

Evolution of the retiolitid *Neogothograptus* (Graptolithina) and its new species from the upper Wenlock of Poland, Baltica

ANNA KOZŁOWSKA, ALFRED LENZ, and MICHAEL MELCHIN



Kozłowska A., Lenz, A., and Melchin, M. 2009. Evolution of the retiolitid *Neogothograptus* (Graptolithina) and its new species from the upper Wenlock of Poland, Baltica. *Acta Palaeontologica Polonica* 54 (3): 423–434. DOI: 10.4202/app.2008.0022.

Neogothograptus reticulatus sp. nov. from the upper Homeric *Colonograptus praedeubeli* Biozone, and *N. thorstinsoni* and *N. alatifformis* from the *Lobograptus progenitor* Biozone, are described for the first time from three localities: borehole, Baltic erratic boulder of East European Platform and Holy Cross Mountains of Poland. *N. reticulatus*, presently the oldest known species of *Neogothograptus*, is also tentatively identified from upper Homeric strata of south-eastern Australia. The two other species are previously known only from Arctic Canada, and possibly China. The morphology of the *Neogothograptus reticulatus* rhabdosome, its appendix, thecal profile, densely reticulated rhabdosome and genicular hoods suggest a close relationship to *N. eximinassa* from *Colonograptus ludensis* Biozone. *N. reticulatus* and *N. eximinassa* are most similar to *Gothograptus nassa*, the earliest-known retiolitid to appear immediately following the *Cyrtograptus lundgreni* extinction event. The biostratigraphic position of *N. reticulatus* suggests it might be considered as a potential ancestor to all younger (Ludlow) species of *Neogothograptus*. Cladistic analysis, however, provides no direct support for such an interpretation and, instead, suggests that *Baculograptus batesi* may be the ancestor. The occurrences of *Neogothograptus*, as well as *G. nassa*, from a number of Silurian terranes mostly from low paleolatitude regions, but also from high paleolatitudes, demonstrate their tolerance to a broad range of paleoenvironments.

Key words: Retiolitidae, *Gothograptus*, *Neogothograptus*, evolution, biostratigraphy, ocean currents, paleolatitude, late Wenlock, Ludlow, Silurian.

Anna Kozłowska [akd@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland; Alfred Lenz [aclenz@uwo.ca], Department of Earth Sciences, University of Western Ontario, London, Ontario N6A 5B7, Canada;

Michael Melchin [mmelchin@stfx.ca], Department of Earth Sciences, St. Francis Xavier University, Antigonish, Nova Scotia, B2G 2W5, Canada.

Received 27 March 2008, accepted 25 June 2009, available online 17 July 2009.

Introduction

The retiolitids (Graptolithina) are a very distinctive group of Silurian graptolites differing from all other graptolites in that the cortical bandages are much better developed than the space-filling, sheet-like fusellae. The bandages forming the meshwork lists provide the structures from which the unique ancora and ancora sleeve structures are developed. The fusellar layer is very thin, and is only very rarely preserved (e.g., Bates 1987; Bates and Kirk 1984, 1992; Lenz 1994; Kozłowska-Dawidziuk 1997). The best-recognized and best-preserved retiolitids come from Arctic Canada and Baltica (e.g., Kozłowska-Dawidziuk 1995, 1997, 2001; Lenz and Kozłowska-Dawidziuk 2001, 2004; Maletz 2008), and detailed studies of these isolated retiolitids have been greatly enhanced through scanning electron microscope studies (Bates and Kirk 1992; Lenz 1994; Kozłowska-Dawidziuk 1997; Lenz and Kozłowska-Dawidziuk 2001, 2002; Maletz 2008), leading to the recognition of many new genera and species. These studies

yielded abundant new data about the construction of retiolitid rhabdosomes and, as a consequence, provided a much better understanding of the complicated rhabdosomal morphology of the retiolitids. In summary, the retiolitids have an additional skeletal element developed as a prolongation of the branching virgella, the ancora, and its continuation, the ancora sleeve, both structures being separate from the thecal framework (Bates and Kirk 1997; Kozłowska-Dawidziuk 2004; Bates et al. 2005).

Retiolitid evolutionary history may be divided into two periods: those before, and those after, the late Wenlock *Cyrtograptus lundgreni* extinction event (Urbanek 1993; Kozłowska-Dawidziuk 2004; Porębska et al. 2004). Taxa from the older strata, those from the middle Llandovery to middle Wenlock, typically exhibit a greater temporal duration in comparison with those appearing after the *Cyrtograptus lundgreni* Event. Their rhabdosomes are generally larger, thecae are long, siculae short, and the bandages have smooth, striated or less commonly, pustulose surfaces. By contrast, the post-ex-

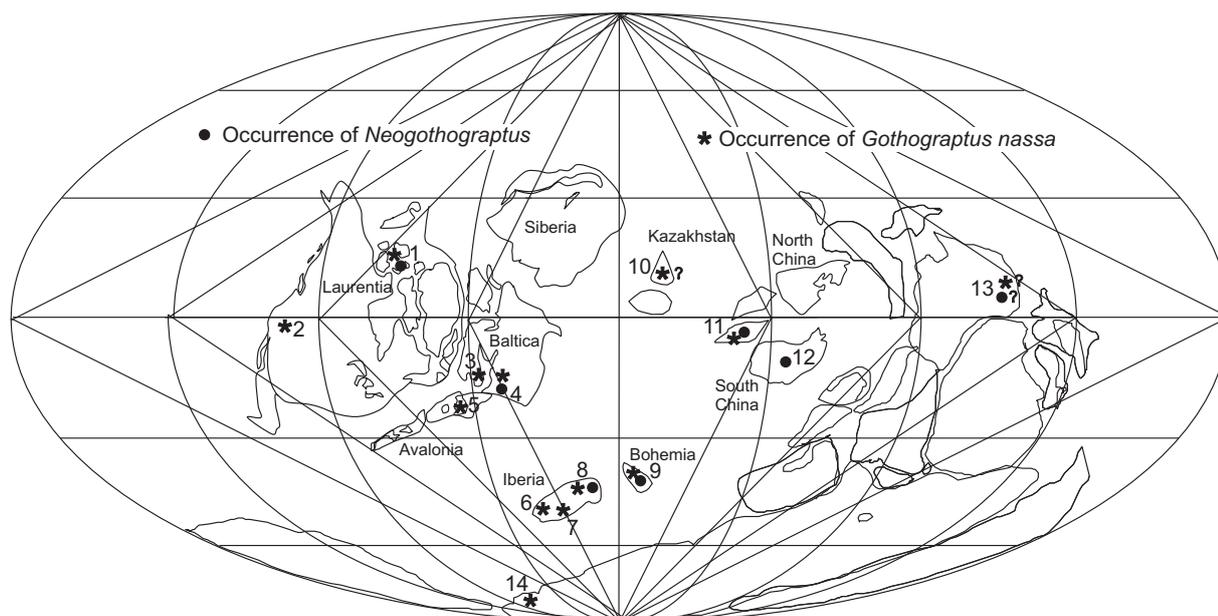


Fig. 1. Silurian paleogeographic map, showing occurrences of *Gothograptus nassa* and *Neogothograptus*. Localities and graptolite data derived from the following literature sources: 1, Arctic Canada: Lenz 1993; Lenz and Kozłowska-Dawidziuk 2004; 2, Nevada: Berry and Murphy 1975; 3, Southern Sweden (Baltica): Holm 1890; 4, Northeastern Poland (Baltica): Kozłowska-Dawidziuk 1995; 5, United Kingdom: Warren 1971; 6, Southern Portugal: Gutiérrez-Marco et al. 1996; 7, Southern Spain: Gutiérrez-Marco et al. 1996; 8, Thuringia (Saxothuringia): Jaeger 1991; 9, Bohemia: Kozłowska-Dawidziuk et al. 2001; 10, Kazakhstan: Koren' et al. 2003; 11, Kyrgyzstan: (AL personal observation 1995); 12, South China: Zhang and Lenz 1997; 13, Southeastern Australia: Rickards et al. 1995; 14, Tunisia, Morocco and Libya: Waterlot 1945, Jaeger et al. 1975.

tion retiolitids are generally characterized by shorter rhabdosomes and thecae, siculae distinctly longer than those of the earlier group, and exclusively pustulose bandages. In retiolitid evolution therefore, there was a strong tendency towards the reduction of the rhabdosomal and thecal size, and a lengthening of the sicula (Kozłowska-Dawidziuk 2004).

The driving forces behind these evolutionary modifications are not well understood, although sea level fluctuations appear to have been one of the strongly correlated factors (Lenz and Kozłowska 2007: fig. 3). For example, during the Llandovery to early Wenlock, the sea level cycles were of longer duration, in comparison with those of the post-*Cyrtograptus lundgreni* time, and retiolitid evolution appears to have closely followed these cycles. The genus *Neogothograptus*, represented in this paper by *Neogothograptus reticulatus* sp. nov., appeared in the *Colonograptus praedeubeli* Biozone, along with retiolitid and monograptid taxa, in coincidence with a global transgression. Further evolution of retiolitids continued into the high sea levels in the Early Ludlow, but completely disappeared from the geological record during the middle Ludlow regression.

Based on biostratigraphic data gathered from a number of globally very well-sampled sections from both warm and cool water paleo-realms (Fig. 1) it has been suggested that all post-extinction, upper Wenlock and Ludlow retiolitids may have been derived from *Gothograptus nassa*, the only known retiolitid species to appear globally immediately following the *Cyrtograptus lundgreni* Extinction Event (e.g., Kozłowska-Dawidziuk 2004). Beginning in the following, post-extinction *Colonograptus praedeubeli* Biozone (the biostratigraphic position of *N. reticulatus*), however, rapid diversifi-

cation of new species followed, culminating in the early Ludlow *Neodiversograptus nilssoni* Biozone (Lenz and Kozłowska-Dawidziuk 2004; Bates et al. 2005).

The two stratigraphically oldest species of *Neogothograptus*, and that are similar to *Gothograptus nassa*, are *Neogothograptus reticulatus* sp. nov. and *N. eximinassa* Maletz, 2008. They occur in the upper Wenlock, *C. praedeubeli* and *C. ludensis* biozones, respectively. The remaining species of *Neogothograptus* occur in the lower and middle Ludlow biozones: *Neodiversograptus nilssoni*–*Lobograptus progenitor* biozones (*N. purus*, *N. balticus*, *N. romani*, *N. thorsteinssoni*, *N. melchiani*, *N. alatiformis*), and *Pleurograptus linearis* Biozone (*N. purus labiatus*) (Table 1). Rhabdosomes of all species of *Neogothograptus* are finite, with a narrow elongate profile and most, if not all, bear an appendix as in *G. nassa* (Fig. 2).

This paper describes *N. reticulatus* sp. nov. from the upper Homeric *C. praedeubeli* Biozone of northeastern and southern Poland. This new discovery fills the gap between the earlier proposed ancestor, *G. nassa* (lowermost to middle Homeric), and the Ludlow species of *Neogothograptus* described in previous studies and therefore, has considerable evolutionary significance. In addition, we have undertaken a phylogenetic analysis to test the hypothesis of the proposed ancestral relationship between *G. nassa* and the later Homeric–early Ludlow retiolitids.

Neogothograptus reticulatus has been recovered from three localities within the East European Platform (EEP) of Poland, a part of the Baltica terrane. These are the Bartoszyce borehole, in northern Poland, a Baltic erratic boulder, and the Prągowiec ravine in the Holy Cross Mountains, southern Po-

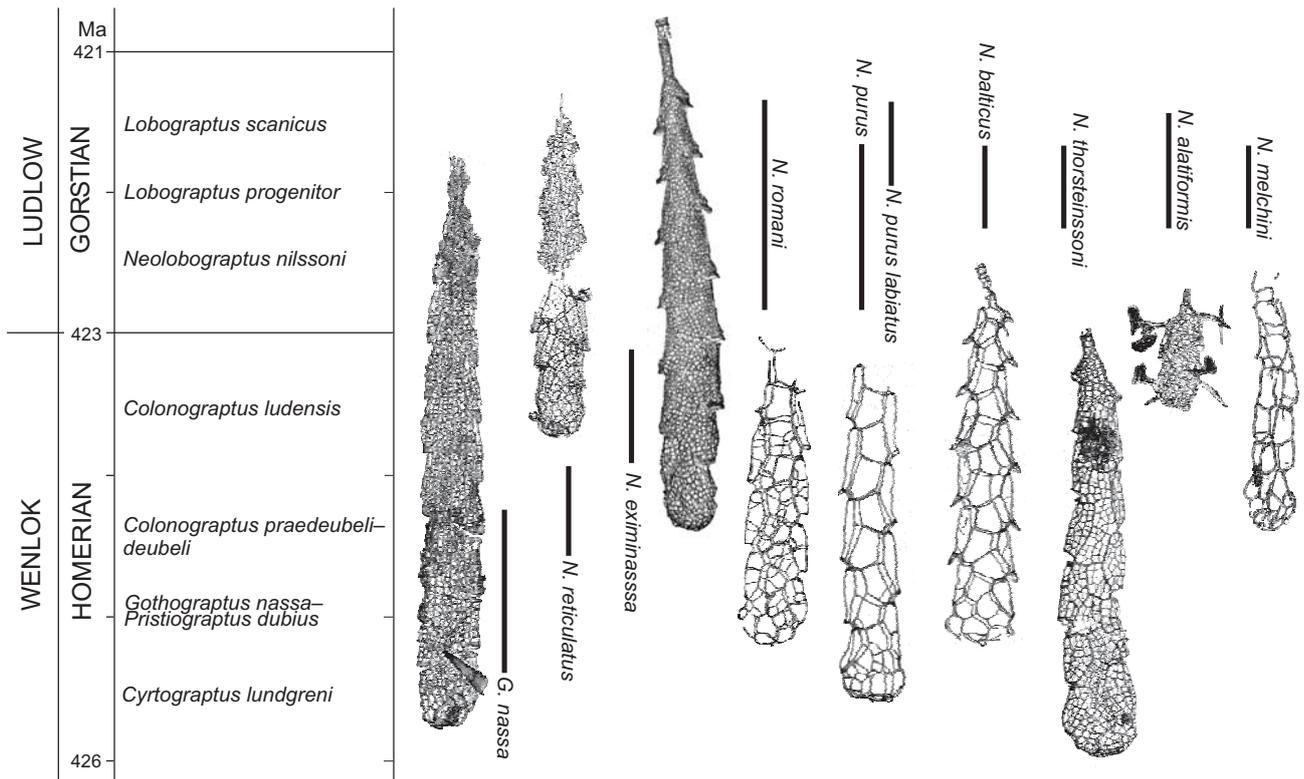


Fig.2. Biostratigraphic ranges of the *Gothograptus nassa* and of eight species of *Neogothograptus*. Most of specimens are shown in lateral view.

land. Two other species, *N. alatifformis* and *N. thorsteinssoni*, previously known only in Arctic Canada, are also described from the Baltica terrane (Fig. 1). All these forms were isolated from rocks by acid extraction and studied by means of scanning electron microscopy.

The new discoveries bring the number of species of *Neogothograptus* to a total of nine (Kozłowska-Dawidziuk 1995; Lenz and Kozłowska-Dawidziuk 2004; Maletz 2008) from a number of widely separated places in the world (Fig. 1), the most important and species-rich regions being the Baltic region and Arctic Canada. Species described from Baltica comprise *N. balticus*, *N. romani*, and *N. purus*, to which list is now added *N. alatifformis* and *N. thorsteinssoni*, and recently *N. eximinassa* and *N. ornatus* (Maletz 2008), and the oldest known species, *N. reticulatus* sp. nov. from the *C. praedeubeli* Biozone. Species found in Arctic Canada comprise *N. purus labiatus*, *N. alatifformis*, *N. melchini*, and *N. thorsteinssoni* (Table 1). A species with a strong affinity to *N. alatifformis* and one now tentatively, assigned to *N.*

ornatus by Maletz (2008), occurs in South China (Zhang and Lenz 1997). Among the species of *Neogothograptus* now known, there is a large variation in number of thecae, degree of reticulation, development of the appendix, and the development of the genicular processes.

Institutional abbreviations.—GSC, Geological Survey of Canada, Ottawa, Canada; ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations.—EEP, East European Platform; MPT, most parsimonious trees; SEM, Scanning Electron Microscope; th, theca.

Evolution of *Neogothograptus*

Morphological and stratigraphic data suggest that the genus *Neogothograptus* may have evolved from either *Gothograptus* (Kozłowska-Dawidziuk, 2004) or *Baculograptus* (Lenz

Table 1. Geographic occurrences of all of the known species of *Neogothograptus*.

| Laurentia, Arctic, Canada | Baltica, Bartoszyce borehole, Poland | Baltica erratic boulders, Poland | Baltica, Holy Cross Mts., Poland | South China, southern Yunnan | Australia, New South Wales | Germany, Baltic boulders | Kyrgyzstan, Central Asia |
|---|--|--|----------------------------------|------------------------------|---|---|---|
| <i>N. thorsteinssoni</i> <i>N. purus labiatus</i> <i>N. melchini</i> <i>N. alatifformis</i> sp. nov. | <i>N. reticulatus</i> <i>N. thorsteinssoni</i> <i>N. romani</i> <i>N. purus</i> | <i>N. reticulatus</i> <i>N. balticus</i> <i>N. romani</i> <i>N. purus</i> <i>N. alatifformis</i> | <i>N. reticulatus</i> | <i>N. ornatus</i> ? | <i>Gothograptus</i> ? probably = <i>N. reticulatus</i> | <i>N. eximinassa</i> <i>N. ornatus</i> | <i>Gothograptus balticus</i> ? <i>Gothograptus</i> sp. |

and Kozłowska-Dawidziuk, 2002). The main similarity among these genera is the construction of a finite rhabdosome terminating in an appendix. *Gothograptus* and several species of *Neogothograptus* possess similarly developed genicular processes (Kozłowska-Dawidziuk 1995), whereas the main difference is the position of the nema (Fig. 2). In all species of *Gothograptus*, the nema is attached throughout, whereas in every species of *Neogothograptus*, as in all other upper Homeric and Ludlow retiolitids, the nema is free (Bates et al. 2005). Species of *Baculograptus* lack genicular processes but have an internal structure that may be an intermediate state in which the nema is free proximally, but attached distally, as in *Eisenackograptus*.

Gothograptus is the only retiolitid genus known to have survived the *Cyrtograptus lundgreni* extinction event (Porębska et al. 2004) and a single species, *Gothograptus nassa*, first appearing in the earliest post-extinction *Pristiograptus dubius*–*Gothograptus nassa* Biozone and ranging into the middle upper Homeric *Colonograptus praedeubeli* Biozone (Kozłowska et al. 2001), is the only known species that spans this interval. By comparison, the genus *Neogothograptus* was, until very recently, known only from the Ludlow, leaving a considerable biostratigraphic gap between the highest occurrence of *Gothograptus* and the lowest occurrence of *Neogothograptus*. The new evidence, presented in this paper, shows that *Neogothograptus* (*N. reticulatus* sp. nov.) first appeared in the *C. praedeubeli* Biozone. This evidence is further enhanced by the very recent discovery of another species of *Neogothograptus* (*N. eximinassa*) from the uppermost upper Homeric, *Colonograptus ludensis* Biozone of Germany (Maletz 2008; and Fig. 3 herein). These gap-closing occurrences suggest that based on biostratigraphic evidence we can suggest that: (i) *Gothograptus nassa* was a possible ancestor to either or both species of the upper Homeric species of *Neogothograptus* and/or *Baculograptus*; and (ii) either of the upper Homeric species of *Neogothograptus* could have been ancestral to the Ludlow species of *Neogothograptus*. Since the first occurrence of species of *Baculograptus* are known from the *C. praedeubeli* Biozone, as in *Neogothograptus*, it is possible that these two genera may show an ancestor-descendant relationship, or be sister taxa, derived from *Gothograptus*.

It is important, however, that too much reliance is not based on our current understanding of the known ranges of species occurrences for phylogenetic interpretations. New studies of isolated faunas (such as this study and Maletz 2008) are still regularly yielding new taxa, so it is clear that our sampling of Homeric retiolitids is still far from complete. It is also clear that the best-known assemblages both in terms morphology and taxonomic diversity have come from collections of isolated material extracted from carbonate strata. Such collections are uncommon in the *Gothograptus nassa*/*Pristiograptus parvus* Biozone in comparison with under- and overlying strata. Therefore, it is likely that despite intensive collection of flattened graptolite assemblages in this interval in many parts of the world, the scarcity of isolated faunas has resulted

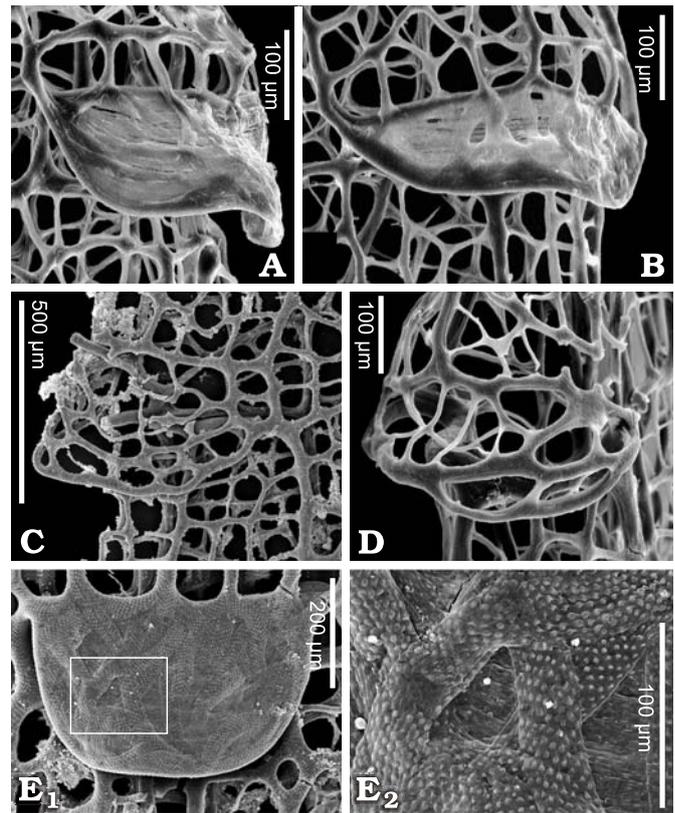


Fig. 3. SEM micrographs showing comparison of the genicular hoods of mature rhabdosomes of *Neogothograptus* Kozłowska-Dawidziuk, 1995 species (A–D) and *Gothograptus nassa* Holm, 1890 (E). A, B. *Neogothograptus eximinassa* Maletz, 2008, Baltic erratic boulder from Wetterhammer, Thuringia, Germany, *Colonograptus ludensis*–*Monograptus gerhardi* Biozone. C, D. *Neogothograptus reticulatus* sp. nov. C. ZPAL G. 41/7, Bartoszyce borehole 1630.7 m, *Colonograptus praedeubeli* Biozone. D. ZPAL G 41/2, Baltic erratic boulder 59, Jarosławiec, Poland. E. *Gothograptus nassa*, Bartoszyce borehole 1655.8 m, *Pristiograptus dubius*–*Gothograptus nassa* Biozone, whole hood (E₁) and enlargement showing bandages covering hood (E₂).

in undersampling of the diversity of retiolitids in this interval. It is therefore possible that other species of *Gothograptus* could have survived the *Cyrtograptus lundgreni* Event to become ancestral to *Neogothograptus*/*Baculograptus*. For example, there are significant similarities between *G. storchi* Lenz and Kozłowska, 2006 from the *Cyrtograptus lundgreni* Biozone and several species of *Neogothograptus* and *Baculograptus*. The finite rhabdosomes ending with an appendix, dense reticulation, similar thecal profile, and well-developed geniculum are very similar in these taxa. A similar possibility is the survival of the *G. kozłowskii*. This species has genicular hoods similar to those in *G. nassa* in the proximal end, and long reticulated hoods in the mesial and distal thecae. *G. kozłowskii*, may then, be ancestral to both *G. nassa*, and later species of *Neogothograptus*.

It is likely then, that further studies will yield more previously unknown species that may help to fill in our understanding of the ranges of morphologies among these genera and their stratigraphic distribution.

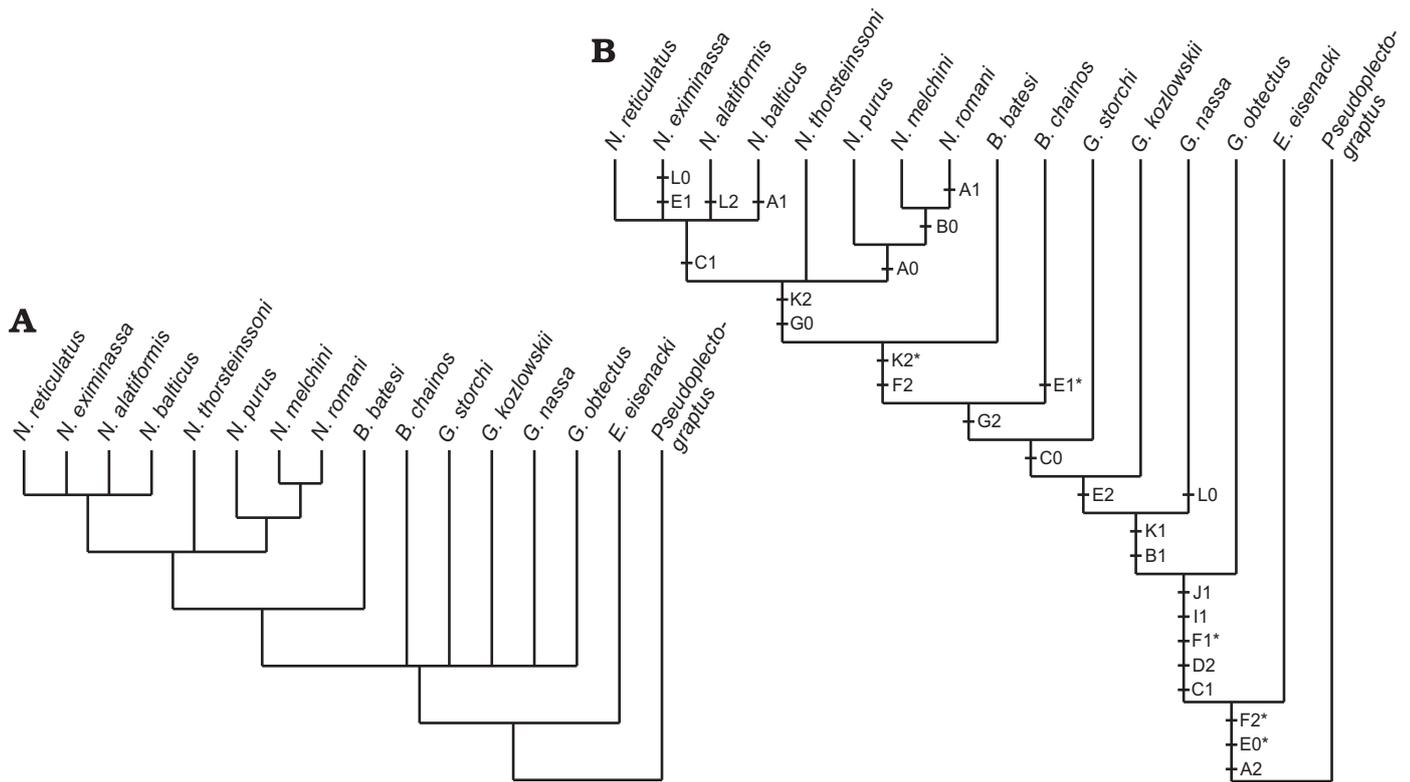


Fig. 4. Cladistic analysis. **A.** Our preferred of four most parsimonious trees (see text for explanation) showing positions of character state changes. Letters (characters) and numbers (states for each character) correspond to codings shown in Appendix 1. Asterisks indicate state changes to a polymorphic condition for groups of taxa above the corresponding node. **B.** Strict consensus tree for the cladistic analysis of the matrix shown in Appendix 2, all characters unordered and unweighted. *Pseudoptectograptus* was used as the outgroup taxon. Tree length: 39; consistency index: 0.769; rescaled consistency index: 0.553; retention index: 0.719; homoplasy index: 0.487. Abbreviations: *B.*, *Baculograptus*; *E.*, *Eisenackograptus*; *G.*, *Gothograptus*; *N.*, *Neogothograptus*.

Cladistic analysis

To test the range of possible evolutionary relationships suggested above, a cladistic analysis was carried out using PAUP 4.0b10 (Swofford 2002) and MacClade version 4.06 (Maddison and Maddison 2001). The fifteen studied taxa comprised *Eisenackograptus eisenacki*, *Baculograptus chainos*, *B. batesi*, *Gothograptus* (*G. storchi*, *G. kozłowski*, *G. obtectus*, *G. nassa*), *Neogothograptus* (*N. reticulatus* sp. nov., *N. alatiiformis*, *N. thorsteinssoni*, *N. balticus*, *N. melchini*, *N. purus* (s.l.), *N. romani*, *N. eximnassa*), and *Pseudoptectograptus*, the last-named serving as the outgroup. Twelve characters, and their varying numbers of character states were employed (Appendix 1) and a matrix was constructed (Appendix 2). A search for the most parsimonious trees (MPTs) was conducted using the branch-and-bound algorithm, with branches collapsed if maximum length was zero (i.e., MPTs may contain polytomies).

The resulting strict consensus tree is shown in Fig. 4B. Although this tree shows several polytomies, only one of these was fully resolved in the four MPTs found in the search. Of the four MPTs, two differed only in the degree of resolution of the polytomy involving some of the derived species of *Neogothograptus* and those differences are not considered significant here. The two remaining MPTs differ

primarily in the relative position in the branching order of *G. nassa* and *B. chainos*. Of the two trees, the one that is most consistent with our current understanding of the relative times of appearance of these two taxa is shown here (Fig. 4A). In neither of the trees is *G. nassa* shown as a sister taxon to *Neogothograptus* and/or *Baculograptus*. On the other hand, *B. batesi* appears as a sister group to *Neogothograptus* in both MPTs, and furthermore, is not distinguished from the node below their point of branching by any autapomorphic traits. This is consistent with the possibility that *B. batesi* is ancestral to the *Neogothograptus* clade, as proposed by Lenz and Kozłowska-Dawidziuk (2002).

Other features of our preferred MPT indicate that both *Baculograptus* and *Gothograptus* are paraphyletic taxa and that *G. storchi* or a species very similar to it was ancestral to *Baculograptus*. This implies that either *G. storchi* or some early form of *Baculograptus* survived the Homeric extinction and occurred within the *Pristiograptus dubius*–*Gothograptus nassa* Biozone. The most significant temporal inconsistencies in the preferred MPT are the relatively low level of *G. nassa* and the high position of *G. storchi* in the branching succession.

The distribution of characters on our preferred MPT suggest that genicular hoods appeared more than once within this clade and cannot be used as a guide for inferring the rela-

tionships between hooded species of *Gothograptus* and *Neogothograptus*. In addition, the tree suggests that the common ancestor of species of *Neogothograptus* did not have genicular hoods and was morphologically similar to, or possibly was, *N. thorsteinssoni*, although the latter possibility is not consistent with the known age range of this species.

It is important to note that the majority of nodes on our strict consensus tree and preferred MPT are supported by only one or two characters and that changes in character coding or included taxa can result in a significantly different outcome. In addition, this also means that the majority of these nodes are not supported by a bootstrap analysis. However, the order of branching our preferred tree is fairly consistent with the known patterns of taxon appearances and also agrees well with at least some of our previous, qualitatively derived hypotheses of relationships among these species.

Palaeogeographical distribution and paleoecology of the genus *Neogothograptus*

To date, species of *Neogothograptus* are known with certainty from six terranes and tentatively from another (Australia). Five of these terranes were close to the Ludlow paleoequator, while two, Bohemia (Perunica) and central Germany (Saxothuringia), were within cool water, mid-paleolatitude regions (Fig. 1). Two of these, Baltica and Laurentia, by far the most prominent, were possibly separated by only a remnant of the Iapetus Ocean. Water circulation could readily have distributed the delicate retiolitid zooplankton between the two nearby terranes. The third and fourth regions are Kyrgyzstan in Central Asia where *Neogothograptus* occurs in the Ludlow, *Lobograptus scanicus* Biozone and, possibly, in the upper Homeric (AL personal observation 1995), and southern Yunnan, South China (Zhang and Lenz 1997; Lenz and Kozłowska-Dawidziuk 2004). For these terranes, the warm and seasonal monsoonal counter currents within the much larger Rheic Ocean could have readily transported the plankton components to these regions. The sixth region is southeastern Australia, also near the paleoequator, where a flattened form apparently from the *Colonograptus ludensis* Biozone (uppermost Homeric) was identified as *Gothograptus* sp. by Rickards et al. (1995). This form, with its dense rhabdosomal meshwork, appendix, and large and strongly reticulated thecal hoods is tentatively considered to be *N. reticulatus*.

By comparison, the slightly older *G. nassa* (earliest late Homeric) ranged paleogeographically from the near-equatorial regions, to the temperate waters of southern Portugal (Fig. 1, locality 6), southern Spain (locality 7), and Saxothuringia, Germany (locality 8), to the presumably cold waters of Tunisia, Morocco and Libya (Jaeger et al. 1975) (locality 14). It appears, therefore, that both *G. nassa* and *Neogothograptus* tolerated considerable ranges in ocean water temperatures.

Material and methods

The new material described in the paper has been isolated from the Bartoszyce borehole, the Prągowiec ravine, Bardo, Holy Cross Mountains, and Baltic erratic boulders from Jarosławiec (all in Poland). The graptolites were recovered following slow dissolution of the host carbonate in acid 5–10% HCl. A fine hairbrush was used to pick and transfer specimens. The material is stored in glycerine and on SEM stubs in ZPAL.

Systematic paleontology

Order Graptoloidea Lapworth, 1873

Family Retiolitidae Lapworth, 1873

Subfamily Plectograptinae Bouček and Münch, 1952

Genus *Neogothograptus* Kozłowska-Dawidziuk, 1995

Type species: Neogothograptus purus Kozłowska-Dawidziuk, 1995, Baltic erratic boulder 149, Jarosławiec, Poland, *Lobograptus scanicus*–*Lobograptus invertus* Biozone, Ludlow.

Diagnosis.—See Maletz 2008: 294.

Species included.—*Neogothograptus balticus* (Eisenack, 1951); *N. romani* Kozłowska-Dawidziuk, 1995; *N. purus* Kozłowska-Dawidziuk, 1995; *N. purus labiatus* Lenz and Kozłowska-Dawidziuk, 2004, *N. alatifomis* Lenz and Kozłowska-Dawidziuk, 2004, *N. melchini* Lenz and Kozłowska-Dawidziuk, 2004, *N. thorsteinssoni* Lenz and Kozłowska-Dawidziuk, 2004, *N. eximinassa* Maletz, 2008, *N. ornatus* Maletz, 2008, and *N. reticulatus* sp. nov.

Neogothograptus reticulatus sp. nov.

Figs. 3, 5–7.

1995 ?*Gothograptus* sp. Rickards, Packham, Wright, and Williamson, 1995: 41, figs. 18K, L, 20J.

Type material: Holotype: ZPAL G. 41/1, proximal end with five first thecae (Fig. 5), Prągowiec ravine; paratypes: ZPAL G. 41/2 to ZPAL G. 41/6, Baltic boulder 59, Jarosławiec; ZPAL G. 41/7 and ZPAL G. 41/8, Bartoszyce borehole, depth 1630.7 m.

Type locality: Prągowiec ravine, Bardo, Holy Cross Mountains, Poland.

Type horizon: *Colonograptus praedeubeli* Biozone, Homeric, Wenlock, Silurian.

Diagnosis.—Dense reticulum of thin lists on ancora sleeve and thecal walls, outer ancora, reticulation well developed. Reticulated hoods fully developed on geniculum. Appendix well developed. Lateral and ventral orifices covered with fine meshworks.

Material.—The material comes from three localities in Poland: Bartoszyce borehole 1630.7 m, stub 210, SEM 011410, five specimens; Baltic erratic boulder 59, Jarosławiec, Ludlow, 25 coarse fragments, and many small fragments; nodules 7, 10, and 11 from Prągowiec ravine, Bardo, Holy Cross Mts., one larger specimen and 20 small fragments. All forms come

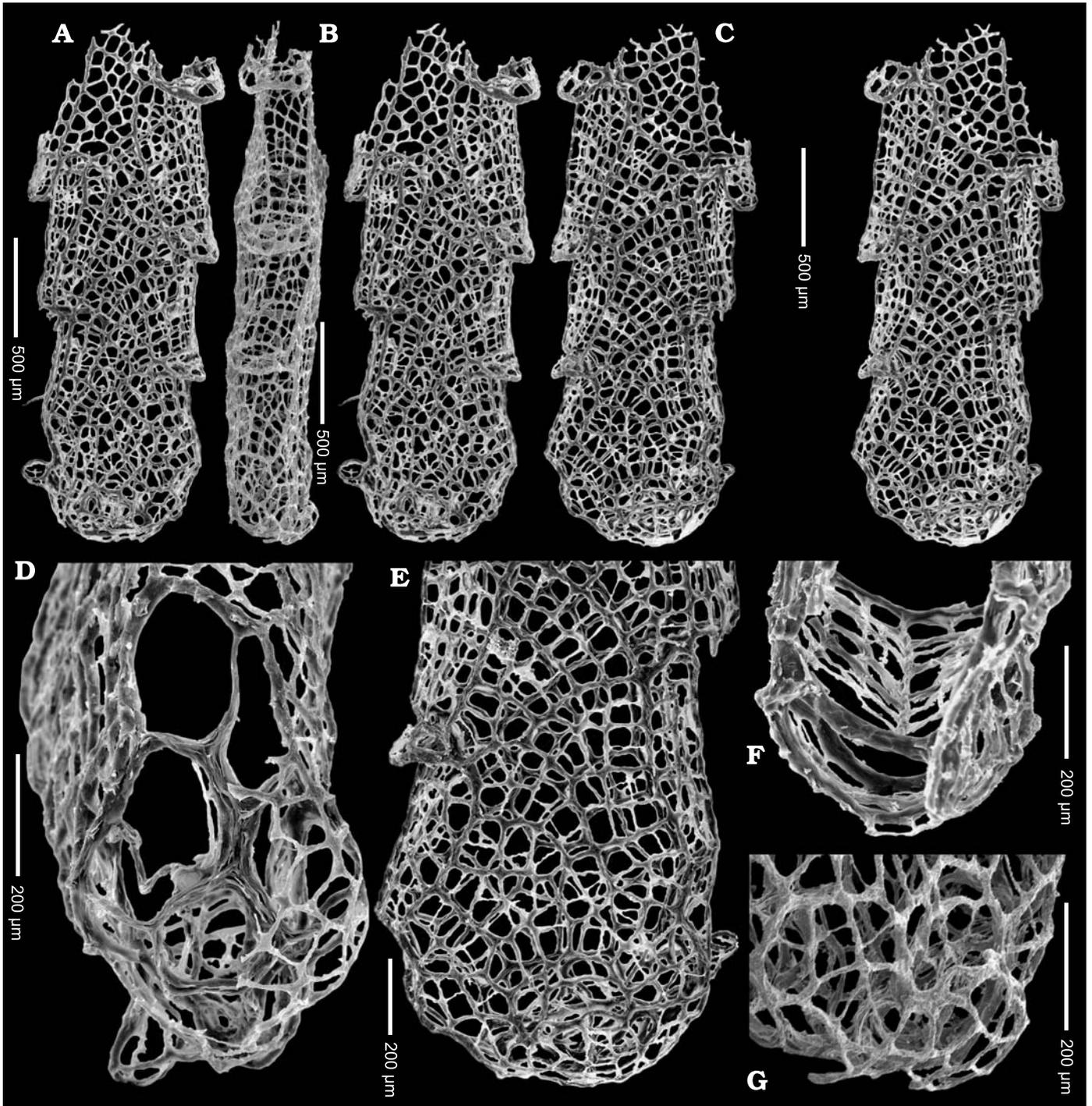


Fig. 5. SEM micrographs of proximal fragment of rhabdosome *Neogothograptus reticulatus* sp. nov., ZPAL G. 41/1, Bardo, Prągowiec, Holy Cross Mountains, Poland, *Colonograptus praedeubeli* Biozone. Stereopair of reverse view: ventral view of thecae 1¹ side (A), stereopair of obverse view (B); outer ancora edge on thecae 1² side, ancora with outer ancora partly destroyed, view from outside (C), closure of proximal end showing outer ancora and reticulum closing orifices, obverse view (D), inside view showing thecal lip, geniculum, and med-ventral list (E), closure of proximal mid-ventral-list (F).

from *Colonograptus praedeubeli* Biozone. Associated fauna: *C. praedeubeli*, *Pristiograptus dubius*.

Description.—Outer ancora well developed in mature rhabdosomes (Figs. 5C, D, 7D). Holotype outer ancora is partly broken on th 1¹ side (Fig. 5A₂). On the second thecal row of the holotype rhabdosome, a well-developed edge is formed by the

outer ancora (Fig. 5A–C). The lateral and ventral proximal orifices are completely obscured by thin reticular lists (Fig. 5D). No complete rhabdosomes are known. The longest specimen, which appears to be almost complete (missing the appendix and the ancora), is 5 mm long and consists of five pairs of thecae (Fig. 7). Width across first theca 0.8–1.0 mm (extrapolated to 1.3–1.55 mm when flattened) and the maximum width

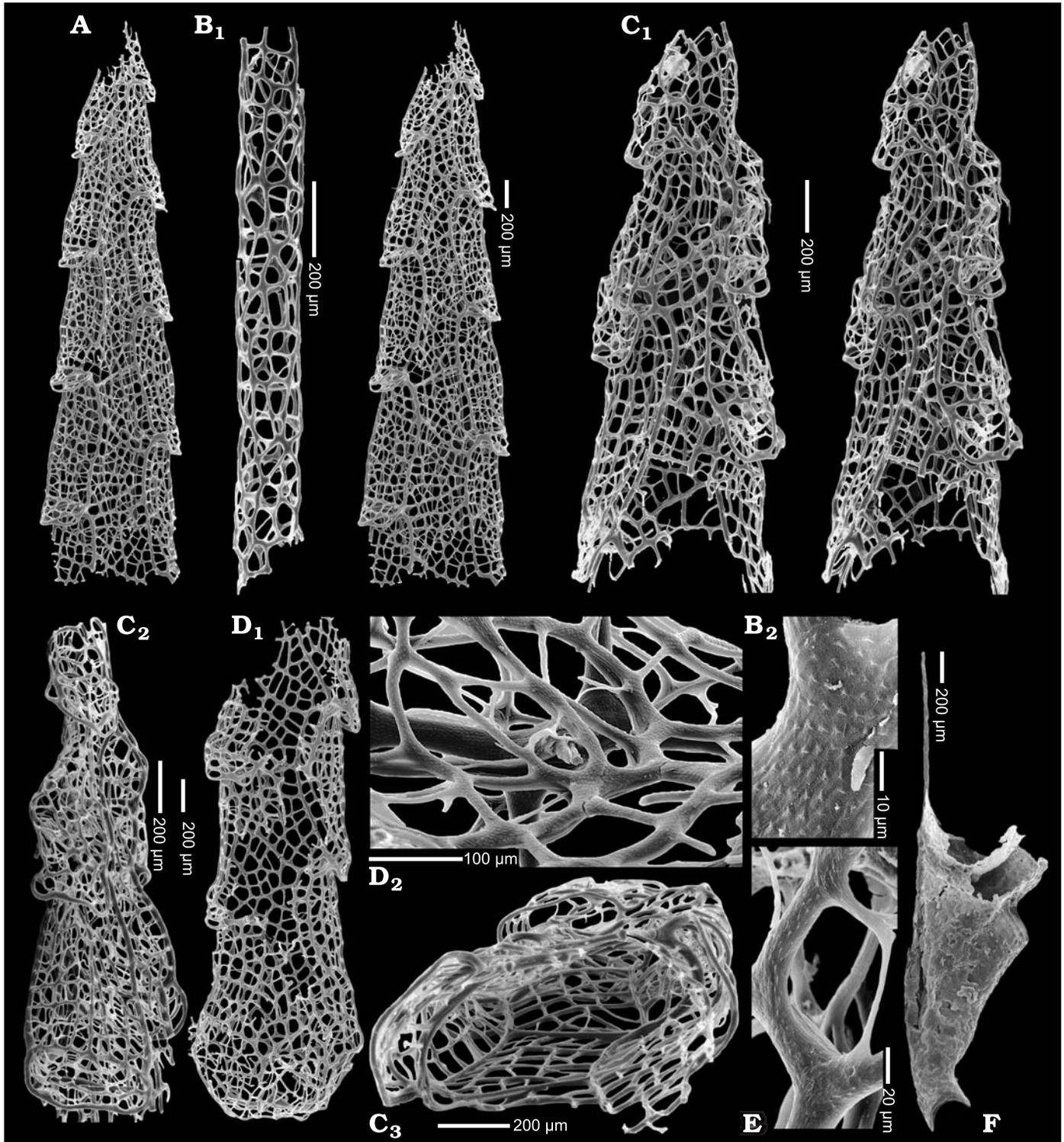


Fig. 6. SEM micrographs of rhabdosomes *Neogothograptus reticulatus* sp. nov. (A–C, E), and *Colonograptus praedeubeli* Jaeger, 1990 (F) from Baltic erratic boulder, Jarosławiec 59, *Colonograptus praedeubeli* Biozone, upper Homerian, Wenlock, Poland. A. Stereopair of lateral view of most distal end with four pairs of thecae, ZPAL G. 41/2. B. Fragment of appendix possibly belonging to *Neogothograptus reticulatus*, ZPAL G. 41/3. C. Stereopair of lateral view of most distal end with five thecae, with long reticulated hoods, and beginning of the appendix, ZPAL G. 41/4, lateral view (C₁), view of the inside (C₂). D. Lateral view of proximal end with two pairs of thecae, ZPAL G. 41/5, view of ancora from the inside (D₁), enlargement of the hood list with pustules (D₂). E. Enlargement of the ancora sleeve list with poorly developed pustules, ZPAL G. 41/6. F. lateral view of *Colonograptus praedeubeli*, rhabdosome of young colony with two thecae.

at the second or third thecal pair is 0.9–1.1 mm, decreasing to 0.6–0.7 mm across the last thecal pair before the appendix.

The two thecae repeat distance in the medial part of the rhabdosome is 1.6–1.8 mm. Theca 1¹ is much shorter than the

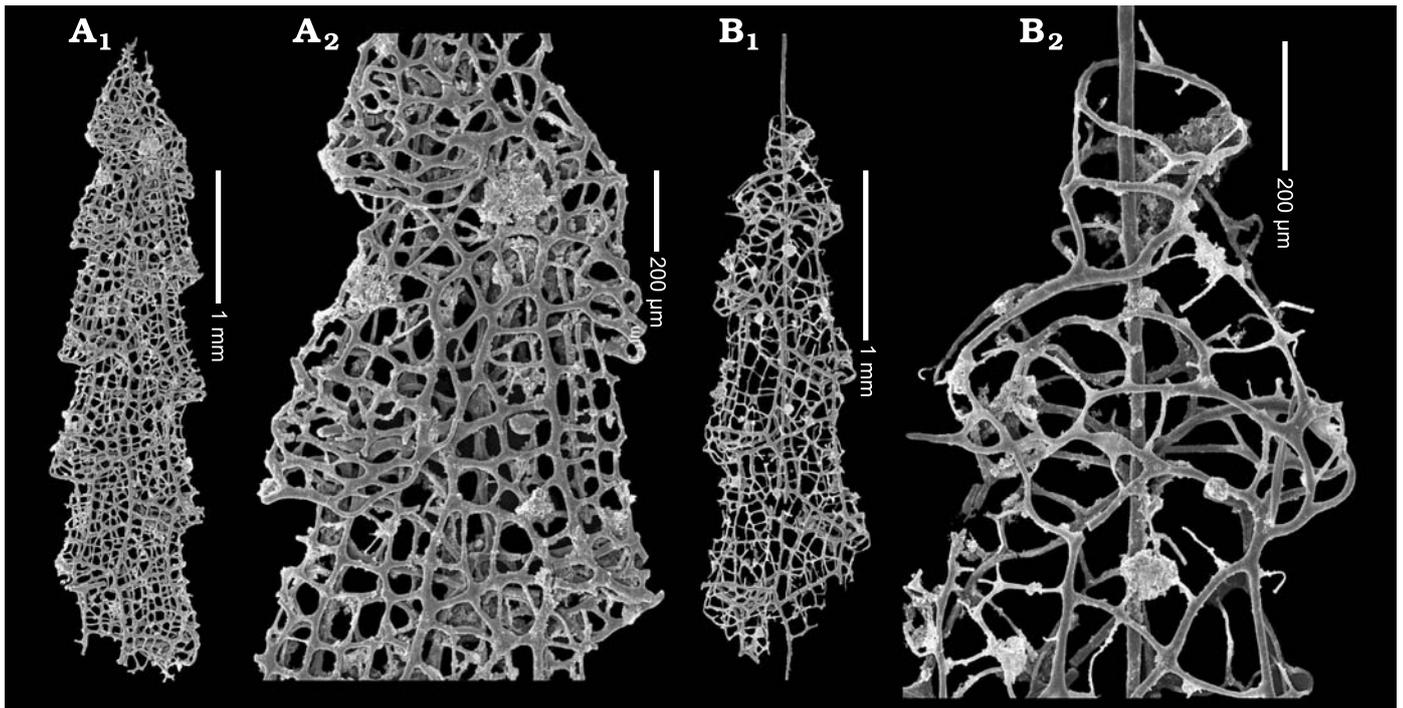


Fig. 7. SEM micrographs of rhabdosome fragments of *Neogothograptus reticulatus* sp. nov., Bartoszyce borehole 1630.7 m, *Colonograptus praedeubeli* Biozone. **A.** Distal end of mature rhabdosome with five pairs of thecae, and beginning of the appendix, ZPAL G. 41/7 (A₁); enlargement of distal part showing long reticulated apertural hoods (A₂). **B.** Distal end of young rhabdosome with three pairs of thecae and growing appendix, ZPAL G. 41/8 (B₁); enlargement of distal part with small appendix and central nema (B₂).

th 1² (Fig. 5). The last theca is also much shorter than the previous one (Fig. 7B). Thecal orifices directed laterally to proximo-laterally, geniculum list projecting ventrally beyond level of thecal lip. Pustules on the bandages are variably developed. They are relatively small on some specimens, e.g. on the distal part of rhabdosome from Bartoszyce borehole (Fig. 6B₁), and from Jarosławiec (Fig. 7D₂). The genicular hoods are densely reticulated (Figs. 5A, B, 6A, B, 7A–D), and the hoods totally cover the apertures, especially in mature rhabdosomes. Nema is not attached to the thecal framework.

Remarks.—The genus *Neogothograptus* was erected quite recently (Kozłowska-Dawidziuk 1995), and is now known to be one of the most species-diverse retiolitid genera, being represented by nine species, one of which consists of two subspecies. The new species, *N. reticulatus*, along with *N. eximinassa*, is a member of the most densely reticulated species-group of *Neogothograptus* with a well-developed outer ancora, dense reticulum over the entire surface, reticulum on proximal orifices, and prominent reticulated genicular hoods.

N. reticulatus shares a considerable number of morphological features with *N. eximinassa*. The primary difference lies in the nature of their genicular hoods: those of *N. reticulatus* are fully reticulated, whereas those of *N. eximinassa* are solid sheet-like hoods such as seen in *G. nassa*. A close examination of all specimens of the two species shows a clean separation between the two types of genicular hoods with no intermediate forms. A further distinction is that in *N. reticulatus* the outer ancora is a well developed mesh outside

of the main ancora umbrella, while that of *N. eximinassa* may consist of only a very few thin lists.

A flattened and moderately preserved form from upper Homeric strata of Australia, and identified as *Gothograptus* sp. by Rickards et al. (1995), is very like *N. reticulatus* in its measurements, shape of rhabdosome, appendix, development of a dense reticulum, and the reticulated genicular hoods. The suggestion that the nema is incorporated into the ancora sleeve wall (Rickards et al. 1995: figs. 18K, L, 20J), is rather questionable, however. More probably, the nema is free as in all upper Homeric and Ludlow retiolitids.

The new species has some features in common with those of *Gothograptus* from the pre-extinction, *Cyrtograptus lundgreni* Biozone. Similar apertural hoods are observed in the most distal theca of the *Gothograptus kozłowskii* Kozłowska-Dawidziuk, 1990 (Kozłowska-Dawidziuk 1990: fig. 4E). The apertural hoods are also reminiscent of those of *G. obtectus* Kozłowska-Dawidziuk, 1990 (Kozłowska-Dawidziuk 1990: fig. 5C, D). In *G. obtectus* the reticulum covering the aperture is continuous along the ventral surface from thecal aperture to thecal aperture. A reticulated genicular hood and dense meshwork are also characteristic of *G. storchi* Lenz and Kozłowska (Lenz and Kozłowska 2006), although its hood does not obscure any part of the thecal orifice.

Neogothograptus purus Kozłowska-Dawidziuk, 1995

Holotype: ZPAL G. XVII/1341.

Type locality and age: Baltic erratic boulder from Jarosławiec, Poland; Lower Ludlow, *Lobograptus scanicus*–*L. invertus* Biozone.

Material.—Ten specimens, mostly fragments from Bartoszyce borehole, depth 1598.0 m, EEP, Poland; *Neodiversograptus nilssoni* Biozone, Ludlow. *N. purus* co-occurs with *Neodiversograptus nilssoni*, *Bohemograptus bohemicus*?, *Colonograptus auctus*, *P. dubius*, *Neogothograptus thorsteinssoni*, *Kirkigraptus inexpectans*, *Spinograptus spinosus*, and *Plectograptus* sp.

Remarks.—The co-occurrence of *Neogothograptus romani* and *N. purus* as earlier found in the *Lobograptus parascanicus* Biozone (Kozłowska-Dawidziuk 1995), and with *Neodiversograptus nilssoni* in this study, demonstrates that *N. purus* ranges from the *Neodiversograptus nilssoni* through to the *Lobograptus parascanicus* biozones (Table 1).

Stratigraphic and geographic range.—Ludlow: *Lobograptus scanicus*–*L. invertus* Biozone from Baltic erratic boulder 149 Jarosławiec, *L. progenitor* Biozone from Mielnik borehole, and *Neodiversograptus nilssoni* Biozone from Bartoszyce borehole of Poland; *Monograptus linearis*–*M. ceratus*, *L. scanicus*, and *L. progenitor* biozones, Arctic Canada.

Neogothograptus thorsteinssoni Lenz and Kozłowska-Dawidziuk, 2004

Fig. 8.

2004 *Neogothograptus thorsteinssoni* sp. nov.; Lenz and Kozłowska-Dawidziuk 2004: 19, pl. 7: 1, 2, 5, 7, 8; pls. 8–10; pl. 26: 5, 6.

2004 *Neogothograptus thorsteinssoni* Lenz and Kozłowska-Dawidziuk, 2004, Maletz 2008: 296, figs. 10, 13I.

Holotype: GSC 125981.

Type locality and age: Northeastern Cornwallis Island, unnamed creek, talus concretion, Arctic Canada; Lower Ludlow, *Lobograptus progenitor* Biozone.

Material.—Thirty specimens, mostly fragments from the Bartoszyce borehole depth 1598.0 m, EEP, Poland; *Neodiversograptus nilssoni* Biozone, Ludlow. It co-occurs with *Neodiversograptus nilssoni*, *Bohemograptus bohemicus*?, *Colonograptus auctus*, *P. dubius*, *Neogothograptus purus*, *Kirkigraptus inexpectans*, *Spinograptus spinosus*, *Plectograptus* sp.

Discussion.—The new material represents well-preserved fragments from every part of the rhabdosome (Fig. 8).

Stratigraphic and geographic range.—Ludlow: *Neodiversograptus nilssoni* Biozone, Bartoszyce borehole, Poland; *Lobograptus progenitor* Biozone, Arctic Canada.

Neogothograptus alatiformis Lenz and Kozłowska-Dawidziuk, 2004

Fig. 9.

2004 *Neogothograptus alatiformis* sp. nov.; Lenz and Kozłowska-Dawidziuk 2004: 18–19, pls. 11–16: 16.

Holotype: GSC 125988.

Type locality and age: Northeastern Cornwallis Island, talus concretion, unnamed creek, Arctic Canada; Lower Ludlow, *Lobograptus progenitor* and *L. scanicus* biozones.

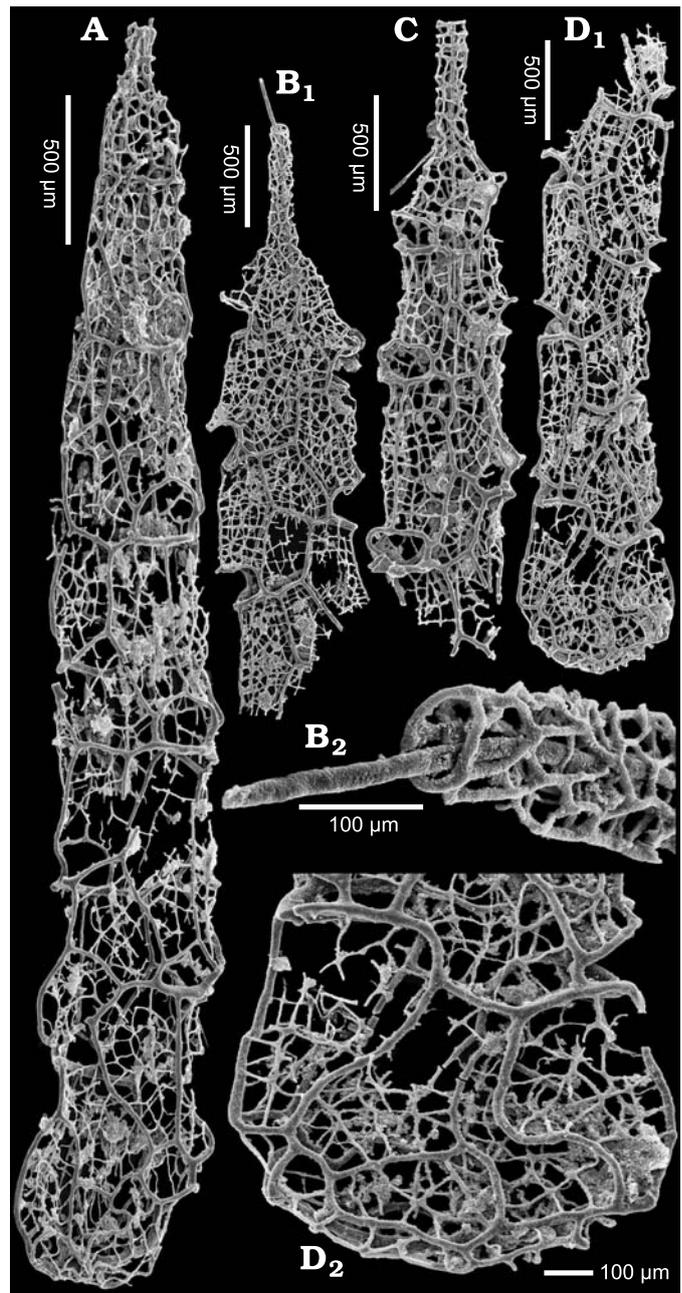


Fig. 8. SEM micrographs of rhabdosomes of *Neogothograptus thorsteinssoni* Lenz and Kozłowska-Dawidziuk, 2004, Bartoszyce borehole 1598.0 m, *Neodiversograptus nilssoni* Biozone. **A.** Obverse view of finite rhabdosome with five pairs of thecae and appendix, lateral-ventral view. **B.** Lateral view of distal end of rhabdosome with appendix and nema (**B**₁); enlargement of distal part of appendix with thick nema (**B**₂). **C.** Ventral-lateral view of distal part of rhabdosome with appendix. **D.** Proximal part of reverse side of rhabdosome with three pairs of thecae (**D**₁); enlargement of ancora region with outer ancora, and first theca (**D**₂).

Material.—Dozens of fragments of rhabdosomes from Baltic erratic boulder 62 from Jarosławiec, Poland, Ludlow; co-occurs with *Saetograptus chimaera*?; several larger fragments from Goldap borehole, depth 1246.3 m, co-occur with *Saetograptus chimaera* and *Lobograptus progenitor*.

Comments.—The material consists of fragments of the prox-

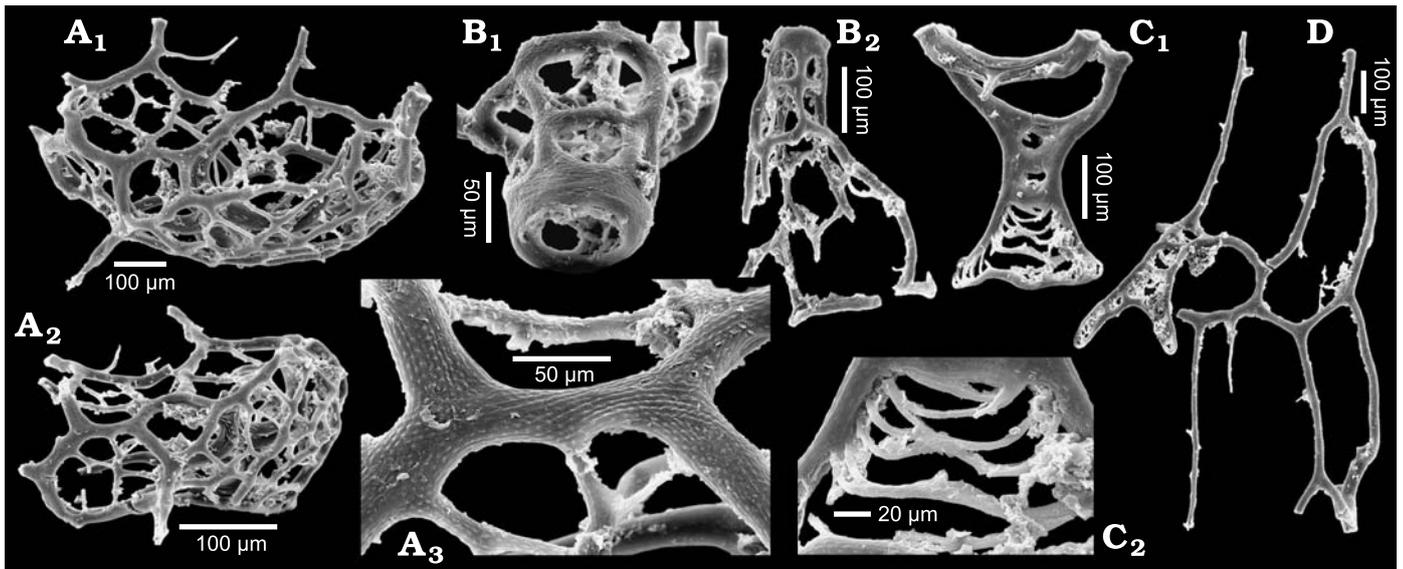


Fig. 9. SEM micrographs of fragments of rhabdosomes of *Neogothograptus alatifformis* Lenz and Kozłowska-Dawidziuk, 2004, Baltic erratic boulder 62 from Jarosławiec, Poland, Ludlow. **A.** Proximal end with outer ancora, lateral view; ventral view (A_1), showing ventral orifice closed by reticulum (A_2), enlargement of ancora list (A_3). **B.** Enlargement of appendix, distal view (B_1), lateral view of appendix (B_2). **C.** Singular apertural process on geniculum, lip with short mid-ventral visible from inside (C_1); inside view of fusellar nature of apertural process (C_2). **D.** Ventral and lateral part of rhabdosome with aperture and apertural process.

imal end, thecal walls, apertural processes, and appendix (Fig. 9). The measurements and proportions of these agree with the type material.

Discussion.—The uniqueness of the *N. alatifformis* rhabdosome, originally described from Arctic Canada, is so distinctive that, with the exception *N. ornatus* Maletz, 2008, the Jarosławiec fragments cannot belong to any other species. From *N. ornatus*, *N. alatifformis* is distinguished by being much shorter (only two pairs of thecae), possessing a very short appendix, and generally larger and more complex genicular processes. Most importantly, the first pair of processes occurs below the first thecal pair.

Stratigraphic and geographic range.—Ludlow, *Lobograptus progenitor* Biozone: Baltic erratic boulder 62 Jarosławiec, and Gołdap borehole of Poland; Arctic Canada; Yunnan, China.

Acknowledgments

Adam Urbanek (ZPAL) is thanked for the donation of the isolated specimens of *N. reticulatus* from the Prągowiec ravine. The late Hermann Jaeger (Museum für Naturkunde, Berlin, Germany) is thanked for very useful unpublished information on retiolitids in Germany. Jorg Maletz (State University of New York, Buffalo, USA) is thanked for the kind donation of the pictures of *Neogothograptus eximinassa*. Aleksandra Holda-Michalska (ZPAL) is thanked for the improvement of the Figs. 3, 5–9, and Grażyna Matriba (ZPAL) for the technical assistance. Jan Zalasiewicz (University of Leicester, UK) and an anonymous reviewer and thanked for comprehensive and helpful reviews of an early version of this paper. AL and MM acknowledge financial support through a Natural Sciences and Engineering Research Council (Canada) Discovery Grant.

References

- Bates, D.E.B. 1987. The construction of graptolite rhabdosomes in light of ultrastructural studies. *Indian Journal of Geology* 59: 1–28.
- Bates, D.E.B. and Kirk, N.H. 1984. Autecology of Silurian graptoloids. In: M.G. Bassett and J.D. Lawson (eds.), *Autecology of Silurian organisms. Special Papers in Palaeontology* 32: 121–139.
- Bates, D.E.B. and Kirk, N.H. 1992. The ultrastructure, mode of construction and functioning of a number of Llandovery ancorate and retiolitid graptolites. *Modern Geology* 17: 1–270.
- Bates, D.E.B., Kozłowska, A., and Lenz, A.C. 2005. Silurian retiolitid graptolites: morphology and evolution. *Acta Palaeontologica Polonica* 50: 705–720.
- Berry, W.B.N. and Murphy, M.A. 1975. Silurian and Devonian graptolites of central Nevada. *University of California Publications in Geological Sciences* 110: 1–109.
- Gutiérrez-Marco, J.C., Lenz, A.C., Robardet, M., and Piçarra, J.M. 1996. Wenlock–Ludlow graptolite biostratigraphy and extinction: a reassessment from the southwestern Iberian Peninsula (Spain and Portugal). *Canadian Journal of Earth Sciences* 33: 656–663.
- Holm, G. 1890. Gotlands graptoliter. *Svenska Vetenskap-Akademiens handlingar* 16: 1–34.
- Jaeger, H., Bonnefous, J., and Massa, D. 1975. Le Silurien en Tunisie; ses relations avec le Silurien de Libye nord-occidentale. *Bulletin Societé géologique de France* 14: 68–76.
- Koren', T.N., Popov, L.E., Degtjarev, K.E., Kovalevsky, O.P. and Modzelevskaya, T.L. 2003. Kazakhstan in the Silurian. In: M.E. Johnson and E. Landing (eds.), *Silurian Lands and Seas: Paleogeography Outside of Laurentia. New York State Museum, Bulletin* 493: 323–343.
- Kozłowska-Dawidziuk, A. 1990. The genus *Gothograptus* (Graptolithina) from the Wenlock of Poland. *Acta Palaeontologica Polonica* 35: 191–209.
- Kozłowska-Dawidziuk, A. 1995. Silurian retiolitids of the East European Platform. *Acta Palaeontologica Polonica* 40: 261–326.
- Kozłowska-Dawidziuk, A. 1997. Retiolitid graptolite *Spinograptus* from Poland and its membrane structures. *Acta Palaeontologica Polonica* 42: 391–412.
- Kozłowska-Dawidziuk, A. 2001. Phylogenetic relationships within the Retiolitidae (Graptolithina) and a new genus *Cometograptus*. *Lethaia* 34: 84–96.

- Kozłowska-Dawidziuk A. 2004. Evolution of retiolitid graptolites—a synopsis. *Acta Palaeontologica Polonica* 49: 505–518.
- Kozłowska-Dawidziuk A., Lenz, A.C., and Štorch, P. 2001. Upper Wenlock and lower Ludlow (Silurian) post-extinction graptolites, Vřeradic section, Barrandian area, Czech Republic. *Journal of Paleontology* 75: 147–164.
- Lenz A.C. 1993. Late Wenlock and Ludlow (Silurian) Plectograptinae (retiolitid graptolites), Cape Phillips Formation, Arctic Canada. *Bulletins of American Paleontology* 104: 1–52.
- Lenz, A. 1994. A sclerotized retiolitid, and its bearing on origin and evolution of Silurian retiolitid graptolites. *Journal of Paleontology* 68: 1344–1349.
- Lenz, A.C. and Kozłowska-Dawidziuk, A. 2001. Upper Wenlock (Silurian) graptolites of Arctic Canada: pre-extinction, *lundgreni* Biozone fauna. *Palaeontographica Canadiana* 20: 1–61.
- Lenz, A.C. and Kozłowska-Dawidziuk, A. 2002. Upper Homeric (Upper Wenlock, Silurian) graptolites from Arctic Canada. *Journal of Paleontology* 76: 321–346.
- Lenz, A.C. and Kozłowska-Dawidziuk, A. 2004. *Ludlow and Pridoli (Upper Silurian) Graptolites from the Arctic Islands, Canada*. 141 pp. NRC Research Press, Ottawa, Ontario.
- Lenz, A.C. and Kozłowska, A. 2006. Graptolites from the *lundgreni* Biozone (Lower Homeric, Silurian), Arctic Islands, Canada: new species and supplementary material. *Journal of Paleontology* 80: 616–637.
- Lenz, A.C. and Kozłowska, A. 2007. Retiolitid diversification and Silurian sea level changes. *Acta Palaeontologica Sinica* 46: 269–277.
- Maddison, W.P. and Maddison, D.R. 2001. *MacClade version 4.06. Analysis of Phylogeny and Character Evolution*. Sinauer Associates, Massachusetts.
- Maletz, J. 2008. Retiolitid graptolites from the collection of Hermann Jaeger in the Museum für Naturkunde, Berlin (Germany). 1. *Neogothograptus* and *Holoretiolites*. *Paläontologische Zeitschrift* 82: 285–307.
- Porębska, E., Kozłowska-Dawidziuk, A., and Masiak, M. 2004. The *lundgreni* event in the Silurian of the East European Platform, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 213: 271–294.
- Rickards, R.B., Packham, G.H., Wright, A.J., and Williamson, P.L. 1995. Wenlock and Ludlow graptolite faunas and biostratigraphy in the Quarry Creek district, New South Wales. *Association of Australasian Palaeontologists Memoir* 17: 68.
- Swofford, D. 2002. *Phylogenetic Analysis Using Parsimony (PAUP), version 4.0b10*. Illinois Natural History Survey, Champaign.
- Urbanek, A. 1993. Biotic crises in the history of Upper Silurian graptoloids: a palaeobiological model. *Historical Biology* 7: 29–50.
- Warren, P.T. 1971. The sequence and correlation of graptolite faunas from the Wenlock–Ludlow rocks of north Wales. *Mémoire de Bureau de Recherche Géologiques et Minières* 73 : 451–460.
- Waterlot, G. 1945. Les graptolites du Maroc. *Service géologique du Maroc, Notes et Mémoires* 63: 45–103.
- Zhang, Y-D. and Lenz, A.C. 1997. Uppermost Wenlock and Ludlow graptolites from southern Yunnan, China. *Canadian Journal of Earth Sciences* 34: 1220–1238.

Appendix 1

Characters and character states:

A – Reticulum development: 0, none; 1, weak; 2, dense

B – Outer ancora: 0, none; 1, yes

C – Genicular processes and hoods: 0, no; 1, yes

D – Geniculum list: 0, none; 1, present/absent; 2, present

E – Width of ancora umbrella vs. width at the level of geniculum: 0, narrower; 1, same; 2, wider

F – Aperture direction: 0, distally; 1, laterally; 2, latero-proximally; 3, disto-laterally

G – Nema: 0, free; 1, attached to ancora sleeve throughout; 2, attached distally

H – Length of theca 1² relative to other thecae: 0, very long; 1, similar length

I – Ancora sleeve bandages: 0, seams on the outside; 1, seams on the inside

J – Transverse rods: 0, present; 1, absent

K – Thecal framework: 0, zigzag; 1, more or less zigzag; 2, more or less rectangular

L – Genicular processes and hoods: 0, *Gothograptus nassa* hood; 1, reticulated hood; 2, *Neogothograptus alatiformis* hood

Appendix 2

Matrix comparing 15 species of *Pseudoplectograptus*, *Eisenackograptus*, *Gothograptus*, *Baculograptus*, and *Neogothograptus*, and 12 morphological characters.

| Species\character | A | B | C | D | E | F | G | H | I | J | K | L |
|---------------------------------------|---|---|---|---|-----|-----|---|---|---|---|-----|---|
| <i>Eisenackograptus eisenacki</i> | 2 | 0 | 0 | 1 | 1/2 | 0/3 | 2 | 0 | 0 | 0 | 0 | – |
| <i>Gothograptus storchi</i> | 2 | 1 | 0 | 2 | 2 | 1/2 | 1 | 1 | 1 | 1 | 1 | – |
| <i>Gothograptus kozłowskii</i> | 2 | 1 | 1 | 2 | 2 | 1/2 | 1 | 1 | 1 | 1 | 1 | 0 |
| <i>Gothograptus obtectus</i> | 2 | 0 | 1 | 2 | 0/1 | 1/2 | 1 | 1 | 1 | 1 | 1 | 0 |
| <i>Gothograptus nassa</i> | 2 | 1 | 1 | 2 | 0/1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 |
| <i>Baculograptus chainos</i> | 2 | 1 | 0 | 2 | 0/1 | 1 | 2 | 1 | 1 | 1 | 1 | – |
| <i>Baculograptus batesi</i> | 2 | 1 | 1 | 2 | 1/2 | 2 | 2 | 1 | 1 | 1 | 1/2 | – |
| <i>Neogothograptus reticulatus</i> | 2 | 1 | 1 | 2 | 2 | 1/2 | 0 | 1 | 1 | 1 | 2 | 0 |
| <i>Neogothograptus eximinassa</i> | 2 | 1 | 1 | 2 | 2 | 2 | 0 | 1 | 1 | 1 | 2 | 2 |
| <i>Neogothograptus alatiformis</i> | 2 | 1 | 1 | 2 | 2 | 2 | 0 | 1 | 1 | 1 | 2 | 1 |
| <i>Neogothograptus thorsteinssoni</i> | 2 | 1 | 0 | 2 | 2 | 2 | 0 | 1 | 1 | 1 | 2 | – |
| <i>Neogothograptus purus</i> (s.l.) | 0 | 1 | 0 | 2 | 2 | 2 | 0 | 1 | 1 | 1 | 2 | – |
| <i>Neogothograptus balticus</i> | 1 | 1 | 2 | 2 | 2 | 2 | 0 | 1 | 1 | 1 | 2 | 0 |
| <i>Neogothograptus melchini</i> | 0 | 0 | 0 | 2 | 2 | 2 | 0 | 1 | 1 | 1 | 2 | – |
| <i>Neogothograptus romani</i> | 1 | 0 | 0 | 2 | 2 | 2 | 0 | 1 | 1 | 1 | 2 | – |