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1 **Reinterpretation of the Enigmatic Ordovician Genus *Bolboporites***
2 **(Echinodermata)**

3

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12

13 **Abstract**

14 *Bolboporites* is an enigmatic Ordovician cone-shaped fossil, the precise nature and systematic affinities of
15 which have been controversial over almost two centuries. For the first time, a wide range of techniques
16 (CT-scan, SEM, cathodoluminescence, XPL, UV epifluorescence, EBSD, FT-IR and XRF spectrometry)
17 were applied to well-preserved specimens of *Bolboporites* from Norway and Russia. Our main finding
18 confirms its echinoderm affinities, as shown by its stereomic microstructure and by the first definitive
19 evidence of its monocrystalline nature. Each cone consists in a single, microporous calcitic crystal with a
20 narrow longitudinal internal canal. These results are combined with all previous data on *Bolboporites* to
21 critically discuss five alternative interpretations of this fossil, namely theca, basal cone, spine, columnal,
22 and holdfast, respectively. The most parsimonious scenario considers *Bolboporites* as an isolated spine,
23 which was articulated in life by a short biserial appendage to the body wall of an unknown echinoderm,
24 possibly of echinozoan affinities.

25

26

27 **Introduction**

28

29 The endoskeleton of echinoderms is a complex, multi-element structure typically consisting
30 of several thousands of individual plates bound together in life by soft tissues (including
31 collagen fibres) and each consisting of monocrystalline calcite. Taphonomic experiments
32 suggest that collagen decays relatively soon after the death of the organism (within days or
33 weeks), thus leading to the collapse and rapid disarticulation of the skeleton into isolated
34 plates and/or sometimes, more resistant modules (Donovan 1991; Brett *et al.* 1997). The
35 assignment of an isolated skeletal element to the phylum Echinodermata is generally
36 straightforward and relies on the presence of a typical three-dimensional meshlike

37 microstructure, the stereom (Smith 1980a; Kouchinsky *et al.* 2012). However, both the
38 potential diagenetic alteration of the stereom and the high morphological disparity of skeletal
39 elements within a same individual (e.g., columnals, holdfast, spines) make it often difficult to
40 identify, and sometimes interpret, such isolated plates, especially in the case of Palaeozoic
41 taxa that have no current representatives (Berg-Madsen 1986; Pisera 1994; Zamora *et al.*
42 2013).

43 The situation is further complicated by the existence of numerous morphological
44 convergences in echinoderms. For example, Palaeozoic deposits have yielded several
45 relatively similar-looking, small, bowl- to cone-shaped structures (e.g., *Cymbionites*
46 Whitehouse, 1941; *Oryctoconus* Colchen & Ubaghs, 1969; *Peridionites* Whitehouse, 1941;
47 *Timorocidaris* Wanner, 1920). Their nature and precise taxonomic assignment (at class level)
48 has often been strongly debated (Bather 1920; Gislén 1947; Schmidt 1951; Ubaghs 1968b,
49 1978a; Smith 1982; Alvaro & Colchen 2002; Seilacher & MacClintock 2005; Zamora *et al.*
50 2009). However, most of them are now convincingly interpreted either as pelmatozoan
51 holdfasts (e.g., *Oryctoconus*; Alvaro & Colchen 2002; Seilacher & MacClintock 2005;
52 Zamora *et al.* 2009), highly specialized columnals (e.g., Sumrall *et al.* 1997), basal thecal
53 plates of eocrinoids (e.g., *Cymbionites*, *Peridionites*; Smith 1982) or highly derived crinoid
54 calices made of few, tightly sutured ('fused') plates (e.g., *Timorocidaris*; Bather 1920;
55 Ubaghs 1978a).

56 On the other hand, the interpretation of some other isolated echinoderm elements remains
57 problematic and controversial. This is the case for the enigmatic Ordovician genus
58 *Bolboporites* Pander, 1830, which corresponds to centimetric cone-shaped calcitic fossils,
59 with a typical honeycomb-like ornamentation on their external lateral surface (Fig. 1B). The
60 base of the cone is smooth, flat to strongly convex, and bears two adjoining, shallow
61 depressions (Fig. 1A). Within this depressed area, a tiny orifice (Fig. 1A) opens into a narrow,
62 longitudinal canal extending internally towards the apex of the cone (Yakovlev 1921;
63 Yeltysheva 1955; Clark & Hofmann 1961; Rozhnov & Kushlina 1994a).

64 *Bolboporites* is particularly widespread and abundant in Baltica, where it is recorded from
65 the Dapingian to the Darriwilian (e.g., Estonia, Russia; Pander 1830; Eichwald 1857; Bassler
66 1911; Yakovlev 1921; Yeltysheva 1955; Smith 1988; Kushlina, 1995, 2007; Federov 2003;
67 Rozhnov & Kushlina 1994a; Rozhnov 2005) and locally to the Sandbian (e.g., Norway,
68 Sweden; Kjerulf 1865; Lindström 1883; Kushlina 1995). This genus also occurs in the late
69 Darriwilian of Laurentia (e.g., New York, Quebec, Virginia; Hall 1847; Billings 1859; Logan
70 *et al.* 1863; Brainerd & Seely 1888, 1896; Miller 1889; Brainerd 1891; Ami 1896; White

71 1896; Ruedemann 1901; Raymond 1905, 1906, 1913; Bassler 1915; Twenhofel 1938; Butts
72 1940; Clark 1944, 1952; Oxley & Kay 1959; Clark & Hofmann 1961; Shaw & Bolton 2011).
73 *Bolboporites* was also reported in the Tramore Limestone Formation of Ireland (Avalonia;
74 Reed 1899), in deposits recently assigned to the late Darriwilian (Wyse Jackson *et al.* 2002).

75 This genus was originally described based on material from the Saint-Petersburg area
76 (Russia) by Pander (1830), who considered that it was closely related to *Dactylopora*
77 Lamarck, 1816 (see also Milne-Edwards & Haime 1851), then interpreted either as a
78 bryozoan or as a foraminiferan, and now assigned to the algae (Dasycladales; see, e.g., Génot
79 & Granier 2011). In North America, the first specimens of *Bolboporites* were reported in
80 Quebec by Hall (1847), who described them as *Chaetetes* Fischer von Waldheim, 1829 (i.e., a
81 genus of hypercalcified sponges; see Stanton *et al.* 2016). This Canadian material was later
82 reidentified as *Bolboporites* by Billings (1859), who interpreted it as a zoophyte. Affinities
83 with anthozoans, and in particular with tabulate corals close to *Favosites* Lamarck, 1816,
84 were frequently suggested for *Bolboporites* (Bronn 1849; Bronn 1851–1856; Eichwald 1857,
85 1860; Fromental 1861; Kjerulf 1865; Zittel 1879; Ruedemann 1901; Butts 1940). Yakovlev
86 (1921) made the first sections through specimens of *Bolboporites*, thus demonstrating the
87 presence of the longitudinal axial canal and internal growth lines. Based on these new
88 observations, he concluded that *Bolboporites* was a highly derived stromatoporoid.

89 Possible echinoderm affinities for *Bolboporites* were first questioned by Logan *et al.*
90 (1863), Quenstedt (1881) and Lindström (1883), based on the observation of stereom
91 microstructure. Miller (1889) interpreted Russian specimens of *Bolboporites* as probable
92 echinoderms, but North American ones as corals. With few exceptions (see above), the
93 assignment of *Bolboporites* to echinoderms was finally accepted by most authors in the late
94 19th century. However, its nature and precise taxonomic affinities remained largely debated
95 and enigmatic (Jaekel 1899; Bassler 1911; Régnell 1956, 1982; Smith 1988). Quenstedt
96 (1881) was the first to point out that the morphology of *Bolboporites* was similar to that of
97 isolated asteroid or echinoid spines. This interpretation was followed by several authors, who
98 interpreted *Bolboporites* as probable spines belonging to various groups of echinoderms:
99 asteroids (Lindström 1883; Yeltysheva 1955; Régnell 1956); echinoids (Wanner 1920); or
100 ‘cystoids’ close to *Palaeocystites tenuiradiatus* (Hall, 1847) (Clarke & Hoffman 1961).

101 An alternative hypothesis was proposed by Ami (1896), who considered that *Bolboporites*
102 was not an isolated spine, but the internal mould of the theca of an unknown ‘cystoid’.
103 Following this interpretation, von Wöhrmann (*in* Jaekel 1899) suggested that *Bolboporites*
104 was possibly the internal mould of a cheirocrinid rhombiferan (see also Régnell 1956). This

105 interpretation of *Bolboporites* as corresponding to the body capsule (theca) of a ‘cystoid’ was
106 further elaborated by Rozhnov & Kushlina (1994a, b), based on the observation of two sets of
107 small skeletal elements articulated into the two depressions on the convex surface of some
108 well-preserved specimens. These two series of plates were interpreted as elements of a single
109 feeding appendage (brachiole), which was inserting onto the convex (oral) surface of a highly
110 derived eocrinoid (Rozhnov & Kushlina 1994a, b; Kushlina 1995, 2006, 2007; Rozhnov
111 2005, 2009). In this interpretation, the central longitudinal canal corresponds to the stem,
112 which was entirely surrounded by massive, fused thecal plates.

113 Recently, the examination by one of us (BL) of numerous individuals of *Coelosphaeridium*
114 Roemer, 1885 (a genus of Ordovician calcareous green algae; see Kato *et al.* 1987; Spjeldnaes
115 & Nitecki 1990; Baarli 2008) from the Sandbian of Norway showed remarkable similarities in
116 size, morphology and external ornamentation with co-occurring specimens of *Bolboporites*
117 from the same levels and localities. This observation thus questioned the echinoderm
118 affinities of *Bolboporites* (Lefebvre 2014, 2017). As a consequence, the aims of this paper
119 were to apply for the first time a wide range of techniques (e.g., cathodoluminescence, CT-
120 scan, FT-IR analyses, SEM, EBSD) on well-preserved specimens of *Bolboporites*, so as to
121 test their putative echinoderm affinities and, if confirmed, to discuss the nature of
122 *Bolboporites* (isolated skeletal element *vs.* body capsule), as well as its systematic position
123 within the phylum Echinodermata.

124

125

126 **Material and Methods**

127

128 **Material.** This study is based on 28 specimens of *Bolboporites* from Norway and Russia. The
129 ten Norwegian specimens were selected within the abundant material of *Bolboporites* sp.
130 (about 100 individuals) belonging to the collections of the Paleontologisk Museum, Oslo
131 (acronym: PMO). All Norwegian specimens of *Bolboporites* were originally collected in 1975
132 by J.F. Bockelie in bioclastic deposits of the Fossum Formation (Sandbian), at Gravastranda,
133 Herøya (Skien-Langesund area, Norway). These levels are generally interpreted as relatively
134 shallow-water deposits yielding abundant and diverse benthic assemblages regularly
135 smothered by storm deposits (Bockelie 1981; Owen *et al.* 1990). The fauna is dominated by
136 brachiopods, bryozoans, echinoderms (caryocystitid and cheirocrinid rhombiferans,
137 eocrinoids, crinoids, edriasteroids) and trilobites, associated to rare cephalopods and
138 graptolites (Bockelie 1981; Owen *et al.* 1990).

139 Eighteen individuals of *Bolboporites mitralis* Pander, 1830, from Russia were made
140 available for this study by S.V. Rozhnov, who donated them to the palaeontological
141 collections of Lyon 1 University (acronym: UCBL). This material was collected on the banks
142 of the Lynna river (Saint-Petersburg area) in the upper member (BII γ , Frizy Limestone) of the
143 Volkhov Formation. This ~3 m thick stratigraphic unit is dated as early Darriwilian, based on
144 the occurrence of both conodonts typical of the *Baltoniodus norrlandicus* Zone and trilobites
145 characteristic of the Scandinavian *Megistaspis simon* Zone (Federov 2003; Dronov 2005).
146 The upper member of the Volkhov Formation consists predominantly of nodular, glauconitic
147 limestones, with several intercalated levels of shales. The bioclastic limestones are generally
148 interpreted as storm-generated deposits, in a shallow-water, temperate setting (Dronov 2005).
149 In these levels, faunal assemblages are dominated by brachiopods, ostracods and isolated
150 pelmatozoan remains, associated to bryozoans, conulariids, graptolites and trilobites (Federov
151 2003).

152

153 **Methods.** As Norwegian specimens are preserved as mouldic impressions in the rock, their
154 original external aspect was revealed by making latex casts, which were coated with
155 ammonium chloride (NH₄Cl) for observation and photographic purposes. External
156 morphological features of *Bolboporites* sp. from Norway were observed at Lyon 1 University,
157 with a Zeiss SteREO Discovery.V8 stereomicroscope binocular and captured with a Zeiss
158 AxioCam MRc5 digital camera.

159 In contrast to the Norwegian material, the Russian specimens are preserved as three-
160 dimensional fossils, thus allowing the application of a wider range of techniques of
161 observation and analyses. Several Russian specimens were embedded in hydrophilic acrylic
162 resin of low viscosity (LR white resin), allowing longitudinal and transverse sections with a
163 Leica SP 1600 saw microtome. Other Russian specimens were set in epoxy resin and cut to
164 make polished thin sections with a thickness of 30 μ m and 130 μ m. Both sections were
165 observed with a Hitachi TM-100 scanning electron microscope (SEM) at the Université de
166 Bourgogne, Dijon, so as to document putative internal structures.

167 Thin sections were observed under plane polarized light (PPL), cross-polarized light (XPL)
168 and epifluorescence UV using a Nikon AZ100 microscope, equipped with a 360 nm exciting
169 source and a Zeiss AxioCam MRc5 (Université de Bourgogne, Dijon). Polished thin sections
170 were also observed under cathodoluminescence using a Leica MZ12 binocular microscope
171 equipped with a Luminoscope ELM-3R device and a Zeiss AxioCam MRc5 camera
172 (Université de Bourgogne, Dijon). Cathodoluminescence (CL) was successfully applied by

173 Gorzelak & Zamora (2013), so as to reveal the internal stereomic microstructure preserved in
174 skeletal elements of various Cambrian echinoderms. This technique was usually shown to be
175 efficient, even in the case of relatively strongly recrystallized specimens.

176 For FT-IR investigations, thin sections were used to extract *in situ* - with the tip of a
177 scalpel blade - small chips of material from different sampling points located both inside the
178 fossil and in the surrounding resin. The extracted materials were then reduced into powders
179 with an agate mini mortar and pestle ($< 10 \mu\text{m}$) and the powder was subsequently analyzed by
180 Fourier transform infrared (FT-IR) spectroscopy, to identify the different mineralogical
181 phases, on a ALPHA FT-IR BRUKER device equipped with an ALPHA-P module. Data
182 acquisition was performed in the $4000\text{-}500 \text{ cm}^{-1}$ wavenumber range (12 scans at a spectral
183 resolution of 4 cm^{-1}), in ATR mode (Attenuated Total Reflectance) with a single reflection
184 diamond crystal adapted to solids. Blank spectra were acquired on resin alone. The qualitative
185 assignment of absorption bands was performed by comparison with known IR spectra found
186 in the literature (Jones & Jackson, 1993).

187 The magnesium content of some Russian specimens of *Bolboporites* was checked with a
188 Bruker S1 Titan spectrometer equipped with a collimated beam and incorporated in a
189 laboratory console. Every measurement consisted of two successive beam phases of 60
190 seconds, with energies of 45 kV and 15 kV. This protocol allows measuring equivalent MgO
191 mass concentrations above 1% in relatively small windows (2 mm in diameter) and directly in
192 the thicker thin sections.

193 The internal structure of one well-preserved *Bolboporites* was also analyzed with electron
194 back-scattered diffraction (EBSD), a technique that permits the characterization of complex
195 polycrystalline materials at nanoscale. In short, it allows measuring and representing - via 2D-
196 coloured maps and pole figures - the crystallographic orientation of individual nanograins
197 with respect to each other. This technique, currently used in materials science, is particularly
198 adapted for calcium carbonate fossil and non-fossil biominerals (Checa *et al.* 2009; Cusack
199 2016). To this end, an embedded sample was manually mirror-polished on $0.05\mu\text{m}$ aluminium
200 oxide powder and further processed on a vibratory polisher. The sample was fixed on a
201 sample holder and analyzed on a JEOL JSM 760 F field emission scanning electron
202 microscope, from which coloured maps were produced, with a step of 250 nm. Measurements
203 were performed at the periphery of the sample and also in different areas of the central zone
204 separated from each other by a few millimeters; this allowed detection of potential
205 crystallographic disorientations at milli-metric scale.

206 Microtomographic observations were performed by using a Bruker CT-scan (Skyscan
207 1174 model) at the Université de Bourgogne, Dijon (Morphoptics Service), to obtain virtual
208 cross-sections through some specimens, and also to reconstruct a three-dimensional model of
209 *Bolboporites*. In recent years, tomography has become a routine technique of imagery, so as
210 to reveal internal structures in various fossils and, in particular, Palaeozoic echinoderms
211 (Sutton *et al.* 2005; Rahman & Clausen 2009; Rahman & Zamora 2009; Rahman *et al.* 2010,
212 2015; Briggs *et al.* 2017). Data acquisition was obtained at 50 kV and 800 μ A. Two images
213 per position (number of frames: 2) were obtained, each of them after an exposure time of
214 2500 ms. The rotation step of the sample was 0.7° and the total acquisition time was 75
215 minutes.

216 Other individuals of *B. mitralis* were kept intact, so as to explore minute details of their
217 external morphology. However, in most specimens, the base of the cone and/or the
218 honeycomb cells on the lateral walls were partly concealed by a thin layer of sedimentary
219 rock. Consequently, fossils were placed in an ultrasonic cleaner containing a solution of dilute
220 ethylenediaminetetraacetic acid (EDTA, 1% wt/vol, pH 8) to remove all pieces of surrounding
221 rock and better expose the external aspect of the specimens. Once cleaned, fossils were rinsed
222 with water, then with ethanol (C₂H₅OH), and finally dried with a hair-dryer. Observation of
223 the external aspect of the specimens was made using both a Zeiss SteREO Discovery.V8
224 binocular stereomicroscope, equipped with a Zeiss AxioCam MRc5 digital camera, at
225 Université Lyon 1, and a Hitachi TM-100 Scanning Electron Microscope (SEM) at the
226 Université de Bourgogne, Dijon.

227 Finally, three dried specimens of the Recent asteroid *Pentacaster mammilatus* (Audouin,
228 1826) were examined and prepared for morphological comparison purposes. This material
229 belongs to the R. Koehler collections, which are part of the zoological collections of Lyon 1
230 University (acronym: UCBL). The specimens were collected between 1895 and 1930 (precise
231 date of sampling not reported on labels) from an unknown locality, possibly in the Red Sea or
232 the western part of the Indian Ocean (Clark & Rowe 1971). Dissection and extraction of some
233 aboral spines was made with a scalpel. Photographs were made with a Nikon D5000 camera
234 in the palaeontological collections of Lyon 1 university (CERESE).

235

236

237 **Results**

238

239 *Chemical and mineralogical analyses.*

240 The FT-IR spectroscopy performed on transverse sections of *Bolboporites mitralis* included
241 in LR white resin generated two contrasting sets of infrared spectra, depending on the position
242 of the sampling points, outside or inside the fossil (Fig. 2). The surrounding LR white resin
243 produced a characteristic reference IR spectrum (Fig. 2B), while infrared spectra obtained in
244 sampling points located within the fossils all showed the three absorption bands that are
245 characteristic of calcite (Fig. 2C-E) at 711-712 cm^{-1} , 871 cm^{-1} , and 1395 cm^{-1} , respectively.
246 This spectrum is clearly distinct from that of aragonite (not shown), characterized by a
247 doublet at 700-713 cm^{-1} and two bands at 858 and 1477 cm^{-1} , in addition to a sharp one at
248 1083 cm^{-1} . No dolomite (identified by absorption bands at 729, 882 and 1441 cm^{-1}) was
249 detected in the central zone, Our data unambiguously showed that the Russian specimens of
250 *Bolboporites* are entirely made of calcite.

251 A slightly more complex infrared spectrum was observed in sampling points located on
252 lateral edges of the fossils, with the three absorption bands typical of calcite, but also some
253 additional minor bands (Fig. 2C, G). Comparison with the 'control' spectrum shows that this
254 signal corresponds to the combination of both calcite and LR white resin infrared spectra,
255 resulting from either the irregular external morphology of the body wall (ornamentation
256 consisting of honeycomb cells), and/or a limited penetration of the resin into micropores and
257 microfractures of the specimens.

258 Finally, a large absorption band of low amplitude in the 3700-3100 cm^{-1} range was
259 observed in one spectrum corresponding to a sampling spot located within the fossil (Fig. 2F).
260 This signal did not result from any contamination from the resin, but more likely
261 corresponded to the vibrations of OH bond, suggesting the occurrence of water, putatively in
262 the form of small fluid inclusions within the calcite.

263 The XRF measurements were made in central and exterior parts of *Bolboporites* sections.
264 Magnesium was only detected, with MgO values between 1 and 5% (mass concentration), in
265 most peripheral parts of the skeleton, where analyzed windows encroach the surrounding
266 sedimentary rock. Close examination of these parts, under SEM and cathodoluminescence
267 (see below) revealed the presence of small dolomite rhombs, thus driving the Mg content. In
268 all other parts of the skeleton, Mg was never found, being below the 1% detection limit. Thus,
269 a low magnesium calcite (LMC) is deduced for their current composition.

270

271 *Microstructures.*

272 Observation of thin sections of *B. mitralis* with a polarizing microscope shows that whole
273 cones are affected by conjugate cleavage planes (Fig. 3A,C), and have a single and right

274 crystal extinction (Fig 3B), typical of monocrystals. This important result is confirmed by our
275 investigations using electron backscattered diffraction (EBSD), the outcome of which is
276 synthesized in Figure 4. When performed on the periphery of the section (Fig. 4A-D), EBSD
277 mapping shows that the crown interface is constituted of a mixture of micritic grains (2 μm or
278 less) surrounding sparitic crystals of about tens to more than 100 microns in diameter (Fig.
279 4B, D) while the upper left corner of the map corresponds to the sample itself, which is
280 symbolized by one unique colour, and is, consequently, monocrystalline. The EBSD mapping
281 performed on the central zone of the sample (Fig. 4E-G) shows that the analyzed area is
282 uniform, with no detectable grain limit. This demonstrates clearly that the structure is
283 monocrystalline. Interestingly, when maps are produced in different central zones distant
284 from each other by few millimetres, one notices a slight change of crystallographic
285 orientation, symbolized by a minor colour change: for example, two zones 1 mm apart (either
286 in X or Y) show a grain orientation spread of about 0.3 - 0.5°. When the distance is larger
287 between two analyzed zones (such as 4 mm between Fig. 4F and G), the disorientation is
288 more important, around 3.73° in the present example. In summary, EBSD mapping confirms
289 that the calcite that constitutes a specimen of *Bolboporites* is monocrystalline, with a very
290 minor and gradual crystalline disorientation at millimetric scale, without any detectable grain
291 limit.

292 Under cathodoluminescence, both transverse and longitudinal sections of *B. mitralis*
293 revealed the same mottled, orange-to-brown luminescent microstructure (Fig. 5C). Orange
294 irregular dots and axes are aligned within a browner sealing calcite crystal, forming a CL
295 pattern usually detected for ancient echinoderm stereoms (e.g., Gorzelak & Zamora 2013).
296 These orange parts probably represent the former porous stereom that has been secondary
297 cemented by a syntaxial brown-luminescent cement. Under XPL and PPL, the same stereom-
298 like microstructure is also detected in some parts of the cones, with the tenuous occurrence of
299 small dark spots aligned along cleavage planes (Fig. 3C). At a larger scale, the stereom of
300 *Bolboporites* exhibits a slightly differentiated, darker, narrow peripheral rim in CL (Fig.
301 5A,B), which probably results either from a diagenetic effect or from a distinct lighter density
302 of the former microstructure. A similar observation was made on virtual cross-sections of *B.*
303 *mitralis* obtained by CT-scan, which show a diffuse peripheral rim, consistently lighter than
304 the darker central part of the fossils (Fig. 6A). In CT-scan imagery, intensity restitution
305 largely depends on the density of the materials. Consequently, the central part of *Bolboporites*
306 is currently made of slightly more porous (less dense) skeleton than the periphery. Views by
307 SEM confirm this deduction, with numerous micropores occurring everywhere in the skeleton,

308 except in its peripheral parts (Fig. 5D), where initial micropores are probably cemented by the
309 diagenetic brown-luminescent calcite. As shown by cathodoluminescence (Fig. 5A-C), the
310 internal canal is also cemented by the brown syntaxial calcite.

311 Finally, contrary to these important observations, no structures have been detected within
312 the cones using UV epifluorescence technique. This is probably due to the absence of
313 fluorescent organic matter within the stereomic calcite microstructure, in probable relation
314 with an intense thermal alteration of the organic matter during the burial history of these
315 Palaeozoic fossils.

316

317 *Internal morphological features.*

318 Sections made through specimens of *B. mitralis* confirm previous reports of a narrow, straight
319 to gently curved, longitudinal canal, extending from the base of the cone towards the apex
320 (Fig. 5A,C; Yakovlev 1921; Yeltysheva 1955; Clark & Hofmann 1961; Rozhnov & Kushlina
321 1994a, b). The observation of this longitudinal canal in all specimens, consistently in the same
322 position, indicates that it corresponds to an original internal structure.

323 In contrast, both transverse and longitudinal sections also demonstrated the presence of
324 additional, randomly distributed tubulars and incurved holes, opening either on the base or on
325 the lateral surface of the cone, and penetrating more or less deeply into it (Fig. 5A,B,D).
326 Optical observations made on thin sections of *B. mitralis* show that these structures are filled
327 by a wackestone to packstone sediment, containing diverse organic fragments (e.g., shell
328 debris, echinoderm skeletal elements) and glauconite grains (Fig. 3). In unprepared Russian
329 specimens (i.e., without ultrasonic cleaning), the nature of this infilling appears to be similar
330 to the surrounding matrix. Consequently, the random distribution of these holes, their variable
331 size and depth, as well as their infilling by sedimentary rock, all indicate that they are not
332 original internal structures, but rather correspond to borings (*Trypanites* isp.) made by
333 unknown drilling organisms. They are morphologically different from the less penetrative,
334 though superficially extensive traces already reported on the basal surface of *B. mitralis*
335 (Kushlina 2006).

336 Apart from the central longitudinal canal and randomly located *Trypanites*-like borings, no
337 other internal morphological macrostructure was apparent in sections of *B. mitralis*.
338 Observations made with a polarizing microscope and EBSD show that each specimen of
339 *Bolboporites* currently consists in a single crystal of calcite (see above). Although the calcite
340 is recrystallized, the diverse observations of an extensive stereom-like microstructure in all
341 parts of a sectioned specimen of *Bolboporites* indicates that each cone was originally a

342 microporous, but unique, monocrystal of calcite, with a central canal forming the unique
343 internal macro-cavity.

344

345 *External morphological features.*

346 Similar external morphological features were observed in all available Norwegian and
347 Russian specimens of *Bolboporites* (Figs 6B,7,8). These features are in good agreement with
348 previous descriptions of the external aspect of *Bolboporites* made on specimens from Baltica
349 (e.g., Yeltysheva 1955; Rozhnov & Kushlina 1994a; Kushlina 1995) and *Laurentia* (e.g.,
350 Clark & Hofmann 1961).

351 Cells on the lateral walls of the cones typically display rounded to hexagonal outlines (Fig.
352 8A) and their diameter decreases in the apical direction (Fig. 7A-C). In contrast, cells located
353 towards the base tend to become larger and more elliptical in shape. Each cell corresponds to
354 a shallow (less than 1 mm deep), gently concave, smooth depression delimited by raised rims,
355 thus forming a characteristic honeycomb pattern on the lateral walls of the cone (Figs 7A-C,
356 8A). After ultrasonic cleaning, SEM observation of Russian specimens revealed the presence
357 of the typical porous, stereomic microstructure on the external surface of the cells (Fig. 8A).
358 No specimens express an orifice at the apex of the cones, thus suggesting that their internal
359 central canal (see above) terminated close to, though not opening at, the apex.

360 The base of the cone is entirely smooth, with the exception of two adjoining circular
361 depressions (or lunules), each surrounded by a low C-shaped ridge (Figs 7D, 8B). These two
362 shallow cavities are not in central positions, but more or less displaced laterally (Fig. 7D).
363 Ultrasonic cleaning of Russian specimens shows that the floor of each depression is gently
364 concave, entirely smooth and displays a well-preserved, porous stereom microstructure (Fig.
365 8B). A small orifice occurs at the junction between the two depressions (Figs 7D, 8B). This
366 opening represents the basal extremity of the internal longitudinal canal (see above). No other
367 conspicuous external morphological structure (e.g., orifice) could be observed on the basal,
368 flat to convex surface of the cones.

369

370

371 **Discussion**

372

373 Cathodoluminescence, applied here for the first time to *Bolboporites*, confirms previous
374 reports of the presence of a former stereomic microporous structure in this fossil (e.g., Logan
375 *et al.* 1863; Lindström 1883; Yeltysheva 1955; Clark & Hofmann 1961). Currently blocked

376 by a diagenetic syntaxial calcite, this microstructure is also detected under SEM and PPL
377 observations. A second important result is that each specimen of *Bolboporites* corresponds to
378 a single, formerly porous, monocrystal of calcite. Taken together, these two points provide
379 definitive evidence for echinoderm affinities. Consequently, overall similarities in shape or
380 ornamentation with algae (e.g., *Coelosphaeridium*), bryozoans, corals or sponges (e.g.,
381 stromatoporoids) are merely superficial.

382 The initial calcite stereom is now entirely cemented and recrystallized into an orange-to-
383 brown luminescent LMC. This low Mg content does not preclude an initial low Mg content
384 that may have been much higher during the formation of this skeletal element, but modified
385 (and lowered) during diagenesis. Such a diagenetic pathway is well documented for most
386 ancient echinoderm stereoms (Gorzalak *et al.* 2016) and for biogenic HMCs in general
387 (Bischoff *et al.* 1993). Despite this recrystallization, the extensive distribution of stereomic
388 microstructure everywhere within the cones suggests that, originally, *Bolboporites* did not
389 contain any internal macro-structure, with the exception of the narrow longitudinal central
390 canal, which opens within the two lunules, on the base of the cone.

391 These results, combined with all available evidence obtained during this study and/or from
392 the literature, make it possible to critically evaluate all plausible interpretations concerning
393 the nature and systematic position of *Bolboporites*. Comparison with other Palaeozoic
394 echinoderm cone-shaped elements suggests that *Bolboporites* can be interpreted in five
395 different ways: (1) internal mould or body wall of a blastozoan theca (by analogy with, e.g.,
396 *Timorocidaris*; Ami 1896; Rozhnov & Kushlina 1994a, b; Kushlina 1995); (2) large
397 infrabasal cone of the body capsule (calyx or theca) of a stemless pelmatozoan (by
398 comparison with, e.g., *Cymbionites*); (3) isolated spine or tuberculated plate of an unknown
399 echinoderm (Quenstedt 1881; Lindström 1883; Wanner 1920; Yeltysheva 1955; Clark &
400 Hofmann 1961); (4) highly modified columnal of a pelmatozoan; and (5) distal holdfast of a
401 stemmed echinoderm ('*Oryctoconus* scenario').

402

403 *Bolboporites* as a theca.

404 In this interpretation, *Bolboporites* represents either the internal mould (Ami 1896; von
405 Wöhrmann *in* Jaekel 1899; Régnell 1956) or the external wall of a blastozoan theca (Rozhnov
406 & Kushlina 1994a, b; Kushlina 1995, 2006, 2007). In blastozoans, the theca was polyplated
407 and entirely made of extraxial skeletal elements (i.e., deriving from the pre-metamorphic
408 larva; David *et al.* 2000; Sprinkle & Guensburg 2001; Nardin *et al.* 2009, 2017). The theca
409 was bearing all main body orifices (anus, hydropore, mouth) and, when present, various kinds

410 of respiratory structures (e.g., epispores, diplopores, rhombs; Kesling 1968; Sprinkle 1973;
411 David *et al.* 2000). In life, the theca housed the main body cavity, which contained all internal
412 organs (e.g., gut; Kesling 1968; Sprinkle 1973; Rahman *et al.* 2015).

413 The interpretation of *Bolboporites* as the internal mould of a blastozoan theca relies on
414 several arguments: (1) its overall morphology is compatible with the cone-shaped aspect of
415 the theca of various blastozoans, such as *Rhopalocystis* Ubaghs, 1963; (2) the honeycomb
416 ornamentation could represent the imprint of thick polygonal thecal plates on the internal
417 mould; (3) the smooth aspect of the basal surface could result from a more finely-plated oral
418 surface; and (4) the lunules could correspond to the imprint left by one (or two) body
419 opening(s). The main problem with this interpretation is that, by definition, the internal mould
420 of a blastozoan theca corresponds to the infilling of this theca by sedimentary rock. This
421 implies that the mineralogical composition of the internal mould should be similar to that of
422 the surrounding rock. However, our results clearly demonstrate that (1) the mineralogical
423 composition of *Bolboporites* is very distinct from that of the surrounding sedimentary rock;
424 and (2) this fossil corresponds to a single echinoderm plate (stereom, monocystal of calcite).
425 Consequently, *Bolboporites* does not represent the internal mould of a blastozoan theca.

426 The second interpretation considers *Bolboporites* as the theca of an eocrinoid blastozoan,
427 preserved either as an external mould (e.g., Norwegian specimens) or as a recrystallised three-
428 dimensional fossil (e.g., Russian material). The main argument supporting this interpretation
429 is the observation of a partially-preserved appendage-like structure inserted onto the lunules,
430 on the smooth basal surface of some specimens from Russia (Rozhnov & Kushlina 1994a, pl.
431 6; Kushlina 2007, pl. 1 fig. 3). When present, this structure occurs consistently in the same
432 location (i.e., perfectly fitting into the lunules), and it always shows a biserial pattern, with
433 two opposite sets of small, thick, semi-circular skeletal elements. A longitudinal groove is
434 running on one side of the appendage, along the suture between the two series of opposite
435 ossicles (see Rozhnov & Kushlina 1994a, pl. 6 fig. 1d). This groove is apparently leading
436 (proximally) into the small orifice located at the junction between the two lunules.

437 This biserial structure was interpreted by Rozhnov & Kuslina (1994a, b) as a feeding
438 appendage (brachiole; see also Kushlina 1995, 2006; Rozhnov 2005, 2009). This
439 identification implies that the groove borne by brachiolar plates probably housed a single ray
440 of the ambulacral system and that, consequently, the mouth was located at the proximal
441 extremity of this ray. The mouth would thus correspond to the small orifice located within the
442 lunule. In their interpretation of *Bolboporites*, Rozhnov & Kushlina (1994a, b) further
443 suggested that: (1) the internal longitudinal canal of *Bolboporites* was probably homologous

444 to the axial canal (lumen) of a pelmatozoan stem, thus implying that the stem was present, but
445 entirely encased within the theca; and (2) all organs (e.g., gut) were not located within the
446 theca, but outside of it, on the smooth surface of the cone.

447 No articulated appendage was preserved in our study material. However, its interpretation
448 as a brachiole is plausible: in echinoderms, axial (ambulacral) flooring plates typically display
449 a comparable biserial, zigzag pattern, resulting from their appearance through ontogeny,
450 alternatively on the left and on the right of a growing ray of the ambulacral system ('ocular
451 plate rule'; David & Mooi 1996, 1999; Mooi & David 1997, 1998, 2008). This identification
452 has several implications: (1) the longitudinal groove borne by the flooring plates is an
453 ambulacral food groove; (2) the orifice located at the proximal extremity of this groove is the
454 mouth; (3) no ambulacral cover plates are apparently present (or preserved) above this
455 groove; and (4) *Bolboporites* possessed one single brachiole. The reduction of the number of
456 feeding appendages is relatively common in Palaeozoic echinoderms. It was documented both
457 in some crinoids (e.g., *Monobrachiocrinus granulatus* Wanner, 1920; Ausich *et al.* 1999) and
458 also in various groups of vagile, epibenthic taxa, such as pleurocystitid rhombiferans (Paul
459 1967; Kesling 1968; Parsley 1970), solutans (Ubaghs 1981; David *et al.* 2000; Lefebvre &
460 Lerosey-Aubril 2018) and stylophorans (Ubaghs 1968a; David *et al.* 2000; Lefebvre 2003).

461 Our results demonstrate that *Bolboporites* corresponds to a single, massive cone-shaped
462 echinoderm skeletal element. This observation has two major implications: if *Bolboporites* is
463 interpreted as the theca of an eocrinoid, then this theca (1) is entirely made of one single plate;
464 and (2) with the exception of the narrow central canal, it does not contain any internal
465 structure. Reduction of the number of plates forming the body capsule is a trend described in
466 various groups of Palaeozoic echinoderms, such as in solutans (e.g., Late Ordovician
467 belemnocystitids from North America; Parsley & Caster 1965; Caster 1968) or in
468 stylophorans (e.g., *Jaekelocarpus* Kolata, Frest & Mapes, 1991 from the Pennsylvanian of
469 Oklahoma; Dominguez *et al.* 2002). Particularly drastic examples of such a reduction in the
470 number of plates can be documented in the calices of several derived, Late Palaeozoic,
471 stemless crinoids, all characterized by convergent, similar-looking cone-shaped
472 morphologies, as, for example, *Agassizocrinus lobatus* Springer, 1926, from the Mississippian
473 of Kentucky (Ettensohn 1975) or *Edriocrinus sacculus* Hall, 1859, from the Lower Devonian
474 of New York (Moore 1978; Seilacher & MacClintock 2005; Herbert & Ettensohn 2018). The
475 stemless Permian crinoid *Timorocidaris* probably represents the most extreme case of
476 reduction in the number of plates, with its bowl-shaped calyx possibly made of a single

477 skeletal element (Ubaghs 1978a; Hess 1999). Consequently, *Bolboporites* could represent a
478 case of convergent acquisition of a single plated body capsule in blastozoans.

479 In all echinoderms, including the most extreme crinoid morphologies, the body capsule
480 always contains an internal cavity housing the viscera. However, our observations show that
481 *Bolboporites* is a massive skeletal element, without any body cavity. If *Bolboporites* was a
482 single-plated theca, then its mouth (i.e., the small orifice located within the lunules, at the
483 proximal extremity of the ambulacral groove) would open into the narrow, distally closed and
484 tapering central canal. This implies that (1) this internal canal cannot be homologous to the
485 axial canal of a stem (in pelmatozoans, the mouth never opens into the stem canal); and (2)
486 the absence of an internal body cavity and of any anal opening both suggest that, from a
487 functional point of view, this interpretation is not valid. The suggestion that soft parts were
488 lying in life over the smooth basal surface of the cone, that is, outside of the theca (see e.g.,
489 Rozhnov & Kushlina 1994a, b), is incompatible with the body plan of the phylum
490 Echinodermata. In all echinoderms, the viscera are always housed within the body capsule,
491 independently of whether it is loosely (e.g., holothurians) or more strongly calcified (most
492 taxa).

493 In summary, our results do not confirm the identification of *Bolboporites* as the theca of an
494 eocrinoid. Although most requirements of this interpretation are plausible (e.g., the biserial
495 pattern of the appendage is similar to that of ambulacral flooring plates; echinoderms with a
496 single feeding appendage did exist, as well as body capsules consisting of a reduced number
497 of elements), this hypothesis has to be rejected, because the implied anatomy would be neither
498 functional (no internal cavity, no viscera, no anus, no hydropore) nor compatible with the
499 echinoderm body plan (extra-thecal viscera, mouth opening into the stem axial canal).

500

501 *Bolboporites* as an *infrabasal cone*.

502 The overall morphology of *Bolboporites* is strongly reminiscent of similar-looking, cone-
503 shaped, massive skeletal elements forming the aboral part of the body capsule in some
504 blastozoans and crinoids. Such aboral (or infrabasal) cones can be made of several tightly
505 sutured plates, as, for example, in *Cymbionites* and *Peridionites*, both from the Cambrian of
506 Australia (Whitehouse 1941; Smith 1982). However, single-plated, massive infrabasal cones
507 have been described in several Cambro-Ordovician eocrinoids (Ubaghs 1963; Clausen 2004;
508 Allaire *et al.* 2017), as well as in some Late Palaeozoic crinoids (Ettensohn 1975, 1980;
509 Seilacher & MacClintock 2005; Webster & Kues 2006). As in *Bolboporites*, massive aboral
510 pelmatozoan cones (plates) also display: (1) a very wide morphological disparity within a

511 same assemblage (see, e.g., Etensohn 1980; Clausen 2004); and (2) a central canal, which is
512 tapering proximally (i.e., towards the apex of the cone) in stemless taxa (e.g., in the
513 Pennsylvanian crinoid genus *Paragassizocrinus* Moore & Plummer, 1940; Etensohn 1980).
514 In contrast, in stemmed taxa, the central canal extends throughout the infrabasal cone and
515 leads proximally into the axial canal of the stem (see, e.g., Ubaghs 1963; Clausen 2004).

516 However, it seems unlikely that *Bolboporites* corresponds to the infrabasal cone of a
517 stemless pelmatozoan. The main difficulty is the smooth aspect of its basal surface: in all
518 pelmatozoans possessing an infrabasal cone, its upper (distal) surface is divided into several
519 concave areas (facets), separated by ridges and corresponding to the insertion of the plates
520 (i.e., basals) belonging to the overlying circlet (Ubaghs 1963; Etensohn 1975, 1980; Clausen
521 2004; Webster & Kues 2006). The absence of such facets in *Bolboporites* implies that its
522 basal surface was not sutured to any overlying plates and, thus, that this fossil does not
523 represent an infrabasal cone. This interpretation is further supported by the strongly convex
524 and particularly high morphology of the basal surface in some specimens of *Bolboporites* (in
525 particular, in *B. americanus* Billings, 1859; see Clark & Hofmann 1961), which is
526 incompatible with the presence of a putative overlying basal circlet. Finally, the biserial
527 appendage articulated to the basal surface of some Russian specimens of *Bolboporites*
528 (Rozhnov & Kushlina 1994a; Kushlina 2007) clearly demonstrates that this surface was not in
529 contact with overlying thecal (or calyx) plates.

530

531 *Bolboporites as a spine*

532 . Spines are highly differentiated, mobile skeletal elements articulated to the body wall of
533 echinoderms (see, e.g., Durham *et al.* 1966; Smith 1980b). Although this character gave its
534 name to the phylum Echinodermata ('spiny skin'), moveable spines indeed occur only in
535 asterozoans, echinozoans (echinoids), edrioasteroids and stylophorans. In asterozoans,
536 echinoids and edrioasteroids, the articulation of spines to the body wall is complex, typically
537 consisting of (1) a concave socket (acetabulum) at the base of the spine; and (2) a
538 corresponding convex ball (mamelon) located at the summit of a tubercle (Durham *et al.*
539 1966; Spencer & Wright 1966; Smith 1980b; Holloway & Jell 1983; Guensburg 1988; Lebrun
540 1998). Attachment and mobility of spines to the body wall are achieved by muscles and/or a
541 ligamentary catch apparatus (Smith 1980b; Lebrun 1998). Spine movements are controlled by
542 nerves, forming either a ring around the tubercle (e.g., in echinoids; Durham *et al.* 1966;
543 Smith 1980b; Lebrun 1998) and/or extending inside the spine itself (e.g., in some ophiuroids;
544 Lebrun 1998). In cornute stylophorans (e.g., chauvelicystids, *Thoralicystis griffei* (Ubaghs,

545 1970)), spines are articulated to various parts of the body wall (proximal aulacophore,
546 supracentral area, thecal margin) by rudimentary balls and sockets (Ubaghs 1970, 1983; Lee
547 *et al.* 2005). In most mitrate stylophorans, the articulation of posterior spines (digital, glossal)
548 consists of complex balls and sockets (e.g., in anomalocystitids; Ubaghs 1968a; Parsley 1991;
549 Ruta & Bartels 1998). In some other taxa (e.g., *Balanocystites primus* (Barrande, 1872)), the
550 posterior spine is connected to the theca by a small column of articulated plates (Lefebvre
551 1999).

552 Spines are thus distinct from spine-shaped tubercles, which are non-articulated (fixed),
553 protruding external structures that can be produced by various elements of the body wall (e.g.,
554 anal plates, calyx or thecal plates, columnals). Tubercles are particularly widespread at
555 phylum-scale. In blastozoans, spine-shaped expansions of thecal plates have been described in
556 aristocystitids (e.g., *Calix sedgwicki* Rouault, 1851; *Lepidocalix pulcher* Termier & Termier,
557 1950; see Chauvel 1941; Makhlof *et al.* 2017), blastoids (e.g., *Thaumatoblastus* Wanner,
558 1924; *Pteratoblastus* Wanner, 1924; see Beaver *et al.* 1968), eocrinoids (e.g., *Rhopalocystis*
559 *havliceki* Chauvel, 1978; see Chauvel & Régnault 1986; Allaire *et al.* 2017) and, to a lesser
560 extent, in glyptocystitids (e.g., *Schizocystis* Jaekel, 1895; Kesling 1968). Strong tubercles also
561 occur in both cinctans (e.g., *Undatacinctus quadricornuta* (Friedrich, 1993); see Smith &
562 Zamora 2009) and solutans (e.g., *Girvanicystis batheri* Caster, 1968; see Daley 1992).
563 Elongate, spine-shaped elements of the body wall also occur in some edrioasteroids
564 (Guensburg 1988), but they are particularly widespread in Palaeozoic crinoids. In this class,
565 such a spiny ornamentation has been described on anal plates (e.g., *Stenopeocrinus* Strimple,
566 1961; *Uperocrinus* Meek & Worthen, 1865; see Ubaghs 1978b; Ausich *et al.* 1999), on
567 brachials (e.g., *Eirmocrinus* Strimple & Watkins, 1969; *Separocrinus* Knapp, 1969; see
568 Moore *et al.* 1978; Ausich *et al.* 1999), on tegmental plates (e.g., *Batocrinus* Casseday, 1854;
569 see Ubaghs 1978b), on calyx plates (e.g., *Calceolispongia* Etheridge, 1915; *Dorycrinus*
570 Roemer, 1854; see Moore *et al.* 1978; Ubaghs 1978b; Brett 1999), and to a lesser extent, on
571 stem elements (e.g., *Aethocrinus moorei* Ubaghs, 1969). Elongate spine-shaped tubercles
572 occur on the proximal brachials of some cornute (e.g., *Reticulocarpos hanusi* Jefferies &
573 Prokop, 1972; *Nanocarpus milnerorum* Ruta, 1999; Jefferies, 1986; Lefebvre 2003) and most
574 mitrate stylophorans (e.g., *Chinianocarpos thoralis* Ubaghs, 1961; *Rhenocystis latipedunculata*
575 Dehm, 1932; Ubaghs 1970; Jefferies 1986; Ruta & Bartels 1998; Lefebvre 2003). Strong
576 spine-shaped skeletal elements are also present on the aboral surface of some Recent
577 oreasterid asteroids (e.g., *Pentaceraster mammilatus*, *Protoreaster nodosus* (Linnaeus, 1758);
578 see Yeltysheva 1955).

579 The cone-shaped morphology of *Bolboporites* is compatible with its interpretation either as
580 an isolated spine or a tuberculated plate of an echinoderm (Quenstedt 1881; Lindström 1883;
581 Wanner 1920; Yeltysheva 1955; Régnell 1956; Clark & Hoffman 1961). Both interpretations
582 imply that (1) the smooth basal surface was facing towards the organism and was either
583 articulated to it (spine) or part of its body wall (tubercle); and (2) the lateral, strongly
584 ornamented walls of the cone were external and directed away from the organism. These two
585 interpretations could explain the wide disparity in size and shape observed in individuals of
586 *Bolboporites* from a same level (Yeltysheva 1955; Clark & Hoffman 1961). Both
587 interpretations would be also in good agreement with the non-random distribution of biofilms
588 produced by encrusting organisms on Russian specimens (Kushlina 2007). When present,
589 thick putative algal-bacterial biofilms are consistently encrusting the lateral sides of
590 *Bolboporites*. They never occur on the smooth, convex surface (Kushlina 2007). This pattern
591 suggests that the biofilms formed when the organism was alive, otherwise biofilms would be
592 present on all surfaces. The distribution of these encrusting biofilms also suggests that the
593 lateral sides of the cones were directly in contact with sea water (i.e., lateral sides were
594 neither buried in the substrate, nor in contact with the body wall). Conversely, the absence of
595 biofilms on the smooth surface supports the view that the basal part of the cones was not
596 exposed to the external medium and, thus, probably in contact with or part of the body wall.

597 As pointed out by Yeltysheva (1955), the overall morphology of *Bolboporites* shows
598 several similarities with the cone-shaped aboral elements of some oreasterid asteroids. For
599 example, the observation and dissection of Recent specimens of *Pentacaster mammilatus*
600 (Fig. 9D,E) showed that a honeycomb pattern is present on the lateral walls of their cone-
601 shaped abaxial tubercles (Fig. 9A). This sculpture, which is similar to that observed in
602 *Bolboporites*, was produced by the thick granulose membrane, which forms the aboral part of
603 the body wall and extends over the cones. However, the dissection of Recent specimens of *P.*
604 *mammilatus* also showed some major morphological differences between *Bolboporites* and
605 oreasterid cone-shaped abaxial elements. The most important one is that the basal surface of
606 oreasterid cones is not smooth and gently convex, but subdivided into several diverging
607 branches (Fig. 9B), connecting the cone with surrounding plates (Fig. 9C). This situation is
608 not unique to oreasterid abaxial cones. All echinoderm spine-shaped tubercles are borne by
609 elements, which are part of the body wall. This implies that tuberculated plates are necessarily
610 in contact with neighbouring skeletal elements and thus always display facets along their
611 sutures. As the basal surface of *Bolboporites* is entirely smooth and does not show any

612 evidence of facets, its interpretation as a putative oreasterid-like cone-shaped element has to
613 be rejected.

614 Finally, although the interpretation of *Bolboporites* as a spine is plausible (cone-shaped
615 morphology, smooth surface in contact with the body wall, wide morphological disparity,
616 encrusting organisms restricted to lateral walls), this hypothesis has implications that can be
617 tested: (1) skeletal evidence supporting an articulation should be present; and (2) soft parts
618 (muscles, ligaments and/or nerves) were very likely involved, too, and should have left some
619 traces. Clearly, the basal surface of *Bolboporites* is entirely smooth and does not show any
620 skeletal evidence suggesting the presence of a socket for articulation onto a putative tubercle
621 on the body wall. Consequently, if *Bolboporites* was a spine, its articulation was different
622 from the most widespread mechanism (balls and sockets) occurring in echinoderms (see
623 above). The only structures occurring on the smooth surface are the two lunules. However,
624 these two concave areas were apparently the place of insertion for a biserial appendage (see
625 discussion above; Rozhnov & Kushlina 1994a; Kushlina 2007). Consequently, if *Bolboporites*
626 was a spine, the small biserial appendage would then have been directed towards the body
627 wall. In the mitrate stylophoran *Balanocystites primus*, a similar-looking short appendage,
628 made of a single column of tiny plates connects the single posterior spine (glossal) to the
629 theca (Lefebvre 1999). By comparison with the situation in *B. primus*, the possibility that
630 *Bolboporites* was a spine, which was connected to the body wall by a short, biserial,
631 articulated appendage cannot be ruled out. If this interpretation is correct, it is thus likely that
632 the smooth aspect of the basal surface of *Bolboporites* is related to the insertion of soft parts
633 (probably muscles or ligaments) on it. Moreover, by analogy with the situation in some
634 ophiuroids (see above; Lebrun 1998), it is then possible to interpret the external longitudinal
635 groove running on the small appendage and extending internally into the central canal of the
636 cone as the probable course of a nerve.

637 The interpretation of *Bolboporites* as a spine is thus plausible and cannot be refuted on
638 available evidence. However, its systematic position remains an open question. The frequent
639 association of *Bolboporites* with skeletal remains of various blastozoans (e.g., cheirocrinids,
640 *Palaeocystites*) questioned the possibility that it could represent isolated spines of one of them
641 (Clark & Hoffman 1961). However, none of the blastozoans found in the same localities as
642 *Bolboporites* in both Baltica and Laurentia shows any evidence suggesting that spines were
643 articulated to its body wall. Indeed, spines are only known in asterozoans, echinozoans,
644 edrioasteroids and stylophorans (see above), thus ruling out any putative blastozoan affinities
645 for *Bolboporites*. The size of *Bolboporites* (from about 2 to 12 mm in height in both North

646 American and Russian specimens; Clark & Hoffman 1961; Rozhnov & Kushlina 1994a)
647 suggests that putative stylophoran affinities are highly unlikely. In this class, the size of the
648 theca is generally comprised between 5 and 30 mm, and it rarely exceeds 30 to 40 mm (e.g.,
649 the largest known mitrate, *Diamphidiocystis drepanon* Kolata & Guensburg, 1979, is about 40
650 mm wide; Lefebvre 1999). The large size and cone-shaped morphology of *Bolboporites* seem
651 to be also incompatible with putative edrioasteroid affinities. When preserved, edrioasteroid
652 spines are consistently consisting of narrow, elongate elements, typically less than 3 mm in
653 length, which were articulated to ambulacral cover plates and/or skeletal elements of the
654 pedunculate zone (Holloway & Jell 1983; Guensburg 1988; Guensburg & Sprinkle 1994).

655 Because of their stratigraphic range and palaeobiogeographic distribution in the
656 Ordovician, asterozoans are more likely candidates: their oldest known representatives have
657 been documented in Lower Ordovician deposits (Thoral 1935; Blake 2013; Jell 2014; Blake
658 & Guensburg 2015), and their presence is recorded in Baltica at least from the Dapingian, i.e.,
659 as early as the oldest known occurrence of *Bolboporites* (Pisera 1994; Hansen *et al.* 2005;
660 Rozhnov 2005; Blake & Rozhnov 2007; Tinn & Ainsaar 2014). However, *Bolboporites*
661 clearly does not show any character supporting its interpretation as an isolated asterozoan
662 spine. The skeletal morphology of Ordovician asterozoans is strongly constrained and, even
663 when preserved as isolated remains, their plates are highly diagnostic (Pisera 1994; Tinn &
664 Ainsaar 2014).

665 Echinozoans possibly appeared and diversified in Baltica during the Middle Ordovician,
666 before spreading to Laurentia in Late Ordovician times (Reich 1999; Smith & Savill 2001;
667 Lefebvre *et al.* 2013). Baltica has yielded the oldest known occurrences of echinoids
668 (Darriwilian; Bockelie & Briskeby 1980; Pisera 1994), holothurians (Darriwilian; Reich
669 2010) and ophiocistioids (Dapingian; Reich 2001; Rozhnov 2005; Reich & Smith 2009). The
670 stratigraphic range and palaeobiogeographic distribution of echinozoans are thus compatible
671 with those of *Bolboporites*. However, the presence of typical tubercles in the oldest known
672 echinoids (including the isolated plates record; Pisera 1994) suggests the existence of
673 mechanisms for spine articulation comparable to those occurring in younger taxa (i.e., balls
674 and sockets). Putative echinoid affinities are thus unlikely for *Bolboporites*. Although spines
675 have not been documented so far in holothurians and ophiocistioids, it cannot be entirely
676 excluded that *Bolboporites* corresponds to isolated spines of a yet unknown primitive
677 echinozoan.

678

679 *Bolboporites* as a columnal.

680 The general aspect of *Bolboporites* reminds in some respects the cone-shaped morphology of
681 some late Cambrian–Early Ordovician pelmatozoan columnals from Utah (Sumrall *et al.*
682 1997) and Spain (Zamora *et al.* 2009), and thus questions its possible identification as a
683 highly differentiated stem plate. This interpretation is in good agreement with (1) the
684 existence of a longitudinal internal canal; (2) the articulation of a biserial appendage on its
685 basal surface (Rozhnov & Kushlina 1994a; Kushlina 2007); and (3) the morphology of the
686 lunules. The biconcave depressed area formed by the lunules, as well as the presence of a tiny
687 orifice opening in between them are morphological features which are reminiscent of
688 synarthrial articulations in crinoids (Ubaghs 1978a; Donovan 1988; Ausich *et al.* 1999).
689 Interestingly, synarthrial articulations were present on the distal columnals of some
690 Ordovician crinoids (e.g., *Ristnacrinus* Öpik, 1934) co-occurring with *Bolboporites* in Baltica
691 (Donovan 1984).

692 It seems, however, difficult to interpret *Bolboporites* as a highly differentiated, massive
693 columnal for several reasons. First, in all pelmatozoan echinoderms, columnals display
694 articulatory facets on their two opposite (proximal and distal) sides, whereas *Bolboporites*
695 would display only one facet (i.e., on its basal surface). A second difficulty is that columnals
696 always display a central canal (lumen), which opens on their two opposite sides: such a canal
697 is present in *Bolboporites*, but it is not in central position and, more importantly, it opens only
698 on one side. Finally, the strongly convex morphology of the basal surface in many North
699 American specimens of *Bolboporites* (see Clark & Hofmann 1961) makes their interpretation
700 as columnals highly improbable.

701

702 *Bolboporites as a holdfast.*

703 Holdfasts are anchoring structures occurring at the distalmost extremity of the stem in
704 various blastozoans and crinoids (Ubaghs 1972, 1978a; Brett 1981; Ausich *et al.* 1999;
705 Seilacher & MacClintock 2005). The massive, cone-shaped morphology of *Bolboporites*
706 shows many similarities with similarly-shaped, isolated pelmatozoan elements (e.g.,
707 *Oryctoconus*), generally interpreted as holdfasts (Colchen & Ubaghs 1969; Alvaro & Colchen
708 2002; Seilacher & MacClintock 2005; Zamora *et al.* 2009). The identification of *Bolboporites*
709 as a putative discoidal holdfast was discussed, but rejected by Rozhnov & Kushlina (1994a).
710 Their main argument was that, if this fossil was a holdfast, its basal surface would then be
711 attached (fixed) to the substrate: this orientation is incompatible with the presence of an
712 appendage articulated to the basal surface of *Bolboporites*. However, it should be stressed that
713 this base-down orientation occurs only in the case of pelmatozoan discoidal holdfasts tightly

714 and permanently encrusted on firmgrounds and hardgrounds (Ubaghs 1978a; Brett 1981;
715 Brett *et al.* 1983; Sumrall *et al.* 1997; Rozhnov 2002). The opposite (base-up) orientation of
716 the cone is observed in most pelmatozoans living on soft substrates and using their distal
717 holdfasts as an anchor or a grapnel, as, for example, the Ordovician eocrinoid *Balantiocystis*
718 Chauvel, 1966, and the Devonian crinoid *Ancyrocrinus* Hall, 1862 ('kite strategy'; Ubaghs
719 1972; Brett 1981; Le Menn 1985; Ausich *et al.* 1999; Alvaro & Colchen 2002; Seilacher &
720 MacClintock 2005; Zamora *et al.* 2009).

721 All above-listed arguments agreeing with the interpretation of *Bolboporites* as a columnal
722 remain valid if this fossil is interpreted as a discoidal terminal holdfast (i.e., internal canal;
723 biserial appendage inserted into the basal surface; lunules forming a facet with a synarthrial-
724 like articulation). However, if *Bolboporites* is a holdfast, the various issues raised for its
725 interpretation as a columnal are no longer problematic: it then makes sense that (1) a single
726 facet is present (on the basal surface); (2) the internal canal does not open distally into the
727 apex of the holdfast; and (3) the inflated morphology of the basal surface in some specimens
728 of *B. americanus* is not incompatible with their interpretation as distal holdfasts. Moreover,
729 the wide morphological disparity observed between specimens of *Bolboporites* from a same
730 level (Clark & Hofmann 1961; Kushlina 1995) is also in good agreement with its
731 interpretation as a holdfast: similar large variabilities in shape have been reported in
732 assemblages of, for example, *Oryctoconus* and grapnel-like holdfasts of *Ancyrocrinus* (Le
733 Menn 1985; Alvaro & Colchen 2002; Zamora *et al.* 2009). Finally, this interpretation is also
734 compatible with the occurrence of *Bolboporites* in deposits corresponding to shallow, storm-
735 generated deposits (see above; Clark & Hofmann 1961; Bockelie 1981; Dronov 2005). In
736 such environmental conditions, stemmed echinoderms and their anchoring structures are
737 generally preserved separately (Brett 1981). Organisms were detached from their anchoring
738 structures probably by autotomy rather than breakages and transported away by storm
739 currents, whereas their holdfasts were preserved in situ (Donovan 2012). Apart from some
740 rare exceptions, such as the eocrinoid *Balantiocystis* or the crinoid *Ancyrocrinus* (Ubaghs
741 1972; Le Menn 1985; Ausich *et al.* 1999), the distalmost part of the stem is unknown in most
742 pelmatozoans and, conversely, most holdfasts cannot be assigned to any specific taxa (e.g.,
743 *Aspidocrinus scutelliformis* Hall, 1859, *Oryctoconus*; Ubaghs 1978a; Brett *et al.* 1983;
744 Sumrall *et al.* 1997; Alvaro & Colchen 2002; Seilacher & MacClintock 2005; Zamora *et al.*
745 2009).

746 The interpretation of *Bolboporites* as a discoidal holdfast has also several implications, that
747 can be tested: (1) the biserial appendage inserting on the lunules would thus probably

748 correspond to the distal-most columnals of a pelmatozoan stem; and (2) if *Bolboporites* was
749 used as an anchor, it was thus at least partly buried into the sediment. If *Bolboporites* was a
750 distal holdfast, the presence of two lunules in all specimens suggests that a dimeric stem was
751 articulated to it. This interpretation is further supported by the observation of a biserial
752 appendage in at least some better preserved individuals from Russia (Rozhnov & Kushlina
753 1994a; Kushlina 2007). Although most Ordovician pelmatozoans possessed holomeric stems
754 (i.e., formed by a single column of plates), tetra-, penta- and hexameric appendages have been
755 also described in several crinoids (e.g., *Aethocrinus moorei*, *Ramseyocrinus* Bates, 1968;
756 Ubaghs 1969, 1983; Donovan 1984, 1985), as well as in some echinosphaeritid and
757 hemicosmitid blastozoans (Jaekel 1899; Bockelie 1981, 1982; Parsley 1998). Dimeric distal
758 stems are the rule in Ordovician solutans (Caster 1968; Ubaghs 1970; Lefebvre *et al.* 2012;
759 Noailles *et al.* 2014). Although they possibly retained an attached post-metamorphic stage,
760 Ordovician solutans were vagile and their stem did not possess any distal discoidal holdfast.
761 With the exception of solutan elements, only few occurrences of tri- and dimeric columnals
762 were documented in Ordovician deposits, and all of them have been assigned to crinoids
763 possibly related to *Ectenocrinus* Miller, 1889 (e.g., Donovan 1985). Consequently, the
764 existence of Ordovician pelmatozoans with a stem comprising dimeric columnals supports the
765 identification of *Bolboporites* as a possible distal holdfast articulated to a biserial appendage.

766 However, contrary to the situation in all echinoderm stem-like appendages, the biserial
767 structure articulated to the basal surface of *Bolboporites* does not contain any lumen (internal
768 central canal), but an external groove (Rozhnov & Kushlina 1994a). This external groove,
769 which probably housed soft parts, communicates with the longitudinal internal canal of
770 *Bolboporites*. In all stemmed echinoderms, the lumen contains coeloms associated with the
771 extraxial part of the body wall (i.e., somatocoels) and, generally, extensions of the nervous
772 system (Ubaghs 1978a; Heinzeller & Welsh 1994; David *et al.* 2000; Mooi & David 2008).
773 The topology observed in *Bolboporites* and its associated appendage thus strongly departs
774 from the situation in pelmatozoan stems (external vs. internal soft parts). This implies that the
775 biserial structure articulated to *Bolboporites* cannot be interpreted as (part of) a stem-like
776 appendage and, consequently, that *Bolboporites* was not a distal holdfast. This conclusion is
777 confirmed by the distribution of biofilms produced by encrusting organisms over the body
778 wall of *Bolboporites* (see above; Kushlina 2007). If this fossil was a discoidal terminal
779 holdfast, comparison with similar structures in pelmatozoans (Ausich *et al.* 1999; Seilacher &
780 MacClintock 2005) suggests that in life, a large part of the cone would have been at least
781 partly buried into and/or in permanent contact with the substrate. This life orientation is not

782 compatible with the observed distribution of epibionts, which produced extensive films on the
783 lateral walls of *Bolboporites*, but are absent from its basal surface (Kushlina 2007).

784 Consequently, although the interpretation of *Bolboporites* as a discoidal distal holdfast is
785 plausible (e.g., massive cone-shaped morphology, wide morphological disparity, articulation
786 to a dimeric appendage; see above), this identification has to be rejected because the structure
787 articulated to its basal surface is not a stem-like appendage (no lumen, external groove
788 housing soft parts). Further, the implied life orientation is not confirmed by the distribution of
789 epibionts on the cones.

790

791

792 **Conclusions**

793

794 Our results not only confirmed the presence of stereomic microstructure in *Bolboporites* (and
795 thus its echinoderm affinities), but they also showed that this fossil is a single, previously
796 microporous, calcitic skeletal element, without any internal macrostructure, except a narrow
797 longitudinal canal opening through a tiny orifice on the basal surface. These results combined
798 with all previous descriptions of *Bolboporites* have made it possible to critically discuss
799 several hypotheses about its nature (e.g., theca, basal cone, spine, columnal, holdfast) and its
800 putative affinities within echinoderms (e.g., asterozoans, blastozoans, crinoids, echinozoans,
801 stylophorans). Most interpretations could be rejected, because they comply with only part of
802 available evidences. Although the identification of *Bolboporites* as a spine remains
803 questionable, it represents the most parsimonious - and likely - interpretation. The precise
804 affinities of *Bolboporites* remain difficult to assess and it is tentatively assigned here to an
805 unknown, possibly basal echinozoan. As this was the case for other problematic fossils (e.g.,
806 conodonts, machaeridians), future discoveries of fully articulated specimens showing
807 *Bolboporites* elements in connection with their host organism will probably help in revealing
808 their actual nature and affinities within echinoderms.

809

810

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812

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834

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836 **References**

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1311 **Figure Captions**

1312

1313 **FIGURE 1.** External morphology of *Bolboporites uncinatus* Pander, 1830, Middle
1314 Ordovician (Dapingian), Saint-Petersburg area, Russia; redrawn and modified from Rozhnov
1315 & Kushlina (1994a, fig. 3b) and Kushlina (1995, pl. 5 fig. 1b). A: Base of the cone, in front
1316 view, showing the two adjoining depressed areas (lunules), and the small orifice
1317 corresponding to the outlet of the longitudinal internal canal. B: Lateral view, showing the
1318 typical honeycomb ornamentation on lateral sides of the cone.

1319

1320 **FIGURE 2.** Fourier transform infrared (FT-IR) spectroscopy made on transverse sections of
1321 *Bolboporites mitralis* Pander, 1830, included in LR white resin; UCBL-FSL 712510, Middle
1322 Ordovician (Dapingian), Saint-Petersburg area, Russia. A: Location of FTIR analyses. B: IF
1323 spectrum of LR white resin (control spectrum). C, G: IF spectra of sampling points located on
1324 the external margin of the specimen (calcite). D-F: IF spectra of sampling points within the
1325 specimen (calcite). Peak values indicated in cm^{-1} .

1326

1327 **FIGURE 3.** Thin section views of *Bolboporites mitralis* Pander, 1830 (Middle Ordovician
1328 (Dapingian), Saint-Petersburg area, Russia; UCBL-FSL 712510) included in the surrounding
1329 sedimentary rock (ss) which is a packstone-wackestone with bioclasts and glauconite grains.
1330 A: Plane-polarized optical light, showing the conjugated cleavage planes (cp) crosscutting the
1331 whole cone. B: Cross-polarized optical light, showing total extinction of the cone. C: Close up

1332 view of A and B (plane polarized light) revealing the tenuous dark-brown patches aligned
1333 along cleavage planes, forming a stereom-like structure.

1334

1335 **FIGURE 4.** EBSD mapping of *Bolboporites mitralis* Pander, 1830; Middle Ordovician
1336 (Dapingian), Saint-Petersburg area, sample UCLB-FSL 712510, cross section, perpendicular
1337 to the cone axis. A: Periphery of the sample observed by SEM. B: corresponding EBSD map,
1338 showing the size heterogeneity of the crystals around the monocrystalline structure; the box
1339 on the down right corner gives the color code for crystallographic axes. C: another peripheral
1340 zone, at higher magnification. D: corresponding EBSD map. E: central zone of *B. mitralis*
1341 visualized by SEM. F and G: two EBSD maps of two areas of the central zone (E) 4 mm
1342 apart. Although the structure is fully monocrystalline on the whole cross-section (no grain
1343 limit detectable), a slight variation of the colour indicates a tiny crystallographic
1344 disorientation ($< 4^\circ$).

1345

1346 **FIGURE 5.** Internal structures of *Bolboporites mitralis* Pander, 1830; Middle Ordovician
1347 (Dapingian), Saint-Petersburg area, Russia. A-C: Cathodoluminescence view of sectioned
1348 *Bolboporites mitralis* Pander, 1830; Middle Ordovician (Dapingian), Saint-Petersburg area,
1349 Russia. A: Longitudinal section through specimen UCBL-FSL 712508, with several randomly
1350 distributed *Trypanites*-like borings (bor) through the body wall. B-C: Cross section through
1351 specimen UCBL-FSL 712510, showing evidence of narrow longitudinal axial canal (int.
1352 canal). B: General view of the sectioned specimen. C: Detail showing the central internal
1353 canal filled with a syntaxial blocky calcite cement (sbc). The surrounding skeleton reveals a
1354 stereom-like structure with aligned luminescent inclusions; specimen UCBL-FSL 712510 D:
1355 This SEM view shows the opening part of a tubular boring crosscutting the stereom-like
1356 microstructure of a *Bolboporites* cone (UCBL-FSL 712508). Note this stereom-like
1357 microstructure is highly cemented near the walls of the boring and at the periphery of the
1358 cone, whereas micropores (mp) are presents in the more internal parts. This boring is partially
1359 filled with a bioclastic and glauconitic packstone (gp) that also surround the cone. More
1360 internal parts of the boring are cemented by dolomite rhombs (dol) and by a syntaxial blocky
1361 calcite cement (sbc).

1362

1363 **FIGURE 6.** CT-scan imagery of *Bolboporites mitralis* Pander, 1830; UCBL-FSL 712509
1364 Middle Ordovician (Dapingian), Saint-Petersburg area, Russia. A: Virtual cross section
1365 showing diffuse peripheral rim, made of denser (less porous) stereom than central part of the

1366 cone, as also shown on SEM imagery (Fig 5B). This view is reminiscent, in part, to a section
1367 through a cidaroid spine (see, e.g., Donovan 2018). Lateral honeycomb cells appear clearly on
1368 external margin of peripheral rim. B: Three-dimensional reconstruction of the specimen, with
1369 line indicating location of cross section in A.

1370

1371 **FIGURE 7.** External aspect and morphological disparity of *Bolboporites*; all specimens from
1372 same locality and level, Upper Ordovician (Sandbian), Skien-Langesund area, Norway. A:
1373 *Bolboporites* sp., lateral side of the cone showing honeycomb ornamentation, and almost flat
1374 base of the cone; PMO 116887. B: *Bolboporites elongatus* Kushlina, 1995, narrow cone in
1375 lateral view, with gently convex base; PMO 218238. C-D: *Bolboporites* cf. *mitralis* Pander,
1376 1830; PMO 218249. C: Wide cone in lateral aspect, with convex base. D: Basal surface with
1377 two lunules in almost central position, and small orifice at their junction.

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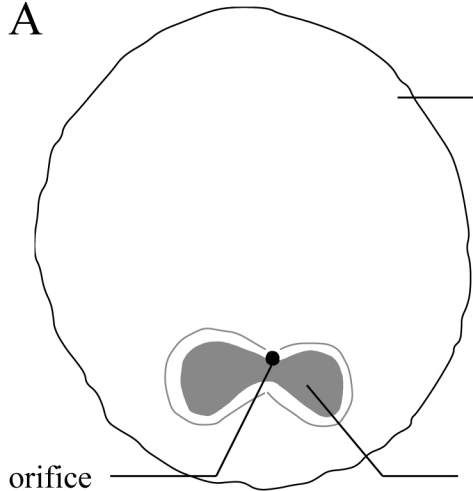
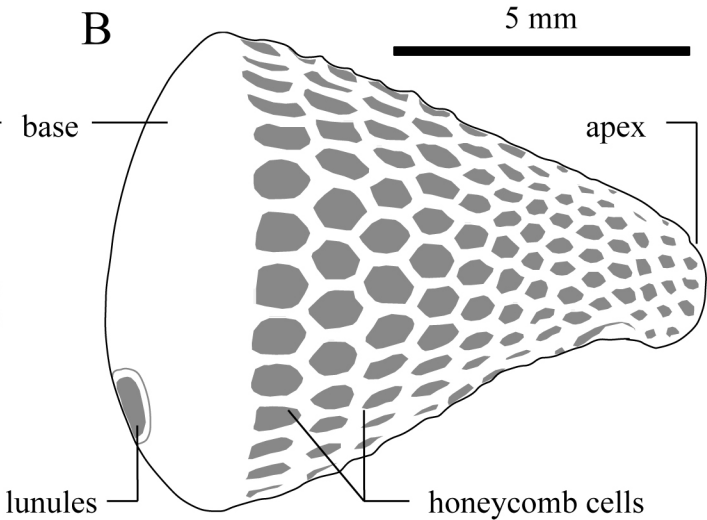
1379 **FIGURE 8.** External morphology of *Bolboporites mitralis* Pander, 1830; Middle Ordovician
1380 (Dapingian), Saint-Petersburg area, Russia. A: Cells forming honeycomb ornamentation on
1381 lateral sides of the cone; SEM view of specimen UCBL-FSL 713254. B: Lunules and
1382 associated small orifice, on the base of the cone; SEM view of specimen UCBL-FSL 713250.
1383 Note also the well-preserved stereom-like microstructure that appears on the wall of these
1384 lunules.

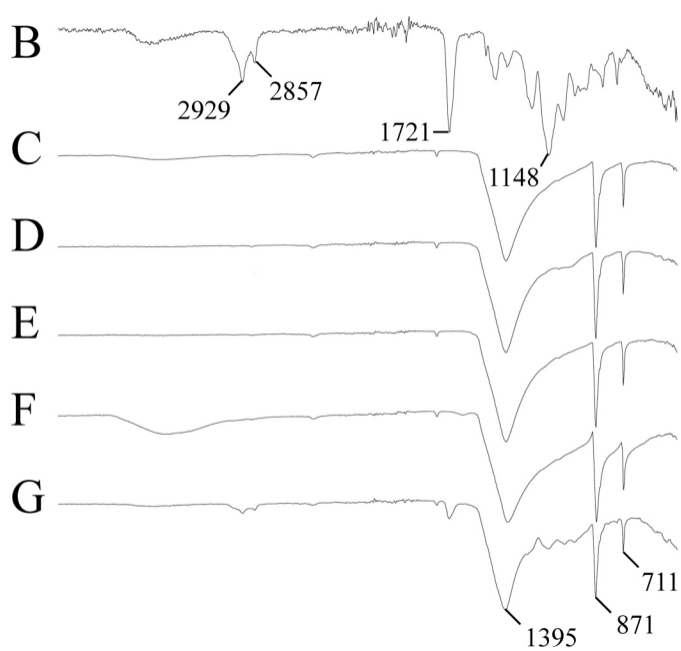
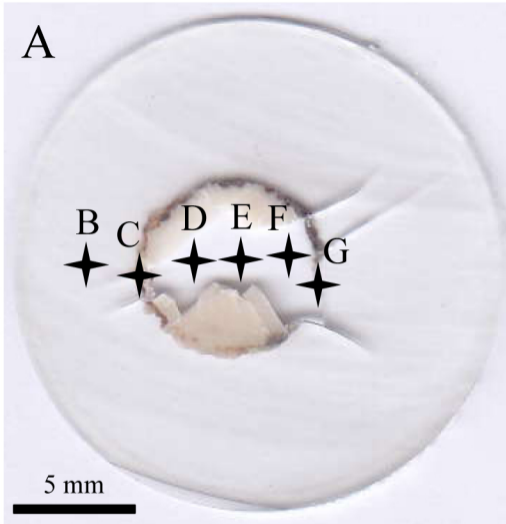
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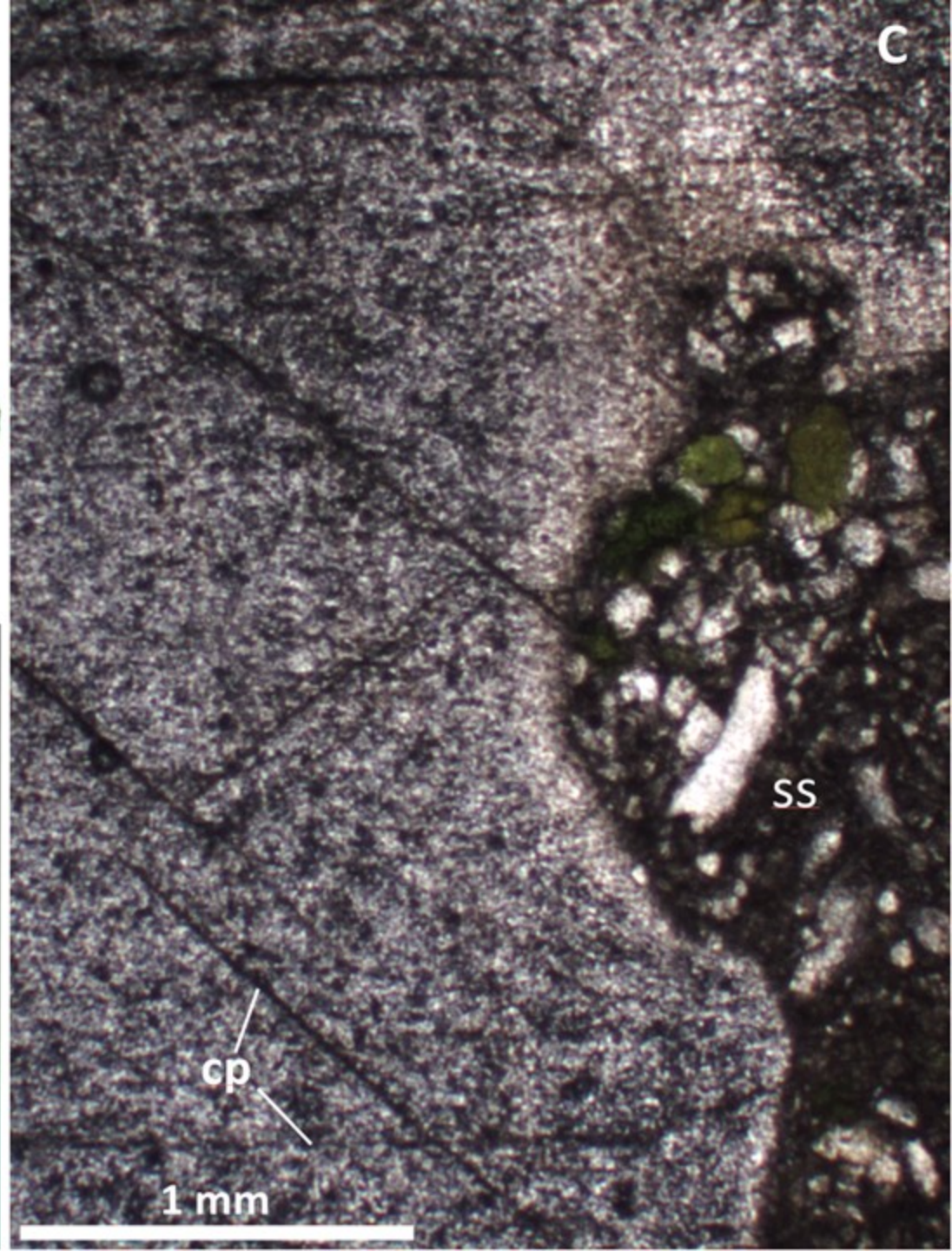
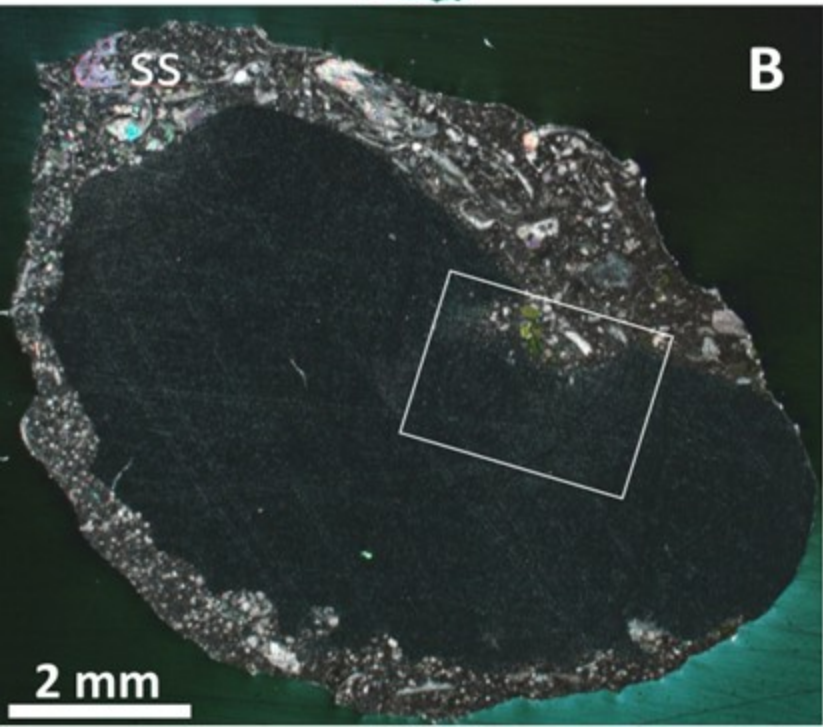
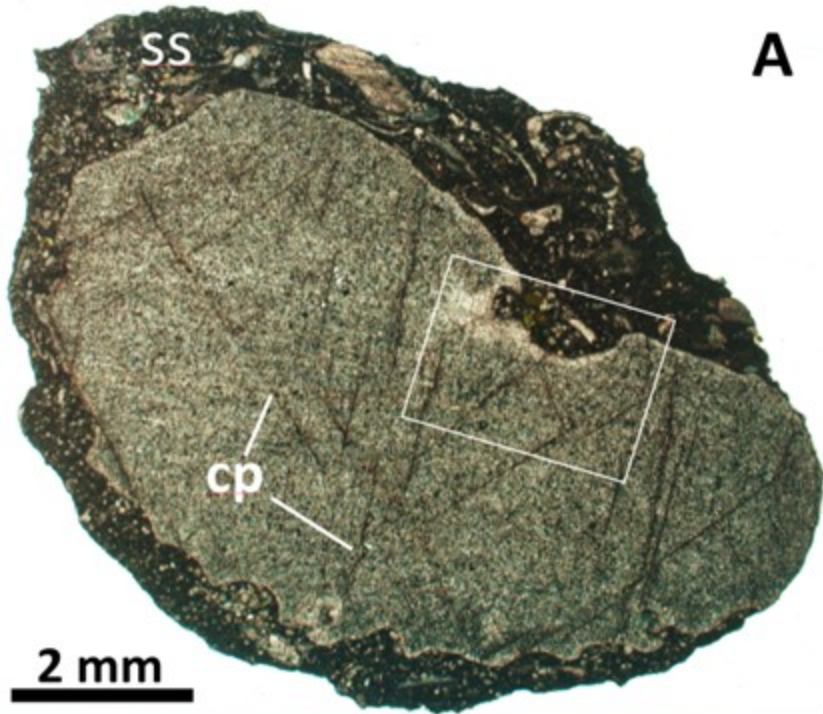
1386 **FIGURE 9.** Aboral tubercles of the Recent oreasterid asteroid *Pentaceraster mammilatus*
1387 (Audouin, 1826). A: Extracted tubercle in lateral view, with its lateral walls covered by thick,
1388 polyplated, granulose aboral membrane; specimen UCBL.2017.01.44. B-E: Specimen
1389 UCBL.2017.01.47. B: Extracted tubercle in oblique view, with its basal surface showing
1390 several diverging branches, connecting it with surrounding aboral plates. C: Cross-section of
1391 extraction site of tubercle shown in (B), on the aboral surface, showing complex articulation
1392 of tubercle-bearing plate with surrounding aboral skeletal elements. D: General view of aboral
1393 surface. E: Close-up of aboral surface showing area of extraction of the spiny tubercle.

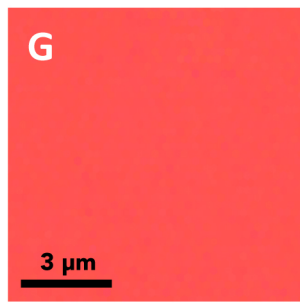
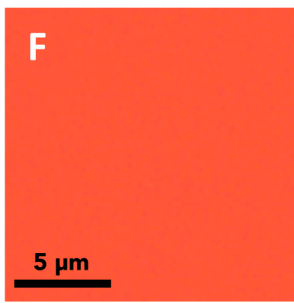
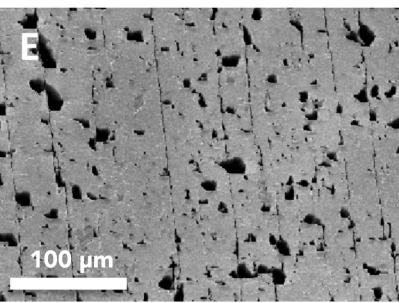
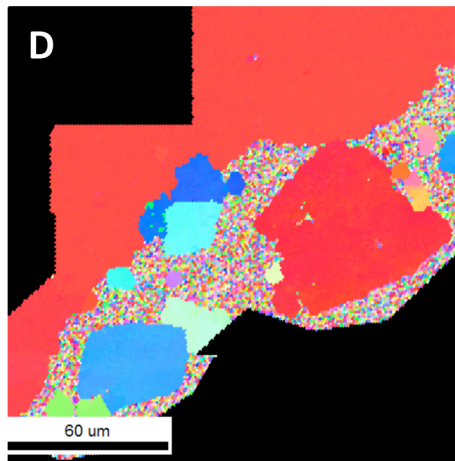
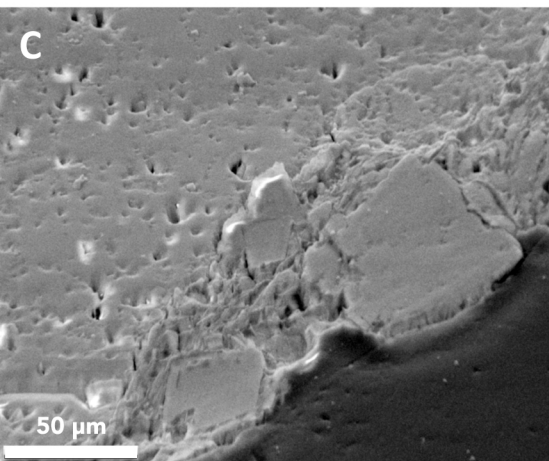
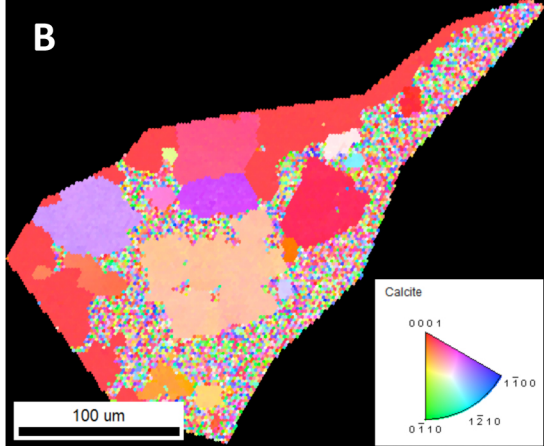
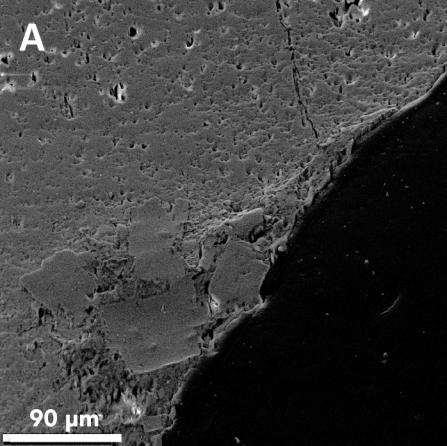
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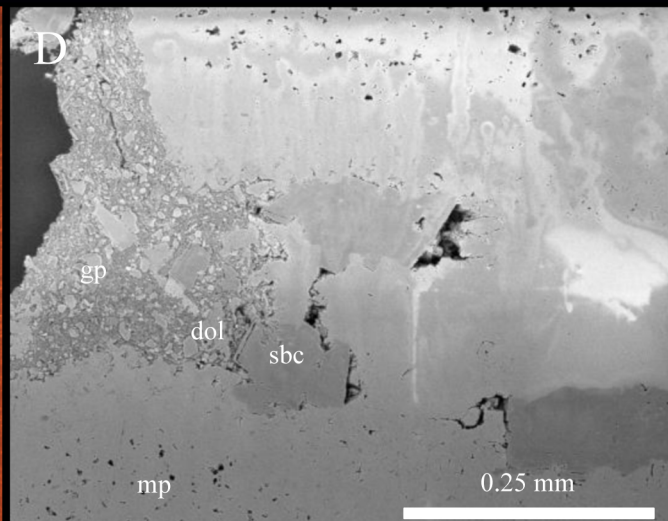
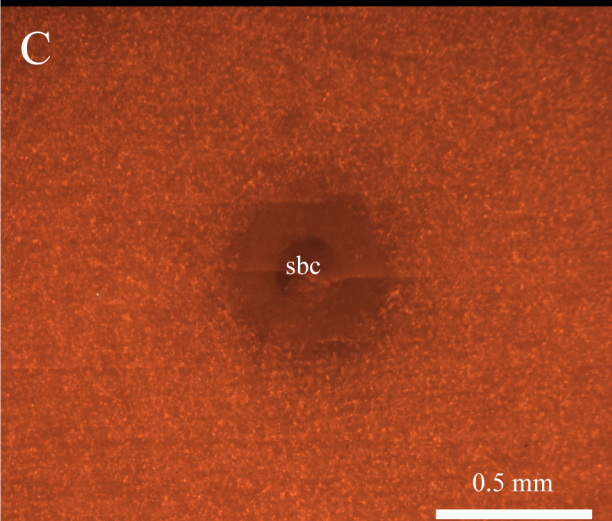
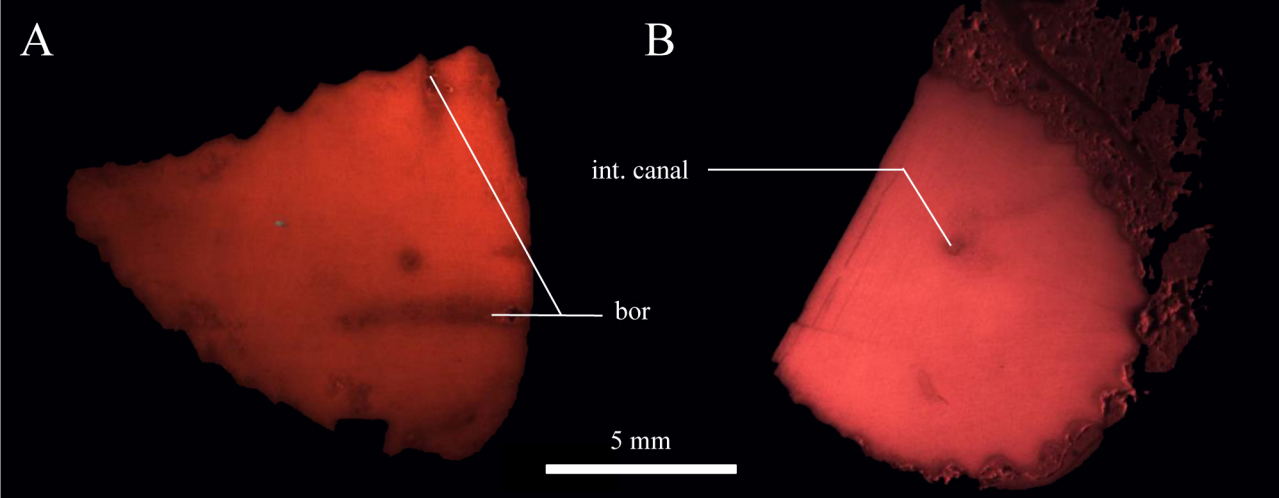
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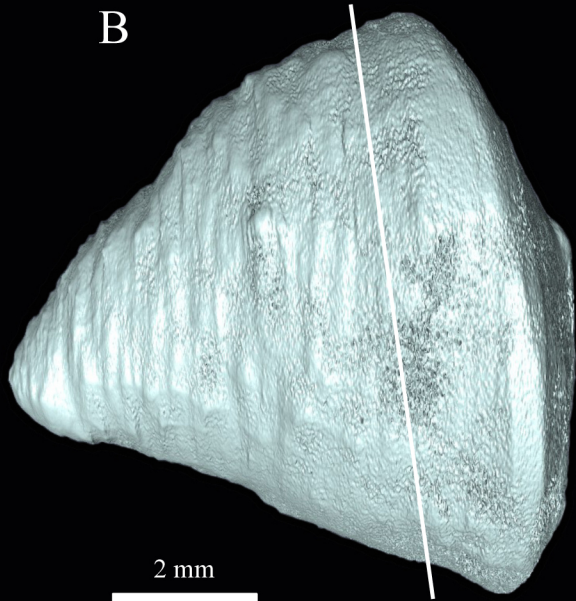
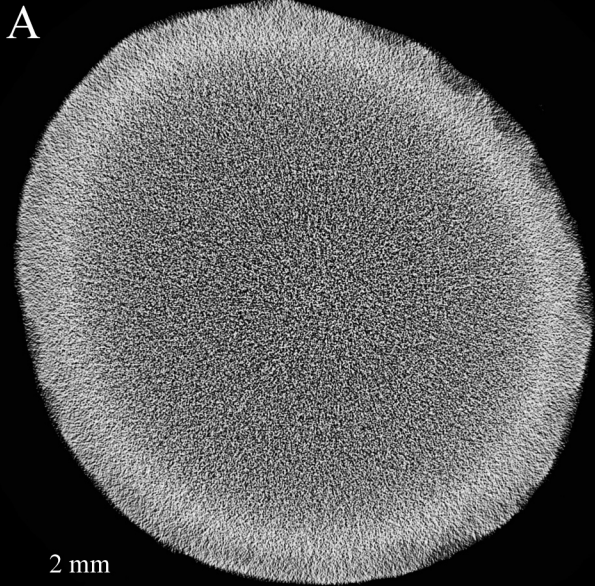
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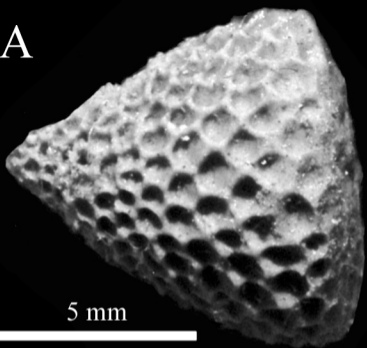
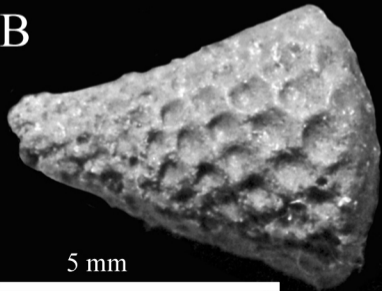










A**B****C****D**

