The morphology and fine structure of the Ordovician *Cephalodiscus*-like genus *Melanostrophus*

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The holotype and a new specimen from the type locality, as well as a few new specimens of *Melanostrophus fokini* Öpik, 1930, an enigmatic invertebrate from the Ordovician of the Baltic region, have been examined using combined LM, SEM and TEM techniques. This form is reinterpreted as a ?cephalodiscid hemichordate. Its skeleton or coenecium is an encrusting assemblage of uniform zooidal tubes, forming a circular or subcircular palisade-like structure.The zooidal tubes are long (up to 50 mm) and slender, similar to zooidal tubes of the extant pterobranch hemichordate *Cephalodiscus* (*Orthoecus*). The fine structure of the skeleton wall is similar to that in graptolites and four components have been recognized within periderm: (i) thick, outer cortical layer, (ii) very thin fusellar layer, constructed of annular growth bands, with their oblique sutures arranged randomly, resembling the fusellar layer of some pterobranchs and primitive graptolites, (iii) inner cortical layer, and (iv) thin, enamel-like inner lining. The periderm is abundantly perforated by pits and holes of different diameters; some of them were probably caused by saprophytic or parasitic borers, but the largest ones (up to 100 μm) are probably primary and mark a tube bifurcation. It is concluded that cortex formation is not a synapomorphy for graptolites.

Key words: Hemichordata, Pterobranchia, *Cephalodiscus*, *Melanostrophus*, ultrastructure, Ordovician, Estonia, erratic boulders.

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Introduction

The problematic fossil genus *Melanostrophus* was proposed by Öpik (1930) in order to embrace two Ordovician species: *Melanostrophus fokini* Öpik, 1930 (type species of the genus) and *M. signum* Öpik, 1930. These forms were recovered from the Kukruse regional stage of Estonia (uppermost Llanvirn–lowermost Caradoc) and regarded as remnants of unknown marine invertebrates, provided with organic-walled tubular exoskeletons. Further findings of these mysterious fossils were obtained by Gothan (1934), Müldner (1934), Eisenack (1937), and Zessin and Puttkamer (1994), all from Ordovician erratic boulders of Baltic origin. A doubtful discovery of *Melanostrophus*-like fossils was reported by Bulman (1944) from the Caradoc of Ayrshire (Scotland).

Various authors were of conflicting opinions about the taxonomic position of the genus under consideration. Öpik (1930) stated that the organic substance of its tubes revealed a superficial resemblance to graptolite periderm. However, he failed to observe any characteristic fusellar growth increments, which were the principal criterion of graptolite affinities; finally, he placed *Melanostrophus* among sedentary polychaete annelids. On the other hand, Gothan (1934) and Müldner (1934) interpreted their findings of *M. fokini* as remnants of plant origin. Eisenack (1937) discovered in his material of the same species the presence of undoubted growth lines, similar to the fusellar structure, and suggested that *Melanostrophus* was related to graptolites. However, he noted that this form is devoid of true thecae and provided with distinctive circular openings in the tube walls. Bulman (1944) considered his form assigned to *?Melanostrophus* sp. as a graptolite *incertae sedis*. Kozłowski (1949) implied that *M. fokini* and *M. signum* were not congeneric and related to two distant groups of sessile graptolites. According to him, the former may represent the poorly-known order Stolonoidea, and the latter was similar to the genus *Graptovermis* Kozłowski, 1949, the only member of the Graptovermida, an enigmatic graptolite-like group. Similarly, Bulman (1955) and Obut (1964) treated *Melanostrophus* as a representative of the graptovermids but with a question mark. Howell (1962) listed *M. signum* among polychaete annelids. Skevington (1963) deliberated similarities between his enigmatic graptolite called ?*Stolonoidea* gen. et sp. indet. and Eisenack's (1937) specimens of *M. fokini*. Thereafter, this genus was transferred tentatively to the stolonoid graptolites by Bulman (1970), and his opinion was later accepted by Zessin and Puttkamer (1994). However, such an affiliation of *Melanostrophus* may be seriously questioned in the light of knowledge of fossil pterobranchs, because the original material of Kozłowski's (1949) stolonoid graptolites seems to

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represent fragments of rhabdopleurid colonies (for detail discussion see Bengtson and Urbanek 1986 and Mierzejewski 1986). Moreover, Mierzejewski (1988) was of the opinion that *M. signum*, similarly as *Graptovermis* Kozłowski, 1949, may represent a resting terminal portion of the stolotheca of an unknown sessile graptolite. In the present situation, *Melanostrophus* may be still regarded as one of the most poorly known graptolite-like fossils.

Because the hemichordate nature of *Melanostrophus* was never convincingly proved, it seemed to us worthwhile to make a restudy of the type material of *M. fokini*, as well as to examine new material of this species using various techniques: light and infrared microscopy, scanning (SEM) and transmission electron microscopy (TEM). This paper is one in a series of our publications devoted to the recognition of the main ultrastructural features in the sessile groups of graptolites (Urbanek et al. 1980, 1992; Urbanek and Mierzejewski 1982, 1984, 1986, 1991).

Material and methods

In 1985, the first author during his stay at the Institute of Geology (previously of the Estonian SSR Academy of Sciences, now Technical University, Tallinn) had an opportunity to reexamine the type material of *Melanostrophus fokini* (unfortunately, the holotype of *M. signum* was missing). This material, described and illustrated by Öpik (1930: pl. 3: 2, 3), was composed of two specimens from two different localities of Ordovician age, at Ubja ($C_2\beta$) and Kohtla (C_2). Moreover, the late Dr. Ralph Männil kindly handed over to the first author a specimen of *M. fokini*, from the undescribed A. Öpik's collection. This specimen originated from the type locality of *M. fokini*. Furthermore, entirely new material of *M. fokini* was discovered in "wet" residues from the erratic boulder No. O.148 of the Lower or Middle Ordovician age (see Kielan-Jaworowska 1966), found in Pleistocene glacial deposits of Poland between Wyszogród and Zakroczym (Valley of the Vistula River).

The isolated material studied in the present paper was etched in 10–15% acetic and formic acids from a limestone matrix. Hot hydrofluoric acid was used to disaggregate and remove the clay minerals and quartz. After acid treatment some fragments of periderm used for TEM were dehydrated in a graded series of acetone and propylene oxide, embedded in Epon 812, sectioned on L.K.B. III ultramicrotome with a diamond knife, and studied using a Tesla BS 500 TEM. Specimens selected for SEM studies were coated with gold or platinum, and examined using a Cambridge Stereoscan 180 and Philips XL 20 electron microscopes. For the purposes of light microscopy several bleaching agents were used (concentrated nitric acid, fuming nitric acid, hydrogen peroxide, Schulze's solution, sodium hypochlorite). Additionally, some fragments of periderm were examined using an infrared microscope. Dimensional data quoted in the text were taken usually directly from the SEM.

Numerous specimens of the Recent hemichordates *Cephalodiscus* (*Cephalodiscus*) *hodgsoni* Ridewood, 1918 and *C.* (*Orthoecus*) *solidus* Andersson, 1907 from Admiralty Bay on King George Island, West Antartica (for origin and morphology of these forms see Urbanek and Zieliński, 1982), were also studied for comparison.

For terminology see Urbanek and Towe (1974) and Urbanek and Mierzejewski (1984).

The described material is deposited in the Institute of Palaeobiology, Polish Academy of Sciences, Warsaw (abbreviated ZPAL) and in the Technical University, Tallinn (unnumbered specimen).

Systematic paleontology

Phylum Hemichordata Bateson, 1885, emend. Fowler, 1892

Class Graptolithoidea Lapworth, 1875 (in Hopkinson and Lapworth 1875) *sensu* Beklemishev, 1951

Order uncertain (Cephalodiscoidea?)

Family Melanostrophidae Zessin and Puttkamer, 1994

Type genus: *Melanostrophus* Öpik, 1930.

Remarks.—The Melanostrophidae were erected by Zessin and Puttkamer (1994: 564) as a family of the graptolite order Stolonoidea to include the single genus *Melanostrophus*; the original diagnosis is as follows: "Kranzartige, ringsherum geschlossene, aus homogenem Filz bestehende Kolonie, mit nach unten in viele einzelne Lappen oder Zotteln ausgehender individuenreicher, verfilzter Röhrenvergesellschaftung. Obere Begrenzung kreisförmig in mehr oder weniger gerader Linie. Einzelne Lappen parallel zur Längsachse nach außen aufgewölbt. Stellung der Lappen einer umgekehrten Krone vergleichbar und leicht nach außen gerichtet. Kolonie immer frei im Sediment vorkommend, niemals auf fremdem Gegenstand haftend. Im gegensatz zur Familie Stolonodendridae ist bentonische Lebensweise wahrscheinlich, die auch die großen morphologischen Differenzen zwischen beiden Familien erklären würde." However, this diagnosis may be questioned because it was based on the misinterpretation of *Melanostrophus* morphology (see below). We do not propose an emendation of the family diagnosis because it is not beyond possibility that the family name Melanostrophidae Zessin and Puttkamer (1994) is a junior synonym of the Cephalodiscidae Harmer, 1905. Under the circumstances, the family affiliation of *Melanostrophus* to the Melanostrophidae should be treated provisionally.

Genus *Melanostrophus* Öpik, 1930

Type species: *Melanostrophus fokini* Öpik, 1930.

Emended diagnosis.—Skeleton composed of long, slender, circular, subcircular or subpolygonal erect zooidal tubes, rarely branched. Zooidal tube wall made of a thin fusellar

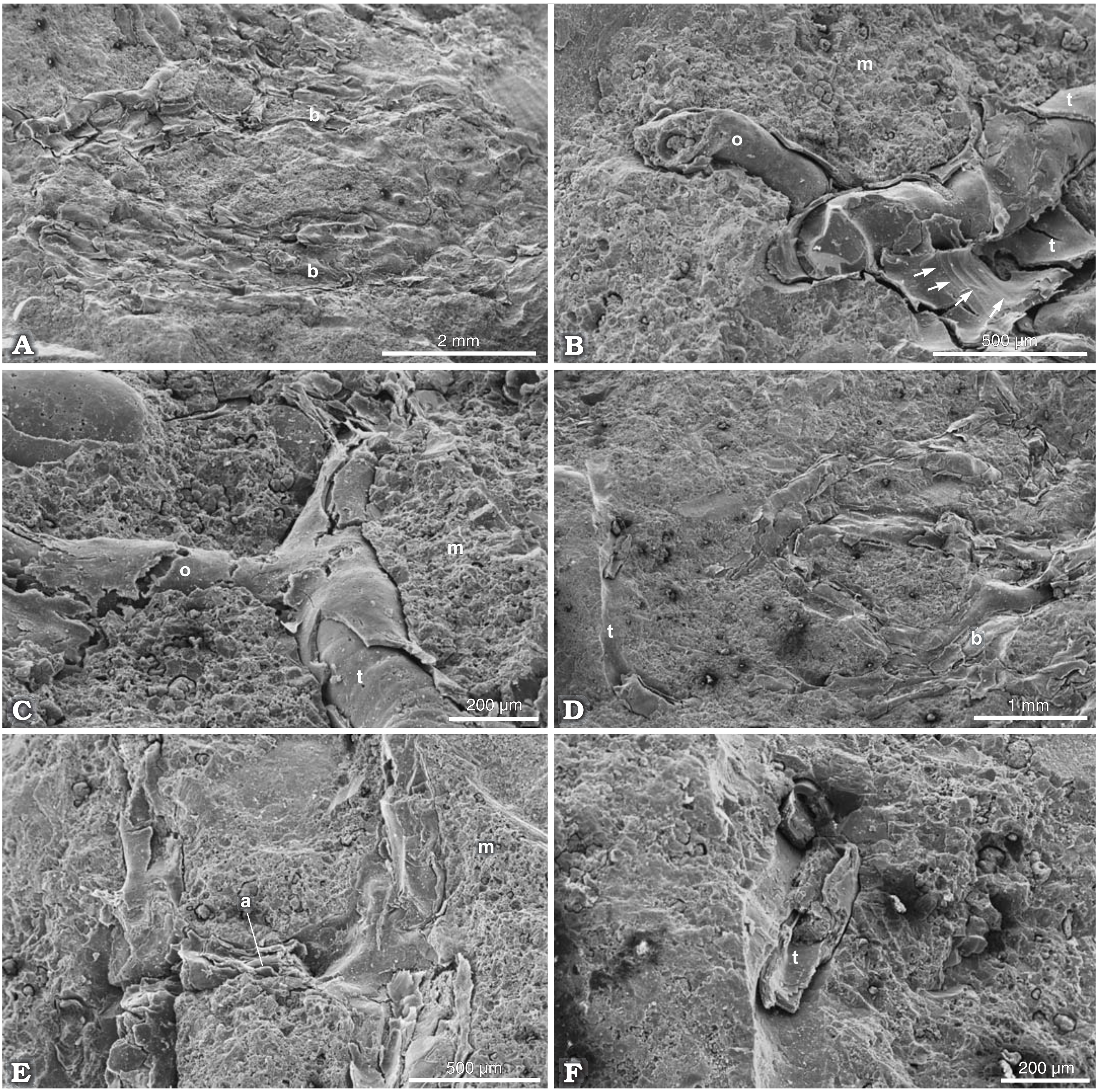

Fig. 1. *Melanostrophus fokini* Öpik, 1930. Upper Ordovician (Kukruse Stage, $C_2\beta$), Ubja (Estonia). Fragment of the specimen, preserved in the limestone matrix; ZPAL Pb 6/1. SEM micrographs. **A**. Fragment of a middle part of the colony made of rather closely packed tubes. **B**, **C**. Lateral offshoots of the tubes. **D**. Tubes connected with the anastomosis. **E**. Part of a distal portion of the colony made of loosely arranged tubes. **F**. Bifurcation of the tube. Abbreviations: a, anastomosis; b, bundle of tubes; m, matrix; o, lateral offshoot of the tube; t, tube. Arrows in B indicate fusellar sutures or their impressions.

layer and very thick outer and inner cortical deposits. Tubes are fused by their walls and form a cup-like colony.

Attachment part of colony unknown.

Species assigned.—Only the type species, *M. fokini* Öpik, 1930.

Remarks.—We challenge the diagnosis of the genus *Melanostrophus* by Zessin and Puttkamer (1994: 564) as based on an erroneous interpretation: the zooidal tubes built of the periderm, composed of fusellar and cortical fabrics, were regarded as graptolite stolons, and the coenecium of *Melanostrophus* as an association of fused stolons.

The other species of *Melanostrophus*, *M. signum* Öpik, 1930 (for illustration see Öpik 1930: pl. 3: 3 or Howell 1962: 104, fig. 14), should be treated as *nomen dubium*. It was based on undeterminable organic remains and no fusellar

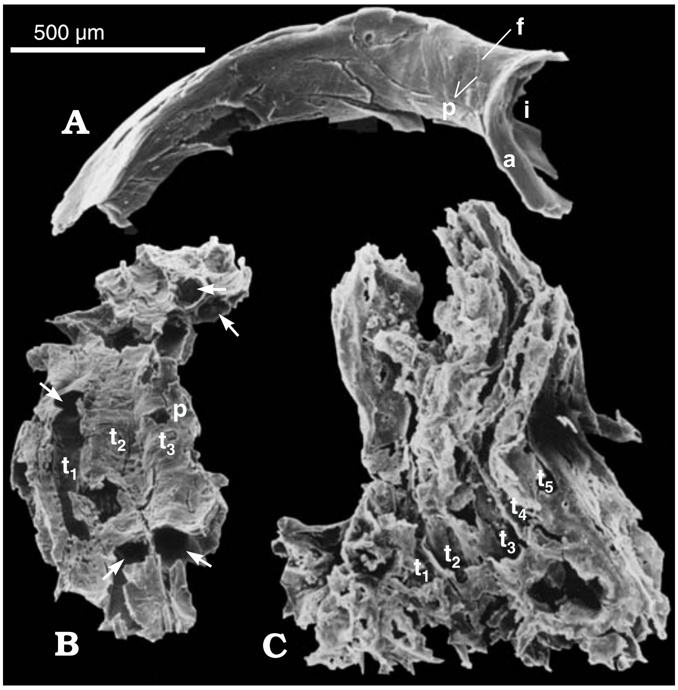

Fig. 2. *Melanostrophus fokini* Öpik, 1930; Upper Ordovician (Kukruse Stage, $C_2\beta$), Ubja (Estonia); ZPAL Pb 6/1. SEM micrographs of chemically isolated fragments. **A**. Fragment of a single tube with a fragment of apertural margin. **B**, **C**. Broken bundles of tubes. Abbreviations: a, apertural margin; f, interfusellar suture; i, interior of the tube; p, periderm perforations; t_1, t_2, etc., adjacent tubes. Arrows show circular cross section of the tubes.

structure was detected. Unfortunately, according to Mierzejewski (1988), the holotype and only specimen of this species is lost. Nevertheless, Zessin and Puttkamer (1994) separated it in a new stolonoid genus (*Stolonofolliculis*) and allocated it to the new family (Stolonofolliculidae) of the order Stolonoidea.

Melanostrophus fokini Öpik, 1930

Figs. 1–9.

Melanostrophus fokini sp. nov.; Öpik 1930: 11, pl. 1: 2, 3.
Melanosrophus fokini Öpik; Gothan 1934: 153, figs. 1–3.
Melanostrophus fokini Öpik; Eisenack 1937: 100, figs. 2–5.
Melanostrophus fokini Öpik; Zessin and Puttkamer 1994: 566, figs. 2–12.

Emended diagnosis.—A *Melanostrophus* species with zooidal tubes a few centimetres long and 0.2–0.3 mm wide.

Material.—The holotype and five specimens etched from matrix.

Description.—All specimens under study are rather small fragments of coenecia (Figs. 1A, 2B, C, 3A). Their fragmentary condition does not permit a closer determination of the general shape of colony, but they distinctly correspond with the morphology of surprisingly well-preserved specimens described by Zessin and Puttkamer (1994). Undoubtedly, they originated from the middle and distal parts of colonies. Unsatisfactorily, all specimens are lacking initial and most distal portions, as well as any traces of attachment surfaces.

The components of the type specimen coenecium are preserved in full relief, undistorted by diagenetic flattening. They are arranged as flat or wavy sheets. These sheets are composed of a great number (several dozen or so) of long, slender, subcylindrical and cylindrical, sometimes subpolygonal tubes. The tubes in the sheets are uniformly oriented and strongly condensed; one may say that their arrangement resembles a palisade. This very regular pattern is disturbed only rarely and only in some areas of the holotype (Fig. 1; see also Öpik 1930: pl. 1: 2). In these parts the sheets are transformed into irregular nets made of loosely packed and irregularly confused tubes. There is a single case when the most distal part of the tube is partially preserved and provided with an incomplete but distinct apertural margin (Fig. 2A). The tubes of the coenecium are unflattened, usually in a satisfactory state of preservation (Fig. 2) Commonly, they are almost straight or more or less bent coiled (Fig. 1E), and only rarely strongly and irregularly, devoid of particular features. No traces of the stolonal system or other skeletal elements have been found. The largest Estonian specimen figured by Öpik (1930: pl. 1: 3) is in the form of a sheet, 16 mm wide and more than 60 mm long.

The colony fragments etched from the erratic boulder (Fig. 3A) are distinctly smaller (4–6 mm wide and up to 12 mm long) and probably originated from the single colony. Their tubes are usually strongly compressed but reveal the same pattern of colony organization as the holotype and Zessin and Puttkamer's specimens (Fig. 3A, B).

Fine structure of periderm

The structure of the wall in the holotype is not easily recognized under a light microscope because of the poor state of preservation. Moreover, some areas of the periderm surface are obscured by mineral impurities. However, the outer surface in the areas without this debris appears completely structureless. Isolated fragments of the periderm are jet black and opaque to visible light. They are strongly carbonized and none of the reagents would bleach them successfully. Thus, using the standard bleaching methods we were unable to find any trace of transverse growth segments, contrary to Eisenack's (1937) but similar to Öpik's (1930) observations. Unfortunately, an application of infrared photomicrography appeared also to be completely useless.

In a majority of cases ultra-thin longitudinal and transverse sections studied in a TEM reveal at first glance resemblance to infrared and visible light microscopy observations. As a rule, TEM micrographs show that the periderm is made of a homogenous material revealing rather uniform electron density (Fig. 4A, B). This material occurs in the form of irregular blocks separated by cracks. Only rarely, between these blocks, one observe isolated straight, udoubtedly cortical fibrils sharing a common orientation. These fibrils are solid, unbranched, devoid of a central core or transverse striation. Neighbouring fibrils are sometimes fused and form bundles.Transverse sec-

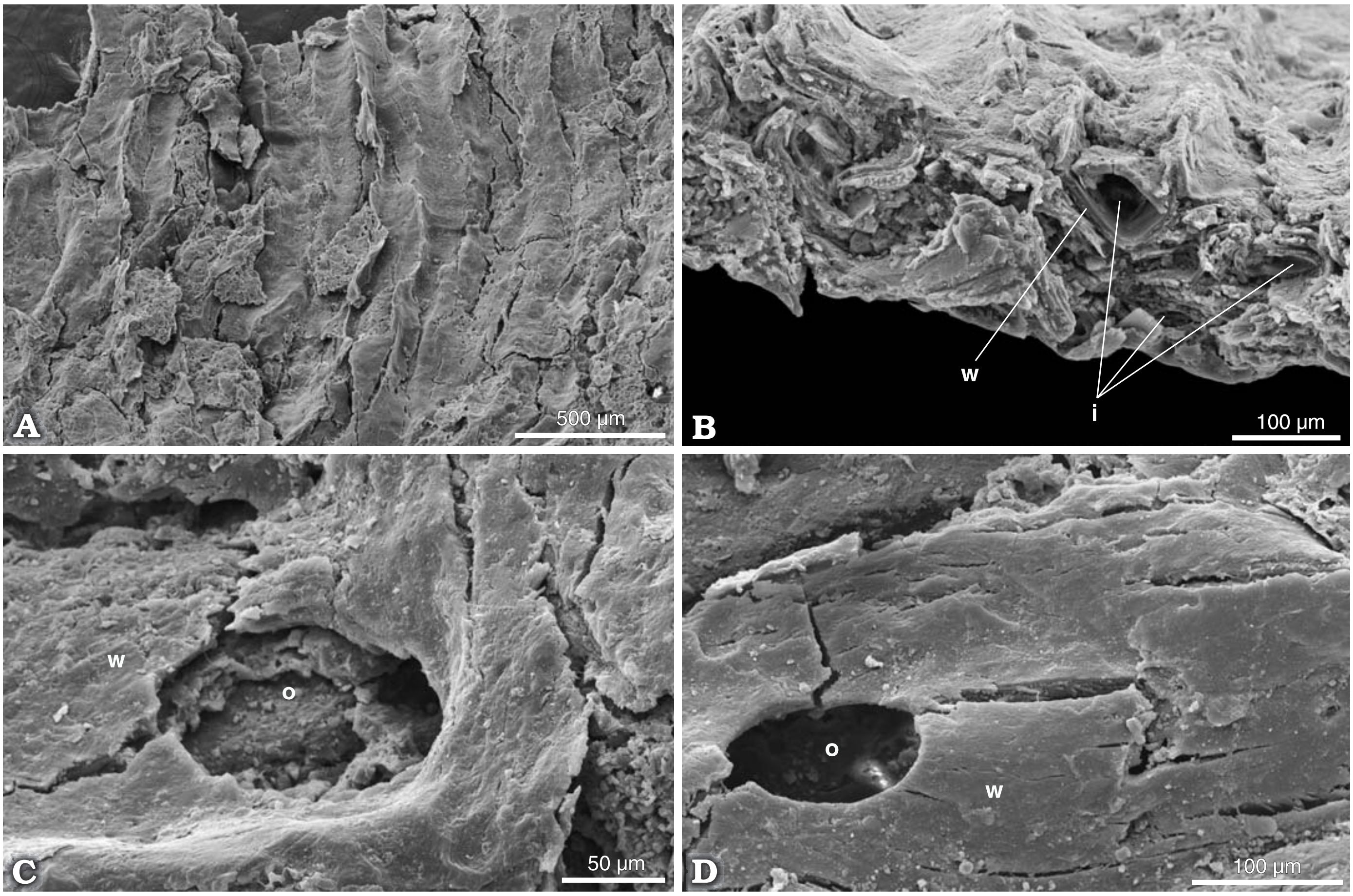

Fig. 3. *Melanostrophus fokini* Öpik, 1930; Ordovician boulder O.148 (Wyszogród/Zakroczym, Poland); ZPAL Pb 6/1. SEM micrographs of a fragment of colony composed of numerous fused zooidal tubes. **A**. General view. **B**. Margin of the specimen showing transversely broken and strongly flattened tubes. **C**, **D**. Large openings in the tube wall. Abbreviatons: i, interior of tube; o, large opening in the wall; w, wall of zooidal tube.

tioned fibrils are subcircular, oval or irregular; their diameter is very variable (90–120 nm). It can be said without hesitation that peridermal blocks of homogenous material were produced secondarily by a fusion of fibrils, as has been observed previously in some dendroid and camaroid graptolites by Urbanek and Mierzejewski (1986, 1991). No traces of sheet and fusellar fabrics, or of interfusellar sutures, have been recognized. It is of interest to note that the tubes contain usually numerous globular bodies, interpreted by Mierzejewski (in preparation) as fossil cyanobacteria.

The application of SEM methods to the present research was fruitful. At a number of places, fractured longitudinal sections of the tubes show that their walls are built of periderm in which different layers may be traced. The structure and arrangement of these layers correspond in all respects to the primary and secondary components of the typical graptolite thecal wall (Fig. 5), according to the model of the graptolite periderm proposed by Urbanek and Towe

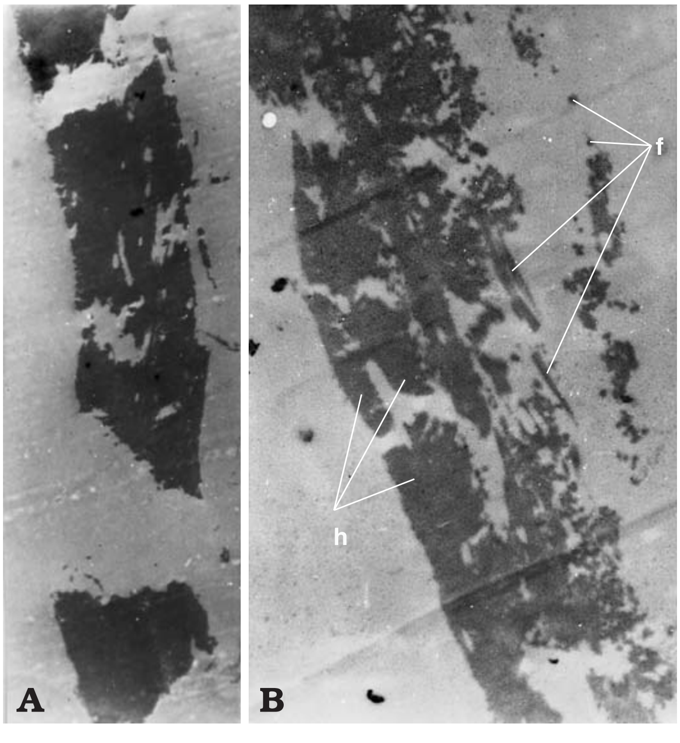

Fig. 4. *Melanostrophus fokini* Öpik, 1930; Upper Ordovician (Kukruse Stage, $C_2\beta$ Ubja); ZPAL Pb 6/1. TEM micrographs. **A**, **B**. Transverse sections of the tube wall showing homogenous and fibrillar ultratructure. Abbreviations: f, fibril; h, homogenous material.

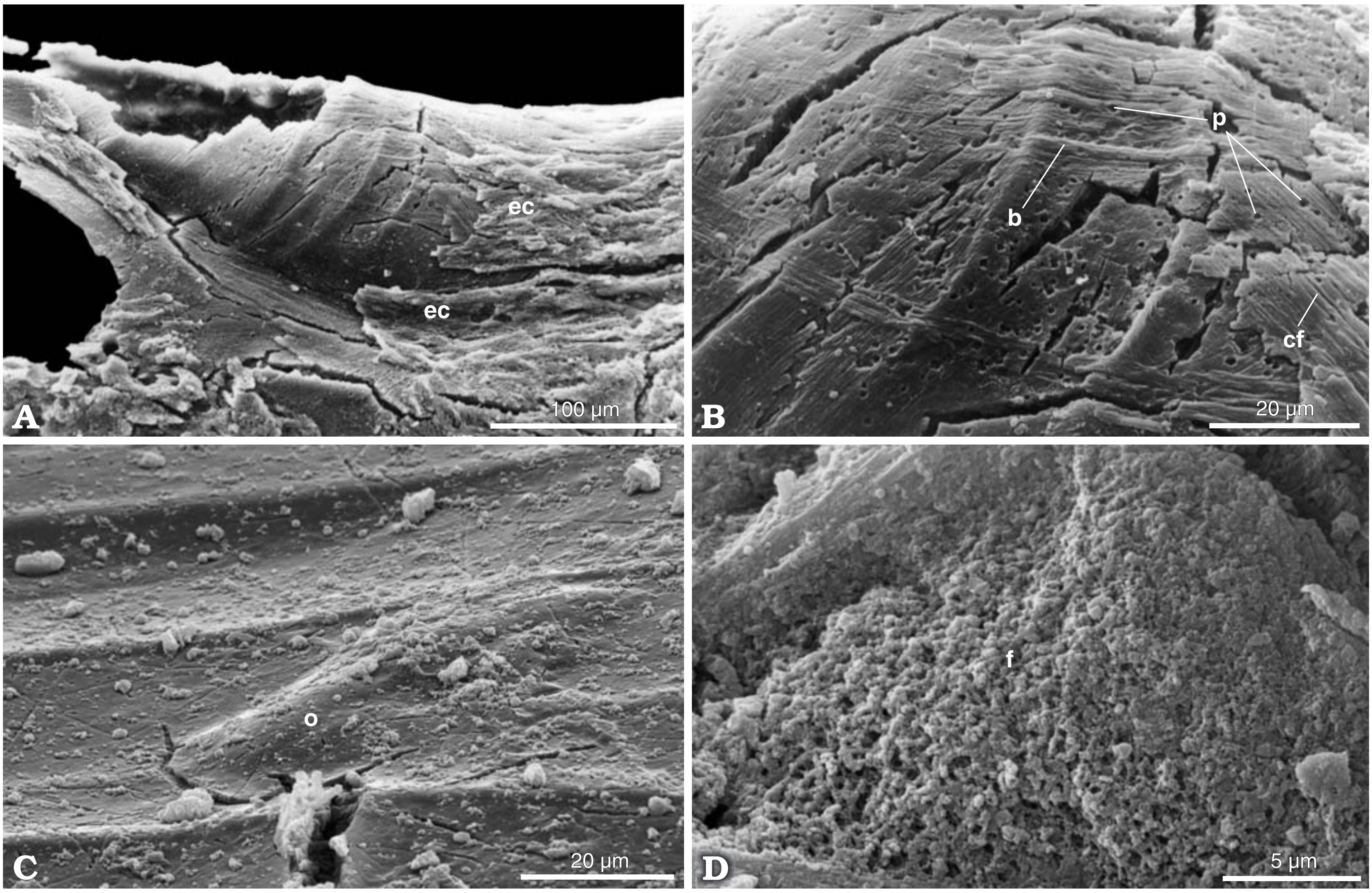

Fig. 5. *Melanostrophus fokini* Öpik, 1930; Upper Ordovician (Kukruse Stage, $C_2\beta$), Ubja (Estonia); ZPAL Pb 6/1. SEM micrographs. Graptolite pattern of tube ultrastructure. **A**. Broken tube wall showing layered ectocortex and fusellar layer. **B**. Parallel bundles of cortical fibrils covering the fusellar layer. **C**. Fuselli arrangement; note the oblique suture. **D**. Details of fusellar fabric. Abbreviations: b, bundle of cortical fibrils; cf, cortical fibril; ec, ectocortical layer; f, fusellar layer; o, oblique fusellar suture; p, pits.

(1974, 1975; see also Crowther and Rickards 1977; Crowther 1981). Thus, the following periderm layers may be traced: (1) ectocortex or ectocortical layer, (2) fusellum or fusellar layer, (3) endocortex or endocortical layer, and (4) inner lining. The cortical layers are here the best-developed components, while the fusellum and inner lining are very thin or lacking.

The ectocortex is the thickest part of the periderm layers (Figs. 5A, 6). It is built of numerous layers of cortical fibrils arranged unidirectionally in particular layers (Fig. 6). The fibrils in adjacent layers show different orientations. They are long, straight or slightly wavy, as a rule smooth (Fig 7). Exceptionally, one may observe some periodicity in fibrils (irregular constrictions). It should be noted that fibril diameter is distinctly varied (90–130 nm), sometimes within a single fibril. As a rule, the cortical fibrils in the ectocortex are tightly packed in bundles (Figs. 4B; 7A, B). Some parts of this layer are often made of homogenous material (Fig. 6C). This material occurs in form of large, irregular blocks.

The fusellar layer is often poorly developed and hardly discernible in some sections of the tubes. If present, the fusellum is manifested in the form of a thin film between the ectocortical and endocortical layers. Sometimes, one may observe details of the fusellar fabric (Fig. 5D). Surprisingly, large parts of the tubes reveal no trace of fusellar layer, even in the form of patches. The interfusellar sutures (= growth lines) are clearly visible (Figs 2A, 6, 7). The fusellum usually comprises complete fusellar rings. An oblique suture of the fuselli is usually hardly visible and irregularly placed (Fig. 7B, C), as in the case of rhabdopleurid zooidal tubes and some cephalodiscids, as well as primitive sessile graptolites. The outer surface of the fusellar layer is completely masked by the ectocortex. However, one can find sometimes areas of the periderm where the outer surface of the fusellum is visible due to removal of the cortical tissue (Fig. 6A, B). The height of the fuselli (i.e., the distance between the growth lines) varies in the range of 17–31 µm.

The endocortex is similar to the ectocortex, but is distinctly thinner. It is surrounded by the fusellum in a rather loose manner (Fig. 8). The cortical fibrils are distributed less regularly and loosely packed (Fig. 8B–D). In some places, the fairly regular arrangement of fibrils is disrupted by the presence of numerous, very thin and often wavy fibrils of the unknown nature (Fig. 8D).

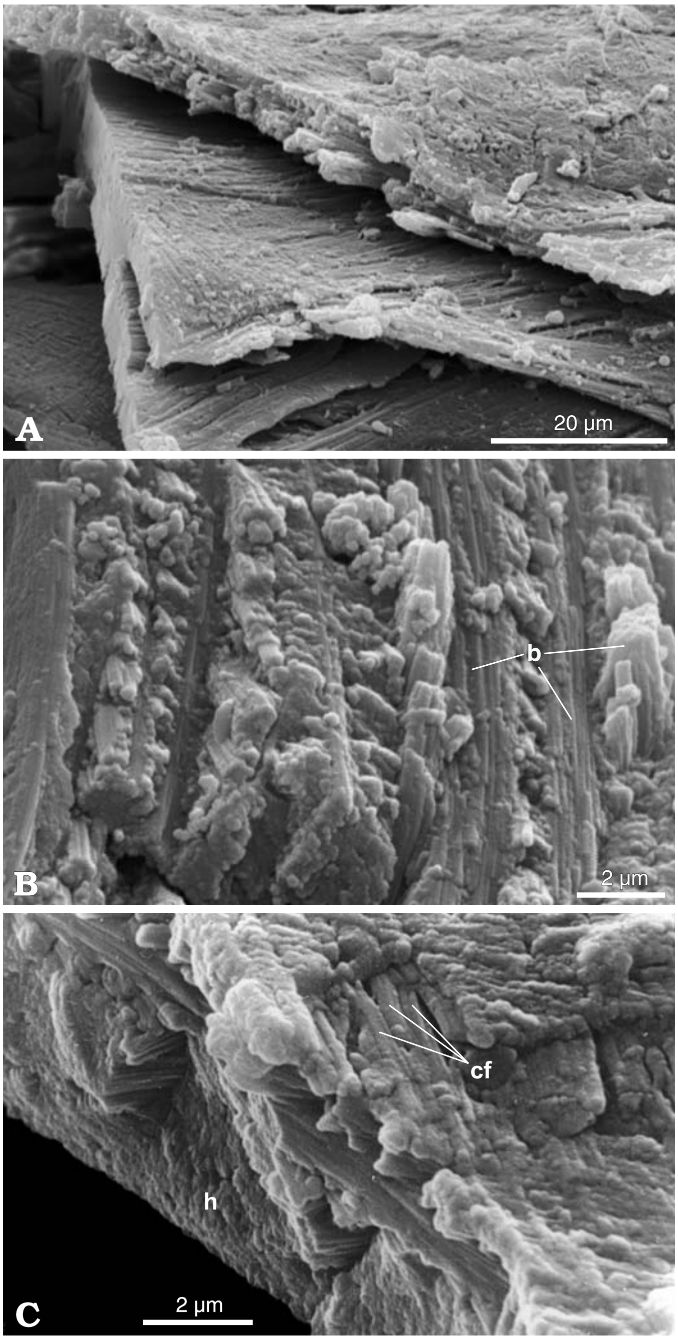

Fig. 6. *Melanostrophus fokini* Öpik, 1930; Upper Ordovician (Kukruse Stage, $C_2\beta$), Ubja (Estonia); ZPAL Pb 6/1. SEM micrographs. **A**–**C**. Details of ectocortex. Abbreviations: b, bundle of cortical fibrils; cf, cortical fibril; h, homogenous material within the cortical tissue.

The inner lining is a thin, enamel-like layer made of homogenous material (Fig. 8A–C). It is usually in close contact with the endocortical layer.

Almost nothing can be said about the micromorphology of the primary outer surface. The outermost parts of the periderm show irregular roughnesses, numerous cracks, deep fissures and holes, undoubtedly as a result of its diagenetic history (Figs. 2, 6B). Because of strong corrosion of the material, one can only rarely find small areas of better preservation. These are devoid of any traces of the outer sheet fabric.

The periderm of *Melanostrophus* commonly abounds in various circular or subcircular pits and openings (Figs. 2, 3C, D, 5A, 9). As a rule, they are irregularly distributed and varying in dimensions. Many of these small, round perforations are similar to those seen in the walls of chitinozoans and other organic microfossils. They are generally attributed to bacteria and parasitic fungi (see Grahn 1981), their diameter

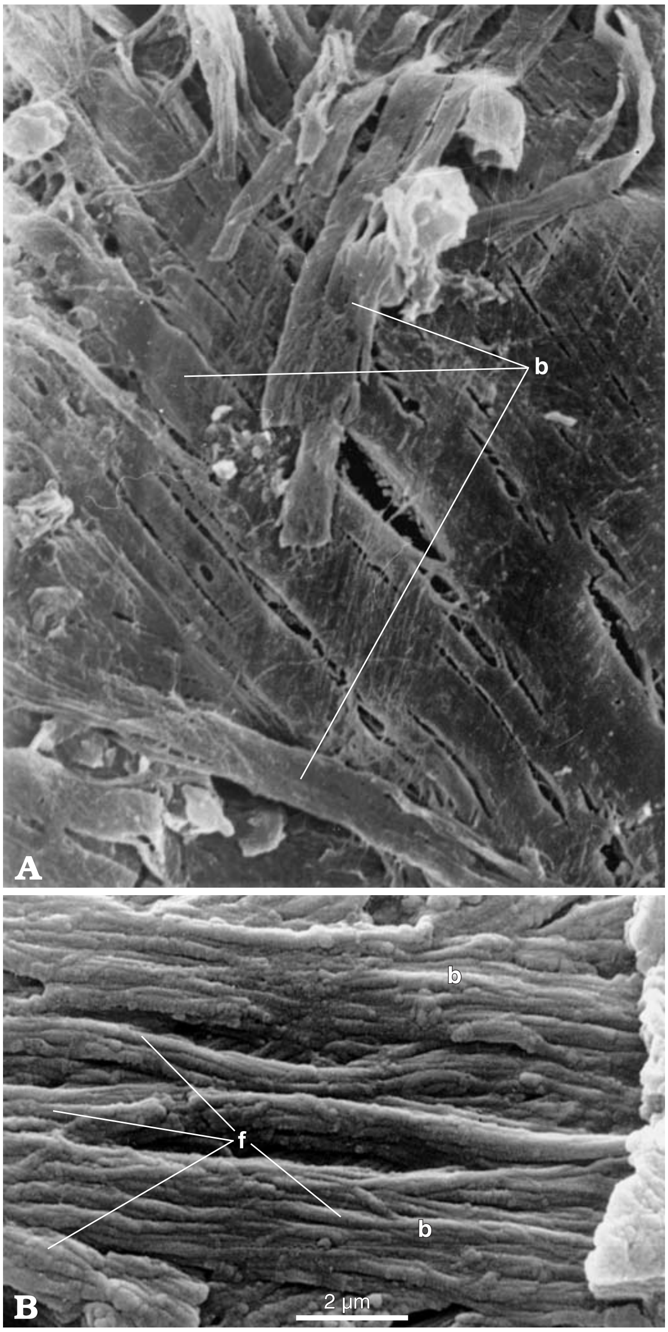

Fig. 7. *Melanostrophus fokini* Öpik, 1930; Upper Ordovician (Kukruse Stage, $C_2\beta$), Ubja (Estonia); ZPAL Pb 6/1. SEM micrographs. Details of cortical fabric in ectocortex. **A**. Bundles of cortical fibrils. **B**. Arrangement of cortical fibrils in bundles. Abbraviations: b, bundle of fibrils, f, cortical fibril.

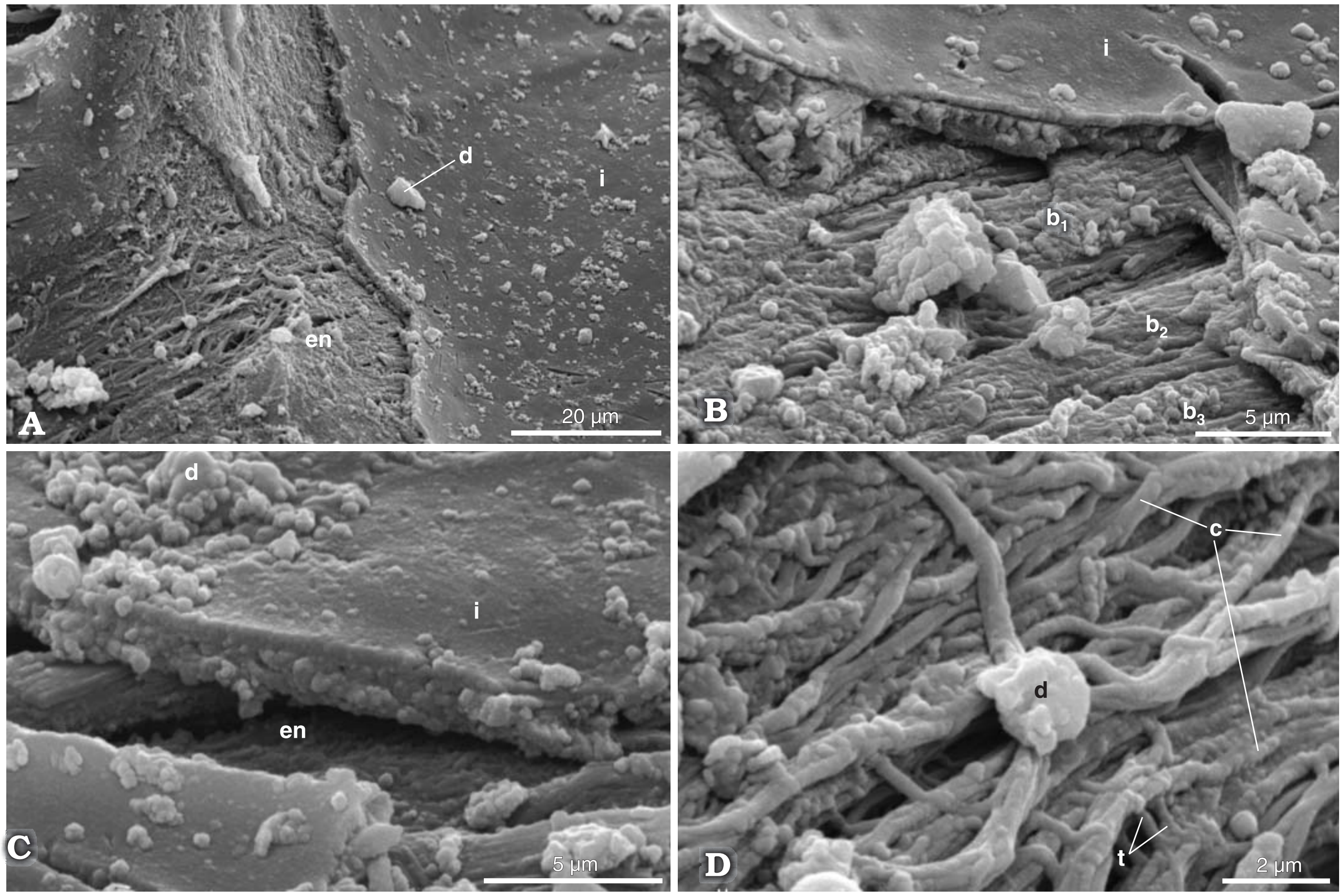

Fig. 8. *Melanostrophus fokini* Öpik, 1930; Upper Ordovician (Kukruse Stage, $C_2\beta$), Ubja (Estonia); ZPAL Pb 6/1. SEM micrographs. **A**–**C**. Inner periderm surface where removal of the enamel-like inner lining reveals cortical fibrils of endocortex beneath. **D**. Enlargement of cortical fabric in endocortex. Abbreviations: b_1, b_2, b_3, adjacent bundles of cortical fibrils; c, cortical fibril; d, mineral debris; en, endocortex; i, inner lining; t, transverse connecting fibril.

varying between 3 and 15 µm. However, zooidal tubes of *Melanostrophus* are proveded also in larger, circular to subovate openings in outline, about 60 to 130 µm in diameter. Margins of these openings are sometimes protruding over the surface (Fig. 3D). Previously, such openings were described by Eisenack (1937). According to him, they served for connection between adjacent tubes rather than were real thecal apertures. Similar openings were found by Skevington (1963: 67, figs. 79 and 81) in his enigmatic graptolite-like fossil named as ?Stolonoidea gen. et sp. indet., identified tentatively as autothecae. The true function of these openings is unclear. However, it seems possible that they only mark tube branching.

Final remarks

The observations presented above clearly indicate that *Melanostrophus* represents an unusual combination of features of extant cephalodiscid and extinct graptolite hemichordates. The overall morphology of the zooidal tubes is strongly reminiscent of cephalodiscids of the Recent subgenus *Cephalodiscus* (*Orthoecus*) Andersson, 1907. Both forms have individual tubes which are very long, slender, and which only rarely branch. According to earlier authors (e.g., Andersson 1907; Johnston and Muirhead 1951) and the present authors' unpublished observations, the tubes in *C.* (*O.*) *densus* Andersson, 1907 and *C.* (*O.*) *solidus* Andeersson, 1907 are closely set and have a tendency to grow together in clusters, often joined together for part of their length, similarly as in *Melanostrophus*. On the other hand, a heavy cortical-like coating, both external and internal, points to a graptolite assignment of the form in question.

Any definitive solution of the problem of the systematic placement of *Melanostrophus* must wait until our knowledge concerning earliest fossil hemichordates becomes more complete. However, at the present state of knowledge it seems safe to conclude that hemichordates—like many other invertebrate groups—passed through a phase of radiation in the Early Cambrian. Some of the clades rreulting from this radiation, became fast established and long lasting, providing a model for understanding the structural plan of fossil hemichordates. Some minor clades were more transient, and represent a non-conventional combination of features. *Melano-*

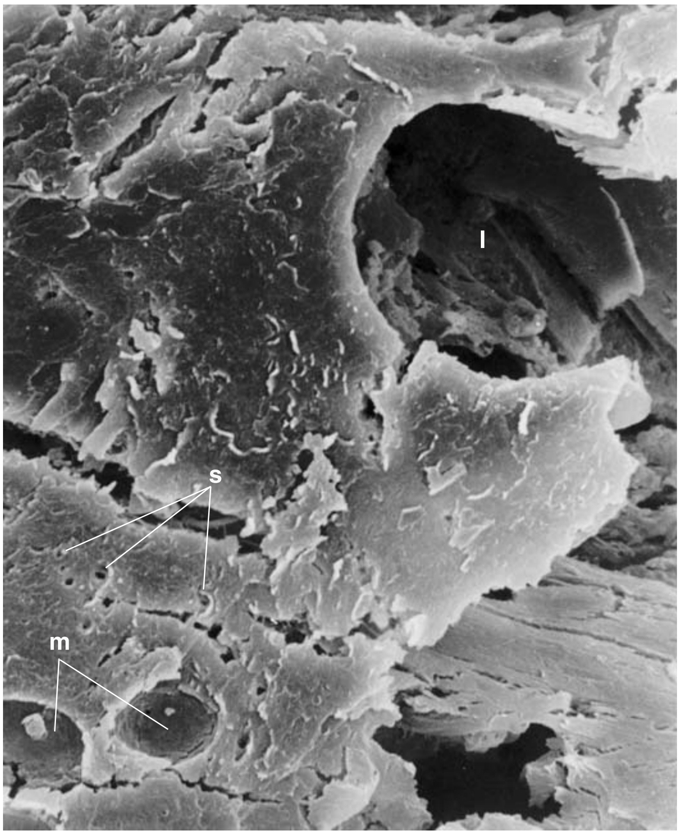

Fig. 9. *Melanostrophus fokini* Öpik, 1930; Upper Ordovician (Kukruse Stage, $C_2\beta$), Ubja (Estonia); ZPAL Pb 6/1. SEM micrograph showing different types of periderm perforation. Abbreviations: l, large opening, m, medium opening, s, small opening.

strophus and *Pterobranchites* (for the fine structure of the latter, see Mierzejewski, 1984) are among such early representatives of pterobranch-like clades, which had an ability to produce thick cortical deposit made of cortical fibrils. Therefore, in the light of recent data, the old belief that the cortex is a novelty (synapomorphy) of the "true" graptolites, acquired relatively late in the morphological evolution, is no longer tenable. Some fossil taxa otherwise representing a pterobranch level of morphology, were able to form cortex. Moreover, as indicated by observations made by Mierzejewski and Kulicki (2001, 2003), both fossil and extant rhabdopleurids were able to lay down cortical fibrils. Cortex could in this way appear prior to the attainment of the graptolite structural grade, being expressed in different clades to different degrees.

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