

Morphology of ctenostome bryozoans: 4. *Pierrella plicata*

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Abstract

The genus *Pierrella* was originally created for a single fossil ctenostome bryozoan species from the Late Cretaceous, which is characterized by runner-like colonies, with zooids possessing a distinctive radial, folded aperture. Not long ago, a few specimens of a recent deep-sea congener, *Pierrella plicata*, were discovered and described from the Russian exploration area of the Clarion-Clipperton Fracture Zone, eastern Central Pacific Ocean. Owing to the lack of data on the internal morphology of this species, we investigated the soft-body morphology of *P. plicata* using serial sectioning and 3D-reconstruction in order to compare it to other more recently investigated ctenostome bryozoans and to infer the systematic position of the genus. The most striking peculiarity of the examined species is the radial aperture formed by multiple cuticular, pleated folds of the cystid wall. The cuticle is thickened into triangular-shaped folds in this area. An orificial sphincter underlies the folded aperture. Apertural muscles are present as a single pair of parieto-diaphragmatic muscles and four duplicature bands. The remaining polypide anatomy is mainly characterized by its miniature design: the lophophore has eight short tentacles and the digestive tract is one of the shortest and most compact ever observed in any bryozoan. A small inter-tentacular organ was detected at the lophophoral base. Taken together the genus *Pierrella* shows unique characters, such as the radial apertural folds that are closed by a series of orificial sphincter muscles, and its particularly small polypide. The general colony morphology resembles arachnidioidean ctenostomes whereas its internal morphology resembles alcyonidioidean species.

KEYWORDS

Alcyonidioidea, Arachnidioidea, ctenostome evolution, orificial sphincter, soft-body morphology

1 | INTRODUCTION

Bryozoa is a phylum of suspension-feeding, almost exclusively colonial lophophorates comprising over 6000 recent species (Bock & Gordon, 2013). Individuals of a colony are termed zooids and comprise a protective body wall and cuticle (cystid) and a tentacle crown and

associated digestive tract (polypide), which is characteristically retractable by retractor muscles (Ryland, 1970). Ctenostome bryozoans are a small clade of paraphyletic, mostly marine forms lacking mineralized skeletons (Schwaha, 2020a; Taylor & Waeschenbach, 2015; Todd, 2000). Owing to the latter, only a few external characters are generally present that can be useful for systematic or phylogenetic inferences. An increasing

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FIGURE 1 *Pierrella plicata*, light microscopical images. (a) Three interconnected zooids encrusting tubular arenaceous foraminiferans, showing the transparent body walls with weakly visible polypides on the right. (b) Lateral view of two polypides from (a) showing broad soma and thin, proximal cauda from the right zooid. Note the apertural folds in both zooids. afo, apertural folds; ap, aperture; int, intestine; pca/cd, proximal cystid appendage/cauda; ply, polypide; py, pylorus; rl, retracted lophophore; v, vestibulum; z, zooid

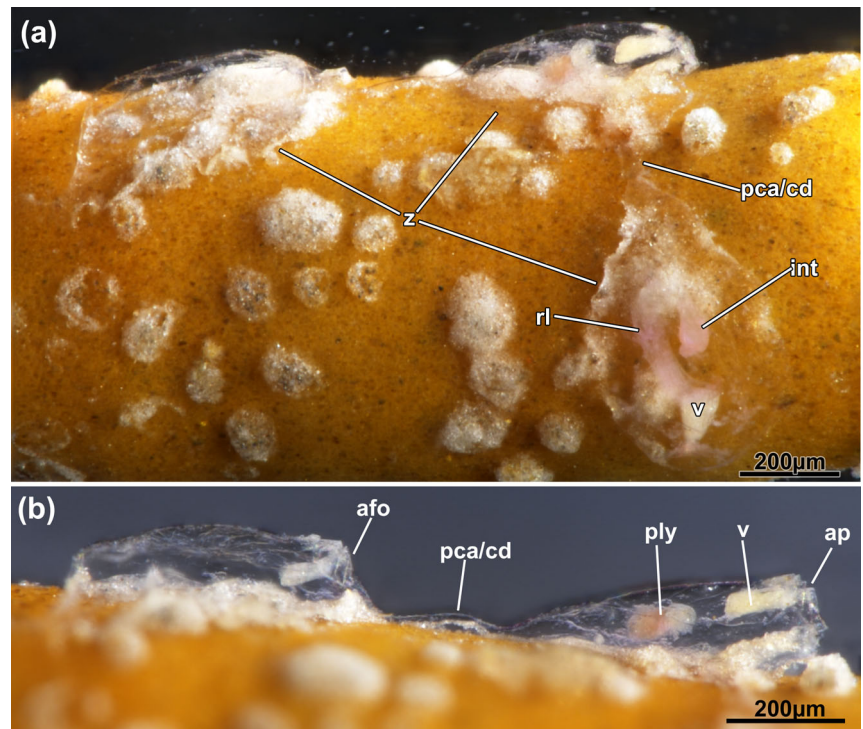
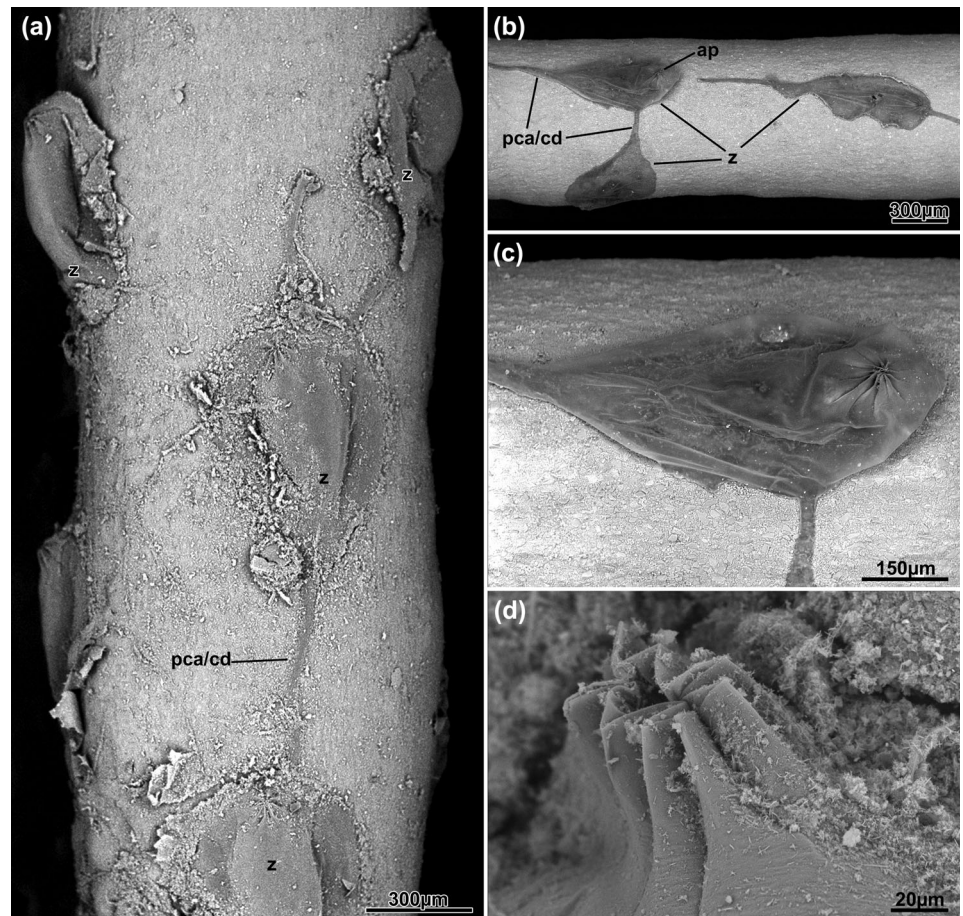


FIGURE 2 *Pierrella plicata*, scanning electron micrographs. (a, b) Overview of uniserial colonies attached to the surface of tubular arenaceous foraminiferans, showing dispersed zooids and thin proximal cystid appendage. (c) Detail of a single zooid. (d) Detail of the apertural folds. ap, aperture; pca/cd, proximal cystid appendage/cauda; z, zooid



number of soft-tissue morphological studies add numerous valuable characters for such implications (Decker et al., 2021; Schwaha, 2020b; Schwaha, 2021; Schwaha et al., 2019; Schwaha & De Blauwe, 2020; Schwaha, Grischenko, & Melnik, 2020; Schwaha, Ostrovsky, & Wanninger, 2020; Schwaha & Wanninger, 2018).

The ctenostome genus *Pierrella* was erected by Wilson & Taylor, 2013 for a fossil species, *P. larsoni*, from the lower Campanian to lower Maastrichtian (Late Cretaceous) of Wyoming and South Dakota, USA. It was preserved on inner shell surfaces of empty body chambers of ammonites by a process interpreted as lithoimmuration. *Pierrella larsoni* is characterized by a simple runner-like colony morphology, with caudate zooids and a radially plicate aperture. It is currently placed in the superfamily Arachnidoidea, which is an artificial assemblage of ctenostome bryozoans that share only plesiomorphic features among most assigned species. The type species, *Arachnidium fibrosum*, has characteristic cystid anastomoses, thin cystid bridges between adjacent zooids (e.g., Hincks, 1880; Marcus, 1938). Such cystid appendages were regarded as the main defining character for the clade (Jebam, 1973, 1986a); they are, however, also present in Nolellidae and Immergentiidae, but only in a few species of Arachnidoidea (Jebam, 1986a). The latter family shows at least two distinct morphologies, distinguishable by the shape of the aperture and the presence of muscular constrictor in the digestive tract (Schwaha & De Blauwe, 2020).

Pierrella plicata Grischenko, Gordon, & Melnik, 2018 was recently described based on six specimens gathered from three stations within the Russian exploration area of the Clarion-Clipperton Fracture Zone, eastern Central Pacific (12.51953–12.91697°N, 128.58775–134.60008°W), from a depth range of 4808–4850 m. Colonies of *P. plicata* encrust tubular arenaceous foraminiferans, which live at the sediment surface (Grischenko et al., 2018). It is the only known recent representative of the genus. The present and fourth contribution in the series “morphology of ctenostome bryozoans” focuses on this exceptionally rare and little-known bryozoan taxon in order to gain insight into its biology and systematic affinity.

2 | MATERIAL AND METHODS

The examined samples were collected as given in detail in the original description by Grischenko et al. (2018). Preparations for scanning electron microscopy were also conducted as mentioned by Grischenko et al. (2018). Samples were analyzed and documented with a Nikon SMZ25 stereomicroscope equipped with a Nikon DsRi2 camera (Nikon). Three specimens were dehydrated with acidified dimethoxypropane followed by infiltration into Agar LVR resin (Agar Scientific) via acetone. Cured resin blocks were serially sectioned with a Leica UC6 ultramicrotome (Leica Microsystems). Sections were stained with toluidine blue, sealed in resin, and documented with a Nikon NiU compound microscope with a Nikon DsRi2 camera. The resulting image stacks were edited with FIJI (Schindelin et al., 2012) before importing them into the visualization software Amira (ThermoFisher). Further processing included section registration, segmentation, and visualization of segmentations as surface models and surrounding tissues as volume rendering.

3 | RESULTS

Zooids of *P. plicata* always have a central portion, the soma, which is round to elliptical in shape and contains the polypide (Figures 1–3). Most zooids have a distinct proximal cystid appendage or cauda, which also represents the budding origin of every zooid. Colonies with caudae have dispersed zooids and display a uniserial, cruciform pattern with interconnections on the distal, proximal, and both lateral sides (Figures 1a and 2a,b).

The aperture or orifice in the distal zone is star-shaped (Figures 2c,d, 3, 4a,b) and comprises multiple cuticular folds. The cuticle, in general, is thin in *P. plicata* (Figures 5, 6), except for the apertural folds that shape the unique aperture (Figure 5b,d–h), and a more proximal area on the cuticle (Figures 4a,b and 6d,e). In both cases, these folds have a similar thickened and triangular form. The staining properties of the outer cuticle are identical to the remaining body wall, but the inner core shaping the triangle stains lighter.

Internally, the apertural folds are lined by an orificial sphincter that is located beneath the apertural folds (Figure 4c–f and 5e–h). From the aperture, the cuticle folds inwards and continues as a vestibular wall toward the diaphragm (Figures 3, 4c–f and 5a). The vestibular wall is wrinkled, elliptical in cross-section (Figure 5c). Accumulated

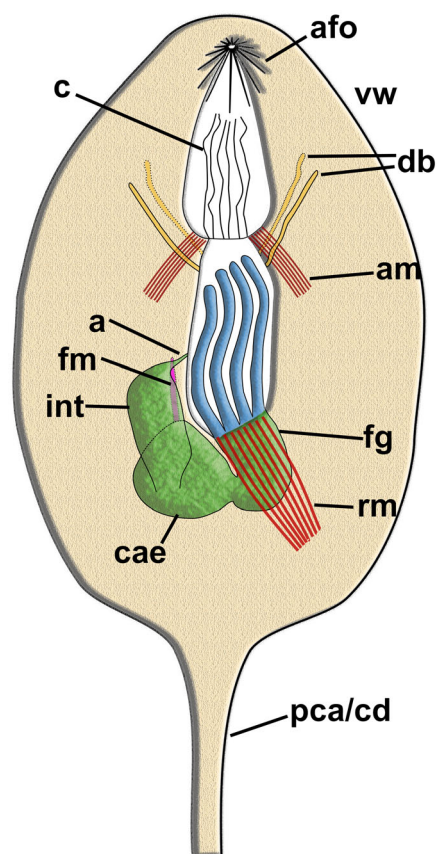


FIGURE 3 *Pierrella plicata*, schematic drawing of a zooid. a, anus; afo, apertural folds; am, apertural muscles; cae, caecum; db, duplicature band; fg, foregut; fm, funicular muscle; int, intestine; pca/cd, proximal cystid appendage/cauda; rm, retractor muscles; vw, vestibular wall

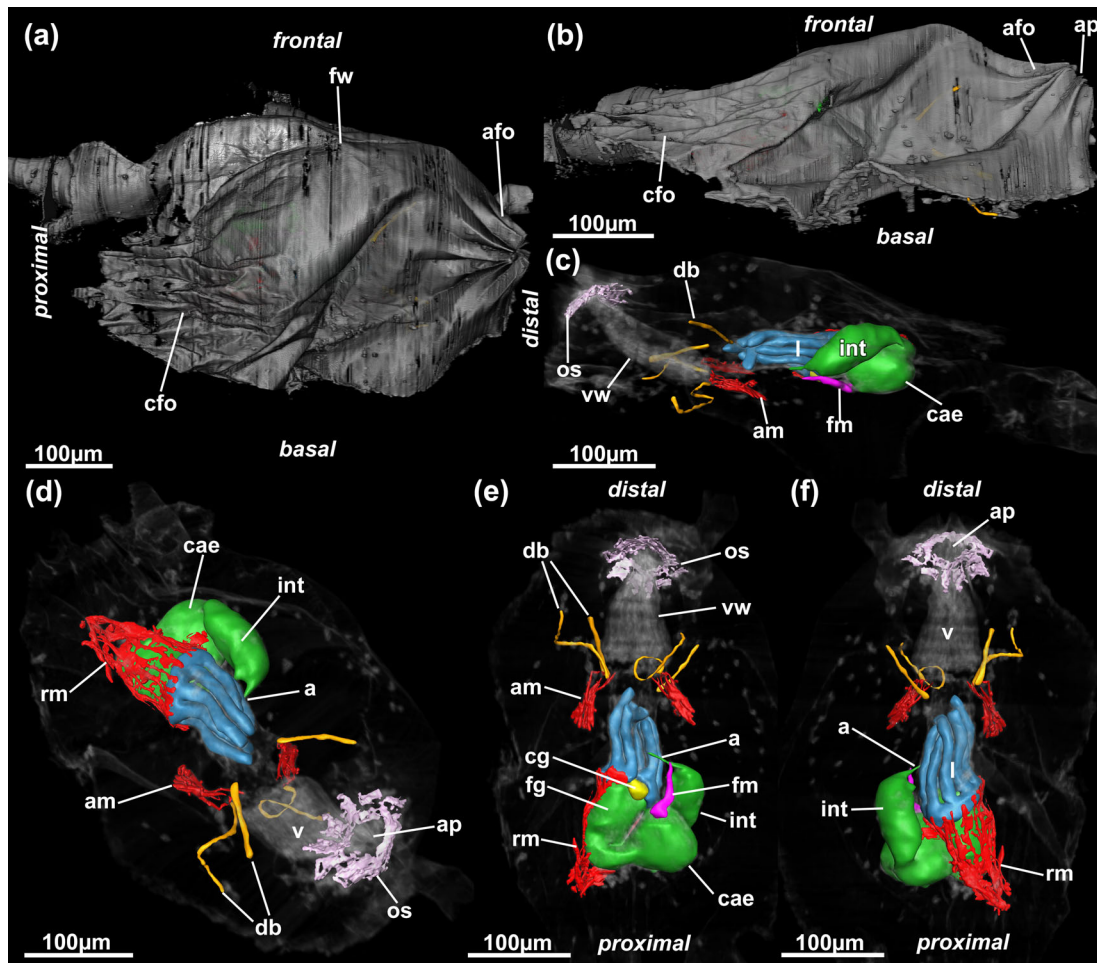


FIGURE 4 *Pierrella plicata*, 3D-reconstruction based on serial sections. (a) Oblique view of a zooid showing the apertural folds on the distal side and regular cystid folds on the frontal side. Volume rendering. (b) Lateral view of the zooids showing the folded cuticular areas. Volume rendering. (c) Cuticle displayed transparently and major organ systems shown as surface rendering. Lateral view. (d) Oblique fronto-distal view. (e) Basal view. (f) Frontal view. a, anus; afo, apertural folds; am, apertural muscles; ap, aperture; cae, caecum; cfo, cuticular folds; cg, cerebral ganglion; db, duplicature band; fg, foregut; fm, funicular muscle; fw, frontal wall; int, intestine; l, lophophore; os, official sphincter; rm, retractor muscle; v, vestibulum; vw, vestibular wall

detritus is enclosed in the vestibulum (Figure 5a–c). At the diaphragm, the collar protrudes along most of the length of the vestibulum (Figures 3 and 5a–c). A single pair of parieto-diaphragmatic muscles are the only prominent apertural muscles associated with the vestibular wall (Figures 3 and 4c–f). Proximally adjoining the vestibular wall lies the tentacle sheath that encloses the retracted lophophore. At its distal end, four duplicature bands extend distally, two on the frontal and two on the basal side (Figures 3 and 4c–f).

The lophophore is small and comprises eight short tentacles. A small cerebral ganglion lies at the lophophoral base (Figures 4e and 6a,c). An intertentacular organ was present in one specimen between the adneurial tentacles. Its inner cavity is filled with unknown contents (Figure 6a) and opens internally slightly above the ganglion (Figure 6b). The digestive tract is short in *P. plicata*. From the mouth opening at the lophophoral base, a short foregut extends proximally, enters the midgut that is ball-shaped, and exits with an intestine in the proximal third of the tentacle sheath (Figures 3, 4c–f and 6d,e). Fecal pellets within the intestine were circular, apparently with concentric layers (Figure 6b,d).

Retractor muscles emerge proximally from the basal wall of the zooid, slightly behind the digestive tract, and insert at the lophophoral base and foregut (Figures 3 and 4d–f). A funicular muscle extends from the midgut (caecum) and projects distally to the level of the anus (Figures 3 and 4c,e). A series of parietal muscles are located next to the polypide (Figure 6c,e).

4 | DISCUSSION

4.1 | Lophophore and gut

The morphology of *P. plicata* is minimalistic and contains the most rudimentary digestive tract ever observed in any bryozoan. The lophophore is small with eight tentacles, a number frequently encountered in many cyclostome and ctenostome bryozoans (Jebram, 1986b). A small intertentacular organ was found in one specimen at the lophophoral base at the adneurial tentacles. Intertentacular organs are

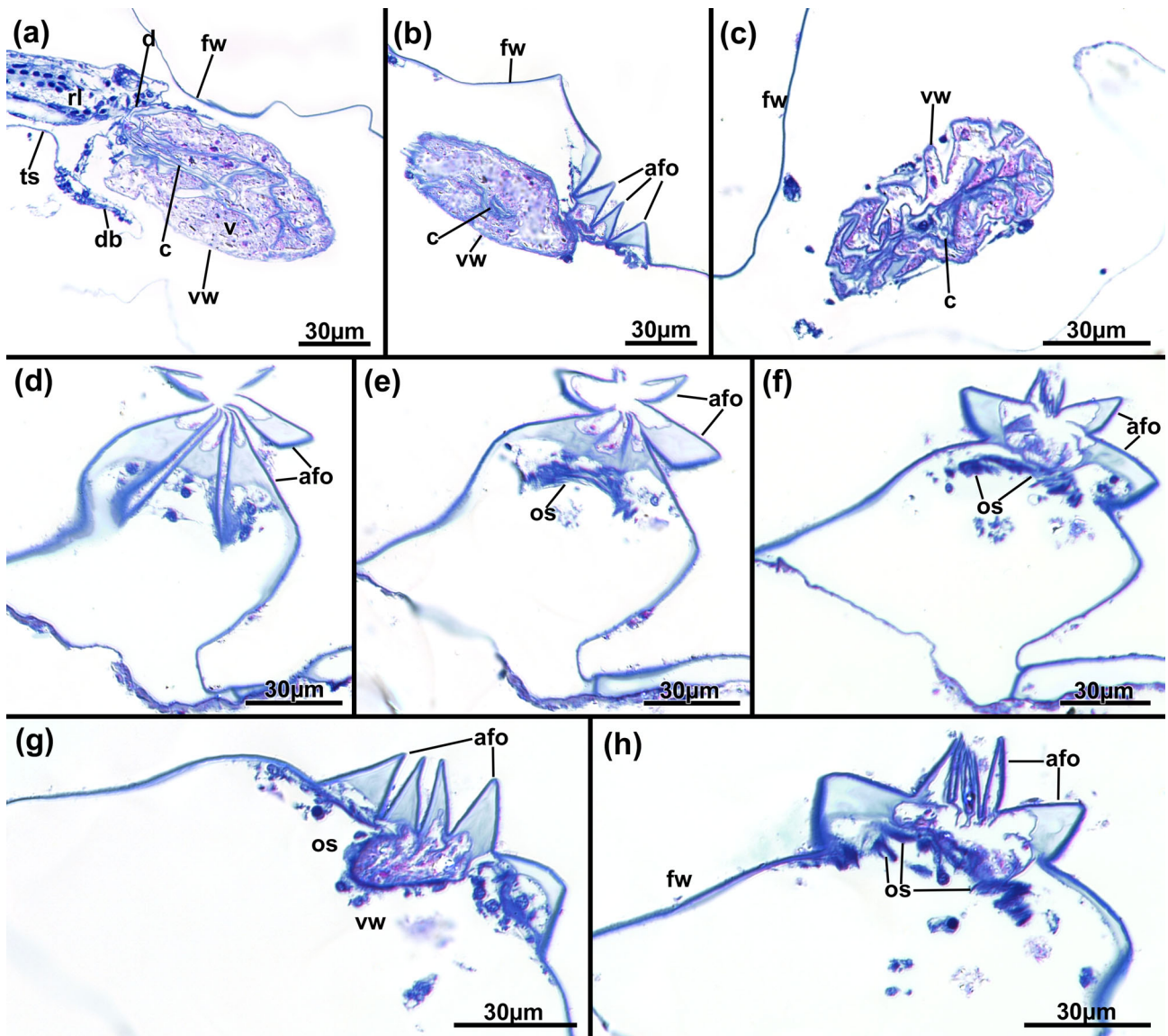


FIGURE 5 *Pierrella plicata*, histological details of the apertural area. Semithin sections. (a) Longitudinal section of the transition of vestibular wall into the tentacle sheath showing the collar and a duplicature band. (b) Longitudinal section of the vestibulum in transition to the aperture and its apertural folds. (c) Cross-section of the vestibular wall and the collar. (d-h) Multiple consecutive cross-sections of the unique apertural area showing the cuticular arrangement of its apertural folds, the connection to the vestibulum and the orificial sphincter. afo, apertural folds; c, collar; d, diaphragm; db, duplicature band; fw, frontal wall; os, orificial sphincter; rl, retracted lophophore; ts, tentacle sheath; v, vestibulum; vw, vestibular wall

widespread among ctenostomes (summarized in Ostrovsky & Porter, 2011; see also Schwaha et al., 2019; Schwaha, Grischenko, & Melnik, 2020; Schwaha, 2021). Usually, it is a temporary structure for the release of gametes, often found in broadcaster species, but also in some brooders (Ostrovsky, 2013). Often, it is two-chambered and distinctly ciliated in other gymnolaemates, but rather inconspicuous and simple in *P. plicata*. However, the histological preservation of the analyzed specimens is not ideal for the detection of specific details. Whether *P. plicata* is a broadcaster or brooder remains elusive, because no signs of gonads were detected.

Whereas other bryozoans show a clearly structured midgut consisting of the cardia, caecum, and pylorus (Schwaha, 2020b;

Silén, 1944), *P. plicata* has a simple sac (termed here as caecum), which shows no distinct regionalization. A pyloric area, however, might be present but remains unrecognizable owing to insufficient preservation.

A specific cardiac constrictor characteristic of numerous ctenostomes (Schwaha, 2020a, 2020b; Schwaha & De Blauwe, 2020) is clearly lacking in *P. plicata*. Lack of such a muscular part of the gut is typical for alcyonidioid ctenostomes, and also in the following taxa: *Paludicella*, *Panolicella*, Aethozoidae, and pentapertural species (Schwaha, 2020a; Schwaha et al., 2019; Schwaha & De Blauwe, 2020). Archanidioid ctenostomes with cystid appendages, such as *Immergentia*, *Noella*, and *A. fibrosum*, show a distinct cardiac constrictor (Schwaha & De Blauwe, 2020; Schwaha & Wanninger, 2018).

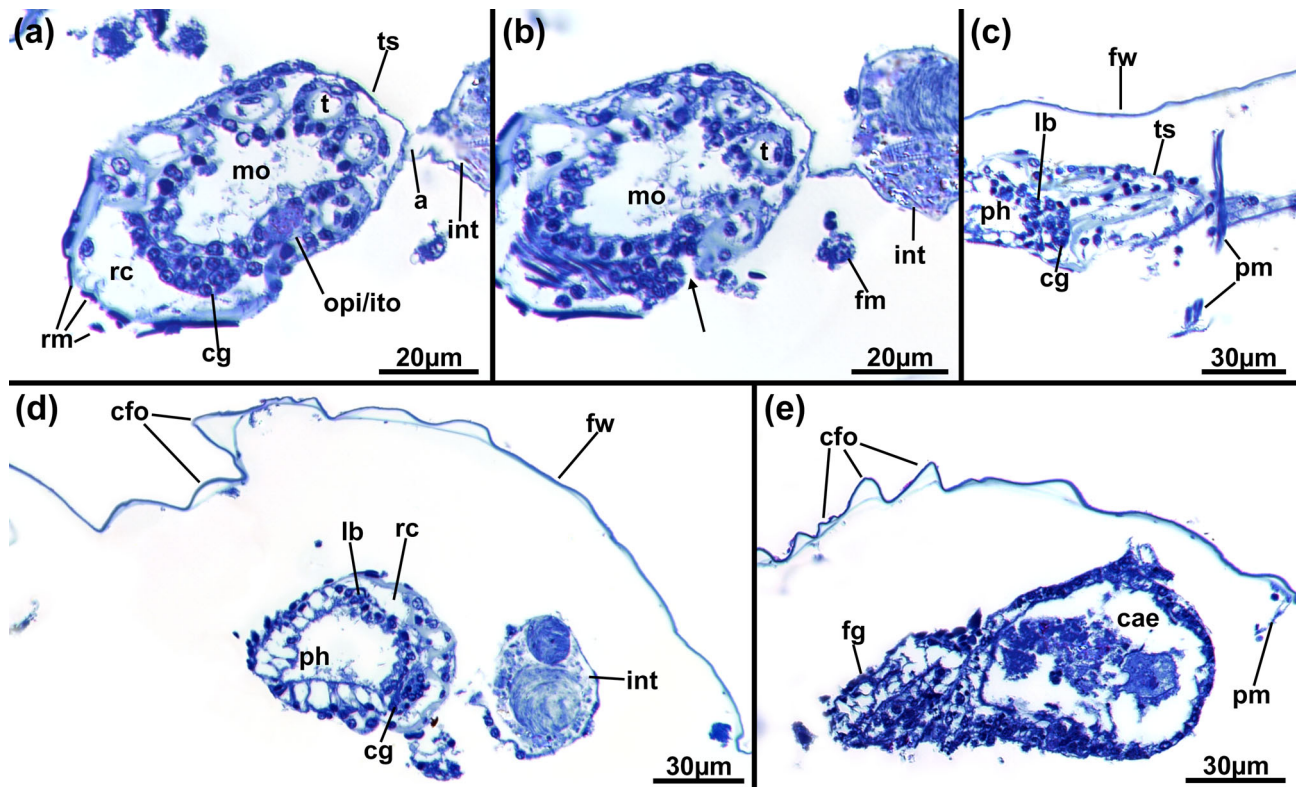


FIGURE 6 *Pierrella plicata*, histological details of the lophophore and digestive tract. Semithin sections. (a) Lophophoral base showing ring canal, anus entry into the tentacle sheath and a small intertentacular organ/ovipositor. (b) Similar section as in (a) but showing the opening of the intertentacular organ to the remaining body cavity. (c) Longitudinal section showing parietal muscles laterally of the retracted polypide. (d) Foregut with highly vacuolar cells and small cerebral ganglion at the lophophoral base. Note the intestine with globular concentric fecal pellets. Note also cuticular folds on the frontal wall. (e) Section of the foregut and midgut. Note cuticular folds on the frontal wall. a, anus; cae, caecum; cfo, cuticular folds; cg, cerebral ganglion; fg, foregut; fm, funicular muscle; fw, frontal wall; int, intestine; lb, lophophoral base; opi/ito, ovipositor/intertentacular organ; pm, parietal muscles; rc, ring canal; rm, retractor muscles; t, tentacle; ts, tentacle sheath

The position of the anus has recently been recognized to be of systematic importance in ctenostome bryozoans (Schwaha, 2020c). The anus in *P. plicata* terminates approximately mid-length of the tentacle sheath, slightly more toward the lophophoral base. Other ctenostomes often have tentacle sheaths and lophophores twice as long compared with *P. plicata*. Consequently, it remains difficult to draw comparisons to other species. A mid-length position of the anus has, for example, been reported for hislopiid ctenostomes, which otherwise show little resemblance to *P. plicata* (Schwaha, 2020a, 2020c).

Funicular muscles are common in bryozoans and ctenostomes particularly show high variation in their position and number (Schwaha, Ostrovsky, & Wanninger, 2020). These muscles usually originate from different parts of the caecum and attach to various regions among ctenostomes. Such variations range from two funicular muscles that attach the caecum to the lateral body wall (*Paludicella*), single ones from the medial side toward the basal body wall as in *Arachnidium* or *Alcyonidium*, or single ones projecting proximo-basally as in *Elzerina* (Schwaha submitted). In *P. plicata*, a single, thicker funicular muscle projects distally toward the basal body wall. This pattern is currently only known in the alcyonidioid genus *Bockiella* (Schwaha, 2021). As variations occur even within a superfamily and a modern phylogeny is still missing,

it remains unknown whether the position of the funicular muscles can aid in resolving certain systematic placements among ctenostomes.

4.2 | Apertural area

Apertural areas including their musculature show a high variation among ctenostome bryozoans (see Pröts et al., 2019; Schwaha, 2020b; Schwaha, 2021; Schwaha et al., 2011, 2019; Schwaha & De Blauwe, 2020; Schwaha, Grischenko, & Melnik, 2020). In *P. larsoni*, the folded imprint of the star-shaped aperture was interpreted as a collar (Wilson & Taylor, 2013). However, based on the structure present in the recent species, it appears more likely that these are also apertural folds, as in *P. plicata*, rather than a collar. Unless partially everted, preservation of the collar would probably be difficult as it usually is a rather thin cuticle. The remaining cuticle, including that of the vestibular wall surrounding the retracted collar, is more likely to be preserved (see e.g., also Olempska, 2016).

The cuticular apertural folds of *P. plicata* are unique and not present in any other known recent ctenostome. Radially arranged apertures are a common feature of alcyonidioid ctenostomes, whereas most others

have quadrangular apertural shapes (Schwaha, 2020a). Likewise, orificial sphincters are currently only known in some alcyonidiid ctenostomes (Schwaha, 2021; Schwaha & Wanninger, 2018).

Apertural muscles include two pairs of duplicature bands in *P. plicata*, which is also the most common condition found in gymnolaemates in general (Schwaha, Ostrovsky, & Wanninger, 2020). Some ctenostomes, such as victorellids and vesicularioideans, lack duplicature bands (Schwaha et al., 2011), whereas only a few species have been reported with more than four, such as *A. fibrosum* (Schwaha & De Blauwe, 2020).

The remaining apertural muscles are present as prominent bundles extending from the lateral or basal cystid wall toward the diaphragm and vestibular wall (Schwaha et al., 2011). In most ctenostomes, these are two sets consisting of four muscles each, the parieto-diaphragmatic muscles inserting proximally at the diaphragm and the parieto-vestibular muscles inserting more distally at the vestibular wall (Schwaha, 2020b). *P. plicata* has a single pair of parieto-diaphragmatic apertural muscles and none attaching to the vestibular wall. Such an arrangement is present in alcyonidioid taxa, such as *Alcyonidium*, *Flustrellidra*, *Elzerina*, and *Bockiella* (see Schwaha 2021), *Haywardozoon* (Schwaha, Grischenko, & Melnik, 2020), or *Pherusella* (Decker et al., 2021). Arachnidioidean ctenostomes of the families Immergentiidae and Nolellidae have four parieto-diaphragmatic and -vestibular muscles (Schwaha & Wanninger, 2018; Soule, 1950). The arachnidid *A. fibrosum* has only two of each of these muscles (Schwaha & De Blauwe, 2020).

5 | CONCLUSION

The deep-sea species *P. plicata* shows multiple unique characters: (a) the apertural area and its closure mechanisms enabled by an orificial sphincter, (b) the most compact polypide in a ctenostome bryozoan, (c) a colony morphology reminiscent of arachnidioidean ctenostomes, but with an internal morphology (aperture shape and muscles, lack of cardiac constrictor) reminiscent of alcyonidoideans. Little data are available for the Arachnididae, which probably comprise two different clades (Schwaha & De Blauwe, 2020), so the phylogenetic position of this unique species will have to await further studies.

AUTHOR CONTRIBUTIONS

Thomas Schwaha: Conceptualization; formal analysis; investigation; methodology; visualization; writing-original draft; writing-review & editing. **Andrei Grischenko:** Investigation; project administration; resources; writing-review & editing. **Viacheslav Melnik:** Resources; writing-review & editing.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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