



Molpadid holothurian calcareous ring material from the early Maastrichtian Rügen Chalk, Germany

Mike Reich^{1,2,3} · Manfred Kutscher⁴ · Tanja R. Stegemann^{1,2}

Received: 4 April 2025 / Accepted: 28 May 2026 / Published online: 14 July 2026
© The Author(s) 2026

Abstract

Molpadid sea cucumbers are important components of the infaunal benthos in today's marine ecosystems. This can also be assumed for Cenozoic and partly Mesozoic times. However, the fossil record to date is more than patchy and also concerns the Upper Cretaceous, for example. From the early Maastrichtian chalk of the Jasmund Peninsula/Isle of Rügen, the world's only second record of late Cretaceous calcareous ring material of molpadid sea cucumbers (*Cretacaudina rugia* gen. et sp. nov.) is described, discussed and subsequently morphologically compared with extant forms.

Keywords Cretaceous · Echinodermata · Holothuroidea · Caudinidae · Eupyrgidae · Molpadiidae · *Heteromolpadia* · X-ray CT

Introduction

Modern members of molpadid Holothuroidea are small- to medium-sized (c. 0.5–25 cm) and more or less sausage-shaped, with the posterior end usually tapering to form a distinct tail (Fig. 1A–B). Representatives of the Molpadida typically live buried or in depressions in soft substrates, from the subtidal zone down to hadal depths (up to 5,700 m; e.g. Pawson, 1977; Pawson & Liao, 1992; Pawson et al., 2001; Pawson & Vance, 2007; Davey & O'Loughlin, 2013;

Gebruk et al., 2014; O'Loughlin & Ong, 2015; Samyn & VandenSpiegel, 2016; Mercier et al., 2024). In suitable habitats, they can form populations of hundreds of specimens per m². Sediment ingestion is non-selective (e.g. Khripounoff & Sibuet, 1980; Pawson et al., 2001) or selective (Mageau & Walker, 1976) using their small, digitate or simple tentacles.

A large part of the Molpadida (Fig. 1A–B) is unique within Holothuroidea in having, besides the usual high-Mg-calcite ossicles (Fig. 1C–D) and other skeletal parts (calcareous ring, anal plates), ferro-phosphatic bodies (e.g. *Heteromolpadia*, *Molpadia*; Fig. 1C–F) embedded in the body wall (Lowenstam & Rossman, 1975; Pawson et al., 1975; Pawson, 1982) as well as chitinous tentacle shovels (*Ceraplectana*; Fig. 1G–I) (Pawson, 1982; Pawson & Kerr, 2001; Reich, 2014).

Today, more than 100 modern species of molpadid sea cucumber taxa, grouped in three families (Molpadiidae, Caudinidae, Eupyrgidae) are known (WoRMS/Paulay et al., 2025).

Fossil members of the Molpadida are lesser known than species of other holothuroid groups (e.g. Apodida) (Gilliland, 1993; Reich, 2013). However, isolated body wall ossicles are frequently reported from Jurassic strata onwards (e.g. Deflandre-Rigaud, 1959, 1962; Górka & Łuszczewska, 1969; Reich, 2002a, 2002b, 2003; Reich & Ansorge, 2014; Caramés et al., 2019) but sometimes misinterpreted. The latter applies, for example, to Sadeddin (1996), who discovered in Albian sediments from Texas/USA distinctive

This work is registered in ZooBank, the LSID is: urn:lsid:zoobank.org:pub:81058683-045C-4B0F-AC8B-1E12C4949B66.

This is a contribution to the special issue honouring Professor Ekkehard Herrig on his 90th birthday.

Handling Editor: Jörg Ansorge.

✉ Mike Reich
m.reich@3landesmuseen.de

¹ Staatliches Naturhistorisches Museum, Gaußstr. 22, 38106 Brunswick, Germany

² paläon Forschungsmuseum, Paläon 1, 38364 Schöningen, Germany

³ Geowissenschaftliches Zentrum, Abt. Geobiologie, Georg-August-Universität Göttingen, Goldschmidt-Str. 3, 37077 Göttingen, Germany

⁴ Dorfstr. 10, 18546 Sassnitz, Germany

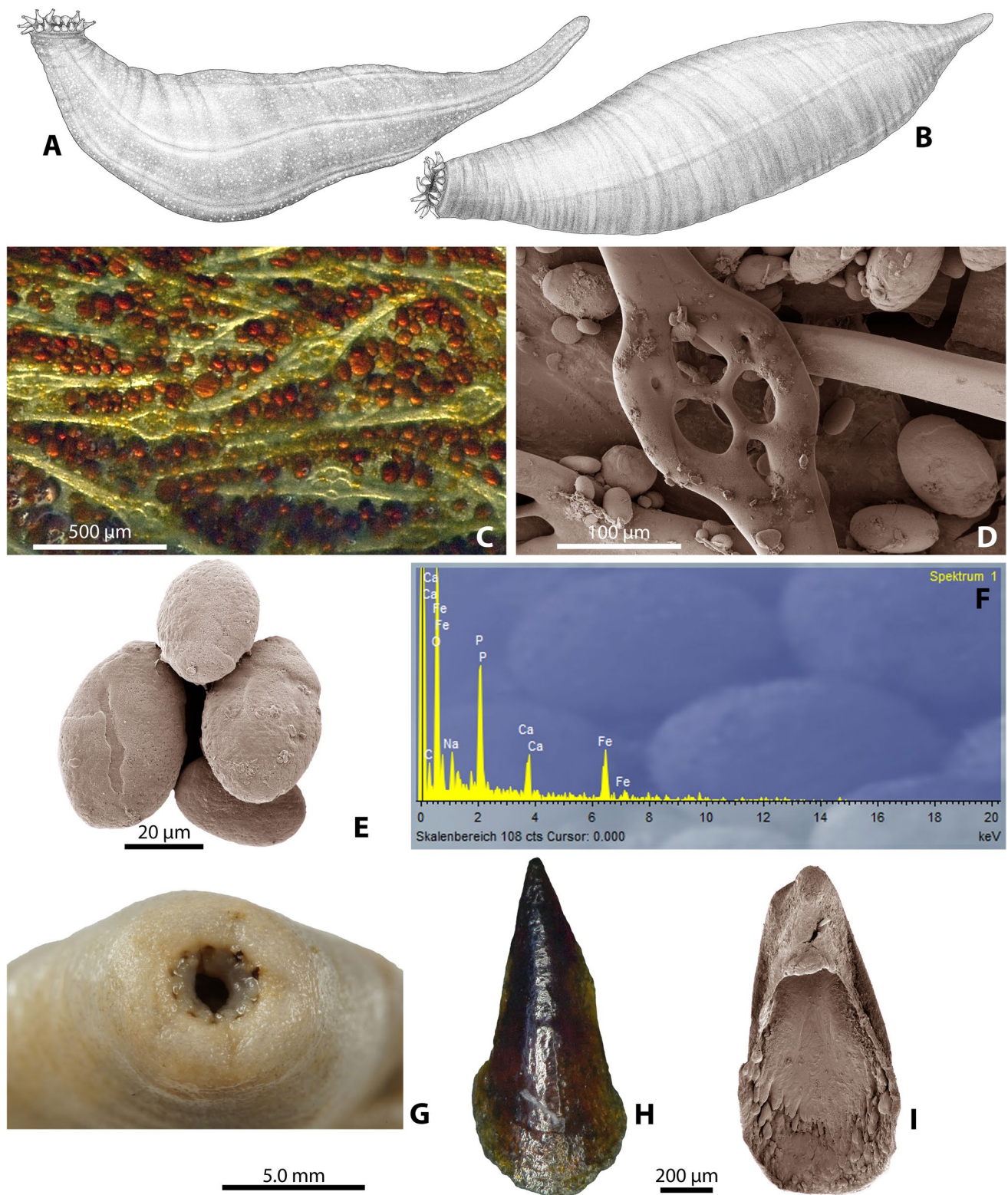


Fig. 1 General morphology and habitus of representatives of the extant molpadid genera; **A** *Paracaudina* (Caudinidae) and **B** *Molpadia* (Molpadiidae). **C–D** Ossicles of high-Mg-calcite associated by iron phosphatic deposits (**C–E**) of the modern *Heteromolpadia marenzelleri* (Molpadiidae); **F** EDS analysis of dermal granules of this species, showing that these contain i.a. phosphate, iron, and calcium. **G–I** Chitinous tentacle sheaths of the extant *Ceraplectana tra-*

chyderma, **G** showing the oral area with 10 retracted (claw-shaped) tentacles; (**H–I**) tentacle sheaths, (**H**) outer and (**I**) inner view. **C–F** SNHMB-N.78702 ex USNM-E.16366 [South Pacific Ocean, New Zealand, off Palliser Bay, 1,006 m water depth], **G–I** SNHMB-N.78703 ex USNM.1074730 [North Pacific Ocean, California, 4,100 m water depth]. **C, G, H** Light microscopic images, **D, E, I** Scanning electron microscopic images

spoon-shaped ossicles (of the Molpadiidae), but described and diagnosed them, in terms of their structure and growth, as table ossicles (Holothuriida/Synallactida) with a base plate and a four-footed stirrup. Articulated specimens of fossil molpadids are missing so far, but isolated elements of the calcareous ring are present in the fossil record (almost exclusively from Jurassic strata; Hess, 1975; Kutscher, 1987, 1988; Kutscher & Hary, 1991; Gilliland, 1992; Kutscher & Reich, 2021), even if these are often overlooked. Further evidence, e.g. from the Lower Cretaceous of Germany and the Neogene of Austria and Slovenia, is still unpublished (Reich & Jäger, Reich & Kroh, Reich & Pollerspöck, Reich, Gašparič et al.).

The only evidence to date of Late Cretaceous molpadid calcareous ring material was reported by Reich (2017) from the “Gerhardtsreiter Schichten” (Gerhardtsreit Formation) in Upper Bavaria, Germany. Fossil molpadid ossicles from Upper Cretaceous sediments have been described by Sadeddin and Saqqa (1997), Al-Tamimi et al. (2001), Al-Tamimi and Saqqa (2008) (all from Jordan) and Reich (2001, 2002b, 2003) (Germany), for example.

The aim of this study is to present the first calcareous ring material belonging to the Molpadida from the Rügen Late Cretaceous chalk.

Geological setting, material and methods

Setting and stratigraphy

During the early Late Cretaceous (Cenomanian) sea-level rise, Central Europe was almost completely flooded and former siliciclastic sedimentation was substituted by the deposition of chalk. Towards the end of the Mesozoic the shelf sea covering much of northern Europe made a final transgression (Campanian) followed by a phased regression (Maastrichtian) (Håkansson et al., 1974; Voigt et al., 2008). In the area of the island of Rügen, NE Germany, Upper Cretaceous sediments reached a maximum thickness of 600 m, whereas 30 kms to the north the thickness was almost twice as great (1,130 m) (Petzka & Reich, 2000; Diener et al., 2004). In Maastrichtian times, the area of Rügen was situated at a latitude of 40°N, far from the coast in the middle of a seaway between the Western European chalk basins and Eastern Europe. A nannofossil ooze or coccolith mud with a non-carbonate content of less than 2% was deposited in the Danish-Polish Trough. Based on the fauna and flora, a water depth of approx. 150–250 (max. 300) metres is assumed for the Rügen Chalk Sea. Oligotrophic and partially oxygen-poor conditions prevailed on the soft, muddy sea floor with unevenly distributed secondary hard substrates (bryozoans, large inoceramid bivalves etc.). The soft bottom itself was intensively bioturbated (due to the activity of infaunal/

semi-infaunal polychaetes, sea cucumbers and sea urchins) (e.g. Frenzel et al., 1998; Frenzel, 2000; Reich & Frenzel, 2002; Reich et al., 2005). The Rügen Chalk is a Liberation Fossil Lagerstätte (Roden et al., 2020)—The fossil species reported so far from here amount to around 1,500 (Reich & Frenzel, 2002; Reich et al., 2018; Knaust & Schnick, 2024).

Surface outcrops of the Rügen chalk are limited to various historical quarries and open-cast mines that are still in operation today, as well as the iconic cliffs between Sassnitz and Lohme at the eastern part of Jasmund Peninsula (Fig. 2B), some of which were deformed by Pleistocene glacial tectonics (e.g. Steinich, 1972; Gehrman et al., 2022).

Stratigraphically, the chalk and flint are early and late Early Maastrichtian (*Belemnella obtusa* to *B. fastigata* belemnite zones; Fig. 2A) in age (Herrig et al., 1996; Reich & Frenzel, 2002; Reich et al., 2018). In addition, high-resolution (regional) bio-zonations based on micromorphic articulate brachiopods, ostracods and foraminifera, among others, have been established (e.g. Steinich, 1965; Herrig, 1966, 1969; Frenzel, 2000; Reich & Frenzel, 2002). Autochthonous sediments of the Late Maastrichtian were recently reported from the nearby south-eastern Arkona Basin (Laschke et al., 2015).

Material

The fossil microscopic/mesoscopic material presented here was collected after storm and chalk erosion events on the chalk cliff north of Sassnitz (Lenzer Bach, see Mehlhorn et al., 2019; fig. 2; Fig. 2B-C).

Extant reference material for comparison (*Molpadia*, *Heteromolpadia*, *Ceraplectana* etc.) was kindly provided by the Smithsonian Institution (D. L. Pawson) and by the Swedish Natural History Museum (S. Stöhr).

Repositories and institutional abbreviations

GZG—Geoscience Centre, University of Göttingen (*Geowissenschaftliches Zentrum, Universität Göttingen*) Göttingen, Germany.

SNHMB—State Natural History Museum (*Staatliches Naturhistorisches Museum*) Brunswick/Braunschweig, Germany.

SNSB—Bavarian Natural History Collections (*Staatliche Naturhistorische Sammlungen Bayerns*) Munich/München, Germany.

USNM—Smithsonian Institution. National Museum of Natural History, Washington, DC, USA.

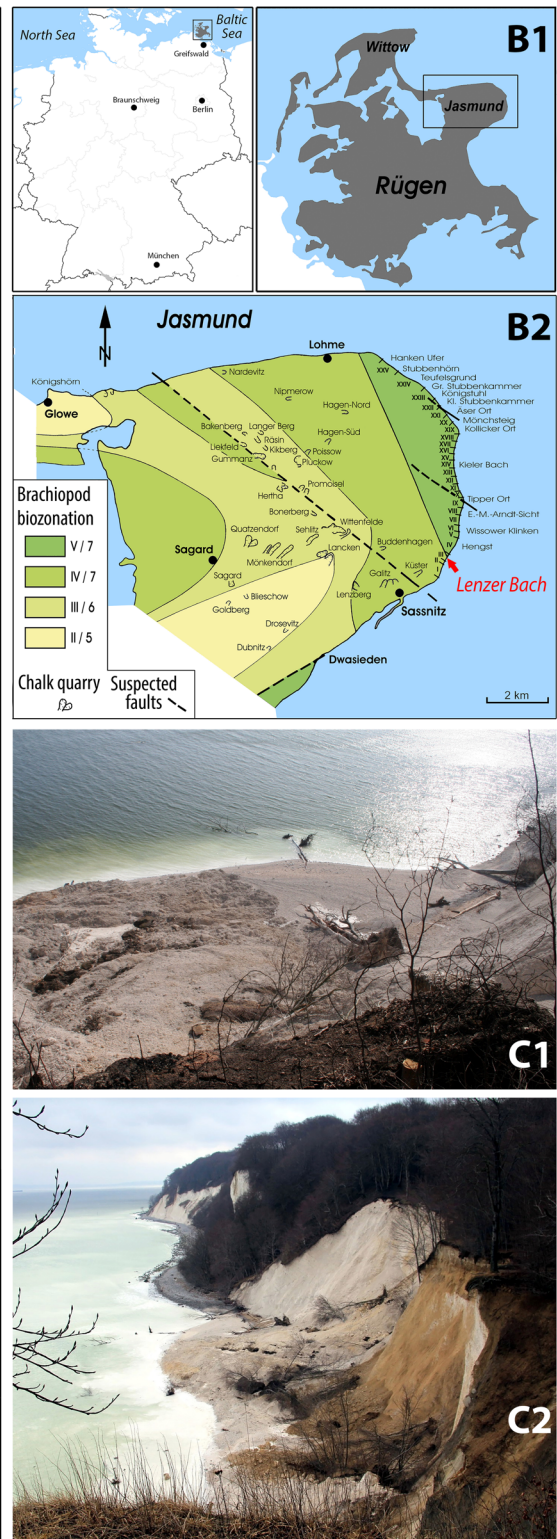


Fig. 2 Litho- and biostratigraphic subdivisions of the Rügen Chalk (A). The orthostratigraphic zonation is based on articulate brachiopods *sensu* Steinich, 1965 and extended by Surlyk, 1970, since the exact belemnite zone (*sensu* Schulz, 1979) boundaries are uncertain (vertical belemnite ranges according to Wehrli, 1967 and Reich, 1994). Furthermore, the subdivision using ostracods *sensu* Herrig, 1966, foraminifera *sensu* Frenzel, 2000 and calcareous nannoplankton (according to Kienel, 1990, 1993) *sensu* Sissingh, 1977 and Perch-Nielsen, 1985 or according to Burnett, 1997 *sensu* Burnett, 1998. **B** Location of outcrops on the cliff (chalk complexes labelled with Roman numerals) and in the centre (quarries and open-cast mines, abandoned and still in operation) of the Jasmund Peninsula (B2), Isle of Rügen (B1). The material presented here comes from the Lenzer Bach (arrow) at the end of chalk complex III. **C** Field photographs of a major coastal collapse at Lenzer Bach (in 2011) (C1, C2), where the material presented here comes from (compiled based on illustrations from Reich & Frenzel, 2002; Herrig, 2004; Kutscher, unpubl.; Reich et al., 2018, modified)

SEM (LEO 1530 Gemini) combined with an INCA X-act EDX (Oxford Instruments) at GZG.

X-ray computed tomography and visualization

The extant molpadid species *Heteromolpadia marenzelleri* (Théel, 1886) was scanned at (SNSB) facility with a phoenixlx-ray nanotom m at 110 kV and 100 µA (0.5 mm aluminium filter). This resulted in 1,440 projections providing a voxel size of 4.9 µm. Visualization and 3D reconstruction were realized with different software applications including SPIERS and VGStudio Max 2.2, 3.0 (at SNHMB and SNSB). Drawings and figures were produced using Adobe Photoshop®.

Systematic palaeontology

The descriptive terminology of *CR* used is based in part on Heding (1933), Gilliland (1992) and Reich (2015), modified. Lettering of *R* and *IR* pieces after Ludwig (1889–1892: figs. 1, 14); Carpenter's (1884) letters for designation of rays corresponds to the following radial elements: A = *RI*; B = *RIII*; C = *RV*; D = *RIV*; E = *RII*.

Systematic abbreviations:

CR—calcareous ring; **IR**—interradial element(s); **R**—radial element(s); **RI**—mid-ventral radial piece of the *CR*; **RII**—left ventral radial piece of the *CR*; **RIII**—right ventral radial piece of the *CR*; **RIV**—left dorsal radial piece of the *CR*; **RV**—right dorsal radial piece of the *CR*; **IRI**—left ventral interradial piece of the *CR*; **IR2**—right ventral interradial piece of the *CR*; **IR3**—left dorsal interradial piece of the *CR*; **IR4**—right dorsal interradial piece of the *CR*; **IR5**—mid-dorsal interradial piece of the *CR*; **irp**—interradial process of anterior margin of calcareous ring; **imm**—insertion mark of longitudinal muscle; **imt**—insertion marks of tentacle muscles/ampullae; **laf**—lateral articulating face

of radial and interradial elements; **mp**—muscular process; **nmp**—non-muscular process; **nt**—notch in anterior margin of muscular process; **pv**—perforation in muscular process; **rp**—radial prolongation of posterior margin of calcareous ring; **CP**—central position of the perforated/notched muscular process, viewed from the outside; **LP**—left position of the perforated/notched muscular process, viewed from the outside; **RP**—right position of the perforated/notched muscular process, viewed from the outside.

Class **Holothuroidea** de Blainville, 1834

Subclass **Actinopoda** Ludwig, 1891

Order **Molpadida** Haeckel, 1896, emend.

Synonyms. Anactinopoda, Molpadiida, Molpadioidea, Molpadonia, Molpadonida.

Earlier diagnoses. See, for example Östergren (1907: 207–210), Heding (1931: 277; 1935: 33–34), Deichmann (1940: 206–207), Pawson (1970: 47, 1977: 98), Madsen and Hansen (1994: 92), Smirnov (2012: 824) and Rowe et al. (2017: 486–487).

Revised and expanded diagnosis. Actinopodid pneumonophorans with 15 (or rarely 10, 13) digitate (or modified simple) tentacles. Body stout and sausage-shaped, in larger and medium-sized forms, here usually with an evident tail; or with a rigid and continuous test in small representatives. Tube feet absent, but anal papillae are present. Anal ring with anal plates ('teeth') sometimes present. Stone canal (with internal madreporite) single and unbranched, either opens externally or blindly terminates at body wall or opens into body cavity. Polian vesicle single. Radial longitudinal muscles divided (one pair) or undivided. Tentacle ampullae (normally) well developed. *CR* well developed, always consisting of 5 *R* and 5 *IR*, often showing secondary bilateral symmetry; *R* with short or distinct posterior bifurcate prolongations (*rp*), due to secondary bilateral symmetry prolongations sometimes reduced in *RIV* + *RV* (= dorsal *R*); *R* with one (muscular; *mp*) or two (a muscular and a non-muscular; *mp* + *nmp*) short anterior process, always notched or perforated for the passage of radial nerve; *IR* smaller or equal in size (in comparison to *R*), with one short anterior process and no distinct posterior prolongations.

Calcareous body wall ossicles may include diagnostic tables or table-like derivatives (cups and fusiform rods), (modified) anchors (also derived from tables) and racquet- or spoon-shaped rods as well as undiagnostic rods, rosettes and perforated plates. Phosphatic bodies in several genera present.

Unique (for echinoderms and sea cucumbers) is the presence of chitineous tentacle shovels in one taxon of this clade.

Included families. Molpadiidae Müller, 1850; Caudinidae Heding, 1931; Eupyrgidae Semper, 1868.

Distribution. Extant representatives of this clade are cosmopolitan and known from all oceans. Fossil molpadid members, including stem-group representatives, are known since Permian/Triassic times (Gilliland, 1993; Reich pers. obs.).

Family **Caudinidae** Heding, 1931

Genus ***Cretacaudina*** nov.

Etymology. Named after the geological period (Cretaceous) from which the material described here originated, and Latin *cauda* = tail, in resemblance to modern caudinid sea cucumbers.

Type species. *Cretacaudina rugia* gen. et sp. nov. Reich, Kutscher & Stegemann.

Diagnosis. Medium-sized molpadids with 15 tentacles. *CR* well developed, with (standard architecture of) 5 *R* and 5 *IR*. *R* longer than wide, slightly widened posteriorly with short bifurcate *rp*. Anterior processes (*nmp* + *mp*) very short. The *mp* notched with a deep median *imm*, which lies posterior to the *mp*. *R* (and presumably *IR* as well) tends to be curved with the inner side being concave.

ZooBank LSID. urn:lsid:zoobank.org:act:B4DF93FF-0967-4ED1-B907-A802DCF78C13.

Comparison. The *R* of *Cretacaudina* are most closely comparable to members of the Caudinidae (Fig. 1A), as can be seen from the size and shape of the anterior processes. The *mp* in the *R* of the Molpadiidae (Fig. 1B) appears almost always (*Molpadida*) or without exception (*Cherbonniera*, *Heteromolpadia*) to be perforated to allow the radial nerve to pass through. The *mp* in the *R* of modern *Acaudina*, *Caudina* and *Paracaudina* species (Caudinidae), on the other hand, are short to very short and notched, as in *Cretacaudina*. *Ceraplectana* can be excluded, as the *R* possess only a centrally located *mp* and not, like all others (*Acaudina*, *Caudina*, *Cretacaudina*, *Eupyrgus*, *Hedingia*, *Heteromolpadia*, *Molpadia*, *Paracaudina*), two anterior processes (*mp* + *nmp*). The monospecific genus *Cherbonniera* is a major exception, in which only the two dorsal (*RIV* + *RV*) and the mid-ventral (*RI*) *R* of the *CR* possess two processes (*nmp* + *mp*), whereas in the left and right ventral *R* (*RII* + *RIII*) there is exclusively a centrally located *mp*. *Eupyrgus* is also excluded on the basis of overall size, morphology and the structure of *mp* + *nmp*, as well as the position of *pv* (Semper, 1867; Clark, 1908; Hôzawa, 1928; O'Loughlin & Ong, 2015; Reich & Rössner, 2016; Reich pers. obs.; Appendix, Fig. 4).

Overall, the attachment area of *Cretacaudina* located on the outer side of the *R* bears some resemblance to *Acaudina*; however, the structure (and length) of the anterior processes does not correspond in detail to that of the modern species within that genus. Also, the material presented here, differs significantly from all previously described Mesozoic (mostly Lower and Middle Jurassic) calcareous ring elements. This is why *Cretacaudina* gen. nov. is being established for this fossil taxon.

Further remarks.

The number of tentacles can always be determined from the total number of the anteriorly situated *mp* and *nmp*: 15 (*Acaudina*, *Caudina*, *Eupyrgus*, *Hedingia*, *Heteromolpadia*, *Molpadia*, *Paracaudina*), 13 (*Cherbonniera*) and 10 (*Ceraplectana*).

Even if only one well preserved *R* is available, a detailed comparison with the *CR* of modern species (of *Caudina*, *Cherbonniera*, *Eupyrgus*, *Hedingia*, *Heteromolpadia*; Reich pers. obs.) and the assumption that the standard architecture of the *CR* (position of the *mp* and right/left orientation of the *rp*; cf. Reich, 2015) of the group has not changed over the last 70 million years, various pieces of information, such as the number of tentacles and their position within the *CR* (dorsal/ventral as well as left and right), can be identified.

Included species. So far monospecific.

Distribution. Early Maastrichtian of Germany.

Cretacaudina rugia sp. nov.

Figure 3

Material. Two, partially incomplete, radial pieces from the calcareous ring (SNHMB-G.30001–30002), both from the Maastrichtian chalk (*Belemnella cimbrica* belemnite zone) north of Sassnitz, Jasmund Peninsula/Isle of Rügen, Western Pomerania, Germany.

Holotype—SNHMB-G.30001 (*RIV* or *RII*).

Paratype—SNHMB-G.30002 (incomplete *R*).

Etymology. Named after the place where the material was found—the island of Rügen (Latin *Rugia*).

Diagnosis. As for genus.

ZooBank LSID. urn:lsid:zoobank.org:act:A47A9432-2B67-4973-8731-514B8BC66393.

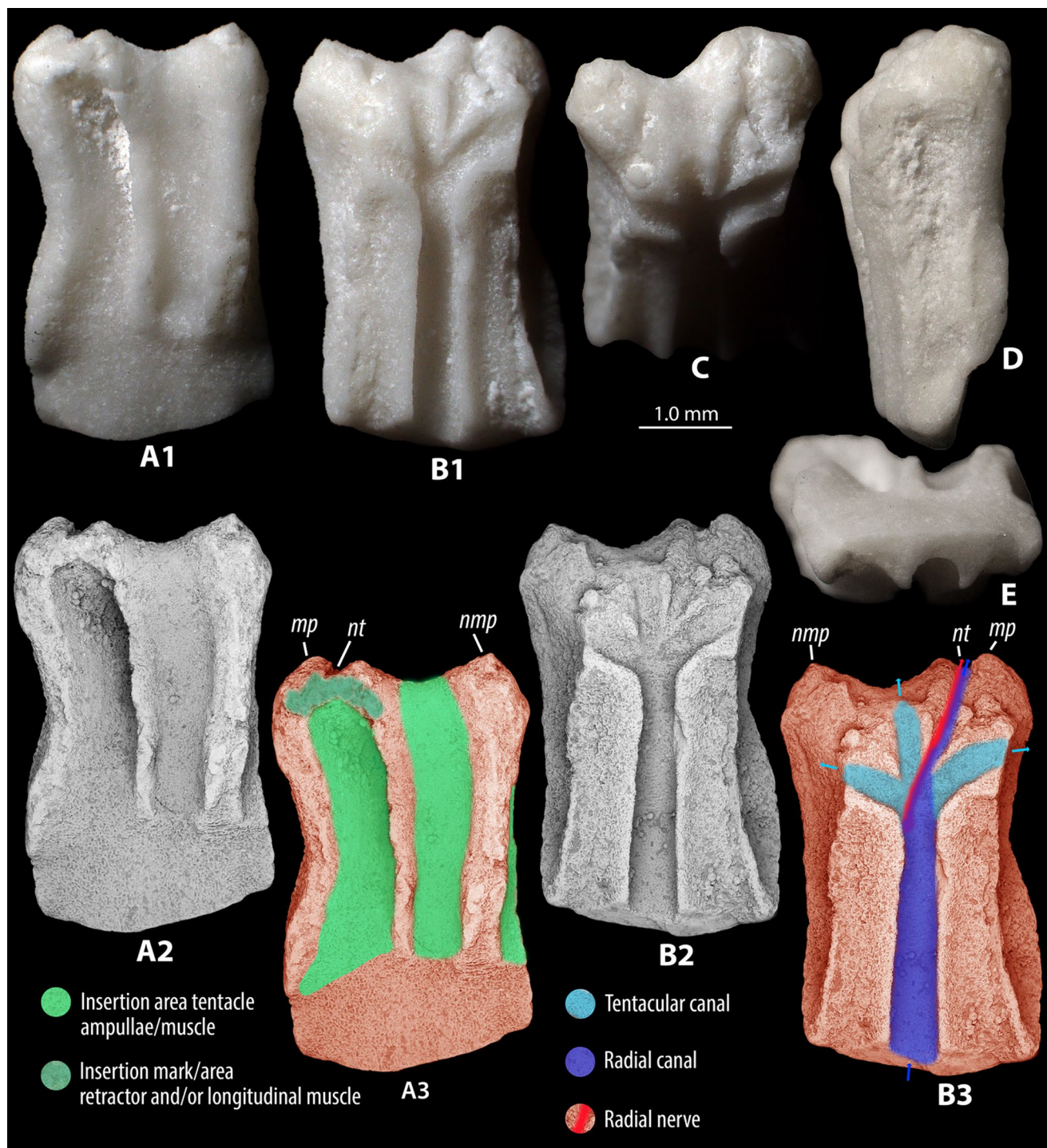


Fig. 3 *Cretacaudina rugia* sp. nov. (Molpadida: Caudinidae) from the upper lower Maastrichtian Rügen Chalk (Lenzer Bach, north of Sassnitz)—*RIV* (or *RII*)=left dorsal (or ventral) element of the cal-careous ring (posterior process broken off). **A1–A2** outer view; **B1–B3** inner view; **C** oblique inner view from anterior; **D** lateral view

from left; **E** posterior view. In **A3** and **B3**, the attachment areas for the water vascular system (radial canal, tentacular canals, tentacle ampullae), nervous system (radial nerve) and muscles were marked in colour. Light microscopic (**A1**, **B1**, **C**, **D**, **E**) and scanning electron microscopic (**A2**, **A3**, **B2**, **B3**) images

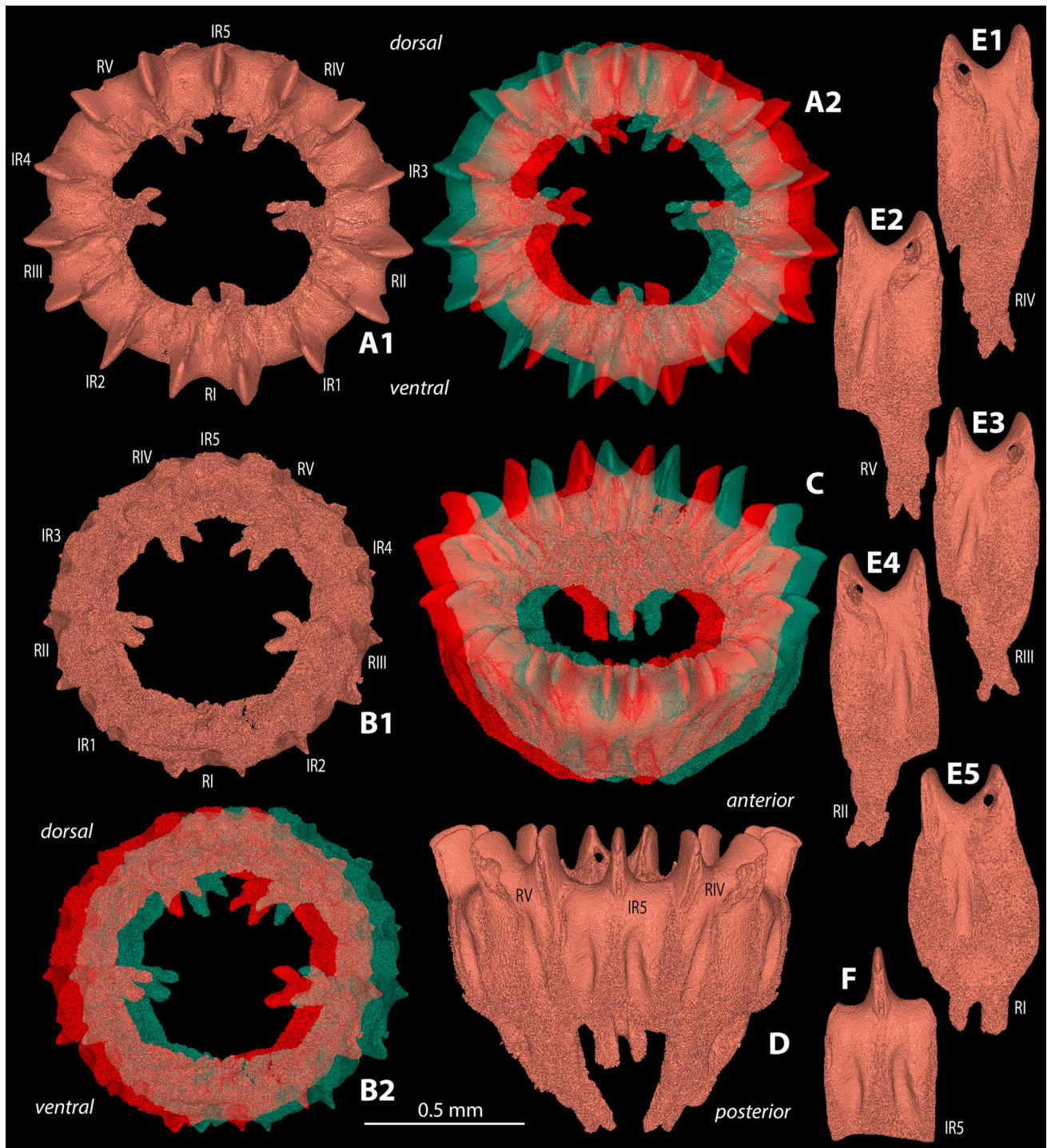


Fig. 4 X-ray computed tomography based digitally reconstructed morphology of the calcareous ring of *Heteromolpadia marenzelleri* (Molpadida: Molpadiidae) from the South Pacific Ocean (New Zealand, off Palliser Bay; water depth of 1,006 m; leg. D. L. Pawson; SNHM-N.78702 ex USNM-E.16366). **A1-A2** anterior view; **B1-**

B2 posterior view; **C** oblique anterior view; **D** lateral view; **E1-E2** dorsal radial elements (RIV-RV) in outer view; **E3-E5** ventral radial elements (RIII-RI) in outer view; **F** interradial element (IR5) in outer view (**A2, B2, C** anaglyph images)

Description. The holotype specimen is complete and very well preserved except for the broken off posterior fork tail. The stereom, although filled in with chalk, is still clearly recognizable and has not undergone any further diagenetic alteration. Almost rectangular in outline, the calcareous ring segment is just over 4 mm long (and thus originally c. 6 mm in total). The deep depression for the tentacle ampullae and the clear anterior incision (notch) on the muscle process for the radial nerve, which is overlaid by the radial canal running to the posterior end of the body, are clearly recognizable on the outside. Both anterior processes (*mp* and *nmp*) are only very short, so that the anterior indentation between the two is only slight. On the inner side of the *R*, the deep incisions for the radial canal and the three tentacular canals branching off from it are clearly visible. The notch for the radial nerve and the narrowing radial canal is also clearly visible.

The paratype specimen is an incomplete fragment of a *R*; as the anterior portion is missing, its position within the *CR* cannot be determined.

Remarks. Based on current knowledge and, in comparison to other extant molpadid species (cf. Appendix and discussion below), of which the *CR* and, to some extent, the ontogeny have been described in detail, e.g. *Paracaudina chilensis* in Hôzawa (1928) and *Molpadia abyssicola* in Pawson (1977), the present new fossil taxon is a caudinid of around 10 cm body length (with an anterior diameter of approx. 2 cm). The number of tentacles is 15, but the detailed (soft part) morphology and thus the number of digits on the tentacle tips are unknown.

Distribution. So far only known from the Rügen Chalk.

Comparison and discussion

Calcareous ring structure of modern Molpadida.—A unifying synapomorphy of all Holothuroidea is the calcareous ring (*CR*) which surrounds the mouth internally, gives support to the pharynx, water vascular system and tentacles, radial nerve ring, and muscle bands (Reich, 2015). Although this structure is probably the most important evolutionary hard part structure within the group of Holothuroidea (Reich & O'Loughlin, 2010), it has so far been little studied and insufficiently documented.

Heding (1931, 1935) used, among other things, the distinctly different morphology of the calcareous ring to differentiate at the genus level within Molpadida. Deichmann (1938) used external morphology and the body wall ossicles to describe molpadid sea cucumbers, without any reference to the calcareous ring, although the author had shortly before (Deichmann, 1936) still referred to the

calcareous ring in her descriptions. Unfortunately, this was not continued and/or further expanded in the scientific literature or by other echinodermologists (see, for example, Pawson, 1963). In the following descriptions of molpadid sea cucumbers, at least some brief descriptions of the *CR* including a 2D drawing with the *R* + *IR* (e.g. Cherbonnier & Féral, 1981; O'Loughlin et al., 2013; Pawson, 1977; Pawson & Liao, 1992; Pawson et al., 2001) were published. Only recently some authors (e.g. O'Loughlin & Ong, 2015; O'Loughlin et al., 2011) also added light micrographs, but again often only of one *R* + *IR* each.

It is certainly a step forward that the *CR* is also increasingly being depicted. However, it is still not very helpful if only a Sect. ($2 \times R + 1 \times IR$) is shown, without precise details of the exact position of the element (e.g. dorsal versus ventral). As we were able to determine in our own research, this is not sufficient, especially for bilateral symmetrical structures. In a preliminary conference presentation, Reich and Rössner (2016) showed clear morphological differences in the calcareous ring of various molpadid sea cucumbers (members of the Caudinidae, Eupyrgidae, Molpadiidae), based on high-resolution x-ray computed tomography analyses. These investigations (cf. Appendix) revealed various details that were previously unknown or had probably been overlooked. This includes several bilateral symmetrical patterns, dorsal/ventral differences, merged anterior processes in radial elements (*R*) of the *CR*, slit-like foramina for the passage of the radial nerve, and furthermore left/right patterns of these foramina, previously only known from some apodid holothurians.

Calcareous ring structure of modern Molpadiidae Müller, 1850 (Synonym: *Trochostomidae* Östergren, 1907)—The members of this family (cf. Heding, 1931: 277–278; Heding, 1935: 34; Deichmann, 1940: 217; Pawson, 1970: 47; Pawson, 1977: 98; Madsen & Hansen, 1994: 93; Smirnov, 2012: 824) are medium- to large-sized molpadids with 15 (*Heteromolpadia* Pawson, 1963; *Molpadia* Cuvier, 1817) or rarely 13 (the monospecific *Cherbonniera* Sibuet, 1974) tentacles. All of these have lateral digits and a terminal digit.

The *CR* is well developed, often bilaterally symmetrical, with 5 *R* and 5 *IR*. All *R* are longer than wide, with long or medium-length bifurcate *rp* as well as with 1–2 anterior processes, of which the *mp* is perforated (or very rarely notched) for the passage of the radial nerve (e.g. Fig. 4; Appendix).

As explained above, the new taxon *Cretacaudina* cannot be classified within the Molpadiidae.

Calcareous ring structure of modern Caudinidae Heding, 1931—Members of this family (cf. Heding, 1931: 282–283; Heding, 1935: 61–62; Deichmann, 1940: 211–212; Pawson,

1970: 49; Smirnov, 2012: 824) are medium- to large-sized molpadids with 15 (*Acaudina* Clark, 1908; *Caudina* Stimpson, 1853; *Hedingia* Deichmann, 1938; *Paracaudina* Heding, 1932) tentacles. These have only lateral digits, without a terminal digit (or are of simple structure).

The *CR* is well developed, often bilaterally symmetrical, with 5 *R* and 5 *IR*. All *R* are longer than wide, with medium-length or long bifurcate *rp* and with 2 anterior processes, of which the *mp* is notched for the passage of the radial nerve.

As explained in detail above, *Cretacaudina* can be classified within the Caudinidae.

Calcareous ring structure of modern *Ceraplectana* Clark, 1908—Given its individual characteristics (tentacles, *CR*) and biomineralisation (Fig. 1G–I), this monospecific genus (currently placed within the Caudinidae) should probably be classified in a separate (new) family as already discussed by Heding (1931: 277) and listed under ‘*incerta sedis*’ (Heding, 1931: 284). However, modern morphological (e.g. X-ray CT) and molecular biological studies are currently lacking for this taxon. The only species known to date (*Ceraplectana trachyderma* Clark, 1908; known from the Northern and Eastern Pacific) is a small- to medium-sized molpadid with 10 tentacles. The tentacles are simple and feature claw-shaped chitinous sheaths arranged in pairs.

The *CR* is well developed, with 5 *R* and 5 *IR*. All *R* are longer than wide, with a medium-length bifurcate *rp* as well as 1 anterior process only, which is the *mp* and perforated for the passage of the radial nerve (cf. Clark, 1908: 183; Clark, 1920: 130–131; Heding, 1931: 284; Pawson & Kerr, 2001).

Given the presence of a single anterior process in all radial elements of *Ceraplectana trachyderma*, *Cretacaudina rugia* gen. et sp. nov. cannot be classified within this group.

Comparison with the Eupyrgidae Semper, 1867—The members of this family (two species of *Eupyrgus* Lütken, 1857, known from the Arctic and North Pacific Ocean; cf. Heding, 1931: 281–282; Heding, 1935: 67–68; Deichmann, 1940: 227; Smirnov, 2012: 824) are small-sized molpadids with 15 tentacles. All tentacles simple, without any digits.

The *CR* is well developed, bilaterally symmetrical, and with 5 *R* and 5 *IR*. The *R* are nearly quadrangular in outline, with short bifurcate *rp*, bearing 2 anterior processes, of which the *mp* is perforated for the passage of the radial nerve (Reich & Rössner, 2016; Reich pers. obs.).

Given the size and morphology of the *R* of the two known species of *Eupyrgus*, it can be excluded that *Cretacaudina rugia* gen. et sp. nov. belongs to the Eupyrgidae or is closely related to it.

Phylogeny and evolutionary diversification of Molpadida.—The exact placement of molpadid representatives within Holothuroidea as well as the relationship between Molpadiidae,

Caudinidae and Eupyrgidae remains uncertain and is still under debate (e.g. Haude, 1992; Kerr & Kim, 2001). This includes, for example, rather heterogeneously distributed characteristics (e.g. the presence of phosphatic deposits or anal plates, or the continuous test in small molpadid species).

We have to reject the long-favoured close relationship between Molpadida and Apodida (e.g. Clark, 1908; Apodacea of Pawson & Fell, 1965), nor is there any close relationship between Molpadida and Dendrochirotida (e.g. Miller et al., 2017; Mongiardino Koch et al., 2023), an assumption shared by almost all holothuriologists since the late nineteenth century (Ludwig, 1889–1892; Ludwig, 1891; Haeckel, 1896; MacBride, 1906). However, a recent study placed Molpadida as a sister group to Synallactida (Miller et al., 2017) which would support in part Östergren’s (1907) and Becher’s (1908, 1909) contrary theories of a closer relationship between molpadid and ‘*aspidochirote*’ (e.g. Holothuriida, Synallactida) sea cucumbers. Östergren based this on shared characteristics like the presence of tentacle ampullae and divided longitudinal muscles which are not present in dendrochirote holothurians. However, these characteristics are also missing in all members of the Synallactidae, Deimatidae and Mesothuriidae (but present in the Stichopodidae and Holothuriidae). A recently published preprint (Whelpley et al., 2025) has clarified the phylogenetic relationships within the Neoholothuriida, placing the Molpadida as a sister group to the Persiculida and the Synallactida as a sister to the Dendrochirotida.

Molecular biological studies or genome analyses of as many known molpadid genera as possible would help immensely to clarify the outstanding questions regarding the phylogeny of the group and its relationships to other holothurian clades.

Conclusion

We describe the world’s second Cretaceous record of molpadid calcareous ring material. The new taxon *Cretacaudina rugia* gen. et sp. nov. is referred to the family Caudinidae, based on the detailed analysis and comparison (x-ray computed tomography data) of the calcareous ring of modern molpadid taxa. The fossil show in part similarities with modern representatives of the caudinid genus *Acaudina* that occurs today almost exclusively in the Indian Ocean. To summarise all the information available to date, *C. rugia* was a small sea cucumber, approximately 10 cm long, with 15 tentacles, which lived exclusively in the soft bottom sediment (nannofossil ooze) of the Rügen Chalk Sea. The new fossil is of exceptional interest because it bridges the gap between Jurassic and Cenozoic times in the calcareous ring (palaeontological) record of the Molpadida. This finding

provides another step towards a better understanding of the sea cucumber diversification and evolution.

Appendix

Description of the calcareous ring structure of modern *Heteromolpadia marenzelleri*—The calcareous ring (CR) as a whole shows a secondary bilateral symmetry and, in a lateral view, a tapering of the diameter from anterior to posterior (Fig. 4A,B, D). The five radial (R) and five interradial (IR) pieces of the ring are arranged alternately (Fig. 4A1, B1). All R are flat cuboid and equipped with anterior processes and posterior prolongations (Fig. 4E1–E5); all IR are similar in shape, but with only one anterior process each (Fig. 4F).

All R possess two anterior processes (Fig. 4E1–E5), the somewhat longer non-muscular process (*nmp*), and the perforated muscular process (*mp* + *pv*), which is relatively shorter (for the passage of the radial nerve and the radial canal). The length of the anterior processes in *RII*, *RIII*, *RIV*, *RV* is almost 20% of the total length of the respective R (Fig. 4E1–E4); in the *RI* it is almost 25% (Fig. 4E5). The position of the muscular process (*mp*) in the R (viewed from the outside) is on the left side (*LP*) for the two left dorsal and ventral R (*RIV* + *RII*) and on the right side (*RP*) for the two right dorsal and ventral R (*RV* + *RIII*) and the mid-ventral R (*RI*) (Fig. 4E1–E5). Below the perforation (*pv*) of the muscular process, there is a depression on the outer side of the R for the insertion of the longitudinal muscle/retractor (*imm*) (Fig. 4E1–E5). The posterior prolongation (*rp*) (in the form of a tapering and bifurcating tail) in *RII*, *RIII*, *RIV*, *RV* (Fig. 4E1–E4), which amounts to about 30% of the total length, is located on the side of the anterior muscular process (*mp*); often the perforation (*rp*) is also bent in this direction.

The perforation of the muscular process (*rp*) of the mid-ventral R (*RI*) is considerably shorter and is restricted to the bifurcation alone (Fig. 4E5). In contrast to the four other R (with the exception of the processes), the outline of *RI* is subcircular (Fig. 4E5). The distal posterior bifurcation serves as an attachment point for the respective radial canals and guides them in a furrow on the inner side of the R (Fig. 4A1, B1, D). This median furrow splits into three channels to make room for each of the three tentacle canals. The radial canal, on the other hand, passes through the perforation together with the radial nerve in order to continue together with the longitudinal muscle through the entire body of the sea cucumber to the anus. A respective ridge on the outside of all R serves as a hold and separation of the tentacle ampullae and lies somewhat to the left or right of the median plane, always on the side of the non-muscular extension (Fig. 4E1–E5).

The respective anterior process of all IR is non-perforated (*irp*) (Fig. 4C, D, F). The total length of the IR compared to the left/right dorsal/ventral R is about 50%. On the outer side, the IR have elongated depressions in the posterior region to the left and right of the median line, running in the antero-posterior axis (Fig. 4C, D, F).

Remarks on the calcareous ring structure of *Heteromolpadia marenzelleri*—The advantages for the documentation and analysis of *Heteromolpadia marenzelleri*, based on the visualisation of the X-ray computed tomography data, are very clear and obvious at first glance, for example with regard to the presence (or absence) of the perforation in each *mp* of the radial elements. In the original description of the genus *Heteromolpadia* and its type species, it was diagnosed (Pawson, 1963: 12) that there are no perforations for the passage of the radial nerve. However, based on our investigations, the corresponding perforations are present and clearly visible (Fig. 4E1–E5).

Acknowledgements This paper is dedicated to Ekkehard Herrig at the occasion of his 90th birthday; he was the academic supervisor of the first author at Greifswald University and is renowned for his research on the Rügen Chalk. MR is grateful for the generous assistance of the following: Andreas Kroh (NHM Vienna, Austria; discussions); Gustav Paulay (FMNH Gainesville, FL, U.S.A.; discussions); Dave L. Pawson (USNM Washington, D.C., U.S.A.; access and donation of material for study); Gertrud E. Rössner (SNSB-BSPG Munich, Germany; for conducting the X-ray CT analysis); Tom Schiøtte (NHM København, Denmark; access to material for study); Sabine Stöhr (NRM Stockholm, Sweden; access to material for study). In addition, we thank the reviewers (Andreas Kroh and Gustav Paulay) for their comments which helped to improve the manuscript.

Author contributions MR conceived the study, analyzed the data, conducted the SEM analysis and the X-ray CT visualization, wrote (with TRS) the manuscript and developed the figures. MK collected the fossil material. All authors reviewed, edited and approved the final version of the manuscript.

Funding EU SYNTHESYS, SE-TAF-2969 and DK-TAF-3795 + State Natural History Museum, Braunschweig (all M. Reich).

Data availability All data are included in the paper.

Declarations

Conflict of interest The authors declare that they have no competing interests.

Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and

your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

References

- Al-Tamimi, M., & Saqqa, W. (2008). Holothurian sclerites from the upper part of Ajlun Group (Late Cretaceous) of Salhoub Area, North Jordan. *Dirasat (Pure Sciences)*, 35(2), 81–95.
- Al-Tamimi, M., Saqqa, W., & Sadeddin, W. (2001). Holothurian sclerites from the Early Late Cretaceous, south of Al-Mastabah Area (North Jordan). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 2001(8), 463–482. <https://doi.org/10.1127/njgpm/2001/2001/463>
- Becher, S. (1908) *Die Stammesgeschichte der Seewalzen. Habilitationsschrift zur Erlangung der Venia legendi einer hohen philosophischen Fakultät der Großherzoglich Hessischen Ludwigs-Universität zu Gießen*. Lippert & Co., Naumburg a. S.
- Becher, S. (1909). Die Stammesgeschichte der Seewalzen. *Ergebnisse und Fortschritte der Zoologie*, 1(3), 403–490.
- Blainville, H. M. D. de (1834). *Manuel d'Actinologie et de Zoophytologie. 2 volumes*. Levrault, Paris & Strasbourg.
- Burnett, J. A. (1997). Nannofossil data from Komplex VIII, Isle of Rügen, Jasmund (4 pp.). Unpublished Report. London: Department of Geological Sciences, University College.
- Burnett, J. A. (1998). Upper Cretaceous. In P. R. Bown (Ed.), *Calcareous Nannofossil Biostratigraphy* (pp. 132–199). Dordrecht: Kluwer Academic Publishers.
- Caramés, A., Martínez, M., Concheyro, A., Remírez, M., & Adamonis, S. (2019). Holothuroidea: New records from the Lower Cretaceous of the Agrio Formation, Neuquén Basin, Argentina. An integrated study with foraminifers and calcareous nannofossils. *Alcheringa*, 43(4), 580–596. <https://doi.org/10.1080/03115518.2019.1641617>
- Carpenter, P. H. (1884). Report upon the Crinoidea collected during the voyage of H.M.S. Challenger during the Years 1873–76. Part I: General morphology, with descriptions of the stalked crinoids. In Thomson C. W., & Murray J. (Eds.), *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–76*, 11(Zoology 32), 1–442.
- Cherbonnier, G., & Féral, J.-P. (1981). Echinodermes: Holothuries. In *Résultats des campagnes MUSORSTOM. I. Philippines (18–28 Mars 1976)* (pp. 357–412). Éd. du Muséum, Paris. (= *Mémoires. Office de la recherche scientifique et technique Outre-Mer*, 91)
- Clark, H. L. (1908) The Apodous Holothurians. A monograph of the Synaptidae and Molpadidae. *Smithsonian Contributions to Knowledge*, XXXV(1723), 1–231.
- Clark, H. L. (1920) Holothuroidea. In *Reports on the scientific results of the expedition to the tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer "Albatross," from August, 1899, to March, 1900, Commander Jefferson F. Moser, U.S.N., Commanding. XXII. + Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer "Albatross," from October, 1904, to March, 1905, Lieut. Commander L.M. Garrett, U.S.N., Commanding. XXXIII. Memoirs of the Museum of Comparative Zoology at Harvard College*, 39(4), 115–154.
- Cuvier, G. (1817). *Le règne animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Tome IV.* Paris: Deterville
- Davey, N., & O'Loughlin, M. (2013). The caudinid sea cucumbers of New Zealand (Echinodermata: Holothuroidea: Molpadida: Caudinidae). *Zootaxa*, 3613(4), 357–368.
- Deflandre-Rigaud, M. (1959). Sur quelques sclérites d'Holothurides de l'Oligocène moyen d'Innien, Holstein. *Revue de Micropaléontologie*, 1(4), 190–200.
- Deflandre-Rigaud, M. (1962). Contribution à la connaissance des sclérites d'Holothurides fossiles. *Mémoires du Muséum National d'Histoire Naturelle (N. S., Série C: Sciences de la Terre)*, 11(1), 1–123.
- Deichmann, E. (1936). Notes on *Molpadia oölitica* (Pourtales). *Proceedings of the New England Zoological Club*, 15, 57–62.
- Deichmann, E. (1938). New holothurians from the western coast of North America and some remarks on the genus *Caudina*. *Proceedings of the New England Zoological Club*, 16, 103–115.
- Deichmann, E. (1940). Report on the holothurians, collected by the Harvard-Havana expeditions 1938 and 1939, with a revision of the Molpadonia of the Atlantic Ocean. *Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey"*, 14(3), 183–240.
- Diener, I., Petzka, M., Reich, M., Rusbült, J., & Zagora, I. (2004). Oberkreide. In G. Katzung (Ed.), *Geologie von Mecklenburg-Vorpommern* (pp. 173–186). Stuttgart: E. Schweizerbart.
- Frenzel, P. (2000). Die benthischen Foraminiferen der Rügener Schreiekreide (Unter-Maastricht, NE-Deutschland). *Neue Paläontologische Abhandlungen*, 3, 1–361.
- Frenzel, P., Herrig, E., Nestler, H., & Reich, M. (1998). Die Rügener Schreiekreide. In M. Reich (Ed.), *Die Kreide Mecklenburg-Vorpommerns, Exkursionsführer zur Geländetagung der DUGW Subkommission für Kreidestratigraphie* (pp. 7–29). Greifswald. <https://doi.org/10.13140/2.1.4532.2560>
- Gebruk, A. V., Smirnov, A. V., & Rogacheva, A. V. (2014). Deep-sea fauna of European seas: An annotated species check-list of benthic invertebrates living deeper than 2000 m in the seas bordering Europe. Holothuroidea. *Invertebrate Zoology*, 11(1), 156–180.
- Gehrmann, A., Schack Pedersen, S. A., & Meschede, M. (2022). New insights into the structural development and shortening of the southern Jasmund Glacitectonic Complex (Rügen, Germany) based on balanced cross sections. *International Journal of Earth Sciences*, 111, 1697–1715. <https://doi.org/10.1007/s00531-022-02216-y>
- Gilliland, P. M. (1992). Holothurians in the Blue Lias of Southern Britain. *Palaeontology*, 35(1), 159–210.
- Gilliland, P. M. (1993). The skeletal morphology, systematics and evolutionary history of holothurians. *Special Papers in Palaeontology*, 47, 1–147.
- Górka, H., & Łuszczewska, L. (1969). Holothurian sclerites from the Polish Jurassic and Tertiary. *Rocznik Polskiego Towarzystwa Geologicznego [= Annales de la Société Géologique de Pologne]*, 39(1), 361–402.
- Haeckel, E. (1896). Systematische Phylogenie der Echinodermen. In E. Haeckel (Ed.), *Entwurf eines natürlichen Systems der Organismen auf Grund ihrer Stammesgeschichte. Zweiter Theil: Systematische Phylogenie der Wirbellosen Thiere (Invertebrata)* (pp. 348–504). Berlin: G. Reimer.
- Håkansson, E., Bromley, R., & Perch-Nielsen, K. (1974). Maastrichtian chalk of north-west Europe—a pelagic shelf sediment. In Hsü K. J., & Jenkins H. C. (Eds.), *Pelagic Sediments: On Land and under the Sea* (pp. 211–233). Oxford: Blackwell Scientific. <https://doi.org/10.1002/9781444304855.ch9>
- Haude, R. (1992). Fossil holothurians: Sclerite aggregates as 'good' species. In Scalera-Liaci L., & Canicatti C. (Eds.), *Echinoderm Research 1991* (pp. 29–33). Rotterdam/Brookfield: A. A. Balkema.
- Heding, S. G. (1931). On the Classification of the Molpadids. Preliminary notice. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København*, 92, 275–284.

- Heding, S. G. (1932). *Paracaudina* nom. nov. A correction, together with some remarks concerning the supposed fossil holothurian *Pseudocaudina brachyura* Broili. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København*, 92, 455–456.
- Heding, S. G. (1933). The *Caudina* of Asamushi, the so-called *Caudina chilensis* (Johs. Müller). *Science Reports of Tôhoku Imperial University (Fourth Series: Biology)*, 8(2), 127–142.
- Heding, S. G. (1935). Holothurioidea. Part I. Apoda.—Molpadi-
oidea.—Gephyrothurioidea. *The Danish Ingolf-Expedition*, 4(9), 1–84.
- Herrig, E. (1966). Ostracoden aus der Weißen Schreibkreide (Unter-Maastricht) der Insel Rügen. *Paläontologische Abhandlungen (A: Paläozoologie)*, 2(4), 693–1024.
- Herrig, E. (1969). Beitrag zur Kenntnis von Ostracoden aus der Oberkreide im Nordosten der Deutschen Demokratischen Republik. *Berichte der Deutschen Gesellschaft für Geologische Wissenschaften (A: Geologie und Paläontologie)*, 14(5), 645–657.
- Herrig, E. (2004). Kreide auf Rügen. In G. Katzung (Ed.), *Geologie von Mecklenburg-Vorpommern* (pp. 186–197). Stuttgart: Schweizerbart.
- Herrig, E., Nestler, H., Frenzel, P., & Reich, M. (1996). Discontinuity Surfaces in the high Upper Cretaceous of Northeastern Germany and their Reflection by Fossil Associations. In Reiter J., Neuweiler F., & Gunkel F. (Eds.), *Global and Regional Controls on Biogenic Sedimentation. II. Cretaceous Sedimentation Research Reports. Göttinger Arbeiten zur Geologie und Paläontologie, Sb3*, 107–111.
- Hess, H. (1975). Die fossilen Echinodermen des Schweizer Juras. *Veröffentlichungen aus dem Naturhistorischen Museum Basel*, 8, 1–130.
- Hôzawa, S. (1928). On the changes occurring with advancing age in the calcareous deposits of *Caudina chilensis* (J. Müller). *Science Reports of Tôhoku Imperial University (Fourth Series: Biology)*, 3(3)[2], 361–378.
- Kerr, A. M., & Kim, J. (2001). Holothuroidea (Echinodermata) inferred from morphology. *Zoological Journal of the Linnean Society*, 133, 63–81. <https://doi.org/10.1006/zjls.2000.0280>
- Khripounoff, A., & Sibuet, M. (1980). La nutrition d'échinodermes abyssaux. I. Alimentation des holothuries. *Marine Biology*, 60(1), 17–26. <https://doi.org/10.1007/BF00395602>
- Kienel, U. (1990) Die Coccolithen der Rügener Schreibkreide (Unter-Maastricht). *Unpublished Diploma Thesis, Sektion Geologische Wissenschaften, University of Greifswald*, 67 pp.
- Kienel, U. (1993) Zur Altersstellung der Rügener Schreibkreide anhand kalkiger Nannofossilien (Unter-Maastricht). In Kohring, R. (Ed), *Miscellanea Palaeontologica 2. Berliner Geowissenschaftliche Abhandlungen (E: Paläobiologie)*, 9, 45–55.
- Knaust, D., & Schnick, H. (2024). Trace fossils from the Maastrichtian chalk of the Isle of Rügen, north-east Germany. In Jagt, J. W. M., Fraaije, R. H. B., Jagt-Yazykova, E. A., & Vellekoop, J. (Eds.), *Aspects of Maastrichtian (Late Cretaceous) stratigraphy and palaeontology. Netherlands Journal of Geosciences*, 103, e12. <https://doi.org/10.1017/njg.2024.6>.
- Kutscher, M. (1987). Die Echinodermen der Callovien-Geschiebe. *Der Geschiebesammler*, 21(2–3), 53–104.
- Kutscher, M. (1988). Zur Invertebratenfauna und Stratigraphie des oberen Pliensbachien von Grimmen (DDR), Echinodermata. *Freiberger Forschungshefte (C: Paläontologie und Stratigraphie)*, 419, 62–70.
- Kutscher, M., & Hary, A. (1991). Echinodermen im Unteren Lias (bucklandi- und semicostatum-Zone) zwischen Ellange und Elvange (SE-Luxemburg). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 182(1), 37–72. <https://doi.org/10.1127/njgpa/182/1991/37>
- Kutscher, M., & Reich, M. (2021). Die Echinodermen-Fauna des Amaltheentons von Buttenheim. In Maisch M. W., & Schweigert G. (Eds.), *Buttenheim. Ein Fenster in die frühe Jurazeit. Fossilien, Sonderheft*, 2021, 67–77.
- Laschke, S., Frenzel, P., & Ustaszewski, K. (2015). Biostratigraphie und Lagerungsverhältnisse der höchsten Oberkreide am SE-Rand des Arkona-Beckens, südliche Ostsee. In Anonymous (Ed.), 79. Tagung der Arbeitsgemeinschaft Norddeutscher Geologen, 26.-29.05.2015 in Güstrow. *Schriftenreihe des Landesamtes für Umwelt, Naturschutz und Geologie Mecklenburg-Vorpommern*, 1/2015, 102–104.
- Lowenstam, H. A., & Rossman, G. R. (1975). Amorphous, hydrous, ferric phosphatic dermal granules in *Molpadida* (Holothuroidea): Physical and chemical characterization and ecologic implications of the bioinorganic fraction. *Chemical Geology*, 15(1), 15–51. [https://doi.org/10.1016/0009-2541\(75\)90011-X](https://doi.org/10.1016/0009-2541(75)90011-X).
- Ludwig, H. (1889–1892). Die Seewalzen. In Bronn, H. G. (Ed.), *Klassen und Ordnungen des Thier-Reichs, wissenschaftlich dargestellt in Wort und Bild. Zweiter Band. Dritte Abtheilung: Echinodermen (Stachelhäuter). I. Buch* (pp. 1–460). Leipzig: C. F. Winter. (1889=pp. 1–176; 1890=pp. 177–240; 1891=pp. 241–376; 1892=pp. 377–460).
- Ludwig, H. (1891). *Ankyroderma musculus* (Risso), eine Molpadi-
ide des Mittelmeeres, nebst Bemerkungen zur Phylogenie und Systematik der Holothurien. *Zeitschrift für Wissenschaftliche Zoologie*, 51(4), 569–612.
- Lütken, C. (1857). Oversigt over Grönlands Echinoderm. *Videnskabelige Meddelelser fra den naturhistoriske Forening i København*, 1857(1–7), 1–109.
- MacBride, E. W. (1906). Echinodermata. In Harmer S. F., & Shipley A. E. (Eds.), *The Cambridge Natural History, Vol. I: Protozoa, Porifera (sponges), Coelenterata and Ctenophora, Echinodermata* (pp. 425–623). London: MacMillan.
- Madsen, F. J., & Hansen, B. (1994). Echinodermata: Holothurioidea. *Marine invertebrates of Scandinavia*, 9, 1–143.
- Mageau, N. C., & Walker, D. A. (1976). Effects of ingestion of foraminifera by larger invertebrates. In Schafer, C. T., & Pelletier, B. R. (Eds.), *First International Symposium on Benthonic Foraminifera of Continental Margins. Part A. Ecology and Biology* (pp. 89–105). Halifax: Maritime Sediments. (=Maritime Sediments, Special Publication, 1).
- Mehlhorn, P., Winkler, L., Grabbe, F.-C., Kenzler, M., Gehrmann, A., Hüneke, H., & Rother, H. (2019). Coastal cliff at Lenzer Bach on Jasmund Peninsula, Rügen Island (Pleistocene Stripe 4): Reconstructed history of glacial tectonic deformation based on fold geometry and microstructural mapping. *DEUQUA Special Publication*, 2, 35–41. <https://doi.org/10.5194/deuquasp-2-35-2019>
- Mercier, A., Gebruk, A., Kremenetskaia, A., & Hamel, J.-F. (2024). An overview of taxonomic and morphological diversity in sea cucumbers (Holothuroidea: Echinodermata). In Mercier A., Hamel J.-F., Suhrbier A., & Pearce C. (Eds.), *The World of Sea Cucumbers. Challenges, Advances, and Innovations* (pp. 3–15). London: Academic Press. <https://doi.org/10.1016/B978-0-323-95377-1.00001-1>
- Miller, A. K., Kerr, A. M., Paulay, G., Reich, M., Wilson, N. G., Carvajal, J. I., & Rouse, G. W. (2017). Molecular phylogeny of extant Holothuroidea (Echinodermata). *Molecular Phylogenetics and Evolution*, 111, 110–131. <https://doi.org/10.1016/j.ympev.2017.02.014>
- Mongiardino Koch, N., Tilic, E., Miller, A. K., Stiller, J., & Rouse, G. W. (2023). Confusion will be my epitaph: Genome-scale discordance stifles phylogenetic resolution of Holothuroidea. *Proceedings of the Royal Society (B: Biological Sciences)*, 290, 20230988. <https://doi.org/10.1098/rspb.2023.0988>

- Müller, J. (1850). Anatomische Studien über die Echinodermen. *Archiv für Anatomie, Physiologie und Wissenschaftliche Medizin*, 1850, 117–155.
- Östergren, H. (1907) Zur Phylogenie und Systematik der Seewalzen. In Anonymous (Ed.), *Zoologiska Studier tillägnade Professor T. Tullberg [Utg.: Naturvet. Studentsällsk.]*. (pp. 191–215). Uppsala: Almqvist & Wiksell.
- O'Loughlin, P. M., Barmos, S., & VandenSpiegel, D. (2011). The paracaudinid sea cucumbers of Australia and New Zealand (Echinodermata: Holothuroidea: Molpadiida: Caudinidae). *Memoirs of Museum Victoria*, 68, 37–65.
- O'Loughlin, P. M., & Ong, J. Y. (2015). New tropical caudinid and synaptid sea cucumbers from the Johor Straits (Echinodermata: Holothuroidea). *Raffles Bulletin of Zoology*, 31(Supplement), 292–302.
- O'Loughlin, P. M., Stępień, A., Kuźniak, M., & VandenSpiegel, D. (2013). A new genus and four new species of sea cucumbers (Echinodermata) from Admiralty Bay, King George Island. *Polish Polar Research*, 34(1), 67–86. <https://doi.org/10.2478/popore-2013-0003>
- Pawson, D. L. (1963). The holothurian fauna of Cook Strait, New Zealand. *Zoology Publications of the Victoria University Wellington*, 36, 1–38.
- Pawson, D. L. (1970). The Marine Fauna of New Zealand: Sea Cucumbers (Echinodermata: Holothuroidea). *New Zealand Oceanographic Institute, Memoir*, 52, 1–69. [= *New Zealand Department of Scientific and Industrial Research, Bulletin*, 201]
- Pawson, D. L. (1977). Molpadiid Sea Cucumbers (Echinodermata: Holothuroidea) of the Southern Atlantic, Pacific, and Indian Oceans. In Pawson D. L. (Ed.) *Biology of the Antarctic Seas VI. Antarctic Research Series*, 26, 97–123.
- Pawson, D. L. (1982). Holothuroidea. In S. P. Parker (Ed.), *Synopsis and Classification of Living Organisms. Volume 2* (pp. 813–818). New York: McGraw-Hill.
- Pawson, D. L., Donnay, G., & Hey, M. H. (1975). Iron phosphate deposits in molpadiid holothurians (Echinodermata: Holothuroidea). *Biom mineralisation*, 8, 16–20.
- Pawson, D. L., & Fell, H. B. (1965). A revised classification of the dendrochirote holothurians. *Breviora. Museum of Comparative Zoology*, 214, 1–7.
- Pawson, D. L., & Kerr, A. M. (2001). Chitin in Echinoderms? Tentacle sheaths in the deep-sea holothurian *Ceraplectana trachyderma* (Holothuroidea: Molpadiida). *Gulf of Mexico Science*, 19(2), 192.
- Pawson, D. L., & Liao, Y. (1992). Molpadiid sea cucumbers of China, with descriptions of five new species (Echinodermata: Holothuroidea). *Proceedings of the Biological Society of Washington*, 105(2), 373–388.
- Pawson, D. L., & Vance, D. L. (2007). *Heteromolpadia joyceae*, a new species of sea cucumber from New Zealand, with a key to New Zealand Molpadiidae (Echinodermata: Holothuroidea: Molpadiida). *Zootaxa*, 1608, 35–39.
- Pawson, D. L., Vance, D. J., & Ahearn, C. (2001). Western Atlantic sea cucumbers of the Order Molpadiida (Echinodermata: Holothuroidea). *Bulletin of the Biological Society of Washington*, 10, 311–327.
- Perch-Nielsen, K. (1985). Mesozoic calcareous nannofossils. In Bolli H. M., Saunders J. B., & Perch-Nielsen K. (Eds.), *Plankton stratigraphy. Volume 1. Planktic foraminifera, calcareous nannofossils and calpionellids* (pp. 329–426). Cambridge: Cambridge University Press.
- Petzka, M., & Reich, M. (2000). Mecklenburg-Vorpommern: Oberkreide. In Stratigraphische Kommission Deutschlands (Ed.), *Die Kreide der Bundesrepublik Deutschland. Courier Forschungsinstitut Senckenberg*, 226, 73–79.
- Reich, M. (1994). Belemnnoidea. In Herrig E., Nestler H., Frenzel P., & Reich M. (Eds.), *Diskontinuitäten in Profilen der höheren Oberkreide und ihre Widerspiegelung in den Fossilgemeinschaften (DFG-Kurzzeichen: Ne 454/1–3)*. Unpublished DFG Report [for 1993–1994], p. 10.
- Reich, M. (2001). Holothurians from the Late Cretaceous of the Isle of Rügen (Baltic Sea). In M. Barker (Ed.), *Echinoderms 2000* (pp. 89–92). Lisse: A. A. Balkema Publishers.
- Reich, M. (2002a). Holothurienreste (Echinodermata) aus dem Oligozän (Rupelium) Norddeutschlands. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 224(1), 97–113. <https://doi.org/10.1127/njgpa/224/2002/97>
- Reich, M. (2002b). Die Holothurien (Echinodermata) der Oberkreide. Unpublished PhD thesis, University of Innsbruck (584 pp.). Innsbruck: Faculty of Natural Sciences.
- Reich, M. (2003). Holothurienreste (Echinodermata) aus der Oberkreide des Ostseeraumes: Teil 5. Molpadiidae J. Müller, 1850. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 229(2), 231–253. <https://doi.org/10.1127/njgpa/229/2003/231>
- Reich, M. (2013). How many species of fossil holothurians are there? In C. Johnson (Ed.), *Echinoderms in a Changing World* (pp. 23–51). Boca Raton: CRC Press Taylor & Francis Group.
- Reich, M. (2014). Phanerozoic echinozoan echinoderms: Palaeobiology, phylogeny and evolutionary history: new evidences from micropalaeontology and fossil lagerstätten. *Unpublished Habilitation thesis, Georg-August University of Göttingen* (77 pp. + 274 pp.). Göttingen: Faculty of Geosciences & Geography.
- Reich, M. (2015). Different pathways in early evolution of the calcareous ring? In Zamora S., & Rábano I. (Eds.), *Progress in Echinoderm Palaeobiology. Cuadernos del Museu Geominero*, 19, 137–145.
- Reich, M. (2017). First report of sea cucumbers (Echinodermata: Holothuroidea) from the latest Cretaceous of Bavaria, Germany. *Zitteliana*, 89, 285–289.
- Reich, M., & Ansoerge, J. (2014). Santonian sea cucumbers (Echinodermata: Holothuroidea) from Sierra del Montsec, Spain. *Göttingen Contributions to Geosciences*, 77, 147–160. <https://doi.org/10.3249/webdoc-3925>
- Reich, M., & Frenzel, P. (2002). Die Fauna und Flora der Rügener Schreibkreide (Maastrichtium, Ostsee). *Archiv für Geschichtsbekunde*, 3(2/4), 73–284.
- Reich, M., & O'Loughlin, M. (2010). Modern holothurian calcareous ring anatomy and stereom structure – the need for more detailed studies and research. In Reich M., Reitner J., Roden V., & Thuy B. (Eds.), *Echinoderm Research 2010: 7th European Conference on Echinoderms, Göttingen, October 2–9, 2010. Abstract Volume and Field Guide to Excursions* (pp. 88–89). Göttingen: Universitätsverlag.
- Reich, M., & Rössner, G. (2016). Unusual calcareous ring morphology in molpadiid sea cucumbers (Echinodermata)? In Reich M., Erpenbeck D., Fleischmann A., Jörgen K., Haszprunar G., & Wörheide G. (Eds.), *17th Annual Meeting of the Gesellschaft für Biologische Systematik, 21.-24. February 2016. Abstracts. Zitteliana*, 88, 41.
- Reich, M., Frenzel, P., & Herrig, E. (2005). Die Schreibkreide: Ein Meer am Ende der Oberkreide. *Biologie in Unserer Zeit*, 35(4), 260–267. <https://doi.org/10.1002/biuz.200410285>
- Reich, M., Herrig, E., Frenzel, P., & Kutscher, M. (2018). Die Rügener Schreibkreide—Lebewelt und Ablagerungsverhältnisse eines pelagischen oberkretazischen Sedimentationsraumes. *Zitteliana*, 92, 17–32. <https://doi.org/10.5282/ubm/epub.57206>
- Roden, V. J., Hausmann, I. M., Nützel, A., Seuss, B., Reich, M., Ulrichs, M., Hagdorn, H., & Kiessling, W. (2020). Fossil liberation: A model to explain high biodiversity in the Triassic Cassian

- Formation. *Palaeontology*, 61(1), 85–102. <https://doi.org/10.1111/pala.12441>
- Rowe, F. W. E., O'Hara, T. D., & Bardsley, T. M. (2017). Class Holothuroidea. In Byrne M., & O'Hara T. D. (Eds.), *Australian Echinoderms. Biology, Ecology and Evolution*. (pp. 447–490). Melbourne: CSIRO Publishing, & Canberra: ABRIS.
- Sadeddin, W. (1996). Holothurian sclerites from the Albian (Early Cretaceous) of the Fort Worth area, Texas, USA. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 200(3), 325–351. <https://doi.org/10.1127/njgpa/200/1996/325>.
- Sadeddin, W., & Saqqa, W. (1997). Holothurian sclerites from the Upper Cretaceous (Lower Turonian) of the Jarash area, North Jordan. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1997(6), 370–382. <https://doi.org/10.1127/njgpm/1997/1997/370>
- Samyn, Y., & VandenSpiegel, D. (2016). Sublittoral and bathyal sea cucumbers (Echinodermata: Holothuroidea) from the Northern Mozambique Channel with description of six new species. *Zootaxa*, 4196(4), 451–497. <https://doi.org/10.11646/zootaxa.4196.4.1>
- Schulz, M.-G. (1979) Morphometrisch-variationsstatistische Untersuchungen zur Phylogenie der Belemniten-Gattung *Belemnella* im Untermaastricht NW-Europas. In *Die Maastricht-Stufe in NW-Deutschland, Teil 1. Geologisches Jahrbuch (A: Allgemeine und regionale Geologie BR Deutschland und Nachbargebiete, Tektonik, Stratigraphie, Paläontologie)*, 47, 3–157.
- Semper, C. (1867–1868) Holothurien. In Semper C. (Eds.), *Reisen im Archipel der Philippinen. Zweiter Theil. Wissenschaftliche Resultate. Erster Band*. Leipzig: W. Engelmann. [1867: pp. 1–100, pls. 1–25; 1868: pp. 101–176, pls. 26–38; 1868: pp. 177–280, pls. 39–40] <https://doi.org/10.5962/bhl.title.11687>
- Sibuet, M. (1974). *Cherbonniera utriculus* gen. nov., sp. nov., petite Holothurie (Molpadonia, Molpadiidae) des vases abyssaux du Nord-Est atlantique. *Comptes Rendus des séances de l'Académie des Sciences (D: Sciences naturelles)*, 279(17), 1443–1445.
- Sissingh, W. (1977). Biostratigraphy of Cretaceous calcareous nanoplankton. *Geologie en Mijnbouw*, 56(1), 37–65.
- Smirnov, A. V. (2012). System of the Class Holothuroidea. *Paleontological Journal*, 46(8), 793–832. <https://doi.org/10.1134/S0031030112080126>
- Steinich, G. (1965). Die artikulierten Brachiopoden der Rügener Schreibkreide. *Paläontologische Abhandlungen (A: Paläozoologie)*, 2(1), 1–220.
- Steinich, G. (1972). Endogene Tektonik in den Unter-Maastricht-Vorkommen auf Jasmund (Rügen). *Geologie*, 20, 1–207. (*Geologie Beiheft*, 71/72).
- Stimpson, W. (1853). Synopsis of the Marine Invertebrata of Grand Manan, or the Region round the Bay of Fundy, New Brunswick. *Smithsonian Contributions to Knowledge*, 6, 1–68.
- Surlyk, F. (1970). Die Stratigraphie des Maastricht von Dänemark und Norddeutschland aufgrund von Brachiopoden. *Newsletters on Stratigraphy*, 1(2), 7–16. <https://doi.org/10.1127/nos/1/1970/7>
- Théel, H. (1886). Report on the Holothuroidea dredged by H.M.S. Challenger during the Years 1873–76. Part II. In Thomson C. W., & Murray J. (Eds.), *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–76*, 14(Zoology 39), 1–290. London: Longmans & Co. etc.
- Voigt, S., Wägreich, M., Surlyk, F., Walaszczyk, I., Uličný, D., Čech, S., Voigt, T., Wiese, F., Wilmsen, M., Niebuhr, B., Reich, M., Funk, H., Michalik, J., Jagt, J. W. M., Felder, P. J., & Schulp, A. S. (2008). Cretaceous. In T. McCann (Ed.), *The Geology of Central Europe. Volume 2: Mesozoic and Cenozoic* (pp. 923–997). London: The Geological Society.
- Wehrli, H. (1967). Das petro- und biostratigraphische Profil der Rügener Schreibkreide. *Wissenschaftliche Zeitschrift der Ernst-Moritz-Arndt-Universität Greifswald (Mathematisch-naturwissenschaftliche Reihe)*, 16(3), 175–188.
- Whelpley, J. M., Uehling, A. T., Paulay, G., & Ryan, J. F. (2025) Phylogenomic analyses of all major sea cucumber lineages provide a robust backbone of Holothuroidea. Preprint: Accessed 2025-12-31. <https://doi.org/10.1101/2025.04.14.648730>
- WoRMS/Paulay, G., Reich, M., & Kremenetskaia, A. (2025). World Register of Marine Species.—Holothuroidea. Available from <https://www.marinespecies.org> at VLIZ. Accessed 2025-04-02. <https://doi.org/10.14284/170>