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SIGNIFICANCE OF ULTRASTRUCTURAL STUDIES FOR GRAPTOLITE RESEARCH

Abstract. — Among many aspects of ultrastructural studies on graptolites of crucial significance is the interpretation of their mode of secretion of periderm. This might contribute to solving the phylogenetic problems and to a better understanding of the development and the function of the colony.

A membrane model of secretion of the graptolite periderm is discussed in some details and compared with alternative interpretations suggested by Andres (1977) and Crowther and Rickards (1977). Both interpretations are evaluated in respect to the entirety of the existing data. A generalized explanation of cortical bandages or ribbons formation due to the presence of the perithecal membrane is offered.

ELECTRON MICROSCOPY IN GRAPTOLITE RESEARCH

The use of electron microscopy in graptolite research has proved to be an invaluable tool for understanding the construction and morphogenesis of graptolite skeleton, and the structural basis of its function. Ultrastructural studies may be used to resolve earlier problems posed by morphological and phylogenetical studies on graptolites but the fantastic range of new details encountered with electron microscopy opens its own problems.

One of the great advantages of electron microscopy is a great economy of sample. Even single specimens or small fragments may be used for ultrastructural studies and minute anatomical details of periderm may be identified as far as their submicroscopic features are concerned (pl. 27). This is why ultrastructural research provides a much safer basis for the understanding of formation and function of graptolite skeleton as compared with classical microanatomy (comp. Urbanek 1976).

Fortunately for the reviewer, the ultrastructural studies on graptolites have a short history. After the first TEM micrographs obtained by Wetzel (1958) which demonstrated that at the existing state of preservation graptolite remains could be studied with EM, pioneering attempts were made by Kraatz (1964, 1968), Berry and Takagi (1970, 1971) and

Berry (1974) himself, Rickards, Hyde and Krinsley (1971). The names of Urbanek and Towe may be mentioned also as their papers provided a foundation for a more systematic interest in further ultrastructural studies on graptolites. A few others have published a number of micrographs, mostly SEM. S. Willefert (Rabat) and H. Mutvei (Stockholm) have made numerous observations and micrographs unfortunately unpublished.

Among numerous aspects of ultrastructural studies as applied to graptolites I will mention only a few and will concentrate later on the crucial problem of morphogenesis and the mode of secretion.

First of all the ultrastructural studies enabled the researchers to recognize the structural units and fabrics involved in the formation of the graptolite skeleton. These data have been published recently (Towe and Urbanek 1972, 1974; Urbanek and Towe 1974, 1975; Urbanek and Rickards 1974). Without going into details, it was found that the graptolite skeleton is made of predominantly fibrous material. Two main kinds of fibrils, the cortical and fusellar fibrils — may be considered, according to our working hypothesis — as collagen-like materials. Considerable diversity of structures observed under the electron microscopy in the peridermal derivatives of graptolites may be classified using a limited set of terms. While retaining the terms tissue (the fusellar and cortical tissue) for larger complexes defined according to Kozłowski in morphogenetic aspect, it was suggested to distinguish certain fabrics and their basis components. A number of fabrics were recognized, each being a portion of periderm with a certain specific pattern and unit elements.

The suggested classification of observed ultrastructural features seems to be largely fruitful for correlation of submicroscopic data with gross structural and light microscopic features in graptolites. This is lucky that from the beginning the ultrastructural studies on graptolites have been clearly related to previous works made with the light microscope and an ordinary microtome.

One of the most striking and unexpected facts discovered with the help of the electron microscope is recognition of a sharp difference in the fabric of fusellar tissue in graptolites and in fossil and recent pterobranchs. These problems were quite recently discussed in my paper (Urbanek 1976a). This observation has doubtlessly a great significance for understanding the phylogenetic relations between both groups, which for decades have been considered (for important reasons) at closely related. The new data seem to indicate that this ancestry was at least rather remote, or may even question the significance of their similarities as having the value of homology.

The recent controversy over the mode of secretion of graptolite skeleton involves two contrary models of morphogenesis — the "membrane" one and the "pterobranch" one. The differences in the opinions are partly

due to different techniques being used, but partly also to different methodological approaches to the problem studied. This controversy is discussed in the next chapters. The present author enjoyed very many discussions with Mr Peter R. Crowther (Cambridge) which were most helpful for a better understanding of his positions. Thanks are also due to Dr Dietmar Andres (West Berlin) for sending his valuable remarks. The present writer has made every effort to follow both his adversaries in their objectivity, but is not certain that he succeeded to avoid being subjective when evaluating the data and lines of reasoning. Sincere thanks are due to Professor Alwyn Williams (Glasgow) for having read the manuscript and given valuable remarks.

THE PROBLEM OF SECRETION AND MORPHOGENESIS OF GRAPTOLITE SKELETON

Among many aspects of ultrastructural studies of graptolites of particular importance are speculations on the mode of secretion of graptolite periderm and on the morphogenesis and evolution of their skeletal tissue.

The crucial significance of a right interpretation of the mode of secretion of peridermal derivatives in graptolites lies in its value 1° for resolving phylogenetic problems, for a better understanding of the 2° development and the function and 3° organization of the colony.

Differences recognized in the fabric of pterobranch and graptolite skeleton, when accompanied by fundamental differences in the mode of its secretion, may certainly rank as very significant, implying lack of homology between the structures considered. The same differences in the fabric with an essentially similar mode of secretion, although indicative of substantial evolutionary changes do not exclude *per se* some degree of affinity (comp. p. 622).

Explanation of the mode of secretion has also a great significance for a better understanding of the relations between the inferred soft parts and the skeleton, a classical paleontological problem, having a crucial significance for comprehension of the biology of every fossil group. Ultrastructural data may shed a new light on this problem, as it is indicated by progress achieved on this way in a number of groups (to mention only molluscs and brachiopods).

At least four models of skeleton secretion have been already suggested and three of them prior to the beginning of ultrastructural research on graptolites. These are namely:

1) a classical (dualistic) model of Kozłowski (1938, 1949),

2) a uniform pterobranch model of Beklemishev (1951),

3) a uniform model posed in two variants by Bohlin (1950) and Kirk (1972),

4) a modified pterobranch model of Rickards (1975).

In view of Kozłowski's (1949, 1966) ideas in the mode of secretion of periderm in graptolites there is a little doubt that secretion of the fusellar component must have been identical with the mode of secretion in Recent *Rhabdopleura*. An extreme similarity of structural units and their pattern in the fuselar tissues of both groups, which was emphasized so strongly by Kozłowski, leaves no place for any other interpretation even though this particular point was not specifically treated in classical Kozłowski's (1949, 1966) papers.

Since secretion of the tubarium in *Rhabdopleura* is usually ascribed to the glands situated on the cephalic disc of the zooid, the fusellar component of graptolite periderm should be formed in the light of Kozłowski's reasoning by a comparable part of the graptolite zooid. The cortical component in graptolite thecal walls was considered by Kozłowski (1949, 1966) as a character newly acquired by the graptolites and which found no counter-part in the skeleton of pterobranchs. By analogy with certain Bryozoa (Cyclostomata) its secretion was considered by Kozłowski to be due to the existence of some soft tissue (extrathecal membrane) enveloping the entire rhabdosome from the outside. Such a membrane may be visualized as a direct extension of the wall of the upper edge of each zooid and uniting all members of the colony.

The essential point in Kozłowski's concept of secretion of the graptolite periderm is that fusellar tissue is primary and cortical tissue is secondary. This secondary cortex was deposited somewhat later over the outer surface of the fusellar component, growing thicker during the colony life and causing a gradual secondary thickening of the thecal walls. An extrathecal membrane could be visualized therefore as present from the very beginning of the formation of any given theca. But in comparison with the pterobranch mode, this would leave no access for the cephalic disc of the zooid available to the growing margin of the theca (fig. 1, *A*). As an alternative a membrane could be imagined gradually spreading distalwards from the preceding thecae (fig. 1, *B*).

Bulman (1955), while accepting the general Kozłowski concept of skeleton formation in graptolites, pointed out that "the precise details of morphology are extremely difficult to visualize, however; and if there were an external membrane uniting all the zooids then the lophophore and proboscis must have been external to this, in which case the fusellar tissue itself can scarcely have been secreted by the proboscis (as it is in the pterobranchs)" (Bulman 1955: 21). Furthemore, he emphasized that "the existence of this enveloping tissue constitutes a significant difference between graptolites and pterobranchs, and its relation to the body of the zooids is certainly difficult to visualize, bearing in mind that the fusellar layer of graptolites must surely have been secreted by some part of the preoral lobe" (Bulman 1970: 25).
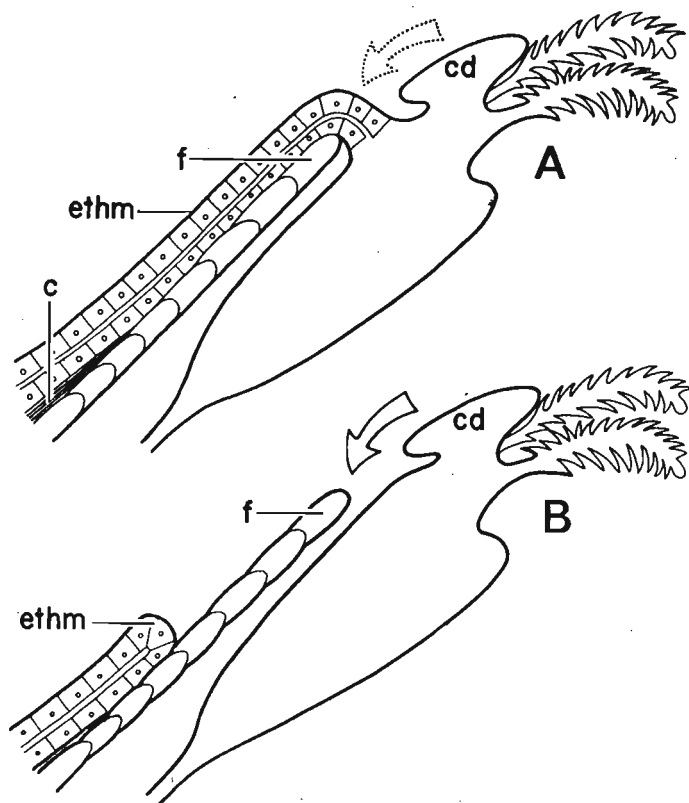
Fig. 1. Diagrammatic representation of inferred relationships of soft parts to the thecal wall in graptolites following the Kozłowski concept. *A* assumes an early formation of an extrathecal membrane as the result of an extension of the lateral walls of the zooid body. *B* assumes a delayed overgrowth of the thecal wall by a membrane spreading distalwards. Arrow (broken line) indicates the lack of access of the cephalic disc (*cd*) to the fusellar wall. In *B* the arrow (solid line) indicates a point of access; *c* cortical component; *f* fusellar component; *ethm* extrathecal membrane (from Urbanek 1976a).

Beklemishev (1951), convinced by Kozłowski's reasoning on the close affinity between graptolites and Pterobranchia, concluded that secretion of the graptolites periderm was due to the pterobranch mode only. He ascribed the formation of the cortical coating to a secretionary activity of the zooids, leaving their zooidal tubes and creeping over the outer surface of the thecae thus covering them with secondary layers of peridermal substance. Beklemishev was also the first to emphasize that formation of fusellar growth bands, so peculiar to both groups, cannot be ascribed to such different parts of the body as the cephalic disc (in Pterobranchia) and an epithelial membrane (in Graptolithina).

Criticism of Kozłowski's concept of periderm formation in graptolites and of their affinities with the pterobranchs was expressed by Bohlin (1950). Some of Bohlin's arguments were clearly based on misinterpretations of graptolite morphology (e.g., his conclusion that graptolites never

formed creeping or incrusting colonies, or his incomplete knowledge of stolonal system). Some of his other arguments are very far reaching but were poorly substantiated by any data. For example, his suggestion that thecal walls were equivalent to the mesoglea of hydroids to support his thesis on the coelenterate affinities of the graptolites (compare also Kozłowski 1966). Some of Bohlin's arguments against the Kozłowski concept of skeletal secretion in graptolites, however, deserve renewed attention.

Bohlin (1950) suggested a uniform mode of secretion of both components of the thecal wall, both being formed in his opinion "in constant contact with soft tissues". The entire thecal wall formed, in his opinion, between two epithecal layers — the outer epithecal layer being responsible for secretion of the cortical component; and the inner epithelial layer for the fusellar component (Bohlin 1950: 112 and figs. 4, 6). This would also explain, according to Bohlin, the substantial difference which exists between fusellar and cortical tissue.

Recently Kirk (1972, 1974, 1975) has considered the problem of the extrathecal tissue. Her conclusions are essentially similar, although not exactly identical, with those of Bohlin (1950). Difficulties in the anatomical and functional association of the cephalic disc responsible for the formation of fuselli, and the extrathecal tissue required to account for the deposition of the cortical layers, led Kirk to doubt whether the fuselli in graptolites could have been secreted by a cephalic disc at all. She suggested, like Bohlin, that both the fusellar and cortical components were secreted by a contiguous epithelium. Secretion of the entire wall of thecae is attributed by Kirk to a double layered epithelial evagination (fold or mantle), the fuselli being secreted from one portion and the cortical layers from another, both within such a structure. In order to explain the bilateral arrangement and alternation of fuselli, Kirk (1972: 4) suggested that the secretion of the fusellar component is due to an upward growth of the "mantle evagination'", first on one side and then on the other. This "rocking-growth" would be accompanied by secretion of successive fusellar half-rings on the outer surface on the zooidal epithelium somewhat behind the proliferating margin. Based on this model of secretion, Kirk offered her restorations showing the relation of the skeleton and soft parts in the dendroid and graptoloid rhabdosome (Kirk 1972: pl. 1, *A—B*).

Rickards (1975) formulated his views just before the main data on ultrastructural anatomy of graptolites were published. He has emphasized that in all probability the hemichordates are the nearest relatives of graptolites, but the "manner of secretion of the cortical and fusellar layers of the graptolite periderm remains the main stumbling block in any reconstruction of the zooid" (Rickards 1975: 431). In the opinion of Rickards a modified pre-oral lobe of an otherwise rhabdopleuracean zooid

has been depicted (Rickards 1975: 429; fig. 76) as a bilobate structure overhanging the thecal walls on both sides and producing in this way a sort of extrathecal tissue derived from individual zooids. In order to explain the formation of the nema, Rickards suggested a second source of extrathecal tissue namely from the nemal tube. In this way the nema was constructed by the migration of secreting cells over its growing tip.

Rickards' interpretation is essentially a dualistic one, the main difference from Kozłowski's views being in the source of extrathecal tissue and in the strong modification of the pre-oral lobe of the graptolite zooid. Thus he has made an attempt to solve the topographical problems posed by Kozłowski's classical scheme.

The recent discovery of ribbon-like cortical units of secretion (the so called "bandages" see p. 610) changes the position of Rickards who is now inclined to accept the scheme proposed by Beklemishev (Crowther and Rickards 1977). However, his previous explanation of the formation of the nema by the external secreting tissue, possibly exuded from the tip of the prosicula is still considered a reasonable suggestion, necessary for understanding the nemal growth (Crowther and Rickards 1977: 10, 18). This introduces an interesting element into the line of recent reasoning of Crowther and Rickards as adherents of the "pterobranch model" of secretion of graptolite skeleton (see also p. 610).

As all these models had already stimulated rather numerous speculations, I thought it very important to collect a certain number of crucial observations which might serve later for evaluation of hypotheses suggested earlier or to elaborate an entirely new point of view. This explains a rather prolonged silence on my part as to the problem of secretion of graptolite skeleton, although within a few months after we started certain preliminary conclusions were formulated and discussed with some colleagues (late Professor O.M.B. Bulman, Dr R.B. Rickards, Dr N.P Dilly, Dr V. Jaanusson and with some others). To avoid a growing number of partial generalizations and short-living working hypotheses I decided to present a more complete picture based on a somewhat broader range of data (Urbanek 1976a). Even a certain risk of loosing priority in some conclusions to less patient colleagues, eager to draw far-reaching conclusions on less complete body of facts already published by us — could not change my attitude to this important problem.

UNIFORM VERSUS DUALISTIC MODE OF SKELETON SECRETION IN GRAPTOLITES

What are the basic facts recognized with the transient electron microscope which shed a new light on the mode of secretion of graptolite periderm?

The classical scheme of Kozłowski (1949) postulates that the cortical

covering is formed secondarily, showing a distinct delay with respect to the secretion of fusellar tissue. In contrast, some of our data indicate that, with hardly any delay, part of the cortical deposit is formed over the wall of the growing thecae. This has been recognized in *Dictyonema* sp. where our data display the presence of a cortical coating (so-called autocortex Urbanek and Towe 1974) on young autothecae. Its appearance precedes therefore the overgrowth by lateral thecae within a given triad (fig. 2, *A—B*). This early formation of an autocortex in
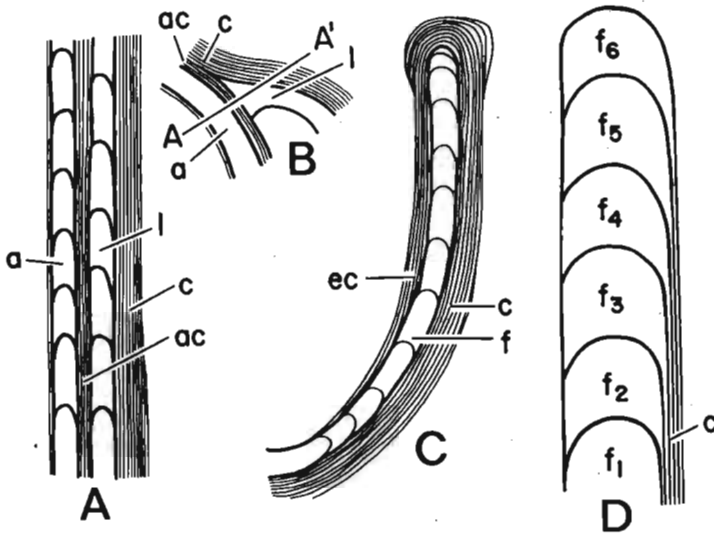

Fig. 2. Anatomical features bearing on the mode of secretion of the skeleton in graptolites. An early formation of cortical coating (*ac* autocortex) over the outer surface of a juvenile autotheca (*a*) preceding the growth of a lateral theca (*l*) and formation of a common cortical envelope (*c* cortex) shown in logitudinal section (*A*) and in transverse section (*B*). *A—A'* in B is the plane of the section shown in *A*. C shows the presence of a cortical deposit on the inner wall of autotheca (*ec* endo-cortex) penetrating deeply into the thecal cavity and continuous with the outer cortical deposit over the aperture: *f* fusellar wall of autotheca. D illustrates the simultaneous formation of successive fuselli (f_1—f_6) and corresponding layers of cortical deposit on the outer surface of the theca in *Didymograptus* sp. (from Urbanek 1976a).

some dendroids is indicative of a continuous secretionary activity during the thecal growth. On this basis it is difficult to visualize either an access for any external parts of the zooidal body (such as the cephalic disc) to the growing margin of thecae, or a delayed overgrowth of the outer surface of thecae by an extrathecal membrane spreading gradually distalwards (compare fig. 1, *A—B*).

Of even greater importance for clarifying the mode of secretion of thecal walls is the presence of an inner cortical deposit, sometimes rather heavy, inside the thecal cavity of some graptolites. According to Kozło-wski (1949, 1966), the cortical tissue would have to be produced only extrathecally and would be found only on the outer surface and around

the thecal aperture. Certain observations indicate the presence of a fairly thick layer of cortical tissue on the inner surface of the thecae, spreading deep into thecal cavity of autothecae ("twigs") in *Acanthograptus* sp. (Urbanek and Towe 1974, pl. 18: 1—2), in the thecae of *Pristiograptus dubius* (Urbanek and Towe 1975, pl. 19: 1—2) and in the thecae of *Climacograptus angulatus* (Urbanek, unpublished). In *Acanthograptus* sp. particular layers of the cortical deposit are continuous over the apertural margin of thecae and pass from an outer into an inner cortical coating of the autotheca penetrating deeply into the thecal cavity (fig. 2, *C*) In *Climacograptus angulatus* the inner cortical deposit is particularly heavy and shows little difference from the outer one. It is this distinct continuity of some of the cortical layers over the aperture that makes us consider secretion of both the outer and inner cortical coatings to be executed by the same part of the zooidal body rather than by different parts of the body.

Inasmuch as the outer member of the entire cortical coating was termed cortex (Urbanek and Towe 1974), it was considered desirable to introduce the term endocortex for its inner member (Urbanek 1976a). The continuity between the cortex and the endocortex may indicate that, in life, the thecal walls were covered from both sides by a membrane of soft tissues capable of the secretion of a cortical fabric over its entire surface.

Additional evidence bearing on the mode of secretion of the skeleton in graptolites is supplied by our observations showing a close relationship between the fusellar and cortical fabrics. An occasional transition from typical fusellar fabric within the body of a fusellus to a cortical-like material at the top of the same fusellus, has been observed in *Dictyonema* sp. (Urbanek and Towe 1974: pl. 13: 1). Further substantiation is provided by the presence of both fusellar and cortical fabric within a single secretionary unit, indeed a single fusellus. This is a paradoxical fact which could be recognized only with the technique of transient electron microscopy. This has been recognized in *Acanthograptus* sp. (Urbanek and Towe: 1974, pl. 6: 1—2), in *Didymograptus* sp. (Urbanek and Towe 1975: pl. 18: 1—2), and in *Pristiograptus dubius* (Urbanek and Towe 1975: pl. 14: 1—3). At some places a transition could be traced from a typical fusellar fibril of fusellus body into a cortical-like fibril in the outer lamella (compare also pl. 30: 3, arrows). This not only indicates the essential chemical similarity of both fusellar and cortical fibrils, but also demonstrates an easy and smooth shift in the secretion from the fusellar to the cortical fabric within a single phase of secretion. It is this fact that provides evidence for the secretion of the graptolite skeleton by the same tissue or portion of the body (Urbanek 1976a).

Such observations on the mode of formation of the cortex in *Didymograptus* sp. are important for understanding the mode of secretion

of thecal walls in general. As established by Urbanek and Towe (1975: pl. 18: 1—2), the formation of the cortex is the result of a large amount of overlap of the outer lamellae of neighbouring fuselli onto the outer surface of the thecal walls. This results in an accumulation of outer lamellae so as to produce an outer cortical covering (c). In this particular case a given fusellus and its corresponding layer of cortex were both secreted simultaneously by the same tissue or part of the graptolite zooid (fig, 2, D).

In conclusion, it is possible to generalize from these ultrastructural studies that a uniform mode of secretion of both components of the graptolite periderm can take place by a shift in the secretionary activity of the cells, which are capable of producing both fuselar and cortical fabric.

Formation of a single fusellus may be described in terms of succession of certain secretionary phases in the activity of such cells. Formation of the body fusellus made of the fusellar fabric only in thus phase 1 (ph_1). Formation of the outer lamella, an essentially cortical element, is phase 2 (ph_2), and secretion of an outer pellicle, made of sheet fabric, is phase 3 (ph_3) respectively (fig. 3, A—B). These phases correspond to the successive changes in secretionary activities of cells responsible for the secretion of skeletal material.

The fuselli of some graptolites, e.g. in *Dictyonema* sp. described by Urbanek and Towe (1974), are relatively simple being composed of the
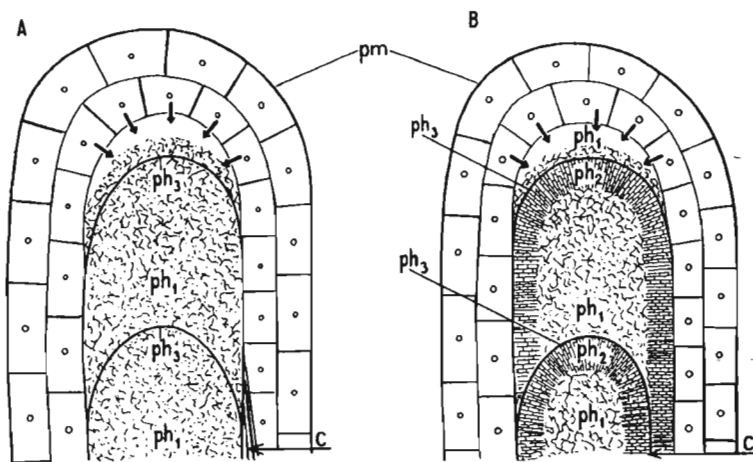

Fig. 3. Ideogram showing presumable relation of secretory part of the perithecal membrane (*pm*) to the growing edge of a thecal wall. *A* in the case of *Dictyonema* type with fuselli lacking the cortical phase of secretion (ph_1—ph_3) and with independent mode of cortex (*c*) formation. *B* in the case of *Acanthograptus* type with fuselli showing the cortical phase of secretion (ph_1—ph_2—ph_3) and with dependent mode of cortex (*c*) formation. Arrows indicate the secretionary activity of epithelial cells and directions of extrusion of their products. Mesodermal component of the perithecal membrane not visualized for the sake of convenience. Note the phase control in formation of fuselli (ph_1, ph_2, ph_3). (from Urbanek 1976b).

body and an outer pellicle only. Thus, the formation of their fuselli may be described as a simple succession (Urbanek 1976b):

$$ph_1 - ph_3 \text{ (fig. 3, } A)$$

omitting phase 2 (ph_2) responsible for the formation of an outer lamella. This omission is most probably a primitive character of some dendroids (*Dictyonema* type of secretion) and lack of an outer lamella in the fuselli may also be an ancestral character of all graptolites. The fuselli in another dendroid (*Acanthograptus* sp.) and some other graptolites have all three components resulting from a secretion according to the formula:

$$ph_1 - ph_2 - ph_3 \text{ (fig. 3, } B)$$

The recent studies on the ultrastructure of microfusellar tissue in *Neocucullograptus kozlowskii* (Urbanek 1976b) are shedding a new light on the mechanism of secretion of graptolite skeleton. The microfusellar tissue is a separate peridermal material, recognized in some monograptids and consisting of very narrow, densely crowded strips (microfuselli). Microfuselli proved to be very important for understanding the morphogenesis of graptolite skeletal tissues in general, and especially for a better understanding of the relation between the fusellar and the cortical tissue. The microfusellar tissue is composed of both fully developed and reduced microfuselli. The fully developed microfuselli show the same succession of secretionary phases as in *Acanthograptus* type, namely:

$$ph_1 - ph_2 - ph_3$$

phase 1 being only distinctly abbreviated which results in an smaller amount of the fusellar fabric produced and, respectively, in a greater narrowness of the strips. The above secretionary phase may undergo a further abbreviation up to a complete reduction and skipping of ph_1. This is how reduced microfuselli are formed according to the sequence:

$$ph_2 - ph_3 \text{ (fig. 4)}$$

Such composition does not differ, however, from that in the cortical tissue. The microfusellar tissue composed of reduced microfuselli still retains therefore a structural organization of a fusellar tissue (the presence of V-shaped growth bands) acquiring at the same time an essentially cortical composition (fabric, nature of unit elements).

As indicated by the sections studied, this transition from an essentially fusellar to an essentially cortical tissue may take place either as a gradual change or an abrupt shift in the secretory activity of cells. A necessary prerequisite for this transformation of fusellar tissue into its cortical derivative is the appearance of a cortical phase within an act of secretion of a single fusellus (as described by Urbanek and Towe 1974, 1975). An outer lamella is composed of tightly packed, more or less ordered fibrils, interconnected by transverse rods, i.e. it bears all the characters of the cortical fabric, although it is secreted as a part of the fusellus and sealed by its outer pellicle. The origin of the outer lamella could be visualized (Urbanek 1976b: fig. 4) as an intensification and ordering of
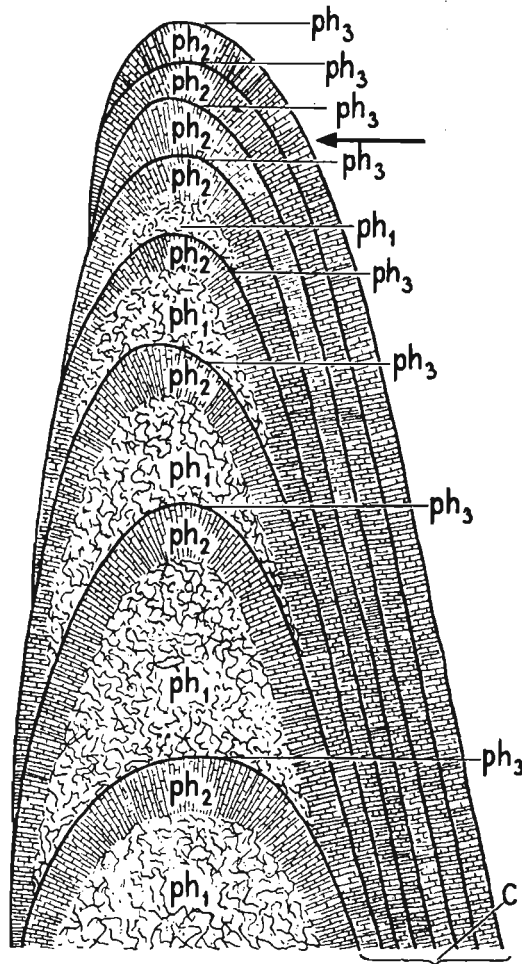
Fig. 4. Diagram showing a gradual depression of fusellar phase of secretion (ph_1) in a series of eight microfuselli seen on a longitudinal section. In result of the above process the fully developed microfuselli pass into reduced ones (at the top). The onset of a complete skipping of ph_1 (indicated by an arrow) results in formation of reduced microfuselli made solely of cortical components (ph_2, ph_3). Note a strongly asymmetric overlap of microfuselli producing in this way a heavy cortical coating (c) on one side (from Urbanek 1976b).

the primarily isolated and dispersed centers of corticization, which had been observed sporadically within the top of fuselli in *Dictyonema* sp. (Urbanek and Towe 1974: pl. 13: 1). The appearance of the outer lamella (pl. 27: 4) produced a prerequisite for the dependent mode of formation of the cortical deposits, especially the outer cortical coating (cortex) as recognized in the thecae of *Didymograptus* sp. (Urbanek and Towe 1975), and the microfusellar additions in *Neocucullograptus kozlowskii*.

It seems therefore, that the independent mode was phylogenetically the primary one, and initially the fuselli were probably closed systems with cortex laid down on them secondarily. The development of an outer

lamella accounts for a later appearance of a dependent mode of cortex formation, due to the overlapping of the fusellar limbs made of cortical fabric. In this way, the fuselli were secondarily transformed into systems opened towards the cortex, each extending into a corresponding layer of the cortex (fig. 5, A—B). Although more data are needed to substantiate the above working hypothesis, the suggested direction of changes from an independent mode of cortex formation seems to me more probable than the reversed one.
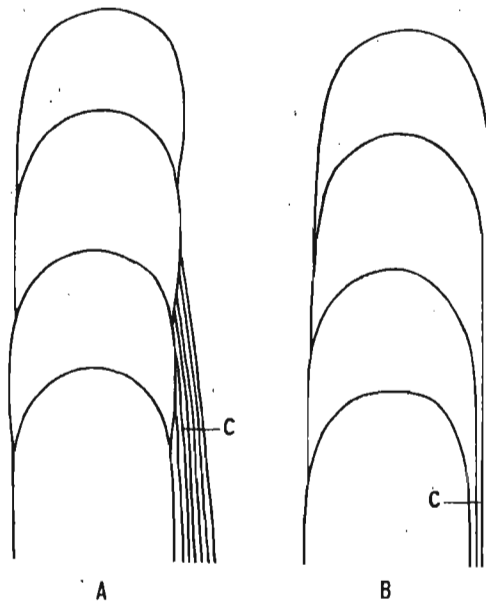

Fig. 5. Diagram showing an independent (A) and dependent (B) mode of cortex (c) formation, as recognized by ultrastructural studies (from Urbanek 1976b).

The mechanism of the appearance of phase 2 (ph_2) as a separate stage in the formation of a fusellus may be interpreted, e.g. as a change in control of secretory behaviour of epithelial cells in the perithecal membrane (soft tissues enveloping the thecal wall from both sides). According to the independent mode of cortex formation, the cortical fabric was laid down with a certain delay by cells which were moved over from the proliferation zone to the outer layer of the perithecal infolding (see fig. 2, A). The control of the secretion was therefore determined by positional (displacement from the edge zone) and temporal (delay in the secretion) factors. The formation of an outer lamella means a complete elimination of positional control (deposition of cortical fabric by cells already at the growing edge) and a drastic reduction of significance of temporal factors with preservation, however, of the previous sequence in the secretory phase (fig. 3, A—B).

The ultrastructural studies on microfusellar tissue supply one more example of close interconnections and transients between the fusellar and the cortical tissue. There is no sharp line delimiting these tissues at the ultrastructural level, as their unit elements as well as major organizational features display transitions. The discrimination between the fusellar and the cortical tissue seems a very relative one, both being only useful descriptive categories, which do not differ from the morphogenetic point of view.

The main generalization which may be drawn from the studies made with the TEM is therefore that both components of graptolite periderm were formed due to the uniform mode of secretion, being produced by the same secretory tissue or part of the body. This view formulated by Urbanek (1976a: 23—24) seems rather safe and is accepted by the recent authors representing otherwise very different opinions on the nature of this tissue or part of the zooid body which was engaged in the secretionary activity.

Although the data supplied by ultrastructural studies are strongly suggestive of a uniform mode of secretion of the graptolite periderm they do not indicate *per se*, which particular part of the body or tissue may be involved in the secretionary activity. The independent origins of the fusellar and the cortical components of the periderm as suggested by Kozłowski (1949, 1966), however, appear untenable in the light of our ultrastructural studies. The dualistic hypothesis of Kozłowski suggesting a "pterobranch" mode of secretion for the fusellar component and a "bryozoan" mode of secretion for the cortical component also appears doubtful, for both anatomical and topographical reasons (compare criticism by Bulman 1955, 1970; also Kirk 1972). These two modes of secretion are mutually incompatible and cannot work together functionally. Therefore Urbanek (1976a) arrived at the opinion that a workable scheme for secretion of the graptolite periderm should be uniform — either "pterobranch-like" (both components produced by the cephalic disc or glands of other parts of the zooid body) or "bryozoan-like" (both components produced by a membrane enveloping the thecal walls). He has found the bryozoan-like model, called later the "membrane model" far more probable than the pterobranch-like one.

THE "MEMBRANE" MODEL OF SECRETION OF GRAPTOLITE SKELETAL TISSUES

The data obtained from ultrastructural studies are easily understandable if one assumes that the formation of the entire graptolite periderm takes place inside an epithelial evagination, for which the term "perithecal membrane" was coined by Urbanek (1976a). The secretory portion

of the perithecal membrane (fig. 3, *pm*) was most probably of epithelial nature, the cells being capable of secretion in either separate phases or in gradation from one type of secretion to the other of both fusellar and cortical fabric. The presence of a mesodermal component (*m*) within the perithecal membrane is doubtless but it is not discussed in details as inessential for our reasoning. The perithecal membrane is supposed to cover the entire outer and a considerable part of the inner surface of the thecae, producing a fold over the thecal aperture or its growing edge. The inner portion of the perithecal membrane probably passed into the body wall of the zooid proper, but an attempt at restoration of their closer relations seems premature.

The presence of some sort of perithecal membrane is suggested by the presence of outer and inner cortical coatings, with distinct continuity of numerous layers over the aperture (as in *Acanthograptus* sp. described above, p. 603).

The collagen in the layered structures, like basal membranes composed of orderly arranged fibrils and similar in many respects to the cortical tissue, is now considered to be secreted mainly or exclusively by epithelial cells (Porter 1964). This may substantiate the presumably epithelial nature of the secretory portion of the perithecal membrane.

In contrast to the earlier views of Bohlin (1950, see above) there is no need to ascribe the secretion of the fusellum to an inner layer of epithelium. The arcuate shape of fuselli and their bilateral overlap are strongly suggestive of the fact that they were produced within a fold of soft tissue, close to the proliferating margin of the epithelial evagination as earlier suggested by Kirk (1972). The same is indicated by the conical shape of microfuselli and the V-shape of their reduced derivatives as mentioned above. The simultaneous formation of fuselli and corresponding layers of cortex (the dependent mode of cortex formation) may be easily explained if we assume that they were formed inside an epithelial evagination — the perithecal membrane (fig. 3, *pm*).

The phase control of secretion as suggested by the ultrastructural features of graptolite periderm, may be ascribed to shifts in secretionary activity of cells within such membrane, showing in this way a remote resemblance to the secretionary activity at the edge of the mantle in molluscs and brachiopods. In certain cases these cells were capable of producing both fusellar and cortical fabrics. Secretion of a greater amount of the cortical fabric (cortex and endocortex was due to a latter polarization of the secretionary activity of the cells which were displaced from the proliferating margin into the surface of the perithecal membrane proper (fig. 3, *A—B*).

The "membrane" hypothesis offers an explanation of formation of the entire graptolite periderm, including such specialized structures as the basal disc (holdfast) of sessile graptolites and the nema (virgula) of plank-

tonic graptolites. The holoperipheral growth lines observed within these peridermal derivatives (pl. 28) may be explained by an assumption that secretion occurs within the envelopes made of soft tissues (comp. Urbanek and Towe 1974: pls. 23—25 and Urbanek and Towe 1975: pls. 2—4).

The "membrane" model is a further development of some earlier ideas suggested by Bohlin (1950) and Kirk (1972, 1974) but it involves substantial corrections of their views based on new data supplied by the transmision electron microscopy.

THE PTEROBRANCH MODEL OF CORTEX FORMATION

This fairly coherent and simple membrane model of secretion of graptolite periderm has been threatened by important observations made independently by Andres (1976, 1977), Crowther and Rickards (1977) and Crowther (1978, this volume). The paper by Crowther and Rickards (1977) presents an excellent review of the data, while the problems related to secretion are discussed in this volume by Crowther.

Using the SEM Crowther has recognized a peculiar and unexpected organization of cortical tissue, namely the presence of numerous, rather narrow and elongated belts called by him "bandages", which cover the surface of the rhabdosome. The preliminary interpretation of these structures, as suggested by Crowther, is that cortex has been secreted in the form of numerous "bandages", which only later accumulated into a cortical covering of the rhabdosome. These "bandages" are usually placed obliquely in respect of the fuselli and pass over a number of them producing in this way an intersecting, criss-cross pattern. According to Crowther, these bandages frequently radiate from a thecal aperture, thus implying that bandages were produced by zooids, when creeping over the fusellar periderm and "dragging or pushing the cephalic shield across the surface of the periderm, secreting as it went. Its size would have been governed by the size and secretory capabilities of the zooid, its course by the direction of motion of the zooid" (Crowther 1977, in lecture). While locally, at any particular level along the rhabdosome, adjacent bandages are uniform in size, there is a gradual increase in bandage size distally along the rhabdosome accompanying the usual increase in the thecal size and in the size of the fuselli.

Similar observations have been made by Andres (1976, 1977) in *Orthograptus gracilis* with light microscope. Numerous and distinct ribbons of probable cortical nature were recognized on the surface of rhabdosome, producing a characteristic pattern of crossing and overlying "bandages". Similar structures were described earlier by Kraft as "Chitinverdückungsbänder" but erroneously considered as placed over the inner surface of the thecae. In opinion of Andres (1977) there is no or only a very slight increase in the width of cortical ribbons distalwards, in contrast to a dis-

tinct increase in the fusellar and theca width. Such ribbons may be interpreted as secretion produced by cephalic discs of individual zooids, creeping over the surface of the rhabdosome, the cortical ribbons being secreted by the adult and the fuselli also by the juvenile zooids. This resembles the cephalodiscid pterobranchs which may produce secondary thickenings over the coenecium due to secretionary activity of particular zooids. Consequently, Andres ascribes the formation of both fusellum and cortex to the pterobranch mode of secretion, along the line suggested by Beklemishev (1951). Thus, Andres rejects Kozłowski's dualistic explanation of the mode of secretion of graptolite skeleton, confirms Beklemishev's uniformistic concept of secretion and in conclusion emphasizes the close affinity between both groups.

Both Anders and Crowther share the opinion that the deposition and accumulation of bandages or similar ribbon-like elements may be compared to a similar process in the recent *Cephalodiscus*. In this latter case the secondary deposition of peridermal material over the wall of coenecium is achieved without any external membrane of soft tissue, solely due to secretion by cephalic discs of zooids creeping outside their tubes. In this way cephalodiscid pterobranch provide a model of cortex formation for graptolites, be it assumed that the bandages are universal units of cortex secretion in all graptolites, including both planktonic and sessile groups. Andres (1977) has found them in a number of graptoloids, emphasizing, however, that they were not recognized so far in sessile graptolites. They may be present there but less distinct as compared with planktonic graptoloids. Andres has found surprising, however, that the electron micrographs published by Urbanek and Towe (1974, 1975) are not especially suggestive of the presence of bandages. Crowther has recognized cortical bandaging on at least 25 species from 15 genera including dendroids, and is convinced that it may well be of universal occurrence. Both authors in question agree, however, that the bandaging is best developed in diplograptids. According to Crowther each bandage is composed of an outer membrane, made of sheet material and an orderly array of fibrils of cortical nature, which are parallel to the bandage margins. Both Andres and Crowther are convinced that the entire is made of ribbon-like elements, without any lining produced by continuous layers of genuine cortex, lying beneath the bandaging.

Crowther (this volume, in discussion of Dr. Dr. Bates' and Kirk's paper) has emphasized that the versatility of the pterobranch mode of secretion is often underestimated. Coenecia in *Cephalodiscus* (*Acoelothecia*) are made of a framework of rods ("ladders") which bear a striking similarity to the retiolitid skeleton. *Cephalodiscus* manages to build these structures, without any soft tissue membrane using only its cephalic disc. Thus, according to Crowther, it seems reasonable to conclude that retiolitids might have a similar capability.

AUXILLIARY HYPOTHESIS TO THE MEMBRANE MODEL: SECRETIONARY INFOLDINGS OF PERITHECAL MEMBRANE

Organization of cortical deposits into numerous ribbons as secretionary units, introduces doubtlessly a new aspect to the much discussed problem of graptolite biology and affinities. It deserves greater attention in order to ensure a reliable interpretation of their formation.

Obviously it seems very tempting to ascribe particular bandages to secretionary activity of individual zooids, presuming along the line suggested already by Beklemishev, that each bandage was secreted by glands of the cephalic shield when the animal was creeping over the surface of the rhabdosome.

Assuming the previous model of continuous perithecal membrane, one could expect secretion of particular cortical layers on larger areas, patches with more or less irregular outline. Secretion of cortex in the form of rather long and narrow belts seems to contradict the perithecal membrane hypothesis as formulated before.

There are, however, also certain limitations of the pterobranch model which in fact offers the explanation of the cortex formation only, taking for granted that the entire fusellum has also been formed according to the pterobranch pattern because of numerous resemblances between fuselli of graptolites and pterobranchs. This approach undervalues the significance of certain important differences recognized in the composition of fusellar tissue of both groups in question (a quite different nature of unit elements, their patterns and biochemical nature) and in morphology (different superposition of fusellar bands, Urbanek 1976a).

A consistent hypothesis concerning the secretion of graptolite periderm should explain the origin of entire periderm and its derivatives. It should provide certain basis for explanation of the origin of fusellar and cortical components of the thecal wall as well as of such specialized, but highly characteristic for graptolite structures as the basal disc (holdfast), the nema (virgula) and its derivatives, the virgella and virgellarium, should explain the formation of the prosicula and later stages. The pterobranch model offers an elegant explanation of certain structures only, leaving the rest of questions to be explained elsewhere. In this way the novelty of a new discovery (the presence of cortical "bandages"!) is dramatically emphasized, while certain difficulties of explanation are ommited.

While, there are certain arguments to attribute the formation of "bandages" to the secretionary activity of individual zooids, there do not seem to be any good reasons to give preference to this hypothesis as a general explanation of morphogenesis of the remaining parts of the rhabdosome. The formation of the nema and simultaneous formation of the fusellum and cortex can hardly be ascribed to the secretionary acti-

vity of individual zooids and their creeping behaviour. This is why *I believe we must seek explanation of the bandages formation within the framework of perithecal membrane hypothesis.*

As the main secretionary activity of the perithecal membrane was presumably concentrated inside the fold of soft tissues close to the growing edges of the thecal part of the rhabdosome, one could suggest that the infoldings of the perithecal membrane are basic secretionary units. Particular layers of cortex were always formed under wrinkle-like, slightly swollen portions of this membrane homologous to the infolding at the thecal edge (see fig. 6, *si*). Such secretionary infoldings would
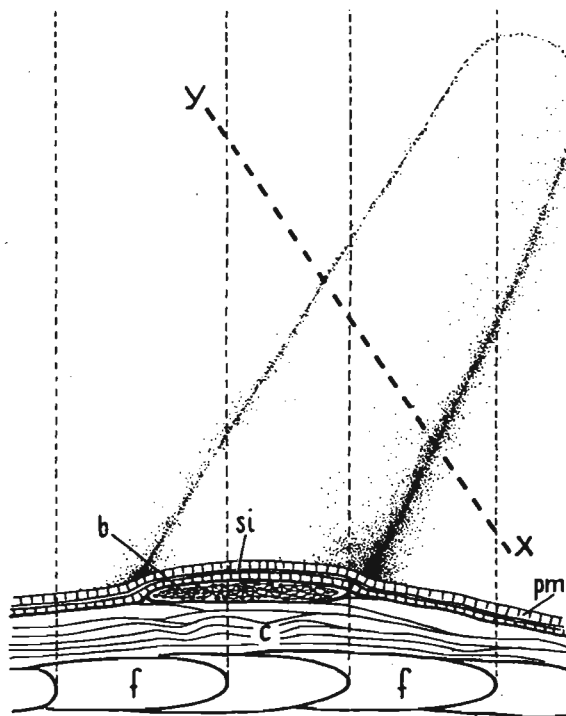

Fig. 6. Ideogram to illustrate the concept of secretionary infoldings (*si*) of the perithecal membrane (*pm*) as the morphogenetic units responsible for the secretion of ribbon-like cortical elements (bandages, *b*). Thecal wall seen in longitudinal section showing genuine cortex (*c*) which may be of dependent or independent type, and fusellar component (*f*); X—Y is a possible orientation of the next secretionary infolding, broken lines are projections of boundaries between fuselli over the wall of the theca.

frequently (or mostly) have a shape of elongated wrinkles, which from time to time migrated and changed orientation ($x-y$ on fig. 6) and were in this way responsible for the origin of "bandages". These bandages were formed due to secretion extruded by cells of such wrinkles or infoldings to be later polymerized in the form of long cortical fibrils, gathered into a single bundle — a "bandage" (fig. 7, *c*).

Even earlier Urbanek and Towe (1975) emphasized that in some grap-
toloids "the cortex is surprisingly uneven showing numerous local swel-
lings that express themselves on the external surface as distinct eleva-
tions followed by depressions" and that "elevations observed on the
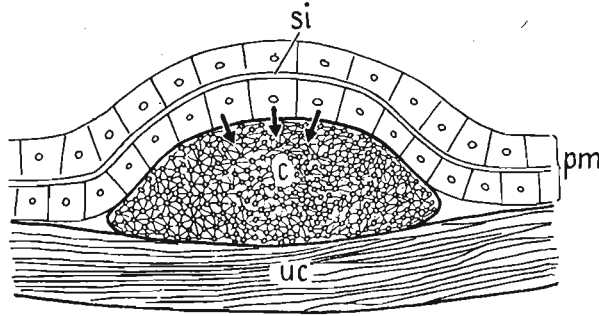outer surface of the cortex are due to either an increased number of

Fig. 7. Diagram to show the presumable relations between the cells of a transver-
selly sectioned secretionary infolding and their products. Secretions of cells are
extruded into the free space beneath the perithecal membrane (as indicated by
arrows) and later subject to fibrogenesis producing the cortical ribbon (c); uc un-
derlying cortical ribbon (bandage).

layers of cortical fabric or a greater thickness of the layers or both"
(op.cit.: 20). The elevations observed by Urbanek and Towe may corres-
pond to the bandages of Rickards and Crowther, although the latter aut-
hors emphasize the fact that each bandage is a separate layer of cortex,
delimited from the adjacent, under-and overlying layers, while Urbanek
and Towe observed rather a continuation of cortical layers from
one elevation to another with only a few cases of tapering. This problem
requires further investigations to solve the basic question — whether the
entire cortex is produced by accumulation of narrow bandages or this
is valid for its outermost portion only. In the latter case the "bandages"
may be considered secondary features — most probably a sort of rein-
forcements superimposed over the largely continuous cortical covering.

Preliminary results obtained by Urbanek and Mierzejewska (1978, in
this volume) on Orthograptus gracilis Roemer may be considered as sup-
porting the last-mentioned view. The thecal wall sectioned with an ultra-
microtome and observed with the TEM reveals the following components:
1. an endocortex, 2. fuselli, 3. a cortex and overlying ribbon-like elements
("bandages") as seen on fig. 6. While the endocortex and cortex are
formed due to a dependent mode overlapping of the outer lamellae of
a number of superimposed fuselli, the "bandages" are made of an almost
homogenous tissue (delicate reticulated material) which differs sharply
from much coarser and denser fibrils in the genuine cortical fabric (see
Urbanek and Mierzejewska 1978: pl. 35: 1; pl. 36: 1—3; pl. 37: 1, 2, this
volume). Thus, in contrast to an earlier belief of Andres (1977 in litt.)

there is a layer of genuine cortical material beneath the secondary deposits organized into ribbon-like elements. And contrary to the observations made by Crowther (1978, in this volume), the "bandages" in *Orthograptus gracilis* were not formed by the cortical fibrils but are made of a peculiar material.

The presence of dependent cortical layers beneath the bandages may be interpreted as an indirect evidence for a secretion under some sort of continuous membrane. On the other hand, a peculiar composition of "bandages" may be considered as an indication of a specialized trend of evolution of these structures, leading to elimination of their primary cortical nature. Our observations on *Pristiograptus dubius* and *Orthograptus gracilis* seem to substantiate the auxilliary hypothesis as to the presence of secretionary infoldings of the perithecal membrane.

The paper by Urbanek and Mierzejewska (1978, in this volume) contains other observations having some significance to the problem considered.

EVALUATION OF THE PTEROBRANCH MODEL OF SECRETION OF THE CORTEX

The pterobranch model of secretion of the graptolite periderm is based first of all on an analogy to secretion of coenecium in cephalodiscid pterobranchs. The wall is produced there by an apposition of numerous fusellar strips, which may be later covered on the inside or on the outside by a secondary deposits forming thin and densely crowded lamellae. In some cases, these secondary deposits appear as a spongy mass made of lamellae or layers interconnecting adjacent zooidal tubes (Harmer 1905; Andersson 1907). In *Rhabdopleura*, a layered inner lining has been found by Andersson (1907) and Kulicki (1971). Quite recently Dilly (1976) has described the vertical fibres on the outside of the erect tube of *Rhabdopleura*, which extend probably across several growth bands (fuselli), being added as an extra material late in the development of the tube.

The above observations speak for a capability of a pterobranch zooid to produce secondary deposits, in some cases substantial (cephalodiscids) in other rather incipient (rhabdopleurids). It must be emphasized, however, that the morphological form of these deposits as described so far, is not necessarilly similar to the classical "bandages" or "railway tracks" recognized in some graptolites. In fact, there is only rather a remote analogy which, however, does not invalidate it as a useful basis for a model of secretion. The phylogenetic thesis usually associated with the pterobranch model of secretion — namely the thesis on close affinity between both groups considered should rest upon a certain number of essential and specific resemblances between the units of secretion (fuselli, "ban-

dages") and in my opinion must be distinguished from a morphogenetic
explanation. This latter may be based on very general and little specific
features such as an ability for external deposition of the material. There-
fore the phylogenetic aspects will be discussed separately (see pp. 621—
623).

As a matter of fact a secondary deposition of layered peridermal ma-
terial has been safely established in cephalodiscids, without reliable evi-
dence for the presence of "bandages" or similar ribbon-like units of se-
cretion. In *Rhabdopleura*, external deposition of secondary material takes
the form of vertically arranged fibres with no specific resemblance to
either "bandages" or "railway tracks". Formation of skeletal structures
in pterobranchs is usually ascribed to a glandular area on the cephalic
disc, but recently some cells of the lophophore were also suggested as
responsible for the secretion of the tubes in *Rhabdopleura* (Dilly 1977,
pers. inform.).

Still more surprising is the lack of convincing evidence for the pre-
sence of "bandages" in sessile graptolites. In the opinion of Andres
(1977) this is because the cortical ribbons may be less clearly outlined in
the sessile graptolites than in the planktonic ones. The evidence present-
ed by Crowther and Rickards (1977: pls. 1—2) of the presence of "ban-
dages" in dendroids seems unconvincing to me as their SEM micrographs
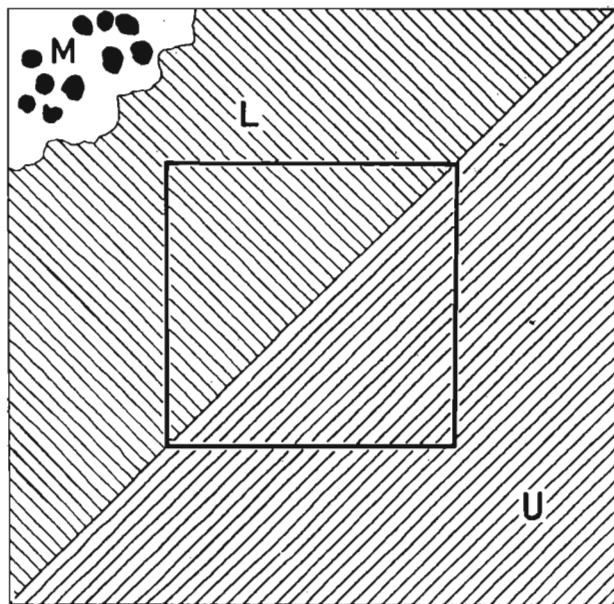

Fig. 8. Diagram to illustrate the possible "pseudo-bandaging effect" in result of the
damage of an upper layer of cortex (*U*) over certain area, thus exposing the under-
lying layer (*L*) and producing an alleged effect of a boundary between two bandages.
In upper left corner — preserved part of sheet fabric (*M* membrane) separating an
underlying (*L*) and overlying (*U*) layer of cortex, with a number of pits (black
spots) which correspond to intramembrane vesicles.

show only a single boundary between the ordinary underlying and overlying layers of cortex, displaying a different orientation of fibrils (see diagram on fig. 8 and explanation to it). There is no indication of narrow belts of secretion here, and such a boundary may be interpreted either as a limit of a larger area of secretion, or simply as an effect of the damage of the upper layer over a certain area, exposing in this way the underlying layer. Some more data which have become recently available and speak against the presence of "bandaging" in sessile graptolites are shown on pls. 28—30.

We are at present facing therefore a rather paradoxical situation: the "bandages" considered as ancestral and universal units of secretion inherited by graptolites from pterobranchs were not recognized so far either in pterobranchs or in primitive sessile graptolites. On the contrary, the only convincing evidence for the presence of "bandages" is for scandent graptoloids, especially for diplograptids. Unless changed by a new discovery this situation disagrees with a presumably primitive nature of these structures and speaks rather in favour of a hypothesis that "bandages" were specialized structures developed for the strengthening of the periderm.

The layered secondary deposits seen on microtome sections of cephalodiscid coenecia do not imply necessarily a rough painting with random orientation of brush and a quick sclerotization of the painted material. The secreted material seems to be rather smoothly spread over larger areas by means of flowing down or by a similar mechanism. Here we have a new possibility to explain the formation of smooth cortical layers over larger areas without assuming the presence of perithecal membrane. One could question, however, whether the main thesis of the pterobranch model as formulated by Andres and Crowther is universal formation of ribbon-like units of secretion due to painting them by the cephalic disc, or this model covers any activities of zooids leading to formation of secondary deposits which may eventually be recognized in pterobranchs?

Certain facts may indicate that a direct relation between the hypothetical cephalic discs of graptolite zooids and the "bandages", in the form postulated by Andres (1977) and Crowther (1978) is simplicistic. It is especially true in respect of a co-relation between the width of "bandages" and fuselli within the same theca as indicative of the size of the cephalic disc (or its secretory part). If the entire periderm was produced by the cephalic disc, as it is assumed by the pterobranch model, the same disc may produce growth bands of quite different width. In neocucullograptids, such different peridermal derivatives as the normal fuselli, microfuselli and presumed "bandages" should be ascribed to the same secretory portion of the cephalic disc. The width of these secretory units cannot be considered as indicative of the size of cephalic disc. On the

other hand, a fairly constant size of bandages at any local portion of the rhabdosome may be roughly related to its diameter or to the area of the free surface of the hypothetical perithecal membrane as factors determining the size of wrinkles (secretionary infoldings).

A number of questions may be raised with regard to functional implications suggested by the pterobranch model. The pterobranch model suggests a sharp and distinct change in the secretionary activity of the graptolite zooids, namely a change from a regular activity, with a rigid bilateral control of secretion (production of fusellar part of the skeleton) to an irregular chaotic deposition of "bandages" over the thecal surface. These two kinds of secretionary activity are not necessarily spaced in time. We know facts of the arrested growth of thecae and formation of a number of apertures, in each case followed most probably by secretion of some cortical material and later on by secretion of additional fuselli. In this way the pterobranch model ascribes to the same zooid an ability of a rigid morphogenetic control (formation of fuselli, astogenetic succession of the thecae) greatly surpassing the degree of control observed in pterobranchs, and uncontrolled random deposition of "bandages". Formation of microfusellar additions producing regular and, in many instances, complex apertural structures (Urbanek 1970) seems to indicate that the ability to control the morphogenesis is preserved for a long time and extended onto a post-matural phase. This implies within the framework of the pterobranch model rather an incoherent picture of the zooid activity, a combination of rigidly controlled secretion of fusellar derivatives with an entirely random behaviour when secreting the cortex.

Considering the mechanism of the formation of peridermal derivatives in cephalodiscids, Urbanek (1958) has arrived at the conclusion that their morphological differentation is accounted rather by the differences in physiology and what was called by him the secretionary behaviour of the zooids. In cephalodiscids, the anatomy of the zooids is fairly constant while coenecia are strongly differentiated. This is true also in respect of *Rhabdopleura*, although the connection between the soft parts and exoskeleton is a bit closer here as compared with cephalodiscids (e.g. sexual dimorphism of the tubes). In pterobranchs, the skeleton is formed due to secretionary activity of the particular zooids and the skeleton anatomy reflects more their secretionary behaviour than the morphology of their soft parts. According to Crowther (1977) and Andres (1977) the above model is valid for graptolites as well.

The other point of view was independently suggested by Bohlin (1950) and Urbanek (1958). It emphasises the high stability and ordering of periderm secretion in graptolites, which results in a very regular succession and budding of thecae and leads in graptoloids to the appearance of a regular morphological gradient with gradual changes or transitions

between the extreme and frequently complicated types of thecae within a single rhabdosome. Such regularity of structure can hardly be ascribed to integration of secretionary behaviour of particular zooids, which probably cannot be controlled with enough precision. The necessary degree of control may be on the other hand ensured by the known mechanisms of cell activities within specialized organs of secretion such as a mantle or a perithecal membrane. Thus, one could believe that the membrane model offers a more adequate explanation of the morphogenesis of the graptolite skeleton than the pterobranch one (see considerations of phase control of secretion in the cells of the hypothetical perithecal membrane, pp. 609). In other words, the membrane model presumes a more realistic mechanism of skeleton formation in graptolites, with a morphogenetic control at the cellular level than at the organismal one (activity of individuals, p. 604). This problem has been recognized also by Crowther and Rickards (1977) when discussing the "enigma of rigid morphogenetic control in graptoloids".

The pterobranch model meets considerable difficulties in explanation of such skeletal structures as the basal disc and nema. The utrastructure and microstructure of the basal disc in *Mastigograptus* (Urbanek and Towe 1975) are indicative of holoperipheral growth lines and give no proof of bandages. Particular growth lines pass gradually into the cortical covering of the stem of the colony (comp. pl. 28 and pl. 29: 3). Formation of the basal disc starts when there is only a single zooid with limited secretionary capacity in its hypothetical cephalic disc, and involves an extensive cortical deposition at a considerable distance from the growing edge.

In nemata investigated so far some layers taper, but the majority is holoperipherical. The growth of nema considerably precedes that of thecae, the contact of its growing tip with underlying zooids being highly improbable. The formation of nema could be hardly ascribed to collective secretionary activity of a number of zooids (comp. also Crowther and Rickards 1977: 18).

Rickards (1975) suggested a hypothesis that the nema and its derivative structures were formed by tissues exuded from the tip of prosicula after its resorption. Certain data published by Urbanek and Towe (1975) and new unpublished observations by the present author on dendroid sicula, make such a resorption hardly probable as a morphogenetic norm. This problem has been discussed earlier (Urbanek and Towe 1975: 7, 12). Moreover if we accept the presence of some sort of extrathecal tissue over the tip of sicula (as suggested by Crowther and Rickards 1977), this introduces an element completely alien to pterobranchs, and we cannot accept the pterobranch model as adequate for explanation of skeletal morphogenesis in graptolites.

EVALUATION OF THE MEMBRANE MODEL OF SECRETION OF THE GRAPTOLITE PERIDERM

When suggesting the membrane model of secretion of the graptolite periderm, Urbanek (1976a) was also the first to emphasize its difficulties. First of all the strong bilateral symmetry and alternate arrangement of fuselli are difficult to explain with the membrane model of secretion. It is obvious that some assumption of an upward growth of the perithecal evagination followed by secretion of fuselli occuring in an alternate way, first on one side of the thecal wall and then on the other (compare suggestion of Kirk 1972), is required. This implies that operation of the perithecal membrane needs a precise physiological control. Any examples of such biletaral control of growth among living organisms are unknown to the present writer.

Another limitation of the model suggested is the difficulty in deriving a clear relationship between the stolonal and perithecal fractions of the tissues in the graptolites, and in reconstructing the growth of the soft parts and the skeleton in the process of budding. Certain suggestions elaborated by Kirk (1972) are very speculative and cannot be verified by the existing data. The fact that due to an abrupt widening, the sheath of stolon in Dendroidea produces membranous internal parts of the thecae, is indicative of an intimate relation between the peridermal sheath of stolon in a mother stolotheca and the thecal walls in a daughter triade. This internal membranous part of the thecae can hardly be explained within the framework of the pterobranch model, as in the last named group the sheath of stolon and zooidal tubes are morphologically quite independent fractions of the periderm. On the other hand, the formation of internal membranous parts of the thecae may be ascribed to the glandular cells of the incipient perithecal membrane of the budding zooids.

The other point raised by Crowther (1977, pers. information) refers to the regular size of secretionary infoldings or wrinckles of the presumed perithecal membrane, responsible for secretion of "bandages" as suggested by the auxilliary hypothesis advanced recently by Urbanek. In Crowther's opinion, there is very little reason for the wrinckles, which are temporary and random structures, to be so much differentiated in size and shape. As already emphasized, however, a "wrinkle" is a descriptive term to denote an elementary secretionary unit, being an infolding of the periderm equivalent to the main infolding at the growing edge of the theca. An idea that such infoldings may have rather stable size at the given spot of the surface of the rhabdosome does not seem so improbable when we take into account the previously mentioned difficulties of the alternative explanation, namely the difficulties to correlate the size of "bandages" with the size of the cephalic disc. They could be formed along the lines of some stress in the periderm as a result of rather a uniform response of the perithecal membrane.

In spite of Crowther's and Rickads' belief (1977: 13) that "the normal method for secreting cortex is independent of fuselli", there is an increasing number of data for a dependent mode of cortex formation (e.g. Urbanek: 1976b, in microfusellar additions). As suggested earlier, this method of secretion is indicative of a membrane model.

Crowther (1977, pers. information) questioned, however, the validity of the dependent mode of the cortex formation as an evidence of the membrane model of secretion of graptolite periderm. He has pointed out that in certain instances cephalodiscid zooids were capable of secretion of fusellar structures with a considerable overlap (comp. e.g. processes of coenecium in *Cephalodiscus (Demiothecia) inaequatus* as figured by Andersson (1907: pl. 3: 14). According to Crowther, the dependent mode of cortex formation may also be explained applying the pterobranch model unless the overlap is very considerable and spreads over large areas.

This problem cannot be solved satisfactorily on the basis of the existing data. In the dependent cortex of *Didymograptus* sp. the overlap which may be traced on longitudinal sections examined with TEM is up to 5—6 fuselli. This does not exceed the range of bandages observed, while the data about the lateral extent of this overlap are lacking. There is a technical difficulty in obtaining ultramicrotome sections good enough over larger areas. An independent cortex in *Acanthograptus* sp. shows layers continuous over 3—5 fuselli, with numerous gradual taperings very much like those in *Dictyonema* sp. Although the decisive evidence is lacking owing to the small size of sections observed I would agree with Andres (1977, pers. information) that the available TEM data are not particularly indicative of the presence of "bandages" in such forms as *Dictyonema, Acanthograptus* and *Mastigograptus* (compare pls 28 and 29).

EXAMINATION OF PHYLOGENETIC THESES

Both the membrane and pterobranch models imply certain phylogenetic solutions. Urbanek (1976a) has chosen the membrane model as appearing to be more readily compatible with the ultrastructural studies. He believes that substantial differences in fabric, pattern and presumed mode of secretion of skeletal tissues in pterobranchs and graptolites present serious obstacles for homology between them. Accordingly, there is little reason to suggest an immediate phylogenetic relationship between the groups in question. In his deliberately agnostic paper, Urbanek (*op. cit.*: 30) expressed a view that the systematic position of graptolites remains an unresolved problem and their close affinity to Pterobranchia seems doubtful.

Recent adherents of the pterobranch model of secretion (Dilly 1976; Andres 1976, 1977; Crowther and Rickards 1977; Crowther 1978, in this

volume) suggest a close affinity between the pterobranchs and grapto-
lites (Andres 1977) and support the classification of graptolites within
the subphylum or phylum Hemichordata (Crowther 1978, in this volume).
The substantial difference in the fabric of fusellar tissue recognized wit-
hin the pterobranchs (loose, straight fibres) and graptolites (mesh or
spongy system of fibres) is explained as being of a secondary, adaptive
nature. The interconnected mesh pattern of fusellar fibres in graptolites
is considered to be an adaptive strengthening of the periderm because of
the erect and more robust habitus of their colonies (Andres 1977: 85).

The latter explanation seems to be inadequate in the light of recent
observations which indicate that *Dendrotubus erraticus*, a sessile encru-
sting tuboid graptolite with some portions of thecae erect but by no
means more than that in *Rhabdopleura*, has a normal spongy fabric in
its fusellar tissue (Urbanek, unpublished). The same is true for the enti-
rely encrusting colonies of crustoids (Urbanek and Rickards 1974). On
the other hand, the erect colonies of Ordovician *Rhabdopleurites* reveal
a typical pterobranch ultrastructure of the tube (loose straight fibrils)
as shown by Urbanek (1976a). Thus the distinct gap at the level of ultra-
structure of the periderm separating the pterobranchs and graptolites is
old and persistent (since Ordovician, Urbanek 1976a). This gap could be
hardly explained as a purely adaptive response to the mode of growth
of the colony.

Phylogenetic inferences should be based on determining homologies
without going into precise definition of homology and its criteria at mi-
croscopic and submicroscopic level (this question was discussed in some
details by Urbanek 1976a). It is enough to state that even in a somewhat
simplicistic approach to this problem suggested by numerical phenetic
taxonomists, "operational homology" still means a great similarity in
g e n e r a l and in p a r t i c u l a r (Sneath and Sokal 1973: 79). Homo-
logy "may be loosely described as compositional and structural corres-
pondence" (*op. cit.*: 77), and the former includes a qualitative resemblance
in terms of chemical constituents. A similar point of view has been pre-
sented by Urbanek (1976a) in respect of the problem of the pterobranch/
/graptolite affinities. Approaching many characters as equal *a priori*, the
chemical constituents or characters should be considered as valid as any
others. This is even more true after weighting the characters and taking
into account that in our case resemblances or dissimilarities reffer to
"informational molecules" (proteins). Their great changes are unlike to
affect exclusively only one class of characters (ultrastructure of skeleton)
without affecting a number of others (e.g. organization of soft parts).
The differences recognized in both groups considered seem rather mean-
ingful as the characters involved are very constant and persistent. One
could not expect here taxonomic incongruencies observed among seden-
tary polychaetes with different composition of the tube almost in each fa-

mily. In my opinion the *extent of observed differences in composition and structure of peridermal derivatives in graptolites and pterobranchs may well indicate that this is a primary not a derived dissimilarity*. In consequence both groups might be considered unrelated or only very distantly related. In any case the differences observed cannot be undervalued or entirely neglected in character weighting when discussing the phyletic aspect of the problem.

As mentioned before (see p. 619), even if the pterobranch model of skeleton secretion will be confirmed as generally true, the thesis on close affinity between the last named group and graptolites would need more substantiation. The secondary thickening of graptolite periderm may occur in a way similar to that recognized in pterobranchs but still remain essentially unhomologous. Nothing is known about nature of the secondary deposits in Cephalodiscoidea — they well may resemble fusellar tissue in pterobranchs, or be produced by accumulation of sheet fabric, while graptolite bandages are essentially cortical. The problem of the validity of this resemblance remains therefore open. The significance of bandages as a criterion of pterobranch ancestry of graptolites is doubtfull to me which, however, does not exclude a possibility of a "pterobranch-like" mode of their formation. One should distinguish, however, a general morphogenetic explanation from establishing the concrete phylogenies. Pterobranchs may be a suitable model for the first purpose and inadequate as an ancestral group in the second case. In opinion of the present writer, a series of transient structures between the genuine cortex and incipient secondary deposits recognized in rhabdopleurids should be established to substantiate safely the pterobranch ancestry of graptolite.

At the present moment a sceptical approach to the problem of graptolite/pterobranch affinity seems heuristically more profitable than the alternative viewpoint as it leads to a careful examination of data and in this way suggests a valuable research programme. This was also an intention of Urbanek (1976a) when he has published his critical paper on the problem of graptolite affinity in the light of the ultrastructural studies, after being for years convinced of a close relation between last named group and pterobranchs.

SOME REMARKS ON THEORY CHANGE AND THEORY REPLACEMENT

There is a widely accepted belief that a properly formulated theory should define conditions of its refutation or falsification. In this way, tentative theories may be criticized and replaced with new and better theories. The other possible outcome may be a less drastic process — the

theory being criticized may be changed (or improved) by introduction
of *ad hoc* auxilliary hypotheses which permits to escape the falsification.

Introduction of an auxilliary hypotheses which ensures the "immu-
nization" of a theory against criticism, may be considered rather a dan-
gerous procedure, except for these cases where the introduction of tes-
table auxilliary hypotheses leads to an increase of informative content
of the emended theory (Popper 1974).

Introduction of an *ad hoc* auxilliary hypothesis of secretionary infol-
dings as structures responsible for the secretion of "bandages", allows to
preserve the body of the membrane model (theory) and at the same time
to explain the shape of these secretionary units, unpredicted by the
unimproved (classical) membrane theory. The problem arose whether it
is a purely evasive move or a fertile manoevre which increases the ex-
planatory content of the theory?

The membrane theory as formulated by Urbanek (1976a) contains no
statements about the shape of cortical deposits. But it is fair to say that
the secretion under the perithecal membrane is most likely to imply a
deposition over larger areas, particular layers being more or less irre-
gular in outline. Therefore regular, narrow belts of secretion ("bandages")
may be considered as falsifying this prediction.

On the other hand, the unimproved (classical) membrane theory logi-
cally implies that any deposition of cortical layers should occur under
slightly swollen portions of the extrathecal tissues, producing in this way
some space for the secrets exuded by the cells. So, the concept of secre-
tionary infoldings although never formulated *expressis verbis* is an inte-
gral part of this working hypothesis. A further suggestion that in some
cases the evolution passed from larger and irregularly shaped units of
secretion (larger areas) into regular and narrow belts ("bandages") seems
to be legitimate. Speculative as it is, these auxilliary hypothesis might be
falsified by the advance of our knowledge on ultrastructure of periderm
especially in sessile graptolites and in pterobranchs.

This latter hypothesis requires that 1) secretion of bandages may be
preceded by deposition of more extensive layers of cortex (formed accor-
ding to the independent or dependent mode), producing in this way an
underlying component, 2) bandages are absent from cortex of sessile
graptolites or at least in some of the sessile orders. These requirements
may be taken as predictions which are provable.

The competing pterobranch hypothesis should be further developed
to span the morphogenesis of entire graptolite skeleton and explain the
formation of specific features of graptolite colonies (as the basal disc,
nema and virgula). In the form suggested by Crowther and Rickards
(1977), this hypothesis is at least inconsistent. *Denying the presence of
any external soft tissue* over the thecae they still find the presence of
some external tissue *necessary* to explain the growth of virgula. In doing

so they refute and take advantage of the membrane hypothesis at one and the same time. Their hypothesis does not explain why this extrathecal tissue, once present, should be restricted to such structures only which, otherwise, are difficult to explain using the pterobranch model. The dualistic model of graptolite periderm secretion in the version suggested by Crowther and Rickards (1977) is perhaps possible, but unlikely, and certainly incompatible with recent knowledge of hemichordate biology.

Recent controversy about the mode of secretion of graptolite periderm resulted in a very interesting situation. There are two opposite theories which most probably cannot be combined or reconciled — one of them should collapse as less adequate in respect to the entirety of the data.

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DISCUSSION

P. R. Crowther:

I wish to comment on several points relating to the applicability of Professor Urbanek's perithecal membrane hypothesis for graptolite periderm secretion.

(i) There is no doubt that TEM evidence taken alone appears to substantiate the idea of secretion within a covering mantle of soft tissue. The arch-shaped fuselli and apparently simply layered nature of the cortex can be adequately explained by growth within an epithelial evagination (Kirk 1972) or perithecal membrane (Urbanek 1976). However, both hypotheses predate the discovery of the bandaged nature of the cortex from many species spanning much of graptolite evolution (Crowther and Rickards 1977; Andres 1977). Cortex appears to be simply layered on TEM micrographs only because their limited field of view makes it unlikely that many, if any, bandage margins would occur in a single micrograph e.g. distal bandages on *Climacograptus typicalis* Hall are 300—400 μm long, 80 μm wide but only 1 μ thick. Having recognised bandages on SEM micrographs, it is possible to identify rare bandage margins on ultramicrotome sections of similar material.

The arch-shaped distal termination of each fusellus is highly suggestive of secretion within a fold of soft tissue but thin sections of pterobranch tubes show a similar pattern (e.g. Harmer 1905). The suggested 'skin" of secretory tissue suggested by Kirk and Urbanek is unnecessary since zooids of the pterobranch *Cephalodiscus* secrete fuselli with equally long, overlapping inner and outer limbs using mainly their cephalic shield, perhaps with the aid of tentacles. The arch-shape of successive fuselli is presumably a reflection of secretion within a cephalic shield, folded over the aperture of the tube.

(ii) Of all the species examined so far and particularly in the diplograptids where the structure is most striking, the entire cortex is bandaged. There is no question of it being merely a superficial layer with a specialised origin and function. Furthermore, bandages are found at all stages of growth, from single siculae up to the mature colony.

(iii) I find Professor Urbanek's attempts to explain secretion of cortical bandages by "wrinkles" in the perithecal membrane unconvincing, partly because it invokes the modification of a hypothesis for periderm secretion that was formulated before the existence of bandaged cortex was suspected, but mainly because it does not adequately explain their form and arrangement. Their strictly constant width at any level along a rhabdosome and the gradual distal increase in size, paralleling the increase in thecal volume (a result of the graptoloid thecal size gradient), could not reasonably be expected to occur if they were the product of secretion beneath

wrinkles in a uniform covering of soft tissue. Why should there be such a rigid control of the size of each wrinkle? Why should wrinkles gradually and uniformly increase in size distally? Why should their sides remain strictly parallel? The arrangement of bandages, sub-parallel on siculae, ventral thecal walls and lateral metathecal walls, more haphazardly criss-crossing at high angles on the lateral walls of diplograptid rhabdosomes and the dorsal wall of *Pristiograptus*, often radiating out from thecal apertures, all point to direct control by the zooid. It seems very doubtful if these patterns could occur, or how they might be maintained, beneath a perithecal membrane.

(iv) One of the major objections to any close affinity between graptolites and the pterobranch *Rhabdopleura* has been the supposed lack of any secondary tissue on the latter. The problem was recognised by Kozłowski (1949) and this, plus his assumption that graptolite cortex was simply layered, forced him to suggest a rather nebulous extrathecal tissue for its secretion extending distally along the rhabdosome some distance behind the growing end. However, Dilly (1976) has recently briefly described a rudimentary deposit of fibrous secondary tissue of *Rhabdopleura compacta* Hincks. More importantly, the secondary tissue that has long been known to exist on several species of *Cephalodiscus* was described by Harmer (1905) as formed from longitudinal strips of periderm. Therefore it appears that the simple pterobranch mode of secretion can produce not only arch-shaped fuselli with overlapping inner and outer limbs but also a cortex in the form of 'strips', both features equally characteristic of graptolite periderm.

(v) Finally, I must emphasize again that cortical bandaging has been found in more than 15 genera of graptolites. It is certainly not of isolated occurrence or some peculiarly specialised development of a restricted group. On the contrary, the only limitation yet to appear is the lack of suitably well preserved material for many species.

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EXPLANATION OF THE PLATES 27—30

Plate 27

Didymograptus sp.

Fine structure of thecal wall as examined with light microscope (1), approx. ×300, and transient electron microscope (2—4). Compare increasing range of details seen in cortical component (1—3, c, connected by lines) under different magnifications. 4 shows a medial part of a fusellus with a distinct outer lamella (o).

Plate 28

Mastigograptus sp.

Fine structure of basal disc as observed with light microscope.
1. Longitudinal section through basal disc and stem of a colony (approx. ×85).
2. Details of basal disc (approx. ×260).
3. Central portion of the basal disc at its passage into the stem of the colony (approx. ×520).

Plate 29

Mastigograptus sp.

1, 2. Fine structure of thecal walls at branching portion of the rhabdosome as examined with light microscope (1) and TEM (2). b branching theca, s stipe proper.
3. Cortical deposits in the transient zone between basal disc and the stem of the colony.

Plate 30

1—2. Fine structure of the thecal walls within the stipe of Mastigograptus sp. as examined with light microscope (1) and TEM (2); c cortex.
3. Transients between fibrils of fusellar-like (spongy) and cortical material within the nema of Didymograptus sp. (arrows indicate places of transition).