



Retiolitid graptolites from the collection of Hermann Jaeger III. *Paraplectograptus*, *Gothograptus* and their relatives

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Abstract

The graptolite collection of Hermann Jaeger at the Museum für Naturkunde in Berlin, Germany includes a number of *Paraplectograptus* and *Gothograptus* specimens. The material provides another glimpse into the dramatic changes affecting retiolitine graptoloids across the *Lundgreni* Extinction Event of the mid Homeric (Wenlock, Silurian) which led to the demise of most earlier groups of retiolitines. The material indicates that the diversity of the pre-extinction retiolitines might have been larger than is already known through the recognition of previously unknown constructional details in earlier *Gothograptus* and *Paraplectograptus* species. Especially, *Gothograptus* shows a much higher diversity in the pre-extinction interval than previously recognized. In the *Pristiograptus parvus*/*Gothograptus nassa* Biozone interval *Gothograptus* re-emerged with new species and *Semigothograptus* is shown to have survived unchanged, indicating that these two genera represent survivors of the extinction event. A number of new genera originated and diversified in the *Pristiograptus dubius*/*Gothograptus nassa* to *Colonograptus praedeubeli/deubeli* Biozone interval, but their evolutionary relationships with earlier taxa are still only partly understood. *Paraplectograptus hermanni* sp. nov., *Gothograptus berlinensis* sp. nov. and *Gothograptus osgaleae* sp. nov. are described as new. Several species are described in open nomenclature due to the lack of sufficiently well preserved material.

Keywords Silurian · Glacial boulder · Graptolites · Retiolitinae · Taxonomy · Evolution

Introduction

Most of the chemically isolated retiolitine graptolites from the Hermann Jaeger collection at the Museum für Naturkunde Berlin, Germany have been described and illustrated in two papers by Maletz (2008, 2010). However, a number of important taxa have not previously been described. These are treated herein and their taxonomy and biostratigraphic is revised.

The retiolitine graptolites from the Hermann Jaeger collection originated from glacial erratic boulders of northern Germany and thus their precise biostratigraphical origin, in relation to an outcrop section, cannot be given. Maletz (2008, Fig. 2) indicated the localities from which the material originated and the biostratigraphical interval covered.

All graptolites are from the ‘Grünlich-Graues Graptolithengestein’ of Heidenhain (1869), Haupt (1878) and Jaekel (1889). This type of rock provided also the retiolitine graptolites described by Münch (1931), Eisenack (1935, 1951) und Reichstein (1962). The stratigraphically older boulders (*Cyrtograptus lundgreni* to *Colonograptus deubeli* Biozone) can be correlated to the *Cyrtograptus* Shale and the higher levels (*Colonograptus ludensis* Biozone and higher) to the Colonus Shale Formation of Scania, southern Sweden (Laufeld et al. 1975; Calner et al. 2013). During the Pleistocene, hard limestones with graptolites were transported to and deposited in northern Germany (Ehlers et al. 2011) and Poland, while the softer shales were not preserved. These rock types are still collected, mostly by fossil collectors, but also investigated by scientists (e.g., Radzevičius et al. 2010; Maletz and Schöning 2017) as they still provide important new scientific information from the included faunas.

During the earlier work on the Jaeger collection graptolites, Alf Lenz (London, Ontario, Canada) provided a preliminary range chart designed by Jaeger (Maletz 2010, Fig. 1) that proved very helpful in identifying the material and providing a general biostratigraphy for the retiolitine faunas. It

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was possible to identify many of the illustrated specimens in the Jaeger collection and, thus, to understand the species concept used by Jaeger in his work. Maletz (2010) described the species originally identified in Jaeger's range chart as *Retiolites (Plectograptus) alfeisenacki* under the name *Cometograptus alfeisenacki* Maletz, 2010. *Neogothograptus eximinassa* Maletz, 2008 and *Neogothograptus ornatus* Maletz, 2008 were also erected to keep the originally proposed, but unpublished names of Jaeger. *Retiolites (Plectograptus) retimarginatus* Jaeger, a nomen nudum in Maletz (2010, Fig. 1) was described as *Papiliograptus retimarginatus* by Kozłowska and Bates (2021). The species is now, however, not based on Hermann Jaeger's material, a single juvenile specimen. Thus, names originally used by Jaeger in his unpublished notes were used to honour his research and identifications of the material. Jaeger was never able to describe his important material and there exists only a single short note on the topic without illustrations in which he (Jaeger 1991a) recognized more than 20 retiolitine species from the ca. 5 Ma-long interval of the *Cyrtograptus lundgreni* Biozone (Wenlock) to the *Saetograptus chimaera* Biozone (Ludlow), the biostratigraphical interval covered by the upper *Cyrtograptus* Shale and *Colonus* Shale of Scandinavia (see Maletz 2010, Fig. 2; Calner et al. 2013). Jaeger (1991a) noted a number of trends in the evolution of the group to simpler colony shapes, the loss of the reticulum, and the reduction of the number of thecae. He considered these changes as rapid, but through a stepwise process. Jaeger (1991a) even postulated the survival of two-to-three lineages of retiolitines across the *Lundgreni* Extinction Event, but this interpretation now has to be revised in the light of re-identification of the material.

The *Lundgreni* extinction event

A number of retiolitine genera are present in the lower Homeric *Cyrtograptus lundgreni* Biozone and most of these are supposed to have become extinct during the *Cyrtograptus lundgreni* Extinction Event as a new compilation of the available data shows (Fig. 1). Some of these taxa (*Paraplectograptus*, *Sokolovograptus* and *Cometograptus*; Kozłowska-Dawidziuk 2001; Lenz and Kozłowska-Dawidziuk 2001a, 2002; Lenz and Kozłowska 2006) attained considerable species level diversity, while others are known from few specimens only (e.g., *Sagenograptoides*; Lenz and Kozłowska-Dawidziuk 2001a; Lenz and Kozłowska 2010). The post-extinction survival interval is quite poor in retiolitines and includes only *Gothograptus* and *Semigothograptus*. The earliest known species of the genus *Hoffmanigraptus* appears with *Hoffmanigraptus karlsteinensis* in the *Pristiograptus parvus*/*Gothograptus nassa* Biozone interval (Kozłowska 2021) (Fig. 1j). It is followed

by the genera *Doliograptus*, *Baculograptus* and *Papiliograptus* (Lenz and Kozłowska-Dawidziuk 2004; Lenz et al. 2012) in the *Colonograptus praedeubeli/deubeli* Biozone interval (Fig. 1 l–n), leading to a considerable diversification of the post-extinction retiolitine faunas. *Plectograptus* and a number of closely related taxa (e.g. *Reticuloplectograptus*, *Valentinagraptus*, *Kirkigraptus*) are not further discussed as they appear only in the early Gorstian (Ludlow) *Neodiversograptus nilssoni* Biozone (Bates et al. 2006; Piras 2006; Kozłowska and Bates 2008; Kozłowska et al. 2010).

The *Lundgreni* Extinction Event ('Große Krise' of Jaeger 1991b) has been described to have resulted in the extinction of all planktic graptolites, except for one retiolitine (*Gothograptus*) and one monograptid (*Pristiograptus dubius*). Urbanek et al. (2012) discussed the evolution of the *Pristiograptus dubius* lineage in some detail and recognized iterative speciation of numerous taxa of the group in the Sheinwoodian (lower Wenlock) to the Pridoli. Probably, only a single monograptid species can be found in the post-*Lundgreni* interval of the *Pristiograptus parvus* Biozone. This diminutive species is generally identified as *Pristiograptus parvus* Ulst, 1974, and is quickly followed stratigraphically by *Pristiograptus dubius frequens* Jaekel, 1889. The precise origin of the two taxa is disputed, however, as the discussion of Urbanek et al. (2012) shows.

In the past, often, the survival of *Gothograptus nassa* across the extinction event was stated (cf. Koren' 1991; Lenz and Kozłowska-Dawidziuk 2001b; Piras 2006), but Lenz and Kozłowska-Dawidziuk (2001b, p. 176) indicated that the identifications of *Gothograptus nassa* in the pre-extinction beds are misidentifications of older species of the genus *Gothograptus*.

Koren' (1991) and Koren' and Urbanek (1994) referred to the survival of the 'plectograptid fauna' with the only surviving retiolitine species being *Plectograptus macilentus* and the appearance of *Gothograptus nassa* above the extinction event. A single species of the genus *Gothograptus*, *Gothograptus nassa*, was considered to be associated with the earliest post-extinction pristiograptids (Porębska et al. 2004). As only the survival of the *Gothograptus* lineage is quite strongly supported through new information, modern knowledge on the biostratigraphical distribution of retiolitines across the extinction event shows a dramatic turnover (Fig. 1).

Jaeger (1991a) indicated the presence of *Plectograptus* in the pre-extinction interval based on the species *Retiolites (Plectograptus) alfeisenacki* (now *Cometograptus alfeisenacki* Maletz, 2010) (Fig. 1e). There is no indication of the presence of true *Plectograptus*, however, in pre-extinction retiolitine faunas, and the connection of *Cometograptus alfeisenacki* to the genus *Plectograptus* cannot be verified, as a number of constructional differences can be observed between the two genera (Lenz et al. 2018).

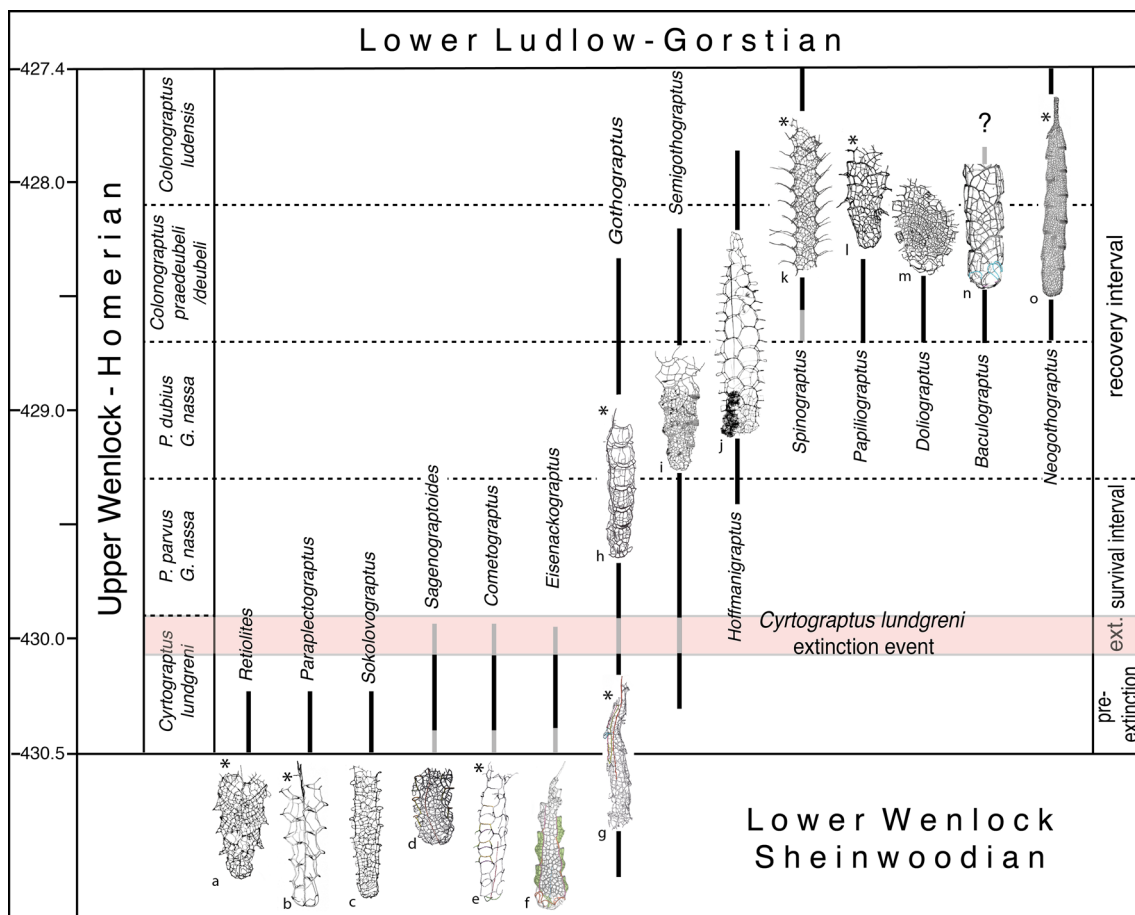


Fig. 1 Retiolitine genera across the *Lundgreni* Extinction Event. **a** *Retiolites geinitzianus* Barrande (MB.G. 1077-06). **b** *Paraplectograptus hermanni* sp. nov. (JM 73-4). **c** *Sokolovograptus textor* (modified from Lenz et al., 2012, pl. 4.1). **d** *Sagenograptoides arctos* (Lenz and Kozłowska-Dawidziuk, 2001a, b), modified from Lenz et al. (2018, Fig. 21.4a). **e** *Cometograptus alfeisenacki* (Maletz, 2010), after Maletz (2010, Fig. 4F). **f** *Eisenackograptus eisenacki* (Obut and Sobolevskaya, 1965), GSC 119,776, after Lenz and Kozłowska-Dawidziuk (2001a, b, pl. 9, Fig. 1). **g** *Gothograptus osgaleae* sp. nov. (SMF 75840). **h** *Gothograptus nassa* (Holm, 1890), drawing by Jaeger (specimen not identified). **i** *Semigothograptus meganassa*

(Rickards and Palmer, 2002), after Kozłowska (2016, Fig. 1). **j** *Hoffmannigraptus varsoviensis* Kozłowska, 2021, after Kozłowska (2021, Fig. 1). **k** *Spinograptus spinosus* (Wood, 1900), from Maletz (2008, Fig. 1B). **l** *Papiliograptus retimarginatus* (after Kozłowska and Bates 2021, Fig. 2D). **m** *Doliograptus latus* Lenz and Kozłowska-Dawidziuk, 2002, after Lenz et al. (2018, Fig. 17.3a). **n** *Baculograptus batesi* (Lenz and Kozłowska-Dawidziuk, 2002), after Lenz and Kozłowska-Dawidziuk (2002, Fig. 9.4). **o** *Neogothograptus eximianassa* Maletz, 2008, after Maletz (2008, Fig. 8L). Specimens not to scale. *Indicates specimens from Jaeger collection

Kozłowska-Dawidziuk (2001) described *Cometograptus* as a link between the then accepted subfamilies Retiolitinae and Plectograptinae, based on a simple, shallow ancora umbrella and the orientation of the inwards directed ancora sleeve list seams with pustules typical of the Plectograptinae. The details of the ancora umbrella are unknown in most species of *Cometograptus* and considerable variability in tubarium construction can be recognized. The development is best known from *Cometograptus apsis* (Lenz and Kozłowska 2001a, b, 2006) with a shallow ancora umbrella showing slight undulation, but no conspicuous lobate features. The lateral orifices are large and directed towards the th¹ side of the colony. This shallow ancora umbrella is similar to that of some *Spinograptus* (Fig. 2b), but other *Spinograptus*

specimens show an ancora umbrella with variable dimensions depending of the species, and extensive ventro-lateral loops (Fig. 2e). *Plectograptus*, however, bears a shallow ancora umbrella with five meshes and an incompletely thickened rim (Bates et al. 2006) (Fig. 2f). As an important character, transverse lists are present in the genus *Cometograptus* (arrows in Fig. 2g). These are not found in any post-extinction taxa, while these generally bear distinct mid-ventral lists, that are not present in *Cometograptus*.

Following Jaeger's (1991a, b) interpretation, the genus *Gothograptus* is represented by three species in the *Cyrtograptus lundgreni* Biozone (pre-extinction interval) and by four species in the post-extinction interval (see Maletz 2010, Fig. 1). The pre-extinction species differ considerably from

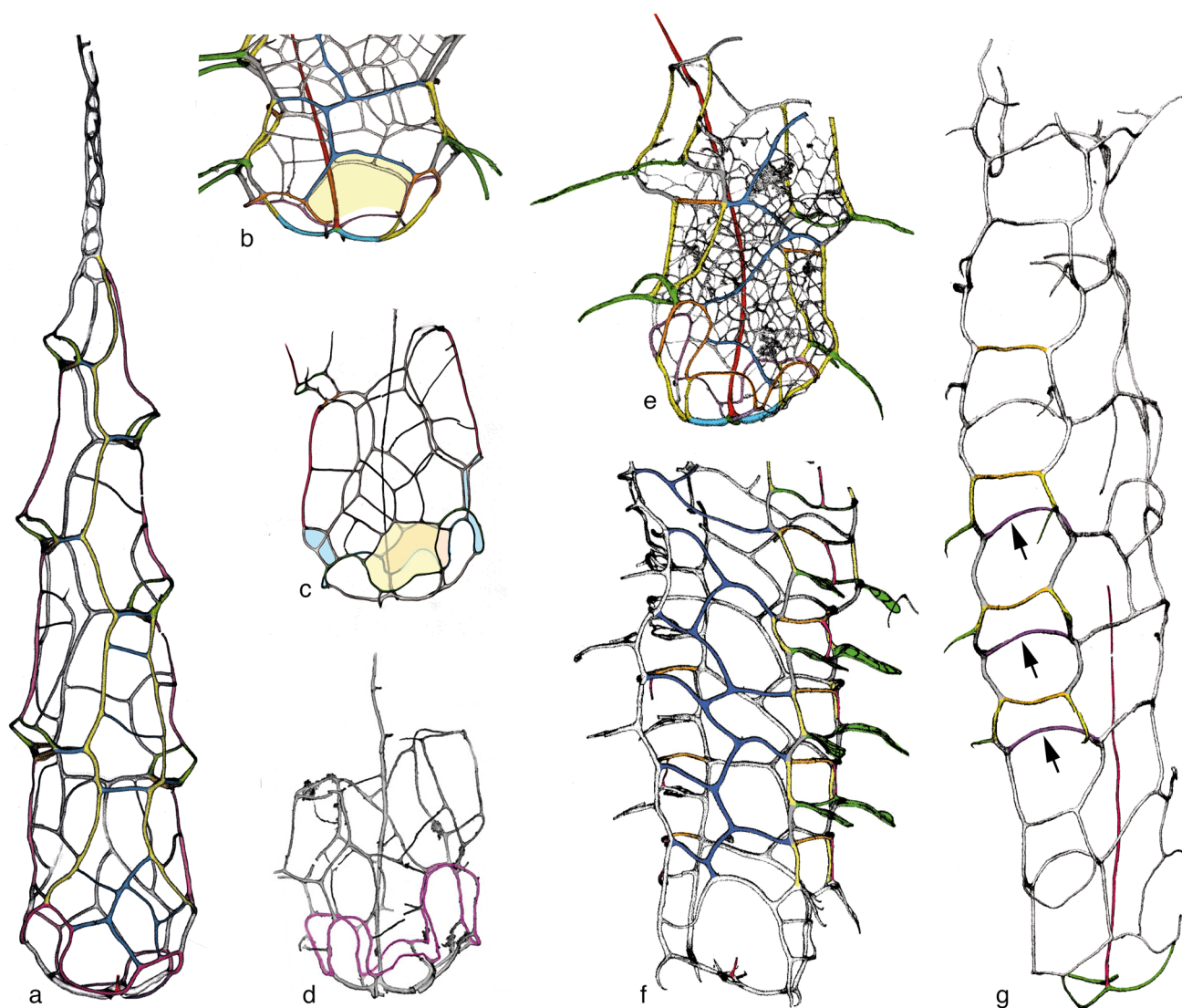


Fig. 2 Retiolitine construction. **a** *Holoretiolites erraticus* (Eisenack, 1951), MB.G. 1085, Sellin/Rügen. **b** *Spinograptus spinosus* (Wood, 1900), MB.G.1090, JM 64, Hiddensee, specimen with shallow ancora umbrella. **c** *Neogothograptus balticus*, juvenile, MB.G. 1082, Spandau/Berlin. **d** *Gothograptus auriculatus* Kozłowska et al., 2019 (modified from Kozłowska et al., 2019, Fig. 4a). **e** *Spinograptus spinosus*

(Wood, 1900)?, MB.G. 1078-5, specimen with deep ancora umbrella and large ventro-lateral lobes. **f** *Plectograptus robustus* (Obut and Zaslavskaya, 1983), MB.G. 1081, Spandau/Berlin. **g** *Cometograptus alfeisenacki* Maletz, 2010, MB.G. 1144-04, paratype (after Maletz 2010, Fig. 4F). See Fig. 3 for colour coding of characters

the post-extinction species and none crosses the event interval. Kozłowska et al. (2019) described the pre-extinction species in some detail and noted the special development of the genicular hoods as a meshwork of lists in these species and also documented the gradational change in the development of the mesh-based genicular hoods and associated veils along the colonies in some taxa. The same development of hoods can be seen in Jaeger's material (*Gothograptus osgaleae* sp. nov. and *Gothograptus berolinensis* sp. nov. herein), but veils are not present in these species. The transverse lists of the veil in earlier *Gothograptus* (Kozłowska et al. 2019) should not be confused with the transverse lists

(Bates et al. 2005) that represent the remains of the interthecal septae in the retiolitine colonies.

Immediately above the extinction event, *Gothograptus nassa* and *Gothograptus diminutus* with their simple, but large genicular hoods secreted from microfusellar tissues appear (Kozłowska et al. 2019). Their tubarium development is comparable to that of the earlier *Gothograptus* species, except for the hood construction. Microfusellar hoods are present in the pre-extinction species in the proximal end only (cf. *Gothograptus kozłowskii*: Kozłowska et al. 2019, Fig. 17). Thus, a distinct change in construction in the genus

Gothograptus can be seen across the extinction interval for which the reason is unclear.

Genicular hoods secreted as microfusellar tissue are present in *Semigothograptus meganassa* (Rickards and Palmer 2002), a taxon previously known only from the post-extinction recovery interval (Kozłowska 2016). Jaeger identified this species as *Gothograptus gigantonassa* (a nomen nudum, see Maletz 2010, Fig. 1). Recently, *Semigothograptus meganassa* was collected from the pre-extinction interval of the Kosov 2 section in the Czech Republic, showing that the genus crosses the boundary interval (Manda et al. 2019) and is more widely distributed stratigraphically than previously thought. The species differs from *Gothograptus* in its much more robust tubarium with a free nema inside the colony. The species also does not have an appendix, and thus does not show the finite growth so typical of all *Gothograptus* species.

The characteristic development of the ancora umbrella with seven meshes and a conspicuously lobate rim (Kozłowska et al. 2019, p. 438) is present in *Semigothograptus* and can be also found in the post-extinction *Baculograptus* and *Papiliograptus* (Lenz and Kozłowska-Dawidziuk 2002), suggesting an evolutionary connection. The depth of this construction is quite variable, however, and a comparable development (Fig. 2a, b) is seen also in the Ludlow species *Neogothograptus balticus* (Maletz 2008, Fig. 7D) and in *Holoretiolites erraticus* (Eisenack, 1951). All of these genera have relatively narrow, slit-like thecal orifices and an appendix, unlike those of *Plectograptus* (Fig. 2f) and its relatives with their large, square thecal orifices and the very shallow and often incompletely preserved ancora umbrella.

The cladistic analysis of Bates et al. (2005, figs. 8–10) regarded *Cometograptus* as ancestral to the clade including the *Plectograptus* and *Gothograptus* groups, that initiated the post-extinction diversification. Their evolutionary tree (Bates et al. 2005, Fig. 9), however, shows diversification into two lineages (*Plectograptus* and *Gothograptus* lineages) already at the base of the *Cyrtograptus lundgreni* Biozone. Kozłowska et al. (2009) discussed the evolution of the genus *Neogothograptus*, but their conclusions were inconclusive. Even though the authors favoured an origin through a *Gothograptus nassa* type ancestor, the cladistic analysis did not provide direct support for the interpretation and suggested that *Baculograptus batesi* may be ancestral to *Neogothograptus*. Thus, it was impossible to trace the lineage downwards into the pre-extinction interval. The origin and early evolution of the post-extinction retiolitines, thus, remain poorly constrained.

Systematic palaeontology

Terminology

The most important morphological terms to describe retiolitines are revised in Bates et al. (2005) and in Lenz et al. (2018). Bates and Kirk (1992, 1997) and Kozłowska-Dawidziuk (1990, 1995) may be consulted for additional information. The terms ‘lists’ and ‘rods’ have been used in earlier literature on retiolitine graptolites for the list construction of their tubaria (e.g., Bates et al. 2005; Melchin et al. 2017). It is here advocated to use the term ‘list’ exclusively (see Fig. 3). The term ‘rod’ should be restricted for round bars formed as spines (e.g., in the lacinia of the *Lasiograptidae*: Maletz 2019), in which no seams are found.

Taxonomy

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).

Repository

All 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. The original SEM numbers (JM XXX) are also provided. Additional material is curated at the Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (SMF).

Phylum **Hemichordata** Bateson, 1885

Class **Pterobranchia** Lankester, 1877

Subclass **Graptolithina** Bronn, 1849

Order **Graptoloidea** Lapworth in Hopkinson and Lapworth, 1875

Suborder **Axonophora** Frech, 1897

Infraorder **Neograptina** Štorch et al., 2011

Superfamily **Retiolitoidea** Lapworth, 1873

Family **Retiolitidae** Lapworth, 1873

Subfamily **Retiolitinae** Lapworth, 1873

Diagnosis. Tubarium generally preserved as framework of lists formed of cortical bandages surrounding highly attenuated and rarely preserved fusellar walls; proximal development of pattern R astogeny; thecal framework lists joined by ancora sleeve, a distal development of the ancora umbrella; fragments of fuselli generally preserved as shards remaining in thecal framework list seams; sricula often preserved in stratigraphically

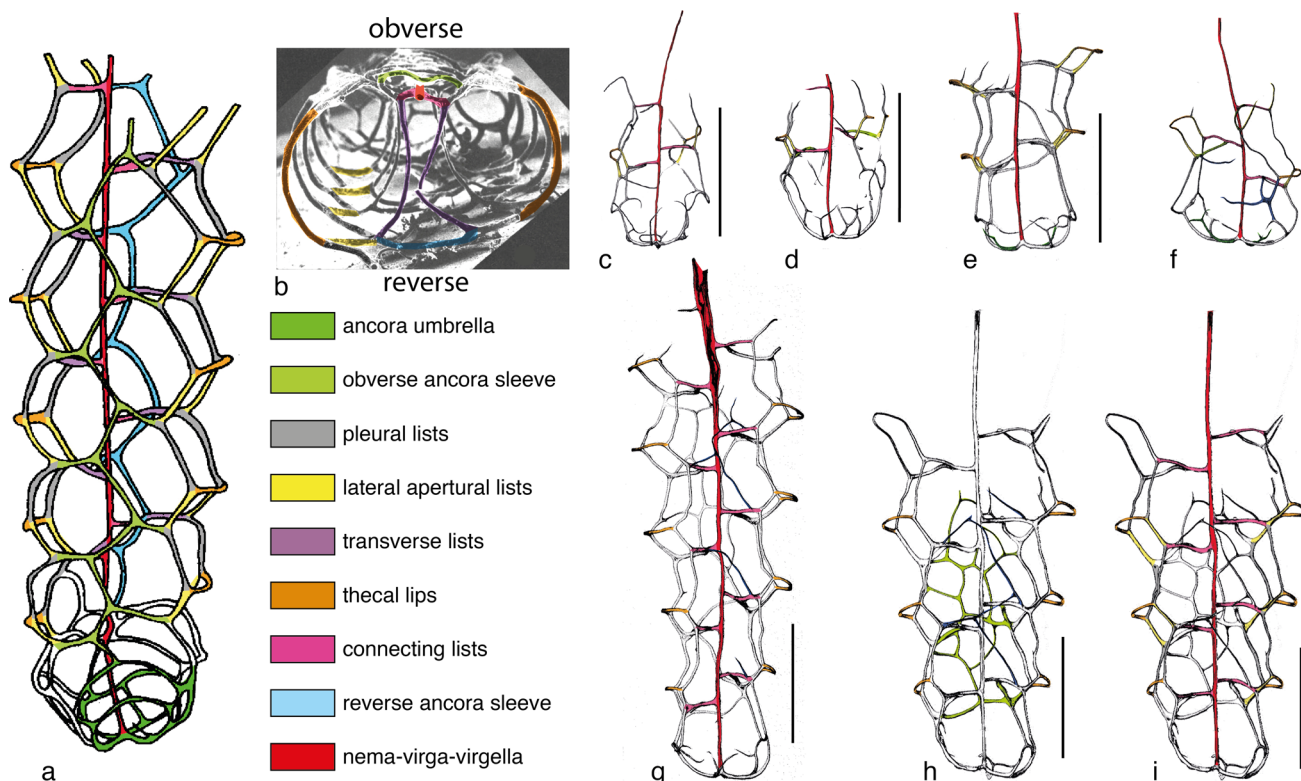


Fig. 3 Interpretation of tubarium construction in *Paraplectograptus*. **a** *Paraplectograptus areticulatus* (after Kozłowska-Dawidziuk, 1995, Fig. 8B: as *Pseudoplectograptus*; based on specimen in Lenz and Melchin, 1987, pl. 3, Fig. 2), reconstruction showing the colour coding of tubarium lists. **b** *Paraplectograptus areticulatus*, cross-section (after Lenz and Melchin, 1987, pl. 3, Fig. 5: as *Paraplectograptus praemacilentus*). **c, d** *Paraplectograptus eiseli*. **c** MB.G. 1084-01,

juvenile. **d** MB.G. 1084-02. **e–i** *Paraplectograptus hermanni* sp. nov. **e** JM 73-3, juvenile. **f** JM 73-8, juvenile. **g** JM 73-4, holotype, mature specimen showing nematularium and a few ancora sleeve list on the obverse side (dark blue). **h–i** JM 76-2, specimen in obverse view, showing ancora sleeve in colour (**h**) and ventral thecal outline and virgella–virga–nema complex (**i**). Scale bars indicate 1 mm

earlier taxa, but generally reduced or not preserved in younger forms; ancora sleeve list surfaces seamed on inside or outside, indicating presence of ancora sleeve membrane; bandages smooth, longitudinally striated or pustulose; virgella and nema connected by virga, a thickened longitudinal list on prosicula (revised from Lenz et al. 2018, p. 10).

Remarks. Lenz and Melchin (1987) differentiated the Plectograptinae from the Retiolitinae based on the surface ornamentation of their lists easily visible in SEM photos. This pustulose surface ornamentation was first recognized by Eisenack (1951, Fig. 11, "Höckerchen"—translatable to pustules) in *Plectograptus tetracanthus* (= *Plectograptus macilentus*) and other retiolitines. Eisenack (1951) also recognized that the virgula (nema) does not show this type of ornamentation. Melchin et al. (2011, 2017) did not support the differentiation of Plectograptinae and Retiolitinae. Melchin et al. (2011) included only *Hercograptus* and *Pseudoretiolites* in their analysis, thus, did not focus on the retiolitids. They, however, regarded *Hercograptus* as a member of their paraphyletic stem group Petalolithinae and separated these from the derived Retiolitinae. Melchin et al.

(2017) demonstrated that 'the simple twofold differentiation of the clade into the subfamilies Retiolitinae and Plectograptinae is not consistent with the phylogenetic relationships among the species'. They, thus decided not to separate the Plectograptinae from the Retiolitinae, a decision accepted by Lenz et al. (2018). A differentiation of the Plectograptinae would make the Retiolitinae a paraphyletic taxon.

Genus *Paraplectograptus* Bouček and Münch, 1952, 1952 [= *Pseudoplectograptus* Obut and Zaslavskaya, 1983].

Type species (monotypy). *Retiolites eiseli* Manck, 1918

Diagnosis. Slender, parallel-sided to distally widening or finite tubarium; ancora umbrella with seven meshes and often incomplete rim; nema with connecting lists; ventral sides formed by thecal lips, short lateral apertural lists and long pleural lists; transverse lists present; ancora sleeve lists well developed to lacking; ancora sleeve lists with seams facing outwards; bandages with pustules (revised from Lenz et al. 2018, p. 23).

Remarks. Lenz et al. (2018) synonymized *Pseudoplectograptus* with *Paraplectograptus*. Both taxa show generally the same tubarium construction, but in species referred to *Paraplectograptus*, the number and development of lists of the thecate tubarium and the ancora sleeve appeared to be reduced. Thus, species referred previously to *Pseudoplectograptus* appeared to have a more complex tubarium. The revision of the diagnosis of *Paraplectograptus* herein acknowledges the high variability in the preservation or development of the ancora sleeve lists. In some species, there are no ancora sleeve lists except for the pleural lists (e.g., *Paraplectograptus eiseli*), while in others (e.g., *Paraplectograptus areticulatus*), complete zigzag parietal lists are found on the obverse and reverse sides. Thus the development of the ancora sleeve is difficult to establish and to compare between species.

Distribution. *Paraplectograptus* species range possibly from the late Llandovery *Spirograptus turriculatus* Biozone to the Lower Homerian *Cyrtograptus lundgreni* Biozone. The genus did not survive the *Lundgreni* Extinction Event. The precise biostratigraphic ranges of most species are still uncertain. The presence of the genus in the *Spirograptus turriculatus* Biozone is based on ?*Paraplectograptus* sp., a species lacking the pustulose ornamentation and, thus, probably not belonging to the genus *Paraplectograptus*. It is based on a few juvenile specimens (Melchin et al. 2017).

Paraplectograptus eiseli (Manck, 1918).

Figures 3c, d, 4a, 5g–i

- 1913 *Retiolites Eiseli* Manck—Manck: 104 (nomen nudum).
- 1918 *Retiolites Eiseli* spec. nov. —Manck: 338, figs. 1–5.
- 1924 *Paraplectograptus Eiseli* (Manck) —Hundt: 81, pl. 11, Fig. 26; pl. 12, figs. 7–10. (Figures copied from Manck).
- ?1951 *Retiolites tenuis* n. sp. —Eisenack: 131, pl. 21, figs. 1–13; pl. 22, figs. 1–3; text-figs. 1,2.
- 1952 *Paraplectograptus eiseli* Manck—Münch: 82, pl. 16b, Fig. 4.
- 1952 *Paraplectograptus eiseli* (Manck) —Bouček and Münch: 136, pl. 1, Fig. 8; text-figs. 11a–h; figs. 11a,b.
- 1954 *Paraplectograptus eiseli* (Manck) —Cope: 322, figs. 2a,b.
- 1987 *Paraplectograptus eiseli* (Manck) —Lenz and Melchin: pl. 3, figs. 4, 11?, 12.
- ?1991b *Ret. (P.) eiseli*—Jaeger: Abb. 1.
- ?1993 *Paraplectograptus eiseli* (Manck) —Lenz: 21, pl. 13, figs. 1–4.

- 1995 *Paraplectograptus eiseli* (Manck, 1917) —Kozłowska-Dawidziuk: 282, Fig. 14a–i; 15d, e; 16a–d.
- 2012 *Paraplectograptus eiseli* (Manck) —Lenz et al.: 15, Fig. 7.1, 7.2, 7.5; pl. 1, figs. 1, 9.
- 2018 *Paraplectograptus eiseli* (Manck) —Lenz et al.: 23, Fig. 19.6c.
- 2019 *Paraplectograptus eiseli* (Manck) —Manda et al.: Fig. 10F.

Type material. Lectotype BAF 8/159, Wetterhammer, Gräfenwarth. The only preserved specimen from the Manck collection was selected by Bouček and Münch (1952) as the lectotype. As the drawings in Manck (1918) are highly stylized, it might not be possible to identify the remaining specimens. The lectotype (Lenz et al. 2018, Fig. 19.6c) is well preserved with a nearly complete proximal end, but the slab is weathered and some details are difficult to determine. Nevertheless, the specimen shows all characteristics of the species as figured by Manck (1918, Fig. 1).

Material. 16 specimens from Jaeger sample 257, MB.G. 1084, Sellin, Rügen island, Baltic Sea, NE Germany; glacial boulder; 11 specimens now preserved on SEM stub; 5 specimens in glycerin. Additional fauna unknown.

Remarks. Lenz et al. (2012) described the species in detail. Thus, a detailed description is not provided here. Jaeger identified a number of specimens from several samples as *Ret. (P.) eiseli*, but only a few of these specimens may be referred to this species. The remaining specimens can be referred to other species. The lectotype specimen shows a nicely preserved long tubarium counting about 14 thecal pairs, but the proximal part is incompletely preserved (see Lenz et al. 2012, Fig. 7.1). Manda et al. (2019, Fig. 10F) illustrated an even longer specimen from the Kosov 2 section of the Czech Republic, preserving about 20 thecal pairs, but the proximal end is lacking in the specimen, indicating that it may have been even longer.

Retiolitine specimens with a parallel-sided tubarium formed from a simple arrangement of lists have commonly been described under this name, but the true identity of some of the material remains uncertain. The lists include the lateral apertural lists, pleural lists, and thecal lips on the ventral sides and the nema–virga–virgella complex with the transverse lists inside (Fig. 3c, d). On the reverse side, there may be an irregular development of parietal lists referable to the ancora sleeve. Ancora sleeve lists on the obverse side have not been illustrated. The precise development of the tubarium and its ancora sleeve lists remains undescribed.

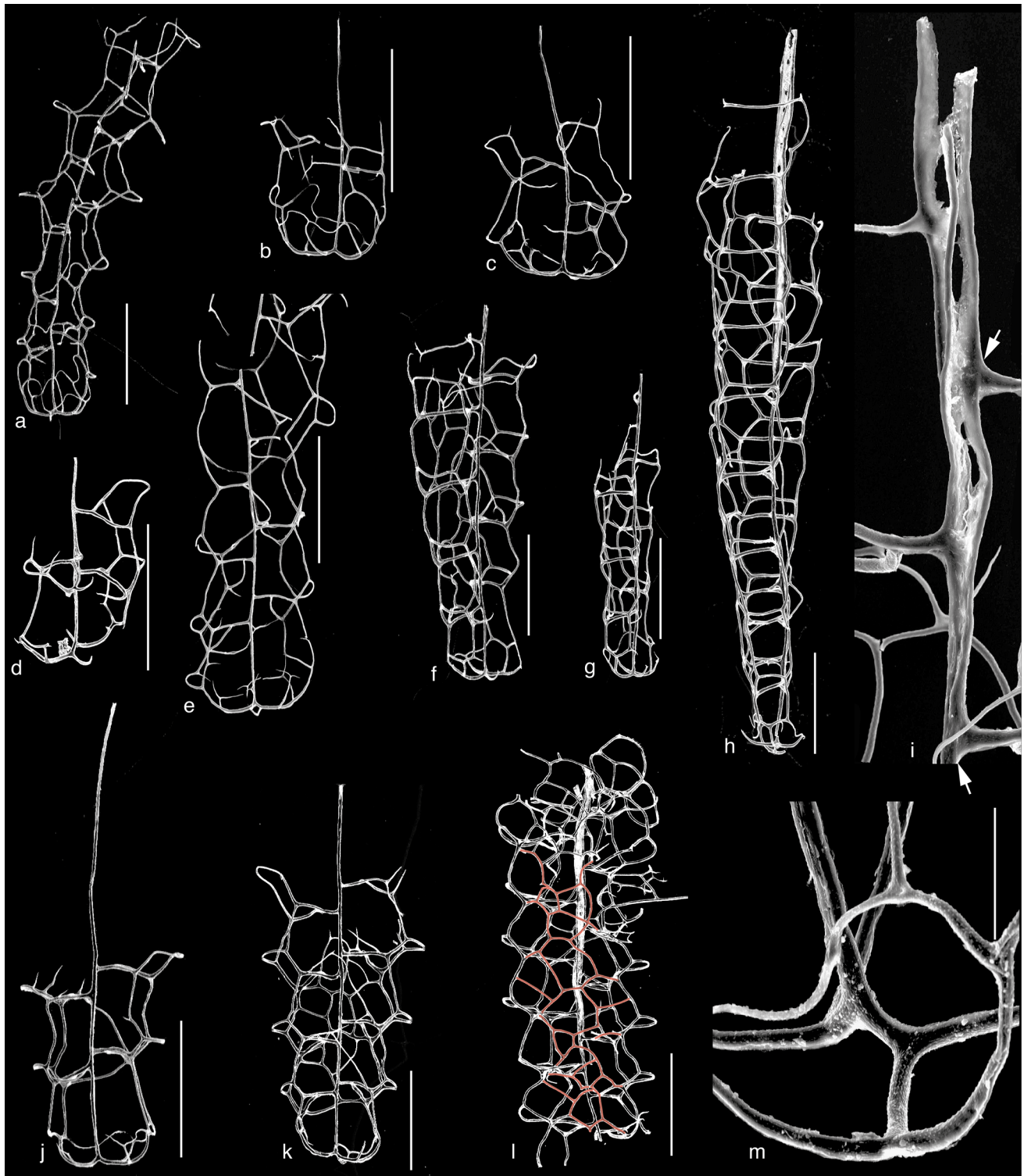


Fig. 4 *Paraplectograptus* specimens. **a** *Paraplectograptus eiseli* (Manck, 1918), JM 73-2. **b–m** *Paraplectograptus hermanni* sp. nov., Sellin, Rügen island. **b** JM 73-07, juvenile, reverse view. **c** JM 73-8, juvenile, reverse view. **d** JM 76-3, juvenile, oblique reverse view. **e** JM 73-9, oblique view. **f** JM 73-13, oblique view. **g** JM 73-6, oblique view, showing strange blob at nema. **h** JM 76-1, ventral view showing

lateral ancora umbrella lobes and distally widening tubarium. **i** JM 73-4, nematularium showing three vanes. **j** JM 73-3, juvenile, obverse view. **k** JM 76-2, obverse view, showing few slender obverse ancora sleeve lists. **l** JM 76-5, robust distal fragment with strong ancora sleeve lists (obverse parietal lists in red) and nematularium. **m** JM 73-11, ancora hub showing pustules. Scale bars indicate 1 mm

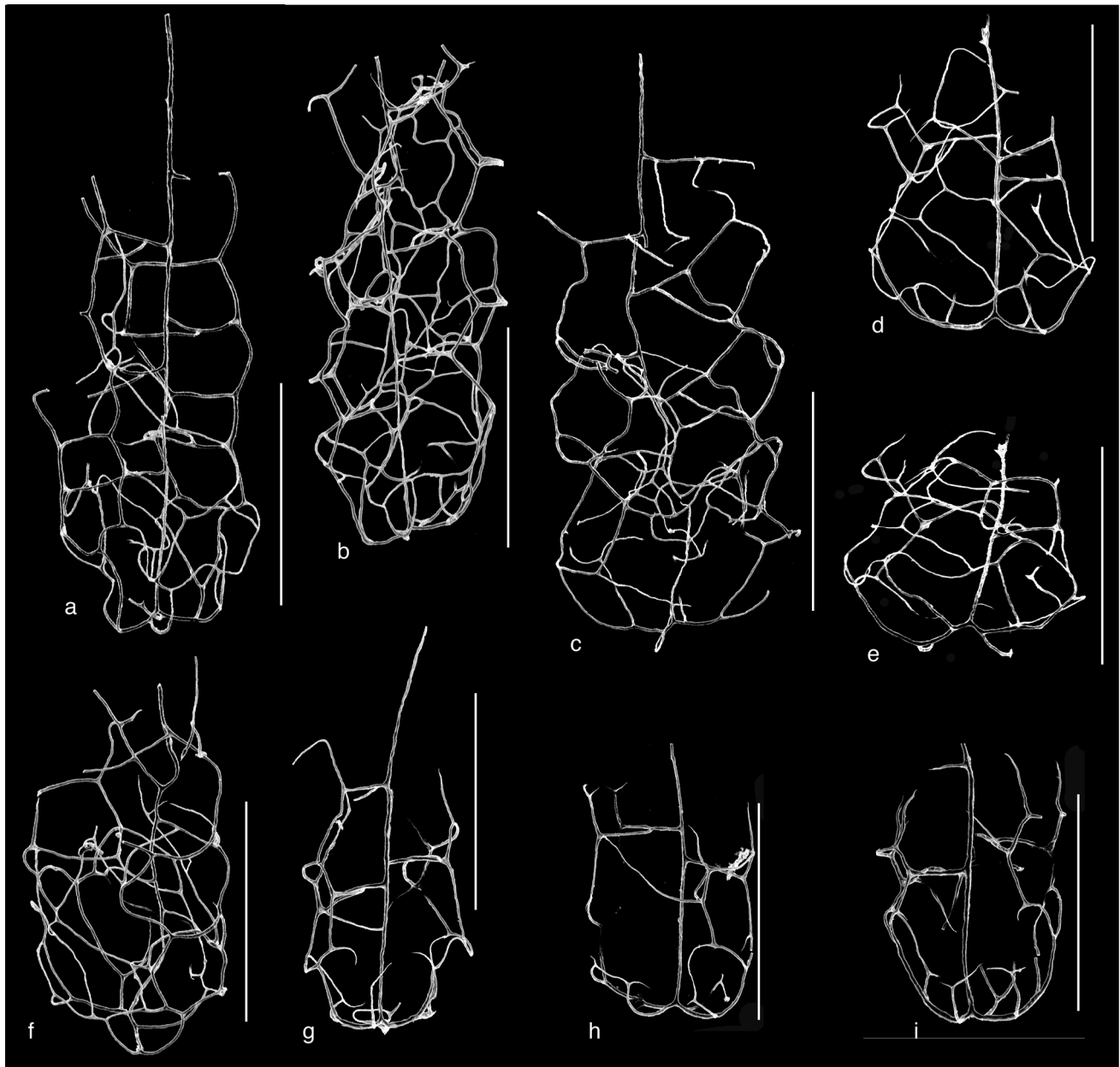


Fig. 5 a–f *Paraplectograptus* sp. a MB.G. 1121, JM 66-02. b MB.G. 1121, JM 66-04. c MB.G. 1121, JM 66-08. d MB.G. 1121, JM 66-12. e MB.G. 1121, JM 66-12, oblique view. f MB.G. 1121, JM 66-09. g–i

Paraplectograptus eiseli (Manck, 1918)?, juveniles. g MB.G. 1084-01. h MB.G. 1084-07. i MB.G. 1084-02. Scale bars indicate 1 mm

Distribution. The species was referred to Zone 18 by Manck (1918), probably correlatable to the *Cyrtograptus lundgreni* Zone of Jaeger (1991a, b, p. 315; his zone 31) and in Jaeger's notes. The use of the various number systems to name the Silurian graptolite zones of Germany is quite confusing and Maletz (2001, p. 171) suggested to abandon it. *Paraplectograptus eiseli* was found to range from the late Llandovery to the *Cyrtograptus lundgreni* Zone in the Cape Phillips Formation of Arctic Canada (Lenz 1993).

***Paraplectograptus hermanni* sp. nov.**

Figures 3e–i, 4b–m.

- ?1991b *Ret. (P.) eiseli*—Jaeger: Abb. 1.
 ?2008 *Paraplectograptus eiseli* (Manck) —Maletz, Fig. 1 J.
 2010 *Pseudoplectograptus* sp. —Maletz: Fig. 2F.

Material. 18 specimens preserved on SEM stubs from Jaeger sample 233 (JM 73, JM 76), Sellin, Rügen island, glacial boulder. The associated fauna includes *Monograptus priodon*, *Pristiograptus dubius* ssp. and *Cyrtograptus lundgreni* (poor fragments) as identified by Jaeger in his notes. All retiolitine specimens are regarded as representing various stages in the astogeny of a single *Paraplectograptus* species, even though a proof is not possible.

Origin of name. The name *hermanni* is used to honour the work of Hermann Jaeger on retiolitine graptolites.

Diagnosis. *Paraplectograptus* species with proximally slightly widening tubarium; a few ancora sleeve lists present; prominent nematularium in mature specimens.

Description. The tubarium is probably about 7–10 mm long in mature specimens. After about 3–4 mm, the nema develops into a long and slender nematularium, approximately 0.2 mm wide. The nematularium may show three-to-four blades (Fig. 4i), but the development is unclear due to the poor preservation in the few available specimens. It may initially have grown in advance of the tubarium (Fig. 3g) and was subsequently incorporated into the growth of the colony. A single distal tubarium fragment shows a ca. 4 mm-long nematularium, broken distally, incorporated completely into the tubarium (Fig. 4l). The specimen also shows the densest development of the ancora sleeve lists and is about 1.9 mm wide. The nematularium shows thickened rims and quite thin membranes in between (Fig. 4i). The nema–virga–virgella complex starts in the centre of the colony, but bends considerably to the obverse side and appears to be incorporated quickly into the lateral tubarium wall (Fig. 4h) before the first thecal pair is developed.

The proximal development of the tubarium is only partially recognizable. In ventral view, distinct lateral lobes of the ancora umbrella can be seen (Fig. 4h), providing a width of 0.6–0.65 mm, while the ventral width of the tubarium is only 0.35–0.4 mm, reaching distal values of ca. 0.6–0.7 mm. Precise measurements are impossible to give, as the delicate specimens show considerable distortion. In lateral view, the tubarium is about 0.9 mm wide at the ancora umbrella and widens to 1.5 mm along the first three thecal pairs, reaching maximum values of ca. 1.8 mm.

The ancora umbrella appears to be quite simple, consisting of few lists, but the details are uncertain in the fragmentary material. There are probably seven meshes and an often incomplete rim, but the partially distorted specimens do not allow to recognize the precise orientation of the lists and the shape of the meshes. Especially, the lateral lobes at the base of the lateral proximal orifices often appear to be broken or missing in the material. The branching of the ancora hub

into second- and third-order branches can be recognized, but a distinct and complete ancora umbrella rim is not recognizable in the available specimens. Two stronger second-order branches form the most prominent features growing to the ventral sides of the tubarium. The lateral second-order branches remain more delicate, but also branch into third-order branches. The third-order branches presumably form the (incompletely preserved or developed) ancora umbrella rim.

The virgella, virga, and nema produce a distinct vertical list in the tubarium, distally developing into the nematularium. Horizontal connecting lists develop from the nema in both ventral directions (Fig. 3g, i). They are produced from alternate obverse and reverse sides of the nema, as can be seen by the presence of distinct seams (arrows in Fig. 4i). A visible seam is present on the reverse side at the junction between the nema and the connecting list of $th1^1$. On the same side the seam between the nema and the connecting list of $th1^2$ is not visible, indicating that it was formed from the other side.

Outwards inclined lateral apertural lists and inwards inclined pleural lists (Fig. 3i) form the edges of the tubarium and produce a distinct zigzag outline. The apertural lips connect the obverse and reverse sides and are more prominent when the tubarium is flattened, but may be much less prominent in three-dimensionally preserved material. The development of the transverse lists is unclear in the material, as they are difficult to see in the lateral preservation shown by most specimens.

The ancora sleeve is recognized on the obverse side by a few thin lists in small specimens with about four thecal pairs (Fig. 3i). On the reverse side, fairly irregular ancora sleeve lists develop (Figs. 3h, 4l), forming a meshwork to counterbalance the obverse side with its thick development of the nema–virga–virgella complex and the connecting lists. The ancora sleeve development may, however, be quite variably expressed and specimens with few lists exist (Fig. 3g).

Remarks. This species is described as new as it is the only species of *Paraplectograptus* with a distinct nematularium, suggesting a finite tubarium growth. A single specimen of *Paraplectograptus eiseli* (Fig. 4a) recognized in the Jaeger collection was associated with this taxon in the sample. Even though not very long, it exceeds the length of *Paraplectograptus hermanni* sp. nov., in which the nematularium growth starts. The specimen does not show any indications of a nematularium and is therefore unlikely to belong *Paraplectograptus hermanni* sp. nov.

Distribution. Jaeger, in his notes, referred the material to the *Cyrtograptus lundgreni* Biozone based on the associated monograptid fauna.

***Paraplectograptus* sp.**

Figure 5a–f

Material. Jaeger sample 61 (MB.G. 1121). 20 isolated specimens on SEM stub and additional ca. 15 specimens in glycerin.

Locality. Kap Arkona, Rügen, NE Germany, glacial erratic boulder. The specimens are associated with *Pristiograptus dubius*, *Monograptus priodon flemingi*, *Cyrtograptus* sp., and *Monoclimacis* sp. of *vomerina* type (all as determined by Jaeger).

Description. The size of the mature specimens of this species is uncertain, as only juvenile specimens are present in the collection. They reach a maximum length of ca. 3 mm and width of 1.3–1.4 mm. All specimens appear to be distorted and the identification of list structures is difficult. The rim of the ancora umbrella is somewhat undulating, but is often incompletely preserved. The lateral proximal orifices are moderate in size and bear only thin lists. They may be overgrown with additional lists in more mature specimens. The ventral sides are outlined by apertural lips, lateral thecal lists, and pleural lists. The nema is connected with connecting lists to the lateral thecal lists and pleural lists on the obverse side, and is overlain by the irregularly developed ancora sleeve lists. Loosely spaced and irregular ancora sleeve lists can be seen on the obverse and reverse side of the tubarium. A distinct orientation or regularity is not observed, but this may be because of the immaturity of the material.

Remarks. As all available specimens are distorted and fragmented, it is not possible to assign the specimens with certainty to a described species. The material is most similar to *Paraplectograptus reticulum* (Lenz et al., 2012) illustrated by two mature specimens from the upper Sheinwoodian of Arctic Canada. The material, however, was not described in detail and the precise development of the ancora sleeve is unclear.

Genus ***Gothograptus*** Frech, 1897

Type species (original designation). *Retiolites nassa* Holm, 1890

Diagnosis. Finite, tubarium with appendix; ancora umbrella with strongly undulating rim and paired ventral lobes; outer ancora in some species; nema with connecting lists, incorporated into obverse ancora sleeve wall above first or second theca; reverse side of ancora sleeve with oblique parietal lists; ventral side with thecal lips, genicular lists, mid-ventral lists, long lateral apertural lists and short pleural lists; ancora

sleeve and ventral thecal walls densely reticulated; genicular hoods; variably formed from microfuselli or a meshwork of lists; extensive veils cover the apertures in some taxa; ancora sleeve lists with seams facing inwards; bandages with pustules (revised from Lenz et al., 2018, p. 20).

Remarks. Kozłowska et al. (2019, p. 440) stated that *Gothograptus* does not have an outer common canal and that the thecal walls are attached to the ancora sleeve wall, ‘distal to the first two thecal orifices, on both the obverse and reverse sides’. This observation raises the question as to whether there are thecal walls and ancora sleeve walls present at all. This would present a constructional feature separating *Gothograptus* from many other retiolitines. A separation of the lateral thecal walls and the ancora sleeve walls is clearly present in many plectograptines as was shown by the preservation of both walls in *Spinograptus praerobustus* Lenz and Kozłowska-Dawidziuk, 2002 (Lenz 1994, figs. 2.2–2.5). A lack of an ancora sleeve wall has to be interpreted for *Gothograptus*, as the nema and the connecting lists of the thecal walls are clearly preserved on the obverse tubarium wall, demonstrated in the material here identified as *Gothograptus storchi*?. Thus, the lateral (obverse and reverse) walls represent the thecal sides, but in the proximal part, remains of the ancora sleeve may still be present. The proximal ancora sleeve walls, thus, grade into the lateral thecal walls.

A number of *Gothograptus* species are found in the *Cyrtograptus rigidus* to the *Cyrtograptus lundgreni* Biozone (Kozłowska-Dawidziuk 1990; Kozłowska et al. 2019) and the genus continues into the *Colonograptus praedeubeli* Biozone. While four closely related *Gothograptus* species are known from the *Cyrtograptus lundgreni* Biozone, these did not survive the *Lundgreni* extinction event, but are replaced by *Gothograptus diminutus* and *Gothograptus nassa* in the post-extinction *parvus-nassa* and *dubius-nassa* intervals (Kozłowska et al. 2019, Fig. 1). *Gothograptus auriculatus* appeared in the *Colonograptus praedeubeli/deubeli* Biozone as the youngest species of the genus.

All *Gothograptus* species possess an ancora umbrella with a strongly undulating rim formed from paired ventrolateral loops (Fig. 6a) and horizontal lateral lobes of the ancora umbrella (Fig. 6c) at the base of the lateral orifices. The asymmetry of the ancora umbrella together with the position of the pre-thecal ventral orifices may be used to identify the obverse and reverse sides of the tubaria (Fig. 6b, c). The obverse side of the tubarium is also recognizable by the incorporation of the nema into the ancora sleeve wall, but it is often difficult to see, due to additional cover of details with cortical bandaging.

The pre-extinction species of *Gothograptus* can be differentiated by the development of their genicular hoods (Fig. 6d, e) and veils from the simple hoods (*nassa* hoods

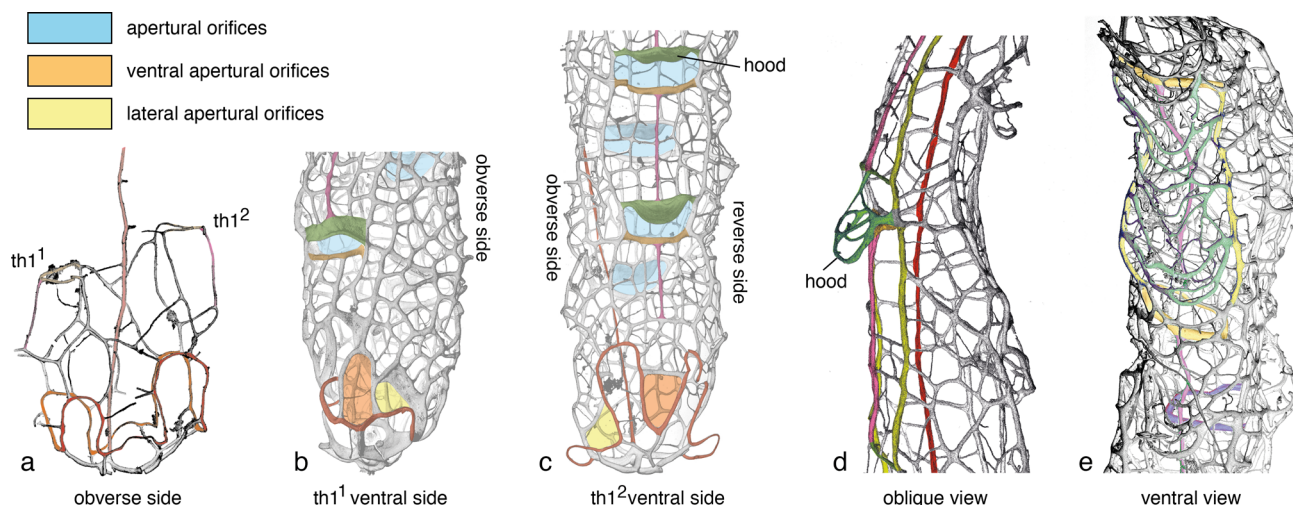


Fig. 6 *Gothograptus* development. **a** *Gothograptus auriculatus* Kozłowska et al., 2019, juvenile showing ancora umbrella rim with extensive ventro-lateral lobes (after Kozłowska et al., 2019, Fig. 4A). **b** *Gothograptus nassa* (Holm, 1890), proximal end of longer specimen, oblique view showing ventral $th1^1$ side (after Kozłowska

et al., 2019, Fig. 11A). **c** *Gothograptus nassa* (Holm, 1890), ventral $th1^2$ side (after Kozłowska et al., 2019, Fig. 11G). **d** *Gothograptus osgalae* sp. nov., showing genicular hood (in green), SMF 75840. **e** *Gothograptus* sp., showing extensive genicular growth of hood (in green), SMF 75835. Illustrations not to scale

of Kozłowska et al. 2019) of the post-extinction species (Fig. 6b, c). The pre-extinction species show a high variability of constructional details and the differentiation of species is difficult in many cases, especially in flattened shale material. Several previously undescribed taxa are recognized in the Jaeger collection and are here compared with the species described by Kozłowska-Dawidziuk (1990) and Kozłowska et al. (2019). The material shows a high species level diversity, but little is known about the precise biostratigraphical distribution of these species. It appears clear that considerable astogenetic variation may cause problems in species differentiation also. The late stage addition of genicular constructions is typical of the genus *Gothograptus* and juveniles of all species are extremely similar.

Kozłowska-Dawidziuk (1990) differentiated the genus *Eisenackograptus*, in which the nema is incorporated in the ventral ancora sleeve wall only distally, from *Gothograptus*, where the nema is completely embedded in the obverse tubarium wall. *Eisenackograptus* (Fig. 1f) bears undulating ventral thecal walls with distally opening apertural orifices, lacking a geniculum and any genicular or apertural hoods or elaborations. Parietal lists are poorly differentiated and often not recognizable, while lateral apertural lists are vertical and combined with short pleural lists. In *Gothograptus*, the lateral apertural lists are more sigmoidal to outwards sloping. The tubarium bears distinct hooded geniculae with the thecal lips often hidden behind these extensive hoods.

Thus, distinct constructional characters separate *Eisenackograptus* and *Gothograptus* and the outline of both taxa may not show a closer phylogenetic relationship.

Unfortunately, the precise development of the ancora umbrella is not described for *Eisenackograptus*.

Gothograptus nassa (Holm, 1890).

Figures 6b, c, 7a–f

- 1890 *Retiolites nassa* n. sp.—Holm: 25, pl. 2, figs. 12–14.
- 1895 *Retiolites nassa* Holm—Wiman: 279, pl. 1, figs. 1–14.
- 1896 *Retiolites nassa* Holm—Wiman: 240, figs. 12–14.
- 1952 *Gothograptus nassa* Holm—Münch: 82, pl. 16b, Fig. 1a.
- 1952 *Gothograptus nassa* (Holm)—Bouček and Münch (English version): 112, pl. 1, figs. 9–11; text-figs. 2a–i; 3a–d.
- 1952 *Gothograptus intermedius* n. sp.—Bouček and Münch (English version): 115, text-figs. 3e–f.
- 1979 *Gothograptus nassa* (Holm)—Obut and Zaslavskaya: 33, pl. 2–3.
- 1991b *Gothograptus nassa* (Holm)—Jaeger: 304, Fig. 1 (no description).
- non 1999 *Gothograptus nassa* (Holm) —Kozłowska-Dawidziuk: 156, Fig. 3B (= *Gothograptus diminutus* Kozłowska et al., 2019).
- 2001 *Gothograptus nassa* (Holm)—Kozłowska-Dawidziuk and Lenz: Fig. 3.1, 3.13.
- 2004 *Gothograptus nassa* (Holm)—Kozłowska-Dawidziuk: Fig. 5D,G.

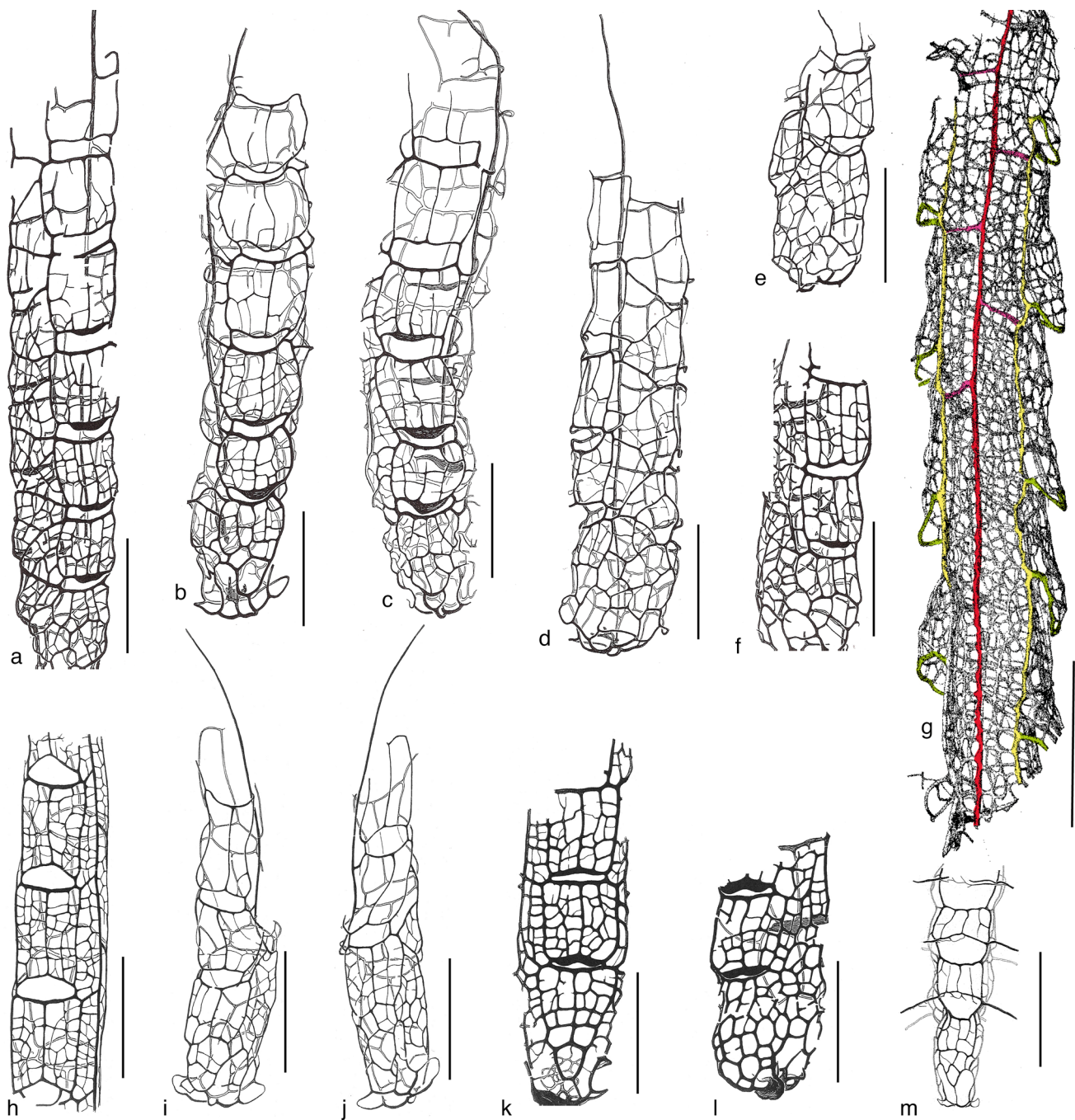


Fig. 7 **a–f** *Gothograptus nassa* (Holm, 1890). Illustrations of Jaeger representing his early form. Original drawings. Material not identified. **b** is shown in Maletz (2010, Fig. 2 K). **g** *Gothograptus berlinensis* sp. nov., JM 84-03, holotype, inverted SEM photo, important constructional details indicated in colour. **h–l** *Gothograptus storchi* Lenz and Kozłowska, 2006?, originally identified as *Gothograptus*

praenassa of Jaeger (nomen nudum), illustrations by Jaeger. **h** SMF 75836, fragment with three thecal pairs. **i, j** juvenile, not preserved. **k** SMF 75839, incomplete proximal end with two thecal pairs. **l** proximal end, not identified. **m** *Papiliograptus retimarginatus* Kozłowska and Bates, 2021, MB.G. 1092, ventral view, drawing by Jaeger. Scale bar indicates 1 mm for all specimens

2006 *Gothograptus nassa* (Holm)—Calner et al.: Fig. 1C–C, E–I.

non 2008 *Gothograptus nassa* (Holm)—Maletz: Fig. 1 N (= *Gothograptus auriculatus*).

2010 *Gothograptus nassa* early form (Frühform)—Maletz: Fig. 2 K.

non 2016 *Gothograptus nassa* (Holm) — Kozłowska: 535, Fig. 1b (= *Gothograptus diminutus* Kozłowska et al., 2019).

Type material. Holm (1890, pl. 2, figs. 12–14) illustrated two fragments of *Gothograptus nassa* from Djupvik, Gotland (Sweden) upside down. Lenz et al. (2018, Fig. 18.3a) provided a photo of the holotype of the species as NRM-PZ Cn0025546 (Natural History Museum Stockholm, Sweden). The specimen shows clearly the ventral pre-theccal opening of the incompletely preserved proximal end. The opening appears as a triangular opening standing on its tip, suggesting that the th¹ side of the colony is represented.

Diagnosis. Robust *Gothograptus* species with dense reticulum in mature specimens; genicular hoods formed from microfusellar tissues.

Remarks. Wiman (1895, 1896) provided a detailed description and illustration of this species from isolated material, even though he misinterpreted the appendix as the proximal end. He also commented on "a certain regularity" of the meshes. Actually, the development of clathria and reticulum is much more irregular than in most of the younger plectograptines, but irregularly placed parietal lists can be recognized in most parts of his specimens (Wiman 1895, pl. 11, figs. 2, 3, 7) that are all shown from the reverse side.

The material of Jaeger identified as *Gothograptus nassa*—early form (see Maletz 2010, Fig. 1, 2) has not been identified. His late form is here identified as *Gothograptus auriculatus*. In a letter to A. Lenz (Jaeger, 29.05.1991), Jaeger stated that his *Gothograptus nassa* (early form) developed the apertural lappets (genicular hoods herein) early in its astogeny, approximately after the first four thecal pairs had grown beginning at the proximal end, spreading distalwards. In his late *Gothograptus nassa* (*Gothograptus auriculatus* herein), the hoods began to grow only when the final size of the colony was attained. They initially grew in the distal part of the colony and spread proximally. Jaeger also produced a number of previously unpublished illustrations of *Gothograptus nassa* that are shown here (Fig. 7a–f).

Obut and Zaslavskaya (1979, pl. 2, figs. 1–5) illustrated a number of juveniles under the name *Gothograptus nassa* in which a complete prosicula with distinct longitudinal lists is visible. This is the only record of a preserved prosicula in *Gothograptus*, but the material may belong to another retiolitine species.

Distribution. The species is common in the *Pristiograptus parvus*/*Gothograptus nassa* and *Pristiograptus dubius*/*Gothograptus nassa* biozones, and ranges into the lower *Colonograptus praedeubeli/deubeli* Biozone (Kozłowska et al. 2019; Fig. 1). Differentiation of smaller specimens from the closely related *Gothograptus auriculatus* may be difficult.

Gothograptus auriculatus Kozłowska et al., 2019

Figures 6a, 8a–n, 9a–s.

- pars 2004 *Gothograptus nassa* (Holm, 1890)—Porębska et al.: Fig. 3 M, N (not figs. 3G, K, N; *Gothograptus nassa*).
- 2006 *Gothograptus nassa*—Calner et al.: 80, Fig. 1E.
- 2008 *Gothograptus nassa* (Holm, 1890)—Maletz: Fig. 1 N.
- 2010 *Gothograptus nassa* (Holm, 1890), late form (of Jaeger)—Maletz, 2010: Fig. 2L, M.
- 2019 *Gothograptus auriculatus* n. sp.—Kozłowska et al.: 451, figs. 2, 3, 4A, B, 13–14.

Material. 24 specimens on SEM stubs, ca. 25 specimens in glycerin, MB.G 1145, Jaeger 347, isle of Hiddensee, near Rügen island, Baltic Sea, NE Germany, glacial erratic boulder (sample includes the type material of *Colonograptus praedeubeli*).

29 specimens on SEM stub, ca. 50 specimens in glycerin, MB.G 1092, Jaeger 354, isle of Hiddensee, near Rügen island, Baltic Sea, NE Germany. Jaeger identified this material as *Retiolites nassa* in his notes. The sample includes also a single proximal end of *Papiliograptus retimarginatus*.

Diagnosis. *Gothograptus* species with genicular hood formed from microfusellar tissue; auriculae formed on the pleural lists; these are often asymmetrically developed or may be present on one side of the thecal aperture only (modified from Kozłowska et al. 2019).

Description. The tubarium has about 12–15 thecal pairs, but complete specimens are not available from the Jaeger collection. However, the longest specimen (Fig. 9s) bears eleven thecal pairs, but is incomplete distally. Kozłowska et al. (2019, table 1) were also unable to recognize the final length of this species. Mature tubaria bear a dense meshwork of ancora sleeve lists (Figs. 8, 9). The density increases during the growth of the colony and juvenile specimens appear to start to secrete ancora sleeve lists at an early stage, probably after one or two thecal pairs are grown. This may be seen in smaller specimens with about three thecal pairs (Figs. 8f, h, m, 9i, j, l), in which a considerable development of the ancora sleeve lists can already be seen. Tubaria with about seven thecal pairs (Figs. 8e, 9d) already show the strong decreasing gradient in the density of the ancora sleeve lists of the growing colony.

The genicular hoods on the thecae appear at a relatively late astogenetic stage. Even specimens with about seven thecal pairs do not possess any genicular hoods (Fig. 9d). The hoods are formed from microfusellar material and appear to be somewhat asymmetrical and often are somewhat pointed

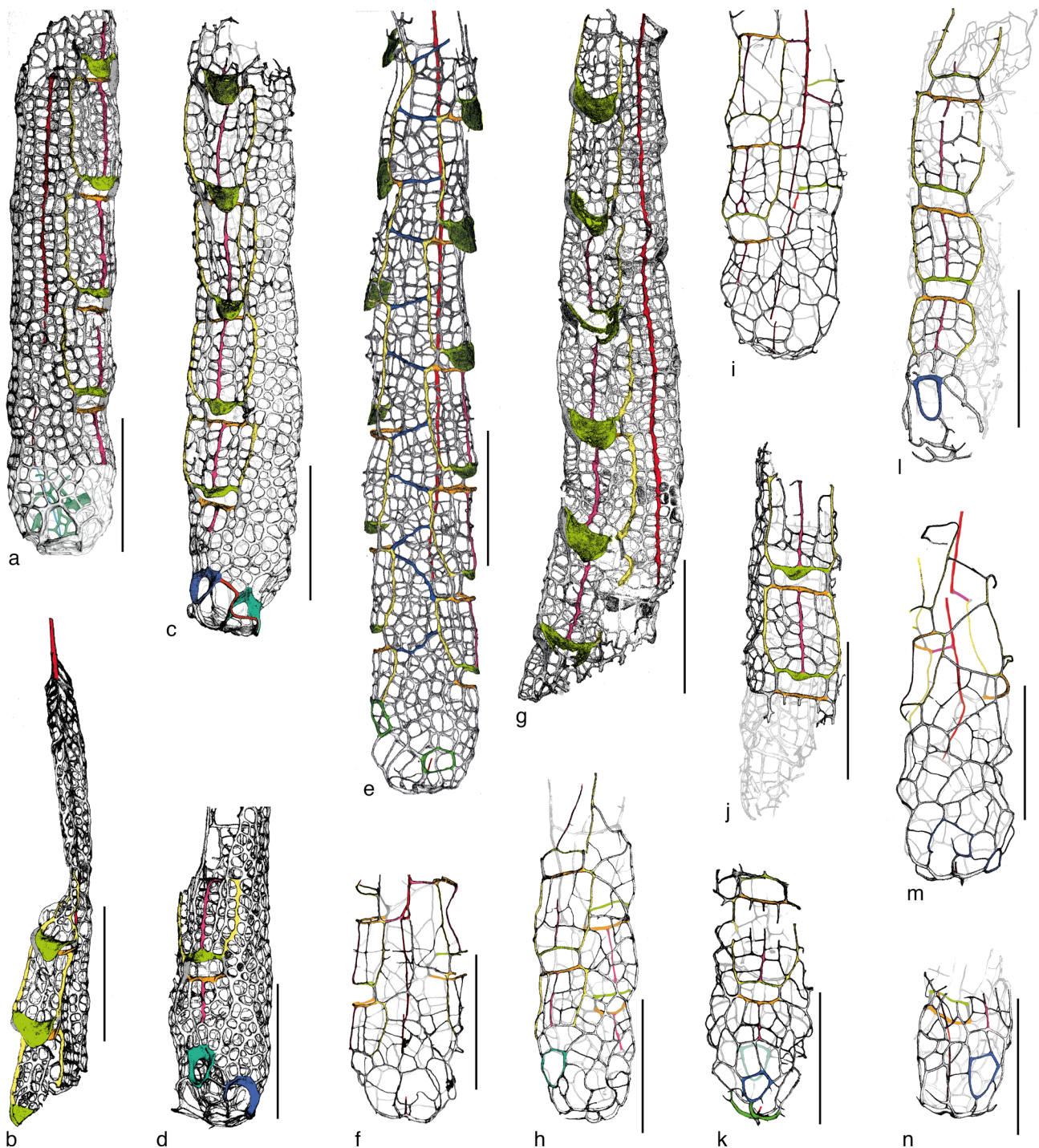


Fig. 8 *Gothograptus auriculatus* Kozłowska et al., 2019, inverted and coloured SEM photos, Hiddensee, near Rügen island, Baltic Sea, NE Germany. **a** MB.G. 1092-6, long proximal fragment, obverse view, note the internal meshwork in proximal end (green). **b** MB.G. 1092-18, mature distal end with appendix. **c** MB.G. 1092-04, proximal fragment in oblique reverse view. **d** MB.G. 1092-17, ventral view. **e** MB.G. 1145-10, specimen with six thecal pairs, lacking the appendix, reverse view, parietal lists in blue. **f** MB.G. 1145-2, juvenile, obverse

view. **g** MB.G. 1092-15, distal fragment, obverse view, appendix broken. **h** MB.G. 1092-5, small specimen in oblique reverse view. **i** MB.G. 1145-3, juvenile, oblique reverse view. **j** MB.G. 1092-7, fragment, ventral view. **k** MB.G. 1145-1, poor proximal end, ventral (th¹ side) view. **l** MB.G. 1092-1, fragment in ventral view. **m** MB.G. 1092-3, juvenile, reverse view. **n** MB.G. 1092-10, juvenile, ventral view. Scale bars indicate 1 mm

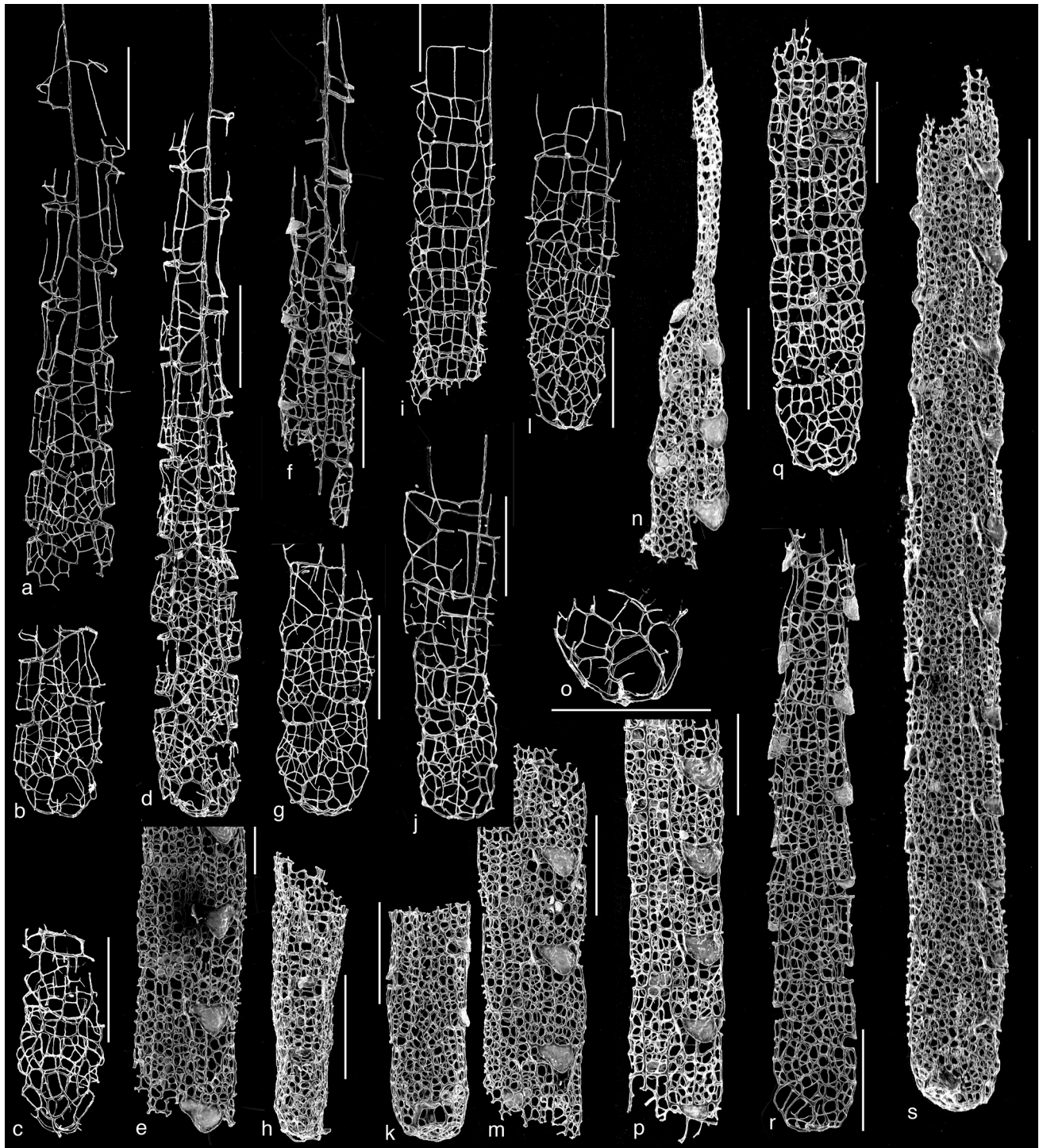


Fig. 9 *Gothograptus auriculatus* Kozłowska et al., 2019, Hiddensee, near Rügen island, Baltic Sea, NE Germany. **a** MB.G. 1145-4, fragment with few ancora sleeve lists, obverse view. **b** MB.G. 1145-2, proximal end in lateral view. **c** MB.G. 1145-01, proximal fragment in ventral view. **d** MB.G. 1145-5, reverse view. **e** MB.G. 1145-6, fragment. **f** MB.G. 1145-11, fragment. **g** MB.G. 1145-3, lateral view. **h** MB.G. 1145-9, proximal fragment in ventral view. **i** MB.G. 1145-2, ventral view. **j** MB.G. 1145-9, ventral view. **k** MB.G. 1145-4, proximal

mal fragment of mature specimen, obverse view. **l** MB.G. 1145-8, oblique ventral view. **m** MB.G. 1145-7, fragment, oblique view. **n** MB.G. 1145-11, distal end of mature tubarium with long appendix. **o** MB.G. 1145-07, juvenile. **p** MB.G. 1145-8, fragment, oblique obverse view. **q** MB.G. 1145-3, oblique view. **r** MB.G. 1145-10, sub-mature specimen lacking distal end, reverse view. **s** MB.G. 1145-5, proximal end of longest specimen, obverse view. Scale bars indicate 1 mm

(Figs. 8g, 9e, m), but this is not invariably seen in the material. There is a distinct gradient in the development of the hoods. The size of the hoods increases considerably along the first six thecal pairs (Fig. 8e). There is barely any development of hoods in the first thecal pair and the final size is reached at thecal pair five or six. In mature specimens, the youngest genicular hoods do not reach the maximum size observed in the middle part of the tubarium, but still cover the thecal orifices completely.

The appendix is up to 2 mm long in mature specimens (Figs. 8b, 9n), starting to grow directly from the top of the last theca. On its obverse side, the nema is incorporated and extends at least 1 mm above the orifice of the appendix. Its free part is slightly more robust than the part incorporated into the appendix. The appendix is about 0.2 mm wide at the start and widens slightly to a width of 0.3 mm at the orifice. The appendix shows a densely reticulated construction.

The tubaria are outlined by a number of main lists that can be regarded as characteristic and useful to understand the development. The thecal orifices are outlined by apertural lips, genicular lists, and pleural lists (Fig. 8l). The apertural lip is connected to the previous genicular list by the mid-ventral list, but irregularly developed secondary lists form a meshwork on this supposed preservation of the supragenicular thecal wall (cf. Bates et al. 2005, Fig. 5D).

The meshwork of the ancora sleeve lists differs on obverse and reverse sides. On the obverse side, a higher regularity of fine meshes is apparent through the straight vertical development of the nema, incorporated into the ancora sleeve wall (Figs. 8a, g, 9p, s). The nema–virga–virgella complex (cf. Bates et al. 2005) is free inside the colony in juvenile specimens up to the second thecal pair before it is incorporated into the ventral ancora sleeve wall and then is easily visible from the outside. This development may show the length of the sicula. Before the incorporation into the lateral ancora sleeve wall, the complex is fairly slender and often broken off (Fig. 8m), but after joining the lateral wall, it becomes much thickened (Fig. 8a, i).

The ancora umbrella is fairly simple, formed from a low number of meshes (Fig. 6a), but is quickly obscured by the addition of secondary lists and may be difficult to observe in mature specimens in which lists are considerably thickened (Fig. 8c, d). The paired ventro-lateral lobes on the th1² side reach much higher than those on the th1¹ side. Thus, the ancora umbrella is quite asymmetrical. The lateral apertural lobes stretch out like paired wings in three-dimensionally preserved specimens (Fig. 8n), but in flattened material appear to be flipped upwards. Thus, the lateral proximal orifices were described as kidney-shaped in the past (Lenz et al. 2018; Kozłowska et al. 2019), but are often more rounded to triangular in lateral view. Parts of the proximal lateral orifices are obscured by secondary lists in mature specimens.

The rims of the proximal ventral orifices are strongly thickened and widened in mature specimens (Fig. 8c, d) and, thus are easily recognized. Thickening and widening can also be seen in the ancora hub lists and in part of the lateral proximal orifices, but details have not been recognized. Kozłowska et al. (2019, figs. 13a, B, D; 14C-F) illustrated the widening, but did not analyze this feature in detail. Thus, it is uncertain, which lists of the ancora umbrella construction are involved. The lateral apertural loops of the ancora umbrella appear to be less involved than the ancora umbrella prong lists (see Kozłowska et al. 2019, Fig. 14C-E).

An internal meshwork of lists can be seen in the proximal part of a few mature specimens (Fig. 8a), but details are unclear. These meshes may represent lists formed on the thecal wall of th1¹, as can be seen in *Eisenackograptus eisenacki* (see Lenz and Kozłowska-Dawidziuk 2001a, b, pl. 9, Fig. 7). This type of development has not been previously recognized in *Gothograptus*.

Remarks. This recently described species has been recognized previously only from the *Colonograptus praedeubeli* Biozone of Poland (Kozłowska et al. 2019) and Sweden (Calner et al. 2006). Kozłowska et al. (2019, p. 451) indicated the presence of *Gothograptus auriculatus* in a drill core in Lithuania, but the material was not illustrated. The here described German material originated from a glacial erratic boulder.

The diagnosis of this species was modified to indicate that the characteristic auriculae are often stronger developed on one side of the thecal orifices, thus show an asymmetrical development of the orifices.

Gothograptus berolinensis sp. nov.

Figures 7g, 10a–h

2010 *Gothograptus osgaleae* Jaeger (nomen nudum)—Maletz: figs. 2A, B.

Material. MB.G. Jaeger sample 142 (JM 84), Spandau (Berlin, Germany). The sample includes 15 specimens preserved on a SEM stub, and a small number of poor fragments in glycerin. Jaeger identified the material as '*Retiolites osgaleae berolinensis* mit sehr langem Visier' (a very long apertural hood) in his notes. Additional species in the sample include *Testograptus testis* and *Paraplectograptus* (several juveniles). The presence of *Testograptus testis* clearly indicates that the material originated from the *Cyrtograptus lundgreni* Biozone. The holotype is JM 84-03 (Figs. 7g, 10c, g, h), a fragmented specimen showing the appearance of the mature colony.

Origin of name. The name of the city of Berlin (latin Bero-linum), the locality from which this species originated, must

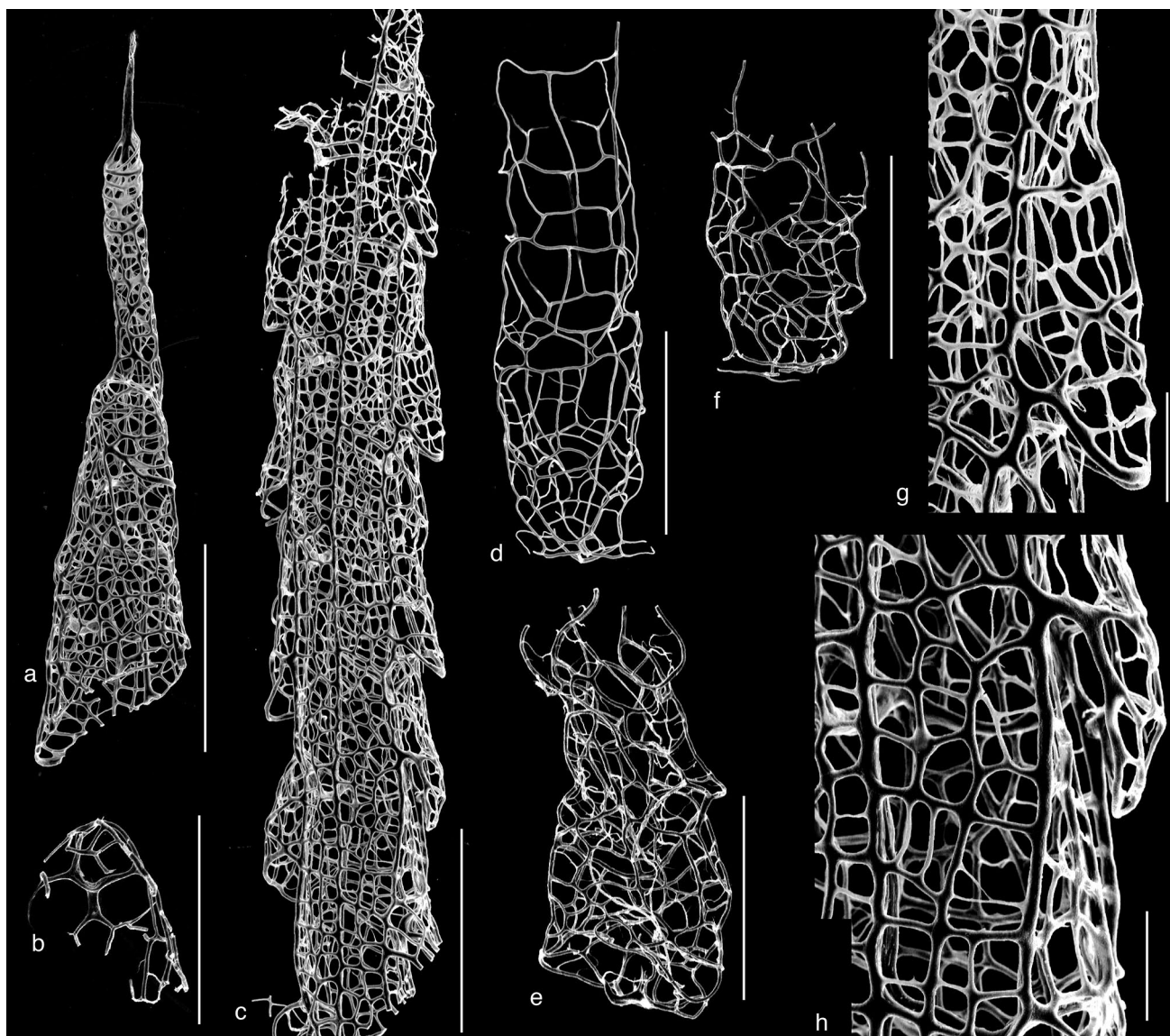


Fig. 10 *Gothograptus berolinensis* sp. nov., MB.G. material. **a** JM 84-05, distal end of mature colony with long appendix. **b** JM 84-07, broken ancora umbrella. **c** JM 84-03, holotype, median fragment in obverse view showing gradient in density of ancora sleeve lists. **d** JM

84-04, juvenile specimen with about three thecal pairs. **e** JM 84-10, distorted proximal end in ventro-lateral view. **f** JM 84-09, juvenile in lateral view. **g**, **h** JM 84-03, holotype, development of genicular hoods. Scale bars are 1 mm, except for **g**, **h**; 0.2 mm

have been the reason for the name used by Hermann Jaeger in his notes.

Diagnosis. Robust *Gothograptus* species with extensive reticular veils and hoods.

Description. Two larger tubarium fragments are here used to describe the main features of the species. A distal fragment of a larger colony preserves about five thecal pairs (Figs. 7g, 10c). It is about 6 mm long and nearly 1 mm wide. The 2TRD is about 1.9 mm. On the obverse side, the robust

and straight nema is incorporated into the lateral tubarium wall (Fig. 7g). The lateral apertural lists and pleural lists run nearly parallel to the nema on the sides of the colony in the form of thickened bars, easily differentiated from the thinner ancora sleeve lists. Further lists and bars are difficult to separate from the slender ancora sleeve lists and connecting lists are only identified in distal parts of the colony on the obverse side (Fig. 7g). The ventral thecal orifices are covered by extensive downward growing veils and hoods (Fig. 10c, g, h), different from the straight rim of the veils in *Gothograptus obtectus* Kozłowska-Dawidziuk, 1990. The

veils cover the complete ventral wall of the previous theca, ending in a rounded hood.

The specimen (Figs. 7g, 10c) is incomplete distally, but shows a distinct thinning of the lists and also a decrease in the number of lists. There is no evidence in this specimen of a reduction of the tubarium width distally or of the presence of an appendix. Thus, the specimen represents a growing end of a relatively long tubarium and the final size of the specimen may have included at least eight-to-ten thecal pairs.

A second larger specimen (Fig. 10a) is a distal fragment from a fully grown colony. It is about 5 mm long and initially about 1 mm wide, showing the reverse side. The width decreases over ca. 2.5–0.5 mm distally, where a 1.5 mm long and 0.3 mm wide appendix can be seen. The nema is incorporated into the obverse wall of the appendix and extends ca. 0.8 mm distally as a stout list. The detailed construction of the distal thecal orifices is difficult to ascertain due to the overgrowth with fine ancora sleeve lists and the precise development of the veils is unclear.

Both fragments are covered by a dense reticulum formed from robust lists, connected with more slender ones. Some regularity in the list development may be seen in individual parts of the colonies, but not in others. Apertural lips and genicular lists of the apertural orifices are difficult to identify as they are fairly thin.

A few juvenile specimens are here included in this species, mainly because they are found in the same sample. They may alternatively represent a different species of *Gothograptus*. The largest one (Fig. 10d) is about 2.8 mm long and has about three thecal pairs. It shows a loose meshwork of bars that diminishes distally, where only the main tubarium lists are found. The specimen shows the ventral view of the theca 1 side. Thecal lips, genicular lists, lateral apertural lists, and pleural lists may be differentiated outlining the thecal orifices. Distinct slender mid-ventral lists are also present. The proximal end clearly shows the lateral extension of the lateral lobes of the ancora umbrella, but many details of the umbrella are unclear. The tubarium width reaches 0.7 mm across the lobes, but distally the tubarium is too distorted to be certain about the original dimensions. The nema starts in the centre of the tubarium, but quickly moves towards to obverse side, which it may reach after about 1.5 mm. It is, however, not clearly visible where the nema is incorporated into the lateral tubarium wall. The nema also does not show any connection to possible lateral lists, but appears to be free before being incorporated into the lateral tubarium wall. Two juveniles (Fig. 10d, f) indicate the presence of the slender connecting lists of the first two thecae ($th1^1$ and $th1^2$).

Remarks. Kozłowska et al. (2019, p. 457) suggested that the material identified as *Retiolites* (*Gothograptus*) *osgaleae* by Jaeger (see Maletz, 2010) may belong to *Gothograptus*

obtectus. The material is here identified as a separate species due to the development of the genicular veils and hoods. Jaeger differentiated *Gothograptus osgaleae* and *Gothograptus osgaleae berlinensis* in his unpublished notes based on the size of the ‘Visier’, in the terminology of Kozłowska et al. (2019) describing the genicular veils and hoods.

***Gothograptus osgaleae* sp. nov.**

Figures 6d, 11a–i.

Non 2010 *Gothograptus osgaleae* Jaeger (nomen nudum)—Maletz: Fig. 1, 2A, B (= *Gothograptus berlinensis* herein).

Material. 6 specimens on SEM stub, SMF 75840–SMF 75843, Sellin, island of Rügen, Baltic Sea, NE Germany (*Monograptus* [= *Testograptus*] *testis* Zone). The species was identified by Jaeger in his notes as *Retiolites* (*Gothograptus*) *osgaleae* mit kurzen Visier (with a short hood) and *Retiolites* n. sp. aff. *nassa* forma A = *osgaleae* on the container. The holotype is SMF 75843 (Fig. 11e, i), the longest and most complete specimen in the collection. All other specimens are regarded as paratypes.

Origin of name. The name is taken from the original notes of Hermann Jaeger, who did not leave any notes on the purpose of suggesting this name. Os (Latin) is bone and galea (Latin) means helmet.

Diagnosis. *Gothograptus* with ventrally lobed genicular list and reticular hood connected at its edges with the apertural lip of the thecal orifice; genicular lists and often also thecal lip thin and inconspicuous.

Description. The description is based on a small number of partly distorted specimens from a single sample. Thus, certain details of the tubarium are not available and others are difficult to interpret. The longest specimen (Fig. 11e) is about 5.5 mm long, but is distally incomplete. There must be at least 5 or 6 thecal pairs in mature colonies. Fragments (Fig. 11b, c) show that the tubarium decreases in width distally and is assumed to end in an appendix, which is not preserved in the material. The ventral width is about 0.6–0.7 mm, while laterally it reaches about 0.9–1.0 mm. The ventral view shows the two lateral lobes of the ancora umbrella extending sideways (Fig. 11h, i) to a width of ca. 0.8–0.9 mm.

The nema is initially free inside the colony, but is later incorporated into the centre of the obverse lateral wall of the ancora sleeve, probably at about the level of the second thecal pair. When it is attached at the obverse lateral wall, the nema starts to become more robust and can easily be recognized as part of the ancora sleeve construction (Fig. 11c).

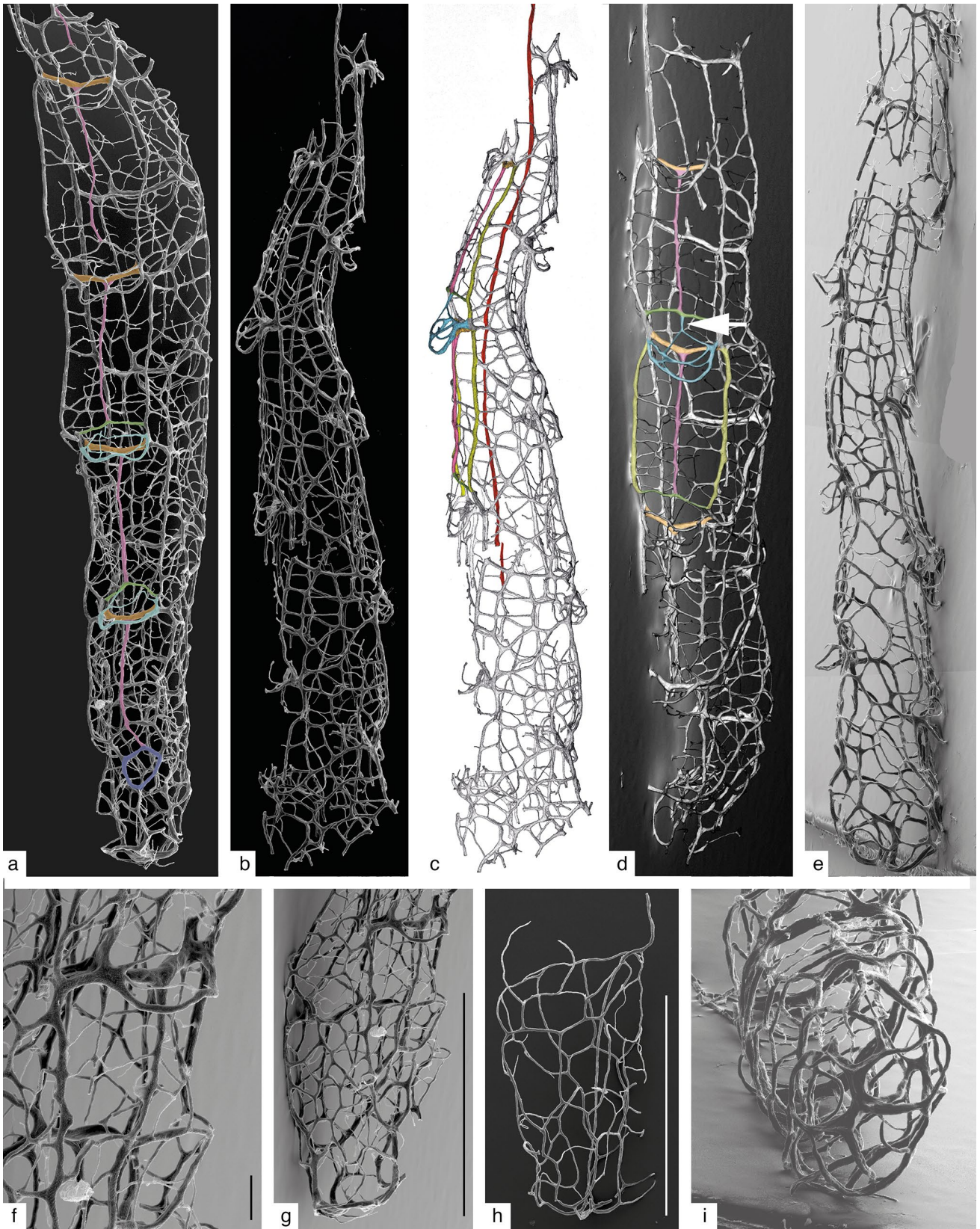


Fig. 11 *Gothograptus osgaleae* sp. nov., Sellin, Island of Rügen, NE Germany. **a** SMF 75840, specimen lacking distal end, oblique reverse view. **b**, **c** JM 116-1, incomplete distal end, reverse view. **d** SMF 75841, oblique ventral view showing thecal development and genicular hood. **e** SMF 75843, holotype, distally incomplete specimen in reverse view, showing hood development. **f** SMF 75840, detail showing pustules. **g** SMF 75840, proximal end in oblique reverse view, showing outer ancora. **h** SMF 75842, juvenile in ventral view. **i** SMF 75843, proximal end showing ancora development. Scale bar is 1 mm in all illustrations, except f (1 µm)

On the reverse side, irregularly placed parietal lists connect the ventral sides of the colony, supported by further thin ancora sleeve lists.

The ancora sleeve lists show a pustulose surface and seams generally on the inside. Outside seams are present on the ancora umbrella, however. Details of the ancora umbrella development are difficult to observe in the distorted material. It is clear that the ancora umbrella consists of few meshes. The precise development of the ancora rim has not been observed and the development of the ventral and lateral orifices of the proximal end is unknown. Thin lists below the ancora umbrella indicate the presence of an outer ancora in mature specimens (Fig. 11g, i).

Short pleural lists and long lateral apertural lists outline the ventral sides of the colony (Fig. 11d). The precise shape of the ventral thecal walls is uncertain due to the distortion of the specimens, but appears to be somewhat undulating. Genicular hoods are present on all thecae and extend outwards ventrally, thus forming a ‘roof-like’ structure over the apertural lip, sheltering the apertural orifice (Fig. 11b). The genicular hood is formed from a number of thickened rims, probably indicating an original fusellar construction in which the rim is thickened before growth continues to enlarge the tubarium (Fig. 11a, d). This development is very similar to the hood growth in *Neogothograptus* (cf. *Neogothograptus balticus*, *Neogothograptus ornatus*; Maletz 2008). The genicular hood is connected at the sides of the apertural lip to the base of the pleural list, however. It completely covers the apertural orifice on the ventral side, but does not grow downwards onto the supragenicular thecal wall below or attach to the lateral apertural list of the previous theca.

During astogeny, the number of ancora sleeve lists increases, as can be seen by comparison of juvenile and mature specimens. Nevertheless, the main tubarium lists remain thin and are often difficult to distinguish from secondary lists. While the genicular lists are very thin, only the apertural lip is somewhat thickened and recognizable. Together with the short pleural lists, the genicular lists and apertural lips form the outline of the apertural orifices, covered by the genicular hoods. The apertural orifices are about 0.2 mm high and appear to be small and slit-like. Mid-ventral lists can be differentiated in the colony, connecting the

genicular lists with the thecal lips. They often continue onto part of the genicular hoods (arrow in Fig. 11d).

Remarks. The species is known from a number of immature specimens found in a single glacial erratic boulder. Kozłowska et al. (2019, p. 447) suggested that the material of *Retiolites (Gothograptus) osgaleae* of Jaeger may belong to *Gothograptus obtectus* Kozłowska-Dawidziuk, 1990. Differences can be found in the development of the genicular hoods and the veil of *Gothograptus obtectus*, in which the hood is extended into a long veil, laterally connected to the lateral apertural lists of the previous theca and bearing a straight, horizontal lower rim. The veil covers the supragenicular ventral wall of the previous theca with a second layer of meshwork (Kozłowska-Dawidziuk 1990, Fig. 5D). There is no veil in *Gothograptus osgaleae* sp. nov., but the looped genicular list develops a hood of moderate size with a second lateral attachment on the lateral tubarium wall directly at the edge of the apertural lip (Figs. 6d, 11c). These hoods appear to be present at each completely developed theca, but become larger in more distal thecae.

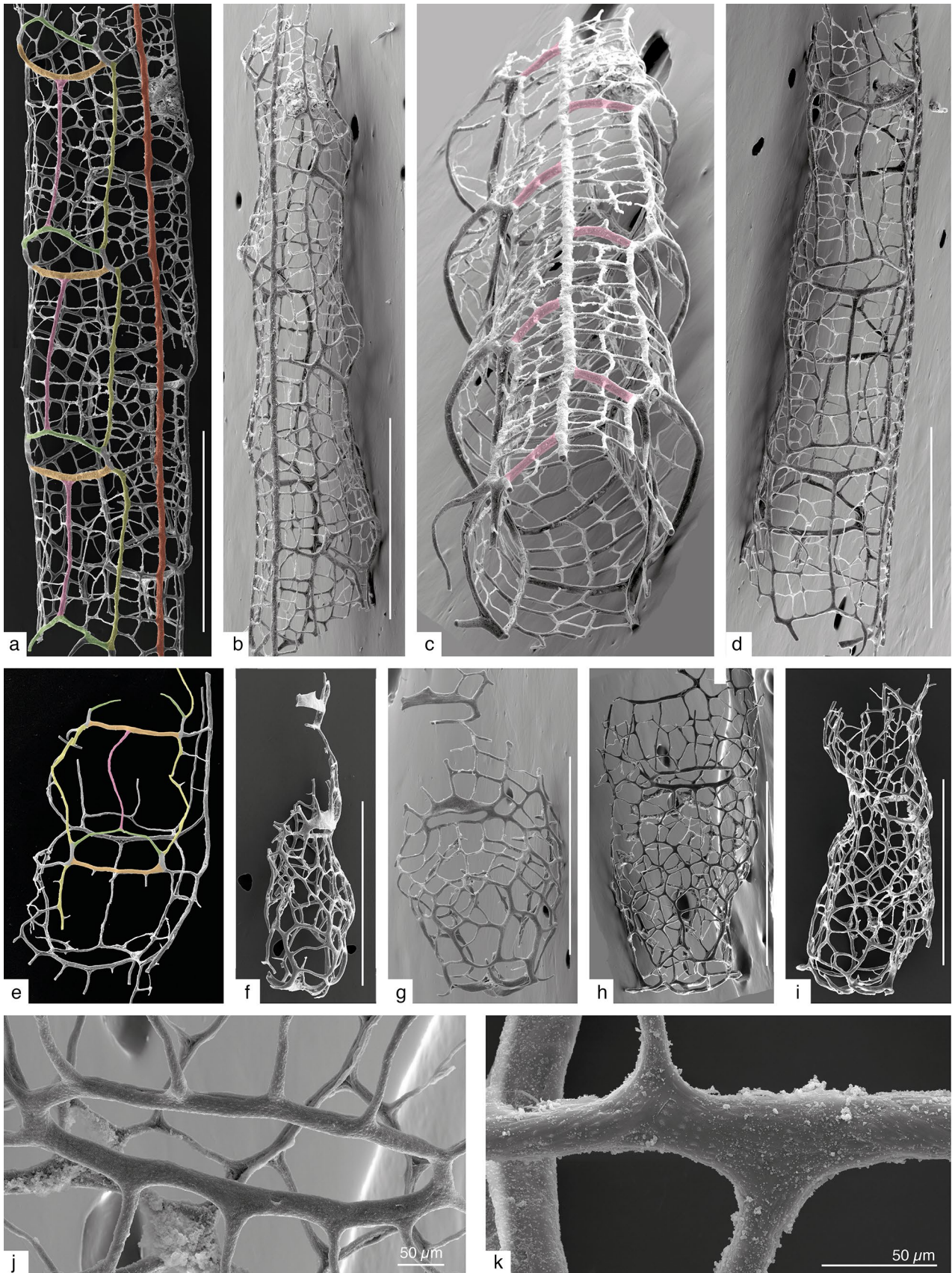
Gothograptus storchi Lenz and Kozłowska, 2006?

Figure 12a–k

- ?2006 *Gothograptus storchi* n. sp.—Lenz and Kozłowska, p. 620, Fig. 6, 7.
2010 *Gothograptus praenassa* Jaeger—Maletz: figs. 2D, E.

Material. 4 specimens from Jaeger sample 188 (JM 115), Spandau (Berlin, Germany), glacial boulder. Jaeger referred the material to the *?Testograptus testis* Biozone (his zone 31B). On his chart (Maletz 2010, Fig. 1), the *Cyrtograptus lundgreni* Biozone is indicated for the origin of the sample. Jaeger’s notes indicate that specimens of *Paraplectograptus* were associated (identified as *Retiolites eiseli*; det. Jaeger).

Description. The best specimen is a fragment with three thecal pairs, ca. 3.3 mm long and 0.9 mm wide laterally. It shows thin apertural lips and equally thin, looped genicular lists on the ventral side, connected by lateral thecal lists and mid-ventral lists (Fig. 12a–d). The looped genicular lists form the edge of the roof over the narrow thecal orifices, bound at the sides by short pleural lists. The thecal orifices are thus oriented proximo-ventrally to the tubarium midline. There is no evidence of any genicular additions in the material, but it is uncertain whether all available specimens belong to a single taxon. One fragmentary proximal end shows wide genicular bands, not seen previously in any gothograptids, on two successive thecal orifices (Fig. 12f, g). A second proximal end has slender thecal lip and genicular



◀**Fig. 12** *Gothograptus storchi* Lenz and Kozłowska, 2006?, collection 188 of Jaeger, Spandau/Berlin, Germany. **a–d** SMF 75836, fragment with three thecal pairs in oblique view (**a**, **b**), view from distal end to show looped genicular lists, indicating connecting lists in pink (**c**) and ventral view (**d**), showing thecal orifices. **e** SMF 75837, fragment showing thecal orifice. **f**, **g** SMF 75838, fragmented proximal end with very wide geniculae, probably not belonging to this species. **h**, **i** SMF 75839, distorted proximal end specimen in ventral (**h**) and lateral (**i**) views. **j** SMF 75839, orifice of th1². **k** SMF 75836, detail showing pustules on bandages and surface covered with small pyrite crystals

lists (Fig. 12h–j) and compares well with the longer fragment. Pustular surfaces (Fig. 12j) are commonly observed in the material, but all surfaces are covered by tiny pyrite crystals (Fig. 12k).

The obverse side of the tubarium shows the nema and the connecting lists as dominant features on the obverse wall (Fig. 12c), suggesting that this is the thecal wall and that an ancora sleeve wall does not exist in the species and in the genus *Gothograptus* as a whole. The reverse wall of the tubarium is then identified as the reverse thecal wall and the oblique lists regarded as thecal lists and not as indications of ancora sleeve (parietal) lists.

Remarks. All specimens represent juveniles or fragments without important characteristics to enable confident specific identification. A few illustrations by Hermann Jaeger (Fig. 7h–l) are available, but not all specimens have been recognized in the collection. The specimens may represent fragments of *Gothograptus storchi*, the only species of the genus without any genicular elaborations known from the pre-*Lundgreni* extinction interval; this species has been found only in the Canadian Arctic so far (Lenz and Kozłowska 2006).

Gothograptus pseudospinosus (Eisenack, 1951).

- 1951 *Retiolites pseudospinosus* n. sp.—Eisenack: 143, pl. 25, figs.1–6.
 1991b *Retiolites (Gothograptus) pseudospinosus*—Jaeger: Fig. 1.
 2010 *Gothograptus pseudospinosus* (Eisenack, 1951)—Maletz: Fig. 2C. 1951

Remarks. The specimens illustrated by Jaeger (1991b) and Maletz (2010) have not been identified in the Jaeger collection. According to Kozłowska et al. (2019), there are several species in the *Cyrtograptus lundgreni* Biozone that may show a similar development of genicular spines or extensions. These ‘paired spines with seams or remnants of reticulum between them’ Kozłowska et al. (2019, p. 454) represent the remains of ventrally extended hoods and should not be

termed spines. Their development has not been investigated in detail yet. Eisenack (1951, p. 144) described the development in *Gothograptus pseudospinosus* as ‘löffelartiger Fortsatz’ and ‘korbartig durchbrochen’ and called it the Visier; he thus was aware that these features represent genicular hoods instead of spines. This is also the reason why he called the species *Gothograptus pseudospinosus*. Kozłowska et al. (2019) illustrated reticulated hoods in their material of *Gothograptus domeyki* and *Gothograptus kozłowskii*.

Gothograptus sp. indet.

Figures 6e, 13a–d

Material. A single specimen from a glacial boulder (SMF 75835), Hafen Vierow, Lubmin, Mecklenburg-Vorpommern, NE Germany. The sample included a few indeterminate fragments of monograptids and is most likely Wenlock in age, based on the recognizable constructional detail in the specimen that are unknown from post-*Lundgreni* extinction species of the genus.

Description. The distally incomplete specimen is about 4 mm long and has a lateral width of ca. 0.7–0.8 mm. The ventral width is 0.5 mm at the ancora umbrella and widens to 0.7–0.8 mm, but considering the considerable distortion, the ventral width should be about 0.5 mm throughout the colony. This can be estimated from the development of the thecal hoods (Fig. 13b). The lateral lists of the ventral tubarium sides show pleural lists ca. 0.1 mm or less long, alternating with 0.7–0.9 mm-long lateral apertural lists. The mid-ventral lists are distinct and can easily be seen below the irregularly developed lists of the genicular hoods (Fig. 13b).

The thecal orifices are outlined by very short pleural lists, genicular lists, and thecal lips, all show considerable thickening. The most distal thecal orifices, however, are difficult to distinguish, as they are fairly delicate. The first pair of thecal orifices is simple, without any genicular elaborations (Fig. 13b). From the second thecal pair on, extremely long genicular hoods are developed, covering the whole ventral side of the previous theca. Many details of this development are impossible to see due to the considerable distortion of the specimen. However, in lateral view (Fig. 13a, c), the hoods are clearly discernible. The hoods grow in stages downwards, shown by the various, somewhat irregularly formed lobes. Minor perpendicular lists can be developed.

Irregular lists can be seen to form the lateral ancora sleeve, but on the obverse side, the nema is incorporated into the ancora sleeve wall in the distal part of the colony (Fig. 13c). The proximal part of the nema is not recognized within the tubarium.

Remarks. The specimen differs from all Wenlock species described by Kozłowska et al. (2019) through the differently

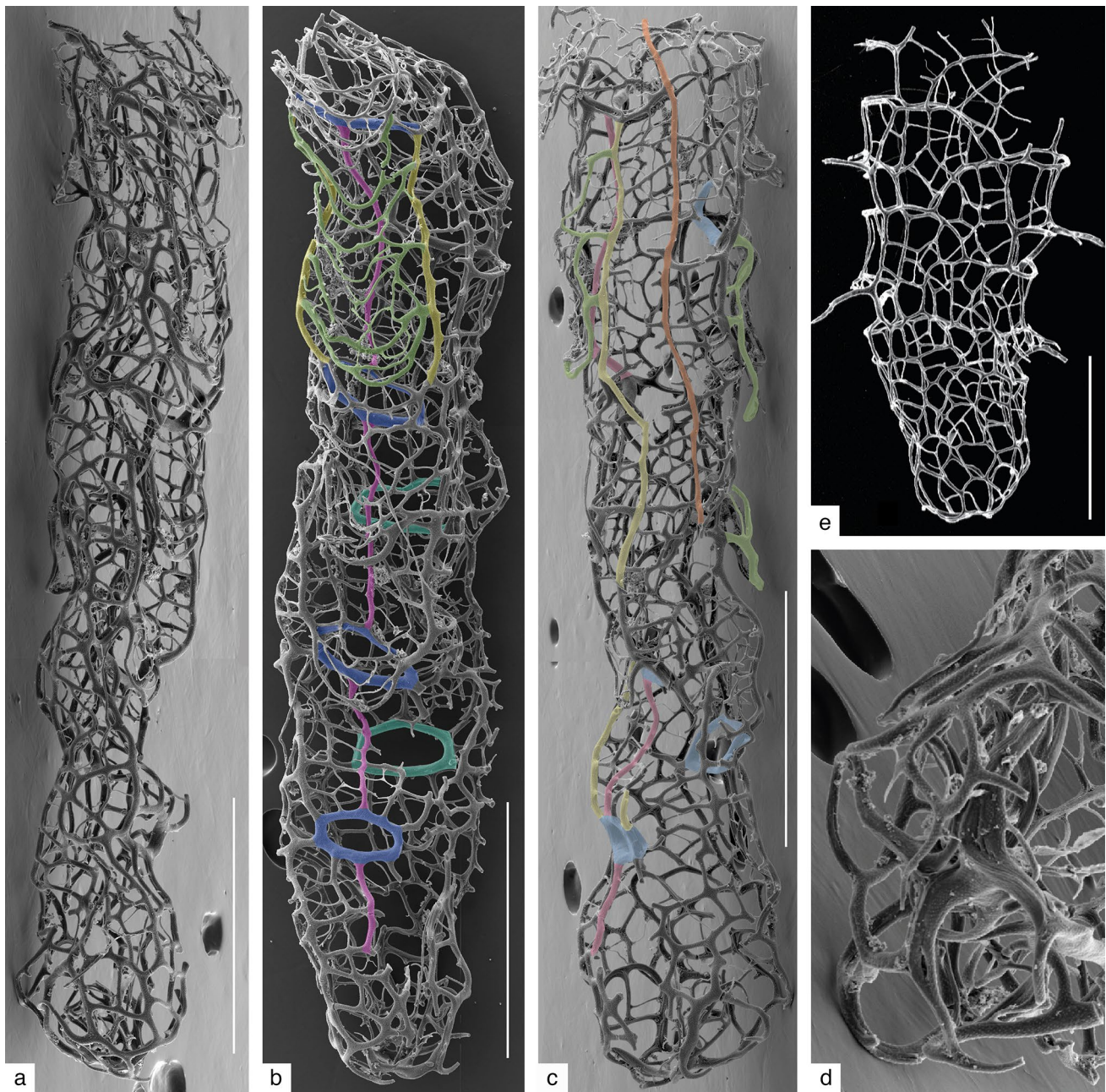


Fig. 13 **a–d** *Gothograptus* sp., Hafen Vierow, Lubmin, NE Germany, coll. Maletz. SMF 75835. **a–c** Specimen in various views showing certain details in colour; **d** ancora development from below, showing

outer ancora; **e** *Papiliograptus retimarginatus* Kozłowska and Bates, 2021. MB.G. 1092. Scale bar is 1 mm for all illustrations

formed genicular hoods and the lack of paired spines on any of the thecal orifices. The downward growth of successive lobes with only minor perpendicular additions is in stark contrast to the irregular development of the genicular veils as illustrated by Kozłowska et al. (2019, Fig. 9). As the material of this taxon consists of a single distorted specimen, it is inadvisable to name it as a new species.

Genus *Semigothograptus* Kozłowska, 2016

Type species (original designation). *Gothograptus? meganassa* Rickards and Palmer, 2002.

Diagnosis. Tubarium initially widening gradually from proximal end; ancora umbrella asymmetrical with undulating rim; nema free; proximal ventral orifices of triangular shape; lateral orifices kidney-shaped; ventral wall represented by thecal lips, genicular lists, long convex lateral apertural lists, short pleural lists and mid-ventral lists; massive genicular

hoods; parietal lists oblique; reticulum irregular; ancora sleeve lists with seams facing inwards; bandages with pustules (revised from Lenz et al., 2018, p. 28).

Remarks. Kozłowska (2016) differentiated the genus from *Gothograptus* through the presence of a free nema within the more robust tubarium in which an appendix indicating a finite growth has not been recognized. All available specimens widen considerably distally. She also considered the long lateral apertural lists with their convex to sigmoidal shape distally as a unique character of the genus *Semigothograptus*.

Semigothograptus Meganassa (Rickards and Palmer, 2002).

- 1991 *Retiolites* (*Gothograptus*) *gigantonassa*—Jaeger, Fig. 1.
 2002 *Gothograptus?* *meganassa* sp. nov.—Rickards and Palmer: 228, text-Fig. 4.
 2010 *Gothograptus gigantonassa* Jaeger—Maletz, Fig. 1, 2 J.
 2016 *Semigothograptus Meganassa* (Rickards and Palmer)—Kozłowska: 536, figs. 1D, 2B, 3, 4B, 7A-D.
 2019 *Semigothograptus Meganassa* (Rickards and Palmer)—Manda et al.: 48, figs. 8 h, 10d.
 2019 *Semigothograptus Meganassa* (Rickards and Palmer)—Štorch and Manda: 48, figs. 3c, 4 g.

Material. Jaeger (1991a, b, Fig. 1) and Jaeger in Maletz (2010) illustrated two fragments of this taxon in small ink drawings as *Retiolites* (*Gothograptus*) *gigantonassa*. The material has not been identified in the Jaeger collection at the Museum für Naturkunde (Berlin, Germany). Jaeger (see Maletz 2010, figs. 1, 2) indicated its origin from the upper *dubius/nassa* to the lower *deubeli* Biozone. Even though the species was not encountered during this study, it appears to provide important clues to the early evolution of the post-extinction retiolitines.

Remarks. The species or at least the genus ranges from the *Cyrtograptus lundgreni* Biozone (see Manda et al. 2019; Štorch and Manda 2019) to the *dubius-nassa* interval and possibly into the early *Colonograptus deubeli* Biozone (see Kozłowska 2016, Fig. 5). The precise age of Jaeger's specimens (see Maletz 2010, Fig. 2) is uncertain as the material has not been identified in the Jaeger collection and the range relies only on the preliminary, unpublished diagram of Jaeger (see Maletz 2010, Fig. 1).

Semigothograptus shows considerably similarities in its general tubarium shape to *Plectograptus* and especially to

Plectograptus wimani. Both share the same general style of tubarium development with a zigzag to sigmoidal curvature of the lateral edges (cf. lateral apertural lists and pleural lists). *Plectograptus wimani*, however, has a less dense reticulum and a poorly outlined ancora umbrella development. The wide and single genicular hoods in *Plectograptus wimani* are made from a number of wider fusellar lists with free spaces in between and not of microfusellar material as in *Semigothograptus*, but gaps in the material of the genicular hoods are also visible in *Semigothograptus*. The difference may be explained by a gradual change of microfusellar material to macrofusellar material and does not represent a major difference. *Plectograptus wimani* develops strong zigzag parietal lists on the lateral ancora sleeve walls, while the parietal lists in *Semigothograptus* only obliquely cross from one side to the other. These differences recall the contrast between the parietal lists in the lateral ancora sleeve construction of *Neogothograptus* and *Holoretiolites* (cf. Maletz 2008, Fig. 3). It is not certain, however, how important these features are phylogenetically. The 'free' internal nema in *Semigothograptus* indicates the presence of an outer common canal and thus the presence of two walls, the thecal wall and the outer ancora sleeve wall, a fundamental difference from *Gothograptus*. It clearly links *Semigothograptus* with the derived post-extinction retiolitines. These never show the incorporation of the nema into the lateral tubarium wall.

Genus ***Papiliograptus*** Lenz and Kozłowska-Dawidziuk, 2002

Type species (original designation). *Papiliograptus papilio* Lenz and Kozłowska-Dawidziuk, 2002

Diagnosis. Finite tubarium, but appendix unknown; ancora umbrella with extensive paired ventral lobes and strongly undulating rim; ventral sides formed by thecal lips, genicular lists, pleural lists, lateral apertural lists and mid-ventral lists; dense reticulum with indistinct zigzag or almost horizontal parietal; reticulate genicular hoods in some species; ancora sleeve lists with seams facing inwards; bandages with pustules (modified from Kozłowska and Bates 2021, p. 200).

Distribution. *Papiliograptus* is known from the *Colonograptus praedeubeli/deubeli* Biozone of the Homeric (Wenlock, Silurian), represented by at least two species. It has been found in Arctic Canada (Lenz and Kozłowska-Dawidziuk 2002) and in the Baltic region (Kozłowska and Radzevičius 2013; Kozłowska and Bates 2021).

Papiliograptus retimarginatus Kozłowska and Bates, 2021 Figs. 7m, 13e.

- 2010 *Papiliograptus retimarginatus* (Jaeger)—Maletz, Fig. 1, 2 N.
 2017 *Papiliograptus* sp.—Maletz et al.: 218, Fig. 12.9D.
 2021 *Papiliograptus retimarginatus* n. sp.—Kozłowska and Bates: 202, figs. 1, 2A, C, D, 3.

Material. MB.G. 1092, Jaeger sample 354, isle of Hiddensee, near Rügen Island, Baltic Sea, NE Germany. Only one juvenile specimen of this species was available. It is associated with numerous specimens of *Gothograptus auriculatus*.

Diagnosis. *Papiliograptus* with single genicular structure formed by long lateral lists, thinning distally and lacking a ventrally continuous (connecting) rim; delicate reticulum in the proximal part of the hoods, growing from geniculum and reaching sideways onto the preserved spiny extensions (Kozłowska and Bates 2021, p. 202).

Description. The single proximal end of the species (Fig. 13e) has about three thecal pairs preserved. The specimen is about 3 mm long and shows a lateral width of ca. 1.3 mm. The ventral width is 0.7 mm at the ancora umbrella and 1.0 mm distally. Kozłowska and Bates (2021) indicated the presence of seven meshes in the ancora umbrella with a fairly asymmetrical development in which the paired ventrolateral lobes on the th₂¹ side reach much higher than the ones on the th₁¹ side. The ancora umbrella is 0.7 mm wide (laterally) and 0.5 mm high. The prominent horizontal lateral lists supporting the butterfly-shaped hoods in mature specimens are easily recognized in ventral view (Fig. 13e) and measure ca. 1.5 mm across. The proximal ventral orifice of the th₁² series side is tetragonal (Fig. 13e).

The lateral orifices are described as kidney-shaped by Kozłowska and Bates (2021) in their flattened material, but are more rounded in the relief specimen (Fig. 7m), in which the lateral lobes of the ancora umbrella are not flipped or rotated upwards. The thecal lips, genicular lips, pleural lists, and lateral apertural lists form the outline of the thecal orifices (Fig. 7m). Thin mid-ventral lists and a slight development of ancora sleeve lists can be found on the ventral supragenicular thecal walls (Fig. 7m). The lateral ancora sleeve walls are outlined by thin lists that start as an irregular development above the proximal lateral orifices. Quickly, they develop distinct stronger zigzag lists and thin secondary ancora sleeve lists on the obverse and reverse sides of the tubarium (Fig. 13e).

Remarks. Kozłowska and Bates (2021) described this species from largely flattened and somewhat distorted material found at a depth of 1647.9 and 1649.0 m in the Bartoszyce IG-1 core, Poland. The material is associated with *Gothograptus auriculatus* Kozłowska et al., 2019. Mature

specimens of *Papiliograptus retimarginatus* possess large laterally extended genicular constructions. These are indicated in the juvenile specimen, but do not reach the dimensions of the mature ones.

The Jaeger collection in the light of the *Lundgreni* Extinction

The Jaeger collection at the Museum für Naturkunde (Berlin, Germany) provides one of the largest and best documented insight into the retiolitine diversity of the late Wenlock to early Ludlow worldwide. It also is probably the best-preserved material, as the specimens are generally preserved in full relief, freed from their limestone matrix. Often juveniles and mature specimens are present in the same sample indicating the astogenetic growth of their tubaria. However, as discussed earlier, numerous other taxa have been collected from various regions in the world that were not recognized in the glacial boulders of northern Germany and Poland.

Maletz (2008) indicated the biostratigraphic range of the glacial boulders from the *Cyrtograptus lundgreni* Biozone of the Homerian (Wenlock) to the *Saetograptus leintwardinensis* Biozone of the Ludfordian (Ludlow). This estimation is, however, largely based on the information by Jaeger (see Maletz 2010, Fig. 1, 2). All boulders from the pre-extinction interval are referred to the *Cyrtograptus lundgreni* Biozone, even though the biostratigraphic evidence is poor and the monograptid faunas from the interval have not been described in enough detail. Urbanek (1966) discussed the oldest level of the glacial erratics and stated that *Retiolites geinitzianus* and *Monograptus priodon* are the oldest graptolites found in them. He referred to the descriptions of Kühne (1953: *Retiolites geinitzianus*) and Roemer (1885: *Monograptus priodon*). Urbanek (1958) and Maletz and Schöning (2017) also described *Monograptus priodon*. The species may not be common in the Grünlich-Graues Graptolithengestein, but its presence indicates that pre-*Cyrtograptus lundgreni* Biozone material may eventually be found.

Biostratigraphic evidence from retiolitine species in documented successions of the late Sheinwoodian to early Homerian is quite limited and may be misleading. A number of species have been included in the genus *Paraplectograptus*, but their precise biostratigraphic ranges are largely unexplored. Kozłowska-Dawidziuk (1995) indicated the presence of *Paraplectograptus areticulatus* from the *Spirograptus turriculatus* Biozone to the *Gothograptus nassa* Biozone, thus even crossing the *Lundgreni* Extinction Event, a range that has not been verified subsequently. Manda et al. (2019) provided some information from the *Cyrtograptus lundgreni* Biozone of the Kosov 2 section in the Czech Republic, but not from older intervals. Eisenack (1951) described *Paraplectograptus tenuis* based on a

number of juvenile specimens found in five glacial boulder, and remarked that the species is not uncommon. Kozłowska-Dawidziuk (1995, p. 282) synonymized the material with *Paraplectograptus eiseli*. The Eisenack (1951) material is immature and a species specific identification may be impossible in this case due to the lack of mature specimens and understanding of the tubarium construction. A revision of the genus *Paraplectograptus* will provide a better indication of the biostratigraphic usefulness of these taxa.

Here, two new species of the genus *Paraplectograptus*, one of these in open nomenclature only, are described, showing previously unknown features like the three-vaaned nematularium found in a number of specimens of *Paraplectograptus hermanni* sp. nov. This vane starts to grow early in the development of the colony and is overgrown and incorporated into the tubarium by the two thecal series.

The genus *Gothograptus* is represented in the Jaeger collection by four pre-extinction and two post-extinction taxa. Other species of the genus mentioned or even illustrated by Jaeger (see *Gothograptus pseudospinosus*: Maletz 2010, Fig. 2) have not been verified in the collection. *Gothograptus berolinensis* sp. nov. and *Gothograptus osgaleae* sp. nov. can be shown to possess previously unrecognized features in their development of genicular hoods and veils, increasing the constructional diversity of the pre-extinction forms of the genus *Gothograptus*. A third species is described in open nomenclature based on a single partly distorted specimen (Fig. 13a–d). *Gothograptus storchi*? is found for the first time outside of its type locality in the Canadian Arctic. If the identification is correct, the claim of an endemism of this species and a restriction to Laurentia (cf. Kozłowska et al. 2019, p. 436) cannot be retained. The limited record of most *Gothograptus* species may indicate our lack of knowledge on the biostratigraphic and biogeographic distribution of the genus and of retiolitine graptolites in general. The spotty knowledge on most retiolitines could also be supported by the distribution of the genus *Cometograptus*, of which most species are only found in the Canadian Arctic and in Poland (Kozłowska-Dawidziuk 2001; Lenz and Kozłowska 2006). A single species is found the North German glacial boulders with *Cometograptus alfeisenacki* Maletz, 2010, but this one again is known from a single sample.

The diversity reported for post-extinction retiolitines is largely due to the record in North German and Polish glacial boulders (Bates et al. 2005, 2006; Maletz 2008, 2010) and to the record in Arctic Canada (Lenz and Kozłowska-Dawidziuk 2002, 2004). Differences in faunal compositions may in part at least be due to collection limitations and failures, not to original faunal differences. Thus, for example, the peculiar *Neogothograptus alatiformis* Lenz and Kozłowska-Dawidziuk, 2004 was only more recently recognized in a few specimens in a Lithuanian drill core. Also, the genus *Papiliograptus* was originally found only

in the Canadian Arctic, but was quoted by Maletz (2010) from the Jaeger collection. It was subsequently described by Kozłowska and Radzevičius (2013) and Kozłowska and Bates (2021) from Lithuania and Poland.

Conclusions

- (1) The diversity of the retiolitines across the *Lundgreni* extinction event is still fairly incompletely known. Especially, the pre-extinction interval needs considerable attention.
- (2) New records of *Gothograptus* species indicate a much higher diversity of this genus in the pre-*Cyrtograptus lundgreni* extinction interval. Considerable variation exists in the development of genicular hoods and veils in this genus.
- (3) The distinct change in the development of the genicular constructions between the pre-extinction and post-extinction *Gothograptus* species might be a good indication of the dramatic changes across this Event horizon.
- (4) While the genus *Paraplectograptus* died out in connection with the *Lundgreni* Extinction Event, the pre-extinction interval either includes a diverse fauna of species referred to this genus or the biostratigraphic interval as identified here, includes a biostratigraphically much longer time span than expected. In this case, the various *Paraplectograptus* species might be useful biostratigraphically in the future.

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Data availability All data are provided in the text and the figures.

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References

- Bates, D.E.B., and N.H. Kirk. 1992. The ultrastructure, mode of construction and functioning of a number of Llandovery anconate diplograptid and retiolitid graptolites. *Modern Geology* 17 (1–3): 1–270.
- Bates, D.E.B., A. Kozłowska, and A.C. Lenz. 2005. Silurian retiolitid graptolites: Morphology and evolution. *Acta Palaeontologica Polonica* 50 (4): 705–720.
- Bates, D.E.B., A. Kozłowska, J. Maletz, N.H. Kirk, and A.C. Lenz. 2006. The Silurian retiolitid graptolite *Plectograptus*: New observations and new species. *Acta Palaeontologica Polonica* 51: 52–540.
- Bates, D.E.B., and N.H. Kirk. 1997. The ultrastructure, construction and functioning of the genera *Stomatograptus* and *Retiolites*, with an appendix on the incremental construction of the rhabdosome in *Petalolithus*, and its comparison with that of the thecal framework in *Retiolites* and *Stomatograptus*. *Institute of Geography and Earth Sciences, University of Aberystwyth Publication* 10: 1–168.
- Bateson, W. 1885. The later stages in the development of *Balanoglossus kowalskii*, with a suggestion to the affinities of the *Enteropneusta*. *Quarterly Journal of Microscopical Science* 25 (81–122): 4–9.
- Bouček, B., and A. Münch. 1952. Retioliti středoevropského svrchního wenlocku a ludlowu. [The central European Retiolites of the Upper Wenlock and Ludlow]. *Sborník Ústředního Ústavu Geologického, Oddíl Paleontologický* 19: 1–151 (1–54, Czech text; 55–103, Russian text; 104–151 English text).
- Bronn, H.G. 1849. *Handbuch der Geschichte der Natur. Dritter Band, Zweite Abtheilung. II. Theil: Organisches Leben (Schluß). Index palaeontologicus oder Ueberblick der bis jetzt bekannten fossilen Organismen*. 1106 pp. Schweizerbart, Stuttgart.
- Bulman, O.M.B. 1955. Graptolithina. In *Treatise on Invertebrate Paleontology, Part V*, ed. R.C. Moore. Lawrence: Geological Society of America and University of Kansas Press.
- Bulman, O.M.B. 1970. Graptolithina. In *Treatise on Invertebrate Paleontology, Part V*, 2nd ed., ed. C. Teichert. Lawrence: Geological Society of America and University of Kansas Press.
- Calner, M., A. Kozłowska, M. Masiak, and B. Schmitz. 2006. A shoreline to deep basin correlation chart for the middle Silurian coupled extinction-stable isotopic event. *GFF* 128 (2): 79–84.
- Calner, M., P. Ahlberg, O. Lehnert, and M. Erlström, eds. 2013. The Lower Palaeozoic of southern Sweden and the Oslo Region, Norway. Field guide for the 3rd annual meeting of the IGCP Project 591. *Sveriges geologiska undersökning, Rapporter och Meddelanden* 133: 1–96.
- Cope, R.N. 1954. Cyrtograptids and retiolitids from County Tipperary. *Geological Magazine* 91 (4): 319–324.
- Ehlers, J., A. Grube, H.-J. Stephan, and S. Wansa. 2011. Pleistocene glaciations of North Germany – new results. *Developments in Quaternary Science* 15: 149–162.
- Eisenack, A. 1935. Neue Graptolithen aus Geschieben baltischen Silurs. *Paläontologische Zeitschrift* 17: 73–90.
- Eisenack, A. 1951. Retioliten aus dem Graptolithengestein. *Palaeontographica* A100: 129–163.
- Frech, F. 1897. *Lethaea geognostica oder Beschreibung und Abbildung für die Gebirgs-Formationen bezeichnendsten Versteinerungen. Herausgegeben von einer Vereinigung von Palaeontologen, I. Teil – Lethaea Palaeozoica*, 544–684. Stuttgart: E. Schweizerbart'sche Verlagshandlung.
- Haupt, K. 1878. Die Fauna des Graptolithengesteines. *Neues Lausitzer Magazin* 54: 29–113.
- Heidenhain, F. 1869. Ueber Graptolithen führende Diluvial-Geschiebe der norddeutschen Ebene. *Zeitschrift Der Deutschen Geologischen Gesellschaft* 21: 143–182.
- Holm, G. 1890. Gotlands Graptoliter. *Bihang till Kongliga Svenska Vetenskaps Akademiens Handlingar* 16 (Afd. 4, No. 7): 1–34.
- Hopkinson, J., and C. Lapworth. 1875. Descriptions of the graptolites of the Arenig and Llandeilo rocks of St. David's. *Quarterly Journal of the Geological Society* 31: 631–672. <https://doi.org/10.1144/GSL.JGS.1875.031.01-04.49>.
- Hundt, R. 1924. *Die Graptolithen des deutschen Silurs*. Leipzig: Verlag Max Weg.
- Jaeger, H. 1991a. Astogenese und Phylogenese der letzten Retioliten. *Mitteilungen aus dem Zoologischen Museum Berlin* 67: 117–118.
- Jaeger, H. 1991b. Neue Standard-Graptolithenzonenfolge nach der "Großen Krise" an der Wenlock/Ludlow-Grenze (Silur). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 182 (3): 303–354.
- Jaekel, O. 1889. Über das Alter des sog. Graptolithengesteins mit besonderer Berücksichtigung der in demselben enthaltenen Graptolithen. *Zeitschrift der Deutschen Geologischen Gesellschaft* 41: 653–716.
- Koren', T.N. 1991. The Lundgreni extinction event in central Asia and its bearing on graptolite biochronology within the Homerian. *Proceedings of the Estonian Academy of Sciences, Geology* 40 (2): 74–78.
- Koren', T.N., and A. Urbanek. 1994. Adaptive radiation of monograptids after the late Wenlock crisis. *Acta Palaeontologica Polonica* 39 (2): 137–167.
- Kozłowska, A. 2016. A new generic name, *Semigothograptus*, for *Gothograptus? meganassa* Rickards and Palmer, 2002, from the Silurian post-lundgreni Biozone recovery phase, and comparative morphology of retiolitids from the lowermost upper Homerian (upper Wenlock). *Zootaxa* 4208 (6): 534–546.
- Kozłowska, A. 2021. *Hoffmanigraptus* n. gen., a new retiolitine (Graptolithina), an early member of the *Plectograptus* lineage from the Silurian of Baltica, Poland. *Comptes Rendus Palevol* 20 (45): 931–939.
- Kozłowska, A., and D.E.B. Bates. 2008. *Kirkigraptus*, a new retiolitid graptolite from Poland. *Acta Palaeontologica Polonica* 53 (1): 105–112.
- Kozłowska, A., and D.E.B. Bates. 2021. *Papiliograptus retimarginatus* n. sp., a new retiolitid (Graptolithina) from the *praedeubeli/deubeli* Biozone (upper Homerian, Wenlock, Silurian), the recovery phase after the *lundgreni* Extinction Event. *Comptes Rendus Palevol* 20 (12): 199–206. <https://doi.org/10.5852/cr-palevol201v20a12>.
- Kozłowska, A., and S. Radzevičius. 2013. Upper Homerian and Gorstian (Silurian) Retiolitidae (Graptolithina) from Lithuania and Latvia. *Memoirs of the Association of Australasian Palaeontologists* 44: 11–23.
- Kozłowska, A., A.C. Lenz, and M.J. Melchin. M. J. 2009. Evolution of the retiolitid *Neogothograptus* (Graptolithina) and its new species from the upper Wenlock of Poland, Baltica. *Acta Palaeontologica Polonica* 54 (3): 423–434.
- Kozłowska, A., D.E.B. Bates, and S. Piras. 2010. A new Silurian graptolite, *Reticuloplectograptus*, and its bearing on retiolitid evolution. *Palaeontology* 53 (6): 1411–1417.
- Kozłowska, A., D.E.B. Bates, J. Zalasiewicz, and S. Radzevičius. 2019. Evolutionary significance of the retiolitine *Gothograptus* (Graptolithina) with four new species from the Silurian of the East European Platform (Baltica), Poland and Lithuania. *Zootaxa* 4568 (3): 435–469.
- Kozłowska-Dawidziuk, A. 1990. The genus *Gothograptus* (Graptolithina) from the Wenlock of Poland. *Acta Palaeontologica Polonica* 35: 191–209.
- Kozłowska-Dawidziuk, A. 1995. Silurian retiolitids of the east European platform. *Acta Palaeontologica Polonica* 40 (3): 261–326.

- Kozłowska-Dawidziuk, A. 2001. Phylogenetic relationships within the Retiolitidae (Graptolithina) and a new genus, *Cometograptus*. *Lethaia* 34: 84–96.
- Kozłowska-Dawidziuk, A., and A.C. Lenz. 2001. Evolutionary developments in the Silurian Retiolitidae (Graptolites). *Journal of the Czech Geological Society* 46 (3–4): 227–238.
- Kühne, W.G. 1953. The prosicula of *Retiolites geinitzianus* Barr. *Geological Magazine*: 444.
- Lankester, E.R. 1877. Notes on the embryology and classification of the animal kingdom: Comprising a revision of speculations relative to the origin and significance of the germ-layers. *Quarterly Journal of Microscopical Science* 17: 399–454.
- Lapworth, C. 1873. Notes on the British graptolites and their allies. 1. On an improved classification of the Rhabdophora, part 2. *Geological Magazine* 10: 555–560. <https://doi.org/10.1017/S0016756800469372>.
- Laufeld, S., J. Bergström, and P.T. Warren. 1975. The boundary between the Silurian *Cyrtograptus* and *Colonus* Shales in Skåne, southern Sweden. *GFF* 97 (3): 207–222.
- Lenz, A.C. 1993. Late Wenlock and Ludlow (Silurian) Plectograptinae (retiolitid graptolites), Cape Phillips Formation, Arctic Canada. *Bulletin of American Paleontology* 104: 1–52.
- Lenz, A.C. 1994. A sclerotized retiolitid, and its bearing on the origin and evolution of Silurian retiolitid graptolites. *Journal of Paleontology* 68: 1344–1349.
- Lenz, A.C., and A. Kozłowska. 2006. Graptolites from the *Lundgreni* Biozone (Lower Homerian: Silurian), Arctic Islands, Canada: New species and supplementary material. *Journal of Paleontology* 80: 616–637.
- Lenz, A.C., and A. Kozłowska. 2010. *Sagenograptoides*, a new name for the retiolitid graptolite *Sagenograptus* Lenz and Kozłowska-Dawidziuk, 2001. *Journal of Paleontology* 84 (1): 156.
- Lenz, A.C., and A. Kozłowska-Dawidziuk. 2001a. Upper Wenlock (Silurian) graptolites of Arctic Canada: Pre-extinction, *lundgreni* Biozone fauna. *Palaeontographica Canadiana* 20: 1–61.
- Lenz, A.C., and A. Kozłowska-Dawidziuk. 2001b. Late Wenlock and early Ludlow graptolite extinction, evolution and diversification: A reassessment. *Special Papers in Palaeontology* 67: 171–183.
- Lenz, A.C., and A. Kozłowska-Dawidziuk. 2002. Upper Homerian (Upper Wenlock, Silurian) graptolites from Arctic Canada. *Journal of Paleontology* 76: 321–346.
- Lenz, A.C., and A. Kozłowska-Dawidziuk. 2004. *Ludlow and Pridoli (Upper Silurian) Graptolites from the Arctic Islands*, 141. Ottawa: NRC Research Press.
- Lenz, A.C., and M.J. Melchin. 1987. Silurian retiolitids from the Cape Phillips Formation, Arctic Islands, Canada. *Bulletin of the Geological Society of Denmark* 35 (3–4): 161–170.
- Lenz, A.C., S. Senior, A. Kozłowska, and M.J. Melchin. 2012. Graptolites from the mid Wenlock (Silurian), middle and upper Sheinwoodian, Arctic Canada. *Palaeontographica Canadiana* 32: 1–93.
- Lenz, A.C., D.E.B. Bates, A. Kozłowska, and J. Maletz. 2018. Part V, revision 2, Chapter 26: Family Retiolitidae Lapworth, 1873: Introduction and taxonomy. *Treatise Online* 114: 1–37.
- Maletz, J. 2008. Retiolitid graptolites from the collection of Hermann Jaeger in the Museum für Naturkunde, Berlin (Germany). I. *Neogothograptus* and *Holoretiolites*. *Paläontologische Zeitschrift* 82 (3): 285–307.
- Maletz, J. 2010. Retiolitid graptolites from the collection of Hermann Jaeger in the Museum für Naturkunde, Berlin (Germany). II. *Cometograptus*, *Spinograptus*, and *Plectograptus*. *Paläontologische Zeitschrift* 84: 501–522. <https://doi.org/10.1007/s12542-010-0065-x>.
- Maletz, J. 2019. Part V, Second Revision, Chapter 22: Suborder Axonophora, Infraorder Diplograptina I (Diplograptidae, Lasiograptidae): Introduction, morphology, and systematic descriptions. *Treatise Online* 127: 1–26.
- Maletz, J., and H. Schöning. 2017. Graptolites from glacial erratics of the Laerheide, northern Germany. *Paläontologische Zeitschrift* 91: 223–235.
- Maletz, J., D.E.B. Bates, A. Kozłowska, and A.C. Lenz. 2017. The retiolitid graptolites. In *Graptolite Paleobiology*, ed. J. Maletz, 207–220. Chichester: Wiley Blackwell.
- Manck, E. 1913. *Retiolites macilentus* Törnq. *Zeitschrift für Naturwissenschaften* 85 (2–3): 101–104.
- Manck, E. 1918. Die Graptolithen der Zone 18, sowie *Retiolites eiseli* spec. nov., *Monogr. bispinosus* spec. nov. und *Diplograptus radiculatus* spec. nov. *Zeitschrift Für Naturwissenschaften* 86: 337–344.
- Manda, Š, P. Štorch, J. Frýda, L. Slavík, and Z. Tasáryová. 2019. The mid-Homerian (Silurian) biotic crisis in offshore settings of the Prague Synform, Czech Republic: Integration of the graptolite fossil record with conodonts, shelly fauna and carbon isotope data. *Palaeogeography, Palaeoclimatology, Palaeoecology* 528: 14–34.
- Melchin, M.J., C.E. Mitchell, A. Naczek-Cameron, J.X. Fan, and J. Loxton. 2011. Phylogeny and adaptive radiation of the Neograptina (Graptoloida) during the Hirnantian extinction and Silurian recovery. *Proceedings of the Yorkshire Geological Society* 58: 1–30.
- Melchin, M.J., A.C. Lenz, and A. Kozłowska. 2017. Retiolitine graptolites from the Aeronian and lower Telychian (Llandovery, Silurian) of Arctic Canada. *Journal of Paleontology* 91 (1): 116–145.
- Münch, A. 1952. Die Graptolithen aus dem anstehenden Gotlandium Deutschlands und der Tschechoslowakei. *Geologica, Schriftenreihe der Geologischen Institute der Universitäten Berlin, Greifswald, Halle, Rostock* 7: 1–157.
- Münch, A. 1931. *Retiolites mancki*. Ein neuer *Retiolites* aus dem norddeutschen Geschiebe. 23. *Bericht der Naturwissenschaftlichen Gesellschaft Chemnitz*, 35–42.
- Obut, A.M., and N.M. Zaslavskaya. 1979. Razvitiye rhabdosom i ekologiya *Gothograptus nassa* (Holm). [The development of rhabdosomes and the ecology of *Gothograptus nassa* (Holm)]. In *Sreda i Zhizn' v Geologicheskom Proshlom; voprosy ekostatigrafii*. [Environment and life in the Geological Past], eds. O.A. Betekhtina, and I.T. Zhuravleva. Sreda i Zhizn' v Geologicheskom Proshlom; voprosy ekostatigrafii. [Environment and life in the Geological Past]. Akademiya Nauk SSSR, Sibirskoye Otdeleniye Instituta Geologii i Geofiziki. Novosibirsk, USSR, 30–33. [in Russian]
- Obut, A.M., and N.M. Zaslavskaya. 1983. Families of retiolitids and their phylogenetic relationships. In *Morfologia i sistematika bespozvonochnykh fanerozoa*, eds. A.S. Dagsy, and V.N. Dubatolov, V.Izdatelstvo Nauka, Moskva, 102–113. [in Russian, for English translation see Obut and Zaslavskaya, 1986]
- Obut, A.M., and N.M. Zaslavskaya. 1986. Families of Retiolitida and their phylogenetic relations. *Geological Society Special Publication* 20: 207–219.
- Piras, S. 2006. *Valentinagraptus* a new genus of plectograptid graptoloid from the lower Ludlow (Silurian) of Barrandian, Bohemia. *Geological Journal* 41: 581–590.
- Porębska, E.E., A. Kozłowska-Dawidziuk, and M. Maasiak. 2004. The *lundgreni* event in the Silurian of the East European Platform, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 213: 271–294.
- Radzevičius, S., P. Raczynski, K. Pluta, and A. Kojele. 2010. Findings Report: Graptolites from Silurian erratic boulders of Mokreszów quarry (Lower Silesia, Poland). *Archiv Für Geschiebekunde* 6 (1): 51–60.
- Reichstein, M. 1962. Conodonten und Graptolithen aus einem Kalk-Mergel-Geschiebe des Unter-Ludlow. *Geologie* 11 (5): 538–547.
- Rickards, R.B., and D.C. Palmer. 2002. *Gothograptus? meganassa* sp. nov., an unusually large retiolitid graptoloid from the Late Wenlock *lundensis* Biozone of Long Mountain, Shropshire, U.K. *Special Papers in Palaeontology* 67: 225–232.

- Roemer, F. 1885. Lethaea erratica oder Aufzählung und Beschreibung der in der norddeutschen Ebene vorkommenden Diluvial-Geschiebe nordischer Sedimentär-Gesteine. *Paläontologische Abhandlungen* 2 (5): 1–173.
- Štorch, P., and Š. Manda. 2019. Little known Homeric (Lower Silurian) graptolites from Kosov quarry near Beroun, the Czech Republic. *Fossil Imprint* 75 (1): 44–58.
- Štorch, P., C.E. Mitchell, S.C. Finney, and M.J. Melchin. 2011. Uppermost Ordovician (upper Katian – Hirnantian) graptolites of north-central Nevada, U.S.A. *Bulletin of Geosciences* 86 (2): 301–386. <https://doi.org/10.3140/bull.geosci.1264>.
- Ulst, R.Z. 1974. The sequence of pristiograptids in conterminous deposits of Wenlock and Ludlow of the Middle Pribaltic (Posledovatelnost pristiograptid v pograničnich otlozheniyich wenloka i ludlova v Sredne Pribaltike). In *Graptolites of the USSR*, ed. A.M. Obut, 105–122. Novosibirsk: Graptolites of the USSR. Publishing House Nauka, Siberian Branch.
- Urbanek, A. 1958. Monograptidae from erratic boulders of Poland. *Palaeontologia Polonica* 9: 1–105.
- Urbanek, A. 1966. On the morphology and evolution of the Cucullograptinae (Monograptidae, Graptolithina). *Acta Palaeontologica Polonica* 11 (3–4): 291–544.
- Urbanek, A., S. Radzevičius, A. Kozłowska, and L. Teller. 2012. Phyletic evolution and iterative speciation in the persistent *Pristiograptus dubius* lineage. *Acta Palaeontologica Polonica* 57 (3): 589–611.
- Wiman, C. 1895. Über die Graptolithen. *Bulletin of the Geological Institute of the University of Uppsala* 2 (4): 239–316.
- Wiman, C. 1896. The structure of the graptolites II. - Retioloidea. *Natural Science* 9: 240–249.