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CONTRASTING MODES OF CONSTRUCTION OF RETIOLITE-TYPE RHABDOSOMES

Abstract. — Investigation of retiolite-type rhabdosomes has so far revealed two contrasting types of construction:

1. In a morphological series including *Reteograptus geinitzianus*, *Gothograptus nassa*, *Holoretiolites* spp. and '*Retiolites*' sp. it is possible to demonstrate that sclerotization of the periderm secreted between the zooid and its mantle evagination became progressively localized, culminating in the formation of the highly specialized and sparse framework of *Holoretiolites* and '*Retiolites*' sp.

2. In *Retiolites geinitzianus* (Barrande) the same kind of peridermal secretion combined with localized sclerotization to produce a superficially similar type of rhabdosome to some of those in the above morphological series, but with a quite different relationship to the secretary tissues of the zooids.

Secretion and sclerotization of fibrous strips or 'bandages' seems to have occurred in many normal graptoloids, but resulting in the formation of a continuous cortex. The restriction of the sclerotized 'bandages' in the retiolites, so as to produce a sparse but resilient framework, suggests that their function was mechanical rather than protective.

PART 1. CONSTRUCTION OF *RETEOGRAPTUS GEINITZIANUS* *GOTHOGRAPTUS NASSA*, *HOLORETIOLITES* AND '*RETIOLITES*' SP.

In 1972 and 1973 Kirk attempted to explain the construction of normal and retiolite-type graptoloid rhabdosomes in terms of a model for graptoloid secretion. This was based on the conventional view that graptolite periderm was dual, made of fusellar increments overlaid by cortical laminae. With Urbanek and Towe's revelation (1974, 1975) that the periderm was formed of successive single increments, arch-shaped in longitudinal section, it became necessary to modify some of the details of rhabdosome construction (Kirk 1974, 1975) though the model invoked for secretion was essentially correct.

Revision of the ideas on retiolite construction was difficult because at first only flattened and carbonized material was available for examination by SEM. Nevertheless it was found possible to work out most

of the details of construction of *Retiolites geinizianus* (Barrande) by systematically chipping away at this material. These conclusions were confirmed and amplified when we were able to examine an isolated distal fragment of this species given to us by Dr. A. C. Lenz. Our understanding of retiolite structure was further increased by the study of isolated material of *Holoretiolites* and *Gothograptus* sent to us by Professor Dr. G. F. Lutze and Dr. H. Jaeger, of *Reteograptus geinitzianus* Hall sent by Dr. S. Finney, and of a species of *Retiolites* sent by Dr. R. B. Rickards. We would like to take this opportunity of expressing our deep indebtedness and gratitude for the gift of these specimens which have provided the key to a truer understanding of retiolite construction.

In *Reteograptus geinitzianus* the sicular periderm is preserved even in young rhabdosomes, and shows good incremental structure in the metasicular part even though this is overlaid by strips or 'bandages' of cortical material showing strong parallel fibres (pl. 4:1). These strips are mainly longitudinal extending without interruption along the thick longitudinal ribs of the prosicula onto the metasicula. In the other direction they extend along the nema. Some of these longitudinal strips are more than half the length of the sicula — about 0.4 mm. There are also a few diagonal strips, and others swing into parallelism with the metasicular rim (pl. 4:2). There is no sign of a prosicular rim. The metasicular rim is also lined with fibrous strips, but these do not seem to extend far into the interior which is lined by a finer fabric. The fibrous strips edging the metasicular rim turn along the virgella on its obverse and reverse sides, but its inner face seems to be covered by fine fabric.
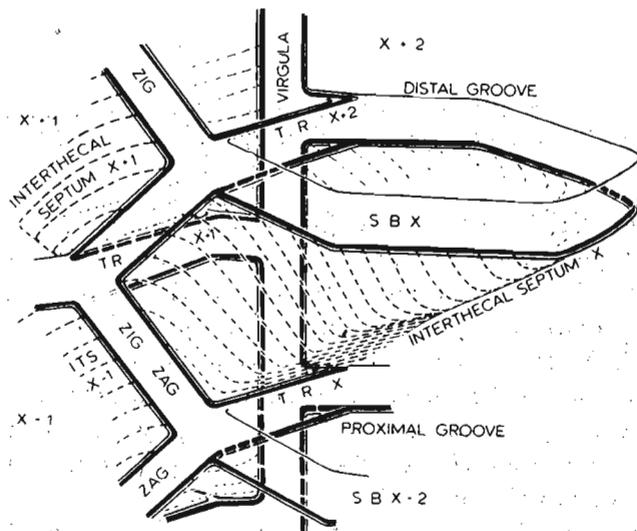

Fig. 1. *Retiolites geinitzianus.* Ideogram showing incremental membranes of three interthecal septa passing into grooves in the framework of list, S.B.X. — septal bar of zooid X, R.R.X.+2 — transverse rod of zooid X+2.

The hood of 1^1 has coarsely fibrous strips on its outer surface, but it is lined by fine fabric which also extends as a broad band across the reverse face of the metasicula to the origin of the ventral list of 1^2 (pl. 1:2; pl. 4:3). It covers and masks the coarsely ribbed longitudinal strips of the metasicula and so is later, though the fibrous strips are themselves clearly later than the 'fusellar' increments.

The ventral lists of 1^1 and 1^2 each receive 2 or 3 ribbed fibrous strips from the metasicula and these can extend, without interruption, to the apertures. They cover the ventral and rather more obverse face of each list, and are separated by a reverse seam and an obverse seam from the fine fabric covering the distal and rather more reverse face (pl. 4:2). This fine fabric links with the hood-lining of 1^1, with the band of fine fabric crossing the sicula to 1^2, and with a hoop-shaped list extending from the ventral list of 1^1 to the dorsal list.

The obverse and reverse prosicular lists arise on the ab-apical side of the thin areas between the prosicular ridges. Coarsely fibrous strips extend from the prosicula along the outer, obverse face of the obverse list, with 2 seams separating them from fine fabric on its reverse face (pl. 5:2).

In young specimens the reverse prosicular list is also seen to receive coarsely fibrous strips from the prosicula, but in other specimens this list and the adjacent prosicula are overlaid by a fine fabric. The other main lists of the juvenile rhabdosome — the ventral longitudinals, the dorsal zig-zag and the horizontal lists, all have coarsely fibrous strips on their outer faces and fine fabric on their inner faces, a seam on each side separating the two fabrics.

It is clear, from older specimens, that the windows in the framework of lists were once closed by incremental periderm (pl. 5:5). Over this periderm was secreted sclerotized sheeting, possibly made up in part of coarsely fibrous strips rather like that covering the sicula. These tend to run along and parallel to the lists, but locally they cross a list and run out over the incremental periderm (pl. 5:3). The resulting membrane seems to have been attached to the lists in such a way that the outer surface of the rhabdosome is very smooth, while the lists project strongly on the inner surface (pl. 5:4).

The reverse prosicular list is wholly internal in the adult colony. The coarsely fibrous strips covering it in very young rhabdosomes could perhaps be related to a stage in astogeny when it was exposed. The obverse face of the obverse prosicular list remains exposed on the obverse side of the colony.

It seems reasonable to conclude from this that the thecae as well as the sicula were formed initially of normal overlapping peridermal increments, arch shaped in longitudinal section. Even in very young rhabdosomes the peridermal increments of the sicula were overlaid by cortex

in the form of coarsely fibrous strips following certain selected paths —
mainly longitudinal — down nema, prosicular ribs and metasicula, but
swinging into parallelism with the metasicular rim, and into the bases
of the sicular and prosicular lists. It is not possible, from examination of
our material by SEM, to say whether these strips of fibrous material
were directly continuous with arch-shaped increments secreted in the
evagination of extrathecal tissue at the growing extremity of the rhab-
dosome. There is, however, little doubt that they were secreted by the
lining of that mantle of evaginated tissue and therefore had potential
continuity with the contemporaneously secreted distal increments.

In the sicula of *Reteograptus* the sclerotized fibrous strips were added
early, before the sicular mantle was withdrawn prior to the secretion
of fine internal fabric over them by the crossing canal of 1^2. They were
also added at the time of the growth of the meta- and prosicular lists,
serving to stiffen them and bind them to the sicula and give them tensile
strength. This early secretion of the fibrous strips led to the preservation
of the initial incremental periderm of the sicula even in very young rhab-
dosomes.

Beyond the sicula the sclerotized fibrous strips were again added early
to the outside of the initial incremental periderm, but evidently only
along selected paths to form the lists. On the inside of the lists a fine-
textured rather soft fabric seems to have been secreted by the zooidal
epithelium so that the lists developed an almost circular cross section.
Beyond these lists the incremental periderm itself was not sufficiently
sclerotized and was not overlaid by sclerotized layers or fibrous strips
soon enough to be preserved in young fossilized rhabdosomes. Traces of
it can be seen as ragged edges along the seams separating the coarsely
fibrous external fabric from the fine internal fabric of the lists.

Probably considerably later the secretion of sclerotized fibrous strips
appears to have spread from the lists over the initial incremental mem-
brane covering the theace. This process started at the oldest, proximal
end of the rhabdosome and spread distally, with the result that in old
colonies the proximal windows between the lists are closed, while in-
creasingly large unsclerotized areas remained over the more distal thecae
and appear as holes in the fossils.

Since traces of parallel fibres are only occasionally visible on the
external surface of the periderm, usually adjacent to the underlying lists,
it would appear possible that the secretion of fibrous bandages was suc-
ceeded by a more general fine textured sheeting which resulted in
a smooth outer surface over the mature rhabdosome.

On the inside a fine textured sheeting also smooths over the junction
between lists and periderm, but the lists project strongly on the inside
suggesting that the sheeting was thick only where it lined the lists but
attenuated rapidly where it passed onto the incremental periderm of the

windows. The tendency to deposit thick cortex on the outside of the incremental periderm and a thin cortical lining on the inside recalls the secretion of 'normal' graptoloids.

The ventral walls of the thecae arise from a distal seam in the postapertural list. A proximal seam on this list can be followed back down the inside of the adjacent longitudinal and horizontal lists and bears traces of an interthecal septum. A seam and ragged fringe can also be traced distally on the inside of the zigzag list from a point between thecae 3^1 and 4^1. This suggests the existence of a median septum which may never have been overlaid by sufficient sclerotized layers for preservation. Proximal to this, the zigzag list is smooth on its inside and the virgula appears to lie free within the rhabdosome.

In *Gothograptus nassa* (Holm) there are no preserved traces of normal incremental periderm, and the interpretation of the structure is therefore more difficult.

In this retiolite the sicula is preserved as a network of lists, but its form and situation within the proximal end of the colony leave no doubt
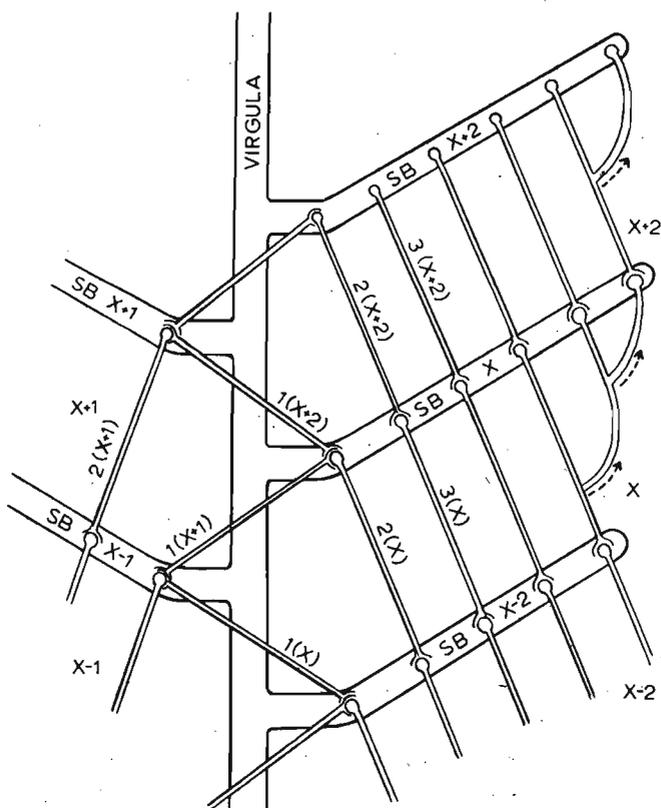

Fig. 2. *Retiolites geinitzianus*. Ideogram showing relationship of reticular threads to septal bars.

of its identity (pl. 6:1). The lists were clearly secreted from the outside, the earliest component strips being visible on the inside (pl. 7:2). The longitudinal strips were earliest — probably serving the same méchanical purpose as the longitudinal fibrous strips in *Reteograptus*. Later transverse strips were deposited outside them. The longitudinal lists extend from what were presumably the prosicular rods to a fairly well defined apertural rim. The principal longitudinal list projects beyond this rim and probably corresponds to the virgella. It forks to form the so called ancora. In our specimen, which may be a rather old colony, the ancora is extremely massive (pl. 6:2). Although it appears to fork again rather irregularly, this may be a somewhat tendentious way of describing what could also be described as a network of ancora lists over the proximal end of the colony (pl. 2). These lists were clearly secreted from the inside — the opposite of the lists forming the sicular reticulum. Where the ancora lists join the apertures of 1^1 and 1^2 their smooth innermost and youngest layer is continuous with the last formed covering of the apertural list (pl. 6:4).

The ancora network lies inside an outer reticular network. This outer network closely resembles that of the sicula and was clearly secreted from the outside. Where it joins the apertures of 1^1 and 1^2 the youngest, outermost, slightly pustulose layer is continuous with the covering of the apertural list (pl. 6:3). The ancora and reticular lists therefore come together at the apertural lists formed in the 'armpits' of the mantle evagination, but otherwise they do not coincide. It is presumed that *G. nassa*, as in *Retograptus geinitzianus*, the fibrous strips forming the ancora and reticular lists were secreted onto the inside and the outside of an initial incremental periderm.

The ancora network is restricted to the proximal end of the rhabdosome where the initial incremental periderm must have been thick, filling the gap between ancora and reticulum. More distally, just proximal to aperture 3^1, some of the more important reticular lists show evidence of an innermost ornamented layer secreted from the inside in contact with the layers secreted from the outside (pl. 7:4). Traces of a seam between the two could mark the insertion of the incremental periderm which becomes thin away from the proximal end.

Where no strips secreted from the inside are preserved one has to suppose that the original incremental periderm underlay the innermost layer of the reticulum, and that the edges of the strips forming the lists once extended as unsclerotized layers on to it (pl. 8:2; pl. 9:1). Evidence for this is provided by a fine, late-formed list which crosses a window at a 'high level'. It was evidently not secreted directly onto the initial incremental periderm but onto a thickness of unsclerotized layers extending over it from the edges of the strips forming the older reticular lists forming the window (pl. 7:1, 3; pl. 8:4, 5). More thin unsclerotized layers may

have lined the incremental periderm on the inside.

The apertural flaps were two sided, secreted within a fold of extra-thecal tissue. The outermost layers were clearly secreted in continuity with the outermost layers of the adjoining reticular lists and have the same kind of pustulose ribbed decoration (pl. 8;3). This follows somewhat irregular, curved paths suggesting that it was laid down in strips or bandages on both the inner and outer surfaces which were completely covered. Where the fibrous strips are thin a fine concentric ridging is visible which seems to represent the original, incremental, possibly micro-fusellar, construction of the flap (pl. 8:1). This seems to be the only trace of the initial incremental periderm in *G. nassa*.

In *Holoretiolites mancki* (Münch) the sicula is not preserved, only the virgella may be represented by a thin rod. From it there extends a forking ancora — clearly secreted from the inside as in *Gothograptus* (pl. 9:2, and pl. 3). The ancora continued to be thickened while the virgella did not — so the sclerotized layers of the ancora end abruptly at the base of the virgella, forming a scar (pl. 9:3).

In this *Holoretiolites* there seems to be no overlaying of an ancora network by a reticular network such as occurred in *Gothograptus*; instead the 'ends' of the ancora lists appear to be grafted onto the 'beginnings' of the reticular lists (pl. 10:1 and 3). The reticular lists, as in *Gothograptus*, were secreted from the outside, with the youngest, ridged and slightly pustulose layer on the outside. If, as seems probable from *Reteograptus*, the lists were sclerotized strips laid down along certain preferred paths over an incremental periderm, one would expect to find traces of this periderm between the outer reticular strips and the inner ancora strips at the grafts. Such traces can be seen, and there is a tendency for the ancora and reticular strips to part along the ragged junction representing this unsclerotized periderm.

As in *Gothograptus*, the apertural lists were presumably formed in the armpit of the extrathecal evagination or mantle. In *Balticograptus*, viewed by transmitted light, apertural flaps somewhat resembling those of *Gothograptus* occasionally preserve a translucent membrane between concentric and radial thickening (pl. 10:2). It would seem that here the fibrous strips following the concentric and radial paths extended over thinner, slightly sclerotized layers in the windows between them. This might be regarded as intermediate between the stage seen in the *Gothograptus* apertural flaps where the incremental periderm was preserved between the fibrous strips, and the stage seen in the thecal walls of *Holoretiolites* and *Gothograptus* where, in the windows between the reticular lists, the original incremental periderm seems never to have been reinforced by sclerotized additions though it undoubtedly existed and thin unsclerotized membranes almost certainly extended on to it from the edges of the sclerotized strips forming the reticular lists (pl. 10:4).

In *G. nassa* and *Holoretiolites* secretion from the inside by the zooidal epithelium produced the ancora lists, and the lining occasionally developed on the inside of some reticular lists. It seems doubtful if unsclerotized layers extended from the strips forming these structures over the inside of the incremental periderm. If they did so extend, it seems likely that they were thin, as in the late lining of the incremental periderm in *Reteograptus geinitzianus* and in the cortical lining of normal graptoloids.

In another retiolite — provisionally called '*Retiolites*' sp. the structural network is even more sparse, but it seems that the virgula continued to be thickened in continuity with the virgella to form a stout axial support to the colony (pl. 10:5). The ancora grew in continuity with it, so there is no scar surrounding its base (pl. 11:2). There is, however, a seam on each side of the virgella, which passes into a seam on the proximal and distal sides of a hoop arising from it. It is suggested that the unsclerotized incremental wall of the sicula extended from these seams, the virgella and hoop representing local sclerotized fibrous additions to the inside and outside of this initial wall.

The ancora network is like a wheel with 4 spokes, the lists forming the rim and spokes all being secreted from the inside — i.e. the sicular side. Presumably the quadrant in line with the hoop would have served as an aperture for the sicular zooid but it seems in no way to differ from the other quadrants. The ventral lists of thecae 1^1 and 1^2 arise from the rim and extend distally till each forks to form an aperture.

In this species of '*Retiolites*' the seam postulated as the remnant of the incremental periderm of the sicula ends on the virgella, and does not extend down any of the spokes of the ancora network. This suggests that the common body of the sicular zooid and the daughter zooids 1^1 and 1^2 budding from it, extended beyond the sicular aperture and communally secreted the ancora network from the inside. In *Gothograptus* the reticular sicula had a sclerotized apertural rim, though the sicular zooid must later have extended beyond it to emerge through a window in the ancora network. In *Holoretiolites* the sicula was unsclerotized and one can only guess at the window in the ancora through which the siculozooid ultimately emerged.

In the '*Retiolites*' specimen the rim of the ancora network has its oldest layer facing away from the colony and continuous with the oldest strip-like layer on the spokes (pl. 11:1). The ventral lists of 1^1 and 1^2 on the other hand, have the oldest strip facing the colony and the youngest on the outside — like the reticular network of *Holoretiolites mancki* and *Gothograptus*. The ventral lists of 1^1 and 1^2 appear to have arisen from the outer side of the rim, possibly at first as a short projecting spine formed in the mantle armpits of zooids 1^1 and 1^2. Later strips of sclerotized material were added on the outside forming typical reticular lists. These ultimately forked presumably at the thecal apertures.

At the origin of the spokes an irregular fibrous network is seen on the outward-facing surface of the oldest, first formed layer (pl. 11:3). It was presumably secreted onto the incremental periderm which is not preserved. It could represent the fusellar core of an increment added distally, though here it represents only that part of its proximal extension which in normal graptoloids constitutes the cortical lining. It seems doubtful if the strips composing the ancora extended as unsclerotized layers over the inside of the incremental periderm in the windows of the ancora network. Whether the sclerotized strips forming the ventral lists of 1^1 and 1^2 extended as unsclerotized layers over the outside of the incremental periderm is also in doubt as the lists do not have the markedly flexed selvedges such as occurred in *G. nassa* and *Holoretiolites*. In fact, in '*Retiolites*' sp. the ancora and reticular lists are rather similar, somewhat cylindrical structures which presumably gave rigidity to the sparse rhabdosome.

Why then should the colony have secreted fibrous strips from the inside on to the incremental periderm to form the ancora network, and from the outside to form the lists of the reticulum? The answer may be suggested by the early development of *Reteograptus*, the most normal of this morphological series. When zooids 1^1 and 1^2 grew across the sicula, the mantle of sicula and zooids 1^1 and 1^2 was withdrawn allowing the zooidal epithelium of zooids 1^1 and 1^2 to secrete internal fabric across the sicula. In *Gothograptus nassa* this seems to have been accompanied by some extension of the siculozooid, and zooids 1^1 and 1^2 secretal internal fabric in continuity with part of the sicular aperture to form the first two branches of the ancora. It would seem, moreover, that in this example, zooid 1^2 passed round the 'obverse' side of the sicula.

In *Holoretiolites* and the '*Retiolites*' sp. the virgella was the only part of the sicula to be sclerotized, but the ancora was presumably again secreted from the inside by the communal zooidal epithelium of the siculozooid and 1^1 and 1^2.

Why was there then a change to secretion of sclerotized fibrous strips from the outside? One has to remember that all periderm is 2 sided, connected, at least potentially, by the incremental arches formed in the armpit of the evaginated extrathecal tissue at the growing ends of the colony. Thickening of the outer surface by secretion of sclerotized cortical sheets was the method adopted by most graptoloids — presumably because it best protected the soft fusellar core of the increments, because it did not reduce the living space of the zooids, and because the cortex, like the extrathecal tissue secreting it, extended without interruption over the whole surface of the rhabdosome. So, after secreting the ancora network, these graptoloids returned to the more orthodox mode of secreting cortex from the outside to produce the reticular network. This requir-

ed, in the morphological series described above, a variety of devices to weld the two networks together.

Secretion from the outside, by the lining of the communal mantle in which thecal boundaries had disappeared, provided the opportunity to construct a reticular network independent of growth increments and thecal boundaries, purely to meet the mechanical requirements of the colony. It is interesting that different combinations of longitudinal, horizontal and diagonal lists have been emlpoyed by different retiolites. Presumably all of these combinations successfully enabled the rhabdosome to resist distortion by the stress resulting from the coordinated ciliary action of the zooids. But the unsclerotized initial incremental periderm, and the unsclerotized layers extending over it from the reticular lists, must have been adequate to afford protection to the zooids. Evidently sclerotization was not essential for protection in graptolites — after all the vital mantle lay outside the periderm — sclerotization must have served a primarily mechanical function. This could account for the fact that overall secretion of sclerotized cortical layers, such as may have occurred in *Didymograptus* (Urbanek and Towe 1975; pl. 18), seems to have been replaced in many graptoloids by secretion of cortical strips or bandages along mechanically selected paths leading eventually to the retiolite condition.

PART. 2. CONSTRUCTION OF *RETIOLITES GEINITZIANUS*

A number of specimens preserved in shale, two specimens in limestone, and the isolated specimen kindly sent to us by Dr. A. C. Lenz formed the material for an investigation which began in 1974.

One of the specimens in limestone showed interthecal septa. These were semi-transparent when viewed by the light microscope, and bore clear traces of incremental boundaries adjacent to the virgula, zigzag list and septal bars (pl. 12:2). Examination by SEM of the zigzag list on the isolated specimen showed the incremental boundaries to be arch-shaped closures of fibrous sheeting which passed into each of the lateral grooves. Where the distal-facing angle between closure and zigzag list was obtuse the groove looked rather smooth, the closure being almost parallel to the surface of the list. But where the distal-facing angle was acute the closures were more clearly seen (pl. 12:1). On the opposite side of the zigzag list the same relationship was observed with the increments of the opposite interthecal septum.

A broken end of the zigzag list showed the increments making the obtuse angle to be attached to the outer layers of the list, while those of the preceding interthecal septum entering the opposite side at an acute

distal-facing angle were continuous with the innermost layers of the zigzag list (pl. 12:3, 4).

The increments of the interthecal septa on the opposite side of the rhabdosome turned distally into the virgula which grew ahead of the thecae, as in other biserial graptoloids. The increments passed into a groove on each side of the virgula and were clearly continuous with its outer layers (pl. 13:1). Successive incremental closures were inserted along the virgular and zigzag grooves and along the septal bar grooves which extended from them. The septal bar turned at right angles into the apertural list, and here the incremental closures became parallel to the list and formed the lining of its groove (pl. 14:1).

What do these relationships imply? It would seem that the zigzag list actually formed as locally-thickened continuations of the closures of the increments of the interthecal septum. The septal bar and apertural list were a continuation of this structure up to the thecal aperture. The increments of the interthecal septum of the next zooid on the opposite side of the rhabdosome (call it X+1) were added to the outside of the zigzag list initiated by the preceding zooid X. The interthecal septum of zooid X+1 began at the transverse rod at its proximal end (fig. 1).

The relationship of transverse rod to zigzag list and virgula could be seen at the confluence of their grooves.

Seen from the proximal side, the transverse rod appears to have developed from the more axial wall of the groove extending from the zigzag list or from virgula to the septal bar. The transverse rod appears to have arisen from this wall at first as a protuberance, a kind of short spine. Later increments presumably extended the reverse spine so that it met a similar spine extending from the obverse side of the rhabdosome. This formed a tube which usually appears as an open groove on the proximal side though later increments can be seen to have closed it adjacent to the zigzag list (pl. 13:2).

On the distal side of the transverse rod a somewhat similar groove occurred, confluent with the grooves on the virgula and zigzag list. This distal groove on the transverse rod never became closed, and it is concluded that it represented the attachment of the membranous interthecal septum. The membrane appears to have been continuous with the outermost layer of the transverse rod, the distal groove being floored by an apparently unbroken cylinder of fibrous sheeting (pl. 13:3 and 4). The transverse rod evidently corresponds to the ab-apertural list figured by Urbanek and Towe (1975: pl. 21). The thin interthecal septum into which it passes seems to be represented by a fringe of fibrils perpendicular to the rod. All these lists were clearly secreted from the outside by enveloping secretory epithelium. The grooves in the lists, and the insides of the arch-shaped increments entering the grooves, were probably once filled with a spongy fusellar fabric, but this is not preserved in our specimens

and it may never have been fully sclerotized. The incremental arches, and the concentric cylinders into which they pass to form the lists, were evidently the fibrous lamellae of the successive increments and must have formed initially in the armpits of the evaginated extrathecal tissue or mantle of the extending zooids.

In our specimen which is a distal fragment, the network or reticulum covering the rhabdosome is only attached to the septal bars. The threads of this network were clearly secreted from the inside, the outermost layers being the first formed — the oldest, the innermost layers being the last formed. The reticular threads joined the septal bars at a number of nodes between the angles and the apertural list. Each node had in it a hole (pl. 14:2—4).

Fractures through the holes show that the uppermost and oldest layer of the reticular thread passed down the hole to become confluent with an older inner layer of the septal bar. Successively formed lower layers of the reticular thread grew in continuity with successively added layers of the septal bar, and the lowest reticular layer was continuous with the outermost covering of the septal bar. Very late-formed reticular threads can be frequently seen passing into the outermost layer on the flank of a septal bar.

How did the growing colony of zooids achieve these relationships between the framework of lists and the threads of the reticulum? Young colonies preserved in shale show the most distal septal bar and apertural list to have formed a loop, with fine reticular threads extending to it from the previous septal bar of the same thecal series. No reticular threads are visible on the distal side of the youngest septal bar. This relationship suggests that the septal bar and apertural list were formed by local thickening of the incremental closures of the interthecal septum, the interthecal septum being at first the dorsal wall of theca X and formed under its evaginated mantle of extrathecal tissue. At this stage the sides of zooid X overlapped it, the theca being strongly concavo-convex in horizontal section. This allowed the zooidal epithelium of the sides to secrete reticular threads from the inside in continuity with the increments and septal bar formed as the dorsal wall of the same zooid X.

At a somewhat later stage zooid X+2 would have extended along the dorsal wall of X (now a true interthecal septum) and the mantle of extrathecal tissue would have been withdrawn from between them. This would have brought the zooidal epithelium of X and of X+2 into contact with the septal bar so that the further thickening of the septal bar would have been by the zooidal epithelia of the two adjacent zooids. Zooid X+2 would by now have been secreting its own dorsal wall edged by a new septal bar, and its sides would have been secreting reticular threads in

continuity with the outer layers of the septal bar of X proximal to it and with the inner layers its own septal bar X+2 along its distal edge.

The bodies of zooids X and X+2 were undoubtedly separated by the interthecal septum extending proximally and inwards from the groove in the septal bar. They were probably also separated outside the septal bar because no fibrous increments are seen to pass over the bar from X to X+2. Instead the fibrous increments formed two series, overlapping one another from the proximal and distal sides (pl. 15:1).

In contrast, where the septal bars bend inwards to meet the ends of the transverse rods, the fibrous increments occasionally pass over the outer face of the septal bar showing that the zooidal epithelia were here confluent, covering a kind of common canal external to the framework of axial lists (pl. 15:2). The order in which the reticular threads were secreted can be determined by an examination of the relationship of the oldest fibrous strips on the outward surface (fig. 2). Thus it is found that the first reticular thread to be secreted by zooid X extended from the oldest hole on septal bar X — 2, to the oldest hole on septal bar X — 1. The second reticular thread secreted by zooid X crossed its flank from the second hole in septal bar X — 2 to the oldest hole in its own septal bar X, reflecting the beginning of the extension of the theca from the common canal. The third reticular thread crossed its flank from the third hole in X — 2 to the 2nd hole in septal bar X and so on. Probably about this time zooid X+1 secreted its first thread diagonally from the oldest hole in septal bar X — 1 to the oldest hole in septal bar X. And a little later still zooid X+2 secreted its first diagonal from the oldest hole in septal bar X to the oldest hole in septal bar X+1.

Of course while new threads were being formed across the axial part of the rhabdosome, and successively away from the axial region along the septal bars towards the apertures, the older reticular threads were being thickened by addition from below in continuity with successive aditions to the outside of the septal bars.

The order of secretion of the reticular threads probably reflected the extension of the thecal walls surrounding the budding and growing zooids. As in most biserial graptoloids, the youngest thecae developing in the axial part of the rhabdosome seem to have formed a fairly even termination with the older thecae flanking them. The side walls appear to have been unsclerotized at first, apart from the fibrous reticular threads secreted across them. The paths chosen for this secretion would most effectively have supported the side walls as they grew, and the linkage of the successive septal bars by diagonals and longitudinals would also have contributed greatly to the resilience of the rhabdosome as a whole. The longitudinal threads were later jointed by transversals to give the reticular network.

At the apertures the extension of each theca beyond that of the preceding one of the same series, led to a slight modification of this pattern.

Transverse reticular threads appear to have grown out from the last complete longitudinal and then to have curved round to become a longitudinal passing into the next hole in the septal bar distal to it. A transversal from this thread may have repeated the process, passing into the next hole, and then yet another may have extended from this to pass into the last hole of the septal bar. As a result the ventral edge of the rhabdosome became straight from theca to theca, and approximately parallel to the long axis of the colony.

In a specimen preserved in shale the reticulum is seen to extend across the distal parts of the proximal 3 or 4 apertures (pl. 1:1). This seems to have been the consequence of an even greater ventral extension of the distal parts of the thecal walls. This resulted in ventral fusion, and reticular threads were secreted across from the reverse to the obverse face. In later thecae the ventral extension became progressively less and the reticular network formed progressively smaller lobes until in the fully adult part of the rhabdosome the extension was only enough to produce the characteristic straight ventral edges.

Although the apertural list probably originated as the thickened closure of the increment completing the dorsal wall of zooid X, as the zooid X+2 extended along it, it became the proximal apertural list of that zooid and it continued to be thickened in the mantle armpit of zooid X+2. The last longitudinal reticular thread adjacent to the proximal part of the aperture of X+2 was also formed in the same mantle-armpit and shared in the prolonged thickening. This produced an outwardly turned flange which framed the more proximal part of the aperture.

In an older etched specimen on limestone some of the reticular threads near to the aperture also show an overturning of the fibrous strips in an axial-proximal direction. This suggests that these, and perhaps all the more-regular, longitudinal, reticular threads, could have originated in the mantle-armpit of the growing zooids.

Viewed from the outside, the fibrous strips composing the reticular threads sometimes show indications of layering. A thin layer of irregularly anastomosing fibrils passes down into closely packed, parallel fibrils (pl. 16:1, and 2).

Viewed from the inside, the reticular threads and closed windows appear only to be formed of successive strips of parallel fibrils, and similar strips are seen to enwrap the framework of lists. The oldest strips, seen on the outside of the reticular threads, are 20—30μ in width and these increase to a width of 50 or 80μ in the case of the youngest, innermost strips, and to 100μ over the lists of the framework. Viewed from the inside the strips end abruptly at their sides where they overlie earlier strips. They terminate longitudinally in a rather irregular fringe of fibrils (pl. 16:3).

The strips of parallel fibrils tend to run parallel to the reticular

threads and to the lists of the framework, but they can also run obliquely across the latter and may form strongly curved wrappings — especially over junctions. A single fibrous strip can also be followed for up to 1000µ along a very irregular path on the inside of the reticulum. This could certainly not have been secreted within a mantle armpit.

The reason for the different appearance of the reticular strips, when viewed from the inside and from the outside, seems to lie in the incremental mode of graptolite secretion. In graptolite periderm each distally added increment consists of a core of fusellar fabric bounded by a lamella of parallel fibrils. The fusellar core is arch-shaped in longitudinal section and the lamella extends back over it to form the limbs of the arch. More proximally the increments on the inside and on the outside of the thecal wall could consist of an attenuated layer of fusellar fabric separated from the secretory epithelium by a lamella of parallel fibrils, though more usually the fusellar layer is omitted.

In *Retiolites geinitzianus* the sclerotized fibrous secretion which formed the reticulum and thickened the framework of lists was secreted by the epithelium covering the zooids. It therefore corresponded to the cortical lining of normal graptolites. It was presumably secreted onto the inside of an incremental periderm which was not sufficiently sclerotized for preservation.

Seen from the outside there is some suggestion that each fibrous strip of the reticulum passed laterally into a thin membrane which once adhered to the inside of the incremental periderm. In the angles of the reticular windows, gaps between successive fibrous strips show signs of having been occupied by loose fusellar fabric (pl. 17:1, 2 and 3). Where the reticular windows eventually became closed by extension of the fibrous strips secreted from the inside, this fusellar fabric thinned out allowing the fibrous strips to form a dense sheeting lining the bulged-out periderm in the windows. The fusellar fabric also thinned out under the window frame so that the late fibrous strips increasingly thickened the dense reticular threads. Being formed as a kind of cortical lining, the strips forming the reticulum and thickening it from the inside would have increasingly reduced the living space of the zooids, causing the incremental periderm to bulge out through the reticular windows. It seems likely therefore that unsclerotized extensions from the fibrous strips on to the incremental periderm would have been reduced to very narrow strips of attachment.

Over the septal bars, between the nodes for the entry of the reticular threads, the fibrous strips overlapped alternately from the proximal and distal sides. It seems impossible that these could have extended as unsclerotized layers lining the incremental periderm. The later formed layers covering the septal bars do not overlap, and there is evidence that the strips composing them extended as a lining to the periderm bulging out

of the windows on either side of the septal bar. Over the apertural lists and adjacent flanges the fibrous strips were secreted in the mantle-armpit and therefore represent true cortex. They are, of course, continuous with and indistinguishable from those of the cortical lining.

The flange framing the more proximal part of the aperture is formed of incremental strips which end in unusually ragged edges (pl. 17:4). It is suggested that during life these extended as unsclerotized layers over the incremental periderm. They would correspond to the outer cortical layers of normal graptoloids, and would have been secreted from the outside by the lining of the mantle. In one of our specimens an unusually extended frange covers the adjacent reticulum, and seems to represent the spread of sclerotized strips on the outside comparable to that which closed the windows on the inside of the incremental periderm.

According to Holm (1890) old specimens of *Stromatograptus* were covered by an outer sclerotized layer masking the outlines of the reticulum. The further spread of sclerotized strips from the extended flange in our specimen, over a thickness of unsclerotized layers extending from the ragged edges of the earlier increments of the flange, could also have had this effect. So it is suggested that in *Retiolites geinitzianus*, as in *Reteograptus geinitzianus* described in the first part of this paper, the unsclerotized incremental periderm 'glazing' the windows of the reticulum, eventually became coated on the inside and on the outside by sclerotized material secreted as cortical lining and cortex by the zooidal epithelium and lining of the mantle.

In the case of the cortical lining there would seem to have been little or no thickness of unsclerotized layers intervening between the incremental periderm and the sclerotized strips which later lined the windows. In the case of the outer cortex there may have been a considerable thickness of unsclerotized layers extending from the ragged edges of the increments of the flange over the incremental periderm, (compare *G. nassa* and *Holoretiolites*). These unsclerotized layers and the underlying incremental periderm would have been increasingly bulged-out by the pressure of the reticular threads as these became progressively thickened from the inside. They would therefore have needed to remain elastic while this thickening continued. Presumably only in old rhabdosomes would secretion of sclerotized strips have extended over these layers, masking the outlines of the reticulum as shown in Holm's illustration, and preventing further bulging.

This could have been a gerontic effect, like the massive thickening of the ancora lists in old specimens of *G. nassa*. It could hardly have been a response to mechanical requirements since the lists of framework and reticulum satisfied these in the earlier growth stages of the colony. And it could hardly have been a response to a need to protect the zooids since the incremental periderm and unsclerotized layers over the windows had

previously afforded adequate protection. Also, as emphasized in the previous section, it has to be remembered that in all graptolites the extrathecal mantle lay outside all peridermal structures and presumably escaped serious damage by some invisible, possibly chemical, protective device and was able to heal minor damage by regeneration of the secretory epithelium preparatory to regeneration of the periderm.

Secretion of cortex and cortical lining in the form of strips of parallel fibrils was not peculiar to retiolite graptoloids. In many normal graptoloids it seems to have taken the place of more continuous sheeting (Crowther and Rickards 1977). It could have been the secretion of such strips which led to the frequency of 'unconformities' between cortical increments as seen in longitudinal section, and to their apparent separation from the distal increments. Many of the strips were very probably not secreted in direct continuity with distally added increments, but potential continuity was always ensured by the continuous secretory epithelium covering the zooids and lining the mantle.

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December 1977

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DISCUSSION

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It should be emphasized that there is no a priori reason for assuming that a retolitid skeletal structure must have been secreted within folds of soft tissue and not by the use of a simple mortaring scheme like that employed by the recent pterobranch hemichordates. The versality of the pterobranch mode of secretion is often underestimated. Even in our present woefully inadequate state of knowledge concerning details of the method used to construct their coenecia, it is clear from John's (1931) description of the subgenus *Cephalodiscus* (*Acoelothecia*) that a swarm of free living zooids is perfectly capable of building a coenecium from a framework of rods. John's illustration of a fragment of distal periderm bears a striking resemblence to the reticulum of *Retiolites geinitzianus densireticulatus* (note, their relative scale is different). He also described a gradual rounding off of 'list' junctions and filling in of the orifices with age, similar to the retiolitid skeleton. Of course, this is not strictly evidence in favour of a similar mode of secretion for retiolid graptolites. But it must be realised that *Cephalodiscus* manages to build a similar structure, without the aid of a covering of soft tissue, using only its cephalic shield (and possibly the tentacles). Thus, it seems reasonable to admit the possibility that retiolitids had a similar capability.

Evidence in favour of a pterobranch mode of secretion for other graptolites is mounting (see Crowther herein; Crowther and Rickards 1977) and is particularly conclusive for the diplograptids, where bandaged cortex is most strikingly observed. Bandaging also occurs on the proximal, sclerotized thecae of *Orthoretiolites* and can be seen on Kirk's micrographs of *Reteograptus*. These observations are in accordance with the generally accepted view that retiolitids originated (polyphyletically) from diplograptid stock. The surface of lists on *Retiolites geinitzianus densireticulatus* are constructed from arrays of parallel fibrils. The arrays often exhibit complex unconformity patterns near list junctions where they overlap, similar to the arrangement of cortical bandages on normal graptolite periderm. Thus, it seems more likely that retiolitid graptolites adapted the secretionary scheme of their ancestors, the diplograptids, to produce a scaffolding-like structure of rods and lists, just as *Acoelothecia* reduced the normal, continuous periderm of other *Cephalodiscus* subgenera to a similar meshwork.

More work must be done on other retiolitid species in conjuction with further research into the ultrastructure and mode of secretion of the cephalodiscan skeleton if the tempting comparison outlined above is to be proved meaningful.

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EXPLANATION OF THE PLATES 1—17

All photographs taken with a Cambridge Stereoscan 600 unless stated otherwise.

Plate 1

Reteograptus geinitzianus

1. Proximal part of rhabdosome, drawn from a specimen preserved in shale.
2. Diagram of young rhabdosome showing sicula and framework of lists seen from reverse side. Bandages of parallel fibres shown by stipple, fine internal fabric shown uncoloured.
   H — hood, *I.* — hoop-shaped list.

Plate 2

Gothograptus nassa

Diagram of proximal end of rhabdosome, (*a*) seen from the inside, (*b*) seen from the outside. Lists of ancora shown white, lists of the reticulum shown stippled.
S — window in ancora-network which may have served as the aperture for the extended siculozooid.

Plate 3

Holoretiolites mancki

Diagram of proximal end of rhabdosome, (*a*) seen from the inside, (*b*) seen from the outside, with outside of reticular lists shown stippled.
S — window which may have served as the aperture for the extended siculozooid.

Plate 4

Reteograptus geinitzianus (Upper Ordovician, USA)

1. Sicula of young specimen showing incremental periderm overlain by bandages with strongly developed parallel fibrils.
2. Apertural part of sicula. Note the fibrous strips running parallel to the aperture and swinging diagonally into the ventral list of theca 1^2.
3. Abapertural edge of band of fine fabric extending across the reverse face of the metasicula and partly masking the coarsely fibrous strips underneath.

Plate 5

Reteograptus geinitzianus (Upper Ordovician, USA)

1. External cortical tissue on sicula, showing the end of a later strip overlying an earlier one. An earlier NNW fibrous strip is overlain by a younger ENE strip with an irregular termination.
2. Obverse prosicular list with seam between the ribbed fabric on the obverse face and fine fabric on the reverse face.

3. Outer surface of mature specimen. The ribbed strips tend to run parallel to the lists but also cross them onto the incremental periderm.
4. Cross-sections of list and membrane of mature specimen outer surface uppermost.
5. Traces of incremental boundaries in periderm filling all windows in the framework of lists in a mature specimen.

Plate 6

Gothograptus nassa (Erratic boulder, FRG)

1. Proximal end of incomplete mature specimen, with sicula partly preserved as a reticulum of liste secreted from the outside.
2. Oblique view of specimen of 1, viewed from the other side, showing thickened ancora secreted from the inside.
3, 4. External and internal views of the aperture of theca 1^1, showing its attachment to the reticulum (R) and to the ancora (A).

Plate 7

Gothograptus nassa (Erratic boulder, FRG)

1, 3. Two external views of a late reticular list, crossing an aperture at a high level. Compare with pl. 8:4, 5 which show internal views of the same list.
2. Close up of the sicula seen in pl. 6:1; V — the main virgellar list.
4. Internal view of reticular list, with additional tissue added internally. Note its rounded surface, and pustulose ornament. Compare with pl. 9:1.

Plate 8

Gothograptus nassa (figs 1 and 3 from Central Wales, figs 2, 4, 5 from erratic boulder, FRG)

1, 3. Latex replicas of the internal and external surfaces of apertural flaps, with growth lines on the internal surface and bands of regular pustules on the external surface.
2. Internal view of junction of ventral reticular list with apertural flap. Note the inturned edges of the strips forming the list.
4, 5. Internal views of the late reticular list, seen in 1 and 3.

Plate 9

Gothograptus nassa (Erratic boulder, FRG)

1. Oblique internal view of reticulum, showing tissue added from the inside (compare with pl. 7:4).

Holoretiolites mancki (Erratic boulder, FRG)

2. Proximal end of rhabdosome, seen from the outside. Reticulum has pustulose ornament facing outwards, ancora has a smooth surface with an external seam in which earlier layers are visible.
3. Close-up of junction of ancora and virgella.

Plate 10

Holoretiolites mancki (Erratic boulder, FRG)

1, 3. Junction of ancora (lower) and reticular list rimming the thecal aperture, external and internal views. The seam between ancora and pustulose reticulum in 1 probably represents the insertion of the incremental periderm.
4. Cross-section of reticular list, showing inwardly turned edges of the component strips.

Balticograptus sp. (Erratic boulder, FRG)

2. Light microscope photograph of apertural flap of theca showing translucent membrane between concentric thickenings or lists.

"Retiolites" sp. (Lower Silurian, Sweden)

5. Proximal end of rhabdosome, seen from the outside;
A — ancora, V — virgella, H — hoop.

Plate 11

"Retiolites" sp. (Lower Silurian, Sweden)

1. Rim of ancora seen from outside looking towards sicular apex, with ventral list of theca 1^1 (VL) at top left, and ancora 'spoke' (AS) to lower right.
2. Ancora and base of virgella (V) seen from inside looking towards sicular aperture.
3. Same, seen from outside showing the first formed layer.

Plate 12

Retiolites geinitzianus (1, 3 and 4 Silurian, Canadian Artic; 2 erratic boulder, FRG)

1. Zig-zag list, looking distally across an angle between "zig" and "zag". Proximally to this angle the groove appears smooth with closure of increments almost parallel to the list. Distally the closures make a higher angle with the list and are more clearly seen.
2. Light microscope photograph of zig-zag list (ZZ) and junctions with septal bar (SB). The increments of three interthecal septa appear as dark lines curving into the zig-zag list and septal bars.
3, 4. Broken end of zig-zag list shown in a composite photograph taken from above (4) and below (3). On the upper side, the increments of ITS X preceded the growth of the list and form its innermost layers. On the lower side increments of ITS X+1 form its outermost layers.

Plate 13

Retiolites geinitzianus (Silurian, Canadian Arctic)

1. View looking distally along the virgula and showing increments of an interthecal septum continuous with the outer layers of the virgula.

2. Junction between transverse rod (TR), zig-zag list (ZZ) and septal bar (SB). A fibrous 'bandage' covers the groove on the proximal side of the transverse bar.
3. Distal face of transverse rod, with a distal groove representing the origin of the interthecal septum late in the development of the rod.
4. Distal side of junction between transverse rod (TR), virgula (V) and septal bar (SB).

Plate 14

Retiolites geinitzianus (Silurian, Canadian Arctic)

1. Groove on septal bar (SB) and apertural list (AL) with traces of incremental closures of the interthecal septum.
2. A node on an 'E-W' septal bar is joined by reticular threads from 'N' and 'S'.
3. Septal bar (SB) with reticular threads entering a node from SW and NE. Later transverse threads cross these from NW to SE, and a very late thread joins an outer layer on the septal bar.
4. Fractured septal bar and reticulum junction. The oldest layers of the reticular thread pass down the hole to become confluent with the innermost layers of the septal bar. The reticular thread entering from the right has been broken off.

Plate 15

Retiolites geinitzianus (Silurian, Canadian Arctic)

1. Outer face of septal bar, between reticular junctions or nodes. The two zooids separated by it have secreted alternately overlapping fibrous layers of which it is constructed.
2. Outer face of internal portion of septal bar between the innermost reticular junction and the junction with the zig-zag list (top). The fibrous bandages occasionally pass right over the bar.
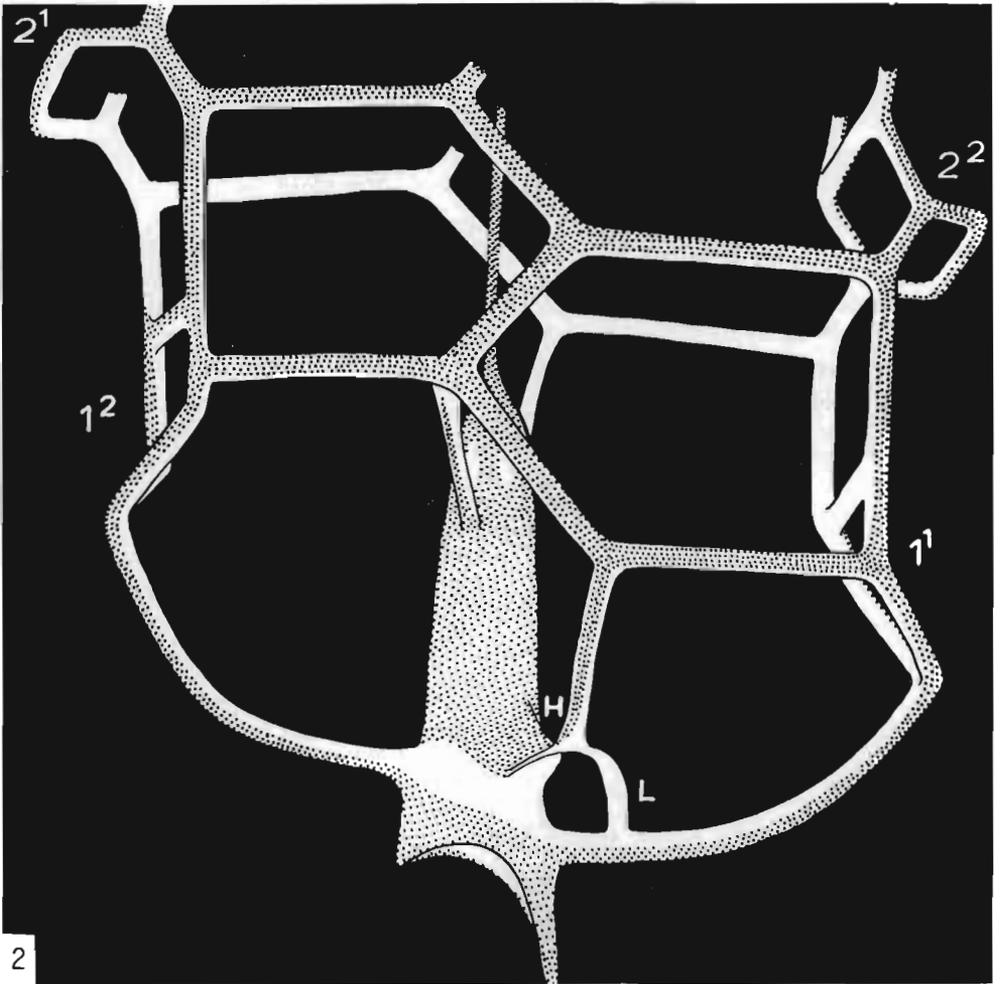
Plate 16

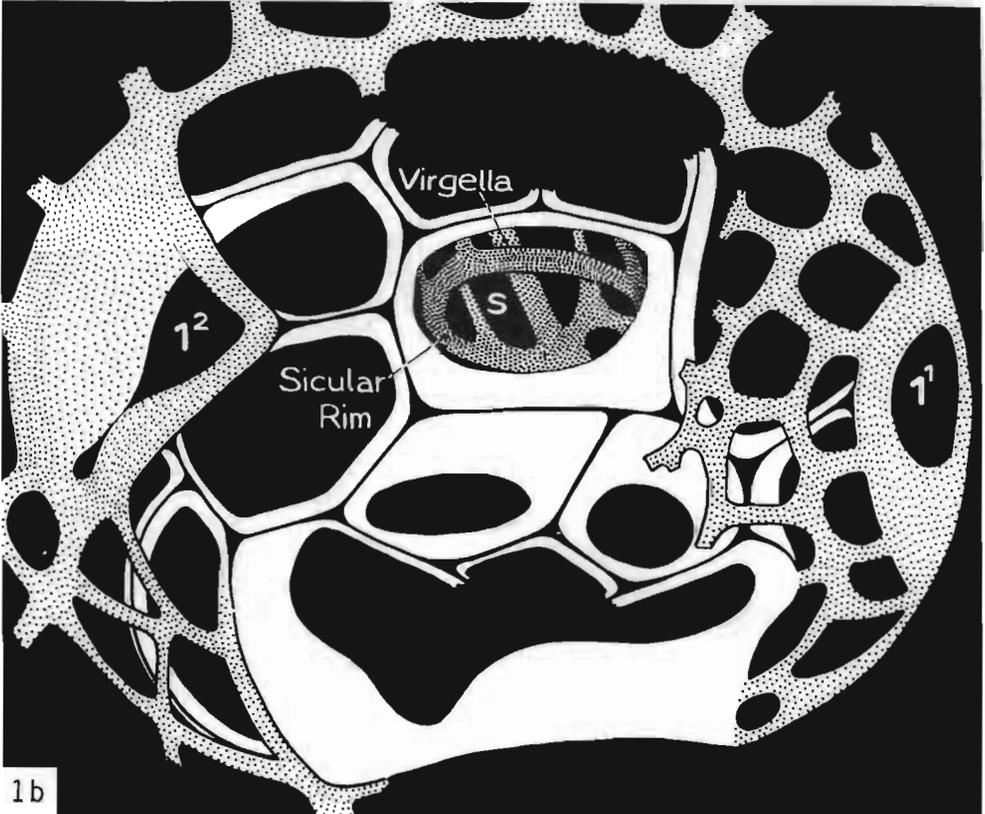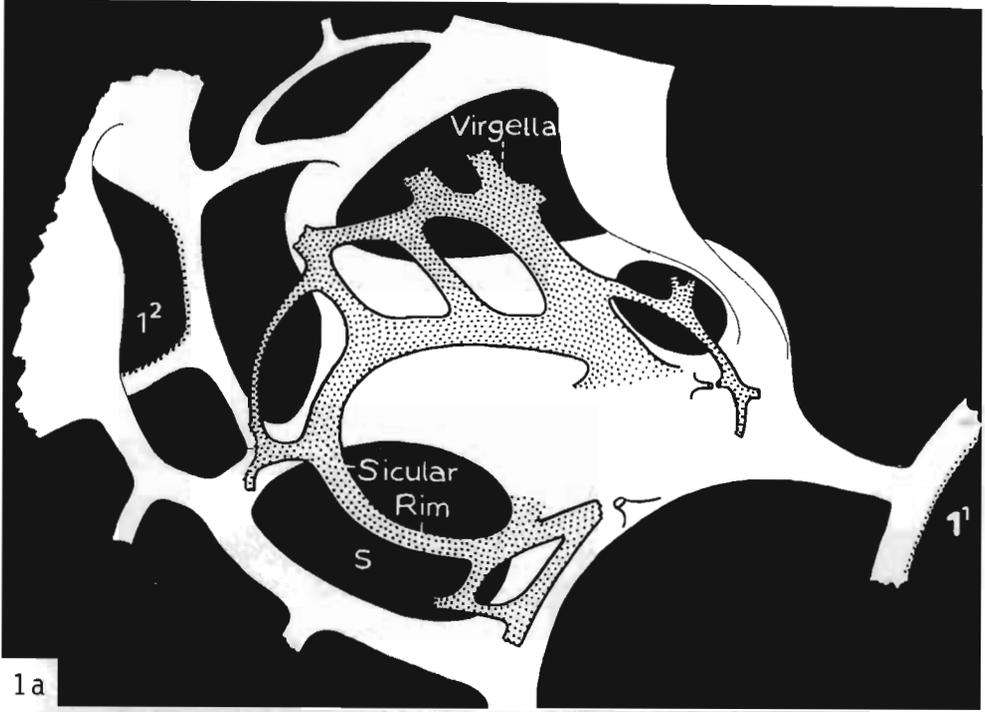### Retiolites geinitzianus (Silurian, Arctic)

1. Junction of reticular threads in external view showing succession of fibrous strips.
2. Close-up of 1, showing irregular anastomosing fibrils above more closely packed parallel fibrils within a fibrous strip.
3. Internal view of reticular junction. The side (A) of one strip of parallel fibrils, and the end (B) of another, can be seen.
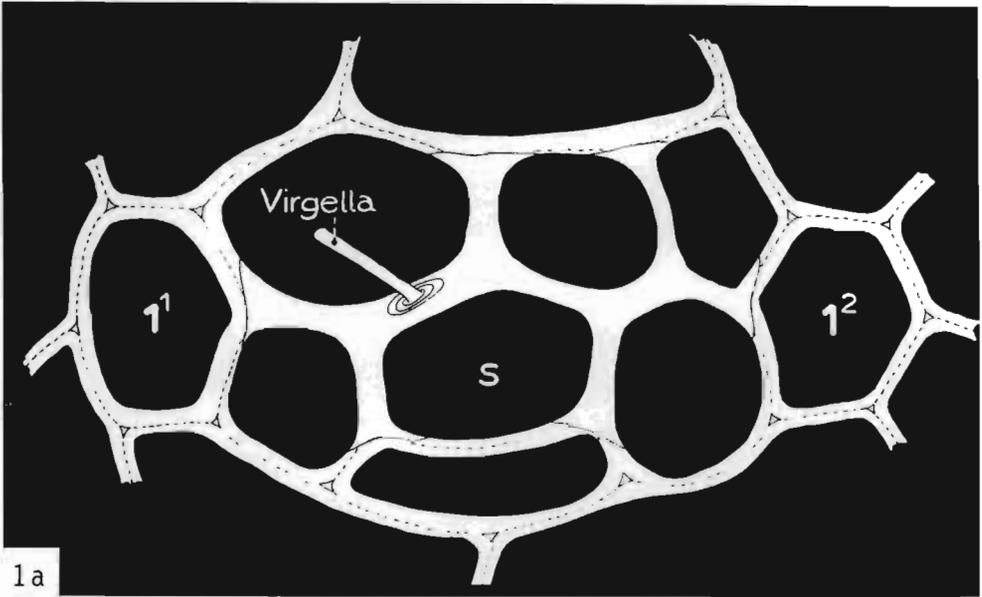
Plate 17

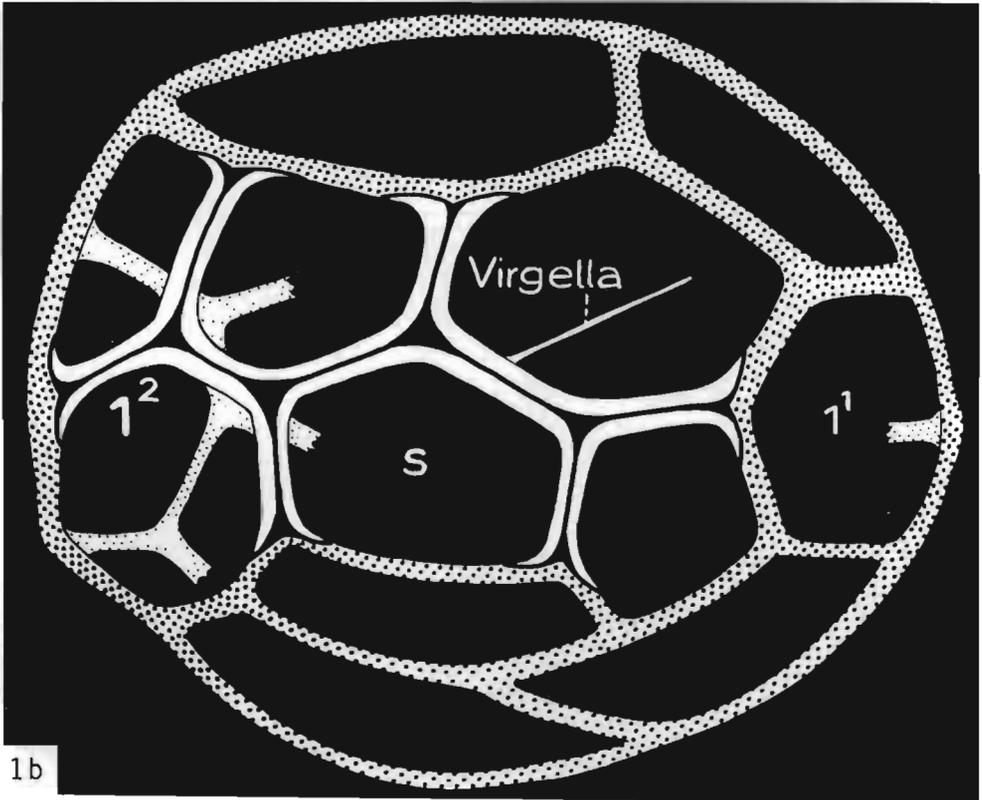### Retiolites geinitzianus (1, 3, 4 Silurian, Canadian Arctic; 2 erratic boulder, FRG)

1. External view of reticular window, with anastomosing fusellar fabric in the gaps between successive strips of packed parallel fibrils.
2. External view of reticular windows closed strips secreted from the inside.
3. Close-up of fusellar fabric of 1, showing the anastomosing fibrils underlain by packed parallel fibrils.
4. Oblique external view of the flange at the side of a thecal aperture.

Virgella

T^2

Sicular
Rim

S

T^1

1a

Virgella

T^2

Sicular
Rim

S

T^1

1b

1a

1b