New and unusual upper Llandovery graptolites from Arctic Canada

ALFRED C. LENZ AND ANNA KOZŁOWSKA

Lenz, A.C. and Kozłowska, A. 2007. New and unusual upper Llandovery graptolites from Arctic Canada. *Acta Palaeontologica Polonica* 52 (3): 489–502.

Three isolated and well-preserved retiolitid taxa, two of them new, and one taxon of unknown affinity, are described from the upper Llandovery of Arctic Canada. All taxa display unusual characteristics The three retiolitids display extraordinary morphological features: *Pseudoplegmatograptus* cf. *obesus* preserves very delicate and lacey or cobweb-like list structures external to the main skeletal lists, structures previously seen only rarely on flattened material; *Pileograptus pileatus* gen. et sp. nov. possesses a thecal framework typical of retiolitines, particularly *Stomatograptus*, but its thecal orifices possess broad, meshwork genicular hoods similar to those in the plectograptines; and *Giganteograptus giganteus*, formerly attributed to *Pseudoplegmatograptus*, with its very coarse and relatively simple skeletal framework, well-developed paired thecal apertural spines, and a pustulose micro-ornamentation on the lists. The latter feature suggests an assignment to the subfamily Plectograptinae, rather than to the Retiolitinae as has been previously presumed. The presence of pustulose lists in *Giganteograptus* adds a further complication to understanding of retiolitid evolution. *Mirorgraptus arcticus* gen. et sp. nov., the fourth taxon and of unknown systematic affinity, lacks the proximal end, but preserves lists with seams and some fusellar material suggestive of some type of new retiolitid. Unlike known retiolitids or other graptolites, however, the skeletal list development is apparently confined to a narrow region along one side of the nema.

Key words: Graptoloidea, Retiolitidae, pustulose micro-ornamentation, Llandovery, Silurian, Arctic.

Alfred C. Lenz [aclenz@uwo.ca], Department of Earth Sciences, University of Western Ontario, London, Ontario N6A 5B7, Canada;
Anna Kozłowska [akd@twarda.pan.pl], Instytut Paleobiologii, PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

Introduction

The advent of SEM technology in recent decades has led to a variety of detailed studies of isolated retiolitid graptolites. These studies have resulted in the recognition of many new taxa (e.g., Kozłowska-Dawidziuk 1990, 1995, 2001; Lenz 1993; Lenz and Kozłowska-Dawidziuk 2001, 2002, 2004); vastly improved the knowledge of their complex macro- and micro-morphology (e.g., Bates 1990; Bates and Kirk 1986, 1992, 1997; Kozłowska-Dawidziuk 1995; Bates et al. 2005, 2006), and have greatly improved understanding of retiolitid classification and evolutionary history (e.g., Lenz and Melchin 1997; Kozłowska-Dawidziuk 2001, 2004; Kozłowska-Dawidziuk and Lenz 2001; Bates et al. 2005, 2006).

Extremely delicate structures, such as finely bifurcating spine tips, fringes and filamentous margins, or lace-like or membranous structures, have been seen only rarely outside of the main body of the rhabdosome of some mature, flattened retiolitid specimens, e.g., in *Pseudoplegmatograptus* spp. (e.g., Elles and Wood 1908; Bouček and Münch 1944; Lenz 1982; Štorch 1992; Lenz et al. 2003). Such delicate structures are even more rarely seen in isolated specimens, possibly because the structures may have been relatively rare to begin with, and/or they may have been developed only on mature specimens. In addition, the acid digestion treatment used to release the graptolites from carbonate concretions, although very gentle, may destroy these delicate structures. The isolated specimens of *Pseudoplegmatograptus* cf. *obesus* (Lapworth, 1877) (Fig. 1) are examples of such a rare and unusual preservation that was illustrated in the holotype specimen of *P. obesus* (Fig. 2A) almost 130 years ago, and only rarely seen since then.

This paper describes and illustrates four graptolite taxa, three of them acknowledged retiolitids, all preserved in full relief, all from the Telychian (upper Llandovery) of Arctic Canada, and all having some unusual or unanticipated morphological or micro-morphological feature. The three retiolitids comprise the "hairy" *Pseudoplegmatograptus* cf. *obesus* (Lapworth, 1877) noted above (Fig. 2), *Giganteograptus giganteus* (Bouček and Münch, 1944), previously described as *Pseudoplegmatograptus*, with a rhabdosome composed of a sparse framework (Fig. 6) and a, previously unknown, pustular micro-ornamentation, affiliating it with the subfamily Plectograptinae. The third form, *Pileograptus pileatus* gen. et sp. nov. (Figs. 3, 4), bears considerable similarities to *Stomatograptus* Tullberg, 1883, but has large, broad genicular hoods. The fourth described taxon, is a bizarre, fragmentary form, *Mirorgraptus arcticus* gen. et sp. nov., totally unlike any known graptolite, but possibly a retiolitid (Fig. 8).

In addition, mature retiolitid specimens, all but one flattened, are separately illustrated to aid and complement taxo-

nomic and morphologic comparisons and to illustrate the preservation of extremely delicate structures. These comprise *Pseudoplegmatograptus obesus* (holotype specimen), *P.* cf. *obesus*, *P. reticulatus* (Bouček and Münch, 1944), and *Giganteograptus giganteus*.

Institutional abbreviations.—BU, the Lapworth Museum, Birmingham University, United Kingdom; GSC, Geological Survey of Canada, Ottawa, Canada; PŠ, Czech Geological Survey, Prague, Czech Republic; ROM, Royal Ontario Museum, Toronto, Canada.

Morphological novelties and their significance

The studied isolated specimens present an opportunity, for the first time in some species, to observe important characters by means of scanning electron microscopy. The study provides unexpected new data, the new characters significant for a broadened understanding of the taxonomy and evolution of retiolitids.

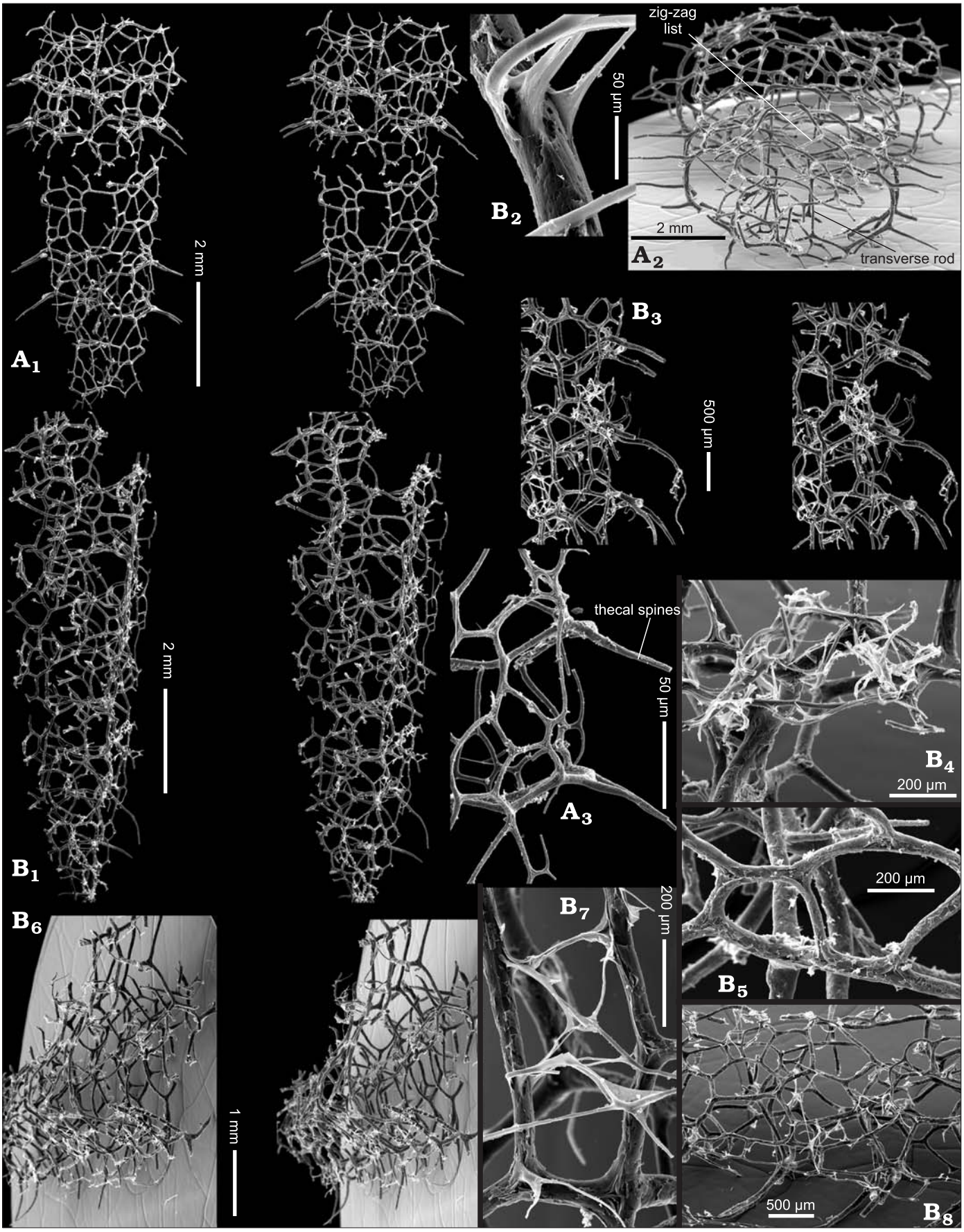
One of the most intriguing finds is the occurrence of pustulose bandages on the rhabdosome lists in a retiolitid belonging to the species described by Bouček and Münch (1944) as *Plegmatograptus giganteus* from the middle Telychian, *Monoclimacis griestonensis–M. crenulata* Biozone. Previously, a pustulose bandaged surface in Telychian retiolitids was known in only three genera, *Paraplectograptus* Bouček and Münch in Přibyl, 1948a, *Pseudoplectograptus* Obut and Zaslavskaya, 1983, and *Sokolovograptus* Obut and Zaslavskaya, 1976 (see Kozłowska-Dawidziuk 2004: fig. 1). Among other characters of the Retiolitidae, surfaces of cortical bandages are strongly differentiated between the "old" retiolitinid genera (as for example *Retiolites, Stomatograptus*, and *Pseudoplegmatograptus*) with smooth or parallel linear patterned bandages, and "young" Plectograptinae faunas with pustulose bandages (such as seen in all post-lower Homerian retiolitids and the older *Sokolovograptus*, *Pseudoplegmatograptus*, and *Paraplectograptus*). It seems that the other members of the *Pseudoplegmatograptus* group created by Přibyl (1948) for *Plegmatograptus* Elles and Wood, 1908, possess smooth or striated bandage surfaces as in *P. obesus* (Bates and Kirk 1992: fig. 217; Fig. 1 herein). As yet, however, the adaptive, morphologic, or evolutionary significance of the changes in bandage ornamentation is unknown, and future detailed study focused specifically on this problem is required. However, the possession of one of the two types of bandage surfaces has been considered to be one of the key characters for the division of the retiolitids into the subfamilies Retiolitinae or Plectograptinae (Lenz and Melchin 1987, Bates et al. 2005). Accordingly, the presence of pustulose micro-ornamentation on *G. giganteus* suggests its affinity lies with the subfamily Plectograptinae, and necessitates recognizing it as a new genus (see below).

The second unusual feature recognized in this study is the preservation of a delicate network of thin lists and finely multi-furcating distal ends of thecal spines, developed outside the ventral walls and ancora sleeve walls in *Pseudoplegmatograptus* cf. *obesus* (Fig. 1). As noted above, such structures are rarely preserved in flattened specimens of *Pseudoplegmatograptus* (see Fig. 1; see also *Pseudoplegmatograptus wenlockianus* Štorch 1992), but have not been previously examined using scanning electron microscopy, although they are recognizable in some images illustrated by Bates and Kirk (1992).

Similar structures have been observed in isolated specimens of *Cometograptus apoxys* Lenz and Kozłowska-Dawidziuk, 2001 (pl. 12: 6), in which there are also thin lists located outside of ancora sleeve and ventral walls. Additionally, however, in the proximal part of *C. apoxys* the lists form stomata with distinctive membranes in their proximal and distal parts, whereas in *P. obesus*, such elaborated stomata are not observed. The layer of thin lists, sometimes connected by a membrane outside the ancora sleeve suggests the possibility of an additional layer outside the ancora sleeve. These delicate structures have occasionally been illustrated as being attached to an almost ephemeral outermost membrane or fringe (e.g., Bouček and Münch 1944: text-figs. 5B, 6). This would have provided the possibility of additional space between ancora sleeve and the new layer (However, an examination by one of us (A.L.) of the same specimens in the Czech National Museum, Prague, provided no convincing evidence of such a fringe, so its presence is in doubt). On the other hand, even though the "hairy" lists were probably not joined to any kind of outer fringe, the presence of the very fine lists alone might have assisted rhabdosomal suspension or orientation in the water column.

The third novel character described in the paper is the occurrence of genicular hoods in the new retiolitid *Pileograptus pileatus* gen. et sp. nov. (Fig. 3), a character observed for the first time in a member of the Retiolitinae. The new form is, in many ways, similar to the well-known genus *Stomatograptus* Tullberg 1883, but differs distinctively in the presence of reticulate genicular hoods above the ventral apertures, a structure that is relatively common in the plectograptines. Apertural hoods are present in *Gothograptus nassa* (Holm, 1890), but they are solid structures, rather than reticulated (Kozłowska-

Fig. 1. SEM micrographs of *Pseudoplegmatograptus* cf. *obesus* (Lapworth, 1877), Snowblind Creek, Cornwallis Island, lower Telychian, *Spirograptus guerichi* Biozone. **A**. Rhabdosome with eight pairs of thecae but without proximal end, GSC38904; A_1, stereopair of lateral view, note zig-zag list; A_2, oblique proximal end view, note transverse rod; A_3, close-up showing well-developed thecal spines and strong thecal lips. **B**. Fragment of rhabdosome with eight pairs of thecae and fine secondary lists, GSC38905; B_1, stereopair of lateral view; B_2, enlargement showing smooth to weakly striated surface of lists; B_3, stereopair of rhabdosome fragment with three thecae, disto-lateral view; B_4, enlargement showing numerous fine, secondary lists; B_5, enlargement of main lists with seams outside; B_6, stereopair of disto-lateral view; B_7, enlargement showing fine, secondary lists; B_8, lateral view showing scattered secondary lists. →


zig-zag list
50 µm
B2
2 mm
A2
transverse rod
2 mm
A1
B3
500 µm
2 mm
B1
thecal spines
50 µm
A3
B4
200 µm
200 µm
B5
B7
200 µm
B6
1 mm
500 µm
B8

Dawidziuk 2004: fig. 5D, G), whereas reticulated genicular hoods are present in, for example *Gothograptus storchi* Lenz and Kozłowska, 2006 (Lenz and Kozłowska 2006: figs. 6, 7), *Papiliograptus papilio* Lenz and Kozłowska-Dawidziuk, 2002 (Lenz and Kozłowska-Dawidziuk 2002: fig. 12), and *Plectograptus wimani* Eisenack, 1951 (Bates et al. 2006: fig. 10). In all Plectograptinae taxa, however, the hoods are attached to distinct thecal geniculae, whereas the reticulated hoods of *Pileograptus pileatus* are connected to lateral apertural rods (and therefore, the lateral thecal walls) that are strongly inclined to the axis of the rhabdosome, a trait typical of all retiolitines such as in *Retiolites* and *Stomatograptus*.

Stratigraphy, biostratigraphy and sample locations

The Cape Phillips Formation, from which all of the study specimens were collected, is the best-known graptolite-bearing unit in the Canadian Arctic Islands(Thorsteinsson 1958), and is justifiably famous for its superb, full-relief preservation of graptolite faunas within calcareous concretions. The study material, all from concretions that were collected from talus, derives from three localities:

(1) Snowblind Creek, central, eastern Cornwallis Island, 75°11' N, 93°56' W (field designation SB04), yielding *Mirorgraptus arcticus* gen. et sp. nov. and *Pseudoplegmatograptus* cf. *obesus*;

(2) Central, western Baillie Hamilton Island, 75°52'47.6" N; 94°47'45" W (GSC locality C61680), yielding *Giganteograptus giganteus* (Bouček and Münch, 1944);

(3) Cape Sir John Franklin, Grinnell Peninsula, Devon Island, 76°42.5' N, 96°53' W (field designation SJF02), yielding *Pileograptus pileatus* gen. et sp. nov.

Mirorgraptus arcticus gen. et sp. nov. and *Pseudoplegmatograptus* cf. *obesus* are associated with a moderately diverse fauna, including *Spirograptus guerichi* Loydell, Štorch, and Melchin, 1993, *Streptograptus* cf. *storchi* Loydell, 1991, *Streptograptus* sp. and *Pseudoretiolites* sp. The first named species suggests a correlation with the lower Telychian *Spirograptus guerichi* Biozone of Loydell et al. (1993), the *Spirograptus turriculatus minor* Biozone of Melchin 1988.

Giganteograptus giganteus is associated with *Oktavites spiralis* (Geinitz, 1852) and *Cyrtograptus* sp. (Fig. 6C, D). The stratigraphic overlap of the two monograptid species clearly indicates a correlation with the uppermost Telychian *Cyrtograptus sakmaricus* Biozone (Melchin 1988), and with the *C. lapworthi-insectus* Biozone (Koren' et al. 1996).

Pileograptus pileatus gen. et sp. nov. is associated with *Retiolites* sp. (immature), *Oktavites spiralis*, *Cyrtograptus*? sp., and *Mediograptus flexuosus* Tullberg, 1883?, among others. The association suggests a correlation with either the *C. sakmaricus* Biozone (if the genus *Cyrtograptus* is correctly identified), or with the generalized upper Telychian *O. spiralis* Biozone of Koren' et al. (1996).

Systematic palaeontology

The described taxa are housed with the National Type Collection of Invertebrate and Plant Fossils of the Geological Survey of Canada, Ottawa, and are assigned curatorial numbers (prefixed GSC) of that institution.

Order Graptoloidea Lapworth, 1873
Family Retiolitidae Lapworth, 1873
Subfamily Retiolitinae Lapworth, 1873
Genus *Pseudoplegmatograptus* Příbyl, 1948b

Type species: *Retiolites perlatus* var. *obesus* Lapworth, 1877, Gala beds, Elwand Water, Melrose, Scotland; Telychian.

Biostratigraphic range: Middle Llandovery *Demirastrites pectinatus–Dm. triangulatus* to mid Wenlock *Monograptus bellerophorus–M. riccartonensis* biozones.

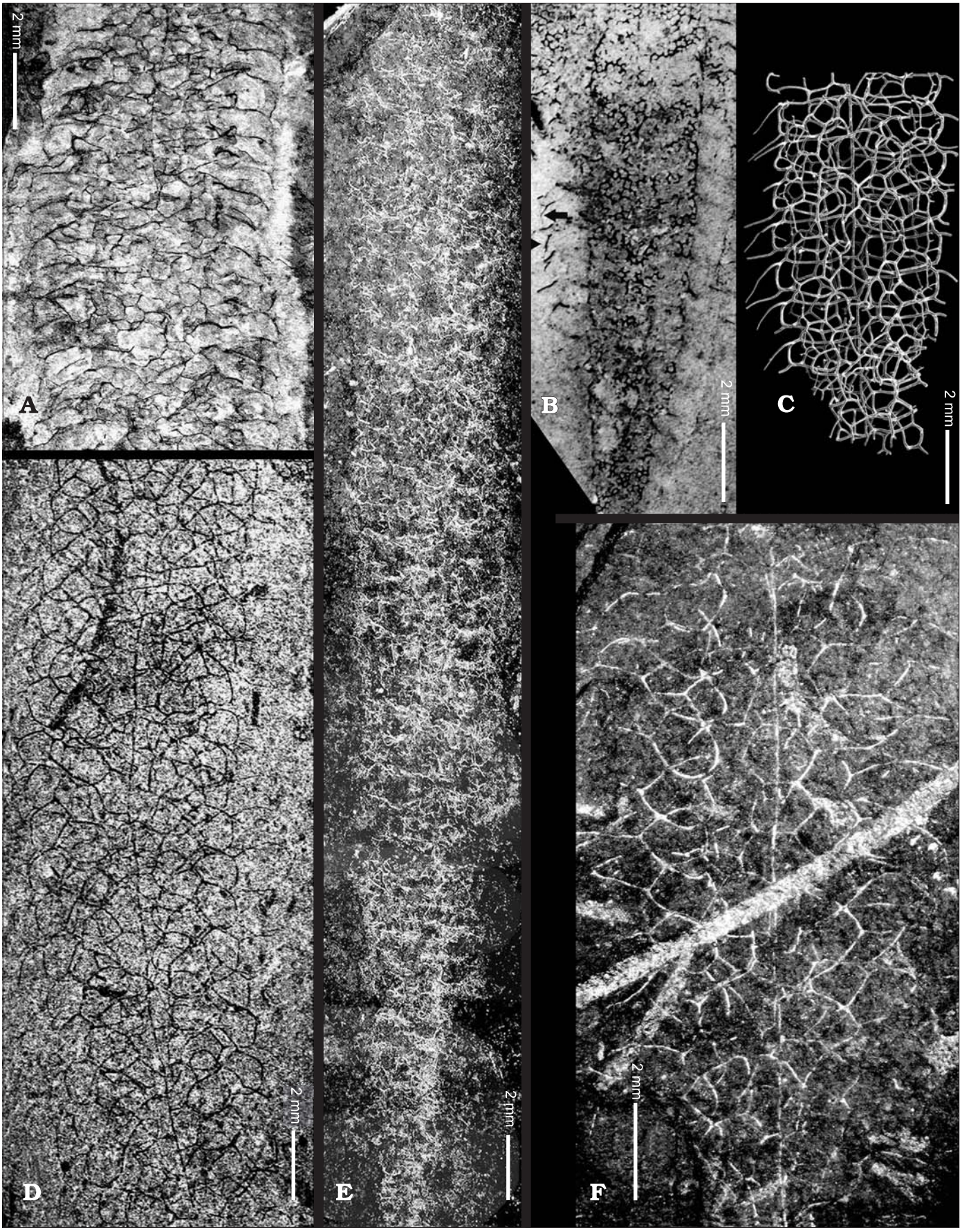
Species included: *Pseudoplegmatograptus obesus* (Lapworth, 1877); *P. reticulatus* (Bouček and Münch, 1944); *P. hexagonalis* (Bouček and Münch, 1944); *P. wenlockianus* Štorch, 1992; *P. relictus* (Bouček and Münch, 1944)?; *P. longispinus* (Bouček and Münch, 1944)?; *P. flaccidus* Wang, 1978?; *Sinostomatograptus mui* Huo, 1957?.

Pseudoplegmatograptus cf. *obesus* (Lapworth, 1877)

Figs. 1, 2A, C, E.

1877 cf. *Retiolites perlatus obesus* sp. nov.; Lapworth 1877: 137, pl. 6: 29.
1944 cf. *Plegmatograptus obesus obesus* (Lapworth, 1877); Bouček and Münch 1944: 6, figs. 1a–g, 2a, b; pl. 1: 1, 2.
1982 *Pseudoplegmatograptus obesus* (Lapworth, 1877); Lenz 1982: 41, figs. 16e; 17a, b.
1987 cf. *Pseudoplegmatograptus obesus obesus* (Lapworth, 1877); Lenz and Melchin 1987: 163, pl. 1: 1 (see Fig. 2C herein).
1992 cf. *Pseudoplegmatograptus obesus* (Lapworth, 1877); Bates and Kirk 1992: 176, pls. 15–20: 171–182, 212–217, 239–249. Non figs. 183–191, 235–238 (= *Pseudoretiolites* sp.)

Fig. 2. **A**, **C**. Flattened or isolated specimens of *Pseudoplegmatograptus obesus* (Lapworth, 1877). **A**. Portion of the holotype specimen, showing distal-end bifurcation and merging of spines, BV1363, Gala beds, Melrose, Scotland, Lower Telychian. **C**. SEM micrograph of isolated specimen, showing typical apertural lips, paired apertural spines and "unadorned" rhabdosome, GSC 78423, lower Telychian, *Spirograptus guerichi* Biozone, Snowblind Creek (= Laura Lakes of Lenz and Melchin 1987), Cornwallis Island. **E**. Mature specimen of *Pseudoplegmatograptus* cf. *obesus* showing abundant intricate and lacey or cobweb-like structures, ROM38884, Peel River, northern Yukon, *Spirograptus guerichi* Biozone (see Loydell 1993: 61 for revision of biostratigraphic level). **B**. Flattened specimen of *Pseudoplegmatograptus reticulatus* (Bouček and Münch, 1944) with well-preserved bifurcating spines (arrows), type 29910 Museum de la Plata, Argentina, from Talacasto region, San Juan, northern Argentina, *Spirograptus turriculatus–Monograptus crispus* Biozone. **D**, **F**. Flattened specimens of *Giganteograptus giganteus* (Bouček and Münch, 1944). **D**. Rhabdosome with coarse meshwork of delicate lists, long paired thecal orifice spines, and clearly attached nema through most of rhabdosome, but possibly free in the distalmost region, type PŠ511a(1), Pankratz, Prague region, Czech Republic. **F**. Distal part of rhabdosome with very coarse meshwork and long, paired spines with nema apparently attached throughout, ROM38886, Delorme Range, Northwest Territories, *Oktavites spiralis* Biozone. Scale bars 2 mm. →


A
2 mm
B
2 mm
C
2 mm
D
2 mm
E
2 mm
F
2 mm

Material.—Two mature, isolated specimens, lacking the proximal-most regions (Fig. 1).

In addition, the holotype specimen of Lapworth (1877) and one isolated specimen of *P. obesus* from the Canadian Arctic (Fig. 2A and C, respectively), and one flattened specimen of *P.* cf. *obesus* from Yukon Territory (Fig. 2E), are illustrated for comparison of the delicate structures.

Description.—Longest specimen 10 mm, proximal end missing; maximum width about 2.6 mm, exclusive of spines. Thecal framework medial region with distinct zigzag lists (Fig. $1A_1$). Transverse rods close to nema (Fig. $1A_2$). Ancora sleeve well developed, well separated from thecal framework, composed of moderate-size polygonal meshes, and some larger, somewhat ill-defined, medially positioned polygonal meshes, probably stomata. Apertural lips thickened (Fig. $1A_3$), with paired, robust and proximolaterally-positioned spines; occasional spine bifurcating or trifurcating distally (Fig. $1B_3$). Arising primarily near the junction of the thecal framework and ancora sleeve are numerous, very fine, frilly, cobweb-like or lacey reticular lists, mostly disorderly; some forming secondary fringelike meshes (Fig. 1B); these structures are clearly similar to those seen in flattened specimen shown in Fig. 2E. List micro-ornament smooth (Fig. $1B_7$, B_5) or with weak, parallel striae (Fig. $1B_2$).

Discussion.—The genus *Pseudoplegmatograptus obesus* Příbyl, 1948b appears to be one of the few retiolitids that occasionally generated delicate structures such as multi-furcated thecal spines that may partially fuse distally, cobweb-like or lacey reticular networks and, still more rarely, apparent membraneous structures (see Elles and Wood 1908: figs. 223a, b; Lenz 1982: fig. 17a–c; Bates and Kirk 1992: figs. 241–243; and holotype specimen of *P. obesus* illustrated in Fig. 2A).

The only other non-retiolitid group featuring such structures relatively commonly are some species of *Petalolithus* Suess 1851 (see some examples in Koren' and Rickards 1996). This parallelism is considered very significant, since the petalolithids and the retiolitids constitute the ancorate graptolites, which are considered to share a common ancestry (Melchin 1998). It is also considered that the retiolitids were derived from some petalolithid (Lenz 1994; Melchin 1999; Kozłowska-Dawidziuk 2004; Bates et al. 2005).

The delicate, multi-furcating thecal spines are only intermittently seen on the two illustrated specimens. However, their relative density where present (preserved) suggests that they were probably originally present on all, or most, of the spines, and that they were broken off during the acid extraction. The presence of thecal spines and rim structures on the species type specimen, *Pseudoplegmatograptus obesus* from Spain (Štorch 1998), *P. reticulatus* from Argentina (Fig. 2A, B, respectively), *P. wenlockianus* described from the Prague region (Štorch 1992), and on some specimens of *Pseudoplegmatograptus obesus* illustrated in Bates and Kirk (1992) supports this conclusion. Whether, however, similar multifurcations were commonly present in all species of the genus is unknown. As a further observation, it appears that *Pseudoplegmatograptus* is one of the few genera to more or less consistently feature border fringes and thecal spine complications.

The study specimens, like the specimens described as *Pseudoplegmatograptus obesus* in Lenz (1982) and illustrated in Fig. 2E, differ from the type species in being somewhat narrower and widening more gradually proximally. In other respects, they are very similar and, accordingly, are identified as *Pseudoplegmatograptus* cf. *obesus*.

Genus *Pileograptus* nov.

Type and only species: *Pileograptus pileatus* sp. nov.

Derivation of the name: From Latin *pileus*, "cap", "capped"; referring to the prominent broad, cap-like thecal hoods.

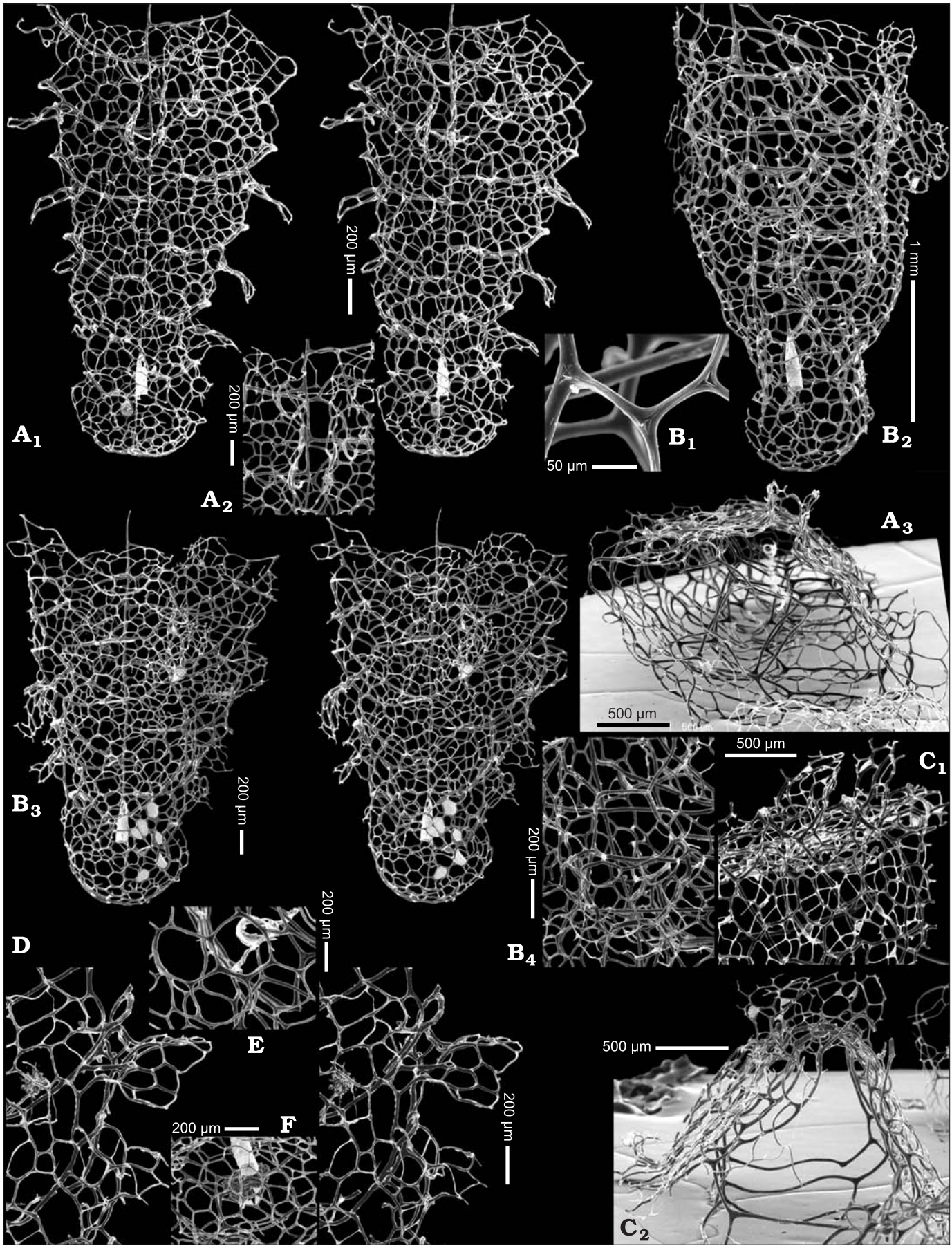
Stratigraphic and geographic range.—Found in the upper Telychian, although it is unclear whether from the *Oktavites spiralis* Biozone or the uppermost Telychian *Cyrtograptus lapworthi–C. insectus* Biozone, Devon Island, Arctic Canada.

Diagnosis.—Ancora umbrella deep, bowl-shaped, composed of uniform, polygonal meshes; prosicula fully preserved; zig-zag forming along one lateral wall of ancora sleeve, transverse rods close to nema, lateral aperture lists moderately curved; thecal aperture capped by prominent, broad meshwork genicular hood that is anchored to lateral apertural lists of succeeding theca; ancora sleeve a fairly dense, polygonal meshwork; stomata chimney-like with meshwork walls; list micro-ornament of weak, parallel striae.

Discussion.—Except for its greater depth, the ancora umbrella of *Pileograptus* gen. nov. is typical of that of *Stomatograptus* Tullberg, 1883 in its bowl-shape and possession of a distinctly polygonal and uniform-size meshwork (see Bates et al. 2005: fig. 6d); also typical of *Stomatograptus*, the immediate post-ancora umbrella part of the rhabdosome is noticeably narrower, imparting a "pinched" profile look, particularly on one side (compare Fig. $3A_1$, B_2, B_3 with Fig. $4A_1$, A_2). The presence of a complete prosicula is also characteristic (as e.g., illustrated in *S. canadensis* in Fig. $4A_2$) of both genera.

The chief difference between *Stomatograptus* and *Pileograptus* gen. nov. rests in the nature of the thecal orifice and

Fig. 3. SEM micrographs of *Pileograptus pileatus* gen. et sp. nov., Devon Island, upper Telychian, *Oktavites spiralis* Biozone. **A**. Holotype showing deep ancora umbrella, well-developed thecal hoods, collar-like stoma, GSC38910; A_1, stereopair of obverse view; A_2, enlargement of stoma; A_3, view of the inside from distal part of rhabdosome, showing canals, transverse rods, and shape of rhabdosome in cross section. **B**. Rhabdosome with five pairs of thecae, and small, elevated stoma, GSC3891; B_1, ancora umbrella lists with smooth surface; B_2, ventral view of rhabdosome; B_3, stereopair of reverse view; B_4, enlargement of a portion of lateral wall showing apertural lists and (behind) transverse rods. **C**. Incomplete specimen with well-developed thecal hood, GSC38912; C_1, lateral view of thecal hood; C_2, distal view, cross-section, broad thecal hood. **D**. Stereopair of fragmentary specimen, showing two well-developed thecal hoods, GSC38913. **E**. Enlargement of portion of ancora, prosicula and virgella, GSC38914. **F**. Enlargement of part of ancora, showing arrangement of ancora umbrella, complete prosicula and virgella, GSC38915. →


A1
200 µm
200 µm
A2
B1
50 µm
1 mm
B2
A3
500 µm
B3
200 µm
200 µm
B4
500 µm
C1
D
200 µm
E
200 µm
F
200 µm
500 µm
C2

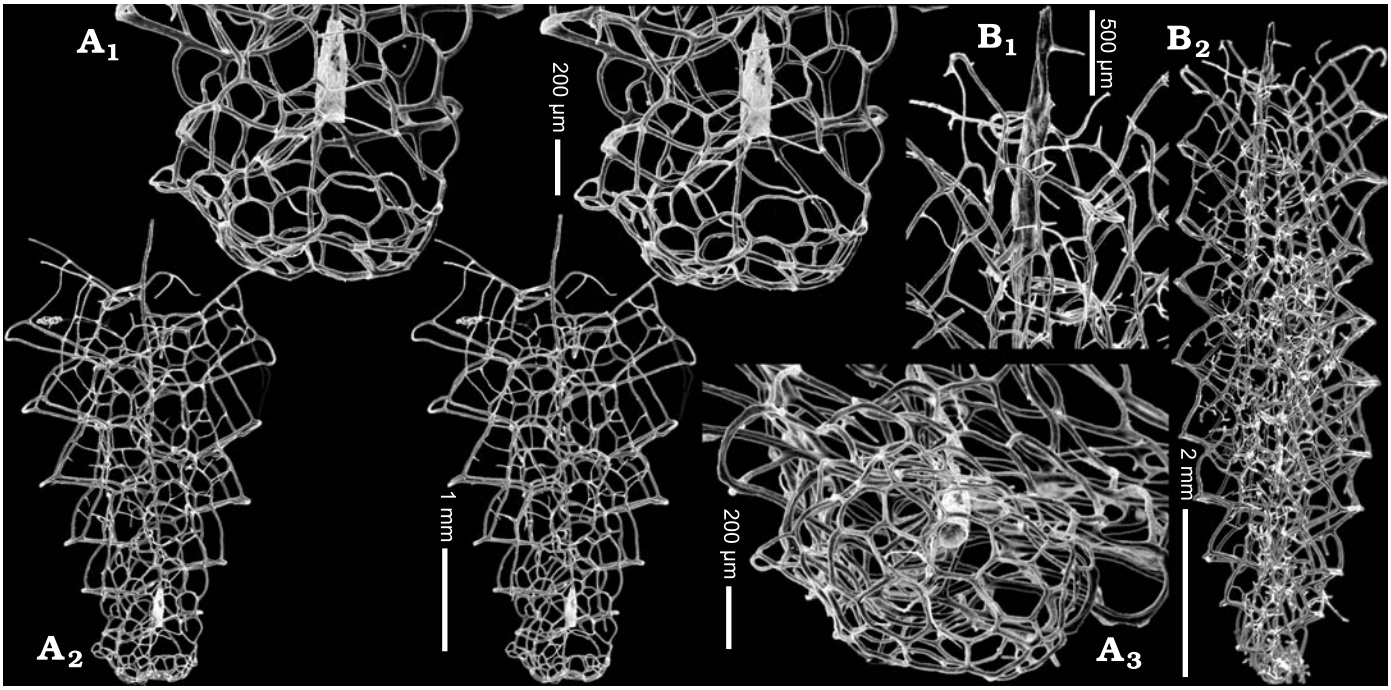


Fig. 4. SEM micrographs of *Stomatograptus canadensis* Lenz, 1988. **A**. Immature specimen with five pairs of thecae, with well-preserved, shallow ancora umbrella, GSC38916, Cape Phillips, Cornwallis Island, Nunavut, Canada, probably *Cyrtograptus centrifugus–C. murchisoni* Biozone; A_1, stereopair enlargement showing sicula and ancora umbrella; A_2, stereopair of obverse view of rhabdosome; A_3, proximal view of the ancora umbrella, showing opening of prosicula. **B**. Rhabdosome with ten pairs of thecae and nematularium, GSC38917, Cape Phillips, Cornwallis Island, Nunavut, Canada, probably *Cyrtograptus centrifugus–C. murchisoni* Biozone; B_1, enlargement of distal part of rhabdosome with nematularium, B_2, latero-ventral view of rhabdosome.

the thecal hoods. In the more common species of *Stomatograptus* such as *S. grandis grandis* (Suess, 1851), *S. grandis imperfectus* Bouček and Münch, 1944; *S. grandis maior* Bouček and Münch, 1944; *S. canadensis* Lenz, 1988; and *S.*? *sinensis* Wang, 1965, the thecal profiles are more clearly orthograptid, and none possesses thecal hoods. Furthermore, in these same species, the stomata on lateral walls of ancora sleeves are all fairly similar in possessing thickened rims and in being less, or not at all, elevated above the surrounding ancora sleeve.

There are also similarities with *Retiolites* Barrande, 1850 in the general arrangement of the rhabdosome, but that genus differs in its much shallower ancora umbrella, absence of a "pinched" profile in immediate post-ancora umbrella region, and straight lateral apertural rods. Thecal hoods are sometimes present in the more proximal region of some species of *Retiolites*, particularly on mature specimens (e.g., Bates and Kirk 1997, figs. 81a, f–j, 82), but these are merely ventral protrusions of the distal rim of the thecal orifice, rather than being distinct hoods that are attached to the proximal side of succeeding thecal lateral rods as in *Pileograptus* gen. nov.

Comparisons can also be made with *Pseudoplegmatograptus* Příbyl, 1948b and *Dabashanograptus* Ge, 1990, both of which also retain the complete prosicula (and occasionally part of the metasicula). From the former, *Pileograptus* gen. nov. differs in its much deeper ancora umbrella, laterally projecting thecal orifices and, particularly, prominent thecal hoods. *Dabashanograptus* Ge, 1990 differs markedly from *Pileograptus* in possessing an extremely simple and open ancora region, somewhat similar to that of the much younger *Plectograptus*; but on the other hand, it appears to possess some type of ventrally projecting and, possibly, meshwork thecal processes (see Bates et al. 2005: fig. 7b). Unfortunately, because of limited preservation, further comparison is impossible.

Pileograptus pileatus sp. nov.

Figs. 3–5.

Derivation of the name: From Latin *pileus*, "cap"; referring to cap-like thecal hoods.

Holotype: GSC38912, Figs. $3A_1$–A_3. Rhabdosome with proximal end well developed five pairs of thecae.

Type locality: Cape Sir John Franklin, Devon Island, Arctic Canada.

Type horizon: Upper Llandovery.

Material.—Twenty specimens, all immature, in various stages of development.

Diagnosis.—As for genus.

Description.—Rhabdosome of most mature specimen with five pairs of thecae 3.7 mm long, maximum distal width 2.4 mm inclusive of thecal hoods. Ancora umbrella deep, bowl-shaped, of *Stomatograptus* type, about 1.0 mm wide, made up of more or less equal-sized and regular hexagonal meshes; well-developed prosicula present in every specimen, length totalling 0.9–1.0 mm, of which about 0.4 mm of the apical end is preserved mostly as longitudinal threads. Thecal framework consists of zigzag lists present on one side

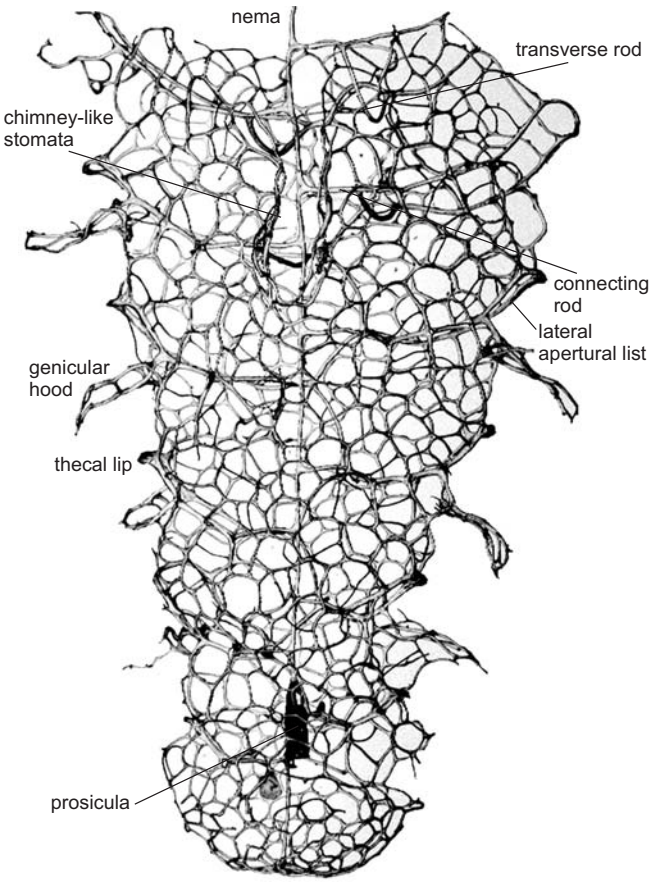


Fig. 5. *Pileograptus pileatus* gen. et sp. nov., labelling relevant parts of the skeletal morphology.

of rhabdosome, transverse rods situated close to the nema (Fig. $3A_2$), concave curved lateral apertural lists inclined overall about 60° to axis of rhabdosome, and apertural rims that are well-developed and slightly thickened; ancora sleeve made of fairly dense meshwork of orderly hexagonal meshes, meshes 0.1–0.2 mm in diameter.

A single prominent ancora sleeve stoma of more or less ovate outline developed about level with third thecal pair on both lateral walls, rimmed by well-developed, but loose collar-like meshwork (Fig. $3A_1$–A_3, B_3). Thecal orifice directed ventrally, with prominent meshwork, genicular hood, reminiscent of the "bill" of a baseball cap. Hood-anchoring lists attached to underside of succeeding thecal lateral apertural lists (Fig. $3A_1$); hood-anchoring lists directed proximoventrally initially, and then abruptly curving ventrally; hood curved ventro-proximally, widening laterally. Lists with weak, parallel micro-ornamentation (Fig. $3B_1$).

Discussion.—The very large and broad thecal hoods of *P. pileatus* are reminiscent of those of the upper Homerian species e.g., *Papiliograptus papilio* Lenz and Kozłowska-Dawidziuk, 2002. In the latter species, however, the hoods are clearly extensions from the geniculum and the thecal structures and thecal framework are completely different.

Stratigraphic and geographic range.—As for genus.

Subfamily Plectograptinae Bouček and Münch, 1952

Genus *Giganteograptus* nov.

Derivation of the name: Referring to the large size of the rhabdosome.

Type and only species: *Giganteograptus giganteus* (Bouček and Münch, 1944).

Species included: *Giganteograptus giganteus* (Bouček and Münch, 1944). It is possible that "*Pseudoplegmatograptus*" *obscurus* Bouček and Münch, 1944, also with a very delicate and coarse skeletal framework, might be assignable to the new genus, although without knowledge of its micro-ornamentation, this cannot be confirmed.

Diagnosis.—Rhabdosome large, with coarse, orderly polygonal meshwork without reticulum. Thecal lists composed of transverse rods, connecting rods present in proximal and medial parts of rhabdosome, lateral apertural rods, and lips with paired apertural spines projecting proximolaterally. Transverse rods close to thin nema similar to *Paraplectograptus* Bouček and Münch, 1948. Nema free in distal part of rhabdosome. Ancora sleeve reduced only to pleural lists, slanted lateral lists. Micro-ornamentation of outward facing pustules.

Discussion.—The lack of any part of the proximal end ancora umbrella in the studied material, as well as in the illustrated Czech material, makes comparisons somewhat difficult. Nevertheless, the rhabdosomal framework is fairly clear (Fig. 2D).

The list surfaces with micro-ornamentation on bandages observed in this species firmly places it in the subfamily Plectograptinae (e.g., Lenz and Melchin 1987; Lenz 1993; Kozłowska-Dawidziuk 2001; Bates et al. 2005).

Stratigraphic and geographic range.—*Monoclimacis griestoniensis–crenulata* Biozone, upper Telychian, Llandovery, Czech Republic; *Cyrtograptus sakmaricus* Biozone, uppermost Telychian, Llandovery, Arctic Canada; and *Oktavites spiralis* Biozone of Delorme Range, Mackenzie Mountains, Northwest Territories, Canada.

Giganteograptus giganteus (Bouček and Münch, 1944)

Figs. 2D, F, 6A, B, 7.

1944 *Plegmatograptus giganteus* sp. nov.; Bouček and Münch 1944: 16, figs. 5b, c; 6a–c.

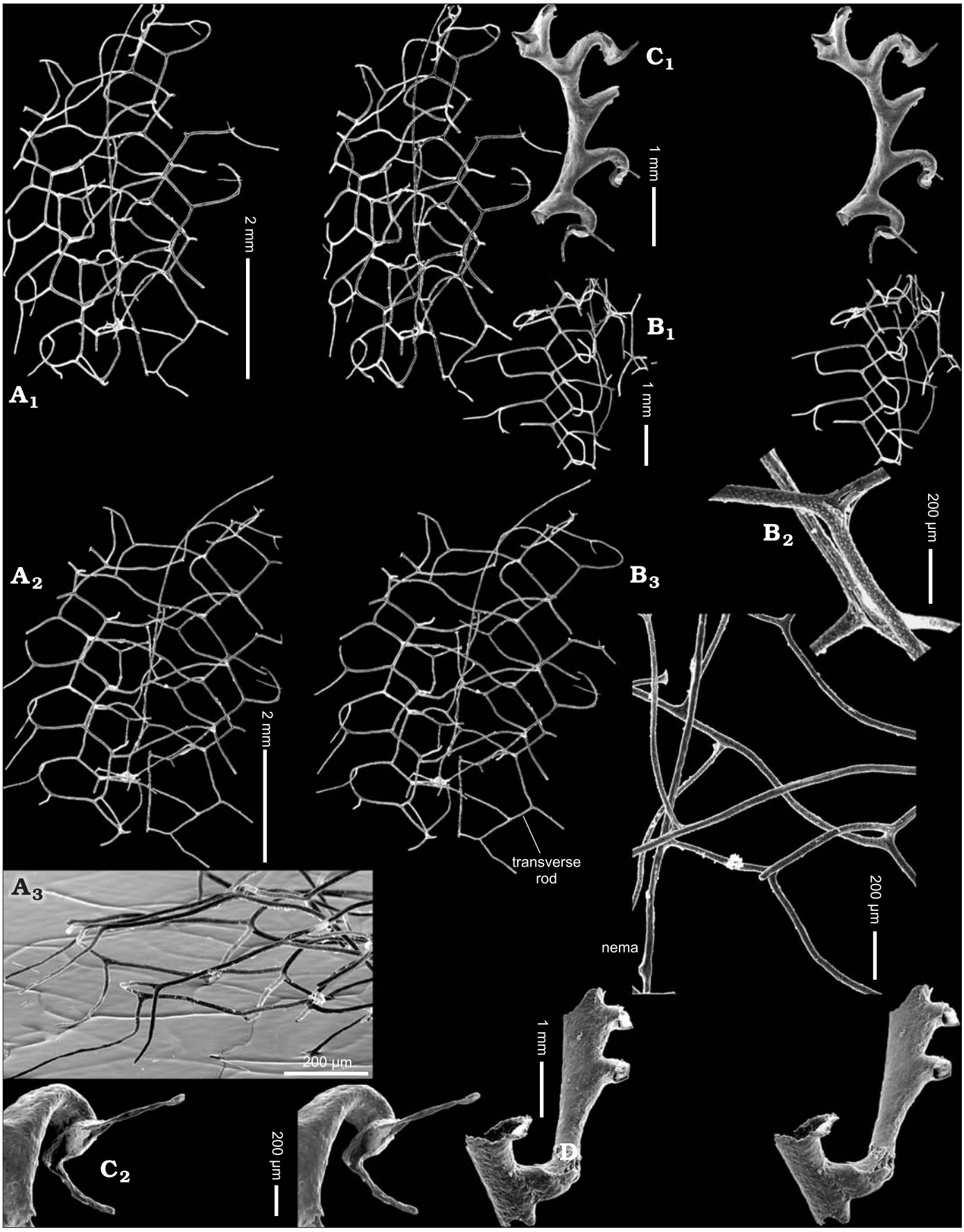
1982 *Pseudoplegmatograptus giganteus* (Bouček and Münch, 1944); Lenz 1982: 41, figs. 17c, d.

1994 *Pseudoplegmatograptus giganteus* (Bouček and Münch, 1944); Štorch 1994: 180, pl. 2: 2.

2003 ?*Pseudoplegmatograptus*? *giganteus* (Bouček and Münch, 1944); Loydell et al. 2003: fig. 7n.

Studied material.—Three incomplete, isolated specimens without proximal ends, two illustrated in Fig. 6. Two mature, flattened specimens, from the Northwest Territories, Canada and the Czech Republic are illustrated for comparison (Fig. 2D, F).

Description.—Rhabdosome incomplete, lacking proximal end; about 5 mm wide exclusive of thecal spines. Skeletal framework of thin lists forming very coarse, orderly, polygonal meshwork, more or less arranged in at least three crude mesh rows. Thecal rims well marked, margins possessing


A1
2 mm
C1
1 mm
B1
1 mm
B2
200 µm
A2
2 mm
B3
transverse rod
A3
200 µm
nema
200 µm
1 mm
C2
200 µm
D

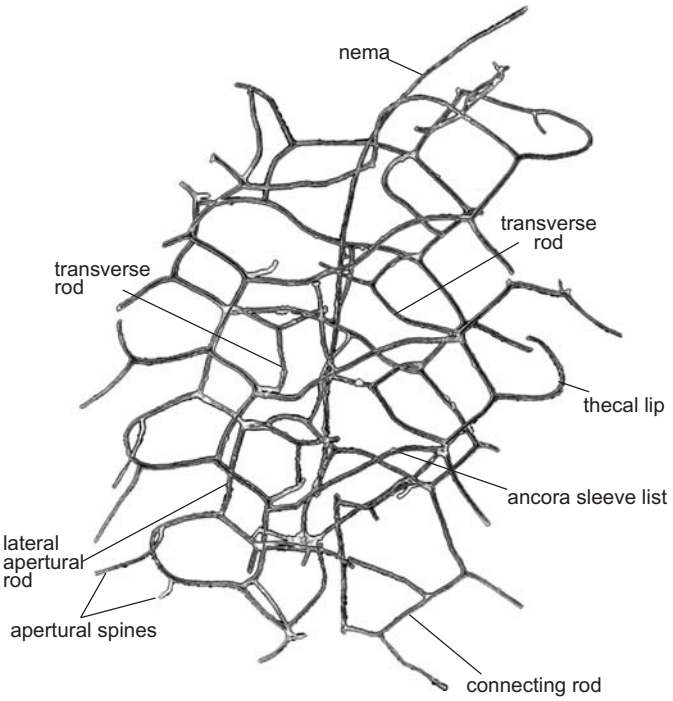


Fig. 7. *Giganteograptus giganteus* (Bouček and Münch, 1944), labelling relevant parts of the skeletal morphology.

well developed, proximolaterally projecting paired spines (Fig. 6A). Nema delicate, attached to thecal framework by connecting rods, possibly free in distal region, extending beyond rhabdosome. Transverse rods well developed, close to nema (Fig. $6A_2$). Pustulose micro-ornamentation on all lists, well developed facing outwards (Fig. $6B_2$).

Discussion.—The thin lists forming a very coarse and crudely polygonal meshwork of three or four rows of meshes are a characteristic of the species. The isolated study material is somewhat narrower than the flattened specimens illustrated in Fig. 2D, F (5 mm *versus* 6–7 mm); nevertheless, the species assignment is considered firm, since some of the greater width of the supplementary material is likely the result of flattening.

The possession of a pustulose micro-ornamentation is, however, entirely unexpected, since the typical *Pseudoplegmatograptus*, like other members of the subfamily Retiolitinae, possesses a smooth or parallel striae micro-ornamentation (see Fig. $1B_2$). The presence of a pustulose micro-ornamentation and well-developed transverse rods are characteristic of the Llandovery and Wenlock genus *Paraplectograptus* Bouček and Münch in Příbyl, 1948a with similarly developed transverse rods and connecting rods, as well as of the late Wenlock *Cometograptus* Kozłowska-Dawidziuk, 2001 (see Kozłowska-Dawidziuk 2001; Lenz and Kozłowska-Dawidziuk 2001) with the transverse rods, but no connecting rods.

The occurrence of pustules on *G. giganteus* at this period of time may be significant, since three other unrelated pustule-bearing genera, *Paraplectograptus*, *Pseudoplectograptus*, and *Sokolovograptus*, also first appear in the Telychian (Kozłowska-Dawidziuk and Lenz 2001).

The species has been reported from Telychian strata of Latvia (Loydell et al. 2003), but that specimen is considered too fragmentary for confident identification.

Stratigraphic and geographic range.—As for the genus.

Family *incertae sedis*, possibly a retiolitid
Genus *Mirorgraptus* nov.

Derivation of the name: From Latin *miror*, "wonder at", "be astonished at"; relating to the most unusual morphology, unlike any known retiolitid or other graptolite.

Type species: *Mirorgraptus arcticus* gen. et sp. nov.

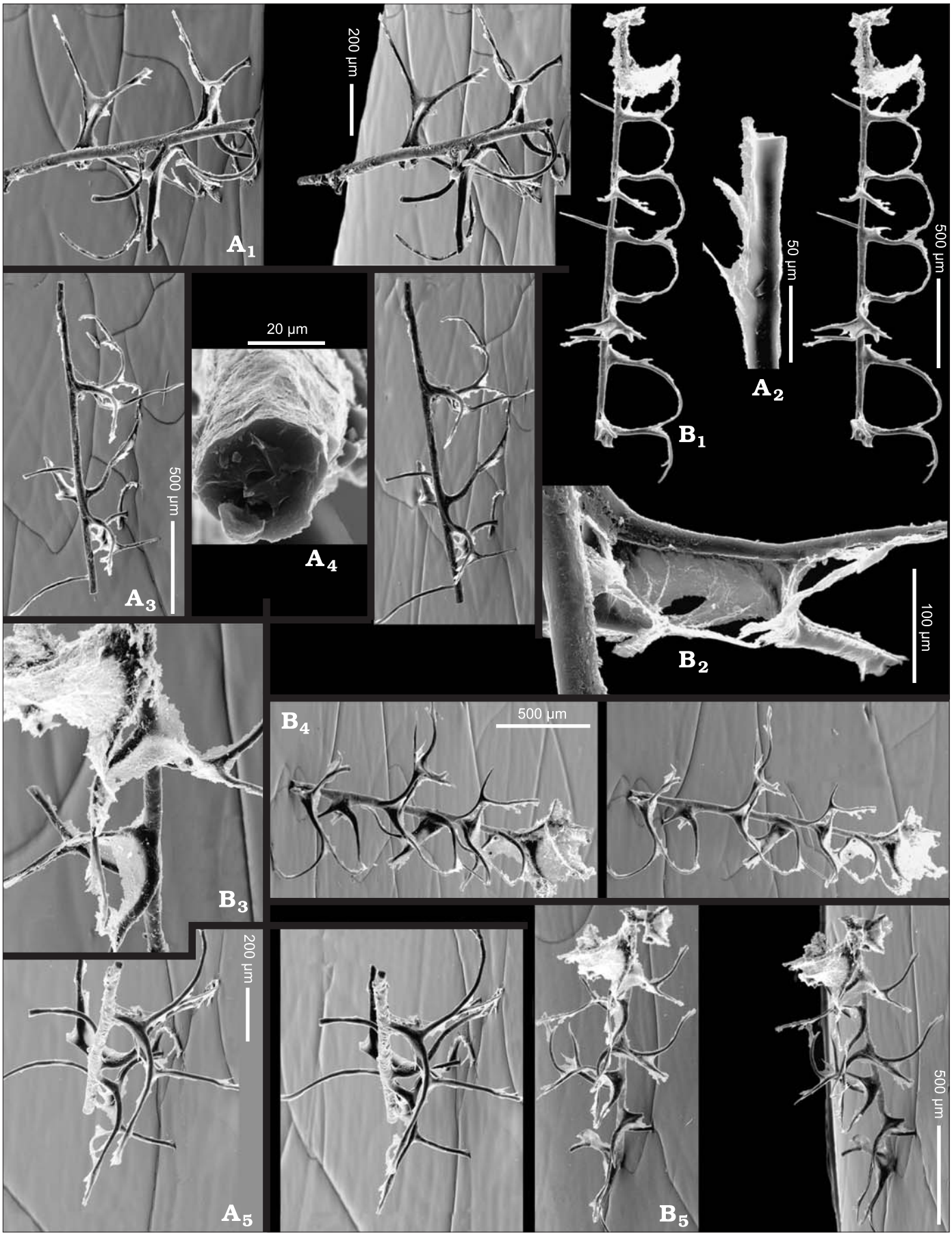
Species included: *Mirorgraptus arcticus* new species.

Diagnosis.—Straight nema with some lists similar to connecting rods in retiolitids arising from more or less the same row along one side of nema and, alternately, curving abruptly left and right, diverging about 180° to each other, between which are loops arising from near base of each connecting rod, oriented 90°. Distally, connecting rods bifurcate and sometimes trifurcate. Connecting rods and vertically oriented loops apparently fully covered by fusellar banding originally.

Discussion.—The lack of any vestige of the proximal region of the rhabdosome, especially of the ancora umbrella, makes it impossible to distinguish proximal and distal ends; furthermore, their absence makes it impossible to assign this taxon to any specific graptolite group with confidence. On the other hand, the presence of what is, almost certainly, a "free-standing" nema, and scattered fusellar tissue and fusellar list seams (Fig. $8A_2$, B_2), suggest that the taxon may be related to a retiolitid, albeit a most unusual one. The petalolithids are the only other graptolite group showing fusellar tissue and list seams in the ancora region, but apart from the narrow focus studies of Bates and Kirk (1997) and Melchin (1999), that group has received no broad-based SEM studies.

A somewhat similar type of list development is known in the rhabdosome of some Ordovician Archaeoretiolitidae; for example some specimens of *Orthoretiolites hami* Whittington 1954 (see Bates and Kirk 1991: particularly fig. 20a)

← Fig. 6. **A**, **B**. SEM micrographs of *Giganteograptus giganteus* (Bouček and Münch, 1944), generalized *Cyrtograptus lapworthi–insectus* Biozone, uppermost Telychian, Baillie Hamilton Island, Arctic Canada. **A**. Stereopairs of fragment of rhabdosome, GSC38906; A_1, ventro-lateral view showing nema attached proximally, possibly free in distal-most region; A_2, lateral view; A_3, disto-lateral view showing thecal spines. **B**. Fragment of rhabdosome with three thecae, showing thecal spines and well-preserved transverse rods, GSC38907; B_1, stereopair of lateral view; B_2, lists with well-developed pustulose micro-ornamentation, and seams inside; B_3, enlargement of fragment of rhabdosome with nema. **C**. Stereopairs of fragment of rhabdosome of *Oktavites spiralis* (Geinitz, 1852) with five thecae, GSC38908, upper Telychian *O. spiralis* Biozone; C_1, dorso-lateral view of entire fragment; C_2, enlargement showing thecal aperture and well-developed paired spines. **D**. Stereopair of fragment of *Cyrtograptus* sp., showing thecal cladium with two thecae, GSC38909, upper Telychian *Oktavites spiralis* Biozone.


A1
200 µm
A2
50 µm
500 µm
B1
A3
500 µm
20 µm
A4
B2
100 µm
B3
B4
500 µm
A5
200 µm
B5
500 µm

which beautifully illustrate a rhabdosome developed only along one side of the nema.

Stratigraphic and geographic range.—Cornwallis Island, Arctic Canada; *Spirograptus guerichi* Biozone, lower Telychian, upper Llandovery.

Mirorgraptus arcticus sp. nov.

Fig. 8.

Derivation of the name: Named after the Arctic from which it was recovered.

Holotype: GSC38908, Fig. 8B. Incomplete specimen.

Type locality: Snowblind Creek, Cornwallis Island, Arctic Canada.

Type horizon: Upper Llandovery.

Material.—Two incomplete specimens without the proximal ends of the rhabdosome.

Diagnosis.—As for the genus.

Description.—Holotype 2.6 mm long, width from tip to tip across left and right diverging connecting lists about 0.9 mm. Nema surface smooth, with central hole (Fig. $8A_4$), robust connecting rods arising from a more or less single region along one side of nema and alternately and consecutively bending sharply left and right, diverging 180° to each other. Connecting rods bifurcated or trifurcated distally, delicate and distinctly Y-shaped, one secondary list curving smoothly in direction of opposite, smooth side of nema; some lists retaining considerable fusellar tissue (Fig. $8B_1$, B_2). Diverging connecting rods spaced at about 0.65 mm. Rising from near base of each connecting rod are almost circular loops that are oriented about 90° to connecting rods. Fusellar tissue and shards of fusellar tissue scattered throughout Fig. 8, suggest that periderm filled spaces between Y-shaped secondary lists region of connecting rod, each loop, and possibly between loops and connecting rods and their secondary branches. Lists surface smooth (Fig. $8B_2$).

Discussion.—This is a most bizarre species, unlike any other graptolite although the preservation of some considerable amount of fusellar periderm and list seams may suggest a possible assignment to a new retiolitid group. While it is impossible to determine which end is the proximal region, it is clear that all construction activity occurred entirely along one relatively narrow region of the nema, leaving most of the nema unadorned. A complete rhabdosome might have shown it to be more or less hemicircular or triangular in cross-section. These combined features separate the species from any other known retiolitid or other graptolite.

Stratigraphic and geographic range.—As for genus.

Acknowledgments

AL acknowledges the continuing financial support from Natural Sciences and Engineering Research Council (Canada) Discovery Grants, and the logistical support of Polar Continental Shelf Project permitting work in the Canadian Arctic Islands. We are grateful to Ray Thorsteinsson (Geological Survey of Canada, Calgary), for the gift of the Arctic specimens of *Giganteograptus giganteus* described in this paper, and to Petr Štorch (Geological Institute, Prague, Czech Republic) for providing digital images of several Czech specimens of *G. giganteus*. The loan of the type specimen of *Pseudoplegmatograptus obesus* by the Lapworth Museum, University of Birmingham is acknowledged. We are grateful to Radvan Horný, former director of the National Museum, Prague, Czech Republic, for permission to examine retiolitids, particularly the several species of *Pseudoplegmatograptus* stored there. David Loydell (School of Earth and Environmental Sciences, University of Portsmouth, Portsmouth, UK) and Mark Williams (British Geological Survey, Nottingham, UK) are thanked for their thorough reviews and constructive comments.

References

Barrande, J. 1850. *Graptolites de Bohême*. 74 pp. Théophile Hasse Fils, Prague.

Bates, D.E.B. 1990. Retiolite nomenclature and relationships. *Journal of the Geological Society* 147: 717–723.

Bates, D.E.B and Kirk, N.H. 1986. Graptolites, a fossil case-history of evolution from sessile, colonial animals to automobile superindividuals. *Proceedings of the Royal Society of London B* 228: 207–224.

Bates, D.E.B and Kirk, N.H. 1991. The ultrastructure, mode of construction and functioning of Ordovician graptolites from the Viola Springs Limestone, Oklahoma. *Modern Geology* 15: 131–286

Bates, D.E.B. and Kirk, N.H. 1992. The ultrastructure, mode and functioning of a number of Llandovery ancorate and retiolitid graptolites. *Modern Geology* 17: 1–270.

Bates, D.E.B and Kirk, N.H. 1997. The ultrastructure, mode of construction and functioning of the genera *Stomatograptus* and *Retiolites*, with an appendix on the incremental construction of the rhabdosome of *Petalograptus*, and its comparison with that of the thecal framework in *Retiolites* and *Stomatograptus*. *Institute of Geography and Earth Sciences, University of Wales, Aberystwyth* 10: 1–168.

Bates, D.E.B., Kozłowska, A., and Lenz, A.C. 2005. Silurian retiolitid graptolites: morphology and evolution. *Acta Palaeontologica Polonica* 50: 705–720.

Bates, D.E.B., Kozłowska, A., Maletz, J., Kirk, N.H., and Lenz, A.C. 2006. The Silurian retiolitid graptolite *Plectograptus*: New observations and new species. *Acta Palaeontologica Polonica* 51: 525–540.

Bouček, B. and Münch, A. 1944. Die Retioliten des mitteleuropäischen Llandovery und unteren Wenlock. *Mitteilungen der tschechischen Akademie der Wissenschaften* 53 (41): 1–53.

Bouček, B. and Münch, A. 1952. Retioliti středoevropského svrchního wenloku a ludlowu. *Sborník Ústředního Ústavu geologického, oddil paleontologicky* 19: 1–151.

Eisenack, A. 1951. Retioliten aus dem Graptolithengestein. *Palaeontographica* 100: 129–163.

← Fig. 8. SEM micrographs of *Mirorgraptus arcticus* gen. et sp. nov., Snowblind Creek, Cornwallis Island, lower Telychian *Spirograptus guerichi* Biozone; the determination of the specimen orientation is arbitrarily chosen. **A**. Fragment of rhabdosome, GSC38918; A_1, stereopair of disto-lateral view; A_2 showing shards of fusellar bands; A_3, stereopair of lateral view; A_4, close-up showing hole in nema; A_5, stereopair of disto-ventral view, showing Y-shaped primary and secondary connecting lists all arising from a single row along nema, and alternating left and right. **B**. Holotype GSC38919; B_1, stereopair of ventral view; B_2, enlargement showing good preservation of fusellar bands; B_3, disto-lateral view, closeup of fusellar bands; B_4, stereopair of ventro-lateral view showing left and right alternation of connecting rods along nema; note considerable amount of fusellar tissue near top end; B_5, stereopair of disto-ventral view.

Elles, G.L. and Wood, E.M.R. 1908. A Monograph of British Graptolites, Pt. 7. *Palaeontographical Society Monograph*, 273–358.

Ge, M.-Y. 1990. Silurian graptolites from Chengkou, Sichuan. *Palaeontologica Sinica* 179, *New Series B* 26: 1–157.

Geinitz, H.B. 1852. *Die Versteinerungen der Grauwacken Formation* (*Die Graptolithen*). 58 pp. W. Engelmann, Leipzig.

Holm, G. 1890. Gotlands graptoliter. *Svenska Vetenskap-Akademiens handlingar* 16: 1–34.

Koren', T.N., Lenz, A.C., Loydell, D.K., Melchin, M.J. Štorch, P., and Teller, L. 1996. Generalized graptolite zonal sequence defining Silurian time intervals for global paleogeographic studies. *Lethaia* 29: 59–60.

Koren', T.N. and Rickards, R.B. 1996. Taxonomy and evolution of Llandovery biserial graptoloids from the southern Urals, western Kazakhstan. *Special Papers in Palaeontology* 54: 1–103.

Kozłowska-Dawidziuk, A. 1990.The genus *Gothograptus* (Graptolithina) from the Wenlock of Poland. *Acta Palaeontologica Polonica* 35: 191–209.

Kozłowska-Dawidziuk, A. 1995. Silurian retiolitids of the East European Platform. *Acta Palaeontologica Polonica* 40: 261–326.

Kozłowska-Dawidziuk, A. 2001. Phylogenetic relationships within the Retiolitidae (Graptolithina) and a new *Cometograptus* genus. *Lethaia* 34: 84–96.

Kozłowska-Dawidziuk, A. 2004. Evolution of retiolitid graptolites—a synopsis. *Acta Palaeontologica Polonica* 49: 505–518.

Kozłowska-Dawidziuk, A. and Lenz, A.C. 2001. Evolutionary developments in the Silurian Retiolitidae (graptolites). *Journal of Czech Geological Society* 46: 227–238.

Lapworth, C. 1873. Notes on the British graptolites and their allies. 1. On an improved classification of the *Rhabdophora*. *Geological Magazine* 10: 500–504, 555–560.

Lapworth, C. 1877. On the graptolites of County Down. *Proceedings of the Belfast Naturalists Field Club* 1: 107–147.

Lenz, A.C. 1982. Llandoverian graptolites of the northern Canadian Cordillera: *Petalograptus*, *Cephalograptus*, *Rhaphidograptus*, *Dimorphograptus*, Retiolitidae, and Monograptidae. *Royal Ontario Museum, Life Sciences Contributions* 130: 1–154.

Lenz, A.C. 1988. Upper Llandovery and Wenlock graptolites from Prairie Creek, southern Mackenzie Mountains, Northwest Territories. *Canadian Journal of Earth Sciences* 25: 1955–1971.

Lenz, A.C. 1993. Late Wenlock and Ludlow (Silurian) Plectograptinae (retiolitid graptolites), Cape Phillips Formation, Arctic Canada. *Bulletins of American Paleontology* 104: 1–52.

Lenz, A.C. 1994. A sclerotized retiolitid, and its bearing on the origin and evolution of Silurian retiolitid graptolites. *Journal of Paleontology* 68: 1344–1349.

Lenz, A.C., Cuerda, A., and Peralta, S. 2003. Graptolites from the Upper Llandovery of the Talacasto area, Central Precordillera, San Juan, Argentina. *Journal of Paleontology* 77: 1198–1202.

Lenz, A.C. and Kozlowska, A. 2006. Graptolites from the *lundgreni* Biozone (lower Homerian, Silurian), Arctic Islands, Canada: new species and supplementary material. *Journal of Paleontology* 80: 616–637.

Lenz, A.C. and Kozłowska-Dawidziuk, A. 2001. Upper Wenlock (Silurian) graptolites of Arctic Canada: pre-extinction *lundgreni* Biozone fauna. *Palaeontographica Canadiana* 20: 1–61.

Lenz, A.C. and Kozłowska-Dawidziuk, A. 2002. Upper Homerian (Upper Wenlock, Silurian) graptolites from Arctic Canada. *Journal of Paleontology* 76: 321–346.

Lenz, A.C. and Kozłowska-Dawidziuk, A. 2004. *Ludlow and Pridoli (Upper Silurian) Graptolites from the Arctic Islands, Canada*. 141 pp. National Research Council Research Press, Ottawa, Ontario.

Lenz, A.C. and Melchin, M.J. 1987. Silurian retiolitids from the Cape Phillips Formation, Arctic Islands, Canada. *Bulletin of Geological Society of Denmark* 35: 161–170.

Lenz, A.C. and Melchin, M.J. 1997. Phylogenetic analysis of the Silurian Retiolitidae. *Lethaia* 29: 301–309.

Loydell, D.K. 1991. The biostratigraphy and formational relationships of the upper Aeronian and lower Telychian (Llandovery, Silurian) formations of western mid-Wales. *Geological Journal* 26: 209–244.

Loydell, D.K. 1993. Upper Aeronian and Lower Telychian (Llandovery) graptolites from western mid-Wales, Part 2. *Monograph of the Palaeontographical Society London* 147: 56–180.

Loydell, D.K., Männik, P., and Nestor, V. 2003. Integrated biostratigraphy of the lower Silurian of the Aizpute-41 core, Latvia. *Geological Magazine* 140: 205–229.

Loydell, D.K., Štorch, P., and Melchin, M.J. 1993. Taxonomy, evolution and biostratigraphical importance of the Llandovery graptolite *Spirograptus*. *Palaeontology* 36: 909–926.

Melchin, M.J. 1988. Llandovery graptolite biostratigraphy and paleobiogeography, Cape Phillips Formation, Canadian Arctic Islands. *Canadian Journal of Earth Sciences* 26: 1726–1746.

Melchin, M.J. 1998. Morphology and phylogeny of some early Silurian "diplograptid" genera from Cornwallis Island, Arctic Canada. *Palaeontology* 41: 263–315.

Melchin, M.J. 1999. Origin of the Retiolitidae: insights from a new graptolite from the early Silurian of Arctic Canada. *Lethaia* 32: 261–269.

Obut, A.M. and Zaslavskaya, N.M. [Zaslavskaâ, N.M.] 1976. New data on the early stages of Retiolitidae develompent [in Russian]. *In*: D. Kalio and T.N. Koren' (eds.), *Graptolity i stratigrafiâ*, 154–162. Izdatelstvo Nauka, Moskva.

Obut, A.M. and Zaslavskaya, N.M. [Zaslavskaâ, N.M.] 1983. The families of retiolitids and their phylogenetic relationships [in Russian]. *Trudy Instytut Geologii i Geofiziki, SSSR, Sibirskoe Otdelenie* 583: 103–113.

Přibyl, A. 1948a. *Bibliographic Index of Bohemian Silurian Graptolites*. 96 pp. Knihovna Státního Geologického Ústavu Československé Republiky, sv. 22, Praha.

Příbyl, A. 1948b. Some new subgenera of graptolites from the families Dimorphograptidae and Diplograptidae. *Věstnik Statního geologického Ústavu Československé Republiky* 23: 37–48.

Štorch, P. 1992. Some new and little known graptolites from the Lower Silurian of Bohemia (Prague Basin, Barrandian area). *Časopis pro mineralogii a geologii* 37 (3): 193–202.

Štorch, P. 1994. Llandovery–Wenlock boundary beds in the graptolite-rich sequence of the Barrandian area (Bohemia). *Journal of the Czech Geological Survey* 39: 163–182.

Štorch, P. 1998. New data on Telychian (Upper Llandovery, Silurian) graptolites from Spain. *Journal of the Czech Geological Society* 43: 113–142.

Suess, E. 1851. Über böhmische Graptolithen. *Haidingers Berlin* 4: 89–134.

Tullberg, S.A. 1883. Skånes graptoliter. II. *Sveriges geologiska Undersökning Afhandlingar C* 55: 1–43.

Thorsteinsson, R. 1958. Cornwallis and Little Cornwallis Islands, District of Franklin, Northwest Territories. *Geological Survey of Canada Memoir* 294: 1–134.

Wang, X.-F. 1965. On the discovery of late Early and Middle Silurian graptolites from N. Gueizhou (Kueichou) and its significance. *Acta Palaeontologica Sinica* 13: 118–127.

Wang, X.-F. 1978. A restudy of the graptolites and the age of the Wentoushan Formation from Liantan, Kwangtung. *Acta Geologica Sinica* 4: 303–317.

Whittington, H.B. 1954. A new Ordovician graptolite from Oklahoma. *Journal of Paleontology* 28: 613–621.