Retiolitid graptolite *Spinograptus* from Poland and its membrane structures

ANNA KOZŁOWSKA-DAWIDZIUK

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Spinograptus reticulolawsoni sp. n., *S. latespinosus* sp. n., *S.* cf. *latespinosus*, and *S.* sp. are described from borecore samples of the late Wenlock (*Colonograptus*? *praedeubeli* Zone), of the Bartoszyce borehole, NE Poland. They represent an early diversification phase of retiolitids, which followed the *Cyrtograptus lundgreni* Event. Some species display a combination of primitive and advanced characters, implying a mosaic pattern of *Spinograptus* evolution. Most of the material studied contains continuous peridermal membranes, suggesting that they may have been universally present in the retiolitids. Long (2 mm) siculae found in two species of *Spinograptus* contrast with short siculae, known for *Retiolites* and *Paraplectograptus*.

K e y w o r d s : graptolites, retiolitids, membrane, phylogeny, Silurian, Poland.

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

Introduction

Until recently (e.g., Bulman 1970; Mitchell 1987), the retiolitids were considered a specialized group of the diplograptids with non sclerotized siculae and thecae, and the periderm reduced to lists. The reticulum was interpreted as being equivalent to the thecal wall. Traces of prosiculae are rarely found, only in the oldest forms, belonging to *Retiolites* Barrande, 1850; *Stomatograptus* Tullberg, 1883; *Pseudoretiolites* Bouček & Münch, 1952; *Paraplectograptus* Bouček & Münch, 1952; and *Sokolovograptus* Obut & Zaslavskaya, 1976 (in Obut & Zaslavskaya 1976; Lenz & Melchin 1987a; Kozłowska-Dawidziuk 1995).

Remnants of the thecal wall were first illustrated by Holm (1890) in *Stomatograptus tornquisti* Tullberg, 1882, and observed in *Retiolites* by Lenz & Melchin (1987b) in SEM micrographs. The presence of the traces of incremental periderm and seams on retiolitid lists led Bates (1990) and Bates & Kirk (1992) to the conclusion that

retiolitids possessed a thecal peridermal wall inside, with the reticulum forming an outer ancora sleeve, formed as a separate membrane by the distal development of virgellar structures. Most of the lists represent part of the ancora sleeve. Well preserved retiolitid membranes of the sicula, thecae, and ancora sleeve have so far been found only by Lenz (1994a, b) in *Agastograptus robustus* Obut & Zaslavskaya, 1983.

The new material described below is of isolated, flattened rhabdosomes of both young and adult growth stages of two species of *Spinograptus* (*sensu* Kozłowska-Dawidziuk 1995), possessing fragments of siculae, thecal and ancora sleeve membrane.

Material

The investigated material comes from the Bartoszyce IG 1 borehole situated on the Peribaltic Syneclise belonging to the Polish part of the East European Platform (Fig. 1). The Silurian of this region has been penetrated by numerous boreholes (Tomczyk 1964, 1968; Teller 1976, 1986). The Bartoszyce core contains grey shales and marls with parallel lamination. Graptolites are randomly dispersed, indicating a very quiet sedimentation regime (Jaworowski 1965). The total thickness of the Silurian rocks in this borehole is about 300 m. The graptolite fauna is generally abundant, but the specimens are more or less compressed.

The retiolitids studied herein come from three horizons: 1642.0 m, 1641.2 m, and 1640.0 m. The associated monograptids *Pristiograptus dubius* (Suess, 1851) and *Colonograptus*? *praedeubeli* (Jaeger, 1990) (Fig. 2) indicate the *C.*? *praedeubeli* Zone of the late Wenlock. Most of them display an almost fully or at least partially preserved thin periderm of both the thecae and the ancora sleeve. Some rhabdosomes are provided with only traces of the periderm, and the state of preservation of this material sometimes makes it difficult to distinguish whether the preserved fragments belong to the thecal walls or to the ancora sleeve.

The material studied is stored in the Institute of Palaeobiology of the Polish Academy of Sciences in Warsaw (abbreviated ZPAL). The abbreviation IG stands for the Polish Geological Institute.

I follow the terminology of Bulman (1970) and Kozłowska-Dawidziuk (1995).

Measurements: In case of flattened material there are problems with accurate measurements. The width of the lateral wall refers to the distance between the pleural lists (Fig. 4). Approximate distances between pleural lists are similar in rhabdosomes flattened laterally or ventrally. In laterally flattened specimens the term of l a t e r a l w i d t h means the width of the lateral wall plus the distance from pleural to medial lists, as in Fig. 7A, but excludes apertural processes.

Membrane periderm in *Spinograptus*

About 80% of the specimens of *Spinograptus* from depth 1640.0 m, and some from depths 1641.2 and 1642.0 m, preserve a more or less fragmentary periderm. The thecal wall periderm cannot be separated from the membrane belonging to the ancora sleeve

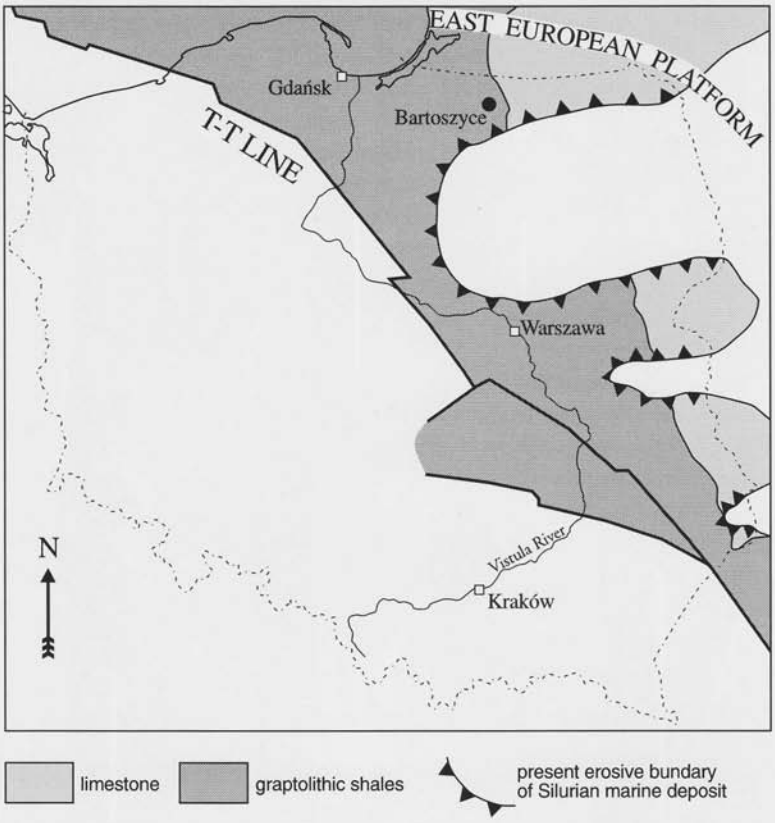

Fig. 1. Sketch map of the north-eastern part of Poland showing the location of the Bartoszyce IG 1 borehole.

in this material. The periderm is thin, translucent, and light brown in colour (Fig. 3), mostly with a spongy texture (Fig. 6C). Only a few fragments of periderm have smoother sheets (Fig. 6B).

Some fragments of the prosicula and metasicula (Fig. 4) are preserved in a young rhabdosome of *Spinograptus* sp. ZPAL G.VIII/90 with four pairs of thecae. The prosicular apex is located level with the aperture of theca 3^1. The prosicula is bordered by the virga (Bates & Kirk 1992) on one side and by a strong longitudinal rod on the opposite side. A fragment of periderm with thin longitudinal rods is preserved at the proximal end of the prosicula. The end of the strong broken rod probably corresponds to the prosicular ring (Fig. 4). Only the medial part of the metasicula is preserved. Part of the edge of the metasicula is readily visible because of its darker periderm. The estimated total length of the sicula is about 2.1 mm.

Possible fragments of the metasicular and prosicular rims are observed in ZPAL G.XIII/89, which represents a young rhabdosome of *Spinograptus* sp. with only the first pairs of thecae (Fig. 5A). The metasicular aperture appears to be close to the ancora. The prosicular apex is at a distance of 2.3 mm from the ancora, indicating that the length of sicula is similar to that in Fig. 4. Also the specimen ZPAL G.XIII/109

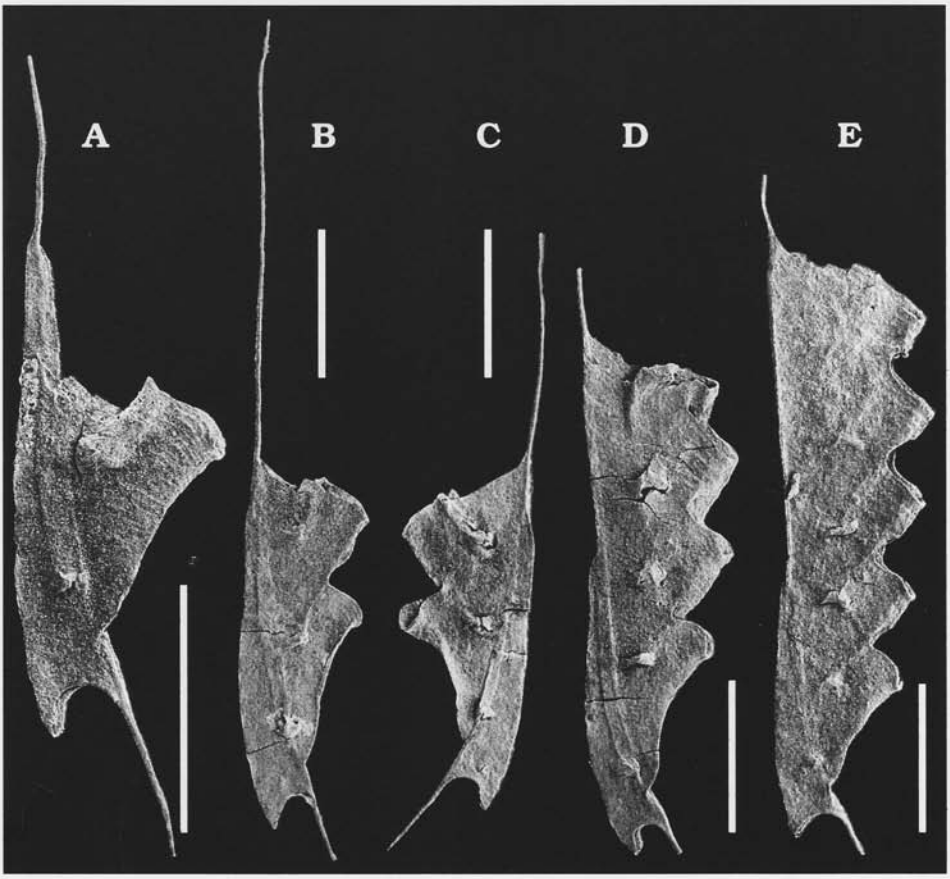

Fig. 2. *Colonograptus? praedeubeli* (Jaeger, 1990), young rhabdosomes, Bartoszyce 1641.2 m. **A**. Sicula with first theca, ZPAL G.XIII/1. **B**. Sicula with two thecae, ZPAL G.XIII/2. **C**. Sicula with two thecae, similar to *Pristiograptus dubius* (Suess, 1851), ZPAL G.XIII/3. **D**. Rhabdosome with the fourth theca starting to grow, ZPAL G.XIII/4. **E**. Rhabdosome with five thecae, showing some *P.? gerhardi* features; ZPAL G.XIII/5. Scale bars 1 mm.

(Fig. 5B) has a long nema, despite its juvenile age. This may suggest a long sicula. Fragments of the prosicula with longitudinal rods and metasicula are illustrated in Fig. 6D.

In the proximal part of the rhabdosomes, some fragments of a membrane presumably belonging to the thecae, are preserved. The structure of this periderm, like that of the metasicula, is without any trace of increments. The widths of the virga and virgella are similar, but the virgula, while proximally thinner, widens in the distal part of the rhabdosome, near the appendix. The first thecae of *Spinograptus reticulolawsoni* sp. n. (Fig. 6F) and *S. latespinosus* sp. n. (Figs 7A, B, 8A, B) are preserved, but flattened. The possible ventral edge of the initial part of the theca 1^1 membrane is situated a little higher than the aperture of the metasicula (Fig. 7B). Membranes are preserved between the lists of some apertural processes (Figs 8D, 10C).

Fig. 3. *Spinograptus reticulolawsoni* sp. n., holotype, finite rhabdosome, reverse view, Bartoszyce 1641.2 m, ZPAL G.XIII/80.

In several specimens, identified as *Spinograptus* cf. *latespinosus,* the periderm of lateral walls is thicker and the contours of the thecae are clearly visible (Fig. 8). It is difficult to distinguish the ancora sleeve from the thecal periderm because of the flattening of the material and poor preservation of the periderm. Thicker periderm may represent thecal and ancora sleeve periderm of lateral walls pressed together (Fig. 8A–C).

Rhabdosome ZPAL G.XIII/80 of *S. reticulolawsoni* sp. n. is flattened ventro-laterally and thecal apertures bordered by continuous periderm are readily visible (Fig. 9A, B). The periderm in this specimen is very thin and transparent under light-microscopy (Fig. 3). This is probably entirely thecal periderm, without any ancora sleeve mem-

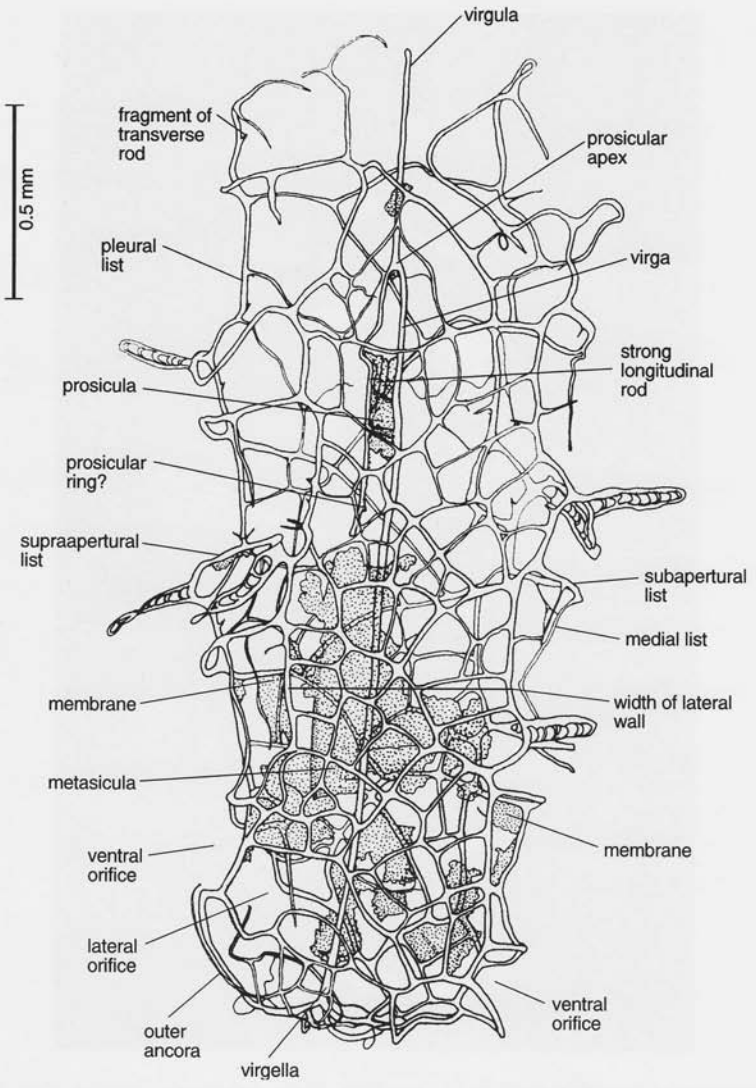

Fig. 4. *Spinograptus reticulospinosus* sp. n., young rhabdosome with preserved prosicula and fragment of metasicula, reverse view, Bartoszyce 1640.0 m, ZPAL G.XIII/90.

brane. The rhabdosome is finite, ending with a short appendix built with a periderm apparently without any lists (Fig. 9B). The virgula is thinner than any other list, and is lunate in cross section along its length, suggesting the presence of a membrane, perhaps to the beginning of the appendix (Fig. 9D). In the distal part of the rhabdosome the virgula is thicker. The thecae are somewhat climacograptid in profile.

The thecal periderm and periderm of the appendix are preserved in *Spinograptus reticulolawsoni* sp. n. ZPAL G.VIII/91 (Fig. 10). This is a fragment of a rhabdosome with four distal pairs of thecae. The rhabdosome is flattened laterally with the profile of the thecae visible. The thecae are strongly curved in their medial parts (Fig. 10A).

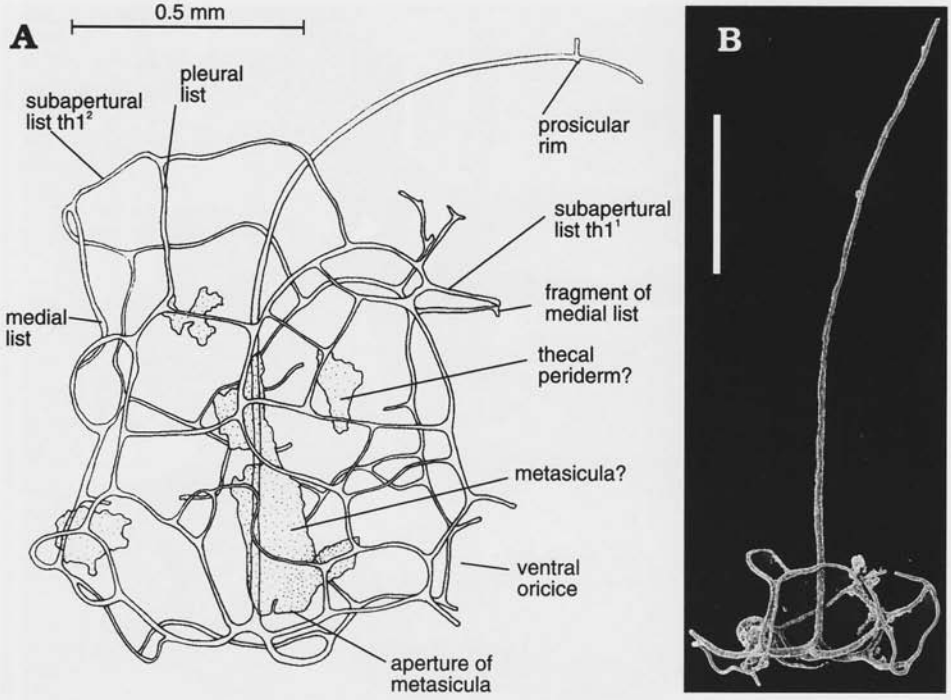

Fig. 5. *Spinograptus* sp., Bartoszyce 1640.0 m. **A**. ZPAL G.XIII/89, young rhabdosome with two first thecae, fragment of metasicula and prosicular rim, reverse view. **B**. ZPAL G.XIII/109, ancora umbrella stage of rhabdosome with long virgula, scale bar 500 μm.

The appendix is a small peridermal tube, situated partly inside the rhabdosome (Figs 10B, 11), similar to ZPAL G.VIII/80 (Fig. 9B). The reticular list ending the appendix has a distal scar with a fragmentary periderm (Fig. 10D). This indicates an initial stage of appendix growth.

Phylogenetic trends in the *Plectograptus* lineage

The genus *Spinograptus* is the oldest representative of the *Plectograptus* lineage (see pp. 402–403). *Spinograptus* is characterized by: presence of medial lists, presence of processes on proximal ventral orifices, and apertural processes which are always reticulofusellar (Fig. 11). Based on previous data (Kozłowska-Dawidziuk 1995), however, it is difficult to say whether changes in *Spinograptus* show reduction of skeletal elements, which apears to be a characteristic general trend among retiolitids. For example, important is the tendency towards reduction of medial lists, which in the stratigraphically older forms are developed in proximal thecae, but in younger ones are almost totally reduced (Fig. 12).

The genus is most species-rich at its appearance in the *Colonograptus*? *praedeubeli* Zone (Fig. 12). The tendency towards finite growth of *Spinograptus* colony with an

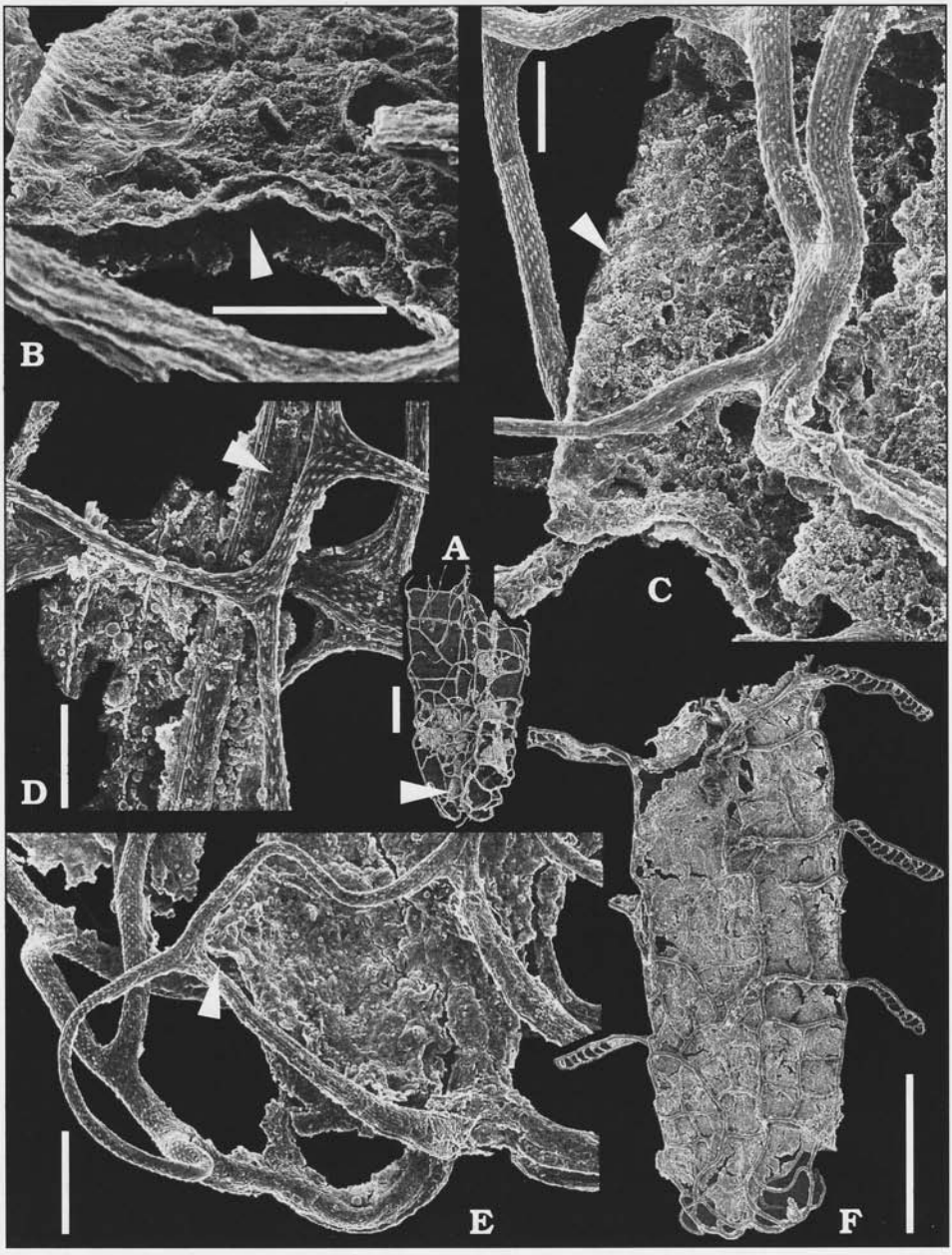

Fig. 6. *Spinograptus reticulolawsoni* sp. n., **A–C**. Young rhabdosome, reverse view, Bartoszyce 1640.0 m, ZPAL G.XIII/93. **A**. Metasicula (arrow); scale bar 500 μm. **B**. Inside view of metasicula with aperture of metasicula (arrow), and smooth surface of periderm (arrow); scale bar 50 μm. **C**. Lateral view of metasicula with spongy periderm arrowed; scale bar 50 μm. **D**. Fragment of prosicula, virga and longitudinal rod arrowed, Bartoszyce 1640.0 m, ZPAL G.XIII/92; scale bar 50 μm. **E, F**. Young rhabdosome flattened ventro-laterally with metasicula and thecal periderm, obverse view, Bartoszyce 1640.0 m, ZPAL G.XIII/93. **E**. Metasicula with possible initial part of theca 1^1 (arrow); scale bar 100 μm. **F**. Scale bar 1 mm.

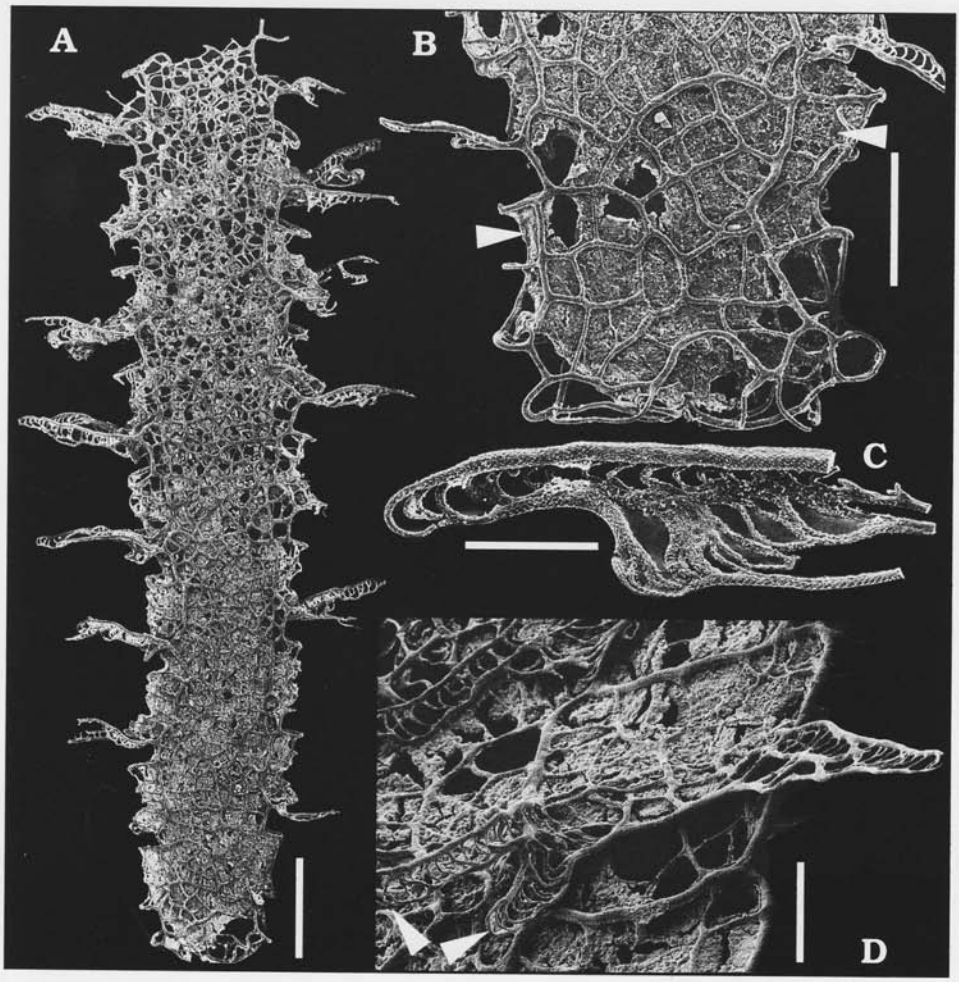

Fig. 7. *Spinograptus latespinosus* sp. n., holotype, Bartoszyce 1640.0 m. **A**. Mature rhabdosome with periderm preserved in proximal and medial part, obverse view, ZPAL G.XIII/100; scale bar 1 mm. **B**. Proximal part of rhabdosome with periderm of thecae 1^1 and 1^2 (arrows); obverse view, ZPAL G.XIII/105, scale bar 500 μm. **C**. Apertural process; scale bar 200 μm. **D**. Fragment of ventral wall showing bifurcate apertural process (arrows), ZPAL G.XIII/101; scale bar 500 μm.

appendix (see diagnosis of *Spinograptus* in Kozłowska-Dawidziuk 1995) is observed in *S. reticulolawsoni* sp. n.

Spinograptus lawsoni (Holland, Rickards & Warren, 1969), *S. reticulolawsoni* sp. n. and *S. latespinosus* sp. n. represent the oldest forms of this genus recognized so far. The two new species occur in the *C.? praedeubeli* Zone in the Bartoszyce borehole. *S. reticulolawsoni* sp. n. is similar to *S. lawsoni* in size of the finite rhabdosome and the presence of medial lists in the proximal part of the rhabdosome, but differs in having a better developed reticulum and apertural processes (Fig. 12). The rhabdosome of *S. latespinosus* sp. n. is longer and more reticulate, and has more complicated, irregular and sometimes

branching apertural processes (Fig. 7C, D). The two species: *S. reticulolawsoni* sp. n. and *S. latespinosus* sp. n. seem to be more primitive than *S. lawsoni*.

Spinograptus lawsoni occurs in the late Wenlock of Shropshire (Holland, Rickards & Warren 1969) and in the Mulde Beds of Gotland (Kozłowska-Dawidziuk 1991); its stratigraphical range is not determined (Lennart Jeppsson personal communication, 1996), but its morphology suggests that the species was probably limited to the lower part of the *Colonograptus? praedeubeli* Zone. The rhabdosome of *S. lawsoni* is small and finite, ending with some lists that indicate the presence of an appendix. The reticulum is poorly developed or absent. Apertural processes are simple and reticulofusellar (Fig. 12), without any additional lists, and are shorter than those of *Spinograptus reticulolawsoni* sp. n. These morphological features suggest that *S. lawsoni* might have developed from *S. reticulolawsoni* sp. n.

The medial lists are almost totally reduced in *Spinograptus clathrospinosus* (Eisenack, 1951), known from the *Colonograptus? praedeubeli* Zone (Jaeger 1991), and from the lower part of the *Neodiversograptus nilssoni* Zone (based on Mielnik borehole material, Kozłowska-Dawidziuk 1995). This species seems to show a combination of advanced and primitive features. *S. clathrospinosus* (Fig. 13A) and the younger *S. spinosus* (Fig. 13C) differ from the remaining species in possessing paired apertural processes (reticulofusellar in their distal parts) at the proximal ventral orifices. *S. clathrospinosus* has a dense reticulum and long, narrow apertural processes (Fig. 13A). Proximal ventral orifices with processes and thin, slender apertural processes (Fig. 13A) are regarded as primitive features for this genus. Short, spine-shaped processes at proximal lateral orifices are known also from the Wenlock representative of the *Gothograptus* lineage – *G. kozlowskii* Kozłowska-Dawidziuk, 1990.

Spinograptus munchi (Eisenack, 1951) a younger species, occurs slightly below the occurrence of the *Neodiversograptus nilssoni* (Kozłowska-Dawidziuk 1995). It contrasts with all other species of *Spinograptus* by its complete lack of reticulum. *S. munchi* is characterised by total lack of medial lists and by dichotomously branching apertural processes.

Spinograptus spinosus (Wood, 1900) occurs in the upper part of the *N. nilssoni* Zone (Kozłowska-Dawidziuk 1995) and locally in the *Colonograptus? ludensis* Zone (Lenz 1993). It has the strongest and most dense reticulum among species of *Spinograptus*, and its apertural processes are simple, long spines with reticulofusellar structure are marked only in their distal parts (see fig. 27: 6 in Obut & Zaslavskaya 1983). It also bears spines at the proximal ventral orifices (Fig. 13C) similar to *S. clathrospinosus*. These features are regarded as primitive in the retiolitid evolution. *S. spinosus* is also characterised by possessing only weak and reduced medial lists.

Summing up, different stages in the development of medial lists are observed in different species of *Spinograptus*. In the oldest species *S. reticulolawsoni* sp. n., *S. latespinosus* sp. n., and *S. lawsoni*, medial lists are well developed in thecae 1^1, 1^2 and 2^1, in rest of the thecae being reduced only to spines or denticles. In the younger *S. clathrospinosus* medial lists are not fully developed, even in the proximal thecae. In theca 1^1 there are only short spines (Fig. 13B), and in the rest of thecae there are denticles or simply no traces of medial lists. Apertural processes at the proximal ventral orifices have been observed in *S. clathrospinosus* (Fig. 13A) and *S. spinosus* (Fig. 13C). They are short and totally covered by peridermal bandages.

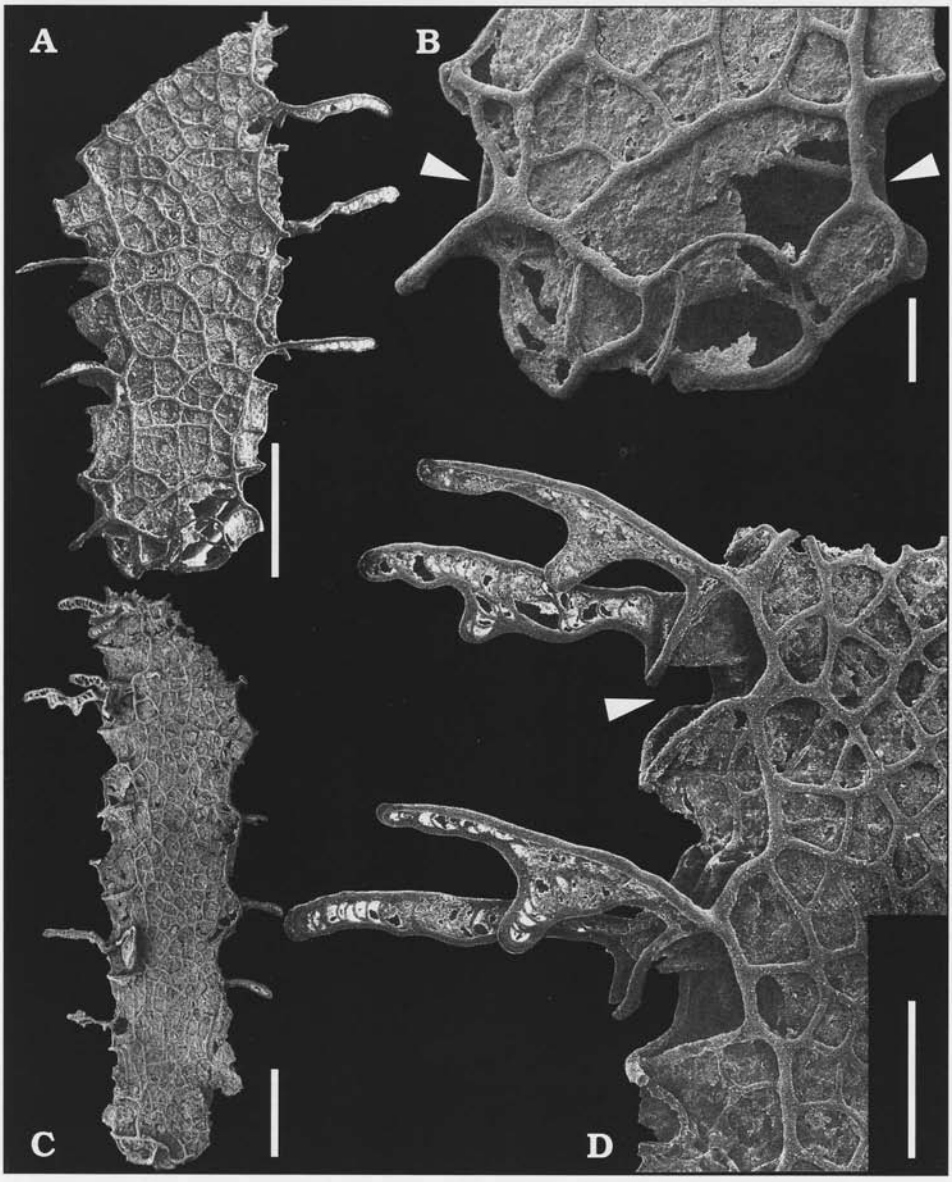

Fig. 8. *Spinograptus* cf. *latespinosus* sp. n., Bartoszyce 1640.0 m. **A**, **B**. Lateral side of proximal part of rhabdosome with periderm, obverse view, ZPAL G.XIII/102. **A**. scale bar 1 mm. **B**. Ancora umbrella, with lateral and ventral orifices (arrows); scale bar 200 µm. **C**. Rhabdosome with periderm, reverse view, ZPAL G.XIII/103; scale bar 1 mm. **D**. Medial part of rhabdosome, aperture of thecae (arrow), ZPAL G.XIII/104; scale bar 500 µm.

Spinograptus clathrospinosus and the stratigraphically younger form *S. spinosus* seem to retain many primitive features. These are the almost total lack of medial lists, the presence of spines at proximal ventral orifices, dense reticulum and spine-shaped

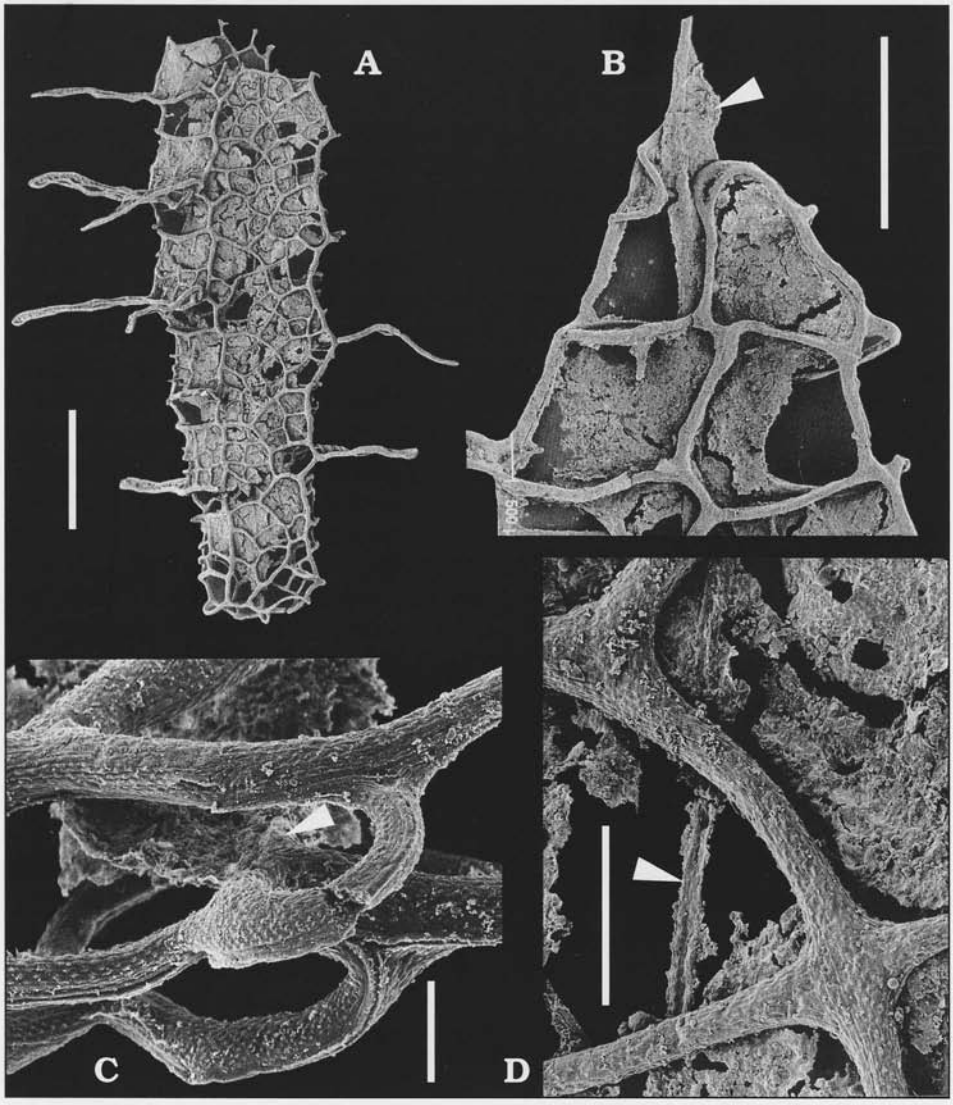

Fig. 9. **A**, **B**. *Spinograptus reticulolawsoni* sp. n., holotype, finite rhabdosome, Bartoszyce 1641.2 m, ZPAL G.XIII/80. **A**. Proximal and medial part, obverse view; scale bar 1 mm. **B**. Distal part with appendix (arrow); scale bar 500 μm. **C**. Inside view of ancora umbrella with virgella (arrow); scale bar 50 μm. **D**. Fragment of the rhabdosome with ancora sleeve lists, thecal periderm and thin, lunate virgula (arrow); scale bar 100 μm.

apertural processes. The older, *S. munchi*, shows both primitive features, like reduced medial lists, and advanced ones like reduced reticulum and well developed apertural processes. The data discussed above indicate the mosaic evolution of the genus *Spinograptus*.

Kozłowska-Dawidziuk (1995) distinguished three lineages in the Plectograptinae Bouček & Münch, 1952: the *Sokolovograptus, Gothograptus* and *Plectograptus* li-

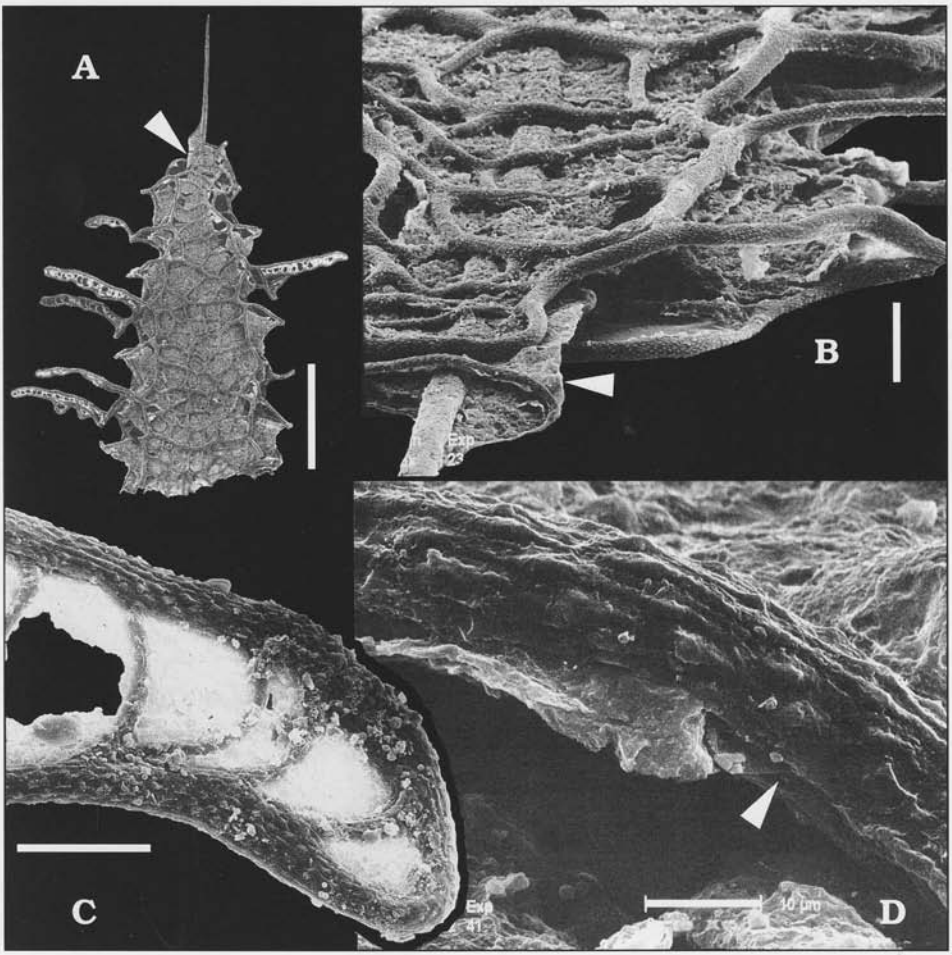

Fig. 10. *Spinograptus reticulolawsoni* sp. n., distal part of finite rhabdosome with appendix (arrow), Bartoszyce 1641.2 m, ZPAL G.XIII/91. **A**. scale bar 1 mm. **B**. Inside view to flattened thecae and appendix (arrow; the area is enlarged in D); scale bar 100 µm. **C**. Apertural process with periderm between lists; scale bar 50 µm. **D**. Distal edge of the appendix with periderm and scar (arrow); scale bar 10 µm.

neages. The most important for retiolitid phylogeny are preserved fragments of periderm of prosiculae and metasiculae. The *Spinograptus* sicula described herein is about 2 mm long, similar to the sicula of *Agastograptus*. Both genera belong to the *Plectograptus* lineage. The long sicula characteristic of the *Plectograptus* lineage contrasts with short siculae of oldest retiolitids belonging to the *Retiolites* lineage: *Retiolites geinitzianus* (Obut & Zaslavskaya 1976), *Pseudoretiolites* cf. *decurtatus* (Lenz & Melchin 1987a; Bates & Kirk 1992); and *Paraplectograptus* sp. (Lenz 1992) belonging to *Paraplectograptus* lineage (Kozłowska-Dawidziuk 1995).

The find of peridermal membranes in *Spinograptus* may suggest their universal presence in retiolite graptolites.

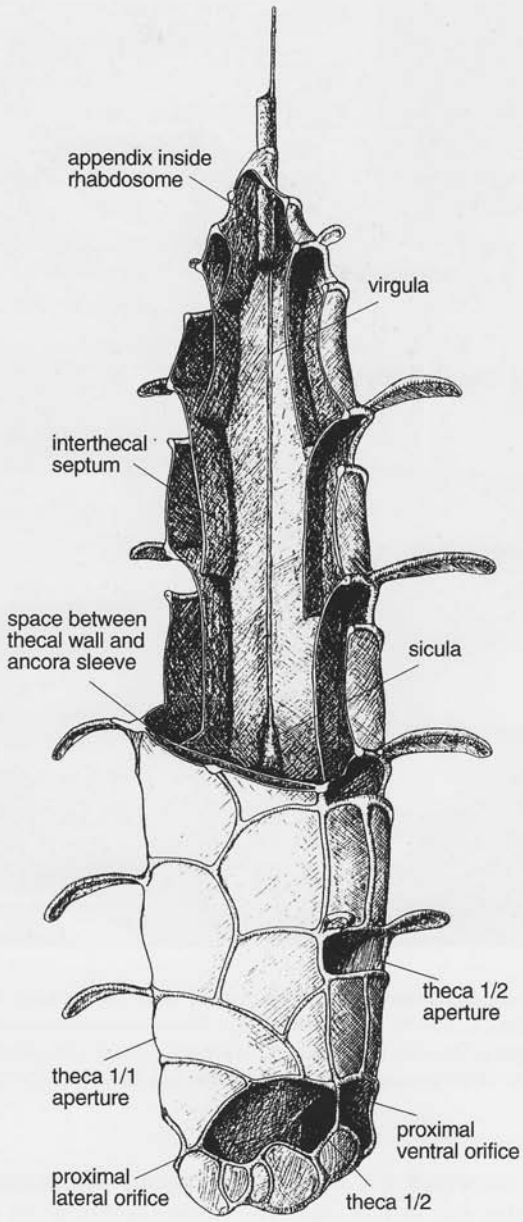

Fig. 11. Hypothetical rhabdosome of *Spinograptus* with thecal and ancora sleeve membranes.

Palaeoecological remarks

The material studied represents the early recovery phase after the *Cyrtograptus lundgreni* Extinction Event (Koren' 1991; Koren' & Suyarkova 1994), which was charac-

terised by environmental changes that were almost lethal for the graptoloid macrozooplankton. The possible causes of these changes have been analysed by many authors and summarized by Koren' & Urbanek (1994). Only two species of graptoloids, representing two different groups, are regarded as survivors of the Event. One of them is *Pristiograptus dubius*, the ancestor of the Ludlow monograptids belonging to *Lobograptus*?, *Colonograptus*? and *Pristiograptus* (see Koren' & Urbanek 1994), all of which occur in the *C.? praedeubeli* Zone. The second is the retiolitid *Gothograptus nassa*, close to possible ancestors of the Ludlow continuation of the *Gothograptus* lineage (see Kozłowska-Dawidziuk 1995).

In Tien Shan (Kyrgyzstan), in the *Colonograptus? praedeubeli* Zone, which follows the *Cyrtograptus lundgreni* Event, the monograptids are represented by five species (Koren' & Urbanek 1994), while in the Arctic Archipelago, Canada (Lenz 1995) there are ten species of monograptids in that Zone. In Bartoszyce material, the diversification of the retiolitids (four species of *Spinograptus*, see Fig. 12) parallels that of the contemporaneous monograptids from Kyrgyzstan.

Taxonomy

Subfamily Plectograptinae Bouček & Münch, 1952

Genus *Spinograptus* Bouček & Münch, 1952

Type species: *Retiolites spinosus* (Wood, 1900),

Emended diagnosis. — Medial lists developed in proximal thecae or reduced to the short lists or denticles, in contrast to *Plectograptus, Semiplectograptus* Kozłowska-Dawidziuk, 1995 and *Plectodinemagraptus* Kozłowska-Dawidziuk, 1995 where medial lists are well developed in all thecae of rhabdosome. Differs from *Plectodinemagraptus* in having the principal parietal lists arranged in zig-zag pattern in lateral walls. Differs from *Plectograptus, Semiplectograptus* and *Plectodinemagraptus* in well developed ancora umbrella, and paired, reticulofusellar apertural processes.

Species included. — *S. spinosus* (Wood, 1900), *S. clathrospinosus* (Eisenack, 1951), *S. munchi* (Eisenack, 1951), *S. lawsoni* (Holland, Rickards & Warren, 1969), *S. reticulolawsoni* sp. n., *S. latespinosus* sp. n., *S.* sp. (this paper).

Spinograptus spinosus (Wood, 1900)

Fig. 13C–D.

Emended diagnosis. — Clathrial lists forming lateral wall fine, poorly visible. Medial lists reduced to denticles in the proximal thecae. Differs from *S. clathrospinosus* in having reticulofusellar structure in the apertural spines covered by external bandages. Differs from *S. munchi, S. lawsoni, S. reticulolawsoni* sp. n., and *S. latespinosus* sp. n. in having the proximal ventral orifice spines.

Spinograptus clathrospinosus (Eisenack, 1951)

Fig. 13A–B.

Emended diagnosis. — Proximal ventral orifices with paired spines, reticulofusellar in distal part.

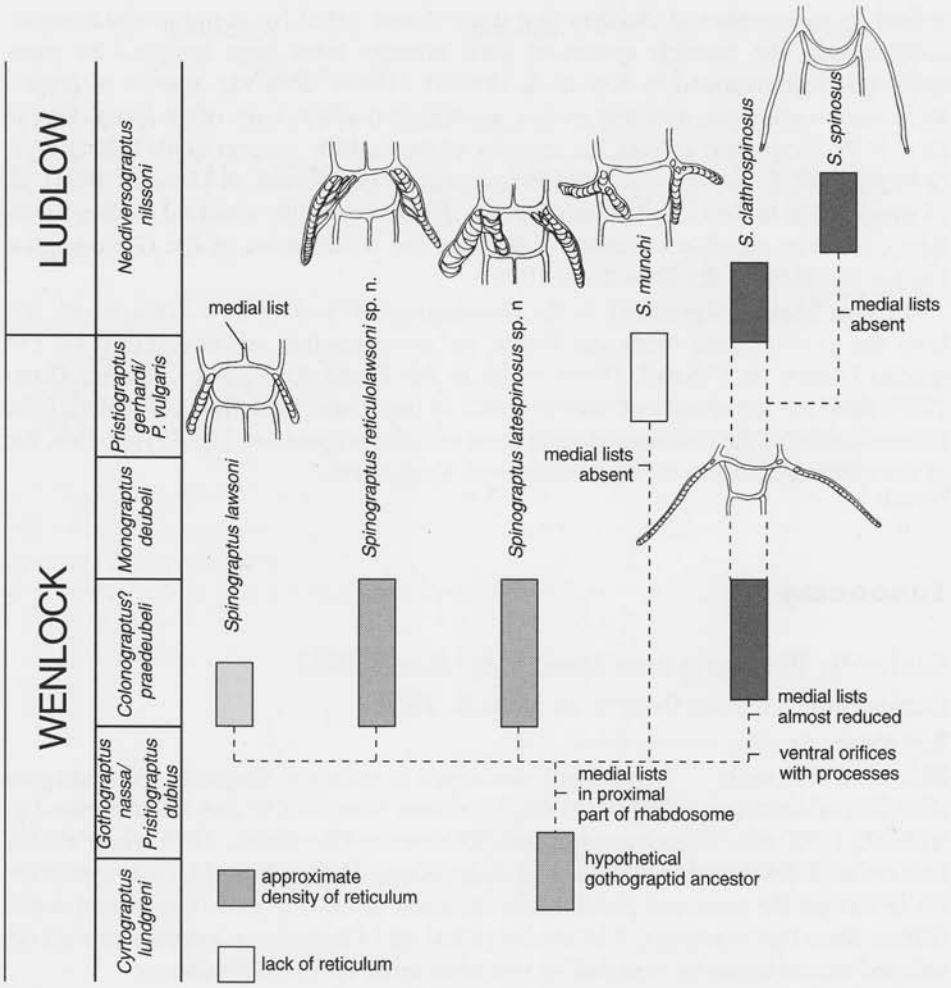

Fig. 12. Stratigraphical sequence and possible relationships of *Spinograptus* taxa based on the Bartoszyce borehole, data of Jaeger (1991), and Kozłowska-Dawidziuk (1995). Note the taxonomical differentiation of *Spinograptus* in the *Colonograptus*? *praedeubeli* Zone.

Spinograptus reticulolawsoni sp. n.

Figs 3, 4, 6, 9, 10, 14.

Holotype: ZPAL G.XVIII/80, finite rhabdosome with appendix, and six pairs of thecae (Figs 3, 9A–D).

Type horizon and locality: Late Wenlock, *Colonogratus*? *praedeubeli* Zone, Bartoszyce IG 1 borehole, depth 1642.1 m, Poland.

Derivation of the name: in recognition of its similarity to *S. lawsoni* (Holland *et al.*, 1969), but possessing a well developed reticulum.

Diagnosis. — Reticulum in ventral and lateral walls well developed. Differs from *S. munchi* in presence of reticulum (absent in *S. munchi*). Medial lists well developed in thecae 1^1, 1^2 and 2^1. Differs from *S. munchi* and *S. spinosus* in having well developed

medial lists in the proximal part of rhabdosome. Unbranched reticulofusellar apertural processes longer in the medial part of the rhabdosome, attain lengths up to 1.2 mm. The width of the lateral wall in the medial part of rhabdosome up to 1.2 mm. Finite rhabdosome up to 6.5 pairs of thecae, ended by a short appendix.

Material. — About one hundred more or less flattened rhabdosomes in young stages of growth and two finite ones. Borehole Bartoszyce IG 1, depths 1641.2 m, 1641.0 m, and 1640.0 m.

Description. — Finite rhabdosome of 5 to 6.5 pairs of thecae. Rhabdosome ended by short appendix (Figs 3, 9B, 10). The total length of the finite rhabdosome is up to 6 mm. Width of the lateral wall is 0.7–0.8 mm above ancora umbrella, 0.7–0.9 mm across the first thecae and medial part, and narrowing to 0.4 mm across last pairs of the thecae.

Almost 70% of the rhabdosomes represent young growth stages. Most of them represent juvenile rhabdosomes with the first pairs of thecae. There are only six fragments of near-finite rhabdosomes, and two finite rhabdosomes.

Remarks. — *S. reticulolawsoni* sp. n. is similar to *S. lawsoni* (see Kozłowska-Dawidziuk 1991). The difference is expressed in a more extended and dense reticulum in the ventral and lateral walls (Figs 9A, 10A). Apertural processes are also better developed and are more complicated than in *S. lawsoni*. Specimens of the new species from depth 1640.0 m very often exhibit a periderm (see pp. 394–397). In *S. lawsoni*, such a sclerotized periderm has not been observed (Kozłowska-Dawidziuk 1995).

Spinograptus latespinosus sp. n.

Fig. 7.

Holotype: ZPAL G.XVIII/100, mature rhabdosome with 8 pairs of thecae (Fig. 7A).

Type horizon and locality: Late Wenlock, *Colonograptus? praedeubeli* Zone, Bartoszyce borehole, depth 1640.0 m, Poland.

Derivation of the name: Latin *latus* – wide, *spina* – spine.

Diagnosis. — Reticulum and medial lists similar to those of *S. reticulolawsoni* sp. n. Differs from *S. reticulolawsoni* sp. n. in having irregular and complex reticulofusellar apertural processes up to 1.2 mm long, which may include additional lists or may bifurcate; in having a wider, up to 1.4 mm lateral wall in medial part of rhabdosome, and narrowing beyond the 10th pair of thecae. In addition, it differs from *S. reticulolawsoni* sp. n. in having a longer rhabdosome, without an appendix.

Material. — Thirty five specimens from Bartoszyce IG 1 borehole, depths 1641.2 m (five young specimens) and 1640.0 m (30 mostly adult specimens).

Description. — Length of rhabdosome to the level of 10th pair of thecae is up to 11.2 mm. Rhabdosome narrows distally, but appendix has not been observed (Fig. 7). Width of lateral wall is 0.5 mm in proximal part of rhabdosome, in medial part width of lateral wall up to 1.4 mm, and lateral width is up to 2.0 mm. Width of lateral wall in distal part narrows to 0.7 mm.

Reticulum is dense in ventral and lateral walls of the rhabdosome. Thecal profile is curved, forming a hood above supraapertural lists (Fig. 7A). Apertural processes are present in proximal and distal parts; in young rhabdosomes they are simpler, developed with almost parallel edges. In the medial part of the rhabdosome, apertural processes are more complicated, and display additional lists on their ventral side (Fig. 7C).

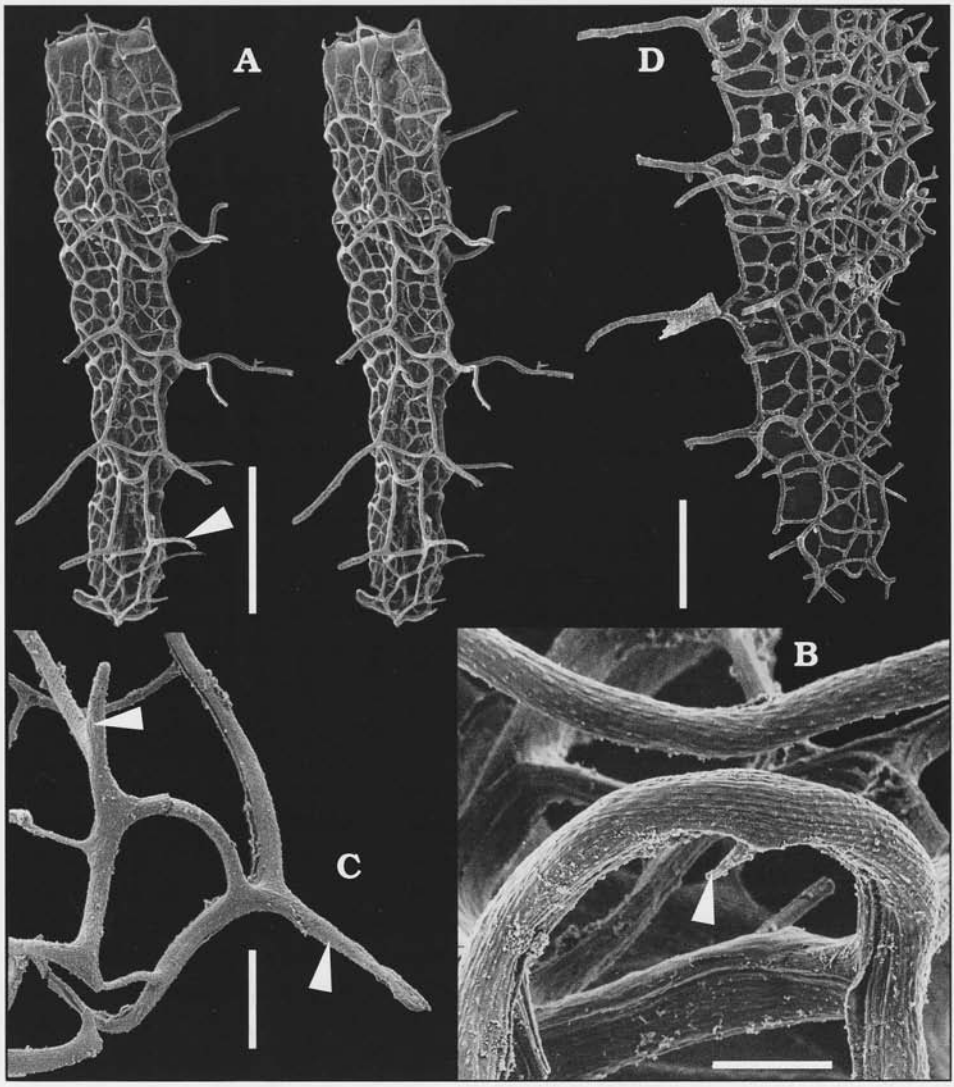

Fig. 13. **A**, **B**. *Spinograptus clathrospinosus* (Eisenack, 1951), Mielnik 1046.9 m. **A**. Steropair of ventral side of rhabdosome; process of proximal ventral orifice is arrowed, ZPAL G.VI/1911; scale bar 1 mm. **B**. Inside view of subapertural list of theca 1^1 with rudimentary medial list (arrow), ZPAL G.VI/1911; scale bar 100 μm. **C**, **D**. *Spinograptus spinosus* (Wood, 1900), Mielnik 1038.9 m. **C**. Ventral proximal orifice with processes (arrows) ZPAL G.VI/1912; scale bar 50 μm. **D**. Fragment of proximal part of rhabdosome, flattened ventro-latrally; ZPAL G.VI/1905, scale bar 400 μm .

Sometimes they are forked (Fig. 7D). Width of virgula is similar to the width of clathrial lists, sometimes wider in medial and distal parts of the rhabdosomes.

Variability. — The arrangement of additional lists in apertural processes is irregular, especially in the medial part of the rhabdosome. Some rhabdosomes are wider in their distal part.

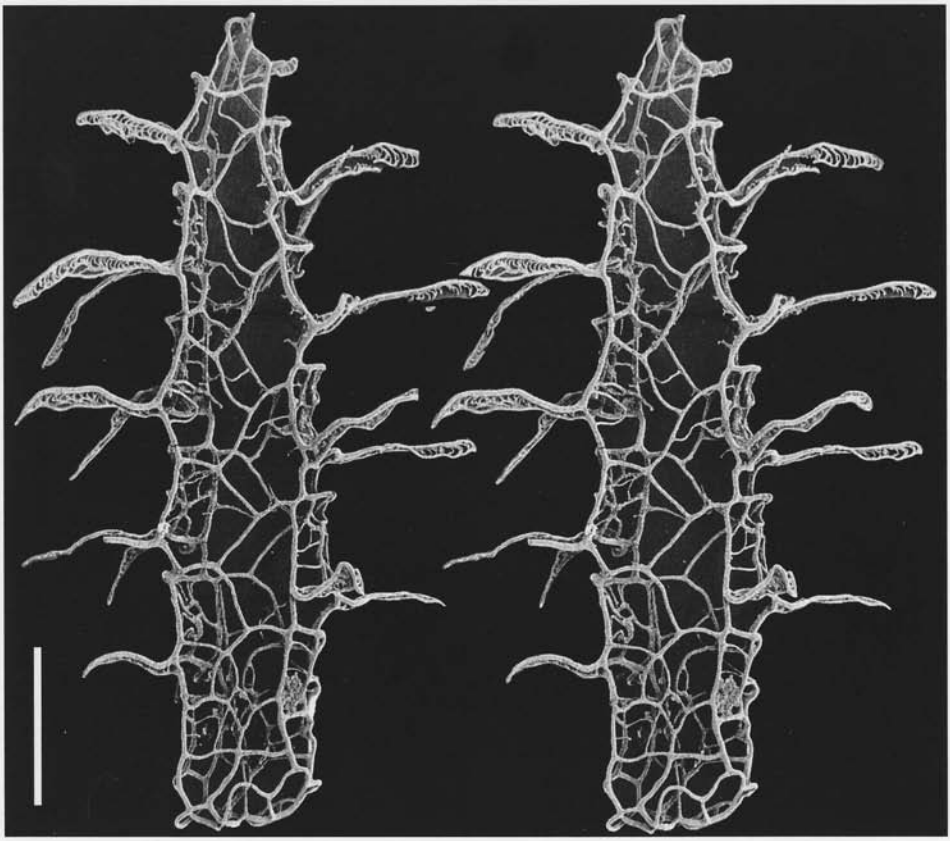

Fig. 14. *Spinograptus reticulolawsoni* sp. n., stereopair of finite rhabdosome without thecal periderm, Bartoszyce 1641.2 m, ZPAL G.XIII/94; scale bar 1 mm.

Spinograptus cf. *latespinosus* sp. n.

Fig. 8.

Material. — Three fragments of rhabdosomes ZPAL GXIII/103–104. Bartoszyce IG 1 borehole, depth 1640.0 m.

Description. — Both specimens represent proximal to medial parts of rhabdosomes. Width of lateral wall is similar to *S. latespinosus*. Apertural processes are simple, regular, sometimes forked in their medial parts (Fig. 8D).

Remarks. — Specimens display a stronger membrane periderm, and more complex and irregular apertural processes than *Spinograptus latespinosus* sp. n. and *S. reticulalawsoni* sp. n.

Spinograptus sp.

Fig. 5.

Material. — Two specimens, Bartoszyce IG 1 borehole, depth 1640.0 m, young rhabdosomes ZPAL G.XIII/89 and ZPAL G.XIII/109.

Description. — Specimen ZPAL G.XIII/89 represents a young rhabdosome with two first thecae. Fragments of prosicula and metasicula are preserved. Specimen ZPAL G.XIII/109 represents a juvenile rhabdosome in the ancora umbrella stage of growth.
Remarks. — The rhabdosomes, due to their juvenile stages of growth, lack features diagnostic at the species level.

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Retiolit *Spinograptus* (Graptolithina) z Polski i jego struktura błoniasta

ANNA KOZŁOWSKA-DAWIDZIUK

Streszczenie

W późnowenlockich szarych iłowcach i marglach wiercenia Bartoszyce IG 1 z platformy wschodnioeuropejskiej (Fig. 1) stwierdzono zespół graptolitów z przewodnią formą *Colonograptus? praedeubeli*. Obserwowany zespół monograptidów i retiolitidów jest świadectwem wczesnej fazy odradzania się makrozooplanktonu po globalej katastrofie późnosylurskiej, znanej jako „zdarzenie *Cyrtograptus lungreni*".

Występują tu retiolity z rodzaju *Spinograptus* reprezentowanego przez *Spinograptus reticulolawsoni* sp. n., *S. latespinosus* sp. n., *S.* cf. *latespinosus* i *S.* sp. Gatunki te różnią się między sobą i od innych gatunków tego rodzaju odmiennie wykształconymi aparatami aperturalnymi o budowie retikulofuzellarnej, stopniem retikulacji rabdozomu zewnętrznego otaczającego teki, zwanego rękawem ankory (ancora sleeve) i liczbą tek w rabdozomach dojrzałych, wykazujących tendencję do zakończonego wzrostu (Fig. 12). U *Spinograptus reticulolawsoni* sp. n. opisano, po raz pierwszy dla tego rodzaju, rabdozom kolonii o zakończonym wzroście z krótkim rurkowatym apendyksem. Wykazano, że ewolucja *Spinograptus* ma charakter mozaikowy.

Wyjątkowy stan zachowania opisywanego materiału, w którym występują membrany perydermalne, pozwolił na szczegółowe zbadanie cech rabdozomu *Spinograp-*

tus, ważnych dla odtworzenia filogenezy retiolitów. Błony perydermalne dostarczają szczegółowych danych o budowie rabdozomów retiolitów (sikul, pierwszych tek) i jednocześnie o pokrewieństwach w obrębie grupy. Bates & Kirk (1992) wnioskowali o obecności membran na podstawie ich śladów na beleczkach rabdozomów retiolitów, co potwierdziło niedawne odkrycie przez Lenza (1994) dobrze zachowanych rabdozomów *Agastograptus robustus* z membranami. Kolejne dowody obecności błon perydermalnych, opisane na podstawie materiału z Bartoszyc u *Spinograptus*, mogą świadczyć o powszechnym występowaniu takich struktur u retiolitów.

Mimo spłaszczenia i często zachowanych jedynie fragmentów membran, w materiale z wiercenia Bartoszyce odnaleziono fragmenty prosikul, metasikul, tek i rękawów ankory. Obecność długiej sikuli u *Spinograptus* (2 mm) potwierdza wcześniejsze przypuszczenia autorki o przynależności tego rodzaju do linii *Plectograptus* (do tej pory sikula o długości 2 mm znana była u jednego przedstawiciela tej linii: *Agastograptus robustus*). Długa sikula w linii *Plectograptus*, kontrastująca z krótkimi sikulami przedstawicieli starszych linii *Paraplectograptus* i *Retiolites* wskazuje, iż retiolity mogą być grupą polifiletyczną.