Graptolite-like fibril pattern in the fusellar tissue of Palaeozoic rhabdopleurid pterobranchs

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The fusellar tissue of Palaeozoic rhabdopleurid pterobranchs has been studied using the SEM techniques. The fibrillar material of Ordovician *Kystodendron* ex gr. *longicarpus* and *Rhabdopleurites primaevus* exhibits a distinct dimorphism, comprising: (1) thinner, wavy and anastomosing/branching fusellar fibrils proper, producing a tight three-dimensional meshwork; and (2) long, more or less straight and unbranched cortical fibrils, sometimes beaded, and arranged in parallel. These fibrils are similar to the fusellar and cortical fibrils of graptolites, respectively. Until now, dimorphic fibrils and their arrangement within fusellar tissue were regarded as unique characters of the Graptolithina. In general, the fibrillar material of these fossils is partially preserved in the form of *flaky material* (new term) composed of *flakes* (new term). Flakes are interpreted as flattened structures originating from the fusion of several neighbouring tightly packed fibrils. A Permian rhabdopleurid, referred to as *Diplohydra* sp., reveals a fabric and pattern of fusellar tissue similar to that of both Ordovician rhabdopleurids but devoid (?) of cortical fibrils. The results presented here question views that: (1) substantial differences in fabric and pattern of fusellar tissue exist between fossil pterobranchs and graptolites; and (2) the ultrastructure of pterobranch periderm has remained unchanged at least since the Ordovician. The Palaeozoic rhabdopleurids investigated are closer ultrastructurally to graptolites than to contemporary pterobranchs. The pterobranchs and the graptolites should be treated as members of one class – the Graptolithoidea.

Key words: Pterobranchs, rhabdopleurids, graptolites, ultrastructure, periderm, taxonomy, Ordovician, Permian.

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Introduction

Living and fossil pterobranchs of the order Rhabdopleurida have an organic sclerotized exoskeleton (also termed coenecium or tubarium) made of regular growth bands

called fuselli or fusellar increments. Comparable growth bands, but more irregular in form and spacing, are known in the other pterobranch order, the Cephalodiscida. According to Kozłowski (1938, 1949, 1966), the fusellar tissues of the Pterobranchia and the Graptolithina are homologues. He was convinced 'that a structure of such type does not occur in any other animal, either Recent or fossil' (Kozłowski 1966: p. 497). Nevertheless, several researchers questioned the homology of skeletal tissues in both groups (e.g., Bohlin 1950; Decker 1956; Hyman 1959; Kirk 1972, 1974, 1975; Urbanek 1976a, b; for a detailed discussion of this question see Urbanek 1986, 1987). In spite of the supposedly sharp differences between the fabric of fusellar tissue in both groups at the submicroscopic level (Urbanek 1976a, b, 1978, 1986, 1987), it is widely accepted that pterobranchs and graptolites are descended from a common ancestor and had formed independent phylogenetic lines as early as in Cambrian times (see for example, Rickards 1975; Crowther 1981; Urbanek 1986; Chapman *et al.* 1996). However, it should be stressed that present knowledge of the fine structure of fossil and living pterobranchs' skeletal tissues is still incomplete and based on a limited number of investigations (see below, p. 351).

Our SEM study examined the fine structure of the fusellar tissue of some Palaeozoic rhabdopleurids in order to verify Urbanek's (1976a, b) claims that the characteristic ultrastructural fabric and pattern of rhabdopleurid skeletal tissue are invariable, have remained unchanged at least since the Ordovician, and are dissimilar to those of graptolites. His publications played a major role in the longstanding debate about the affinities of graptolites (for historical details of this discussion see Urbanek 1986, 1987). Urbanek's morphogenetic and phylogenetic theses were based on TEM studies of the fusellar tissue of both fossil and Recent Pterobranchia; he strongly questioned Kozłowski's (1938, 1949, 1966) ideas concerning a pterobranch ancestry for graptolites but failed to win acceptance (e.g., Andres 1977, 1980; Crowther & Rickards 1977; Crowther 1978, 1981; Crowther in Urbanek 1978: p. 627). Nevertheless, his ultrastructural observations and his conclusions regarding the supposedly substantial and invariable differences between the fusellar components of graptolite and pterobranch skeleton (Urbanek 1976a, b) have been widely adopted and gone largely unchallenged for a quarter of a century.

The Ordovician and Permian material selected for the present study represents different rhabdopleurid families. The Ordovician *Kystodendron* ex gr. *longicarpus* (Eisenack, 1937) and *Rhabdopleurites primaevus* Kozłowski, 1967 are members of the Rhabdopleuridae and the Rhabdopleuritidae, respectively (for taxonomy of the Rhabdopleurida see Mierzejewski 1986). Both examples were derived from Gilbergabrottet 1, a well-known exposure of the Ontikan Limestones of Valaste age (lower Llanvirn) deposits in northernmost Öland, Sweden (for details of location, lithology, fauna and biostratigraphy, see Bohlin 1949 and Grahn 1980). Using 10–15% acetic acid the material was etched out of a sample of grey glauconitic limestone (ca. 0.5 kg), collected by the first writer (together with Dr. S. Stouge) in 1985 during his stay at the Institute of Historical Geology and Palaeontology, University of Copenhagen. The *incertae familiae* Permian rhabdopleurid referred to as *Diplohydra* sp. comes from the core Dia 84-31 (sample P3, depth 10.18–10.40 m), Svalis Dome, central Barents Sea, Norway; it was obtained from an undescribed microfossil collection made by A. Mørk, H.A. Nakrem, and H. Szaniawski. The age of this material has been estimated as Kazanian on the basis

of palynomorphs (Nilsson *et al.* 1996); an associated rich assemblage of scolecodonts is discussed by Nakrem *et al.* (in press). The specimen was etched from a cherty mudstone matrix using acetic and hydrofluoric acid.

All specimens studied were coated with platinum and examined using a Philips SEM XL 20. Dimensional data quoted in the text were taken directly from the SEM. The rhabdopleurid material described has been deposited in the Institute of Palaeobiology, Polish Academy of Science, Warsaw (abbreviated ZPAL).

The standard terminology for graptolite periderm ultrastructure (defined by Urbanek & Towe 1974) is adhered to in this work. However, two new terms are introduced: (1) flake – structure composed of several tightly packed fibrils lying approximately in the same plane and cemented together to form an irregular plate; (2) flaky material – material composed of flakes, usually intermingled with free-lying fibrils.

Previous EM studies of pterobranch skeletal tissues

TEM studies of rhabdopleurid pterobranch skeletal tissues began with work of Wetzel (1958). He compared the fine structure of the fusellar zooidal tube of Recent *Rhabdopleura* with the prosicular non-fusellar periderm of an Ordovician diplograptid, *Orthograptus gracilis* (Roemer). He found no resemblance but noted that both rhabdopleuracean and graptolite skeletal tissues are made predominantly of fibrous material. Rickards & Dumican (1984: p. 176) emphasized that Wetzel was also the first to discover 'the contrast in dimensions between the fibrils in *O. gracilis* and *Rhabdopleura*, the latter being finer and, apparently, often straighter and needle-like even in thin sections'.

The frame of reference for all future ultrastructural studies of rhabdopleurid periderm was set by Dilly (1971) in his excellent study of Recent *Rhabdopleura compacta* (Hincks). According to Dilly, the fusellar tissue of this pterobranch is built of a mass of keratin-like straight fibrils, loosely dispersed in an almost structure-free matrix. The fibrils are of three different types when classified by their ultrastructural features and vary considerably in length, from a few nanometers to over 5 mm. The thickest fibrils have a diameter of about 25–30 nm and contain a double helix of fine fibrils. As demonstrated by Urbanek (1976a, b), the coenecium of the living cephalodiscid pterobranch *Cephalodiscus (Cephalodiscus) inaequatus* (Andersson) is ultrastructurally very similar to that of Recent *Rhabdopleura*. Unfortunately, the state of preservation of his material precluded any closer analysis of the *Cephalodiscus* fibrils. Later, Urbanek, Dilly, & Mierzejewski (in Mierzejewski 1984b) found that the skeletal tissue of Recent *Cephalodiscus solidus* Andersson is built of straight, unbranched fibrils which possess a large lucent core. The diameter of these fibrils varies in the range 19–22 nm. Regretably, extensive SEM and TEM studies by P.N. Dilly, A. Urbanek and P. Mierzejewski made in 1981 on three living species of *Cephalodiscus* remain unpublished; only some of their observations and conclusions are mentioned by Mierzejewski (1984b), Urbanek (1986) and herein. Dilly's (1993) SEM and TEM studies showed that spines of Recent *Cephalodiscus graptoloides* Dilly have an identical structure to a graptolite nema. Additional TEM and SEM observations were made by Andres (1980) and Crowther (1981) on the fine structure of Recent cephalodiscid and rhabdopleurid coenecial tissue, respectively.

Ultrastructural studies of fossil pterobranchs also have a short history and are restricted only to the TEM and SEM investigations of Urbanek (1976a, b), Andres (1980), Mierzejewski (1984a, 1986), and Urbanek *et al.* (1992); Rickards *et al.* (1984: p. 27) unsuccessfully applied SEM techniques to the periderm of Silurian *Rhabdopleura hollandi.* The observations and conclusions of Urbanek (1976a, b) are of special significance. He investigated the fusellar tissue of two fossil rhabdopleurids: the Ordovician *Rhabdopleurites primaevus* Kozłowski, 1967 and the Jurassic *Rhabdopleura kozlowskii* Kulicki, 1969. He concluded that the nature and arrangement of fusellar fibrils within the Pterobranchia are invariable and have remained unchanged since at least the Ordovician. He also concluded that the striking dissimilarity between fibrillar material of Pterobranchia and Graptolithina rules out any close affinity of between them. Previous TEM studies carried out by Towe & Urbanek (1972), Berry & Takagi (1973) and Urbanek & Towe (1974, 1975) demonstrated that the fusellar tissue of graptolites is composed of a different fibrillar fabric from that of Recent *Rhabdopleura.* Graptolite fusellar fibrils, presumably of a collagenous nature, are distinctly thicker and their average diameter varies usually in the range 60–110 nm (Crowther 1981), and reaches up to 130 nm (Bates 1997). Moreover, they are not straight and loosely dispersed but wavy, branching or anastomosing, creating a three-dimensional spongy meshwork.

In these circumstances, the discovery that the coenocia of Recent cephalodiscid and rhabdopleurid pterobranchs are collagenous (Armstrong *et al.* 1984) appeared to be of great importance. It reinforced the hypothesis that pterobranchs and graptolites are phylogenetically closely related and explained differences at the ultrastructural level as a secondary effect of the arrangement of tropocollagen units within the collagen fibrils. In connection with this discovery, Urbanek (1986, 1987) introduced the term 'ultrastructural anomaly' for the ultrastructural differences between the fibrillar material of both groups, and he attached great significance to the distinction. He regarded such ultrastructural differences as 'one of the best criteria for the pterobranch-graptolite boundary in phylogeny and classification' (Urbanek 1986: p. 211) and stated later that 'Perhaps they are among the best diagnostic features of the graptolite grade of the rhabdosome construction' (Urbanek 1987: p. 228). It is the more remarkable then that the periderm of the Middle Cambrian *Rhabdotubus johanssoni* Bengtson and Urbanek (one of the two oldest known rhabdopleurids) reveals in some cases a delicate network of interconnected fibrils, indicating an essentialy graptolite grade of periderm fine structure (Urbanek *et al.* 1992: fig. 1).

Observations

Kystodendron ex gr. *longicarpus* (Eisenack, 1937)

Figs. 1–4.

Description. — The specimen examined is a small fragment of coenecium consisting of an upright zooidal tube joined to a piece of creeping tube (Fig. 1A). The fossil is preserved undistorted and in full relief. With regard to the state of preservation, it differs from all other chemically isolated Ordovician rhabdopleurids (described by Kozłowski 1967, 1970, and Mierzejewski 1986) in the considerable rigidity of its periderm and a strong pigmentation.

The preserved fragment of creeping tube is semicircular in transverse section, ca. 300 mm long and 90 mm wide, with a flat lower wall (the basal membrane) and a convex upper wall. The lower
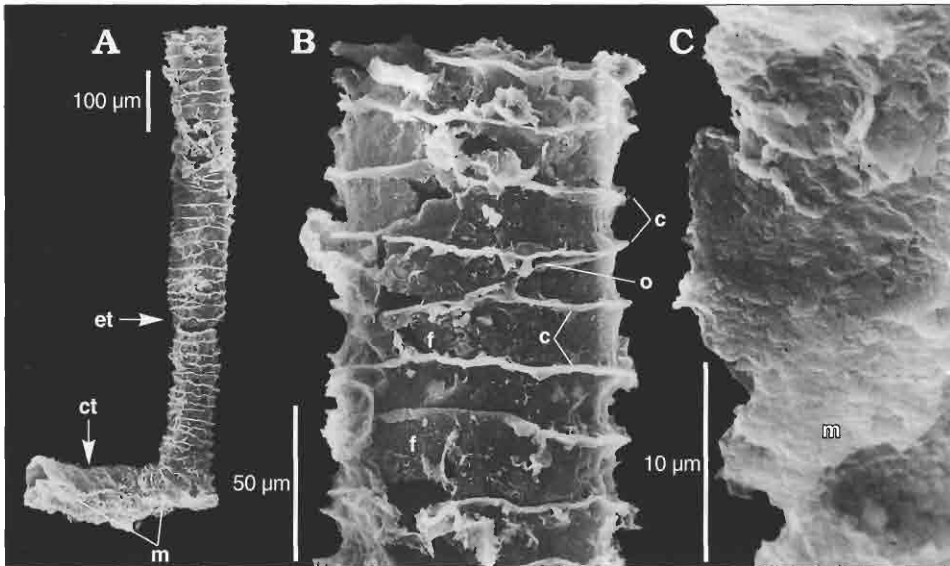
Fig. 1. *Kystodendron* ex gr. *longicarpus* (Eisenack, 1937). Lower Llanvirn (Ontikan Limestones of the Valaste age), Gilbergabrottet 1, Öland (Sweden). SEM micrographs. Specimen consisting of erect tube and incompletely preserved creeping tube (ZPAL Pb/0/1). **A**. Lateral view of the specimen; × 110. **B**. Distal part of the erect tube; × 550. **C**. Upper surface of the margnal memebrane; × 3500. Abbreviations: c, collar of fusellus; ct, creeping tube; et, erect tube; f, fusellus; m, marginal membrane; o, oblique suture of fuselli.

wall, which was attached to the substratum during the organism's life, is light brown, semi-transparent and looks strongly crumpled; it shows no traces of fibrillar structure. The upper wall is dark brown, opaque and displays a distinctly fusellar structure. Fuselli occur on both sides of the upper wall and join each other at a constant angle to form a characteristic zigzag suture. The width of the fuselli varies considerably, between 10.5 mm and 13.1 mm. The creeping tube is bordered by a narrow, structureless marginal membrane, which is colourless and almost translucent (Fig. 1C).

The zooidal tube is 730 mm long, built of very clear fuselli and extends perpendicular to the creeping tube (Fig. 1A, B). It is almost cylindrical, robust, and mostly dark brown and opaque; the most distal section is lighter in colour. There is a distinct and rather gradual increase in width of the zooidal tube, from 61 mm at the base to 90 mm at the aperture. Fuselli of the zooidal tube are complete rings, with a single oblique suture – similar to those of most rhabdopleurids (Figs. 1B, 2). The upper margins of the fuselli protrude strongly to produce a characteristic fusellar collar (Figs. 1A, B, 2). The spacing of fusellar increment spacing is about 60 per mm; the height of the fuselli (i.e. the distance between the growth lines) ranges between 16.5 and 21.4 mm.

The fine structure of the surface of the fusellar periderm is very well preserved. The outer surface was primarily covered with a smooth, presumably homogenous, enamel-like pellicle (Fig. 2). Only in some places is the pellicle fractured; minor foldings and finely comminuted debris make original features less distinct. Most of the debris is probably composed of exfoliated fusellar pellicle (Fig. 3A). Usually the pellicle is robust and masks the inner fusellar structure, but in some places, it seems to be more delicate and reflects the shape and orientation of underlying fusellar fibrils (Fig. 3B). However, the fibrillar material becomes especially clear when the fusellar pellicle has been damaged and removed. Here the fusellar fibrils can be subdivided into two categories according to their shape and thickness: (1) short, wavy, branched or anastomosing fusellar fibrils proper; and (2) long and straight, distinctly thicker cortical fibrils. However, sometimes fibrils intergrade between these two types. Fibrils of the first category build the main fibrillar component of the fusellar tissue. They are usually ca. from 70 to 90 nm in diameter, sometimes reaching to 110 nm or more. Fusellar fibrils are usually
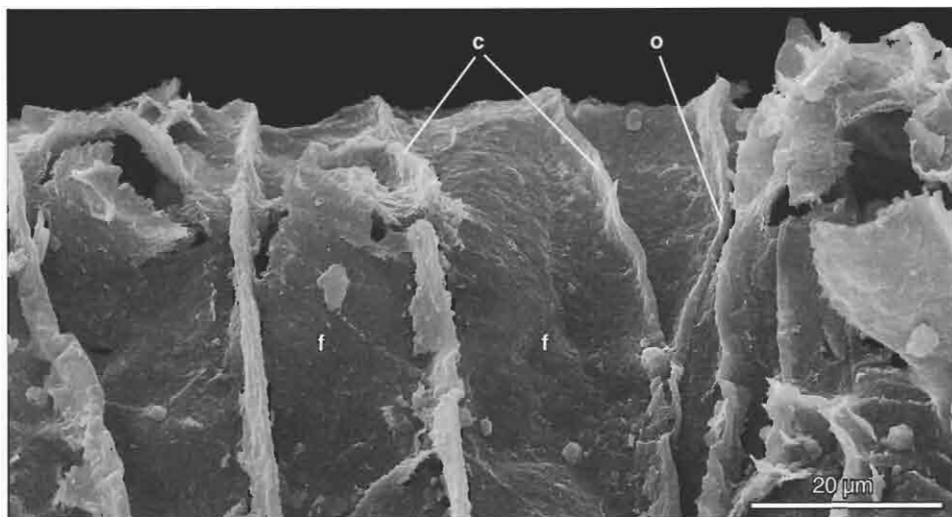
Fig. 2. *Kystodendron* ex gr. *longicarpus* (Eisenack, 1937). Lower Llanvirn (Ontikan Limestones of Valaste age), Gilbergabrottet 1, Öland (Sweden) ZPAL Pb/0/1. Well-preserved outer surface of fusellar increments; ca. × 2000. SEM micrograph. Abbreviations: f, fusellus; c, collar of fusellus; o, oblique suture of fuselli.

more or less close-packed and produce a characteristic, three-dimensional, reticulate pattern (Figs. 3B, 4). At some places the packing together of the fibrils appears distinctly loose (Fig. 4B). There are also intercalations of almost homogenous material which we term flakes (Fig. 4). In some cases, the flakes pass gradually into strongly packed and then loose-lying fibrils (Fig. 4C). Fibrils of the second category occur exclusively in the collars of fuselli (Fig. 3). SEM micrographs distinctly show that each fusellar collar is built of closely packed or even cemented cortical fibrils. They are arranged uniformly and parallel to the margins of collars, forming a band-like, solid construction. Like the fibrils of the first category, the cortical fibrils are not uniform in thickness, with thinner fibrils being scattered among thicker ones; their diameter varies from 150 to 200 nm. Sometimes, extremely thick cortical fibrils occur, up to 290 nm in diameter, but presumably these result from the fusion of two or more thinner fibrils. When examined at higher magnification, neither fusellar fibrils proper nor cortical fibrils show show traces of substructure or annular ringing. There is no indication of a preserved ground substance in between the fibrils.

Remarks. — The morphology of this specimen of *Kystodendron* ex gr. *longicarpus* matches the zooidal and creeping tubes of living members of the genus *Rhabdopleura* Allman, 1869. Almost identical specimens, composed of erect and creeping tubes, were described from Ordovician erratic boulders by Kozłowski (1970) and Mierzejewski (1986), who referred them to Eorhabdopleura urbaneki Kozłowski (this specific name is treated as a *nomen dubium*, see Mierzejewski 1986: p. 184) and *Kystodendron longicarpus* (Eisenack, 1937), respectively. The first author of the present paper examined several similar specimens from the Ordovician of Estonia (found in the undescribed collection of the late Dr. Ralph Männil) which, by rhabdopleurid standards, represent an exceptionally small sized pterobranch; it may be best compared with the smallest known forms of the fossil Rhabdopleuridae, i.e. *Kystodendron tener* Mierzejewski, 1986 and *K.* ex gr. *longicarpus* (Eisenack), known from Ordovician and Silurian glacial drift boulders (Mierzejewski 1986). As in *Rhabdopleura* (see Urbanek & Dilly 2000), the zooidal tubes of *Kystodendron* have only limited value in the identification of species, so the use of open nomenclature is necessary.

SEM studies of the ultrastructure of zooidal tubes of recent *Rhabdopleura compacta* Hincks, 1880 have revealed the presence of fibrils on the outer surface of fuselli (Dilly 1976). These fibrils are external to the main body of the periderm; long fibrils which cross several increment rings, and short fibrils which run along the height of each fusellus can be distinguished. The
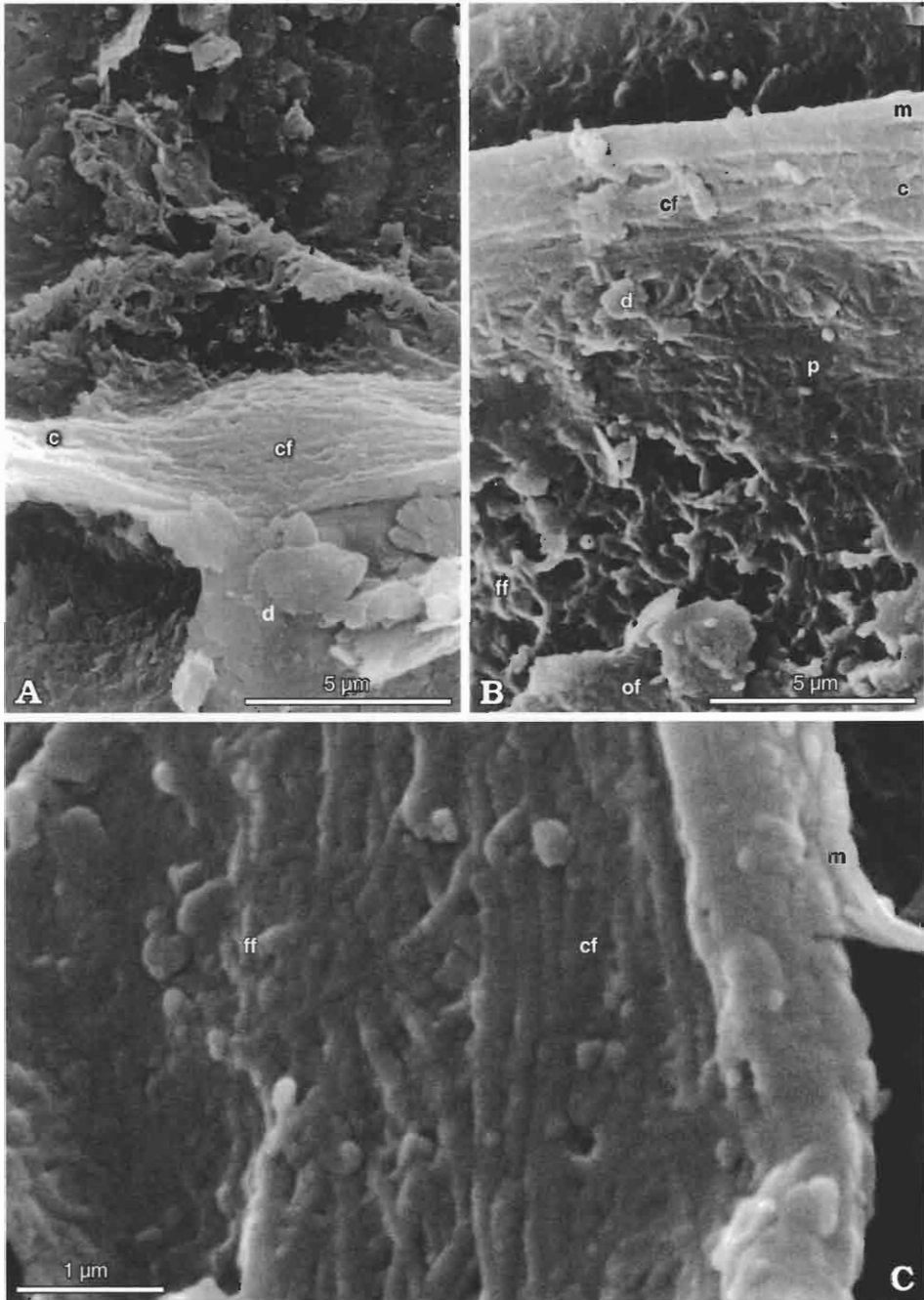
Fig. 3. *Kystodendron* ex gr. *longicarpus* (Eisenack, 1937). Lower Llarnvirn (Ontikan Limestones of Valaste age), Gilbegrabrottet 1, Öland (Sweden). SEM micrographs. ZPAL Pb/0/1. Fine structure of fusellar collars. **A**, × ca. 5500; **B**, × ca. 5500; **C**, × 21000. Abbreviations: c, collar of fusellus; cf, cortical fibril; of, outer pellicle of fusellus; d, debris of peeled off pellicle; ff, fusellar fibrils proper; m, margin of fusellar collar; p, delicate periderm reflecting underlying fusellar fibrils.
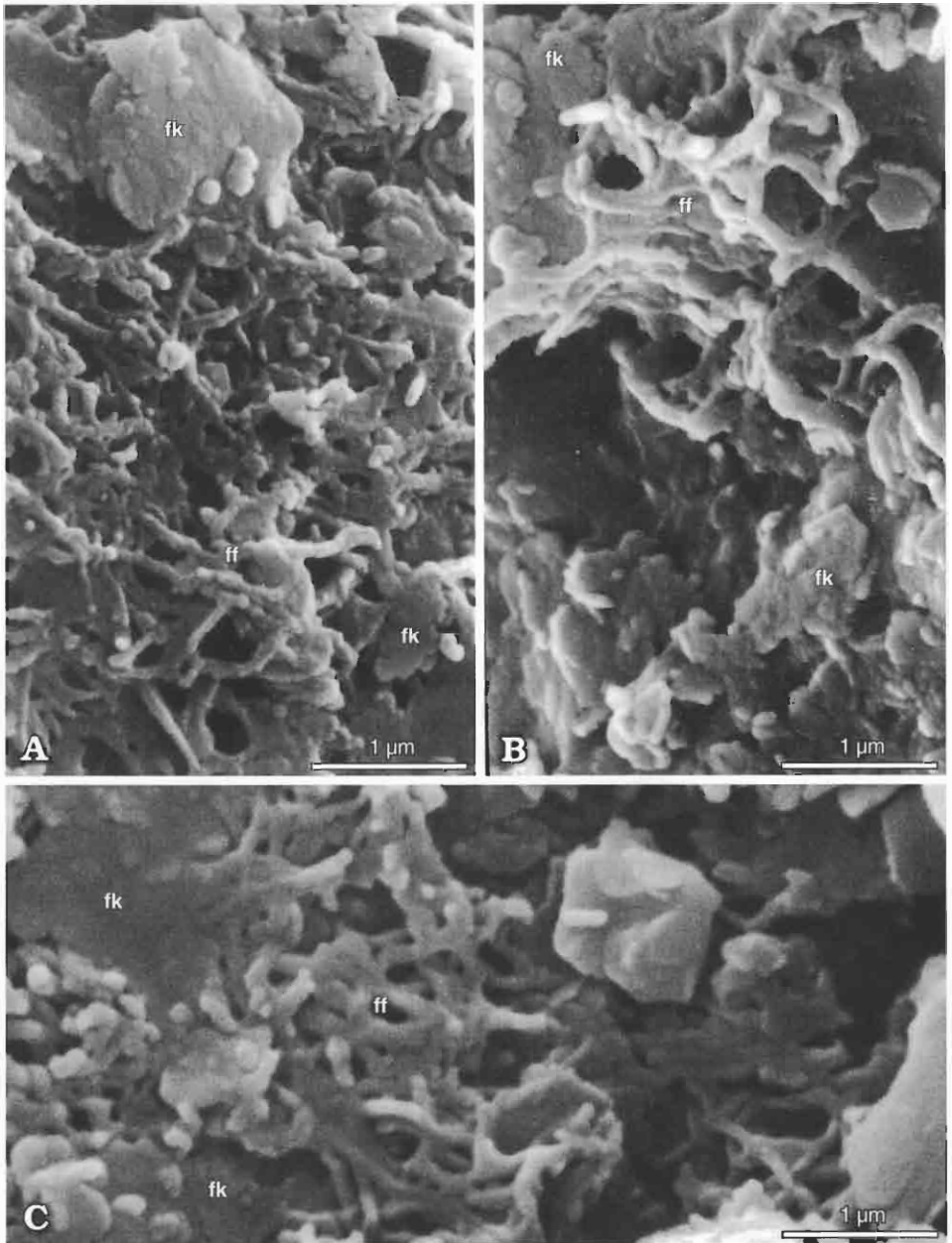
Fig. 4. *Kystodendron* ex gr. *longicarpus* (Eisenack, 1937). Lower Llanvirn (Ontikan Limestones of Valaste age), Gilbergabrottet 1, Öland (Sweden). SEM micrographs. ZPAL Pb/0/1. Anastomosing and/or branching fusellar fibrils proper intermingled with flakes. **A**, ca. × 21000; **B**, ca. × 21000; **C**, × 21000. Abbreviations: ff, fusellar fibril; fk, flake.

periderm of the specimen described here is entirely devoid of such external fibrils. It rather resembles the smooth, enamel-like external surface of the periderm of various sessile graptolites (see Urbanek *et al.* 1980).
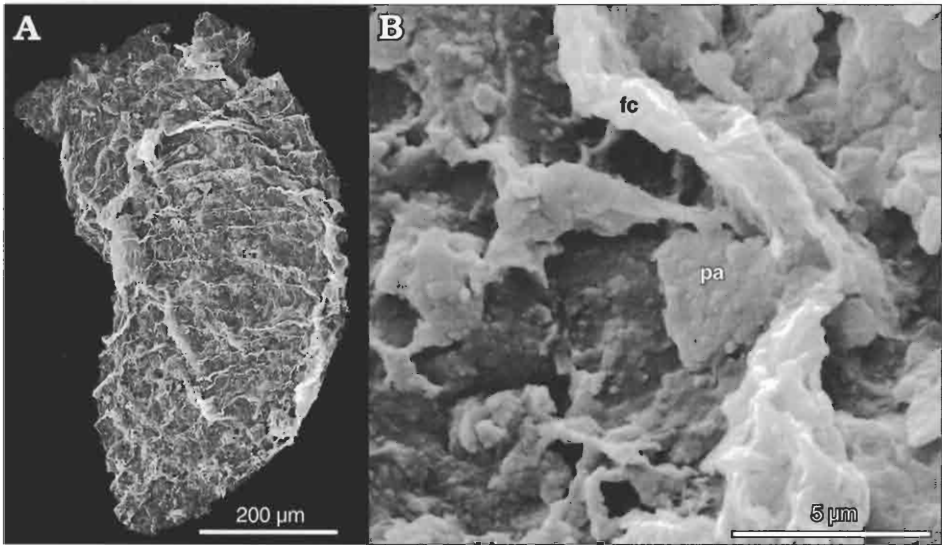
Fig. 5. *Rhabdopleurites primaevus* Kozłowski, 1967. Lower Llanvirn (Ontikan Limestones of Valaste age), Gilbergabrottet 1, Öland (Sweden). SEM micrographs. ZPAL Pb/0/2. **A.** Fragment of the strongly flattened zooidal tube; × 90. **B.** Surface of the periderm; × 5200. Abbreviations: fc, fusellar collar; pa, 'patch'.

The fine structure of the non-fusellar skeletal elements of the tubarium of *Kystodendron* (stolons and sterile bud cysts) was studied under the TEM by Mierzejewski (1986). The material comprising these elements appears to be completely homogenous.

Rhabdopleurites primaevus **Kozłowski, 1967**

Figs. 5, 6.

Description. — The specimen studied (Fig. 5A) is a fragment of a strongly flattened zooidal tube measuring 760 mm in length and ca. 340 mm in width. It is composed of delicate, flexible, light-brown and translucent periderm. The fusellar increments are usually ring-like, only rarely exhibit an oblique suture and vary from 30 to 61 mm in width. The fusellar collars are weak and indistinct; some appear to be empty.

The periderm surface is patchy (as defined by Urbanek 1986: p. 210) and rough (Fig. 5B). No distinct fibril network can be identified in the periderm material. The fusellar tissue is composed largely of strongly condensed flaky, material with rare meshes (Fig. 6). Most flakes appear to be structureless (to the limits of SEM resolution). In some, however, more or less wavy and free-laying fusellar fibrils pass into flakes, or flakes are clearly built of aggregations of tightly packed and cemented fibrils (Fig. 6). The diameter of these fibrils varies between wide limits, from as little as 90 nm up to 200 nm. Moreover, the straighter and thicker cortical fibrils (usually 200–240 nm in diameter) occur sporadically in fusellar collars (Fig. 6E). These fibrils possess annular thickenings with a rather irregular periodicity of about 150 nm.

Remarks. — The specimen agrees closely in shape and dimensions with those from Ordovician glacial boulders described by Kozłowski (1967, 1970) and Mierzejewski (1986), and studied ultrastructurally under the TEM by Urbanek (1976a, b). Previously Skevington (1965) erroneously described these forms from the Ordovician of Öland by as ?Graptovermid sp., gen. et sp. indet., as noted by Andres (1977) and Mierzejewski (1977, 1986). Contrary to Skevington's specimens, ours is devoid of an inner secondary layer (first recognized in rhabdopleurid pterobranchs by Kulicki 1971).

The nature of certain characteristic 'patches' on the periderm surface is unclear. They may result from corrosion of the primary surface prior to fossilization and represent the remnants of a fusellar
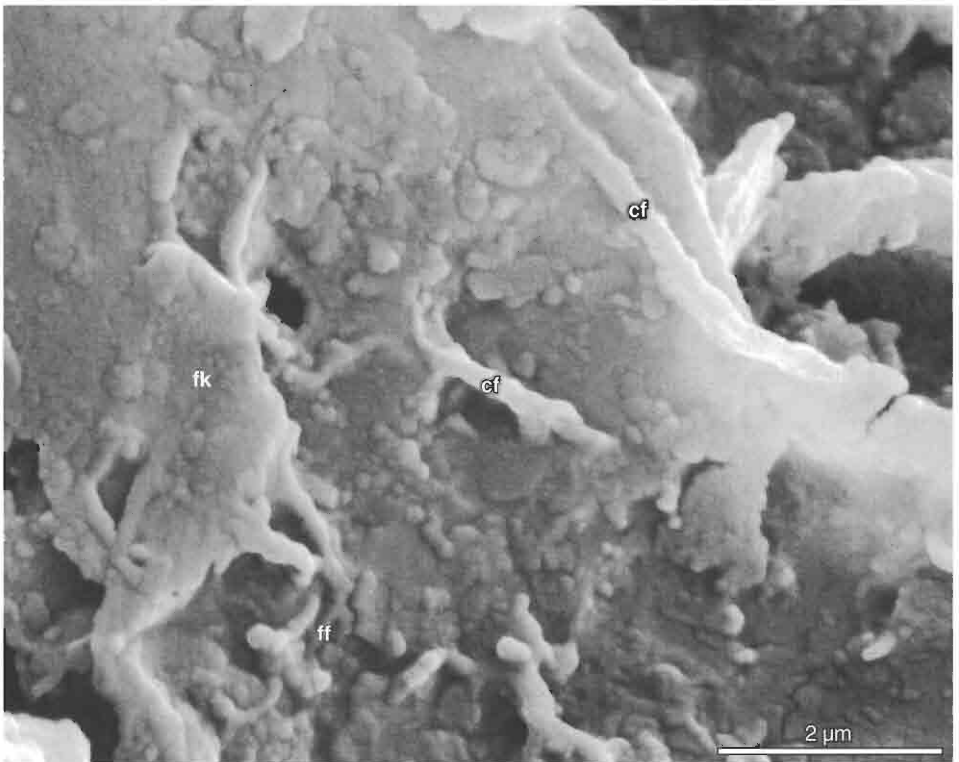
Fig. 6. *Rhabdopleurites primaevus* Kozlowski, 1967. Lower Llanvirn (Ontikan Limestones of Valaste age), Gilbergabrottet 1, Öland (Sweden). ZPAL Pb/0/2. SEM micrograph showing fine structure of the fusellar tissue; × 15500. Abbreviations: c, fusellar collar; cf, cortical fibril; ff, fusellar fibril; fk, flake.

pellicle fused with flaky material. On the other hand, they reveal a striking similarity to the 'patches' which cover the surface of living tubes of some Recent cephalodiscid pterobranchs, as discovered by Dilly, Urbanek and Mierzejewski (unpublished), and subsequently interpreted as secondary deposits (cf. Urbanek 1986: p. 210).

The fine structure of the fusellar tissue of *Rhabdopleurites primaevus* is of crucial importance both for Urbanek's (1976a, b) claim that substantial differences exist between pterobranch and graptolite fibrllar material and for the existence of his 'ultrastructural anomaly'. His investigation, micrographs and conclusion are reinterpreted below and compared with the SEM studies reported here. The ultrastructure of the remaining elements of the coenecium was investigated by Mierzejewski (1986), who discovered that non-fusellar tubes are built of periderm showing a clearly laminar ultrastructure, whereas stolons are built of very thin, long and straight fibrils, cemented together.

Diplohydra sp.

Fig. 7.

Description. — The specimen studied represents a fragment of a rhabdopleurid coenecium; it is composed of several branching, tangled stolons connected to remnants of fusellar tubes. A detailed morphological description of this fossil is outside the scope of the present paper and will be published elsewhere (Mierzejewski & Kulicki in preparation). Like the stolons, the fragments of the fusellar tubes are generally flattened, and their micromorphological details (e.g., sutures between fuselli or fusellar collars) are difficult to observe. However, the fine structure of the fusellar tissue is well seen under the SEM (Fig. 7A). The predominant component is flaky material together with some fibrils
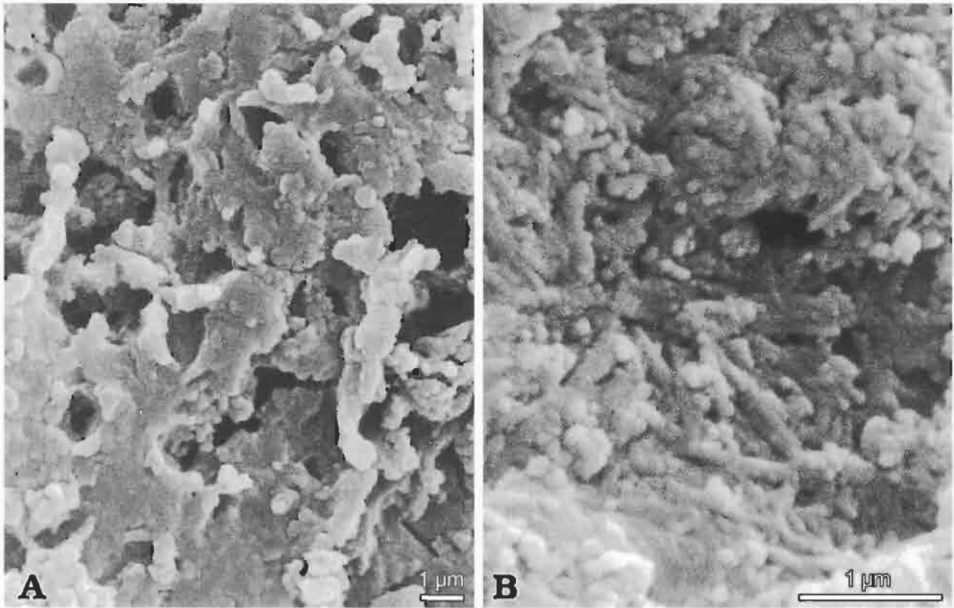
Fig. 7. *Diplohydra* sp. Kazanian (Upper Permian), core Dia 84-31 (sample P3, depth 10.18–10.40 m), Svalis Dome, central Barents Sea (Norway). SEM micrographs. **A.** Flake material from the fusellar tissue with indinstinct traces of fusellar fibrils and numerous meshes. ZPAL Pb/0/4; × 5500. **B.** Fibrous material covering the outer surface of the stolon, ZPAL Pb/0/5; × 19500.

(diameter 100–150 nm), producing an irregular three-dimensional network. The characteristic meshes of this network are distributed randomly and attain a diameter of 0.7–1.1 mm. The gradual passage from free-lying fibrils into more or less condensed flakes is observed.

Sometimes, the fibrillar material is seen on the outer surface of the stolon, forming a layer of very tightly packed fibrils (Fig. 7B). These fibrils are randomly oriented and seem to be rather short and wavy; their diameter varies between 110 and 170 nm. Flaky material is not observed among these fibrils.

No trace of any long straight fibrils, similar to that of *Kystodendron* and *Rhabdopleurites*, are found in the fusellar tissue or on the outer surface of the stolon.

Remarks. — While the pattern of fusellar tissue in the fossil under discussion differs from that of living *Rhabdopleura compacta* (see Dilly 1971), it is very similar to that of Ordovician *Kystodendron* and *Rhabdopleurites* (herein), apart from the lack of long, thick, parallel packed cortical fibrils. On the other hand, the mass of fibrils covering the stolons of *Diplohydra* sp. is strikingly similar to a condensation of thick fibrils incorporated within the stolonal wall of Recent *Rhabdopleura compacta* (Hincks) (Dilly 1975: fig. 12), and of Ordovician *Rhabdopleurites primaevus* Kozłowski (Mierzejewski 1986: pl. 27: 2).

It is noteworthy that *Diplohydra* sp. is the first pterobranch (and the first representative of the phylum Hemichordata) to be found in Permian deposits.

Discussion

The results of this SEM study of Palaeozoic rhabdopleurid pterobranchs are in sharp contrast with those of Urbanek's (1976a, b) TEM studies. Urbanek stated that the fabric of the fusellar tissue in pterobranchs differs essentially from that of graptolites, and

that the nature and arrangement the fusellar fibrils within the Pterobranchia have not changed since the Ordovician.

In contrast, we have found no fundamental ultrastructural difference between the fusellar tissues of graptolites and Palaeozoic rhabdopleurid pterobranchs. The fusellar tissue of Ordovician *Kystodendron* ex gr. *longicarpus* (Eisenack) and *Rhabdopleurites primaevus,* as well as Permian *Diplohydra* sp., reveals a fabric made of fibrils strikingly similar to those recognized in graptolites. The fusellar fibrils of these forms are not thin and needle-like, as in Recent *Rhabdopleura*, but thick and wavy, as in graptolites. Moreover, the diameter of graptolite fusellar fibrils (60–110 nm according to Crowther 1981; exceptionally up to 130 nm, see Bates 1997) and that of Palaeozoic rhabdopleurids (70–150 nm, sporadically up to 200 nm, herein) is similar whereas fusellar fibrils in Recent *Rhabdopleura* are distinctly thinner (25–30 nm according to Dilly 1971). The fusellar fabric in the body of the fusellus in *Diplohydra* sp. is typical of graptolite fusellar fabric, as defined by Urbanek & Towe (1974: p. 5), i.e. it is a spongy meshwork of interconnecting fibrils (compare also Crowther 1981, pl. 1: 6, pl. 4: 6). The fuselli of this form closely resemble the simple fuselli of some graptolites because they are composed only of the body and an outer pellicle. The formation of such fuselli may be compared to the *Dictyonema* type of secretion in Urbanek's (1976c) classification. On the other hand, the fuselli of both Ordovician forms include straight, unbranched cortical fibrils, parallel to one another, and sometimes closely packed or even cemented. These fibrils may be slightly intermingled with the fusellar fibrils proper. This gradual transition from fusellar fibrils proper to the ordered cortical fibrils in the collar regions of fuselli is fully comparable with a transition from fusellar to cortical fabric within the body of a graptolite fusellus (as described by Urbanek & Towe 1974 and Rickards & Dumican 1984). In the fuselli of some graptolites, these 'criss-cross fibrils become more closely packed, forming a layer or lamella of fibrils usually orientated parallel to the circumference of the half-ring', as Bates & Kirk (1985: p. 210) so clearly showed. Some of their SEM micrographs (especially pl. 2: 12) show a fibril pattern very similar to that of *Kystodendron* ex gr. *longicarpus* (Fig. 3; see also Bates 1986: fig. 2). Undoubtedly, the fuselli of *Kystodendron* and *Rhabdopleurites* may be compared to graptolite fuselli comprising all three fusellar components (i.e. body, pellicle and outer lamella), which are consistent with the *Acanthograptus*-type of secretion of Urbanek's (1976c) classification.

The flaky material of Palaeozoic rhabdopleurids described herein has its equivalent in the ultrastructure of some sessile graptolites and should be regarded only as a preservational artifact of normal fibrous material (see below).

So why do our SEM results conflict with Urbanek's (1976a, b) TEM investigations? Could it be a product of the two very different techniques? SEM microscopy has the advantage that surfaces and fractured sections of the periderm can be examined, whereas TEM microscopy provides only a two-dimensional and very limited field of view. Some TEM-base interpretations of graptolite ultrastructure (e.g., a 'ground substance' of the cortical fabric, or the existence and nature of the cortical bandages) have been strongly challenged (e.g., see Crowther & Rickards 1977; Crowther in Urbanek 1978: p. 627; Crowther 1981; Rickards & Dumican 1984), and it can be argued that TEM micrographs may sometimes be positively misleading. Nevertheless, we are of the opinion that the discrepancy in our conclusions and those of Urbanek (1976a, b) is only partly due to the

different techniques adopted. It is now possible to reinterpret his micrographs in the light of new ultrastructural data concerning pterobranchs and graptolites.

The fine structure of Ordovician *Rhabdopleurites* has been crucial to Urbanek's (1976a, b, 1978, 1986, 1987) arguments which claim that substantial ultrastructural differences exist between the Pterobranchia and the Graptolithina, and that the fibrillar pattern in pterobranch fusellar tissue has changed little since Ordovician times. Thanks to scale bars on Urbanek's (1976a, b) micrographs, it is possible to measure fibril diameter. Astonishingly: fibril diameters are generally more than 100 nm and less than 200 nm, which is within the limits of dimensional data measured in the rhabdopleurids described herein. While we share Urbanek's view that the general arrangement of fibrils in his specimens of *Rhabdopleurites* is similar to that of living *Rhabdopleura*, they are unquestionably of graptolite dimensions. It should be stressed that this shape and fibril arrangement is also strikingly similar to the ultrastructural pattern found in some graptolites (e.g., fusellar fibrils of graptoblasts described by Mierzejewski 1984b and Urbanek *et al.* 1986). The fusellar fibrils of the camaroid graptolite *Tubicamara coriacea* Kozłowski, 1949 are long, slightly wavy and only rarely seem to be branched (Urbanek & Mierzejewski 1991: fig. 11). Similar fusellar fibrils were recognized by Urbanek *et al.* (1982: fig. 14) in the nematularium of the graptoloid *Cystograptus vesiculosus* (Nicholson).

The Jurassic *Rhabdopleura kozlowskii* Kulicki, 1969 was the second fossil rhabdopleurid pterobranch studied under the SEM by Urbanek (1976a, b). We agree with him that remarkable differences between its fine structure and that of two living species of *Rhabdopleura* are a result of fossilization and diagenesis. However, we claim that the fine structure of *Rh. kozlowskii* reveals distinct similarities to the ultrastructure of some graptolites. The structures recognized by Urbanek (1976b: pl. 4) as matrix of 'numerous filamentous materials' distinctly resemble the fusellar fabric of the metasicula of *Orthograptus quadrimucronatus* Hall, as illustrated under the TEM by Berry & Takagi (1973: fig. 2). On the other hand, the obscure 'foamy structures' in the periderm of *Rh. kozlowskii* may be best compared with the 'reticulated fabric' discovered by Urbanek & Mierzejewski (1986) in dendroid graptolites, and with similar structures found in camaroid graptolites (Urbanek & Mierzejewski 1991); these are interpreted as an unusual state of aggregation of the fibrous material. Such 'foamy structures' in Jurassic *Rhabdopleura* are most probably the result of the fusion of originally straight and parallel fibrils, similar to the flaky material identified in three Palaeozoic forms herein. Our preliminary SEM studies of *Rh. kozlowskii* suggest the presence of heteromorphic fibrillar material in its fusellar tissue and in the wall of a sterile bud cyst (Fig. 8; Mierzejewski & Kulicki in preparation). In some cases the outer surface of skeletal elements exhibits a complex network of linear features, strikingly similar to poorly preserved graptolite cortical bandages (cf. Crowther & Bergström 1980: pl. 1: 3 and Crowther 1981: pl. 19: 2). Moreover, we interpret a series of electron-dense membranes on Urbanek's (1976b: pl. 4C) TEM micrograph as a secondary deposit within the zooidal tubes, recognized by Kulicki (1971) in this species by means of light microscopy. It seems, therefore, that while our SEM observations contradict Urbanek's (1976a, b) interpretations and conclusions, they are nevertheless consistent with his ultrastructural data.

Our observations also shed a new light on Urbanek's (1986, 1987) concept of an 'ultrastructural anomaly' (see above, p. 352) and its significance for pterobranch/ graptolite taxonomy and phylogeny. Such a supposedly clear distinction at the ultra-
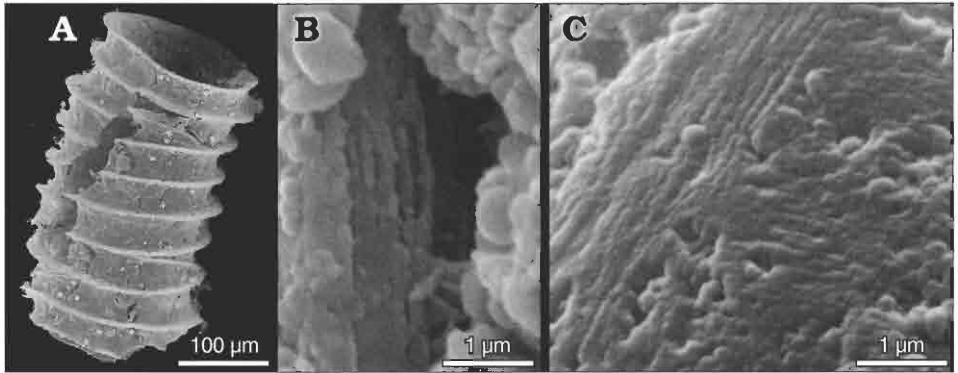
Fig. 8. *Rhabdopleura kozlowskii* Kulicki, 1969. Callovian (Jurassic), Łapiguz clay pit, Łuków (Poland). SEM micrographs. ZPAL Pb/0/6. **A**. Fragment of a zooidal tube; × 210. **B**. Fissure in the periderm: arrow indicates a presumably bunch of cortical fibrils; × 14000. **C**. Unconformity between two presumably bunches of cortical fibrils on the surface of a sterile bud cyst. Note a striking similarity to cortical bandages in graptolites! × 14300.

structural level between the two groups was not immediately apparent. Dilly (1975) found a reticulum of coarse fibres very similar to the fusellar fabric of graptolites in the repent tube of living *Rhabdopleura compacta* Hincks, 1880. He regarded his discovery as indicative of a close evolutionary origin for cephalodiscids, rhabdopleurids and graptolites (Dilly 1975, 1976). The value of Dilly's observations and conclusions was underestimated by Urbanek (1976b: p. 18; but see also Urbanek 1986: p. 204 and Crowther 1981). Andres (1980) found the fine structure of fusellar tissue in living *Rhabdopleura* and in an unidentified Ordovician crustoid graptolite to be very similar, but his observations were questioned by Urbanek & Mierzejewski (1984). Crowther (1981: p. 27) observed that 'Fusellar fabrics of graptolites and *Rhabdopleura* bear a superficial resemblance on SEM micrographs'. Mierzejewski (1984b) noted that the apparent structural gap between the fusellar tissue of pterobranchs and the graptolites was partly filled by some unusual fibrils in the periderm of an Ordovician graptoblast (see also Urbanek *et al.* 1986: p. 103, fig. 7A). These fibrils were of cephalodiscid pterobranch ultrastructure, yet of graptolite dimensions. This is consistent with the view of Armstrong *et al.* (1984) that ultrastructural differences between the skeletel tissues of the Pterobranchia and the Graptolithina are probably less important for phylogenetic considerations than was previously suggested. Mierzejewski's (1984b) discovery was discussed by Urbanek (1986: p. 204, fig. 12A) who considered it 'indicative of relative lability between the newly acquired graptolite and the phylogenetically old pterobranch systems of fibrillogenesis', suggesting that the presence of unusual fibrils 'may be explained as biochemical regression to a more primitive stage of fibrillogenesis, owing to the inhibition of growth (...), which disturbs also the processes of fibrillogenesis.' Most significant of all is the case of the Ordovician *Pterobranchites antiquus* Kozłowski, 1967, which was initially interpreted as a cephalodiscid pterobranch (Kozłowski 1967; Bulman 1970). As stated by Mierzejewski (1984a), this fossil may be regarded as intermediate in form between cephalodiscids and graptolites: all the features of morphological features of its skeleton fall within the limits of variability of the Cephalodiscida, yet the ultrastructure of its periderm (in-

cluding a typical graptolite-like cortex) appears much closer to graptolites than pterobranchs. In the light of our new observations, the systematic position of the genus *Pterobranchites* must be reconsidered. Finally, *Cephalodiscus solidus* Andersson provides further evidence for 'bridging a gap' between the ultrastructural organization of the Pterobranchia and the Graptolithina (Dilly, Urbanek, & Mierzejewski, unpublished TEM observations), in that some parts of its coenecium are built of a fabric similar to the cortical fabric of graptolites. This fabric comprises long, unbranched fibrils with a translucent core (previously illustrated by Mierzejewski 1984b: pl. 16), loosely packed in layers and separated by sheets. In each layer the fibrils are arranged parallel or subparallel, while succesive layers are oriented at different angles. We conclude from all these observations that there is no evidence for an 'ultrastructural anomaly'.

The evolution of graptolite skeletal tissues is beyond the scope of this paper, but our work also sheds new light on this problem (addressed previously by, for example, Urbanek 1976c; Andres 1980; Crowther 1981; Rickards *et al.* 1982; Urbanek & Mierzejewski 1984; Urbanek 1986; Urbanek *et al.* 1992). Issues include the molecular evolution of collagen and its derivatives within the Pterobranchia and the Graptolithina, fibrillogenesis, corticization, and the origin of the outer lamella in graptolite fuselli. In our view it no longer justifiable to asign the orders of rhabdopleurid pterobranchs (Rhabdopleurida) and sessile graptolites (Camaroidea, Crustoidea, Dendroidea, Tuboidea) to two separate hemichordate classes (i.e. Pterobranchia and Graptolithina) respectively. We agree with Beklemishev (1951) that they should all be treated as members of a single class of the Graptolithoidea (see also Urbanek 1986, 1994). Finally, our investigations have created a new 'Problem Situation' for the debate on graptolite affinities, as defined by Urbanek (1986, 1987). Continuing Urbanek's historical sequence (PS 1–10), PS 11 may be called rejection of the concept of the 'ultrastructural anomaly'.

Conclusions

- The fine structure of fusellar tissue in Palaeozoic rhabdopleurid pterobranchs is distinct from that of Recent Pterobranchia; there are differences in shape, dimensions and arrangement of the fusellar fibrils. Recent *Rhabdopleura* and *Cephalodiscus* have their fusellar tissue made exclusively of thin (20–30 nm) needle-like fibrils loosely dispersed in matrix, whereas fibrils of fossil pterobranchs are of two categories: (1) fusellar fibrils proper, distinctly thicker (70–150 nm in diameter), often branched/ anastomosed, forming a solid three-dimensional spongy network; and sometimes; (2) *cortical fibrils*, thicker still (usually 150–200 nm in diameter), straight, unbranched and forming band-like constructions.
- There is no significant difference in the fusellar component of the skeleton of graptolites and fossil rhabdopleurid pterobranchs. Thus, contrary to Urbanek (1986, 1987), the so-called 'ultrastructural anomaly' is not diagnostic of the graptolite grade of rhabdosome construction because there is no such anomaly among Palaeozoic forms. The fusellar tissue of both groups is made predominantly of fusellar fibrils *sensu stricto* forming a spongy meshwork of anastomosing/branching fibrils, sometimes accompanied by ordered cortical fibrils.
- This heteromorphy of fibrous material (a three-dimensional network composed of anastomosing/branching fibrils, with fragments of fuselli built up of ordered fibrils)

is not unique to graptolites. Such features were presumably attained by the common ancestor of pterobranchs and graptolites.

*   There is no reason to regard pterobranchs and graptolites as two separate classes of the phylum Hemichordata. We share Beklemishev's (1951, 1970) opinion that they should be treated as members of one class – the Graptolithoidea.

Acknowledgements

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Graptolitowy typ ultrastruktury tkanki fuzellarnej paleozoicznych rabdopleuridów

PIOTR MIERZEJEWSKI i CYPRIAN KULICKI

Streszczenie

Przeprowadzono badania ultrastrukturalne perydemy trzech paleozoicznych pióroskrzelnych (Pterobranchia) z rzędu Rhabdopleurida: ordowickich *Kystodendron* ex gr. *longicarpus* (Eisenack) i *Rhabdopleurites primaevus* Kozłowski, oraz permskiego *Diplohydra* sp. Wykazano, że tkanka fuzellarna form ordowickich składa się z tego samego tworzywa co u graptolitów oraz wykazuje typowy dla nich dymorfizm fibrylarny i układ przestrzenny: tworzą ją stosunkowo cienkie, rozgałęziające się, powyginane włókna fuzellarne oraz grube, często równolegle ułożone włókna kortykalne. Włókien kortykalnych nie stwierdzono u *Diplohydra* sp., która zachowała jednak typowo graptolitowy charakter włókien fuzellarnych. Między włóknami wszystkich zbadanych form występują struktury określone jako płatki (*flakes*), powstałe wskutek cementacji kilkunastu lub więcej sąsiadujących ze sobą włókien. Materiał peridermalny zbudowany z płatków (*flaky material* – nowy termin) obserwowany był uprzednio u graptolitów. Stwierdzony w badanym materiale dymorfizm fibrylarny był dotąd uważany za właściwy jedynie graptolitom, podczas gdy tkanka fuzellarna pióroskrzelnych, zarówno kopalnych jak i współczesnych miała być zbudowana wyłącznie z cienkich, nierozgałęziających się włókien. Uzyskane wyniki potwierdzają trafność koncepcji Beklemiszewa (1951) o traktowaniu współczesnych i kopalnych pióroskrzelnych jako przedstawicieli gromady Graptolithoidea.