Silurian retiolitid graptolites: Morphology and evolution

DENIS E.B. BATES, ANNA KOZŁOWSKA, and ALFRED C. LENZ


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 the 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 Retiolitinæ and Plectograpitinæ. 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 Retiolitinæ and Plectograpitinæ, 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 Retiolitinæ, as the subfamily Archiretiolitinæ (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-
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 ancora 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, *Colonoograptus praedeubeli*–*C. deubeli* biozone, Wenlock. A. ZPAL G.37/1; A1, stereopair of exterior proximal end showing ancora, well-preserved sicula, base of theca 11 (directly below sicula), double fusellar walls, thecal apertures and spino-reticular genicular processes; A2, reverse view showing ancora and ancora umbrella, and partially preserved thin fusellar layer that fills in space between the zigzag (bandaged) lists; A3, Proximal-lateral stereopair view. B. Stereopair showing sicula, theca 12 on lower right side of sicula, aperture of theca 12, 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 Stenkyrkheus fyr, Gotland, Sweden, Lower Visby Marl, uppermost Llandovery; C1, ventro-lateral view; C2, view to the inside of rhabdosome showing sicula and thecal walls. Abbreviations: as, ancora sleeve; s, sicula; th, theca.
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.
Appendix.—Tubular structure developed at the distal end of rhabdosome formed of reticulum, sometimes incorporating nema (Fig. 3J). It may be regarded 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, A2, 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).

Nematarium.—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 and th1) 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 ancorula (Fig. 5G; Bates and Kirk 1984: text-fig. 4), (d) stoma 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, virgella, 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 nema (or cauda?); the prosicular to metasicular boundary by the ancora sleeve which connect with each other in the mid-dorsal area to give a “zigzag” appearance (Figs. 1B, 5G).

**Virga.**—That part of the nema to virgella list of retiolitids corresponding to the prosicula, formed of bandages deposited on the prosicula 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 Graptoloida, 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 (Storch and Serpagli 1993). It is probable that the dimorphograptids and petalolithids were derived from some common ancestor with a particular synapomorphy—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; Storch 1985, 1998; Melchin 1998) as well as in *Cephalograptus* Hopkinson, 1869, (Storch 1998), *Dimorphograptoides Koren’* and Rickards, 1996, and possibly in *Victorograptus Koren’* and Rickards, 1996 (Storch 1998) and *Corbograptus Koren’* and Rickards, 1996. In *Petalolithus* and...
**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 ancora 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 ancora 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 ancora 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 Diplograptidae derived from within it. 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 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.
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-
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. 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.
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 (*Retio−

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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* Příbyl, 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 polytymous 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 paratax 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 *Cometo−

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References


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 with 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 theca; 2, probably two layers on each side of theca: one with seams outside, second with seams inside; 3, one layer with seams inside on both sides of theca.

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, approximately equal; 2, wider; 3, wider than well.

18. lateral proximal orifices: 0, none; 1, small, taller than wide; 2, small, wider than tall; 3, large, taller than wide.

19. ancora umbilical 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. intertheal 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.