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Ultrastructure of the buccal complex of *Pricea multae* (Monogenea: Polyopisthocotylea, Gastrocotylidae)

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Abstract. The 'buccal complex' of *Pricea multae* Chauhan, 1945 consists of two buccal suckers, the pharynx, a putative taste organ and the mouth cavity. The two suckers are dorsal to the mouth cavity, and the pharynx posterior to them. The septum in each sucker consists of connective tissue containing muscle filaments, lined by tegument with short irregular microvilli. The mouth cavity and the lumen of the suckers are lined by tegument with short irregular lamellae and by tegument with long bulbous, interconnected lamellae, separated from each other and from the body surface tegument by septate junctions. A ventral extension of the mouth cavity is also lined by tegument with short irregular lamellae. An anterior 'taste organ' is lined by 'normal' (body) tegument and tegument with short irregular lamellae. Glandular ducts open into it, and it contains many small uniciliate and multiciliate receptors, as well as two receptor complexes each consisting of a large non-ciliate receptor surrounded by small and large uniciliate receptors, with multiciliate receptors closeby. The four types of receptors are described in detail. The anterior part of the pharyngeal lumen is lined by an epithelium with dense surface lamellae and is penetrated by non-ciliate receptors. Attention is drawn to significant differences between the buccal complexes of the polyopisthocotylean monogeneans *Pricea multae* (Gastrocotylidae), *Gotocotyla secunda* (Tripathi, 1956) (Gastrocotylidae), *Polylabroides australis* (Murray, 1931) (Microcotylidae), *Zeuxapta seriolae* (Meserve, 1938) (Axinidae) and *Diclidophora merlangi* (Kuhn, 1832) (Diclidophoridae).

Few studies on the fine structure of the anterior end of the polyopisthocotylean Monogenea have been made (Rohde 1974, 1979, 1981, Halton and Morris 1975, Halton and Stranock, 1976, Rohde and Watson 1995), and only one of these (Rohde and Watson 1995) examined the ultrastructure of the septate suckers and associated sensory receptors of a species (*Polylabroides australis* [Murray, 1931], Microcotylidae) based on semi-serial ultrathin sections. Even in that study, a detailed reconstruction of the various organs in front of the suckers was not made. In the present study, we examine the fine structure of the anterior end of the gastrocotylid *Pricea multae* Chauhan, 1945, based on two complete sets of semithin longitudinal sections, and on one set of semiserial ultrathin cross-sections. This paper represents one of a series of papers on the ultrastructure of the anterior end of monogeneans, with the aim of establishing a basis for comparing different taxa within the Monogenea, thus contributing to a phylogeny of the group, and for an analysis of the function of various organs and receptor types. To make a comparison with similar structures of other species possible, descriptions have to be detailed and illustrations sufficient to show all details referred to in the descriptions; sequences of electron-micrographs of a particular structure are therefore often given. Only structures are included that appear to be useful for a phylogenetic analysis. Histochemical studies may well yield interesting results concerning the function of the various structures described, but are beyond the scope of this paper.

MATERIALS AND METHODS

Scomberomorus commerson Lacépède, 1800 (Spanish mackerel) were collected by trolling near Edward Island, in the Whitsunday Group off the coast of Queensland, Australia, in October 1994. *Pricea multae* were removed from the gills and fixed in 3 % glutaraldehyde in 0.1 M sodium cacodylate buffer made with seawater, pH 7.3 at 4°C for 8 days. They were then washed in the same buffer, post-fixed in 1 % OsO_4 in buffer, dehydrated through a graded series of alcohol and embedded in Spurr resin. Two series of longitudinal semi-thin sections of 3.0–3.5 µm were cut through the anterior region of two worms and stained with toluidine blue. Semiserial ultrathin transverse sections through another individual from the anterior end of the suckers to midway through the pharynx were stained with uranyl acetate and lead citrate and examined under a JEOL 1200EX electron microscope at 60 kV.

RESULTS

Light-microscopic morphology of the anterior end

Figure 1 illustrates the position of the main organs in a diagrammatic sagittal section. In the dorsal part of the protruded head end, the tegument forms a deep

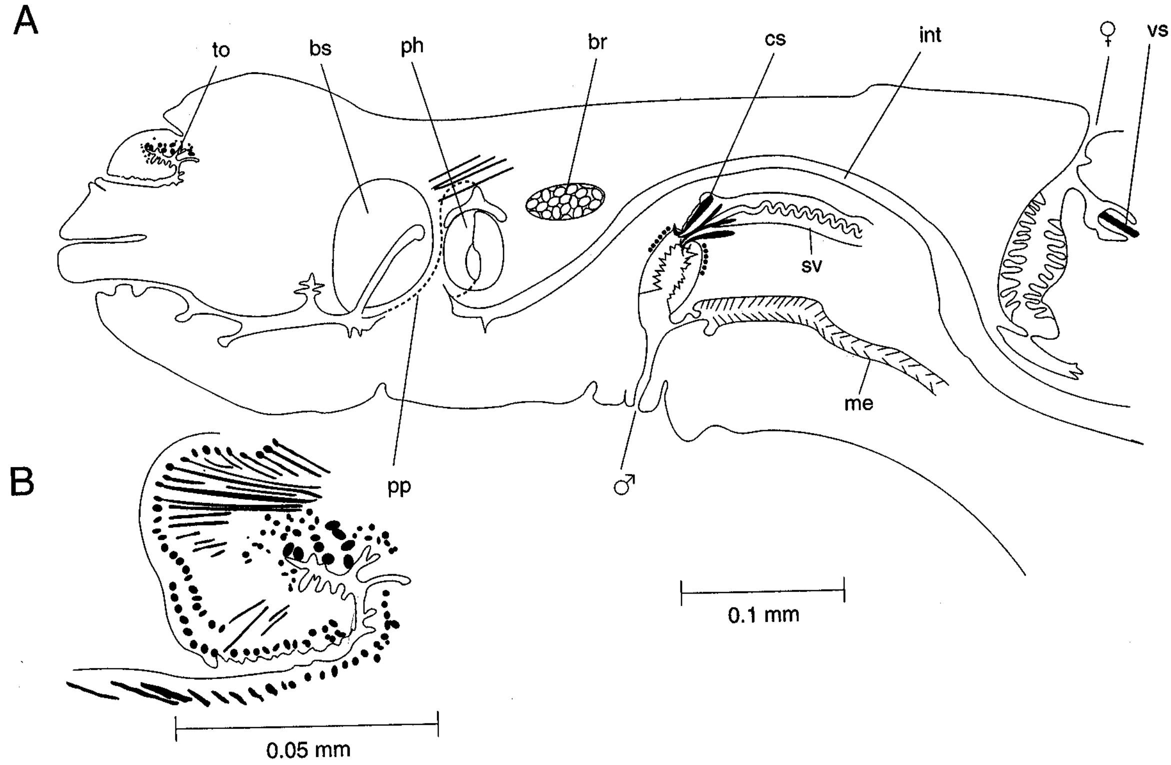

Fig. 1. Diagram of sagittal section through anterior part of body based on serial semithin sections (**A**), and diagram of sagittal section through taste organ (**B**).

invagination which first turns dorsally and then anteriorly, with numerous small side branches (Fig. 2C). Glandular secretion, some perikarya containing the same kind of secretion, and numerous muscle filaments are close to the anteriorly directed end of the invagination (Figs. 1A, B, 2C). This organ is, subsequently, referred to as the 'taste organ'. It had exactly the same position in the two specimens that were sectioned longitudinally, but appeared as a dorsal invagination of the mouth cavity in the cross-sectioned ultrathin sections (Figs. 2B–D). There were also some shallower invaginations of the tegument (Fig. 1A) at the anterior end of the longitudinally sectioned specimens. The mouth cavity has several dorsal and ventral invaginations and is continuous with the lumen of each sucker and a ventral extension below the sucker (Figs. 1A, 2H, I). The two buccal suckers lie dorsal to the mouth cavity (Figs. 1A, 2E–I). The pharynx, in all three specimens examined, was oriented dorso-ventrally behind the buccal suckers, with the anterior end directed dorsally. Connections of the pharynx lumen with the mouth cavity and intestine are very thin and could not be traced completely. Their likely course is indicated by interrupted lines in Fig. 1. The brain lies posterior to the pharynx, and the intestine curves dorsally above the seminal vesicle, and then again ventrally, below the vagina (Fig. 1A). Metraterm and the seminal vesicle, its anterior end surrounded by the cirrus spines, open into a common cavity leading to the ventral gonopore. The vaginal opening is dorsal, and the large vaginal cavity has many infoldings. A vaginal spine protrudes into a cavity connected to the dorso-posterior part of the vaginal duct (Fig. 1A).

Ultrastructure of the mouth cavity and buccal suckers

The buccal suckers are strongly muscular organs, their lumina continuous with the more ventral mouth cavity (Figs. 3A, 4A, 5A). They are lined by a basal lamina continuous with that of the tegument lining the mouth cavity, the lumen of the suckers (Fig. 3A–C) and the septa (Fig. 3B, C). Closely packed muscle bundles separated from each other by connective tissue (Figs. 3A, 4A, B, 5A) mostly run in a anterior-posterior direction. Some have a ventral-dorsal and largely transverse orientation (Fig. 5A), conspicuously crossing the anterior-posterior muscles. A band of densely packed anterior-posterior muscle filaments is located outside and adjacent to the basal lamina surrounding the dorsal, lateral and medial parts of the suckers (Figs. 3A, 5A). In the most posterior parts of the suckers, these muscles extend all around the suckers, except for a small ventral

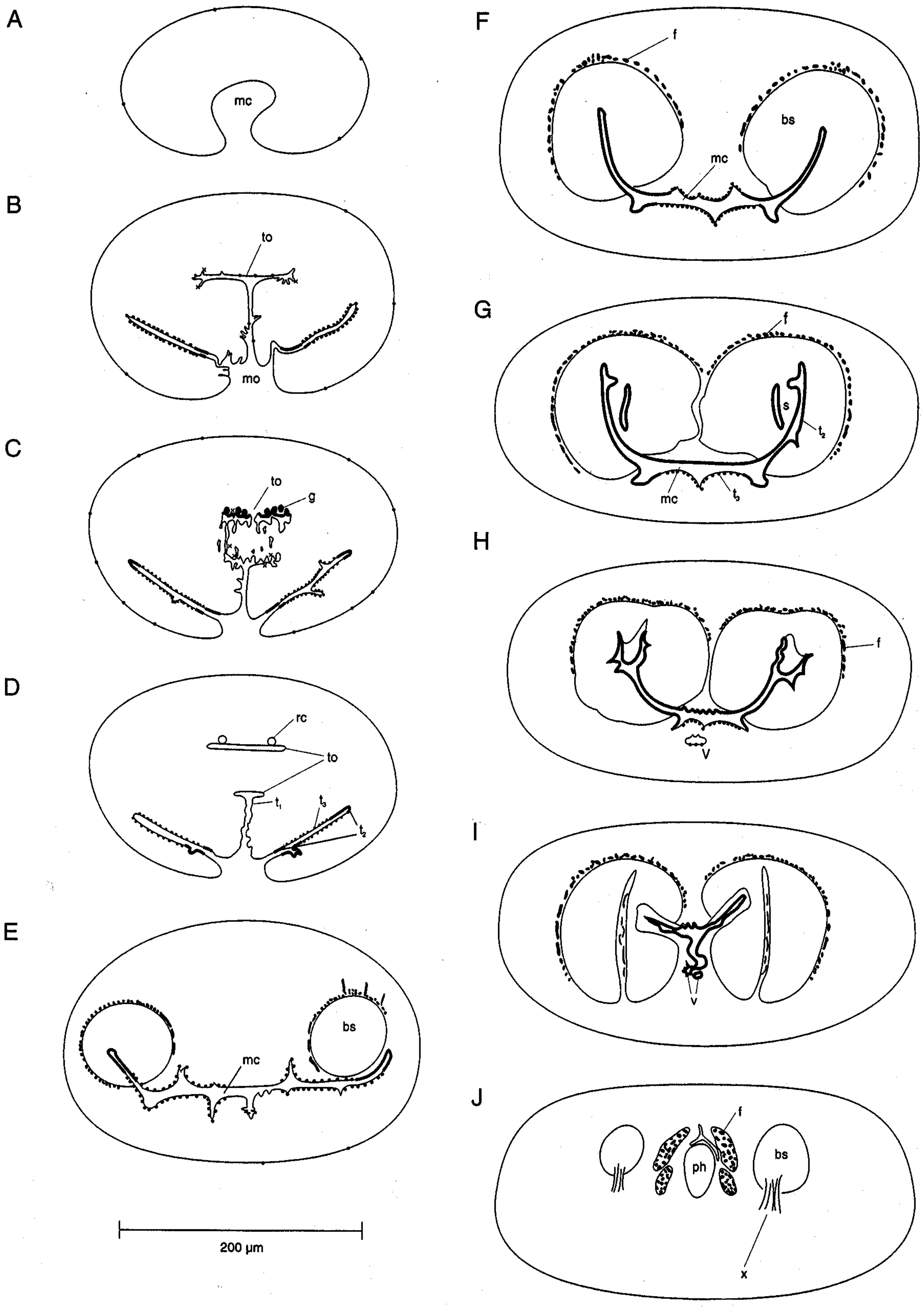

Fig. 2. Diagrams of cross-sections through anterior part of body based on ultrathin sections, at level of anterior tip (**A**), taste organ (**B–D**), anterior end of suckers (**E–F**), septum (**G–H**), posterior part of suckers (**I**), and pharynx (**J**). Note: (x) bundle of fibres extending from between muscle filaments of sucker into parenchyma. — 'normal' tegument (t_1), ▬ tegument with short irregular lamellae (t_2), ... tegument with long bulbous, interconnected lamellae (t_3). Also note: lining of prepharynx and pharynx with lamellae that differ from those of t_2 and t_3.

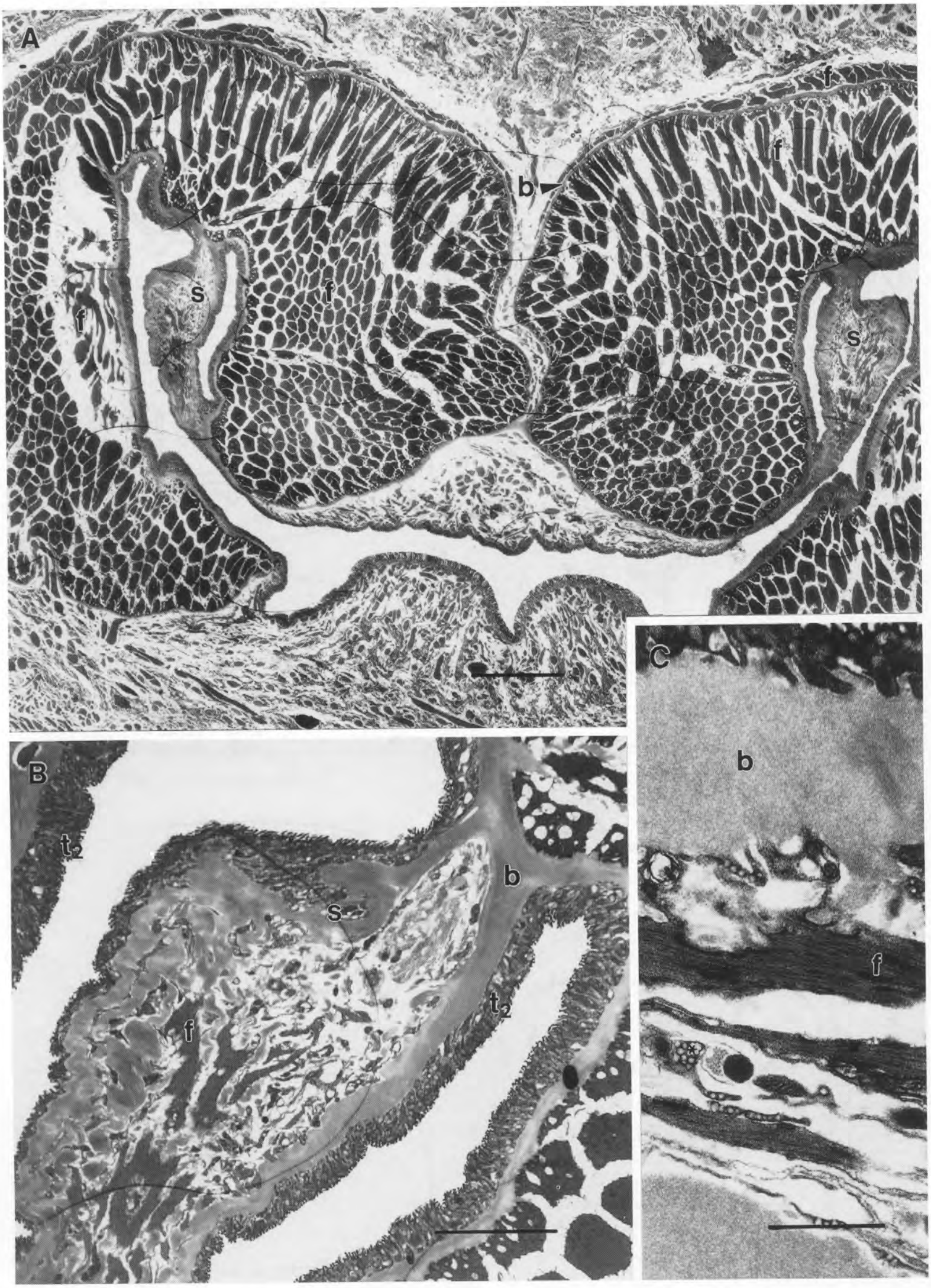

Fig. 3. A – cross-section through buccal suckers at level of septa (s). Note basal lamina (b) around suckers and the layer of muscle filaments (f) outside basal lamina. **B** – Septum at higher magnification. Note basal lamina (b), and muscle filaments (f) in loose connective tissue. Also note tegument with short irregular lamellae (t_2) lining lumen of sucker. **C** – Detail of septum showing very thick basal lamina, vesiculate fibres (asterisk), and muscle filaments. Scale bars = 20 μm (A), 5 μm (B) and 1 μm (C).

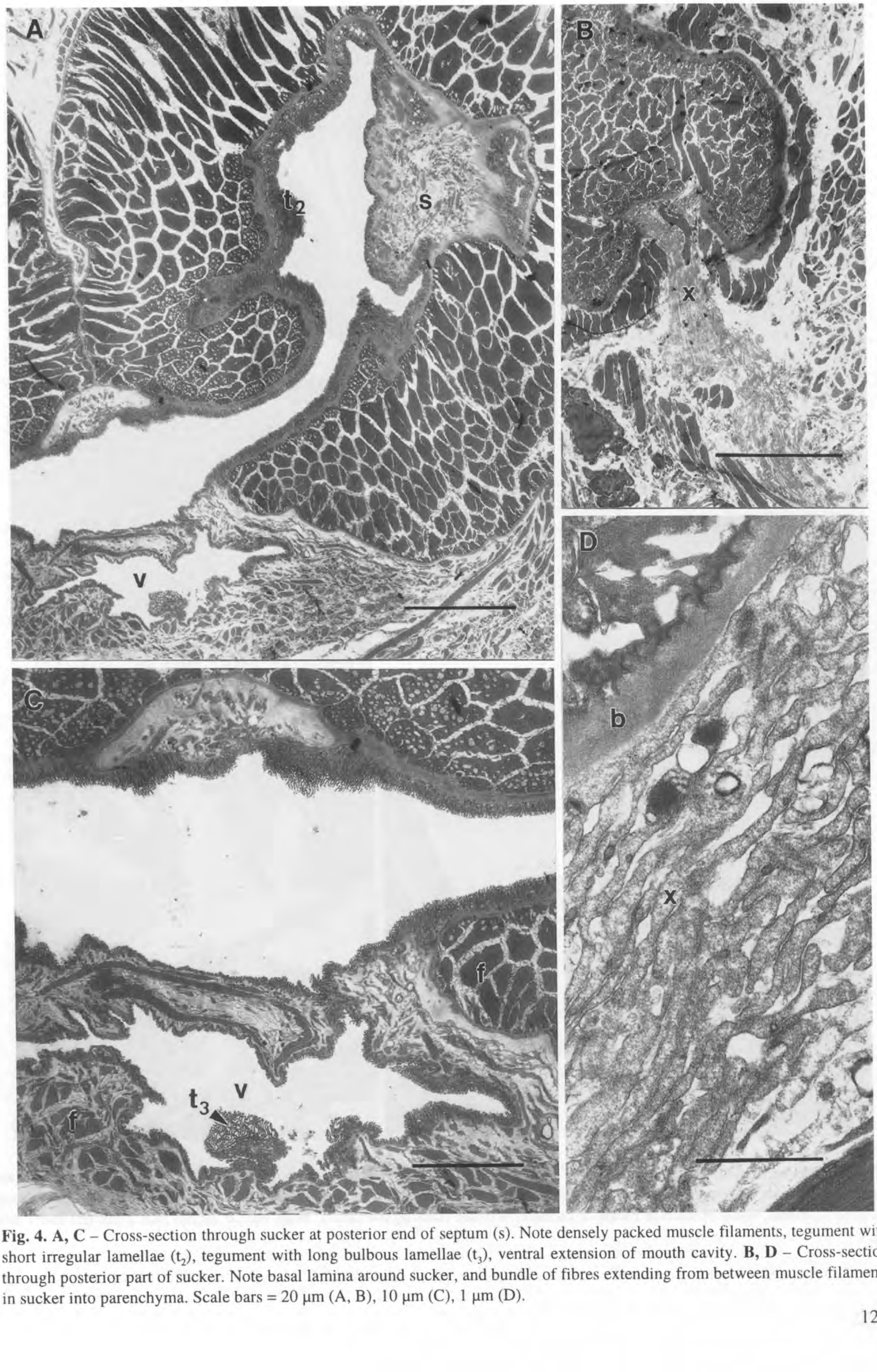

Fig. 4. A, C – Cross-section through sucker at posterior end of septum (s). Note densely packed muscle filaments, tegument with short irregular lamellae (t_2), tegument with long bulbous lamellae (t_3), ventral extension of mouth cavity. **B, D** – Cross-section through posterior part of sucker. Note basal lamina around sucker, and bundle of fibres extending from between muscle filaments in sucker into parenchyma. Scale bars = 20 μm (A, B), 10 μm (C), 1 μm (D).

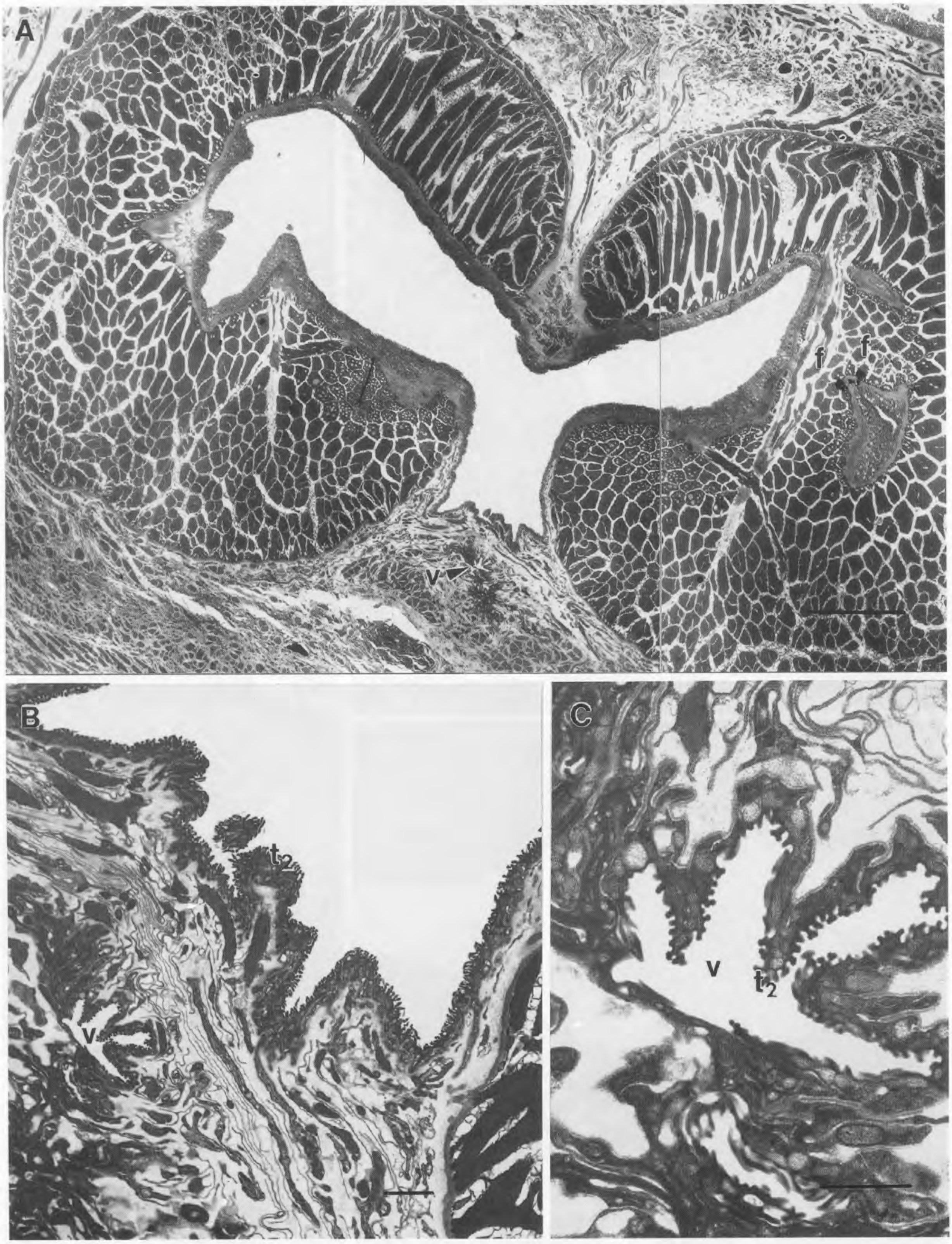

Fig. 5. Cross-sections through middle parts of suckers behind septum on left and at posterior margin of septum on right. Note tegument with short irregular lamellae (t_2), lining lumen of suckers and ventral extension of lumen. Also note densely packed muscle filaments, some of them in bands of connective tissue crossing the others. Scale bars = 20 µm (A), 2 µm (B) and 1 µm (C).

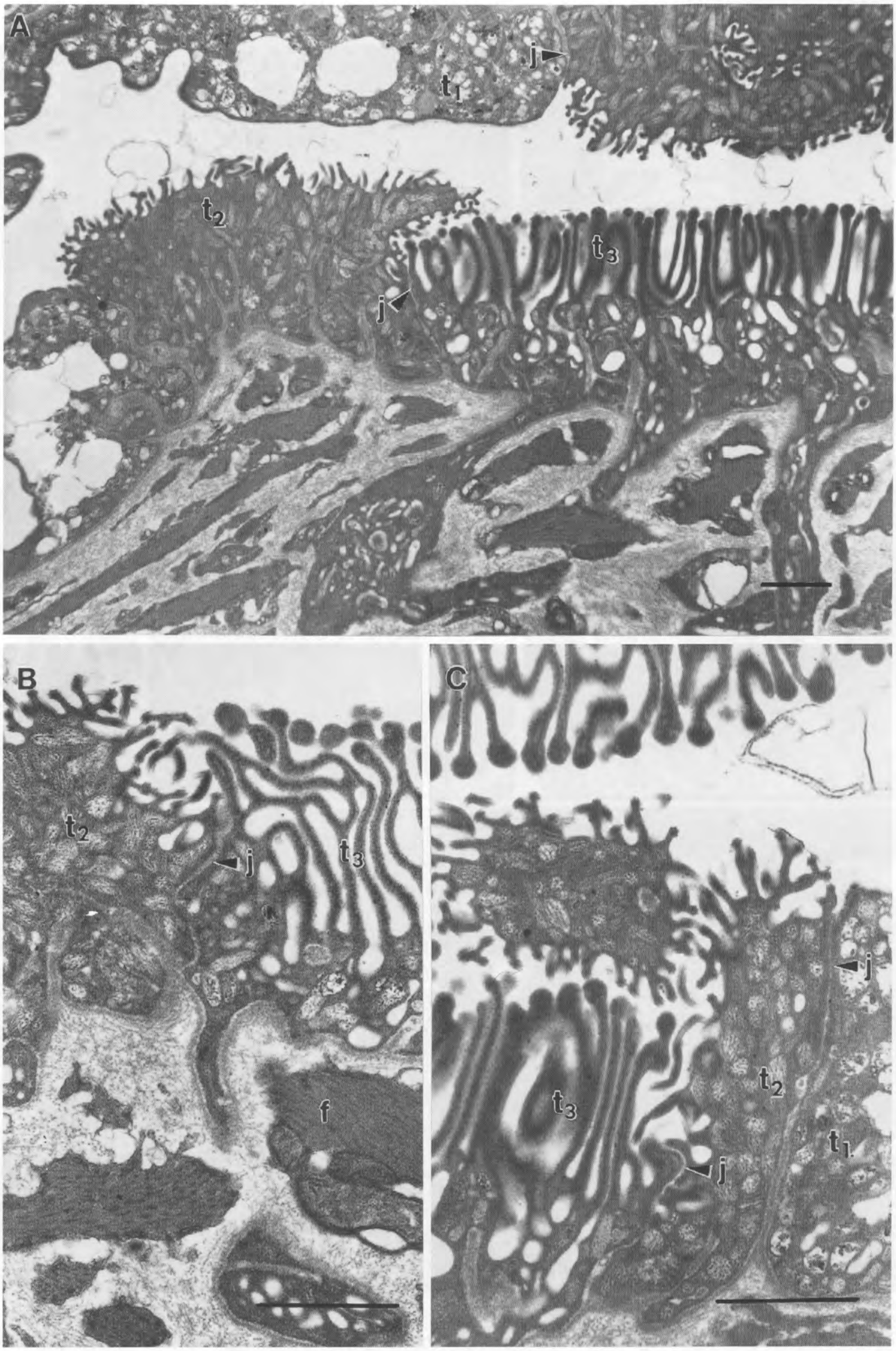

Fig. 6. Tegument lining parts of mouth cavity leading to buccal suckers (Fig. 2D). t_1 – 'normal' tegument identical with that covering the body surface, t_2 – tegument with short irregular lamellae, t_3 – tegument with long bulbous, interconnected lamellae. Different types of tegument connected by septate junctions. Note large number of muscle filaments below tegument. Scale bars = 1 μm.

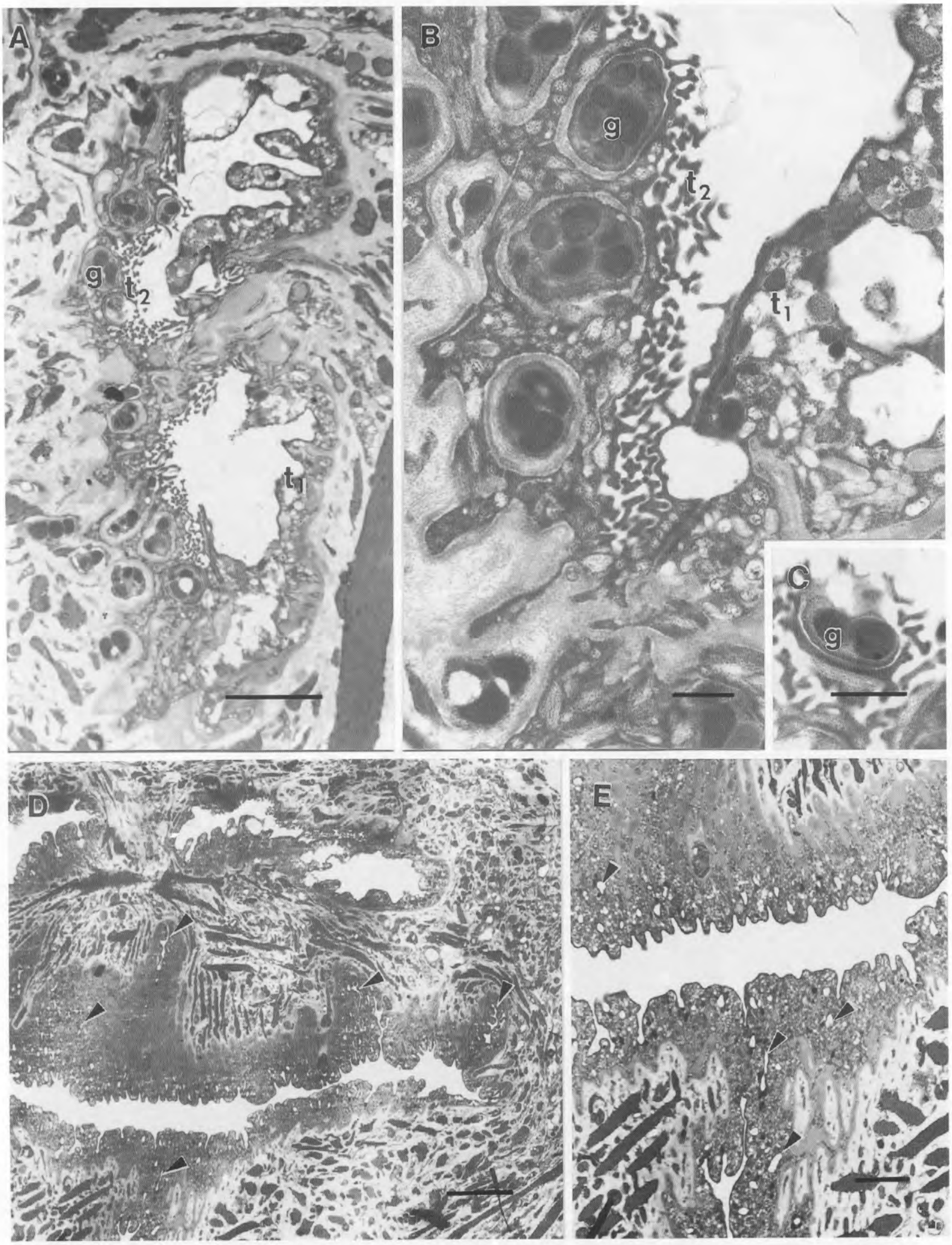

Fig. 7. Glandular secretion of taste organ. Note ducts lined by 'normal' tegument (t_1) and tegument with short irregular lamellae (t_2) in **A** and **B**. Also note numerous sieve-like invaginations of tegument of taste organ (arrowheads) in **D** and **E**. In D, the taste organ is sectioned through both 'loops', due to the turning back on itself of the organ. Note: ventral side in A and B on the right. Scale bars = 2 µm (A), 0.5 mm (B, C), 5 µm (D) and 2 µm (E).

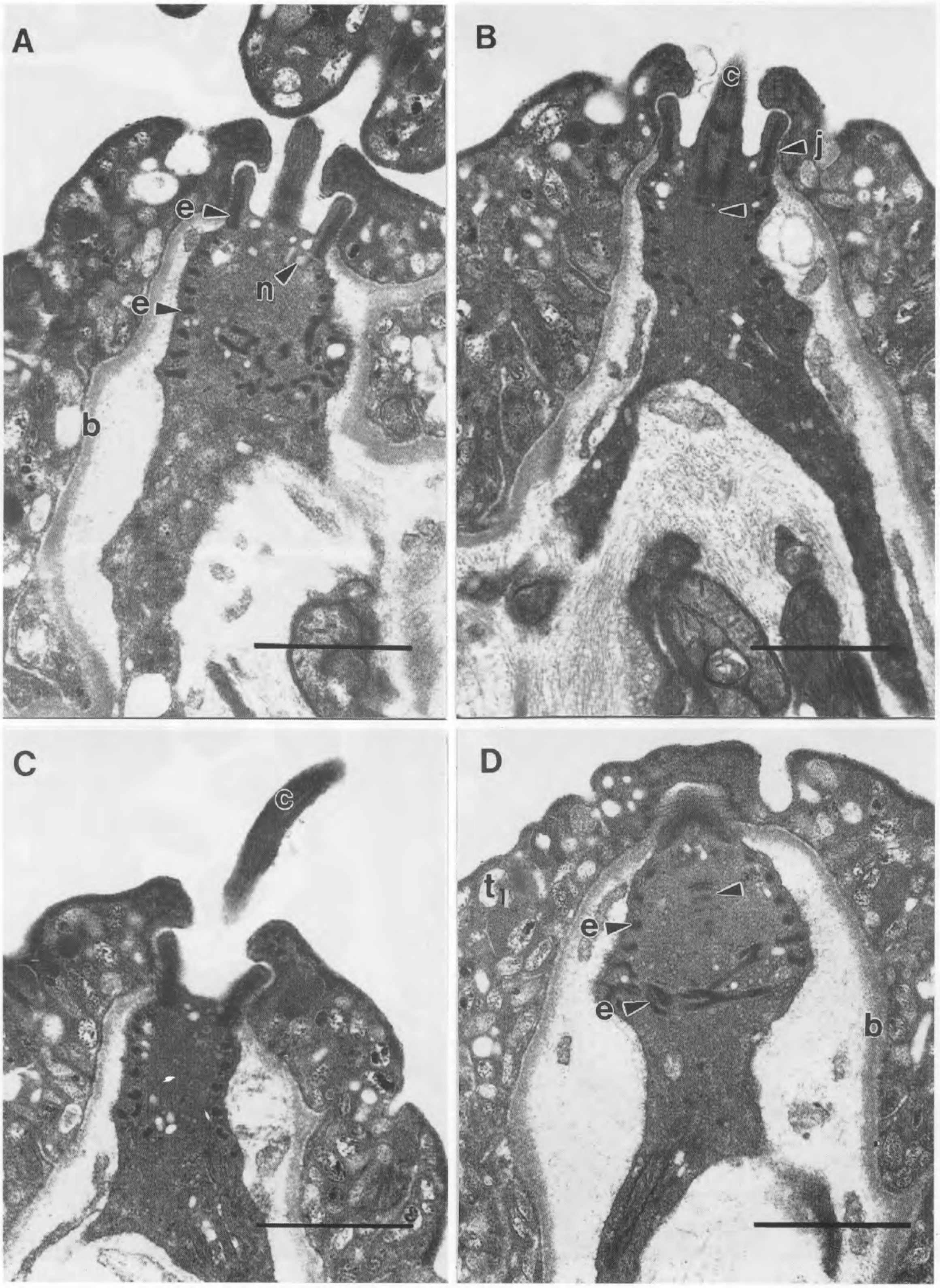

Fig. 8. Uniciliate receptors. Note large number of electron-dense collars, interconnected in a reticulate manner (in **D**), neurovesicles, indistinct cross-striated ciliary rootlet (arrowheads). The receptor in **A** is in a duct of the taste organ, the others are surface receptors. (t_1) body tegument, (asterisk) rootlet. Scale bars = 1 μm.

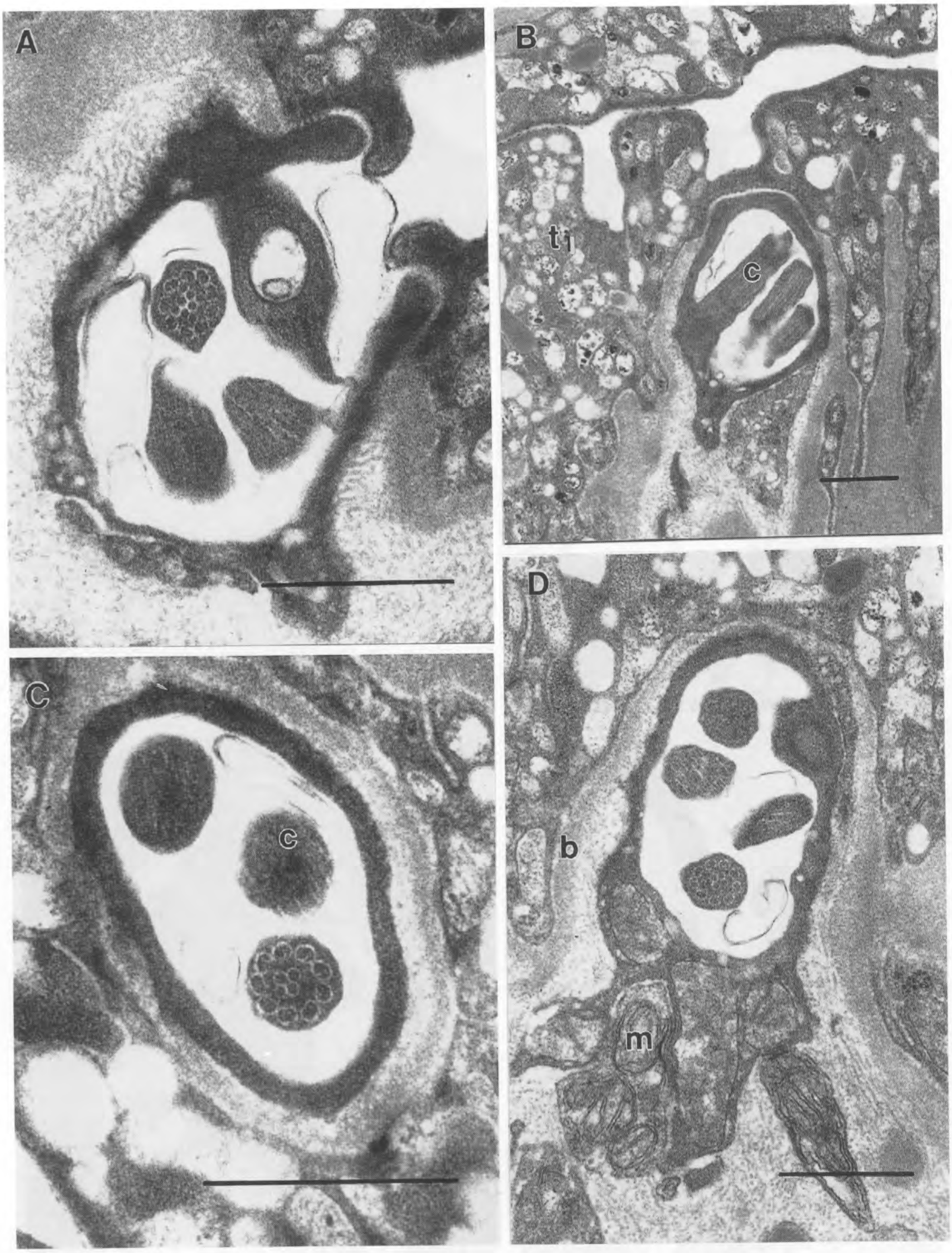

Fig. 9. Multiciliate receptor in the taste organ. Note short cilia (c, usually three) not protruding beyond the tip of the tegument and containing 9 peripheral doublets of microtubules whose lumina are indistinct, as well as several (4 in **C**, at least 6 in **A**) single microtubules in the centre. Also note numerous densely packed mitochondria, and dense cytoplasm of the receptor which obscures the electron-dense collar(s). Scale bars = 0.5 μm.

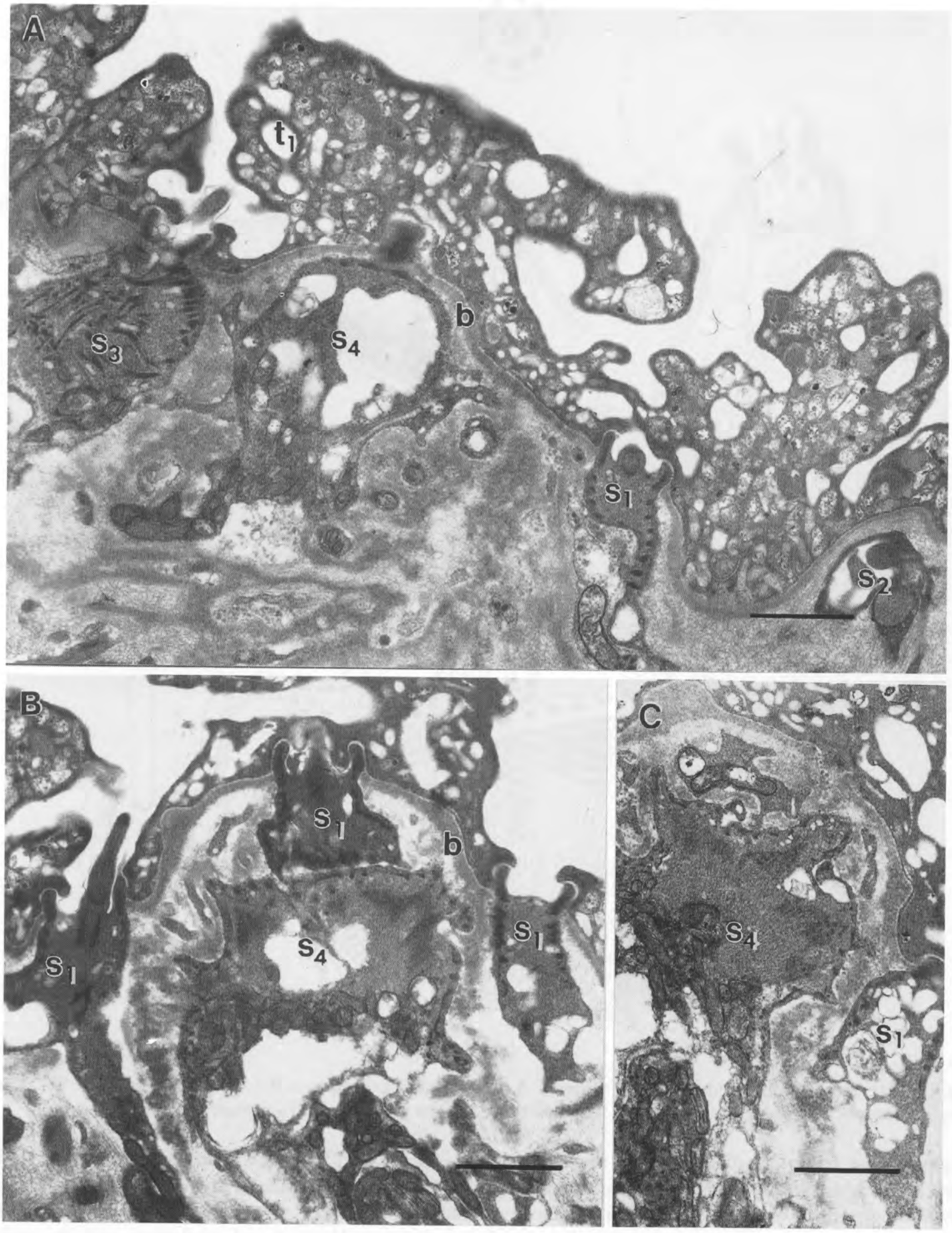

Fig. 10. Receptor complex of taste organ, consisting of large non-ciliate receptor (S_4), large uniciliate receptor with many interconnected electron-dense collars (S_3), and several small uniciliate receptors (S_1). Note large number of electron-dense collars, extensive cross-striated rootlets and densely packed fibres in non-ciliate receptor. The receptor complexes are located in those parts of the ducts of the taste organ lined by 'normal' tegument (t_1). Multiciliate receptors (S_2) are closeby. Scale bars = 1 μm.

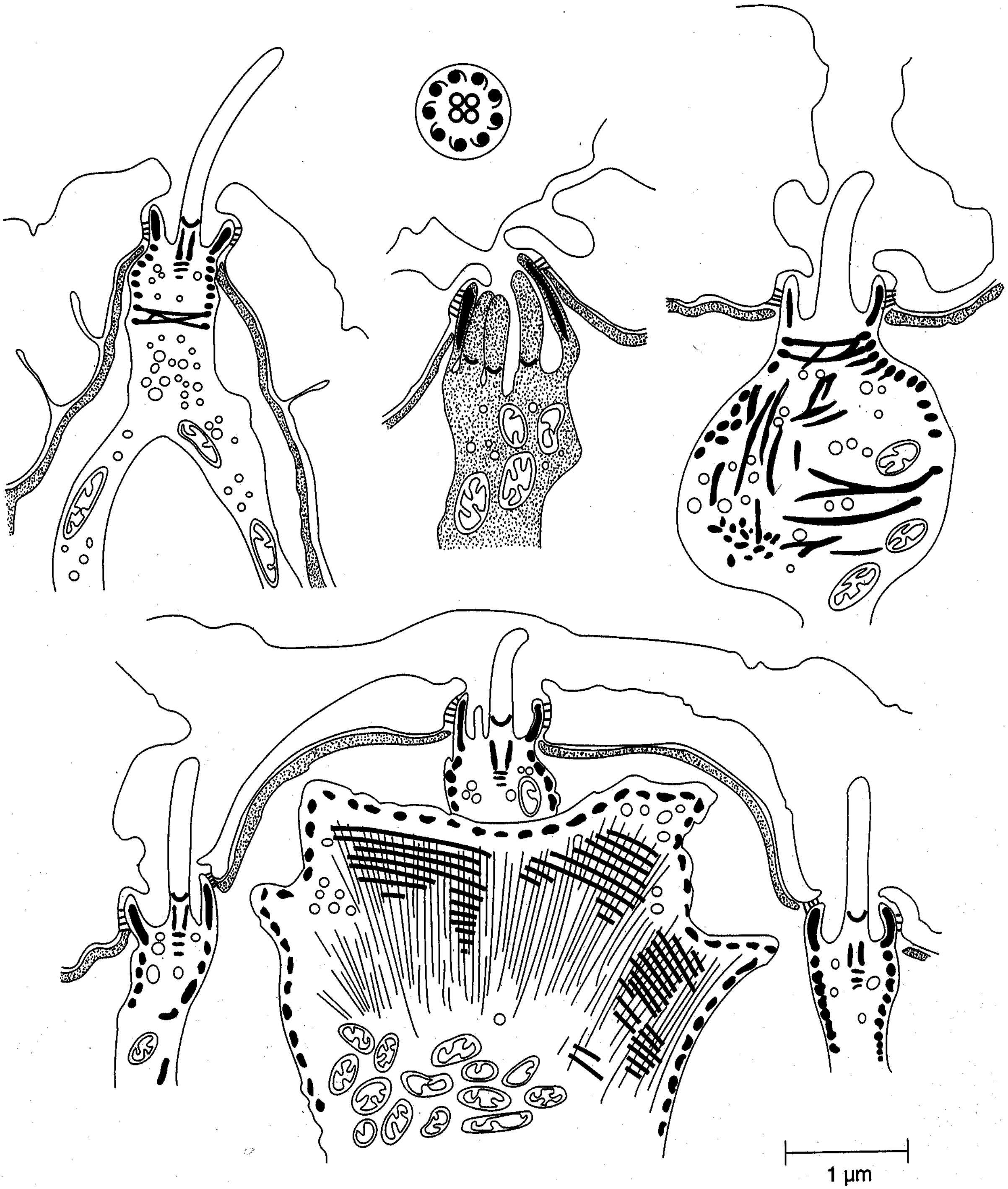

Fig. 11. Diagrams of non-pharyngeal sensory receptors. **A** – Small uniciliate receptor. **B** – Multiciliate receptor. **C** – Large uniciliate receptor. **D** – Receptor complex with large non-ciliate receptor and some small uniciliate receptors.

-region where dense bundles of nerve fibres extend from between the muscle fibres in the suckers into the surrounding parenchyma (Fig. 4B, C). The septa extend between the medio-dorsal and medio-ventral parts of the suckers (Fig. 3A, B). They contain much connective tissue, muscle filaments and vesiculate fibres (Figs. 3B, C). A ventral extension of the mouth cavity (Figs. 4A, C, 5A–C) arises at the level of the middle parts of the suckers and joins the mouth cavity again some distance more posteriorly.

Mouth cavity, lumina of the suckers and the ventral extension of the mouth cavity are lined by tegument, of which three types can be distinguished. The 'normal' tegument is identical and continuous with the surface tegument. It lacks microvilli or lamellae (Fig. 6A, C). A second type has shorter branching microvilli that give an 'irregular' appearance due to the branching and the variability in thickness (Fig. 6A–C), and a third type has long interconnected lamellae possessing bulbous endings (Fig. 6A–C). Different types of tegument are joined

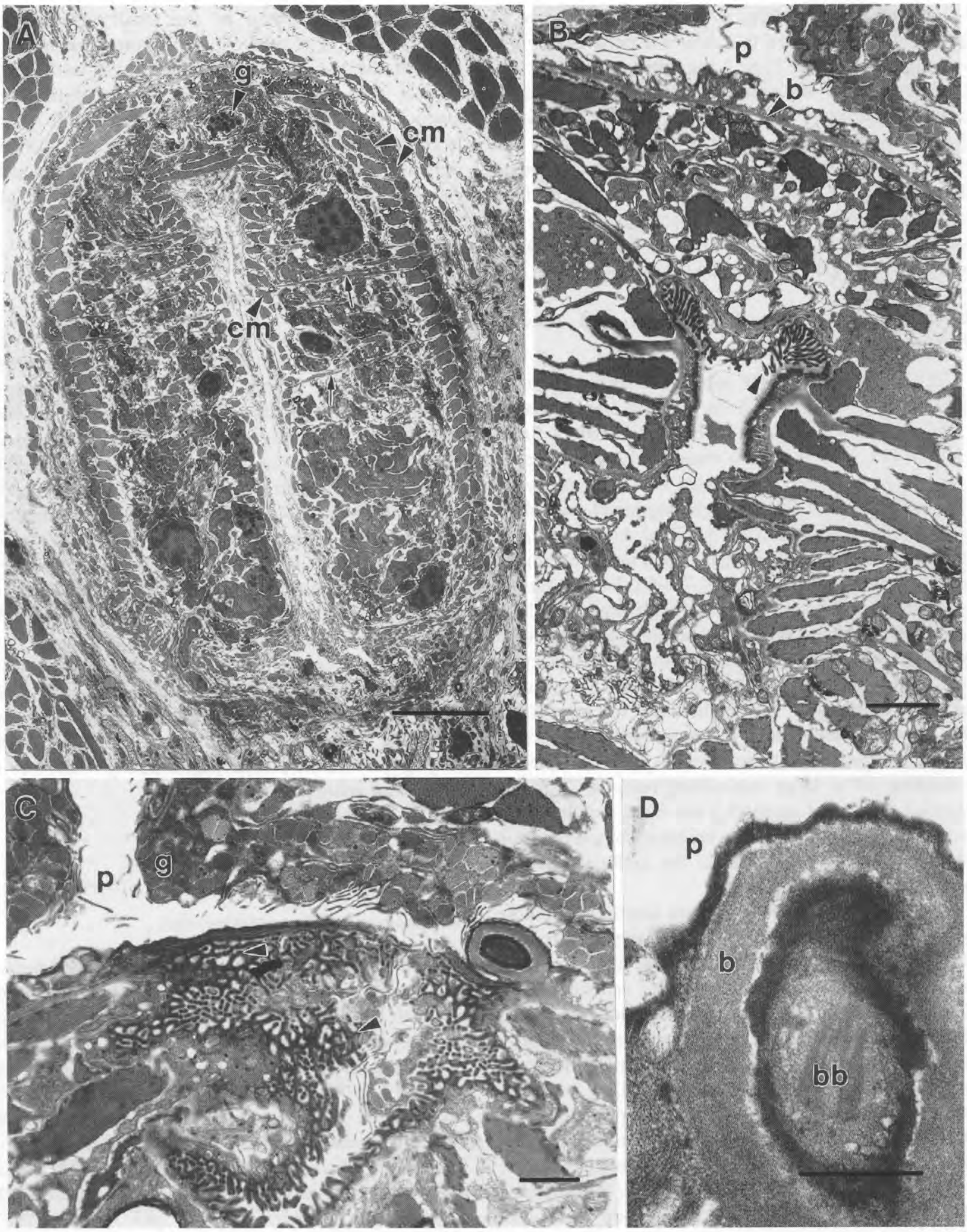

Fig. 12. Longitudinal sections through pharynx. **A–B** – Note two outer layers of circular muscles, and inner circular muscles, radial muscles (arrows), gland duct, and dense outfoldings of pharynx epithelium in anterior part of pharynx (arrowheads). Also note prepharyngeal cavity, and basal lamina-like sheath (b) around pharynx. **C–D** – Sensory receptor at anterior margin of pharynx. Note basal body and basal lamina around receptor. Scale bars = 10 µm (A), 2 µm (B), 1 µm (C) and 0.5 µm (D).

by septate junctions (Fig. 6A–C). All three types of tegument are connected to subsurface perikarya by cytoplasmic processes. Type 1 tegument covers the surface of the body, the mouth cavity close to the mouth opening, and much of the taste organ (Figs. 2, 7A–E). Type 2 tegument covers most of the mouth cavity and its ventral extension, the lumen of the suckers including the septa (Figs. 2, 3A, B, 4A, C, 5A–C), and parts of the taste organ around the glandular openings (Figs. 7A–C), and Type 3 tegument covers parts of the mouth cavity and parts of its ventral extension (Figs. 2, 4A, C).

Ultrastructure of the taste organ and sensory receptors

The invagination of the tegument forming the taste organ widens at the end in a transverse T-shaped fashion and bends back on itself (Figs. 1 and 2). Some sections therefore show two transversely extending cavities (Fig. 7D), the more dorsal one lined partly by 'normal' tegument and partly by tegument with short irregular lamellae (Fig. 7A–C). Gland ducts with large electron-dense secretory droplets open into the terminal part of the invagination (Figs. 1, 7A–C). The transversely widened cavity has many small side branches, those of the anteriorly and posteriorly running part of the taste organ probably connected, leading to a sieve-like structure of the tissue around it (Fig. 7D, E). Many small uniciliate (Fig. 8A) and multiciliate receptors (Fig. 9A–D) are scattered along the main cavity and its side branches. Also present are two receptor complexes, consisting of a large non-ciliate receptor (S_4) surrounded by several small (S_1) and large uniciliate (S_3) receptors (Fig. 10A–C). The receptor complexes lie a short distance on either side of the midline (Fig. 2D, only one illustrated).

The small uniciliate receptors are identical with those of the surface tegument. They have a single cilium with short cross-striated ciliary rootlet, dense cytoplasm containing neurovesicles and mitochondria, and many interconnected (up to 9 were counted) electron-dense collars (Fig. 8A–D). Multiciliate receptors were only seen in the taste organs and are usually concentrated in small pits, i.e. invaginations of the tegument. They have several (usually three) short cilia that do not protrude above the tegumental surface (Fig. 9). The electron-dense collar(s) is indistinct due to the very dense appearance of the cytoplasm, and there are many mitochondria (Fig. 9D). The axonemal microtubules are somewhat abnormal: the peripheral doublets have an indistinct lumen, and there are several (4 to at least 6 counted) central singlets (Figs. 9A, C, D). One large uniciliate receptor was seen in each receptor complex (Fig. 10A). It resembles the small uniciliate receptor, but has a larger dentritic ending and more electron-dense collars in a much less regular arrangement than those of the small uniciliate receptors. One large non-ciliate receptor was seen in each of the two receptor complexes. It has a large number of electron-dense collars, a fine striation extending from the periphery to the base, and several large cross-striated rootlets representing the more peripheral parts of the 'fine striation'. Numerous mitochondria are present in the basal part of the receptor (Fig. 10A–C).

Diagrams of the receptors are given in Fig. 11.

Ultrastructure of the pharynx

The pharynx is surrounded by a sheath resembling a basal lamina (Fig. 12B). There are two rows of external circular muscles, internal circular muscles forming a single row in the middle and posterior parts of the pharynx, and at least two rows in the anterior part, and radial muscles (Fig. 12A). Various cell types, some containing glandular secretion, are scattered between the muscle fibres (Fig. 12A). The anterior part of the lumen of the pharynx is lined by epithelium with conspicuously dense surface layer and many dense evaginations (Fig. 12B, C). Dense irregular bodies are closely associated with muscle fibres and the cytoplasmic processes between them. The prepharyngeal lumen is lined by cytoplasm with long lamellae (Fig. 12B, C) and many gland ducts discharge in this region. Four non-ciliate receptors, with a basal body, electron-dense collars and numerous vesicles, and surrounded by basal lamina bulging out into the prepharyngeal cavity, were seen in the anterior epithelium (Fig. 12C, D).

DISCUSSION

Morphology of the anterior end

In none of the other polyopisthocotylean Monogenea examined was the anterior end reconstructed on the basis of serial semi- and ultrathin sections (*Polystomoides malayi* Rohde, 1963 – Rohde 1974; *Diclidophora merlangi* (Kuhn in Nordmann, 1832) – Halton and Morris 1975; *Pricea multae, Gotocotyla secunda* (Tripathi, 1956), *Heteromicrocotyloides mirabilis* Rohde, 1977, *Heteromicrocotyla australiensis* Rohde, 1977 – Rohde 1979; *Zeuxapta seriolae* (Meserve, 1938), *Paramicrocotyloides reticularis* Rohde, 1978 – Rohde 1981; *Polylabroides australis* – Rohde and Watson 1995). Nevertheless, the information available permits certain comparisons. In *P. malayi* (Polystomatidae), the single anterior, non-septate sucker is not delimited from the surrounding parenchyma by a complete sheath of connective tissue or a basal lamina, as it is in *P. multae*; the pharynx is located directly behind the sucker, its large lumen a direct posterior continuation of the sucker lumen. A large ventral extension connects the mouth cavity anterior to the pharynx with the oesophagus behind the pharynx (Rohde 1974). A ventral extension is also present in *Pricea*, but it is a thin canal and a connection to the postpharyngeal digestive tract could not be traced, although its existence is possible. The pharynx of *P. malayi* has a much more complex structure than that of *Pricea multae* with extensive radial muscles, circular muscles forming a complete ring in the anterior part, an external and internal ring in the middle part, and a distinct sphincter at the posterior end of the pharynx. Longitudinal muscles extend along the pharynx.

In *Z. seriolae* (Axinidae), the two suckers lack a septum. They are located on the sides of the large mouth cavity, their large lumina representing lateral pouches of the mouth cavity and not separated from it by a narrow canal or sphincter (Rohde 1981). In *D. merlangi* (Diclidophoridae), the suckers, as in *Zeuxapta*, are laterally attached to the large mouth cavity, their large lumina representing lateral pouches of the mouth cavity. The lumen of the large pharynx is a direct posterior continuation of the mouth cavity via the prepharynx (Halton and Morris 1975). In *H. australiensis* (Heteromicrocotylidae), the suckers lack septa. They are shallow muscular cups, dorsal to the mouth cavity (Rohde 1979). The suckers of *G. secunda* (Gastrocotylidae) resemble those of *Pricea* most closely. The suckers are septate and the sucker lumina are lateral narrow continuations of the more ventral mouth cavity (Rohde 1979).

From a phylogenetic point of view, the structure of the oral sucker of *Polystomoides* (single, no sheath, more anterior location), different from those of other polypisthocotyleans, indicates that it is unlikely to be homologous with them. Futhermore, lack of septa in the suckers in a number of taxa of the order Microcotyloidea (Heteromicrocotylidae, Axinidae), suggests that lack of a septum in this order is secondary because most taxa of the order have septa. Most likely, the character 'pair of septate suckers' is a synapomorphy for a large taxon within the Polyopisthocotylea that comprises the Microcotylidea and Diclidophoroidea and possibly some other groups.

Ultrastructure of the mouth cavity and buccal suckers

The three types of tegument lining the mouth cavity and lumina of the suckers in *Pricea multae* have not been described from other polyopisthocotyleans. In *Zeuxapta seriolae* only one type, lacking microvilli or lamellae, was seen (Rohde 1981) and it is unlikely that other types are present, in view of examination of sections through various parts of the mouth cavity and suckers. In *D. merlangi*, Halton and Morris (1975) described a tegument in the 'mouth region and buccal cavity' that is structurally similar to that of the body surface. However, the tegument of the buccal cavity, including that of the buccal suckers, is thinner than in the mouth, with numerous insertions of the thick basal lamina. The tegument of the suckers furthermore has a dense, subsurface layer and a surface plasma membrane 'bearing parallel rows of small bristles or spines'. These spines are not similar to the lamellae of the tegument in *P. multae*. In *Gotocotyla secunda*, tegument with long lamellae, some with swollen endings distinctly different from those of *P. multae* was seen (Rohde 1979), but complete or almost complete series of sections were not examined, and a detailed comparison is therefore not possible. In *Polylabroides australis*, mouth cavity and suckers are lined by normal surface tegument (Rohde and Watson 1995).

Thickening of the surface layer of the tegument around parts of the suckers, the so-called 'rim', was seen in *P. australis* (Rohde and Watson 1995) and *Z. seriolae* (Rohde 1981). It is absent in *P. multae*.

A 'valve apparatus', specialized structures near the anterior part of the pharynx, apparently regulating the uptake of material by the pharynx, has been described so far only in *P. australis* (Rohde and Watson 1995). It is absent in *P. multae*. In the buccal suckers of *P. australis*, Rohde and Watson (1995) illustrated thick cytoplasmic bands containing lipid vacuoles between the radial muscle fibres. In contrast, the suckers of *P. multae* are much more muscular and conspicuous cytoplasmic bands are absent. However, the bulk of the densely packed muscle filaments, running in a more or less anterior-posterior direction, is traversed by some thin bands of connective tissue containing some muscle fibres, running in a dorso-ventral or transverse direction. These bands appear to correspond to the so-called 'ducts', seen by Rohde (1979) in serial paraffin sections and arranged in a characteristic, regular way.

Information available to date clearly shows that related polyopisthocotylean Monogenea, all blood feeders (indicated by the presence of blood pigment in the digestive tract), differ markedly in the structure of the mouth cavity and buccal suckers. Apparently, different species have adapted to life in similar (gill) habitats in different ways.

Ultrastructure of the taste organ and sensory receptors

Detailed ultrastructural studies of sensory receptors and the 'taste organ' have been made only for two species, *Polylabroides australis* and *Pricea multae*. In the former species, Rohde and Watson (1995) described altogether nine types of receptors in the anterior end of the body, compared with only four in the latter. Multiciliate receptors, resembling each other in their short cilia not projecting above the tegument and (usually) found in tegumental pits, are present in both species. Uniciliate receptors are also found in both species, but a greater variety occurs in *P. australis*. A large non-ciliate receptor, found in a 'receptor complex' also containing uniciliate receptors, and adjacent multiciliate receptors, are characteristic of both species. However, the large non-ciliate receptor of *Polylabroides* contains, in addition to electron-dense collars and some cross-striated rootlets, a dense bundle of parallel fibres crossed by thick electron-dense bands. Furthermore, the shape of the receptor differs markedly from that of *P. multae*.

Glandular ducts open near the receptor complexes in both species. However, in *Pricea* the tegument near the glandular openings has short irregular lamellae, whereas in *Polylabroides* a small region around the glandular openings is covered by a tegument resembling type 3 tegument of *Pricea*, with long lamellae (Rohde and Watson 1995).

In the two sets of serial longitudinal semithin sections of *P. multae* examined, the taste organ was located at the anterior end of the body, in a deep, posteriorly-directed invagination of the tegument that turns back on itself. In the only set of semi-serial ultrathin sections examined, the taste organ was in a deep dorsal invagination of the tegument arising from the anterior part of the mouth cavity. This indicates that the anterior end can be retracted into the mouth cavity, or at least that it can be bent and distorted so strongly that the taste organ appears to lie in a cavity continuous with the mouth cavity. It may be protruded in order to bring it and the taste organ into contact with the tissue (gill filament). In the lack of experimental evidence, we can only speculate on the function of the "taste organ". That it is indeed a sense organ is indicated by the large number of receptors of several types, and by its sieve-like structure, which increases the surface area of the organ. The glandular ducts opening between the receptors contain a secretion likely to be histolytic, dissolving surface tissue of the gill filaments to facilitate 'tasting' of blood. The numerous muscle filaments around the inner end of the taste organ may either contribute to sucking in the blood to be tasted, or press the sensory receptors and the glandular openings in the taste organ closer to the surface during 'tasting'.

Ultrastructure of the pharynx

Dense surface lamellae of the cytoplasm lining the anterior part of the pharyngeal lumen, similar to those found in *Pricea multae*, were also seen in *Polylabroides australis* (Rohde and Watson 1995). Symmetrically arranged non-ciliate receptors with a basal body and electron-dense collars are present in both species and may play a role in regulating food intake into the pharynx, although experimental evidence is lacking.

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Abbreviations. b – basal lamina; bb – basal body; br – brain; bs – buccal sucker; c – cilium; cm – inner circular muscle fibre; cs – copulatory spine; e – electron – dense collar; f – muscle filament; g – glandular secretion; int – intestine; j – septate junction; m – mitochondrion; mc – mouth cavity; me – metraterm; mo – mouth opening; n – neurovesicles; p – prepharyngeal cavity; ph – pharynx; pp – prepharynx; rc – receptor complex; s – septum; sv – seminal vesicle; to – "taste organ"; v – ventral extension of mouth cavity; vs – vaginal spine; x – filamentous bundle extending from between muscle filaments of sucker into parenchyma; ♂ – male gonopore; ♀ – vaginal opening.

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