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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 (helicoidal 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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ADDITIONAL KEYWORDS: Atelostomata – classification – Echinoidea – Holasteroida – morphology – sea urchins – Spatangoida.

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, sytematic 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 relicta* 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	*Holanthus expergitus* (Lovén, 1874)
Suborder Micrasterina Fischer, 1966	Family Micrasteridae Lambert, 1920	*Isopatagus obovatus* Mortensen, 1948
	Family Aeropsidae Lambert, 1896	*Aeropsis fulva* (A. Agassiz, 1898)
Suborder Brissidina Stockley, Smith Littlewood & MacKenzie-Dodds, 2005	Family Loveniidae Lambert, 1905	*Breynia australasiae* (Leach, 1815)
		Echinocardium cordatum (Pennant, 1777)
		Echinocardium mediteraneum (Forbes, 1844)
		Lovenia elongata (Gray, 1845)
		Lovenia subcarinata Gray, 1851
	Family Spatangidae Gray, 1825	*Spatangus capensis* Döderlein, 1905
		Spatangus purpureus Müller, 1776
		Spatangus raschi Lovén, 1870
	Family Maretiidae Lambert, 1905	*Granobrissoides hirsutus* (Mortensen, 1950)
		Gymnopatagus magnus Agassiz & Clark, 1907
		Homolampas sp.
		Maretia planulata (Lamarck, 1816)
		Nacospatangus laevis (H.L. Clark, 1917)
		Nacospatangus tylota (H.L. Clark, 1917)
		Spatagobrissus mirabilis H.L. Clark, 1923
	Family Palaeotropidae Lambert, 1896	*Paleotrema loveni* (A. Agassiz, 1879)
	Family Eurypatagidae Kroh, 2007	*Eurypatagus ovalis* Mortensen, 1948
		Eurypatagus parvituberculatus (H.L. Clark, 1924)
		Linopneustes fragilis (de Meijere, 1903)
		Linopneustes longispinus (A. Agassiz, 1878)
		Linopneustes murrayi (A. Agassiz, 1879)
		Paramaretia multituberculata Mortensen, 1950
	Family Brissidae Gray, 1855	*Anametalia regularis* (H.L. Clark, 1925)
		Brissopsis lyrifera (Forbes, 1841)
		Brissus agassizii Döderlein, 1885
		Brissus latecarinatus (Leske, 1778)
		Brissus obesus Verrill, 1867
		Meoma ventricosa grandis Gray, 1851
		Meoma ventricosa ventricosa (Lamarck, 1816)
		Metalia nobilis Verrill, 1867
		Plagiobrissus grandis (Gmelin, 1791)
		Rhynobrissus hemiasteroides A. Agassiz, 1879
		Rhynobrissus pyramidalis 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, Maretiidae, 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	*Abatus cavernosus* (Philippi, 1845)
		Abatus cordatus (Verrill, 1876)
		Aceste bellidifera Thomson, 1877
		Brisaster capensis (Studer, 1880)
		Brisaster fragilis (Düben & Koren, 1846)
		Moira atropos (Lamarck, 1816)
		Protenaster australis (Gray, 1851)
		Schizaster compactus (Koehler, 1914)
		Schizaster edwardsi Cotteau, 1889
		Tripylaster philippii (Gray, 1851)
	Family Prenasteridae Lambert, 1905	*Agassizia scrobiculata* Valenciennes, 1846
		Tripylus excavatus Philippi, 1845
	Paleopneustine	*Amphipneustes lorioli* Koehler, 1901
		Amphipneustes marsupialis (Koehler, 1926)
	unnamed clade	*Heterobrissus hystrix* (A. Agassiz, 1880)
	Superfamily Paleopneustidea A. Agassiz, 1904	
	Family Paleopneustidea A. Agassiz, 1904	*Paleopneustes cristatus* A. Agassiz, 1873
		Plesiozonus diomedeae Mortensen, 1948
	Family Pericosmidae Lambert, 1905	*Faorina chinensis* Gray, 1851
		Pericosmus akabanus Mortensen, 1939
		Pericosmus macronesius 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	*Plexechinus spectabilis* Mortensen, 1948
	Family Corystusidae Foster & Philip, 1978	*Corystus relictus* (de Meijere, 1903)
	Family Pourtalesiidae A. Agassiz, 1881	*Ceratophysa ceratopyga valvaecristata* Mironov, 1976
		Ceratophysa rosea (A. Agassiz, 1879)
		Cystocrepis setigera (A. Agassiz, 1898)
		Echinocrepis rostrata Mironov, 1973
		Echinosigra (*Echinogutta*) *amphora* Mironov, 1974
		Echinosigra (*Echinosigra*) *phiale* (Thomson, 1873)
		Echinosigra (*Echinosigra*) *vityazi* Mironov 1997
		Pourtalesia heptneri Mironov, 1978
		Pourtalesia jeffreysi Thomson, 1873
		Pourtalesia laguncula A. Agassiz, 1879
		Pourtalesia thomsoni Mironov, 1976
	Family Urechinidae Duncan, 1889	*Cystechinus loveni* A. Agassiz, 1898
		Pilematechinus vesica (A. Agassiz, 1879)
		Urechinus naresianus A. Agassiz, 1879
	Family Carnarechinidae Mironov, 1993	*Carnarechinus clypeatus* (A. Agassiz, 1879)
	Family Calymnidae Mortensen, 1907	*Sternopatagus sibogae* de Meijere, 1903

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)

Cystechinus wyvillii A. Agassiz, 1879	pl. XL, figs. 59–60
Calymne relicta Thomson, 1877	pl. XL, figs. 64, 65
Cystechinus wyvillii A. Agassiz, 1879	pl. XLI, figs. 24–27
Echinocrepis cuneata A. Agassiz, 1879	pl. XLI, fig. 31
Spatagocystis challengeri A. Agassiz, 1879	pl. XLI, fig. 40
Ceratophysa ceratopyga (A. Agassiz, 1879)	pl. XLI, figs, 44–46
Pourtalesia hispida A. Agassiz, 1879	pl. XLI, figs. 47, 48
Helgocystis carinata (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 (plastronal 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, plastronal). Scale bar: 1 cm.

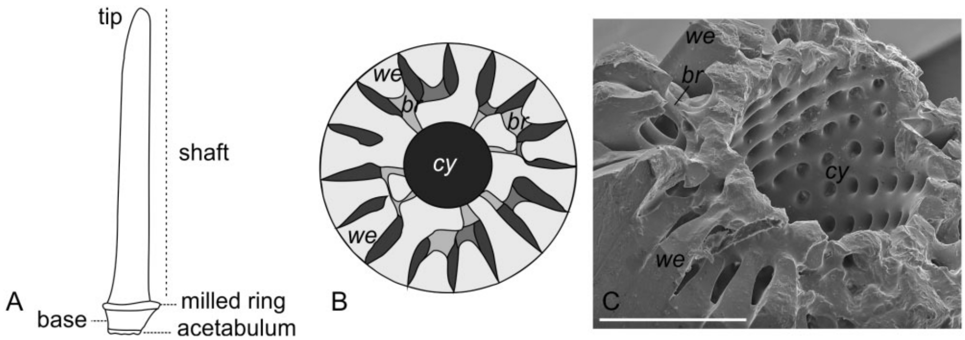

Figure 2. Spine morphology: general (A), spatangoid spine in section (B), and internal structure in a broken spine of *Spatangus raschi* (C). Abbreviations: *br*, bridges; *cy*, cylinder; *we*, wedge.

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).

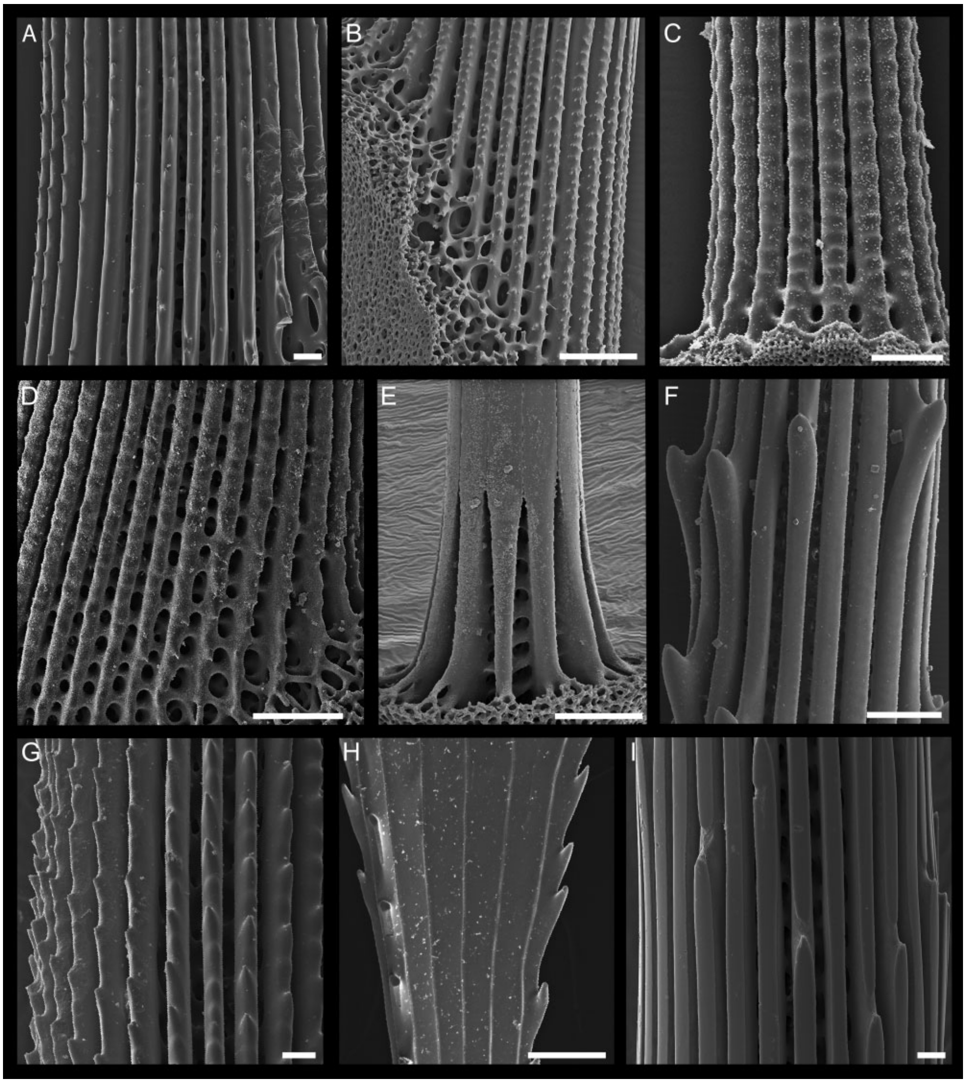

Figure 3. Ornamentation of spines: A, *Abatus cordatus* (ZMB.Ech 2230_5); B, *Breynia australisae* (ZMUC-ECH-610); C, *Tripylaster philippii* (ZMUC-ECH-612); D, *Moira atropos* (ZMUC-ECH-613); E, *Pourtalesia heptneri* (ZMUC-ECH-655); F, *Paleopneustes cristatus* (ZMUC-ECH-113); G, *Amphipneustes lorioli* (ZMUC-ECH-666); H, *Echinosigra 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.

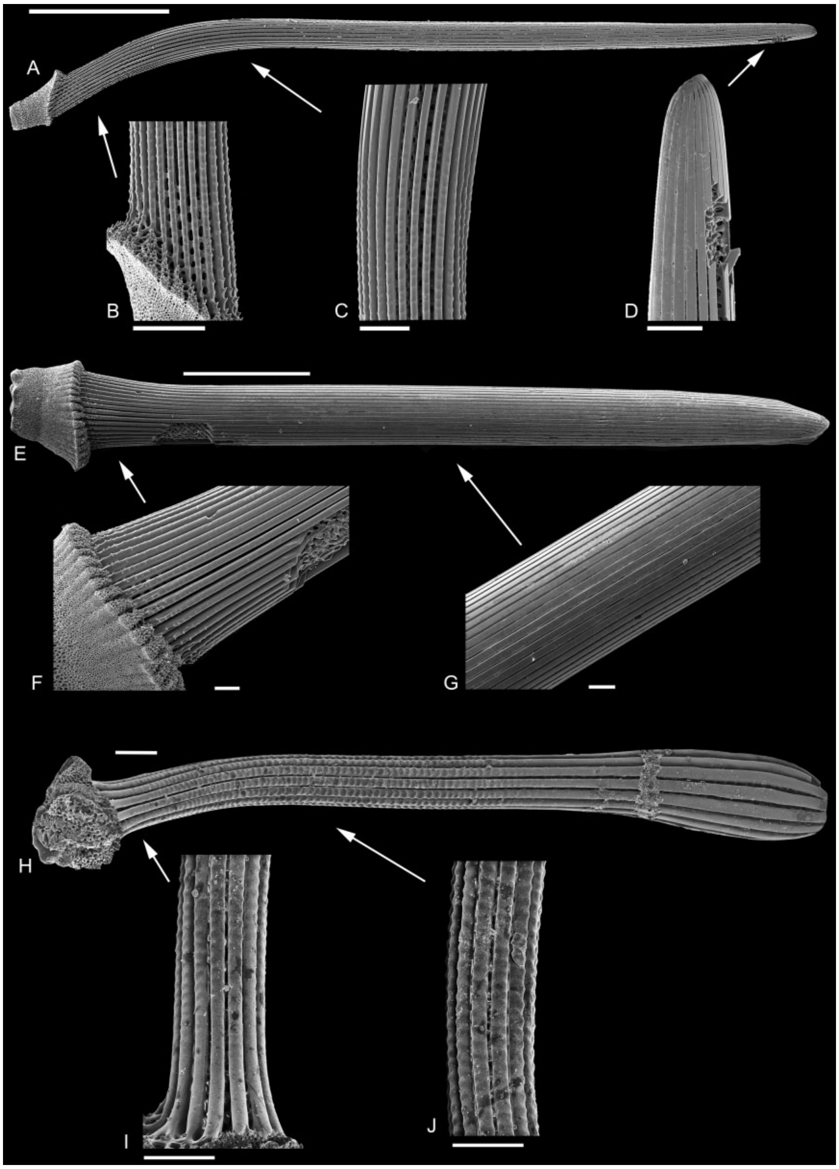

Figure 4. Ornamentation of spines: A–D, *Echinocardium cordatum* (GZG.INV.78890); E–G, *Brissus agassizii* (GZG.INV.78900); H–J, *Holanthus expergitus* (ZMUC-ECH-651). Scale bars: (A) 200 µm; (B–D) 40 µm; (E) 1 mm; (F–J) 100 µm.

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, *Moira 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

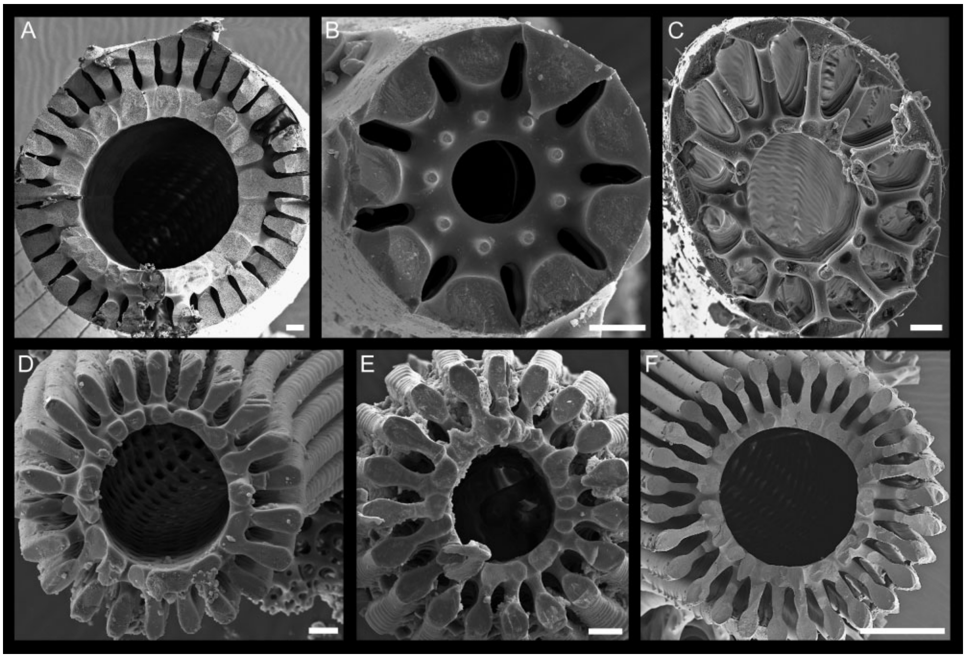

Figure 5. Wedge shapes: A, *Echinocardium* group, *Linopneustes fragilis* (ZMUC-ECH-643); B, *Brissus* group, *Sternopatagus sibogae* (ZMB.Ech-7426); C, *Brissus* group, *Echinocardium mediteraneum* (ZMUC-ECH-622); D, *Prenaster* group, *Tripylus excavatus* (ZMUC-ECH-637); E, *Prenaster* group, *Plesiozonus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

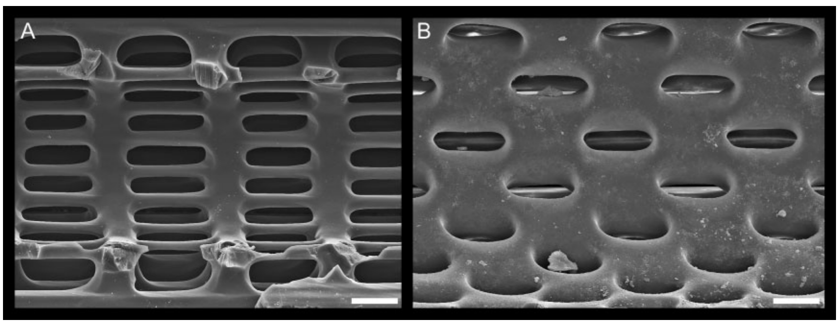

Figure 6. Perforation of the internal cylinder: A, horizontal arrangement in *Ceratophysa rosea* (ZMB.Ech-7419); B, helicoidal arrangement in *Gymnopatagus magnus* (ZMUC-ECH-641). Scale bars: 20 μm.

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, Maretiidae, 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

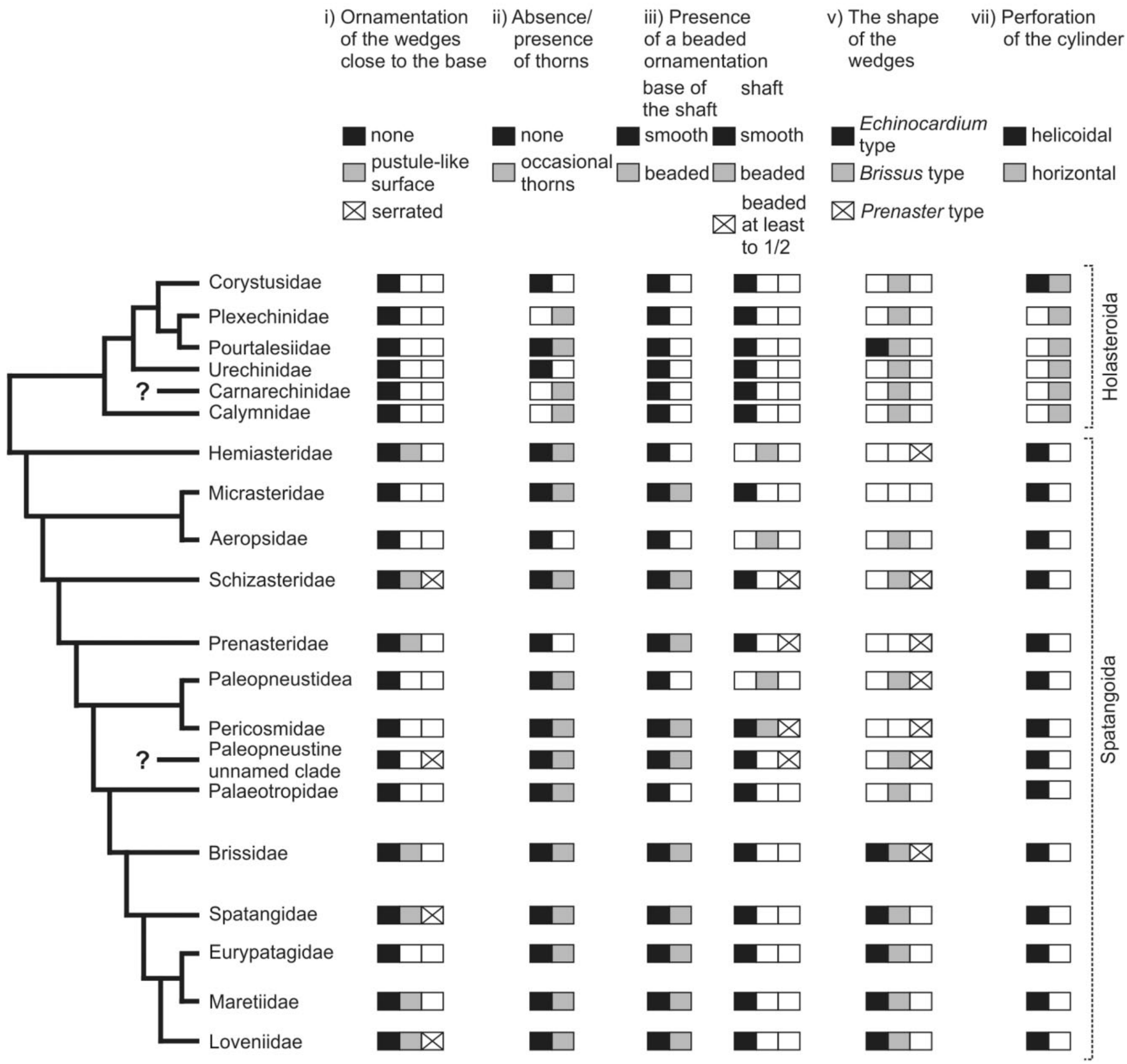

Figure 7. Simplified phylogenetic tree showing the different observed characters for each family (after Kroh & Smith, 2010; for a more detailed phylogeny of the Holasteroida, see Smith, 2004; Mironov, Dilman & Krylova, 2013).

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.

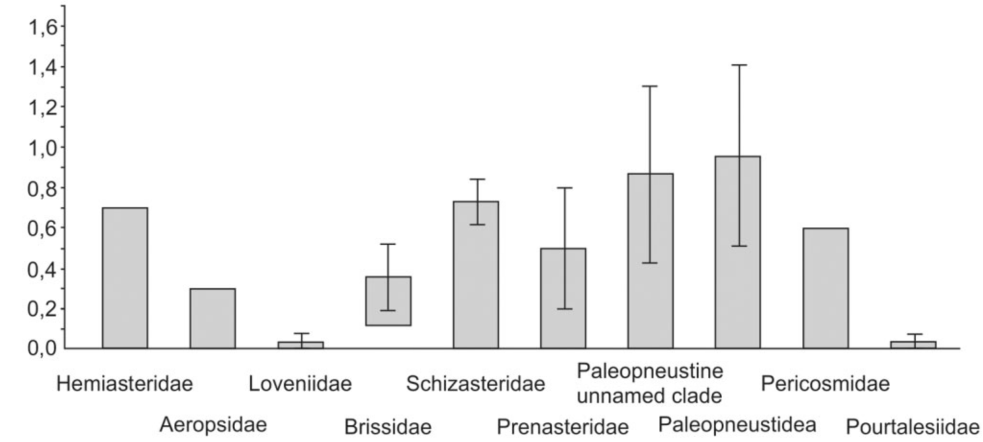

Figure 8. Box plot showing the mean values and ranges of distance between wedges for the atelostomate families studied (the numbers on the vertical axis represent distance between the wedges/width of the wedges); families that show no distance between wedges are not presented (Micrasteridae, Spatangidae,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

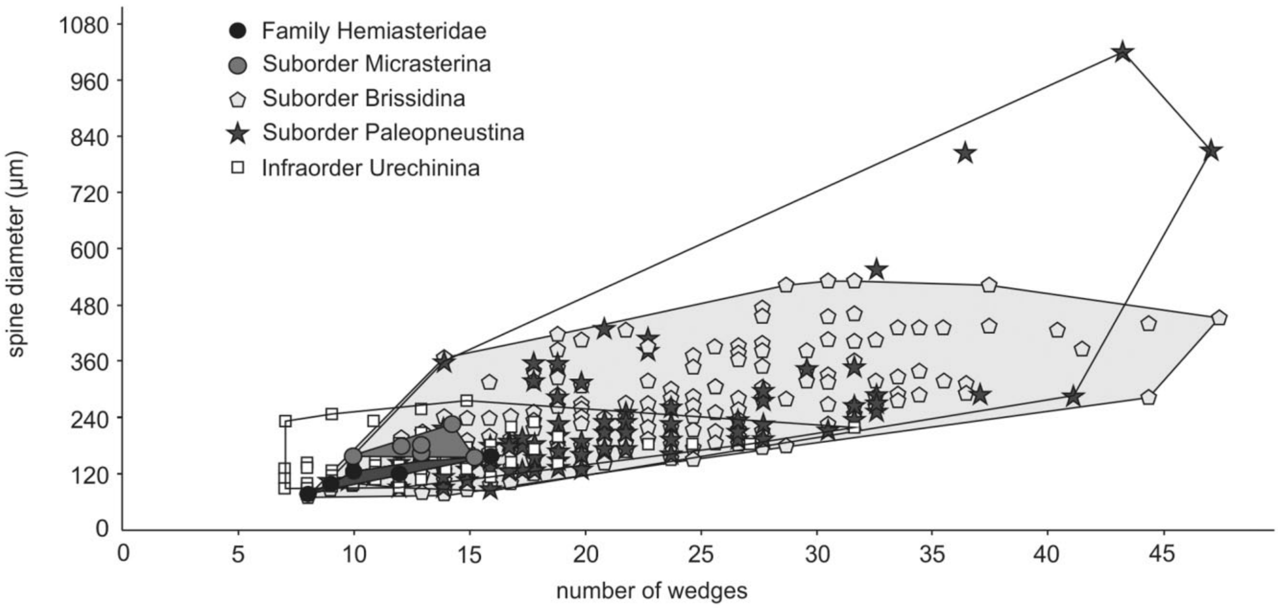

Figure 9. Scatter plot showing the relationship between number of wedges and spine diameter, including convex hulls for each group; for a better overview only higher systematic levels are distinguished, where possible.

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 contrast, 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,

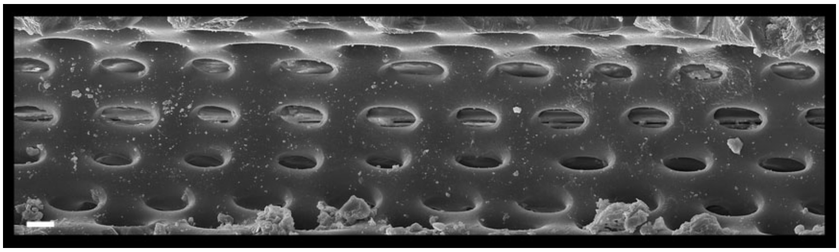

Figure 10. View of the inner side of the cylinder of a spine of *Corystus relictus* (ZMUC-ECH-605): pores are arranged in a horizontal pattern (left half), but from approximately half of the image this changes to a helicoidal pattern. Scale bar: 20 µm.

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 Holasteroida (horizontal pore orientation in the internal cylinder) and Spatangoida (helicoidal pore orientation in the cylinder) (Fig. 7).

Finally, a beaded surface and other ornaments like pustules or serrations are exclusively found in the Spatangoida, but never occur in the Holasteroida, 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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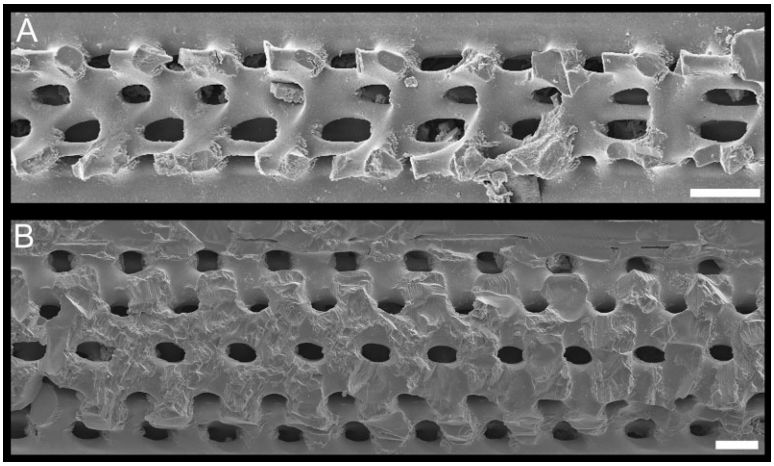

Figure 11. View of the cylinder of spines of atelostomate echinoids of early–middle Albian age (Falkland Plateau; A, GZG.INV.94999; B, GZG.INV.95000). A, view on the inner side: pores are arranged in a horizontal pattern (right half of the image), but from approximately half of the image the pattern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

Agassiz A. 1872–1874. Revision of the Echini. *Illustrated Catalogue of the Museum of Comparative Zoölogy at Harvard College* **7:** i–xii. 1–378, pls. 1–49 [1872]; (3): 379–628 + 1, pls. 50–77 [1873]; (4): 629–762, pls. 78–94 [1874].

Agassiz A. 1878. Reports on the Results of Dredging, under the Supervision of Alexander Agassiz, in the Gulf of Mexico, by the United States Coast Survey Steamer 'Blake', Lieutenant-Commander C. D. Sigsbee, U.S.N., Commanding. Report on the Echini. *Bulletin of the Museum of Comparative Zoölogy at Harvard College* **5:** 181–195.

Agassiz A. 1879. Preliminary report on the Echini of the Exploring Expedition of H.M.S 'Challenger'. *Proceedings of the American Academy of Arts and Sciences, New Series* **6:** 190–212.

Agassiz A. 1880. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Caribbean Sea in 1878–79, and along the Atlantic Coast of the United States during summer of 1880, by the U.S. Coast Survey Steamer 'Blake'. IX. Preliminary report on the Echini. *Bulletin of the Museum of Comparative Zoölogy at Harvard College* **8:** 69–84.

Agassiz A. 1881. *Report on the scientific results of the voyage of H.M.S. 'Challenger' during the years 1873–1876, zoology, Vol. III, part ix, report on the echinoidea*. London: Longmans & Company.

Agassiz A. 1898. Reports on the dredging operations off the west coast of Central America to the Galápagos, to the west coast of México, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Streamer 'Albatross', during 1891, Lieut. Commander Z. L. Tanner, U.S.N., Commanding. XXIII. Preliminary report on the Echini. *Bulletin of the Museum of Comparative Zoölogy* **32:** 71–86.

Agassiz A. 1904. The panamic deep sea Echini. *Memoirs of the Museum of Comparative Zoölogy at Harvard College* **31: ix+** 1–243.

Agassiz A, Clark HL. 1907. Preliminary report on the echini collected, in 1902, among the Hawaiian Islands, by the U.S. Fish Commission steamer 'Albatross', in charge of Commander Chauncey Thomas, U.S.N., commanding. *Bulletin of the Museum of Comparative Zoölogy at Harvard College* **50:** 231–259.

Agassiz L. 1840. *Catalogus systematicus Ectyporum Echinodermatum fossilium Musei Neocomiensis, secundum ordinem zoologicum dispositus; adjectis synonymis recentioribus, nec non stratis et locis in quibus reperiuntur. Sequuntur characteres diagnostici generum novorum vel minus cognitorum*. Neuchâtel: Petitpierre.

Barker PF, Dalziel IWD, Dinkelman MG, Elliot DH, Gombos AM, Jr, Lonardi, A, Plafker, G, Tarney, J, Thompson, RW, Tjalsma, RC, von der Borch, CC, Wise, SW, Jr, Harris, W, Sliter, WV. 1977. Evolution of the southwestern Atlantic Ocean basin; results of Leg 36, deep sea drilling project. *Initial Reports of the Deep Sea Drilling Project* **36:** 993–1014.

Clark HL. 1917. Hawaiian and other Pacific Echini. The Echinoneidae, Nucleolitidae, Urechinida, Echinocorythidae, Calymnidae, Pourtalesiidae, Palaeostomatidae, Aeropside, Palaeopneustidae, Hemiasteridae, and Spatangidae. *Memoirs of the Museum of Comparative Zoology at Harvard College* **46:** 81–283.

Clark HL. 1923. The echinodermfauna of SouthAfrica. *Annals of the South African Museum* **13:** 221–435.

Clark HL. 1924. Echinoderms from the South African Fisheries and Marine Biological Survey, Part I: Sea-Urchins (Echinoidea). *Fisheries and Marine Biological Survey Report* **4:** 1–16.

Clark HL. 1925. *A catalogue of the recent sea-urchins (echinoidea) in the collection of the British Museum (Natural History)*. London: Oxford University Press.

Coppard SE, Kroh A, Smith AB. 2012. The evolution of pedicellariae in echinoids: an arms race against pests and parasites. *Acta Zoologica* **92:** 125–148.

Cotteau GH. 1889. Description de trois Échinides vivants recueillis par le Dr J. Jullien, sur les côtes de Guinée (Libéria). In: Blanchard RAÉ, ed. *Compte-rendu des séances du Congrès International de Zoologie à Paris, Comptes Rendus Scientifique*. Paris: Société zoologique de France, 281–292.

Cotteau GH, Triger J. 1857–1869. *Echinides* du *Département* de la *Sarthe considérés* au *point* de *vue zoologique* et *stratigraphique*. Paris: Baillière et fils.

Döderlein L. 1885. Seeigel von Japan und den Liu-Kiu-Inseln. *Archiv für Naturgeschichte* **51:** 73–112.

Döderlein L. 1905. Ueber Seeigel der deutschen Tiefsee-Expedition. *Zoologischer Anzeiger* **282:** 621–624.

Düben MW, Koren J. 1846. Ofversigt af skandinaviens echinodermer. *Kungliga Vetenskaps-Akademiens Handlingar* **[1844]:** 229–328.

Duncan PM. 1889. A revision of the genera and great groups of the Echinoidea. *Journal of the Linnean Society, Zoology* **23:** 1–311.

Durham JW, Melville RV. 1957. A classification of echinoids. *Journal of Paleontology* **31:** 242–272.

Eble GJ. 2000. Contrasting evolutionary flexibility in sister groups: disparity and diversity in Mesozoic heart urchins. *Paleobiology* **26:** 56–79.

Fischer AG. 1966. Spatangoids. In: Moore RC, ed. *Treatise on invertebrate paleontology, part U. Echinodermata. 3 (2)*. Lawrence, Kansas: Geological Society of America and University of Kansas Press, U543–U628.

Forbes E. 1841. *A history of British starfishes and other animals of the Class Echinodermata*. London: Van Voorst.

Forbes E. 1844. Read also a continuation of the series of memoirs] On the *Radiata* of the Eastern Mediterranean. *Proceeding of the Linnean Society of London* **1:** 184–186.

Foster RJ, Philip GM. 1978. Tertiary holasteroid echinoids from Australia and New Zealand. *Palaeontology* **21:** 791–822.

Gibson G, Dworkin I. 2004. Uncovering cryptic genetic variation. *Nature Reviews. Genetics* **5:** 681–690.

Gmelin JF. 1791. *Caroli a Linné, systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I.* Editio decima tertia, aucta, reformata. Lipsiae [=Leipzig]: G. E. Beer.

Goldfuss A. 1826–1829. *Petrefacta Germaniæ tam ea, quae in Museo Universitatis Regiae Borussicae Fridericiae Wilhelmiae Rhenanae servantur, quam alia quaecunque in Museis Hoeninghusiano Muensteriano aliisque extant, Iconibus et Descriptionibus illustrata. Abbildungen und Beschreibungen der Petrefacten Deutschlands und der angränzenden Länder, unter Mitwirkung des Herrn Grafen Georg zu Münster*. Düsseldorf: Arnz & Co.

Gray JE. 1825. An attempt to divide the Echinida, or Sea Eggs, into natural families. *Annals of Philosophy, New Series* **10:** 423–431.

Gray JE. 1845. Description of two new invertebrated animals from Australia. In: Eyre EJ, ed. *Journals of expeditions of discovery into Central Australia and overland from Adelaide to King Georg's Sound in 1840–41*. Volume 1. London: T. & W. Boone, 435–436.

Gray JE. 1851. Descriptions of some new genera and species of Spatangidae in the British Museum. *Annals and Magazine of Natural History, Series* **2:** 130–134.

Gray JE. 1855. *Catalogue of the recent echinida, or sea eggs, in the collection of the British museum. Part I. Echinida irregularia*. London: Woodfall & Kinder.

Hesse E. 1900. Die Mikrostructur der fossilen Echinoideenstacheln und deren systematische Bedeutung. *Neues Jahrbuch für Mineralogie, Geologie und Palaeontologie, Beilagen-Band* **13:** 185–264.

Kier PM. 1974. Evolutionary trends and their functional significance in the post-Paleozoic echinoids. *The Paleontological Society, Memoir* **5:** 1–95. [Supplement to Journal of Paleontology 48].

Koehler R. 1901. *Expédition antarctique Belge. Resultats du voyage du S.Y 'Belgica'. Zoologie; Échinides et Ophiures*. Anvers: Buschmann.

Koehler R. 1914. *Echinides du Musée Indien à Calcutta.I. Spatangidés. Echinoderma of the Indian Museum. Part 8, Echinoidea (1)*. Calcutta: Zoological Survey of India.

Koehler R. 1926. Echinodermata Echinoidea. In: Harrison L, ed. *Australasian antarctic expedition, 1911–14. Under the leadership of sir douglas mawson, D.Sc., B.E., F.R.S. scientific reports. Series C.-zoology and botany*. Vol. 8, 1–134.

Kroh A. 2002. Die Echiniden (Echinodermata) aus dem Karpatium des Korneuburger Beckens und der Kreuzstettener Bucht (Niederösterreich, Untermiozän). *Beiträge zur Paläontologie* **27:** 305–315.

Kroh A. 2007. Hemipatagus, a misinterpreted loveniid (Echinodermata: Echinoidea). *Journal of Systematic Palaeontology* **5:** 163–192.

Kroh A, Smith AB. 2010. The phylogeny and classification of post-Palaeozoic echinoids. *Journal of Systematic Palaeontology* **8:** 147–212.

de Lamarck J-BPM. 1816. *Histoire Naturelle des Animaux sans Vertébres, présentant les caractéres géneraux et particuliers de ces animaux, leur distribution, leur classes, leurs familles, leurs generes, et le citation des principales espèces qui s'y rapportent; précédée d'une Introduction offrant la Détermination des caractéres essentiells de l'animal, sa distinction du végétal et des autres corps naturels, enfin, l'Exposition des Principes fondamentaux de la Zoologie. Tome Troisième*. Paris: Verdière.

Lambert J. 1896. Notes sur quelques Échinides Crétacés de Madagascar. *Bulletin de la Société Géologique de France, Série* **3:** 313–332.

Lambert J. 1905. Notes sur quelques Échinides éocéniques de l'Aude et de l'Hérault. In: Doncieux L, ed. *Catalogue descriptif des fossiles nummulitiques de l'Aude et de l'Hérault.*

Annales de l'Université de Lyon, Nouvelle Série, I. Sciences, Médecine. Vol. 17, 129–164.

Lambert J. 1920. Etude sur quelques formes primitives de Spatangidés. *Bulletin de la Société des Sciences Historiques et Naturelles de l'Yonne* **73:** 1–41.

Laube GC. 1871. Die Echinoiden der oesterreichischungarischen oberen Tertiärablagerungen. *Abhandlungen der Kaiserlich-königlichen Geologischen Reichanstalt* **5:** 55–74.

Leach WE. 1815. *The zoological miscellany; being descriptions of new, or interesting animals*. Vol. II. London: Nodder.

Leske NG. 1778. Jacobi Theodori Klein naturalis dispositio echinodermatum . . . , edita et descriptionibus novisque inventis et synonomis auctorem aucta. Addimenta ad I. T. Klein naturalem dispositionem Echinodermatum. Lipsiae [= Leipzig]: G. E. Beer.

Linnaeus C. 1758. *Systema Naturæ per Regna tria Naturæ, secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis. Edito Decima, Reformata*. Tomus I. Impensis Direct. Laurentii. Holmiæ: Salvii.

Lovén S. 1870. En ny art af slägtet *Spatangus* från Nordsjön. *Öfversigt af Kongl. Vetenskaps-Akademiens Förhandlingar* **26 [1869]:** 733–735.

Lovén S. 1874. Études sur les échinoïdés. *Kongelige Svenska Vetenskaps-Akademiens Handlingar* **11:** 1–91.

Markov AV, Solovjev AN. 2001. [Echinoids of the family Paleopneustidae (Echinoidea, Spatangoida), morphology, taxonomy, phylogeny]. *Trudy Paleontologicheskogo Instituta, Rossijskaya Akademiya Nauk* **280:** 1–108. [In Russian].

de Meijere JCH. 1903. Vorläufige Beschreibung der neuen, durch die Siboga-Expedition gesammelten Echiniden. *Tijdschrift der Nederlandsche Dierkundige Vereeniging* **8:** 1–16.

Mironov AN. 1973. New deep-sea species of sea urchins of the genus Echinocrepis and the distribution of the family Pourtalesiidae (Echinoidea, Meridosterniana)]. *Trudy Instituta Okeanologii Akademii Nauk SSSR* **91:** 240–247. [In Russian].

Mironov AN. 1974. [Pourtalesiid sea urchins of the Antarctic and Subantarctic (Echinoidea: Pourtalesiidae)]. *Trudy Instituta Okeanologii Akademii Nauk SSSR* **98:** 240–252.

Mironov AN. 1976. [Deep-sea urchins of the northern Pacific]. *Trudy Instituta Okeanologii, Akademii Nauk SSSR* **99:** 140–164. [In Russian].

Mironov AN. 1978. Meridosternous echinoids (Echinoidea: Meridosternina) collected during the 16th cruise of the R V^{-1} 'Dm. Mendeleev']. *Trudy Instituta Okeanologii Akademii Nauk SSSR* **113:** 208–226. [In Russian].

Mironov AN. 1993. [Deep-sea echinoids (Echinodermata: Echinoidea) of the South Atlantic]. *Trudy Instituta Okeanologii Akademii Nauk SSSR* **127:** 218–227. [In Russian].

Mironov AN. 1997. [Holasteroid sea urchins. 4. Echinosigra]. *Zoologicheskij Zhurnal* **76:** 173–186.

Mironov AN, Dilman AB, Krylova EM. 2013. Global distribution patterns of genera occurring in the Arctic Ocean deeper 2000 m. *Invertebrate Biology* **10:** 167–194.

Mooi R, David B. 1996. Phylogenetic analysis of extreme morphologies: deep-sea holasteroid echinoids. *Journal of Natural History* **30:** 913–953.

Mortensen T. 1907. The danish ingolf-expedition *1895–1896. Vol. 4, no. 2. Echinoidea, pt. 2*. Copenhagen: Bianco Luno.

Mortensen T. 1939. New Echinoida (Aulodonta). Preliminary Notice. *Videnskabelige Meddelelser fra Danks naturhistorisk Forening i København* **103:** 547–550.

Mortensen T. 1948. Report on the Echinoidea Collected by the United States Fisheries Steamer 'Albatross' during the Philippine Expedition 1907–1910 Part 3: the Echinoneidae, Echinolampadidae, Clypeastridae, Arachnoididae, Laganidae, Fibularidae, Urechinidae, Echinocorythidae, Palaeostomatidae, Micrasteridae, Palaeopneustidae, Hemiasteridae, Spatangidae. *United States National Museum Bulletin* **100:** 89–140.

Mortensen T. 1950. New Echinoidea (Spatangoida). Preliminary notice. *Videnskabelige Meddelelsar Dansk Naturhistoriske Forening i Kjøbenhavn* **112:** 157–163.

Mortensen T. 1950. *A monograph of the echinoidea. V, 1. Spatangoida I. Protosternata, meridosternata, amphisternata i. palæopneustidæ, palæostomatidæ, aëropsidæ, toxasteridæ, micrasteridæ, hemiasteridæ*. Copenhagen: C. A. Reitzel.

Mortensen T. 1951. *A monograph of the echinoidea. V, 2. Spatangoida II. Amphisternata II. Spatangidæ, loveniidæ, pericosmidæ, schizasteridæ, brissidæ*. Copenhagen: C. A. Reitzel.

Müller OF. 1776. Zoologicæ Danicæ prodromus, seu animalium Daniæ et Norvegiæ indigenarum characteres, nomina, et synonyma imprimis popularium. Havniae [= Copenhagen]: Impensis auctoris.

Pennant T. 1777. *British zoology.Vol. IV. Crustacea, mollusca, testacea*. London: White.

Philippi RA. 1845. Beschreibung einiger neuer Echinodermen nebst kritischen Bemerckungen über einige weniger bekannte Arten. *Archiv für Naturgeschichte* **11:** 344–359.

Polak M, ed. 2003. *Developmental instability: causes and consequences*. New York: Oxford University Press.

R Development Core Team. 2013. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Rasmuson M. 1960. Frequency of morphological deviants as acriterion of developmental stability. *Hereditas* **46:** 511–535.

Saucède T, Mironov AN, Mooi R, David B. 2009. The morphology, ontogeny, and inferred behaviour of the deep-sea echinoid *Calymne relicta* (Holasteroida). *Zoological Journal of the Linnean Society* **155:** 630–648.

Smith AB. 1980. The structure and arrangement of echinoid tubercles. *Philosophical Transactions of the Royal Society B* **289:** 1–54.

Smith AB. 1984. *Echinoid palaeobiology*. London: Allen & Unwin.

Smith AB. 2004. Phylogeny and systematics of holasteroid echinoids and their migration into the deep-sea. *Palaeontology* **47:** 123–150.

Smith AB, Crame JA. 2012. Echinoderm faunas from the Lower Cretaceous (Aptian-Albian) of Alexander Island, Antarctica. *Palaeontology* **55:** 305–324.

Stephenson DG. 1963. The spines and diffuse fascioles of the

Cretaceous echinoid *Echinocorys scutata* Leske. *Palaeontology* **6:** 458–470.
Stolley E. 1892. Die Kreide Schleswig-Holsteins. *Mittheilungen aus dem Mineralogischen Institut der Universität Kiel* **1:** 191–384.
Studer T. 1880. Übersicht über die während der Reise S.M.S. Corvette Gazelle um die Erde 1874–76 gesammelten Echinoiden. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin* **[1880]:** 861–885.
Thomson CW. 1873. *Depths of the Sea: an account of the General Results of the Dredging Cruises of H.M.SS. 'Porcupine' and 'Lightning' During the Summers of 1868, 1869, and 1870 under the Scientific Direction of Dr. Carpenter, F.R.S., J.Gwyn Jeffreys, F.R.S., and Dr. Wyville Thomson, F.R.S.* London: MacMillian and Co.
Thomson CW. 1877. *The voyage of the 'Challenger'. The Atlantic. A preliminary account of the general results of the exploring voyage of H.M.S. 'Challenger' during the year 1873 and the early part of the year 1876. Volume I.* London: Macmillan & Co.
Thuy B, Gale AS, Kroh A, Kucera M, Numberger-Thuy LD, Reich M, Stöhr S. 2012. Ancient Origin of the Modern Deep-Sea Fauna. *PLoS ONE* **7:** 1–11. e46913. doi:10.1371/journal.pone.0046913.
Valenciennes A. 1846. Zoophytes. In: **du Petit-Thouars A, ed.** *Voyage autour de monde sur la frégate 'La Vénus', pendant 1836–1839. Atlas de Zoologie*. Paris: Ministre de la Marine, 1–15.
Verrill AE. 1867–1871. Notes on the Radiata in the Museum of Yale College, with descriptions of new genera and species. *Transactions of the Connecticut Academy of Arts and Sciences* **1:** 247–613.
Verrill AE. 1876. Annelids and echinoderms. In: Kidder JH, ed. *Contributions to the natural historry of kerguelen Island*. Washington: United States Government Printing Office, 64–75.
West-Eberhard MJ. 2003. *Developmental plasticity and evolution*. New York: Oxford University Press.
Wiese F, Schlüter N, Reich M, Zirkel J, Herrle J. 2015. From bycatch to main dish – spines of irregular echinoids as monitors for macrofaunal dynamics in the deep sea during the Cenozoic critical intervals? A pilot study. In: Litt T, Oberhänsli R, Erbacher J, eds. *IODP/ICDP kolloquium 2015, Bonn. Abstract volume*, Bonn: Steinmann-Institut, Universität Bonn, 134–135.
Ziegler A, Stock SR, Menze BH, Smith AB. 2012. Macro- and microstructural diversity of sea urchin teeth revealed by large-scale mircro-computed tomography survey. Proceedings of SPIE 8506: 85061G.
von Zittel KA. 1879. *Echinodermata. Handbuch der paläontologie: paläozoologie. Vol. 1. Pt. 1.* München & Leipzig: R. Oldenbourg.

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 anaylsed.
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.