RESEARCH ARTICLE

Morphology of ctenostome bryozoans: 2. *Haywardozoon pacificum*, with implications of the phylogenetic position of the genus

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Abstract

The genus *Haywardozoon* represent a little known genus of ctenostome bryozoans that has only been found in the deep-sea. It forms small, mostly uniserial colonies lacking polymorphs. Zooids have a conspicuous apertural closure mechanism consisting of a cuticular lower lip that closes the aperture. The systematic placement of the genus remains uncertain, detailed morphological studies that include soft-body morphological traits are missing. Consequently, this is the first study analyzing *H. pacificum* by means of histological serial sections and 3d-reconstruction. Zooids are ovoid and in some cases solitary, that is, showing no interconnected zooids. Most prominent is the large vestibular wall that can be more than half of the total length of the zooid. Its vestibular wall is particularly lined by a complex, multilayered and branched cuticle. A single pair of lateral parieto-diaphragmatic muscles is present. The polypide is small and comprises about 17 tentacles. The digestive tract is short, has an elongated cardia, a vestigial caecum and a vestibular anus. An ovipositor/intertentacular organ and several oligolecithal oocytes were detected. Several aspects of zooidal morphology, including the structure of the bilateral aperture, parieto-diaphragmatic muscles, general structure of the gut and the thick cuticle, clearly indicate an association to the ctenostome superfamily Alcyonidioidea. Therefore, we reject the previous placement into Hislopioidea and suggest a possible association to pherusellid ctenostomes. New reproductive characters show that *H. pacificum* is a broadcaster contrary to some other deep-sea forms that are brooding.

Research Highlight: Morphology of ctenostome bryozoans remain little investigated. This contribution is the second of a series of detailed morphological analyses of this understudied clade of bryozoans. The morphological investigation of *Haywardozoon pacificum* revealed numerous characters that show a closer relationship to Flustrellididrae rather than Hislopiidae as previously assumed.

KEYWORDS

Alcyonidioidea, ctenostome evolution, cuticular lip, *Flustrellidra*, Gymnolaemata

1 | INTRODUCTION

Ctenostome bryozoans are a small and still insufficiently investigated group of the phylum Bryozoa (Schwaha, 2020a). Systematics currently divides ∼350 recent described species into approximately 7–8 superfamilies (Jebram, 1973, 1986; Todd, 2000). Classification is almost entirely based on colony and cystid characters. Recent advances in molecular studies have shown that most of these characters can be highly homoplasious (e.g., Waeschenbach, Cox, Littlewood, Porter, & Taylor, 2009; Waeschenbach, Taylor, & Littlewood, 2012). Soft-body morphological features are still little studied for inferring evolutionary relationships, but have a high potential for revealing phylogenetic relationships (see also Schwaha, 2020a, 2020b, 2020c). The present study is the second in a series just started by Schwaha and De Blauwe (submitted) dealing with precise soft-body morphological analyses of ctenostome bryozoans. Herein, we analyze the newly described deep-sea species *Haywardozoon pacificum* Grischenko, Gordon, & Melnik, 2018.

Haywardozoon inarmatum is the type species of the genus *Haywardozoon*, which is even often allocated to a separate family. Originally described as *Flustrellidra inarmata*, it was collected from 2,939–3,213 m depth in the Norwegian Sea (Hayward, 1978). Suggestive of its species name, the species lacks any spinozooids otherwise characteristic for the family Flustrellidridae and members of the genus *Flustrellidra* (Cook, 1964; Silén, 1947). *Haywardozoon* and Flustrellidridae share a flattened bilateral apertural area and polygonal zooids. The closing mechanism was described as opercular-like (d'Hondt, 1983; d'Hondt & Hayward, 1981). Two other species of the genus also occur in the deep-sea. *Haywardozoon atlantae* d'Hondt & Hayward, 1981 has been described from the southwestern Atlantic (∼36°S, 52°W) from 2,440–2,480 m depth. The most recently described *Haywardozoon pacificum* Grischenko, Gordon, & Melnik, 2018 has been documented from eight stations within the Russian exploration area of the Clarion–Clipperton Fracture Zone, eastern Central Pacific, from a depth range 4,741–5,050 m. All species are characterized by simple, uniserial colonies with flattened zooids, and the aforementioned specific closure mechanism of the aperture.

The phylogenetic placement and systematic affinity of *Haywardozoon* is not clear. Originally assigned to the alcyonidioidean Flustrellidridae (Hayward, 1978), it was subsequently shifted to a separate genus, family and superfamily, presumably closely related to hislopioidean ctenostomes (see Bock & Gordon, 2013; d'Hondt, 1983). However, no detailed morphological analysis has been undertaken for any of these three species and their systematic position remains poorly defined. Hence, the main aim of this study is to clarify the systematic status of the genus *Haywardozoon* by analyzing its soft-body morphology and also to supplement data on its biology.

2 | MATERIAL AND METHODS

Colonies of *Haywardozoon pacificum* were collected as given in detail by Grischenko et al. (2018). Specimens were collected in the Clarion-Clipperton Fracture Zone, eastern Central Pacific, from a depth range 4,741–5,050 m. Specimen documentation was conducted with a Nikon

SMZ25 stereromicroscope (Nikon, Tokyo, Japan) equipped with a Nikon Ds-Ri2 microscope camera. Samples were embedded in Agar LVR epoxy resin (Agar Scientific, Essex, UK). Serial sectioning of four specimens was conducted on a Leica UC6 Ultramicrotome (Leica Microsystems, Wetzlar, Germany) with a section thickness of 1 μm. Sections were stained with toluidine blue and analyzed and documented with a Nikon NiU compound microscope with the same camera as described above. Serial images were imported into Amira 2019.4 (Thermo Fisher) for 3D-reconstruction (see Ruthensteiner, 2008 for details).

3 | RESULTS

Zooids of *Haywardozoon pacificum* are elongated, roundish, or irregular in shape (Figures 1-3). Zooids appear arranged as uniserial chains, sometimes in close proximity, distally to laterally (Figure 2a). All sectioned specimens are solitary and show no connections to other zooids, or any sign of asexual budding. The lateral margins are composed of thin elongated sheets of cuticle (Figure 4c). Lateral cystid extensions of zooids appear to be connections between zooids (Figure 2c), which, however, were not verified by histological methods. Some extensions are also directed towards other zooids, but do not reach them (Figure 2d). Zooids in close proximity show significant size differences indicating various ontogenetic stages, including an ancestrula (Figure 2d). Apertures are generally orientated in the same direction, but can also be directed towards opposite sides (Figure 2b,c).

The ectocyst is thin, like the general cystid wall. In the distal area of the zooid, the cuticle thickens towards the apertural area and is distinctly multilayered with an outer more prominently staining layer that forms internal cuticular inclusions (Figure 4a–d). The aperture or orifice is bilabiate and rounded. A distinct opercular-like fold plugs the orifice, leaving only a thin slit-like space entering the retracted zooid (Figures 2b–d, 3, 4a,b, and 5c). This basal lip has no associated musculature involved in its opening or closure. Its cuticle shows a thick rim closing the aperture (Figure 4a,b,f). The orifice continues with the vestibular wall towards the diaphragm that separates the vestibule from the atrium, which is the cavity enclosed by the retracted tentacle sheath. The vestibular wall can be extremely long and ranges from about a third to over half of the entire zooidal length (Figures 1, 3, 4a, and 5a,b,e). Like the cuticle of the orificial area, the cuticle lining the vestibular wall is thick and extremely sculptured in form of arborescent branching structures that attach other particles to its surface (Figure 4a,b,h). A pair of apertural muscles, the parieto-diaphragmatic muscles, insert laterally at the proximal transition of the vestibular wall to the diaphragm (Figures 3 and 5a,b,e). These originate from the basal surface of the zooid and are the only muscles associated with the aperture and vestibular wall. From the diaphragm, a prominent cone extends distally and appears to carry the diaphragmatic sphincter (Figures 3 and 4a,e,h). Internally, a short, membranous cuticular collar resides within the cone (Figure 4e). Four duplicature bands extend proximally of the diaphragm from the tentacle sheath distally. The two frontal bands are more prominent than the basal bands (Figures 3 and 5b,e).

The polypide is small and has a mid-sized lophophore comprising around 17 tentacles. A prominent ovipositor/intertentacular organ is
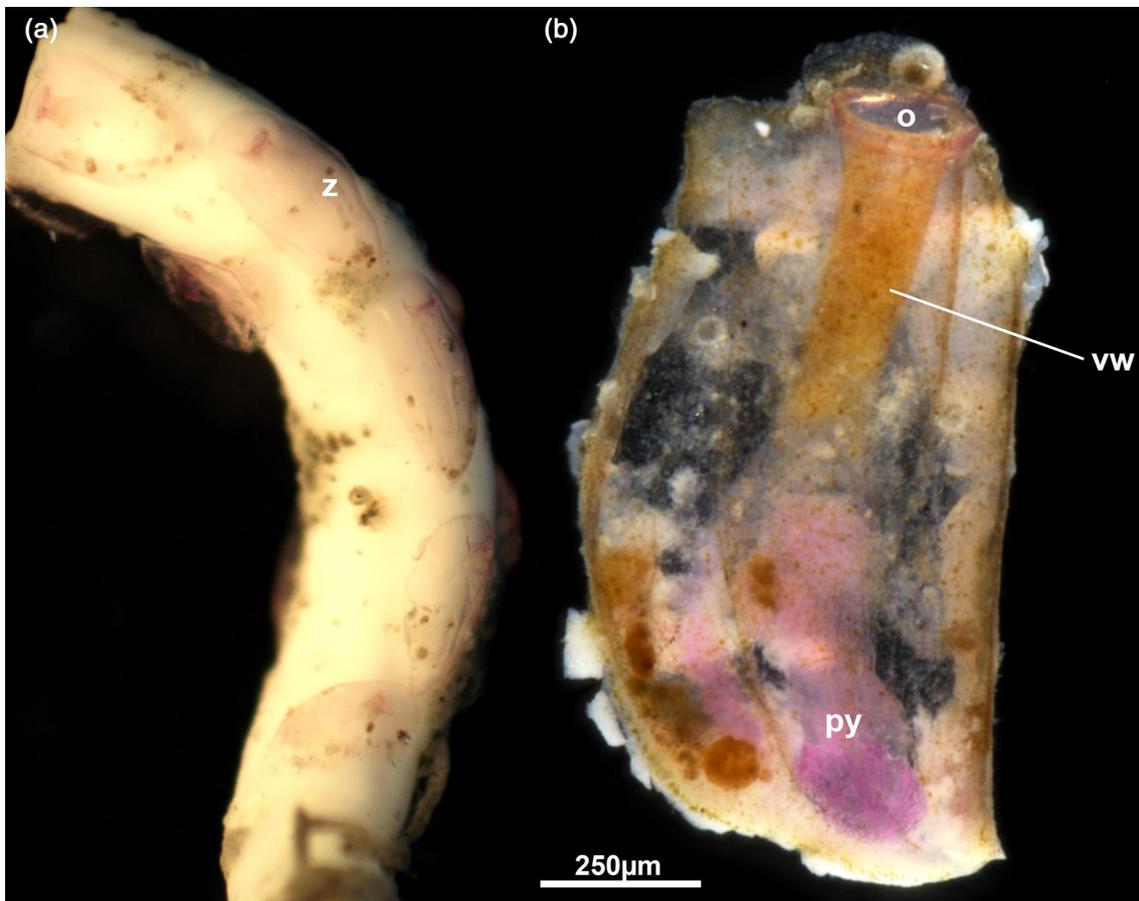
FIGURE 1 *Haywardozoon pacificum*, light microscopical images. (a). Overview of several zooids. (b). Detail of a single zooid. o, orifice; py, polypide; vw, vestibular wall; z. zooid

present at the anal side of the lophophoral base (Figures 5d and 6a). The ovipositor/intertentacular organ is a ciliated tube that connects the visceral cavity with the external medium enabling release of fertilized oocytes/zygotes (in other species with similar ovipositior or intertentacular organ). The gut is simple with a short foregut, an enlarged cardia, a vestigial caecum and short intestine terminating with a vestibular anus on the basal side (Figures 3, 5(b), (e)). From the proximal margin of the zooid, a set of retractor muscles extends towards the proximal side of the polypide and attaches to the lophophoral base, and the foregut (Figures 3, 5b,d,e, and 6b).

Laterally of the polypide, a series of parietal muscles traverse the basal to frontal side of the zooid (Figures 3 and 5b,e). In the proximal area, clusters of oogonia and (primary) oocytes are located, often associated with the cystid wall. They are small, oligolecithal cells (Figures 5b,e and 6c,d).

4 | DISCUSSION

4.1 | Gross morphology

The general zooidal morphology of *Haywardozoon pacificum* is simple, with flattened oval zooids, similar to other species of *Haywardozoon* which all form uniserial colonies. Interconnectivity of zooids is difficult to assess because all four sectioned specimens were solitary without interconnections to other zooids. Lateral cystid extensions of those appear to be solely cuticular and lack any blastogenic tissue. The presence of a distinct ancestrula is indicative that several colonies are present on the same limited substrate area. Interestingly, the orientation of the majority of zooids, however, is identical, indicating either astogenetic processes during uniserial budding, or metamorphosis leads to similarly oriented zooids owing to an unknown stimulus. Apart from zooids arising from the metamorphosis of different larvae, change or loss of zooidal polarity can also occur, which results in different proximo-distal axis of a bud, as has been earlier observed in *H. inarmatum* (d'Hondt, 1983). Budding in *Haywardozoon* otherwise appears to occur mostly on the distal side (or distolateral side) of zooids (d'Hondt, 1983). Parallel zooids with identical proximo-distal axis have been encountered in *H. inarmatum* (Hayward, 1978) and *H. pacificum* (Grischenko et al., 2018). In case of lateral buds, the budding pattern is similar to other alcyonidioideans in terms of orientation of the zooids. In contrast, hislopiids have lateral buds with proximo-distal axis in 90° relative to the mother zooid (see for example, d'Hondt, 1983).

The tentacle number was not determined by Grischenko et al. (2018), but determined as 17 in the current study. This number is within known range of the two other congeners and ranges between 12 and 18 (12 in *H. atlantae*, 14–18 in *H. inarmatum* (d'Hondt, 1983)).
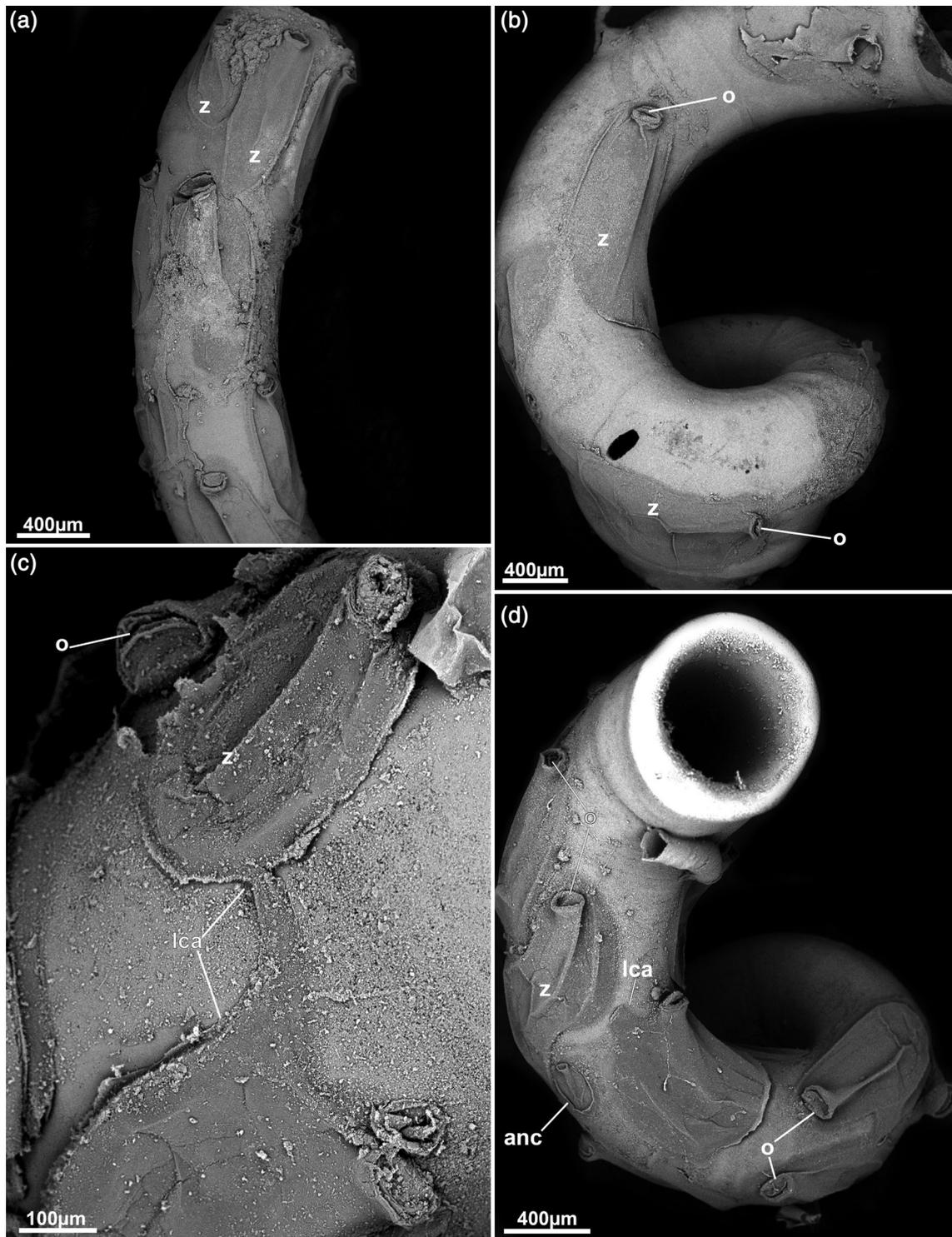
FIGURE 2 *Haywardozoon pacificum*, scanning electron micrographs. (a). Serpulid tube encrusted by several zooids in close proximity, with identical orientation. (b). Group of zooids, showing no distinct connection between them. (c). Close-up of few zooids showing a lateral cystid appendage between adjacent zooids. (d). Group of zooids including a small ancestrula situated in between older ones. anc, ancestrula; lca, lateral cystid appendage; o, orifice; z, zooid

4.2 | Apertural muscles

Haywardozoon has a single pair of lateral parieto-diaphragmatic muscles, which is identical to flustrellidrids, such as *Flustrellidra* or *Elzerina*,

or phersuellids (Decker, Wanninger, & Schwaha, 2020). The closely related Alcyonidiidae slightly differs from *Haywardozoon* in having an orificial sphincter, parieto-diaphragmatic muscles and a series of irregular more distal apertural muscles (Schwaha & Wanninger, 2018).
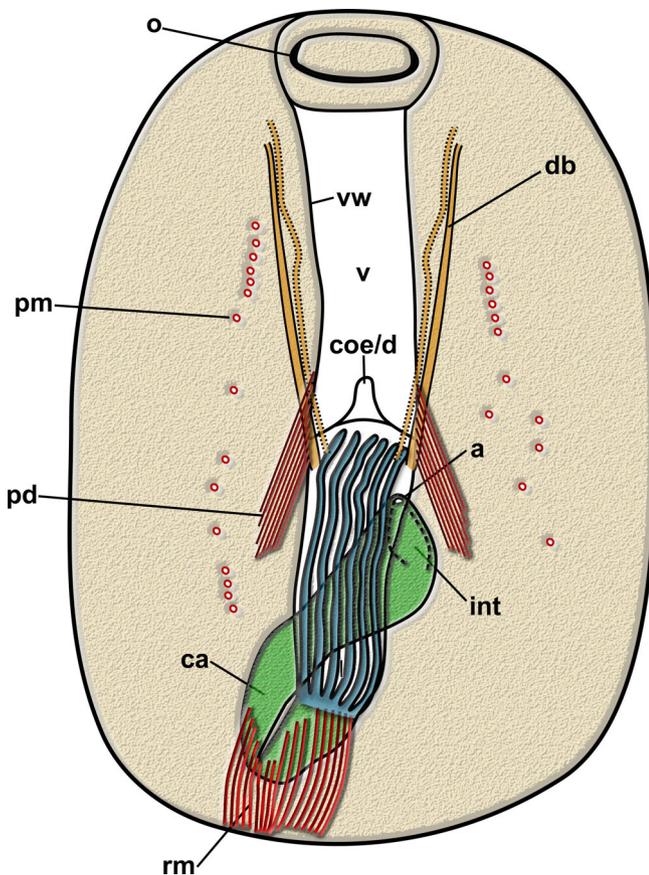
FIGURE 3 Schematic drawing of *Haywardozoon pacificum*. a, anus; ca, cardia; cae, caecum; coe, collar epithelium; d, diaphragm; db, duplicature band; int, intestine; l, lophophore; o, orifice; pd, parieto-diaphragmatic muscle; pm, parietal muscles; rm, retractor muscle; v, vestibulum; vw, vestibular wall

These appear more radially arranged and not in bilateral manner. However, only few alcyonidiid species have been properly analyzed with respect to their apertural musculature. The genus *Hislopia*, of the Hislopioidea, to which *Haywardozoon* has often been associated to (e.g., Bock & Gordon, 2013), differ in their apertural muscles. Besides vestibular wall muscles that are, due to the thick cuticle, apparently missing in *H. pacificum*, they possess four prominent apertural bundles inserting at the diaphragm and large areas of the vestibular wall. In addition, *Hislopia* lacks duplicature bands (Schwaha, Wood, & Wanninger, 2011), which, however, are present in *Haywardozoon* (this study), *Alcyonidium* and related genera (Schwaha et al., 2011), flustrellidrids and pherusellids (Decker et al., 2020). In most cases, there are four bands—as also found in *H. pacificum* in the present study (Table 1).

4.3 | The aperture

Apertures in ctenostomes can range from bilateral/bilabial to round, quadrangular or even pentagonal (Schwaha, 2020a). Bilateral apertures such as present in *Haywardozoon* are found in Flustrellididrae and Farrellidae. In these two taxa, they seem to have evolved

independently as supported by the characteristically bilabiate aperture and distinct cuticular rims present only in Flustrellidrae (e.g., Cook, 1964; d'Hondt, 1983; Marcus, 1926; Schwaha, 2020a). Hislopiids, on the other hand, have a quadrangular aperture similar to numerous other ctenostomes such as victorellids or vesicularioideans (Schwaha, 2020a); another indication for a closer relationship of *Haywardozoon* to flustrellidrid bryozoans (Table 1).

Additional support for such a relationship comes from the specific distal cuticular, "opercular-like" fold of the aperture of *H. pacificum* that is identical to *Neoflustrellidra schopfi* (d'Hondt, 1976, Figure 7). In *H. pacificum* there is no muscle associated with the closure or opening of this protective fold. *Neoflustrellidra schopfi* is another deep-sea monospecific genus and species that forms erect colonies with alternating series of zooids developing back-to-back. Its general zooidal appearance differs from *Haywardozoon*, but the aperture is identical. The erect stems appear to grow from a small encrusting base on the substrate, and a comparable repent encrusting part of the colony, which could show more similarities to *Haywardozoon*, is not present.

4.4 | The cuticle

Cuticle properties have never been comparatively analyzed among bryozoans. Such studies require histology, the application of which is still not common in ctenostomes. In many bryozoans the cuticle is thin and inconspicuous (e.g., Mukai, Terakado, & Reed, 1997). The cuticle of the apertural area, especially the vestibular wall, of *Haywardozoon pacificum*, however, is prominent, multilayered and also with arborescent branching structures. Such structures are not described in any other ctenostome bryozoans.

4.5 | The guts

The gut in *Haywardozoon pacificum* has an elongated cardia, short to vestigial caecum, vestibular anus (Schwaha, 2020b), and lacks a cardiac constrictor found in many ctenostomes (Schwaha, 2020c; Schwaha & Wanninger, 2018). These characteristics are identical to the morphology found in alcyonidioideans (Schwaha & De Blauwe, submitted; d'Hondt, 1983; Schwaha, 2020a; Schwaha & Wanninger, 2018). In contrast, species of the genus *Hislopia* have a mid-sized cardia, extremely large caecum (see also Hirose & Mawatari, 2011; Schwaha et al., 2011), a mid-tentacle sheath anus (Schwaha, 2020b) and a prominent cardiac, muscular proventriculus (Schwaha et al., 2011; Table 1).

### 4.6 | Reproductive ecology of Haywardozoon

The presence of an intertentacular organ is surprising and is indicative of broadcasting species (Ostrovsky, 2013; Ostrovsky & Porter, 2011), which are also characterized by small oligolecithal eggs as confirmed by the present study. Such a reproductive mode
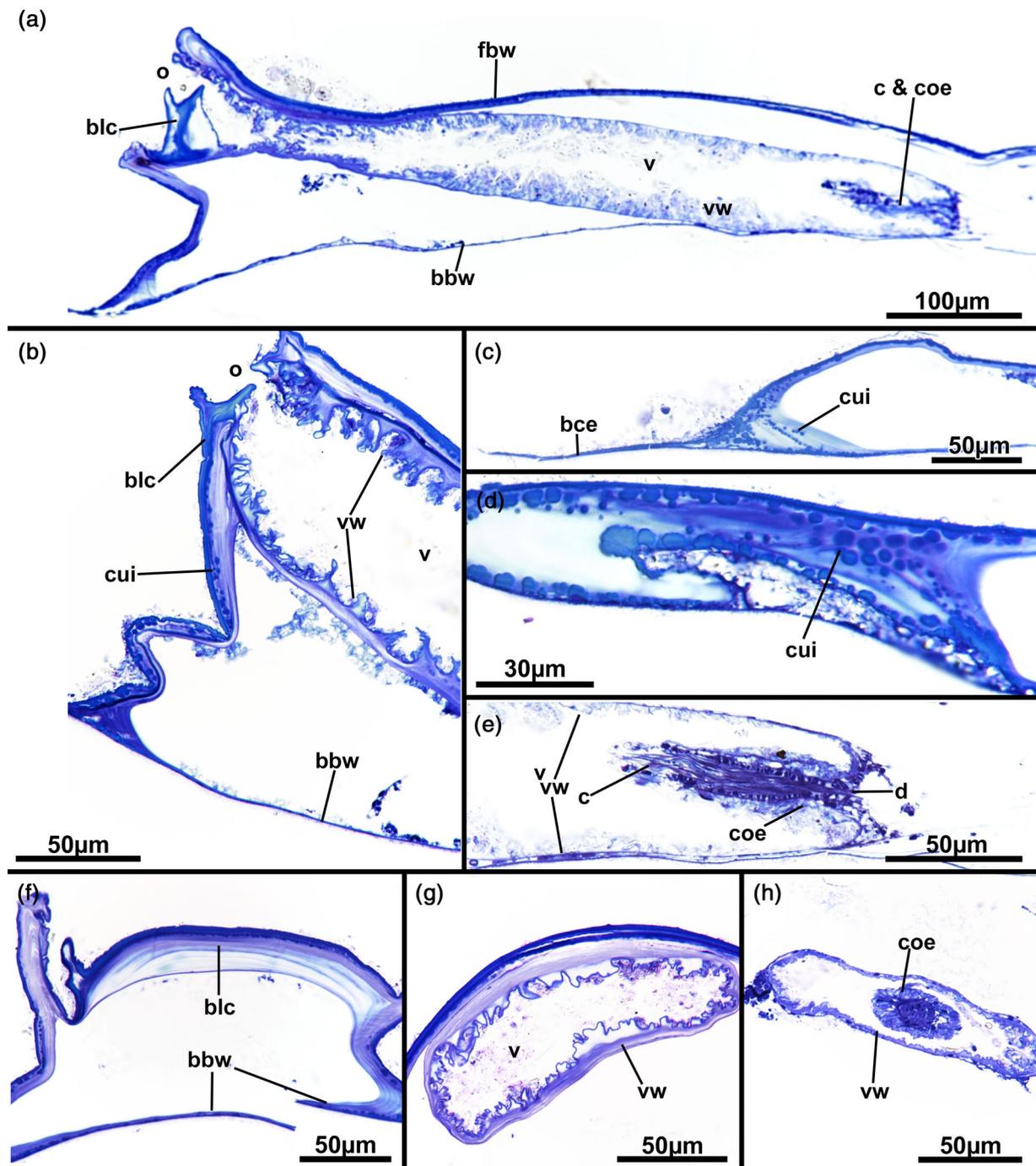
FIGURE 4 *Haywardozoon pacificum*, histology of the apertural area. (a). Longitudinal section of the apertural area showing the long vestibular wall. (b). Detail of the aperture and the thick cuticle, particularly on the basal lip. (c). Section showing basal cuticular extension of a zooid. (d). Section of the multilayered cuticle showing distinct cuticular inclusions. (e). Detail of the diaphragm and collar. (f). Cross-section of the basal cuticular lip closing the orifice. (g). Cross-section of vestibular wall showing distinct, wrinkled cuticle. (h). Cross-section of the collar epithelium. bbw, basal body wall; bce, basal cuticular extension; blc, basal lip cuticle; c, collar; coe, collar epithelium; cui, cuticular inclusions; d, diaphragm; fbw, frontal body wall; o, orifice; v, vestibulum; vw, vestibular wall

is typically associated with the development of planktotrophic, gymnolaemate-specific cyphonautes larvae (Gruhl, 2020; Reed, 1991). As planktotrophs, these are self-nourishing, produced in larger numbers and capable of living several months prior to settlement and metamorphosis. This reproductive mode is interesting for deep-sea habitats that would be expected to be rather deprived of large amounts of nutrition for larvae, but is also found in other deep-sea ctenostomes such as aethozooids that also show an inter-tentacular organ and small oligolecithal oocytes (Schwaha, Edgcomb, Bernhard, & Todaro, 2019).
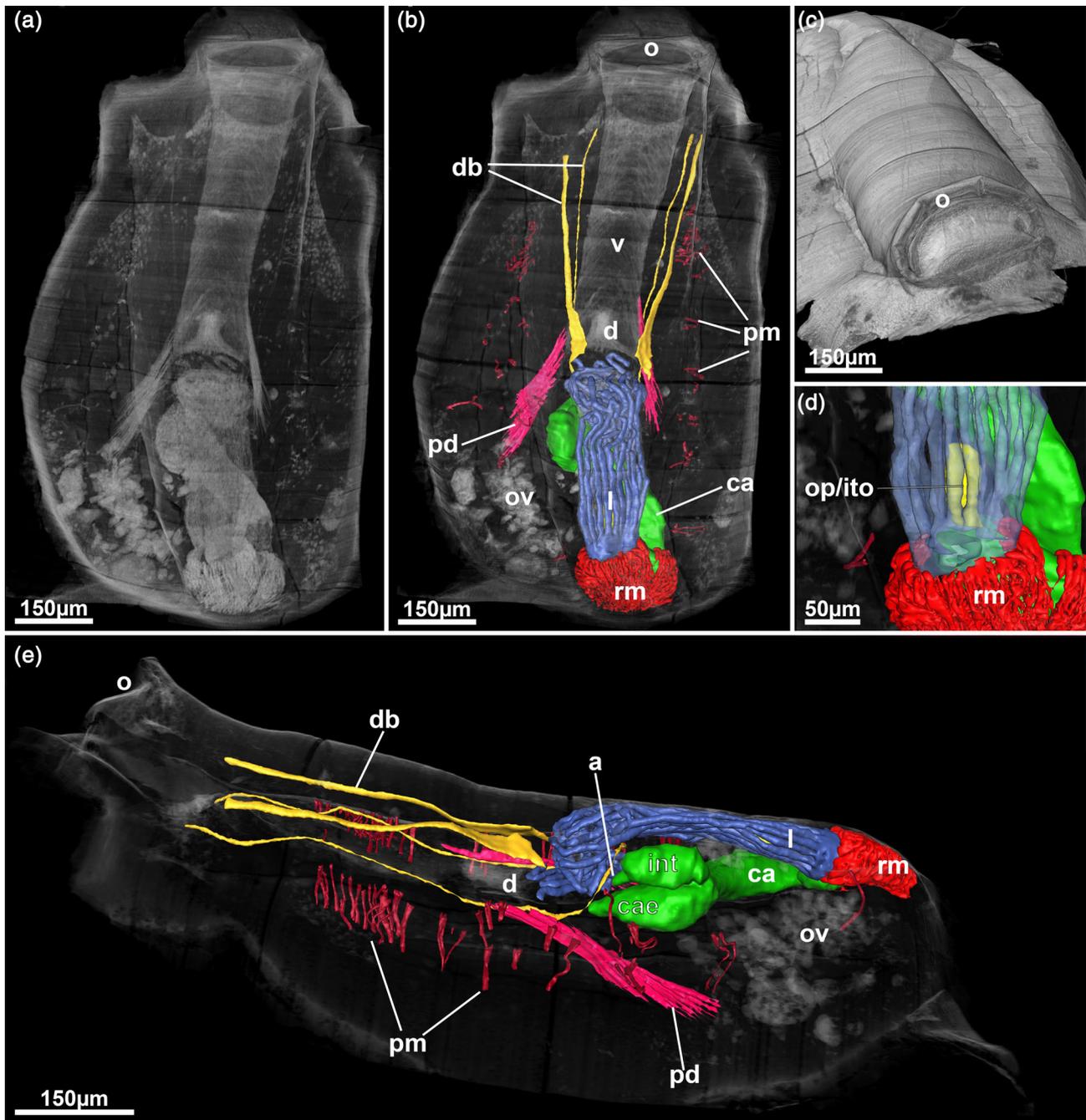
FIGURE 5 *Haywardozoon pacificum*, 3D-reconstruction of a zooid based on serial semithin sections. Volume and surface renderings combined in different variations. (a). Overview of the reconstructed zooid. (b). Same view as in A. with different reconstructed organs as surface models. (c). Distal view of the aperture showing the basal cuticular lip closing the orifice. (d). Detail of the lophophoral base with the tentacles displayed transparently to show the ovipositor/intertentacular organ. (e). Oblique view of the zooid. a, anus; ca, cardia; cae, caecum; d, diaphragm; db, duplicature band; int, intestine; l, lophophore; o, orifice; op/ito, intertentacular organ; ov, ovary; pd, parieto-diaphragmatic muscle; pm, parietal muscles; rm, retractor muscle; v, vestibulum

Although generally assumed long-living, larvae of such broadcasters might also be short-living and undergo metamorphosis shortly after their release. In the original description, an ancestrula of *Haywardozoon pacificum* was found close to other zooids (Grischenko et al., 2018). This indicates that either larvae from the same or different spawnings settled on the same substrate. Differences in zooidal sizes and ontogenetic states slightly favor the latter; however, both possibilities remain speculative. In light of restricted data and difficulties in obtaining material, especially larvae, it remains the only source of information for inferring ecological and life-cycle events of such species. The harsh environment, lack of distinct zooidal connections and signs of asexual budding indicates that possibly they form larvae that settle on the same substrate as the parent colonies.
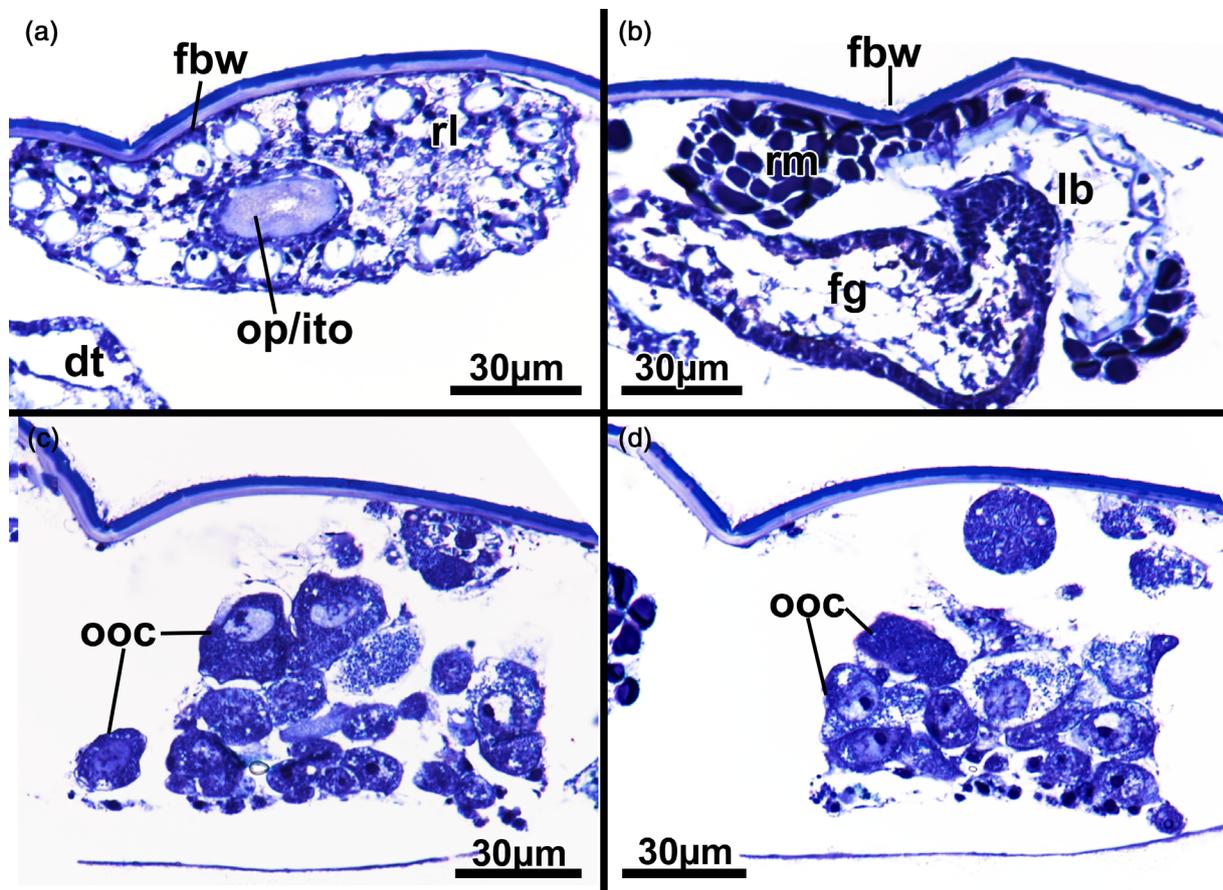
FIGURE 6 *Haywardozoon pacificum*, histological micrographs. (a). Cross-section showing the ovipositor/intertentacular organ in the retracted lophophore. (b). Section of the lophophoral base. (c, d). Two different sections showing an ovary with different oogonia and oocytes. dt, digestive tract; fbw, frontal body wall; fg, foregut; lb, lophophoral base; ooc, oocyte; op/ito, intertentacular organ; rl, retracted lophophore; rm, retractor muscle

TABLE 1 Morphological characters of hislopiid and flustrellididrid ctenostomes, compared to *Haywardozoon*

| Characters	Hislopiidae	Flustrellididrae	*Haywardozoon*
Colony morphology	Serial, runner-like	Dense, non-serial	Serial, runner-like
Apertural muscles	4 vestibular muscles, no duplicature bands	2 parieto-diaphragmatic muscles, four duplicature bands	2 parieto-diaphragmatic muscles, four duplicature bands
Aperture	Quadrangular	Bilateral	Bilateral, with basal cuticular lip
Cuticle	Simple	Multi-layered	Multi-layered
Gut	With prominent muscular proventriculus	No muscular cardia	No muscular cardia

5 | CONCLUSION

The analysis of *Haywardozoon pacificum* has shown the presence of numerous characters that clearly support its placement in Alcyonidioidea, presumably close to the multiporate flustrellidrids or pherusellids. An earlier assumed relationship to hislopiids is only superficially given by the rounded-oval shape of the zooid, but in detail has little in common with *Haywardozoon* (see also Table 1). Associating this genus to hislopioideans is therefore uncalled for and more, erection of a separate superfamily "Hawardozoonoidea" is superfluous as it seems affiliated to the multiporate alcyonidioideans. New insights into its reproductive biology indicate that it is a broadcasting species that potentially might form solitary colonies.

AUTHOR CONTRIBUTIONS

Thomas Schwaha: Conceptualization; formal analysis; investigation; methodology; visualization; writing-original draft; writing-review and editing. **Andrei Grischenko:** Investigation; project administration; resources; writing-review and editing. **Viacheslav Melnik:** Resources; writing-review and editing.
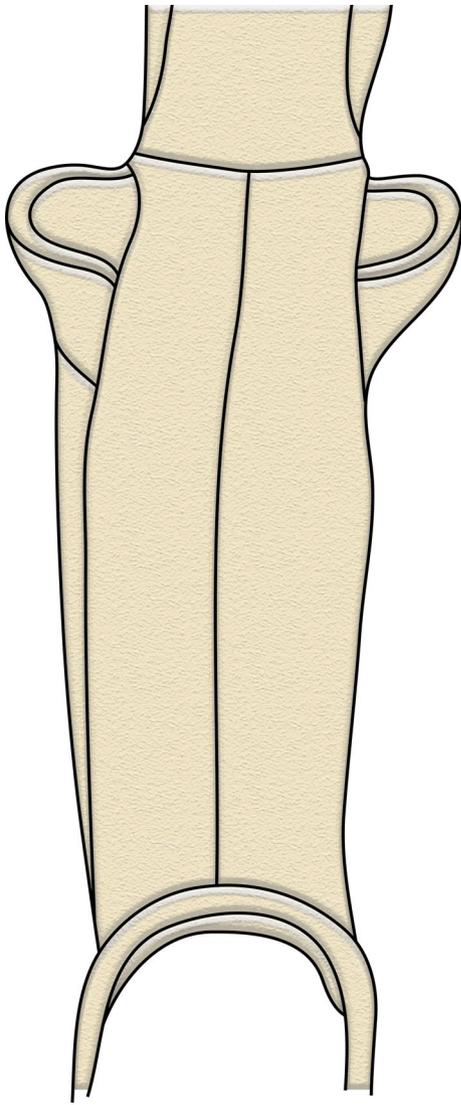
FIGURE 7 Schematic drawing of *Neoflustrellidra schopfi*, redrawn from d'Hondt, 1976

DATA AVAILABILITY STATEMENT

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