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THE PROBLEM OF GRAPTOLITE AFFINITIES IN THE LIGHT OF ULTRASTRUCTURAL STUDIES ON PERIDERMAL DERIVATIVES IN PTEROBRANCHS

Abstract. — The ultrastructure of the organic coenecium in living *Cephalodiscus* (*Cephalodiscus*) *inaequatus* (Andersson) studied with the transmission electron microscope reveals a fabric and pattern very similar to that recognized in living *Rhabdopleura compacta* (Hincks) by Dilly (1971). The same techniques used to study the ultrastructure of Jurassic *Rhabdopleura kozlowskii* Kulicki and Ordovician *Rhabdopleurites primaevus* Kozlowski indicate that the nature of the fibrous unit elements of the periderm and their characteristic pattern remain unchanged within the Pterobranchia, at least since the Ordovician.

The results combined with those of previous studies on the ultrastructure of peridermal derivatives in graptolites (Towe & Urbanek, 1972; Urbanek & Towe, 1974, 1975), reveal a substantial difference at the submicroscopic level between the fusellar component of the periderm in the Pterobranchia and that of the Graptolithina. The presumed homology between fusellar tissues of both groups constitutes the main argument in Kozłowski's suggestion (1938, 1949, 1966a) of a close affinity between pterobranchs and graptolites. A reevaluation of his line of reasoning enables us to conclude that Kozłowski's main criterion of homology was the specificity of the structures involved. This requirement is not fulfilled at the ultrastructural level because of substantial differences in the nature of the unit elements and their pattern. Moreover, other data on the ultrastructural anatomy of graptolites (very early deposition of cortical tissue over juvenile thecae; presence of cortical deposits over the inner surface of thecae; simultaneous secretion of successive fuselli and corresponding layers of cortical tissue) contradict the mode of secretion of the graptolite skeleton as suggested in the classical Kozłowski hypothesis.

In contrast to the independent origin of fusellar and cortical tissue suggested by Kozłowski, each being secreted by a different part of the body, the ultrastructural data are indicative of a uniform mode of secretion. A secretion of the entire periderm within an epithelial evagination — the perithecal membrane — appears to be more readily compatible with the ultrastructural studies.

Substantial differences in fabric, pattern, and mode of secretion of fusellar extracellular tissues in pterobranchs and graptolites produce serious obstacles for homology between them. Accordingly, there is little reason to suggest an immediate phylogenetic relationship between Pterobranchia and Graptolithina. The systematic position of the latter group within the Bilateria remains an unresolved problem.

INTRODUCTION

The aim of the present paper is to study the ultrastructure of the periderm in the Pterobranchia (phylum Hemichordata) as an extension of earlier studies on the graptolites (Towe & Urbanek, 1972, 1974; Urbanek & Towe, 1974, 1975). Interpretation of the ultrastructural investigations on graptolites in comparison with data obtained for Recent and fossil pterobranchs is important since both groups have been considered closely related.

In a representative attempt to study the ultrastructure of the periderm in the Pterobranchia a graded series of forms of different age has been investigated. This includes a Recent representative of the Cephalodiscoidea — *Cephalodiscus (Cephalodiscus) inaequatus* and two fossil representatives of the Rhabdopleuroidea, a Jurassic *Rhabdopleura kozlowskii* and an Ordovician *Rhabdopleurites primaevus*. Combined with data published by Dilly (1971) on the ultrastructure of the periderm in Recent *Rhabdopleura compacta*, this has provided a reasonably complete picture of exoskeletal fabrics and patterns in the pterobranchs. The material selected also provides some estimate on the effect of fossilization on the preservation of ultrastructural features.

The data obtained for pterobranchs and graptolites are compared in order to attempt to solve the problem of homology of their fusellar tissues. The problem of the mode of secretion of peridermal derivatives is considered and conclusions are used in both cases to evaluate the classical Kozłowski hypothesis (Kozłowski, 1938, 1949, 1966a) regarding the close affinity of Graptolithina and Pterobranchia. This problem commands the attention of both paleontologists and biologists and may be considered one of the more interesting problems of contemporary phylogenetics.

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MATERIAL AND METHODS

The Recent pterobranch examined is *Cephalodiscus* (*Cephalodiscus*) *inaequatus* Andersson from material collected by the Swedish Antarctic Expedition 1901—1903, in Graham's Region of Antarctica, north from Joinville Island (locality 94 of Andersson, 1908, p. 1). Specimens were obtained through the courtesy of Professor E. Stensiö of the Swedish Museum of Natural History of Stockholm, who presented them to Professor R. Kozłowski and who, in turn, made them available for the present study. The material represents coenecia fixed in alcohol and stored in glycerine.

The fossil pterobranchs include two species. The first is a Jurassic *Rhabdopleura kozlowskii* Kulicki, etched from calcareous concretions occurring in Callovian clays near Łuków, Poland (Kulicki, 1969) and from calcareous-marly concretions in the Bathonian clays of Zawiercie, Poland (Kulicki, 1971). The stratigraphic position, lithology, associated fossil remains and origin of the material are discussed by Kulicki (1969, 1971). The specimens were etched from the matrix with hydrochloric acid, washed and stored in glycerine.

The second fossil pterobranch is an Ordovician *Rhabdopleurites primaevus* Kozlowski etched from erratic boulders numbered 0.400 and 0.533 in the collection of the Institute of Palaeontology, Warsaw University. Both were found at the Mochty locality (approximately 60 km north of Warsaw, central Poland) in the moraine deposits of the high bank of the Vistula River. The age of the material is Middle Ordovician (Viruan) as indicated by the associated graptolite fauna. They are probably the equivalents of the Uhaku and Kukruse Stage in the Estonian sequence (see Kozłowski, 1966b, 1967, 1970). The basic structure of this species was described by Kozłowski (1967, pp. 127—129, fig. 13A, D; 1970, pp. 6—8, pl. 2, figs 1-5). These specimens were etched with acetic acid rinsed and stored in glycerine. In both the Jurassic *Rhabdopleura* and the Ordovician *Rhabdopleurites* small fragments of the erect portion of the tubarium (the zooidal tubes proper) were used for ultrastructural studies.

The principal methods used in the study of the present material with the transmission electron microscope have been described earlier (Urbanek & Towe, 1974). They included embedding in Durcupan AMC (Fluka)

and ultramicrotomy with the use of a diamond knife. The living material was stained with either phosphotungstic acid (PTA) or uranyl acetate (UAC), or double stained with both. The fossil pterobranchs were studied without bleaching or staining. All material was examined with a Philips EM 200 operated at either 60 or 80 kV. Staining procedures were ineffective with the fossil material as a result of diagenetic changes in the chemical nature of the organic material during fossilization.

ULTRASTRUCTURE OF THE COENECIUM IN
CEPHALODISCUS (CEPHALODISCUS) INAEQUATUS

The coenecium in Cephalodiscoidea is an exoskeletal structure secreted by members of a pseudocolony — a swarm-like assemblage of zooids. This is a structure composed of a basal mat and a number of separated erect tubes cemented to the mat, each housing a zooid (*Cephalodiscus (Orthoecus)*). In other instances it is a much more integrated structure with the individual zooidal tubes of the coenecium either embedded in the common peridermal substance (as in *Cephalodiscus (Idiothecia)*), or communicating with one another to produce a common cavity occupied by all the zooids of a given colony. Such coenecia are frequently dendroid in form with a characteristic spinose appearance. Spines surround the superficial openings (ostia) and lead through passages into the common cavity (*Cephalodiscus (Cephalodiscus)*). The coenecium of our species·belongs to this last type and its morphological details have been described by Andersson (1908, pp. 17—19; Pl. 2, figs 1-2; Pl. 3, figs 12-14).

The structural elements of coenecia, both in the walls of the zooidal tubes proper and in the common peridermal substance filling the spaces between them, are growth bands laid down irregularly and deposited in multiple layers. They are usually considered homological with the regularly arranged fusellar bands of *Rhabdopleura* (Andersson, 1908; Kozłowski, 1949, 1966a). The opinion of Hyman (1959) that fusellar structure occurs only in *Rhabdopleura* and is not recorded in *Cephalodiscus* seems erroneous in the light of our investigations which have revealed an essential similarity in the components of the peridermal derivatives in both genera.

Transverse ultrathin sections taken through the wall of the coenecium and examined with the electron microscope of low magnification reveal this structural principle showing particular growth bands as extremely variable in size and form. The delicate matrix of the body of each fusellus is covered by thin, electron-dense outer membranes (pl. I, fig. *A*). Higher magnification micrographs show details of both the matrix (pl. I, fig. *B*) and the membranes (pl. II). The body of each growth band contains deli-

cate fibrils loosely and irregularly dispersed. They vary in length and are embedded in an abundant electron-lucent ground substance (pl. I, fig. *B*). The longest fibril observed is about 1 μm long. Ultrastructural details of these fibrils are poorly resolved, which may be ascribed to alcohol fixation and long storage before embedding (some 70 years!). Nevertheless, the majority of fibrils when examined at higher magnification show traces of substructure (pl. I, fig. *B*). There are outlines of loop-like or beaded structures which, liberally interpreted, may be considered as remnants of intrafibrillar helices made of a more electron-dense substance. In this respect they resemble some of the fibrils recognized in the periderm of *Rhabdopleura compacta* by Dilly (1971). The state of preservation of the material precludes closer identification of the observed fibrils with one of the three fibril types recognized by Dilly (1971, p. 503) on his well-preserved material of *Rhabdopleura*. The ground substance itself appears amorphous, except for numerous irregular and randomly dispersed areas of somewhat greater density (pl. I, fig. *B*). Frequent inclusions have been encountered within the wall of the coenecium (pl. I—II). Some contain bacteria and other foreign particles and cilia-like structures (pl. II, fig. *A*, i). Similar inclusions have been found within the wall of zooidal tubes in *Rhabdopleura* (Dilly, 1971).

Each growth band is covered by a thin, electron-dense outer membrane. On suitably oriented sections examined at higher magnification some of these membranes consist of an inner and outer electron-dense layer, separated by a more lucent middle region (pl. II). In this respect they are similar to the well-known trilaminar unit or plasma membrane. Adjacent fuselli are separated by multiple depositions composed of several membranes packed together (pl. II, fig. A). The membranes themselves are complex structures which when sectioned obliquely are shown to consist of densely matted fibrillar material (pl. II, figs B—C). This fibrillar material originated in the electron-dense layers of the membrane as indicated by its own electron density and gradual transition.

The trilaminar membranes are similar to structures recognized on the outer and inner edges of the fuselli in *Rhabdopleura compacta* (Dilly, 1971, figs 1, 13, 14, p. 512). The inner edge in particular shows a double layer — two dense lines separated by a lucent space. This is very similar to our membrane, although Dilly does not refer to it as a membrane. At places the trilaminar nature of this structure is less distinct and on the outer surface it is completely obscured, which according to Dilly, may be secondary and due to environmental influences. Strikingly similar membranes, called triple-unit membranes, were described in the periostracum (external cuticle) of some Recent bryozoans (Tavener-Smith & Williams, 1972). A difference between these and that of pterobranchs is the presence of a filamentous brush on the external surface of their triple-unit membrane — not unlike a glycocalyx on the plasma membrane of some cells.

An accessory laminated deposit covering the outer surface of the coene-
cium as described in some Cephalodiscoidae by Ridewood (1907), has not
been found in the material examined.

In summary, the coenecium in *Cephalodiscus (Cephalodiscus) inaequa-
tus* shows a similarity in the matrix, in the nature of its fibrous consti-
tuents, and in the structure of its membranes, to *Rhabdopleura compacta*
as described by Dilly (1971). In spite of the considerable differences in the
arrangement of growth bands in the genera in question they both display
an essential similarity at the ultrastructural level.

ULTRASTRUCTURE OF THE TUBARIUM IN *RHABDOPLEURA KOZLOWSKII*

The tubarium in Rhabdopleuroidea is an exoskeletal structure com-
posed of a number of interconnected tubes separated into individual com-
partments housing the zooids. Each compartment consists of a stolonal
portion, usually creeping over and cemented to the substratum, and a
distal, erect portion, occupied by the zooid itself. Longitudinal and trans-
verse ultrathin sections of fragments of these erect zooidal tubes were
studied. The erect portions of the zooidal tube are composed of a number
of superimposed growth bands, the fuselli. Each fusellus is a fusiform
belt, an annular segment of the tube which overlaps the underlying fu-
sellus on the inner surface and protrudes on the outer side below the over-
lying fusellus in the form of a collar. Details of the fusellar structure of
Rhabdopleura kozlowskii are described by Kulicki (1969, 1971).

Longitudinal sections through the wall of the zooidal tube, examined
at low magnification, reveal the principles of fusellar structure showing
the particular fuselli and their superposition (text-fig. 1 *A*). Schematic-
ally, each fusellus may be subdivided into a base (b) (which overlaps con-
siderably the underlying growth band from its inner surface and rests
over its head), a narrow trunk (t) and again a wider head (h), producing
a protruding edge (collar of Kulicki, 1969). The fuselli overlap unilaterally
on the inner surface only. Each fusellus is composed of a matrix and is
coated by an electron-dense outer membrane (pl. III). The matrix is dis-
continuously distributed within the body of the fusellus, certain places
with disrupted membranes being filled only be the embedding medium
(pl. IV, fig. *A*). This is most probably the result of fossilization or sample
preparation procedures used prior to embedding. The matrix consists of
numerous filamentous materials. At some places this filamentous material
has a reticulated or foamy aspect (pl. IV, fig. *B*).

Transverse sections proved to be difficult to obtain and the quality of
the majority of such sections was poor. Nevertheless, some of them reveal
the filamentous pattern of organization of the matrix, and the presence of
electron-dense membranes on their inner and outer surfaces (pl. IV, fig. *C*).

There are considerable differences in the ultrastructure of the Jurassic *Rhabdopleura kozlowskii*, and the living *Rhabdopleura compacta* (Dilly, 1971) or *Rhabdopleura normani* (Wetzel, 1958). These differences could be the result of secondary changes in the primary constituents of the periderm as a result of fossilization and diagenesis. Medium-dense material within the fuselli of the Jurassic material may be identified as probable
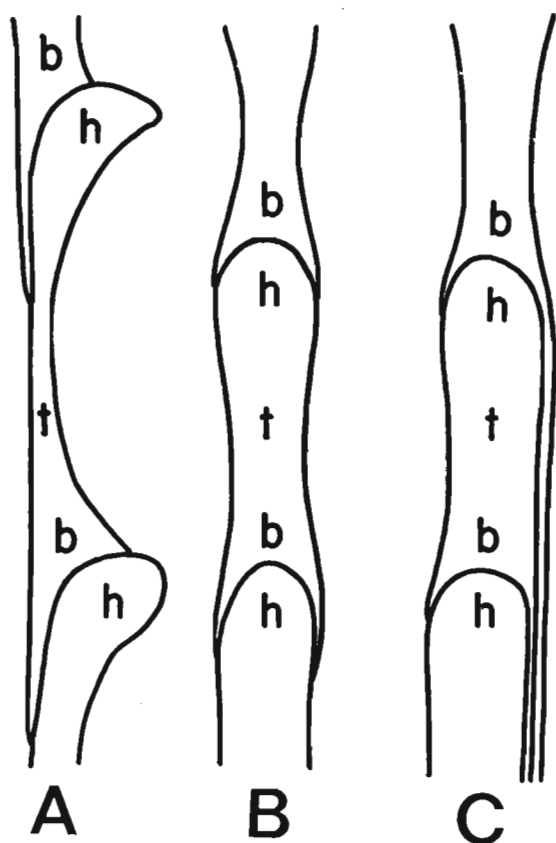

Fig. 1. Unilateral overlap of fusellar bands as recognized on longitudinal section of an erect portion of a zooidal tube in *Rhabdopleura* (A). Bilateral overlap on longitudinal sections of thecal walls in graptolites, *Acanthograptus* (B) and *Didymograptus* (C), b, h, t = base, head, trunk of the fuselli.

remnants of the ground substance, while the electron-dense granular filaments are remnants of a fibrous component of the fusellar matrix. As stated above, the discontinuous distribution of this material is probably the result of chemical and physical changes caused by fossilization and/or the techniques used. The specimens examined show no traces of a secondary laminated layer producing an inner lining in the zooidal tubes of *Rhabdopleura kozlowskii*, as recognized by Kulicki (1971).

ULTRASTRUCTURE OF THE TUBARIUM IN
RHABDOPLEURITES PRIMAEVUS

In general appearance the tubarium of *Rhabdopleurites* resembles that in *Rhabdopleura* (Kozłowski, 1967). Both the stolonal and zooidal tubes were probably erect, stretching above the surface of the substratum (Kozłowski, 1970). The delicate remains of such zooidal tubes were used in the present study.

In spite of the considerable age of these fossils, the main structural elements are exceptionally well preserved (pl. V). The fuselli are coated with an electron-dense membrane, while the body of the fusellus is filled with a loose fibrous material. The electron micrographs reveal that the fibrous elements are primarily linear, some being rod-like or even granular. In a few cases medium-dense linear trails have granular, headed densities. It is possible that these elements correspond to primary fibrils at different stages of degradation. There are no traces of preserved ground substance, the background having the density of the embedding medium. Any ground substance originally present appears to have been leached out leaving only the fibrous components preserved. This may indicate a greater degree of degradation of the primary constituents of the periderm as compared with the Jurassic *Rhabdopleura*, where remnants of the ground substance were preserved.

Pl. V, fig. *B* shows the junctional region of two overlapping fuselli as seen in transverse section. There is a close resemblance to structures described from living *Rhabdopleura* (Dilly, 1971, fig. 13 and pl. VI in this paper based on a micrograph made available to the present author by courtesy of Dr. P. N. Dilly). The general pattern of ultrastructure in the Ordovician *Rhabdopleurites* is reasonably similar to that in the living *Rhabdopleura* (compare pl. V and pl. VI).

ANALYSIS OF THE KOZŁOWSKI CRITERIA FOR HOMOLOGY
BETWEEN FUSELLAR TISSUES OF GRAPTOLITES AND PTEROBRANCHS

According to Kozłowski (1938, 1949, 1966a), the most characteristic feature of graptolites is the very specific microstructure of the periderm. The walls of thecae are made of an organic substance composed of a successive superposition of growth bands referred to by Kozłowski as the fuselli. This characteristic structure of graptolites is therefore commonly called "fusellar" structure and it is recorded in all graptolites as well as in Recent and fossil representatives of the Pterobranchia. It was this similarity that Kozłowski considered as essential and indicative of a close phylogenetic relationship between both groups. There is no doubt regarding the homological significance of this structure in the thinking of Kozłowski.

According to Kozłowski (1949, 1966a), the homology of peridermal derivatives showing fusellar structure is based on the following criteria: (1) both skeletal formations are made of the same elementary components, namely spindle-shaped growth bands (swollen in the middle and pointed at both ends); (2) these elementary components are disposed transversely to the longitudinal axis of the thecae or zooidal tubes; and (3) they show an irregular (Cephalodiscoidea among the pterobranchs), partly ordered (Rhabdopleuroidea among the pterobranchs, some graptolites) or highly ordered arrangement, so as to produce a perfect bilateral disposition with wedge-shaped terminations indenting each other to form two zigzag sutures (vast majority of graptolites).

In addition to these main criteria, another less emphasized and somewhat confusing argument was offered by Kozłowski based on the presumed chemical nature of the organic skeleton in graptolites and pterobranchs. First, the graptolites were considered as "chitinous" on the basis of certain physical properties of their skeleton. The term "chitin" was used commonly at that time as a general term to describe any organic, flexible skeletal structures without reference to their chemical composition (see Kozłowski, 1949, pp. 47—68, 68). Later, when the first biochemical data that accumulated on the chemical composition of the Pterobranchia and Graptolithina indicated its non-chitinous and probably proteinaceous nature, Kozłowski (1966, p. 498) included biochemical data into his criteria of homology.

Kozłowski's view of the essential similarities in microstructure of the fusellar organic skeleton in graptolites and pterobranchs as evidence of their close affinity can be evaluated from Remane's (1956) views on the criteria for homology. In this important work the circular reasoning inherent in many approaches to homology is avoided. Remane distinguished three major criteria for evaluating homologies:
   (1) The positional relationship of a structure to other anatomical parts.
   (2) The specificity or uniqueness of a given structure (composition, fabric, function).
   (3) The presence of transitional structures involving gradations between extremes considered.

The first criterion has a limited value with respect to the relationships between fusellar structures because of the basic simplicity of the geometric relations between the particular parts of the skeleton in both of the groups in question. Such features as the transverse disposition of the fuselli with respect to the thecal axis and their junction with oblique sutures (a result of their spindle-like shape) have little value as criteria of homology.

The third criterion is also of minor significance, since the structural transitions represent only a very general change from an irregular to an ordered arrangement of fusellar bands. The presence of the structural transitions is may be one of the strongest criteria of homology, under the

condition, however, that it involves a number of structural characters. In our case the transition from irregular to an ordered arrangement of fusellar bands is a simple geometric change. In all other respects the fuselli of pterobranchs and graptolites are different and separated by the same gap since Ordovician (compare pls I—VII). This is why a gradual increase in the ordering of the fuselli has per se only a limited significance as a proof of homology.

A reevaluation of Kozłowski's arguments leads one to the conclusion that he used the second criterion — that of the specific compositional quality of the structure — as the main criterion of homology between fusellar derivatives in the Pterobranchia and Graptolithina. The specificity of the fusellar structure according to Kozłowski (1949, 1966a) lies in the form of the elementary units (the fuselli) and in their arrangement which produce examples of extreme similarity (Kozłowski, 1949, fig. 13; Kozłowski, 1966a, text-figs 8, 9). The restricted distribution of such structures in the animal kingdom was also noted. According to Kozłowski (1966a, pp. 496—497), "such a structure is recorded in all graptolites, as well as in Recent and fossil representatives of the Pterobranchia... in both the Graptolithina and Pterobranchia, the walls of theca have an identical and very specific structure." Fusellar structure was thus considered by Kozłowski as characteristic and indicative for systematic position among the invertebrates, much as the presence of feathers is used among the vertebrates. The extreme similarity and uniqueness of the structures involved constituted the basis of Kozłowski's views on the close affinities between graptolites and pterobranchs.

Combining Kozłowski's arguments with the Remane (1956) views on the criteria of homology, it is reasonable to consider as additions to the structural specificity of fusellar derivatives not only the characteristic shape of the unit elements, but also their mode of secretion, and the chemical composition and nature of their ultrastructural fabric.

As regards the added criteria of chemical composition and nature of the submicroscopic components, one might expect an essential similarity in these aspects for closely related homologous structures. But the significance of ultrastructural features for establishing homology is limited by observations which indicate considerable variation at the ultrastructural level in structures whose homology has been safely established by the use of other criteria. For example, the cuticle of some polychaetes is composed of regularly ordered layers of extracellular collagen fibrils while in others these fibrils are lacking (Storch & Welsch, 1970). The cuticles of annelids and arthropods are considered homologous but a different ultrastructure and chemical composition exists in both groups. The annelids share collagen-like fibrous materials embedded in carbohydrate matrices, while in the arthropods chitin is the predominant material. Homology between the cartilaginous precursors of replacement bones and their ossified counter-

parts in vertebrates is another example of substantial submicroscopic and microscopic differences in homologous structures.

The addition of further criterion of the specificity of structure not only makes any homology more difficult to demonstrate but also avoids the criticism (i.e., Bohlin, 1950) that even a striking similarity in shape and arrangement of growth bands may be superficial and does not necessarily express a fundamental structural interconnection.

It is convenient to examine the homology of the anatomical features involved from the following points of view:

(1) structural specificity of the fusellar derivatives at the microscopic level,

(2) nature of their ultrastructural fabric,

(3) chemical composition,

(4) mode of their secretion.

STRUCTURAL SPECIFICITY OF THE FUSELLAR DERIVATIVES AT THE MICROSCOPIC LEVEL

Although there are striking similarities between the creeping stolonal tubes of the Rhabdopleuroidea and the stolothecae of some crustoids or the autothecae of tuboid graptolities, the fusellar structure of free zooidal tubes and thecae differs in several ways. In the rhabdopleuroids with erect zooidal tubes (*Rhabdopleura, Eorhabdopleura, Rhabdopleurites*) each tube is made of a superposition of annular fusiform growth bands, while in graptolites the thecae are composed of semiannular fuselli arranged bilaterally producing two regular zigzag sutures (compare diagram, text-fig. 2, A—B).

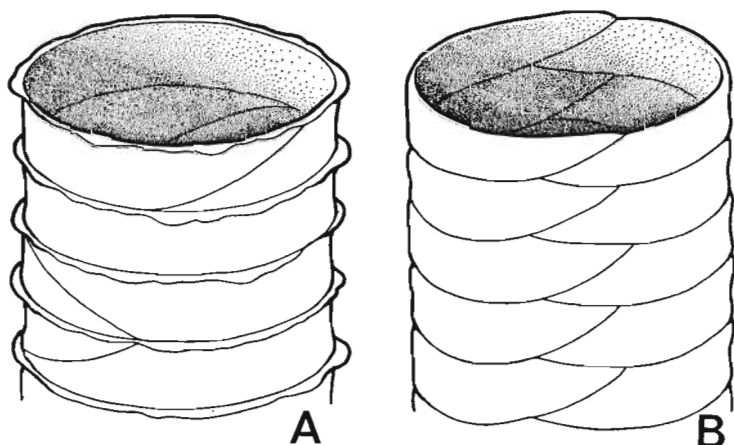More important are the differences in the superposition and mode of

Fig. 2. Diagram comparing the arrangement of fuselli as seen in the erect zooidal tube of *Rhabdopleura* (A) and in a graptolite theca (B).

overlap between adjacent fuselli in rhabdopleuroid pterobranchs and in
graptolites that are revealed by my microtome sections (text-fig. 1, *A—C*).
In pterobranchs the fuselli show only unilateral overlap, the adjacent fu-
selli being fused at some distance on the inner side of the zooidal tube. In
the graptolites the degree of overlap is somewhat smaller and is bilateral,
although not always symmetrical. As a result, each fusellus of a zooidal
tube in the rhabdopleuroids forms a distinctly protruding outer edge or
collar (text-figs 1, *A*). In graptolites, as a result of the bilateral overlap the
outer surface, like the inner one, is rather smooth (text-figs 1, *B—C*; text-
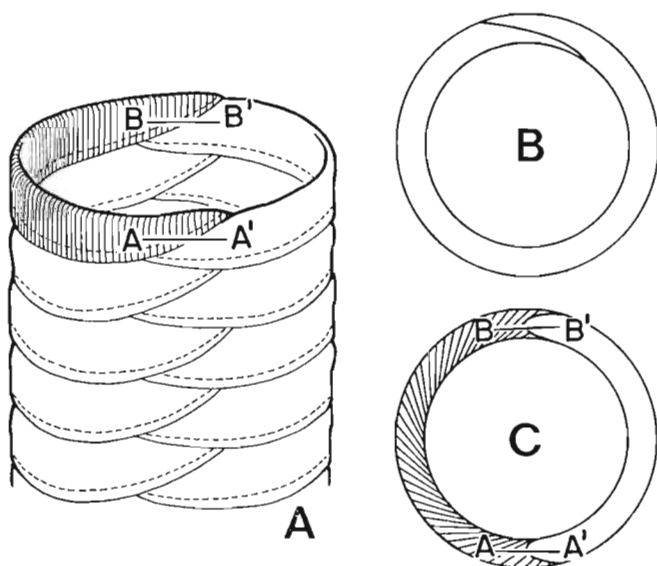fig. 3, *A*).

Fig. 3. *A* — Principle of superposition of fuselli in graptolites as seen on transparent
thecal walls. Stippled area = overlying fusellus. *A—A'* and *B—B'* indicate the plane
of section through an oblique suture of two adjacent fuselli. Compare a transverse
section in *Rhabdopleura B* with that of a graptolite in *C*.

A different mode of deposition of fusellar growth bands in rhabdopleu-
roid pterobranchs and in graptolites produces a different picture on trans-
verse sections across the boundary of two overlapping fuselli. In the former
group, this intersection appears as a more-or-less straight line (text-fig. 3,
B), while in the latter it always appears as a concave-convex line (text-
fig. 3, *A, C*). A concave-convex line is a direct result of a section through
the bilateral overlap of the two adjacent fuselli, the underlying fusellus
being overlapped on both sides by the overlapping one, not only along the
lower fusellar suture but also along its oblique suture (text-fig. 3, *A*).

Thus the classical Kozłowski view of the microstructure of thecal walls
in graptolites (Kozłowski, 1949, text-fig. 5) correctly shows the *longitudinal*
interrelations of superimposed fuselli, but the *transverse* image is errone-
ous and contradicts both the data obtained by Urbanek & Towe (1974,

pl. 1 and fig. 1) and the sections figured by Kozłowski himself (1949, pl. 3, fig. 21; Pl. 21, figs 11—27). These small but distinct differences in the superposition of the fuselli between pterobranchs and graptolites lead to the conclusion that the mode of formation of the fusellar tissue was not identical.

The mode of secretion of fusellar growth bands in living *Rhabdopleura* has not been investigated in any detail. Preliminary results agree with the early speculations of Dawydoff (1948) and show that it is likely that certain glands present on the preoral disc (cephalic shield) are involved in their formation (Stebbing, 1970; Dilly, 1971, pp. 512, 514). The secretory part of the cephalic disc is in some way "painted" over the edge of the zooidal tube and onto the inner surface of the last formed fusellus which is later subject to sclerotization. The bilateral overlap of superimposed fuselli in graptolites indicates a different method of formation, namely by secretion of a continuous soft tissue membrane producing an infolding over the growing margin of the thecae.

DIFFERENCES BETWEEN FUSELLAR TISSUES OF GRAPTOLITES AND PTEROBRANCHS AT THE SUBMICROSCOPIC LEVEL

Early light microscopic studies of the fabric within the fuselli of graptolites based on microtome sections (Kozłowski, 1949, p. 40) revealed only that they are composed of delicate, brownish, semi-transparent and apparently structureless matter. More advanced techniques involving ultramicrotomy and higher resolution with the electron microscope proved that the fusellar fabric is a monotypic system composed solely of a meshwork of wavy and anastomosing fibrils with little or no preserved ground substance (Towe & Urbanek, 1972; Urbanek &Towe, 1974, 1975).

Because of probable preservational difficulties involving the ground substance, comparison of the ultrastructure of fusellar tissue in pterobranchs with that in graptolites must be reduced to an evaluation of their fibrous components. Here there are differences in a number of features concerning both the nature of the unit elements and their pattern (pls VI—VII). The fibrils of the fusellar tissue in dendroid and graptoloid graptolites are coarse (diameter ~ 600 Å), loosely packed and interconnected, and either branched or irregularly anastomosing. This produces a very characteristic mesh or spongy pattern (pl. VII). By comparison, the fibrils of the fusellar tissue in pterobranchs, as revealed by Wetzel (1958), Dilly (1971) and the present study (pl. VI), are narrow, straight, and loosely dispersed, never producing an interconnected meshwork. The diameter of the fibrils in *Rhabdopleura* varies according to Dilly (1971) in the range of 250—300 Å. The fusellar tissue in graptolites and pterobranchs is thus composed of a different fibrous fabric — a fact which provides little support for this aspect of homology between the two groups.

As regards the biochemical nature of the fibrous components of pterobranch periderm, early qualitative data obtained by Andersson (1908, pp. 19—20) for *Cephalodiscus* indicated that it is proteinaceous. Later, Rudall (1955) excluded the presence of chitin from the periderm of *Rhabdopleura*, and Foucart *et al.* (1965) reported a number of amino acids in the periderm of *Cephalodiscus* and also proved its proteinaceous nature in *Rhabdopleura*. In an electron microscope study Dilly (1971) distinguished three types of fibrils embedded in an electron-lucent matrix for *Rhabdopleura compacta*. Two of them, which have internal helical electron-dense lines surrounded by a sheath of less electron-dense material, were tentatively described by Dilly (1971, pp. 513—514) as keratin-like. This interpretation was based on histochemical investigations using the Alcian Blue technique where the intensive black staining of the helices was ascribed to the presence of sulphur, especially disulphide bonds, and thus would be consistent with keratin. The nature of the third type of fibrils, which are rather long, thick and without any substructure, remains obscure. On the other hand, amino acid analysis of the periderm in *Rhabdopleura normani* made by Dr. P. E. Hare (Geophysical Laboratory of the Carnegie Institution, Washington), failed to detect any substantial amounts of the sulphur containing amino acids (cysteine and methionine) whose presence would be indicative of the keratin-group of fibrous proteins in this species. Dilly's conclusion was also criticized by Bairati (1972) who felt that too many diagnostic keratin characteristics were lacking — an X-ray diffraction pattern, high sulphur content and microfilament organization. Bairati also felt that the extracellular position of the material was evidence against its being true keratin. To add further to the confusion, Dr. Dilly (personal communication) has recently obtained from fibrils in *Rhabdopleura compacta* X-ray diffraction patterns which he judges as characteristic of keratin.

Thus at the present moment evidence about the chemical nature of the fibrous components in *Rhabdopleura* is confusing and further work needs to be done. It seems safe, however, to conclude that none of the fibrils recognized in the periderm of *Rhabdopleura* is in the least suggestive of collagen or collagen-like material, nor do the amino acid analyses indicate the presence of hydroxyproline or hydroxylysine as would be characteristic of collagens. This is of primary significance because in the graptolites the collagen-like fibrils are a principal skeletal-building material (Towe & Urbanek, 1972, 1974; Urbanek & Towe, 1974, 1975).

The data obtained from paleobiochemical analysis of graptolite periderm are also confusing. Early opinions based on the physical properties of graptolite periderm and its elementary composition are summarized by Kozłowski (1949) but are of very limited significance for the solution of the problem. More recent attempts are contradictory. Manskaya and Drozdova (1962) detected the presence of the amino-sugar glucosamine which would

be indicative of a chitinous nature for the graptolite periderm. However, Foucart *et al.* (1965*a*, *b*, 1966) found no traces of glucosamine, but recognized in three graptoloid species a number of amino acids, among them high amounts of glycine, serine and alanine. These amino acids observed in their hydrolysates were considered as evidence for the scleroproteic nature of the graptolite periderm.

Amino acid analyses of periderm hydrolysates from our *Dictyonema* sp. made independently by D. von Endt and P. E. Hare (see Towe & Urbanek, 1972) point up the major biochemical degradation of graptolite periderm due to diagenetic fossilization. The periderm is very resistant to acid hydrolysis (boiling 6 *N* HCl, 36 hours) and such hydrolysates analyzed by column chromatography show only traces of amino acids and no glucosamine at a sensivity of 10^{-9} moles. These amino acids are more likely due to contamination rather than to residues of primary paleoproteins. The results obtained by Foucart *et al.* need further control work in view of Hare's (1965) observation on possible sources of contamination, especially by HCl. In any case the absence of glucosamine in analyses of fossil organic material of such age means only that the graptolite periderm is not now chitinous in the same way that the almost total lack of amino acids in our hydrolysates means only that the carbonized periderm is not now proteinaceous. These negative data, therefore, provide no reliable information regarding the original composition of the periderm.

It seems clear that for the present, ultrastructural studies remain the only reliable source of information on the original chemical nature of the fibrous components of graptolite periderm. These studies point to the collagen-like nature of this material in the cortical fabric (Towe & Urbanek, 1972) as shown by the appearance of the unit elements and their characteristic pattern. Fusellar fibrils also may be considered collagenous because of the gradual transition of a single fusellar fibril into a cortical fibril in the outer lamella within a single fusellus and because of their general resemblance to organization of extant collagen materials as for example within the Bowman membrane of ocular tissue. These conclusions suggesting the collagen class of fibrous proteins as the main structural component of graptolite periderm were reinforced by a more recent discovery of a new kind of fibrous fabric within the rods of the clathrium of certain retiolitids (Towe & Urbanek, 1974; Urbanek & Towe, 1975). These fibrils, which differ in some respects from the previously recognized fibrous materials in graptolite periderm (presence of oblique striations along the fibril and internal septations visible on transverse sections), show, nevertheless, an important resemblance to collagen since the vertical d-repeat is near 700 Å and obliquely banded collagens have been reported (Kühn, Kühn & Schuppler, 1964; Bruns, Trelstand & Gross, 1973; Doyle *et al.*, 1974; Rayns, 1974). It seems therefore that collagen-like material was the main structu-

ral component of the graptolite skeleton and it was physically organized in a number of different patterns.

A substantial gap in the nature of unit elements and patterns recognized within pterobranch and graptolite periderm seems, at least in certain aspects, to be filled by most recent observations by Dilly (1975). He has found a reticulum of coarse silver staining fibres in the repent part of the tubarium in *Rhabdopleura*. This tissue surrounds the dormant buds and forms a matrix in close proximity of the black stolon. According to Dilly this reticulum is very similar to the fusellar fabric of graptolites and "may perhaps suggest an affinity between the graptolites and the pterobranchs (Dilly, 1975, p. 397).

The biochemical nature of thick fibres recognized by Dilly is obscure but they clearly differ from anything seen in erect tubes of *Rhabdopleura* and in coenecium of *Cephalodiscus*. The reticulated tissue produced by these fibres really show a certain resemblance to the fusellar fabric of graptolites. Examination of thin sections of the repent part of tubarium of *Rhabdopleura compacta* (kindly made available by Dr P. N. Dilly) shows that fibers in question are distinctly coarser than fusellar fibrils recognized in graptolites so far studied, and are rather ribbon shaped. The similarity produced by a reticulated arrangement of these fibers to the fusellar tissue may be therefore superficial. Conclusion of Dilly that these coarse fibers become incorporated to form the sclerotized thick wall of the stolon "in a manner similar to that which made the fusellar fabric of the periderm of fossil graptolites" (Dilly, 1975, p. 387) is confusing. The thecal walls of graptolites made of fusellar fabric never condense into electron opaque layers. On the other hand stolons in *Acanthograptus* are made mainly of an electron dense, homogenous material defined as crassal fabric. Stolons are joined with the wall of the stolotheca by some spongy material of fusellar aspect (Urbanek & Towe, 1974, pls 27—28), but there is no indication of any morphogenetic relation of both fabrics.

Phylogenetic significance of resemblance between reticulum of coarse fibers found in repent tubes of *Rhabdopleura* to the fusellar fabric of graptolites remains doubtful to the present author. Its intimate relation to the sheath of black stolons is *ex situ* and can not be considered as a proof of affinity. In order to be considered as an indication of kinship of both groups in question, this material should occur *in situ*, being related to the formation of erect portion of zooidal tubes (= autothecae). Nevertheless this finding by Dilly is of a great interest for our phylogenetic speculations.

The assumption that pterobranchs and graptolites are closely related would imply a profound transformation at the molecular level in order to bridge the gap in the nature and pattern of the fabrics recognized in their fusellar tissues. Such a transformation could be achieved by a shift in the secretionary activity of the cells responsible for the formation of the skeleton. Although this assumption does not exclude affinities between pterobranchs and graptolites, it does imply a more distant relationship between these groups than is currently believed by the majority of zoologists and paleontologists.

THE MODE OF SECRETION OF THE PERIDERM IN GRAPTOLITHINA

In view of Kozłowski's (1949, 1966a) ideas on the mode of secretion of the periderm in graptolites there is 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 fusellar 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, 1966a) 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, 1966a) as a character newly acquired by the graptolites and which found no counterpart 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's 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 (text-fig. 4, *A*). As an alternative a membrane could be imagined gradually spreading distalwards from the preceding thecae (text-fig. 4, *B*).

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 mesogloea of hydroids to support his thesis on the coelenterate affinities of the graptolites (compare also Kozłowski, 1966a). 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 was formed, in his opinion, between two epithelial layers — the outer epithelial layer being res-

ponsible for secretion of the cortical component; and the inner epithelial layer for the fusellar component (Bohlin, 1950, p. 112 and figs 4, 6). This would also explain, according to Bohlin, the substantial difference which exists between fusellar and cortical tissue. Evidence for such a mode of formation was based not so much on reconsideration of graptolite micro-
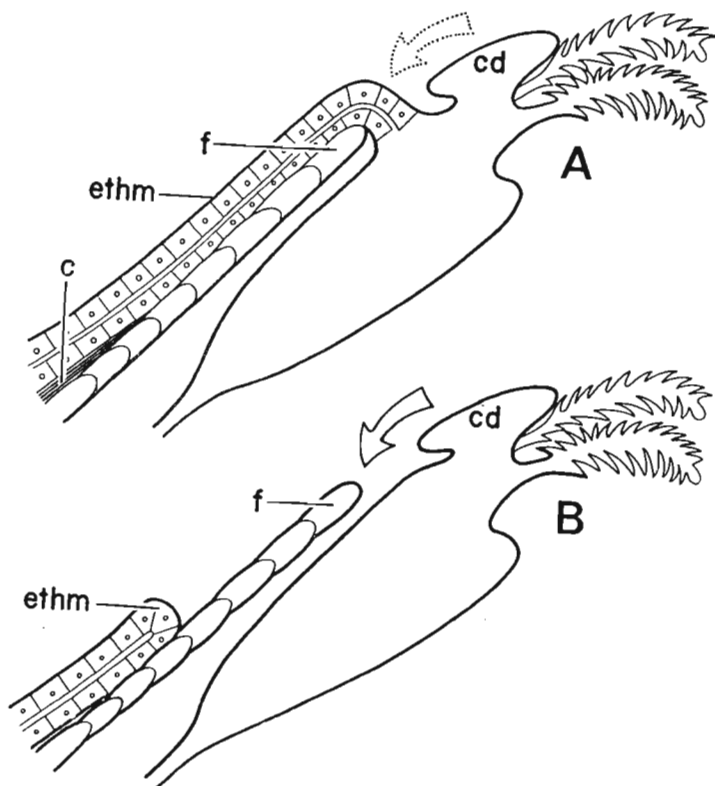

Fig. 4. Diagrammatic representation of inferred relationships of soft parts to the thecal wall in graptolites following the Kozłowski concept. *A* — assumes an early formation of an extrathecal membrane as the result of an extension of the lateral walls of the zooid body. *B* — assumes a delayed overgrowth 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) indicate a point of acces; *c* = cortical component; *f* = fusellar component; ethm = extrathecal membrane.

structure as on the fact that graptolite rhabdosomes show a very regular succession of thecae — a regular morphological gradient with gradual changes or transitions between the extreme types of thecae within a single rhabdosome. This regularity of structure, according to Bohlin, cannot be explained by any secretionary behaviour of the zooids, which could not be controlled with precision, and thus indicates secretion within a specialized organ on the surface or at the base of the epithelium.

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).

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, p. 21). Furthermore, 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, p. 25).

Recently Kirk (1972) has considered the problem of the extrathecal tissue. Her conclusions are essentially similar, although not exactly identical, with those of Bohlin (1953). 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, p. 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*).

THE MODE OF SECRETION OF GRAPHOLITE SKELETON IN THE LIGHT OF ULTRASTRUCTURAL DATA

Ultrastructural studies on the graptolite periderm and its derivatives made by Towe and Urbanek (Towe & Urbanek 1972, 1974; Urbanek & Towe, 1974, 1975) shed new light on the mode of formation of the skeleton in graptolites and provides a basis for establishing a relation between the soft parts and the skeleton. The electron microscopy provides the possibility to identify the structural nature of the minute strips of the peridermal material and to produce in this way a reasonably complete picture of their secretion.

The classical scheme of Kozłowski (1949), postulates that the cortical covering is formed secondarily, having 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 indicate that the presence of a cortical coating (so-called autocortex, Urbanek & Towe, 1974) on young autothecae, its appearance preceding the overgrowth by lateral thecae within a given triad (text-fig. 5, *A*, *B*). This early formation of an autocortex in some dendroids is indicative of the
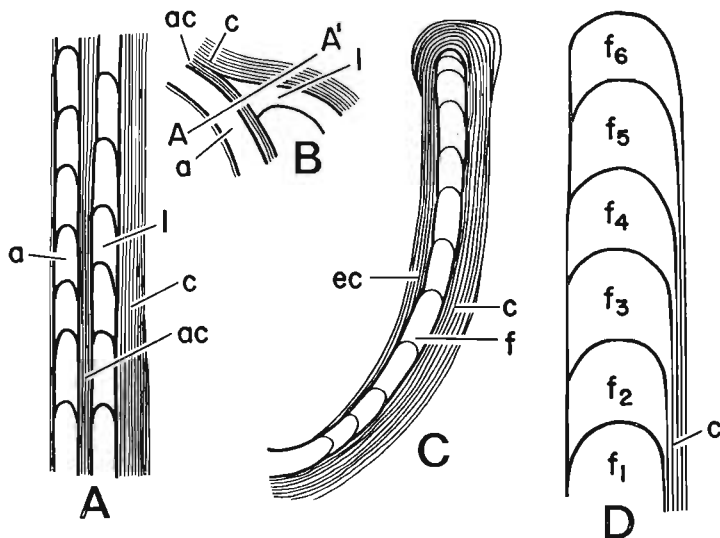

Fig. 5. Anatomical features bearing on the mode of secretion of the skeleton in graptolites. An early formation of cortical coating (*ac* = autocortex) over the outer surface of a juvenile autotheca (*a*) preceding the growth of a lateral theca (*l*) and formation of a common cortical envelope (*c* = cortex) shown in longitudinal 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* = = endocortex) 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.

continuous presence of a secretionary extrathecal membrane during the growth of thecae. 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 text-fig. 4, *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 Kozłowski (1949, 1966a), the cortical tissue would have to be produced only extrathecally and would be found only on the outer surface and around the aperture of thecae. Our observations indicate the presence of a fairly thick layer of cortical tissue on the inner surface of the thecae, spreading deep into the thecal cavity of autothecae ("twigs") in *Acanthograptus* sp. (Urbanek & Towe, 1974, pl. 18, figs 1—2), in thecae of *Pristiograptus dubius* (Urbanek & Towe, 1975, pl. 19, figs 1-2) and in 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 and penetrating deeply into the thecal cavity (text-fig. 5, *C*). In *Climacograptus angulatus* the inner cortical deposit is particularly heavy and differs little from the outer one. In *Acanthograptus* sp. the inner cortical deposit can show some differences from the outer one, principally due to greater amounts of sheet fabric. Such an accumulation of sheet fabric is observed, however, also in the peripheral zone of the outer cortical deposit. The important and decisive point which makes it necessary to consider secretion of both the outer and inner cortical coatings by the same part of the zooidal body rather than as similar secretions produced by different parts of the body, is the distinct continuity of the cortical layers over the aperture.

Inasmuch as the outer member of the entire cortical coating has been termed *cortex* (Urbanek & Towe, 1974), it seems desirable to introduce the term *endocortex* at this time for its inner member. The continuity between the cortex and the endocortex indicates 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. A 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 & Towe, 1974, pl. 13, fig. 1). Further substantiation is provided by the presence of both fusellar and cortical fabric within a single secretionary unit, indeed a single fusellus. This has been recognized in *Acanthograptus* sp.

(Urbanek & Towe, 1974, pl. 6, figs 1—2), in *Didymograptus* sp. (Urbanek & Towe, 1975, pl. 18, figs 1—2), and in *Pristiograptus dubius* (Urbanek & Towe, 1975, pl. 14, figs 1—3). At some places a transition could be traced from a typical fusellar fibril of the body of the fusellus into a cortical-like fibril of the outer lamella. This not only indicates the essential chemical similarity of both fusellar and cortical fibrils, but also demonstrates an easy and smooth change in the secretion of both fusellar and cortical fabric within a single phase of secretion. It is this which provides evidence for the secretion of the graptolite skeleton by the same tissue or portion of the body (text-fig. 6, *B*).

Such observations on the mode of formation of the cortex in *Didymograptus* sp. have an important significance for understanding the mode of secretion of thecal walls in general. As established by Urbanek & Towe (1975, pl. 18, figs 1—2), the formation of the cortex is the result of a large amount of overlap from 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 (text-fig. 5, *D*).

On the basis of these and other observations, a hierarchy in the events of secretion of the components of the graptolite periderm may be established (text-figs 5, 7): 1. The secretion is separated into two phases with a distinct interval between the secretion of the fusellum and the formation of the cortical coating (this is probable for the majority of graptolites, text-fig. 7); 2. The secretion takes place with a very short time interval between the formation of both components of the periderm (our *Dictyonema* sp., see above, text-fig. 5, *A*, *B*); 3. A simultaneous secretion of subsequent fuselli and corresponding layers of the cortex takes place (our *Didymograptus* sp., see above, text-fig. 5, *D*).

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

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 ana-

tomical 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.

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 the body wall of the zooid), or "bryozoan-like" (both components produced by a membrane enveloping the thecal walls). A bryozoan-like model is far more probable. The data obtained from ultrastructural studies are more easily understandable if one assumes that the formation of the entire graptolite periderm takes place inside an epithelial evagination (text-fig. 6, A). Here the cells would be capable of secretion in either separate phases or in gradation from one type of secretion to the other of both fusellar and cortical fabric (text-fig. 6, B). Numerous previous reports of regeneration or repair of the damaged thecal walls also strongly suggest the presence of such a perithecal membrane (summarized by Bul-
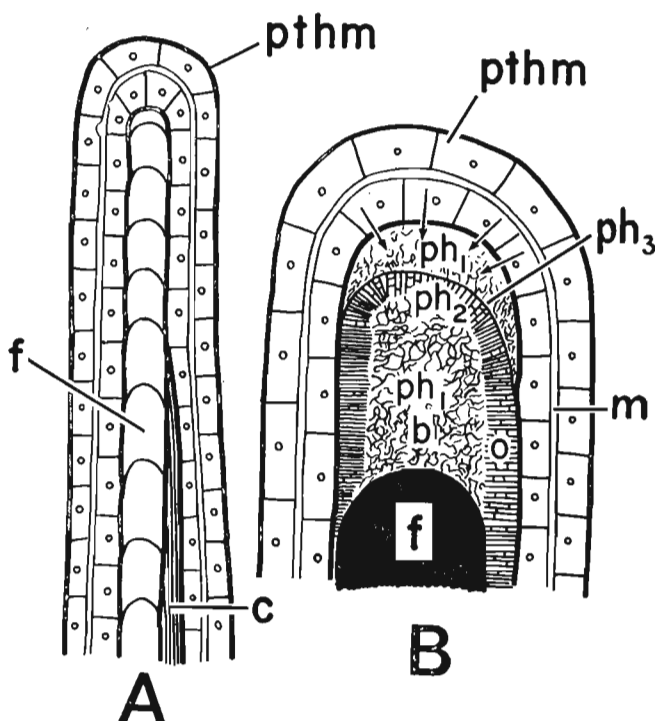

Fig. 6. A — Presumed relationship of soft-parts and thecal wall in graptolites as inferred from the present study suggests the formation of both a fusellar (f) and cortical (c) component of the thecal wall within an epithelial evagination (pthm = perithecal membrane). In B the cells of the epithelial membrane were capable of secreting both fusellar fabric (arrows) in the body of the fusellus (b) and cortical fabric in the outer lamella of the fusellus (c) in successive phases of secretion (ph₁, ph₂, ph₃ ...). Overlap and extension of outer lamellae may contribute to outer layers of the cortex (compare text-fig. 5. D) Preceding fusellus (f) shown in solid black, presumable mesodermal component of the perithecal membrane (m).

man, 1970, pp. 70—71). Furthermore, secretion of collagen in the layered structures, like basal membranes composed of orderly arranged fibrils and similar in many respects to the cortical tissue, are 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 (text-fig. 6, pthm). The presence of a mesodermal component (m) within the perithecal membrane is doubtless but it is not discussed in detail as inessential for our reasoning.

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 epithetium. 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). In certain cases these cells were capable of producing both fusellar and cortical fabric. Secretion of a greater amount of the cortical fabric (cortex and endocortex) was due to a later polarization of the secretionary activity of the cells which were displaced from the proliferating margin onto the surface of the perithecal membrane proper (text-fig. 6, A; 7, A—B).
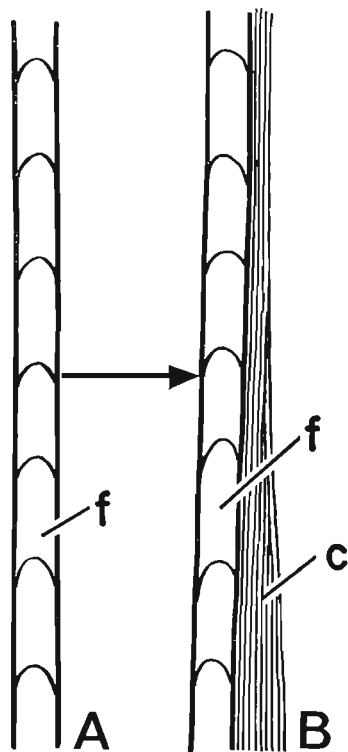

Fig. 7. Primary (A) and secondary (B) structure of thecal walls and delayed formation of outer cortical deposit (c) over the fusellar component (f). Probably characteristic for the majority of graptolites.

Kirk (1974b) has recently suggested a generalized model of cortex formation in dendroid graptolites based on observations by Urbanek and Towe (1974). This model implies that in *Dictyonema* sp. and probably in all dendroids, the entire cortex was formed due to lateral transition from fusellar into cortical fabric in outer limbs of mutually overlapping fuselli ("corticization of the outer limb" in Kirk's terminology). Just the contrary our studies indicate that in *Dictyonema* sp. the fuselli were closed systems and cortex was laid down quite independently (see above). The model suggested by Kirk (1974b, Diagram 2) is wrong in the case of our *Dictyonema* sp., being inadequate as well for the rest of the graptolites studies so far. Our *Didymograptus* sp. (see text-fig. 5, D) in this paper demonstrates a formation of cortex due to a mutual overlap of the outer limbs of fuselli, without any gradual lateral corticization, however. Each layer of the cortex corresponds to an extension of an outer lamella, the latter being present already within the fusellus proper.

A number of questions concerning the mode of secretion of the graptolite skeleton, however remain unresolved. The strong bilateral symmetry and alternate arrangement of fuselli are difficult to explain with the suggested "bryozoan-like" model of secretion. It is obvious that some supposition of upward growth of the perithecal evagination followed by secretion of fuselli occurring 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 requires a precise physiological control. Any examples of such bilateral control of growth among living organisms are unknown to the present writer.

A more serious limitation to the value 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 to reconstruct the growth of the soft parts and the skeleton in the process of budding. The explanation elaborated by Kirk (1972) assumes a number of purely hypothetical processes (investment of the bud by a parental "mantle"; the later breaking through of mouth, anus, and lophophore of the young zooid proper; the withdrawal of the mantle, etc.), without providing analogies to living models. These speculations cannot be verified at the moment.

RELATIONSHIP BETWEEN PTEROBRANCHIA AND GRAPTOLITHINA IN THE
LIGHT OF THE ULTRASTRUCTURAL DATA

The hypothesis elaborated by Kozłowski (1949, 1966) on the close phylogenetic relationship between pterobranchs and graptolites, was based on three main morphological criteria: (1) the presence of fusellar tissue in the periderm of both groups which was considered to be a unique feature in the animal kingdom; (2) the presence of internal stolons (a stolon within

its own thecal tube — stolotheca) recognized only in some pterobranchs and in the graptolites; (3) a particular form of budding of the zooids through perforation of the thecal walls (all zooids in *Rhabdopleura*; the first blastozooid in the majority of graptolites). Of crucial significance in Kozłowski's concept of graptolite affinities is the similarity of the fusellar tissue. Kozłowski's concept had great heuristic value providing a basis for further studies on the biological interpretation of graptolite remains and the arguments presented by Kozłowski have been accepted during the last three decades by the vast majority of paleontologists, the present author included.

Following Kozłowski's reasoning, Kirk (1974a) has recently concluded that the common ancestry of Pterobranchia and Graptolithina is "not too remote". This was unexpected because she had earlier argued the fundamental differences in the mode of secretion of the skeleton in both groups (Kirk, 1972). Kirk (1974a) solved the problem of pterobranch-graptolite affinities by assuming a hypothetical common ancestor provided with a pair of lateral secretory organs situated beneath the lophophore. The unilateral, uneven growth of the zooidal stalk is considered responsible for the semiannular deposition of fuselli, first on one side and then on the other (Kirk, 1974a, pl. 2, J). In the evolutionary line toward pterobranchs these paired secretory organs were fused to produce a median secretory cephalic disc, which secretes fusellar rings and half rings in *Rhabdopleura* (Kirk, 1974a, pl. 2, J, K). In the other evolutionary line leading to the dendroid and graptoloid graptolites (Kirk, 1974, pl. 2, L—O), a hypothetical extension of primarily paired secretory organs resulted first in the formation of a secretory band folded over the margin of the theca and later in the formation of a "mantle" covering the outer surface of the thecae. The unilateral left and right growth of this mantle at the proliferation zone, below the lophophore resulted in the secretion of the semiannular fuselli.

A difficulty in her reasoning, however, is that the factors responsible for the arrangement of fusellar increments in the periderm are in one case delegated to paired lateral secretory organs (in the common ancestor), in a second case to an unpaired cephalic disc (in rhabdopleuroids), and in a third case to the unilateral growth of the mantle margin alone (in graptolites). It is unclear why such different secretory organs should operate by different mechanisms to maintain "the intermitted left and right advance of the ancestral zooid" so as to produce a striking similarity of the fusellar pattern. If one were to assume a similar number of steps and similar hypothetical, but radical transformations of the soft body and skeleton, one could derive the graptolites as easily from the Coelenterata or the Bryozoa. In addition, Kirk neglects the important differences which occur in the fusellar microstructure of rhabdopleuroid pterobranchs and graptolites and pays little attention to the ultrastructural fabric of the fusellar tissue because of an erroneous feeling that within closely related taxa

"striking differences of skeletal composition can also occur" (Kirk, 1974a, p. 4), and pays no attention to the fact that in the case of graptolites and pterobranchs this would imply a real revolution in secretion!

The mode of secretion of the periderm in the graptolites suggested here, combined with the differences recognized at the ultrastructural level provide no basis for homology between the fusellar tissues in Pterobranchia and Graptolithina. Because of the differences in the ultrastructure and formation of the fusellar tissue which we consider fundamental, any other similarities are difficult to evaluate. This is especially true with respect to the stolons although their internal position is clearly unique. The peridermal sheath of stolons in *Rhabdopleura* (Dr. P. N. Dilly, personal communication) is also strikingly similar to that in *Acanthograptus* (Urbanek & Towe, 1974, pl. 28). Both are, however, made of homogeneous, featureless crassal fabric which prevents biochemical comparison on morphological grounds.

Far more important for the problem of homology is the fact that both morphogenetic role and relation of peridermal sheath of stolon to the thecal walls, are quite different in dendroid graptolites and in pterobranchs. In the former, as recognized by Kozłowski (1949), the sheath of stolon produces, just above the node, due to an abrupt widening a membranous internal part of a given theca. Further up it passes into the fusellar wall of theca proper. This is indicative of an intimate relation between the peridermal sheath of stolon in a mother stolotheca and the thecal walls in a daughter triade, which is a derivative of the stolonal sheath. In pterobranchs, however, the sheath of stolon and zooidal tubes are morphologically quite independent fractions of the periderm. These fundamental differences diminish considerably the morphological significance of the resemblance between internally placed "black stolons" of Pterobranchia and Graptolithina. In spite of the above similarities they could be hardly considered homologous.

Other striking resemblances in the early stages of colony development in *Rhabdopleura* (embryonic vesicle) and in the prosicula of sessile graptolites (Kozłowski, 1971) may be coincidental features or may indicate only a distant phylogenetic relationship. There is no safe reason, however, on the basis of these data, to suggest any close phylogenetic connection between the pterobranchs and the graptolites. The wall of the prosicula in the dendroid and graptoloid graptolites is always composed of a spirally coiled band (helical band, see also Urbanek & Towe, 1975, figs 3 A-D), and the helical line is usually distinct. Traces of the helical line are discernible even in some of the bottle-shaped discophorous prosiculae of sessile graptolites, which otherwise resemble the embryonic vesicle of *Rhabdopleura* (Kozłowski, 1963, 1971). The lack of a helical line in the prosiculae of some idiotubids described by Kozłowski (1971) may be a preservational feature, as is the case in some other graptolites. The helical

line might be lacking in some advanced graptolites, like monograptids (Urbanek & Towe, 1975), as a presumably result of a secondary evolutionary change, whereas its presence is indispensable in primitive graptolites and their ancestors. But no helical line has ever been observed in the embryonic vesicle of *Rhabdopleura*, and the resemblance of the latter to the prosicula of some sessile graptolites (crustoids and tuboids) may well be a superficial one. This of course does not exclude their fundamental biological analogy, both being an envelope of young larval forms, as pointed out by Kozłowski (1949, 1971).

Furthermore Hutt (1974, p. 89) has emphasized that "the conical prosicula is not entirely homologous with the (embryonic) vesicle and that it represents a structure at a more advanced stage of organization not represented in *Rhabdopleura*". As justification for this conclusion is another observation by Hutt (1974, p. 91) that because of the presence of cortical derivatives on the outer wall of prosicula, the planktonic graptolite prosicula would be, or could become, an essentially internal skeleton. This last conclusion appears valid not only for the planktonic groups but also for the sessile graptolites. This is not exclusively because of the prosicula but also because of their later stages of development. This produces another serious obstacle for any homology between the peridermal derivatives of the groups considered, including their early stages of astogeny.

On the basis of a few rather randomly taken micrographs Wetzel (1958) made an attempt to substantiate a closer affinity of the graptolites to bryozoans than to pterobranchs. He has mistakenly compared a structureless membrane of the non-fusellar prosicula in a diplograptid with the fusellar zooidal tube of *Rhabdopleura*, and found no resemblance. The present studies provide neither a basis for favorable comparison of graptolite and pterobranch periderm nor for favorable comparison of the former with the bryozoan cuticle.

Pterobranchs certainly provide a useful model for biological comparison with graptolites, but on the basis of existing data there is little reason to postulate any definitive systematic relationship of both groups. A strongly emphasized bilateral symmetry places graptolites clearly among the Bilateria and their highly differentiated organic skeleton indicates most probably a coelomic grade of organization. They may represent, however, a rather separate phylum among the Coelomates. Their relationships to the Hemichordata remain for the time being an unresolved problem.

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PROBLEM POCHODZENIA GRAPTOLITÓW W ŚWIETLE BADAŃ NAD ULTRASTRUKTURĄ UTWORÓW PERYDERMALNYCH U PIÓROSKRZELNYCH

Streszczenie

Ultrastruktura szkieletu organicznego u współczesnego *Cephalodiscus* (*Cephalodiscus*) *inaequatus* (Andersson), rozpoznana za pomocą transmisyjnego mikroskopu elektronowego, składa się z tego samego tworzywa co u współczesnej *Rhabdopleura compacta* Hincks zbadanej przez Dilly'ego (1971). Te same metody zastosowane do badania ultrastruktury jurajskiej *Rhabdopleura kozlowskii* Kulicki i ordowickiego *Rhabdopleurites primaevus* Kozłowski pozwoliły ustalić, że elementarne jednostki strukturalne perydermy i ich charakterystyczny układ przestrzenny pozostawały wśród Pterobranchia niezmienione co najmniej od ordowiku.

Równocześnie porównanie wyników powyższych badań z rezultatami wcześniejszych prac nad ultrastrukturą utworów perydermalnych u graptolitów (Towe i Urbanek, 1972; Urbanek i Towe, 1974, 1975) wykazało zasadnicze różnice na poziomie struktury submikroskopowej między fusellarnymi komponentami perydermy pióroskrzelnych i graptolitów.

Homologia między tkanką fusellarną obu wspomnianych grup stanowiła główny argument klasycznej hipotezy Kozłowskiego (1938, 1949, 1966) o bliskich związkach filogenetycznych między Pterobranchia i Graptolithina. Analiza tej koncepcji, przeprowadzona w świetle współczesnych poglądów na kryteria homologii wykazuje, że w ujęciu Kozłowskiego głównym jej kryterium była swoista jakość rozważanych struktur. To kryterium nie jest jednak spełnione na poziomie ultrastruktury, ze względu na zasadnicze różnice w naturze elementarnych jednostek strukturalnych i w sposobie ich ułożenia. Ponadto szereg danych odnoszących się do anatomii submikroskopowej graptolitów nie potwierdza modelu sekrecji szkieletu graptolitów postulowanego przez klasyczną hipotezę Kozłowskiego. Do tych faktów należą: wczesne odkładanie się tkanki korowej na powierzchni młodocianych tek, obecność utworów korowych na powierzchni wewnętrznej tek oraz stwierdzona u niektórych graptolitów równoczesna sekrecja kolejnych fusellusów i odpowiadających im warstewek tkanki korowej.

W przeciwieństwie do heterogenicznego modelu sekrecji tkanki fusellarnej i kortykalnej postulowanego w klasycznej hipotezie Kozłowskiego i przypisującym sekrecję tych tkanek odmiennym częściom ciała zooidów, dane ultrastrukturalne wskazują raczej na jednorodny sposób ich wytwarzania. Powstawanie perydermy wewnątrz fałdu nabłonkowego — tzw. błony perytekalnej — najlepiej odpowiada wynikom badań ultrastrukturalnych.

Tak więc zasadnicze różnice w tworzywie i jego rozkładzie przestrzennym oraz w sposobie sekrecji tkanki fusellarnej u pióroskrzelnych i u graptolitów uniemożliwiają jej homologizowanie. Powyższe rozważania nie dają uzasadnienia dla kon-

cepcji o ścisłych związkach filogenetycznych między Pterobranchia i Graptolithina. Stanowisko systematyczne tych ostatnich pozostaje w chwili obecnej problemem otwartym.

АДАМ УРБАНЕК

ПРОИСХОЖДЕНИЕ ГРАПТОЛИТОВ В СВЕТЕ ИССЛЕДОВАНИЙ УЛЬТРАСТРУКТУРЫ ПРОИЗВОДНЫХ ПЕРИДЕРМЫ У КРЫЛОЖАБЕРНЫХ

Резюме

Изучение ультраструктуры органического скелета современного *Cephalodiscus* (*Cephalodiscus*) *inaequatus* (Andersson) с помощью трансмиссионного электронного микроскопа показало, что он построен из такого же материала, что и скелет современной *Rhabdopleura compacta* Hincks, который был исследован Дилли (Dilly, 1971). Применение аналогичных методов для исследования ультраструктуры юрской *Rhabdopleura kozlowskii* Kulicki и ордовикского *Rhabdopleurites primaevus* Kozłowski позволило установить, что элементарные структурные единицы перидермы, равно как и их пространственное расположение сохраняются у крыложаберных без изменений, по крайней мере, начиная с ордовика.

В то же время сопоставление результатов вышеуказанных исследований с данными ранее опубликованных работ по ультраструктуре скелета граптолитов (Towe и Urbanek, 1972; Urbanek и Towe, 1974, 1975) продемонстрировало существенные различия между фюзеллярными компонентами перидермы у крыложаберных и граптолитов на субмикроскопическом уровне.

Гомология фюзеллярных тканей этих групп животных составляла основу доказательств в классической гипотезе Козловского (Kozłowski, 1938, 1949, 1966) относительно близких филогенетических связей между Pterobranchia и Graptolithina. Анализ данной концепции в свете современных взглядов на критерии гомологии обнаружил, что в представлении Козловского главным её критерием являются специфические качества рассматриваемых структур („Kriterium der speziellen Qualität der Strukturen" по A. Remane, 1956). Однако указанный критерий не выдерживается на ультраструктурном уровне из-за существенных различий в природе элементарных структурных единиц и в способе их расположения. Кроме того, целый ряд данных по субмикроскопической анатомии граптолитов не подтверждает той модели секреции их скелета, которую мы находим в классической гипотезе Козловского. К данным этого рода относятся: раннее отложение кортикальной ткани на наружной поверхности тек, присутствие

кортикального материала на внутренней поверхности тек, а также обнаруженное у некоторых граптолитов одновременное образование новых фюзеллюсов и соответствующих им слоёв кортикальной ткани.

В отличие от гетерогенной модели секреции фюзеллярной и кортикальной тканей, выдвинутой в классической гипотезе Козловского, которая приписывает создание этих тканей различным частям тела зооида, ультраструктурные исследования свидетельствуют скорее в пользу единообразного способа их возникновения. Результаты ультраструктурных исследований также позволяют говорить с достаточной убедительностью о возникновении перидермы внутри эпителиальной складки, так называемой перитекальной мембраны.

Таким образом, существенные различия в материале и его пространственной организации, а также в способе образования фюзеллярной ткани у крыложаберных и граптолитов делают невозможным вывод об их гомологии.

Приведенные выше доказательства не дают оснований для установления тесных филогенетических связей между Pterobranchia и Graptolithina. Вопрос о систематическом положении этой последней группы до сих пор остается не разрешенным.

EXPLANATION OF PLATES

Plate I

Cephalodiscus (Cephalodiscus) inaequatus (Andersson)

A - Fusellar growth bands as seen on transverse ultrathin sections through the wall of the coenecium. i = inclusion bodies. PTA staining. Scale bar 0.5 μm.
B - High magnification view of the fusellar matrix material. UAC staining. Scale bar 0.1 μm.

Plate II

Cephalodiscus (Cephalodiscus) inaequatus (Andersson)

A - Fusellar bands separated by multiple deposition of trilaminar membranes. i = = inclusion body. UAC staining. Scale bar 0.5 μm.
B, C - Matted fibrillar nature of trilaminar membrane material as seen on sections with oblique views. PTA UAC staining. Scale bar 0.5 μm.

Plate III

Rhabdopleura kozlowskii Kulicki

Longitudinal ultrathin section of fuselli and details of the unilateral overlap at the boundary of two adjacent fuselli, f_1 and f_2. Scale bar 1.0 μm. Compare with diagram in text-fig. 3A.

Plate IV

Rhabdopleura kozlowskii Kulicki

Details of tubarium ultrastructure as seen on longitudinal (A) and transverse (C) ultrathin sections. A foamy structure is recognized at some places and may be a diagenetic product. (B) Scale bars 1.0 μm.

Plate V

Rhabdopleurites primaevus Kozlowski

Tubarium ultrastructure as seen on transverse ultrathin section. A fusellar boundary (fb) is labelled in B. Scale bar 1.0 μm. Compare with Plate VI.

Plate VI

The fusellar boundary and fabric as seen in an ultrathin section of recent *Rhabdopleura compacta* Hincks. Glutaraldehyde-osmium fixation. UAC staining. Scale bar 1.0 μm. Electron micrograph courtesy of Dr. P. N. Dilly.

Plate VII

The fusellar boundary and fabric of a dendroid graptolite (A) and a graptoloid graptolite (B). Compare with plate VI. Scale bar 1.0 μm.