

RESEARCH ARTICLE

Morphology of ctenostome bryozoans: 3. *Elzerina*, *Flustrellidra*, *Bockiella*

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Email: thomas.schwaha@univie.ac.at**Abstract**

Ctenostome bryozoans are a small group of bryozoans whose soft-tissue morphology has received only little attention. The present study represents the third in a series of articles dealing with the morphology of this clade of bryozoans. The morphology of three genera of Alcyonidioidea, that is, *Bockiella* (Alcyonidiidae), *Elzerina* and *Flustrellidra* (both Flustrellidridae), are analyzed using histology and 3D-reconstruction techniques. The general zooidal morphology is similar and externally differs by the shape of the aperture. Zooids of *Elzerina binderi* are elongated in the fronto-basal axis, whereas the other two are more flattened in this axis. All species show multiple pore-complexes in their zooidal walls ranging from ~66 in *E. binderi*, to ~30 in *F. hispida* and to less than 10 in *Bockiella*. The aperture is bilabiate in flustrellidrids and roundish in *Bockiella*. Apertural muscles are present as parieto-diaphragmatic muscles. The flustrellidrids have a large frontal duplicature band that further splits into four separate bands. The collar is diaphragmatic in *Bockiella*, but vestibular in the flustrellidrids. Lophophores are similar among the investigated species with a rejection tract in the flustrellidrids. The digestive tract shows differences in the extent and proportions of the caecum, which is large in the flustrellidrids and small in *Bockiella*; the anus is vestibular in all species. A funicular muscle of variable location is present in each species. *Elzerina binderi* has additional thin strands emanating from the digestive tract to the body wall. The parietal muscles show a unique situation in *E. binderi* with five bundles being present, two laterals and one distal. Several features aid in defining characters for the entire superfamily and the families Flustrellidridae and Alcyonidiidae. Besides the shape of the aperture, the frontal duplicature band, the vestibular collar and the large caecum are important. The set of characters also confirms recent notions that *Bockiella* belongs to the Alcyonidiidae.

KEYWORDSAlcyonidioidea, *Bockiella* sp., ctenostome evolution, *Elzerina binderi*, *Flustrellidra hispida*, soft-body morphology

1 | INTRODUCTION

Bryozoa is a phylum of suspension-feeding, benthic, and aquatic lophotrochozoans that are almost entirely colonial (Ryland, 1970). Colonies are formed by iterated modules termed zooids that usually each possess a ciliated tentacle crown (lophophore) and a u-shaped digestive tract. In feeding or undisturbed position, the lophophore is extended from the zooidal surface. In all bryozoans, prominent retractor muscles can retract the lophophore and digestive tract (polypide) into the body wall (Mukai et al., 1997).

From the two main clades of bryozoans, Phylactolaemata and Myolaemata, gymnolaemates are the largest clade with the Cheilostomata comprising over 5000 species (Martha et al., 2020). Ctenostome bryozoans are a small clade of paraphyletic Gymnolaemata lacking a mineralized skeleton (Taylor & Waeschenbach, 2015; Todd, 2000). More than 350 species have currently been described (Schwaha, 2020a), but there are still dozens of undescribed species that remain to be described. Few fossils are known of ctenostomes, mostly as borings or bioimmured specimens (Ernst, 2020). Ctenostome systematics rely on colonial or zooidal characters (e.g., d'Hondt, 1983; Hayward, 1985), which, however, are problematic because they show a high level of homoplasy. Soft tissues morphology has been recently advocated to provide new characters for resolving phylogenetic and systematics relationships (Schwaha, Ostrovsky, & Wanninger, 2020). A series of morphological studies of ctenostome bryozoans was started to analyze the details of soft-tissues by sectioning and 3D reconstruction techniques. (Schwaha, Grischenko, &

Melnik, 2020; Schwaha & De Blauwe, 2020). This contribution is the third in the series providing new morphological data on three different genera of the Alcyonidoidea.

The Alcyonidoidea is a large superfamily of ctenostomes comprising five families (Schwaha, 2020a). Histological data and detailed information is available for the family Alcyonidiidae (e.g., Matricon, 1960; Porter, 2004; Porter et al., 2001; Porter & Hayward, 2004; Silbermann, 1906), which is also necessary for proper species identification in the genus *Alcyonidium*. Other families of the superfamily are little studied with the exception of a recent revision of the Pherusellidae (Decker et al., in press). Two of the studied species herein belong to the Flustrellidridae: *Elzerina binderi* and *Flustrellidra hispida*. The latter species has been extensively studied in regard to feeding (e.g., Best & Thorpe, 1983, 1991, 1996, 2002), and reproduction and development (e.g., Prouho, 1890, 1892; Pace, 1906; d'Hondt, 1977, Wood & Seed, 1992; Gruhl, 2008, 2009; Kvach et al., 2019). Despite the number of investigations, little is known of the detailed morphology of this species with few details being published by Atkins (1932) on lophophore and gut morphology and Smith (1973) on tentacle structure. The genus *Elzerina* differs in colony shape and the extent of polymorphic zooids (heterozooids) and has received little attention (see Cook, 1964). The geographical distribution of the genus is restricted to South Africa, Australia and New Zealand. Morphological studies of internal structures are entirely lacking. Merely a single section image of *E. blainvillii* has been published (Cheetham & Cook, 1983). The third species belongs to the

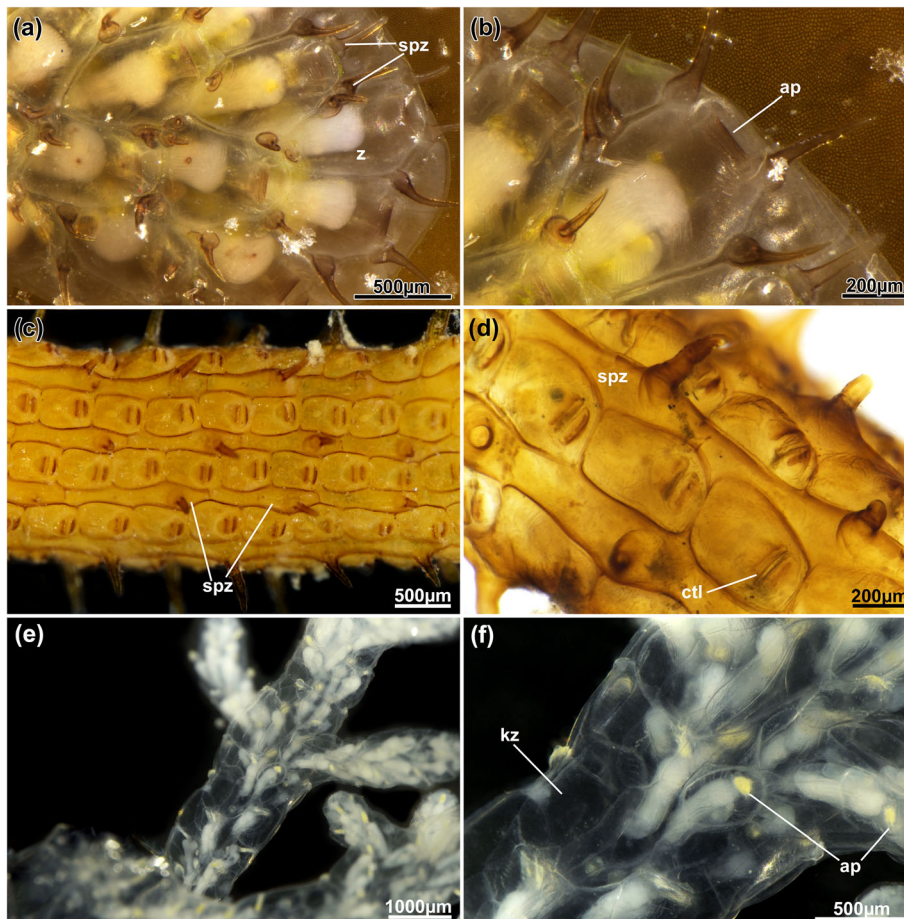


FIGURE 1 Overview images showing zooids of the three investigated taxa. (a, b) *Flustrellidra hispida*. (c, d) *Elzerina binderi*. (e, f) *Bockiella* sp. ap, aperture, kz, kenozooid, spz, spinozooid, z, zooid

genus *Bockiella*, which had been previously assigned to the family Flustrellididae (d'Hondt, 1983; Hayward, 1985), but was recognized to belong to the Alcyoniidae (Cook et al., 2018). The aim of the

current study is to provide detailed morphological data in the frame of the current series to find characters suitable for systematic and phylogenetic inferences.

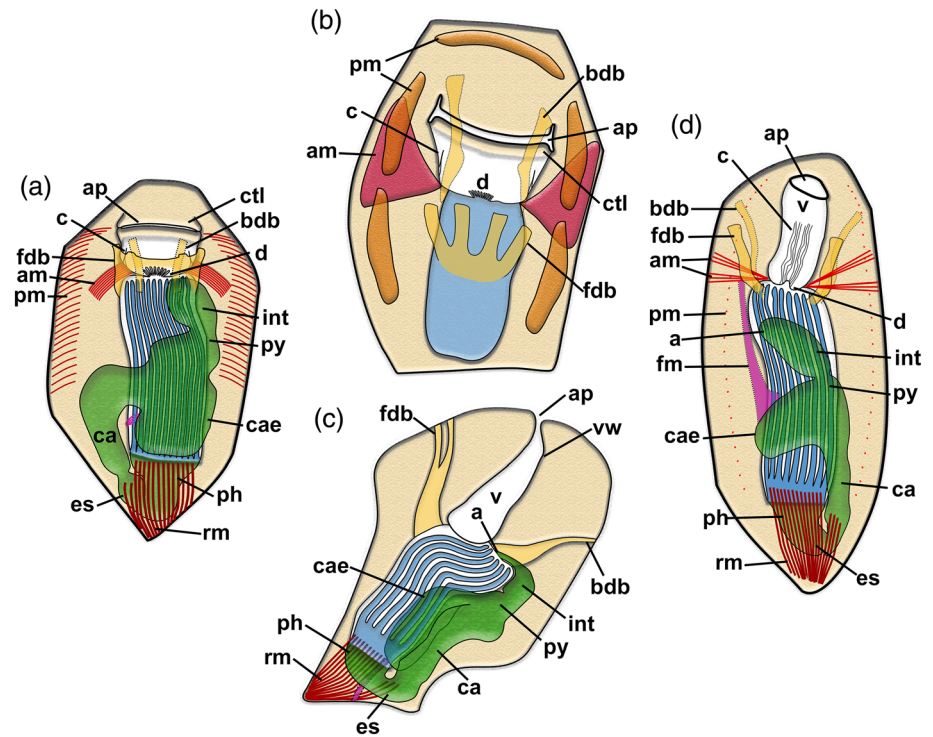


FIGURE 2 Schematic drawings of *Flustrellidra hispida* (a), *Elzerina binderi* (b, c) and *Bockiella* sp. (d) showing main morphological features. All views are from the frontal side except (c) which is from the lateral side. a, anus, am, apertural muscles, ap, aperture, bdb, basal duplicature band, c, collar, ca, cardia, cae, caecum, d, diaphragm, es, esophagus, fdb, frontal duplicature band, fm, funicular muscle, int, intestine, ph, pharynx, pm, parietal muscles, py, pylorus, rm, retractor muscles, v, vestibulum

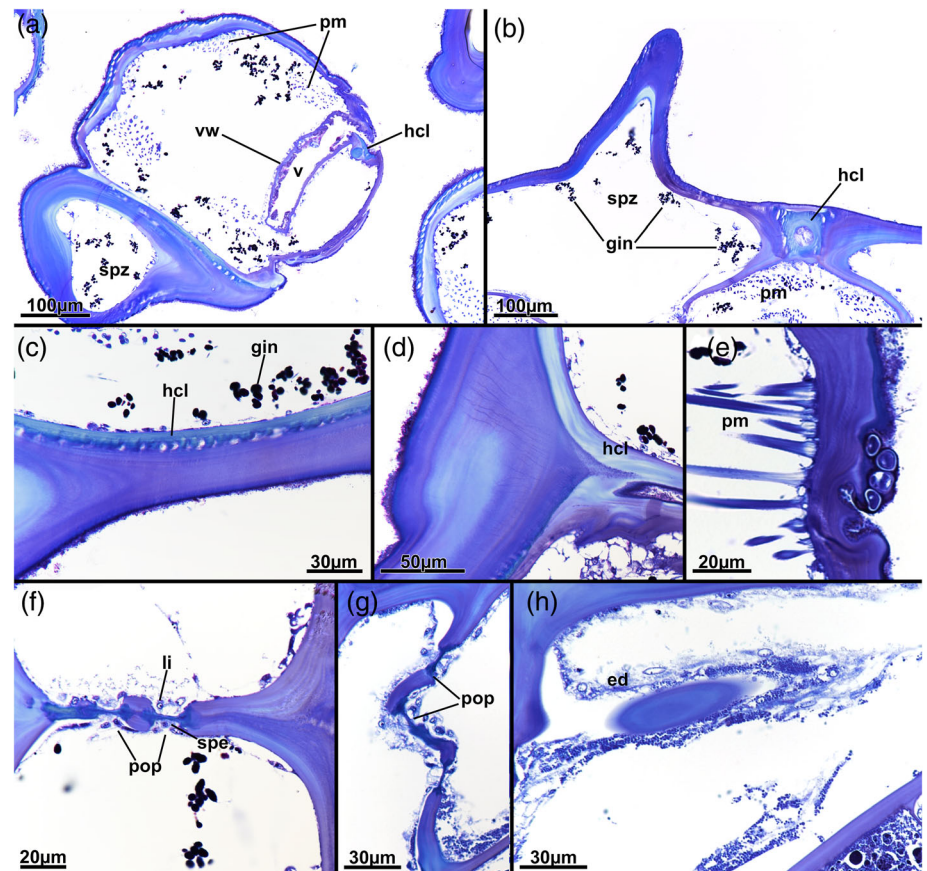


FIGURE 3 *Elzerina binderi*, histological details of the cuticle and pore plates. (a) Frontal section showing autozooid with vestibulum opening exteriorly and an adjacent spinozooid. (b) Section of a cuticular spine of a spinozooid showing the thick cuticle. (c, d) Sections showing the multilayered cuticle including different staining properties. Note the brittle and tattered appearance of parts of the upper cuticular layer. (e) Attachment of parietal muscles to the cuticle. (f, g) Section of pore plates showing several pore complexes. (h) Oblique section showing granular inclusions in the epidermis lining the cuticle. ed, epidermis, fw, frontal wall, gin, granular inclusions, hcl, homogenous cuticular layer, li, limiting cell, pm, parietal muscles, pop, pore plate, rm, retractor muscle, spe, special cell, spz, spinozooid, tw, transverse wall, v, vestibulum, vw, vestibular wall

2 | MATERIAL AND METHODS

Flustrellidra hispida (Fabricius, 1780) was collected from *Fucus* leaves in the intertidal zone at Ile de Batz, opposite Roscoff marine biological station, France. Samples were primarily fixed in 2% glutaraldehyde in 0.1 mol L⁻¹ sodium cacodylate buffer (10% sucrose added). Post fixation was done with 1% aqueous osmium tetroxide for 1 hour at room temperature. Colony pieces from *Elzerina binderi* (Busk, 1861) were taken from the collection of the Natural History Museum London (NHMUK, 1993.11.22.1), whereas *Bockiella* sp. was provided from the

personal collection of Masato Hirose (Kitasato University, Japan). The latter two species were fixed in ethanol.

Specimens were photographed and documented with a Nikon SMZ25 (Nikon, Tokyo, Japan) stereomicroscope equipped with a Ds-Ri2 camera, or a Hirox RH-2000 (Hirox, Tokyo Japan). For embedding, sectioning and 3D-reconstruction, samples were processed as previously described previously (e.g., Decker et al., 2020; Schwaha, Grischenko, et al., 2020; Schwaha & De Blauwe, 2020). In brief, samples were dehydrated with acidified dimethoxypropane, embedded into epoxy resin and afterwards serially sectioned at 1 µm thickness at a Leica UC6

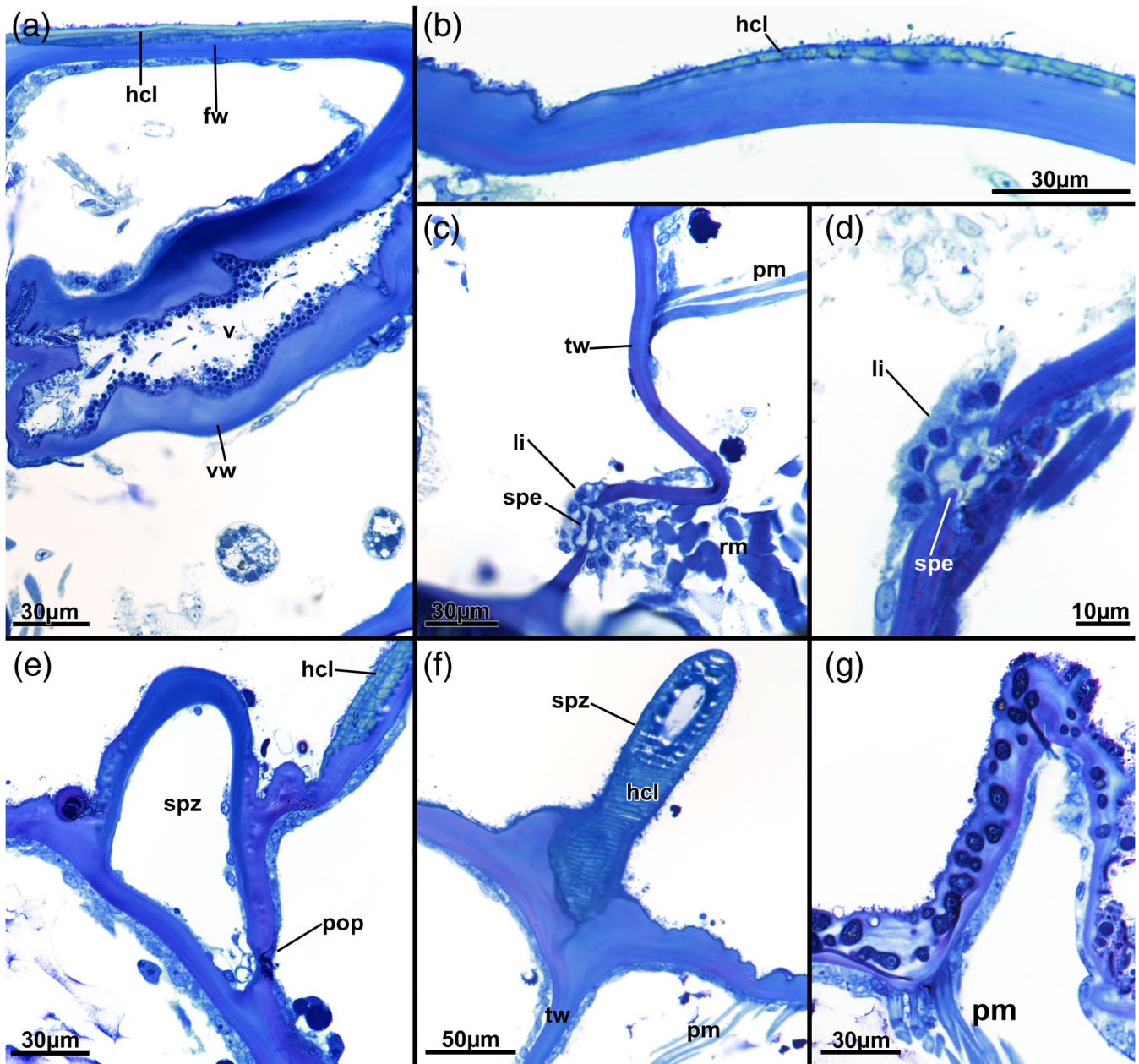


FIGURE 4 *Flustrellidra hispida*, histological details of the cuticle and pore plates. (a) Longitudinal section showing the cuticle of the frontal and vestibular wall. (b) Frontal wall with distinct superficial layer of different staining property. (c, d) Pore plates in the lateral cystid walls. Each pore plate has several pore complexes. (e, f) Section of adventitious spinozoids. (g) Cuticle with multiple intruding organisms. fw, frontal wall, li, limiting cell, pm, parietal muscles, pop, pore plate, rm, retractor muscle, spe, special cell, spz, spinozoid, tw, transverse wall, v, vestibulum, vw, vestibular wall

ultramicrotome (Leica Microsystems, Wetzlar Germany). Sections were stained with toluidine blue, analyzed and photographed with a Nikon NiU compound microscope equipped with a Nikon DsRi2 microscope camera (Nikon, Tokyo, Japan). Image stacks were aligned, segmented and 3D-reconstructed with Amira 2020.2 (ThermoFisher).

3 | RESULTS

3.1 | General morphology

Zooids have three main body axes: the proximo-distal axis with the proximal side at the origin of the zooid and distal at the growth/budding edge; the lateral axis in direction of the lateral sides, and the basal-frontal axis with the basal side toward the substrate and the frontal one pointing externally and carrying the aperture. *Elzerina binderi* and *Bockiella* sp. show similar erect, branching colony forms with the erect branches being entirely composed of zooids (Figure 1(c–f)). *Flustrellidra hispida* forms encrusting sheets that predominantly occur on the seaweed *Fucus* (Figure 1(a, b)). Zooids in the colony are generally polygonal and are connected to multiple neighboring zooids over the entire range of their cystid walls. In *Bockiella* sp. and *F. hispida* zooids are flat and show only a short basal-frontal axis, whereas they are deeply elongated in *E. binderi*

(Figure 2(c)). Zooids within the colony are either autozooids (functional feeding zooids) or specialized kenozooids (functional feeding zooids) or specialized kenozooids. *E. binderi* and *F. hispida* have spinozooids, that is, special kenozooids lacking any polypide and with chitinous spines (Figure 1(a–d)). These are vicarious in *E. binderi* and adventitious in *F. hispida*. *Bockiella* sp. has simple, non-spinous vicarious kenozooids (Figure 1(e, f)). Spines are generally sclerotized giving them a darker appearance. Colonies of *E. binderi* are generally yellow to brown in color, *Bockiella* sp. forms transparent colonies with the vestibular areas showing a darker coloration (Figure 1).

3.2 | Cuticle and pore-plates

The cuticle in the flustrellidrids *Elzerina binderi* and *Flustrellidra hispida* is thick and multi-layered (Figures 3 and 4). In some more sclerotized parts, such as the spines of kenozooids, an additional homogenous layer is present (Figures 3(a–c) and 4 (a,b,e,f)). In particular, the cuticular lips lining the proximal and distal edge of the aperture in *E. binderi* show this probably highly-sclerotized cuticle (Figure 5(g)). It often appears brittle or broken in sections (Figures 3(a–c), 4(f), and 5(g)). Both flustrellidrids have cuticular inclusions or cysts in the basal or lateral walls (Figures 6 and 7(a,d)). Such cuticular inclusions are not present in every zooid and are ovoid to globular bodies lined by a thin

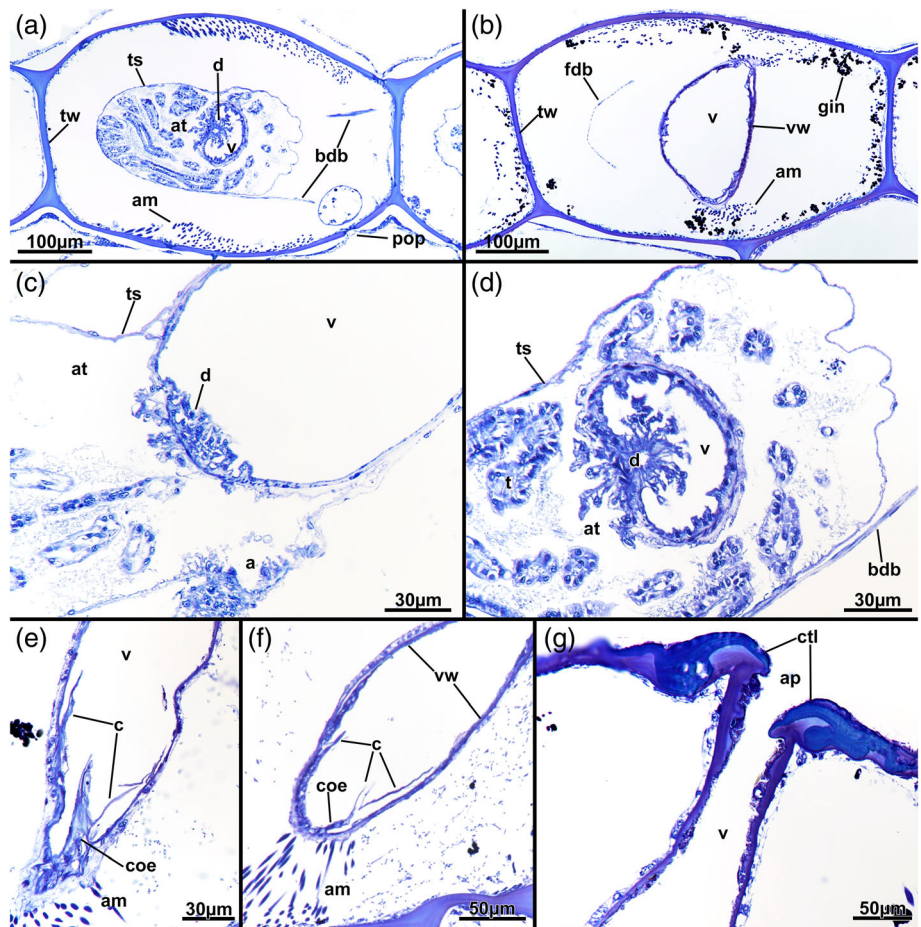


FIGURE 5 *Elzerina binderi*, histological details of the apertural area. (a) Frontal section of the diaphragm and the basal duplicature bands. (b) Frontal section of the vestibulum showing apertural muscle attachment and the broad frontal duplicature band. (c, d) Longitudinal sections of the diaphragm showing its folds into the vestibulum and atrium. (e, f) Sections of the collar epithelium and collar. (g) Section of the cuticular lips. a, anus, am, apertural muscles, ap, aperture, at, atrium, bdb, basal duplicature band, c, collar, coe, collar epithelium, ctl, cuticular lip, d, diaphragm, fdb, frontal duplicature band, hcl, homogenous cuticular layer, t, tentacle, ts, tentacle sheath, v, vestibulum, vw, vestibular wall

cuticle or membrane that is immersed in the cystid cuticle (Figure 6). In *F. hispida*, the cysts can be rather small, composed of cells (Figure 6(a,b)), whereas larger ones lack distinct cells and contain heteromorphic material (Figure 6(c–e)). In *E. binderi*, the cuticular cysts appear always large (Figures 6(g–j) and 7(a,d)). Their contents vary from a few, loosely arranged inclusions (Figure 6(g–i)) to tight compact masses (Figure 6(j)). The cuticular cysts resemble presumptive brown bodies located in the body cavity of the zooids, because of their similar linings (compare also Figure 6(g, i)). However, the contents of the brown bodies show different inclusions (Figures 6(g), 7(a), and 8), sometimes even regularly arranged structures (Figure 8(b,d)). Besides the brown bodies, *E. binderi* also shows conspicuous granular inclusions dispersed in the body cavity (Figures 3(c) and 5(b)).

The cuticle in *Bockiella* sp. is thin and inconspicuous (Figure 9). Only in a few areas, the frontal wall of some zooids appeared multi-layered (Figure 9(a)). At the apertural and on the vestibular walls, the cuticle is thicker than on the remaining body wall, similar to the flustrellidrid species (Figure 10).

Epizootic organisms are common on the external surface of the cuticle. In some zooids of *F. hispida*, seemingly unicellular organisms were also found within the cuticular layers (Figure 4(g)). Some of these organisms extended as far as the epidermis of the zooid.

Multiple pore-plates are present between adjacent zooids. These were most abundant in *E. binderi* with 66 pore complexes counted on a single zooid (Figure 11(b,c,f,g)). Thirty were encountered in *F. hispida* and only eight in *Bockiella* sp. Each pore-plate can have multiple pore

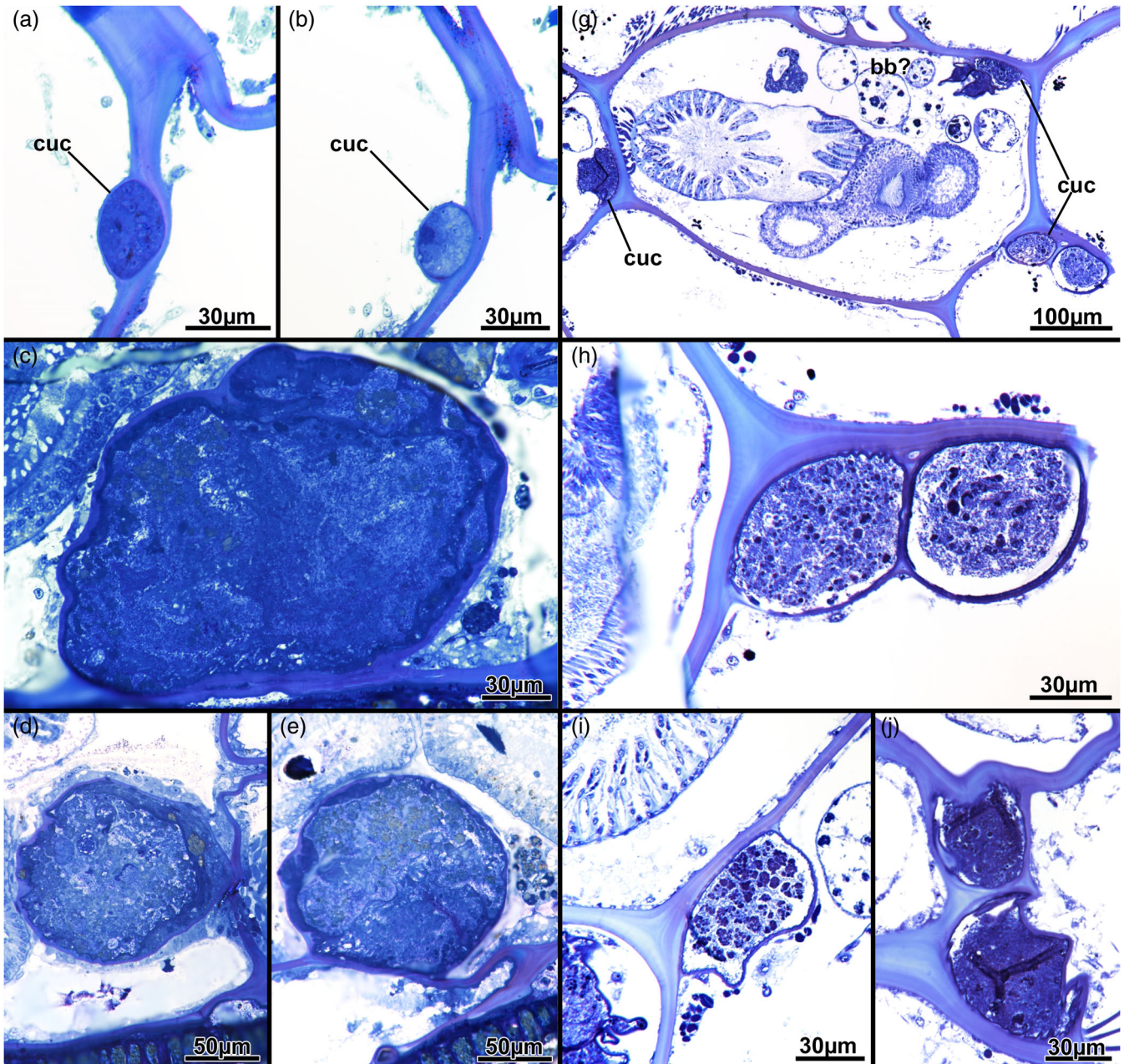


FIGURE 6 Cuticular inclusions in the Flustrellidridae. (a–e) *Flustrellidra hispida*. (g–j) *Elzerina binderi*. bb, brown body, cuc, cuticular cysts

complexes (Figures 3(f,g), 4(c,d), and 9(c,d)). The cuticle is thin between adjacent zooids and is centrally perforated by a minute pore of approximately 1–2 μm size. In *E. binderi*, the cuticle of the pore-plate has different staining properties than the remaining cuticle (Figure 3(f,g)). One or two ‘Special Cells’ line the cuticle on each side of the pore and plug the small pore. In *F. hispida* and *E. binderi*, several ‘Limiting Cells’ are located adjacent to the ‘Special Cells’ on both sides of the pore plate. In *Bockiella* sp., such additional cells are present but not abundant (Figure 9(b,c)). Cincture cells were not observed in any species.

3.3 | Apertural area including muscles

The aperture is bilabiate in the flustrellidrids *E. binderi* and *F. hispida* (Figures 1(b,d), 2, 11(a), and 12(a)), and approximately circular in *Bockiella* sp. (Figure 1(f) and 2). The cuticular lips of *E. binderi* and *F. hispida* are located on the proximal and distal edges of the aperture.

These are slightly elevated in *F. hispida* and protrude from the frontal surface (Figures 12(a) and 13(a–c)). In *E. binderi*, they are rather flat and at the same level as the remaining frontal wall (Figure 11(a)). In both species, the cuticle shows distinct staining properties probably indicating increased sclerotization. The aperture enters the vestibulum in retracted zooids, which is lined by the vestibular wall (Figure 2). The latter is of moderate and similar size in the three investigated species and ranges from 150 to 200 μm in length (Figures 2, 10(a), 11(d), 12(b, c), and 14(b–e)). The vestibular wall possesses a thick cuticle that is continuous with the remaining ectocyst. Proximally and basally the vestibular wall terminates in the diaphragm (Figures 2, 5(a,c,d), and 10, and 15(a–c,e)), which in retracted zooids separates the distal vestibulum from the proximal atrium. A diaphragmatic sphincter is present and constricts the area between the two cavities in retracted zooids. In *F. hispida*, the vestibular wall is proximally folded and bends frontally with the diaphragm always being located basally of the retracted lophophore (Figure 15(b,c)). In *Bockiella* sp., a distinct collar emanates distally from the diaphragm (Figures 2 and 10)

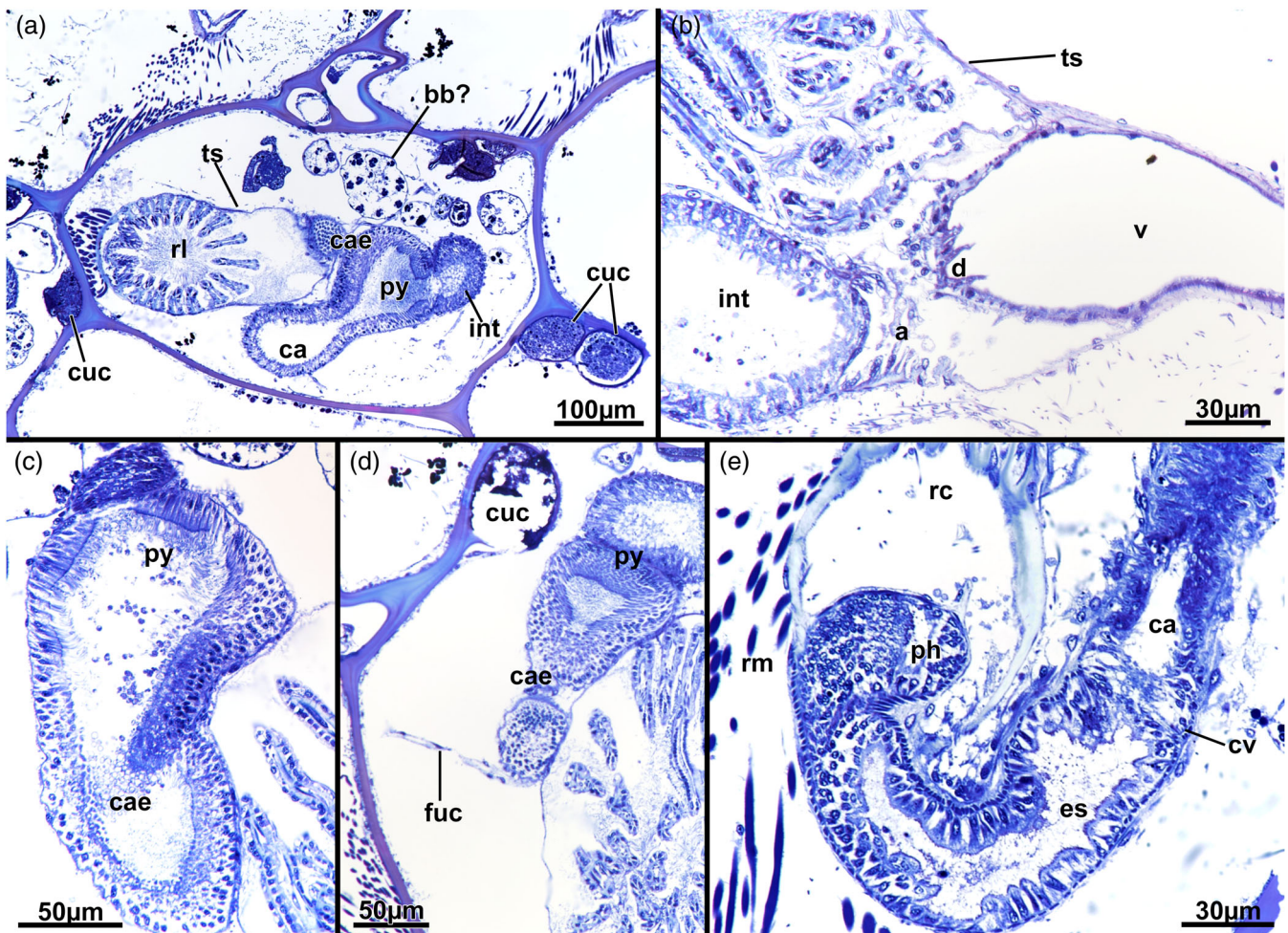


FIGURE 7 *Elzerina binderi*, histological details of the lophophore and digestive tract. (a) Frontal section of the mid- and hindgut. (b) Section of the fimbriated anus close to the diaphragm. (c) Section of the pylorus showing dense ciliation. (d) Section showing a thin tissue cord extending from the caecum to the lateral body wall. (e) Section of the foregut and its transition to the midgut at the cardiac valve. a, anus, bb, brown body, ca, cardia, cae, caecum, cuc, cuticular cysts, cv, cardiac valve, d, diaphragm, es, esophagus, fuc, funicular cord, int, intestine, ph, pharynx, py, pylorus, rc, ring canal, rl, retracted lophophore, rm, retractor muscle, ts, tentacle sheath, v, vestibulum

approximately half way along the vestibulum. The collar is a radially folded cuticular projection produced from the collar epithelium at the diaphragm, which is cone-shaped in this genus. In *F. hispida* and *E. binderi*, the epithelia of the diaphragm are folded on both sides, the distal one into the vestibulum and the proximal one into the atrium (Figures 2, 5(c,d), and 15(a,c,e)). A collar is not present at the

diaphragm in these two species. Instead, it arises more distally from folds of the vestibular wall (Figures 2, 5(e,f), and 15(b,d,f,g)). Hence, the collar is vestibular contrary to the diaphragmatic collar of *Bockiella* sp.

Apertural muscles are present as parieto-diaphragmatic muscles and duplicature bands. The former are present as a single pair

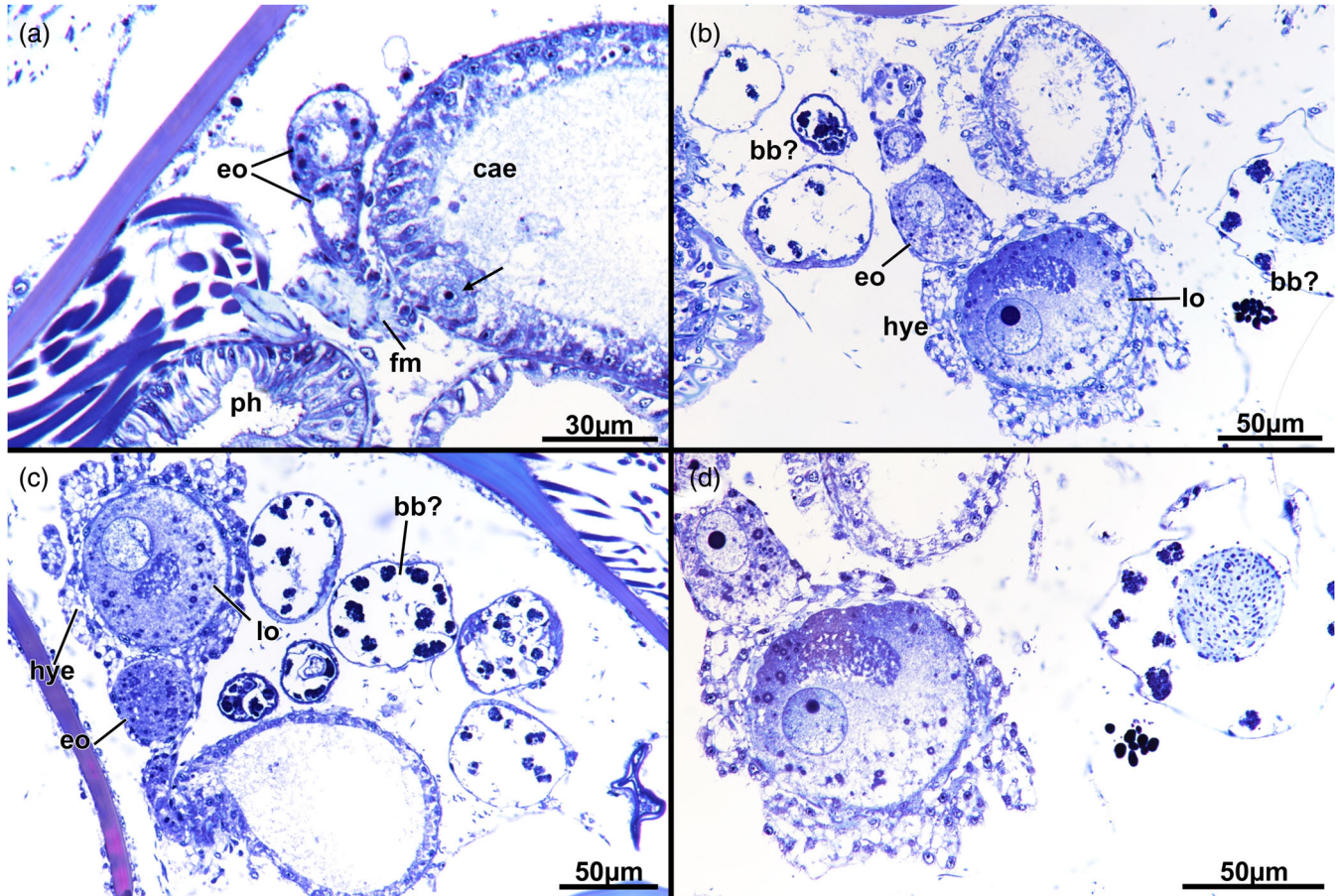


FIGURE 8 *Elzerina binderi*, oogenesis and oocytes. (a) Early oocyte tube attached to the proximal caecum end, close to the funicular muscle. (b, c) Sections of two oocyte tubes showing various early oocytes and one later oocyte at the distal end of the tube. (d) Detail of a late oocyte surrounded by a hypertrophied follicular epithelium. Note also the peculiar inclusions in the presumed brown body on the right. bb, brown body, cae, caecum, eo, early oocyte, fm, funicular muscle, hye, hypertrophied epithelium, lo, late oocyte, ph, pharynx

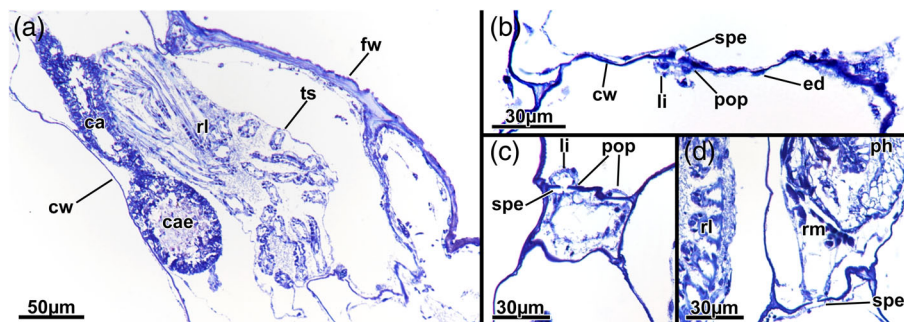


FIGURE 9 *Bockiella* sp. histological details of the cuticle and pore plates. (a) Longitudinal section showing the frontal wall and otherwise mostly thin cuticle. (b-d) Sections of the thin cuticular walls showing pore plates and very small pore complexes. ca, cardia, cw, cystid wall, ed, epidermis, fw, frontal wall, li, limiting cell, ph, pharynx, pop, pore plate, rl, retracted lophophore, rm, retractor muscle, spe, special cell, ts, tentacle sheath

originating from the lateral and basal wall in *E. binderi* and *F. hispida*, respectively, and insert in the area of the diaphragm (Figures 2, 11(c,g, h), 12(c,d), and 15(a,f)). In *Bockiella* sp., two pairs are situated on each side of the diaphragm (Figures 2, 10(a), and 14(b–e)). The duplicature

bands each arise from the tentacle sheath, close to the diaphragm, and project distally (in retracted zooids). They can be categorized into basal and frontal bands according to their location in the zooid. The basal bands are similar in all examined species and consist of a single

FIGURE 10 *Bockiella* sp. histological details of the apertural area.

(a) Longitudinal section of the aperture and vestibular area. (b) Details of the diaphragmatic sphincter and collar. (c, d) Section of the diaphragm showing the folded collar epithelium. am, apertural muscles, ap, aperture, c, collar, coe, collar epithelium, d, diaphragm, db, duplicature band, dis, diaphragmatic sphincter, fw, frontal wall, rl, retracted lophophore, ts, tentacle sheath, v, vestibulum, vw, vestibular wall

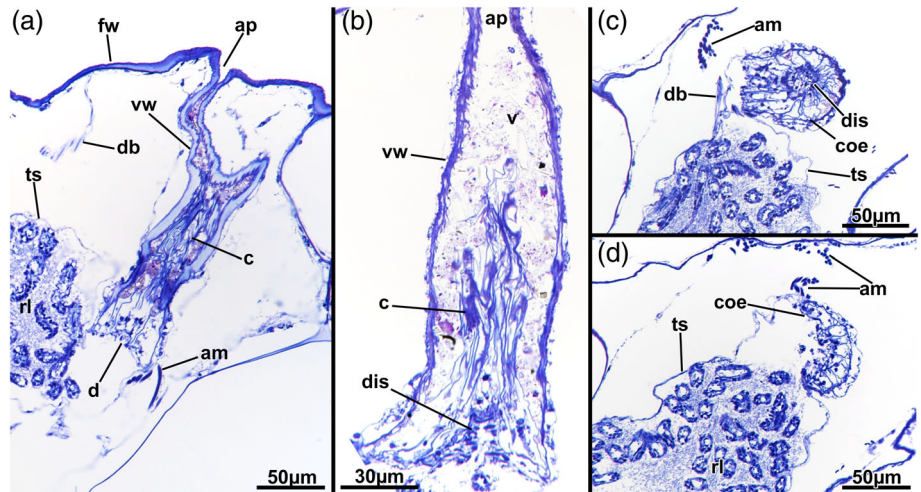
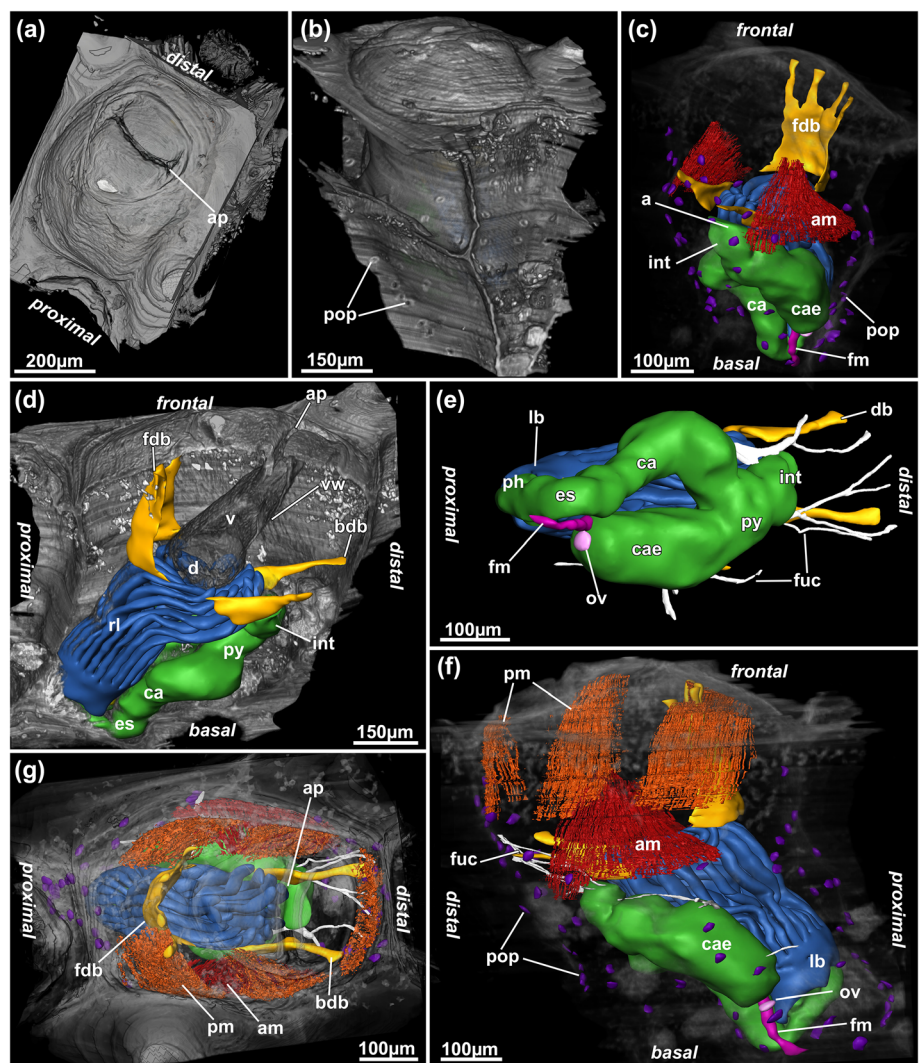


FIGURE 11 3D reconstruction based on serial sections of *Elzerina binderi* showing a zooid with major organ systems. (a) Frontal view showing the bilabiate aperture, volume rendering. (b) Lateral view showing pore plates, volume rendering. (c) Surface rendering showing the crown-shaped frontal duplicature band and the apertural muscles. (d) Lateral view of digestive tract, lophophore and duplicature bands as surface rendering and surrounding tissues as volume rendering. (e) Basal view of the digestive tract and funicular structures. (f) Lateral view showing parietal and apertural muscles. (g) Frontal view of the parietal and apertural muscles. a, anus, am, apertural muscles, ap, aperture, bdb, basal duplicature band, ca, cardia, cae, caecum, d, diaphragm, db, duplicature band, es, esophagus, fdb, frontal duplicature band, fm, funicular muscle, fuc, funicular cord, int, intestine, lb, lophophoral base, ov, ovary, pm, parietal muscles, pop, pore plate, py, pylorus, rl, retracted lophophore, v, vestibulum, vw, vestibular wall



pair (Figures 2, 11(d-f), 12(b-d), and 14(b-e)), which is also the case for the frontal bands of *Bockiella* sp (Figures 2 and 14(b-e)). A single broad frontal duplicature is present in *E. binderi* and *F. hispida*, which in its distal direction splits into four separate bands (Figures 2, 11(c,d), and 12(c,d)). In *F. hispida*, each of the four bands is short, but they are elongated in *E. binderi*. In *Bockiella* sp., a single lateral duplicature band was found in the reconstructed specimen (Figure 14(d,e)). Vestibular wall muscles are not present in any of the species.

3.4 | Lophophore and lophophoral base

The lophophore is large in all investigated species and carries 22–23 tentacles in *Bockiella* sp., 22 in *E. binderi* and 28–29 in *F. hispida*. In retracted zooids, they are tightly packed, for most of their part straight within the tentacle sheath but distally convoluted, which is especially evident in the large lophophore of *F. hispida*. Close to the lophophoral base, the two tentacles lining the median plane on the oral side are

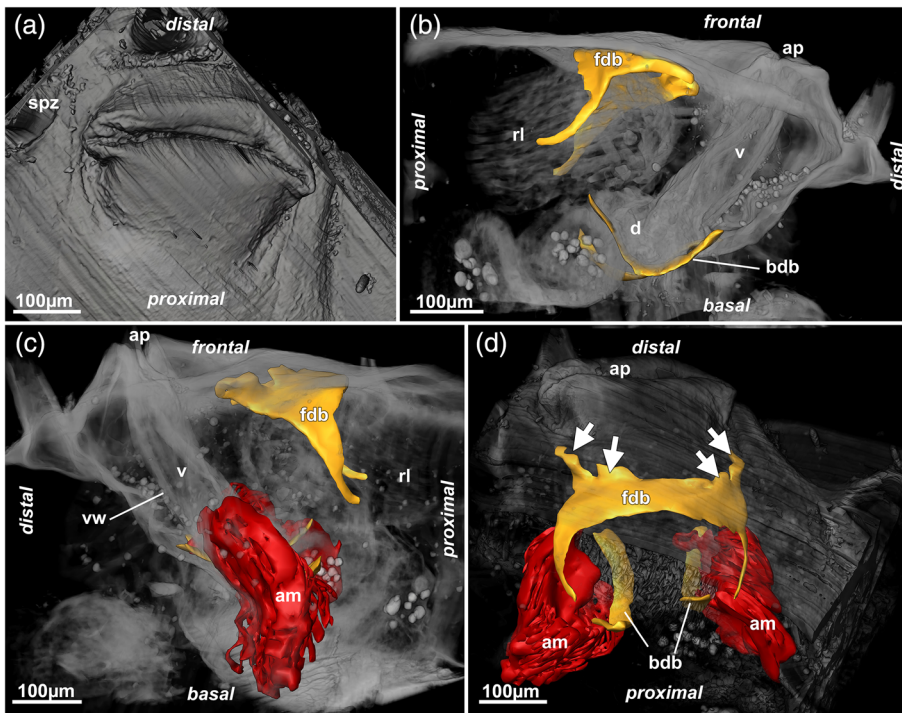


FIGURE 12 3D reconstruction based on serial sections of the apertural area of *Flustrellidra hispida*. (a) Frontal view of the aperture, volume rendering. (b) Lateral view showing the duplicature bands, aperture displayed transparently as volume rendering. (c) Similar view as in (b) but with apertural muscles included as surface rendering. (d) Frontal view of the frontal duplicature band. Arrows show the short four extensions. am, apertural muscles, ap, aperture, bdb, basal duplicature band, d, diaphragm, fdb, frontal duplicature band, rl, retracted lophophore, v, vestibulum, vw, vestibular wall

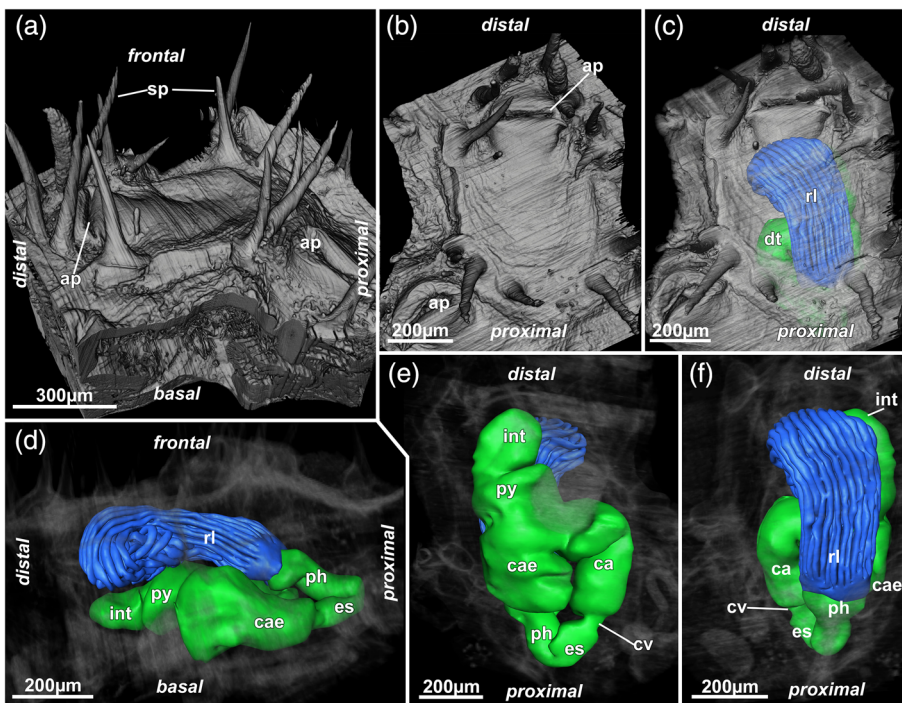


FIGURE 13 3D reconstruction based on serial sections of *Flustrellidra hispida* showing a zooid with kenozooidal spines (spinozooids). (a) Oblique view showing spinozooids, volume rendering. (b) Frontal view, volume rendering. (c) Similar view as in (b) but displayed more transparent and the lophophore and digestive tract as surface models. (d–f) Lateral (d), basal (e) and frontal (f) views of the lophophore and digestive tract, surface renderings. ap, aperture, ca, cardia, cae, caecum, ctl, cuticular lip, cv, cardiac valve, dt, digestive tract, es, esophagus, int, intestine, ph, pharynx, py, pylorus, rl, retracted lophophore, sp, spines

slightly enlarged and comma-shaped in cross-section in *E. binderi* and *F. hispida* (Figure 16(a)). Proximally, in the direction of the mouth, they continue as a small groove on the oral side of the foregut to form the so-called rejection tract.

A coelomic compartment, the ring canal, is present at the lophophoral base and unites the coelomic cavities of the individual tentacles (Figures 7(e) and 17(b,c)). Regularly arranged radial muscles traverse the ring canal, the buccal dilators, and occasionally sperm was encountered in the ring canal of *E. binderi* (Figure 17(b)). The ring canal is in open connection to the remaining body cavity at the anal side of the lophophoral base where also the cerebral ganglion is located. The latter is a small nerve concentration that has lateral extensions, which form the circum-oral nerve ring in an oral direction at the lophophoral base (Figures 16(c), 17, and 18(b)). In *E. binderi*, a small ganglionic lumen was detected (Figure 17(a,b)).

3.5 | Digestive tract

The digestive tract comprises three areas: the fore-, mid-, and hindgut. The foregut adjoins the lophophoral base with a short pharynx and esophagus, which terminates at the cardiac valve at the junction with the midgut (Figures 2, 7(c,e), 11(d–g), 13(d–f), 14(b–d), 16(b,c), 17(b,c), and 18(a,b)). The following cardia is the first part of the midgut, elongated in all three species and extending distally below or next to the retracted lophophore. The flustrellidrids *E. binderi* and *F. hispida* have a large caecum that extends proximally to the area of the lophophoral base (Figures 2(a,c), 11(c,e,f) and 13(d–f)). In *Bockiella* sp., only a small caecal pouch is present (Figures 2(d) and 14(b–e)). The last section of

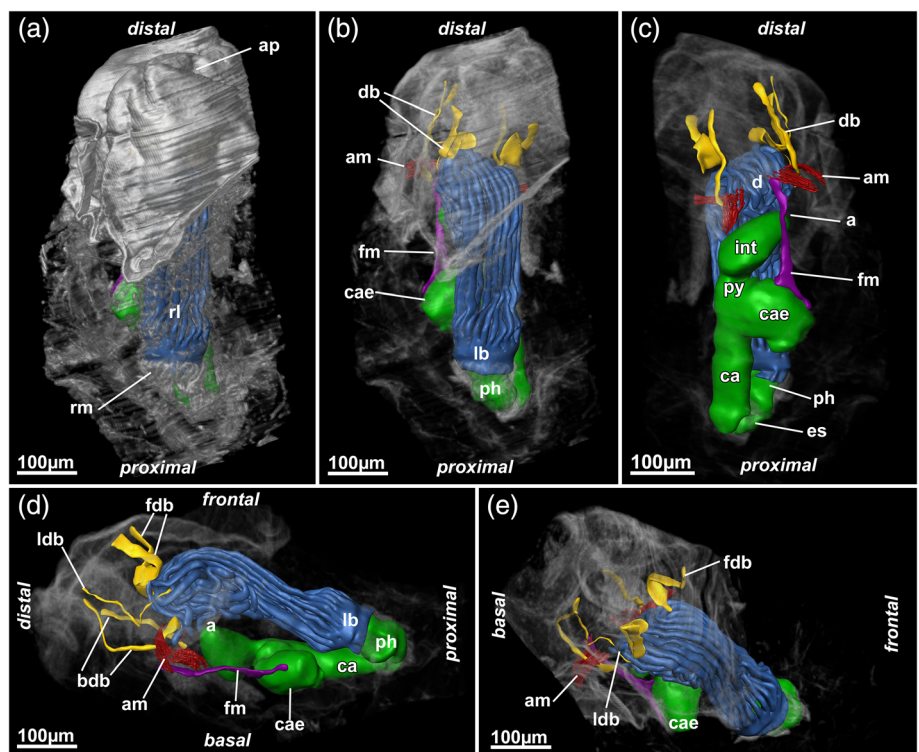
the midgut is the ciliated pylorus, which enters the intestine in the distal area of the zooid (Figures 2, 7(a), 11(c–e), 13(d–f), 14(c,d), 15(a,b), 16(d,e) and 18(b–d)). From the intestine, a vestibular anus enters the tentacle sheath, close to the diaphragm (Figures 2, 5(c), 11(c), 14(c,d), and 16(d,e)). The anus is fimbriate in the two flustrellidrids and shows multiple thin folds at its entry into the tentacle sheath.

A funicular muscle is present in all three species but varies in its position and extent in each species. In *E. binderi*, it is a short, muscular peritoneal strand from the proximal tip of the caecum that attaches to the closely located basal body wall (Figures 2(c), 8(a), 11(c,e,f)). In *F. hispida*, a short muscle is present on the medial side of the caecum, in the proximal third of the zooid, and attaches to the basal body wall approximately in the median plane of the zooid (Figures 2(a) and 16(f)). In *Bockiella* sp., a longer funiculus extends from the caecal pouch distally to the basal body wall (Figures 2(d) and 14(b–e)). In addition to the funicular muscle, thin cellular strands extend from the mid- and hindgut to various locations of the body wall (Figures 7(d) and 11(e–g)).

3.6 | Reproductive organs

Data on reproductive organs can only be provided for *E. binderi*. The analyzed specimens of *Bockiella* sp. and *F. hispida* had no gonads. Spermatogenetic tissue in *E. binderi* is uniformly located on the lateral cystid walls of ripe zooids. An early ovary was detected at the proximal end of the caecum, close to the funicular muscle, and contains only a few early oocytes (Figures 8(a) and 11(e,f)). In general, the ovary is tubular in this species with an external thin follicular lining and a series of progressive oogenetic stages

FIGURE 14 3D reconstruction based on serial sections of *Bockiella* sp. (a) Frontal view of a zooid showing surrounding tissues as volume rendering. (b) Same as in (a) but displayed more transparently. (c) Basal view of the polypide, surface rendering. (d) Lateral view of the polypide, surface rendering. (e) Oblique view from the distal side. a, anus, am, apertural muscles, ap, aperture, bdb, duplicature band, ca, cardia, cae, caecum, d, diaphragm, db, duplicature band, es, esophagus, fdb, frontal duplicature band, fm, funicular muscle, int, intestine, lb, lophophoral base, ldb, lateral duplicature band, ph, pharynx, rm, retractor muscle



(Figure 8(a–c)). The latest encountered stages are surrounded by a conspicuously hypertrophied follicular epithelium. The oocyte itself contains a large granular body (“yolk nucleus,” Balbiani body) next to the nucleus, and numerous yolk inclusions in the peripheral part of the cytoplasm (Figure 8(b–d)).

An intertentacular organ or ovipositor is present at the lophophoral base in *E. binderi* (Figure 17). Between the gut shanks of

the digestive tract, proximally of the cerebral ganglion, the peritoneal epithelium is thickened and forms a ciliated gutter (Figure 17(a,c)). In a distal direction, it enters the opening of the intertentacular organ above the ganglion. The epithelial lining of the organ is conspicuous. The proximal lumen seems constricted toward the distal larger cavity that exits into the lophophoral base above the mouth opening (Figure 17).

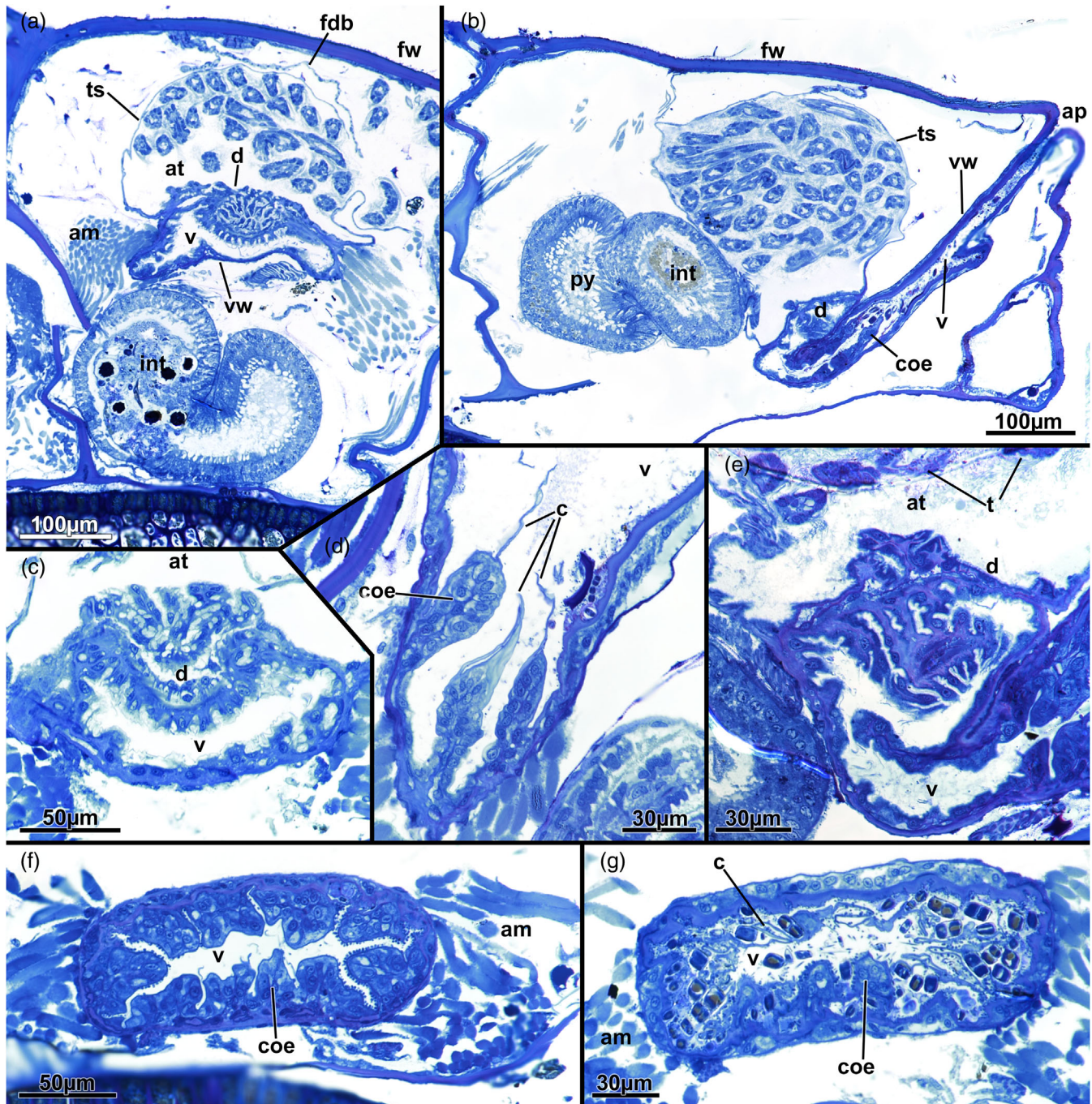
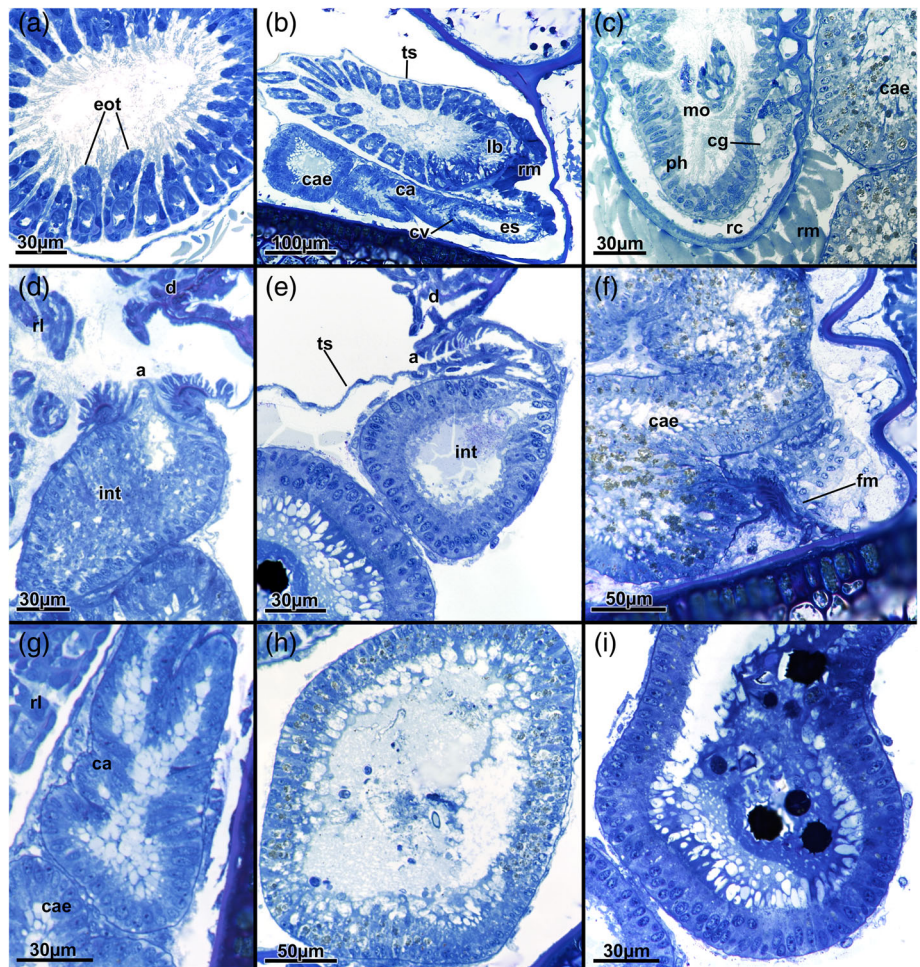


FIGURE 15 *Flustrellidra hispida*, histological details of the apertural area. (a) Cross-section of the diaphragm. (b) Longitudinal section of the vestibulum. (c) Detail of the diaphragm, cross section. (d) Longitudinal section of the collar epithelium and collar. (e) Detail of the diaphragm, longitudinal section. (f, g) Cross sections of vestibular wall showing folded epithelium. am, apertural muscles, ap, aperture, at, atrium, c, collar, coe, collar epithelium, d, diaphragm, fdb, frontal duplicature band, fw, frontal wall, int, intestine, py, pylorus, t, tentacle, ts, tentacle sheath, v, vestibulum, vw, vestibular wall

FIGURE 16 *Flustrellidra hispida*, histological details of the lophophore and digestive tract. (a) Cross-section of the tentacles close to the lophophoral base showing the elongated oral tentacles. (b) Longitudinal section showing the transition of the esophagus to the midgut. (c) Detail of the lophophoral base. (d, e) Details of the anus. (f) Detail of the funicular muscle extending from the caecum to the basal body wall. (g) Transition of the cardia to caecum. (h) Detail of the intestine. (i) Food particles located in the midgut. a, anus, ca, cardia, cae, caecum, cg, cerebral ganglion, d, diaphragm, eot, elongated oral tentacles, es, esophagus, fm, funicular muscle, int, intestine, lb, lophophoral base, mo, mouth opening, ph, pharynx, rc, ring canal, rl, retracted lophophore, rm, retractor muscle, ts, tentacle sheath



3.7 | Retractor and parietal muscles

Retractor muscles are similar in all investigated species and consist of multiple fibers that originate from the proximal side of the zooid and insert at the lophophoral base and the foregut (Figure 2). Some fibers also attach to the area of the esophagus-cardia transition. The parietal muscles are a series of thin muscles on the periphery of the zooids (Figure 2). In *F. hispida*, they originate from the lateral cystid wall, in *Bockiella* sp. from the basal wall, and in both species attach to the frontal wall. The parietal muscles reach into the distal area of the zooid next to the aperture. In *E. binderi*, there are five distinct parietal muscle bundles, four emanating from the lateral sides of the zooid and one from the distal transverse wall, all of which insert at the frontal wall (Figures 2(b) and 11(f,g)).

4 | DISCUSSION

4.1 | General structure

Typical for most members of the superfamily Alcyonidoidea, zooids are polygonal and form tightly arranged colonies (see, e.g., d'Hondt, 1983). The general structure of the zooids thus corresponds to previous

descriptions (see also, e.g., Cook, 1964). However, the elongation and deep extension of the zooids of *E. binderi* into the cylindrical branches has not been reported before for the genus, but is present in some species of *Alcyonidium* (Hayward, 1985).

4.2 | Cuticle and pore plates

The cuticle is generally thick and multi-layered in the three investigated species, although the cuticle in *Bockiella* only showed a few thicker areas, such as the frontal wall. It should, however, be emphasized that preservational issues might also be present and comparison of the three samples should be undertaken with caution, since primary fixation differs. Multi-layered, thicker cuticles are also present in Alcyonidiidae (e.g., Chrétien, 1957; Matricon, 1960), Pherusellidae (Decker et al., in press), *Haywardozoon* (Schwaha, Grisichenko, et al., 2020) and Hislopiidae (Schwaha, 2020b). Cuticles of other stenostomes are usually thin and do not show any distinct layers. From the multi-layered families, hislopiids are the only clade not closely related to the Alcyonidoidea, but form a separate superfamily (Schwaha, 2020a). Specific superficial layers of different staining properties (in sections), as encountered in *E. binderi* and *F. hispida*, were, however, not encountered in hislopiids, but occur in pherusellids and

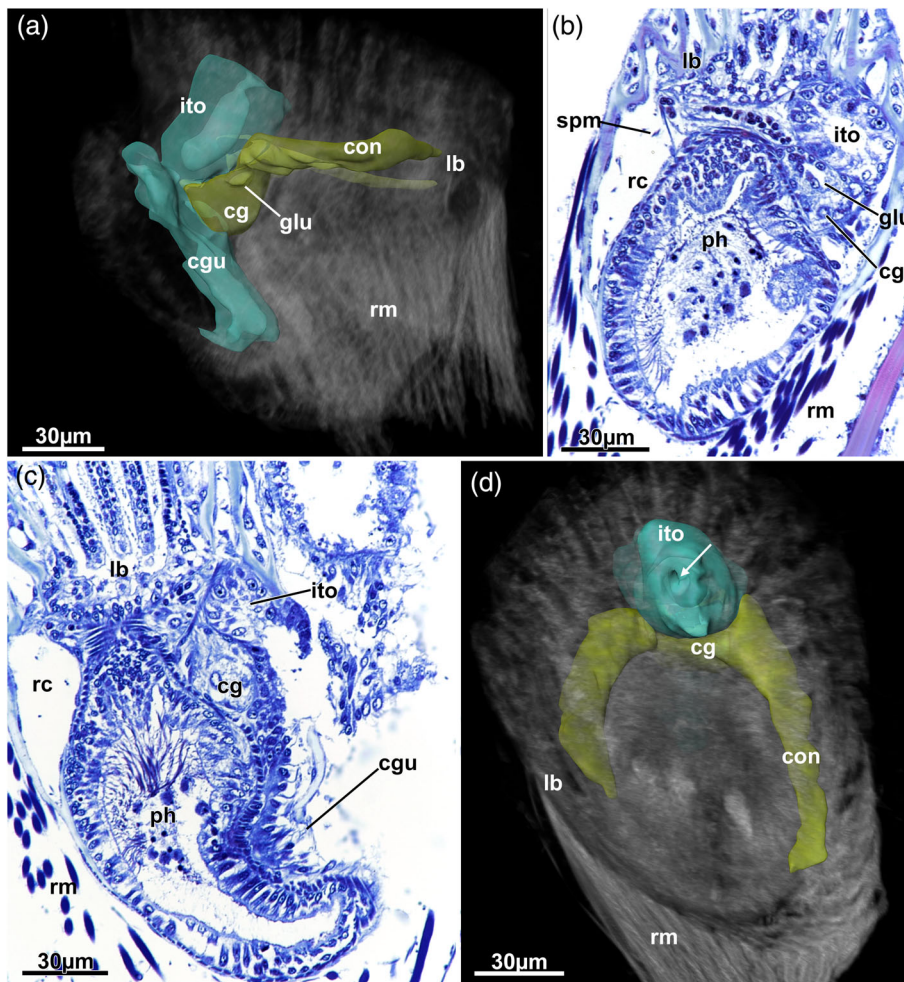


FIGURE 17 *Elzerina binderi*, intertentacular organ/ovipositor at the lophophoral base. (a, d) 3D reconstruction based on serial sections. (b, c) Semithin sections. (a) Lateral view showing lumen of intertentacular organ and ganglion. (b) Location of the intertentacular organ above the ganglion, which contains a lumen. (c) Thickened peritoneal layer proximal to the ganglion carrying long cilia to form a ciliated gutter. (d) Frontal view showing the opening of the intertentacular organ in the lophophoral space (arrow). cg, cerebral ganglion, cgu, ciliated gutter, con, circum-oral nerve ring, glu, ganglion lumen, ito, intertentacular organ, lb, lophophoral base. ph, pharynx, rc, ring canal, rm, retractor muscle, spm, sperm

Haywardozoon. Although not specifically tested, these superficial layers appear more sclerotized than the remaining cuticle, which would explain their shredded or broken appearance along the sectioning direction.

Cuticular inclusions of presumed brown bodies as found in the two flustrellidrid species have partially only been reported in pherussellids (Decker et al., in press). The degeneration products of the polypide recycling events, the brown bodies, are either expelled from the newly regenerated zooid by various mechanisms or alternatively remain in the body cavity, which consequently indicates the number of recycling events in the lifetime of the zooid (Gordon, 1977).

Pore-plate structures vary among ctenostomes, and most species or clades usually have a single pore-plate on each side of the zooid (twice lateral, proximal and distal) (Schwaha, 2020a; Schwaha, Ostrovsky, et al., 2020). Each pore complex consists of up to three different cell types: “Special Cells” in the pore, “Limiting Cells” surrounding the “Special Cells,” and “Cincture Cells” lining the cuticle between the Special Cell plug (Mukai et al., 1997; Schwaha, 2020b). Multiple pores in the cystid walls are rare among ctenostomes and were originally only recorded in the genera *Pherusella* and *Sundanella*, although their presence in *Flustrellidra* had already been shown (Schwaha 2020a, 2020b). This study brings the first real

confirmation of multiple pores in the Flustrellidridae, exemplified by the genera *Flustrellidra* and *Elzerina*. Together with other characters, this supports a close relationship of the multiporate ctenostomes *Pherusella*, *Flustrellidra*, *Elzerina*, and *Sundanella*, as recently indicated (Schwaha, 2020a).

4.3 | Aperture and associated muscles

Bilabiate apertures are not common among ctenostomes and are characteristic of the family Flustrellidridae (d'Hondt, 1983, Schwaha, 2020a), the genus *Farrella* (Hayward, 1985; Marcus, 1926) and the genus *Haywardozoon* (Schwaha et al. 2020b). The Alcyonidiidae typically have a rounded aperture (Schwaha, 2020a), which corresponds to the situation found in *Bockiella* sp. Among the remaining Alcyonidioidea, clavoporids and pachyzoids share a round aperture, whereas pherussellids have a rectangular aperture (Schwaha, 2020c, Decker et al., in press).

Another character typical for this superfamily is the highly cuticularized vestibular wall, which has also been described for other members of the clade (*Alcyonidium*, Matricón, 1963; *Haywardozoon*, Schwaha, Grischenko, et al., 2020; *Pherusella*, Decker et al., in press).

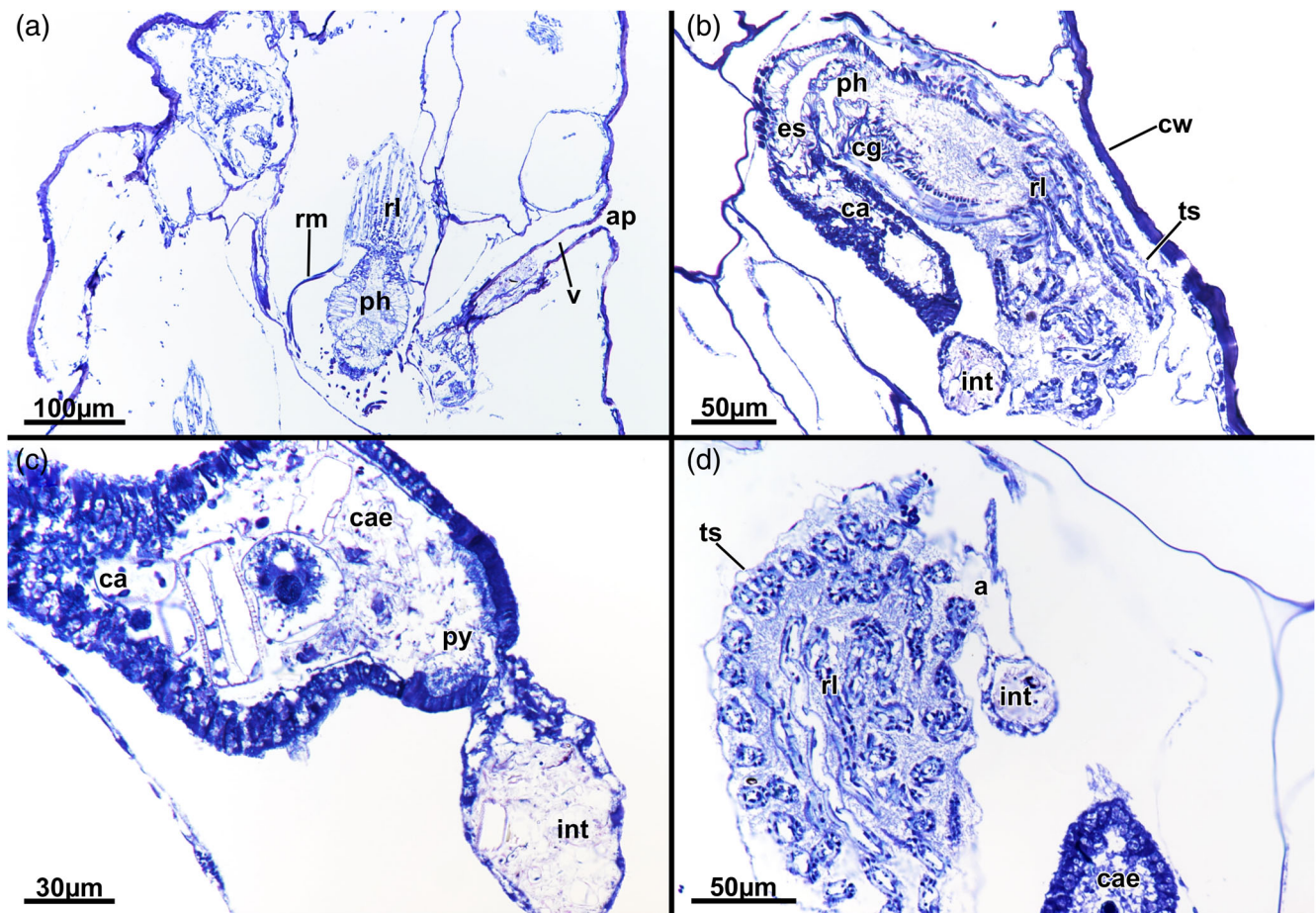


FIGURE 18 *Bockiella* sp., histological details of the lophophore and digestive tract. (a) Longitudinal section of the colony. (b) Detail of the lophophoral and foregut including the transition into the cardia. (c) Detail of the midgut and hindgut. (d) Detail of the anus entering the tentacle sheath. a, anus, ap -aperture, ca, cardia, cae, caecum, cg, cerebral ganglion, cw, cystid wall, es, esophagus, int, intestine, ph, pharynx, py, pylorus, rl, retracted lophophore, rm, retractor muscle, ts, tentacle sheath, v, vestibulum

In most other ctenostome superfamilies, the cuticle of the vestibular wall is thin (see, e.g., Braem, 1890, 1951; Schwaha et al., 2019; Schwaha & De Blauwe, 2020). Apertural muscles are present as parieto-diaphragmatic muscles, which insert only at the proximal end of vestibular wall. These consist of a single pair in the flustrellidrids *E. binderi* and *F. hispida*, similar to those found in pherussellids (Decker et al., 2020, in press) and the genus *Haywardozoon* (Schwaha, Grischenko, et al., 2020). *Bockiella* has two bundles on each side, which corresponds to the presumed ancestral condition of the apertural muscles in ctenostomes (Schwaha, Ostrovsky, et al., 2020), but also lacks parieto-vestibular muscles like the flustrellidrids. The situation among the remaining Alcyonidoidea (Alcyoniidae, Clavoporidae, Pachyzoidae) is not entirely clear. A set of the latter muscles attaching to the distal vestibular wall, arranged as discrete bundles, was shown in *Alcyonidium* (Prouho, 1892; Reed, 1991; see also Schwaha et al., 2011), but a recent study based on confocal laser scanning microscopy reported such muscles as diffuse and rather chaotic in *Alcyonidium* and the clavoporid genus *Ascorhiza* (Schwaha & Wanninger, 2018). As shown in the current study, the parietal muscles are also located in the far distal area of zooids, next to the aperture, in

the three analyzed species. This implies that the muscles shown by early researchers (Prouho, 1892 and especially the copy of Reed [1991]) and found in recent studies (Schwaha & Wanninger, 2018) probably are in fact parietal muscles and not apertural muscles. Owing to the large size of zooids and colonies of alcyonidoideans, dissection of colony pieces or zooids for techniques such as confocal microscopy is often required, which probably resulted in distortion of the original traverse of these muscles and led to the misinterpretation of apertural muscles. However, additional specimens of Alcyoniidae and other families should be studied histologically for confirmation. The far distal displacement of the parietal muscles functionally compensates for the absence of parieto-vestibular muscles. Parieto-vestibular muscles are required for the lateral displacement of the vestibular wall during the protrusion process and thus prevent body cavity fluid from entering the distal area of the zooid (Schwaha, 2020b). In the species for this study, and probably most alcyonidoideans, this function seems to be carried out by the parietal muscles. The functional significance of these different hydrostatic systems is not clear.

In addition to the parieto-diaphragmatic muscles, an orificial sphincter is present in alcyonidiid and clavoporid ctenostomes

(Schwaha & Wanninger, 2018), and also monobryozoids (Ott & Schwaha, 2020). It was considered as a possible synapomorphy of alcyonidioid ctenostomes, but is clearly lacking in the flustrellidrids, and also *Bockiella*. Hence, it appears to be restricted to certain clades of this superfamily and might be apomorphic for family-level grade taxa.

Duplicature bands are a second set of apertural muscles extending from the tentacle sheath to the body wall and are present in all phylactolaemates and cheilostomes, and most ctenostomes (Schwaha, 2020b; Schwaha et al., 2011; Schwaha & Wanninger, 2018). In *Bockiella* sp., these are arranged as four bands (sometimes with a fifth one), which corresponds to the situation found in most clades. In the two investigated flustrellidrid species, the broad frontal duplicature band that further splits into four bands is unique and has not been observed in any other ctenostome. *Pherusella minima* is the only other bryozoan to show a single frontal duplicature, which, however, has only a short proximal connection and splits into two separate bands. In the pheruselid *Pherusella liowae*, the proximal part of the frontal duplicature bands is widened, but still distinguishable as two distinct bands that are not medially connected (Decker et al., in press).

The collar is a gymnolaemate-specific character and present in almost all ctenostomes (Schwaha, Ostrovsky, et al. 2020). In most ctenostomes, the collar is formed at the diaphragm and projects distally into the vestibulum (Schwaha, 2020a, 2020b). It can have a wide variety of shapes, the largest one being setigerous and found in the genus *Aeverillia* (see McKinney & Dewel, 2002). In ctenostomes, such as *Elzerina*, *Flustrellidra*, and *Pherusella*, the collar was described as nearly absent and reduced (Banta, 1975), implying that “opercular”-like closing mechanism of the aperture of these genera correlates with collar reduction. However, as shown in the current study on *Elzerina* and *Flustrellidra*, and a recent study on pheruselids (Decker et al., in press), the collar is present, but vestibular rather than diaphragmatic. The term “vestibular collar” is applicable when the collar-forming epithelium is located on the vestibular wall, usually slightly distal of the diaphragm, whereas “diaphragmatic collar” is used for collars formed directly at the diaphragm. Vestibular collars are certainly smaller than diaphragmatic ones. The significance of the different position remains unknown. However, it enables the diaphragm to form multiple folds as observed in the three genera mentioned above (this study, Decker et al., in press), but also membraniporine cheilostomes (see Lutaud, 1984, 1993). At least for flustrellidrid and pheruselid ctenostomes the vestibular collar and folded diaphragm is a useful apomorphic character. Whether this implies that they share a common ancestor with cheilostomes (as implied by Banta [1975]) remains unknown.

4.4 | Lophophore and ganglion

The lophophore in *Bockiella* sp. and *E. binderi* has ~22 tentacles, which corresponds to data previously reported for both genera (Cook, 1964). Similarly, the observed 29 tentacles of *Flustrellidra hispida* correspond to the range of 28–40 given by Hayward (1985). Tentacle ranges show a

higher variation in the genus *Flustrellidra*. Although little data is provided for other species of the genus, most reports range from 18 to 22 tentacles (*F. akkeshiensis* 22–24, *F. filispina* 20–22 (Mawatari, 1971), *F. armata* 18 (Grischenko et al., 2010), *F. corniculata* 18 (Smitt, 1872)).

The oral tentacles in *E. binderi* and *Flustrellidra hispida* are elongated at the lophophoral base and medially line the rejection tract which extends proximally into the pharynx. Such a rejection tract was first recognized in *F. hispida* (Atkins, 1932) and forms a ciliated groove on the oral side of the foregut. Along with the adjacent elongated tentacles, it is used for rejecting incurrent particles at the lophophoral base prior to ingestion. It is also present in the genus *Sundanella* (Braem, 1939) and all pheruselids (Decker et al., in press). It seems restricted to multiporate ctenostomes and probably is a synapomorphy.

The ganglion at the lophophoral base corresponds to the situation of other bryozoans, including ctenostomes (Schwaha, 2020b). A small ganglion lumen was detected in *E. binderi*. Such a ganglionic lumen is characteristic of all phylactolaemates, and has also been found in two clades of ctenostomes (Temereva & Kosevich, 2016; Weber et al., 2014) and most recently in a cyclostome bryozoan (Temereva & Kosevich, 2018).

4.5 | Retractor and parietal muscles

The retractor muscles of the investigated species are similar to other ctenostome bryozoans and attach to the lophophoral base and parts of the foregut, distally to the first parts of the cardia (see Schwaha, 2020b; Schwaha, Grischenko, et al., 2020; Schwaha & De Blauwe, 2020). There are only a few exceptions to this general pattern, such as the aethozooid *Aethozooides uraniae* where additional retractor muscle fibers insert at the caecum too (Schwaha et al., 2019).

The parietal muscles of *F. hispida* and *Bockiella* sp. are similar to those described in other cteno- and cheilostomes (Cheatham & Cook, 1983; Mukai et al., 1997). The parietal muscles in these two species also extend far distally in the area of the aperture (see also above concerning the confusion of parietal-apertural muscles and functional implications). The situation in *E. binderi* is unique in having parietal muscles organized in a few discrete bundles. The distal position, in front of the aperture is especially unusual, since these muscles are normally restricted to the lateral sides of zooids (Cheatham & Cook, 1983). This particular arrangement of the parietal muscles probably correlates with the extreme elongation of the fronto-basal axis of the zooids in *E. binderi*.

4.6 | Digestive tract and funicular structures

The digestive tract of all three species has several similarities: short foregut, elongated cardia and a vestibular anus (cf. Schwaha, 2020c). A short vestigial caecum is typical for the Alcyonidiidae (see Le Brozec, 1955; d'Hondt, 1983), which supports the position of *Bockiella* in this family. In contrast, flustrellidrids (this study) and pheruselid species (Decker et al., in press) have a large and medium-sized caecum, respectively, which represents another character for distinguishing these families. An additional character found exclusively in

flustrellidrids and pherussellids is a fimbriate anus (this study, Decker et al., in press).

Funicular structures in the form of funicular muscles are common in ctenostomes (Schwaha, Ostrovsky, et al., 2020). Considerable variation exists in the number and location of funicular muscles. In most ctenostomes, they originate from the caecum and insert at the lateral or proximal body wall. As shown in this study, all three studied species show a different structure of the funicular muscle: *E. binderi* with a short one from the caecum tip to the proximal/basal body wall as for example also observed in *P. liowae* (Decker et al., in press); *F. hispida* with a short muscle extending from the medial caecal area to the basal body wall, as also found in the genus *Alcyonidium* (Prouho, 1892) and *Arachnidium fibrosum* (Schwaha & De Blauwe, 2020); and *Bockiella* sp. showing a thicker, longer muscle extending from the distal area of the caecum further distally. The latter condition does not seem to have been described for any ctenostome. In *E. binderi*, additional thin tissue strands are present that connect parts of the gut with the body wall. Such networks of peritoneal strands are not common among ctenostomes but are considered typical for cheilostome bryozoans (Schwaha, Ostrovsky, et al., 2020). However, among alcyonidiodieans it has been indicated, but not verified, in the genus *Lobiancopora* (see Hayward, 1985). Similar, irregular peritoneal strands were recently reported in *A. fibrosum* (Schwaha & De Blauwe, 2020). Whether such strands evolved multiple times or not, and also their functional significance, remains unknown.

4.7 | Reproduction in Flustrellidridae

Data on the reproduction of the genus *Elzerina* has hitherto been entirely unknown. The current investigation provides first data on oogenesis and the presence of an intertentacular organ or ovipositor. Ovaries are present as elongated tubes with progressive ripening showing small oogonia on the proximal end and ripe, large ones at the distal end of the tube. Oocytes at the distal end are small (less than 100 µm), oligolecithal and few in number, which corresponds to pattern 2 of Ostrovsky (2013), which is also found in other Alcyonidiodiea and in general involves few meso- to macrolecithal oocytes and brooding. Growth and yolk increase past the encountered stages appears likely since the follicular epithelium surrounding larger oocytes is hypertrophied, which indicates additional, heterosynthetic production of yolk for the surrounded oocyte. Also, a “yolk nucleus” as encountered in the closely-related *F. hispida* (Pace, 1906) was present in the observed oocytes of *E. binderi*. This structure is temporary in *F. hispida* (Pace, 1906) and corresponds to the Balbiani body of other organisms.

An intertentacular organ has been found in numerous ctenostomes including several species of the genus *Alcyonidium* (Ostrovsky & Porter, 2011). So far, it was not encountered in any member of Flustrellidridae. Its presence is often associated with a broadcasting reproductive strategy, but is also found in many brooders. In the case of broadcasters, a high number of oligolecithal

oocytes is typically present (Reed, 1991). The genus *Flustrellidra* and the closely related multiporate ctenostome family Pherussellidae possess so-called pseudocyphonautes larvae, which are lecithotrophic, shelled and brooded within the tentacle sheath of degenerated mother zooids (Decker et al., 2020, in press). To date, no intertentacular organ has been described in *Flustrellidra* or *Pherusella*. Nonetheless, it appears likely that *Elzerina* also shows a similar mode of development with brooded embryos developing into lecithotrophic larvae (pseudocyphonautes?), but additional studies are required to confirm this.

5 | CONCLUSIONS

The present study adds another important piece into our understanding of the soft body morphology of ctenostomes. Characters such as the aperture and its associated muscles, details of the digestive tract and the first confirmation of multiporate cystid walls in Flustrellidridae are essential for resolving systematic and phylogenetic position. The multitude of newly established characters will be especially important for reconstructing character evolution in this same clade of bryozoans once a robust phylogenetic tree is available.

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AUTHOR CONTRIBUTIONS

Thomas Schwaha: Conceptualization; formal analysis; investigation; methodology; project administration.

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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