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On Mesozoic laetmogonid sea cucumbers (Echinodermata: Holothuroidea: Elasipodida)*

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Abstract

A comparative systematic survey of fossil Mesozoic laetmogonid sea cucumbers (Elasipodida) and their relatives is presented. A re-examination of the fossil record shows that only 13 fossil taxa can be recognised as belonging to this group. Four further known 'laetmogonid' taxa can be regarded as *incertae sedis*. An analysis of the results supports the following taxonomic changes. Palaeocaudinidae Boczarowski, 2001 represents a junior synonym of the Laetmogonidae Ekman, 1926. The subfamily Staurocaudininae Boczarowski, 1997 is restricted to the type species of *Staurocaudina*. The new family Palaeolaetmogonidae comprises probable stem group members of the Laetmogonidae. Three new species (*Palaeocaudina rugia*, *Priscolaetmogone oloughlini*, *Palaeolaetmogone frankwiesei*) are described from Late Cretaceous sediments of Europe. Two new genera (*Palaeolaetmogone*, *Priscolaetmogone*) are erected. The geographic distribution and phylogenetic relationships of Mesozoic and Cenozoic laetmogonid holothurians are analysed and discussed.

Key words: Europe, India, Triassic, Jurassic, Cretaceous, systematics, Elasipodida, Holothuroidea, Echinodermata, new genus, new taxa

Introduction

Macroinvertebrate communities of the deep sea are characterised by high biodiversity (*e.g.*, Belyaev 1966; Hessler & Sanders 1967; Zenkevič 1970; Wolff 1977; Grassle 1989; Rex *et al.* 1993). This includes various groups of the Holothuroidea, like the Myriotrochidae (Apodida), Synallactidae (Aspidochirotida), Deimatidae, Elpidiidae, Psychropotidae and Laetmogonidae (all Elasipodida) confined to bathyal, abyssal and hadal depths (*e.g.*, Agatep 1967; Hansen 1956, 1967, 1975; Gebruk 1990; Lambert & Boutillier 2011).

Modern laetmogonid sea cucumbers (Figs. 1–2) were first recorded from the "Challenger" expedition of 1872–76 (Théel 1879, 1882) and were later reported from nearly all marine deep-water environments (*e.g.*, Sluiter 1901; Mitsukuri 1912; Hansen 1975; Pawson 1978, 1983; Madsen & Hansen 1994; Thandar 1998, 1999; Rogacheva *et al.* 2009; Solís-Marín *et al.* 2009; Massin & Hendrickx 2011).

Members of this family are medium-sized with an elongate, more or less cylindrical gelatinous body and well-defined diagnostic wheels. Up to the present, 6 genera with around 17 modern species

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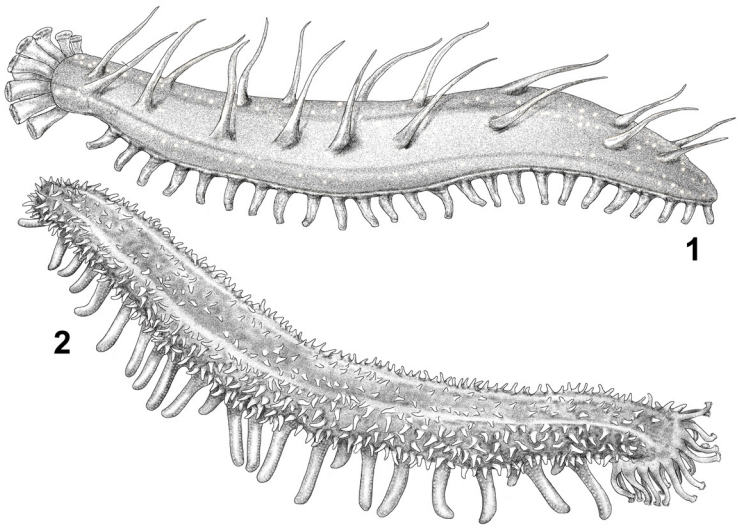


FIGURE 1. Schematic drawings of modern members of the Laetmogonidae. 1: *Laetmogone* [body length: ~10 cm]; 2: *Pannychia* [body length: ~15 cm].

are known. These are: *Laetmogone* Théel, 1879; *Benthogone* Kœhler, 1895 and *Pannychia* Théel, 1882 as well as the monotypic *Apodogaster* Walsh, 1891; *Psychronaetes* Pawson, 1983 and *Gebrukothuria* Rogacheva & Cross, 2009 in Rogacheva *et al.* 2009. Laetmogonid representatives are found in the deep sea (bathyal to abyssal) only, with cosmopolitan and endemic species. All are exclusively epifaunal detritus feeders and grazers.

The first fossil laetmogonid holothurians from Mesozoic sediments were described by Marthe Deflandre-Rigaud in 1946 (Jurassic, Oxfordian of the Normandy, France), followed by a few other descriptions (Mostler 1970; Soodan 1977; Singh *et al.* 1981; Lipiec 1992; Jamnik & Ramovš 1993; Sztejn 1993; Reich 1995; Krainer *et al.* 1994; Krainer & Mostler 1997) or mentions only (*e.g.*, Soodan 1972), mostly from Europe.

In this article, I strive to critically evaluate published records of Mesozoic Laetmogonidae. My report also presents new records and observations, including several new taxa, to set a baseline for future studies on fossil Elasipodida.

Material

This study is based on review of records in the literature and of samples of isolated fossil calcareous holothurian ossicles from different Mesozoic European localities, as follows:

(1) ENCI-HeidelbergCement Group quarry, south of Maastricht, The Netherlands. The material (sampled in 1999) described herein comes from partly silicified limestones embedded in glauconitic, grey chalky marls of the Vijlen Member (Gulpen Formation; Felder 1997, Felder & Bosch 1998), which are late Early Maastrichtian in age (*Belemnella cimbrica* Zone; Keutgen *et al.* 2010, Jagt & Jagt-Yazykova 2012). The present laetmogonid body-wall ossicles are associated with sclerites of chiridotid (Apodida; Reich 2003b), dendrochirotid, holothuriid, and molpadiid sea cucumbers (Reich & Jagt 2001). Jagt (1999) noted echinoderm bioclasts predominate in the Vijlen Member, considering sedimentation in a low-energy setting below storm wave base.

(2) Peninsula Jasmund, Isle of Rügen, western Pomerania, Germany. The material described below, was preliminarily described in Reich (1997b) and originates from the standard section of

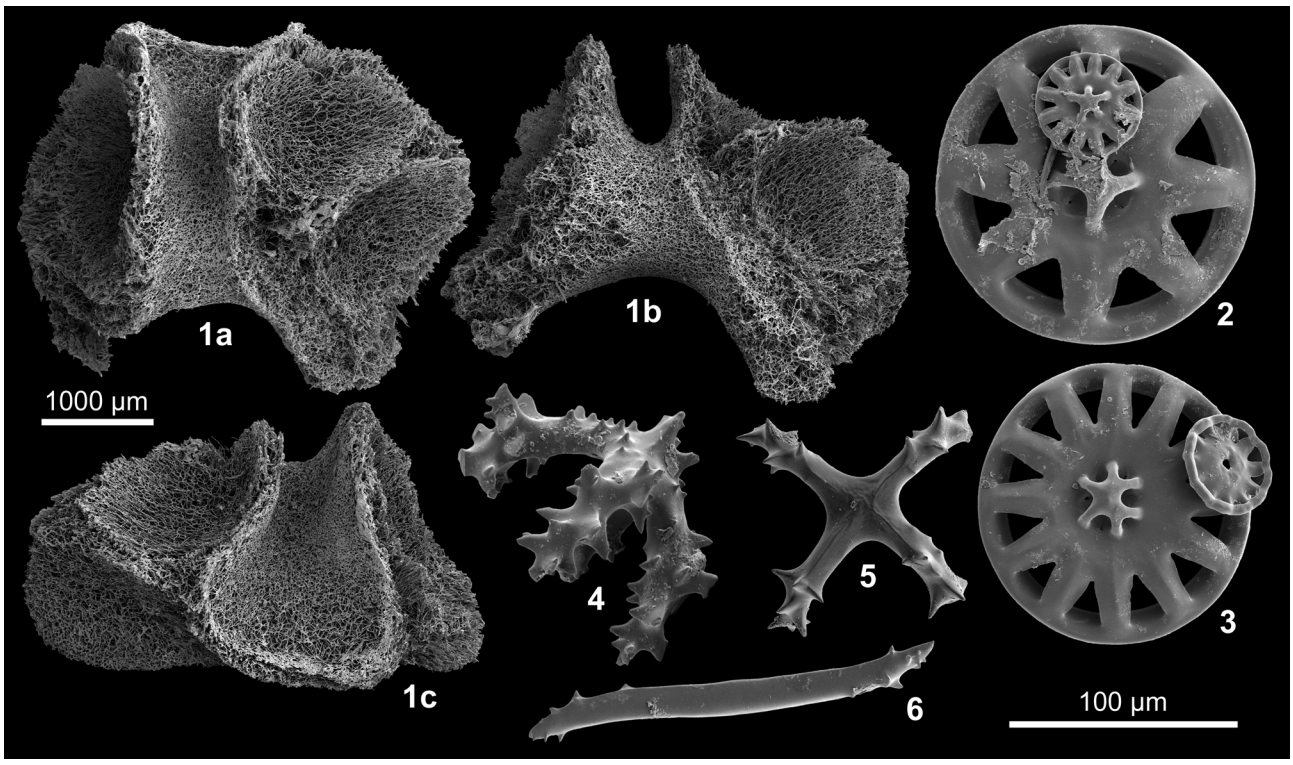


FIGURE 2. Calcareous hard parts of *Laetmogone violacea* Théel, 1879 (specimen 6 cm long; SMNH 110035–110037). 1a–1c: radial element of the calcareous ring notched for the passage of the radial nerves and showing a fragile network of stereom structure; 1a: anterior view; 1b: inner view; 1c: outer view; 2–3: wheels of large and small type, lower side showing the cone formed by the primary cross, which is directed inwards in the body wall, and upper side showing the perforated calcareous membrane covering the nave; 4–6: spinous cross- (4–5) and rod-shaped (6) ossicles. Recent, North Atlantic Ocean, between Faroe Islands and Scotland, 1015 m water depth (coll. H. Théel). Scale bar 1000 µm = 1a–1c; Scale bar 100 µm = 2–6.

the 'Rügen chalk' at complex VIII north of Sassnitz, Jasmund peninsula (Reich & Frenzel 2002; Herrig 2004b). Rügen is a classic fossil type locality of the European Upper Cretaceous, where the succession is built up by 90 m of chalk sediment, Early Maastrichtian in age (*Belemnella obtusa*, *B. sumensis*, *B. cimbrica*, *B. fastigata* belemnite Zones).

The elasipodid body-wall ossicles are associated with other members of the Apodida, Molpadiida, Aspidochirotida, Dactylochirotida, Dendrochirotida (Reich 2001a, 2002, 2003a, 2003b, 2003c, 2003d; Reich *et al.* 2004). The whole sedimentation interval of the Rügen Chalk contains a highly diverse and typical 'boreal' (Northern Temperate Realm) faunal association of the outer shelf to upper bathyal (~150–300 m water depth; Herrig *et al.* 1996).

(3) Late Cretaceous geschiebes (glacial erratic boulder) from northeastern Germany and the Baltic Sea bottom. These grey- and whitish-coloured flints (collected in the 1980s and 1990s) were formed in their early diagenesis by secondary matrix silicification within Upper Cretaceous chalks and limestones. The age of these sediments was precisely dated using foraminifers and ostracods (mostly Maastrichtian), and the source area of this type of geschiebe is presumed to be the bottom of the Baltic Sea, most likely the Adlergrund, SW off the Isle of Bornholm (Herrig 2004a).

These partly silicified limestones contain, in addition to other invertebrates, a rich and diverse assemblage of sea cucumbers, with members from all modern orders (Reich 1995, 1997a, 2002, 2003b). Herrig (2004a) considered after investigation of ostracods a deposition of the chalk in a water depth of ~100 m.

(4) Isle of Wolin, Województwo zachodniopomorskie, Poland. The Upper Turonian material (*Subprionocyclus neptuni* ammonite Zone; sampled in 1991 and 2000) described herein, originates from a small abandoned quarry near Kępa (see Reich & Wiese 2010), where flint-bearing chalk was exposed.

The ossicles of the Laetmogonidae were mentioned by Reich (1995, p. 685) for the first time and are associated with numerous other holothurian ossicles (Apodida, Aspidochirotida, Dendrochirotida; Reich 2000, 2001b, Reich & Wiese 2010). Reich & Wiese (2010) assumed open shelf settings with a depositional depth of ~100–120 m for this environment.

Additional extant and fossil material was investigated at several institutions (IGPI, MNHN, NHM, and SMNH).

Methods

Fossil holothurian ossicles from chalk and calcareous marls were isolated using 'Nötzold's method' with acetic acid (96–100 %) and copper (II) sulphate, those from clays using hydrogen peroxide (10 %) or hot water. Most of the material comes from partly silicified limestones, isolated by hydrofluoric acid (30–40 %) (see Wissing & Herrig 1999). The latter method delivered very well-preserved material due to early diagenetic impregnation of the sediment matrix by SiO_2 without any further compaction (Herrig 1982, 1993). After washing (sieve sizes: >0.063 mm and 1 mm), the residues were dehydrated at a temperature of ~70°C.

Modern holothurian ossicles were obtained by maceration of distinct parts or entire specimens in hypochlorous acid or diluted household bleach, followed by washing in distilled water through a microbiological filter (size 2 µm) to acquire all hard parts.

All specimens were studied under a binocular microscope first and later mounted on stubs and coated with Au/Pd or Au for investigation and documentation using scanning electron microscopy (SEM) and field-emission scanning electron microscopy (FEM).

All the figured and type material of Reich 1995ff. (cf. Reich 1999) was transferred in 2002 from FGWG to GZG, due to the missing curatorial support of the Greifswald palaeontological collections at that time. For terminology and orientation of wheel-shaped ossicles of laetmogonid holothurians see Fig. 3.

Institutions are abbreviated as follows: DAG = Deutsches Archiv für Geschiebeforschung, Ernst-Moritz-Arndt University Greifswald, Germany; FGWG = old acronym of the (today's) Institute of Geography and Geology, Ernst-Moritz-Arndt University Greifswald, Germany; GZG = Geoscience Centre, Georg-August University Göttingen, Germany; IGPI = Institute of Geology and Palaeontology, University of Innsbruck, Austria; MNHN = Muséum national d'Histoire naturelle, Paris, France; NHM = Natural History Museum, Department of Palaeontology, London, UK; SMNH = Swedish Museum of Natural History, Stockholm, Sweden.

Systematic Palaeontology

Class Holothuroidea de Blainville, 1834
Order Elasipodida Théel, 1882

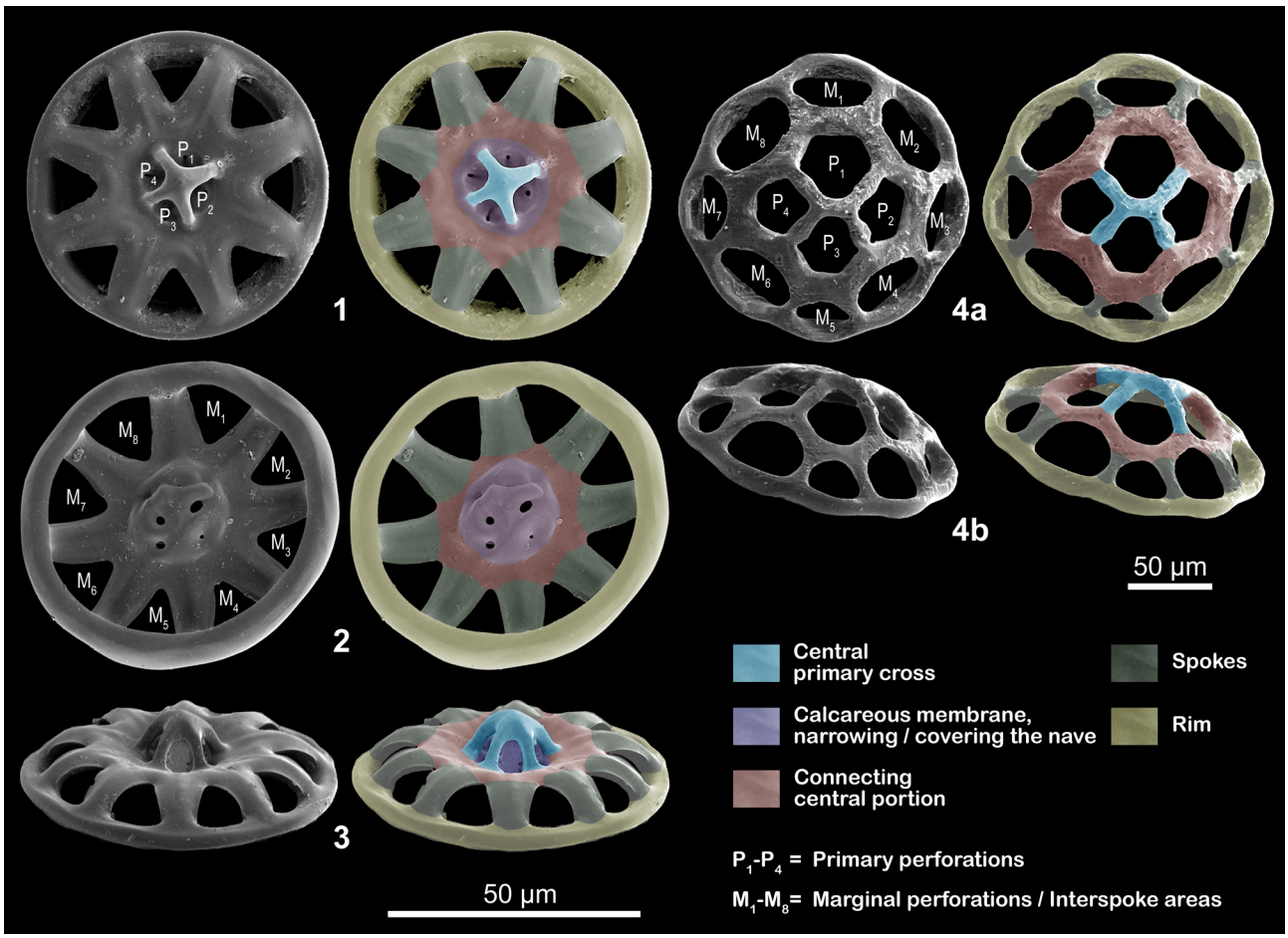


FIGURE 3. Terminology and orientation of wheel-like ossicles in laetmogonid holothurians. 1–3: *Laetmogone violacea* Théel, 1879 (SMNH 110036), Recent, North Atlantic Ocean (cf. Fig. 2); 1: lower side; 2: upper side; 3: lower side, lateral-oblique view; 4: *Palaeocaudina dorsetensis* (Soodan & Whatley, 1988) (GZG.INV.91199), early Oxfordian, Villers-sur-Mer, Normandy, France (coll. M. Reich); 4a: lower side; 4b: lower side, lateral-oblique view.

Family Laetmogonidae Ekman, 1926

Laetmogonidae n. fam. Ekman, 1926: 480
Lætmogonidæ—Mortensen 1927: 360–361
Laetmogonidae Ekman 1926—Deichmann 1930: 118–119
Laetmogonidae Ekman, 1925—Pawson 1965a: 19
Laetmogonidae Ekman, 1926—Hansen 1975: 47–48; Rogacheva *et al.* 2009: 479–480
Protocaudinidae cohors nov. vel parafam. nov. Deflandre-Rigaud, 1961: 103–104 [*pro parte*]
Protocaudinidae cohors nov. vel parafam. nov. Deflandre-Rigaud, 1962: 96–97 [*pro parte*]
Protocaudinidae Deflandre-Rigaud, 1961—Frizzell & Exline, 1966: U668–U669 [*pro parte*]
Protocaudinidae Deflandre-Rigaud—Mostler 1970: 351 [*pro parte*]
Palaeocaudinidae fam. n. Boczarowski, 1997: 336 [*nomen nudum*]
Palaeocaudinidae fam. n. Boczarowski, 1999: 73 [*nomen nudum*]
Palaeocaudinidae fam. n. Boczarowski, 2001: 150

Included genera. *Laetmogone* Théel, 1879 [syn. *Bathygone* Pawson, 1965a; *Cryodora* Théel, 1879; p.p. *Ilyodaemon* Théel, 1879*; Laetmenoecus* Clark, 1913]; *Pannychia* Théel, 1882 [syn. *Laetmophasma* Ludwig, 1894]; *Apodogaster* Walsh, 1891; *Benthogone* Kœhler, 1895 [syn. *Benthophyces* Kœhler & Vaney, 1905; p.p. *Ilyodaemon* Théel, 1879]; *Psychronaetes* Pawson, 1983; *Palaeocaudina* Boczarowski, 1997 [fossil]; *Gebrukothuria* Rogacheva & Cross, 2009 in Rogacheva *et al.* 2009.

Remarks. Rogacheva *et al.* (2009: 480) recently amended the diagnosis of the family Laetmogo-

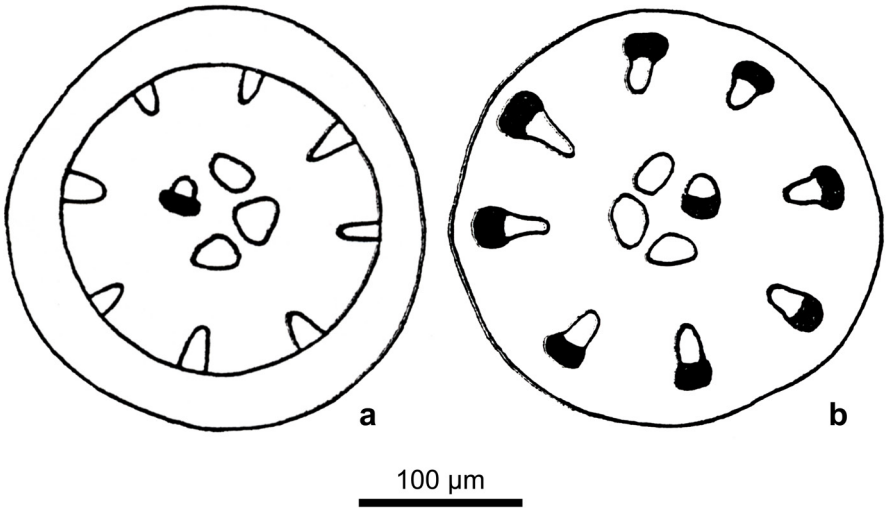


FIGURE 4. Holotype of *Palaeocaudina acmaea* (Matyja, 1972) from the Late Jurassic (Oxfordian) of central Poland (Tokarnia near Kielce, Holy Cross Mountains). a: upper side; b: lower side. Reproduced from Matyja (1972: Text-fig. 12a-b; modified) with permission of the publisher.

nidae Ekman, 1926 to accommodate the new genus *Gebrukothuria* Rogacheva & Cross in Rogacheva *et al.* 2009. But this new definition has not turned out well due to the fact that the new diagnosis does not contain all described species any more. This concerns the modern *Laetmogone interjacens* (Sluiter, 1901) and *L. perplexa* Thandar, 1998, for example. Both species have a lateral brim (cf. Thandar 1998: table 3) contrary to the new diagnosis given by Rogacheva *et al.* (2009: 480; "…never fused into a brim…"). Furthermore I doubt that the "Calcareous ring is reduced or not calcified." (Rogacheva *et al.* 2009: 480) in the entire family (see Fig. 2). The latter is possibly a conservational or maceration artefact: *Gebrukothuria profundus* was even erected on a single specimen only and does not have a calcareous ring.

In the opinion of the author, the diagnostic laetmogonid wheels (cf. also Smirnov 2012: 814) are a distinctive synapomorphy of the family, which are, unfortunately, not present in *Gebrukothuria*.

In 1997, Boczarowski erected the new fossil family Palaeocaudinidae without any diagnosis, publishing a corresponding diagnosis only a few years later (Boczarowski 2001: 150). However, this family (parafamily) represents a younger synonym of the Laetmogonidae.

Besides the listed fossil *Palaeocaudina*, which is more related to the extant *Laetmogone* and *Benthogone*, Thuy *et al.* (2012: Fig. 2O) figured recently a new laetmogonid wheel-type (currently under description by the author), which represents probably the forerunner of the disctinct modern laetmogonid genus *Pannychia*.

Genus *Palaeocaudina* Boczarowski, 1997

Type species. *Protocaudina hexagonaria* Martin, 1952 *emend.* Gutschick & Canis, 1971

Palaeocaudina gen. n. Boczarowski, 1997: 336
Palaeocaudina gen. n. Boczarowski, 1999: 73
Palaeocaudina Boczarowski, 1997—Boczarowski 2001: 150–151

Diagnosis. "Sclerites with the central pore cross have contained four pores, none and marginal girdle have had no indentation on the edge." [Boczarowski 1997: 336].

Remarks. This genus has to be revised due to several reasons: (1) the diagnosis given by Boczarowski (1997) covers also a large part of wheels of modern laetmogonids; (2) the proposed type species *Protocaudina hexagonaria* Martin, 1952 *emend.* Gutschick & Canis, 1971 as well as other Palaeozoic members are not clear laetmogonids and were included by some authors within *Praecaudina* Mostler, 1970 *emend.* Gaździcki *et al.* 1978. *Praecaudina* Mostler, 1970 on the other hand, originally established for concavo-convex sclerites with hexagonal to octagonal outline, 4 central perforations, 1–2 marginal rows of perforations and a dentate rim, is dubious momentarily: Mostler (1970) published a drawing only and stated very clearly on the always dentated rim of *Praecaudina*, whereas Gaździcki *et al.* 1978 emending this genus, not mentioning this feature any more. All later figured and established species of *Praecaudina* show non-dentated rim.

In sum, we need a modern overview on laetmogonid wheel-like ossicles using SEM studies to establish a detailed catalogue of characteristics, also applicable in fossil elasipodid wheel-ossicles.

Included species. *Protocaudina acmaea* Matyja, 1972; *Protocaudina dorsetensis* Soodan & Whatley, 1988; *Protocaudina herrigi* Reich, 1995; *Palaeocaudina rugia* n. sp.; *Protocaudina* sp. *sensu* Singh *et al.* 1981; *Protocaudina* sp. 1 *sensu* Sztejn 1993.

Palaeocaudina acmaea (Matyja, 1972)

Figures 4, 19(6)

Protocaudina acmaea Matyja, 1972: 243–244, Fig. 12
Protocaudina acmaea Matyja—Mostler 1972: 9
Palaeocaudina acmaea (Matyja, 1972)—Boczarowski 1997: 336; Boczarowski 1999: 73
Protocaudina n. sp. Fenninger & Holzer, 1971: Pl. 2 (Fig. 10) [*?*]
P. n. sp. Fenninger & Holzer—Mostler 1972: 9 [*?*]

Type locality, horizon and age. Tokarnia village, 18 km SW of Kielce, central Poland; Late Jurassic, Middle Oxfordian, *Gregoryceras transversarium* ammonite Zone. [Matyja 1972: 243; modified]

Diagnosis. "Wheel-shaped scrlerite [*sic!*] with quadruplicate perforation in the centre. Central plate, perforated in this way, is connected to the rim by 8 wide, lanceolate spokes. Both edges of lower margins of every spoke roll-like thickened." [from Matyja 1972: 243]

Discussion. *P. acmaea* differs from all other known *Palaeocaudina* species in possessing very wide short spokes in connection with a large central portion. There are no known modern relatives with these characteristics.

Occurrence. Known from the late Middle Oxfordian of Poland; with additional, questionable material from the Kimmeridgian of Austria.

Palaeocaudina dorsetensis (Soodan & Whatley, 1988)

Figures 5, 19(7–8)

Protocaudina dorsetensis n. sp. Soodan & Whatley, 1988: 120, Pl. 2 (Fig. 1)
Protocaudina triperforata Schallreuter, 1968—Soodan & Whatley 1988: 120, Pl. 2 (Fig. 2)

Type locality, horizon and age. Crook Hill, Dorset, U.K.; Late Jurassic Oxford clay (Callovian). [Soodan & Whatley 1988: 120; modified]

Diagnosis. Not given by Soodan & Whatley (1988), only a description: "Sclerites in the form of a medium size disc, oval in shape, smooth periphery; eight very short spokes; interspoke area oval, large, elongated, parallel to the margin of the rim; central area with 4 central perforations, central

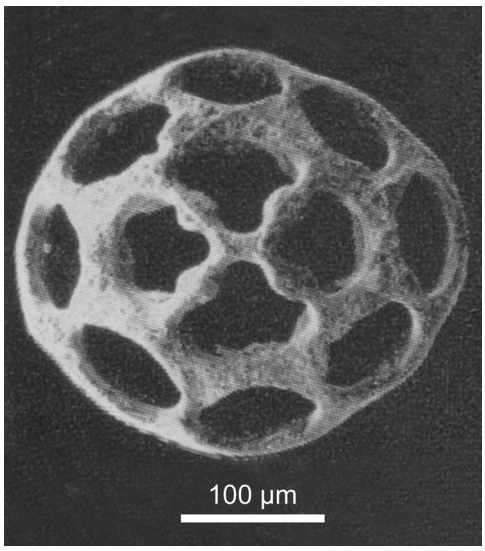


FIGURE 5. Holotype of *Palaeocaudina dorsetensis* (Soodan & Whatley, 1988) from the Middle Jurassic (Callovian) of South West England (Crook Hill, Dorset); lower side. Reproduced from Soodan & Whatley (1988: Pl. 2, Fig. 1; modified).

perforations equally spaced; central cross with rays having enlarged middle part; rim inclined to the plane of the disc; curved upwards and inwards. Diameter varies from .27 mm to .30 mm." [from Soodan & Whatley 1988: 120]

Discussion. *P. dorsetensis* differs from all other known *Palaeocaudina* species in possessing a distinct concavo-convex shape and a prominent primary cross. This fossil species is probably more closely related to the modern *Benthogone* or *Psychronaetes* (cf. Pawson 1965b, 1983; Hansen 1975) than to *Laetmogone*.

Occurrence. Known from the Callovian Oxford Clay of Dorset, England as well as from the early Oxfordian of Normandy, France (pers. observ.).

Palaeocaudina herrigi (Reich, 1995)

Figures 6, 19(10)

Protocaudina herrigi n. parasp. Reich, 1995: 683–685, Text-figs. 1–4 [*vidimus*]
Palaeocaudina herrigi (Reich, 1995)—Boczarowski 1997: 337; Boczarowski 1999: 73; Reich & Jagt 2001: Text-fig. 1 [*vidimus*]

Material. Holotype GZG.INV.91202 (formerly FGWG 109/1); Paratypes GZG.INV.91203, 91204, 91205 (formerly FGWG 109/2) (all from the type locality and horizon); GZG.INV.91200 (formerly FGWG 270/1), 91201 (ENCI quarry Maastricht, The Netherlands; upper Lower Maastrichtian).

Type locality, horizon and age. Zarrenthin near Jarmen, Western Pomerania, Germany; Geschiebe (glacial erratic boulder) that origined from the southern Baltic Sea; Late Cretaceous, upper Upper Maastrichtian. [Reich 1995: 683; modified]

Diagnosis. "Eine Art der Paragattung *Protocaudina* mit subzirkularem bis annähernd oktogonalem Umriß, leicht gewölbter Nabe und sich nach oben biegenden Speichen, acht kurzen, breiten Speichen, die sich zur Felge hin verjüngen, subtriangulären Speichenzwischenräumen, sowie einer annähernd x-förmigen Stütze (Primärkreuz sensu EKMAN 1926) im zentral perforierten Bereich der Nabe." [from Reich 1995: 684]

Translation (herein): "A species of the paragenus *Protocaudina* with subcircular to nearly octogonal outline, sligthly concave hub and spokes curving upward, eight short and wide spokes, that are narrower at the rim, subtriangular interspoke areas as well as a roughly x-shaped support (primary

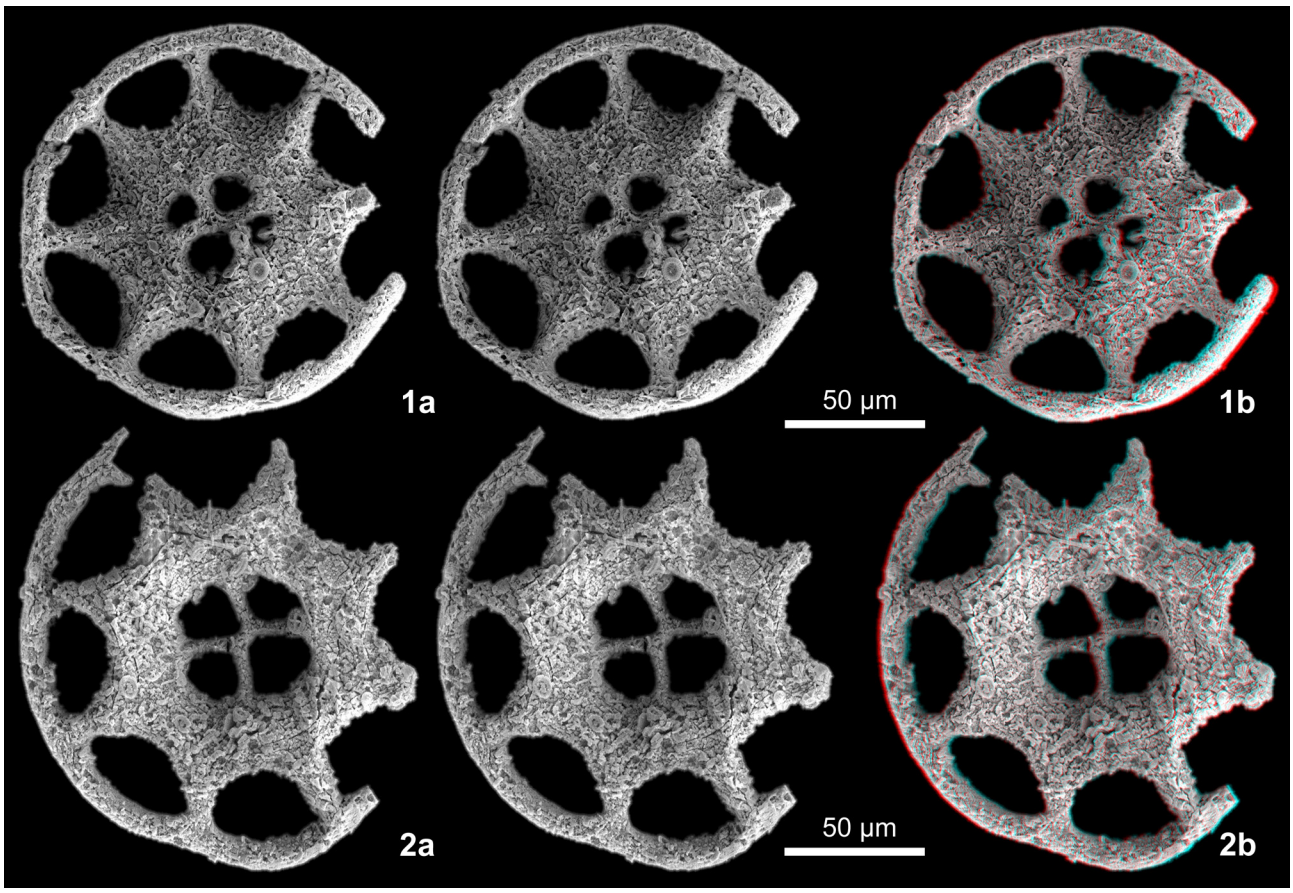


FIGURE 6. *Palaeocaudina herrigi* (Reich, 1995). 1: upper side (GZG.INV.91200); 1a: stereoscopic images; 1b: anaglyph image; 2: lower side (GZG.INV.91201); 2a: stereoscopic images; 2b: anaglyph image. Both specimens from the Vijlen Member of the Gulpen Fm. (upper Lower Maastrichtian), ENCI quarry Maastricht, The Netherlands (coll. M. Reich).

cross *sensu* Ekman 1926) in the centrally perforated area of the hub."

Discussion. Boczarowski (1997: 337) assigned this species to his new genus *Palaeocaudina*. New material of *P. herrigi* from partly silicified limestones from the Vijlen Member (Gulpen Formation) of Maastricht are even better preserved than the type material from the Baltic Sea bottom. Note the well-preserved primary cross, which rises gradually in the direction of the upper side. *P. herrigi* is more closely related to the modern *Laetmogone*, than to other Recent genera.

Occurrence. So far known only from the Early Maastrichtian chalk the Netherlands, and the Late Maastrichtian of the Baltic Sea area.

***Palaeocaudina rugia* n. sp.**

Figures 7, 19(9)

Protocaudina n. parasp. 1 Reich, 1997a: Pl. 15 (Fig. 14) [*vidimus*]
Protocaudina parasp. nov. a Reich, 1997b: 90–91, Fig. 60, Pl. 5 (Fig. 4) [*vidimus*]
"*Protocaudina*" parasp. nov. a Reich & Frenzel, 2002: 197; Reich *et al.* 2004: 501
"*Protocaudina*" parasp. nov. A Reich, 2001a: Pl. 1 (Fig. 11) [*vidimus*]

Etymology. After *Rugii*, the East Germanic tribe which lived at the southern shore of the Baltic Sea in the first century, and *Rugia*, Latin for the Isle of Rügen.

Material. Holotype GZG.INV.91206; Paratype GZG.INV.91207 (both from the type locality and horizon); GZG.INV.91208 (formerly FGWG 126/14) (geschiebe DAG 2013 from Ladebow near

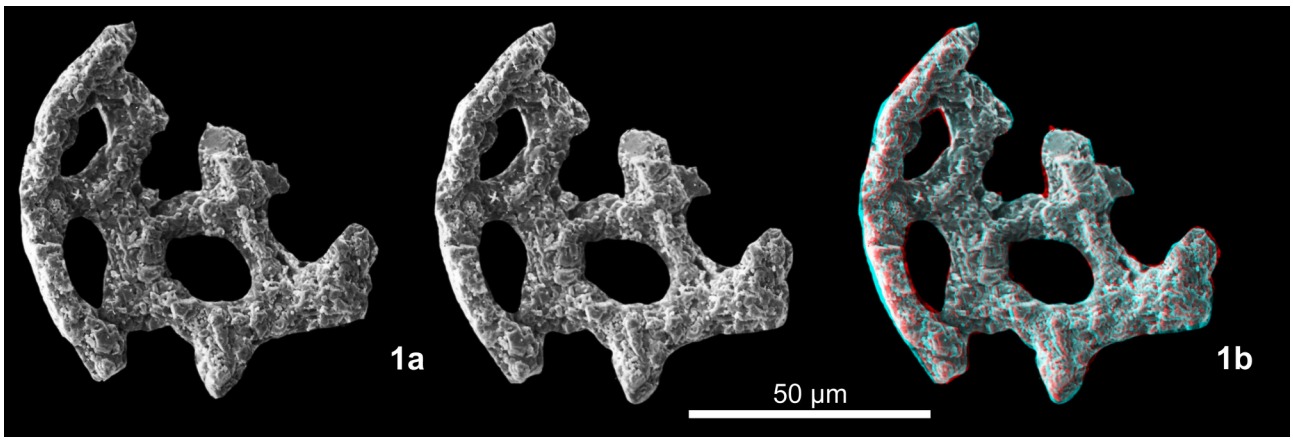


FIGURE 7. *Palaeocaudina rugia* n. sp. 1a: upper side (GZG.INV.91206), stereoscopic images; 1b: anaglyph image. From the Rügen Member of the Hemmoor Fm. at standard section, north of Sassnitz, Peninsula Jasmund, Isle of Rügen, Pomerania, Germany, complex/sample VIII/04 (upper Lower Maastrichtian; *Belemnella fastigata* belemnite Zone).

Greifswald, Pomerania; upper Upper Maastrichtian, cf. Reich 2003b: 367).

Type locality. Standard section of the 'Rügen chalk' north of Sassnitz, Peninsula Jasmund, Isle of Rügen, Pomerania, Germany.

Type horizon and age. Cretaceous: upper Lower Maastrichtian (*Belemnella fastigata* belemnite Zone).

Diagnosis. A laetmogonid species with *Palaeocaudina*-type wheels, roughly circular in outline, with a large central primary cross, and a narrow connecting central portion. Primary perforations prominent, suboval to subtriangular, always larger than the strongly suboval to oval marginal perforations. 8 very short spokes. Rim inclined relative to the plane of the central portion. Struts of the primary cross, spokes and rim of equal thickness.

Description. These laetmogonid wheels, roughly circular in outline, with a diameter of ~140 µm, bear a very prominent large central primary cross. The connecting central portion between the primary cross and the spokes is very small. As diagnostic for *Palaeocaudina*, there is no dentation along the primary and marginal perforations. Primary perforations suboval to subtriangular, and always larger than the smaller marginal perforations. With 8 very short spokes, connecting the small central portion and the rim, rim slightly inclined. All spokes and struts as well as the rim are of equal thickness.

Discussion. *P. rugia* differs from other Cretaceous laetmogonids, like *P. herrigi*, in possessing a prominent large primary cross and a much smaller central portion. It is probably more closely related to the modern *Benthogone* than to other modern genera, concerning the shape of the central portion.

Occurrence. So far known only from the Early Maastrichtian chalk of Rügen, Germany, and the Late Maastrichtian of the Baltic Sea area.

***Palaeocaudina* sp. 1**

Figure 8

Protocaudina sp. Singh *et al.* 1981: Fig. 2

Discussion. The specimen of Singh *et al.* (1981: Fig. 2) is too poorly figured to add to our knowledge of this genus without investigation of the original material.

Occurrence. So far only known from the Upper Bathonian of Rajasthan, India.

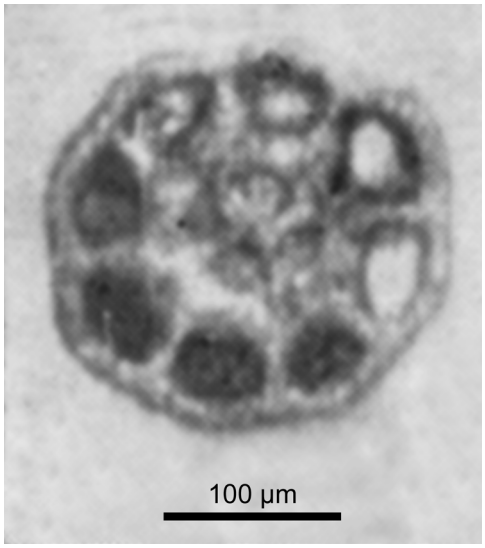


FIGURE 8. *Palaeocaudina* sp. 1 [= *Protocaudina* sp. of Singh *et al.* 1981] from the Middle Jurassic Jaisalmer Formation (Jaisalmer Member, Upper Bathonian) of Rajasthan, Northwest India. Reprinted with the permission of the Indian Academy of Sciences, Bangalore, from Singh *et al.* (1981: Fig. 2, modified).

Palaeocaudina sp. 2

Figure 9

Protocaudina sp. 1 Sztejn 1993: 125, Pl. 3 (Fig. 4)

Discussion. The specimens recorded by Sztejn (1993) unfortunately are too poorly preserved and filled with sediment to be identify in a satisfactory manner.

Occurrence. So far only known from the Early Kimmeridgian of Poland.

Family Palaeolaetmogonidae n. fam.

Type genus. *Palaeolaetmogone* n. gen.

Protocaudinidae Deflandre-Rigaud—Mostler 1970: 351 [*pro parte*]
Staurocaudininae subfam. n. Boczarowski, 1997: 334 [*pro parte*]
Staurocaudininae subfam. n. Boczarowski, 1999: 73 [*pro parte*]
Staurocaudininae subfam. n. Boczarowski, 2001: 130–131 [*pro parte*]

Diagnosis. Elasipodid sea cucumbers with distinctive concavo-convex wheels bearing a typical central primary cross (covered or not covered by a calcareous membrane), with marginal perforations (upper side) and/or at primary perforations possessing denticulated margins.

Included genera. *Palaeolaetmogone* n. gen.; *Priscolaetmogone* n. gen.; "*Neomicroantyx* Mostler in Krainer, Mostler & Haditsch, 1994".

Remarks. Boczarowski (1997: 334) originally erected a new subfamily (Staurocaudininae) within the Cucumariidae Ludwig, 1894 *emend.* Pawson & Fell, 1965 (Dendrochirotida) for some new Devonian material (*Staurocaudina*), as well as some Mesozoic holothurian species, like *Protocaudina mortenseni* Deflandre-Rigaud, 1946 and *P. khadirensis* Soodan, 1977. He considered *Staurocaudina* to be related to the modern *Staurocucumis* Ekman, 1927, because both possess denticulated primary and marginal perforations in their ossicles.

However, only the type species of *Staurocaudina* (*S. canina*) has entire marginal perforations with fine toothlets, probably similar to those found in the modern *Staurocucumis liouvillei* (cf. Ekman 1925; Hansen 1988; Massin 1994). All Mesozoic '*Protocaudina*' species included by Boczarowski in

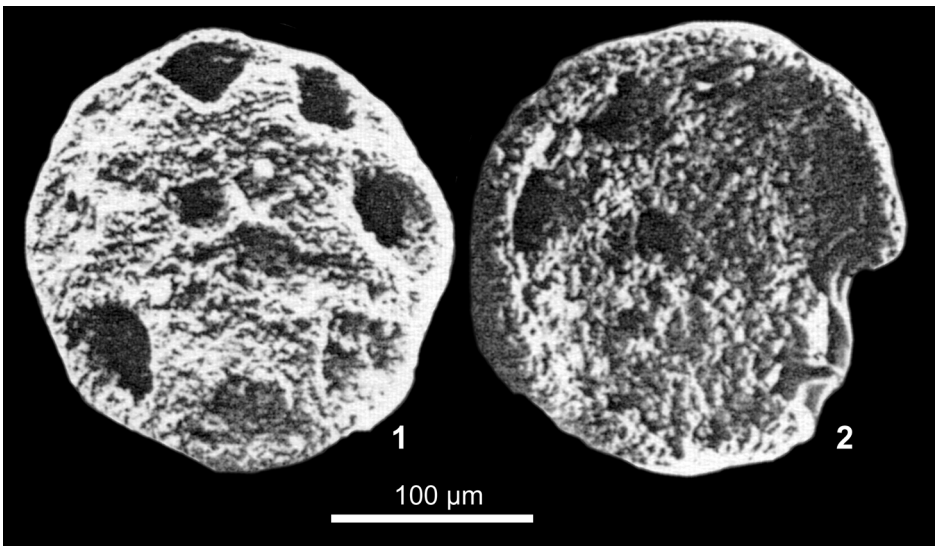


FIGURE 9. *Palaeocaudina* sp. 2 [= *Protocaudina* sp. 1 of Sztejn 1993] from the Late Jurassic (Kimmeridgian) of central Poland (Łódź trough, Bełchatów PD-2B borehole). 1: lower side; 2: upper side. Reproduced from Sztejn (1993: Pl. 3, Figs. 4a, 4c; modified) with permission of the publisher (Polish Academy of Sciences, Warsaw).

the Staurocaudininae are definitively members of the Elasipodida and related to the Laetmogonidae, probably to stem group laetmogonids.

In my opinion there are two diagnostic characters of stem group laetmogonids: (1) toothlets at the periphery of the marginal and/or primary perforations, and (2) complete covering of the nave/primary cross by a calcareous membrane. Both characteristics can also be found in Palaeozoic laetmogonid relatives, including species of '*Protocaudina*' and '*Microantyx*' are known.

A revision of all Palaeozoic '*Protocaudina*' and '*Microantyx*' species is urgently needed using SEM studies, because their relationships have become confused. Boczarowski (1997) transferred most of these species ('stem group laetmogonids', herein) to the Rotasacciidae Haude & Langenstrassen, 1976, a family of the Palaeozoic Ophiocistioidea (see Reich & Haude 2004, Reich 2010) without clear evidence. Boczarowski hereby definitively missed Early Jurassic records (Krainer *et al.* 1994; Krainer & Mostler 1997) of 'his ophiocistioid wheels' (*e.g.*, '*Microantyx*'; Boczarowski 1997, 1999), whereas undisputed ophiocistioids are known from the Palaeozoic only (Reich 2007, 2010).

Genus *Palaeolaetmogone* n. gen.

Type species. *Protocaudina mortenseni* Deflandre-Rigaud, 1946

Unnamed genus "Protocaudina" Frizzell & Exline, 1966: U668

Etymology. After Greek παλαιός (= ancient) and the modern holothurian genus *Laetmogone*.

Diagnosis. Elasipodid sea cucumbers with distinctive concavo-convex wheels bearing a typical central primary cross, not covered by a calcareous membrane, and with peripherally-denticulated marginal (or rarely) primary perforations.

Included species. *Protocaudina mortenseni* Deflandre-Rigaud, 1946; *Protocaudina khadirensis* Soodan, 1977 [syn. *Protocaudina elliptica* Soodan, 1977]; *Palaeolaetmogone frankwiesei* n. gen. et n. sp.; *Protocaudina rigaudae* Mostler, 1970.

Occurrence. Upper Triassic (Carnian) to Late Cretaceous (Turonian) of Europe and India.

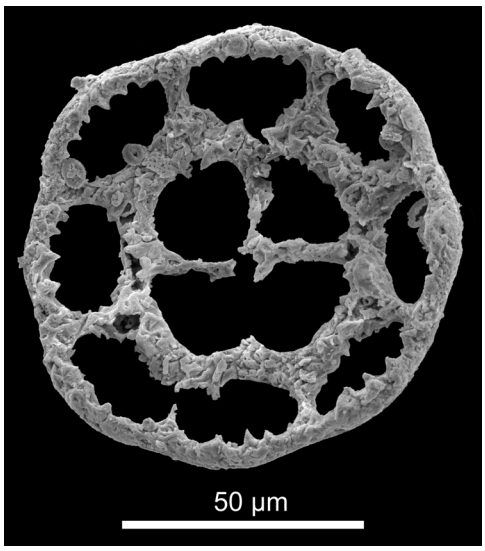


FIGURE 10. *Palaeolaetmogone frankwiesei* n. gen. et n. sp. (GZG. INV.91211), upper side. From Kępa, Isle of Wolin, NW Poland (Upper Turonian; *Subprionocyclus neptuni* ammonite Zone).

***Palaeolaetmogone frankwiesei* n. gen. et n. sp.**
Figures 10, 19(4)

Etymology. Named after friend and colleague Dr. Frank Wiese (Göttingen), in recognition of his numerous contributions to Turonian stratigraphy and palaeontology.

Material. Holotype GZG.INV.91211, Paratype GZG.INV.91212.

Type locality. Kępa, Isle of Wolin, Województwo zachodniopomorskie, Poland.

Type horizon and age. Cretaceous: Upper Turonian (*Subprionocyclus neptuni* ammonite Zone).

Diagnosis. A species of *Palaeolaetmogone* with wheels circular in outline and a prominent primary cross with large primary perforations. Primary cross plane not curved upward or inward. 8 short spokes connect the central portion with the rim. All marginal perforations are denticulated at their periphery with medium-sized toothlets.

Description. These small (~80 µm) palaeolaetmogonid wheels are circular in outline and slightly concave. The central portion with a prominent primary cross and large somewhat triangular primary perforations covers around 50% of the wheel diameter. The primary cross lies in a plane, and has fragile, thin struts, that do not curve upward or inward. 8 short spokes connect the central portion with the rim. All marginal perforations, equal in size, with 5–6 medium-sized toothlets at the periphery.

Discussion. *P. frankwiesei* differs from other palaeolaetmogonid species, like *P. mortenseni*, in possessing a prominent large plane primary cross, covering around 50% of the whole wheel. There are no similar modern representatives.

Occurrence. Known only from the Late Turonian of northwestern Poland.

***Palaeolaetmogone khadirensis* (Soodan, 1977)**
Figure 11

Protocaudina khadirensis Soodan, 1977: 181–182, Pl. 1 (Figs. 1–2)
Protocaudina elliptica Soodan, 1977: 181, Pl. 1 (Figs. 3–4)
Staurocaudina khadirensis (Soodan, 1977)—Boczarowski 1997: 335; Boczarowski 1999: 73

Type locality, horizon and age. Khadir Island, Kutch, India; Middle Jurassic, lower part of the

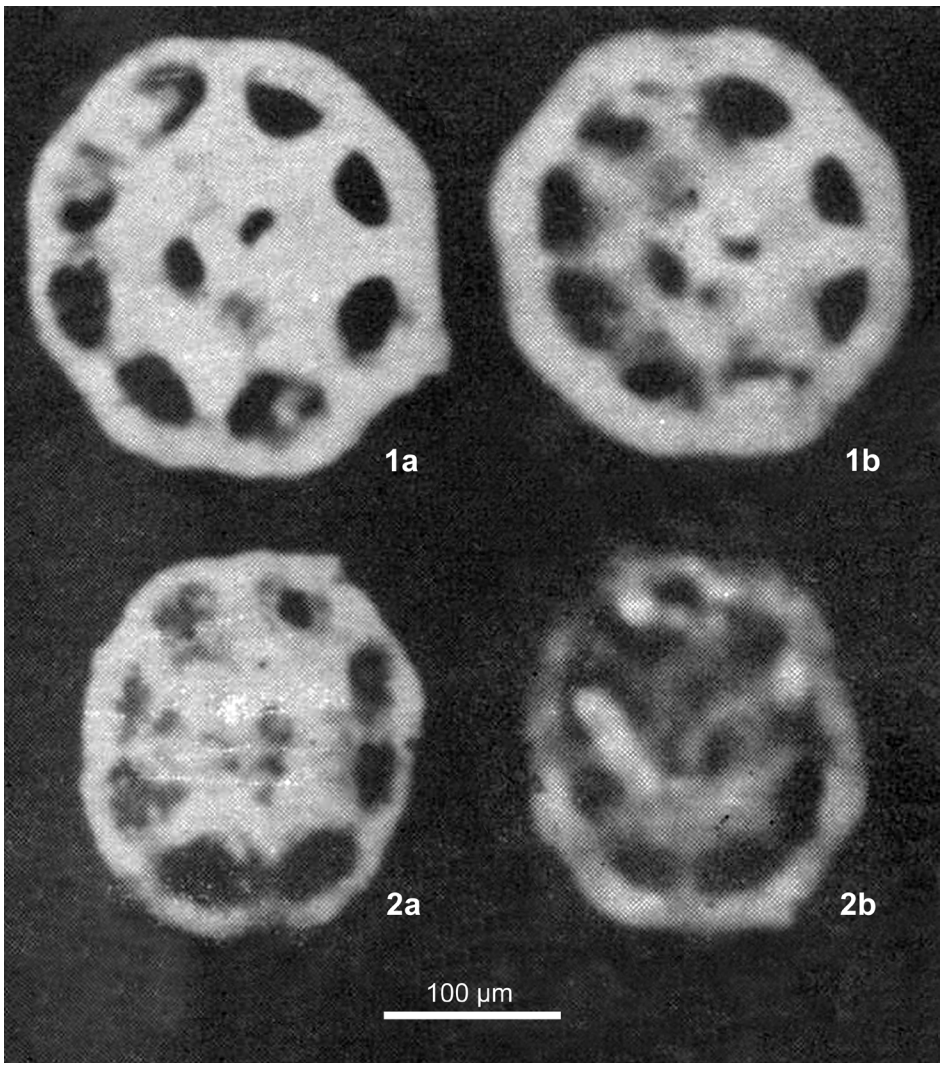


FIGURE 11. *Palaeolaetmogone khadirensis* (Soodan, 1977) from the Middle Jurassic Khadir Formation (lower part, ?Callovian) of Kutch, India. 1a: lower side; 1b: upper side (holotype, originally described as *Protocaudina khadirensis*); 2a: lower side; 2b: upper side (originally described as *Protocaudina elliptica*). Reproduced from Soodan (1977: Pl. 1, Figs. 1–2; modified) with permission of the publisher (The Palaeobotanical Society, Lucknow).

Khadir Formation, ?Callovian. [Soodan 1977: 181; modified]

Diagnosis. "Sclerite in the form of medium-sized concavo-convex wheel; periphery scalloped, scallops opposite the interspoke-space ; eight spokes, short, broad near the centre, thinner towards the periphery ; interspoke-space almost triangular with outer margins arched along the scallops ; rim inclined to the plane of wheel, curved upwards and inwards, inner margin finely dentate ; central part of the sclerite large with four perforations, two large and nearer than the smaller which are widely spaced, diameter 0.25 mm." [from Soodan 1977: 181]

Discussion. The two species, described by Soodan in 1977 from the same locality and stratum, are clearly synonymous. Soodan did not consider the interspecific variability; *Protocaudina elliptica* Soodan, 1977 differs from *Protocaudina khadirensis* Soodan, 1977 only slightly by a more elliptical outline. The figures published by Soodan (1977) are too poor to make any further comparison.

Occurrence. So far only known from the Middle Jurassic (?Callovian) of Kutch, India.

***Palaeolaetmogone mortenseni* (Deflandre-Rigaud, 1946)**

Figures 12, 19(3)

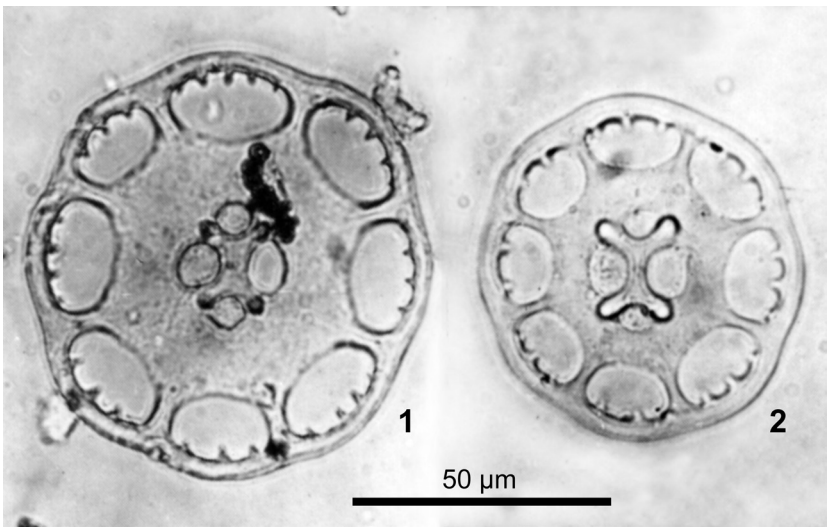


FIGURE 12. *Palaeolaetmogone mortenseni* (Deflandre-Rigaud, 1946) from the Late Jurassic "Marnes de Villers" (Early Oxfordian; *Quenstedtoceras mariae* ammonite Zone) of Normandy (Villers-sur-Mer), northwestern France. 1: lower side (holotype); 2: lower side (paratype). Reproduced from the unpublished PhD thesis (1961) of Marthe Deflandre-Rigaud (MNHN).

Protocaudina Mortenseni n. sp. Deflandre-Rigaud, 1946: Text-fig. 1–2 [*vidimus*]
Protocaudina mortenseni Deflandre-Rigaud, 1946—Deflandre-Rigaud 1952: 6
Protocaudina mortenseni Deflandre-Rigaud, 1946—Lipiec 1992: 442, Pl. 2 (Figs. 3–4) [*?*]
Protocaudina mortenseni Defl.-Rig.—Deflandre-Rigaud 1953: Text-fig. 14 [*vidimus*]
Protocaudina mortenseni Deflandre-Rigaud—Sieverts-Doreck 1958: Pl. 6 (Fig. 6); Deflandre-Rigaud 1961: 105–106, Text-figs. 148–149, Pl. 3 (Figs. 1–2) [*nom. nud.*, *vidimus*]; Deflandre-Rigaud 1962: 98, Text-figs. 148–149, Pl. 3 (Figs. 1–2); Frizzell & Exline 1956: 138, Pl. 8 (Figs. 13–14) [all *vidimus*]
Protocaudina mortenseni—Frizzell & Exline 1958: 1 card
"*P.*" *mortenseni* Deflandre-Rigaud—Frizzell & Exline 1966: U668; Mostler 1972: 9
P. mortenseni—Soodan 1972: 225 [*?*]
Protocaudina paucispinosa cent. nov. vel parasp. nov. Deflandre-Rigaud, 1961: 106, Text-fig. 145, Pl. 3 (Fig. 3) [*nom. nud.*, *vidimus*]
Protocaudina paucispinosa cent. nov. vel parasp. nov. Deflandre-Rigaud, 1962: 98, Text-fig. 145, Pl. 3 (Fig. 3) [*vidimus*]
"*P.*" *paucispinosa* Deflandre-Rigaud, 1961—Frizzell & Exline 1966: U668; Mostler 1972: 9
"*Protocaudina*"—Frizzell & Exline 1966: Text-fig. 527 (1d) [*vidimus*]
Staurocaudina mortenseni (Deflandre-Rigaud, 1946)—Boczarowski 1997: 335
Staurocaudina mortenseni (Deflandre and Rigaud, 1946) [*sic!*]—Boczarowski 1999: 73

Type locality, horizon and age. Villers-sur-Mer, Normandy, France; Late Jurassic "Marnes de Villers", Oxfordian. [Deflandre-Rigaud 1961: 105; 1962: 98; modified]

Diagnosis. "Sclérite disciforme à contour subcirculaire ou un peu elliptique légèrement festonné; huit perforations marginales, elliptiques allongées à bord externe aplati, parallèle au contour du sclérite, et pourvu de quelques courtes dents (deux à cinq); croisillon en X allongé, nettement bombé et en étrier, situé au centre d'une aire médiane assez grande, et determinant quatre perforations subégales deux à deux." [Deflandre-Rigaud 1961: 105; 1962: 98]

Translation (herein): "Discus-shaped sclerites with subcircular outline or slightly elliptical arched; eight short dentate marginal perforations, elliptical in outline, with flattened rim, parallel to the contour of the sclerite; in the centre a stirrup-like X-shaped structure with four roughly equal perforations, arranged in pairs."

Description [from Frizzell & Exline 1956: 138]: "Sclerite in form of a very small wheel; rim inclined to plane of wheel, coarsely dentate; periphery slightly scalloped; with 8 very short and narrow spokes; interspoke spaces low and wide, inner margins arched, outer margins nearly straight;

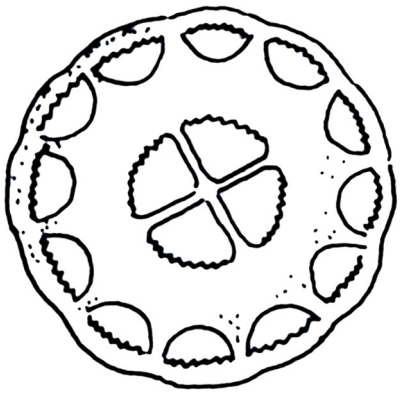


FIGURE 13. Holotype (lower side) of *Palaeolaetmogone rigaudae* (Mostler, 1970) from the Upper Triassic (Carnian) of the Salzkammergut (Raschberg), Austria. Reprinted from Mostler (1977: Text-fig. 5: 21) with the permission of the Naturwissenschaftlich-Medizinischer Verein in Innsbruck. The exact size is not known and was not indicated in Mostler (1970, 1977) either.

teeth restricted to interspoke perforations, from 2 to 5 above each perforation; central perforations in 2 unequal pairs, larger perforations contiguous and separating smaller perforations; diameter, about 0.07 to 0.09 mm."

Discussion. *P. mortenseni* and *P. paucispinosa*, both described by Marthe Deflandre-Rigaud from the same locality and stratum, are clearly synonymous (pers. observ. on the type material). Unfortunately, Deflandre-Rigaud did not consider interspecific variability. There are no similar modern representatives: Wheel ossicles of modern *Pannychia* are have similar inward teeth at the rim (Solís-Marín *et al.* 2009: Pl. 47C), but these are much larger than in *P. mortenseni* and in *Pannychia* the number of these teeth always corresponds to the number of marginal perforations.

Occurrence. So far only known from the Upper Jurassic (Oxfordian) of Normandy, France and questionably from the Callovian/?Lower Oxfordian of the Polish Tatra Mts.

Palaeolaetmogone rigaudae (Mostler, 1970)

Figures 13, 19(1)

Protocaudina rigaudae n. sp. Mostler, 1970: 352, Pl. 3 (Figs. 5–6)
Protocaudina rigaudae Mostler—Kozur & Mock 1972: Pl. 4 (Fig. 8); Kozur & Mock 1974: Pl. 2 (Fig. 23); Mostler 1977: Text-fig. 5 (Figs. 21–22)
Protocaudina rigaudae Mostler—Kozur & Mock 1972: Pl. 4 (Figs. 9–10); Kozur & Mock 1974: Pl. 2 (Fig. 22) [both *non*]
Protocaudina cf. *rigaudae* Mostler, 1971—Jamnik & Ramovš 1993: 30, Pl. 3 (Fig. 2)
Staurocaudina rigaudae (Mostler, 1970)—Boczarowski 1997: 335–336; Boczarowski 1999: 73

Type locality, horizon and age. Raschberg, Salzkammergut, Austria; Late Triassic, Carnian. [Mostler 1970: 352; modified]

Diagnosis. "Eine Art der Gattung *Protocaudina* CRONEIS 1932 mit folgenden Besonderheiten: Im Zentralfeld 4 gleich große oben bezahnte Poren, die durch sehr schmale Nabenspeichen voneinander getrennt sind. Von der breiten, gewölbten Nabenfelge biegen 10–12 kurze, im Querschnitt runde Speichen steil zur Felge hinauf." [Mostler 1970: 352]

Translation (herein): "A species of the genus *Protocaudina* CRONEIS 1932 with the following characteristics: In the central area 4 spokes equally in size and dentate at the periphery. Wide convex hub with 10–12 short, in cross-section round, spokes curving upward to the rim."

Discussion. *P. rigaudae* differs from other palaeolaetmogonid species in possessing small toothlets at the periphery of the marginal and primary perforations. There are no similar modern representatives bearing a dentate periphery at primary perforations.

Occurrence. So far only known from the Late Triassic (Carnian) of Austria and the Norian of Slovak Republic and the Kamnik-Savinja Alps, Slovenia.

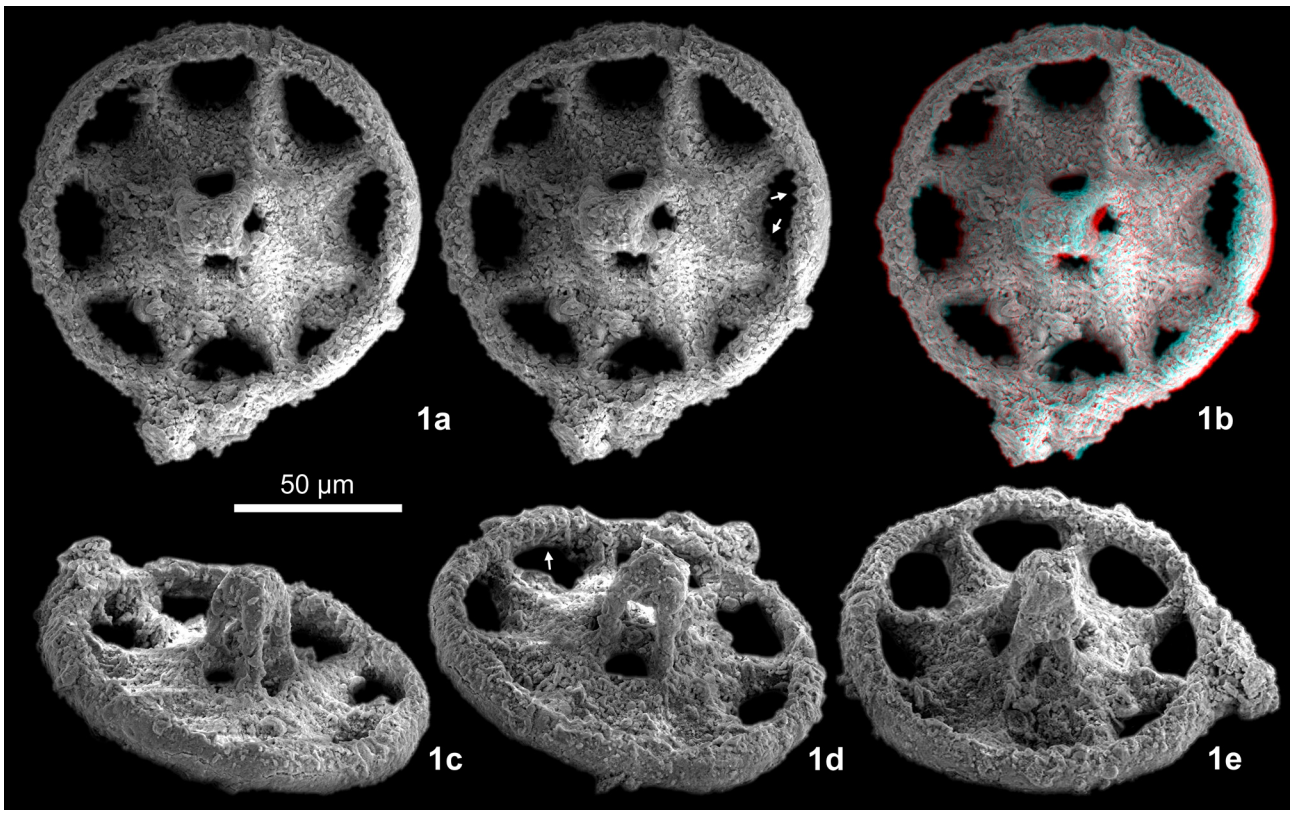


FIGURE 14. *Priscolaetmogone oloughlini* n. gen. et n. sp. (GZG.INV.91210). 1a: upper side, stereoscopic images; 1b: upper side, anaglyph image; 1c–e: upper side, picture series of lateral-oblique view. Please note the small dentation (arrows in 1a and 1d) around the interspoke areas. From Vierow near Greifswald, Pomerania, Germany; geschiebe (glacial erratic boulder) with origin at the southern Baltic Sea bottom (lower Upper Maastrichtian).

Genus *Priscolaetmogone* n. gen.

Type species. *Priscolaetmogone oloughlini* n. gen. et n. sp.

Etymology. After Latin *prisco* (= ancient) and the modern holothurian genus *Laetmogone*.

Diagnosis. Moderately warped concave laetmogonid wheels with a four-pillared top centered over the primary cross of the nave.

Included species. Type species *P. oloughlini* n. gen. et n. sp. (Later Cretaceous, Baltic Sea area) and one undescribed species from the Kimmeridgian of Austria (pers. comm. H. Mostler, 2001).

Occurrence. Late Jurassic (Kimmeridgian) to Late Cretaceous (Maastrichtian) of Europe (Austria and the Baltic Sea area).

Priscolaetmogone oloughlini n. sp.

Figures 14, 19(5)

Etymology. Named after P. Mark O'Loughlin (Melbourne), in recognition of his numerous contributions to holothurian systematics and for supporting my research with comparative modern sea cucumber material.

Material. Holotype GZG.INV.91210, Paratype GZG.INV.91209.

Type locality. Vierow near Greifswald, Pomerania, Germany. Geschiebe (glacial erratic boulder) that origined from the southern Baltic Sea bottom.

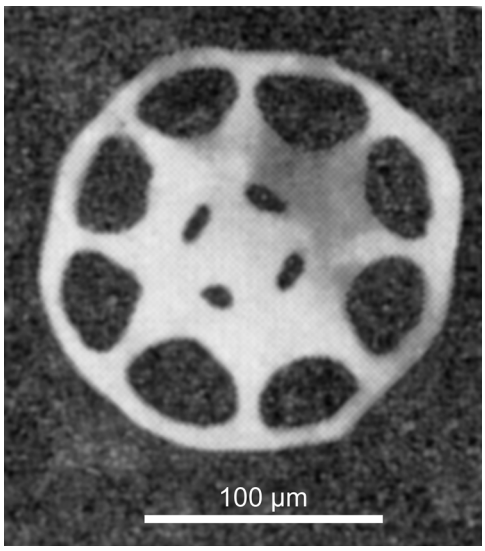


FIGURE 15. *Priscolaetmogone*? n. sp. (upper side; originally figured as "*Priscopedatus* n. sp.") from the Kimmeridgian of the Hubkogel at Bad Ischl, Upper Austria. Reproduced from Fenninger & Holzer (1971: Pl. 2, Fig. 9; modified) with permission of the Naturwissenschaftlicher Verein für Kärnten.

Type horizon and age. Cretaceous: lower Upper Maastrichtian; partly silicified limestone (DAG 1015; cf. Reich 2003b: 366).

Diagnosis. A laetmogonid with wheels of *Priscolaetmogone* n. gen., the latter circular to subcircular in outline. 8 short spokes, connecting the large central portion with the rim. Marginal perforations finely dentate. A small- to medium-sized four-pillard top is centered over a small primary cross of the nave.

Description. These unusual laetmogonid wheels, circular to subcircular in outline, are ~100 µm in diameter and bear a small- to medium-sized four-pillared top over the nave. This top and the primary cross are equal in size and thickness. There are no connecting cross-beams within this top. The central portion of the wheel is large, and 8 short spokes connect this area with a smooth rim. The rim is inclined to the plane of the central portion, but lower than the four-pillared top. All marginal perforations are equal in size and shape: straight on one side, and rounded on the opposite side, all fine dentate.

Discussion. Besides the undescribed Kimmeridgian species of *Priscolaetmogone* n. gen. from Austria [= '*Priscopedatus* sp.' in Fenninger & Holzer 1971: Pl. 2 (Fig. 9)], no other similar fossils are known. Even within the members of the 6 modern laetmogonid genera, there is no species known with comparable wheel ossicles. It seems very likely that this four-pillared top has a functional morphological role, probably penetrating the outer skin and aiding in defence or helping in locomotion.

Occurrence. So far known only from the type locality and horizon.

***Priscolaetmogone*? n. sp.**

Figure 15.

Priscopedatus n. sp. Fenninger & Holzer, 1971: Pl. 2 (Fig. 9)

Discussion. This new species probably represents the oldest record of the genus *Priscolaetmogone*, was first figured by Fenninger & Holzer (1971) and is currently under description (pers. comm. H. Mostler, 2001).

Occurrence. Known only from the Kimmeridgian (Rettenbach limestones: "limestones with *Saccocoma*") of Upper Austria.

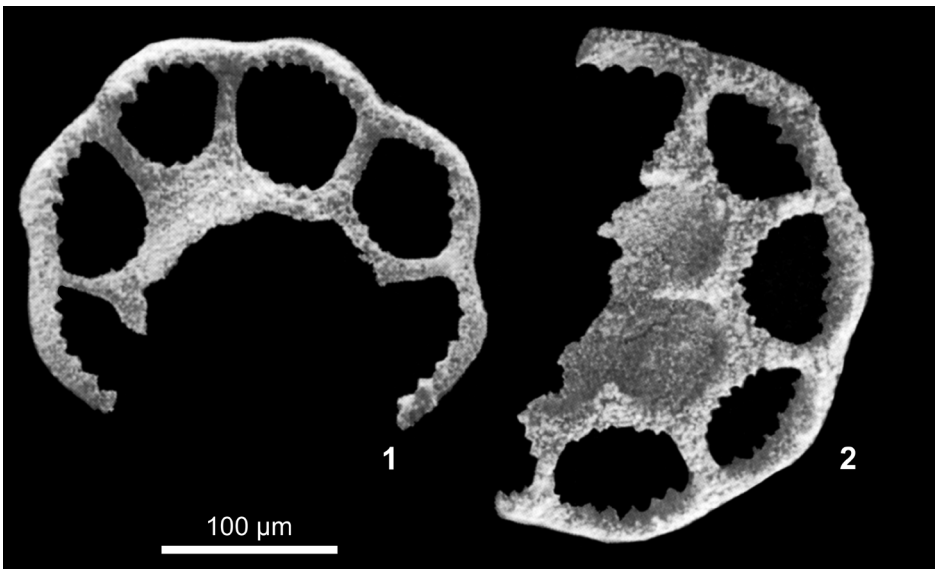


FIGURE 16. "*Neomicroantyx ingridae* Mostler in Krainer, Mostler & Haditsch, 1994" [*nomen nudum*] from the Lower Toarcian of the Northern Calcareous Alps near Lofer (Hochkranz near Weißbach, Salzburg, Austria). 1: upper side; 2: lower side. Reprinted from Krainer *et al.* (1994: Pl. 4, Figs. 11, 15; modified) with the permission of the publisher, the Geological Survey of Austria.

Genus "*Neomicroantyx* Mostler in Krainer, Mostler & Haditsch, 1994" [*nomen nudum*]

Proposed type species. "*Neomicroantyx ingridae* Mostler in Krainer, Mostler & Haditsch, 1994"

Diagnosis. Not given by Mostler in Krainer *et al.* 1994, therefore this name is a *nomen nudum*.

Included species. "*Neomicroantyx ingridae* Mostler in Krainer, Mostler & Haditsch, 1994".

Occurrence. Early Jurassic of Austria and Middle Jurassic of Poland.

"*Neomicroantyx ingridae* Mostler in Krainer, Mostler & Haditsch, 1994" [*nomen nudum*]

Figures 16, 19(2)

Neomicroantyx ingridae Mostler n. gen. n. sp.—Krainer *et al.* 1994: Pl. 4 (Figs. 11–12, 15–16)
Neomicroantyx ingridae Mostler—Krainer & Mostler 1997: Pl. 4 (Fig. 16), Pl. 5 (Fig. 10)
Staurocaudina sp.—Boczarowski 2012: Text-fig. 9 (A1–A2) [*?*]

Proposed type locality, horizon and age. Hochkranz near Weißbach, Salzburg, Austria; Early Jurassic, Lower Toarcian.

Diagnosis. Not given by Mostler in Krainer *et al.* 1994.

Discussion. Since a description and diagnosis of this taxon is still lacking, the species described by Mostler in Krainer *et al.* (1994) remains a *nomen nudum*. However, this new species and new genus shows a typical Palaeozoic '*Microantyx*'-type wheel from early Jurassic sediments, which is quite important due to the fact that several authors (*e.g.*, Kozur & Mostler 1989; Gilliland 1993a; Boczarowski 1997) thought that this ossicle type belongs to the Ophiocistioidea. However, ophiocistioids are definitively known from the Palaeozoic only (Reich & Haude 2004; Reich 2007, 2010), and due to similar morphology with laetmogonid wheels we can assume that '*Microantyx*'-/'*Neomicroantyx*'-type are more likely attributable to the Holothuroidea (Elasipodida). Recently Boczarowski (2012) published a probable juvenile ossicle of this species from the Bathonian of Poland, unfortunately without description, but presenting a picture of the upper side (Boczarowski 2012: Fig. 9A).

"*Neomicroantyx ingridae*" shows distinct characteristics, probably of stem group laetmogonids.

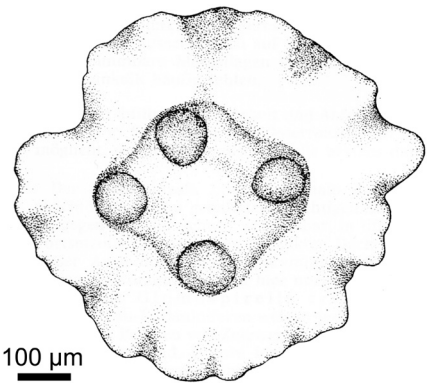


FIGURE 17. Holotype of "*Protocaudina antyx"* Kristan-Tollmann, 1964 from the Late Triassic (Rhaetian) Zlambach marls of Styria (Leislingbach near Bad Aussee), Austria. Reproduced from Kristan-Tollmann (1964: Text-fig. 1, Fig. 5; modified) with permission of the publisher.

There are no similar modern representatives.

Occurrence. So far only known from the Lower Toarcian and Sinemurian/Pliensbachian of Austria, as well from the Upper Bathonian of Poland.

Class Holothuroidea de Blainville, 1834

incerti ordinis et incertae familiae [proposed "laetmogonids"]

"*Protocaudina antyx*" Kristan-Tollmann, 1964 [*nomen dubium*]

Figure 17

Protocaudina antyx Kristan-Tollmann, 1964: Text-fig. 1 (5)

Discussion. "*Protocaudina antyx*" from the Late Triassic of Austria is based on a single incomplete large ossicle (~780 µm), of which the complete rim and all spokes are missing. This specimen unfortunately is too poorly preserved and filled with sediment to determine with certainty the taxonomic identity, therefore I consider this nominal species to be a *nomen dubium*.

Occurrence. Known only from the Rhaetian Zlambach marls of Styria, Austria.

"*Protocaudina latifolia* Mostler, 1972" [*nomen nudum*]

P. latifolia Mostler, 1972: 9

Discussion. "*Protocaudina latifolia*" is probably a manuscript name only. I was not able to track down this name (cf. Reich 2013, in press).

Occurrence. Jurassic, other details unknown.

"*Laetmophasma*" *sensu* Gowda, 1954

Figure 18

Laetmophasma ?—Gowda 1954a: 14
Lætmophasma—Gowda 1954b: 152, Text-fig. 4

Discussion. The specimen figured by Gowda (1954b: Text-fig. 4) is within a thin-section and too poorly preserved to be identified in a satisfactory manner, but it looks more like an chiridotid wheel, rather than an laetmogonid wheel. First listed as "*Laetmophasma*?" in Gowda (1954a), Gowda mentioned two species of *Laetmophasma* in an abstract one year later (1955). Unfortunately, I was not able to find a description of these species.

Occurrence. So far known only from Late Cretaceous of southern India.

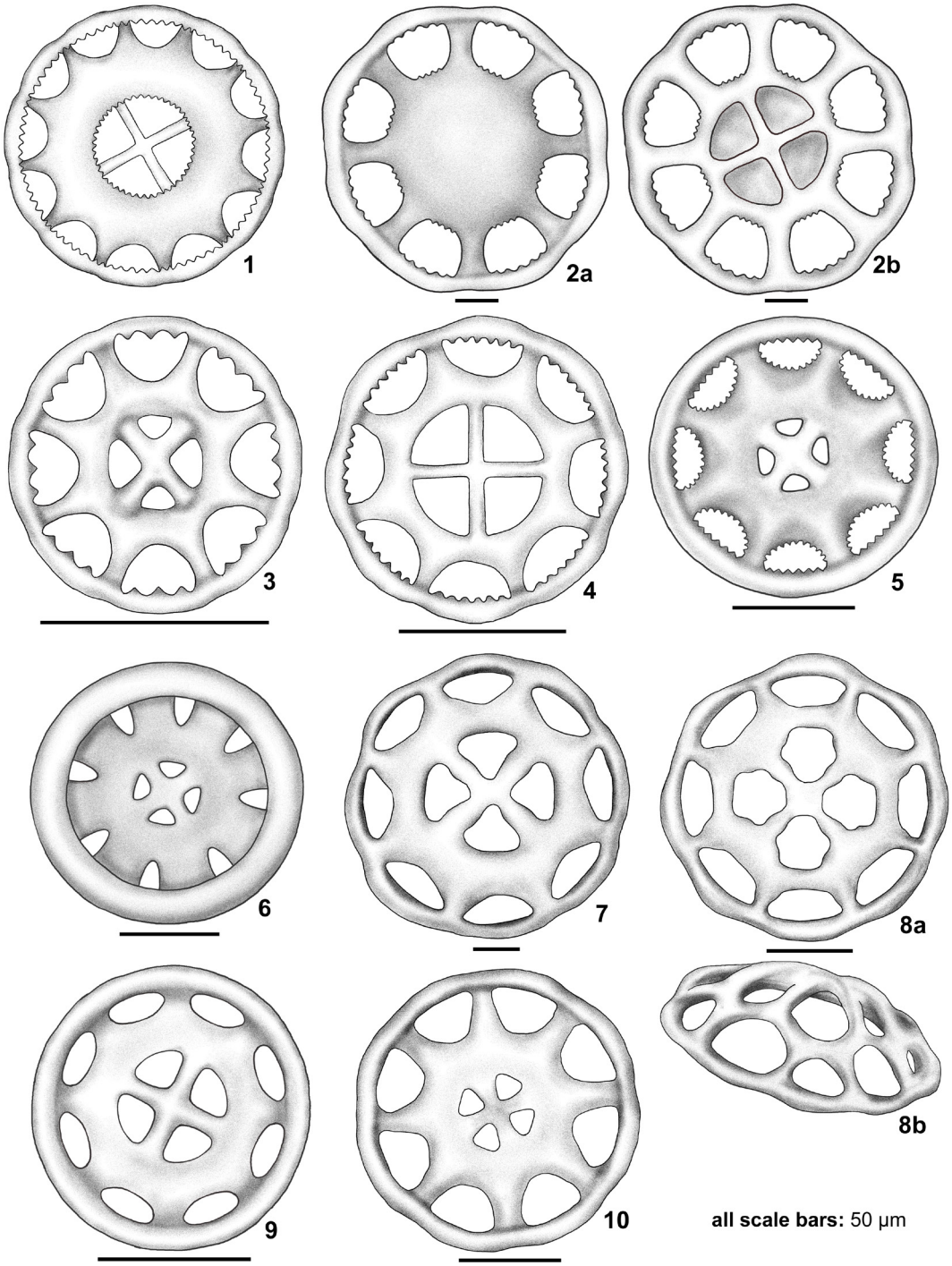


FIGURE 19. Schematic drawings of several fossil laetmogonid wheels (Triassic–Cretaceous) for comparison. 1: *Palaeolaetmogone rigaudae* (Mostler, 1970), upper side, from the Upper Triassic (Carnian) of the Salzkammergut, Austria [the exact size is not known]; 2: "*Neomicroantyx ingridae* Mostler in Krainer, Mostler & Haditsch 1994" from the Lower Toarcian of the Northern Calcareous Alps, Austria, 2a: upper side, 2b: lower side; 3: *Palaeolaetmogone mortenseni* (Deflandre-Rigaud, 1946), lower side, from the Late Jurassic (Early Oxfordian) of Normandy, northwestern France; 4: *Palaeolaetmogone frankwiesei* n. gen. et n. sp., upper side, from the Late Cretaceous (Upper Turonian) of the Isle of Wolin, Northwest Poland; 5: *Priscolaetmogone oloughlini* n. gen. et n. sp., upper side, from the Late Cretaceous (Upper Maastrichtian) of the southern Baltic Sea bottom; 6: *Palaeocaudina acmaea* (Matyja, 1972) from the Late Jurassic (Oxfordian) of central Poland, a: upper side, b: lower side; 7: *Palaeocaudina dorsetensis* (Soodan & Whatley, 1988), lower side, from the Middle Jurassic (Callovian) of South West England; 8: *Palaeolaetmogone dorsetensis* (Soodan & Whatley, 1988), from the Late Jurassic (Early Oxfordian) of Normandy, northwestern France, 8a: lower side, 8b: oblique view; 9: *Palaeocaudina rugia* n. sp., upper side, from the Late Cretaceous White Chalk (upper Lower Maastrichtian) of Rügen, Pomerania, Germany; 10: *Palaeocaudina herrigi* (Reich, 1995), upper side, from the Late Cretaceous Gulpen Fm. (upper Lower Maastrichtian) of the Maastricht area, the Netherlands.

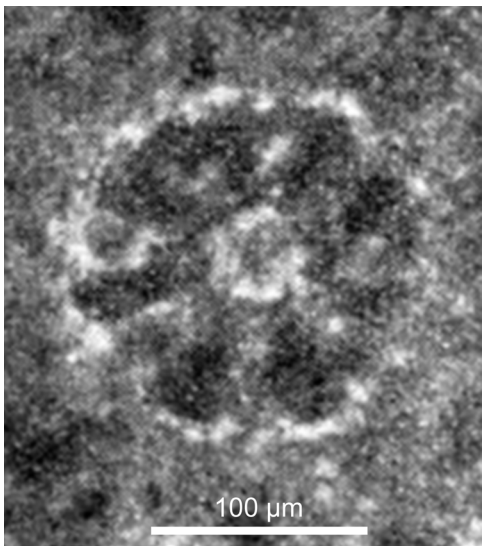


FIGURE 18. A probable chiridotid wheel-like ossicle in a petrographic thin section of Cretaceous rocks from Trichinopoly (today Tiruchirappalli), southeasternmost India, figured by Gowda (1954) as a "transverse section of *Lætmophasma*" (which is a junior synonym of the laetmogonid *Pannychia*). Reproduced from Gowda (1954: Fig. 4; modified) with permission of the publisher, the Indian Academy of Sciences, Bangalore.

Discussion and Conclusions

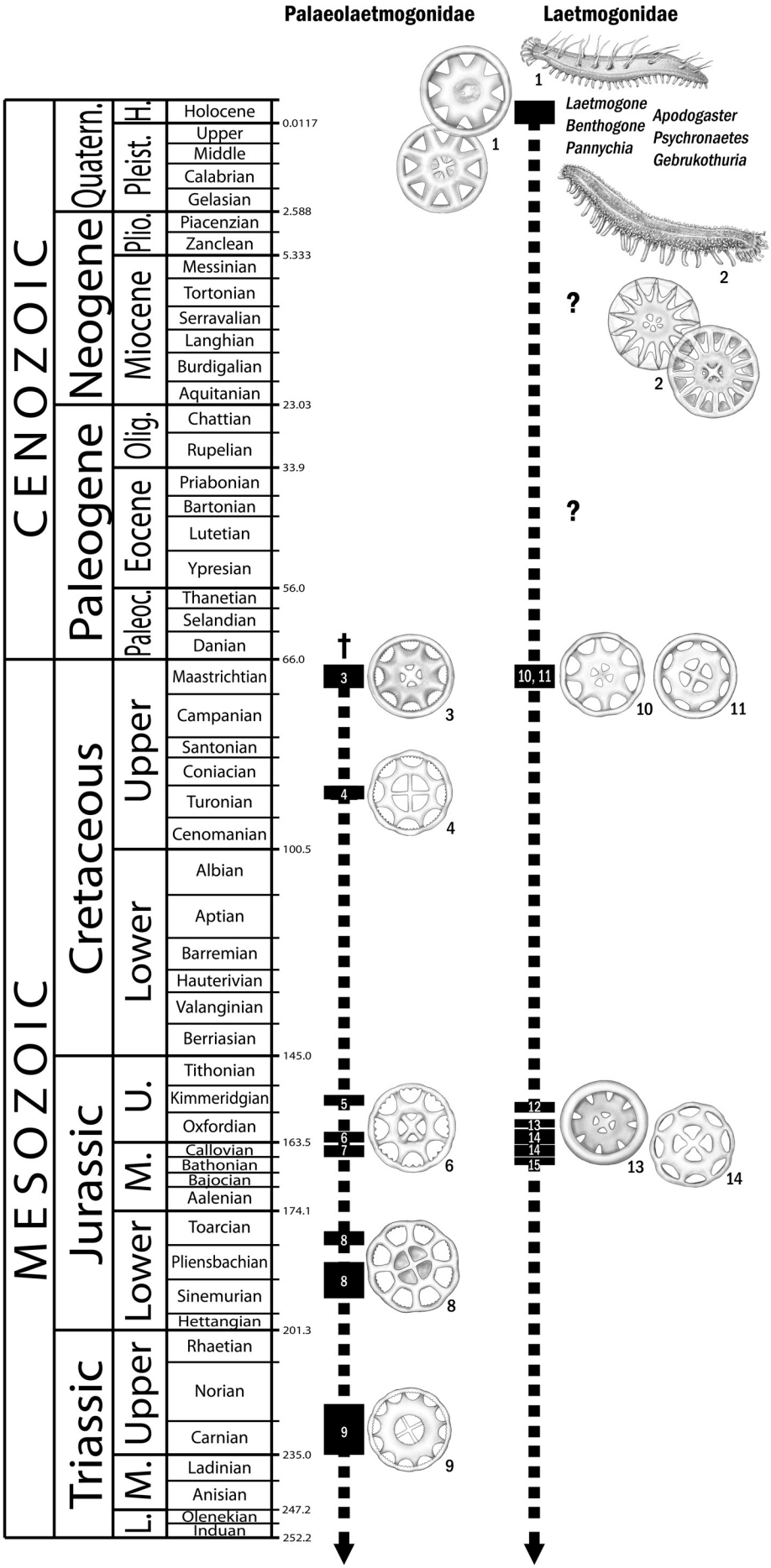
At first glance one might conclude that the fossil record of laetmogonid sea cucumbers and relatives is quite good (Gilliland 1993a, 1993b; Boczarowski 1997, 2001) and goes back to the early Palaeozoic. However, a more thorough review reveals numerous gaps (Fig. 20) and large discrepancies. One particularly problematic issue is distinguishing ossicles of 'naked' ophiocistioids (Haude & Langenstrassen 1976), which possess 'elasipodid'-like wheel ossicles, from ossicles of holothurians. Several erroneous transfers of former holothurian species/genera (*Protocaudina*, *Microantyx*) to the Ophiocistioidea (Rotasacciidae) were proposed (*e.g.*, Kozur & Mostler 1989; Boczarowski 1997).

The fossil record of laetmogonid sea cucumbers, however, is not as good as it seems. Nearly 20 laetmogonid species were named from Palaeozoic sediments, around a dozen from Mesozoic strata (Figs. 19–20) and none from the Cenozoic (cf. Reich 2013, in press). As yet nothing is known about the timing of divergence of elasipodid families and relationships within the Elasipodida (cf. Gilliland 1993a; Kerr & Kim 2001). This is in part caused by missing detailed descriptions and SEM studies of modern wheel-shaped ossicles of the Laetmogonidae and Elpidiidae (both Elasipodida). Almost all published documentations regarding the hard parts of these families are based on simple drawings (*e.g.*, Hansen 1975; Gebruk 1990, 2008) only. Unfortunately, including SEM pictures in descriptions (*e.g.*, Thandar 1998, 1999; Solís-Marín *et al.* 2009) remains the exception. This makes interpretations of fossil elasipodid sea cucumbers difficult.

Above I provided an overview of all Mesozoic taxa of laetmogonids and their close relatives, to set a baseline for future studies on elasipodid evolution. Nearly all of these taxa were reported from Europe and India. A few overlooked or new species have proven especially informative concerning the Post-Palaeozoic diversity of the Laetmogonidae as well as the origin of some modern laetmogonids.

However, future studies using SEM and/or X-ray computer tomography on both fossil and extant

FIGURE 20. Stratigraphic range chart for Mesozoic members of the Laetmogonidae and Palaeolaetmogonidae (Elasipodida). 1: *Laetmogone violacea* Théel, 1879; 2: *Pannychia moseleyi* Théel, 1882; 3: *Priscolaetmogone oloughlini* n. gen. et n. sp.; 4: *Priscolaetmogone*? n. sp.; 5: *Palaeolaetmogone frankwiesei* n. gen. et n. sp.; 6: *Palaeolaetmogone mortenseni* (Deflandre-Rigaud, 1946); 7: *Palaeolaetmogone khadirensis* (Soodan, 1977); 8: "*Neomicroantyx ingridae* Mostler in Krainer *et al.*, 1994"; 9: *Palaeolaetmogone rigaudae* (Mostler, 1970); 10: *Palaeocaudina herrigi* (Reich, 1995); 11: *Palaeocaudina rugia* n. sp.; 12: *Palaeocaudina* sp. 2; 13: *Palaeocaudina acmaea* (Matyja, 1972); 14: *Palaeocaudina dorsetensis* (Soodan & Whatley, 1988); 15: *Palaeocaudina* sp. 1.


Palaeolaetmogonidae
Laetmogonidae
CENOZOIC
MESOZOIC
Paleogene
Neogene
Quatern.
Cretaceous
Jurassic
Triassic
Paleoc.
Eocene
Olig.
Miocene
Plio.
Pleist.
H.
Upper
M.
L.
Lower
U.
Holocene
Upper
Middle
Calabrian
Gelasian
Piacenzian
Zanclean
Messinian
Tortonian
Serravalian
Langhian
Burdigalian
Aquitanian
Chattian
Rupelian
Priabonian
Bartonian
Lutetian
Ypresian
Thanetian
Selandian
Danian
Maastrichtian
Campanian
Santonian
Coniacian
Turonian
Cenomanian
Albian
Aptian
Barremian
Hauterivian
Valanginian
Berriasian
Tithonian
Kimmeridgian
Oxfordian
Callovian
Bathonian
Bajocian
Aalenian
Toarcian
Pliensbachian
Sinemurian
Hettangian
Rhaetian
Norian
Carnian
Ladinian
Anisian
Olenekian
Induan
0.0117
2.588
5.333
23.03
33.9
56.0
66.0
100.5
145.0
163.5
174.1
201.3
235.0
247.2
252.2
Laetmogone
Benthogone
Pannychia
Apodogaster
Psychronaetes
Gebrukothuria
?
?
†
1
2
3
4
5
6
7
8
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10, 11
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14
15

elasipodid wheel-shaped ossicles are urgently needed. In the future, increased detailed character sampling should allow more accurate determinations of fossil sea cucumber material as well as better assessment of diversification and evolutionary relationships within the Holothuroidea.

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References

Agatep, C.P. (1967) Some elasipodid holothurians of Antarctic and subantarctic seas. *In*: Llano, A. & Schmitt, W.L. (Eds.), Biology of the Antarctic Seas III. *Antarctic Research Series*, 11, 49–72.

[Belyaev, G.M.] Беляев, Г.М. (1966) *Донная фауна наибольших глубин (ультраабиссали) Мирового океана. [Donnaā fauna naibolš'ih glubin (ul'traabissali) Mirovogo okeana; Hadal bottom fauna of the World Ocean]*. Наука, Москва [Nauka, Moskva], 246 pp.

Blainville, H.M.D. de (1834) *Manuel d'Actinologie ou de Zoophytologie, vol. 1 (text)*. Levrault, Paris, viii + 694 pp.

Boczarowski, A. (1997) Mistaken identity of wheel-shaped sclerites of Ophiocistioidea and Holothurioidea. *Slovak Geological Magazine,* 3(4), 331–340.

Boczarowski, A. (1999) Mistaken identify of wheel-shaped sclerites of Ophiocistioidea and Holothurioidea. *Mineralia Slovaca,* 31(1–2), p. 73.

Boczarowski, A. (2001) Isolated sclerites of Devonian non-pelmatozoan echinoderms. *Palaeontologia Polonica,* 59, 3–220.

Boczarowski, A. (2012) Palaeoenvironmental interpretation of echinoderm assemblages from Bathonian ore-bearing clays at Gnaszyn (Kraków-Silesia Homocline, Poland). *In*: Gedl, P. & Kaim, A. (Eds.), Palaeoenvironmental reconstruction of the Bathonian (Middle Jurassic) ore-bearing clays at Gnaszyn, Krákow-Silesia Homocline, Poland. *Acta Geologica Polonica,* 62(3), 351–366.

Clark, H.L. (1913) Echinoderms from Lower California, with descriptions of new species. *Bulletin of the American Museum of Natural History*, 32(8), 185–235.

Deichmann, E. (1930) The Holothurians of the Western Part of the Atlantic Ocean. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 71(3), 41–226.

Deflandre-Rigaud, M. (1946) Sur les divers types de sclérites d'Holothurides oxfordiens des marnes de Villers-sur-Mer. *Memoires, Comptes Rendus de l'Académie des Sciences*, 223(14), 513–515.

Deflandre-Rigaud, M. (1952) Contribution à la systématique des sclérites d'Holothurides fossiles. *Bulletin de l'Institut Océanographique*, 49(1012), 1–12.
Deflandre-Rigaud, M. (1953) Classe des Holothurides (Holothurioidea Zittel 1883). *In*: Piveteau, J. (Ed.), *Traité de Paléontologie, Tome III*. Masson et C^{ie}, Paris, pp. 948–957.
Deflandre-Rigaud, M. (1961) Contribution à la connaissance des sclérites d'Holothurides fossiles. *[Unpublished] Thèse Docteur de l'Universite Paris (Laboratoire de Micropaléontologie de l'École Pratique des Hautes Études)*. Institut de Paleontologie du Museum, Paris, v + 135 pp.
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.
Ekman, S. (1925) Holothurien. *In*: Odhner, T. (Ed.), *Further Zoological Results of the Swedish Antarctic Expedition 1901–1903 under the direction of Dr. Otto Nordenskjöld*, 1(6), 194 pp.
Ekman, S. (1926) Systematisch-phylogenetische Studien über Elasipoden und Aspidochiroten. *Zoologische Jahrbücher (Abt. für Anatomie und Ontogenie der Tiere),* 47(4), 429–540.
Ekman, S. (1927) Holothurien der Deutschen Südpolar-Expedition 1901–1903 aus der Ostantarktis und von den Kerguelen. *In*: Drygalski, E. von (Ed.), *Deutsche Südpolar-Expedition 1901–1903*, 19(9) [= Zoologie 11(9)], 359–419.
Felder, P.J. (1997) The Vijlen Chalk Member (Maastrichtian, Late Cretaceous) in the Meuse-Rhine region. *Annales de la Société géologique de Belgique,* 119[for 1996](2), 119–133.
Felder, P.J. & Bosch, P.W. (1998) Geologie van de St. Pietersberg bij Maastricht. *In*: Limburgnummer 9A: Geologie van de St. Pietersberg. *Grondboor & Hamer*, 52(3), 53–63.
Fenninger, A. & Holzer, H.-L. (1971) Die Entwicklung der Rettenbachkalke im Raume des Hubkogels bei Bad Ischl. *In*: Festschrift zum 70. Geburtstag von Hon.-Prof. Hofrat Dr. Franz Kahler. Naturwissenschaftliche Beiträge aus dem Kärntner Raum. *Carinthia II, Sonderheft*, 28, 31–49.
Frizzell, D. L. & Exline, H. (1956) Monograph of Fossil Holothurian Sclerites. *Bulletin of School of Mines and Metallurgy (Technical Series)*, 89[for 1955](1), 204 pp.
Frizzell, D. L. & Exline, H. (1958) *The Frizzell-Exline Card Catalogue of Holothurian* Sclerites, The McLean Paleontological Laboratory, Alexandria, Vir., 216 cards incl. suppl.
Frizzell, D. L. & Exline, H. (1966) Holothuroidea – Fossil Record. *In*: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology*, *U, Echinodermata 3 [Asterozoa-Echinozoa] (2)*. University of Kansas Press, Lawrence, Kans. & Geological Society of America, Boulder, Colo., pp. U646–U672.
Gaździcki, A., Kozur, H., Mock, R. & Trammer, J. (1978) Triassic microfossils from the Korytnica limestones at Liptovská Osada (Slovakia, ČSSR) and their stratigraphic significance. *Acta Palaeontologica Polonica,* 23(3), 351–373.
[Gebruk, A.V.] Гебрук, А.В. (1990) *Глубоководные голотурии семейства Elpidiid. [Glubokovodnye goloturii semejstva Elpidiid; Elpidiid deep sea holothurians]*. Наука, Москва [Nauka, Moskva], 160 pp.
Gebruk, A.V. (2008) Holothurians (Holothuroidea, Echinodermata) of the northern Mid-Atlantic Ridge collected by the *G.O. Sars* MAR-ECO expedition with description of four new species. *Marine Biology Research*, 4, 48–60.
Gilliland, P.M. (1993a) The skeletal morphology, systematics and evolutionary history of holothurians. *Special Papers in Palaeontology*, 47, 147 pp.
Gilliland, P.M. (1993b) Class Holothuroidea de Blainville, 1834. [*In*: Simms, M.J., Gale, A.S., Gilliland, P.M., Rose, E.P.F. & Sevastopulo, G.D.: Echinodermata]. *In*: Benton, M.J. (Ed.), *The Fossil Record 2*. Chapman & Hall, London, pp. 509–513.
Gowda, S.S. (1954a) Fossil Holothuroidea from the Trichinopoly Cretaceous Rocks. *Proceedings of the Indian Science Congress Association*, 41(4), p. 14.
Gowda, S.S. (1954b) Fossil Holothuroidea from the Trichinopoly Cretaceous (S. India). *Current Science*, 23(5), 152–153.
Gowda, S.S. (1955) New "frontier" in the Micropalaeontology of the Trichinopoly marine beds. *Proceedings of the Indian Science Congress Association*, 42(4), p. 9.
Grassle, J.F. (1989) Species diversity in deep-sea communities. *Trends in Ecology and Evolution,* 4(1), 12–15.
Gutschick, R.C. & Canis, W.F. (1971) The holothurian sclerite genera *Cucumarites, Eocaudina*, and *Thuroholia* – restudy of *Eocaudina* and *Protocaudina* from the Devonian of Iowa. *Journal of Paleontology*, 45(2), 327–337.
Hansen, B. (1956) Holothurioidea from depths exceeding 6000 meters. *Galathea Reports. Scientific Results of the Danish Deep-Sea Expedition Round World (1950–1952),* 2, 33–54.
Hansen, B. (1967) The taxonomy and zoogeography of the deep-sea holothurians in their evolutionary aspects. *Studies in tropical Oceanography,* 5, 480–501.
Hansen, B. (1975) Systematic and Biology of the Deep-sea Holothurians. Part 1. Elasipoda. *Galathea Reports. Scientific Results of the Danish Deep-Sea Expedition Round World (1950–1952),* 13, 1–262.
Hansen, B. (1988) The genus *Staurocucumis* Ekman and its possible affinity with *Echinocucumis* Sars (Holothuroidea, Dendrochirota). *In*: Burke, R.D., Mladenov, P.V., Lambert, P.V. & Parsley, R.L. (Eds.), *Echinoderm Biology. Proceedings of the Sixth International Conference, Victoria, 23–28 August 1987*. A. A. Balkema, Rotterdam, pp. 301–308.
Haude, R. & Langenstrassen, F. (1976) *Rotasaccus dentifer* n. g. n. sp., ein devonischer Ophiocistioide (Echinodermata) mit „holothuroiden" Wandskleriten und „echinoidem" Kauapparat. *Paläontologische Zeitschrift*, 50(3/4), 130–150.

Herrig, E. (1982) Zur Erhaltung von kalkschaligen Mikrofossilien in verkieselten Sedimenten, dargestellt am Flint aus der Schreibkreide (Unter-Maastricht) der Insel Rügen. *Zeitschrift für geologische Wissenschaften*, 10(10), 1357–1379.
Herrig, E. (1993) The Preservation of Ostracod Shells in Siliceous Chalk oft he Danish-Polish Furrow (Baltic Sea). *Facies*, 28, 77–86.
Herrig, E. (2004a) Neue Oberkreide-Ostrakoden aus Pleistozän-Geschieben: Bythocytheridae und Paradoxostomatidae. *Archiv für Geschiebekunde*, 4(5), 279–304.
Herrig, E. (2004b) 3.8.3 Kreide auf Rügen. *In*: Katzung, G. (Ed.), *Geologie von Mecklenburg-Vorpommern,* Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 186–197.
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*: Reitner, 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.
Hessler, R.R. & Sanders, H.L. (1967) Faunal diversity in the deep-sea. *Deep-Sea Research,* 14(1), 65–78.
Jagt, J.W.M. (1999) Late Cretaceous–Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium – Part 1: Introduction and stratigraphy. *Scripta Geologica*, 16, 1–57.
Jagt, J.W.M. & Jagt-Yazykova, E.A. (2012) Stratigraphy of the type Maastrichtian – a synthesis. *In*: Jagt, J.W.M., Donovan, S.K. & Jagt-Yazykova, E.A. (Eds.), Fossils of the type Maastrichtian (Part 1). *Scripta Geologica, Special Issue*, 8, 5–32.
Jamnik, A. & Ramovš, A. (1993) Holoturijski skleriti in konodonti v zgornjekarnijskih (tuvalskih) in norijskih apnencih osrednjih Kamniških Alp. *Geologija*, 35[for 1992], 7–63.
Kerr, A.M. & Kim, J. (2001) Phylogeny of Holothuroidea (Echinodermata) inferred from morphology. *Zoological Journal of the Linnean Society,* 133(1), 63–81.
Keutgen, N., Jagt, J.W.M., Felder, P.J. & Jagt-Yazykova, E.A. (2010) Stratigraphy oft he upper Vijlen Member (Gulpen Formation; Maastrichtian) in northeast Belgium, the southeast Netherlands and the Aachen area (Germany), with special reference to belemnitellid cephalopods. *Netherlands Journal of Geosciences [= Geologie en Mijnbouw],* 89(2), 109–136.
Kœhler, R. (1895) Rapport préliminaire sur les Ėchinodermes. Dragages profonds executes a bord du »Caudan« dans le Golfe de Gascogne. *Revue Biologique du Nord de la France*, 7[1894/1895], 439–496.
Kœhler, R. & Vaney, C. (1905) An account of the deep-sea Holothurioidea collected by the Royal Indian Marine Survey Ship Investigator. [Holothuries recueillies par l'Investigator dans l'Océan Indien. I. Les Holothuries de Mer profonde.] *In*: *Echinoderma of the Indian Museum. I. Holothurioidea*, The Indian Museum, Calcutta, v + 123 pp. + (ii).
Kozur, H. & Mock, R. (1972) Neue Holothurien-Sklerite aus der Trias der Slowakei. *Geologisch-Paläontologische Mitteilungen Innsbruck*, 2(12), 47 pp.
Kozur, H. & Mock, R. (1974) Holothurien-Sklerite aus der Trias der Slowakei und ihre stratigraphische Bedeutung. *Geologický Zborník [= Geologica Carpathica],* 25(1), 113–143.
Kozur, H. & Mostler, H. (1989) Echinoderm Remains from the Middle Permian (Wordian) from Sosio Valley (Western Sicily). *Jahrbuch der Geologischen Bundesanstalt*, 132(4), 677–685.
Krainer, K. & Mostler, H. (1997) Die Lias-Beckenentwicklung der Unkener Synklinale (Nördliche Kalkalpen, Salzburg) unter besonderer Berücksichtigung der Scheibelberg Formation. *Geologisch-Paläontologische Mitteilungen Innsbruck*, 22, 1–41.
Krainer, K., Mostler, H. & Haditsch, J.G. (1994) Jurassische Beckenbildung in den Nördlichen Kalkalpen bei Lofer (Salzburg) unter besonderer Berücksichtigung der Manganerz-Genese. *In*: Festschrift zum 60. Geburtstag von Erik Flügel. *Abhandlungen der Geologischen Bundesanstalt in Wien*, 50, 257–293.
Kristan-Tollmann, E. (1964) Beiträge zur Mikrofauna des Rhät. I. Weitere neue Holothuriensklerite aus dem alpinen Rhät. *Mitteilungen der Gesellschaft der Geologie- und Bergbaustudenten in Wien*, 14[for 1963], 125–134.
Lambert, P. & Boutillier, J. (2011) Deep-sea Echinodermata of British Columbia, Canada. *Canadian Technical Report of Fisheries and Aquatic Sciences,* 2929, 143 pp.
Lipiec, M. (1992) Some Jurassic holothurian sclerites from the High-Tatric Series of the Tatra Mts., Poland. *Kwartalnik Geologiczny [= Geological Quarterly]*, 36(4), 435–450.
Ludwig, H. (1894) XII. The Holothurioidea. *In*: Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer "Albatross", during 1891, Lieut. Commander Z. L. Tanner, U. S. N. commanding. *Memoirs of the Museum of Comparative Zoölogy at Harvard College,* 17(3), 183 pp.
Madsen, F.J. & Hansen, B. (1994) Echinodermata: Holothuroidea. *Marine Invertebrates of Scandinavia*, 9, 143 pp.
Martin, W.R. (1952) Holothuroidea from the Iowa Devonian. *Journal of Paleontology*, 26(5), 728–729.
Massin, C. (1994) Ossicle variation in Antarctic dendrochirote holothurians (Echinodermata). *Bulletin de l'Institut Royal des Sciences naturelles de Belgique (Biologie) [= Bulletin van het Koninklijk Belgisch Institut voor Naturwetenschappen (Biologie)]*, 64, 129–146.
Massin, C. & Hendrickx, M.E. (2011) Deep-water Holothuroidea (Echinodermata) collected during the TALUD cruises off the Pacific coast of Mexico, with the description of two new species. *Revista Mexicana de Biodiversidad,* 82, 413–443.

Matyja, B.A. (1972) Holothurian sclerites from the Oxfordian limestones of the Holy Cross Mts. *Acta Geologica Polonica*, 22(2), 233–246.
Mitsukuri, K. (1912) Studies on Actinopodous Holothurioidea. *Journal of the College of Science, Tokyo Imperial University,* 29(2), 284 pp.
Mortensen, T. (1927) *Handbook of the Echinoderms of the British Isles*, Oxford University Press, London *etc.*, viii [x] + 471 pp.
Mostler, H. (1971) Über einige Holothurien-Sklerite aus der süd- und nordalpinen Trias. *In*: Mostler, H. (Ed.), *Beiträge zur Mikrofazies und Stratigraphie von Tirol und Vorarlberg. [= Festband des Geologischen Institutes anläßlich der 300-Jahr-Feier der Universität Innsbruck],* Universitätsverlag Wagner, Innsbruck & München, pp. 339–360. [preprints 1970; published date of the volume 1971]
Mostler, H. (1972) Holothuriensklerite aus dem Jura der Nördlichen Kalkalpen und Südtiroler Dolomiten. *Geologisch-Paläontologische Mitteilungen Innsbruck,* 2(6), 1–29.
Pawson, D.L. (1965a) The Bathyal Holothurians of the New Zealand Region. *Zoology Publications of the Victoria University Wellington*, 39, 1–33.
Pawson, D.L. (1965b) Some Echinozoans from North of New Zealand. *Transactions of the Royal Society of New Zealand (Zoology)*, 5(15), 197–224.
Pawson, D.L. (1978) Some aspects of the biology of deep-sea echinoderms. *In*: Zavodnik, D. (Ed.), Proceedings of the Second Echinoderms Conference. Rovinj, Yugoslavia, 26th September–1st October, 1975. *Thalassia Jugoslavica*, 12[for 1976](1), 287–293.
Pawson, D.L. (1983) *Psychronaetes hanseni*, a new genus and species of elasipodan sea cucumber from the eastern central Pacific (Echinodermata: Holothuroidea). *Proceedings of the Biological Society of Washington*, 96(1), 154–159.
Pawson, D.L. & Fell, H.B. (1965) A revised classification of the dendrochirote holothurians. *Breviora. Museum of Comparative Zoology,* 214, 1–7.
Reich, M. (1995) Erster sicherer Nachweis der Elasipoda (Holothuroidea, Echinodermata) aus der Kreide, sowie Bemerkungen zu den Holothurienresten der Oberkreide. *Archiv für Geschiebekunde,* 1(11), 681–688.
Reich, M. (1997a) Fossile Holothurienreste (Echinodermata) aus Geschieben – Ein Überblick. *In*: Zwanzig, M. & Löser, H. (Eds.), *Berliner Beiträge zur Geschiebeforschung,* CPress, Dresden, pp. 81–89.
Reich, M. (1997b) Die Holothurienreste (Echinodermata) der Schreibkreide (Unter-Maastrichtium), Insel Rügen/Ostsee. *Unpublished Diploma thesis, Institute of Geological Sciences, University of Greifswald,* Greifswald, 138 pp.
Reich, M. (1999) Catalogue of palaeontological types and figured specimens of the University of Greifswald. Part I: Echinodermata, Hemichordata, Cephalochordata, Tunicata and Craniata. *Greifswalder Geowissenschaftliche Beiträge,* 6, 519–535.
Reich, M. (2000) Holothurians from the Turonian of the Isle of Wolin (Pomerania, NW-Poland). *In*: Anonymous (Ed.), *6th International Cretaceous Symposium, August 27 to September 4, 2000, Vienna, Austria. Abstracts, List of Participants,* Vienna, p. 113.
Reich, M. (2001a) Holothurians from the Late Cretaceous oft he Isle of Rügen (Baltic Sea). *In*: Barker, M. (Ed.), *Echinoderms 2000. Proceedings of the 10th International Echinoderm Conference, Dunedin, 31 January–4 February 2000*, A. A. Balkema Publishers, Lisse *etc.*, pp. 89–92.
Reich, M. (2001b) *Pravuscucumis deeckei* paragen. et parasp. nov. (Echinodermata: Holothuroidea) aus dem Turonium des Ostseegebietes. *Geschiebekunde aktuell,* 17(2/3), 97–106.
Reich, M. (2002) Holothurien (Echinodermata) aus der Oberkreide des Ostseeraumes: Teil 1. Myriotrochidae Théel, 1877. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen,* 224(3), 373–409.
Reich, M. (2003a) Holothurien (Echinodermata) aus der Oberkreide des Ostseeraumes: Teil 2. Ypsilothuriidae Heding, 1942. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte,* [2003](8), 498–512.
Reich, M. (2003b) Holothurien (Echinodermata) aus der Oberkreide des Ostseeraumes: Teil 3. Chiridotidae Östergren, 1898. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen,* 228(3), 363–397.
Reich, M. (2003c) Holothurien (Echinodermata) aus der Oberkreide des Ostseeraumes: Teil 4. Synaptidae Burmeister, 1837. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen,* 229(1), 75–95.
Reich, M. (2003d) Holothurien (Echinodermata) aus der Oberkreide des Ostseeraumes: Teil 5. Molpadiidae J. Müller, 1850. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen,* 229(2), 231–253.
Reich, M. (2007) *Linguaserra spandeli* sp. nov. (Echinodermata: Ophiocistioidea) from the Late Permian (Zechstein) of Thuringia, Germany. *In*: Special Volume – A tribute to Prof. Georges Ubaghs (1916–2005) – Part 2. *Annales de Paléontologie,* 93(4), 317–330.
Reich, M. (2010) Evolution and diversification of ophiocistioids (Echinodermata: Echinozoa). *In*: Harris, L.G., Böttger, S.A., Walker, C.W. & Lesser, M.P. (Eds.), *Echinoderms: Durham. Proceedings of the 12th International Echinoderm Conference, Durham, New Hampshire, USA, 7–11 August 2006*, Taylor & Francis, London *etc.*, pp. 51–54.
Reich, M. (2013, in press) How many species of fossil holothurians are there ? *In*: Johnson, C. (Ed.), *Echinoderms in a changing world. Proceedings of the 13th International Echinoderm Conference, University of Tasmania, Australia, 5–9 January 2009*, Taylor & Francis, London *etc.*

Reich, M. & Frenzel, P. (2002) Die Fauna und Flora der Rügener Schreibkreide (Maastrichtium, Ostsee). *Archiv für Geschiebekunde,* 3(2/4), 73–284.
Reich, M. & Haude, R. (2004) Ophiocistioidea (fossil Echinodermata): an overview. *In*: Heinzeller, T. & Nebelsick, J. (Eds.), *Echinoderms: München. Proceedings of the 11th International Echinoderm Conference, Munich, Germany, 6–10 October 2003*, Taylor & Francis, London *etc.*, pp. 489–494.
Reich, M. & Jagt, J.W.M. (2001) Holothurien aus dem Maastrichtium der Niederlande und Belgiens. *In*: Reich, M. & Hinz-Schallreuter, I. (Eds.), 1. Arbeitstreffen deutschsprachiger Echinodermenforscher, Greifswald, 11. bis 13. Mai 2001 – Arbeiten und Kurzfassungen der Vorträge und Poster. *Greifswalder Geowissenschaftliche Beiträge*, 9, p. 42.
Reich, M., Villier, L. & Kutscher, M. (2004) The Echinoderms of the Rügen White Chalk (Maastrichtian, Germany). *In*: Heinzeller, T. & Nebelsick, J. (Eds.), *Echinoderms: München. Proceedings of the 11th International Echinoderm Conference, Munich, Germany, 6–10 October 2003*, Taylor & Francis Group, London *etc.*, pp. 495–501.
Reich, M. & Wiese, F. (2010) Apodid sea cucumbers (Echinodermata: Holothuroidea) from the Upper Turonian of the Isle of Wolin, NW Poland. *Cretaceous Research,* 31(4), 350–363.
Rex, M.A., Stuart, C.T., Hessler, R.R., Allen, J.A., Sanders, H.L. & Wilson, G.D.F. (1993) Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature*, 365(6447), 636–639.
Rogacheva, A., Cross, I.A. & Billett, D.S.M. (2009) *Gebrukothuria profundus*, a new genus and species of laetmogonid holothurian (Elasipodida, Laetmogonidae) from around the Crozet Plateau in the Southern Indian Ocean. *In*: Brökeland, W. & George, K.H. (Eds.), Deep-sea taxonomy – a contribution to our knowledge of biodiversity. *Zootaxa,* 2096, 479–483.
Schallreuter, R. (1968) Die ältesten sicheren Holothuroideenreste (Ordoviz). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, [1968](9), 522–529.
Sieverts-Doreck, H. (1958) Spezielle Arbeitsgebiete der Mikropaläontologie 3. Echinodermen. *In*: Freund, H. (Ed.), *Handbuch der Mikroskopie in der Technik. Bd. II. Teil 3. Mikroskopie in der Geologie sedimentärer Lagerstätten (Mikropaläontologie)*. Umschau-Verlag, Frankfurt a. M., pp. 238–264.
Singh, S.N., Kulshreshtha, S.K., Garg, R. & Saxena, R.K. (1981) Preliminary note on the presence of Jurassic holothuroids from Jaisalmer, Rajasthan. *Current Science*, 50(13), 589–591.
Sluiter, C.P. (1901) Die Holothurien der Siboga-Expedition. *In*: Weber, M. (Ed.), *Siboga-Expeditie, XLIV*. E.J. Brill, Leiden, 141 pp.
Smirnov, A.V. (2012) System of the Class Holothuroidea. *Paleontological Journal*, 46(8), 793–832.
Solís-Marín, F.A., Arriaga-Ochoa, J.A., Laguarda-Figueras, A., Frontana-Uribe, S.C. & Durán-González, A. (2009) *Holoturoideos (Echinodermata: Holothuroidea) del Golfo de California*. Comisión Nacional par el Conocimiento y Uso de la Biodiversidad & Instituto de Ciencias del Mar y Limnología, UNAM, México, D.F., 177 pp.
Soodan, K.S. (1972) Fossil holothurian sclerites from the Upper Cretaceous and Paleocene sequence of Kutch, India. *Proceedings of the Indian Science Congress Association*, 59(3), 224–225.
Soodan, K.S. (1977) Fossil Holothuroidea from Kutch, India – Part IV. *Geophytology*, 7(2), 179–182.
Soodan, K.S. & Whatley, R. (1988) Fossil Holothuroidea from the Jurassic Rocks of Great Britain. Part II. *Geoscience Journal,* 9(2), 117–130.
Sztejn, J. (1993) Upper Jurassic and Lower Cretaceous Sclerites from the Łódź Trough of the South-Eastern Slope of the Kujawy Swell. *Bulletin of the Polish Academy of Sciences (Earth Sciences),* 41(2), 115–126.
Thandar, A.S. (1998) A new genus and three new species of deep-sea holothuroids from the west coast of South Africa (Echinodermata). *Journal of Zoology*, 244(1), 79–88.
Thandar, A.S. (1999) Deep-sea holothuroids taken by the R.V. *Africana II* in 1959, from off the west coast of the Cape Peninsula, South Africa. *Annals of the South African Museum [= Annale van die Suid-Afrikaanse Museum]*, 105(9), 363–409.
Théel, H. (1879) Preliminary Report on the Holothuridæ of the exploring voyage of H. M. S. "Challenger", under Professor Sir C. Wyville Thomson. Part I. *Bihang till Kongliga Svenska Vetenskaps-Akademiens handlingar*, 5(19), 1–20.
Théel, H. (1882) Report on the Holothurioidea dredged by the H.M.S. Challenger, during the years 1873–1876. Part I. *In*: *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–76. Zoology,* 4(13): 176 pp.
Thuy, B., Gale, A.S., Kroh, A., Kucera, M., Numberger-Thuy, L.D., Reich, M. & Stöhr, S. (2012) Ancient Origin of the Modern Deep-Sea Fauna. *PLoS ONE*, 7(10), 1–11. [e46913]
Walsh, J.H.T. (1891) Natural History Notes from H.M. Indian Marine Survey Steamer "Investigator"... No. 24. List of deep-sea holothurians, collected during seasons 1887–91, with description of new species. *Journal of the Asiatic Society of Bengal (2: Natural Sciences),* 60, 197–204.
Wissing, F.-N. & Herrig, E. with cooperation of M. Reich (1999) *Arbeitstechniken der Mikropaläontologie. Eine Einführung*, Enke-Verlag, Stuttgart, 191 pp.
Wolff, T. (1977) Diversity and faunal composition of the deep-sea benthos. *Nature*, 267 (5614), 780–785.
[Zenkevič, N.L.] Зенкевич, Н.Л. (1970) *Атлас фотографий дна Тихого океана*. [*Atlas fotografij dna Tihogo okeana; An photographic atlas of the deep-sea.]*, Наука, Москва [Nauka, Moskva], 135 pp.