



# Absurdaster, a new genus of basal atelostomate from the Early Cretaceous of Europe and its phylogenetic position<sup>☆</sup>



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## ABSTRACT

Field work in the Lower Cretaceous of the Dolomites (Italy) has resulted in the recovery of a new genus of 'disasteroid' echinoid, which successively was also discovered in slightly older strata in Northern Hungary. This new genus, *Absurdaster*, is characterized by its highly modified, disjunct apical disc in which all genital plate except genital plate 2 are reduced or fused. The gonopores (which may be multiple) have shifted and pierce interambulacral plates. Anteriorly ambulacrum III is distinctly sunken and forms a distinct frontal notch, while the posterior end is pointed and features a small sharply defined posterior face bearing the periproct.

Two new species are established: *Absurdaster puezensis* sp. nov. from the Upper Hauterivian to Lower Barremian Puez Formation of Northern Italy is characterized by its rudimentary ambulacral pores in the paired ambulacra, high hexagonal ambulacral plates aborally and multiple gonopores in the most adapical plates of interambulacral columns 1b and 4a. *Absurdaster hungaricus* sp. nov. from the Lower Hauterivian Bersek Marl Formation of Northern Hungary, in contrast, shows circumflexed ambulacral pores, low ambulacral plates, a single gonopore each in the most adapical plates of interambulacral columns 1b and 4a and a flaring posterior end, with sharp margin and invaginated periproct. In addition to those two species *Collyrites meriani* Ooster, 1865 from the uppermost Berriasian to basal Barremian of Switzerland is attributed to the new genus. Despite the poor knowledge on this form it seems to be distinguished from the new species by its smaller ambulacral plates and higher interambulacral/ambulacral plate ratio.

Phylogenetic analyses based on previous work by Barras (2007) and Saucède et al. (2007) indicate that the new genus is a highly derived stem-group member of the Atelostomata close to the split of holasteroids and spatangoids. A combined analysis based on a subset of the characters employed in these two studies for the first time results in a fully resolved tree for 'disasteroids'.

*Absurdaster*, shows two notable morphological peculiarities: 1) it is one of the first echinoids to develop fascioles and exhibits a yet unknown type of fasciole circling the periproct, termed circumanal fasciole here; 2) it is extraordinary among echinoderms as its extraxial skeleton is reduced to a single plate, the madreporite (genital plate 2), and because its genital pores pierce axial elements rather than extraxial ones.

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## 1. Introduction

Early Cretaceous echinoids are among the least known of all Post-Palaeozoic echinoids, despite the fact that this period represents one of the most interesting times in echinoid evolution, with

the emergence of the earliest holasteroids and spatangoids from stem-group atelostomates (Barras, 2007, 2008) and a first migration of 'disasteroid' echinoids to the deep sea (Smith and Stockley, 2005). This paucity of echinoids can in part be explained by the 'Neocomian transgression' which led to the drowning of the widespread Jurassic carbonate platforms (Bodin et al., 2006) and thus to a loss of shallow-water environments rich in echinoids. While echinoids can be extremely well preserved and abundant in some outcrops in France (e.g., David, 1980), preservation is often far from encouraging in the Lower Cretaceous marl and marl-limestone alternations of the Alps. The thin-shelled tests of

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the 'disasteroid' echinoids inhabiting these off-shore environments often are heavily crushed and/or dissolved. The latest Jurassic to early Early Cretaceous interval also represents a period of which comparatively little sedimentary rock is exposed on the surface (Smith, 2001) in Western Europe, adding a further bias to our knowledge of faunas from that time.

During the research on such an off-shore echinoid fauna from the Hauterivian and Barremian of the Dolomites of Northern Italy (Kroh and Lukeneder, in preparation) we discovered a novel echinoid taxon with unusual morphology and apical disc plating. First results on this enigmatic echinoid were presented at the International Conference on Echinoderms in Brussels, 2012, where we realized that one of us (JG) was independently working on apparently similar specimens from the Hauterivian of Northern Hungary. Upon realizing that the material was likely congeneric, if not conspecific we decided to join forces to document these novel echinoids and to elucidate their phylogenetic affinities.

## 2. Geological setting

### 2.1. The Puez section

The Permian to Cretaceous deposits of the Dolomites in northern Italy constitute an internal part of the Southern Alps that emerged during the deformation of the passive continental margin of the Adriatic (= Apulian) Plate of the South Alpine–Apennine Block (Stampfli and Mosar, 1999; Scotese, 2001; Stampfli et al., 2002; Bosellini et al., 2003). This block was limited by the Peninic Ocean (= Alpine Tethys) to the north and the Vardar Ocean to the southeast (Scotese, 2001; Stampfli et al., 2002). During the Early Cretaceous, the Dolomites formed a part of the Trento Plateau that extended from the area around Trento in the south to the Puez region in the north (Bosellini et al., 2003). It was one of the several topographic highs located in the Tethys that contributed to the complex palaeogeography of the Early Cretaceous (Dercourt et al., 1993). The Trento Plateau was formerly surrounded by two basins: the Lombardian Basin to the west and the Belluno Basin to the east (Lukeneder, 2010; Lukeneder et al., 2012; Lukeneder and Grunert, 2013).

The studied section Puez 1 is located on the Puez-Odle-Gardenaccia Plateau in the northern Dolomites, about 30 km northeast of Bozen (Fig. 1; N 46°35'30", E 011°49'15"). Biostratigraphic constraints from ammonites and microfossils indicate a Valanginian to Albian age for the hemipelagic to pelagic deposits (Lukeneder, 2010, 2012). The lithology shows a transition from

limestones and marly limestones into a marl–marly limestone alternation in the upper half of the section (Lukeneder, 2010).

### 2.2. The Veveyse de Châtel-Saint-Denis section

The section at Veveyse de Châtel-Saint-Denis (Ooster, 1860; Sarasin and Schöndelmayer, 1901, 1902) encompasses sediments from uppermost Berriasian to basal Barremian (Pourtoy, 1989; Busnardo et al., 2003; Baudin et al., 2006) and is located in the canton of Fribourg, western Switzerland (Fig. 1). The outcrop is located along the La Veveyse stream. The area is part of the tectonic unit 'Ecaille de Riondonnaire' which belongs to the Ultrahelvetetic realm, primarily located on the northern Tethyan shelf margin (Trümpy, 1960; Weidmann et al., 1993; Busnardo et al., 2003; Godet et al., 2006). The lithology of the Lower Cretaceous within this part of the 'Prealps externes' is dominated by alternations of hemipelagic to pelagic deposits with limestones, marly limestones and marls.

### 2.3. The Bersek Quarry section

The Bersek Quarry lies on the Bersek Hill in the Gerecsé Mountains, close to the Danube River, south of the village Lábatlan, Komárom-Esztergom County, central N Hungary (Fig. 1; N 47°43'13", E 018°31'42"). The region belongs to the Transdanubian Range, representing the northeastern segment of the Bakony Unit (Kázmér, 1986) and it is the Austroalpine part of the AlCaPa terrane (Csontos and Vörös, 2004). The major part of the quarry corresponds to monotonous, grey marls of the Bersek Marl Formation (Császár, 1996) that, in their upper part turn reddish in colour, are composed of calcareous and argillaceous couplets and represent the Hauterivian stage. These sediments were deposited on a mud- or silt-dominated submarine slope, most likely with a linear feeding system (Fogarasi, 1995).

Based on the most recently published biostratigraphy of the Bersek Quarry (Fözy and Janssen, 2009) the levels in which the echinoids occur (221, 226, 228 and 233 at Section C) correspond to the *Acanthodiscus radiatus* Zone of the Lower Hauterivian.

## 3. Material and methods

The echinoid material from the Puez section was collected bed-by-bed during a period of three years within the FWF project P20018-N10 and is stored in the South Tyrol Museum of Natural Sciences and the Natural History Museum in Vienna. In addition,



Fig. 1. Origin of the samples.

material from the Museum de Gherdëina and the Museo Paleontologico Rinaldo Zardini was consulted in order to study the oral surface of the echinoids, which was incompletely preserved in any of the specimens collected by us. Preservation of the specimens is rather poor and most are strongly crushed and distorted. Therefore, extensive measurements were impossible and the description restricted to qualitative features. Due to the hard nature of the enclosing sediment many specimens could not be fully exposed. Cleaning was only possible using a combination of mechanical (vibrotools, sandblasting) and chemical (KOH) preparation.

Material from the Bersek Quarry section come from the Fülöp collection preserved at the Hungarian Natural History Museum and derives from bed-by-bed collecting during 1963 and 1964 (see Fözy and Janssen, 2009). Like in the Puez section echinoids are comparatively rare and rather poorly preserved. Most specimens are strongly distorted and preserved in hard siltstone, they were exposed using sandblasting. Fortunately, the distortion happened at a time when the sediment was still soft, but the connective tissue of the echinoid test already decayed, allowing movement along the sutures, which therefore are usually well visible in the Bersek Quarry specimens.

The Swiss material comes from the historical Ooster collection housed at the Naturhistorisches Museum Bern. The exact (stratigraphic) origin of most specimens is not clear and their preservation is usually poor.

### 3.1. Cladistic analysis

The phylogenetic analysis was carried out using the matrices of Barras (2007) and Saucède et al. (2007), with the new taxa added, as well as a new matrix based on a combination of the characters employed in these two studies. For parsimony analysis, PAUP\* 4.0b10 (Mac OSX) (Swofford, 2005) was used, facilitating the heuristic search with 1000 random addition sequences. Other than character 1 for the analysis using the matrix of Barras (2007) all characters were treated as unordered and of equal weight. Bootstrap percentages are based on 10,000 fast (simple addition without branch swapping) heuristic searches in PAUP\*. Bremer support (Bremer, 1994) values were calculated manually with PAUP\*. After completion of the initial analysis, characters were

reweighted by their rescaled consistency index and the parsimony analysis repeated under the new weighting scheme. Missing data are scored as “?”, inapplicable characters as “–”. The emended character list is provided in Appendix 1, the data matrices in the Appendix 2. Trees were drawn using the software TreeGraph 2 (Stöver and Müller 2010).

### 3.2. Abbreviations

CI	Consistency Index
HI	Homoplasy Index
HNHM	Hungarian Natural History Museum, Budapest, Hungary
MG	Museum de Gherdëina, St. Ulrich, Gröden, Italy
MNHN	Muséum national d'Histoire naturelle, Paris, France
MPTs	most parsimonious trees
NHMW	Naturhistorisches Museum Wien, Austria
NMBE	Naturhistorisches Museum Bern, Switzerland
RC	Rescaled Consistency Index
RI	Retention Index
STMN	Naturmuseum Südtirol, Bozen, Italy
TL	test length

## 4. Systematic palaeontology

The higher classification used herein follows that of Kroh and Smith (2010).

Class Echinoidea Leske, 1778

Infraclass Acroechinoidea Smith, 1981

Irregularia Latreille, 1825

Atelostomata von Zittel, 1879

Stem group Atelostomata ['disasteroids']

Family Collyritidae d'Orbigny, 1853

Genus *Absurdaster* nov. gen.

*Type-species.* *Absurdaster puezensis* sp. nov., designated herein.

*Etymology.* Referring to the puzzling morphology exhibited by the type-species (Fig. 2).

*Diagnosis.* Collyritid with highly modified, disjunct apical disc in which only genital plate 2 is retained and forms a bilaterally

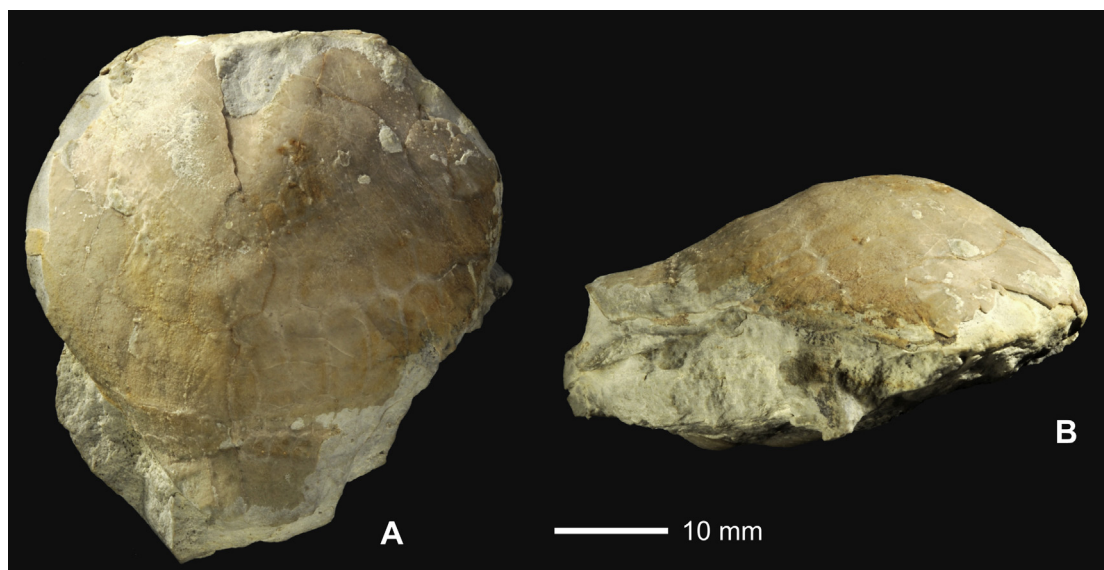


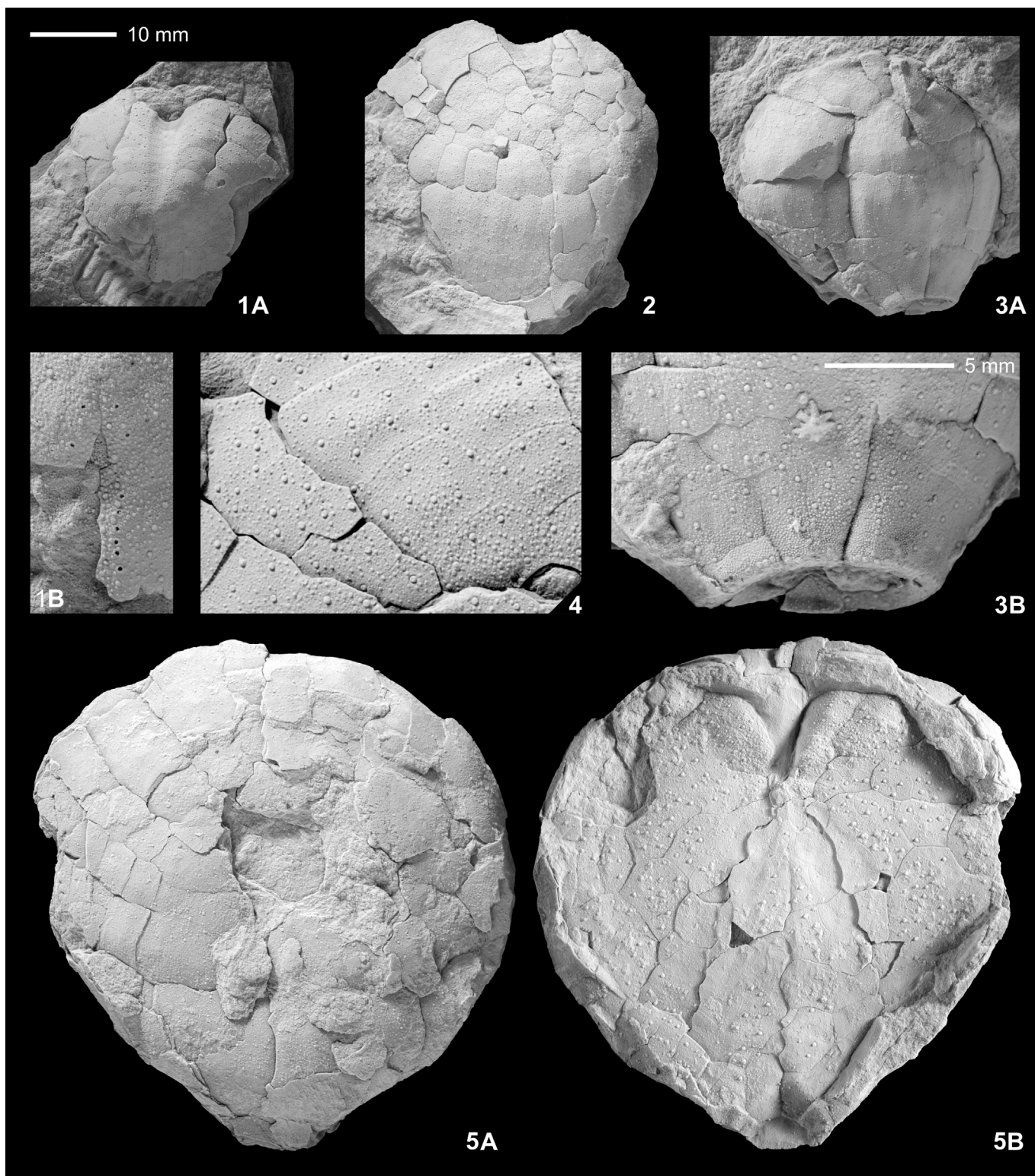
Fig. 2. *Absurdaster puezensis* sp. nov.: Holotype STMN PZO 341 (A: aboral view; B: right lateral view).



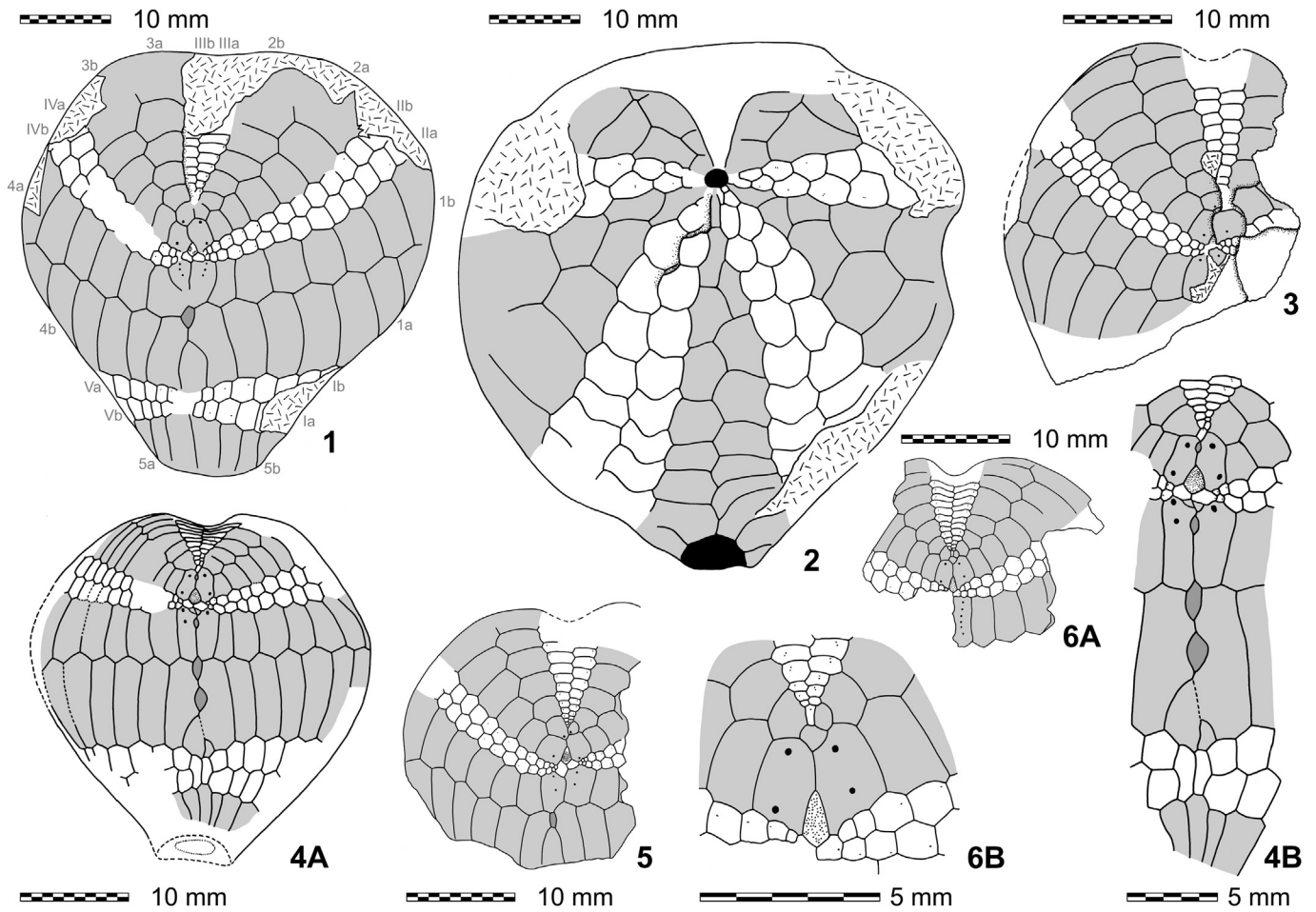
symmetrical madreporite located along midline of test. Multiple genital pores located on the most adapical interambulacral plates may be present. Ambulacrum III sunken at the ambitus and differentiated from the paired ambulacra. Periproct located low on

ambitus on a small, sharply defined, vertically truncated posterior face.

**Remarks.** Both new species of *Absurdaster* exhibit a rather unusual apical disc structure (Figs. 3.1B, 4.4B, and 8.1B). First of all it



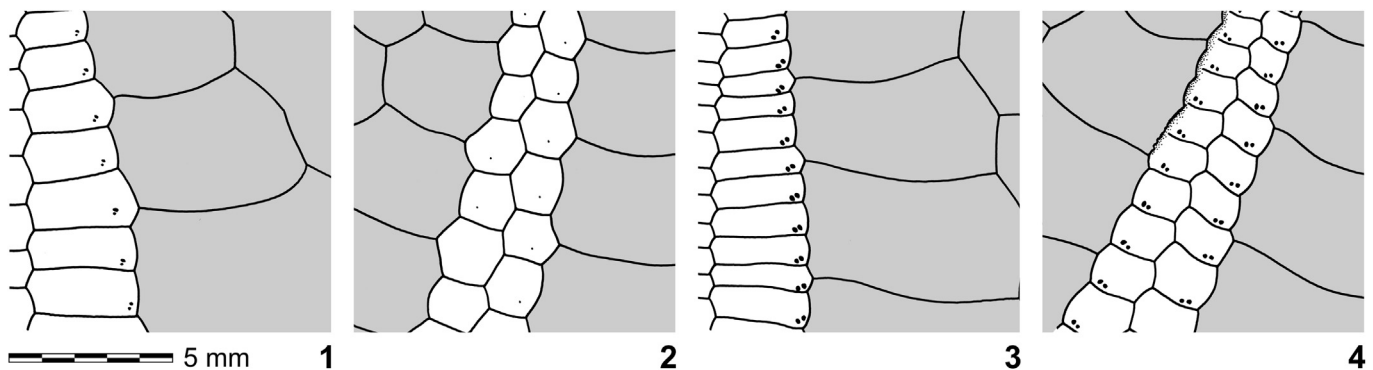
**Fig. 3.** *Absurdaster puezensis* sp. nov.: Paratype NHMW 2011/0405/0007 (A: aboral view; B: apical disc); 2: Paratype NHMW 2011/0386/0027 (aboral view); 3: Paratype STMN PZO 325 (A: aboral view; B: posterior end with circumanal fasciole); 4: NHMW 2011/0387/0003 (aboral tuberculation detail); 5: Paratype MG P-257 (A: aboral view; B: oral view). All specimens whitened with ammonium chloride.



**Fig. 4.** *Absurdaster puezensis* sp. nov.: camera lucida drawings. 1: Holotype STMN PZO 341 (aboral view); 2: Paratype MG P-257 (oral view); 3: NHMW 2011/0387/0007 (aboral view); 4: Paratype NHMW 2011/0415/0001 (A: aboral view; B: apical disc); 5: Paratype NHMW 2011/0385/0003 (aboral view); 6: Paratype NHMW 2011/0405/0007, (A: aboral view; B: trivium). Interambulacra shaded in light grey, complementary plates in dark grey; uncertain sutures stippled. Numbering of the plate columns according to Lovén's system is indicated in grey font.

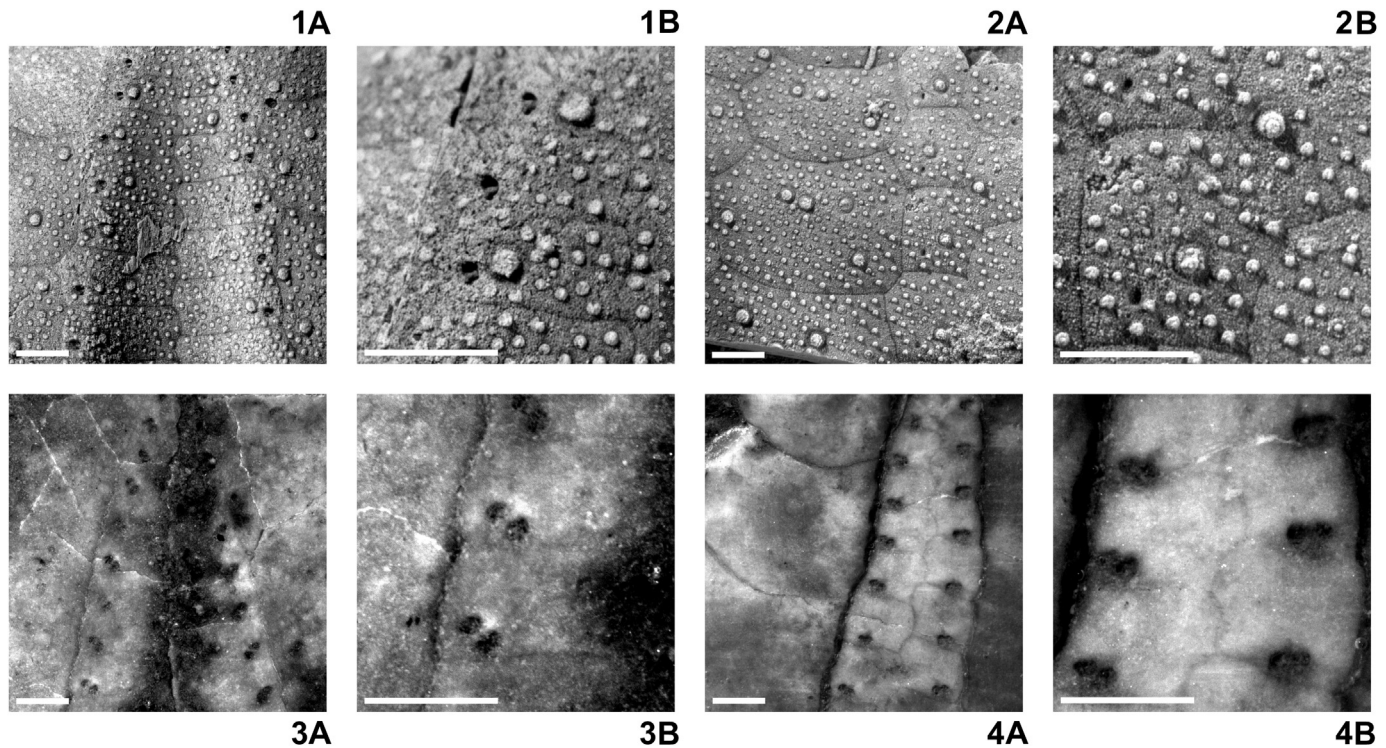
shows two rather than one disjunctions: the posterior disjunction between bivium and trivium typical for most 'disasteroids' and an anterior one within the trivium that separates ocular plate III from the remaining plates of the trivium. The gonopores (which vary in number) are unusual since they pierce interambulacral plates (i.e., axial elements) rather than the genital plates. The latter appear to be largely reduced – the apical disc of *Absurdaster* contains remarkably few plates apart from the oculars: a large one with

madrepore pores (here interpreted as genital plate 2) in central position along the midline of the test and zero (*A. hungaricus*, Fig. 8.1A, B) or one to four (*A. puezensis*, Fig. 4.1 vs. 4.4A) small unperforated plates that apparently do not follow the opercular plate rule (Mooi et al., 1994) and thus must represent extraxial elements: unperforated genital plates or complementary plates. Interpretation as modified, unperforated genital plates, such as occur in some modern pourtalesiid and plexechinids (Saucède



**Fig. 5.** Comparison of *Absurdaster* ambulacral plating. 1, 2: *A. puezensis* sp. nov.; 3, 4: *A. hungaricus* sp. nov. (1, 3: supraambital ambulacrum III, 2, 4: supraambital ambulacrum IV; 1: Paratype NHMW 2011/0397/0001, 2: Paratype NHMW 2011/0385/0003, 3: Holotype HNHN PAL 2013.30.1., 4: Paratype HNHN PAL 2013.32.1.). Interambulacra shaded.





**Fig. 6.** Comparison of *Absurdaster* ambulacral pores. 1, 2: *A. puezensis* sp. nov., whitened with ammonium chloride; 3, 4: *A. hungaricus* sp. nov., immersed in water; A: overview, B: detail of A. (1, 3: supraambital ambulacrum III, 2, 4: adapical ambulacrum IV; 1, 2: Paratype NHMW 2011/0405/0007, 3: Holotype HHNM PAL 2013.30.1., 4: Paratype HHNM PAL 2013.32.1.). Scale bars equal 1 mm.

et al., 2004) might seem the most parsimonious explanation at first. As such one would expect the presence of a pair of plates located where the interradiial sutures of interambulacra 1 and 4 meet the central suture (as in pourtalesiids). Only one plate is found in this position, however, the other plates (when present) are variably placed along the midline of the test (Fig. 4.4B). In addition, their number varies from one to four in *A. puezensis*, while they are completely lacking in *A. hungaricus*. So neither placement nor plate number fit well with an interpretation as unperforated posterior genital plates. Thus we favour an interpretation as complemental plates here, which also fits well with the apical disc structure of the presumed closest relatives (*Cardiopelta*/*Collyropsis*-group), which show a discontinuous string of complemental plates between the bivium and trivium, but retain genital plates. The positions of the complemental plates in these species [e.g., “*Collyropsis*” *carinatus* (Leske, 1778) illustrated by A.B. Smith in Smith and Kroh, 2013] perfectly match those in *A. puezensis*.

Despite the peculiar apical disc morphology of this taxon, it clearly seems to be derived from ‘collyritid’ ancestors. With them it shares a disjunct apical disc in which the posterior ocular plates are widely removed from the periproct. As mentioned above the disc configuration is the closest to that of *Cardiopelta*. It differs from that taxon, however, by the apparent loss of the genital plates 1, 3 and 4 and by the dislocation of the madreporite, which lacks a genital pore, to the midline of the test, as well as the highly posterior position of the bivium. Additionally, there is a second disjunction of the apical disc between the madreporite and ocular plate III.

Multiple disjunctions within the apical are also known from some modern pourtalesiids and plexechinids (Saucède et al., 2004), but in these forms the additional disjunctions occur between the posterior genital plates and the anterior ocular plates and (in some plexechinids) between genital plate 2 and ocular plates II and IV. In *Absurdaster*, in contrast, the additional disjunction is located

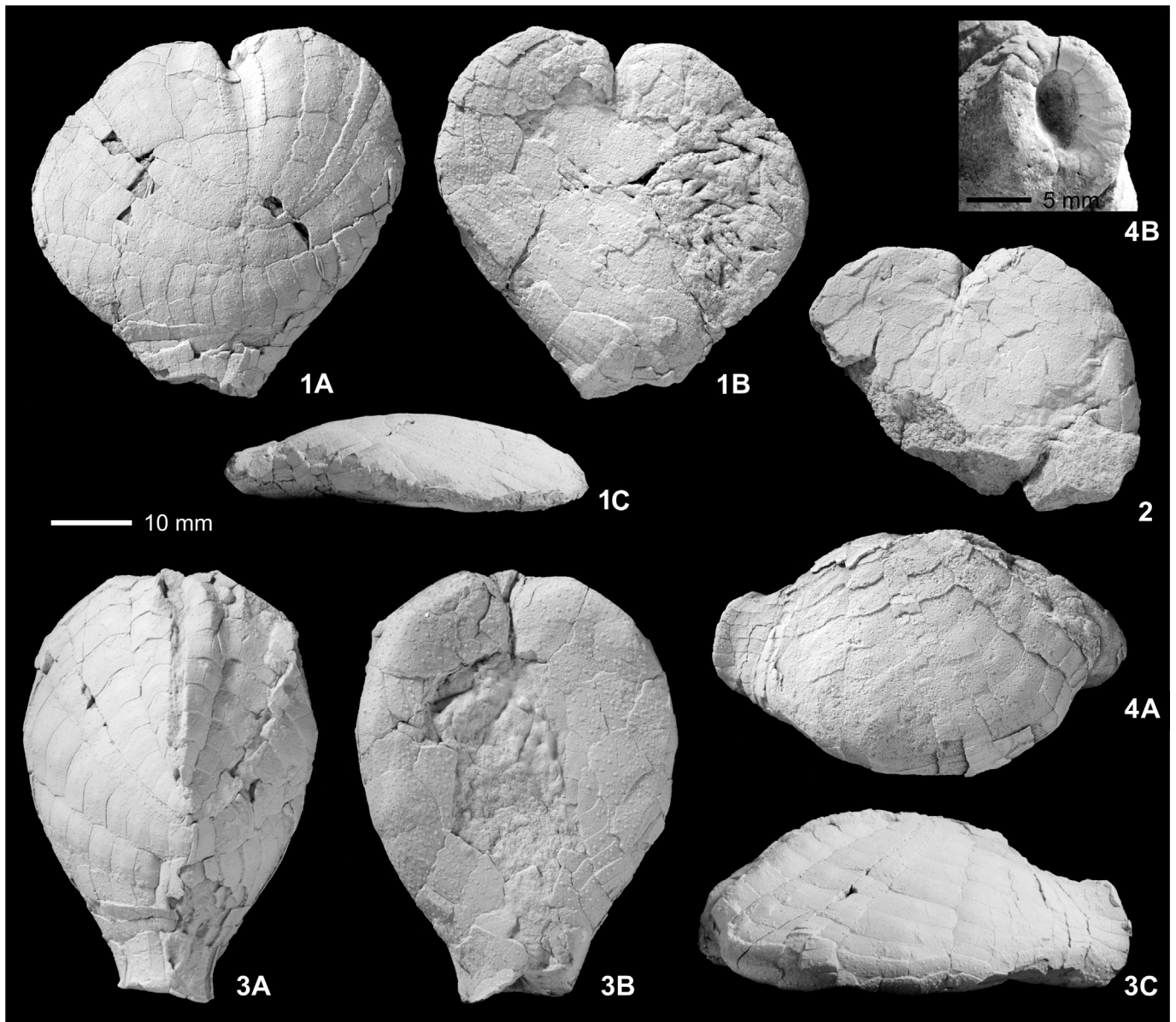
anteriorly, between ocular plate III and genital plate 2. Multiple disjunction of the apical disc alone can thus not be used as a synapomorphy and does not indicate any close relation between the new taxon and modern deep-water holasteroids.

The loss of genital plates is not unparalleled in echinoid evolution, in the closely related tithoniids genital plates 2 and 4 are apparently lost or highly reduced and the posterior genital pores translocated to ocular plates II and IV. Likewise, multiple genital pores, as observed in the type-species *A. puezensis*, are known from other taxa too: in *Lampadaster* and *Guettaria*, ocular plates II and IV bear two additional gonopores each. Such an extreme case of gonopore multiplication, as observed in *A. puezensis*, however, is known only from an extant pedinoid echinoid from New Zealand, so far: *Caenopedina otagoensis* McKnight, 1968. In this sexually dimorphic species the females have three to six genital pores per genital plate, while males have only one per plate. It is possible that the variation in gonopore number observed in *A. puezensis* is related to sexual dimorphism too.

*Absurdaster*, furthermore, shows a peculiar type of fasciole circling the periproct. This new type of fasciole is termed circumanal fasciole here. It can also be observed in some ‘disasteroids’ supposedly related to *Cardiopelta* (e.g., ‘*Collyropsis*’ *acutocordatus* Szörényi, 1960, ‘*Collyrites*’ *meyrati* Ooster, 1865).

Among the echinoids species described to date (Lambert and Thiéry, 1909–1925; Kier and Lawson, 1978; Kroh, 2010; Kroh and Mooi, 2013; Smith and Kroh, 2013), there is no taxon with comparably modified apical disc and test shape. We thus have decided to propose a new genus for the present material, despite its fragmentary nature and rarity. Based on the characters of the apical disc even crushed specimens of the taxon can readily be identified.

Among ‘disasteroids’ there are only three other genera with a distinct frontal notch: *Cardiopelta* Pomel, 1883 (= *Collyropsis*

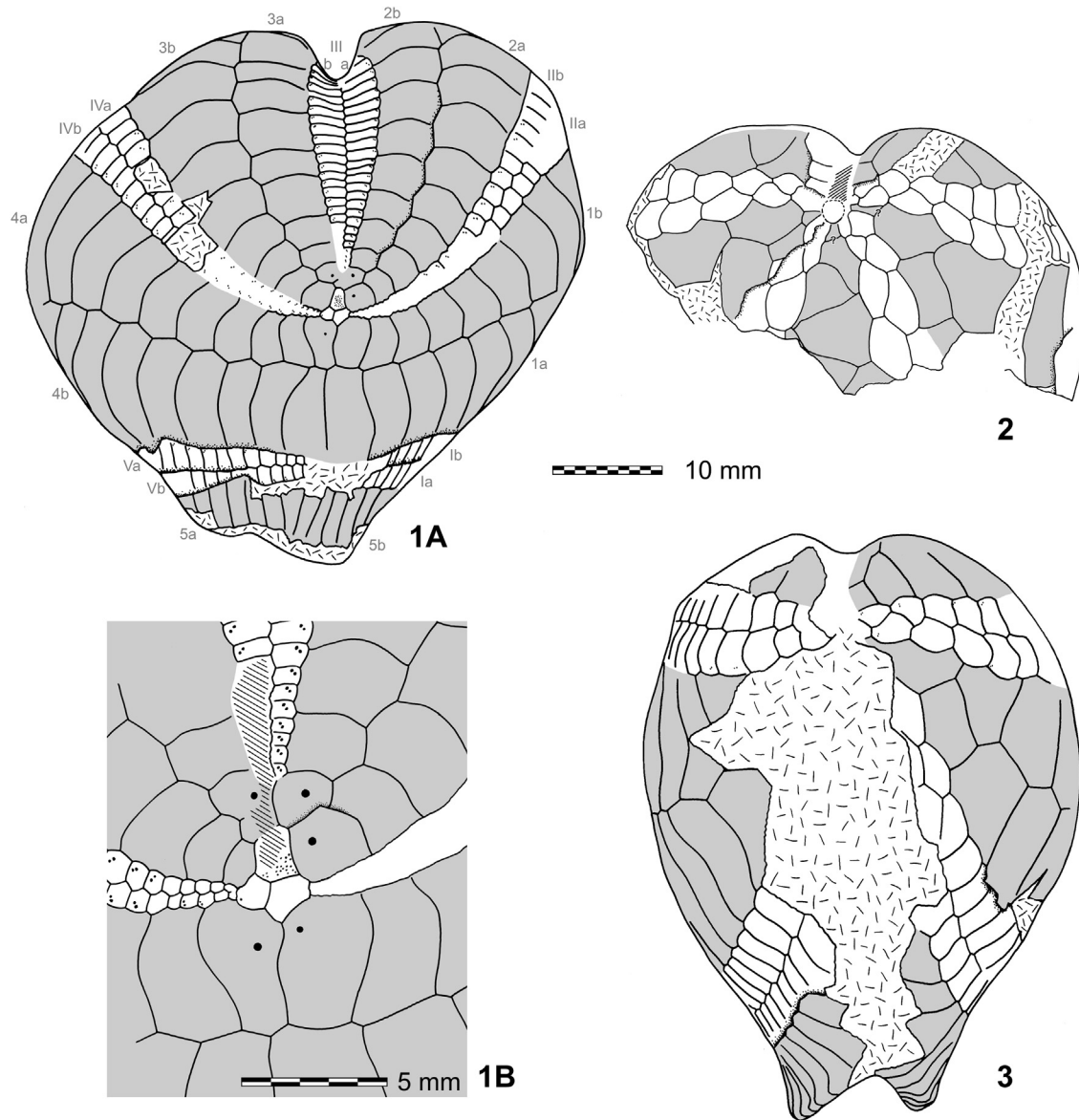


**Fig. 7.** *Absurdaster hungaricus* sp. nov.: 1: Holotype HNHM PAL 2013.30.1. (A: aboral, B: oral, and C: right lateral view); 2: Paratype HNHM PAL 2013.31.1. (oral view); 3: Paratype HNHM PAL 2013.32.1. (A: aboral, B: oral, and C: left lateral view); 4: Paratype HNHM PAL 2013.33.1. (A: right lateral view of distorted test; B: posterior face). All specimens whitened with ammonium chloride.

Gauthier, 1896), *Cardiolampas* Pomel, 1885 and *Laticlypus* Szörényi, 1966. From the former *Absurdaster* can easily be distinguished by its modified apical disc. Differentiation from the latter two genera, in contrast, is severely hampered by the poor knowledge on their plating patterns and structure of their apical discs. *Laticlypus* differs from *Absurdaster* by its overall shape (transversely elongated), aboral periproct, which is situated in a distinct sulcus, and by the short distance between the trivium and bivium, the latter of which might even be in contact with the periproct. *Cardiolampas* differs by its less elongated outline and subambital periproct. Apical disc structure in that genus is virtually unknown, but incomplete data on a specimen from the Upper Oxfordian of Tunisia (MNHN J01.431; Smith in Smith and Kroh, 2013) indicates that the trivium of *Cardiolampas* is made up from ocular plates II to IV and genital plates 2 and 3 and an additional plate located centrally, here interpreted as complementary plate. There is no information on the posterior genital plates and the bivium, but it is evident that the disc

is distinctly different from that of *Absurdaster*. *Cardiolampas* specimens with a similarly pointed and elongated posterior as in *Absurdaster* were illustrated by Beurlen (1934: fig. 23), but it is conceivable that these are in fact misidentified *Absurdaster* specimens, since the syntypes of *Cardiolampas friburgensis* (Ooster, 1865) preserved in the Naturhistorisches Museum der Bürgergemeinde Bern (NMBE 5015009, 5015010, 5015011, and 5015012) do not show such an outline. Some of them (e.g., NMBE 5015011) even show a vertically truncated posterior end with different periproct position. Despite the claim by Beurlen (1934: p. 118) that *C. friburgensis* can be easily recognized, it seems that published illustrations and descriptions of this species are based on a mixture of different taxa from different ages. A specimen (NMBE 5017081) from the Late Cretaceous red marls of Wimmis, Switzerland (then considered as Late Jurassic) attributed to *C. friburgensis* by Ooster (1869: p. 4, pl. 2, fig. 6), for example, seems to be a misidentified stegasterid [possibly *S. subtrigonatus* (Catullo, 1827)], as already suggested by





**Fig. 8.** *Absurdaster hungaricus* sp. nov.: camera lucida drawings. 1: Holotype HNHM PAL 2013.30.1. (A: aboral view, B: apical disc detail); 2: Paratype HNHM PAL 2013.31.1. (oral view); 3: Paratype HNHM PAL 2013.32.1. (oral view). Lines marked by question marks in 2 are interpreted as fractures rather than sutures here. Interambulacra shaded; areas covered by sediment hatched. Numbering of the plate columns according to Lovén's system is indicated in grey font.

Steinmann in Lorenz (1902: p. 45)] instead, because the configuration of the aboral ambulacra suggests that it has a compact apical disc. For clarification of the true morphology of *Cardiolampas* topotypic material with well-preserved apical disc is urgently needed, but has so far not been available for study.

Apart from these three genera there is also *Proholaster* Gauthier, 1896, which has only an incipient frontal notch. It is different from *Absurdaster* in terms of overall shape, being more circular than cordiform and having a vertically truncated posterior face with the periproct high on the margin. The apical disc of *Proholaster*, in addition, is of standard collyritid design, except for its lack of complemental plates.

*Absurdaster puezensis* sp. nov.

Figs. 2; 3.1–3.4; 4.1–4.6; 5.1–5.2; 6.1–6.2

**Etymology.** Referring to the type locality.

**Holotype.** Naturmuseum Südtirol STMN PZO 341 (CP172) (Figs. 2A–B).

**Paratypes.** Seven specimens: Museum de Gherdëina MG P-257; Naturhistorisches Museum Wien NHMW 2011/0385/0003, 2011/0386/0027, 2011/0397/0001, 2011/0405/0007, 2011/0415/0001; STMN PZO 325 (all from the type locality).

**Type-locality.** southern side of Piz de Puez, Puez-Odle-Gardenaccia Plateau, Dolomites, about 30 km northeast of Bozen, Italy (Lukeneder, 2012: fig. 1).

**Type-stratum.** Puez Limestone Member of the Puez Formation; Upper Hauterivian “*Pseudothurmannia ohmi*” Zone (*Pseudothurmannia mortilleti* Subzone) to Lower Barremian *Moutoniceras moutonianum* Zone.

**Additional material studied.** Seven additional, less well-preserved specimens: NHMW 2005z0245/0023, 2011/0386/0036, 2011/0387/0003, 2011/0387/0004, 2011/0387/0007, 2011/0415/0013; STMN PZO 324 (CP 170) (all from the type locality).

**Diagnosis.** An *Absurdaster* species with rudimentary pores and large, high, hexagonal plates in the aboral and ambital part of the anterior paired ambulacra; ambulacrum III forming a wide frontal



notch and bearing strongly oblique, almost vertical pores aborally; multiple gonopores in the most adapical plates of interambulacral columns 1b and 4a; posterior end without sharp margin, periproct flush or slightly sunken only.

**Description.** Test of small to medium size, less than 50 mm in length. In aboral view the test is cordiform (Figs. 2A and 3.2) with a distinct frontal notch starting close to the apical disc and becoming progressively more depressed towards the ambitus. Posterior margin narrow and transversely truncated (Fig. 3.3B). Oral surface flattened. In profile test wedge shaped, with high, rounded anterior end and posterior end sloping gently from the apex toward a low vertically face featuring the periproct. Coronal wall very thin, varying between 290 and 520  $\mu\text{m}$  (in c. 40 mm TL specimens) depending on position of measurement. Consequently all specimens are crushed, precluding the exact measurements of length, width and height.

Apical disc highly modified with just a single genital plate (here interpreted as genital plate 2) in central position bearing the madreporic pores (Figs. 3.1B, 4.4B, 4.5, 4.6B). The disc is twice disjunct: 1) between ocular plates I + V and II + IV; 2) between genital plate 2 and ocular plate III (separated by interambulacral plates). Multiple genital pores present (Fig. 3.1B). Four are located on the interambulacral plates immediately anterior of the madreporite, with two pores in each interambulacrum. Another four to twelve pores are located on the most adapical plate of interambulacral columns 1b and 4a, where they form anterior-posteriorly extended lines of two to six pores each. Not only does the number of gonopores vary considerably between specimens, but also their position. In some specimens (e.g., NHMW 2011/0405/0007, 2011/0415/0001) all anterior genital pores lie on the adapical-most plates of columns 2a and 3b (i.e., the posterior columns; Fig. 4.6B), in other specimens (e.g., NHMW 2011/0385/0003; Figs. 4.1, 4.3) they pierce the plates of the anterior columns too. Diameter of genital pores varies between c. 160 and 190  $\mu\text{m}$ . Ocular plate III is tiny, rectangular and antero-posteriorly elongated. Ocular plates II and IV are small, abutting each other and the madreporite. Posterior oculars are elongated antero-posteriorly and in direct contact with each other, but not in contact with the periproct which is far removed from the apical disc. One to three isolated complemental plates present between the trivium and bivium, located along the suture between interambulacra 1 and 4 (Fig. 4.4B).

Paired ambulacra simple throughout (Figs. 3.4, 4.1, 4.3), with minute unipores aborally, which are located in the adoral/adradial corner of the plates (Figs. 5.2 and 6.2). On the adoral plates the pores are slightly larger, with well-defined attachment area, and lie roughly in the centre of the plates. They neither show plate crowding nor phyllodes-formation or plate occlusion. Aboral plates roughly hexagonal and slightly elongated vertically, oral plates with distinctly convex sutures. At the ambitus each interambulacral plate abuts three ambulacral plates (Fig. 5.2). Aboral surface of the ambulacra flush, with small tubercles similar to that found on the interambulacra. On the oral side ambulacra II and IV bear large well-defined “primary” tubercles, while ambulacra I and V are naked, bearing miliary and very sparse secondary tuberculation only. Ambulacrum III flush adapically, but increasingly sunken towards the ambitus, where it forms a distinct frontal notch. On the oral side the peristome is connected by a sunken groove to the anterior margin. In aboral ambulacrum III plates are distinctly lower than wide, with three to four ambulacral plates abutting each interambulacral. Pores are small, but larger than those of the paired ambulacra and consisting of strongly oblique (to almost vertical) double pores of the circumflexed type (*sensu* Barras, 2007).

At the ambitus interambulacra are much wider than ambulacra. They are covered by sparse, small primary tubercles and

dense miliary tuberculation. Adorally, the interambulacra show a heterogeneous tuberculation, with rather large, widely scattered, superficial primary tubercles (Fig. 3.5B). Many of those are detached in a similar way as in some modern palaeopneustid and lovenioid echinoids (see David and Néraudeau, 1989). Interambulacrum 1 appears to be amphisternous, while interambulacrum 4 seems to be meridosternous (Fig. 4.2) if interpreted correctly (deciphering of plating structure is complicated by the crushed nature of the material, presence of fractures and the general poor visibility of plate sutures in the most adoral plates in most ‘disasterids’). The basicoronal plates of interambulacra 1, 4 and 5 are rather large, extending at least to the third or fourth adjacent ambulacral plate and have a strongly oblique, concave suture. In interambulacrum 5 (Fig. 4.2) plates 5.a.2 to 5.a.3 are not significantly enlarged (protosternous condition), but plate 5.b.2 takes up the full plastron width, precluding direct contact between the labrum and plate 5.a.2 (meridosternous condition).

Periproct located low on the ambitus on a low vertically truncated posterior face, with well defined edge. Periproct outline oval, laterally elongated. The first plates to contact the periproct are 5.a.8 and 5.b.8 and the periproct is framed by at least six plates on either side, possibly more.

On the posterior end of the test, along the edge of the posterior face a distinct band of dense granules can be observed which form a ring (Fig. 3.3B). While the band is well defined along the posterior edge, it grades into the surrounding tuberculation anteriorly. The pattern is similar to that of parafascioles shown by toxasterids (Néraudeau et al., 1998).

**Remarks.** At the first glance the Puez material is highly similar to the slightly older specimens from Lábatlan (Hungary). Upon closer examination, however, considerable differences become apparent, mainly affecting ambulacral plating and pores (Figs. 5 and 6), which are listed in Table 1. Given low variation of these features within the two ‘populations’ it seems justified to regard them as two different species.

The only similar form described earlier – *Collyrites meriani* Ooster, 1865 – is, unfortunately, poorly known. It is based upon three specimens, two of which are preserved in the collections of the Naturhistorisches Museum Bern. These specimens, as discussed in more detail below, are incompletely preserved and it is thus difficult to establish whether or not they are conspecific with the Puez material described here. Aboral plate sutures are preserved in patches on the holotype (e.g., in interambulacrum 1 and ambulacrum II), which is an internal cast. These suggest that ambital ambulacral plate shape is similar to the Puez material, but that

**Table 1**

Key diagnostic features of the two new *Absurdaster* species recognized here (amb. = ambulacra; iamb = interambulacra).

Feature	<i>A. puezensis</i>	<i>A. hungaricus</i>
Frontal notch	Wide	Narrow
Posterior end	Low, bluntly pointed	Flaring, trumpet-shaped, sharp margin of posterior face
Genital pore no. (ant./post.)	4/4–12	4/2
Ratio amb./iamb. plates (ambital paired amb.)	2:1	3:1
Ratio amb./iamb. plates (amb. III)	2–3:1	3–4:1
Ambital amb. plate height	High	Low
Aboral pores, paired amb.	Unipores	Double pores
Orientation pores, aboral amb. III	Almost vertical (70–80°)	Oblique (35–55°)
Periplastral areas	Naked	Tuberculate
Periproct	Not invaginated	Invaginated

plates are smaller and the ratio between interambulacral plates and ambulacral plates is different. (5:1 vs. 2:1 in *A. puezensis*). Consequently we prefer not to attribute the Puez material to Ooster's species for the time being.

**Occurrence.** Known only from the type locality.

*Absurdaster hungaricus* sp. nov.

Figs. 5.3–5.4; 6.3–6.4, 7.1–7.4, 8.1–8.3, 9

**Etymology.** Referring to the country of origin.

**Holotype.** Hungarian Natural History Museum HNHM PAL 2013.30.1.

**Paratypes.** Hungarian Natural History Museum HNHM PAL 2013.31.1., PAL 2013.32.1., and PAL 2013.33.1.

**Type-locality.** Bersek Quarry, Látatlan, Komárom-Esztergom county, Hungary (Gerecse Mountains, Transdanubian Range) (Fözy and Janssen, 2009).

**Type-stratum.** Bersek Marl Formation; Lower Hauterivian, *Acanthodiscus radiatus* Zone.

**Diagnosis.** An *Absurdaster* species with circumflexed pores and low plates in the ambital part of the anterior paired ambulacra; ambulacrum III forming a narrow frontal notch and bearing oblique (c. 45°) pores aborally; single gonopore each in most adapical plates of interambulacral columns 1b and 4a; posterior end flaring, with sharp margin, periproct invaginated.

**Description.** Test of medium size, up to 50 mm in length. In aboral view the test is cordiform with a distinct, but narrow frontal notch (Fig. 7.1A). Posterior half tapering to a trumpet-shaped, transversely truncated posterior face (Fig. 7.3a, 7.4b). Oral surface flattened, with slightly raised plastronal area. In profile test arched, gently sloping from the trivium in all directions. Towards the posterior the test rises again, to form the flaring margin of the vertically face featuring the periproct. Coronal wall very thin, varying between 320 and 430 µm (in a c. 50 mm TL specimen) depending on position of measurement. All specimens are crushed, precluding the exact measurements of length, width and height.

Apical disc highly modified with just a single genital plate (Fig. 8.1B), as in *A. puezensis* described above. In contrast to that

species, however, complementary plates are lacking and there seem to be just two genital pores on the most adapical plate of interambulacral columns 1b and 4a. In all other details the apical disc is identical to that of *A. puezensis*.

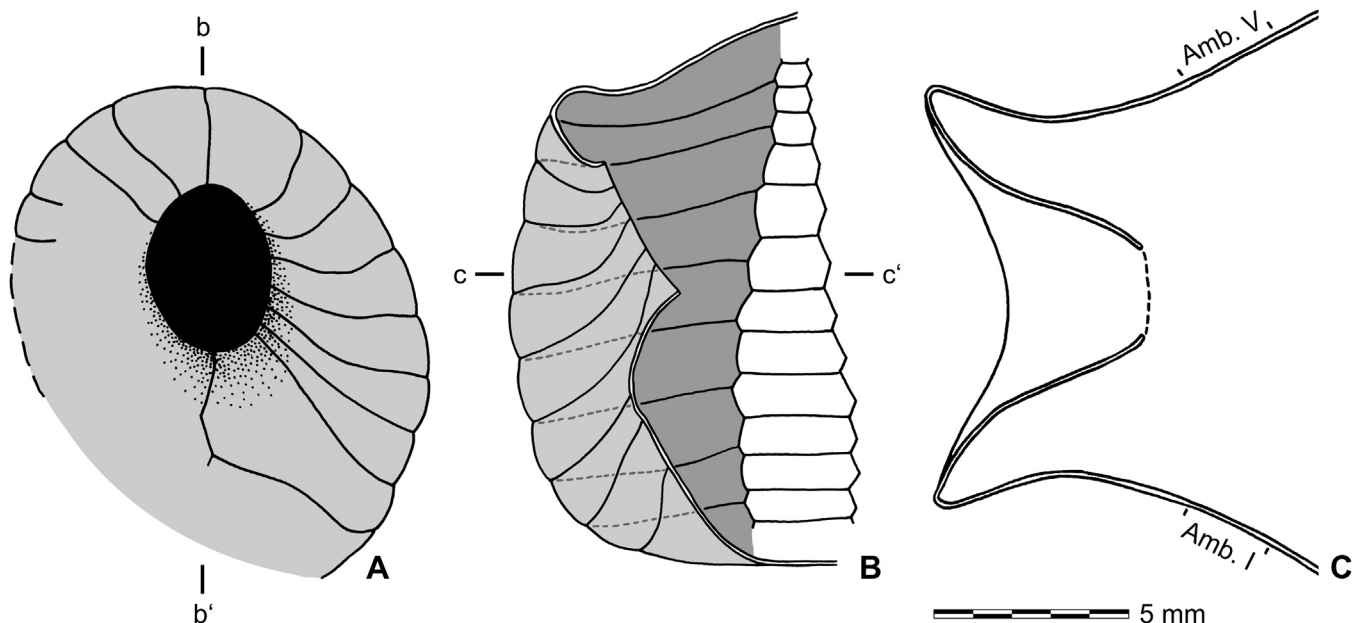
Paired ambulacra simple throughout, with moderately large partitioned isopores aborally, which are located in the adoral/adradial corner of the plates (Figs. 5.4 and 6.4). Adoral ambulacra poorly preserved, but show neither phyllode formation by plate occlusion, nor by plate crowding (Fig. 8.2, 8.3). Adapical plates hexagonal and high, gradually becoming lower towards the ambitus, where their height equals about half their width. Each interambulacral plate borders four ambulacral plates at the ambitus. Adoral plates again increase in size towards the peristome and show distinctly convex sutures.

Ambulacrum III flush adapically, but increasingly sunken towards the ambitus, where it forms a distinct, but narrow frontal notch. On the oral side the peristome is connected by a sunken groove to the anterior margin. In aboral ambulacrum III plates are distinctly lower than wide, with four to five ambulacral plates abutting each interambulacral plate. Pores are small, oblique partitioned isopores (Figs. 5.3 and 6.3).

As far as can be recognized despite the poor preservation of the oral surface in all available specimens, the paired interambulacra appear to be amphisternous, with large basicoronal plates extending to the second or third adjacent ambulacral plate (Fig. 8.2). In interambulacrum 5 plates 5.a.2 and 5.a.3 are not significantly enlarged (protosternous condition), but take up almost the full width of the interambulacrum (Fig. 8.2), reminiscent of the situation in early cardiasterids.

Aboral tuberculation not preserved; oral tuberculation apparently was heterogeneous as in *A. puezensis*, but is poorly preserved in all available specimens. The periplastral areas, seem to have been tuberculated.

Periproct invaginated (Fig. 9A–C) and located in the centre of the vertically truncated posterior face (Fig. 7.4B). Periproct of circular shape and framed by eight plates on either side (Fig. 9A). These plates are acutely bent where they curve around the edge of the posterior face, producing a sharply defined crest (Fig. 9C).



**Fig. 9.** *Absurdaster hungaricus* sp. nov.: Posterior face with invaginated periproct in paratype HNHM PAL 2013.33.1. (A: outside view of posterior face, B: vertical section, C: horizontal section viewed from above). Interambulacra shaded.



Fascioles, if some were originally present, are not preserved.

**Remarks.** *A. hungaricus* can easily be different from *A. puezensis* based on structural test characters (compare discussion above and Table 1). Likewise, it differs from Ooster's *A. meriani* by its different posterior end, which has a distinct trumpet shape.

**Occurrence.** Known only from the type locality.

*Absurdaster meriani* (Ooster, 1865) comb. nov.

Fig. 10

1865 *Collyrites meriani* Ooster, p. 58, pl. 9, figs. 10–12.

**Holotype.** Naturhistorisches Museum der Bürgergemeinde Bern NHMBE 5015015 (Ooster, 1865: pl. 9, fig. 10; from Veveyse).

**Paratypes.** NMBE 5015016 (Ooster, 1865: pl. 9, fig. 12; from Veveyse). The repository of the third specimen (Ooster, 1865: pl. 9, fig. 11, from “Gantrischkumli” [= Chumml, Mt. Gantrisch, Rüeggisberg, Bern-Mittelland, Switzerland]) is unknown.

**Type-locality.** Valley of the Veveyse River, Fribourg, Switzerland.

**Type-stratum.** “Néocomien-Urgonien” of Ooster (1865: p. 58). The Veveyse outcrop encompasses sediments from uppermost Berriasian to basal Barremian (Busnardo et al., 2003). Sediments similar to the matrix adhering to the types are present at numerous levels in that section and the exact stratigraphic provenance of the types thus remains unknown.

**Diagnosis.** An *Absurdaster* species with numerous small, hexagonal plates in the supraambital part of the anterior paired ambulacra; ambulacrum III forming a wide frontal notch; posterior end without sharp margin.

**Description.** The general form of the test shows a cordiform outline and pointed posterior end with small, vertically truncated posterior face presumably featuring the periproct. The frontal notch is rather wide and deep, starting close to the apex and becoming increasingly depressed towards the margin.

The apical disc is poorly preserved but its disjunct nature can be clearly seen in the holotype (which is an internal mould), as can be the additional disjunction within the trivium.

Aborally the anterior paired ambulacra show numerous hexagonal plates, about five or six per adjacent interambulacral plate.

**Remarks.** Ooster's species *Collyrites meriani* is based on three incomplete specimens. At least one of them – the holotype (Fig. 10.1; NMBE 5015015; Ooster, 1865: pl. 9, fig. 10) – clearly belongs to the new genus described herein. It is, however, an internal mould of the aboral surface only, thus preserving mainly the gross shape of the echinoid test but not the detailed plating structure. Given the minute differences (plate numbers, pore development) which separate the Italian and Hungarian species of *Absurdaster* (Table 1) it is thus impossible to judge if the Swiss specimen is conspecific with either of them and we prefer to keep it separate for the time being. If additional, better preserved material from the type-locality of *A. meriani* becomes available it might be possible to judge if one of the two newly established specimens belongs into the synonymy of Ooster's species. The few details of the plating patterns that can be seen in the holotype indicate that *A. meriani* is indeed different, its aboral ambulacrum II appears to consist of numerous small hexagonal plates, five or six of which seem to abut one interambulacral plate in the supraambital region. This situation differs both from *A. puezensis*, which has few large plates and from *A. hungaricus*, which has many plates, but of different shape (lower than wide).

Ooster's other specimens represent an echinoid half embedded in the matrix, exhibiting the oral surface (NMBE 5015016; Ooster, 1865: pl. 9, fig. 12) and a crushed specimen (Ooster, 1865: pl. 9, fig. 11), which could not be located. The morphology of the oral surface in specimen NMBE 5015016 is compatible with that of *Absurdaster puezensis*, but reveals no additional details, since its adoral region is largely destroyed and/or covered by adhering sediment.

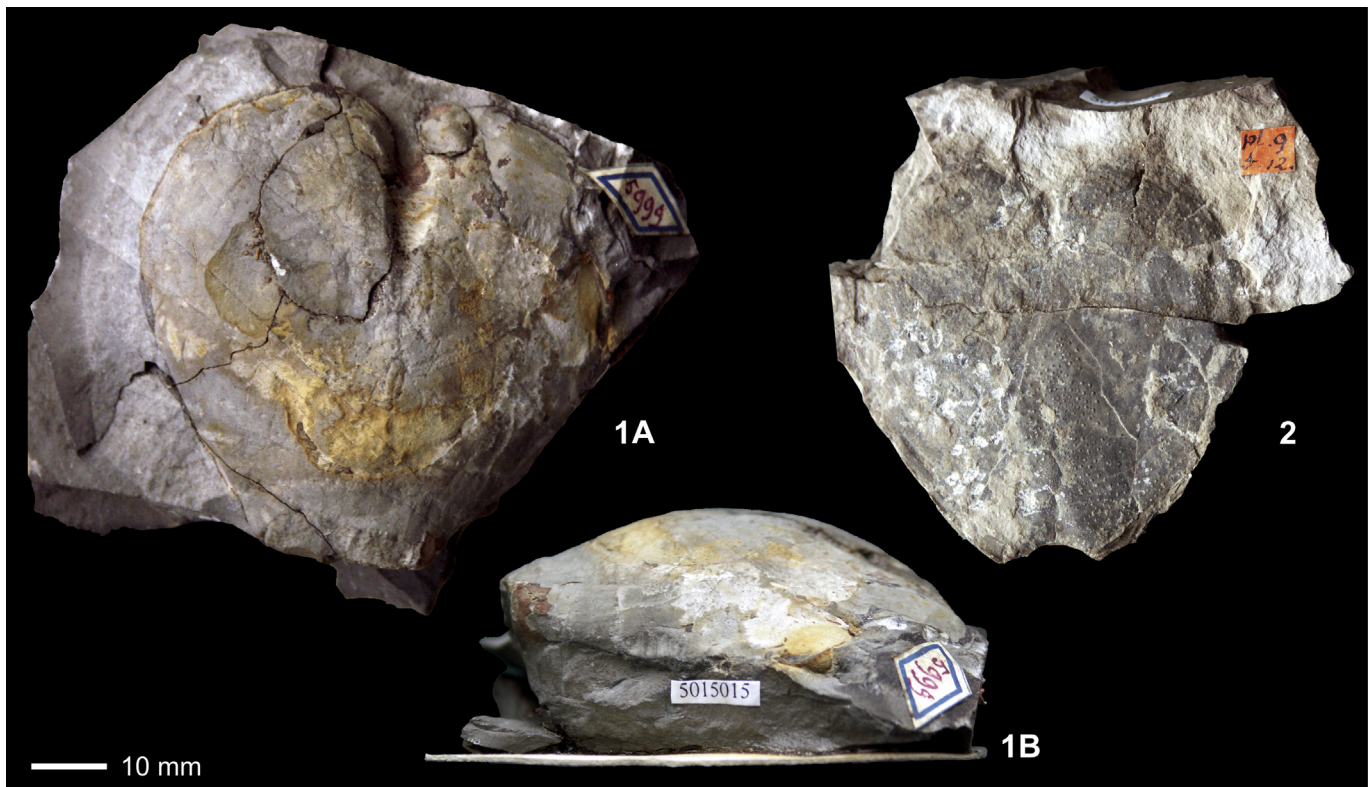


Fig. 10. *Absurdaster meriani* (Ooster, 1865): 1: Holotype NHMBE 5015015 (A: aboral view; B: right lateral view); 2: Paratype NMBE 5015016 (oral view).

Lambert and Thiéry (1924: p. 392) have considered *C. meriani* as a junior synonym of *Cardiolampas friburgensis* (Ooster, 1865). While it is true that both genera have a similar overall shape their posterior end is distinctly different. In addition, evidence available at present indicates that *Cardiolampas* does not possess the twice disjunct disc of *Absurdaster* (see above for detailed discussion) and it thus seems unlikely that the two species really are conspecific.

**Occurrence.** Known only from the uppermost Berriasian to basal Barremian of SW Switzerland.

## 5. Phylogenetic analysis

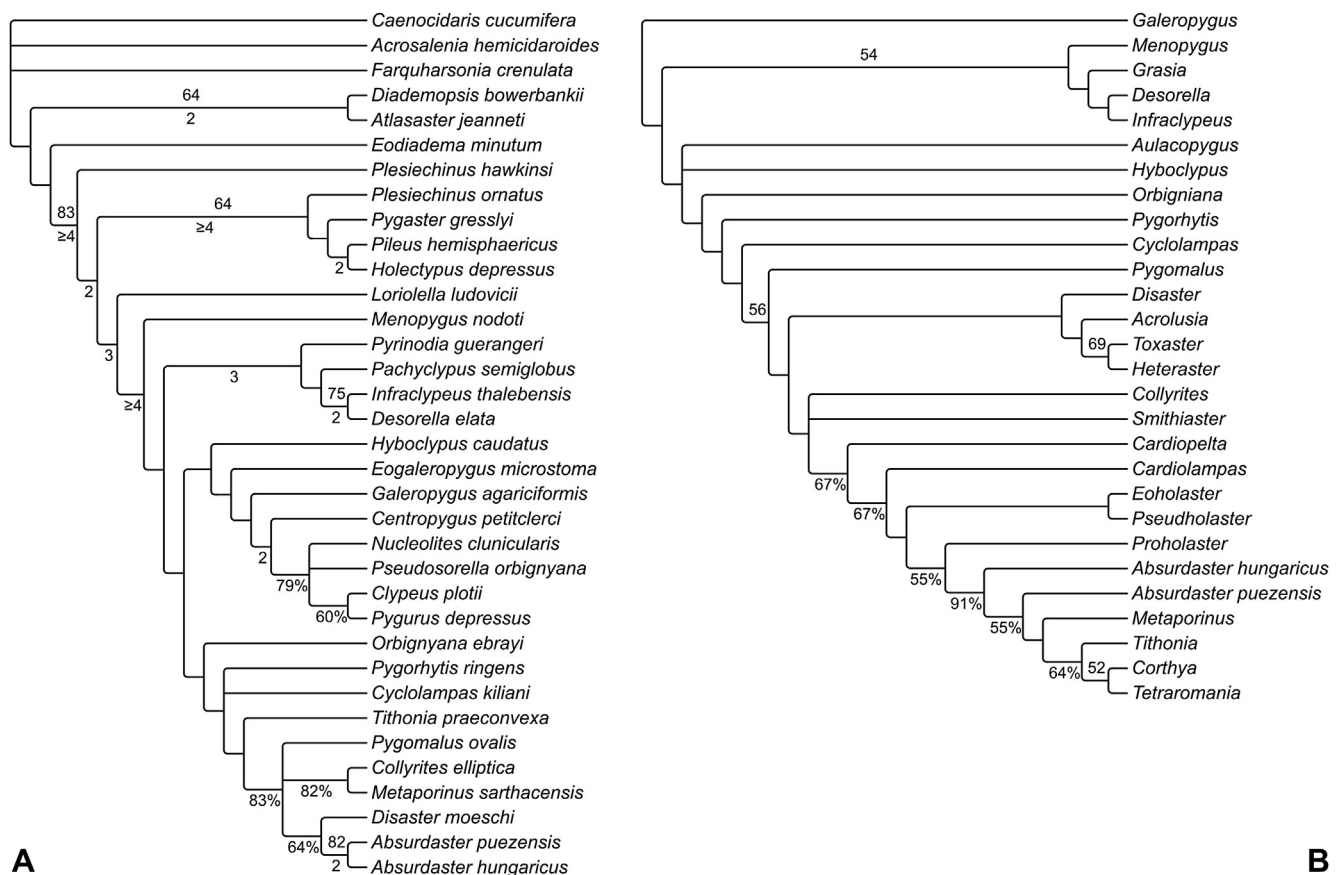
**Previous work.** The phylogeny of early irregular echinoids was recently studied independently by Barras (2006, 2007) and Saucède et al. (2007), who analysed different sets of characters and taxa. In order to test our ad-hoc assumption that *Absurdaster* represents an advanced stem-group atelostomate and to check whether it belongs into the holasteroid or spatangoid branch, we added the two new species of *Absurdaster* to the matrices of Saucède et al. (2007) and Barras (2007) respectively and re-run their analyses.

**Cladistic analysis.** An analysis of the taxon and character set of Saucède et al. (2007) extended by the inclusion of *Absurdaster* results in 2430 most parsimonious trees (MPTs) of 157 steps length. In the strict consensus tree (not shown; CI = 0.355, RI = 0.709, RC = 0.252, HI = 0.645) the two *Absurdaster* species are resolved as sister taxa rooted within an unresolved clade containing *Collyrites*, *Disaster*, *Metaporinus*, *Pygomalus* and *Tithonia*. In the 50%-majority-

rule consensus tree (Fig. 11A) the resolution within this clade is marginally better and shows *Disaster* as outgroup to the *Absurdaster* clade in an unresolved trichotomy with *Pygomalus* and *Collyrites*+*Metaporinus*, while *Tithonia* is placed as sister taxon to all of those taxa. As in the original analysis by Saucède et al. (2007) bootstrap support is low for the majority of the clades found. The position of *Absurdaster* within the ‘disasterids’ is not affected by renewed analysis after reweighing the characters by their RC (18 MPT, 45.14658 steps; CI = 0.542, RI = 0.847, RC = 0.459, HI = 0.458), but finds a sister-group relationship between *Absurdaster* spp. and *Collyrites*+*Metaporinus* which nest in an unresolved trichotomy with *Pygomalus* and *Disaster*. The new genus thus clearly is a stem-group member of the Atelostomata.

Interpretation of the supernumerary plates between the trivium and bivium as unperforated genitals does not change the result of the analysis, since none of the characters scores for the number of genital plates. The only character affected is the one scoring for the presence of complemental plates (character 6), which would thus need to be scored identical for both taxa (most specimens of *A. puezensis* have just one or two supernumerary plates, so no complemental plates are present if these plates are considered genitals – as in *A. hungaricus*).

The second analysis employed the characters and matrix of Barras (2007). While the former could be used without any modifications to the existing scoring, some modifications were necessary for the latter: character 2 of Barras (2007) was found to be erroneously scored, with the published matrix contradicting the

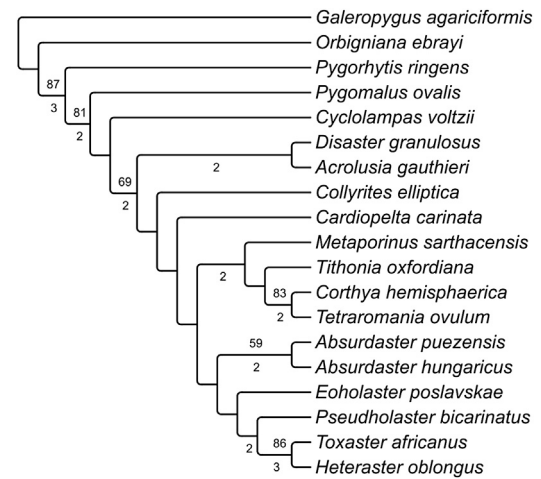


**Fig. 11.** Results of the phylogenetic analyses: A: 50%-majority-rule consensus tree of the analysis based on the matrix of Saucède et al. (2007), which indicates that *Absurdaster* is a stem-group members of the Atelostomata; B: 50% majority-rule consensus tree using Barras' (2007) matrix, which places *Absurdaster* within stem-group holasteroids, albeit with low support. Numbers above branches indicate bootstrap values above 50%, those below indicate Bremer indices above 1 (all other nodes collapse one step away from the shortest tree) respectively the percentage of trees that include the respective node for nodes that are not fully supported in the full set of MPTs.



accompanying character description. The corrected matrix including the scoring for the new taxa is provided in [Appendix 2](#). Analysing the modified matrix with *Absurdaster* added to the analysis results in 1965 MPTs of 53 steps length (CI = 0.547, RI = 0.771, RC = 0.422, HI = 0.453). It differs from the tree published in [Barras \(2007: fig. 13A\)](#) only by placement of *Metaporinus*, *Tithonia* and *Corthya*+*Tetraromania* in an unresolved trichotomy rather than a set of nested clades. The two *Absurdaster* species are placed within the large unresolved clade containing all stem-group holasteroids and stem-group spatangoids. The 50% majority rule tree shows more resolution within that clade and the *Absurdaster* species are rooted as sister taxa to a tithoniid clade to which *Proholaster* forms an outgroup. Bootstrap and Bremer support are almost non-existent. Re-running the analysis under a new weighting scheme (reweighing by RC) results in 33 MPTs of 22.27047 steps length (CI = 0.700, RI = 0.886, RC = 0.620, HI = 0.300). The strict consensus differs from that of [Barras \(2007: fig. 13B\)](#) mainly by the lower resolution within stem-group holasteroids. In the 50% majority rule consensus ([Fig. 11B](#)) the two *Absurdaster* species are again placed as successive outgroups to the tithoniid clade, within stem-group holasteroids (sensu [Barras, 2007](#)), albeit with low support.

The character sets of the two analyses are very different. Since the analysis of [Saucède et al. \(2007\)](#) was originally designed to resolve the radiation of early irregular echinoids, it contains numerous characters that are not relevant for the placement of *Absurdaster*. It does, however, include a number of characters not employed by [Barras \(2007\)](#) which may help to better resolve the divergence of ‘disasteroids’ and stem-group members of the holasteroid and spatangoid clades. Moreover, additional data on some of the taxa included in these two analyses have become available, mainly on *Cyclolampas* ([Saucède et al., 2013](#)) and *Tithonia* ([Gaillard et al., 2011](#)). To better resolve the relationship of *Absurdaster* the taxon set was restricted to forms found to be stem-group atelostomates in the previous analyses. Characters uninformative for this reduced taxon set were excluded, as were duplicate characters. In addition, some of the characters were found to add a considerable amount of noise [e.g., [Barras, 2007](#) character #2 (B2), [Saucède et al., 2007](#) characters #9 and #39 (S9, S39 respectively)]. Because of the way it is defined character B2 performs much worse than S6, although both are basically aimed at the same feature. S9 accounts for the presence of complementary plates between ocular plates I and V. These, however, are apparently highly variable, within genera and possible even species [in some specimens of *Collyrites* complementary plates are sandwiched between the posterior oculars (e.g., [Saucède et al., 2007: fig. 3f](#)), in others the oculars abut each other (e.g., [Kroh and Smith 2010: fig. 9M](#))]. S39 scores for test profile, which is highly variable in the taxon set analysed – globular forms appear in several unrelated clades. Consequently, these three characters (B2, S9 and S39) were omitted. Where necessary character definitions were adapted to fully capture the morphology exhibited by *Absurdaster*. The final character list is provided in [Appendix 1](#). Heuristic analysis of the resulting matrix found 129 MPTs of 61 steps length (CI = 0.574, RI = 0.755, RC = 0.433, HI = 0.426), but revealed problems with the placement some of the taxa (*Cardiolampas*, *Proholaster*, and *Cardiopelta*), caused by the high number of missing scores for the former two. If these two taxa are excluded, the analysis results in a single, fully resolved MPT of 60 steps length ([Fig. 12](#); CI = 0.583, RI = 0.752, RC = 0.439, HI = 0.417). Support values are not high, but much better than for the analyses of the original datasets. Tree topology is largely compatible with that resulting from the analysis of [Barras’](#) matrix, but differs in placement of *Toxaster* and *Heteraster*, which together with *Eoholaster* and *Pseudoholaster* form the sister group of *Absurdaster*. *Disaster* and *Acrolusia*, in contrast to [Barras’s](#) result are thus not members of stem-group Spatangoida, but an early stem-group



**Fig. 12.** Results of the phylogenetic analyses based on the revised matrix: single most parsimonious tree. Conventions as for [Fig. 11](#).

atelostomate side-branch. *Absurdaster* is resolved as very close to the split between spatangoids and holasteroids, but is not referable to either group. Unlike the analysis based on [Saucède et al.’s](#) matrix and in agreement with [Barras \(2007\)](#) the tithoniids are recovered as monophyletic clade and sister to crown-group atelostomates plus *Absurdaster*.

## 6. Discussion

### 6.1. Morphological plasticity in echinoids

The large majority of fossil and extant echinoids follow a very limited number of different designs, which govern the construction of their corona: 1) the cidaroid-type, 2) the echinacean-type, 3) the ‘cassiduloid’ type, 4) the sand-dollar type, and 5) the heart-urchin type. While there are abundant exceptions of this, the general pattern is recognizable in most forms. Three echinoid lineages, however, broke out of this pattern and developed much higher plasticity both in terms of body shape and test construction. The best known among these are the pourtalesiids with their remarkable variety of different forms ranging from standard heart-urchin type forms (e.g., *Spatagocystis*) to highly aberrant vase- to stylus-shaped ones (e.g., *Echinostigma*), in which test construction deviates severely from that of other taxa. Another such group are cardias-terids, in which the *Infulaster-Hagenowia* lineage ([Gale and Smith, 1982](#)) developed profound modifications of the standard holasteroid heart-urchin type test construction.

A similar situation seems to be present in the lineage leading from *Collyrites* via *Cardiopelta* to *Absurdaster*. While the exact relationship of these forms can at present not be reconstructed by cladistics analysis (see above) it is nevertheless easy to derive *Cardiopelta* from *Collyrites* by elongation of the posterior end, anterior displacement of the peristome, development of an incipient frontal notch and loss of complementary plates. Continued progression along these trends leads to the shape of *Absurdaster*, which is distinguished by additional plate loss in the apical disc. These changes could be interpreted as an example of peramorphic evolution leading to a reduction of extraxial elements expressed by less derived forms of the clade. A similar trend has been observed in pourtalesiids ([David, 1990; Saucède et al., 2004](#)).

It is not clear what triggers this sudden appearance of morphological plasticity at different times and in different lineages. It is apparent, however, that this always seems to happen in off-shore mud-bottom environments, possibly because of lower

predation pressure or competition for resources. *Absurdaster*, like *Hagenowia*, however, seems to have been an evolutionary dead end since no younger forms are known that share their particular modified test construction.

## 6.2. *Absurdaster* and the Extraxial-Axial-Theory (EAT)

Mooi et al. (1994) developed a system of skeletal homologies applicable across all echinoderm clades and identified two different types of body wall in echinoderms: axial and extraxial elements. Echinoids represent a special case among echinoderms: while the extraxial skeleton forms a large part of the body in most groups, it is reduced to a minimum in sea urchins: just the genital plates and the periproctal scales (David and Mooi, 1996, 1999).

During the evolution of echinoids the amount of extraxial elements was further reduced: one of the genital plates was lost in the large majority of the irregular echinoids and in a large subset of them genital plate 2 strongly exceeds the size of the remaining genital plates and dominates the apical disc (the monobasal apical disc of cassiduloids and clypeasteroids). In a few groups additional genital plates have been lost: e.g., tithoniids, some representatives of the cardiasterids genera *Infulaster* and *Hagenowia*, and some aeropsids and schizasterids. In pourtalesiids this trend is carried to the extreme, and in the adults of some *Pourtalesia* species only a single genital plate is left (Saucède et al., 2004). The new 'disasteroid' genus described herein had arrived at this condition some 130 Million years before pourtalesiids and took this trend even one step further: unlike most other echinoids the genital pores do not pierce extraxial elements in *Absurdaster*, but have been relocated to the axial plates of the interambulacra, thereby violating one of the axioms of the EAT. This situation is very uncommon, but not unknown in other echinoids, in some species of *Clypeaster* and some fibulariids (e.g., in females of *Echinocyamus bisex* Kier, 1968) the gonopores lie also outside the apical disc, within interambulacral plates. In contrast to the statement of Saucède et al. (2004: p. 152) opening of gonopores in axial elements cannot be considered as a synapomorphy of pourtalesiids only, but evolved independently at least seven different times (*Goniopygus*, pourtalesiids, tithoniids, *Absurdaster*, fibulariids, clypeasterids, and laganids).

In *Absurdaster* the size of the sole remaining genital plate is shrunken to a minimum and is completely covered by madreporic pores. An interpretation of the supernumerary plates between the trivium and bivium as unperforated genitals (see discussion above) would further support the conclusion that the new *Absurdaster* species are members of a peramorphic clade, with *A. hungaricus* being more derived than *A. puezensis*. This is also indicated by the more pronounced trumpet-shape of the periproctal region and loss of complemental plates in *A. hungaricus*. As already suggested by Saucède et al. (2004: p. 153) it seem that further reduction of the extraxial skeleton is severely hampered by the fact that echinoids do not seem to be able to form madreporic pores within axial elements [although there are some rare examples where madreporic pores extend to other apical disc plates, including ocular plate III – e.g., *Plesiohemipneustes revestensis* (Lambert, in Lambert and Thiéry, 1924) see Smith and Wright, 2003: text-fig. 194B; *Hemipneustes pyrenaicus* Hébert, 1875 see Smith and Jeffery, 2000: text-fig. 124B; *Hemipneustes arabicus* Ali, 1989 see Smith, 2004: text-fig. 1F].

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## Appendix A. Supplementary data

Supplementary data related to this article can be found online at <http://dx.doi.org/10.1016/j.cretres.2013.11.013>.