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ORIGINAL PAPER

The identity of the Silurian retiolitine genera *Paraplectograptus* and *Sagenograptoides* (Graptoloidea, Retiolitinae)

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Abstract

The genus *Paraplectograptus* includes a small number of retiolitine species with an identical development of the main thecal and ancora sleeve lists. A complete virgella-virga-nema development with connecting lists is formed on the obverse side of the tubarium, while the only thecal lists on the reverse side are the lateral apertural lists, connected through the pleural lists of the ancora sleeve. Obverse and reverse sides of the tubarium are connected by the thecal lips on the ventral sides. The characteristic zigzag thecal lists of the reverse side of many early retiolitines are not present in the genus. The development and extent of the reticular ancora sleeve lists on the obverse and reverse sides of the tubarium are quite variable and range from lacking entirely to dense. The genus *Pseudoplectograptus* is regarded as a junior synonym of *Paraplectograptus*. *Pseudoplectograptus sagenus* is transferred to the genus *Sagenograptoides*. Its type species '*Sagenograptoides arctos*' was known only from small, immature or fragmentary specimens of the associated *Sagenograptoides sagenus*. This species bears a characteristic reticulum on the ventral thecal walls, not found in the genus *Paraplectograptus*, but which is present in other *Cyrtograptus lundgreni* Biozone retiolitines.

Keywords Graptolites · Retiolitinae · *Paraplectograptus* · *Pseudoplectograptus* · *Sagenograptoides* · Tubarium construction · Biostratigraphy

Introduction

Numerous problems still exist in the understanding of retiolitine graptolite genera, their tubarium construction and their evolutionary patterns and relationships in the Silurian. Especially the Telychian yielded less information than most other biostratigraphic intervals in which retiolitines can be found (see Maletz 2022, fig. 8). Important information is available for some of the early taxa, the Petalolithinae, showing aspects of the ancora umbrella development, but likely representing side-lines of the general retiolitine evolution. They generally show a completely preserved thecal fusellum and often (paired) apertural spines that are not found in any Retiolitinae. These spines may not indicate a phylogenetic connection with the ancora sleeve development of the Retiolitinae. The early retiolitine genera *Aeroretiolites* and *Eorograptus* appear to be far removed from this early stock and their construction is thus difficult to be compared with that of the Petalolithinae. The spiral development of their ancora umbrella, so characteristic of *Pseudoretiolites*, can be found in the genus *Hercograptus* and may be followed back to *Pseudorthograptus obuti* or closely related petalolithine taxa (see Bates and Kirk 1992). However, the ancora umbrella in the younger *Retiolites* and *Stomatograptus* differs considerably through its meshwork development, lacking the distinct spiral construction (see Bates and Kirk 1997). Without the few available chemically isolated early retiolitines, our understanding of the evolutionary history of the clade would be restricted to the robust taxa referred to *Pseudoretiolites*, *Retiolites* and *Stomatograptus*. These show a considerable tubarium differentiation already and their ancora umbrella and ancora sleeve development indicates a strong diversification. It is difficult to relate these taxa phylogenetically to the younger taxa from the late Wenlock to Ludlow with their simpler ancora development.

Considerably diverging interpretations have been published in recent years regarding the genera *Paraplectograptus* and *Pseudoplectograptus* and their potential evolutionary relationships to the robust retiolitine genera *Retiolites* and *Stomatograptus*. Lenz et al. (2018) and Maletz (2022, 2023a) considered *Paraplectograptus* and *Pseudoplectograptus* to be synonymous as they possessed no definitive constructional

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characters to show a sufficient separation of the included species, but Kozłowska-Dawidziuk (1995, 2004) and Bates et al. (2023, p. 52) separated the genera based largely on their tubarium dimensions ('*Pseudoplectograptus* has a more robust and wider rhabdosome whereas that of *Paraplectograptus* is slender and parallel-sided').

Bates et al. (2023) supported the long-held view of a long ranging genus *Paraplectograptus* from the lower Telychian (Llandovery) *Spirograptus turriculatus* Biozone to the lower Homerian (Wenlock) *Cyrtograptus lundgreni* Biozone (see also Lenz and Melchin 1997, fig. 4; Kozłowska-Dawidziuk 2004, fig. 1; Melchin et al. 2017, fig. 6), based apparently largely on unpublished information and on range charts without specimen illustrations (cf. Lenz and Melchin 1987; Melchin et al. 2017). Maletz (2022) indicated a more limited range of the genus from the Sheinwoodian (Wenlock) *Monograptus riccartonensis* Biozone to the *Cyrtograptus lundgreni* Biozone, rejecting the poorly known ?*Paraplectograptus* sp. of Melchin et al. (2017) as a member of the genus *Paraplectograptus*. The species lacks the pustulose ornamentation of the lists of *Paraplectograptus* and bears a simple ancora resembling that of *Rotaretiolites* (Maletz, 2022, p. 11).

A specimen from the *Cyrtograptus centrifugus* Biozone was initially identified as *Paraplectograptus praemacilentus* (Štorch 1994, pl. 3, fig. 4), but subsequently listed as *Paraplectograptus* cf. *eiseli* (Štorch 2023, p. 36). Štorch (2023, fig. 16) indicated a range from the upper part of the *Cyrtograptus insectus* Biozone to the top of the *Cyrtograptus murchisoni* Biozone for this species, of which only a single specimen was ever illustrated. The specimen clearly shows similarities to a *Paraplectograptus* with few lists, but a definite identification is impossible. If this specimen represents *Paraplectograptus*, the origin of the genus would be found much earlier than suggested elsewhere in this paper, filling part of the gap in the Telychian to early Sheinwoodian discussed by Maletz (2022).

Bates et al. (2023) based their interpretation of the early evolution of the Retiolitinae and the phylogenetic connection on the genera *Retiolites* and *Stomatograptus* entirely on this possible early record of *Paraplectograptus*. Kozłowska-Dawidziuk (1995) discussed the *Paraplectograptus* lineage, at the time incorporating the genera *Paraplectograptus* and *Pseudoplectograptus*. A fresh view appears to be necessary to understand the constructional details of the two genera and their phylogenetic relationships to early retiolitines. Based on the interpretation of Maletz (2022 , fig. 8), *Paraplectograptus* has to be regarded as a stratigraphically fairly young retiolitine taxon, first appearing in the mid-Sheinwoodian (Wenlock). The genera *Retiolites* and *Stomatograptus* originated in the early Telychian (Llandovery), thus at least six million years earlier. Thus, there is a considerable interval in our record in which basically no data for the construction of the retiolitines and their evolution are available. Due to the rapid evolution of the group, this gap prevents a better understanding of the tubarium construction of the Retiolitinae and the evolution of the group.

Paraplectograptus construction

The tubarium construction of *Paraplectograptus* is based on chemically isolated material of a number of species, as the interpretation of shale material is difficult and easily leads to misinterpretations. Interpretations of single specimens have changed considerably over time and modifications have been added that may or may not be recognisable in the genus. For example a prosicular ring was illustrated for *Paraplectograptus* (Bates et al. 2023, fig. 2), but neither the identity of the species nor the precise origin of the material (cf. Cape Phillips Formation, uppermost Llandovery) is verifiable. The illustration of complete specimens would be needed to identify the genus and species. Specimens referred to *Paraplectograptus* sp. from an 'isolated nodule near locality 3; age: probably late Llandovery or early Wenlock' (Lenz 1993, explanation to pl. 13) suggest a taxon similar to *Paraplectograptus* in which a prosicula with four longitudinal rods is preserved.

Kozłowska-Dawidziuk (1998, pl. 1, fig. 1) illustrated a single specimen as *Paraplectograptus eiseli* from the Zawada borehole with a preserved prosicula. The oblique, flattened preservation makes it difficult to reconstruct the tubarium shape and development and the assignment to *Paraplectograptus* remains tentative. The specimen clearly represents a species with very few thecal and ancora sleeve lists. It is not recognisable in the illustration whether the specimen bears a pustular ornamentation of the lists.

Previous interpretations: A number of conflicting reconstructions have been offered in the literature for *Paraplectograptus*. In general, only genus names are provided for these reconstructions, even though they are usually based on particular specimens of distinct species. Thus, the more recent reconstruction of *Paraplectograptus* in Lenz et al. (2018, fig. 10.4) (Fig. 1) is based on the specimen of Lenz (1993, pl. 14, fig. 5), identified as *Paraplectograptus praemacilentus* (Fig. 1a, b), a species later referred to *Pseudoplectograptus* (cf.Kozłowska-Dawidziuk 1995; Lenz et al. 2012; Bates et al. 2023). The specimen is from locality 4, Cape Phillips, CP850 (244-250m; *Cyrtograptus lundgreni-Testograptus testis* Biozone; associated with *Paraplectograptus eiseli, Sokolovograptus textor* and others: Lenz 1993, p. 26). In time, the reconstruction was modified and now three distinctly different reconstructions of this specimen exist (Fig. 1c-e). Lenz et al. (2018) and Bates et al. (2023) even added

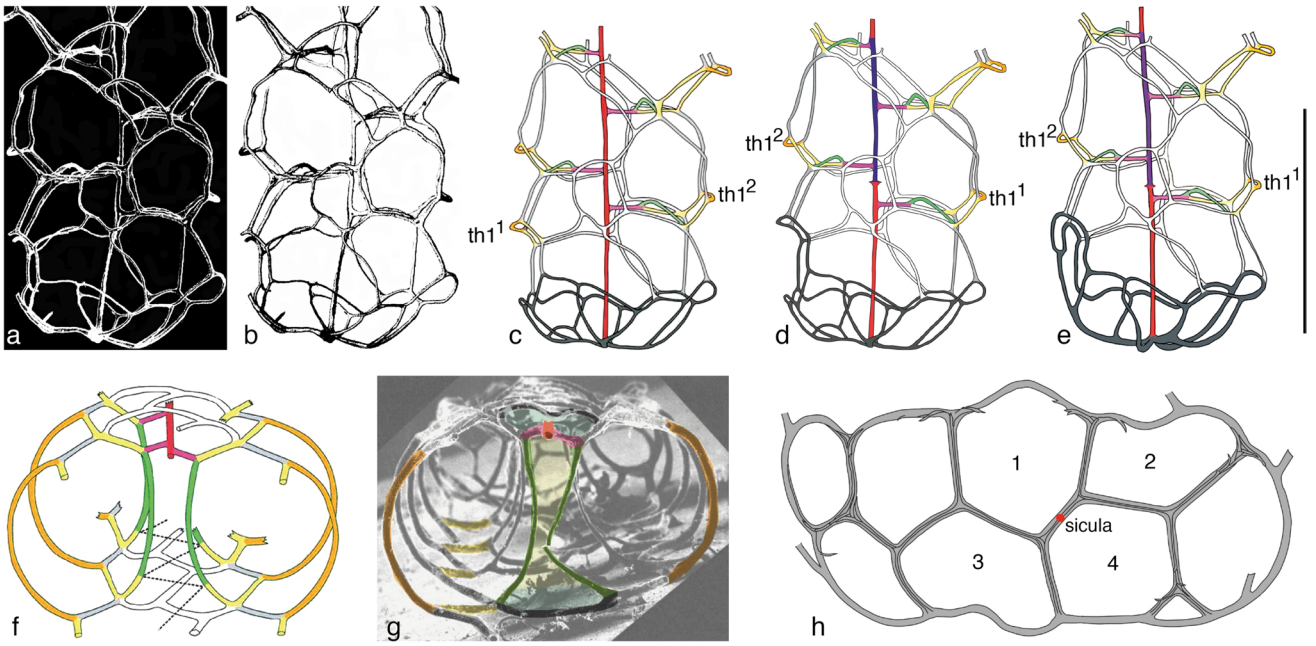

Fig. 1 Previous reconstructions of *Paraplectograptus*. **a-e** *Paraplectograptus areticulatus* (Kozłowska-Dawidziuk 1995), GSC 104044 from Arctic Canada (**a-b**) and reconstructions based on this specimen (**c-e**). **a-b** from Lenz (1993, pl. 14, fig. 5: *Paraplectograptus praemacilentus*), SEM photo (**a**) and inverted version (**b**). **c** Bates et al. (2005, fig. 5), interpreted as *Pseudoplectograptus* in obverse view. **d** Lenz et al. (2018, fig. 10.4), interpreted as *Paraplectograptus* in reverse view. **e** Bates et al. (2023, fig. 1A), interpreted as *Pseudoplectograptus* sp. in reverse view. There is no indication of a prosicular ring in the specimen, but it is shown in the reconstructions (**d-e**). Scale bar is 1 mm. **f** *Paraplectograptus* cross section in Bates et al. (2023, fig. 1D; based on Lenz, 1993, pl. 14, fig. 3: later identified as *Pseudoplectograptus areticulatus* by Kozłowska-Dawidziuk 1995). **g** *Paraplectograptus areticulatus* (Kozłowska-Dawidziuk, 1995), holotype, cross section (Maletz 2022, fig. 2C; photo originally by Lenz and Melchin 1987, pl. 3, fig. 5). **h** *Paraplectograptus eiseli* (Manck, 1918), ancora umbrella from outside showing seams, based on Bates et al. (2023, fig. 3), ZPAL G.47/6; same specimen probably illustrated as *Paraplectograptus* sp. in Bates et al. (2023, fig. 5E). For colour-coding of characters in all illustrations see Maletz (2022, fig. 4)

indications of a prosicular ring that is not recognisable in the specimen. The interpretation shows a change from an obverse view (see theca 1^1 on left side in Fig. 1c; Bates et al. 2005) to a reverse view (Fig. 1d, e: theca 1^1 on right side; Lenz et al. 2018; Bates et al. 2023). The interpretation as a reverse view is more likely, as the first connecting list (base of $th2^1$) of the obverse side of the tubarium grows to the right side (see Maletz 2022, fig. 1E, F: *Retiolites*).

The cross section referred to *Paraplectograptus* by Bates et al. (2023, fig. 1D) (Fig. 1f, g) was originally illustrated as an SEM photo by Lenz and Melchin (1987, pl. 3, fig. 5: *Paraplectograptus praemacilentus*) and also a lateral view of the specimen was provided (Lenz and Melchin 1987, pl. 3, fig. 2). Kozłowska-Dawidziuk (1995, p. 290) identified the specimen as the holotype of her new species *Pseudoplectograptus areticulatus*. Maletz (2022, fig. 2C) used the cross section as an example (Fig. 1g) and identified the species as *Paraplectograptus areticulatus*. His interpretation is nearly identical to the one provided by Bates et al. (2023, fig. 1D), but the latter (Fig. 1f) indicated a theoretical zigzag homologue of the reverse zigzag lists of *Retiolites*, suggesting that the transverse lists in Maletz (2022) may include parts of the lateral apertural lists on the reverse side of the tubarium.

New interpretation: As the type specimen of *Paraplectograptus eiseli* is preserved as a flattened, poorly preserved specimen in shale (photo in Lenz et al. 2012, fig. 7.1), its details are only in part available and a comparison with chemically isolated material is difficult. Therefore, the identification of chemically isolated material as *Paraplectograptus eiseli* may be questionable and may not serve to provide a reasonable example to identify this species. Thus, a new interpretation of the tubarium construction of the genus *Paraplectograptus* (Fig. 2a-c) is here provided, based on *Paraplectograptus hermanni* Maletz, 2023a, a species quite similar to *Paraplectograptus eiseli*, but based on chemically isolated three-dimensionally preserved material.

Paraplectograptus hermanni shows the typical development of the thecal and ancora sleeve lists on the obverse side (Fig. 2a). Here the virgella-virga-nema complex is connected with the horizontal connecting lists to the zigzag line of the lateral apertural lists and pleural lists forming the edges of the tubarium. The obverse side, thus include the thecal lists and the pleural lists as the only ancora sleeve lists. On the reverse side, the pleural ancora sleeve lists and the lateral apertural lists are the only lists remaining from the outline of the tubarium. A zigzag thecal list

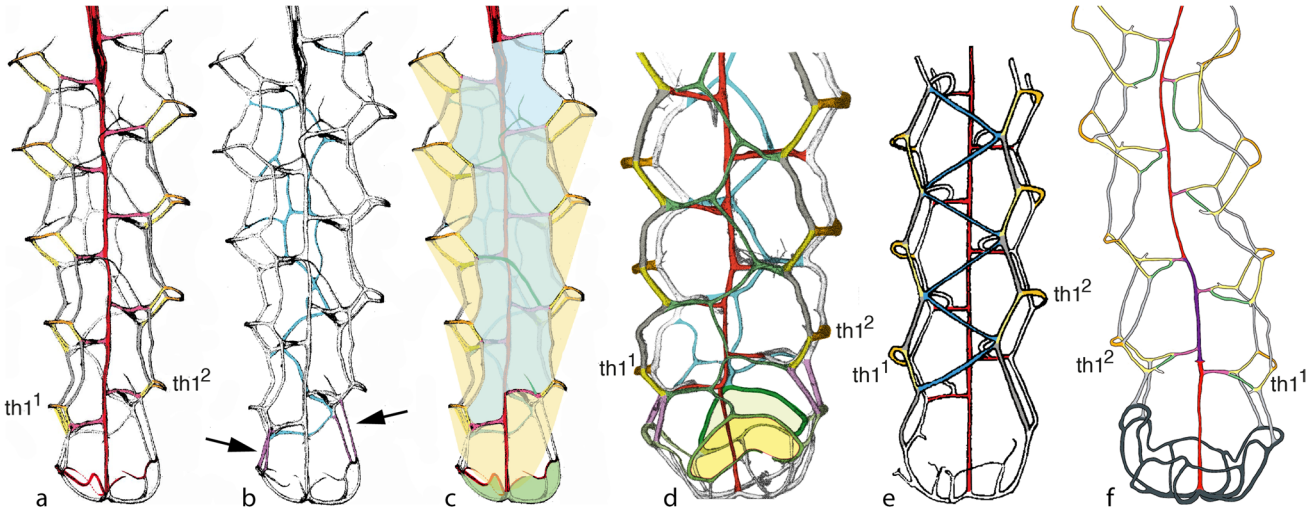

Fig. 2 *Paraplectograptus* interpretations. **a-c** *Paraplectograptus hermanni* Maletz, 2023a, interpretation of holotype in obverse view. **a** Interpretation showing virgella-virga-nema-complex, lateral thecal lists and pleural lists (ancora sleeve lists) and thecal lips in colour. **b** Same specimen showing reverse ancora sleeve lists in blue. **c** Interpretation showing thecal membranes (yellow), obverse ancora sleeve membranes (light blue) and possible ancora umbrella extension (green). **d** *Paraplectograptus areticulatus* (Kozłowska-Dawidziuk, 1995), obverse view (based on Palmer and Rickards 1991, pl. 66). **e** *Paraplectograptus eiseli*, interpretation showing reverse parietal lists in blue (based on Kozłowska-Dawidziuk 1995, fig. 8C). **f** *Paraplectograptus*, reverse view, specimen showing slight indications of ancora sleeve lists only (from Bates et al. 2023, fig. 1B). Specimens not to scale

as seen in *Retiolites* and *Stomatograptus* (see Maletz 2022, fig. 1E, F) is lacking. The thecal lips connect obverse and reverse sides on the ventral sides. Secondary ancora sleeve lists or reticulum can be seen on the reverse side (Fig. 2b: blue). Few secondary ancora sleeve lists are found on the obverse ancora sleeve membranes (Fig. 2c: green).

The ancora sleeve is connected to the ancora umbrella by four lists (purple lists; arrows in Fig. 2b), here interpreted as the initial pleural lists. These lists appear to connect the ancora umbrella rim with the junction of the lateral apertural and the connecting list on the obverse side and to the lateral apertural list on the reverse side. These initial pleural lists probably outline the sides of the ventral proximal orifices, as suggested for *Paraplectograptus eiseli* by Bates et al. (2023, fig. 4). It is, thus, impossible to tell if proximal lateral orifices were developed in this taxon. Therefore, the ancora sleeve membrane is indicated to start at the connecting lists of the first thecal pair in the interpretation (Fig. 2c), but likely originated earlier. Distinct lateral proximal orifices are visible in *Paraplectograptus areticulatus* (Fig. 2d), but do not reach the pleural lists.

The outline of the ancora umbrella shows thin lists that may easily be broken and thus incompletely preserved. Therefore its development is difficult to ascertain. Bates et al. (2023, fig. 3) illustrated a drawing of the ancora umbrella of a specimen, possibly belonging to *Paraplectograptus eiseli*, with nine meshes of variable sizes (Fig. 1h). The specimen number (ZPAL47/6, stub 313) is identical to a fragment in Bates et al. (2023, fig. 5F) not showing the ancora umbrella. Further information is not available for the ancora umbrella construction in *Paraplectograptus*.

In *Paraplectograptus areticulatus*, a species with more extensive ancora sleeve lists, the ancora sleeve can be interpreted to reach down to the rim of the ancora umbrella and the development includes proximal lateral orifices (2d). The fairly regular zigzag lists with their short horizontal connections to the junction of the lateral apertural lists and pleural lists on the obverse and reverse sides can be recognised as ancora sleeve lists (parietal lists) with their seams on the outside. Thus, a zigzag thecal list on the reverse side as in *Retiolites* and *Stomatograptus*, is not present. The precise development of the transverse lists is still unclear in *Paraplectograptus*.

Density of ancora sleeve lists: The development and density of the ancora sleeve lists can be quite variable in the various species of *Paraplectograptus*, and shows the difficulty to separate between clathrial and reticular lists (Maletz 2022, p. 7). The pleural lists of the ancora sleeve can be identified as clathrium, forming the edges of the ancora sleeve membranes together with the lateral apertural lists. The identification of the lateral zigzag parietal lists as clathrium is more problematic. They may be quite regularly developed as in *Paraplectograptus areticulatus* (Fig. 2d).

A more dense development of the list construction than on the obverse side can be seen on the reverse side *Paraplectograptus hermanni*. The parietal lists on the reverse side of the tubarium initially are quite regular, but distally

the irregularity increases (Fig. 2b) in this species. On the obverse side only few lists can be noted (Fig. 2c).

Highly irregular mesh development can be found, filling out secondarily the regular zigzag parietal list construction in some *Paraplectograptus* species and forming an irregular meshwork of lists as in *Paraplectograptus simplex* or *Paraplectograptus reticulum*. A similar development is also recognisable in other taxa (cf. *Hoffmanigraptus* in Kozłowska 2021, fig. 4A, B; *Plectograptus* in Bates et al. 2006). A clear development of parietal lists is not discernible in *Sagenograptoides sagenus* (Fig. 3b: blue lists) in which a dense irregular meshwork of reticular lists is found on the ancora sleeve.

The reticulum development in *Paraplectograptus eiseli* is unclear, as the type specimen (Fig. 4a) does not show all the details. The development of zigzag parietal lists connecting directly the lateral edges of the tubarium on the reverse side (cf. Bouček and Münch 1952, fig. 11D, F, H) has not been demonstrated for chemically isolated material, except for a single poor illustration in Kozłowska-Dawidziuk (1995, fig. 4) and in Lenz et al. (2012, pl. 1, fig. 9). Kozłowska-Dawidziuk (1995, fig. 8C) figured a reconstruction of this type that, according to the thecae, shows an obverse view, but has the zigzag parietal lists on this side (Fig. 2e), which cannot be correct, as the obverse side invariably shows the virgella-virga-nema complex in *Paraplectograptus*. Specimens referred to *Paraplectograptus eiseli* with a strongly reduced amount of ancora sleeve lists have been illustrated suggesting the presence of minor amounts of reticulum on the obverse side of the ancora sleeve at least (cf. Lenz et al. 2012, pl. 1, fig. 9). Specimens lacking ancora sleeve reticulum completely (cf. Lenz et al. 2012, pl. 1, fig. 2) appear to be incompletely developed early astogenetic stages or are possibly incompletely preserved as specimens (cf. Bates et al. 2023, fig. 1B). The reticulum on the ancora sleeve wall membranes is only developed in more mature specimens and its density should not be regarded as a species defining character in smaller or juvenile specimens of *Paraplectograptus*.

The thecal shape: The true thecal shape of retiolitines is difficult to observe as only few specimens with

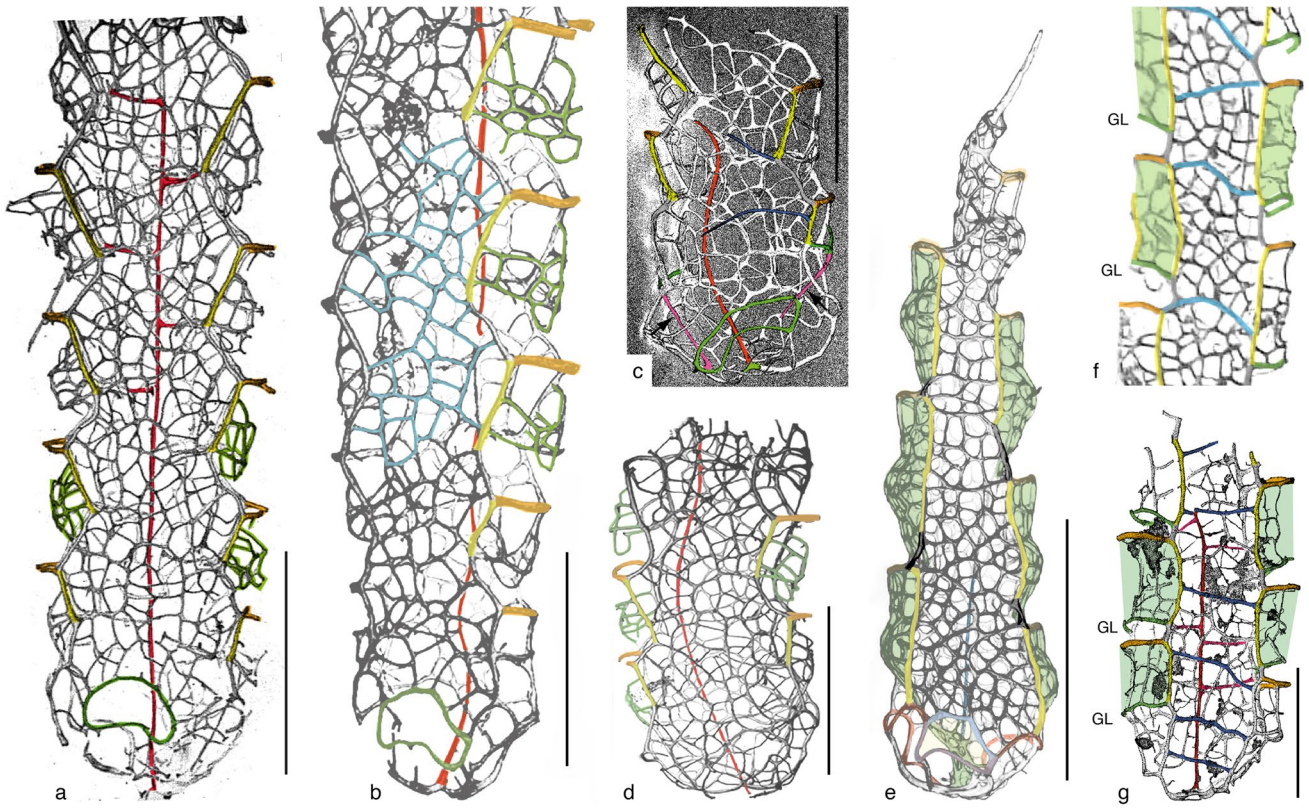

Fig. 3 Reticulum and the ventral thecal walls. **a-d** *Sagenograptoides sagenus* (Lenz, 1993). **a** holotype, GSC 104048 (after Lenz 1993, pl. 15, fig. 9). **b** GSC 126924, reverse view of mature tubarium (after Lenz and Kozłowska 2006, fig. 5.4). **c** paratype of *Sagenograptoides arctos*, GSC 119775, obverse view (after Lenz and Kozłowska-Dawidziuk 2001, pl. 8, fig. 1). **d** holotype of *Sagenograptoides arctos*, GSC 99179 (after Lenz and Kozłowska-Dawidziuk 2001, pl. 8.5). **e** *Eisenackograptus eisenacki* (Obut and Sobolevskaya, 1965), GSC 99146, Arctic Canada (after Lenz 1993, pl. 9.9). **f** ?*Eisenackograptus eisenacki* (Obut and Sobolevskaya, 1965), part of longer specimen (after Kozłowska-Dawidziuk 1990, pl. 25, fig. 1). **g** *Virgellograptus perrarus* Kozłowska 2015, holotype (after Kozłowska 2015, fig. 1E). Ventral thecal walls and/or reticulum on these in green. Scale bars are 1 mm

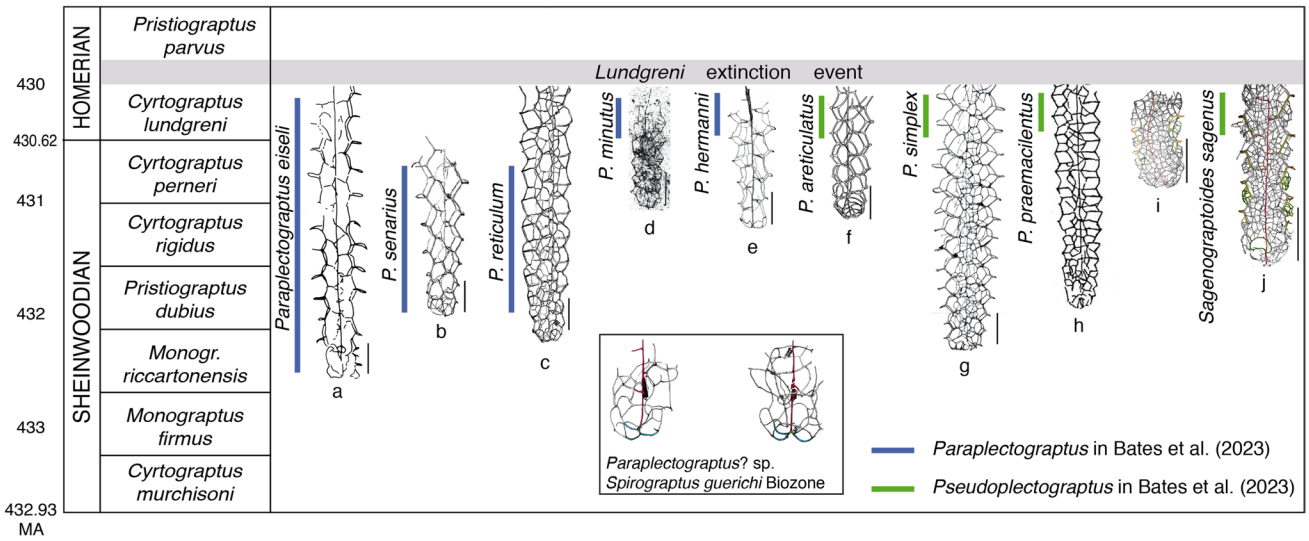

Fig. 4 Biostratigraphy of *Paraplectograptus* and *Sagenograptoides*. **a** *Paraplectograptus eiseli* (after Blumenstengel et al. 2006, pl. 1.1). **b** *Paraplectograptus senarius* (after Lenz et al. 2012, fig. 7.3). **c** *Paraplectograptus reticulum* (after Lenz et al. 2012, fig. 7.4). **d** *Paraplectograptus minutus* (from Rickards et al. 1995, fig. 20A). **e** *Paraplectograptus hermanni* (after Maletz 2023a, fig. 3G). **f** *Paraplectograptus areticulatus* (after Palmer and Rickards 1991, pl. 66). **g** *Paraplectograptus simplex* (after Lenz et al. 2012, pl. 2.1). **h** *Paraplectograptus praemacilentus* (after Bouček and Münch 1952, fig. 8B). **i** *Sagenograptoides sagenus* (type of *S. arctos*; after Lenz et al. 2018, fig. 21.4a). **j** *Sagenograptoides sagenus* (after Lenz 1993, pl. 15, fig. 7). *Paraplectograptus*? sp. modified from Melchin et al. (2017, figs. 15.1, 15.2). Scale bars indicate 1 mm

preserved thecal walls have been found. The best available interpretation of the thecal walls in *Paraplectograptus* is based on the model prepared by Nancy Kirk (see Bates et al. 2023, fig. 7B: as *Pseudoplectograptus*) as preserved thecal wall membranes are unknown for the genus. It shows a highly inclined ventral thecal wall and also strongly inclined apertures without a geniculum or the vertical to inwards inclined thecal walls found in many post-lundgreni extinction taxa (cf. Kozłowska et al. 2019; Maletz 2023b: *Holoretiolites*, *Neogothograptus*). This development (see Fig. 2c) is similar to that in *Retiolites* (Maletz 2022, fig. 1E-G), *Pseudoretiolites* (Maletz, 2022, fig. 3B) and even *Hercograptus* (Melchin 1999), but the inclination of the ventral thecal walls is steeper here. A highly inclined ventral thecal wall can also be seen in *Sagenograptoides*, here covered in part by the reticulum (Fig. 3a-d: green). Other genera from the pre-lundgreni extinction interval in the lower Homerian *Cyrtograptus lundgreni* Biozone show a distinct geniculum and vertical thecal walls (cf. *Virgellograptus*, *Cometograptus*, *Gothograptus*, *Semigothograptus*).

Reticulate ventral thecal walls: In early retiolitines, the lateral ancora sleeve walls often show a distinct mesh of reticulate lists, but reticular lists are not present on the thecal walls. A reticular meshwork on the thecal walls (Fig. 3) and sometimes even on the sicula is characteristic of the genus *Gothograptus* (cf. Kozłowska et al. 2019) and can be found in other retiolitines from the *Cyrtograptus lundgreni* Biozone onwards (see Maletz 2022, fig. 8: *Cometograptus*, *Sagenograptoides*, *Semigothograptus*, *Virgellograptus*). The reason for this construction is unclear as is the origin. The oldest taxa with a reticulum on the ventral thecal walls include *Eisenackograptus* (Fig. 3e) with a ventral thecal wall lacking a geniculum and the poorly known *Virgellograptus* (see Kozłowska 2015, fig. 2A) with a strong genicular list (GL in Fig. 3g). Both genera are first found in the *Cyrtograptus perneri* Biozone of late Sheinwoodian (Wenlock, Silurian) age.

Eisenackograptus is similar in its thecal form to *Sagenograptoides*, but has a finite tubarium with relatively few thecal pairs and a tubarium that narrows distally ending in an appendix (cf. Kozłowska-Dawidziuk 1990; Lenz, 1993). *Eisenackograptus eisenacki* (Obut and Sobolevskaya, 1965) possesses an undulating, reticulated ventral thecal wall that reaches deep into the tubarium at least in the first thecal pair (Maletz 2022, fig. 3C) and does not bear a geniculum (Fig. 3e). Long specimens referred to *Eisenackograptus eisenacki* by Kozłowska-Dawidziuk (1990, pl. 25) from the *Cyrtograptus rigidus* Biozone of Poland show a distinct genicular list without infragenicular reticulum (Fig. 3f), as does the reconstruction of a specimen in Kozłowska-Dawidziuk (1995, fig. 9A). A few longer fragments illustrated by Lenz (1993, pl. 8) and Lenz and Melchin (1987, pl. 3) lack the geniculum and have the undulating ventral thecal walls of typical *Eisenackograptus eisenacki*. It is unclear, whether this can be regarded as the intraspecific variation of a single species or whether more than one species is covered under this name.

The supposed homology of the genicular list in the younger retiolitines with the geniculum in earlier graptoloids needs clarification. The supragenicular wall in these retiolitines shows a reticulum, while there is no reticulum below the genicular list (infragenicular wall) and it is unclear whether there has been a thecal wall and that the genicular list can be homologized constructionally (not evolutionarily) with the geniculum in the climacograptids for example or represents an independently developed feature.

The surface ornamentation of lists: All species of *Paraplectograptus* bear the characteristic pustulose surface ornamentation of the stratigraphically younger retiolitines (cf. Lenz and Melchin 1987: Plectograptinae; Lenz et al. 2018). The presence of pustules is unknown in the material identified as *Paraplectograptus* cf. *eiseli* by Štorch (1994, 2023). According to Maletz (2022, fig. 8), the oldest retiolitine taxa with pustulose surface ornamentation belong to the genera *Giganteograptus* Lenz and Kozłowska, 2007 and *Sokolovograptus* Obut and Zaslavskaya, 1974.

The seams in seamed lists of the obverse and reverse ancora sleeve are found on the outside in all species known in enough detail (see Palmer and Rickards 1991, pl. 66: *Paraplectograptus areticulatus*). The seams are also present on the outside of the ancora umbrella lists (see Bates et al. 2023, fig. 3). In younger (late Wenlock to Ludlow) retiolitines, the ancora sleeve lists are seamed on the inside (Lenz et al. 2018; Maletz 2022, 2023a). The transition between the two types has not been traced so far, but a number of late Sheinwoodian species show some evidence of both (cf. *Cometograptus*: Kozłowska-Dawidziuk 2001).

Paraplectograptus? sp. of Melchin et al. (2017) from the *Spirograptus guerichi* Biozone (basal Telychian, Llandovery) shows a surface ornamentation of weak longitudinal striae or a smooth surface, unlike any other species of *Paraplectograptus*. The authors indicate a sicula only 0.4-0.49 mm long, but this is clearly the length of the well-preserved prosicula. The available specimens are quite small and immature (Fig. 4) and their inclusion in *Paraplectograptus* is unlikely as they bear only an apparently simple ancora umbrella with lists representing a single thecal pair. The distal development of the tubarium is unknown.

Sicula length: Kozłowska-Dawidziuk (1998, 2004) considered the length of the sicula in the retiolitines as an important character to understand the evolutionary changes within the clade. Kozłowska-Dawidziuk (1998, p. 206) suggested a possible polyphyletic origin of the retiolitids (now the Retiolitinae) based on the length of the sicula. The length of the sicula apparently varies between 1.0 and 1.5 mm within the genus *Paraplectograptus* (Kozłowska-Dawidziuk 2004, fig. 3), but Bates et al. (2023, p. 52) stated a length of 0.9-1.15 mm. The sicula length has not been demonstrated in most species and thus, further comments cannot be made. If the specimens of *Paraplectograptus*? sp. of Melchin et al. (2017) are not included in the genus *Paraplectograptus*, the length of the prosicula is also not known for the genus as further specimens showing the preservation of the prosicula are not published. Kozłowska-Dawidziuk (1995, fig. 4) and Kozłowska-Dawidziuk (1998, pl. 1.1) indicated the presence of specimens of *Paraplectograptus eiseli* with preserved prosiculae from the lower Wenlock (?*Cyrtograptus centrifugus* Biozone) of the Zawada-1 drillcore, Poland. The identity of this material remains unclear, however.

Astogeny and intraspecific variation

The astogeny is an often neglected feature in graptolite taxonomy, but may be quite important for taxonomic purposes. Maletz (2023b) discussed the astogenetic changes for a number of species in the genera *Holoretiolites* and *Neogothograptus* and indicated the problems for the identification of juvenile specimens. Juvenile specimens of *Paraplectograptus* with less than four theca cannot be referred to a certain species, unless a growth series has been recovered from the sample. Therefore, for example the specimens of *Paraplectograptus*? sp. of Melchin et al. (2017) from the *Spirograptus guerichi* Biozone of Arctic Canada (Fig. 4: box) are unidentifiable at the species level (see note in Maletz 2022, p. 11).

Astogentic changes and variation in *Paraplectograptus* and *Sagenograptoides* are not restricted to the final size of the specimens, but include also the density of the reticulum in these. Kozłowska-Dawidziuk (1995; fig. 15C) illustrated a specimen of *Sagenograptoides sagenus*, indicating a finite tubarium. However, the specimen may be incomplete distally, but it clearly shows the decrease of the density of the reticulum distally. Also the specimens illustrated by Lenz (1993) show the distal decrease of the reticulum density in this species. This development can be seen in all species of the genus *Paraplectograptus* in which a secondary reticulum is present. In all taxa the reticulum is the latest addition to the tubarium and much of it is formed at a fairly late stage in the construction of the colony.

A restricted growth may be indicated by the nematularium in *Paraplectograptus hermanni* (Fig. 4e), but the final length for the colonies is unknown for most species. A nematularium is unknown in any further species of the genus *Paraplectograptus* and has not been recognised in *Sagenograptoides*. Manda et al. (2019, fig. 10F) illustrated a specimen as *Paraplectograptus eiseli* with at least 20 thecal pairs, probably the longest known specimen of *Paraplectograptus*. It was apparently still growing as the distally extending nema shows. Other species are distally widening, but none shows distal tapering of the tubarium or the indication of an appendix suggesting a finite growth.

Intraspecific variation may also play a role in the identification of retiolitines (Maletz 2023b), but has

rarely been investigated. The intraspecific variation of *Paraplectograptus* has never been explored and most species have been described from very few specimens. A good example is *Paraplectograptus areticulatus*, a species of which only about 3-4 specimens have ever been illustrated. The species looks like it is well known and common, but only the holotype specimen was illustrated again and again (cf. Lenz and Melchin 1987; Palmer and Rickards 1991; Kozlowska-Dawidziuk 1995; Lenz 1993; Lenz et al. 2018; Maletz 2022; Bates et al. 2023). Reichstein's (1962) publication on *Holoretiolites simplex* (Eisenack, 1935) is the only example for the indication of a distinct intraspecific variation of mature specimens of retiolitines in general.

Biostratigraphical distribution

Lenz and Melchin (1997, fig. 2) illustrated a slightly idealized and simplified version of an early retiolitine from the Aeronian (*Lituigraptus convolutus* Biozone) under the name '*Paraplectograptus*', but later (Melchin et al. 2017, p. 137) identified it as *Eorograptus spirifer*. *Paraplectograptus*? sp. from the *Spirograptus guerichi* Biozone of Arctic Canada (Melchin et al. 2017, p. 141) was considered as the oldest species of this genus (cf. Kozłowska-Dawiziuk 2001), but the authors also considered that it may represent a new genus. The micro-ornamentation of the ancora sleeve lists consists of fine parallel striae, thus differing from the pustules found in *Paraplectograptus*. It also bears a completely preserved prosicula in all known specimens. A specimen identified only as *Paraplectograptus* sp. (see Bates et al. 2023, fig. 2C, D) bears a thickened prosicular rim and lacks a pustular surface of the cortical bandages. The origin of this material unfortunately is unknown. Another taxon from the late Llandovery or early Wenlock (found in an isolated nodule) bears a complete prosicula and shows a pustular surface of the ancora sleeve lists (Lenz 1993, pl. 13, figs. 5-10: *Paraplectograptus* sp.) and is not comparable to *Paraplectograptus*? sp. of Melchin et al. (2017). None of these records verify an origin of the genus *Paraplectograptus* before the mid-Sheinwoodian.

The latest data are used here to show the biostratigraphic ranges of all accepted *Paraplectograptus* species (Fig. 4). The apparently longest biostratigraphic range is that of *Paraplectograptus eiseli*, but many identifications of this species need to be verified. Lenz et al. (2018, p. 23) indicated an origin of the lectotype of *Paraplectograptus eiseli* from the mid-Telychian *Monoclimacis griestoniensis* Biozone, even though Manck (1918) clearly stated Zone 18 at Wetterahammer (*Monograptus riccartonensis* Biozone of Eisel 1899, 1903), which is approximately mid-Sheinwoodian in modern biostratigraphy. Jaeger (1991, fig. 1) indicated the presence of *Paraplectograptus eiseli* in the *Cyrtograptus lundgreni* Biozone at Wetterahammer. Lenz et al. (2012) identified *Paraplectograptus eiseli* from the *Monograptus instrenuus- Cyrtograptus kolobus* to the *Cyrtograptus perneri* Biozone in Arctic Canada, the latter correlated to the *Monograptus riccartonensis* Biozone of the mid-Sheinwoodian (Maletz 2021, fig. 6).

Lenz et al. (2012) identified their species *Paraplectograptus reticulum* and *Paraplectograptus senarius* from the *Monoclimacis flumendosae* to the *Cyrtograptus perneri* biozones. Both species differ mostly in the density of the reticulum in mature specimens. All further species are found exclusively in the *Cyrtograptus lundgreni* Biozone (Fig. 4). The data show that the genus *Paraplectograptus* is biostratigraphically restricted to the interval from the mid-Sheinwoodian to the basal Homerian and does not represent an early retiolitine genus (cf. Bates et al. 2023, p. 46: 'one of the earliest retiolitines'). Little can be learnt about its phylogenetic origin and connections and the subsequent evolutionary change before it went extinct during the lundgreni extinction event. The robust *Retiolites* and *Stomatograptus* bear ancora umbrellae with a complex meshwork of lists that theoretically may be reduced to the type found in *Paraplectograptus*. A considerable differentiation and re-arrangement of the ancora sleeve reticulum would also be necessary, especially as *Retiolites* does not possess defined pleural lists (Maletz 2022, p. 8).

Systematic Palaeontology

Remarks: The systematics of the Graptolithina follows the latest Treatise version (Lenz et al. 2018; Maletz (coordinating author), 2023c).

Subfamily Retiolitinae Lapworth, 1873
Genus *Paraplectograptus* Bouček and Münch, 1952, 1952 [= *Pseudoplectograptus* Obut and Zaslavskaya, 1983; syn. Lenz et al. 2018, p. 23]

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 (Maletz (coordinating author), 2023c, p. 409).
Included species: *Retiolites eiseli* Manck, 1918; *Retiolites tenuis* Eisenack, 1951; ?*Paraplectograptus hemmanni* Bouček and Münch, 1952; *Plectograptus praemacilentus* Bouček and Münch, 1952; *Pseudoplectograptus areticulatus* Kozłowska-Dawidziuk, 1995; *Paraplectograptus simplex* Kozłowska-Dawidziuk, 1995; *Paraplectograptus minutus* Rickards et al., 1995; *Paraplectograptus reticulum* Lenz et al., 2012; *Paraplectograptus senarius* Lenz et al., 2012; *Paraplectograptus hermanni* Maletz, 2023a

Remarks: The genus *Pseudoplectograptus* is synonymized with *Paraplectograptus* as was already done by Lenz et al. (2018, p. 23), but both were used without explanation as separate genera by Bates et al. (2023). The type species of *Pseudoplectograptus* is *Plectograptus praemacilentus* Bouček and Münch, 1952, a species originally described from flattened shale material. Chemically isolated material described under this name includes specimens described by Lenz and Melchin (1987, 1991) and Lenz (1993) from Arctic Canada. Kozłowska-Dawidziuk (1995) erected the species *Pseudoplectograptus areticulatus* based on some of this material. Bates et al. (2023, fig. 1D) used the holotype of *Pseudoplectograptus areticulatus* Kozłowska-Dawidziuk, 1995 (see Lenz 1993, pl. 14, fig. 3) to understand the development of *Paraplectograptus*. Maletz (2022, fig. 2C: cross section) used the same specimen to illustrate the development of *Paraplectograptus* and illustrated an interpretation of the specimen (Maletz 2022, fig. 5D) to show the development of the zigzag-shaped parietal lists in this taxon (Fig. 2d). Thus, *Paraplectograptus* and *Pseudoplectograptus* have been used to demonstrate the tubarium construction of a single genus, here identified as *Paraplectograptus*.

Notes are provided here for all recognised species of the genus *Paraplectograptus*. The differentiation is based on the presence and density of the secondary or reticular ancora sleeve lists (cf. Maletz 2022, p. 7). The diagnoses of species have been emended in cases that additional characters were regarded as important. Emendations for poorly known species and synonyms are not provided.

Paraplectograptus areticulatus (Kozłowska-Dawidziuk, 1995), ex *Pseudoplectograptus*
(Figs. 1a-g; 4f)

Diagnosis: *Paraplectograptus* species with zigzag parietal lists on obverse and reverse sides of the tubarium; additional reticular lists on the ancora sleeve lacking.
Remarks: The species was found in the *Cyrtograptus lundgreni* Biozone of Arctic Canada. Kozłowska-Dawidziuk (1995, p. 290) stated its presence from the *Spirograptus turriculatus* Biozone to the *Gothograptus nassa* Biozone, but published no evidence for this distribution. The species is known from its commonly re-illustrated holotype and very few additional specimens in Lenz and Melchin (1987) and Lenz (1993). There is no information on a wider biogeographical distribution.

Paraplectograptus eiseli (Manck, 1918), ex *Retiolites*
(Figs. 1h?; 2f; 4a)

Diagnosis: Slender and long, parallel-sided *Paraplectograptus* species with wide loops of the apertural lips; obverse side with horizontal connecting list attached to nema; no parietal lists on obverse side of tubarium; parietal lists on reverse side probably in contact at junction with pleural lists; secondary reticulum lacking.
Remarks: The reconstruction in Kozłowska-Dawidziuk (1995, fig. 8C; identified as *Paraplectograptus* only) is misleading as it shows parietal lists of the reverse side, but the thecal symmetry of the specimen indicates an obverse view (see Fig. 2e). It appears to be based on the reconstruction of the species in Bouček and Münch (1952, fig. 11H), in which a proximal end is not present. However, Kozłowska-Dawidziuk (1995, fig. 4) provided a poor, small illustration of a specimen that may support part of this construction. The precise development of the parietal list on the reverse side is unclear in the type specimen (Fig. 4a).

Paraplectograptus hemmanni Bouček and Münch, 1952 was based on a single specimen from Ronneburg, Thuringia, *Testograptus testis* Biozone. The specimen is indeterminable and its inclusion in *Paraplectograptus* cannot be verified.

Paraplectograptus hermanni Maletz, 2023a
(Figs. 2a-c; 4e)

Diagnosis: Small (5-7 thecal pairs), distally widening *Paraplectograptus* with distinct nematularium; irregular reticulum on the reverse side, but few reticular lists on obverse side.
Remarks: The species is characterised by a relatively short tubarium with a distinct, elongate nematularium, that is incorporated into the obverse side of the tubarium (Maletz 2023a, fig. 4H, L). There is an irregular meshwork of the reticulum on the reverse side, but only few isolated lists on the obverse side. Distinct lateral lobes of the ancora umbrella can be seen at the proximal end in ventral view (Maletz 2023a, fig. 4H) and may be recognisable in all *Paraplectograptus* species in the ventral view of the tubarium. These lobes are also characteristic in the post-lundgreni extinction taxa (cf. Maletz 2023a, fig. 6C: *Gothograptus nassa*).

Paraplectograptus minutus Rickards et al., 1995 (Fig. 4d). *Cyrtograptus lundgreni/Testograptus testis* Biozone, New South Wales, Australia. The species may be referred to *Paraplectograptus*, but the tubarium details are unclear, as the material is poorly preserved as flattened specimens in shale, often found in oblique orientation. The species shows a moderate development of the reticulum.

Paraplectograptus praemacilentus (Bouček and Münch, 1952), ex *Plectograptus*
(Figs. 2d; 4h)

Diagnosis: Robust, initially distally widening *Paraplectograptus* species with irregular ancora sleeve lists

on obverse and reverse sides; single proximo-ventrally directed looping list on the ventral tubarium sides.
Remarks: The species is based on three shale specimens and appears to show a relatively dense reticulum on the reverse and obverse sides in mature specimens. The detailed construction of the clathrium and reticulum in the type material is uncertain due to the preservation as flattened specimens. Many specimens initially referred to this species have been re-assigned to *Paraplectograptus areticulatus* by Kozłowska-Dawidziuk (1995). Lenz et al. (2012, p. 16) referred to the 'proximo-ventrally directed looping list' as the main characteristic feature of the species.

Paraplectograptus reticulum Lenz et al., 2012 (Fig. 4c). The species was described from the *Monoclimacis flumendosae* to *Cyrtograptus perneri* Biozone of Arctic Canada. It was illustrated from only two somewhat distorted specimens. There is evidence of the reticulum on the reverse side of the ancora sleeve, but it may be absent on the obverse side.

Paraplectograptus senarius Lenz et al., 2012 (Fig. 4b). Arctic Canada, very similar to *Paraplectograptus eiseli*. Differs apparently through the development of the zigzag ancora sleeve list on the reverse side. *Paraplectograptus eiseli* apparently has zigzag parietal lists connected directly to the lateral apertural lists and pleural lists (Fig. 2e), while those in *Paraplectograptus senarius* have short horizontal connection lists (cf. Fig. 4b).

Paraplectograptus simplex (Kozłowska-Dawidziuk, 1995), ex *Pseudoplectograptus* (Fig. 4g). Robust form with distally widening tubarium. Ancora sleeve reticulum present, maybe on obverse and reverse sides, but details were not described. Reticulum is irregular, no clear zigzag parietal lists. *Cyrtograptus lundgreni/Testograptus testis* Biozone or *Cyrtograptus radians* Biozone, Poland. Could by synonymous with *Paraplectograptus praemacilentus*.

Paraplectograptus tenuis (Eisenack, 1951), ex *Retiolites*. Eisenack (1951) described the species from a number of juvenile specimens. The holotype (Eisenack 1951, pl. 21, fig. 10) shows one thecal pair. The material most likely belongs to *Paraplectograptus eiseli* or a closely related taxon based on the proximal end with an ancora umbrella connected to the ancora sleeve with four pleural lists only. A species-specific identification is not possible.

Genus *Sagenograptoides* Lenz and Kozłowska, 2010 (=*Sagenograptus* Lenz and Kozłowska-Dawidziuk, 2001; homonym of *Sagenograptus* Obut and Sobolevskaya, 1962)

Diagnosis: Tubarium parallel-sided; ancora umbrella shallow; nema free; proximal lateral orifices kidney-shaped; ventral wall defined by thecal lips, pleural lists, lateral apertural lists; mid-ventral lists on thecae 11 and 12 attached to ancora umbrella rim; transverse lists in first pairs of thecae; irregular reticulum on ventral thecal walls and ancora sleeve; lists of ventral walls with pustules and seams inside; ancora sleeve lists with seams facing outward; outer ancora sleeve lists with seams facing inward may be present (Maletz (coordinating author), 2023c, p. 411).
Included species: *Paraplectograptus sagenus* Lenz, 1993; *Sagenograptus arctos* Lenz and Kozłowska-Dawidziuk, 2001 (syn. of *Sagenograptoides sagenus*; herein).
Remarks: The genus was originally named *Sagenograptus* by Lenz and Kozłowska-Dawidziuk (2001), but had to be re-named *Sagenograptoides*, as the name was already used for a Tremadocian anisograptid genus (Lenz and Kozłowska, 2010). Its type species *Sagenograptoides arctos* (Lenz and Kozłowska-Dawidziuk, 2001) is here regarded as a junior synonym of *Sagenograptoides sagenus* (Lenz, 1993), a species first described as *Paraplectograptus sagenus*.

Sagenograptoides sagenus (Lenz, 1993) ex *Paraplectograptus* (Figs. 3a-d; 4i, j)

Remarks: *Sagenograptoides arctos* was originally identified from the *Cyrtograptus lundgreni/Testograptus testis* Biozone of Arctic Canada. The description was based on a small number of broken proximal ends showing at most a length of 2 mm with three thecal pairs and an apparently free virgella-virga-nema complex inside the tubarium (Fig. 3c, d). It is also characterised by a dense reticulum on the ancora sleeve and also on the ventral thecal membranes. *Sagenograptoides arctos* and *Paraplectograptus sagenus* are both listed from samples SBC 10B and SB90 E41m (see Lenz and Kozłowska-Dawidziuk 2001), thus occur together. The specimens of *Paraplectograptus sagenus* possess a dense reticulum on the ancora sleeve and on the ventral thecal membranes (Fig. 3a, b). The thecal lips in both taxa are free loops, while the reticulum starts lower down on the supposed thecal membranes and does not touch the thecal lips. The reticulum shows an outward inclined ventral thecal side as in *Paraplectograptus*. *Sagenograptoides sagenus* specimens are much longer than the associated *Sagenograptoides arctos* specimens (reaching at least 6-7 thecal pairs in 5 mm and a length of 8 mm: Lenz 1993, p. 22). The virgella-virga-nema complex is secured in the tubarium with lateral connecting lists at least from the third thecal pair onwards where the connecting lists to the virgella-virga-nema complex are recognisable (Fig. 3a), but appears to be free initially (cf. Fig. 3b).

The development of a reticulum on the ventral thecal walls is common in many late Sheinwoodian retiolitines (e.g. *Virgellograptus, Cometograptus, Eisenackograptus, Semigothograptus, Gothograptus*), but is barely known from earlier taxa. It is characteristic for all post-lundgreni extinction taxa (cf. Maletz 2023b: *Holoretiolites*, *Neogothograptus*). The oldest taxon with a ventral thecal reticulum appears to be *Sokolovograptus* (see Lenz and Kozłowska 2006, fig. 4: *Sokolovograptus* cf. *S. parens*), but the distribution of this feature in the genus is quite variable as the example of *Sokolovograptus polonicus* with its strongly reduced meshwork of lists suggests (Kozłowska-Dawidziuk 1995; Lenz et al. 2012). *Sokolovograptus* differs from *Sagenograptoides* and related taxa through the presence of ancora sleeve lists with seams on the inside and a closer phylogenetic relationship is difficult to establish at the moment.

The development of the ventral thecal reticulum appears to be connecting many late Sheinwoodian to Homerian and younger retiolitines, but the origin of this character is unclear. The relationship of *Sagenograptoides* to *Paraplectograptus* cannot be verified at the moment, even though many tubarium features are quite similar.

Conclusions

Species of the genus *Paraplectograptus* are restricted biostratigraphically from the mid-Sheinwoodian (*Monograptus riccartonensis* Biozone) to early Homerian (*Cyrtograptus lundgreni* Biozone) with most species found only in the *Cyrtograptus lundgreni* Biozone.

Paraplectograptus differs from earlier taxa through the pustulose ornamentation of the cortical bandages and the loss of the reverse zigzag thecal lists. The ancora sleeve lists density varies considerably from dense to lacking.

The ancora umbrella appears to be quite simple, but details are unknown and the ancora umbrella rim is often difficult to recognise. It may be reduced and a distinct rim may not be developed.

Paraplectograptus may be phylogenetically related to genera in which a reticulum is present on the ventral thecal membranes as in *Sagenograptoides*, *Eisenackograptus*, *Virgellograptus* and others. These taxa also share lists with pustulose surfaces and seams on the outside.

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Declarations

Conflict of interest The author declares no conflict of interest.

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