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Reinterpretation of the enigmatic Ordovician genus *Bolboporites* (Echinodermata)

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Abstract

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

Introduction

The endoskeleton of echinoderms is a complex, multi-element structure typically consisting of several thousands of individual plates bound together in life by soft tissues (including collagen fibres) and each consisting of monocrystalline calcite. Taphonomic experiments suggest that collagen decays relatively soon after the death of the organism (within days or weeks), thus leading to the collapse and rapid disarticulation of the skeleton into isolated plates and/or sometimes, more resistant modules (Donovan 1991; Brett *et al.* 1997). The assignment of an isolated skeletal element to the phylum Echinodermata is generally straightforward and relies on the presence of a typical three-dimensional meshlike microstructure, the stereom (Smith 1980a; Kouchinsky *et al.* 2012). However, both the potential diagenetic alteration of the stereom and the high morphological disparity of skeletal elements within a same individual (e.g., columnals, holdfast, spines) make it often difficult to identify, and sometimes interpret, such isolated plates, especially in the case of Palaeozoic taxa that have no current representatives (Berg-Madsen 1986; Pisera 1994; Zamora *et al.* 2013).

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

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derived crinoid calices made of few, tightly sutured ('fused') plates (e.g., *Timorocidaris*; Bather 1920; Ubaghs 1978a).

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

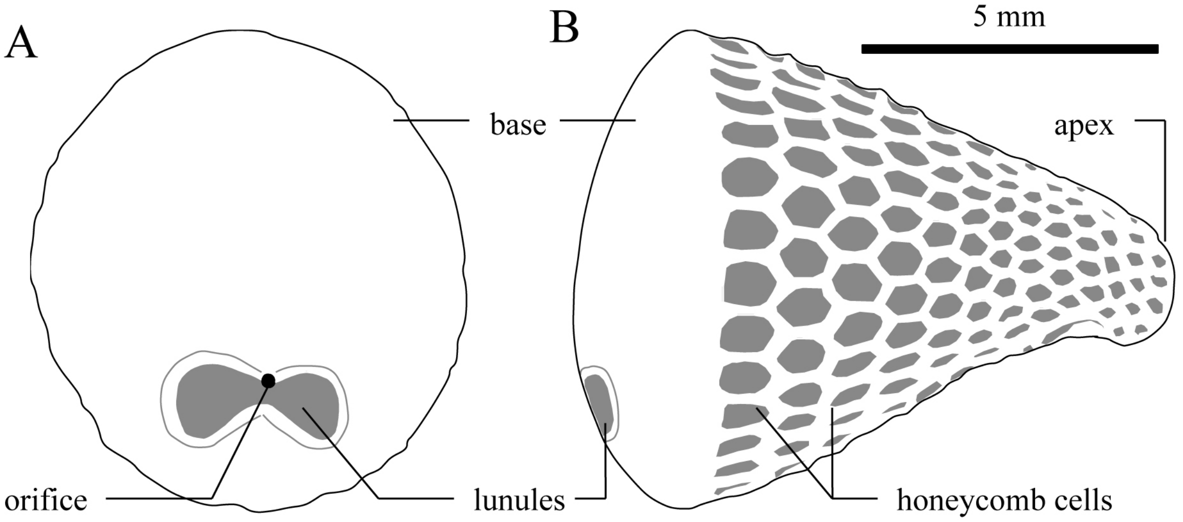

FIGURE 1. External morphology of *Bolboporites uncinatus* Pander, 1830, Middle Ordovician (Dapingian), Saint-Petersburg area, Russia; redrawn and modified from Rozhnov & Kushlina (1994a, fig. 3b) and Kushlina (1995, pl. 5 fig. 1b). A: Base of the cone, in front view, showing the two adjoining depressed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

Bolboporites is particularly widespread and abundant in Baltica, where it is recorded from the Dapingian to the Darriwilian (e.g., Estonia, Russia; Pander 1830; Eichwald 1857; Bassler 1911; Yakovlev 1921; Yeltysheva 1955; Smith 1988; Kushlina, 1995, 2007; Federov 2003; Rozhnov & Kushlina 1994a; Rozhnov 2005) and locally to the Sandbian (e.g., Norway, Sweden; Kjerulf 1865; Lindström 1883; Kushlina 1995). This genus also occurs in the late Darriwilian of Laurentia (e.g., New York, Quebec, Virginia; Hall 1847; Billings 1859; Logan *et al.* 1863; Brainerd & Seely 1888, 1896; Miller 1889; Brainerd 1891; Ami 1896; White 1896; Ruedemann 1901; Raymond 1905, 1906, 1913; Bassler 1915; Twenhofel 1938; Butts 1940; Clark 1944, 1952; Oxley & Kay 1959; Clark & Hofmann 1961; Shaw & Bolton 2011). *Bolboporites* was also reported in the Tramore Limestone Formation of Ireland (Avalonia; Reed 1899), in deposits recently assigned to the late Darriwilian (Wyse Jackson *et al.* 2002).

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

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

An alternative hypothesis was proposed by Ami (1896), who considered that *Bolboporites* was not an isolated spine, but the internal mould of the theca of an unknown 'cystoid'. Following this interpretation, von Wöhrmann (*in* Jaekel 1899) suggested that *Bolboporites* was possibly the internal mould of a cheirocrinid rhombiferan (see also Régnell 1956). This interpretation of *Bolboporites* as corresponding to the body capsule (theca) of a 'cystoid' was further elaborated by Rozhnov & Kushlina (1994a, b), based on the observation of two sets of small skeletal elements articulated into the two depressions on the convex surface of some well-preserved specimens. These two series of plates were interpreted as elements of a single feeding appendage (brachiole), which was inserting onto the convex (oral) surface of a highly derived eocrinoid (Rozhnov & Kushlina 1994a, b; Kushlina 1995, 2006, 2007; Rozhnov 2005, 2009). In this interpretation, the central longitudinal canal corresponds to the stem, which was entirely surrounded by massive, fused thecal plates.

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

Material and Methods

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

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

Methods. As Norwegian specimens are preserved as mouldic impressions in the rock, their original external aspect was revealed by making latex casts, which were coated with ammonium chloride (NH_4Cl) for observation and photographic purposes. External morphological features of *Bolboporites* sp. from Norway were observed at Lyon 1 University, with a Zeiss SteREO Discovery.V8 stereomicroscope binocular and captured with a Zeiss AxioCam MRc5 digital camera.

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

Thin sections were observed under plane polarized light (PPL), cross-polarized light (XPL) and epifluorescence UV using a Nikon AZ100 microscope, equipped with a 360 nm exciting source and a Zeiss Axiocam MRc5 (Université de Bourgogne, Dijon). Polished thin sections were also observed under cathodoluminescence using a Leica MZ12 binocular microscope equipped with a Luminoscope ELM-3R device and a Zeiss Axiocam MRc5 camera (Université de Bourgogne, Dijon). Cathodoluminescence (CL) was successfully applied by Gorzelak & Zamora (2013), so as to reveal the internal stereomic microstructure preserved in skeletal elements of various Cambrian echinoderms. This technique was usually shown to be efficient, even in the case of relatively strongly recrystallized specimens.

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

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

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

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

Other individuals of *B. mitralis* were kept intact, so as to explore minute details of their external morphology. However, in most specimens, the base of the cone and/or the honeycomb cells on the lateral walls were partly concealed by a thin layer of sedimentary rock. Consequently, fossils were placed in an ultrasonic cleaner containing a solution of dilute ethylenediaminetetraacetic acid (EDTA, 1% wt/vol, pH 8) to remove all pieces of surrounding rock and better expose the external aspect of the specimens. Once cleaned, fossils were rinsed with water, then with ethanol (C_2H_5OH), and finally dried with a hair-dryer. Observation of the external aspect of the specimens was made using both a Zeiss SteREO Discovery.V8 binocular stereomicroscope, equipped with a Zeiss AxioCam MRc5 digital camera, at Université Lyon 1, and a Hitachi TM-100 Scanning Electron Microscope (SEM) at the Université de Bourgogne, Dijon.

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

Results

Chemical and mineralogical analyses

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

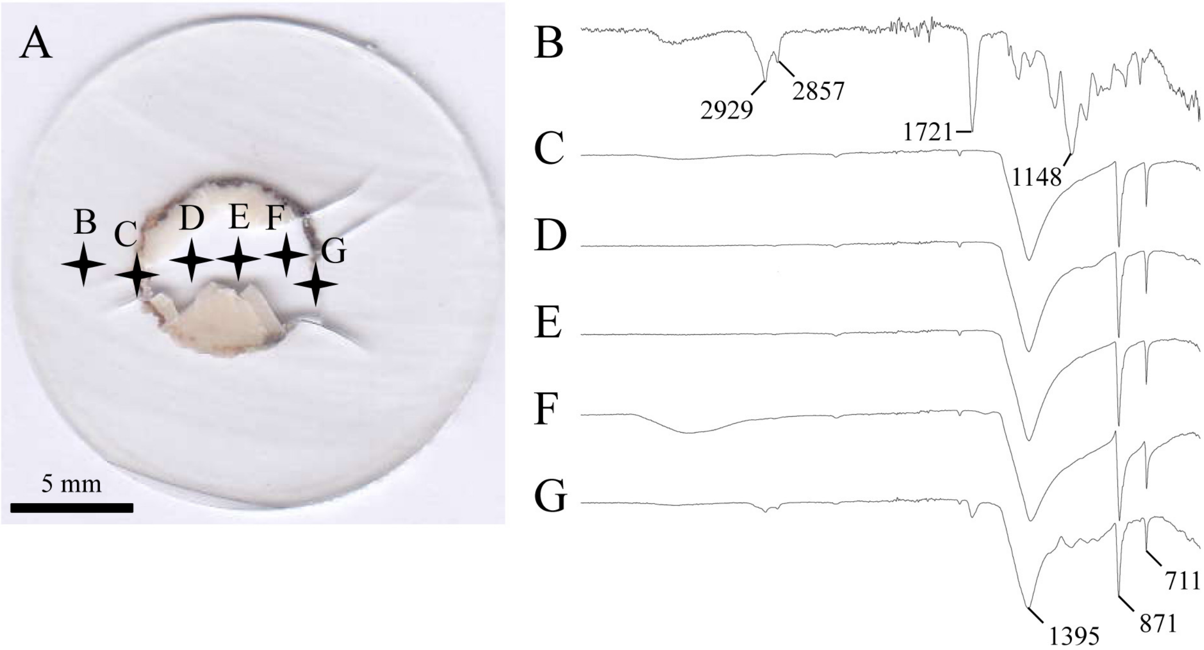

FIGURE 2. Fourier transform infrared (FT-IR) spectroscopy made on transverse sections of *Bolboporites mitralis* Pander, 1830, included in LR white resin; UCBL-FSL 712510, Middle Ordovician (Dapingian), Saint-Petersburg area, Russia. A: Location of FTIR analyses. B: IF spectrum of LR white resin (control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

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

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

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

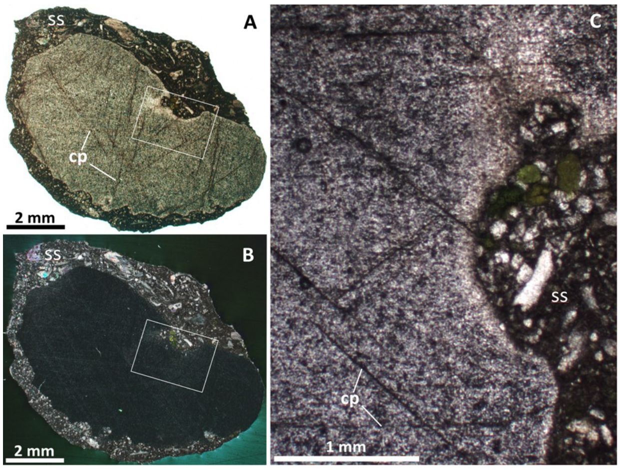

FIGURE 3. Thin section views of *Bolboporites mitralis* Pander, 1830 (Middle Ordovician (Dapingian), Saint-Petersburg area, Russia; UCBL-FSL 712510) included in the surrounding sedimentary rock (ss) which is a packstone-wackestone with bioclasts and glauconite grains. A: Plane-polarized optical light, showing the conjugated cleavage planes (cp) crosscutting the whole cone. B: Cross-polarized optical light, showing total extinction of the cone. C: Close up view of A and B (plane polarized light) revealing the tenuous dark-brown patches aligned along cleavage planes, forming a stereom-like structure.

Microstructures

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

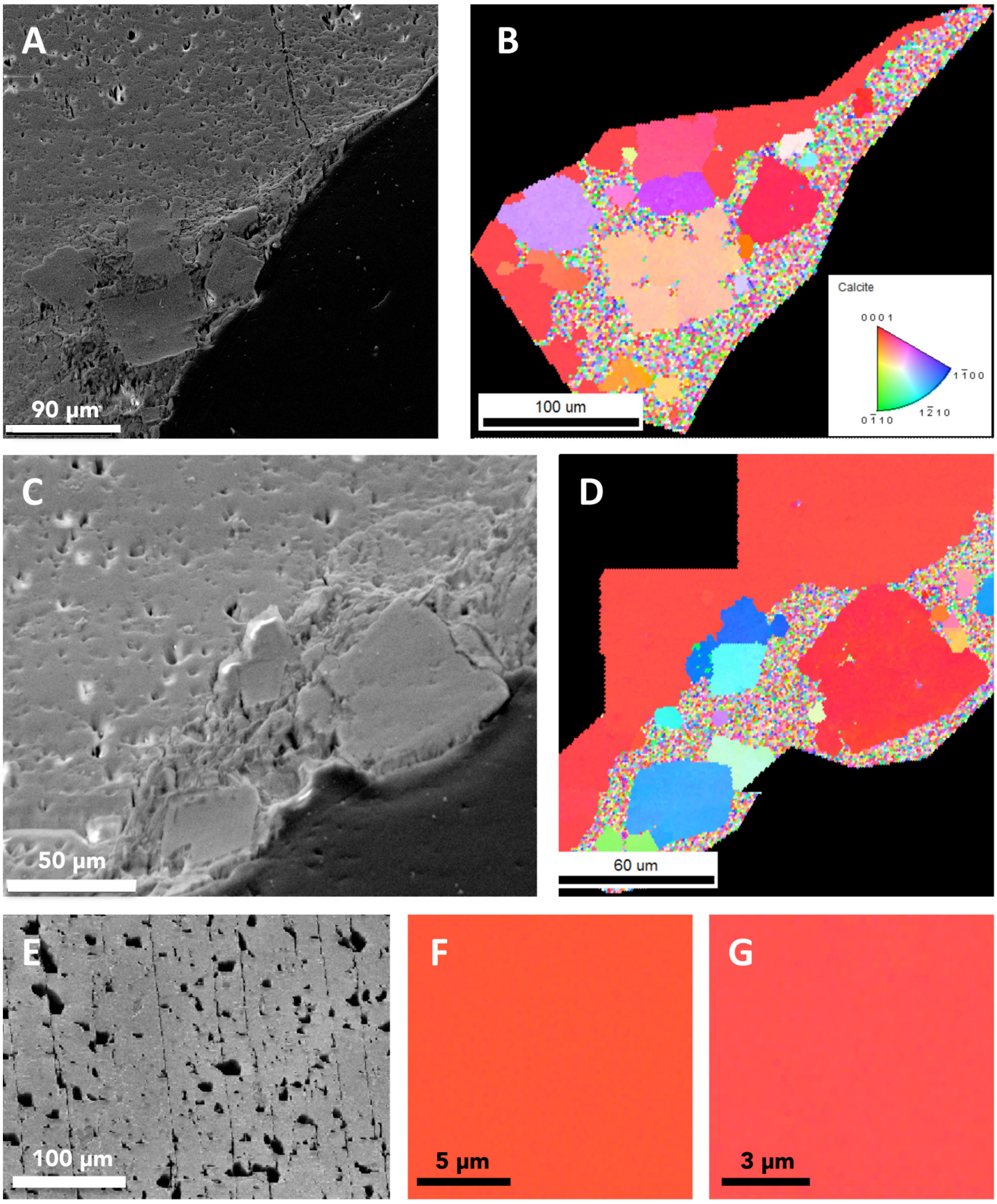

FIGURE 4. EBSD mapping of *Bolboporites mitralis* Pander, 1830; Middle Ordovician (Dapingian), Saint-Petersburg area, sample UCLB-FSL 712510, cross section, perpendicular to the cone axis. A: Periphery of the sample observed by SEM. B: corresponding EBSD map, showing the size heterogeneity of the crystals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

Under cathodoluminescence, both transverse and longitudinal sections of *B. mitralis* revealed the same mottled, orange-to-brown luminescent microstructure (Fig. 5C). Orange irregular dots and axes are aligned within a browner sealing calcite crystal, forming a CL pattern usually detected for ancient echinoderm stereoms (e.g., Gorzelak & Zamora 2013). These orange parts probably represent the former porous stereom that has been secondary cemented by a syntaxial brown-luminescent cement. Under XPL and PPL, the same stereom-like microstructure is also detected in some parts of the cones, with the tenuous occurrence of small dark spots aligned along cleavage planes (Fig. 3C). At a larger scale, the stereom of *Bolboporites* exhibits a slightly differentiated, darker, narrow peripheral rim in CL (Fig. 5A,B), which probably results either from a diagenetic effect or from a distinct lighter density of the former microstructure. A similar observation was made on virtual cross-sections of *B. mitralis* obtained by CT-scan, which show a diffuse peripheral rim, consistently lighter than the darker central part of the fossils (Fig. 6A). In CT-scan imagery, intensity restitution largely depends on the density of the materials. Consequently, the central part of *Bolboporites* is currently made of slightly more porous (less dense) skeleton than the periphery. Views by SEM confirm this deduction, with numerous micropores occuring everywhere in the skeleton, except in its peripheral parts (Fig. 5D), where initial micropores are probably cemented by the diagenetic brown-luminescent calcite. As shown by cathodoluminescence (Fig. 5A–C), the internal canal is also cemented by the brown syntaxial calcite. Finally, contrary to these important observations, no structures have been detected within the cones using UV epifluorescence technique. This is probably due to the absence of fluorescent organic matter within the stereomic calcite microstructure, in probable relation with an intense thermal alteration of the organic matter during the burial history of these Palaeozoic fossils.

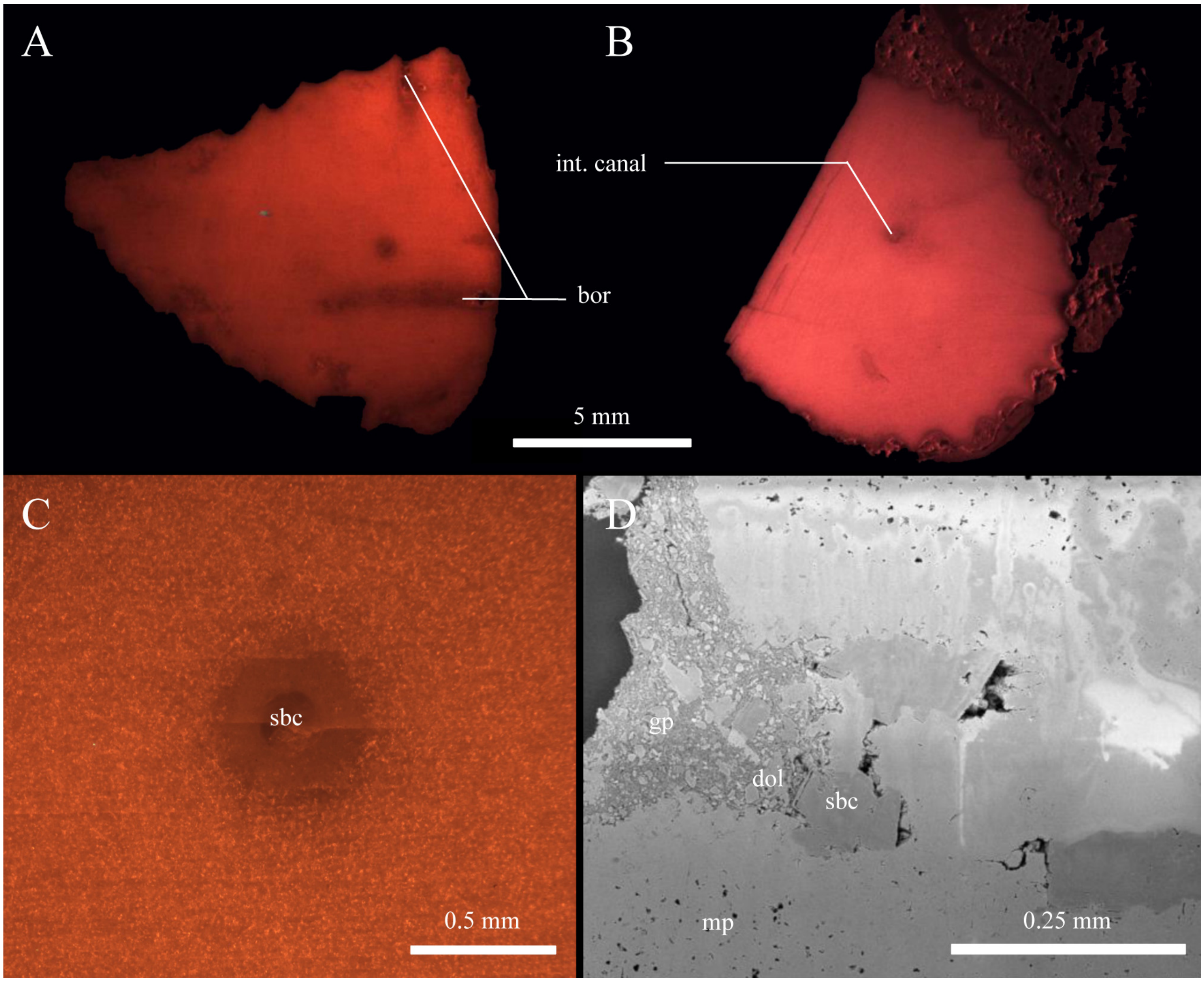

FIGURE 5. Internal structures of *Bolboporites mitralis* Pander, 1830; Middle Ordovician (Dapingian), Saint-Petersburg area, Russia. A–C: Cathodoluminescence view of sectioned *Bolboporites mitralis* Pander, 1830; Middle Ordovician (Dapingian), Saint-Petersburg area, Russia. A: Longitudinal section through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

Internal morphological features

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

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

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

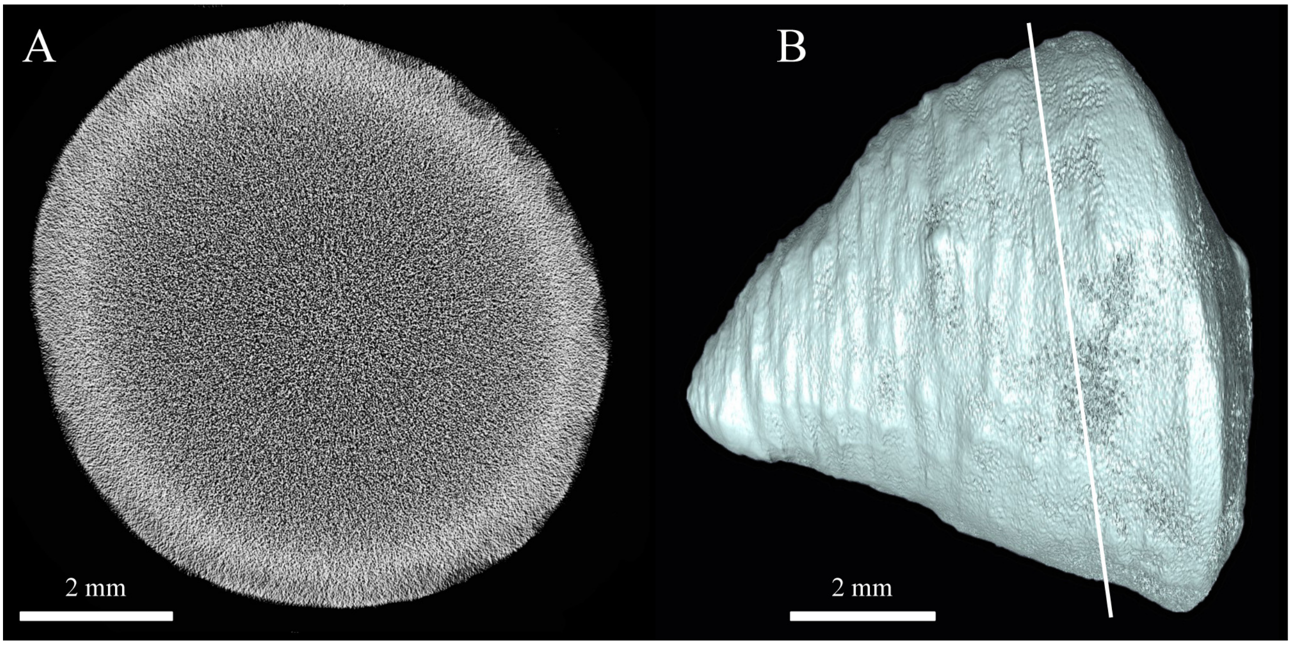

FIGURE 6. CT-scan imagery of *Bolboporites mitralis* Pander, 1830; UCBL-FSL 712509 Middle Ordovician (Dapingian), Saint-Petersburg area, Russia. A: Virtual cross section showing diffuse peripheral rim, made of denser (less porous) stereom than central part of the cone, as also shown on SEM imagery (Fig 5B). This view is reminiscent, in part, to a section through a cidaroid spine (see, e.g., Donovan 2018). Lateral honeycomb cells appear clearly on external margin of peripheral rim. B: Three-dimensional reconstruction of the specimen, with line indicating location of cross section in A.

External morphological features

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

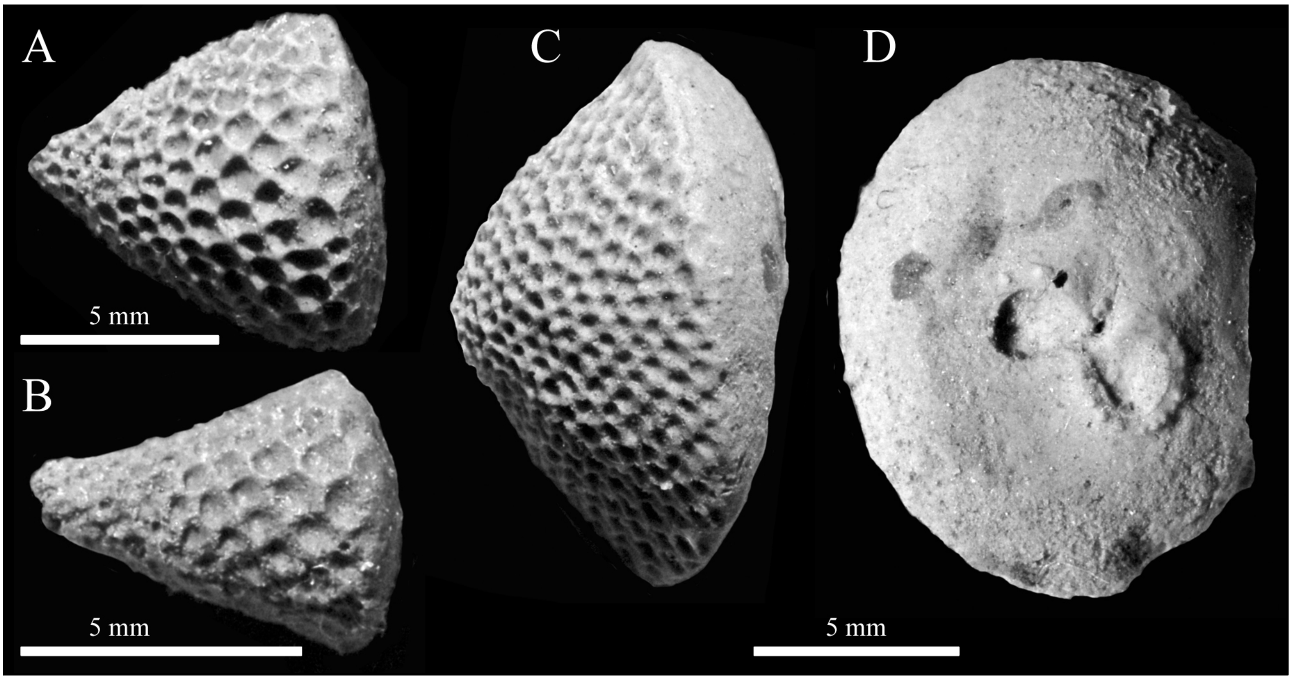

FIGURE 7. External aspect and morphological disparity of *Bolboporites*; all specimens from same locality and level, Upper Ordovician (Sandbian), Skien-Langesund area, Norway. A: *Bolboporites* sp., lateral side of the cone showing honeycomb ornamentation, and almost flat base of the cone; PMO 116887.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

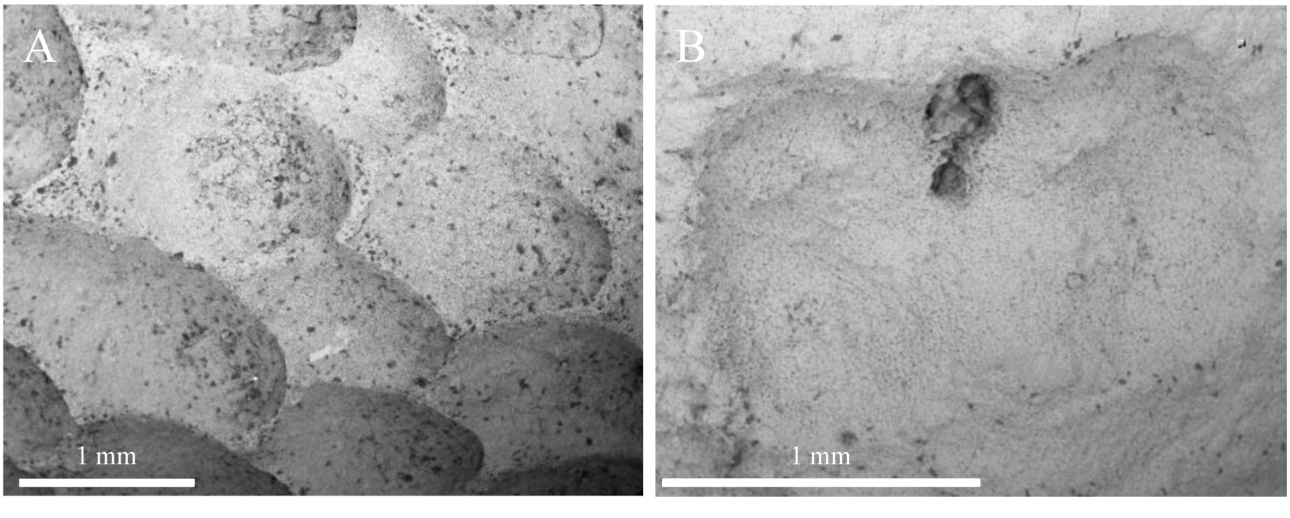

FIGURE 8. External morphology of *Bolboporites mitralis* Pander, 1830; Middle Ordovician (Dapingian), Saint-Petersburg area, Russia. A: Cells forming honeycomb ornamentation on lateral sides of the cone; SEM view of specimen UCBL-FSL 713254. B: Lunules and associated small orifice, on the base of the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

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

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

Discussion

Cathodoluminescence, applied here for the first time to *Bolboporites*, confirms previous reports of the presence of a former stereomic microporous structure in this fossil (e.g., Logan *et al.* 1863; Lindström 1883; Yeltysheva 1955; Clark & Hofmann 1961). Currently blocked by a diagenetic syntaxial calcite, this microstructure is also detected under SEM and PPL observations. A second important result is that each specimen of *Bolboporites* corresponds to a single, formerly porous, monocrystal of calcite. Taken together, these two points provide definitive evidence for echinoderm affinities. Consequently, overall similarities in shape or ornamentation with algae (e.g., *Coelosphaeridium*), bryozoans, corals or sponges (e.g., stromatoporoids) are merely superficial.

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

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

Bolboporites *as a theca*

In this interpretation, *Bolboporites* represents either the internal mould (Ami 1896; von Wöhrmann *in* Jaekel 1899; Régnell 1956) or the external wall of a blastozoan theca (Rozhnov & Kushlina 1994a, b; Kushlina 1995, 2006, 2007). In blastozoans, the theca was polyplated and entirely made of extraxial skeletal elements (i.e., deriving from the pre-metamorphic larva; David *et al.* 2000; Sprinkle & Guensburg 2001; Nardin *et al.* 2009, 2017). The theca was bearing all main body orifices (anus, hydropore, mouth) and, when present, various kinds of respiratory structures (e.g., epispires, diplopores, rhombs; Kesling 1968; Sprinkle 1973; David *et al.* 2000). In life, the theca housed the main body cavity, which contained all internal organs (e.g., gut; Kesling 1968; Sprinkle 1973; Rahman *et al.* 2015).

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

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

This biserial structure was interpreted by Rozhnov & Kuslina (1994a, b) as a feeding appendage (brachiole; see also Kushlina 1995, 2006; Rozhnov 2005, 2009). This identification implies that the groove borne by brachiolar plates probably housed a single ray of the ambulacral system and that, consequently, the mouth was located at the proximal extremity of this ray. The mouth would thus correspond to the small orifice located within the lunule. In their interpretation of *Bolboporites*, Rozhnov & Kushlina (1994a, b) further suggested that: (1) the internal longitudinal canal of *Bolboporites* was probably homologous to the axial canal (lumen) of a pelmatozoan stem, thus implying that the stem was present, but entirely encased within the theca; and (2) all organs (e.g., gut) were not located within the theca, but outside of it, on the smooth surface of the cone.

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

Our results demonstrate that *Bolboporites* corresponds to a single, massive cone-shaped echinoderm skeletal element. This observation has two major implications: if *Bolboporites* is interpreted as the theca of an eocrinoid, then this theca (1) is entirely made of one single plate; and (2) with the exception of the narrow central canal, it does not contain any internal structure. Reduction of the number of plates forming the body capsule is a trend described in various groups of Palaeozoic echinoderms, such as in solutans (e.g., Late Ordovician belemnocystitids from North America; Parsley & Caster 1965; Caster 1968) or in stylophorans (e.g., *Jaekelocarpus* Kolata, Frest & Mapes, 1991 from the Pennsylvanian of Oklahoma; Dominguez *et al.* 2002). Particularly drastic examples of such a reduction in the number of plates can be documented in the calices of several derived, Late Palaeozoic, stemless crinoids, all characterized by convergent, similar-looking cone-shaped morphologies, as, for example, *Agassizocrinus lobatus* Springer, 1926, from the Mississipian of Kentucky (Ettensohn 1975) or *Edriocrinus sacculus* Hall, 1859, from the Lower Devonian of New York (Moore 1978; Seilacher & MacClintock 2005; Herbert & Ettensohn 2018). The stemless Permian crinoid *Timorocidaris* probably represents the most extreme case of reduction in the number of plates, with its bowl-shaped calyx possibly made of a single skeletal element (Ubaghs 1978a; Hess 1999). Consequently, *Bolboporites* could represent a case of convergent acquisition of a single plated body capsule in blastozoans. In all echinoderms, including the most extreme crinoid morphologies, the body capsule always contains an internal cavity housing the viscera. However, our observations show that *Bolboporites* is a massive skeletal element, without any body cavity. If *Bolboporites* was a single-plated theca, then its mouth (i.e., the small orifice located within the lunules, at the proximal extremity of the ambulacral groove) would open into the narrow, distally closed and tapering central canal. This implies that (1) this internal canal cannot be homologous to the axial canal of a stem (in pelmatozoans, the mouth never opens into the stem canal); and (2) the absence of an internal body cavity and of any anal opening both suggest that, from a functional point of view, this interpretation is not valid. The suggestion that soft parts were lying in life over the smooth basal surface of the cone, that is, outside of the theca (see e.g., Rozhnov & Kushlina 1994a, b), is incompatible with the body plan of the phylum Echinodermata. In all echinoderms, the viscera are always housed within the body capsule, independently of whether it is loosely (e.g., holothurians) or more strongly calcified (most taxa).

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

Bolboporites *as an infrabasal cone*

The overall morphology of *Bolboporites* is strongly reminiscent of similar-looking, cone-shaped, massive skeletal elements forming the aboral part of the body capsule in some blastozoans and crinoids. Such aboral (or infrabasal) cones can be made of several tightly sutured plates, as, for example, in *Cymbionites* and *Peridionites*, both from the Cambrian of Australia (Whitehouse 1941; Smith 1982). However, single-plated, massive infrabasal cones have been described in several Cambro-Ordovician eocrinoids (Ubaghs 1963; Clausen 2004; Allaire *et al*. 2017), as well as in some Late Palaeozoic crinoids (Ettensohn 1975, 1980; Seilacher & MacClintock 2005; Webster & Kues 2006). As in *Bolboporites*, massive aboral pelmatozoan cones (plates) also display: (1) a very wide morphological disparity within a same assemblage (see, e.g., Ettensohn 1980; Clausen 2004); and (2) a central canal, which is tapering proximally (i.e., towards the apex of the cone) in stemless taxa (e.g., in the Pennsylvanian crinoid genus *Paragassizocrinus* Moore & Plummer, 1940; Ettensohn 1980). In contrast, in stemmed taxa, the central canal extends throughout the infrabasal cone and leads proximally into the axial canal of the stem (see, e.g., Ubaghs 1963; Clausen 2004).

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

Bolboporites *as a spine*

Spines are highly differentiated, mobile skeletal elements articulated to the body wall of echinoderms (see, e.g., Durham *et al*. 1966; Smith 1980b). Although this character gave its name to the phylum Echinodermata ('spiny skin'), moveable spines indeed occur only in asterozoans, echinozoans (echinoids), edrioasteroids and stylophorans. In asterozoans, echinoids and edrioasteroids, the articulation of spines to the body wall is complex, typically consisting of (1) a concave socket (acetabulum) at the base of the spine; and (2) a corresponding convex ball (mamelon) located at the summit of a tubercle (Durham *et al*. 1966; Spencer & Wright 1966; Smith 1980b; Holloway & Jell 1983; Guensburg 1988; Lebrun 1998). Attachment and mobility of spines to the body wall are achieved by muscles and/or a ligamentary catch apparatus (Smith 1980b; Lebrun 1998). Spine movements are controlled by nerves, forming either a ring around the tubercle (e.g., in echinoids; Durham *et al.* 1966; Smith 1980b; Lebrun 1998) and/or extending inside the spine itself (e.g., in some ophiuroids; Lebrun 1998). In cornute stylophorans (e.g., chauvelicystids, *Thoralicystis griffei* (Ubaghs, 1970)), spines are articulated to various parts of the body wall (proximal aulacophore, supracentral area, thecal margin) by rudimentary balls and sockets (Ubaghs 1970, 1983; Lee *et al.* 2005). In most mitrate stylophorans, the articulation of posterior spines (digital, glossal) consists of complex balls and sockets (e.g., in anomalocystitids; Ubaghs 1968a; Parsley 1991; Ruta & Bartels 1998). In some other taxa (e.g., *Balanocystites primus* (Barrande, 1872)), the posterior spine is connected to the theca by a small column of articulated plates (Lefebvre 1999).

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

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

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

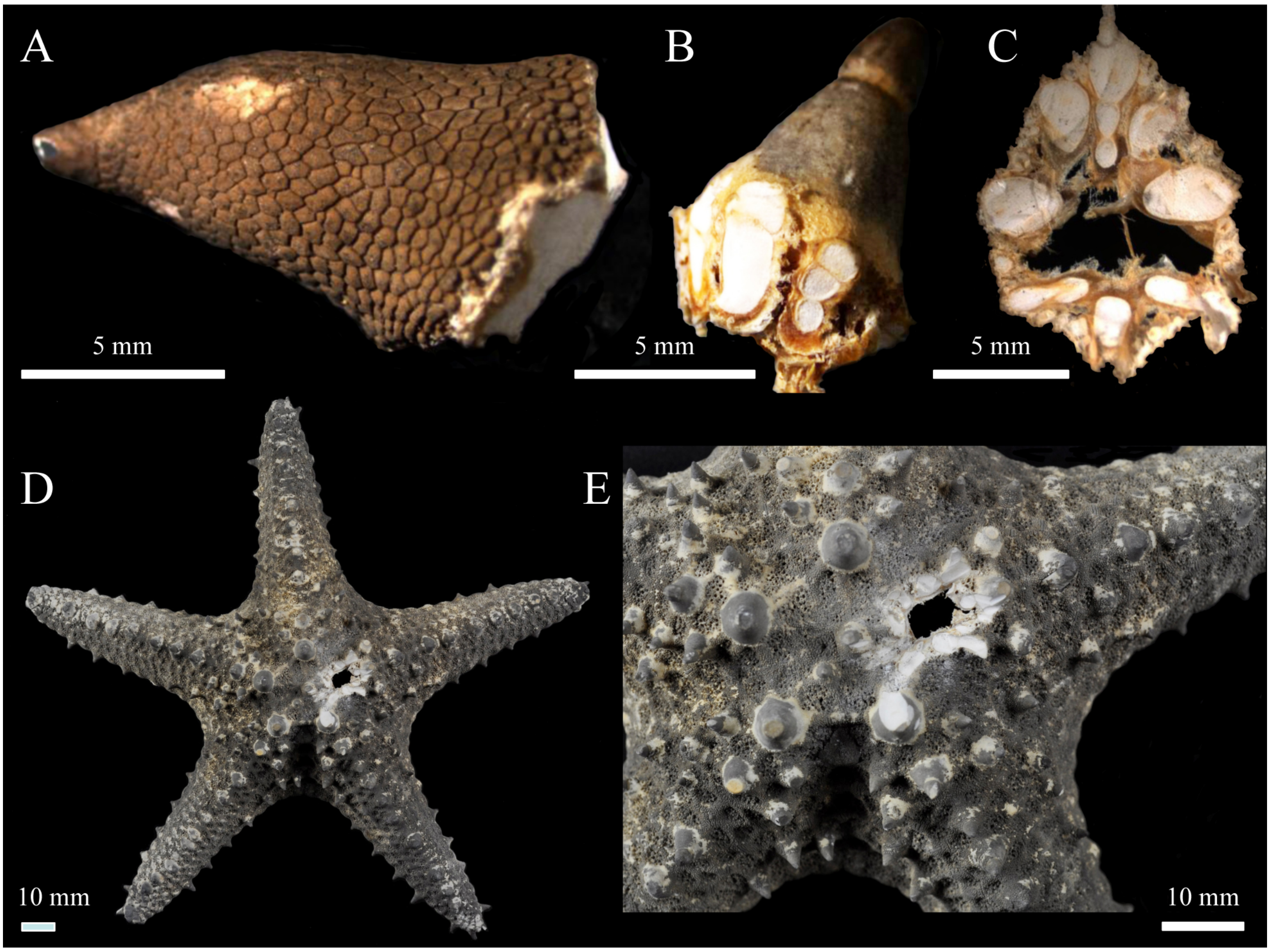

FIGURE 9. Aboral tubercles of the Recent oreasterid asteroid *Pentaceraster mammilatus* (Audouin, 1826). A: Extracted tubercle in lateral view, with its lateral walls covered by thick, polyplated, granulose aboral membrane; specimen UCBL.2017.01.44. B–E: Specimen UCBL.2017.01.47. B: Extracted tubercle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

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

The interpretation of *Bolboporites* as a spine is thus plausible and cannot be refuted on available evidence. However, its systematic position remains an open question. The frequent association of *Bolboporites* with skeletal remains of various blastozoans (e.g., cheirocrinids, *Palaeocystites*) questioned the possibility that it could represent isolated spines of one of them (Clark & Hoffman 1961). However, none of the blastozoans found in the same localities as *Bolboporites* in both Baltica and Laurentia shows any evidence suggesting that spines were articulated to its body wall. Indeed, spines are only known in asterozoans, echinozoans, edrioasteroids and stylophorans (see above), thus ruling out any putative blastozoan affinities for *Bolboporites*. The size of *Bolboporites* (from about 2 to 12 mm in height in both North American and Russian specimens; Clark & Hoffman 1961; Rozhnov & Kushlina 1994a) suggests that putative stylophoran affinities are highly unlikely. In this class, the size of the theca is generally comprised between 5 and 30 mm, and it rarely exceeds 30 to 40 mm (e.g., the largest known mitrate, *Diamphidiocystis drepanon* Kolata & Guensburg, 1979, is about 40 mm wide; Lefebvre 1999). The large size and cone-shaped morphology of *Bolboporites* seem to be also incompatible with putative edrioasteroid affinities. When preserved, edrioasteroid spines are consistently consisting of narrow, elongate elements, typically less than 3 mm in length, which were articulated to ambulacral cover plates and/or skeletal elements of the pedunculate zone (Holloway & Jell 1983; Guensburg 1988; Guensburg & Sprinkle 1994).

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

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

Bolboporites as a columnal

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

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

Bolboporites *as a holdfast*

Holdfasts are anchoring structures occurring at the distalmost extremity of the stem in various blastozoans and crinoids (Ubaghs 1972, 1978a; Brett 1981; Ausich *et al.* 1999; Seilacher & MacClintock 2005). The massive, cone-shaped morphology of *Bolboporites* shows many similarities with similarly-shaped, isolated pelmatozoan elements (e.g., *Oryctoconus*), generally interpreted as holdfasts (Colchen & Ubaghs 1969; Alvaro & Colchen 2002; Seilacher & MacClintock 2005; Zamora *et al.* 2009). The identification of *Bolboporites* as a putative discoidal holdfast was discussed, but rejected by Rozhnov & Kushlina (1994a). Their main argument was that, if this fossil was a holdfast, its basal surface would then be attached (fixed) to the substrate: this orientation is incompatible with the presence of an appendage articulated to the basal surface of *Bolboporites*. However, it should be stressed that this base-down orientation occurs only in the case of pelmatozoan discoidal holdfasts tightly and permanently encrusted on firmgrounds and hardgrounds (Ubaghs 1978a; Brett 1981; Brett *et al.* 1983; Sumrall *et al.* 1997; Rozhnov 2002). The opposite (base-up) orientation of the cone is observed in most pelmatozoans living on soft substrates and using their distal holdfasts as an anchor or a grapnel, as, for example, the Ordovician eocrinoid *Balantiocystis* Chauvel, 1966, and the Devonian crinoid *Ancyrocrinus* Hall, 1862 ('kite strategy'; Ubaghs 1972; Brett 1981; Le Menn 1985; Ausich *et al.* 1999; Alvaro & Colchen 2002; Seilacher & MacClintock 2005; Zamora *et al.* 2009).

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

The interpretation of *Bolboporites* as a discoidal holdfast has also several implications, that can be tested: (1) the biserial appendage inserting on the lunules would thus probably correspond to the distal-most columnals of a pelmatozoan stem; and (2) if *Bolboporites* was used as an anchor, it was thus at least partly buried into the sediment. If *Bolboporites* was a distal holdfast, the presence of two lunules in all specimens suggests that a dimeric stem was articulated to it. This interpretation is further supported by the observation of a biserial appendage in at least some better preserved individuals from Russia (Rozhnov & Kushlina 1994a; Kushlina 2007). Although most Ordovician pelmatozoans possessed holomeric stems (i.e., formed by a single column of plates), tetra-, penta- and hexameric appendages have been also described in several crinoids (e.g., *Aethocrinus moorei*, *Ramseyocrinus* Bates, 1968; Ubaghs 1969, 1983; Donovan 1984, 1985), as well as in some echinosphaeritid and hemicosmitid blastozoans (Jaekel 1899; Bockelie 1981, 1982; Parsley 1998). Dimeric distal stems are the rule in Ordovician solutans (Caster 1968; Ubaghs 1970; Lefebvre *et al.* 2012; Noailles *et al.* 2014). Although they possibly retained an attached post-metamorphic stage, Ordovician solutans were vagile and their stem did not possess any distal discoidal holdfast. With the exception of solutan elements, only few occurrences of tri- and dimeric columnals were documented in Ordovician deposits, and all of them have been assigned to crinoids possibly related to *Ectenocrinus* Miller, 1889 (e.g., Donovan 1985). Consequently, the existence of Ordovician pelmatozoans with a stem comprising dimeric columnals supports the identification of *Bolboporites* as a possible distal holdfast articulated to a biserial appendage.

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

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

Conclusions

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

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