The Silurian retiolitid graptolite *Plectograptus*: New observations and new species

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The Ludlow genus *Plectograptus*, with the type species *Retiolites macilentus* Törnquist, 1887, collected from Thuringia (Germany), has been a widely-identified, monospecific, but poorly understood taxon for almost one hundred years. This was due to poor and incomplete preservation of the type material, and misidentification by subsequent authors up to 1995. The original, and only, type specimen of *P. macilentus* collected by Törnquist being lost, a neotype is herein selected from a small collection of Thuringian material. The genus has now been redefined and based on this, and SEM studies of isolated material, the defining characteristics of the genus are (i) the possession of a simple ancora umbrella with five radial lists with an incompletely developed rim; (ii) an ancora umbrella separated from lateral ancora sleeve walls by exceptionally large lateral orifices; (iii) the possession of mid-ventral lists; (iv) simple, orderly zigzag lateral wall ancora sleeve lists. Recently, two additional species, *P. robustus* and *P. wimani*, previously placed in different genera, were assigned to *Plectograptus*. This study recognizes three new species: *P. mobergi*, *P. toernquisti*, and *P. trijunctus*, bringing the total number of species to six. Species are distinguished by the presence or absence of genicular processes, inclination of the thecal ventral walls and mid-ventral lists, presence or absence of reticular lists, and three-way or four-way sleeve/lateral rod/apertural lip junctions.

Key words: Graptoloidea, Retiolitidae, *Plectograptus*, rhabdosome, Silurian, Ludlow.

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Introduction

The genus *Plectograptus* was erected by Moberg and Törnquist (1909) for the species *Retiolites macilentus* Törnquist, 1887. Although the genus was monospecific for a long time, it became one of the best-known retiolitids of the Upper Silurian (e.g., Bouček and Münch 1952). The first isolated material was described and illustrated by Eisenack (1951), as *Retiolites* (*Plectograptus*) *tetracanthus* from Baltic erratic boulders. Kozłowska-Dawidziuk (1995, 2002) included two more species in the genus: *Plectograptus wimani* (Eisenack, 1951) and *P. robustus* (Obut and Zaslavskaya, 1983).

A serious problem for taxonomic stability, however, has long been posed by the poor preservation and incompleteness of the type material of *P. macilentus*. Only a schematic diagram with no scale was used to illustrate the species (Törnquist 1887: fig. 3; reproduced here as Fig. 1B) in the original description, but a photograph of the type was later provided by Moberg and Törnquist (1909: pl. 1: 10). This specimen lacks the proximal (ancora) end.

The original Törnquist type specimen of 1887 from the Wetterahammer area, Thuringia has presumably been lost. However, a collection of several specimens, not part of the original collection, but like the type, derived from the Lower Graptolitic Shales of the Wetterahammer area, are present in the collections of the Senckenberg Forschungsinstitut und Naturmuseum (Frankfurt/Main, Germany). The best specimen of that collection is herein chosen as the neotype (Fig. 1G). That specimen clearly shows several of the significant characteristics necessary for genus and species identification, although it lacks a complete proximal end, so necessary for the recognition of the "*Plectograptus* ancora" (see below), and for the overall recognition of the subfamily Plectograptinae Bouček and Münch, 1952.

Scanning electron microscopy (SEM) of three-dimensionally preserved, isolated material is now routinely applied to study retiolitids in more detail. SEM study reveals important new characters not normally shown in flattened material. Material recently isolated from Baltic erratic boulders and other localities shows a variety of rhabdosomal

[1] Nancy H. Kirk passed away on 4th September 2005.

characters sufficient to justify the recognition of a number of distinct species and, thus, specimens shown as SEM micrographs and assigned by Lenz (1993) and Kozłowska-Dawidziuk (1995) to *Plectograptus macilentus* (*sensu* Bouček and Münch 1952), are herein recognized as new species (see below).

The purpose of this paper is to elucidate the morphology of the genus *Plectograptus*, to redefine the existing species, to designate a neotype for *P. macilentus* and to describe new species.

Institutional abbreviations.—LO, Lund University Museum, Lund, Sweden; MB.G, Museum für Naturkunde, Berlin, Germany; NMW, National Museum of Wales, Cardiff, United Kingdom; SMF, Forschungsinstitut Senckenberg, Frankfurt/Main, Germany; SMD, Staatliches Museum für Mineralogie, Dresden, Germany; ZPAL, Institute for Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations.—EEP, East European Platform.

Terminology and morphology

General terminology for the retiolitids has been listed by Bates et al. (2005). The term pleural list has been used for the thickening of the sides of the aperture in the Glossograptidae and Retiolitidae (e.g., Lenz 1993). However, with the identification in the retiolitids of the ancora sleeve as being an outer extrathecal structure, it is clear that in most retiolitids the apertural openings and, particularly those of all higher forms are not homologous with the thecal apertures of other graptolites (Bates and Kirk 1984, 1992). Instead, each opening, or orifice, is bounded proximally by the thecal lip, distally by the next thecal lip, e.g., in *Retiolites* (Bates et al. 2005) or genicular list, e.g., in *Spinograptus praerobustus* Lenz and Kozłowska-Dawidziuk, 2002 (Fig. 2A, C), and laterally by longitudinal lists of the ancora sleeve, the pleural lists (Fig. 2) (see Bates et al. 2005: 710). Proximal to the first two thecae, the pre-th1^1 and pre-th1^2 orifices are bounded proximally by portions of the rim of the ancora umbrella, and laterally by the most proximal pleural lists (Figs. 2B, 3).

The lists of the ancora sleeve may be divided into primary lists, which are formed at the growing end of the sleeve, marking stages in its extension, and secondary lists (reticular lists), formed on the already extended sleeve. Two different types of primary lists (A and B) are found in *Plectograptus* (Figs. 4–6). In type A lists the initial list has a proximally-facing insertion seam (Fig. 5A) which marks the extension of the initial (presumed) fusellum of the ancora sleeve. These lists run largely transversely, and are usually convex distally, as in *P. toernquisti* sp. nov. (Fig. 4B). They also mark pauses in the extension of the sleeve, as it grew in synchronicity with the thecae. Type B primary lists have an initial, first formed portion which has a concentric structure (Fig. 5B). The core is similar to the fusellar core of the spines found in both retiolite and other graptolites, and is surrounded by concentric, but asymmetric, layers of cortical appearance. Each list would appear to have grown forwards, initially as a spine, towards the genicular region of the thecal wall, making contact with it at the end of the genicular list (at the socket, see below, Fig. 6B$_5$). The side of the sleeve enwraps the thecal lateral apertural rods, being extended slightly later than the thecal wall. Beyond the thecal lip, the sleeve was again extended forwards as a spine. The extension of the fusellum of the next portion of the sleeve is then marked by an enwrapping seam on the list (Fig. 5B$_2$) and further thickening of the list is then by bandaging, which no longer forms as concentric structures. In effect, the type A list forms at the margin of a panel of fuselli; the type B list as a spinose projection with a fusellar core.

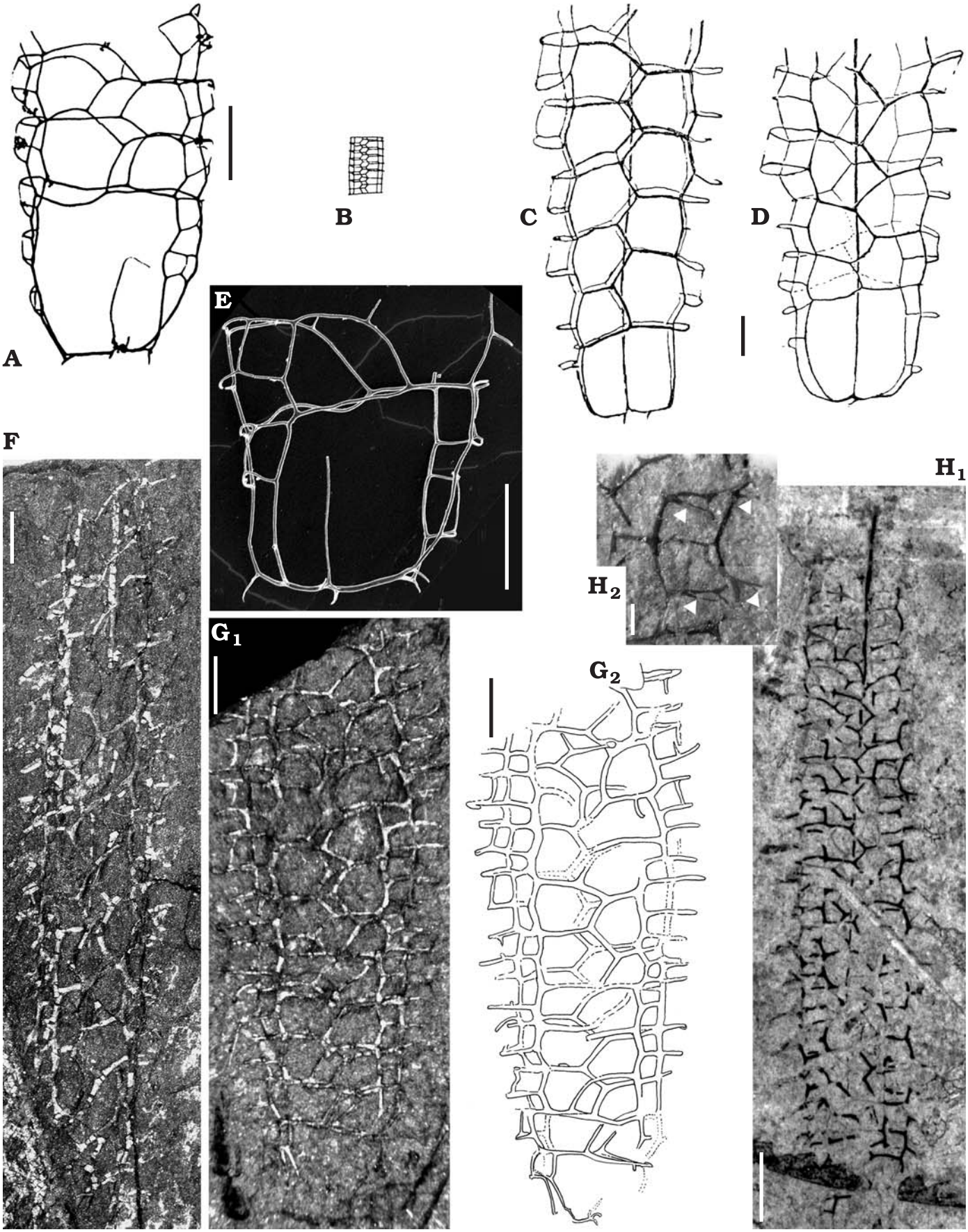
In species such as *P. toernquisti* there are quadruple (four-way) list junctions at the ends of the thecal lips (Fig. 4B): the fourth list of the junction being the succeeding pleural list of type B, which extends to the next genicular list. In contrast, in other species, these junctions are triple or three-way (Fig. 4A), the succeeding ancora sleeve list being of type A, and growing across the ancora sleeve. The succeeding type B list now has its origin on the sleeve list, distal to the triple junction.

At the proximal end of the rhabdosome in *Plectograptus* there are four initial type B pleural lists separating the proximal orifices. The lists extend from the rim of the ancora umbrella (Figs. 2B, 3). These have no seams, as they separate the dorsal obverse and reverse proximal orifices from the ventral pre-th1^1 and pre-th1^2 orifices.

Secondary lists on the ancora sleeve are developed in most retiolitids, but in only one species of *Plectograptus*, *P. wimani*, except for the presence of the mid-ventral lists. They are produced as accumulations of bandages on pre-existing fusellar panels. The mid-ventral list of the thecal framework is also a secondary list, and bears on its inner face the imprint of the fusellar closures of the thecal wall, with some indications of the mid-ventral zigzag suture (Bates 1987: fig. 7b, pl. 6: 2).

The sockets are depressions on the lists, and occur at the junctions of the genicular lists with the lateral apertural rods and the pleural sleeve lists (Figs. 2B, 6A, B) and, by definition, are absent if transverse rods are developed. They are particularly prominent because the sleeve list is of type B.

Fig. 1. **A–G**. *Plectograptus macilentus* Törnquist, 1887. **A**. Eisenack's (1952) light photograph of isolated specimen, from Baltic erratic boulder, Kalinigrad area, Russia, Ludlow. **B**. Original drawing of original size by Törnquist 1887. **C**, **D**. Bouček and Münch's (1952) drawings of mature flattened material, from Bohemia, Czech Republic. **E**. SEM picture of MB.G 1091, Stoltera, Baltic erratic boulder, Germany. **F**. Photograph of whole flattened specimen LO7398 from Zeulenroda, Thuringia, Germany. **G**. Neotype SMF XXIV 433, from Wetterahammer, Thuringia, Germany; photograph of whole specimen (G_1), line drawing showing main skeletal lists (G_2). **H**. *Plectograptus robustus* (Obut and Zaslavskaya, 1983); H_1, light photograph of specimen LO2198 (Moberg and Törnquist 1909: fig. 1.1), originally identified as *Plectograptus macilentus*, Röddinge, Scania, Sweden; H_2, enlargement showing genicular processes (arrowed). Scale bars 1 mm. →


A
B
C
D
E
F
G1
G2
H1
H2

Figs. 2, 4, and 6 illustrate the complex relationships between the ancora sleeve and the thecal walls occurring at this juncture, due to the linkage of these two approaching structures (the lateral apertural rods are part of the thecal framework, being lateral parts of the thecal aperture, whereas the pleural lists, as here defined, are ancora sleeve lists).

The proliferating ventral and lateral walls of the thecae meet the growing tips of the spines of the ancora sleeve, fusing to produce the initial contacts between theca and sleeve. At the same time, the next section of the ventral walls of the thecae links across between the two socket areas. This must have initially formed as a fusellar-cored spine, before extending forwards as the next section of ventral thecal wall. If it was subsequently thickened, it would have formed a transverse rod or genicular list, as in older retiolitids, and exceptionally in younger taxa such as *Spinograptus praerobustus* Lenz and Kozłowska-Dawidziuk, 2002. For comparison, the transverse rod found in *Spinograptus* with rarely preserved membranes (Lenz 1994; Bates et. al. 2005) is shown diagrammatically in Fig. 2A, C.

From the sockets the geniculum runs across the ventral face of the rhabdosome, and the thecal wall extends as a lateral apertural rod, with an insertion seam for the thecal wall, to the thecal lip. A mid-ventral list (the interpleural list of Lenz 1993) connects the mid-point of the geniculum with that of the thecal lip. In contrast to the other lists, the mid-ventral list is quite flat on its inner side, where it was emplaced on the outer surface of the thecal wall. It is formed entirely of bandages (Figs. 7, 8C).

Material and preparations.—New material described in the paper is isolated and has been recovered from the erratic boulders from northern Germany and Poland, and nodules from Arctic Canada. The graptolites were recovered following slow dissolution of the host carbonate in acid (1–10% HCl, the strength of the acid varying with the chemistry of the hosting carbonates). A fine hairbrush or eyedropper was used to pick and transfer specimens. The material is stored in glycerine in plastic containers, or on the SEM stubs.

Systematic part

Order Graptoloidea Lapworth, 1873

Family Retiolitidae Lapworth, 1873

Subfamily Plectograptinae Bouček and Münch, 1952

Genus *Plectograptus* Moberg and Törnquist, 1909

Type species: *Retiolites macilentus* Törnquist, 1887, from Wetterahammer near Gräfenwarth, Thuringia, Unterer Graptolithenschiefer (Lower Graptolite Shale), Ludlow.

Biostratigaphic range.—Typically ranging through Gorstian, Lower Ludlow globally, but rare and geographically restricted in upper Homerian, upper Upper Wenlock.

Emended diagnosis.—Simple ancora umbrella with five radial lists and an incompletely developed rim. Ancora umbrella separated from lateral ancora sleeve walls by large lateral orifices. Nema free throughout the rhabdosome. Lateral walls of simple, orderly zigzag lists. Reticulum and genicular processes present in some species. Mid-ventral lists present.

Species included.—*Plectograptus macilentus* (Törnquist, 1887), *Plectograptus robustus* (Obut and Zaslavskaya, 1983), *Plectograptus wimani* (Eisenack, 1951), *Plectograptus toernquisti* sp. nov., *Plectograptus mobergi* sp. nov., *Plectograptus trijunctus* sp. nov.).

Description.—Virgella thin, rarely preserved as far as the prosicular rim; nema free, but probably was within the obverse thecal wall, and may be extended as a nematularium in mature specimens (Figs. 1F, H, 9B).

The *Plectograptus* type ancora umbrella is simple, with five radial lists (two near the center of origin being rudimentary) defining five meshes and an incompletely preserved rim (Figs. 2B, 3A). Primary ancora lists bifurcate, one branch to give a thin obverse list and a stronger secondary list meeting the ancora rim and the proximal side of the pre-th1^1 ventral orifice; other primary list forking to give a thin reverse list and a stronger secondary list which divides to give two lists leading to the ancora rim. Apparent pre-th1^2 ventral orifice is in part the fifth mesh of the ancora, the ancora rim being unthickened where it forms the proximal edge of the true pre-th1^1 ventral orifice.

Thecal walls defined only by lateral apertural rods, horizontal thecal lips, genicular lists, and with mid-ventral lists formed of external bandaging running from geniculum to lip. Processes may be present on genicular lists. No transverse rods; instead sockets at junctions of pleural lists (Fig. 6), lateral apertural rods and genicular lists (Fig. 2). Nematularium may be present.

Large proximal orifices on the obverse and reverse sides of rhabdosome, extending beyond the lips of th1^1 and th1^2 (Fig. 2B).

Ancora sleeve defined by lists with a zig-zag pattern in the mid-dorsal part of the wall, formed of lists which become horizontal ventral-wards; the ventral edges of the meshes formed of pleural lists and lateral apertural rods (Figs. 2, 4). Bandages pustular (Fig. 10E, G, H). Seams face inwards (Fig. 10H).

Discussion.—When erecting the type species Törnquist (1887) provided only a schematic drawing, without a proximal end, reproduced here as Fig. 1B. This drawing is completely generalized and shows neither the genicular or mid-ventral lists. The first photograph, of flattened material without a proximal end, was provided by Moberg and Törnquist (1909: pl. 1: 10) with an annotation that this is the "original" of *Plectograptus macilentus* from Wetterahammer, Thuringia. This specimen has not been located in the Lund collection, and is presumed lost.

A single other specimen from the original Törnquist collection remains (Fig. 1F), although that specimen, as suggested by the original labels written by Robert Eisel, was not part of Törnquist's 1887 collection, and was collected from

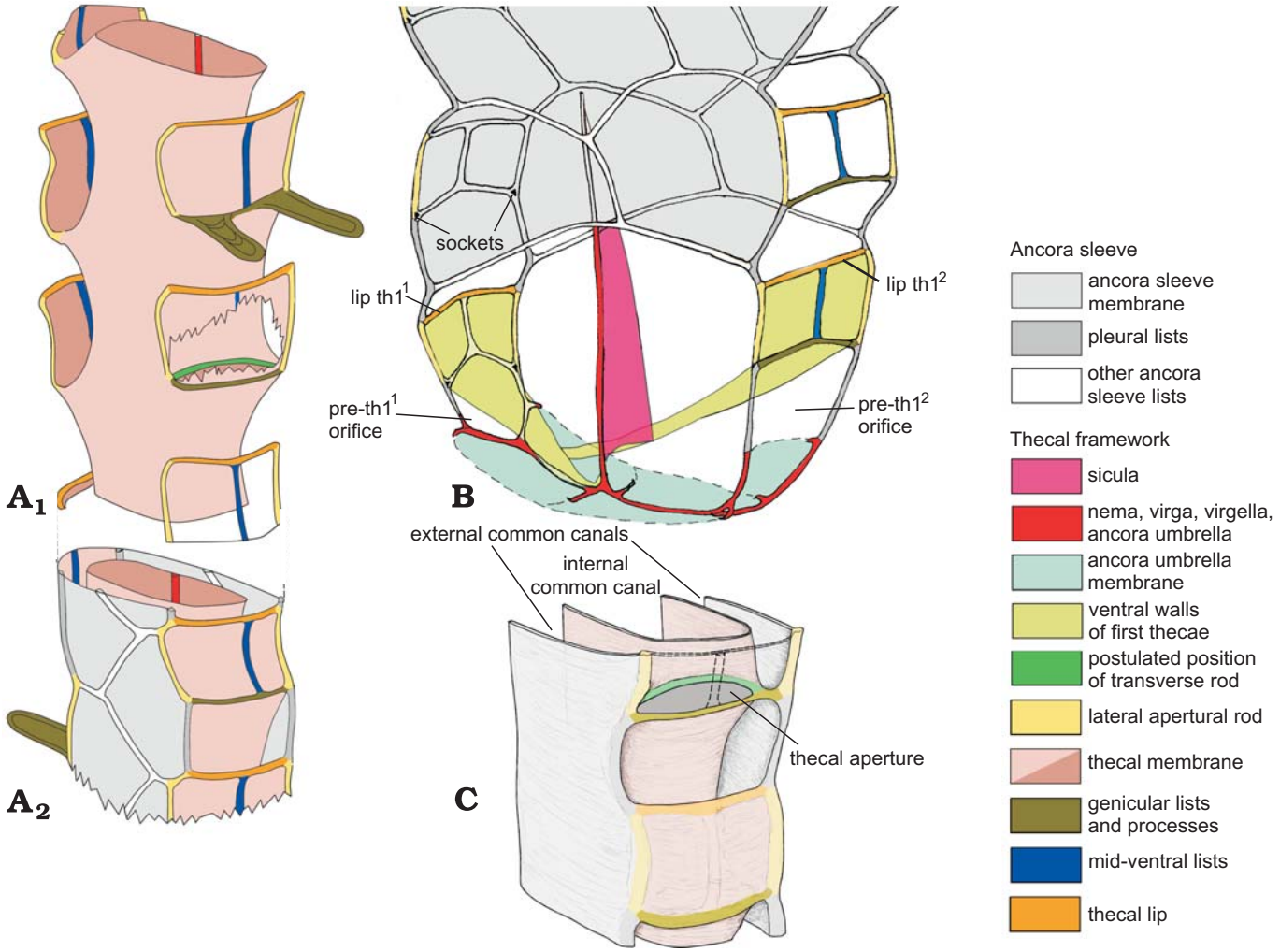


Fig. 2. Schematic drawings of rhabdosomes showing coloured thecal framework and ancora sleeve structures with lists and postulated membrane of *Spinograptus praerobustus* (Lenz and Kozłowska-Dawidziuk, 2002) and *Plectograptus* Moberg and Törnquist, 1909. **A**. Fragment of medial part of rhabdosome of *S. robustus*: thecate part of rhabdosome (A_1), thecate part and ancora sleeve (A_2). **B**. Proximal fragment of illustrating the position of actual thecal aperture and proximal orifices. **C**. Fragment of *Plectograptus* rhabdosome with postulated membranes, common canals and thecal aperture.

the Zeulenroda locality, near Gräfenwarth, Thuringia. The Zeulenroda specimen is not chosen as a neotype because it does not come from the type locality and does not show the main important characteristics of the species.

A neotype was selected from material collected at the original type locality by Maletz (Fig. 1G). Justification for the selection of a neotype from that collection is as follows: the specimen has been collected from the same locality and the same strata as the original, and it clearly shows some of the morphology considered characteristic of the genus. These include the simple and very orderly zigzag pattern of lateral ancora sleeve lists, the distinctly climacograptid thecae, each with complete genicular, apertural and mid-ventral lists, and absence of genicular processes. The ancora umbrella, however, is only partly preserved in the specimen and a nema and nematularium is not visible.

The remainder of the material illustrated by Moberg and Törnquist (1909: figs. 1.1–1.9) comes from Röddinge in Scania, Sweden, and although bearing genicular processes, was originally identified as *P. macilentus*. All those specimens, including fig. 1.1, illustrated herein (Fig. 1H) are here identified as belonging to *P. robustus*.

The first good illustrations, showing proximal end characters, were by Eisenack (1951), using isolated, but immature material from Baltic erratic boulders (Fig. 1A). This material, described as a new species by Eisenack, is clearly assignable to *P. macilentus*. Bouček and Münch (1952) illustrated flattened, but well-preserved and mature specimens from Bohemia (Fig. 1C, D) and used the genus to establish the subfamily Plectograptinae. Paradoxically, in taxonomic practice, it has been primarily from Bouček and Münch's (1952) elucidation of the Bohemian material that the basic understanding of the morphological characteristics of the proximal end of the genus has been derived. The first SEM studies of isolated material were by Lenz (1993) and Kozłowska-Dawidziuk (1995), and these considerably enlarged the understanding of the genus although as noted above, the illustrated specimens described by them are herein recognized as new species.

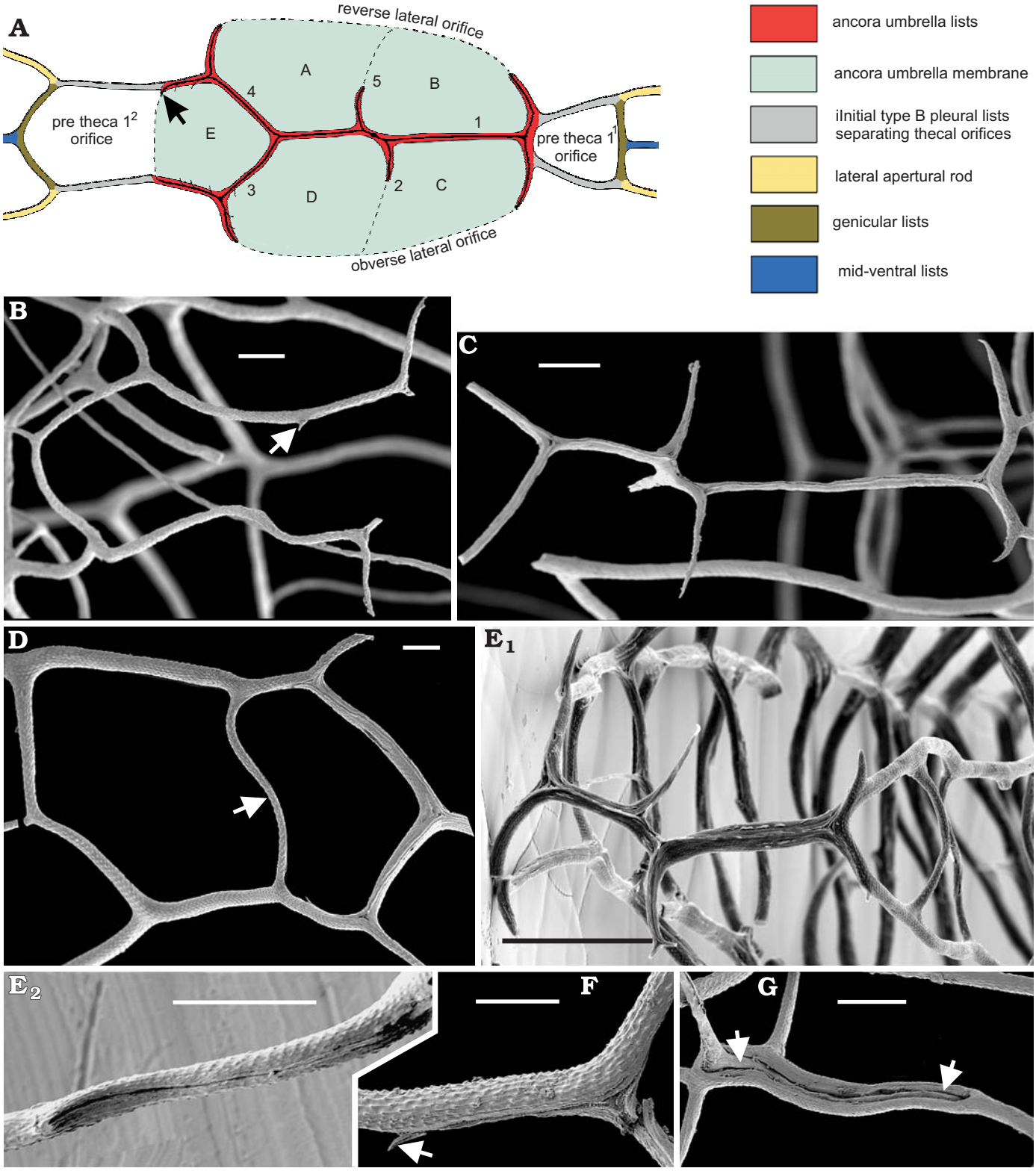


Fig. 3. Proximal end of *Plectograptus toernquisti* sp. nov. **A**. Schematic drawing with insertion seams on ancora umbrella in black, arrow indicates the change from ancora umbrella rim to pleural list (the small curved "twigs" are fusellar shards). The numbers 1–5 are indicative of radial lists reaching the rim only, the letters A–E shows five meshes of ancora umbrella, the solid color region indicating the extent of the ancora umbrella. **B**–**G**. SEM micrographs of fragments showing ancora umbrella. **B**. Ancora umbrella and pre-th 1^2 orifice, arrow indicates the change from ancora umbrella rim to pleural list, NMW 91.52G.1698, Bramsche, Baltic erratic boulder Nr. B9/96, Germany, Gorstian, Lower Ludlow. **C**. Ancora umbrella from the outside, NMW 91.52G.1701, Baltic erratic boulder, Stoltera, Germany, Gorstian. **D**. Outside view of pre-th1^2 orifice with complete list of ancora umbrella rim (arrow), NMW 91.52G.1697, Baltic erratic boulder B4/97, Nienhagen, Germany, Gorstian. **E**. Outside view of ancora umbrella ZPAL G.39/2, st. A92, Jarosławiec, Baltic erratic boulder Nr. 22, Poland, Ludlow; E_1, whole ancora umbrella; E_2, outside view of part of ancora umbrella region arrowed on A. →

The simple ancora umbrella (Figs. 2, 3), with a minimum of radial lists, and an incompletely thickened peripheral rim, is comparable to that in other late retiolitids, such as *Semiplectograptus* and *Plectodinemagraptus* (Kozłowska-Dawidziuk 1995: fig. 34). This is the *Plectograptus* type ancora umbrella. It is joined to the rest of the rhabdosome by four pleural lists. These separate the four proximal orifices, and are unseamed. The pre-th1[2] lists can be divided into two portions: a distal portion (the true pleural list) without seams, where they separate the pre-th1[2] ventral orifice from the lateral orifices, and a proximal portion where they form part of the ancora rim. The ventral part of the rim is not normally thickened into a list, but can be traced in growth as seams along the lists, with fusellar increments projecting from them (Fig. 3), culminating in a prominent "twig" (on the reverse list) marking the final growth of the ancora rim (shown by the arrows in Fig. 3A, B, F). In other late Silurian genera, such as *Spinograptus* and *Holoretiolites*, the ancora umbrella is more complex, with more radial list forkings, and the pleural lists do not form the only lists linking the ancora umbrella to the rest of the rhabdosome (Bates et. al. 2005).

The thecal framework of *Plectograptus* is reduced to lateral apertural rods, thecal lips, genicular lists and mid-ventral lists, similar to *Spinograptus* (Fig. 2A, C). Sockets on the inner face of the junction between pleural lists, genicular lists and lateral apertural rods, mark the conjunction of the thecal walls with the ancora sleeve (Figs. 2B, 6). These take the place of the transverse rods, as seen in genera such as *Cometograptus*, marking the proximal ends of the ventral thecal walls (Kozłowska-Dawidziuk 2001).

Very large proximal obverse and reverse orifices are prominent and unique features of *Plectograptus*, contrasting markedly with the smaller and more restricted orifices seen in all other genera of the plectograptine group (among the retiolitines, only the poorly known taxon *Dabashanograptus chengkouensis* Ge, 1990 appears to have large obverse and reverse orifices (Bates et al. 2005: fig. 7B). On their distal sides the first primary lists of the ancora sleeve make conjunctions with the pleural lists distal to the lips of the first two thecae, although there is some variation in the level of contact. The highest position noted is just below the lip of th3[1] on the first thecal series, and at the level of the thecal lip of th 2[2] on the others (Fig. 1A). In contrast, in other genera such as *Neogothograptus* and *Holoretiolites*, the distal margins of the first lateral orifices make contact with lists proximal to the lateral apertural rods of the first thecae. Succeeding dorsal lists of the sleeve alternate from side to side, suggesting that the sleeve grew as a series of lobes (Fig. 4). These were extended in parallel with the thecal walls, with which they make conjunctions only along the lateral apertural rods.

A nematularium is preserved in some flattened specimens of *Plectograptus* (Moberg and Törnquist 1909; Bouček and Münch 1952; Tomczyk 1956) (Fig. 1F, H_1). It has not been observed in any isolated material.

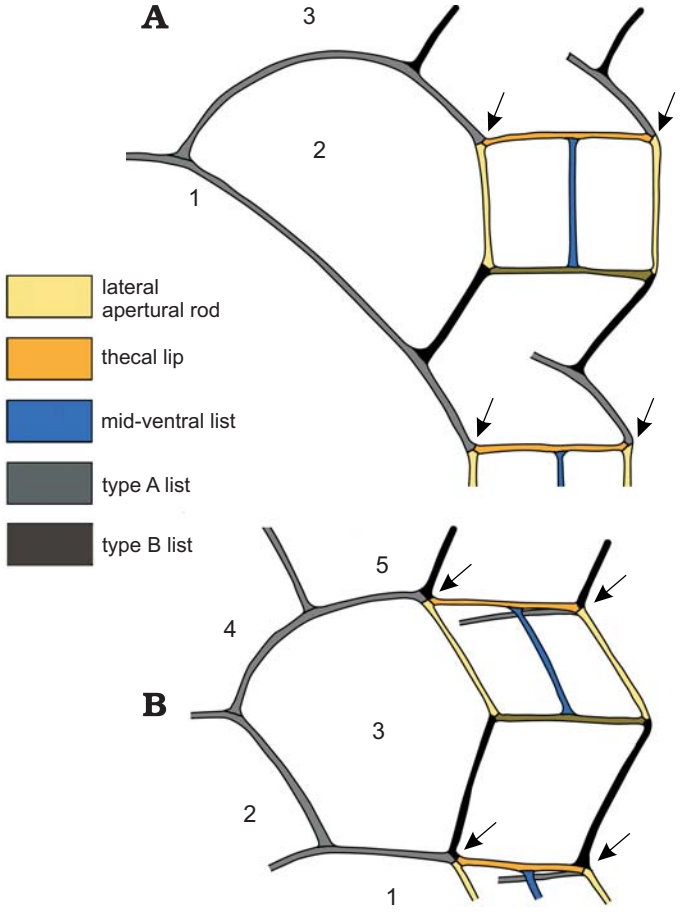


Fig. 4. Schematic diagrams of the ancora sleeve growth in *Plectograptus* Moberg and Törnquist, 1909. Numbers indicate the order of growth of ancora sleeve panels. **A**. *P. mobergi* sp. nov. with triple junctions of lists (arrows). **B**. *P. toernquisti* sp. nov. with quadruple junctions of lists (arrows).

Plectograptus? *bouceki* Rickards, 1967 is not assignable to *Plectograptus*, because it has sleeve walls which are formed of a reticulum without any major lists, and the proximal end does not have large lateral orifices. Rickards recognized that it resembled *Plectograptus*? *textor* Bouček and Münch, 1952, which was placed in *Sokolovograptus* by Kozłowska-Dawidziuk (1995: 291). *Plectograptus*? *carlsteinensis* Kozłowska-Dawidziuk et al. 2001 and *Plectograptus*? *ovatus* Kozłowska-Dawidziuk et al. 2001 are excluded from *Plectograptus*, as they have different proximal end structures (Kozłowska-Dawidziuk et al. 2001). Their generic assignment is unknown.

Recently acquired material of *Plectograptus* has some characters not seen in the type species, permitting the recognition of three new species, described below.

The pleural list is without a seam. **F**. Lateral view of the same region as on A, NMW 91.52G.1686, Baltic erratic boulder No. B9/96, Bramsche, Germany, Gorstian, arrow indicates the change from ancora umbrella rim to pleural list. **G**. Inside view of ancora hub region with th1[1] scar (arrowed), NMW 91.52G.1688B, Baltic erratic boulder No. B9/96, Bramsche, Germany, Gorstian. Scale bars: B–E, G 100 μm; F, 50 μm.

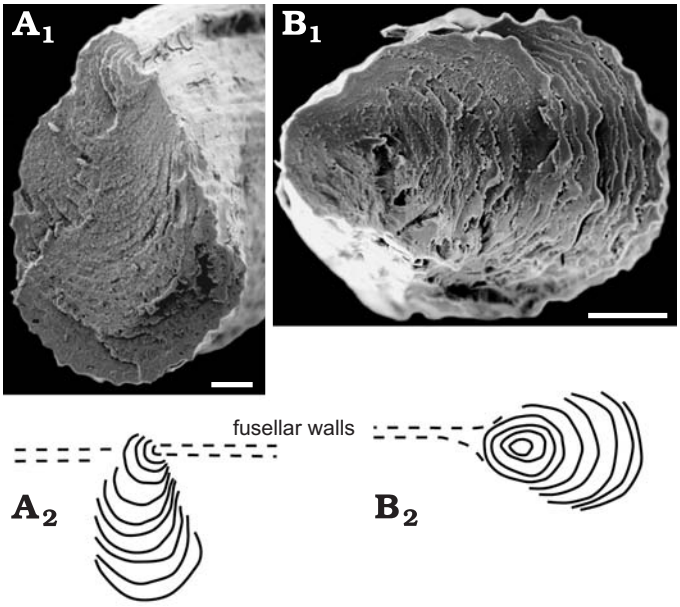


Fig. 5. Two types of ancora sleeve lists in representatives of *Plectograptus* Moberg and Törnquist, 1909 shown in cross sections. **A**. Lists type A with insertion seam, *P. wimani* (Eisenack, 1951), ZPAL G.39/1, Mielnik borehole, depth 1405.0 m, EEP, Poland, Ludlow: SEM micrograph (A_1), schematic diagram (A_2). **B**. Lists type B with spinose core, *P. toernquisti* sp. nov., NMW 91.52G.1700, Bramsche, Mecklenburg-Vorpommern, Baltic erratic boulder No. B9/96, Germany, Gorstian, Lower Ludlow: SEM micrograph (B_1) and schematic diagram (B_2). Schematic diagrams of the lists with lines suggest fusellar wall. Scale bars 10 μm.

Species distinguished here are:
- *Plectograptus macilentus* Törnquist, 1887
- *Plectograptus toernquisti* sp. nov.
- *Plectograptus mobergi* sp. nov.
- *Plectograptus robustus* (Obut and Zaslavskaya, 1983)
- *Plectograptus trijunctus* sp. nov.
- *Plectograptus wimani* (Eisenack, 1951)

Plectograptus macilentus (Törnquist, 1887)

Figs. 1A–G, 6D.

1887 *Retiolites macilentus* sp. nov.; Törnquist 1887: 491, fig. 3.
?1908 *Retiolites* (*Gothograptus*) *spinosus* (Wood); Elles and Wood 1908: 345, text-fig. 226d (non a–c).
1909 *Plectograptus macilentus* (Törnquist, 1887); Moberg and Törnquist 1909: 13, fig. 10. (non figs. 2–9).
1951 *Plectograptus tetracanthus* Eisenack 1951: 140, pl. 23: 6–8; pl. 24: 8; pl. 25: 9; text-figs. 4, 5.
1952 *Plectograptus macilentus* (Törnquist 1887); Bouček and Münch 1952: 22, fig. 7a–f; pl. 1–4.
1956 *Plectograptus macilentus* (Törnquist1887); Tomczyk 1956: 44, pl. 1: 2a, b; text-fig. 9a–c.
1971 *Retiolites* (*Plectograptus*) *macilentus* Törnquist 1887; Schauer 1971: 85, pl. 39: 11,12; pl. 40: 7, 8.
?1889 *Plectograptus macilentus* (Törnquist 1887); Pashko 1989: 117, fig. 2.
non 1993 *Plectograptus* (*Plectograptus*) *macilentus* (Törnquist 1887); Lenz 1993: 13, pl. 1: 6–8.
1994 *Plectograptus macilentus* (Törnquist 1887); Koren' 1994: 140, pl. 2: 6.
non 1995 *Plectograptus macilentus* (Törnquist 1887); Kozłowska-Dawidziuk 1995: 317, fig. 33.
1995 *Plectograptus macilentus* (Törnquist 1887); Maletz et al. 1998: pl. 1: 2, 5.
1998 *Plectograptus macilentus* (Törnquist 1887); Kozłowska-Dawidziuk, Lenz and Štorch 1998: fig. 1E.
2004 *Plectograptus macilentus* (Törnquist 1887); Lenz and Kozłowska-Dawidziuk 2004: 21, pl. 23: 1–5; pl. 24: 4–6, 8–12; pl. 26: 15.

Neotype: SMF XXIV 433, Wetterahammer, Thuringia, Germany, Gorstian, *Neolobograptus nilssoni* Zone (Fig. 1G). The slabs associated with the neotype specimen (SMF XXIV 433 to SMF XXIV 442) include a number of specimens of *P. macilentus*, *Spinograptus spinosus*, *Neogothograptus balticus*, *Neolobograptus nilssoni* (fragments), and *Pristiograptus dubius*. The graptolites are preserved as greenish pressure shadow minerals with some remaining parts of the periderm in a tectonized black shale.

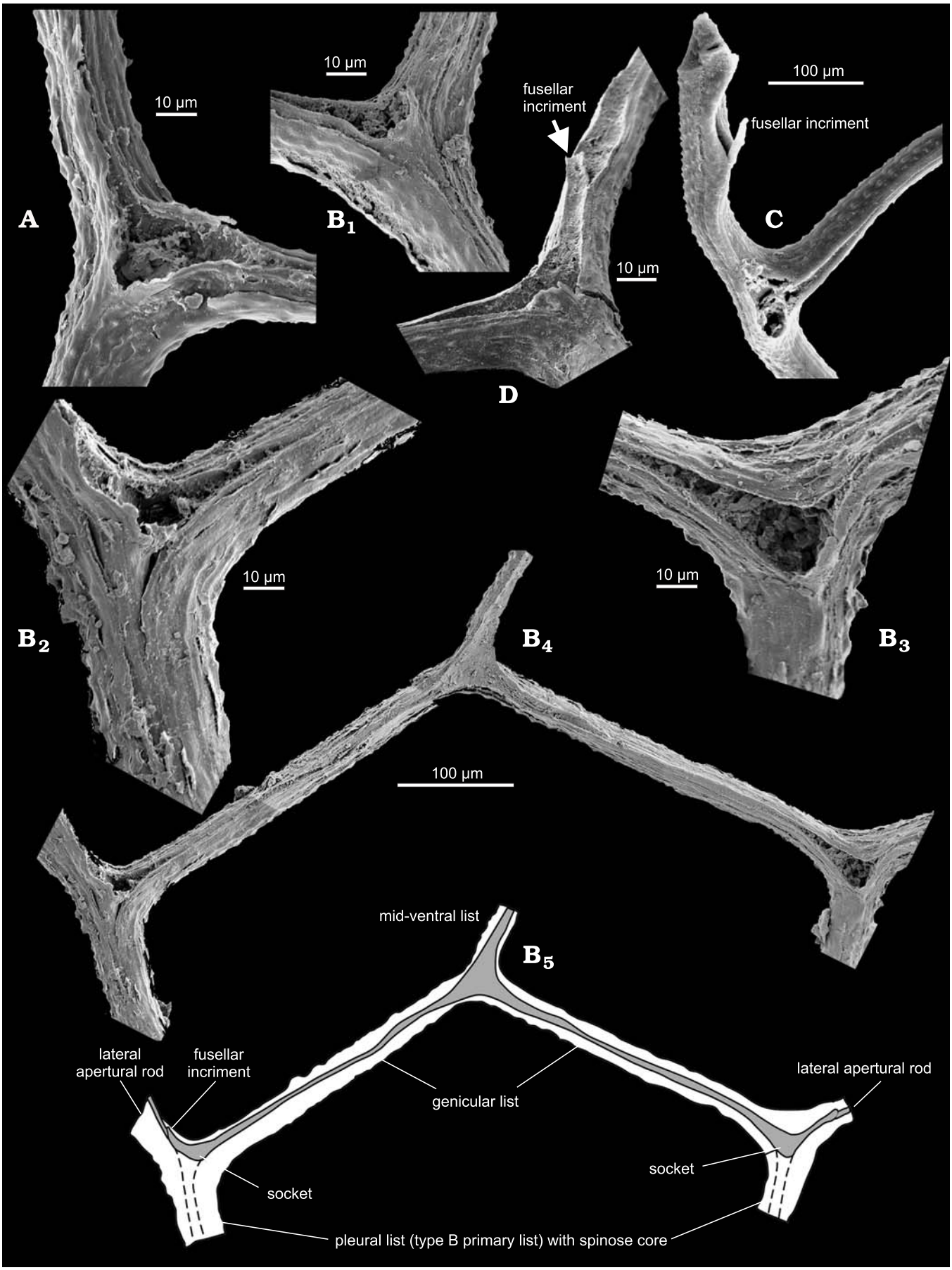
Type locality: The original Wetterahammer or Wetterhammer locality was discussed by Hundt (1910) as his locality No. 6 (see also Zimmermann 1912: 46). He remarked on the presence of *Plectograptus macilentus* in Zone 19 at the locality. Jaeger (1991) described the biostratigraphy of the remaining modern Wetterahammer locality, which has been modified through road and railroad construction since Törnquist's visit, showing its biostratigraphic extent crossing the Wenlock–Ludlow boundary and representing an important succession for the documentation of the *Cyrtograptus lundgreni* extinction event.

Diagnosis.— Ancora sleeve with only primary lists. Junctions between ancora sleeve lists, pleural lists, thecal lips and lateral apertural rods forming a quadruple junction. Mid-ventral lists vertical, pleural lists relatively vertical. No genicular processes.

Table 1. Distinguishing characters of the species of *Plectograptus*.

Species characters	*P. macilentus*	*P. toernquisti*	*P. mobergi*	*P. robustus*	*P. trijunctus*	*P. wimani*
genicular processes	absent	absent	absent	paired	paired	single
mid-ventral inclination	±vertical	inclined	vertical	vertical	vertical	inclined
sleeve/ lateral apertural rod/lip junctions	4 way	4 way	3 way	4 way	3 way	4 way
reticulum	absent	absent	absent	absent	present	present

Fig. 6. **A**–**C**. *Plectograptus toernquisti* sp. nov. lists showing sockets occurring at the junctions of the genicular lists with the lateral apertural rods and the pleural sleeve lists. **A**. ZPAL G.27/2, Bartoszyce borehole, depth 1627.0 m, EEP, Poland, Ludlow. **B**. NMW 91.52G.1686, Bramsche, Baltic erratic boulder No. B9/96, Germany, Gorstian: B_1–B_4, SEM micrographs; B_5, schematic drawing of B_4 showing connections of lists and positions of sockets, insertion seams are shown in grey. **C**. ZPAL G.39/2, Jarosławiec, Baltic erratic boulder No. 22, Poland, Ludlow. **D**. *Plectograptus macilentus* Törnquist, 1887 lists with well developed fusellar increments, NMW 91.52G.1695, Stoltera, Baltic erratic boulder, Germany, Gorstian. All SEM micrographs. →


10 µm
A
10 µm
B1
fusellar
incriment
10 µm
D
100 µm
fusellar incriment
C
10 µm
B2
10 µm
B3
B4
100 µm
mid-ventral list
B5
lateral
apertural rod
fusellar
incriment
genicular list
lateral apertural rod
socket
socket
pleural list (type B primary list) with spinose core

Description.—Mature rhabdosome ≥ 15–20 mm long, width of lateral wall about 2 mm, total width including thecal loops about 4 mm. Rhabdosome more or less parallel-sided throughout, but may taper slightly towards the distal end. Thecae 10–12 in 10 mm. Genicular lips and thecal lists about same size throughout, joined by mid-ventral lists that are more or less vertically oriented. Fairly robust nematularium developed in larger specimens, beginning well inside rhabdosome and projecting well beyond. Without thecal (genicular) processes. Quadruple junctions, as noted in diagnosis.

Discussion.—The species was described as *Retiolites macilentus* by Törnquist in 1887, from poor material from Thuringia, Germany. Moberg and Törnquist erected the genus *Plectograptus* in 1909, following the study of better-preserved material from Scania, Sweden. When erecting the species in 1887, from Thuringia, Törnquist published only a diagrammatic illustration, reproduced in Fig. 1B. Subsequently, when erecting the genus *Plectograptus*, Moberg and Törnquist (1909) provided photographs of additional flattened material of *P. macilentus* from Sweden and the type from Thuringia. Most of the material, which was incorrectly identified as *P. macilentus* by Moberg and Törnquist in 1909 (e.g., fig. 1.1; illustrated herein as Fig. 1H), is stored in the Lund University Museum (LO 2198–2208).

The simple and orderly zig-zag nature of lateral walls of the rhabdosome, and the "climacograptid" profile of the thecae were clearly evident in the original studies of the type material by Törnquist (1887) and Moberg and Törnquist (1909), and these features alone are sufficient to recognize the genus *Plectograptus*, and most of its species, including *P. macilentus*. However, one important problem is the absence of the proximal (ancora) end of the rhabdosome in the original type and thus, the very basis of the family Plectograptinae and of the nature of the "*Plectograptus* ancora". This problem has essentially been solved by the universal acceptance of the morphological characteristics of mature specimens described and illustrated in Bouček and Münch (1952) and, subsequently, supplemented, elaborated on, and fully confirmed by the recent SEM studies of isolated material. The second problem, concerns the presence or absence of the thecal processes, and an error involving material studied by the original authors. Moberg and Törnquist (1909) illustrated 10 specimens (including the original type, fig. 1.10) all identified as *P. macilentus*. Our examination of the nine other specimens, including the best specimen (Fig. 1H), shows them to possess thecal (genicular) processes (see Fig. 9B), and thus are assignable to *P. robustus* (see below).

Plectograptus toernquisti sp. nov.

Figs. 3B–G, 6A–C, 7.

1993 *Plectograptus* (*Plectograptus*) *macilentus* (Törnquist, 1887); Lenz 1993: 13, pl. 1: 6–8.

Derivation of the name: In honour of the late Swedish paleontologist S.L. Törnquist who erected the species *P. macilentus*.

Holotype: NMW 91.52G.1702. *Paratypes* NMW 91.52G.1686, NMW 91.52G. 1688A, NMW 91.52G. 1693, NMW 91.52G. 1697, NMW 91.52G. 1698, NMW 91.52G. 1701.

Type locality: Bramsche, Mecklenburg-Vorpommern, Baltic erratic boulder No. B9/96, Germany.

Type horizon: Specimens are associated with specimens of *Saetograptus chimaera*, Gorstian, Lower Ludlow.

Material.—Baltic erratic boulder No. B9/96, Germany; Cornwallis Island, Arctic Canada field collection SB E-68 m, Gorstian, *Lobograptus progenitor* Biozone.

Diagnosis.—Ancora sleeve with only primary lists. Junctions between ancora sleeve lists, pleural lists, thecal lips and lateral apertural rods quadruple. Mid-ventral lists and lateral apertural rods distinctly inclined inwards from genicular lists to thecal lips. No genicular structures.

Description.—Minimum calculated length of rhabdosome 9.5 mm, with nine thecal pairs. Dorso-ventral width gradually increasing from 1.26 mm at the ancora to 2.7 mm at about the 6th thecal pair, then gently narrowing. Scalariform width 1.7 mm. Width of thecal lips 0.84–0.98 mm, height of free ventral walls from geniculum to lip 0.38 mm and from lip to geniculum 0.46 mm. The lateral profile distinctly "saw-toothed" (Fig. 7B), with lateral apertural rods and mid-ventral lists inclined inwards at about 30–40°, and pleural lists inclined outwards at about the same angle. Genicular lists longer than thecal lips, so that they are convex outwards, and the mid ventral lists therefore longer than the lateral apertural rods (Figs. 4B, 7A, B). Pleural lists join the lateral ancora sleeve lists at the junction with the lateral apertural rods and thecal lips, forming quadruple junctions (Figs. 4B, 7B). As a result the ancora sleeve meshes are hexagonal. Pleural lists are composed entirely of type B lists (Fig. 4B).

Discussion.—The material described by Lenz (1993) as *Plectograptus macilentus* belongs to this new species, having quadruple junctions at the thecal lips, and markedly inward inclined lateral apertural lists.

Geographic and stratigraphic range.—EEP and Arctic Canada, Gorstian, *Neolobograptus nilssoni* and *Lobograptus progenitor* biozones, respectively.

Plectograptus mobergi sp. nov.

Fig. 8.

1995 *Plectograptus macilentus* (Törnquist, 1887); Kozłowska-Dawidziuk 1995: 317, fig. 33.

2002 *Plectograptus macilentus* (Törnquist, 1887); Kozłowska-Dawidziuk 2002: 460–462, fig. 2A.

Derivation of the name: In honour of the late Swedish paleontologist J.C. Moberg who, with S.L. Törnquist, studied *Plectograptus macilentus*.

Holotype: MB.G 1091.6 (Fig. 8B).

Type locality: MB.G. 1091, Glacial erratic boulder, Stoltera, Mecklenburg-Vorpommern, northern Germany, coll. H. Jaeger (Orig. No. 353).

Type horizon: Ludlow, sample includes fragments of a cucullograptid indet.

Material.— Nine specimens mounted on SEM stubs and additional fragments including juveniles preserved in glycerine, preserved in Museum fuer Naturkunde, Berlin under the

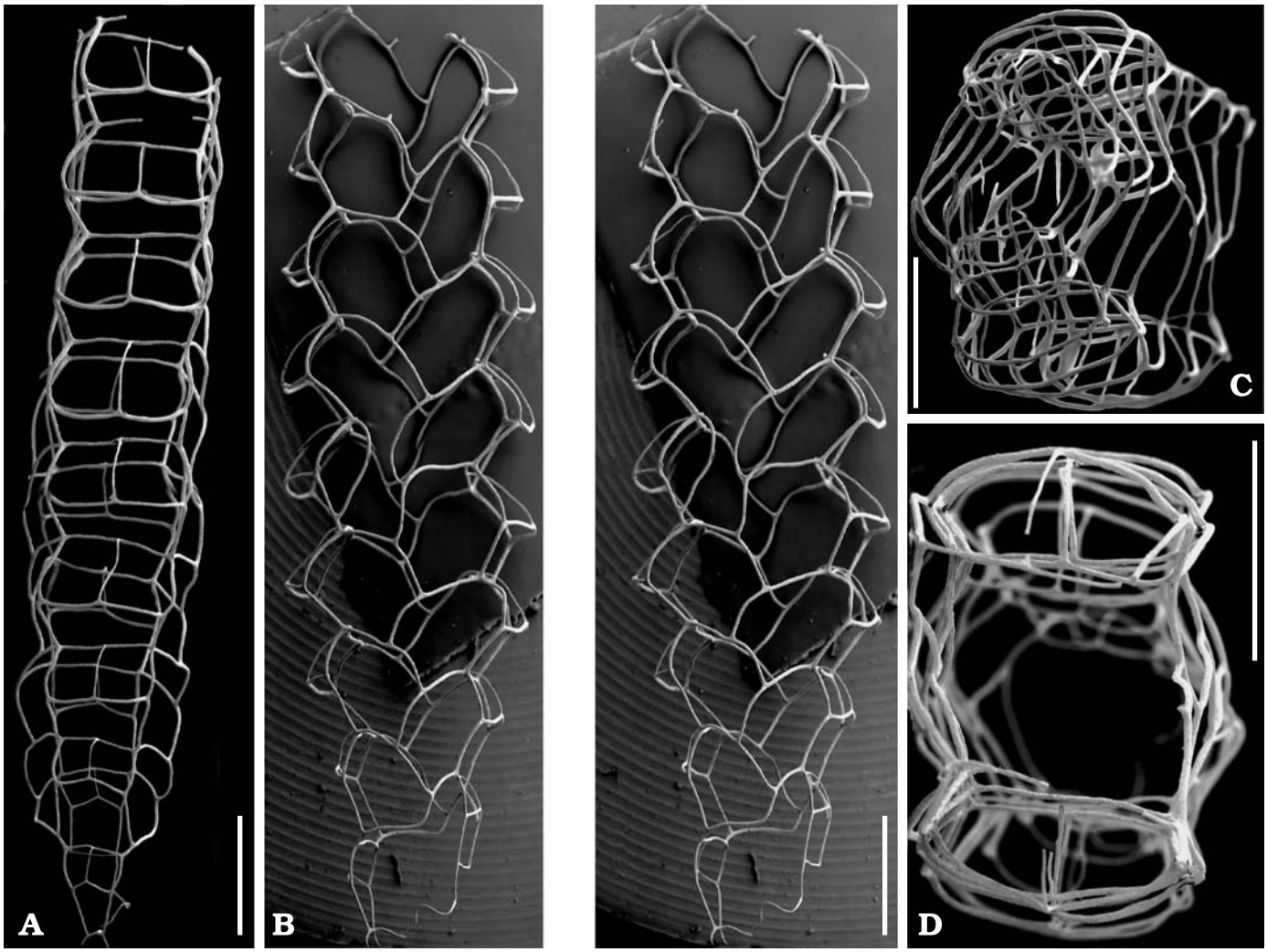


Fig. 7. SEM micrographs of *Plectograptus toernquisti* sp. nov. mature rhabdosome, NMW 91.52G.1702, holotype, Baltic erratic boulder No. B9/96, Bramsche, Germany, Gorstian. **A**. Ventral view . **B**. Stereopair of the obverse view of specimen. **C**. Oblique view looking distally. **D**. Proximal view. Scale bars 1 mm.

type number MG.B 1091. Other illustrated material from Baltic erratic boulders No. 22, Jarosławiec, Poland; Mielnik borehole, depth 978.9 m, Poland, Ludlow.

Diagnosis.—Ancora sleeve with only primary lists, mid-ventral lists vertical. The ancora sleeve list junctions with pleural lists are triple; otherwise like *P. macilentus*. Pleural lists slightly undulating. No genicular processes.

Description.—Maximum length with 12 pairs of thecae 10.1 mm, ancora width 1.2–1.8 mm. Rhabdosome gently widening from 1.74 mm at first thecal pair to 2.16 mm at fourth thecal pair (but parallel sided or tapering gently towards distal end from 2.5–2.0 mm. Scalariform width 0.66 mm proximally. Proximal obverse and reverse orifices 1.3 mm wide by 1.3 mm high. Thecal lips of th1[1] 0.83 mm distal from ancora hub, of th1[2] 1 mm distal. Lateral profile with thecal walls from genicular list to lips almost vertical. Pleural lists in two sections, the first inclined inwards from the thecal lips at about 30°and curving inwards to the centre of the ancora sleeve and bearing a proximally facing insertion seam; the second branching from the first about 0.18 mm from the lip junction, inclined outwards at about 6°, running to the next genicular list.

Discussion.—The new species has the ancora sleeve lists junctions with pleural lists (Figs. 4A, 8A$_1$, B, C, D$_1$) triple in contrast to those of *Plectograptus toernquisti* sp. nov.

One specimen shows aberrant growth in the distal part of rhabdosome at the level of th 5[1] (Fig. 8D), and at the level of the next theca it becomes regular again. Theca 5[1] is incomplete. The distal part of the rhabdosome is displaced towards the reverse side (Fig. 8D$_2$), and is a little narrower than the proximal portion. The distal lists are thinner than the proximal ones suggesting regeneration of the colony.

Geographic and stratigraphic range.—EEP, Ludlow.

Plectograptus robustus (Obut and Zaslavskaya, 1983)

Figs. 1H, 9B, C.

1909 *Plectograptus macilentus* (Törnquist, 1887); Moberg and Törnquist 1909: 13, pl. 1: 1.

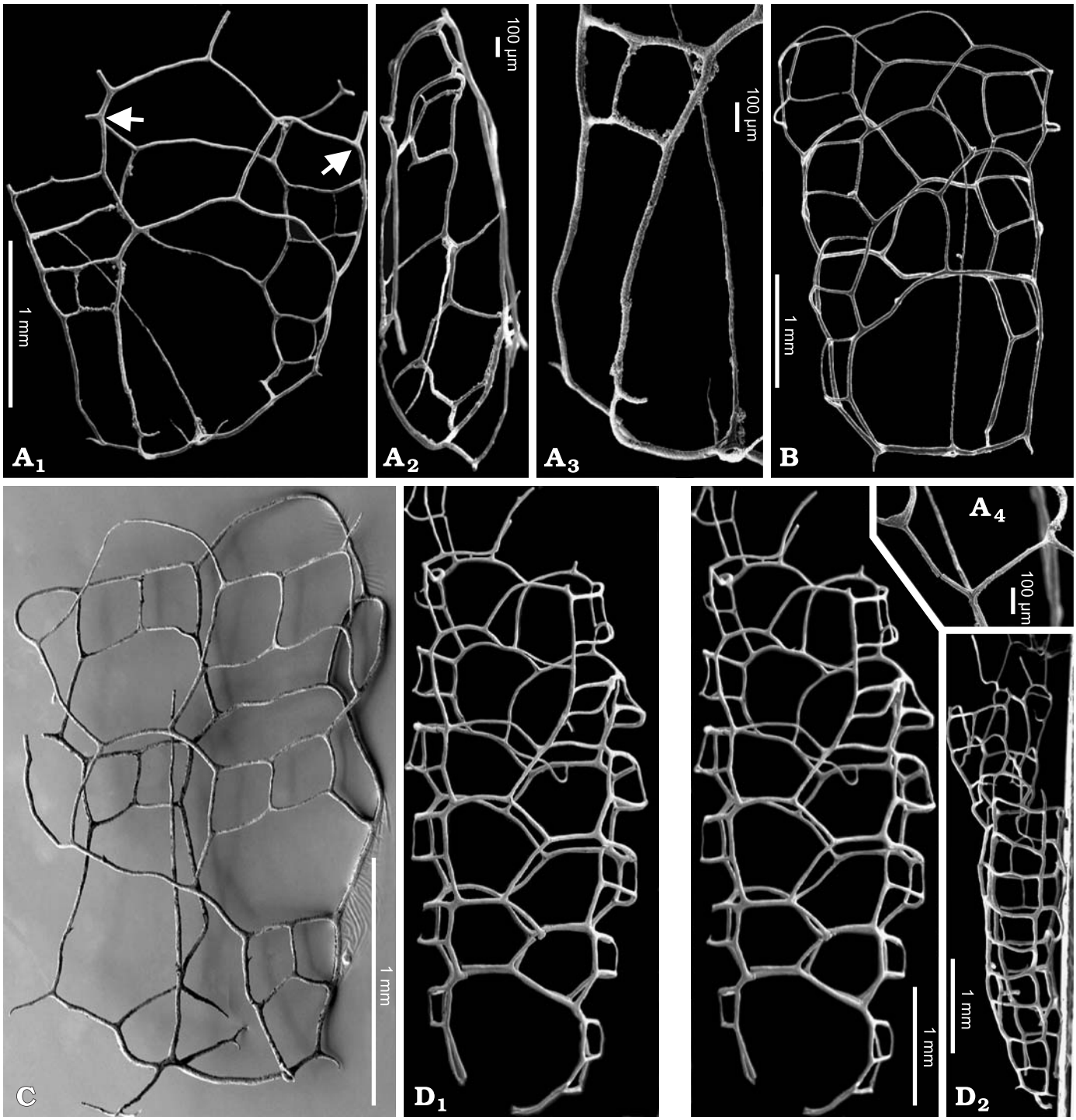


Fig. 8. SEM micrographs of *Plectograptus mobergi* sp. nov. **A**. Immature rhabdosome, ZPAL G.27/1, Baltic erratic boulder No. 46, Jarosławiec, Poland, Ludlow; A_1, reverse view of proximal fragment, triple junctions of ancora sleeve with pleural lists indicated by arrows; A_2, inside view showing shape of ancora umbrella and shape of rhabdosome in cross section; A_3, enlargement with part of ancora umbrella and theca 1^2; A_4, outside view of ancora umbrella proximal to theca 1^1. **B**. Obverse view of rhabdosome with three pairs of thecae and long virgella preserved, holotype, Stoltera, Germany, MB.G 1091, Stoltera, Germany, Ludlow. **C**. Oblique view of theca 1^1 side of immature specimen, ZPAL G.39/3, Mielnik borehole, depth 978.9 m, Poland, Ludlow. Note that the obverse and reverse lists of the ancora umbrella are unusually long, and have portions of the ancora rim attached to them. **D**. Mature rhabdosome, with malformation and regeneration in the distal part of the rhabdosome, ZPAL G.39/4, Jarosławiec, Baltic erratic boulder No. 54, Poland, Ludlow: D_1, reverse view of rhabdosome—stereopair; D_2, ventral view of theca 1^1 side.

1983 *Agastograptus robustus* Obut and Zaslavskaya, 1983: 108. pl. 24: 1–3.

pars 2002 *Plectograptus robustus* (Obut and Zaslavskaya, 1983), Kozłowska-Dawidziuk 2002: 462, fig. 2D.

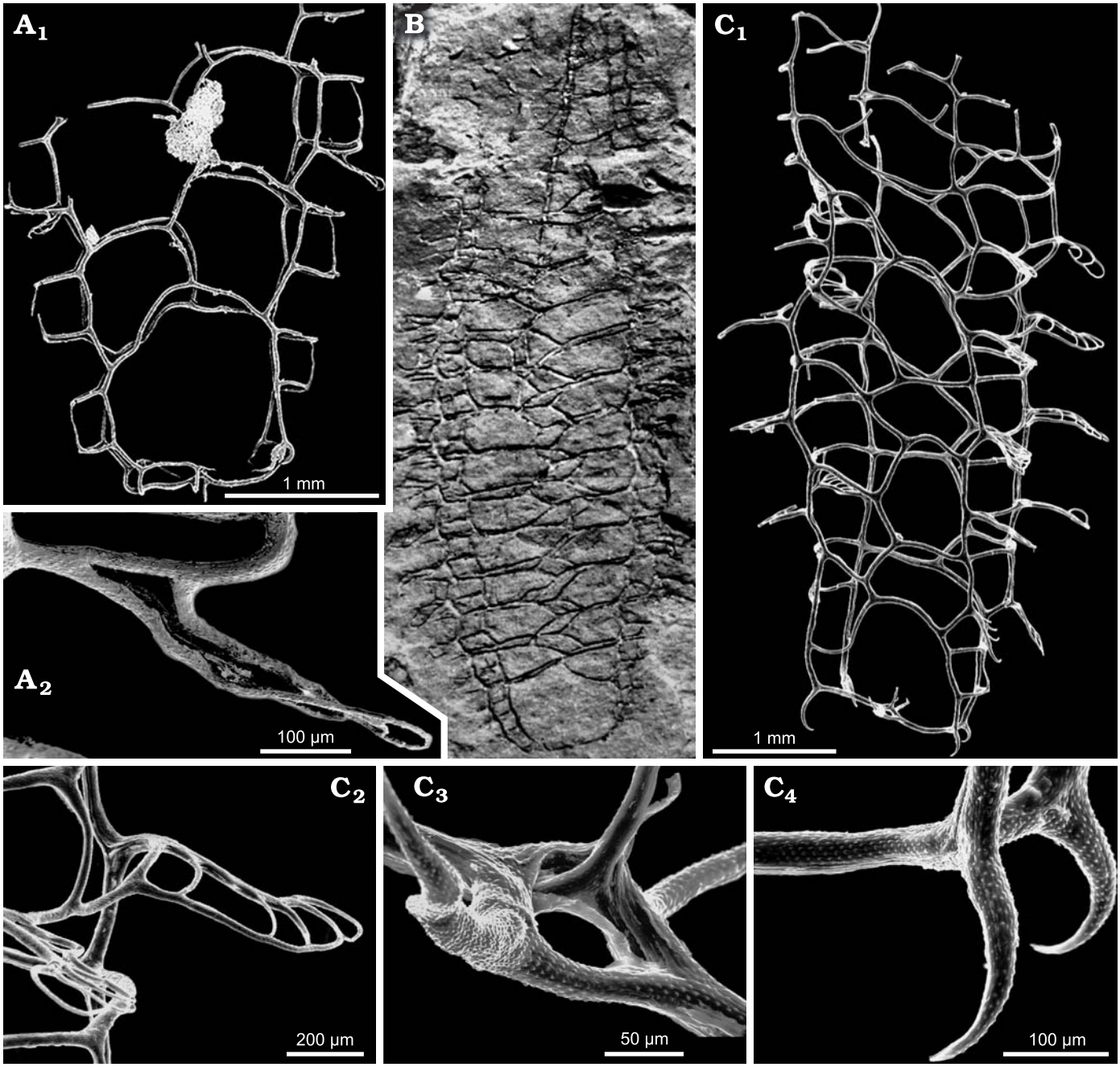


Fig. 9. **A**. SEM micrographs of *Plectograptus trijunctus* sp. nov., holotype ZPAL G.27/2, Bartoszyce borehole, depth 1627 m, EEP, Poland, late Homerian; A_1, whole rhabdosome, reverse view; A_2, enlargement of apertural process. **B**, **C**. *Plectograptus robustus* (Obut and Zaslavskaya, 1983). **B**. Light photograph of reverse of mature rhabdosome with nematularium, SMD-SAS 217, Grube "Frisch Glueck" near Zwickau, south of Stenn, Germany, Ludlow; not to scale. **C**. SEM micrographs of a mature rhabdosome, MB.G 1081, Spandau bei Berlin, Germany, Ludlow: C_1, obverse view; C_2, paired apertural process; C_3, ancora hub; C_4, enlargement of ancora umbrella fragment.

non 2002 *Plectograptus robustus* (Obut and Zaslavskaya, 1983); Kozłowska-Dawidziuk 2002: 462, fig. 2C.

2004 *Plectograptus robustus* (Obut and Zaslavskaya, 1983); Lenz and Kozłowska-Dawidziuk 2004: 22, pl. 24: 1–3, 7; pl. 26: 3, 4, 8, 9, 11–14.

Emended diagnosis.—Ancora sleeve with only primary lists, mid-ventral lists vertical. Quadruple junctions among ancora sleeve lists, pleural lists, thecal lips and lateral apertural rods. Pleural lists slightly undulating. Paired reticulofusellar genicular processes as in *Plectograptus trijunctus* sp. nov.

Material—Three specimens, glacial erratic boulder, Spandau bei Berlin, Germany, coll. H. Jaeger (Orig. No. 173), MB.G 1081; one flattened specimen from Grube "Frisch Glueck" near Zwickau, south of Stenn, Germany, Ludlow, *Neolobograptus nilssoni* Biozone.

Description.—Maximum length of rhabdosome with 6 pairs of thecae 5.5 mm, ancora width about 1.5 mm. Rhabdosome gently widening to about 2.5 mm distally. Pleural lists in two sections, similar to *P. mobergi*.

One flattened specimen from Grube "Frisch Glueck" near Zwickau represents a mature rhabdosome of *P. robustus* with 18 thecal pairs and a well-developed nematularium, which is preserved only inside the distal part of the rhabdosome (Fig. 9B). The rhabdosome distinctly tapers distally. Genicular processes are not developed in the distalmost thecae.

Discussion.—The material identified as *Plectograptus robustus* by Kozłowska-Dawidziuk (2002: 462, fig. 2C) is assigned to the new species *Plectograptus trijunctus* based on it having a triple junction and genicular processes (Fig. 9A).

The specimen from Central Asia illustrated in Koren' (1994: pl. 2: 6) may represent *P. robustus*, since the quadruple junction is clear. There is no proximal end preserved and possible genicular processes are visible only in proximal thecae. The specimen of *Plectograptus robustus* illustrated in Fig. 9C has a quadruple junction in all thecae except th1[1]. There are also some distortions in the proximal and distal parts of the rhabdosome.

Geographic and stratigraphic range.—EEP, lower Gorstian, *Neolobograptus nilssoni* Biozone.

Plectograptus trijunctus sp. nov.

Fig. 9A.

2002 *Plectograptus robustus* (Obut and Zaslavskaya, 1983); Kozłowska-Dawidziuk 2002: 462, fig. 2c.

Derivation of the name: From the Latin tri and junctus, for a three junction.

Holotype: Holotype ZPAL G.27/2 (Fig. 9A).

Type locality: Bartoszyce borehole, 1627.0 m, Poland.

Type horizon: Gorstian, *Neolobograptus nilssoni* Biozone.

Material.—One immature specimen and several fragments from Bartoszyce borehole, 1627.0 m, Poland.

Diagnosis.—Ancora sleeve only primary lists, mid-ventral lists vertical. The ancora sleeve list junctions with pleural lists triple. Thecal walls inclined inwards from genicular to apertural lists, similar to *Plectograptus mobergi* and *P. wimani*. Paired reticulofusellar genicular processes similar to those of *P. robustus*.

Description.—Proximal obverse and reverse orifices as well as thecal profiles similar to *Plectograptus robustus*. Lateral profile with thecal walls from genicular list to lips slightly undulating. Pleural lists in two sections, similar to *P. mobergi*. Genicular processes on immature specimen with three thecal pairs, developed only on third pair of thecae. See also Kozłowska-Dawidziuk (2002) for additional description.

Discussion.—The new species is similar to *Plectograptus robustus* in having similar apertural processes and thecal profiles, but in contrast to *Plectograptus robustus,* the ancora sleeve list junctions with the pleural lists are triple rather than quadruple.

Geographic and stratigraphic range.—EEP, lower Gorstian, *Neolobograptus nilssoni* Biozone.

Plectograptus wimani (Eisenack, 1951)

Fig. 10.

1951 *Retiolites wimani* sp. nov.; Eisenack 1951: 145, pl. 25: 8.
1951 *Retiolites* sp. indet. Eisenack 1951: 146, figs. 6, 7.
1995 *Plectograptus wimani* (Eisenack, 1951); Kozłowska-Dawidziuk 1995: 318, fig. 27E.

Emended diagnosis.—Ancora sleeve with secondary lists, quadruple list junctions at ends of apertural lists. Thecal walls inclined inwards from genicular to apertural lists. Singular reticulated genicular hood as wide as a length of genicular list.

Material.—Three mature specimens, partly damaged, and one at ancora stage of growth (Kozłowska-Dawidziuk 1995), Mielnik Borehole, Poland, depth 1044.9 m, Gorstian, *Neolobograptus nilssoni* Biozone.

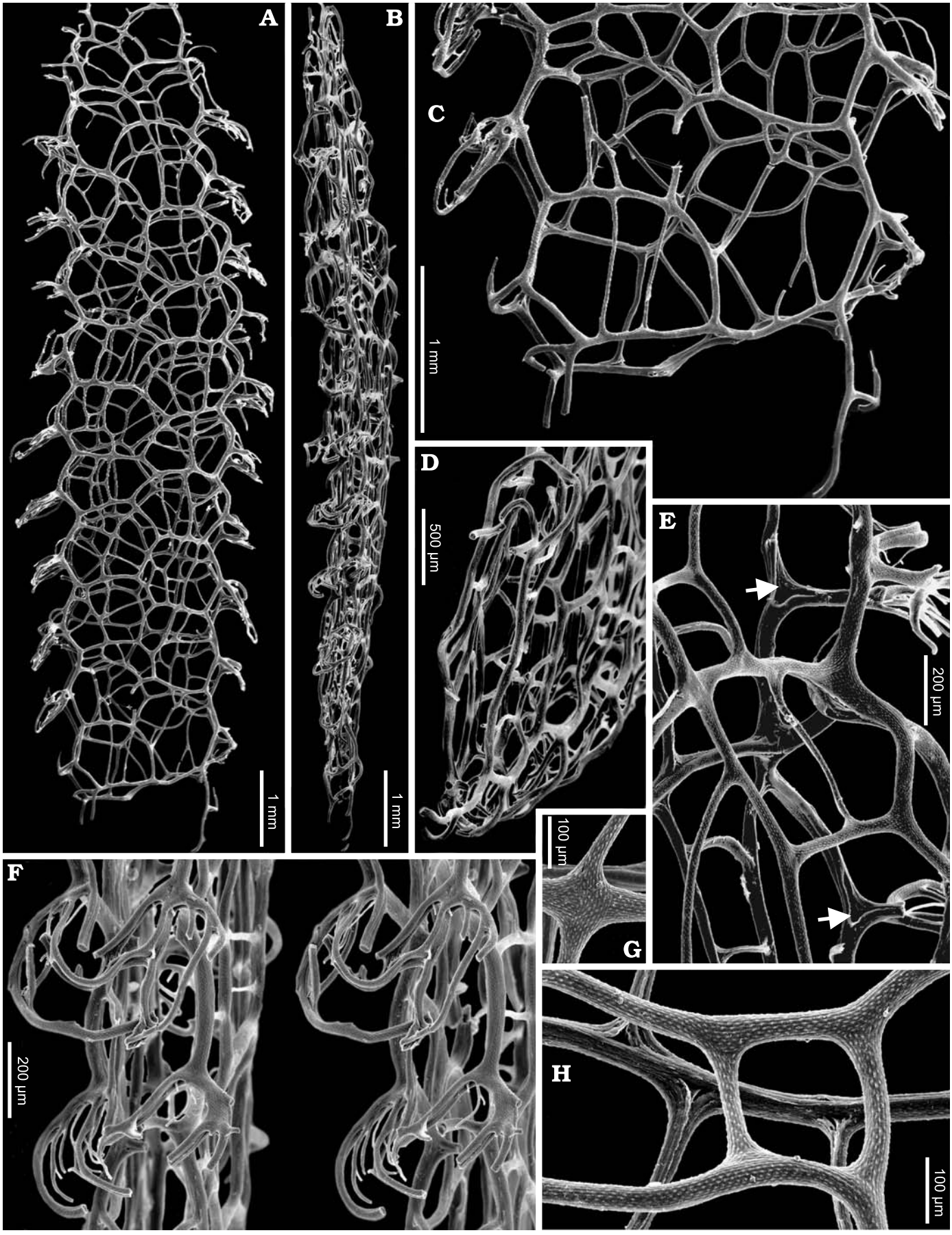
Description.—Largest specimen with 12 pairs of thecae, compressed almost flat, resulting in outward bulging of the thecal lips and genicular lists (Fig. 10). Ancora umbrella and distal end broken off (Fig. 10A). Width of ancora sleeve gradually increasing from 2.05 mm at the level of the first geniculum to 2.62 mm at the 7th thecal pair, gradually decreasing to 2.05 mm at the level of the 10th thecal pair. Total length estimated at 11.7 mm. Thecal orifices calculated as 1.00 mm wide by 0.36 mm from lip to geniculum, and cross-sectional obverse to reverse width of rhabdosome 2.08 mm. Primary ancora sleeve lists joining the lateral apertural rod/ thecal lip/pleural list junction. Secondary (reticular) lists of the sleeve form a stout meshwork between the primary lists. Genicular processes complex and loop-shaped (Fig. 10F), inclined proximally at about 30° from the horizontal (Fig. 10A).

The genicular processes are formed of primary curving lists, each bearing an insertion seam on its inner face, and secondary lists which are oblique to the primary lists, having seams on their inner or outer sides.

Discussion.—The illustrated specimen (Fig. 10) represents a more mature rhabdosome than the holotype (Eisenack 1951: pl. 25: 8), which has thinner lists and only incipient genicular processes. Two fragmentary rhabdosomes illustrated by Eisenack (1951: figs. 6, 7) represent more mature stages of growth, with better developed genicular processes, similar to the Polish material.

The insertion seams on the inner face of the primary lists making the genicular processes, show that the processes

Fig. 10. SEM pictures of mature rhabdosome of *Plectograptus wimani* (Eisenack, 1951), ZPAL G.XVI/1607, Mielnik borehole 1044.0 m, Poland, Ludlow → in obverse (**A**) and ventral (**B**) views. **C**. Enlargement of proximal end. **D**. Oblique view of proximal end. **E**. Thecae showing sockets (arrowed) and genicular hoods. **F**. Stereopair of two genicular hoods formed of primary lists and reticulum. **G**. Mid-ventral list and thecal lip. **H**. Ancora sleeve walls showing surface of lists from outside and inside.


A
1 mm
B
1 mm
C
1 mm
D
500 µm
E
200 µm
F
200 µm
G
100 µm
H
100 µm

were formed initially with a (fusellar) membrane. The secondary lists with their inner or outer seams therefore were formed on the outer and inner faces respectively of the process.

Geographic and stratigraphic range.—EEP, lower Gorstian, *Neolobograptus nilssoni* Biozone.

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