Santonian sea cucumbers (Echinodermata: Holothuroidea) from Sierra del Montsec, Spain

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Göttingen Contributions to Geosciences
www.gzg.uni-goettingen.de

77: 147-160, 8 figs. 2014

Recent discovery of disarticulated sea cucumber material from Font de la Plata (Sierra del Montsec, Lleida, Catalonia, Spain) resulted in the identification of at least six holothurian taxa, belonging to the Apodida (Synaptidae, Chiridotidae), Molpadiida (?stem group Molpadiidae), and Aspidochirotida (Holothuriidae). Three new genera (*Cruxopadia*, *Eoleptosynapta*, *Eorynkatorpa*) and four new species (*Cruxopadia mesozoica, C. reitneri*, *Eoleptosynapta jaumei*, *Eorynkatorpa catalonica*) are described from Late Cretaceous sediments of Spain, and in part from the Late Jurassic of France. The new fauna increases our knowledge of holothuroid echinoderms from Santonian strata worldwide.

Received: 12 June 2013
Accepted: 01 August 2013

Subject Areas: Palaeontology, Zoology

Keywords: Echinodermata, Holothuroidea, Jurassic, Oxfordian, France, Normandy, Cretaceous, Santonian, Spain, Catalonia, systematics, phylogeny

LSID: urn:lsid:zoobank.org:pub:9C2E58EE-77E4-44F1-9511-4337496D7823

Introduction

The Sierra del Montsec, situated in the southern marginal zone of Pyrenees, presents classical outcrops and excellent preserved fossils of early and late Cretaceous age. Among them are also members of eleutherozoan echinoderms, such as echinoids, asteroids, and ophiuroids; only holothurians were missing up to now.

Holothuroid echinoderms are not common as fossils in general (e.g., Frizzell & Exline 1956, 1966; Gilliland 1993), the skeleton is rarely robust and consists of microscopic ossicles embedded in the body wall as well as of larger calcareous ring elements, encircling the pharynx at the inner side of the mouth. Consequently they disarticulate rapidly after death and have left a rather poor fossil record (e.g., Reich 2013a).

Santonian holothurians have so far been recorded only from Germany and the U.K. Lommerzheim (1976, 1991) reported their occurrence from Westphalia (Germany), but, unfortunately, without any descriptions. Upton (1917) mentioned a chiridotid wheel (Apodida) from the "Upper Chalk" of Purley (Surrey, England). Recently, a nearly articulated find from the "Upper Chalk" of England, belonging to the Holothuriidae (Aspidochirotida), was presented by Reich (2008, 2013b) and is currently under description by Reich & Gale.

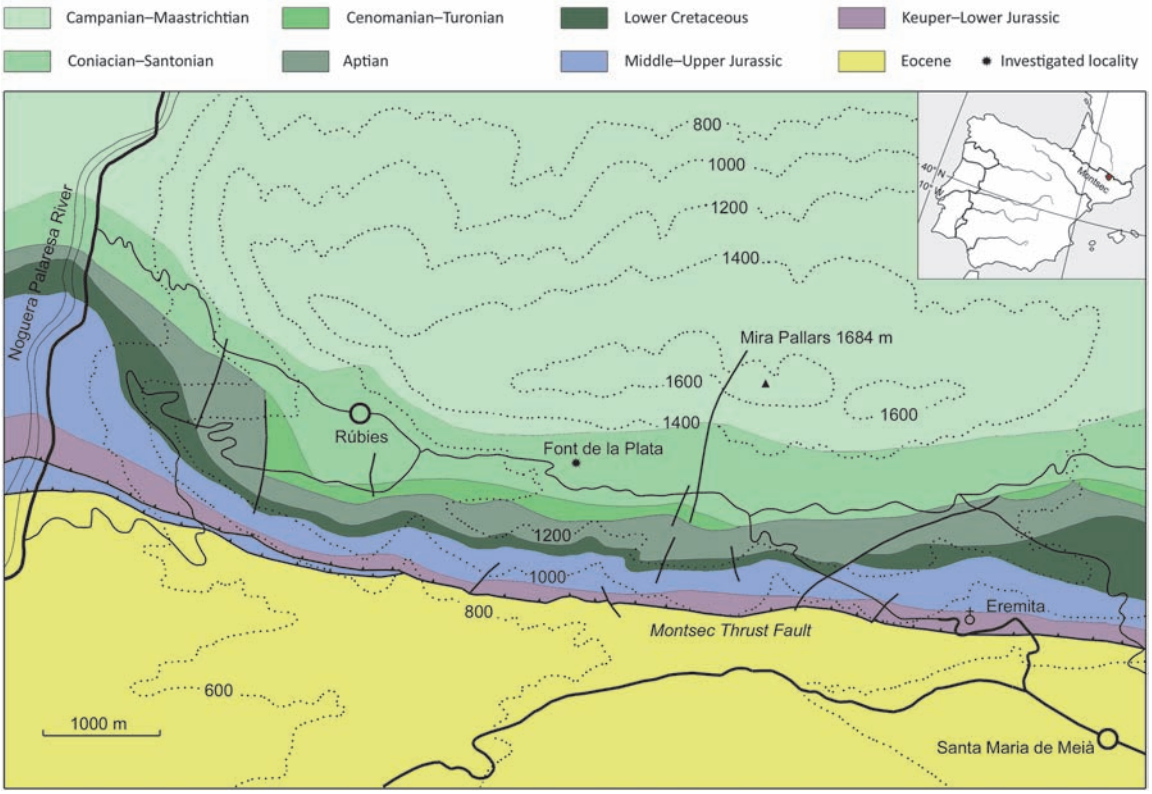


Fig. 1: Location of the sampled outcrop at Font de la Plata, east of Rúbies, Sierra del Montsec, Catalonia, Spain. Geological map from Ansorge (1991, modified).

Geological setting and material

The studied microfossil material from the late Santonian ("Santon E" of Krusat 1966) of the Font de la Plata (Montsec de Rúbies; Figs. 1–2) was sampled by JA in September 1996 and includes around 50 isolated holothurian ossicles. This formation (> 100 m) contains grey and/or yellowish calcareous marls and marly limestones interbedded by limestones and sandstones (Krusat 1966: 60f.). It can be correlated with the "Unit 5" of Caus & Cornella (1983) or with the "Montsec marls" of Caus & Gómez-Garrido (1989).

The rich associated fauna (e.g., Krusat 1966) comprises abundant scleractinian corals and rudist bivalves, calcareous algae, chaetetid sponges, decapod crustaceans, bivalves, gastropods, cephalopods, articulate brachiopods, larger foraminifera and teleost fishes (e.g., Bataller 1937a, 1953; Hottinger 1966; Cornella 1977; Caus et al. 1978; Hottinger et al. 1989; Nolf 2003; Garassino et al. 2009; Hottinger & Caus 2009). Echinoderms are also reported with representatives of the Echinoidea and Asteroidea (e.g., Bataller 1937b: 590, 1953: 57ff.; Krusat 1966: 58; Neumann & Hess 2001: 7ff.).

The pachydont bivalves *Hippuritella maestrei* (Vidal), *Hippuritella sulcatissima* (Douvillé), and *Vaccinites galloprovincialis* (Matheron) (systematics updated after Vicens 1992, Vicens et al. 1998 and Steuber 2002) reported by Krusat (1966: 84) are biostratigraphically useful and are considered to be late Santonian in age, which is in agreement with other fossils (see Llompart 1979; Caus et al. 1999). This Santonian environment corresponds to an open shallow-water platform (e.g., Llompart 1979).

The studied samples include besides the isolated holothurian ossicles also typical other calcareous microfossils, such as foraminifera and ostracods, as well as microscopic remains of macrofossils, like octocoral scleres (Alcyonacea), echinoid spines, and ophiuroid ossicles (lateral side shields, vertebrae etc.).

In the systematic description we also introduce a new molpadiid genus (*Cruxopadia* Reich gen. nov.) with its genotype *C. mesozoica* Reich sp. nov. from the early Oxfordian of Villers-sur-Mer (Calvados, France). Early Oxfordian mudstones of the *Quenstedtoceras mariae* Zone are exposed at longer cliff sections of the English Channel coast between Houlgate and Villers-sur-Mer, Normandy (e.g., Dugué et al. 1998; Merle 2011). Holothurians from the Oxfordian marls of Villers-sur-Mer are known for a long time (e.g., Deflandre-Rigaud 1946, 1962). Samples were taken by MR in 1999 and 2012.

Methods

The microscopic fossils from clayey and calcareous marls were isolated using hot water and/or hydrogen peroxide (10 %). After washing (sieve sizes: >0.063 mm, 0.1 mm and 1 mm), the residues were dehydrated at a temperature of ~70°C (cf. Wissing & Herrig 1999). 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).

All figured specimens are deposited at the Geoscience Centre of the Georg-August University Göttingen, Germany (GZG).

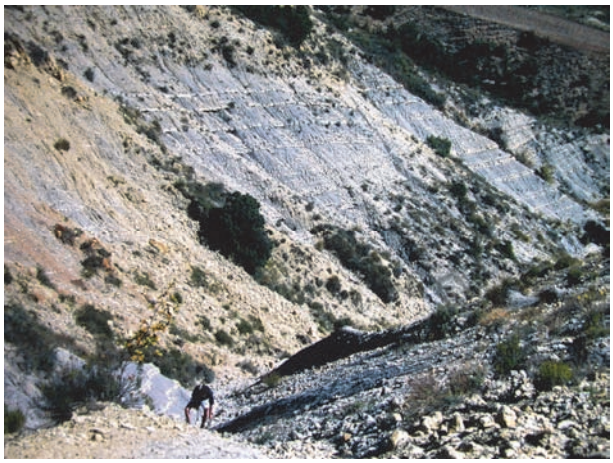


Fig. 2: Outcrop at Font de la Plata, east of Rúbies, showing the interbedded strata of calcareous marls and limestones (September 1996).

Systematic palaeontology

Phylum **Echinodermata** Bruguière, 1791 [ex Klein, 1734]
Subphylum **Eleutherozoa** Bell, 1891
Class **Holothuroidea** de Blainville, 1834
Subclass **Holothuriacea** Smirnov, 2012
Order **Molpadiida** Haeckel, 1896

Family (?stem group) **Molpadiidae** J. Müller, 1850

Genus ***Cruxopadia*** Reich gen. nov.

Type species. – *Cruxopadia mesozoica* Reich sp. nov. from the early Oxfordian of Normandy, France.

Etymology. – Named after Latin *crux, crŭcis* = cross, and in remembrance of the modern holothurian genus *Molpadia*. The generic name is of feminine gender.

Diagnosis. – Solid cross-shaped plates with four central perforations.

Comparison. – The new genus differs from the related *Priscolongatus* Górka & Luszczewska, 1969 (syn. *Fletcherina* Soodan, 1975; *Brianella* Huddleston, 1982; *Hannaina* Soodan, 1975; *Koteshwaria* Tandon & Saxena, 1983) in being not table-like and therefore in having no spire or stirrup. The synonymy of genera/paragenera within this '*Priscolongatus* group' was briefly discussed by Gilliland (1993: 81–82).

Occurrence. – Hitherto known only from the late Jurassic (Oxfordian) to the late Cretaceous (Santonian) of Europe (France, Spain).

Cruxopadia mesozoica Reich sp. nov.

Figs. 3A–B

Material. – One cross-shaped ossicle (GZG.INV.91405; holotype; Fig. 3A); two further (broken) ossicles (GZG.INV.91406–91407; paratypes).

Type locality. – Villers-sur-Mer, Normandy, France.

Type horizon. – "Marnes de Villers", *Quenstedtoceras mariae* Zone (late Jurassic: early Oxfordian).

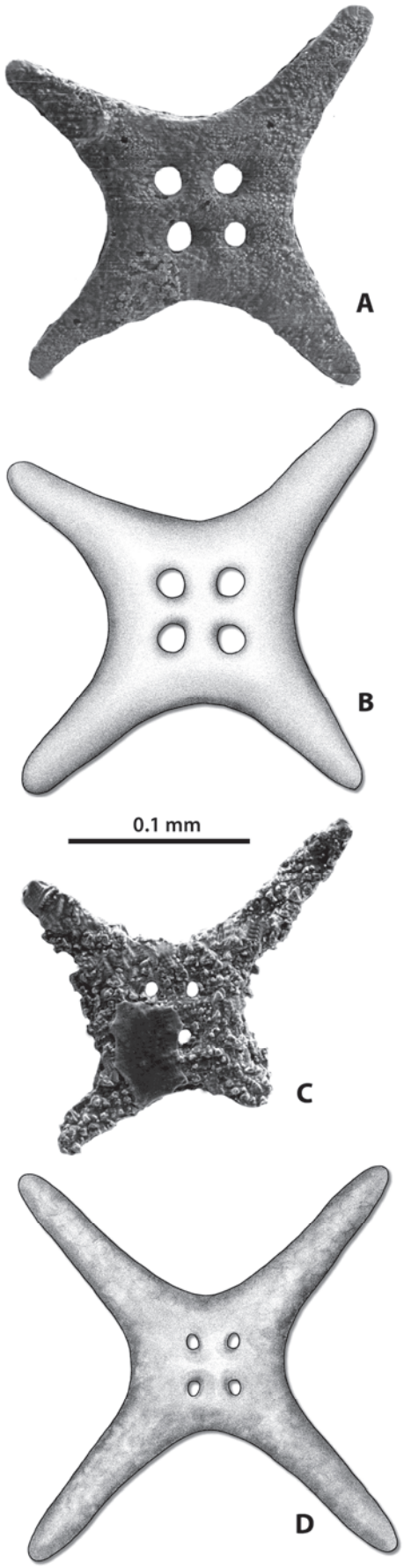
Etymology. – Species name refers to the "Mesozoic" era.

Diagnosis. – A species of *Cruxopadia* with the following characteristics: ossicle in one plane, four solid radiating arms at (nearly) right angles, medium-sized in length and tapering distally. All arms are more or less of equal length. Four central perforations are cross-shaped arranged, and medium-sized in diameter.

Description. – The ossicles of *C. mesozoica* are cross-shaped (Fig. 3A; diameter ~250–260 μm) and in one plane with four solid radiating arms at nearly right angles (±90°) or so with respect to each other. These arms are medium-sized (~100–110 μm) and more or less of equal length and tapering distally. Four central perforations with a medium-sized diameter (~16–17 μm) are cross-shaped arranged and circular to suboval in outline. The square of these perforations is covering approx. 20 % of the whole central portion of the ossicle. The central portion takes approx. 60 % of the total ossicle area (diameter). No spire or stirrup is present. The surface is fine-grained (Fig. 3A).

Comparison. – *C. mesozoica* differs from *C. reitneri* Reich sp. nov. in having shorter and more robust arms as well as in having much larger central perforations. Also the central portion is much larger, by covering more than 60 % of the total ossicle area (diameter).

Remarks. – The new material extends the fossil record of the 'fusiform rod' molpadiid morphotype back to the Mesozoic, and furthermore shows that Cenozoic and modern 'fusiform rods' probably evolved from primarily cross-shaped ossicles with an evolutionary trend to decrease the number of central perforations (4 to 3) and the formation



of arms (4 to 2). Modern molpadiid members with 'fusiform rods' have 2–3(4) arms and (2)3–4 prominent central perforations (e.g., Pawson 1977; Pawson et al. 2001).

The new species bearing this type of ossicles lived probably, as all other members of the Molpadiida, infaunal as an active burrower and deposit feeder.

Occurrence. – The new species occurs in the "Marnes de Villers" of Calvados (Normandy), early Oxfordian of France.

Cruxopadia reitneri Reich sp. nov.

Figs. 3C–D

Material. – One cross-shaped ossicle (GZG.INV.91408; holotype; Fig. 3C); one further (broken) ossicle (GZG.INV.91409; paratype).

Type locality. – Font de la Plata, Sierra del Montsec, Catalonia, Spain.

Type horizon. – Marly limestones of the "Santon E", (Cretaceous: late Santonian).

Etymology. – Named after Joachim Reitner (*1952), Göttingen, in recognition of his contributions to the study of Spanish Mesozoic strata and in celebration of his 60th birthday.

Diagnosis. – A species of *Cruxopadia* with the following characteristics: ossicle in one plane, four delicate and solid radiating arms at (nearly) right angles; arms long and tapering distally. Four central perforations are cross-shaped arranged, and small in diameter.

Description. – The ossicles of *C. reitneri* are cross-shaped (Fig. 3C) and in one plane with four solid radiating arms at nearly right angles (±90°) or so with respect to each other. These arms are long and delicate, 110–120 μm in length and tapering distally. Four central perforations with a small diameter (~9–11 μm) are cross-shaped arranged and circular to suboval in outline. The square of these perforations are covering approx. 20 % of the whole central portion of the ossicle. The central portion takes approx. 30 % of the total ossicle area (diameter). No spire or stirrup is present. The surface is coarse-grained (Fig. 3C).

Comparison. – *C. reitneri* differs from *C. mesozoica* in having longer and more delicate arms as well as in having much smaller central perforations. Also the central portion is much smaller, in covering only 30 % of the total ossicle area (diameter). No spire or stirrup is present.

Fig. 3: Representative ossicles of molpadiid sea cucumbers. **(A–B)** *Cruxopadia mesozoica* gen. et sp. nov.; **(A)** GZG.INV.91405, holotype, upper side; **(B)** Schematic drawing, upper side. **(C–D)** *Cruxopadia reitneri* gen. et sp. nov.; **(C)** GZG.INV.91408, holotype, upper side; **(D)** Schematic drawing, upper side. Early Oxfordian; Villers-sur-Mer, Normandy, France (A–B). Late Santonian; Font de la Plata, east of Rúbies, Catalonia, Spain (C–D). Scale bar = 0.1 mm.

Remarks. – See under *C. mesozoica*.

Occurrence. – The new species occurs in the late Santonian of Spain.

Order **Aspidochirotida** Grube, 1840
Family **Holothuriidae** Burmeister, 1837

[p. p.] Paragenus ***Priscopedatus*** Schlumberger, 1890

Type species. – *Priscopedatus pyramidalis* Schlumberger, 1890 from the Middle Eocene (Lutetian) of Chaussy, Paris Basin, France.

Remarks. – The paragenus *Priscopedatus* (cf. Soodan 1975) needs a comprehensive revision, since table-like ossicles are present in species of all orders of the Holothuriacea (Aspidochirotida, Molpadiida, Dendrochirotida). A modern comprehensive overview of these table-like ossicles (including SEM pictures) is, however, missing so far. We therefore use the paragenus name in quotation marks.

'Priscopedatus' sp.

Fig. 4A

Material. – One incomplete table ossicle (GZG.INV.91449).

Description. – Incomplete table-like ossicle (diameter ~165 μm), nearly suboval in outline with a short stirrup over a suboval central hole with around 8–10 peripheral perforations.

Remarks. – The described ossicle taxon belongs to the *Priscopedatus/Feddenella* group of Gilliland (1993: 66ff.), and can clearly be assigned to the Holothuriidae (Aspidochirotida) due to the typical "holothuriid cross".

Occurrence. – This taxon occurs in the late Santonian of Spain.

[p. p.] Paragenus ***Parvispina*** Kornicker & Imbrie, 1958

Type species. – *Stichopites spinosus* Frizzell & Exline, 1956 from the Mississippian of Illinois, U.S.A.

Remarks. – The paragenus *Parvispina* also needs to be revised in comparison to other members (e.g., *Rhabdotites*, *Stichopites*) of the paraphyletic parafamily Stichopitidae (e.g., Gilliland 1993: 65-66). We therefore use the paragenus name in quotation marks.

'Parvispina' sp.

Fig. 4B

Material. – One holothuriid rod (GZG.INV.91447).

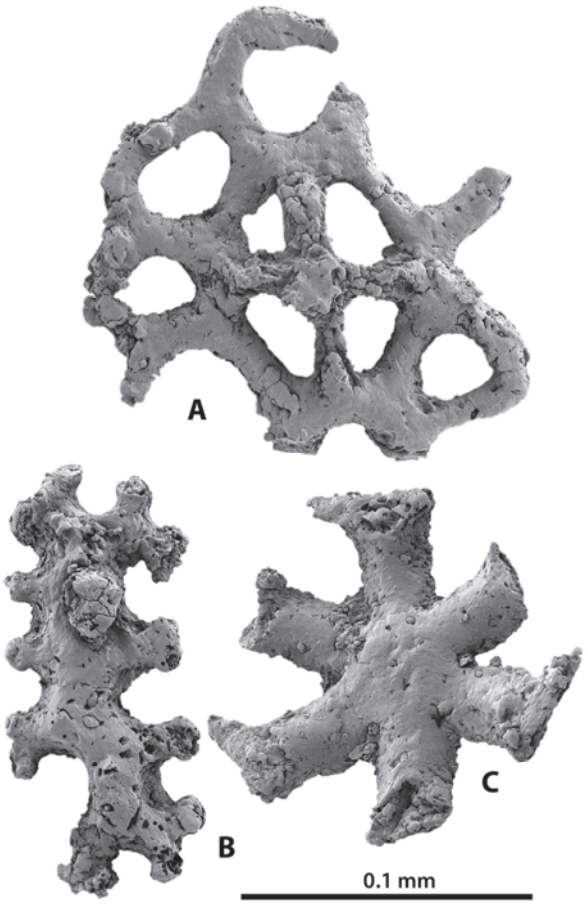


Fig. 4: Representative ossicles of holothuriid **(A–B)** and chiridotid **(C)** sea cucumbers. **(A)** incomplete table ossicle *'Priscopedatus'* sp. (Holothuriidae), GZG.INV.91449, upper side; **(B)** rod-like ossicle *'Parvispina'* sp. (Holothuriidae), GZG.INV.91447. **(C)** not fully developed wheel, gen. et sp. indet. (Chiridotinae), GZG.INV.91448, upper side.
All from the late Santonian; Font de la Plata, east of Rúbies, Catalonia, Spain. Scale bar = 0.1 mm.

Description. – Straight and slightly arched rod, around 150 μm in length, and short dichotomously branched, not spinose.

Remarks. – This ossicle taxon can be clearly assigned to the Holothuriidae, where most ancient members, like *Actinopyga*, *Bohadschia* and *Holothuria (Halodeima)* (Samyn et al. 2005) bear this type of rod in the body-wall and (partly) tube-feet (e.g., Rowe 1969; Massin 1996, 1999; Samyn 2003).

Occurrence. – This taxon occurs in the late Santonian of Spain.

Both holothuriid taxa lived probably, as (nearly) all other members of the Holothuriidae, as epibenthic deposit feeders.

Subclass **Synaptacea** Cuénot, 1891
Order **Apodida** Brandt, 1835 [= Synaptida Cuénot, 1891 *sensu* Smirnov, 2012]
Suborder **Synaptina** Smirnov, 1989

Family **Chiridotidae** Östergren, 1898
Subfamily **Chiridotinae** Östergren *sensu* Smirnov, 1998

gen. et sp. indet.

Fig. 4C

Material. – One (not fully developed) wheel (GZG.INV.91448).

Description. – The single specimen is a typical, not fully developed, (6-spoked) chiridotid wheel. The diameter is ~123 μm.

Remarks. – Further statements are not possible due to the missing rim (dentation etc.). This small wheel-ossicle represents the first record of a member of the Chiridotidae (Chiridotinae) from Santonian strata worldwide (cf. Fig. 8).

Occurrence. – This taxon occurs in the late Santonian of Spain.

Family Synaptidae Burmeister, 1837 *sensu* Östergren, 1898

Paragenus ***Calcancora*** Frizzell & Exline, 1956

Type species. – *Calcancora mississippiensis* Frizzell & Exline, 1956 from the Paleogene (Oligocene) of Mississippi, U.S.A.

Calcancora sp. 1

Fig. 6A

Material. – One incomplete anchor (GZG.INV.91410).

Description. – Incomplete anchor ossicle, with preserved flukes only, which are long (~115 μm) and serrated with 8–10 teeth on each fluke.

Remarks. – The described anchor ossicle probably belongs to *Eorynkatorpa catalonica* gen. et sp. nov. (Rynkatorpinae), where such serrated anchors (with >5 teeth on each fluke) are common.

Occurrence. – This taxon occurs in the late Santonian of Spain.

Calcancora sp. 2

Fig. 6B

Material. – One incomplete anchor (GZG.INV.91411).

Description. – Incomplete anchor ossicle of medium length (~250 μm) with two moderately long (~95 μm) flukes, and 4–5 small teeth on lower side of each fluke. Knob not branched and with no visible denticulation.

Remarks. – The described anchor ossicle probably belongs to *Eoleptosynapta jaumei* gen. et sp. nov. (?stem Leptosynaptinae), where such sparsely serrated anchors combined with this type of (unbranched) knob are known.

Occurrence. – This taxon occurs in the late Santonian of Spain.

Family **Synaptidae** Burmeister, 1837 *sensu* Östergren, 1898
Subfamily **Rynkatorpinae** Smirnov, 1989

Genus ***Eorynkatorpa*** Reich gen. nov.

Type species. – *Eorynkatorpa catalonica* Reich sp. nov. from the late Santonian of Catalonia, Spain.

Etymology. – Named after Greek ἕως = dawn, and in remembrance of the modern holothurian genus *Rynkatorpa*. The generic name is of feminine gender.

Diagnosis. – Synaptid sea cucumbers with distinct anchor plates, which are more or less elongate and slightly irregular in outline; with less than 15 perforations, of which the two in the center of the plate are prominent, much larger and elongated. All perforations have smooth margins.

Comparison. – The new genus differs from the related modern *Rynkatorpa* Rowe & Pawson, 1967 in having less than 25 perforations and even a different articulation area (cf. also Clark 1908; Rowe & Pawson 1967; Smirnov 1997; Pawson & Vance 2005). No fossil representatives or relatives of *Rynkatorpa* are known up to now.

Occurrence. – Hitherto known only from the late Cretaceous (Santonian) of Spain.

Eorynkatorpa catalonica Reich sp. nov.

Figs. 5A–D

Material. – One cluster of two anchor plate ossicles (GZG.INV.91450; holotype); one further anchor plate (GZG.INV.91451; paratype).

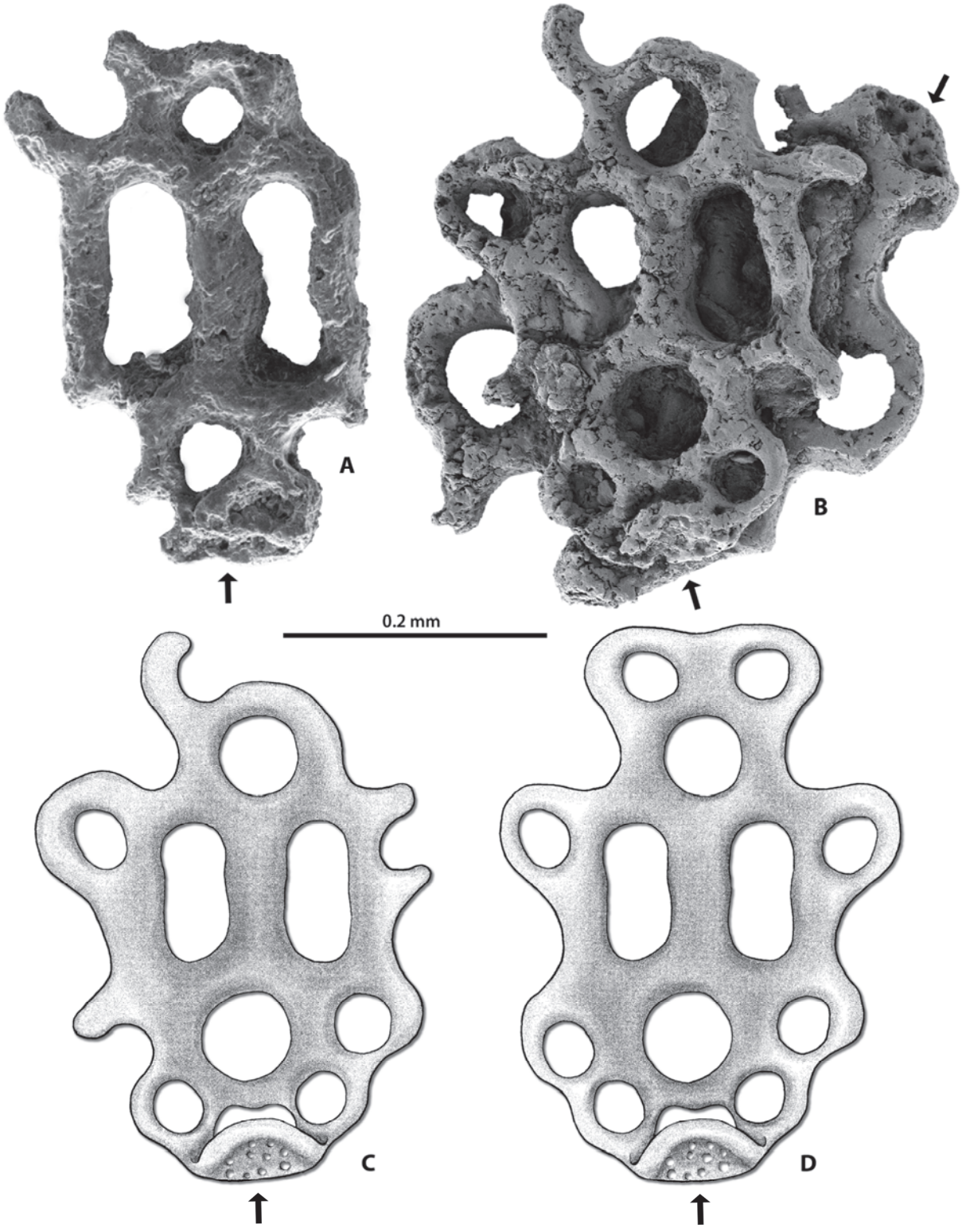


Fig. 5: Representative ossicles of a new synaptid sea cucumber **(A–D)**, *Eorynkatorpa catalonica* gen. et sp. nov. **(A)** incomplete anchor plate GZG.INV.91451, paratype, upper side; **(B)** cluster of two anchor plates GZG.INV.91450, holotype, upper side; **(C–D)** schematic (interpretative) drawing of the upper side, showing a more irregular **(C)** or a regular **(D)** outline of the anchor ossicle.
The arrows mark the articulation areas for the anchor ossicles. All from the late Santonian; Font de la Plata, east of Rúbies, Catalonia, Spain. Scale bar 0.2 mm.

Type locality. – Font de la Plata, Sierra del Montsec, Catalonia, Spain.

Type horizon. – Marly limestones of the "Santon E", (Cretaceous: late Santonian).

Etymology. – Named after the region ("Catalonia") where the new species, described in this paper, was found.

Diagnosis. – As for the genus.

Description. – The new anchor plates are more or less elongate and slightly irregular in outline, 420–450 µm long and 280–300 µm wide. All ossicles with 8–13 perforations, of which the two central perforations are very prominent, angular in outline and three times larger than any other present perforation. The articular end is simple, forming a turned over edge, slightly curved and finely perforated. All perforations have smooth margins.

Comparison. – See under *Eorynkatorpa*.

Remarks. – The two large prominent perforations in the centre are typical for representatives of the extant genus *Rynkatorpa* Rowe & Pawson, 1967. Members of this genus are currently known with around a dozen species from bathyal [*R. albatrossi* (Fisher); *R. bicornis* (Sluiter); *R. challengeri* (Théel); *R. coriolisi* Smirnov; *R. duodactyla* (Clark); *R. felderi* Pawson & Vance; *R. pawsoni* Martin; *R. sluiteri* (Fisher); *R. timida* (Koehler & Vaney)] and shallow-water [*R. bisperforata* (Clark); *R. gibbsi* Rowe; *R. hickmani* Rowe & Pawson; *R. uncinata* (Hutton)] depths, mostly from the Pacific Ocean (e.g., Clark 1908; Rowe & Pawson 1967; Smirnov 1983a, 1983b; Pawson & Vance 2005). Only one representative was reported from the Atlantic Ocean (*R. felderi* Pawson & Vance, 2005).

All species of *Rynkatorpa* are detritus/deposit feeders with specimen lengths between 0.5 and 13 cm, living as burrowers in soft substrates.

The present new species represents the oldest unequivocal record related to this group (cf. also Fig. 8). Smirnov (2012: 811) also assigned the sclerite association of *Rigaudites punctatus* Mutterlose, 1982 and *Calcancora michaeli* Mutterlose, 1982 (both from the Albian of northern Germany) to the extant genus *Rynkatorpa*, which is, in opinion of the first author, not clearly supportable. The anchor plate *R. punctatus* with its four medium-sized central perforations surrounded by numerous smaller perforations does not match the definition of the subfamily Rynkatorpinae (Smirnov 1998: 520, 2012: 811) or the genus *Rynkatorpa* (Rowe & Pawson 1967: 31; Pawson & Vance 2005: 16). Our new species *Eorynkatorpa catalonica* is rather a *Rynkatorpa*-stem group representative, in which the two typical central large (angular) perforations were formed by fusion of four central medium-sized perforations (e.g., *Rigaudites punctatus*, cf. Mutterlose 1982: pl. 8.6-2, fig. 23).

Occurrence. – The new species occurs in the late Santonian of Spain.

Subfamily (?stem group) **Leptosynaptinae** Burmeister, 1837 *sensu* Östergren, 1898

Genus ***Eoleptosynapta*** Reich gen. nov.

Type species. – *Eoleptosynapta jaumei* Reich sp. nov. from the late Santonian of Catalonia, Spain.

Etymology. – Named after Greek ἔως = dawn, and in remembrance of the modern holothurian genus *Leptosynapta*. The generic name is of feminine gender.

Diagnosis. – Synaptid sea cucumbers with distinct anchor plates, which are more or less reverse pear-shaped in outline; with 3(–4) horizontal rows of prominent medium-sized perforations (8–15), and an inconspicuous ledge for the articulation of the anchor. All perforations have smooth margins.

Comparison. – The new genus differs from related modern genera like *Leptosynapta* Verrill, 1867, *Epitomapta* Heding, 1928, and *Eupatinapta* Heding, 1928 (e.g., Clark 1924; Heding 1928; Cherbonnier 1953b, 1988; Thandar & Rowe 1989) in having smooth perforation margins. Only *Patinapta* Heding, 1928 has (in part) no serrations at the margins of perforations (e.g., Heding 1928, 1929; Cherbonnier 1953a, 1954, 1955, 1988), but can be distinguished from *Eoleptosynapta* gen. nov. by a different arrangement of anchor plate perforations. Within the Leptosynaptinae only members of *Eupatinapta* have more than the 7 (6 + 1) perforations in the main part of anchor plates, but these are serrated. In contrast to Reich (2003b: 81, 86), Smirnov (2012: 811) also assigned the sclerite association of *Rigaudites nudus* Reich, 2003b and *Calcancora pomerania* Reich, 2003b (both from the early Maastrichtian of northern Germany) to the Leptosynaptinae, which is, in opinion of the first author, not convincing. No related Mesozoic representatives are known up to now, however, members of the Leptosynaptinae from Cenozoic strata are well-known (e.g., Frizzell & Exline 1956, 1957; cf. Smirnov 2012).

Occurrence. – Hitherto known only from the late Cretaceous (Santonian) of Spain.

Eoleptosynapta jaumei Reich sp. nov.

Figs. 6C–F, 7A–C

Material. – 35 nearly complete or partly broken anchor plates (GZG.INV.91412–91446).

Type locality. – Font de la Plata, Sierra del Montsec, Catalonia, Spain.

Type horizon. – Marly limestones of the "Santon E", (Cretaceous: late Santonian).

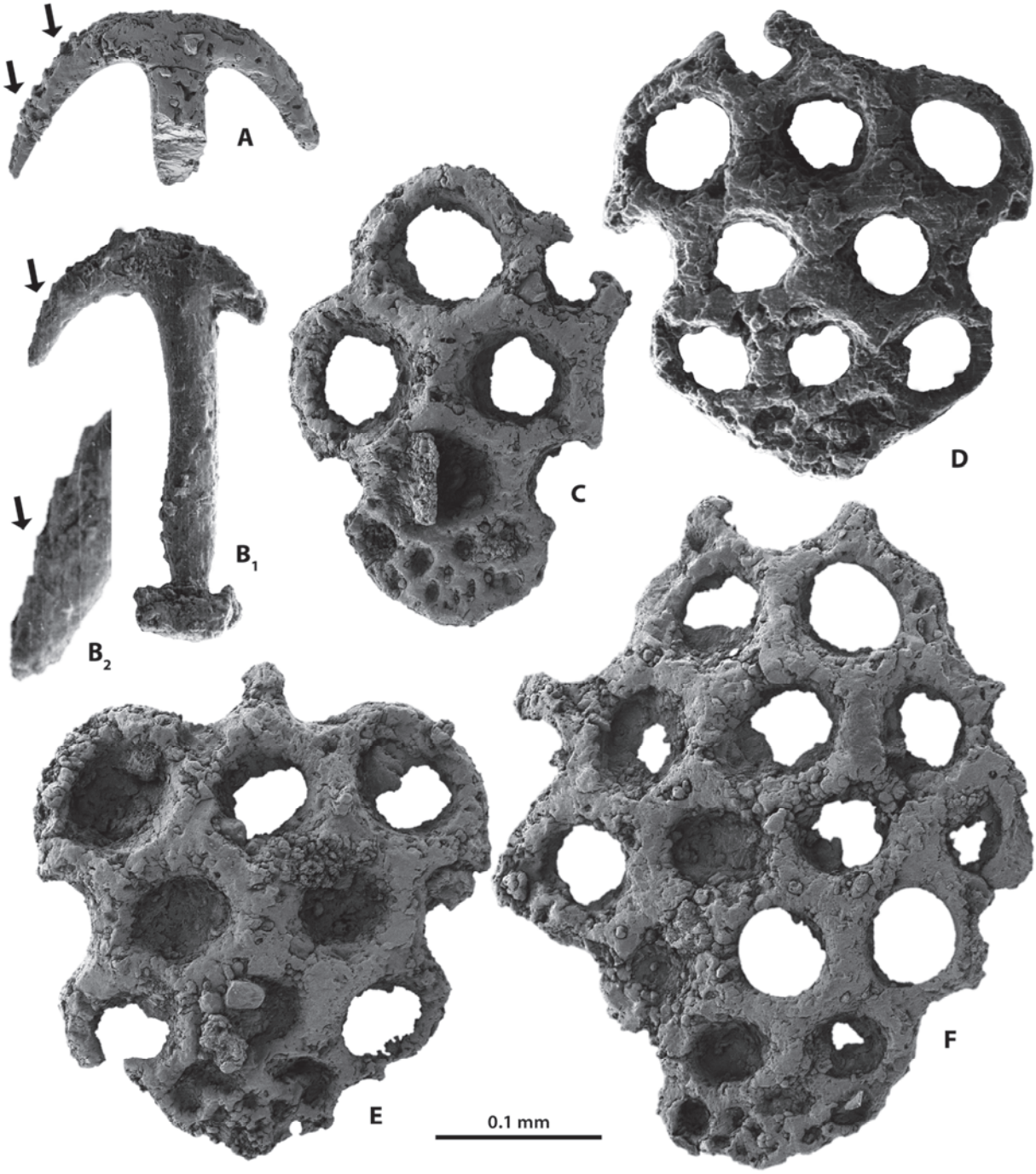


Fig. 6: Representative ossicles of synaptid sea cucumbers. **(A)** *'Calcancora'* sp. 1 (Rynkatorpinae), incomplete anchor GZG.INV.91410, upper side, **(A_1)** total view, **(A_2)** detail of one fluke showing few fine denticles; **(B)** *'Calcancora'* sp. 2 (Rynkatorpinae), incomplete anchor GZG.INV.91411, upper side; **(C–F)** *Eoleptosynapta jaumei* gen. et sp. nov.; **(C)** juvenile anchor plate GZG.INV.91412, paratype, lower side; **(D)** ?subadult/adult anchor plate GZG.INV.91413, paratype, lower side; **(E)** ?subadult/adult anchor plate GZG.INV.91414, holotype, lower side; **(F)** incomplete adult anchor plate GZG.INV.91415, paratype, lower side.
Perforations in anchor plates are partly filled with sediment. The arrows in (A) and (B) mark the preserved teeth at anchor flukes. All specimens from the late Santonian; Font de la Plata, east of Rúbies, Catalonia, Spain. Scale bar 0.1 mm.

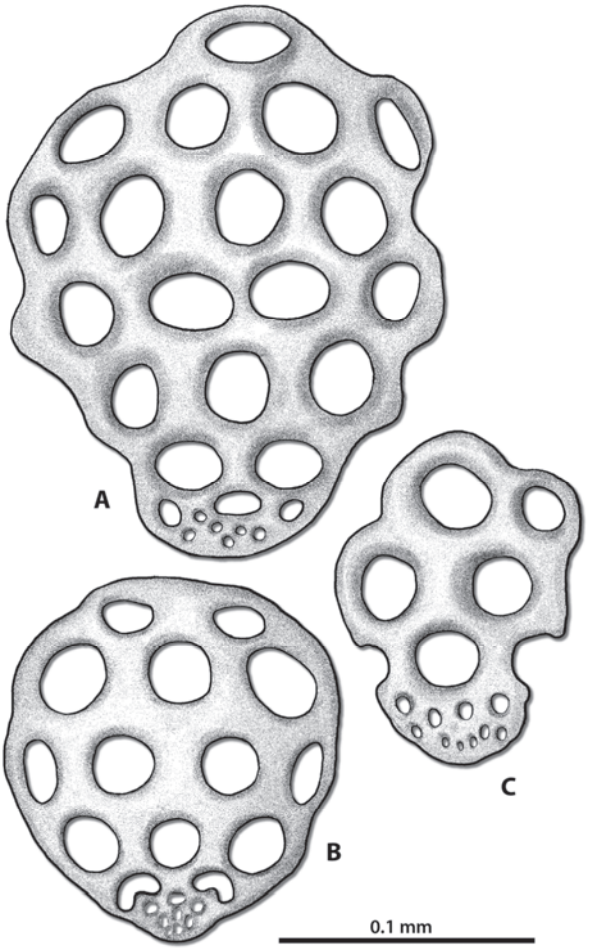


Fig. 7: Schematic drawings of representative ossicles of a new synaptid sea cucumber **(A–C)**, *Eoleptosynapta jaumei* gen. et sp. nov. **(A)** adult anchor plate, lower side; **(B)** ?subadult anchor plate, lower side; **(C)** juvenile anchor plate, lower side.
All from the late Santonian; Font de la Plata, east of Rúbies, Catalonia, Spain. Scale bar 0.1 mm.

Etymology. – Named after Jaume Gallemí (*1954), Barcelona, in recognition of his contributions to Cretaceous echinoderms from Spain.

Diagnosis. – As for the genus.

Description. – The new anchor plate ossicles are more or less pear-shaped in outline, and ~250–430 µm long and ~200–330 µm wide, with 3(–4) rows of medium-sized perforations. These rows contain altogether 8–15 perforations (each 45–55 µm in diameter) with smooth margins. The articulation area for the anchor ossicle is build up by an inconspicuous ledge with numerous very small perforations of subcircular and suboval outline.

Comparison. – See under *Eoleptosynapta*.

Remarks. – The present ossicle association probably presents a stem group member of the Leptosynaptinae, due to the clearly arranged medium-sized perforations of the anchor plates. Representatives of the more Cenozoic and modern Leptosynaptinae + Synaptinae (cf. Frizzell & Exline 1957; Smirnov 1999) normally contain 6 + 1 prominent perforations in the main part of anchor ossicles (see Smirnov 2012: 811f.). It would be conceivable that two rows were reduced during early diversification and later evolution (cf. also Fig. 8).

Species of related leptosynaptid sea cucumbers are quite larger than rynkatorpid species, with specimen lengths normally between 10 and 20(30) cm. They developed different lifestyles; most modern species are infaunal deposit feeders ("funnel-feeders") living in U- or L-shaped tubes (e.g., Roberts et al. 2000), but also facultative swimmers are known (e.g., Costello 1946; Glynn 1965).

Occurrence. – This taxon occurs in the late Santonian of Spain.

Discussion

The species described and discussed herein belong to three holothurian groups: Apodida, Aspidochirotida, and Molpadiida. There are six recognised taxa: (1) *Cruxopadia mesozoica* gen. et sp. nov., (2) *C. reitneri* gen. et sp. nov. (both Molpadiida: ?stem group Molpadiidae), (3) *Eorynkatorpa catalonica* gen. et sp. nov. (Apodida: Synaptidae: Rynkatorpinae), (4) *Eoleptosynapta jaumei* gen. et sp. nov. (Apodida: Synaptidae: Leptosynaptinae), (5) gen. et sp. indet. (Apodida: Chiridotidae: Chiridotinae), and (6) gen. et sp. indet. (Aspidochirotida: Holothuriidae). The two different described anchor ossicles (paragenus *Calcancora*) probably belong either to *Eorynkatorpa catalonica* (*Calcancora* sp. 1) or to *Eoleptosynapta jaumei* (*Calcancora* sp. 2). The both holothuriid ossicles (table = '*Priscopedatus*' sp. and rod = '*Parvispina*' sp.) probably also form a biological species. Most of the fossil species encountered herein were infaunal detritus/deposit feeders (1–5); only holothuriid sea cucumbers normally live as epibenthic detritus/deposit feeders (6).

The sea cucumber material reported in our paper represents the first Santonian holothurian fauna ever described worldwide, helping to fill in some gaps in the fossil record (cf. Fig. 8). Especially the synaptid (Figs. 5–7) and probably also the molpadiid (Fig. 3) holothurians underwent a period of rapid diversification in the Cretaceous. Our results provide new insight in the early diversification of the Synaptidae (Apodida) as well as will help to improve calibration points of divergence times for sea cucumber groups in future studies.

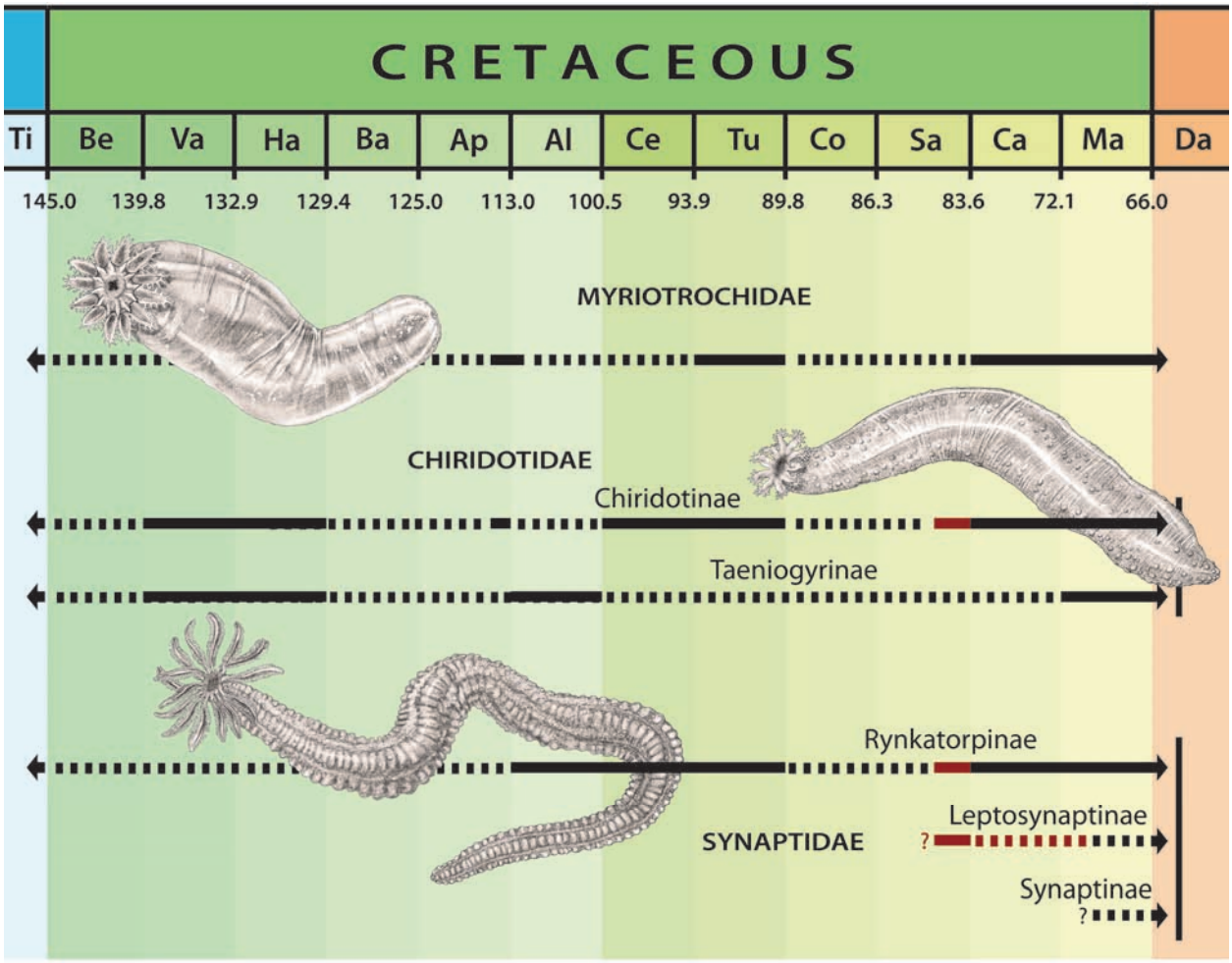


Fig. 8: Evolutionary history of Cretaceous apodid sea cucumbers. Red bars showing the filled gaps in the Fossil Record due to the here described Santonian fauna (Fossil Record of Apodida after Reich in Herrig et al. 1997; Reich 2002, 2003a, 2003b; Reich & Wiese 2010 and Reich unpubl., modified).

Acknowledgements

We thank A. Bartolini (Paris), T. Ewin (London), A. Kroh (Vienna), R. Panchaud (Basel), O. Schmidt (Basel), A.B. Smith (London), M.-T. Vénec-Peyré (Paris), T. Wiese (Hannover) for access to fossil echinoderm material housed in their institutions.

Stimulating discussions on holothurians with R. Haude (Göttingen), D. L. Pawson (Washington, D.C.), A. Smirnov (St. Petersburg), and other colleagues are also gratefully acknowledged.

This study was supported in part by Synthesys grants (AT-TAF-787, FR-TAF-1618) to MR, a programme financed by European Community Research Infrastructure Action. Partially funding (MR) of this project by the German Science Foundation (DFG HE2476/2-1, RE2599/6-1, 6-2) is also gratefully acknowledged.

Additional thanks are due to Andrew S. Gale (Portsmouth), his comments greatly improved the final version of our manuscript. We would also like to thank D. Hause-Reitner, C. Hundertmark and T. R. Stegemann (all Göttingen) for technical assistance.

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Cite this article: Reich, M. & Ansorge, J. (2014): Santonian sea cucumbers (Echinodermata: Holothuroidea) from Sierra del Montsec, Spain. *In:* Wiese, F.; Reich, M. & Arp, G. (eds.): "Spongy, slimy, cosy & more…". Commemorative volume in celebration of the 60th birthday of Joachim Reitner. *Göttingen Contributions to Geosciences* **77**: 147–160.

http://dx.doi.org/10.3249/webdoc-3925