

Evolution of retiolitid graptolites—a synopsis

ANNA KOZŁOWSKA-DAWIDZIUK



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Twenty million years of retiolitid evolution reflect environmental changes, the most severe being the Silurian *Cyrtograptus lundgreni* Event. Five biostratigraphically and morphologically constrained retiolitid faunas are distinguished and characterized according to their rhabdosomal modifications: (1) the oldest and long-ranging Llandovery group of mostly large and morphologically complex rhabdosomes, (2) the less diverse Telychian-Sheinwoodian group, (3) the *Cyrtograptus lundgreni* Biozone varied group of intermediate size, and two short-ranged (4) late Homerian, and (5) early Ludlow groups with small rhabdosomes. Although the evolutionary history of retiolitids was complex and not linear, a common tendency toward reduction of rhabdosome size in most lineages is observed. The greatest reduction in both number and volume of thecae, and in skeletal elements is demonstrated in the *Gothograptus* and *Plectograptus* faunas. Contrary to the thecal decrease, a distinctive increase of sicula size is observed in retiolitids. Two types of colonies are distinguished: L-colonies with a small sicula and numerous large thecae of similar size, and S-colonies with a long sicula and a few, small thecae. These changes imply modification of the soft body: an increase in siculozoid length and a decrease in the size of the zooids. Thus, the siculozoid probably produced great amounts of morphogen inhibiting zooid growth. In consequence the phenomenon of colony reduction occurred. The most extreme stages of rhabdosome reduction in Ludlow retiolitids can be seen in *Plectodinemagraptus gracilis* of the *Plectograptus* lineage and in the new species *Holoretiolites helenaewitoldi*, possibly representing the last stage of skeletal reduction in the *Gothograptus* lineage; the next hypothetical stage would be its total loss. The sicula length of *Holoretiolites*, about 2 mm, is reported herein for the first time.

Key words: Graptoloidea, Retiolitidae, Silurian, Ludlow, rhabdosome reduction, *Holoretiolites*.

Anna Kozłowska-Dawidziuk [akd@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

Introduction

Retiolitids were planktic graptolites that evolved through about 20 Ma of the Silurian, from the Aeronian to the Ludfordian (Fig. 1). During that time, their diversity increased and decreased, and only sometimes developed in parallel with those of the better known patterns seen in an estimated eleven monograptid-based extinction events (Melchin et al. 1998). Specifically three extinction events strongly affected the retiolitids, these being the *Cyrtograptus lapworthi* Event, the *Cyrtograptus lundgreni* Event and the *Saetograptus leintwardinensis* Event (Fig. 1). During the first event, *Pseudoplegmagraptus* and *Pseudoretiolites* appear to have become extinct, while other taxa *Paraplectograptus*, *Sokolovograptus*, and *Retiolites* continued unchanged. The next event, the *Cyrtograptus lundgreni* Event, however, had a profound effect on both retiolitids and monograptids, resulting in the extinction of more than 90% of the species (Lenz and Kozłowska-Dawidziuk 2001). This was followed by the recovery and expansion during the subsequent late Wenlock and early Ludlow and, finally, the retiolitids became extinct during the *S. leintwardinensis* Event (Urbanek 1993; Kozłowska-Dawidziuk 1995; Melchin et al. 1998).

The retiolitids are an extraordinary group of late-appearing diplograptids having unique skeletons built of thecal and ancora sleeve walls, both represented by lists, although the

true nature of the retiolitid skeleton was not recognized for a long time. The ancora sleeve probably provided some functional ability to survive crises during times when other diplograptids became extinct. Studies of retiolitids progressed slowly during the 19th to mid-20th century, principally those by Barrande (1850), Törnquist (1887), and Bouček and Münch (1944) who described only flattened material. While this preservation makes graptolites difficult to work with taxonomically, it provides important information on retiolitid overall diversity, geographic distribution, endemism, and biostratigraphy, but also contributes to the recognition of delicate structures such as long nematularia, or long spines, both of which are destroyed in the recovery of isolated specimens. Flattened retiolitids are widely known from, e.g., the Barrandian region (Bouček and Münch 1944, 1952; Kozłowska-Dawidziuk et al. 2001), China (Huo 1957; Lenz et al. 1996; Liu 1985; Ge 1990; Zhang and Lenz 1997; Ni and Lin 2000), Central Asia (Koren' 1994), Arctic Canada (Lenz and Melchin 1991, Lenz 1995), and Australia (Rickards et al. 1995). Studies of isolated forms commenced much later, see for example Münch (1931), Eisenack (1951), and Obut and Zaslavskaya (1976, 1983).

Among the recent zooplankton the most abundant and diverse crustacean groups are the copepods and euphausiids, which are widely adapted to midwater marine environments. They are active swimmers capable of considerable vertical

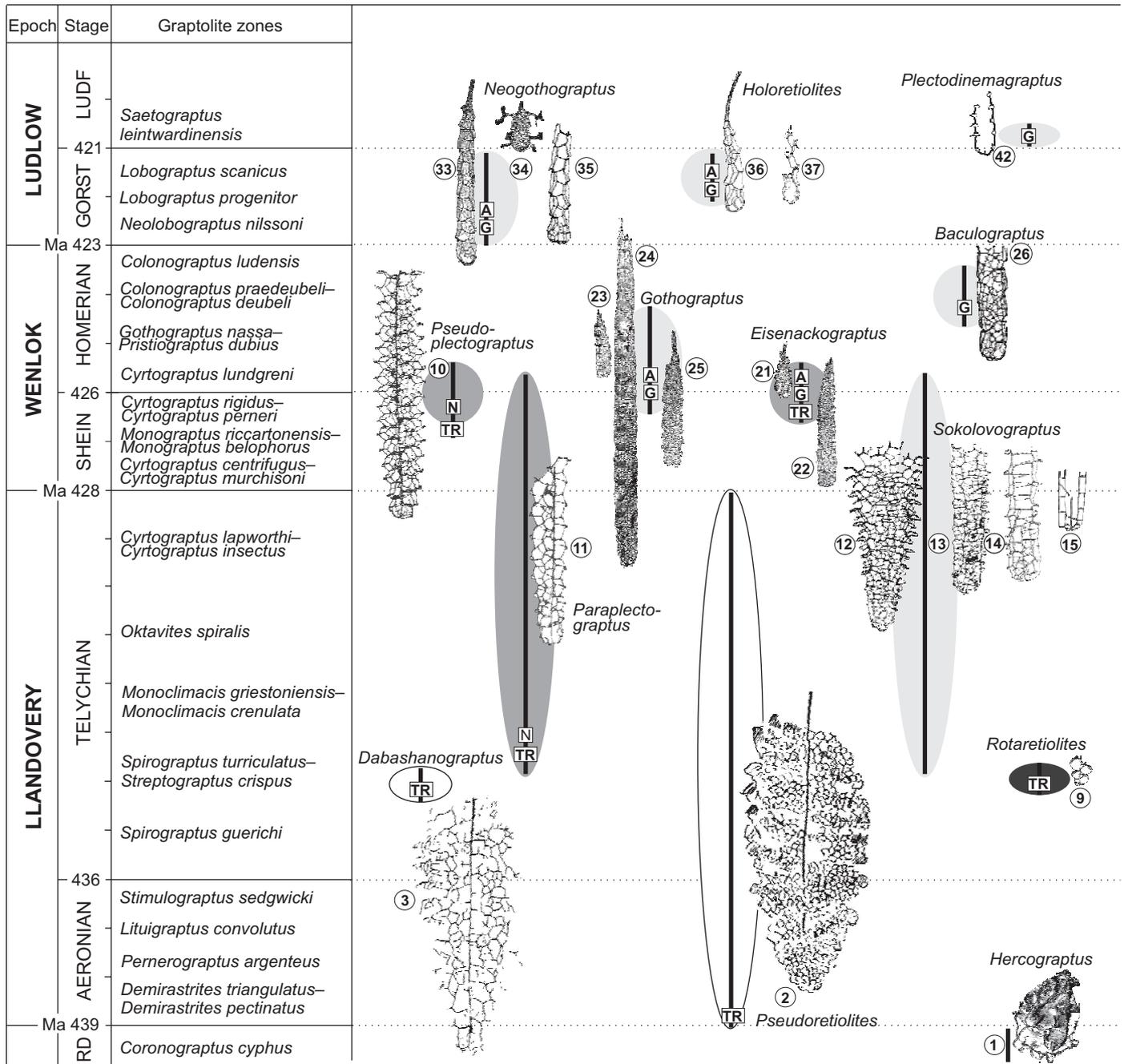
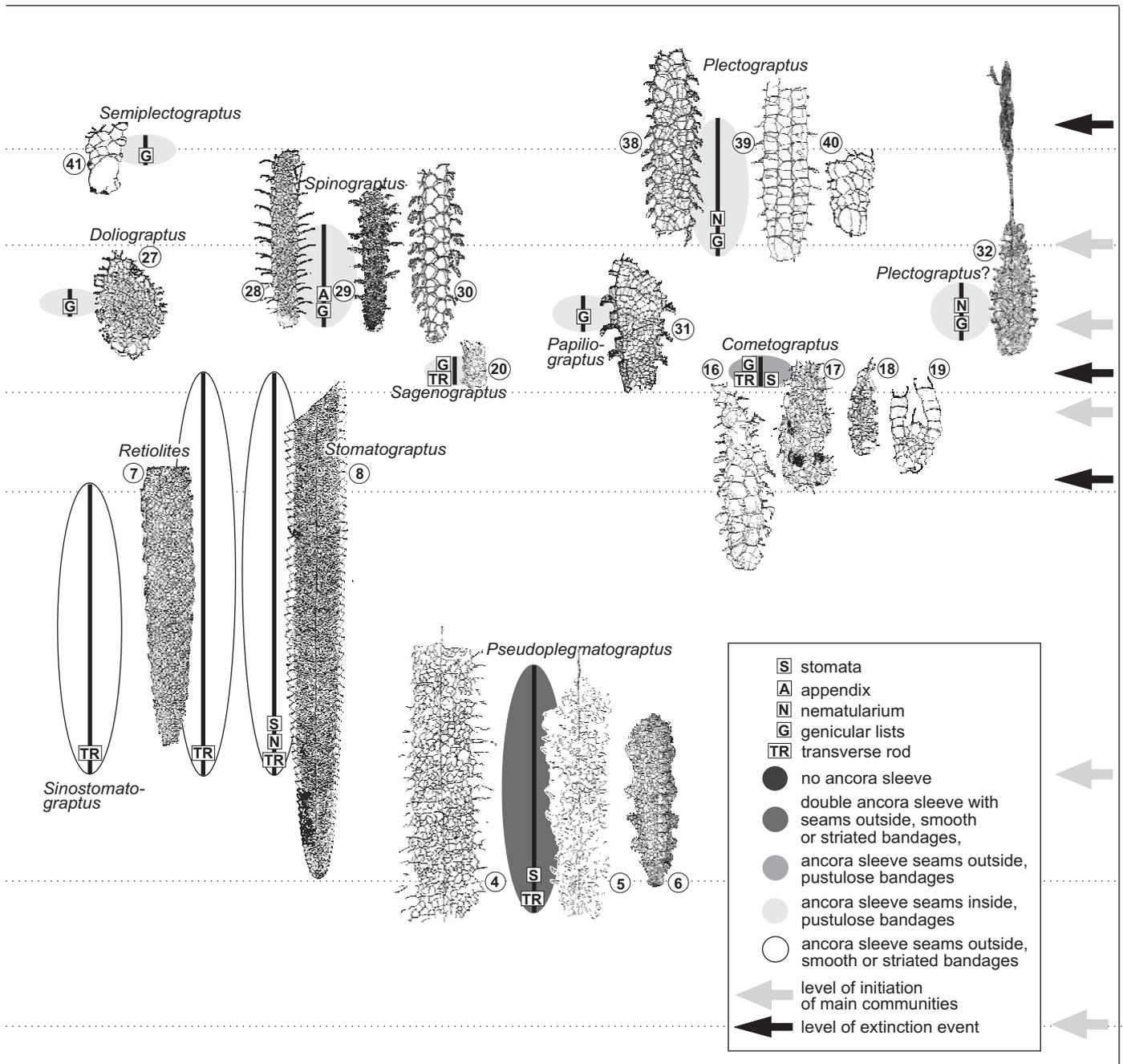


Fig. 1. Ranges of the retiolite genera with illustration of the characteristic species with their main synapomorphies. Numbered species: 1. *Hercograptus introvertus* Melchin, 1999, *C. cyphus* Biozone, Arctic Canada. 2. *Pseudoretiolites decurtatus* (Bouček and Münch, 1944), *Rastries linnaei* Biozone, Thuringia. 3. *Dabashanograptus chengkouensis* Ge, 1990, *S. turriculatus* Biozone, China. 4, 5. *Pseudoplegmagraptus longispinus* (Bouček and Münch, 1944), *R. linnaei* Biozone, Barrandian. 6. *Pseudoplegmagraptus obesus* Lapworth, 1877, *S. turriculatus* Biozone, Sweden. 7. *Retiolites angustidens* Elles and Wood, 1908, Lower Visby Formation, Sweden. 8. *Stomatograptus grandis* Suess, 1851, *M. spiralis* Biozone, Barrandian. 9. *Rotaretiolites exutus* Bates and Kirk, 1992, *S. turriculatus* Biozone, Sweden. 10. *Pseudoplectograptus praemacilentus* (Bouček and Münch, 1952), *C. lundgreni* Biozone, EEP, Poland. 11. *Paraplectograptus eiseli* Manck, 1917, *C. lundgreni* Biozone, EEP, Poland. 12. *Sokolovograptus diffusus* Kozłowska-Dawidziuk, 1995, *C. perneri* Biozone, EEP, Poland. 13. *Sokolovograptus parens* Obut and Zaslavskaya, 1976, *C. perneri* Biozone, EEP, Poland. 14. *Sokolovograptus zawadensis* Kozłowska-Dawidziuk, 1995, *C. perneri* Biozone, EEP, Poland. 15. *Sokolovograptus polonicus* Kozłowska-Dawidziuk, 1995, *C. lundgreni* Biozone, EEP, Poland. 16. *Cometograptus tomczyki* Kozłowska-Dawidziuk, 2001, *C. lundgreni* Biozone, EEP, Poland. 17. *Cometograptus apoxys* (Lenz, 1993), *C. lundgreni* Biozone, Arctic Canada. 18. *Cometograptus marsupium* (Lenz, 1993), *C. lundgreni* Biozone, Arctic Canada. 19. *Cometograptus kirki* Lenz and Kozłowska-Dawidziuk, 2001, *C. lundgreni* Biozone, Arctic Canada. 20. *Sagenograptus arctos* Lenz and Kozłowska-Dawidziuk, 2001, *C. lundgreni* Biozone, Arctic Canada. 21. *Eisenackograptus eisenacki*, short morphotype, *C. lundgreni* Biozone, Arctic Canada. 22. *Eisenackograptus eisenacki* (Obut and Sobolevskaya, 1965), long morphotype, *C. lundgreni* Biozone, EEP, Poland. 23. *Gothograptus nassa* (Holm, 1890), short form, Bartoszyce borehole, EEP, Poland. 24. *Gothograptus nassa*, long form, EEP, Poland. 25. *Gothograptus obtectus* Kozłowska-Dawidziuk, 1995, *C. lundgreni* Biozone, Balic erratic boulder, Poland. 26. *Baculograptus batesi* Lenz and Kozłowska-Dawidziuk, 2002, *C. praedubeli/C. debubeli* Biozone, Arctic Canada. 27. *Doliograptus latus* Lenz and Kozłowska-



Dawidziuk, 2002, *C. praedubeli/C. deubeli* Biozone, Arctic Canada. 28. *Spinograptus spinosus* Wood, 1900, *L. nilssoni* Biozone, EEP, Poland. 29. *Spinograptus latospinosus* Kozłowska-Dawidziuk, 1997. 30. *Spinograptus munchi* Eisenack, 1951, *C. praedubeli/C. deubeli* Biozone, EEP, Poland. 31. *Papiliograptus papilio* Lenz and Kozłowska-Dawidziuk, 2002, *C. praedubeli/C. deubeli* Biozone, Arctic Canada. 32. *Plectograptus? karlsteinensis* Kozłowska-Dawidziuk, Lenz, and Štorch, 2001, *C. praedubeli/C. deubeli* Biozone, Barrandian. 33. *Neogothograptus thorsteinssoni* Lenz and Kozłowska-Dawidziuk, 2004, *L. progenitor* Biozone, Arctic Canada. 34. *Neogothograptus alatiformis* Lenz and Kozłowska-Dawidziuk, 2004, *L. progenitor* Biozone, Arctic Canada. 35. *Neogothograptus purus* Kozłowska-Dawidziuk, 1995, EEP, Poland. 36. *Holoretiolites mancki* (Münch, 1931). 37. *Holoretiolites helenaewitoldi* sp. nov., *L. progenitor* Biozone, EEP, Poland. 38. *Plectograptus wimani* Eisenack, 1951, *N. nilssoni* Biozone, Baltic erratic boulder, Poland. 39. *Plectograptus robustus* Obut and Zaslavskaya, 1983, *L. nilssoni* Biozone, EEP, Kaliningrad. 40. *Plectograptus macilentus* Törnquist, 1887, *L. scanicus* Biozone, Baltic erratic boulder, Poland. 41. *Semiplectograptus urbaneki* Kozłowska-Dawidziuk, 1995, *Cucullograptus hemiaversus/C. aversus* Biozone, EEP, Poland. 42. *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk, 1995, *Cucullograptus hemiaversus/C. aversus* Biozone, EEP, Poland. Figures adapted from: 1, Melchin (1999); 2, 4–5, Bouček and Münch (1944); 3, holotype photographed by A. Lenz; 6, 9, Bates and Kirk (1992); 7, Bates and Kirk (1997); 8, Štorch (1994); 10–15, 38, 40–42, Kozłowska-Dawidziuk (1995); 16, Kozłowska-Dawidziuk (2001); 17–21, Lenz and Kozłowska-Dawidziuk (2001); 22, 25, Kozłowska-Dawidziuk (1990); 23, 35, photo taken by author; 24, 32, Kozłowska-Dawidziuk et al. (2001); 26, 27, 31, Lenz and Kozłowska-Dawidziuk (2002a); 28, 35, photo taken by author; 29, Kozłowska-Dawidziuk (1997); 30, Kozłowska-Dawidziuk 2002; 36, Kozłowska-Dawidziuk and Lenz (2001); 37, this paper; 39, Obut and Zaslavskaya (1983). Not to scale. Abbreviations: RD, Rhuddanian; SHEIN, Sheinwoodian; GORST, Gorstian; LUDF, Ludfordian. Biozonal scheme after Koren^o et al. 1996; Geological time scale by International Commission on Stratigraphy, International Union of Geological Sciences 2004 (www.stratigraphy.org).

diurnal migration (Vannier et al. 2003) living in oxygen-poor, but nutrient- and nitrogen-rich waters. These particular crustaceans have been suggested as analogs for planktic graptolites (Berry and Wilde 1990), the common group of early Palaeozoic zooplankton recognized globally as rapidly evolving and therefore highly important biostratigraphically. Furthermore graptolites represent a wide variety of adaptations to quiet but variable environments. Although their soft body evolution cannot be recognized and studied, we may relate them to the recent hemichordate pterobranchs (Kozłowski 1949). The detailed study of well-preserved graptolite skeletons has provided us with information on general evolutionary processes such as the introduction of new characters, parallelisms, homoeomorphisms, repopulations, and radiations or simplifications during about 95 Ma of the group's history (e.g., Urbanek 1960, 1970; Bulman 1970; Bates and Kirk 1984, 1986; Loydell et al. 1993; Melchin et al. 1998).

The nature of the retiolitid skeletal structure has long been misunderstood. The skeleton was traditionally regarded as a normal diplograptid in which the periderm was reduced to lists. In the absence of ultrastructure studies early authors were unable to recognize the real nature of retiolitid skeleton. Retiolitid research has accelerated in recent years with the advent of scanning electron microscopy technology. SEM observations permitted the recognition of fundamental features of the retiolitid skeleton, leading to a better understanding of its nature (e.g., Bates 1990; Bates and Kirk 1984, 1992, 1997). The turning point of these studies came with the recognition of the double-layer nature of the skeleton; i.e., diplograptid thecae, outside of which was an additional layer, the ancora sleeve, a structure developed from the bifurcation and subsequent distal development of the virgella. Continuous fusellar membranes that form the thecal walls and ancora sleeve are extremely thin and only rarely preserved, whereas the much thicker and multi-layered cortical periderm forming lists built of bandages is typically well-preserved. As a consequence, the only consistently preserved element of the rhabdosome is the cortex, and rarely the sicula. Exceptionally and uniquely, however, the continuous periderm of the thecae and ancora sleeve may be rarely preserved, as seen for example, in some forms of *Spinograptus* (Lenz 1994a, b; Kozłowska-Dawidziuk 1997).

Evolutionary trends through time have been recognized in general in graptolites as a whole, among them being the reduction of the rhabdosome size and number of branches, and an increase in the degree of thecal complexity, e.g., Bulman (1970), Mitchell (1990). More studies focused at the lower level, for example family and subfamily, have demonstrated broadly similar repetitions of morphological types following extinction events, and increasing complexity of thecal characters, e.g., Urbanek (1966, 1997). In none of the previous studies, however, had there been a concerted effort to look at trends in retiolitid evolution with the exception of some preliminary studies by Kozłowska-Dawidziuk and Lenz (2001) and Lenz and Kozłowska-Dawidziuk (2002b) as detailed studies of even isolated graptolites were impossible before

the advent of SEM technology. That permitted ultrastructural and detailed morphologic studies and, these in turn, increased knowledge of retiolitid evolution. In particular, these studies have documented numerous species of the genus *Cometograptus* Kozłowska-Dawidziuk, 2001 in the *C. lundgreni* Biozone faunas (early Homerian) of Poland and of Arctic Canada (Kozłowska-Dawidziuk 2001; Lenz and Kozłowska-Dawidziuk 2001); have enabled recognition of several new genera in the upper Homerian faunas of Arctic Canada (Lenz and Kozłowska-Dawidziuk 2002a); and enabled description of new taxa of Wenlock and Ludlow retiolitids from Polish Part of the East European Platform (EEP) (Kozłowska-Dawidziuk 1995, 1997, 1999). All these data provided new information on retiolitid diversity and on unique morphological features such as spines on the ancora sleeve in *Cometograptus* or complex genicular processes in other taxa which, in turn, supplied further information on their phylogenetic relationships (Kozłowska-Dawidziuk 2001).

These studies further showed that the history of the group was severely affected by the *C. lundgreni* Extinction Event (Fig. 1) when 95 per cent of more than 50 species of graptolites became extinct. As a result, retiolitids were on the edge of extinction, considering that only one retiolitid species, *Gothograptus nassa* Holm, 1890 (Kozłowska-Dawidziuk 1999; Lenz and Kozłowska-Dawidziuk 2002b), and one monograptid species, *Pristiograptus dubius*, survived. Retiolitids flourished and diversified again during the late Homerian and the very early Ludlow, but subsequently gradually diminished in diversity, becoming extinct in about mid-Ludlow times (Kozłowska-Dawidziuk 1995; Kozłowska-Dawidziuk and Lenz 2001), that is, during the *S. leintwardinensis* Event (see Urbanek 1993), possibly as a result of environmental changes such as sea level changes (Johnson and McKerrow 1991) or spatial fluctuations in trophic resources connected with palaeoceanographic changes such as suggested by Elżbieta Porębska (personal communication 2001).

A significant trend towards a decrease in rhabdosome size and structural complexity is observed in the Wenlock *Sokolovograptus* and *Cometograptus*, and in the Ludlow *Plectograptus* and *Gothograptus* lineages (lineages used in this paper are *sensu* Kozłowska-Dawidziuk, 2001). In all these forms, the reduction is directed toward the loss of the lateral walls of the ancora sleeve. This reduction is seen in *Holoretiolites helenaewitoldi* sp. nov. of the *Gothograptus* lineage, described herein from the Ludlow. This new species demonstrates the greatest rhabdosome reduction in the *Gothograptus* lineage, comparable to that developed in *Plectodinmagraptus gracilis* Kozłowska-Dawidziuk, 1995 of the *Plectograptus* lineage (Fig. 2).

In the light of limited ecological data, it is difficult to discuss the causes of retiolitid fauna changes and trends. However, it is reasonable to assume that the retiolitids would have been under the influence of factors similarly to those affecting recent zooplankton. They probably reacted by similar varied strategies, e.g., maximizing efficiency of their feeding

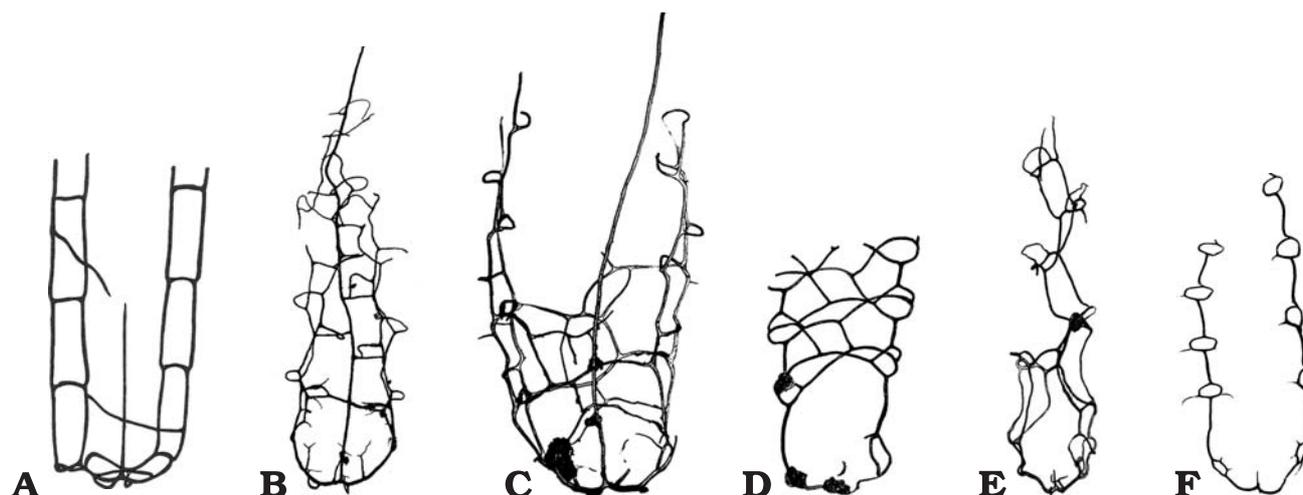


Fig. 2. Examples of the most reduced retiolitid rhabdosomes. A. *Sokolovograptus polonicus* Kozłowska-Dawidziuk, 1995. B. *Paraplectograptus eiseli* Manck, 1917, ZPAL G.34/12, Bartoszyce borehole, 1690.6 m. C. *lundgreni*/*T. testis* Biozone. C. *Cometograptus kirki* Lenz and Kozłowska-Dawidziuk, 2001. D. *Semiplectograptus urbaneki* Kozłowska-Dawidziuk, 1995. E. *Holoretiolites helenaewitoldi* sp. nov., holotype ZPAL G.34/2. F. *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk, 1995. Figures modified from: A, D, F, Kozłowska-Dawidziuk (1995); C, Lenz and Kozłowska-Dawidziuk (2001); B, E, originals. Not to scale.

strategies and for minimizing the risk of predation by means of vertical migration, varying with reproductive strategies, and changing of visibility, size and mobility (Gliwicz 1986; Saito and Hattori 2000).

The paper discusses the history of retiolitid evolution, using a different approach than previously applied (Kozłowska-Dawidziuk 2001; Kozłowska-Dawidziuk and Lenz 2001), showing their diverse faunas reflecting environmental changes and events, and demonstrating the overall trend of rhabdosome reduction supplemented by the description of a new and structurally most reduced *Holoretiolites* form.

History of evolutionary changes in retiolitid faunas

Five large biostratigraphically and morphologically constrained retiolitid faunas are recognized herein. The oldest Llandovery fauna is long-ranging and begins in the earliest Aeronian *Demirastrites triangulatus*–*D. pectinatus* Biozone and extends to the end of the Llandovery (Fig. 1). The second fauna appears in the Telychian *Spirograptus turriculatus*–*Monograptus crispus* Biozone and ends in the Sheinwoodian *Cyrtograptus rigidus*–*C. perneri* Biozone. The next, short-range retiolitid fauna is confined to the early Homerician *C. lundgreni* Biozone and comprises a diverse fauna including the recently-described and multi-species element, *Cometograptus* (Kozłowska-Dawidziuk 2001). The fourth fauna, restricted to the upper Homerician, is also one of short duration, and is made unique by survival of the species *Gothograptus nassa* and its successors. The Ludlow fauna begins in the earliest Ludlow *Neodiversograptus nilssoni* Biozone and continues to the extinction of

the retiolitids within the *S. leintwardinensis* Biozone. Noteworthy in this last-named interval is the skeletal reduction of both the *Plectograptus* lineage, as witnessed in *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk, 1995, and that of the *Gothograptus* lineage ending with *Holoretiolites helenaewitoldi* sp. nov. Details of the retiolitid faunas are presented below.

The Llandovery fauna.—The oldest retiolitids probably derived from an ancestor such as *Hercograptus introvertus* Melchin, 1999, a form occurring in *Coronograptus cyphus* Biozone (Fig. 1). Most of the Llandovery forms are long-ranging. Llandovery species belong to *Pseudoretiolites*, *Pseudoplegmagraptus*, and *Dabashanograptus*. Members of this group form large colonies with numerous similar-sized, orthograptid-shaped thecae, small common canals, and a well developed, dense, reticulated ancora sleeves, with seams outside, and smooth or striated bandages on lists. Most of the species have wide rhabdosomes, ranging from 2.5 to 8 mm. In *Pseudoretiolites* and *Pseudoplegmagraptus* the ancora sleeve may be the complicated by having a double, outside layer (Bates and Kirk 1992). The sicula, as is typical of other members of this group, is short (Fig. 3), about 1 mm (Kozłowska-Dawidziuk 1998), and is usually preserved, including preservation of part of the metasacula in some taxa. The ancora umbrella was spiralled, and deep or shallow. Some forms have lips or genicular processes on thecae. An exception among Llandovery retiolitids is the very small *Rotaretiolites exutus* Bates and Kirk, 1992. This has only two to three pairs of thecae, and an ancora sleeve limited only to a single list connecting the simple ancora umbrella to the thecal lists. It seems that the form may have disappeared with no descendants. The oldest members of the Llandovery fauna disappeared during the *Cyrtograptus lapworthi* Event (Fig. 1).

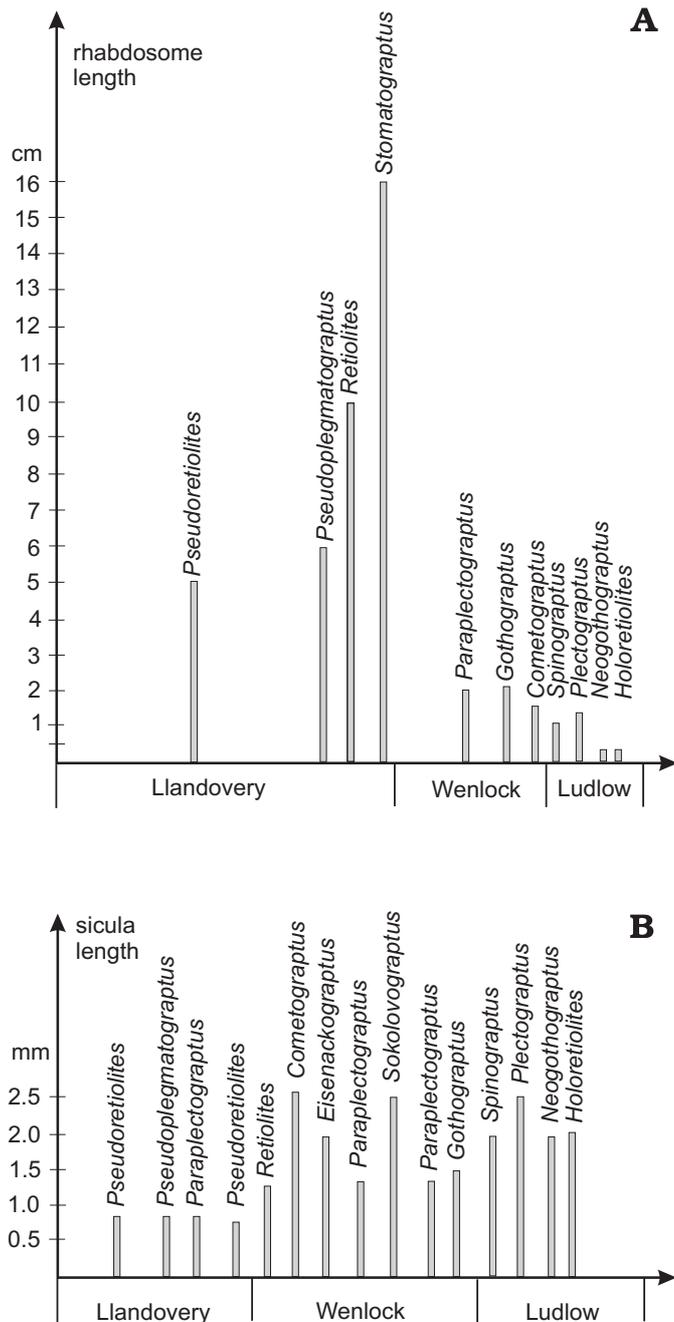


Fig. 3. Diagrams showing: lengths of rhabdosomes (A) and lengths of siculae (B) in common retiolitid genera.

The Telychian–Sheinwoodian fauna.—The new retiolitid fauna overlaps with the Llandovery fauna through the late Llandovery, and ranges up to the end of Sheinwoodian (Fig. 1). The three long-ranging retiolitid groups (*Paraplectograptus*, *Sokolovograptus*, *Retiolites*) appear in the *S. turriculatus*–*M. crispus* Biozone (Lenz and Melchin 1987; Kozłowska-Dawidziuk and Lenz 2001) and range through to the lower part of the *C. lundgreni* Biozone. The largest known retiolitid rhabdosome, *Stomatograptus grandis* Suess, 1851, described in Bouček and Münch (1944) from the *M. spiralis* Biozone of Barrandian region, is an incomplete rhabdosome

160 mm long. Characteristic structures in *Stomatograptus* are the openings, stomata, along the ancora sleeve wall. Fusellar fragments of the thecal floor and the prosicula are fairly commonly preserved in this taxon.

Much smaller retiolitids belong to *Sokolovograptus*, a form that flourished and proliferated in, particularly, the *C. perneri* Biozone in the EEP, Poland (Kozłowska-Dawidziuk 1995). Characteristic of the genus is a pseudoglyptograptid thecal shape. Unusually for retiolitids during this time period, the ancora sleeve list seams were on the inside and there were pustules on the bandages. The sicula of *Sokolovograptus* is long, reaching about 2.5 mm (Kozłowska-Dawidziuk 1998), a feature typical of the youngest retiolitids. The *Sokolovograptus* lineage is similar to the post-*C. lundgreni* retiolitids except for important features such as the lack of a geniculum and a zigzag pattern on the ancora sleeve. There is a strong tendency toward ancora sleeve reduction, the most pronounced being in *S. polonicus* Kozłowska-Dawidziuk, 1995 (Fig. 2). The other important member of this fauna is *Paraplectograptus* that has a relatively simple and narrow rhabdosome some 1.5 mm in width. This lineage is characterized by a pseudoglyptograptid thecal pattern, poor development of the ancora sleeve, and reduced ancora umbrella (Figs. 1, 2). The characteristic form, *P. eiseli*, was much smaller than co-occurring forms, its length being up to about 25 mm. Sicula length increases up the stratigraphic column from short in the oldest, to medium (< 2 mm), in younger forms. Some forms of a possible *P. eiseli* from the *C. lundgreni* Biozone have a very reduced ancora umbrella and no ancora sleeve (Fig. 2), perhaps representing some stage of advanced reduction of the ancora sleeve or some simple, ecophenotypic form of the *P. eiseli*. On the other hand more complex forms, such as *Pseudoplectograptus praemacilentus* ranging from the *C. perneri* Biozone up to the lower part of the *C. lundgreni* Biozone (Fig. 1), widen distally and have a well developed ancora sleeve. *Paraplectograptus* like *Sokolovograptus* possesses pustules on the bandages, a feature that appeared more or less simultaneously for the first time in both groups. Significantly, the morphological features of *Paraplectograptus* suggest that it may be an intermediate stage between old and young retiolitids, and *P. eiseli* is regarded as the ancestor of *E. eisenacki* (Fig. 1).

The most advanced form among the Wenlock retiolitids is *Eisenackograptus eisenacki*, appearing in the *C. perneri*–*C. rigidus* Biozone but proliferating in the early Homerian. It is regarded as the ancestor for the *Gothograptus* lineage (Kozłowska-Dawidziuk 1990, 2001), a lineage characterized by a finite rhabdosome ending with an appendix. For the first time in retiolitid development, the point at which an appendix appears on any one rhabdosome marks the end of the colony growth, the appendix being a modified and most distal theca. *Eisenackograptus eisenacki* has two to nine pairs of thecae. The pseudoglyptograptid shape of thecae with genicular lists, a large common canal, a large sicula, and bandages on lists with pustules are characteristic of the surviving retiolitids, appearing after the *Cyrtograptus lundgreni* Event.

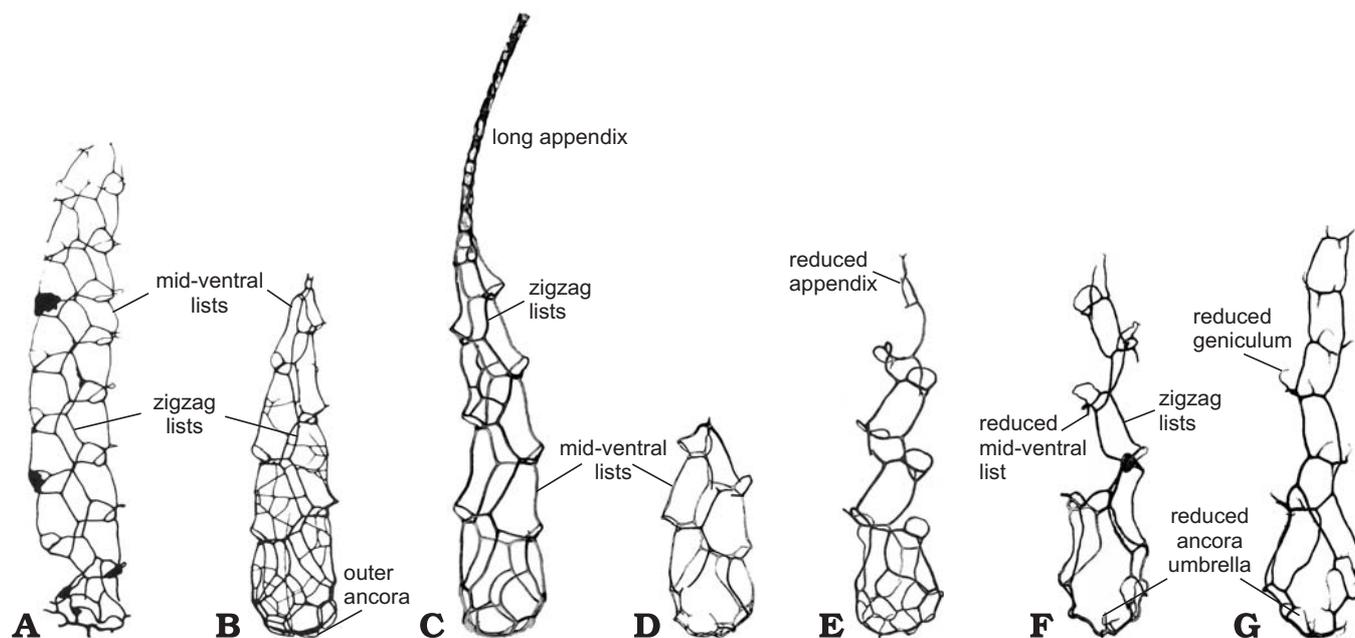


Fig. 4. Species of *Holoretiolites* showing successive steps of rhabdosomal changes. **A.** Largest rhabdosome of *H. manckoides* Kozłowska-Dawidziuk, 1995. **B.** *H. romani* Kozłowska-Dawidziuk, 1995 with reticulum. **C.** *H. mancki* with long appendix. **D.** *H. simplex* Eisenack, 1951 having short rhabdosome with two pairs of thecae and reduced ancora sleeve. **E.** *H. atrabecularis*, Kozłowska-Dawidziuk, 1995 with ancora sleeve preserved only in the proximal part and reduced mid-ventral lists. **F, G.** *H. helenaewitoldi* sp. nov. with strongly reduced ancora umbrella, ancora sleeve, and mid-ventral lists; ZPAL G.34/2 (F) and ZPAL G.34/4 (G). Figures modified from: A, B, E, Kozłowska-Dawidziuk (1995); C, Kozłowska-Dawidziuk and Lenz (2001); D, Eisenack (1951); E–G, originals. Not to scale.

The *Cyrtograptus lundgreni* fauna.—The greatest diversification in the legacy of retiolitid history is seen in the *C. lundgreni* Biozone. In the lower part of the biozone, uncommon occurrences of *Paraplectograptus*, *Sokolovograptus*, *Retiolites*, and *Stomatograptus* (Lenz and Kozłowska-Dawidziuk 2001; Kozłowska-Dawidziuk and Lenz 2001) can still be found. Their disappearance marked the end of the record of the old retiolitid generations (Fig. 1), although *Sagenograptus*, a form that appears to be affiliated to the old group, occurs in the upper part of the *C. lundgreni* Biozone (Lenz and Kozłowska-Dawidziuk 2002a). The *Gothograptus* lineage is represented by several species.

A new and significant development was the appearance of *Cometograptus* (Fig. 1), a genus that underwent significant speciation, and was confined entirely to the *C. lundgreni* Biozone (Kozłowska-Dawidziuk 2001; Lenz and Kozłowska-Dawidziuk 2001). *Cometograptus* forms possess a well developed ancora sleeve, and various species show a considerable range of variations, such as in the development of large stomas bordered by membranes or unique, long spines connected by membranes, perhaps being some kind of stabilizing structure (Fig. 1). One form, *C. kirki* has a strongly reduced rhabdosome, mostly of the ventral walls (Figs. 1, 2), whereas *C. tomczyki* (Kozłowska-Dawidziuk 2001) has a relatively reduced ancora sleeve with lists forming a zigzag structure, similar to those of the *Plectograptus* lineage of the post-*C. lundgreni* interval. The significant difference between these forms are that the seams on lists are outside in *Cometograptus* and inside in *Plectograptus*.

Sagenograptus and *Pseudoplectograptus* (a form very close to, but more complex than *Paraplectograptus*) ranged to the end of the *C. lundgreni* Biozone (Lenz and Kozłowska-Dawidziuk 2002a). The earliest representatives of the *Gothograptus* lineage (e.g., *G. obtectus* Kozłowska-Dawidziuk, 1990; *G. kozłowskii* Kozłowska-Dawidziuk, 1990), characterized by a narrow rhabdosome with an appendix, and varied genicular processes developed on the genicular lists, appeared at this time. The *Gothograptus* lineage assumed an extremely important role in retiolitid history, since *Gothograptus nassa* was the only retiolitid to survive the *C. lundgreni* Event (Kozłowska-Dawidziuk 1999; Lenz and Kozłowska-Dawidziuk 2002b).

Upper Homeric fauna.—As noted above, only one retiolitid, *Gothograptus nassa* and one or two monograptids, *Pristiograptus dubius*, survived the *C. lundgreni* Event, and both are typical of the earliest Homeric. *G. nassa* appears to have been ancestral to the succeeding late Homeric fauna. The rhabdosome of *G. nassa* is relatively small and narrow, with thecal apertures covered by hoods. The size of *G. nassa* ranges from five to 23 pairs of thecae (Figs. 1, 5), and the maximum length of the rhabdosome is 26 mm including the appendix.

The late Homeric retiolitid proliferation commenced with a recovery phase in the *C. praedeubeli*–*C. deubeli* Biozone during which they appeared in great numbers. Presumed descendants of *G. nassa* include the recently described genera *Baculograptus*, *Spinograptus*, *Doliograptus*,

Papiliograptus, and *Plectograptus*? (Kozłowska-Dawidziuk et al. 2001; Lenz and Kozłowska-Dawidziuk 2002b). All these forms share common features such as a medium-sized rhabdosome with a small ancora umbrella, a long sicula (about 2.5 mm), a well developed ancora sleeve with a dense to reduced reticulum, and often, paired or singular genicular processes. *Baculograptus* represents some form intermediate between the *Gothograptus* and *Plectograptus* lineages. It possesses the rhabdosomal shape and thecal pattern of *Gothograptus*, whereas its ancora sleeve pattern has a zigzag typical of the *Plectograptus* lineage. *Doliograptus* has a wide rhabdosome with no genicular processes, whereas the remaining forms have medium-width rhabdosomes and a large variety of genicular processes as seen for example in *Spinograptus* and *Papiliograptus*. An intriguing form is the recently described *Plectograptus? karlsteinensis* Kozłowska-Dawidziuk, Lenz, and Štorch, 2001 with a long spiralled nematularium. It might be ancestral to *Plectograptus*, having a similar rhabdosome structure and size, although its preservation only in flattened form prevents detailed studies.

Ludlow fauna.—The youngest retiolitids were less diverse than those in the late Homerian, having the last and most reduced representatives of two lineages, comprising the *Gothograptus* lineage with two genera, *Neogothograptus* and *Holoretiolites* (Fig. 5), and the more diverse *Plectograptus* lineage with the last representatives of *Spinograptus* (up to the *L. progenitor* Biozone). The genus *Plectograptus* is represented by three species: *P. wimani*, *P. robustus*, and *P. macilentus* (Fig. 1), representing different stages of ancora sleeve reduction beginning with a large opening in the proximal part of the ancora sleeve wall (Kozłowska-Dawidziuk 2002). Two succeeding species of the *Plectograptus* lineage are known only from the Polish part of the EEP: *Semiplectograptus urbaneki*, Kozłowska-Dawidziuk 1995 and *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk, 1995 and represent significant successive stages in the reduction of the ancora sleeve. The last species is presently regarded as the most reduced retiolitid form (Kozłowska-Dawidziuk 1995).

Neogothograptus and *Holoretiolites* are well developed in the Polish part of the EEP (Kozłowska-Dawidziuk 1995, 2002) and in Arctic Canada (Lenz 1993, 1994b).

As in the *Plectograptus* lineage, there are successive steps of rhabdosome reduction represented by species of *Neogothograptus* and *Holoretiolites* (Figs. 1, 4, 5). The discovery of *Holoretiolites helenaewitoldi* sp. nov. demon-

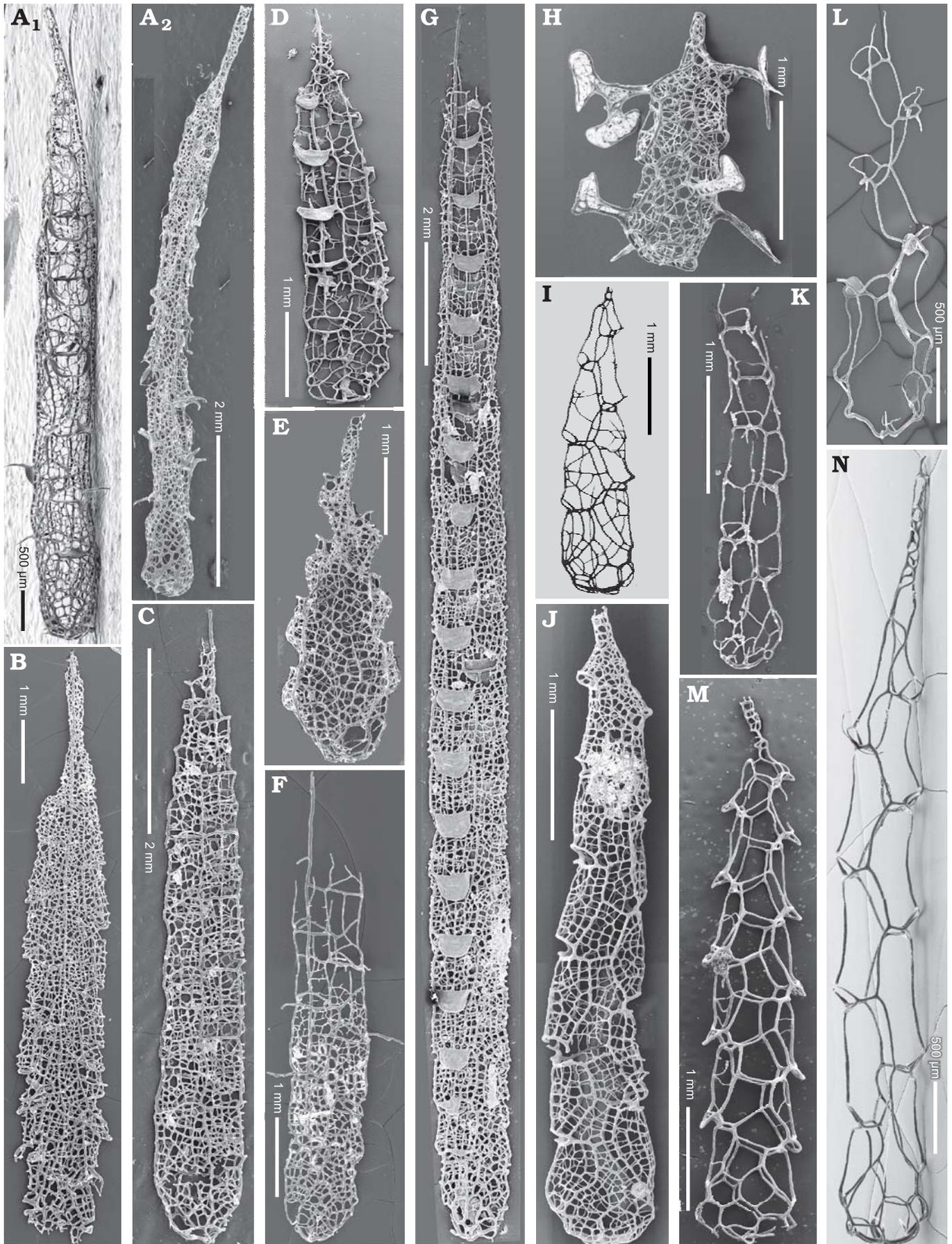
strates the last stage of rhabdosome reduction in the *Gothograptus* lineage. It has a framework reduction almost as great as that seen in *Plectodinemagraptus gracilis* (Figs. 1, 2), but with different elements being reduced.

Changes in organization of retiolitids colonies

The retiolitid faunas described reflect evolutionary histories that followed environmental changes culminating at the end of the *C. lundgreni* Biozone. The ensuing *C. lundgreni* Event reduced the variety of forms to one species, *Gothograptus nassa*, a species that was possibly the only ancestor of the subsequent new late Homerian and Ludlow forms following repopulation. As a result, two major significant types of retiolitid colonies appeared during their history, and are distinguished herein. The oldest type, termed L-colonies represents the large rhabdosomes with small siculae. They range from the Aeronian and Telychian–Sheinwoodian as long-ranging faunas, perhaps indicating relatively stable environmental conditions. The L-colonies of numerous thecae (Figs. 1, 7A) typically contain about 80 pairs of slightly increasing large thecae. The small size of the siculae in these early large forms (Fig. 3) shows that the colonies developed from very small siculozooids. The younger S-colonies, by contrast, represent small rhabdosomes with long siculae and a limited number of thecae (Fig. 7B). These forms were short-ranging. The S-colonies replaced the L-colonies in the Homerian, possibly indicating more variable environments.

The diverse forms from the *C. lundgreni* Biozone (see above) as well as the *Sokolovograptus* and *Paraplectograptus* lineages represent some kind of intermediate forms between two the types of colonies, although the presence of medium-length and long siculae makes them more allied to the S-colonies. The typical S-colonies appeared in the late Homerian and continue through the Ludlow retiolitids with relatively small to very small rhabdosomes, following a trend toward size reduction in progressively younger forms. The thecal lengths in longer forms of S-colonies (e.g., *G. nassa*, Fig. 5G) increase up to the middle part of the rhabdosome and then decrease distally, whereas in the shortest forms (e.g., *H. mancki*, Fig. 4C) thecal length lessens steadily distally. As many as a dozen thecal pairs occur in *Plectograptus* type forms such as *Papiliograptus*, *Spinograptus*, and

Fig. 5. Species of the *Gothograptus* lineage showing evolutionary change; arranged from older forms to younger (from left to right of the figure). **A.** *Gothograptus kozłowskii* Kozłowska-Dawidziuk, 1990, holotype ZPALG.XIII/43, Poland, EEP; A₁, ventral view of the 1st side of rhabdosome with well developed apertural processes, reticulum of ventral wall and ancora sleeve; A₂, reverse side of rhabdosome. **B.** *Gothograptus obtectus* Kozłowska-Dawidziuk, 1990, holotype, ZPAL G.XIII/23, EEP, Poland, reverse side of rhabdosome with well developed apertural processes covering thecal openings. **C.** *Eisenackograptus eisenacki* Obut and Sobolevskaya, 1965. C. ZPAL G.34/1, Zawada borehole, 1603.1–1609.1 m, EEP, Poland. **E.** GSC 119776, Arctic Canada. **D.** *G. Gothograptus nassa* (Holm, 1890), short form, ZPAL G.29/21, Poland, EEP. **G.** Long form, ZPAL G.28/1, Poland, EEP. **F.** *Gothograptus pseudospinosus* Eisenack 1951, ZPAL G.XIII/42, EEP, Poland. **H.** *Neogothograptus* sp. 1, GSC 125988, Arctic Canada. **I.** *Holoretiolites erraticus* Eisenack, 1951, ZPAL.G XVI/1373, Poland, EEP. **J.** *Neogothograptus* sp. 2, GSC 125981, Arctic Canada. **K.** *Neogothograptus* sp. 3, GSC 126003, Arctic Canada. **L.** *Holoretiolites helenaewitoldi* sp. nov., ZPAL G.34/2, Bartoszyce borehole, depth 1579.9 m, Poland, EEP. **M.** *Neogothograptus balticus* ZPAL G.27/3, Poland, EEP. **N.** *Holoretiolites mancki*, ZPAL G.34/3, erratic boulder 48, Jarosławiec, Poland. All SEM photographs except I, which is light microscope photograph. →



Plectograptus. The complete rhabdosome of *Plectograptus? karlsteinensis* Kozłowska-Dawidziuk, Lenz, and Štorch, 2001, with a well developed nematularium, distinctly shows a distal decrease of thecal length.

A final type of growth colony with a clearly limited number of thecae appeared in the *Gothograptus* lineage in the early Homerian, and continued into the Ludlow. In these forms, the rhabdosome growth is arrested by a last-modified theca, the appendix (Fig. 5). The maximum number of thecal pairs in the lineage reached 19 in *G. nassa* in the *P. dubius*–*G. nassa* Biozone, whereas in Late Homerian and Ludlow forms the maximum is ten pairs and, in most cases, fewer. The smallest colony represented by, e.g., *Neogothograptus* sp. 1 possessed only two pairs of thecae (zooids) (Fig. 5H). Thus the smallest Ludlow retiolitids have about 40 times fewer thecal pairs than the longest Llandovery species. At the same time the ratio of the sicula length to the mature rhabdosome length is 1:0.8, whereas in L-colonies it is 1:0.008. In the same vein, simple calculations suggest that the volume of individual thecae in S-colonies was approximately one-quarter that in the L-colonies, whereas its sicula was about twice the length of that in L-colonies (Fig. 3). Thus in extreme cases of the S-colony the siculozooid would be twice bigger whereas zooids would be four times smaller than in some extreme L-colony.

What was the cause of this trend of colony size reduction? Many factors promote varying survival life strategies, including the strategy, characteristic for rapid maturation, and reproduction of small forms in recent zooplankton. The small size organisms were mortality-controlled; when mortality is heavy it is optimal to start reproduction when the organism is small (Kozłowski 1992). On the other hand, the body size is one of the most important determinants of the relative abundance of planktonic animals in nature (Gliwicz 1990). Recent large-bodied plankton is more exposed to predation by visually feeding planktivorous fishes and must therefore, take evasive action such as moving into relatively deep, dark water. In like manner, retiolitids might have been preyed upon by contemporaneous oceanic-dwelling fishes. According to Bates and Kirk (1984, 1986), the reduction of colony size to a few zooids is connected to an adaptation to automobility. They suggested that ciliated extrathecal tissue enclosed the whole rhabdosome and that these would produce ciliary propulsion as a method of locomotion as well as producing feeding currents. Melchin and DeMont (1995), on the other hand, presented a hydrodynamic approach to the mobility that is in agreement with the pterobranch model of graptolite affinity. They propose dual functions of the cephalic shield in planktonic graptoloids: rhabdosomal secretion and locomotion, similar to benthic pterobranchs (Dilly 1985). Further enhancement of the cephalic shield to one or two lobes being expanded into swimming wings, may have significantly added to the drag and reduction in the sinking rate. As such, small colonies of retiolitids, having several zooids and their wings (Fig. 6), could have been active micro-swimmers, perhaps as active as recent copepods. This latter idea of graptolite locomotion seems to be likely in comparison with recent zooplankton; e.g., some

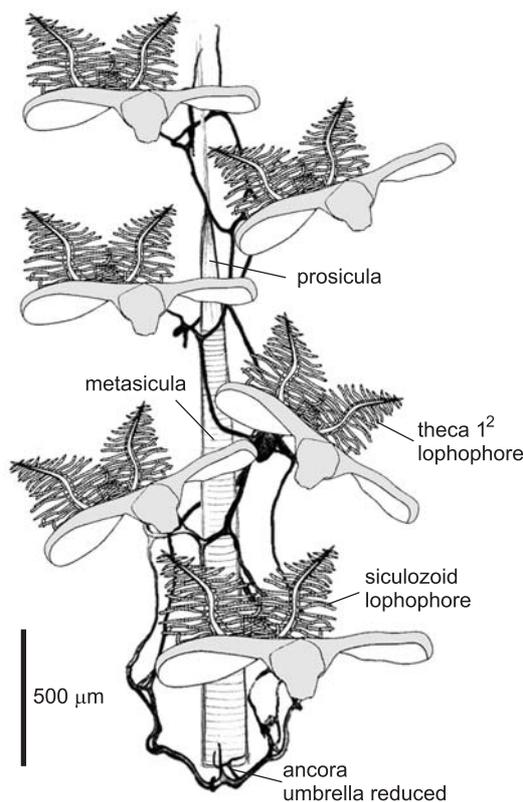


Fig. 6. Rhabdosome of the holotype *Holoretiolites helenaewitoldi* sp. nov. with the sicula reconstructed and hypothetical lophophores; the rest of soft body is omitted. The hypothetical lophophores are modified after Melchin and DeMont 1995.

cladocerans aggregate at the surface during the day and descend into the water column at night to reduce the predation risk from visual predators (Saito and Hattori 2000). There are many other factors influencing behavior and life strategies in the recent zooplankton, some of them only recently discovered; e.g., the life-history of *Daphnia* responses to chemicals released by fish predators leads to a decrease in mature size (Hanazato et al. 2001).

The morphological theory of organization of graptolite colonies (Urbanek 1960, 1973, 2004) would explain morphological gradient of thecae, as well as the process of reduction of the retiolitid colony size during astogeny. The morphogenetic substance implied is regarded as an inhibitor for the growth of genetically identical thecae. Only the sexually created siculozooid was able to produce the active substance and that gradually decreased in concentration distally, leading to a size gradient in succeeding thecae. Simultaneously, the sicula was omitted from these changes. Thus, the distal thecae become larger and more variable in, for example, monograptids as well as in L-colonies of retiolitids having a large number of big thecae (Figs. 1, 7). By comparison, the opposite process took place in, e.g., Ordovician Corynoididae, in which a large sicula, with differentiation of the apertural region, was accompanied by only two simple thecae. This phenomenon is similar to that of S-colonies of retiolitids (Figs. 4D, 5H). Additionally there is a remarkable

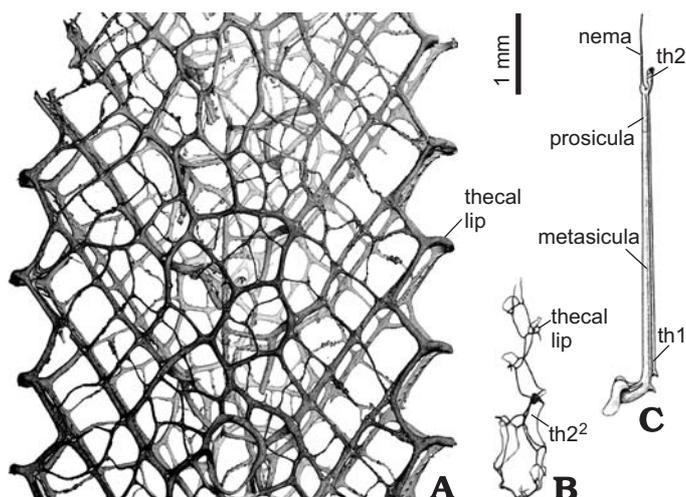


Fig. 7. Comparison of an L-colony rhabdosome (A) with two rhabdosomes of S-colony (B, C). A. *Stomatograptus* sp., ZPAL G. 34/12, unknown Arctic Canada locality, Llandovery?, fragment of distal part of rhabdosome with five thecae. B. *Holoretiolites helenaewitoldi* sp. nov., ZPAL G.34/2. C. *Corynites wyszogrodensis* Kozłowski, 1956, ZPAL G.IV, Ordovician.

similarity between the last vestigial theca in *Corynites wyszogrodensis* Kozłowski, 1956 (Fig. 7C) and the appendix (the last modified theca) in the *Gothograptus* lineage (Fig. 4C), although the first one is twisted. The appearance of such small colonies was explained by Urbanek (1960, 1973) as a result of production of a great amount of the morphogenetic substance by the hypertrophic siculozoid. The morphogen thus acts as a strong inhibitor for zooid growth, resulting in an abridged number of thecae, that shorten distalwards.

The evolutionary process leading to the development of S-colonies was a presumably a response to selective pressure from the environment (suggestions above) promoting small colonies with small zooids, selecting for specific morphogen activity. Thus colony growth was replaced by increased growth of the siculozoid (Kozłowski 1956), a process that may be regarded as a failure of coloniality.

Material and abbreviations.—The new three-dimensional material described in this paper is isolated and well-preserved, and has been recovered from the Bartoszyce borehole from north-east Poland, a part of the EEP. Graptolites come from one core sample (about 150 g) from the Bartoszyce borehole. The graptolites were recovered following slow dissolution of the host carbonate in acid (5–10% HCl). A fine hairbrush was used to pick and transfer specimens. The material is stored in glycerine in plastic containers. Figured specimens of the new material are on SEM stubs No 292, 293, and 297 housed in the Institute of Palaeobiology, Polish Academy of Sciences (abbreviated ZPAL). Specimens illustrated in Fig. 5E, H, J are housed in the Geological Survey of Canada (abbreviated GSC).

Terminology.—The terminology for anatomical details of the rhabdosome follows Kozłowska-Dawidziuk (1997, 2002).

Systematic paleontology

Order Graptoloidea Lapworth, 1873

Family Retiolitidae Lapworth, 1873

Subfamily Plectograptinae Bouček and Münch, 1952

Genus *Holoretiolites* Eisenack, 1951

Type species: *Holoretiolites mancki* (Münch, 1931), Baltic erratic boulder, Uckemark, Templin, Germany; Silurian.

Species included: *H. mancki* (Münch, 1931), *H. erraticus* Eisenack, 1951; *H. manckoides* Kozłowska-Dawidziuk, 1995, *H. atrabecularis* Kozłowska-Dawidziuk, 1995, *H. helenaewitoldi* sp. nov.

Holoretiolites helenaewitoldi sp. nov.

Figs. 4F, 5L, 7B, 8A, B, E–I.

Holotype: ZPAL G.34/2, Bartoszyce borehole, 1579.9 m, EEP, Poland, upper part the *Lobograptus progenitor* Biozone, Silurian.

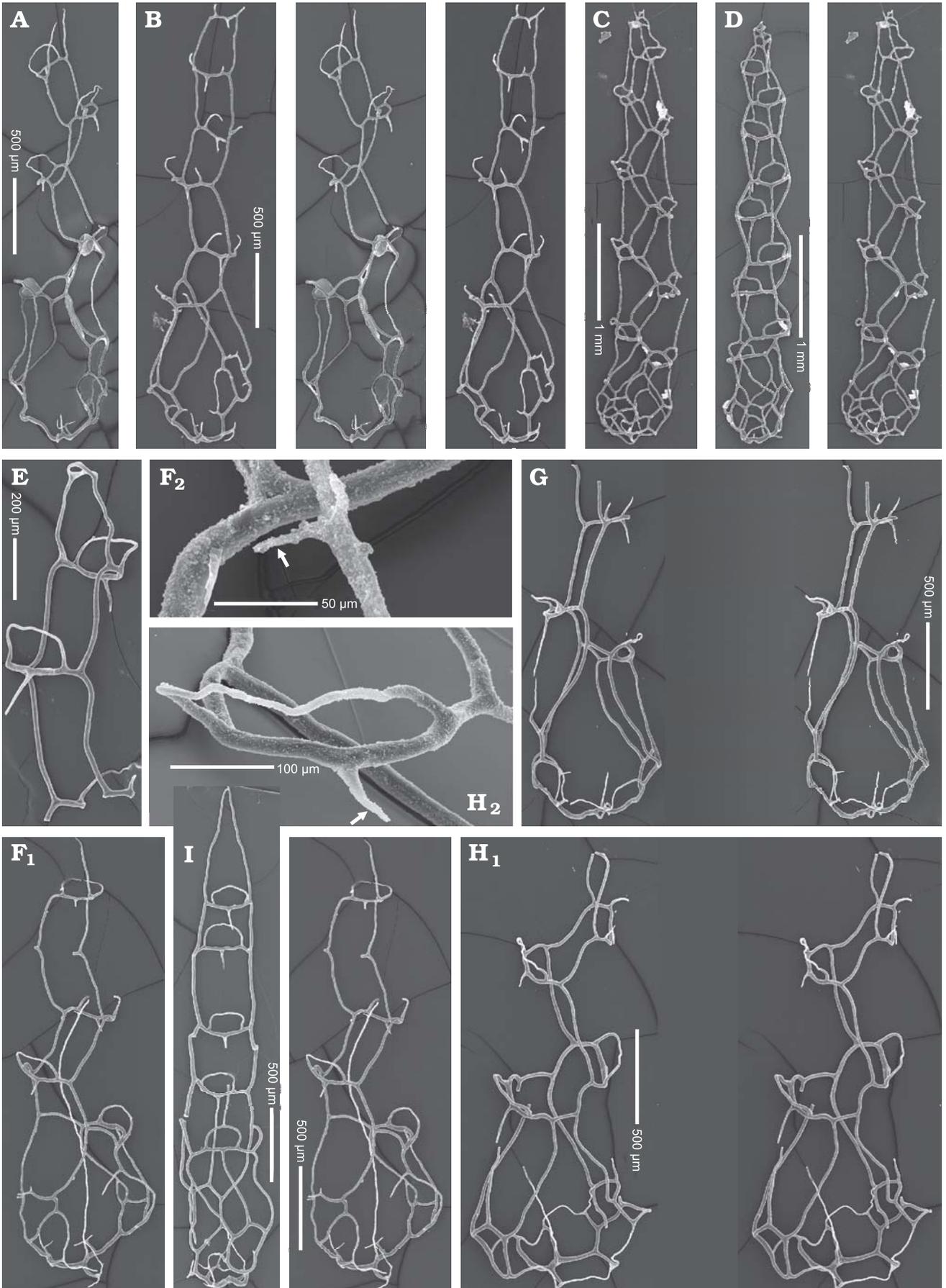
Derivation of the name: In honour of my parents Helena and Witold Kozłowski.

Diagnosis.—*Holoretiolites* with almost completely reduced ancora sleeve lists, a partly reduced ancora umbrella, and mid-ventral lists. Differs from *H. atrabecularis* in the greater reduction of ancora sleeve lists and of the ancora umbrella, and in possessing no ancora sleeve lists on lateral sides of rhabdosome.

Studied material.—Ten rhabdosomes and 20 fragments. Bartoszyce borehole, depth 1579.9 m.

Description.—Rhabdosomes with two to three pairs of thecae. Ancora umbrella in most specimens reduced to small lists, in a few specimens lists are more or less complete (Fig. 8), very thin. Maximum length of rhabdosome containing three pairs of thecae is 3.5 mm. Width of proximal part (corona) is 0.6 mm. Length of lips about 0.25 mm. Lips and primary ancora umbrella lists much stronger than the secondary ancora umbrella lists, genicular lists, and reduced mid-ventral lists (Fig. 8H). In some specimens the genicular lists are partly reduced. Appendix not observed, although some distal list suggests its presence, possibly simplified (Fig. 8E). Long virgella with preserved prosicular rim, observed in one specimen (Fig. 8F). The prosicular rim is 1.6 mm from the ancora, suggesting a sicula length of about 2 mm. There are no ancora sleeve lists on the lateral sides of the rhabdosome.

Discussion.—*Holoretiolites helenaewitoldi* sp. nov. represents the most advanced stage of rhabdosomal reduction in the *Gothograptus* lineage. The new species is most similar to *H. atrabecularis* in the reduction of mid-ventral lists. *H. atrabecularis* has a well developed ancora umbrella and ancora sleeve lists, and a reticulum in the proximal part, whereas *H. helenaewitoldi* sp. nov. has a strongly reduced ancora umbrella and ancora sleeve lists. The zigzag lists, which may in part, be thecal lists and ancora sleeve lists, are similarly developed in these two species. In some specimens of *H. helenaewitoldi* sp. nov., the reduction of the ancora umbrella is more advanced (Fig. 8A, F) and similar to that in *Plectograptus macilentus*, *Semiplectograptus urbaneki*, and



Plectodinemagraptus gracilis (Fig. 2) from the *Plectograptus* lineage.

Holoretiolites mancki is regarded as a possible ancestor of *H. atrabecularis*. The next evolutionary stage is *Holoretiolites helenaewitoldi* sp. nov., representing the most extreme skeletal reduction. The measurable length of sicula in *H. helenaewitoldi* convincingly indicates, for the first time, the sicula length in the genus *Holoretiolites* in general.

Plectodinemagraptus gracilis in the *Plectograptus* lineage, and *Holoretiolites helenaewitoldi* sp. nov. of the *Gothograptus* lineage (Figs. 2, 4, 5) represent the final stages of two kinds of rhabdosomal reduction. In both species the ancora umbrella is similarly simple whereas there are differences in the construction of the rhabdosome lists. In *H. helenaewitoldi* sp. nov., zigzag lists and lips are well developed in contrast to *P. gracilis*, which retains only mid-ventral lists, lips and well developed genicular lists (Figs. 2, 4).

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← Fig. 8. Two species of *Holoretiolites*: *H. helenaewitoldi* sp. nov. (A, B, E–I) and *H. mancki* (C, D, H). A, B, E–I. *Holoretiolites helenaewitoldi* sp. nov., Bartoszyce borehole, 1579.9 m, *L. progenitor* Biozone. A. Holotype ZPAL G.34/2, stereopair of obverse view of specimen with five thecae, note reduced ancora umbrella. B. ZPAL G.34/4, stereopair of obverse view of specimen with three pairs of thecae, lists bordering apertures are partly reduced. E. ZPAL G.34/5, fragment of distal part of rhabdosome with two thecae and beginning of appendix. F. ZPAL G.34/6, F₁, ventro-lateral view of specimen with prosicular rim preserved on virgella; F₂, enlargement of the prosicular rim (arrow). G. ZPAL G.34/7, reverse side of proximal part of rhabdosome showing no ancora sleeve in corona part. H. ZPAL G.34/8; H₁, obverse view of wider rhabdosome with two pairs of thecae, well developed ancora umbrella and fragment of virgella preserved; H₂, enlargement of thecal orifices lists with short mid-ventral list (arrow). I. ZPAL G.34/9, ventral view of theca 1¹ side. C, D. *Holoretiolites mancki* Münch, 1931, Bartoszyce borehole, 1576.1 m, *L. scanicus parascanicus* Biozone, showing differences with *H. helenaewitoldi* in developed mid-ventral lists and more complex proximal part. C. ZPAL G.34/10, stereopair of reverse side of rhabdosome with five thecae and appendix. D. ZPAL G.34/11, ventro-lateral view of rhabdosome.

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