# *Agastograptus*, a synonym of *Plectograptus* (Retiolitidae, Graptolithina)

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*Agastograptus robustus* Obut and Zaslavskaya, 1983, the type species of the genus *Agastograptus* is herein recognized as a species of *Plectograptus*. Large proximal lateral orifices are one of the significant characters of *Plectograptus*. *P. robustus* differs from the type species, *Plectograptus macilentus* Törnquist, 1887, in possessing paired apertural processes. Other species of *Agastograptus* have been assigned to three different genera: *Spinograptus, S. clathrospinosus* (Eisenack, 1951), *S. munchi* (Eisenack, 1951), *Neogothograptus*, *N. balticus* (Eisenack, 1951), and *Cometograptus*, *C. nevadensis* (Berry and Murphy, 1975). The main diagnostic feature used for *Agastograptus*, the spinoreticular paired apertural processes, is recognized as a species feature, characteristic mostly for *Spinograptus*, whereas the generic features are the arrangement of the proximal end, ventral walls, and ancora sleeve of the rhabdosome. Therefore the genus *Agastograptus* is a synonym of *Plectograptus*.

Key words: Graptolithina, Retiolitidae, *Agastograptus*, Silurian, taxonomy.

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## Introduction

The study of retiolitids dates back to the nineteenth century (Barrande 1850). One hundred years later, Eisenack (1951) and Bouček and Münch (1952) described most of the known retiolitid species and provided the first division of the Retiolitidae Lapworth, 1873, based on flattened and isolated material. The next attempt at a comprehensive taxonomic study of retiolitids was by Obut and Zaslavskaya (1983) in which they established the genus *Agastograptus* and assigned five species to that genus. These comprised three species described by Eisenack (1951) as *Retiolites clathrospinosus*, *Retiolites munchi*, and *Retiolites balticus*, a fourth, *Retiolites nevadensis* described by Berry and Murphy (1975), and the fifth was a new species *A. robustus* Obut and Zaslavskaya, 1983. One of the main diagnostic characters of this genus was the "spinoreticular" nature of its apertural processes, as in the type species, *A. robustus* (Fig. 2D).

However, in a later study (Kozłowska-Dawidziuk 1995: 290, 304) morphology of apertural processes was considered diagnostic only at species level, while the generic diagnoses were based on the following features: ancora umbrella, ancora sleeve, ventral walls, and position of the nema. The present study further shows that proximal lateral orifices can also be important diagnostic generic features.

Detailed study of different species of *Agastograptus* showed considerable variation in the apertural processes of different species, as well as different arrangements of the proximal ends, ventral walls and ancora sleeve lists. In the study of Kozłowska-Dawidziuk (1995), *A. clathrospinosus* and *A. munchi* were moved to the genus *Spinograptus* Bouček and Münch, 1952, and *A. balticus* (Eisenack, 1951) was assigned to the genus *Neogothograptus* Kozłowska-Dawidziuk, 1995. *Agastograptus nevadensis*, assigned to *Spinograptus* by Lenz (1993), was recently reassigned to *Cometograptus* (Kozłowska-Dawidziuk 2001), a new upper Wenlock genus (see below). Finally, a new species described from Arctic Canada by Lenz (1993), as *Agastograptus quadratus*, is recognized herein as a species of *Spinograptus*, having the ancora umbrella, ventral walls, and ancora sleeve, characteristic for that genus. *A. robustus*, the type species of *Agastograptus*, is herein recognized as a species of *Plectograptus*, with characteristic large proximal orifices of the ancora sleeve, a small, simple ancora umbrella composed of four meshes, and central nema, long sicula and mid-ventral lists.

The purpose of this paper is to demonstrate that the type species of *Agastograptus* belongs to *Plectograptus*, and that *Agastograptus* is a synonym of the genus *Plectograptus*. Furthermore, the paper shows that species originally assigned to the *Agastograptus* belong to four different genera and lineages (Fig. 1), and proposes their phylogenetic position by showing their different features, as well as presenting the relationships among them.

*Material and abbreviations*.—Well preserved material described in this paper has been chemically prepared. Pictures, except of Fig. 2D, were taken under SEM. Figured specimens are housed in the Institute of Paleobiology of the Polish Academy of Sciences, Warsaw (ZPAL), except for the specimen in Fig. 2D, which is stored in the Institute of Geology, Geophysics and Mineralogy of the Russian Academy of Sciences, Novosibirsk (UIGGM SB RAS) and specimens in Fig. 3C, D are at the Geological Survey of Canada, Ottawa (GSC). My study of the retiolitids from Poland (Baltic erratic boulders and Bartoszyce borehole) has been complemented by comparisons with retilitid materials stored in the following institutions: All-Russian Geological Institute, VSEGEI, St. Petersburg; Institute of Geology, Geophysics and Mineralogy, Novosibirsk; Lund University; Museum für Naturkunde, Berlin; University of Cambridge; University of Tübingen; University of Western Ontario, London. The East European Platform is abbreviated EEP.

*Terminology*.—The terminology for anatomical details of the rhabdosome follows Bates (1992), Bates and Kirk (1997), and Kozłowska-Dawidziuk (1995, 1997, 2001). The term reticulum is applied for thin lists, specifying whether they are part of the ancora sleeve or thecal framework.

# Systematic palaeontology

## Order Graptoloidea Lapworth, 1873
## Family Retiolitidae Lapworth, 1873
## Subfamily Plectograptinae Bouček and Münch, 1952
## Genus *Plectograptus* Moberg and Törnquist, 1909

*Type species*: *Retiolites macilentus* Törnquist, 1887, from Wetterhammer area (Colonusskiffern), Thüringia, Ludlow.

*Emended diagnosis*.—Ancora umbrella simple, small, usually partly preserved. Sicula about 2.6 mm long, rarely preserved as traces of the prosicular rim, and indicated by seams on the virgella. Nema free, possibly extended as a nematularium in mature specimens. Ancora sleeve lists of hexagonal meshes with zigzag pattern in the mid-dorsal part of wall. First zigzag lists of ancora sleeve located in region of the lips of $th1^1$and $th1^2$. Large proximal orifices on obverse and reverse sides of rhabdosome, outlined by the ancora umbrella lists (rarely preserved), and first zigzag lists of the ancora sleeve. Mid-ventral list present. Ancora sleeve and thecal lists with seams from the inside and distinctive pustules on bandages.

*Species included*.—*Plectograptus macilentus* (Törnquist, 1887), *P. robustus* (Obut and Zaslavskaya,1983), *P. wimani* (Eisenack, 1951).

*Discussion*.—The type species *Plectograptus macilentus* (Törnquist, 1887) was originally assigned to the genus *Retiolites*, based on poor material from Thüringia. Moberg and Törnquist (1909) established a new genus *Plectograptus* for *R. macilentus*, following the study of better preserved material from Skåne, Sweden. They illustrated a flattened type specimen of *P. macilentus* with large proximal openings (Moberg and Törnquist 1909: pl. 1: 10). The main diagnostic features of large proximal orifices as well as paired reticulofusellar apertural processes occur in one species of *Plectograptus*, *P. robustus*. Similar processes are characteristic of species of *Spinograptus* (see Kozłowska-Dawidziuk 1997), including *S. clathrospinosus* from the *Colonograptus praedeubeli* Biozone which precedes the appearance of *P. robustus* and *P. macilentus*, both of which occur in the Ludlow *Neodiversograptus nilssoni* Biozone. *Spinograptus* is considered to be an ancestor of *Plectograptus* (Kozłowska-Dawidziuk 1995). The main differences between these two genera are the presence in *Plectograptus* of large lateral proximal orifices, and a nematularium. Nematularia have only been found in flattened material (Moberg and Törnquist 1909; Eisenack 1951; Bouček and Münch 1952; Tomczyk 1956). The rhabdosome of *Spinograptus* typically tapers distally, and in most species ends with an appendix (Lenz 1994a; Kozłowska-Dawidziuk 1997).

### *Plectograptus macilentus* (Törnquist, 1887)

Fig. 2A, B.

*Retiolites macilentus* n. sp.; Törnquist 1887: 491, fig. 3.
*Plectograptus macilentus* (Törnquist); Moberg and Törnquist 1909: 13, pl. 1: 1–12.
*Plectograptus tetracantus* n. sp.; Eisenack 1951: 140, pl. 23: 6–8, pl. 25: 9, text-figs. 4, 5.
*Plectograptus macilentus* (Törnquist); Bouček and Münch 1952: 120, fig. 7a–f, pl. 1: 1–4.
*Plectograptus* (*Plectograptus*) *macilentus* (Törnquist); Lenz 1993a: 13–14, pl. 1: 6–8.
*Plectograptus macilentus* (Törnquist); Kozłowska-Dawidziuk 1995: 317, fig. 33.
non *Retiolites* (*Plegmatograptus*) *obesus* var. cf. *macilentus*; Elles and Wood 1908: 343, pl. 34; 13a, b, fig. 224.

*Emended diagnosis*.—Ancora sleeve and thecal walls without reticulum, as in *P. robustus*. Differs from *P. robustus* in absence of apertural processes.

*Description*.—The new material represents the same features as the material described before

*Discussion*.—The first detailed description and discussion of the species was by Bouček and Münch (1952). The authors carefully studied the previously described material of *Plectograptus macilentus*, and other species incorrectly included in this species. They noticed the presence of large openings above the ancora, central position of nema, which in mature specimens projects distally as a thickened "ramification", which was regarded by them as a "teratological phenomenon". This feature is regarded as a three-vaned nematularium (Kozłowska-Dawidziuk 1995).

Bouček and Münch (1952) also mentioned the variation in the development of the proximal part of rhabdosome. These differences are also observed by the author, and are expressed in the location of the first lists of the ancora sleeve walls, which may appear at the level of the either the first or second theca, accounting for differences in the size of the ancora sleeve proximal orifices. More material is needed to study the significance of this feature.

The ancora umbrella with incomplete lists is similarly developed in *P. macilentus* from a Baltic erratic boulder (Fig. 2A, B) (see also Kozłowska-Dawidziuk 1995: fig. 33B) and

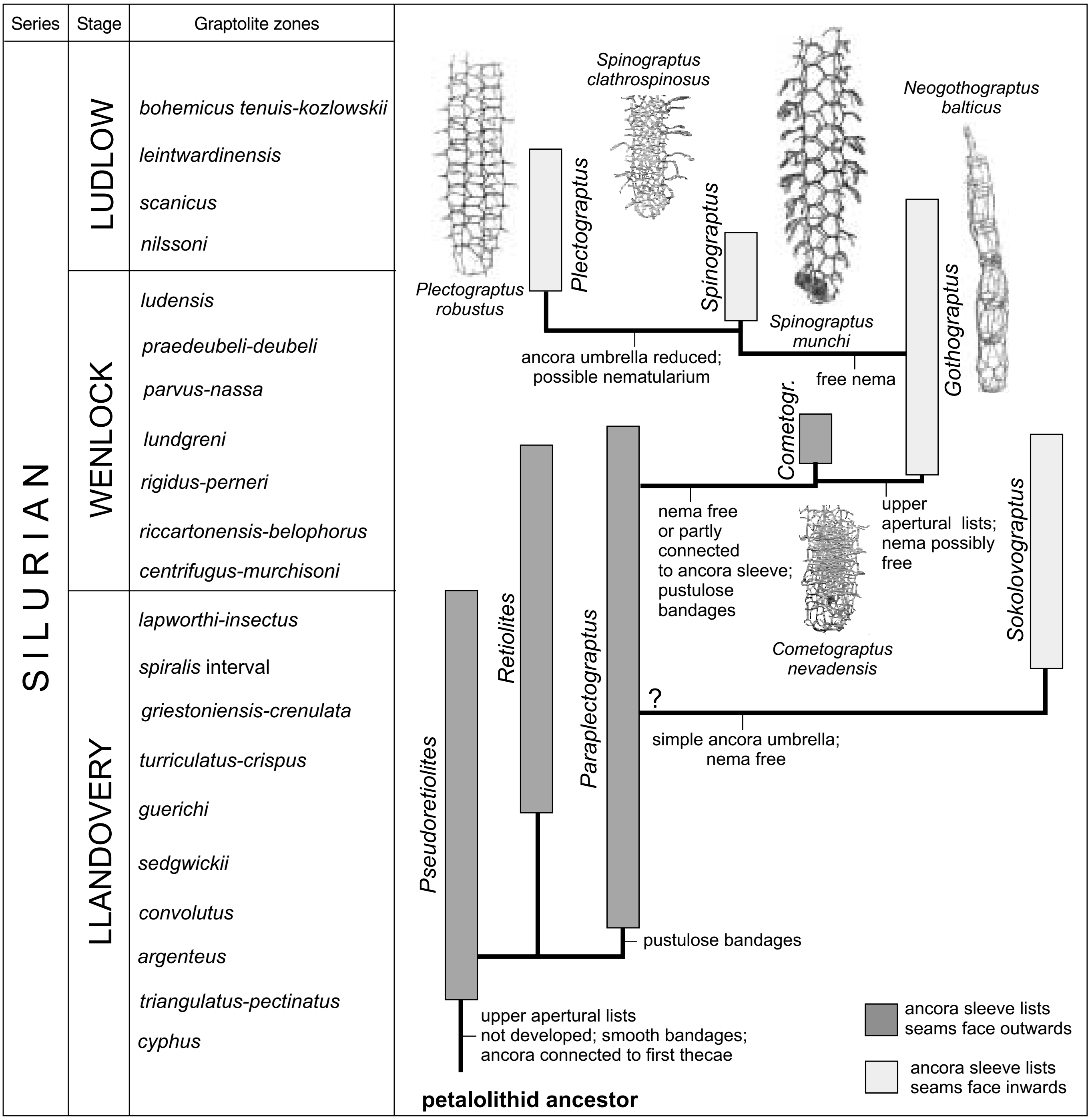


Fig. 1. Phylogenetic relationships among the retiolitids (modified after Kozłowska-Dawidziuk 2001) with synapomorphies, and pictures of species originally included in the genus *Agastograptus* Obut and Zaslavskaya, 1983, showing their position in the *Plectograptus*, *Spinograptus*, *Gothograptus*, and *Cometograptus* lineages. Graptolite zonation after Koren' et al. 1995.

in *P. robustus* from the Kaliningrad area (Fig. 2D), whereas the specimen of *P. robustus* from the EEP possesses better-developed ancora umbrella lists (Fig. 2C), forming an almost complete rim on the ancora. The primary difference between *P. macilentus* and *P. robustus* lies in the presence of paired apertural processes in the latter.

*Material*.—Five specimens representing fragments of rhabdosomes come from Baltic erratic boulder 46 from Jarosławiec, Poland. It co-occurs with *N. balticus*, *Saetograptus chimaera*, *Bohemograptus bohemicus*, *Neodiversograptus beklemishevi*, *Pristiograptus dubius*, *Monoclimacis* sp., and *Crinitograptus crinitus*?.

*Occurrence*.—*P. macilentus* is restricted to the Lower Ludlow, *Neodiversograptus nilssoni* Biozone in Sweden (Törn-

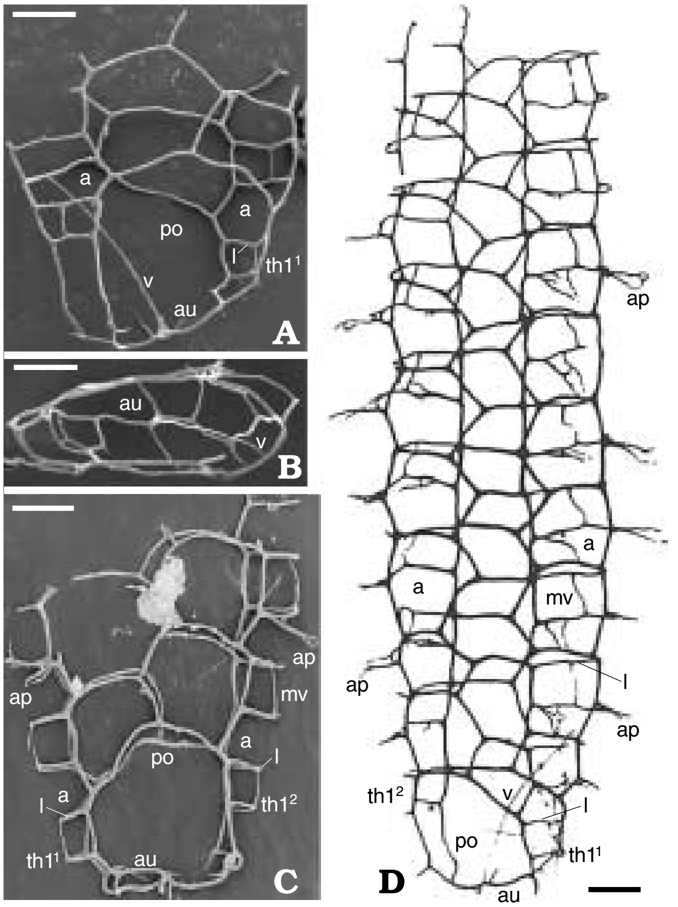


Fig. 2. **A**, **B**. *Plectograptus macilentus* (Törnquist, 1887), ZPAL G. 27/1; Baltic erratic boulder 46 Jarosławiec (photo D. Bates). **A**. Reverse view of proximal fragment of immature rhabdosome. **B**. Inside view showing shape of ancora umbrella and shape of rhabdosome in cross section. **C**, **D**. *Plectograptus robustus* (Obut and Zaslavskaya, 1983). **C**. ZPAL G.27/2, EEP, Bartoszyce borehole, depth 1627.0 m, obverse view of immature rhabdosome. **D**. UIGGM SB RAS 251/42-4/1, holotype, Kaliningrad District, North Kaliningrad borehole, depth 2094.0–2105.5 m (courtesy of N. Sennikov). Scale bars 0.5 mm. Abbreviations: a, aperture; ap, apertural process; au, ancora umbrella; l, lip; mv, mid-ventral list; po, proximal orifice; v, virgella.

quist 1887), Czech Republic (Bouček and Münch 1952; Kozłowska-Dawidziuk et al. 2001), Kyrgyzstan (Koren' 1991), Arctic Canada (Lenz, 1993), Poland (Kozłowska-Dawidziuk 1995), China (Lenz et al. 1996) and Iberia (Gutiérrez-Marco et al. 1996).

## *Plectograptus robustus* (Obut and Zaslavskaya, 1983)

Fig. 2C, D.

*Agastograptus robustus* n. sp.; Obut and Zaslavskaya 1983: 108, pl. 24, tab. 24: 1–3.

*Agastograptus robustus* Obut and Zaslavskaya; Obut and Zaslavskaya 1986: 210, fig. 1a–c.

non *Agastograptus robustus* Obut and Zaslavskaya; Lenz 1994a: fig. 2: 1–7, fig. 3: 1–9.

non *Agastograptus robustus* Obut and Zaslavskaya; Lenz 1994b: fig. 2: 1–5, fig. 3: 1–4, 6.

non *Agastograptus robustus* Obut and Zaslavskaya; Rickards, Packham, Wright and Williamson 1995: 32, fig. 18I, J.

*Emended diagnosis*.—Similar to *P. macilentus*, but differs in possession of paired reticulofusellar apertural processes. Reticular lists of the ancora sleeve and thecal walls are absent.

*Description*.—The longest (3 mm) specimen contains 3 pairs of thecae, and represents growing rhabdosome (Fig. 2C). Width of ancora umbrella is about 1 mm. Some lists of ancora umbrella are present, forming almost complete rim on the ancora. Rhabdosome width increases up to 2 mm on the level of 3rd pair of thecae. Apertural processes absent in two first pairs of thecae. Length of first apertural processes is 0.5 mm. Virgella is not preserved.

*Discussion*.—The holotype of *A. robustus* number UIGGM SB RAS 251/42-4/1 (there is also number 251/42-44 for the same specimen, see Obut and Zaslavskaya 1983: 108, 175) illustrated on Fig. 2D represents a mature specimen built of relatively strong lists with the distinctive zigzag pattern of the ancora sleeve wall, and mid-ventral lists on the ventral side of rhabdosome, as well as paired reticulofusellar spines. This specimen, shown in reverse view, possesses a large lateral orifices outlined by the ancora sleeve lists located close to lip of th1¹ and in region of the lip of the th1². The specimen UIGGM SB RAS 251/42-2/2 from type collection (Obut and Zaslavskaya 1983: fig. 24: 3) represents early stage of growth with first theca developed. It is similar to the specimen representing early growth stage of the species from the author's collection.

Specimens from Arctic Canada assigned to *A. robustus* by Lenz (1994a, b) have a unique preservation or different development of the thecal and ancora sleeve membranes. These specimens, although similar in size to *P. robustus*, are assigned to *Spinograptus* because of possession of an appendix, proximal lateral orifices of similar position and size (see Kozłowska-Dawidziuk 1997: fig. 4) to *Spinograptus*, as well as paired reticulofusellar apertural processes. The prime first zigzag list of the sleeve above the ancora umbrella is connected to the ancora umbrella lists (Lenz 1994a: fig. 2: 1; fig. 3: 3). The lateral proximal orifices in the holotype of *P. robustus,* as in *P. macilentus* (Fig. 2), are larger than those in *A. robustus* from the Arctic, and the prime first zigzag lists are connected to ventral lists on the levels of the first theca apertures. The features described above, as well as occurrence in the *Colonograptus ludensis* Biozone, show that the Arctic forms belong to *Spinograptus*, and assigned to a new species, *S. praerobustus* Lenz and Kozłowska-Dawidziuk, 2002. Specimens from Australia assigned to *A. robustus* by Rickards et al. 1995 show similar features as specimens from the Arctic Canada (Lenz 1994a, b; Lenz and Kozłowska-Dawidziuk 2002), as well as developed reticulum which is absent in *P. robustus*. Australian specimens do not have the specific membrane present in the Arctic species.

*Material*.—One immature specimen (Fig. 2C) and several fragments from depth 1627.0 m, Bartoszyce borehole, Po-

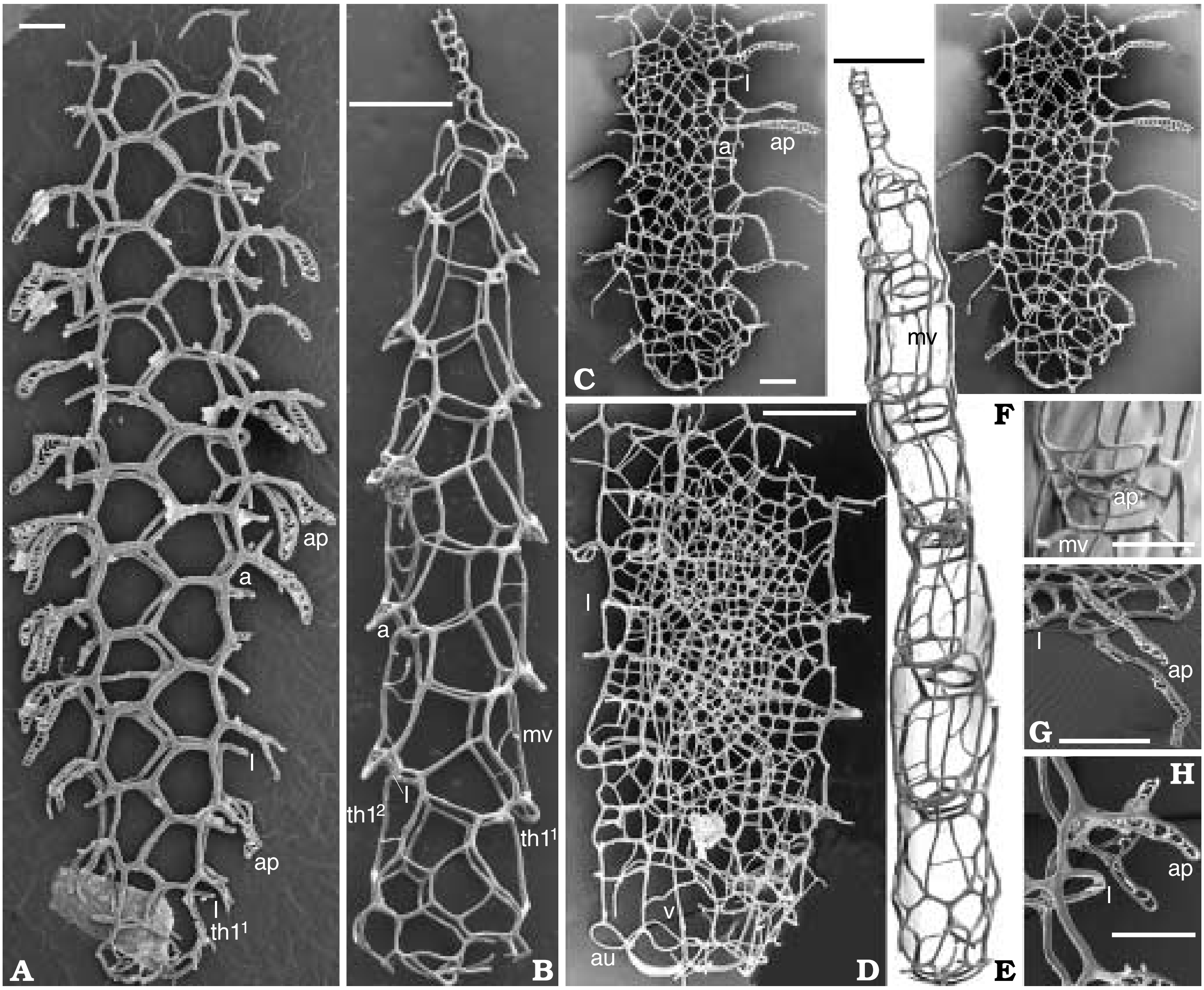


Fig. 3. **A**, **H**. *Spinograptus munchi* (Eisenack, 1951), **A**. ZPAL G. 27/3, EEP, Bartoszyce borehole, depth 1626.6 m, reverse view of mature rhabdosome. **H**. ZPAL G. 27/7, EEP Mielnik borehole, depth 1044.0 m, enlargement of paired apertural processes of distal theca. **B**, **E**, **F**. *Neogothograptus balticus* (Eisenack, 1951), Baltic erratic boulder 46 from Jarosławiec. **B**, **E**. ZPAL G. 27/4 mature rhabdosome with appendix (photo D. Bates). **B**. Reverse view. **E**. Ventral view of thecae $1^2$ side. **F**. ZPAL G. 27/5 enlargement of single reticular apertural process. **C**, **G**. *Spinograptus clathrospinosus* (Eisenack, 1951), **C**. GSC120736, Arctic Canada, Cornwallis Island, AB-97 25 m, stereopair of immature rhabdosome, reverse view (modified after Lenz and Kozłowska-Dawidziuk 2002: fig. 13: 6). **G**. ZPAL G. 27/6, EEP, Bartoszyce borehole, depth 1631.2 m, paired apertural processes of medial theca. **D**. *Cometograptus nevadensis* (Berry and Murphy, 1975), GSC 99161, Arctic Canada, Cornwallis Island, SBC10E (modified after Lenz 1993: pl. 19: 1), ventro-latral view of rhabdosome. Scale bars 1 mm except for **D**, **F**–**H** which is 0.5 mm. Abbreviations as Fig. 2.

land; co-occur with *Colonograptus jaegeri*, *C. praedeubeli*, *C. gerhardi*?, *Pristiograptus dubius*, *Spinograptus munchi*.

*Occurrence*.—*Plectograptus robustus* occurs in *Neodiversograptus nilssoni* Biozone of North Kaliningrad, Russia, and late Homerian of Poland.

## Genus *Spinograptus* Bouček and Münch, 1952

*Type species*: *Retiolites spinosus* Wood, 1900.

*Species included*.—*Spinograptus spinosus* (Wood, 1900), *S. munchi* (Eisenack, 1951), *S. clathrospinosus* (Eisenack, 1951), *S. lawsoni* (Holland, Rickards and Warren, 1969), *S. quadratus* (Lenz, 1993), *S. reticulolawsoni* Kozłowska-Dawidziuk, 1997, *S. latespinosus* Kozłowska-Dawidziuk, 1997, *S. praerobusus* Lenz and Kozłowska-Dawidziuk, 2002.

## *Spinograptus munchi* (Eisenack, 1951)

Fig. 3A, H.

*Retiolites munchi* n. sp.; Eisenack1951: 136, pl. 22: 9–12, pl. 23: 3–5, pl. 24: 1.

*Agastograptus munchi* (Eisenack); Obut and Zaslavskaya 1983: 111–112, pl. 22: 4, pl. 26: 1–4.

*Spinograptus munchi* (Eisenack); Kozłowska-Dawidziuk 1995: 316–317, figs. 31A, 32A, B.

non *Agastograptus munchi* (Eisenack); Richards, Packham, Wright and Williamson 1995: 32, figs. 18E–H, 19D–H.

*Diagnosis*.—See Kozłowska-Dawidziuk 1995.

*Description*.—The longest specimen of 10 mm, with robust lists, represents mature rhabdosome with 10 pairs of thecae. Ancora umbrella is about 1 mm wide, composed of lists thinner than in the rest of the rhabdosome. Maximum width of lateral walls (between pleural lists) is 1.6 mm at the level of 5$^{th}$ pair of thecae, and is the same to end of the rhabdosome. Paired apertural processes well developed of typical shape for the species. Two first pairs of thecae possess smaller and thinner processes, the strongest are in the middle part of rhabdosome. In the distal part they are not present, probably broken off. The rest of specimens represent fragments of mature and younger (thinner lists) stages. Virgella is preserved in young rhabdosomes.

*Discussion*.—The new material represents the rhabdosome features as in the type material (Eisenack 1951) as well as the material described from Všeradice, Czech Republic (Kozłowska-Dawidziuk et al. 2001). *S. munchi* differs from other species of *Spinograptus* in lacking an ancora sleeve reticulum and mid-ventral lists (see Kozłowska-Dawidziuk 1995, 1997). It possesses distinctive, paired bifurcated reticulofusellar apertural processes, (Fig. 3A, H). Material described by Rickards et al. (1995) may represent some *Spinograptus* species, similar to *S. latespinosus*, with a developed reticulum. The difference between *S. munchi* and *S. latespinosus* is in the lack of reticulum of ancora sleeve and ventral walls, different shape of apertural processes as well as absence of a mid-ventral list and appendix in *S. munchi*.

*Material*.—The new material consists of dozens of fragments and 9 more complete rhabdosomes, and comes from Poland, Bartoszyce borehole depths: 1626.6 m, 1627.0 m, 1634.5 m, 1635.5 m, 1641.0 m.

*Occurrence*.—*Spinograptus munchi* probably occurs in the *Colonograptus ludensis* Biozone (uppermost upper Homerian) from unknown locality of erratic boulders of the Eisenack material (personal examination by the present author 1998), the *Gothograptus nassa* Biozone from Kaliningrad, Russia (Obut and Zaslavskaya 1983), the lower part of the *Neodiversograptus nilssoni* Biozone (Kozłowska-Dawidziuk 1995) and *Colonograptus praedeubeli* and *C. deubeli* biozones of Poland, and in the middle part of *C. praedeubeli–C. deubeli* Biozone of Všeradice, Barrandian, Czech Republic (Kozłowska-Dawidziuk et al. 2001).

## *Spinograptus clathrospinosus* (Eisenack, 1951)

Fig. 3C, G.

*Retiolites clathrospinosus* n. sp.; Eisenack 1951: 139, pl. 23: 1, 2.

*Spinograptus* cf. *spinosus* (Wood); Lenz 1978: 636, pl. 7: 3, 4.

*Agastograptus clathrospinosus* (Eisenack); Lenz 1993: 15–16, pl. 3:1, 2, 4, 7, pl. 4: 6, 8.

*Spinograptus clathrospinosus* (Eisenack); Kozłowska-Dawidziuk 1995: 314, pl. 31B, pl. 32C.

*Agastograptus clathrospinosus* (Eisenack); Richards, Packham, Wright and Williamson 1995: 34: fig. 18D.

*Spinograptus clathrospinosus* (Eisenack); Kozłowska-Dawidziuk 1997: 405, fig. 13A, B.

*Agastograptus clathrospinosus* (Eisenack); Zhang and Lenz 1997: 1225, fig. 3G–J.

non *Agastograptus clathrospinosus* (Eisenack); Lenz 1993: 15–16, pl. 3: 3, 5, 6, pl. 4: 1–5, 7.

*Diagnosis*.—See Kozłowska-Dawidziuk 1997.

*Description*.—The new material displays similar preservation and features as those described before (Eisenack 1951; Lenz 1993; Kozłowska-Dawidziuk 1995).

*Discussion*.—*S. clathrospinosus* displays a well developed reticulum of the ancora sleeve with a marked zigzag in its dorsal part, and poorly developed mid-ventral lists, as well as long, thin apertural processes with reticulofusellar structure clearly visible throughout their length (Fig. 3C, G). *S. clathrospinosus* is similar to *S. spinosus* in size of rhabdosome, weak mid-ventral lists and ancora sleeve reticulum, but differs in apertural processes, which are thinner in *S. spinosus*, with reticulofusellar structure marked only at their distal ends.

*Material*.—Seven fragments from depth 1631.2 m, Bartoszyce borehole, Poland, EEP.

*Occurrence*.—*Neodiversograptus nilssoni* Biozone of erratic boulders from an undescribed location (Eisenack 1951), in Kaliningrad area, Russia (Obut and Zaslavskaya 1983), and Poland (Kozłowska-Dawidziuk 1995), *Colonograptus predeubeli–C. debeli* and *C. ludensis* biozones of Arctic Canada (Lenz 1993), *C. ludensis* and *L. progenitor* biozones in South China (Zhang and Lenz 1997), and the upper part of the *Pristiograptus parvus–Gothograptus nassa* Biozone at Všeradice, Barrandian, Czech Republic (Kozłowska-Dawidziuk et al. 2001).

## *Spinograptus quadratus* (Lenz, 1993)

*Agastograptus quadratus* n. sp.; Lenz 1993: 16, pl. 5: 1–10.

*Emended diagnosis*.—Apertural processes relatively short, simple and broad, close to mid-ventral list. Mid-ventral list well developed, straight. Minimal reticulum. Ancora sleeve with distinct zigzag. *Plectograptus*-like thecal profile.

*Discussion*.—*S. quadratus* is similar to *S. latespinosus* in thecal shape, and size of rhabdosome, although the lateral wall in *S. quadratus* is wider proximally, and narrower distally. The difference is in a shape of apertural processes and lack of reticulum in the ventral walls. The mid-ventral list in *S. quadratus* is well developed in every theca, whereas in other species of *Spinograptus* that list is usually well developed only in proximal thecae (*S. lawsoni*, *S. reticulolawsoni*, *S. latespinosus*) or not developed (*S. clathrospinosus*, *S. spinosus*, *S. munchi*).

*Material and occurrence*.—*S. quadratus* is known only from Arctic Canada, Cape Sir John Franklin, Devon Island, *Lobograptus progenitor* Biozone.

### Genus *Neogothograptus* Kozłowska-Dawidziuk, 1995

*Type species*: *Neogothograptus purus* Kozłowska-Dawidziuk, 1995; Baltic erratic boulder 22 from Jarosławiec, Poland.

*Species included*.—*Neogothograptus purus* Kozłowska-Dawidziuk, 1995; *Neogothograptus balticus* (Eisenack, 1951), *Neogothograptus romani* Kozłowska-Dawidziuk, 1995.

### *Neogothograptus balticus* (Eisenack, 1951)

Fig. 3B, E, F.

*Retiolites balticus* Eisenack; Eisenack 1951: 134–136, pl. 22: 4–8, pl. 24: 5.
*Gothograptus nassa* (Holm); Moberg and Törnquist 1909: 19, pl. 1: 14.
*Holoretiolites* (*Balticograptus*) *balticus* Eisenack; Bouček and Münch 1952: 17–19, fig. 5b.
*Neogothograptus balticus* (Eisenack); Kozłowska-Dawidziuk 1995: 304, fig. 27I.

*Diagnosis*.—See Kozłowska-Dawidziuk 1995.

*Description*.—The preservation and features (measurements of thecae, ancora umbrella, ancora sleeve, apertural processes) of the new material are consistent with *N. balticus* described before (Eisenack 1951; Kozłowska-Dawidziuk 1995).

*Discussion*.—*Neogothograptus balticus* demonstrates the presence of a strong, clearly single, reticular apertural hood (Fig. 3E, F), in contrast to the paired processes of *Spinograptus* (Fig. 3C, G).

The specimen described as *G. nassa* by Moberg and Törnquist (1909) was examined by the author in 1993 in Lund University, and was recognized to be *N. balticus*. It possesses less ancora sleeve reticulum than *G. nassa*, distinctive single reticular apertural processes, and an ancora sleeve list arrangement characteristic of *N. balticus*, as well as a free nema. These features contrast to the dense ancora sleeve reticulum, solid microfusellar apertural hood, and nema incorporated to the ancora sleeve wall of *G. nassa* (see Kozłowska-Dawidziuk 1999), a species restricted to the *P. dubius*–*G. nassa* Biozone. The Moberg and Törnquist specimen co-occurs with the same Ludlow assemblage of graptolites *Neodiversograptus nilssoni*, *Plectograptus macilentus*, and *Spinograptus spinosus*, like the type.

*Material*.—16 specimens from Baltic erratic boulder 46 from Jarosławiec, Poland, containing of *N. balticus* and *Plectograptus macilentus, Saetograptus chimaera, Bohemograptus bohemicus, Neodiversograptus beklemishevi, Pristiograptus dubius, Monoclimacis* sp., and *Crinitograptus crinitus*?.

*Occurrence*.—*Neogothograptus balticus* occurs in *Neodiversograptus nilssoni* Biozone from erratic boulder of Kaliningrad area, Russia (Eisenack 1951), in *Lobograptus progenitor* (Kozłowska-Dawidziuk 1995) and in *Bohemograptus bohemicus* biozones of Poland (see above).

### Genus *Cometograptus* Kozłowska-Dawidziuk, 2001

*Type species*: *Cometograptus tomczyki* Kozłowska-Dawidziuk, 2001.

*Species included*.—*Cometograptus nevadensis* (Berry and Murphy, 1975), *C. apoxys* (Lenz, 1993), *C. bicladis* (Lenz, 1993), *C. marsupium* (Lenz, 1993), *C. tomczyki* Kozłowska-Dawidziuk, 2001, *C. koreni* Kozłowska-Dawidziuk, 2001, *C. apsis* Lenz and Kozłowska-Dawidziuk, 2001, *C. kirki* Lenz and Kozłowska-Dawidziuk, 2001.

### *Cometograptus nevadensis* (Berry and Murphy, 1975)

Fig. 3D.

*Retiolites nevadensis* n. sp.; Berry and Murphy 1975: 100, pl.15: 5, 6.
*Agastograptus nevadensis* (Berry and Murphy); Obut and Zaslavskaya 1983: 107.
*Spinograptus nevadensis* (Berry and Murphy); Lenz 1993: 23, pl. 19: 1–6, pl. 20: 1–7.
*Cometograptus nevadensis* (Berry and Murphy); Lenz and Kozłowska-Dawidziuk 2001: 18, pl. 11: 1–6.

*Diagnosis*.—See Kozłowska-Dawidziuk 2001.

*Discussion*.—*Cometograptus nevadensis* is recognized as a species of the *Cometograptus* group restricted to the *Cyrtograptus lundgreni* Biozone (Kozłowska-Dawidziuk 2001). The crucial difference between *Plectograptus* and *Cometograptus* is in the position of seams on the ancora sleeve lists, which may indicate the mode of list secretion, whether from the outside or from the inside (Bates and Kirk personal communication 1999). In *Cometograptus* seams on lists face out, the opposite of *Plectograptus*. There are also differences in arrangement of the ventral wall lists, presence of transverse rods, and development of apertural processes as a spine-like genicular hoods with seams, probably signifying some kind of membrane between them.

*Occurrence*.—*Cometograptus nevadensis* occurs in two places: Arctic Canada and Central Nevada, North America, both in *Cyrtograptus lundgreni* Biozone.

## Phylogenetic position of species assigned to *Agastograptus*

Six species originally assigned to *Agastograptus* are recognized herein as forms belonging to the four different generic groups: *Cometograptus*, *Gothograptus*, *Spinograptus*, and *Plectograptus*.

The *Cometograptus* group is the characteristic retiolitid element within the *Cyrtograptus lundgreni* Biozone, and contains at least six species, that appeared and disappeared rapidly (Fig. 1). The group is characterized by ancora sleeve lists with seams facing outward (opposite to the post *lundgreni* retiolitids), well-developed transverse rods situated close to the ventral walls, and a long sicula (Kozłowska-Dawidziuk 2001). There is a large variation in forms belonging to *Cometograptus*, ranging from those with a dense reticulum to forms with regular clathrial lists of the ancora sleeve; and with stoma on lateral rhabdosome walls or with a small appendix situated distally (Lenz 1993; Lenz and Kozłowska-Dawidziuk 2001). This group is possibly derived from *Paraplectograptus* (Fig. 1), and it is likely ancestral of the

*Gothograptus* lineage (Kozłowska-Dawidziuk 2001). This may be significant, assuming that only one species of *Gothograptus* survived the *Cyrtograptus lundgreni* Event (see Koren' and Urbanek 1994). *Cometograptus* combines features that link this group with oldest retiolitids (seams on ancora sleeve lists facing on the outside, transverse rods) and features of younger retiolitids (pustules on lists, long sicula). *C. nevadensis* was earlier assigned to *Agastograptus*.

The *Gothograptus* lineage ranges from the *Cyrtograptus lundgreni* Biozone to the *Cucullograptus hemiaversus* Biozone. This lineage contains four genera: *Eisenackograptus*, *Gothograptus*, *Neogothograptus*, and *Holoretiolites*, and is characterized by thin rhabdosomes with a variable number of thecae, from two to 23 pairs, ending with a well-developed appendix (Lenz 1993; Kozłowska-Dawidziuk et. al. 2001). Usually the stratigraphically older and the younger forms were built of fewer thecae. In older species the ancora sleeve is densely-reticulated (*Eisenackograptus*, *Gothograptus*), whereas the younger forms possess almost only clathrial ancora sleeve lists (*Neogothograptus*, *Holoretiolites*). *Neogothograptus* is a younger form occurring in the *Lobograptus progenitor* Biozone (Kozłowska-Dawidziuk 1995), and is characterized by a large reduction of thecal and ancora sleeve lists. Single apertural processes are observed in one species, *N. balticus*, a form previously assigned to *Agastograptus*.

The *Spinograptus* group is one of the first to appear in Late Homerian, after the *Cyrtograptus lundgreni* Event, and continues into the *Neodiversograptus nilssoni* Biozone (Fig. 1). Its forms possess regular clathrial lists on the ancora sleeve forming zigzag, which in some species is hidden by well-developed thin reticular lists. Some forms possess a short appendix (Lenz 1994; Kozłowska-Dawidziuk 1997), not so well developed as in *Gothograptus*. A characteristic feature of *Spinograptus* is the presence of paired apertural processes, which range from thin "spines" (*S. spinosus*) to wide paddle-shaped structures of *S.* sp. (see Kozłowska-Dawidziuk et. al. 2001), all reticulofusellar in nature. *S. clathrospinosus*, *S. munchi*, and *S. quadratus* were assigned earlier to *Agastograptus*.

The *Plectograptus* group is well known from *Neodiversograptus nilssoni* to *Saetograptus leintwardinensis* biozones, although the author's personal observation of material from the Bartoszyce borehole of the EEP, shows earlier appearance of *Plectograptus* species in Late Homerian. The group contains three genera; two species of the *Plectograptus* (*P. macilentus* and *P. robustus*), and one species each of the two genera *Semiplectograptus* and *Plectodinemagraptus* (the youngest retiolitid form). This lineage possesses forms with the biggest (*Plectograptus*), and the smallest (*Plectodinemagraptus*) retiolitid rhabdosomes of the Ludlow. This group is characterized by ancora sleeve lists with seams facing inwards, a large lateral opening in the proximal part of the rhabdosome, long sicula, possible nematularium, and a very reduced reticulum on the ancora sleeve. A regular hexagonal pattern with a zigzag on the lateral wall of the ancora sleeve is characteristic for the genus *Plectograptus*. A nematularium is recognized in *P. macilentus* although it is common only in more complete flattened material. The *Plectograptus* lineage may have evolved from *Spinograptus* (Kozłowska-Dawidziuk 1995), or from another group of retiolitids with nematularia, beginning in the *Pristiograptus parvus–nassa* to *Colonograptus praedeubeli–C. deubeli* biozones (see Kozłowska-Dawidziuk et. al. 2001). The proposed phylogenetic relationships of the retiolitids are shown in Fig. 1.

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