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# Kirkigraptus, a new retiolitid graptolite from Poland

#### ANNA KOZŁOWSKA and DENIS E.B. BATES



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The new retiolitid graptolite *Kirkigraptus inexpectans* gen. et sp. nov., from the *Neodiversograptus nilssoni* Biozone of the Bartoszyce borehole, Poland is described. It is unique among the retiolitids not having a preserved virgella or ancora. Instead the most proximal structures are two round proxi-lateral lists, joining the two genicular lists of the first thecae, connecting the two sides of the rhabdosome. The lists are interpreted as a possible homologue of the distal edge of the ancora umbrella in typical retiolitids. The size of rhabdosome with large proximal lateral orifices, and the ventral panels of thecae with mid-ventral lists, are similar to those of *Plectograptus*, whereas the two ancora sleeve panels consisting of spaced horizontal lists only, resemble those of *Valentinagraptus*. It is possible that the new retiolitid may represent a new pattern of development of the proximal end of the rhabdosome, different from that in all other retiolitids.

Key words: Graptolithina, Retiolitidae, Kirkigraptus, ancora, proxi-lateral list, Silurian.

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## Introduction

In the last ten years the study of isolated retiolitids, many of them coming from boreholes of the East European Platform (EEP) of Poland, has identified a number of new taxa. It seems that every section of borehole contains novel forms. In addition the possibility of isolating the retiolitids from the rock, and studying them under the scanning electron microscope (SEM) has allowed the opportunity to trace their new characters in detail. In the case of the retiolitids the mode of construction is such that most of the skeleton is unpreserved.

The retiolitids are a specific group of graptolites characterised by incrementally deposited fusellar layers, supported by strong lists formed of cortical bandages. Usually only the rod-like bandaged lists of the retiolitid rhabdosome are preserved. This development of the walls together with the development of a new structure, the ancora, and its prolongation as the ancora umbrella and ancora sleeve, make the retiolitids uniquely differentiated group group within the diplograptids. The ancora sleeve forms outer lateral walls to the colony, with spaces, the external common canals, between them and the thecal walls.

Thus the retiolitid skeleton contains lists belonging to the thecae and to the ancora sleeve. Studying the ultrastructures of lists we may recognize to which part of rhabdosome they belong. A complication in studying retiolitids is the fact that only a small part of the rhabdosome, that formed as lists made of bandages, is normally preserved, and hence the ultrastructure of the lists is important, as they show traces of the membranes of the thecal walls. There are only a few exceptions where the fusellar membranes are present, as in *Retiolites* from the Llandovery (Bates and Kirk 1997), and *Spinograptus* from the

*Colonograptus praedeubeli* Biozone (Lenz 1994; Kozłowska-Dawidziuk 1997). Only extremely well preserved retiolitids are useful for studying their evolution. There are only a few places in the world currently yielding a retiolitid fauna both varied and well preserved for ultrastructural study, in particular Arctic Canada, and the EEP.

In this paper a new, well preserved and unexpected form of retiolitid, Kirkigraptus gen. nov., is presented. In this most unusual retiolitid, no ancora umbrella is preserved. The most proximal structures are two rounded lists, joining the two genicular lists of first thecae, observed for the first time in retiolitids. However, the limited number of complete specimens does not allow us to be certain of the true nature of these lists, although it is probable that the lists may represent the distal edge of the ancora umbrella. The new form also possesses ancora sleeve lists which are horizontal, simple but distinctive, similar to those of Valentinagraptus Piras, 2006. Otherwise the arrangement of ventral panels and the character of their lists show some similarities to those of Plectograptus Moberg and Törnquist, 1909. Thus it seems that Kirkigraptus is closely related to these both retiolitids. However, the crucial differences do not allow the inclusion of Kirkigraptus in either of these genera. In addition there is a distinctively different proximal end with the new structures.

The new form is also not an aberrant form, with only one specimen among the population e.g., in *Rhapidograptus toernquisti* (Elles and Wood, 1906), with the origin of the virgellar prolongation not from the virgella itself but from the side of the sicula (Zalasiewicz and Tunnicliff 1994: fig. 8J). *Kirkigraptus* is different from other known retiolitids, and the new development of the proximal end is regarded herein as a new character.

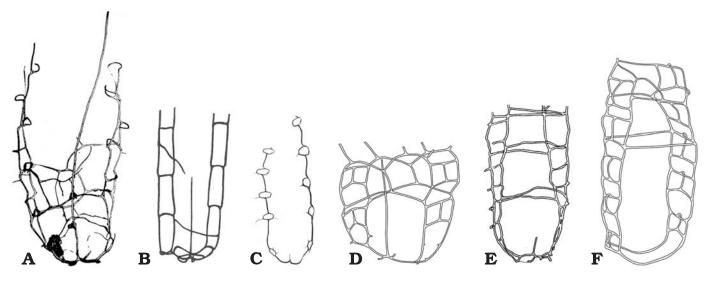


Fig. 1. Drawings of representatives of retiolitids with strongly reduced ancora umbrella and ancora sleeve. A. *Cometograptus kirki* Lenz and Kozłowska-Dawidziuk, 2001. B. Reconstruction of *Sokolovograptus polonicus* Kozłowska-Dawidziuk, 1995. C. Reconstruction of *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk, 1995. D. *Plectograptus mobergi* Bates, Kozłowska, Maletz, Kirk, and Lenz, 2005. E. Reconstruction of *Valentinagraptus simplex* Piras, 2006 after Piras 2006, modified. F. Reconstruction of *Kirkigraptus inexpectans* gen. et sp. nov.

For these unique proximal lists, the new term "proxi-lateral lists" is introduced. For the rest of terminology see Bates et al. (2005, 2006).

*Institutional abbreviation.*—ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

# New aspects in the evolution of the retiolitids

The evolution of the retiolitids has been intensively studied and better recognized during recent years (Bates and Kirk 1984, 1992; Kozłowska-Dawidziuk and Lenz 2001; Lenz and Kozłowska-Dawidziuk 2002; Kozłowska-Dawidziuk 2004). One striking trend in retiolitid evolution is that of rhabdosome reduction, especially during the Wenlock and Ludlow (Kozłowska-Dawidziuk 2004: figs. 1, 7). Thus during about 20 million years such elements of the rhabdosome as the ancora umbrella and ancora sleeve, as well as the size of the rhabdosome, are consistently reduced.

The trend of the reduction of the ancora umbrella, with accompanied reduction of the ancora sleeve, is observed in e.g., *Sokolovograptus polonicus* Kozłowska-Dawidziuk, 1995, *Paraplectograptus eiseli* Manck, 1917, *Cometograptus kirki* Lenz and Kozłowska-Dawidziuk, 2001, *Valentinagraptus* Piras, 2006, and *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk, 1995 (Fig. 1). This trend is significant in retiolitids and starts almost from the beginning of the history of this group. Thus only the first Llandovery retiolitids possess a deep, spiral ancora umbrella (Bates and Kirk 1992) like that of *Pseudoplegmatograptus obesus* (Lapworth, 1877). Simpler ancora umbrellas occur in the rest of the retiolitids

(Kozłowska-Dawidziuk 2004: fig. 1). The new retiolitid Kirkigraptus inexpectans gen. et sp. nov. has no ancora preserved, and there are only the proxi-lateral lists forming the possible ancora umbrella rim. This may be a new pattern of reduction of the rhabdosome. This pattern of reduction is different from that in other retiolitids, where the virgella and ancora are retained. Such strong, differential reduction of the ancora is thus observed in retiolitids for the first time. If a teratological development, it would have affected only the proximal end of rhabdosome. The rest of rhabdosome of the new form consists of a simple thecal framework of two regular, almost parallel ventral walls, similar to that of Plectograptus mobergi Bates, Kozłowska, Maletz, Kirk, and Lenz, 2006 (Fig. 1). The ancora sleeve of the new form is similar to the ancora sleeve in the recently described *Valentinagraptus* Piras, 2006 of the same age as the new form, the Neodiversograptus nilssoni and Lobograptus progenitor biozones of the Barrandian. The strongly reduced ancora sleeve is represented by a few almost horizontal main lists linking the ventral walls.

The new material represents only the adult stage of colony growth; there are no young stages with the proximal end. There is a possibility that the ancora umbrella lists were not bandaged and thence not preserved.

Thus we may have an example of opportunistic development of the proximal end in the retiolitids.

## Material

The new material described in the paper is isolated and comes from the Bartoszyce borehole, Poland, East European Platform. The graptolites were recovered following slow dis-

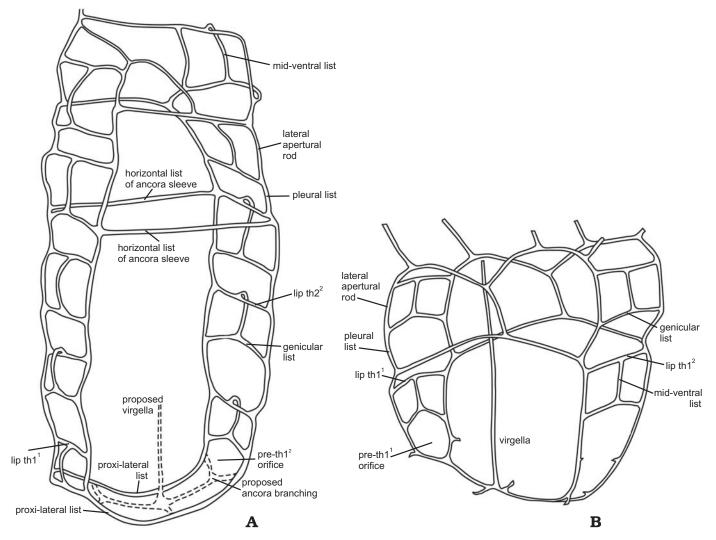


Fig. 2. Drawings showing comparison of A: reconstruction of *Kirkigraptus*, with a postulated ancora umbrella and virgella, with B: *Plectograptus mobergi* Bates, Kozłowska, Maletz, Kirk, and Lenz, 2006.

solution of the host carbonate in acid 5-10% HCl. A fine hairbrush was used to pick and transfer specimens. The material is stored on the SEM stubs and in glycerine.

## Systematic paleontology

#### Order Graptoloidea Lapworth, 1873 Family Retiolitidae Lapworth, 1873

*Emended diagnosis.*—Diplograptid rhabdosome composed of cortical bandages forming lists with the sicular and fusellar walls not usually preserved. Ancora present, a structure of four lists formed by forking at the end of the virgella; from the ancora there develops the ancora umbrella and its prolongations composing the ancora sleeve which encloses the thecae. The thecal framework comprises the nema, virga, virgella, transverse rods, lateral apertural rods, thecal lips, and connecting rods. Some structures of the rhabdosome may be reduced.

*Discussion.*—The last diagnosis of the retiolitids was published by Obut and Zaslavskaya (1983), who also included the Ordovician Archietiolitidae. Subsequently many investigations of retiolitids have been made mostly using the scanning electron microscope (e.g., Bates and Kirk 1984, 1992, 1997; Bates 1990; Lenz 1994, 1995; Lenz and Kozłowska-Dawidziuk 2001, 2004; Kozłowska-Dawidziuk 2002, 2004; Lenz and Kozłowska 2006). The new data allow us to understand better and define the retiolitid structures as well as the evolutionary tendencies of the group. The terminology of retiolitids is explained in Bates et al. (2005).

One of the main tendencies in retiolitid evolution is reduction of the rhabdosome elements; thus as a result there are many forms with rhabdosome structures reduced, e.g., instead of transverse rods only sockets occur in most Plectograptinae; and no ancora sleeve is developed in *Rotaretiolites exutus* Bates and Kirk, 1992. In the new form described herein, *Kirkigraptus inexpectans* sp. nov., there is no ancora. This is the first record of such an absence.

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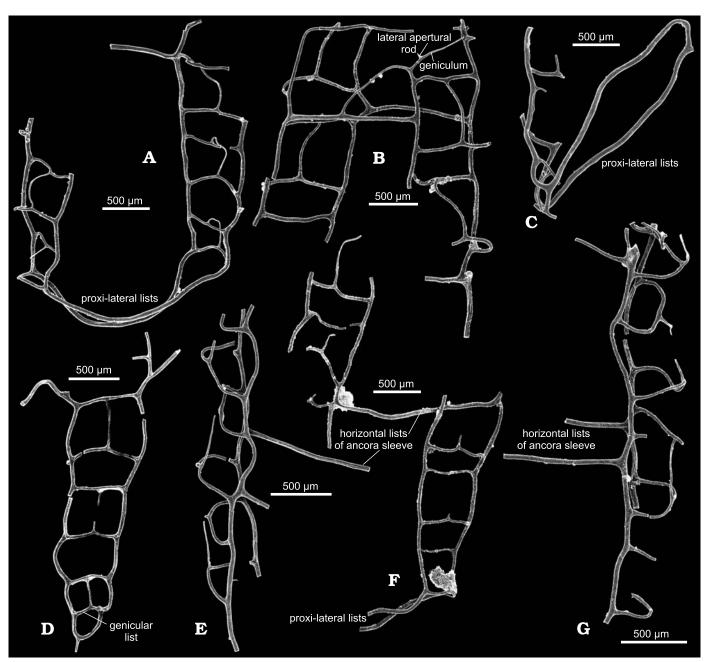


Fig. 3. SEM micrographs of plectograptine retiolitid *Kirkigraptus inexpectans* gen. et sp. nov., *Neodiversograptus nilssoni* Biozone, Ludlow, Poland. A. Rhabdosome with proximal end and two thecal rows, ZPAL G. 40/01, holotype. B. Distal growing end with malformation of the last thecal orifice on the right hand side, ZPAL G. 40/02, paratype. C. Fragment of proximal end with proxi-lateral lists complete, ZPAL G. 40/03, paratype. D. Fragment of one thecal row with proximal end, and with malformation proximal to the first genicular list, view from the inside, ZPAL G. 40/04, paratype. E. One thecal row fragment of rhabdosome with two fragments of horizontal lists of ancora sleeve, lateral view, ZPAL G. 40/05, paratype. F. Fragment of rhabdosome with two rows of thecae, ZPAL G. 40/06, paratype. G. Fragment of rhabdosome with one row of thecae, and three pieces of horizontal lists of ancora sleeve, ZPAL G. 40/07, paratype.

#### Subfamily Plectograptinae Bouček and Münch, 1952 Genus *Kirkigraptus* nov.

Type species: Kirkigraptus inexpectans sp. nov., monotypic.

*Derivation of the name*: After Nancy Kirk, the renowned palaeontologist, who discovered the actual structure of the retiolitids.

Species included.—Kirkigraptus inexpectans gen. et sp. nov.

Diagnosis .-- Proximal end without ancora; two proxi-lat-

eral lists join the two genicular lists of the first thecae, connecting the two sides of the rhabdosome. Thecal framework formed only of genicular lists, lateral apertural rods, thecal lips and mid-ventral lists. The ventral panels of lists (apertural and pleural lists) are straight. Ancora sleeve built of pleural lists and horizontal lists between the two rows of thecae. No transverse rods are present, their positions being marked by sockets. Large lateral proximal orifices are bor-

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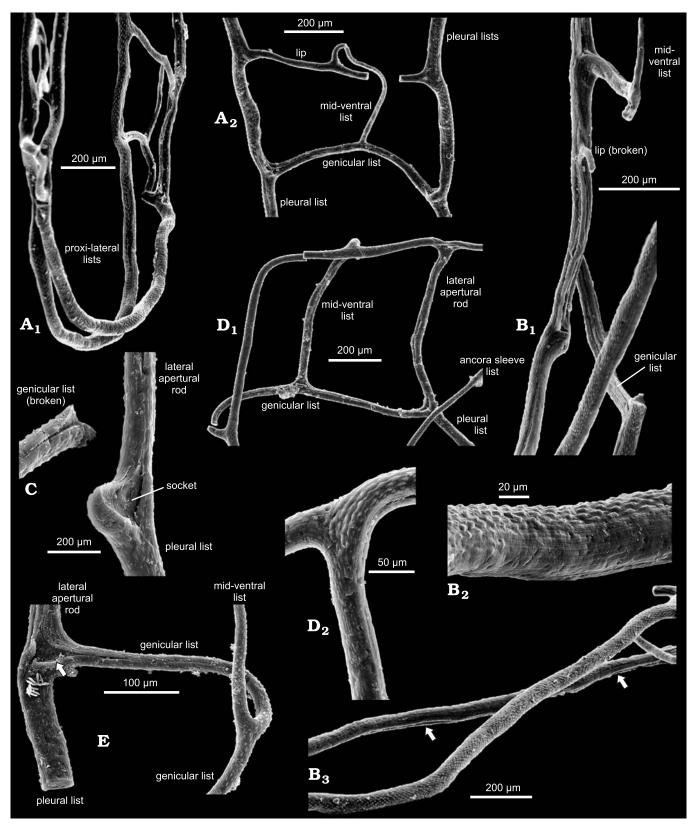


Fig. 4. SEM micrographs of plectographine retiolitid *Kirkigraptus inexpectans* gen. et sp. nov., *Neodiversograptus nilssoni* Biozone, Ludlow, Poland. A. Proximal end of fragment of specimen, oblique view, ZPAL G. 40/01; A<sub>1</sub>, oblique view, showing curved proxi-lateral lists; A<sub>2</sub>, thecal orifice, internal view. B. Fragment of rhabdosome with one side of thecae, ZPAL G. 40/03; B<sub>1</sub>, oblique view with seam on inside of lateral apertural rod; B<sub>2</sub>, proxi-lateral list, with pustular or nament on the exterior; B<sub>3</sub>, proxi-lateral lists looking proximally with seam (arrows). C. Fragment of lists showing socket, at junction of pleural list with genicular list (broken) and lateral apertural rod, ZPAL G. 40/05. D. Distal theca with last genicular list and thecal lip, ZPAL G. 40/02; D<sub>1</sub>, whole view; D<sub>2</sub>, external view of thecal lists, with two sizes of pustular ornament. E. Fragment of rhabdosome with lateral apertural list, geniculum and socket (arrowed), ZPAL G. 40/07.

dered by proxi-lateral lists and the first horizontal lists of the ancora sleeve.

*Discussion.*—The most striking feature of *Kirkigraptus* is that it is unique among the retiolitids in having no conventionally preserved ancora. The two lists, termed here the proxi-lateral lists, which unite the two ventral panels of lists, may in part represent some of the lists of a conventional ancora umbrella. Most probably the proxi-lateral lists are homologues of the distal edge of the ancora umbrella of typical retiolitids. There appear to be some seams on them, but with the limited material available, it is not possible to ascertain either their length or nature (insertion or enwrapping). The virgella and nema are also not preserved. Figure 2 shows the relationship of the two observed lists to a postulated ancora umbrella.

There are no young stages of the colony growth with the proximal end in the new material. Thus there is a possibility that the ancora umbrella had been developed in early stage of growth, but not thickened by bandages.

By analogy with the situation in *Plectograptus*, proximal to the th1<sup>1</sup> and th1<sup>2</sup> genicular lists, would be the two ventral orifices, each flanked by pleural list portions of the proxi-lateral lists. The central portions of these lists would be part of the ancora umbrella rim. But there are no broken lists or other traces found indicating the presence of an ancora umbrella connected with the proxi-lateral lists.

The size of rhabdosome of the new genus, and the arrangement of ventral panels of lists (thecal and ancora sleeve) resemble those of *Plectograptus* Moberg and Törnquist, 1909. However, whereas Plectograptus has principal lateral ancora sleeve lists forming an alternating, zig-zag arrangement, the new genus has only simple sub-horizontal lists connecting its two sides. The new genus Kirkigraptus is also similar to Valentinagraptus simplex Piras, 2006, a new form from the Neodiversograptus nilssoni and Lobograptus progenitor biozones of the Barrandian area of central Bohemia, Czech Republic. The similarities are in the size of rhabdosome, the horizontal arrangement of ancora sleeve lists, and the ventral rows of the thecal lists. However, without better study of Barrandian material (i.e., isolated in 3D) it is difficult to be sure of which portions of the longitudinal lists are the pleural and which the lateral apertural. It appears that Valentinagraptus Piras, 2006 has a normal ancora and well developed nema (Fig. 1). The difference is in lack of mid-ventral lists in the ventral walls of Valentinagraptus, whereas the lists are well developed in Kirkigraptus. There is also a difference in shape of the longitudinal (pleural and lateral apertural) lists: they are straight in Kirkigraptus gen. nov., whereas in the Barrandian form they look distinctly concave, giving a "scalloped" appearance to the lateral profile of the graptolite. The Ludlow age as well as the strong similarities of the new form with Valentinagraptus Piras, 2006 suggests a close relationship between the two forms.

The new form shows some similarities to the form described as *Sokolovograptus* (?) (Maletz et al. 1998). The form is associated with *Plectograptus macilentus* and *Spinograptus clathrospinosus*, suggesting the lower Ludlow age (Maletz et al. 1998: table 1). There is only one flattened specimen to compare (Maletz et al. 1998: pl. 1A). The form has similar horizontal ancora sleeve lists starting at about the level of theca 1<sup>2</sup>. This is much lower than in the new form. Together with the well developed nema, *Sokolovograptus* (?) sp. is most similar to the *Valentinagraptus*. But it is difficult to recognize the details of the proximal end, as well as the presence of the mid-ventral lists. For the constructive comparison we need to study an isolated specimen under SEM.

There is some similarity of *Kirkigraptus* to *Sokolovo-graptus* Obut and Zaslavskaya, 1983, especially to the most reduced form, *Sokolovograptus polonicus* (Fig. 1B). The ancora umbrella in *S. polonicus* is simple but well developed, built of strong lists. The distal edge of the ancora umbrella is rounded, similar to the proxi-lateral lists of the *Kirkigraptus*.

*Stratigraphic and geographic range.*—Bartoszyce borehole depths 1598.0 m and 1599.6 m, EEP, Poland; *Neodiverso-graptus nilssoni* Biozone, Ludlow.

#### Kirkigraptus inexpectans sp. nov.

Figs. 3, 4.

Derivation of the name: Inexpectans—after Latin inexpectus, not expected.

*Holotype*: ZPAL G. 40/01, well preserved specimen with proximal end, Fig. 3A.

*Material.*—Three specimens (two of them with complete proximal end, Fig. 3A, C; and one with partly preserved proximal end, Fig. 3F) from Bartoszyce depth 1598.0 m; five specimens without proximal end from depth 1599.2 m, eight fragments from depth 1599.6 m. Other graptolites: depth 1598.0 m: *Neogothograptus thorsteinssoni* Lenz and Kozłowska-Dawidziuk, 2001, *Pristiograptus dubius* (Suess, 1851), *Saetograptus chimaera* Barrande, 1850; depth 1599.2 m: *Neodiversograptus nilssoni* Lapworth, 1876, *Pristiograptus dubius*, *S. chimaera*, *Spinograptus spinosus*, *P. ludensis* (Murchison, 1839).

#### Diagnosis.—As for the genus.

*Description.*—The best preserved specimen (ZPAL G. 40/01) represents the proximal end and two rows of thecae: the first thecal row with two thecae, the second row with three thecae. Distance between thecal walls proximally is 2.1 mm. The distal part of the rhabdosome, represented by a fragment with four distal thecae (ZPAL G. 40/02, Fig. 3B), tapers to a width between thecal walls of about 1.5 mm. The mid-ventral lists are convex and longer than the lateral apertural rods (Fig. 3). The ventral panels of lists (apertural and pleural lists) are straight. The lateral apertural lists increase in length distally, from 0.35 mm for the most proximal, to 0.7 mm for the most distal ones. The first pleural lists are about 0.35 mm in length, but succeeding lists are about 0.28 mm in length (Fig. 3).

The first horizontal ancora sleeve list appears at the level of theca 3<sup>2</sup>, about 2 mm from the proximal end of the rhabdosome. Subsequent lists are spaced at 1.6 mm intervals (ZPAL G. 40/07, Fig. 3G).

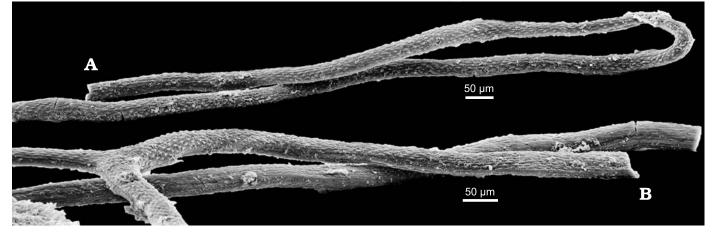


Fig. 5. SEM micrographs of plectograptine retiolitid *Kirkigraptus inexpectans* gen. et sp. nov., ZPAL G. 40/06, *Neodiversograptus nilssoni* Biozone, Ludlow, Poland. View of proxi-lateral lists, proximal (A) and distal (B) sides.

*Discussion.*—Because of the limited number of specimens, and their position on the SEM stubs, it is difficult to ascertain some of the detail of branchings and seams. Hence it is difficult to reconstruct the form of the ancora umbrella, if it existed. An attempt at reconstruction is presented in Fig. 2A. The form of the proxi-lateral lists is shown in Figs. 4B<sub>3</sub>,  $F_1$ ,  $F_2$ , and 5, the seams present are largely hidden.

Two of the specimens show what may be abnormalities. Specimen 302A (Fig. 3B) shows the growing distal end with the last thecal orifice not finished. The right hand side lists of the orifice are normal in size whereas the left hand side lists are thin, with a short list which might be a beginning of the growing genicular list on the lateral apertural rod. The last ancora sleeve list on the nearer side runs obliquely, from a junction with a horizontal sleeve list, to join the pleural list. The first orifice in the ventral wall of specimen ZPAL G. 40/04 (Fig. 3D) is much smaller than the other orifices and has a different shape, being rounded especially in its proximal part. The position and shape of the orifice make it similar to the pre-theca 1<sup>1</sup> orifice in *Plectograptus mobergi* Bates, Kozłowska, Maletz, Kirk, and Lenz, 2006 (Fig. 1). Such an orifice is not observed in the best preserved specimen (Fig. 3A) but its possibility of preservation is marked in the reconstruction of the new form on Fig. 2.

The pustular ornament, as is typical of Plectograptinae, is largely on the outer sides of the lists. An unusual feature is that ornament with pustules of two different sizes is present (Fig.  $4D_2$ ).

Stratigraphic and geographic range.—As for the genus.

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## References

- Barrande, J. 1850. *Graptolites du Bohême*. 74 pp. Théophile Hasse Fils, Prague.
- Bates, D.E.B. 1990. Retiolite nomenclature and relationships. *Journal of the Geological Society* 147: 717–723.
- Bates, D.E.B. and Kirk, N.H. 1984. Autecology of Silurian graptoloids. Special Paper in Palaeontology 32: 121–139.
- Bates, D.E.B. and Kirk, N.H. 1992. The ultrastructure, mode of construction and functioning of a number of Llandovery ancorate diplograptid and retiolitid graptolites. *Modern Geology* 17: 1–270.
- Bates, D.E.B. and Kirk, N.H. 1997. The ultrastructure, mode of construction and functioning of the genera *Stomatograptus* and *Retiolites*, with an appendix on the incremental construction of the rhabdosome of *Petalolithus*, and its comparison with that of the thecal framework in *Retiolites* and *Stomatograptus*. *Institute of Geography and Earth Sciences, University of Wales, Aberystwyth* 10: 1–168.
- Bates, D.E.B., Kozłowska, A., and Lenz, A.C. 2005. Silurian retiolitid graptolites: morphology and evolution. *Acta Palaeontologica Polonica* 50: 705–720.
- Bates, D.E.B., Kozłowska, A., Maletz, J., Kirk, N.H., and Lenz, A.C. 2006. The Silurian retiolitid graptolite *Plectograptus*: New observations and new species. *Acta Palaeontologica Polonica* 51: 525–540.
- Bouček, B. and Münch, A. 1952. Retioliti středoevropského svrchního wenloku a ludlowu. Sborník Ústředního Ústavu geologického, oddil paleontologicky 19: 1–151.
- Eisenack, A. 1951. Retioliten aus dem Graptolithengestein. Palaeontographica 100: 129–163.
- Kozłowska-Dawidziuk, A. 1995. Silurian retiolitids of the East European Platform. Acta Palaeontologica Polonica 40: 261–326.
- Kozłowska-Dawidziuk, A. 1997. Retiolitid graptolite *Spinograptus* from Poland and its membrane structures. *Acta Palaeontologica Polonica* 42: 391–412.
- Kozłowska-Dawidziuk, A. and Lenz, A.C. 2001. Evolutionary development in the Silurian Retiolitidae (Graptolites). *Journal of the Czech Geological Society* 46: 227–238.
- Kozłowska-Dawidziuk, A. 2002. Agastograptus, a synonym of Plectograptus (Retiolitidae, Graptolithina). Acta Palaeontologica Polonica 47: 459–467.
- Kozłowska-Dawidziuk, A. 2004. Evolution of retiolitid graptolites—a synopsis. Acta Palaeontologica Polonica 49: 505–518.
- Lapworth, C. 1873. On an improved classification of the Rhabdophora. *Geological Magazine* 10: 500–504, 555–560.
- Lapworth, C. 1876. On Scottish Monograptidae. *Geological Magazine* 13: 544–552.

- Lapworth, C. 1877. On the graptolites of County Down. *Proceedings of the Belfast Naturalists Field Club* 1: 107–147.
- Lenz, A.C. 1994. A sclerotized retiolitid, and its bearing on origin and evolution of Silurian retiolitid graptolites. *Journal of Paleontology* 68: 1344–1349.
- Lenz, A.C. 1995. Upper Homerian (Wenlock, Silurian) graptolites and graptolite biostratigraphy, Arctic Archipelago, Canada. *Canadian Journal of Earth Sciences* 32: 1378–1392.
- Lenz, A.C. and Kozłowska, A. 2006: Graptolites from the *lundgreni* Biozone (lower Homerian, Silurian), Arctic Islands, Canada: new species and supplementary material. *Journal of Paleontology* 80: 616–637.
- Lenz, A.C. and Kozłowska-Dawidziuk, A. 2001. Upper Wenlock (Silurian) graptolites of Arctic Canada: pre-extinction, *lundgreni* Biozone fauna. *Palaeontographica Canadiana* 20: 1–61.
- Lenz, A.C. and Kozłowska-Dawidziuk, A. 2002. Late Wenlock and early Ludlow graptolite extinction, evolution and diversification. *Special Papers in Paleontology* (C.H. Holland commemorative volume) 67: 171–183.
- Lenz, A.C. and Kozłowska-Dawidziuk, A. 2004. Ludlow and Přidoli (Upper Silurian) Graptolites from the Arctic Islands, Canada. 141 pp. NRC Research Press, Ottawa, Ontario.
- Manck, E. 1917. Die Graptolithen der Zone 18, sowie *Retiolites eiseli* sp. nov. *Zeitschrift für Naturwissenschaft* 86: 337–344.

- Maletz, J., Königshof, P., Meco, S., and Schindler, E. 1998. Late Wenlock to Early Ludlow graptolites from Albania. *Senckenbergiana Lethaea* 78: 141–151.
- Moberg, J.C. and Törnquist, S.L. 1909. Retiolitoidea från Skånes Colonusskiffer. Sveriges Geologiska Undersökning C 213: 1–20.
- Murchison, R.I. 1839. The Silurian System, Founded on Researches in the Countries of Scalop, Hereford, Montgomery, Carmarthen, Brecon, Pembroke, Monmouth, Glucester, Worcester, and Stafford: with Description of the Coal-Fields and Overlaying Formation. xx+523 pp. John Murray, London.
- Obut, A.M. and Zaslavskaya, N. 1983. Families of retiolitids and their phylogenetic relationships [in Russian]. In: A.S. Dagys and V.N. Dubatolov (eds.), Morfologiâ i sistematika bespozvonočnyh fanerozoâ, 103–113. Izdatelstvo Nauka, Moskva.
- Piras, S. 2006. Valentinagraptus a new genus of plectograptid graptoloid from the lower Ludlow (Silurian) of Barrandian, Bohemia. Geological Journal 41: 581–590.
- Suess, E. 1851. Über böhmische Graptolithen. Naturwissenschaftliche Abhandlungen 4: 87–134.
- Zalasiewicz, J. and Tunnicliff, S. 1994. Uppermost Ordovician graptolite biostratigraphy of the Wye Valley, central Wales. *Palaeontology* 37: 695–720.