

The ultrastructure of some Ordovician graptoloid prosiculae

DENIS E.B. BATES



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The graptoloid prosicula (conus and cauda) forms the first part of the growing colony, and was probably secreted during a single continuous episode of growth. The wall is composed of a central unit of criss-cross fibrils (*fusellar fabric*), interlaced with parallel fibrils whose grouping appears as the spiral line (*spiral line fabric*). The conus is lined with a granular or felted sheet (*sheet fabric*). The diaphragm, at the apex of the conus, appears to be formed of fusellar fabric. The cauda is formed of fusellar and spiral fabrics with a central cavity apparently not open to the conus interior. An outer layer (*diamond mesh fabric*) of fibrils forming a diamond mesh covers both conus and cauda, and is itself overlain by longitudinal rods. The apex of the cauda is formed of a second domed diaphragm of criss-cross fibrils, covered by a sheet fabric. The nema is extended distally as a series of finger-shaped increments, overlain by bandages. An outermost layer of clustered fibrils (*stellate fabric*) is occasionally present, lying on, or formed by a modification of, the diamond mesh fibrils of the conus.

Key words: graptoloids, prosiculae, ultrastructure, stellate fabric, secretion.

Denis Bates, Institute of Earth Studies, University of Wales Aberystwyth, Aberystwyth, Dyfed SY23 3DB, U.K.

Introduction

The graptolite prosicula is the first-formed part of the growing rhabdosome, and was probably formed by the sicular zooid after metamorphosis of a free-living larva. Though the ultrastructural details of the graptoloid metasicula and thecate portion of the rhabdosome have been fully described (Towe & Urbanek 1973; Urbanek & Towe 1974, 1975; Crowther & Rickards 1977; Crowther 1981; Rickards & Dumican 1984; Bates & Kirk 1985, 1986a, 1986b; Bates 1987; Andres 1980), the detail of the prosicula has hitherto only been incompletely known (Urbanek & Towe 1975; Crowther & Rickards 1977; Bates & Kirk 1985, 1986b). This paper extends

their work, using siculae from the Upper Ordovician Viola Springs Limestone of Oklahoma, U.S.A.

It is difficult to assign any of the material to the species found in the Viola Springs Limestone, as graptoloid siculae are, with some exceptions, extremely uniform in character and dimensions. It is probable that all of the material belongs to diplograptid species, and that most belongs to *Geniculograptus typicalis*, which is by far the most common species.

Material has been examined in the light microscope, and by the S.E.M. and T.E.M. Material has been prepared for S.E.M. investigation in a number of ways: (1) whole siculae have been isolated from limestone using acetic or hydrochloric acid, washed in alcohol and deposited on the stub, (2) similarly isolated material has been broken, by pricking it with a needle, after deposition on the stub, (3) careful fracturing of rock, generally along the bedding planes, using a pair of carpenter's pincers.

Material obtained by fracturing is usually in the form of counterpart pieces, irregularly broken along the sicular and thecal walls, and reveals internal details in three dimensions, when viewed as stereopair photographs. This material has not been subject to any chemical treatment; loose fragments are blown off the surface prior to coating.

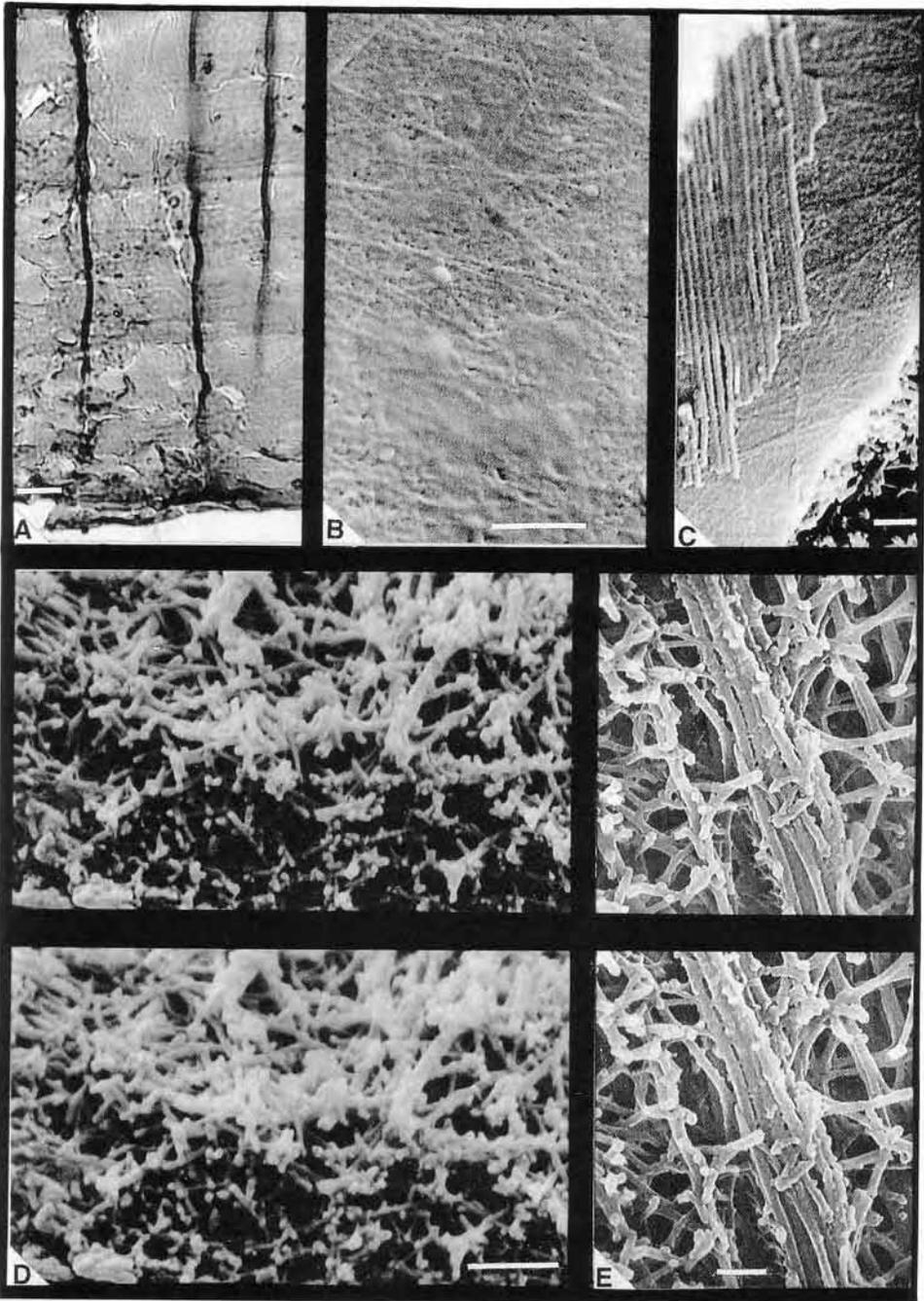
Material described in this paper has been deposited in the National Museum of Wales, Cardiff (abbreviated NMW), under the accession number 91.52G. Each stub is individually numbered: e.g. the full number of Stub 784 is 91.52G.784. Where several specimens are on a stub they are lettered as, for example, 487/B. Negatives are also deposited under this accession number.

Previous work on the structure of the prosicula and nema

Light microscopy of prosiculae, metasiculae and early thecate stages, often using cleared specimens, has revealed the general structure and stages of growth of the sicula (e.g. Kraft 1926; Bulman 1932–1936, 1944–1947, 1970; Kozłowski 1949, 1971; Hutt 1974).

The prosicula always appears complete, and is generally thought to have been secreted in a single 'increment' of growth (Kozłowski 1971; Rickards 1975), presumably as the housing of a sexually produced larval siculozoid. The main cup is the hollow conical *conus*, with a proximal prolongation of its apex forming the *cauda* (or *nema prosiculae* of Kraft

Fig. 1. □A. Light micrograph of the spiral line fabric in a chemically isolated prosicula. Parallel dark lines increase in density towards each turn of the spiral line itself. The dark vertical lines are longitudinal rods. NMW 91.52G.23128, neg. 84/39/1. Scalebar 10 μ m. □B. Inner surface of prosicula. Finely granular inner sheet fabric is overlain by sparse random fibrils. The smooth areas in the lower half of the picture may not be part of the rhabdosome, but a post-mortem deposition of material. Stub NMW 91.52G.753/A, neg. 86/37/26. Scalebar 1 μ m. □C. Inner surface of prosicula, with internal bandage overlying the inner sheet fabric.



The bandage has no covering sheet fabric. Stub NMW 91.52G.15/D2, neg. 85/15/6. Scalebar 2 μ m. \square D. Stereopair photograph of fusellar fabric of the core of the prosicular wall. Stub NMW 91.52G.631/C, neg. 86/39/35-36. Scalebar 1 μ m. \square E. Stereopair photograph of spiral line and fusellar fabrics, at the spiral line itself, aperture of prosicula to the left. The two fabrics are meshed together. Stub NMW 91.52G.763/A, neg. 86/45/9-10. Scalebar 0.2 μ m.

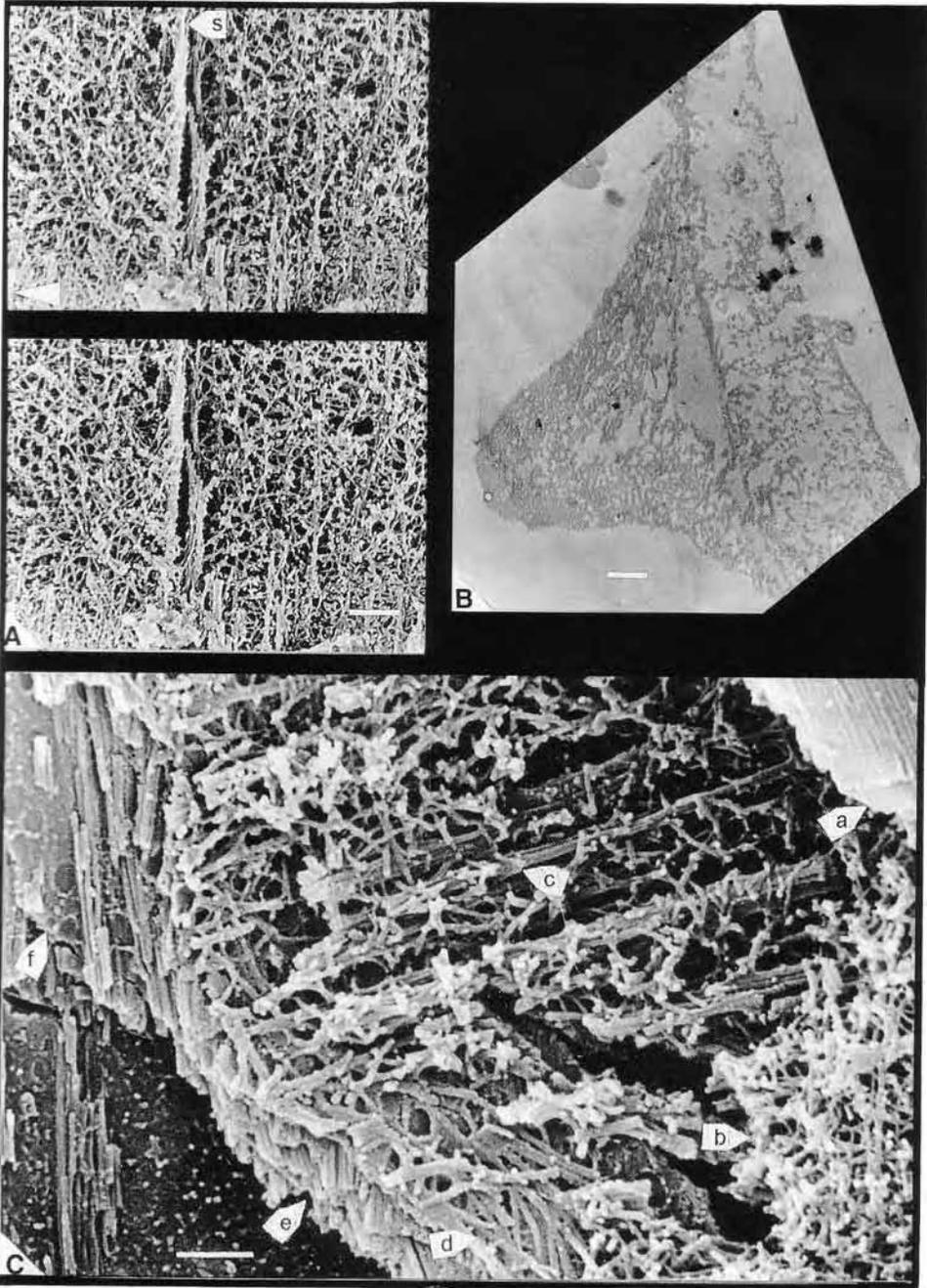
1926). The cauda has a rounded end (in the Tremadocian forms described by Hutt (1974)). Both the cauda and the *diaphragm*, a dark partition across the neck of the conus, are thought to be invariably present in the planktonic graptoloids (Hutt 1974: p. 80). The spiral line, coiled with either a left or right handed thread (apparently in equal proportions), forms a steep spiral in the cauda and a gentler one in the conus. In transmitted light the line actually marks the apertural edge of a band of parallel lines, becoming darker towards the edge (Fig. 1A). The band has the same width in both the cauda and the conus, and this accounts for the different spiral angles. Towards the aperture of the prosicula, however, the width of the band decreases, so that it becomes tangential to the aperture.

The next stage is marked by the appearance of the longitudinal rods, running along the length of the both conus and cauda. They do not all run the full length of both, but appear to be spaced so that they occur at intervals around the conus of about 50 μm : this means that some rods do not extend onto the cauda, but appear to taper out on the shoulder of the conus. Others do not reach the aperture. They appear to increase in number by interpolation of later rods between earlier ones (Bulman 1970: fig. 48).

With the addition of metasicular increments and, later, the first thecae, the sicula becomes more opaque as cortical tissue is added. This is now known from scanning electron microscope investigation to be in the form of cortical bandages (Crowther & Rickards 1977), but the bandages can be seen under the light microscope (Wiman 1895; Kraft 1926; Bulman 1932–1936, 1944–1947; Andres 1980; Crowther 1981).

Electron microscopy of the nema and prosicula commenced with the classic work of Urbanek & Towe (1975) using the transmission electron microscope. This showed that the nema in *Didymograptus* (Urbanek & Towe 1975: pl. 2: 1) has an external wall, 40 μm in diameter, surrounding a central 'canal' of 15m diameter, filled with a loose mat of fibrils, considered by them to be similar to the fusellar fabric of thecae. The wall structure they described as being similar to that of the cortex of the thecae. Close to the apex of the conus (Urbanek & Towe 1975: pl. 7), the cauda appeared similar to the nema, but with condensations of fibrils within the central portion marking, according to Urbanek & Towe (1975), growth lines. In *Pristiograptus* the central canal was narrower (1–1.6 μm diameter) and appeared to be alternately filled with fibrils or empty. They considered

Fig. 2. □A. Stereopair photograph of spiral line and fusellar fabrics, at the spiral line itself (S). Arrow points to the aperture of the prosicula. At the spiral line, its parallel fibrils appear to be present within the full thickness of the fusellar fabric layer; elsewhere they are mainly towards the surface of this layer. Stub NMW 91.52G.763/A, negs 86/38/37-8. Scalebar 2 μm . □B. TEM Micrograph of the thickness of the prosicular wall and a longitudinal rod. The bulk of the wall thickness is formed of the fusellar fabric, the inner continuous layer is the inner sheet fabric, and the outer layer represents the diamond mesh fabric. It is clearly overlain by the longitudinal rod. This appears to be filled with a denser apparently random mesh: however, as can be seen in Fig. 3C the fabric here is of parallel fibrils linked by cross



pieces. Neg. NMW 91.52G.84/42/4362. Scalebar 1 μm . □C. Fractured cross-section of prosicular wall, viewed from inside. Stub NMW 91.52G.15/D1, neg. 85/13/3. Scalebar 1 μm . Abbreviations: a – inner sheet lining with internal bandage; b – fusellar fabric; c – spiral line fabric meshing with fusellar fabric; d – diamond mesh fabric; e – external bandages; f – external sheet fabric of a bandage with granules and vesicles.

it unlikely that the central 'canal' contained soft tissues (Urbanek & Towe 1975: p. 7).

Urbanek & Towe (1975) described the conus as having an outer cortical layer similar to that of the thecae, continuous with that of the nema, a central wall of a loose mat of fibrils with arcuate condensations of fibrils rather like those of thecal increments, and a compact sheet-like inner layer (Urbanek & Towe 1975: p. 9). At the prosicular apex they were uncertain about the detailed structure, but thought that the middle layer was likely to be continuous with the fibrous filling of the cauda. The diaphragm appeared to be formed of a double layer of condensations of fibrous material (Urbanek & Towe 1975: p. 12).

Scanning electron microscope investigation of prosiculae commenced with the work of Crowther & Rickards (1977: pl. 5: 3-4), illustrating the prosicula of *Climacograptus inuiti*. Bates & Kirk (1985, 1986b) illustrated and described the various fabrics making up the prosicular wall, together with the ultrastructure of the longitudinal rods. However they did not examine the cauda, or the relationship between the conus, cauda and nema which is necessary for an understanding of the nature and growth of the rhabdosome.

Andres (1980: fig. 67) figured a TEM longitudinal section of a nema showing an infilling of fibrils, and a dome-shaped closure of a dense material. More recently Mitchell & Carle (1986) have described the nema and nemal vane of *Pseudoclimacograptus scharenbergi*, which appears to be hollow in transverse section under the TEM.

Primary prosicular fabrics

The prosicular wall is normally three layered (Bates & Kirk 1985, 1986b), having: (1) an inner prosicular sheet layer; (2) a middle fibrous layer, comprising two components: (a) fusellar fabric and, (b) spiral line fabric; and (3) an outer layer with fibrils arranged in a diamond mesh.

It is possible that these three layers were secreted sequentially, but in all the material examined all three layers are present. It may be that, even if the layers were secreted successively, the prosicula was not sufficiently robust to be normally preserved until all three layers were deposited. The fusellar and spiral line fabrics are intimately intermingled, and must have been secreted at the same time.

Fig. 3. □A. Apertural end of a longitudinal rod, with diamond mesh fabric beneath and lateral to it. Stub NMW 91.52G.765, neg. 86/52A/31. Scalebar 5 µm. □B. Diamond mesh fabric, with spiral line (s) just beneath and interrupting it. Longitudinal rod on right. Stub NMW 91.52G.655/F, neg. 88/11/13. Scalebar 2 µm. □C. Internal fabric of a longitudinal rod. Fibrils parallel to its length are connected by irregular cross-pieces. Stub NMW 91.52G.211,



neg 86/29/17. Scalebar 0.2 μ m. □D. Fractured longitudinal section of a cauda. Arrows point to successive passes of the spiral line. Stub NMW 91.52G.646, negs 86/34/3-4. Scalebar 5 μ m. □E. Stereopair photograph of fractured longitudinal section of cauda. Fusellar fabric lines the central cavity, and is surrounded by and meshed with orientated fibrils of the spiral line fabric. Stub NMW 91.52G.739/A, negs 87/1/35-36. Scalebar 2 μ m.

Inner sheet fabric. — This forms a lining to the conus: it fades out at the apertural rim (Bates & Kirk 1985: fig. 1b), and may also form a dome at the apex of the conus (see below).

The sheet fabric (Fig. 1B, C) is thin, some 0.07 μm in thickness, with a fine granular texture. Sparse randomly orientated fibrils about 0.06 μm in diameter cover its inner surface.

In sections viewed by the TEM (Urbanek & Towe 1975: pl. 5: 3–4) it appears as a thin continuous black line, but is thickened by the addition of secondary internal cortex. This is formed, like the outer cortex, of bandages, each a single layer of parallel fibrils without any covering sheet fabric (Figs 1C, 2C; Bates & Kirk 1985, 1986b).

Fusellar fabric. — This fabric (*criss-cross fabric* of Bates & Kirk 1985) forms the bulk of the wall thickness of the conus. It appears to be identical to the similar fusellar fabric which makes up the bulk of fusellar increments (Urbanek & Towe 1975; Bates & Kirk 1985, 1986b): it is made of fibrils about 0.06 μm in diameter, which apparently do not anastomose (Figs 1C–D, 2C). They are parallel-sided or cylindrical in form, and are linked by what appears to be a 'gluey' or *ground* substance. There is no sign of the annulations figured by Crowther (1981) in cortical fibrils (which could have been caused by a degradation or chemical alteration of the fibrils). The ground substance itself may be a degradation product of another organic substance: Bates & Kirk (1985: pp. 389–390, 1986b) have suggested that in life the fibrils may have been secreted and suspended in a gel of organic material. The fibrils of the fusellar fabric appear to become more closely packed in the region of the diaphragm.

It should be noted that in fractured material (Figs 1C–C, 2C) there is no mineral infilling or cement in the interstices within this layer, even though the enclosing rock is a well cemented limestone. The organic material (or pore fluid) that occupied these spaces when the material was entombed evidently had little communication with the pore fluids in the sediment itself.

The 'spiral line'. — The spiral line (Figs 1A, D, 2C) is formed by spirally arranged parallel fibrils, also of 0.06 μm diameter, *within* the fusellar fabric of the middle layer. The fibrils are held together, and also bound to the fusellar fibrils, by the same ground substance which holds the latter together. The fibrils increase in number towards the 'spiral line' itself, giving the increased opacity seen in the light microscope (Fig. 1A). At the spiral line, the fibrils form a cluster which extends through the thickness of the middle layer (Figs 1E, 2A). Elsewhere the spiral line fibrils are concentrated towards the outer and inner surfaces of the middle layer (Figs 2A, C), and their spacing increases proximally, until there are very few adjacent to the previous pass of the spiral line (Figs 1A, 2A). The overall disposition of these fibrils then gives the appearance of a crude arch-shaped increment. This pattern also agrees with the illustrations of Urbanek & Towe (1975: pls 6, 7).

It is conceivable that this middle layer was formed as a continuously proliferating single 'fusellar' increment of growth, rather like the addition of a continuous strip of clay to form a coil pot (Kozłowski 1971: p. 327; Rickards 1975). However, both authors point out that growth stages of the prosicula have never been found, Kozłowski stating that 'the spiral band ... was developed in the larva simultaneously over its entire length'. He went on to suggest that the band continued to grow proximally, thus forming the nema. In contrast, it could be argued that (1) growth may have been very rapid, so that incomplete forms would be rarely found, and (2) in the absence of the outer and inner layers this prosicula would have been too delicate to have been preserved.

However, in the absence of incomplete prosiculae this cannot be proved, and it is equally possible that the whole prosicula, including the cauda, was formed at once.

At the aperture of the prosicula the height of the spiral line 'arch' decreases, so that the 'arch' itself forms the rim of the prosicula (comp. with Urbanek & Towe 1975: pl. 8: 2). This would correspond with the tapering out of a fusellar increment at a zig-zag suture.

At the apex of the conus the material shows that the preferred interpretation of Urbanek & Towe (1975), illustrated in their fig. 2A, is correct: the fusellar and spiral line fabrics are continuous from the cauda to the conus. The variations in the placing and density of the fusellar fabric as described above account for the differences in density described by them.

Outer diamond-mesh fabric. — The entire conus and cauda is covered by a thin (about two fibrils thick) layer of fibrils, again about 0.06 μm in diameter (Figs 2C, 3A-B). The fibrils form a set which has an overall orientation inclined at about 15° to the long axis of the prosicula, but at right angles to the spiral line in the conus (Fig. 3B; Bates & Kirk 1985: fig. 1a, f; 1986: pls 1: 6, 2: 7, 9). Most fibrils are inclined at about 15° to this overall orientation, and they cluster together at intervals to produce a meshwork with elongated diamond-shaped gaps. These fibrils also seem to be cemented together by a ground substance. Towards the aperture (Figs 3A, 6C) the fabric becomes more random, and eventually the fibrils become parallel to one another and to the aperture.

This layer was not detected by Urbanek & Towe (1975), but it would have been difficult to have done so given only TEM thin sections. It may show up in their pl. 5: 4 as a slightly denser concentration of fibrils to the left of their middle component.

Longitudinal rods

The longitudinal rods are clearly secondary (Bulman 1970: fig. 48; Bates & Kirk 1985, 1986b), as some siculae lack them. They are T-shaped in cross section, having a broad base and a central raised portion (Figs 2B, 3A). Urbanek & Towe (1975) thought that their central cores (in *Didymo-*

graptus) were swellings of the middle layer of the prosicula, but in fractured cross-sections they are clearly seen to be a separate component of growth, formed entirely of longitudinal fibrils and deposited outside the diamond-mesh fabric (Bates & Kirk 1985: fig. 2c, 1986: pl. 1: 4). This is also clearly shown in the TEM section of Fig. 2B. In the section of the prosicula of *Pristiograptus* illustrated by Urbanek & Towe (1975: pl. 10: 3) the middle wall and its outer layer of diamond mesh is overlain by an apparently fusellar fabric filling in the core of the longitudinal rod. However in the SEM this infilling is seen to be a more ordered fabric (Fig. 3C) in which spaced parallel longitudinal fibrils are linked by spaced transverse fibrils. The apertural end of a longitudinal rod is shown in Fig. 3A: the parallel fibrils tending to splay out as the aperture is approached.

The prosicula of *Pristiograptus* was thought by Urbanek & Towe (1975) to be distinctly different from that of *Didymograptus*, but this appears to be mainly due to the increased corticization of the former: the layers shown in their pl. 10 being formed of about 10 bandages, burying the longitudinal rod.

Cauda

The cauda, as shown by the continuity of the spiral line, forms with the conus a single unit of secretion. Its apertural end is marked by a mat of fibrils forming the diaphragm, its apex by a dome convex towards the nema. Thus the interior of the cauda would appear to be blocked both from the living space within the conus and from the exterior at its apex.

The cauda is cylindrical in form, with fusellar and spiral line fibrils, as described above, forming the innermost component of the wall, beneath diamond mesh fabric, longitudinal rods, and cortical bandaging (Fig. 3E-F). The inner sheet layer of the conus is not present. However the central core of the cauda seems to have been largely empty. This is suggested by the way in which it is preserved in a flattened form in material such as Stub G211 (Fig. 4A). Here a dense meshwork of these two fabrics is present, yet it is not sufficient in volume to have filled the originally cylindrical space, and does not appear to have been compacted to a greater density than elsewhere. In unflattened fractured material SEM stereopairs clearly confirm this (Fig. 3F).

The spiral line fabric has been illustrated by Urbanek & Towe (1975: pl. 2: 2) in TEM cross-section. The fusellar fabric is also present apically of the diaphragm, as is seen in their pl. 7: 1, where the whole of the cauda appears to have been infilled by fusellar fabric.

Fig. 4. □A. Spiral line fabric meshed with fusellar fabric in fractured cross-section of flattened cauda. Note the increase in density of parallel fibrils approaching the spiral line itself. Stub NMW 91.52G.211, neg. 86/29/25. Scalebar 1 μ m. □B-C. Fractured longitudinal section of



cauda and proximal portion of nema, part and counterpart. Stub NMW 91.52G.764/A-B, negs 86/37/7-8, 86/37/13-14. Scalebar 5 μ m. □D-E. Close-up stereopair photographs of the diaphragm of Fig. 4B-C. NMW 91.52G, negs 86/46/17,19-21. Scalebar 0.5 μ m. Abbreviations: d - diaphragm at apex of cauda, a - wide portion of nema, with central cavity lined with fusellar fabric, b - narrower portion of nema, completely filled with fusellar fabric.

At the apex of the cauda in the specimen of Stub G764 there is a dome-shaped closure, apparently of sheet fabric, convex towards the nema (Fig. 4B–E). This is reinforced by some fibrils lying on its inner surface (Fig. 4D–E); just underneath it the fusellar fabric may not be present, where there may be a hollow: this could however be simply due to damage in the fractured longitudinal section.

As the proscicula lacks any outer sheet fabric, it is probable that the sheet fabric of this domed closure was deposited during the extension of the nema from the cauda. It would then correspond with the sheet fabric described by Bates & Kirk (1985) as forming the basal component of a fusellar increment.

The diaphragm

The diaphragm (membrane of Kraft 1926) of *Clonograptus/Adelograptus* was described by Hutt (1974: p. 81) as being a dark crescentic band across the apex of the conus. She thought that it was incomplete in most specimens, having a gap 'on one or on either side', and that it may have been produced after the secretion of the proscicula itself. As illustrated and described from a TEM section of *Didymograptus* by Urbanek & Towe (1975: p. 13; pl. 7: 1) it appears to be a condensation of fibrous material showing 'a number of disruptions filled by loose fibrous material'. These disruptions they thought were either primary imperfections or secondary preservational features.

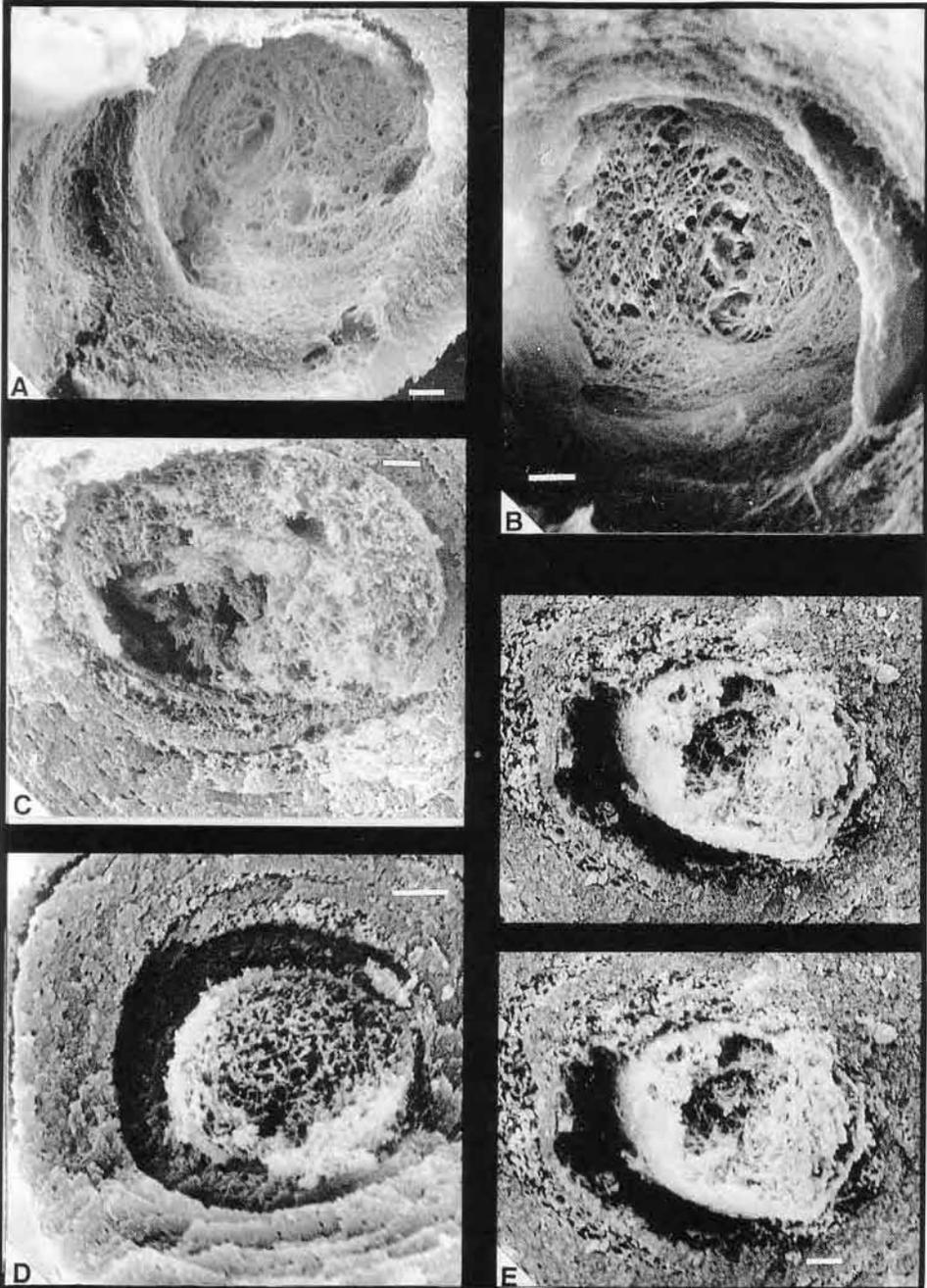
From this material, it is not possible to determine the structure of the diaphragm with complete confidence. In isolated material broken on the stub in the hope of revealing the diaphragm (Fig. 5A–B), the apex of the interior of the conus is plugged by fusellar fibrils of the middle layer of the proscicula, without any inner sheet fabric. Therefore the inner sheet fabric of the conus should die out before reaching the diaphragm, but none of the material shows this.

Fractured and flattened material does not show the diaphragm clearly. Some material (Stubs G209A, G763C) shows a condensation of fusellar fabric which apparently blocks the apex of the conus, though this region does not photograph well. It is not clear what has happened to the sheet fabric at this place.

The nema

As described by Urbanek & Towe (1975) the nema in *Didymograptus* is a thick walled tube with a central core about 15 μm in diameter. This core

Fig. 5. □A. Apex of proscicula with diaphragm at the base of the cauda, seen from the interior of the proscicula. Stub NMW 91.52G.799/A3, neg. 87/8/4. Scalebar 1 μm . □B. As Fig. 5A.



Stub NMW 91.52G.768/C5, neg. 87/5/31. Scalebar 1 μ m. \square C. Fractured cross-section of nema, completely filled with fusellar fabric. Stub NMW 91.52G.806, neg. 87/5/32. Scalebar 1 μ m. \square D. As Fig. 5C. Stub NMW 91.52G.806, neg. 87/5/36. Scalebar 2 μ m. \square E. Stereopair photographs of core of nema, probably a damaged incremental closure. Stub NMW 91.52G.805/H, negs 87/10/14-5. Scalebar 1 μ m.

is filled with a loose material of delicate fibrils about 400 Å in diameter. The wall appears identical in their sections with transverse sections of typical cortical tissue, or bandages. In *Pristiograptus* they describe a primary nema in a young specimen, though in the majority of adult specimens this has been replaced by a regenerated nema. The two types of nema apparently do not differ in ultrastructure. Their pl. 4 shows the primary nema as having a central region only about 1–1.6 µm in diameter, sometimes empty or sometimes filled with 'porous material'; the two conditions perhaps being repeated alternately along the nema. The transverse sections of the nema also show that individual cortical bandages taper out around the circumference of the nema. The fibrils are shown as having a distinctive internal lamination, and to be separated by dark or electron-dense material, the term *virgular fabric* being used to describe it.

Urbanek & Towe (1975) regard the two types of cortical fabric (normal in *Didymograptus*, 'virgular' in *Pristiograptus*) as being related to the different mechanical properties needed in the two genera: *Didymograptus* is axonilipous and *Pristiograptus* axonophorous.

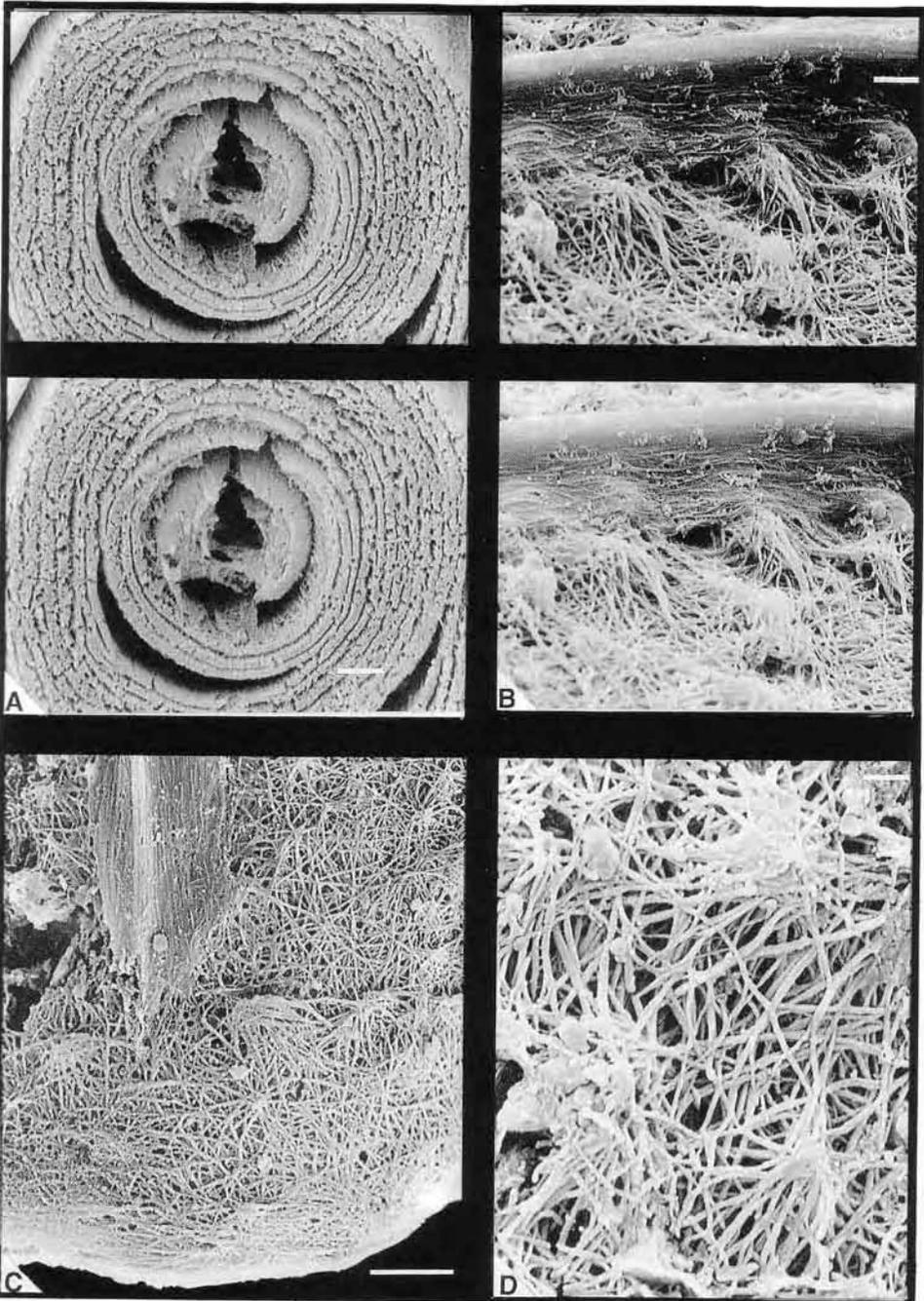
Andres (1980: fig. 67) has also figured longitudinal sections of a nema, showing a core of fusellar fabric, and closures convex distally.

Fractured longitudinal sections of the nemata of *Viola siculae* show that the central core is, as Urbanek & Towe (1975) showed, alternately filled with fusellar fabric or largely empty, the fusellar fabric in the latter portions being confined to a layer lining the outer walls (Fig. 4B–C). Fractured cross-sections of filled portions of isolated material show the fusellar fabric clearly (Fig. 5C–E).

The walls are formed principally of layers of bandages showing, in section, fabrics identical with the rest of the cortex. The dominant fabric is formed of parallel fibrils (Fig. 4C–E), separated by thin sheets with granules (Fig. 4E). The parallel fibrils are closely packed, or are separated by spaces, with irregular linkages between them. They do not show the virgular fabric (which probably reflects a structure internal to the fibrils), neither do they show flanged connections, as described by Rickards & Dumican (1984) in dendroids. The innermost layers of the wall will in fact be formed by the overlapping of successive increments of extension of the nema, i.e. form microfusellar extensions of each increment.

The nema grew distally from the apex of the cauda, and therefore should show increments of growth. These, as for the lacinial spines of *Phormograptus* (Bates & Kirk 1985, 1986b, 1987, 1991) should show dome-shaped closures formed by the sheet fabric sealing each increment, convex distally. These have so far not been recognized in any of the longitudinally fractured sections we have managed to make, but have been observed in isolated material. An incomplete or damaged increment was illustrated in Bates & Kirk (1986a: fig. 2b), and further examples are

Fig. 6. □A. Stereopair photographs of damaged closure in core of nema, viewed from the distal end of the nema. Stub NMW 91.52G.784/B, negs 86/53/16–7. Scalebar 2 µm. □B. Stereopair



photographs of stellate fabric overlain by a longitudinal rod. Stub NMW 91.52G.787/H, negs 87/1/10–11. Scalebar 2 μ m. □C. External surface and rim of proscicula. The stellate fabric gives way to a fabric of fibrils parallel to the rim, which probably strengthened it. Note also the end of a longitudinal rod. Stub NMW 91.52G.787/H, neg. 86/53/26. Scalebar 5 μ m. □D. Stellate texture. Stub NMW 91.52G.655/O, neg. 88/11/18. Scalebar 1 μ m.

shown here, in stereopairs (Figs 5D, 6A). In each case the dome-shaped end of the increment, which is convex distally, is damaged.

The increments of growth of a typical nema are probably much more widely spaced than those in the lacinia of *Phormograptus*. For example, in a Silurian orthograptid sicula with only a few metasicular increments the nema can be seen to have reached a length of 2 mm. This would explain the difficulty of observing them, particularly in TEM cross-section.

Stellate fabric

Specimens UCWG655/0, G787H, prosciculae of an unknown species, have an unusual fabric either external to the diamond mesh fabric or perhaps forming a modification of it (Fig. 6B–D).

The outermost fibrils are arranged randomly over much of the surface, but aggregate to form 'stars'. These are clumps of fibrils, which are raised above the general surface level (Fig. 6B). Individual fibrils may run across a star from one side to the other, or they may end on the summit or flanks of the star: there is no definite relationship between them and the topography of the star, apart from their concentration on the stars (Fig. 6D). The longitudinal rods overlie the stellate fabric, and their flanks bulge upwards where they cross the stars (Fig. 6B).

Discussion

Although the structure of the proscicula differs markedly from that of the later incremental rhabdosome, there are nevertheless striking similarities between the fabrics which make up the two portions of the rhabdosome: the fusellar fabric is similar to that of thecal increments; the spiral line and diamond mesh fabrics compare well with the parallel fibrils of a lamella present beneath the outer sheet fabric of an increment, both in parallelism and position; the longitudinal rods have similarities with bandages.

Four main conclusions may be drawn from the observations made above:

(1) The secretion of the main body of the conus and cauda was probably a single event. This is shown by the continuity of the spiral line and fusellar fabrics through both portions of the proscicula. The inner sheet fabric and the outer diamond mesh fabric *may* both have been deposited later, to give rigidity to the young proscicula. The longitudinal rods were later additions, although they were added before the start of growth of the metasicula (Fig. 6C).

(2) The fabrics which make up the proscicula are at least analogous to those of the metasicula and the rest of the rhabdosome (both of fusellar increments and cortical bandages).

(3) The interiors of the cauda and the nema were not empty, forming in life a conduit for soft tissue, but are filled or intermittently blocked by skeletal tissues.

(4) The nema in these axonophorous graptolites was formed by the addition of finger-like increments of growth, extending distally from the end of the cauda. It appears to have been made in the same way as other spines and lists, such as the virgella, scopular spines and lacinial lists (Bates & Kirk 1986b, 1987; Bates 1987).

Two main hypotheses have been proposed for the deposition of the graptolite skeletal tissue: the extrathecal tissue model and the mortaring model. According to the extrathecal tissue model, the entire graptolite rhabdosome was enveloped in soft tissue, beneath which the skeleton was deposited (e.g. Kirk 1972, 1994 and references therein; Urbanek *et al.* 1982). A colony constructed like that of the hemichordate *Rhabdopleura* is envisaged in the mortaring model, with the rhabdosome (a coenocidium, not a skeleton) formed by material exuded from the pre-oral lobes of zooids free to wander from their thecal tubes over the outer surface (e.g. Kozłowski 1949; Rigby 1994). A dual mode of secretion has also been proposed, by Rickards (1975), Crowther & Rickards (1977), Mitchell & Carle (1986) and Mitchell (1995). The first two authors suggested that soft tissue passed up the interior of a hollow nema, exuding out of the open growing end to deposit the skeletal tissues beneath it. Mitchell & Carle (1986) proposed that the soft tissue within the nema laid down the skeletal tissue on the *inside* of the nema, which would have been gradually inflated as more material was added. Mitchell (1995) has recently suggested that in the early (axonolipous) graptoloids the nema was indeed secreted internally, forming a homologue of the pterobranch stolon, but that in some of the later (axonophorous) graptoloids it was secreted by external mortaring.

It is clear that the nema, in this material, was secreted from the outside: the evidence does not support the concept of a hollow nema; it contains closures and can be filled with fusellar fabric. This is probably true also for the material described by Hutt (1974), which was of flattened material examined only by light microscope. That material also shows a similar spiral line and diaphragm, the appearance of a hole in the latter (Hutt 1974: p. 81) may be due to the flattening and consequent distortion of the diaphragm. Again it is not clear from her photographs that the apex of the cauda is indeed broken or resorbed before extension of the nema.

The ultrastructure of the prosicula does not provide unequivocal evidence for either the extrathecal model or the mortaring model. However, the number and range of fabrics seen in the prosicula exceed those described in pterobranchs. It is difficult to envisage the contortions of shape necessary for the pre-oral lobe to secrete, in one phase of secretion, the conus and cauda with their four initial fabrics, followed by the very much slimmer longitudinal rods.

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References

- Andres, A. 1980. Feinstrukturen und Verwandtschaftsbeziehungen der Graptoliten *Paläontologische Zeitschrift* **54**, 129–170.
- Bates, D.E.B. 1987. The construction of graptolite rhabdosomes in the light of ultrastructural studies *Indian Journal of Geology* **59**, 1–28.
- Bates, D.E.B. & Kirk, N.H. 1985. The fine structure of graptolite periderm. In: A. Bairati & R. Garrone (eds) *Biology of Invertebrate and Lower Vertebrate Collagens*, 389–395. Plenum Publishing Co.
- Bates, D.E.B. & Kirk, N.H. 1986a. Mode of secretion of graptolite periderm, in normal and retiolite graptolites. In: C.P. Hughes & R.B. Rickards (eds) *Palaeoecology and Biostratigraphy of Graptolites. Geological Society of London Special Publication* **20**, 221–236. (Proceedings of the Second International Graptolite Conference, Cambridge 1981)
- Bates, D.E.B. & Kirk, N.H. 1986b. Graptolites, a fossil case-history of evolution from sessile, colonial animals to automobile superindividuals. *Proceedings of the Royal Society of London* **B228**, 207–224.
- Bates, D.E.B. & Kirk, N.H. 1987. The role of extrathecal tissue in the construction and functioning of some Ordovician and Silurian retiolitid graptolites. *Bulletin of the Geological Society of Denmark* **35**, 85–102.
- Bates, D.E.B. & Kirk, N.H. 1991. The ultrastructure, mode of construction and functioning of Ordovician retiolitid graptolites from the Viola Springs Limestone, Oklahoma. *Modern Geology* **15**, 131–286.
- Bulman, O.M.B. 1932–1936. On the graptolites prepared by Holm, I–VII. *Arkiv für Zoologie* **24A**, 1–46; **26A**, 1–52; **28A**, 1–107.
- Bulman, O.M.B. 1944–1947. Monograph of Caradoc (Balclatchie) graptolites from limestones in Laggan Burn, Ayrshire. *Monograph Palaeontographical Society London*, 1–78.
- Bulman, O.M.B. 1970. Graptolithina, with sections on Enteropneusta and Pterobranchia. *Treatise on Invertebrate Paleontology, Part V, 2nd Edition*, i–xxxii; V1–V163. Geological Society of America and University of Kansas Press.
- Crowther, P.R. 1981. The fine structure of graptolite periderm. *Special Paper in Palaeontology* **26**, 1–119.
- Crowther, P.R. & Rickards, R.B. 1977. Cortical bandages and the graptolite zooid. *Geologica Palaeontologica* **11**, 9–46.
- Hutt, J. 1974. The development of *Clonograptus tenellus* and *Adelograptus hunnebergensis*. *Lethaia* **7**, 79–92.
- Kirk, N.H. 1972. Some thoughts on the construction of the rhabdosome in the Graptolithina, with special reference to extrathecal tissue and its bearing on the theory of automobility. *Publications of the Department of Geology Universtiy College of Wales, Aberystwyth* **1**, 1–21.
- Kirk, N.H. 1994. Coordination of construction and functioning of the graptolite colony. In: Chen Xu, D.-D. Erdtmann, & Ni Yu-nan (eds) *Graptolite Research Today*, 197–216. Nanjing University Press. (Proceedings of the 4th International Graptolite Conference)
- Kozłowski, R. 1949. Les graptolithes et quelques nouveaux groupes d'amimaux du Tremadoc de la Pologne. *Palaeontologica Polonica* **3**, 1–235.

- Kozłowski, R. 1971. Early development stages and the mode of life of graptolites. *Acta Palaeontologica Polonica* **16**, 313–343.
- Kraft, P. 1926. Ontogenetische Entwicklung und Biologie von *Diplograptus* and *Monograptus*. *Paläontologische Zeitschrift* **7**, 207–249.
- Mitchell, C.E. 1995. An alternative pterobranch model for secretion of the nema and associated structures in graptolites. *Abstracts for the Fifth International Graptolite Conference of the Graptolite Working Group of The International Palaeontological Association*. Published in *Graptolite News* No. 8, 54–56. Department of Geology, State University of New York, Buffalo, New York.
- Mitchell, C.E. & Carle, K.J. 1986. The nematularium of *Pseudoclimacograptus scharenbergi* (Lapworth) and its secretion. *Palaeontology* **29**, 373–390.
- Rickards, R.B. 1975. Palaeoecology of the Graptolithina, an extinct class of the Phylum Hemichordata. *Biological Reviews* **50**, 397–436.
- Rickards, R.B. & Dumican, L.W. 1984. The fibrillar component of graptolite periderm. *Irish Journal of Geology* **6**, 175–203.
- Rigby, S. 1994. Hemichordate skeletal growth, shared patterns in *Rhabdopleura* and graptoloids. *Lethaia* **27**, 317–324.
- Towe, K.M. & Urbanek, A. 1973. Collagen-like structures in Ordovician graptolite periderm. *Nature* **237**, 443–445.
- Urbanek, A., Koren, T.N., & Mierzejewski, P. 1982. The fine structure of the virgular apparatus in *Cystograptus vesiculosus*. *Lethaia* **15**, 207–228.
- Urbanek, A. & Towe, K.M. 1974. Ultrastructural studies on graptolites, 1: The Periderm and its Derivatives in the Dendroidea and in *Mastigograptus*. *Smithsonian Contributions to Paleobiology* **20**, 1–48.
- Urbanek, A. & Towe, K.M. 1975. Ultrastructural studies on graptolites, 2: The Periderm and its Derivatives in the Graptoloidea. *Smithsonian Contributions to Paleobiology* **22**, 1–48.
- Wiman, C. 1895. Über die Graptoliten. *University of Uppsala, Geology Institute Bulletin* **2**, 239–316.

Streszczenie

Proscicula graptolitów jest najwcześniej tworzoną częścią rabdozomu i była najprawdopodobniej budowana przez pierwszego zooida tuż po jego metamorfozie ze swobodnie żyjącej larwy. Przedmiotem niniejszej pracy jest ultrastruktura prosciculi z późnoordowickiego wapienia Viola Springs. Proscicule z tej formacji skalnej zapewne należą do dwuseryjnych graptolitów, których najpospolitszym występującym tam gatunkiem jest *Geniculograptus typicalis*. Na przełamach ścianek prosciculi obserwowanych w skaninowym mikroskopie elektronowym ukazuje się ich trójwarstwowa budowa, z wyściółką wewnątrz o nieregularnie orientowanych włóknach, środkową ścianą z wplecionymi włóknami tworzącymi linię spiralną oraz zewnętrzną warstwą o włóknach krzyżujących się w rombowy splot. Środkowa warstwa ściany tworzona była zapewne w jednorazowym akcie sekrecji ale jej struktura nie różni się istotnie od fuzellarnych elementów rabdozomu. Nema powstawała jako seria palcowatych przyrostów okrytych przez bandaże; jej wnętrze jest lite, nie pozostawia miejsca na jakiegokolwiek miękkie tkanki.