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Re-assessment of the aberrant brittle star genus *Astrosombra* (Echinodermata, Ophiuroidea), based on an exceptionally preserved specimen from the Upper Cretaceous of Rügen, north-east Germany

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Abstract

Amongst the most extraordinary extinct ophiuroids is the genus *Astrosombra* from the Upper Cretaceous of Germany. Initially known from isolated ossicles only, the extremely expanded lateral arm plates suggested an aberrant body shape comparable to that seen in the extraordinary astrophiurid genus *Astrophiura*. Here, we describe the first articulated specimen of *Astrosombra rammsteinensis*, the type and only known species of the genus, from the type locality of the taxon, showing the highly modified lateral arm plates in their anatomical context and providing insights into the general skeletal morphology. The new specimen confirms the presence of extremely widened arms, formed by the aberrantly expanded lateral arm plates articulating with unusually wide vertebrae and covered dorsally by multiple rows of dorsal arm plates. The width of the arms is further increased by large, flat, feather-like arm spines. MicroCT images of the articulated disc revealed morphological details, in particular, high oral plates with wing-like expansions, suggesting transfer of *Astrosombra* from the Amphilimnidae to the Ophiopsilidae. In analogy with *Astrophiura*, the extremely widened arms, the fringe of flat arm spines, the large tentacle pores and the overall flat body shape suggest that *Astrosombra* inhabited the small, patchy hard substrates formed by the skeletal remains of other organisms.

Key Words

Astrosombra rammsteinensis, Chalk Sea, Echinodermata, Maastrichtian, ophiuroid, Systematic placement

Introduction

Brittle stars or ophiuroids constitute the most speciose of the five extant classes of echinoderms and represent an important component of marine benthic communities (Stöhr et al. 2012). Although their basic anatomy – a round central disc with five slender arms – appears simple and monotonous at first sight, ophiuroids do display a surprisingly wide range of morphological variation, both in terms of gross body shape (e.g. number of arms, length of arm spines) and at the microscopic level (e.g. arrangement of mouth papillae) (Stöhr et al. 2012; O'Hara et al. 2018).

Amongst all the morphological variants, some diverge so strikingly from the basic ophiuroid bauplan that they were long considered synapomorphies of higher-level taxa. The family Hemieuryalidae Verrill, 1899, for example, was traditionally diagnosed by a combination of characters that appeared to be unique amongst non-euryalid brittle stars, in particular, by their small size, reduced disc plating and coiling arms (e.g. Fell (1960)). Recent advances in molecular and morphological phylogeny, however, have revealed that many former hemieuryalid genera in fact belong to other families, implying that the seemingly unique characters were independently

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acquired adaptations to an epizoic lifestyle (O'Hara et al. 2017, 2018). On a more general level, revision of ophiuroid higher-level classification has demonstrated that the group is particularly prone to convergent evolution (O'Hara et al. 2018).

Amongst the most remarkable examples of convergent evolution in the fossil record of brittle stars is the case of the extinct genus *Astrosombra* Thuy, Gale & Numberger-Thuy, 2019. This taxon was originally described on the basis of dissociated lateral arm plates that showed an unusual combination of spine articulations typically found in members of the family Amphilimnidae O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018, plus a highly modified plate outline otherwise known solely from the highly aberrant genus *Astrophiura* Sladen, 1879. The conclusion reached by Thuy et al. (2019) was that *Astrosombra* represented an extinct amphilimnid with widely expanded lateral arm plates that increased overall body surface beyond the disc edge, as in *Astrophiura*.

Here, we describe the fortuitous find of an articulated specimen of the type species of *Astrosombra*, *A. rammsteinensis* Thuy, Gale & Numberger-Thuy, 2019, which enables novel insights into the anatomy of this highly aberrant brittle star genus. Using a combination of light and electron microscopy and microCT scanning, we here provide an exhaustive morphological description of this specimen, revise the higher systematic position of *Astrosombra* and discuss potential palaeoecological implications of its peculiar anatomy.

Geological context

The Upper Cretaceous chalk succession of the Isle of Rügen (Mecklenburg-Vorpommern, north-east Germany, Fig. 1), represents one of the most extensive and well-studied pelagic chalk deposits in Europe. During the late early Maastrichtian (Late Cretaceous), this succession accumulated within a broad epicontinental seaway that inundated large parts of northern Europe. On the Jasmund Peninsula, this chalk crops out in coastal cliffs and former quarries (Fig. 1). At present, a single active quarry remains, where more than 90 metres of section are accessible, in spite of strong glaciotectonic deformation linked to movements of Pleistocene ice sheets (Reich and Frenzel 2002).

During the Maastrichtian, the present-day Rügen area formed part of the Rügen Basin, a subsidiary trough along the south-western margin of the Fennoscandian Shield. The Basin occupied the south-easterly extension of the Danish Sub-basin within the Danish-Polish Trough (Reich and Frenzel 2002; Reich et al. 2018). Deposition occurred during a period of relative tectonic quiescence and regional subsidence, although later inversion movements produced slumps, seismites and displaced sediment masses within the chalk succession (Reich et al. 2018).

The chalk ooze accumulated in an oligotrophic, warm-temperate, open-marine shelf environment at approximately 40° palaeolatitude (Reich and Frenzel 2002). Water depths of roughly 150–250 metres, possibly reaching up to 300 metres, placed the depositional setting below the storm wave base, but within the lower photic zone (Reich and Frenzel 2002; Reich et al. 2018). The seafloor consisted of soft calcareous ooze, largely produced by coccolithophores, with benthic islands of secondary hardgrounds formed by skeletal remains of benthic organisms such as bryozoans or other hard-shelled biota (e.g. bivalves, echinoids and cephalopods) (Nestler 1965). These hard substrates, very limited in extent, were inhabited by a diverse fauna of sessile benthic organisms, such as solitary corals, crinoids and serpulid polychaetes. The sediment experienced intense bioturbation by infaunal and semi-infaunal organisms, such as decapod arthropods, sea cucumbers, echinoids and polychaetes (Reich and Frenzel 2002; Reich and Kutscher 2018; Knaust and Schnick 2024). In general, sedimentation rates were low, around 35 mm per 1,000 years (Reich and Frenzel 2002). Nevertheless, these deposits yield diverse benthic and planktic faunal assemblages that are often well preserved (at times, excellently so), allowing details of microscopic stereom structure in echinoderms to be observed. Amongst brittle stars, several dozens species have been recognised to date (Kutscher and Jagt 2000; Kutscher 2011).

Biostratigraphically, the upper lower Maastrichtian chalk of Rügen is subdivided primarily using index taxa amongst belemnitellid coleoids (Schulz 1979), articulate brachiopods (Steinich 1965; Surlyk 1984) and ostracods (Herrig 1966) (Fig. 1).

Material and methods

The specimen described in the present paper was collected by one of us (NS) at the active Promoisel chalk pit, operated by Vereinigte Kreidewerke Dammann GmbH. At this quarry, most of the section exposed belongs to the *Belemnella sumensis* belemnite Zone (upper lower Maastrichtian), based on personal observations by one of us (NS) and finds of the index brachiopod *Trigonosemus pulchellus* (Nilsson, 1827), indicative of brachiopod zone II (*sensu* Steinich (1965); see also Surlyk (1984, 2025)) (Fig. 1).

The brittle star was found loose in scree below a part of the quarry face containing an interval with several debris-flow events, from which it most likely originated. These debris-flow intervals are characterised by abundant macrofossils and generally small, angular to moderately rounded chalk clasts measuring only a few millimetres to centimetres in size, rarely larger, embedded in a darker grey matrix, corresponding to the so-called "Brockenhorizont" (Steinich 1967, 1972). This particular interval is interpreted as a debris flow that transported and subsequently buried organisms and skeletal remains within calcareous ooze prior to decay.

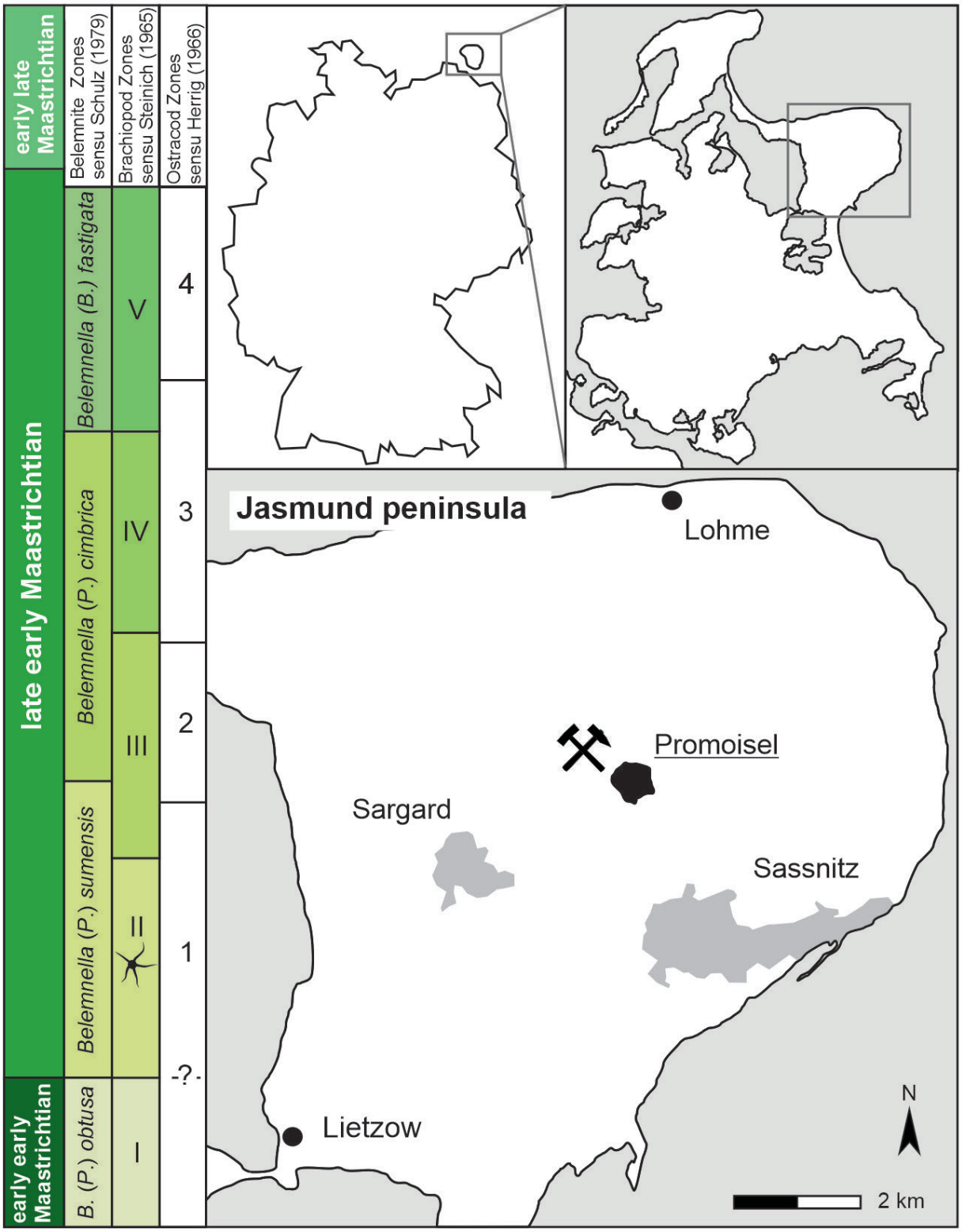

Figure 1. Biostratigraphic framework and subdivision of the Upper Cretaceous succession of the Rügen Chalk, modified after Reich et al. (2018), showing the correlation of belemnite, brachiopod and ostracod zones. The brittle star symbol marks the fossil horizon; Brachiopod Zone II corresponds to the *Trigonosemus pulchellus* Zone. The maps show the location of the Jasmund Peninsula on Rügen and the position of the Promoisel chalk pit, from which the studied material was collected.

The specimen was discovered after splitting a piece of chalk, which broke the skeleton into a ventral and a dorsal part. The rock was then reassembled using water-soluble wood glue. Afterwards, the disc and arms were carefully prepared and manually cleaned with a brush and needle in order to expose the dorsal surface. The ventral side was left unprepared on account of the extreme fragility of the specimen; it was visualised virtually by means of microCT scanning.

The studied specimen was first scanned using a YXLON FF35 CT scanner, equipped with a Perkin Elmer Y.Panel 4343 CT detector at the Natural History Museum of Vienna (NHMW) using the YXLON 225 kV Microfocus Direct Beam x-ray tube. The scans were performed with a tube voltage of 160 kV, a current of 200 µA, 3600 projections, 1 × 1 binning and an exposure time of 1 sec. An isotropic voxel size of 35.6 µm was achieved. Visualisation was carried out using the Dragonfly software, Version 2022.1 for Windows (Object Research Systems, Montreal, Canada, 2022) using volume renderings. The raw data were deposited in the NHMW data repository (Winkler et al. 2026, https://doi.org/10.57756/c8kp23).

Images of the specimen were taken using a Keyence VHX-6000. Isolated arm ossicles were removed from the matrix, cleaned in an ultrasonic bath, mounted on aluminium stubs and gold-coated for scanning electron microscopy using a JEOL NeoScope JCM-5000. The specimen is now housed in the collections of the National Museum of Natural History Luxembourg (acronym MNHNL). We adopt the classification of ophiuroids outlined by O'Hara et al. (2017, 2018) and use the terminology proposed by Stöhr et al. (2012), Thuy and Stöhr (2016) and Hendler (2018).

Results

Systematic palaeontology

Class Ophiuroidea Gray, 1840
Subclass Myophiuroidea Matsumoto, 1915
Infraclass Metophiurida Matsumoto, 1913 (crown-group of Ophiuroidea)
Superorder Ophintegrida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Order Amphilepidida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Suborder Ophiopsilina Matsumoto, 1915
Superfamily Ophiopsiloidea Matsumoto, 1915
Family Ophiopsilidae Matsumoto, 1915

Genus *Astrosombra* Thuy, Gale & Numberger-Thuy, 2019

Type and sole species known. *Astrosombra rammsteinensis* Thuy, Gale & Numberger-Thuy, 2019.

Emended diagnosis. Ophiopsilid with dorsal disc covered by a continuous ring of very large, thick radial shields showing densely arranged small tubercles with slightly larger, prominent tubercles scattered across the surface and lacking discernible disc spines or granules; arms extremely widened, composed of very wide, short vertebrae, a row of very wide primary dorsal arm plates bordered on each side by three rows of accessory dorsal arm plates and strongly modified, notably expanded lateral arm plates arranged in an imbricating row leaning towards the disc, with the ventro-distal portion of a lateral arm plate overlapped by the dorso-proximal portion of the succeeding plate; lateral arm plates with coarsely tuberculate outer surface ornamentation and with continuous, but heterogeneous row of spine articulations, with the ventral spine articulations small and composed of thin, close-set ridges carrying small, short, conical arm spines and the dorsal spine articulations much larger and composed of thicker, widely spaced ridges carrying very large, flat, feather-like arm spines.

Astrosombra rammsteinensis Thuy, Gale & Numberger-Thuy, 2019

Figs 2–4

Description. MNHNL OPH322 is an articulated skeleton preserved in the process of disintegration. It exposes the dorsal side and all arms broken at their base, except for one arm preserving at least 20 proximal to median segments. The disc is round and has a diameter of 13 mm. Its dorsal surface is covered to a large extent by a continuous ring of very large, thick, scalene-triangular dorsal radial shields (Fig. 2). The latter have an outer surface stereom covered by densely arranged small tubercles with slightly larger, prominent tubercles scattered across the surface. The radial and abradial edges of the radial shields are strongly bevelled and form wide contact surfaces that were originally covered by thick polygonal disc scales, including a bar-like proximal scale and several smaller distal ones, all showing the same outer surface tuberculation as the radial shields. The centre of the disc (Fig. 2) shows a jumble of small, thick, polygonal scales, some of which could correspond to the central and/or radial primary plates. The interradial notches between the radial shields (Fig. 2) are covered by lozenge- to wedge-shaped scales. There is no trace of spines or granules that originally would have covered the dorsal disc, although it cannot be ruled out that such structures were lost to incipient decay and/or preparation.

The arm stumps preserved are extremely large (Fig. 3A–D). One of them exposes the dorsal side of proximal vertebrae (Fig. 3C). These are approximately four times wider than long and show a deep dorso-distal notch interlocking with a dorso-proximal protrusion of the succeeding vertebra. The proximal lateral arm plates (Fig. 3C, E, F) are extremely widened and articulate only with the lateral tips of the vertebrae, thereby doubling the total width of the arm. They are arranged in an imbricating row leaning towards the disc, with the ventro-distal portion of a lateral arm plate overlapped by the dorso-proximal portion of the succeeding lateral arm plate. The lateral arm plates each carry up to four very large, feather-like arm spines (Fig. 3D, G) sitting perpendicular to the arm axis on the three dorsalmost spine articulations and expanding the width of the arm, followed ventrally by up to four much smaller, extremely short, conical, pointed arm spines. The dorsal surface of

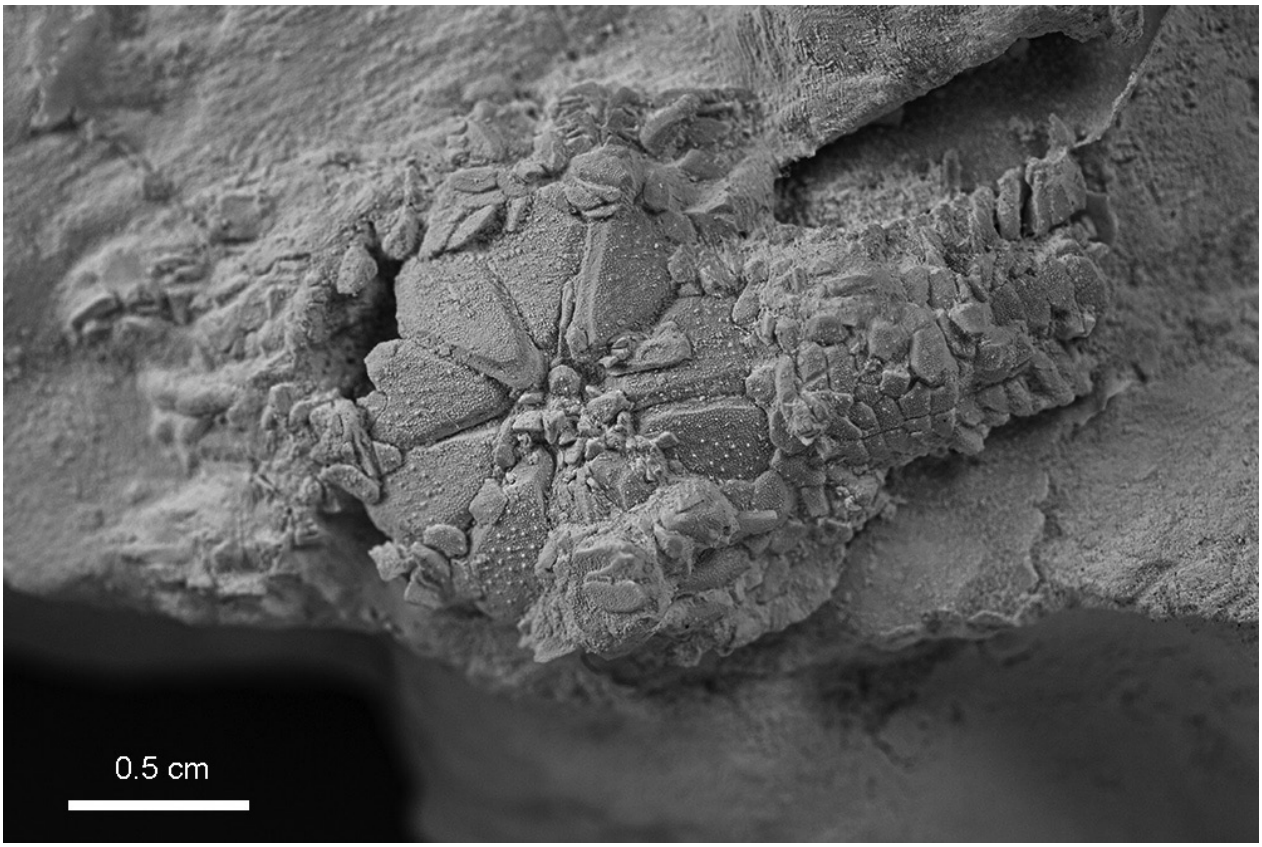

Figure 2. *Astrosombra rammsteinensis*, MNHNL OPH322, from the upper lower Maastrichtian (Upper Cretaceous) of Rügen, north-east Germany, in dorsal view.

the arm (Fig. 3A, B) is covered along its mid-line by a contiguous row of wide, roughly hexagonal, thick primary dorsal arm plates, almost twice wider than long and with a coarsely reticulate dorsal surface stereom that consists of tubercles merging into small, vermiform ridges close to the edges of the plate. The primary dorsal arm plate is laterally bordered on either side by three accessory dorsal arm plates, two irregularly pentagonal ones and a wedge-shaped one at the edge that covers the interstice between successive lateral arm plates and reaches the spine articulations of the latter. All accessory dorsal arm plates have the same outer surface stereom as the primary ones.

The microCT scan (Fig. 4) of the specimen confirms the imbricate arrangement of the lateral arm plates and suggests that the tentacle openings emerge from a relatively large, angular junction between the lateral arm plates and the vertebrae, encompassed between lateral arm plate pairs and the ventral arm plates. A radial furrow along the mid-line of the ventral side of the lateral arm plates (Fig. 3E) potentially enabled the abradial extension of the tube foot. The ventral arm plates (Fig. 4C) are almost three times wider than long and have an expanded distal portion with a straight to weakly concave distal edge and proximalwards converging lateral edges that lead to a wide, straight to slightly convex proximal edge. All ventral arm plates preserved are widely contiguous. The oral skeleton (Fig. 4B–D) includes relatively small, approximately pentagonal oral shields that are as wide as long and have concave proximal and lateral edges and a convex distal edge. The adoral shields are short and very wide and broadly abut in front of the oral shield. The oral plates (Fig. 4B, D) are relatively short and slender when seen in ventral view and very high when seen in lateral view. Their adradial flange is expanded into a wing-like structure. The set of oral papillae and teeth is largely dissociated, but the few elements that remain close to their original anatomical position suggest long, slender and spine-like teeth and oral papillae *sensu lato*.

A lateral arm plate (Fig. 3E, F) that was detached from the specimen and examined using scanning electron microscopy is extremely widened and dorso-ventrally flattened. The outer surface, i.e. the abradially facing surface of the plate, is reduced to a narrow edge carrying up to eight spine articulations (Fig. 3F) in a continuous row. The four dorsal spine articulations are largest and composed of thick dorsal and ventral lobes that are parallel and proximally separated by two to three short, small knobs and that encompass muscle and nerve openings of similar size. The four ventral spine articulations are much smaller and show a ventralward decrease in size. They are composed of very thin, parallel dorsal and ventral lobes. The ventro-distal and dorso-proximal portions of the lateral arm plates show surface stereom ornamented by coarse tubercles, whereas the ventro-proximal and dorso-distal portions are transformed into contact surfaces with the preceding and succeeding lateral arm plates,

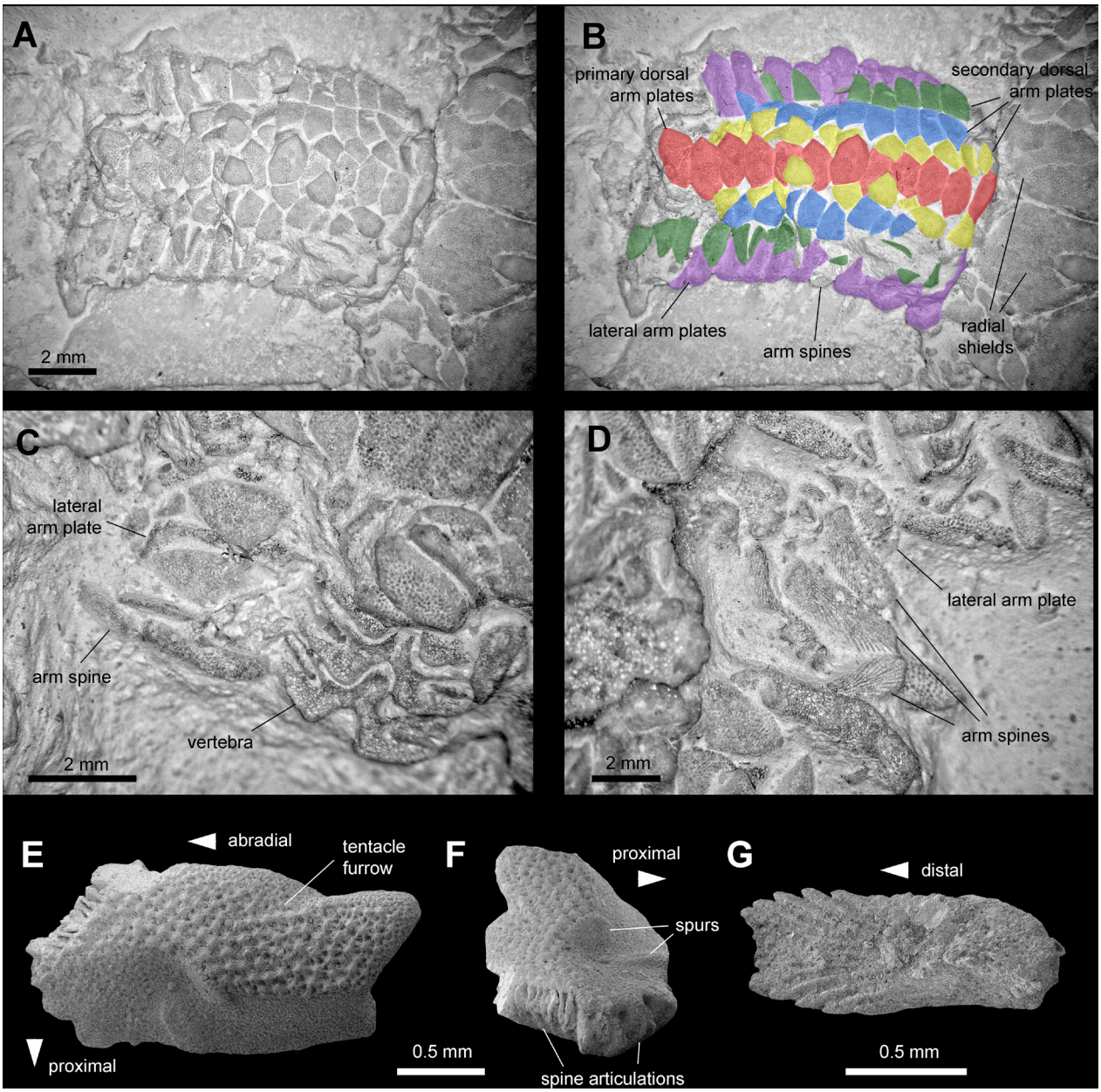

Figure 3. *Astrosombra rammsteinensis*, MNHNL OPH322, from the upper lower Maastrichtian (Upper Cretaceous) of Rügen, north-east Germany. **A, B.** Detail of the dorsal arm plating in plain view (**A**) and with plate types and corresponding rows of accessory dorsal arm plates colour-coded (**B**); **C.** Detail of an arm base in dorsal view exposing the vertebrae; **D.** Detail of arm spines sitting on proximal lateral arm plates in dorsal view; **E, F.** Isolated lateral arm plate removed from the articulated specimen in ventral (**E**) and abradial (**F**) views; **G.** Isolated arm spine removed from the articulated specimen.

respectively, showing finely meshed stereom devoid of ornamentation. The ventro-proximal edge of the lateral arm plate is deeply incised by the dorso-proximal contact surface and shows two conspicuous spurs. The adradial edge of the lateral arm plate corresponds to the vertebral articular surface and shows a single perforation and a poorly discernible single knob.

An arm spine (Fig. 3G) detached from the specimen has a conspicuous feather-like shape. Its base is thickened and shows two parallel ridges. The main body is flattened and ornamented with coarse, distalward diverging ridges that terminate in pointed lateral tips.

Discussion

Taxonomic affinities

The unique shape of the lateral arm plates, one of which could be detached (Fig. 3E, F) and examined exhaustively from all sides, unambiguously identifies the newly-collected specimen described here as *Astrosombra rammsteinensis*. This species was originally described on the basis of dissociated lateral arm plates from the same deposit that yielded the new individual, i.e. the upper lower Maastrichtian chalk of Rügen (Thuy et al. 2019).

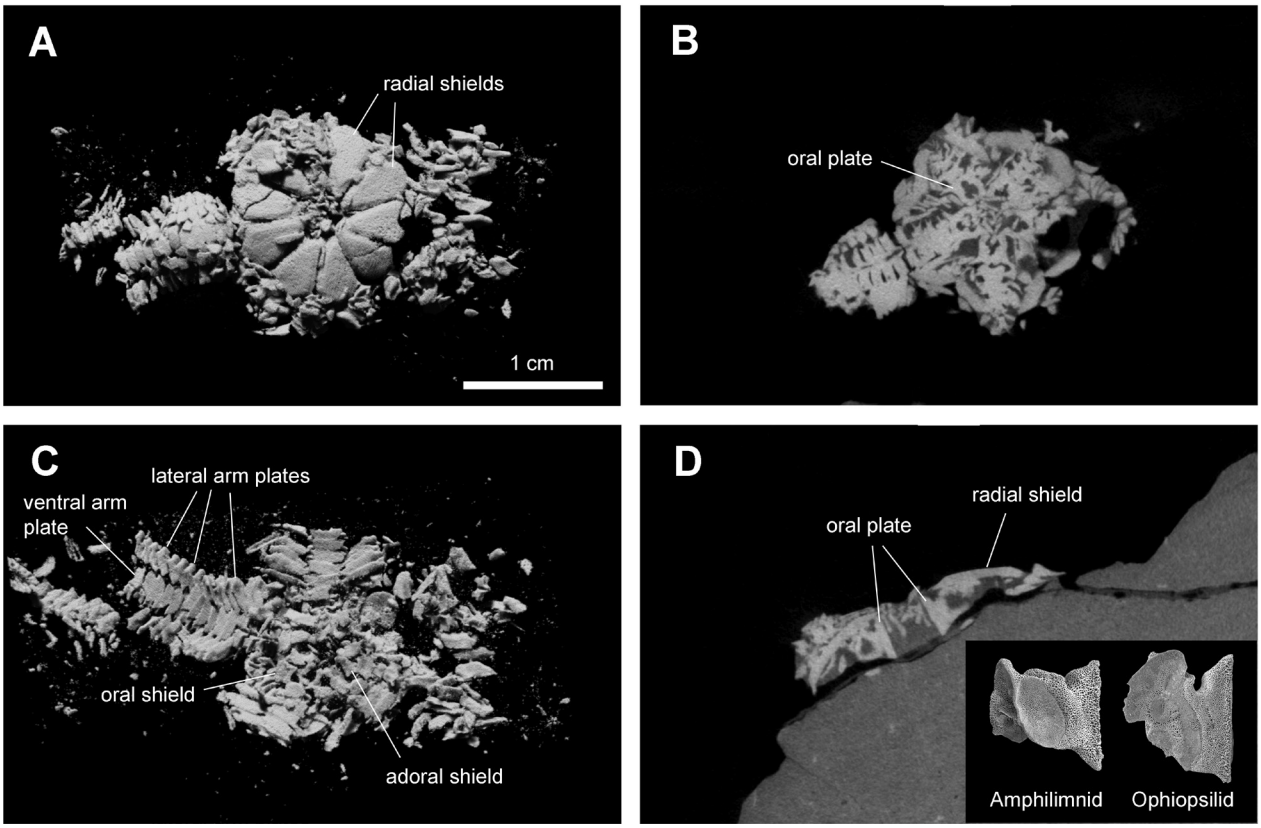

Figure 4. *Astrosombra rammsteinensis*, MNHNL OPH322, from the upper lower Maastrichtian (Upper Cretaceous) of Rügen, north-east Germany. **A–D.** microCT scans showing the dorsal surface (**A**), a horizontal section (**B**), the ventral surface (**C**) and a vertical section (**D**). Oral plates in abradial view of a recent amphilimnid and ophiopsilid, respectively, for comparison.

The aberrant anatomy of *A. rammsteinensis* was already inferred on the basis of the unusual shape of the dissociated lateral arm plates. The new semi-articulated skeleton before us, however, allows us to re-evaluate the conclusions drawn from dissociated lateral arm plates and unlocks previously unavailable insights into disc morphology.

The articulated arm fragments of the new specimen confirm the extremely widened nature of the arms and the imbricating arrangement of lateral arm plates. In addition, it reveals that the lateral arm plates in the original description were misorientated, with the dorsal side erroneously labelled as ventral side and *vice versa* (Thuy et al. 2019). Furthermore, microCT scans of the new specimen suggest that the actual tentacle notch is restricted to the space between the lateral arm plate and the vertebra. The structure that was incorrectly interpreted in the original description as a very wide tentacle notch (Thuy et al. 2019) is here re-interpreted as an articular surface for the preceding lateral arm plate. Nevertheless, the size of the junction between the lateral arm plates and the vertebrae implies relatively large tube feet and the radial furrow along the mid-line of the ventral side of the lateral arm plates, newly discovered in the present study, suggests that the tube feet could extend abradially.

These new insights into the general skeletal morphology of *Astrosombra rammsteinensis* permit a re-evaluation of the systematic position of that taxon. Based on the spine articulation morphology of the type specimens, Thuy et al. (2019) assigned *A. rammsteinensis* to the family Amphilimnidae, although they did mention that the Ophiopsilidae had superficially similar spine articulations. However, the new specimen lacks the long disc spines typically found in members of the Amphilimnidae. Furthermore, the oral plates of the new specimen are higher than long and show an adradial flange expanded into a wing-like structure. The latter, combined with the naked disc, favour ophiopsilid affinities. We therefore transfer *Astrosombra rammsteinensis* to the Ophiopsilidae and thereby add a second genus to this originally monotypic family.

Palaeoecology

As outlined above, the Maastrichtian Chalk of Rügen represents a predominantly soft-bottom environment composed of calcareous ooze. Such a soft-bottom environment requires many benthic organisms to develop adaptations, generally dubbed “snowshoe” adaptations, that reduced the risk of sinking into the ooze during resting or locomotion. Such adaptations have been recorded for several biotic groups (see, for example, Carter (1972)), including epibenthic echinoderms (e.g. Nestler (1965, 1980); Schlüter et al. (2012)). The unusual body shape modifications seen in *Astrosombra rammsteinensis*, in particular, the extremely widened arms, appear at first sight to serve a similar “snowshoe” effect by increasing the body surface. However, in

present-day oceans, muddy seafloors are commonly inhabited by ophiuroids (Stöhr et al. 2012) that fail to show any particular anatomical adaptations related to substrate conditions, for example, to prevent sinking. The same holds true for the bulk of the Chalk ophiuroids (Kutscher and Jagt 2000). Therefore, it seems very unlikely that the aberrant morphology of *A. rammsteinensis* is an adaptation to the soft bottom of the Chalk Sea.

Extremely widened arms such as those observed in *A. rammsteinensis* are rarely seen in ophiuroids, both amongst recent and extinct taxa. The most conclusive insights available to date are based on observations on recent species of the astrophiurid *Astrophiura*, suggesting that the extremely widened arms typically found in members of this genus, together with the overall flat body, the large tube feet and the fringe of flattened spines along the margin of the disc and expanded arm bases enable a more efficient adhesion to hard substrates (Fujita and Hendler 2001). This limpet-like lifestyle is well in accordance with submersible observations of live animals caught predominantly on hard substrates such as rocks, shells or even discarded beer bottles (Pawson 2018). *Astrosombra rammsteinensis* aligns with species of the genus *Astrophiura* when it comes to its conspicuous anatomical modifications, in particular, the extremely widened arms, the overall flat body, the large tentacle pores and the large, flat arm spines along the margins of the arms. It is, therefore, reasonable to assume a similar, limpet-like lifestyle in *Astrosombra*.

As a consequence and in direct analogy with recent species of *Astrophiura*, the most likely habitats of *A. rammsteinensis* were small and spatially restricted hard-substrate patches, so-called secondary hardgrounds, formed by the skeletal remains of other organisms, such as bryozoans and molluscs, including large inoceramid shells (Nestler 1965; Reich and Frenzel 2002). These were inhabited by a diverse fauna of sessile benthic organisms as well as mobile organisms adapted to hard substrates, such as *A. rammsteinensis*. The patchy occurrence of these hard-substrate islands within an otherwise ooze-dominated seafloor might provide an explanation for the relative scarcity of *A. rammsteinensis* compared to other elements of the Chalk Sea ophiuroid fauna (Kutscher and Jagt 2000; Thuy et al. 2019).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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NS collected and prepared the fossil specimen. BT took the lead in conceiving the project and writing the manuscript. AK and VW produced the microCT scans. BT and NS compiled the figures. JWMJ, NS, AK and VW contributed to the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text.