

SHELL STRUCTURE OF THE SIPHONOTRETACEAN BRACHIOPODA

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ABSTRACT. The shell of the inarticulate brachiopod genera *Helmersenia*, *Multispinula*, and *Siphonotreta*, is finely banded in section with layers of apatite crystallites separated by relatively more homogeneous units presumably representing concentrations of proteinaceous derivatives. The surface texture of the protegulum and adult shell is smooth, and the most conspicuous ornamentation consists of regularly arranged prostrate spines with central canals, either communicating with the shell interior throughout life, or terminating proximally just below the external base of the spine. Consideration of the growth and distribution of spines suggests that they probably acted as protective grilles, sieving coarse particles from inhalent currents entering the commissural gape and reducing the incidence of microbenthic colonization of the shell exteriors.

A RECENT investigation of the shell surface of inarticulate brachiopods belonging to the Acrotretida showed a noteworthy differentiation in the external micro-ornamentation of certain species (Biernat and Williams 1970). In fossil and living representatives of the Craniacea and Discinacea, the surface of the first-formed shell, the protegulum, is essentially like that of the adult. Minor differences, other than the presence of growth-lines on the surface of the extra-prottegular shell, do occur. Concentric ridges or lamellae may be more prominent in, or even restricted to, adult growth stages, but their development has never reflected any fundamental change in the regime of shell secretion. In all acrotretacean species examined, however, the protegulum differs significantly from the adult shell in being ornamented by closely distributed shallow pits. The pits usually fall into two distinct sizes, averaging 3 μm and 350 nm in *Torynelasma*, with the larger pits separated from one another by clusters of the smaller. The pattern is like the mould of a bubble raft and is interpreted as having been caused by deposition of calcium phosphate crystallites on the inner surface of the sealing membrane of a highly vesicular periostracum. The absence of pits from the adult part of the shell is believed to indicate the development of a strong post-prottegular thickening of the inner sealing membrane which masked the vesicular topography of the rest of the periostracum.

During that investigation, the only siphonotretacean material examined consisted of *Helmersenia* and *Siphonotreta* valves dissolved out of Tremadocian cherts by hydrofluoric acid. The entire external surfaces of these shells bore densely distributed pits which were solution features although they may have included shallow depressions formed during skeletal secretion and enlarged during etching (Biernat and Williams 1970, p. 495, pl. 100, fig. 6). This possibility remained unchecked until recently when, with the ready help of Dr. L. R. M. Cocks of the British Museum, Dr. G. A. Cooper of the U.S. National Museum, and Dr. V. Y. Goryansky of Leningrad, to whom we are greatly indebted, well-preserved specimens of *Helmersenia*, *Multispinula*, and *Siphonotreta* became available for comparative study. Well-preserved shells of *Alichovia*, *Schizambon*, and *Dysoristus*, the only other genera assigned to the superfamily (Rowell in Williams *et al.* 1965, p. H288; Goryansky 1969, p. 97) could not be obtained. But the shell structure of *Alichovia* and *Schizambon* is unlikely to differ significantly from that

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of the closely related *Multispinula*; and although the protegular surface of *Dysoristus* still has to be examined, the absence of spines precludes consideration of the shell structure of that stock in relation to other Siphonotretacea. In fact, as will be shown below, the development of two distinct sets of spines, and not the nature of the protegulum, is the most distinctive feature of the siphonotretacean shell.

Materials and methods. The skeletal fabric of four siphonotretacean species has been examined in detail: *Helmersenia ladogensis* (Jeremejev) from the Tremadocian Pakerortskij sandstones of Staraja Ladoga and Ivanogorod in the Leningrad area; *Multispinula perspinosa* Cooper from the Caradocian Bromide limestones, Rock Crossing, Oklahoma; *Siphonotreta unguiculata* (Eichwald) from the Caradocian Kukerskij argillaceous limestones at Kerstovo and Diatlitz near Leningrad; and *S. verrucosa* (Eichwald) from the 'Ordovician of Volkov near Leningrad' (BB 33159-33161). For the study of shell topography, 10% acetic acid was used to remove adherent rock matrix from internal and external surfaces of valves which were then washed in a weak detergent. For the preparation of sections, specimens were left in the rock and the cut surfaces were polished with tin oxide or alumina and subsequently etched in 2% EDTA for 20 min. Both sections and shell surfaces were coated with gold-palladium for study under the Cambridge Stereoscan scanning electron microscope purchased by N.E.R.C. grant GR/3/443.

THE PROTEGULUM

The protegulum, as the first-formed mineral layer simultaneously secreted over the larval mantle, is that part of the umbonal surface of each adult valve bounded by the earliest discernible growth-line. In four brachial valves of *Helmersenia ladogensis*, the subcircular protegulum averages 380 μm in length (Pl. 75, fig. 1). Dorsal protegula of *Siphonotreta unguiculata* and *Multispinula perspinosa* Cooper have comparable lengths of 450 and 400 μm respectively. These are up to three times as large as the typical acrotretacean protegulum, which is about the same order of difference as that of the absolute size of adult shells. There is, moreover, no trace of the regular pattern of shallow pits so characteristic of the Acrotretacea. Instead, the protegular surface of all three species is pock-marked with irregularly distributed depressions, up to 3 μm in diameter and usually connected to one another by anastomosing shallow grooves (Pl. 75, fig. 3). The surface may also show a fine layering exposed at different levels (Pl. 75, fig. 2). These features are clearly solution phenomena differentially etched, during recovery of the valves from rock matrix, out of well segregated mineral layers which cannot be much

EXPLANATION OF PLATE 75

Figs. 1-6. Scanning electron micrographs. 1. Umbonal region of brachial valve of *Helmersenia ladogensis* to show the extent of the protegulum and the restriction of spines to the post-protegular part of the valve ($\times 120$). 2-3. Details of protegular surfaces of brachial valves of *Multispinula perspinosa* and *Siphonotreta verrucosa* respectively showing solution pits ($\times 2800$). 4. Detail of oblique fracture surface through brachial valve of *Siphonotreta unguiculata* showing layers of apatite crystallites; exterior towards top of micrograph ($\times 2200$). 5. Differentially etched section of brachial valve of *Siphonotreta verrucosa* showing origin of small spines to left and internal blade-like projection in top right; anterior of valve to bottom of micrograph ($\times 250$). 6. Differentially etched section of brachial valve of *Siphonotreta unguiculata* showing banding; exterior at top left hand corner of micrograph ($\times 1200$).

more than 400 nm thick in *Helmersenina*. The skeletal ultrastructure of living Acrotretida suggests that these layers represent extensive laminae of apatite separated from one another by residues of the chitino-proteinaceous sheets on which the apatite crystallites were originally deposited. The distribution of solution pits and their disposition more or less normal to the protegular surface further suggests that the crystallites were secreted with their long axes vertical to the chitino-proteinaceous sheets.

The fact that the surface of the siphonotretacean protegulum is smooth in its unweathered state indicates that the inner sealing membrane of the periostracum, which acted as a seeding sheet for the outermost mineral layer of the shell, was also featureless. Thus the periostracum itself may have been a homogeneous mucopolysaccharide layer as in living crinaceans, or a vesicular layer with a thick inner sealing membrane as inferred for the adult acrotretacean shell.

THE ADULT SHELL

The siphonotretacean adult shell is structurally similar to that of other chitino-phosphatic inarticulate brachiopods. The ultrastructure is best studied in oblique natural fractures (Pl. 75, fig. 4) and prepared sections (Pl. 75, fig. 6) of the relatively thick shell of *Siphonotreta unguiculata*; and the arrangement seen in that species is typical of other siphonotretacean stocks. The shell is finely layered with 15 bands having an average thickness of 1 μm . The commonest type of band is made up of fine crystallites rarely more than 500 nm across. It has not been possible to decide whether the crystallites are epitaxially arranged from one band to the next. In any event it is likely that the banding, as in the protegulum, represents apatitic laminae that were originally separated from one another by chitino-proteinaceous sheets. Indeed, oblique fractures commonly show groups of 2-5 closely spaced bands with surfaces that are homogeneous at the resolutions possible with a scanning electron microscope. These bands are probably composed mainly of proteinaceous derivatives and would have been deposited during periodic changes in the secretory regime of the *Siphonotreta* mantle.

In *Siphonotreta* and *Multispinula*, narrow strips of shell, as interwoven lines with angular junctions, usually occur on the shell exteriors anastomosing around spinal bases (see bottom left-hand corner Pl. 76, fig. 2). Each strip has a slightly undercut edge so that it forms an overlapping film of shell about 1 μm wide. In living articulate brachiopods, the shell surface immediately beneath the periostracum may bear furrows or ridges which are presumably mineral casts either reflecting inequalities in the inner surface of the periostracum, or coinciding with intercellular boundaries. Polygonal areas enclosed by the strips on siphonotretacean shell surfaces are too large to represent cell outlines. Provisionally, they are interpreted as having been secreted within microscopic folds in the seeding surface of the periostracum.

In *Helmersenina* but especially in *Multispinula* and *Siphonotreta*, concentric lamellae, up to 150 μm long, regularly occur. The last two genera are also characterized both externally and internally by raised concentric ridges (Pl. 76, figs. 1, 5). In *Multispinula* they occur externally as more or less continuous asymmetrical ridges at intervals of about 150 μm in the middle regions of the shell with the steeper side facing anteriorly. In *Siphonotreta*, similarly disposed asymmetrical ridges, about 20 μm high, occur. These tend to be impersistent over the immature shell surface but are more continuous and

more widely spaced, at intervals of about 300 μm , in the adult shell. In both genera, internal concentric features occur at intervals of 500–700 μm as blade-like projections extending posteriorly for about 30 μm (Pl. 75, fig. 5). In no species, however, is any ornamentation so conspicuous as the prostrate spines distributed in different patterns over the surface of the adult shell.

Distribution of spines. The spines are restricted to the post-protegeral part of the adult shell where they form dense arrays as defined by Rudwick (1965, p. 605). The simplest array is found in *Helmersenia ladogensis*. In this species, the spine bases, which are distributed alternately and radially at intervals of about 100–200 μm , must have borne spines of only one size grade. The bases are usually oval in outline with their major diameters, averaging about 45 μm , aligned radially (Pl. 76, fig. 3) and frequently coincident with slightly raised ridges trailing off for a few micrometres on either side. Although no spines have been seen it is evident, from the slope of fracture surfaces defining their bases, that they must have lain sub-parallel, or at a small angle, to the shell surface (compare the rare remnants of spines in *H. ladogensis* figured by Goryansky 1969, pl. 19, figs. 1 and 2). Each spine base communicates with the shell interior by a central canal, about 10 μm in diameter, which is disposed normal to the surface of the valve.

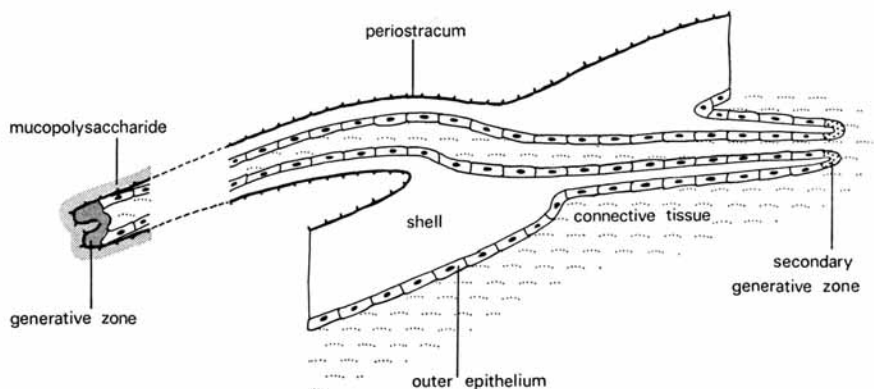
The arrays found in *Siphonotreta* and *Multispinula* are more complicated because they involve two sets of spines as already noted by Cooper (1956, p. 268) in his study of the latter genus. These sets can be distinguished by differences in their structural relationship to the shell as well as in their mean diameters (cf. Pl. 76, figs. 1, 5). The average lengths of the sets must also differ significantly, although both kinds of spines have been broken off the shell near their bases and no reliable estimates were obtained during this study. Some indication, however, can be given of the minimum length of the spines; in *Multispinula*, for example, the larger spines are at least 6 mm long (Cooper 1956, p. 268) and the smaller ones 1.3 mm according to our investigations. Presumably a comparable order of difference is characteristic of the two spine sets developed in other siphonotretacean species.

In *Siphonotreta verrucosa*, a set of larger spines, which correspond to those of *Helmersenia*, occurs radially and alternately at about 1 mm intervals (Pl. 76, figs. 1, 2). These external spines are subcircular in section near their bases where they average 220 μm in diameter for 4 estimates. Each is pierced by a central canal with an average diameter of 80 μm . The canal runs obliquely through the valve to communicate with the shell interior by an inwardly directed spine which is up to 360 μm long and tapers to a diameter of about 50 μm . The internal spines (Pl. 76, fig. 4) are usually fluted longitudinally at

EXPLANATION OF PLATE 76

Figs. 1–6. Scanning electron micrographs. 1–2. Exterior near antero-lateral margin of brachial valve of *Siphonotreta verrucosa* to show two sets of spines; valve margin beyond top left hand corner ($\times 30$, $\times 150$). 3. Exterior of brachial valve of *Helmersenia ladogensis* with spine broken off at base to show canal piercing shell ($\times 2400$). 4. Interior of brachial valve of *Siphonotreta verrucosa* showing internal extension of a large spine ($\times 300$). 5. Exterior near antero-medial margin of brachial valve of *Multispinula perspinosa* showing two sets of spines; valve margin beyond bottom left hand corner ($\times 120$). 6. Interior of brachial valve of *Multispinula perspinosa* showing internal extensions of large spines ($\times 575$).

their junctions with the valve surface by subdued impersistent ridges up to $4\ \mu\text{m}$ wide. The larger spines of *M. perspinosa* also occur radially and alternately, but they are usually concentrated at intervals of about $100\ \mu\text{m}$ in two closely set rows along the crest of a concentric lamella (Pl. 76, fig. 5). They are somewhat smaller than their counterparts in *Siphonotreta* and are oval in section at the base with an average major diameter of $125\ \mu\text{m}$ disposed parallel to the lamella and an average minor diameter of $85\ \mu\text{m}$ for 8 estimates. Here the canals are about $30\ \mu\text{m}$ in diameter and again pass obliquely through the valve to become the axes of tapering internal spines up to $25\ \mu\text{m}$ long and about $22\ \mu\text{m}$ in diameter (Pl. 76, fig. 6).



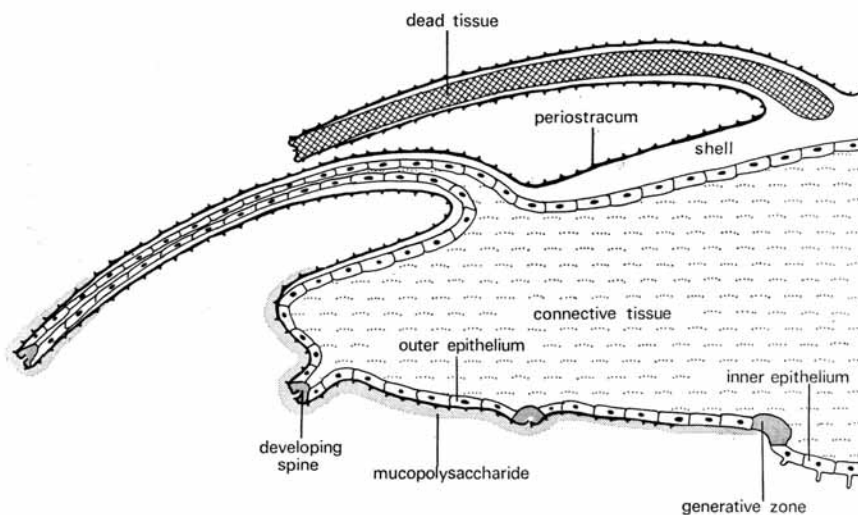
TEXT-FIG. 1. Stylized reconstruction of the soft parts in relation to a large spine of *Siphonotreta* as seen in longitudinal section.

The smaller spines of *Siphonotreta* have subcircular sections and occur at intervals of about $100\ \mu\text{m}$ in alternating rows with as many as 8 or 9 belonging to one row intervening between the larger spines (Pl. 76, figs. 1, 2). Ten of them averaged $45\ \mu\text{m}$ in diameter just above the base where the central canal had a mean diameter of $18\ \mu\text{m}$. The smaller spines of *Multispinula* are oval in section and have an average major diameter of $62.5\ \mu\text{m}$ in 5 estimates with proportionately sized canals. They intervene singly between adjacent larger spines (Pl. 76, fig. 5). Thus these spines appear to be simply small-scale versions of the larger sets in their respective genera. Yet all smaller spines are fundamentally alike in the termination of their central canals within the shell just below their junctions with the external surfaces of the valves. In no section examined has a canal extended into the shell for more than $35\ \mu\text{m}$ where it is invariably sealed off from the interior by outwardly concave shell layers (Pl. 75, fig. 5).

Growth and function of spines. The structure and distribution of spines give a good indication of the way they grew and even of their function.

The canals of all large spines seen in longitudinal section penetrated the shell to communicate with the interior. In living specimens, therefore, the canals would have been lined with outer epithelium surrounding a central core of connective tissues (text-fig. 1). Remnants forming the basal stumps of spines taper distally in thickness and the mineral

layer forming the tips of spines up to 6 mm long must be very thin indeed. Such tips could only have been deposited by newly formed outer epithelium and must mark the sites of tissue capable of generating outer epithelium throughout the life of the animal. Assuming this tissue to be persistent patches of the intramarginal generative zones that controlled the expansion of shell and mantle, one would expect outer epithelium released at the tips of spines to follow the full secretory regime characteristic of the mantle



TEXT-FIG. 2. Stylized reconstruction of the mantle edge of *Siphonotreta* to show the relationship between small spines and the outer mantle lobe.

generally. Judging from the regimes of living Acrotretida (Williams and Wright 1970, p. 14), each large siphonotretacean spine would have borne a continuously replenished cap of mucopolysaccharide covering a nozzle of periostracum which supplied the more persistent organic cover of the spine and acted as the seeding sheet for the mineral components of the skeleton. Each generative tip would have remained active as long as the canal through the shell remained open for the free circulation of nutrients from the mantle. In this way each spine was capable of growing externally up to half the length of the shell.

The internal extension of the spine must have been effected by a localized ring of proliferating tissue which was unlike a generative tip because it gave rise to outer epithelium depositing shell only and not the entire succession of a complete secretory regime.

The small spines must have begun growing in the same way as the larger ones, but their walls are never more than 10–15 μm thick which is only about one-seventh the medial thickness of the valve. Consequently growth must have ceased when a spine was only a short distance within the expanding margin of the shell (text-fig. 2). At this stage

in development, the canal was constricted and then closed by accelerated shell deposition within a narrow ring-like zone forming the canal base. The outwardly concave disposition of growth surfaces defining the proximal end of the canal shows that secretion continued on both sides of the constriction until the canal was completely sealed off. Living tissue must, therefore, have occupied the canal up to the moment of its closure. Thereafter, following severance of all mantle connections, the tissue within a small spine would have died and no vital function could have been carried out by the feature.

In his functional interpretation of the spines of *Acanthothiris* which were proximally closed like small siphonotretacean spines, Rudwick (1965, p. 610) explored a number of possibilities but concluded that they acted as sensory mechanisms and protective grilles. In so far as spines have always been advantageous to brachiopods, their dense distribution in grille-like arrays, protecting both the commissure and the shell surface, is probably the most significant benefit bestowed by their growth. The degree of sensitivity of the spine tips, which must always have been adequately covered by layers of mucopolysaccharide and periostracum, is unknown. It cannot be relevantly assessed by comparing spine tips with the mantle edge which normally bears long setae serving as highly efficient tactile organs. Indeed our own impression is that the mantle edge of living *Crania*, which lacks setae, is much less sensitive to physical changes in the environment than that of setae-bearing species like *Terebratulina*. In contrast, as Shiells (1968, p. 503) pointed out, the tendency for prostrate spines to form interlocking grilles around the commissural gape of feeding animals ensures an effective sieving of inhalant currents. Even for the shell surface, a dense spine mesh serves a protective function. One of the most striking aspects of the typical brachiopod exterior is the richness of the benthic microfauna living on the periostracum and burrowing into the shell. In particular, overlapping growths of bryozoans, sponges, algae, etc., which encroach on the commissural zone of the brachiopod shell, must have deleterious effects. Dense mats of spines are less suitable substrates for such growths and so reduce successful colonization of the brachiopod exterior by microbenthos.

Thus both types of siphonotretacean spines are more likely to have protected the shell and acted as a feeding sieve than to have served as a sensory mechanism. In this context there appears to be no difference between the two sets except that the continuously growing larger spines, row by row, may have kept pace with the expansion of the shell margin and so formed an ever-present outer grille. This barrier would have prevented the coarsest particles carried by the inhalant current from reaching an inner grille of finer spines immediately peripheral to the shell edge.

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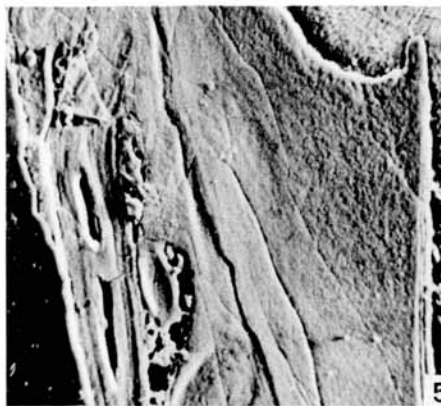
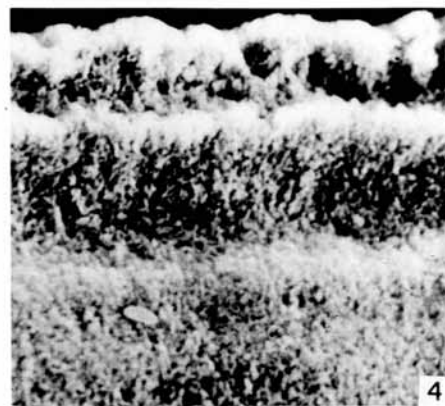
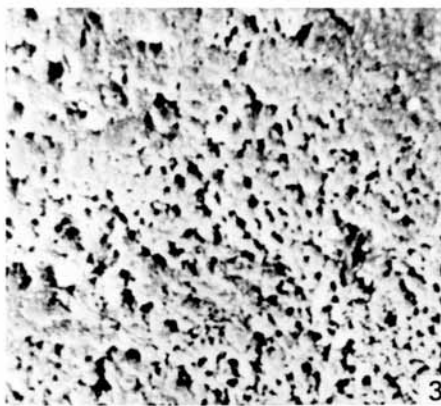
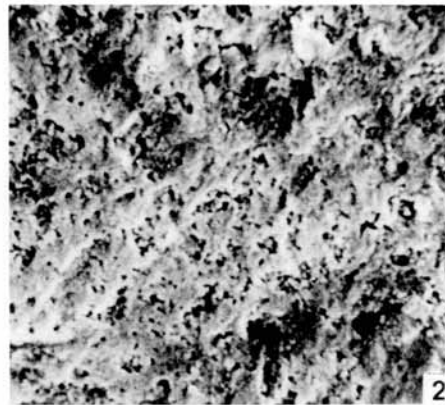
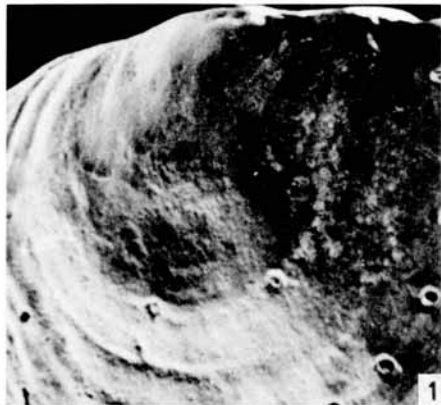
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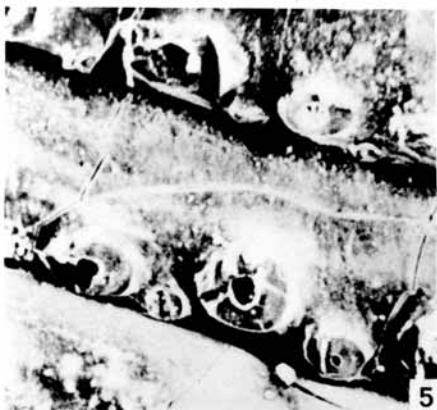
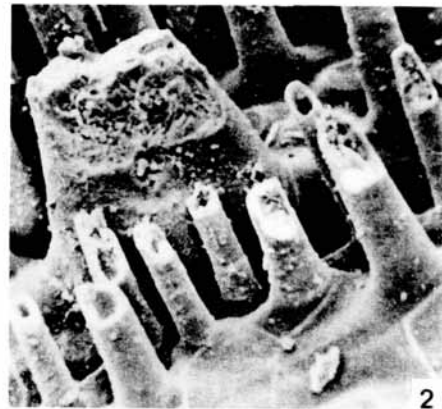
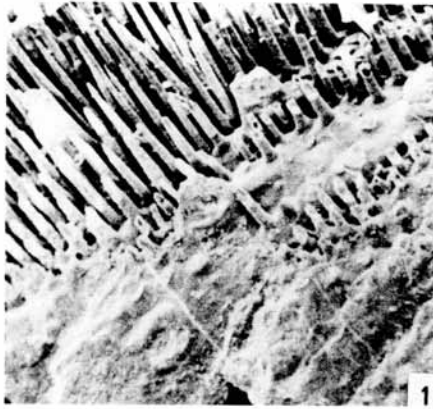
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