The Ultrastructure and Building of Graptolite Dissepiments

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ADAM URBANEK and PIOTR MIERZEJEWSKI

Dissepiments or connecting bars between adjacent stipes in rhabdosomes of dendroid graptolites were studied by means of electron microscopy (SEM and TEM). The material, chemically isolated from rock matrix, originating from the Ordovician of Estonia and glacial boulders of Baltic origin found in Poland, is assigned provisionally to the genus "*Dictyonema*" sensu lato. Early growth stages of dissepiments are made only of the fusellar component. Older dissepiments are composed of the central core and the outer envelope: the central core is made of rather irregularly arranged growth units made of the fusellar tissue, whereas the outer envelope has a distinct cortical appearance. TEM observations indicate that the fusellar component is made of both typical fusellar and microfusellar tissues (the latter with complete and reduced microfuselli). The cortical component of dissepiments is made both of dependent and independent cortex. The opinion is advanced that the dissepiments were constructed externally by the mortaring activities of zooids, similar to that of Recent *Cephalodiscus*. Our observations indicate that bizooids were most probable dissepiment constructors. These results, in general, does not support earlier opinions that dissepiments are made of cortical tissue acquiring a fusellar aspect in some cases, and that dissepiments were produced by the extrathecal membrane surrounding the rhabdosome.

Key words: Hemichordata, Graptolithoidea, Dendroidea, *Dictyonema*, dissepiments, skeletal tissues, ultrastructure, Ordovician.

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Introduction

In some sessile, as well as planktic dendroid graptolite colonies, the adjacent branches are connected by transverse or oblique skeletal structures called the dissepiments. Undoubtedly, they served to maintain the branches at a certain distance from each other and to strengthen the densely branched colony. These peculiar skeletal structures are especially abundant in two well-known genera, namely *Dictyonema* Hall, 1851 (Dendrograptidae) and *Rhabdinopora* Eichwald, 1855 (Anisograptidae). Sporadically, they occur in other graptolites, for example, *Ptiograptus* Ruedemann, 1908, *Callograptus* Hall, 1865, *Desmograptus* Hopkinson, 1875, or *Dendrograptus* Hall, 1858. Moreover, there are some dissepiment-bearing gerontic morphs of *Staurograptus* Emmons, 1855 and *Anisograptus* Ruedemann, 1937. It seems possible that the structures under discussion are present in rhabdosomes of some tuboid graptolites (Tuboidea): according to Bouček (1957), a few species of *Reticulograptus* Wiman, 1901 have their stipes connected by crossbars interpreted as dissepiments. On the other hand, Bulman and Rickards (1966) were of the opinion that this tuboid is devoid of true dissepiments. The skeletal meshwork created by dissepiments resulted in a "fenestrate" morphology of the colony (Starcher and McGhee 2003), implying important influence on water flow and filtering by the zooids. These functional aspects are, however, beyond the scope of the present paper.

The only known example of strands connecting the adjacent stipes in graptoloid colonies are apertural spines described in turbo-spiral rhabdosome of *Monograptus turriculatus* (Elles and Wood 1913). According to the recent re-examination by Zalasiewicz (1993) each such dissepiment is a single apertural spine spanning from a theca of the lower whorl and attaching to the dorsal wall of the succeeding whorl. Their resemblance to dissepiments of dendroid graptolites is very remote and there is no doubt that they developed secondarily as a homoplastic feature.

This paper presents our results of SEM and TEM investigations of the dissepiments of Ordovician *Dictyonema*-like dendroid graptolites, as well as some deliberation on the mode of their formation. Moreover, we compare the fine structure of dissepiments and the mode of their secretion with some other hemichordate skeletal structures (for example a virgella or other apertural spines). Until now, the dissepiments have not been studied ultrastructurally, though the fine structure of periderm and its derivatives in *Dictyonema*-like forms were studied by a few authors (e.g., Towe and Urbanek 1972; Urbanek and Towe 1974; Urbanek et al. 1980; Crowther 1981; Chapman and Rickards 1982).

Material and methods

The material used in this investigation comes from: (1) the Ordovician erratic calcareous boulders of Baltic origin, numbered O.62, O.129, and O.331 (the lithological characteristics and the assemblages of fossils in Urbanek and Towe 1974, Kozłowski 1959, and Mierzejewski 1986, respectively), collected by the late Professor Roman Kozłowski and his students on Pomerania's beaches and from the Quaternary moraines in Central Poland, and (2) the Caradoc limestone from the core of deep boring at Chudovo, depth 33 m (Estonia), collected by the late Dr. Ralph Männil.

The material was extracted by dissolving the rock matrix in 10–15% hydrochloric or/and acetic acids, using standard techniques for graptolite work. Stipes of graptolites were cleaned of mineral impurities in hydrofluoric and nitric acids, dehydrated in graded ethanol solutions and propylene oxide. Specimens selected for scanning electron microscopy were mounted on SEM stubs and coated with gold or platinum, then investigated with Cambridge Stereoscan 180 at 30 kV (at Plant Breeding and Acclimatization Institute, Radzików, Poland) and Philips XL 20 (at ZPAL). The graptolites intended for study with TEM were embedded in Epon 812 and sectioned on a L.K.B. ultramicrotome with a diamond knife. The sections were studied with a Tesla BS 500 electron microscope at the Institute of Botany, Warsaw University, Poland.

As a result of the fragmentary nature of our material (with the exception for *Dictyonema* cf. *cervicorne* Holm, 1890) makes that the general rhabdosomal characters are not known and this does not permit determination of the systematic position of graptolites under study. According to present knowledge, the taxonomy of *Dictyonema*- and *Rhabdinopora*-like forms is very difficult and unclear, because numerous taxa have been treated as "form-species", intraspecific variants or astogenetic morphs (e.g., Erdtmann 1986a, b). In this situation, to avoid any taxonomic implications, we have decided to assign all of the "dictyonemid" material under study to *Dictyonema* sensu lato (cf. Bulman 1955, 1970).

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

Historical background

As a rule, the dissepiments are usually in form of partially hollow (in light microscopy), more-or-less regular threads, connecting neighboring rhabdosome branches or stipes. Sometimes, they are completely irregular, plate-like or even provided with spines and processes. In general, the dissepiments are 0.5–3.0 mm long and their thickness is about 0.1 mm. They seem to be extraordinarily regular in certain species, as well as erratic in spacing and direction in others. Sometimes they are very closely-set, in other cases only widely spaced. In the past, many authors regarded the shape, spacing and arrangement of dissepiments as a very important
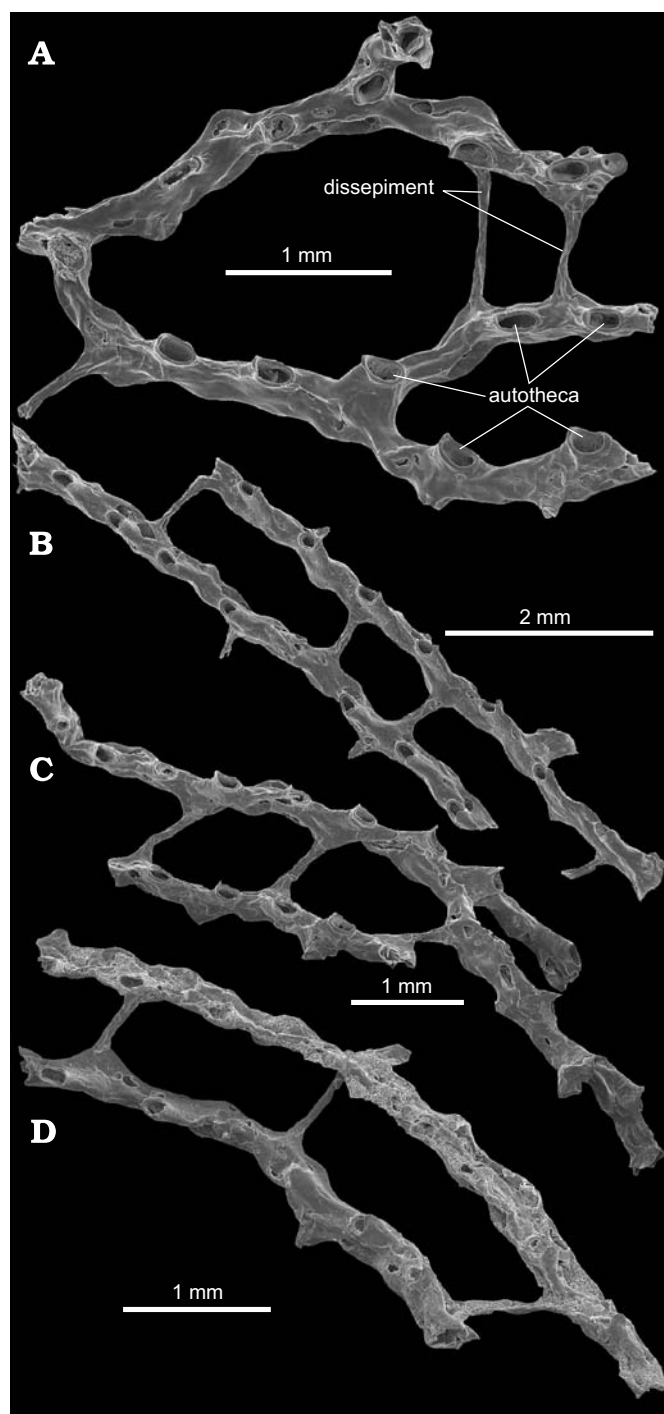

Fig. 1. Dendroid graptolite "*Dictyonema*" sp. 1. Fragments of stipes connected with dissepiments, SEM micrographs. Caradoc limestone, borehole Chudovo, depth 33 m, Estonia. **A**. ZPAL G.39/1. **B**. ZPAL G.39/2. **C**. ZPAL G.39/3. **D**. ZPAL G.39/4.

diagnostic taxonomic feature. Bouček (1957) was of opinion that in the same species the dissepiments even from different localities and from different material (limestone, shale) are built conformably and there is no great difference in character. However, it was suggested by Erdtmann (1986a: 77), that: "the secretion of dissepiments is not phylogenetically controlled and thus not a taxonomically relevant factor, but is
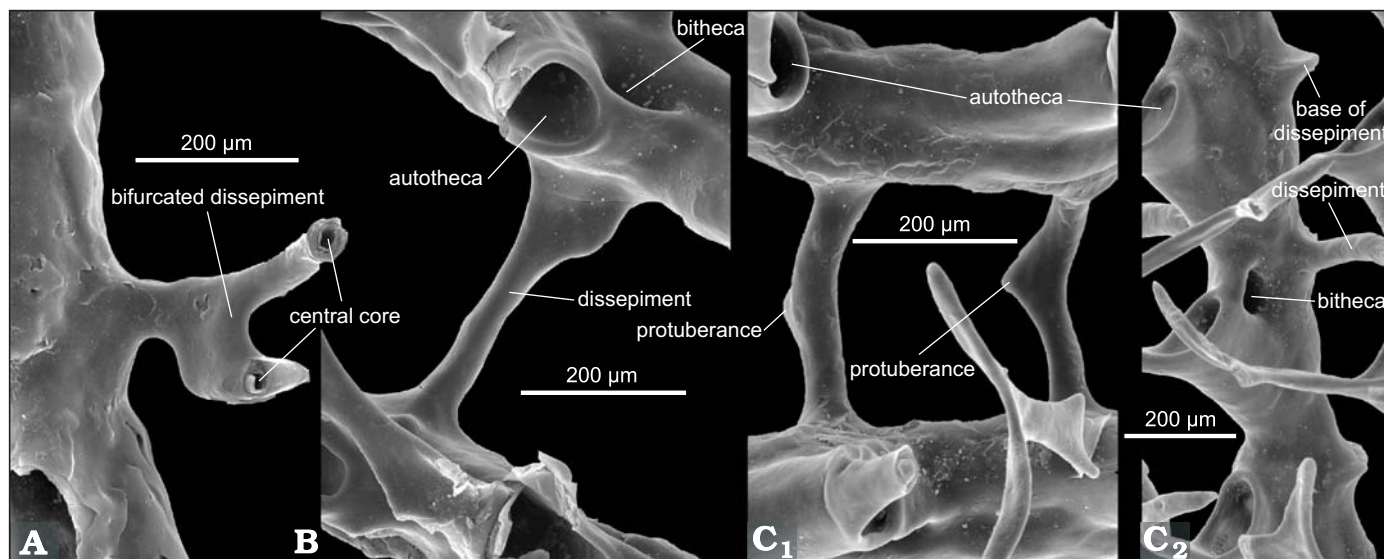
Fig. 2. Morphology and variability of dissepiments of dendroid graptolites, SEM micrographs. **A**, **B**. "*Dictyonema*" sp. 1. Caradoc limestone, borehole Chudovo, depth 33 m, Estonia. **A**. Broken bifurcated dissepiment showing central core. ZPAL G.39/5. **B**. Dissepiment with broad, plate-like base. ZPAL G.39/2. **C**. *Dictyonema* cf. *cervicorne* Holm, 1890. ZPAL G.39/6. Ordovician boulder O.331. C_1, dissepiments with distinct protuberances; C_2, abnormally developed dissepiments and abandoned attempts at their formation.

rather caused by the requirement of a frequently branching rhabdosome to prevent adjacent stipes from coming into direct contact with one another".

The formation and microstructure of the dissepiments have previously been discussed only by a few authors. The first studies were done by Gerhard Holm about 1894, but his results were never published. Bulman (1933) illustrated a few Holm's slides showing a finely laminated microstructure of dissepiments with rather irregular translucent core in *Dictyonema flabelliforme* (Eichwald, 1840). According to Bulman (1938), the formation of dissepiments was in some way connected in the certain manner to the bithecae. He noted that there is a distinct relation between so-called mesh structure (i.e., density of branches and dissepiments) and the arrangement of the bithecae along adjacent branches.

The most important observations on the microstructure of the dissepiments were made by Kozłowski (1949) on the *Dictyonema*-like material isolated from upper Tremadoc cherts. His specimens were either bleached and studied on transparencies, or embedded in parafine and sectioned by microtome. According to Kozłowski (1949), these structures are entirely extrathecal in origin, secreted by the hypothetical extrathecal living tissue and are composed of the cortical tissue. His observations on the skeletal microstructure of *Dictyonema wysoczkianum* (Kozłowski 1949: 42, pl. 4: 6) are especially interesting: a core of its dissepiment is made primarily of the cortical tissue of a pseudofusellar aspect and later becoming a normally laminated cortical tissue, producing a sort of outer sleeve. His bleached specimens of *Dictyonema* (Kozłowski 1949: text-figs. 30, 33) display numerous irregularly, placed fusellar growth bands within the dissepiment. Bulman (1970) defined the dissepiments in *Dictyonema* as cortical derivatives.

Results

The specimens of "*Dictyonema*" sp. 1 are in form of small isolated fragments of rhabdosomes from which it is difficult to judge the characters of the mesh (Fig. 1). However, it seems delicate but irregular; stipes are slender (0.3–0.35 mm wide), rather sinuous and connected by dissepiments. The autothecae are slightly isolate at their distal ends, with oval apertures and blunt processes from the ventral apertural margin. The bithecae are not usually visible: possibly their apertures are situated inside cavities of the autothecae.

The dissepiments are usually delicate, ca. 0.1 mm wide and 0.5–0.8 mm long, mostly straight, and distinctly expanded at their bases (Figs. 2, 3). The dissepiment bases pass gradually into the stipe walls. However, one can observe in some cases more-or-less visible fissures suggesting the presence of sutures between dissepiments and the stipe proper. The dissepiments are irregularly spaced, perpendicular or oblique to the axis of stipes. Two specimens are provided additionally with broad, plate-like dissepiments.

In general, the condition of the periderm, including that of dissepiments, is excellent (Fig. 4A, B). Its surface appears remarkably smooth or showing lineations that reflect a regular arrangement and parallel orientation of the underlying cortical fibrils. At some spots of dissepiments minute subcircular pits, 0.2 μm in diameter cover the surface. They are arranged in a close-packed fashion and are usually interpreted as intrasheet vesicles of cortical tissue (e.g., Crowther and Rickards 1977; Urbanek and Mierzejewski 1984).

SEM micrographs of transversally fractured dissepiments taken near their base (Fig. 4A) and in their middle portion (Fig. 4B) reveal that they are composed of an outer, solid en-
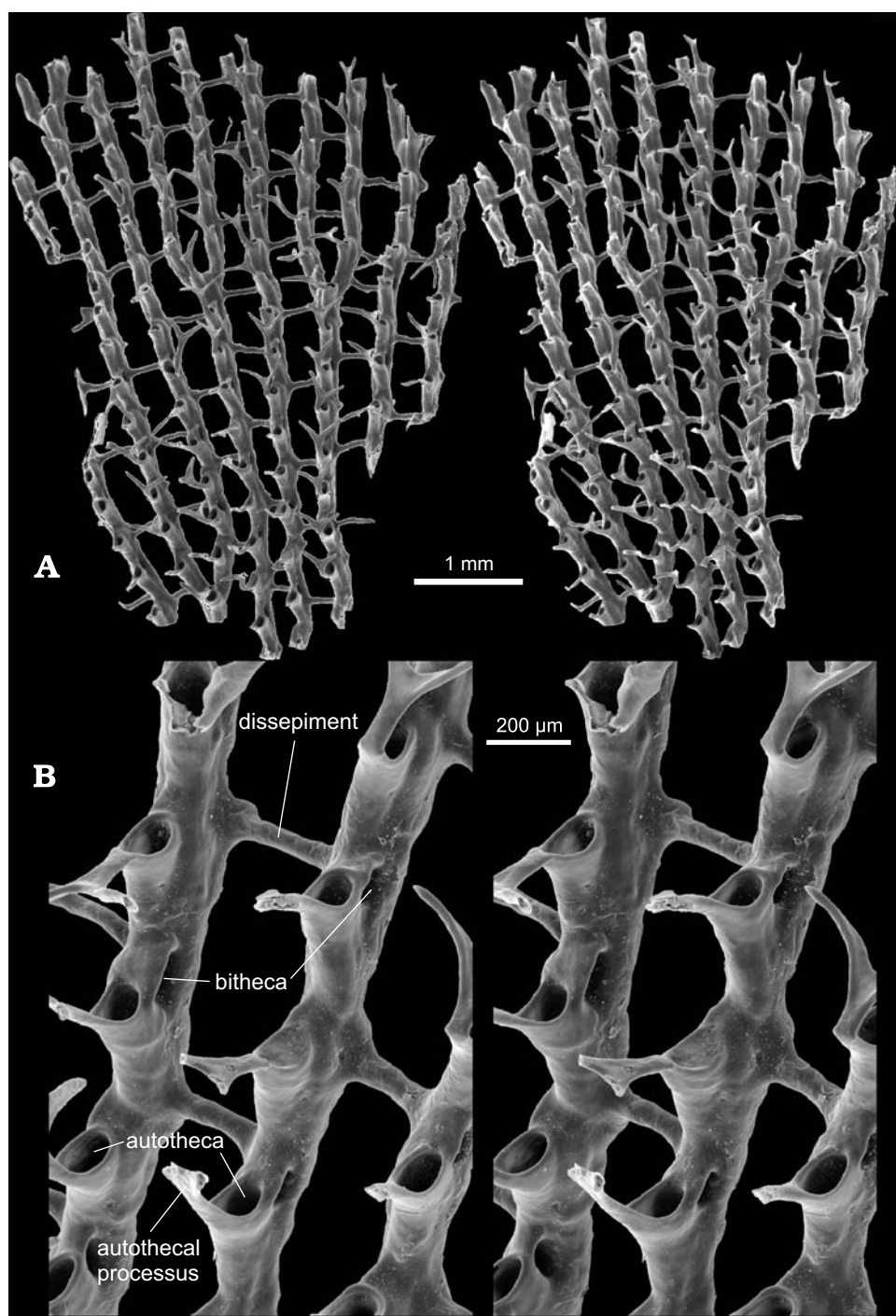
Fig. 3. Dendroid graptolite *Dictyonema* cf. *cervicorne* Holm, 1890. Ordovician, boulder No. O.331, SEM micrograph stereopairs, ZPAL G.39/6. **A**. General view of specimen. **B**. Details of morphology.

velope and a wide, central core. The envelope has a distinct cortical appearance, being layered with fibrils arranged uniformly within a given layer (Fig. 4C, D). The core is made of irregular fusellar component and contains irregularly distributed holes.

However, only the application of TEM technique based on ultrathin sections, permitted the identification of even the smallest portions of skeletal material in dissepiments, thus revealing their true structure (Fig. 5, diagram). Ultrathin lon-

gitudinal sections through the dissepiments of "*Dictyonema*" sp. (specimen 2 and specimen 3) provided a clear picture of their ultrastuctural components (Fig. 6) and support the SEM observations. One can observe a typical ultrastructure of fusellar, microfusellar and cortical tissues as recognized by Towe and Urbanek (1972), Urbanek and Towe (1974). The central fusellar core consists of superimposed fusellar and microfusellar bands. The fusellar bands are also the main component of the expanded dissepiment base (Fig. 7A).
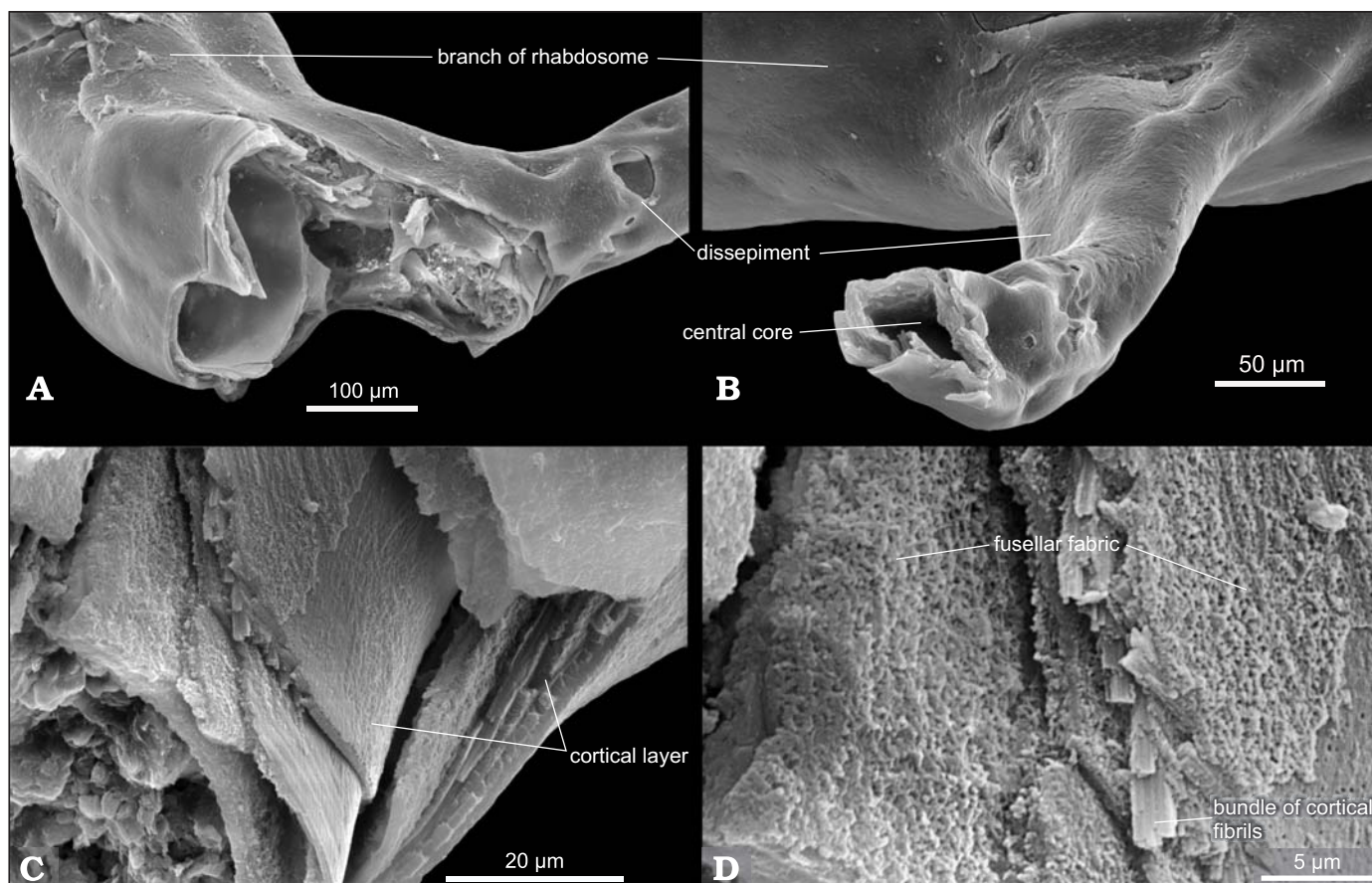
Fig. 4. Dendroid graptolite "*Dictyonema*" sp. 1. Fine structure of the dissepiment, Caradoc limestone, borehole Chudovo, depth 33 m, Estonia, SEM micrographs, ZPAL G.39/2. **A**. Broken expanded base of the dissepiment revealing fusellar core and cortical envelope. **B**. Broken dissepiment in the middle part showing central core. **C**. Layering of the cortical envelope. **D**. Ultrastructural details of fusellar and cortical fabrics in the dissepiment.

They are made of a subtle network of loosely dispersed fusellar fibrils. The more distal portion of the dissepiment core is composed of series of subconical fuselli with strongly overlapping lateral limbs (Fig. 6, core). Each fusellus body is made of a delicate meshwork produced by the fusellar fabric and of an outer lamella made of fibrils oriented normally to the outer pellicle enveloping the entire structure (Fig. 8A, C). The share of the mentioned structural components varies in particular growth bands: some have fusellar meshwork reduced (Fig. 8B), and thus resemble the microfuselli, while exceptionally growth bands may be even reduced to the outer

lamella alone (Fig. 9A). Each dissepiment is composed of two twigs (Fig. 5) growing out from adjacent branches of the rhabdosome so as to meet and fuse in the center. This is indicated by heads of fuselli situated on each twig and oriented in the opposite direction (Figs. 5, 6). In the middle they usually produce a protuberance due to the small overlap of their tips. Lamellar growth bands with little or none fusellar content are spread between the two twigs, producing in this way a sort of cortical envelope surrounding the entire structure. The origin of this envelope is complex: it appears partly by merging of outer lamellae in adjacent growth bands (Fig. 9A) and pro-
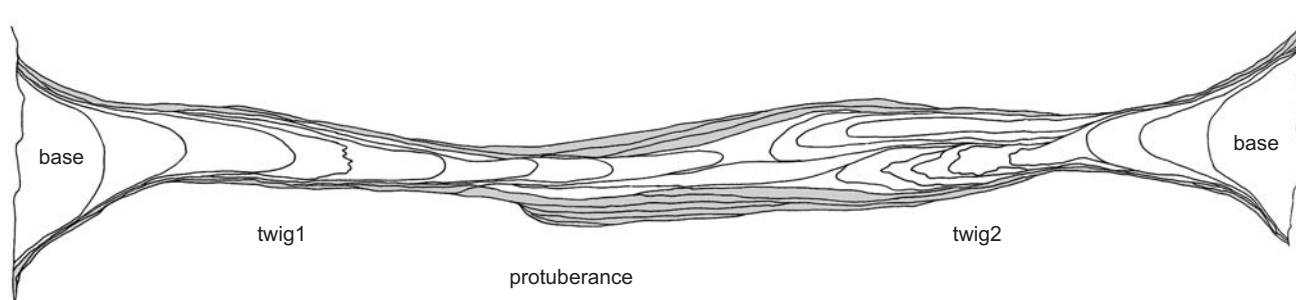

Fig. 5. A generalized ultrastructural pattern of a dissepiment in dendroid graptolite *Dictyonema* sensu lato as seen with TEM on a longitudinal section. Fusellar core made of superimposed fuselli and microfuselli—white, cortical envelope—shaded. Not to scale.
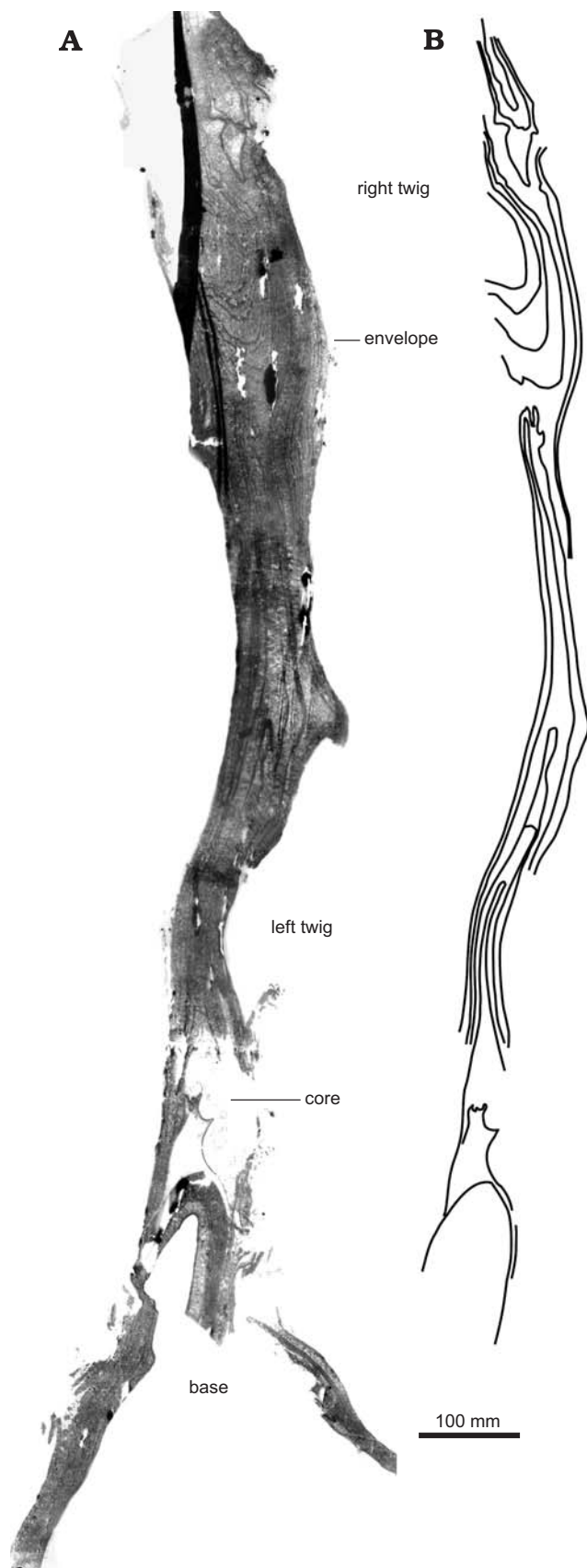
Fig. 6. Longitudinal section through dissepiment mounted from a number of TEM micrographs of dendroid graptolite "*Dictyonema*" sp. 2. Ordovician boulder No. O.62. **A**. TEM micrographs. **B**. Drawing of the same structure.

ducing so-called dependent cortex (as defined in Urbanek and Mierzejewski 1984), and partly by the independent deposition of cortical material in form of cortical bandages (Fig. 8D) . Presence of both the subconical and the lamellar fusellar growth bands (Fig. 9B) is a distinctive feature of dissepiment ultrastructure. At places numerous intersheet vesicles (pits), being a standard ultrastructural trait of graptolite skeletal structures, are present (Fig. 9B, C) . Therefore early growth stages of dissepiments are made only of the fusellar component. Older dissepiments are composed of the central core and the outer envelope: the central core is made of rather irregularly arranged growth units made of the fusellar tissue, whereas the outer envelope has a distinct cortical appearance.

Discussion and conlusions

Our SEM and TEM observations support, in general, the first microstructural studies on the dissepiments in *Dictyonema* made by earlier authors. Gerhard Holm in 1890s made longitudinal serial sections through dissepiments of *D. flabelliforme*, which were published many years later by Bulman (1933, pl. 1: 8; pl. 2), showing that their central parts and expanded bases contain distinct portions made of a very loose substance. Later, similar observations were made by Kozłowski (1949) in *D. wysoczkianum*; he interpreted the loose substance partially infilling the dissepiments as a special pseudofusellar form of cortical tissue which was secreted by a hypothetical extrathecal tissue membrane covering the outer surface of the rhabdosome (analogy with ctenostome bryozoan secretion). Moreover, Kozlowski (1949: 42–43) was inclined to think that both cortical and fusellar tissue are made of very much the same skeletal material, and differ only by the course of growth lines which are parallel in the first case or strongly convex in the second. According to our TEM observations the loose material is nothing but true fusellar fabric. Therefore, the dissepiments are constructed of the same fabrics (cortical, fusellar, and sheet fabrics, according to Urbanek and Towe's [1974] classification) as the periderm of typical graptolite thecae. The alleged canals and hollows observed under SEM in some portions of dissepiment are in fact areas of extremely loose fusellar fabric.

Historically, there were two conflicting concepts concerning the mechanism for the construction of the dissepiments, i.e., the thecal construction hypothesis of Bulman (1933, 1938) connecting dissepiment formation with the zooid activity, and extrathecal hypothesis of Kozłowski (1949), suggesting their origin trough secretion by the hypothetical extrathecal tissue membrane, generally involved in the production of the elaborate secondary thickening of graptolite skeletal constructions.. Later his views were accepted by Bulman (1970: 32) who stated that "dissepiments have been shown to be extrathecal in origin and composed of cortical tissue secreted by the extrathecal living tissue". However, Kozłowski's (1949) concept of the extrathecal tissue is no longer tena-
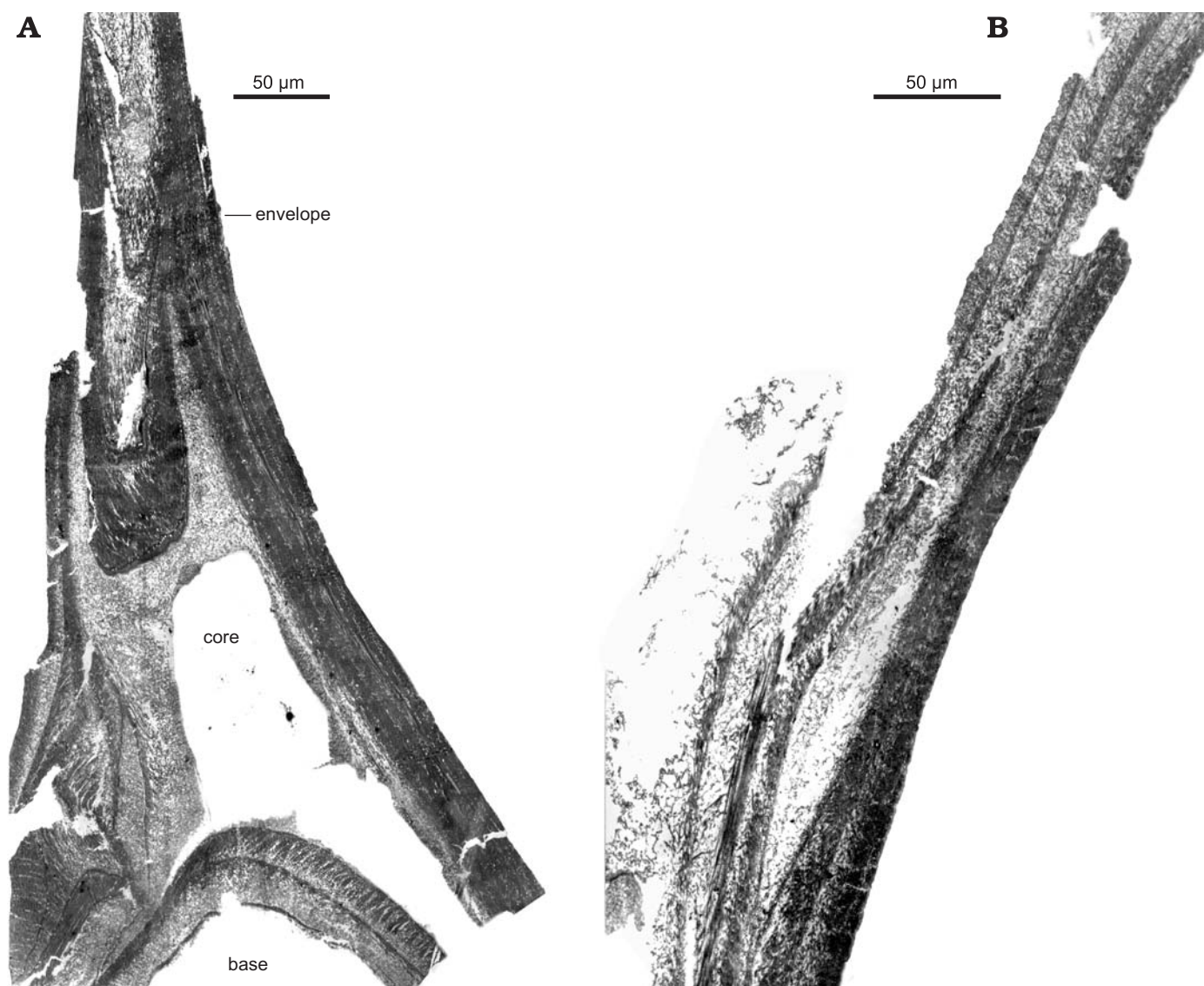
Fig. 7. Dendroid graptolite "*Dictyonema*" sp. 2, TEM micrographs. **A**. Ordovician boulder No. O.62. Longitudinal section through the expanded base of a dissepiment showing delicate fusellar fabric filling the first conical growth bands and producing the fusellar core enveloped by a heavy cortical deposit. **B**. Laminar growth bands with cortical content.

ble because of a radical change of general opinion on the origin of secondary thickening of graptolite skeletal structures following the arguments raised by Beklemishev (1951) and other authors (for discussion see also Andres 1980; Crowther 1981; Urbanek 1986; Mitchell 1995).

As was observed by some authors (e.g., Bulman 1933; Kozłowski 1949), the dissepiments are situated as a rule near bithecae apertures. Thus, when accepting the dissepiment formation by the mortaring zooid activities according to the pterobranch model of secretion, one may regard bizooids as the dissepiment constructors. This conclusion seems especially convincing when disepiment is closely related to the aperture of a bitheca and constitutes a sort of its apertural spine (as is the case of *Dictyonema longilinguae* and *D. wysoczkianum*, described by Kozłowski 1949: figs. 30, 33). In the instance of *Dictyonema* cf. *cervicorne*, studied in the present pa-

per, the relations between bithecae and dissepiments are different but also very close each other. The bithecae reveal a strong elongation, turn above the autothecal aperture to open on the opposite side of the branch (Figs. 2C$_2$, 3B). The dissepiments, when present, connect two bithecae placed on adjacent branches just below the point of the bending of their thecal tubes. Therefore, dissepiments are produced between bithecae situated on adjacent branches with apertures oriented in opposite directions ("back to back", Fig. 10). Because of alternating position of bithecae every second triad may be involved in dissepiment formation. The astogeny of species in question follows essentially this rule (Figs. 3A, 10). The growth of a multiramous rhabdosome was probably concomitant, triad by triad being added on the tips of their branches. Hence, the bithecae on adjacent branches were in unison position, oriented either "back to back" or "face to face".
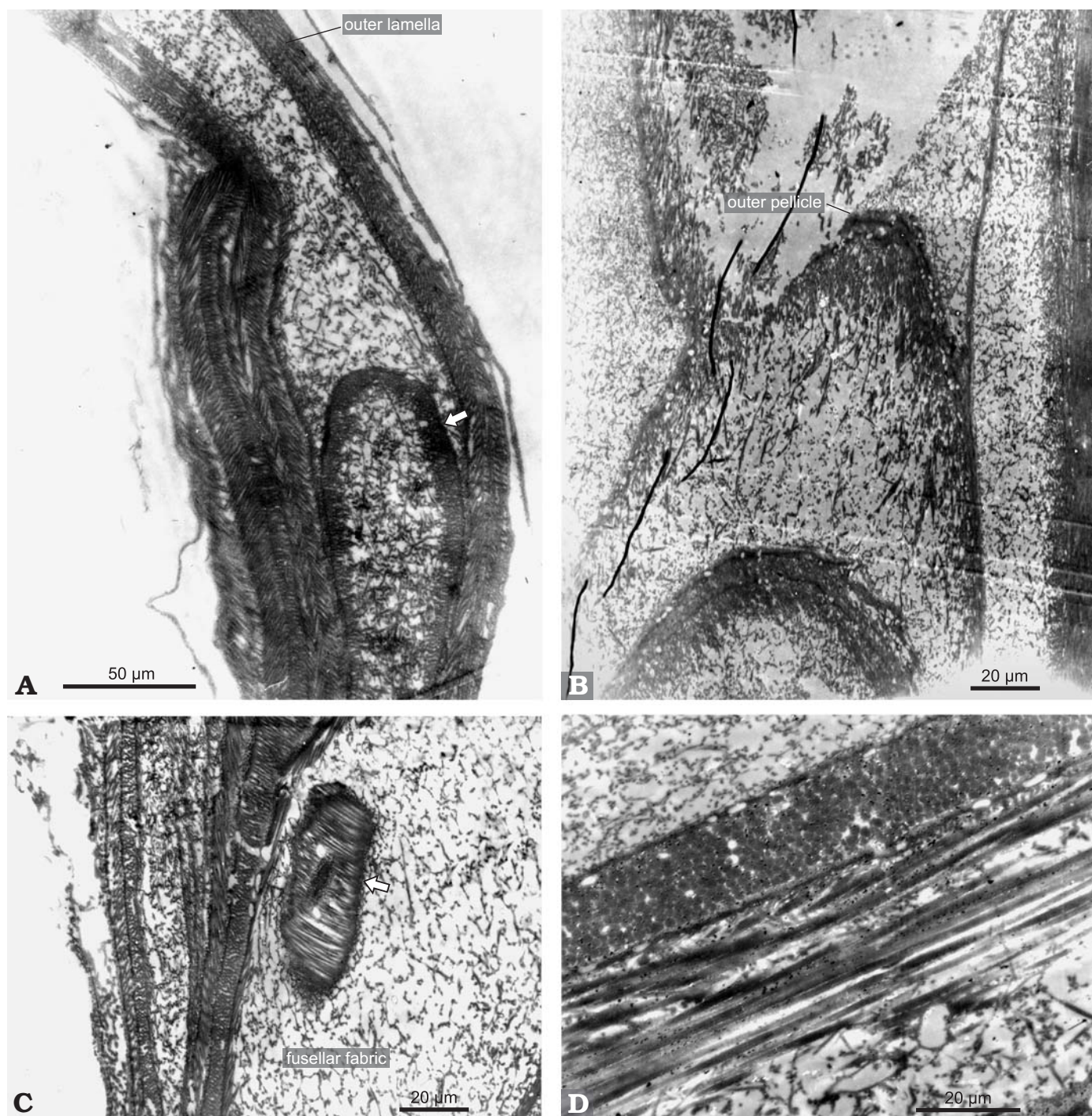
Fig. 8. Dendroid graptolite "*Dictyonema*" sp. 2. Ordovician boulder No. O.62, TEM micrographs of fuselli as components of a dissepiment. **A**. Fusellus with head and trunk normally developed, note that lateral limbs of adjacent fuselli merge to produce condensed layers of dependent cortex (arrow). **B**. Fuselli with reduced trunk resembling microfuselli. **C**. Ultrastructural details of fusellar and cortical fabric within a fusellus. **D**. Cortical and fusellar material within a dissepiment.

Erdtmann (1982) in his imaginative reconstruction of the life habit of *Rhabdinopora* ascribed dissepiment building to autozooids. Nevertheless, our observations discussed above suggest that bizooids were most probable dissepiment constructors. Whether the same is true in respect of dissepiments situated between autothecae and on other places of the rhabdosome is a matter of further considerations.

In general the structural pattern exhibited by the *Dictyonema* dissepiments is remarkably similar to that recognized in thecal and apertural spines in many graptoloids. From a comparative—anatomical point of view the dissepiment may be seen as a composite structure made of two spines growing from adjacent branches with their tips fused in the middle. Coordination of secretion and behavior of two zooids, needed for
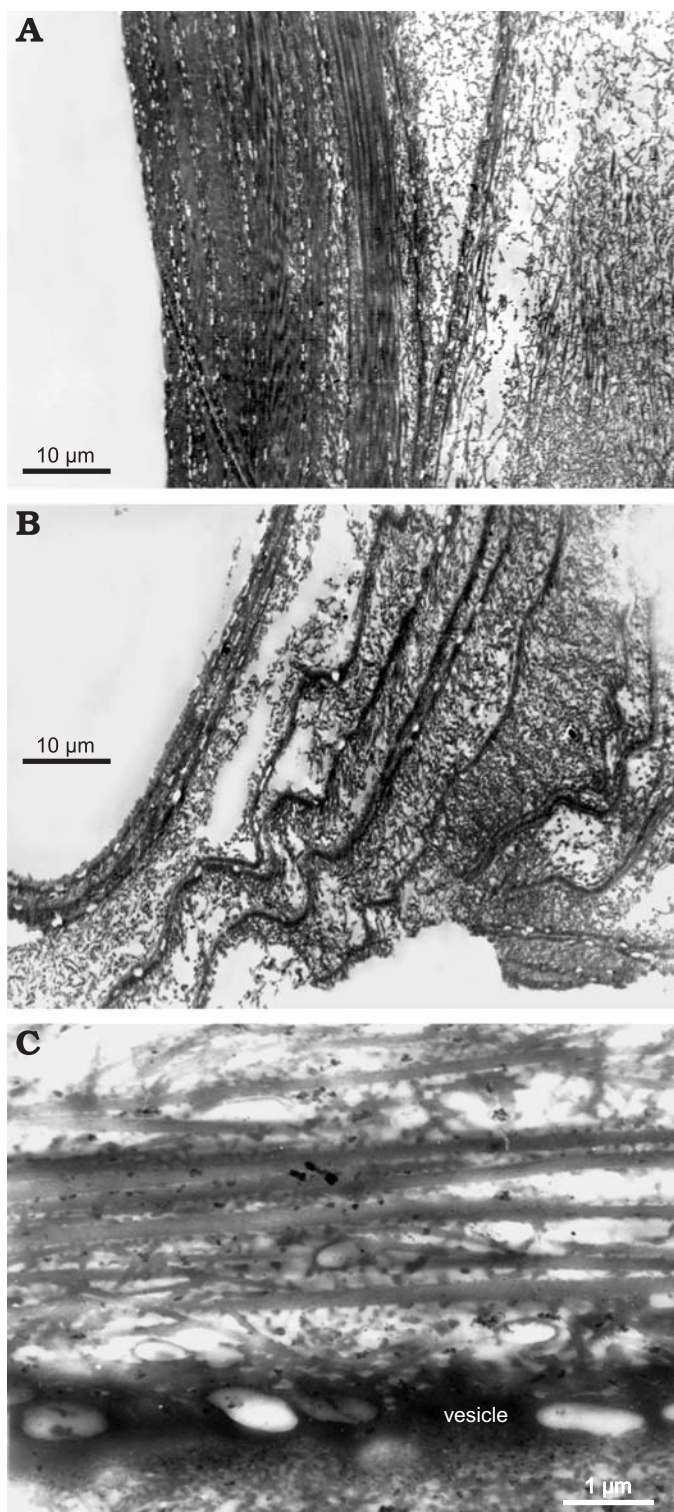
Fig. 9. Dendroid graptolite "*Dictyonema*" sp. 2. TEM micrographs of ultrastructural components of a dissepiment. Ordovician boulder No. O.62. **A**. Superimposed fuselli made mainly of outer lamellae merging laterally into multilayered cortical envelope. **B**. Laminar growth bands with fusellar fabric and intrasheet vesicles. **C**. Details of intrasheet vesicles.

the building of the composite structure such as a dissepiment, might perhaps be best explained by an assumption that each zooid would be attracted by the other being a source of some

signals (physical or chemical, like a pheromone compare Hammer 2000). So long the counterpart was present on a proper place and time the cooperative activity continued. Nevertheless, the co-ordination of the process was not perfect: numerous protuberances visible on the surface of the branches may be probably interpreted as abandoned attempts at dissepiment formation (Fig. 2D, base of dissepiment) because the counterpart zooid was not available, while exceptionally the dissepiment may be produced in "face-to-back" position (Fig. 2D). Thus the building of complete dissepiments resulted from lateral interactions between zooids situated on adjacent branches of the rhabdosome.

Generally, there is a striking resemblance between the fine structure of the "dictyonemid" dissepiments and of some other trabecular skeletal elements in the Hemichordata as cephalodiscid or graptoloid spines (see for example Andres 1980; Dilly 1993): they are all made of a loose core and a solid, cortical envelope. This similarity may suggest that the mode of construction and growth should be similar or even identical in all these hemichordate structures.
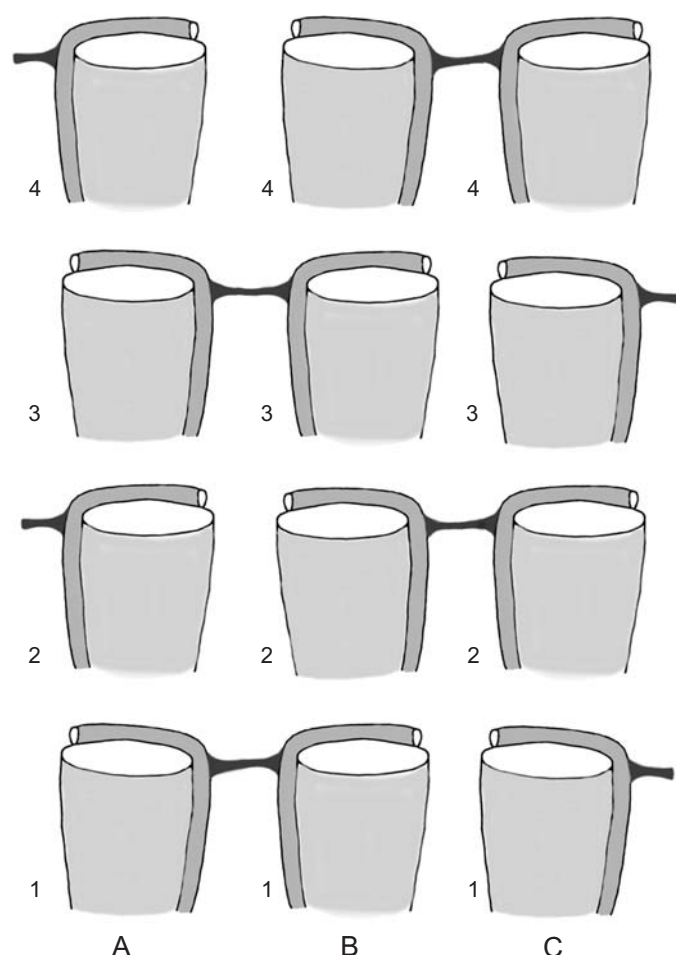

Fig. 10. Diagram showing relation between bithecae (shaded) and dissepiments (black) within a fragment of dendroid graptolite *Dictyonema* cf. *cervicorne* Holm, 1890 rhabdosome. Note that dissepiments are formed between adjacent bithecae in "back to back" position (e.g., A1–B1). Abbreviations: A, B, C fragments of adjacent branches; 1–4 successive triads.

Acknowledgements

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