Exceptional Soft-Tissue Preservation in Boring Ctenostome Bryozoans and Associated "Fungal" Borings from the Early Devonian of Podolia, Ukraine

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Colonies of boring ctenostome bryozoans and microborings of "fungi" that occur in the Early Devonian (Lochkovian, ~416 Ma) of Podolia, western Ukraine, have soft-tissue preserved by phosphatization. These comprise exceptional three-dimensional body walls of feeding zooids with probable parietal muscles inserted on the cystid wall, and setigerous collars twisted within the vestibulum. The presence of collars in this Early Devonian ctenostomes proves the existence of this feature for more than 416 Ma of ctenostome evolution. Phosphatized remains of the zooid walls are interpreted as relicts of the originally chitinous cystid walls. This is the first record of soft-tissue fossilization in a boring bryozoan. The presence of cavities (specialized heterozooids), empty or filled with laminated calcium phosphate, is also documented in bryozoans for the first time. These cavities are interpreted as "store-rooms" in which the bryozoans accumulated nutrients. The new taxon, *Podoliapora doroshevi* gen. et sp. nov. is described. In additional, phosphatised fungi-like endoliths co-occur with bryozoans.

Key words: Bryozoa, Fungi, phosphatization, soft-tissue, demineralization, Devonian, Podolia, Ukraine.

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Introduction

The lack of mineral skeleton is a diagnostic feature of the bryozoan order Ctenostomata. In extant boring ctenostomes the basal part of each feeding zooid is completely immersed within the calcareous substrates, only the flexible polypide may protrude to the surface while opening its lophophore (e.g., Hayward 1985; Mukai et al. 1997; Schwaha et al. 2011). The lophophore and setigerous (or pleated) collar which projects from the neck of the autozooid around the lower parts of the lophophore, are the only parts of the bryozoan animal that extend periodically above the surface of the inhabited object when the polypide is feeding (e.g., Pohowsky 1978). The setigerous collar has a comb-like appearance, hence the name of the order (Prenant and Bobin 1956; Banta et al. 1995; McKinney and Dewel 2002; McKinney 2008).

Bryozoans, as with other boring organisms such as cyanobacteria, fungi, algae, and sponges, that use mostly molluscan shells or corals as a substrate, have an important role in destroying shells and enhance fine grain sediment production (e.g., Schneider and Torunski 1983; Tribollet et al. 2002; Tribollet 2008; Ehrlich et al. 2008, 2009; Garcia-Pichel et al. 2010).

Boring bryozoans have long geological record, having been identified within calcareous substrates from the Early Ordovician onwards (e.g., Soule and Soule 1969; Pohowsky 1978; Todd 2000; Wilson and Palmer 2006; Rosso 2008). The oldest, though as yet unpublished, record of a boring bryozoans is from the Volkhov Stage of the St Petersburg region (Taylor and Ernst 2004). The boring ctenostomes have not been frequently studied since the important papers by Marcus (1938), Silén (1946, 1947), Soule and Soule (1969), Pohowsky (1978) and Vogt and Soule (1973).

Extant boring bryozoans most frequently infest the shells of living and dead molluscs (Soule and Soule 1969; Pohowsky 1978) and serpulid worm tubes (Bertling 1995). Palaeozoic bryozoan borings are mostly found in brachiopod shells and in crinoids (Pohowsky 1978), the oldest examples from Volkhov are in trilobites (Taylor and Ernst 2004).

The soft anatomy of boring bryozoans is known only in a few species (Marcus 1938; Silén 1946, 1947; Prenant and Bobin 1956; Soule and Soule 1969). The morphology of boring traces has been studied mostly in resin casts with subsequent decalcification of the shells in acid (Golubic et al. 1970, 1975; Pohowsky 1978; Vogel et al. 1987). They have been treated either as body fossils (Pohowsky 1974, 1978;

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Voigt and Soule 1973; Viskova and Pakhnevich 2010), or as trace fossils (e.g., Boekschoten 1970; Bromley 1970; Mayoral 1988, 1991; Casadío et al. 2001). Ichnotaxonomic nomenclature is also applied to endolithic fungi (Radtke 1991), recorded here in association with the bryozoans.

The non-boring, exclusively soft-bodied ctenostomes are occassionally overgrown by organisms possessing hard skeletons and preserved in the fossil record as bioimmurations (Taylor 1990a, b; Todd 1993, 1994, 1996; Taylor and Todd 2001; Taylor and Ernst 2008), or as epibiont shadows (Palmer et al. 1993).

In this paper the state of preservation is described and mode of boring discussed in colonies of ctenostomes and "fungal" microborings from the Early Devonian, collected at Doroshiv in the western part of Podolia, Ukraine (Fig. 1). The studied bryozoans have three-dimensionally preserved zooids (Figs. 2, 3) with cuticular body walls, presumed parietal muscles within these walls, and setigerous collars, all impregnated with or replaced by calcium phosphate (Figs. 4, 5). In one autozooid, the displaced presumed lophophore and encircling collar are preserved (Fig. 5D). Additionally, inside one, partly retracted collar, the presumed base of the lophophore is preserved (Fig. 5E).The identity of the host shells remains unknown, although replicas of their microstructures are preserved in details (Figs. 6–8). Most probably, they are bivalves which were preserved as internal moulds on the bedding planes of many investigated limestone samples from the locality. At low magnifications the boring bryozoans are also visible as fine brown pyritized structures in moulds of the molluscan shells. The associated fungal-like colonies have phosphatized three-dimensionally preserved filaments and swellings (Figs. 9, 10).

Institutional abbreviations.—ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

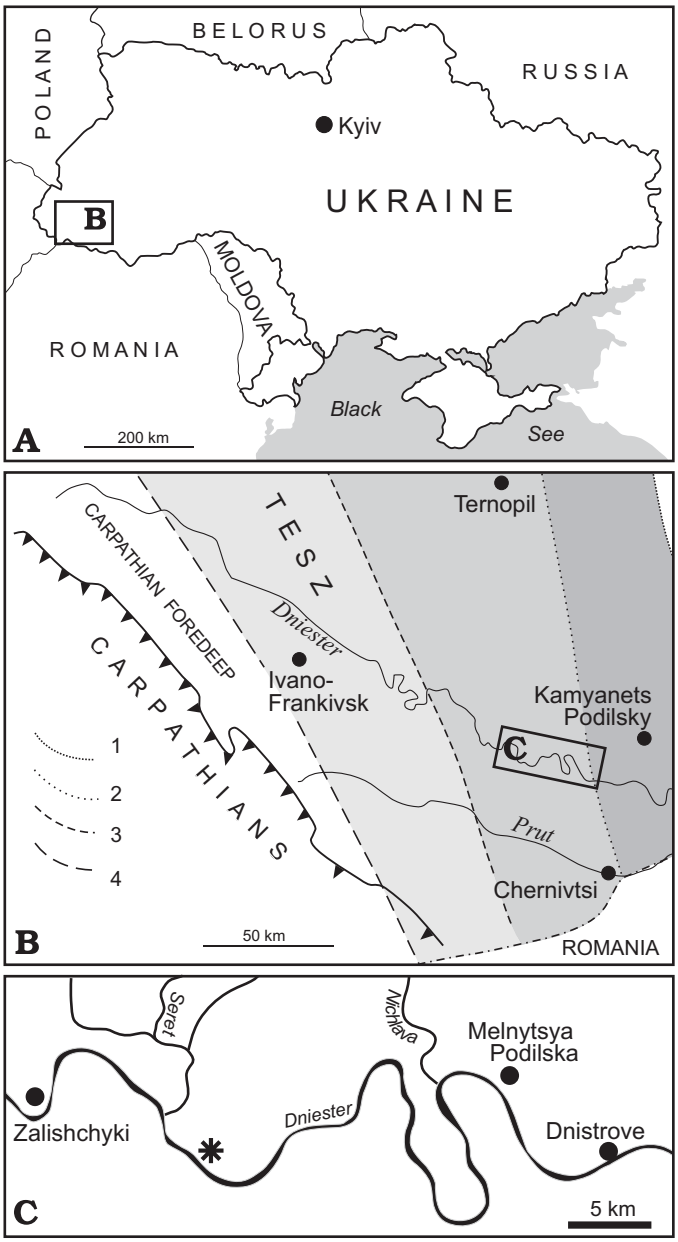

Fig. 1. Location map of the studied section, Lower Devonian, middle Lochkovian, Chortkiv Formation in Doroshiv, Podolia Ukraine. **A**. Map of Ukraine showing location of the study area; rectangle indicates general locality, enlarged in B and C. **B**. Distribution of the Silurian and Devonian deposits in Podolia, SW Ukraine; 1, Eastern extent of the Silurian deposits; 2, Eastern extent of the Devonian deposits; 3, Eastern extent of the Old Red Sandstone-type deposits; 4, Trans European Suture Zone. **C**. Location of the Doroshiv outcrop in the vicinity of Dniestr valley. Modified from Małkowski et al. (2009).

Geological setting

The Late Silurian–Early Devonian fossil sediments in Podolia, western Ukraine, are of marine origin and were deposited in an epicontinental environment in southern Baltica, a continent located at that time in the Southern Hemisphere at about 10° to 20°S (see Kozłowski 2003; Voichyshyn 2011). Podolia is known as a classical geological site in Europe and has attracted the interest of many palaeontologists working on vertebrate and invertebrate faunas (e.g., Baliński 2010, 2012; Drygant and Szaniawski 2012; Filipiak et al. 2012; Racki et al. 2012; Voichyshyn and Szaniawski 2012).

The study area is located along the Dniester River (Fig. 1). The specimens studied were found in the middle part of the marine Lochkovian succession outcropping in the right escarpment of the Dniester River close to the village of Doroshiv, section number 77 of Nikiforova et al. (1972) and Małkowski et al. (2009) (coordinates: N48°35'45.5" E25°53'17.4"). The strata belong to the Chortkiv Formation of the Tyver Group (Małkowski et al. 2009; Drygant and Szaniawski 2012; Voichyshyn 2011), and are composed of alternating dark grey argillaceous shale, thin-bedded fine-grained limestone, and brownish and reddish claystone. The fossil bryozoans were found in the middle and upper part of the section. The carbonate deposits at Doroshiv have yielded a diverse fossil assemblage composed of brachiopods, ostracods, bivalves, gastropods, and agnathan remains.

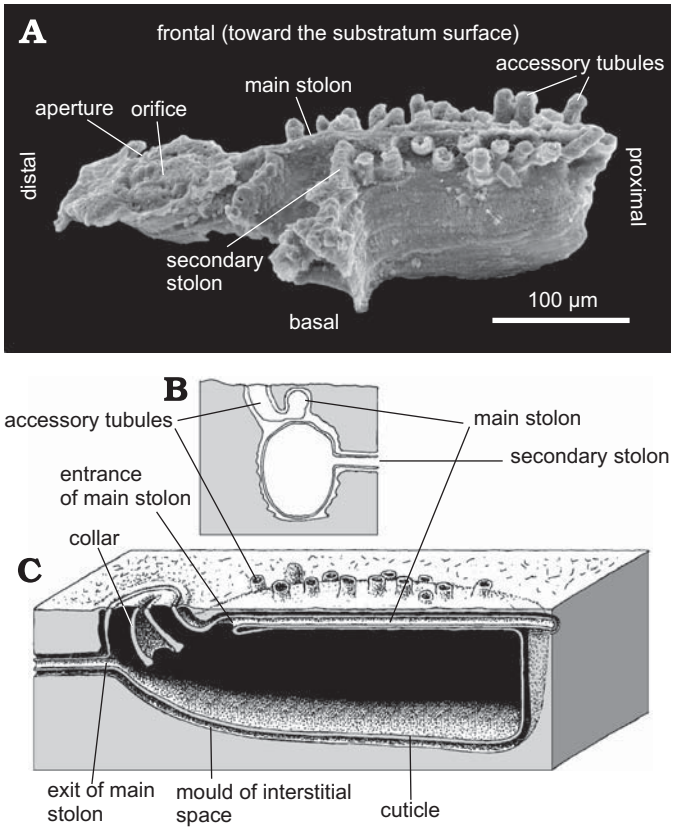

Fig. 2. Early Devonian bryozoan *Podoliapora doroshivi* gen. et sp. nov., from the Doroshiv section, Podolia, Ukraine. **A**. Lateral view of a single autozooid showing external morphological features, ZPAL Br XIV/102. **B**. Reconstruction in transverse section. **C**. Reconstruction in longitudinal section.

A phosphatized podocopid ostracod with three-dimensionally preserved soft-parts have been described from the Early Devonian of the Ivanye Zolote site in Podolia by Olempska et al. (2012).

Material and methods

Numerous samples from various stratigraphical levels of the Early Devonian of Podolia were dissolved mostly for conodonts and other non-calcareous fauna (see Małkowski et al. 2009; Drygant and Szaniawski 2012). The boring ctenostomes and fungal-like traces preserved three-dimensionally were found in acid-resistant residues of the limestone from in the Doroshiv section. The fossils were extracted from carbonate matrix using 10% acetic acid. Colonies had been fragmented in small pieces of approximately 1–2 mm^2 in size (Fig. 3), probably by mechanical destruction during the dissolution process. In extreme cases the bryozoans are represented by isolated single autozooids (Fig. 2). Several dozens of specimens display phosphatized remains of soft-tissue. In addition, phosphatized fungal-like traces are associated with bryozoan colonies in five specimens.

The present study is based on the examination of 150 fragments of bryozoan colonies. In most specimens, the substrate had been moderately to very densely bored by bryozoan. Up to 40 autozooids and "heterozooids" may be present on ~1 mm^2 the substrate surface. The material also contains numerous fragments of pyritized bryozoan colonies of the same boring species, but their state of preservation is rather poor.

Specimens were photographed using a Philips XL 20 Scanning Electron Microscope and equipped with energy spectrometer EDAX-Dx4i, Genesis in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Mode of preservation

In the studied material, the colonies of boring Bryozoa and "fungi" are secondarily phosphatizated. The original host shell material is not preserved, being dissolved in the process of limestone samples dissolution. The phosphatization preserved the shape of the zooids and "fungal" filaments, and formed the calcium phosphate coating up to 1.5 µm thick, around the specimens (Figs. 3–8). However, this precluded the possibility of observing of the external surface of phosphatised cuticular wall details. The external surface is visible in the places where the coating has been destroyed (Fig. 6B). The phosphate has also replaced the soft-tissue inside the bryozoan zooids.

The external surfaces of some host shells are preserved in part, because they were covered by the thin layer of calcium phosphate. Bryozoan and "fungal" colonies are attached underneath of this layer. The EDAX analyses show that 90–92% of the coating by weight is comprised of Ca, P, and O, with smaller amounts of Fe, Si, Al, and Na.

The phosphatized zooidal cavities are preserved in two ways: (i) the bryozoan colonies are phosphatized throughout their thickness, and all zooid walls are coated by a thin 1–1.5 µm layer of calcium phosphate, and therefore zooids are visible only externally (Figs. 2A, 3D–F); (ii) zooids are coated by a layer of calcium phosphate, but occasionally only the frontal (toward the surface of the substratum), and side walls of the zooids are preserved; basal walls, probably due to a different degree of phosphatization, collapsed during acid dissolution. Therefore these zooids are "half-open" and show soft-tissues partly preserved inside (Fig. 3A–C).

On the surface of the coating layer, details of the host shell microstructure are exceptionally preserved (Figs. 3, 4) in negative replica. The phosphate particles forming the coating layer have an amorphous appearance.

Two main patterns of microstructure replicas can be distinguished in the bryozoan colonies from Podolia. The base of the first type structure, close to substrate surface, is preserved as two thin, amorphous-like or microgranular layers, the first ~4.9 µm thick, and second ~2.5 µm thick. The layer above, ~15 µm thick, is composed of poorly preserved imprints of gently inclined or vertically oriented closely joined prismatic crystallites. In some places this layer has the appearance of fine-grained aggregations. These two layers are best visible on the coating layer covering the vestibular parts of autozooid

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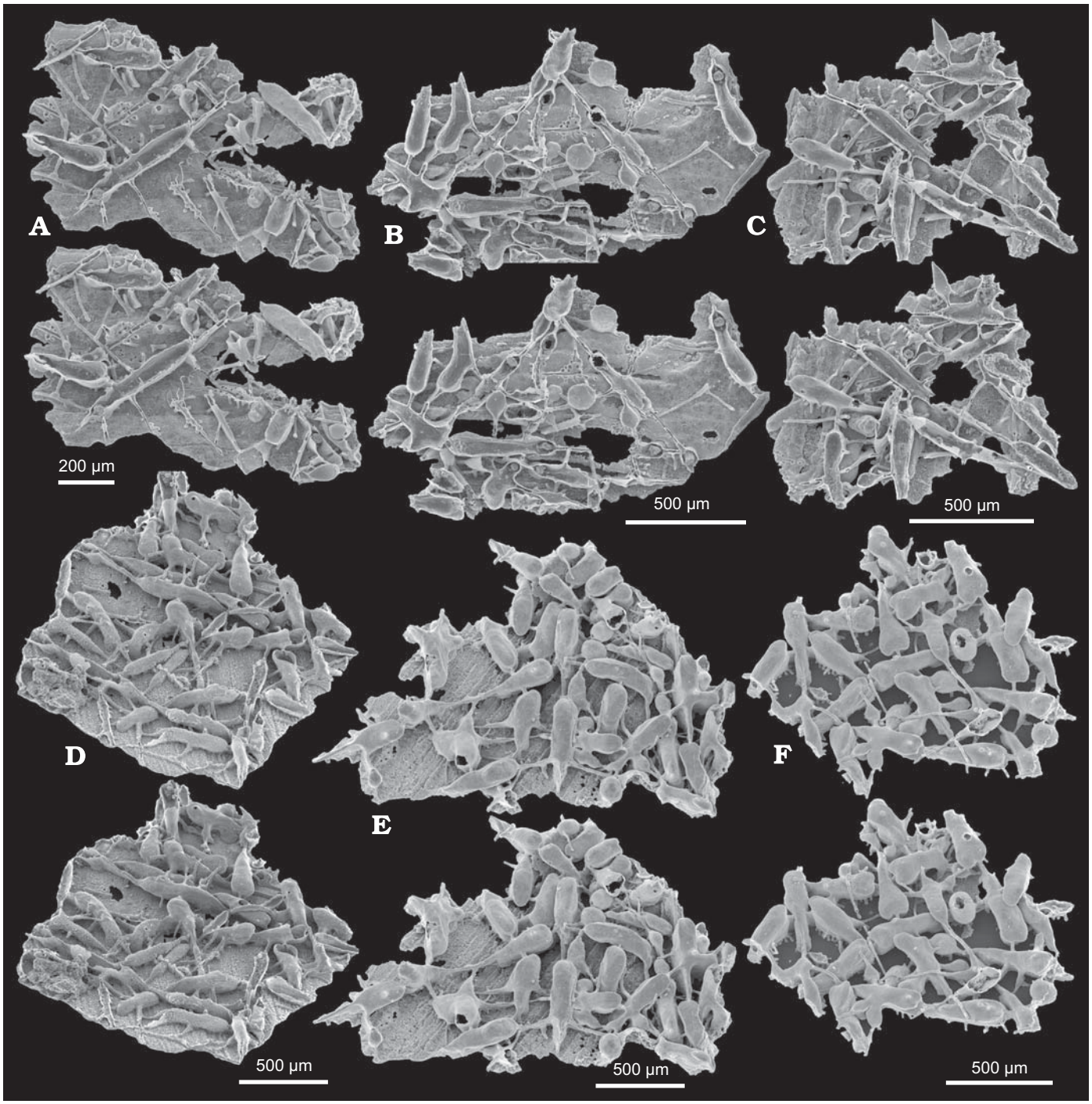

Fig. 3. Early Devonian bryozoan *Podoliapora doroshivi* gen. et sp. nov., from the Doroshiv section, Podolia, Ukraine. Stereo-pairs of phosphatized colonies in basal view; frontal parts of the colonies and orifices are not visible as they opened onto the surface of the host shell. **A**–**C**. Internal views of partly preserved zooids with basal walls collapsed, soft-tissue preserved inside autozooids, and orifices visible at the distal ends of autozooids. **A**. ZPAL Br XIV/008. **B**. ZPAL Br XIV/009. **C.** ZPAL Br XIV/015. **D**–**F**. Basal views of the colonies with zooid completely preserved. **D**. ZPAL Br XIV/002. **E**. ZPAL Br XIV/155. **F**. ZPAL Br XIV/157.

borings (Fig. 6H). They may represent imprints of uncalcified periostracum and prismatic layers of the mollusc shells. However, they are rather poorly preserved. All the deeper parts of the zooid walls, toward their basal parts, are composed very thin numerous horizontal layers of flat tablets (Fig. 6). Tablets vary in size in different specimens but usually range from 0.7 to 0.8 µm in thickness. This microstructure pattern shares many similarities with the nacre of molluscan shells (e.g., Mutvei 1983; Carter 1990; Addadi et al. 2006; Checa et al. 2009; De Paula and Silveira 2009).

On the surface of autozooids, discontinuities in the host microstructure are often preserved. It seems likely that these lines reflect successive stages of the boring process connected with the direction and stages of autozooid growth (Fig. 6D).

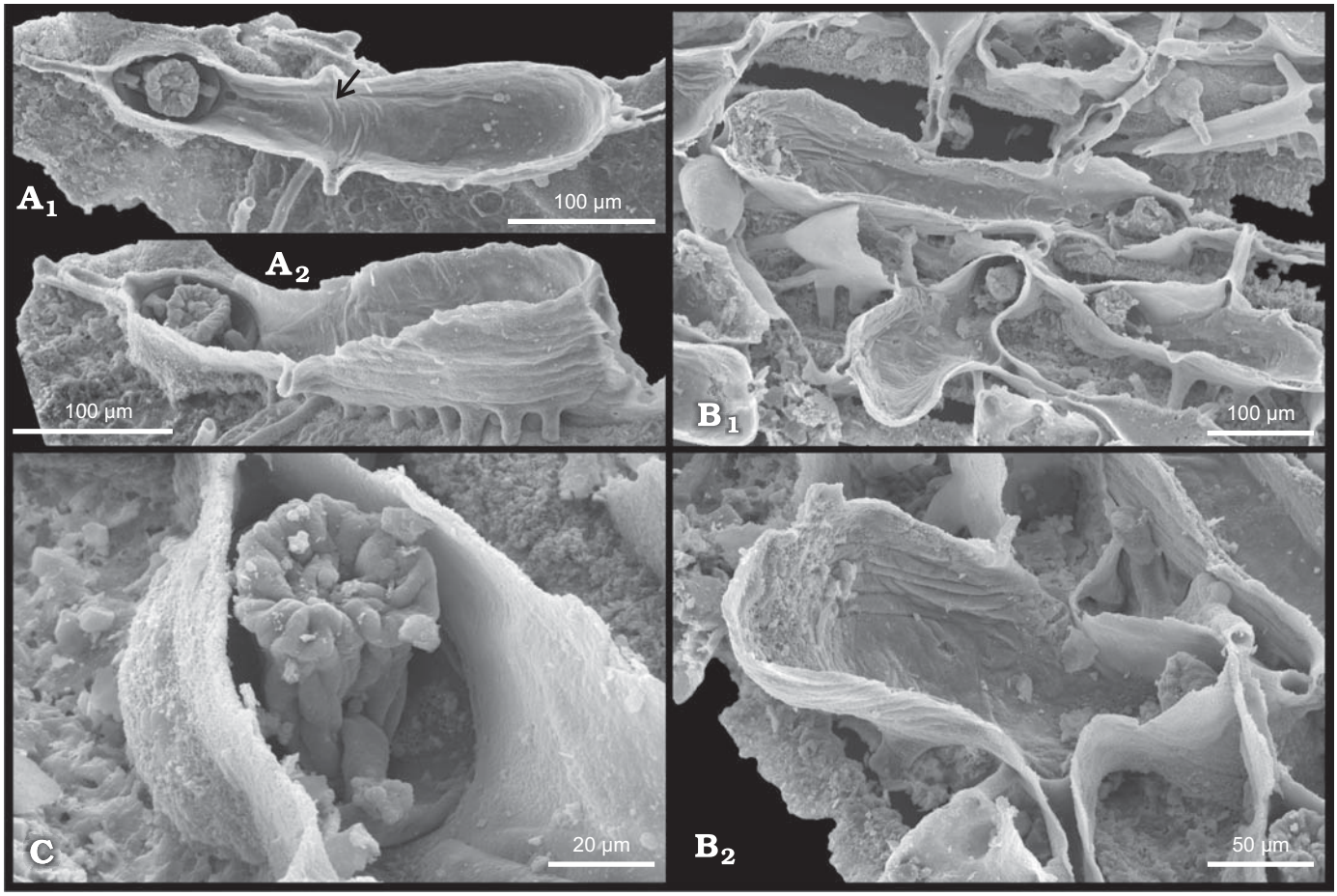

Fig. 4. Early Devonian bryozoan *Podoliapora doroshivi* gen. et sp. nov., from the Doroshiv section, Podolia, Ukraine. SEM photographs showing phosphatized soft-tissue preserved inside autozooids. ZPAL Br XIV/009. **A**. Internal view (A_1) showing wrinkling frontal (arrow) and lateral cystid walls, setigerous collar twisted within the vestibulum, entrance of the main stolon into the autozood is preserved below the vestibulum, secondary-order "stolons" partly preserved in both sides of the autozooid, oblique lateral view (A_2) showing accessory tubules and imprints of the host shell microstructure preserved on the surface of the coating layer. **B**. Internal view of autozooid (B_1) and close-up showing longitudinal parietal muscles and irregular shape of autozooids occurring in dense colonies (B_2). **C**. Internal view showing setigerous collar twisted within vestibulum.

A second type of host shell microstructure has been found only in a few specimens. It differs fundamentally from the first type and is composed of an extremely fine, nanomicron-scale network of microfibrils (Fig. 7). Basal layers are not visible. This microstructure is somewhat similar to the fibrous secondary layer of brachiopod shells (e.g., Williams et al. 2000; Schmahl et al. 2008), however, brachiopod fibres are much coarser (Carter 1990).

The bryozoan cuticle is preserved as a layer of phosphate crystals about 1 µm thick, oriented perpendicular to the surface, visible in the vestibulae area of broken specimens (Fig. $6M_1$, M_2). Some parts of the cystid walls, especially in proximal parts of the autozooids show an empty spaces between their internal and external surfaces (Fig. 6K). This suggests that they may represent mould of the cystid wall. A thin suture is visible between the coating layer and the phosphatised cuticle layer (Fig. 6K). Pyrite fromboids are often attached to the internal cuticle walls of the autozooids (Fig. 5H).

"Fungal" filaments and swellings (Fig. 9) are also coated by a thin layer of calcium phosphate, 1.65–1.85 µm thick. The style of phosphatization is exceptionally fine, such that the imprints of the host shell microstructure are preserved on surface of swellings and filaments. The pattern of the microstructure of the host shell preserved on "fungal" filaments is exactly the same as in co-existing bryozoan specimens. In broken "fungal" swellings, hollow interiors inside are visible (Fig. $9B_6$, B_7). This may indicate the position of the soft-tissue of fungus.

The co-occurring fossils in the limestone samples from the Doroshiv section retain their calcite composition and have been dissolved during the process of dissolution. Commonly occurring coproliths and fecal pellets are phosphatized.

Bryozoan remains

Some fragments of studied bryozoan colonies *Podoliapora doroshivi* gen. et sp. nov., contain well preserved feeding zooids (autozooids) and possible heterozooids linked laterally and frontally by stolon-like tunnels of first-, second-, and

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third-order (terms used in the sense of Pohowsky 1978). The autozooids are oriented nearly horizontally in the substrate, lying immediately beneath the substrate surface. Autozooids are asymmetrical in lateral view (Fig. 2), usually cylindrical to elongate ovoidal, 340–450 μm long. When the substrate is densely bored by bryozoans the shape of the autozooids becomes more irregular. All autozooids are interconnected by main "stolons", developed along their frontal walls, close to the substrate surface (Figs. 2, 5A–C). Original soft-tissues preserved inside the autozooids, include fragments of cuticular body sac together with presumed parietal muscles inside the cuticular wall, and setigerous collars twisted within the vestibule (Fig. 4). The phosphatized fragment of presumed lophophore with encircling collar, and presumed base of the lophophore, inside one, partly retracted collar are also preserved (Fig. 5D, E). The supposed parietal muscles are preserved as thickened wrinkle-shaped folds of the cuticle on the internal surface of the zooid walls (Figs. $4A_1$, B_2, 5F, H, $7B_3$, B_4). Usually, 3–4 semi-circular folds (muscles?) are preserved below the vestibule. Numerous longitudinal U-shaped presumed muscles are arranged along walls in the proximal part of the autozooids (Figs. $4B_1$, $7B_3$). The cuticle is also folded irregularly in some places. The cuticular layer of the autozooids is about 2 μm thick. In places where parietal muscles are present inside the cuticle, the layer is much thicker. No other internal tissues such as the digestive tract or retractor muscle are preserved. The internal walls of the "stolons" are smooth, but soft tissue is not recognizable. The setigerous collars display various degrees of preservation, ranging from excellent preservation to different stages in the postmortem decay process.

In the studied bryozoan colonies, besides the autozooids, there are cavities, empty (Fig. 5G) and partly (Fig. 5F) or fully filled (Fig. 8) with thin laminae composed of amorphous-like calcium phosphate, which form cone-in-cone patterns. The laminae are almost parallel to the substrate surface and slightly concave in its middle part (Fig. 8). The thickness of individual laminae reaches up to 2.6 μm. These laminae are composed of numerous, extremely thin lamellae, ranging from 130 to 160 nm in thickness (Fig. $8A_1$). The laminae are seen as fine striations on the surface of the cavities when the external coated layer is partly removed (Fig. $8C_2$, C_3) or the basal walls of the cavities are not preserved.

These "heterozooid" cavities are mostly cylindrical in shape, rarely ovate or more irregular (Figs. 5G, 8). Their dimensions range from 70 to 120 μm and they are connected to two or three autozooids by stolon-like tubules of third- order and rarely by primary- and secondary-order "stolons" (Figs. 3B, C, 5F, G, 8B, C_1). Outside the bryozoans colonies, such structures have not been found. In dense populations, cavities filled with amorphous calcium phosphate are numerous (Figs. 3, 8B). In extant bryozoans, the polymorphism occurs as "discontinuous variation in the morphology of zooids" (Mukai et al. 1997: 59). The zooids characterized by a reduction of the polypide are termed heterozooids and they are connected with e.g., sexual reproduction, defensive function or cleaning function (Mukai et al. 1997).

The function of the "heterozooids" is unknown. It is speculated that these cavities are "store-rooms" in which the bryozoans accumulated a stock of dissolved food, preserved by phosphatization.

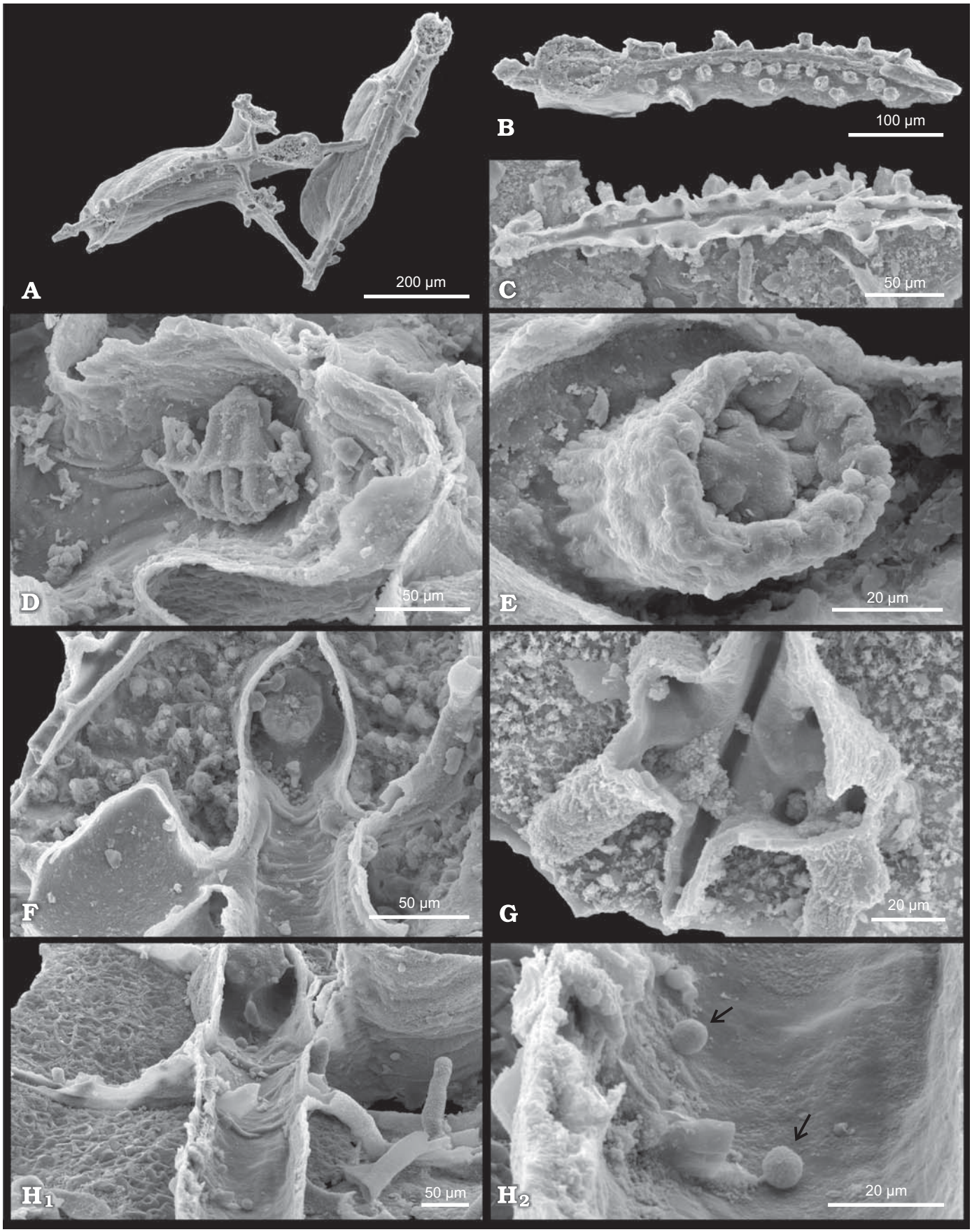
Similar heterozooids filled with granules ("granulations réfringentes") were described by Prenant and Bobin (1956) in living *Spathipora comma* (Soule, 1950). According to Pohowsky (1978), the function and mode of origin of granules is unknown.

The presence of "sac zooids" (heterozooids) have been noted in *Ropalonaria venosa* Ulrich, 1879 from the Upper Ordovician of Ohio, and also *Ropalonaria arachne* (Fischer, 1866) from the Middle Jurassic of France (Pohowsky 1978; Taylor and Ernst 2008). Heterozooids occur also in *Orbignyopora devonica* (Richards, 1974) from the Middle Devonian of New York State, USA (Vogel et al. 1987). They are developed along the main stolons, between the autozooids; their function remains unknown. Rare circular cavities connected to autozooidal cavities and to the primary stolon tunnels have been described in the boring *Pinaceocladichnus cristatus* Botquelen and Mayoral, 2005 from the Early Devonian of France (Botquelen and Mayoral 2005).

In *Podoliapora doroshivi*, the autozooids and "heterozooids" are connected to the substrate surface by a number of short accessory tubules (max. 17 μm in length and 13.0–15.9 μm in external diameter, 7.9–10.6 μm diameter of internal canal) which project from the frontal surface of zooids (Figs. 2, $4A_2$, 5A–C, 6G, J, L, $7B_2$, 8). In the autozooids they are developed close to the main "stolons". Their internal canals with probably original cuticular walls, as well as surrounding interstitial space (preserved as calcium phosphate moulds) opened on the substrate surface. The cuticular walls of the canals were probably connected with the soft-tissue of the main "stolon", but are not connected with the body cavity of the autozooids.

In some living genera (e.g., *Penetrantia*), accessory tubules project out from stolons and extend to the substrate surface. In species lacking these tubules, the stolons are located close to the surface of the shell and communicate with the exterior by frontal pores (Pohowsky 1978: text-fig. 3).

Fig. 5. Early Devonian bryozoan *Podoliapora doroshivi* gen. et sp. nov., from the Doroshiv section, Podolia, Ukraine. **A**, **B**. External frontal views of autozooids showing main "stolons" and accessory tubules. **A**. ZPAL Br XIV/174. **B**. ZPAL Br XIV/092. **C**. Internal view of partly preserved autozooid (vestibular part not preserved), ZPAL Br XIV/129. **D**. Internal view of autozooid showing displaced presumed lophophore, ZPAL Br XIV/078. **E**. Internal view of autozooid showing presumed base of the lophophore preserved inside the setigerous collar, ZPAL Br XIV/168. **F**. Internal view showing cystid walls, setigerous collar and connection with partly filled "heterozooid" cavity, basal walls collapsed, ZPAL Br XIV/007. **G**. Internal view of empty "heterozooid" cavity showing place of stolon and entrances of accessory tubules preserved on the surface of the frontal wall, ZPAL Br XIV/189. **H**. Internal view of autozooid (H_1) and close-up showing pyrite framboids (H_2) attached to the internal cuticle walls, ZPAL Br XIV/008. →



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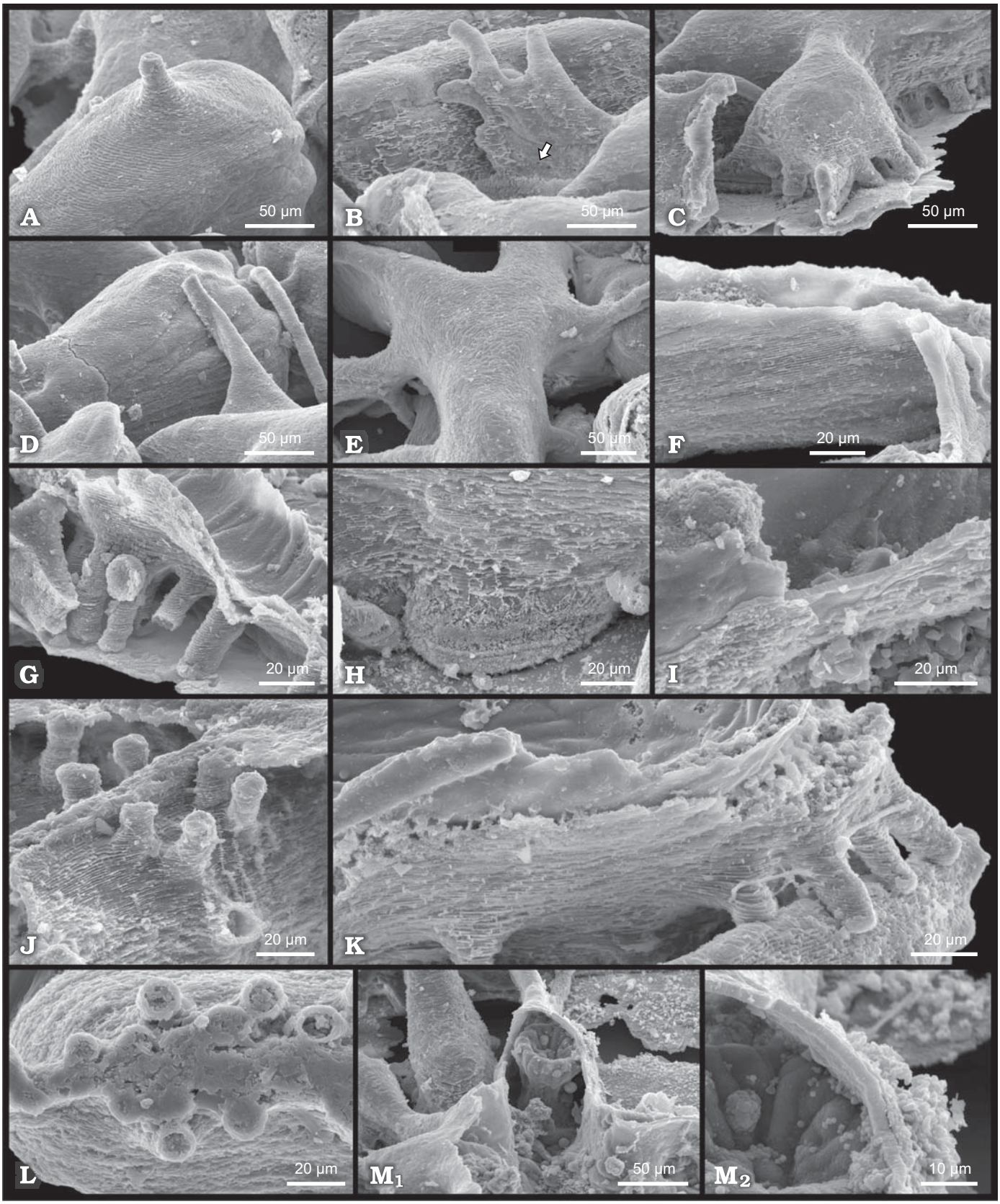

Fig. 6. Early Devonian bryozoan *Podoliapora doroshivi* gen. et sp. nov., from the Doroshiv section, Podolia, Ukraine. SEM photographs showing imprints of the molluscan host shell microstructures preserved on the surface of the coating layer (internal mould of the interstitial space). **A**. Basal part of the autozooid specimen, ZPAL Br XIV/155. **B**. Oblique lateral view showing the coating layer with host shell microstructure preserved; the external surface of cuticle is visible only in places where the coating layer have been damaged; arrow shows poorly visible micro-pore on the surface of cuticle, ZPAL Br XIV/002. →

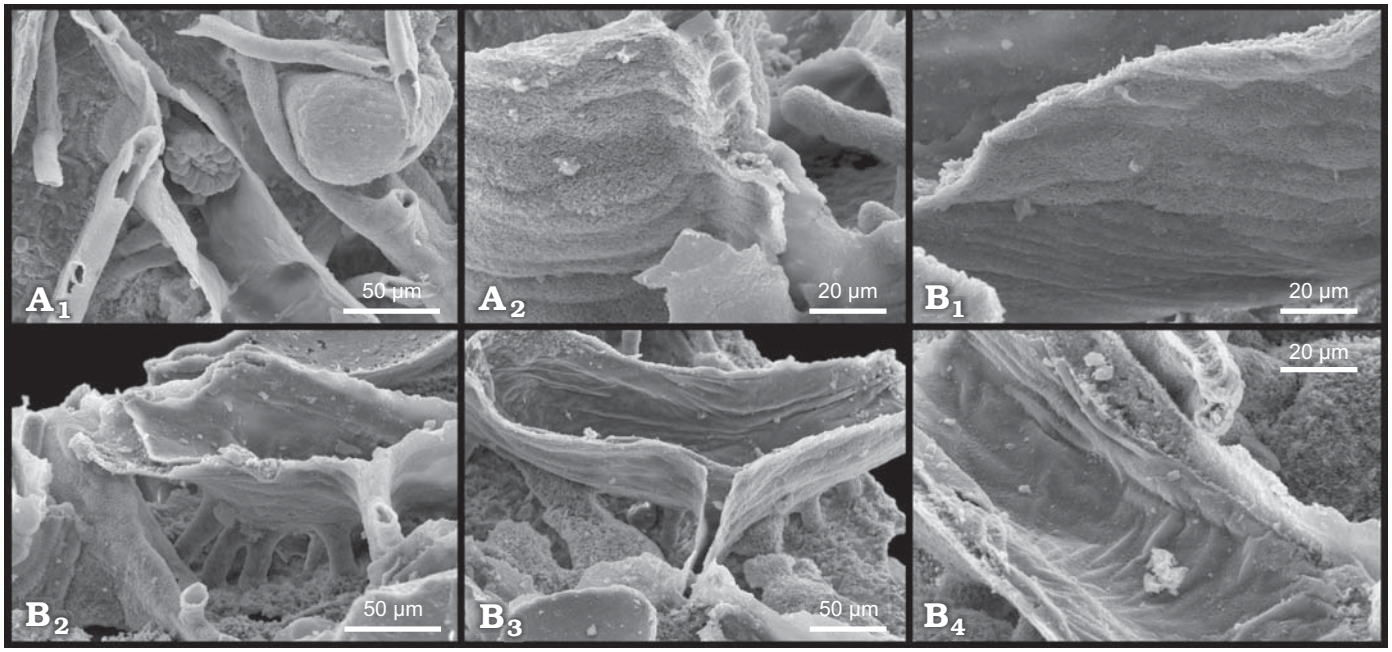

Fig. 7. Early Devonian bryozoan *Podoliapora doroshivi* gen. et sp. nov., from the Doroshiv section, Podolia, Ukraine. SEM photographs of zooids coated by micro-fibrils of host shell microstructure. **A**. ZPAL Br XIV/008. Basal view of partly preserved autozooid, cylindrical-heterozooid and "stolons" (A_1). Lateral view of proximal part of autozooid showing partly preserved main tunnel-like stolon (A_2). **B**. ZPAL Br XIV/009. Lateral view of side wall of autozooid (B_1). Partly preserved autozooid with accessory tubules and internal view showing cuticle layer preserved inside the zooid and external coated layer with imprint of host shell microstructure (B_2). Obliquely internal view of autozooid (vestibular part not preserved) showing cuticle with folds of longitudinal parietal muscles preserved (B_3). Internal view of autozooid showing folds of circular and longitudinal muscles (B_4).

Fungal-like remains

Organic matrix, which is a component of mineralized skeletons, frequently serves as food sources for endolithic heterotrophic microorganisms such as "fungi" (Golubic et al. 1975, 2005).

Associated with some fragments of the studied boring bryozoan colonies are microendolithic borings comparable to those produced by recent fungi. Two specimens (morphotype A) (Fig. 9), are similar to the boring of "fungi" *Saccomorpha terminalis* Radtke, 1991, illustrated by Wisshak et al. (2005: fig. 10D) from an experimental station located in the northern Kosterfjord area, SW Sweden. They are also similar to the boring *Orthogonum appendiculatum* Glaub, 1994, described from the Jurassic (Bajocian) of France (Glaub 1994).

They are also similar to the chlorophyte microboring *Rhopaliacaten ata* as described by Radtke (1991) and recently established *Rhopalia clavigera* by Golubic and Radtke (2008). There also is some similarity to the ubiquitous chlorophyte microboring *Ichnoreticulina elegans* as revised and described by Radtke and Golubic (2005) and by Wisshak et al. (2011).

The network of fine filaments of almost uniform diameter, ranging from 4.4 to 4.7 µm in diameter, are close and almost parallel to the substrate surface. Branches are perpendicular to the filaments and abruptly end after 13–14 µm (Fig. $9B_2$). At the ends of branches, small openings, 1.6–1.7 µm in diameter are visible (Fig. $9B_4$). Large, 12–16 µm diameter irregularly bulbous swellings also occur (Fig. $9A_4$, B_5–B_7). Some swellings appear longitudinally subdivided. This feature occurs only in large swellings (Fig. $9B_7$). The narrow filaments, 870–880 nm in diameter, co-occur within the colony (Fig. $9B_4$).

In one sample, an unknown fungal-like species (morphotype B) is associated with the boring bryozoans (Fig. 10). Only the filaments preserved in the deeper part of the bored host shell are visible; they are numerous and straight. They are almost uniform in diameter, 4.5–5.0 µm in width. Branches of filaments are short (16–21 µm in length) and perpendicular to

C. Oblique lateral view showing partly preserved coating layer and accessory tubules preserved on the frontal part of zooids, ZPAL Br XIV/002. **D**. Basal surface of the autozooid wall, showing dislocation lines possibly reflecting successive stages of autozooid growth, ZPAL Br XIV/157. **E**. Close-up of autozooid showing basal wall and imprints of host shell nacre microstructure; note the irregular shape of the autozooid, ZPAL Br XIV/004. **F**. Lateral view of the autozooid wall showing imprint of the host nacre microstructure, ZPAL Br XIV/117. **G**. Oblique internal view of autozooid with host shell microstructure preserved on the surface of accessory tubules and permineralized cuticle layer visible inside the zooid, ZPAL Br XIV/122. **H**. Lateral view of vestibular part of the autozooid showing different layers of host shell microstructure, ZPAL Br XIV/135. **I**. Partly preserved vestibular part of autozooid showing damaged coating layer, note the external and internal surfaces of cuticular layer visible inside, ZPAL Br XIV/134. **J**. Frontal part of autozooid showing accessory tubules and main" stolon", ZPAL Br XIV/142. **K**. Lateral view of proximal part of partly preserved autozooid showing coating layer and cuticle layer visible inside, ZPAL Br XIV/055. **L**. Frontal wall of autozooid showing accessory tubules, ZPAL Br XIV/103. **M**. Lateral internal view of vestibulum showing setigerous collar (M_1) and close-up showing cuticular layer and its external coating layer, visible in transverse section (M_2), ZPAL Br XIV/136.

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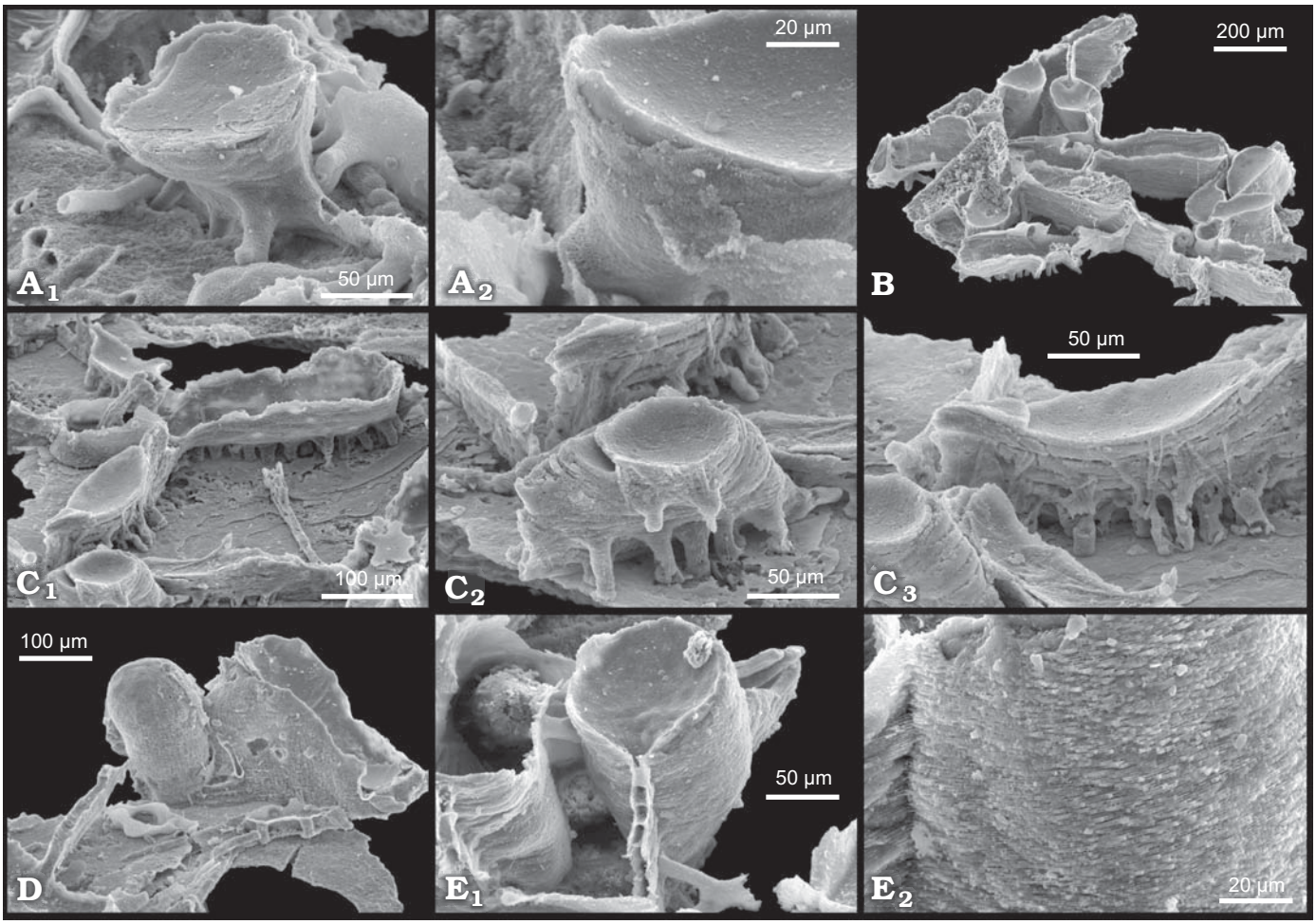

Fig. 8. Early Devonian bryozoan *Podoliapora doroshivi* gen. et sp. nov., from the Doroshiv section, Podolia, Ukraine. **A**. ZPAL Br XIV/009. Lateral view of cylindrical-shaped heterozooid cavity, basal wall collapsed (A_1). Close-up showing external coating layer and internal lamellae, basal wall collapsed (A_2). **B**. ZPAL Br XIV/011. Oblique view of the partly preserved colony showing cylindrical heterozooids, basal wall collapsed. **C**. ZPAL Br XIV/112; Lateral view showing autozooids and ovate-shaped heterozooids (C_1), lateral views of heterozooids showing layers infilling the interior of the cavity, visible in places where the coating layer has not been preserved (C_2, C_3), basal walls collapsed. **D**. ZPAL Br XIV/071. Fragmentary preserved colony in oblique view showing heterozooid cavity with basal wall preserved. **E**. ZPAL Br XIV/137. Oblique view of cylindrical heterozooid with basal wall collapsed (E_1), close-up showing host shell microstructure preserved on the surface of the coating layer (E_2).

the main hyphae (Fig. 10C). The boring differs from the species described above in the absence of swellings. Imprints of the host shell microstructure are poorly visible on these "fungal" filaments.

Many of the fine branches of both "fungal" borings may show the "infestation" of bryozoan zoods (Figs. $9A_2$, A_3, B_2–B_4, 10D–F). "Fungal" branches are usually very short, but those "infesting" bryozoans are much longer and directed towards the surface of the feeding zooids (Fig. $9B_4$). "Fungal" filaments have not been found inside zooids with preserved collars which were likely to have been alive shortly before phosphatization.

Comparable infestation of endolithic algae by parasitic fungi has been noted in many Recent examples (e.g., Gatrall and Golubic 1970; Priess et al. 2000; Bentis et al. 2000; Golubic et al. 2005). Bentis et al. (2000) reported fungal attacks on coral polyps and algal filaments by hyphal branches and then growth inside these algal filaments.

Systematic palaeontology

Phylum Bryozoa Ehrenberg, 1831

Class Gymnolaemata Allman, 1856

Order Ctenostomata Busk, 1852

Genus *Podoliapora* nov.

Etymology: From Podolia and Latin *pori,* pora; common ending of bryozoans names.

Type species: *Podoliapora doroshivi* sp. nov.; see below.

Diagnosis.—Non-pedunculate boring ctenostome with long, cylindrical or irregularly developed autozooids, disposed parallel to substratum surface, along main "stolon". Aperture rounded-ovate disposed symmetrically along "stolon", orifice narrow slit-like.

Podoliapora doroshivi sp. nov.

Figs. 2–8.

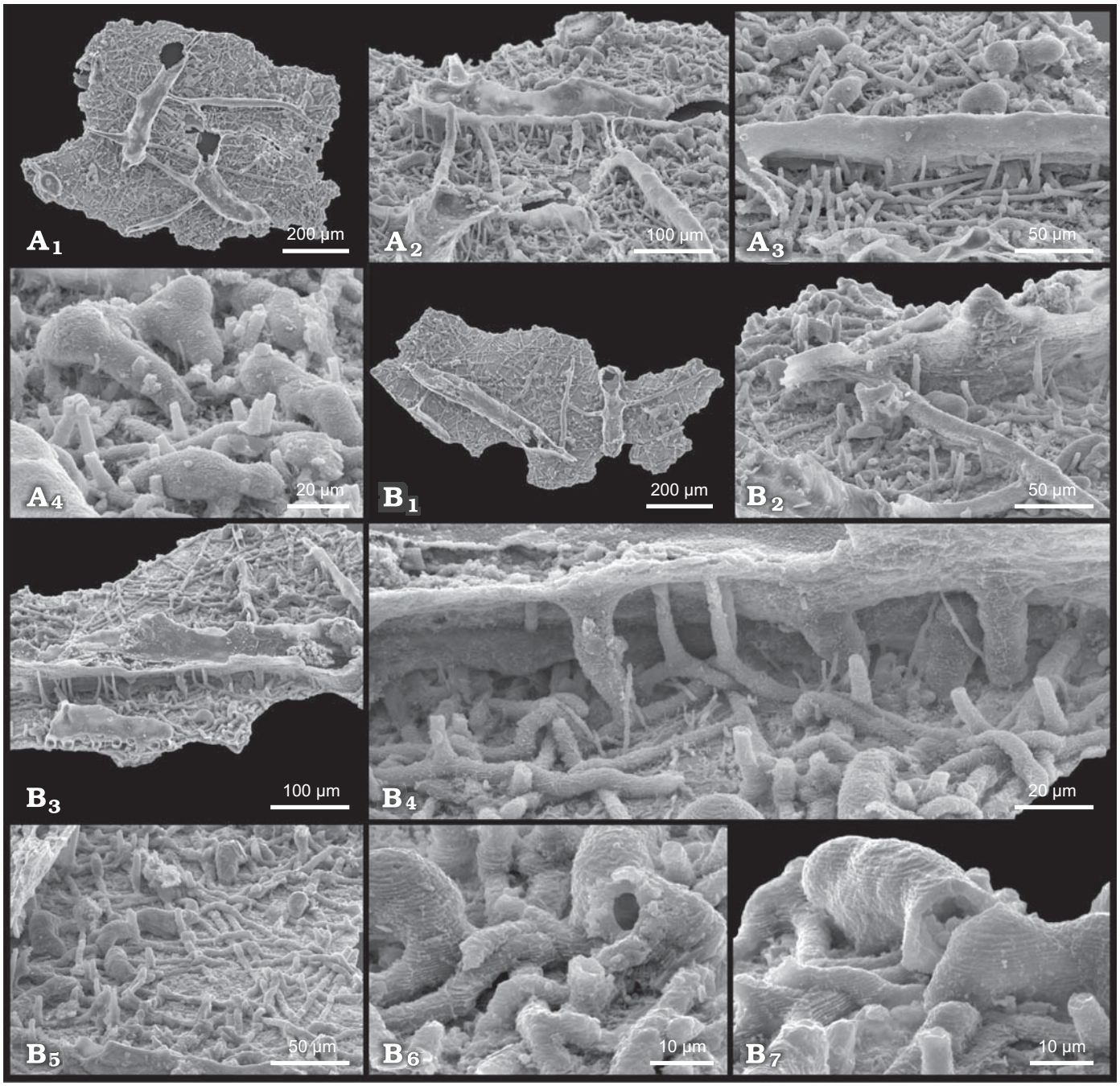

Fig. 9. SEM photographs of phosphatized endolithic community of bryozoans and "fungi" (morphotype A) from the Early Devonian of Doroshiv section, Podolia, Ukraine. **A**. ZPAL Br XIV/067. Fragmentary colony showing a network of irregularly branched filaments and rare bryozoan zooids (A_1). Oblique view showing partly preserved bryozoans autozooids and 'fungal' hyphae (A_2). Oblique view showing fungal attack on supposed juvenile bryozoan autozooid (A_3). Close-up showing "fungal" filaments with branches and irregularly shaped swellings, note imprints of host shell microstructure preserved on the coating layer (A_4). **B**. ZPAL Br XIV/101. Pattern of fungal filaments and bryozoans zooids (B_1). Close-up of partly preserved bryozoan zooids attached by "fungal" hyphae (B_2). Oblique view showing partly preserved autozooid with accessory tubules visible, attacked by fungal branches (B_3). Close-up of autozooid attacking by "fungal" branching (B_4). Oblique view of "fungal" colony (B_5). Close-up of irregularly shaped "fungal" swellings showing hollow interiors, note the host shell microstructure imprints preserved on the coating layer (B_6, B_7).

Etymology: After the type locality.

Holotype: ZPAl Br XIV/009, phosphatized colony (Fig. 3B).

Type horizon: Early Devonian, Lochkovian, Chortkiv Formation of the Tyver Group.

Type locality: Doroshiv, Podolia, Ukraine.

Material.—More than 150 fragments of colonies.

Diagnosis.—A *Podoliapora* which characterized by cylindrical or irregularly developed autozooids, aperture rounded-ovate disposed symmetrically along "stolon", with the dimension ranging from 58 to 64 µm, covered inside by the mem-

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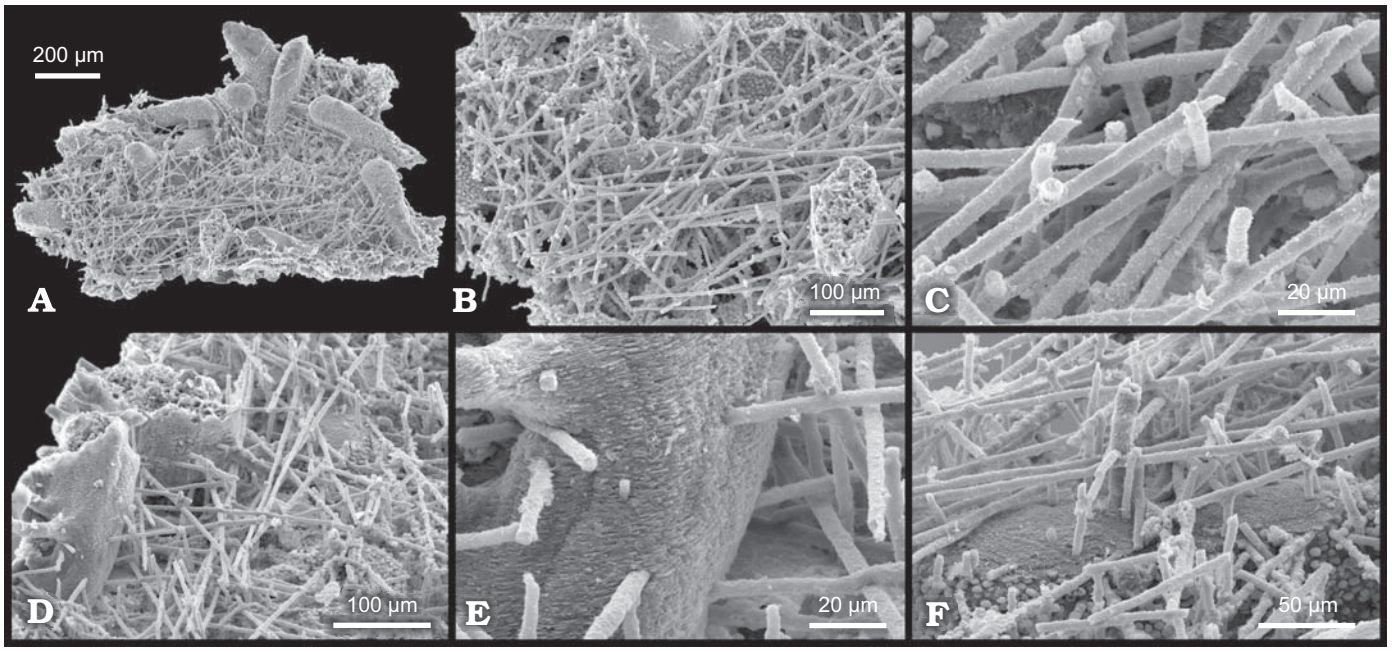

Fig. 10. SEM photographs of phosphatized endolithic community of bryozoans and "fungi" (morphotype B) from the Early Devonian of Doroshiv section, Podolia, Ukraine. ZPAL Br XIV/154. **A**. Fragmentary preserved colony in basal view. **B**. Oblique view showing filaments with perpendicular branches. **C**. Close-up of branching filaments. **D–F**. Side views of bryozoan autozooid perforated by endolithic "fungal" hyphae.

brane with narrow slit-like orifice in its middle part. Two rows of accessory tubules occur along both sides of main "stolon" on autozooids. Up to four lateral stolon-like tubules are located on both sides of the autozooid. "Heterozooids" are numerous, mostly cylindrical in shape, rarely ovate or more irregular; connected to two or three autozooids by "stolons". Fossilized setigerous collar and cuticular body sac are preserved.

Discussion.—*P. doroshivi* differs from similar species of *Orbignyopora* Pohowsky, 1978 in the presence of numerous lateral stolon-like tubules and the presence of specialized heterozooids, presumed to function as store-rooms. Further study is required to determine its family and superfamily range (see discussion in Todd 2000).

Stratigraphic and geographic range.—Type locality only.

Discussion

Phosphatization.—Phosphatization of soft-tissues and skeletal remains provides an insight into the anatomy of many extinct animals. Three-dimensional preservation of soft-tissue is usually associated with environmental conditions enabling early diagenetic secondary phosphatization capable of preserving exceptionally fine detail (e.g., Allison 1988; Briggs et al. 1993; Briggs and Kear 1994; Briggs and Wilby 1996; Hof and Briggs 1997; Porter 2004; see also Dornbos 2011, and Hendy 2011 for reviews).

Examples of phosphatization of soft-tissues have been reported mostly from the Cambrian–Early Ordovician, but there are also examples from the Cretaceous, Eocene and rarely from other epochs (e.g., Walossek 1993; Weitschat 1995; Maas et al. 2003, 2006; Dong et al. 2004; Klug et al. 2005; Trinajstic et al. 2007; Olempska et al. 2012).

The taphonomy of the phosphatized bryozoans from Podolia indicates rapid replacement of tissues before decay of the bryozoan body was completed. Relatively decay-resistant materials, such as the originally chitinous cystid walls and membraneous collar, survived as organic remains. In living non-boring ctenostomes, the collar is attached to the atrial sphincter (diaphragm) (Mukai et al. 1997; McKinney and Dewel 2002). This diaphragm is not preserved in *Podoliapora doroshivi*. Tissues such as the lophophore, digestive tract, tentacle sheath and retractor muscles, have not been preserved, apparently because these tissues were more labile and their decay was faster than the phosphatization process. Rogick (1945: 211) noted that in Recent ctenostome *Aeverrillia setigera* (Hincks, 1887) the setigerous collar "is often found in excellent condition even when all the zooid contents except the zooecial wall have disintegrated".

It is likely that the decaying tissues of bryozoans and/or the host organisms may have provided phosphate ions. Among the fossils in the Doroshiv section, phosphatized coprolites and fecal pellets are common remains. Coprolites contain large quantities of mineral phosphate (e.g., Chin et al. 2003) and it is likely that this facal material may have been one of the sources of phosphorus. The boring habit, small size of the bryozoan zooids, subsequent anoxia in their living habitat, perhaps due to burial, and low pH may have played important roles in the soft-tissue preservation (e.g., Briggs et al. 1993).

Bryozoan boring mechanism.—Boring autotrophic and heterotrophic microorganisms actively penetrate the hard carbonate substrates which they inhabit (Golubic et al. 1981). The processes of biomineralization and demineralization (bioerosion) have been studied since the 19th century (reviewed by Ehrlich et al. 2008, 2009 and references therein). It has been suggested by many authors that substrate dissolution results from the production of acid or chelating fluids at the apical cells of euendolithic organisms (Schneider and Le Campion-Alsumard 1999). Alexandersson (1975) suggested the existence of specialised boring organelles in the boring cyanobacterium *Hermatonema*.

Recently, Garcia-Pichel et al. (2010) found in experimental investigations, that the boring photoautotrophic cyanobacteria (strain BC008) could decrease the extracellular Ca^{2+} concentration at the excavation front, via the active intracellular pump transport of Ca^{2+} along cyanobacterial trichoms, and re-precipitate it as a micrite mud at the distal end of the borehole. The uptake and transport was driven by the enzyme P-type Ca^{2+}-ATPase (Garcia-Pichel et al. 2010).

Micrite is commonly associated with algal and cyanobacteria borings (e.g., Bathurst 1966; Alexanderson 1975; Kobluk and Risk 1977; Schneider and Le Campion-Alsumard 1999; Chacón et al. 2006; Garcia-Pichel 2006; Garcia-Pichel et al. 2010). The precipitation of micrite as cements within the matrix of bioeroded carbonates in tropical environments is a fast process, almost contemporaneous with boring (Chacón et al. 2006).

The physiological mechanisms by which bryozoans are able to excavate calcareous substrates remains unknown; however, most authors have postulated that this process is chemical in nature because of the absence of mechanical devices for excavation (Marcus 1938; Silén 1947; Pohowsky 1978).

The exact mechanisms that enable bryozoans to dissolve solid $CaCO_3$ (host shell) and transport away Ca^{2+} produced during the boring process are unknown. Re-precipitation of the Ca^{2+} ions may potentially occur simultaneously outside and inside the bryozoan colony. It seems possible that efflux of Ca^{2+} occurred from the boring front with transportation of Ca^{2+} through the interstitial space surrounding the canals of accessory tubules by extracellular circulation/diffusion and deposition of micrite out of the colony at the surface of the host shell or its excretion into the external environment. However, intracellular transport of Ca^{2+} (via the stolonal funiculus?) to the vacated cavities (heterozoids) and local deposition as carbonate mud also seems possible.

The interstitial space may also provide for the passage of water into a space surrounding the body wall of the autozooids to permit extrusion of the lophophore (see also Pohowsky 1978). The function of canals is not clear. In modern ctenostomes, the parietal muscle bundles which are associated with the cystid wall deform the autozooid wall and assist in protrusion of the lophophore. Retraction is a very rapid process (Hayward 1985; Mukai et al. 1997).

Voigt and Soule (1973: 29, pl. 4: 1) illustrated pale areas surrounding around the orifice of the bryozoans boring *Penetrantia gosaviensis* Voigt and Soule, 1973, from the Cretaceous of Austria, suggesting "a chemical alteration of the shell-matrix affected by the zooids". Pohowsky (1978: pl. 11: 1) illustrated Recent *Penetrantia densa* Silén, 1946 from South Africa with calcium carbonate secreted by the bryozoan around the apertures and along stolons on the substrate surface.

The host shell microstructure.—The imprints of the host shell microstructure, preserved on the apatite coating layer may have originated when the calcium phosphate filled the space between the still intact animal body and bored shell. This space ("interstitial space" of Garcia-Pichel 2006) was probably filled by dissolving acids or chelating fluids and residues of the dissolution process by the bryozoan. The imprints of host shell microstructure described here became phosphatized during early diagenesis.

Imprints of the host shell microstructure on the surface of resin casts or phosphate fillings of the tunnels were noticed in several species of microborers (e.g., Golubic 1969; Alexanderson 1975; Golubic et al. 1975; Runnegar 1985; Mao Che et al. 1996). According to Mao Che et al (1996), fungi are common boring microorganisms in the nacreous layer of the mollusc shell of black pearl oyster *Pinctada margaritifera* var. *cumingii* penetrating up to 3 mm into the shell.

Imprints of shell microstructure preserved as phosphatic moulds and casts are common in mollusc shells from the Cambrian (e.g., Runnegar 1985; Kouchinsky 1999, 2000; Feng and Sun 2003; Vendrasco et al. 2010, 2011). The earliest nacre structure is known from the Ordovician (Mutvei 1983).

Conclusions

Boring microorganisms were an important component of the early Palaeozoic ecosystems. The setigerous collar is a conserved feature which these exceptional fossils show to have existed for at least 416 Ma. Specialized "heterozooids" filled with laminated amorphous calcium phosphate, are interpreted as store-rooms in which the bryozoans built a stock of nutrients (in the form of lipids?).

The heterotrophic bryozoans were able to dissolve calcium carbonate and simultaneously micrite mud has been re-precipitated on the substrate surface and/or in the vacated heterozoids.

Associated "fungal" borings include examples of associations between "fungi" and bryozoans.

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