Silurian retiolitid graptolites: Morphology and evolution

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Developmental mode and proximal structures are commonly accepted as the best for the recognition of high-level taxonomic categories within the Graptoloidea. The petalolithids and retiolitids are unique in possessing a virgellar ancora and in the latter, distal ancora development. The ancora structures are considered homologous, and the ancorate petalolithids are considered to be the direct ancestors to the retiolitids. The Retiolitidae are unique among the diplograptoids in possessing (1) outer, lateral, ancora sleeve walls (derived from distal extension of the ancora), and (2) a skeletal framework of bandaged lists between which are a succession of very thin and rarely preserved fusellar layers. Retiolitids possess different kinds of thecal profiles and two types of micro-ornamentation on the lists, and these have served to distinguish between the subfamilies Retiolitinae and Plectograptinae. Complete retiolitid morphological terminology is clarified and explained. Cladistic analysis of the retiolitids provides some measure of a better understanding of retiolitid evolution, but adds only modest support for the retention of the two subfamily categories.

Key words: Graptoloidea, Retiolitidae, Petalolithidae, ancora, cladistic analysis, Silurian.

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Introduction

By virtue of their possession of a meshwork skeletal framework, retiolitids have since at least the time of Lapworth (1873) been accorded a separate familial and subfamilial status within the suborder Diplograptina Lapworth, 1880. A later departure from this simple classification was the work of Bouček and Münch (1952) that divided the retiolitid family into the subfamilies Retiolitinae and Plectograptinae, based primarily on their known stratigraphic positions, as well as on some generalized morphological differences. Coincidentally, the much later SEM studies of Lenz and Melchin (1987) on isolated retiolitids from Arctic Canada showed the presence of a smooth to striated micro-ornamentation on retiolitine lists and a pustulose micro-ornamentation on plectograptine lists, adding support to the twofold subfamilial division of the retiolitids. The distinctive micro-ornamentation on bandages is unique among graptolites.

The Ordovician archiretiolitids have hitherto been included in the family Retiolitidae, as the subfamily Archiretiolitinae (e.g., Bulman 1970). However, they have a markedly different morphology (Bates and Kirk 1986, 1991), and appear to be unrelated to the Silurian retiolitids. While their thecal framework is formed in a similar manner to that of the retiolitids, the external lacinia is not formed from an ancora, and its lists are unseamed.

The retiolitids have been misunderstood for a long time, in part because it had been tacitly assumed that their immediate ancestors were "normal" diplograptoids that had simply lost their continuous periderm, retaining only a skeletal framework devoid of any intervening fusellar periderm and, in part, because there had been no recognition of the unique double-layer nature of the retiolitid skeletal structure. It was primarily following the long and detailed SEM studies of Bates and Kirk (e.g., 1984, 1987, 1992) who, working with isolated, three-dimensionally preserved material, clearly showed that retiolitids possess a framework unlike any other diplograptoid. To wit, while retiolitid thecae originate from the sicula as in all other graptolites, and thereby form the thecal framework, the outermost lateral walls of the rhabdosome (the ancora sleeve of Bates 1990, partly the equivalent of the "reticulum" and/or "clathrium" in a morphological sense) are exclusively the product of the distal extension and development of the ancora meshwork that partially envelopes and/or ventrally joins with the thecal framework. Thus the retiolitids are unlike all other graptolites in that most possess double lateral walls: an inner one being the homologue of the "normal" diplograptoid lateral walls ("thecal wall" in Fig. 1) within which the virgula is normally found, and an outer wall derived entirely from the distal extension of the ancora ("ancora sleeve wall" in Fig. 1). These walls, built from very thin and incrementally deposited fusellar layers supported by strong lists formed exclusively from bandages, are only very rarely completely preserved (Fig. 2). Normally, therefore, only the rod-like bandaged lists of the retiolitid rhabdosome are preserved (Fig. 3H–J), and ultrastructural investigation is needed to reconstruct the thin, largely fusellar membranes. A "nor-

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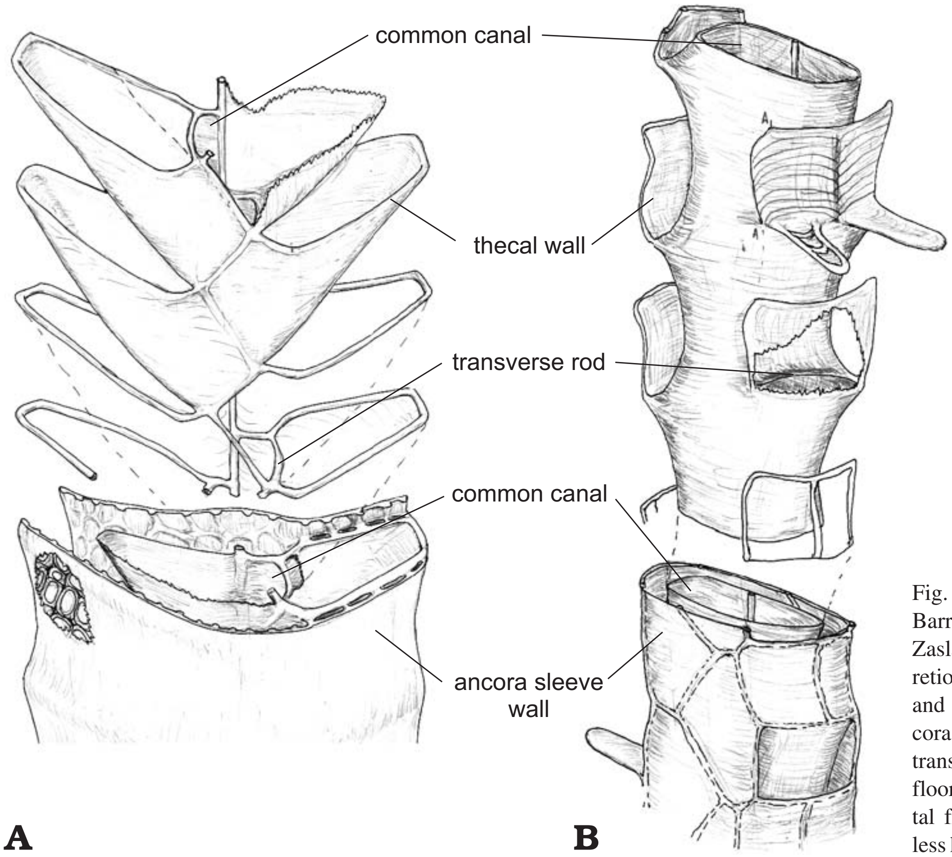


Fig. 1. Reconstruction of: **A**. *Retiolites geinitzianus* Barrande, 1850. **B**. *Plectograptus robustus* (Obut and Zaslavskaya, 1983) showing double-wall nature of retiolitids, orthograptid shape of thecae in *Retiolites*, and relationship between the thecal framework, ancora sleeve and common canal in both species. The transverse rod marks the internal limit of the thecal floor. Note that, in life, the list-like, bandaged skeletal framework would probably have been more or less hidden by the continuous fusellar layer periderm.

mal" single-walled diplograptoid, e.g., pictured in Melchin (1998), compared with those rare retiolitids in which the periderm (fusellar layer) has been fully preserved (e.g., Lenz 1994a, b; Kozłowska-Dawidziuk 1997), illustrates the spectacular distinction between the two taxonomic groups.

The retiolitid ancora is more complex and highly developed than typical of the petalolithids (Figs. 4, 5), being extended to form the ancora umbrella, and then the ancora sleeve, which is integrated with the thecal framework. However, in early growth stages, the ancorae of the retiolitids and the petalolithids are basically identical (Figs. 3A–D, 4), and are consequently regarded as homologous structures (Mitchell 1987; Bates 1990). Moreover the petalolithids, possessing ancora structures, are now widely accepted as being ancestral to the retiolitids (Bates and Kirk 1984, 1992; Bates 1987, 1990; Mitchell 1987; Lenz 1993, 1994a; Lenz and Melchin 1997; Melchin 1998, 1999; Lenz and Kozłowska-Dawidziuk 2001).

This paper is written with the aim of (1) pointing out the evolutionary relationships between "ancorate" petalolithids and retiolitids (that is, the ancora is a fundamental synapomorphic feature), (2) updating the morphological terminology for the retiolitids, (3) emphasizing the morphologic diversity and uniqueness of the most complex ancorate forms within the Diplograptacea, the Retiolitidae, and, (4) studying the evolutionary relationships of the retiolitids using cladistics.

Material.—The isolated material illustrated herein comes from nodules of the Arctic Canada, from erratic boulders and boreholes of Poland, Germany, and Sweden. The graptolites were recovered following slow dissolution of the host carbonate in acid (1–10% HCl). A fine hairbrush was used to pick and transfer specimens. The material is stored in glycerine in plastic containers, as well as on the SEM stubs.

Institutional abbreviations.—CNIGR, Chernyshev Central Scientific-Research Geological Exploration Museum, St. Petersburg, Russia; GSC, Geological Survey of Canada, Ottawa, Canada; NIGP, Nanjing Institute of Geology and Palaeontology, Nanjing, China; NMW, National Museum of Wales, Cardiff, United Kingdom; PS, Czech Geological Survey, Prague, Czech Republic; ZPAL, Institute of Paleobiology Polish Academy of Sciences, Warszawa, Poland.

Retiolitid terminology

Ancora.—Structure of four lists formed by forking at the end of the virgella (Figs. 3A–D, 6A).

Ancora umbrella.—Umbrella-shaped structure of lists developed from the ancora, comprising fusellar walls (not usually preserved), initial radially forking lists and subsequent spiral (Figs. 3I, 6C) or polygonal lists (Fig. 6D) and, in some genera (e.g., *Rotaretiolites*) a circular rim with (e.g., Fig. 3F, *Pseudorthograptus*) or without (Fig. 5B) further looping lists.

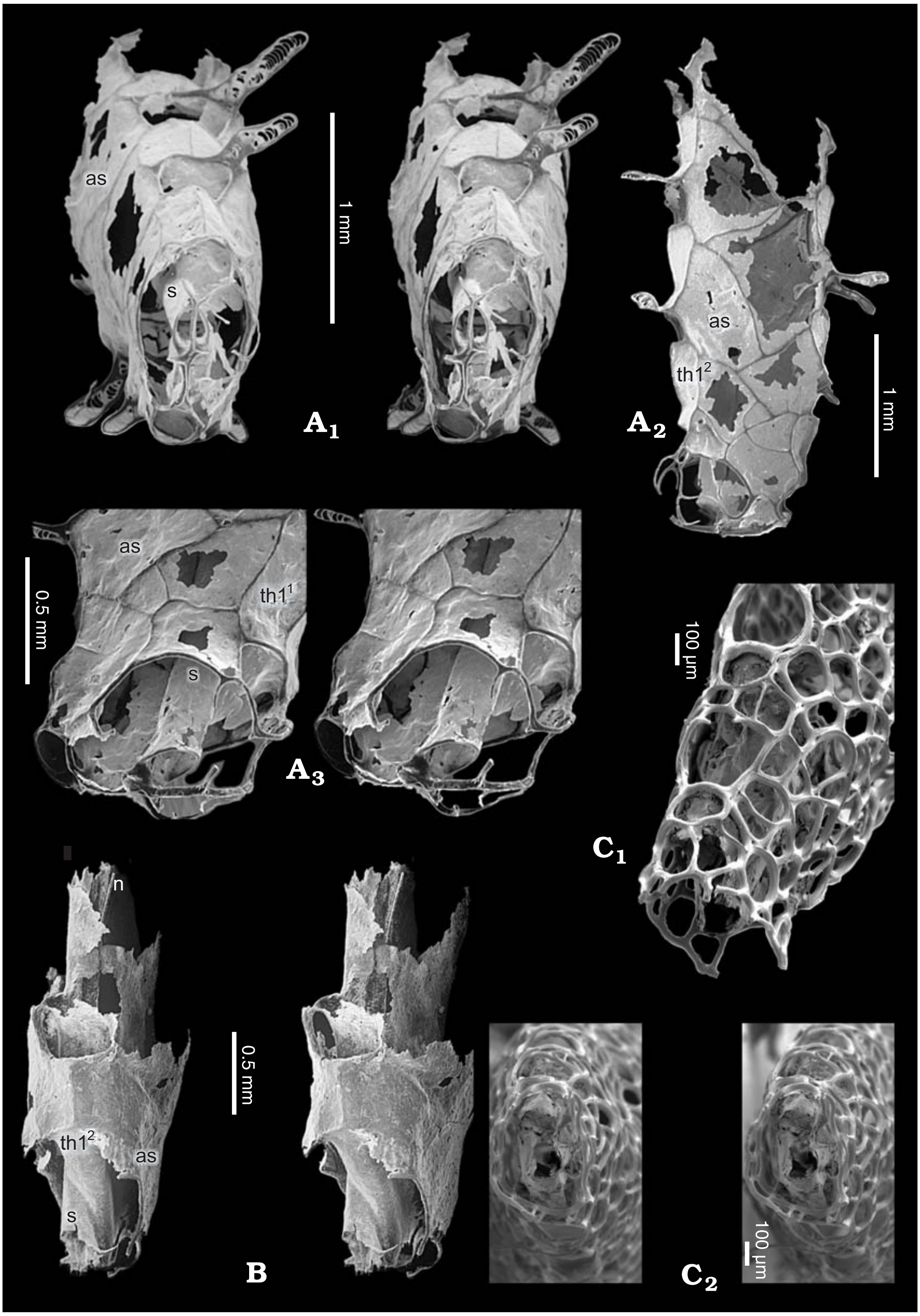


Fig. 2. Ancorae sleeve membranes in Silurian retiolitids. **A**, **B**. *Spinograptus praerobustus* Lenz and Kozłowska-Dawidziuk, 2002, specimens with preserved thecal and ancora sleeve membranes, Cornwallis Island, Arctic Canada, ABa3-98, 21 m, *Colonograptus praedeubeli–C. deubeli* Biozone, Wenlock. **A**. ZPAL G.37/1; A_1, stereopair of exterior proximal end showing ancora, well-preserved sicula, base of theca 1^1 (directly below sicula), double fusellar walls, thecal apertures and spino-reticular genicular processes; A_2, reverse view showing ancora and ancora umbrella, and partially preserved thin fusellar layer that fills in space between the zigzag (bandaged) lists; A_3, Proximal-lateral stereopair view. **B**. Stereopair showing sicula, theca 1^2 on lower right side of sicula, aperture of theca 1^2, inner and outer (ancora sleeve) fusellar layers, and thin nema, GSC 107928. **C**. Proximal end of *Retiolites angustidens* Elles and Wood, 1908 with broken ancora umbrella, NMW 91.52G.812, 500 m south of Stenkyrkehuks fyr, Gotland, Sweden, Lower Visby Marl, uppermost Llandovery; C_1, ventro-lateral view; C_2, view to the inside of rhabdosome showing sicula and thecal walls. Abbreviations: as, ancora sleeve; s, sicula; th, theca.

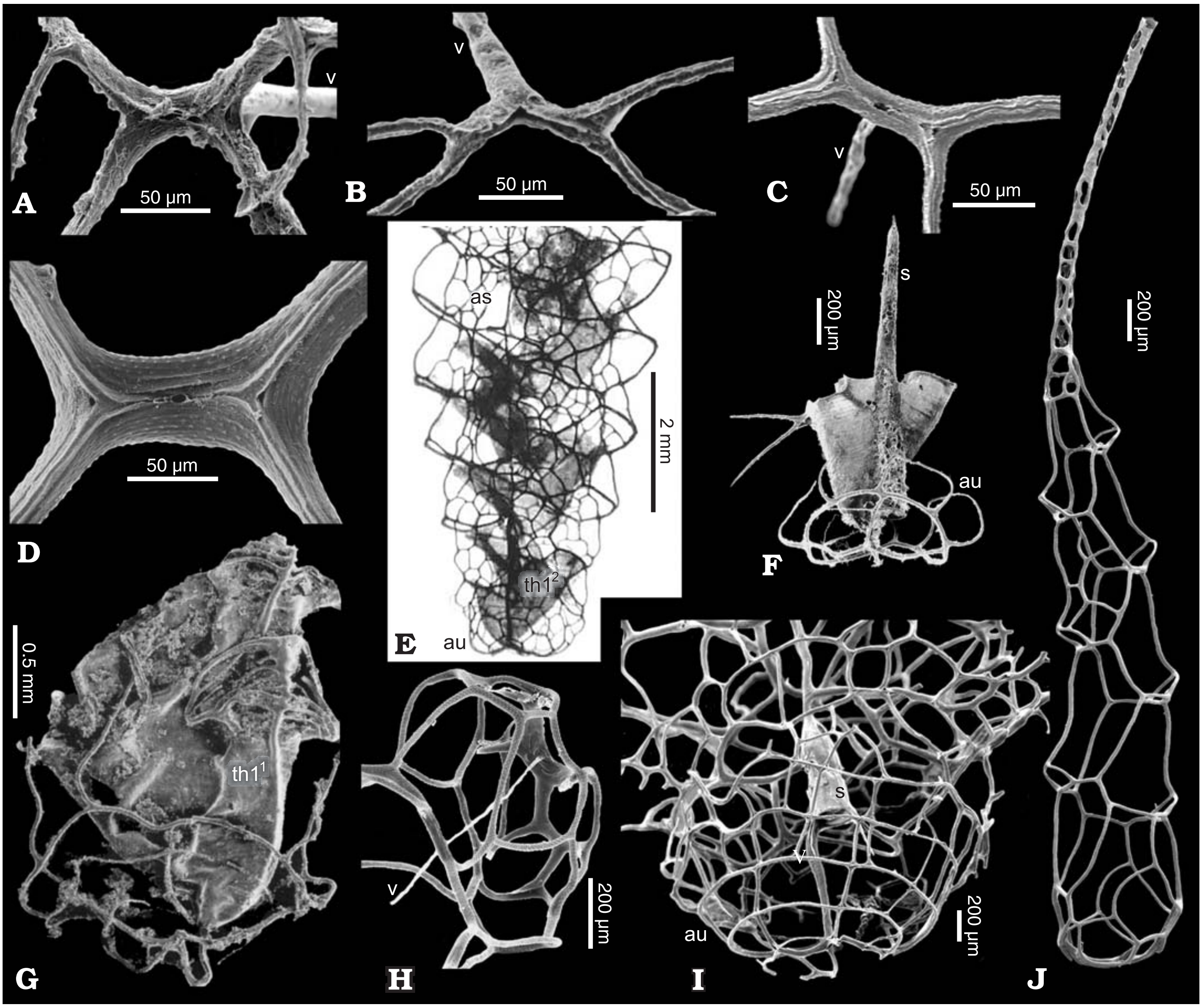


Fig. 3. Ancorae of Silurian retiolitids. **A**–**D**. Outside views of ancorae. **A**. *Pseudoretiolites* sp., specimen NMW 91.52G856, negative No. 88/34/16, field designation ML64, Cornwallis Island, Arctic Canada, Llandovery. **B**. Petalolithid early growth stage, specimen NMW 91.52G450E, Kallholn, Sweden, Llandovery. **C**. *Holoretiolites* sp., Baltic erratic boulder, Rerik, Germany, stub NMW 91.52G.1711, Ludlow. **D**. *Spinograptus lawsoni* (Holland, Rickards and Warren, 1969), Däps 1, Gotland, Sweden, ZPAL GXIII/55, *Colonograptus ludensis* Biozone, Wenlock. **E**. *Stomatograptus* sp. obverse view of specimen with well preserved fusellar thecal walls, GSC115529, after Lenz and Thorsteinsson (1997), Arctic—location unknown, probably late Llandovery. **F**. *Pseudorthograptus inopinatus* (Bouček, 1944), young stage of rhabdosome with ancora umbrella, GSC9819, field designation CM-93 #3, Arctic Canada, probably *Coronograptus cyphus* Biozone, Llandovery. **G**. *Hercograptus introvertus* Melchin, 1999, GSC104936, fragment of proximal end with ancora umbrella and first theca, Cornwallis Island, Cape Manning, *Coronograptus cyphus* Biozone, Llandovery, after Melchin 1999. **H**. *Holoretiolites mancki* (Münch, 1931), ZPAL G.32/1, Baltic erratic boulder, Jarosławiec 48, inside view showing ancora with virgella (v). **I**. *Pseudoretiolites* sp., Cornwallis Island, Arctic Canada, ML64, GSC114223, *Lituigraptus convolutus* Biozone, Llandovery. **J**. *Holoretiolites mancki*, mature rhabdosome with lists of ancora umbrella and ancora sleeve partly integrated with thecal walls; well developed appendix, ZPAL G.28/1, Baltic erratic boulder, Jarosławiec 48, Poland, *Lobograptus progenitor* Biozone, Ludlow. Abbreviations: au, ancora umbrella; s, sicula; th, theca; v, virgella.

Ancora sleeve.—Prolongation of the ancora umbrella to enclose the thecae on both the obverse and reverse sides of the rhabdosome (Figs. 1, 5A, D). Formed of a fusellar wall (not usually preserved) with bandaged lists secreted on one or both sides. Contact with the thecal walls is only along the lateral apertural rod (septal bar) portions of the apertural lists of the thecae.

[Thecal] Aperture.—Opening at the mouth of the theca, bounded entirely by lists of the thecal framework (Fig. 5A). These comprise the transverse rods, lateral apertural rod, thecal lips and, in some genera, genicular lists.

Apertural list.—Comprises the lateral apertural rod, thecal lip, and transverse rod.

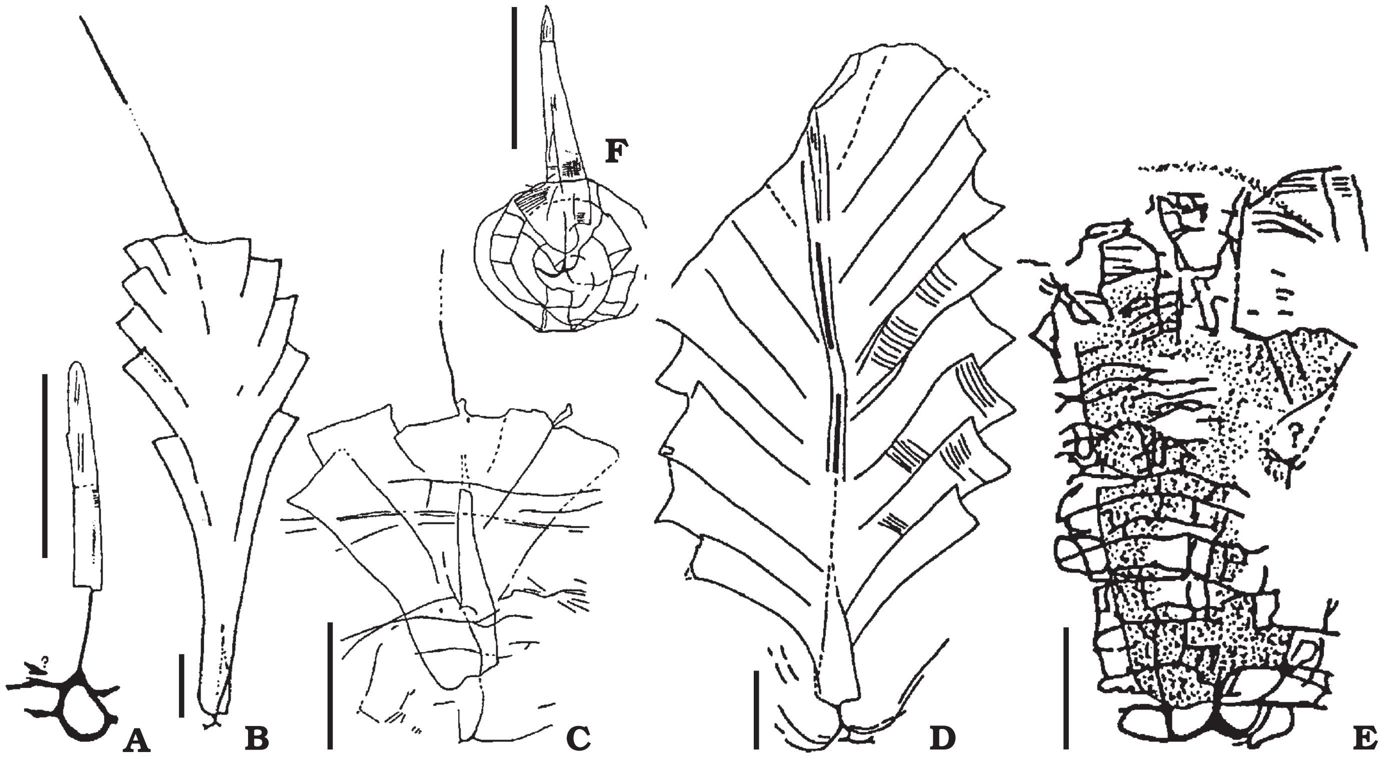


Fig. 4. **A**. *Akidograptus ascensus* Davies, 1929, young stage representing sicula and virgella with irregular ancora-like structures, CNIGR 201/12879, *Akidograptus ascensus–Parakidograptus acuminatus* Biozone, Ordovician. **B**–**F**. Examples of ancora-bearing taxa, showing various levels of ancora development, Llandovery, Silurian. **B**. *Pethalolithus krizi* Štorch, 1998, *Litiugraptus convolutus* Biozone, rhabdosome with small ancora, PS 781. **C**, **D**. *Petalolithus ovatoelongatus* (Kurck, 1882), *Spirograptus guerichi* Biozone. **C**. Reverse view of young rhabdosome with well-developed ancora, CNIGR 121/12879. **D**. Reverse view of incomplete rhabdosome with partly preserved ancora, CNIGR 116/12879. **E**. *Pseudorthograptus* (*Pseudorthograptus*?) sp. C, *Coronograptus cyphus* or *Coronograptus gregarius* Biozone, proximal fragment of rhabdosome with thecae enveloped in ancora and its extension, CNIGR 79E. **F**. *Pseudorthograptus* (*Pseudorthograptus*) *obuti* (Rickards and Koren', 1996), *Coronograptus gregarius* Biozone, sicula with the beginning of first theca and ancora umbrella, CNIGR Museum 162/12879. A, C–F after Koren' and Rickards 1996, B after Štorch 1998. Scale bars 1 mm.

Appendix.—Tubular structure developed at the distal end of rhabdosome formed of reticulum, sometimes incorporating nema (Fig. 3J). It may be regard as a terminal modified theca.

Clathrium. "Skeletal framework of rods (lists) composing rhabdosome, in some supporting reticulum or attenuated periderm" (Bulman 1970). Included in this definition are lists of both the thecal framework and the ancora sleeve.

Connecting rod.—Rod linking transverse rod and nema (Fig. 5B, E).

Genicular process.—Structure developed on the genicular list (Figs. 2A$_1$, A$_2$, 5D). Includes hoods, spines, spino-reticular processes.

Genicular list.—Transverse list marking the distal side of the thecal orifices in plectograptine retiolitids Fig. 5D). It marks the position of an abrupt bend in the thecal wall.

Geniculum.—Angular bend, generally abrupt, in the ventral thecal wall (Figs. 2A, B, 5D).

Lateral apertural rod.—That part of the thecal apertural list having connection with the lists of the ancora sleeve Fig. 5A, D). Originally named septal bar, in the belief that the list marked the conjunction between the interthecal septum and the lateral thecal walls.

Lip.—(Subapertural list. Lower apertural list). Ventral proximal list of thecal aperture, beyond the lateral apertural rod (septal bar) portion (Fig. 5A, D).

List.—Skeletal rod strengthening periderm by cortical bandages.

Mid-ventral list.—Centrally placed longitudinal list running from the transverse rod to thecal lip (Fig. 5A–D, G).

Nematularium.—Nema with distal development of vane, or a spiral structure.

Orifice.—Opening in the rhabdosome, partially or entirely rimmed by lists of the ancora sleeve: (a) thecal orifices are bounded by thecal lips and the pleural lists of the ancora sleeve (Fig. 2C1), and in the plectograptines by the genicular lists (Fig. 5D, G), (b) proximal ventral (pre th1^1 and th1^2) orifices are bounded proximally by the ancora umbrella, laterally by lists of the ancora sleeve, and distally by the lips or genicular lists of the first pair of thecae (Fig. 5C, G), (c) proximal lateral (obverse and reverse) orifices, are bounded proximally by the ancora umbrella, and laterally and distally by lists of the ancora sleeve (Fig. 5G; Bates and Kirk 1984: text-fig. 4), (d) stomata are more distal lateral orifices entirely bounded by lists of the ancora sleeve in genera such as *Stomatograptus* (Bates and Kirk 1984: text-fig. 4; 1997: fig. 6, pl. IV).

Outer ancora.—Additional lists outside of, but connecting with, the normal ancora (Fig. 6H).

Pleural list.—Literally, "side list". Lateral longitudinal lists of the ancora sleeve, connected to successive lateral apertural rods (septal bars) (Fig. 5A, D–G). This term has been used for the longitudinal lists which mark the corners of the rhabdosome, between the lateral walls and the ventral walls and orifices. In genera such as *Retiolites* these lists are entirely of ancora sleeve origin; in the plectograptines they are formed of a succession of lateral apertural rods of thecal origin, and lists of ancora sleeve origin.

Pustule.—Regularly placed low protuberance on the sheet fabric bounding bandages of lists, found only in retiolitids.

Reticulum.—Delicate irregular network of lists on the ancora sleeve and thecal wall.

Septal bar.—The term is now considered obsolete (see lateral apertural rod); originally named in the belief that the list marked the conjunction between an interthecal septum and the lateral thecal walls.

Stoma (stomata).—Lateral (obverse and reverse) orifices in the ancora sleeve, sometimes bounded by chimney-like reticular walls.

Thecal framework.—Regular network of lists, of thecal origin (i.e., excluding the lists of the ancora sleeve), in retiolitids (Fig. 5). Comprises nema, virga, virgella, transverse rods, lateral apertural rods, lips, connecting rods.

Transverse rod.—List at the base of a thecal wall, bearing a seam which marks the attachment to it of the fusellum of the wall (Fig. 5A, D–F). Homologous with the aboral list of non-retiolitid graptoloids, but, as the retiolitids have no interthecal septum, forms the distal part of the thecal aperture. In later retiolitids transverse rods are not present.

Virga.—That part of the nema to virgella list of retiolitids corresponding to the prosicula, formed of bandages deposited on the prosicular wall (Fig. 7A). It has a flattish inner side, and a convex outer side. The apex of the prosicula is marked by a change to the concentric construction of the nema (or cauda?); the prosicular to metasicular boundary by a change to the concentric construction of the virgella.

Zig-zag lists structure.—There are two types of zig-zag list structures. In Retiolitinae (e.g., *Retiolites*) the zig-zag is made by reverse mid-dorsal lists of the thecal framework, which link with the transverse rods and lateral apertural rods (Figs. 1A, 5A). In Plectograptinae the zig-zag is made by major lists of the ancora sleeve which connect with each other in the mid-dorsal area to give a "zigzag" appearance (Figs. 1B, 5G).

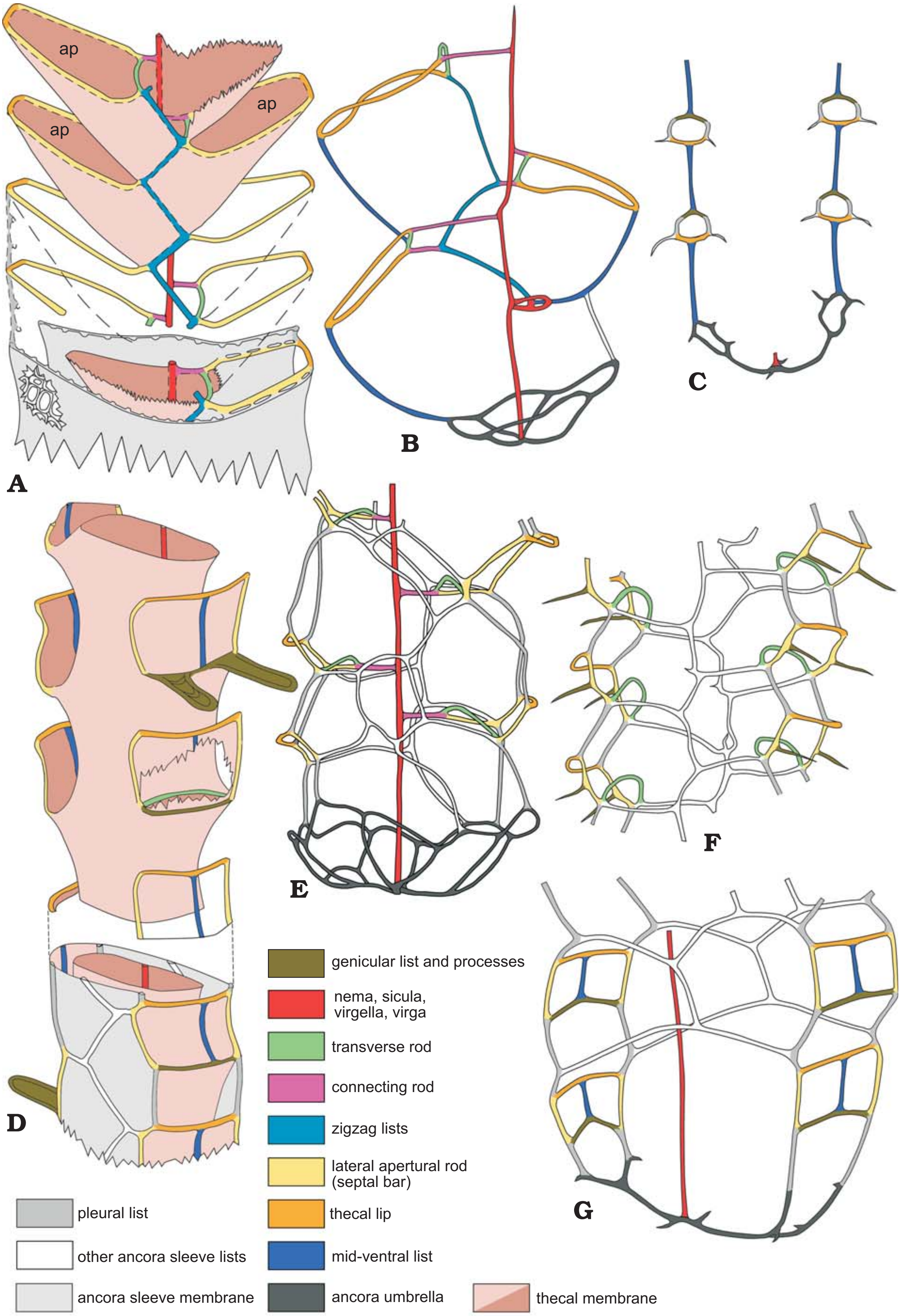
Ancora structure in Silurian diplograptoids

The ancora was defined by Bulman (1970: V8) as the "anchor-shaped initial growth stage of retiolitids, apparently formed of virgella with two distal bifurcations". Fortey and Cooper (1986) emphasized the significance of the development mode and structure of the proximal end as fundamental features for classification of higher level taxa within the Graptoloidea, an approach followed, and considerably expanded by Mitchell (1987). The ancora and its distal complex development appear to be such features.

It is now recognized that the true ancora is developed in all diplograptid Pattern I and I' forms and in retiolitid Pattern R (Melchin 1998). About the same time that the true ancora appeared, some irregular branching virgellar structures at the distal end of the virgella were developed in the Dimorphograptidae Elles and Wood, 1908, representing Pattern J (Melchin 1998). For example, the virgella of *Akidograptus ascensus* Davies, 1929 (Fig. 4A) is divided into triple spines, and that in *Parakidograptus acuminatus* (Nicholson, 1867) into irregular root-like branches (Štorch and Serpagli 1993). It is probable that the dimorphograptids and petalolithids were derived from some common ancestor with a particular synapomorph—the potential for ancora production (see Melchin 1998: text-fig. 5). These irregular structures are not considered to be homologues of the ancora.

Thus the first true ancora, beginning with a bifurcation (Figs. 3B, 6A), was developed in petalolithids representing Pattern I forms (Melchin 1998) probably late in the Rhuddanian Stage. Some evolution of the ancorae from small and simple to more complex is observed (Fig. 4), although there has been no detailed study of the petalolithid group focusing on the astogenetic and historic development of ancorae. A well developed ancora, sometimes with a spiral structure, is manifested in *Petalolithus* Suess, 1851 (Fig. 4B–D) and *Pseudorthograptus* Legrand, 1987 (Rickards and Koren' 1974; Bates and Kirk 1984; Koren' and Rickards 1996; Štorch 1985, 1998; Melchin 1998) as well as in *Cephalograptus* Hopkinson, 1869, (Štorch 1998), *Dimorphograptoides* Koren' and Rickards, 1996, and possibly in *Victorograptus* Koren' and Rickards, 1996 (Štorch 1998) and *Corbograptus* Koren' and Rickards, 1996. In *Petalolithus* and

Fig. 5. Diagrams of seven retiolitid genera showing morphology. Thecal framework lists and membrane are coloured; ancora sleeve lists and membrane in white and grey. **A**. *Retiolites* Barrande 1850. The upper part of the diagram shows the thecal framework only; ap, aperture. **B**. *Rotaretiolites* Bates and Kirk, 1992. **C**. *Plectodinemagraptus* Kozłowska-Dawidziuk, 1995. **D**. *Spinograptus* Bouček and Münch, 1952; diagram based on *Spinograptus praerobustus* Lenz and Kozłowska-Dawidziuk, 2002, the upper part of the diagram shows the thecal framework only. **E**. *Pseudoplectograptus* Obut and Zaslavskaya, 1983. **F**. *Cometograptus* Kozłowska-Dawidziuk, 2001. **G**. *Plectograptus* Moberg and Törnquist, 1909. →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mid-ventral list
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pleural list
other ancora sleeve lists
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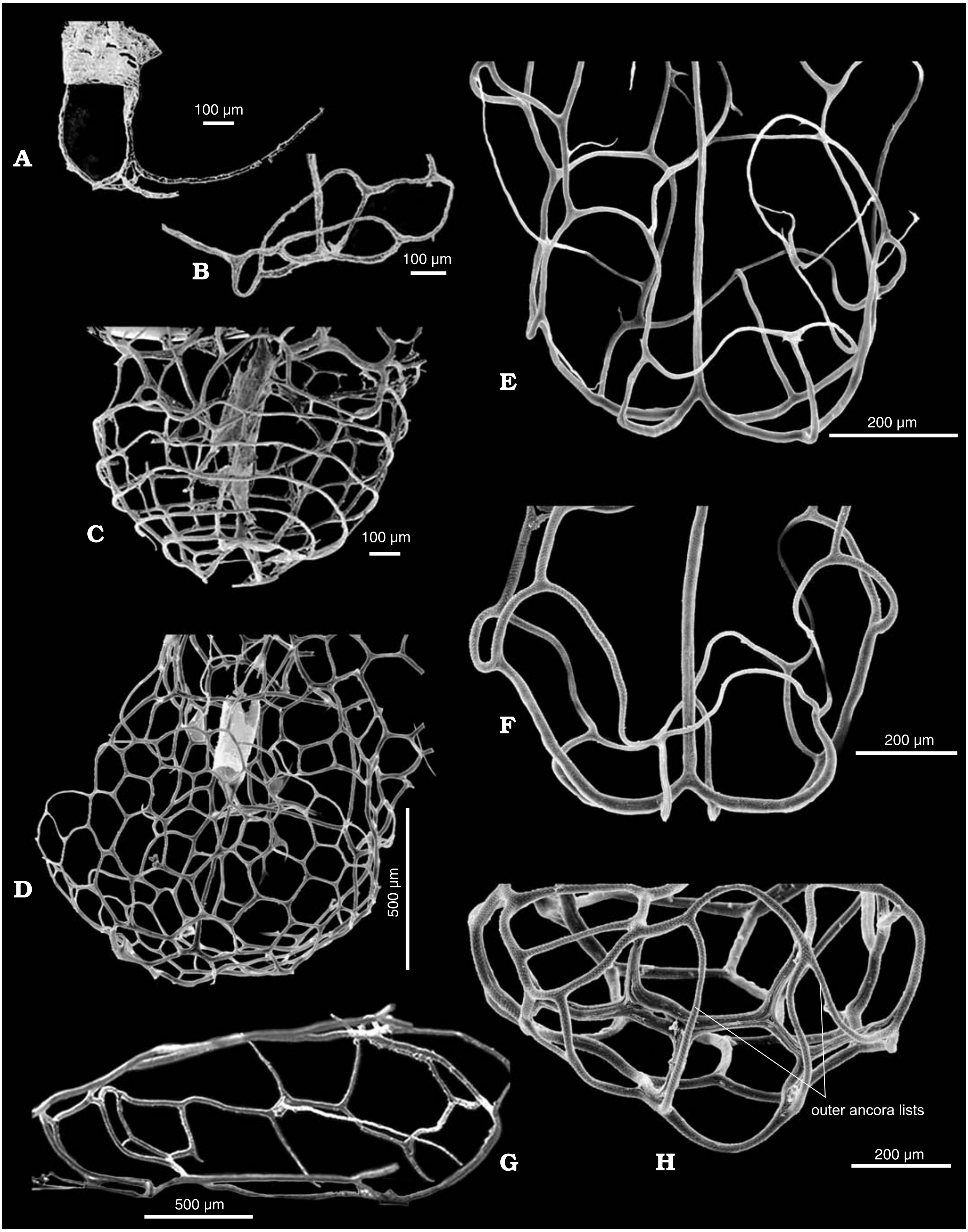
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Pseudorthograptus there is sometimes considerable distal growth beyond the ancora umbrella to the point of partial envelopment of the post-sicular region of the rhabdosome (e.g., Koren' and Rickards 1996; see Fig. 4C, E). In *Pseudorthograptus* the large ancora sometimes supports a continuous membrane. Melchin (1998) suggested that "*Pseudorthograptus* and possibly *Victorograptus* may show some connection between the ancora sleeve and distal thecal apertures". The most studied ancorate petalolithid *Hercograptus* Melchin, 1999, possesses an ancora umbrella connected to the thecae (Fig. 3G). Because the thecal walls are built in typical diplograptid mode, Melchin (1999) placed *Hercograptus* in the family Petalolithidae, although the apertural region of thecae is reduced to a meshwork of lists.

We regard the ancorate petalolithids (*Pseudorthograptus*, *Petalolithus*, *Cephalograptus*, *Dimorphograptoides*, *Victorograptus*, *Hercograptus*, *Corbograptus*) as a sister group with the retiolitids (see Melchin 1999: text-fig. 5), having generally the same astogenetic pattern, the only difference being in the connection of the ancora to thecal skeleton—Pattern R in retiolitids—as well as the modification of the thecal walls into a thecal framework. Some ancorate petalolithid such as *Pseudorthograptus* was probably the ancestor to the retiolitids involving two synapomorphic features: (1) presence of the ancora with some potential to develop the ancora sleeve structure, (2) potential for the reduction of the thecal wall to a thecal framework. The most studied petalolithid closely related to the retiolitids—*Hercograptus*—has an ancora umbrella, the beginning of ancora sleeve lists, and well developed thecal walls with lists on their distal parts. *Hercograptus* is regarded as an intermediate stage between the Petalolithidae and Retiolitidae (Melchin 1999). According to Melchin (1998) the Petalolithidae appears to be a paraphyletic group since the Retiolitidae derived from within it. For the above reasons, Kozłowska-Dawidziuk et al. (2003) tentatively proposed a radical departure, suggesting that the petalolithids and retiolitids be united into a single superfamily; i.e., the equivalent to the diplograptaceans. Since, however, the diplograptaceans are considered to be ancestral to both the petalolithids and retiolitids, we now consider that proposal to be untenable, although the strong phylogenetic relationship between the (ancorate) petalolithids and retiolitids unquestionably remains.

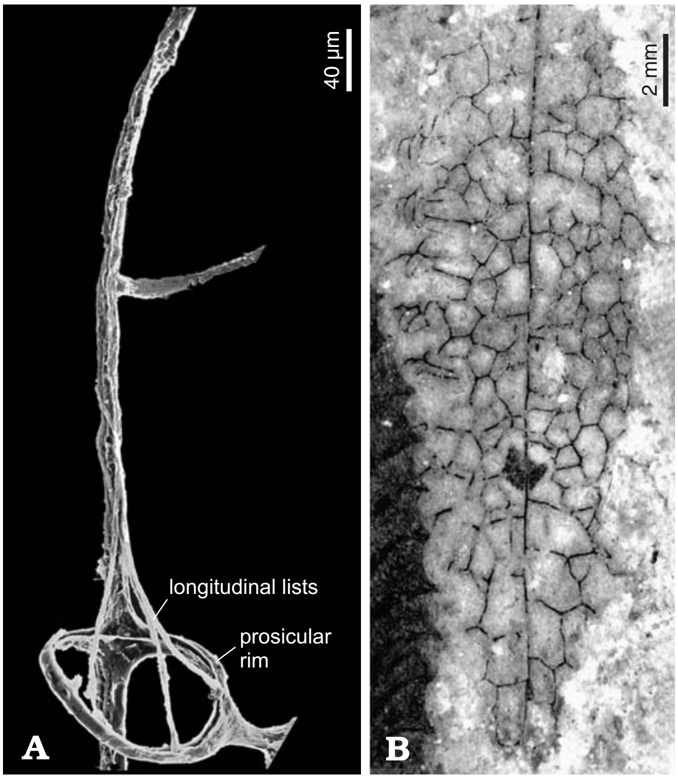

Fig. 7. **A**. Virga with prosicular rim and longitudinal rods. *Rotaretiolites exutus* Bates and Kirk, 1992, NMW 91.52G610, Osmundberget, Sweden, *Spirograptus turriculatus* Biozone, Llandovery, Silurian. **B**. *Dabashanograptus chengkouensis* Ge, 1990, holotype [NIGP21147(2b)], Sichuan, China, Llandovery, Silurian.

The next and most advanced stage of ancora development occurs in the Retiolitidae in the form of an ancora sleeve. Examination of growth stages shows that it appears to have grown in synchronicity with the thecal framework (e.g., Bates and Kirk 1997: fig. 53). The ancora sleeve is deeply integrated with the thecal skeleton, which in addition, is built mostly by lists similar to those of the ancora (see introduction). Thus, detailed ultrastructural studies are required to distinguish between the ancora sleeve and the thecal framework. These two features, the ancora sleeve and thecal framework, are fundamental for the retiolitids. The retiolitid ancora sleeve may form walls outside the thecal skeleton, making an additional internal environment. The ancora sleeve wall may possess orifices and some further structures such as large stomas or long spines on the obverse and reverse sides of the rhabdosome (Bates and Kirk 1997; Kozłowska-Dawidziuk 2001, 2002, 2004; Lenz and Kozłowska-Dawidziuk 2001).

Concluding, the retiolitid ancora structures, along with the thecal framework (both composed of bandaged lists), and originating from the petalolithids, are unique within the Graptolithina in having the ability to build a double-walled rhabdosome.

← Fig. 6. Silurian ancora types. **A**. Petalolithid. *Petalolithus minor* Elles, 1897, NMW 91.52G1464, limestone nodule, Kallholen, Sweden, *Pernerograptus argenteus* Biozone, Llandovery. **B**. Shallow spiralled, *Rotaretiolites* Bates and Kirk, 1992, NMW 91.52G284, Osmundberget, Sweden, *Spirograptus turriculatus* Biozone, Llandovery. **C**. Deep spiralled. *Pseudoretiolites* cf. *decurtatus* Bouček and Münch, 1944, NMW 91.52G853, Arctic Canada, *Demirastrites triangulatus* to *Spirograptus turriculatus* Biozone, Llandovery. **D**. Hexagonal mesh, *Stomatograptus* sp., GSC 10334, Llandovery. **E**. Gothograptid, *Gothograptus* sp., ZPAL G. 37/2, Blähal 1, Gotland, *Cyrtograptus lundgreni* Biozone, Wenlock. **F**. Paraplectograptid, *Paraplectograptus eiseli* (Manck, 1917), ZPAL G. 37/3, Proniewicze borehole, depth 550.8-551.7 m, *Cyrtograptus lundgreni* Biozone, Wenlock. **G**. Plectograptid, *Plectograptus robustus* (Obut and Zaslavskaya, 1983), ZPAL G.37/4, Bartoszyce borehole, depth 1627.0 m, Wenlock. **H**. Outer ancora, *Neogothograptus purus* Kozłowska-Dawidziuk, 1995, ZPAL G. 37/5, Baltic erratic boulder 46, Jarosławiec, Poland, *Lobograptus scanicus* Biozone, Ludlow. A–C after Bates and Kirk 1992, G after Kozłowska-Dawidziuk 2002.

Table 1. Matrix for 24 retiolitid genera and 26 characters. For list of characters see Appendix 1.

	01	**02**	**03**	**04**	**05**	**06**	**07**	**08**	**09**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**
Pseudorthograptus	0	0	0	0	0	0	0	0,2	0	0	0	0	0	1	0	1	0	0	0	0	0,2	2	0	1	0	0
Hercograptus	1	1	0	1	0	?	1	0	?	0	0	0	0	0	1	1	0	?	0	?	2	2	0	1	?	0
Baculograptus	4	2	4	6	1	4	3	?	2	2	1	0	0	0	7	3	1	1	0	4	0	1	2	2	2	1
Cometograptus	5	2	7	6	1	2	1	0	2	0,2	2	2	0,1	1	2	3	1,2	1	1	2	1	1	1	1	2	1
Dabashanograptus	?	2	2	2	0	4	?	2	1	0	0	0	0	0	1	0	0	0	0	?	?	2	?	1	?	1
Doliograptus	5	2	4	5	1	4	3	?	2	2	0	0	1	0	2	3	0	1	0	2	2	2	2	1	2	1
Eisenackograptus	4	2	7	3	2	5	4	0	2	0,2	1	0	0,1	0	7	3	0	1	0	4	2	0	1	1,2	1	1
Gothograptus	4	2	7	4	1	4	3	1	2	2	1	0	1	0	7	3	3	1	0	4	0	0	2	1,2	2,3	1
Holoretiolites	5	2	7	1	1	4	3	0	2	2	1	0	1	0	6	2	1	1	0	4	0	0	2	2	4	1
Neogothograptus	5	2	7	1	1	4	3	?	2	2	1	0	1	0	6	3	3	1	0	4	0	0	2	2	4	1
Papiliograptus	5	2	4	5	1	4	3	?	2	2	0	0	1	0	2	3	3	1	0	2	0	0	2	1	4	1
Paraplectograptus	5	2	5	2	3	0	1	1,2	1	0,2	0	0	0	0	5	4	0	2	0	2	1	1	1	1	2	1
Plectodinemagraptus	6	2	6	5	1	4	3	?	2	2	0	0	1	0	8	2	1	1	0	1	1	1	2	2	4	1
Plectograptus	6	2	7	1	1	4	3	0	2	2	0	0	1	0	2	3	1	1	0	3	0	0,1	2	1	4	1
Pseudoplectograptus	5	2	5	2	3	0	1	1	1	0,2	0	0	0	1	2	4	0	2	0	2	1	1	1	1	2	1
Pseudoplegmatograptus	7	2	2	2	0	2	2	2	1	0	0	1	0	0	1	0	0	0	0	1	2	2	1	0	2	1
Pseudoretiolites	1	2	1	2	0	1	2	2	1	0	0	1	0	0	1	0	0	0	0	1	2	2	1	1	1	1
Retiolites	3	2	5	2	0	0	1	2	1	0	0	0	0	0	1	0	0	0	0	2	0	2	1	0	1	1
Rotaretiolites	2	2	3	2	3	1	0	2	1	1	0	0	0	0	0	1	0	2	0	0	0	2	1	2	0	1
Sagenograptus	5	2	7	?	3	3	5	1	2	2	0	0	1	0	1	3,4	0	1	0	2	0	1	1	2	2	1
Semiplectograptus	6	2	6	5	1	4	3	?	2	2	0	0	1	0	4	2	1	1	0	3	1	1	2	2	4	1
Sokolovograptus	5	2	5	1	3	0	3	0	2	2	0	0	0	0	3	4	0	1	0	2	1	1,2	2	1	2	1
Spinograptus	5	2	5	6	1	4	3	0	2	2	1	0	1	0	2	3	4	1	0	2	0	1	2	1	2	1
Stomatograptus	3	2	2	2	0	0	1	2	1	0	0	1	0	0	1	0	0	0	0	2	0	2	1	0	1	1

Phylogenetic analysis of the retiolitids

The first attempt at phylogenetic analysis of the retiolitids using a cladistic approach was that of Lenz and Melchin (1997). That study, involving 16 taxa and two parataxa (i.e., informally identified taxa, tentatively using the names of existing taxa), and 22 characters, generally supported the twofold division of the retiolitids into the Retiolitinae and Plectograptinae. Since then, a great deal more has been learned about the overall morphology of the retiolitids; in particular and among others, there is now a far better understanding of their early astogenetic stages, the relationship and distinguishing features of the ancora sleeve and the thecal framework, and the internal development and makeup of the thecae, and these have strongly influenced the choice of characters. Added to this, a number of new genera from the late Wenlock and early Ludlow have been erected (Kozłowska-Dawidziuk 1995, 2001; Lenz and Kozłowska-Dawidziuk 2001, 2002), whereas several species previously assigned to the genus *Agastograptus* Obut and Zaslavskaya (1983) were later recognized by Kozłowska-Dawidziuk (2002) to belong to either *Cometograptus*, *Spinograptus*, *Plectograptus*, or *Neogothograptus*.

This study, involving 24 genera, was based on isolated, uncompressed material, except for the genus *Dabashanograptus* Ge, 1990 (Fig. 7B). The parataxa "*Rotaretiolites*" and "*Paraplectograptus*", used by Lenz and Melchin (1997), were not used in this study, since these warrant future detailed study. Cladistic parsimony analyses (unweighted and unordered), involving 26 characters, were carried out using PAUP 4.0 (Swofford 2000) and MacClade 4 (Maddison and Maddison 2001). *Pseudorthograptus*, particularly as exemplified in, but not exclusively restricted to, the features in *P. inopinatus* (Bouček, 1944), is used as the outgroup taxon. Since *Pseudorthograptus* has a very well-developed ancora it is considered to represent the generalized ancestral form for the retiolitids. *Hercograptus* on the other hand appears to represent a transitional form (Melchin 1999). The characters are listed in the same order as they appear in the data matrix table (Table 1).

Discussion of the cladograms

For this study, the size of the matrix prompted a more thorough analysis than provided through the default heuristic search. Thus, in the heuristic search option, the stepwise addi-

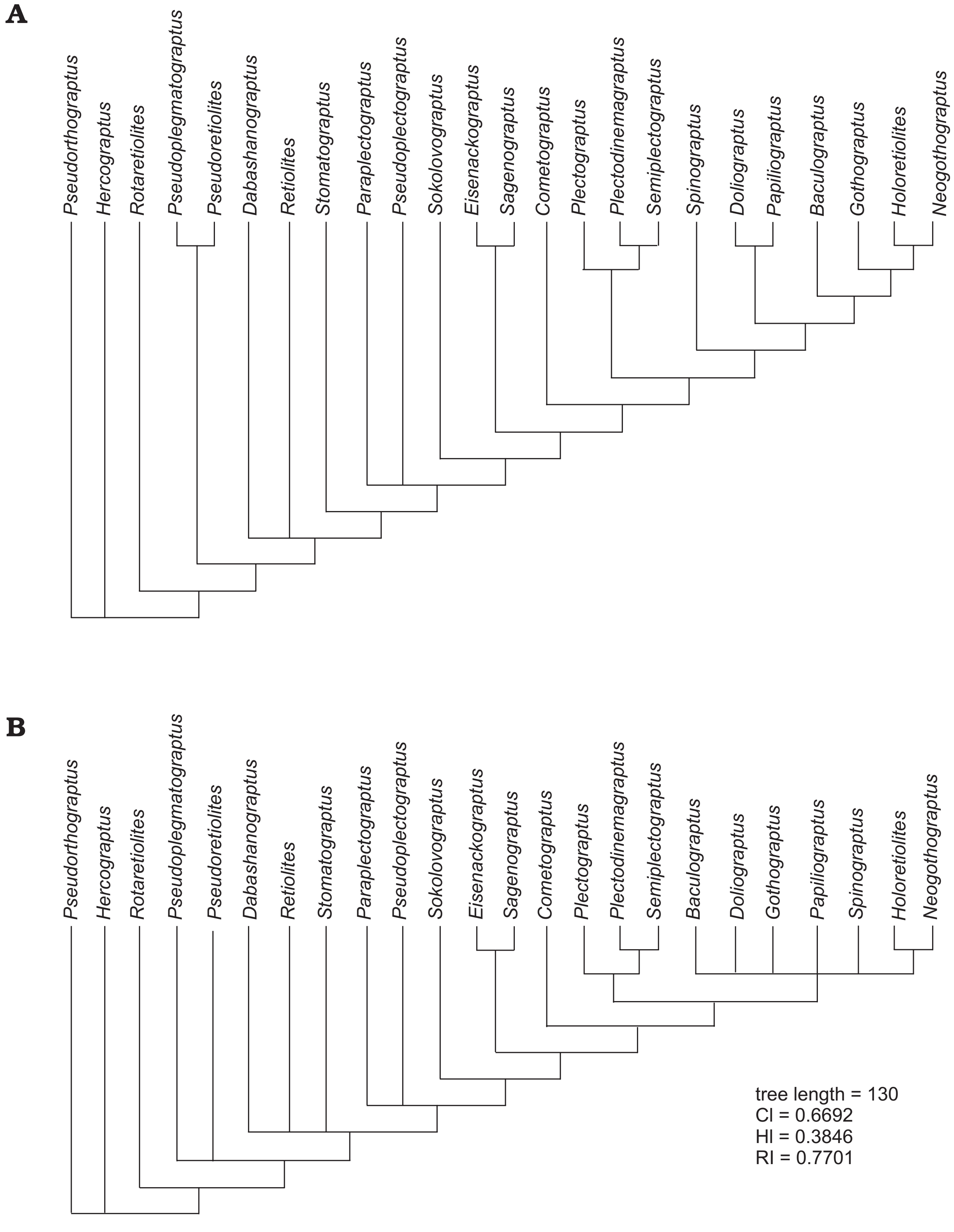

Fig. 8. Consensus trees. **A**. Strict consensus tree. **B**. 50% Majority-rule consensus tree for 100 trees. Abbreviations: CI, Consistency Index; HI, Homoplasy Index; RI, Retention Index.

tion option with 100 representatives, and in the parsimony settings, the multistate taxa and "polymorphism" options were chosen. It was felt that these modifications would provide a much more thorough search for the most parsimonious trees and, in fact, the resulting trees showed some modest differences from those produced in the default search. The PAUP analysis, scoring characters as unordered and unweighted and designating *Pseudorthograptus* as the outgroup, produced 100

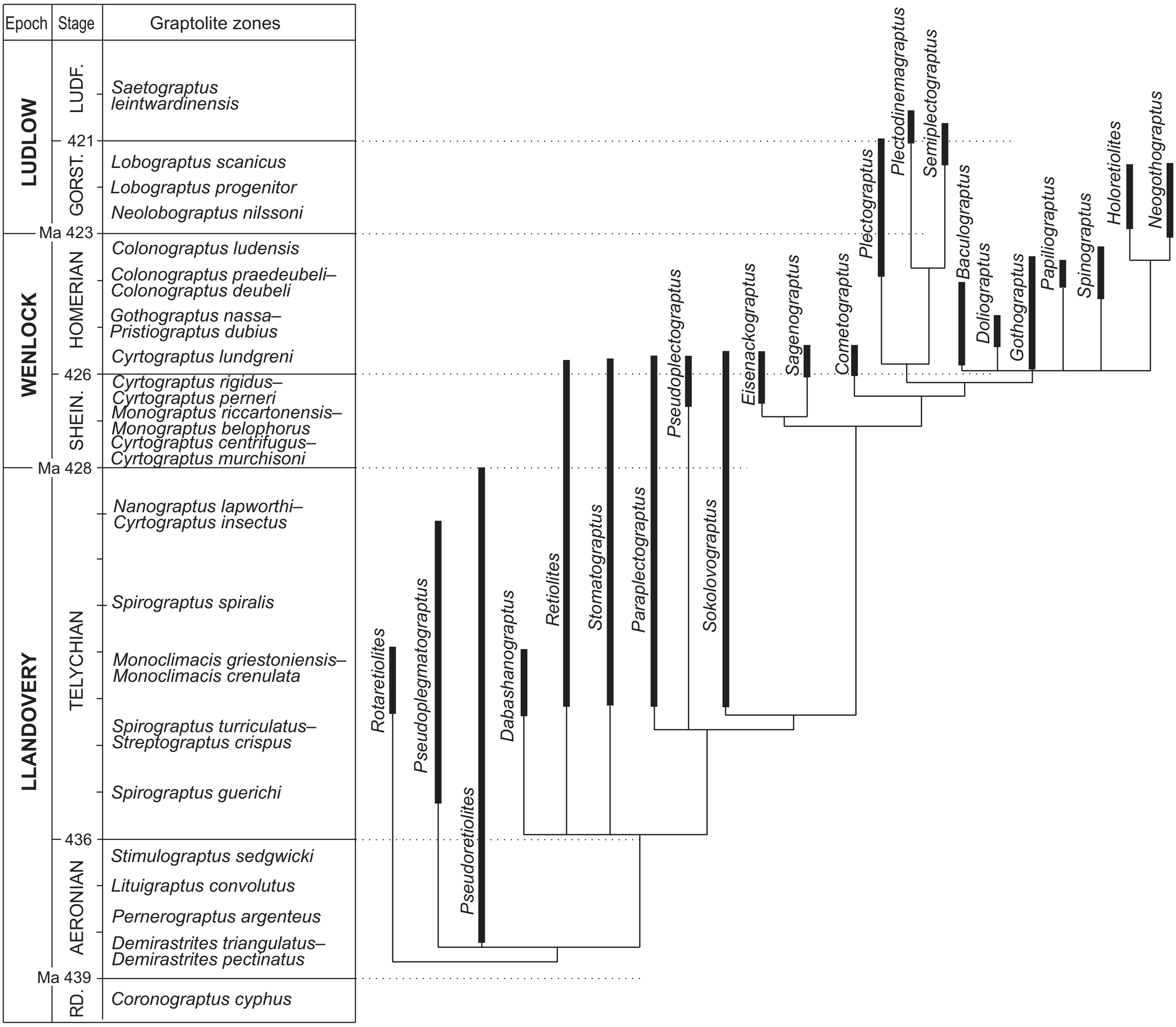

Fig. 9. Evolutionary tree of the family Retiolitidae calibrated against the graptolite biostratigraphic record, using the Strict Consensus tree as a template. The biozonal scheme is that used in the Generalized Graptolite Zonation of Koren' et al. (1996). Abbreviations: GORST., Gorstian; LUDF., Ludfordian; RD., Rhuddanian; SHEIN., Sheinwoodian.

arbitrarily selected trees with the following descriptions: Tree length = 130, Consistency index = 0.6692, Retention index = 0.7701, Homoplasy index = 0.3846), the first two representing moderately rigorous resolutions, and the third indicating only modest homoplasy. The resulting strict consensus tree and majority rule 50% consensus tree are shown in Fig. 8, and in neither case is the twofold division into retiolitine and plectograptine subfamilies clearly displayed, a situation also true of all of the 100 trees produced through the extended heuristic analysis. The position of *Rotaretiolites* Bates and Kirk, 1992 is ambiguous in that it is shown in a more primitive and in a paraphyletic position relative to the other retiolitines (*Retiolites* Barrande, 1850; *Stomatograptus* Tullberg, 1883; *Dabashanograptus* Ge, 1990; *Pseudoplegmatograptus* Přibyl, 1948; and *Pseudoretiolites* Bouček and Münch, 1944). However, *Rotaretiolites* is known only on the basis of very few and, perhaps, immature specimens, so that its complete morphology might not be understood.

On the other hand, *Pseudoretiolites*, the earliest known retiolitid and considered by us to most probably represent the stem group, is shown to be closely linked to *Pseudoplegmatograptus.* The remaining retiolitines, *Retiolites, Stomatograptus*, *Dabashanograptus* are shown in a polytomous relationship (i.e., several or more taxa rooted on the same node) which is reasonable, since we consider the three taxa to be closely related, even though the full biostratigraphic range

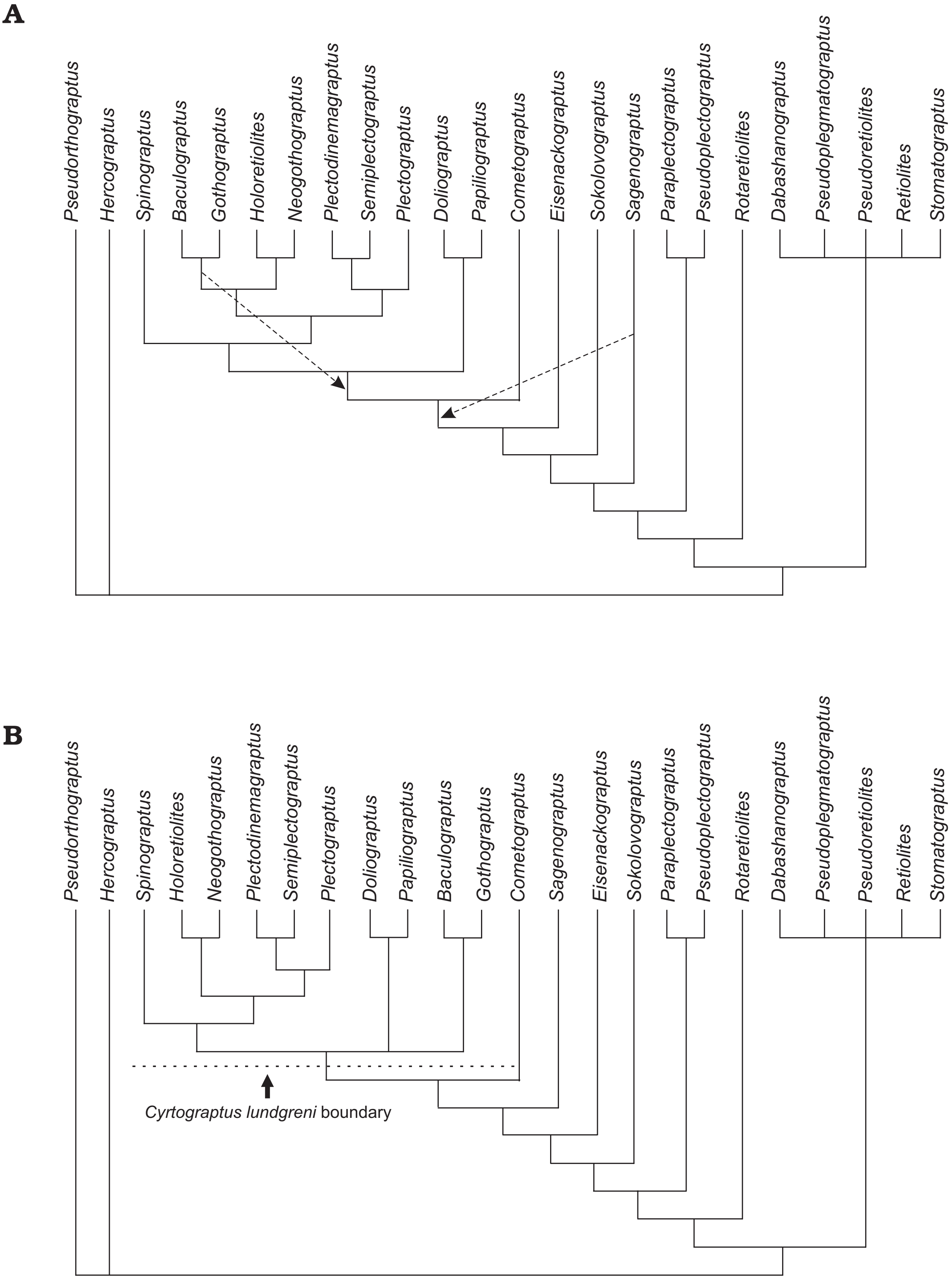

Fig. 10. **A**. MacClade default tree with a tree length of 135 with arrows showing movement of nodes to new positions. **B**. Modified MacClade tree with tree length also of 135 and the one showing much better agreement with the biostratigraphic ranges of (principally) the plectograptines. Specifically, the right-hand arrow shows the shifting of the *Sagenograptus* node to a position immediately below the *Cometograptus* node, and left-hand arrow shows the shifting of the *Baculograptus* and *Gothograptus* node to a position indicated by the head of the arrow, both moves resulting in derived tree B, but still retaining a tree length of 135 as in the default tree.

and morphological details of *Dabashanograptus* are not known. It should be pointed out, however, that Llandovery and early Wenlock retiolitids have received relatively few detailed studies in comparison with those of younger plectograptine retiolitids, and future detailed studies are almost certain to turn up new taxa (see for example, Lenz and Melchin 1987 who tentatively recognized two new parataxa in the Llandovery).

Paraplectograptus Bouček and Münch, 1948 and *Pseudoplectograptus* Obut and Zaslavskaya, 1983 are shown in a bitomous relationship, undoubtedly due to their possession of intergradational morphologies, and *Sokolovograptus* Obut and Zaslavskaya, 1983 is shown as a sister group to the more "advanced" and biostratigraphically much higher plectograptines. *Paraplectograptus* and *Sokolovograptus*, both possessing pustulose lists and a much enlarged central canal (compared with older or other contemporary taxa), are considered to be the earliest members of the plectograptine subfamily. *Eisenackograptus* Kozłowska-Dawidziuk, 1990 and *Cometograptus* Kozłowska-Dawidziuk, 2001 are shown in an intermediate position between *Sokolovograptus* and the much younger plectograptines, a position considered by us to be reasonable, since they pre-date the *Cyrtograptus lundgreni* extinction event. *Sagenograptus* Lenz and Kozłowska-Dawidziuk, 2001 appears in a somewhat anomalous position with *Eisenackograptus*; however, it is a pre-extinction form and it does possess some primitive characteristics such as a complete thecal ventral list on theca 1^1, and glyptograptid profile thecae.

The remainder of the plectograptine group, representing late Homerian and younger forms, is portrayed in unsatisfactory and mostly polytomous arrangements, although the group does form a fairly distinct clade. The clade is divided into two subclades: a *Plectograptus* subclade formed of three genera (*Plectograptus* Moberg and Törnquist, 1909; *Plectodinemagraptus* Kozłowska-Dawidziuk, 1995; and *Semiplectograptus* Kozłowska-Dawidziuk, 1995) and a second *Spinograptus* subclade of seven genera. It appears to be reasonable that *Plectograptus* might have been ancestral to *Plectodinemagraptus* and *Semiplectograptus*, but the position of *Gothograptus* Frech, 1897 in the *Spinograptus* subclade is most troubling since it occurs in a very derived position (particularly in the 50% Majority-rule consensus tree). *Gothograptus* is the only retiolitid genus known to range from the lower Homerian into the upper Homerian and, therefore, to survive the *Cyrtograptus lundgreni* extinction event, making it the ideal candidate to be ancestral to all subsequent plectograptines. In summary, the analysis provides some modest support for the division of the Retiolitidae into the retiolitine and plectograptine subfamilies.

An evolutionary tree has been produced by linking the strict consensus tree with the biostratigraphic ranges of the retiolitids (Fig. 9). The evolutionary tree shows some agreement relative to the ranges of the retiolitines, less so to that of the plectograptines, particularly those noted above. In particular, there is a considerable ghost lineage in the Aeronian, and a very expanded one through the Telychian and most of the Wenlock. It is eminently possible that taxa such as *Eisenackograptus*, *Sagenograptus*, and *Cometograptus* may have originated somewhat earlier than presently known. The appearance of the remainder of the plectograptine group during, or prior to, the early Homerian and thus prior to the *Cyrtograptus lundgreni* extinction event seems to us to be untenable since, as noted above, it is widely recognized that only *Gothograptus* survived the extinction event (Kozłowska-Dawidziuk 2001; Lenz and Kozłowska-Dawidziuk 2001). Nevertheless, the evolutionary tree shows four evolutionary "bursts": a modest one during the Aeronian, a prominent one in the early Telychian, a moderate one in the late Sheinwoodian and early Homerian, and a final and drawn-out one following recovery from the *Cyrtograptus lundgreni* extinction event and extending into the Ludlow.

The single default tree (Fig. 10A) generated by MacClade was utilized for its ability of being able to move nodes while continuously showing tree lengths, the object being to see which nodes could be moved without increasing the tree length. This is particularly useful when working with stratocladistics; that is, the linking of the cladogram with the biostratigraphic positions of the various taxa. The default tree, having a tree length of 135, shows *Sagenograptus* in a more primitive position relative to *Sokolovograptus* and *Eisenackograptus*, whereas *Gothograptus* (along with *Baculograptus* Lenz and Kozłowska-Dawidziuk, 2002) is placed in a very derived position. However, by shifting the *Sagenograptus* node to just below *Cometograptus*, and that of *Gothograptus* and *Baculograptus* to a more basal position, shown by the arrows, results in a tree (Fig. 10B) still with a length of 135, but one that is much more in line with the biostratigraphic ranges of the plectograptines and, with the exception of *Baculograptus*, fully recognizes the effects of the *Cyrtograptus lundgreni* extinction event. Specifically, it shows *Gothograptus* (along with *Baculograptus*) as a sister group, and probably ancestral to, the remaining younger post-extinction retiolitids. By comparison, the movements of any other nodes resulted in increased tree lengths, and were thus unacceptable.

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Appendix 1

List of characters and their character states, where 0 is considered the plesiomorphic state:

1. ancora umbrella: 0, petalolithid type; 1, deep spiralled; 2, small shallow spiralled; 3, spiralled with hexagonal meshwork; 4, hexagonal meshwork; 5, *Gothograptus* type; 6, *Paraplectograptus* type; 7, *Plectograptus* type.
2. thecal development: 0, fuselli of normal graptolite mode; 1, fuselli proximally; lists only at distal part of theca; 2, thecal framework.
3. sicula preservation and virga: 0, complete; 1, prosicula and part of metasicula; 2, prosicula only; 3, virga and prosicular ring; 4, virga only; 5, usually virga; prosicula rare; 6, not preserved; 7, virga and prosicular ring rarely.
4. nema position: 0, may be attached to partially developed median septum; 1, free; 2, attached to thecal wall; 3, attached to thecal wall and ancora sleeve distally; 4, attached to thecal wall and ancora sleeve throughout; 5, free, rarely attached to thecal wall and ancora sleeve distally.
5. thecal profile: 0, orthograptid everted; 1, orthograptid introverted; 2, climacograptid; 3, pseudoglyptograptid; 4, glyptograptid everted.
6. mid-ventral list: 0, none developed; 1, complete from transverse rod to thecal lip; 2, present in distal part of theca, attached only to thecal lip; 3, present in distal part of theca, attached only to thecal lip, sometimes completely developed in first theca; 4, attached from genicular list to thecal lip.
7. ancora sleeve development. 0, none (not developed); 1, one layer with seams outside on both sides of thecae; 2, probably two layers on each side of thecae: one with seams outside, second with seams inside; 3, one layer with seams inside on both sides of thecae.
8. sicula length: 0, long or short (< 1.0, > 2 mm); 1, short (< 1.0 mm); 2, medium (1.0–1.9 mm); 3, long (> 2.0 mm).
9. connecting rod: 0, no; 1, yes; 2, lost.
10. micro-ornamentation: 0, finely striated; 1, parallel ridges; 2, pustules well-developed.
11. appendix: 0, no; 1, yes; 2, some species.
12. stomata: 0, no; 1, yes; 2, sometimes.
13. genicular list: 0, no; 1, yes.
14. ancora sleeve structures: 0, no; 1, mesh (no clathrium); 2, mid dorsal zigzag, reticulum mesh; 3, reticulum and sometimes horizontal clathrial lists on distal part; 4, mid dorsal zigzag no reticulum; 5, zigzag and reticulum sometimes; 6, gently inclined lists with reticulum sometimes; 7, gently inclined lists with reticulum; 8, lost.
15. lateral apertural rod (septal bar): 0, not present; 1, horizontally oriented; 2, vertically oriented; 3, inclined; 4, partial; 5, curved.
16. genicular processes: 0, no geniculum, no processes; 1, geniculum with no processes; 2, paired spines; 3, singular hood; 4, paired spino-reticular processes.
17. common canal: 0, narrow; 1, wide; 2, medium.
18. lateral proximal orifices: 0, none; 1, small, taller than wide; 2, small, wider than tall; 3, large, taller than wide.
19. ancora umbrella width versus distal part of rhabdosome width: 0, narrower; 1, approximately equal; 2, wider.
20. transverse rods: 0, none; 1, yes; 2, not preserved.
21. size of rhabdosome: 0, > 20 mm; 1, 10–20 mm; 2, 5–10 mm; 3, < 5 mm.
22. proximal ventral orifices: 0, no orifice; 1, oriented latero-distally; 2, laterally; 3, distally; 4, latero-proximally.
23. interthecal septum: 0, yes; 1, no.
24. virga: 0, no; 1, yes; 2, not preserved.
25. presence outer ancora: 0, no; 1, yes.
26. genicular presence: 0, not developed; 1, yes.