Fossilized soft tissues in Palaeozoic bryozoans

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Abstract: Thin sections of three Palaeozoic bryozoans reveal fossilized soft tissues that show the position of organic cuticle and internal structures such as the membranous sac and gut. The fossilization occurred apparently due to fast burial under anoxic conditions. The position of a membranous sac in the Permian trepostome *Rhombotrypella superangustata* is indicative of a progressive polypide cycle. The position of the polypide in the Ordovician *Graptodictya delicata* behind the superior and interior hemisepta suggests a protective function of the hemisepta.

Key words: morphology, Bryozoa, fossilization, Palaeozoic.

BRYOZOANS are colonial, mostly marine, suspension feeders that often produce calcareous skeletons. Their proven fossil record starts in the Cambrian (Zhang et al. 2021). The majority of Palaeozoic bryozoans belong to the group called Palaeostomata Ma et al., 2014. These are calcified bryozoans represented by c. 600 genera with the major occurrence from the Early Ordovician to the Late Triassic (e.g. Ernst 2020).

Individuals of bryozoan colonies (called zooids) share the basic anatomy of bryozoans, namely they are divided into cystids and polypides (e.g. Schwaha 2020). The cystids comprise the entirety of the body walls, which cover the hard parts of the zooecial chamber (or zooecium). Polypides are developed from the tissues of the cystids and contain a lophophore with a tentacle crown and digestive apparatus (Fig. 1). The mouth is situated inside the tentacle crown, leading to a U-shaped gut that ends with an anus outside of the tentacle crown (Ectoprocta). Polypides are normally retracted inside the cystids (Fig. 2A, B, D), and are protruded for feeding (Fig. 2C, E). Polypides undergo periodic degeneration–regeneration cycles.

The protrusion of the polypid occurs under hydrostatic pressure (e.g. Taylor 1981). Uncalcified bryozoans such as ctenostomes establish the necessary pressure by the action of various groups of muscles, which contract the flexible membrane of the outer wall (e.g. Hayward 1985; Winston & Migotto 2020). Bryozoans with calcified walls (internal or external) evolved various mechanisms to establish hydrostatic pressure inside the cystid (e.g. Taylor 1981).

Stenolaemate bryozoans share the presence of a membranous sac, which produces hydrostatic pressure inside the rigid cystid (e.g. Borg 1926; Nielsen & Pedersen 1979; Winston & Migotto 2020). The membranous sac envelops the polypid, and its contraction by annular muscles pushes the polypid outwards (Fig. 1).

There is no exact knowledge about the internal morphology of the extinct Palaeostomata. However, their zooids are thought to have a similar morphology to those of modern Cyclostomata (e.g. Boardman 1971, 1973, 1999). The finding of fossilized remnants of soft parts in Palaeostomata can facilitate the understanding of the internal morphology of this group (e.g. McKinney 1969; Boardman 1973, 1998). Fossil bryozoans often contain so-called brown deposits that indicate remnants of soft tissues (e.g. Boardman & McKinney 1976; Ernst & Voigt 2002).

The present paper describes three newly found examples of fossilized soft parts in autozooecial chambers of Palaeostomata in a trepostome, a fenestrate, and in a cryptostome species.

MATERIAL AND METHOD

Bryozoans were studied in thin sections (24 × 48 mm). The studied material comes from three localities. Trepostome *Rhombotrypella superangustata* Morozova, 1970 (Fig. 3A, B) comes from the Assistance Formation, Permian (Roadian) of Lake Hazen, Ellesmere Island, Canada (Ernst & Nakrem 2022). The studied sample (one thin section) is deposited at the Canadian Museum of Nature, Ottawa, Canada, and is part of the Nunavut Collections (NUIF 2755b).

The fenestrate *Hemitrypa* sp. comes from the Nims Member of the Upper Junkerberg Formation (Eifelian, Middle Devonian) near the village Gondelsheim, Prüm Syncline, Eifel, Germany (Ernst 2008). The studied material (four thin sections) is housed at the Research Institute and
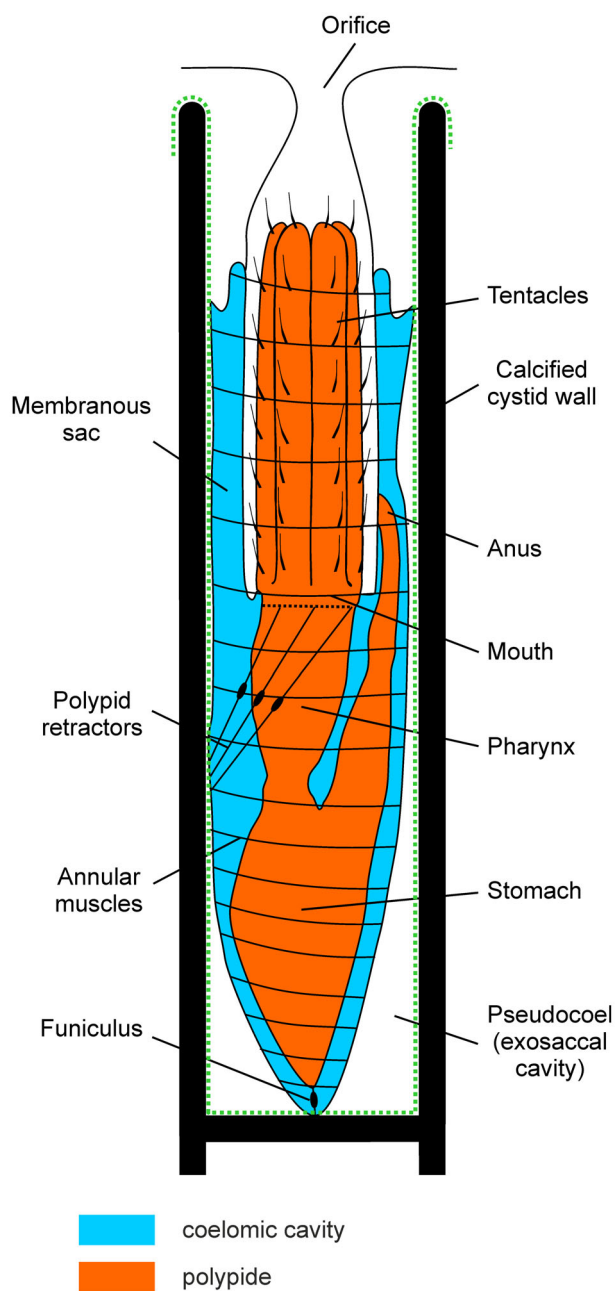
FIG. 1. Schematic drawing of a palaeostomate zooid with retracted polypide. The green dotted line represents the peritoneum with inner epidermis. Modified after Boardman (1971) and Nielsen (2013).

Natural History Museum (Frankfurt am Main, Germany), under the numbers SMF 64233–64237.

The cryptostome *Graptodictya delicata* Männil *in* Gorjunova & Lavrentjeva, 1993, comes from the Steinvika Formation (Sandbian–Katian, Ordovician) of Steinberg, Norway (59°45.637′; 009°59.036′). The studied material (two thin sections) is housed at the Natural History Museum in Oslo, Norway, under the numbers PMO 222.298 and PMO 222.300.

Samples of living ctenostomes *Alcyonidium gelatinosum* (Linnaeus, 1761) and *Amathia* sp. and a cheilostome *Electra pilosa* (Linnaeus, 1767) were collected in the Baltic Sea near Kiel in the summer of 2010 (Fig. 2).

RESULTS

Studied thin sections (longitudinal sections, cut along the growth direction) contain transparent partitions (formed by sparite, or blocky calcite) inside the autozooecia. These partitions are in immediate contact with the skeletal walls and differ in their transparency from the surrounding matrix.

Rhombotrypella superangustata *Morozova, 1970*

This trepostome bryozoan developed branched ramose colonies. Autozooecia in *Rhombotrypella superangustata* are long and prismatic, and have a polygonal shape in transverse section. Ring septa, or perforated diaphragms, occur at regular distances in the exozone. The object inside the autozooecium (Fig. 3A, B) represents a sac-shaped structure attached to the zooecial wall at its apical part. The wall of the sac is thin, dark-coloured, and sharply defined. Inside of the sac, a remnant of a U-shaped brownish structure is visible (arrow). The sac is constrained between two successive ring septa.

Hemitrypa *sp.*

The fenestrate *Hemitrypa* sp. developed a reticulate, apparently funnel-shaped colony. This species possesses short autozooecia, pentagonal in mid-tangential section, with apertures positioned at the distal end of the chamber. Several autozooecia in the studied sample contain a transparent partition lining the wall of the autozooecial chamber (Fig. 3C, D). These partitions are sharply separated from the microsparitic matrix outside in the area of aperture (red arrows), and contain centrally positioned invaginations. The walls of the invaginations are partly covered with brownish and black deposits.

Graptodictya delicata *Männil in Gorjunova & Lavrentjeva*

The cryptostome (ptilodictyine) species *Graptodictya delicata* developed flat branched colonies with autozooecia
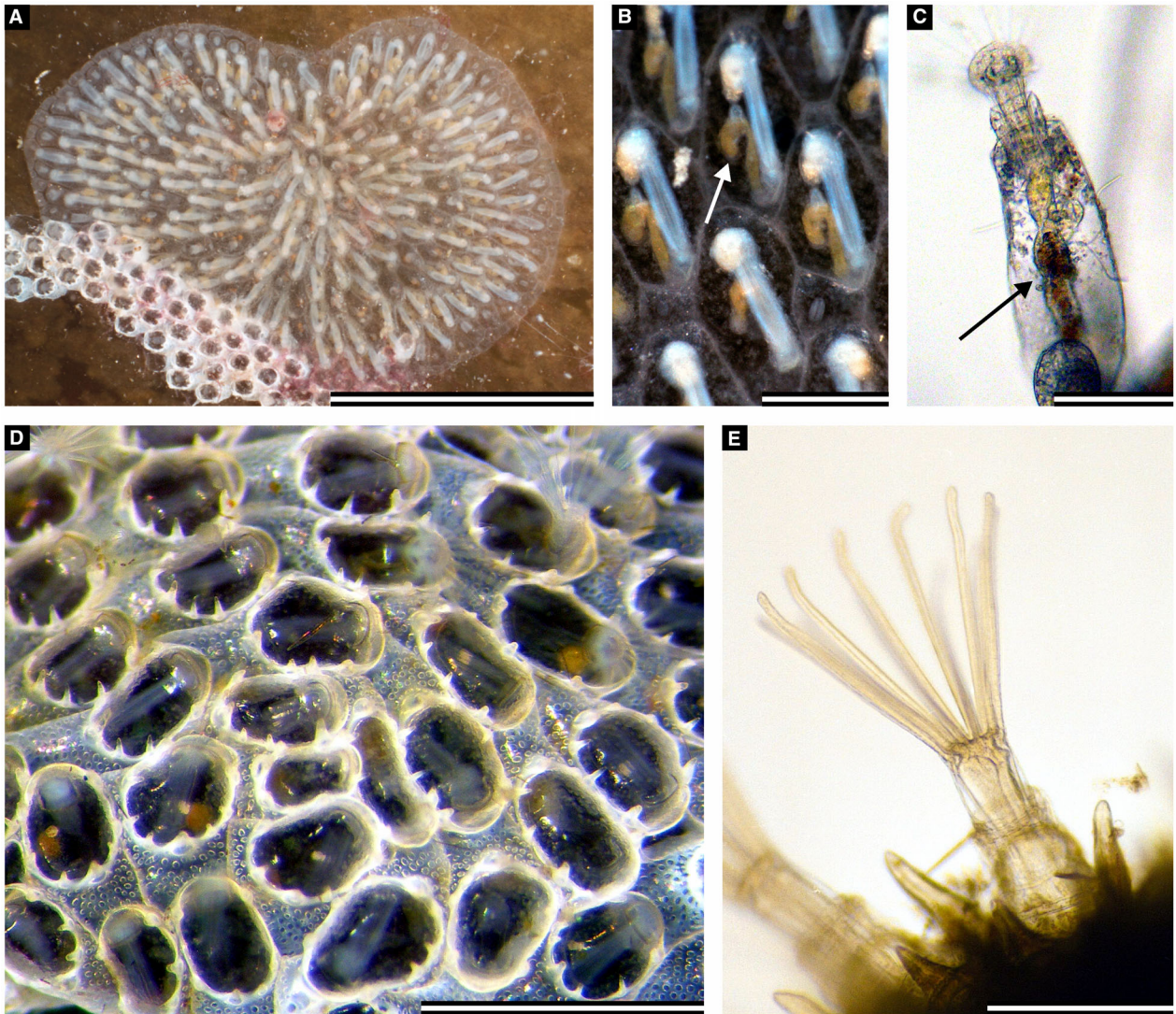
FIG. 2. Living bryozoans. A–B, ctenostome *Alcyonidium gelatinosum* (Linnaeus), Baltic Sea: A, encrusting colony on red alga overgrowing *Electra pilosa*; B, fragment of the colony surface showing retracted polypides, the arrow indicates the gut. C, ctenostome *Amathia* sp., Baltic Sea, single zooid with everted tentacle crown; arrow indicates the gut. D–E, cheilostome *Electra pilosa* (Linnaeus), Baltic Sea: D, colony surface showing autozooecia with both everted and retracted polypides; E, tentacle crown of an everted polypid. Scale bars represent: 5 mm (A); 0.5 mm (B); 0.2 mm (C, E); 1 mm (D).

growing along mesotheca and bending in the exozone. They possess two hemisepta, inferior and superior. Inferior hemisepta are long, thin, curved distally, positioned on the basal (proximal) wall of autozooecia. Superior hemisepta are blunt, short, positioned distally in the zooecial chamber on the transition between endozone and exozone. Autozooecia in the studied colony contain transparent partitions with sac-shaped invaginations filled by black granular material (Fig. 3C, D). The invaginations have narrow vestibules connected to the microsparitic matrix outside of the autozooecial chamber, and widened proximal parts that are positioned behind the inferior hemisepta.

DISCUSSION

Preservation

The presence of the blocky calcite in these areas implies precipitation of calcitic material during early marine-burial diagenesis inside voids (e.g. Melim *et al.* 1995; Flügel 2010). Such sparite can be formed only in low Mg conditions, which is usually the case inside pores or during meteoric diagenesis (A. Munnecke, Erlangen, pers. comm.). The (partial) preservation of soft tissues can be explained by extremely fast burial of bryozoans and precipitation of sparite in voids formed by the outer
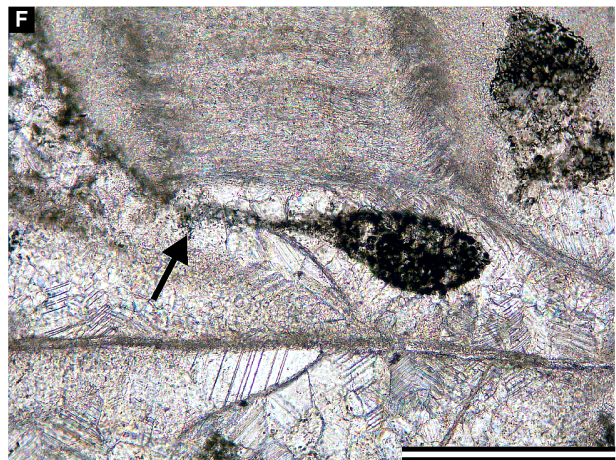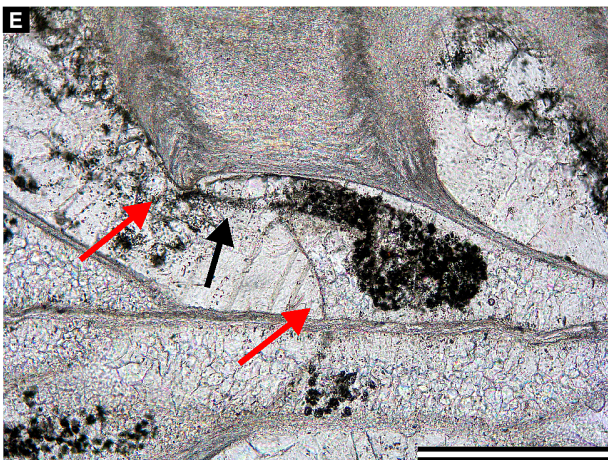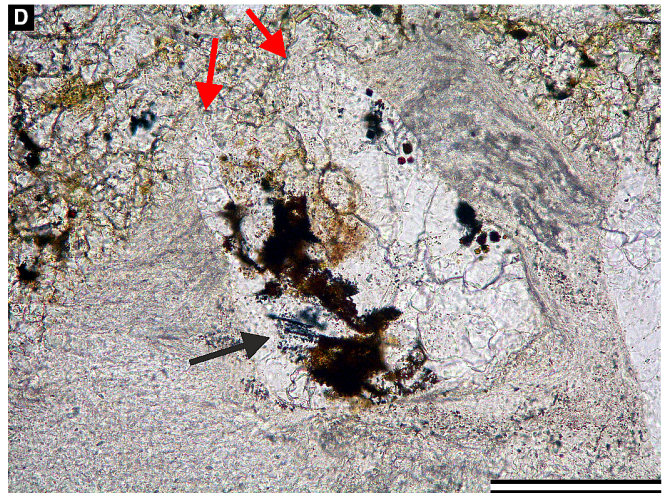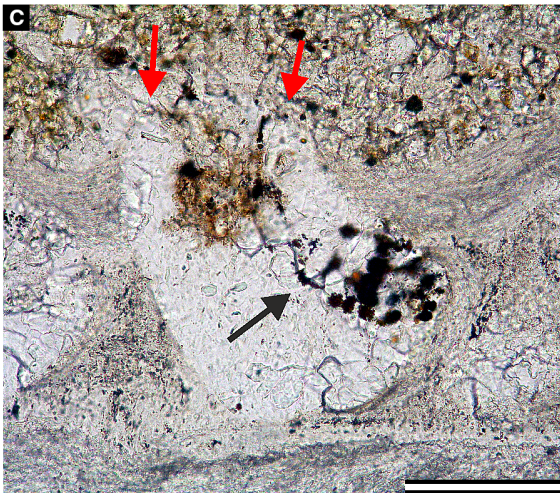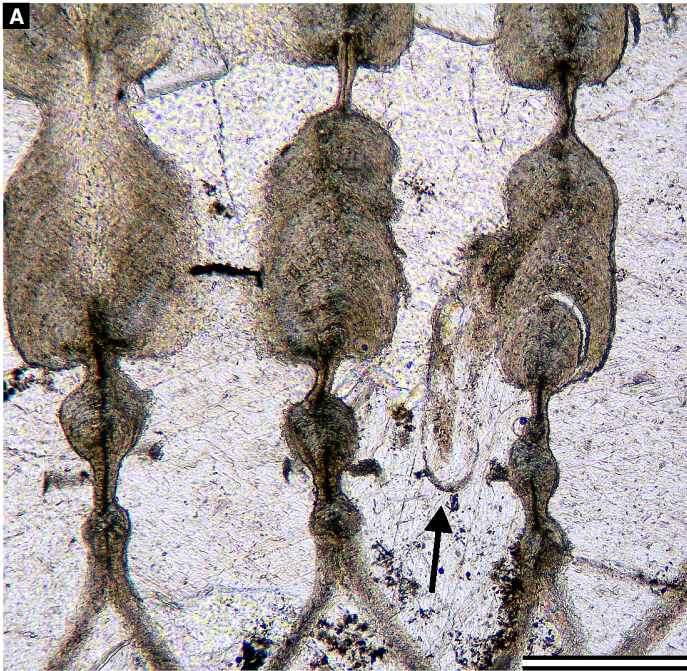
FIG. 3. All images show longitudinal thin sections of autozooecial chambers. A–B, *Rhombotrypella superangustata* Morozova, NUIF 2755b, Assistance Formation, Permian (Roadian); Lake Hazen, Ellesmere Island, Canada, fossilized polypid (black arrow) inside the autozooecial chamber; the red arrow indicates the supposed remnant of a gut. C–D, *Hemitrypa* sp., SMF 64235, Middle Devonian, Germany, fossilized remnants of soft tissue inside the autozooecial chambers; red arrows, indications of outer cuticula; black arrows, invaginations with supposed remnants of polypides. E–F, *Graptodictya delicata* Männil *in* Gorjunova & Lavrentjeva, Steinvika Formation, Upper Ordovician (Sandbian–Katian), Steinberg, Norway; supposed remnants of polypides; black arrows, vestibules; red arrows, inferior (lower) and superior (upper) hemisepta; E, PMO 222.300; F, PMO 222.298. Scale bars represent: 0.2 mm (A, E, F); 0.1 mm (B–D).

membrane of bryozoans (indicated by the sharp boundary between sparitic partitions and enveloping microsparitic matrix).

Internal structures such as apparent remnants of a gut (e.g. *Rhombotrypella superangustata*) contain brownish or black parts that are composed of iron minerals. Their presence may mark the position of organic structures after decay, for example, biogenic iron from the tissue could be bound in sulphates under reduction conditions in anoxic environments (e.g. Briggs 2003; Saleh *et al.* 2020).

Bryozoan anatomy

The majority of known Palaeozoic examples of soft-tissue preservation have been reported from trepostome bryozoans. McKinney (1969) noted remnants of polypides in the Mississippian *Tabulipora*. This trepostome has a similar morphology to *Rhombotrypella* in possessing ring septa. In contrast to the present material, the membranous sac with the polypid in *Tabulipora* stretches from the bottom of the autozooecial chamber (McKinney 1969, pl. 50, figs 1–6), whereas the studied material of *Rhombotrypella superangustata* has a short membranous sac constrained between two successive ring septa (Fig. 3A, B). The U-shaped brownish structure inside the proposed membranous sac resembles the gut of modern bryozoans (cf. Fig. 2B, C).

Bryozoans undergo degeneration–regeneration cycles of their polypides during the life cycle (e.g. Borg 1926; Gordon 1977; Boardman 1998). During regeneration, the body of the polypide collapses and degenerated cells are encapsulated within an organic membrane. Such brown bodies can be stored in the bottom of the living chamber or removed from it. The new polypide is formed from the tissues of a cystid. Boardman (1998) distinguished two types of this process in Cyclostomata: progressive and stationary polypide cycles. In species with attachment organs, polypides develop as the growth of a bryozoan advances, so that the distance to the orifice remains constant (progressive cycle). In species without attachment organs, polypides develop on the bottom of their living chambers, so that the distance to the orifice (and,

subsequently, the distance to their protrusion) increases during growth (stationary cycle). As a result, the length of the zooid increases with its growth. The position of the proposed remnants of polypides in *Tabulipora* described by McKinney (1969) would correspond to the stationary polypide cycle, whereas the present material of *Rhombotrypella superangustata* instead implies a progressive polypide cycle. The progressive polypide cycle supposes the presence of attachment organs that are not preserved in the present material.

Boardman & McKinney (1976) reported several examples of brown deposits indicating the position of degenerated polypides in Ordovician trepostomes. It was shown that structures such as basal diaphragms and funnel cystiphragms restrict the living space of a zooid. The brown deposits are stored at the bottom of the living chamber, similar to the position of brown bodies in living Cyclostomata. Such accumulations of brown deposits have been reported in different trepostome genera of the Ordovician age (e.g. Corneliussen & Perry 1973; Morrison & Anstey 1979; Ernst & Voigt 2002; Ernst 2022*a*). Those are thought to be remnants of 'encapsulated' brown bodies produced during degeneration–regeneration cycles.

Mineralized diaphragms in modern Cyclostomata are rare (e.g. Boardman 1998, 2001). They are precipitated on membranes that comprise the floor of living spaces in autozooecial chambers. With each new polypide cycle, diaphragms mark the bases of living chambers; therefore, the number of diaphragms in autozooecia corresponds to the number of polypide cycles (Boardman 2001). It appears that ring septa (or 'perforated' diaphragms) in *Tabulipora*, *Rhombotrypella* and related genera may also correspond to polypide cycles.

Reports of indications for soft parts are rare in other groups of Palaeostomata. McKinney & Wyse Jackson (2015, fig. 36) presented various examples of mineralized inferred soft-tissue remains in autozooecia of Mississippian fenestrate bryozoans. Ernst (2022*b*) illustrated similar structures in the Devonian fenestrate *Rectifenestella aculeata* (Sandberger & Sandberger, 1856). The usually singular rounded or cylindrical structures could remain in abandoned zooecia that are closed by terminal diaphragms. Utgaard (1973, pp. 332–333) described examples of possible polypide remnants in cystoporate bryozoans. Blake (1983) mentioned

remnants of brown deposits in the Suborder Rhabdomesina (Order Cryptostomata).

Previous records of indications of soft parts in the Suborder Ptilodictyina are unknown. The present material of *Graptodictya delicata* is interesting because it shows the position of the polypide behind the hemisepta (Fig. 3E, F). Hemisepta are shelf- or spoon-shaped projections that extend from the zooecial wall into the cavity of autozooecial chambers (e.g. Karklins 1983). Hemisepta are often slightly curved, hook-shaped, but can also be straight when viewed in longitudinal section of the autozooecial chamber. The role of the hemisepta has been discussed as an attachment surface, protrusion aid, or protective structure (e.g. Blake 1973; Hinds 1973; Boardman 1983, 1998). Remarkably, hemisepta in Palaeostomata are often curved proximally, whereas those in modern Cyclostomata are usually curved distally (e.g. Boardman 1983, fig. 39.4; Ernst 2020, fig. 8.9F). Unusually for palaeostomates, the inferior hemisepta in *Graptodictya delicata* are curved distally (Fig. 3E, F).

The position of the proposed polypides (membranous sacs) behind the hemisepta in *Graptodictya delicata* might support the protective function of this structure, whereas another function in different taxa appears possible. Blake (1983) noted that some taxa have a variable distribution of hemisepta within the same colony, whereas others have them in all autozooecia. Such a distribution may point to a microenvironmental influence such as periodical exposure to predators.

CONCLUSION

Thin sections of three samples of Palaeozoic bryozoans show structures that are apparently remnants of soft parts of zooids that have been preserved, probably due to extremely fast burial. Their shape and position generally correspond to the anatomical Bauplan of modern Bryozoa including sac-shaped (retracted) polypides (within a membranous sac in Stenolaemata) and a U-shaped gut. The position of the membranous sac in *Rhombotrypella superangustata* constrained within two subsequent ring septa suggests a progressive polypide cycle in this species and the possible presence of attachment organs (not preserved). The proposed membranous sacs of the cryptostome *Graptodictya delicata* are constrained by superior and inferior hemisepta. The position of the hemisepta is suggestive of a protective function.

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