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

ANNA KOZŁOWSKA, ALFRED LENTZ, and MICHAEL MELCHIN


*Neogothograptus reticulatus* sp. nov. from the upper Homerian *Colonograptus praedeubeli* Biozone, and *N. thorsteinssoni* and *N. alatiformis* 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 Homerian strata of southeastern 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.

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Introduction

The retiolitids (Graptolithina) are a very distinctive group of Silurian graptolites differing from 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 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).

Reticulitid 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-
tinction 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 diversification 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–Labograptus progenitor biozones (N. purus, N. balticus, N. romani, N. thorsteinssonii, N. melchini, 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 Homerian C. praedeubeli Biozone of northeastern and southern Poland. This new discovery fills the gap between the earlier proposed ancestor, G. nassa (lowermost to middle Homerian), 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 Homerian–early Ludow 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-
Table 1. Geographic occurrences of all of the known species of Neogothograptus

<table>
<thead>
<tr>
<th>Region</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baltica, Arctic, Canada</td>
<td>N. thorsteinsoni, N. purus labiatus, N. melchini, N. alatiformis sp. nov.</td>
</tr>
<tr>
<td>Baltic, Bartoszyce borehole, Poland</td>
<td>N. reticulatus, N. thorsteinsoni, N. romani, N. purus, N. alatiformis</td>
</tr>
<tr>
<td>Baltic, Holy Cross Mts., Poland</td>
<td>N. reticulatus, N. balticus, N. romani, N. purus, N. alatiformis</td>
</tr>
<tr>
<td>South China, southern Yunnan</td>
<td>N. reticulatus</td>
</tr>
<tr>
<td>Australia, New South Wales</td>
<td>N. ornatus</td>
</tr>
<tr>
<td>Germany, Baltic boulders</td>
<td>N. eximinasssa, N. romani</td>
</tr>
<tr>
<td>Kyrgyzstan, Central Asia</td>
<td>N. balticus</td>
</tr>
</tbody>
</table>

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. alatiformis and N. thorsteinsoni, previously known only in Arctic Canada, are also described from the Baltic 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 Baltic comprise N. balticus, N. romani, and N. purus, to which list is now added N. alatiformis and N. thorsteinsoni, and recently N. eximinasssa and N. ornatus (Maletz 2008), and the oldest known species, N. reticulatus sp. nov. from the C. praedebeli Biozone. Species found in Arctic Canada comprise N. purus labiatus, N. alatiformis, N. melchini, and N. thorsteinsoni (Table 1). A species with a strong affinity to N. alatiformis 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 gerinical 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...
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 geniculat 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 Homerian 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 Pristograptus dubius–Gothograptus nassa Biozone and ranging into the middle upper Homerian Colonograptus praedeubeli Biozone and into the uppermost upper Homerian Colonograptus lundensis 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 Homerian species of Neogothograptus and/or Baculograptus; and (ii) either of the upper Homerian 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 Homerian 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 nassaiPristograptus 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 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. kozlowski, 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. kozlowski, 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. kozlowski, 2006 from the Cyrtograptus lundgreni Biozone and several species of Neogothograptus and Baculograptus.
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 (Madison and Maddison 2001). The fifteen studied taxa comprised Eisenackograptus eisenacki, Baculograptus chainos, B. batesi, Gothograptus (G. storchi, G. kozlowski, G. obtectus, G. nassa), Neogothograptus (N. reticulatus, N. alatiformis, N. thorsteinssoni, N. balticus, N. melchini, N. purus (s.l.), N. romani, N. eximnassa), and Pseudoplectograptus, 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 Kozlowska-Dawidziuk (2002).

Other features of our preferred MPT indicate that both Baculograptus and Gothograptus are paraphyletic taxa and that G. storchi or some early form of Baculograptus survived the Homerian 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 suggests 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. thorsteinssonii, 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, Bactria 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 Rhioc 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 rhadosomal 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 ans 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 invercis Biozone, Ludlow.

Diagnosis.—See Maletz 2008: 294.


Neogothograptus reticulatus sp. nov.
Figs. 3, 5–7.
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
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. 5A3). 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

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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
th 1^2 (Fig. 5). The last theca is also much shorter than the previous one (Fig. 7B). Thecal orifices directed laterally to proximolaterally, 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 Homerian 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 Homerian 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 kozlowskii* 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. XVI/1341.

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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 thorsteinssonii, 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 thorsteinssonii Lenz and Kozłowska-Dawidziuk, 2004

Fig. 8.

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


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.


Holotype: GSC 125988.

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

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-
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. alatiformis* 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. alatiformis* is distinguished by being much shorter (only two pairs of thecae), possessing a very short appendix, and generally larger and more complex geniculal 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.

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References


Fig. 9. SEM micrographs of fragments of rhabdosomes of *Neogothograptus alatiformis* Lenz and Kozłowska-Dawidziuk, 2004, Baltic erratic boulder 62 from Jarosławiec, Poland, Ludlow. A. Proximal end with outer ancora, lateral view; ventral view (A1), showing ventral orifice closed by reticulum (A2), enlargement of ancora list (A3). B. Enlargement of appendix, distal view (B1), lateral view of appendix (B2). C. Singular apertural process on geniculum, lip with short mid-ventral visible from inside (C1); inside view of fusellar nature of apertural process (C2). D. Ventral and lateral part of rhabdosome with aperture and apertural process.

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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 – Genicular 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 1 relative to other thecae: 0, very long; 1, similar
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 Peudoplectograptus, Eisenackograptus, Gothograptus, Baculograptus, and Neogothograptus, and 12 morphological characters.

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

Species/character
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 – Genicular 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 1 relative to other thecae: 0, very long; 1, similar
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