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Differentiation and Growth of the Brachiopod Mantle

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SYNOPSIS Cell differentiation in the mantle edge of *Notosaria, Thecidellina* and *Glottidia*, representing respectively, the impunctate and punctate calcareous articulate and chitinophosphatic inarticulate brachiopods, is described. Comparison of electron micrographs suggests that outer epithelium which secretes periostracum and mineral shell, is separated from inner epithelium by a band of "lobate" cells, of variable width, exuding an impersistent mucopolysaccharide film or pellicle. The lobate cells always occupy the same relative position on the inner surface of the outer mantle lobe; but the outer epithelium is commonly connected with the inner surface of the periostracum by papillae and protoplasmic strands which persist during mineral deposition and ensure that both shell and attached mantle remain *in situ* relative to the outwardly expanding inner surface of the outer mantle lobe. In the prototypic brachiopod, the lobate cells are likely at first to have occupied the hinge of the mantel fold but later to have been displaced into their present position by the rigid outward growing edge of the mineral shell.

INTRODUCTION

The pair of epithelial folds, constituting the brachiopod mantle, perform two distinct functions. They secrete the organic-mineral valves which protect the soft parts and act as a rigid frame for various organs. They also enclose the mantle cavity and thereby sustain an appropriate milieu for the efficient working of the lophophore.

Both functions are promoted by epithelial specialization. The inner epithelium is more or less the same in all species so far investigated (Figs. 3, 11). It consists of a layer of cuboidal, microvillous, ciliated cells with plasmalemmas disposed in folds especially adjacent to the basal lamina, and well developed smooth endoplasmic reticulum, mitochondria and Golgi complexes. Vesicles and membrane-bound droplets of varying electron density, representing glycoproteins, mucoproteins and mucopolysaccharides, are very common. These inclusions together with the products of widely distributed mucous cells are continuously exuded so that the fibrillar coats of the microvilli are always impregnated with a mucin-like substance. The flow of mucin along the microvillous surface of the inner epithelium and the rhythmic beat of regularly spaced cilia preclude microbenthic settlement and assist in the circulation of water within the mantle cavity.

The outer epithelium, as befits its different secretory rôle, is morphologically and histologically much more variable than the inner epithelium. Cell shape can vary from cuboidal or columnar (Fig. 12) to a flattened rhomboidal structure with the secretory plasmalemma depressed into an outward facing concavity to accommodate the inwardly directed secondary fibres of articulate brachiopods (Fig. 1). The shape is related to the contours of the rigid skeletal surface to which the outer epithelium is adherent. This relationship also accounts for the highly characteristic nature of the secretory plasmalemma which is devoid of cilia and a microvillous mat but is normally studded with hemidesmosomes. These are terminations of bundles of tonofibrils permeating the cell and they attach the external plasmalemma to proteinous membranes secreted between lenses, laminae, blades or fibres of calcium carbonate or phosphate (Fig. 1). Membrane-bound droplets of glycoprotein and mucopolysaccharide occur, but less frequently than in the inner epithelium while rough endoplasmic re-

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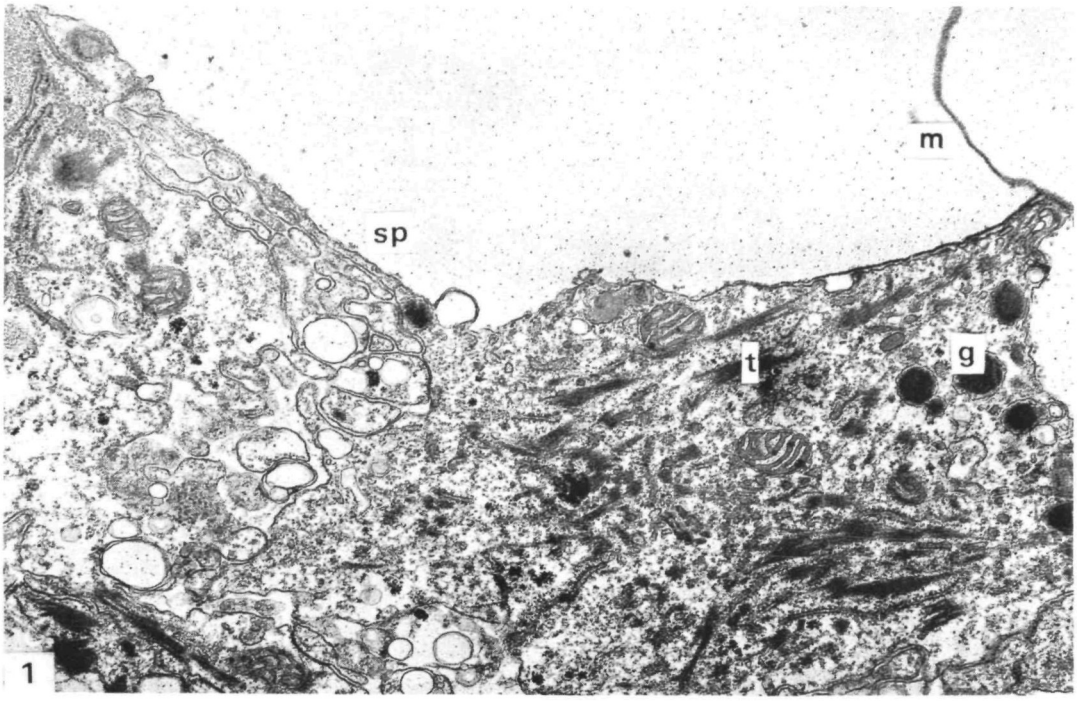

FIG. 1. Section of outer epithelium of *Waltonia inconspicua* (Sowerby) showing: glycoprotein (g); protein membrane (m); secretory plasmalemma (sp); tonofibrils (t). × 20,000.

ticulum is normally much more conspicuous than the smooth.

These epithelial differences must first become apparent very early in brachiopod ontogeny because, shortly after the reversal of mantle lobes in inarticulates or their forward growth in articulates, the protegulum, consisting of percursory periostracum and underlying primary carbonate or phosphate, is secreted by the external surfaces of the lobes. Yet if one thinks of the mantle as a sheet of epithelium tightly folded to enclose a flat layer of connective tissue, the hinge of the fold, which coincides with the free edge of a mantle lobe, must be a very important transitional zone.

The mantle edge is very much alike in most living species (Fig. 13). It is usually divided by a groove into a pair of asymmetric lobes with the more distal larger outer one underlying the shell edge. The mantle groove accommodates regularly occurring setal follicles except where these structures are absent as in the thecideidines and craniaceans. Species of the latter group are also exceptional in lacking a groove and an inner lobe although this deficiency does not affect the concentric differentiation of cells which is the same as that found in other brachiopods.

The concentric differentiation of cells at the mantle edge can be correlated with the regular layering of the exoskeleton which is understood to include the mineral layers, the periostracum and any impersistent organic coat external to it. It has long been known that the periostracum originated on the mantle lobes. In 1900, Blockman, for example, clearly identified a groove on the inner face of the outer mantle lobe of *Lingula* out of which arose the first-formed periostracum. No thought, however, was given to the question of how cells became differentiated to secrete a diversity of materials always in the correct order of deposition. Such a process can be effected by two contrasted methods of mantle growth. First, an incremental expansion of the mantle can be sustained by uniformly distributed mitosis keeping pace with the areal increase in the shell so that the same cells, or their re-

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placements, always secrete the same skeletal components in the same relative position on the internal shell surface. Alternatively the mantle can grow by peripheral addition of cells, proliferated from a narrowly defined generative zone at the closure of the mantle groove. As each cell "migrates" around the outer mantle lobe to become incorporated in the outer epithelial layer it secretes a variety of exoskeletal components in the same chronological order as their occurrence in the shell succession. In effect, except for adjustment during interphase and rare mitosis, each cell remains in proximity to that part of the shell it had secreted *ab initio*. The term "conveyor belt system" has been applied to the second mode of growth (Williams, 1968*a*). In fact both kinds of growth involve the conveyor belt principle but whereas epithelium moves radially outwards independent of the shell in the former (partial conveyor belt system), both move in unison independently of a circumferential generative zone in the latter (full conveyor belt system).

The nature of the relationship between the outer epithelium and shell of many living brachiopods suggests that the growth of the mantle involves a continuous migration of cells from a mitotic zone more or less restricted to the closure of the mantle groove (Williams, 1956). In terebratulides, the mantle is covered with papillae (caeca) which penetrate the mineral part of the exoskeleton to connect with the periostracum through perforated canopies of the primary carbonate shell (compare Fig. 8). The perforations (brush) must be formed by secretion of primary shell around microvilli attached to the inner surface of the periostracum. Microvilli of the right size persist in fully developed caeca immediately below the canopies. Although no secretions have yet been prepared showing the origin of caeca, there is no doubt that contact between the periostracum and the microvilli can only occur on the inner surface of the tip of the outer lobe. Since it is unlikely that the topographically complex inner surface of a densely perforated shell could freely migrate across mantle-bearing papillae of such intricacy, it seems highly probable that the papillae anchor the entire mantle to that part of the shell with which their microvillous heads first made contact. Moreover, the majority of brachiopod orders include species with penetrative skeletal perforations which must have contained epithelial outgrowths varying from protoplasmic strands as in some lingulides (*Lingula*) or mantle projections which secreted the external spines of the strophomenide productidines, to the storage papillae of the terebratulides, thecideidines, orthide enteletaceans and some spiriferides (MacKinnon, 1971).

Such an intimate physical connection between the mantle and shell of brachiopods seems to preclude any form of growth other than that involving the full conveyor belt system. Indeed a generative zone along the mantle groove would not only separate the inner epithelium from the outer but would also contribute to the expansion of both layers as well as the intercalated connective tissue. In other phyla, however, the growth of exoskeletons of similar design seems much more variable. A process similar to that suggested for brachiopods has been assumed to take place in bivalves, cephalopods and chitons (Dunachie, 1963; Kennedy, Taylor, and Hall, 1969; Mutvei, 1964; Beedham and Trueman, 1967). Other researchers, however, have taken a contrary view of molluscan shell growth. Kniprath (1975) has shown that mitosis is not restricted to a specific part of the mantle edge in *Lymnaea* and that cells in the outer mantle lobe of that genus remain in the same position and exude the same components of the shell succession throughout life. Saleuddin (1974) has reached the same conclusion concerning secretion of the periostracum of the bivalve *Astarte*.

Although the differences between the partial and full conveyor belt systems are fundamental, they are not necessarily mutually exclusive. Both types may simultaneously contribute to the formation of the bryozoan skeleton (zooecium). The growing tip of cheilostomes (Lutaud, 1961; Tavener-Smith and Williams, 1972),

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for example, is encased in a continuous cover of periostracum which expands by intussusception and is secreted by an apical cap of palisade cells, each with a conspicuous Golgi complex, globular vesicle, smooth endoplasmic reticulum and many secretion droplets underlying the microvillous external plasmalemma. In sagittal section two narrowly defined mitotic zones are identifiable: one in the basal part, and another proximally, of the frontal part of the palisade cell cap. They are interpreted as sections of a continuous ring of generative tissue giving rise proximally to secretory epithelium and distally to palisade cells at least along the basal sector. Evidently palisade cells secrete only periostracum and do not migrate proximally with that layer to become incorporated within the epithelium lining zooecia. However, behind the growing tip, differentiation of zooids which includes the development of papillae penetrating the zooecia of some species, precludes much movement of epithelium relative to the exoskeleton once the periostracum has moved into place. Consequently differences in the carbonate successions deposited on the periostracum must reflect changes in the secretory regime of a static epithelium.

VARIATION IN THE BRACHIOPOD MANTLE

Despite indications that both partial and full conveyor belt systems could simultaneously contribute to the development of a lophophorate skeleton, a similar style of growth was not identified among brachiopods until *Thecidellina* had been investigated (Williams, 1973). The evidence leading to this conclusion, which is reviewed below, is at least as strong as that supporting the traditional view of brachiopod mantle growth. Consequently, the question now arises whether the mantle growth determined for *Thecidellina* is also more characteristic of other brachiopod groups than previously believed and, if so, whether a generalized model for living species affords any indication of the likely structure of the mantle and shell of prototypic brachiopods. The data available for such a reappraisal are limited although comprehensive enough in respect of extant Orders. In addition to that of *Thecidellina*, the mantle edges of the lingulides *Lingula* and *Glottidia*, the acrotretide *Crania,* the rhynchonellides *Hemithyris* and *Notosaria* and the terebratulides *Kraussina, Liothyrella, Macandrevia, Terebratulina* and *Waltonia*, have been investigated. However, sections of only *Glottidia, Lingula, Notosaria* and *Thecidellina* have so far unequivocally shown all the first-formed periostracum in its position of growth on the inner surface of the outer mantle lobe, although its disposition at the mantle edge of the other species studied can confidently be inferred. Fortunately *Glottidia, Notosaria* and *Thecidellina* belong to widely different Orders and it seems reasonable to regard them as typical of species with chitino-phosphatic, impunctate carbonate and punctate carbonate shells respectively. Comparison of them should, therefore, afford a reliable measure of the variation in the differentiation and growth of the brachiopod mantle.

Growth of the Notosaria *mantle*

When the mantle edge of *Notosaria nigricans* (Sowerby) was first described (Williams, 1968*a, b*), it was regarded as typical of the phylum; and the six different secretory processes carried out in chronological order by the outer epithelium during synthesis of the full skeletal succession, were described as the "standard secretory regime." *Notosaria* now seems less representative of the phylum with respect to mantle growth than was first believed although, within the last seven years, more data, some of them relevant to the present discussion, have come to light and have been incorporated in the following account.

The first exoskeletal layer to be secreted consists of a medium dense finely granular film which is probably a mucopolysaccharide (Figs. 2, 3). It is secreted by up to four cells, immediately distal of ciliated and regularly microvillous inner epithelium, which, in section, are elongately lobate and inclined outwards overlapping one another in that direction. The film

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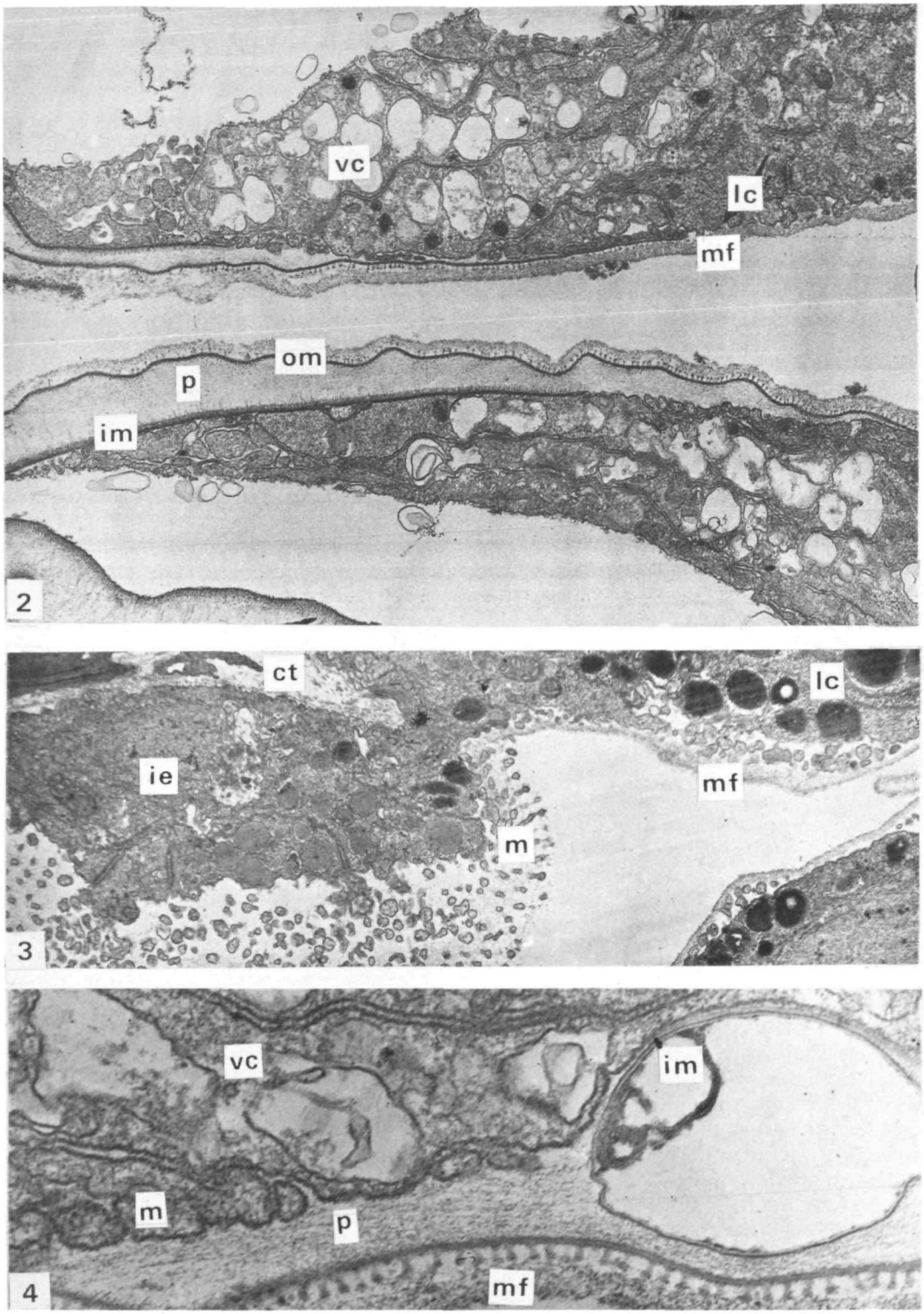

FIG. 2. Section of decalcified mantle grooves of *Notosaria nigricans* (Sowerby) showing: inner 3-unit membrane (im); lobate cell (lc); mucopolysaccharide film (mf); outer 3-unit membrane (om); periostracum (p); vesicular cell (vc). × 27,500.

FIG. 3. Section of mantle grooves of *Notosaria nigricans* showing: connective tissue (ct); inner epithelium (ie); lobate cell (lc); microvilli (m); mucopolysaccharide film (mf). × 13,700.

FIG. 4. Section of inner surface of outer mantle lobe of *Notosaria nigricans* showing: origin of inner 3-unit membrane (im); microvillus (m); mucopolysaccharide film (mf); periostracum (p); vesicular cell (vc). × 82,000.

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emerges with a sharp but undifferentiated external surface from under an outwardly disposed fringe of inner epithelial microvilli to attain a thickness of about 100 nm although it rarely, if ever, persists beyond the tip of the outer lobe. Adjacent plasmalemmas of the lobate cells are irregularly disposed as ill-fitting folds and cylindroids, here and there loosely linked by septate desmosomes, or widely separated by intercellular spaces. The external plasmalemmas through which the mucopolysaccharide film is extruded is also thrown into a series of prostrate cylindroid projections up to 200 nm thick, like the microvilli of the inner epithelium but neither as fibrillar nor as regular in distribution. In many sections, the microvilli of the first lobate cell are difficult to distinguish from those of the inner epithelium except that they lie beneath the film. Indeed, in a few sections, even the microvilli immediately overlying the film at its orgin may belong not to the inner epithelium but to the lobate cell secreting the film. The lobate cells are packed with vesicles and membrane-bound secretion droplets of glyco- and muco- proteins especially in the distal parts of the cells where smooth endoplasmic reticulum is the chief membranous feature. Glycogen aggregates occur throughout and, together with clusters of small vesicles, are densely distributed within the Golgi complexes during the preliminary stages of droplet synthesis.

The five or six cells responsible for the secretion of the periostracum also overlap one another as tongue-like extensions. They are, however, distinguishable from the lobate cells in being crowded with vesicles, usually culminating in one large structure immediately beneath the secreting plasmalemma (Fig. 2). In other respects both types of cells are very much alike. Common features include an abundance of glycogen, the complicated microtopography of the plasmalemmas with their folds and cylindroids, and the rarity of fibrillar ties between crudely fitting adjacent plasmalemmas.

The periostracum, which can be about 1 μm thick, is a complex mixture of proteins and polysaccharides derived from the vesicles which themselves are sporadically evacuated intact to become constituents of the main layer (Fig. 4) where fibrillar proteins also polymerize out of the matrix after secretion has been completed. The most complicated features, however, are its two triple-unit bounding membranes (Figs. 2, 4). The outer one is studded externally with regularly spaced rods which are probably compressed fibrillar coils; the inner one bears a dense mat of fibrils of uniform height, which may only differ from the rods of the outer bounding membrane in their morphology and distribution. Both membranes may first appear either as superficial sheets resting on relatively planar parts of the secreting plasmalemma or within indentations, up to 150 nm deep, between irregular projections of the plasmalemma. They do not originate within intercellular spaces nor is there any evidence that pieces of either membrane are assembled within cells and then secreted in a prefabricated state.

Mantle projections, like caeca or strands, do not penetrate the *Notosaria* shell as in *Thecidellina* or *Glottidia*. However, the front sector of each outer epithelial cell is permeated by bundles of tonofibrills, which pass into desmosomal attachments between the external plasmalemma and a proteinous sheet being secreted by it (compare Fig. 1). This sheet is part of an interconnecting system of sheaths encasing carbonate fibres which are simultaneously being secreted by the back parts of cells. This intimate relationship between the internal organisation of the cell and the fabric of the exoskeleton suggests that the growth of a fibre and one-half of a sheath is controlled by the same cell and that both mantle and shell "migrate" together away from a circumferential generative zone.

Growth of the Thecidellina *mantle*

The mantle edge of *Thecidellina barretti* (Davidson) is morphologically unlike those known in other brachiopods because a fibrillar triple-unit layer, constituting the outer surface of the periostracum, arises within an intercellular slot, about 5 μm

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deep, between distal vesicular and proximal lobate cells (Figs. 5, 6, 9). The elongate vesicular cells at the tip of the mantle lobe exude the remainder of the evenly granular periostracum and the beginnings of the primary carbonate shell. In section, the lobate cells, which intervene between the periostracal slot and the most distal part of the inner epithelium, are normally grouped around a large mucin cell. This body stretches the cells so that they usually appear as flattened structures, overlapping one another anteriorly in tongue-like lobes, with taut uncrenulated plasmalemmas. The secretory plasmalemmas may also be distended into smooth surfaces devoid of projections except for lateral flaps overlying the intercellular openings leading from terminal bars. However when the mucin body is small, intercellular membranes become folded and prostrate microvilli appear in the secretory plasmalemmas. The lobate cells contain many vesicles and membrane-bound droplets of mucoproteins and, together with the mucin cells, sustain a mucopolysaccharide film (Fig. 7) which persists for some distance beyond the slot as an external coat to the periostracum. The preperiostracal cell may even contribute to the formation of the outer filamentous layer of the periostracum *sensu stricto*.

Secretion of periostracum in the manner described above is inconsistent with the theory that the mantle groove is the site of a generative zone from which cells migrate around the outer mantle lobe to become part of the outer epithelial layer. The lobate cells lie proximal to the slot and no rational pathway can be visualized along which they may migrate around the slot before changing into vesicular cells. On the other hand, the thecideidine shell is penetrated by densely distributed caeca (Fig. 8), each encased in a proteinous membrane which also lines the brush and is continuous with the overlying periostracum. The caeca are attached to their membranous covers by fibrillar connexions although detachment does occur. Thus as the shell thickens, caeca shift inwardly with the retreating mantle and periodically deposit proteinous partitions sealing off the more distal parts of puncta. This evidence of epithelial movement relative to the shell, however, does not diminish the likelihood that caeca originate at the tip of the outer mantle lobe in intimate connexion with the periostracum, and that both periostracum and caeca and, presumably, the entire mantle, migrate posteriorly together.

Growth of the Glottidia *mantle*

The morphology of the mantle edge of *Glottidia pyramidata* (Stimpson) and *Lingula anatina* Lamarck is more complicated than that of other living orders. In section, bilobation of the mantle, accentuated by the occurrence of closely spaced setal follicles, superficially resembles that of articulates; but the boundary between outer and inner epithelium is actually located in a notch (periostracal groove) opening posteriorly on the inner face of the outer mantle lobe (Figs. 10, 13). Here the first-formed constituent of the skeletal succession, a medium dense granular mucopolysaccaride film, about 50 nm thick, is secreted by one or two cell(s) adjacent to regularly microvillous and ciliated inner epithelium (Fig. 11). This cell(s) tends to encroach proximally like a tongue over the basal part of its neighbour and is usually partly bounded by larger intercellular spaces. It contains numerous vesicles and membrane-bound secretion droplets in various stages of accumulation and dispersion as they migrate to the external plasmalemma which is prolonged into a number of prostrate, non-fibrillar microvilli lying beneath the mucopolysaccharide film. Where the film emerges from under the fringe of forward projecting inner epithelial microvilli, its external surface polymorizes into a fibrillar triple-unit membrane about 10 nm thick which normally persists as a detached bag-like cover to a small posteriorly projecting lip (periostracal lobe) which forms the inner boundary of the periostracal groove. The 20 or so additional cells seen in sagittal section of the periostracal lobe and those making up the remainder of the distal part of the outer mantle lobe, are responsible for se-

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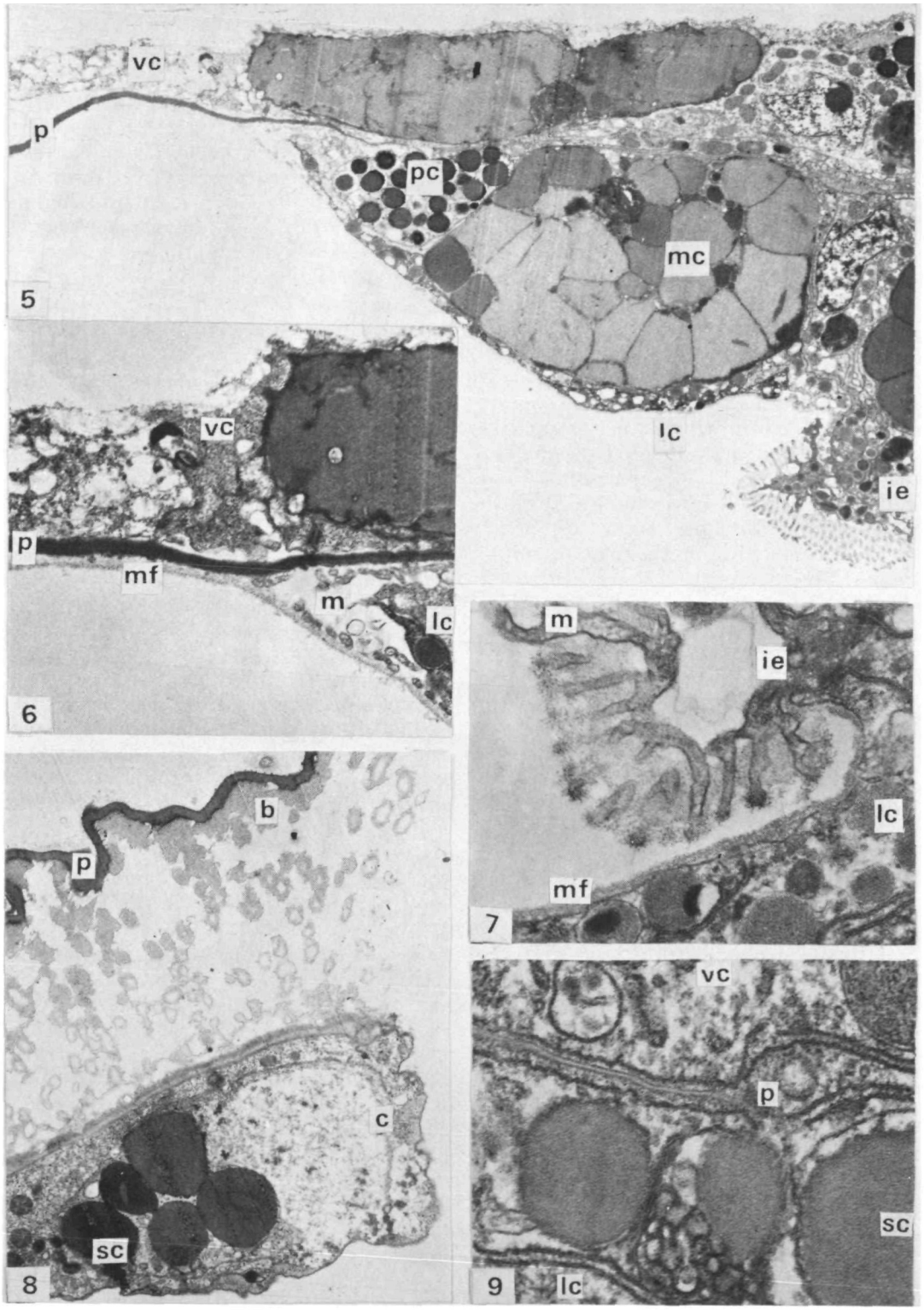

FIG. 5. Section of decalcified mantle edge of *Thecidellina barretti* (Davidson) showing: inner epithelium (ie); lobate cells (lc); mucin cell (mc); periostracum (p); pre-periostracal cell (pc); vesicular cell (vc). × 4,100.

FIG. 6. Section of inner surface of outer mantle lobe of *Thecidellina barretti* showing: lobate cell (lc); microvillus (m); mucopolysaccharide film (mf); periostracum (p); vesicular cell (vc). × 8,200.

FIG. 7. Section of closure of mantle groove of *Thecidellina barretti* showing: inner epithelium (ie); lobate cell (lc); microvillus (m); mucopolysaccharide film (mf). × 27,500.

FIG. 8. Section of decalcified shell of *Thecidellina barretti* showing: brush (b); caecum (c); periostracum (p); secretion droplet (sc). × 5,500.

FIG. 9. Section of outer mantle lobe of *Thecidellina barretti* showing: lobate cell (lc); origin of periostracum (p); secretion droplet (sc); vesicular cell (vc). × 82,000.

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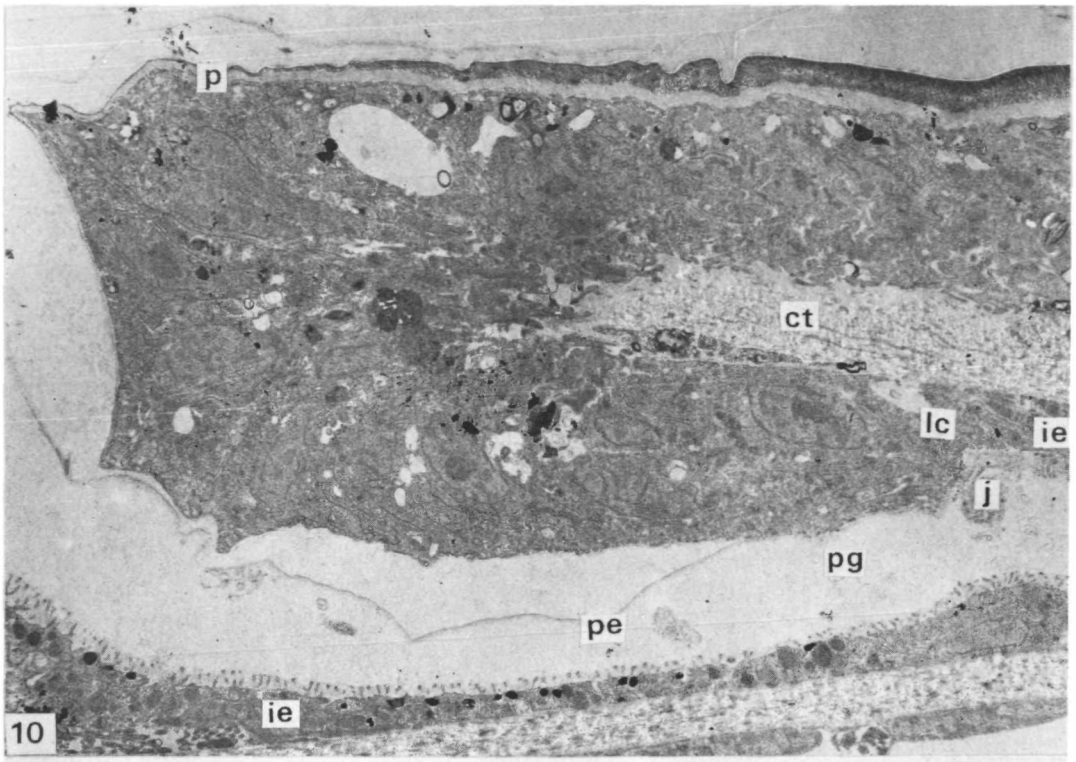

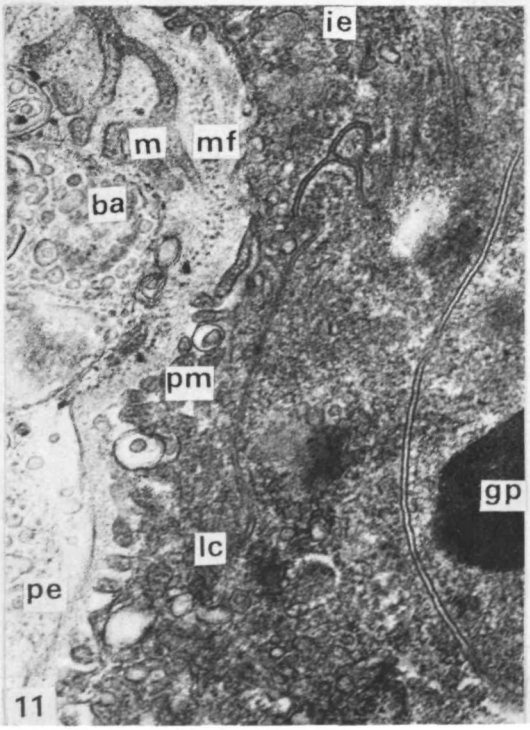

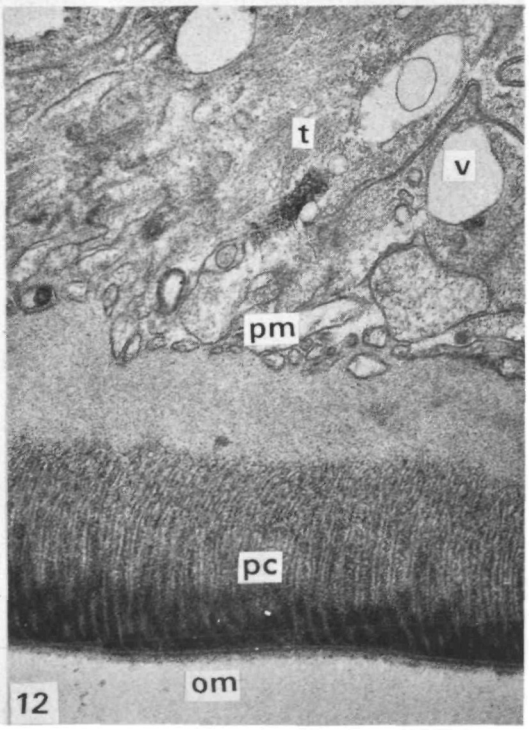

FIG. 10. Section of the periostracal lobe of *Glottidia pyramidata* (Stimpson) showing: connective tissue (ct); junction (j) between inner epithelium (ie) and lobate cells (lc); periostracum (p); pellicle (pe); periostracal groove (pg). × 4,500.

FIG. 11. Section of the junction between the inner epithelium (ie) and lobate cells (lc) of *Glottidia pyramidata* showing: bacteria (ba) immediately above the mucin (mf) of the inner epithelium with microvilli (m) and the lobate cells with prostrate microvilli (pm); glycoprotein droplet (gp); pellicle (pc). × 66,000.

FIG. 12. Section of the distal part of lobate cells and associated periostracum of *Glottidia pyramidata* showing: outer 3-unit membrane (om); periostracum differentiated into proteinous cylinders and median rods (pc); prostrate microvilli (pm); tonofibrils (*t*); vesicle (v). × 35,500.

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creting the periostracum proper.

A coarsely fibrillar triple-unit membrane polymerises early in the exudation of the periostracum to form an outer surface, but internal differentiation does not take place until the layer is about 250 nm thick (Fig. 12). This involves the appearance of electron-dense partitions which connect with one another to define a series of cylinders each containing a solid or beaded electron-dense rod. The partitions and their rods polymerize inwardly, from the external surface but remain separated from the outer epithelium by undifferentiated inner periostracal layers. The periostracum-secreting cell is typically columnar with many vesicles (some containing smaller packages of mucoprotein), secretion droplets, bundles of fibrils, and with smooth endoplasmic reticulum replacing the rough towards the external plasmalemma which is thrown into a series of irregular, prostrate microvilli (Fig. 12) and indented by evacuating vesicles.

The movement of the lingulid mantle and shell independently of each other is subject to the same sort of constraint found in *Thecidellina*. The shell of *Lingula* (and probably that of *Glottidia* too, which has not yet been examined under the electron microscope) is penetrated by minute canals about 700 nm in diameter. The canals are lined with a membrane connecting the inner surface of the periostracum with the external plasmalemma of the outer epithelium, and although they are mainly occupied by small, closely packed vesicles, they also contain, proximally at least, some glycogen and evaginations of the plasmalemma. Like caeca, these protoplasmic strands must anchor outer epithelium to the inner sealing surface of newly secreted periostracum at the tip of the outer mantle lobe.

There are few other indications of the relative movement of mantle and shell. The electron dense cylinders with their median rods polymerizing within the periostracum and the proteinous strands trailing from the inner periostracal surface, can be used as strain figures to determine stress couples operating within the layer. They show that, relative to its interface with epithelium, the periostracum "moves" steadily away from the periostracal groove around the outer mantle lobe. This pattern simply confirms the direction of periostracal migration determined from the skeletal succession but, at least, it indicates that *in vivo* strain features are not distorted during the fixing of specimens and preparation of sections. Orientation of the intercellular boundaries, however, affords a much more complex picture. Along the outer limb of the periostracal lobe, the boundaries are convex posteriorly indicating that cells are actually moving away from the inner epithelial boundary towards the lobe hinge at a faster rate than the periostracum. However, on the inner limb they are also convex posteriorly suggesting either a movement towards the lobe hinge or a faster movement of periostracum in an anterior direction. The deposition of cells around the outer mantle lobe affords a much more incongruous stress system. All cells in the inner and outer limbs of the lob slope towards their junction with the periostracum (and shell). This would accord with the forward movement of periostracum on both limbs. The only way to explain these anomalous orientations of cells in the outer mantle lobe is to assume that they reflect a maximum strain directed postero-radially. Such a strain could have been imposed by the pull of the setal protractor muscles.

CONCLUSIONS

Model for mantle growth

Before comparing mantle growth and differentiation in *Notosaria, Thecidellina,* and *Glottidia,* it is relevant to resolve ambiguities arising from the terminology used to describe the morphology of the mantle edges (Fig. 13). In all articulate species examined, the junction between inner epithelium and the non-ciliated cells secreting an impersistent outer cover to the periostracum (lobate cells), is located in the hinge of the mantle fold. In section, the median layer of connective tissue forming the core of the mantle edge ends in a

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rounded boundary within which the basal lamina traces a concentric fold. This folded termination lies in the vicinity of the mantle groove and is, therefore, more or less alined with the inner epithelium-lobate cell junction. A similar alinement occurs in *Crania* despite the absence of a groove. In *Glottidia* (and *Lingula*), however, the junction is not in the hinge of the periostracal groove but on the outer wall of the periostracal lobe. Moreover in these chitinophosphatic inarticulates, closure of the connective tissue core is effected by two folds: a major more distal one occupying the middle of the outer mantle lobe and a minor one, which is a posteriorly directed digitation from the lower limb of the major fold, occupying the middle of the periostracal lobe slightly in advance of the junction. Thus to compare this arrangement with that found in articulates, the periostracal lobe should be rotated through 180° and correlated with the outer mantle lobes of *Notosaria* and *Thecidellina* (Fig. 13). In this context, the "outer mantle lobe" of *Glottidia*, represents an extra loop of mantle accomodating an abnormally long strip of periostracum-secreting epithelium which lines the inner limb of the fold.

Comparison of the growth and secretory regimes of the three mantle edges described above shows that there are several features in common (Fig. 13).
They include:

(1) The first layer of the exoskeleton is secreted by lobate cells and consists of a mucopolysaccharide film or polymerized pellicle which does not persist outside the mantle cavity.

(2) The lobate cells, in sagittal section, vary from one to about eight in the three species studied, but are otherwise alike when allowance is made for the distorting effect of the mucin cell in the mantle lobe of *Thecidellina*. Among the similarities are: irregularly folded intercellular plasmalemmas which are loosely and sporadically linked; secreting plasmalemmas with prostrate non-fibrillar microvilli; large nuclei; and abundant secretion droplets.

(3) The junction between the lobate cells and inner epithelium is distinguished by the appearance of the mucopolysaccharide film overlying non-fibrillar, prostrate microvilli. In detail the distinction is less sharply drawn. The inner epithelium also exudes a mucin-like substance but it coats the fibrillar mesh extending between erect microvilli. In the absence of cilia which have not yet been seen in a cell at the junction, the difference reduces to the fibrillar nature and erect habit of the inner epithelial microvilli.

(4) The periostracum is secreted by vesicular cells which differ from the lobate cells in the greater frequency of vesicles and the irregular aspect of the prolongations of the secreting plasmalemmas. These, however, remain prostrate like the more regularly shaped microvilli of the lobate cells.

(5) The intercellular secretion of a continuous outer bounding membrane to the periostracum of *Thecidellina* precludes migration of lobate cells into the position occupied by vesicular cells. This arrangement is neither confirmed nor contradicted by the relationship between periostracum and vesicular and lobate cells in other species.

(6) Strands or microvillous portions of the secretory plasmalemmas of vesicular cells become attached to the inner sealing membrane of the periostracum. This membrane is deposited by inward facing cells at the tip of the outer lobe.

These features delineate a consistent pattern of mantle growth and differentiation for all living brachiopods if two inferences are drawn. The first is that the lobate cells are not involved in any conveyor belt movement around the tip of the outer mantle lobe; they are concerned solely with the secretion of an outwardly migrating impersistent mucopolysaccharide layer. The second is that, following attachment of the vesicular cells to the periostracum, the inner surface of the outer mantle lobe, including newly formed vesicular cells must move antero-radially, relative to the fixed shell edge with its attached older vesicular cells. The outer epithelium may, therefore, be redefined as that part of the mantle responsible for the secretion of periostracum and shell. It

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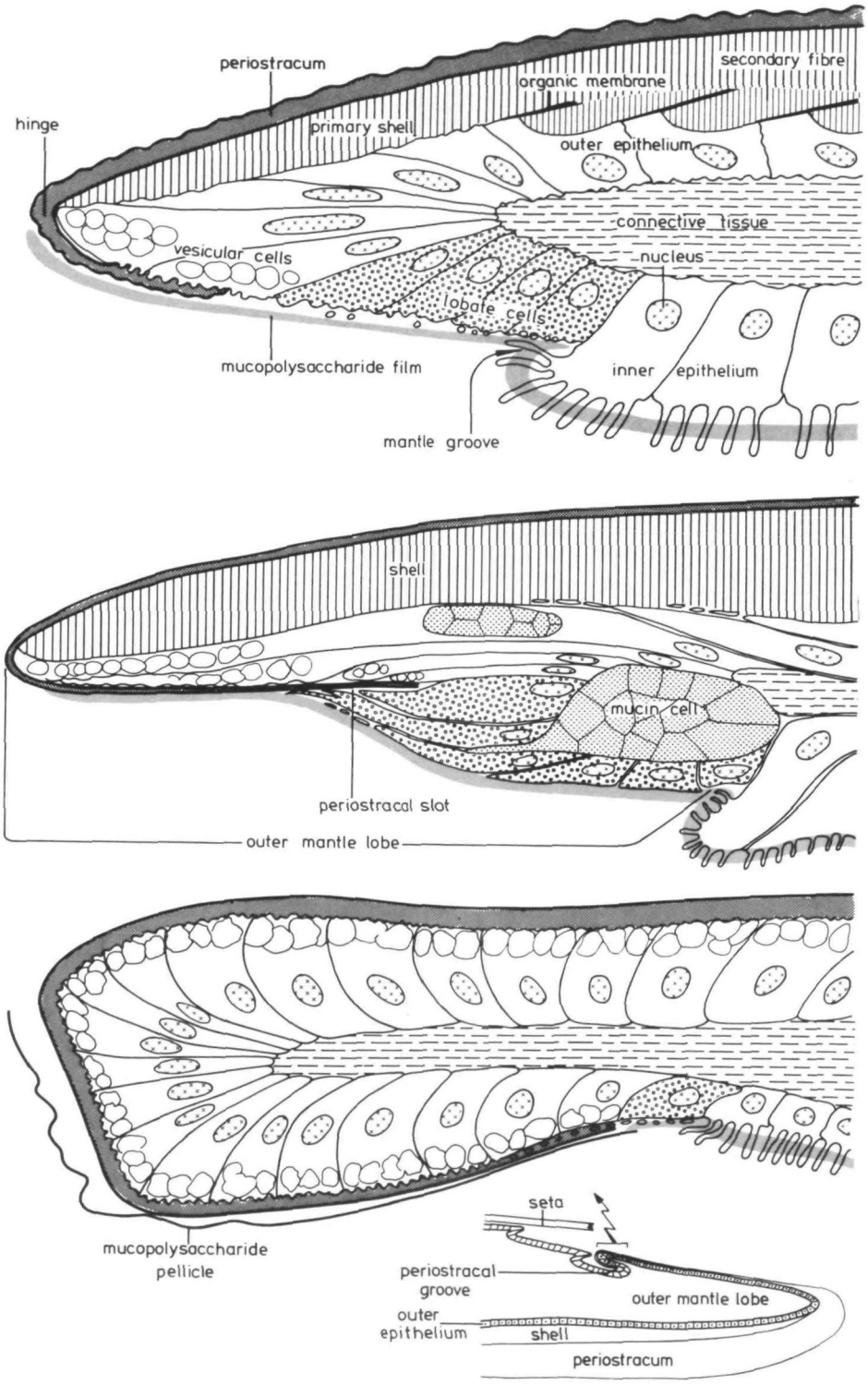

FIG. 13. Diagrammatic sagittal sections of the edge of the valves of *Notosaria* (above), *Thecidellina* (middle) and *Glottidia* (below) illustrating common features in mantle differentiation.

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must include a zone in the tip of the outer lobe where cells are proliferated at a sufficient rate to keep pace with the peripheral expansion of the shell. It does not, however, include the lobate cells separating it from the inner epithelium. In fact it may be significant that the lobate cells more closely resemble the inner epithelium in many ways; but whether the former are specialized versions of, or can give rise to, the latter has still to be investigated.

The prototypic mantle

A concluding note on the prototypic mantle seems appropriate because awareness of the antiquity of *Lingula*, which is much older than any thecideidine and at least as old as the earliest rhynchonellide, may prompt the view that the mantle of the ancestral brachiopod was like that of *Glottidia*. This is unlikely, unless the earliest brachiopods were burrowers for which there is no geological evidence. In *Glottidia* (and *Lingula*) the abnormal length of the outer mantle lobe is probably related to the extraordinary use made of the setae by lingulids to maintain burrows and form siphon-like tubes for feeding (Chuang, 1956). Each setal follicle is controlled by three sets of muscles all inserted within the outer mantle lobe which, by natural selection, would tend to become longer thereby providing extra accommodation for muscle bases and protective peripheral cover during burial. Indeed consideration of the model derived from the study of living species suggests that the prototypic mantle may not have been bilobed at all. If the threefold differentiation of mantle epithelium is as early as its invariable development in living species suggests, and if the fold in the prototypic mantle had been symmetric about a median plane, the lobate cells would have occupied the hinge of the fold and would have been flanked by an external and internal generative zone, maintaining outer and inner epithelium respectively (Fig. 14). At this stage in evolution the lobate cells at the mantle edge would have been protected by mucilaginous secretion and the outer epithelium by a fibrillar three-unit periostracum (Williams, 1968*a*). However, with the secretion of mineral layers there would have been a tendency for the inflexible edge of the exoskeleton to form a protruding ledge overlying the hinge of the mantle. The protection thus afforded the sensitive rim of the mantle

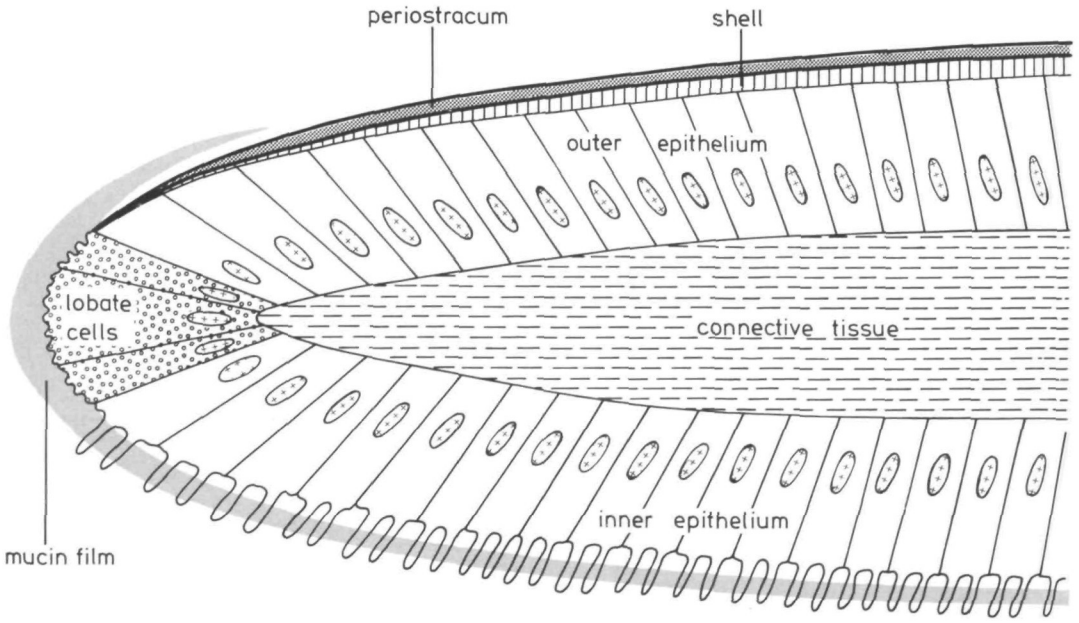

FIG. 14. Diagrammatic reconstruction of a sagittal section of the mantle edge of a prototypic brachiopod.

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would have promoted a selection pressure in favour of a more strongly projecting shell edge which would have concomitantly displaced the lobate cells and both generative zones on to the inner surface of the mantle. Bilobation of this inner surface, which can exist even in the absence of setae might, therefore, be a vestige of a postero-medial retreat of the original mantle edge.

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