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REGULAR RESEARCH ARTICLE

An unusual assemblage of ophiuroids (Echinodermata) from the late Maastrichtian of South Carolina, USA

Ben Thuy[1] · Lea D. Numberger-Thuy[1] · John W. M. Jagt[2]

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Abstract

A small, albeit diverse, assemblage of dissociated ophiuroid ossicles, mostly lateral arm plates, from the upper Maastrichtian Peedee Formation temporarily (August 1998) exposed at North Myrtle Beach (Horry County, South Carolina), is described and illustrated. This lot comprises at least seven species, five of which are new and formally named herein. The assemblage is of note in providing a significant expansion of the palaeobiogeographical record of latest Cretaceous brittle stars. Furthermore, it includes a new genus and species of the family Asteronychidae that is transitional between the stem euryalid *Melusinaster* and Recent asteronychids, as well as the oldest unambiguous fossil representative of the family Amphiuridae. Finally, this assemblage stands out in lacking *Ophiotitanos* and ophiomusaids, two of the most widely distributed and abundant brittle star taxa during the Late Cretaceous. Instead, it is dominated by members of the Amphilimnidae, Amphiuridae and Euryalida, which are amongst the rarest components in the faunal spectrum of modern-day equivalents. The assemblage represents a unique combination of taxa unknown from any other outcrops of upper Mesozoic rocks and seems to document the onset of modern shallow-sublittoral ophiuroid assemblages.

Keywords Late Cretaceous · North America · New species · Palaeoecology

Introduction

Records of latest Cretaceous brittle stars generally are rare with most material known from localities across Europe. In North America, there are only a handful of records of mid- to Late Cretaceous ophiuroids; most of these are of (near-)complete individuals on bedding planes (Clark 1893; Alexander 1931; Berry 1941). However, as far as we are aware, nothing comparable to the European approach of attaining ophiuroids by bulk sampling of sediments, i.e. washing, sieving and handpicking, has ever been undertaken on a large scale in the United States. Through bulk sampling of Jurassic and Cretaceous strata in France England, Germany, Switzerland and the Czech Republic ophiuroid diversity has been considerably increased over recent decades (Hess 1960b, 1962a, b, 1964, 1965; Smith et al. 1995; Kutscher and Villier 2003; Thuy 2005, 2011, 2013, 2015; Štorc and Žítt 2008; Thuy and Kroh 2011; Thuy and Stöhr 2011; Thuy and Meyer 2012; Thuy et al. 2013, 2014; Numberger-Thuy and Thuy 2015; O'Hara et al. 2014). Even material from bulk samples recovered from deep-sea boreholes in oceanic basins has been described (e.g. Thuy et al. 2012), thus significantly expanding the ophiuroid fossil record to include otherwise virtually inaccessible palaeoenvironments. Since the pioneering work by Hess (1962a), the diagnostic value of ophiuroid microfossils and in particular the spine-bearing lateral arm plates has been extensively studied (Thuy and Stöhr 2011). It was recently shown that dissociated lateral arm plates can be identified to species level (Thuy and Stöhr 2011) and included in phylogenetic estimates (Thuy and Stöhr 2016, 2018), thus unlocking the ophiuroid microfossils record.

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✉ Ben Thuy
ben.thuy@mnhn.lu

John W. M. Jagt
john.jagt@maastricht.nl

[1] Musée National d'Histoire Naturelle de Luxembourg, Section Paléontologie, 25 Rue Münster, 2160 Luxembourg, Luxembourg

[2] Natuurhistorisch Museum Maastricht, de Bosquetplein 6-7, 6211 KJ Maastricht, The Netherlands

The study of Late Cretaceous ophiuroids from Europe has a long tradition, but it is also biased towards more or less complete material (Spencer 1905–1908; Hess 1960a; Jagt 1991, 2000, 2001; Stuwe 2000) and portions of arms, plus dissociated ossicles (Valette 1915; Müller 1950; Rasmussen 1950, 1952, 1972; Helm et al. 1999; Jagt 1999, 2000; Jagt and Odin 2001; Kutscher 2011). Amongst the most remarkable works on material exclusively derived from bulk samples is the study by Kutscher and Jagt, *in* Jagt (2000), who described as many as 38 ophiuroid species from the lower Maastrichtian of Rügen (Germany) and Møn (Denmark), 24 of which were new.

We here record the first assemblage of dissociated ophiuroid skeletal plates to be handpicked from bulk samples from upper Maastrichtian strata of the eastern United States (compare also Rasmussen 1952). All taxa identified to the species level are new, which emphasises the utility of using bulk sampling techniques to explore the fossil record of brittle stars. The assemblage described is unusual as far as its taxonomic composition is concerned: firstly, it lacks taxa that are otherwise almost ubiquitous in other Upper Cretaceous localities (e.g. ophiomusaids and *Ophiotitanos*) and, secondly, it is dominated by taxa that are amongst the rarest components in the faunal spectrum of modern-day equivalents.

Materials and methods

Herein, we describe material that was handpicked from sieving residues of a screen-washed bulk sample taken in August 1998 from clayey quartz sands assigned to the upper Maastrichtian Peedee Formation at North Myrtle Beach (South Carolina; see Fig. 1). The sampling site was a road ramp construction for the present-day RT501 that connects North Myrtle Beach with Conway (South Carolina), at 10021 North King's Highway (co-ordinates 33°47′22.38″N, 78°46′12.05″W).

During the course of the works, overlying strata assigned to the Socastee/Canepatch (Pleistocene) and Waccamaw formations (Cenozoic; see Dubar 1971; Clements 1999) were removed and put on spoil heaps, while the harder Peedee Formation (upper Maastrichtian, Upper Cretaceous) was brought to the surface and used for the construction of the road ramp (Fig. 2). While the open pit was available, collections were made from the surrounding spoil heaps that had a small amount of white shell hash of the Waccamaw Formation mixed with the harder, siltier and dark greyish green Peedee Formation matrix. The Peedee Formation here consists of a light to dark greyish green, unconsolidated, loosely cemented clayey quartz sand with some mica and glauconite; elsewhere, there are patches of sandy limestone with molluscan moulds in the upper part of the unit (Wheeler and Curran 1974; Harris 1976; Brouwers and Hazel 1978; Sohl and Owens 1991; Wingard 1993; Landman et al. 2004; https://mrdata.usgs.gov/; https://ngmdb.usgs.gov/). This unit represents deposition in an outer neritic, open-shelf setting in the lower part, which grades into an inner neritic setting in the upper part (Harris and Self-Trail 2006). The Cenozoic Waccamaw Formation comprises smaller clasts of white shell hash and loose sediments (Dubar 1971).

Approximately 2.2 kg of this matrix was collected for microfaunal studies. First, the sample was dry screened to remove larger (> 2.3 mm) material, after which the < 2.3 mm fraction (weighing approximately 800 g) was further split. The fractions of < 2.3 mm to > 0.5 mm were chosen for analysis of microfossil content (ostracods and other biota); these were lightly washed with tap water to remove loosely attached clay/silt and subsequently oven dried and screened under magnification (Series Forty binocular dissecting microscope). Microfaunal elements were picked with a 000 sable brush. The fraction of < 1.5 to > 0.5 mm (around 100 g) yielded the highest diversity of dissociated ophiuroid ossicles, as well as pelagic microcrinoids that are comparable to the assemblage recently described from the Peedee Formation of North Carolina (Gale et al. 2018).

At the Natural History Museum Luxembourg, the handpicked ophiuroid microfossils were cleaned in an ultrasonic bath to remove remains of adhering clay and debris. Selected ossicles were mounted on stubs and gold-coated for scanning electron microscopy using a JEOL Neoscope JMC-5000. Type specimens and material illustrated and/or referred to in the text are now deposited in the collections of the Natural History Museum Luxembourg (MnhnL) and the Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands (NHMM). Terminology follows (Stöhr et al. 2012) and (Thuy and Stöhr 2011, 2016). We use the classification recently published by (O'Hara et al. 2017, 2018).

Systematic descriptions

EtymologyClass Ophiuroidea Gray, 1840

Subclass Myophiuroidea Matsumoto, 1915

Infraclass Metophiurida Matsumoto, 1913

Superorder Euryophiurida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017

Order Euryalida Lamarck, 1816

Family Asteronychidae Ljungman, 1867
Genus *Lillithaster* nov.

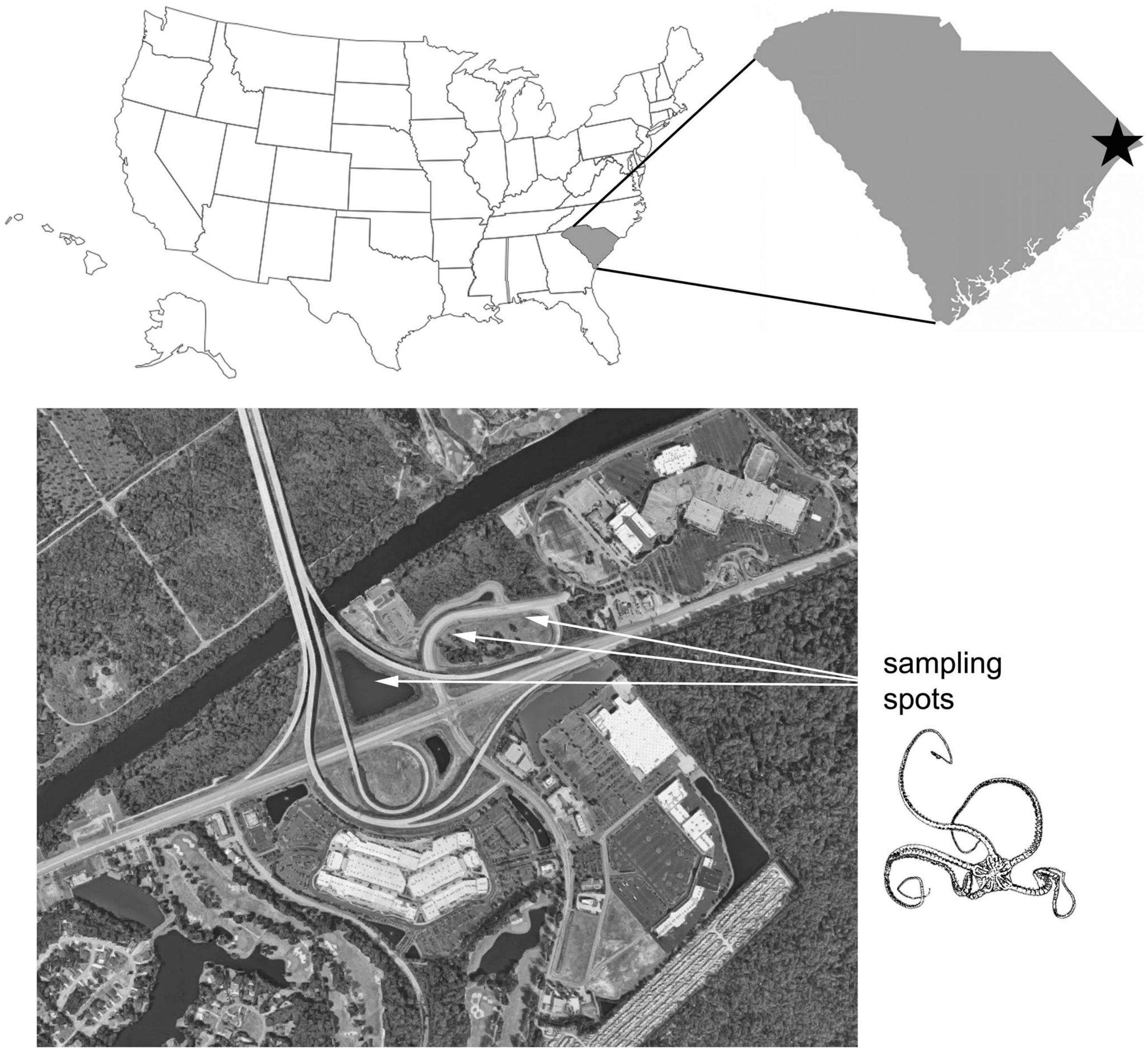


Fig. 1 Map to show the position of the study area (indicated by star), and aerial view (http://www.googlemaps.com) of the southwestern outskirts of North Myrtle Beach (Horry County, South Carolina), to show the position of the temporary outcrop during road ramp construction in August 1998

Etymology In reference to Lillith, a figure of Jewish mythology; she was created at the same time and from the same dirt as Adam but refused to become subservient to him.

Type and sole known species Lillithaster lamentatiofelium sp. nov.

Diagnosis: Asteronychid known exclusively from dissociated lateral arm plates and vertebrae and a single partially articulated arm fragment; lateral arm plates tall, strongly arched, with protruding tongue-shaped ventral portion; proximal lateral arm plates with up to seven spine articulations, the two ventralmost of which having a large, semicrescentic muscle opening widely separated from a much smaller, circular nerve opening by a large and prominent, albeit poorly defined knob; remaining spine articulations developed as large, prominent tubercles with small, near-central perforation; inner side of lateral arm plates with slender, well defined and prominent ridge; lateral arm plates articulating with vertebrae in a latero-ventral position.

Lillithaster lamentatiofelium sp. nov.
Figs. 3, 4

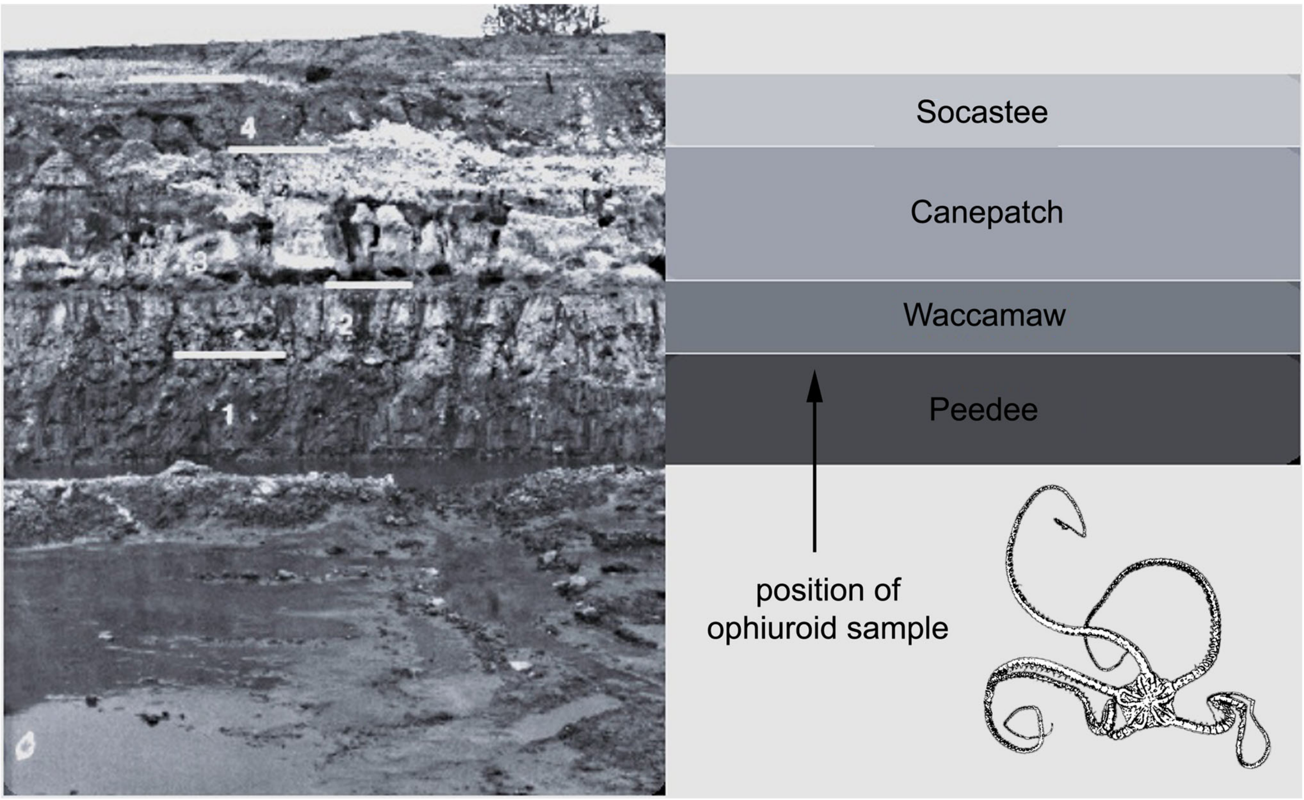


Fig. 2 Section exposed at the road ramp construction site at North Myrtle Beach (Horry County, South Carolina; see Fig. 1), with indication of lithostratigraphical units exposed (modified from Clements 1999) and position of ophiuroid sample

Etymology Species name composed of Latin 'lamentatio' (= mourning) and 'felium' (= of cats), honouring the Norwegian folk rock band Katzenjammer, in recognition of their energy-loaded approach to music and their masterpiece 'Demon Kitty Rag'.

Holotype MnhnL OPH050.

Paratypes NHMM 2018 011 (one lateral arm plate) and MnhnL OPH051 (a single semi-articulated arm fragment).

Additional material MnhnL OPH052 (seven dissociated lateral arm plates) and MnhnL OPH053 (12 dissociated vertebrae).

Diagnosis as for genus.

Locus typicus Road ramp construction at 10021 North King's Highway (Figs. 1, 2), North Myrtle Beach (Horry County, South Carolina).

Stratum typicum Peedee Formation, *Discoscaphites conradi* Zone (Landman et al. 2004), upper Maastrichtian (Upper Cretaceous).

Description of the holotype MnhnL OPH050 (Fig. 3a) is a dissociated proximal lateral arm plate with the dorso-proximal edge obscured by debris; lateral arm plate approximately 2.5 times taller than long, with rounded dorsal edge and strongly protruding tongue-shaped ventral portion with evenly rounded ventral tip; outer surface with moderately finely meshed stereom, devoid of spurs, enlarged trabecular intersections or any other elements of ornamentation; distal portion of lateral arm plate (apart from ventral tongue) strongly bulging, with seven spine articulations; two ventral spine articulations (Fig. 3a3) low, with very large semi-crescentic muscle openings distally bordered by very large, poorly defined, albeit prominent knob; two round nerve openings on distal edge of large knobs, much smaller than muscle openings and closely spaced; five dorsal spine articulations (Fig. 3a4) developed as large, prominent tubercles with small perforation near the centre of the slightly flattened top, presumably corresponding to the muscle opening; dorso-distal edge of tubercles with small, inconspicuous and poorly defined perforation probably corresponding to the nerve opening; dorsalmost tubercle protruding beyond the dorsal edge of the lateral arm plate. Inner side of lateral arm plate with a single, continuous, slender and prominent ridge (Fig. 3a2); dorsal and ventral tips of ridge most prominent and best defined; ridge composed of only slightly more finely meshed stereom; no perforations or spurs discernible on inner side of lateral arm plate.

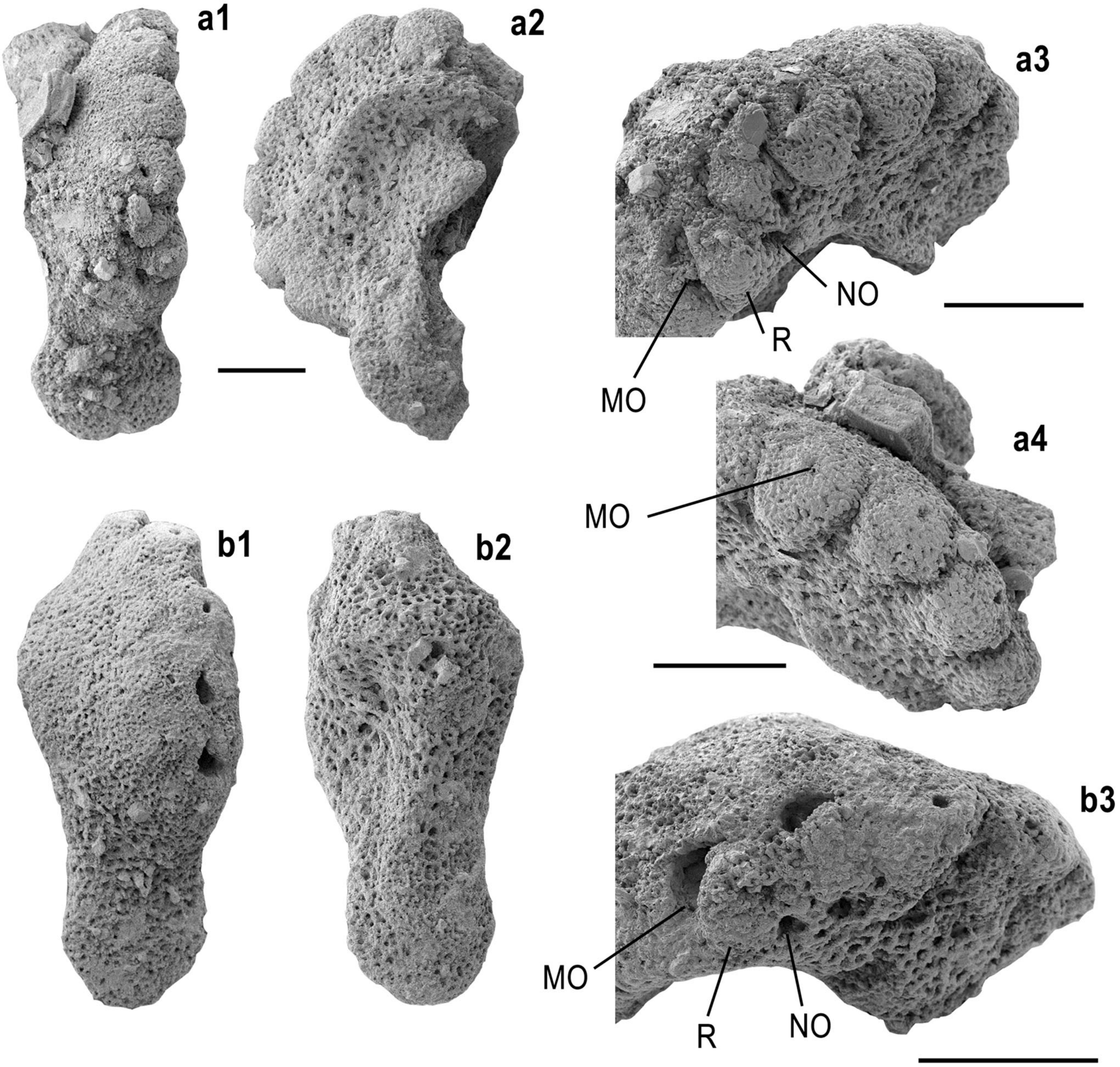


Fig. 3 *Lillithaster lamentatiofelium* sp. nov. from the Peedee Formation (upper Maastrichtian, Upper Cretaceous) at the road ramp construction site in North Myrtle Beach (Horry County, South Carolina). **a** MnhnL OPH050 (holotype), dissociated proximal lateral arm plate in external (1) and internal (2) views, and with details of spine articulations in ventro-distal (3) and dorso-distal (4) views. **b** NHMM 2018 011 (paratype), dissociated median lateral arm plate in external (1) and internal (2) views, and with details of spine articulations in ventro-distal (3) and dorso-distal (4) views. *MO* muscle opening, *NO* nerve opening, *R* ridge. Scale bars equal 0.2 mm

Paratype supplements NHMM 2018 011 (Fig. 3b) is a dissociated median lateral arm plate, approximately 2.2 times taller than long; overall shape and outer surface stereom as in holotype but of better preservation; five spine articulations (Fig. 3b3), the two ventralmost of which are as in the holotype; three dorsal spine articulations developed as prominent tubercles comparable to five dorsal arm spine articulations in the holotype but with flattened, round, smooth top with central perforation presumably corresponding to the muscle opening.

MnhnL OPH051 (Fig. 4) is a semi-articulated arm fragment composed of two vertebrae in articulation and a displaced lateral arm plate; width of vertebrae exceeding height, with very deep dorsal furrow (Fig. 4c), near-straight oblique lateral edges of the dorsal muscle fossae and an angle between lateral edges of dorsal and ventral muscle fossae, resulting in a conspicuously angular overall

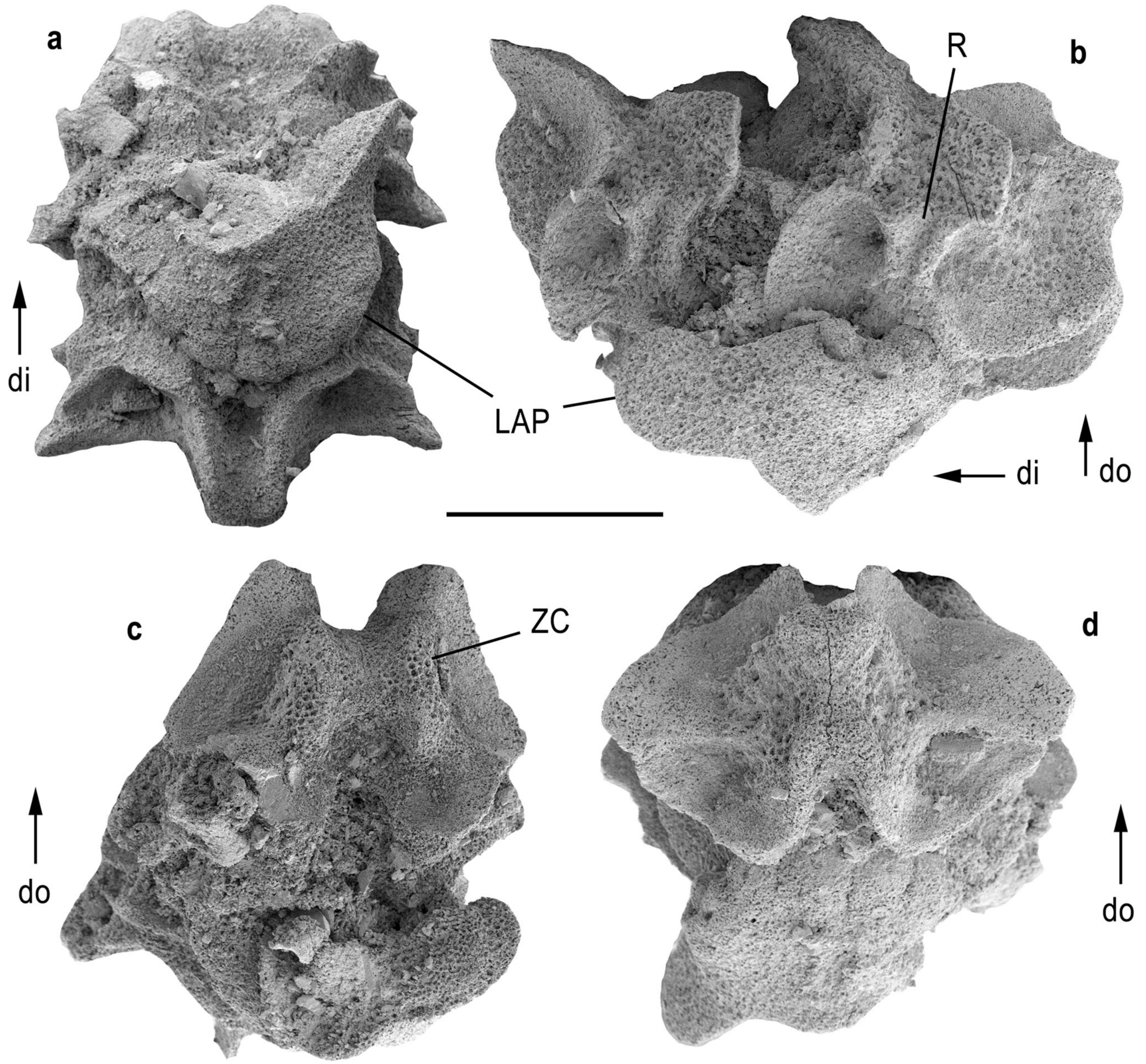


Fig. 4 *Lillithaster lamentatiofelium* sp. nov. from the Peedee Formation (upper Maastrichtian, Upper Cretaceous) at the road ramp construction site in North Myrtle Beach (Horry County, South Carolina), Mnhnl OPH051 (paratype), semi-articulated arm fragment composed of two vertebrae and a displaced lateral arm plate in ventral (**a**), lateral (**b**), distal (**c**) and proximal (**d**) views. *di* distal, *do* dorsal, *LAP* lateral arm plate, *R* ridge, *ZC* zygocondyle. Scale bar equals 1 mm

outline of both the distal and proximal vertebral faces; ventral groove open (Fig. 4d); distal zygocondyles (Fig. 4c) composed of coarsely meshed stereom, proximal ones (Fig. 4d) of more finely meshed stereom; no zygosphene; lateral saddle S-shaped, with short vertical, well-defined groove (Fig. 4b) approximately at the same height as the dorsal half of the ventro-distal muscle fossa, presumably articulating with the ridge on the inner side of the lateral arm plates when in original anatomical position, thus suggesting a ventro-lateral position of the lateral arm plates on the vertebrae.

Remarks The shape of the spine articulations, in combination with the unornamented outer surface stereom and the hourglass-shaped vertebral articulation unambiguously, places this material in the order Euryalida. Within this group, the strongest affinities are shared with members of the family Asteronychidae on account of the shape of the lateral arm plates, the arrangement of the tubercle-like spine articulations and the wide vertebrae with open ventral groove and S-shaped lateral saddles.

Extant asteronychids currently comprise the genera *Asteronyx* Müller and Troschel, 1842, *Astrodia* Verrill, 1899b, *Astronebris* Downey, 1967 and *Ophioschiza* H.L. Clark, 1911. Of these, only *Asteronyx* has more than three arm spines (Downey 1967). With respect to the arrangement of arm spine articulations, the present Late Cretaceous specimens indeed share striking similarities to the lateral arm plates of the type species, *Asteronyx loveni*, inclusive of the tubercle-like spine articulations. In modern-day euryalids, such tubercle-like spine articulations carry hooks (e.g. Martynov 2010), suggesting a similar function in the fossil equivalents described herein. However, unlike lateral arm plates of *Asteronyx*, the Cretaceous material has a strongly protruding, tongue-shaped ventral portion and a semi-crescentic (rather than round) muscle opening in the ventralmost spine articulations, precluding assignment to the same genus. For this reason, we erect a new taxon, *Lillithaster lamentatiofelium*, for the accommodation of these specimens.

Other extinct asteronychid occurrences known to date are ambiguous, at best. Vertebrae described by Rasmussen (1950, p. 121, pl. 18, fig. 11) as a new species, *Asteronyx*? *ornatus*, from the upper Maastrichtian of Sjælland, eastern Denmark, were tentatively transferred by Jagt (2000, p. 8) and Kutscher and Jagt (2000, pp. 51, 52) to *Trichaster* L. Agassiz, 1836 within the family Euryalidae Gray, 1840. Considering the much wider vertebrae of Recent species of *Asteronyx*, we explicitly endorse this transfer to the Euryalidae, although there seem to be stronger affinities with *Asteroschema* Örstedt & Lütken *in* Lütken, 1856 than with *Trichaster*. *Asteronyx*? sp. from the Danian of Denmark (Rasmussen 1950, p. 122, pl. 18, fig. 12) and *Asteronyx*? *simplex* A. H. Müller, 1950 (p. 22, pl. 2, fig. G1–5) from the lower Maastrichtian of Germany (Kutscher and Jagt, *in* Jagt 2000) are dissociated vertebrae that lack characters pointing at a particular family, e.g. a high width/length ratio, a covered ventral groove, conspicuous lateral ridges or knobs or branching distal articulations; for this reason, they might or might not belong to the Asteronychidae. *Asteronyx*? *spinulosa* Kutscher and Jagt, *in* Jagt, 2000 (p. 50, pl. 30, figs. 1–4) from the lower Maastrichtian of Germany, Denmark and the southeast Netherlands is based primarily on dissociated lateral arm plates and might well belong to the Asteronychidae on account of general shape, lack of outer surface ornamentation and shape of the ridge on the inner side. However, the tubercle-like spine articulations appear to have a fundamentally different morphology, precluding assignment to *Lillithaster* gen. nov. and possibly even challenging asteronychid affinities altogether.

Lateral arm plates of *Lillithaster* gen. nov. share remarkable similarities to those of the recently described basal euryalid *Melusinaster* Thuy and Stöhr, 2018 from the Jurassic, in particular on account of the tongue-shaped, protruding ventral portion of the lateral arm plates and the shape of the ventralmost spine articulations. With respect to lateral arm plate morphology, *Lillithaster* gen. nov. seems to hold a transitional position between *Melusinaster* and Recent asteronychids. Amongst the most interesting aspects of this assumed morphological succession is that the spine articulations in *Lillithaster* gen. nov. provide insights into the origin of the hook-bearing tubercles found in *Asteronyx* and many other modern euryalids. The tubercle itself seems to be a massively enlarged and morphologically transformed knob that originally separated the muscle and nerve openings in the non-tubercle spine articulations, and the perforation on top of the tubercle is a shrunk muscle opening while the nerve opening is reduced to a tiny perforation on the dorso-distal edge of the tubercle, if preserved at all. Thus, the discovery of *Lillithaster* gen. nov. significantly adds to our understanding of the fossil record of euryalids, and future phylogenetic analyses including this new fossil taxon have the potential to elucidate the evolution of the Euryalida further.

Family Gorgonocephalidae Ljungman, 1867

Gorgonocephalid gen. et sp. indet.

Fig. 5a–b

Material studied Two dissociated vertebrae (MnhnL OPH054 and OPH056) and a single dissociated lateral arm plate (MnhnL OPH055).

Description MnhnL OPH054 (Fig. 5a) is a dissociated proximal vertebra of approximately equal height and width, but much taller than long and of a rounded, ovoid outline, wider dorsally than ventrally; dorsal and ventral furrows (Fig. 5a1) relatively narrow, but deep, not covered; distal and proximal muscle fossae almost vertical, relatively small; distal zygocondyles (Fig. 5a1) conspicuously large and converging ventralwards, composed of finely meshed stereom towards the lateral edges and of more coarsely meshed stereom towards the centre; proximal zygocondyles (Fig. 5a3) hourglass shaped, slightly wider dorsally, with well-defined, prominent area of more coarsely meshed stereom on both sides of the hourglass waist. Lateral sides of vertebra (Fig. 5a2) with very large, conspicuous, sharply defined dorsal knob, ventrally bordered by two pairs of smaller yet similarly sharply defined knobs.

MnhnL OPH055 (Fig. 5b) is a dissociated proximal lateral arm plate that probably belonged to the same species as the vertebra MnhnL OPH054; almost three times taller than long, with a straight proximal edge, rounded

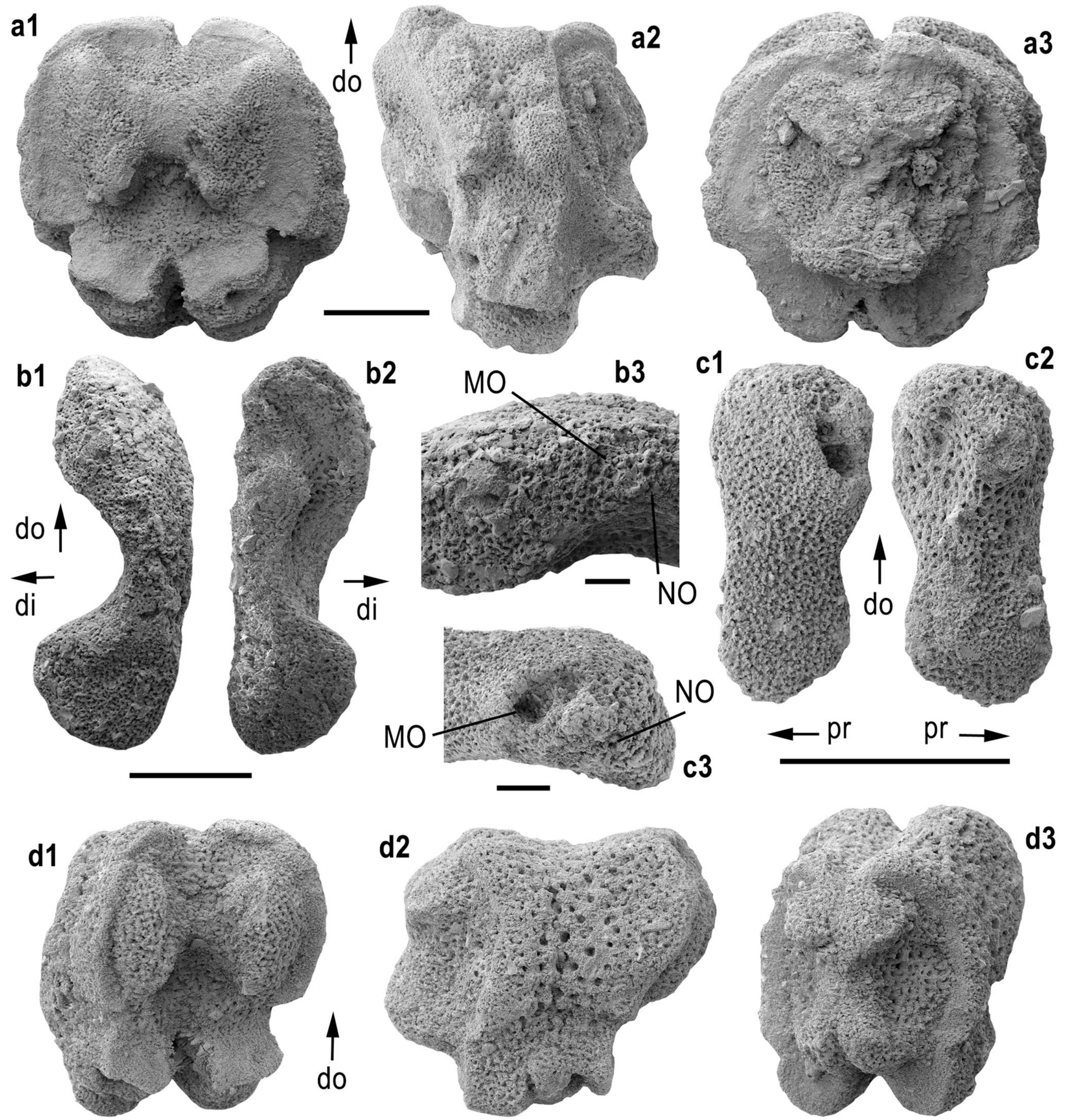


Fig. 5 Gorgonocephalid gen. et sp. indet. from the Peedee Formation (upper Maastrichtian, Upper Cretaceous) at the road ramp construction site in North Myrtle Beach (Horry County, South Carolina), **a** Mnhnl OPH054, dissociated proximal vertebra in distal (1), lateral (2) and proximal (3) views; **b** MnhnL OPH055, dissociated proximal lateral arm plate in external (1) and internal (2) views, and with detail of spine articulations (3) *Squamophis*? sp. indet. from the Peedee Formation (upper Maastrichtian, Upper Cretaceous) at the road ramp construction site in North Myrtle Beach (Horry County, South Carolina), **c** Mnhnl OPH057, dissociated lateral arm plate in external (a) and internal (b) views, and with detail of spine articulation in distal (c) view; **d** MnhnL OPH058, dissociated vertebra in distal (a), lateral (b) and proximal (c) views. Abbreviations: di: distal; do: dorsal; MO: muscle opening; NO: nerve opening; pr: proximal. Scale bars equal 0.5 mm (**a–e**, **h–l**) and 0.1 mm (**f–g**)

dorsal and ventral tips and a deeply concave distal edge resulting in a strongly waisted plate outline; outer surface stereom undifferentiated, lacking spurs or any other ornamentation; at least two poorly discernible spine articulations (Fig. 5b3) integrated into the distal edge of the dorsal lateral arm plate portion, composed of a large but poorly defined depression distally bordered by a very faint ridge and a second much smaller but similarly poorly defined depression. Inner side of lateral arm plate (Fig. 5b2) with wide, strongly prominent S-shaped ridge with sharply defined dorsal tip and moderately well-defined ventral tip.

Remarks Vertebrae, including the one described above, display the typical combination of a disc-shaped outline with deep, uncovered dorsal and ventral furrows and conspicuously large, hourglass-shaped zygocondyles that are commonly found in modern gorgonocephalids (e.g. Kroh 2003). The very limited number of specimens available precludes a reliable identification beyond the family level, especially in consideration of the low morphological disparity of gorgonocephalid vertebrae (Kroh 2003). The two vertebrae available both show simple articulations and thus can neither confirm nor exclude the presence of arm branching. The conspicuous ornamentation on the lateral sides of the vertebrae might well be of diagnostic value. However, in the absence of any systematic survey of gorgonocephalid vertebral morphology, we cannot be more specific at this stage. We, therefore, describe the material at hand as an indeterminate gorgonocephalid record, stressing, however, that it significantly extends the known fossil record of the family (Kroh 2003).

Comparisons with vertebrae described by Rasmussen (Rasmussen 1950, 1952, as *Asteronyx*? *ornatus*) and Kutscher and Jagt, *in* Jagt (2000, as *Trichaster*? *ornatus*) from the Upper Cretaceous of Denmark, southern Sweden, Germany and the Maastricht area reveal similarities with respect to the large, sharply defined knobs on the lateral sides and the dorsal and ventral muscle fossae that form a continuous disc. Differences in the frontal outline (broader ventrally in *T.*? *ornatus*), the orientation of the distal zygocondyles (parallel in *T.*? *ornatus* rather than converging ventralwards) and in the size pattern and arrangement of the lateral knobs, however, preclude assignment to the same species. Nonetheless, the otherwise close similarities to the vertebrae described here challenge the position of *T.*? *ornatus* within the Euryalidae but instead favour gorgonocephalid affinities. Anyway, assignment to the genus *Trichaster* is untenable because of the open ventral furrow. Assuming that *T.*? *ornatus* had unbranched arms, as is suggested by the lack of vertebrae with double distal articulations (Kutscher and Jagt, *in* Jagt 2000), the species should be transferred to a genus of gorgonocephalid with unbranched arms. However, with our current patchy knowledge of gorgonocephalid arm plate micromorphology (lateral arm plates and vertebrae are invisible in most illustrations as they are concealed by soft tissue in unmacerated specimens), we are unable to narrow down the genus-level placement of *T.*? *ornatus*. We, therefore, leave it as it is, at least for now.

The lateral arm plate described above has unambiguous euryalid affinities on account of general shape, the unornamented outer surface stereom and the development of spine articulations. We tentatively associate it with the gorgonocephalid vertebrae because they represent the best fit with respect to size and shape between the ridge on the inner side of the lateral arm plate and the latero-ventral ridge on the lateral surface of the vertebra. Again, the lack of any systematic survey of gorgonocephalid arm plates precludes a more exhaustive morphological interpretation of the lateral arm plate available.

Family Euryalidae Gray, 1840

Genus *Squamophis* Okanishi, O'Hara & Fujita, 2011

Squamophis? sp. indet.

Fig. 5c–d

Material studied 13 dissociated vertebrae (MnhnL OPH057 and OPH059; NHMM 2018 012) and two dissociated lateral arm plates (MnhnL OPH058 and OPH060).

Description MnhnL OPH057 (Fig. 5d) is a dissociated proximal vertebra that is slightly taller than long, with moderately deep dorsal furrow and conspicuously deep, but uncovered ventral furrow (Fig. 5d1, d3); dorsal muscle fossae evenly rounded, narrow; ventral muscle fossae clearly separated from dorsal ones, small, squarish, protruding ventralwards; distal zygocondyles (Fig. 5d1) conspicuously large, occupying almost entire dorsal portion of vertebra, horizontally hourglass shaped, with parallel lateral extremities composed of coarsely meshed stereom and with more finely meshed stereom in the hourglass waist; proximal zygocondyles (Fig. 5d3) vertically hourglass shaped with bifid dorsal and ventral extremities and narrow, less prominent waist surrounded by elevated area of coarsely meshed stereom; lateral saddle of vertebra (Fig. 5d2) with very coarsely meshed stereom and some of the trabecular intersections developed as irregularly scattered, slightly enlarged tubercles.

MnhnL OPH058 (Fig. 5c) is a dissociated proximal or median lateral arm plate two times taller than long, with rounded dorsal and ventral tips and gently concave distal and proximal edges; ventral portion of lateral arm plate projecting ventralwards, tongue shaped; outer surface stereom finely meshed with simple trabecular intersections; no spurs or any other elements of ornamentation; single conspicuously large spine articulation (Fig. 5c3) on swollen dorso-distal edge of lateral arm plate, composed of a very large, round muscle opening that is dorso-distally separated from a very small nerve opening by a large, prominent, moderately well-defined knob. The inner side of lateral arm plate (Fig. 5c2) with two poorly defined, round knobs, a more prominent one on the dorsal portion of the inner side and a weakly protruding one on the ventral portion, with a very faint vertical ridge connecting both knobs; no perforations discernible.

Remarks We consider the type of lateral arm plates and vertebrae described above to have belonged to the same species on account of the matching size relationships and similarities in shape between the knobs on the inner side of the lateral arm plates and the knobs on the ventro-lateral side of the vertebrae. Both the lateral arm plates and the vertebrae independently show affinities with the equivalent skeletal plates of the extant genus *Squamophis* within the family Euryalidae (Okanishi et al. 2011; Stöhr 2011): the lateral arm plates have a single, conspicuously large spine articulation and a ventral portion that projects ventralwards, while the vertebrae show clearly separate dorsal and ventral muscle fossae and an open ventral furrow. However, since knowledge of euryalid arm plate micromorphology is poor at the moment, we consider assignment to *Squamophis* to be tentative.

These lateral arm plates are unlike any other types currently known from the fossil record. It should be stressed here that the discovery of these plates was a major achievement by Kevin R. Shannon, the collector, because the plates are very small, inconspicuous and likely to be confused with poorly preserved and/or broken lateral arm plates of non-euryalids. The vertebrae described herein differ from those recorded by Rasmussen (1950) and Kutscher and Jagt, *in* Jagt (2000) in having clearly separate dorsal and ventral muscle fossae.

Superorder Ophintegrida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017

Order Ophiacanthida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017

Suborder Ophiacanthina O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017

Family Ophiotomidae Paterson, 1985

Genus *Ophiotreta* Verrill, 1899a

Ophiotreta sadorfi sp. nov.

Fig. 6a–c

Etymology Species named in honour of Eric M. Sadorf, in recognition of his palaeontological and stratigraphical studies in North and South Carolina (see Case et al. 2017; Stringer et al. 2018).

Holotype MnhnL OPH061.

Fig. 6 *Ophiotreta sadorfi* sp. nov. from the Peedee Formation (upper Maastrichtian, Upper Cretaceous) at the road ramp construction site in North Myrtle Beach (Horry County, South Carolina). **a** MnhnL OPH061 (holotype), dissociated proximal lateral arm plate in external (1) and internal (2) views. **b** NHMM 2018 013 (paratype), dissociated median lateral arm plate in external (1) and internal (2) views. **c** MnhnL OPH062 (paratype), dissociated distal lateral arm plate in external (1) and internal (2) views. *Amphilimna intersepultosetme* sp. nov. from the Peedee Formation (upper Maastrichtian, Upper Cretaceous) at the road ramp construction site in North Myrtle Beach (Horry County, South Carolina), **d** MnhnL OPH064 (holotype), dissociated proximal lateral arm plate in external (1) and internal (2) views, and with detail of spine articulations in distal (3) view; **e** NHMM 2018 023 (paratype), dissociated proximal lateral arm plate in external (1) and internal (2) views, and with detail of spine articulations in distal (3) view; **f** MnhnL OPH065 (paratype), dissociated median lateral arm plate in external (1) and internal (2) views; **g** MnhnL OPH065 (paratype), dissociated distal lateral arm plate in external (1) and internal (2) views. Abbreviations: di: distal; do: dorsal; pr: proximal; SP: spur. Scale bars equal 0.2 mm

▶

Paratypes NHMM 2018 013 and MnhnL OPH062.

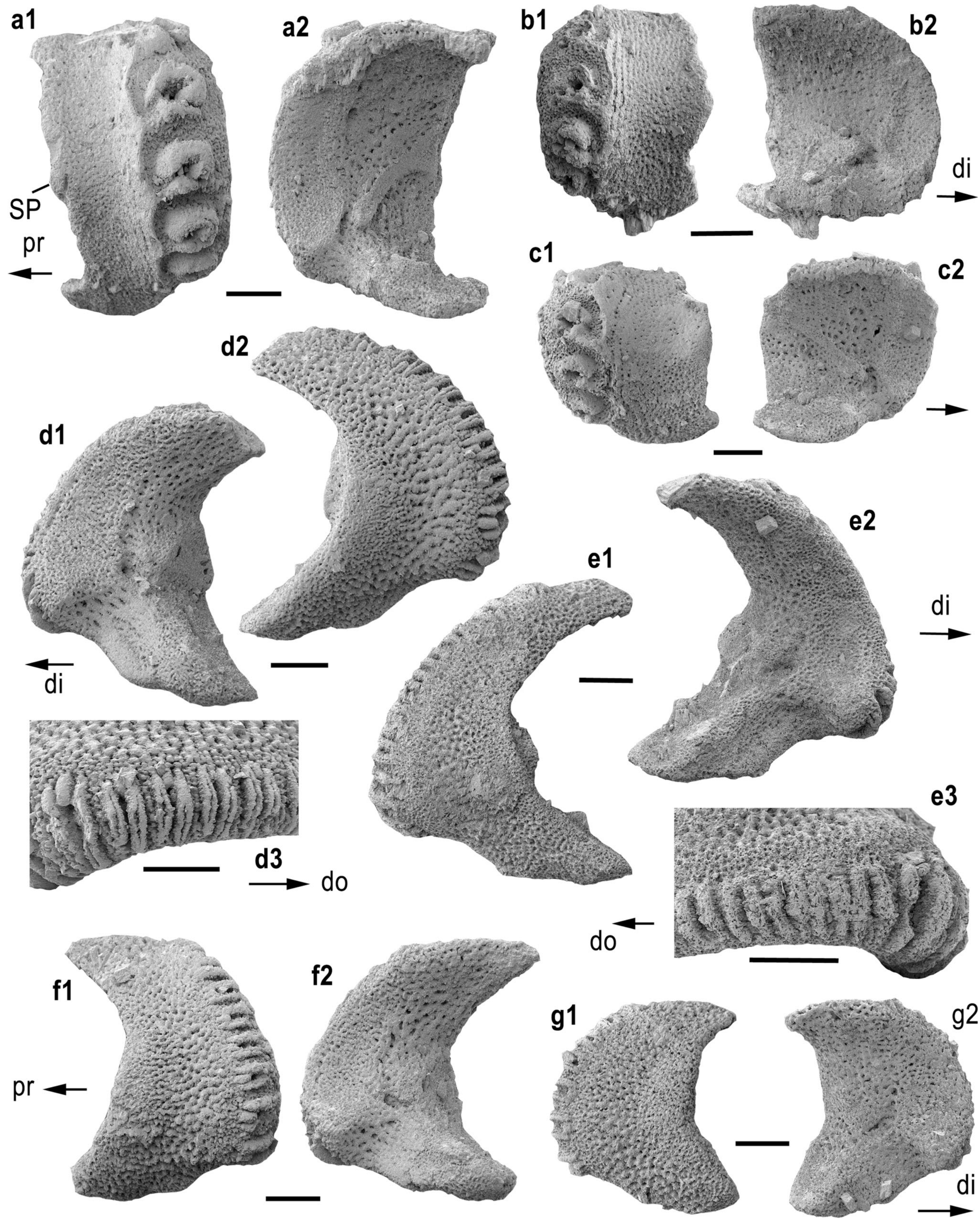
Additional material MnhnL OPH063 (four dissociated lateral arm plates).

Diagnosis Small species of *Ophiotreta* with up to five large spine articulations with a moderately well-developed connection between the ventral lobe and vertical ridge proximally bordering spine articulations; very weakly developed spur on the outer proximal and inner distal edges; vertical striation on outer surface poorly developed and restricted to a narrow band along ridge bordering spine articulations.

Locus typicus Road ramp construction at 10021 North King's Highway (Figs. 1, 2), North Myrtle Beach (Horry County, South Carolina).

Stratum typicum Peedee Formation, *Discoscaphites conradi* Zone (Landman et al. 2004), upper Maastrichtian (Upper Cretaceous).

Description of the holotype MnhnL OPH061 (Fig. 6a) is a dissociated proximal lateral arm plate approximately 1.5 times taller than long, with an evenly convex distal edge, a slightly wavy proximal edge, a concave dorsal edge and a ventro-proximally protruding ventral portion; very weakly developed, slightly protruding spur on outer proximal edge (Fig. 6a1); outer surface with very weak striation on the edge of the ridge carrying the spine articulations, otherwise finely meshed stereom with trabecular intersections transformed into very small, inconspicuous tubercles only in ventral and dorsal areas of the outer surface; distal portion of lateral arm plate strongly elevated and proximally bordered by sharply defined, wavy ridge; five very large, ear-shaped spine articulations (Fig. 6a1) on elevated distal plate portion, in a continuous vertical row, separated from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the distal edge of the lateral arm plate by a narrow band of finely meshed stereom; dorsalward increase in size of gaps separating spine articulations; second dorsalmost spine articulation largest; spine articulations composed of a very large, semi-circular dorsal lobe and a smaller, near-straight ventral lobe, with both lobes distally connected by a sigmoidal fold and proximally separated by a shallow, poorly defined furrow; proximal tip of ventral lobe weakly connected with wavy ridge proximally bordering row of spine articulations; muscle opening large, enclosed by dorsal lobe, nerve opening much smaller and encompassed proximally by sigmoidal fold.

Inner side of lateral arm plate (Fig. 6a2) with slender ridge composed of oblique, well-defined central part and a vertical, poorly defined dorsal part lining the proximal edge of the lateral arm plate; kink between the two parts of the ridge with a ventro-proximally pointing projection; no spurs discernible on inner distal edge of lateral arm plate; shallow, poorly defined vertical furrow with moderately large perforations.

Paratype supplements NHMM 2018 013 (Fig. 6b) is a dissociated median lateral arm plate, slightly taller than long, well in agreement with holotype but with only very weakly concave dorsal edge, with slightly better-developed spur on outer proximal edge (Fig. 6b1); vertical striation developed on a slightly larger portion of the outer surface than in holotype; five spine articulations (Fig. 6b1) as in holotype but with dorsalmost one much smaller than others; inner side (Fig. 6b2) as in holotype but with less well-developed vertical furrow.

MnhnL OPH062 (Fig. 6c) is a dissociated distal lateral arm plate, of nearly equal length and height, well in agreement with holotype but with slightly better-developed spur (Fig. 6c1) on the outer proximal edge; four spine articulations (Fig. 6c1) of similar shape and arrangement as those of holotype; ridge on inner side (Fig. 6c2) almost exclusively consisting of oblique central part, with only very short vertical dorsal part; poorly defined area of more densely meshed stereom on inner distal edge corresponding to spur on outer proximal edge.

Remarks The shape of the ridge on the inner side, especially the typical ventro-proximally pointed projection at the kink between the central and dorsal parts of the ridge, places these lateral arm plates in the ophiacanthid family Ophiotomidae as recently redefined by O'Hara et al. (2018). Within this family, affinities are greatest with the extant genera *Ophiotreta* Verrill, 1899b and *Ophiopristis* Verrill, 1899, because of the poorly defined spur on the outer proximal edge, the vertical striation on the outer surface, the sharp ridge that borders the spine articulations distally and the connection between this ridge and the ventral lobe of the spine articulations (Thuy 2013). The two genera seem to share closely similar lateral arm plate morphologies, at least when taking into account the species studied by Thuy (2013). Pending a study of lateral arm plate morphologies of the type species of both genera, we tentatively assign the present material to *Ophiotreta* because the lateral arm plates in this genus more commonly display a connection between the ventral lobe of the spine articulations and the vertical ridge that borders these (Thuy 2013).

As far as fossil species currently assigned to *Ophiotreta* are concerned, the present specimens share greatest similarities to *Ophiotreta hedone* Thuy, 2013 from the Eocene of France. Differences mostly pertain to the better-developed vertical striation and slightly smaller spine articulations in *O. hedone* and, albeit minor, these traits support assignment of the new Cretaceous material to a distinct, new species. The substantial stratigraphical and geographical distance provides further support for a species level distinction.

Order Amphilepidida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017

Suborder Ophionereidina O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017

Superfamily Ophionereidoidea Ljungman, 1867

Family Amphilimnidae O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018

Genus *Amphilimna* Verrill, 1899a

Amphilimna intersepultosetme sp. nov.

Fig. 6d–g.

Etymology Species name consisting of Latin "inter sepultos et me", translating into "between the buried and me", to honour the eponymous progressive metal band.

Holotype MnhnL OPH064.

Paratypes NHMM 2018 023, MnhnL OPH065 and OPH066.

Additional material MnhnL OPH067 (85 dissociated lateral arm plates).

Diagnosis Species of *Amphilimna* with stout lateral arm plates; outer surface stereom with trabecular intersections swollen into smooth, low, irregular tubercles; up to ten spine articulations showing a strong ventralward increase in size.

Locus typicus Road ramp construction at 10021 North King's Highway (Figs. 1, 2), North Myrtle Beach (Horry County, South Carolina).

Stratum typicum Peedee Formation, *Discoscaphites conradi* Zone (Landman et al., 2004), upper Maastrichtian (Upper Cretaceous).

Description of holotype MnhnL OPH064 (Fig. 6d) is a dissociated proximal lateral arm plate, taller than long, strongly arched, crescent shaped, with pointed dorsal and ventral tips, evenly convex distal edge and evenly concave proximal edge; ventro-distal edge with large and gently concave incision for tentacle notch; outer surface stereom with trabecular intersections swollen into smooth, low, irregular tubercles decreasing in size towards the row of spine articulations and towards the proximal edge and dorsal and ventral tips; large, poorly defined, prominent, yet non-protruding, area in the centre of the outer proximal edge (Fig. 6d2), composed of much more finely meshed stereom than surrounding outer surface; then spine articulations (Fig. 6d3) in a continuous row on the distal edge of a slightly bulging distal portion of the lateral arm plate; distance between spine articulations increasing dorsalwards; size of spine articulations increasing ventralwards, with the two ventralmost ones much larger than others (Fig. 6d3); spine articulations composed of straight, horizontal, parallel ventral and dorsal lobes, both lined by a thin horizontal groove, tightly encompassing the muscle and nerve openings, and proximally separated by a single short, horizontal ridge approximately as thick as the dorsal and ventral lobes; two ventralmost spine articulations approximately 1.5 times larger than remaining ones and with a much larger ridge separating dorsal and ventral lobes at their proximal end.

Inner side of lateral arm plate (Fig. 6d1) with two knobs merged into a large, rounded triangular knob in the centre of the inner proximal edge, projecting proximalwards beyond the edge of the lateral arm plate; single large perforation near the ventro-distal tip of the knob, at the ventral end of a moderately well-defined vertical furrow; very large tentacle notch, with coarsely meshed, horizontally stretched stereom and elongate ridge along the proximal half of the notch projecting ventralwards beyond the edge of the lateral arm plate.

Paratype supplements and variation: NHMM 2018 023 (Fig. 6e) is a dissociated proximal lateral arm plate, taller than the holotype but otherwise in good agreement; ten spine articulations (Fig. 6e3) as in holotype but with the ventralmost even larger compared to the remaining ones; inner side (Fig. 6e2) as in holotype except for slightly better discernible two components of merged central knob.

MnhnL OPH065 (Fig. 6f) is a dissociated median lateral arm plate, less tall than holotype, with shorter and less strongly protruding ventral portion, with less clearly developed area of finely meshed stereom in the centre of the outer proximal edge and with less clearly developed vertical band of coarsely meshed stereom in the middle of the outer surface; eight spine articulations (Fig. 6f1) as in holotype but with smaller ventralward increase in size; inner side (Fig. 6f2) as in holotype but with less well-defined knob and vertical furrow.

MnhnL OPH066 (Fig. 6g) is a dissociated distal lateral arm plate, of almost equal length and height, with shorter and less strongly protruding ventral portion, with less well-developed area of finely meshed stereom in the centre of the outer proximal edge (Fig. 6g1), with weaker contrast between coarsely meshed stereom in the centre of the outer surface and the more finely meshed stereom at the edges; seven arm spine articulations (Fig. 6g1) as in holotype but near-equally spaced and with much weaker ventralward increase in size; inner side of lateral arm (Fig. 6g2) plate as in holotype but with less well-defined knob and vertical furrow.

Remarks These lateral arm plates show the highly characteristic combination of features typically found in extant species of *Amphilimna* (Thuy et al. 2014). This amphiurid genus is highly disparate within the Amphilepidida, in agreement with the latest phylogenetic evidence supporting separation of *Amphilimna* at the family level (O'Hara et al. 2017, 2018). Because of the unique lateral arm plate morphology, assignment of the present material to the recently erected family Amphilimnidae (O'Hara et al. 2018) is beyond doubt. However, on the generic level, too little is known about the morphological variation of extant species of amphilimnids, especially with respect to lateral arm plates. For this reason, we assign our material to the sole currently known genus in the family.

The first and previously sole known fossil occurrence of amphilimnids is rare finds from the Aptian of Spain that were described by Thuy et al. (2014) in open nomenclature. The present material represents the second record of extinct members of the family and is based on much richer and better-preserved material. It differs from the Spanish specimens in having up to ten spine articulations with a strong ventralward increase in size.

Interestingly, *Ophiothrix*? *bongaertsi* Kutscher and Jagt, *in* Jagt, 2000 (p. 72, pl. 29, figs. 9–10) from the upper Campanian to upper Maastrichtian of Rügen, northeast Belgium and the southeast Netherlands, and *Amphiura*? *plana* Kutscher and Jagt, *in* Jagt, 2000 (pp. 21, 71, pl. 10, fig. 11; pl. 11, fig. 1; pl. 29, figs. 1–5; pl. 33, fig. 3) from the upper Campanian to upper Maastrichtian of Rügen, Denmark, southern Sweden, northeast Belgium and the southeast Netherlands both show the typical characters of amphilepidid lateral arm plates, in particular with respect to general outline, shape of the spine articulations and morphology of the inner side. For this reason, we here transfer both species to the genus *Amphilimna*. Both differ from *Amphilimna intersepultosetme* sp. nov. in the lower number of spine articulations and the much weaker ventralward increase in the size of the spine articulations.

Suborder Gnathophiurina Matsumoto, 1915

Superfamily Amphiuroidea Ljungman, 1867

Family Amphiuridae Ljungman, 1867

Genus *Amphiura* Forbes, 1843

Amphiura shannoni sp. nov.

Fig. 7a–c

Etymology Species named in honour of Kevin R. Shannon of Martinsville (Virginia, USA), for supply of the North Myrtle Beach echinoderm material.

Holotype MnhnL OPH068.

Paratypes NHMM 2018 024 and MnhnL OPH069.

Additional material MnhnL OPH070 (43 dissociated lateral arm plates).

Diagnosis Species of *Amphiura* with very tall, sickle-shaped lateral arm plates, central part of proximal edge straight in proximal lateral arm plates and evenly convex in median to distal ones; up to ten spine articulations with a strong ventralward increase in size; narrow, well-defined vertical furrow with few small perforations on inner side of lateral arm plates.

Locus typicus Road ramp construction at 10021 North King's Highway (Figs. 1, 2), North Myrtle Beach (Horry County, South Carolina).

Stratum typicum Peedee Formation, *Discoscaphites conradi* Zone (Landman et al., 2004), upper Maastrichtian (Upper Cretaceous).

Description of holotype MnhnL OPH068 (Fig. 7a) is a dissociated proximal lateral arm plate, approximately three times taller than long, sickle shaped, with pointed dorsal and ventral tips, distal edge evenly convex, proximal edge concave with a straight central part (Fig. 7a1); ventral portion protruding ventro-proximally; outer surface stereom with trabecular intersections transformed into small tubercles, except for a small, semi-circular area of more finely meshed stereom near centre of outer proximal edge corresponding to straight part of proximal edge contour; ten large spine articulations (Fig. 7a3) evenly distributed along distal edge of lateral arm plate on same level as outer surface stereom, with a ventralward increase in size and a dorsalward increase in distance between neighbouring spine articulations; spine articulations composed of straight, parallel, horizontal, near-equal and massive dorsal and ventral lobes, separated distally and proximally and encompassing nearly equal-sized muscle and nerve openings.

Inner side of lateral arm plate (Fig. 7a2) with three small, poorly defined and weakly prominent knobs, two at the inner proximal edge of lateral arm plate and another one in a central position halfway between proximal and distal edges at same level as the ventral knob at proximal edge; tentacle notch large but shallow, resulting in a weakly concave ventro-distal edge of lateral arm plate; conspicuous perforation at ventral edge of central knob; narrow and well-defined vertical furrow (Fig. 7a2) comprising at least three smaller perforations.

Paratype supplements and variation NHMM 2018 024 (Fig. 7b) is a dissociated median lateral arm plate approximately 2.5 times taller than long, sickle shaped but with rounded rather than pointed ventral edge; proximal edge outline with evenly convex rather than straight central part (Fig. 7b1); outer surface as in holotype; seven spine articulations (Fig. 7b1) as in holotype, except for stronger ventralward increase in size; inner side (Fig. 7b2) as in holotype but with better-defined knobs and with fewer perforations in a less sharply defined vertical furrow at the dorsal edge of the central knob.

MnhnL OPH069 (Fig. 7c) is a dissociated distal lateral arm plate slightly more than twice taller than long, with rounded ventral and proximal edge with an evenly convex rather than straight central part (Fig. 7c1); outer surface as in holotype; six spine articulations as in holotype; inner side of lateral arm plate (Fig. 7c2) as in holotype, except for poorly discernible vertical furrow and associated perforations.

Remarks The spine articulations composed of straight, parallel, horizontal, near-equal and distally separated dorsal and ventral lobes and the three knobs on the inner side of the lateral arm plates unambiguously place these specimens in the family Amphiuridae. The fossil record of this family is sparse (Jagt 2000) and many of the records previously assigned to this family are either dubious (e.g. *Nullamphiura felli* Skwarko, 1963, based on a virtually unidentifiable specimen from the Cenomanian of Bathurst Island, northern Australia) or have by now been transferred to other families (e.g. *Amphiura*? *senonensis* Valette, 1915 from the Campanian of France transferred tentatively to *Ophiocoma* L. Agassiz, 1836 by Kutscher and Jagt, *in* Jagt 2000). Following an examination of the type specimen of *Amphiura cretacea* Spencer, 1907 from the Cenomanian of southeast England at the Natural History Museum in London (specimen registration number E 5059), we challenge its amphiurid affinities and instead suggest a position within the Ophiotomidae Paterson, 1985 based on the lateral arm plate morphology and in particular the shape of the spine articulations.

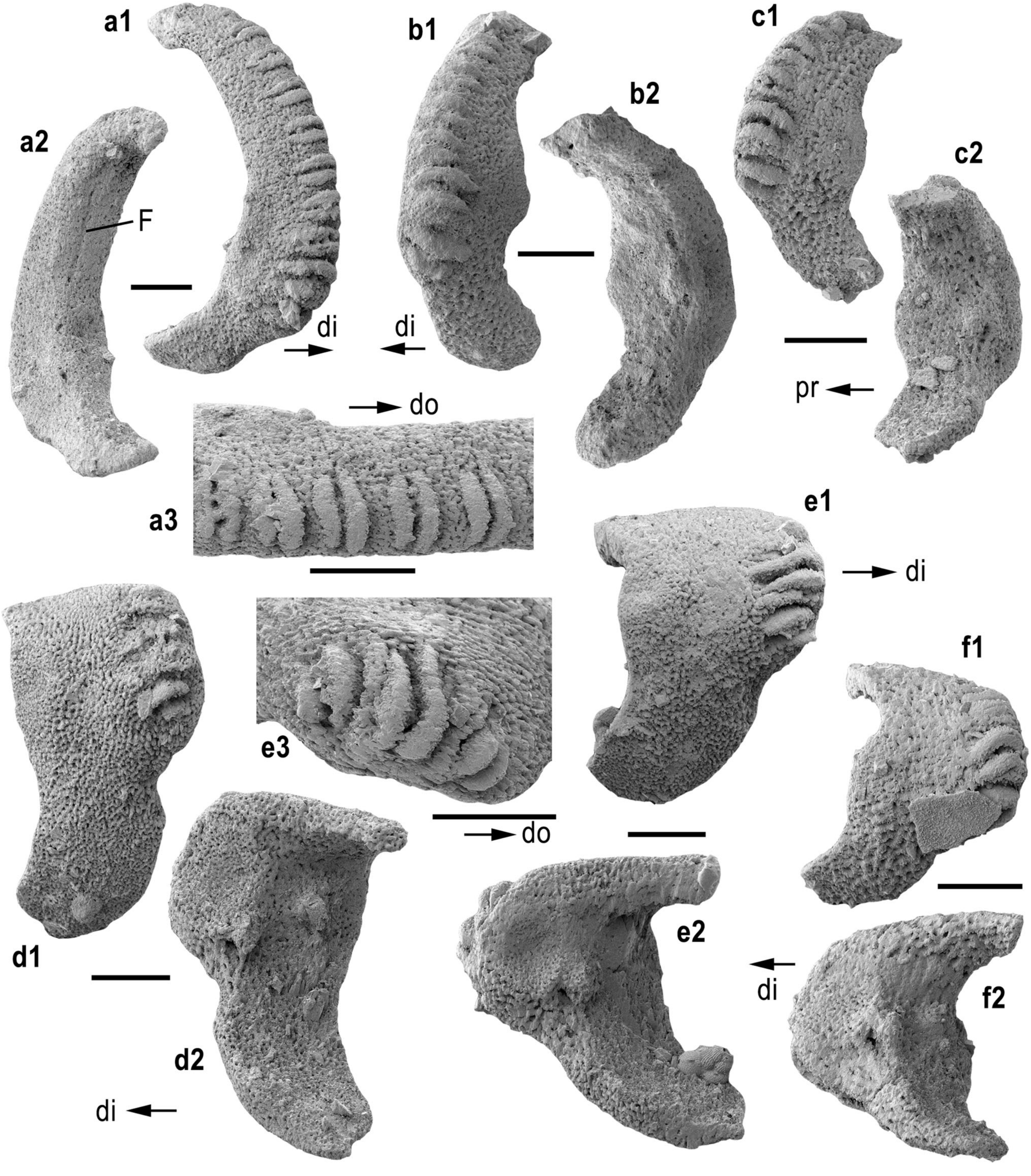

Fig. 7 *Amphiura shannoni* sp. nov. from the Peedee Formation (upper Maastrichtian, Upper Cretaceous) at the road ramp construction site in North Myrtle Beach (Horry County, South Carolina), **a** MnhnL OPH068 (holotype), dissociated proximal lateral arm plate in external (1) and internal (2) views, and with detail of spine articulations in distal (3) view; **b** NHMM 2018 024 (paratype), dissociated proximal lateral arm plate in external (1) and internal (2) views; **c** MnhnL OPH069 (paratype), dissociated distal lateral arm plate in external (1) and internal (2) views. *Amphioplus clementsi* sp. nov. from the Peedee Formation (upper Maastrichtian, Upper Cretaceous) at the road ramp construction site in North Myrtle Beach (Horry County, South Carolina), **d** MnhnL OPH068 (holotype), dissociated proximal lateral arm plate in external (1) and internal (2) views, view; **e** NHMM 2018 025 (paratype), dissociated proximal lateral arm plate in external (1) and internal (2) views, and with detail of spine articulations in distal (3); **f** MnhnL OPH069 (paratype), dissociated distal lateral arm plate in external (1) and internal (2) views. Abbreviations: di: distal; do: dorsal; F: furrow; pr: proximal. Scale bars equal 0.2 mm

For the few remaining extinct amphiurid occurrences, family level assignment relied on general skeletal characters that are not, or no longer, exclusive features of the Amphiuridae according to the most recent classification (O'Hara et al. 2018). In particular, the presence of a pair of infradental papillae was long considered diagnostic for the amphiurids (e.g. Fell 1960). However, it has recently been shown that the terms oral papillae, apical papillae, infradental papillae, tooth papillae and teeth have been applied to non-homologous structures across the Ophiuroidea, thus causing considerable confusion (O'Hara et al. 2018). Ontogenetically defined, infradental papillae designate oral papillae at the ventral or ventro-lateral edge of the dental plate that develop laterally at the dental plate and subsequently move below the teeth. As such, true infradental papillae occur not only in the Amphiuridae but also in the Amphilepididae, Ophiothamnidae and Ophiactidae (O'Hara et al. 2018). In Recent specimens, infradental papillae can be differentiated from apical oral papillae because they do not articulate with sockets on the dental plate. However, in extinct individuals, the presence or absence of sockets on the dental plate can only rarely be seen and a pair of apical papillae is, therefore, easily misinterpreted as a pair of infradental papillae.

Against this background, the amphiurid affinities of the Cretaceous genera *Xanthamphiura* Hess, 1970 and *Deckersamphiura* Jagt and Kutscher, *in* Jagt, 2000 require critical re-assessment because they were based primarily on the assumed presence of infradental papillae. Further insights into more diagnostic characters, in particular the micromorphology of arm spine articulations, are called for in order to enable unambiguous family level placement of those two genera.

Thus, the specimens described herein represent the sole unambiguous amphiurid record from the upper Mesozoic to date, along with the material described below as *Amphioplus clementsi* sp. nov. Assignment to the extant genus *Amphiura* is tentative, being based on the superficial resemblance with lateral arm plates of the genus as illustrated by Thuy and Stöhr (2011). However, it should be emphasised that our knowledge of lateral arm plate morphology of modern amphiurids is still very limited. To make matters worse, the major extant genera within the Amphiuridae, including the type genus *Amphiura*, are polyphyletic in their current composition (O'Hara et al. 2017).

Genus *Amphioplus* Verrill, 1899a

Amphioplus clementsi sp. nov.

Fig. 7d–f

Etymology Species named in honour of Don Clements (North Carolina Museum of Natural History, Raleigh, North Carolina), in recognition of his palaeontological and stratigraphical work on the Upper Cretaceous of the Atlantic Coast of the United States (see Stringer et al. 2018).

Holotype MnhnL OPH071.

Paratypes NHMM 2018 025 and MnhnL OPH072.

Additional material OPH073 (11 dissociated lateral arm plates).

Diagnosis Species of *Amphioplus* with a very large ventral portion, accounting for almost half of the entire height of the lateral arm plate; three equal-spaced spine articulations at the distal edge of the dorsal half of the lateral arm plate; median spine articulation largest; inner side of lateral arm plate with three knobs.

Locus typicus Road ramp construction at 10021 North King's Highway (Figs. 1, 2), North Myrtle Beach (Horry County, South Carolina).

Stratum typicum Peedee Formation, *Discoscaphites conradi* Zone (Landman et al. 2004), upper Maastrichtian (Upper Cretaceous).

Description of holotype MnhnL OPH071 (Fig. 7d) is a dissociated proximal lateral arm plate approximately two times taller than long, with a dorso-proximally pointing dorsal tip, a convex distal edge and a concave proximal edge with a large, weakly convex central part; ventral portion of lateral arm plate (Fig. 7d1) very large, long, accounting for almost half of the entire lateral arm plate height, ventro-proximally pointing, with a constriction dorsally; outer proximal edge with a poorly defined central area of finely meshed stereom, devoid of spurs; outer surface stereom with trabecular intersections transformed into small, inconspicuous tubercles; three equally spaced spine articulations (Fig. 7d1) integrated into the outer surface stereom at the distal edge of the dorsal half of the lateral arm plate; median spine articulation largest; spine articulations composed of two near-straight lobes, doral lobe very weakly dorsally arched, horizontal, massive, ventral lobe parallel to dorsal but slight shorter, is straight, horizontal and massive; both lobes proximally separated and encompassing nearly equal-sized muscle and nerve openings.

Inner side of lateral arm plate (Fig. 7d2) with three knobs, one well defined and prominent in the centre of the dorsal half of the lateral arm plate, a second well defined and prominent one near the tentacle notch at the midline between the dorsal and ventral halves of the lateral arm plate, and a third, much smaller, much less well defined and less prominent one in the centre of the inner proximal edge; single large, well defined perforation at the ventro-distal edge of the second knob; large, but rather shallow tentacle notch.

Paratype supplements and variation NHMM 2018 025 (Fig. 7e) is a dissociated median lateral arm plate approximately 1.5 times taller than long; well in agreement with holotype except for slightly more strongly convex central part of the proximal edge; outer surface stereom with trabecular intersections transformed into small- to medium-sized tubercles; three spine articulations (Fig. 7e3) as in holotype; inner side of lateral arm plate (Fig. 7e2) as in holotype.

MnhnL OPH072 (Fig. 7f) is a dissociated distal lateral arm plate of almost equal height and length; generally in agreement with holotype but with much more strongly convex central part of proximal edge (Fig. 7f1) and with much coarser outer surface stereom; three spine articulations (Fig. 7f1) as in holotype but partially covered by debris; inner side (Fig. 7f2) as in holotype.

Remarks These lateral arm plates can unambiguously be identified as amphiurid on account of the spine articulations that are composed of straight, parallel, horizontal, near-equal and distally separated dorsal and ventral lobes and the three knobs on the inner side of the lateral arm plates. As explained above (see *Amphiura shannoni* sp. nov.), the amphiurid remains described herein represent the only confirmed Mesozoic records of the family Amphiuridae to date.

The present lateral arm plates differ from those of the co-occurring *Amphiura shannoni* sp. nov. most conspicuously in the lower number of spine articulations, the greater length and the much larger ventral portion. The differences even suggest distinction at the generic level; indeed, these lateral arm plates show little resemblance with those of Recent species of *Amphiura* as illustrated by Thuy and Stöhr (2011). There are closer similarities to lateral arm plates of extant species of *Amphioplus* (Rodrigues et al. 2011; B. Thuy, unpublished observations). However, as noted above, our knowledge of lateral arm plate morphology amongst Recent amphiurids is still insufficient. Assignment to the genus *Amphioplus* should, therefore, be considered tentative.

Discussion

At first sight, the present note is yet another systematic description of a fossil ophiuroid assemblage that is based on dissociated skeletal parts. However, in the light of the taxa found, it provides an unexpectedly far-reaching addition to the ophiuroid fossil record. This is because the present assemblage was collected from a fundamentally different palaeogeographical context than previously described coeval assemblages (e.g. Jagt 2000) and, probably as a result, shares no species with them. Instead, all the taxa identified in the North Carolina assemblage are new to science, although some need to remain unnamed pending the discovery of more material. Obviously, ophiuroid faunas of latest Cretaceous age are still flawed by a considerable geographical sampling bias, despite being amongst the best known (e.g. Jagt 2000; Kutscher and Jagt, *in* Jagt, 2000). Thus, our study emphatically encourages geographical expansion of sampling of the ophiuroid fossil record, even for the better-known time intervals. Similar conclusions were put forward by Thuy et al. (2014), who compared ophiuroid assemblages from the Aptian of Spain and Texas on opposite sides of the proto-Atlantic.

Not only does the present assemblage consist exclusively of previously unknown species, it furthermore shows a composition that fundamentally differs from other coeval assemblages as far as genera or even families are concerned. Late Cretaceous ophiuroid assemblages from Europe are commonly dominated by representatives of the extinct genus *Ophiotitanos* and those of the suborder Ophiomusina (e.g. Helm et al. 1999; Jagt 2000; Kutscher and Jagt, *in* Jagt 2000; Štorc and Žítt 2008). These two groups are completely missing from the North Carolina assemblage. Instead, the most abundant component is a new species assignable to the family Amphilimnidae (*Amphilimna intersepultosetme* sp. nov.), which had previously been recorded only once from the fossil record (Thuy et al. 2014). In modern oceans, this family is widespread, albeit rare. Dredging samples from deep shelf or shallow bathyal areas occasionally yield very few specimens assignable to *Amphilimna*. Only in exceptional cases are samples dominated by an amphilimnid species, e.g. Albatross station 5222 of (Koehler 1922) or samples NAD40V, NAD52E and NAD55C of A.M. Clark (1974). The present assemblage could well be a latest Cretaceous equivalent of such settings, but in order to substantiate such a comparison further, more research needs to be undertaken into the causes for a modern locality to be dominated by amphilimnid species.

Euryalids are not uncommon in the uppermost Cretaceous (e.g. Kutscher and Jagt, *in* Jagt 2000) although the diversity of the order in the present assemblage is remarkable. Never before has a fossil ophiuroid fauna been shown to include representatives of all three currently recognised euryalid families. Another notable aspect is the presence of a new genus of asteronychid (*Lillithaster* gen. nov.) that holds a transitional position between the stem euryalid *Melusinaster* and Recent asteronychids. Finally, the South Carolina assemblage yields the oldest known unambiguous records of the family Amphiuridae.

It has been shown that the taxonomic composition of Mesozoic shallow-marine ophiuroid assemblages differs from that of living equivalents in shallow seas (e.g. Thuy et al. 2013, 2014). Specifically, many Mesozoic sites yield groups that are currently restricted to or predominantly found at bathyal or abyssal depths (e.g. Thuy 2013; Thuy et al. 2013). The assemblage described herein originates from sublittoral palaeo-depths but fails to follow this pattern and lacks typical deep-sea groups. Even the sole representative of the suborder Ophiacanthina, whose members predominantly inhabit the deep sea, belongs to the Ophiotomidae, the family within this suborder that is known from the most shallow-water occurrences (Thuy 2013). The present assemblage thus seems to document the onset of modern shallow-sublittoral ophiuroid assemblages.

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