From feeding to sensing: microanatomy and ultrastructure of the rudimentary polypide in the avicularia of *Arctonula arctica* (Bryozoa: Cheilostomatida)

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ABSTRACT: Exaptations are among the most interesting evolutionary phenomena, involving a change of function in organs that were not originally adapted for that task. In the colonies of most cheilostome bryozoans, some basic feeding modules (autozooids) with protective operculum were transformed to avicularian polymorphs equipped with an enlarged defensive/cleaning mandible. The tentaculate, sensing, food-gathering and digesting apparatus of autozooids — the retractile polypide — was reduced to a tiny sensory organ retaining a limited mobility. Our first ultrastructural and immunocytochemical study on the adventitious sessile avicularia of *Arctonula arctica* focuses on muscular and nervous elements of the rudimentary polypide and also shows the presence of an associated unpaired gland. The overall structure suggests a mechano- and/or chemoreceptor function of the vestigial polypide. Based on the presence of the accessory gland, we also assume a chemical defense function of the avicularium.
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KEY WORDS: colonial invertebrates, polymorphism, ultrastructure, exaptations.

От питания к ощущению: микроанатомия и ультраструктура рудиментарного полипида авикулярев *Arctonula arctica* (Bryozoa: Cheilostomatida)

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РЕЗЮМЕ: Экзаптации являются одним из интереснейших эволюционных явлений, характеризующих смену функций органов. В колониях большинства хейлостомных мшанок некоторые питающиеся модули (аутозооиды) с защитным оперкулюмом и щупальцевым пищедобывающим и пищеварительным аппаратом — полипидом, трансформировались в авикулярии с увеличенной защитной/чистящей мандибулой и сенсорным органом, состоящим из крошечного рудиментарного полипида. Кроме того, наше ультраструктурное и иммуноцитохимическое исследование адвентивных сидячих авикуляриев мшанки *Arctonula arctica* обнаружило наличие связанной с полипидом непарной железы. Общая структура, включая мышечные и нервные элементы, предполагает возможность как механо-, так и/или хеморецепторной функций рудиментарного полипида. Наличие дополнительной железы позволяет также предположить наличие еще одной функции — химической защиты.
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КЛЮЧЕВЫЕ СЛОВА: колониальные беспозвоночные, полиморфизм, ультраструктура, экзаптации.

Introduction

Among colonial invertebrates the phylum Bryozoa demonstrates one of the most striking examples of morpho-functional polymorphism or "division of labor" manifested via the emergence of modules specialized in performing certain functions (Lidgard *et al*., 2012). While the bryozoan class Phylactolaemata entirely lacks polymorphic zooids (or heterozooids), the classes Stenolaemata and Gymnolaemata both show a high diversity of zooid types (Boardman *et al*., 1983; Schack *et al*., 2019). Among them, the gymnolaemate order Cheilostomatida exceeds other bryozoan clades in having the largest variety of polymorphs including several unique types (Cheetham, Cook, 1983; Schack *et al*., 2018, 2019).

Bryozoans are almost exclusively colonial filter-feeders that, together with sponges and cnidarians, dominate many benthic ecosystems (Ryland, 1970, 2005; Taylor, 2020; Schwaha, 2021). Each colony is formed by the iterative budding of modules (zooids), most of which are capable of feeding and termed autozooids. Every autozooid consists of (1) a polypide, including a retractable crown of ciliated tentacles (lophophore), a gut, and associated muscular and nerve elements, and (2) a cystid, which is a rigid or elastic body wall enveloping the polypide when it is retracted (Hyman, 1959; Mukai *et al*., 1997). In the retracted state, the lophophore is surrounded by the wall of the tentacle sheath, which continues distally into a small chamber of the vestibulum. In cheilostome bryozoans the latter opens to the external environment via an orifice covered by a chitinized flap or operculum. When the polypide is protruded, the operculum is uplifted, and the everting tentacle sheath (often termed introvert) constitutes the stalk-like lower part supporting the lophophore (Shunkina *et al*., 2015). In cheilostomes the vestibulum also receives the ducts of paired or unpaired organs, known as periopercular organs and vestibular glands (Repiachoff, 1875; Ostroumoff, 1886; Waters, 1892; Marcus, 1939; Lutaud, 1964, 1986; Hageman, Lutaud 1982). The function of the gland secretion is unknown and is thought to either provide a lubricant protecting tentacles from mechanical damage during protrusion and retraction, or to be a mucus retaining food particles on the tentacle surface. Some of these organs contain bacteria (Lutaud, 1965, reviewed in Hyman, 1959; Mukai *et al*., 1997).

In comparison to basic autozooidal structure, zooidal polymorphs are characterized by varying degrees of reduction or even a total loss of the polypide, and by a significant modification of the cystid. The evolutionary transformation of

autozooids to heterozooids in most cases were also accompanied by a strong restructuring and reduction of both nervous and muscular systems (Silén, 1938, 1977; Marcus, 1939; Lutaud, 1977; Carter *et al*., 2010, 2011; Serova *et al*., 2017, 2022).

Bryozoans from the order Cheilostomatida exhibit several types of heterozooids among which avicularia are the most diverse. Depending on the size, position, and structure, four main types of avicularia are distinguished: vicarious, interzooidal, adventitious (sessile and pedunculate), and a separate type called vibracularia. All have a movable mandible — a roundish, triangular, hook-, paddle-, spoon-like or otherwise — sclerotinized part that evolutionarily originated from the operculum of the autozooid. In vibracularia the mandible is more or less long, often transformed into a seta (Hincks, 1880; Silén, 1938; Kluge, 1975; Carter *et al*., 2010; Schack *et al*., 2018, 2019; Serova *et al*., 2022). The different shapes, sizes and arrangement of the avicularia presumably reflect different functions performed by these polymorphs in the colony. Indeed, direct observations indicate that avicularia are mostly defensive and cleaning structures, whereas vibracularia can provide cleaning, defense, colony support as well as locomotion, sensory and certain other functions (e.g. Marcus, Marcus, 1962; Cook, 1973; Cook, Chimonides, 1978; Chimonides, Cook, 1981; Winston, 1984, 1986, 1991, 2010; Shunatova *et al*., 2022; reviewed in Serova *et al*., 2022).

The general assumption is that the ability of the avicularia to detect (and, eventually, to react to) inputs from the environment is based on a receptor function of the vestigial polypide (Hyman, 1959; Mukai *et al*., 1997; Winston, Migotto, 2021). Early researchers considered a rudimentary polypide having a bundle of cilia to be an organ of tactile reception (e.g. Busk, 1854; Hincks, 1880; Calvet, 1900). Experimental work, however, suggested the presence of both mechano- and chemoreception (Rey, 1927; Forbes, 1933; Winston, 1991). The latter can be also assumed because some avicularia possess secretory cells and, sometimes, paired or unpaired glands, reminiscent of the vestibular glands in the autozooids (e.g. Marcus, 1939; Marcus, Marcus, 1962; Lutaud, 1964, 1965).

Most studies on avicularian microanatomy involved histological sections and, incidentally, used vital staining (Lutaud, 1977). These techniques provided little information on the structure of the miniature vestigial polypide. Carter was the first to apply confocal laser scanning microscopy (CLSM) and transmission electronic microscopy (TEM) for this purpose when studying adventitious "bird's-head" avicularia and pedunculate avicularia in two bugulid cheilostomes (Carter, 2008; Carter *et al*., 2010, 2011). Her data were recently significantly supplemented by the work of Shunatova with co-authors (2022), who also studied the bird's-head avicularium of another bugulid. While glandular cells were described in the vestigial polypide of two studied species, those authors suggested only a mechanoreceptor function, although Shunatova wrote that sensory cells of the polypide detect "different stimuli" (Shunatova *et al*., 2022: 22).

Until now the sessile adventitious avicularia of the cheilostome bryozoans have not been studied by modern techniques. Using TEM and CLSM, we for the first time examined the microanatomy and ultrastructure of a vestigial polypide in the sessile avicularium of *Arctonula arctica*, focusing on its nervous and muscular elements. Based on the results, we discuss its probable functions and the evolutionary transformations of the polypide that occurred during the transition from the feeding module (autozooid) to the avicularian heteromorph.

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connected with a fold of vestibulum (asterisk: gland cavity). D — longitudinal section of avicularium with mandible open (only distal part of retractor muscle shown; ganglion is out of section plane; palate is folded, broken wall of avicularium shown by arrowhead, cilia of reduced lophophore by arrow); E — total mount of avicularim with closed mandible (avicularian cystid and mandible outlined by white, vestigial polypide with gland and ganglion by red dashed lines; frontal wall elevated as a result of deformation; retractor muscle contracted); F — Scheme of avicularium with opened mandible showing all major elements, including muscles and vestigial polypide (retractor muscles contracted).

Abbreviations: az — autozooid; dm — diaphragmatic muscles; cw — cystid wall; fm — frontal membrane; g — ganglion; gl — avicularian gland; lm — longitudinal muscles of tentacle sheath; lph — lophophore; mab — abductor; mad — adductor; md — avicularian mandible; pa — palate; rl — rudimentary lophophore; rm — retractor muscles; ts — tentacle sheath; ve — vestibulum; zc — zooidal cavity.

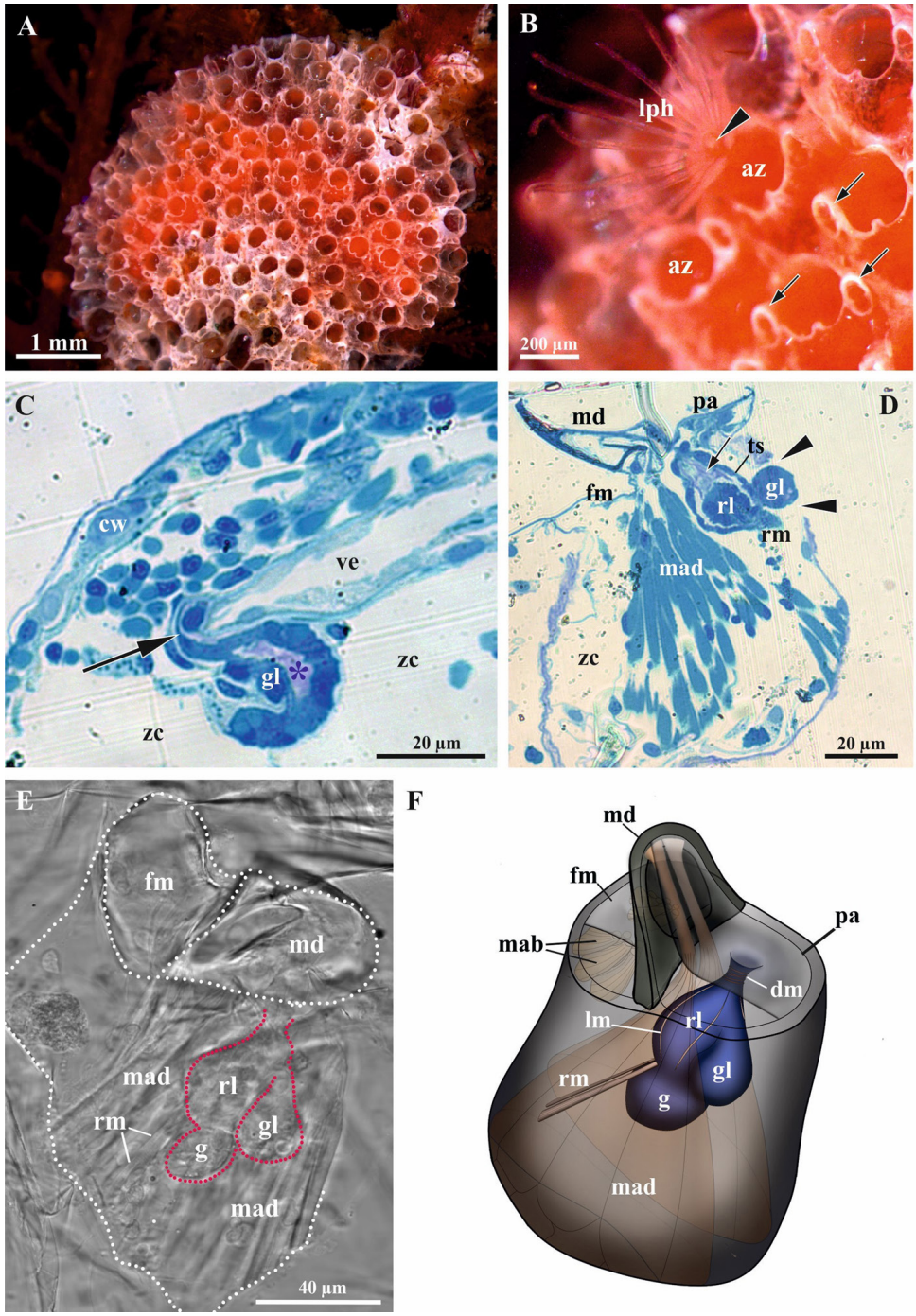

Fig. 1. Morphology and anatomy of autozooids and sessile adventitious avicularia in *Arctonula arctica* (stereomicroscope, light microscopy, total mounts and stained histological sections). A — general view of living colony (red areas: autozooids with functional polypides). B — close-up of colony area showing autozooids with retracted polypides and expanded lophophore (arrowhead: mouth; arrows: paired lateral avicularia near zooidal orifices). C — tangential section of autozooid showing vestibular gland with its duct (arrow)

Material and methods

Colonies of *Arctonula arctica* (M. Sars, 1851) growing on red algae (Fig. 1A) were collected by boat dredging from 7–10 m depth near the Educational and Research Station "Belomorskaia", Saint Petersburg State University (Chupa Inlet, Kandalaksha Bay, White Sea, Russia) in the summer field seasons 2011–2022. Colonies were anesthetized for 2–4 h in a magnesium chloride solution at 4 °C. For histological studies, some colonies were fixed in Bouin's fluid without acetic acid, then dehydrated in ethanol of increasing concentrations (40°-50°-70°-80°-90°-96°) and acetone, and embedded in resin (TAAB 812 kit, Sigma-Aldrich, St. Louis, USA). Serial semi-thin sections (1–2 µm thick) were prepared using the ultramicrotome Leica EM UC7 (Leica Microsystems Europe, Germany). Sections were stained using Richardson's stain for 1–3 minutes (Richardson *et al*., 1960). Images were made using a Nikon DS-Fi1 photocamera (Nikon, Japan) connected with a Leica DM2500 stereomicroscope and an AxioImager A1, Zeiss microscope (Zeiss, Oberkochen, Germany).

For confocal laser scanning microscopy (CLSM), some colonies were fixed in 4% paraformaldehyde (PFA) in 0.1 M phosphate buffer solution (PBS, pH=7) for 4 h at 25 °C. Next, the samples were decalcified in a solution of 10% EDTA (Amresco LLC, Solon, USA) in 0.1 M PBS at 25 °C for 2–4 h. The material was then washed in PBS (three times for 0.5 h) and stored in it with 0.1% NaN_3 at 4 °C, followed by washing in PTA (PBS with 0.1% Triton X-100 (Amresco LLC, Solon, USA) and 0.3% NaN_3 (Sigma-Aldrich, St. Louis, 27, USA)) three times for 20 min. To prevent nonspecific binding of antibodies, colony fragments after additional washing were kept in PTA Block (PTA containing 6% serum albumin (Amresco LLC, Solon, USA) for 5 h. Indirect immunohistochemical staining was applied to visualize the nervous system using antibodies to α-tubulin (acetylated mouse monoclonal antibodies (Sigma-Aldrich, St. Louis, USA, catalog number T6793)), serotonin (rabbit polyclonal antibodies (Sigma-Aldrich, USA, catalog number S5545)) and FMRFamide (rabbit polyclonal antibodies (Immunostar, USA, catalog number 20091)). Fragments were incubated for 12 h at 4 °C in PTA Block containing either 1:500 diluted both serotonin antibody and α-tubulin antibody, or 1:500 diluted both FMRF-amide antibody and α-tubulin antibody, followed by washing in PTA Block for 12 h at 4 °C with three changes. They were then placed in a PTA Block containing 1:500 diluted solution of secondary goat-anti-mouse and goat-anti-rabbit antibodies conjugated with CF 633 (Sigma-Aldrich, St. Louis, USA, catalog number SAB4600148) and with CF 488A (Sigma-Aldrich, St. Louis, USA, catalog number SAB4600044), respectively, for 12 h at 4 °C. After washing from secondary antibodies in 0.1 M PBS three times for 15 min the colony fragments were stained with 1 µg/ml TRITC-conjugated phalloidin (Sigma, P1951) in 0.1 M PBS (1 h at 25 °C) to visualize the muscular system and, after washing in 0.1 M PBS for 15 min, stained with HOECHST 33258 dye (H1398, Invitrogen) for 5 min to visualize cell nuclei. Finally, the samples were placed on glass slides in a drop of glycerol with PBS at a ratio of 9:1, and analyzed using a confocal scanning laser microscopes Leica TCS SP5 and Leica TCS SP5 MP (Leica Microsystems, Wetzlar, Germany). Images were processed by ImageJ software (FiJi).

For transmission electron microscopy (TEM), some colonies were fixed during 3–4 h after collecting in 2.5% glutaraldehyde (buffered in 0.1M Na-cacodylate buffer containing 10% sucrose (pH 7.4)) at 4 °C and stored for two weeks. They were then washed with the same buffer three times for 5 min and postfixed with a buffered 1% solution of osmium tetroxide (OsO_4). After three washes (for 5 min each) in the same buffer, colonies were decalcified for 24 h in 2% aqueous solution of EDTA (Amresco LLC, Solon, USA), washed again in the same buffer for 15 min, and cut into fragments. The fragments were dehydrated in a graded ethanol series (30-50-70-80-90-100%), then in a mixture of alcohol and acetone (3:1 – 1:1 – 1:3) and in pure acetone and embedded in epoxy resin (TAAB 812 kit, Sigma-Aldrich, St. Louis, USA). Embedded specimens were sectioned using a Leica EM UC7 ultramicrotome (Leica Microsystems, Wetzlar, Germany). Ultrathin sections were picked up with copper grids with formvar support film and contrasted first with uranyl acetate for 1–3 min, then with lead citrate for 1–2 min, washing after each step with distilled water. Ultrathin sections were examined with Jeol JEM-1400 and Jeol JEM-2100 microscopes (JEOL Ltd., Japan).

Altogether, fifteen avicularia were examined; five of them were sectioned.

Results

Microanatomy and ultrastructure of vestigial polypide (TEM)

Each autozooid in the colony possesses two miniature adventitious sessile avicularia symmetrically placed on both sides of zooidal orifice (Fig. 1B). Each avicularium is embedded into the skeletal wall of the autozooid. The frontal side of the polymorph is oval, consisting of two parts, the distal palatal and proximal postmandibular areas. Whereas the flexible postmandibular area corresponds to the frontal wall of the autozooid, the palate corresponds to the lower wall of the vestibulum and is covered by the lowered mandible, which is a modified operculum (Fig. 1D–F).

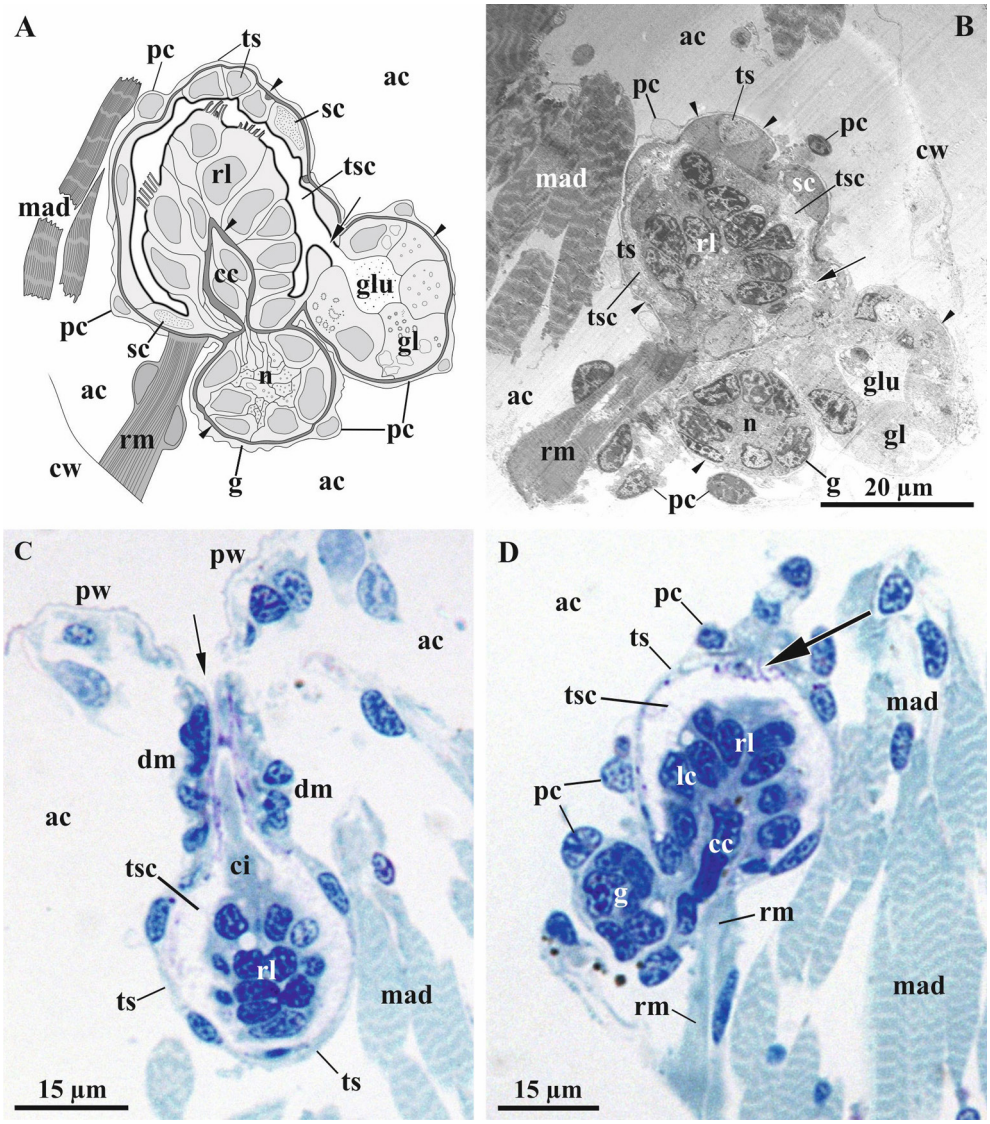

Fig. 2. Microanatomy of vestigial polypide in avicularium of *Arctonula arctica* (A — scheme; B — TEM; C, D — light microscopy, stained histological sections). A — scheme of longitudinal section showing main parts of polypide and associated unpaired gland with a duct (arrow) opening into tentacle sheath cavity (arrowheads point to basal lamina shown in dark-grey). B — oblique section through vestigial polypide showing reduced lophophore, gland, ganglion and retractor muscle (in A and B avicularian orifice is out of section plane; duct of gland (arrow) is only partially visible in B; arrowheads: electron-transparent basal lamina). C — tangential section through distal part of vestigial polypide showing lophophore tip, surrounded by tentacle sheath narrowing towards orifice (small arrow) in palate wall; tuft of cilia is visible in narrow 'neck' together with muscle cells of diaphragmatic sphincter. D — diagonal section through rudimentary polypide showing its proximal half with cerebral ganglion (large arrow: folds of tentacle sheath "neck").

Abbreviations: ac — cavity of avicularian cystid; cc — central cells of rudimentary lophophore; ci — cilia; cw — wall of the avicularian cystid; dm — muscle cells of diaphragmatic sphincter; g — cerebral ganglion; gl — gland; glu — gland lumen; lc — epidermal cells of vestigial lophophore; mad —, adductor muscles; n — ganglion neuropile; pc — peritoneal cell; pw — palatal wall; rl — rudimentary lophophore; rm — retractor muscles; sc — secretory cells of tentacle sheath wall; ts — tentacle sheath wall; tsc — tentacle sheath cavity.

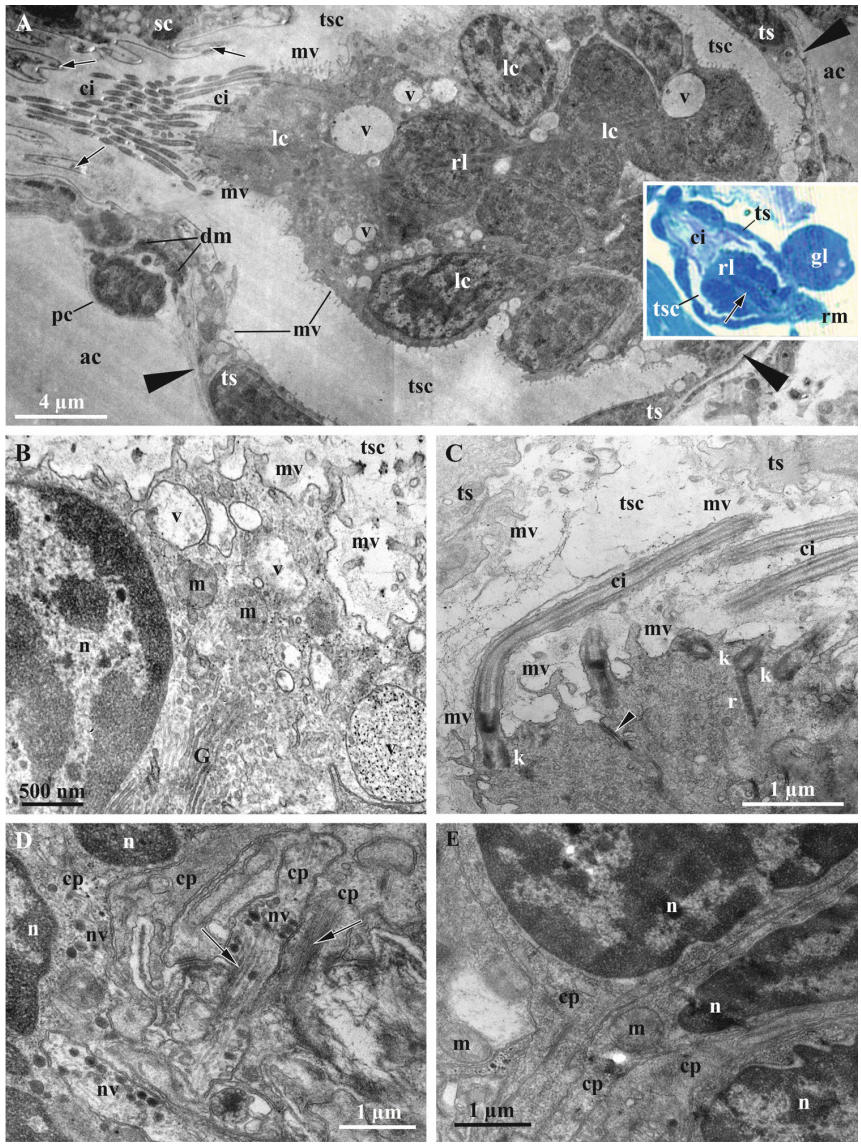

Fig. 3. Microanatomy and ultrastructure of rudimentary lophophore in avicularium of *Arctonula arctica* (TEM, light microscopy, stained histological section). A — sagittal section through vestigial polypide showing tentacle sheath surrounding lophophore composed of ciliary and non-ciliated cells, some with large vacuoles (arrowheads: basal lamina; arrows: folds in distal part of tentacle sheath; central cells are out of section plane); inset, longitudinal section through vestigial polypide, central cells shown by arrow. B — apical part of non-ciliated epidermal cell showing microvilli, mitochondria, Golgi dictyosomes and numerous vacuoles with flocculent and "granular" content fusing with apical membrane. C — apical membrane of ciliary cells of lophophore showing cilia, kinetosomes, cross-striated rootlets (microvilli are visible both on cells of lophophore and tentacle sheath; arrowhead: tight junction between cells). D, E — proximal parts of epidermal sensory cells forming processes that contain mitochondria, neurosecretory vesicles and microtubules (arrows).

Abbreviations: ci — cilia; cp — receptor cell processes; dm — diaphragmatic muscles; g — cerebral ganglion; G — Golgi dictyosomes; k — kinetosome; lc — epidermal cells of vestigial lophophore; lm — mitochondria; mv — microvilli; n — nucleus; nv — neurosecretory vesicles; pc — peritoneal cell; r — striated roots; rl — rudimentary lophophore; rm — retractor muscles; sc — secretory cells of tentacle sheath wall; ts — tentacle sheath wall; tsc — tentacle sheath cavity.

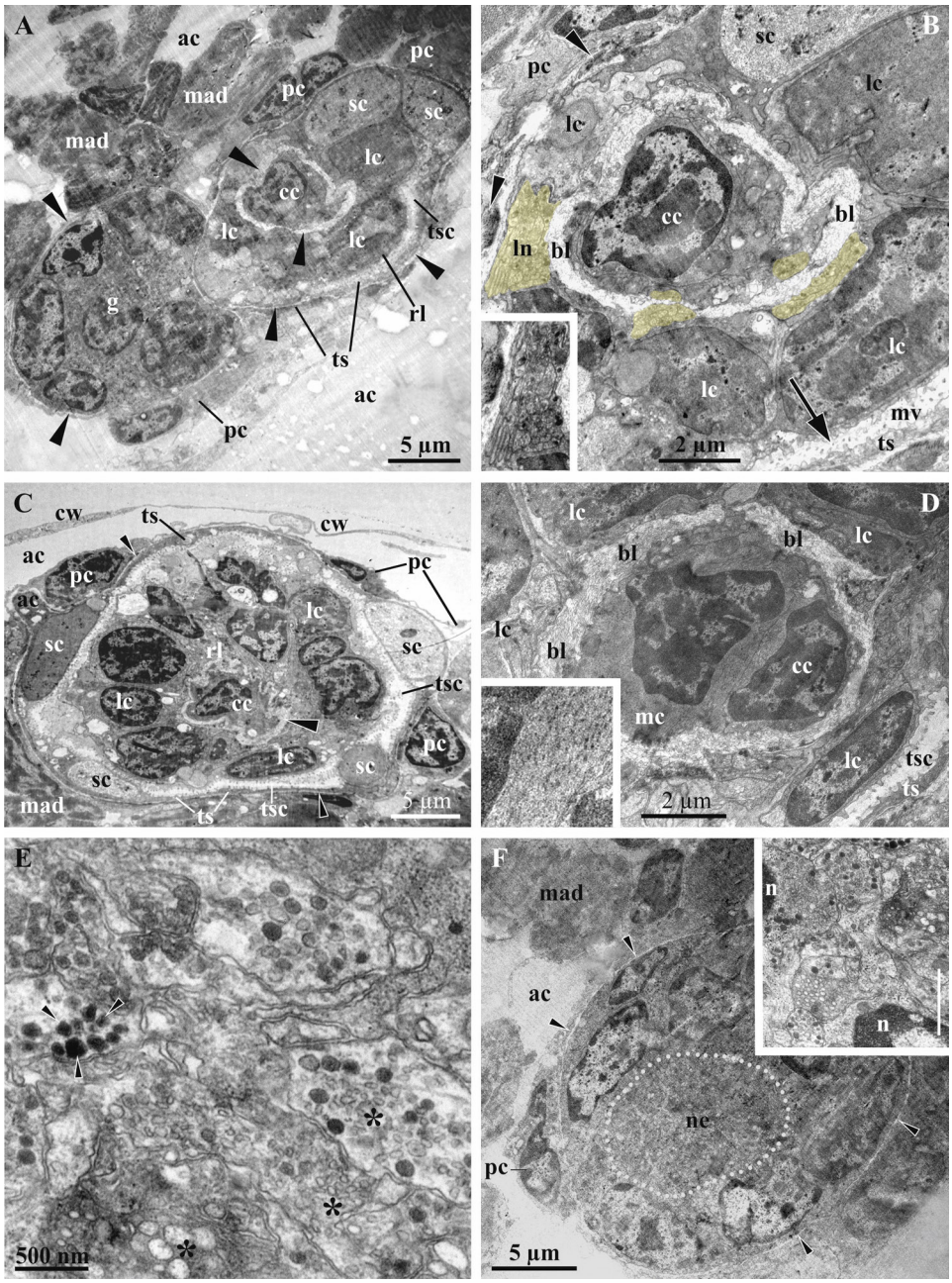

Fig. 4. Microanatomy and ultrastructure of rudimentary lophophore and ganglion in avicularium of *Arctonula arctica* (TEM). A — diagonal section through basal part of lophophore and upper part of ganglion (epidermal cells of lophophore base continue to tentacle sheath wall close to two large secretory cells; tentacle sheath cavity visible as short slit; basal lamina shown by arrowheads; neuropile is off section plane). B — magnified area of the same vestigial lophophore showing epidermal cells, basal lamina surrounding two central cells, the lophophoral nerves (in yellow) below and above it, and longitudinal muscles (arrowheads) of tentacle sheath wall (arrow: cavity of tentacle sheath; microvilli are visible on apical membranes of both lophophore and tentacle sheath cells); inset: cross-section of left lophophore nerve. C — cross section of vestigial pol-

The rudimentary polypide of the avicularium consists of two major parts. The upper/distal part is a modified lophophore enclosed by a tentacle sheath, and the lower/proximal part is either an oval or rounded (in sagittal/longitudinal sections) cerebral ganglion (Figs 1D–F, 2, 9). The polypide is situated underneath the palate in the distal part of the avicularian cystid, between the adductor muscles (Fig. 1D–F). The wall of the tentacle sheath distally forms a narrow 'neck' associated with a slight invagination in the center of the palate. This 'pit' surrounds a small orifice through which the cavity of the tentacle sheath communicates with the environment (Figs 1F, 2C, 6A, 9).

Also, a non-paired gland is associated with a tentacle sheath (Figs 1D–F, 2A, B, 5, 9). Similarly, the autozooids contain paired glands, each having a duct communicating with an introvert via opening at the border of the vestibulum and tentacle sheath (Fig. 1C).

The rudimentary lophophore is oval in sagittal/longitudinal sections (40×30 μm) and mostly consists of the large epidermal multiciliary cells. The cilia (having a single cross-striated short rootlet each) form a bundle on the tip of the rudimentary lophophore (Figs 2A, C, 3A, inset, 5A, 7A, C, 9). Epidermal cells without cilia form the lophophore base. Such cells were also present between the ciliary cells (Figs 2, 3A). Dense and septate cell contacts (not shown in the figures) were noted between the apical areas of some epidermal cells (Fig. 3C). Some of them form long processes at the base, descending to the cerebral ganglion. These processes contain neurosecretory vesicles and microtubules (Fig. 3D, E). Together, these processes form thin nerves running to the ganglion close to the basal lamina (Figs 4B, 9).

The apical membrane of lophophoral cells, both ciliary and non-ciliated, forms numerous microvilli with slightly widening tips bearing "star-like' outgrowths of dense glycocalyx. Microvilli are also formed on the apical membrane of the tentacle sheath cells (Figs 3A–C, 6B, C). In both cases microvilli were embedded in a loose glycocalyx.

Various inclusions are also typical for the epidermal cells of the rudimentary lophophore. Their cytoplasm contains a large number of mitochondria, Golgi dictyosomes (especially in the apical part of the ciliary cells), microvesicles and vacuoles of various sizes (Fig. 3A, B). In some non-ciliated cells, the vacuoles with either granular or flocculent content are fused with the apical membrane between microvilli releasing their content into the cavity of the tentacle sheath. This indicates their secretory function. All epidermal cells showed a large active nucleus with heterochromatin dispersed through the nucleoplasm.

Epidermal cells of the lophophore are underlain by a basal lamina that continues to the corresponding laminae of the tentacle sheath, ganglion and gland (Figs 2A, B, 3A, 4A–C, F, 5B, C, E, F, 9). At the base of the lophophore, the basal lamina envelopes small cells, which we designated as "central cells" (Figs 2A, D, 3A, inset, 4A–D). The precise number of these cells is currently unclear. TEM study showed two cells in a cross-sectioned lophophore, one with muscle fibers (Fig. 4D), and the immunocytochemical method revealed two parallel myofibrils, positionally corresponding to two "central cells" there (Fig. 8A).

Up to five nerves were detected in the central part of the rudimentary lophophore: 2–3 were subepidermal, situated between the epidermal cells and basal lamina, and two were recorded in one polypide below the lamina (Fig. 4B). This indicates that whereas some nerves (formed by the receptor cells of the lophophore) run to the ganglion directly, others pierce the basal lamina and run close to the central muscle cells, possibly innervating them.

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ypide showing circular cavity of tentacle sheath (arrowheads: basal lamina). D — magnified cross-section of lophophore rudiment showing central cells (one with miofilaments) surrounded by basal lamina; inset: cytoplasm of muscle cell with miofilaments. E — magnified area of neuropile, showing processes of nerve cells containing numerous electron-dense (arrowheads) and electron-transparent (asterisks) neurosecretory vesicles. F — diagonal section of ganglion, consisting of a peripheral layer of nerve cells and a central neuropile (outlined) (arrowheads: basal lamina); inset: part of neuropil showing processes of nerve cells and perykaria with neurosecretory vesicles inside (scale bar 1 μm).

Abbreviations: ac — cavity of avicularian cystid; bl — basal lamina; cc — central cells; cw — cystid wall; g — cerebral ganglion; lc — epidermal cells of vestigial lophophore; mad — adductor muscles; mc — muscle central cell; mv — microvilli; n — nucleus; ne — neuropile of cerebral ganglion; pc — peritoneal cell; rl — rudimentary lophophore; sc — secretory cells of tentacle sheath wall; ts — tentacle sheath wall; tsc — tentacle sheath cavity.

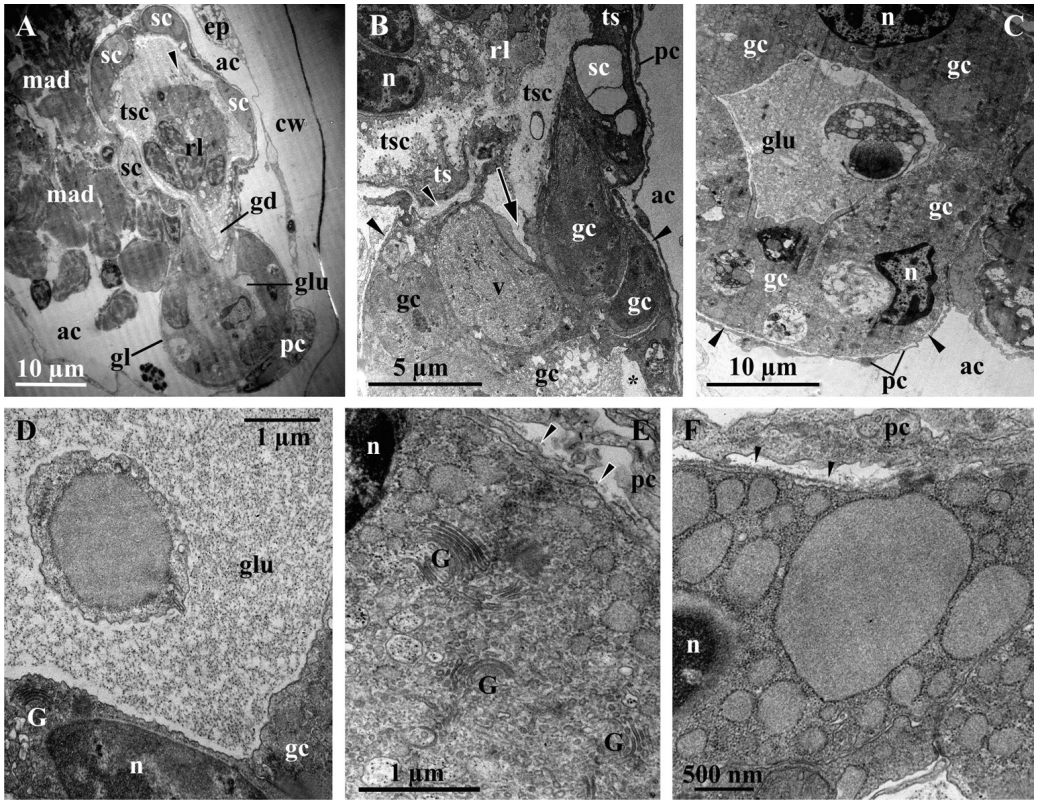

Fig. 5. Microanatomy and ultrastructure of rudimentary lophophore and associated gland in *Arctonula arctica* (TEM). A — diagonal section through rudimentary polypide and gland showing duct of gland opening into cavity of tentacle sheath (arrowhead: cilia of epidermal cells of lophophore). B — magnified partial view of vestigial polypide (upper left corner) and gland whose duct (arrow) opens into cavity of tentacle sheath (duct lumen indicated by asterisk; microvilli visible on apical membrane of both lophophore and tentacle sheath cells). C, D — partial view of two glands showing their central lumen filled by flocculent secretion (fragments of secretory cells inside lumen indicate apocrine secretion). E, F — close-up of gland cells showing numerous Golgi apparatuses and vacuoles. Basal lamina between secretory and peritoneal cells shown by arrowheads. Abbreviations: ac — avicularian cavity; cw — cystid wall; ep — epithelial cell of cystid wall; G — Golgi dictyosomes; gc — gland cell; gl — gland; gd — duct of gland; glu — gland lumen; mad — adductor muscles; n — nucleus; pc — peritoneal cell; rl — rudimentary lophophore; sc — secretory cells of tentacle sheath wall; tsc — tentacle sheath cavity; v — vacuole.

The ganglion is connected to the narrow lophophoral base (Fig. 2A, B, D, 4A, F, 7B–D, F, 8B inset, 9). It consists of a peripheral layer of neurons covered by a thin basal lamina and a single layer of peritoneal cells, and of a central neuropile – a cluster of nerve cell processes (Fig. 4F). The perikarya, in addition to large active nuclei, contain Golgi dictyosomes, mitochondria, neurosecretory vesicles as well as a large number of cytoskeletal elements such as microtubules and filaments (Fig. 4F, inset).

The processes of nerve cells in the neuropile contain a large number of neurosecretory vesicles differing in content and size. Among them there are vesicles with electron-dense content ("dense-cored" vesicles) of smaller or larger size (depending on this, the width of the electron-transparent rim of the vesicle differs), as well as rounded and oval vesicles with electron-transparent content (Fig. 4E, F inset). The diameter of the vesicles with electron-dense content is approximately 100 nm, and that of the light rounded ones 50 nm; the oval vesicles measure 50×30 nm.

The wall of the tentacle sheath consists of the flattened epidermal cells containing large active nucleus and a fairly large number of inclusions, for example, vacuoles with flocculent content. These cells often partially overlap, being underlain by a

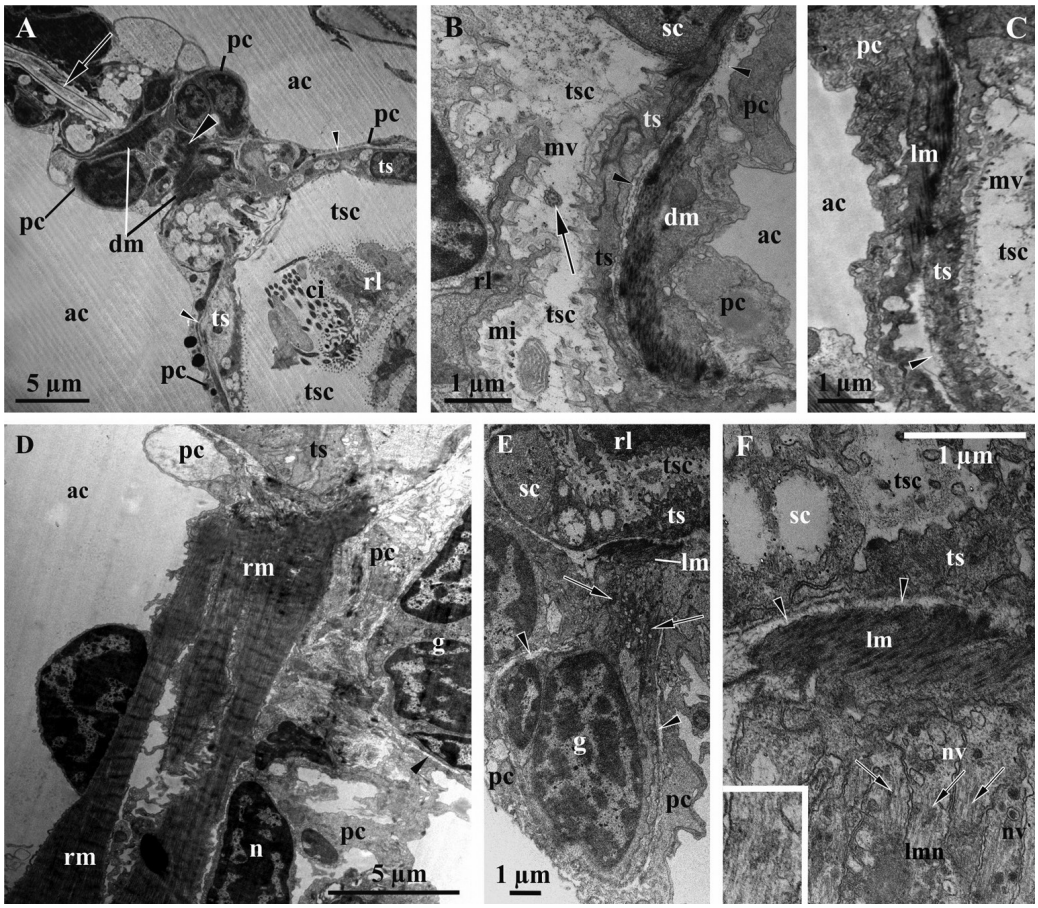

Fig. 6. Muscular and neural elements associated with vestigial polypide in avicularia of *Arctonula arctica* (TEM). A — longitudinal section through distal part of rudimentary polypide showing diaphragmatic and longitudinal (arrowhead) muscles in narrowing upper part of tentacle sheath (arrow shows its lumen and fold). B — transverse section through distal portion of lophophore (to left) and tentacle sheath wall showing numerous microvilli and diaphragmatic muscle cell (arrow: cilium of lophophore). C — oblique section through vestigial polypide showing longitudinal muscles in tentacle sheath wall. D — distal ends of retractor muscles attached to tentacle sheath wall close to ganglion. E, F — Innervation of the longitudinal muscles of the tentacle sheath wall (in E nerve is shown by arrows, in F, microtubules inside processes of nerve cells are shown with arrows, magnified in inset).

Arrowheads point to basal lamina. Abbreviations: ac — avicularian cavity; ci — cilia of lophophore cells; dm — diaphragmatic muscles; g — ganglion; lm — longitudinal muscles of tentacle sheath wall; lmn — nerves of longitudinal muscles; mv — microvilli; nv — nerve cell processes; pc — peritoneal cell; rl — rudimentary lophophore; rm — retractor muscles; sc — secretory cells of tentacle sheath wall; ts — tentacle sheath wall; tsc — tentacle sheath cavity.

basal lamina and peritoneal epithelium. In addition, individual glandular (secretory) cells with a very large vacuole were recorded in the epidermis of the tentacle sheath (Fig. 2A, B, 3A, 4A–C, 6B, C). The cells forming its narrow distal part bear numerous elongated folds facing the tentacle sheath cavity and covered by a thin ectocyst (Figs 3A, 6A, 9). Proximally, the tentacle sheath wall joins the base of rudimentary lophophore: its epidermis continues with the lophophoral epidermis, and so do the basal lamina and peritoneal lining (Figs 2A, B, D, 3A inset). Using both TEM and CLSM, we detected annular diaphragmatic and longitudinal muscles in the tentacle sheath wall (Figs 2C, 6A–C, E, F, 8A).

The gland of the rudimentary polypide in *A. arctica* is situated near the ganglion and connected to the tentacle sheath by a short duct (Fig.

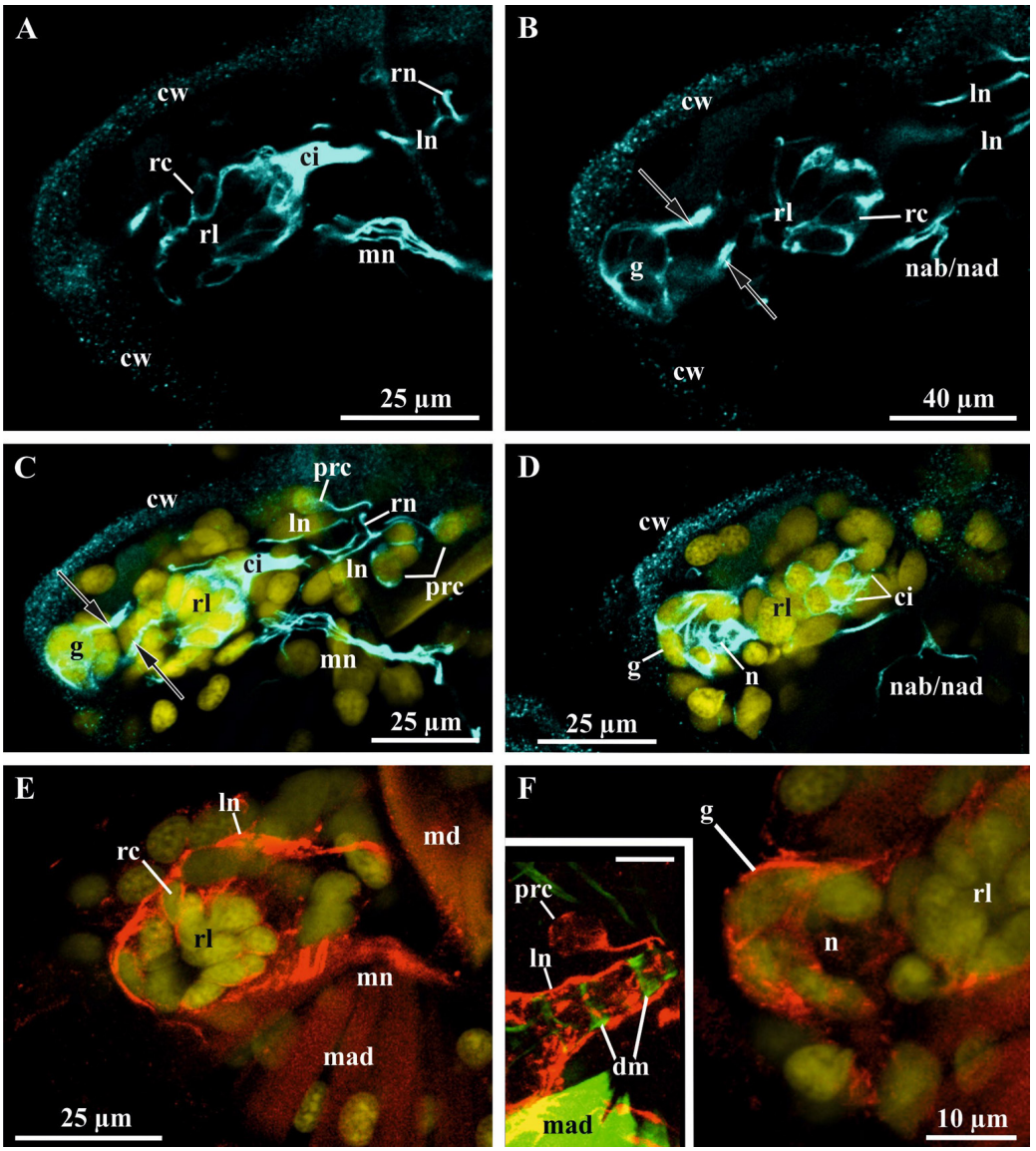

Fig. 7. Nervous system of vestigial polypide in avicularia of *Arctonula arctica* (CLSM). A–D — treatment with antibodies to α-tubulin (blue), C–F — nuclear staining with HOECHST (yellow), E–F — treatment with antibodies to FMRF-amide (red)). A–D — lateral view of rudimentary polypides, showing putative epidermal receptor cells of lophophore, circular and longitudinal nerves of tentacle sheath, and nerves (arrows) coming to ganglion and entering neuropile. E — nerve elements of rudimentary polypide. F — magnified ganglion showing nerve processes inside neuropil and pericarya on its periphery; inset: upper part of tentacle sheath with innervation of ring diaphragmatic and longitudinal muscles (large receptor cell of palate is visible; scale bar 10 µm).

Abbreviations: ci — cilia of lophophore cells; cw — cystid wall; g — ganglion; lmn — nerves of longitudinal muscles; md — mandible; mn — mixed nerve; n — neuropile; nab, nad — processes innervating the abductor and adductor muscles; prc — receptor cells of palate; rc — putative receptor cells of reduced lophophore with basal process; rl — rudimentary lophophore; rn, ring nerve of diaphragmatic muscles.

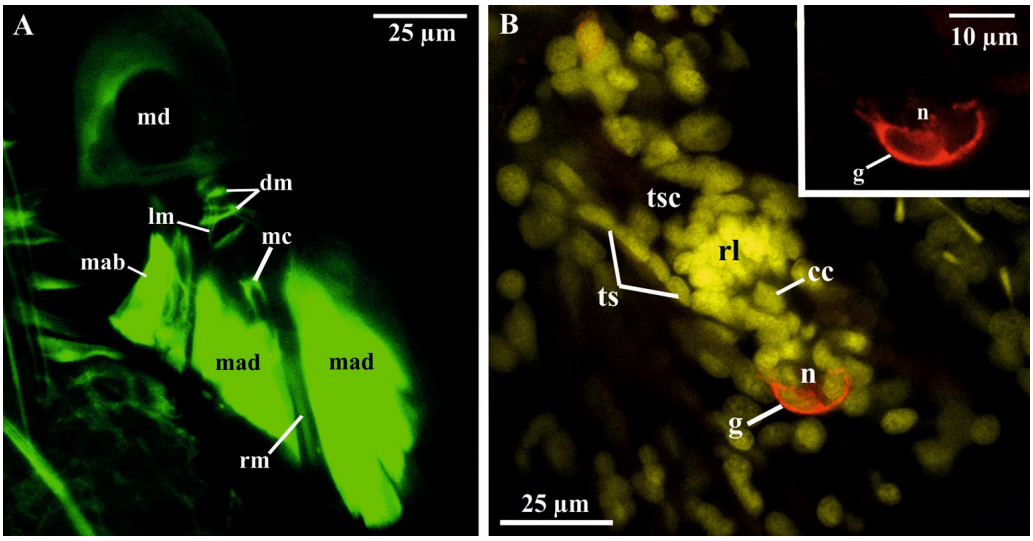

Fig. 8. Muscular and neural elements associated with vestigial polypide in avicularia of *Arctonula arctica* (CLSM, phalloidin staining (green), serotonin (red), staining of nuclei with HOECHST (yellow)). A — muscular system of avicularium showing diaphragmatic and longitudinal muscles of tentacle sheath, muscle (central) cells of the rudimentary lophophore and retractors of rudimentary polypide. B — cell composition of vestigial polypide; inset: ganglion.

Abbreviations: cc — central cells of rudimentary lophophore; dm — diaphragmatic muscles; g — ganglion; lm — longitudinal muscles of tentacle sheath wall; mab — abductor muscle; mad — adductor muscle; md — mandible; mc — muscle (central) cells of lophophore; rm — retractor muscle; rl — rudimentary lophophore.

2A, B, 5A, B, 9). The gland wall consists of large secretory cells underlaid by a basal lamina and a layer of peritoneal cells. The gland lumen is connected with the cavity of the tentacle sheath. The oval cells of the gland wall contain a large active nucleus, a well-developed endoplasmic reticulum and the Golgi multiple apparatuses (Fig. 5C–F). Their cytoplasm is filled with vacuoles of different sizes with homogeneous content. In contrast, the lumens of both the gland and the duct are filled with flocculent material. In addition, fragments of secretory cells were detected in the gland lumen, presumably indicating apocrine secretion (Fig. 5C, D).

Neuro-muscular system of vestigial polypide (CLSM)

The main muscles of the adventitious avicularia in *Arctonula arctica* are two large, symmetrical, striated adductors that close the mandible. They occupy most of the volume of the avicularian cystid. Smooth paired abductors are situated behind them. When abductors contract, the frontal membrane bends and the mandible opens (Figs 1D, F, 8A).

The diaphragm of the tentacle sheath wall consists of 3–4 annular fibers forming a narrow, loose "cone" situated in the uppermost narrow part of the tentacle sheath. The tentacle sheath wall also has 7-8 thin longitudinal muscle fibers. The upper ends of these muscles intersect with the fibers of the lower half of the diaphragm (Fig. 8A). In addition to the diaphragmatic and the longitudinal muscles, the rudimentary polypide is provided with 2–3 retractors (Figs 2A, B, D, 6D, 8A) consisting of 2–4 fibers each. These retractors attach to the vestigial polypide in the lower part of the tentacle sheath (Figs 2A, B, D, 6D). The muscle cells are anchored to the basal lamina of the tentacle sheath wall. The proximal ends of the retractors are attached to the basal cystid wall of the avicularium (Fig. 8A). In some confocal and TEM images, the transverse striation of the retractors is visible (Fig. 6D). Two muscle fibers (Fig. 8A) were recorded in the central part of the rudimentary lophophore.

Treatment with antibodies to α-tubulin revealed putative receptor epidermal cells of the lophophore with cilia, circular and longitudinal

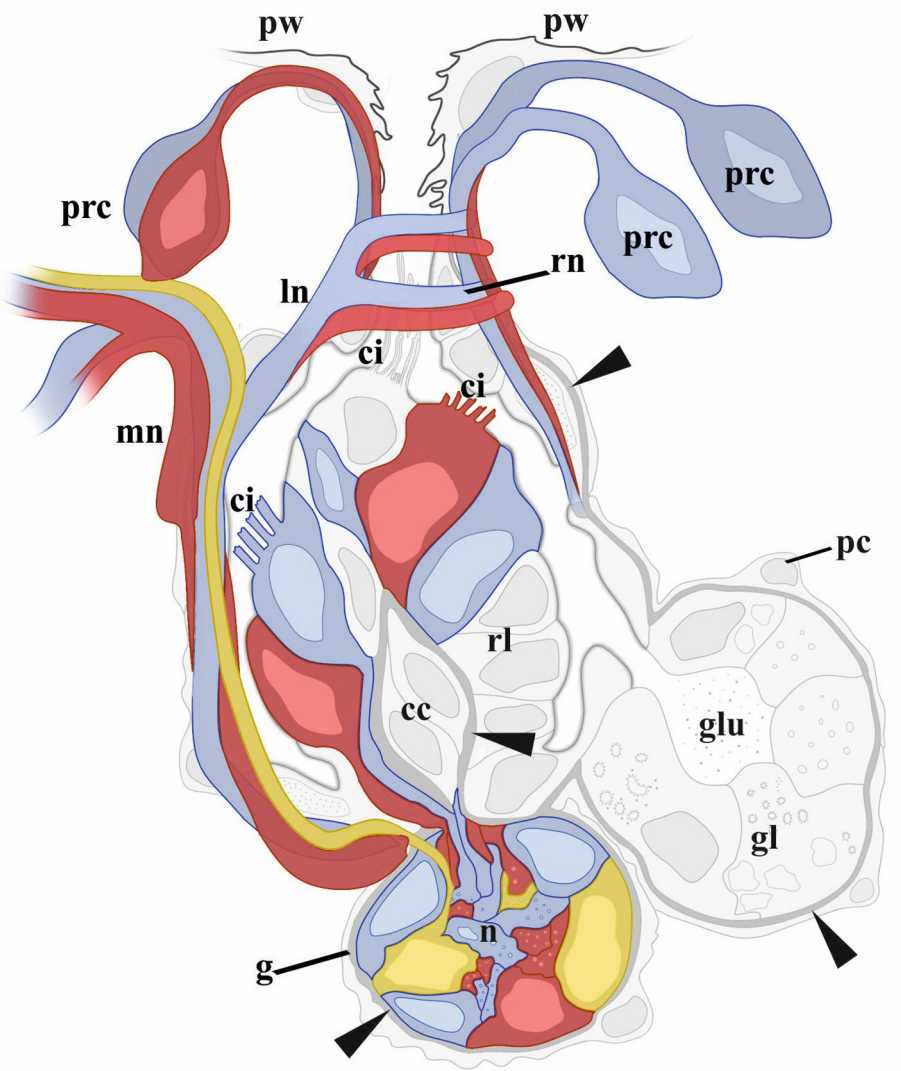

Fig. 9. Scheme of distribution of nervous elements in rudimentary polypide of sessile adventitious avicularia of *Arctonula arctica* (treatment with antibodies to serotonin shown by yellow, treatment with antibodies to α-tubulin by blue, treatment with antibodies to FMRF-amide by red; arrowheads: basal lamina; cilia only partially shown).

Abbreviations: ci — cilia of rudimentary lophophore; cc — central cells; g — ganglion; gl — gland; glu — gland lumen; ln — longitudinal nerves of tentacle sheath wall; n — neuropile; pc — peritoneal cell; prc — receptor cell of palate; rl — rudimentary lophophore; ts — tentacle sheath wall; tsc — cavity of tentacle sheath.

nerves of the tentacle sheath, nerves coming to the ganglion and entering the neuropile, and nerve branches running to the main elements of the avicularium musculature (Fig. 7A–D).

FMRF-amide has been detected in some, presumably sensory cells of the rudimentary lophophore and neurons of the cerebral ganglion as well as in the nerve branches running to the the avicularium musculature (Fig. 7E, F). Annular and longitudinal nerve fibers, also detected by treatment with antibodies to FMRF-amide, were recorded in the wall of the tentacle sheath together with the longitudinal and diaphragmatic muscles (Fig. 7F inset). The 5-HT immunopositive ele-

ments include neurons and nerve processes of the ganglion (Fig. 8B inset).

In the upper part of the tentacle sheath under the palate, 6–7 nerve cells (presumably sensory) were detected by treatment with antibodies to FMRF-amide and α-tubulin. No peripheral processes were recognizable in these cells, but their central processes approach the wall of the tentacle sheath and descend along it to the cerebral ganglion (Fig. 7C, F inset). Note that these nerve fibers are sometimes not distinguishable from those innervating the longitudinal muscles of the tentacle sheath.

Discussion

General organization of a rudimentary polypide

All bryozoan polymorphs evolved via transformation of autozooids, and their parts are therefore homologous to the corresponding autozooidal elements (Nitsche, 1871; Darwin, 1872; Hincks, 1880; Marcus, 1926, 1939; Silén, 1938, 1977; Carter *et al*., 2010, 2011; reviewed in Shunatova *et al*., 2022 and Serova *et al*., 2022). The rudimentary (vestigial) polypide of the adventitious avicularia in *Arctonula arctica* comprises a reduced lophophore situated inside the cavity of the rudimentary tentacle sheath, the tentacle sheath itself, a miniature ganglion with a few nerve branches of the tentacle sheath, and a gland that is, in contrast to autozooids, unpaired. When comparing to an autozooid, the main part that is missing is a gut. Muscular elements associated with a vestigial polypide include retractors, diaphragmatic and longitudinal muscles of the tentacle sheath wall, and the central muscle cells of the lophophore. Overall, the polypide structure in the adventitious sessile avicularium is generally very similar to that described in the adventitious avicularia of the other types — "bird's head" avicularia (in *Bugulina flabellata* (Thompson in Grey, 1848) and *Dendrobeania fruticosa* (Packard, 1863)) and pedunculated avicularia (in *Nordgaardia cornucopioides* d'Hondt, 1983) (Carter *et al*., 2010, Shunatova *et al*., 2022). Note, however, that in *N. cornucopioides* the rudimentary lophophore has a large coelomic cavity that is absent in all other studied species (see also below). Among the homologies, we point to the folded surface of the narrow distal part of the tentacle sheath covered by the ectocyst. Similar folds, although much larger and with much thicker ectocyst, are known in the most proximal part of the vestibulum in cheilostome autozooids (Bogdanov, Ostrovsky, in preparation).

The cells covering the vestigial polypide from the outside in the avicularia of *D. fruticosa* were previously designated as "accessory cells" (Shunatova *et al*., 2022). In our study, we designate them as "peritoneal cells" based on their position. In *A. arctica* these cells cover the surface of the ganglion, gland and the wall of the tentacle sheath of the rudimentary polypide, facing the avicularian cystid cavity.

Lophophore

The distal part of the rudimentary polypide enveloped by the tentacle sheath wall is sometimes called a reduced lophophore (Shunatova *et al*., 2022; Serova *et al*., 2022). In contrast, Carter with co-authors (2010) considered it, depending on the species, as a single or a group of rudimentary tentacles. That point of view is based on the comparison between the vestigial polypide of *N. cornucopioides* and a tentacle of a gymnolaemate autozooid, both having epidermal ciliated and non-ciliated cells underlain by a basal lamina and prominent coelomic lumen lined by the peritoneal and mioepithelial cells (Mukai *et al*., 1997; Carter *et al*., 2010; Shunatova, Tamberg, 2019). Thus, both views are valid, and we follow the former terminological variant (Shunatova *et al*., 2022) because it is more general.

Similar to all three aforementioned cheilostomes with adventitious avicularia, the vestigial lophophore of *A. arctica* consists of an epidermal layer of multiciliated (some of which are receptor cells with long central process) and non-ciliated (some of which are seemingly secretory) cells, a basal lamina and "central cells" that correspond to the mioepithelial cells of the tentacle in the autozooid. Two cell types, ciliary and non-ciliated, both with "numerous granulated vesicles" in their cytoplasm, were described in *B. flabellata* (Carter *et al*., 2010). Four cell types, including two sensory, with long central process containing either microtubules or microvesicles, and at least one secretory cell type, were described in the rudimentary lophophore of the adventitious "bird's head" avicularia of *D. fruticosa* (Shunatova *et al*., 2022). Only ciliary cells were mentioned in the "vestigial tentacle" of *N. cornucopioides*

(Carter *et al*., 2010), and those authors suggested that they remove the secretions produced by the glandular cells of the tentacle sheath to the environment. We agree with this interpretation, based on the consideration that the presence of both a gland and the secretory cells in the wall of the tentacle sheath requires having cells with motile cilia in the reduced lophophore in order to remove the mucus from the vestigial polypide in *A. arctica*. In contrast, the receptor cells of the lophophore should have rigid cilia.

The apical membrane of the epidermal cells and the cells of the tentacle sheath wall are covered with microvilli embedded in a loose glycocalyx. Microvilli and a layer of glycocalyx are also known in autozooids, in both cells of the tentacles and of the tentacle sheath (Gordon, 1974; Shunatova, Nielsen, 2002), presumably protecting them from mechanical damage during polypide excursions (Smith, 1973; Mukai *et al*., 1997). Microvilli in the cells of the vestigial polypide have been previously described in the avicularia of *N. cornucopioides* and *D. fruticosa*, whereas only irregularly shaped outgrowths have been recorded in *B. flabellata* (Carter, 2008; Carter *et al*., 2010; Shunatova *et al*., 2022).

Interestingly, in three of four species studied by TEM the microvilli were not lost entirely despite very restricted (if any) ability of the vestigial polypide for movements. This mobility is evidenced by the presence of retractors, diaphragmatic and longitudinal muscles of the tentacle sheath wall, as well as recorded changes in the position of the vestigial polypide in accord with the mandible movements (Carter *et al*., 2010, 2011; Shunatova *et al*., 2022; Serova *et al*., 2022; our data).

The presence of the muscle cells in the central part of the rudimentary polypide of *A. arctica* is confirmed by both TEM and CLSM studies. These two cells were mistakenly described as the distal parts of the retractors in an earlier paper by Serova with co-authors (2022, Fig. 8A), but now stands corrected by the current study. Similarly, the presence of smooth muscle cells lining the coelomic cavity of the reduced lophophore has been documented by TEM in *N. cornucopioides* (Carter *et al*., 2010). Although their function is unknown, we suggest that in both cases they are homologous to the mioepithelial cells lining the coelomic cavity of the autozooidal tentacles. No muscular cells in the lophophore were reported in either *B. flabellata* or *D. fruticosa* (Carter *et al*., 2010, 2011; Shunatova *et al*., 2022).

2–3 miniature basepithelial nerves formed by processes of receptor cells were recorded in the lophophore of *A. arctica*. They were also found in *D. fruticosa*, but were shown underneath the basal lamina of the lophophore between the non-muscular "central" cells (Shunatova *et al*., 2022). We also acknowledge that 1–2 tiny nerve process were detected below the basal lamina in *A. arctica* too (see also below).

Tentacle sheath

The wall of the tentacle sheath of the vestigial polypide of *A. arctica* generally has the same structure as that of an autozooid: a layer of microvillate epithelium underlaid by the basal lamina, and circular diaphragmal (in the distal part) and longitudinal muscle fibers covered by the peritoneal cells. In addition, we recorded the individual glandular cells containing a large vacuole in the distal and the proximal part of the tentacle sheath. Similarly, Shunatova with co-authors (2022) described several putative secretory cells with vacuoles filled with fibrillar material in the tentacle sheath of *D. fruticosa* avicularia. In contrast, the wall of the tentacle sheath of the reduced lophophore of *N. cornucopioides* is "hypertrophied into an extensive ... arrangement of glandular cells" (Carter *et al*., 2010: 200–201).

Gland

The rudimentary polypide of the adventitious sessile avicularia of *A. arctica* contains an unpaired gland whose wall consists of an internal layer of secretory cells covered by a basal lamina, and an external layer of peritoneal cells. The basal lamina of the gland continues to the corresponding laminae of the tentacle sheath and ganglion. The structure and position of the gland indicate its homology to the vestibular glands of the autozooids.

Glands in avicularia were first described by Waters (1888) followed by several authors (reviewed in Marcus, 1939). Differing in size and shape, most of these glands were unpaired, although paired and 'bilobate' glands were recorded in some species too. Later, bacteria were found in the vestibular glands of both autozooids and avicularia (Lutaud, 1964, 1965, 1986).

Glandular secretions into the cavity of the tentacle sheath potentially could protect the

vestigial lophophore during its movements, as was suggested for the lophophore of autozooids (Mukai *et al*., 1997). Other possible functions include chemoreception and even a chemical defense, as was proposed for avicularia in general (Schopf, 1977; Winston, 1991; Carter *et al*., 2010, reviewed in Winston, 1984), but this issue remains open (see also below).

Ganglion

In bryozoan zooids the cerebral ganglion performs an integrative function, receiving and processing information from different receptor cells as well as controlling activities of the main muscle elements. In autozooids it is usually oval and situated on the posterior/dorsal side of the pharynx. For example, the ganglion in the autozooid of *Electra pilosa* (Linnaeus, 1767) consists of three cell complexes – central, distal and proximal — located around the eccentric neuropile occupying the proximal and central (deep) part of the ganglion. The ganglion consists of 4–5 groups of neurons separated by the axon bundles in *Cryptosula pallasiana* (Moll, 1803) (Gordon 1974). On average, the ganglion of marine bryozoans ranges from 30 to 60 μm in diameter and contains approximately 30-40 cells (Lutaud, 1969, 1977; reviewed in Mukai *et al*., 1997).

The ganglion in various types of avicularia is located at the base of the rudimentary polypide and consists of a peripheral layer of neuronal bodies and a central neuropile, represented by nerve cell processes (Carter *et al*., 2010; Shunatova *et al*., 2022; our data). The ganglion of the adventitious "bird's head" avicularia in *D. fruticosa* reaches a diameter of 25–30 μm and include approximately 20 neurons (Shunatova *et al*., 2022). The diameter of the avicularian ganglion of *A. arctica* is even smaller (20 μm), although it contains a similar number of neurons (about 20 μm). Note that the avicularian ganglia of both species are significantly smaller than that of the autozooidal ganglion (50 μm) and accordingly contain fewer neurons.

The processes of the sensory cells in the rudimentary lophophore and in the neuropile of the ganglion contain a large number of neurosecretory vesicles. Based on their ultrastructural diversity, these processes probably contain different neurotransmitters, which are presumably transported in different types of vesicles (reviewed in Sakharov, 1974; Breidbach, Kutsch, 1995; Schmidt-Rhaesa *et al*., 2015). The most numerous are round vesicles with electron-dense content. Some of them (so-called "dense-cored" vesicles) are surrounded by a light rim of varying width, which presumably indicates the presence of neuropeptides. In our study, we detected the FMRF-amide and serotonin in both the neurons and the neuropile region of the avicularian ganglion of *A. arctica*. However, although both this species and *D. fruticosa* revealed similar microvesicles in the processes of the neuropile by TEM, immunocytochemical methods failed to show the presence of neurotransmitters in the peripheral neurons of the ganglion in the latter species (Shunatova *et al*., 2022).

Function of rudimentary polypide

Our ultrastructural data indicating the presence of the receptor and nerve cells in the rudimentary lophophore of *Arctonula arctica* were confirmed by the immunocytochemical studies (Fig. 9). We detected α-tubulin in some peripheral lophophoral cells (including multiciliary) and in their cilia in the apical part of the lophophore, in the neurons of the ganglion, in the receptor cells underneath the palate, close to the tentacle sheath, as well as in the central processes running from these cells. The presence of α-tubulin in the ciliary structures, neurons and their processes, and in the central nervous system has also been shown in various invertebrates (e.g. Schmidt-Rhaesa *et al*., 2015; Zaitseva *et al*., 2022; Starunova *et al*., 2024).

Also, we detected serotonin in the avicularian ganglion of *A. arctica*, in both neurons and neuropile. Carter (2008) previously noted that the ganglion of the "bird's head" avicularia in *Bugulina flabellata* contains serotonin, but the quality of the illustrative material hinders reliable conclusions. The presence of serotonin in the autozooidal ganglion has also been shown in all major bryozoan clades — phylactolaemates, gymnolaemates and stenolaemates (Shunkina *et al*., 2013, 2015; Schwaha, Wanninger, 2015; Temereva, Kosevich, 2016, 2018; Worsaae *et al*., 2020). In addition, we detected FMRF-amide in the presumed sensory cells of the reduced lophophore and palate, neurons of the ganglion and their processes running to all groups of avicularian muscles including muscles of the polypide in *A. arctica*. The distribution of FMRF-amide

suggests that it is involved in the transmission of signals to the muscles in invertebrates, including bryozoans (see also e.g. Yu *et al*., 2015; Serova *et al*., 2017; Zaitseva, Shumeev, 2017; Li *et al*., 2019).

Presumed sensory cells were previously described in the tentacles and introvert of autozooids in both freshwater and marine bryozoans (including *A. arctica*), using CLSM, SEM and TEM. The ultrastructure of some of these multiciliary cells indicates that they are mechanoreceptors (Mukai *et al*., 1997; Nielsen, Riisgård, 1998; Shunatova, Nielsen, 2002; Tamberg, Shunatova, 2017).

Our ultrastructural data gave no definitive answer to the question whether the vestigial polypide has a mechano- or chemoreceptor function (or both) in *A. arctica*. It is thought that dopaminergic neurons with ciliary receptive structures act as either mechano- and/or chemoreceptors (e.g. Schlavny *et al*., 1991; Zaitseva *et al*., 2022; Barmasova *et al*., 2022). The visualization of catecholamines enabled recognizing multiple intraepithelial cells corresponding to laterofrontal cells with a (mechano)sensory cilium in the autozooidal tentacles of the freshwater bryozoan *Cristatella mucedo* (Shunkina *et al*., 2014, 2015). The central processes of these cells, as part of the tentacular nerves (frontolateral and abfrontal), eventually reached the cerebral ganglion. Similarly, the central processes of the sensory cells in the lophophore rudiment of avicularia also go to the ganglion (Shunatova *et al*., 2022; our data). Recently, our unpublished study showed positive staining for tyrosine hydroxylase in the rudimentary polypide of the adventitious sessile avicularium of another cheilostome, *Tegella armifera*, but that result still provied no answer whether it contains mechanoreceptors.

If present, the chemoreception in some avicularia is likely based on the activity of the gland(s) and/or individual/multiple secretory cells in the lophophore and in the wall of the tentacle sheath (Lutaud, 1964, 1965; Carter *et al*., 2010; our data). Mucus secreted by these glands and cells can serve as a medium that facilitates the perception of chemical stimuli from the environment by receptor cells that are presumably present in the avicularian lophophore.

Another possibility is a defensive function of the mucus produced by the gland. An earlier suggestion was that it can work as a lubricant during polypide excursions in autozooids (see above). However, only a small percentage of cheilostome species have such vestibular glands, leading to the question why then these glands are so rare? Moreover, the movements of the rudimentary lophophore in avicularia are very restricted: in some species, only its tip is projected from the orifice, whereas in others it never appears outside. Is a lubricant required for such very limited movements? Or is the secretory activity of some polypide cells sufficient to fulfil that function? Alternatively, toxic mucus could deter micropredators. Although the chemical defense was mostly discussed in connection with symbiotic bacteria (see, e.g. Winston, 1984), it is also possible that the bryozoans themselves produce toxic substances. Of course, both functions — chemoreceptory and defensive, could co-exist.

Conclusion

In support and extension of previous studies, our research on the cheilostome *Arctonula arctica* showed that, together with the loss of the food-gathering and digestive apparatus, its avicularian polypide transformed to a sensory — mechano- and/or chemoreceptor — structure, incapable of feeding and digestion, but still retaining limited mobility. Another possible function that we highlight based on the presence of the gland and/or secretory cells of the tentacle sheath is a chemical defense. Although we did not detect symbiotic bacteria that are considered responsible for producing toxic metabolites in their bryozoan hosts (reviewed in Bogdanov *et al*., 2022, 2023) in the gland of *A. arctica*, some bryozoans are thought to produce toxic substances themselves (Maltseva *et al*., 2016; discussed in Karagodina *et al*., 2018).

The morpho-functional transformation of bryozoan autozooids to polymorphs can be considered as another example of exaptation — "characters, [that] evolved for other usages…, and later [were] "coopted" for their current role" (Gould, Vrba, 1982: 6; Gould, 2002). Dorn (1875) also formulated the principle of functional changes, namely the weakening of the main and the strengthening of the secondary function that leads to a restructuring of the morphology of the organ such that one of its secondary functions becomes the main one, and the main function in the ancestors either

becomes secondary or disappears (reviewed in Severtzoff, 1928, 1939; Severtsov, 1990). Whereas the operculum in autozooids passively protects the orifice, its modified version — the mandible — became an active defensive tool (see Introduction). It still covers the zooidal orifice, but that function is has become secondary. Autozooidal polypides perform multiple functions including food capture and digestion (primary functions), sensing (involved in gathering food particles and avoidance reactions), gamete manipulation and, sometimes, cleaning (reviewed in Winston, 1977, 1978; Shunatova, Ostrovsky, 2001). Whether the function of the vestiular glands is connected with either chemical defense or chemoreception in autozooids is unknown. In avicularia, polypide lost most of these functions, and sensing became the primary function. Thus, the term exaptation can be applied here to the evolutionary transformation both of zooids and their parts (mandible) (for other examples among bryozoans, see Nekliudova *et al*., 2021). Transformation of the avicularian polypide to the sensory organ should not be considered as exaptation, however, because the polypides in autozooids also have a sensory function. Still, exaptation can occur if the function of the gland has been changed.

Interestingly, reduced or vestigial lophophores with fewer tentacles (sometimes of various length) and small, non-functional or totally missing gut are also known in the sexual polymorphic zooids, female and male (sometimes, dwarf), in certain cyclostome and cheilostome bryozoans (Cook, 1968; Ostrovsky, 1998, 2013; Nekliudova *et al*., 2019, 2021). They sometimes demonstrate special tentacle behavior, whose only function is sperm manipulation, its catch (cyclostomes) or release (cheilostomes).

The polypide reduction strongly transformed the associated muscular and nervous elements. Changes affecting the muscular system include the complete disappearance of the digestive system muscles, some apertural muscles, the duplicature bands, and the partial reduction and diminishing of the muscles of the diaphragm, longitudinal muscles of the tentacle sheath and of the retractors. The remaining parts of the nervous systems include the cerebral ganglion, branches innervating the muscles of the tentacle sheath wall, adductors, abductors and retractors, as well as the sensory cells associated with the palate and the frontal membrane. The reduction also affected an avicularian gland, which became very small and unpaired.

Despite the long history of research on avicularia, their anatomical, ultrastructural and functional diversity is still not fully known and understood. The changes that affected parts of avicularia of different cheilostomes also differ, raising questions related to the independent modifications of heterozooids in different cheilostome lineages and to the transformation of feeding modules towards more highly specialized polymorphs. Altogether, studies on avicularia will further contribute to the development of ideas about the emergence and further evolution of polymorphism in modular organisms in general.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

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