The epidermis of *Phoronis psammophila* Cori (Phoronida, Lophophorata): an ultrastructural and histochemical study

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The principal cell types of the trunk epidermis of *Phoronis psammophila* are categorized and described on the basis of their ultrastructural and histochemical properties. There are seven cell types: uniciliated supporting cells with a well-developed microvillar layer, fine-granule-containing cells with distinctive finger-like processes that contain vesicles and extend into the microvillar layer, and five types of generalized gland cells distinguished mainly by the fine structure of their secretory granules. Gland cells lack cilia but possess intact basal body complexes within the cytoplasm in close association with the Golgi complex. This is an unusual feature for gland cells, and suggests that they may have recently evolved from more typical ciliated epithelial cells. The secretory product of the gland cells contains either acidic mucopolysaccharides, which are mostly sulfated, or neutral mucopolysaccharides and protein. The possible functions of these cell types are discussed. The supporting cells are presumably involved in direct uptake of nutrients and (or) the protection and cleaning of the epidermis. The fine-granule-containing cells may help the animal adhere to the tube, whereas the gland cells probably function in the secretion of the tube.

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L'épiderme du tronc de *Phoronis psammophila* est composé de sept types cellulaires, décrits d'après leurs caractéristiques ultrastructurales et histochimiques : cellules de soutien monociliées à microvillosités bien développées, cellules à granules fins, à digitations dans la bordure en brosse, et cinq types de cellules glandulaires distinctes surtout par la microstructure de leurs granules sécréteurs. Malgré l'absence d'un cil externe, les cellules glandulaires possèdent des structures ciliaires basales en étroite relation avec l'appareil de Golgi. Ces structures, rares dans les cellules glandulaires, permettent de croire à l'évolution récente de ces cellules à partir de cellules épithéliales monociliées typiques. Les sécrétions sont soit des mucopolysaccharides acides, de type sulfaté, soit des mucopolysaccharides neutres associés à des protéines. Les fonctions possibles des différents types cellulaires sont examinées. Les cellules de soutien interviennent probablement dans l'absorption directe des nutriments ainsi que dans la protection et le nettoyage de l'épiderme; les cellules à granules fins semblent faciliter l'adhésion de l'animal (en position normale) à son tube; les cellules glandulaires semblent principalement responsables de la formation et de l'entretien du tube.

Introduction

The Phoronida are tubicolous and free living within their tubes. The tube of *Phoronis psammophila* Cori is composed of sand grains and various particles aggregated by epidermal secretions. The epidermis of phoronids is a simple epithelium, the cells of which are taller in the trunk region of the body than in the ampulla and tentacles. The epidermal cells contain a brush border of microvilli (Emig 1971) and rest upon a basement membrane. A basiepithelial nerve plexus occurs among the epidermal cells. Several types of epidermal cells, including gland cells which are mainly involved in tube secretion, have been previously identified, using light microscopy, in the body wall of the same species (see Pourreau 1979; Emig 1982).

This paper is the first ultrastructural investigation of a phoronid epidermis to provide a detailed description of the various cell types and their distribution along the body wall. The ultrastructure and histochemistry are discussed with reference to previous observations on the behavior and natural history of phoronids.

Material and methods

Adult *Phoronis psammophila* were collected along the Spanish Atlantic coast, in the intertidal zone of the Meira beach, Ría de Vigo, in northeastern Spain.

The specimens were fixed in 4% glutaraldehyde buffered with 0.1 M cacodylate (pH 7.4) and postfixed in 1% osmium tetroxide in seawater. Pieces of tissue were then dehydrated in acetone, stained en bloc with 2% uranyl acetate during dehydration, and embedded in Araldite via propylene oxide. The blocks were sectioned with an LKB III ultramicrotome. After staining in lead citrate, the sections were viewed and photographed using a Philips EM 201 electron microscope.

For histochemical tests, the specimens were embedded in paraffin wax after fixation in neutral buffered formalin or Bouin's fluid. The blocks were sectioned at 5–7 μm. The following histochemical techniques were used (for details see Lison 1960; Pearse 1968; Gabe 1968): for mucopolysaccharides: periodic acid – Schiff (PAS); Alcian Blue 8GX (AB) at pH 2.5 and 1.5; AB–PAS; Toluidine Blue (TB) at pH 4.2–1.5. For chemical conversion the techniques of methylation and sequential methylation–saponification (KOH) were used. The enzyme was hyaluronidase (from ovine testes; Sigma); for proteins: the tetrazo reaction, with or without previous treatment by dinitrofluorobenzene (DNFB), performic oxidation, benzoylation, and deamination.

Results

The epidermis of *Phoronis psammophila* consists of several cell types: supporting cells, fine-granule-containing (FG) cells, and at least five types of gland cells (Figs. 1, 2). The epidermal cells are joined to one another by zonulae adhaerentes near the apical surface and by septate junctions below. Interdigitations of the lateral cell membranes also occur.

Numerous basiepithelial nerve cell processes containing both clear and dense-core vesicles lie directly above the basement membrane. The single giant nerve fiber lies in the epidermis on the left side of the trunk in *P. psammophila* (Fig. 3A). The fiber is surrounded by a myelin-like sheath consisting of spirally arranged and irregularly spaced lamellae (Fig. 3B).

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Neighboring cells, possibly glial cells, appear to form an additional sheath. In transverse section the lamellae exhibit a pattern of major and minor bands like that of vertebrate myelin.

Supporting cells

The term supporting cell is used here for epidermal cells that are specialized as neither gland cells nor FG cells.

The supporting cells have a well-developed brush border of regularly spaced microvilli covered by a moderately electron-dense mucoid glycocalyx. The glycocalyx is composed of filaments oriented parallel to the epidermal surface, where they pass among the microvilli, and perpendicular to it over the brush border (Figs. 1, 2, 4). Long bundles of filaments inside the microvilli extend deep within the cell. Numerous pinocytotic invaginations are present among the bases of the microvilli and appear to be forming coated vesicles. Pinocytotic vesicles also occur at some distance from the apical plasma membrane in close association with multivesicular bodies.

Supporting cells bear a single centrally located cilium (Figs. 4, 5), with the usual 9 × 2 + 2 pattern of microtubules, a diplosomal basal body (i.e., with both a proximal and a distal centriole), and two striated rootlets. The largest rootlet is directed basally and the secondary rootlet extends parallel to the cell surface. Apical to the nucleus (Figs. 1, 2), spherical membrane-bound granules (about 0.5 μm) with homogeneous electron-dense material occur in association with the Golgi apparatus, which in turn lies near the basal complex of the cilium. Other organelles, e.g., free ribosomes, rough endoplasmic reticulum (RER), and mitochondria with a dense matrix, are also present (Figs. 4, 5). Cells extruding large amounts of cytoplasmic material and granules have been observed, but these may be abnormal or dying cells (Fig. 6).

Large bundles of longitudinally oriented filaments occur in the basal region of the supporting cells. They are attached by hemidesmosome-like junctions to the basal cell membrane, which in turn lies directly above the relatively thick collagenous basal lamina (Fig. 7).

Fine-granule-containing cells

The elongated FG cells increase in number from the anterior (upper) trunk region down to the ampulla where they are abundant (Figs. 1, 2, 8). Each cell bears a single cilium with a diplosomal basal body and a striated rootlet (Fig. 9). The cytoplasm is nearly filled with small ovoid granules (0.3 × 0.1 μm on average) that contain electron-dense material. The FG cells are expanded apically, with a variable number of lobular, finger-like processes that extend beyond the epidermal surface but below the tips of the microvilli (Figs. 8, 9, 14). These apical extensions are filled with the same ovoid electron-dense granules as the rest of the cell and each is encircled by a collar of microvilli belonging to the neighboring supporting cells (Figs. 10, 14). Other cell organelles, i.e., free ribosomes, RER, mitochondria, and an apical Golgi complex, are also present. The nucleus, which is ovoid and elongated, is located in the basal third of the cell and contains abundant heterochromatin.

Gland cells

Gland cells are interspersed among the supporting cells. Each cell has an apical concavity lined by very short microvilli. The nucleus and most of the cytoplasmic organelles are located in the basal region of the cell. Ciliary basal structures association with the Golgi complex are present, although a ciliary axoneme is lacking.

On the basis of the histochemical data, the gland cells are divided into two main classes: acidic mucus (AM) cells and non-acidic mucus (NAM) cells. Based mainly on the fine structure of their secretory granules, a total of five cell types can be identified: AM1, AM2, NAM1, NAM2, and NAM3 cells (Table 1).

Acidic mucus cells

AM cells secrete acidic mucopolysaccharides. This is shown by their strong metachromatic response with TB at pH 4.5 and an intense alcianophilia with AB at pH 2.5. The resistance of the metachromasia to dehydration and its retention below pH 3 indicate that the acidic mucopolysaccharide is sulfated. This hypothesis is supported by an observed alcianophilia at pH 1.5, by the susceptibility of the TB metachromasia to methylation, and by the fact that a weak metachromasia is restored upon subsequent saponification. The weakness of this reaction suggests the presence of carboxyl groups.

Secretory granules were PAS negative and sometimes weakly stained, and the response to the combined AB–PAS technique indicated that the acidic mucosubstance predominates, i.e., the granules are strongly alcianophilic. However, a blue–purple color, suggesting the presence of a neutral mucosubstance, appeared occasionally.

Hyaluronidase, applied for 4–26 h at 37°C prior to AB treatment, did not abolish the response to AB, so the positive histochemical results to testing for acidic mucosubstances are not due to the presence of hyaluronic acid.

All tests for protein were negative.

The AM1 cell type: AM1 cells constitute the most abundant gland cell type in the anterior trunk epidermis (Table 1). They are filled with low to moderately electron-dense, membrane-bounded secretory granules (0.6–1 μm in diameter) (Fig. 11). The contents have a finely fibrillar substructure with randomly arranged darker strands, giving the granules a mottled appearance (Fig. 12). Maturing cells have an RER system containing moderately electron-dense material and a prominent, cup-shaped Golgi complex. Numerous small vesicles and condensing vacuoles enclosing fibrillar material occur near the mature face and lateral edges of the Golgi cisternae (Figs. 11, 12).

The AM2 cell type: AM2 cells, scattered mainly in the median and posterior trunk regions (Table 1), contain rounded to polygonal secretory granules (ca. 0.8 μm in diameter) of moderate electron density and homogeneous appearance. Some granules, however, exhibit a mottled substructure. The well-developed Golgi complex is apical and lateral in position (Figs. 1, 2, 13, 15, 17, 21). Micrographs showing the extrusion of the secretory product suggest an apocrine mechanism (Fig. 16).

Non-acidic mucus cells

The results of tests for acidic mucopolisaccharides were all negative in NAM cells, but the presence of neutral mucopolysaccharides is indicated by the positive reaction obtained with the PAS test. The number of positive cells and the degree of response were not uniform. Positive results for proteins were obtained using the tetrazo reaction, and the presence of tyrosine and tryptophan was detected by previous chemical conversion with DNFB and performic acid. The absence of histidine is supported by the negative results of the benzoylation–tetrazo reaction.

The NAM1 cell type: NAM1 cells (Fig. 1) are more numerous in the middle and posterior regions of the trunk (Table 1). They are completely filled with secretory granules (about 1.5–2 μm in diameter), which are spherical, or polyhedric as a

TABLE 1. Distribution of the gland cells and fine-granule-containing cells along the trunk epidermis of *Phoronis psammophila*

Cells	Anterior	Middle		Posterior		Ampulla*
AM1	++++	+++	++	0	++	++
AM2	0	0	+++	+++	+++	0
NAM1	++	+++	+++	++	++	+++
NAM2	0	+	++	++	++	++
NAM3	+	++	+++	+++	+++	+++
FG	+	+	++	++	++	+++

*Excludes the posterior part of the ampulla where mostly supporting cells occur.

result of compression. The granules have either a single large dark core or several smaller ones distributed throughout a homogeneous paler matrix (Fig. 17). Both the matrix and the cores show a paracrystalline substructure (Fig. 18). NAM1 cells contain numerous free ribosomes, mitochondria, a well-developed RER with swollen cisternae, but a poorly developed Golgi complex. Extrusion of the secretory product appears to be apocrine.

The NAM2 cell type: NAM2 cells (Fig. 1) increase in number toward the posterior trunk region (Table 1). They contain generally ellipsoidal secretory granules (2 × 1 μm) whose contents have a distinct, banded substructure (Fig. 19, 20). Immature granules contain filamentous bundles of moderate electron density (Fig. 20). NAM2 cells contain numerous free ribosomes and highly dilated RER cisternae enclosing a moderately electron-dense material. The Golgi saccules appear to be closely associated with the RER.

The NAM3 cell type: NAM3 cells are numerous from the middle trunk region to the ampulla (Table 1). The secretory granules are characterized by a homogeneous and highly electron-dense material. They become larger toward the apex of the cell and subsequently coalesce to form a large secretory mass within the cell (Figs. 1, 2, 21). The extrusion process apparently proceeds by an apocrine mechanism (Fig. 22). Following the extrusion NAM3 cells sometimes exhibit a dense cytoplasm, which may indicate cellular morbidity.

Discussion

The epidermis of *Phoronis psammophila* contains a variety of specialized cell types. Only the supporting cells and fine-granule-containing cells bear cilia, although in all gland cells, intact ciliary basal complexes occur, usually associated with the Golgi apparatus. These basal complexes could be remnants of the primitive ciliated epithelial cells from which the gland cells are supposed to have evolved. The hypothesis that the gland cells originate from supporting ciliated cells has been suggested for other marine invertebrates (e.g., enteropneusts, see Atamanova 1978; Pardos and Benito 1989). Throughout the epidermis, the cilia have the classical 9 × 2 + 2 pattern of microtubules. They probably have at least two important functions: (*i*) cleaning the surface of the epidermis and the space between it and the tube, using a ciliary–mucoid mechanism of removing waste (e.g., the material extruded by the supporting cells); and (*ii*) producing a continuous water flow within the tube (Emig 1982) for gas and nutrient exchange, which would also help in waste removal.

The well-developed brush border of microvilli with the associated glycocalyx coat may have several functions, including increasing the epithelial surface for direct uptake of dissolved organic substances through the epidermis (Emig and Thouveny 1976), and functioning in respiratory gas exchange, as has recently been found for the lophophoral brush border in the same species (Pardos *et al.* 1991). The bundles of filaments inside the microvilli undoubtedly function as a cytoskeleton to maintain the structural integrity of the brush border.

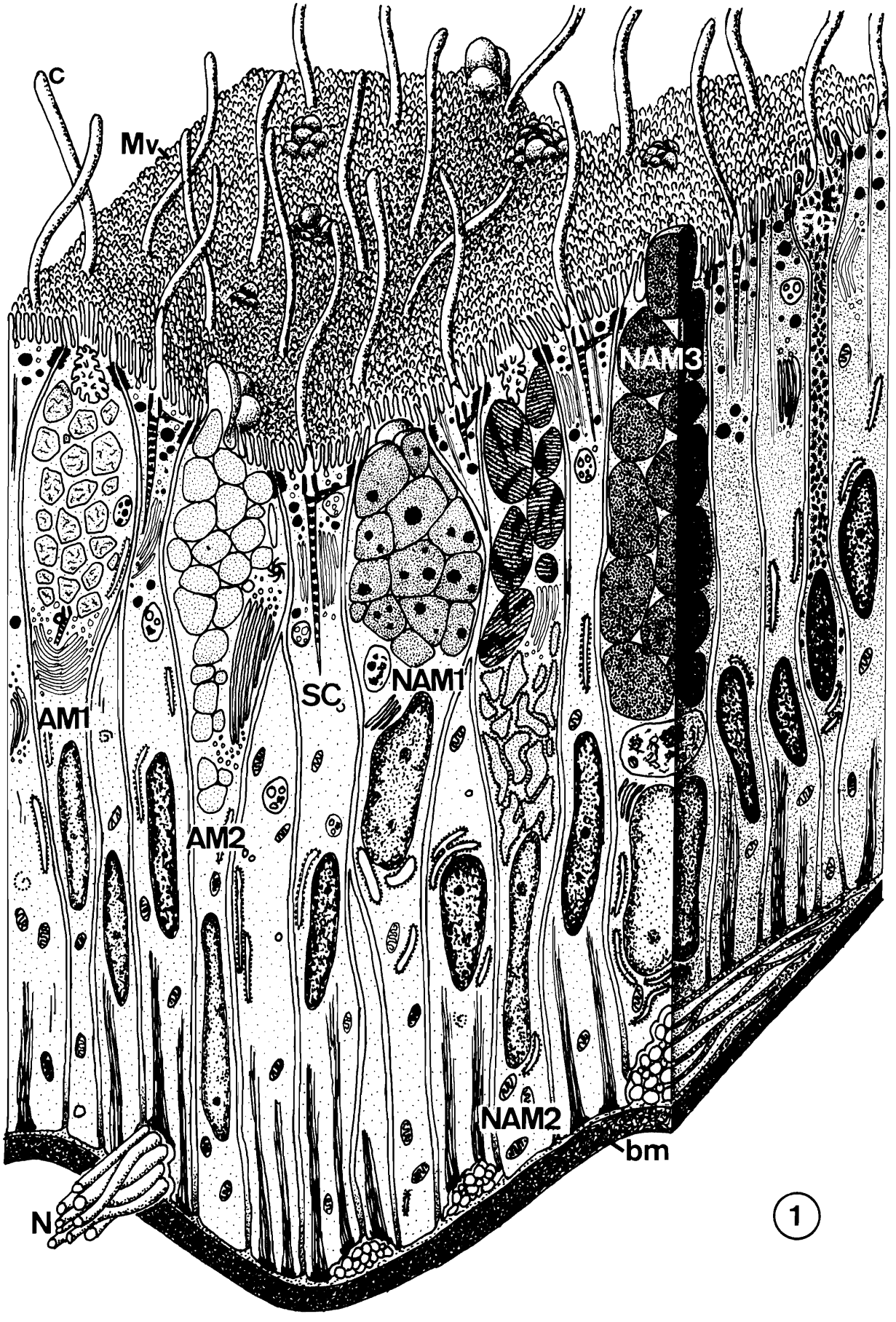
The glycocalyx is generally covered by a mucoid coat histochemically resembling the secretory content of AM cells. The secretory product of these cells is an acidic mucopolysaccharide which is predominantly sulfated, with a few carboxylated groups and neutral mucopolysaccharides. Ultrastructurally, cells containing granules that are intermediate between those found in AM1 and AM2 cells have sometimes been observed. This suggests that these two cell types may be different developmental stages of a single gland cell type. This is further supported by the variable response of their secretion to histochemical tests. We suggest that the AM cells may be involved in lubricating the trunk and thus minimizing abrasion when the animal is moving in its tube. The absence of protein and hyaluronic acid suggests that the secretory product has a low viscosity, which could facilitate the formation of a film for gaseous exchange. AM cells correspond to the B-cell type described by Pourreau (1979). Histological tests have suggested that these cells secrete the thick central coating layer of the tube (Pourreau 1979; Emig 1982).

ABBREVIATIONS: AM1 and AM2, acidic mucopolysaccharide cell types 1 and 2, respectively; Bc, basal complex; *bm*, basement membrane; *c*, cilium; *co*, dense core in secretory granules; F, fingerlike extensions of the fine-granule-containing (FG) cells; G, Golgi complex; GF, giant nerve fiber; Gl, glycocalix; Ms, myelin sheath; Mv, microvilli; N, nerve fibers; NAM1, NAM2, and NAM3, non-acidic mucopolysaccharide cell types 1, 2, and 3, respectively; R, rough endoplasmic reticulum; SC, supporting cell; SG, secretory granule.

FIG. 1. Diagram of the epidermis of *Phoronis psammophila.*

FIG. 2. General view of a longitudinal section of the epidermis of *Phoronis psammophila*, showing several AM2, NAM3, and FG cells, and one NAM1 cell, among the supporting cells. Scale bar = 3 μm. FIG. 3A. Cross section of the giant nerve fiber. Scale bar = 2 μm. FIG. 3B. Detail of the myelin sheath, showing its irregular packing. Scale bar = 0.1 μm. FIG. 4. Apical region of a supporting cell; note the single cilium, the brush border of microvilli, and the associated glycocalyx. Scale bar = 1 μm. FIG. 5. Golgi complex associated with the ciliary basal structures in a supporting cell. Scale bar = 1 μm.

FIG. 6. Extrusion of cytoplasmic material and granules from a supporting cell (arrow). Scale bar = 1 μm. FIG. 7. Bundles of longitudinal filaments in the basal region of a supporting cell, showing their hemidesmosome-like structures with the basement membrane (arrow). Scale bar = 1 μm. FIG. 8. Elongated FG cell filled with small ovoid electron-dense granules. Scale bar = 2 μm. FIG. 9. Apical part of an FG cell, showing the single cilium and finger-like extensions filled with granules. Scale bar = 1 μm. FIG. 10. Cross section at the level of the brush border, showing the arrangement of the finger-like extensions of an FG cell encircled by the microvilli of the neighboring supporting cells (see Fig. 14). Scale bar = 1 μm. FIG. 11. AM1 cell filled with secretory granules of varying shape and electron density. Scale bar = 2 μm. FIG. 12. Detail from Fig. 11, showing the fine fibrillar substructure with darker strands in the secretory granules and the highly developed Golgi complex. Scale bar = 1 μm. FIG. 13. An AM1 cell. Scale bar = 1 μm.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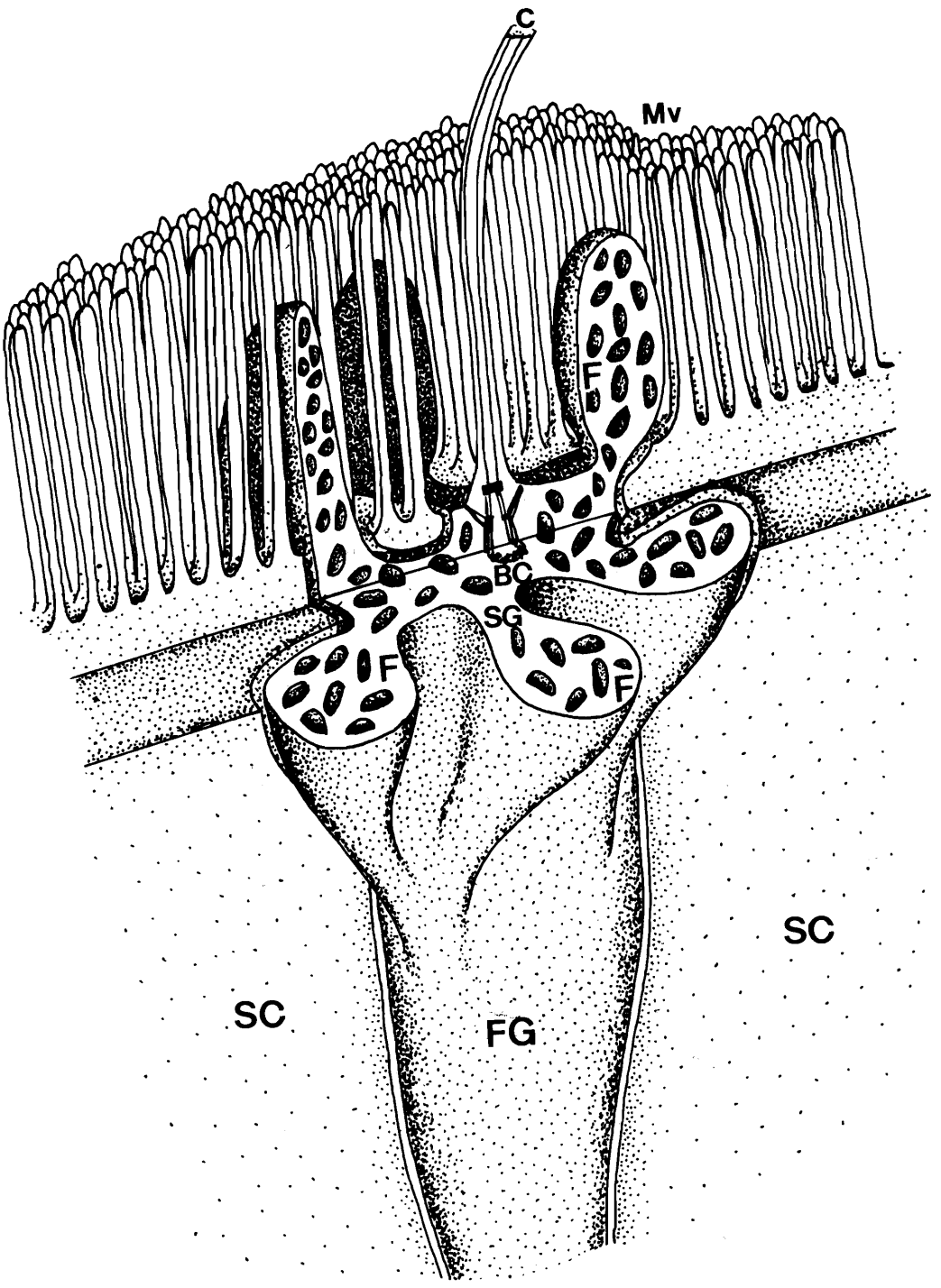
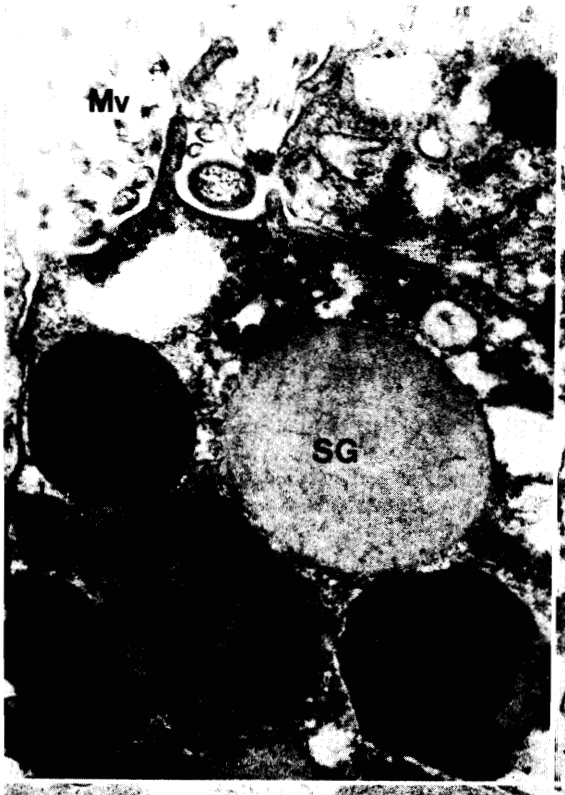


FIG. 14. Diagram of an FG cell.

FIG. 15. Secretory granules in an AM2 cell; note their mottled structure. Scale bar = 0.5 μm. FIG. 16. Extrusion of the secretory products of an AM2 cell (arrow). Scale bar = 1 μm. FIG. 17. An NAM1 cell; the polyhedric secretory granules have single or multiple dark cores. Scale bar = 2 μm. FIG. 18. Detail of two secretory granules of an NAM1 cell, showing the paracrystalline patterns in the matrix and dense cores. Scale bar = 0.5 μm. FIG. 19. Ellipsoidal secretory granule of an NAM2 cell with a banded substructure. Scale bar = 0.5 μm. FIG. 20. Secretory granule production by an NAM2 cell. Note the presence of very dilated RER cisternae and secretory granules showing patches of high and low electron density as well as banding. The arrow points to filamentous bundles in an immature granule. Scale bar = 1 μm. FIG. 21. An NAM3 cell filled with homogeneous and highly electron-dense granules. In some cases these contain flocculent fibrillar material (arrow). Scale bar = 2 μm. FIG. 22. Extrusion of secretory material by means of an apocrine mechanism in an NAM3 cell. Scale bar = 0.5 μm.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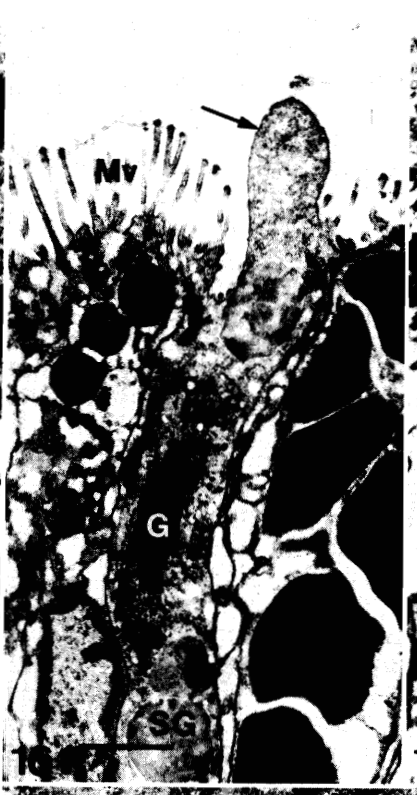
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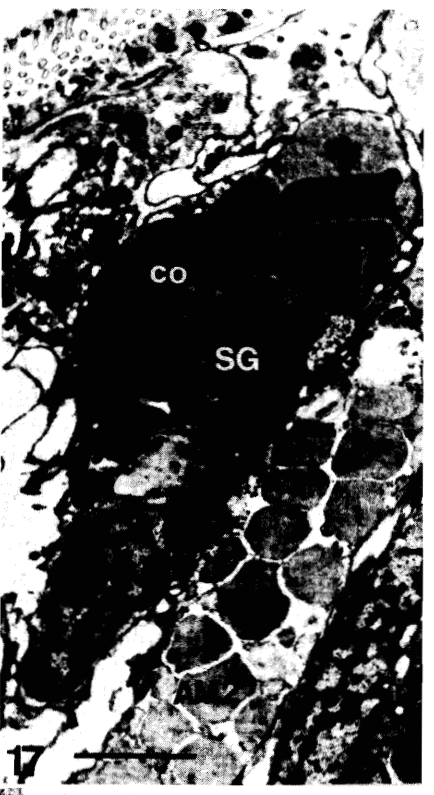
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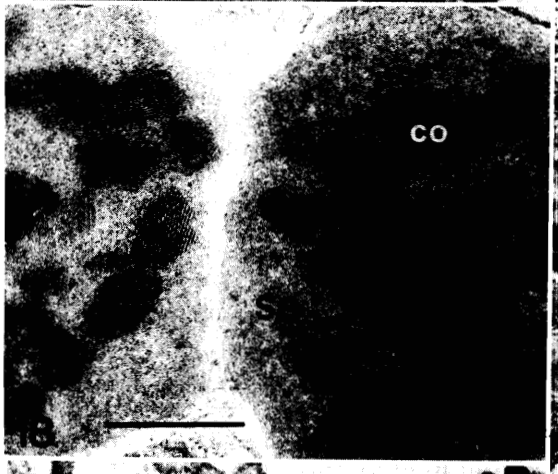
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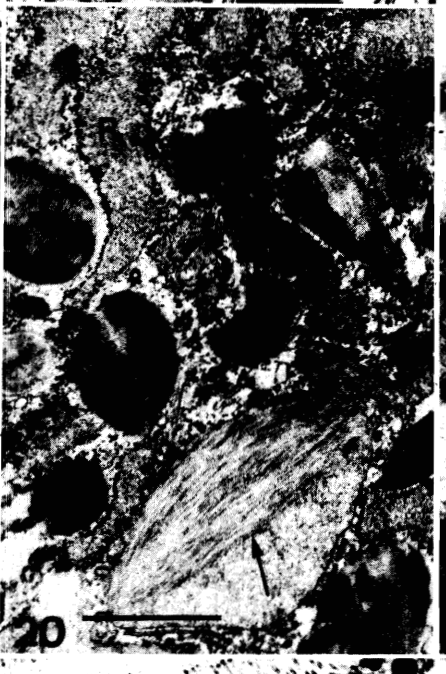
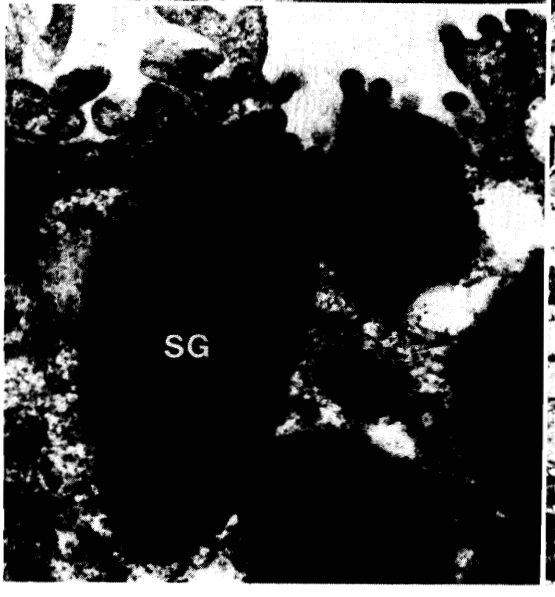



Mv
SG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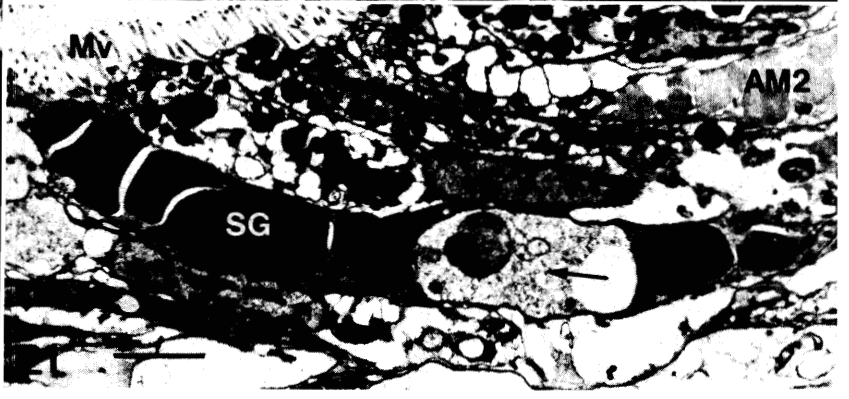
Mv
AM2
SG

NAM cell types have the cytological feature that characterizes glycoprotein-secreting cells: an extensive RER which is associated with the Golgi complex. The histochemical tests used in this study demonstrate the coexistence of neutral mucopolysaccharides and proteins containing tyrosine and tryptophan in all the NAM cell types. NAM1 and NAM2 cells show similar characteristics to the A and B′ cell types described by Pourreau (1979), and their distribution is similar to Pourreau's curve A. The NAM3 type corresponds to Pourreau's C-cells and the so-called corps-en-massue of Selys-Longchamps (1907), but these cells occur all along the trunk rather than being restricted to the base of the lophophore, as stated by both authors. Based on the structure of the tube (Pourreau 1979; Emig 1982), the NAM cell types are probably involved in forming the internal and external tube layer, which aggregates grains of sand and various types of detritus around the tube.

In ultrastructural features, the FG cells closely resemble the "viscid gland cells" of the duo-gland adhesive systems of turbellarians, gastrotrichs, and some archiannelids (Boaden 1968; Tyler 1976; Martin 1978; Reuter 1978), in that the microvilli of the neighboring supporting cells surround the finger-like projections of the FG cells in a collar-like fashion. Consequently, we suggest that the secretory material of the FG cells may help the animal adhere to its tube and thus minimize the muscular action needed to keep the phoronid extended in the tube.

A further remarkable feature of the integumentary epithelium is the well-developed subepidermal nerve plexus. It is most likely that the nerve fibers control the ciliary and perhaps the secretory activities of the epidermis. However, no sensory cells have been recorded in the trunk epidermis, probably because the trunk is isolated from the environment by the tube. Thus, stimuli are received through the sensory cells in the epidermis of the tentacles, which are in direct contact with the surrounding medium (Pardos *et al.* 1991).

The giant nerve fiber in *Phoronis psammophila* generates a powerful contraction of the longitudinal trunk musculature for a quick retraction of the animal into the tube (Silén 1954). Further studies are obviously needed to established the detailed construction and relationships of this giant nerve fiber.

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