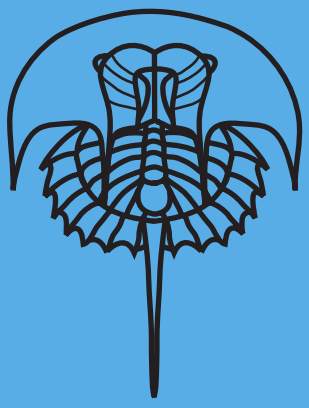

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Part V, Second Revision, Chapter 26: Family Retiolitidae: Introduction, Morphology, and Systematic Descriptions

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PART V, SECOND REVISION, CHAPTER 26: FAMILY RETIOLITIDAE: INTRODUCTION, MORPHOLOGY, AND SYSTEMATIC DESCRIPTIONS

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Family RETIOLITIDAE Lapworth, 1873

[Retiolitidae LAPWORTH, 1873, table 1, facing p. 555]

Axonophorans (Neograptina) with scandent, biserial, dipleural, bistipular to unistipular tubarium; mostly pattern I astogeny or derived pattern, but development unknown in most taxa with poorly preserved fusellum; ancora umbrella and ancora sleeve weakly developed in derived petalolithines, well developed in all retiolitines; sicula and fusellum fully preserved in petalolithines, rarely in retiolitines. *Upper Ordovician (Hirnantian* Metabolograptus persculptus *Biozone)–Silurian, Ludlow (lower Ludfordian* Saetograptus leintwardinensis *Biozone):* worldwide.

Melchin and others (2011) revised the family Retiolitidae based on a cladistic analysis and extended the concept considerably to include a number of non-ancorate taxa previously not referred to the Retiolitidae, although Melchin (1998) already combined the ancorate and non-ancorate taxa. They defined the Retiolitidae as "the first species that acquired a unistipular (aseptate) biserial rhabdosome in the clade that contains *Paramplexograptus madernii* and *Retiolites geinitzianus* and all its descendants (Melchin & others, 2011, p. 298 node 4, fig. 2–3)." Melchin, Lenz, and Kozłowska (2017) followed this usage, even though Maletz (2014) preferred a more restricted definition of the superfamily Retiolitoidea and the family Retiolitidae. He differentiated the family Retiolitidae into two subfamilies, the paraphyletic Petalolithinae and the derived, monophyletic Retiolitinae, based on the presence or absense of the fusellum of the thecate part of the tubarium, respectively.

Even though the absence of the fusellum has to be regarded as a preservational aspect, it most easily separates the two groups in the fossil record. The recognition of tubarium characters, especially in the Retiolitinae, is based on chemically isolated material, which may differ considerably in preservation from shale specimens (Fig. 1.3–1.4). Specimens of *Pseudoretiolites perlatus* sometimes show the preservation of the fusellum in shale material (e.g., Elles & Wood, 1908; Bouček & Münch, 1944; Obut, Sobolevskaya, & Merkureva, 1968). By comparison, the chemically isolated material provides a full three-dimensional view of the lists, while fusellar structures are recognized only in a relatively few taxa (Bates & Kirk, 1992, 1997; Lenz, 1994b, Lenz & Kozłowska-Dawidziuk, 2002b; Kozłowska-Dawidziuk, 1997, Kozłowska & others, 2013). Bouček and Münch (1944) commented on the preservation of an outer (ancora sleeve) membrane covering the list structure in *Retiolites*. Holm (1890, pl. 2,*5*) described and illustrated the preservation of thecae inside the lists of the ancora sleeve in this genus.

Lenz, Alfred C., Denis E. B. Bates, Anna Kozłowska, and Jörg Maletz. 2018. Part V, Second Revision, Chapter 26: Family Retiolitidae: Introduction, morphology, and systematic descriptions. Treatise Online 114:1–37, 24 fig.

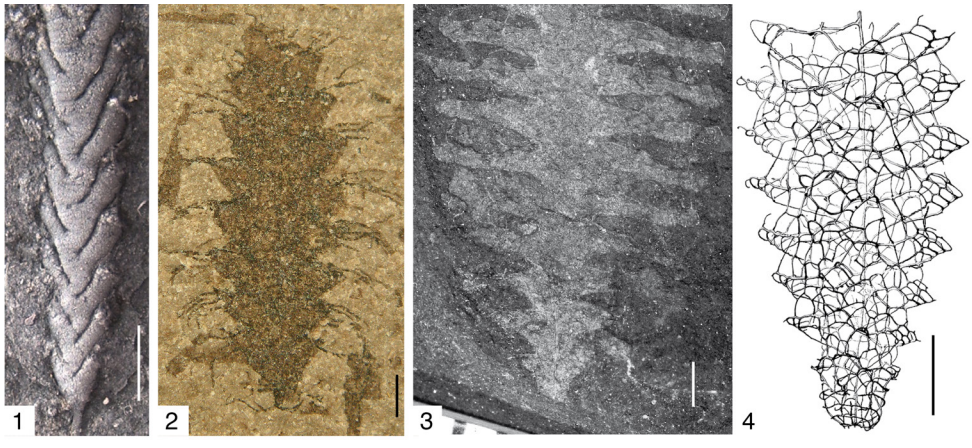


Fig. 1. *1, Rivagraptus bellulus* (Törnquist, 1890), PMU 31837, proximal end in reverse view and full relief, showing preserved thecae, Tomarp, Scania, Sweden (new); *2, Spinadiplograptus inopinatus* (Bouček, 1944), PŠ 3632b, flattened specimen showing fusellum of the thecae, ancora umbrella, and thecal spines, *Demirastrites triangulatus* Biozone, Czech Republic (Štorch, 2015, fig. 9A); *3–4, Pseudoretiolites perlatus* (Nicholson, 1868a); *3,* NIGP 168459, flattened specimen in shale showing fusellum and ancora sleeve mesh, Yesanguan, Badong County, Hubei, China (new; specimen provided by Wang Chuanshang, Wuhan, China); *4,* GSC 137613, chemically isolated specimen in three dimensions showing ancora sleeve meshes, Llandovery, upper Aeronian, *Lituigraptus convolutus* Biozone, Arctic Canada (inverted SEM photo, Melchin, Lenz, & Kozłowska, 2017, fig. 3,*1*). Scale bars, 1 mm.

THE ANCORA

The ancora is a branched virgellar spine that bears four lateral branches, from which an ancora umbrella and the ancora sleeve may develop (Fig. 2.2–2.4). Early growth stages can be readily recognized by the initially four-pronged construction of the ancora. Bates and Kirk (1992) described the ancora umbrella for three species of *Pseudorthograptus* and *Petalolithus* and compared the construction with that of the derived retiolitines. The ancora and ancora umbrella form a generally saucer- or umbrella-shaped construction below the aperture of the sicula (Fig. 2.4–2.6), with the addition of spiral or polygonal cortical lists (Bates & Kirk, 1992, 1997). In addition, the ancora sleeve may form, originating from the upward growing ancora umbrella lists and connecting with the lateral thecal walls at the lateral apertural rods. In *Pseudorthograptus* (Fig. 2.8) and *Spinadiplograptus*, in addition to the ancora umbrella, lateral thecal apertural spines may be formed, but there is no evidence of a fully developed ancora sleeve. Extremely long spines connect to a possible ancora sleeve in *Victorograptus*, but the poor preservation prevents recognition of such details.

The construction is clear in derived retiolitids, the Retiolitinae: The ancora sleeve attaches to the thecal framework mainly to the lateral apertural rods (see Bates, Kozłowska, & Lenz, 2005) and apertural spines are present in *Pseudoplegmatograptus* and *Giganteograptus*. The ancora sleeve forms the secondary, lateral tubarium walls in the Retiolitinae (Fig. 2.9), although the lateral thecal walls of the tubarium are seldom preserved. The reason for the evolution of the ancora is unclear, although a number of other taxa, considered to be unrelated to the Retiolitidae, independently developed a branched virgella (e.g., *Akidograptus* Davies, 1929; *Parakidograptus* Li & Ge, 1981).

FUSELLUM REDUCTION

The Petalolithinae bear complete thecal walls made of fusellar tissue (Fig. 2.4–2.8). The thecal walls appear to have become reduced in thickness during the evolution of the Retiolitidae and are rarely preserved in the Retiolitinae, although shards and seams in

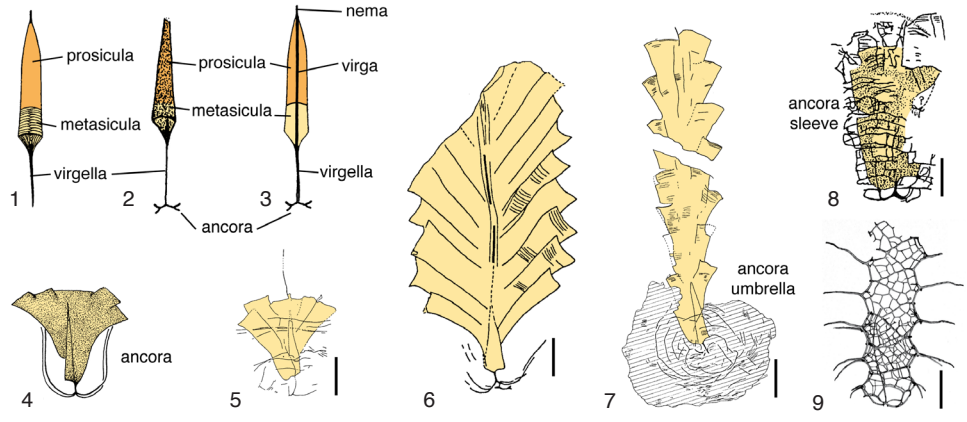


FIG. 2. The ancora and ancora sleeve. *1,* Axonophoran sicula with ventral virgella (Bulman, 1970, fig. 48); *2,* retiolitid sicula with ancora on ventral virgella (Bates & Kirk, 1986, fig. 28); *3,* retiolitine sicula from virgellar side showing virga as connection between virgella and nema (new); *4, Petalolithus* SUESS, 1851 sp., juvenile showing ancora with long extensions (Bates & Kirk, 1986, fig. 28); *5, Petalolithus ovatoelongatus* (KURCK, 1882) with possible ancora sleeve development (Koren' & Rickards, 1996, fig. 11D); *6, Petalolithus ovatoelongatus* (KURCK, 1882) showing extension of ancora (Koren' & Rickards, 1996, fig. 10J); *7, Dimorphograptoides physophora* (NICHOLSON, 1868a) showing extensive ancora umbrella development (Koren' & Rickards, 1996, fig. 19A); *8, Pseudorthograptus* LEGRAND, 1987 sp. showing ancora umbrella and ancora sleeve lists (Koren' & Rickards, 1996, fig. 18F); *9, Spinograptus spinosus* (WOOD, 1900) with thecal clathrium and ancora sleeve, lacking fusellar membranes (Maletz, 2010, fig. 5A). Sicula and thecate tubarium highlighted in color; scale bars in *5–9*, 1 mm.

the clathrium and reticulum are interpreted as remains of fusellar walls. A number of the Retiolitinae show preservation of the thecal walls and ancora sleeve walls, e.g., *Pseudoretiolites, Spinograptus praerobustus* (see LENZ & KOZŁOWSKA-DAWIDZIUK, 2002a), but in general, the walls are not preserved. In early Retiolitinae, the prosicula is routinely fully preserved, whereas the metasicula may be fully to partially preserved to absent, while in younger taxa, the prosicula may or may not be present, and a construction of clathrial and reticular lists is all that remains of the tubarium. A thickened apertural list is common in *Pseudorthograptus* specimens in which the thecal walls are complete, whereas further tubarial lists, including a mid-ventral list on the thecae, appear in *Hercograptus* in addition to the ancora sleeve lists (ŠTORCH, 2015).

THECAL FRAMEWORK AND ANCORA SLEEVE

The thecal framework consists of lists of nema, virga, virgella, transverse rods, lateral apertural rods, lips, connecting lists, ventral lists, and zigzag lists (BATES, KOZŁOWSKA, & LENZ, 2005). The ancora sleeve consists of lists developing from the ancora umbrella and connects to the thecal framework, generally the first thecal pair. The thecal framework lists are more robust than those of the ancora sleeve, although both may vary in width, but it appears that only the seams of thecal framework lists commonly bear shards, interpreted as remnants of fusellar walls, whereas ancora sleeve lists yield no evidence of a fusellar covering, although varying amounts of bandaging may occur at localized sites. Not all taxa possess ancora sleeve lists. By way of explanation, the terms clathrium and reticulum (ELLES & WOOD, 1908, p. 334; BOUČEK & MÜNCH, 1944, 1952), used to differentiate tubarium lists, are informal, subjective terms and mostly correspond to more robust and narrower lists, respectively.

EVOLUTION

According to MELCHIN and others (2011), the Retiolitidae originated from a neodiplograptid ancestor close to *Paraclimacograptus* PŘIBYL 1947. The early petalolithines—

Glyptograptus, *Sudburigraptus,* and *Paramplexograptus*—appeared in the late Ordovician (Hirnantian) and diversified in the early Silurian (Rhuddanian) into a number of genera. Ancorate taxa appeared in the mid-Rhuddanian with the genus *Pseudorthograptus*. It is clear that the development of the ancora umbrella and ancora sleeve of the Retiolitidae originated in the Rhuddanian from a simple branching of the virgella at a point close to the sicular aperture. Similar developments occurred independently in a number of taxa during the late Ordovician and early Silurian. *Climacograptus baragwanathi* (Hall, 1906), from the Eastonian 2 (mid-Katian) of Victoria, Australia, appears to be the earliest taxon producing a meshwork of bars at the end of the virgella (VandenBerg & Cooper, 1992, fig. 9D). However, it is very unlikely that a phylogenetic relationship existed between the Late Ordovician graptoloids bearing a virgellar meshwork and the ancorate Retiolitidae.

Taxa showing branching at the virgella, but not considered to be closely related to the retiolitoids, appeared in the earliest Silurian in the *Akidograptus ascensus* Biozone. Stein (1965), Koren' and Rickards (1996), and Štorch and Feist (2008) illustrated juvenile specimens of *Akidograptus ascensus* (Davies, 1929) with at least three branching divisions of the virgella. A short virgella with two horizontal branches is also present in *Avitograptus avitus*, but it is unlikely to be a homologous structure of the ancora of the Retiolitidae (Melchin & others, 2011). *Normalograptus minor* (Huang, 1982) from the *Metabolograptus persculptus* Biozone (Hirnantian, upper Ordovician) also bears multiple branching divisions of the virgella. Thus, the addition of further constructional complexities from the virgella was common in the early Silurian, but only in the retiolitoid clade did they become a standard, with a long and successful period of development.

Subfamily PETALOLITHINAE Bulman, 1955

[Petalolithinae Bulman, 1955, p. 87, *nom. correct.* Melchin & others, 2011, p. 298 *ex* Petalograptinae Bulman, 1955, p. 87]

Axonophorans (Neograptina) with long, nearly straight thecae, often with gentle ventral curvature and variable thecal overlap; thecal apertures straight, outwards inclined, sometimes with variable number of apertural spines; pattern I astogeny or derived pattern; tubarium often tabular, exaggeratedly rectangular in cross section; incomplete median septum on obverse side in many taxa; ancora development in derived taxa present, sometimes with poorly developed, unattached ancora sleeve. *Upper Ordovician (Hirnantian,* Metabolograptus persculptus *Biozone)–Silurian, Llandovery (Telychian,* Spirograptus guerichi *Biozone):* worldwide.

Bulman (1970) did not refer to the Petalolithinae, but included *Petalograptus* (now *Petalolithus;* see Loydell, 1992, p. 36) in the Diplograptidae, even though he had earlier erected the subfamily Petalograptinae for the genera *Petalolithus* and *Cephalograptus* (see Bulman, 1955). Štorch and Serpagli (1993) extended the Petalolithinae to include the genus *Glyptograptus*.

Melchin and others (2011, p. 298) defined the Petalolithinae as the "partial clade that includes the first species that acquired a unistipular (aseptate) biserial rhabdosome in the clade that contains *Paramplexograptus madernii* and *Retiolites geinitzianus* and its descendants, but excluding the taxa included in the subfamily Retiolitinae." Thus, the authors defined the Petalolithinae as a paraphyletic taxon, referring to the genus *Petalolithus*, but also revised and enlarged the taxon considerably.

THE MEDIAN SEPTUM

The existence of a partial median septum in some petalolithines has been known for a long time. Törnquist (1893) noted this in his material of *Diplograptus palmaeus* Barrande, 1850 (=*Petalolithus minor* Elles, 1897, see Maletz, 2014, fig. 23) and was recognized in the same species by Bates and Kirk (1992, fig. 41) (Fig. 3.2–3.4). The median septum is visible on the obverse side but not on the reverse side. *Petalolithus folium* also has a median septum on the obverse

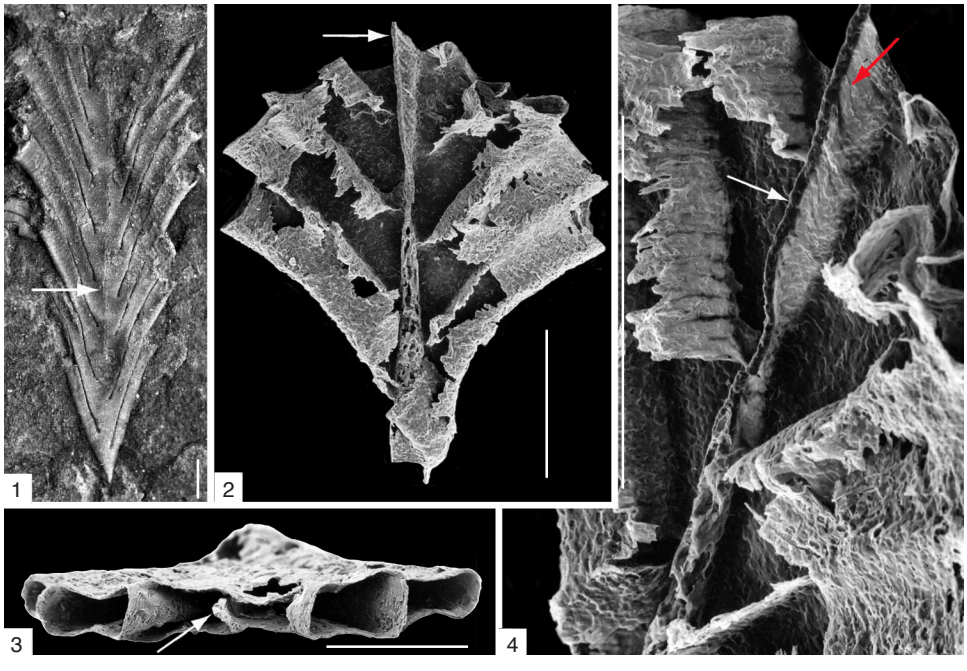


FIG. 3. The median septum. *1, Petalolithus folium* (HISINGER, 1837), LO 11863t, Röstånga, Sweden, reverse view, showing break (*arrow*) due to collapsed lateral wall (Maletz & others, 2014, fig. 1N); *2–4, Petalolithus minor* ELLES, 1897, Kallholn, Sweden; *2, 4,* NMW 91.52G.448A, broken specimen showing partial median septum on obverse side and bound by nema (*white arrow*), fuselli are visible in the partial median septum (*red arrow*) (new); *3,* NMW 91.52G.505, distal end of small tubarium showing partially collapsed wall and median septum with nema (new). Scale bars, 1 mm in *1–3;* 100 µm in *4*.

side, but on the reverse side only a fine line is visible in partially collapsed specimens, possibly indicating breakage of the thecal wall due to the presence of the nema and partial median septum (Fig. 3.1). BULMAN (1955, fig. 63,*7a*) indicated the presence of a partial median septum in *Cephalograptus.*

ANCORATE TAXA

Petalolithus SUESS, 1851, p. 100, *nom. nov. pro Diprion* BARRANDE, 1850, p. 14, homonym of *Diprion* SCHRANK, 1802, p. 209, Hymenoptera [**Prionotus folium* HISINGER, 1837, p. 114; SD LAPWORTH, 1873, table 1, facing p. 555] [=*Petalograptus* SUESS, 1851, *sensu* LAPWORTH, 1873, table 1, facing p. 555 (type, *P. folium,* OD); =*Corbograptus* KOREN' & RICKARDS, 1996, p. 86 (type, *C. enigmatica,* OD) herein]. Robust petalolithine with pattern I astogeny, possessing rectangular thecae with either straight or concave ventral sides; cross section of tubarium rectangular to oval; ancora present, sometimes also partial ancora sleeve with lists; partial median septum on obverse side. *Silurian, Llandovery (Aeronian,* Demirastrites triangulatus *Biozone–Telychian,* Spirograptus guerichi *Biozone):* worldwide.——FIG. 4,*2a–c.* **P. folium* (HISINGER); *2a,* NRM-PZ Cn 69037, (new); *2b,* lectotype (designated by BOUČEK & PŘÍBYL, 1942, p. 8), NRM-PZ Cn 69040 (new); *2c,* PŠ 821, showing ancora and long, slender nematularium, Tmaň, Czech Republic (Štorch, 1998, fig. 5,*2c*). Scale bars, 1 mm.——FIG. 4,*2d. Petalolithus* sp., holotype of *Corbograptus enigmatica* KOREN' & RICKARDS, 1996, CNIGR 197/12879, southern Urals, Russia, scale bar, 1 mm (Koren' & Rickards, 1996, fig. 20i).

Cephalograptus HOPKINSON, 1869, p. 159, original spelling as *Cephalograpsus* changed in ICZN, Opinion 650, 1963 [**Diplograpsus cometa* GEINITZ, 1852, p. 26; OD]. Petalolithine with pattern I astogeny and strongly elongated thecae but short sicula; thecae with fairly straight ventral sides; number of thecae often reduced; ancora present in some; partial median septum on obverse side. *Silurian, Llandovery (Aeronian*, Lituigraptus convolutus–Stimulograptus halli *Biozones):* worldwide.——FIG. 4,*1a–d.* **C. cometa* (GEINITZ); *1a,* type specimen not preserved, scale unclear (Geinitz, 1852, pl. 1,*28a*); *1b,* LO 1120t, reverse view, latex cast; *1c,* LO 1121t, obverse view showing median septum, latex cast; *1d,* LO 1124t, proximal end in

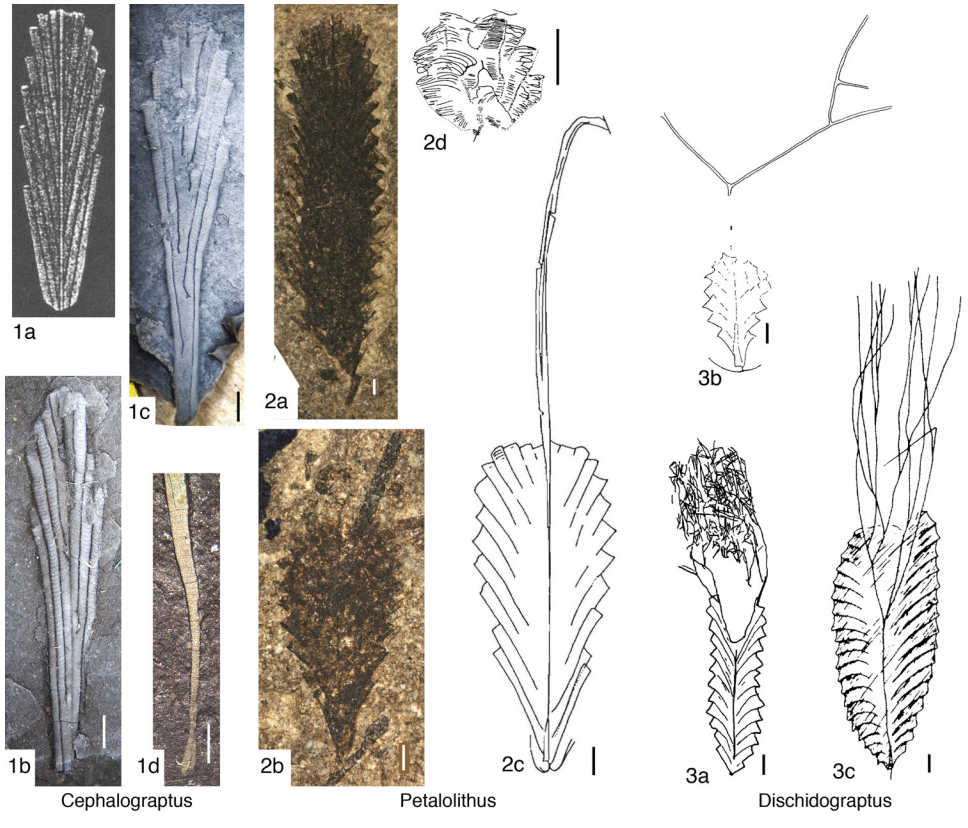


FIG. 4. Retiolitidae (Petalolithinae) (p. 5–6).

obverse view; *1b–1d,* Tommarp, Scania, Sweden, scale bars, 1 mm (new).

Dischidograptus NI, 1978, p. 399 [**Petalolithus mirabilis* MU & others, 1974, p. 213; OD]. Robust petalolithine with pattern I astogeny, possessing square thecae with concave ventral sides; ancora present; tubarium splitting into two separate stipes, following the first branching division of the nema; nema branching several times dichotomously at regular distances, eventually forming tangled mesh of rods. [Inclusion of *D.* (?) *regius* (HUNDT, 1957) in *Dischidograptus* uncertain due to lack of ancora]. *Silurian, Llandovery (Aeronian,* Lituigraptus convolutus *Biozone–?Telychian,* Spirograptus turriculatus *Biozone):* China, ?Germany.——FIG. 4,*3a–b.* **D. mirabilis* (MU & others); *3a,* holotype, NIGP 121427, showing branched nema but lacking proximal end, Hubei, China, scale bar, 1 mm (Melchin, 1998, fig. 6U); *3b,* NIGP 168329, YD-1, drill core, proximal end with ancora and branched nema, scale bar, 1 mm (new).——FIG. 4,*3c. D.*(?) *regius,* holotype, BAF H4217, Thuringia, Germany, scale bar, 1 mm (Schauer, 1971, pl. 13,*8*).

Dimorphograptoides KOREN' & RICKARDS, 1996, p. 85, *ex Pseudorthograptus* (*Dimorphograptoides*) KOREN' & RICKARDS, 1996, p. 85, herein [**Diplograpsus physophora* NICHOLSON, 1868b, p. 56; OD]. Petalolithine with short uniserial part; proximal pattern unknown; thecae with thickened apertural rims; ventral thecal walls straight to concave; ancora umbrella with four prongs and additional spiral lists and with probable ancora sleeve. *Silurian, Llandovery (Rhuddanian,* Cystograptus vesiculosus–Coronograptus cyphus *Biozones):* UK, Czech Republic, Germany, Russia.——FIG. 5,*1a–b.* **D. physophora* (NICHOLSON); *1a,* holotype, NHMUK PM 1891(4), Garpol Linn, Birkhill Shale, Moffat area, Scotland, UK (Nicholson, 1868b, fig. 7); *1b,* SM A210464a, Dob's Linn, Birkhill Shale, Scotland, UK, scale bar, 1 mm (Koren' & Rickards, 1996, fig. 19D).

Dittograptus OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968, p. 69 [**D. fortuitus;* OD]. Petalolithine with pronounced ancora and extensive scopular membranes, reaching distally to at least 29th thecal pair; proximal development of pattern I astogeny; thecae simple, possibly with ventral apertural spines. *Silurian, Llandovery (lower Aeronian,* Demirastrites triangulatus–Pribylograptus leptotheca *Biozones):* Czech Republic, Germany,

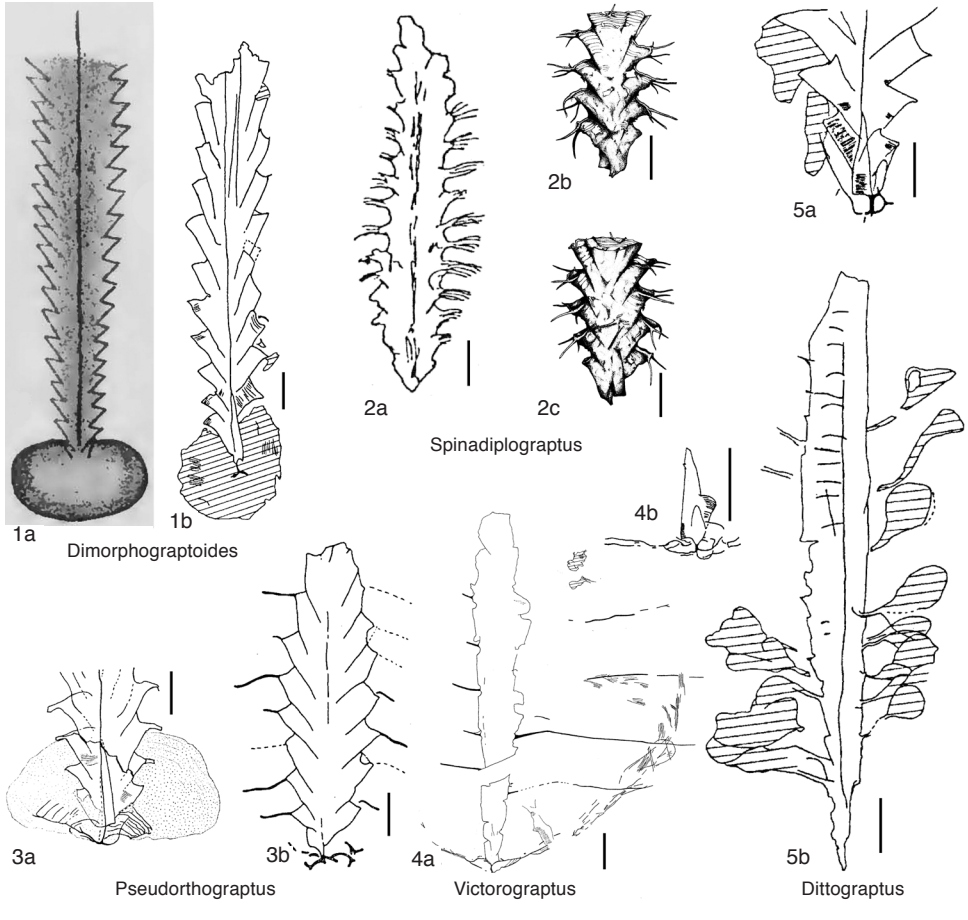
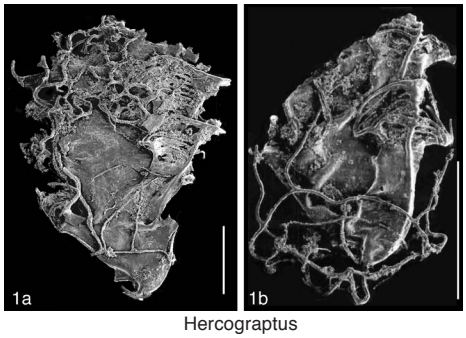


FIG. 5. Retiolitidae (Petalolithinae) (p. 6–8).

Russia.——FIG. 5,*5a–b. *D. fortuitus; 5a,* holotype, CNIGR 61/9765, proximal end in lateral view; *5b,* CNIGR 64/9765, adult specimen in scalariform view; scale bars, 1 mm (Koren' & Rickards, 1996, fig. 20G–H; for photos of complete specimen, see Obut, Sobolevskaya, & Merkureva, 1968, pl. 6,*1,* pl. 6,*4*).

Hercograptus MELCHIN, 1999, p. 263 [**H. introversus;* OD]. Petalolithine with partly attenuated fusellum; proximal development pattern I astogeny; ancora umbrella with spiral lists extending to form ancora sleeve connected to lateral thecal apertural margins; thecal apertures considerably widened laterally; fusellum at thecal apertures reduced to conspicuous list structure. *Silurian, Llandovery (upper Rhuddanian,* Coronograptus cyphus *Biozone–lower Aeronian,* Campograptus curtus *Biozone):* Czech Republic, Canada (Arctic).——FIG. 6,*1a–b. *H. introversus; 1a,* holotype, GSC 104935, Cape Manning section, Arctic Canada, scale bar, 1 mm (new, provided by M. Melchin); *1b,* paratype, GSC 14936, proximal end with ancora umbrella, showing lateral widening close to thecal aperture, Cape Manning section, Arctic Canada, scale bar, 1 mm (Melchin, 1999, fig. 1B).

Pseudorthograptus LEGRAND, 1987, p. 62 [**Diplograpsus insectiformis* NICHOLSON, 1869, p. 236; OD]. Petalolithine with concave first thecal pair and pattern I astogeny; partial median septum present; thecal apertures with ventrolateral processes developed as gentle lateral cusps to paired spines; ventral thecal walls straight to concave; ancora with four prongs and additional spiral lists. *Silurian, Llandovery (Rhuddanian,* Lituigraptus convolutus *Biozone–Aeronian,* Coronograptus gregarius *Biozone):* worldwide.——FIG. 5,*3a. P. obuti* (RICKARDS & KOREN', 1974), SVEGEI material, no number, Alimbet Creek, South Urals, Russia, scale bar, 1 mm (Rickards & Koren', 1974, fig. 9).——FIG. 5,*3b. *P. insectiformis* (NICHOLSON); NHMUK PM Q3112, specimen from holotype slab, scale bar, 1 mm (Rickards & Koren', 1974, fig. 4).



Hercograptus

FIG. 6. Retiolitidae (Petalolithinae) (p. 7).

Spinadiplograptus HUNDT, 1965, p. 21 [**Orthograptus* (?) *inopinatus* BOUČEK, 1944, p. 2; SD herein]. Petalolithine with concave first thecal pair and pattern I astogeny; median septum lacking; thecal apertures with paired lateral spines at the thecal apertures; ventral thecal walls straight to concave; small, shallow ancora umbrella; no ancora sleeve. *Silurian, Llandovery (Aeronian,* Demirastrites triangulatus–Lituigraptus convolutus *Biozones):* Canada (Arctic); Czech Republic; Germany; Sweden.——FIG. 5,*2a–c*. **S. inopinatus* (BOUČEK); *2a,* holotype, NMP L2732, Velká Chuchle, Czech Republic (Bouček, 1944, fig. 1b); *2b–c,* SM X.25935, chemically isolated specimen in reverse (*b*) and obverse (*c*) views, Cape Phillips Formation, Arctic Canada, scale bars, 1 mm (Koren' & Rickards, 1996, fig. 17).

Victorograptus KOREN' & RICKARDS, 1996, p. 45 [**V. morosus;* OD]. Petalolithine with long genicular thecal spines; proximal development and thecal style incompletely known; wide and shallow ancora umbrella with extremely wide possible ancora sleeve possibly connected to genicular spines. *Silurian, Llandovery (Aeronian,* Coronograptus gregarius *Biozone):* Russia.——FIG. 5,*4a–b*. **V. morosus; 4a*, holotype, CNIGR 106/12879; *4b,* paratype, CNIGR 107/12879; southern Urals, Russia, scale bars, 1 mm (Koren' & Rickards, 1996, fig. 9a and 9b, respectively).

NON-ANCORATE TAXA

Agetograptus OBUT & SOBOLEVSKAYA, in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968, p. 78 [**A. secundus;* OD] Petalolithine with pattern I' proximal development type; tubarium aseptate with free central nema; thecae with straight outwards inclined or slightly curved ventral thecal wall without geniculum; uniserial first theca by redirection of growth of second theca; thecal apertures straight, outwards inclined, paired apertural spines may be present; virgella strongly elongated. *Silurian, Llandovery, (upper Rhuddanian,* Coronograptus cyphus *Biozone–Aeronian,* Pribylograptus leptotheca *Biozone):* Canada, China, Russia, Sweden.——FIG. 7,*1a–c*. **A. secundus; 1a–b,* holotype, CNIGR 91/9765; *1c,* paratype, CNIGR 91/9766, showing long virgella; scale bars, 1 mm (Obut, Sobolevskaya, & Merkureva, 1968, pl. 8).——FIG. 7,*1d*. *A. spiniferus* OBUT & SOBOLEVSKAYA, in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968, GSC 104885, Arctic Canada, scale bar, 1 mm (Melchin, 1998, pl. 7,*1*).

Comograptus OBUT and SOBOLEVSKAYA, in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968, p. 60 [**C. comatus;* OD]. Petalolithine with a pattern I proximal development type; thecae sharply geniculate; no median septum; nema free and central; sicular aperture with at least three spines projecting outwards from sicula; additional sicular and thecal spines produced during maturation of colony. *Silurian, Llandovery (upper Rhuddanian,* Coronograptus cyphus *Biozone–Aeronian,* Stimulograptus sedgwicki *Biozone):* Canada, China, UK, Czech Republic, Germany, Russia.——FIG. 7,*2a–c*. **C. comatus; 2a,* holotype, CNIGR 27/9765, proximal and distal part of tubarium, lower *Demirastrites triangulatus* Biozone, Norilsk region, Siberia, Russia (Koren' & Rickards, 1996, fig. 6g); *2b,* specimen from Arctic Canada (Russel-Houston, 2001, pl. 2h); *2c,* juvenile with three proximal spines (Russel-Houston, 2001, pl. 2j). All scale bars, 1 mm.

Rivagraptus KOREN' & RICKARDS, 1996, p. 62 [**Diplograptus bellulus* TÖRNQUIST, 1890, p. 28; OD]. Petalolithine with Pattern I or N proximal development and curved to straight ventral thecal walls; tubarium aseptate with free, central nema; sicular length reduced. *Silurian, Llandovery (Rhuddanian,* Coronograptus cyphus *Biozone–Aeronian,* Lituigraptus convolutus *Biozone):* worldwide.——FIG. 7,*3a–d*. **R. bellulus* (TÖRNQUIST); *3a,* lectotype, selected herein (lectotype selection by PŘÍBYL, [1948, p. 11] of specimen in TÖRNQUIST, 1890, pl. 1,*25* is based on missing specimen), LO 948t, flattened proximal end in reverse view, showing thecal spines (new); *3b,* lectotype, LO 948t, original illustration showing long virgella (Törnquist, 1890, pl. 1,*27*); *3c,* GSC 135129, reverse view, infra-red photo, Arctic Canada (Melchin & others, 2011, fig. 5l); *3d*, LO 11859t, proximal end in obverse view, Röstånga drill core at 33.65-33.55 m (new). Scale bars, 1 mm.——FIG. 7,*3e*. *R. kayi* (CHURKIN & CARTER, 1970), GSC 135128, isolated proximal end in reverse view, infra-red photo, Arctic Canada, scale bar, 1 mm (Melchin & others, 2011, fig. 5j).

Glyptograptus LAPWORTH, 1873, table 1, facing p. 555 [**Diplograpsus tamariscus* NICHOLSON, 1868a, p. 526; OD] Petalolithine with pattern I proximal development type; nema embedded in obverse wall of tubarium or with narrow, obverse partial median septum; thecae with rounded to flowing geniculum. *Upper Ordovician (Hirnantian,* Metabolograptus persculptus *Biozone)–Silurian, Llandovery (Telychian,* Streptograptus crispus *Biozone):* worldwide.——FIG. 8,*1a–c*. **G. tamariscus* (NICHOLSON); *1a,* paralectotype, NHMUK PM Q.578, Birkhill Shale, Wamphray, Dumfries, Scotland,

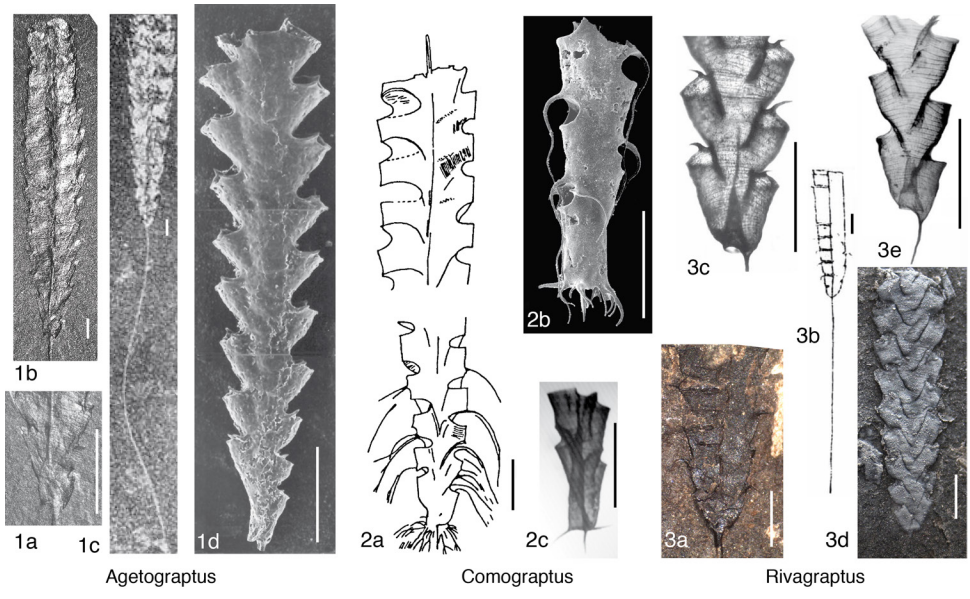


FIG. 7. Retiolitidae (Petalolithinae) (p. 8).

UK (Zalasiewicz, 2008); *1b,* lectotype (selected by PŘÍBYL, 1948, p. 10), NHMUK PM Q.579, Birkhill Shale, Wamphray, Dumfries, Scotland, UK (Zalasiewicz, 2008); *1c,* GSC 104864, proximal end in reverse view, Arctic Canada (Melchin, 1998, pl. 5,*2*). Scale bars, 1 mm.——FIG. 8.*1d. G. tamariscus,* ssp. GSC 104874, long specimen in reverse view, broken into three pieces, scale bar, 1 mm (Melchin, 1998, pl. 6,*1*).

Paramplexograptus MELCHIN & others, 2011, p. 298 [**Paraorthograptus paucispinus* LI, in Anhui Geological Survey Team, 1982; OD]. Petalolithine with pattern H' proximal development type or derived one; colony parallel-sided or widening slowly from proximal end; sicular aperture with slight dorsal flare; median septum lacking; nema attached to bases of the interthecal septa; thecae with sharp genicular thickenings or ventral flanges, slightly to moderately inclined, usually concave subapertural walls; apertures everted. *Upper Ordovician (upper Hirnantian,* Metabolograptus persculptus *Biozone)–Silurian, Llandovery (lower Rhuddanian,* Atavograptus atavus *Biozone):* Canada, China, Russia.——FIG. 8,*2a–b. *P. paucispinus* (LI in Anhui Geological Survey Team), southern Anhui, China (Melchin & others, 2011, fig. 6h–i). *2a,* lectotype, NIGP 67260; *2b,* topotype, NIGP 1540281; scale bars, 1 mm.——FIG. 8,*2c. P. madernii* (KOREN' & MIKHAILOVA, in KOREN', MIKHAYLOVA, & TZAJ, 1980), GSC 135122, Cape Manning, Nunavut, Canada, scale bar, 1 mm (Melchin & others, 2011, fig. 5b).

Parapetalolithus KOREN' & RICKARDS, 1996, p. 57 [**P. dignus;* OD] [=*Parapetalolithograptus* RICKARDS, WRIGHT, & THOMAS, 2009, p. 71; misspelling of *Parapetalolithus*]. Petalolithine with pattern I proximal development type; first thecal pair straight, V-shaped; no median septum; nema free and central or embedded in obverse wall, often with extended nematularium; moderately inclined thecae with nearly straight ventral side and outwards inclined, straight thecal apertures. *Silurian, Llandovery (upper Aeronian,* Stimulograptus halli *Biozone–Telychian,* Monoclimacis griestoniensis *Biozone):* worldwide.——FIG. 8,*3a–b. *P. dignus; 3a,* holotype, CNIGR 124/12879, obverse view, Zhaksy-Kargala Valley, southern Urals, Russia; *3b,* CNIGR 123/12879, Kos-Istek region, southern Urals, Russia; scale bars, 1 mm (Koren' & Rickards, 1996, fig. 11j and 11k, respectively).——FIG. 8,*3c. P. conicus* (BOUČEK, 1932), lectotype, NMP L 25043, Zelkovice, Bohemia, Czech Republic, scale bar, 1 mm (Štorch, 2000).

Sudburigraptus KOREN' & RICKARDS, 1996, p. 47 [**Orthograptus eberleini* CHURKIN & CARTER, 1970, p. 29; OD]. Petalolithine with pattern H' and possibly pattern I astogeny; tubarium aseptate with non-geniculate thecae; colonies show slight dorsal curvature of proximal end and slightly flared dorsal sicular margin. *Silurian, Llandovery (Rhuddanian,* Cystograptus vesiculosus–Coronograptus cyphus *Biozones):* Canada, USA, UK.——FIG. 8,*4a. *S. eberleini* (CHURKIN & CARTER), holotype, USNM 161783, Alaska, USA, scale bar, 1 mm (Melchin & others, 2011, fig. 6n).——FIG. 8,*4b. Sudburigraptus* sp. 1, GSC 135127, infra-red photo, reverse view, southern Urals, Russia, scale bar, 1 mm (Melchin & others, 2011, fig. 5h).

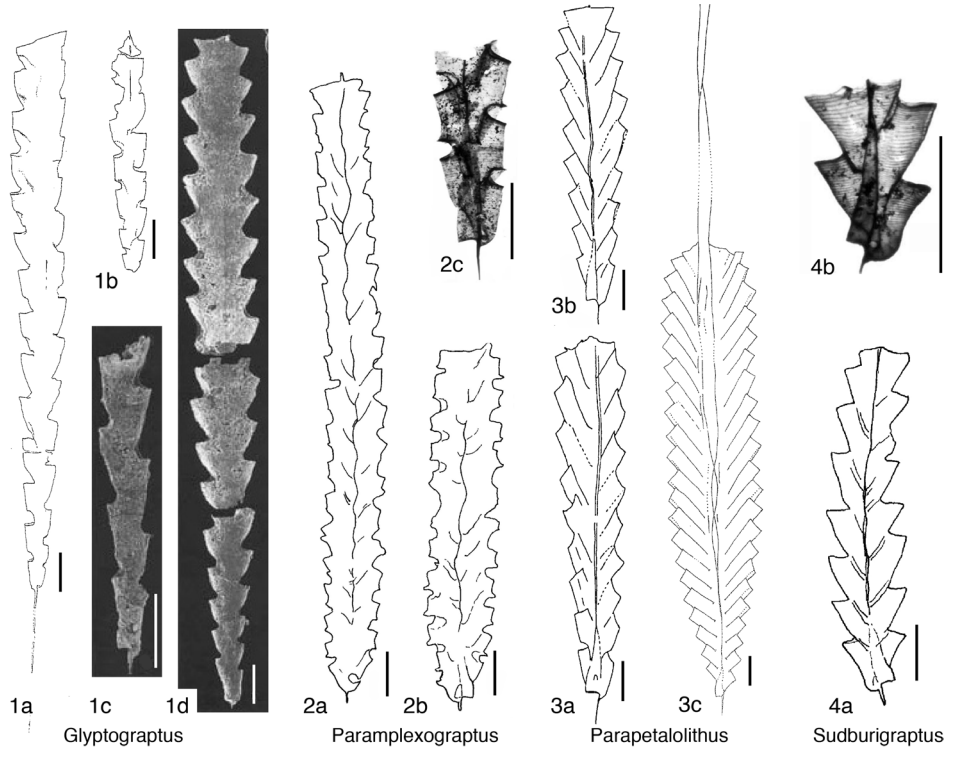


FIG. 8. Retiolitidae (Petalolithinae) (p. 8–9).

Subfamily RETIOLITINAE Lapworth, 1873

[Retiolitinae LAPWORTH, 1873, table 1, facing p. 555] [incl. Plectograptinae BOUČEK & MÜNCH, 1952, p. 10 (Czech text), p. 110 (English text); Pseudoretiolitinae OBUT & ZASLAVSKAYA, 1974, p. 159 (English version, 1976, p. 123); Gothograptinae OBUT & ZASLAVSKAYA, 1983, p. 112 (English version, 1986, p. 218); Pseudoplegmatograptinae OBUT & ZASLAVSKAYA, 1983, p. 105 (English version, 1986, p. 209); Cometograptinae, Neogothograptinae, Paraplectograptinae, Rotaretiolitinae, Sokolovograptinae, and Spinograptinae KOZŁOWSKA-DAWIDZIUK, LENZ, & BATES, 2003, p. 51]

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; sicula often preserved in stratigraphically earlier taxa, but reduced or not preserved in younger forms, although with rare exception of some occurrences of *Spinograptus* spp. (LENZ, 1994b; KOZŁOWSKA-DAWIDZIUK, 1997); thecae with variable inclination, lacking interthecal septa and thecal overlap; thecal apertures often strongly enlarged; ancora sleeve list surfaces seamed inside or outside, indicating presence of ancora sleeve membrane; bandages smooth, longitudinally striated or pustulose; virgella and nema connected by virga, a thickened longitudinal rod on prosicula. *Silurian, Llandovery (Aeronian,* Demirastrites triangulatus/ Demirastrites pectinatus *Biozone)–Ludlow (Ludfordian,* Saetograptus leintwardinensis *Biozone):* worldwide.

MELCHIN and others (2011, p. 300) emended the Retiolitinae as "the first ancora-bearing graptolite species within the clade that includes *Retiolites geinitzianus* that acquired thecae constructed of a full framework of lists and reduced or absent fusellar walls, and all of its descendents."

The retiolitines have been misunderstood for a long time, in part because of

the tacit assumption that their immediate ancestors were axonophorans with a fully developed fusellum that had simply lost their continuous fusellar coverings, retaining only a meshwork of lists (e.g., BULMAN, 1955, 1970). A second reason was the lack of recognition of the unique double-layer nature of the retiolitid tubarium construction with its internal thecal framework and the external ancora umbrella and ancora sleeve (Fig. 9–Fig. 10). It is only since the advent of scanning electron microscopy (SEM) that this has come fully to light. Three-dimensional specimens showing the dual construction had been recovered and illustrated by TÖRNQUIST (1880, 1890) and HOLM (1890), but these apparently were subsequently overlooked or forgotten. The detailed SEM studies instituted by BATES and KIRK (e.g., 1978, 1984, 1987, 1991, 1992, 1997), working with isolated, three-dimensionally preserved material, clearly showed that retiolitines possess a framework unlike that of any other neograptines (Fig. 10). The Late Ordovician Lasiograptidae (see ŠTORCH & others, 2011) mirrored some features found in the Retiolitinae, but their external meshwork (lacinia) is based on growth and branching of thecal spines and does not bear indications of the presence of membranes (BATES & KIRK, 1991).

MORPHOLOGY

In the vast majority of instances, retiolitine tubaria are preserved with only cable-like lists arranged in a meshwork pattern. However, originally there were also two membrane-based constructions: the thecal framework inside, formed from the fusellum (Fig. 9.1), and a second layer, the ancora sleeve, on the outside (Figs. 9.2,5–6). The retiolitine membranes are very thin and usually not preserved, but their presence was already noted on flattened and relief material (e.g., TULLBERG, 1883; TÖRNQUIST, 1890; PERNER, 1897; ELLES & WOOD, 1908; LENZ & THORSTEINSSON, 1997). The incrementally deposited fusellar membrane, predominantly the thecal framework, is found only in a very few taxa, e.g., *Retiolites, Pseudoretiolites* (Fig. 1.3), *Stomatograptus* (Fig. 9.1), and a number of *Spinograptus* species (KOZŁOWSKA-DAWIDZIUK, 1997, KOZŁOWSKA, DOBROWOLSKA, & BATES, 2013).

The ancora sleeve consists of meshes made of lists formed of cortical bandages derived from the ancora umbrella. The lists of the thecal framework have seams, which are U-shaped in cross section (Fig. 11.3). Very commonly, the seams demonstrate evenly spaced, U-shaped increments or shards (Fig. 11.5) that BATES and KIRK (1992) interpreted as remnants of fusellar sheets. The ancora sleeve consists of meshes made of lists formed of cortical bandages derived from the ancora umbrella. It is not clear, however, whether fuselli or cortical bandages fully or partially covered these membranes.

The first theca of retiolitines emerged through a sicular resorption foramen (Fig. 12), from which was derived a column of successively developed thecae, forming the thecal framework. Further development of the retiolitine tubarium is difficult to ascertain. The proximal development type probably is comparable to the pattern I astogeny, but details are not preserved and MELCHIN (1998) defined the pattern as pattern R, differentiated from pattern I astogeny by the presence of the ancora and its incorporation into the framework of the first thecal pair. The thecae of the Retiolitinae do not show any thecal overlap and, thus, lack an interthecal septum, as can be shown in the genera *Retiolites* and *Pseudoretiolites* (see BATES & KIRK, 1992, 1997).

The ancora umbrella was constructed before the thecae of the tubarium appeared. It was followed by the upward extension of the ancora umbrella, constituting the ancora sleeve (BATES, 1990), which in turn linked up with the thecal framework, giving rise to the outermost lateral walls of the tubarium. The ancora sleeve is, therefore, exclusively the product of the distal extension from the ancora umbrella that partially envelops and laterally and ventrally joins with the underlying thecal framework (Fig. 9).

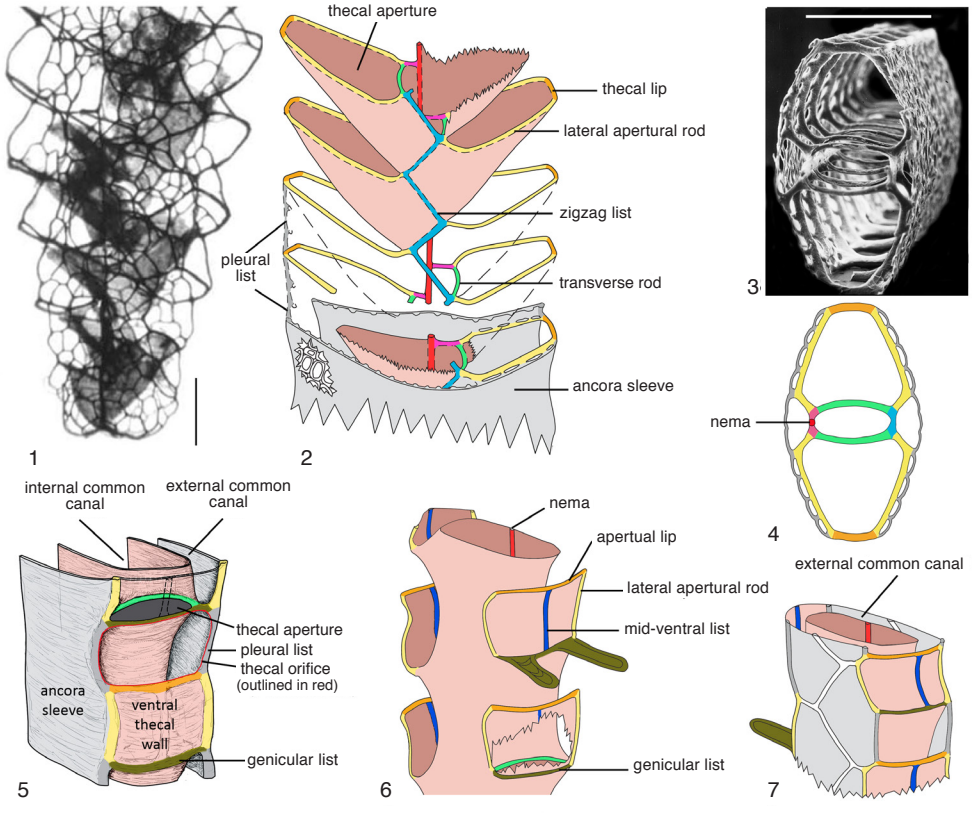


FIG. 9. Morphology and morphological terminology. *1, Stomatograptus* TULLBERG, 1883, showing preservation of thecal walls composed of sheetlike fusellar bands, scale bar,1 mm (Lenz & Thorsteinsson, 1997, fig. 1); *2, Retiolites* BARRANDE, 1850, reconstruction of median part, showing thecal framework and connection to ancora sleeve (*gray*); *3, Retiolites*, cross section showing strong transverse rods and nema, scale bar, 1 mm (Bates, 1989, fig. 11); *4, Retiolites*, cross section showing thecal framework (in *colors*); ancora sleeve (*gray*) (adapted from Bates & Kirk, 1997, fig. 127b); *5–7, Spinograptus praerobustus* (LENZ & KOZŁOWSKA–DAWIDZIUK, 2002a), reconstruction of median part of colony showing thecate part, ancora sleeve, and list development (*2, 5–7,* adapted from Bates & others, 2006, fig. 1–2).

The retiolitines are thus unique among the graptolites in that most possess double lateral walls: an inner one being the homologue of the normal neograptid (or axonophoran) thecal walls within which the nema is found, and an outer wall (ancora sleeve) derived entirely from the distal extension of the ancora (Fig. 9.2).

The early growth stages of the ancora-derived structures in both the retiolitines and the petalolithines are basically identical at the level of the ancora and ancora umbrella (Fig. 13). As a consequence of the great similarities between the ancoras and ancora umbrellas of the petalolithines and retiolitines, these structures are regarded as homologous (MITCHELL, 1987; BATES, 1990). The petalolithines are thus widely accepted as being ancestral to the retiolitines (BATES & KIRK, 1984, 1987, 1991, 1992; MITCHELL, 1987; LENZ, 1993a, 1994a, 1994b; LENZ & MELCHIN, 1997; MELCHIN, 1998, 1999; LENZ & KOZŁOWSKA-DAWIDZIUK, 2001; MELCHIN & others, 2011, fig. 3). Further support for concluding that the retiolitine and the petalolithine subgroups share a common origin is that both are part of the group that shares the astogenetic pattern I (BATES, KOZŁOWSKA, & LENZ, 2005). One of the differences seen in early growth stages

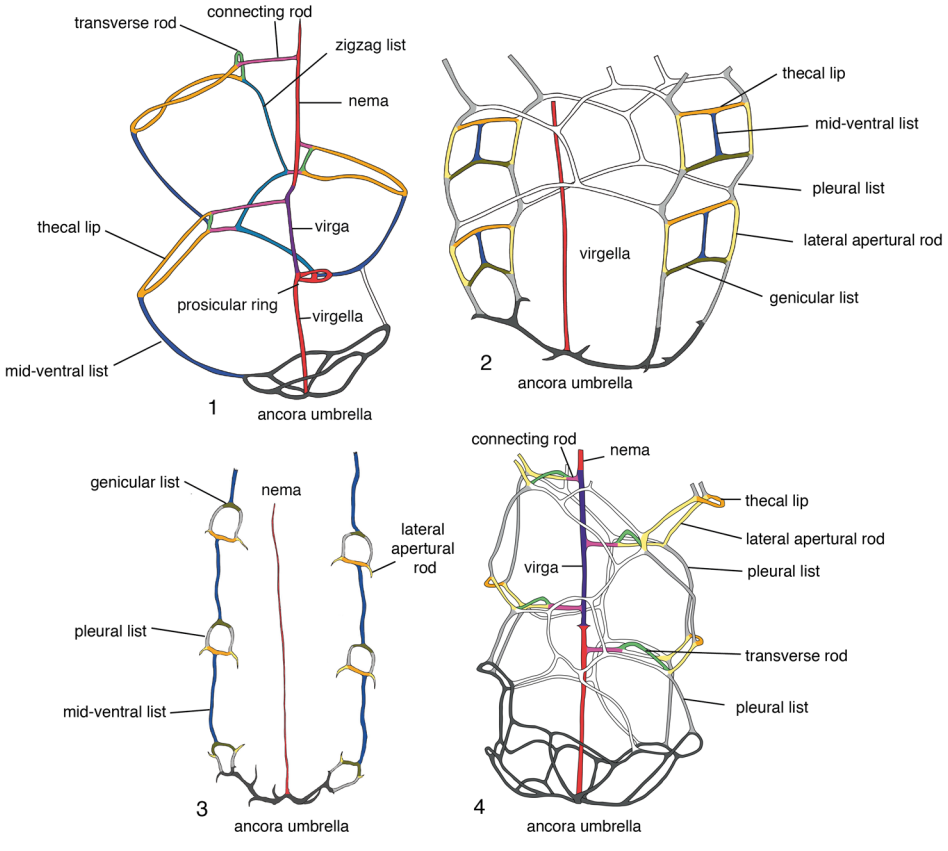


FIG. 10. Terminology of thecal lists in the Retiolitinae. *1, Rotaretiolites* BATES & KIRK, 1992, possessing only thecal framework, prosicular ring, and simple ancora umbrella; *2, Plectograptus* MOBERG & TÖRNQUIST, 1909, showing very simple ancora umbrella and large lateral and ventral orifices; *3, Plectodinemagraptus* KOZŁOWSKA-DAWIDZIUK, 1995, showing strongly reduced framework; *4, Paraplectograptus* PŘÍBYL, 1948, tubarium with strong ancora umbrella, lacking reticulum (all adapted from Bates, Kozłowska, & Lenz, 2005, fig. 5).

is the presence of the virga, a thickened longitudinal cortical list on the prosicula connecting the virgella with the nema in the Retiolitinae, but not in the Petalolithinae.

Ancora umbrellas of the retiolitines range from very simple, comprising a few branches (e.g., *Paraplectograptus*) (Fig. 13.3), some smoothly bounded by a rim (e.g., *Rotaretiolites*) (Fig. 10.1), to very complex, comprising many meshes, to those with numerous radial and spiral lists (e.g., *Pseudoretiolites*) (Fig. 13.5), and from a shallow saucer-shape to a deep cup-shape in profile (Fig. 13.5–13.6). In general, the ancora umbrella structures are more complex, including a spiral structure, in the Llandovery (Fig. 13.2), and generally simpler in the Wenlock and Ludlow taxa (Fig. 13.3,6). In some retiolitines there is an outer ancora situated outside of the main ancora. In these, the seams of the ancora membranes are outward facing on the inner ancora, and inward facing on the outer ancora (Fig. 14).

The earlier retiolitines possess ancora sleeve seams on the outside of the ancora sleeve, as was demonstrated for *Retiolites angustidens* ELLES & WOOD, 1908 by BATES and KIRK (1997, fig. 118). In most derived retiolitines, the seams of the ancora sleeve are facing inward, except for the ancora umbrella, and the lists are pustulose (KOZŁOWSKA-DAWIDZIUK & LENZ, 2001).

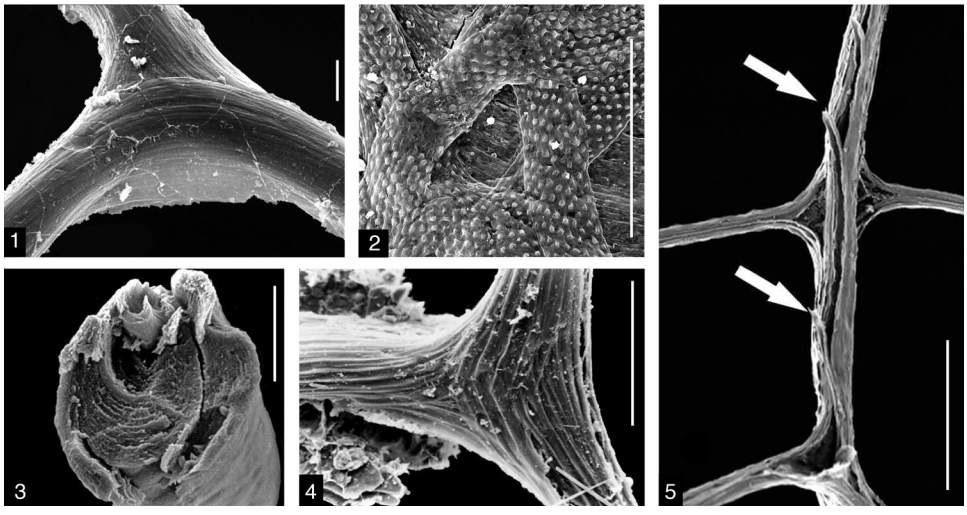


Fig. 11. General morphology and micromorphology of retiolitines. *1, Eorograptus spirifer* Melchin, Lenz, & Kozłowska, 2017, lists showing fine striation (Melchin, Lenz, & Kozłowska, 2017, fig. 9,*4*); *2, Gothograptus nassa* (Holm, 1890), ZPAL G.54.6, cortical bandages on genicular hood showing well-developed pustules (Kozłowska, Lenz, & Melchin, 2009, fig. 3); *3,* NMW 91.52G.95, cross section of a list of *Retiolites* Barrande, 1850, showing concentric cortical bandage layers and insertion seam (new); *4, Rotaretiolites* Bates & Kirk, 1992, NMW 91.52G.52, with robust parallel striae (new); *5, Gothograptus nassa,* ZPAL G.66/2, seams with shards indicated by *white arrows* (new). Scale bars, 10 µm in *1, 3–4;* 100 µm in *2,5*.

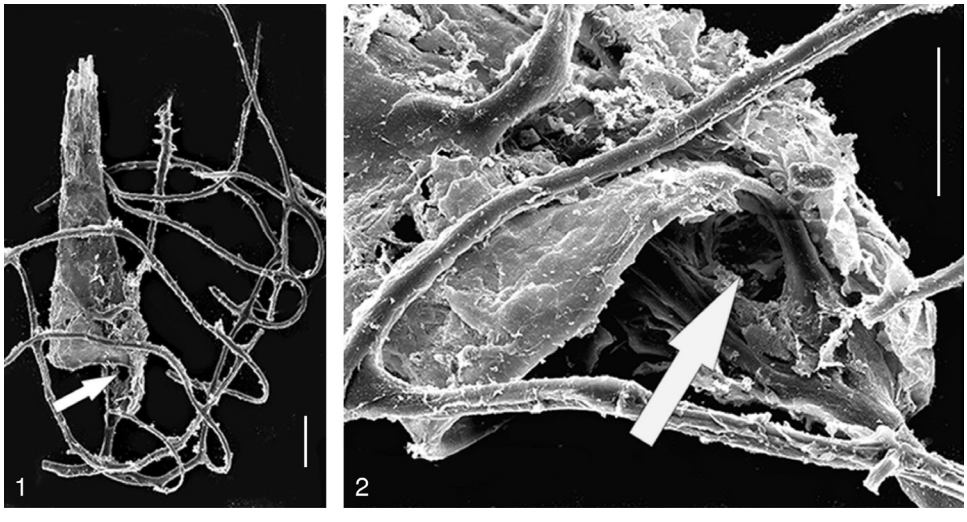


Fig. 12. Resorption foramen. *Pseudoretiolites* Bouček & Münch, 1944 sp., GSC 137638, distal end of metasicula, showing downward curvature of theca 1^1 and well rounded foramen (*arrows*), Llandovery, middle Aeronian, upper *Campograptus curtus* Biozone, Arctic Canada; *1,* complete distal end of sicula, ancora, and four spiral lists, scale bar, 0.5 mm; *2,* enlargement showing well-rounded porus, scale bar 50 µm (*1–2,* Melchin, Lenz, & Kozłowska, 2017, fig. 11,*2*).

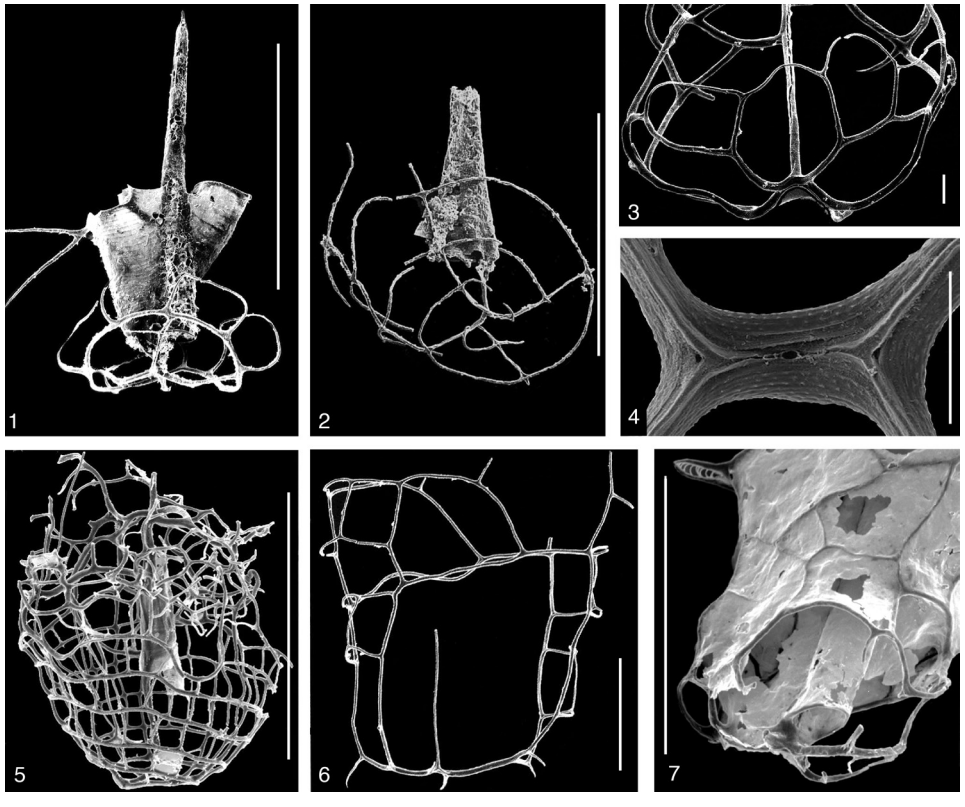


FIG. 13. Ancoras and ancora umbrellas. *1, Spinadiplograptus inopinatus* (BOUČEK, 1944) (petalolithine), GSC 9819, complete ancora umbrella, Arctic Canada (Bates, Kozłowska, & Lenz, 2005, fig. 3F); *2,* ancora umbrella of *Pseudorthograptus* sp. cf. *P. obuti* RICKARDS and KOREN', 1974 (petalolithine) with spiral and radial lists (Bates & Kirk, 1992, fig. 44); *3,* simple ancora umbrella of *Paraplectograptus* PŘÍBYL, 1948 (retiolitine), Arctic Canada; *4, Spinograptus* BOUČEK & MÜNCH, 1952, (retiolitine) ancora, showing pustules and seams on outside (Bates & others, 2005, fig. 3D); *5,* complex, spiraled ancora umbrella of *Pseudoretiolites hyrichus* (Melchin, Lenz, & Kozłowska, 2017, fig. 10,*2*) (retiolitine); *6,* very simple ancora umbrella of *Plectograptus* MOBERG & TÖRNQUIST, 1909 (retiolitine) (Bates & others, 2006, fig. 1E); *7, Spinograptus praerobustus* LENZ & KOZŁOWSKA-DAWIDZIUK, 2002a, proximal end showing rarely preserved, complete fusellar walls between cortical lists and fully preserved sicula (Bates & others, 2005, fig. 2A). Scale bars, 1mm in *1–2, 5–7;* 0.1 mm in *3–4.*

The retiolitine girder-like structures, the cortical lists, are the mainstays for retiolitine preservation, and show three styles of surface micro-ornamentation built up concentrically, layer by layer: pustulate, parallel ridges, and smooth to finely striated. Taxa with smooth to finely striated surfaces (Fig. 11.1) appeared in the early Aeronian, extended through the Telychian and, in a more limited way, into the Wenlock, and disappeared at the end of the early Homerian. Strong parallel ridges occurred only in *Rotaretiolites* in the Telychian (Fig. 11.4). Taxa with pustule ornamentation and finely stiated lists (Fig. 11.2) appeared in the mid-Telychian and continued until the extinction of the retiolitids in the mid-Ludlow. Thus, two forms of micro-ornamentation were present in late Llandovery to early Wenlock, whereas only pustular ornamentation remained following the late Wenlock graptolite extinction. In reference to smooth cortical lists, however, it should be kept in mind that at least some of the list smoothness might be attributable to abrasion, rather than being of biological origin. The function of the micro-ornamentations is unknown.

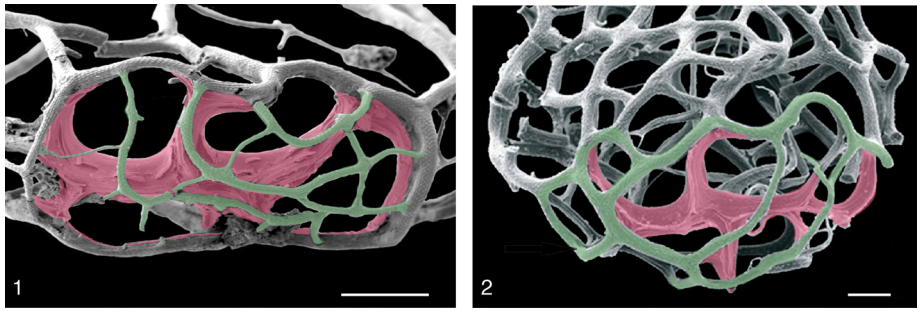


FIG. 14. The outer ancora. *1, Neogothograptus* sp., ZPAL G.66/3, specimen with well-developed ancora umbrella with seams facing outward (*pink*) (new); *2, Baculograptus chainos* (Lenz, 1993a), GSC 120711, showing well-developed outer ancora with seams facing inward (*green*); Arctic Canada; scale bars, 100 µm (new).

More than one type of ornamentation can be present in a single taxon. In *Eisenackograptus,* for example, the external bandaging on the ancora sleeve is pustular, while that on the inside of the ancora umbrella, sleeve and thecal framework is striated.

Retiolitine distal ends fall into two groups. One group has an open distal end (e.g., *Retiolites* and *Stomatograptus*), and is universal in the Llandovery and early Wenlock, although a very few range as high as the Lower Ludlow (e.g., some species of *Plectograptus,* and *Spinograptus*). The other group includes those with a finite tubarium, most of which possessed a tubular appendix (e.g., *Eisenackograptus, Gothograptus, Neogothograptus;* see KOZŁOWSKA, DOBROWOLSKA, & BATES, 2013, p. 88), generally regarded as a single final theca. Alternatively, a few taxa show a closed end with no appendix and only a nema projecting beyond the distal end of the tubarium (e.g., *Spinograptus praerobustus*, *Spinograptus tubothecalis, Cometograptus marsupium* (LENZ, 1993A). A special development can be seen in *Cometograptus bicladis* (LENZ, 1993b), in which the tubarium splits distally into two uniserial stipes.

PHYLOGENETIC ANALYSIS AND SYSTEMATICS

Cladistic studies of retiolitids began with LENZ and MELCHIN (1997), in which all of the then-known genera were included. It was followed by the studies of BATES, KOZŁOWSKA, and LENZ (2005) and KOZŁOWSKA, LENZ, and MELCHIN (2009), the last being a study of only those with pustular micro-ornamentation. The most recent study by MELCHIN, LENZ, and KOZŁOWSKA (2017) (Fig. 15) is of taxa that originated in the Aeronian and early Telychian (Llandovery). It is especially important as it shows the roots of the subgroups of the retiolitines and the links to the petalolithines.

There are four major clade groups in the cladogram (Fig. 15): (A) a paraphyletic stem group, *Pseudoretiolites*, being ancestral to all subsequent taxa; (B) the monophyletic *Pseudoplegmatograptus* clade, typical of traditional retiolitines with fine, parallel striation to smooth surfaces of the cortical bandages and, normally, complex morphology; these became extinct at the end the lower Homerian (upper Wenlock); (C) a monophyletic group with *Aeroretiolites, Rotaretiolites,* and other members of this subclade that ranged from the *Lituigraptus convolutus* Biozone (Aeronian, Llandovery) to the *Spirograptus guerichi* Biozone (Telychian, Llandovery); and (D) a monophyletic group with *Eorograptus, Paraplectograptus,* and *Sokolovograptus,* in which the earlier taxa *Eorograptus* and *Paraplectograptus* have parallel micro-ornamentation, and the somewhat later occurring taxa (*Sokolovograptus* and *Paraplectograptus*) have pustular bandages. As such, in this subclade, some taxa

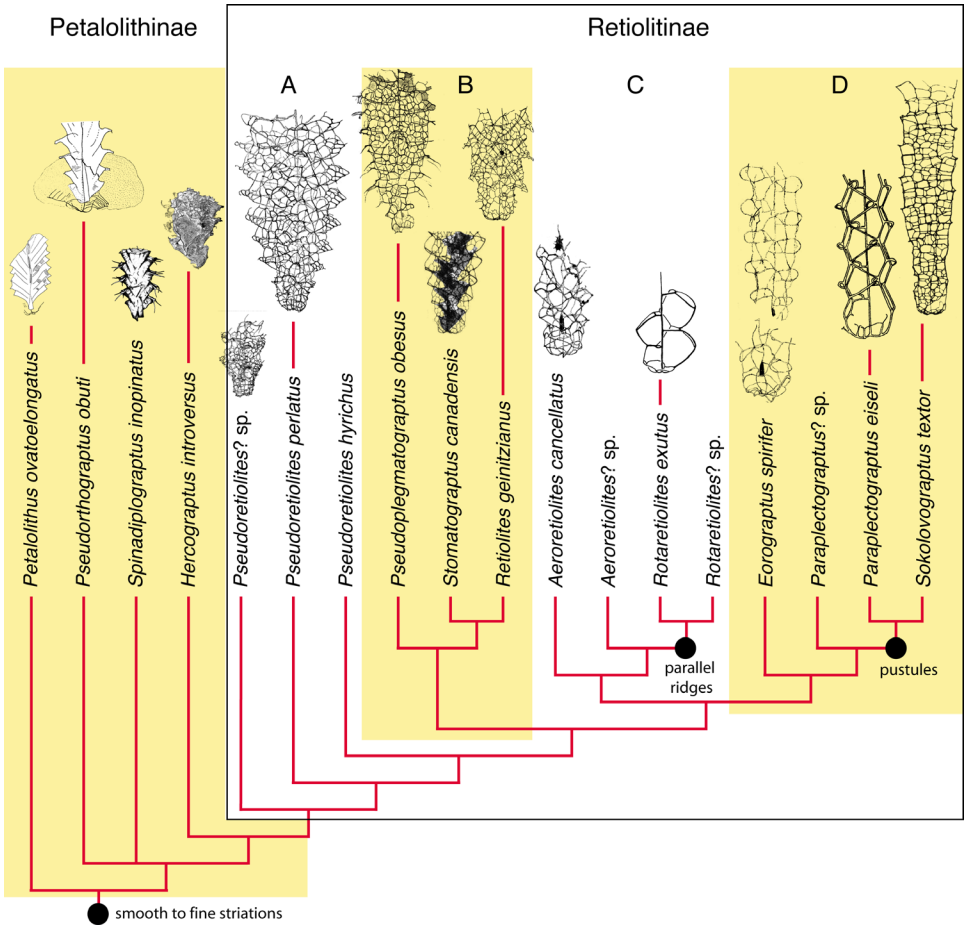


FIG. 15. Cladogram resulting from the analyses that included all taxa in the study of MELCHIN, LENZ, and KOZŁOWSKA (new; based on Melchin, Lenz, & Kozłowska, 2017, fig. 5).

have parallel micro-ornamentation and others, somewhat later developed, have a pustulose ornamentation. *Sokolovograptus* and/or *Paraplectograptus* are considered ancestral to all of the stratigraphically higher taxa, and can be directly linked to the cladogram in KOZŁOWSKA, LENZ, and MELCHIN (2009), where the earliest taxon is shown as *Pseudoplectograptus* (synonym of *Paraplectograptus,* herein). The result is that all taxa previously recognizable as Silurian retiolitids are now considered to be members of a single subfamily Retiolitinae.

Retiolites BARRANDE, 1850, p. 68, *nom. conserv.,* ICZN, Opinion 199, 1954 [**Gladiolites geinitzianus* BARRANDE, 1850; M] [=*Gladiolites* BARRANDE, 1850, *nom. suppr.,* ICZN, Opinion 199, 1954; =*Gladiograptus* HOPKINSON & LAPWORTH, 1875, p. 633 (type, *G. geinitzianus* BARRANDE, 1850, p. 68, M); =*Dimykterograptus* HABERFELNER, 1936, p. 92 (type, *D. bončevi,* M), see BOUČEK & MÜNCH, 1944, p. 31)]. Tubarium initially slightly widening, then parallel sided, ovate in cross section; thecal framework fusellum very rarely preserved, showing thecal apertures inclined at ~45°, lacking interthecal septa and accordingly thecal overlap; no geniculum; strongly developed thecal framework; ancora umbrella shallow, saucer-shaped with few polygonal meshes; ancora sleeve without fusellum and with dense reticulum; lateral apertural rods inclined at 45° to 60° to tubarium axis, thecal aperture defined by transverse rods, lateral apertural rods and thecal lips; without mid-ventral lists; thecal orifices more or less vertical; proximal thecae

occasionally with reticular hoodlike structures; nema attached to transverse rods by connecting rods on obverse side; reverse side with zigzag lists; ancora sleeve without stomata; ancora sleeve lists with finely striated surface and seams facing outwards. *Silurian, Llandovery (Telychian,* Spirograptus turriculatus/Streptograptus crispus *Biozone)–Wenlock (Homerian,* Cyrtograptus lundgreni *Biozone):* worldwide.——Fig. 16,*1a*. **R. geinitzianus* (Barrande), neotype (selected by Loydell & Štorch, 1996 and accepted by ICZN, Opinion 1901, 1998), NM L31612, Llandovery, *Cyrtograptus murchisoni* Biozone, Vyskočilka, Czech Republic, scale bar, 10 mm (new).——Fig. 16,*1b*. *R. australis* M'Coy, 1875, GSC137748, ?lower Wenlock, Arctic Canada, scale bar, 1 mm (new).——Fig. 16,*1c*. *Retiolites* sp., GSC 114221, with proximal thecal hoods, Llandovery, Upper Telychian, *Cyrtograptus sakmaricus* Biozone, Arctic Canada, scale bar, 1 mm (Kozłowska-Dawidziuk & Lenz, 2001, fig. 2,*2*).

Aeroretiolites Melchin, Lenz, & Kozłowska, 2017, p. 139 [**A. cancellatus;* OD]. Ancora umbrella comprises radial lists with continuous undulating rim with up to three whorls of spiral lists; thecae with everted to horizontal apertural loops supported by slightly convex mid-ventral lists; pleural lists present, joined to lateral apertural rods; lists bear weak, parallel striations; ancora sleeve weakly developed; prosicula present. *Silurian, Llandovery (Aeronian,* Lituigraptus convolutus *Biozone):* Arctic Canada.——Fig. 16,*3a–b*. **A. cancellatus; 3a,* holotype, GSC 137651, proximal end; *3b,* paratype, GSC 137653, distal fragment; Arctic Canada; scale bars, 1 mm (Melchin, Lenz, & Kozłowska, 2017, fig. 14).

Baculograptus Lenz & Kozłowska-Dawidziuk, 2002a, p. 329 [**Gothograptus chainos* Lenz, 1993a, p. 17; OD]. Tubarium parallel sided, with appendix; ancora umbrella saucer-shaped; continuous rimlike list around ancora marking edge of robust outer ancora; nema incorporated into appendix; thecal orifices moderately shallow, directed ventrally or proximoventrally; rectangular to round in outline, with thickened apertural rim; reticulum of uniform-sized meshes; lists with pustules; seams on ancora sleeve inside. *Silurian, Wenlock (upper Homerian*, Colonograptus praedeubeli/deubeli–Colonograptus ludensis *Biozones):* Arctic Canada; UK, ?Australia (New South Wales).——Fig. 16,*2a–c*. **B. chainos* (Lenz); *2a,* holotype, GSC 104004, ventrolateral view (Lenz, 1993a, pl. 7,*6*); *2b,* GSC 120709, lateral view (Lenz & Kozłowska-Dawidziuk, 2002a, fig. 10,*1*); *2c,* GSC120717, distal end with appendix; Wenlock, upper Homerian, *Colonograptus ludensis* Biozone, Arctic Canada, scale bars, 1 mm (Lenz & Kozłowska-Dawidziuk, 2002a, fig. 10,*6*).

Cometograptus Kozłowska-Dawidziuk, 2001, p. 84 [**C. tomczyki;* OD]. Robust and parallel sided to distinctly widening tubarium with or without genicular processes; genicular structures developed as spines, loops, or hoods; simple, shallow ancora umbrella with six meshes; kidney-shaped proximal lateral orifices more than half width of tubarium; nema free; mid-ventral lists partially developed; some species with large stomata; long mid-lateral spines on ancora sleeve wall in some species; lists with pustules; ventral wall seams inside, ancora sleeve seams outside. *Silurian, Wenlock (lower Homerian,* Cyrtograptus lundgreni *Biozone):* Kazakhstan, Czech Republic, Germany, Poland, USA (Nevada); Canada (Arctic).——Fig. 17,*2a*. **C. tomczyki*, holotype, ZPAL G.24/8, Bartoszyce core, northeastern Poland, scale bar, 1 mm (Kozłowska-Dawidziuk, 2001, fig. 5b).——Fig. 17,*2b*. *C. apsis* Lenz & Kozłowska-Dawidziuk, 2001, GSC 126935, with portions of bandages on lateral wall of theca, Arctic Canada, scale bar, 1 mm (Lenz & Kozłowska, 2006, fig. 8,*6*).

Dabashanograptus Ge, 1990, p. 82 [**D. chengkouensis;* OD]. Robust and distinctly widening tubarium; prosicula preserved; ancora umbrella shallow, apparently very simple; large lateral orifices above ancora umbrella; reticulum with coarse polygonal meshes of more or less equal size; ventral thecal wall with zigzag lists distally. *Silurian, Llandovery (Telychian,* Spirograptus guerichi *Biozone):* China (Sichuan).——Fig. 16,*4a–b*. **D. chengkouensis*, holotype, NIGP 21147a–b (part and counterpart), Chengkou, Sichuan, China; scale bars, 1 mm (Ge, 1990, pl. 10).

Doliograptus Lenz & Kozłowska-Dawidziuk, 2002a, p. 321 [**D. latus;* M]. Ovate tubarium with well-developed reticulum and slightly coarser lists of ancora sleeve walls in more or less zigzag pattern; transverse rods absent; mid-ventral lists well developed; thecal profile rectangular, thecal apertures deep in some with genicular processes; simple, shallow ancora umbrella; lateral proximal orifices large, kidney-shaped; lists with pustules. *Silurian, Wenlock (upper Homerian,* Colonograptus praedeubeli/deubeli *Biozone):* Canada (Arctic).——Fig. 17,*3a–b*. **D. latus; 3a,* holotype, GSC 104678, scale bar, 1 mm (Lenz & Kozłowska-Dawidziuk, 2001, fig. 10.6); *3b,* GSC 104679, large, fairly complete specimen, note glue covering thecal outer walls; scale bar, 1 mm (Lenz, 1994a, fig. 6,*7*).

Eiseligraptus Hundt, 1959, p. 15 [**Plegmatograptus eisenacki* Hundt, 1951, p. 56, fig. 13; OD]. Robust, largely parallel-sided tubarium; nema free inside, forming distinct branched nematularium with several stout branches emanating from a single point, beginning within the mature tubarium; ancora umbrella apparently very simple; lateral orifices large; meshwork composed of three or more distal rows of more or less equal-sized hexagonal meshes; pleural lists strongly inclined, connecting thecal lip to succeeding lateral apertural list. *Silurian, Llandovery (Telychian* Spirograptus turriculatus *Biozone):* Germany.——Fig. 17,*1a*. **E. eisenacki* (Hundt), holotype, BAF H4667, Weinberg bei Hohenleuben, Germany, scale bar, 1 mm (new).——Fig. 17,*1b*. *E. cystifer* Hundt, 1959, holotype, BAF 67 H4104, Weinberg bei Hohenleuben, Germany, scale bar, 1 mm (new).

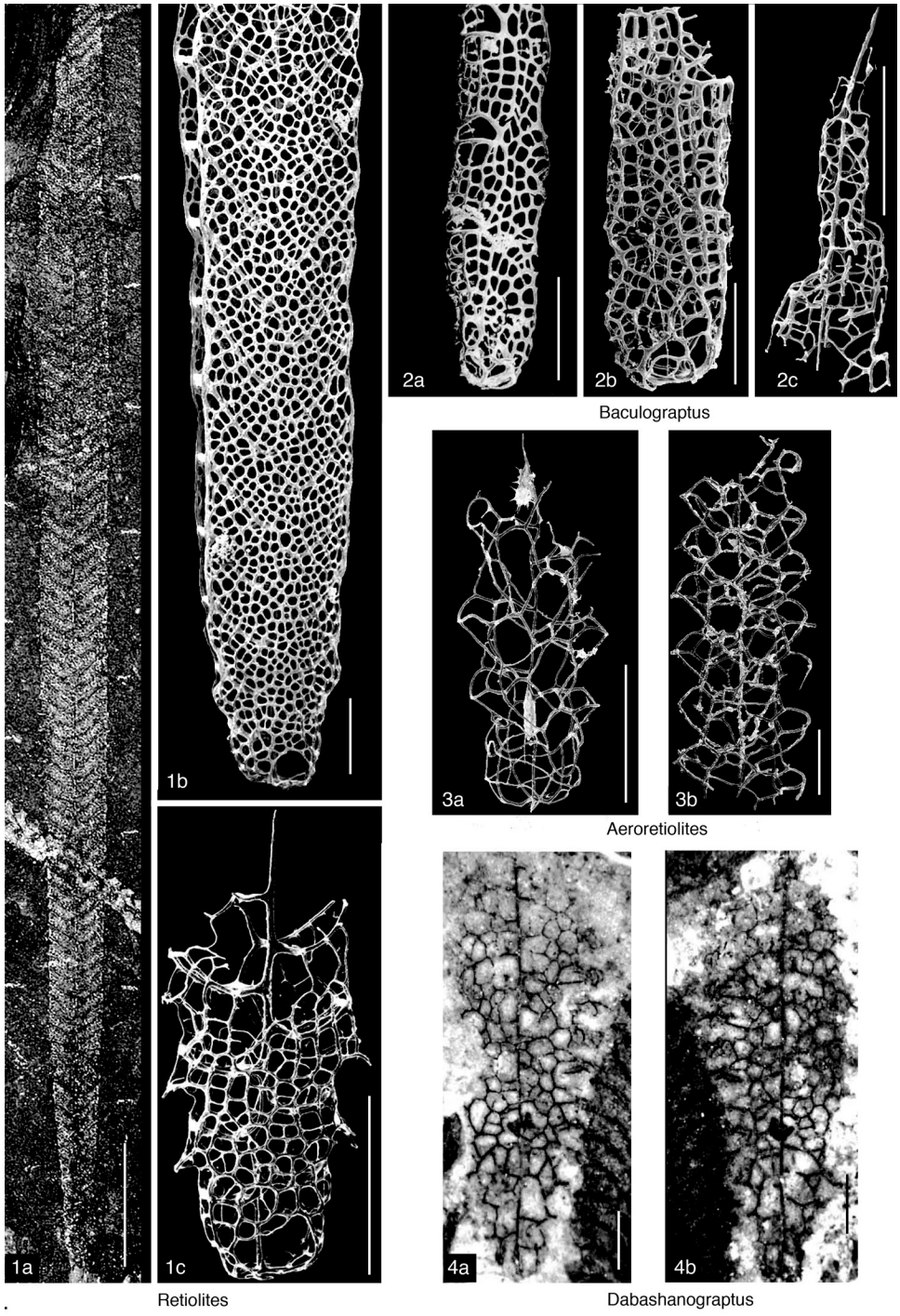


FIG. 16. Retiolitidae (Retiolitinae) (p. 17–18).

Eisenackograptus Kozłowska-Dawidziuk, 1990, p. 203, *ex Gothograptus* (*Eisenackograptus*) Kozłowska-Dawidziuk, 1990, p. 203, Kozłowska-Dawidziuk, 1995, p. 272 [**Gothograptus eisenacki* Obut & Sobolevskaya, 1965, p. 41; OD]. Tubarium finite, narrowing distally, with prominent appendix; nema free, but incorporated into wall at base of appendix; ventral thecal walls undulose; partial mid-ventral lists; transverse rods present; ancora umbrella shallow, simple, asymmetrically developed; proximal lateral orifices kidney shaped, oriented towards the theca 1^2 side of the tubarium; large proximal ventral orifice below theca 1^2; outer ancora may be present; ancora sleeve lists made up of moderately coarse lists running from lateral edge of one thecal lip to the next, and meshwork of smaller lists; seams of reticulum facing outwards; thecal orifices directed distolaterally; long, reticulated wall of theca 1^2 extending nearly to ancora; genicular lists absent; lists weakly pustulose to almost smooth and, occasionally, some striate. *Silurian, Wenlock (upper Sheinwoodian* Cyrtograptus perneri *Biozone–lower Homerian* Cyrtograptus lundgreni *Biozone):* Russia (Taimyr), Poland, Canada (Arctic), Latvia.——Fig. 17,*4a–b.* **E. eisenacki* (Obut & Sobolevskaya); *4a,* holotype, CINGR 33/8783, 1087a/24 *Testograptus testis* Biozone, central Taimyr, Russia, scale bars, 1 mm (Sobolevskaya, 2011, p. 259; specimen lost); *4b,* GSC 104017, very well-preserved specimen, Wenlock, Lower Homerian, *Cyrtograptus lundgreni* Biozone, Arctic Canada, scale bar, 1 mm (new).

Eorograptus Sennikov, 1984, p. 54 [**Pseudoplegmatograptus singularis* Sennikov, 1976, p. 160; OD]. Tubarium parallel sided; prosicula present, nema connected throughout to thecal lists by horizontal connecting rods and transverse rods; ancora umbrella shallow bowl-shaped, with spiral threads; thecal apertural lips looping, horizontal, alternating on either side in orderly, ladderlike succession; pleural lists parallel, vertical on both sides of tubarium, continuous between each lateral thecal list; zigzag lists of ancora sleeve on reverse side. *Silurian, Llandovery (upper Aeronian* Lituigraptus convolutus *Biozone–lower Telychian* Spirograptus minor/Rastrites linnaei [=Spirograptus guerichi] *Biozone):* Siberia; Canada (Arctic).——Fig. 18.*1a.* **E. singularis* (Sennikov), holotype, image inverted to show better contrast, Llandovery, lower Telychian, *minor/linnaei* Biozone (=*guerichi* Biozone), Altai, Siberia, scale bar, 1 mm (Sennikov, 1976, pl. 8).——Fig. 18,*1b–c, E. spirifer* Melchin, Lenz, & Kozłowska, 2017; *1b,* paratype, GSC 137646, distal part showing horizontal thecal loops, parallel pleural lists, and prosicula; *1c,* GSC 137650, proximal end showing prosicula and spiraled ancora umbrella, Landovery, Aeronian, *Lituigraptus convolutus* Biozone, Arctic Canada; scale bars, 1 mm (Melchin, Lenz, & Kozłowska, 2017, fig. 13.8–13.9).

Giganteograptus Lenz & Kozłowska, 2007, p. 497 [**Plegmatograptus giganteus* Bouček & Münch, 1944, p.17 (p. 543, German text); OD]. Tubarium with orderly polygonal, coarse meshwork composed of relatively thin lists; thecal lists composed of transverse rods, lateral apertural rods, and lips with paired apertural spines projecting proximolaterally; nema attached to connecting rods proximally, free in distal part of tubarium; ancora umbrella unknown; lists with pustulose surface; seams facing inward. *Silurian, Llandovery (Telychian,* Monoclimacis griestoniensis–Cyrtograptus sakmaricus *Biozones):* China (Ziyang), UK, Czech Republic, Germany, Canada (Arctic).——Fig. 18,*2a–c.* **G. giganteus* (Bouček & Münch); *2a,* PŠ5.11a, holotype; *2b,* paratype, PŠ84a, ancora umbrella missing, Llandovery, Telychian, *Monoclimacis griestoniensis* Biozone, Czech Republic (Lenz & Kozłowska, 2007, fig. 2); *2c*, GSC 38906, isolated fragment, Llandovery, Telychian, *Cyrtograptus sakmaricus* Biozone, Arctic Canada (Lenz & Kozłowska, 2007, fig. 6). Scale bars, 1 mm.

Gothograptus Frech, 1897, p. 670 [**Retiolites nassa* Holm, 1890, p. 25; OD]. Finite tubarium with appendix; sicula 1.3–1.4 mm long; ancora umbrella simple, asymmetrical, more pronounced on theca 1^2 side; outer ancora in some species; proximal lateral orifices kidney shaped; ventral proximal orifice on theca 1^2 side larger; ancora sleeve and thecal walls densely reticulated; nema incorporated into ancora sleeve wall above first or second theca; obverse side of ancora sleeve composed of horizontal lists connected to nema, reverse side with oblique lists; transverse rods not developed; mid-ventral lists well developed; genicular hoods, sometimes of solid microfusellar tissue, overlain by random bandages showing pustules; ancora sleeve lists with pustules. *Silurian, Wenlock (Homerian,* Cyrtograptus lundgreni–Colonograptus praedeubeli/deubeli *Biozones):* worldwide.——Fig. 18,*3a–c.* **G. nassa* (Holm); *3a,* holotype, NRM-PZ Cn0025546, Wenlock, upper Homerian, *Gothograptus nassa* Biozone, Gotland, Sweden (Holm, 1890, pl. 2,*12*); *3b,* proximal end of long form, MB.G. Jaeger sample 347, JM 75/5, glacial boulder, Hiddensee, Rügen, Baltic Sea, from boulder with type material of *Pristiograptus praedeubeli* Jaeger in Barca & Jaeger, 1990 (new); *3c,* ZPAL G.29/21, short form, Wenlock, upper Homerian, *Gothograptus nassa* Biozone, northeastern Poland (Kozłowska-Dawidziuk, 2004, fig. 5D). Scale bars, 1 mm.

Holoretiolites Eisenack, 1951, p. 153. [**Retiolites mancki* Münch, 1931, p. 35; OD] [=*Balticograptus* Bouček & Münch, 1952, p. 117 (type, *Retiolites erraticus* Eisenack, 1951, p. 136, OD), see Maletz, 2008, p. 304]. Finite tubarium with appendix; sicula 1.95 mm long; nema free throughout; simple, shallow ancora umbrella with six meshes; outer ancora in some species; distinct proximal ventral orifices; proximal lateral orifices close to theca 1^2; mid-ventral lists may be reduced; transverse rods absent; lateral apertural rods absent; lateral ancora sleeve wall lists zigzag; reticulum poorly developed or absent, sometimes only on appendix; no genicular processes; bandages with pustules. *Silurian, Ludlow (Gorstian,* Neodiversograptus nilssoni–Lobograptus scanicus *Biozones):* Kyrgyzstan, Germany, Poland,

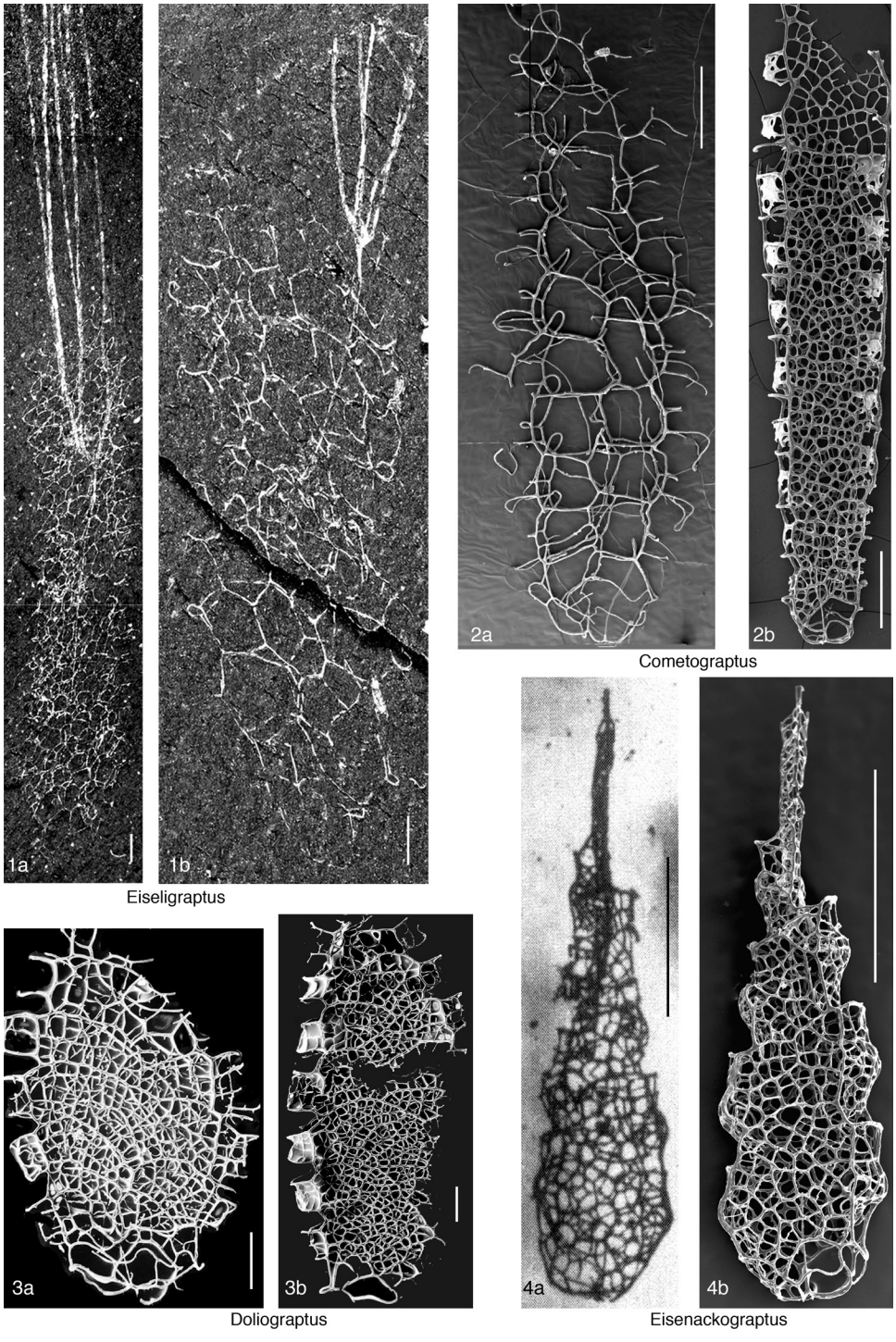


FIG. 17. Retiolitidae (Retiolitinae) (p. 18–20).

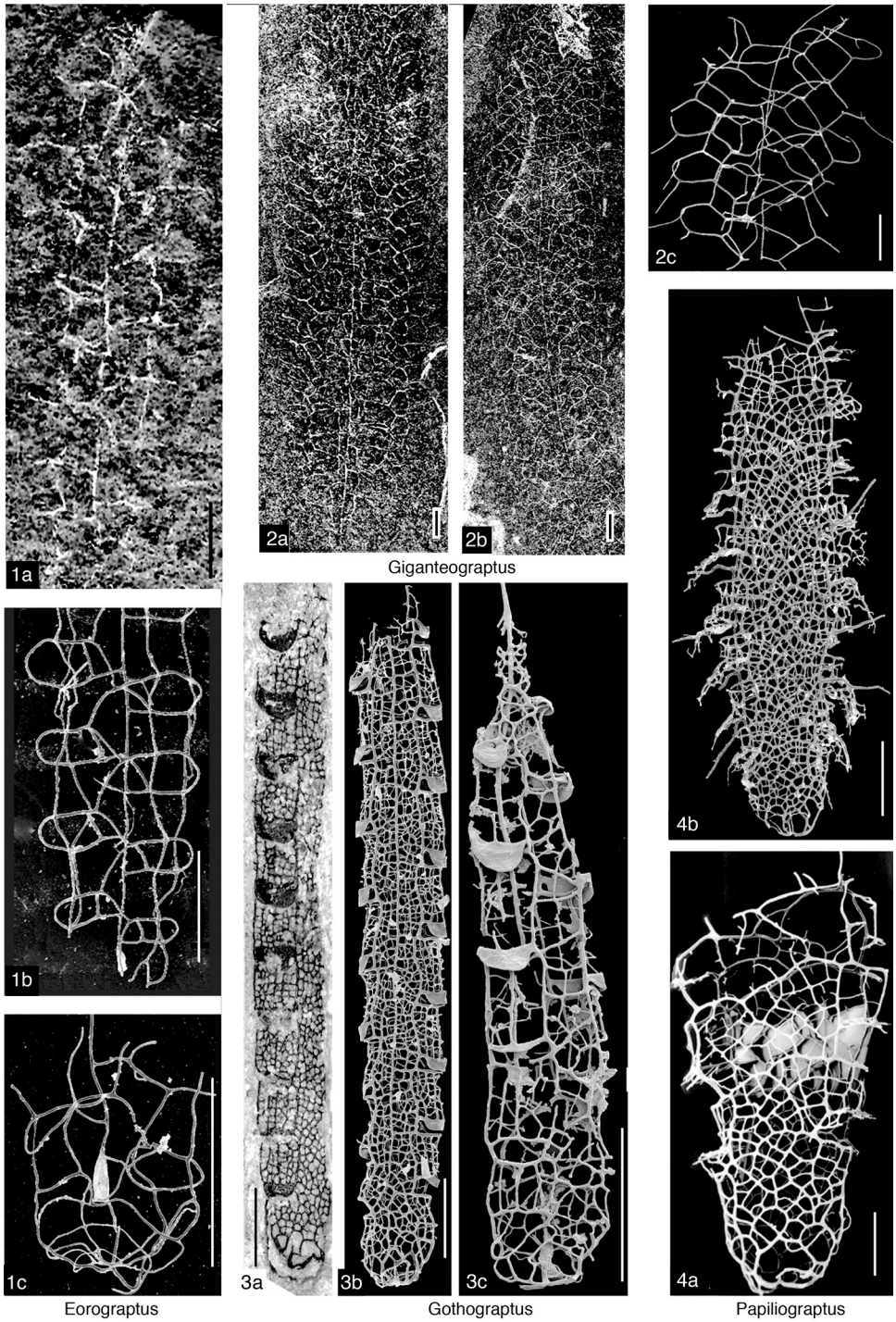


FIG. 18. Retiolitidae (Retiolitinae) (p. 20–23).

Canada (Arctic).——Fig. 19,*2a–c*. **H. mancki* (Münch); *2a,* ZPAL G.28/1, Baltic glacial boulder specimen with long appendix, Ludlow, *Lobograptus scanicus* Biozone, Jarosławiec, northeastern Poland (Kozłowska-Dawidziuk & Lenz, 2001, fig. 3,*4*); *2b,* idealized reconstruction, ventral view of specimen (Münch, 1931, fig. 4); *2c,* holotype, whereabouts unknown, Baltic glacial erratic, Ludlow, Gorstian, Uckermark, northern Germany (Münch, 1931, fig. 5). Scale bars, 1 mm.

Kirkigraptus Kozłowska & Bates, 2008, p. 108 [**K. inexpectans;* M]. Proximal end without ancora; no virga or nema; two proximolateral lists join two genicular lists of first thecae, connecting the two sides of tubarium; thecal framework formed only of genicular lists, lateral apertural rods, thecal lips, and mid-ventral lists; ventral panels of lists (lateral apertural rods and pleural lists) straight; transverse rods absent; ancora sleeve built of pleural lists and horizontal lists between two rows of thecae; large proximal lateral orifices bordered by proximolateral lists and first horizontal lists of ancora sleeve; bandages with pustules. *Silurian, Ludlow (Gorstian,* Neodiversograptus nilssoni *Biozone):* Poland.——Fig. 19,*3a–b*. **K. inexpectans; 3a,* ZPAL G. 40/02, distal end of tubarium; *3b,* holotype, ZPAL G. 40/1, proximal part of tubarium; northeastern Poland; scale bars, 1 mm (Kozłowska & Bates 2008, fig. 3).

Neogothograptus Kozłowska-Dawidziuk, 1995, p. 303 [**N. purus;* OD]. Finite, distally tapering tubarium with appendix; sicula 1.9 mm long; nema free throughout tubarium; transverse rods absent; pleural and mid-ventral lists present; simple, shallow ancora umbrella; outer ancora in some; ancora sleeve lists almost horizontal; reticulum dense to absent; genicular hoods or processes in some, rarely also on proximal ventral orifices; lists with pustules; seams inside. *Silurian, Wenlock (upper Homerian,* Colonograptus praedeubeli/deubeli *Biozone)–Ludlow (Gorstian,* Lobograptus scanicus *Biozone):* Kyrgyzstan, Poland, Germany, Canada (Arctic), ?Australia.——Fig. 19,*1a–b*. **N. purus; 1a,* ZPAL G.XVI/1353, small finite specimen; *1b,* holotype, ZPAL G.XVI/1341, Ludlow, Gorstian, *Lobograptus scanicus* Biozone, Baltic erratic boulder, Jarosławiec, northern Poland, scale bars, 1 mm (Kozłowska-Dawidziuk, 1995, fig. 27F–27G).——Fig. 19,*1c*. *N. thorsteinssoni* Lenz & Kozłowska-Dawidziuk, 2004, MB.G. 1083.2, Ludlow, Baltic glacial boulder, scale bar, 1 mm (Maletz, 2008, fig. 1o).

Papiliograptus Lenz & Kozłowska-Dawidziuk, 2002a, p. 331 [**P. papilio;* OD]. Tubarium narrowing distally, but appendix unknown; pleural and mid-ventral lists present and well developed; ancora umbrella simple; dense reticulum with zigzag or almost horizontal coarser ancora sleeve lists; proximal lateral orifices large, circular to kidney shaped; thecal orifices deep; reticulate genicular hoods in some species; lists with pustules. *Silurian, Wenlock (upper Homerian,* Colonograptus praedeubeli/deubeli *Biozone):* Lithuania, Poland, Germany, Canada (Arctic).——Fig. 18,*4a–b*. **P. papilio; 4a,* holotype, GSC 104681, white infilling is glue, scale bar, 1 mm (Lenz & Kozłowska-Dawidziuk, 2002a, fig. 12.1); *4b,* VU RET-1, complete tubarium, Šiupyliai-69 borehole, Lithuania, scale bar, 1 mm (Kozłowska & Radzevičius, 2013, fig. 3a).

Paraplectograptus Bouček & Münch, 1952, p. 37 (also cited as *Paraplectograptus* Bouček & Münch in Příbyl, 1948, p. 21, *nom. nud.*) [**Retiolites eiseli* Manck, 1918, p. 338; M] [=*Pseudoplectograptus* Obut & Zaslavskaya, 1983, p. 110 (type, *Plectograptus praemacilentus* Bouček & Münch, 1952, p. 26, Czech text; p. 124, English text, OD, herein)]. Slender, parallel-sided tubarium; thecal framework formed of nema, virga, virgella, connecting rods, transverse rods, lateral apertural rods, and thecal lips only; ancora umbrella simple, orderly, with or without well-defined rim; ancora sleeve lists variably developed, with reticulum in some species; ancora sleeve lists may be with finely striated surface or pustules; ancora sleeve seams outside, lists of ventral wall seams inside. *Silurian, Llandovery (Telychian* Spirograptus turriculatus *Biozone)–Wenlock (lower Homerian* Cyrtograptus lundgreni *Biozone):* worldwide.——Fig. 19,*6a*. **P. praemacilentus,* holotype, NM L2727, Wenlock, lower Homerian, *Cyrtograptus lundgreni* Biozone, Bítov, Czech Republic, scale bar, 1 mm (new).——Fig. 19,*6b*. *P. simplex* Kozłowska-Dawidziuk, 1995, GSC 119772, Wenlock, *Cyrtograptus perneri* Biozone, Arctic Canada, scale bar, 1 mm (Lenz & Kozłowska-Dawidziuk, 2001, pl. 7).——Fig. 19,*6c*. **P. eiseli* (Manck) lectotype, BAF 8/159, ancora umbrella portion missing, Llandovery, mid-Telychian, *Monoclimacis griestoniensis* Biozone, Wetterahammer, Thuringia, Germany, scale bar, 1 mm (new).——Fig. 19,*6d*. *P. senarius* Lenz & others, 2012, GSC134631, Wenlock, *Cyrtograptus perneri* Biozone, Arctic Canada, scale bar, 1 mm (Lenz & others, 2012, pl. 1).

Pileograptus Lenz & Kozłowska, 2007, p. 494 [**P. pileatus;* M]. Robust retiolitines with deep, bowl-shaped ancora umbrella formed from uniform polygonal meshes, and distinctly widening tubarium; sicula 0.8–0.9 mm long; prosicula preserved; lateral apertural lists moderately curved; prominent and broad genicular hoods anchored to lateral apertural lists of succeeding thecae; thecal orifices more or less vertical with thickened apertural lips; ancora sleeve fairly dense, polygonal meshwork; chimneylike stomata with meshwork walls present; lists with finely striated surface. *Silurian, Llandovery (upper Telychian,* Oktavites spiralis or Cyrtograptus lapworthi-C. insectus *Biozone):* Arctic Canada.——Fig. 20,*2a–b*. **P. pileatus; 2a,* holotype, GSC 38910, whole specimen; *2b,* enlargement of holotype, showing thecal hood; Arctic Canada; scale bars, 1 mm (Lenz & Kozłowska, 2007, fig. 3).

Plectodinemagraptus Kozłowska-Dawidziuk, 1995, p. 322 [**P. gracilis;* M]. Diminutive, reduced parallel-sided tubarium; simple ancora umbrella with no rim, more pronounced on theca 1^2 side;

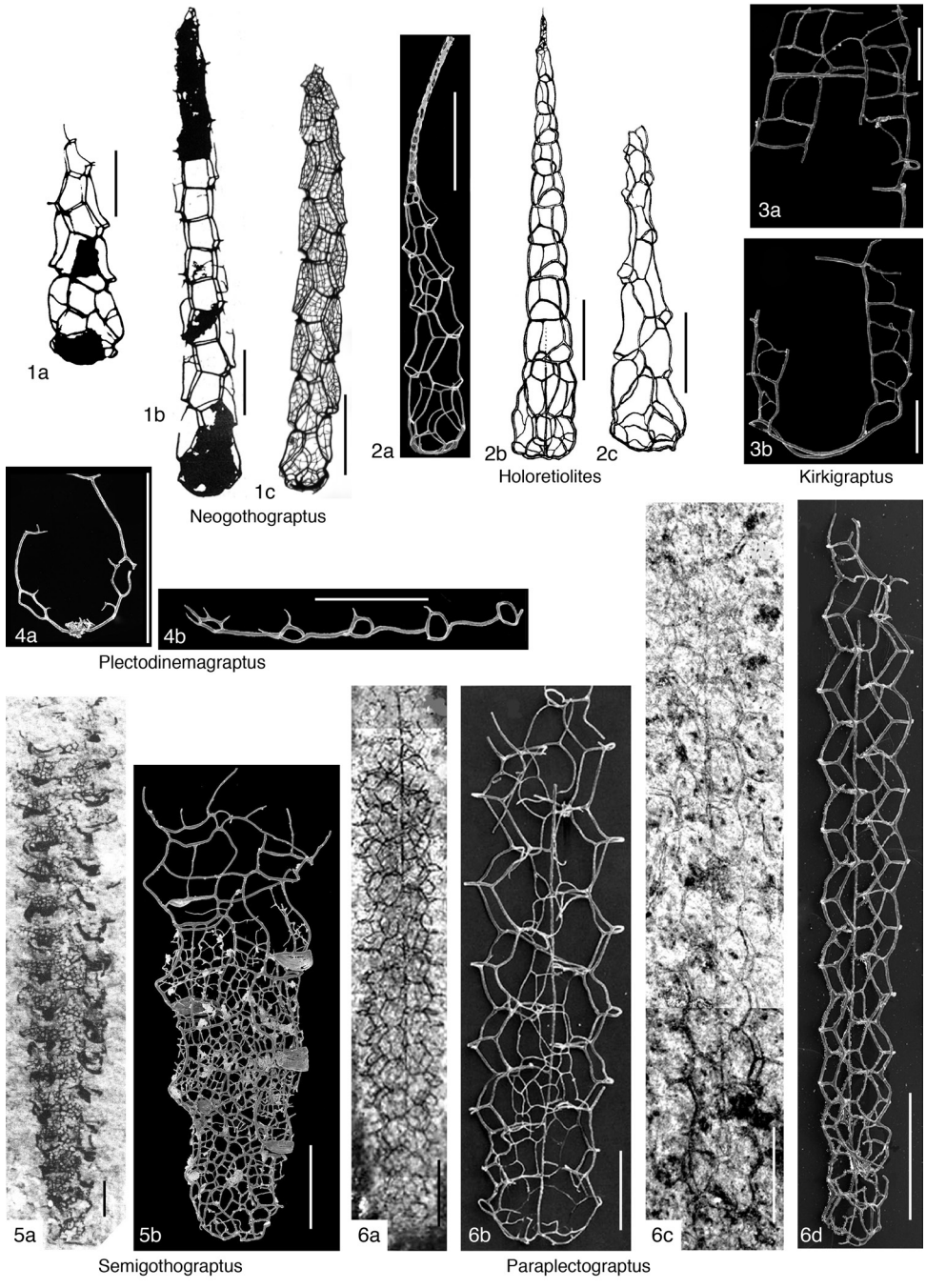


FIG. 19. Retiolitidae (Retiolitinae) (p. 23–28).

ventral walls formed by thecal lip, genicular list, mid-ventral lists, pleural lists, and reduced lateral apertural rods; ancora sleeve represented by pleural lists only; proximal ventral orifices of hexagonal shape; lists with pustules; seams on inside; reticulum lacking. *Silurian, Ludlow (Ludfordian,* Saetograptus leintwardinensis *Biozone):* Poland.——Fig. 19,*4a–b*. **P. gracilis; 4a,* holotype, ZPAL G.XVI/1406, proximal end of specimen showing ancora umbrella, two ventral orifices and mid-ventral lists of first thecae; *4b,* ZPAL G. XVI/1408, showing proximal ventral orifices and four thecae of one side of tubarium; northeastern Poland; scale bars, 1 mm (Kozłowska-Dawidziuk, 1995, fig. 34).

Plectograptus Moberg & Törnquist, 1909, p. 18 [**Retiolites macilentus* Törnquist, 1887, p. 491; OD] [=*Agastograptus* Obut & Zaslavskaya, 1983, p. 107, English translation, Obut & Zaslavskaya, 1986, p. 210 (type, *A. robustus,* OD), see Kozłowska-Dawidziuk, 2002, p. 459]. Parallel-sided tubarium with or without paired genicular processes; sicula 2.45 mm long; nema free throughout the tubarium; nematularium may be present; transverse rods absent; mid-ventral lists present; shallow ancora umbrella with five meshes and only partially developed rim; large proximal lateral orifices; reticulum present in some species; lateral walls of ancora sleeve formed by strong zigzag lists; lists with pustules. *Silurian, Wenlock (upper Homerian* Colonograptus praedeubeli/deubeli *Biozone)–Ludlow (Gorstian* Lobograptus scanicus *Biozone):* worldwide.——Fig. 21,*1a–b*. **P. macilentus* (Törnquist); neotype, SMFXXIV 433, photograph and line drawing of specimen, Ludlow, Gorstian, *Neodiversograptus nilssoni* Biozone, Wetterahammer, Thuringia, Germany, scale bars, 1 mm (Bates & others, 2006, fig. 1).——Fig. 21,*1c*. **P. robustus* (Obut & Zaslavskaya, 1983), holotype, CNIGR 251/42-2, chemically isolated specimen, scale bar, 1 mm (Obut & Zaslavskaya, 1986, fig. 1).

Pseudoplegmatograptus Přibyl, 1948, p. 22 [**Retiolites perlatus obesus* Lapworth, 1877, p. 137; OD] [=?*Sinostomatograptus* Huo, 1957 (type, *S. mui,* OD): Lenz & Kozłowska, 2007, p. 492]. Robust tubarium, slowly widening distally; sicula 0.8 mm long; thecal lips horizontal with long, paired spines; spines rarely distally extended by fine, or lacelike bifurcations or multifurcations; mid-ventral lists present only in more distal thecae; prosicula present; ancora umbrella shallow saucer-shaped, with coarse, polygonal meshes; pleural lists more or less vertical; ancora sleeve meshes finely to coarsely polygonal, may form double layer in mature specimens; stomata often present on lateral walls; lists with finely striated surface. *Silurian, Llandovery (Aeronian,* Stimulograptus sedgwickii *Biozone)–Wenlock (Sheinwoodian,* Monograptus riccartonensis *Biozone):* worldwide.——Fig. 20,*1a–d*. **P. obesus* (Lapworth); *1a–b,* holotype, BU 1363; *1a,* whole specimen; *1b,* enlarged portion of specimen showing single curved thecal spines, some showing secondary to tertiary branching, Llandovery, lower Telychian, *Spirograptus turriculatus* Biozone, County Down, Ireland (Elles & Wood, 1908, pl. 34,*12b*); *1c,* NMW 91.52G, immature specimen with stoma (*arrow*) and shallow ancora umbrella made of few meshes, lower Telychian, *Spirograptus turriculatus* Biozone, Osmundsberget, Sweden (Bates & Kirk, 1992, fig. 180); *1d,* GSC 78423, mature specimen without ancora umbrella, Llandovery, lower Telychian, *Spirograptus turriculatus* Biozone, Arctic Canada (Lenz & Melchin, 1987, pl. 1,*1*). Scale bars, 1 mm.

Pseudoretiolites Bouček & Münch, 1944, p. 22, *ex Retiolites* (*Pseudoretiolites*), Bouček & Münch, 1944, p. 22, see Obut, Sobolevskaya, & Nikolaev, 1967, p. 82 [**Retiolites perlatus* Nicholson, 1868a, p. 530; OD] [=?*Tscharyschograptus* Sennikov, 1984, p. 51 (type, *T. altaicus* Sennikov, 1984, p. 51, OD): Loydell, 1993, p. 61]. Robust, distally widening, parallel-sided or ovate tubarium; sicula 0.5–0.8 mm long; sicula and even thecae may be partially or completely preserved; ventral thecal sides highly inclined (~60° to 80° to tubarium axis) as seen from mid-ventral lists, showing no thecal overlap; thecal apertures often nearly horizontal; thecal apertures with distinct zigzag lists distally; mid-ventral lists present, becoming distinctly zigzag in ventral region of all thecae; ancora umbrella deep, spiraled; thecal profile prominently orthograptid; ancora sleeve well developed with dense meshwork; small lateral orifices present proximally; stomata present in some species; lists with finely striated surface; seams on outside. *Silurian, Llandovery (Aeronian,* Demirastrites triangulatus *Biozone–Telychian,* Cyrtograptus insectus *Biozone):* worldwide.——Fig. 20,*3a–d*. **P. perlatus* (Nicholson); *3a,* GSC 137613, complete specimen with well-developed spiral ancora umbrella and well-preserved zigzag list thecal ventral walls, Llandovery, upper Aeronian, *Lituigraptus convolutus* Biozone, Arctic Canada (Melchin, Lenz, & Kozłowska, 2017, fig. 7,*1*); *3b, 3d,* holotype, BU 1361, Llandovery, upper Aeronian, Cumbria (Lake District), UK (new); *3c,* GSC 137617, ancora umbrella showing well-developed spiral pattern and sicula, Llandovery, upper Aeronian, *Lituigraptus convolutus* Biozone, Arctic Canada (Melchin, Lenz, & Kozłowska, 2017, fig. 7,*6*). Scale bars, 1 mm.

Reticuloplectograptus Kozłowska, Bates, & Piras, 2010, p. 1412 [**R. serpaglii;* M]. Parallel-sided tubarium with paired genicular processes; nema free throughout tubarium; ancora umbrella simple with incompletely developed rim similar to *Plectograptus;* ancora sleeve with small lateral and ventral proximal orifices; ventral wall of tubarium similar to *Plectograptus* with well-developed, almost vertical mid-ventral lists and with well-developed reticulum; lateral walls of the ancora sleeve built of oblique lists showing distinct zigzag pattern and dense reticulum; paired genicular reticulofusellar processes widening distally; lists with pustules. *Silurian, Ludlow (Gorstian,* Neodiversograptus nilssoni–Lobograptus progenitor *Biozones):* Czech Republic, Poland.——Fig. 21,*3a–b*. **R. serpaglii;*

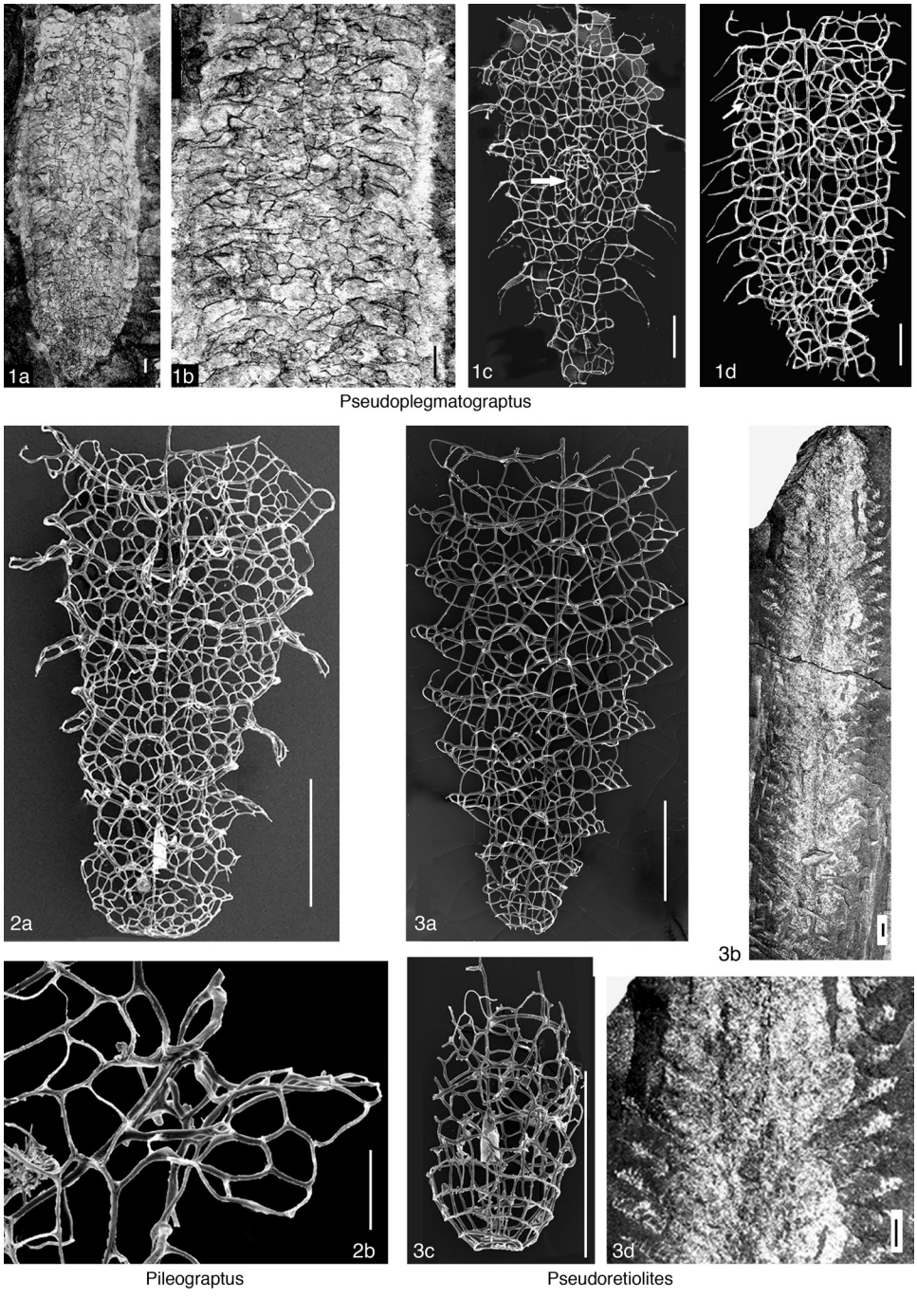


FIG. 20. Retiolitidae (Retiolitinae) (p. 23–25).

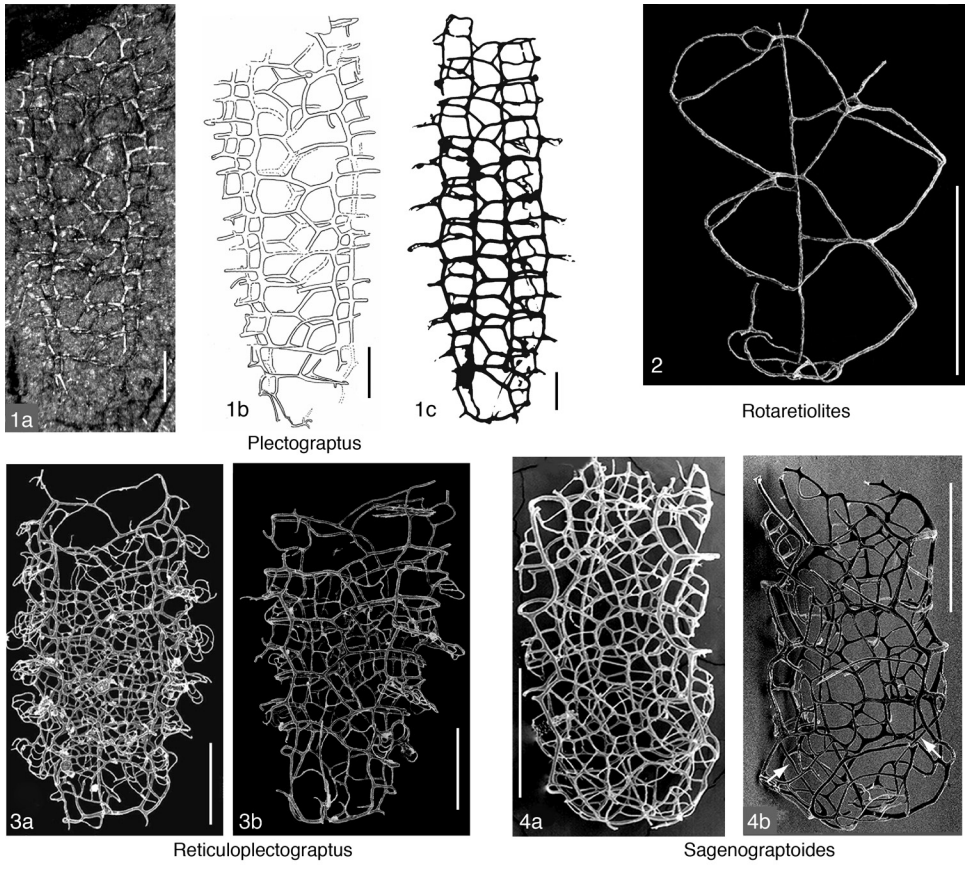


FIG. 21. Retiolitinae (p. 25–28).

3a, holotype, ZPAL G.43/01; *3b,* paratype, ZPAL G.43/02, less mature specimen, complete ancora umbrella, Ludlow, *Neodiversograptus nilssoni* Biozone, northeastern Poland, scale bars, 1 mm (Kozłowska, Bates, & Piras, 2010, fig. 6–7).

Rotaretiolites BATES & KIRK, 1992, p. 265 [**R. exutus;* OD]. Sicula represented by prosicular apertural ring; zigzag list on reverse side extends from prosicular ring; thecae represented by everted apertural loops, dorsal transverse rod and single, mid-ventral list arising from center of transverse rod of previous theca; mid-ventral list of theca 1^1 attached directly to ancora umbrella rim, that of 1^2 to zigzag list close to prosicular ring; some with spines on mid-ventral lists and lateral thecal rims; ancora umbrella with four radial ribs terminating in subcircular rim; ancora umbrella rim joined to mid-ventral list of 1^2 by unseamed list; ancora sleeve not recognized; thecal lists and ancora umbrella lists with coarse parallel striae. *Silurian, Llandovery (Telychian,* Spirograptus guerichi–Spirograptus turriculatus *Biozones):* Sweden, Canada (Arctic).——FIG. 21,*2. R. exutus,* holotype, NMW91.52G.345, lower Telychian, *Spirograptus turriculatus* Biozone, Dalarna, Sweden, scale bar, 1 mm (Bates & Kirk, 1992, fig. 66).

Sagenograptoides LENZ & KOZŁOWSKA, 2010, p. 156, *nom. nov.* pro *Sagenograptus* LENZ & KOZŁOWSKA-DAWIDZIUK, 2001, p. 15, non *Sagenograptus* OBUT & SOBOLEVSKAYA, 1962, p. 74 (Anisograptidae) [**S. arctos* LENZ & KOZŁOWSKA-DAWIDZIUK, 2001, p. 15; M]. Tubarium parallel sided; nema free most of length, but some weak lists may connect nema to transverse rods distally; mid-ventral lists present only on thecae 1^1 and 1^2; geniculum weakly developed, better developed in proximal thecae, distally represented by fewer lists; strong, curving pleural lists; proximal lateral orifices kidney-shaped; outer ancora sleeve present; lists with pustules; ancora sleeve with seams outside; outer ancora sleeve present in some specimens. *Silurian, Wenlock (lower Homerian,* Cyrtograptus lundgreni *Biozone):* Canada (Arctic).——FIG. 21,*4a–b*. **S. arctos; 4a,* holotype, GSC 99179; *4b,* GSC 119775, showing

complete mid-ventral lists of th1[1] and th1[2] (*arrows*); Wenlock, lower Homerian, *Cyrtograptus lundgreni* Biozone, Arctic Canada, scale bars, 1 mm (Lenz & Kozłowska-Dawidziuk, 2001, pl. 8).

Semigothograptus Kozłowska, 2016, p. 536 [**Gothograptus*? *meganassa* Rickards & Palmer, 2002, p. 228; OD]. Tubarium widening gradually from proximal end; nema free; ancora umbrella simple with pair of large looping meshes on each side of tubarium; proximal ventral orifices of triangular shape; proximal lateral orifices kidney shaped; ventral wall represented by mid-ventral lists, lips, genicular lists and long lateral apertural rods convex towards the centre of lateral wall, which become distinctly sigmoidal the more distal they are; oblique clathrial lists on lateral walls. *Silurian, Wenlock (upper Homerian,* Gothograptus nassa/Pristiograptus parvus–Colonograptus deubeli *Biozones):* UK, Czech Republic, Germany, Poland.——Fig. 19,*5a–b. *S. meganassa* (Rickards & Palmer); *5a,* SMX 28550a, holotype, Shropshire, UK, scale bar, 1 mm (Rickards & Palmer, 2002, fig. 4A); *5b,* ZPAL G54/1, Bartoszyce drill core at 1649.2 m, Poland, scale bar, 1 mm (Kozłowska, 2016, fig. 1D).

Semiplectograptus Kozłowska-Dawidziuk, 1995, p. 320 [**S. urbaneki;* M]. Tubarium parallel sided; nema free throughout; simple ancora umbrella with no rim, more pronounced on theca 1[2] side; ventral wall formed by mid-ventral lists, thecal lips and genicular lists; mid-ventral lists of first thecal pair about twice as long as those on remaining thecae; proximal ventral orifices and thecal orifices rhomboid; large proximal lateral orifices; first ancora sleeve list on level of first pair of thecae; oblique ancora sleeve lists forming zigzag; lists with pustules; reticulum lacking. *Silurian, Ludlow (lower Ludfordian,* Cucullograptus hemiaversus–Cucullograptus aversus *Biozones):* Poland.——Fig. 22,*1a–b. *S. urbaneki; 1a,* holotype, ZPAL G.XVI/1392; *1b,* paratype, ZPAL G.XVI/1394; Ludfordian, *Saetograptus leintwardinensis* Biozone; northeastern Poland; scale bars, 1 mm (Kozłowska-Dawidziuk, 1995, fig. 34a and fig. 27j, respectively).

Sokolovograptus Obut & Zaslavskaya, 1974, p. 161 (English text, Obut & Zaslavskaya, 1976, p. 127) [**Plectograptus*? *textor* Bouček & Münch, 1952, p. 29; OD]. Tubarium parallel sided or widening slowly distally; sicula 2.3 mm long; nema free throughout; ventral wall built of looping apertural lips, exceptional genicular lists, and short pleural lists; simple, shallow ancora umbrella with four branches and sometimes incompletely developed rim; outer ancora may be present; proximal lateral orifices present; proximal ventral orifices on both sides; ancora sleeve with irregular meshwork proximally, and sometimes almost horizontal arrangement of oblique lists distally; lists with pustules, seams of thecal framework inside. *Silurian, Llandovery (Telychian,* Spirograptus turriculatus *Biozone)–Wenlock (lower Homerian,* Cyrtograptus lundgreni *Biozone):* worldwide.——Fig. 22,*2a–c. *S. textor* (Bouček & Münch); *2a–b,* holotype, NM L2740, complete specimen and enlargement, Wenlock, *Cyrtograptus rigidus* Biozone, Czech Republic (both images inverted to increase contrast), scale bars, 1 mm (new, photo by Petr Štorch); *2c,* GSC 134638, Wenlock, *Cyrtograptus perneri* Biozone, Arctic Canada, scale bar, 1 mm (Lenz & others, 2012, pl. 3).

Spinograptus Bouček & Münch, 1952, p. 130 [**Retiolites spinosus* Wood, 1900, p. 485; OD] [=*Quattuorgraptus* Dobrowolska, 2013, p. 14 (type, *Retiolites muenchi* Eisenack, 1951, p. 138, *nom. correct*. Maletz, 2010, p. 512 *pro Retiolites münchi* Eisenack, 1951, p. 138, OD)]. Tubarium parallel sided, rarely narrowing distally, ending in a short appendix; sicula 1.9 mm long; ventral wall formed of genicular lists, lips, pleural lists, and complete to incomplete mid-ventral lists; genicular processes paired, reticulofusellar, simple to complex; tubarium very rarely preserved with complete fusellar wall cover, including complete sicula; ancora umbrella with six meshes, highly asymmetrical in lateral profile, looping ventrally below theca 1[2]; pronounced proximal lateral orifices, but in some mature specimens overgrown by reticulum; ancora sleeve formed of lists arranged in strong zigzag pattern, reticulum well developed to absent; lists with pustules. *Silurian, Wenlock (upper Homerian,* Colonograptus praedeubeli/deubeli *Biozone)–Ludlow (Gorstian,* Neodiversograptus nilssoni *Biozone):* worldwide.——Fig. 22,*3a–b. *S. spinosus* (Wood); *3a,* lectotype, BU 1366, Ludlow, *Neodiversograptus nilssoni* Biozone, Wales, UK, scale bar, 1 mm (new); *3b,* ZPAL G. XVI1/1904, Ludlow, *Neodiversograptus nilssoni* Biozone, northeastern Poland, scale bar, 1 mm (new).——Fig. 22,*3c. S. clathrospinosus* (Eisenack, 1951), GSC 104663, specimen with completely preserved fusellar wall, Arctic Canada, scale bar, 1 mm (Lenz & Kozłowska-Dawidziuk, 2002a, fig. 14).——Fig. 22,*3d–e. S. muenchi* (Eisenack); *3d,* holoype, GPIT 180, Nr. 11; *3e,* longer specimen; Baltic erratic boulder, Germany, scale bars, 1 mm (Eisenack, 1951, pl. 22,*9* and 24,*1* (not preserved).

Stomatograptus Tullberg, 1883, p. 42 [**S. toernquisti;* M, =*Retiolites grandis* Suess, 1851, p. 99, see Törnquist, 1890, p. 8]. Tubarium up to 16 cm long, slowly widening initially; prosicula present, but sometimes fusellum of thecae preserved completely; sicula 0.7 mm long; mid-ventral lists absent; pleural lists strongly inclined, connecting thecal lip to succeeding lateral apertural list; nematularium present internally and externally in some specimens; thecae with straight, outward-inclined ventral side; ancora umbrella shallow to moderately bowl-shaped, with orderly hexagonal meshwork; ancora sleeve well developed, with polygonal to quadrilateral meshes; stomata present in all species; lists with finely striated surface; seams on outside of ancora sleeve lists. *Silurian, Llandovery (Telychian,* Spirograptus turriculatus

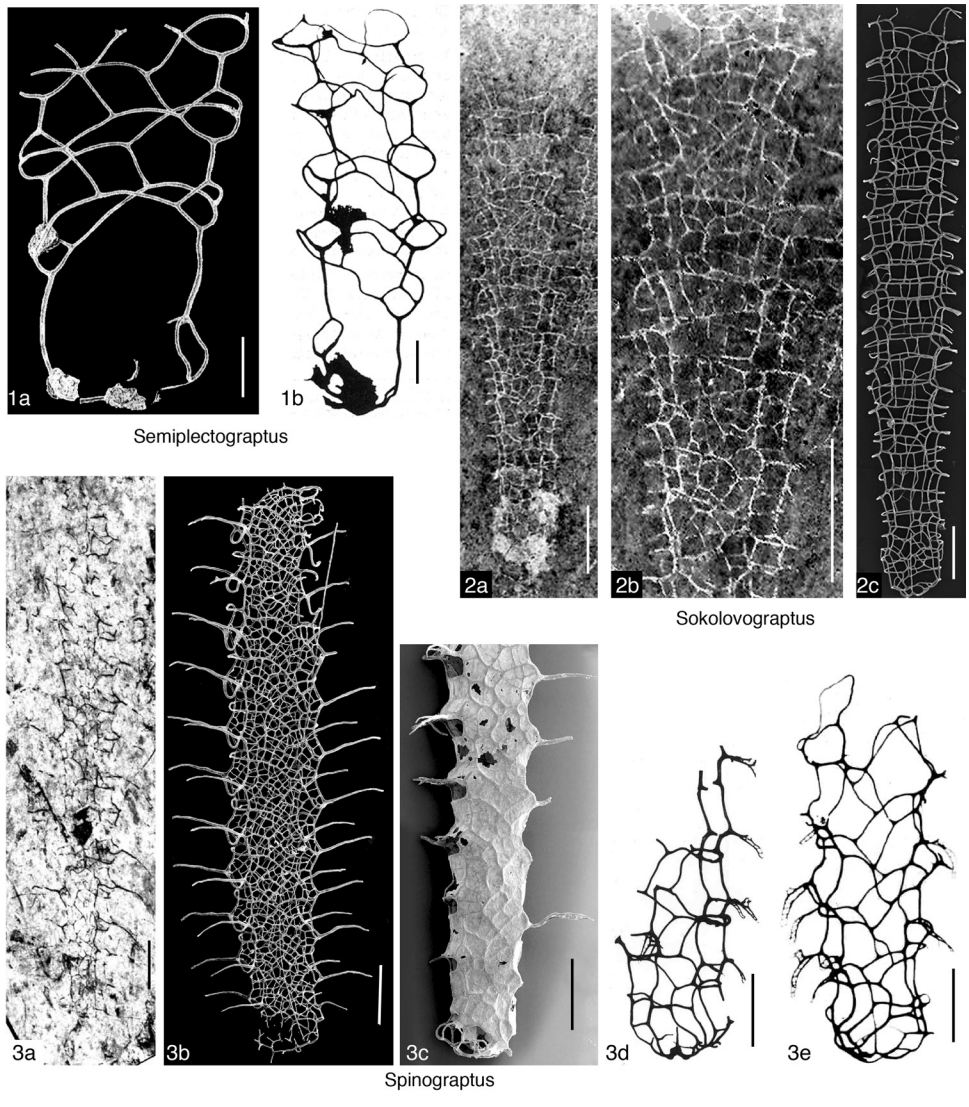


FIG. 22. Retiolitidae (Retiolitinae) (p. 28).

Biozone)–Wenlock (lower Homerian, Cyrtograptus lundgreni *Biozone):* worldwide.——FIG. 23,*1a–b*. *S. grandis* (SUESS); *1a,* neotype, NM L31630 (selected by ŠTORCH, SERPAGLI, & BARCA, 2002, p. 103), Llandovery, upper Telychian, *Cyrtograptus lapworthi* Biozone, Prague region, Czech Republic (new); *1b,* GSC 78432, thecal fusellar floors partially preserved, Llandovery, *Cyrtograptus centrifugus* or *Cyrtograptus murchisoni* Biozone, Arctic Canada (new). Scale bars, 1mm.——FIG. 23,*1c*. *S. canadensis* LENZ, 1988, GSC, Llandovery, *Cyrtograptus sakmaricus* Biozone, Arctic Canada (new).——FIG. 23,*1d–e*. **S. toernquisti; 1d,* holotype, LO 481T, Röstånga, Scania, Sweden; *1e,* Lo 482t, Motala, Östergötland, Sweden (specimen missing); scale bars, 1 mm (Tullberg, 1883, pl. 1).

Valentinagraptus PIRAS, 2006, 584. [**V. simplex;* M]. Tubarium parallel sided, formed from few thecal and ancora sleeve lists; nema free; ventral walls composed of parallel pleural lists, lateral apertural rods, genicular lists and thecal lips; thecal apertures rectangular; ancora umbrella four branches, without developed rim; large proximal lateral orifices; ancora sleeve developed as horizontal lists. *Silurian, Ludlow (Gorstian,* Lobograptus progenitor *Biozone):* Albania, Czech Republic.——FIG. 23,*2*.

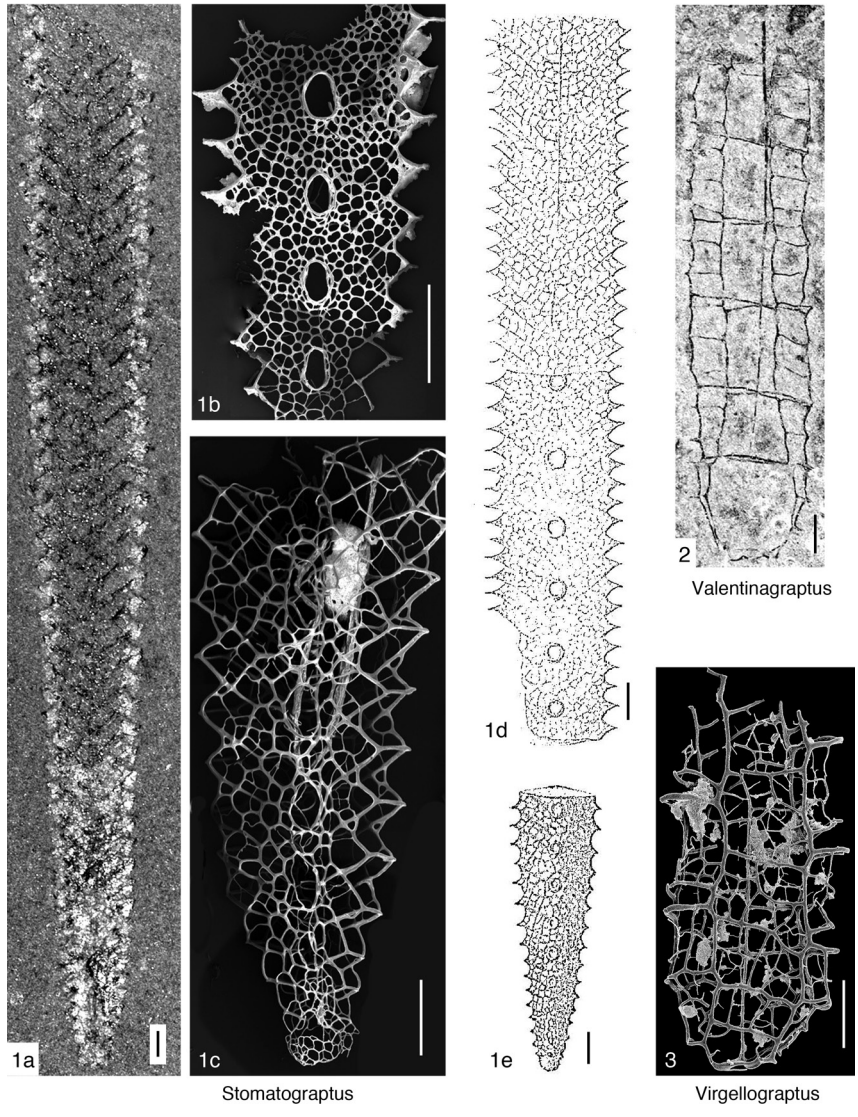


FIG. 23. Retiolitidae (Retiolitinae) (p. 28–30).

**V. simplex,* holotype, CGS SP 183a, Bykoš, Czech Republic, scale bar, 1 mm (Piras, 2006, fig. 7a).

Virgellograptus KOZŁOWSKA, 2015, p. 454. [**V. perrarus;* M]. Slender, parallel-sided tubarium, long sicula; virgella connected to lateral wall; simple ancora umbrella with four meshes; nema free; ventral wall formed by thecal lips, lateral apertural rods, genicular lists, and pleural lists; ancora sleeve built on oblique lists; proximal ventral orifices and proximal lateral orifices overgrown by reticulum in mature colonies; lists with pustules; seams of ancora sleeve on inside; reticulum present. *Silurian, Wenlock (upper Sheinwoodian* Cyrtograptus ellesae *Biozone):* Poland.——FIG. 23,*3*. **V. perrarus,* holotype, ZPAL G.52/1, Wenlock, Bartoszyce IG-1 drill core, Poland, scale bar, 1 mm (Kozłowska, 2015, fig. 2).

Family UNCERTAIN

A number of genera have to be regarded as Retiolitidae *incertae sedis* due to incomplete or fragmentary preservation of the material. The genera *Demicystograptus, Parademicystograptus,* and *Thecocystograptus* were introduced by Hundt (1950) based on the construction of

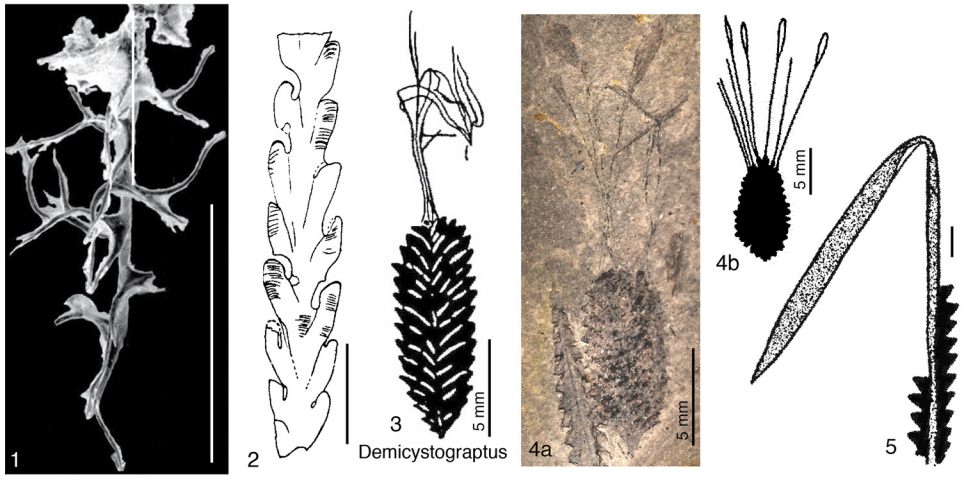


FIG. 24. Retiolitidae *incertae sedis* (p. 31).

their nematularia. The illustrated material originated from the Aeronian to Telychian of Germany and may be related to *Parapetalolithus,* but due to the poor preservation and illustration, the material cannot be identified with certainty.

Demicystograptus HUNDT, 1950, p. 293 (also cited as *Demicystograptus* HUNDT, 1944 in HUNDT, 1953, p. 40) [**D. nindeli;* herein] [=*Demicystifer* HUNDT, 1959, pl. 6,*1, nom. nud.* (misspelling of *Demicystograptus* HUNDT, 1950)]. [The genus was not recognized by BULMAN (1970) and was rejected by JONES and RICKARDS (1967). Some species included in the genus *Demicystograptus* may be referred to *Parapetalolithus.*] *Silurian, Llandovery (Aeronian,* Lituigraptus convolutus *Biozone):* Germany.——FIG. 24,*3.* **D. nindeli*, BAF H4/68/2295, Igelsberg bei Ronneburg, Thuringia, Germany, scale bar, 1 mm (Hundt, 1950, fig. 11).

Mirorgraptus LENZ & KOZŁOWSKA, 2007, p. 499 [**M. arcticus;* OD]. Straight nema with some lists similar to connecting rods arising from more or less same row along one side of nema and, alternately curving to left or right, diverging 180° to each other, between which loops arise from near base of each connecting rod, oriented 90°, distally connecting rods bifurcate and trifurcate; connecting rods and vertically oriented loops probably fully covered by fusellar banding originally. [The type material of *Mirorgraptus* consists of poorly preserved fragments of a long and robust nema with some lists and attached remains of membranes. It may represent a fragment of a retiolitid, but could alternatively be identified as a poorly preserved biserial indet., not necessarily related to the retiolitids.] *Silurian, Llandovery (Telychian,* Spirograptus guerichi *Biozone):* Canada (Arctic).——FIG. 24,*1.* **M. arcticus,* holotype, GSC 38919, oblique view, Silurian, Llandovery, Canada, scale bars, 1 mm (Lenz & Kozłowska, 2007, fig. 7).

Neoglyptograptus RICKARDS & others, 1995, p. 26 [**N. sussmilchi;* OD]. Small, biserial, with strongly alternating thecae having flowing sigmoidal curvature, but with strongly introverted thecal apertures, pronounced lateral excavations, and thickened rims; possibly aseptate distally; fusellum possibly reduced proximally. [The taxon is based on a single incomplete specimen, lacking the proximal end. It may be interpreted as a fragment close to the genus *Gothograptus.*] *Silurian, Wenlock (Homerian,* Colonograptus ludensis *Biozone):* Australia.——FIG. 24,*2.* **N. sussmilchi;* holotype, AMF 81743 (G4/3440), Locality G4, New South Wales, Australia, scale bar, 1 mm (Rickards & others, 1995, fig. 18c).

Parademicystograptus HUNDT, 1950, p. 293 (no type species named). [Genus uncertain based on distal fragment of tubarium with long nematularium, most probably a fragment of a *Parapetalolithus* species]. *Silurian, Llandovery (Aeronian,* Rastrites peregrinus *Biozone):* Germany.——FIG. 24,*5.* No specimen number (the specimen, part of the Hundt collection at Bergakademie Freiberg, has not been identified), Kanigsberg bei Lichtenberg bei Ronneburg, Thuringia, Germany, scale bar, 1 mm (Hundt, 1950, fig. 3).

Thecocystograptus HUNDT, 1950, p. 293 [**T. polycystus;* M]. Biserial tubarium with eight possible floats. *Silurian, Llandovery (Aeronian,* Lituigraptus convolutus *Biozone):* Germany.——FIG. 24,*4a–b.* **T. polycystus; 4a,* NIGP 168459, Dingjiapo, Hubei Province, China; *4b,* BAF 186/4707, Wachtelberg/Frankenberg, Thuringia, Germany (Hundt, 1950, fig. 14).

ABBREVIATIONS FOR MUSEUM REPOSITORIES

BAF: Palaeontological collection, Department of Geology, TU Bergakademie Freiberg, Germany
BU: Lapworth Museum, Birmingham University, UK
CGS: Czech Geological Survey, Prague, Czech Republic
CNIGR: A. P. Karpinsky All-Union Geological Research Institute (VSEGEI), St. Petersburg, Russia
GPIT: Paläontologische Sammlungen, Universität Tübingen, Germany
GSC: Geological Survey of Canada, Ottawa, Canada
LO: Lunds Originale, Department of Geology, Lund University, Sweden
MB.G.: Museum für Naturkunde, Berlin, Germany
NHMUK PM: The Natural History Museum, London, UK
NIGP: Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China
NMP: National Museum, Department of Paleontology, Prague, Czech Republic
NMW: National Museum of Wales, Cardiff, UK
NRM-PZ Cn: Naturhistoriska Riksmuseet Stockholm, Sweden
PMU: Palaeontological Collections, Museum of Evolution, Uppsala University, Sweden
PŠ: Petr Štorch collection, Palaeontological collections, Czech Geological Survey, Prague, Czech Republic
SM: Sedgwick Museum of Earth Sciences, Cambridge, UK
SMF: Naturmuseum Senckenberg, Frankfurt am Main, Germany
VSEGEI: F. N. Tchernyshev Central Geological Museum, St. Petersburg, Russia
VU: Geological Museum, Department of Geology and Mineralogy, Vilnius University, Vilnius, Lithuania
ZPAL G: Insitute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland

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