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Authors: Kozłowska, Anna, Dobrowolska, Kinga, and Bates, Denis E.B.

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A new type of colony in Silurian (upper Wenlock) retiolitid graptolite *Spinograptus* from Poland

ANNA KOZŁOWSKA, KINGA DOBROWOLSKA, and DENIS E.B. BATES



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The new retiolitid species, *Spinograptus tubothecalis*, is described from the *Colonograptus praedeubeli* and *C. deubeli* biozones from two localities in Poland: a borehole on the East European Platform and the Holy Cross Mountains. This was a recovery phase after the severe Silurian *Cyrtograptus lundgreni* Event. The new species has a unique, previously undescribed form of finite rhabdosome. Unlike the species *Spinograptus reticulolawsoni* and *S. lawsoni*, in which the finite rhabdosomes taper distally, its rhabdosome is parallel-sided with the two distal thecae developed as isolated tubes without genicular processes, with a small appendix between them. The new species also has preserved membranes of the sicula, thecae and ancora sleeve, similar to a few species of *Spinograptus* from the lower Homerian. *Spinograptus tubothecalis*, like *Spinograptus clathrospinosus* and *S. spinosus*, has paired reticulofusellar genicular processes on the pre-thecal ventral orifices, similar to but shorter than thecal processes. Transverse rods, a rare character in post-*Cyrtograptus lundgreni* Event retiolitids occur in the new species in rudimentary form.

Key words: Graptoloidea, Retiolitidae, *Spinograptus*, finite colony, Silurian, Poland.

Anna Kozłowska [akd@twarda.pan.pl] and Kinga Dobrowolska [kdobrowolska@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland;
Denis E.B. Bates [deb@aber.ac.uk], Institute of Geography and Earth Sciences, Aberystwyth University, Aberystwyth, Ceredigion SY23 3QQ, UK.

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Introduction

The last 25 years of study of retiolitid graptolites has brought to light more information about the evolution, anatomy, astogeny, and mode of life of these colonial organisms (Bates and Kirk 1984, 1992, 1997; Lenz and Melchin 1987; Lenz 1993; Kozłowska-Dawidziuk 1995, 1997, 2004) than the previous one hundred years. This is largely due to the use of isolated specimens and the scanning electron microscope (SEM).

Spinograptus spinosus was one of the first retiolitids to be described, about 110 years ago, by Wood (1900). It was illustrated in three small line drawings of flattened specimens. Today we know of eight species of *Spinograptus*, and the ultrastructural details of three dimensional specimens. They vary in many characters, such as the development of the paired reticulofusellar processes on the geniculum, and the development of the reticulum of the ancora sleeve and thecae (Kozłowska-Dawidziuk 1997; Kozłowska-Dawidziuk et al. 2001). These species appeared during a diversification phase of the plectograptinid retiolitids (Porębska et al. 2003), which followed the *Cyrtograptus lundgreni* Event, one of the most severe extinction events experienced by graptolites. The youngest species of *Spinograptus* known is from the *Neodiversograptus nilssoni* Biozone (Fig. 1), except in Arctic Canada where two species reach the *Saetograptus linearis–Monograptus ceratus* Biozone (Lenz and Kozłowska-Dawidziuk 2004).

The paper describes the new species *Spinograptus tubothecalis* with its new, unique type of finite rhabdosome.

Institutional abbreviations.—ZPAL, Institute of Paleobiology Polish Academy of Sciences, Warsaw, Poland.

New observations on retiolitid colony development

Many retiolitids, as with most other graptoloids, grew rhabdosomes along linear stipes that are open-ended. They have almost parallel walls or widen distally, such as *Stomatograptus* Tullberg, 1883 and the youngest and smallest, *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk, 1995 (Kozłowska-Dawidziuk 2004: fig. 1).

There are some retiolitids, as well as some other graptolites (e.g., *Corynites wyszogrodensis* Kozłowski, 1956), that

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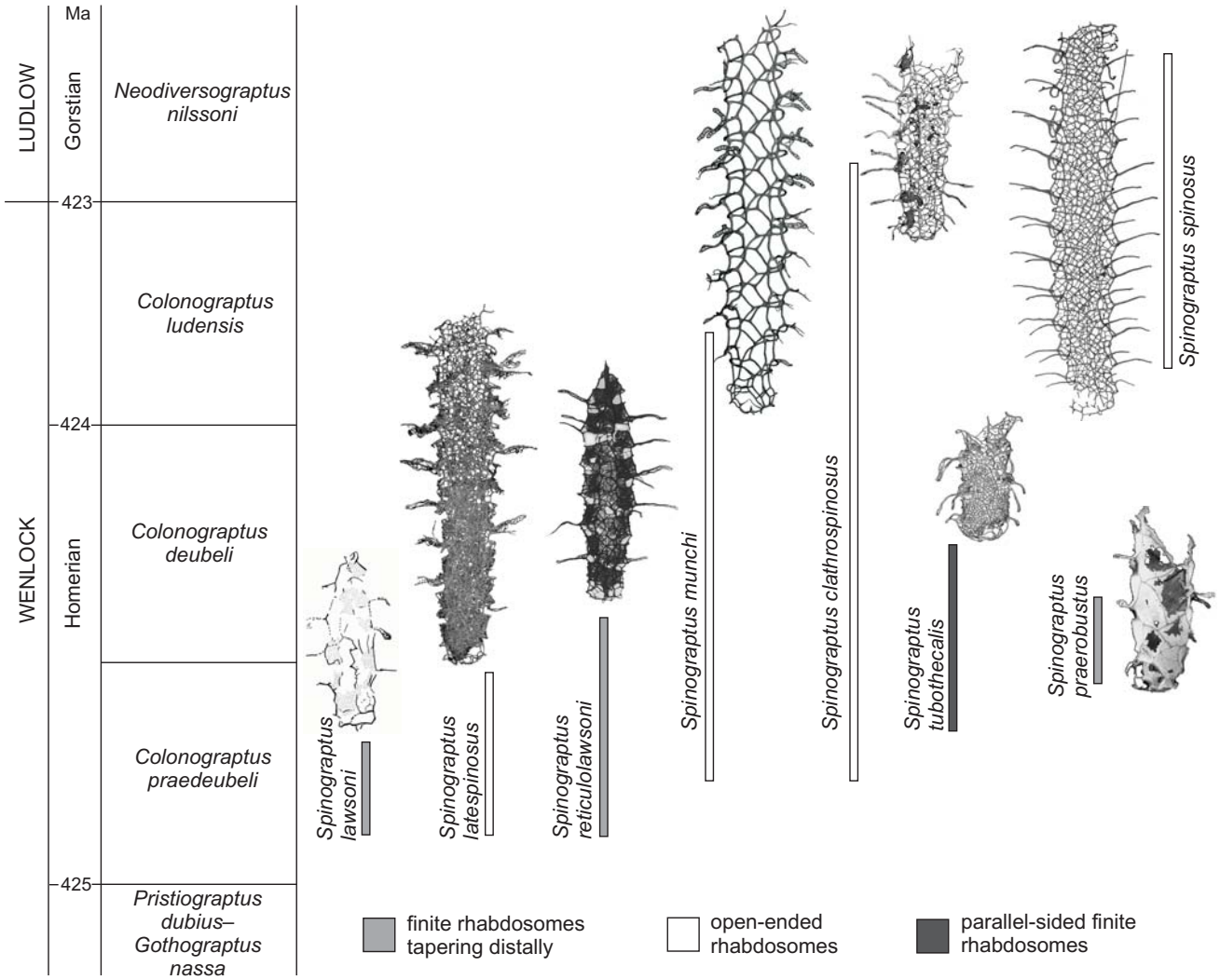


Fig. 1. Stratigraphical sequence of the *Spinograptus* species, with new data from this paper and Kozłowska-Dawidziuk 1997: fig. 12. The ranges of *Spinograptus spinosus* (Wood, 1900) and *S. clathrospinosus* Eisenack, 1951 reach the *Saetograptus linearis–Monograptus ceratus* Biozone in the Arctic Canada (Lenz and Kozłowska-Dawidziuk 2004), which is not marked herein.

have finite ends to their colonies. Many retiolitids have rhabdosomes that taper distally and are ended by an appendix. They belong to the *Gothograptus* lineage, appearing in the late Sheinwoodian, (e.g., *Gothograptus* Frech, 1897 and *Eisenackograptus* Kozłowska-Dawidziuk, 1990), and continue to the end of the Gorstian (*Neogothograptus* Kozłowska-Dawidziuk, 1995 and *Holoretiolites* Eisenack, 1951). The rhabdosomes vary from 23 pairs of thecae in *Gothograptus nassa* Holm, 1890 to two pairs of thecae in *Neogothograptus alatiformis* Lenz and Kozłowska-Dawidziuk, 2004 (Kozłowska-Dawidziuk 2004: fig. 1).

The genus *Spinograptus* has quite a large variation of forms with strong differences in the development of characters, such as reticulum density and the shape of the reticulofusellar genicular processes (Fig. 1). The most striking and variable character is the end of the colony. There are three different types of endings of *Spinograptus* rhabdosomes: open ended (e.g., *S. spinosus* Wood, 1900), finite tapering distally ended by an appendix (*S. reticulolawsoni* Kozłowska-Dawidziuk, 1997, *S. praerobustus* Lenz and Kozłowska-Dawidziuk, 2002, and *S. lawsoni* Holland, Rickards, and Warren, 1969), and the new type described here. It is finite and parallel-sided distally, with a short appendix (Figs. 2–5), isolated from the distal thecae.

The finite rhabdosome with parallel walls to the end of the rhabdosome represents a newly discovered type of colony, found only in the new species *Spinograptus tubothecalis* (Figs. 2–5). Its rhabdosome is short, having three to four pairs of thecae with a diminutive appendix between the last two thecae. In this new type the nema is connected to the wall just below the appendix (Figs. $2A_1$, A_3, 4A, B_3), whereas in *Gothograptus* and *Eisenackograptus* it is connected in the proximal and distal part of the rhabdosome respectively, and runs along the wall of a usually long appendix. The two distal thecae are developed differently from the others, being partly isolated tubes without characteristic paired genicular processes (Figs. $2A_1$, 3C, 4, 5). Their orifices are surrounded by thecal lip, genicular and pleural lists (Fig. 3B, C).

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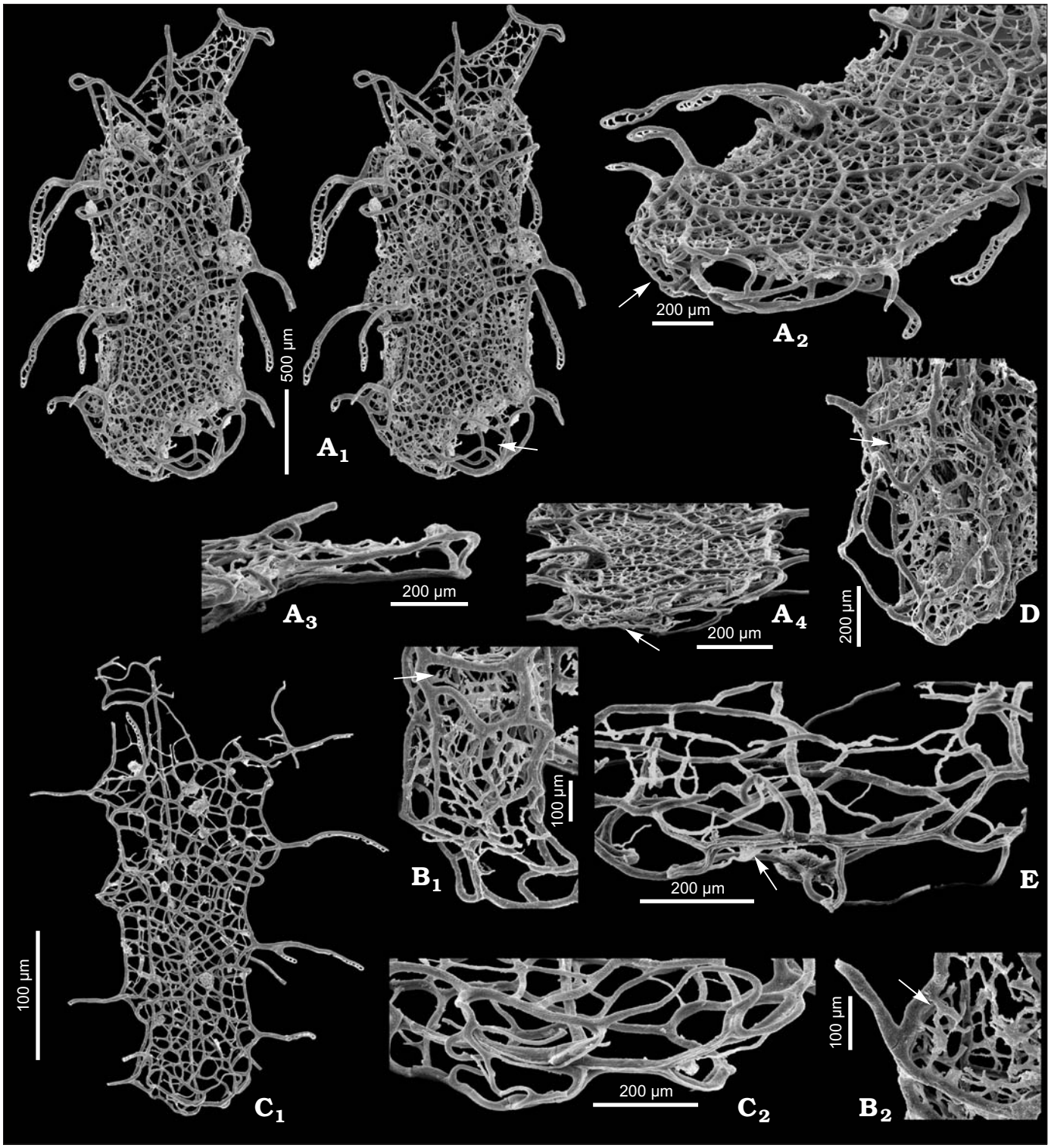


Fig. 2. Retiolitid graptolites *Spinograptus tubothecalis* sp. nov. and *Spinograptus clathrospinosus* Eisenack, 1951 from the Gołdap IG-1 borehole, Poland. **A**, **B**, **D**, **E**. *Spinograptus tubothecalis* sp. nov., depth 1267.0 m, *Colonograptus deubeli* Biozone, Wenlock. **A**. ZPAL G. 47/1, holotype, stereopair of obverse view of finite rhabdosome, proximal lateral orifice (arrow) (A_1); proximal view of rhabdosome (A_2), outer ancora arrowed; proximal view of isolated last theca and nema (A_3); ancora umbrella and dense outer ancora at th 1^1 side of rhabdosome (arrow) (A_4). **B**. ZPAL G. 47/5, th 1^1 side view of proximal part of rhabdosome showing dense outer ancora and pre-thecal ventral orifice overgrown by reticulum (arrow) (B_1), rudimentary transverse rod (arrow) (B_2). **D**. ZPAL G. 47/8, th 1^2 side view of proximal part of rhabdosome showing overgrown pre-thecal ventral orifice (arrow). **E**. ZPAL G. 47/9, proximal view of immature rhabdosome showing ancora umbrella and outer ancora starting to grow (arrow). **C**. *Spinograptus clathrospinosus* Eisenack, 1951, ZPAL G. 47/10, depth 1259.0 m, *Colonograptus ludensis* Biozone, Wenlock, open-ended rhabdosome with three pairs of thecae, lateral view (C_1), obverse view of proximal end of rhabdosome (C_2) showing ancora umbrella and outer ancora at th 1^1 side of rhabdosome.

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Methods

The graptolites were recovered following slow dissolution of the host carbonate in acid (1–10% HCl). A fine hairbrush was used to pick up and transfer specimens. The material is stored in plastic containers in glycerin and on SEM stubs (10b, 18b, 19b, 324) at ZPAL.

Systematic paleontology

Order *Graptoloidea* Lapworth, 1873

Family *Retiolitidae* Lapworth, 1873

Subfamily *Plectograptinae* Bouček and Münch, 1952

Genus *Spinograptus* Bouček and Münch, 1952

Type species: *Retiolites spinosus* Wood, 1900. Lectotype BU 1366, figured Wood 1900: pl. 25: 29A, selected and refigured Elles and Wood 1908: pl. 34: 16a (Strachan 1971: 48). Lower Ludlow, *Neodiversograptus nilssoni* Biozone, West borderland, United Kingdom.

Species included.—*Retiolites spinosus* Wood, 1900; *Retiolites clathrospinosus* Eisenack, 1951; *R. münchi* Eisenack, 1951; *Holoretiolites* (*Balticograptus*) *lawsoni* Holland, Rickards, and Warren, 1969; *Agastograptus quadratus* Lenz, 1993; *Spinograptus reticulolawsoni* Kozłowska-Dawidziuk, 1997; *S. latespinosus* Kozłowska-Dawidziuk, 1997; *S. praerobustus* Lenz and Kozłowska-Dawidziuk, 2002; *S. tubothecalis* sp. nov.

Emended diagnosis (modified from Maletz 2010).—Nema free, exceptionally in two species attached distally, to obverse wall of short appendix; shallow ancora umbrella; outer ancora may be present; pre-thecal ventral orifices sometimes with paired processes, sometimes overgrown by reticulum; proximal lateral orifices above ancora umbrella medium sized; ventral wall formed of lip, genicular and lateral apertural lists; rudimentary mid-ventral lists and transverse rods sometimes present; ancora sleeve formed of oblique lists arranged in zigzag pattern; reticulum may be present on ventral and lateral walls; paired, reticulofusellar genicular processes. Rhabdosomes may be open-ended or finite with short appendices, the finite rhabdosomes may taper distally or exceptionally be parallel-sided with two distal isolated thecae with openings directed distally.

Remarks.—Our observations of the new species *Spinograptus tubothecalis* show a new character within *Spinograptus*, which is also unique among post *Cyrtograptus lundgreni* retiolitids: the nema attached distally to the obverse wall. This character is also possible in *S. reticulolawsoni*, but is not so clearly seen because of the presence of membranes in a flattened specimen (Kozłowska-Dawidziuk 1997: fig. 10A, B). An outer ancora, not mentioned in Maletz's (2010) diagnosis, is present in three species: *S. reticulolawsoni*, *S. clathrospinosus*, and *S. tubothecalis* sp. nov. Maletz (2010) described parietal lists of the lateral walls often arranged in an irregular zigzag pattern, but in the referred material the zigzag pattern is rather regular.

Spinograptus tubothecalis sp. nov.

Figs. 2A, B, D, E, 3A–D, 4.

Etymology: From Latin *tubo*, tube and *theca,* theca; due to the shape of the two last thecae.

Type material: Holotype ZPAL G. 47/1, stub 18b, Figs. 2A, 3C; paratype ZPAL G. 47/6, stub 324, Fig. 4A.

Type locality: Gołdap IG-1 borehole, depth 1267.0 m, Poland, East European Platform.

Type horizon: *Colonograptus deubeli* Biozone, Homerian, Wenlock, Silurian.

Referred material.—The well preserved isolated, slightly flattened specimens come from two localities: the Gołdap IG-1 borehole, depth 1267.0 m and a nodule from Prągowiec 2, Holy Cross Mountains, Poland. Gołdap IG-1 contains one finite rhabdosome and 65 fragments, mostly proximal parts of young and mature rhabdosomes of *S. tubothecalis* sp. nov.; *Plectograptus robustus*, and monograptids: *Colonograptus deubeli*, *Pristiograptus dubius ludlowensis*, *Pristiograptus ludensis*, representing the *Colonograptus deubeli* Biozone. From the second location, Prągowiec 2, are 800 specimens, mostly of the medial part of rhabdosomes, several proximal and distal ones, together with *Neogothograptus reticulatus* Kozłowska, Lenz, and Melchin, 2009; *Plectograptus*? and *Colonograptus colonus*, representing the *Colonograptus praedeubeli* Biozone.

Diagnosis.—Parallel-sided, densely reticulated rhabdosome terminated by small appendix located between two distal thecae. Rhabdosomes contain three to four pairs of thecae. Pre-thecal ventral orifices with paired short, apertural processes; in mature rhabdosomes orifices may be overgrown by reticulum. Paired reticulofusellar apertural processes similar to *Spinograptus clathrospinosus*. Two distal thecae tube-shaped, and isolated, having rounded openings built by lip, lateral apertural rod and geniculum without processes. Reticulated outer ancora present in some specimens. Nema free through rhabdosome except species with finite rhabdosomes where most distal part of nema is included in the appendix wall.

Description.—The holotype ZPAL G. 47/1, a well preserved finite rhabdosome, is 2.64 mm long, and bears three pairs of thecae (Figs. $2A_1$, 3C). There are some fragments, especially from Prągowiec 2, indicating rhabdosomes with four pairs of thecae. It is about 1 mm wide between the pre-thecal ventral orifices, and about 0.93 mm between the second pair of thecae. The ancora umbrella is asymmetric, typical for *Spinograptus*, with proximal lateral orifices located on $th1^2$ side (Fig. $2A_1$, A_2). The reticulum on the ancora umbrella, as well as on the outer ancora is developed only on the $th1^1$ side, mainly in mature rhabdosomes in specimens from Gołdap (Fig. $2A_4$, B_1, D). The reticulum is denser in specimens from Gołdap than from Prągowiec 2 (see Figs. 2A, B, D, 4). The pre-thecal ventral orifices have paired processes half the size of the thecal processes. The orifices are sometimes over-

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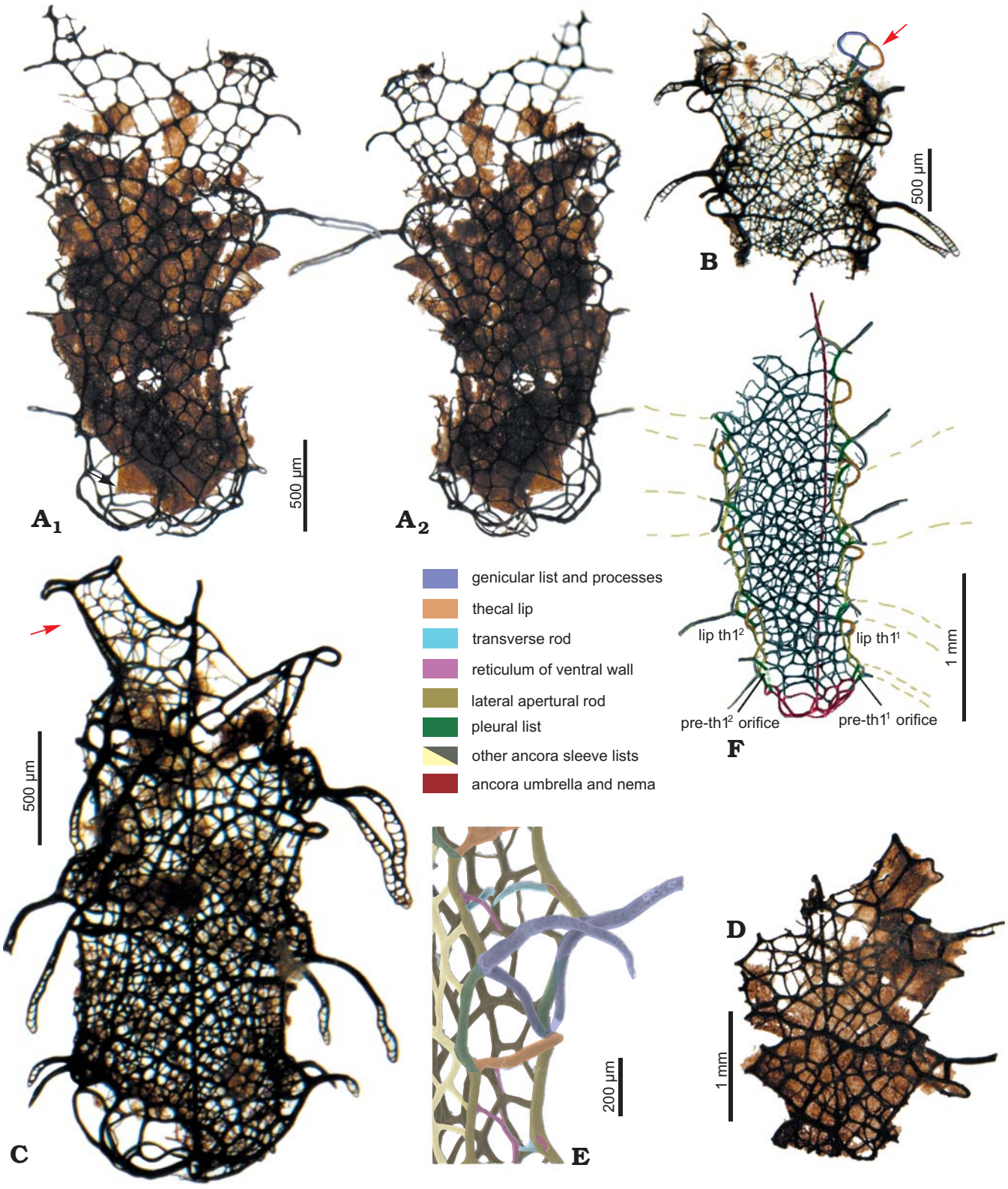


Fig. 3. Retiolitid graptolite *Spinograptus tubothecalis* sp. nov. rhabdosomes (A–D) showing thecal membranes (brown) and *Spinograptus spinosus* (Wood, 1900) (E, F) showing morphological details. **A**, **B**, **D**. Fragments of rhabdosomes from Prągowiec 2, *Colonograptus deubeli* Biozone. **A**. ZPAL G. 47/2, well preserved proximal end and three pairs of thecae obverse (A_1) and reverse (A_2) views, metasicula arrowed. **B**. ZPAL G. 47/3, tuboid distal theca arrowed. **D**. ZPAL G. 47/4, well preserved membranes and tuboid distal theca. **C**. Finite rhabdosome, holotype from Gołdap IG-1 borehole (1267.0 m), *Colonograptus deubeli* Biozone, ZPAL G. 47/1, obverse view with isolated distal theca (arrow). **E**. *Spinograptus spinosus* (Wood, 1900) from Gołdap IG-1 borehole (1250.0 m) *Neodiversograptus nilssoni–Lobograptus progenitor* Biozone, ZPAL G. 47/12, morphology of ventral wall. **F**. *Spinograptus spinosus* (Wood, 1900) from Jarosławiec K2, ZPAL G. 47/11, young rhabdosome, dotted lines show possible broken spines. Light microscope pictures (A–D), SEM pictures (E, F).

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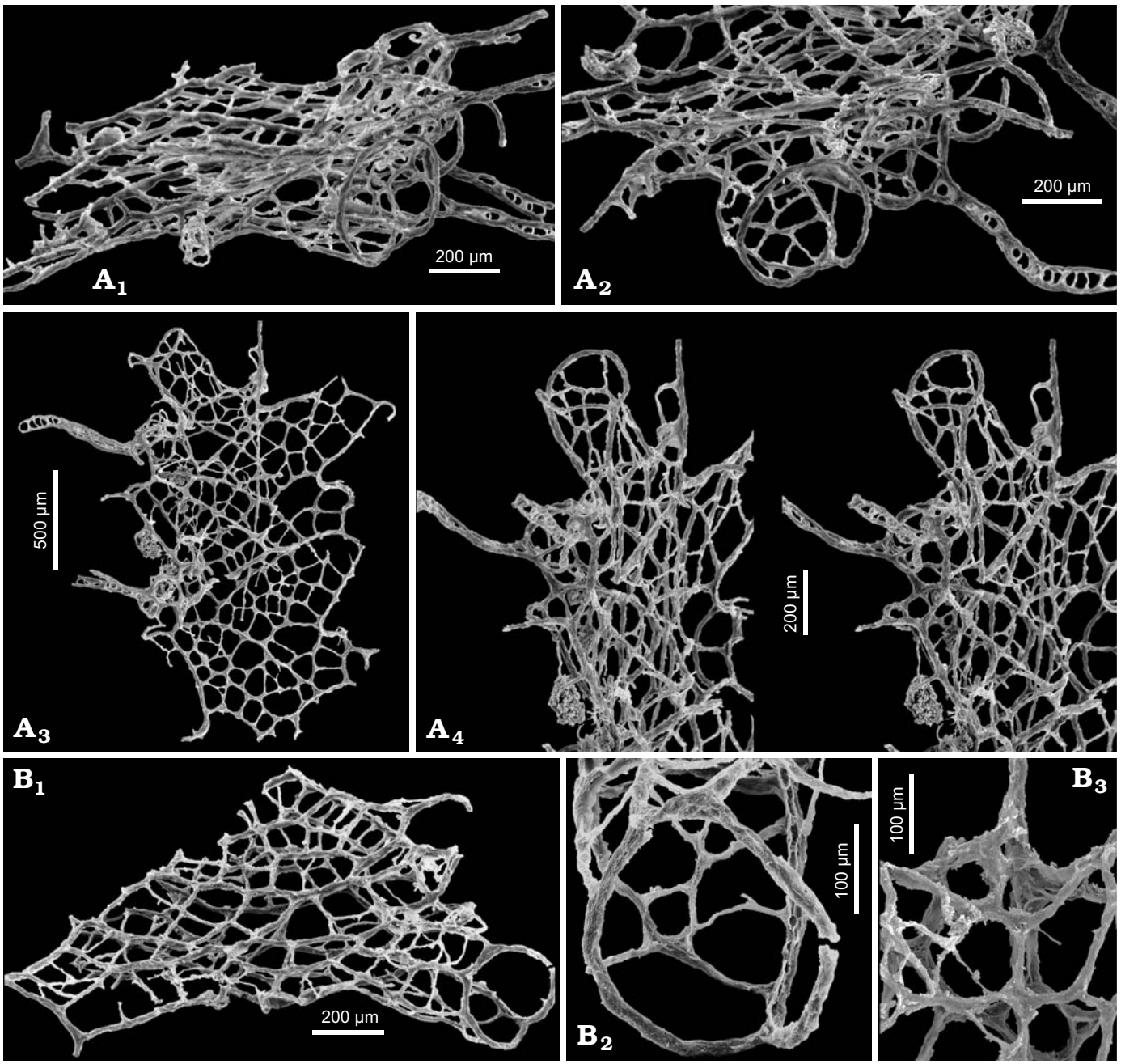


Fig. 4. Retiolitid graptolite *Spinograptus tubothecalis* sp. nov. from Prągowiec 2, *Colonograptus deubeli* Biozone. **A**. ZPAL G. 47/6, paratype, distal end of rhabdosome with three well preserved thecae on one side and small appendix; distal view (A_1), view towards the inside of last theca (A_2), lateral view of whole specimen (A_3), stereopair of the better preserved thecae (A_4). **B**. ZPAL G. 47/7, distal end of rhabdosome with two last thecae and terminal structure; distal view of the whole fragment (B_1); view to the inside of last theca (B_2); terminal structure (B_3).

grown by reticulum (Fig. $2B_1$, D). The apex of the well preserved sicula reaches to the end of second pair of thecae; the length of sicula is 1.1 mm. The two first pairs of thecae have paired reticulofusellar processes about 0.7 mm long. The last theca in the holotype is developed as a partly isolated tube with rounded openings made by the genicular, pleural and thecal lip lists without paired apertural processes (Fig. $2A_1$). The specimens from Prągowiec 2 have two distal thecae (Fig. 4) similarly developed as the last theca in the holotype. The isolated parts of the distal thecae are about 0.5 mm long. Between the distal thecae is a small appendix of about 60 µm diameter (Figs. $2A_1$, 4A). In a young specimen with one theca developed the outer ancora has already started to grow (Fig. 2E). Mid-ventral lists are short, developed only at the first pair of thecae (Fig. $2A_1$). The rudimentary transverse rods are at first pair of thecae (Fig. $2B_2$). The dense reticulum of the ventral walls makes it difficult to check the presence of transverse rods in the most distal thecae. The nema is free up to the appendix, where it is attached to the wall on the obverse side of the rhabdosome (Figs. $2A_1$, A_3, 4A, B_3). Very

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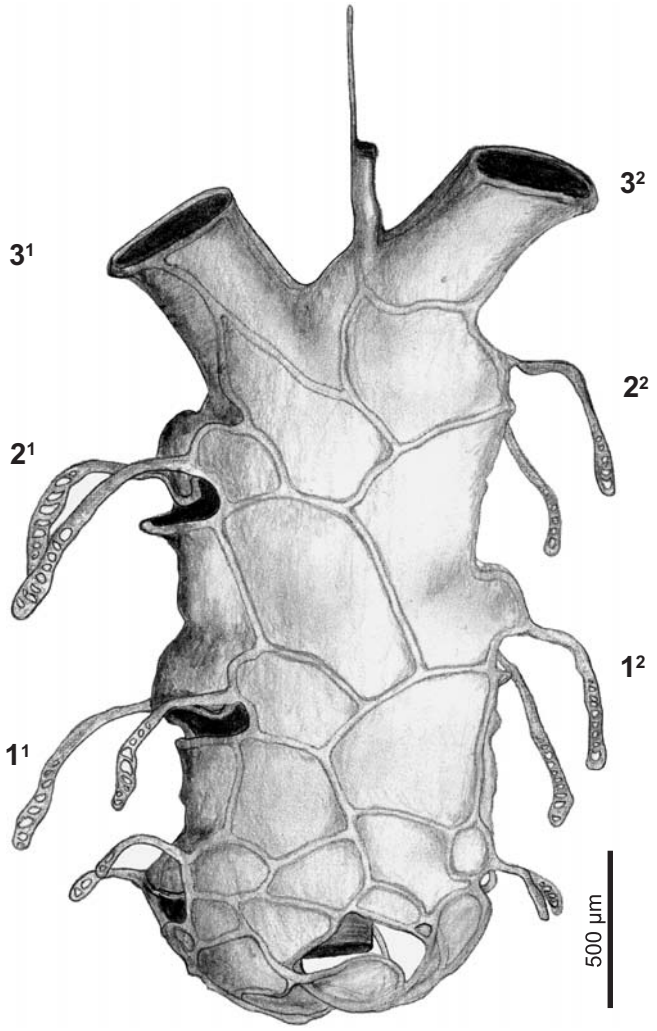


Fig. 5. Drawing of retiolitid graptolite *Spinograptus tubothecalis* sp. nov., in obverse view, with reconstructed membranes. The ancora umbrella membrane is hypothetical. Note the short finite rhabdosome with characteristic two last tube-shaped thecae without genicular processes and very small and narrow appendix. Drawing AK.

dense reticulum occurs in mature rhabdosomes, developed in the thecal and ancora sleeve walls (Fig. $2A_1$). Among specimens from both localities there are several with the sicular and thecal membranes preserved (Fig. 3A–D).

Discussion.—The distal end of the new species differs from that in other species of *Spinograptus*. The last two thecae, partly isolated, have unusual rounded openings without genicular processes (Figs. $2A_1$, A_3, 3B, C, 4A, B_1, B_2). Such openings are unique among all retiolitids. The rudimentary appendix in the new form is similar to that in other species of *Spinograptus* with appendixes, but does not extend more distally than the last thecae.

Spinograptus tubothecalis sp. nov. belongs to the older group of *Spinograptus* species, occurring in *Colonograptus praedeubeli* and *C. deubeli* biozones (Fig. 1). Most of them have, unusually for the retiolitids, well preserved peridermal membranes, both thecal and ancora sleeve (*S. lawsoni*, *S. latespinosus*, *S. reticulolawsoni, S. praerobustus*, and *S. tubothecalis* sp. nov.). This kind of preservation does not usually occur in other retiolitids (Lenz 1994a, b; Kozłowska-Dawidziuk 1997; Lenz and Kozłowska-Dawidziuk 2002). The new species probably had an ancora sleeve membrane (Fig. 5), which was too thin to be preserved.

Finite rhabdosomes occur in four species of *Spinograptus* together with the new one; the new species representing at the same time the new type of the finite rhabdosome. The new species is similar to *S. reticulolawsoni* Kozłowska-Dawidziuk, 1997 in having a finite colony ended by a short, rudimentary appendix. The most significant difference is in the sides of the finite rhabdosomes, which taper distally in *S. reticulolawsoni* and are parallel in the new species (Fig. 1).

The older species of *Spinograptus*: *S. reticulolawsoni*, *S. latespinosus*, and *S. clathrospinosus* have a dense reticulum. The new species *S. tubothecalis* has the densest reticulum of all the *Spinograptus* species, not only on the ancora umbrella and the thecal and ancora sleeve walls, but the reticulum of the outer ancora is also much denser than in other species, e.g., *S. clathrospinosus*, and is located at the $th1^1$ side of rhabdosome (Fig. $2C_2$). The pre-thecal ventral orifices are sometimes overgrown by dense reticulum. Among *Spinograptus* species the paired genicular processes, present in the new species, occur also in *S. spinosus* and *S. clathrospinosus.* Another feature of the new species is the presence of a rudimentary transverse rod, which is characteristic in pre-*Cyrtograptus lundgreni* retiolitids.

Geographic and stratigraphic range.—Gołdap IG-1 borehole, East European Platform, and Prągowiec 2, Holy Cross Mountains, Poland; *Colonograptus deubeli* Biozone and *Colonograptus praedeubeli* Biozone respectively.

Conclusions

There is a large variation in the development of retiolitid rhabdosomes, e.g., open ended with many thecae to finite with few thecae. Typical for some finite rhabdosomes is the appendix, possibly a modified last theca ending the rhabdosome. Usually one type of rhabdosome is characteristic of each retiolitid genus. However, in *Spinograptus* we observe some variation of rhabdosome development, both open ended and finite. *S. tubothecalis* sp. nov. represents a new type of finite rhabdosome, never observed before. Its short rhabdosome has two tube-shaped, isolated distal thecae, with rounded openings built by thecal lip, genicular and pleural lists, without processes. The thecae are directed upwards and between them there is the small appendix.

The transverse rods found in *S. tubothecalis* sp. nov., a character present in pre-*Cyrtograptus lundgreni* Event, shows a combination of primitive and advanced characters in *Spinograptus*, implying a mosaic pattern of its evolution. The new material gives us new data about graptolite evolution.

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