



Systematic assessment of the Atelostomata (Spatangoida and Holasteroida; irregular echinoids) based on spine microstructure

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Spines of irregular echinoids occur in very high abundance in each specimen, and display distinct architecture as a result of the specialized functions of the spines; however, studies on spine microstructure in atelostomate echinoids have rarely been carried out. Accordingly, little is known about their specific morphology. This work aims to elaborate differences in the spine morphology of selected Atelostomata (Spatangoida and Holasteroida) in detail, and to discuss spine microstructure for its potential systematic value. Based on 82 atelostomate species (56 spatangoids and 26 holasteroids), we show that the perforation pattern in the internal cylinder of the spine (helical versus horizontal pattern) provides a safe distinction between the Spatangoida and Holasteroida. According to this character we discuss the geological history of atelostomate echinoids, in particular their migration into the deep sea, based on well-preserved records of fossil spines.

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INTRODUCTION

Holasteroid and spatangoid echinoids (the only extant atelostomate irregular echinoids) evolved around 145 Mya (Eble, 2000; Kroh & Smith, 2010), and became an important component of the Cretaceous shelf benthos (Kier, 1974; Smith, 1984; Eble, 2000); however, systematic approaches to these atelostomates predominantly rely on test architecture. The appendages of echinoids in general have been studied in detail elsewhere (pedicellariae, including atelostomate taxa, Mortensen, 1950, 1951; Coppard *et al.*, 2012; teeth of regular

echinoids, Ziegler *et al.*, 2012); however, there is little knowledge on the morphology and microstructure of atelostomate spines. Agassiz (1872–1874: 651) gave detailed descriptions on spine microstructure in the major extant echinoid groups, also including sections (Agassiz, 1872–1874: plates XXXV, XXXVI, XXXVII). Mooi & David (1996) documented some miliary spines from selected Holasteroida, and Stephenson (1963; on *Echinocorys scutata* Leske, 1778) and Saucède *et al.* (2009; on *Calymne relictata* Thomson, 1877) presented the spine morphology of a single species in great detail. Other studies treated spines cursorily (Agassiz, 1881; Hesse, 1900; Mortensen, 1950, 1951; Stephenson, 1963; Kroh, 2002) and, because of their apparently poorly variable and thus insignificant morphological

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Table 1. List of taxa investigated

Superorder Atelostomata		
von Zittel, 1879		
Order Spatangoida		
L. Agassiz, 1840		
	Family Hemiasteridae H. L. Clark, 1917	<i>Holanthus expergitus</i> (Lovén, 1874)
Suborder	Family Micrasteridae Lambert, 1920	<i>Isopatagus obovatus</i> Mortensen, 1948
Micrasterina Fischer, 1966	Family Aeropsidae Lambert, 1896	<i>Aeropsis fulva</i> (A. Agassiz, 1898)
Suborder	Family Loveniidae Lambert, 1905	<i>Breynia australasiae</i> (Leach, 1815)
Brissidina Stockley, Smith		<i>Echinocardium cordatum</i> (Pennant, 1777)
Littlewood & MacKenzie-		<i>Echinocardium mediteraneum</i> (Forbes, 1844)
Dodds, 2005		<i>Lovenia elongata</i> (Gray, 1845)
		<i>Lovenia subcarinata</i> Gray, 1851
	Family Spatangidae Gray, 1825	<i>Spatangus capensis</i> Döderlein, 1905
		<i>Spatangus purpureus</i> Müller, 1776
		<i>Spatangus raschi</i> Lovén, 1870
	Family Maretidae Lambert, 1905	<i>Granobrissoides hirsutus</i> (Mortensen, 1950)
		<i>Gymnopatagus magnus</i> Agassiz & Clark, 1907
		<i>Homolampas</i> sp.
		<i>Maretia planulata</i> (Lamarck, 1816)
		<i>Nacospatangus laevis</i> (H.L. Clark, 1917)
		<i>Nacospatangus tylota</i> (H.L. Clark, 1917)
		<i>Spatagobrissus mirabilis</i> H.L. Clark, 1923
	Family Palaeotropidae Lambert, 1896	<i>Paleotrema loveni</i> (A. Agassiz, 1879)
	Family Eurypatagidae Kroh, 2007	<i>Eurypatagus ovalis</i> Mortensen, 1948
		<i>Eurypatagus parvituberculatus</i> (H.L. Clark, 1924)
		<i>Linopneustes fragilis</i> (de Meijere, 1903)
		<i>Linopneustes longispinus</i> (A. Agassiz, 1878)
		<i>Linopneustes murrayi</i> (A. Agassiz, 1879)
		<i>Paramaretia multituberculata</i> Mortensen, 1950
	Family Brissidae Gray, 1855	<i>Anametalia regularis</i> (H.L. Clark, 1925)
		<i>Brissopsis lyrifera</i> (Forbes, 1841)
		<i>Brissus agassizii</i> Döderlein, 1885
		<i>Brissus latecarinatus</i> (Leske, 1778)
		<i>Brissus obesus</i> Verrill, 1867
		<i>Meoma ventricosa grandis</i> Gray, 1851
		<i>Meoma ventricosa ventricosa</i> (Lamarck, 1816)
		<i>Metalia nobilis</i> Verrill, 1867
		<i>Plagiobrissus grandis</i> (Gmelin, 1791)
		<i>Rhynobrissus hemiasteroides</i> A. Agassiz, 1879
		<i>Rhynobrissus pyramidalis</i> A. Agassiz, 1872

characters, atelostomate spines were not seriously considered to be taxonomically significant (but see Kroh & Smith, 2010).

In order to gauge the possible systematic value of atelostomate spines, we studied the morphology and microstructure of 973 spines of 74 extant atelostomate taxa (for details, see Figure S3), following the systematic classification of Kroh & Smith (2010): 56 Spatangoida, with members of the Hemiasteridae, Micrasteridae, Loveniidae, Spatangidae, Maretidae, Palaeotropidae, Eurypatagidae, Brissidae, Loveniidae, Schizasteridae, Prenasteridae, Palaeopneustine unnamed

clade, Paleopneustidea, and Pericosmidae; 18 Holasteroida, with species of the Plexechinidae, Corystusidae, Pourtalesiidae, Urechinidae, Carnarechinidae, and Calymnidae (Tables 1–3). In addition, published drawings (A. Agassiz, 1881) from eight holasteroid taxa were studied for the perforation of the internal cylinder (see Table 4).

MATERIAL AND METHODS

Most of the material comes from the Theodor Mortensen collection (Natural History Museum Copenhagen), which

Table 2. List of taxa investigated (continuation of Table 1)

Order Spatangoida L. Agassiz, 1840		
Suborder Paleopneustina Markov & Solovjev, 2001	Family Schizasteridae Lambert, 1905	<i>Abatus cavernosus</i> (Philippi, 1845) <i>Abatus cordatus</i> (Verrill, 1876) <i>Aceste bellidifera</i> Thomson, 1877 <i>Brisaster capensis</i> (Studer, 1880) <i>Brisaster fragilis</i> (Düben & Koren, 1846) <i>Moira atropos</i> (Lamarck, 1816) <i>Protenaster australis</i> (Gray, 1851) <i>Schizaster compactus</i> (Koehler, 1914) <i>Schizaster edwardsi</i> Cotteau, 1889 <i>Tripylaster philippii</i> (Gray, 1851)
	Family Prenasteridae Lambert, 1905	<i>Agassizia scrobiculata</i> Valenciennes, 1846 <i>Tripylus excavatus</i> Philippi, 1845
	Paleopneustine	<i>Amphipneustes lorioli</i> Koehler, 1901 <i>Amphipneustes marsupialis</i> (Koehler, 1926)
	unnamed clade	<i>Heterobrissus hystrix</i> (A. Agassiz, 1880)
	Superfamily Paleopneustidea A. Agassiz, 1904	
	Family Paleopneustidea A. Agassiz, 1904	<i>Paleopneustes cristatus</i> A. Agassiz, 1873 <i>Plesiozonus diomedea</i> Mortensen, 1948
	Family Pericosmidae Lambert, 1905	<i>Faorina chinensis</i> Gray, 1851 <i>Pericosmus akabanus</i> Mortensen, 1939 <i>Pericosmus macronesius</i> Koehler, 1914

Table 3. List of taxa investigated (continuation of Table 2)

Order Holasteroida Durham & Melville, 1957		
Infraorder Urechinina Duncan, 1889	Family Plexechinidae Mooi & David, 1996 Family Corystusidae Foster & Philip, 1978 Family Pourtalesiidae A. Agassiz, 1881	<i>Plexechinus spectabilis</i> Mortensen, 1948 <i>Corystus relictus</i> (de Meijere, 1903) <i>Ceratophysa ceratopyga valvaecristata</i> Mironov, 1976 <i>Ceratophysa rosea</i> (A. Agassiz, 1879) <i>Cystocrepis setigera</i> (A. Agassiz, 1898) <i>Echinocrepis rostrata</i> Mironov, 1973 <i>Echinosigra (Echinogutta) amphora</i> Mironov, 1974 <i>Echinosigra (Echinosigra) phiale</i> (Thomson, 1873) <i>Echinosigra (Echinosigra) vityazi</i> Mironov 1997 <i>Pourtalesia heptneri</i> Mironov, 1978 <i>Pourtalesia jeffreysi</i> Thomson, 1873 <i>Pourtalesia laguncula</i> A. Agassiz, 1879 <i>Pourtalesia thomsoni</i> Mironov, 1976 <i>Cystechinus loveni</i> A. Agassiz, 1898 <i>Pilematechinus vesica</i> (A. Agassiz, 1879) <i>Urechinus naresianus</i> A. Agassiz, 1879 <i>Carnarechinus clypeatus</i> (A. Agassiz, 1879) <i>Sternopatagus sibogae</i> de Meijere, 1903
	Family Urechinidae Duncan, 1889	
	Family Carnarechinidae Mironov, 1993	
	Family Calymnidae Mortensen, 1907	

is one of the largest collections of recent echinoids worldwide. Further taxa come from the Natural History Museum of Berlin and the Geoscience Museum of the University of Göttingen. There is a mismatch between the number of Holasteroida and the number of

Spatangoida in the collections: today, Holasteroids are restricted to the deep sea, and given the fragile nature of their tests and spines, specimens often lack the complete spine canopy, or spine tips are broken off as a result of the collecting technique (e.g. dredging).

Table 4. Holasteroid species, which reveal a horizontal arrangement in pores in the internal cylinder (A. Agassiz, 1881)

<i>Cystechinus wyvillii</i> A. Agassiz, 1879	pl. XL, figs. 59–60
<i>Calymne relictata</i> Thomson, 1877	pl. XL, figs. 64, 65
<i>Cystechinus wyvillii</i> A. Agassiz, 1879	pl. XLI, figs. 24–27
<i>Echinocrepis cuneata</i> A. Agassiz, 1879	pl. XLI, fig. 31
<i>Spatagocystis challengerii</i> A. Agassiz, 1879	pl. XLI, fig. 40
<i>Ceratophysa ceratopyga</i> (A. Agassiz, 1879)	pl. XLI, figs. 44–46
<i>Pourtalesia hispida</i> A. Agassiz, 1879	pl. XLI, figs. 47, 48
<i>Helgocystis carinata</i> (A. Agassiz, 1879)	pl. XLI, figs. 50–52

INSTITUTIONAL ABBREVIATIONS

GZG, Geowissenschaftliches Zentrum der Georg-August-Universität Göttingen, Göttingen, Germany; ZMB, Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Berlin, Germany; ZMUC, Zoological Museum, Natural History Museum of Denmark, Copenhagen, Denmark.

GENERAL MORPHOLOGY OF SPINES IN ATELOSTOMATE ECHINOIDS

Irregular echinoids are armed with a dense coat of often small spines (Fig. 1). These play a very important role in the differing lifestyles of the echinoids. With the distinct functions of the spines (e.g. locomotion, protection, and transport of food particles), the architecture of the spines is highly adapted to the function. Smith (1980) gave a detailed description on the overall shape and function of spines (for characters mentioned in the text, see Fig. 1). The proximal part of the spine, the acetabulum, is articulated to the mamelon of the tubercle. The base is connected via muscles to the areole, which surrounds the mamelon. The shape of the base varies because of the function of the spine. If the movement of the spine is preferentially unidirectional, the area of muscle attachment is enlarged in the corresponding direction, both in the areole and in the base. The widened area at the top of the base is called the milled ring, which also serves for muscle attachment. The shaft of a spine is generally slender, with either a pointed or a spatulate tip towards the distal ends. The spatulate tip is often found in spines specialized for burrowing/locomotion, and is localized on the oral and possibly on the lateral side also. The spines show a distinct longitudinal striation, which is produced by longitudinal wedges running over the whole length of the shaft. The wedges are generally wedge- or club-shaped in cross section (Fig. 2B). The hollow centre of the spines (lumen or axial cavity, Fig. 2B) is encompassed by a cylinder ('*Axialscheide*' of Hesse,

1900), which is perforated (Fig. 2C). The blade-like wedges are connected to the cylinder via bridges (Fig. 2A, B).

METHODS

The spines were extracted from the oral side (plastral area), lateral side and apical side of the tests (see Fig. 1), if spines were available in these areas. These areas could not always be sampled in all specimens because of incomplete spine preservation. The spines were macerated and cleared of organic remains with hypochlorous acid (3%), and afterwards were washed in distilled water. For longitudinal sections, to assess the perforation of the cylinder, spines were glued on stubs and opened with a nail file. Prior to SEM investigation, samples were sputtered with gold, and analyses and photographic documentation were performed at the Section of Palaeontology, Freie Universität Berlin, with a Zeiss Supra 40VP scanning electron microscope. All measurements were made with ImageJ, three measurements were made and averaged, and the correlation analysis was performed in R v. 3.0.1 (R Development Core Team, 2013).

SYSTEMATIC ASSESSMENT

We tested seven spine characters (one internal and six external) for a systematic assessment.

1. Ornamentation of the wedges close to the base
Four states can be discriminated: a serrated-like appearance of the wedges (Fig. 3A); a distinct, horizontal, or scattered running pustulation in the wedges (Fig. 3B); beaded ornamentation (Fig. 3B–D); or naked wedges throughout (Fig. 3E). It appears that some states occur together in a single spine (e.g. Fig. 3B).
2. Absence/presence of thorns
One internal and six external thorns were generally treated as being absent or present. We did not distinguish between distinct shapes of the thorns (see Figs. 3F–I).
3. The presence of beaded ornamentation
We distinguished between spines with a beaded structure (see Fig. 4A–C, H–J) and spines without any ornamentation. Furthermore, the position and extension of the beaded structure on the spine was considered: (1) spines with a beaded base only; (2) the beaded structure extended at least to half the length of the spine; (3) the base of the shaft is smooth and the beaded structure starts higher; (4) naked spines.
4. The distances between the wedges
The distance between the wedges was related to the width of the wedges. Wedges were measured at the widest point of each wedge, and in between them.

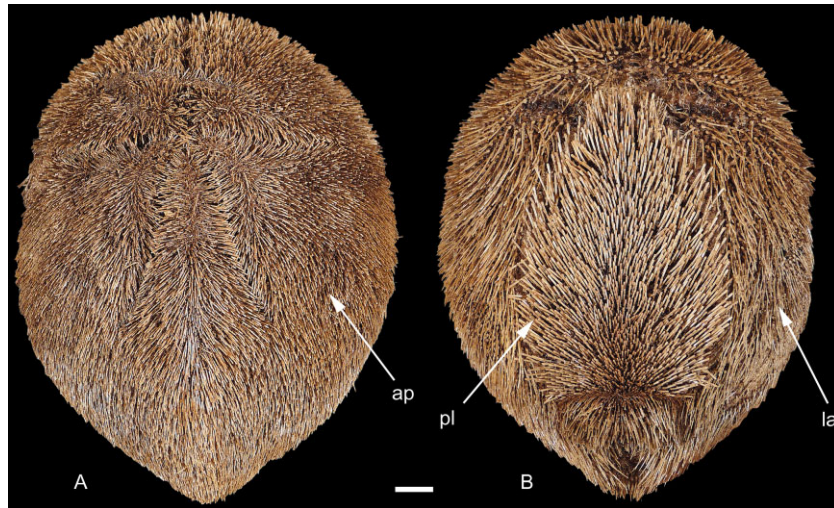


Figure 1. Test with spines (*Brissus latecarinatus*, ZMUC-ECH-602): apical side (A), oral side (B). Arrows indicate, approximately, the locations from where spines were generally collected (ap, apical; la, lateral; pl, plastral). Scale bar: 1 cm.

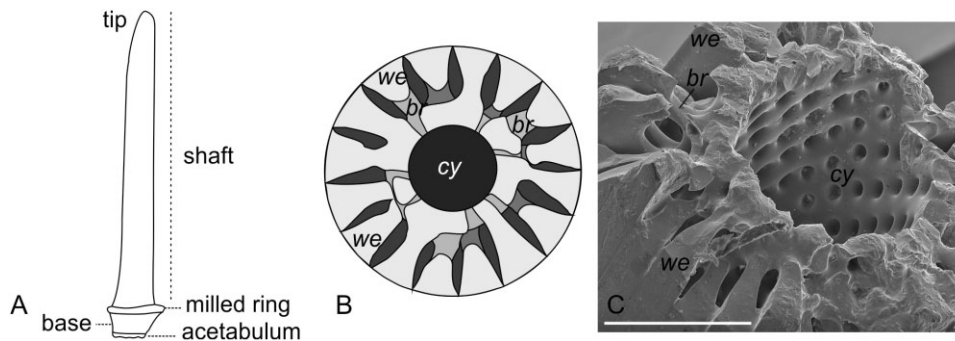


Figure 2. Spine morphology: general (A), spatangoid spine in section (B), and internal structure in a broken spine of *Spatangus raschi* (C). Abbreviations: *br*, bridges; *cy*, cylinder; *we*, wedge.

To gain a descriptive parameter for statistical analysis, the distance between the wedges was divided by the width of the wedges. The smaller the distance between the speta, the smaller the result: a result of 0 means no distance between the wedges, and a result of 1 means the distance between the wedges and the width of the wedges are equal.

5. The shape of the wedges

The shape of the wedges was suggested by Hesse (1900) as a systematic character. He distinguished the following groups: (1) *Echinocardium* group, based on cuneiform wedges (flatter outer surface and triangular shape; Fig. 5A); (2) *Brissus* group, based on a fan-shaped appearance of the proximal parts of the wedges (after a thinner bridge, connecting cylinder and wedges, the width of the wedges increases rapidly towards the periphery), the surface of the wedges is more flatter (Fig. 5B, C); (3) *Prenaster* group, based on club-shaped wedges (rounded to well-rounded outer surface; Fig. 5D–F).

6. Number of wedges

The diameter of the spine was measured at three different sites of the spine: close to the base of the shaft, the middle part, and at the top. These measurements were averaged and then correlated with the number of wedges. The correlation of these data was performed for all species grouped together.

7. Perforation of the cylinder

The arrangement of the pores was differentiated between pores running horizontally (Fig. 6A) and helicoidally (Fig. 6B).

RESULTS

A detailed compilation of the results of the analyses can be obtained from the table provided in Figure S1. A generalized overview of the results for each family is given in a simplified phylogenetic tree of the Spatangoida and the Holasteroida (Fig. 7).

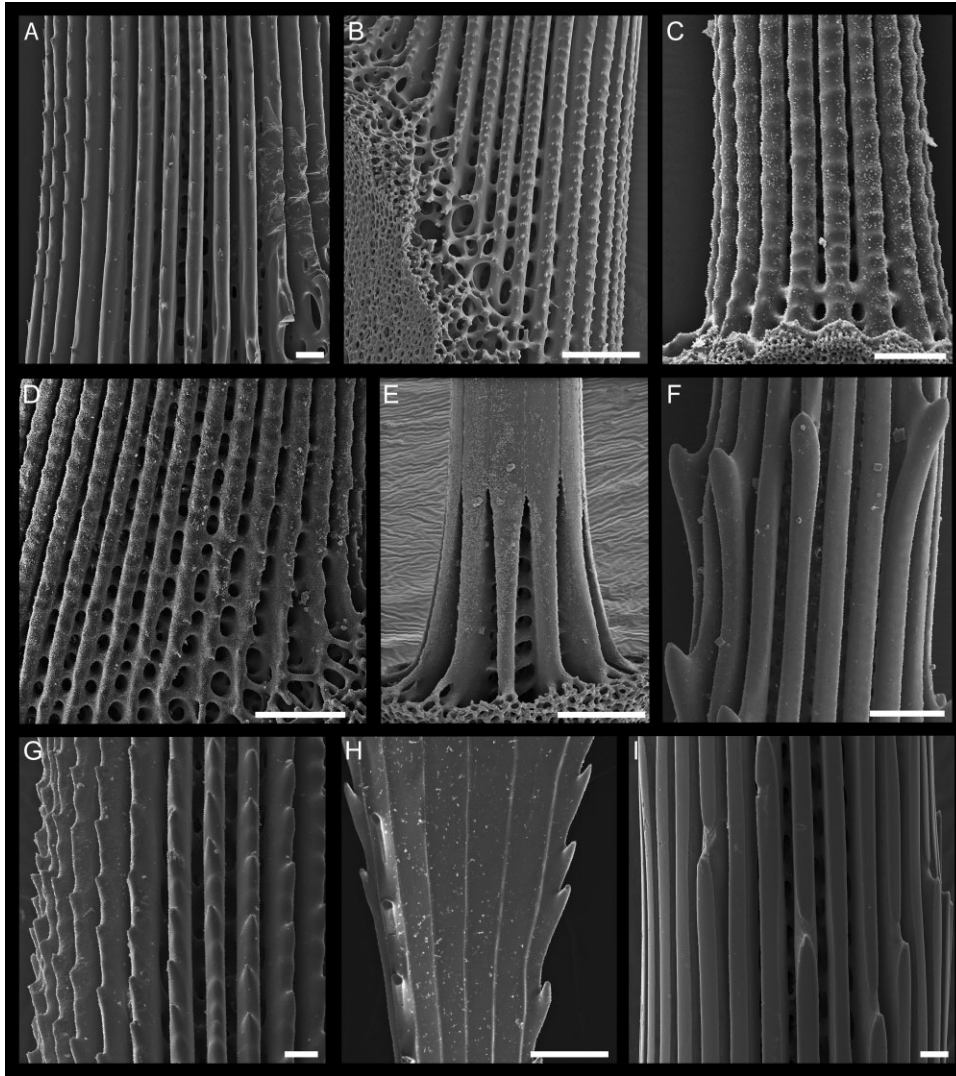


Figure 3. Ornamentation of spines: A, *Abatus cordatus* (ZMB.Ech 2230_5); B, *Breynia australisae* (ZMUC-ECH-610); C, *Tripylaster philippii* (ZMUC-ECH-612); D, *Moira atropos* (ZMUC-ECH-613); E, *Pourtalesia heptneri* (ZMUC-ECH-655); F, *Paleopneustes cristatus* (ZMUC-ECH-113); G, *Amphipneustes lorioli* (ZMUC-ECH-666); H, *Echinosisgra phiale* (ZMB.Ech 5436_2); I, *Rhynobrissus pyramidalis* (GZG.INV.78903). Scale bars: (A) 30 μm ; (B–F, H) 100 μm ; (G, I) 20 μm .

ORNAMENTATION OF THE WEDGES CLOSE TO THE BASE

It appears that the development of a pustulation, or serration, is a shared apomorphy among several spatangoid taxa, as these features could not be observed in holasteroid spines. An occurrence of distinct ornamentation states in spatangoids, which follows a systematic grouping at the family level, could not be detected. The development of ornamentation is possibly more stable at the genus level than at the family level: both species of *Abatus* share the same state (serrated ornamentation), the species of *Nacospatangus* (naked and pustule-like surfaces) and *Linopneustes*

(naked throughout). By contrast, species of *Echinocardium* differ from one another: whereas *Echinocardium cordatum* (Pennant, 1777) has spines with a pustulated surface, *Echinocardium mediterraneum* (Forbes, 1844) has naked wedges at the base. Moreover, individuals occur with both types of spines.

1. Absence/presence of thorns

Thorns occur in holasteroids as well as in spatangoids. Spines with thorns occur scattered among several families. The simple presence or absence of thorns does not reveal a systematic pattern in this study.

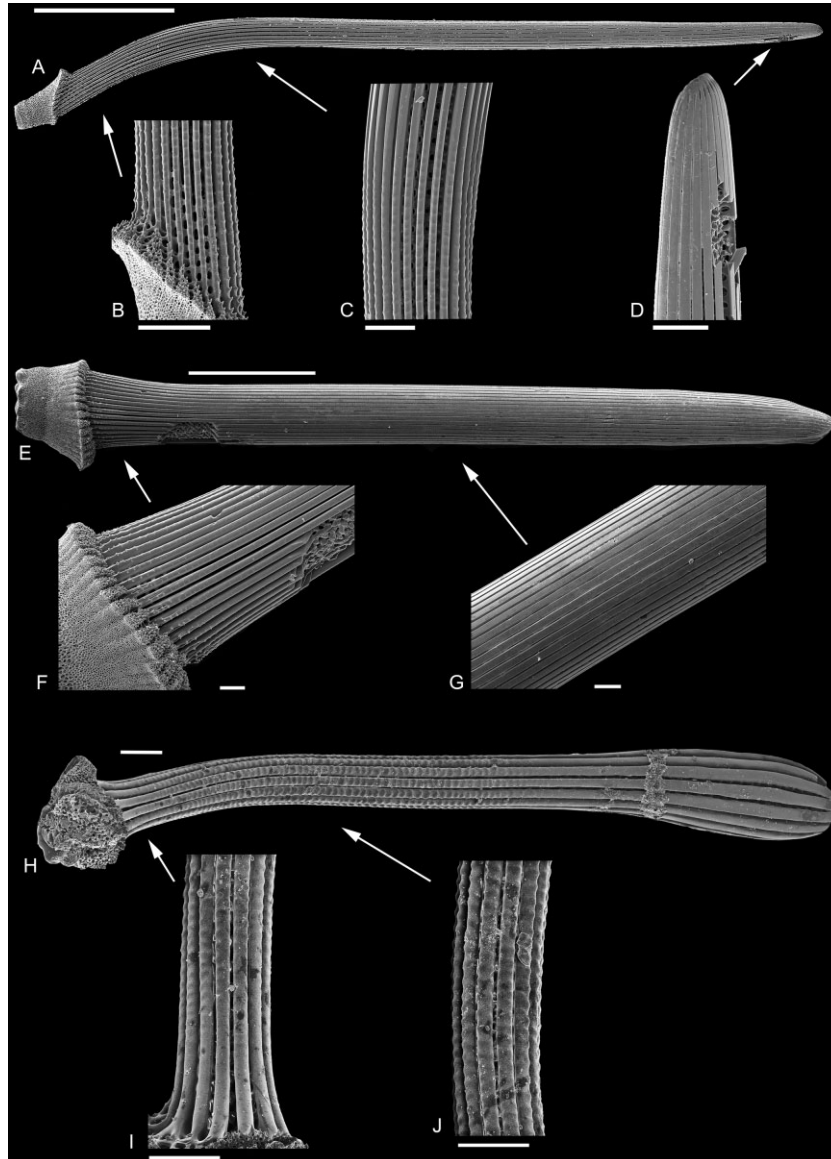


Figure 4. Ornamentation of spines: A–D, *Echinocardium cordatum* (GZG.INV.78890); E–G, *Brissus agassizii* (GZG.INV.78900); H–J, *Holanthus expergitus* (ZMUC-ECH-651). Scale bars: (A) 200 µm; (B–D) 40 µm; (E) 1 mm; (F–J) 100 µm.

2. Presence of beaded ornamentation

Holasteroid echinoids never display such ornamentation, which is why we believe that beaded ornamentation is in part apomorphic to the Spatangoida; however, this state seems to occur randomly in spatangoids. Regarding simple availability, it does not strictly follow any systematic grouping: taxa with beaded ornamentation present or absent are found in species regardless of their natural grouping.

Furthermore, this feature is variable even in a single echinoid, which can possess beaded as well as naked spines.

On the other hand, the degree of expansion of the beaded structure might bear some limited systematic

value at the family level. Taxa of the suborders Micrasterina, Brissidina, and the hemiasterid *Holanthus expergitus* (Lovén, 1871) have beaded ornamentation on the lower part of the shaft only, whereas there are several species in the suborder Palaeopneustina [*Abatus cavernosus* (Philippi, 1845), *Abatus cordatus* (Verrill, 1876), *Amphipneustes lorioli* Koehler, 1901, *Brisaster capensis* (Studer, 1880), *Brisaster fragilis* (Düben & Koren, 1844), *Faorina chinensis* Gray, 1851, *Moiria atropos* (Lamarck, 1816), *Pericosmus macronesius* Koehler, 1914, *Protenaster australis* (Gray, 1851), *Schizaster edwardsi* Cotteau, 1889, *Schizaster compactus* (Koehler, 1914), and *Tripylus excavatus* Philippi, 1845] in which the beaded ornamentation continues beyond

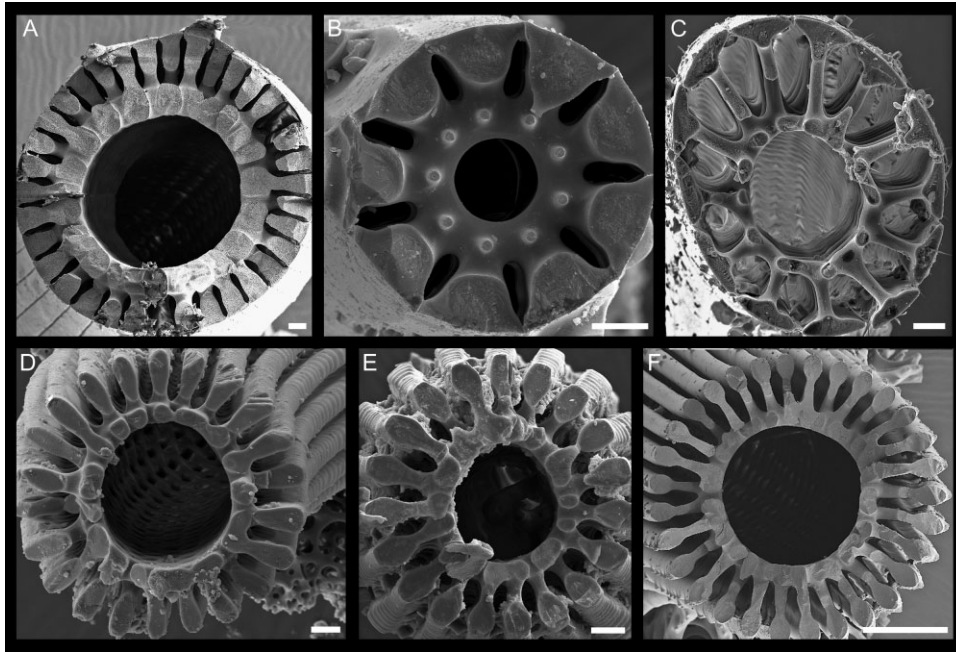


Figure 5. Wedge shapes: A, *Echinocardium* group, *Linopneustes fragilis* (ZMUC-ECH-643); B, *Brissus* group, *Sternopatagus sibogae* (ZMB.Ech-7426); C, *Brissus* group, *Echinocardium mediteraneum* (ZMUC-ECH-622); D, *Prenaster* group, *Tripylus excavatus* (ZMUC-ECH-637); E, *Prenaster* group, *Plesiozonus diomedea* (ZMUC-ECH-135); F, *Prenaster* group, *Amphipneustes marsupialis* (ZMUC-ECH-640). Scale bars: (A, B, D, E) 20 μ m; (C) 10 μ m; (F) 100 μ m.

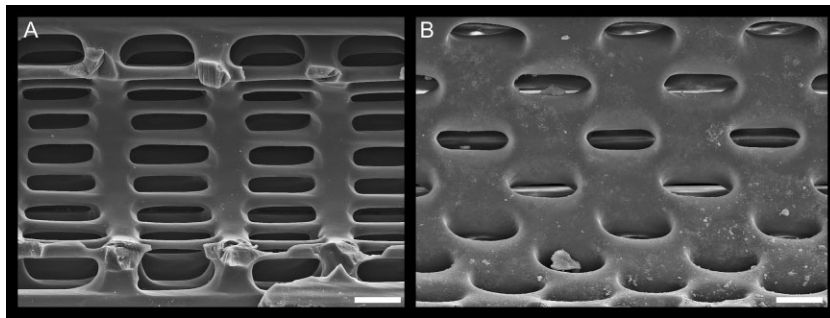


Figure 6. Perforation of the internal cylinder: A, horizontal arrangement in *Ceratophysa rosea* (ZMB.Ech-7419); B, helicoidal arrangement in *Gymnopatagus magnus* (ZMUC-ECH-641). Scale bars: 20 μ m.

half the length of the shaft. This observation, however, is in need of verification by analysing larger numbers of taxa.

3. Distances between the wedges

This character potentially bears some limited value for systematics in atelostomate echinoids. The members of the families Spatangidae, Maretidae, and Eurypatagidae studied here have spines in which the wedges are more fused to each other, similar to the families Palaeotropidae and Micrasteridae, although these are represented by a single taxon only, and are thus not significant. Pericosmids and schizasterids have mostly distanced wedges (compare Fig. 8), and *Aceste*

bellidifera Thomson, 1877 is the only schizasterid species with spines that are largely fused wedges. Admittedly, this conclusion is putative and needs to be evaluated for its systematic value with larger data sets.

5. The shape of the wedges

It appears that all types of wedge shapes can occur together in different spines of the same species (*Rhynobrissus hemiasteroides*, A. Agassiz, 1879). Furthermore, the variability of shape types within families can be relatively large, where all types of shapes are present (e.g. Loveniidae and Brissidae). By contrast, schizasterids have the *Brissomorpha* (= *Prenaster*) type only, except

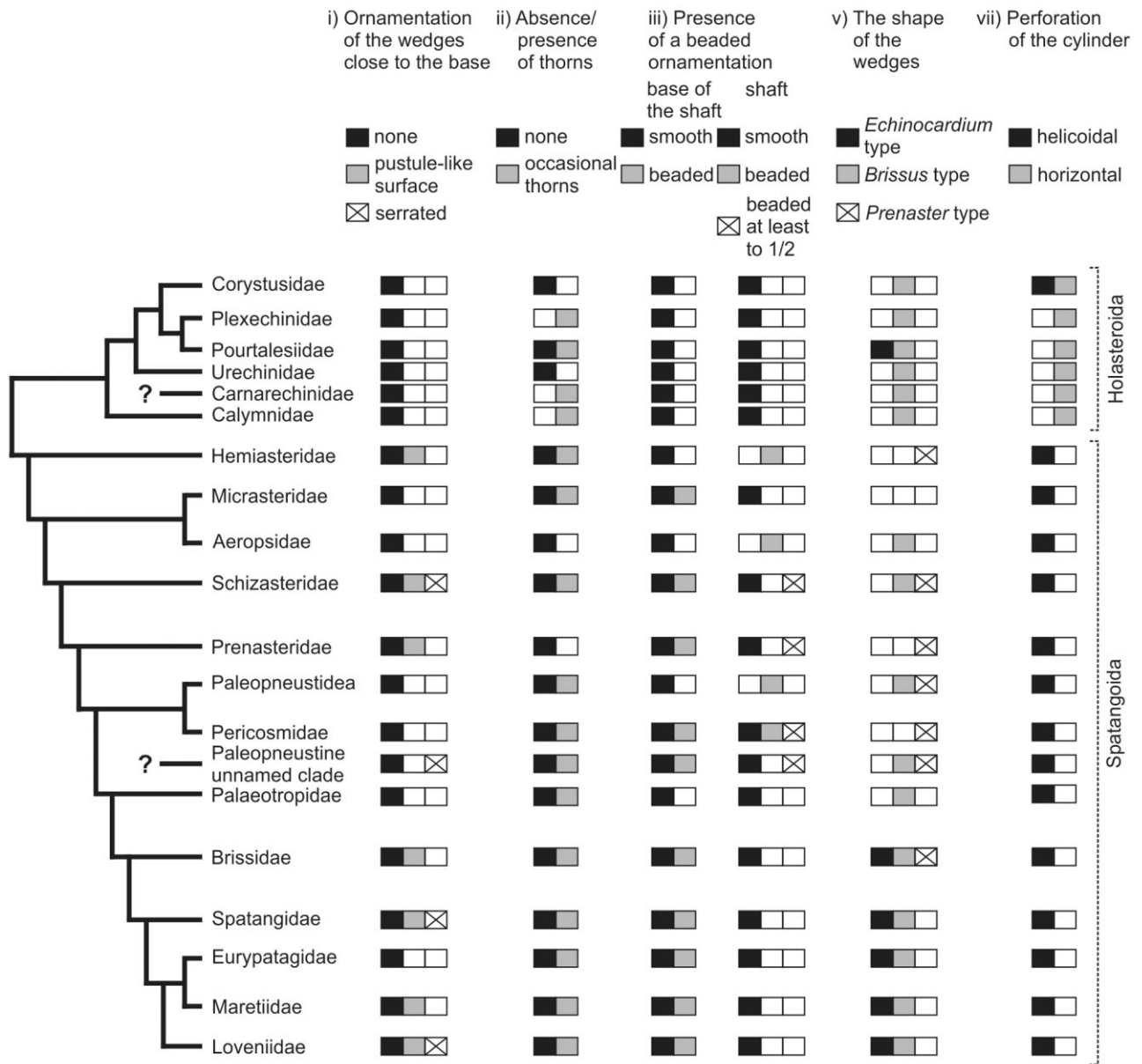


Figure 7. Simplified phylogenetic tree showing the different observed characters for each family (after Kroh & Smith, 2010; for a more detailed phylogeny of the Holasteroidea, see Smith, 2004; Mironov, Dilman & Krylova, 2013).

for *Aceste bellidifera* and comparable monotonous holasteroids, which have only the *Brissus* type, except for *Pourtalesia jeffreysi* Thomson, 1873. Hesse (1900) grouped 15 atelostomate taxa (fossil and recent) based on the shape of the wedges in section into three groups: (1) *Echinocardium* group with *Echinocardium cordatum*, *Spatangus* sp., *Hemipatagus hoffmanni* (Goldfuss, 1829), *Spatangus purpureus* Leske, 1778, *Schizaster canaliferus* (Lamarck, 1816), *Maretia planulata* (Lamarck, 1816), *Stegaster facki* Stolley, 1892 [probably misidentified, possibly a junior synonym of *Plesiocorys* (*Sternotaxis*)

heberti (Cotteau in Cotteau & Triger, 1860) or a similar species]; (2) *Brissus* group with *Brissus* sp. and *Brissus carinatus* (Lamarck, 1816) [= *Brissus latecarinatus* (Leske, 1778)]; (3) *Prenaster* group with *Prenaster fuchsi* (Laube, 1871), *Micraster* sp., *Schizaster* sp., *Echinocorys ovata* (Leske, 1778), *Hemipneustes striatoradiatus* (Leske, 1778), and *Metalia maculosa* (Gmelin, 1791) (= *Metalia spatagus* Linnaeus, 1758).

This clustering does not reflect the natural systematic grouping, and our data support that this character is of no value for a systematic assessment.

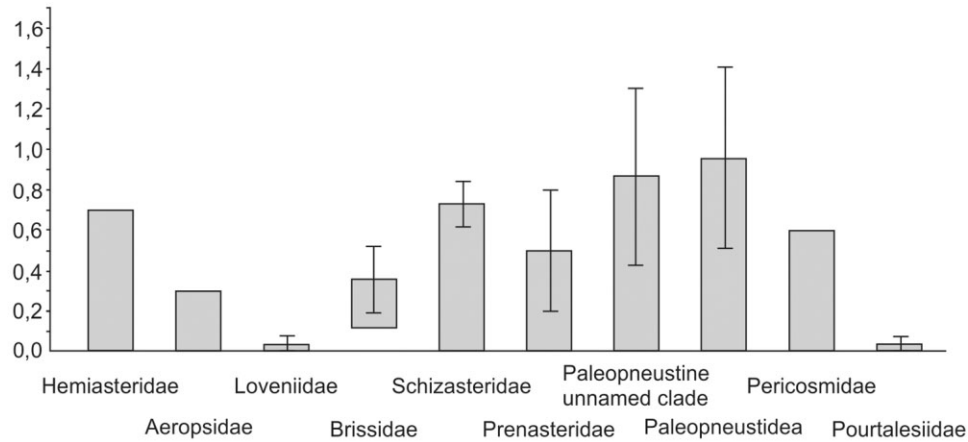


Figure 8. Box plot showing the mean values and ranges of distance between wedges for the atelostomate families studied (the numbers on the vertical axis represent distance between the wedges/width of the wedges); families that show no distance between wedges are not presented (Micrasteridae, Spatangidae, Maretidae, Palaeotropidae, Eurypatagidae, Plexechinidae, Corystusidae, Urechinidae, Carnarechinidae, and Calymnidae).

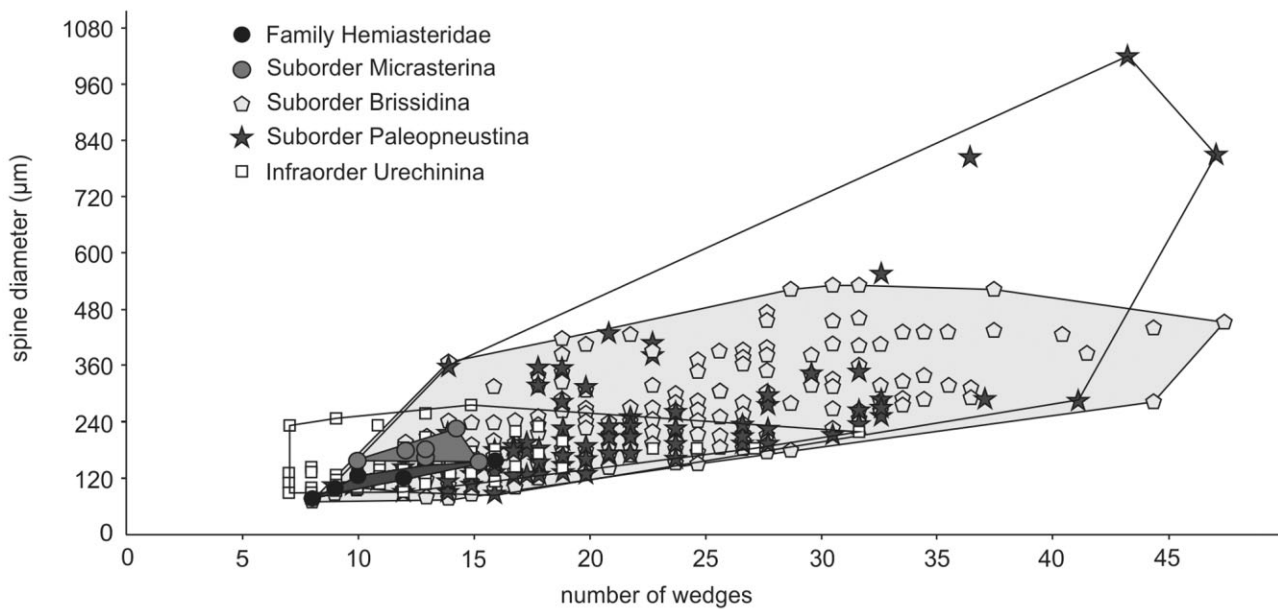


Figure 9. Scatter plot showing the relationship between number of wedges and spine diameter, including convex hulls for each group; for a better overview only higher systematic levels are distinguished, where possible.

6. Number of wedges

The number of wedges and diameter of the spine are strongly positively correlated (Fig. 9, Pearson's correlation coefficient = 0.74; Figure S2). This suggests that the number of wedges is simply related to a growth factor, and hence is not relevant for systematic purposes.

7. The perforation of the cylinder

Spatangoid spines reveal cylinders with a helicoidal pore arrangement in the cylinder throughout. In con-

trast, in holasteroid spines the pores are exclusively arranged horizontally. Additionally, the drawings of holasteroid spines from eight taxa in Agassiz (1881) reveal a horizontal pore pattern in the cylinder also (Table 4). The only outlier in this group is *Corystus relictus* (de Meijere, 1902), which, in contrast, has helicoidally arranged pores. Both patterns were found in a single spine, however (Fig. 10). Given that the spiral pattern is the target phenotype in spines of *C. relictus*, this phenomenon can be interpreted as a phenodeviant, sporadically occurring abnormal morphology (Rasmuson,

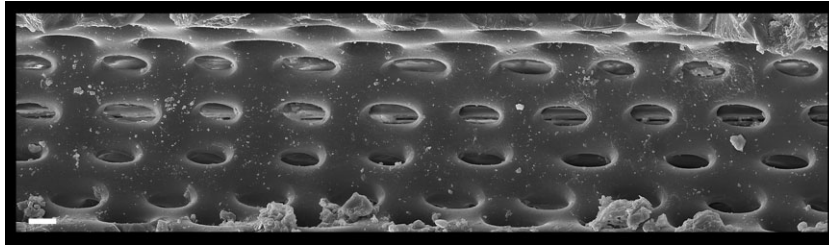


Figure 10. View of the inner side of the cylinder of a spine of *Corystus relictus* (ZMUC-ECH-605): pores are arranged in a horizontal pattern (left half), but from approximately half of the image this changes to a helicoidal pattern. Scale bar: 20 μm .

1960). Phenodeviants can be the result of developmental instability, caused by genetic and/or environmental perturbations (Polak, 2003). Those perturbations have an effect on the gene regulatory cascade, and thus potentially reveal cryptic genetic variation (Gibson & Dworkin, 2004). We postulate a scenario that could explain this aberrancy: genetic information from both pore arrangement patterns is available in this specimen, and the developmental pathway for horizontal pores has been reactivated, or switched, as a result of perturbations. This might also hold true for the species *C. relictus*. Even rare abnormalities can give important clues to evolutionary development (West-Eberhard, 2003). We propose that the arrangement of the holes perforating the cylinder turns out to be a reliable character to delineate between holasteroid and spatangoid spines, at least for the majority of the taxa investigated here.

CONCLUSION

From the seven characters investigated, only the perforation of the cylinder provides a feature of unequivocal systematic value, enabling a discrimination of the Holasteroidea (horizontal pore orientation in the internal cylinder) and Spatangoidea (helicoidal pore orientation in the cylinder) (Fig. 7).

Finally, a beaded surface and other ornaments like pustules or serrations are exclusively found in the Spatangoidea, but never occur in the Holasteroidea, which bears some potential for systematic assessments. Our work suggests that spine morphology can serve in parts as a supplementary source for phylogenetic analysis in atelostomate echinoids. The results also bear implications for the evaluation of Atelostomata occurrences in the geological record: from the early–middle Albian (Lower Cretaceous, 110 Myr old), we found Atelostomata spines in deep-sea sediments of Deep Sea Drilling Project (DSDP) Site 327 (eastern Falkland Plateau). These spines exhibit both helicoidal and horizontal pore arrangements, as indicated by astonishingly well-preserved microstructures of the spines (Fig. 11). Interestingly, the horizontal state co-occurs

in a single spine with the helicoidal pattern, similar to the deviant spine of *Corystus*. As disasteroid echinoids (stem-group members of the Atelostomata) still occur today (Smith & Crame, 2012), we cannot exclude the possibility that these spines were belonging to other atelostomates than holasteroids and spatangoids. A post-mortem down-slope transport of the spines from shallower areas is unlikely. This area, as the name suggests, is a plateau since the early/middle Albian, surrounded by deeper basins (Barker *et al.*, 1977). Nevertheless, these finds indicate that the colonization of the deep sea by the Atelostomata happened earlier than has previously been thought (Smith, 2004). These data are in good accordance with the results of Thuy *et al.* (2012), who showed that the origin of some modern deep-sea echinoderm faunas (especially ophiuroids and holothuroids) dates back at least to the early Cretaceous (Aptian, c. 120 Mya). In addition, it is the spines of the Atelostomata and not the echinoids test, which are preserved in Integrated Ocean Drilling Program (IODP) deep-sea samples in large numbers (Wiese *et al.*, 2015). Thus, our results potentially provide a new tool to assess this as yet unexplored source of information in order to reconstruct the distribution and dispersal of the Atelostomata in the deep sea through time.

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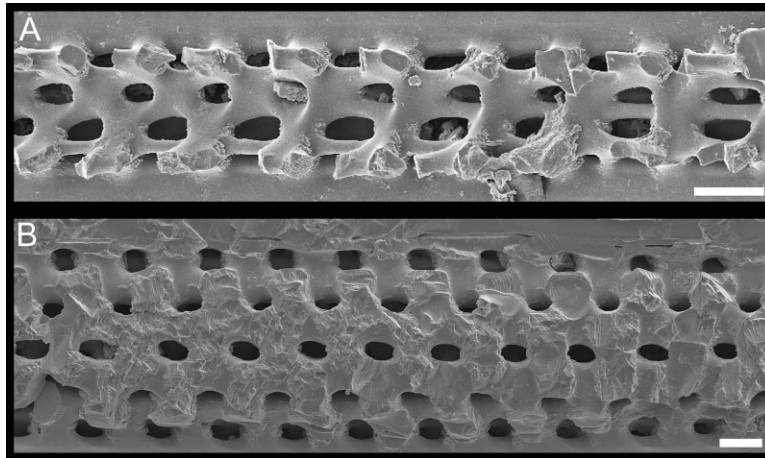


Figure 11. View of the cylinder of spines of atelostomate echinoids of early–middle Albian age (Falkland Plateau; A, GZG.INV.94999; B, GZG.INV.95000). A, view on the inner side: pores are arranged in a horizontal pattern (right half of the image), but from approximately half of the image the pattern changes to helicoidal. B, view on the outer side: pores are arranged in a helicoidal pattern throughout. Scale bars: 20 µm.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Figure S1. List of taxa investigated and summary of the results.

Figure S2. List of taxa, with number of wedges and diameter for each spine analysed.

Figure S3. List of taxa, collection numbers, and number of spines investigated, separated into spines for external and internal analyses, and provenance (with coordinates, if available) of the specimens.