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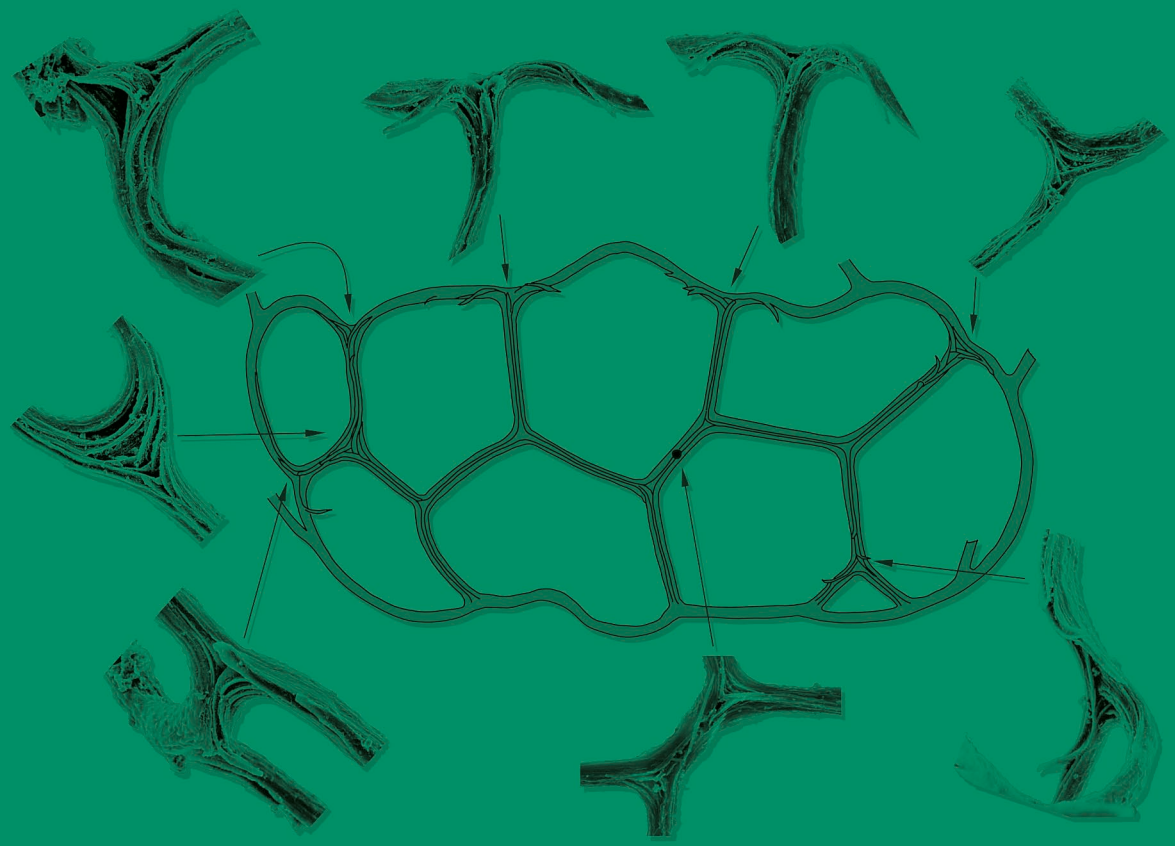
Denis E. B. BATES, Nancy H. KIRK† & Anna KOZŁOWSKA



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Morphology and reconstruction of the retiolitines: Silurian graptolites of the *Paraplectograptus* lineage (Graptolithina)

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ABSTRACT
The long ranging Silurian retiolitines belonging to the *Paraplectograptus* lineage (*Spirograptus turriculatus* to *Cyrtograptus/lundgreni* Biozone), represented by the genera *Paraplectograptus* Bouček & Münch, 1952 and *Pseudoplectograptus* Obut & Zaslavskaya, 1983 are described in detail based on well preserved, three-dimensional material from the Canadian Arctic and Poland. For the first time, reconstructions of their structure are attempted, and comparisons are made with the related genera, *Stomatograptus* Tullberg, 1883 and *Retiolites* Barrande, 1850. Ultrastructural details vary somewhat between the genera: the bandaging on the *Paraplectograptus* lineage and *Pseudoplectograptus* has a characteristic pustulose ornament, while that of *Retiolites* and *Stomatograptus* shows a surface of longitudinal striations. Prosicular preservation is generally incomplete, represented merely by the prosicular apex and prosicular rim. The thecal part of the *Paraplectograptus* and *Pseudoplectograptus* tubaria (rhabdosomes) possesses transverse rods, connecting rods, lateral apertural rods and lips. The ancora sleeve lists are variably developed but lack a dorsal/zigzag list, which is present in *Stomatograptus* and *Retiolites*. The *Paraplectograptus* lineage appears to mark an intermediate stage in the evolution of the retiolitines, from the early Silurian forms, with strong thecal and ancora sleeve frameworks (e.g. *Retiolites*, *Stomatograptus*), to late Silurian descendants with strong ancora sleeves, minimal thecal frameworks and pustular ornament, with no transverse rods.

KEY WORDS
Graptolithina,
Retiolitinae,
Paraplectograptus,
Silurian,
tubarium (rhabdosome)
morphology,
reconstruction.

RÉSUMÉ
Morphologie et reconstruction des retiolitines : graptolites siluriennes de la lignée Paraplectograptus *(Graptolithina).*
Les rétiolitines siluriennes appartenant à la lignée *Paraplectograptus* de longue durée (biozones *Spirograptus turriculatus* à *Cyrtograptus lundgreni*), représentées par les genres *Paraplectograptus* Bouček & Münch, 1952 et *Pseudoplectograptus* Obut et Zaslavskaya, 1983, sont décrites en détail sur la base du matériel tridimensionnel bien conservé de l'Arctique canadien et de la Pologne. Pour la première fois, des reconstructions de leur structure ont été tentées et des comparaisons ont été réalisées avec les genres apparentés, *Stomatograptus* Tullberg, 1883 et *Retiolites* Barrande, 1850. Les détails ultrastructuraux varient quelque peu entre les genres, la surface des bandages est noduleuse chez *Paraplectograptus* et *Pseudoplectograptus*, tandis que celle des *Retiolites* et *Stomatograptus* se caractérise par des stries longitudinales. La partie thécale des tubaria du *Paraplectograptus* et du *Pseudoplectograptus* possède des tiges transversales, des tiges de connexion, et des listes et lèvres aperturales latérales. Les manches de l'ancora sont développées de manière variable, mais il leur manque une structure dorsale en forme de zigzag qui est présente chez *Stomatograptus* et *Retiolites*. Le tubarium de la lignée phylogénétique *Paraplectograptus* semble marquer une étape intermédiaire dans l'évolution des rétiolitines, depuis les premières formes du Silurien avec des parties thécales fortement developpées et un nacra sleeve (par exemple, *Retiolites*, *Stomatograptus*), jusqu'aux descendants du Silurien tardif avec des manches de l'ancora solide, des parties thécales réduites et une ornementation pustulaire, sans tiges transversales.

MOTS CLÉS
Graptolithina,
Retiolitinae,
lignée *Paraplectograptus*,
Silurien,
tubarium (rhabdosome),
morphologie,
reconstruction.

INTRODUCTION

One of the most fascinating planktic groups of the graptolites is the retiolitines. They differ from the other graptolites in having the tubarium (rhabdosome) comprising fuselli, which are mostly thin and only rarely preserved, and an extrathecal ancora sleeve forming a layer outside the lateral thecal walls. The bandages are developed as lists, forming a mesh-like framework to make a tubarium unlike that of any other retiolitids (*sensu* Melchin *et al.* 2011). Detailed scanning electron microscope (SEM) studies on isolated three-dimensionally preserved material (e.g. Bates & Kirk 1978, 1984, 1987, 1992, 1997; Bates 1987, 1990; Lenz & Melchin 1987; Lenz 1993, 1994a; Kozłowska-Dawidziuk 1997; Lenz & Thorsteinsson 1997), have helped in understanding this type of rhabdosome.

The retiolitines evolved during the Silurian, from the Llandovery, up to the early Ludfordian (late Ludlow). They survived the dramatic environmental crisis, the Homerian *lundgreni* Event (Jaeger 1991; Lenz & Kozłowska-Dawidziuk 2001), after which they successfully recovered (Kozłowska-Dawidziuk *et al.* 2001; Lenz & Kozłowska-Dawidziuk 2002; Kozłowska 2016), and then slowly went into a decline, finally becoming extinct in the *leintwardinensis* Event (Koren' 1987; Urbanek 1993; Kozłowska-Dawidziuk 1995, 2004; Lenz & Kozłowska-Dawidziuk 2004, Kozłowska *et al.* 2019).

One of the stratigraphically earliest retiolitines is *Paraplectograptus eiseli* (Manck, 1917), which is known from around the world, e.g. Avalonia (Elles & Wood 1908), Laurentia (Lenz & Melchin 1987; Lenz 1993, 1994b; Lenz *et al.* 2012), the Barrandian (Bouček & Münch 1952; Štorch & Manda 2019) and Baltica (Eisenack 1951; Kozłowska-Dawidziuk 1995; Maletz 2010: fig. 1). It is found in strata from the *Spirograptus turriculatus* Biozone up to the *Cyrtograptus lundgreni* Biozone (Kozłowska-Dawidziuk 2004).

This paper is a continuation of the study of retiolitine tubarium (rhabdosome) construction and function initiated by Nancy Kirk and Denis Bates (Bates & Kirk 1978, 1984, 1987, 1992) based on detailed study of their structures under the SEM, which was innovative at that time for the study of graptolites. Based on the SEM pictures, Nancy Kirk made large models, up to 70 cm, of retiolitid tubaria (Bates & Kirk 1997). Some of them are presented in this paper.

This current study is based mostly on well preserved retiolitines from Arctic Canada donated by Alf Lenz, and from Poland. In this paper, we focus attention on the overall morphological characteristics, and the reconstruction of the tubaria of the genera *Paraplectograptus* Pribyl, 1948 and *Pseudoplectograptus* Obut & Zaslavskaya, 1983, comprising the *Paraplectograptus* lineage. Comparison of their construction is made with that of *Retiolites* Barrande, 1850 and *Stomatograptus* Tullberg, 1883, which belong to the oldest group of retiolitines.

The aim of this paper is to present the detailed morphology of the *Paraplectograptus* rhabdosome and development of the colony based on SEM pictures.

MATERIAL AND METHODS

The majority of the material derives from Arctic Canada; two specimens come from Poland. The specimens studied for the paper have been isolated from the rock following slow dissolution of the host carbonate in 5-10% HCl. A fine hairbrush was used to pick and transfer specimens to a box with glycerin or onto SEM stubs. The material is stored in glycerin in plastic containers, as well as on the SEM stubs, in the Institute of Paleobiology, Polish Academy of Sciences, number collection ZPAL G.

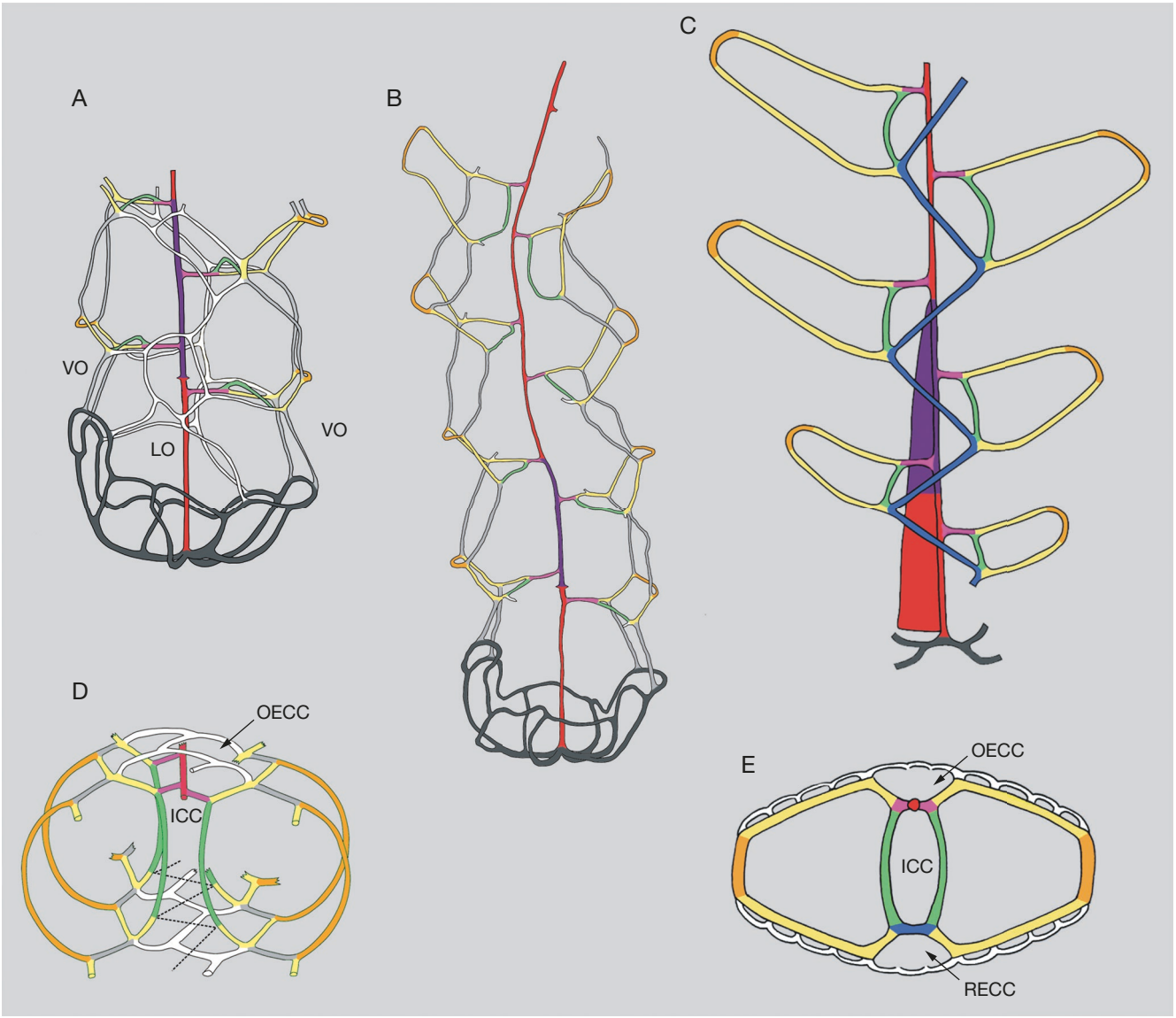

Fig. 1. — Diagrams showing comparison of the thecal framework, ancora sleeve and common canals in *Pseudoplectograptus* Obut & Zaslavskaya, 1983, *Paraplectograptus* Pribyl, 1948 and *Retiolites* Barrande, 1850: **A**, *Pseudoplectograptus* viewed from the reverse sides; **B**, **D**, *Paraplectograptus*: **B**, viewed from the reverse sides; **D**, cross-section of *Paraplectograptus* based on Lenz 1993, pl. 14, fig. 3; **dotted lines** suggest the presence of zigzag homologues to the zigzag of *Retiolites*; **C**, **E**, *Retiolites*: **C**, viewed from the reverse sides, ancora umbrella and ancora sleeve lists are omitted; **E**, cross section showing thecal framework and pleural lists of ancora sleeve (adapted from Bates & Kirk 1997: fig. 127b). Colours: **red**, nema, metasicula, virgella; **purple**, virga, prosicula; **pink**, connecting rods; **dark gray**, ancora umbrella; **green**, transverse rod; **yellow**, lateral apertural list; **orange**, thecal lip; **light gray**, pleural list; **white**, other ancora sleeve lists; **blue**, zigzag (dorsal). Abbreviations: **ICC**, internal common canal; **LO**, proximal lateral orifice; **OECC**, obverse external common canal; **RECC**, reverse external common canal; **VO**, proximal ventral orifice.

The 3D retiolitine models were made by Nancy Kirk based on detailed observation and measurement of many specimens under the SEM. The material used for making models is sheathed wire and paper tape painted in different colours corresponding to certain morphological features.

The complete retiolitine morphological terminology is clarified and explained in Bates *et al.* 2005 and Lenz *et al.* 2018. The classification of the graptolites follows Melchin *et al.* 2011.

Abbreviations

Institutions

NMW National Museum of Wales, Cardiff;

ZPAL Institute of Paleobiology Polish Academy of Sciences, Warszawa.

Other

HCl hydrochloric acid;

SEM scanning electron microscope.

HISTORY OF RESEARCH ON THE *PARAPLECTOGRAPTUS* LINEAGE

Research on *Paraplectograptus* started more than 100 years ago, when Manck (1917) erected the species *Retiolites eiseli* Manck, 1917. This new form was characterised by a slender

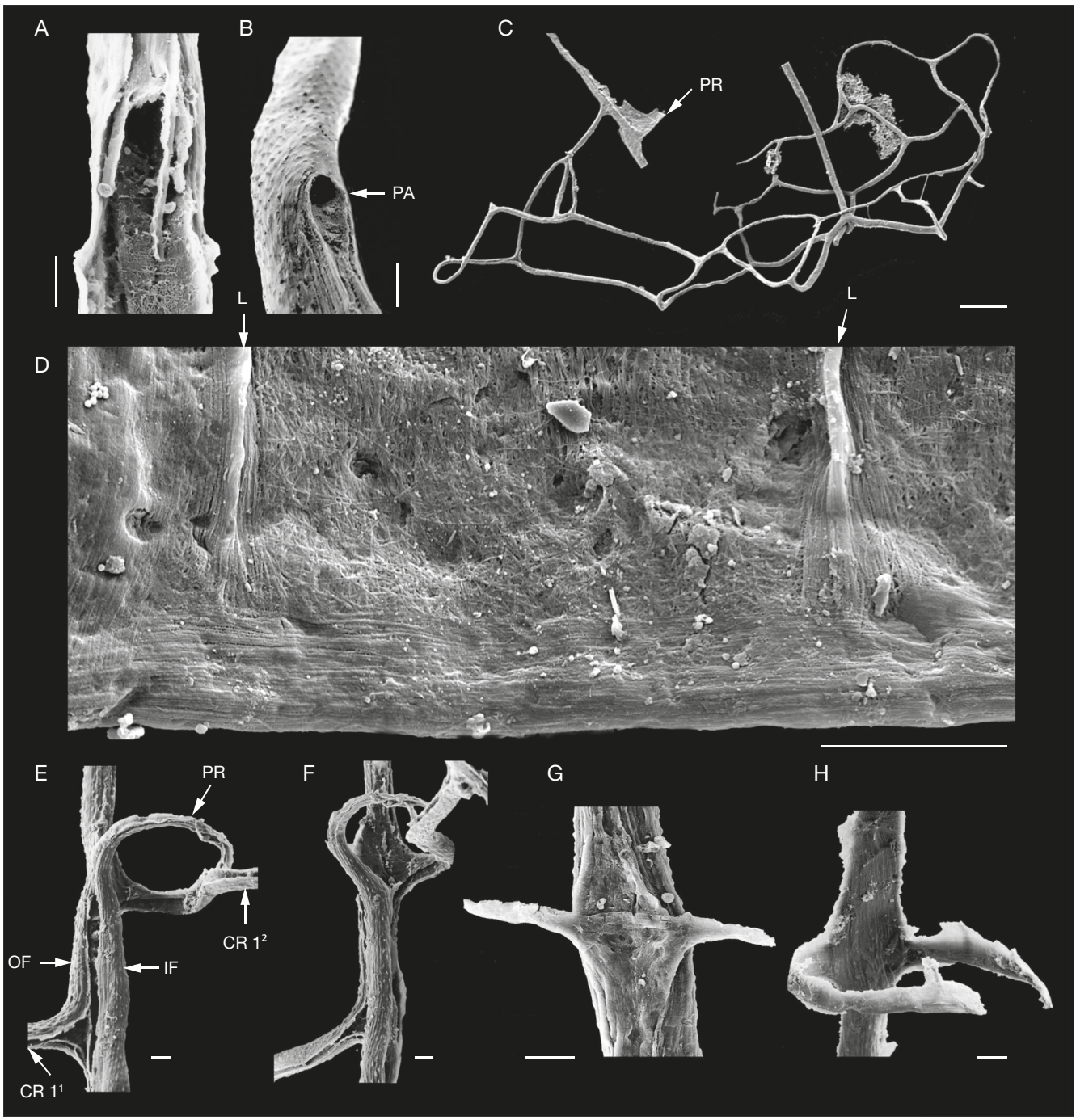

FIG. 2. — Prosicula and metasicula remnants of *Paraplectograptus* sp.: **A**, apex of prosicula with remains of three longitudinal rods beneath the later bandaging of the nema; remains of the spiral line and fusellar fabrics are preserved on the innermost enwrapping bandage of the virga, Cornwallis Island, Arctic Canada, uppermost Llandovery, ZPAL G.47/1, stub 1267M; **B**, apex of prosicula showing a succession of bandages secreted over the outer face of the prosicular wall to form the virga, and enwrapping beyond the apex to form the cylindrical nema, Cape Phillips Formation, Arctic Canada, stub 324D, ZPAL G.47/2; **C**, **D**, proximal end with ancora umbrella and lists of th1¹, ZPAL G.47/3, stub 1597B, locality unknown: **C**, whole specimen; **D**, close-up of prosicular rim, with two longitudinal rods (**L**) superimposed on a fabric of randomly oriented fibrils, and parallel fibrils marking the rim, the longitudinal rods lose their relief, and their fibrils splay out, as they approach the rim; **E**, **F**, two views of a complete prosicular rim, Cape Phillips Formation, Arctic Canada, uppermost Llandovery, ZPAL G.47/4, stub 1258A: **E**, the obverse half of the complete prosicular rim (**PR**) is lined and supported by bandages extending from the inner face (**IF**) of the virgella, the connecting rod for th1¹ (**CR1¹**) is seen to arise from the outer face (**OF**) of the virgella just outside the slot for the obverse metasicular wall; **F**, view from the inside of metasicula; bandaging on the inner side of the virgella is pustular; **G**, a very vestigial prosicular rim extends as a pair of prongs, Zawada 1 core, 1597.7 m, Poland, *lundgreni* Biozone, ZPAL G.47/5, stub 1220; **H**, bandages with pustules extend from the inside of the virgella onto the inside of the virga, where they become non-pustular, the remains of longitudinal rods extend adapically from the prosicular rim, Zawada 1 core, 1597.7 m, Poland, *lundgreni* Biozone ZPAL G.47/1, stub 1267. Abbreviations: **CR**, connecting rod; **IF**, inner face; **L**, longitudinal rod; **OF**, outer face; **PA**, prosicular apex; **PR**, prosicular rim. Scale bars: 10 µm.

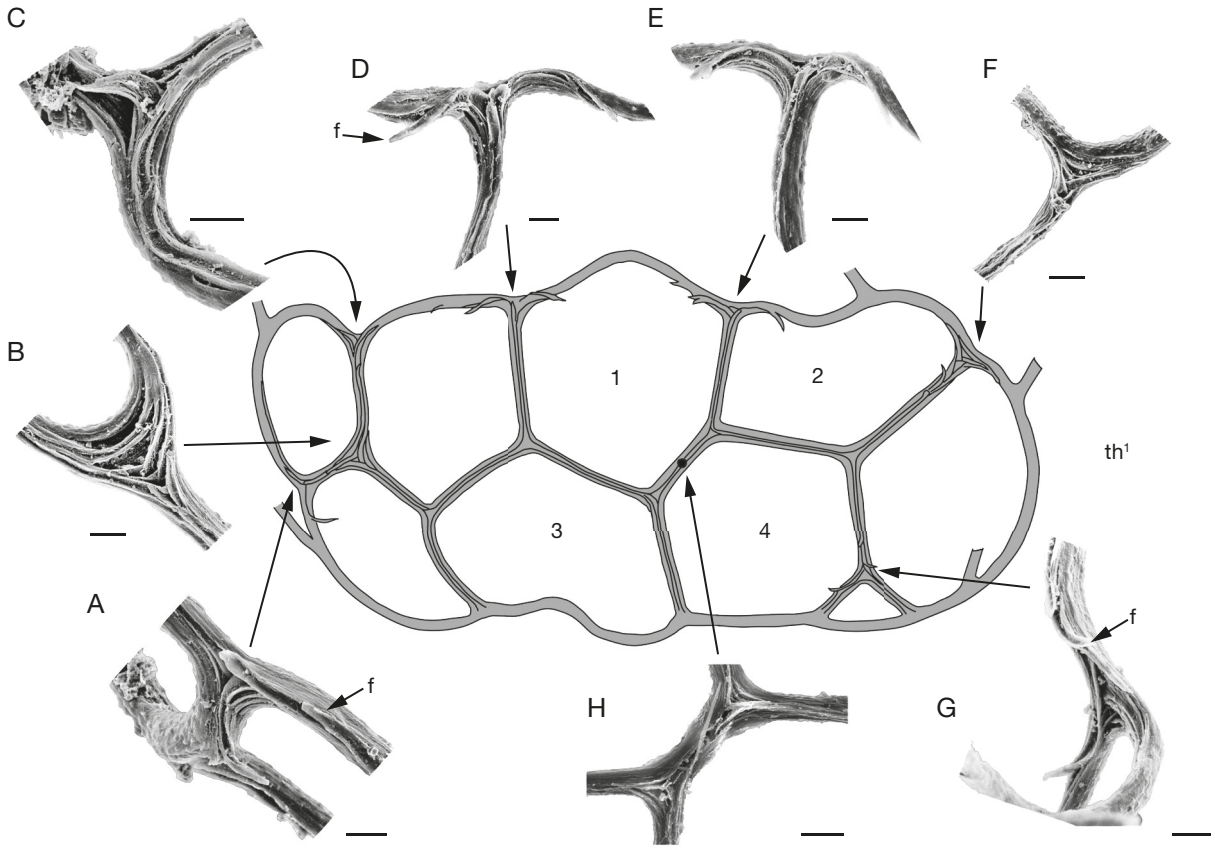

FIG. 3. — The ancora umbrella of *Paraplectograptus eiseli* (Manck, 1917), diagram and SEM pictures of the details, viewed from the outside, Cape Phillips Formation, Arctic Canada, ZPAL G.47/6, stub 313: **A**-**G**, enlargements showing the remnants of fuselli at branchings of the umbrella; **H**, ancora umbrella hub. **Numbers 1**-**4**, four central meshes of the ancora umbrella. Abbreviation: **f**, remains of fuselli. Scale bars: 10 µm.

tubarium with almost no reticulum, and a nema connected by the connecting rods to the obverse thecal wall (Fig. 1B). The genus *Paraplectograptus* was established by Bouček & Münch (1952) for *Retiolites eiseli*. *Paraplectograptus eiseli* is a long ranging species known from the *S. turriculatus*/*Streptograptus crispus* Biozone of the Llandovery to the *C. lundgreni* Biozone of the Wenlock. Its occurrence in the *S. turriculatus* Biozone in Arctic Canada was recorded by Thorsteinsson (1958); other records from Poland, Arctic Canada and the Czech Republic come from the *Testograptus testis* and *C. lundgreni* biozones (e.g. Lenz & Melchin 1987; Kozłowska-Dawidziuk 1995; Lenz & Kozłowska-Dawidziuk 2001; Štorch & Manda 2019).

Bouček & Münch (1952) described the new species *Paraplectograptus hemmanni*, and included *Retiolites tenuis* Eisenack, 1951 in the genus. Both species come from the *T. testis* Biozone. Later these species were questionably placed in *Paraplectograptus* by Lenz & Melchin (1987) and Kozłowska-Dawidziuk (1995). *Plectograptus*? *lejskoviensis*, described by Bouček (1931), and *Plectograptus praemacilentus* described by Bouček & Münch (1952), both from the *T. testis* Biozone, were included by Lenz & Melchin (1987) in *Paraplectograptus*, based on the development of the main characters, e.g. the connecting rods linking the transverse rods of the thecal wall with the nema.

The material of *Paraplectograptus eiseli* described by Manck (1917) was flattened on the rock surface. The breakthrough in research came thanks to observations under the SEM of three-dimensional specimens of *Paraplectograptus*, started by Lenz & Melchin (1987). Further research gradually revealed the diversity of species within *Paraplectograptus*. Lenz *et al.* (2012) described *P. senarius* Lenz, Senior, Kozłowska & Melchin, 2012 and *P. reticulum* Lenz, Senior, Kozłowska & Melchin, 2012, occurring in Arctic Canada, from the *Monoclimacis flumendosae* to *Cyrtograptus perneri* biozones. They differ in the development of the ancora sleeve lists, which in *P. senarius* have hexagonal meshes with a thin reticulum, which are present mostly at the proximal end, while in *P. reticulum* the reticulum is mainly developed in the middle part of the ancora sleeve.

Obut & Zaslavskaya (1983) erected the new genus *Pseudoplectograptus* for *Plectograptus praemacilentus* (Bouček & Münch, 1952), based on material described by Bouček & Münch (1952) from the Barrandian, *T. testis* Biozone. According to the morphological similarity of *Paraplectograptus* and *Pseudoplectograptus* (Fig. 1A, B) Kozłowska-Dawidziuk (2001) distinguished the *Paraplectograptus* lineage comprising these two genera (Lenz & Kozłowska 2006).

Later studies of new material from the Arctic Canada and Poland showed the large diversity of these genera with the following species described: *Paraplectograptus eiseli* (Manck, 1917); *Paraplectograptus senarius* Lenz, Senior, Kozłowska & Melchin, 2012; *Paraplectograptus reticulum* Lenz, Senior,

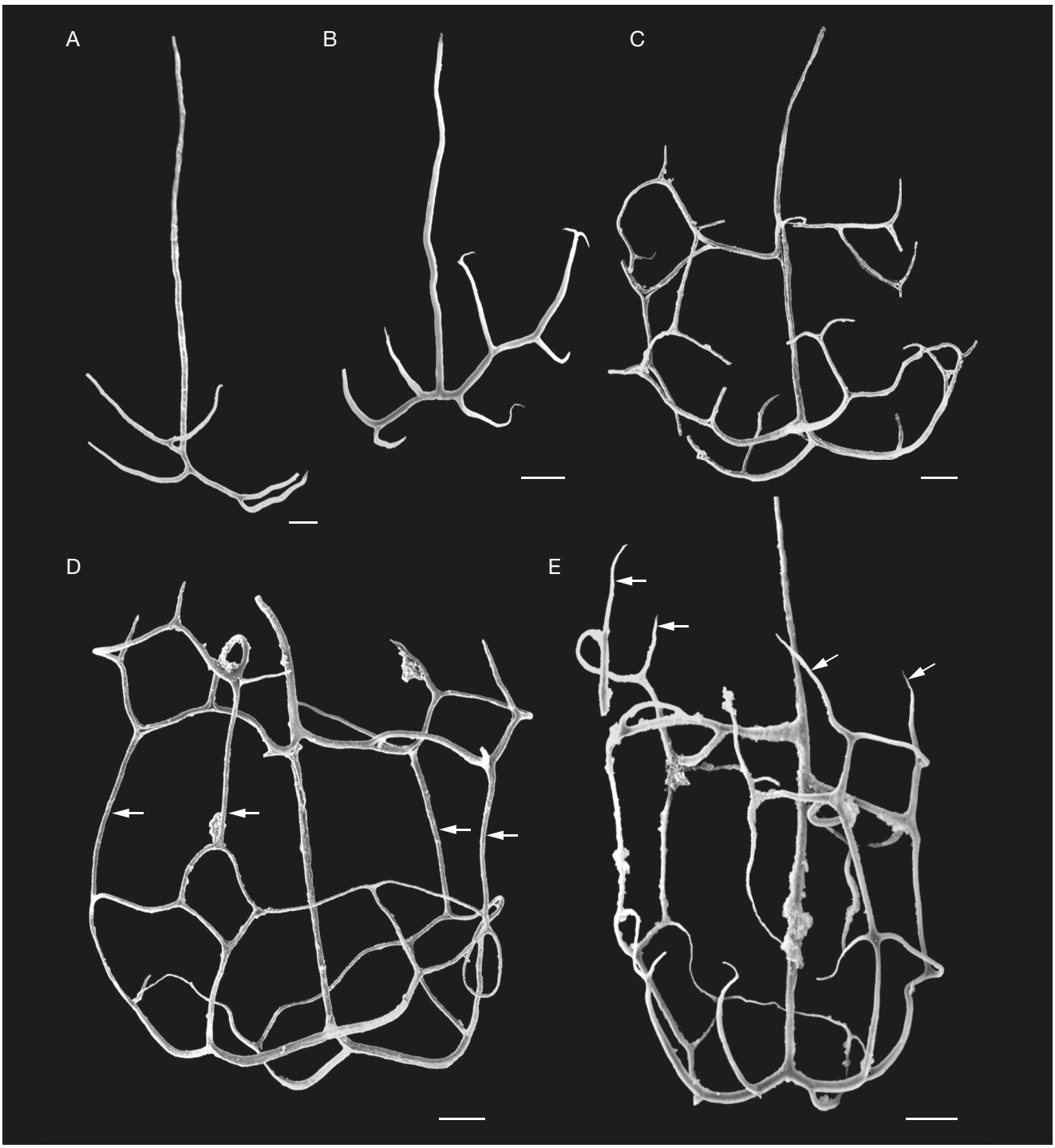

Fig. 4. — Growth stages of *Paraplectograptus eiseli* (Manck, 1917): **A**, early growth stage, with five ancora umbrella lists, stub 3, 201901, ZPAL G.47/7; **B**, growth stage with seven ancora lists, with branching indicating the growth of the ancora umbrella rim (compare with ancora umbrella diagram, Fig. 3), stub 1F, ZPAL G.47/9; **C**, growth stage in obverse view, with incomplete ancora umbrella, and lists joining ancora to th1^{1} complete; those to th1^{2} partial, Cape Phillips Formation, Arctic Canada, uppermost Llandovery, stub 1258A ZPAL G.47/10; **D**, reverse view, with complete ancora umbrella, and four lists (**arrowed**) leading towards the first two thecae, stub 1257A, ZPAL G.47/11; **E**, growth stage with two first thecae, reverse view, lists of the lateral panels of the ancora sleeve (**arrowed**) tapering proximally, are developed in addition to the four initial lists as seen in **D**, in addition, pleural sleeve lists (**arrowed**), tapering distally, are now being developed, and project forwards from the thecal lips of the first two thecae, stub 1B, 201901, ZPAL G.47/12. Scale bars: 100 µm.

Kozłowska & Melchin, 2012; *Pseudoplectograptus praemacilentus* (Bouček & Münch, 1952); *Pseudoplectograptus sagenus* (Lenz, 1993); *Pseudoplectograptus simplex* Kozłowska-Dawidziuk, 1995; *Pseudoplectograptus areticulatus* Kozłowska-Dawidziuk, 1995.

The oldest form, questionably assigned to *Paraplectograptus*, is described from the lower Telychian *Spirograptus guerichi* Biozone and possibly the Aeronian *Demirastrites convolutus* Biozone of the Llandovery (Melchin *et al.* 2017). It shows

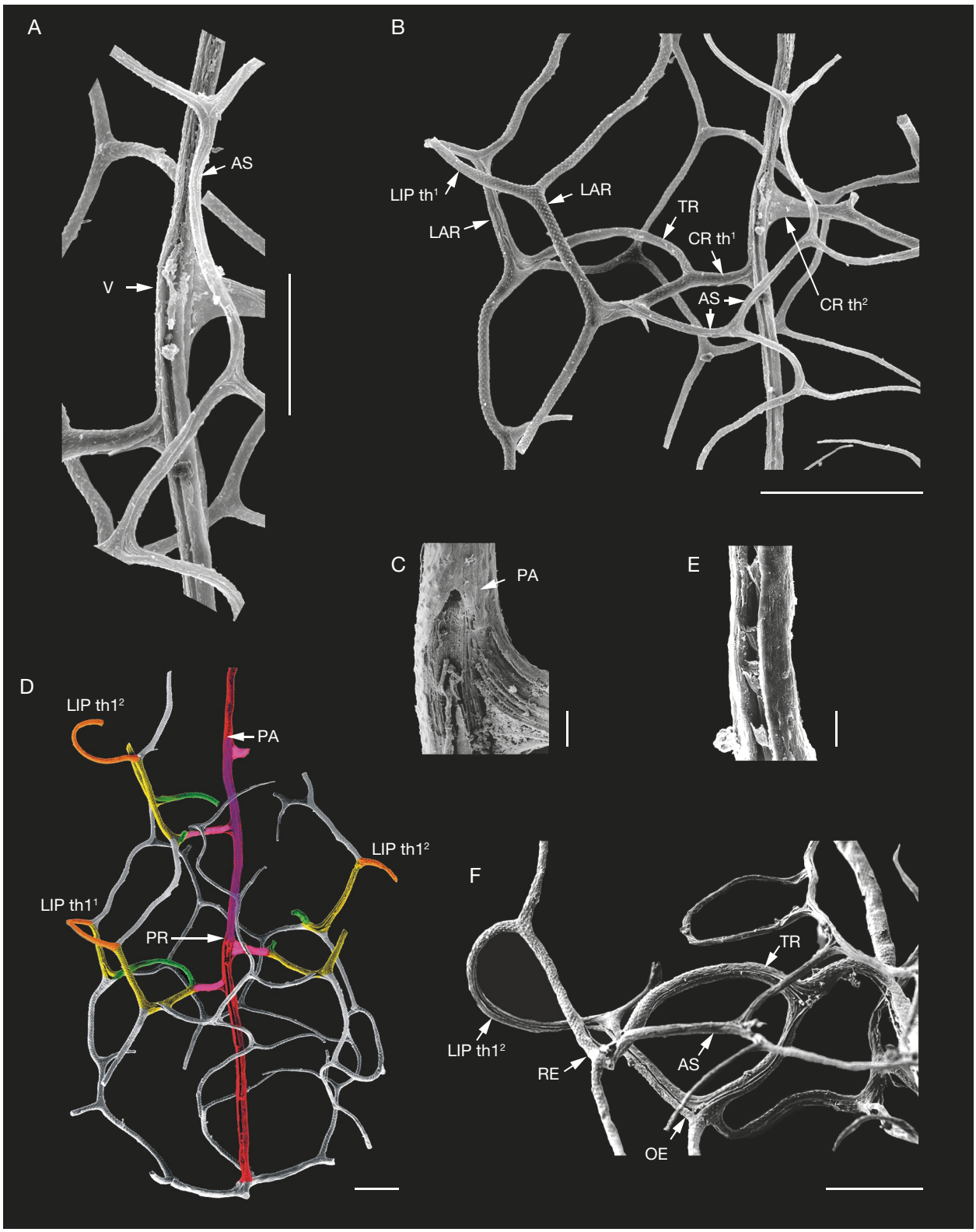

FIG. 5. — Details of *Paraplectograptus* sp. tubarium: **A**-**D**, tubarium with destroyed ancora umbrella, obverse view, Arctic Canada, Cape Phillips Formation, stub 319, ZPAL G.47/8: **A**, enlargement showing the prosicular rim and seams of the prosicular and metasicular walls; **B**, the relationship of the thecal framework of th1^1, the connecting rod (**CR1^1**), transverse rod (**TR**) and lateral apertural rods (**LAR**) with the virgella, seen from the obverse side, and the connecting rod (**CR1^2**) marking the attachment of th1^2 to the reverse side of the sicula opposite the prosicular rim; **C**, enlargement of prosicular apex; **D**, whole specimen with coloured tubarium structures, **arrows** mark length of prosicula (**green**, transverse rods; **orange**, lip; **pink**, connecting rod; **purple**, virga; **red**, virgella and nema; **yellow**, other thecal part); **E**, four metasicular increments are seen inserting into a slot between bandaging over the inner and outer faces of the virgella, Zawada 1 core, 1597.7 m, Poland, *lundgreni* Biozone, ZPAL G.47/16, stub 324; **F**, fragment of tubarium, th1^1 seen from the reverse side and from slightly proximal, ZPAL G.47/6, stub 313. Abbreviations: **AS**, ancora sleeve lists; **CR**, connecting rod; **LAR**, lateral apertural rod; **LIP**, lip; **OE**, obverse edge; **PA**, prosicular apex; **PR**, prosicular rim; **RE**, reverse edge; **TR**, transverse rod; **V**, virga. Scale bars: A, D, F, 100 µm; B, 200 µm; C, E, 10 µm.

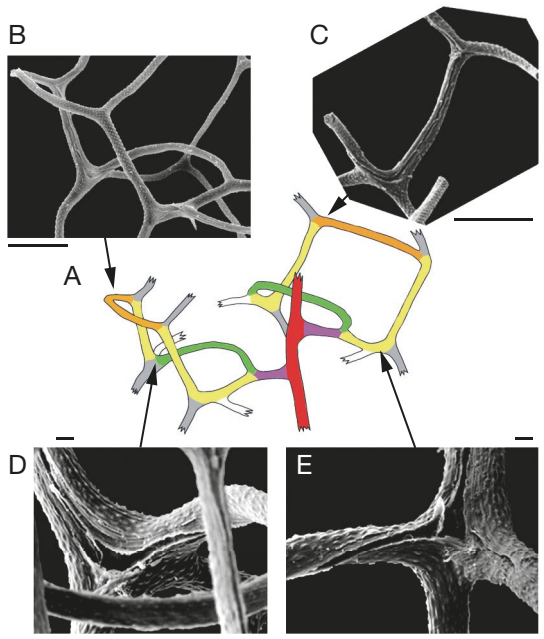

Fig. 6. — Details of thecal framework lists of two thecae of *Paraplectograptus eiseli* (Manck, 1917), with the course of the insertion seams associated with them, viewed obliquely from the obverse side: **A**, diagrammatic picture; **B**, **C**, Cape Phillips Formation, Arctic Canada, stub 319, ZPAL G.47/8; **D**, **E**, Cornwallis 156 m, Arctic Canada, uppermost Llandovery, stub 1267M, ZPAL G.47/1. Colours: **red**, nema; **pink**, connecting rods; **green**, transverse rod; **yellow**, lateral apertural list; **orange**, thecal lip; **gray**, pleural list; **white**, other ancora sleeve lists. Scale bars: B, C, 100 µm; D, E, 10 µm.

a similarity of the tubarium construction to *Paraplectograptus*, but differs in having a simple ancora umbrella consisting of four meshes and a short sicula, 0.4-0.49 mm long, whereas the ancora umbrella of *Paraplectograptus eiseli* has eight meshes and a longer sicula, about 0.9-1.15 mm long. The micro-ornamentation of its tubarium bandages consists of fine parallel striae, in contrast to the pustular ornamentation of *Paraplectograptus*. The fact that this taxon occurs in the Llandovery is important since it may represent both a temporal and phylogenetic link between typical Aeronian retiolitines and the more derived taxa in later Telychian and younger strata.

In conclusion, the *Paraplectograptus* lineage is a relatively diverse group of retiolitines, comprising two genera, *Paraplectograptus* and *Pseudoplectograptus*, and seven species (Kozłowska-Dawidziuk 1995, 2004; Lenz *et al.* 2012). It is a long ranging group, occurring from the lower Telychian, *S. turriculatus*/*Str. crispus* Biozone up to the upper part of the *C. lundgreni* Biozone in the Homerian.

MORPHOLOGY

General characteristics

Paraplectograptus and *Pseudoplectograptus* differ mostly in the size of tubaria and arrangement of the lateral walls of ancora sleeve and ventral walls (Kozłowska-Dawidziuk 1995; Lenz *et al.* 2012). They have distally open-ended tubaria, which may contain about 20 pairs of thecae in the longest specimens. *Pseudoplectograptus* has a more robust and wider rhabdosome whereas that of *Paraplectograptus* is slender and parallel-sided. Their thecal frameworks include: connecting rods linking transverse rods with the nema, lateral apertural rods, and thecal lips (Fig. 1). Their ancora umbrellas are simple, orderly, with well-defined rims, sometimes very thin and not preserved (Figs 1-4). The ancora sleeves of *Paraplectograptus* and *Pseudoplectograptus* are variably developed, from more or less regular simple lists, to a reticulated wall (Lenz *et al.* 2012).

The ancora sleeve reticulum is better developed in *Pseudoplectograptus* species. The lists of the ventral wall have seams inside with well-developed pustules on their outer sides, as opposed to ancora sleeve lists with seams outside and inner smooth surfaces.

Sicula and nema

As with most retiolitines, the earliest part of the *Paraplectograptus* tubarium to survive is the composite list which comprises the proximal part of the nema, the virga, which forms part of the prosicula; and, with the development of the metasicula, the virgella. The length of the prosicula, based on the position of the prosicular apex and prosicular rim, is about 0.4 mm. The sicular length is about 0.9-1.15 mm.

The preservation of the prosicula is commonly incomplete, generally limited to the prosicular rim (Fig. 2). This rim is very variable, ranging from a complete, circular rim (Fig. 2E, F) to scarcely visible vestiges on the inner face of the virga-virgella (Fig. 2G). Where the rim is more fully preserved, traces of longitudinal rods can occasionally be seen extending from the adapical edge of the prosicular rim (Fig. 2D).

The structure of the prosicula and longitudinal rods is similar to that of Ordovician diplograptid species (Bates 1996), suggesting that their construction is a very conservative feature. The wall is formed of randomly oriented fibrils; the longitudinal rods are formed of parallel fibrils making a keel which fades towards the prosicular aperture; and the prosicular rim has parallel fibrils, probably forming a bandage (Fig. 2D).

The virga, the unique structure for retiolitines, is formed on the outer face of the prosicula by the deposition of bandages, and has a concave internal face. On this there may be traces of the prosicular wall, including fibrils which may be parallel to the spiral line (Fig. 2A). The ab-apertural end of the virga, and the transition to the nema, is marked by the end of the concave face; it becomes "internal" at the apex of the prosicula (Figs 2A, B; 5C). It should be noted that it has not been possible to establish the presence of a cauda (Bates 1996) apically from the conus.

Distal to the virga, the nema is characterised by having a concentric structure, around a central, largely hollow, axis. The thickening of the nema was by the deposition of bandages, with a pustular ornament (Fig. 2B).

The virgella of *Paraplectograptus* is very similar to that of most retiolitines, including those of both *Retiolites* and *Stomatograptus.* It is formed of a fusellar core, thickened both internally and externally by bandages running along its length (Fig. 5A, E). Traces of metasicular fusellar closures are usually only preserved in the slots on the obverse and reverse faces

of the virgella nearer to the metasicular aperture (Fig. 5E). They sweep forwards into the slots, indicating the forwards sweep of the fuselli themselves.

Ancora umbrella

In *Paraplectograptus* the ancora umbrella commences, as in other ancorate retiolitines, by forking of the virgella to form the first two lists (Figs 3; 4A, B). These are inclined at an angle of about 40°, anticlockwise (viewed looking from outside the specimen) from the plane of symmetry of the two thecal series. A second forking then results in four secondary lists separating the four central meshes of the umbrella. Two of these lists extend to the rim of the ancora umbrella adjacent to the obverse and reverse proximal lateral orifices. The other two lists fork again to give rise to lists which define a minor mesh proximal to th1^1, and three minor meshes proximal to th1^2 (Fig. 3).

The resulting ancora umbrella is consequently oval in plan and asymmetrical about the virgella, being more elongated where it arches over the sicular aperture and ventral wall of th1^2. In some other tubaria, and possibly in certain *Paraplectograptus* species, the number of minor meshes in the umbrella reticulum became greater, but a similar asymmetrical oval form seems to have been retained.

The ancora umbrella of *Paraplectograptus* is completed with a definite rim. This is similar to that in most retiolitines like *Pseudoplegmatograptus* (Bates & Kirk 1992: figs 212, 213) but is in contrast to the umbrella in both *Retiolites* and *Stomatograptus*, in which there is no distinct rim (Bates *et al.* 2005: fig. 6B; Lenz & Kozłowska 2007: fig. 4).

The rim is a somewhat lobate oval list closure, with a centripetally facing insertion slot continuous with the attachment grooves over the absicular faces of the adjoining radiating lists of the umbrella reticulum. Distinctive shards of possible fuselli are associated with the list/rim junctions (Fig. 3A-G).

The ancora umbrella is connected to the thecal framework by four main pleural lists, which mark the "corners" of the tubarium between the ventral and lateral sides (Fig. 4D, E).

Growth of tubarium walls

In the growth of any graptolite, bandages are always laid down on a pre-existing surface, not produced "in space". So, in the growth stages illustrated, all of the lists, as preserved, are represented by the bandaging which was laid down on a fusellum: this can be either a wall, as in the sicula and ancora umbrella, or a spine, as in the nema, the pleural lists and the four initial lists joining the ancora umbrella to the first two thecae (Fig. 4D, E). Therefore, each growth stage illustrated is actually a record of the appearance of the secondary bandaging, not of the actual growth.

The earliest growth stage is the production of the prosicula and the associated nema (Fig. 4A). Both the nema and the virga are preserved because they were thickly bandaged. The succeeding walls of the metasicula are only preserved as the deep seams which have within them the traces of the fuselli (Fig. 5E). These are angled forwards in the direction of growth, as is seen in the growth of most siculae.

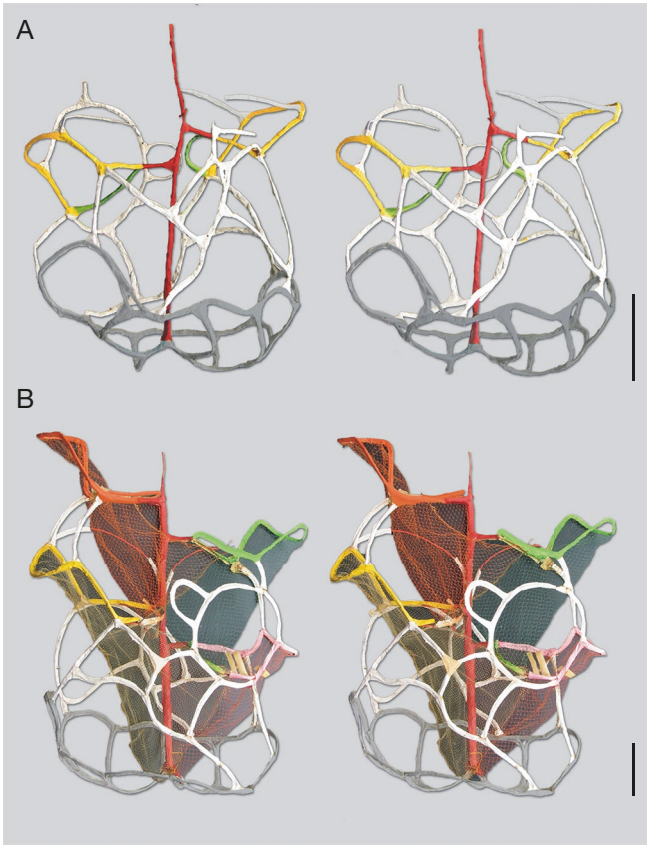

FIG. 7. — Stereopairs of two *Pseudoplectograptus* models made by Nancy Kirk: **A** model with one pair of thecae, ZPAL G.47/13, obverse view: **red**, nema, virga, connecting rods; **gray**, ancora umbrella; **green**, transverse rod; **yellow**, lateral apertural list; **orange**, thecal lip; **white**, pleural list and other ancora sleeve lists; **B** model with two pairs of thecae and postulated thecal walls, ZPAL G.47/14, reverse view, colours indicate: **pink**, th1^1; **green**, th2^1; **yellow**, th1^2; **red**, th2^2. Scale bars: 10 cm.

The early growth stages show the development of the ancora umbrella; in Figure 4A the radial lists do not extend to the rim, in Figure 4B and C forkings of some of these lists show the position of the ancora umbrella rim. This forking is also seen in Figure 3, in a mature ancora umbrella.

The appearance of the lists of th1^1 and th1^2 is shown in Figure 4C, those of th1^1 being more complete than those of th1^2 (which lacks the apertural lip). Together with these, the first pleural lists of the ancora sleeve have already joined the ancora rim to the lateral apertural lists of th1^1. At this stage, however, the lists on th1^2 are not complete: they give the appearance of pairs of spines projecting towards one another.

In Figure 4D the umbrella rim is bandaged sufficiently to be preserved as a complete rim. Both initial thecae are complete, and the next four pleural lists are projecting forwards. The four pleural lists are now completely present proximal to the first thecae, marking the presence of the four proximal orifices (Fig. 4D).

The development of the ancora sleeve lists is shown in Figure 4E. Two lists are projecting proximally towards the ancora umbrella rim, and other lists of the sleeve are starting to form the sleeve growing distally. As further thecae are generated, this pattern of growth is continued.

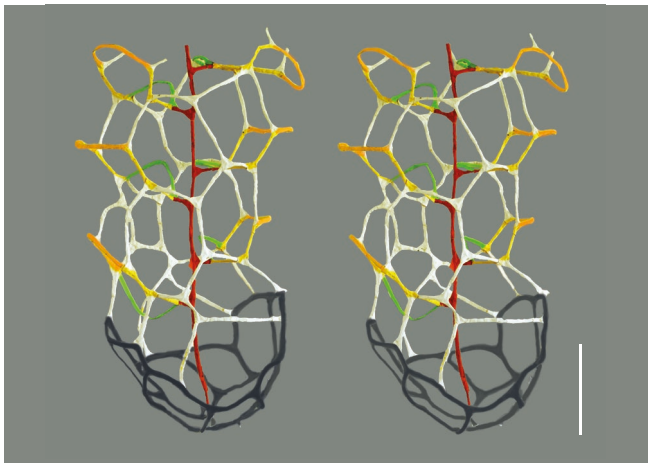

FIG. 8. — Stereopair of the *Paraplectograptus* model made by Nancy Kirk, with three thecal pairs, viewed from the reverse side of tubarium, ZPAL G.47/15. Colours: **red**, nema, virga, connecting rods; **dark gray**, ancora umbrella; **green**, transverse rod; **yellow**, lateral apertural list; **orange**, thecal lip; **white**, pleural and other ancora sleeve lists. Scale bar: 10 cm.

Thecal framework

Paraplectograptus has a thecal framework which differs from that of *Retiolites* and *Stomatograptus* principally in having no dorsal or zigzag list (Fig. 1), a structural element which is also noticeably attenuated in *Stomatograptus* (Bates & Kirk 1997). The thecal framework is again supplemented by ancora sleeve lists extending from the proximal ancora umbrella. Examination at the ultrastructural level shows the strongly notched ventral margins of the *Paraplectograptus* rhabdosome, like those of *Stomatograptus*, to be due to an alternation of lateral apertural thecal lists (yellow) and pleural ancora sleeve lists (gray) bordering the proximal ventral orifices (Figs 1; 4; 5). There are also obverse and reverse orifices adjacent to the rim of the ancora umbrella, but no stomata.

Thecae 1^1 and 1^2 are defined by lists with seams arising from the region of the prosicula (Figs 1; 5). $Th1^1$ probably had its origin in a porus on the sicula, growing proximally before turning distally towards its aperture, defined by the first transverse rod, lateral apertural rods and thecal lip (Fig. 6A). The aperture of $th1^2$ is similarly marked by the equivalent lists on the other side (Fig. 6C). Subsequent thecae have their apertures also formed of transverse rods, lateral apertural rods, and thecal lips (Figs 1; 6). Details of the fusellar seams of *Paraplectograptus eiseli* can be seen in all four photographs on Figure 6B-E: note that the seams are rotated as they pass from proximal-facing on the transverse rods to inward-facing on the lateral apertural rods.

The transverse rod marks the initiation of the ventral thecal wall of successive thecae (Figs 5B; 6A). It is probably homologous with the ab-apertural list in diplograptids and monograptids. In these the list forms the base of the interthecal septum and forms initially as a spine (perhaps a pair of spines extending towards one-another) extending from side to side of the tubarium. It is also found in *Retiolites* and *Stomatograptus*, with the thecal wall extending distally from it to the thecal lip. In *Rotaretiolites* (Bates & Kirk 1992: fig. 114) the transverse rod also has a strong seam on its proximal side.

On the obverse side of the tubarium the thecal walls include the nema and connecting rods, in a continuous lateral wall, inside the lists of the ancora sleeve (Figs 1A-C; 6A). The same arrangement is found in both *Retiolites* (Fig. 1E) and *Stomatograptus*. Note that the sleeve lists are secreted from the inside, implying that there was a space between the thecal wall and the ancora sleeve, the obverse external common canal (Fig. 1E). On the reverse side there is no zigzag or dorsal list, as is found in *Retiolites* and *Stomatograptus*. However, the ancora sleeve lists here, in *Paraplectograptus*, are also secreted from the inside, and it is probable that the reverse external wall lay inside the ancora sleeve, with an external common canal between them.

The walls of successive thecae would have overlapped one another (Fig. 7B), but there was no thickening along their junctions, which would have generated the zigzag list (cf. the generation of the zigzag list in *Retiolites* (Bates & Kirk 1978: pl. 12)).

Ancora sleeve

The ancora sleeve of *Paraplectograptus* is formed of lists which have outward-facing seams (Fig. 5A, B), as have those in *Retiolites* and *Stomatograptus*, in which they form a continuation of the lists of the ancora umbrella. This indicates that the bandages were laid down on the inner side of the sleeve, in spaces between the sleeve and the thecal framework, the external common canals. In the absence of a preserved dorsal or zigzag list on the reverse side of *Paraplectograptus*, it is not possible to be certain of the presence of an external common canal on this side. However, the bandages of the sleeve lists here were also laid down on the inside, so there was probably a space internal to the sleeve, but outside the thecal framework –the reverse external common canal.

In *Retiolites* and *Stomatograptus* the dorsal list marks the proliferation of successive thecae (thn^2 succeeding thn^1), its bandaging being laid down before the wall of thn^2 is deposited (Bates & Kirk 1997). It is presumed to have been present here also, but, without any bandaging to thicken and so form the lists, it is not preserved; its likely path is indicated in Figure 1D. Pleural lists mark the ventral limits of the ancora sleeve, and occupy similar positions to those of both *Retiolites* and *Stomatograptus*.

The sleeve bandages have a pustular ornament (Fig. 5A, B), unlike those of *Retiolites* and *Stomatograptus*, which are simply striated. The pustular ornamentation is an advanced feature characteristic of all post-*lundgreni* period retiolitines. *Paraplectograptus* is one of a few pre-*lundgreni* retiolitines having pustules on its bandages (Kozłowska-Dawidziuk 2004: 510).

Proximal lateral orifices

Proximal lateral orifices form a prominent feature of many retiolitines, and, together with the proximal ventral orifices, form a circlet of four proximal orifices. In young specimens of *Paraplectograptus* they are separated only by four single lists (Fig. 4D, E). However, as growth continues, other lists of the ancora sleeve are developed, and they constrain the shape of the proximal lateral orifice. This, in common

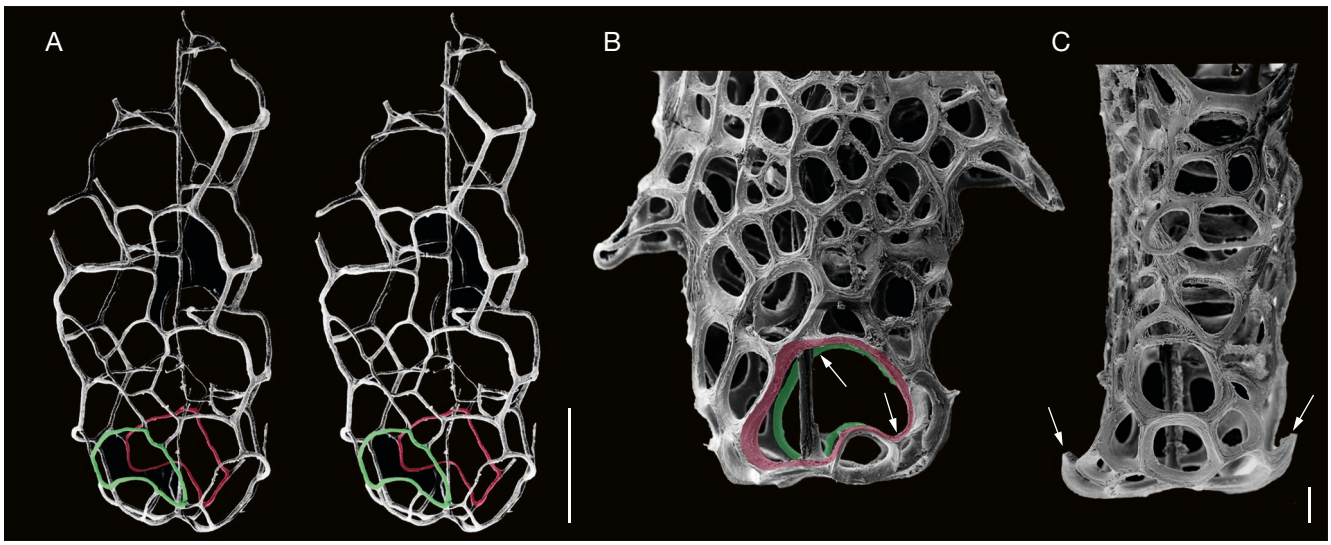

FIG. 9. — **A**, Stereopair image of *Pseudoplectograptus* sp. in reverse view; **B**, **C**, *Retiolites angustidens* Elles & Wood, 1908; Cape Phillips Formation, Cornwallis Island, Canadian Arctic, precise horizon unknown, NMW 91.52G.127: **B**, proximal end in obverse view; **C**, ventral view, arrows show lateral edges of ancora umbrella rim. **Arrows** mark edges of proximal lateral orifices; **pink**, the obverse proximal lateral orifice rim; **green**, the reverse one. Scale bars: A, 500 µm; B, C, 100 µm.

with that of a number of other genera of retiolitines, has a kidney-shaped appearance (Figs 1A; 7-9A, B). The rim of the ancora umbrella bends outwards and upwards to form a re-entrant shape when viewed laterally, while the other section of the rim is convex. In flattened specimens this feature can be accentuated, as the ancora rim section is bent upwards.

CONCLUSIONS

The morphology and reconstruction of the *Paraplectograptus* lineage, containing the two genera *Paraplectograptus* and *Pseudoplectograptus*, is described herein based on well-preserved three-dimensional material from Arctic Canada and Poland. Based on these data, comparison is made with the Llandovery retiolitines *Retiolites* and *Stomatograptus*. The similarities of their tubaria are shown in the main construction of the thecal wall and ancora sleeve.

The development of the transverse rods and their connection to the nema in *Paraplectograptus* and *Retiolites* make for a strong rhabdosome (tubarium) construction in both the *Paraplectograptus* lineage and *Retiolites*. The construction is made by the well-developed transverse rods (the basal part of thecae) connected to the nema, as well as the lateral apertural rods and lips. The lengths and angles between these lists are different in both groups of retiolitine.

There is a similar arrangement of the ancora sleeve in all the genera, which defines external common canals outside the internal common canal. The ancora sleeve of *Paraplectograptus* and *Pseudoplectograptus* is formed by more irregular and thinner lists. In both groups the ancora sleeve is secreted from the inside, which is typical for the older retiolitines.

In spite of the early appearance of *Paraplectograptus*, in the lower Telychian, its tubarium shows some advanced features compared with *Retiolites*. It is one of the first retiolitines having the later feature of pustular bandages, characteristic of all post-*lundgreni* period retiolitines. The bandages of *Retiolites* are smooth, typical of the older retiolitines.

Another important feature, used in retiolitine classification, is the development of the ancora umbrella. The ancora umbrella of *Paraplectograptus* and *Pseudoplectograptus* has a well-defined rim, in contrast to those of *Retiolites* and *Stomatograptus*.

The proximal lateral orifices are similar in shape in both the *Paraplectograptus* lineage and in *Retiolites* and *Stomatograptus*. Their patterns are widespread in the retiolitines.

One other difference is in size of tubaria, which are strong and large in *Retiolites* and *Stomatograptus*, as opposed to the small and slender *Paraplectograptus* tubaria, which are similar to most post-*lundgreni* forms.

To conclude, the *Paraplectograptus* lineage has features typical of the older Llandovery retiolitines, as well as advanced ones characteristic of all post-*lundgreni* forms. It may be regarded as an evolutionary link between the two groups.

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REFERENCES

BATES D. E. B. 1987. — The construction of graptolite rhabdosomes in light of ultrastructural studies. *Indian Journal of Geology* 59: 1-28.
BATES D. E. B. 1990. — Retiolite nomenclature and relationships. *Journal of the Geological Society* 147 (4): 717-723. https://doi.org/10.1144/gsjgs.147.4.0717

Bates D. E. B. 1996. — The ultrastructure of some Ordovician graptoloid prosiculae. *Acta Palaeontologica Polonica* 41 (1): 39-57.
Bates D. E. B. & Kirk N. H. 1978. — Contrasting modes of construction of retiolite-type rhabdosomes. *Acta Palaeontologica Polonica* 23: 427-448.
Bates D. E. B. & Kirk N. H. 1984. — Autecology of Silurian graptoloids. *Special Papers in Palaeontology* 32: 121-139.
Bates D. E. B. & Kirk N. H. 1987. — The role of extrathecal tissue in the construction and functioning of some Ordovician and Silurian retiolitid graptolites. *Bulletin of the Geological Society of Denmark* 35: 85-102. https://doi.org/10.37570/bgsd-1986-35-10
Bates D. E. B. & Kirk N. H. 1992. — The ultrastructure, mode of construction and functioning of a number of Llandovery ancorate and retiolitid graptolites. *Modern Geology* 17: 1-270.
Bates D. E. B. & 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 *Petalolithus*, and its comparison with that of the thecal framework in *Retiolites* and *Stomatograptus*. *Institute Geography and Earth Sciences University of Wales, Aberystwyth* 10: 1-168.
Bates D. E. B., Kozłowska A. & Lenz A. C. 2005. — Silurian retiolitid graptolites: Morphology and evolution. *Acta Palaeontologica Polonica* 50: 705-720.
Bouček B. 1931. — Předběžná zpráva o některých novych druzích graptolitu z Českého gotlandienu. *Věstník Státního geologického ústavu, CSR* VII-3: 29-313.
Bouček B. & Münch A. 1952. — Retioliti středoevropského svrchního wenloku a ludlowu. *Sborník Ústředního* Ústavu *geologického, oddil paleontologicky* 19: 1-151.
Elles G. L. & Wood E. M. R. 1908. — *Monograph of British graptolites*. Part 7. Palaeontographical Society, London: cxxi-cxlviii, 273-358.
Eisenack A. 1951. — Retioliten aus dem Graptolithengestein. *Palaeontographica* 100: 129-163.
Jaeger H. 1991. — Neue Standard-Graptolithenzonenfolge nach der "Grossen Krise" an der Wenlock/Ludlow-Grenze (Silur). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 182: 303-354. https://doi.org/10.1127/njgpa/182/1991/303
Koren' T. N. 1987. — Graptolite dynamics in Silurian and Devonian time. *Bulletin of the Geological Society of Denmark* 35: 149-159. https://doi.org/10.37570/bgsd-1986-35-16
Koren' T. N., Lenz A., Loydell D. K., Melchin M.J, Štorch P. & Teller L. 1996. — Generalized graptolite zonal sequence defining Silurian time intervals for global paleogeographic studies. *Lethaia* 28 (2): 137-138. https://doi.org/10.1111/j.1502-3931.1995.tb01603.x
Kozłowska A. 2016. — A new generic name, *Semigothograptus*, for *Gothograptus*? *meganassa* Rickards & Palmer, 2002, from the Silurian post-*lundgreni* Biozone recovery phase, and comparative morphology of retiolitids from the lowermost upper Homerian (upper Wenlock). *Zootaxa* 4208 (6): 534-546. https://doi.org/10.11646/zootaxa.4208.6.2
Kozłowska A., Lenz A. & Melchin M. 2009. — Evolution of the retiolitid *Neogothograptus* (Graptolithina) and its new species from the upper Wenlock of Poland, Baltica. *Acta Palaeontologica Polonica* 54 (3): 423-434. https://doi.org/10.4202/app.2008.0022
Kozłowska A., Bates D. E. B., Zalasiewicz J. & Radzevičius S. 2019. — Evolutionary significance of the retiolitine *Gothograptus* (Graptolithina) with four new species from the Silurian of the East European Platform (Baltica), Poland and Lithuania. *Zootaxa* 4568 (3): 435-469. https://doi.org/10.11646/zootaxa.4568.3.2
Kozłowska-Dawidziuk A. 1995. — Silurian retiolitids of the East European Platform. *Acta Palaeontologica Polonica* 40 (3): 261-326.
Kozłowska-Dawidziuk A. 1997. — Retiolitid graptolite *Spinograptus* from Poland and its membrane structures. *Acta Palaeontologica Polonica* 42 (3): 391-412.
Kozłowska-Dawidziuk A. 2001. — Phylogenetic relationships within the Retiolitidae (Graptolithina) and a new genus, *Cometograptus*. *Lethaia* 34 (1): 84-96. https://doi.org/10.1080/002411601300068314
Kozłowska-Dawidziuk A. 2004. — Evolution of retiolitid graptolites: a synopsis. *Acta Palaeontologica Polonica* 49 (4): 505-518.
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. 1994a. — A sclerotized retiolitid, and its bearing on origin and evolution of Silurian retiolitid graptolites. *Journal of Paleontology* 68 (6): 1344-1349. https://doi.org/10.1017/S0022336000034326
Lenz A. C. 1994b. —Uppermost Wenlock and lower Ludlow plectograptine graptolites, Arctic Islands, Canada: new isolated material. *Journal of Paleontology* 68 (4): 851-860. https://doi.org/10.1017/S0022336000026305
Lenz A. C. & Melchin M. J. 1987. — Silurian retiolitids from the Cape Phillips Formation, Arctic Islands, Canada. *Bulletin of the Geological Society of Denmark* 35: 161-170. https://doi.org/10.37570/bgsd-1986-35-17
Lenz A. C. & Thorsteinsson R. 1997. — Fusellar banding in Silurian retiolitid graptolites. *Journal of Paleontology* 71 (5): 917-920. https://doi.org/10.1017/S0022336000035836
Lenz A. C. & Kozłowska-Dawidziuk A. 2001. — Upper Wenlock (Silurian) graptolites of Arctic Canada: pre-extinction *lundgreni* Biozone fauna. *Palaeontographica Canadiana* 20: 1-61.
Lenz A. C. & Kozłowska-Dawidziuk A. 2002. — Upper Homerian (Upper Wenlock, Silurian) graptolites from Arctic Canada. *Journal of Paleontology* 76 (2): 319-344. https://doi.org/10.1017/S0022336000041731
Lenz A. C. & Kozłowska-Dawidziuk A. 2004. — Ludlow and Přidoli (Upper Silurian) Graptolites from the Arctic Islands, Canada. *NRC Research Press, Ottawa, Ontario, Canada*: 1-41. https://doi.org/10.1139/9780660193267
Lenz A. C. & Kozłowska A. 2006. — Graptolites from the *lundgreni* Biozone (Lower Homerian, Silurian), Arctic Islands, Canada: new species and supplementary material. *Journal of Paleontology* 80 (4): 616-637. https://doi.org/cq4k2j
Lenz A. C. & Kozłowska A. 2007. — New and unusual upper Llandovery graptolites from Arctic Canada. *Acta Palaeontologica Polonica* 52 (3): 489-502.
Lenz A. C., Senior S., Kozłowska A. & Melchin M. 2012. — Graptolites from the Mid Wenlock (Silurian), Upper Sheinwoodian, Arctic Canada. *Palaeontographica Canadiana* 32: 1-93.
Lenz A. C., Bates D. E. B., Kozłowska A. & Maletz J. 2018. — Part V, second revision, Chapter 26: Family Retiolitidae: Introduction, morphology, and systematic descriptions. *Treatise Online* 114: 1-37. https://doi.org/10.17161/to.v0i0.6534
Maletz J. 2010. — Retiolitid graptolites from the collection of Hermann Jaeger II: *Cometograptus*, *Spinograptus* and *Plectograptus*. *Paläontologische Zeitschrift* 84: 501-522. https://doi.org/10.1007/s12542-010-0065-x
Manck E. 1917. — Die Graptolithen der Zone 18, sowie *Retiolites eiseli* spec. nov., *Monogr. bispinosus* spec. nov. und *Diplograptus radiculatus* spec. nov. *Zeitschrift für Naturwissenschaften* 86: 337-344.
Melchin M. J., Mitchell C. E., Naczk-Cameron A., Fan J. X. & Loxton J. 2011. — Phylogeny and adaptive radiation of the Neograptina (Graptoloida) during the Hirnantian Mass Extinction and Silurian recovery. *Proceedings of the Yorkshire Geological Society* 58 (4): 1-30. https://doi.org/10.1144/pygs.58.4.301
Melchin M. J., Lenz A.C & Kozłowska A. 2017. — Retiolitine graptolites from the Aeronian and lower Telychian (Llandovery, Silurian) of Arctic Canada. *Journal of Paleontology* 91 (1): 116-145. https://doi.org/10.1017/jpa.2016.107

OBUT A. M. & ZASLAVSKAYA N. 1983. — Families of retiolitids and their phylogenetic relationships, *in* DAGYS A. S. & DUBATOLOV V. N. (eds), *Morphology and Taxonomy of Phanerozoic Invertebrata*. Nauka, Moscow: 103-113 [in Russian].

ŠTORCH P. & MANDA Š. 2019. — Little known Homerian (lower Silurian) graptolites from Kosov quarry near Beroun, the Czech Republic. *Fossil Imprint* 75: 44-58. https://doi.org/10.2478/if-2019-0003

THORSTEINSSON R. 1958. — Cornwallis and Little Cornwallis islands, District of Franklin, Northwest Territories. *Geological Survey of Canada*, *Memoir* 294: 1-134. https://doi.org/10.4095/100516

URBANEK A. 1993. — Biotic crises in the history of Upper Silurian graptoloids: a palaeobiological model. *Historical Biology* 7 (1): 29-50. https://doi.org/10.1080/10292389309380442

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