

Evolutionary history of the *Gothograptus* lineage of the Retiolitidae (Graptolithina)

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Received 10 July 2014, accepted 8 October 2014

Abstract. Evolutionary trends of the *Gothograptus* lineage (Graptolithina, Retiolitidae) from the lower Homeric to lower Ludfordian, Silurian are described. Gothograptids evolved towards simplification of the tubarium and decrease in the number of thecae. The lineage is characterized by finite growth, ending with a tubular appendix in most species, long sicula and singular genicular processes in some forms. Species belonging to the genera of the *Gothograptus* lineage (*Gothograptus*, *Baculograptus*, *Neogothograptus* and *Holoretiolites*) occur continuously from the *Cyrtograptus lundgreni* to the *Saetograptus leintwardinensis* biozones. *Gothograptus nassa* is the only retiolitid known to appear immediately after the *lundgreni* event. The oldest genera of the lineage, *Gothograptus* and *Baculograptus*, have a well-developed tubarium with a dense reticulum and nema incorporated into the lateral wall. Younger genera have a free nema and, in general, gradually reduced number of thecae, lists, reticulum and apertural processes, whereas the sicula becomes longer. The best-developed apertural processes occur in *Gothograptus*. *Holoretiolites* Eisenack, 1951, the last known representative of the lineage, has the most reduced tubarium with three pairs of thecae, few lists and no apertural processes. This is one of the last representatives of the retiolitids, which became extinct in the *S. leintwardinensis* Biozone.

Key words: graptolites, retiolitids, Silurian, *Gothograptus* lineage, evolution, *lundgreni* event.

INTRODUCTION

The evolutionary pattern of graptolites is one of the best recognized patterns due to their well-documented fossil record of flattened and isolated material. Evolutionary trends through time have been recognized in graptolites as a whole, including the reduction of the rhabdosome (tubarium) size and number of branches and an increase in the degree of thecal complexity, e.g., Bulman (1970) and Mitchell (1990).

Some good examples of the simplification and reduction of graptolite colonies are shown in the retiolitids (Retiolitidae) evolving from the Llandovery to the mid-Ludlow, Silurian (Kozłowska-Dawidziuk 2004). The group is unlike all other graptolites in mostly possessing double lateral walls: an inner one which is the homologue of the 'normal' diplograptoid lateral walls (thecal walls) and an outer wall (ancora sleeve wall) derived entirely from the distal extension of the ancora (e.g. Bates & Kirk 1984; Bates et al. 2005). These walls are rarely completely preserved (Lenz & Melchin 1987; Kozłowska-Dawidziuk 1997; Lenz & Kozłowska-Dawidziuk 2002), being built from very thin and incrementally deposited fusellar layers supported by strong lists formed from bandages. Normally, therefore, only the rod-like bandaged lists of the retiolitid tubarium are preserved.

The phenomenon of limited growth of the colony (ending with an appendix) in retiolitids may be regarded as gradual loss of coloniality (Kirk 1978; Kozłowska-Dawidziuk 2004). It means that during their evolution, the siculozoid became larger, while zooids were small in size and reduced in numbers (Kozłowska-Dawidziuk 2004, fig. 7). As a consequence, the large siculozoid could have had a dominant role for the colony of a few small zooids. There are large colonies of earlier Silurian retiolitids with no appendix, containing about 80 pairs of thecae with small siculae, whereas some of the youngest retiolitids possess a finite tubarium with a large sicula and as few as three thecae (Kozłowska-Dawidziuk 2004, fig. 7). Similar relationships between the siculozoid and zooids occur exceptionally in Ordovician graptolites, such as *Corynites* Kozłowski, 1956 (Kozłowska-Dawidziuk 2004). Some significantly reduced rhabdosomes are also observed among Llandovery retiolitids, such as *Rotaretiolites* Bates & Kirk, 1992, but its sicula is short as in other Llandovery forms and the appendix is not known.

Limited colony growth is clearly recognized in the *Gothograptus* lineage, identified by the presence of the finite tubarium terminated by an appendix (Kozłowska-Dawidziuk 2004). The number of thecae in species of this lineage varies from 18 in older taxa to three pairs

in the youngest forms. The lineage is regarded herein as a group that includes the genera *Gothograptus*, *Baculograptus*, *Neogothograptus* and *Holoretiolites*, which evolved during the Homerician *Cyrtograptus lundgreni* Biozone to the lower Ludfordian, to the *Saetograptus leintwardinensis* Biozone (Kozłowska-Dawidziuk 1995; Dobrowolska 2013).

The fossil record shows that among retiolitids only gothograptids survived the *C. lundgreni* event (e.g. Koren' 1991; Kozłowska-Dawidziuk et al. 2001), making it the ideal form to be ancestral to all subsequent plectograptines (Bates et al. 2005, fig. 9). The *lundgreni* event is regarded as one of the most profound, global graptolite extinction events (Jaeger 1991; Koren' & Urbanek 1994; Lenz 1995).

The purpose of this paper is a new synthesis of hypotheses about relationships between the species of the *Gothograptus* lineage, in light of new observations and the new insights derived from the cladistic studies of Bates et al. (2005) and Kozłowska et al. (2009).

The specimens figured are housed at the Institute of Paleobiology, Polish Academy of Sciences (abbreviation ZPAL).

HISTORY OF THE *GOTHOGRAPTUS* LINEAGE

Finite growth of tubaria is characteristic of some of the upper Wenlock and Ludlow retiolitids. According to the fossil record, *Eisenackograptus* from the *Cyrtograptus perneri* Biozone is the earliest retiolitid of limited growth of colony ending with an appendix (Lenz & Melchin 1987). The genus was regarded as an ancestor of the *Gothograptus* lineage by Kozłowska-Dawidziuk (2001) and Kozłowska-Dawidziuk & Lenz (2001). According to the cladistic analysis (Bates et al. 2005), *Eisenackograptus* forms a separate group with the appendix independently derived from the appendix in *Gothograptus*. *Eisenackograptus* differs from gothograptids in a more complicated proximal end having a thecal ventral list on theca 1¹, well-developed transverse rods and an ancora sleeve with seams facing out (Bates et al. 2005).

The *Gothograptus* lineage is regarded herein as a clade consisting of the genera *Gothograptus*, *Baculograptus*, *Neogothograptus* and *Holoretiolites* based on the cladistic analyses presented in Bates et al. 2005 (fig. 10A). The members of the *Gothograptus* lineage are characterized by tubaria tapering distally, most of them by a well-developed appendix, and singular genicular hoods as well as characteristic features of the proximal end, and thecae (e.g. Kozłowska-Dawidziuk 1995, 2004; Bates et al. 2005). Closely related to these

forms are *Cometograptus* Kozłowska-Dawidziuk, 2001 from the *C. lundgreni* Biozone, *Doliograptus* Lenz & Kozłowska-Dawidziuk, 2002 and *Papiliograptus* Lenz & Kozłowska-Dawidziuk, 2002 from the *Colonograptus praedeubeli*–*Col. deubeli* Biozone (Bates et al. 2005).

The remnants of the sicula are rarely preserved, but the available data show that the length of the sicula is 1.2 mm in *Gothograptus* and 1.8 mm in the youngest genus *Holoretiolites* (Kozłowska-Dawidziuk 2004). The last form of the *Gothograptus* lineage is *Holoretiolites mancki* (Münch, 1931) known from the *S. leintwardinensis* Biozone (Kozłowska-Dawidziuk 1995; Dobrowolska 2013). Bigger reduction of the tubarium than that of *H. mancki* show *H. helenaewitoldi* Kozłowska-Dawidziuk, 2004 occurring in the *Lobograptus progenitor* Biozone and *H. atrabecularis* Kozłowska-Dawidziuk, 1995 in the *Lobograptus parascanicus* (Kozłowska-Dawidziuk 1995) and *Cucullograptus hemiaversus* biozones (author's unpublished data).

Genus *Gothograptus*

The oldest three species of the genus *Gothograptus*, *G. kozłowskii* Kozłowska-Dawidziuk, 1990 (Fig. 1A), *G. obtectus* Kozłowska-Dawidziuk, 1990 and *G. storchi* Lenz & Kozłowska, 2006, appeared in the *C. lundgreni* Biozone. They have densely reticulated tubaria, nema incorporated into the lateral wall and the largest and the most variable singular genicular processes, which may extend proximally covering the apertures and part of the theca (Kozłowska-Dawidziuk 1990). The sicula length is about 1.2 mm (author's unpublished data).

Gothograptus nassa Holm, 1890 has characteristic solid genicular hoods built of densely packed parallel bandages (Figs 1B, 2B). They are almost identical to the proximal thecal hoods of the older species *G. kozłowskii*, which may indicate their close relationship. *Gothograptus nassa* has the largest number of thecae of any species of the *Gothograptus* lineage, up to 18 pairs. This is the only retiolitid known to appear in the earliest post-extinction *Pristiograptus dubius*–*G. nassa* Biozone (Koren' 1991; Koren' & Urbanek 1994; Poreńska et al. 2004) (see Introduction). However, the cladistic analysis suggests that the ancestor of the *Plectograptus* lineage could have spanned this interval as well (Bates et al. 2005, fig. 9).

Genus *Baculograptus*

Two species of *Baculograptus* Lenz & Kozłowska-Dawidziuk, 2002 are known from the *Colonograptus praedeubeli* Biozone, *B. chainos* Lenz, 1993 and *B. batesi* Lenz & Kozłowska-Dawidziuk, 2002. The genus is characterized by a reticulated rhabdosome with the nema

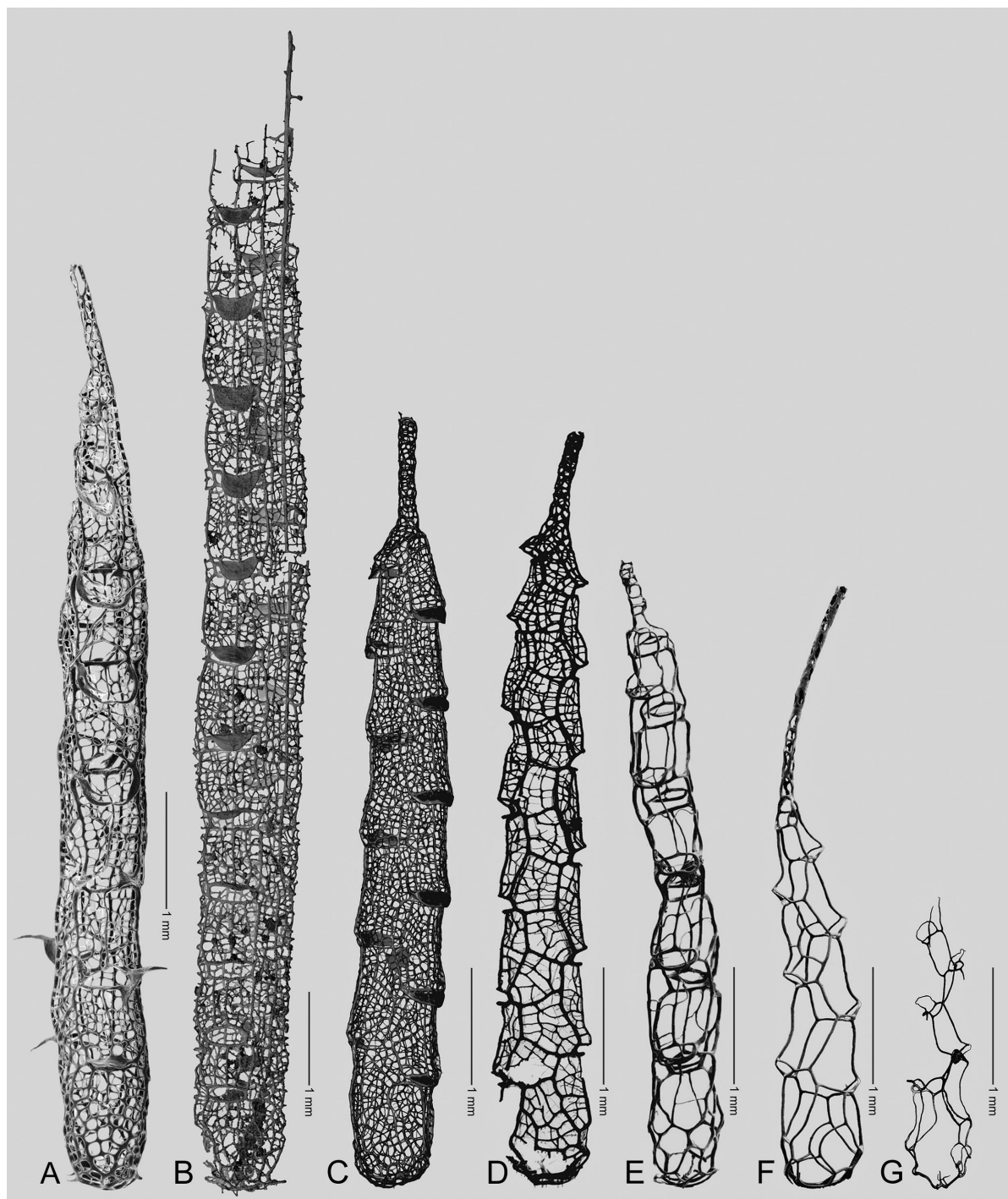


Fig. 1. SEM pictures of representatives of the *Gothograptus* lineage: **A**, *Gothograptus kozłowskii* Kozłowska-Dawidziuk, 1990, ZPAL G.XIII/43, *Cyrtograptus lundgreni* Biozone, Baltic erratic boulder, Jarosławiec, Poland. **B**, *Gothograptus nassa* Holm, 1890, ZPAL G.29/11, Bartoszyce IG-1 core, depth 1655.8 m, *Pristiograptus dubius*–*Gothograptus nassa* Biozone, Poland, EEP. **C**, *Neogothograptus eximinassa* Maletz, 2008, MB.G. 1123, JM 61/13, Baltic erratic boulder, Wetterhammer, Germany, *Colonograptus ludensis*–*Monograptus gerhardi* Biozone. **D**, *Neogothograptus thornsteinssoni* Lenz & Kozłowska-Dawidziuk, 2004, GSC 125978, *Lobograptus progenitor* Biozone, Arctic Canada. **E**, *Neogothograptus balticus* (Eisenack, 1951), ZPAL G.27/4, Baltic erratic boulder, Jarosławiec 49, Poland. **F**, *Holoretiolites mancki* (Münch, 1931), ZPAL G.53/1, Baltic erratic boulder, Jarosławiec 48, Poland, *Lobograptus scanicus parascanicus* Biozone. **G**, *Holoretiolites helenawitoldi* Kozłowska-Dawidziuk, 2004, ZPAL G.34/2, Bartoszyce IG-1 core, 1579.9 m, *Lobograptus progenitor* Biozone. Figures modified from: A, Kozłowska-Dawidziuk 1990; B, E, Lenz & Kozłowska-Dawidziuk 2002; C, Maletz 2008; D, Lenz & Kozłowska-Dawidziuk 2004; F, G, Kozłowska-Dawidziuk 2004.

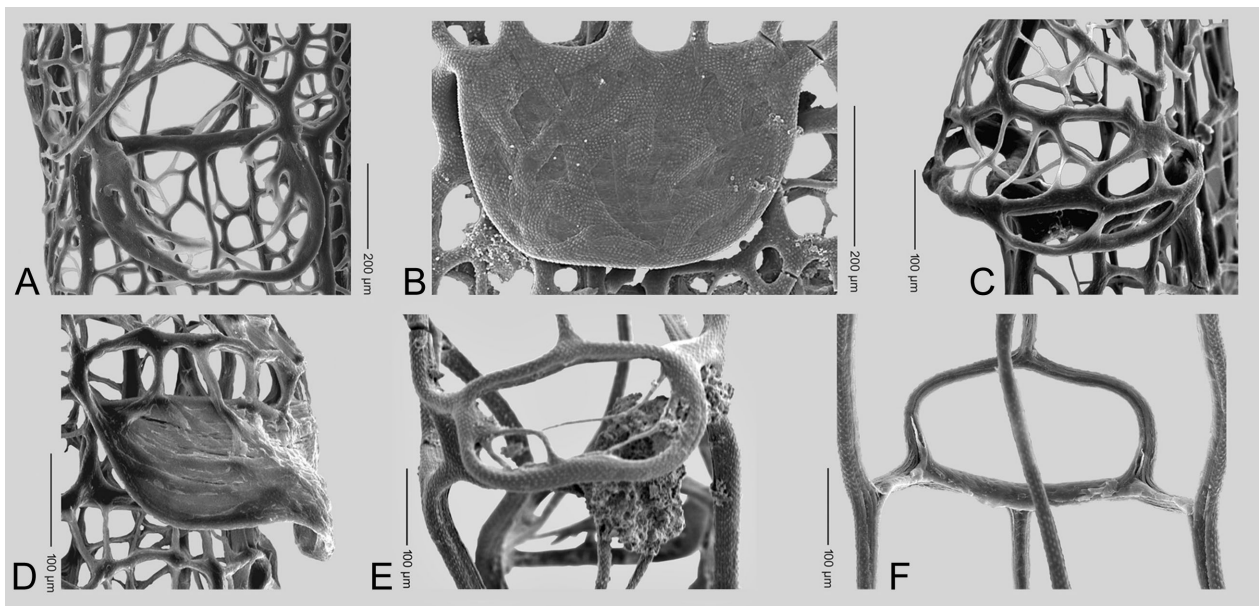


Fig. 2. SEM pictures of apertural hoods of gothograptids: **A**, reticulated hood of *Gothograptus kozłowskii* Kozłowska-Dawidziuk, 1990, ZPAL G.XIII/43, *Cyrtograptus lundgreni* Biozone, Baltic erratic boulder, Jarosławiec, Poland. **B**, hood of mature specimen, *Gothograptus nassa* Holm, 1890; Bartoszyce IG-1 core, 1655.8 m, *Pristiograptus dubius*–*Gothograptus nassa* Biozone. **C**, reticulated hood, *Neogothograptus reticulatus* Kozłowska, Lenz & Melchin, 2009, ZPAL G.41/2, Baltic erratic boulder 59, Jarosławiec, Poland. **D**, solid hood of *Neogothograptus eximinassa* Maletz, 2008, Baltic erratic boulder from Wetterhammer, Thuringia, Germany, *Colonograptus ludensis*–*Monograptus gerhardi* Biozone. **E**, slightly reticulated hood of *Neogothograptus balticus* (Eisenack, 1951), ZPAL G.27/4, Baltic erratic boulder, Jarosławiec 49, Poland. **F**, thecal aperture from the inside with no hood, *Holoretiolites mancki* (Münch, 1931), ZPAL G.53/2, Baltic erratic boulder, Jarosławiec 48. Figures B, C, D, modified from Kozłowska et al. (2009).

incorporated in its distal part of the lateral wall, and a lack of genicular hoods. Given that the first occurrence of species of *Baculograptus* is from the *Col. praedeubeli* Biozone, as is the case with *Neogothograptus* Kozłowska-Dawidziuk, 1995, it is possible that these two genera may show an ancestor–descendant relationship, or be sister taxa, derived from *Gothograptus* (Kozłowska et al. 2009).

Genus *Neogothograptus*

Species of *Neogothograptus* flourished continuously from the *Col. praedeubeli* Biozone up to the *Lobograptus scanicus* Biozone (Lenz & Kozłowska-Dawidziuk 2002; Kozłowska et al. 2009). This is the first group of gothograptids with a free nema, which is a typical feature of Ludlow retiolitids.

Neogothograptus is the most diverse among gothograptid genera, with nine species. The great similarity of genicular solid hoods of *N. eximinassa* Maletz, 2008 (Figs 1C, 2D) suggests possible close relationship with *G. kozłowskii* and *G. nassa*, although the results of the cladistic analysis of Kozłowska et al. (2009) suggest that the hoods could have been derived independently. *Neogothograptus balticus* (Eisenack, 1951)

and *N. reticulatus* Kozłowska, Lenz & Melchin, 2009 have similar hoods built of a reticulum (Figs 1E, 2C, E).

Neogothograptus thornsteinssoni Lenz & Kozłowska-Dawidziuk, 2004 (Fig. 1D) from the *Neodiversograptus nilssoni* and *Lobograptus progenitor* biozones exhibit a mix of characters of older gothograptids, having a dense reticulum, and of younger forms in the absence of genicular processes (Fig. 1D).

Neogothograptus alatiformis Lenz & Kozłowska-Dawidziuk, 2004 is the smallest form of this genus with only three thecae and a well-developed, dense reticulum, especially in mature colonies. This species possesses unique, well-developed singular genicular processes with a distal shelf-like projection. Similar processes are present in the most proximal part of the tubarium. These structures are unusual in the *Gothograptus* lineage (Lenz & Kozłowska-Dawidziuk 2004).

Species of *Neogothograptus*, like most of the Ludlow retiolitids, display a strong tendency to reduction of the reticulum and genicular hoods. The species *N. purus* Kozłowska-Dawidziuk, 1995 and *N. melchini* Lenz & Kozłowska-Dawidziuk, 2004, from the *L. progenitor* Biozone, possess tubaria with no reticulum or genicular structures.

Genus *Holoretiolites*

The greatest degree of rhabdosomal structural reduction occurs in the youngest gothograptids, species of *Holoretiolites*. The reduction of mid-ventral lists in *H. atrabecularis* shows the next step in reduction of the tubaria in this lineage. In addition, four of the species of this genus, *H. mancki* (Münch, 1931), *H. erraticus* Eisenack, 1951, *H. atrabecularis* and *H. helenawitoldi*, have extremely reduced, small rhabdosomes with a simple proximal end, no reticulum and no genicular hoods (Fig. 1F). The two most reduced species of the genus, *H. atrabecularis* and *H. helenawitoldi* (Fig. 1G), have a reduced appendix. The sicula in *H. helenawitoldi* is about 1.8 mm long (Kozłowska-Dawidziuk 2004). Only *H. manckoides* Kozłowska-Dawidziuk, 1995 from the *Cucullograptus hemiaversus* Biozone has a larger tubarium and no reticulum.

According to the stratigraphical record, the species of *Holoretiolites* – *H. mancki*, known from the *S. leintwardinensis* Biozone, represents the last known species of the *Gothograptus* lineage, although two the most reduced forms *H. helenawitoldi* and *H. atrabecularis* occur in the *Lobograptus progenitor* and *L. parascanicus* biozones.

SUMMARY

The *Gothograptus* lineage ranges through the upper Homeric to the lower Ludfordian of the Silurian, thus survived the *lundgreni* extinction event. Most of its members, the genera *Gothograptus*, *Baculograptus*, *Neogothograptus* and *Holoretiolites*, have a finite tubarium terminating with an appendix, except for some of the most reduced species of *Holoretiolites*. The appendix, regardless of its length, marks the end of colony growth and is considered to be a modified distalmost theca.

A characteristic feature of some gothograptids is the presence of singular hoods, developed on the genicular list of thecal apertures. They are built of a reticulum or densely packed parallel bandages, having different shapes and sizes in different species. Hoods are absent in species of *Baculograptus*, *Holoretiolites* and some species of *Neogothograptus*.

Reduction of tubaria complexity, size, numbers of zooids and increase in sicula length lead to the smallest forms represented by some species of *Holoretiolites*. A comparable degree of reduction, but with a different rhabdosomal structure, is known in *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk, 1995 from the *S. leintwardinensis* Biozone (Kozłowska & Bates 2014).

Acknowledgements. I thank Alf Lenz from the University of Western Ontario, Canada and Joerg Maletz from Institut für Geologische Wissenschaften Freie Universität, Germany for the kind donation of the pictures of *Neogothograptus thorsteinssoni* and *Neogothograptus eximinassa*. The reviewers Alf Lenz and Michael Melchin are thanked for their constructive comments which greatly improved this manuscript. This paper is a contribution to IGCP Project 591 ‘The Early to Middle Palaeozoic Revolution’.

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