



# The tubarium construction in *Holoretiolites*, *Neogothograptus* and related taxa (Graptolithina, Retiolitinae): clues to their astogeny and species identification

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Received: 2 September 2022 / Revised: 31 October 2022 / Accepted: 5 December 2022 / Published online: 3 February 2023  
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## Abstract

The Homeric (Wenlock) to Ludfordian (Ludlow), late Silurian, retiolitine genera *Neogothograptus* and *Holoretiolites* and their relatives are revised. These are often considered as the youngest and smallest retiolitine taxa, characterised by a finite growth indicated by the appendix, leading to the extinction of the clade. The tubarium construction of the genera is analysed and compared, showing the loss of the pleural and parietal lists in *Holoretiolites* and the development of a central zigzag construction on the obverse and reverse sides of the tubarium. This construction is not homologous to similar constructions in earlier retiolitines, as it is based on the modification of the lateral apertural lists. It is also found in the closely related *Semiplectograptus* and *Plectodinemagraptus*. Useful details to understand the astogeny of these taxa include the development of the reticulum, the genicular processes and the outer ancora. These features are described for the first time for most species. Details of the outer ancora and its construction in the genus *Neogothograptus* are still poorly understood. *Holoretiolites helenawitoldi* is synonymised with *Holoretiolites atrabecularis*. *Holoretiolites manckoides* is transferred to *Semiplectograptus*.

**Keywords** Graptolithina · Retiolitinae · *Holoretiolites* · *Neogothograptus* · Astogeny · Biostratigraphy · Evolution

## Introduction

‘If the siculozoid in *Holoretiolites* had become sexually mature the budding of the last six blastozooids could have been omitted altogether and the sclerotized framework could have disappeared. But the holoretiolite stock need not have become extinct’ (Kirk 1978, p. 546).

Nancy Kirk’s views on the disappearance of retiolitine graptolites, even though not an accepted view today (see Rigby 1993), certainly shows the problems we deal with, struggling to understand these strange organisms. The Retiolitinae represent one of the most fascinating groups of the planktic graptolites. Even though many details of their tubarium construction have been elucidated in some detail in recent years (e.g. Lenz et al. 2018; Maletz 2022), little is known or has been considered about the preservational aspects in the taxonomy of the group. The investigated material

is usually fragmented and simple questions about the size of the colonies and their astogenetic modifications may be difficult or impossible to answer. A size limitation can often be recognised when the colonies bear an appendix at the distal end, a simple tube. The appendix appears first in the late Sheinwoodian (Wenlock) in *Eisenackograptus eisenacki* Kozłowska-Dawidziuk, 1990 (Maletz, 2022, fig. 8) and in the species of the genus *Gothograptus* Frech, 1897. An appendix is also characteristic for *Holoretiolites* Eisenack, 1951 and *Neogothograptus* Kozłowska-Dawidziuk, 1995 in the late Wenlock to Ludlow. However, even in the post Lundgreni Extinction interval a number of genera appear to show unlimited growth (e.g. *Semigothograptus* Kozłowska-Dawidziuk, 2016, *Plectograptus* Moberg and Törnquist, 1909, *Spinograptus* Bouček and Münch, 1952) or an appendix is not known (e.g. *Plectodinemagraptus* Kozłowska-Dawidziuk, 1995; *Semiplectograptus* Kozłowska-Dawidziuk, 1995). Most genera, however, include members with and without growth limitations. A good example is the genus *Spinograptus* with its various and quite variable species. While *Spinograptus spinosus* (Wood, 1900), *Spinograptus clathrospinus* (Eisenack, 1951) and *Spinograptus muenchi* (Eisenack, 1951) appear to show

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unlimited growth (an appendix or a distal decrease in tubarium width is not known), *Spinograptus tubothecalis* Kozłowska et al. 2013 has only three pairs of thecae of which the distal two thecae are reduced to a simple tubular form. The species also shows the indication of an appendix between the two distal thecae (Kozłowska et al. 2013, fig. 5). *Spinograptus reticulolawsoni* Kozłowska-Dawidziuk 1997 has a finite tubarium with about six to seven thecal pairs and possibly a short appendix (Kozłowska-Dawidziuk 1997, fig. 3).

Finite growth is common in graptolites and has been recognised in a number of biserial axonophorans. Thus, it is a general feature without any important phylogenetic relevance. Mitchell (1988) described the lasiograptine genus *Brevigraptus* for biserial specimens with only four thecal pairs. Earlier taxa with supposedly finite growth include *Apiograptus clavus* (Mu in Mu et al., 1979) as illustrated by Chen et al. (1995, fig. 26A, pl. 4A) from the latest Dapingian. Maletz et al. (2011, fig. 7P) illustrated a finite tubarium of *Archiclimacograptus* sp. from the Table Head Group of western Newfoundland. Finite growth occurs with *Corynoides* and *Corynites* in the Glossograptina (see Maletz and Zhang 2016). Finite growth is present in the Monograptidae with the best example being *Coronograptus maxiusculus* Štorch, 1988, consisting of the strongly elongated sicula and a single short theca. All examples show that the finite or limited growth of the colonies is not defined by genus level. Individual species may reduce their growth capacity, while other species of the same genus retain their (supposedly) infinite growth.

### The tubarium construction

Maletz (2022) discussed the construction of the Silurian Retiolitinae in some detail and provided a key to the identification, homologization and interpretation of the various lists of these organisms. Due to the investigation largely based on chemically isolated material, the genera *Holoretiolites* and *Neogothograptus* from the Ludlowian (Silurian) were considered well known – at least for general biostratigraphic purposes (Kozłowska-Dawidziuk 2004; Maletz 2022). Both genera are interpreted as closely related due to similarities in tubarium construction and *Holoretiolites* may easily be derived from *Neogothograptus* (e.g. Kozłowska-Dawidziuk 2004; Bates et al. 2005; Kozłowska 2015), but the biostratigraphic ranges of the individual species have only been evaluated previously for the genus *Neogothograptus* (Kozłowska et al. 2009, fig. 2). The biostratigraphic ranges of the *Holoretiolites* species are shown here (Fig. 1).

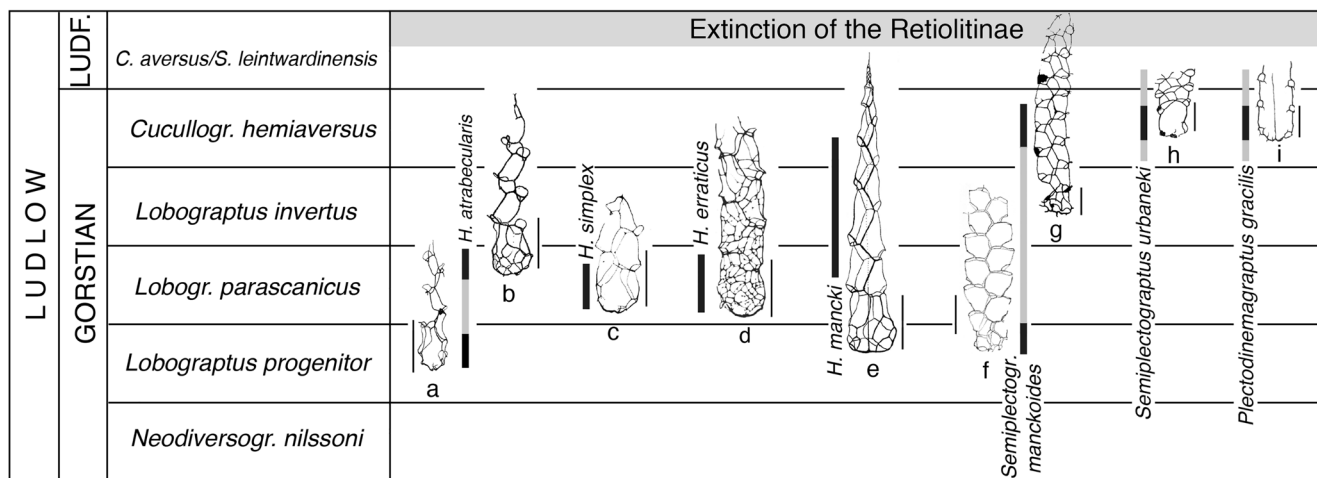
Maletz (2022) discussed and revised the terminology of the retiolitine list construction and also provided the latest concept for the understanding and differentiation of the clathrium and reticulum in retiolitine graptolites. In *Neogothograptus* and *Holoretiolites*, the differentiation is usually quite easy, as most

species do not possess much reticulum. The reticulum can generally be considered as a secondary development, formed during the maturation of the colonies.

**Obverse and reverse sides of tubarium:** The obverse and reverse tubarium sides of *Holoretiolites* and *Neogothograptus* can usually be differentiated easily by the position of the ventral pre-thecal orifices and the thecal orifices (Fig. 2a–b, e). The top of these orifices can also be recognised by the attachment of the mid-ventral list of the first thecal pair. The ventral proximal orifices are generally hexagonal in shape in *Holoretiolites* and *Neogothograptus* (see Maletz 2008, fig. 5). The ancora umbrella is somewhat asymmetrical with the pre-th1<sup>1</sup> orifice in a lower position than the pre-th1<sup>2</sup> orifice position in reverse view (Fig. 2a, b, e). The development of the lateral clathrium is identical or very similar on both sides. Complete colonies appear to have identical numbers of thecae on each ventral side, but the distal thecae are considerably reduced in size and the tubaria generally end in a centrally positioned appendix.

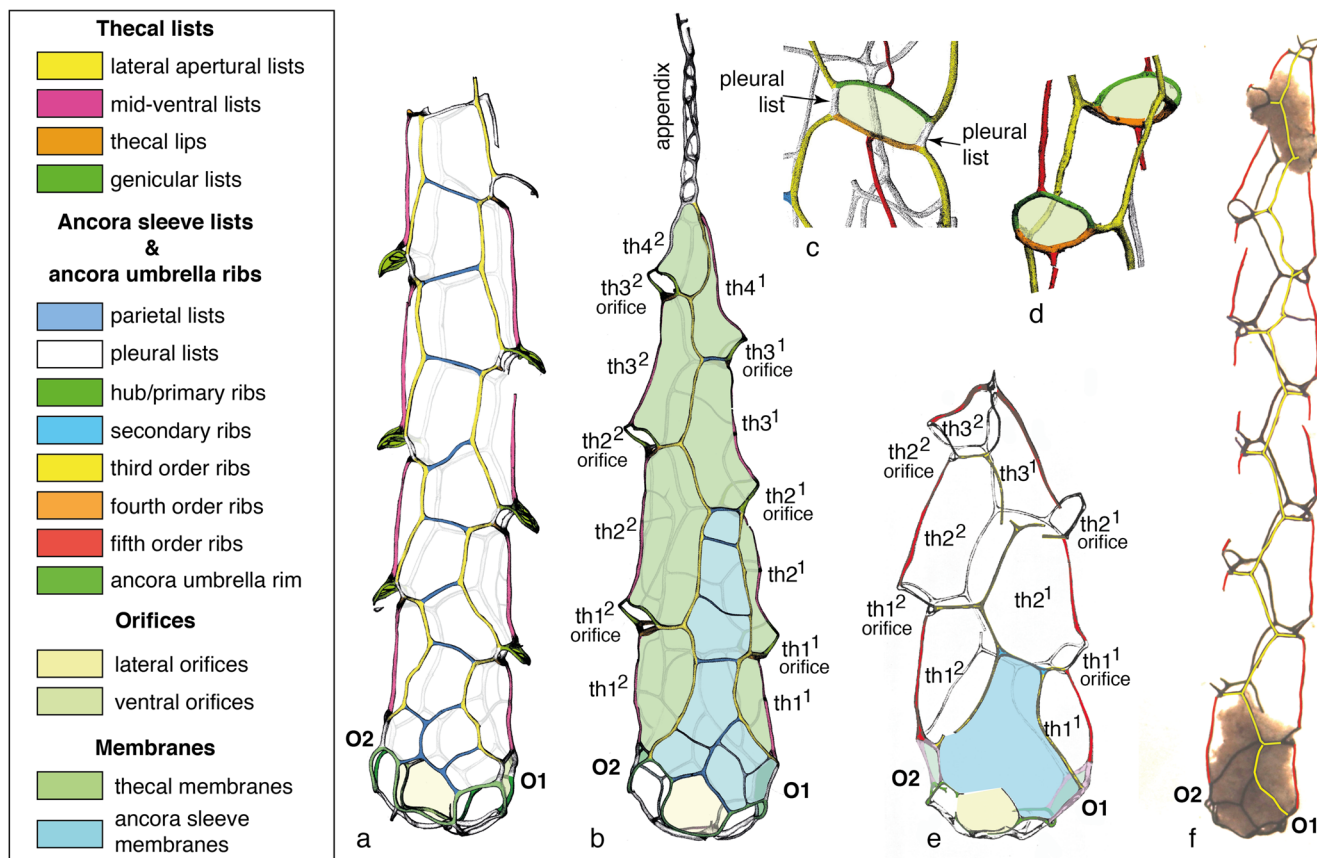
**Tubarium size:** The size of the tubaria in the genera *Holoretiolites* and *Neogothograptus* is quite variable and between three thecal pairs (*Holoretiolites simplex*) and nine thecal pairs (*Neogothograptus balticus*) have been counted. It appears that all species form finite colonies, but an appendix is not documented for all species due to the fragmentary preservation of the material. So far it is unclear whether the number of thecae is constant in a particular species or how much variation is possible. The thecae can easily be counted when the mid-ventral lists are recognised (see Fig. 2). The thecal orifice can be found at the top of its mid-ventral list. It is difficult to understand the distal part of the colonies with the strongly reduced last thecal pair that lacks an orifice and merges smoothly into the appendix (Fig. 2b). A last orifice is only seen at the tip of the appendix. It is especially easy in *Holoretiolites simplex* to count the number of thecae, as in this species the ventral sides of the thecae are represented solely by the mid-ventral list, even in the most distal thecal pair (Fig. 2e).

**The ancora umbrella:** The ancora umbrella is formed as an extension from the virgella and develops as a complex umbrella-shaped construction of which only the meshwork is preserved in the form of a number of ribs (Bates and Kirk 1992). In all taxa considered here, the ancora umbrella is formed of about five to seven meshes, but this number has to be taken with care as it has not been verified for some species and the consistency of the number of ribs is unclear. The branching divisions of the virgella are here labeled as a succession of dichotomous branchings (Fig. 3). A maximum of five orders of branching have been recognised (Fig. 3c), but four orders are more common (Fig. 3a–b). The ancora umbrella meshes, here labeled 1–4, starting on the th1<sup>1</sup> ventral-



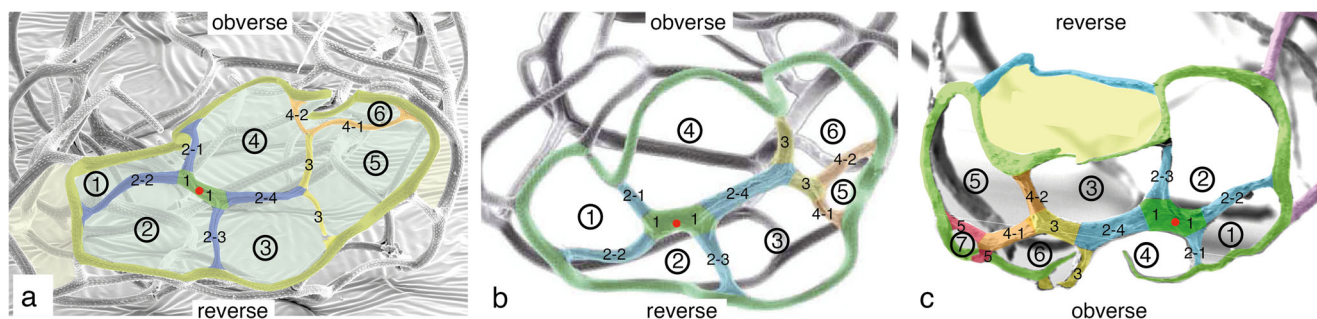
**Fig. 1** The biostratigraphic ranges of the known *Holoretiolites*, *Semiplectograptus* and *Plectodinemagraptus* species. **a–b** *Holoretiolites atrabeularis* Kozłowska-Dawidziuk, 1995. **a** paratype of *Holoretiolites helenaewitoldi* Kozłowska-Dawidziuk, 2004 (after Kozłowska-Dawidziuk 2004, fig. 4F). **b** paratype (after Kozłowska-Dawidziuk 1995, fig. 29B). **c** *Holoretiolites simplex* (Eisenack, 1935), holotype (after Eisenack 1951, pl. 7, fig. 1). **d** *Holoretiolites erraticus* Eisenack, 1951, holotype (after Eisenack 1951, pl. 24, fig. 4). **e** *Holoretiolites*

*mancki* (after Münch 1931, fig. 3). **f–g** *Holoretiolites manckoides* (Kozłowska-Dawidziuk, 1995). **f** Arctic Canada (after Lenz and Kozłowska-Dawidziuk 2004, pl. 18, fig. 5). **g** holotype, Poland (after Kozłowska-Dawidziuk 1995, fig. 27B). **h** *Semiplectograptus urbaneki* Kozłowska-Dawidziuk, 1995, holotype (after Kozłowska 2018b). **i** *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk, 1995, reconstruction (Lenz et al. 2018, fig. 10.3). Scale bars indicate 1 mm for each specimen



**Fig. 2** Constructional interpretation of *Holoretiolites* and *Neogothograptus*. **a** *Neogothograptus balticus*, MB.G. 1082/2, reverse view (after Maletz 2008, fig. 71). **b** *Holoretiolites erraticus*, MB.G. 1085/03, reverse view ancora sleeve panels in blue, ventral thecal membranes in green. **c** *Neogothograptus romani*, SMF 75844, JM 118/06, showing short pleural lists, thecal lip and geniculum outlining orifice. **d**

*Holoretiolites mancki*, SMF 75848, JM 125/08, Lichtenrade, Berlin. **d** normal light photo (see fig. 11a). **e** *Holoretiolites simplex*, complete tubarium in reverse view, after Eisenack (1935, pl. 7, fig. 1). Colour code also for all further illustrations. O1 and O2 indicates the ventral pre-thecal orifices on the th<sup>1</sup> (O1) and th<sup>2</sup> (O2) sides



**Fig. 3** Ancora hub terminology, generation of ribs labeled (1-5), meshes labeled 1-6. **a** *Neogothograptus romani*, SMF 75845, JM 118/03. **b** *Holoretiolites manckoides*, ZPAL G. 48/5 (after Dobrowolska 2013,

fig. 8B). **c** *Holoretiolites simplex* (photo provided by D. E. B. Bates, Aberystwyth, Wales, UK)

obverse side with mesh 1 and labeling in clockwise sense from the underside (abscicular side), are formed from the first and second generation ribs (Fig. 3a). Meshes 5 and 6 are on the  $th1^2$  ventral side, formed from the ribs of the third and fourth generation.

A complete rim (ancora umbrella rim) can be seen surrounding the ancora umbrella, to which the ends of the ribs are connected. These ribs clearly show seams as remains of a previously existing membrane on the outside (abscicular face) (Fig. 3a-c). The ribs are initially relatively slender, but may widen considerably towards maturity of the colony. Considerably widened ribs of the first one or two generations of ribs can be seen in *Baculograptus chainos* (Lenz et al. 2018, fig. 14B) and in *Neogothograptus purus* (Dobrowolska 2013, fig. 10C), but may be more widely distributed. A considerable widening of the ribs is also visible in some mature specimens of *Gothograptus nassa* (cf. Kozłowska et al. 2019, fig. 11A), here associated with the widening of the rims of the lateral proximal orifices.

In *Holoretiolites* and *Neogothograptus* there are three ribs of the second order connected to the ancora rim (Fig. 3a-b), while the fourth rib produces another generation of ribs (third order) of which the obverse one connects to the ancora rim. The reverse third order rib branches again at least once to form another pair of ribs (fourth order). The obverse fourth order rib may branch again (Fig. 2e: *Holoretiolites simplex*) in one observed example, but this seems to be an exception, in which the ancora umbrella also has seven meshes. The interpretation is difficult when the ribs are strongly enlarged (see Lenz et al. 2018, fig- 14A: *Neogothograptus* sp.). In this specimen, there appear to be only five meshes and a maximum of three orders of ribs in the ancora umbrella. Four orders of ancora umbrella ribs and six meshes were also identified in *Semiplectograptus manckoides* (Dobrowolska 2013, fig. 8B).

The connection of the ribs to the ancora rim in can be recognised in *Neogothograptus romani* (Fig. 3a). Rib 2-2, the longest of the four second order ribs, is connected to the base of the ventral prothecal orifice on the  $th1^1$  side. Rib 4-1 is connected to the same position of the ventral prothecal orifice of  $th1^2$  side, on the opposite side of the tubarium. Due to the

distortion, the precise connection is, however, not possible to determine in many specimens.

**Lists on the ventral sides:** The ventral sides of the tubarium are the sides where the thecal orifices are found. These sides are outlined in *Neogothograptus* by long lateral apertural lists and short pleural lists (the lateral apertural orifice lists) forming the edges of the tubarium and the apertural lips and genicular lists connecting these lists on the obverse and reverse sides (Fig. 2a). Thus, the thecal orifices are formed from the horizontal lower thecal lip, the equally horizontal genicular list and on the sides by the short pleural lists (Fig. 2c). The long, curved lateral apertural lists connect at two places to the thecal orifices; at the base and top of the short pleural lists (Fig. 2C, arrows). Distinct more or less vertical to somewhat distally inward inclined mid-ventral lists are generally formed on the thecal membranes and connect the genicular lists with the overlying thecal lips.

In *Holoretiolites*, the lateral apertural lists are moved away from the edge of the tubarium towards the mid-line of the lateral sides, forming a central zigzag list. The zigzag list bears horizontal lists as the connection to the thecal orifices (Fig. 2e, f). Thus, there is only a single connection of the thecal orifices to the obverse and reverse (lateral) sides of the tubarium and there are no pleural lists, suggesting that there is no ancora sleeve.

Lateral zigzag lists are common in retiolitine graptolites, but that does not mean they are all homologous constructions. Bates et al. (2005) differentiated the zigzag lists on the reverse side in early taxa (e.g. *Retiolites*, *Pseudoretiolites*, *Rotaretiolites*) (see Loydell et al. 1997, fig. 1), formed as thecal lists, from the zigzag ancora sleeve (parietal) lists in younger taxa (*Plectograptus*, *Spinograptus*) (see Bates et al. 2006, fig. 1). These are found on both the obverse and reverse sides of the tubarium. Zigzag parietal lists can also be found on the reverse and obverse sides in *Paraplectograptus areticulatus* Kozłowska-Dawidziuk, 1995 (Maletz, 2022, fig. 5D), but not in other species of the genus. The zigzag lists in *Holoretiolites* are formed from the lateral apertural lists, thus, are not homologous to the reverse side zigzag thecal lists

or the ancora sleeve parietal zigzag lists discussed by Bates et al. (2005). Therefore, we have at least three independent instances of the evolution of zigzag lists on the lateral sides of the tubarium of the retiolitines, a great example of parallel or convergent evolution in the retiolitines.

**Lists on the obverse and reverse sides:** The parietal lists connect the obverse and reverse sides of the tubarium in *Neogothograptus*, where they are attached to the lateral apertural lists (Fig. 2a). The earliest list identified as a parietal list forms the arch of the dorsal side of the lateral proximal orifice (Fig. 2a) and connects the paired ventral lobes of the ancora umbrella rim on the  $th1^1$  and  $th1^2$  sides. The following parietal lists are somewhat irregular, but quickly the development becomes more regular and further parietal lists form at regular distances and are only slightly inclined alternately to the two different sides (Fig. 2a).

In *Holoretiolites*, parietal lists are only found in the proximal end, reaching upwards approximately to the orifices of  $th1^1$  as is seen in *H. simplex* (Fig. 2e). In one specimen of *H. erraticus* (Fig. 2b), the evidence shows a more extensive development of parietal lists, but above the orifice of  $th2^1$  the central zigzag list typical of the genus *Holoretiolites* is present.

**The interpretation of the thecal and ancora sleeve membranes:** The identification and interpretation of the list construction in *Neogothograptus* and *Holoretiolites* can easily be used to understand the membrane development in these taxa. The parietal lists in *Neogothograptus* indicate the development of the lateral ancora sleeve membranes, connected at the sides with the thecal membranes through the lateral apertural lists (Maletz 2022, fig. 13D).

In *Holoretiolites*, the zigzag of the lateral apertural list starts at the  $th1^1$  orifice (Fig. 2e: *Holoretiolites simplex*) and there are no parietal lists above this point. Thus, species of *Holoretiolites* are characterised by zigzag lateral apertural lists connected with horizontal lists to the thecal orifices (Fig. 2f), and at least distally lack an ancora sleeve development.

The situation in a specimen of *Holoretiolites erraticus* (Fig. 2b) shows the origin of the zigzag lateral apertural list at the top of the  $th2^1$  orifice and the ancora sleeve membrane panels disappear only at this point. Thus, a considerable development of ancora sleeve panels (membranes) can be seen before the lateral apertural lists form the zigzag list. A specimen referred to *H. erraticus* illustrated by Kozłowska-Dawidziuk (1995, fig. 27H) seems to show a different development, but is hard to interpret from the light photo. Kozłowska-Dawidziuk (1995, fig. 9D) provided a reconstruction clearly based on the specimen that shows the basic construction of *Holoretiolites*, in which the zigzag list starts at the orifice of  $th1^1$ . Thus, it appears that the development in *H. erraticus* may be variable, providing an intermediate development between *Neogothograptus* and *Holoretiolites*.

## Astogeny

Astogeny describes the growth of a colony as the equivalent of the ontogeny of a single organism. Ruedemann (1904) introduced the term for the graptolites based on the discussion of growth stages in the development of the Bryozoa by Cumings (1904). Ruedemann (1902) initially described the astogeny of the genus *Goniograptus* from numerous growth stages as the ‘ontogeny of the species’, but later identified it as the astogenetic series (Ruedemann, 1904, p. 526), now generally called the astogeny of the colony. Urbanek (1963, p. 148) differentiated astogeny and cladogeny, but identified cladogeny as an astogenetic process, producing additional stipes, while defining astogeny as the ‘complete process of colonial development’. Maletz et al. (2014) defined the term astogeny – slightly misleadingly – as the ‘combined growth of individuals of a colonial organism’, a phrasing that suggested that only the zooidal development was included and not the tubarium construction. Ruedemann (1904), however, clearly understood the term to identify the growth of the graptolite tubarium. The term should be used for the growth of the graptolite tubarium, but also including the addition and differentiation of the clonal zooids within the tubarium. All stages from the earliest phase to the gerontic modification are here understood as the tubarium astogeny.

Astogenetic considerations have rarely played a role in the investigation of retiolitine graptolites, even though the astogeny presents a serious problem in species identification and interpretation of poorly or incompletely preserved material. A good example is the species *Gothograptus nassa*, first described by Holm (1890) based on a few fragmentary shale specimens. Wiman (1895) provided the first description of chemically isolated material of this species from Gotland, Sweden. He illustrated a number of specimens, some without and others with fairly dense reticulum. He considered these different specimens as showing intraspecific variation (Ausdruck der Variation) and not representing astogenetic stages (Altersstadien). Bouček and Münch (1952) erroneously described some of Wiman’s (1895) material as their new species *Gothograptus intermedius*, based on the lack of the reticulum. These specimens are, however, immature colonies of *Gothograptus nassa*, as can be shown by the numerous specimens now available of this species and of the closely related *Gothograptus auriculatus* showing the astogenetic variation (see Kozłowska et al. 2019; Maletz 2023, in press).

The most important character to determine the astogeny of the retiolitines may not be the size of the tubarium, as most taxa discussed here show a finite growth. Thus, the final length of the tubaria may be reached quite early in the astogeny of the colony. A number of other characters can be recognised that determine the maturity and the astogenetic stage of the specimens. These characters include the density of the reticulum, the development of genicular modifications and the outer ancora

development. All these characters appear only in advanced stages of the colony growth, but differences in the timing of their construction can be seen in the various species.

**The reticulum:** The reticulum represents a secondary development of lists in the retiolitine tubarium in the form of irregular to highly regularly secreted lists (cf. Maletz 2022). Retiolitine graptolites are quite variable in this character and the reticulum ranges from non-existent to extremely dense. Juvenile specimens of retiolitines usually do not possess any reticular lists, but it is uncertain at what stage in the astogeny the construction of the reticulum starts. In the Ludlow (upper Silurian) quite a number of taxa without any reticulum appear, while closely related taxa may show considerable development of the reticulum. These cannot be identified as juveniles, but may represent examples of neoteny in retiolitines.

The genus *Neogothograptus* shows a quite variable development of the reticulum. Very dense reticulum is present in *Neogothograptus reticulatus* and *Neogothograptus eximinassa* (Fig. 4), but *Neogothograptus purus* and *Neogothograptus melchini* lack any reticulum (see Kozłowska et al. 2009). It is, however, clear that the development of the reticulum shows a distinct trend in the genus *Neogothograptus* in which early species possess a fairly dense reticulum in mature specimens, but younger species show less reticular development or do not show a reticulum at all (Fig. 5).

Maletz (2008) discussed the astogeny of *Neogothograptus eximinassa* and illustrated a number of immature and mature specimens from a single sample. The available specimens indicate that the mature colony has about 6–7 thecal pairs and a distinct appendix, ca. 0.8 mm long (Fig. 4g–h). Specimens with about 1 to 3 or 4 thecal pairs do not possess any preserved reticulum (Fig. 4a–c). One specimen has about 6 thecal pairs, but is distally incomplete (Fig. 4f). It also shows a gradational decrease of the reticulum development towards the distal end. One supposedly immature fragment (Maletz 2008, fig. 8J), a proximal end with about 3 thecal pairs, the distal most one incompletely preserved, has small indications of the genicular hoods and a fairly dense reticulum (Maletz 2008, fig. 9K). Irregular reticular lists also cover the proximal orifices during the astogeny of the colony and form an outer ancora (Maletz 2008, fig. 8J), but it is uncertain at what stage this development starts. A few outer ancora lists are already present in a specimen with six thecal pairs and a highly incomplete development of the reticulum (Fig. 4f).

A clear astogenetic trend is also visible in the reticulum of *Neogothograptus ornatus* Maletz, 2008 (Fig. 6), but is more incompletely known due to the fragmentary nature of the available material. A number of juvenile specimens with up to two thecal pairs do not show any evidence of the reticulum. The appendix is known from two fragments and is about 0.7 mm long (Fig. 6a, i), but a number of incomplete

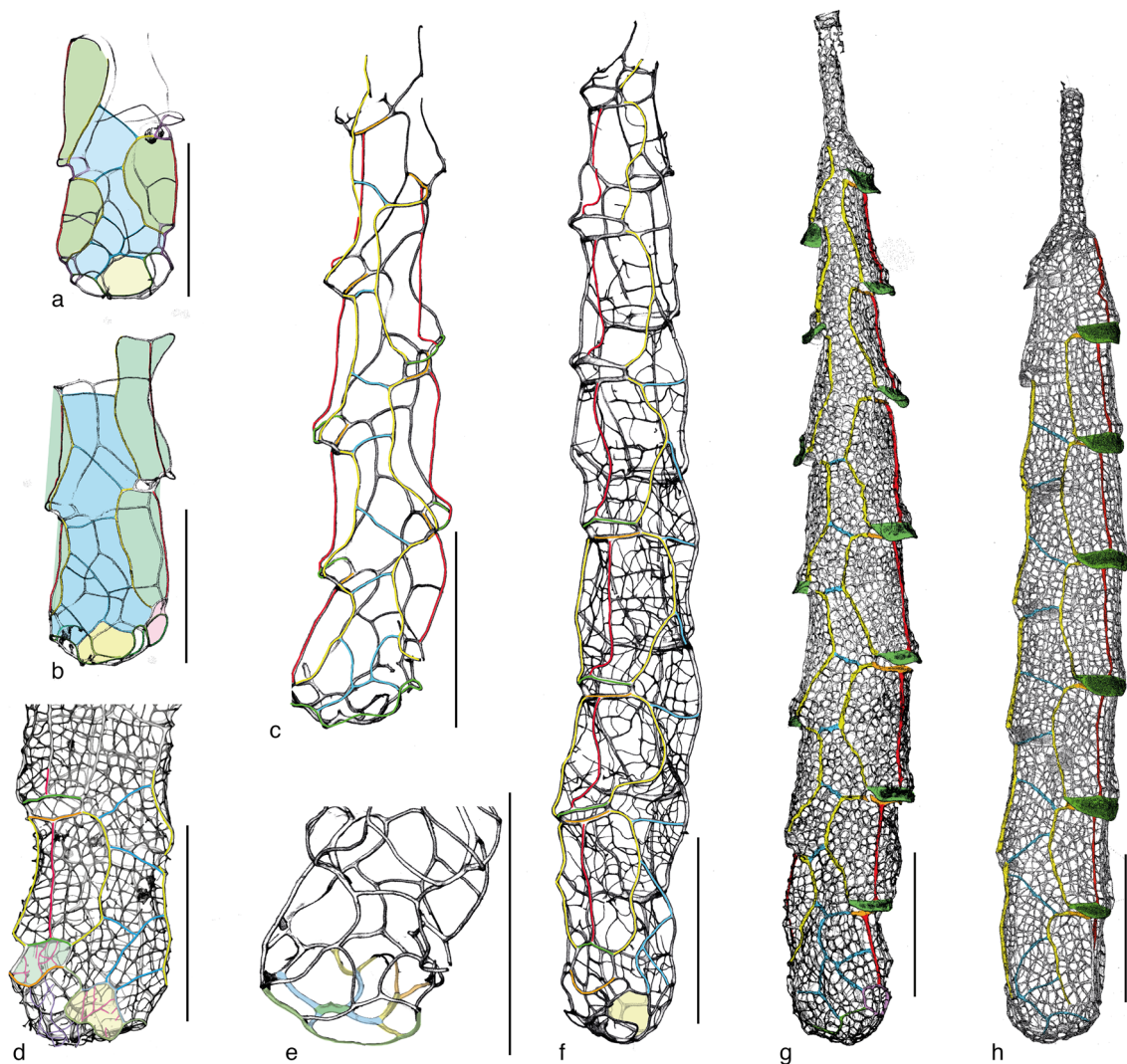
specimens show clearly the distal narrowing colony indicating a finite growth, even though they do not show a preserved appendix. The horizontal lists on the appendix may also be identified as reticular lists. The longest specimen with a proximal end has about four thecal pairs (Maletz 2008, fig. 10J). It shows a distally diminishing reticulum and robust genicular processes (Fig. 6b). The reticulum appears relatively regular as was also seen in a shale specimen illustrated by Štorch et al. (2016, fig. 3A).

**Genicular processes:** Genicular additions in the form of hoods, spines or other features are not uncommon in retiolitines. While single features are often identified as hoods, paired structures are invariably been called processes. It is here preferred to identify all extensions as processes, especially as single ‘hoods’ can, through astogeny, be modified into more complex constructions. The wide genicular processes in *Papiliograptus papilio* start to develop as paired lobes and processes are even more extended into apparent paired spines connected through a meshwork of reticulum in *Papiliograptus retimarginatus* (see Lenz et al. 2018; Kozłowska and Bates 2021).

Kozłowska et al. (2019) differentiated ‘*nassa*’ hoods and reticulated hoods in the genus *Gothograptus*. Their ‘*nassa*’ hoods are processes formed from microfusellar material as relatively massive constructions, while reticular processes are formed of a meshwork of bars or lists. The ‘*nassa*’ hoods are here more generally identified as microfusellar processes, as the term ‘*nassa*’ hood suggests a limitation of their distribution to *Gothograptus nassa*. They can also be found in *Semigothograptus* (see Kozłowska 2016) and *Neogothograptus* (see *N. eximinassa* herein). The phylogenetic relevance of this feature is unclear as is the detailed construction of these processes.

Considerable astogenetic differences can be seen in the presence and development of the genicular processes in *Gothograptus nassa*. Kozłowska et al. (2019) described this development in some detail. They stated that specimens with up to six thecal pairs may not possess evidence of genicular processes. The authors did not, however, illustrate such immature specimens. Their immature specimens (Kozłowska et al. 2019, fig. 10) show a decrease in the density of the reticulum, but all have quite extensive genicular processes. The longest specimen bears about 18 thecal pairs, but is incomplete distally.

The genicular processes start in *Neogothograptus eximinassa* with the addition of a thin accretion of microfusellar material at the thickened genicular rim that grows wider as the specimen matures (Fig. 7l–m). In the finished process, a wide slightly thickened rim appears (Fig. 7n). As a late stage addition, bandages starting from the reticular meshwork of the theca are laid down perpendicular or irregularly on the processes (Fig. 7n–o). The genicular processes are smaller on the first thecal pair and increase in size distally. In



**Fig. 4** Astogeny of *Neogothograptus eximinassa*, MB.G. 1123. **a** MB.G. 1123/10, juvenile with three thecae. **b** MB.G. 1123/11, small specimen with two thecal pairs, lacking reticulum. **c**, **e** MB.G. 1123/08, specimen with four thecal pairs, lacking any reticulum. **c** complete specimen in lateral view. **e** oblique th<sup>1</sup> view, showing ancora umbrella development in colour. **d** MB.G. 1123/07, proximal end with outer

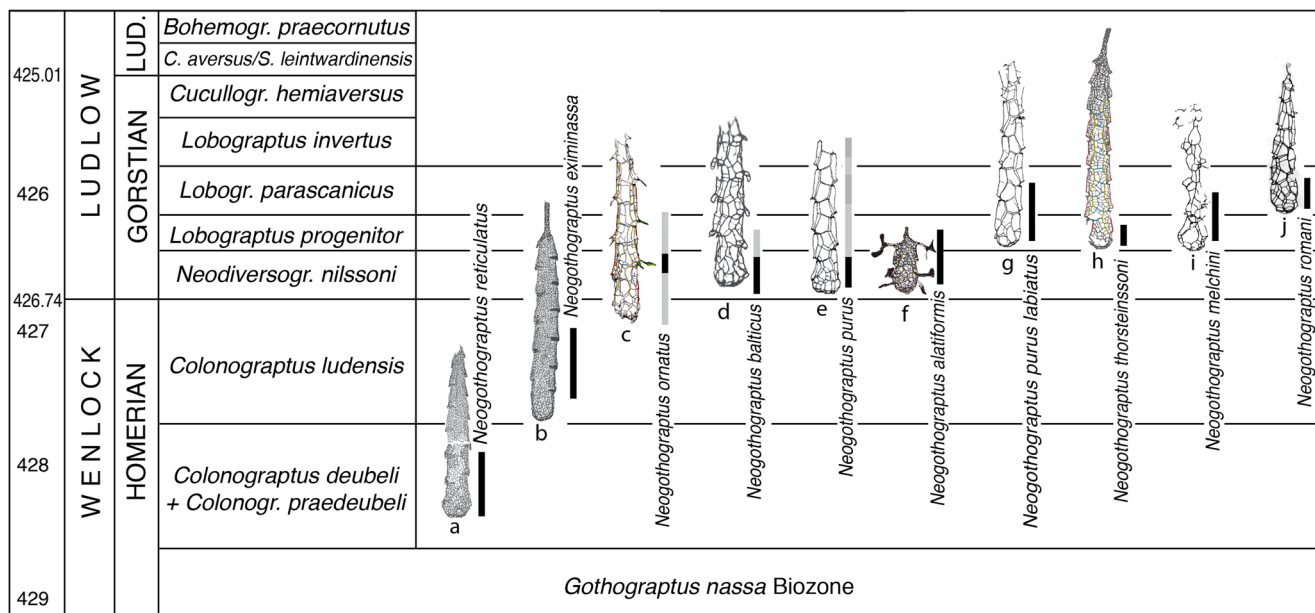
ancora and dense ancora sleeve meshes. **f** MB.G. 1123/05, growing specimen with six thecal pairs, showing gradational development of reticulum. **g** MB.G. 1123/14, mature specimen in reverse view. **h** MB.G. 1123/13, mature specimen in reverse view. All scale bars are 1 mm

immature specimens there might not be a genicular process on the first thecal pair, but subsequent thecae already possess considerable process development. The processes might reach a length of more than 150  $\mu\text{m}$  in mature specimens. Their development does not differ from the processes in *Gothograptus* (Fig. 7e–g) and *Semigothograptus* as illustrated by Kozłowska (2016, fig. 7). Also in these, bandages crossing over the surface of the microfusellar processes can commonly be recognised.

The genicular processes in *Neogothograptus balticus* are formed somewhat differently (Fig. 7a–d). There is no preservation at least of microfusellar material. The growth develops in a number of stages with the secretion of a thickened rim at each stage. Thus, this type of process is identified as a reticular process. Sometimes, intermittent isolated bandages appear to

be secreted on the pre-existing surface of the process (Fig. 7a). Seams on the inside suggest that that the processes initially were formed as the thickened rim of a membrane. The material of Eisenack (1951, pl. 24, fig. 5) indicates that several generations of rim extensions can be formed and the processes are elongated considerably. A similar situation may be inferred from the specimen illustrated by Štorch et al. (2016, fig. 4C), the most mature specimen known of this species. It also shows a quite dense reticulum and long, extended genicular processes. More complex reticular lists are also present in a chemically isolated, robust specimen illustrated by Kozłowska and Radzevičius (2013, fig. 7A).

Paired reticular extensions at the geniculum can be seen in *Neogothograptus ornatus* (Fig. 7h–k). They are constructionally identical to the single processes in *Neogothograptus*



**Fig. 5** Biostratigraphic distribution of *Neogothograptus*. **a** *Neogothograptus reticulatus* (Kozłowska et al. 2009, fig. 6). **b** *Neogothograptus eximinsassa* (after Kozłowska 2015, fig. 1C). **c** *Neogothograptus ornatus* Maletz, 2008, holotype (after Maletz 2008, fig. 10J). **d** *Neogothograptus balticus* (Eisenack, 1951), holotype (from Eisenack 1951, pl. 22, fig. 4). **e** *Neogothograptus purus* Kozłowska-Dawidziuk, 1995 (after Lenz and Kozłowska-Dawidziuk 2004, fig. 15A). **f** *Neogothograptus alatiformis* Lenz and Kozłowska-Dawidziuk,

2004, holotype (from Kozłowska 2018a). **g** *Neogothograptus purus labiatus* Lenz and Kozłowska-Dawidziuk, 2004, holotype (after Lenz and Kozłowska 2004, pl. 3, fig. 9). **h** *Neogothograptus thorsteinssoni* Lenz and Kozłowska-Dawidziuk, 2004 (from Kozłowska 2015, fig. 1D). **i** *Neogothograptus melchini* Lenz and Kozłowska-Dawidziuk, 2004, holotype (after Lenz and Kozłowska 2004 pl. 17, fig. 4). **j** *Neogothograptus romani* Kozłowska-Dawidziuk, 1995 (from Maletz 2008, fig. 13C). Specimens not to scale

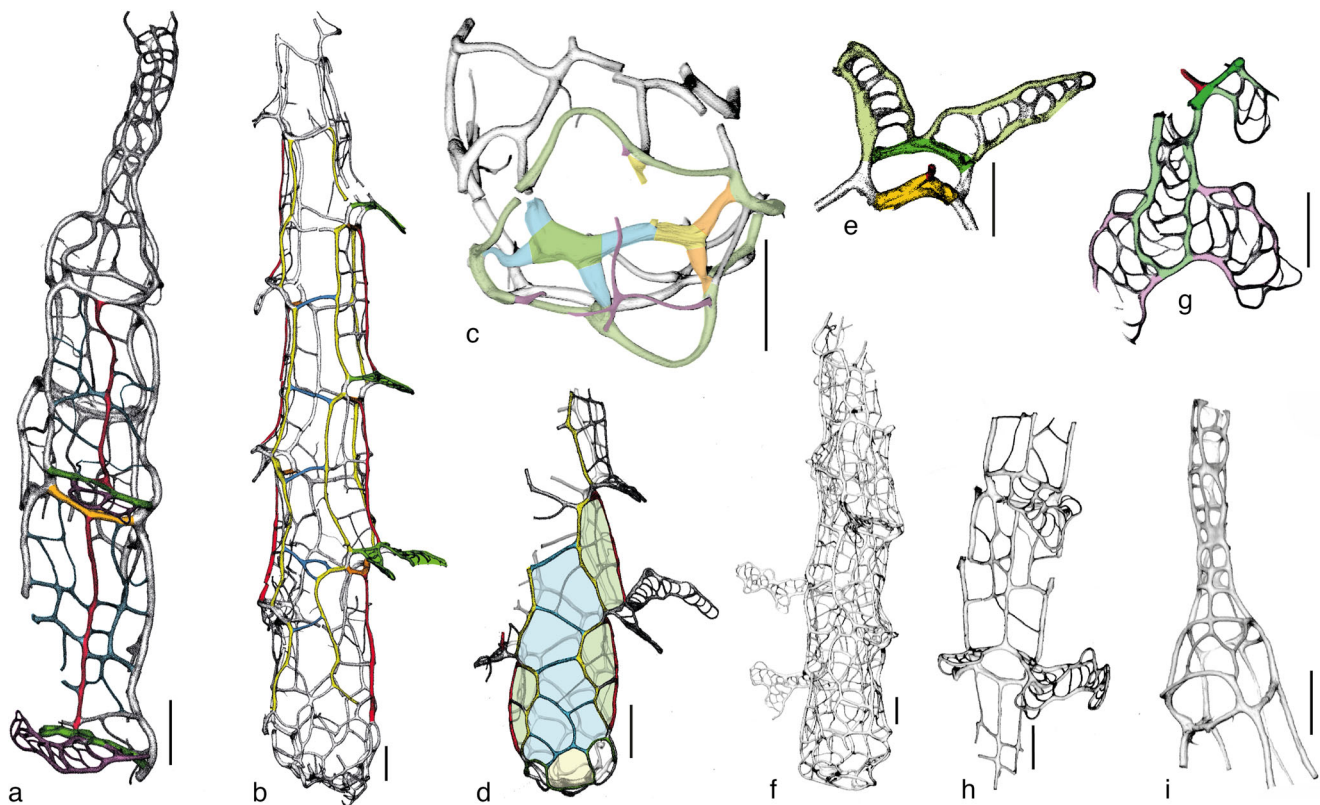
*balticus*, but develop more complexly and grow larger. They are quite variable in shape, from paired simple, but long, distally narrowing extensions with several meshes (Figs. 6e and 7h) to irregularly branched extensions or processes (Fig. 7k), that appear to be paired with relatively simple and smaller ones (Figs. 6g and 7i, j). The outer rims of the extensions are generally thicker than the more variable internal ones. These developments are identical to the ones found in *Neogothograptus alatiformis*, in which, however, remains of the membranes are present in many specimens (see Lenz and Kozłowska-Dawidziuk 2004, pl. 11). Genicular processes are also present at the rim of the pre-thecal ventral orifices in *Neogothograptus alatiformis*, but have not been found in *Neogothograptus ornatus*. The processes in *Neogothograptus alatiformis* are quite spectacular, starting as single outgrowths from the geniculum of the second thecal pair, branching distally into two large sails (Lenz and Kozłowska-Dawidziuk 2004, pl. 11, fig. 2). Interestingly, the processes at the pre-thecal ventral orifices are paired, but otherwise similar in shape (Fig. 9i–j).

**The outer ancora:** The outer ancora is a feature at the proximal end of the retiolitines, covering the ancora umbrella on the outside. The development of an outer ancora (Fig. 8) can be seen in a number of retiolitines, but its exact construction is still unknown. It is clearly a late stage development and differs from the ancora umbrella in the orientation of the seams. The ancora

umbrella invariably bears seams on the outside, while the outer ancora has its seams on the inside (Lenz et al. 2018, p. 13). Lenz et al. (2018) suggested the presence of an outer ancora in *Spinograptus* and *Sokolovograptus*, but this has not been verified. The earliest taxa with an outer ancora appear to be species of the genus *Gothograptus* and *Eisenackograptus* in the pre-lundgreni extinction interval and an outer ancora is also present in the post-lundgreni extinction interval in *Holoretiolites* and *Neogothograptus*. An outer ancora may also be present in *Sagenograptoides* (Lenz and Kozłowska, 2010), but has never been described or illustrated in any detail. Its construction needs to be investigated as well as the possible phylogenetic interpretation to determine the possible homology of this feature.

Kozłowska et al. (2019, p. 451; figs. 4F and 12D) indicated that an outer ancora umbrella is rarely developed in *Gothograptus nassa*. However, the figure explanation to their fig. 4F indicates that the specimen is the holotype of *Gothograptus kozłowskii* (see Fig. 8b). Thus, an outer ancora is not verified for *Gothograptus nassa*. Kozłowska et al. (2019, fig. 4) included a number of quite robust specimens in *Gothograptus nassa*, showing extreme development of the ancora umbrella ribs and a distinct reticulated metasicula (see also Bates and Kirk 1978, pl. 2.1). These features are not seen in any other published material of *Gothograptus nassa* and the identification may be questionable. A minor development of an outer ancora is visible in one of these specimens (Kozłowska et al. 2019, fig. 4E).





**Fig. 6** The astogeny of *Neogothograptus ornatus*, Hiddensee, NE Germany. **a** MB.G. 1079/02, distal fragment with appendix. **b** MB.G. 1079/03, incomplete longer, but immature specimen with incomplete development of the reticulum. **c** MB.G. 1079/21, proximal end showing outer ancora (in pink). **d** MB.G. 1079/04 proximal fragment, lateral view, showing mature genicular extensions, but immature reticulum. **e** MB.G.

1079/23, paired genicular processes. **f** MB.G. 1079/13, robust, distally incomplete specimen with extensive genicular processes and relatively dense reticulum. **g** MB.G. 1079/22, fragment of complex, asymmetrically developed genicular processes. **h** MB.G. 1079/16 fragment showing asymmetry of genicular processes. **i** MB.G. 1079/19, fragment with appendix. Scale bars are 200 µm

Kozłowska et al. (2019, p. 440) illustrated specimens of *Gothograptus kozłowskii* Kozłowska-Dawidziuk, 1990, *Gothograptus domeyki* Kozłowska et al., 2019 and *Gothograptus velo* (Kozłowska et al., 2019, fig. 22C) in which the outer ancora is visible. An outer ancora is also present in *Gothograptus storchi* Lenz and Kozłowska, 2006, but details have not been described or illustrated. The presence of an outer ancora in *Eisenackograptus* (Lenz et al. 2018) needs to be proven.

The outer ancora in *Holoretiolites*, *Neogothograptus* and *Baculograptus* may consist of a few lists or a complex meshwork covering the ancora umbrella completely (Lenz et al. 2018, fig. 14). Kozłowska-Dawidziuk (1995, fig. 15H, 30) indicated an outer ancora in *Holoretiolites erraticus*, but the feature is based on very few lists. Otherwise there is no evidence of an outer ancora in the genus *Holoretiolites*.

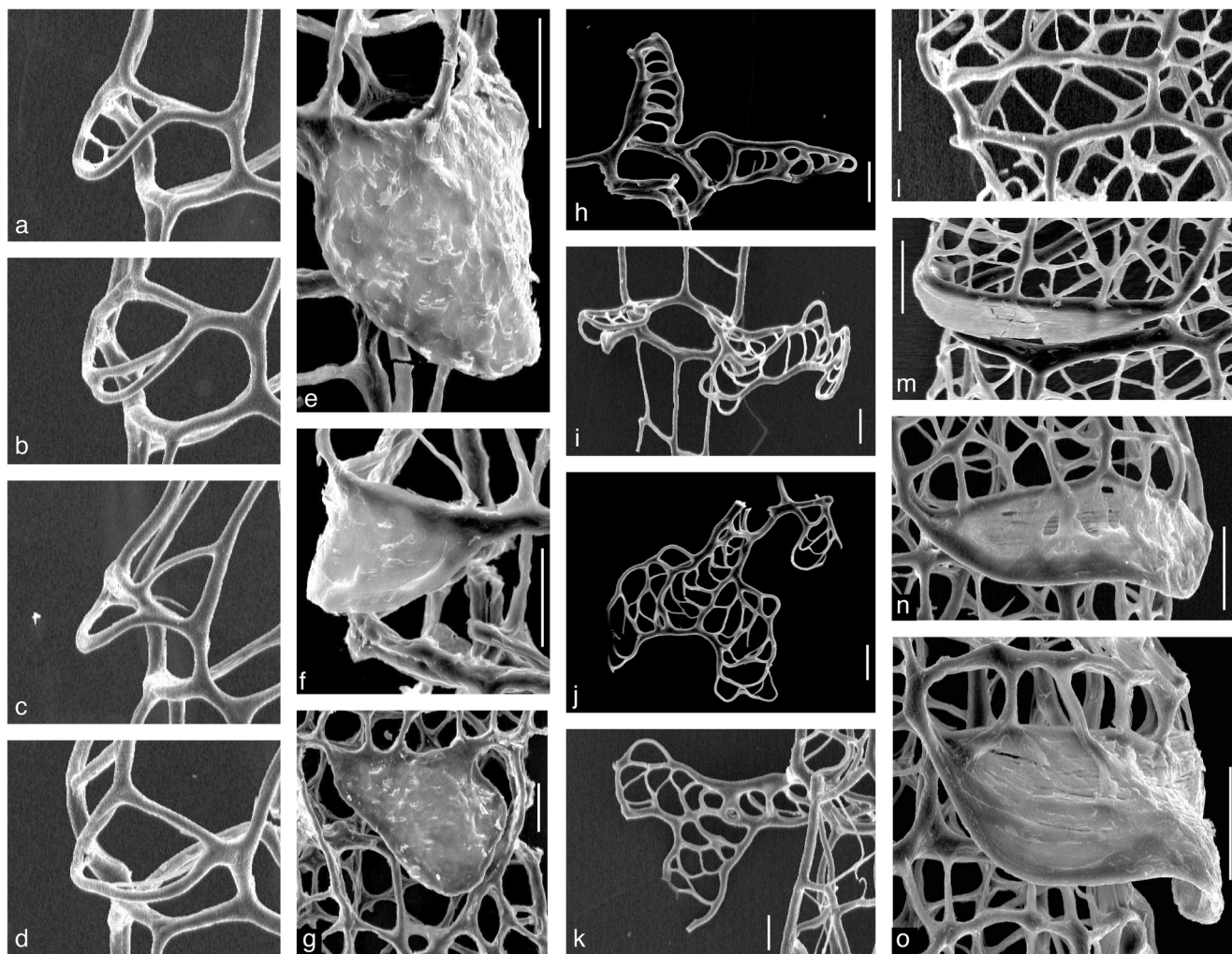
Bates et al. (2005, fig. 6h) illustrated the proximal end as *Neogothograptus purus* with an extensive outer ancora, even though the species barely shows any reticulum. The identity of the specimen remains uncertain, as the complete specimen is not illustrated. Specimens of *Neogothograptus purus* with an outer ancora have never been illustrated and the species is thus unlikely to bear an outer ancora. In *Neogothograptus balticus*

an outer ancora covers with its coarse mesh the whole ancora umbrella (Fig. 8d, e, g). The outer ancora in this species starts initially with lists crossing from the obverse to the reverse side of the tubarium (Fig. 8c-e). These lists then form additional connections to the ancora rim and eventually form a meshwork around the ancora rim, probably growing upwards to cover the ventral and lateral proximal orifices. The strongest development of the outer ancora is initially on the th1<sup>1</sup> side of the colony (Fig. 8c), the side at which the ancora umbrella has only two generations of ribs. The th1<sup>2</sup> side of the ancora usually bears three to four generations of ribs (see Fig. 3c).

*Neogothograptus ornatus* can develop an outer ancora, but the extent is known only from one specimen in the form of thin lists (Fig. 5c). *Neogothograptus eximinassa* shows an extensive outer ancora (see Maletz 2008) that is difficult to outline as it covers the proximal orifices and grades into the ancora sleeve meshes.

### Evolutionary changes

The genera discussed here represent the latest development of the Retiolitinae and clear trends are visible during the



**Fig. 7** Genicular processes in retiolitines. **a–d** *Neogothograptus balticus*, MB.G. 1082/04, all processes from one specimen. **e–g** *Gothograptus auriculatus*. **e** MB.G. 1145, JM 74/10. **f** MB.G. 1145, JM 74/11. **g** MB.G. 1145, JM 75/07. **h–k** *Neogothograptus ornatus*. **h** MB.G. 1079/23. **i** MB.G. 1079/16. **j** MB.G. 1079/22. **k** MB.G. 1079/13. **l–o**

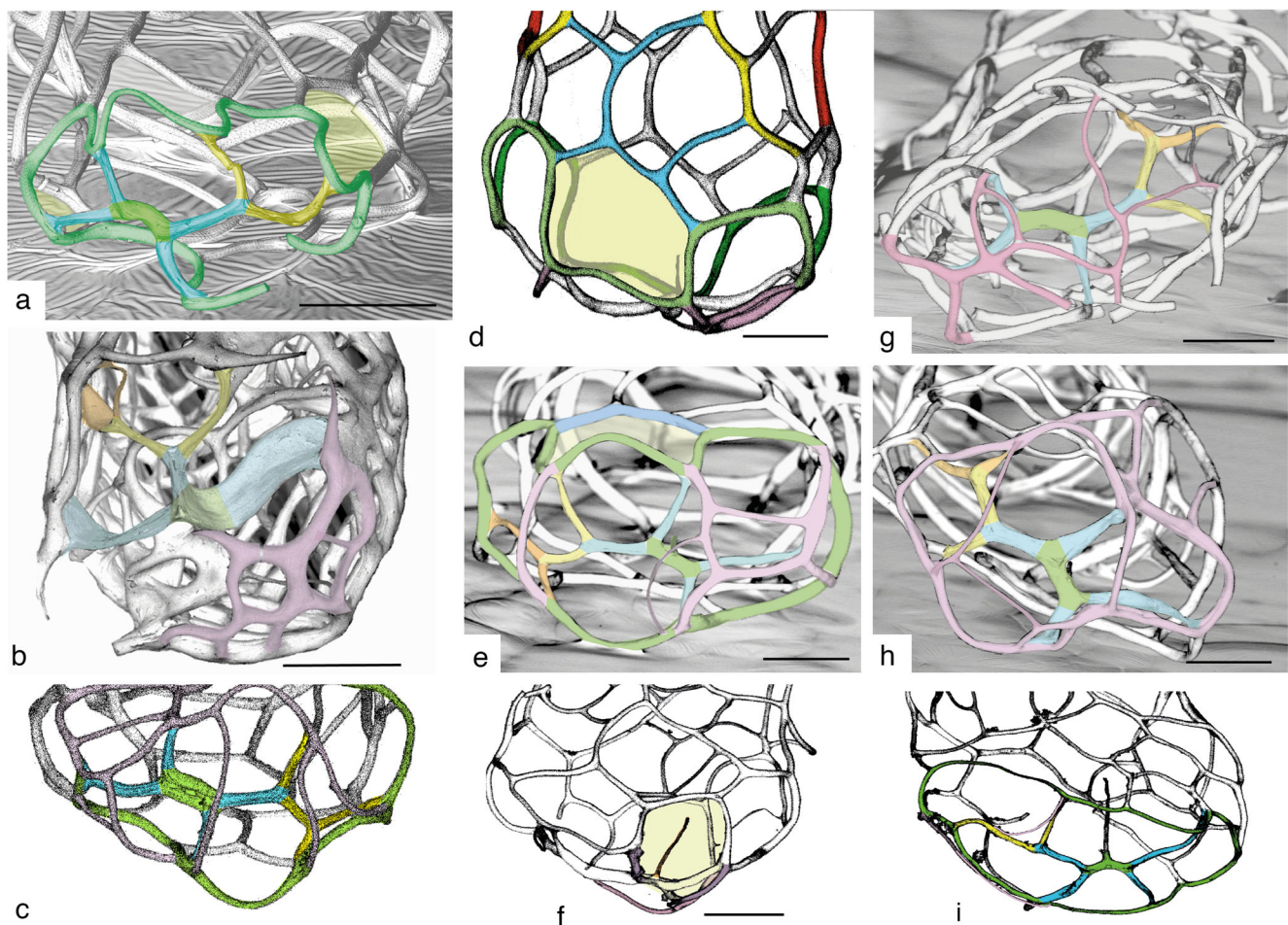
*Neogothograptus eximinassa*. **l** MB.G. 1123/07, th<sup>1</sup> orifice. **m** MB.G. 1123/07, th<sup>2</sup> orifice. **n** MB.G. 1123/13, th<sup>4</sup> orifice. **o** MB.G. 1123/01, third thecal orifice on right side of distal tubarium fragment. Scale bars are 100  $\mu$ m

evolution of this group. Certain aspects of the general evolutionary changes for the latest retiolitines were discussed by Kozłowska-Daidziuk (1995) and Kozłowska (2015). Most taxa possess a limited growth shown in the development of the appendix, a symplesiomorphic character for the group, already present in *Eisenackograptus* from the pre Lundgreni extinction interval (Maletz 2022, fig. 8) and found in all *Neogothograptus* and *Holoretiolites* species. However, the apparently youngest retiolitines of the genera *Semiplectograptus* and *Plectodinemagraptus* are known only from very few fragmented specimens and a finite growth cannot be demonstrated for these forms as an appendix is unknown.

**Reticulum:** Early *Neogothograptus reticulatus* possesses a dense reticulum. The reticulum is completely lost in *N. purus* and *N. melchini*, but a variable development of

the reticulum can still be seen in the youngest known member of the genus, *N. romani* (see Fig. 5). The genus *Holoretiolites* has lost the reticulum completely, except for *H. erraticus*, in which a moderate reticulum may still be present (Fig. 1d).

**Genicular processes:** The development of genicular processes in the genus *Neogothograptus* ranges from microfusellar processes to reticular and even complexly branching ones. A reduction and loss is first found in *N. purus*, but can also be seen in *N. thorsteinssoni* and in the younger species *N. melchini* and *N. romani* (Fig. 5). None of the *Holoretiolites* species show any evidence of genicular processes, thus indicating a further reduction of their tubarium construction. Genicular processes have also not been recognised in the fragmentary material of *Semiplectograptus* and *Plectodinemagraptus*,



**Fig. 8** The outer ancora (in pink or purple). **a** *Neogothograptus romani* showing ancora umbrella without outer ancora, SMF 75846, JM 118/05 (complete specimen in Fig. 9i). **b** *Gothograptus kozłowskii*, after Kozłowska et al. (2019, fig. 18C). **c** *Neogothograptus purus* (Bates et al. 2005, fig. 6H). **d–e, g–i** *Neogothograptus balticus* with outer ancora. **d–e**

MB.G. 1082/02 in lateral (**d**) and apertural (**e**) views. **g** MB.G. 1082/07 (complete specimen in Fig. 9b). **h** MB.G. 1082/04 (complete specimen in Fig. 9d). **i** MB.G. 1082/03 (complete specimen in Fig. 9c). **f** *Holoretiolites erraticus*, MB.G. 1085/01, minor development of outer ancora (complete specimen in Fig. 10i). Scale bars are 200  $\mu\text{m}$

the youngest known retiolitines from the *Saetograptus leintwardinensis* Biozone.

**Clathrium reduction:** Initially, the clathrium of the retiolitines consists of the meshwork of the thecal part and the ancora part of the tubarium (Maletz 2022, fig. 4). In *Neogothograptus*, *Holoretiolites* and related taxa, thecal clathrium is only found on the ventral sides of the tubarium in the lateral apertural lists, the mid-ventral lists, the thecal lips and geniculum. The clathrium of the ancora sleeve is found in the variously developed parietal lists. While the remaining clathrial lists of the tubarium are completely preserved in nearly all *Neogothograptus* and *Holoretiolites* species (see Fig. 2a, b, e), including a fully developed ancora umbrella, a reduction of the mid-ventral lists may be recognised in *H. atrabecularis* (Fig. 1a, b) and in *N. melchini* (Fig. 5i) as the first step in the reduction of the clathrial lists. A reduction and modification of the clathrium can be seen in *Holoretiolites*, where the parietal lists disappear and the lateral apertural lists of the  $th1^1$  and  $th1^2$

sides merge and form a lateral zigzag lateral apertural list indicating the loss of the ancora sleeve membranes. This development connects *Holoretiolites* with the genera *Semiplectograptus* and *Plectodinemagraptus*. *Semiplectograptus* has lost the last parietal lists (Fig. 1f), but bear a full succession of the lateral zigzag lists with connecting lists to the thecal orifices. In *Plectodinemagraptus* (Fig. 1i), also the zigzag lateral apertural lists are lost and the two stipes appear to be unconnected at least in the few available fragments. The only connection between the thecal orifices can be seen in the mid-ventral lists.

**Pleural lists and lateral apertural lists:** The presence of pleural lists associated with the parietal lists invariably demonstrates the presence of the ancora sleeve, as they show the free edge of the ancora sleeve at the thecal orifices (see Maletz 2022). Short pleural lists are present at the sides of the thecal orifices in *Neogothograptus* (Fig. 2c). These are lost in *Holoretiolites*, where horizontal lists connect to the sides of

the thecal lips and the arch of the genicular lobe (Fig. 2d). The same development is present in *Semiplectograptus* (Fig. 1f–h) and can be seen in *Plectodinemagraptus* (Fig. 1i). *Semiplectograptus*, however, shows also the lateral zigzag thecal lists, that are lost in *Plectodinemagraptus*. If this development is not just a preservational aspect, the loss of the zigzag lateral apertural lists is the last stage in the reduction of the retiolitine tubarium.

### Preservation and identification

The preservation is an important aspect to recognise and identify graptolites properly. Maletz (2020) discussed the preservational aspects of graptolite faunas in connection with geological modifications (diagenesis, metamorphism, tectonics, etc.), showing that the organic material of the graptolites leads to distinct modes of preservation not found in mineralized fossils (e.g. shells, bones). Maletz (2020, fig. 13) demonstrated the variable preservation of (?) *Kiaerograptus supremus* Lindholm, 1991 in various modes and under variable geological conditions. Most of these modes do not concern the work with retiolitine graptolites, as these are generally isolated with the help of acetic or formic acid from limestones. As graptolites would be destroyed through thermal heating and tectonic deformation and would not be isolatable any more, only limestones with a negligible thermal history can be used to gain this type of material. Surprisingly, however, it is possible to chemically isolate graptolites from the Silurian limestones of Dalarna, central Sweden (e.g. Hutt et al. 1970; Loydell and Maletz 2004, 2009), that have endured an asteroid impact (Maletz 2021).

The chemical isolation of retiolitine graptolites, even though done very carefully, usually results of largely fragmented material. Larger specimens (see *Pseudoretiolites perlatus* in Melchin et al. 2017, fig. 8.1) are rare and difficult to handle, as they are usually quite fragile. It also appears that juvenile specimens are rarely found associated with larger and more mature material, but this could be due to the delicate nature of the material and the difficulty in handling small specimens. Thus, generally, only few specimens are available or are illustrated in the description of new taxa. A good example is the description of *Sagenograptoides arctos* (Lenz and Kozłowska-Dawidziuk 2001; Lenz and Kozłowska 2010) based on seven small specimens that might represent a species originally growing to a much larger size. All specimens have a maximum of three thecal pairs and are broken distally. There are no juveniles available and nothing is known about the final size of this species.

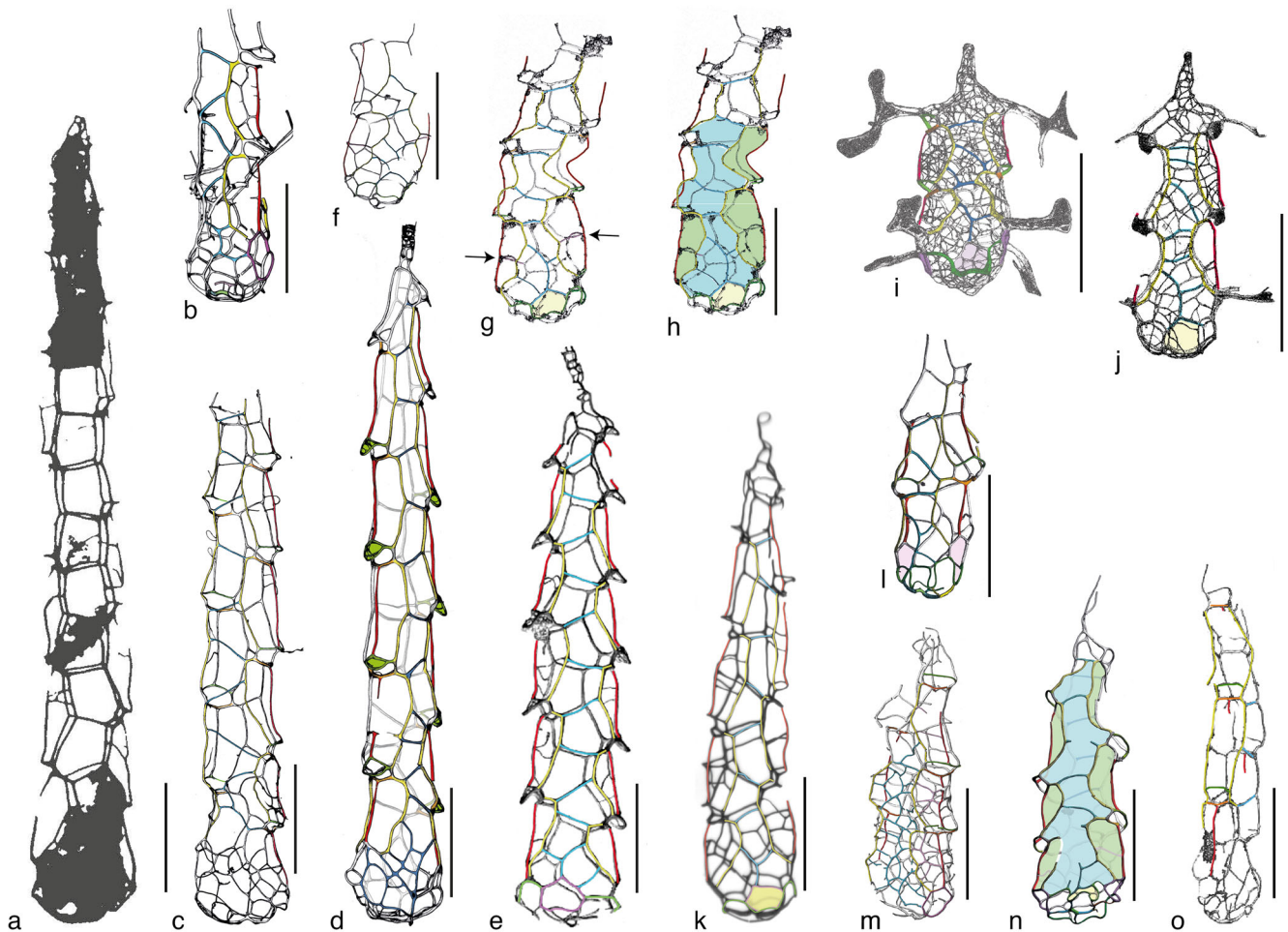
The paper by Reichstein (1962) is one of the few demonstrating the intraspecific and preservational variation of a single retiolitine species, *Holoretiolites simplex*. Reichstein (1962, pl. 2) illustrated 12 specimens from the sample in

oblique to lateral view. All show four thecal orifices and the third thecal pair is considerably reduced in size. It does not bear orifices and the colony ends in the appendix. A short nema is visible in some specimens and the ancora umbrella may be incompletely preserved. The collection shows a considerable variation in width and length, even though it has to be assumed that all specimens belong to a single species. Specimens shown in oblique or ventral view are distinctly more slender than perfectly lateral views (Reichstein 1962, pl. 2). The material does not show any differences to the specimens illustrated here (Fig. 11e–h).

Incomplete or immature specimens of *Holoretiolites simplex* bearing only a single thecal pair could easily be misidentified with a number of other *Holoretiolites* species like *Holoretiolites mancki* or *Holoretiolites erraticus*. The same can be seen with juveniles of the genus *Neogothograptus*. Juveniles without the presence of genicular processes or a reticulum may be impossible to differentiate. A good example is a sample MB.G. 1090 (Jaeger sample 351) from Sassnitz, Rügen Island, NE Germany. The sample includes a number of *Spinograptus spinosus* specimens (illustrated in Maletz 2008) and two specimens of *Neogothograptus* sp. (Fig. 9f–h). The larger specimen is parallel-sided and bears three thecal pairs and the remains of a fourth one. There are no reticular lists, except for a horizontal one crossing the ventral thecal membranes of the first thecal pair at about the middle (arrow in Fig. 9g). The specimen could be identified as *Neogothograptus balticus*, *Neogothograptus eximianassa*, *Neogothograptus purus* or even *Neogothograptus romani* and additional growth stages would be needed to provide a proper identification. The record of proximal ends, juveniles or incomplete specimens, thus, would not allow a definite identification of many retiolitines. Especially juvenile specimens of many retiolitines can only be identified to species level by the presence of further growth stages and mature material. The astogeny of the species changes considerably the appearance of the tubarium and most species described from fragmented material are in need of revision.

### Material and methods

A few remarks are here given to explain the style of retiolitine illustrations used herein. The original SEM photos of most specimens were modified and adjusted digitally in Adobe Photoshop CS6 and Illustrator CS6. Photos were often inverted to get rid of the black or dark background and to make the meshwork of the retiolitines more readily visible in contrast to a white background. This method has been used frequently for retiolitines in the past and appears to be quite useful for the interpretation of the tubarium construction of these complex forms (cf., Kozłowska et al. 2009, 2019; Kozłowska 2016). Colour was applied to mark important characters, to identify, interpret and



**Fig. 9** *Neogothograptus* comparison. **a** *Neogothograptus purus*, holotype (after Kozłowska-Dawidziuk 1995, fig. 27F). **b–e** *Neogothograptus balticus*. **b** MB.G. 1082/07, proximal fragment. **c** MB.G. 1082/03, immature specimen with five thecal pairs. **d** MB.G. 1082/04, complete specimen with six+ thecal pairs. **e** Robust specimen from Poland, ?glacial erratic boulder (after Kozłowska-Dawidziuk 2004 fig. 5M). **f–h** *Neogothograptus* sp. indet, MB.G. 1090. **f** juvenile, MB.G. 1090/11. **g–h** MB.G. 1090/10, immature specimen with three thecal pairs, (**h**) showing ancora sleeve and thecal membranes in colour. **i**

*Neogothograptus alatiformis*, morph A, holotype (after Kozłowska, 2018a, Folio 3.3). **j** *Neogothograptus alatiformis*, morph B (after Lenz and Kozłowska-Dawidziuk 2004, pl. 14, fig. 9). **k–n** *Neogothograptus romani*. **k** MB.G. 1117/02, the most complete specimen, five thecal pairs and appendix (after Maletz 2008, fig. 13C). **l** SMF 75846, JM 118/05. **m** SMF 75847, JM 118/04. **n** SMF 75845, JM 118/03. **o** *Neogothograptus melchini*, paratype (after Lenz and Kozłowska-Dawidziuk 2004, pl. 17, fig. 11). All scale bars are 1 mm

compare the list construction of the individual taxa (cf., Kozłowska 2016; Maletz 2022). Only in a few cases original light photos were used for the interpretation (cf. Fig. 2f; specimen subsequently mounted for SEM work; see Fig. 11a).

Illustrated specimens from the Jaeger collection are preserved in the type collection at the Museum für Naturkunde, Berlin, Germany (MB.G.) together with the non-illustrated material preserved in glycerin. Additional material is curated at the Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (SMF). Further material is preserved at the Geological Survey of Canada (GSC) in Ottawa, Canada. Specimens marked ZPAL G. are preserved in the collection at the Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

## Systematic palaeontology

**Taxonomy and terminology:** The taxonomy of the Retiolitidae follows the revision of the Treatise (Bulman 1955, 1970) by Lenz et al. (2018). Genus diagnoses have been corrected and revised for consistency to the style and content in which they will appear in the book version of the ‘Graptolite Treatise’ (Maletz et al. 2023, in press). The most important morphological terms to describe retiolitines are revised in Bates et al. (2005) and in Lenz et al. (2018, 2022). Bates and Kirk (1992, 1997) and Kozłowska-Dawidziuk (1990, 1995) may be consulted for additional information.

Order Graptoloidea Lapworth, 1873

Suborder Axonophora Frech, 1897

Infraorder Neograptina Štorch et al., 2011  
 Superfamily Retiolitoidea Lapworth, 1873  
 Family Retiolitidae Lapworth, 1873  
 Subfamily Retiolitinae Lapworth, 1873

Genus *Neogothograptus* Kozłowska-Dawidziuk, 1995

**Type species:** *Neogothograptus purus* Kozłowska-Dawidziuk, 1995 (OD), Baltic erratic boulder, Jarosławiec, N. Poland. *Lobograptus scanicus* Biozone, Gorstian, Ludlow, Silurian.

**Species:** *Retiolites balticus* Eisenack 1951; *Neogothograptus purus* Kozłowska-Dawidziuk, 1995; *Neogothograptus romani* Kozłowska-Dawidziuk, 1995; *Neogothograptus alatiformis* Lenz and Kozłowska-Dawidziuk, 2004; *Neogothograptus melchini* Lenz and Kozłowska-Dawidziuk, 2004; *Neogothograptus purus labiatus* Lenz and Kozłowska-Dawidziuk, 2004; *Neogothograptus thorsteinssoni* Lenz and Kozłowska-Dawidziuk, 2004; *Neogothograptus eximinassa* Maletz 2008; *Neogothograptus ornatus* Maletz 2008; *Neogothograptus reticulatus* Kozłowska et al., 2009

**Diagnosis:** Finite tubarium; strongly reduced distalmost thecal pair without orifices opening into appendix; shallow, asymmetrical ancora umbrella with six or seven meshes and strongly undulating rim; outer ancora may be present; nema free; ventral sides with thecal lips, genicular lists, short pleural lists, long lateral apertural lists, and mid-ventral lists; genicular processes in some, rarely also on proximal ventral orifices; parietal lists on ancora sleeve walls almost horizontal; reticulum dense to absent; ancora sleeve lists with seams facing inward; bandages with pustules (revised from Lenz et al. 2018).

**Remarks:** The presence of an outer ancora was not mentioned by Lenz et al. (2018), but is here verified for several species. The number of meshes in the ancora umbrella is more variable and may range from five to seven, probably even eight, but is most commonly six.

*Neogothograptus purus* Kozłowska-Dawidziuk, 1995 (Figs. 5e, 9a)

1995 *Neogothograptus purus* sp. n. – Kozłowska-Dawidziuk, p. 303, figs. 6, 9C (reconstruction based on specimen in Fig. 6, identified as *Neogothograptus* sp.), 27F–G.

2004 *Neogothograptus purus purus* Kozłowska-Dawidziuk – Lenz and Kozłowska-Dawidziuk, textfig. 15 (no description; ZPAL G. 35/1, probably from Poland; see Lenz and Kozłowska-Dawidziuk, 2004, p. 18).

2005 *Neogothograptus purus* Kozłowska-Dawidziuk – Bates et al., fig. 6H (ZPAL G. 37/5, Baltic erratic boulder 46, Jarosławiec, Poland).

2009 *Neogothograptus purus* Kozłowska-Dawidziuk – Kozłowska et al., p. 431, fig. 2 (specimen also in Lenz and Kozłowska-Dawidziuk, 2004, text-fig. 15).

2013 *Neogothograptus purus* Kozłowska-Dawidziuk – Dobrowolska, fig. 10C (ZPAL G. 48/24; locality not given) (no description, robust, but incompletely preserved ancora umbrella, six meshes).

?2013 *Neogothograptus purus purus* Kozłowska-Dawidziuk – Kozłowska and Radzevičius, p. 20, fig. 8 (Virbalis-5 borehole, Lithuania, at 983.0 m, *Neodiversograptus nilssoni* Biozone; immature specimen, not identifiable to species level).

**Type specimen:** The holotype is ZPAL G. XVI/1341, boulder 149, Jarosławiec (Fig. 9a). The only additionally illustrated specimen is ZPAL G. XVI/1353, boulder 22 from Jarosławiec is from a different boulder and should not be regarded as a paratype.

**Tubarium characteristics:** Simple *Neogothograptus* species; length reaches up to eight thecal pairs; appendix unknown, probably due to incomplete preservation of material; outer ancora may be present; no reticulum(?); no genicular processes.

**Astogeny:** The few available specimens do not allow to understand the astogeny, but longer specimens probably develop a few reticular lists and thickened genicular lists, but apparently no genicular processes.

**Remarks:** There are only two specimens illustrated in the original description and the intraspecific variation remains unknown. Specimens with up to at least eight thecal pairs and specimens with only four thecal pairs were mentioned, indicating high intraspecific variation in size. Very little detail has been described from the type material. These specimens could easily be immature specimens of *Neogothograptus balticus*. A distally incomplete specimen with four thecal pairs (Lenz and Kozłowska-Dawidziuk 2004, fig. 15) shows a few reticular lists and apparently an apertural loop on the third theca of the left side that may be indication of the subsequent growth of genicular processes. The origin of this specimen is unknown.

*Neogothograptus purus labiatus* Lenz and Kozłowska-Dawidziuk, 2004

(Fig. 5g)

1993 *Holoretiolites mancki* Eisenack – Lenz, p. 20, pl. 12, figs. 1–5, 8–12.

2004 *Neogothograptus purus labiatus* n. subsp. – Lenz and Kozłowska-Dawidziuk, p. 17, pl. 3, figs. 1–12, pl. 4, figs. 1–11, pl. 5, figs. 1–9, pl. 6, figs. 1–10, pl. 7, figs. 3, 4, 6, 9, 10, ?pl. 26, fig. 7.

**Type specimen:** The holotype GSC 125964, loc. BH-57.6 m (Lenz and Kozłowska-Dawidziuk 2004, pl. 3, figs. 1, 3–12). The parallel-sided tubarium of the specimen has at least six thecal pairs (broken distally or immature) and does not show indications of an appendix.

**Tubarium characteristics.** Simple *Neogothograptus* species; three to six thecal pairs; appendix unknown, probably due to incomplete preservation of material; outer ancora may be present; labiae on genicular lists often characteristic; outer ancora represented by few lists; few reticular lists.

**Astogeny.** The known examples are largely mature specimens. Clathrial lists are delicate in some specimens in which no reticulum and outer ancora is present; robust in others with increased reticulum and some outer ancora lists. The size of the tubarium appears to vary considerably from three thecal pairs in mature specimens to six or seven thecal pairs in immature specimens.

**Remarks.** This taxon could easily represent mature to gerontic specimens of *Neogothograptus purus* and may be synonymised with it. Even *Neogothograptus balticus* is very similar and a differentiation may be questionable. A new investigation should be made to separate or synonymise these taxa.

*Neogothograptus alatiformis* Lenz and Kozłowska-Dawidziuk, 2004 (Figs. 5f, 9i, j)

?1997 *Agastograptus* sp. 2 – Zhang and Lenz, p. 1226, fig. 3C (Yunnan, China).

2004 *Neogothograptus alatiformis* n. sp. (morphotype A) – Lenz and Kozłowska-Dawidziuk, p. 18, pl. 11, figs. 1-3; pl. 12, figs. 1-6; pl. 3, figs. 1-5.

2004 *Neogothograptus alatiformis* n. sp. (morphotype B) – Lenz and Kozłowska-Dawidziuk, p. 18, pl. 14, figs. 1-10; pl. 15, figs. 1-10; pl. 16, figs. 1-10.

?2004 *Neogothograptus* cf. *alatiformis* n. sp. – Lenz and Kozłowska-Dawidziuk, fig. 17 (Yunnan, China).

?2009 *Neogothograptus alatiformis* Lenz and Kozłowska-Dawidziuk – Kozłowska et al., fig. 2, fig. 9 (glacial boulder from Jarosławiec, Poland, specifically indeterminate small fragments)

2013 *Neogothograptus alatiformis* Lenz and Kozłowska-Dawidziuk – Kozłowska and Radzevičius, p. 20, fig. 9 (Siupyliai-69 drill core, Lithuania at 958.4 m; material from 967.4 m not illustrated)

2018a *Neogothograptus alatiformis* Lenz and Kozłowska-Dawidziuk. – Kozłowska, Atlas of Graptolite Type Specimens 3.3. (holotype, inverted SEM)

**Type specimen:** The holotype is GSC 125988 (Lenz and Kozłowska-Dawidziuk 2004, pl. 11, figs. 1-3), representing morphotype A (Fig. 9i). Morphotype B differs in the presence and construction of the genicular processes and a more slender, less reticulate tubarium (Fig. 9j).

**Tubarium characteristics:** Small tubarium with three thecal pairs; construction of ancora unclear; extensive genicular processes on thecal orifices and sometimes on ventral pre-thecal

orifices; parietal lists fairly irregular; reticulum dense in mature specimens; massive outer ancora and overgrowth of lateral and ventral proximal orifices (details unknown).

**Astogeny:** All illustrated specimens appear to show a fully grown tubarium with three thecal pairs and a short appendix. The density of the reticulum increases with maturity and also the proximal lateral and ventral orifices are overgrown. An extensive outer ancora may be present, but has not been described or illustrated in detail (see Kozłowska and Radzevičius 2013, fig. 9D).

**Remarks:** Lenz and Kozłowska-Dawidziuk (2004) discussed two morphotypes of this species. Their relationship is unclear. As morphotype B invariably looks much more slender and bears less reticulum in apparently mature specimens, it may represent a different species. It bears distinct paired reticular processes or hoods on the four thecal orifices (Fig. 9j) not found in morphotype A. Thus, it is unlikely to represent immature specimens of morphotype A.

*Neogothograptus balticus* (Eisenack, 1951) (Figs. 2a, 5d, 7a-d, 9b-e)

1951 *Retiolites balticus* sp. nov. – Eisenack, p. 134, pl. 22, figs. 4-8, pl. 24 fig. 5. Exact age and faunal association unknown.

1952 *Holoretiolites (Balticograptus) balticus* (Eisenack) – Bouček and Münch: 17, fig. 5b [copy of Eisenack 1951, pl. 22 fig. 4].

? 1995 *Neogothograptus* cf. *balticus* (Eisenack). – Kozłowska-Dawidziuk, p. 304, fig. 6, 27i.

pars 2001 *Neogothograptus balticus* (Eisenack) – Kozłowska-Dawidziuk and Lenz, fig. 3.17 (boulder 49, Jarosławiec, ZPAL G 27/2) [non fig. 3.16 = *Neogothograptus thorsteinsoni*] (no description).

2002 *Neogothograptus balticus* (Eisenack) – Kozłowska-Dawidziuk, p. 465, figs. 3b, e, f. Glacial boulder 46, Jarosławiec, Poland (ZPAL G. 27/4).

2004 *Neogothograptus balticus* (Eisenack) – Kozłowska-Dawidziuk, fig. 5M (no description).

2008 *Neogothograptus balticus* (Eisenack) – Maletz, p. 294, Figs. 6A–C, 7A–K. Glacial boulder.

2013 *Neogothograptus balticus* (Eisenack) – Kozłowska and Radzevičius, p. 20, fig. 7. (Lithuania, drill core at 968.1 m).

2015 *Neogothograptus balticus* (Eisenack) – Kozłowska, fig. 1E, 2E (no description).

2016 *Neogothograptus balticus* (Eisenack) – Štorch et al., fig. 3D, 4C (shale, mature specimen, Czech Republic).

**Type specimen:** As the originally planned ‘Typus’ (holotype: Eisenack 1951, pl. 24, fig. 5), the only complete specimen illustrated, was considered lost during the war and prior to the publication of the paper, Eisenack (1951, p. 129; explanation for pl. 24) designated the specimen on his pl.

22, fig. 4 (specimen 181, Nr. 6) as the ‘Typus-Exemplar’. This specimen (Fig. 5d) should therefore be regarded as the holotype. The specimen is distally incomplete, but consists of at least four thecal pairs and represents the proximal fragment of a mature specimen with robust clathrium and reticular lists.

**Tubarium characteristics:** Medium sized *Neogothograptus* with six to nine thecal pairs, slowly narrowing distally; ancora with five to six meshes; short appendix formed by three or four vertical lists; genicular lists bear sometimes extensive, reticular processes with thickened rims in mature specimens; lateral sides with slightly oblique parietal lists; outer ancora in mature specimens; moderate development of reticulum.

**Astogeny:** It appears that the colony is fully developed in this form before the genicular hoods are formed (Fig. 9c). Thus, juvenile specimens may easily be misinterpreted as another species when found separately from gerontic specimens (Maletz 2008, p. 296). Insert of reticular lists at various stages visible. First reticular lists can be seen in juveniles with only one thecal pair. Here horizontal lists cross the ventral thecal membranes.

A considerable outer ancora is visible in a few mature specimens. Its origin and detailed construction are impossible to interpret with the few specimens at hand. An outer ancora is, however, not visible in the robust specimen of Kozłowska and Radzevičius (2013, fig. 7A).

**Remarks:** A number of somewhat different populations are here referred to *Neogothograptus balticus*. All can be united by the development of reticulate genicular processes formed from successively formed thickened lobes in mature specimens. The development of reticular lists is quite variable, ranging from none to dense. The type specimen has five thecal pairs, of which the distalmost one is incomplete, as the specimen is broken. The most complete specimen of Eisenack (1951, pl. 24, fig. 5) is not preserved, but consisted of eight thecal pairs and a short appendix. It also had fairly extensive genicular processes. Maletz (2008) described material with six thecal pairs and minor development of reticulum, while the specimen of Štorch et al. (2016) has nine thecal pairs and a fairly dense reticulum. It also appears to have much longer and more complex genicular processes. Kozłowska-Dawidziuk (2002, 2004) illustrated a specimen with fairly robust clathrium and very scarce and slender reticular lists (Fig. 9e).

*Neogothograptus eximinassa* Maletz, 2008  
(Figs. 4a-h, 5b, 7l-o)

- 1991 *Retiolites (Gothograptus) eximinassa* – Jaeger, p. 304, fig. 1 [nomen nudum].  
 ?2001 *Neogothograptus cf. balticus* (Eisenack) - Kozłowska-Dawidziuk et al., p. 153, figs. 7.5, 7.9.  
 2008 *Neogothograptus eximinassa* n. sp. – Maletz, p. 299, Figs. 1 P, 5D-E, 8A-M, 9A-K (glacial boulder, Spandau/Berlin).

- 2009 *Neogothograptus eximinassa* Maletz – Kozłowska, fig. 2, 3A, B (holotype).  
 2015 *Neogothograptus eximinassa* Maletz – Kozłowska, fig. 1C (no description).  
 2016 *Neogothograptus eximinassa* Maletz – Štorch et al., figs. 3B, 4B (shale material), Czech Republic, common and widely found in section.  
 2019 *Neogothograptus eximinassa* Maletz – Manda et al., fig. 10A (no description; shale specimen). Kosov section, Czech Republic.

**Type specimen:** The holotype is MB.G. 1123/14 (Maletz 2008, p. 299), a specimen with seven thecal pairs and a moderately long appendix. The mature specimen shows a dense reticulum, also overgrowing the proximal orifices (Fig. 4g).

**Tubarium characteristics:** Tubarium with moderately long appendix and about six to seven thecal pairs; genicular hoods formed of microfusellar material present in mature specimens; mature tubaria with dense reticulum; outer ancora in mature specimens.

**Astogeny:** Maletz (2008) described the astogeny of the species as his collection included a number of juvenile and immature specimens. In specimens with about three to four thecal pairs (Fig. 4c), the clathrium is well developed, but there is no reticulum. A specimen with six thecal pairs bears a gradational development of the reticulum (Fig. 4f), but lacks the genicular hoods present in mature specimens. A distally incomplete specimen shows minor development of the genicular hoods on the second and third thecal orifice, but not on the first one (Maletz 2008, fig. 8J). The reticulum is relatively dense and indications of an outer ancora are present. The proximal orifices are covered by the reticulum in mature specimens. Considerable development of an outer ancora and covered proximal orifices may be seen in mature specimens (Fig. 4g-h).

**Remarks:** The species is known from a single sample providing immature and mature specimens (Maletz 2008) and one specimen from the Kosov quarry, Czech Republic (Štorch et al. 2016).

*Neogothograptus melchini* Lenz and Kozłowska-Dawidziuk, 2004  
(Figs. 5i, 9o)

- 1993 *Holoretiolites mancki* - Lenz, p. 20, pl. 12, figs. 6, 7.  
 2004 *Neogothograptus melchini* n. sp. - Lenz and Kozłowska-Dawidziuk, p. 19, pl. 17, figs. 1-13. type GSC 126003 (pl. 17, fig. 4). Samples MCM-91 (st. 112, 113), MCM-90 (st. 112), BH 86 m; SB-97, 1.5 m; SB-97, 2 m. There are quite a number of specimens (165) mentioned. The specimens are delicate and poorly preserved, partly flattened and distorted.



**Type specimen:** The holotype is GSC 126003 (Lenz and Kozłowska-Dawidziuk 2004, pl. 17, fig. 4), a poorly preserved specimen lacking the distal end (Fig. 5i).

**Tubarium characteristics:** Tubarium with three to four thecal pairs and possibly a short appendix (Lenz and Kozłowska-Dawidziuk 2004, pl. 17, fig. 7, 8); no reticulum; mid-ventral list reduced after the first thecal pair; outer ancora unknown.

**Astogeny:** Even though quite a number of specimens were available, there is no information on the astogeny due to the poor preservation of the small specimens and only two specimens of this species have been illustrated.

**Remarks:** The species is defined through the reduced mid-ventral lists and a complete lack of the reticulum. All specimens are highly fragmented and distorted, as they are quite delicate with thin lists. The oblique parietal lists are sometimes visible supporting the inclusion in *Neogothograptus* (Fig. 9o).

*Neogothograptus ornatus* Maletz, 2008

(Figs. 5c, 6a-i, 7h-k)

2008 *Neogothograptus ornatus* n. sp. – Maletz, figs. 1H, I (Hiddensee, Rügen), 3A, 5A-C, 10A-M, 11A-I (glacial boulder, Spandau/Berlin).

2013 *Neogothograptus ornatus* Maletz – Dobrowolska, fig. 6A (ZPAL G. 48/8), 10B (ZPAL G. 48/23, locality info not provided).

2016 *Neogothograptus ornatus* Maletz - Štorch et al., fig. 3A, 4E, shale specimen (upper part of *Neodiversograptus nilssoni* Biozone; Czech Republic)

**Type specimen:** The holotype is MB.G. 1079/03, a distally incomplete specimen with indications of an outer ancora (Fig. 6b). Complete specimens are not available.

**Tubarium characteristics:** Tubarium with probably four to six thecal pairs and an appendix of median length; appendix outlined by four vertical lists connected with horizontal rings or connecting lists; large paired and unpaired reticulate genicular processes at thecal orifices; dense reticulum in mature specimens.

**Astogeny:** Specimens with one to two thecal pairs lack any reticulum (Maletz 2008, fig. 10A-D). The specimens do not show any genicular additions at this stage. Larger specimens develop a reticulum and immature specimens show a gradation to less density of the reticulum in the distal part of the tubarium. Genicular extensions show a gradation along the tubarium with the largest ones found at the orifices of the first thecal pair. There is an outer ancora (Fig. 6c), but its development is unclear from the few available specimens.

**Remarks:** Štorch et al. (2016, fig. 3A, 4E) identified the species in the upper *Neodiversograptus nilssoni* Biozone of their section near Nesvacily, Prague synform, Czech Republic. This is the best biostratigraphic information available for the species, otherwise only known from a single glacial boulder.

The specimen shows the large genicular processes of a mature specimen, the detailed development of which cannot be recognised.

*Neogothograptus reticulatus* Kozłowska et al., 2009 (Fig. 5a)

?1995 ?*Gothograptus* sp. - Rickards et al., p. 41, figs. 18K, L, 20J. New South Wales, SE Australia.

2009 *Neogothograptus reticulatus* Kozłowska et al., 2009, p. 428, figs. 3, 5-7.

**Type specimen:** The holotype is ZPAL G. 41/1, a proximal end with five thecae (Kozłowska et al. 2009, fig. 5A-G). The nearly parallel-sided specimen is broken at the third thecal pair and may have been much longer. It is mature with dense reticulum and considerable development of an outer ancora that is incompletely preserved.

**Tubarium characteristics:** Robust tubarium with at least four or five thecal pairs, known only from fragments of probably considerably longer mature colonies; dense reticulum, covering also proximal orifices; large reticulate genicular processes, the precise development of which is unknown; extensive outer ancora; ?long appendix (associated with, but not connected to specimens).

**Astogeny:** All illustrated specimens are fragments of mature specimens and astogenetic changes are not recognisable in the material.

**Remarks:** This is a quite distinct species, but it is found in a single sample and has not been reported from other regions. The identity of the Australasian specimen in Rickards et al. (1995) remains uncertain.

*Neogothograptus romani* Kozłowska-Dawidziuk, 1995

(Figs. 2c, 3a, 5j, 8a, 9k-n)

1995 *Neogothograptus romani* n. sp. – Kozłowska-Dawidziuk, p. 306, fig. 6 (based on a single poor illustration, glacial boulder 45 from Jarosławiec, Poland).

?2001 *Neogothograptus* sp. – Kozłowska-Dawidziuk and Lenz, fig. 3.2.

non 2004 *Holoretiolites romani* Kozłowska-Dawidziuk - Kozłowska-Dawidziuk, p. 511, fig. 4B [specimen also illustrated as *Holoretiolites erraticus* Eisenack in fig. 5i] (= *Holoretiolites erraticus*).

2008 *Neogothograptus romani* Kozłowska-Dawidziuk, - Maletz, p. 299, figs. 13A-C. (Cap Arkona, Rügen, glacial boulder).

2009 *Neogothograptus romani* Kozłowska-Dawidziuk – Kozłowska et al., fig. 2 (no description).

2022 *Neogothograptus romani* Kozłowska-Dawidziuk – Maletz, fig. 13C (no description). The specimen shows a robust clathrium, but no additional reticular lists.

**Type specimen:** The species was originally only illustrated in the range chart from a single specimen (Kozłowska-Dawidziuk 1995, fig. 6), now recognised as the holotype. Better illustrations of the specimen, identified as ZPAL G. XVI/1355, are not available.

**Tubarium characteristics:** Tubarium with four thecal pairs; short appendix; reticular list density variable; appendix with two longitudinal lists and short horizontal loops.

**Astogeny:** The specimens in Kozłowska-Dawidziuk (1995) and Maletz (2008) are quite uniform, possessing five thecal pairs and a short appendix with two vertical lists. Additional reticular lists are formed at a late stage in the development, starting with horizontal lists on the ventral sides of the first two to three thecae. Only a small number of additional reticular lists are seen in probably more mature specimens. There is no outer ancora. Additional material referred to *Neogothograptus romani* (Fig. 9l-n) bears only four thecal pairs and the indication of an appendix formed from two lists. The specimens appear to form a robust tubarium from the clathrial lists, before they add reticular lists on the ventral thecal membranes and also on the lateral ancora sleeve panels. There is a complete specimen (Fig. 9n) without any reticular lists, but others from the sample show reticular lists in probably much earlier astogenetic stages. It is unclear, whether all specimens from the sample can be referred to a single species.

**Remarks:** The new SEM JM 118 (SMF 75844-75847) material is from Sellin, Island of Rügen, NE Germany (Fig. 9l-n). The specimens are associated with *Pristiograptus dubius*, *Monograptus micropoma*, *M. operculatus* (det. Jaeger). The specimens were originally identified as *Ret. erraticus tetrathecatus* by Hermann Jaeger (*nomen nudum*).

*Neogothograptus thorsteinssoni* Lenz and Kozłowska-Dawidziuk, 2004 (Fig. 5h)

- 1994 *Holoretolites (Balticograptus) erraticus* (Eisenack) – Lenz, p. 858, figs. 6.1–6.6, 6.9, 6.11. (locality 2, south shore of Baillie Hamilton Island, 57.6 m).
- 2001 *Neogothograptus balticus* (Eisenack)? – Kozłowska-Dawidziuk and Lenz, fig. 3.16. (loc. See Lenz, 1994).
- 2004 *Neogothograptus* sp. 2. – Kozłowska-Dawidziuk, fig. 1.33, 5j. (no description).
- 2004 *Neogothograptus thorsteinssoni* n. sp. – Lenz and Kozłowska-Dawidziuk, p. 19, pl. 7 figs. 1-8, pl. 8 figs. 1-11, pl. 9 figs. 1-5, pl. 10 figs. 1-7, pl. 26, figs. 5-6.
- 2008 *Neogothograptus thorsteinssoni* Lenz and Kozłowska-Dawidziuk – Maletz, p. 296, figs. 10, 13I. (glacial boulder, locality unknown as label was lost, preserved in glycerin).
- 2009 *Neogothograptus thorsteinssoni* Lenz and Kozłowska-Dawidziuk – Kozłowska et al., p. 432, fig. 2 (holotype), fig. 8A-D (Bartoszyce borehole at 1598 m, Poland).

2015 *Neogothograptus thorsteinssoni* Lenz and Kozłowska-Dawidziuk – Kozłowska, fig. 1D (no description; GSC 125978).

**Type specimen:** The holotype, GSC 125981, NE Cornwallis Island, Arctic Canada is a complete, mature specimen with six thecal pairs and a short appendix (Lenz and Kozłowska-Dawidziuk 2004, pl. 9, fig. 3).

**Tubarium characteristics:** Tubarium with six to seven thecal pairs; appendix of median size; dense reticulum in mature specimens; extensive outer ancora in mature specimens, covering also proximal orifices.

**Astogeny:** The species is known exclusively from relatively mature specimens and the only changes that can be seen is the thickness of the reticular lists. The apertural lips are thickened considerably in mature specimens, bearing distinct labiae.

**Remarks:** The species bears a quite regular reticulum and cannot be mixed with other species of the genus. The best specimens are from Arctic Canada (Lenz and Kozłowska-Dawidziuk 2004), but Maletz (2008) found good material in a glacial erratic boulder from NE Germany.

Genus *Holoretolites* Eisenack, 1951

**Type species:** *Retiolites mancki* Münch, 1931 (OD), Baltic erratic boulder, Uckermark, Templin, NE Germany, Ludlow, Silurian.

**Species:** *Retiolites mancki* Münch, 1931; *Retiolites simplex* Eisenack, 1935; *Holoretolites erraticus* Eisenack, 1951; *Holoretolites atrabecularis* Kozłowska-Dawidziuk, 1995; *Holoretolites helenawitoldi* Kozłowska-Dawidziuk, 2004 (syn. of *Holoretolites atrabecularis* Kozłowska-Dawidziuk, 1995; herein).

**Diagnosis:** Finite tubarium with appendix and strongly reduced distalmost thecal pair without orifices; shallow, asymmetrical ancora umbrella with six to seven meshes; outer ancora in some species; nema free; proximal ventral orifices of hexagonal shape; ventral sides with thecal lips, genicular lists and long mid-ventral lists; zigzag lateral apertural lists on obverse and reverse sides; some parietal lists proximally; reticulum poorly developed to absent; ancora sleeve lists with seams facing inward; bandages with pustules (revised from Lenz et al. 2018).

**Remarks:** The species of *Holoretolites* are invariably found in chemically isolated material. There are no descriptions from shale material available. Thus, minor differences may have been taken as important characters to separate taxa. Lenz et al. (2018) did not mention the presence of an outer ancora in some species in their diagnosis.

The lateral zigzag lists in *Holoretolites* are not homologous to the zigzag thecal lists in *Retiolites* and related taxa or the zigzag parietal lists of derived retiolitines (cf. Bates et al. 2005; Maletz 2022). They clearly originate as remains

of the lateral apertural lists when the ancora sleeve on the reverse and obverse sides disappears except for two panels at the proximal end (Figs. 10e, 11d). Thus the reduction of the lists indicates a simplification of the tubarium with the loss of the dual wall construction.

*Holoretiolites mancki* (Münch, 1931)

(Figs. 1e, 2d, f, 10a–e, 11a)

1931 *Retiolites mancki* n. sp. - Münch, pp. 35–42, pl. 1, figs. 1–13. Grünlich-Graues Graptolithengestein, Templin, Uckermark, NE Germany. 75 specimens were in the Münch collection, but only about six complete ones.

1951 *Holoretiolites mancki* Münch - Eisenack, pl. 24, fig. 6; text-fig. 10 (no detailed description). Glacial erratic boulder, ‘Ostpreussisches Silurgeschiebe’.

1952 *Holoretiolites (Holoretiolites) mancki* (Münch) – Bouček and Münch, p. 3, fig. 11–1B (copy of Münch, 1931); 4A (copy of Eisenack, 1951).

pars 1993 *Holoretiolites mancki* (Münch) – Lenz, p. 20, pl. 12, fig1-5, 8–12 (non pl. 12, figs. 6 and 7; =*Neogothograptus melchini*)

pars 1995 *Holoretiolites mancki* (Münch) - Kozłowska-Dawidziuk, p. 307, figs. 6, 27A, 28D. *Lobograptus parascanicus* Biozone, Mielnik drill core, Poland.

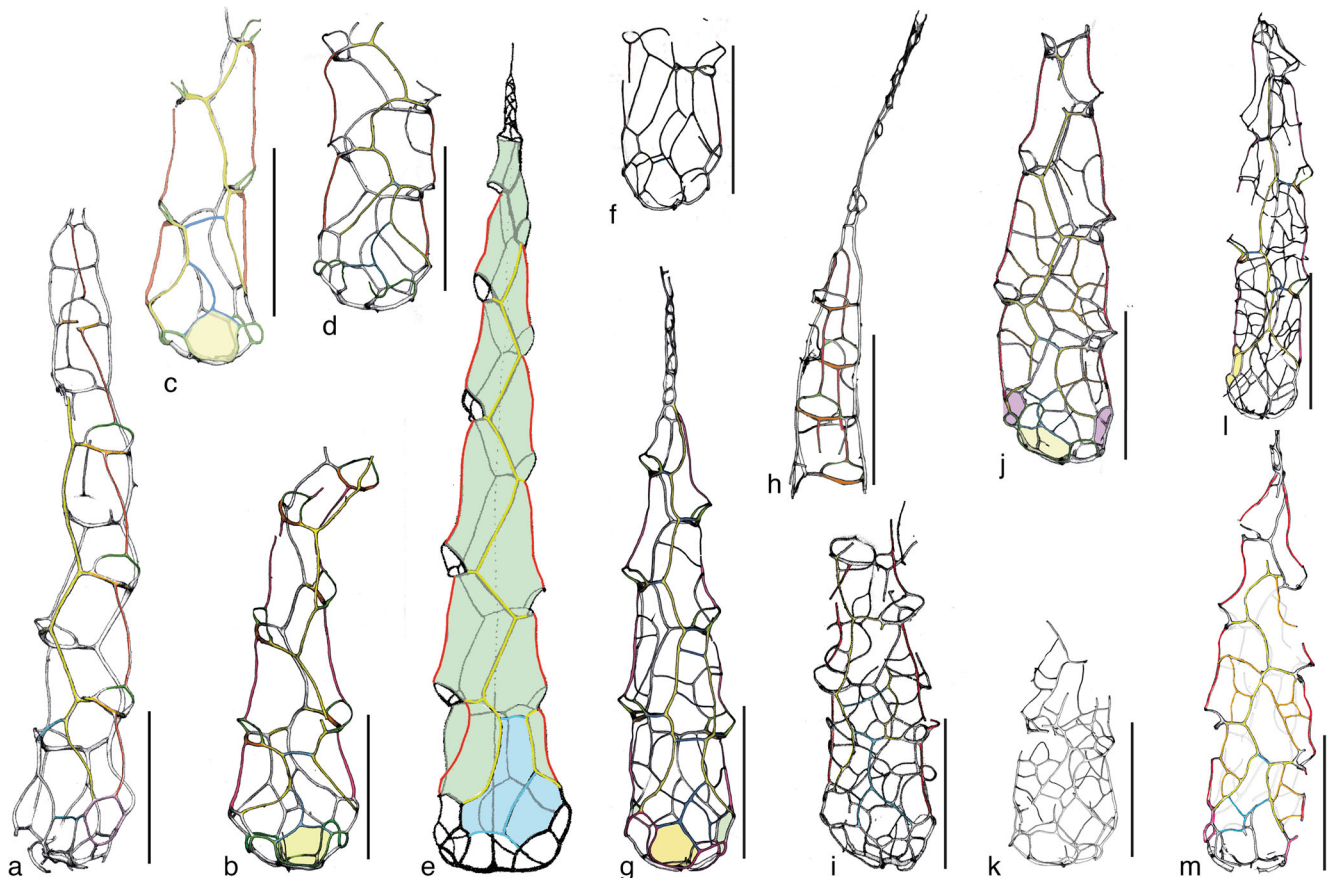
2004 *Holoretiolites mancki* (Münch) – Kozłowska-Dawidziuk, fig. 1.36, 4C, 5N (erratic boulder 48, Jarosławiec, Poland) (no description).

2008 *Holoretiolites mancki* (Münch) – Maletz, fig. 1L, 14A–G.

2014 *Holoretiolites mancki* (Münch) – Kozłowska and Bates, fig. 1B (erratic boulder 48, Jarosławiec, Poland) (no description).

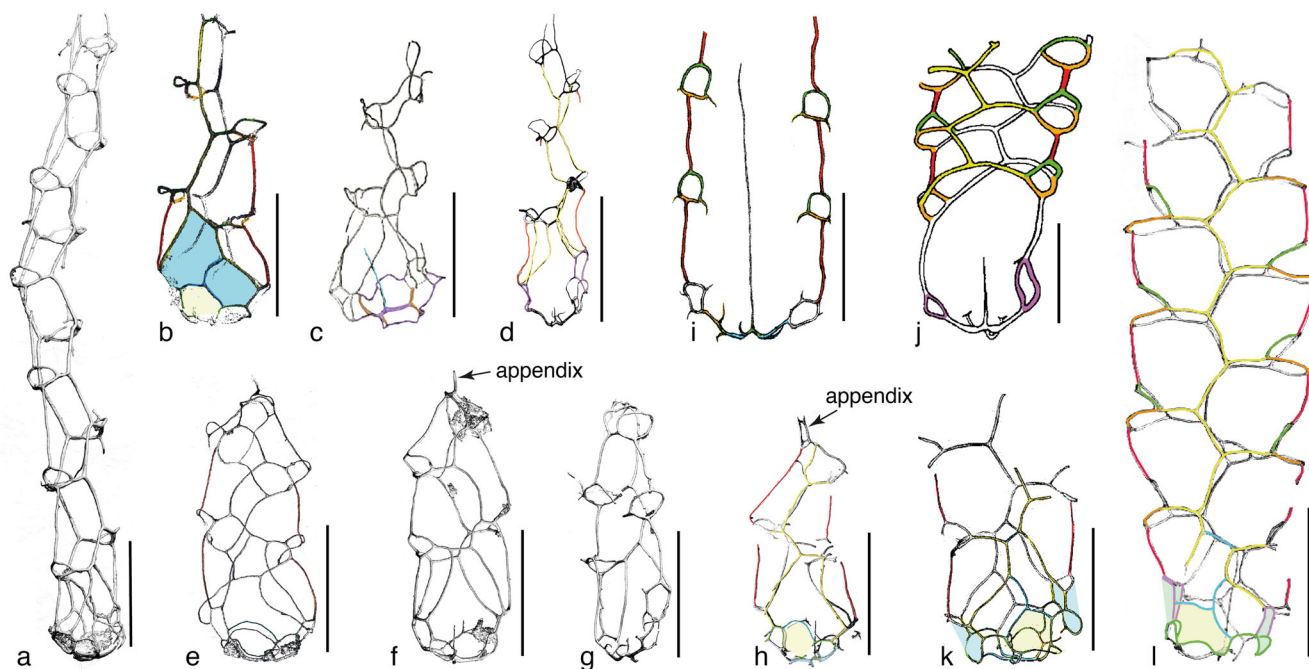
2015 *Holoretiolites mancki* (Münch) – Kozłowska, fig. 1F, erratic boulder 48, Jarosławiec, Poland (no description).

**Type specimen:** Münch (1931) did not select a type specimen and the whereabouts of his material are unclear. The specimen



**Fig. 10** *Holoretiolites* species. **a–e** *Holoretiolites mancki*. **a** MB.G. 1120/02, incomplete specimen with about four thecal pairs in oblique view. **b** MB.G. 1120/08, nearly complete tubarium, lacking appendix. **c** MB.G. 1120/01, immature specimen showing incomplete rims of the second pairs of thecal orifices. **d** MB.G. 1120/09, specimen with two thecal pairs. **e** Typical specimen, slightly reconstructed by Münch (after Münch 1931, fig. 3). **f–m** *Holoretiolites erraticus*. **f** MB.G. 1085/23, possibly a juvenile with one complete thecal pair. **g** MB.G. 1085/03, most

complete specimen. **h** MB.G. 1085/04, distal end with appendix. **i** MB.G. 1085/01, incomplete specimen with two preserved thecal pairs and evidence of outer ancora. **j** MB.G. 1085/10, specimen lacking distal end, apertural orifice of  $th_2^3$  is present. **k** MB.G. 1085/06, proximal fragment with thin lists. **l** MB.G. 1085/02, incomplete specimen, distalmost theca missing. **m** MB.G. 1085/08, nearly complete specimen with indication of appendix. All scale bars are 1 mm. No scale available for (e)



**Fig. 11** *Holoretiolites* and related forms. **a** *Holoretiolites mancki*, oblique view, SMF 75848, JM 125/08 (see also Fig. 2b; light photo of same specimen). **b–d** *Holoretiolites atrabecularis*. **b** paratype (after Kozłowska-Dawidziuk 1995, fig. 29A). **c–d** type material of *Holoretiolites helenaewitoldi*. **c** paratype, showing complete ancora umbrella (after Kozłowska-Dawidziuk 2004, fig. 8H). **d** holotype, obliquely distorted specimen (after Kozłowska 2015, fig. 1G). **e–g** *Holoretiolites simplex*, Lichtenrade/Berlin, Germany, glacial boulder. **e** SMF 75850, JM 125/05. **f** SMF 75849, JM 125/01. **g** SMF 75851, JM 125/07. **h** *H. simplex*, SMF 75852, JM 120/05, Rerik, Mecklenburg-

Vorpommern, NE Germany, glacial boulder, mature specimen, collapsed on transfer, showing short appendix. **i** *Plectodinemagraptus gracilis*, reconstruction, based on Kozłowska and Bates (2014, fig. 2). **j** *Semiplectograptus urbaneki*, reconstruction based on holotype in Kozłowska-Dawidziuk (1995, figs. 20, 10C). **k–l** *Semiplectograptus manckoides*, Arctic Canada. **k** GSC 126016, proximal end (after Lenz and Kozłowska-Dawidziuk 2004, pl. 19, fig. 4). **l** GSC 126007, nearly complete, but largely flattened specimen with colour interpretations (after Lenz and Kozłowska-Dawidziuk 2004, pl. 18, fig. 5). Scale bars are 1 mm

illustrated in Münch (1931, fig. 4) is regarded as characteristic and used as a tool for the identification of this species. The designation of a neotype for name stability does not seem to be necessary. Münch (1931, p. 37) indicated that the illustration is slightly schematic (etwas schematisiert) and the sicula (now identified as the appendix) is added. The specimen shows the main relevant characters as is indicated by the coloured interpretation in which ancora sleeve panels (blue) and thecal membranes (green) are highlighted (Fig. 10e). The specimen has six thecal pairs and an appendix.

**Tubarium characteristics:** Species with four to six thecal pairs; ancora sleeve panels and parietal lists in proximal ends; mid-ventral lists robust, outlining the tubarium; complete ancora umbrella; appendix present.

**Astogeny:** The tubarium of this species is quite simple, without any indications of a reticulum or an outer ancora. Thus, little can be learned from the astogeny of its tubarium.

**Remarks:** Münch (1931) described the species from a collection of 75 specimens, of which only a few were complete. All his complete specimens appear to have six thecal pairs and a short appendix, and thus differ from the material of Kozłowska-Dawidziuk (1995) and Maletz (2008), that are shorter, not having more than four thecal pairs.

*Holoretiolites atrabecularis* Kozłowska–Dawidziuk, 1995 (Figs. 1a–b, 11b–d)

1995 *Holoretiolites atrabecularis* sp. n. Kozłowska-Dawidziuk, p. 310, fig. 6; fig. 28A–C; 29A–C. Holotype ZPAL G. XVI/1529 not illustrated, Mielnik drill core at 972.9 m, Poland.

2004 *Holoretiolites atrabecularis* Kozłowska-Dawidziuk – Kozłowska-Dawidziuk, fig. 4E. (same as in Kozłowska-Dawidziuk, 1995, fig. 29B).

2004 *Holoretiolites atrabecularis* Kozłowska-Dawidziuk – Lenz and Kozłowska-Dawidziuk, p. 20, pl. 20, figs. 1–11. (Arctic Canada; RC-01-1, 22m, 20 fragments; associated with *Holoretiolites manckoides*; the locality and level are not listed in the appendix. Thus, the precise age is uncertain).

2004 *Holoretiolites helenaewitoldi* n. sp. – Kozłowska-Dawidziuk, p. 515, figs. 4F, 6, 5L, 7B, 8A, B, E–I. Upper part of the *Lobograptus progenitor* Biozone, Bartoszyce drill core at 1579.9 m, Poland.

2014 *Holoretiolites helenaewitoldi* Kozłowska-Dawidziuk – Kozłowska and Bates, fig. 1C (holotype, no description).

2015 *Holoretiolites helenaewitoldi* - Kozłowska-Dawidziuk – Kozłowska, fig. 1G (holotype, no description).

**Type specimen:** Kozłowska-Dawidziuk (1995, p. 310) designated ZPAL G. XVI/1529 as the holotype of the species, but did not illustrate the specimen. The concept of the species is therefore based on the specimens illustrated in Kozłowska-Dawidziuk (1995, fig. 29A-B; ZPAL G. XVI/1530, 1531) (Fig. 11b). The most complete specimen shows four thecal pairs and the indication of an appendix (Fig. 1d). The first two or three thecae have complete mid-ventral lists (Kozłowska-Dawidziuk 1995, fig. 29B).

**Tubarium characteristics:** Tubarium with about four thecal pairs and possibly appendix; mid-ventral lists reduced or lacking in the distal thecae, but complete in the first two or three thecae; ancora umbrella complete, but delicate rim may not be preserved in its entirety.

**Remarks:** *Holoretiolites helenaewitoldi* Kozłowska–Dawidziuk, 2004 is here regarded as a synonym of *Holoretiolites atrabecularis*. The species is known from a few distorted and incompletely preserved specimens. Especially the holotype appears to be more slender in the proximal end than other specimens, based on an oblique preservation and partial compression (Fig. 11d). Kozłowska-Dawidziuk (2004, p. 515) indicated a strongly reduced ancora umbrella and ancora sleeve lists for the species, but also illustrated specimens with a complete ancora umbrella (Fig. 11c). The preservation of the mid-ventral lists is variable, but generally the mid-ventral lists of the first thecal pair are complete, while the distal ones may be only partially formed or preserved. Kozłowska-Dawidziuk (2004, p. 515) interpreted *Holoretiolites helenaewitoldi* as the most reduced species of *Holoretiolites* and regarded *Holoretiolites mancki* as a possible ancestor, even though this species appears to be considerably older than *Holoretiolites mancki* with a less reduced tubarium (see Fig. 1).

*Holoretiolites erraticus* (Eisenack, 1951)  
(Figs. 1d, 2b, 8f, 10f-m)

1951 *Retiolites erraticus* n. sp. – Eisenack, p. 136, pl. 24, figs. 2–4, pl. 25, fig. 7, text-fig. 3. Silurian glacial erratic, Eastern Prussia.

1952 *Holoretiolites (Balticograptus) erraticus* (Eisenack) – Bouček and Münch, p. 17, fig. 5a (copy of Eisenack 1951, pl. 24 fig. 4).

1995 *Holoretiolites erraticus* Eisenack – Kozłowska-Dawidziuk, p. 312, figs. 27C, H; 30.

2004 *Holoretiolites romani* Kozłowska-Dawidziuk – Kozłowska-Dawidziuk, fig. 4B.

2004 *Holoretiolites erraticus* Eisenack – Kozłowska-Dawidziuk, fig. 5I (same specimen as *Holoretiolites romani* in fig. 4B).

2008 *Holoretiolites erraticus* Eisenack – Maletz, p. 304, figs. 1M, 12A-F, 13D-H.

**Type specimen:** Eisenack (1951) selected the specimen on his pl. 24, fig. 4 as the ‘type’, thus it is now identified as the holotype (Fig. 1d). The specimen bears the number ‘Präparat 177 Nr. 5’, preserved at Tübingen University. The specimen bears indications of four thecal pairs and is nearly parallel-sided, indicating an even longer colony. The reticulum decreases distally in the specimen from the complete ancora umbrella to the distal part, where the specimen is broken off. **Tubarium characteristics:** Tubarium with three to four thecal pairs and often long appendix; mid-ventral lists robust, outlining the tubarium; density of reticulum variable; outer ancora may be present.

**Astogeny:** The precise astogeny of this species is difficult to estimate, as juveniles have not been described. The material of Eisenack (1951) includes four fragmented specimens of which three show the ancora umbrella and a more or less parallel-sided tubarium with three to four thecal pairs, broken distally. Eisenack (1951, fig. 3) referred a single distal fragment with indications of an appendix to this species. All specimens show a moderately dense development of the reticulum on the ancora sleeve.

A considerable variation in the density of the reticulum may be present in this species as described by Maletz (2008), as the most complete specimen (Fig. 10g) bears a relatively coarse mesh in comparison to other, more fragmentary specimens (Fig. 10i-l).

Mature specimens may show a relatively long appendix (Fig. 10h), formed from two longitudinal lists connected by irregularly placed circular ones. Mature specimens may bear an outer ancora, but this construction is known from a single specimen only (Fig. 8f).

**Remarks:** The type material has at least four thecal pairs, but complete specimens are not present to show the complete tubarium (Eisenack 1951) and may have been considerably longer. The ancora sleeve has some development of reticulum, especially in mature specimens. The material of Maletz (2008) is shorter, with less development of the reticulum and a distinctly narrowing tubarium distally. Also the material of Kozłowska-Dawidziuk (1995) has only four thecal pairs and an appendix and is clearly identical in size to the material of Maletz (2008). An outer ancora is not mentioned by Eisenack (1951), but this feature was unknown at the time and may not have been recognised.

There is no information on the intraspecific variation in size available and all specimens may easily be referred to *Holoretiolites erraticus*. All specimens from a single sample appear to show a consistent number of thecae.

*Holoretiolites simplex* Eisenack, 1935  
(Figs. 1c, 2e, 3c, 11e-h)

- 1935 *Retiolites simplex* n. sp. – Eisenack, p. 84, pl. 4, fig. 16, pl. 7, fig. 1. (glacial erratic boulder, ‘Ostpreussisches Silurgeschiebe’).
- 1951 *Retiolites simplex* Eisenack – Eisenack, pl. 24, fig. 7 (holotype; no description).
- 1952 *Holoretiolites (Holoretiolites) simplex* (Eisenack) – Bouček and Münch, p. 18, fig. 4B (copy from Eisenack, 1951).
- 1962 *Retiolites simplex* Eisenack – Reichstein, p. 539, figs. 3–8, pl. 1, figs. 5–12; pl. 2, figs. 1–12. (Löbber Ort, Rügen; map in Reichstein, 1962, p. 538).
- 1987 *Holoretiolites simplex* (Eisenack) – Bates and Kirk, p. 99, fig. 13 (specimen from Jaeger collection).
- ?1987 *Holoretiolites simplex* (Eisenack) – Lenz and Melchin, pl. 2, figs. 3, 12 (no description; Lower Ludlow, Laura Lakes area, Arctic Canada. Field number LL10).
- 1995 *Holoretiolites mancki (simplex form)* – Kozłowska-Dawidziuk, p. 308, fig. 6.
- 2010 *Holoretiolites simplex* (Eisenack) – Maletz, fig. 1, 2 (Jaeger material, no description).

**Type specimen:** Eisenack (1935) illustrated a single specimen that has to be identified as the holotype. Eisenack (1951) re-illustrated the specimen with the number ‘Präparat 178 Nr. 3’. It is preserved in the collection at the University of Tübingen. The specimen is nearly complete, with three thecal pairs and the indication of an appendix (Fig. 2e).

**Tubarium characteristics:** Tubarium with three thecal pairs; small and incomplete appendix may be present; a single panel indicates the remains of the ancora sleeve (Fig. 2e); one parietal list approximately at the level of the th1<sup>1</sup> orifice; no reticular lists; ancora umbrella with six to seven meshes.

**Astogeny:** Nothing can be said about the astogeny of the species, as juveniles and immature specimens are not available.

**Remarks:** The species is one of the smallest retiolitines and has rarely been described, as it is only found in chemically isolated material so far. Reichstein (1962) provided the best description of *Holoretiolites simplex* and also indicated the intraspecific variation of this species, as he illustrated a number of specimens in various orientations and preservations.

Kozłowska-Dawidziuk (1995) considered the species to be a synonym of *Holoretiolites mancki*. However, she (Kozłowska-Dawidziuk 1995, fig. 6) indicated the ‘*simplex*’ form to be present at a lower level in the *Lobograptus parascanicus* Biozone of the drill core. The species can be associated with *Holoretiolites mancki* (sample JM 125; Lichtenrade, Berlin, Germany; SMF 75848-75851), but both species do not show any biometric overlap and can easily be separated (see Fig. 11a, e-h).

Genus *Semiplectograptus* Kozłowska–Dawidziuk, 1995

**Type species:** *Semiplectograptus urbaneki* Kozłowska-Dawidziuk, 1995 (M). Mielnik borehole at 973 m, Poland, *Cucullograptus hemiaversus/Cucullograptus aversus* Biozone, Ludlow, Silurian.

**Species:** *Semiplectograptus urbaneki* Kozłowska-Dawidziuk, 1995; *Holoretiolites manckoides* Kozłowska-Dawidziuk, 1995.

**Diagnosis:** Tubarium parallel sided; ancora umbrella incompletely known; nema free; ventral wall formed by thecal lips, genicular lists, and mid-ventral lists; proximal ventral orifices and thecal orifices rhomboid; large proximal lateral orifices in one species; zigzag lateral apertural lists start at level of first pair of thecal orifices; no reticulum; ancora sleeve lists with seams facing inward; bandages with pustules (revised from Lenz et al. 2018).

**Age:** Kozłowska-Dawidziuk (1995) identified *S. urbaneki* from the *Cucullograptus hemiaversus-Cucullograptus aversus* Biozone, but in Kozłowska-Dawidziuk (2004, fig. 1) she showed a range into the overlying *Saetograptus leintwardinensis* Biozone. Lenz et al. (2018, p. 27) again indicated the *Cucullograptus hemiaversus-Cucullograptus aversus* Biozone for the age, but in the figure explanation indicated the *Saetograptus leintwardinensis* Biozone. Thus, the precise age of the species remains uncertain.

**Remarks:** The genus has only been found once before and its development was quite incompletely known from only two illustrated specimens of *Semiplectograptus urbaneki* Kozłowska-Dawidziuk, 1995. Bates and Kozłowska (2014, fig. 4C) illustrated the ancora umbrella of this taxon showing six meshes and the two mid-ventral lists connecting the ancora umbrella on the ventral sides to the remains of the tubarium. This illustration may be a reconstruction, but it is unclear whether it is based on actual material (see also reconstruction in Kozłowska-Dawidziuk 1995, fig. 10C).

The lateral zigzag lists in *Semiplectograptus* (Fig. 11i-j) may be interpreted as homologues of the lateral apertural lists in *Holoretiolites* and parietal lists are lacking. This development does not indicate a connection with *Plectograptus*, in which distinct lateral apertural lists and pleural lists are present, connected with zigzag parietal lists. The long mid-ventral lists of the first thecal pair in *Semiplectograptus urbaneki* may be a specific character of this species, but not useful for further interpretation. The distinct zigzag lists with the long connections to the thecal orifices and the relatively short mid-ventral lists are comparable to the construction in *Holoretiolites manckoides* (Fig. 111) that is here transferred to *Semiplectograptus*. The large lateral orifices in *Semiplectograptus urbaneki* can easily be explained by the loss of the parietal lists (or the ancora sleeve panels) in the proximal end. These are still present in *Semiplectograptus manckoides* (blue in Fig. 111).

*Semiplectograptus urbaneki* Kozłowska–Dawidziuk, 1995 (Figs. 1h, 11j)

- 1995 *Semiplectograptus urbaneki* n. sp. - Kozłowska-Dawidziuk, p. 320, figs. 27J, 34A.
- 2004 *Semiplectograptus urbaneki* Kozłowska-Dawidziuk – Kozłowska-Dawidziuk, fig. 1.41, 2D.
- 2014 *Semiplectograptus urbaneki* Kozłowska-Dawidziuk – Kozłowska and Bates, fig. 4C.
- 2018b *Semiplectograptus urbaneki* Kozłowska-Dawidziuk, 1995. Atlas of Graptolite type Specimens 3.94.

**Type specimen:** Kozłowska-Dawidziuk (1995, fig 34A) identified ZPAL G. XVI/1392 as the holotype. The specimen (Fig. 11j) is from the depth of 973 m in the Mielnik IG-1 core, Poland; *Cucullograptus hemiaversus/Cucullograptus aversus* Biozone.

**Tubarium characteristics:** Robust, largely parallel sided tubarium; ancora umbrella incompletely known, but probably with six meshes; nema free; ventral tubarium wall formed by thecal lips, genicular lists, and relatively short mid-ventral lists; zigzag lateral apertural lists start on level of first pair of thecal orifices, connected to thecal orifices by horizontal lists; proximal ventral orifices and thecal orifices rhomboid; no reticulum.

**Remarks:** This species is known from two specimens only. The reconstruction of Kozłowska-Dawidziuk (1995, fig. 10C) shows a more complete ancora than the one visible in the specimens. Kozłowska and Bates (2014, fig. 4C) illustrated the ancora of *Semiplectograptus urbaneki* with six meshes, but the basis for this interpretation is unclear.

*Semiplectograptus manckoides* (Kozłowska-Dawidziuk, 1995) (Figs. 1f-g, 3b, 11k-l)

- 1995 *Holoretiolites manckoides* n. sp. – Kozłowska\_Dawidziuk, p. 309, fig. 6, 27B.
- 2004 *Holoretiolites manckoides* Kozłowska-Dawidziuk - Kozłowska-Dawidziuk, fig. 4A.
- 2004 *Holoretiolites manckoides* Kozłowska-Dawidziuk; Lenz and Kozłowska-Dawidziuk, p. 20, pl. 18, figs. 1-8, pl. 19, figs. 1-10. (listed as *Neogothograptus manckoides* in Fig. 3, Abbott River section, from top of *progenitor* Biozone).
- 2013 *Holoretiolites manckoides* Kozłowska-Dawidziuk – Dobrowolska, figs. 3C, 8B (no detailed description of species; ZPAL G. 48/5. Locality not mentioned).

**Type specimen:** Kozłowska-Dawidziuk (1995, p. 309) identified ZPAL G. XVI/1347 as the holotype of this species, but did not illustrate the specimen. Thus, there is only one illustrated specimen from the type series (ZPAL G. XVI/1350), collected from the Mielnik borehole at 954.0-960.0 m level available (Kozłowska-Dawidziuk 1995, fig. 6; fig. 27B). This specimen is obliquely preserved, possibly flattened and does not show much detail (Fig. 1g).

**Tubarium characteristics:** Robust, largely parallel sided tubarium; ancora umbrella incompletely known, but probably with six meshes; nema free; ventral tubarium wall formed by thecal lips, genicular lists, and mid-ventral lists; mid-ventral lists relatively short, outwards inclined; parietal lists and ancora sleeve panels in proximal end; zigzag lateral apertural lists start at level of first pair of thecal orifices, connected to thecal orifices by horizontal lists; proximal ventral orifices and thecal orifices rhomboid; no reticulum (based on material from Arctic Canada: Fig. 11i).

**Astogeny:** The few specimens from the Canadian Arctic (Lenz and Kozłowska-Dawidziuk 2004) show a simple growth of the tubarium by the addition of thecae, but little later thickening of lists can be observed. Even the ancora umbrella ribs show little subsequent thickening. There is no evidence of additional reticulum or thickening of clathrial lists.

**Remarks:** The species is poorly known and the inclusion of the material from Arctic Canada (Lenz and Kozłowska-Dawidziuk 2004) cannot be verified from the poor original illustration of the species. *Semiplectograptus manckoides* was found initially in the Mielnik borehole of Poland, but has subsequently recognised in Arctic Canada (Lenz and Kozłowska-Dawidziuk 2004). Kozłowska-Dawidziuk (1995, p. 309) also mentioned fragments from a Polish glacial boulder, but did not illustrate the material.

*Semiplectograptus manckoides* (Kozłowska-Dawidziuk, 1995) has originally been referred to the genus *Holoretiolites*, but differs in many details and is here included in *Semiplectograptus*. The tubarium construction has many similarities to *Holoretiolites*, but differs considerably in other characters, especially the outwards inclined, short mid-ventral lists and the almond-shaped, large thecal orifices. The largest specimen from Arctic Canada (Fig. 11i) shows a slight reduction of thecal size distally, but there is no evidence of a finite growth or the presence of an appendix.

**Age:** The Canadian material originated from the *Lobograptus progenitor* to *Lobograptus scanicus* biozone interval, while the Polish material is younger, from the *Cucullograptus hemiaversus/Cucullograptus aversus* Biozone. It is, however, unclear whether the material can be included in a single species.

Genus *Plectodinemagraptus* Kozłowska–Dawidziuk, 1995

**Type species:** *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk, 1995 (M). Mielnik borehole at 946.9 m and 940.5 m, Poland, *Cucullograptus hemiaversus/Cucullograptus aversus* Biozone, Ludlow, Silurian.

**Species:** *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk, 1995.

**Diagnosis:** ?Parallel-sided tubarium; ancora umbrella with six meshes and partially developed rim; ventral walls formed by

thecal lips, genicular lists, long mid-ventral lists and reduced lateral apertural lists; proximal ventral orifices of hexagonal shape; lists with seams facing inward; bandages with pustules. (revised from Lenz et al. 2018).

**Age:** Kozłowska-Dawidziuk (1995) identified *P. gracilis* from the *Cucullograptus hemiaversus*-*Cucullograptus aversus* Biozone, but in Kozłowska-Dawidziuk (2004, fig. 1) and Lenz et al. (2018, p. 27) the species is referred to the *Saetograptus leintwardinensis* Biozone.

*Plectodinemagraptus gracilis* Kozłowska-Dawidziuk, 1995 (Figs. 1i, 11i)

- 1995 *Plectodinemagraptus gracilis* sp. nov. - Kozłowska-Dawidziuk, p. 322, fig. 2B, 6, 10D, 27D, 34B-E.  
 2001 *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk – Kozłowska-Dawidziuk and Lenz, figs. 3.7, 3.9.  
 2004 *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk – Kozłowska-Dawidziuk, fig. 1.  
 2005 *Plectodinemagraptus* Kozłowska-Dawidziuk – Bates et al., fig. 5C.  
 2014 *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk – Kozłowska and Bates, p. 147, figs. 1D, 2, 3.  
 2014 *Plectodinemagraptus* Kozłowska-Dawidziuk – Kozłowska and Bates, p. 147, fig. 1D.  
 2018 *Plectodinemagraptus gracilis* Kozłowska-Dawidziuk – Lenz et al., p. 23, fig. 10.3, fig. 19.4a-b.

**Remarks:** The species is based on very few specimens that may be interpreted either as juveniles or fragments and the size and development of the species is largely unclear. Kozłowska and Bates (2014, fig. 2) provided a reconstruction based on specimens from the Bartoszyce borehole at 1554.6 m, but the material on which the reconstruction was based was never illustrated. Kozłowska and Bates (2014, fig. 4b) also provided a reconstruction of the ancora umbrella of the species, showing six meshes. A different reconstruction (Kozłowska and Bates (2014, fig. 1D), based on material from the Mielnik borehole shows lack of detail in the ancora umbrella. It suggests hexagonal pre-thecal orifices and at least four thecal pairs and does not provide information on the final size of the species. Thus, the tubarium construction of this species is based on small fragments and a number of different and not verifiable reconstructions (see also Kozłowska-Dawidziuk 1995, fig. 10D; Bates et al. 2005, fig. 5C).

The highly fragmented pieces of *Plectodinemagraptus gracilis* show only a few features that can be compared with other taxa. While the development of the ancora umbrella is speculative and will not be discussed herein, the hexagonal pre-thecal orifices are clearly illustrated (Kozłowska-Dawidziuk 1995, fig. 34B) and should be considered proven. The same can be said for the shape of the thecal orifices, showing the horizontal thecal lip and a loop representing the

geniculum (Kozłowska-Dawidziuk 1995, fig. 34E). Bates et al. (2005, fig. 5C) and Lenz et al. (2018, fig. 10.3) understood this genicular loop as a combination of the geniculum and the pleural lists. Robust mid-ventral lists connect the genicular loops with the thecal lips as in *Holoretiolites* and *Semiplectograptus* as discussed earlier. The paired lateral ‘spines’ originating from the thecal lips can be interpreted as remains of the lateral connections to the lateral zigzag lists as seen in *Holoretiolites* and in *Semiplectograptus*. They would suggest, as in *Holoretiolites*, that there are no remains of pleural lists. The loss of the lateral zigzag list would be the only change from *Semiplectograptus* to *Plectodinemagraptus*. Nothing can be said about the maximum size of the tubaria of these taxa from the available fragments.

**Acknowledgements** Special thanks to Denis Bates (Aberystwyth, Wales, UK), Alf Lenz (London, Ontario, Canada) and Anna Kozłowska (Warsaw, Poland) for numerous discussions on retiolitines over the years and for providing illustrations of published and unpublished specimens in their care. Michael Steiner (FU Berlin, Germany) helped with the SEM work at FU Berlin. Michael J. Melchin (Antigonish, Nova Scotia, Canada) and an anonymous reviewer provided important insight and help to improve the manuscript.

**Funding** Open Access funding enabled and organized by Projekt DEAL. There was no funding available for this project.

**Data availability** Please see chapter “Material and methods”.

## Declarations

**Conflict of interest** The author declares no conflict of interest.

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