THE NEMATULARIUM OF *PSEUDOCLIMACOGRAPTUS SCHARENBERGI* (LAPWORTH) AND ITS SECRETION

by CHARLES E. MITCHELL *and* KAREN J. CARLE

ABSTRACT. The nematularium of *Pseudoclimacograptus scharenbergi* (Lapworth) is a three-vaned structure derived from its hollow nema. The apex of the structure is sealed. The vanes are solid, lack a thickened rim, and comprise thin, irregular lamellae that parallel the semicircular vane outline. Each lamella consists of a body of anastomosing fibrils overlain by a dense outer pellicle. Although the thecae have a bandaged cortex, the vanes lack cortical layers. The nematularium is strikingly irregular in shape and lamella geometry compared to *P. scharenbergi* thecae. The structure of the nematularium is inconsistent with its secretion by an enveloping epithelium but is explained well by the pterobranch model. Both the nema and the nematularium were probably secreted externally to soft tissue (nematocaulus) confined within the lumen of the nema. A similar mode of secretion could have produced most of the other structures derived from the nema of planktic graptolites. This 'naked' nematularium could not have added to the colony's buoyancy but would have added preferentially to the viscous drag forces that slowed its rate of sinking. Thus, the nematularium and a variety of other structures evolved by planktic graptolites may have helped these graptolites to maintain their preferred depth in the oceans.

PALAEOBIOLOGISTS continue to be frustrated in their attempts to understand many of the most fundamental features of graptolite biology. During the first one hundred years of study, even the zoological affinities of graptolites were obscure. Kozłowski (1938, 1949, 1966), Bulman (1944–1947, 1955, 1970, and elsewhere), and Beklemishev (1970) have given graptolites a comfortable home among the Hemichordata. Yet considerable debate remains about the closeness of this suggested relationship with the pterobranch hemichordates in particular, and about how graptolites secreted their skeletons. Recently, Andres (1977, 1980), Crowther (1978, 1981), Crowther and Rickards (1977), and others have generated considerable interest in the pterobranch model of peridermal secretion originally supported by Beklemishev (1970 and earlier) with their discovery that the cortical layers in a wide range of graptoloids were deposited as distinct strips or bandages covering the surfaces of the thecae. Alternatively, Kirk (1972), Urbanek and Towe (1974, 1975), Urbanek (1976, 1978), Bates and Kirk (1978), Urbanek *et al.* (1982), and others have argued in favour of a non-pterobranch model in which all of the peridermal components, including the fuselli, were produced beneath an enveloping epithelium (the extrathecal tissue model).

Relying on data from the ultrastructure of the thecae or thecal clathria and lacinia, the debate has reached in impasse. The ultrastructure and patterns of growth of the nema and its associated structures provide a critical test of the pterobranch and epithelial models. Several diplograptid graptolites, including *Pseudoclimacograptus scharenbergi* (Lapworth), produced a three-vaned, float-like organ (a type of nematularium) at or near the apex of the colony's nema. Urbanek *et al.* (1982), in their study of the *Cystograptus vesiculosus* nematularium, have proposed that the graptoloid nema and the terminal nematularium were produced by an enveloping epithelium similar to that associated with the thecae in the extrathecal tissue model. Crowther (1978, 1981) and Crowther and Rickards (1977), however, note that the nema of most nematophorous graptolites was hollow and, as suggested by Kozłowski (1971) and Hutt (1974), probably contained tissue (called the nematocaulus by Hutt) capable of secreting the nema and associated structures. Indeed, a dual mode of peridermal secretion of exactly this sort exists in the pterobranch *Rhabdopleura* (see Schepotieff 1906, 1907; Hyman 1959).

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The black rind of their stolon is secreted from within by the gymnocaulus (the organ that occupies the central lumen of the stolon, and from which the zooids bud).

The pterobranch model and the extrathecal tissue model each lead to different expectations for the formation and ultrastructure of the diplograptid nematularium. The pterobranch model, with its double mode of secretion, implies that the graptoloid nema and nematularium must have been produced by the nematocaulus *from within* as an external cuticle in like fashion to the pectocaulus of *Rhabdopleura*. Ultrastructurally, the tissue of a nematularium should resemble that of the nema rather than the fuselli and should include no multi-layered cortical tissue or cortical bandages since these components of cortical periderm were produced by the cephalic disc of differentiated zooids. Alternatively, the extrathecal tissue model implies that the nema and nematularium were secreted *from without* by the external epithelium. The ultrastructure of the nematularium in this case should be similar not only to the nema but also to the thecae.

Our intent in this paper is to report the results of our investigation of the peridermal structure and ultrastructure of the nematularium of *P. scharenbergi* and to compare these observations with the expectations generated by the different models of graptolite peridermal secretion. We also present a revised interpretation of the function of these float-like structures.

MATERIAL AND METHODS

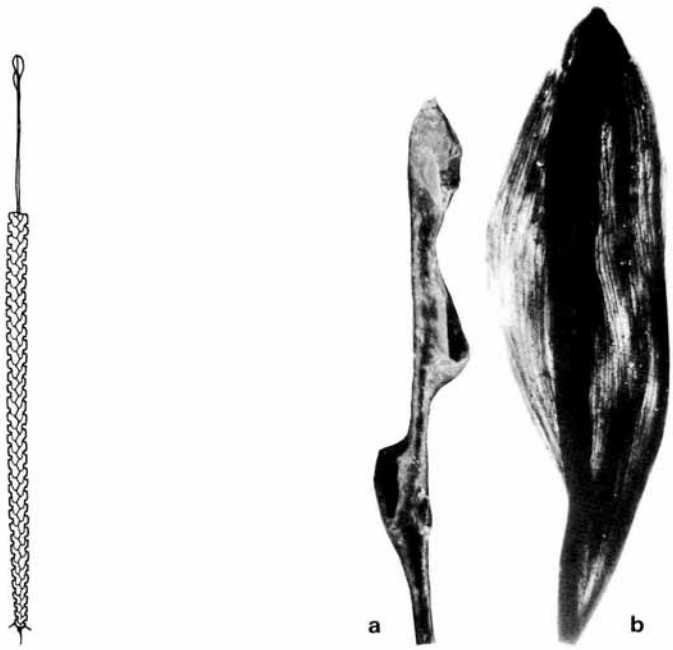
We obtained several complete and numerous fragmentary specimens of nematularia from a silty limestone sample in the collections of the Museum of Comparative Zoology, Harvard University. The sample is from the '*Climacograptus* band' of the Balclatchie beds exposed in Laggan Burn, Ayrshire, Scotland. The three-dimensionally preserved graptolite fauna of this Caradoc unit has been described by Bulman (1944–1947). Bulman also recovered specimens of the nematularia, and tentatively referred them to the species *Climacograptus brevis* Elles and Wood. Neither Bulman's specimens nor ours were recovered attached to rhabdosomes. Their referral to *P. scharenbergi* is based on reports of similar, but flattened, structures at the apex of the nema of this species preserved in shales (Bulman 1964; see also text-fig. 1).

The limestone sample was soaked in an approximately 10% solution of hydrochloric acid for about one month, with the spent solution being periodically exchanged for fresh as the carbonate dissolved. When all reaction ceased the highly siliceous residue was carefully washed to remove the remaining Ca^{++}, and a dilute hydrofluoric acid solution was then added. After about two weeks the sample had become completely reduced to an oozy sediment that was again carefully washed to remove the fine organic detritus. The freed graptolites were pipetted from this residue. Additional details concerning the processing of graptolite-bearing limestone samples can be found in Bulman (1944–1947) and especially in Wiman (1895).

Specimens used for light and transmission electron microscopy were dehydrated in a graded series of acetone, embedded in Spurr's Low Viscosity Resin, and sectioned on a Sorvall MT-2B Ultramicrotome with glass knives. The thin sections were picked up on copper grids and viewed on a Zeiss EM-9 TEM. Light micrographs were taken on a Zeiss Photomicroscope III using Panatomic-X film. Specimens for SEM study were mounted on aluminum stubs using gum tragacanth, coated lightly with gold/palladium, and examined at 20 kV using an AMRAY 1000A SEM. Micrographs were taken on Polaroid 4X5 land film type P55 Positive-Negative, handled according to package directions.

DESCRIPTION OF THE NEMATULARIUM

Nematularium form. The nematularium consists of three vanes radiating at roughly 120° to one another from the central nema (text-fig. 2; Pl. 28, figs. 1, 3–6; Pl. 29, fig. 2). The vanes are very thin and delicate. The overall size of the nematularium varies from specimen to specimen but ranges up to about 1·5 mm in width and 5·0 mm in length. The proportions of the structure are also somewhat variable. The length: breadth ratio ranges from about 5:1 to approximately 2·5:1. Individual vanes within a nematularium are generally all of different lengths: that is, they extend to different distances down the nema. At the apex of the structure all three vanes unite to form a triangular cap that completely occludes the end of the nema (Pl. 28, fig. 1). The nematularium has a central lumen (40–45μm in diameter) that corresponds to the lumen of the nema (Pl. 28, figs. 4, 6; Pl. 29, figs. 1, 2).



TEXT-FIG. 1 (*left*). Complete rhabdosome of *Pseudoclimacograptus scharenbergi* showing a nematularium at the tip of the nema, approx. × 2 (reconstructed in part from Bulman 1964, fig. 5*c*).

TEXT-FIG. 2 (*right*). *P. scharenbergi* nematularia (sample location and horizon as in Plate 28). *a*, SEM of tip of a slender nema showing terminal bulb and two lateral swellings, × 60 (specimen accidentally destroyed). *b*, nematularium, MCZ 9432, viewed in transmitted light, × 33 (specimen subsequently sectioned for transmission electron microscopy).

The vanes themselves are solid and exhibit no traces of being the collapsed remnants of a globular, hollow vesicle (Pl. 29, fig. 2).

Under transmitted light (text-fig. 2*b*) the vanes show narrow, irregular growth lines that more-or-less parallel the outline of the vane and are sub-parallel to the length of the nema. The growth lines are roughly concentric about what appears to be their point of origin from the nema. These centres are at different locations along the nema for each of the three vanes and are further from the apex of the structure the longer the vane. The concentric arrangement of the thin growth lines is commonly interrupted by variations in width of the growth increment, by pinching out of individual lamellae, and in some cases by what appear to be periodic shifts along the nemal axis of the centre about which the growth lines are concentric. Thus, the locus of most active growth in an individual vane appears to have shifted abruptly from time to time. As Bulman (1944–1947, p. 65) noted, the edge of each vane is markedly more opaque but not thicker than the remainder. This condition contrasts sharply with the situation in the nematularium of *Cystograptus penna* and *C. vesiculosus* (Jones and Rickards 1967; Urbanek *et al.* 1982) where the vanes have a thickened rim.

Individual growth lamellae are narrow compared to the width of fuselli in the thecae of *P. scharenbergi*. They average 18 μm in width (range 10–30 μm) while the fuselli of distal metathecae have an average width of 70 μm (range 50–120 μm). In addition to being much narrower than the fuselli the growth bands are also much longer. Individual bands commonly extend from one end

of a vane to the other, over a distance of as much as 5 mm. Apart from the similar microfuselli of the *C. vesiculosus* nematularium, we know of no other peridermal structures in which the constituent growth bands are even approximately of the proportions of these nematular growth lamellae. A potential exception, but as yet unproved, may be the growth lamellae of the nema itself (see Berry 1974).

Among graptolite colonial structures, nematularia are highly atypical. Both in the arrangement of the constituent growth lamellae and in the overall form of the structure, they are strikingly less regular than are the thecae and other principal structures of graptoloid rhabdosomes.

Nematularium growth stage. Our collections include one specimen that we interpret as an early growth stage in the formation of the *P. scharenbergi* nematularium (text-fig. 2*a*). This specimen is a small distal fragment of a nema, the tip of which is bulbous and may be sealed. It also bears two localized swellings located a short distance down the nema, on nearly opposite sides. The walls of the swellings and the bulbous tip appear to be thin and somewhat collapsed; they consist of narrow growth lamellae that parallel the outline of the swellings. Structures like these were described as early stages in the growth of the similar virgular apparatus of *Climacograptus parvus* by Ruedemann (1908). Unfortunately, our specimen was destroyed accidentally during handling of the SEM stub on which it was mounted.

Nematularium ultrastructure. Under SEM examination the vanes appear slightly shrunken and cracked. The surfaces of the nematularium are irregularly pitted, probably as a result of their diagenetic history. Where well preserved the vane surfaces reveal subparallel fibrils (about 0·15–0·18 μm in diameter) that, like the growth lamellae, are concentric with the edge of the vane. Also present are minute oval pits whose long axis is parallel to the fibrils. These pits are similar to those associated with sheet fabric (Crowther 1981).

The nematularia exhibit no traces of either cortical deposits in general or bandaging in particular. The broken ends of several nematularia examined with the SEM reveal the layered fibrillar structure of the periderm (Pl. 28, figs. 2, 6). Individual growth lamellae are crescentic or chevron-shaped, overlapping, and comprise sub-parallel, anastomosing fibrils. The fibril diameter is approximately 0·15–0·18 μm. TEM cross-sections corroborate this picture of lamella geometry and show that each growth lamella consists of a body of a loosely-packed, fibrillar mesh enclosed in a thin, electron-dense outer pellicle (Pl. 29, fig. 3). Under SEM examination this outer pellicle is seen to consist of densely packed, sub-parallel fibrils.

A comparison of cross-sections of the nema just proximal to the nematularium (Pl. 29, fig. 1) and of the nematularium proper (Pl. 29, fig. 2) confirms that the vanes are produced by a progressive elaboration of the walls of the nema. Both nema and nematularium enclose a relatively spacious

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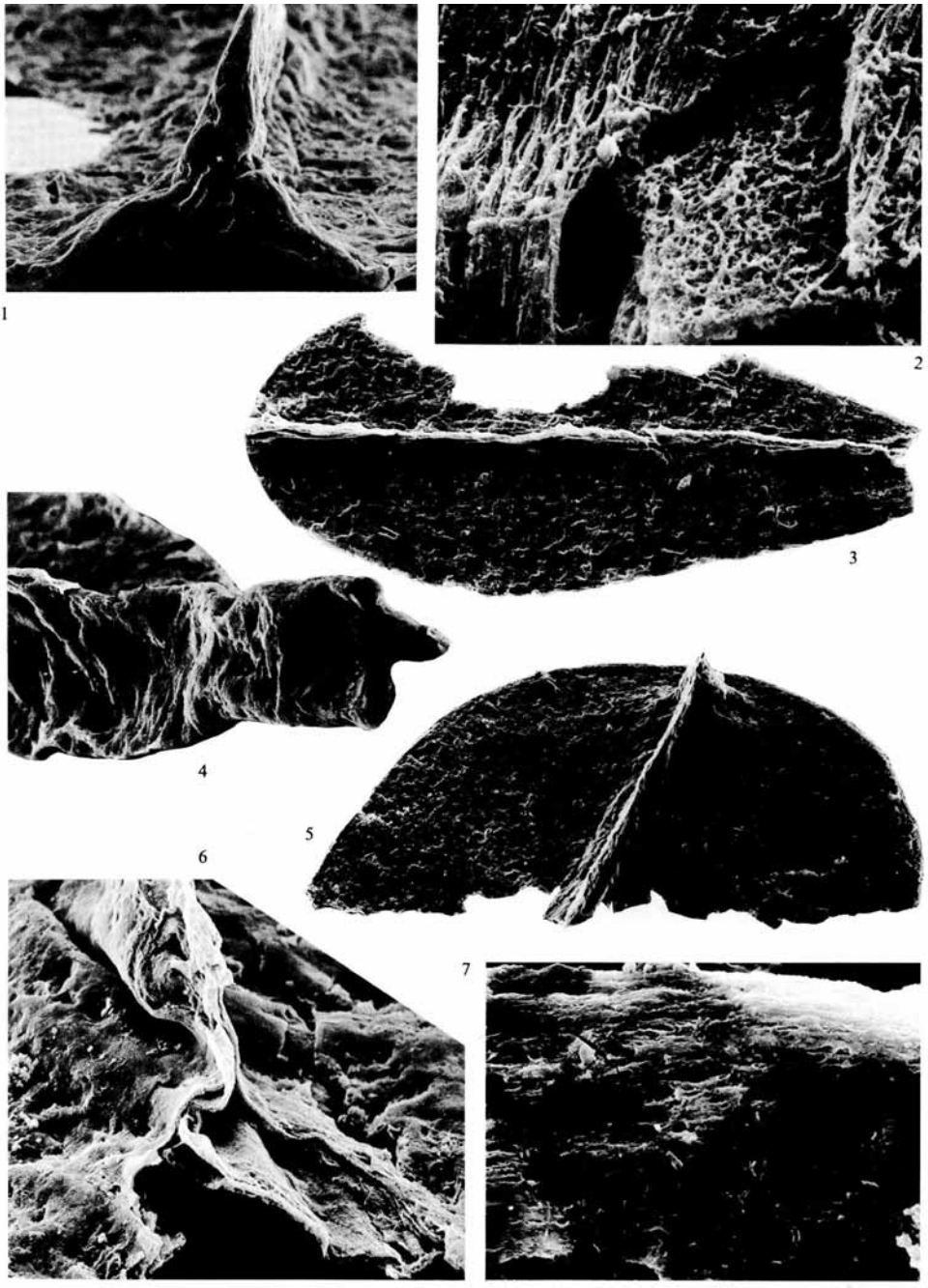
EXPLANATION OF PLATE 28

Figs. 1–7. *Pseudoclimacograptus scharenbergi* (Lapworth) nematularia, isolated from silty limestone of the '*Climacograptus* band', Laggan Burn, Ayrshire, Scotland. 1,3,6, MCZ 9430: 1, apical view showing sealed apex where the three vanes join at about 120°, × 190; 3, lateral view showing blunt apex with vanes tapering proximally, and third vane and nema broken away, × 47; 6, enlarged view of broken proximal end showing overlapping, chevron-shaped growth lamellae in end view of broken vertical vane above the triangular central lumen, × 470. 2, 4, MCZ 9431: 2, high magnification view of surface near proximal end of specimen in fig. 4, showing subparallel arrangement of fibrils on outer surface (= pellicle) and more irregular, mesh-like arrangement of fibrils below, × 5200; 4, proximal view showing merging of nematularium with nema (note three-lobed central lumen), × 230. 5, 7, MCZ 9429: 5, lateral view showing irregular surface and no signs of cortical bandaging, × 72; 7, high magnification view of vane surface and edge in upper left area of specimen, showing parallelism of fibrils and vane edge (at top of figure) as well as numerous minute elliptical pits like those typical of sheet fabric (large irregular pits and hummocks are probably preservational artifacts), × 1500.

All SEMs.



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lumen, 40–45 μm in diameter. There is a great similarity between the nematularium growth lamellae and those of the nemata studied by Berry (1974, especially pl. 8).

The structural basis of the growth lines visible in the vanes under transmitted light is apparent in TEM cross-sections. The three regions between the vanes consist of approximately four growth lamellae. In contrast the vanes consist of a large number of growth lamellae. In their broader portions we estimate (the irregular lamellae are difficult to count accurately) that the vanes are comprised of thirty or more growth lamellae. Plate 29, fig. 3 shows the junctions of several lamellae (arrowed); these junctions are staggered at intervals, and it is this overlap that results in the appearance of growth lines when the vanes are viewed in transmitted light. Ideally, a vane seen in cross-section resembles a stack of bowls that become narrower and deeper towards the top of the stack. The innermost growth lamellae, adjacent to the central lumen, are broadly crescentic with a curvature similar to that of the lumen wall. Growth lamellae located successively further out into the vanes become more chevron-shaped and overlap one another extensively.

Not all lamellae in the nematularium have a pellicle of the same thickness. Those of the outermost four or five lamellae in the vanes and all lamellae of the nema have a pellicle that is substantially thicker than that of the lamellae found in the inner portions of the vanes. The outer lamellae, with their thicker pellicle, usually extend about one-third the circumference of the nematularium (Pl. 29, fig. 2); they make up most of the thickness of the structure between the vanes and reach nearly completely around each vane. In the axial area of a vane, adjacent to the lumen, the lamellae have a thin pellicle and are asymmetrical; they occupy only about one-sixth of the circumference of the lumen and extend from the region between the vanes to just past the vane axis, towards the next inter-vane region. An idealized reconstruction of this structure is illustrated in text-fig. 3.

A GROWTH MODEL FOR NEMATULARIA

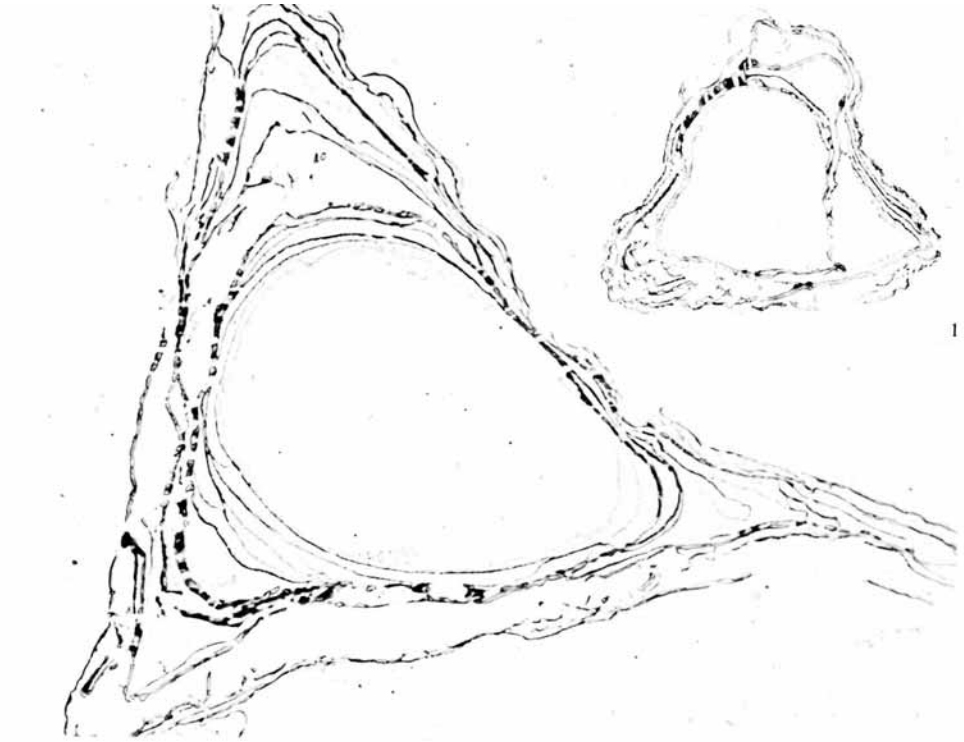
Growth of the P. scharenbergi *nematularium*

We propose that the structure of the nematularium indicates that it was secreted by an organ, the nematocaulus, that lay within its central lumen and within the nema. We further propose that this secretion occurred in distinct pulses. Six principal factors dictate this mode of secretion:

1. Growth lamellae are irregularly offset and change geometry markedly from the inner to the outer portions of the nematularium vanes.
2. The number of growth lamellae in the vanes and in the regions between the vanes are greatly different, yet the outermost lamellae in the vanes enclose most or all of each vane and lap on to the intervane areas.
3. The outer pellicles of the outermost several lamellae in the vanes and in the regions between the vanes are markedly thicker than those in the inner portions of the vanes. However, they appear identical to those of the nema just below the nematularium and to the lamellae of the nemata illustrated by Berry (1974, pl. 8).
4. This zone with thicker pellicles coincides with the more opaque edges of the vanes, which appear to be present in all nematularia regardless of the size of the vanes or the size of the structure as a whole.
5. The apex of all of the nematularia examined are sealed, regardless of the state of maturation of the structure.

EXPLANATION OF PLATE 29

Fig. 1–3. *Pseudoclimacograptus scharenbergi* (Lapworth) nematularium. MCZ 9432, sample location and horizon as in Plate 28. 1, light micrograph of cross-section of nema just proximal to base of nematularium × 650. 2, light micrograph of cross-section of proximal end of nematularium showing arrangement of growth lamellae surrounding its central lumen, × 1150. 3, TEM of portion of vane of nematularium in cross-section × 10000. pe, pellicle.



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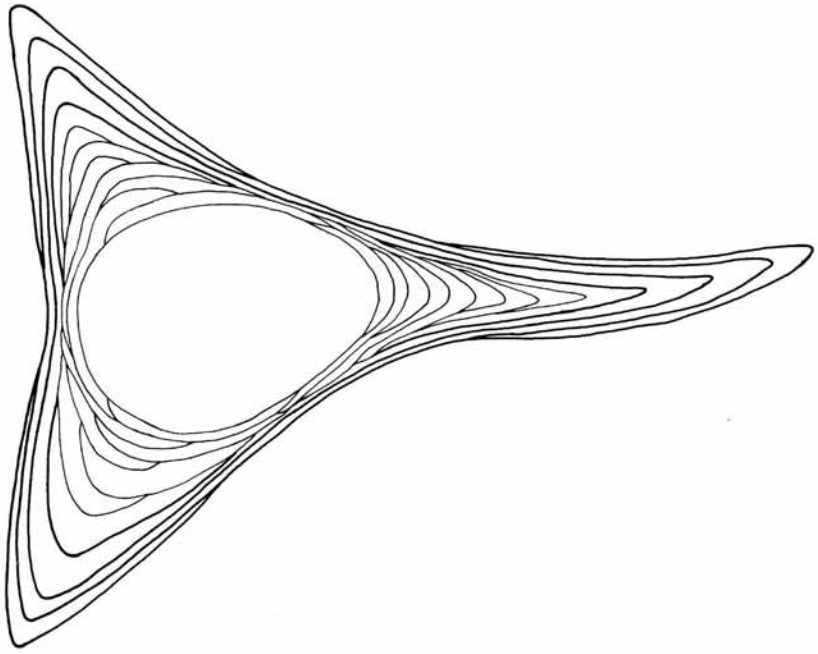


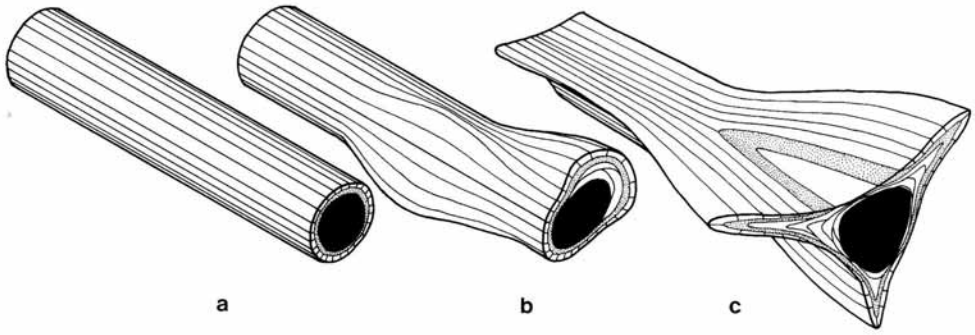
TEXT-FIG. 3. Reconstructed and idealized cross-section of the *Pseudoclimacograptus scharenbergi* nematularium showing the structure and geometry of growth lamellae, approx. × 250 (based on cross-sections illustrated in Plate 29).

6. In none of our specimens is the external surface covered by any secondary (cortical) peridermal material.

Text-fig. 4 presents schematically our interpretation of the growth of the *P. scharenbergi* nematularium. The outer, more opaque lamellae were derived directly from the pre-existing nema during the early phases of nematularium growth. This opaque rim comprises lamellae with a thick pellicle and appears to be present on all vanes throughout all stages of nematularium growth. Growth commenced with the secretion of small, wedge-shaped lamellae in three linear zones arrayed around the circumference of the nema and between the epithelium of the nematocaulus and the pre-existing periderm. As each new layer was secreted, it fused with the last-secreted layer in inter-vane regions. The formation of new lamellae pushed the pre-existing lamellae outwards with the result that the periderm between the inter-vane areas buckled outward to form the vanes. As succeeding layers were added internally, each outer layer was pushed further outwards, stretched and buckled to an even greater extent. Why did the layers fuse only in the three inter-vane areas? These areas may have been the most active sites of periderm secretion or the sites where secretion occurred first at a given level of the nematularium. The newly secreted and still unpolymerized periderm fused with the previously secreted layer before it began to push the previous layer outward and before secretion was initiated in the vane areas.

This scheme requires only the existence of a simple secretion-inducing morphogen that diffused in a proximal-to-distal direction along the axis of the nematularium to regulate growth. The immature nematularium pictured in text-fig. 2*a* shows that all three vanes originated along a single spiral pathway and could, therefore, have originated from a single morphogen gradient. The configuration

of vane lengths, widths, and level of origin along the nema, together with their positioning at about 120° to one another shows numerous parallels with the phenomena of phyllotaxis. This configuration indicates that the apparently high degree of order exhibited in the nematularium's form may have arisen, as it does in phyllotaxis, as a forced consequence of the physical constraints of growth and the requirement that elements of finite size be added where there is sufficient room for them to grow (Thompson 1948; Wardlaw 1953; see also Gould and Katz 1975). Thus, we need not invoke any *ad hoc* or particularly complex regulatory mechanism to explain the nematularium's growth.



TEXT-FIG. 4. Idealized cut-away views of the *Pseudoclimacograptus scharenbergi* nematularium illustrating its derivation from the nema and subsequent growth by the addition of new lamellae in generative zones beneath the vanes. The boundaries of approximately every second lamella are shown. Lamellae with similar added patterning were formed synchronously. The longitudinal stripes added to the outer lamella emphasizes its three-dimensional form and do *not* indicate growth lines.

Application of the model

If our model for nematularium growth in *P. scharenbergi* is correct it should also be applicable to most or all of the other float-like nematularia found among the nematophorous graptolites. We base this conclusion on two lines of reasoning:

1. Nematularia occur sporadically among a wide variety of graptolites including the dendroid *Rhabdinopora flabelliformis* (Bulman and Størmer 1971), anisograptid dendroids (Jackson 1974), and in representatives of all of the graptoloid families (see Ruedemann 1904, 1908; Bulman 1964; Müller and Schauer 1969; Kozłowski 1971; Rickards 1975; Finney 1979). This wide but scattered occurrence of nematularia means that, although they evolved independently in several different lineages, the *capacity* to develop these structures was a general, shared feature of the nematophorous graptolites as a group.
2. In reconstructing the mode of secretion of the *P. scharenbergi* nematularium we have based many of our inferences on several fundamental similarities between the anatomy and skeletal structures of graptolites and pterobranchs. If these similarities are indeed true homologies, as we believe them to be, then the proposed mode of secretion should be a widely shared capacity among the graptolites—a capacity based on the nature of the nema of the nematophorous graptolites.

In all but a very few cases, nematularia are known only from small numbers of non-isolated, flattened specimens. Although we can point out some features of these organs that are consistent with our explanations, their structures and patterns of growth are not known well enough to permit us to determine the details of their morphogenesis. Thus, they do not constitute a test of our model. Only two other nematularia have been studied from isolated preparations.

Finney (1979) described a vesicular structure associated with a *Dicellograptus* specimen from the middle Ordovician Athens Shale in Alabama; Finney (pers. comm.) has since discovered additional specimens of this nematularium in the Athens Shale. The structure was a hollow, apparently single-walled globe that was attached to the end of a somewhat expanded, hollow nema of a young *Dicellograptus*. The minute vesicle was only 0·4 mm in diameter, had no external opening, and lay about 0·8 mm from the apex of the prosicula. This configuration agrees well with the mode of secretion that we have proposed for the *P. scharenbergi* nematularium. It is of the same magnitude as the hollow nodes developed in the early growth stage of the nematularium described above and likewise may have formed externally, around a localized enlargement of the nematocaulus. The periderm of the *Dicellograptus* nematularium appears to be structureless because it formed by a simple ballooning outward of the layered nema, without the secretion of additional periderm to form a more elaborated structure like that of the *P. scharenbergi* nematularium. As Kozłowski (1971) and Finney (1979) noted, the 'attachment discs' of many dendroid and dichograptid species described by Ruedemann probably represent hollow vesicles of this sort.

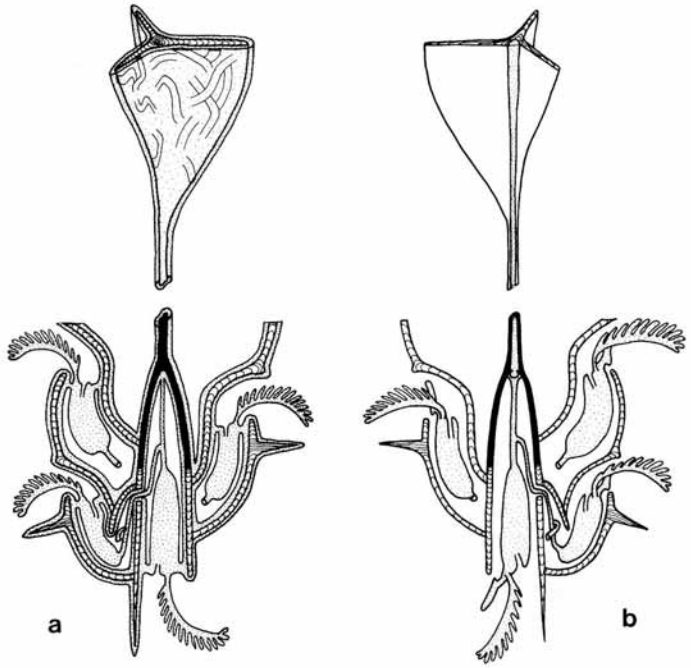
It is more difficult to interpret the mode of growth of the *Cystograptus vesiculosus* nematularium. Although Urbanek *et al.* (1982) believed that it provided an example of secretion beneath an epithelial membrane, they did not give any detailed reconstruction of how this structure, with its thickened rim, grew. Since this apparatus appears to have no central lumen in the region they studied, it must have been formed by a mechanism somewhat different from that which we envisage as responsible for most other graptolite nematularia.

Urbanek *et al.* (1982) concluded that the ultrastructure of both the vanes and the thickened rims of the *C. vesiculosus* nematularium was quite distinct from the ultrastructure of the diplograptid nema. From this they inferred that the nematularium was not a highly modified derivative of the nema but rather a replacement for the nema. If this is true then it may not be unduly troubling that this nematularium type has a different morphogenetic pattern from that of *P. scharenbergi*, Finney's *Dicellograptus* specimens, and nematularia of the *scopaeculare* type (see Müller and Schauer 1969, for a classification of nematularium forms), all of which are unambiguously derived from a normal and intact nema.

A solution to the exact mode of secretion of the *C. vesiculosus* nematularium must await more detailed information about its growth stages, its relationship to the nema and prosicula, the timing of growth, and of its enclosure by the upward growing rhabdosome. The form of the *C. vesiculosus* nematularium is not easily explained by the extrathecal tissue model either. The thickened rim of the vanes was probably present throughout the ontogeny of the apparatus (Jones and Rickards 1967 observed thickened rims on the immature vanes of *C. penna*). Accordingly, it seems unlikely that the nematularium could have been secreted by external addition of growth increments without also undergoing extensive and continuous remodelling. The cross-sections figured by Urbanek *et al.* (1982) show no signs of such remodelling. Data from other species that possess a nematularium with thickened rims and no central nema (such as *Petalograptus speciosus* and others with an apparatus of the *vinculare* and *bullare* type; see Kozłowski 1971) may also be relevant.

IMPLICATIONS FOR THE MODE OF PERIDERMAL SECRETION

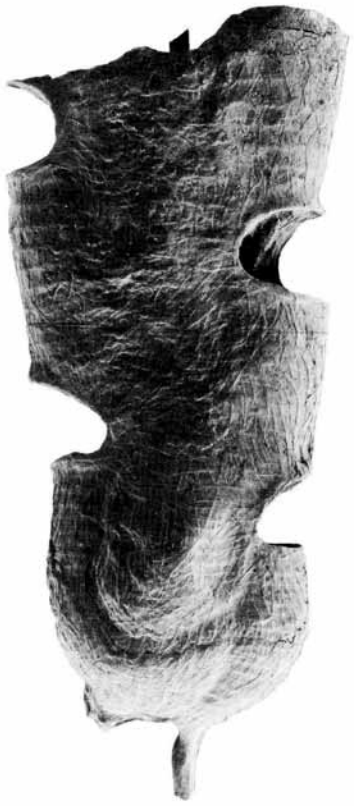
In the introduction we outlined the features of the two models of peridermal secretion that provide the best explanation of the data available on colony form and construction (see text-fig. 5). Our data on the growth of the *Pseudoclimacograptus scharenbergi* nematularium are inconsistent with the extrathecal tissue hypothesis but fit well with the pterobranch hypothesis. If our model is corroborated in studies of other nematularia, we believe that it, taken together with the data on cortical bandaging described by Crowther and Rickards (1977), Crowther (1978, 1981), and Andres (1977, 1980), will require the extrathecal tissue hypothesis to be abandoned as a general explanation for graptolite peridermal secretion. In this section we develop the argument that underlies this conclusion.



TEXT-FIG. 5. Ideogram of relationships between the graptolite zooids and the rhabdosome of a pseudoclimacograptid as predicted from *a*, the extrathecal tissue hypothesis and *b*, the pterobranch hypothesis. The rhabdosome is shown in cross-section, as is the nematularium in *b*. The prosicula and lower portion of the nema are black; thecal periderm is indicated by chevroned fuselli and soft tissues are stippled. The median septum is omitted for clarity. *a*, zooids reconstructed as bryozoan-like, according to the suggestions of Urbanek (1978); note that the nema is a solid rod the secretion of which is unrelated to the funiculus-like stolon of the siculozooid; the nematularium is enveloped in secretory extrathecal tissue and its primary periderm coated with cortical bandages. *b*, zooids are reconstructed as pterobranch-like; the nema is secreted by an internal extension of the stalk of the siculozooid; the nematularium is 'naked' and bears no secondary cortex.

Like all diplograptids the rhabdosome of *P. scharenbergi* has a thick cortical layer covering the fusellar periderm and obscuring the fuselli. Unfortunately, preservation in our Balclatchie graptolite sample shows a strong bias against the robust species with their thick cortex. Colonies of *Amplexograptus leptotheca*, *Climacograptus brevis*, and the nematularia are moderately well preserved, but those of larger species, such as *Orthograptus apiculatus* and *P. scharenbergi*, are poorly preserved. Both *A. leptotheca* and *C. brevis* exhibit clear cortical bandaging but all the rhabdosome surfaces of the *P. scharenbergi* specimens we examined are corroded and fractured. The cortical structures have been obliterated for the most part, although a few specimens exhibit vague traces of bandaging. Broken edges of the thecae reveal that diagenesis has destroyed all traces of the fibrillar nature of both the fusellar and cortical tissues.

Crowther (1981) observed bandaging in Bulman's *P. scharenbergi* material (particularly in *P. s. stenostoma*). The closely related species *P.* sp. aff. *P. caudatus*, from strata of the *C. pygmaeus* Biozone



TEXT-FIG. 6. Composite SEM of young rhabdosome of *Pseudoclimacograptus* sp. aff. *P. caudatus* (Lapworth) (despite its nearly straight supragenicular walls, this species has a strongly zig-zag median septum and an early astogeny identical to that of *P. scharenbergi*), MCZ 9433, from lower Viola Springs Formation (Alberstadt's 1973 section O, 47 m above outcrop base), upper *Climacograptus pygmaeus* Zone (probably coeval with *P. linearis* Zone of Welsh succession). Note strikingly bandaged cortex with nearly all bandages radiating from thecal apertures or from the sicular aperture; note also that some bandages extend across the apertural selvage on to the infragenicular wall, × 60.

(Caradoc) in the Viola Springs Formation of Oklahoma, shows a strikingly bandaged cortex (text-fig. 6). Andres (1980) also figured micrographs of a *Pseudoclimacograptus* species that is strongly bandaged. In both of these species, bandages densely coat the entire periderm and virtually all bandages radiate from a thecal aperture or from the sicular aperture.

There is a sharp contrast between the periderm of the *P. scharenbergi* and other diplograptid nematularia on the one hand, and the periderm of the corresponding rhabdosomes on the other. (Urbanek *et al.* 1982 did not report on the ultrastructure of the thecate portion of the *C. vesiculosus* rhabdosome, but the peridermal fabrics of its nematularium were like those described here.) The major differences include the following:

1. Nematularia appear to be either structureless or to consist of thin, irregular, microfuselli-like growth increments of great length. The thecal fuselli, in contrast, are relatively much shorter and extend only one half the circumference of the theca.

2. Nematularia completely lack cortical deposits in general and bandaged cortex in particular. Diplograptid rhabdosomes, including those of *P. scharenbergi*, have a thick, multi-layered, and usually bandaged cortex that overlies the notably regularly arranged fuselli.

3. Growth lamellae of nematularia are formed approximately parallel to the longitudinal axis of the structure and are extremely long (up to several millimetres). In contrast, the fuselli of diplograptid

thecae and median septa are short (of the order of 0·5 mm) and are formed nearly perpendicular to the longitudinal axis of these structures.

4. Nematularia are markedly irregular, both in their overall size and shape and in the arrangement of their constituent growth lamellae. Graptolite colonies and their constituent thecae exhibit outstanding regularity in their form (shape, growth gradients, branching pattern, and the like) and arrangement of fuselli.

In summary, the nematularia and rhabdosomes differ in the suite of peridermal tissues that constitute the structure, in their geometric arrangement, and regularity. The existence of such differences could not have been predicted from the extrathecal tissue model of graptolite peridermal secretion. On the contrary, this model leads one to expect more substantial similarities than we observed. For example, in an effort to reconcile the presence of cortical bandages with his extrathecal tissue hypothesis, Urbanek (1978) postulated that the bandages were a low mass means of strengthening the rhabdosome. Yet, despite the probability that a means for producing a high strength, low mass periderm would have been at a similar or even greater premium on the *P. scharenbergi* or *C. vesiculosus* nematularium compared to the rhabdosome proper, the nematularia lack a bandaged cortex or any cortex at all. We suggest that the striking contrasts outlined above are not compatible with the hypothesis that both the rhabdosome and nematularium were secreted in the same manner under a common extrathecal membrane.

However, these contrasts between the fabric, structures, and peridermal tissues present in the nematularia and the thecate portions of the rhabdosome are precisely what we should expect given the pterobranch hypothesis. In this case the rhabdosome is the product of a dual mode of secretion. The thecate part of the rhabdosome was secreted by the mobile, pterobranch-like zooids and so exhibits fabrics, tissues, and geometries reflective of this mode of origin: regularly arranged, short fuselli deposited around the growing edge of the lengthening thecal tube; cortical tissues deposited secondarily in parallel-sided bandages comprised of densely packed fibrils that are themselves parallel to the edge of their bandage. The nema and nematularium were secreted by soft tissue associated solely with this organ and so exhibit a different set of fabrics, tissues, and geometries reflective of this mode of origin: highly elongate, somewhat irregular lamellae that parallel the length of the vanes and the nema; absence of secondary (externally added) cortical deposits; lamellar geometries suggestive of internal formation adjacent to the nematularium's lumen. Andres's (1980) observations of bandaging on the nema of diplograptids is not in conflict with our proposals but rather indicates that secondary, cortical deposits may be added to the outside of the nema in regions near the thecate portion of the rhabdosome during colony growth.

Rickards (1975), Rickards and Crowther (1978), Crowther and Rickards (1977), and Crowther (1978, 1981) have suggested that the nematocaulus may have extended from the tip of the nema to cover its outer surface. This also does not seem possible in the case of the *P. scharenbergi* nematularia at least. As we noted above the apex of the nema was apparently sealed during the entire ontogeny of the nematularium.

FUNCTION OF THE NEMATULARIUM

The nematularium growth model that we suggest requires a dramatically different view of the function of these structures than has previously been considered. The most commonly accepted hypothesis is that the nematularium functioned as a float and was either hollow and gas-filled (as seems plausible for the organ described by Finney (1979) or was solid and enveloped in vacuolated or ciliated soft tissue (Rickards 1975; Urbanek *et al.* 1982). Our model of the *P. scharenbergi* nematularium postulates a naked structure with a relatively small amount of soft tissue confined to its central lumen. Urbanek *et al.* (1982, p. 225) stated that naked 'floats', as implied by the radical pterobranch hypothesis of Andres (1980), could not have aided the buoyancy of the colonies; this applies equally well to our model. Given Andres's model, Urbanek *et al.* (1982) suggested that nematularia could only have functioned as stabilizers to prevent rotation or as a kind of sail. They further suggested, and we agree, that neither proposal seems particularly plausible. However, a different function is likely.

As a consequence of their small size and the low velocities at which they probably moved through the water column (as is common for zooplankton, many of which follow a vertical diurnal migration through the photic zone; see Banse 1964), graptolite colonies must have lived in a world dominated by the high viscous forces characteristic of hydrodynamic situations with low Reynolds number. The magnitude of such forces are determined by size, surface area, and shape. Under these circumstances, body forces, such as the inertial forces generated by the acceleration of the colony's mass due to gravity, will be relatively low or even negligible. Hence, buoyancy (essentially a body force of sign opposite to that of the gravitational force) may also have been of little importance in the dynamics of colony motion and stability. Drag forces are the dominant forces in highly viscous situations. (For a qualitative review of these relationships see Shapiro 1961.)

The extremely thin-vaned nematularium must have contributed relatively much more to the colony's surface area than to its mass. The frictional drag experienced by a colony is a consequence of shear forces that arise due to motion through a viscous fluid. These forces are proportional to the surface area of the colony and tend to retard motion. Sinking occurs as a consequence of gravity, which generates an inertial body force proportional to the mass of the colony. Thus, the effect of the addition of a nematularium must be to preferentially increase the colony's frictional drag. Drag for planktic colonies would enhance depth stability by tending to slow movement up or down in the water column. Erdtmann (1976) and Kaljo (1978) (following on from the earlier suggestions of Berry 1962, among others) provided substantial evidence from the facies associations of graptoloids which indicated that they lived a depth stratified existence. Given this ecology, a mechanism that allowed planktic graptolites to maintain their preferred depth (as opposed to simply remaining afloat in the pleuston) by utilizing passive drag may have been of considerable ecological and evolutionary significance to graptoloids.

It is possible to estimate the mass and viscous drag that a nematularium would have contributed to a mature *P. scharenbergi* colony, given a few simple assumptions about the velocity of colony motion and periderm density. Unfortunately, we lack sufficient information about graptolite palaeobiology and palaeoecology to define criteria by which to judge the significance of the drag enhancement when simply computed in this isolated fashion. Accordingly, we have not undertaken these calculations.

Considerable qualitative support for the suggestion that drag enhancement was the primary function of nematularia can be deduced from among the range of graptolite colonial structures. Many graptolites display organs that must have added principally to colony drag. In several cases these novel structures could scarcely have had any other function and do not appear to be an outcome of constructional constraints on form (i.e. they do not appear to be primarily a reflection of the *Bautechnischer aspekt* of form, in Seilacher's 1970 terminology).

Several multi-branched, horizontal dichograptids such as *Loganograptus logani*, *L. kjerulfi*, and *Tetragraptus headi* possess a central webbing that connects the proximal regions of their many stipes (summarized by Bulman 1964, 1970). Lenz (1974) described a similar membrane-bearing rhabdosome of *Cyrtograptus*. In the anisograptid *Clonograptus callavei*, the sides of the stipes are drawn out as lateral flanges. Specimens of *Rhabdinopora flabelliformis* often possess an apical bundle of fibres (Bulman 1972) corresponding to a much-divided nema (Hutt 1974 described a young growth stage of either *Adelograptus hunnebergensis* or *C. tenellus* that exhibited a nema divided into three separate branches) as do several Silurian diplograptids grouped by Müller and Schauer (1969) as the *scopaeculare* flotation apparatus.

Speculation that the membrane structures strengthened the rhabdosome, or that these and the *scopaeculare*-type nematularia were covered by vacuolated or ciliated soft tissue (Bulman, 1964) remains possible, but it is *certain* that these structures would have added preferentially to the viscous drag forces acting on the colony and, accordingly, would have slowed vertical motion. The problematic virgellarium of *Linograptus posthumus* (Urbanek 1963), and the large proximal spines and webbed spines of *Climacograptus bicornis*, *C. longispinus*, *C. papilio*, *C. ensiformis*, and others, as well as the large paddle-shaped vane of *Monograptus pala* (see Bulman 1964; Riva, 1974) must have had similar effects. Furthermore, as Bulman (1970, p. V94) noted, if the functional significance

(assuming they were adaptations in the narrow sense) of these diplograptid and monograptid proximal-end structures was to aid buoyancy, the colonies must have possessed a reversed orientation compared to that usually considered likely for graptoloids (the thoughts of Kirk 1969 not withstanding; see Rickards 1975 on her suggestions). If these structures served primarily to enhance drag and depth stability, their proximal position imposes no such inversion.

Finally, a variety of suggestions have been offered to account for the independent evolution of retiolitid colony forms. Kirk (1979) stressed the importance of selection for reduction in rhabdosome mass as an aid to increased mobility. Other plausible suggestions include selection for an economizing of the energy and material expended during periderm construction. Regardless of whether or not these suggestions are correct, again it is certain that the reduction of the colony's periderm to a series of rods would also have had a great effect on the ratio of frictional drag forces to inertial body forces. This effect arises from the inescapable negative allometry between surface area (proportional to frictional drag forces) and volume (proportional to mass and so to inertial forces). Hence, the relative increase in surface drag forces compared to reduction in periderm mass would greatly retard the colony's rate of sinking. The development of a lacinia must have further added to this effect, as both Kirk (1972) and Rickards (1975) noted, yielding immobile holoplanktic colonies.

In summary, we believe that a wide variety of characteristics of both dendroids and graptoloids can be interpreted as primarily having affected colony drag. These include: 1, evolutionary trends toward peridermal reduction or reduction accompanied by formation of clathria and lacinia; 2, astogenetic shape changes which accompanied the progressive elaboration of spines and lacinia or the development of a nematularium; and 3, the frequent acquisition of one of a wide range of structures (spines, genicular flanges, clathria, lacinia, proximal webs and vanes, and a variety of nematularia) that preferentially add to a colony's surface area. These features of graptolite colonies evolved not only very commonly, but also independently by convergence and parallelism in many different lineages. All of these features must have affected differentially the drag forces experienced by planktic colonies; such features were probably adaptations to enhance the depth stability of graptolite colonies.

CONCLUSIONS

The graptolite nematularium, by virtue of its distance from the thecae and its anatomical association with the nema, offers unique insights into the method of graptolite peridermal secretion. Data on the suite of peridermal fabrics and their geometry match the predictions of the pterobranch model, while conflicting sharply with the predictions of the extrathecal tissue model. Thus, we advocate the acceptance of the pterobranch model and the rejection of the extrathecal tissue model as a general explanation for the secretion of graptolite periderm.

This corroboration of the pterobranch model has important implications for our understanding of graptolite palaeobiology and evolution. Through their work on pterobranch and graptolite peridermal ultrastructure, Towe and Urbanek (1972), Urbanek and Towe (1974, 1975), and Urbanek (1976, 1978) have stimulated a great deal of interest in and debate about the nature of the graptolite zooid and its phylogenetic relationship to pterobranchs. Urbanek (1976, 1978) suggested that the many structural and constructional similarities between coenecia of pterobranchs and graptolite rhabdosomes, as well as the inferred anatomical similarities, are all analogous homoplasies, and so indicate no close relationship between these groups. This view has become progressively less tenable as additional information about graptolite and pterobranch periderm has accumulated. Armstrong *et al.* (1984), in contrast to suggestions by Dilly (1971), showed that the fibrillar material comprising the bulk of the periderm in both groups is probably collagen. Andres (1980) has shown that the very different density of the fibrillar fabrics employed by pterobranchs and graptoloids is bridged among the benthic graptolites, such as the crustoids and tuboids. Hutt's (1974) work on the early growth stages of *A. hunnebergensis* and *Clonograptus tenellus* and our work on the *P. scharenbergi* nematularium demonstrate that the nema and associated structures are probably

homologous with the pterobranch pectocaulus and that the mode of peridermal formation is wholly similar in the two groups. Thus, this work reaffirms the close phylogenetic relationship between the Graptolithina and the Pterobranchia that Kozłowski (1949, 1966) forcefully developed and that Crowther (1981) and others have recently stressed.

Our model of nematularium formation has additional implications for graptolite palaeobiology. The frequent and independent evolution of nematularia among nematophorous graptolites indicates that these structures served an important function in the ecology of these species. This function apparently was to enhance depth stability through their disproportionate contribution to the colony's drag. The depth stratification model of graptolite ecology supported by Erdtmann (1976) and Kaljo (1978), among others, now appears more likely to be a useful model. The maintenance of a preferred depth through drag (perhaps, but not necessarily, in combination with lophophore-generated currents) may have been a pervasive factor in graptolite evolution. Further study of graptolite structure and palaeoecology employing these concepts will probably provide data essential to our understanding of the major features of graptolite evolutionary history.

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CHARLES E. MITCHELL
Department of Geological Sciences
State University of New York at Buffalo
Amherst, New York 14226, USA

KAREN J. CARLE
Department of Biology
Osborn Memorial Laboratory
Yale University, New Haven
Connecticut 06511, USA

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