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The fossil record of the family Benthopectinidae (Echinodermata, Asteroidea), a reappraisal

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Abstract. Fossils assigned to the predominantly deep-sea asteroid family Benthopectinidae Verrill, 1894 are described and their affinities reappraised. Detailed comparative morphology of ambulacrals, adambulacrals and marginal ossicles has revealed that only some extinct taxa fall within the morphological range of the modern representatives of the family. These include *Jurapecten hessi* Gale, 2011, *J. infrajurensis* sp. nov. (both Jurassic), *J. dhondtae* sp. nov. (Upper Cretaceous) and *Nearchaster spinosus* (Blake, 1973) comb. nov. (Lower Oligocene). A new Late Cretaceous genus, *Punkaster* gen. nov. (*P. spinifera* gen. et sp. nov. and *P. ruegenensis* gen. et sp. nov.), appears to be a highly derived benthopectinid. A possible benthopectinid is described from the Upper Triassic (Carnian) of China. Other described records are distantly related to, but convergent in gross morphology with, benthopectinids. Thus, *Plesiastropecten hallovensis* Peyer, 1944 is here referred to the Jurassic spinulosidan family Plumasteridae Gale, 2011 and *Xandarosaster hessi* Blake, 1984 is interpreted as Spinulosida Perrier, 1884 incertae sedis. The mid-Cretaceous *Alkaidia sumralli* Blake & Reid, 1998 is reassigned to the Forcipulatida (Zorocallina). The "fossil benthopectinid" of Spencer & Wright in Moore (1966) is shown to belong to the goniopectinid genus *Chrispaulia* Gale, 2005, of which two new Cretaceous species are described, *C. wrightorum* sp. nov. and *C. spinosa* sp. nov. Finally, we consider *Henricia*? *venturana* Durham & Roberts, 1948 to be an indeterminate asteroid.

Keywords. Neoasteroidea, Mesozoic, North America, Europe, new taxa.

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Introduction

Benthopectinids form a small but well-characterised family of predominantly deep-sea asteroids, of very widespread distribution in the deeper bathyal and abyssal regions of the world's oceans. Eight genera are now recognised (Clark 1981; Clark & Downey 1992), of which only two, *Pontaster* Sladen, 1885 and *Cheiraster* Studer, 1883, extend onto the continental shelves, and then only at high northern latitudes. Approximately 75 species are currently considered valid (Clark & Downey 1992; Mah 2020a) and, although the taxonomy of benthopectinids has been described in considerable detail, their biology is poorly known. Gage *et al*. (1982) described the reproductive biology of three Atlantic species and concluded that they underwent direct development from large yolky eggs. The presence of special longitudinal muscles in the arms of benthopectinids has led to suggestions that they either swim or raise the arms for filter feeding. In-situ deep-sea photographs (Mah 2020b) show a partially buried specimen of *Cheiraster* cf. *echinulatus* (Perrier, 1875) with superomarginal spines projecting above the substrate. Mah (2020b) also recorded other (unnamed) benthopectinids sitting on open substrates.

Over the last 40 years, a number of authors have identified extinct species of asteroid as benthopectinids. In the *Treatise of Invertebrate Paleontology*, Spencer & Wright (1966) recorded a fossil benthopectinid from the Albian (mid-Cretaceous) of the United Kingdom, but failed to provide more details. The specimen upon which this record was based is now in the C.W. and E.V. Wright Collection at the Natural History Museum, London (NHMUK). Blake (1973) described the ossicular morphology of benthopectinids for the first time, and recorded a new genus and species of benthopectinid, *Mistia spinosa* Blake, 1973, from the Lower Oligocene of Oregon. Subsequently, Blake (1984) identified two fossils from the Jurassic of Switzerland as benthopectinids, namely *Plesiastropecten hallovensis* Peyer, 1944 (of Hettangian age) and *Xandarosaster hessi* Blake, 1984 (of Bajocian age), which he placed in a new subfamily, the Paleobenthopectininae. In the same paper, he referred *Henricia*? *venturana* Durham & Roberts, 1948, from the Cretaceous of California, to the benthopectinids. Villier *et al.* (2009) transferred *Xandarosaster* and *Plesioastropecten* to the Order Velatida Perrier, 1884. A further genus and species, *Alkaidia sumralli* Blake & Reid, 1998, from the upper Albian–Cenomanian of Texas, was referred to the subfamily Paleobenthopectininae. This has subsequently been transferred to the forcipulatacean family Terminasteridae Gale, 2011 by Gale (2011a) and Ewin & Gale (2020). Blake & Jagt (2005) recorded a benthopectinid, *Cheiraster*? sp., from the upper Maastrichtian of the Netherlands, and Jagt (2000) had earlier identified two (or more) benthopectinid species, benthopectinid sp. 1 (? spp.) and benthopectinid sp. 2, on the basis of both isolated and associated ossicles from the upper Campanian and Maastrichtian of northeast Belgium, southeast Netherlands and the Aachen area (Germany). Gale (2011a, 2011b) described *Jurapecten hessi* from the Upper Jurassic (Oxfordian) of the French Jura, based on isolated and associated ossicle groups. ASG had previously collected further material of Jagt's "benthopectinid 2" from the Cenomanian–Campanian Chalk of England. Subsequently, we set about to describe this material, augmented by an associated set of ossicles from the uppermost Maastrichtian of Stevns Klint, eastern Denmark, herein described as *Punkaster spinifera* gen et sp. nov. From that study followed a reappraisal of the taxonomic affinities of all fossils so far assigned to the Benthopectinidae, their relationships with extant genera and the phylogeny of the family.

Two new species of the genus *Jurapecten* Gale, 2011 are described, one of Jurassic (middle Toarcian), the other of Cretaceous (late Maastrichtian) age, while *Mistia spinosa* is reassigned to the Recent genus *Nearchaster* Fisher, 1911. In addition, one new Late Cretaceous genus, *Punkaster* gen. nov. (with two species, *P. spinifera* gen. et sp. nov. and *P. ruegenensis* gen. et sp. nov.), which appears to be a highly derived benthopectinid, is erected. *Plesiastropecten hallovensis* Peyer, 1944 is reassigned to the Jurassic spinulosidan family Plumasteridae Gale, 2011, *Xandarosaster hessi* interpreted as Spinulosida incertae sedis and *Alkaidia sumralli* placed in the Forcipulatida Perrier, 1884 (Zorocallina Downey, 1970). Lastly, two new Cretaceous species of the goniopectinid genus *Chrispaulia* Gale, 2005 are erected, *C. wrightorum* sp. nov. and *C. spinosa* sp. nov., and *Henricia*? *venturana* is considered to be an indeterminate asteroid.

Material and methods

The present study is based on fossil material contained in several North American and European museums (see list of institutional abbreviations below). Comparative Recent material of several taxa housed in a few institutional collections (Table 1) has also been used, as have partially macerated (bleach) specimens in the A.S. Gale Collection; the latter have not been formally registered. Specimens used for SEM examination were gold-palladium coated and imaged in a Jeol SEM.

Morphological terminology follows Gale (2011a, 2011b) and Ewin & Gale (2020).

Institutional abbreviations

BGS = British Geological Survey, Keyworth, United Kingdom
IoS = Institute of Oceanographic Sciences, Southampton, UK
MHI = Muschelkalkmuseum Hagdorn, Ingelfingen, Germany
MZA = Museum zu Aller Heiligen, Schaffhausen, Switzerland
Nds LH = Niedersächsisches Landesmuseum, Hannover, Germany
NHMM = Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands (JJ – J.W.M. Jagt Collection; MD – M.J.M. Deckers Collection)
NHMUK = The Natural History Museum, London, United Kingdom
NMB = Naturhistorisches Museum Basel, Switzerland
SNSB-BSGP = Bavarian State Collection of Palaeontology and Geology, Munich, Germany
UCMP = University of California, Museum of Paleontology, Berkeley, California, USA
USNM = United States National Museum, Washington DC, USA

Abbreviations for asteroid morphology

ab = abactinal ossicle
abiim = abactinal interradial interoral muscle (oral)
abr = abactinal ridge (on amb)
abtam = abactinal transverse amb muscle
aciim = actinal interradial interoral muscle
actam = actinal transverse amb muscle
actf = actinal face (of oral)
ad = adambulacral ossicle
ada1 = single distal amb-adamb articulation
ada1a = distal adradial amb-adamb articulation
ada1b = distal abradial amb-adamb articulation
ada2 = proximal adradial amb-adamb articulation
ada3 = proximal abradial adamb-amb or adamb-adamb articulation
adada = adamb-adamb articulation
adadm = interadambulacral muscle
adamb = adambulacral
adp = adambulacral process
adpm = adambulacral prominence
amb = ambulacral ossicle
ambb = base of ambulacral ossicle
ambh = head of ambulacral ossicle
ambsh = shaft of ambulacral ossicle
amn = ambulacral notch
apo = apophyse on oral
car = caries-like holes on articulation surfaces of amb, adamb
ce = centrale
co = circumoral ossicle
coh = circumoral head
dadam = distal amb-adamb muscle

dcoa = distal circumoral articulation on oral
dcp = distal circumoral process on circumoral
de = dentition (orals, ambs, peds)
doda = distal odontophore articulation (on oral, odontophore)
fs = furrow spine
iioa = interradial interoral articulation (on oral)
im = inferomarginal
ima = articulation surface between adjacent inferomarginals
ma = inferomarginal articulation
lia = longitudinal interamb articulation
lim = longitudinal interambulacral muscle
ms = marginal spine
odom = oral-odontophore muscle
or = oral ossicle
orada = adambulacral articulation (on oral)
oradm = oral adambulacral muscle
osp = attachment of oral spine
padam = proximal adamb-amb muscle
pb = proximal blade (oral ossicle)
pcoa = proximal oral-circumoral articulation
pcp = proximal circumoral process (on circumoral)
pir = primary interradial ossicle
poda = proximal odontophore articulation (on oral and odontophore)
pr = primary radial ossicle
ra = radial
riom = radial interoral muscle
rng = ring nerve groove on oral
rvg = ring vessel groove on oral
sads = subadambulacral spine
sm = superomarginal
sos = attachment of suboral spine

Results

Morphological characteristics of extant benthopectinids

In basic construction, benthopectinids are similar to other Paxillosida Perrier, 1884 in possessing relatively elongated, tapering arms, with acutely angled to rounded interradii and conspicuous, spine-bearing marginals that frame disc and arms and a flat abactinal surface that is made of small ossicles set in a flexible integument (Figs 1–2). Indeed, astropectinid taxa such as *Dytaster* Sladen, 1889, which bear single spines on each marginal ossicle and in which intermarginal fascioles are poorly developed, are superficially similar to benthopectinid genera like *Pontaster*. More detailed inspection of both the external and internal morphology, however, reveals that all extant benthopectinids share numerous distinctive characters; these are discussed below. Whether or not the presence of these justifies the elevation of the family to an order (i.e., Notomyotida Ludwig, 1910) has been the source of controversy amongst taxonomists. In the phylogeny of Gale (2011a), benthopectinids belong to the Paxillosida, sister group to the other four families making up the group. Molecular studies suggest that benthopectinids are sister taxon to the Pseudarchasteridae, and belong to a clade which includes all Paxillosida (Mah & Foltz 2011: fig. 1).

Distinctive features of benthopectinids include the following:

- The presence of longitudinal muscles in the arms, which attach to specialised ridges on the ambulacrals (***abr***; see Fig. 3I), the dorsal body wall and the insides of the inferomarginals (Clark 1981).

- Papulae (specialised respiratory structures) are restricted to specific regions, called papularia, at the base of the arms on the abactinal surface. These are oval, or V-shaped, stand proud of the surface and are made up of distinctively thickened, triangular abactinal ossicles between which the papulae extrude (Fig. 1A).
- The presence of distinctive comb-like, multivalved pectinate (attached to more than one ossicle) and fasciculate (attached to a single ossicle) pedicellariae, in the form of a double comb of two opposing rows of valves (Fisher 1911; Jangoux & Lambert 1988). These bear a distinctive sculpture on the

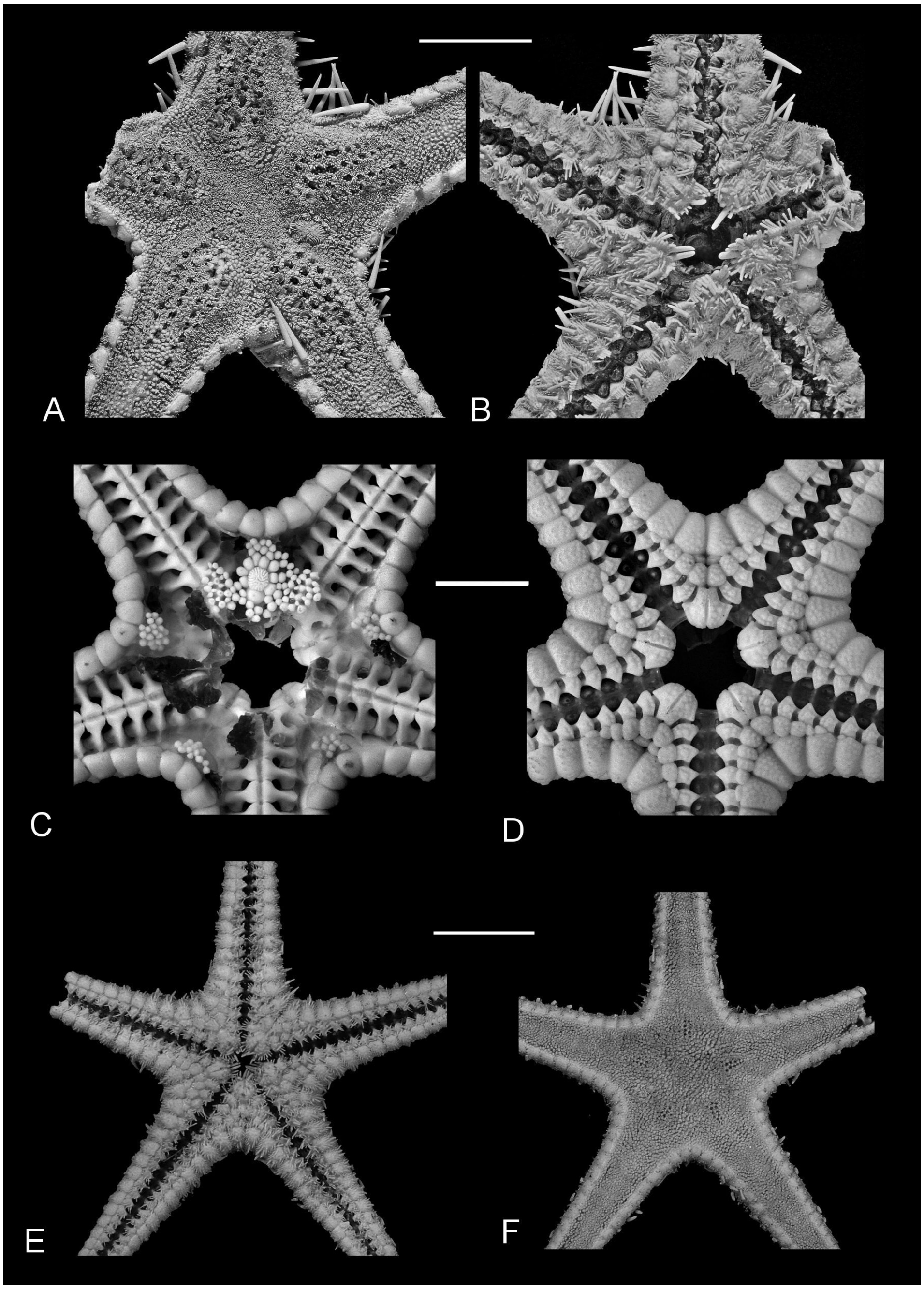

Fig. 1. A–B. *Cheiraster gazellae* Studer, 1883, Recent, in abactinal (A) and actinal (B) views (A.S. Gale collection, unregistered). **C–F**. *Pontaster tenuispinus* (von Düben & Koren, 1846), Recent, in various views (A.S. Gale collection, unregistered), Rockall Trough, NE Atlantic. Scale bars: A–B = 7 mm; C–D = 5 mm; E–F = 10 mm.

exterior of the valves. *Pontaster* has bivalved pedicellariae only (Clarke & Downey 1992). The precise homology with pedicellariae in other asteroid groups is uncertain.

- The lateral surfaces of the ambulacrals articulate with the inner sides of the inferomarginals, except on the 4–5 most proximal plates (Fig. 4A).

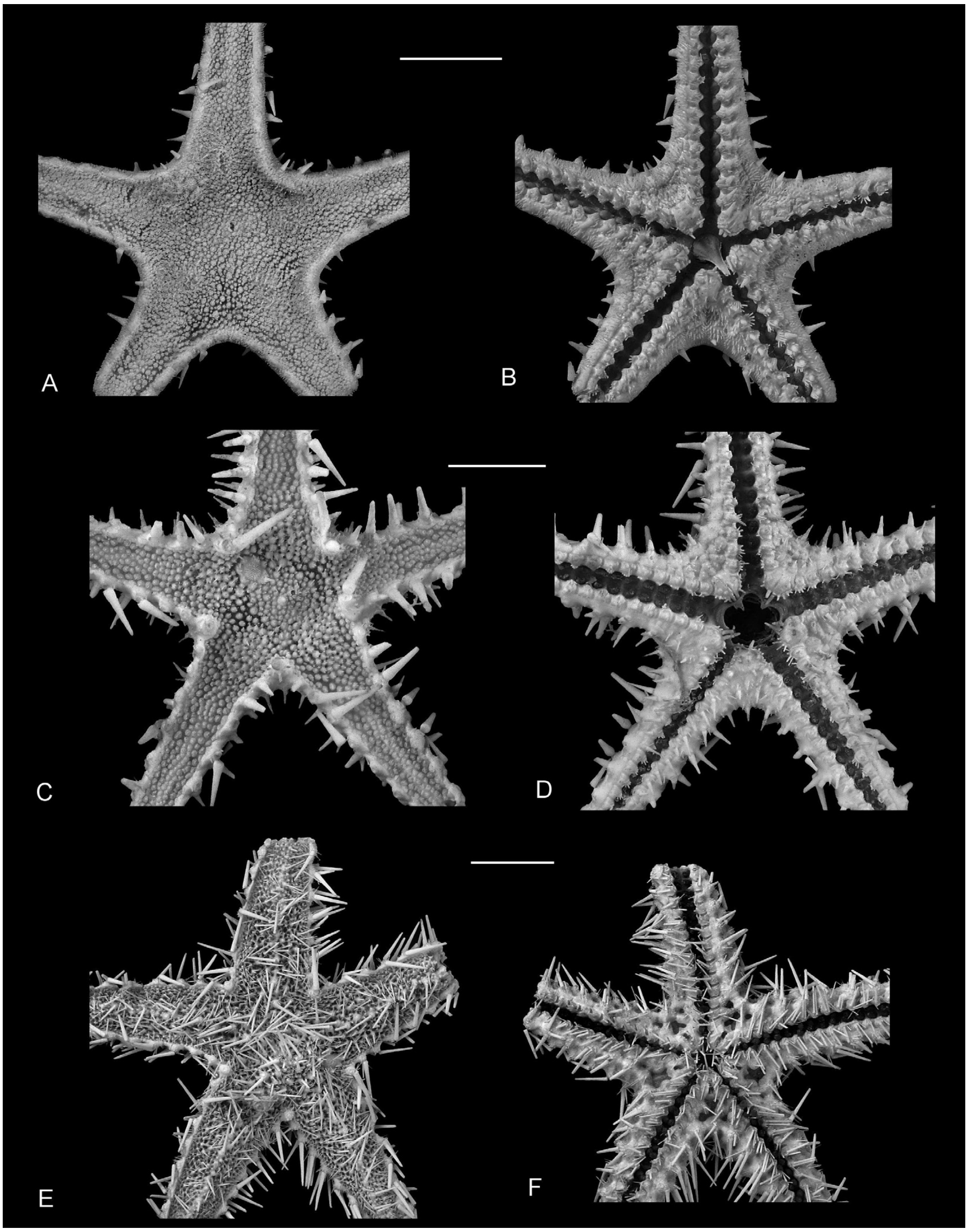

Fig. 2. A–B. *Pectinaster filholi* Perrier, 1885, Recent, in abactinal (A) and actinal (B) views, Porcupine Trough, NE Atlantic (A.S. Gale collection, unregistered). **C–D**. *Benthopecten simplex* (Perrier, 1881), Recent, in abactinal (C) and actinal (D) views, Rockall Trough, NE Atlantic (NHMUK EE 13563). **E–F**. *Nearchaster aciculosus* (Fisher, 1910), Recent, in abactinal (E) and actinal (F) views, NE Pacific (USNM, unregistered). Scale bars: A–B = 7 mm; C–D = 6 mm; E–F = 20 mm.

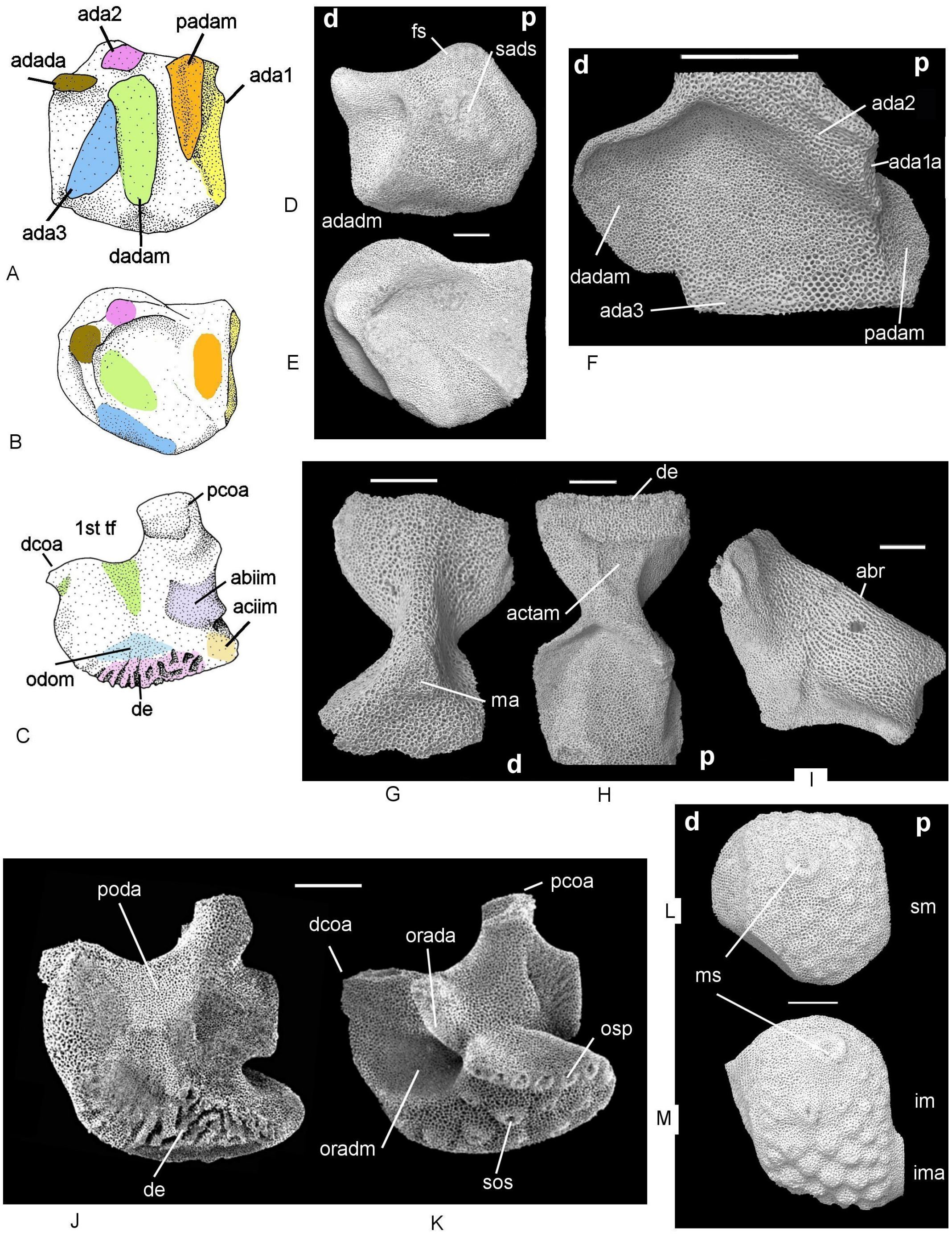

Fig. 3. **A–C**. Terminology used for adambulacrals and orals in the present paper. **A**. Actinal view of adambulacral of *Luidia* sp. — **B–F**. *Benthopecten simplex* (Perrier, 1881), Recent (NHMUK EE 13563). **B**. Abactinal view of adambulacral. **C**. Interradial view of oral ossicle. **D–E**. Adambulacral in actinal (D) and abactinal (E) views. **F**. Base of ambulacral in actinal view. — **G–I**. *Cheiraster gazellae* Studer, 1883, Recent (A.S. Gale collection, unregistered), ambulacral ossicles in abactinal (G), actinal (H) and proximal (I) views; note raised abactinal ridge (abr) and inferomarginal articulation (ma). — **J–M**. *Pontaster tenuispinus* (von Düben & Koren, 1846), Recent (A.S. Gale collection, unregistered). **J–K**. Oral ossicle in radial (K) and interradial (J) aspects. **L–M**. Supero- and inferomarginal pair. Abbreviations: d = distal; p = proximal; see Material and methods; after Gale 2011a: figs 10, 16. Scale bars: 1 mm.

- All but the few most proximal infero- and superomarginals alternate with each other (Fig. 4B–E).
- The articulation between successive inferomarginals is specialised. A flange is present on the proximal actinolateral surface of each inferomarginal, which carries a strip of smooth imperforate stereom for articulation with the distal part of the adjacent ossicle (Figs 3M, 4W).
- The ambulacrals are hourglass-shaped, with equally expanded triangular head and base (Fig. 5I–M). The ambulacral heads of successive ambulacrals abut, and do not imbricate.
- The ambulacral-adambulacral contact is highly modified (Blake 1973; Gale 2011a) in comparison to other paxillosidans (Fig. 3A–B). Articulation ***ada3*** is elongated and positioned on the abradial margins of ambulacrals and adambulacrals (Fig. 3B, F). ***Adada*** and ***ada2*** are set on a raised ridge on the adambulacrals and the ***ada2*** articulation surface is present on a ridge on the ambulacral base (Fig. 3F). The central part of the ambulacral base adjacent is concave and sites of attachment of the ambulacral-adambulacral muscles (***padam***, ***dadam***) are strongly asymmetrical, with a reduced ***padam*** (Fig. 3F). The muscle attachment site ***padam*** is carried on short, wing-like flanges on the ambulacral bases. No other asteroids have this complex and highly derived ambulacral-adambulacral contact (Gale 2011a).
- The adambulacral construction and spination. The adradial margin of the ambulacrals projects into the groove, with an angled or rounded margin which carries a row of numerous adambulacral furrow spines. The central portion of the actinal adambulacral surface bears one or two large subadambulacral spines.
- The morphology and spination of the oral ossicles (Fig. 3C, J–K). The oral ossicles are trapezoidal in outline, with a convex actinal margin which carries a fringe of suboral spines. The inner face of the oral ossicles has dentition on the actinal border only.
- The presence of parapaxillae: distinctively modified abactinal ossicles. Although these are diverse in form, they have a common structure – a broad flat, rounded base, with a bevelled rim, and a raised central region which carries a centrally placed spine base, commonly surrounded by smaller spine bases (Fig. 4X–Z). Parapaxillae are unique to benthopectinids.
- Enlarged abactinal and marginal spines, when present, have a distinctive construction, being cylindrical, tapering, with a concavity on the base for articulation with the underlying ossicle. They are made up of thorny stereom similar in form to the verticillate structure in echinoid spines.
- The odontophore is shield-shaped and flattened, and the surfaces articulating with the oral ossicles extend along the length of the plate. This is unlike the odontophore of any other asteroids (Gale 2011a).

Fig. 4 (next page). **A, D, J–M, O–P, S–W, Z**. *Pontaster tenuispinus* (von Düben & Koren, 1846), Recent (A.S. Gale collection, unregistered). **A**. Denuded radius, abactinal view. **D**. Lateral view of denuded arm. **J–M**. Superomarginals, lateral view. **O–P, S, W**. Inferomarginals, in lateral (O–P, S) and proximal (W) views. **T**. Circumoral ossicle. **U–V**. Oral ossicle. **Z**. Abactinal ossicle. — **B, N, R, X**. *Nearchaster aciculosus* (Fisher, 1910), Recent (A.S. Gale collection, unregistered). **B**. Lateral view of denuded arm. **N, R**. Marginal pair. **X**. Abactinal ossicle. — **C, F–G, Y**. *Pectinaster filholi* (Perrier, 1885), Recent (A.S. Gale collection, unregistered). **C**. Denuded arm, in lateral view. **F–G**. Marginal pair. **Y**. Abactinal ossicle. — **E, Q**. *Cheiraster gazellae* Studer, 1883, Recent (A.S. Gale collection, unregistered). **E**. Lateral view of denuded arm. **Q**. Lateral view of superomarginal. — **H–I**. *Benthopecten simplex* (Perrier, 1881), Recent (A.S. Gale collection, unregistered), lateral view of supero-/inferomarginal pair. Abbreviation: d = distal. See Fig. 3 for detailed morphological terminology. Scale bars: A–E = 5 mm; F–W = 1 mm; X–Z = 0.5 mm.

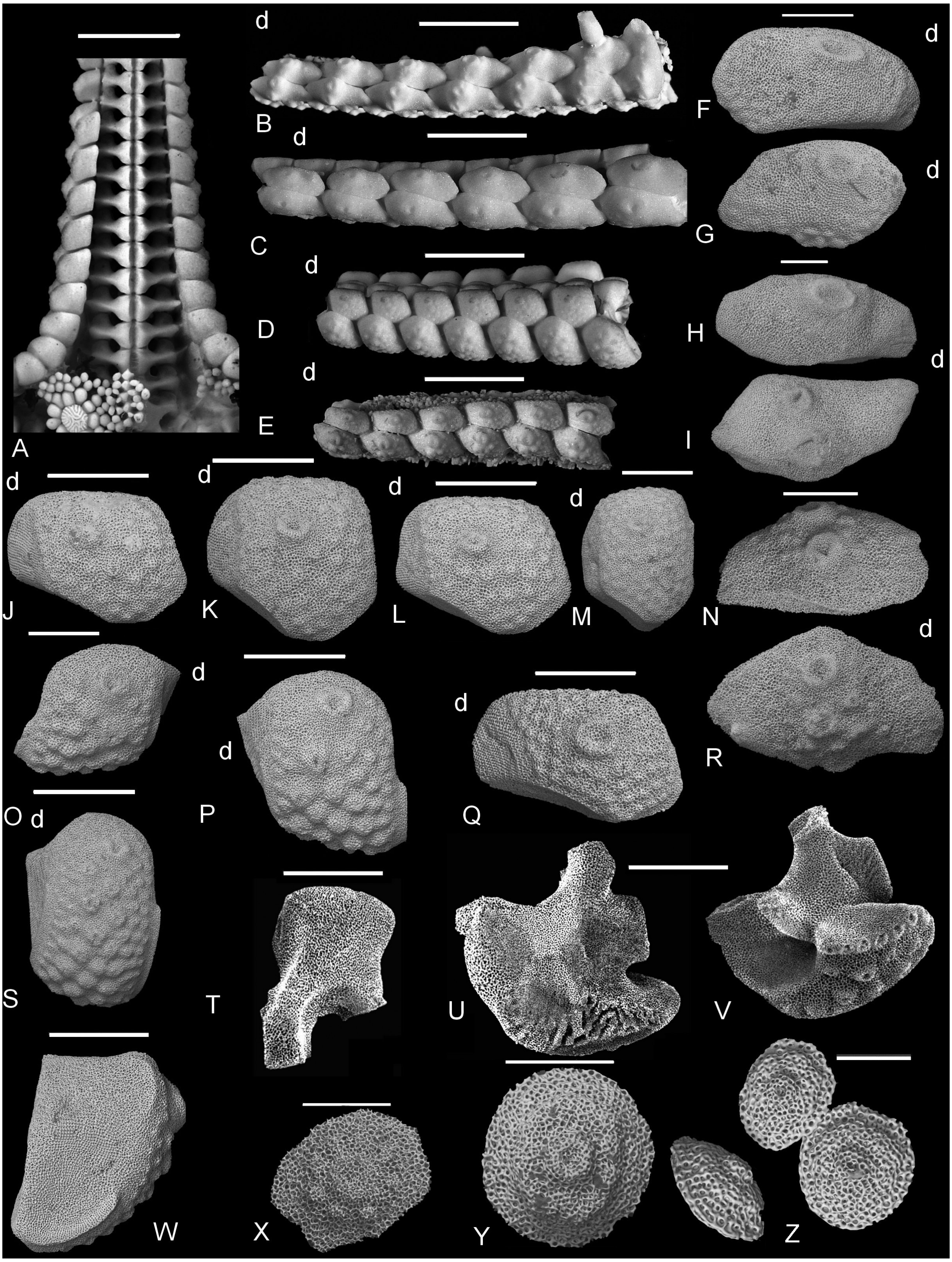
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Table 1. Modern benthopectinids used for present study.

Species	Collection	Locality
Pectinaster filholi Perrier, 1885	IoS Southampton	Porcupine Trough, NE Atlantic
Pontaster tenuispinus (Duben & Koren, 1846)	IoS Southampton	Porcupine Trough, NE Atlantic
Benthopecten simplex (Perrier, 1881)	IoS Southampton	Porcupine Trough, NE Atlantic
Nearchaster aciculosus (Fisher, 1910)	USNM	NE Pacific
Cheiraster gazellae Studer, 1883	USNM	SW Pacific

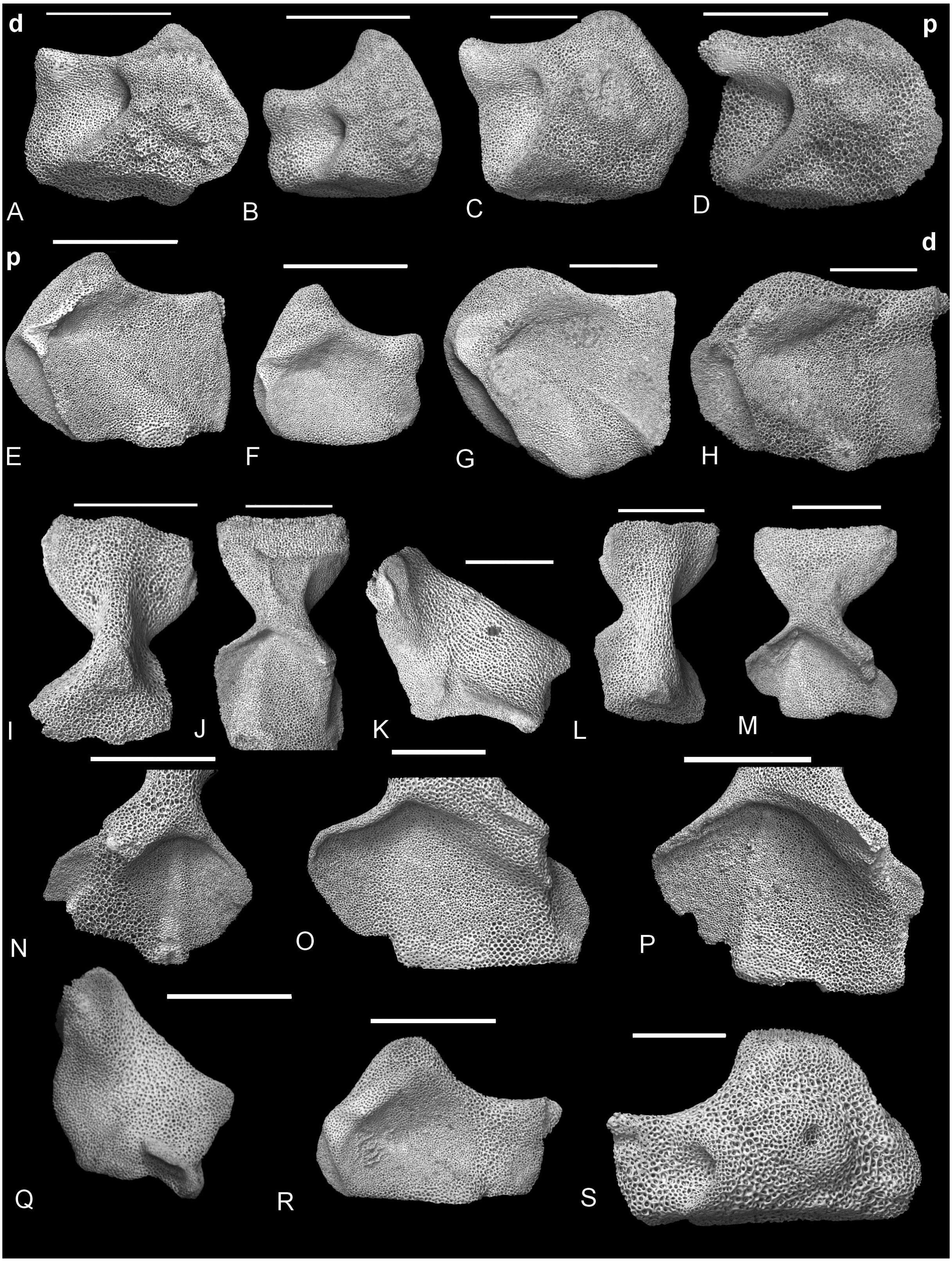
The most recent revision of benthopectinids at the generic level was made by Clark (1981) and the Atlantic species of the family were thoroughly revised by Clark & Downey (1992; see also Mah 2020a). There has been a long debate about both the number of extant benthopectinid genera, and the assignation of species to these genera. Clark (1981) summarised the taxonomic history of the family and provided a tabular key to benthopectinid taxa, of which she recognised eight genera and four subgenera. In the present study, additional characters were found to be of taxonomic value, most especially the shape, sculpture and articulation of the marginal ossicles.

Morphological diversity of extant benthopectinids

The morphology of five living benthopectinids is illustrated here with photographs of entire, dried specimens of *Pontaster tenuispinus* (Duben & Koren, 1846), *Cheiraster gazellae* Studer, 1883 (Fig. 1), *Pectinaster filholi* Perrier, 1885, *Benthopecten simplex* (Perrier, 1881) and *Nearchaster aciculosus* (Fisher, 1910) (Fig. 2). The most conspicuous differences are the variable development of marginal spines; short and small in *P. tenuispinus*, larger and longer in the other taxa. *Nearchaster aciculosus* has elongated abactinal spines. The shape of the denuded marginal plates (Fig. 4B–E) is significantly different, as these are short and broad in *Pontaster tenuispinus* and *Cheiraster gazellae* (Fig. 4D–E) and elongated with a proximal and distal taper in *Pectinaster filholi* and *Benthopecten simplex* (Fig. 4B–C).

The skeletal morphology of five species of extant benthopectinids (Table 1) has also been examined, using bleach preparation and SEM examination of ossicle types (Figs 3–5), in order to make comparisons with fossil taxa.

Fig. 5 (next page). **A, E, I–K**. *Cheiraster gazellae* Studer, 1883 (A.S. Gale collection, unregistered). **A, E**. Adambulacral, in actinal and abactinal views, respectively. **I–K**. Ambulacrals, in abactinal, actinal and proximal views, respectively. — **B, F, L–M**. *Pontaster tenuispinus* (von Düben & Koren, 1846) (A.S. Gale collection, unregistered). **B, F**. Adambulacral, in actinal and abactinal views, respectively. **L–M**. Ambulacral, in abactinal and actinal views, respectively. — **C, G, P**. *Benthopecten simplex* (Perrier, 1881) (A.S. Gale collection, unregistered). **C, G**. Actinal and abactinal views of adambulacral, respectively. **P**. Enlarged view of actinal surface of ambulacral base. — **D, H, N**. *Nearchaster aciculosus* (Fisher, 1910) (USNM, unregistered). **D, H**. Adambulacral in actinal and abactinal views, respectively. **N**. Enlarged view of actinal surface of ambulacral base. — **O, Q–S**. *Pectinaster filholi* (Perrier, 1885) (A.S. Gale collection, unregistered). **O**. Enlargement of ambulacral base, actinal view. **Q**. Proximal view of ambulacral. **R–S**. Abactinal and actinal views of adambulacral, respectively. Abbreviations: d = distal; p = proximal. See Fig. 3 for detailed morphological terminology. Scale bars: A–N, P–S = 1 mm; O = 0.5 mm.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Phylogeny of the Benthopectinidae Verrill, 1894

The fossil material described in the present paper provides evidence of the timing and order of appearance of evolutionary novelties within the family. Firstly, the highly derived ambulacral-adambulacral articulation (see above) is ubiquitously present in all genera, and had evolved by the Lower Jurassic. Secondly, the abactinal ridges on the ambulacrals, and the presence of an articulation between the ambulacral base and the inferomarginals is a feature restricted to the crown group benthopectinids (all living taxa, plus their common ancestor) which did not appear until the Oligocene. The Mesozoic representatives of the family represent the stem group.

Phylum Echinodermata Bruguière, 1791 (ex Klein, 1734)
Class Asteroidea de Blainville, 1830
Subclass Neoasteroidea Gale, 1987
Order Paxillosida Perrier, 1884
Family Benthopectinidae Verrill, 1894

Genus ***Nearchaster*** Fisher, 1911

Nearchaster Fisher, 1911: 91.

Type species

Acantharchaster aciculosus Fisher, 1910, by original designation.

Nearchaster spinosus (Blake, 1973) comb. nov.

Mistia spinosa Blake, 1973: 48, pl. 16 figs 30–44, pl. 17 figs 1–21, 35–36.

Brisingid (?) – Zullo *et al*. 1964: 334.

Material examined

UCMP A-5018 (holotype no. 10675) is the type and only specimen; it exposes a partly disarticulated abactinal surface showing the disc and proximal portions of four arms. Large marginal spines and smaller abactinal ones are visible. Marginals, adambulacrals, ambulacrals and abactinal ossicles of the holotype were figured individually by Blake (1973).

Occurrence

Keasey Formation (Lower Oligocene) near Mist, Oregon (USA).

Description

The abactinal surface of UCMP A-5018, embedded in matrix (Blake 1973: pl.16 fig. 44), shows part of the disc and four proximal arms. Although the outline is retained, the ossicles are jumbled and largely dissociated, such that adambulacrals and ambulacrals are visible on the actinal surface. The marginal spines, largely in place, are elongated and tapering. The abactinal spines are much smaller, perhaps one-fifth the size of those on the marginals. The adambulacrals are well preserved, subrectangular, with 2–3 large subadambulacral spine bases, and the concave inner (abactinal) surface and ridge bearing ***ada2*** and ***ada3***, characteristic of benthopectinids. The ambulacrals have the typical hourglass shape of benthopectinids, and asymmetry of the interambulacral muscles (P1 small, P2 large) is seen. The marginals are longer than broad with a convex, mound-like outer surface which carries 1–2 large spine bases and a number of sparsely scattered smaller ones. The inner surface of the marginals is flat. The abactinal ossicles are parapaxillae, with centrally placed, single spine bases, surrounded by a ring of smaller spines.

Remarks

As recognised by Blake (1973), the distinctive characters of the ambulacral, adambulacral and marginal ossicles place this form firmly in the Benthopectinidae. Comparison with extant benthopectinid species studied here indicates that *Mistia spinosa* shares important characters with the Recent Pacific genus *Nearchaster*, including the following:

1. Adambulacrals are nearly identical in shape to those of *Nearchaster aciculosus*, and both carry 2–3 bases for subambulacral spines.
2. Marginals are closely similar to those of *N. aciculosus* in both shape and distribution of spine bases.

The overall form of the body, with large marginal spines, and shorter abactinal spines on the disc is broadly similar to the development in the genera *Benthopecten*, *Nearchaster* and *Myonotus* Fisher, 1911 (see Fisher 1911: pls 22–26). The proportionate sizes and distributions of spines in *Mistia spinosa* are closest to those in *Benthopecten claviger* Fisher, 1910, *Myonotus intermedius* (Fisher, 1910) and *Nearchaster aciculosus* (Fisher, 1910) (see Fig. 2E–F herein).

The abactinal parapaxillae of *Mistia spinosa* are very close in structure to those of *N. aciculosus*, with a central spine base surrounded by a ring of smaller ones.

In conclusion, *Mistia spinosa* is a benthopectinid which has remarkably detailed similarities of ossicle morphology to the present-day Pacific species *Nearchaster aciculosus* and it is therefore provisionally placed in that genus. The genus thus has a history in the Pacific Ocean of at least 33 million years.

Genus ***Jurapecten*** Gale, 2011

Jurapecten Gale, 2011a: 84, pl. 19.

Type species

Jurapecten hessi Gale, 2011, by original designation.

Diagnosis

Benthopectinids which possess strongly rugose marginals; rugosities conjoined by thin radiating strips of imperforate stereom; ambulacrals lack abactinal ridges and inferomarginal articulation.

Assigned species

In addition to the type species, *J. infrajurensis* sp. nov. and *J. dhondtae* sp. nov., both described below.

Remarks

Jurassic–Cretaceous benthopectinids are locally common among isolated ossicles in washed residues. All share the same distinctive sculpture type of prominent imperforate rugosities, conjoined by radiating strips of stereom (e.g., Figs 6N–O, 7G, I–J), absent on extant genera. In the extant genera *Pontaster* and *Cheiraster*, the rugosities on the superomarginals are smaller and more widely spaced (e.g., Fig. 4J–M, Q), although the inferomarginal sculpture is similar to that seen in *Jurapecten* (Fig. 6C–E). *Jurapecten* also lacks a number of characters seen in all extant taxa, including an abactinal ridge on the ambulacrals (compare Fig. 7N–O with Fig. 5I, K–L, Q), and there is no ambulacral articulation surface with the inferomarginal (compare Fig. 7N–O with Fig. 5I, K, Q). Additionally, the ambulacral heads are more elongated in *Jurapecten* (e.g., Figs 6J, L, 8Q–U). The absence of the abactinal ridge, to which the longitudinal arm muscles attach in all living genera (Clark 1981), is a plesiomorphic feature of *Jurapecten*.

Jurapecten hessi Gale, 2011

Figs 6C, G, 7K–Y

Jurapecten hessi Gale, 2011a: 84, pl. 19 figs 1–6, 8–12, pl. 20 figs 6–10, 12–14, 19.

Jurapecten hessi – Gale 2011b: 76, fig. 6a–h.

Diagnosis

Jurapecten in which the marginals bear a sculpture of discrete, rounded rugosities and 1–3 larger spine bases on inferomarginals. Ambulacral base short.

Material examined

The type specimen, NHMUK EE 13594, consists of a set of associated ossicles from the upper Oxfordian (Couches d'Effingen, *bifurcatus* ammonite Zone, *stenocycloides* ammonite Subzone) at Savigna, near Orgelet (Département du Jura, France; see Gale 2011a, 2011b). Additional material comprises several hundred ossicles and groups of associated ossicles from the type locality (NHMUK collections).

Remarks

There is little new information or material since the original description by Gale (2011a, 2011b); differences with *J. infrajurensis* sp. nov. are discussed under that species (see below).

Jurapecten infrajurensis sp. nov.

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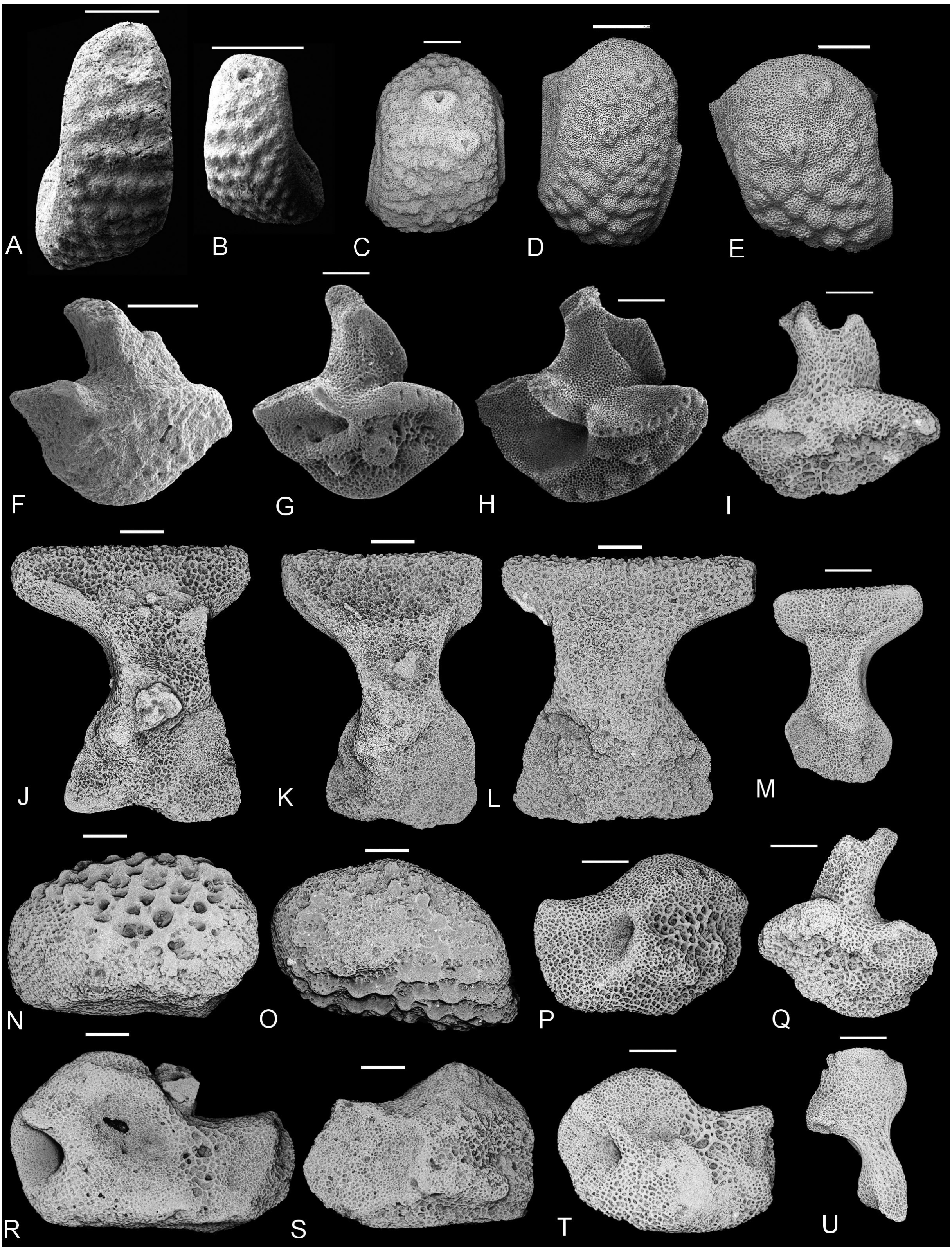
Figs 6I–U, 7A–J

Diagnosis

Jurapecten in which the ambulacral base broadens abradially; sculpture of superomarginals comprises a reticulum of conjoined rugosities.

Fig. 6 (next page). **A–B, F**. ? Benthopectinidae. **A–B**. Inferomarginals, in lateral aspect (MHI 2183/7, MHI 2183/8). **F**. Oral ossicle in radial view (MHI 2183/9). — **C, G**. *Jurapecten hessi* Gale, 2011. **C**. Inferomarginal, in lateral view (NHMUK PI EE 17988). **G**. Oral ossicle, in radial view (NHMUK EE 13606; the original of Gale 2011a: pl. 20 fig. 10). — **D–E, H**. *Pontaster tenuispinus* (von Düben & Koren, 1846). **D–E**. Lateral view of inferomarginals. **H**. Oral ossicle (A.S. Gale collection, unregistered). — **I–U**. *Jurapecten infrajurensis* sp. nov. **I**. Oral ossicle, radial view (SNSB-BGSP2020XLV 31). **J–M**. Ambulacral ossicles, in actinal views (J = holotype, NHMUK PI EE 17989; K–L = paratypes, NHMUK PI EE 17990–17991; M = SNSB-BGSP2020XLV16). **N–O**. Marginal ossicles (paratypes, NHMUK PI EE 17992–17993). **P, R–T**. Adambulacral ossicles (paratypes), in actinal (P, R) and abactinal (S–T) views (R–S = NHMUK PI EE 17994–17995; P, T = SNSB-BGSP2020XLV 17, SNSB-BGSP2020XLV 19). **I, Q**. Oral ossicles, in radial view (paratypes: SNSB-BGSP2020XLV 15, SNSB-BGSP2020XLV 18). **U**. Circumoral ossicle (paratype: SNSB-BGSP2020XLV 20). Provenance: A–B, F. Maantang Formation (Carnian, Upper Triassic), sample C30, Jiancougou, Sechuan Province, China. C, G. Upper Oxfordian (Couches d'Effingen, *bifurcatus* ammonite Zone, *stenocycloides* ammonite Subzone), Savigna, near Orgelet, Département du Jura, France (Gale 2011b). D–E, H. Recent, Porcupine Trough, NE Atlantic. I, M, P–Q, T–U. Upper Toarcian–lower Aalenian (possibly *aalensis* ammonite Zone), Quedlinburg (Landkreis Harz, northern Germany; Hess 2014). J–L, N–O, R–S. Middle Toarcian, Le Clapier (Département d'Aveyron), 62 km WNW of Montpellier, southern France (Thuy 2012). See Fig. 3 for detailed morphological terminology. Scale bars: A–H = 0.4 mm; I–U = 0.2 mm.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Etymology

From the Latin '*infra*', in allusion to the occurrence of the species in the Lower Jurassic.

Material examined

The ambulacral illustrated here (Fig. 6J) is the holotype (NHMUK PI EE 17989); paratypes are NHMUK PI EE 17990–17995. All specimens are from middle Toarcian strata at Le Clapier (Département d'Aveyron, 62 km WNW of Montpellier, southern France; see Thuy 2012). Additional paratypes are fifteen ossicles (SNSB-BGSP 2020 XLV 16–30) from the upper Toarcian–lower Aalenian (possibly *aalensis* ammonite Zone) at Quedlinburg (Landkreis Harz, northern Germany; see Hess 2014).

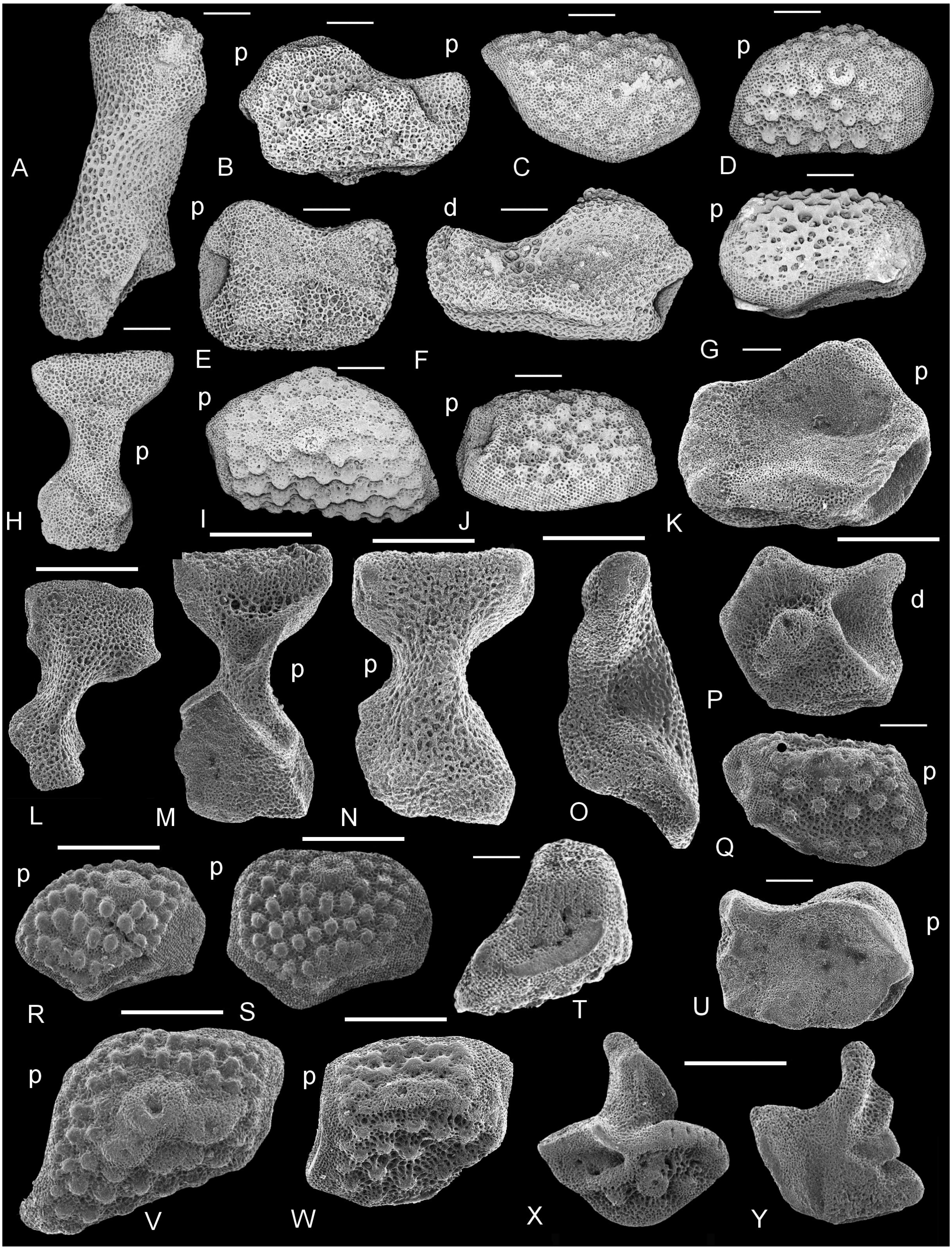
Description

Marginals block-like, length slightly exceeding height, carrying a sculpture of rugosities, on inferomarginals aligned into transverse rows parallel with arm (Figs 6O, 7I). On proximal superomarginals (Fig. 7C–D) rugosities discrete and centrally placed single spine base present; on distal superomarginals rugosities conjoined by narrow radial struts, forming a reticulum of imperforate stereom (e.g., Figs 6N, 7G). Ambulacrals (Figs 6J–M, 7A, H) waisted, with elongated heads and broad flat bases; abactinal ridge absent (Fig. 7A). Bases with broad ***padam*** site, slightly shorter than ***dadam*** (Fig. 6J–L). Adambulacrals (Figs 6P, R–T, 7B, E–F) with deep ***adadm*** site, distally placed ***padam*** and broad ***ada1*** (best seen in Fig. 6R); ***ada3*** diffuse. Orals (Fig. 6I, Q) with tall, distally recurved ***apo***, concave actinal face, low, lozenge-shaped body. Circumoral (Fig. 6U) with elongated ***poda***, short ***doda***.

Remarks

Jurapecten infrajurensis sp. nov. differs from *J. hessi* (see above) in the more elongated ambulacral base, and the more coarsely rugose sculpture of both infero- and superomarginals, which lack enlarged spine pits.

Fig. 7 (next page). **A–J**. *Jurapecten infrajurensis* sp. nov., various ossicle types (paratypes). **A, H**. Ambulacrals, in lateral and actinal aspects, respectively (SNSB-BGSP2020XLV 21,SNSB-BGSP2020XLV 28). **B, E–F**. Adambulacrals, in actinal and abactinal views (SNSB-BGSP2020XLV 22, SNSB-BGSP2020XLV 25–26). **C, G, J**. Superomarginals, in lateral views (SNSB-BGSP2020XLV 23, SNSB-BGSP2020XLV 27, SNSB-BGSP2020XLV 30). **D, I**. Inferomarginals, in lateral views (SNSB-BGSP2020XLV 24, SNSB-BGSP2020XLV 29). — **K–Y**. *Jurapecten hessi* Gale, 2011. **K, P, U**. Adambulacral ossicles. **K**. Abactinal view (NHMUK PI EE 17996). **P**. NHMUK EE 13598 (the original of Gale 2011a: pl. 19 fig. 11). **U**. NHMUK EE 13599, the original of Gale (2011a: pl. 20 fig. 12). **L**. Circumoral ossicle (NHMUK EE 13605, the original of Gale 2011a: pl. 20 fig. 13). **M–N**. Ambulacral ossicles, in actinal and abactinal views, respectively (NHMUK EE 13595–13596, the originals of Gale 2011a: pl. 19 figs 8–9). **O**. Ambulacral, in proximal/distal view (NHMUK 13597). **Q–S**. Superomarginal ossicles (NHMUK EE 13601–13602; the originals of Gale 2011a: pl. 20 figs 6–7). **T, V–W**. Inferomarginals (NHMUK EE 13600, EE 13603–13604, EE 13608, the originals of Gale 2011a: pl. 20 figs 5, 8, 16). **X–Y**. Oral ossicles (NHMUK EE 13606–13607, the originals of Gale 2011a: pl. 20 figs 10, 14). Provenance: A–J. Upper Toarcian–lower Aalenian (possibly *aalensis* ammonite Zone), Quedlinburg (Landkreis Harz, northern Germany; see Hess 2014). K–Y. Upper Oxfordian (Couches d'Effingen, *bifurcatus* ammonite Zone, *stenocycloides* ammonite Subzone), Savigna, near Orgelet, Département du Jura, France (Gale 2011b). Abbreviations: d = distal; p = proximal. See Fig. 3 for detailed morphological terminology. Scale bars: A–J = 0.2 mm; K–Y = 0.5 mm.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Jurapecten dhondtae sp. nov.

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Fig. 8A–H, J–V

benthopectinid sp. 1 (? spp.) – Jagt 2000: 393, pl. 6 figs 1–4.

Cheiraster? sp. – Blake & Jagt 2005: 190, pl. 5 figs 1–7.

Diagnosis

Jurapecten in which the marginal ossicles possess a coarsely rugose sculpture and the inferomarginals bear a single, large, laterally directed spine base.

Etymology

Named after Annie V. Dhondt (1942–2006), specialist of Cretaceous bivalves and close friend.

Material examined

The inferomarginal illustrated here (Fig. 8F) is the holotype (NHMM JJ 10490a), while the other figured ossicles in lot NHMM JJ 10490 are paratypes. Additional material includes around 50 isolated ossicles (lot NHMM JJ 9591). All material is from the upper Maastrichtian (Maastricht Formation, Emael Member, Lava Horizon) at the CBR-Romontbos Quarry, Eben Emael (Liège, northeast Belgium).

Description

Superomarginals (Fig. 8A–D) block-like, nearly equidimensional, elongating distally. Outer face with sculpture of dense rugosities of similar size and single, crater-rimmed spine base positioned towards abactinal-distal margin. Inferomarginals (Fig. 8E–H, J–K) asymmetrical, proximal margins broader than distal margins; inter-inferomarginal articulation facet close to actinal surface of plate (Fig. 8J), forming short projection. External face of inferomarginal with sculpture of coarse, rounded rugosities and single, large crater-rimmed spine base, positioned centrally, or slightly towards abactinal margin. Ambulacrals (Fig. 8Q–V) with elongated, bar-like ***ambh***, broad, flat ***ambb***, with large, flat surface for ***dadam*** and ***ada3***, ***padam*** on short wing. Abactinal ridge and inferomarginal articulation absent (Fig. 8V). Adambulacrals (Fig. 8L–M) with concave abactinal face, actinal face with single subambulacral spine base. Enlargement of ***dadam*** (Fig. 8P) shows irregularly ridged region, similar to that seen on extant *Pectinaster filholi* (Perrier, 1885) (Fig. 8I).

Remarks

The marginal ossicles (Fig. 8A–H, J–K) are closely similar to those of *Pontaster tenuispinus* (von Düben & Koren, 1846) (compare with Fig. 4J–M, O–Q) in shape, sculpture and spine base development,

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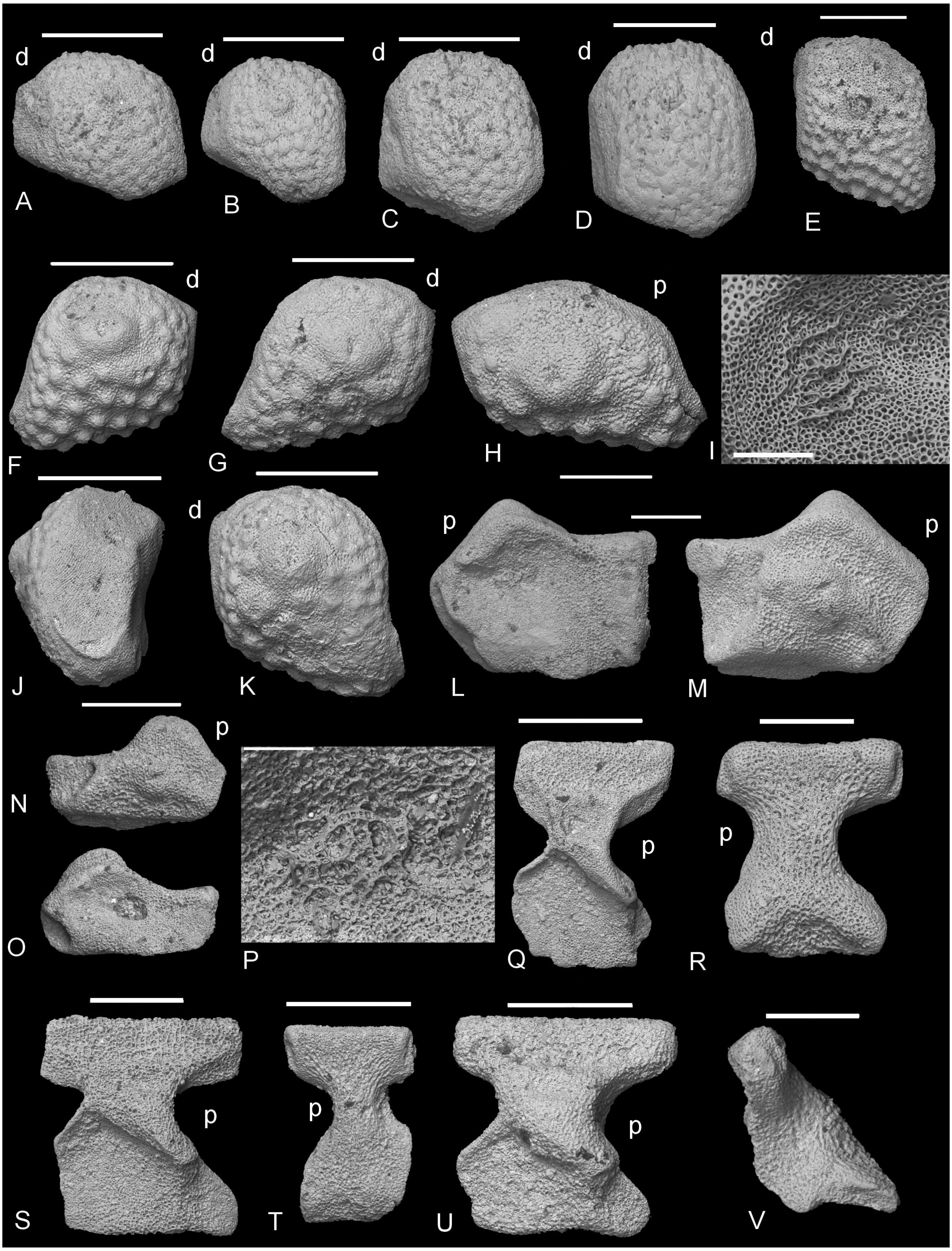
Fig. 8 (next page). **A–H, J–V**. *Jurapecten dhondtae* sp. nov. **A–D**. Superomarginals in lateral view (NHMM JJ 10490b–e). **E–H, J–K**. Inferomarginals (NHMM JJ 10490f–j), in lateral (E–H, K) and distal (J) views. **E**. Original of Jagt (2000: pl. 6 fig. 2; NHMM JJ 9591i). **F**. Holotype (NHMM JJ 10490a). **L–P**. Adambulacrals, in actinal (M–N) and abactinal (L, O) views, with (P) enlargement to show ridges (lot NHMM JJ 9591). **Q–V**. Ambulacrals, in actinal (Q, S, U), abactinal (R, T) and proximal/distal (V) views (lot NHMM JJ 9591). — **I**. *Pectinaster filholi* (Perrier, 1885) (A.S. Gale collection, unregistered), enlargement of area on actinal surface of ambulacral. Provenance: A–H, J–V. Upper Maastrichtian, CBR Romontbos quarry, Eben Emael (Liège, NE Belgium), Maastricht Formation, Emael Member (Lava Horizon). I. Recent, Rockall Trough, northeast Atlantic. Abbreviations: d = distal; p = proximal. See Fig. 3 for detailed morphological terminology. Scale bars: A–H, J–O, Q–V = 1 mm; I, P = 0.2 mm.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but the ambulacrals (Fig. 8Q–V) possess elongated heads and lack abactinal ridges and inferomarginal articulation structures, and compare better with those of *Jurapecten hessi* and *J. infrajurensis* sp. nov. (see Figs 6J–M, 7M–O).

The partially preserved specimen (NHMM MD 4105), described and illustrated by Blake & Jagt (2005), may be conspecific, but recrystallisation of all ossicle types precludes detailed comparison of the sculpture of infero- and superomarginal ossicles and ambulacral ossicles are too poorly preserved. The type material of *J. dhondtae* sp. nov., from the middle Emael Member, is ca 200 000 years younger than NHMM MD 4105, from the basal Gronsveld Member (compare Keutgen 2018).

Genus ***Punkaster*** gen. nov.

urn:lsid:zoobank.org:act:D63466E2-7CA4-4896-BFD2-4D156A280AA8

Type species

Punkaster spinifera gen. et sp. nov.

Diagnosis

Highly derived form in which the marginal ossicles are very elongated, proximal infero-and superomarginal pairs occasionally fused, and marginals may possess 1–2 large rounded bases for attachment of conical spines. Adambulacrals with deep rounded notch to allow extension of tube feet and very large furrow spines.

Etymology

From the similarity of the marginal spination to the 1980s punk hairdos.

Assigned species

In addition to the type species, *P. ruegenensis* gen. et sp. nov. (see below).

Remarks

The highly unusual marginal ossicles of this new genus (Fig. 9E, I–J, M, P) have been known for over 60 years, but they remained undescribed and it has hitherto not been possible to assign them to any family. The new material includes ambulacral and adambulacral ossicles, which demonstrate a likely affinity with benthopectinids in the elongated, bar-like ambulacral heads and, especially, in the nature of the ambulacral/adambulacral articulation. This is typically benthopectinid, in the abradial position of ***ada3***, the position of ***padam*** on a short wing-like process and the presence of ***ada2*** on a steep ridge. The abactinal ossicles are closely similar to parapaxillae of modern benthopectinids. The presence of an abactinal ridge on the ambulacrals of *P. spinifera* gen. et sp. nov. may indicate that the species possessed longitudinal muscles in the arms. The genus perhaps represents a highly specialised offshoot from the mainline benthopectinids.

Punkaster spinifera gen. et sp. nov.

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Figs 9–11, 12J–K

Zwischenplatten QA, RA – Müller 1953: 45, pl. 10 figs qa–ra.
indeterminate “cryptozonid” – Jagt 1999: pl. 2 figs 1–2, 4.
benthopectinid sp. 2 – Jagt 2000: 394, pl. 6 figs 5–6, 8, 10–12, pl.7 figs 1–2.

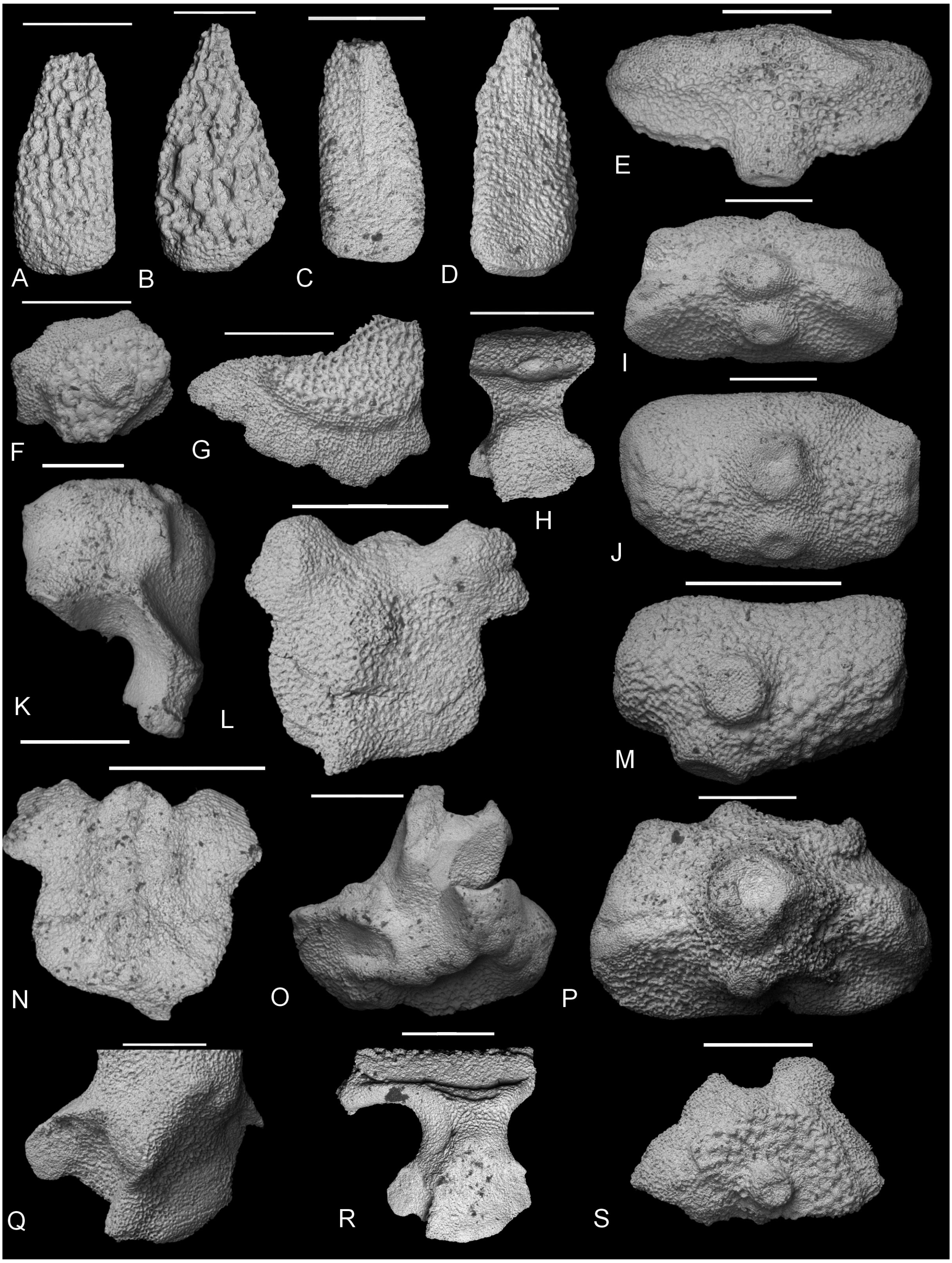

Fig. 9. *Punkaster spinifera* gen. et sp. nov. (holotype**,** NHMM JJ 11736). **A–D**. Subadambulacral or suboral spines. **E, I–J, M, P**. Marginal ossicles. **F–G, S**. Abactinal ossicles. **H, Q–R**. Ambulacrals, in actinal view. **K**. Circumoral, in actinal view. **L, N**. Odontophore, in abactinal and actinal views. **O**. Oral ossicle, in radial view. Provenance: uppermost Maastrichtian, ca 12 m below K/Pg boundary, Kulsti Rende, Stevns Klint, eastern Denmark. Scale bars: A–D = 5 mm; E–S = 1 mm.

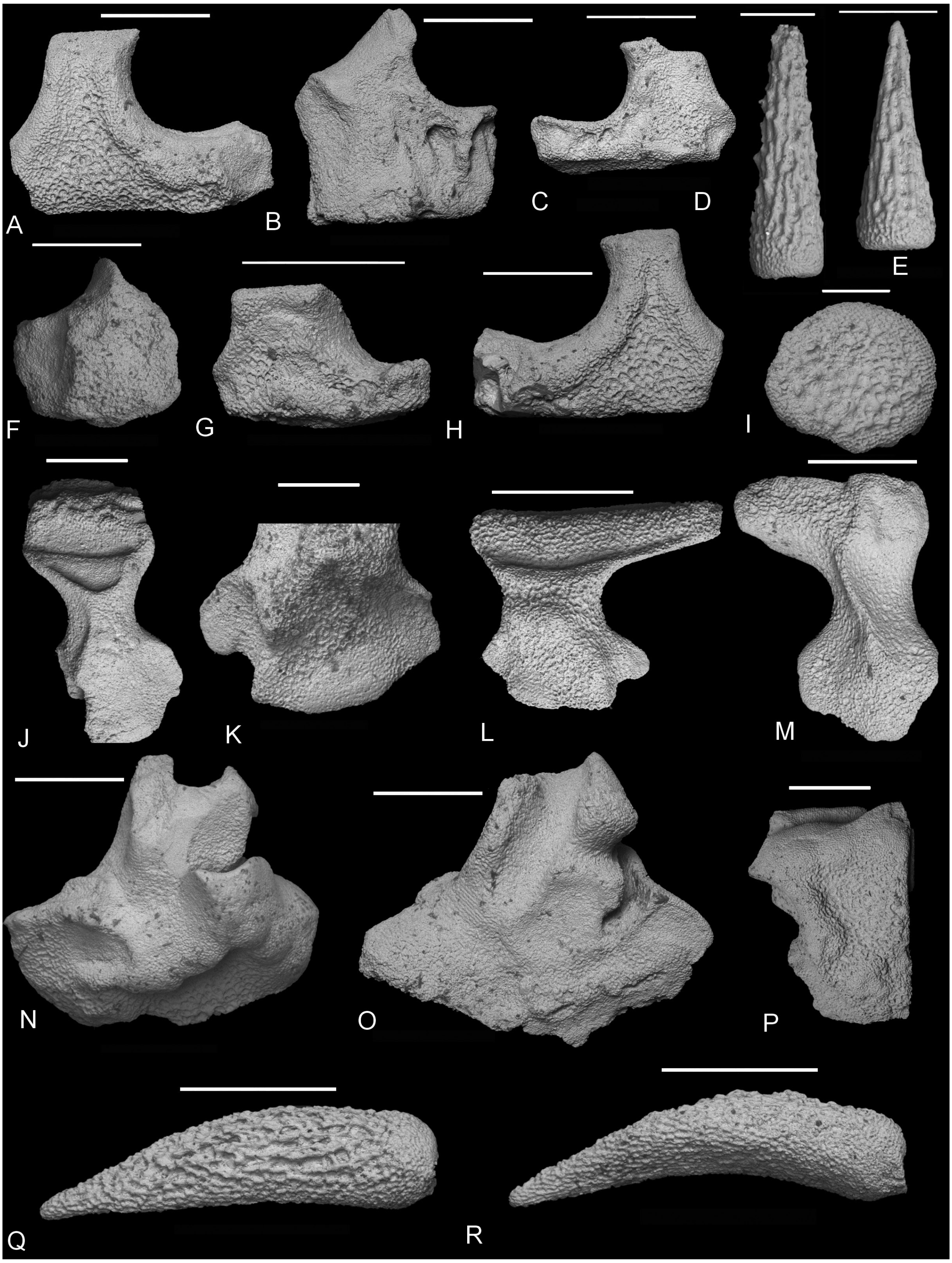

Fig. 10. *Punkaster spinifera* gen. et sp. nov. (holotype, NHMM JJ 11736). **A–C, F–H**. Adambulacral ossicles, in actinal (A, C, H) and abactinal (B, F–G) views. **D–E**. Abactinal or marginal spines. **I**. Abactinal ossicle. **J–M**. Ambulacral ossicles, in actinal (J–L) and abactinal (M) views. **N–P**. Oral ossicle, in radial (N), interradial (O) and actinal (P) views. **Q–R**. Large spines of uncertain position. Provenance: uppermost Maastrichtian, ca 12 m below K/Pg boundary, Kulsti Rende, Stevns Klint, eastern Denmark. Scale bars: A–C, F–R = 1 mm; D–E = 0.5 mm.

Diagnosis

Punkaster gen. nov. in which the marginal ossicles carry 1–2 cylindrical spine bases, which bore conical spines.

Etymology

Derived from the Latin '*spinifera*', meaning bearing spines.

Material examined

A set of > 100 associated ossicles (marginals, a single terminal, abactinals, actinals, orals, circumorals, odontophores, adambulacrals, ambulacrals, marginal spines, adambulacral spines and oral spines) from ca 12 metres below the Cretaceous-Paleogene (K/Pg) boundary in the upper Maastrichtian Højerup Member (Tor Formation; Surlyk *et al.* 2006) at Kulsti Rende, Stevns Klint, eastern Denmark, is the holotype (NHMM JJ 11736). Additional material includes disarticulated, yet associated, ossicles of another individual from the same locality and stratigraphical unit, as well as isolated marginal ossicles from several localities exposing Cenomanian–Maastrichtian rocks in the United Kingdom (Kent, Hampshire), Belgium, Germany (Rügen, SNSB-BGSP collections; Aachen area) and the Czech Republic, including ossicles from the lower Campanian Chalk of Downend, Hampshire (Gale 1980).

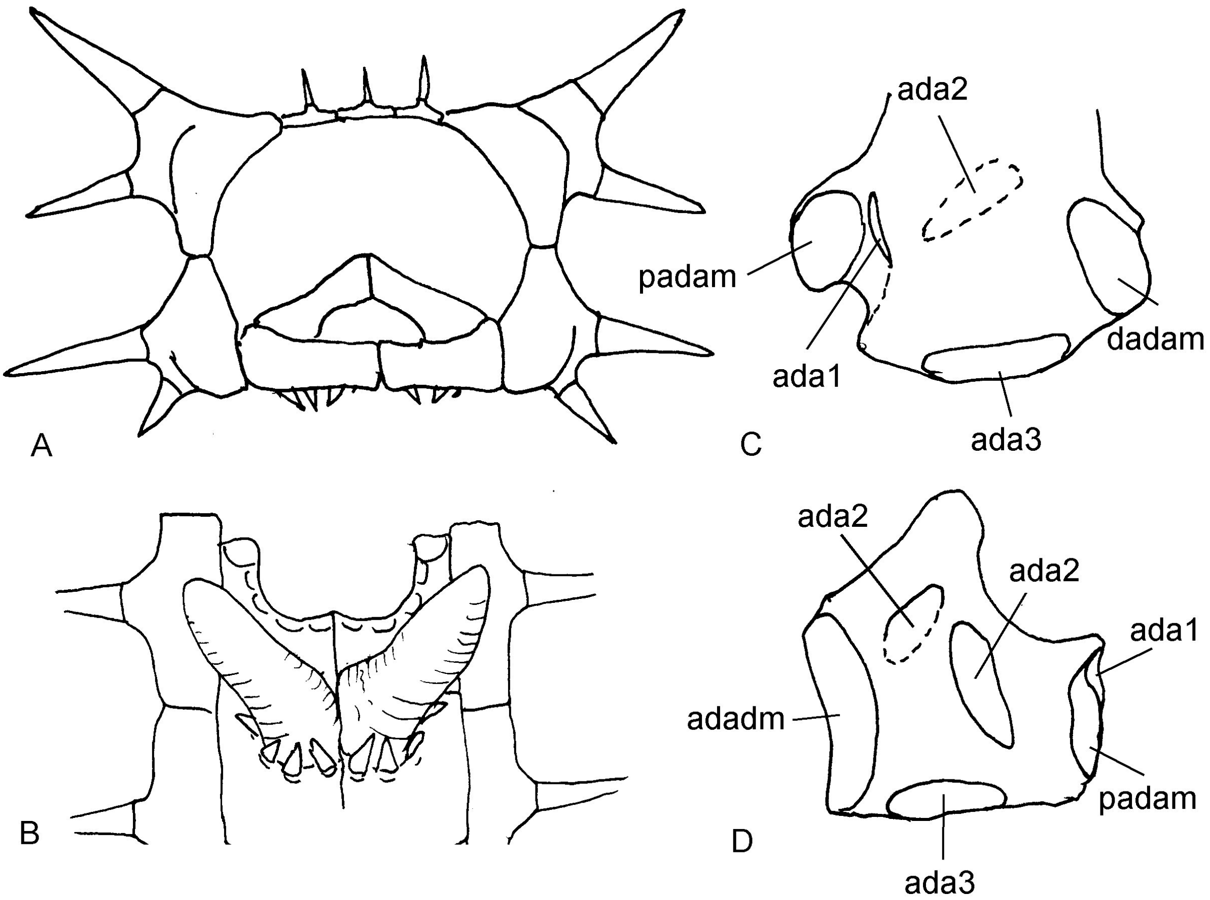

Fig. 11. *Punkaster spinifera* gen. et sp. nov., reconstructions and interpretation. **A**. Reconstruction of cross-section of arm. **B**. Reconstruction of ambulacral groove, with large podial basins and furrow spines. **C**. Ambulacral base, in actinal view. **D**. Abactinal face of adambulacral. Abbreviations: see Material and methods, and Fig. 3 for detailed morphological terminology.

Description

Marginals are highly distinctive plates; supero- and inferomarginals elongated, broadly rectangular in lateral-abactinal aspect, with a length-parallel central rounded ridge, single oninferomarginals, bifurcating towards distal and proximal margins of superomarginals. Central, raised part of ridge carrying 2–3 spine bases, borne on cylindrical protrusions projecting from surface of ossicles. Superomarginals (Fig. 9E, I, P) with thin, narrow abactinal portion and opposing inferomarginals. Inferomarginals (Fig. 9J, M) with distinctive facet on internal surface for contact with adambulacrals. External surface of supero- and inferomarginals with complex sculpture comprising numerous small, rounded rugosities interconnected by network of stereom. Marginal spines (Fig. 10D–E) conical, thorny.

Adambulacrals boot-shaped in actinal and abactinal aspect, large ***adp*** forming heel, narrow distal extension (Fig. 10A, H); adradial margin deeply concave to accommodate large tube feet. Three to four attachment sites for ***fs***, ***sads*** not present; probable ***fs*** large, lanceolate (Fig. 9A–D). Abactinal surface (Fig. 11D) of adambulacrals showing ***ada3*** on abradial margin, poorly defined ***ada2***. Ambulacrals (Figs 9H, Q–R, 10J–M) in proximal position (Fig. 10J) short, broad, distal ambulacrals with elongated ***ambh*** (Fig. 10L). Abactinal ridge present (Fig. 10M). Ambulacrals (Figs 9Q–R, 10K, 11C) with separate wing for ***padam***, ***ada3*** on abradial margin, ***dadam*** large, ***ada2*** poorly defined, ***ada1*** large. Oral ossicles robust, subtriangular, actinal surface trapezoidal, concave centrally (Fig. 10P). Proximal margin with three oral spine bases and two suboral spine bases on distal margin; ***apo*** stout, with shallow ***rng***.

Abactinal ossicles flattened parapaxillae, with irregular lobed outlines and bevelled rim (Fig. 9F–G, S). Raised central area with finely rugose stereom which probably carried small spines. Some abactinals with single, outwardly directed spine base.

Remarks

Punkaster spinifer gen. et sp. nov. differs from *P. ruegenensis* gen. et sp. nov. (see below) in the unfused proximal supero- and inferomarginals and in the presence of large marginal spine bases. As seen in our reconstruction (Fig. 11), the marginals were paired, not alternating, and carried a transverse fan of 4–6 outwardly directed, large conical thorny spines (Fig. 11A). The species had very large tube feet, protected by large, lanceolate furrow spines (Fig. 11B).

Punkaster ruegenensis gen. et sp. nov.

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Fig. 12A–I, L–M

Diagnosis

Punkaster gen. nov. in which the proximal supero- and inferomarginals form fused pairs; distally, they are separate. Large marginal spine bases absent.

Etymology

Named after the island of Rügen (northeast Germany) in the Baltic Sea.

Material studied

The interradial marginal pair (Fig. 12A) is the holotype (SNSB-BGSP 2020 XLV 31); the other eight ossicles illustrated here are paratypes (SNSB-BGSP 2020 XLV 32–39), all from the upper lower Maastrichtian Chalk of Rügen, northeast Germany. Additional material includes over 30 marginal ossicles and other ossicles from the same locality (lot SNSB-BGSP 2020 XLV 32).

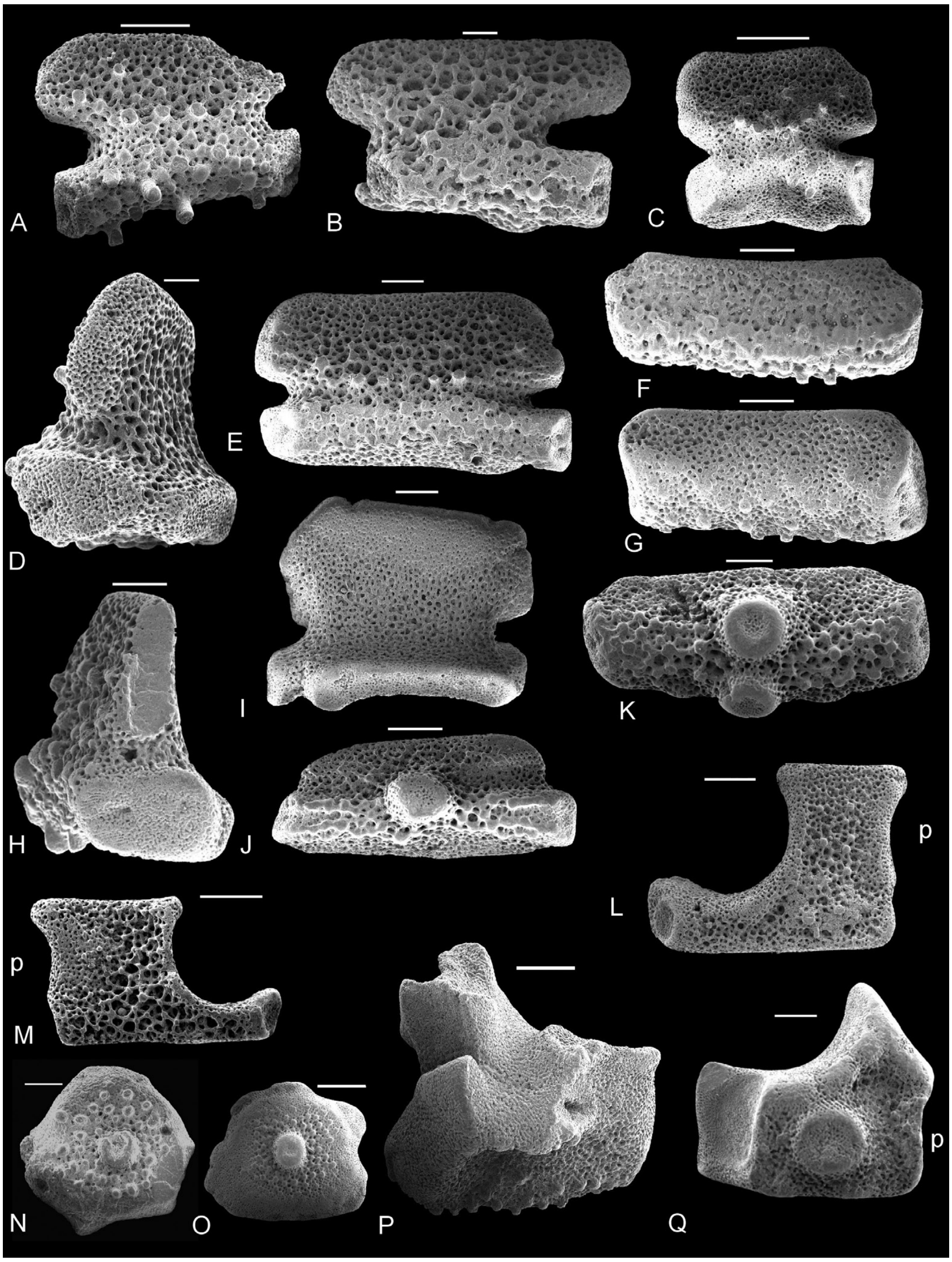


Fig. 12. A–I, L–M. *Punkaster ruegenensis* gen. et sp. nov. **A–E, H–I**. Fused marginal pairs, in lateral (A–C, E: SNSB-BGSP2020XLV 31–33, SNSB-BGSP2020XLV 35) views, at right angles to margin (D, H: SNSB-BGSP2020XLV 34, SNSB-BGSP2020XLV 38) views and internal view (I: SNSB-BGSP2020XLV 39). **F–G**. Distal inferomarginals in lateral view (SNSB-BGSP2020XLV 36–37). **A**. Holotype (SNSB-BGSP2020XLV 31). **B–I**. Paratypes (SNSB-BGSP2020XLV 32–39). **L–M**. Probable adambulacrals, actinal view (lot SNSB-BGSP2020XLV 32). — **J–K**. *Punkaster spinifera* gen. et sp. nov., marginals (SNSB-BGSP2020XLV 40–41). — **N–O**. *Punkaster* gen. nov., sp. indet., abactinal ossicles (SNSB-BGSP2020XLV 42–43). — **P**. ? *Punkaster* gen. nov., sp. indet., oral ossicle, external view (SNSB-BGSP2020XLV 44). — **Q**. *Punkaster* gen. nov., sp. indet., adambulacral, actinal view (SNSB-BGSP2020XLV 45). All specimens are from the upper lower Maastrichtian of Rügen, NE Germany. Abbreviation: p = proximal. See Fig. 3 for detailed morphological terminology. Scale bars: A, C–Q = 0.5 mm; B = 0.2 mm.

Description

Proximal marginals fused, bilobed; actinal part formed by a low, elongated, concave inferomarginal, abactinal part a subrectangular flange, formed by superomarginal (Fig. 12A–E, H–I). Infero- and superomarginals separated by a notch of variable size. Proximal/distal profile L-shaped, articulation facets for adjacent marginal plates oval (Fig. 12D). External sculpture of coarse reticulate stereom network, with rugosities, and small cylindrical projections which carried spines. Distal inferomarginals (Fig. 12F–G) rectangular, elongated, with similar sculpture to proximal plates. Presumed adambulacral (Fig. 12L–M) boot-shaped, with deep podial notch and narrow distal portion. Large ***fs*** bases present, central actinal face slightly inset, coarsely reticulate, rugose.

Remarks

The marginal ossicles are most unusual in that supero- and inferomarginal pairs are fused, perhaps uniquely amongst asteroids. The overall shape and sculpture of the ossicles suggest affinity with the type species, *Punkaster spinifera* gen. et sp. nov. (see above), but the present form differs in the fused proximal marginals and in the absence of large spine bases.

? **Benthopectinidae** Verrill, 1894

Fig. 6A–B, F

? Benthopectinidae Verrill, 1894: 217.

Material

Seventeen marginal ossicles; the inferomarginal figured (Fig. 6A) is MHI 2183/7; the other inferomarginal and oral ossicle illustrated here are MHI 2183/8 and 9. All are from the Maantang Formation (Carnian, Upper Triassic; sample C30) at Jiancougou, Sechuan Province, China.

Description

The inferomarginal and oral ossicles are strongly reminiscent in shape and external sculpture of those of benthopectinids; compare Fig. 6A–B with benthopectinid marginals (Fig. 6C–E), and the oral (Fig. 6F) with those of benthopectinids (Fig. 6G–I).

The inferomarginals share a number of similarities to those of benthopectinids (Fig. 6A–E), notably the coarse, longitudinally arranged rows of rugosities, the presence of a large spine (or pedicellaria) base close to the abactinal margin of the plate, and the marked asymmetry of the distal inferomarginals, in which the distal height is less than the proximal one. The oral ossicles (Fig. 6F) are remarkably similar to those of benthopectinids in the evenly convex actinal margin, the distally angled apophyse and the shape of the adambulacral articulation (Fig. 6G–I). However, the material available to date is too limited, and in the absence of ambulacrals and adambulacrals, this referral is very tentative.

Family Goniopectinidae Fisher, 1916

Genus ***Chrispaulia*** Gale, 2005

Chrispaulia Gale, 2005: 2, fig. 4a–c.

Type species

Nymphaster radiatus Spencer, 1905, by original designation (see Fig. 13A–C).

Diagnosis

Arms long, narrow; disc small, with rounded interbrachial arcs; superomarginals meeting over radius along length of arm; distal marginals imbricate (emended from Gale 2005).

Assigned species

In addition to the type species, *Chrispaulia jurassica* Gale, 2011 (Gale 2011a), *C. wrightorum* sp. nov. and *C. spinosa* sp. nov.

Remarks

The record in the *Treatise of Invertebrate Paleontology* (Part U; Spencer & Wright 1966) of a benthopectinid from the "Albian of England" is based on an arm fragment from the Albian Red Chalk of Yorkshire, United Kingdom (C.W. Wright, pers. comm. to ASG, 1978). We have examined this specimen (NHMUK PI EE 17997), which comprises five marginal ossicles reconstructed on plasticene. The shape of the ossicles indicates that this specimen belongs to the genus *Chrispaulia*; it is here described as a new species, *C. wrightorum* sp. nov. (see below). In addition, we record another species from the Hauterivian (Lower Cretaceous) of northeast England and northern Germany.

Chrispaulia wrightorum sp. nov.

urn:lsid:zoobank.org:act:DC13434F-62E3-47A9-9F62-327F77141670

Fig. 13F–G

?*Benthopecten* sp. – Spencer & Wright in Moore 1966: U48.

Diagnosis

Chrispaulia with smooth marginal ossicles, in which the distal superomarginals possess a single large spine pit close to their distal, abactinolateral border.

Etymology

After the late brothers C.W. and E.V. Wright, who collected the specimen.

Material examined

The arm fragment (NHMUK PI EE 17997) from the Albian Red Chalk (Hunstanton Formation) at Speeton, Yorkshire (United Kingdom) is the holotype and single specimen known to date. The specimen was originally articulated; it was subsequently reconstructed on plasticene by the Wright brothers.

Description

Arm elongated, narrow; supero- and inferomarginals opposed, shortening rapidly distally (Fig. 13F–G). Superomarginals bearing single, distally directed, crater-like spine base on distal, abactinolateral margin. Supero- and inferomarginals smooth, grooves for cribriform organs between infero-/superomarginal pairs poorly defined.

Remarks

Chrispaulia wrightorum sp. nov. differs from all congeners in the smooth marginal ossicles, lacking rugosities.

Chrispaulia spinosa sp. nov.

urn:lsid:zoobank.org:act:4C003A9F-1F91-44BC-91AB-2910B8EA756A

Fig. 13D–E, H–O

Diagnosis

Chrispaulia in which distal inferomarginals bear an oblique row of large, bifid spine attachment sites, which carried long, flattened spines.

Etymology

Latin for 'bearing spines', in reference to the row of spine attachment sites on distal inferomarginals.

Material examined

A distal arm fragment (Nds LH 105.107), comprising five marginal pairs, with articulating spines preserved, is the holotype; it is from the lower Hauterivian (*Endemoceras amblygonium* ammonite Zone) at Engelbostel near Hannover (northern Germany). Paratypes (NHMUK PI EE 17998–18004) are 35 marginal ossicles and a single oral ossicle from the upper 3 metres of the Tealby Clay (Hauterivian) at Nettleton, Lincolnshire (United Kingdom).

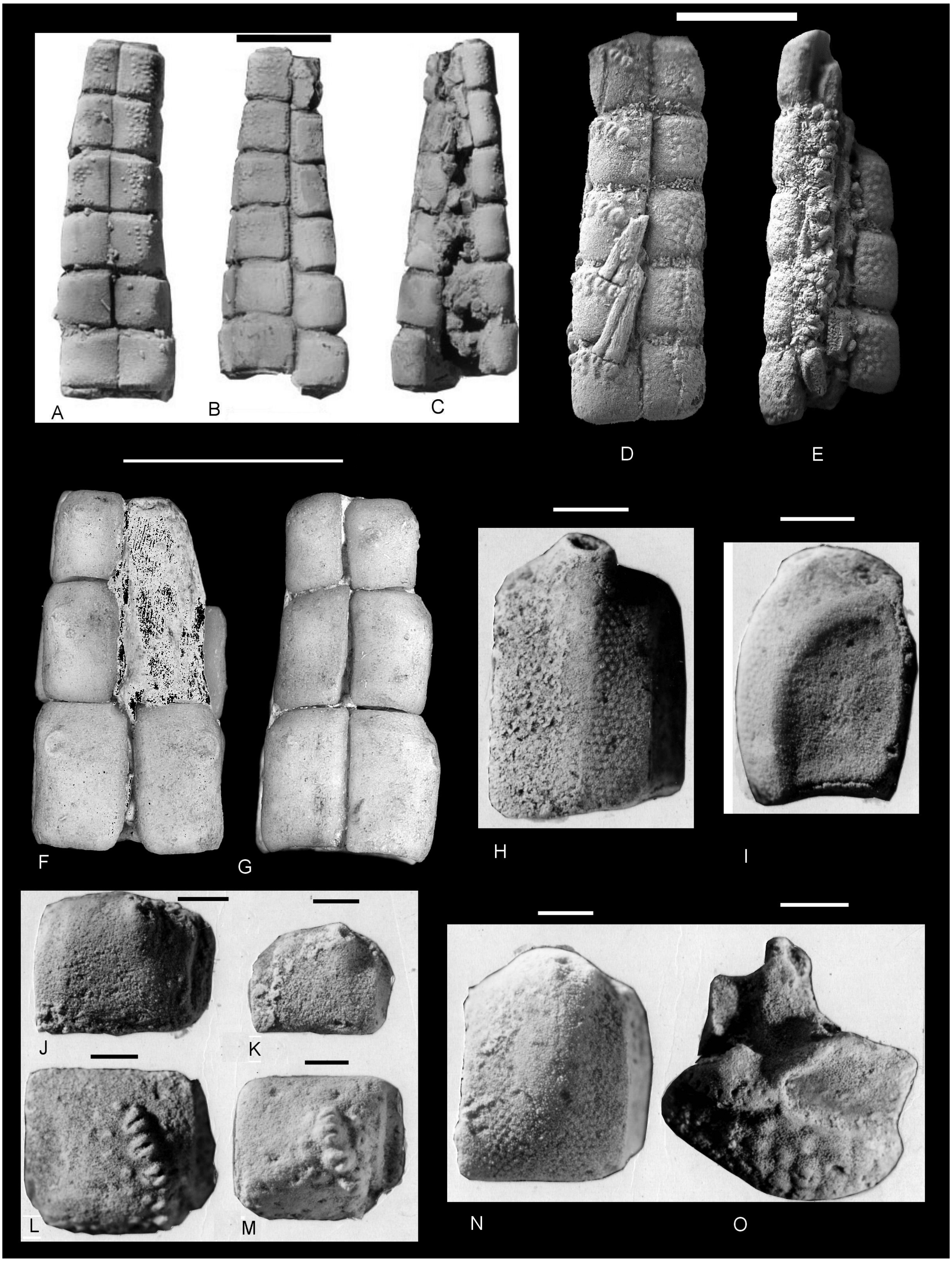
Description

Arms elongated, narrow, tapering slowly (Fig. 13D–E); proximal superomarginals tall, block-like, bearing a single, abactinally directed, crater-like spine base. Central region of external face narrow, poorly defined, lateral surfaces broad with small rugosities for attachment of tiny cribriform spines (Fig. 13H–I, N; spines still articulated in Fig. 13D). Distal superomarginals with or without an abactinally situated, distally directed large spine base (Fig. 13I–J), rugose (Fig. 13D) or smooth (Fig. 13I–J). Distal infero- and superomarginals thin, imbricating proximally; distal inferomarginals with oblique row of large, bifid spine bases, which bore flattened, lanceolate spines (Fig. 13D). Sharply defined grooves for cribriform organs between each infero-/superomarginal pair. Oral ossicle (Fig. 13O) with broad actinal face, bearing large rugosities for attachment of ***sos***; large elongate ***oradm***, low, broad apophyse.

Remarks

Chrispaulia spinosa sp. nov. differs from its congeners in its possession of 3–4 bifid spine pits on distal inferomarginals.

Fig. 13 (next page). **A–C**. *Chrispaulia radiatus* (Spencer, 1905) (BGS 108650), arm of individual in abactinal, lateral and actinal views, respectively (the original of Gale 2005: fig. 5). — **D–E, H–O**. *Chrispaulia spinosa* sp. nov. **D–E**. Holotype (Nds LH 105.107), arm fragment in lateral and actinal views, respectively. **H–O**. Isolated ossicles, all paratypes. **H–I, N**. Median superomarginals (NHMUK PI EE 17998, 18003). **J–K**. Distal superomarginals in lateral view (NHMUK PI EE 17999–18000). **L–M**. Distal inferomarginals in lateral view (NHMUK PI EE 18001–18002). **O.** Oral ossicle, in radial aspect (NHMUK PI EE 18004). — **F–G**. *Chrispaulia wrightorum* sp. nov., holotype, reconstructed distal arm, in abactinal and lateral views, respectively (NHMUK PI EE 17997). Provenance: A–C. Cenomanian (Lower Chalk), Dover, Kent, United Kingdom. D–E. Lower Hauterivian (*Endemoceras amblygonium* ammonite Zone), Engelbostel near Hannover, Germany. F–G. Albian, Hunstanton Formation, Speeton, Yorkshire, United Kingdom. H–O. Upper 3 m of Tealby Clay, Hauterivian, Nettleton, Lincolnshire, United Kingdom. Scale bars: A–G = 5 mm; H–O = 1 mm.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Order Spinulosida Perrier, 1884

Family **Plumasteridae** Gale, 2011

Plumasteridae Gale, 2011b: 82, fig. 13.

Diagnosis

Five- to multi-armed asteroids possessing broad, short concavo-convex adambulacrals which possess a single row of large, transverse spine pits; adambulacrals articulate by means of transversely arranged specialised surfaces; abactinal ossicles stellate, large, with a central boss with which a long, glassy spine articulates.

Assigned genera

Plumaster Wright, 1863 and *Plesiastropecten* Peyer, 1944.

Remarks

Although *Plesiastropecten* is 5-rayed, the adambulacrals, abactinal ossicles and marginals are closely similar to those of *Plumaster* (see Gale 2011b) and the genus is accommodated here.

Plesiastropecten Peyer, 1944

Plesiastropecten Peyer, 1944: 320, pls 7–8.

Type species

Plesiastropecten hallovensis Peyer, 1944, by monotypy.

Diagnosis

Five-rayed plumasterid, in which the abactinal ossicles are stellate and which bears a fringe of elongated marginal spines.

Plesiastropecten hallovensis Peyer, 1944
Fig. 14

Plesiastropecten hallovensis Peyer, 1944: 320, pls 7–8.

Plesiastropecten hallovensis – Blake 1984: 633, fig. 1a–h.

Diagnosis

As for genus.

Material examined

The holotype (MZA L13a) is a complete asteroid in a claystone matrix, comprising part and counterpart, from the Lower Jurassic (Hettangian, *liasicus* ammonite Zone) of Hallau, Canton Schaffhausen, Switzerland (Peyer 1944). It is contained in the collections of the Museum zu Aller Heiligen, Schaffhausen, and has suffered from considerable over-preparation. Additional material includes a suite of specimens from the same locality and horizon, most notably, specimen MZA L 13b/32a-e, which is a partially dissociated individual of which one arm is well preserved (Blake 1984: fig. 1a–g). This specimen is coated with a glue-like substance which obscures much detail and requires specialist preparation. The present description is based on these two individuals.

Description

The overall form is well shown by the type specimen (Fig. 14A); the arms are moderately long and tapering, the interbrachial angles acute (R:r = approximately 6:1). The arms bear an even fringe of closely spaced marginal spines. The marginals are numerous, narrow and short with a three-tiered structure, resembling tiny 'cottage loaves' of bread (Fig. 14F). They are clearly visible in MZA L 13b/32a-e, and are robustly paxilliform, bearing a single large spine pit centrally. The abactinal ossicles are conspicuous and relatively large, convex to flat and carry four to six, lobe-like lateral projections. Each abactinal has a single, large and centrally placed crater-like spine pit (Fig. 14B, D). The ossicles imbricate, and the lobes are notched on their inside (actinal) surfaces for contact with adjacent ossicles. These ossicles are more or less radially symmetrical in the disc, but elongated in the arm, where the abactinal ossicles are arranged in three rows comprising radials and two adradials (Fig. 14B). In the distal arm, the large radial and adradials are separated from adjacent ossicles of the same row by smaller inset ossicles. The adambulacrals were prepared in a small part of specimen MZA L 13b/32b. They are very broad and short (3:1), and carry 5–6 large, horseshoe-shaped spine bases arranged in a single transverse row (Fig. 14E). The adambulacrals of opposing rows are slightly angled (150°) in a proximal direction. The ambulacrals are only seen in abactinal view, and the ***ambh*** forms a conspicuous, elongated triangular proximal wing which overlaps the more proximal adjacent ambulacral (Fig. 14D). The ***ambb*** is oval and symmetrical. The marginal spines are conspicuous, forming an even comb-like fringe to the starfish. Each marginal plate carries a single tapering spine with a unique construction. The cross section is a shallow U-shape, and the abactinal surface bears a groove. The rounded actinal surface is made up of 4–6, length-parallel coalescing rods of trabecular stereom. The lateral margins of the spines carry outwardly directed short barbs, probably lost on the holotype through over-preparation. The base of the spine is swollen and rounded, and a simple socket on the base articulates with a boss on the marginal. The abactinal spines are shorter, and round in cross section; these are also composed of elongated trabeculae. The 5–6 adambulacral spines articulate with horseshoe-shaped bases, and are long and gently curved.

Remarks

The robust paxilliform construction of the marginals is not found in any benthopectinid asteroid, but is characteristic of modern solasterids and the Jurassic genus *Plumaster*, and each marginal carries only a single spine. We cannot agree with Blake (1984) that these resemble marginals of benthopectinids, other than in that they carry large spines. The large, oval or rounded, imbricating abactinal ossicles which are alternately large and spine-bearing and small and spineless in the arm are quite different from the parapaxillae of benthopectinids. The construction of the marginal and abactinal spines, with elongated trabeculae running along the length of the spines and a semicircular, concavo-convex cross section bearing two rows of lateral thorns, are dissimilar to benthopectinid spines, which are conical, cylindrical and carry numerous, irregular, distally directed thorns. The concavo-convex construction is otherwise seen only in the multi-armed Early Jurassic *Plumaster ophiuroides* (Wright, 1863). The transversely broad, short adambulacrals, carrying 5–6 large curved adambulacral spines, are quite unlike adambulacrals of benthopectinids which are narrow and rather elongated, but are similar to those of *Plumaster* (Gale 2011b: figs 13–14). The elongated, imbricating proximal flanges of the ambulacral heads are not found in any benthopectinid, where the ambulacral heads are short, upright and do not imbricate, as in all paxillosidans (Gale 2011a), but are similar to those of *Plumaster* (Gale 2011b: fig. 14b–c). Other than a superficial similarity in shape and the presence of elongated marginal and abactinal spines (also found in other asteroids), *Plesiastropecten hallovensis* does not show any of the characteristics of the Benthopectinidae, but bears a close similarity to the Pliensbachian–Aalenian multi-armed genus *Plumaster*, with which it shares broad, short adambulacrals with 5–6 large transversely arranged, hyaline spines and the flanged, imbricating abactinal ossicles (Gale 2011b).

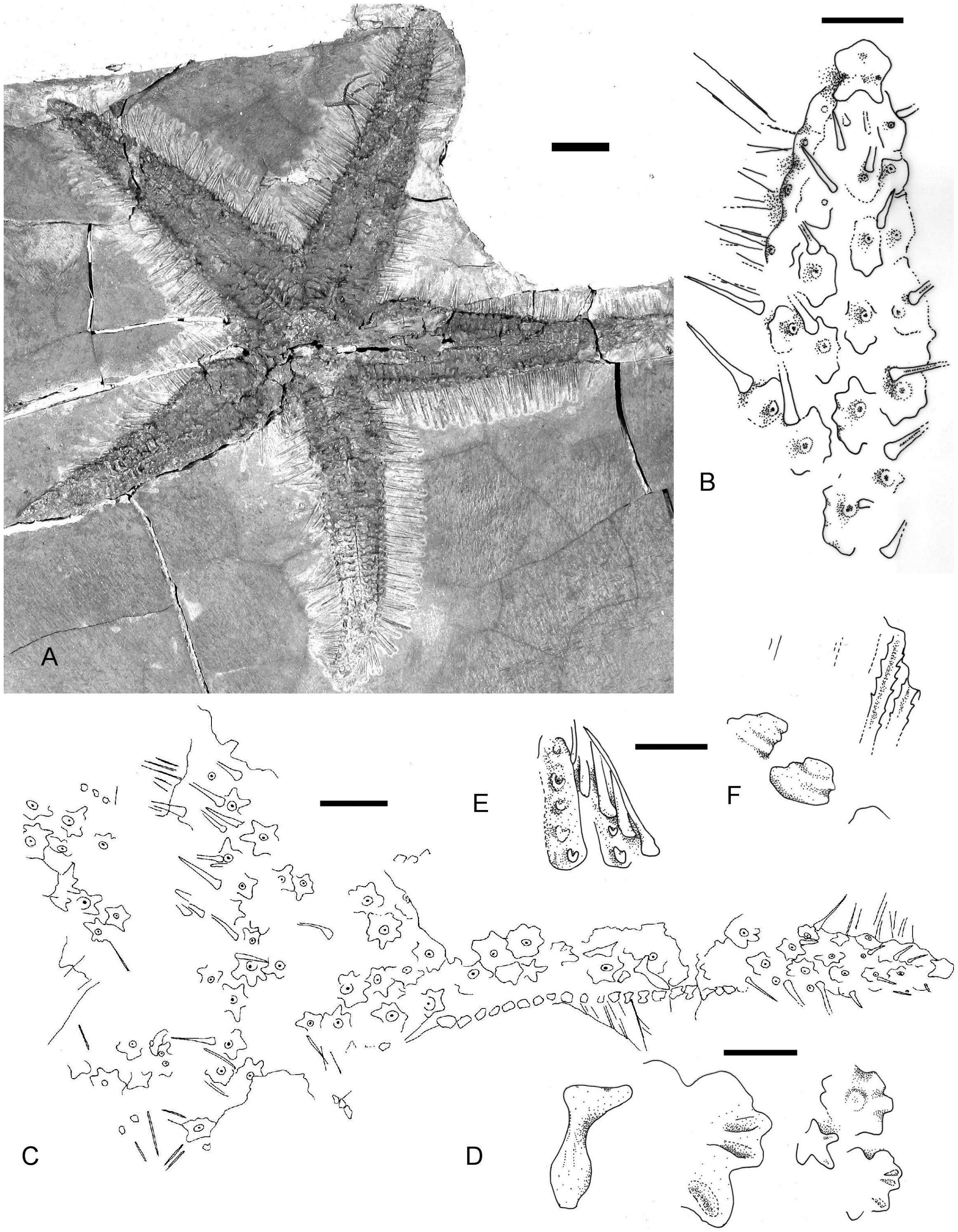

Fig. 14. *Plesiastropecten hallovensis* Peyer, 1944. **A**. Holotype (MZA L13a), the original of Peyer (1944: pl. 7) and Blake (1984: fig. 1a–h). **B**. Enlargement of distal arm. **C–F**. Line drawings of MZA L 13b/32a–e. **C**. Ossicle distribution of entire individual; note large, stellate abactinal ossicles which each carry a large boss for attachment of a single spine. **D**. Ambulacral ossicle, in abactinal view, and two abactinal ossicles. **E**. Adambulacral ossicle with spines attached. **F**. Two marginal ossicles, with serrated spines attached. Provenance: Lower Jurassic (Hettangian, *liasicus* ammonite Zone) of Hallau, Canton Schaffhausen, Switzerland. Scale bars: A = 10 mm; B–C = 5 mm; D–G = 2 mm.

Spinulosida incertae sedis

Xandarosaster hessi Blake, 1984
Fig. 15A–C

Xandarosaster hessi Blake, 1984: 638, figs 2a–i, 3.

Material examined

The single specimen available (NMB M9683) comprises fragments of three arms and dissociated ossicles, intimately entwined with an isocrinid crinoid on a single slab, from the Bajocian of Reigoldswil (Canton Baselland, Switzerland). The specimen is very fragmentary and is not easy to interpret, because pressure solution has welded scraps of calcite onto most ossicles, making discrimination of features difficult.

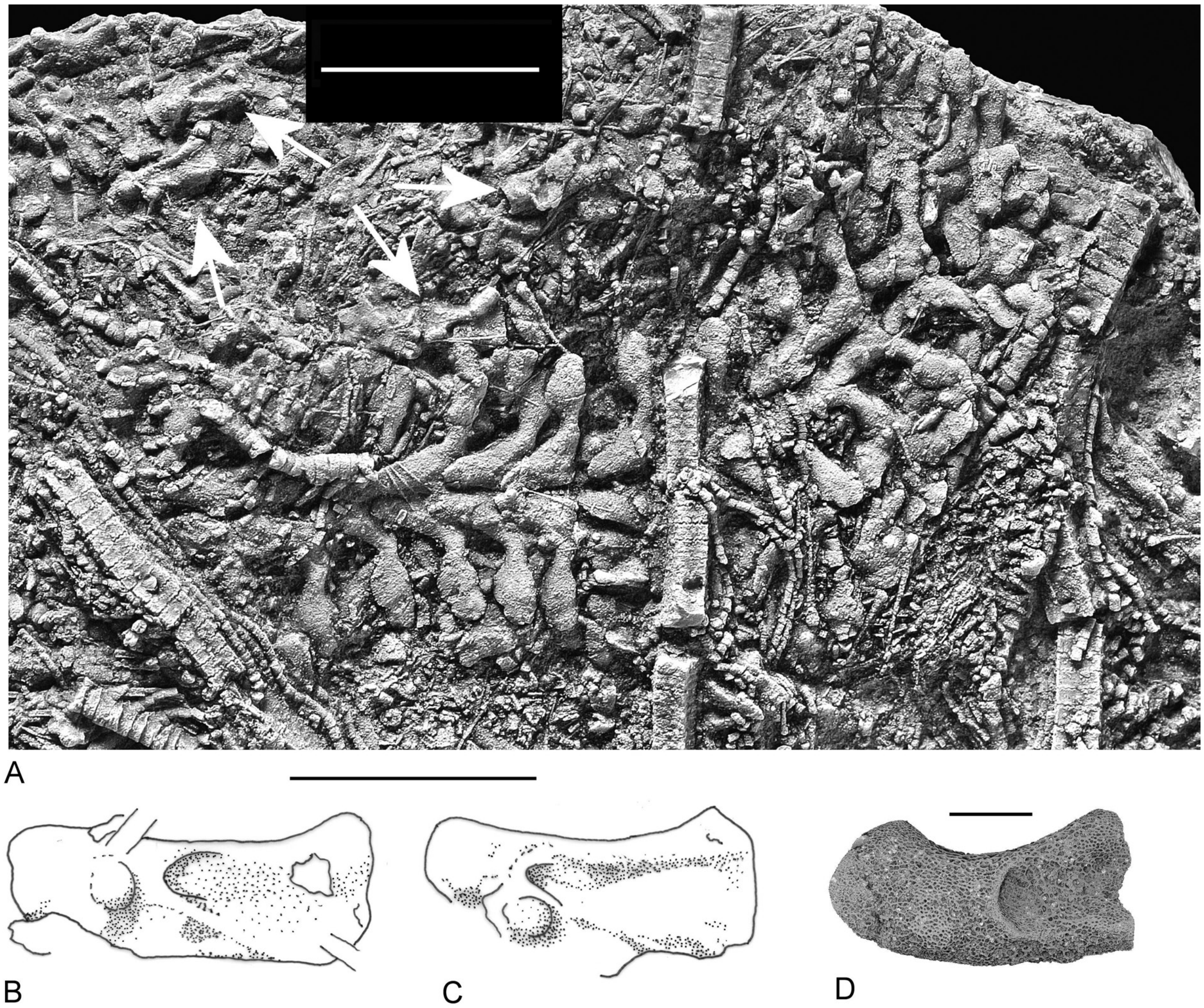

Fig. 15. A–C. *Xandarosaster hessi* Blake, 1984. **A**. Holotype slab (NMB M9683), showing articulated ambulacral ossicles and isolated adambulacrals (arrowed); the original of Blake (1984: fig. 2a1–3). **B–C**. Line drawings of actinal views of adambulacrals; note extreme elongation, long interadambulacral muscle insertion site and boss for a single, large subadambulacral spine. **D**. Similar adambulacral ossicle of indeterminate form (NHMUK PI EE 18008). Provenance: A–C. Bajocian of Reigoldswil, Canton Baselland, Switzerland. D. Oxfordian, Andelot-Morval, Jura, France (for details of locality, reference is made to Gale 2018: fig. 20). Scale bars: A = 10 mm; B–C = 5 mm; D = 0.5 mm.

Description

The ossicles of the ambulacral groove are the best preserved and most distinctive part of this specimen (Fig. 15A). The ***ambh*** imbricate strongly proximally, and are elongated and triangular. The ambulacrals are waisted, and the ***ambb*** carry short asymmetrical flanges for ***padam*** and ***dadam***, and articulation surfaces ***ada1*** and ***ada2***. The adambulacrals are rectangular and very elongated, being approximately three times longer than broad; half to two-thirds of the actinal face is occupied by a V-shaped depression for the ***adadm*** (Fig. 15B–C). An oblique ridge runs from the proximal part of the V to the distal abradial margin. Proximal ***adambs*** carry two large swollen spine bases set obliquely on the proximal face of the ossicle, and more distal ***adamb*** have a single spine base.

Several oral ossicles are visible. These are very broad and gently convex on the external surface, and an adambulacral articulation ridge and deep V-shaped concavity for the ***oradm*** muscle are present. The abactinal ossicles are of even, small size, have a lobed base and carry a large centrally placed, rounded spine boss. Possible marginals are elongated-rectangular and imbricate distally, with a very large round spine base on the proximal part of the external face. The abactinal and marginal spines are conical and moderately long, and have swollen bases. They are made up of elongated trabeculae of stereom.

Remarks

The ambulacral/adambulacral articulation of *X. hessi* is utterly dissimilar to that of benthopectinids. The ***ambh*** is broad and short in *X. hessi*, with a strong, short transverse actinal ridge. In benthopectinids, the ***ambb*** is triangular and elongated. *Xandarosaster hessi* has short, oval and nearly symmetrical facets for ***padam*** and ***dadam***, which are triangular and strongly asymmetrical in benthopectinids. In *X. hessi* **ada2** and ***adada*** are fused and ***ada3*** is absent. In benthopectinids, all three facets are discrete, and ***ada2*** and ***adada*** are placed on a ridge adjacent to a concavity on both ambulacrals and adambulacrals.

The construction of the spines, with elongated hyaline trabeculae, is unlike that of benthopectinids in which the spines are made of thorny stereom with distally directed barbs. Moreover, the elongated, strongly imbricating, asymmetrical ***ambh*** are not present in benthopectinids, where the heads are short and do not imbricate.

In summary, *X. hessi* does not possess a single character of the Benthopectinidae, but has features unique to the Spinulosida (sensu Gale 2011a), including spines constructed of elongated hyaline trabeculae and elongated, triangular proximal ***ambh*** which strongly imbricate proximally. Its affinity with other spinulosidans is uncertain, although some aspects of the ambulacrals and adambulacrals are broadly comparable with those of solasterids. The very elongated rectangular adambulacrals are unique to *X. hessi*. Adambulacrals of this type, currently indeterminate (Fig. 15D), are also found uncommonly in Jurassic sedimentary rocks such as the lower Oxfordian of Andelot-Morval, France.

Order Forcipulatida Perrier, 1884
Suborder Zorocallina Downey, 1970

Family **Terminasteridae** Gale, 2011

Terminasteridae Gale, 2011a: 92, fig. 8.

Diagnosis

Zorocallinids with extra-axial arm constructed of seven rows of ossicles organised with one row of radials, two rows of adradials, two rows of superomarginals and two rows of inframarginals; both marginal rows extend to arm tip.

Assigned genera

Alkaidia Blake & Reid, 1998 and *Terminaster* Hess, 1974.

Remarks

The family Terminasteridae is sister group to the Eocene–Recent Zoroasteridae Sladen, 1889, which is widespread in bathyal to abyssal depths of the present-day oceans.

Alkaidia Blake & Reid, 1998

Alkaidia Blake & Reid, 1998: 529, fig. 8.

Type species

Alkaidia sumralli Blake & Reid, 1998, by original designation.

Diagnosis

Terminasteridae with elongated rhombic superomarginals directed obliquely towards radials; inferomarginals with tall, distally swollen central spine bases and prominent groove for spine attachment; radials (except primary radial) rhombic in outline.

Assigned species

In addition to the type species, *A. megaungula* Ewin & Gale, 2020.

Remarks

Alkaidia ranges from the Barremian to Cenomanian and appears to be restricted to the western Tethys.

Alkaidia sumralli Blake & Reid, 1998

Figs 16A–C, 17B–E, H, K

Alkaidia sumralli Blake & Reid, 1998: 529, fig. 9/1–14.

Alkaidia sumralli – Ewin & Gale 2020: 13, figs 10.1–10.2, 13.3, 13.8, 13.11–13.12.

Diagnosis

Alkaidia in which the primary radial ossicles are elongated and the terminal ossicle is not deeply notched on its proximal margin.

Material examined

The holotype (Texas Memorial Museum, number 1786 TX1) is from the Grayson Formation (lower Cenomanian) at the Waco shale pit (Waco, Mclennan County, Texas, USA). Additional material comprises a magnificent individual (NHMUK PI EE 15225), collected by Frank Holterhoff from the Grayson Formation (lower Cenomanian) of Dottie Lynn, Fort Worth, Texas and illustrated here (Fig. 16A–C), as well as numerous dissociated ossicles from the same locality (NHMUK PI EE 18005–18007, 18009).

Remarks

The affinities of *A. sumralli* have recently been discussed in some detail by Ewin & Gale (2020) and the evidence for its inclusion in the Forcipulatida (Zorocallina) and the family Terminasteridae can be summarised briefly as follows: the presence of abundant, straight ‘duck-billed’ forcipulate pedicellariae is a characteristic of the Zorocallina (Fig. 16D); the construction of the abactinal surface is closely

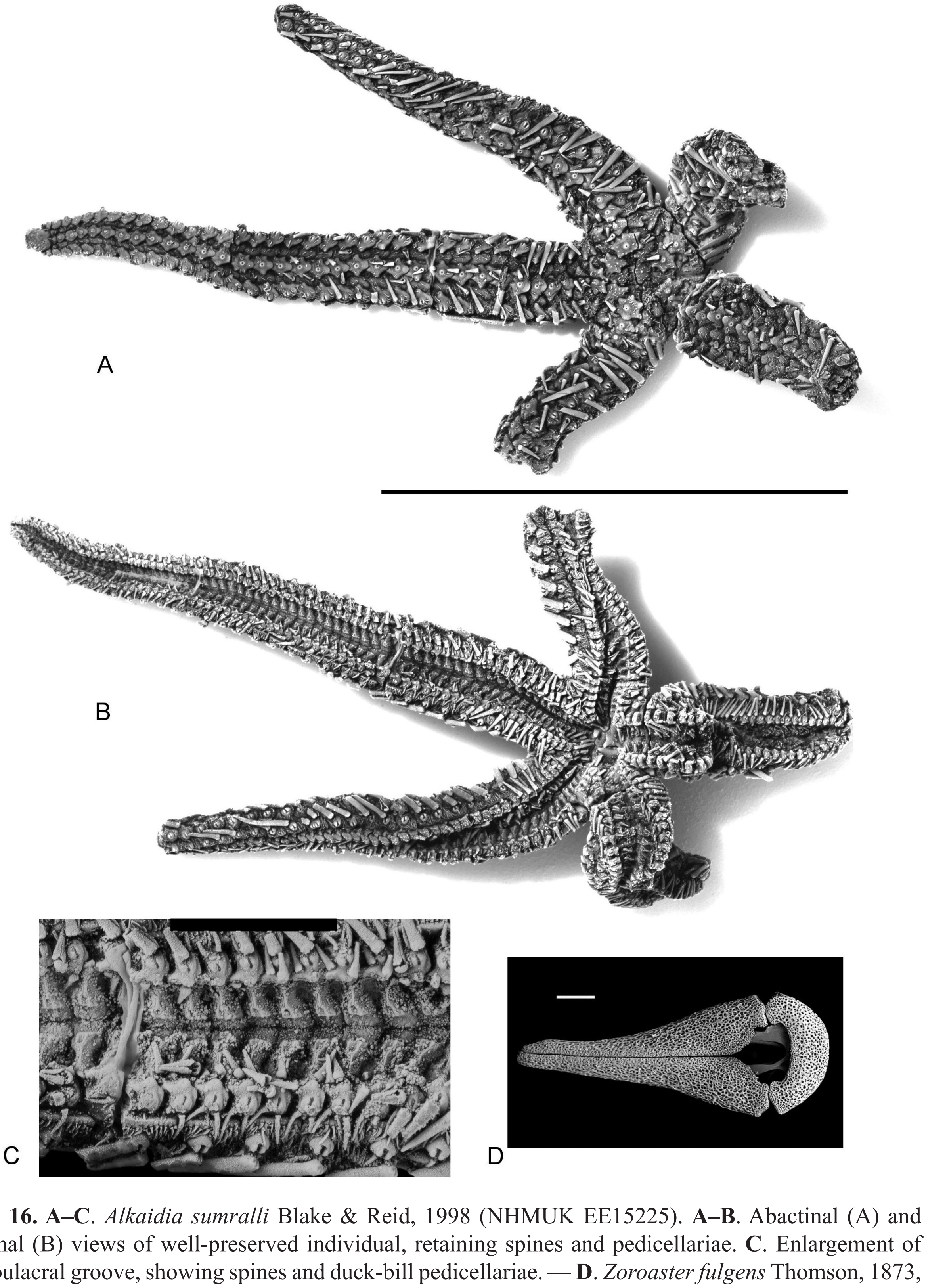

Fig. 16. A–C. *Alkaidia sumralli* Blake & Reid, 1998 (NHMUK EE15225). **A–B**. Abactinal (A) and actinal (B) views of well-preserved individual, retaining spines and pedicellariae. **C**. Enlargement of ambulacral groove, showing spines and duck-bill pedicellariae. — **D**. *Zoroaster fulgens* Thomson, 1873, duck-billed pedicellaria of a zoroasterid (A.S. Gale collection, unregistered). Provenance: A–C. Grayson Formation, *Graysonites wacoense* ammonite Zone, Dottie Lynn Lane, Fort Worth, Texas, USA (for details of locality, reference is made to Hess 2015 and Gale *et al.* 2021). D. Recent, Rockall Trough, northeast Atlantic. Scale bars: A–B = 50 mm; C = 5 mm; D = 0.5 mm.

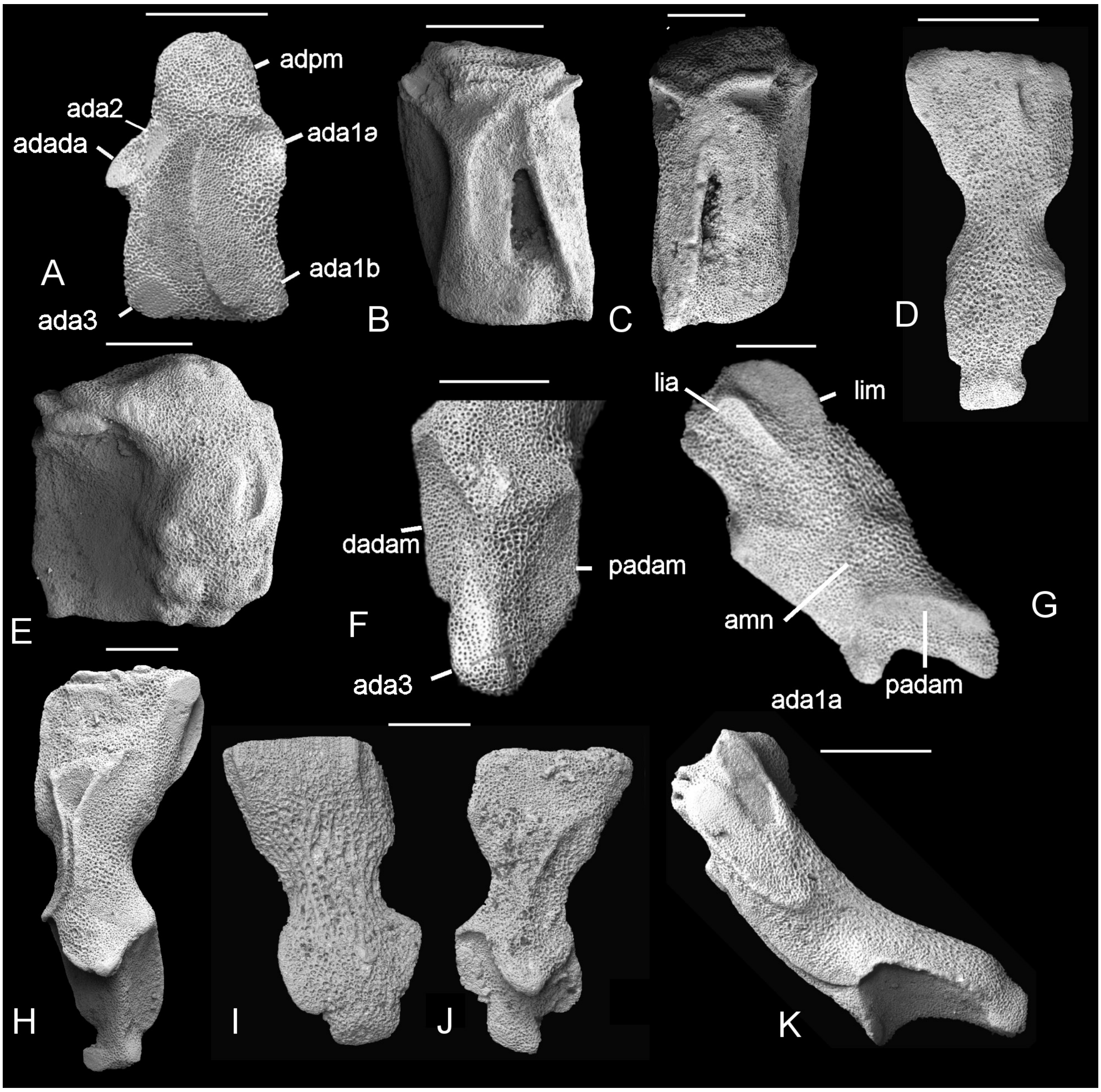

Fig. 17. A, F–G. *Zoroaster fulgens* Thomson, 1873 (A.S. Gale collection, unregistered). **A**. Adambulacral, in abactinal view; the original of Gale (2011a: pl. 8 fig. 5). **F**. Ambulacral base, in actinal view; the original of Gale (2011a: pl. 8 fig. 8). **G**. Ambulacral, in proximal view. — **B–E, H, K**. *Alkaidia sumralli* Blake & Reid, 1998, isolated ambulacrals and adambulacrals. **B–C**. Abactinal views of adambulacrals (NHMUK PI EE 18005–18006). **D**. Abactinal view of ambulacral (NHMUK PI EE 18007). **E**. Actinal view of adambulacral (NHMUK PI EE 18008). **H**. Actinal view of ambulacral (NHMUK PI EE 18008). **K**. Proximal view of ambulacral (NHMUK PI EE 18010), the original of Gale (2011a: pl. 8 fig. 9). — **I–J**. *Terminaster cancriformis* (Quenstedt, 1876) (NMB M 9036), ambulacral, in abactinal and actinal views; the original of Gale (2011a: pl. 26 figs 11–12). Provenance: A, F–G. Recent, Rockall Trough, northeast Atlantic. B–E, H, K. Grayson Formation, *Graysonites wacoense* ammonite Zone, Dottie Lynn Lane, Fort Worth, Texas, USA (for locality details, reference is made to Hess 2015 and Gale *et al.* 2021). I–J. Upper Oxfordian (Couches d'Effingen, *bifurcatus* ammonite Zone, *stenocycloides* ammonite Subzone), Savigna, near Orgelet, Département de Jura, France (Gale 2011b). See Material and methods for abbreviations. Scale bars: 1 mm.

similar to that of zoroasterids and terminasterids, which also have large, Y-shaped first superomarginals and a row of robust, lobed, quadrangular radial ossicles which imbricate proximally and each carry a centrally placed conical spine (Ewin & Gale 2020).

Additionally, the morphology of the adambulacrals and ambulacrals, and the nature of their articulation is similar in zoroasterids, *Terminaster* and *Alkaidia* (Fig. 17). ***Ada1a*** and ***ada2*** are concave on the adamulacrals (Fig. 17A–C) and positioned on a process on the ambulacrals (Fig. 17G–H, J–K). The ***dadam*** and ***padam*** facets are subequal in size, broad and short (Fig. 17A–C).

The abactinal construction is never seen in extant benthopectinids, in which the abactinal ossicles in the arms are small and parapaxilliform or very small, and never imbricate. Additionally, in benthopectinids the abactinal surface is invariably flat, and the arm section is not subcylindrical.

Indeterminate asteroid

Henricia*? *venturana Durham & Roberts, 1948

Henricia? *venturana* Durham & Roberts, 1948: 437, pl. 66 figs 1, 3.

Remarks

The unique holotype, from the Upper Cretaceous Chico Formation of the North Fork of Matilija Creek, Ventura County (California, USA), is contained in the palaeontological collections of the University of California. Part (number 4866B) and counterpart (4866A) show the abactinal and actinal surfaces, respectively.

The type specimen is an external mould of a near-complete asteroid with moderately long, narrow arms and a small disc, which has lost the abactinal ossicles and exposes the ambulacrals on the abactinal surface. Unfortunately, parts of the moulds have been worn by erosion and few details are well preserved. The ambulacral heads are elongated, and the adambulacral ossicles are clearly visible, as are probable small marginal ossicles bearing spines. The groove is very wide. Although Blake (1984) assigned the taxon to the Benthopectinidae, there does not seem to be any compelling evidence for its taxonomic affinity, and it is considered here to be an indeterminate asteroid.

Discussion

The hypothesis that Mesozoic asteroids (Table 2) which bear conspicuous, elongated marginal and abactinal spines are members of, or closely related to, the extant deep-sea family Benthopectinidae is tested, using comparative morphology of diverse ossicle types. It is concluded that all three members of the subfamily Paleobenthopectininae Blake, 1984 are convergent in gross morphology with certain extant benthopectinids and should be correctly assigned to distantly related groups (i.e., Spinulosida, Plumasteridae; Forcipulatida, Terminasteridae). The other fossil benthopectinid cited in the literature (Spencer & Wright, 1966) is here assigned to a new species of the goniopectinid genus *Chrispaulia*.

In the present study, we demonstrate the taxonomic value of characters ubiquitously present in extant benthopectinids. In particular, the ambulacral/adambulacral morphology is of value, specifically the nature of the articulation between the ambulacrals and adambulacrals; this provides an excellent criterion for correct recognition of fossil benthopectinids (see also Gale 2011a). The distinctive benthopectinid ambulacral/adambulacral articulation appeared early in the Jurassic (Toarcian) and is retained in all members of the family to the present day. Possible benthopectinid ossicles are already present in the Triassic (see above), but in the absence of ossicles of the ambulacral groove and mouth frame this identification is uncertain.

Table 2. Affinities of fossils assigned to the Benthopectinidae Verrill, 1894, by date of publication.

Name	Age	Locality	Assignation
Plesiastropecten hallovensis Peyer, 1944	Early Jurassic Hettangian	Switzerland	Spinulosida, Plumasteridae
Henricia ? *venturana* Durham & Roberts, 1948	Cretaceous	California	Indeterminate asteroid
Benthopectinid Spencer & Wright 1966	Albian	Yorkshire, England	Goniopectinidae, *Chrispaulia wrightorum* sp. nov.
Mistia spinosa Blake, 1973	Oligocene	Mist, California	Benthopectinidae, *Nearchaster spinosus*
Xandarosaster hessi Blake, 1984	Middle Jurassic, Bajocian	Switzerland	Spinulosida, affinity uncertain
Alkaidia sumralli Blake & Reid, 1998	Cretaceous, Albian–Cenomanian	Texas	Forcipulatida, Terminasteridae
Benthopectinid 1 Jagt 2000	Late Cretaceous	Netherlands	Benthopectinidae, *Jurapecten dhondtae* sp. nov.
Benthopectinid 2 Jagt 2000	Late Cretaceous, Cenomanian–Maastrichtian	Netherlands, UK, Denmark, Germany, Czech Republic	Benthopectinidae, *Punkaster spinifera* gen. et sp. nov.

The Benthopectinidae is represented in the Jurassic and Cretaceous (Toarcian–Maastrichtian) by the genus *Jurapecten*, which resembles the extant *Pontaster* in the morphology of the marginal plates and spines attached to these (squat, block-like; spines short), but in which the ambulacrals lack a raised transverse abactinal ridge; they did not articulate with the inferomarginals, as is the case in all extant genera. The absence of the abactinal ridge can be taken as evidence that *Jurapecten* lacked longitudinal muscles in the arm. The new genus *Punkaster* gen. nov., from the Upper Cretaceous, appears to be a highly derived benthopectinid, in which the marginals are elongated, sometimes in fused interradial pairs, and carried large conical spines. The main evidence of assignation of *Punkaster* gen. nov. to the family is the nature of the ambulacral/adambulacral articulation. The oldest representative of extant benthopectinid genera is *Nearchaster* (formerly *Mistia*) *spinosus* comb. nov. from the Lower Oligocene of Oregon, USA (Blake 1973).

The transition between the plesiomorphic Mesozoic-type benthopectinid morphologies (lack of abactinal ridges on ambulacrals, ambulacrals not articulating with the inferomarginals) and derived Cenozoic types in which the abactinal ridges supported longitudinal muscles, is poorly known, but the oldest Cenozoic fossil benthopectinid (*Nearchaster spinosus* comb. nov.) is present in the Early Oligocene. It is therefore likely that the radiation of the family took place during the early Paleogene. The presence of a number of derived characters in all living and Cenozoic benthopectinid taxa supports their monophyly. However, the very fragmentary nature of the benthopectinid fossil record (mostly isolated ossicles) does not lend itself to cladistic analysis of the group.

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