Cytomorphology of the pedal aperture glands of *Mya arenaria* L. (Mollusca, Bivalvia)

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A glandular cushion, called the pedal aperture gland in this paper, lies adjacent and internal to each of the two mantle margins composing the pedal aperture of the soft-shelled clam *Mya arenaria*. Two types of glandular cells are found in the glands. The principal type (bacillary mucous cell) manufactures secretory vesicles that contain discrete protein-rich fibers in a matrix of glycoprotein. The second type (mucous goblet cell) produces sulfated and nonsulfated mucosubstances. The glands function in the formation of pseudofeces from particulate material, especially burrow sediments that enter the mantle cavity through the pedal aperture. Their possible phylogenetic relationship to similar glands in other bivalves is discussed briefly.

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Un coussin glandulaire, appelé glande de l'ouverture du pied dans cette article, s'étend à l'intérieur de chacune des deux bordures du manteau qui constituent l'ouverture du pied chez la mye *Mya arenaria*. Les glandes contiennent deux types de cellules glandulaires. Le type principal (cellules muqueuses bacillaires) produit des vésicules sécrétrices qui contiennent des fibres discontinues riches en protéines, dans une matrice de glycoprotéines. Le second type (cellules muqueuses caliciformes) produit des mucosubstances sulfatées et non sulfatées. Les glandes jouent un rôle dans la formation de pseudofèces à partir de matières particulaires, notamment des sédiments du terrier qui pénètrent dans la cavité du manteau par l'ouverture du pied. Les relations phylogénétiques possibles entre ces glandes et des glandes semblables trouvées chez d'autres bivalves sont examinées.

[Traduit par la revue]

Introduction

Mya arenaria Linnaeus, 1767, the common soft-shelled clam, is a deep burrower in muddy and sandy marine habitats and becomes essentially sessile as an adult (Trueman 1966). The latter habit is consonant with the adult having a reduced foot, long siphons, and the entire mantle margin fused except for the small pedal aperture (Trueman 1966). Glands associated with the pedal gape have been all but forgotten in recent reviews, although they appear to be a key adaptive feature in one or more lineages of burrowing bivalves (e.g., Morton 1984, 1985).

A variety of glandular structures located in the mantle cavity of an assortment of bivalve mollusks was described during the early proliferation of comparative anatomical work on bivalves (e.g., Pelseneer 1891, 1911). Vlès (1909, Fig. 7) first drew attention to a pair of "corps bruns" in *M. arenaria*, which he described as brownish glandular cushions lying along the internal surface of the anterior mantle margins that form the pedal aperture. According to Yonge (1947, 1951*a*, 1951*b*, 1951*c*), similar glands, which we consider to be probable homologues, are found in the Myacean families Myidae (e.g., *Cryptomya californica* (Conrad), *Platyodon cancellatus* (Conrad), and *Sphenia binghami* Turton) and Corbulidae (e.g., *Aloidis gibba* (Olivi)). Similarly positioned glands are known from other members of the order Myoida: the Gastrochaenacea (e.g., *Gastrochaena* Spengler (Morton 1982)), the Hiatellacea (e.g., *Hiatella* Daudin (Hunter 1949) and other genera (Yonge 1971)), and the Pholadacea (e.g., most of the Pholadidae (Purchon 1955; Morton 1986*a*)), but also from at least two more-distant relatives, *Calyptogena magnifica* Boss & Turner (Veneroida) (Morton 1986*b*) and *Clavagella australis* Sowerby (Anomalodesmata) (Morton 1984).

Cursory accounts of the histology of some of these glands were presented by Hunter (1949) and Morton (1985, 1986*a*, 1986*b*). Hunter (1949) and Yonge (1951*a*, 1951*b*, 1951*c*) considered the pedal aperture glands in the Hiatellaceans studied by them to be principal agents in consolidating pseudofeces in the mantle cavity. This function was inferred largely from the strategic location of these glands at the base of the ventral rejection tract. Vlès (1909) supposed that these structures might be sensory as well as glandular. The fine structure and histochemistry of the pedal aperture glands of *M. arenaria* are examined here to test these inferences.

Materials and methods

Mya arenaria were collected from spring through fall from an intertidal mudflat at the mouth of Northeast Creek on Mount Desert Island, Maine. They ranged from 2.5 to 6 cm in shell length and were maintained in running seawater for 2 or 3 days. The clams were dissected by cutting the anterior adductor, the mantle edge, and the siphons along the ventral midline. The anterior portion of each valve, including all of the pedal aperture gland, was immersed in one of several different fixatives for about 10 min. Then the mantle edge of the pedal aperture was separated from its shell and the gland was quickly cut out. This was placed into fresh fixative. For light microscopy and histochemistry, samples were fixed in Hollande's picri-formal-acetic solution (Humason 1979) or Halmi's (Gabe 1976), Helly's, or Zenker's solution (Humason 1979) and post-treated appropriately. The tissues were dehydrated through absolute ethanol, embedded in polyester wax (90/10) (Steedman 1960), and sectioned serially at 5 μm. Sections were mounted on albumenized slides and dried at room temperature for 24 h. Heidenhain's iron hematoxylin and Azan techniques were used in routine staining. Histochemical staining was with the periodic acid – Schiff (PAS) method and diastase control for glycogen (Humason 1979), alcian blue (AB) pH 1.0 and 2.5, AB pH 1.0 alcian yellow (AY) pH 2.5 (AB/AY) (Wendellaar Bonga 1970), alcian blue – critical electrolyte concentration (AB–CEC) (Pearse 1968), PAS/AB (Pearse 1968) procedures for mucosubstances, and the mercuric bromphenol blue (Pearse 1968) method for protein. Although Johannes and Klessen (1984) provide evidence that the sequence AB/PAS may provide more reliable results than the sequence PAS/AB, this is not critical in interpreting our results.

Samples for scanning electron microscopy (SEM) were rinsed

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vigorously in 7% $MgCl_2$ before fixation, to reduce the amount of residual surface mucus. For transmission electron microscopy (TEM) and SEM, samples were fixed in phosphate-buffered 2.5% glutaraldehyde (pH 7.5, 980 mosmol/kg H_2O) (Cloney and Florey 1968) for 4 h and postfixed for 2 h in phosphate-buffered 2% OsO_4. Samples were rinsed and dehydrated in graded steps of ethanol. For TEM, specimens were transferred to propylene oxide and embedded in Epon. Thin sections (70–90 nm) were cut on a diamond knife, collected on copper grids, stained with uranyl acetate and bismuth (Barrett *et al.* 1977), and examined at 60 kV with a Philips EM 400. Some samples for SEM were first embedded in Steedman's polyester wax and sectioned on a rotary microtome using razor blades until a desired position in the gland was reached. The block surface was then ultraplaned on a glass knife and the remaining block was de-embedded in absolute alcohol (Norenburg and Barrett 1987). Samples for SEM were critical-point dried in CO_2, lightly coated with silver, and examined with an AMR-1000A SEM at 20 or 30 kV.

Results

The pedal aperture glands lie in the mantle cavity along the two mantle edges forming the pedal aperture at the anterior of the clam (Fig. 1). Each gland is a pale, brownish cushion which is raised as much as 1.5 mm above the adjacent mantle epithelium (Fig. 3). It is lanceolate in shape (Fig. 2), being broadest dorsally where it extends onto the ventral surface of the anterior adductor muscle. It tapers and ends in a blunt point just ventrad to the pedal aperture. The surface is uniformly ciliated but a few widely dispersed collar cells are also present (Fig. 6).

In transverse section, the glandular epithelium appears pseudostratified (Figs. 4 and 5). There is a surface layer of short (about 15 μm), columnar, ciliated cells which are similar to those of the adjacent mantle epithelium. Among these cells are numerous necks of the two types of flask-shaped glandular cells that compose the bulk of the gland's mass. Numerous muscle fibers crisscross the gland (Figs. 4 and 5). Between the gland cells are cytoplasmic processes that contain electron-dense granules and resemble the gliointerstitial system described from the epidermis of other mollusks (Nicaise 1973) and a variety of other invertebrates.

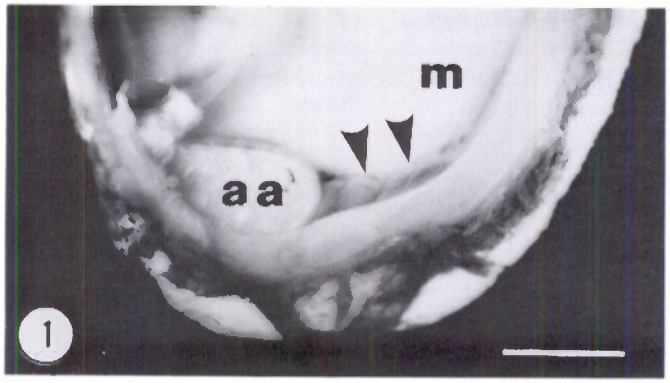
The gland is dominated by two types of secretory cells. We refer to one as the mucous goblet cell. It contains relatively amorphous (homogeneous), finely granular material in numerous spheroidal vesicles about 0.3–0.6 μm in diameter (Fig. 10). The mucus is easily extracted in aqueous fixatives, resulting in cells with an empty, goblet-like appearance. The second cell type is more numerous and contains discrete, refringent vesicles (Figs. 4 and 5) which are well preserved in most fixatives. We refer to this as a bacillary mucous cell, following the usage of Pierantoni (1908) and Norenburg (1985*a*) for cells with similar refringent secretory material. In the basal region of the gland, within the bacillary cells, are numerous large bodies containing heterogeneously stained granules and vesicles (Fig. 18). These bodies retain their natural brown color with most of the staining procedures used, and probably are the source of the gland's brown color. They appear to be degenerative bodies formed in recycling of glandular elements. Table 1 summarizes the principal histochemical characteristics of the two types of secretory material, the extracellular matrix (ECM), and the degenerative bodies.

The mucous goblet cell is also found in the adjacent mantle tissue. The "goblet" consists of numerous vesicles about 0.3–0.6 μm in diameter (Fig. 10). With the routine fixatives employed in this study, the vesicles are relatively electron-lucent, containing only a fine web of fibers. Although many of the vesicles appear to be coalescing, the observations of Ichikawa *et al.* (1982) indicate that this is probably a fixation artifact. The histochemical properties of the secretory vesicles are similar to, but more intense than, those of the surrounding ECM, except for the cyanophilous reaction in the Azan procedure. Thus, these vesicles stain positively for sulfated and nonsulfated mucosubstances.

The bacillary cells vastly outnumber the mucous goblet cells and may be considered to characterize the pedal aperture gland; their distribution appears to be restricted to the gland. This type of cell is characterized by its distinctive secretory product (Fig. 5) and extensive profiles of highly distended rough endoplasmic reticulum (ER) (Figs. 11–13). The bacillary vesicles are oblate spheroids in outline, about 2–3 μm along the major axis, and remain discrete entities until they reach the surface of the gland (Figs. 5 and 7–9). The histochemical properties of the vesicles suggest to us that they consist predominantly of nonsulfated mucosubstances (Table 1). Each vesicle consists of an electron-lucent core of finely granular material enclosed in a highly ordered array of electron-dense fibers (Fig. 5). Golgi profiles in these cells are relatively thick (Fig. 13). Other vesicles are found in addition to the abundant mature vesicles. They are considerably fewer and probably represent early phases in the production of the secretory material. Adjacent to the trans face of the Golgi apparatus are vesicles with finely granular content (Fig. 11). Some of these vesicles are slightly larger than the mature bacillary vesicles. Vesicles that have marginal, relatively electron-lucent fiber profiles are sometimes observed near a Golgi apparatus (Fig. 12). Maturing vesicles that have electron-dense fibers are frequently surrounded by the distended cisternae of rough ER (Figs. 12 and 13). The remainder of the maturing vesicle is often filled with granules that are more electron-dense and discrete but similar to the content of much of the adjacent rough ER. In a few vesicles these granules form a highly ordered reticular substructure (Fig. 14). In a given section, many mature vesicles contain a relatively dense, homogeneous distribution of granules, whereas others appear to have fewer, more dispersed granules (Fig. 14). In the latter, there is often some of the reticular structure described earlier. A single electron-dense body is frequently found within the granular core of these same vesicles (Fig. 16).

The fibers of mature bacillary vesicles apparently do not form a fully closed capsule (Fig. 9). Although the fibers are highly orientated with respect to their neighbors, the overall pattern of winding around the granular core is variable. Rarely, the fibers are dispersed as a loose tangle (Fig. 17). The latter are usually in the vicinity of degenerative bodies and may be headed for

FIGS. 1–5. *Mya arenaria*. Fig. 1. Right valve. Anterior adductor (*aa*), mantle (*m*), pedal aperture gland (arrowheads). Scale bar = 1 cm. Fig. 2. SEM of pedal aperture gland (*ag*) and lip (*l*) (= mantle edge) of right valve. Ventral is to the right, and anterior adductor is just off the left side. Scale bar = 1 mm. Fig. 3. SEM of transversely sectioned and de-embedded gland. *ag*, pedal aperture gland; *l*, lip; *m*, mantle. Arrow indicates epidermis. Scale bar = 1 mm. Fig. 4. Apical half of transversely sectioned gland (by light microscopy). Arrows indicate bacillary cell necks with secretory vesicles, arrowheads indicate muscle fibers. *bl*, basal lamina. Scale bar = 50 μm. Fig. 5. TEM of apical half of gland, showing epidermal cells and upper subepidermal bacillary cells. *bv*, bacillary packets; *, large cisternae of rough ER; *m*, muscle fiber. Scale bar = 10 μm.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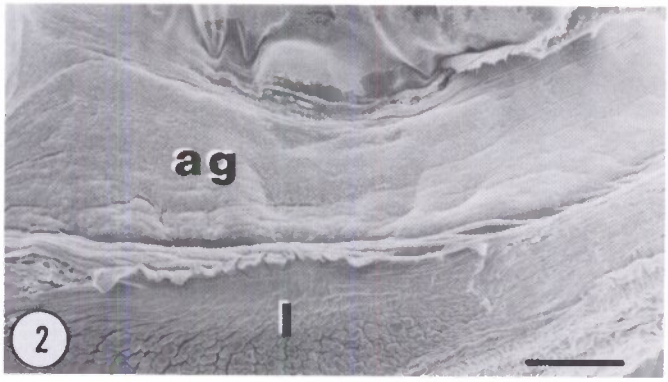
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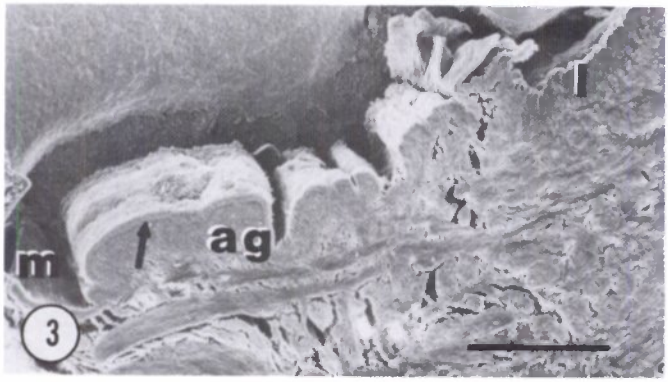
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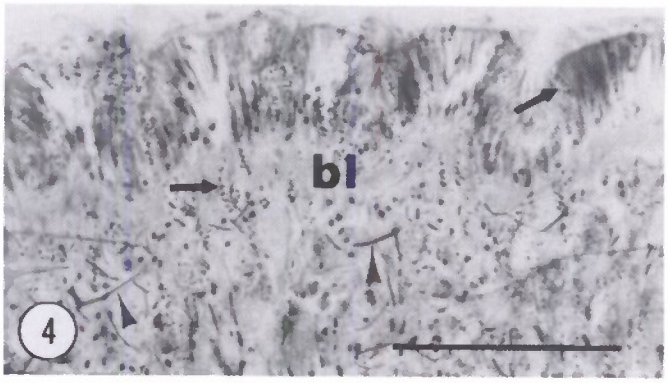
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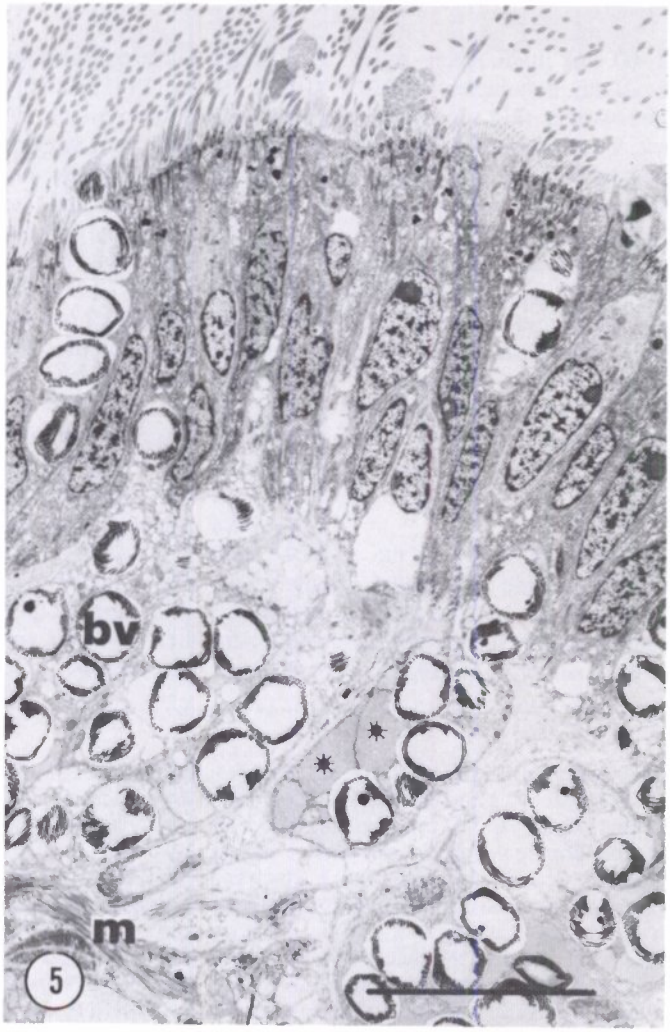
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TABLE 1. Select histochemistry of the pedal aperture gland

	Mucous "goblet"	Bacillary vesicles	Extracellular matrix	Degenerative bodies
Alcian blue (AB)				
pH 2.5	+ + +	+	+ +	*
pH 1.0	+ +	+	+	*
Alcian yellow (AY), pH 2.5	+ + +	+	+	*
AB pH 1.0/AY pH 2.5				
Blue	+ +	−	+	*
Yellow	−	+	−	*
Alcian blue CEC				
0.1 M $MgCl_2$	+ +	+	+ +	+
0.2 M $MgCl_2$	+	+	+	*
0.5 M $MgCl_2$	+	−	+	*
0.6 M $MgCl_2$	+	−	+	*
0.8 M $MgCl_2$	+/−	−	+	*
1.0 M $MgCl_2$		−	−	*
Periodic acid – Schiff	+ +	+ +	+	+ + − +
PAS diastase	+ +	+ + +	+	+ + − +
PAS/AB	Pink	Magenta	Pink	Red
Mercuric bromphenol blue	Yellow	Blue	Yellow	*
	+ + −	+	+	
Azan	Blue	Blue	Blue	*
	+ /	+ +	+ + +	
Hematoxylin	Brown	Blue	Brown	*

NOTE: CEC, critical electrolyte concentration.
*Brown but unstained

recycling. Each fiber is about 55–60 nm in diameter and contains an electron-lucent core, 15–20 nm in diameter, about which two electron-dense strands are wound (Fig. 15). The strands are approximately 10 nm thick, wound in a double helix at about 30° of pitch, and separated by less electron-dense material (Fig. 16). In a transverse section of a fiber these strands often are cut tangentially, which makes them appear as two dense smudges (Fig. 15). Geometric analysis and the appearance of crossed strands in fibers cut longitudinally (Fig. 16) confirms the presence of two strands. Optical examination of the mercuric bromphenol blue reaction demonstrates that the matrix of the granules is yellowish to olive in color, and a blue region can be observed within it, i.e., the fibers of the granules stain positively for protein, as do adjacent muscle fibers.

Discussion

Historical background

Kellogg (1915) demonstrated that waste particles on the mantle surface are carried to vortices on either side of the pedal aperture and from there pass along the mantle fusion to the base of the inhalant siphon. Although the pedal aperture glands of *M. arenaria* and *Platyodon cancellatus* were shown in Kellogg's (1915) figures, he made no reference to them in the text. Yonge (1923, 1951*a*, 1951*b*, 1951*c*), Hunter (1949), and Purchon (1955) noted that ciliary currents at the pedal aperture are directed inward. They suggested that the pedal aperture glands are part of the mechanism for eliminating pseudofeces. Morton (1985, 1986*a*) speculated that the pholad "pedal gape glands" contribute chemically in burrow formation.

Hunter (1949) found distinct pedal aperture glands in boring adults of *Hiatella gallicana* and *H. arctica*, but only a few subepithelial glandular cells in the vicinity of the pedal aperture in nonboring individuals. *Hiatella* bores by mechanical abrasion; the abraded material is removed from the burrow via the mantle cavity. Hunter (1949) concluded that the glands develop by hypertrophy as a response to continual contact with irritant material. He described the glandular cells of nonboring individuals as "goblet-shaped with granular contents," about 20 times the volume of an epithelial cell, and having "approximately the same staining reactions as typical mucous cells," whereas the glandular cells of boring individuals extend "under almost all the mantle epithelium round the pedal opening" and "are each about a hundred times the volume of an epithelial cell." These cells were described as goblet-shaped, opening to the mantle

FIGS. 6–18. *Mya arenaria*. Fig. 6. SEM of apical surface of collar cell. Scale bar = 5 μm. Fig. 7. SEM of bacillary secretion on surface of gland, showing uncoiled bacillary fibers (arrow). Scale bar = 5 μm. Figs. 8 and 9. SEM of bacillary packets in cell neck, showing discoid shape, irregular (arrowhead) and incomplete wrapping by fibers. Scale bars = 2 μm. Fig. 10. TEM of mucous goblet. Scale bar = 5 μm. Figs. 11–18. TEM of some bacillary cells. Fig. 11. Golgi apparatus with forming vesicle (*) at trans face and maturing vesicles (*bv*) laterally. Scale bar = 2 μm. Fig. 12. Maturing vesicles (*bv*) surrounded by rough ER. Scale bar = 5 μm. Fig. 13. Thick Golgi profiles (*g*) and forming vesicles (*). Scale bar = 5 μm. Fig. 14. Maturing granules among rough ER (*er*). Note the different forms of granulation in vesicles (arrows). Vesicles at upper right and lower left show remnants of reticular organization of granules. Scale bar = 2 μm. Fig. 15. Cross-sectional profiles of fibers, each with two dense regions (arrowheads), the helical threads. Scale bar = 0.1 μm. Fig. 16. Mature vesicle with central electron-dense core. Crossings of helical strands can be observed in some of the dense medial sections of fibers (arrowheads). Scale bar = 1 μm. Fig. 17. Vesicle with irregular tangle of fibers, apparently undergoing autolysis. Scale bar = 1 μm. Fig. 18. Degenerative bodies with bacillary vesicles in various stages of re-absorption. Scale bar = 5 μm.


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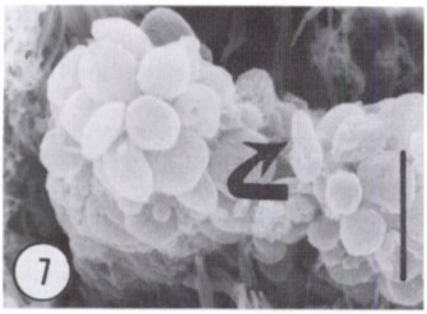
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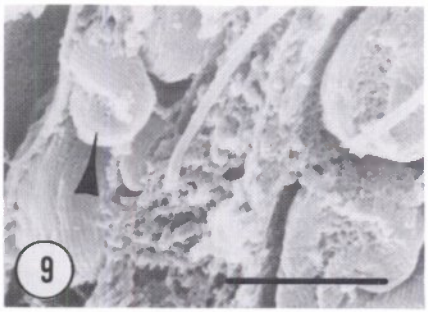
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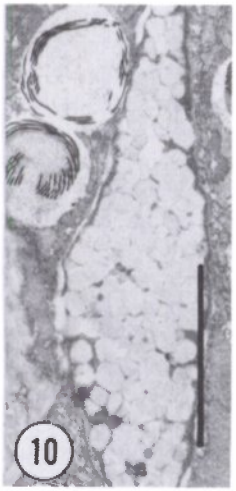
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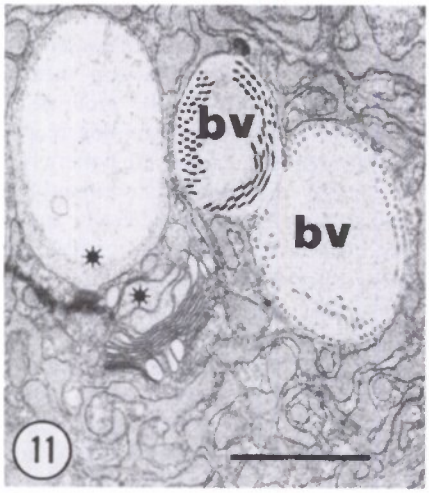
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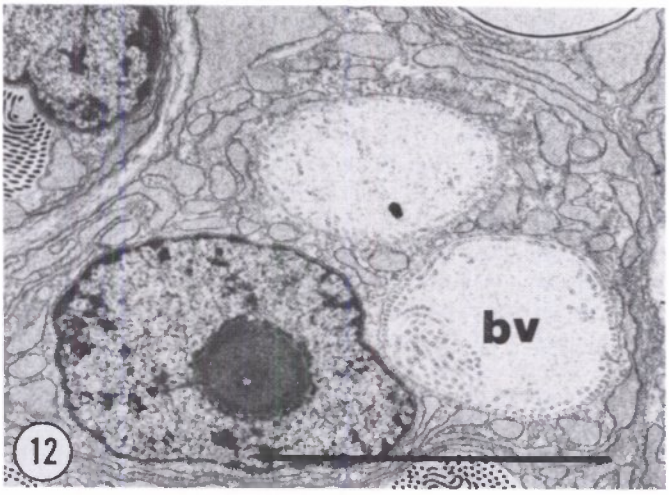
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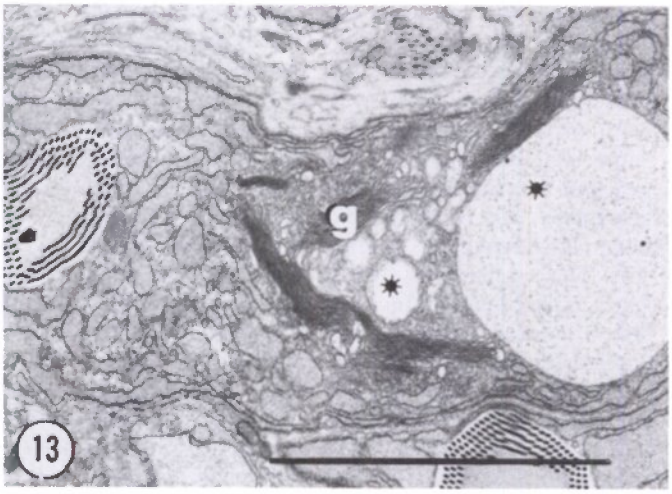
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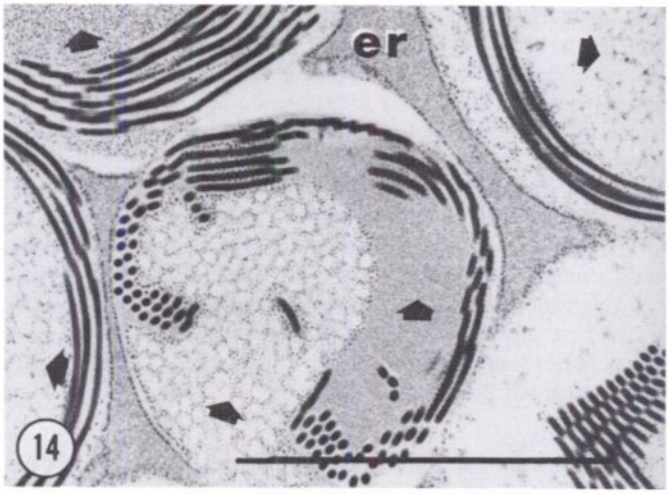
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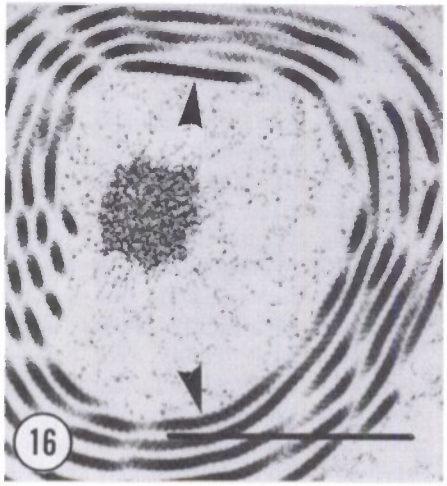
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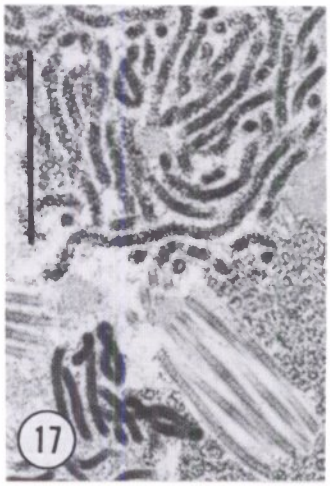
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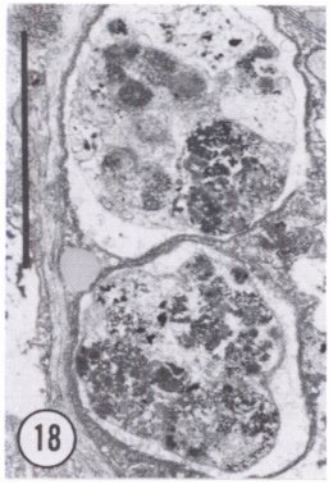
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surface by necks between the epithelial cells, staining "heavily with nuclear stains such as haematoxylin, methylene blue, toluidine and thionin," and the content consisting "throughout of small rod-shaped granules" (Hunter 1949). This compares favorably with the structure of the pedal aperture glands in *M. arenari*. However, in *M. arenaria* the glands are raised cushions, whereas in *Hiatella* the gland is depicted as submerged, often with folds. Yonge (1971, p. 10 and Fig. 6) noted that the glands of nonboring *Hiatella* that he examined "could hardly have been more extensive" and disputed Hunter's (1949) observations. Glands located adjacent to the anterior adductor in other bivalves were alluded to by Pelseneer (1911, p. 83, "glandes palléales latérales"), but we have been unable to find detailed descriptions of these. Within the order Myoida, mucous glands associated with the pedal aperture are known from (*i*) Myidae (Yonge 1951*a*, 1951*b*, 1951*c*), (*ii*) Corbulidae (Yonge 1947), (*iii*) Hiatellidae (Hunter 1949), (*iv*) Gastrochaenidae (Morton 1982), and (*v*) Pholadidae (Purchon 1955; Morton 1985, 1986*a*). We know of only two similar occurrences outside the Myoida, in *Clavagella australis* of the Anomalodesmata (Morton 1984) and *Calyptogena magnifica* of the Veneroida (Morton 1986*b*). At this time it seems reasonable to hypothesize, on the basis of distribution, that the pedal aperture glands within the order Myoida are homologues, although more detailed comparative information would enhance this considerably. The unique ultrastructure of the glandular cells described here should provide a firm basis for testing such homology. Although the conclusion seems warranted that the pedal aperture glands of the Gastrochaenacea are among the most apomorphic for the Myoida, Morton (1983) provides a tantalizing description of the type C gland cells in *Eufistulana mumia* Spengler: these cells are subepidermal, along the inner surface of the inner mantle fold, and contain "many spherical inclusions" (as in *Mya*, but they are eosinophilic, unlike those of *Mya*). Whether the glands of *C. australis* and *C. magnifica* represent homology or convergence in pedal aperture glands is problematic, especially as the latter appears not to burrow, though other *Calyptogena* probably do (Boss and Turner 1980).

At this time there is no structural, positional, or functional evidence to suggest that the pedal aperture glands have any phylogenetic relationship to the radial mantle glands (cf. Prezant 1981) of the Anomalodesmata.

Sensory function

Vlès's (1909) comment that these glands might also be sensory is now substantiated by the finding of collar cells, whose putative sensory nature, in many phyla, is established on the basis of their strategic anatomical position. We would predict that in this case they are mechanoreceptors. These provide a potential means for regulating secretion of the gland, perhaps mediated by the gliointerstitial system, relative to the frequency of their stimulation by particles. Furthermore, such direct stimulus might influence the degree of development of the gland in *Hiatella*.

Glandular structure and function

The bacillary mucous cell, by virtue of its apparently limited distribution, can be presumed to be the primary functional unit for activity of the pedal aperture glands in *M. arenaria*. In contrast, the mucous goblet cell is found also in the adjacent mantle surface; its fine-structural and general histochemical characteristics are similar to those of relatively nonspecialized ciliated epidermal surfaces of many other invertebrates. Similar, but not necessarily identical, mucous goblet cells in bivalves are present in the mantle (Beedham 1958; Richardson *et al.* 1981; Morton 1986*a*), marginal folds (Mane and Patil 1980), and surface of the foot (Banu *et al.* 1979*a*, 1979*b*). These cells, in many species, have in common the production of mucus rich in acidic glycoproteins; in the present study they are particularly rich in sulfuric acid groups. This mucous cell presumably produces the watery mucus that provides surface lubrication for ciliary activity.

The bacillary mucous cell resembles a variety of invertebrate mucous cells whose secretory products display paracrystalline patterns. Welsch *et al.* (1984) noted that the electron-dense patterns in such secretions are protein sites. The extensive rough ER of the bacillary cell, characteristic of protein synthesis, and the positive staining reaction with mercuric bromphenol blue provide evidence for the proteinaceous nature of the fibers. However, the general staining reactions, particularly alcianophilia at pH 2.5, suggest that there is a significant component of acidic glycoprotein (predominantly carboxylated) present. The relationship between the Golgi apparatus and the rough ER in the material available is enigmatic. Lack of alternative evidence suggests that the content of the rough ER bypasses the Golgi apparatus and contributes directly to forming the secretory vesicles, one of several possible routes presented by Hand and Oliver (1984). Thus, the vesicle formed at the trans face of the Golgi apparatus could contain primarily acidic glycoproteins. The significance of the organizational state of granules in the maturing vesicles also is not self-evident, although there is some evidence that the structure of the secretory content may be related in some instances to the presence of a highly ordered reticular substructure within the maturing vesicle (Hand and Oliver 1981). In this study, however, condensed fibers are found in vesicles uniformly filled with granules and in vesicles with dispersed granules. The dense core found in many of the latter vesicles appears to be a massive aggregation of granules, whereas the pattern of the remaining granules in these vesicles resembles, and is probably derived from, the highly ordered reticular pattern that is observed only infrequently (Figs. 13 and 14). The similarity of this derived pattern of granules to the extracellular matrix which is fixed in like manner suggests that the influence of fixation is a variable in the ontogeny of the vesicles that we are unable to evaluate now.

The fibrous nature of the secretory packet is reminiscent of the thread cells of the hagfish slime gland (Downing *et al.* 1981), but fibers of the latter are up to 1.5 μm in diameter and only a single secretory packet, with major axes of up to 0.5 × 1 mm, is produced by a cell. The principal component of this thread is a protein subunit with a molecular weight of approximately 63 500. Downing *et al.* (1981) conclude that threads from this packet become embedded in mucus released by adjacent cells, thus increasing the overall viscosity of the mucus.

The observations of Kellogg (1915), Yonge (1923, 1951*a*, 1951*b*, 1951*c*), and Hunter (1949) provide strong circumstantial evidence that the function of the pedal aperture glands most likely involves the formation of pseudofeces, although Norenburg (1985*b*) considered the possibility of a role in sealing the pedal aperture or consolidating the burrow. Each of these might be served by a highly viscous, adhesive mucus; the first is explained most readily. We believe that the glands deal especially with particulate matter entering the mantle cavity through the pedal aperture, whether by ciliary currents or on the foot. *Hiatella* actively routes sediment through the mantle cavity to "clean" its burrow (Hunter 1949). It is noteworthy that a pedal aperture gland is lacking in *Pholadidea loscombiana*, a

species in which the foot becomes progressively reduced until it is lacking in the adult and in which the pedal aperture is a "minute hole" (Purchon 1955); presumably, little sediment is brought in.

Bacillary packets on the surface of the fixed gland are often uncoiled, and one may presume that, as in the hagfish slime gland, the fibers separate and become distributed in mucus. We expect that bacillary mucus is adhesive and directly traps particulates and is then brought into one of the lateral ciliary vortices or directly into the ventral rejection tract. For efficiency, this adhesive mucus probably remains at the surface of the mucus that lubricates the cilia. We consider this to represent an example of the dual nature of adhesion espoused by Hermans (1983), rather than a simple modulation of viscosity; the nature of the bacillary mixture of glycoprotein and proteinaceous fibers is adhesive and that of the "goblet" mucus is de-adhesive.

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