

Cortical fibrils and secondary deposits in periderm of the hemichordate *Rhabdopleura* (Graptolithoidea)

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Coenecia of extant hemichordates *Rhabdopleura compacta* and *Rh. normani* were investigated using SEM techniques. Cortical fibrils were detected in their fusellar tissue for the first time. The densely packed cortical fibrils form a characteristic band-like construction in fusellar collars, similar to some Ordovician rhabdopleurids. No traces of external secondary deposits are found in coenecia. Two types of internal secondary deposits in tubes are recognized: (1) membranous deposits, composed of numerous, tightly packed sheets, similar to the crustoid paracortex and pseudocortex; and (2) fibrillar deposits, devoid(?) of sheets and made of cortical fibrils, arranged in parallel and interpreted as equivalent to graptolite endocortex. There is no significant difference in either the shape or the dimensions of cortical fibrils found in *Rhabdopleura* and graptolites. The cortical fabric of both rhabdopleuran species studied is composed of long, straight and more or less wavy, unbranched fibrils arranged in parallel; their diameters vary from 220 to 570 μm . The study shows that there is no significant difference between extinct and extant Graptolithoidea (= Pterobranchia) in the histological and ultrastructural pattern of their primary and secondary deposits of the periderm. The nonfusellar periderm of the prosicula is pitted by many depressions similar to pits in the cortical tissue of graptolites.

Key words: *Rhabdopleura*, Pterobranchia, Hemichordata, periderm, sicula, ultrastructure, fibrils.

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Introduction

The colonial hemichordate *Rhabdopleura* Allman, 1869 is the only living member of the graptolite (*sensu* Beklemishev 1951, 1970) order Rhabdopleuroidea Beklemishev, 1951, and is sometimes referred to as one of the oldest “living fossils” because some doubtful remains attributed to this genus have been reported from the Middle Cambrian (Durman and Sennikov 1993). However, true *Rhabdopleura* is unknown before the Middle Jurassic (Kulicki 1969, 1971; see also Mierzejewski 1986 and Urbanek and Dilly 2000). According to Mierzejewski (1986), *Rhabdopleura* may be a descendant of the Palaeozoic genus *Kystodendron* Kozłowski, 1959. The taxonomy of *Rhabdopleura* remains confused and needs further investigations. At present, the genus comprises seven extant and six extinct species, but most taxa seem questionable and in need of reexamination (see Kulicki 1971; Dilly and Ryland 1985). *Rhabdopleura* is exceptionally valuable in the study of graptolite palaeobiology because it is most closely related to the presumed ancestor of graptolites (Schepotieff 1905, 1910; Kozłowski 1949, 1966; Urbanek 1986).

Until quite recently, it has been generally accepted that there were sharp differences between the skeletal tissues of rhabdopleurans and graptolites at the submicroscopic level (e.g., Urbanek 1976, 1986; Urbanek et al. 1980; Andres

1980; Crowther 1981; Urbanek and Mierzejewski 1984; Rickards and Dumican 1984). However, recent SEM investigations by Mierzejewski and Kulicki (2001) revealed that the fusellar tissue of both fossil rhabdopleurids and graptolites is composed predominantly of fusellar fibrils, forming a spongy meshwork, accompanied by ordered cortical fibrils. This discovery sheds new light on the evolution of graptolite skeletal tissues and conflicts with the observations and/or conclusions of some earlier authors (see Mierzejewski and Kulicki 2001 for references) who reported remarkable differences between the fibrous material of pterobranchs and graptolites. It also proves that there is no justification for separating graptolites from fossil rhabdopleurid pterobranchs on the basis of their fusellar tissue and consequently no reason to treat the Pterobranchia Lankester, 1877 and the Graptolithina Bronn, 1849 as two distinct classes within the phylum Hemichordata Bateson, 1885. Following Beklemishev (1951, 1970), we now unite them in a single class—the Graptolithoidea (Mierzejewski and Kulicki 2001, 2002; see also Urbanek 1986, 1994). However, in our research we have encountered the problem of ultrastructural differences between the periderm of fossil *Rhabdopleura* (and *Rhabdopleura*-like forms) and that of recent *Rhabdopleura*, examined by Dilly (1976) and Andres (1980). It seems especially surprising that we have observed distinct traces of cortical fibrils in both the

primary and secondary deposits of the Jurassic *Rhabdopleura kozłowskii* Kulicki, 1969, whereas the fusellar tissue of extant *Rh. compacta* lacks cortical fibrils (accordingly to older reports). Consequently, we focussed our studies on the supposed ultrastructural differences between the periderm of fossil and recent Rhabdopleuroidea. The primary aim of this paper is to reexamine previous authors' investigations into the peridermal fine structure of extant *Rhabdopleura*, and to clarify the alleged differences from graptolite periderm.

Material and methods

The three young colonies of *Rh. compacta* Hincks used in this study were collected alive by Dr. A.R.D. Stebbing in 1967 while dredging off Stoke Point (50°17' N, 04°03' W, depth 21–24 m), South Devon, England. He presented some of this material to Professor R. Kozłowski who, in turn, made them available to one of us (C.K.) for further investigations. The colonies were attached to the concave surfaces of disarticulated shells of the bivalve *Glycymeris glycymeris* (compare Stebbing 1968). For SEM study, they were etched intact from the shell with a weak solution of acetic acid. The specimens were frozen in a small amount of water and desiccated by sublimation using a vacuum dessicator in the presence of silica gel at 72 K. After mounting on aluminum stubs with double-sided adhesive tape, the specimens were coated with platinum and examined using a Philips SEM XL 20. Dimensional data were taken directly from the SEM (using the measurements option). For element composition, the EDAX (x-ray energy dispersive spectrometer) with a DX4i detector was used. A small fragment of the coenecium of *Rh. normani* Allman, 1869 from Bergen, Norway, from the late Professor R. Kozłowski's collection, was similarly investigated. A few specimens of *Rh. kozłowskii* Kulicki, 1969 from the Bathonian and Callovian of Poland were also studied, as comparative material. The SEM stubs have been deposited in the Institute of Palaeobiology of the Polish Academy of Sciences (ZPAL).

Because *Rhabdopleura* is interpreted herein as a member of the class Graptolithoidea, we adopt the standard terminology for graptolite peridermal ultrastructure employed by Urbanek and Towe (1974) and Urbanek and Mierzejewski (1984), with additional terms introduced by Mierzejewski and Kulicki (2001). Because the skeleton of the initial zooid (oozooid) of a *Rhabdopleura* colony is almost indistinguishable from that of extinct sessile graptolites (compare Kozłowski 1971; Dilly 1985a; Urbanek 1986), three graptolite terms are used as follows:

sicula—skeleton of the initial zooid of a colony, comprising the *prosicula* and *metasicula*; synonyms include “prosiculum” (Dilly 1985a, 1986) and “embryonal vesicle” (partim) (Urbanek 1979, 1986).

prosicula—proximal, subsphaerical part of the sicula, built up of nonfusellar periderm; synonyms include “vesicle”

(Kozłowski 1971), “settling vesicle” (Dilly 1986), “dome” (Dilly 1985a, 1986), “embryonal or embryonic vesicle” (Dilly 1986; Urbanek 1986).

metasicula—distal, tubular part of the sicula, made of fusellar periderm; synonyms include: “repent tube + erect tube” (Stebbing 1970b), “horizontal tube + erect tube” (Dilly 1985), “prosicular tube” (Dilly 1986), “primary repent tube” (Urbanek 1986).

Current knowledge of the rhabdopleurid secondary deposits

The key to understanding the evolution of graptolite skeletal tissues centres undoubtedly around the problem of rhabdopleurid and cephalodiscid secondary tissues, deposited on the primary fusellar wall (see Urbanek 1986 for discussion and references). Urbanek and Mierzejewski (1984: 76) defined “secondary deposits” as follows: “Any skeletal material laid on the primary thecal wall, independently of its position and structure, and resulting in a thickening of the periderm”. Graptolite secondary deposits almost exclusively take the form of a cortex or cortical layer (for the definition of cortex, and a classification of cortex based on topographical criteria, structural features and mode of formation, see Urbanek and Mierzejewski 1984). In the long phylogenetic debate on the affinities of graptolites (reviewed by Urbanek 1986), the alleged lack of secondary deposits and a cortical layer in *Rhabdopleura* was for decades a firmly established idea of great significance. Kozłowski (1966: 497) wrote: “...the tubarium of the Rhabdopleuroidea are built only of fusellar tissue and are not covered on the outside with any accessory layers” (see also Kozłowski 1949; Bulman 1955, 1970).

Investigation of rhabdopleurid secondary deposits began with the work of Kulicki (1971), who was the first to recognize under a light microscope a secondary layer which lined internally the ascending parts of zooidal tubes in *Rh. kozłowskii* Kulicki, 1969 (from the Jurassic of Poland; Figs. 1A–C, 8). These deposits took the form of one or two-layered, longitudinally striated tubes, visible only under high magnification (Fig. 1A–C). Kulicki noted that both the presence and the thickness of secondary deposits depended on the length and diameter of the tubes and on environmental conditions; he concluded that this skeletal structure played a reinforcing role (see Dilly 1976). Later, very similar deposits were observed by Mierzejewski (1977) in Lower Ordovician rhabdopleurid zooidal tubes (Fig. 1D); these had previously been misinterpreted by Skevington (1965) as ?graptovermid remains (see also Andres 1977; Mierzejewski 1986). Under TEM examination, the secondary deposits of fossil and Recent rhabdopleurids appeared to be an accumulation of sheets and intersheet material devoid of cortical fibrils (Andres 1980; Dilly 1976, 1985a, b; Mierzejewski 1986; and Urbanek's 1976 micrographs reinterpreted by Mierzejewski and

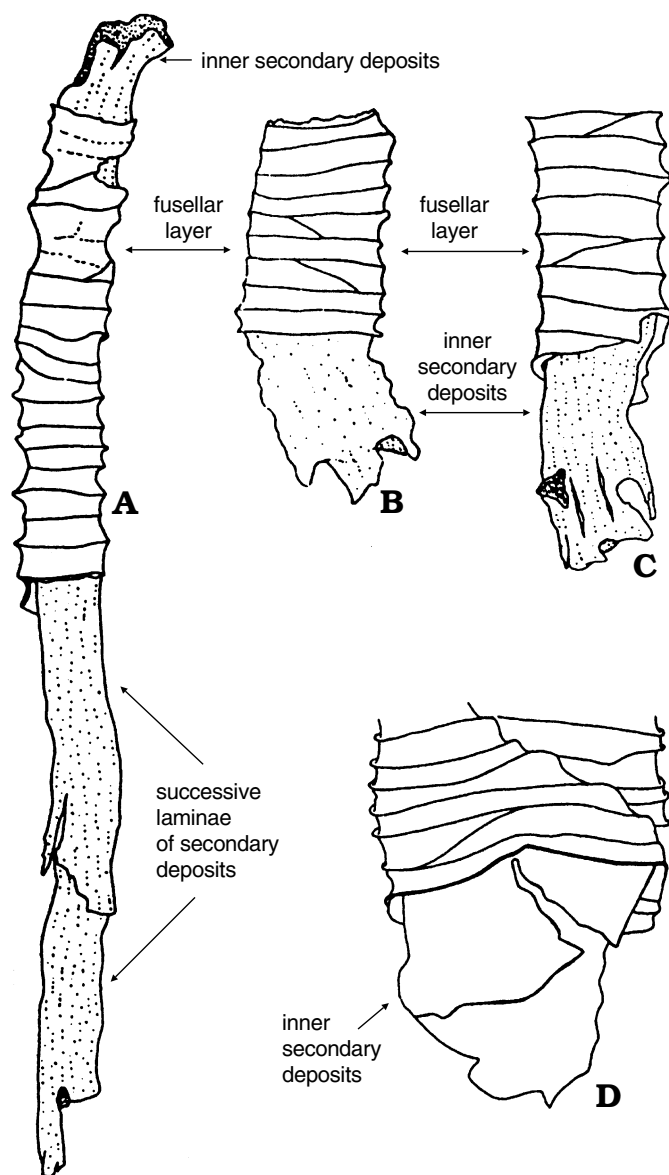


Fig. 1. Inner secondary deposits in zooidal tubes of fossil Rhabdopleuroidea. A–C. *Rhabdopleura kozlowskii* Kulicki, 1969; Bathonian and Callovian of Poland. After Kulicki 1971, modified; A, ZPAL Pb.II/8; B, ZPAL Pb.II/9; C, ZPAL Pb.II/10. D. *Rhabdopleurites primaevus* Kozłowski, 1967; Lower Ordovician of Öland, Sweden. After Skevington 1965, modified.

Kulicki 2001). According to Dilly (1985a: 173) these structures “are reminiscent of the cortical bandages of graptolites and may support a close affinity between *Rhabdopleura* and graptolites”. He stressed that the bandages in *Rhabdopleura* are not as abundant as they are in graptolites. Recently, Mierzejewski and Kulicki (2001) reported the presence of bunches of cortical fibrils on the surface of dormant bud capsules of the Callovian *Rh. kozlowskii*. Undoubtedly these structures may be identified as the remains of inner secondary deposits. It should be stressed that these bunches exhibit a striking similarity to cortical bandages (secondary deposits) of extinct graptolites.

Apart from the above claims, there has been so far only Dilly’s (1976) observations of presumed secondary deposits on the outer surface of *Rh. compacta* tubes. He noted that many striations on the periderm run vertically and he compared them to the cortical fibrils of graptolites (Dilly 1976). He thought that some vertical fibrils were restricted to a single fusellar ring, whereas others ran across several fuselli. Urbanek et al. (1980: 206) considered these fibrils to be “entirely unconvincing as equivalents of bandages, and their origin may be rather ascribed to the lophophore than to the cephalic disc”. Even the primary nature of these structures was called into question by Andres (1980), who interpreted Dilly’s vertical fibrils as “shrinkage wrinkles”, caused by drying out (see also below p. 106).

SEM observations

Rhabdopleura compacta Hincks, 1880

Figs. 2–6.

Morphologically, the coenecia of the young colonies under investigation fit the descriptions by Stebbing (1970a, b) and Dilly (1986). They are about 0.8–2.9 mm in diameter and form irregular, compact and encrusting mats of adhering repent tubes, from which arise 2, 3, or up to 10 erect tubes (Fig. 2). A frayed marginal membrane runs around the periphery of the attached part of each coenecium. The coenecium is composed of a sicula, constructed by the primary zooid (oozooid), and a series of daughter tubes (i.e., equivalent to the thecae of other graptolites), made by blastozooids. There is no indication of the so-called “embryonal ring”, recognized only by Schepotieff (1907) and Dilly (1985b) in *Rh. normani*. The coenecia are all devoid of dormant buds and their capsules. Under the light microscope almost all elements of the coenecia are nearly colourless and transparent or semitransparent; only the siculae and the oldest parts of creeping tubes are slightly brownish and rather opaque.

The sicula is easily identifiable in the central regions of the two smaller colonies (Figs. 2A–C, 3A). The sicula’s general appearance resembles those described by Stebbing (1970b), Dilly (1985a, 1986) and Dilly in Urbanek (1986: fig. 4B). The prosicula is a subspherical vesicle, with a large, flat attachment surface and a convex upper surface. Unfortunately, only the upper surface is easily visible because its lateral slopes are tightly overgrown and surrounded by younger elements of the coenecium. The upper surface of the prosicula is covered with abundant foreign material of an unknown (algal? inorganic?) nature, apparently incorporated partially into its structure (Fig. 3). However, this enigmatic material does not completely mask the primary details of the dome. Its upper surface is covered by many small sub-circular, polygonal, and irregular depressions or pits (Fig. 3A, B) which are distributed in a chaotic and uneven way. We have distinguished two types of these structures, based on their morphology and dimensions:

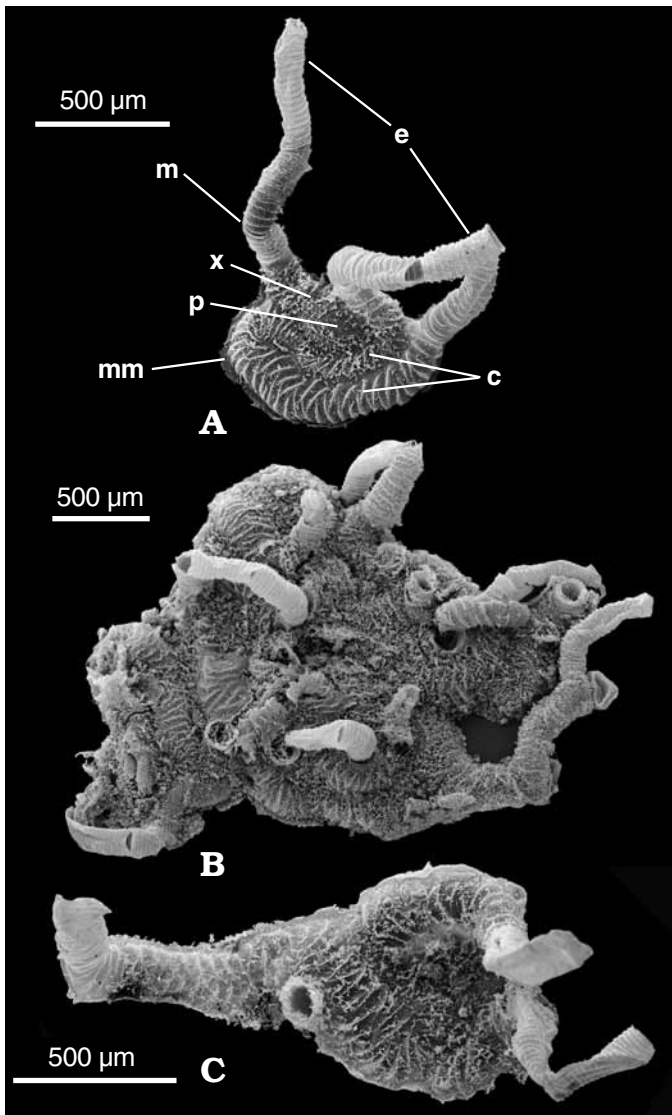


Fig. 2. *Rhabdopleura compacta* Hincks, 1888, Recent. SEM micrographs of complete coenecia. A. Young coenecium composed of a sicula and two zooids (ZPAL Pb.5/1). B. Adult coenecium consisting of a sicula and a dozen or so zooids (ZPAL Pb.5/2). C. Young coenecium built of a sicula and three zooids (ZPAL Pb.5/3). Abbreviations: c, creeping tube; e, erect tube; m, metasicula; mm, marginal membrane; p, prosicula; x, boundary between prosicula and metasicula.

(1) Large pits (Fig. 3B–F), corresponding to those described first by Dilly (1985a, see also 1986). They are surrounded by prominent rings made of curved fibril-like elements. In general, they are about 3.2–8.6 μm in diameter, and the thickness of the fibril-like elements is ca. 0.35 μm . They are often tightly grouped into clusters. The bottom of each large pit is covered with several (usually 4–13) of the tiny pits, irregularly distributed, described next.

(2) Tiny pits (Fig. 3C–G), described herein for the first time. They are usually 0.54–1.27 μm in diameter, with a rather indistinct margin, and are built of a homogenous material identical to the prosicular wall. These tiny pits are irregu-

larly scattered both between and within the large pits; some appear to coalesce.

The metasicular part of the sicula (which is inhabited by the primary zooid after its metamorphosis) is sharply distinguished from the prosicula not only by its fusellar structure but also by a lack of pits (Fig. 3A, B). Both metasiculae closely resemble the material described by Stebbing (1970) and Dilly (1986).

The bulk of each coenecium is made of a mass of repent and erect tubes (Fig. 2); their width is approximately 0.12–0.15 mm and 0.16–0.25 mm, respectively. The fuselli of creeping tubes are typically built of half segments, deposited alternately to left and right, which form a characteristic and very distinct median zigzag suture (Figs. 2, 4A). The transition from creeping to erect tube is marked by a discontinuity in the fusellar structure. All erect tubes are made of complete fusellar rings, with each being intersected by a single oblique suture, irregularly placed (Figs. 1, 5A, D). This suture marks the beginning and end of a fusellus. As a rule, the upper part of a fusellus takes the form of a collar (*sensu* Kulicki 1969) which is very characteristic of rhabdopleurid fusellar tubes (Fig. 5). Fusellar heights varies within 45–55 μm in creeping tubes, and 26–37 μm in erect tubes. Unlike Dilly and Ryland (1985), we failed to find any non-fusellar sections of tubes to match the nonfusellar periderm of fossil rhabdopleurids discussed by Mierzejewski (1986).

In general, the outer surfaces of coenecia are not smooth. Even under low magnification, various irregular, plate-like or often filamentous structures cover the surface (Figs. 2–5). We interpret this debris as foreign to the rhabdopleuran skeletal tissue, probably representing the remains of dense agglutinations of minute organic and inorganic particles (see Dilly 1975). The nature of these particles remains obscure, but they may equate with material known in some cephalodiscid skeletons, i.e. various epibionts, diatoms, sponge spicules, minute fragments of shells, and grains of sand (see Andersson 1907; Urbanek et al. 1980; Crowther 1981). Some plate-like particles on the outer surface of the coenecium produced on x-ray energy dispersive spectrum typical of layered silicates. Occasionally, where this foreign material has been removed mechanically from the primary outer surface of the periderm (Fig. 5A), the surface appears smooth, with little relief at low magnification. There is no evidence for any secondary deposits on the primary fusellar layer similar to graptolite ectocortex or to the isolated thick fibres described by Dilly (1975). However, some fusellar surfaces are more or less distinctly wrinkled forming a longitudinal undulation. The outer surface of each fusellus is a robust sheet fabric which usually hides the underlying fibril orientation. However, in some places at high magnification, fine parallel lineations cover the periderm and may indicate underlying fibrous material. In contrast, sheet fabric on the margins of collars displays distinct parallel lineations which unquestionably reflect more or less straight fibrils (Figs. 4A, 5B, C). We conclude that fusellar collars are built of closely packed fibrils, arranged

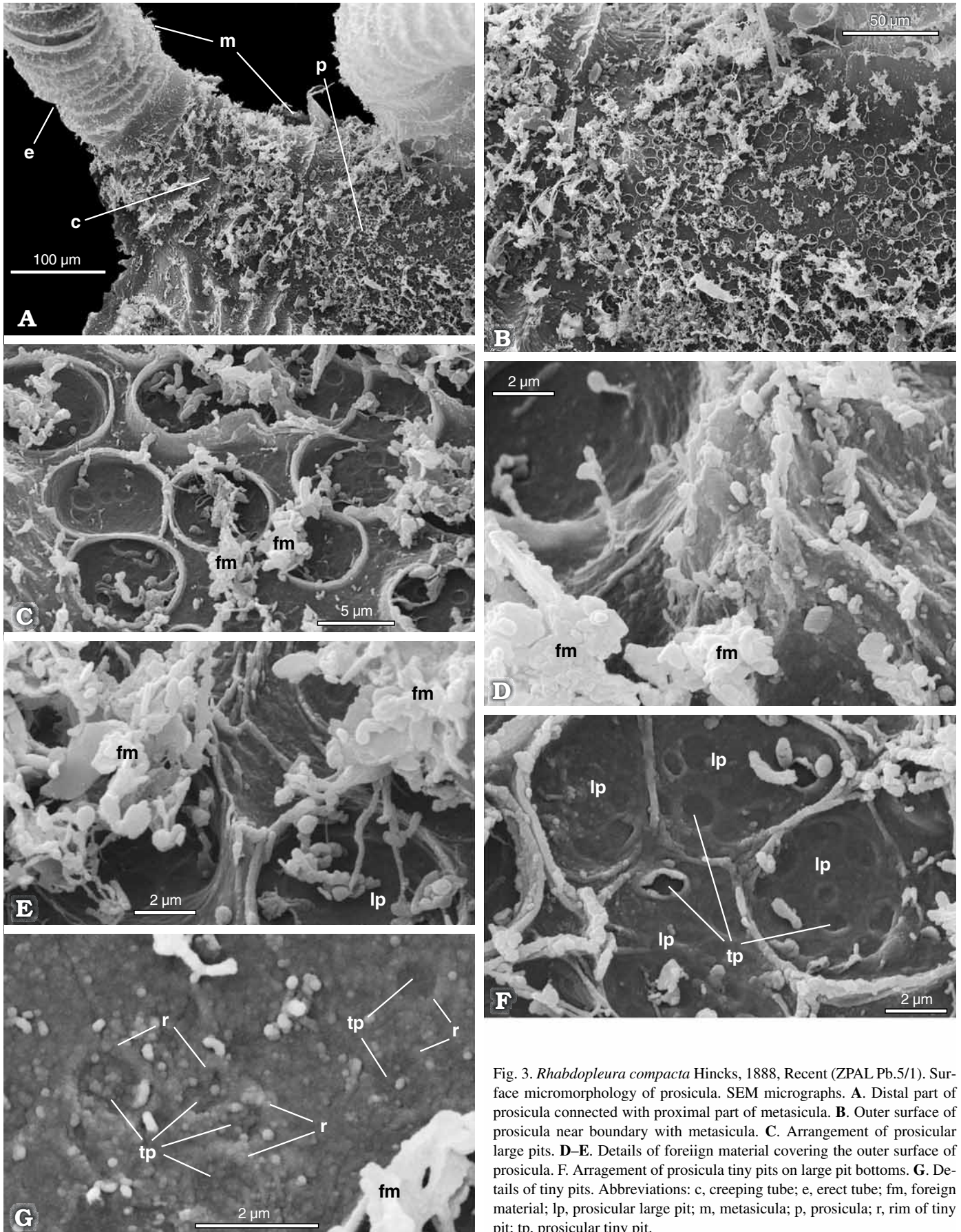


Fig. 3. *Rhabdopleura compacta* Hincks, 1888, Recent (ZPAL Pb.5/1). Surface micromorphology of prosicula. SEM micrographs. **A**. Distal part of prosicula connected with proximal part of metasicula. **B**. Outer surface of prosicula near boundary with metasicula. **C**. Arrangement of prosicular large pits. **D–E**. Details of foreign material covering the outer surface of prosicula. **F**. Arrangement of prosicula tiny pits on large pit bottoms. **G**. Details of tiny pits. Abbreviations: c, creeping tube; e, erect tube; fm, foreign material; lp, prosicular large pit; m, metasicula; p, prosicula; r, rim of tiny pit; tp, prosicular tiny pit.

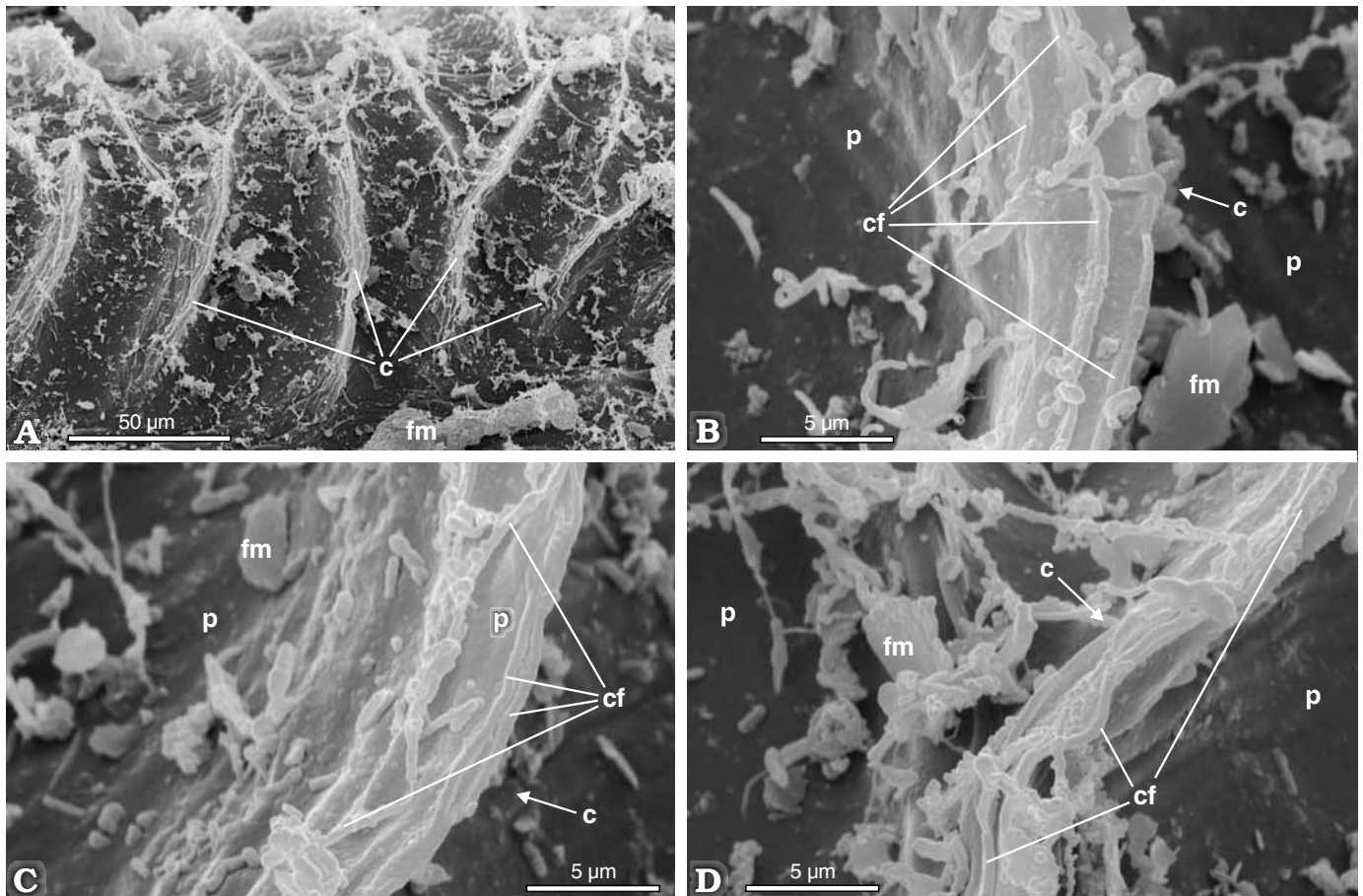


Fig. 4. *Rhabdopleura compacta* Hincks, 1880, Recent (ZPAL Pb.5/1). SEM micrographs. Micromorphology of outer surface of creeping tubes. **A.** Fragment of creeping tube with prominent zig-zag suture. **B–D.** Cortical fibrils in fusellar collars. Abbreviations: c, fusellar collar; cf, cortical fibril; fm, foreign material; p, fusellar pellicle.

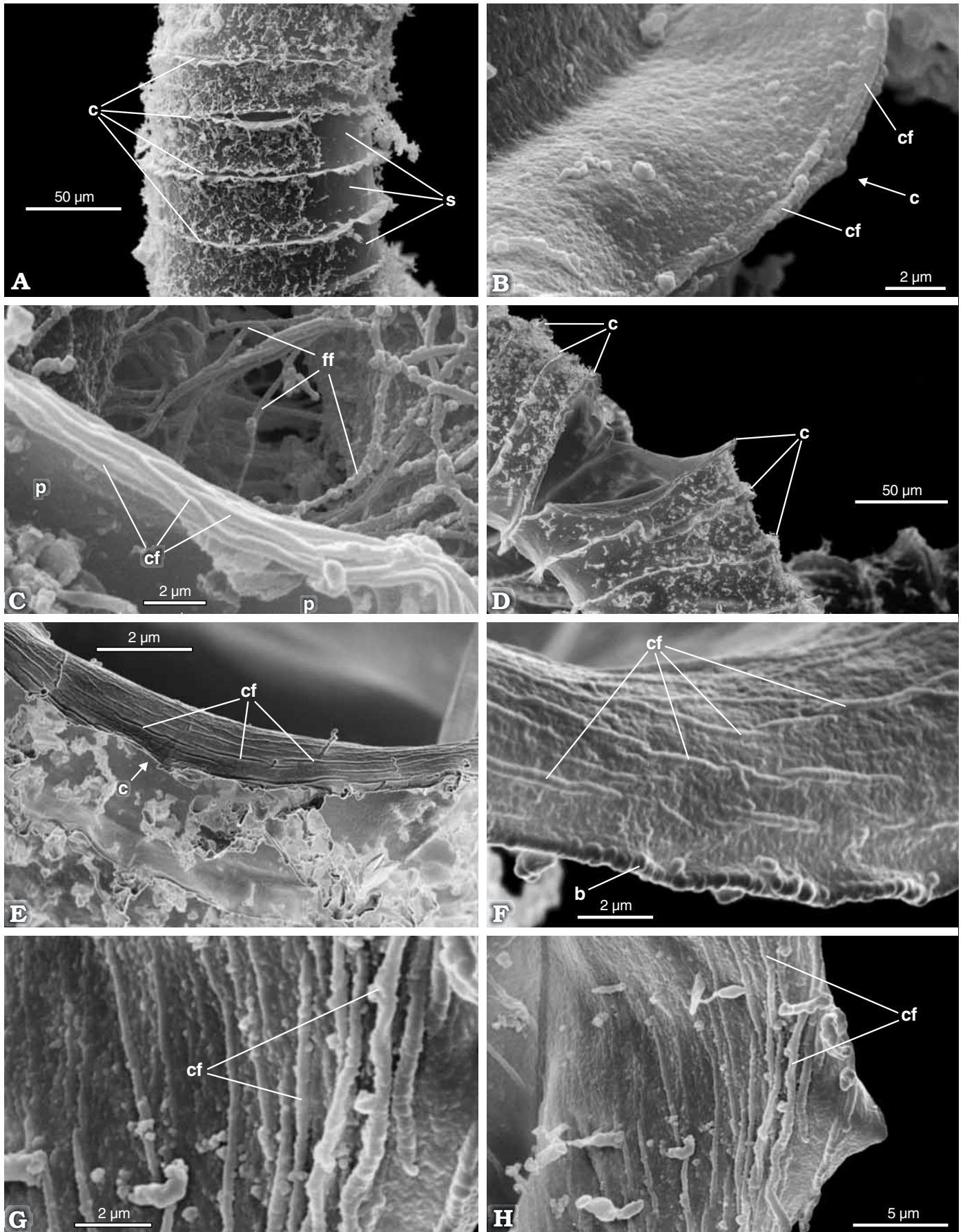
uniformly and parallel to their margins. Sometimes, more or less distinct traces of periodicity can be observed along a single fibril.

A dimorphic arrangement of the fibrillar material becomes clear where the periderm has been mechanically damaged (Fig. 5C–H), i.e. fusellar fibrils proper and cortical fibrils (Fig. 5C). Fusellar fibrils predominate in fusellar tissue; they are more or less wavy, produce a chaotic three-dimensional meshwork, and vary widely in diameter, from as little as 40 nm to nearly 300 nm. Strikingly, in some areas structures similar to the mingling of fusellar fibrils with flaky material described by Mierzejewski and Kulicki (2001: fig. 4) from the Ordovician *Kystodendron* Kozłowski, 1959 and *Rhabdopleurites* Kozłowski, 1967, were observed. Cortical fibrils are distinctly thicker, with a diameter of 150–520 nm. They are the basic component of the fusellar collars, with their characteristically solid, band-like construction, similar to those of Ordovician rhabdopleurids. The shape of these fibrils is rather unstable; they can be almost straight or slightly bent, smooth or annulated. The annulated fibrils display a distinctly variable periodicity. Morphological details of the cortical fibrils are best seen in the fissure between two adjacent fuselli (Fig. 5E–H).

The inner surfaces of erect and creeping tubes are rather smooth, with only a small amount of foreign material. Sometimes, however, there are some areas of these surfaces covered distinctly with layers of secondary deposits. We have been able to recognize two different types of these deposits: (1) membranous inner secondary deposits, and (2) fibrillar inner secondary deposits.

Deposits of the first type, known since Kulicki's (1971) and Andres' (1980) light EM and TEM investigations, appear distinctly laminated (Fig. 6B). They are constructed of distinct and numerous (up to 10 or more) tightly packed membranes or sheets. No traces of any substructure have

Fig. 5. *Rhabdopleura compacta* Hincks, 1880, Recent (ZPAL Pb.5/1). SEM micrographs. Micromorphology of outer surface of erect tubes. **A.** Section of an erect tube densely covered with foreign material. **B.** Detail of fusellar collar provided with weak band-like construction. **C.** Detail of strong band-like construction and a comparison of cortical and fusellar fibrils. **D.** Section of erect tube with disconnected fuselli; **E–F.** Upper surface of fusellar collar. **G–H.** Ordered cortical fibrils on upper surface of disconnected fusellar collar, presumably made of thickly beaded cortical fibril; c, fusellar collar; cf, cortical fibril; ff, fusellar fibrils; m, foreign material; p, fusellar pellicle; s, primary smooth outer surface of fuselli.



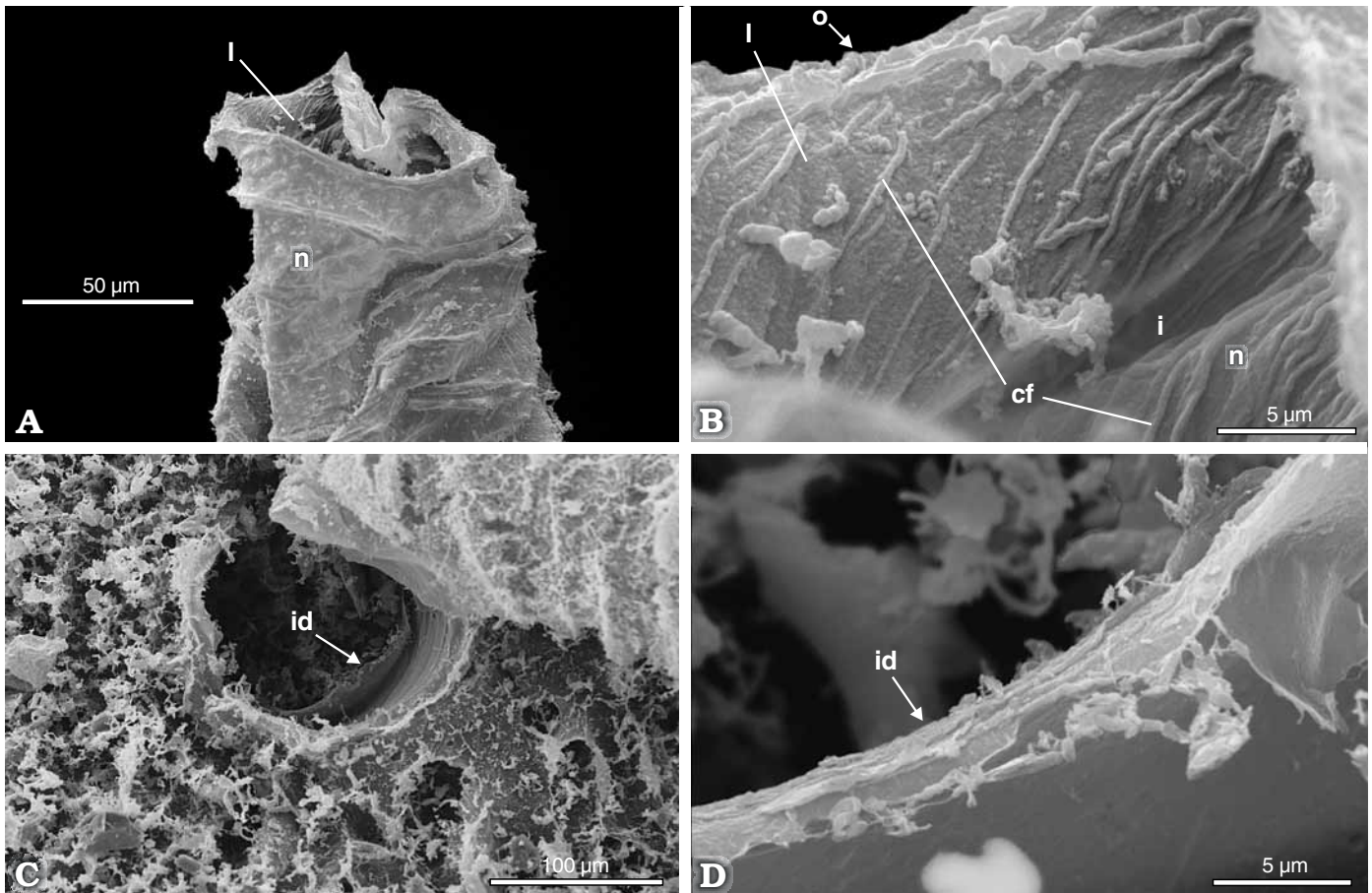


Fig. 6. *Rhabdopleura compacta* Hincks, 1880, Recent (ZPAL Pb.5/3). SEM micrographs. Secondary inner deposits in erect tubes. **A.** Growing end of an erect tube with inner cortical deposits. **B.** Detail of Fig. 5A showing an arrangement of cortical fibrils. **C.** Broken erect tube near its base showing membranous inner deposits. **D.** Multilayered structure of inner membranous deposits. Abbreviations: cf, cortical fibril; i, interfusellar suture; id, inner deposit; l, last fusellus; n, next to the last fusellus; o, outer edge of an erect tube.

been recognized within these sheets. The intersheet material, if present, is completely devoid of any discernible fibrous material. The membranous inner secondary deposits were found only in the basal i.e. oldest part of erect tube, near the horizontal creeping tube.

Fibrillar inner secondary deposits, described herein for the first time (Fig. 6C, D), take the form of a thin layer, only one fibril thick. Fibril diameter is generally 260–570 nm and they can be identified as cortical fibrils. They are rather loosely distributed, straight and arranged more or less in parallel. There is little evidence that a membrane-like structure ever covered these fibrils.

Rhabdopleura normani Allman, 1869

Fig. 7.

The specimen studied is a small fragment of coenecium consisting of a branching creeping tube joined to an erect tube (Fig. 7A). Its periderm is composed of typical fusellar components, with a very distinct zig-zag suture in the creeping tube, and the classical ring-like segments with irregularly distributed oblique sutures in the erect tube; the shape and arrangement of fuselli are very similar to those of *Rhabdo-*

pleura compacta. The height of the fuselli varies according to their position in the coenecium: 32–55 µm for the creeping tube, 15–45 µm for the erect tube. Fusellar collars of the creeping tube are distinctly less prominent than in *Rh. compacta* (Fig. 7D). On the other hand, collars of the erect tube are rather large, with an indistinct band-like structure composed of cortical fibrils (Fig. 7G). These cortical fibrils are quite clear with a diameter of 270–510 nm. The condition of the coenecium's surface varies; large areas of periderm are covered with foreign material, but some parts are rather smooth and reveal details of fine structure. There is no evidence for secondary deposits on either the outer or inner surfaces. Some areas lack the fusellar pellicle, altogether and reveal the presence of extremely densely packed fusellar fibrils (Fig. 5E). The fusellar fibrils seem to be rather short, wavy, and anastomosing with a diameter of 70–105 nm. Broken edges of periderm reveal further details. As in extinct graptolites, the bulk of the fibrils is concentrated just beneath the inner and outer surfaces of fuselli (Fig. 7E). Occasionally, the outer fusellar surface appears to be longitudinally striated (Fig. 7F), but this sculpture is nothing more than wrinkling of the periderm.

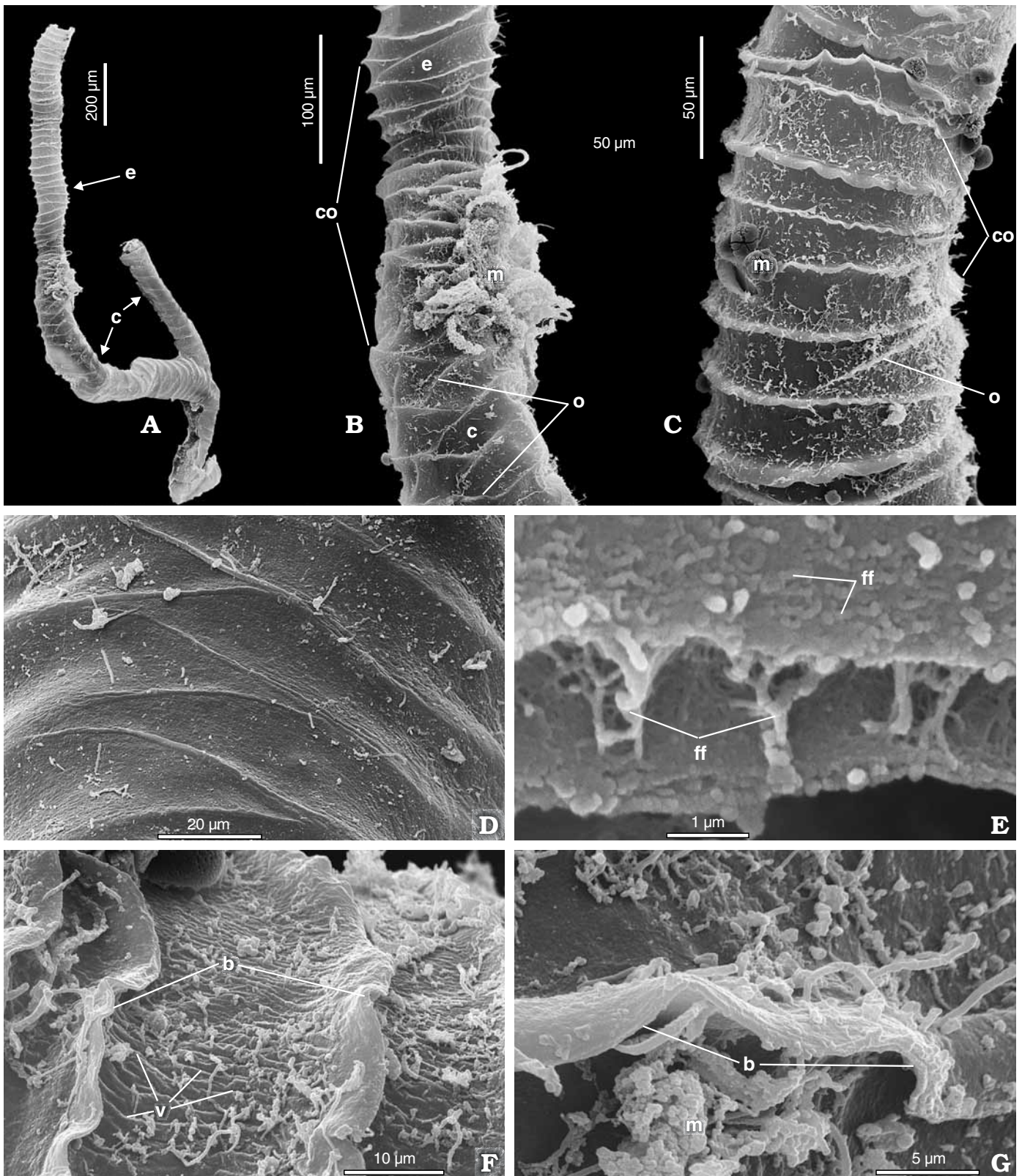


Fig. 7. *Rhabdopleura normani* Allman, 1869, Recent (ZPAL Pb.5/4). SEM micrographs. **A.** Fragment of coenecium composed of an erect tube connected with a branched creeping tube. **B.** Connection of creeping tube with erect tube. **C.** Erect tube. **D.** Outer surface of creeping tube devoid of pellicle. **E.** Details of broken periderm showing arrangement of fusellar fibrils. **F.** Short vertical fibrils on periderm of erect tube. **G.** Periderm of the same erect tube devoid of vertical wrinkles. Abbreviations: b, band-like structure composed of cortical fibrils; c, creeping tube; co, fusellar collar; e, erect tube; ff, fusellar fibrils; m, foreign material; o, oblique suture; v, wrinkle.

Discussion

The discovery of cortical fibrils in the coenecium of *Rh. compacta* and *Rh. normani* is particularly significant. Until recently, such fibrils were completely unknown in the skeletal tissues of Recent Rhabdopleuroidea, although Mierzejewski and Kulicki (2001) have reported their presence in the fusellar tissue of Ordovician *Kystodendron* ex gr. *longicarpus* (Eisenack, 1937) and *Rhabdopleurites primaevus* Kozłowski, 1967, and some very distinct traces in the Jurassic *Rhabdopleura kozłowskii* Kulicki, 1969. These observations suggest that there is no significant difference between the fusellar component of graptolites (in the conventional sense) and fossil rhabdopleurids, because the fusellar tissue of both groups is made of fusellar fibrils *sensu stricto* arranged in a spongy meshwork, accompanied by ordered cortical fibrils. The discovery of cortical fibrils in fossil representatives of the Rhabdopleuroidea sheds new light on the problem of the evolution of graptolite skeletal tissues and contradicts the opinions of some earlier authors (e.g., Urbanek 1976, 1986; Andres 1980; Urbanek and Mierzejewski 1984; Dilly 1986). We have previously claimed a striking difference between the fine structure of fusellar tissue in fossil and Recent rhabdopleurids, involving the shape, dimensions and arrangement of fibrils (Mierzejewski and Kulicki 2001). An alleged lack of cortical fibrils in Recent *Rhabdopleura* was based upon Dilly's (1971) and, to some degree, Andres' (1980) TEM investigations. According to Dilly (1971), the periderm of *Rh. compacta* is built of three types of fibrils, loosely dispersed in an almost structureless matrix. These fibrils are very thin, only about 4–30 nm in diameter, and from just a few nanometers to over 5 μm long—and thus completely dissimilar to cortical fibrils. Two of Dilly's (1971) fibrils, exhibited internal, helical, electron-dense lines surrounded by a sheath of keratin-like, less electron-dense material, while the nature of the third structureless fibril type was obscure (compare Bairati 1972; Armstrong et al. 1984; and Urbanek 1986 for chemical composition of rhabdopleuran fibrils). Now, the SEM observations reported herein have caused us to reverse our previous opinion and to conclude that there are no ultrastructural differences between skeletal tissues of fossil and Recent Rhabdopleuroidea: both have fusellar tissue built mainly of loosely dispersed fusellar fibrils proper but with the addition of cortical fibrils arranged in parallel in fusellar collars. There are no essential differences in shape, dimensions, arrangement and distribution between the cortical fibrils in the coenecia of extinct and extant rhabdopleurids. Such fibrils are always long, almost straight or slightly bent, circular or oval in cross section, sometimes with a more or less regular periodicity (annulated or beaded fibrils). Strikingly, the cortical fibrils observed in the Rhabdopleuroidea have the same dimensions and appearance as their equivalents in other orders of the Graptolithoidea (for details of graptolite cortical fibrils see: Towe and Urbanek 1972; Urbanek and Towe 1974, 1975; Crowther and Rickards

1977; Crowther 1981; Rickards and Dumican 1984) and graptolite-like Palaeozoic forms of uncertain position (Mierzejewski 1984; Mierzejewski and Urbanek unpublished). The diameter of cortical fibrils in graptolite tissues varies within wide limits, from as little as 100 nm (Urbanek and Towe 1974; Crowther 1981) to 700–900 nm (Chapman and Rickards 1982; Bates 1997), or even 1 μm (Denis Bates personal communication 2001; Mierzejewski and Kulicki unpublished). Thus, it is consistent with rhabdopleurid fibrils measuring 220–570 nm in Recent *Rhabdopleura* (herein) and 200–290 nm in Ordovician forms (Mierzejewski and Kulicki 2001). Moreover, it is noteworthy that fusellar fibrils in *Rh. normani* are of the same diameter as these of extinct graptolites, i.e. 70–105 nm and 60–110, respectively.

Our new SEM observations also supply important data concerning the presence and nature of the secondary deposits in Recent *Rhabdopleura*. It is of considerable interest that two types of these skeletal elements, differing distinctly in their fine structure, may be distinguished. Both the membranous deposits (made of several sheets with ill-defined intersheet material) and the fibrillar deposits (made of a thin layer of the cortical fibrils running parallel to the surface of the fusellar layer) have their exact equivalents in the periderm of extinct Graptolithoidea. The membranous deposits are strikingly similar to the paracortex and the pseudocortex of crustoid graptolites, while the fibrillar deposits resemble eucortex (for details and explanation of these terms, see Urbanek and Mierzejewski 1984). The fibrillar deposits in *Rh. compacta* are strikingly similar in their structure to the endocortical bandages of *Monograptus communis communis* Lapworth, 1876 and *Cyrtograptus* sp. described by Crowther (1981) (see also Bates 1987), i.e., they are usually only one fibril thick and lack sheet fabrics. Additionally, our preliminary SEM investigations of Jurassic *Rh. kozłowskii* suggest that its inner secondary deposits were made of densely crowded and matted fibrils similar to fusellar fibrils proper (compare Figs. 7E and 8B). Taking into consideration all previous reports, especially those of Dilly (1971, 1976) and Andres (1980), as well as our present results, we conclude that the zooids of *Rhabdopleura* can secrete inner secondary deposits, although only under certain circumstances.

We have found no evidence of outer secondary deposits. We agree with Andres' (1980) opinion that the alleged vertical fibrils on the outer surface of rhabdopleuran zooidal tubes are nothing but wrinkles, due to shrinkage. Similar wrinkles are present in our material. It appears that *Rhabdopleura* zooids can only secrete secondary material on to the inside of fusellar tubes.

It is of great significance for our understanding of how graptolite tissue evolved that cortical fibrils can occur in both the primary and the secondary deposits of rhabdopleuran periderm, just as in fossil graptolites. There is also now no doubt that the parallel alignment of cortical fibrils is not a unique character of graptolites, as has been claimed (see e.g.: Urbanek 1976, 1986; Crowther 1981; Mierzejewski 1984). Although these fibrils are not as abundant in *Rhabdopleura* as

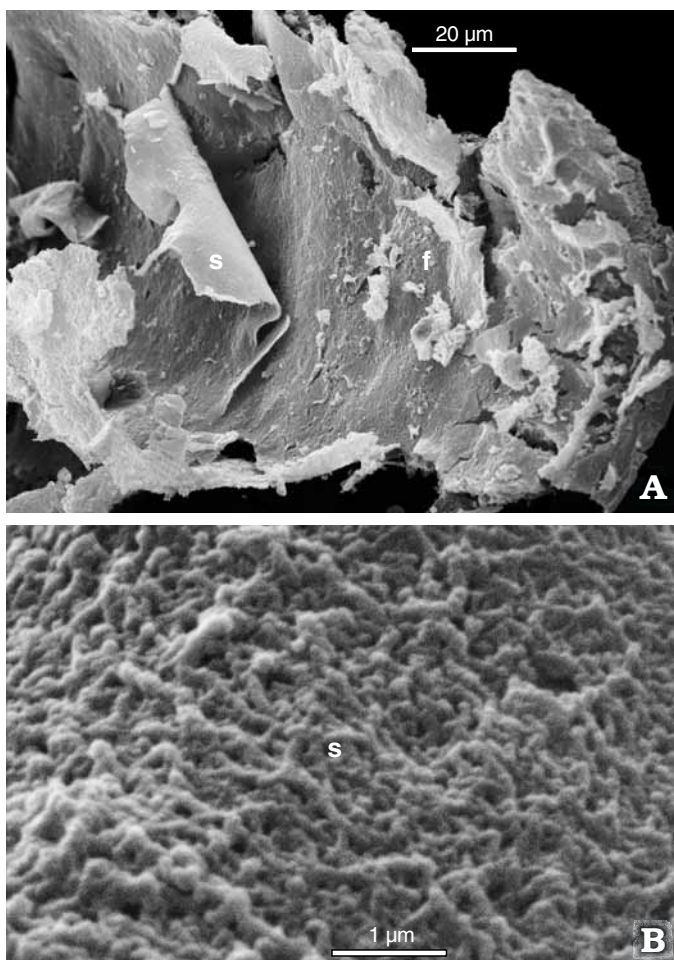


Fig. 8. *Rhabdopleura kozłowskii* Kulicki, 1969; Callovian of Poland (ZPAL Pb.5/5). SEM micrographs. A. Fragment of erect tube with inner deposits. B. Fibrillar nature of the inner deposit material. C. Pits in the fusellar tissue. Abbreviations: f, fusellar layer; s, secondary inner deposits.

they are in graptolite periderm, they do form incipient or rudimentary equivalents of the outer lamella and cortical deposits in graptolites. We therefore conclude that there are no significant differences between the fine structure of the periderm in extant *Rhabdopleura* and in extinct graptolites. This supports the view that there is no reason to regard pterobranchs and graptolites as two separate classes of the phylum Hemichordata. With Beklemishev (1951, 1970), we are of the opinion that they should be treated as members of one class, namely Graptolithoidea sensu Beklemishev (Mierzejewski and Kulicki 2001; see also Urbanek 1986: 222). Independently, Kinman (1994) proposed to treat pterobranchs and graptolites as representatives of his new class Pterobranchia. It follows that *Rhabdopleura* is not only a “living fossil” but also a living graptolite (for the similar case of *Cephalodiscus* M’Intosh see: Dilly 1993; Rigby 1993; Urbanek 1994).

The surface micromorphology of the rhabdopleuran prosicula is difficult to explain. The origin and significance of the large and tiny pits is still obscure. Some speculations were offered by Dilly (1985a) who excluded the possibility

that they serve as a channel for metabolite transport, since they only penetrate a short distance. He concluded that they are the traces of microorganisms which became stuck to the outer surface of the prosicular periderm and were then partially incorporated into the coenecium. However, it is interesting to note that the distribution of pits is restricted to the outer surface of the prosicula. Strikingly, no traces of similar surface structures were found on the metascula or any other elements of the coenecium, even if the outer layer of the rhabdopleuran periderm shows traces of destructive influences of external environment and is frequently covered with foreign organic and inorganic material (comp. Dilly 1971, 1986). These observations suggest that the pits are not secondary and foreign to the prosicular periderm. In this situation it would be interesting to search for similar structures in skeletons of other graptolite hemichordates. However, there is no evidence for any pit-like structures on the skeletal material of three Recent species of the genus *Cephalodiscus*, as studied by Urbanek, Dilly and Mierzejewski (*unpublished*). On the other hand, very similar pits were previously recognized in fossil hemichordates, i.e. in the Jurassic *Rhabdopleura kozłowskii* Kulicki, 1969 (Fig. 8C) and in graptolites (Crowther and Rickards 1977, Urbanek et al. 1980; Crowther 1981; see also Urbanek and Mierzejewski 1984 for discussion). Strikingly, just as in *Rhabdopleura* two basic types of pits may be distinguished in graptolites, i.e. (a) large pits (1–2 µm in diameter) delineated by well-defined and ill-defined rims, and (b) tiny pits (ca. 0.05 µm in diameter). According to Crowther and Rickards (1977), these pits are nothing more than the intrasheet vesicles of Urbanek and Towe (1974). The nature of these intrasheet vesicles is enigmatic, but they may equate to the rhabdopleuran “vesicular inclusions” mentioned by Dilly (1985). It should be stressed that the presence of numerous intrasheet vesicles is an important feature of the graptoloid graptolite prosicula, as was recognized by Urbanek and Towe (1975) and most likely observed by Rickards et al. (1971). It is generally accepted (e.g., Kozłowski 1971; Urbanek 1979, 1986; Dilly 1985a) that the sicula of *Rhabdopleura* is almost indistinguishable from those of encrusting graptolites. Paradoxically, the prosicula of the only encrusting graptolite studied in detail, the tuboid *Kozłowskitubus erraticus* (Kozłowski, 1963), lacks any trace of pits or intrasheet vesicles (Urbanek 1979). This striking resemblance between rhabdopleuran prosicular pits and graptolite pits, and what it might mean in terms of their origin and significance, cannot be properly evaluated until more is known about their fine structure. We regard the prosicular pits as primary anatomical features.

Conclusions

- The fibrillar material of fusellar tissue in Recent *Rhabdopleura* exhibits a distinct dimorphism, comprising: (1) thinner, anastomosing/branching fusellar fibrils proper, condensed or loosely dispersed in a matrix and forming a

three-dimensional spongy network; and (2) thicker, long, unbranched, closely packed, parallel cortical fibrils, forming band-like constructions. There is no difference between the fusellar component of skeletal tissues in either Recent or fossil members of the Rhabdopleuroidea.

- Zooids of *Rhabdopleura* can secrete material only on to the inner surface of their coenecium, to form inner secondary deposits. There is no evidence for the presence of outer secondary deposits.
- There are two types of inner secondary deposits in *Rhabdopleura*: (1) membranous deposits (equivalent to the paracortex or pseudocortex of crustoid graptolites), and (2) fibrillar deposits (equivalent to graptolite eucortex).
- There is a distinct resemblance in the shape, dimensions and distribution of cortical fibrils between *Rhabdopleura* and extinct graptolites.

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