# FAMILY RETIOLITIDAE

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## Family RETIOLITIDAE Lapworth, 1873

[Retiolitidae Lapworth, 1873b, 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 (2014b) 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. 259.3–259.4). Specimens of *Pseudoretiolites perlatus* (Nicholson, 1868a) 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, whereas fusellar structures are recognized only in a relatively few taxa (Bates & Kirk, 1992, 1997; Lenz, 1994a, Lenz & Kozłowska-Dawidziuk, 2002b; Kozłowska-Dawidziuk, 1997, Kozłowska, Dobrowolska, & Bates, 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.

## MORPHOLOGY

### 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. 260.2–260.4). 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. 260.4–260.6), 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

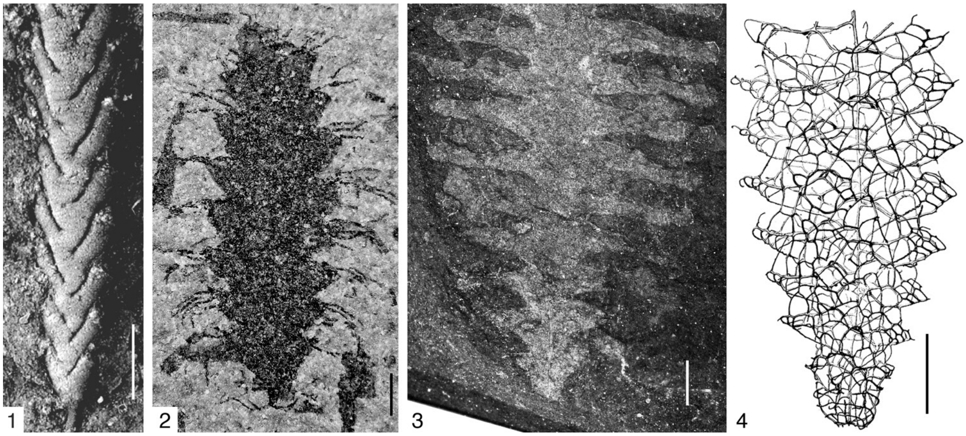


FIG. 259. *1, Rivagraptus bellulus* (TÖRNQUIST, 1890), PMU 31873, proximal end in reverse view and full relief, showing preserved thecae, Tomarp, Scania, Sweden (new); *2, Spinadiplograptus inopinatus* (BOUČEK, 1944), PŠ 3632b, flattened specimen showing fusellum of the thecae, ancora umbrella, and thecal 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.

thecal walls at the lateral apertural lists. In *Pseudorthograptus* (Fig. 260.8) 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 lists (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. 260.9), 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. 260.4–260.8). 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 the clathrium and reticulum are interpreted as remains of fusellar walls. A few Retiolitinae specimens have preserved thecal walls and ancora sleeve walls, e.g., *Pseudoretiolites, Spinograptus praerobustus* (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 or absent. 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 lists, lateral apertural lists, thecal lips, connecting lists,

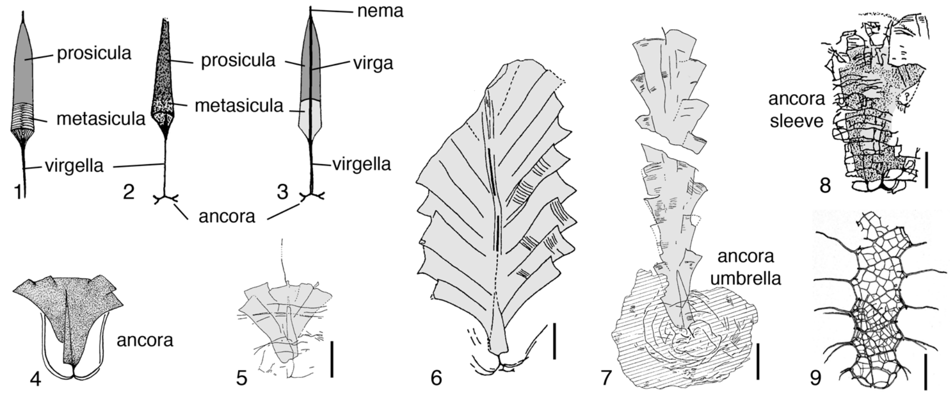


FIG. 260. The ancora and ancora sleeve. *1,* Axonophoran sicula with ventral virgella (Bulman, 1970, fig. 48); *2,* retiolitid sicula with ancora on ventral virgella (Bates & Kirk, 1986, fig. 28); *3,* retiolitine sicula from virgellar side showing virga as connection between virgella and nema (new); *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 and ancora sleeve lists, lacking fusellar membranes (Maletz, 2010b, fig. 5A). Sicula and thecate tubarium in gray; scale bars in *5–9*, 1 mm.

mid-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. However, 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 during the Late Ordovician (Hirnantian) and diversified during the early Silurian (Rhuddanian) into a number of genera. Ancorate taxa appeared during the mid-Rhuddanian with the genus *Pseudorthograptus*. It is clear that the development of the ancora umbrella and ancora sleeve of the Retiolitidae originated during 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* (T. S. HALL, 1906), from the Eastonian 2 (middle 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 with branching at the virgella but not considered to be closely related to the retiolitoids appeared in the earliest Silurian

*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* (DAVIES, 1929), 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, outward inclined, sometimes with variable number of apertural spines; pattern I astogeny or derived pattern; tubarium commonly 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 palmeus* BARRANDE, 1850 (=*Petalolithus minor* ELLES, 1897, see MALETZ, 2014b, fig. 23), and it was recognized in the same species by BATES and KIRK (1992, fig. 41) (Fig. 261.2–261.4). The median septum is visible on the obverse side but not on the reverse side. *Petalolithus folium* (HISINGER, 1837) also has a median septum on the obverse 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. 261.1). 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, 1873b, table 1, facing p. 555] [=*Petalograptus* SUESS, 1851, *sensu* LAPWORTH, 1873b, table 1, facing p. 555 (type, *P. folium,* OD); =*Corbograptus* KOREN' & RICKARDS, 1996, p. 86 (type, *C. enigmatica,* OD), syn. 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. 262,*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 nematu-

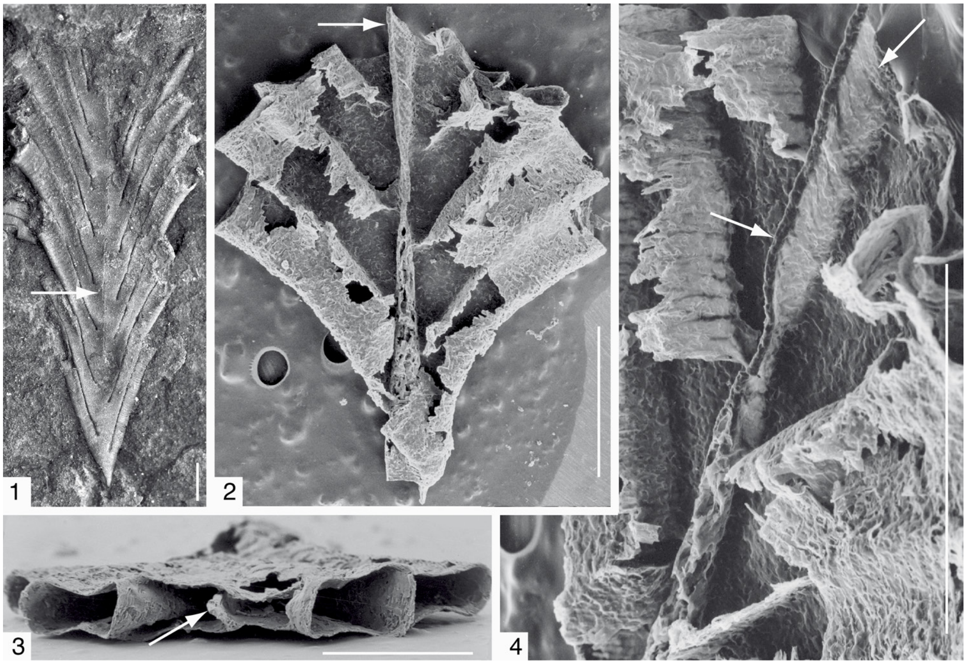


FIG. 261. The median septum. *1, Petalolithus folium* (HISINGER, 1837), LO 11863t, Röstånga, Sweden, reverse view, showing break (*arrow*) due to collapsed lateral wall (Maletz, Ahlberg, & others, 2014, fig. 1N); *2–4, Petalolithus minor* ELLES, 1897, Kallholn, Sweden; *2, 4,* NMW 91.52G.448A, broken specimen showing partial median septum on obverse side and bound by nema (*lower arrow*), fuselli are visible in the partial median septum (*upper 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*.

larium, Tmaň, Czech Republic (Štorch, 1998a, fig. 5,*2c*). Scale bars, 1 mm.——FIG. 262,*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 *Cephalograpsu*s 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* Biozone–*Stimulograptus halli* Biozone): worldwide.——FIG. 262,*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 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, 1957a) in *Dischidograptus* uncertain due to lack of ancora]. *Silurian, Llandovery* (*Aeronian, Lituigraptus convolutus Biozone*–?*Telychian, Spirograptus turriculatus* Biozone): China, ?Germany.——FIG. 262,*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. 262,*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, 1868c, 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* Biozone–*Coronograptus cyphus* Biozone): UK, Czech Republic, Germany, Russia.——FIG. 263,*1a–b.* **D.*

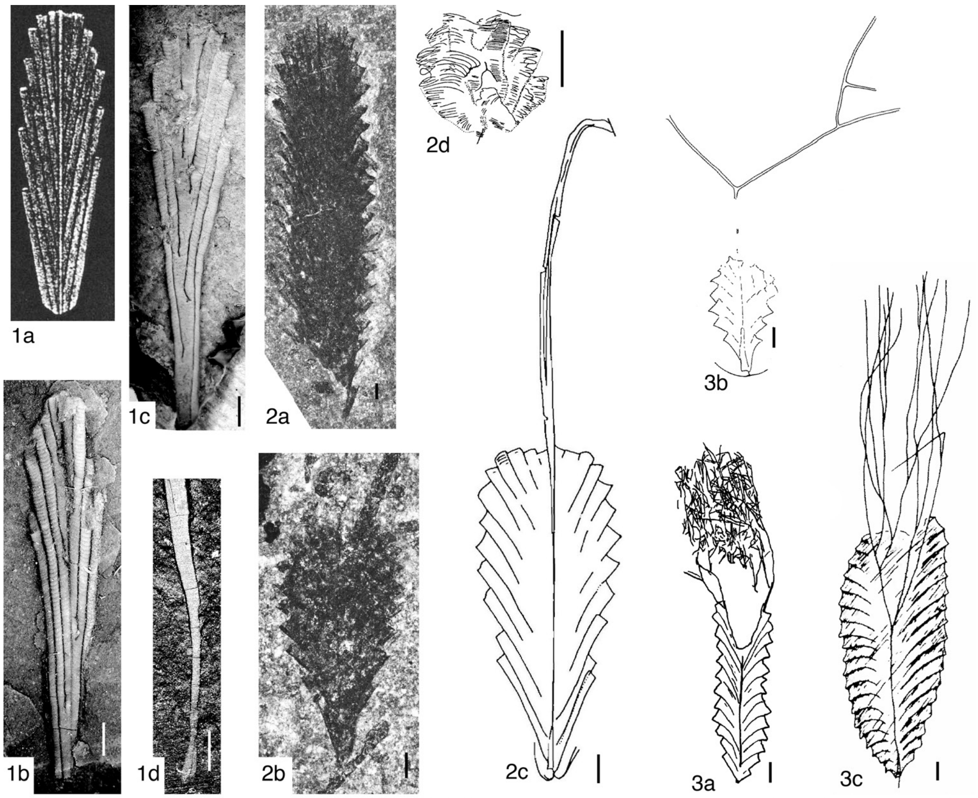


FIG. 262. Retiolitidae (Petalolithinae) (p. 390–391).

*physophora* (NICHOLSON); *1a,* holotype, NHMUK PM 1891(4), Garpol Linn, Birkhill Shale, Moffat area, Scotland, UK (Nicholson, 1868c, 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* Biozone–*Pribylograptus leptotheca* Biozone): Czech Republic, Germany, Russia.——FIG. 263,*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; nema free. *Silurian, Llandovery* (*upper Rhuddanian, Coronograptus cyphus* Biozone–*lower Aeronian, Campograptus curtus* Biozone): Czech Republic, Canada (Arctic).——FIG. 264,*a–b.* **H. introversus; a,* holotype, GSC 104935, Cape Manning section, Arctic Canada, scale bar, 1 mm (new; provided by M. Melchin); *b,* 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, Coronograptus gregarius* Biozone–*Aeronian, Lituigraptus convolutus* Biozone): world-

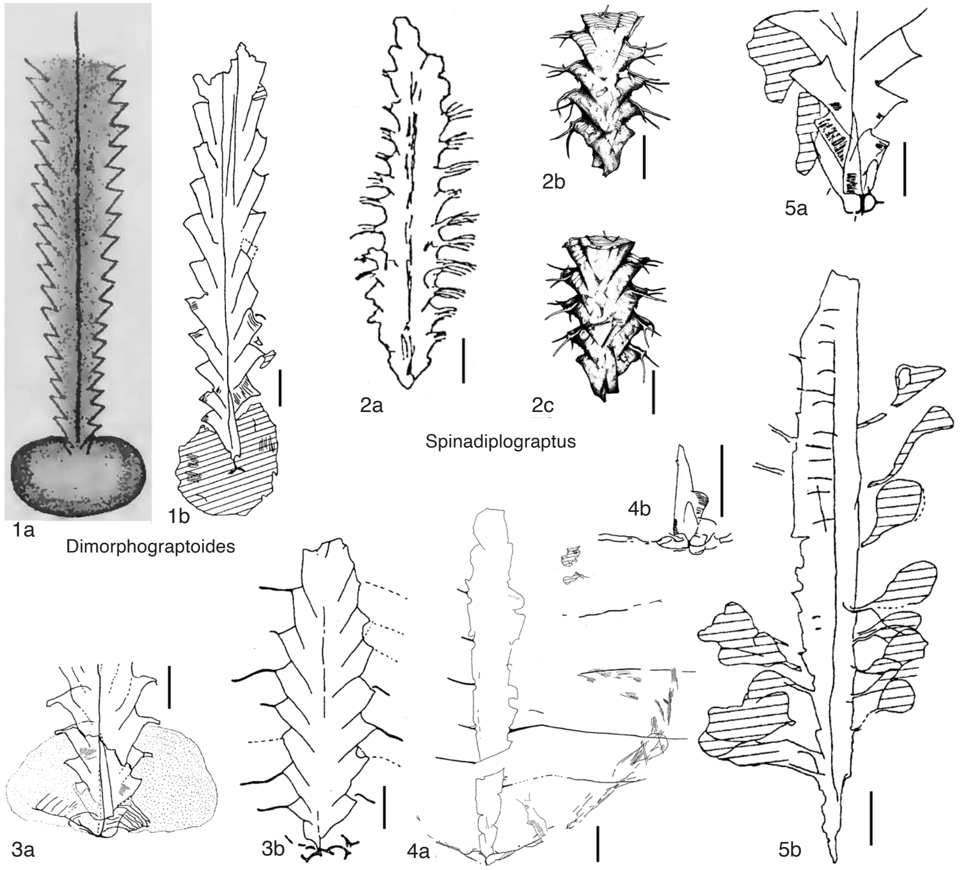


FIG. 263. Retiolitidae (Petalolithinae) (p. 391–393).

wide.——FIG. 263,*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. 263,*3b.* **P. insectiformis* (NICHOLSON); NHMUK PM Q3112, specimen from holotype slab, scale bar, 1 mm (Rickards & Koren', 1974, fig. 4).

**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* Biozone–*Lituigraptus convolutus* Biozone): Canada (Arctic); Czech Republic; Germany; Sweden.——FIG. 263,*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. 263,*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 outward-inclined or

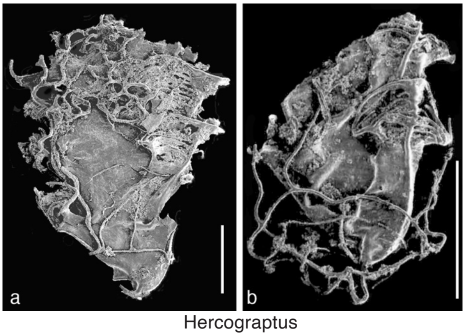


FIG. 264. Retiolitidae (Petalolithinae) (p. 392).

slightly curved ventral thecal wall without geniculum; uniserial first theca by redirection of growth of second theca; thecal apertures straight, outward 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. 265,*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. 265,*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 outward from sicula; additional sicular and thecal spines produced during maturation of colony. *Silurian, Llandovery* (*upper Rhuddanian, Coronograptus cyphus* Biozone–*Aeronian, Stimulograptus sedgwickii* Biozone): Canada, China, UK, Czech Republic, Germany, Russia.——FIG. 265,*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. 265,*3a–d*. **R. bellulus* (TÖRNQUIST); *3a,* lectotype, selected herein (lectotype selection by PŘÍBYL, [1948a, 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, infrared 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. 265,*3e. R. kayi* (CHURKIN & CARTER, 1970), GSC 135128, isolated proximal end in reverse view, infrared photo, Arctic Canada, scale bar, 1 mm (Melchin & others, 2011, fig. 5j).

**Glyptograptus** LAPWORTH, 1873b, 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. 266,*1a–c*. **G. tamariscus* (NICHOLSON); *1a,* paralectotype, NHMUK PM Q.578, Birkhill Shale, Wamphray, Dumfries, Scotland, UK (Zalasiewicz, 2008b, Atlas, Folio 2.88); *1b,* lectotype (selected by PŘÍBYL, 1948a, p. 10), NHMUK PM Q.579, Birkhill Shale, Wamphray, Dumfries, Scotland, UK (Zalasiewicz, 2008b, Atlas, Folio 2.88); *1c,* GSC 104864, proximal end in reverse view, Arctic Canada (Melchin, 1998, pl. 5,*2*). Scale bars, 1 mm.——FIG. 266,*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, MITCHELL, NACZK-CAMERON, FAN, & LOXTON. 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 gradually 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 B*iozone): Canada, China, Russia.——FIG. 266,*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. 266,*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

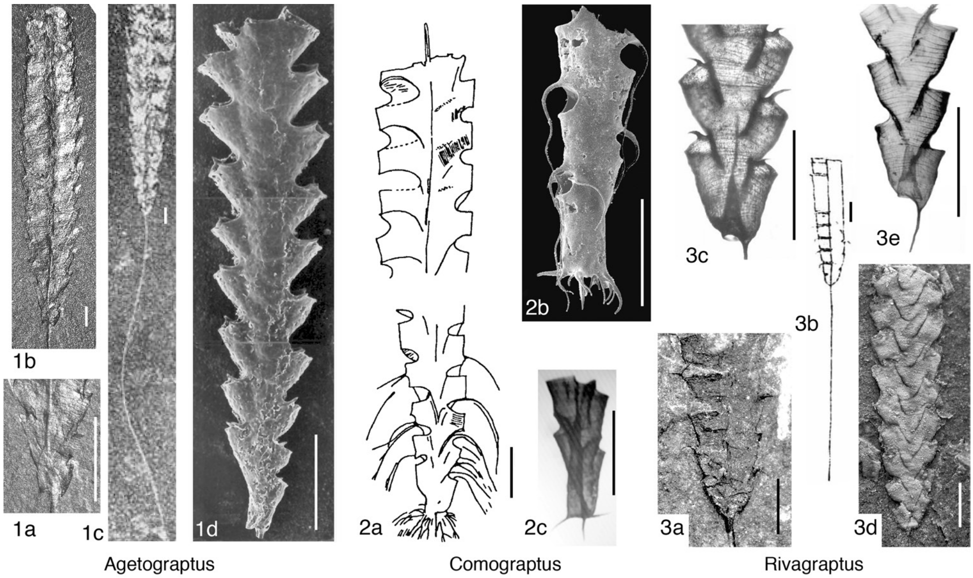


FIG. 265. Retiolitidae (Petalolithinae) (p. 393–394).

and central or embedded in obverse wall, typically with extended nematularium; moderately inclined thecae with nearly straight ventral side and outward-inclined, straight thecal apertures. *Silurian, Llandovery* (*upper Aeronian, Stimulograptus halli* Biozone–*Telychian, Monoclimacis griestoniensis* Biozone): worldwide.——FIG. 266,*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. 266,*3c. P. conicus* (BOUČEK, 1932), lectotype, NMP L 25043, Zelkovice, Bohemia, Czech Republic, scale bar, 1 mm (Štorch, 2000a).

**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 with slight dorsal curvature of proximal end and slightly flared dorsal sicular margin. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone–*Coronograptus cyphus* Biozone): Canada, USA, UK.——FIG. 266,*4a*. **S. eberleini* (CHURKIN & CARTER), holotype, USNM 161783, Alaska, USA, scale bar, 1 mm (Melchin & others, 2011, fig. 6n).——FIG. 266,*4b*. *Sudburigraptus* sp. 1, GSC 135127, infrared photo, reverse view, southern Urals, Russia, scale bar, 1 mm (Melchin & others, 2011, fig. 5h).

## Subfamily RETIOLITINAE Lapworth, 1873

[Retiolitinae LAPWORTH, 1873b, 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 typically preserved in stratigraphically earlier taxa, but reduced or not preserved in later forms, with the rare exception of some occurrences in *Spinograptus* spp. (LENZ, 1994a; KOZŁOWSKA-DAWIDZIUK, 1997); thecae with variable inclination, lacking interthecal septa and thecal overlap; thecal apertures generally considerably 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

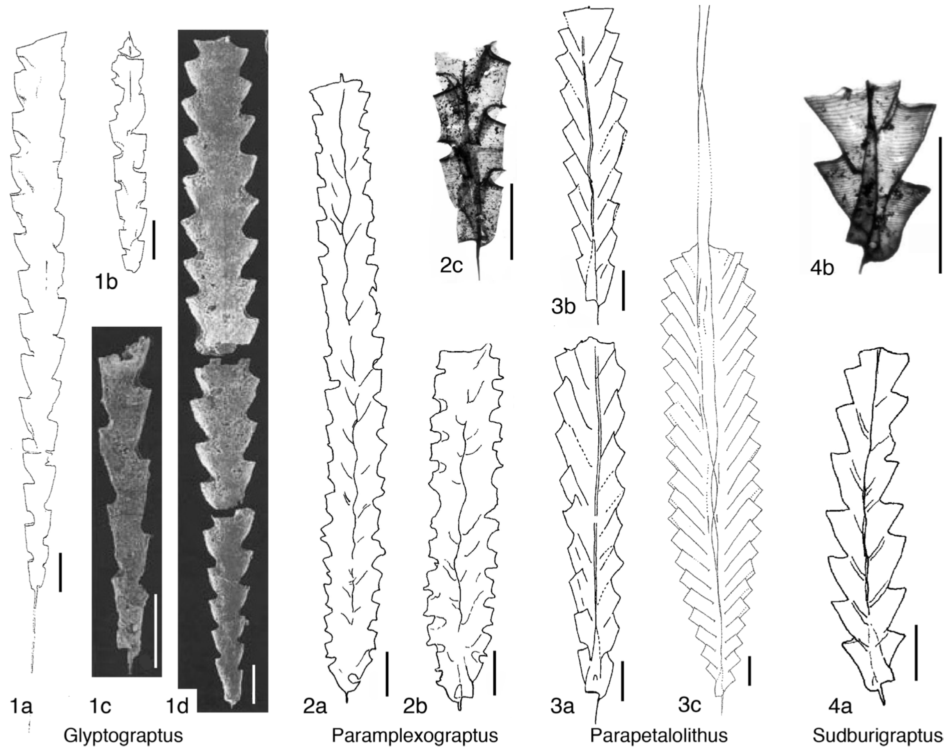


FIG. 266. Retiolitidae (Petalolithinae) (p. 394–395).

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. 267–Fig. 268). 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. 268). 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. 267.1), and a second layer, the ancora sleeve, on the outside (Fig. 267.2, 267.5–267.6). 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 present in only a very few taxa, e.g., *Retiolites, Pseudoretiolites* (Fig. 259.3), *Stomatograptus* (Fig. 267.1), 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. 269.3). Very commonly, the seams demonstrate evenly spaced, U-shaped increments or shards (Fig. 269.5) 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. 270), 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.

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. 267). 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 present, and an outer wall (ancora sleeve) derived entirely from the distal extension of the ancora (Fig. 267.2).

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. 271). 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, 1993b, 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

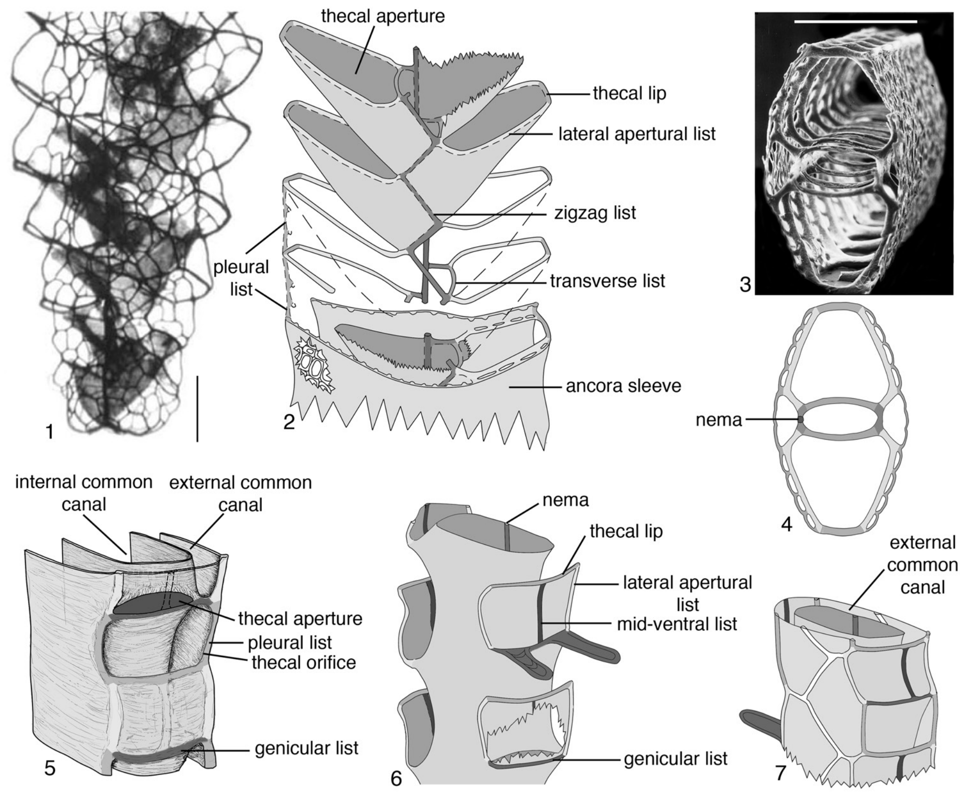


FIG. 267. Morphology and morphological terminology. *1, Stomatograptus* TULLBERG, 1883, showing preservation of thecal walls comprised of sheetlike fusellar bands, scale bar,1 mm (Lenz & Thorsteinsson, 1997, fig. 1); *2, Retiolites* BARRANDE, 1850, reconstruction of median part, showing thecal framework and connection to ancora sleeve (*gray*); *3, Retiolites*, cross section showing strong transverse lists and nema, scale bar, 1 mm (Bates, 1989, fig. 11); *4, Retiolites*, cross section showing thecal framework; ancora sleeve (*light 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 astogenetic pattern I (BATES, KOZŁOWSKA, & LENZ, 2005). One of the differences in early growth stages 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, comprised of a few branches (e.g., *Paraplectograptus*) (Fig. 271.3) with some smoothly bounded by a rim (e.g., *Rotaretiolites*) (Fig. 268.1), to very complex, comprised of many meshes, to those with numerous radial and spiral lists (e.g., *Pseudoretiolites*) (Fig. 271.5), and range from a shallow saucer-shape to a deep cup-shape in profile (Fig. 271.5–271.6).

In general, the ancora umbrella structures are more complex, including a spiral structure, during the Llandovery (Fig. 271.2), and generally simpler structures during the Wenlock and Ludlow taxa (Fig. 271.3, Fig. 271.6). 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. 272).

The earlier retiolitines possess ancora sleeve seams on the outside of the ancora sleeve, as was demonstrated for *Retiolites angustidens*

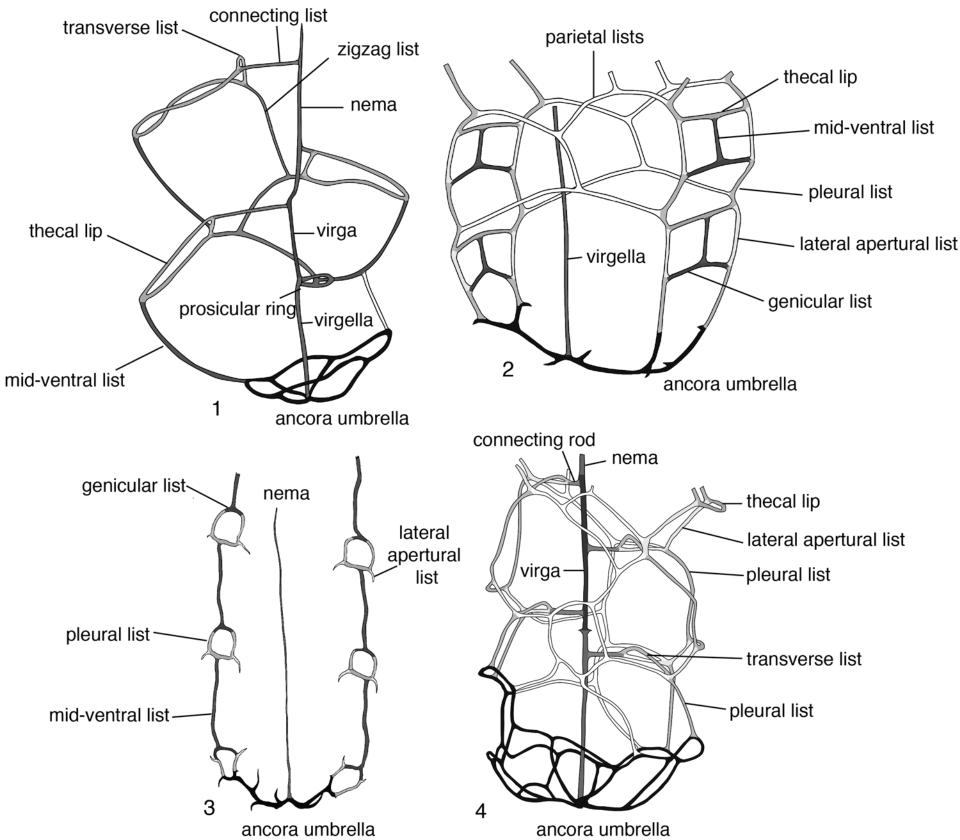


FIG. 268. Terminology of thecal lists in the Retiolitinae. *1, Rotaretiolites* BATES & KIRK, 1992, possessing only thecal framework, prosicular ring, and simple ancora umbrella; *2, Plectograptus* MOBERG & TÖRNQUIST, 1909, showing very simple ancora umbrella and large lateral and ventral orifices; *3, Plectodinemagraptus* KOZŁOWSKA-DAWIDZIUK, 1995, showing strongly reduced framework; *4, Paraplectograptus* PŘÍBYL, 1948a, tubarium with strong ancora umbrella, lacking reticulum (all adapted from Bates, Kozłowska, & Lenz, 2005, fig. 5). Color version of illustrations available in *Treatise Online* 114.

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).

The retiolitine girder-like structures, the cortical lists, are the mainstays for retiolitine preservation and have 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. 269.1) appeared during the early Aeronian, extended through the Telychian, and in a more limited way into the Wenlock, then disappeared at the end of the early Homerian. Strong parallel ridges occurred only in *Rotaretiolites* during the Telychian (Fig. 269.4).

Taxa with pustule ornamentation and finely striated lists (Fig. 269.2) appeared during the middle Telychian and continued until the extinction of the retiolitids during the middle Ludlow. Thus, two forms of micro-ornamentation were present from the 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

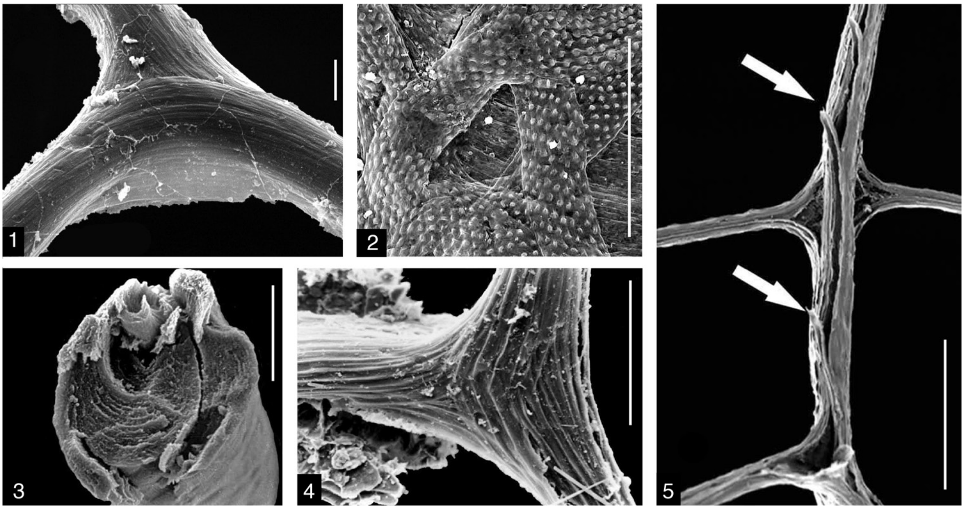

FIG. 269. General morphology and micromorphology of retiolitines. *1, Eorograptus spirifer* MELCHIN, LENZ, & KOZŁOWSKA, 2017, lists showing fine striation (Melchin, Lenz, & Kozłowska, 2017, fig. 9,*4*); *2, Gothograptus nassa* (HOLM, 1890), ZPAL G.54.6, cortical bandages on genicular hood showing well-developed 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*.

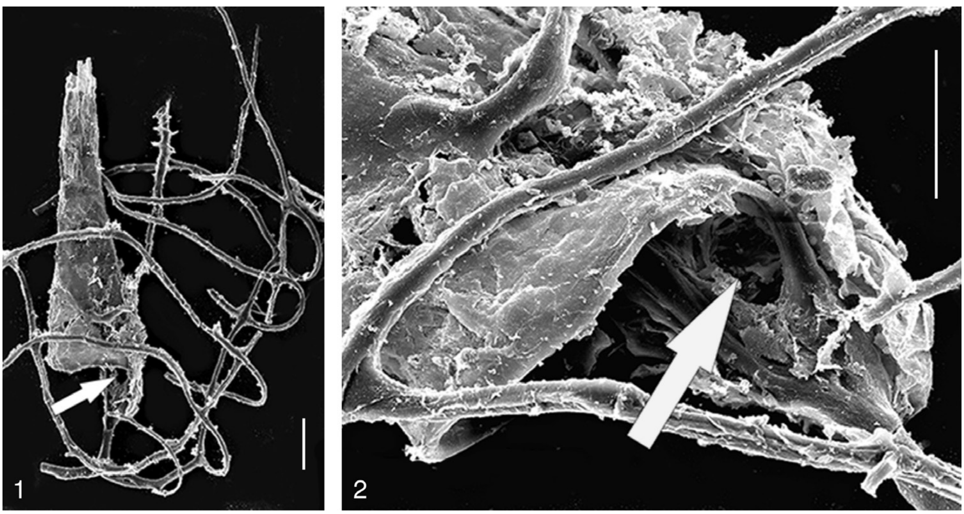

FIG. 270. Resorption foramen. *Pseudoretiolites* BOUČEK & MÜNCH, 1944 sp., GSC 137638, distal end of metasicula, showing downward curvature of theca $1^1$ and well rounded foramen (*arrows*), Llandovery, middle Aeronian, upper *Campograptus curtus* Biozone, Arctic Canada; *1,* complete distal end of sicula, ancora, and four spiral lists, scale bar, 0.5 mm; *2,* enlargement showing well-rounded porus, scale bar 50 µm (Melchin, Lenz, & Kozłowska, 2017, fig. 11,*2*).

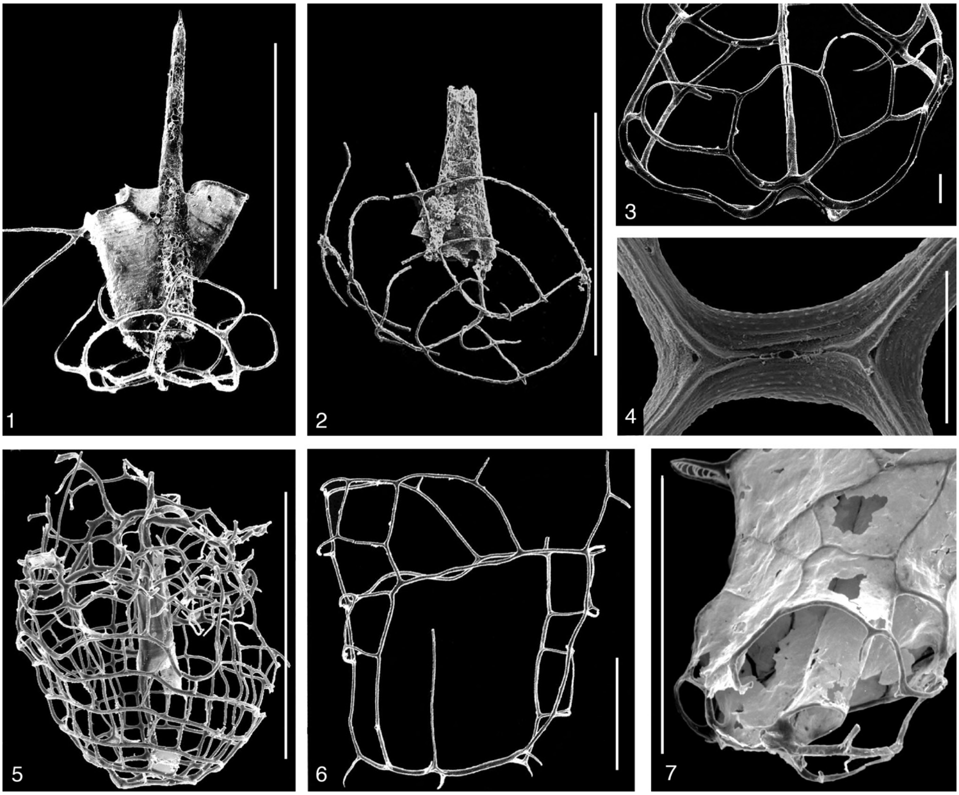


FIG. 271. Ancoras and ancora umbrellas. *1, Spinadiplograptus inopinatus* (BOUČEK, 1944) (petalolithine), GSC 9819, complete ancora umbrella, Arctic Canada (Bates, Kozłowska, & Lenz, 2005, fig. 3F); *2,* ancora umbrella of *Pseudorthograptus* sp. cf. *P. obuti* RICKARDS & KOREN', 1974 (petalolithine) with spiral and radial lists (Bates & Kirk, 1992, fig. 44); *3,* simple ancora umbrella of *Paraplectograptus* PŘÍBYL, 1948a (retiolitine), Arctic Canada; *4, Spinograptus* BOUČEK & MÜNCH, 1952, (retiolitine) ancora, showing pustules and seams on outside (Bates, Kozłowska, & Lenz, 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, Kozłowska, & Lenz, 2005, 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, Kozłowska, & Lenz, 2005, fig. 2A). Scale bars, 1mm in *1–2, 5–7;* 0.1 mm in *3–4.*

smoothness might be attributable to abrasion rather than biological origin. The function of the micro-ornamentations is unknown.

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, but the ornamentation 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 was universal during the Llandovery and early Wenlock, with a very few ranging as high as the early 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), which is generally regarded as a single final theca. Alternatively, a few taxa had a closed end with no appendix and only a nema projecting beyond the distal end of the tubarium, for instance, *Spinograptus praerobustus; Spinograptus tubothecalis* KOZŁOWSKA,

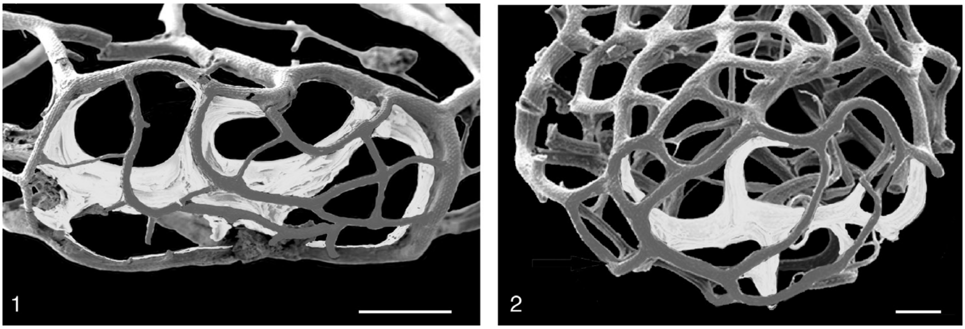


FIG. 272. The outer ancora. *1, Neogothograptus* sp., ZPAL G.66/3, specimen with well-developed ancora umbrella with seams facing outward (*light gray*) (new); *2, Baculograptus chainos* (Lenz, 1993b), GSC 120711, showing well-developed outer ancora with seams facing inward (*dark gray*); Arctic Canada; scale bars, 100 µm (new).

DOBROWOLSKA, & BATES, 2013; and *Cometograptus marsupium* (LENZ, 1993b). A special development occurred in *Cometograptus bicladis* (LENZ, 1993a), in which the tubarium split 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. 273) is of taxa that originated during the Aeronian and early Telychian (Llandovery) and was of special importance because it showed the roots of the subgroups of the retiolitines and the links to the petalolithines.

There are four major clade groups in the cladogram (Fig. 273): (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 of 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 have parallel micro-ornamentation and others have a pustulose ornamentation, which developed somewhat later. *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, 1954c; =*Gladiograptus* HOPKINSON & LAPWORTH, 1875, p. 633 (type, *G. geinitzianus* BARRANDE, 1850, p. 68, M); =*Dimykterograptus* HABERFELNER, 1936, p. 92 (type, *D. bončevi,* M), syn. by BOUČEK & MÜNCH, 1944, p. 31)]. Robust, initially widening tubarium; ancora umbrella shallow, saucer-

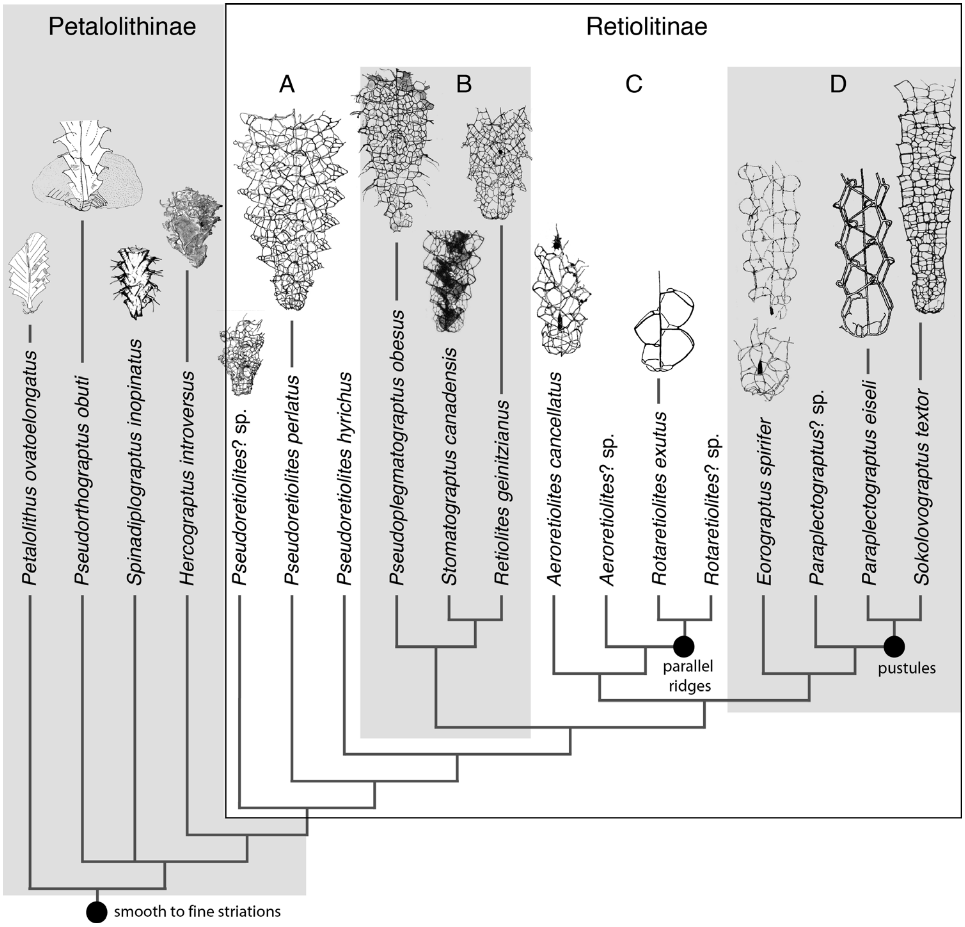


FIG. 273. Cladogram resulting from the analyses that included all taxa in the study of MELCHIN, LENZ, and KOZŁOWSKA (new; based on Melchin, Lenz, & Kozłowska, 2017, fig. 5).

shaped with few polygonal meshes; nema with connecting lists; triangular proximal lateral orifices and small subcircular proximal ventral orifices; reverse side thecal walls with zigzag list; ventral sides defined by horizontal thecal lips and vertical pleural lists; lateral apertural lists inclined at 45° to 60° to tubarium axis; proximal thecal orifices occasionally with reticular hoods formed from the ancora sleeve; unornamented thecal membrane; ancora sleeve with dense and robust reticulum; narrow external common canals without stomata; ancora sleeve lists with seams facing outward; bandages finely striated. *Silurian, Llandovery* (*Telychian, Spirograptus turriculatus/Streptograptus crispus* Biozone)–*Wenlock (Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——FIG. 274,*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. 274,*1b*. *R. australis* M'COY, 1875, GSC137748, ?lower Wenlock, Arctic Canada, scale bar, 1 mm (new).——FIG. 274,*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]. Slender tubarium with few lists; prosicula present; ancora umbrella with spiral lists and continuous undulating rim; ventral side bears pleural lists, looped apertural lists and inclined mid-ventral lists connected to transverse lists; nema with connecting lists on obverse side; pleural lists joined to middle of lateral apertural lists; ancora sleeve weakly developed; ancora sleeve lists with seams facing outward; bandages finely striated. *Silurian, Llandovery* (*Aeronian, Lituigraptus convolutus* Biozone): Arctic Canada.——FIG. 274,*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 with appendix; ancora umbrella strongly asymmetrical, with paired ventral lobes; nema distally incorporated into lateral wall and in appendix; kidney-shaped ventral orifices; ventral walls with thecal lips, geniculum, long lateral apertural lists, short pleural lists, and mid-ventral lists; parietal lists initially zigzag, distally oblique; reticulum present; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*upper Homerian, Colonograptus praedeubeli/deubeli–Colonograptus ludensis* Biozones): Arctic Canada; UK, ?Australia (New South Wales).——FIG. 274,*2a–c*. **B. chainos* (LENZ); *2a,* holotype, GSC 104004, ventrolateral view (Lenz, 1993b, 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, variably shaped tubarium; shallow ancora umbrella with six meshes; nema free; large proximo-lateral orifices more than half width of tubarium; ventral sides with thecal lips, pleural lists, and lateral thecal lists; mid-ventral lists may be partially developed; genicular structures lacking or developed as spines, loops, or hoods; stomata may be present; long mid-lateral spines with seams on ancora sleeve wall in some species; lists of ventral walls with seams inside; ancora sleeve seams outside; bandages with pustules. *Silurian, Wenlock* (*lower Homerian, Cyrtograptus lundgreni* Biozone): Kazakhstan, Czech Republic, Germany, Poland, USA (Nevada); Canada (Arctic).——FIG. 275,*2a*. **C. tomczyki*, holotype, ZPAL G.24/8, Bartoszyce core, northeastern Poland, scale bar, 1 mm (Kozłowska-Dawidziuk, 2001, fig. 5b).——FIG. 275,*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 unknown; nema with connecting lists; reticulum with coarse polygonal meshes of more or less equal size. *Silurian, Llandovery* (*Telychian, Spirograptus guerichi* Biozone): China (Sichuan).——FIG. 274,*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. 331 [**D. latus;* M]. Ovate tubarium; shallow ancora umbrella with undulate rim; nema free; kidney-shaped lateral proximal orifices; ventral walls with thecal lips, genicular lists, pleural lists, lateral thecal and mid-ventral lists; ancora sleeve walls with vague zigzag pattern; dense reticulum; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*upper Homerian, Colonograptus praedeubeli/deubeli* Biozone): Canada (Arctic).——FIG. 275,*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, 1994b, fig. 6,*7*).

**Eiseligraptus** HUNDT, 1959, p. 15 [**Plegmatograptus eisenacki* HUNDT, 1951a, p. 56, fig. 13; OD]. Robust, largely parallel-sided tubarium; free nema with branched nematularium emanating from a single point; ancora umbrella incompletely known; ancora sleeve with regular hexagonal meshes. *Silurian, Llandovery* (*Telychian Spirograptus turriculatus* Biozone): Germany.——FIG. 275,*1a*. **E. eisenacki* (HUNDT), holotype, BAF H4667, Weinberg bei Hohenleuben, Germany, scale bar, 1 mm (new).——FIG. 275,*1b*. *E. cystifer* HUNDT, 1959, holotype, BAF 67 H4104, Weinberg bei Hohenleuben, Germany, scale bar, 1 mm (new).

**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]. Finite tubarium with prominent appendix; shallow, asymmetrically developed ancora umbrella; proximal lateral orifices kidney-shaped; nema incorporated into wall at base of appendix; thecal orifices directed distally; ventral thecal walls undulose, formed from thecal lips, short pleural lists, long lateral apertural lists, and partial mid-ventral lists; transverse lists present; reticulated ventral thecal walls extending downward into tubarium; irregular reticulum with indistinctly developed oblique parietal lists; outer ancora may be present; ancora sleeve lists with seams facing outward; bandages pustulose to almost smooth and occasionally striate. *Silurian, Wenlock* (*upper Sheinwoodian, Cyrtograptus perneri* Biozone*–lower Homerian, Cyrtograptus lundgreni* Biozone): Russia (Taimyr), Poland, Canada (Arctic), Latvia.——FIG. 275,*4a–b*. **E. eisenacki* (OBUT & SOBOLEVSKAYA); *4a,* holotype, CINGR 33/8783, 1087a/24 *Testograptus testis* Biozone, central Taimyr, Russia, scale bar, 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 without virga; nema with connecting lists; ancora umbrella shallow, bowl-shaped, with spiral threads; ventral side formed by vertical pleural lists and looping horizontal thecal lips; zigzag lists on reverse side;

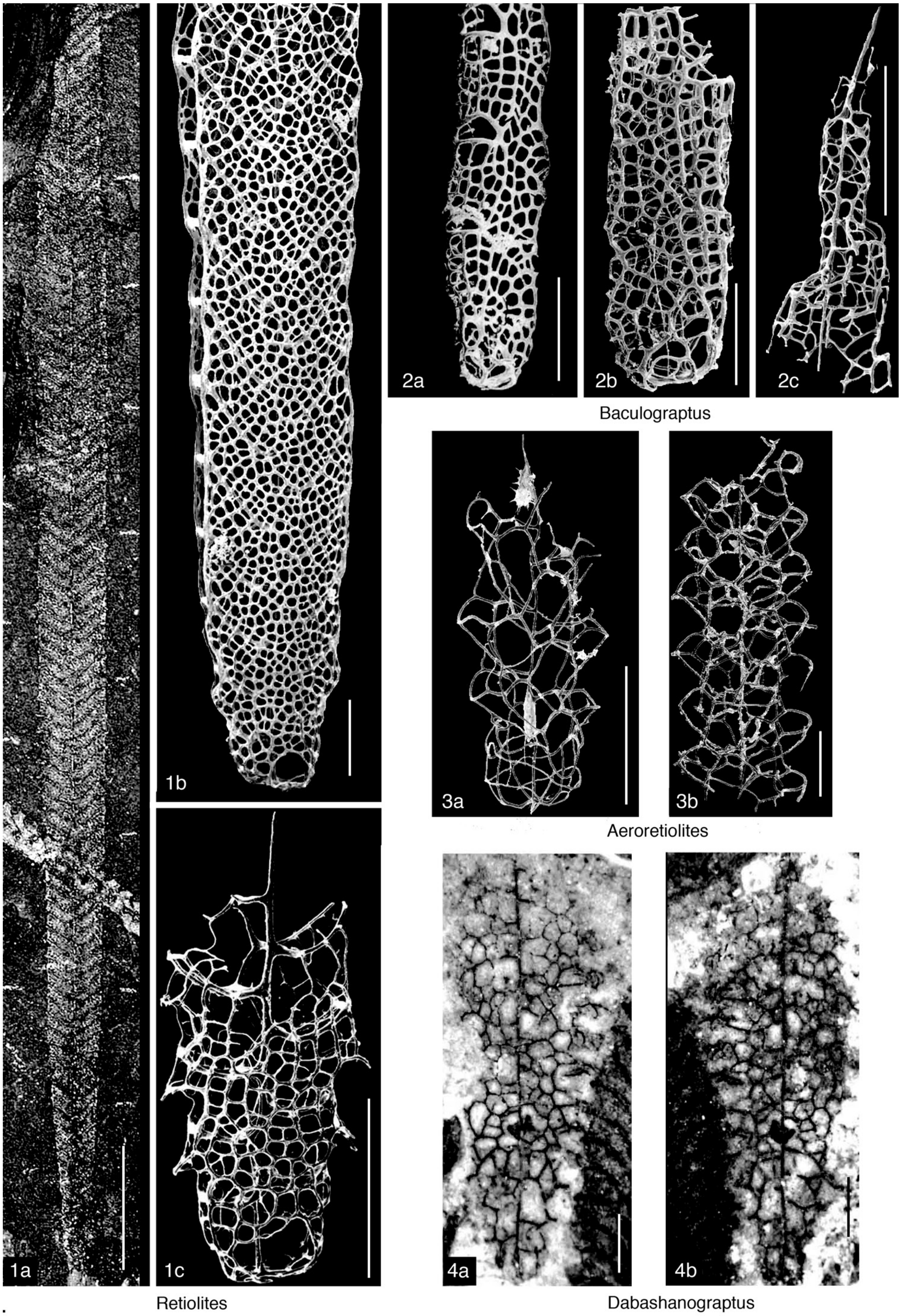


FIG. 274. Retiolitidae (Retiolitinae) (p. 402–404).

transverse lists connect obverse and reverse sides of tubarium; no reticulum; ancora sleeve lists with seams facing outward; bandages finely striated. *Silurian, Llandovery* (*upper Aeronian, Lituigraptus convolutus* Biozone–*lower Telychian, Spirograptus minor/Rastrites linnaei* [=*Spirograptus guerichi*] Biozone): Siberia; Canada (Arctic).——Fig. 276,*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. 276,*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]. Large tubarium with coarse meshwork of relatively thin lists; ancora umbrella unknown; nema with connecting lists joined to middle of transverse lists; thecae outlined by transverse lists, lateral apertural lists, and thecal lips with paired proximolaterally projecting spines; parietal lists on obverse side with zigzag structure, oblique lists on reverse side; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Llandovery* (*Telychian, Monoclimacis griestoniensis* Biozone–*Cyrtograptus sakmaricus* Biozone): China (Ziyang), UK, Czech Republic, Germany, Canada (Arctic).——Fig. 276,*3a–b.* **G. giganteus* (Bouček & Münch); *3a,* paratype, PŠ84a, ancora umbrella missing, Llandovery, Telychian, *Monoclimacis griestoniensis* Biozone, Czech Republic (Lenz & Kozłowska, 2007, fig. 2); *3b,* GSC 38906, isolated fragment, Llandovery, Telychian, *Cyrtograptus lapworthi* 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; ancora umbrella with strongly undulating rim and paired ventral lobes; outer ancora in some species; nema with connecting lists, incorporated into obverse ancora sleeve wall above first or second theca; reverse side of ancora sleeve with oblique parietal lists; ventral side with thecal lips, genicular lists, mid-ventral lists, long lateral apertural lists, and short pleural lists; ancora sleeve and ventral thecal walls densely reticulated; genicular hoods variably formed from microfuselli or a meshwork of lists; extensive veils cover the apertures in some taxa; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone–*Colonograptus praedeubeli/deubeli* Biozone): worldwide.——Fig. 276,*4a–b.* **G. nassa* (Holm); *4a,* holotype, NRM-PZ Cn0025546, Wenlock, upper Homerian, *Gothograptus nassa* Biozone, Gotland, Sweden (Holm, 1890, pl. 2,*12*); *4b,* mature form, Bartoszyce IG-1 drill core, Poland (Kozlowska, 2016, fig. 1A). Scale bars, 1 mm.——Fig. 276,*4c, G. diminutus* Kozłowska, Bates, Zalasiewicz, & Radzevičius, 2019, holotype *4c,* ZPAL G.29/21, Wenlock, upper Homerian, *Gothograptus nassa* Biozone, northeastern Poland (Kozłowska-Dawidziuk, 2004, fig. 5D). Scale bar, 1 mm.

**Hoffmanigraptus** Kozłowska, 2021, p. 933 [*H. varsoviensis;* OD]. Finite tubarium of variable length, widening from proximal end; ancora umbrella shallow with six meshes; nema free, may bear a nematularium; kidney-shaped lateral proximal orifices; ventral wall formed by thecal lips, genicular lists, lateral thecal lists and pleural lists; mid-ventral lists absent to well developed; reticulofusellar genicular processes may be present; zigzag parietal lists on obverse and reverse sides; reticulum well developed to absent; ancora sleeve lists with seams facing inward; bandages with pustules.——Fig. 276,*2.* **H. varsoviensis,* holotype, obverse view; scale bar, 1 mm (Kozłowska, 2021, fig. 1A2).

**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), syn. by Maletz, 2008, p. 304]. Finite tubarium; shallow, asymmetrical ancora umbrella with six meshes; outer ancora in some species; nema free; proximal ventral orifices of hexagonal shape; ventral side with thecal lips, genicular lists, pleural lists(?), and long mid-ventral lists; zigzag lateral apertural lists on main parts of obverse and reverse sides; reticulum poorly developed to absent; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone–*Lobograptus scanicus* Biozone): Kyrgyzstan, Germany, Poland, Canada (Arctic).——Fig. 277,*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]. Parallel sided tubarium; ancora umbrella and nema unknown; lateral (parietal?) lists connect the genicular lists of the first thecal pair; ventral side formed by thecal lips, geniculum, pleural lists, lateral apertural lists, and mid-ventral lists; horizontal parietal lists start at fourth thecal pair level; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone): Poland.——Fig. 277,*3a–b.* **K. inexpectans; 3a,* ZPAL G. 40/02, distal end of tubarium; *3b,*

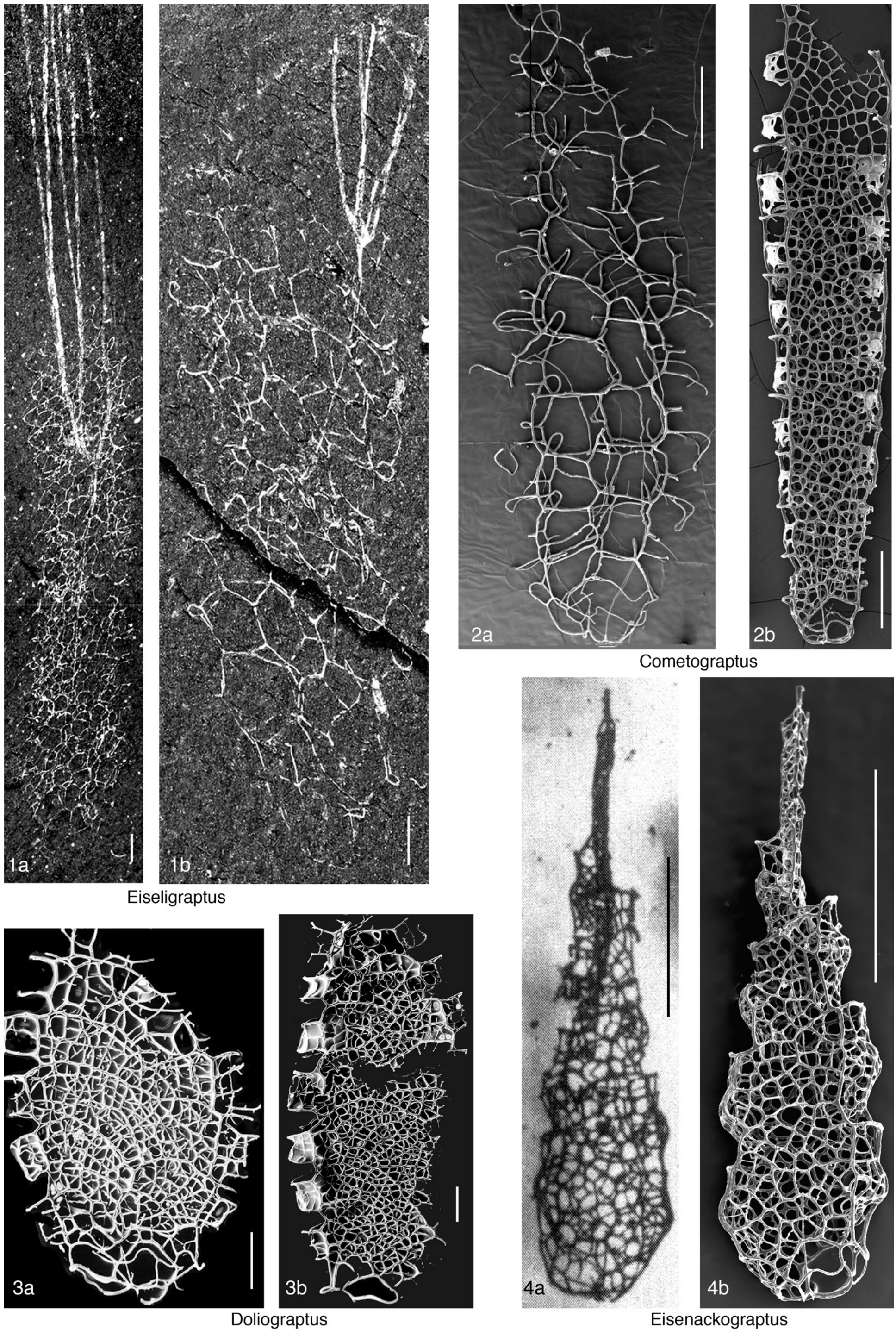


FIG. 275. Retiolitidae (Retiolitinae) (p. 404).

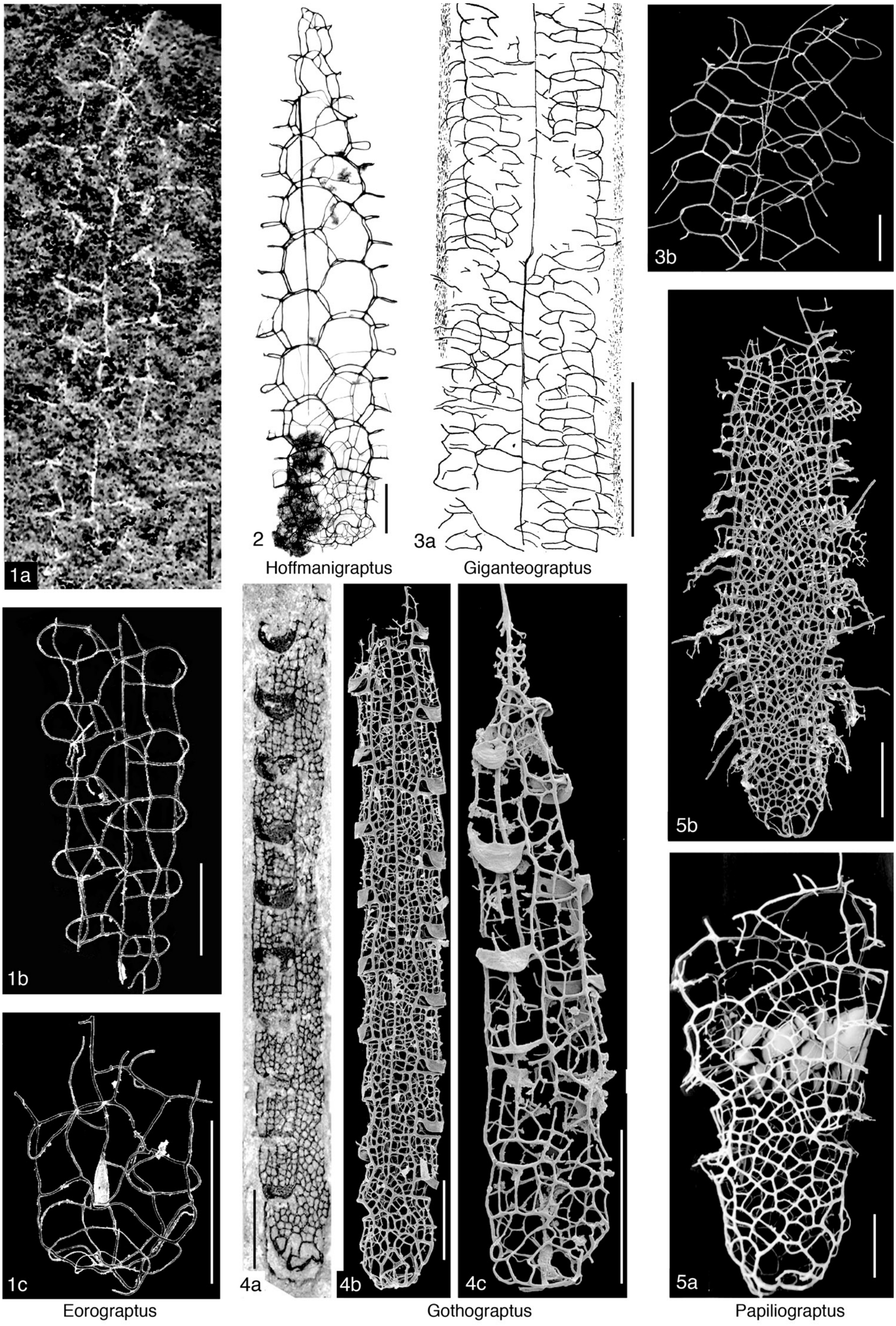


FIG. 276. Retiolitidae (Retiolitinae) (p. 404–409).

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 tubarium with appendix; shallow, asymmetrical ancora umbrella with seven meshes and strongly undulating rim; outer ancora may be present; nema free; ventral side with thecal lips, genicular lists, short pleural lists, long lateral apertural lists, and mid-ventral lists; genicular hoods or processes in some, rarely also on proximal ventral orifices; parietal lists on ancora sleeve walls almost horizontal; reticulum dense to absent; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*upper Homerian, Colonograptus praedeubeli/deubeli* Biozone)*–Ludlow* (*Gorstian, Lobograptus scanicus* Biozone): Kyrgyzstan, Poland, Germany, Canada (Arctic), ?Australia.——Fig. 277,*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. 277,*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]. Finite tubarium, but appendix unknown; ancora umbrella with extensive paired ventral lobes and strongly undulating rim; ventral sides formed by thecal lips, genicular lists, pleural lists, lateral apertural lists, and mid-ventral lists; dense reticulum with indistinct zigzag or almost horizontal parietal lists; reticulate genicular hoods in some species; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*upper Homerian, Colonograptus praedeubeli/deubeli* Biozone): Lithuania, Poland, Germany, Canada (Arctic).——Fig. 276,*5a*. **P. papilio,* holotype, GSC 104681, white infilling is glue, scale bar, 1 mm (Lenz & Kozłowska-Dawidziuk, 2002a, fig. 12.1).——Fig. 276,*5b*. *P. retimarginatus* Kozłowska & Bates, 2021, 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, 1948a, p. 21, *nom. nud.*) [**Retiolites eiseli* Manck, 1918, p. 338; M] [=*Pseudoplectograptus* Obut & Zaslavskaya, 1983, p. 110 (type, *Plectograptus praemacilentus* Bouček & Münch, 1952, Czech text, p. 26; English text, p. 124, OD), syn. herein)]. Slender, parallel-sided to distally widening or finite tubarium; ancora umbrella with seven meshes and often incomplete rim; nema with connecting lists; ventral sides formed by thecal lips, short lateral apertural lists, and long pleural lists; transverse lists present; ancora sleeve lists well developed to lacking; ancora sleeve lists with seams facing outward; bandages with pustules. *Silurian, Wenlock* (*Sheinwoodian, Monograptus riccartonensis* Biozone*–lower Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——Fig. 277,*6a*. *P. praemacilentus,* holotype, NM L2727, Wenlock, lower Homerian, *Cyrtograptus lundgreni* Biozone, Bítov, Czech Republic, scale bar, 1 mm (new).——Fig. 277,*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. 277,*6c*. **P. eiseli* (Manck) lectotype, BAF 8/159, ancora umbrella portion missing, Llandovery, middle Telychian, *Monoclimacis griestoniensis* Biozone, Wetterahammer, Thuringia, Germany, scale bar, 1 mm (new).——Fig. 277,*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, initially widening tubarium; deep, bowl-shaped ancora umbrella with uniform polygonal meshes; prosicula preserved; nema with connecting lists; ventral side outlined by thecal lips, lateral apertural lists, and pleural lists; transverse lists present; thecal orifices with reticulated hoods; ancora sleeve with fairly dense, polygonal meshwork; chimney-like stomata with meshwork walls; ancora sleeve lists with seams facing outward; bandages finely striated. *Silurian, Llandovery* (*upper Telychian, Oktavites spiralis* or *Cyrtograptus lapworthi-C. insectus* Biozone): Arctic Canada.——Fig. 278,*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]. Parallel-sided tubarium; ancora umbrella with six meshes and partially developed rim; ventral walls formed by thecal lips, genicular lists, long mid-ventral lists, pleural lists, and reduced lateral apertural lists or parietal lists; proximal ventral orifices of hexagonal shape; bandages with pustules. *Silurian, Ludlow* (*Ludfordian, Saetograptus leintwardinensis* Biozone): Poland.——Fig. 277,*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), syn. by Kozłowska-Dawidziuk, 2002, p. 459]. Tubarium parallel sided or narrowing distally; shallow ancora umbrella with five meshes and only partially developed rim; nema free, may bear a nematularium; large proximal lateral orifices of tubarium width;

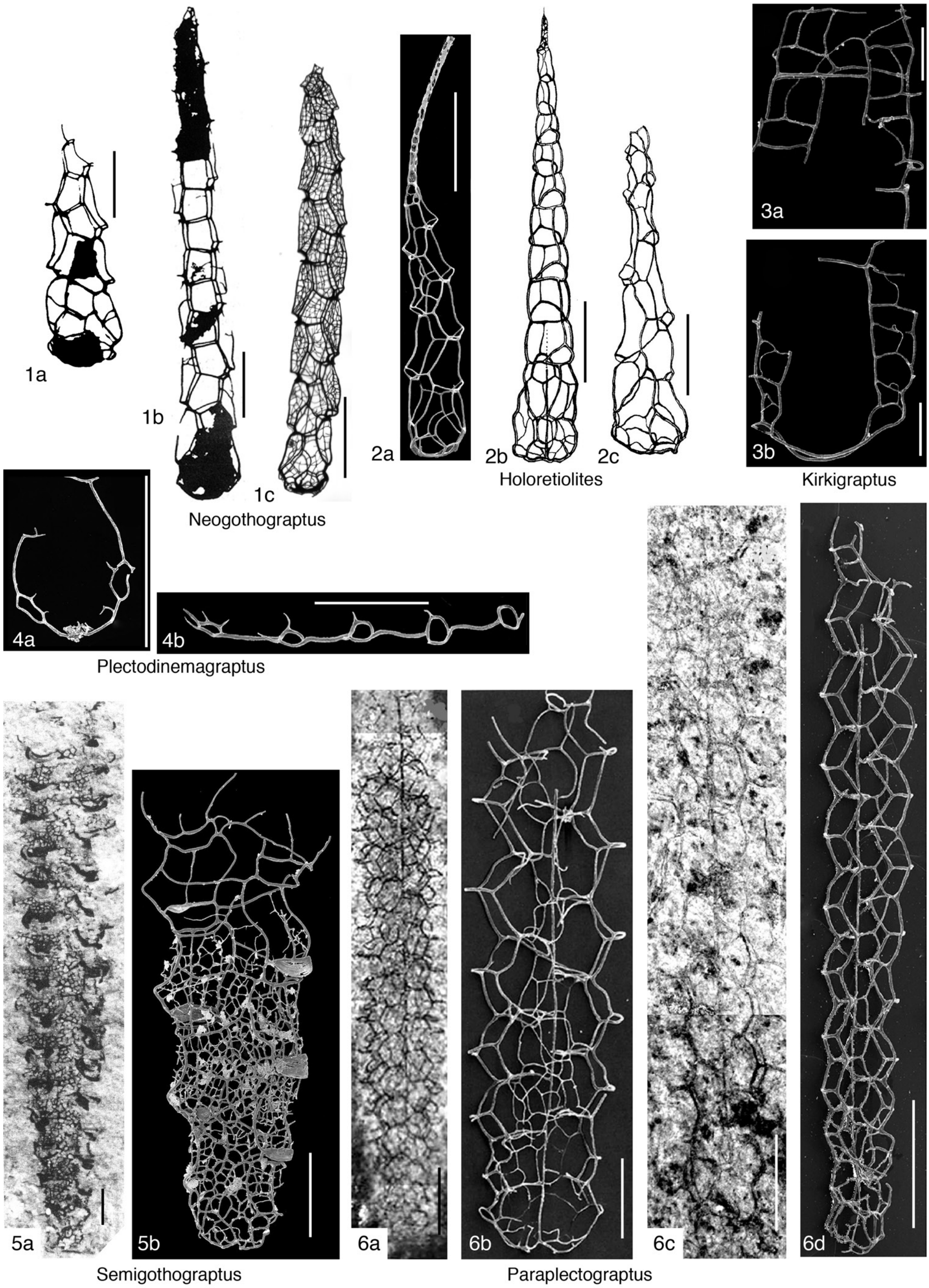


FIG. 277. Retiolitidae (Retiolitinae) (p. 406–413).

ventral sides formed by thecal lips, genicular lists, lateral apertural, lists pleural lists, and mid-ventral lists; single or paired genicular processes in some species; reticulum well developed to absent; zigzag parietal list lists; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni–Lobograptus scanicus* Biozone): worldwide.——Fig. 279,*1a–b*. **P. macilentus* (Törnquist); neotype, SMF XXIV 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. 279,*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, 1948a, p. 22 [**Retiolites perlatus obesus* Lapworth, 1877, p. 137; OD] [=?*Sinostomatograptus* Huo, 1957 (type, *S. mui,* OD), syn. by Lenz & Kozłowska, 2007, p. 492]. Tubarium widening distally; ancora umbrella with polygonal meshes; nema with connecting lists; no virga; thecal orifices with paired apertural spines; ventral sides defined by thecal lips and pleural lists; reticular lists on ancora sleeve irregular; narrow, but deep external common canal with large stomata; inner and outer reticula of ancora sleeve present; ancora sleeve lists with seams facing outward; bandages finely striated. *Silurian, Llandovery* (*Aeronian, Stimulograptus sedgwickii* Biozone)–*Wenlock* (*Sheinwoodian, Monograptus riccartonensis* Biozone): worldwide.——Fig. 278,*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, 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), syn. by Loydell, 1993, p. 61]. Robust, distally widening, parallel-sided or ovate tubarium; prosicula preserved; deep, spiraled ancora umbrella; nema with connecting lists; thecal lists on reverse side with zigzag; ventral sides defined by looping thecal lips and curved pleural lists; mid-ventral lists with distinct ventral zigzag structure distally; ancora sleeve with dense, irregular meshwork; small lateral orifices present proximally; stomata present in some species; ancora sleeve lists with seams facing outward; bandages finely striated. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone–*Telychian, Cyrtograptus insectus* Biozone): worldwide.——Fig. 278,*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 (English 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]. Robust tubarium; ancora umbrella shallow with incompletely developed rim; nema free; medium size proximal lateral orifices; ventral wall with thecal lips, genicular lists, pleural lists, lateral thecal lists, and mid-ventral lists; paired, reticular genicular processes; ancora sleeve with small lateral and ventral proximal orifices; dense reticulum on ancora sleeve and ventral thecal walls; zigzag parietal list on obverse and reverse sides; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone–*Lobograptus progenitor* Biozone): Czech Republic, Poland.——Fig. 279,*3a–b*. *R. serpaglii; 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]. Minute tubarium with few thecae; nema with connecting lists; sicula represented by prosicular apertural ring; shallow ancora umbrella with four radial ribs and subcircular rim; ancora umbrella rim joined to mid-ventral list of theca $1^2$ by unseamed list; thecae outlined by everted apertural loops, transverse lists, and mid-ventral lists; zigzag list on reverse side extends from prosicular ring; mid-ventral list of theca $1^1$ attached directly to ancora umbrella rim; spines on mid-ventral lists and lateral thecal rims may be present; ancora sleeve not recognized; bandages with coarse parallel striae. *Silurian, Llandovery* (*Telychian, Spirograptus guerichi* Biozone–*Spirograptus turriculatus* Biozone): Sweden, Canada (Arctic).——Fig. 279,*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)

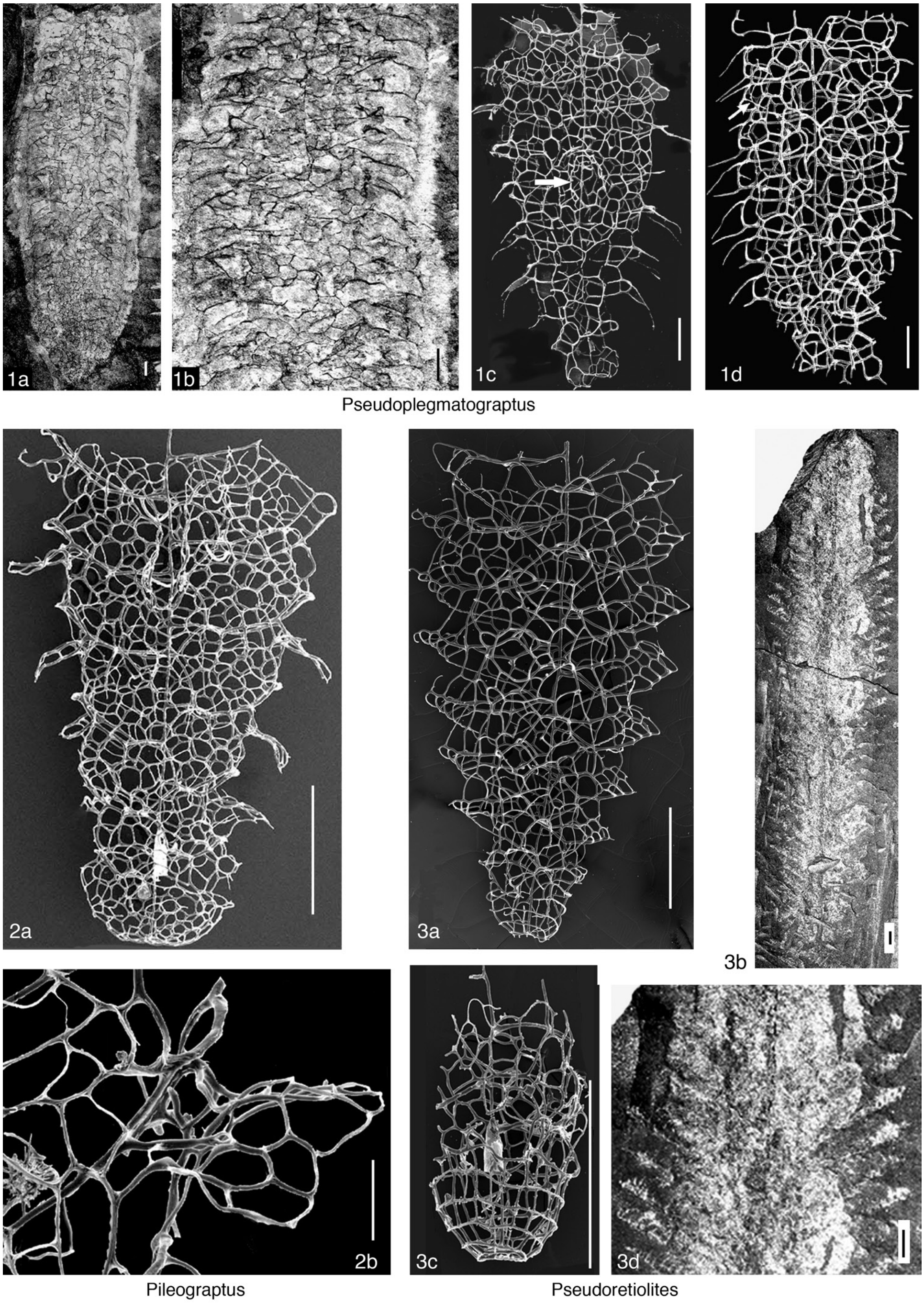


FIG. 278. Retiolitidae (Retiolitinae) (p. 409–411).

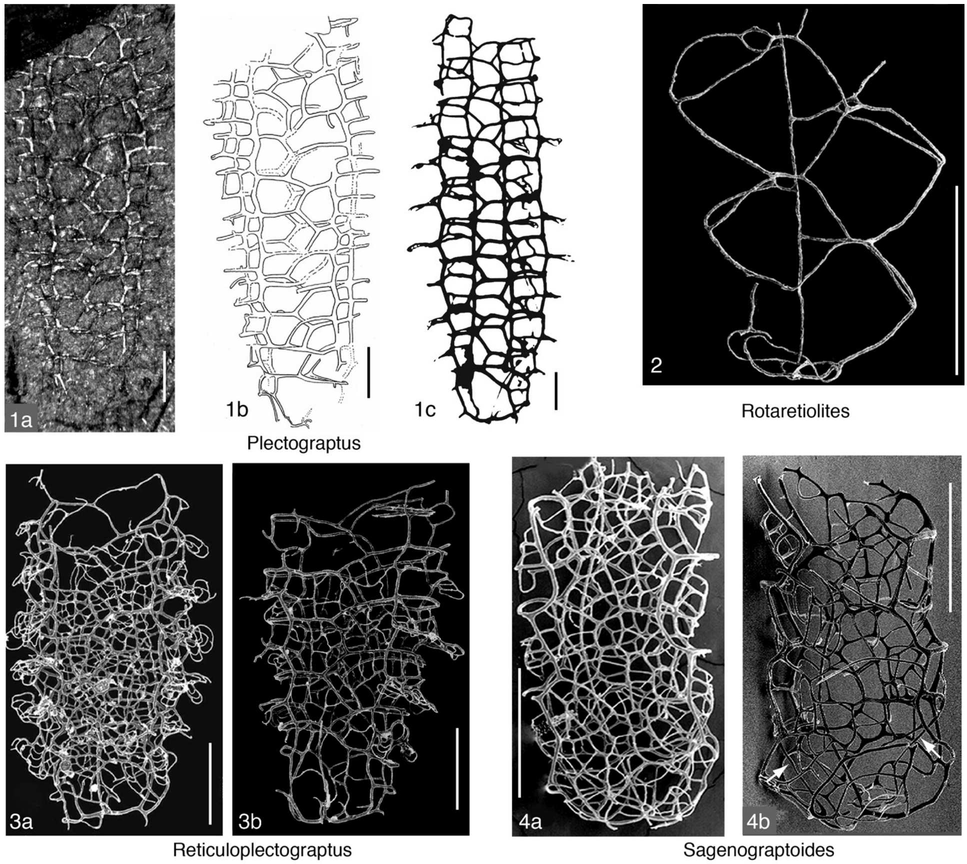


FIG. 279. Retiolitidae (Retiolitinae) (p. 409–413).

[**S. arctos* LENZ & KOZŁOWSKA-DAWIDZIUK, 2001, p. 15; M]. Tubarium parallel sided; ancora umbrella shallow; nema free; proximal lateral orifices kidney-shaped; ventral wall defined by thecal lips, pleural lists, and lateral apertural lists, mid-ventral lists on thecae $1^1$ and $1^2$ attached to ancora umbrella rim; transverse lists in first pairs of thecae; irregular reticulum on ventral thecal walls and ancora sleeve; lists of ventral walls with pustules and seams inside; ancora sleeve lists with seams facing outward; outer ancora sleeve lists with seams facing inward may be present. *Silurian, Wenlock* (*lower Homerian, Cyrtograptus lundgreni* Biozone): Canada (Arctic).——FIG. 279,*4a–b*. **S. arctos; 4a,* holotype, GSC 99179; *4b,* GSC 119775, showing complete mid-ventral lists of th$1^1$ and th$1^2$ (*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 initially widening gradually from proximal end; ancora umbrella asymmetrical with undulating rim; nema free; proximal ventral orifices of triangular shape; lateral orifices kidney-shaped; ventral wall represented by thecal lips, genicular lists, long convex lateral apertural lists, short pleural lists, and mid-ventral lists; massive genicular hoods; parietal lists oblique; reticulum irregular; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone–*Colonograptus deubeli* Biozone): UK, Czech Republic, Germany, Poland.——FIG. 277,*5a–b*. **S. meganassa* (RICKARDS & PALMER); *5a,* SM X28550a, 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; ancora umbrella incompletely known; nema free; ventral wall formed by thecal lips, genicular lists, and mid-ventral lists; proximal ventral orifices and thecal orifices rhomboid; large proximal lateral orifices; zigzag parietal lists start on level of first pair of thecal orifices; no reticulum; ancora sleeve lists with seams facing inward; bandages with pustules.

*Silurian, Ludlow* (*lower Ludfordian, Cucullograptus hemiaversus* Biozone–*Cucullograptus aversus* Biozone): Poland.——Fig. 280,*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 distally; shallow ancora umbrella with four or more meshes and sometimes incompletely developed rim; outer ancora may be present; nema free; ventral wall built of looping thecal lips and vertical pleural lists; proximal lateral orifices of variable shape and size; ancora sleeve with or without irregularly positioned parietal lists; reticulum variable, from dense to lacking, formed irregularly; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Llandovery* (*Telychian, Cyrtograptus lapworthi* Biozone)–*Wenlock* (*lower Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——Fig. 280,*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, 2010b, p. 512 *pro Retiolites münchi* Eisenack, 1951, p. 138, OD), syn. herein]. Tubarium parallel sided or finite, ending with appendix; ancora umbrella shallow with six meshes; outer ancora possible; nema free; kidney-shaped lateral proximal orifices; ventral sides formed of thecal lips, genicular lists, lateral apertural lists, pleural lists; mid-ventral lists absent to well developed; reticulofusellar genicular processes paired, simple to complex, sometime also on ventral prethecal orifices; parietal lists zigzag to irregular; reticulum well developed to absent; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*upper Homerian, Colonograptus praedeubeli/deubeli* Biozone)–*Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone): worldwide.——Fig. 280,*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. 280,*3c*. *S. clathrospinosus* (Eisenack, 1951), GSC 104663, specimen with completely preserved ancora sleeve wall, Arctic Canada, scale bar, 1 mm (Lenz & Kozłowska-Dawidziuk, 2002a, fig. 14).——Fig. 280,*3d–e*. *S. muenchi* (Eisenack, 1951); *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 gradually widening initially; ancora umbrella bowl-shaped, with hexagonal meshwork; prosicula present; nema with connecting lists; transverse lists present; ventral walls defined by thecal lips, strongly inclined lateral apertural lists and pleural lists; pleural lists attached to middle part of outward-inclined lateral apertural lists; ancora sleeve well developed, with polygonal meshes; narrow external common canal with stomata; ancora sleeve lists with seams facing outward; bandages finely striated. *Silurian, Llandovery* (*Telychian, Spirograptus turriculatus* Biozone)–*Wenlock* (*lower Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——Fig. 281,*1a–b*. *S. grandis* (Suess); *1a,* neotype, NM L31630 (selected by Štorch, Serpagli, & Barca, 2002, p. 102), 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. 281,*1c*. *S. canadensis* Lenz, 1988c, GSC, Llandovery, *Cyrtograptus sakmaricus* Biozone, Arctic Canada, scale bar, 1 mm (new).——Fig. 281,*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; ancora umbrella with four branches, without developed rim; nema free, with nematularium; large proximal lateral orifices; ventral walls composed of vertical pleural and lateral apertural lists, genicular lists and thecal lips; parietal lists more or less horizontal; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Ludlow* (*Gorstian, Lobograptus progenitor* Biozone): Albania, Czech Republic.——Fig. 281,*2*. **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]. Parallel-sided tubarium; connecting lists link virgella with lateral wall on obverse side; nema free; shallow ancora umbrella with four meshes; ventral wall formed by thecal lips, genicular lists, long lateral apertural lists, and short pleural lists; ancora sleeve with oblique parietal lists on reverse side; reticulum irregularly developed; ancora sleeve lists with seams facing inward; bandages with pustules. *Silurian, Wenlock* (*upper Sheinwoodian, Cyrtograptus ellesae* Biozone): Poland.——Fig. 281,*3*. **V. perrarus,* holotype, ZPAL G.52/1, Wenlock, Bartoszyce IG-1 drill core, Poland, scale bar, 1 mm (Kozłowska, 2015, fig. 2).

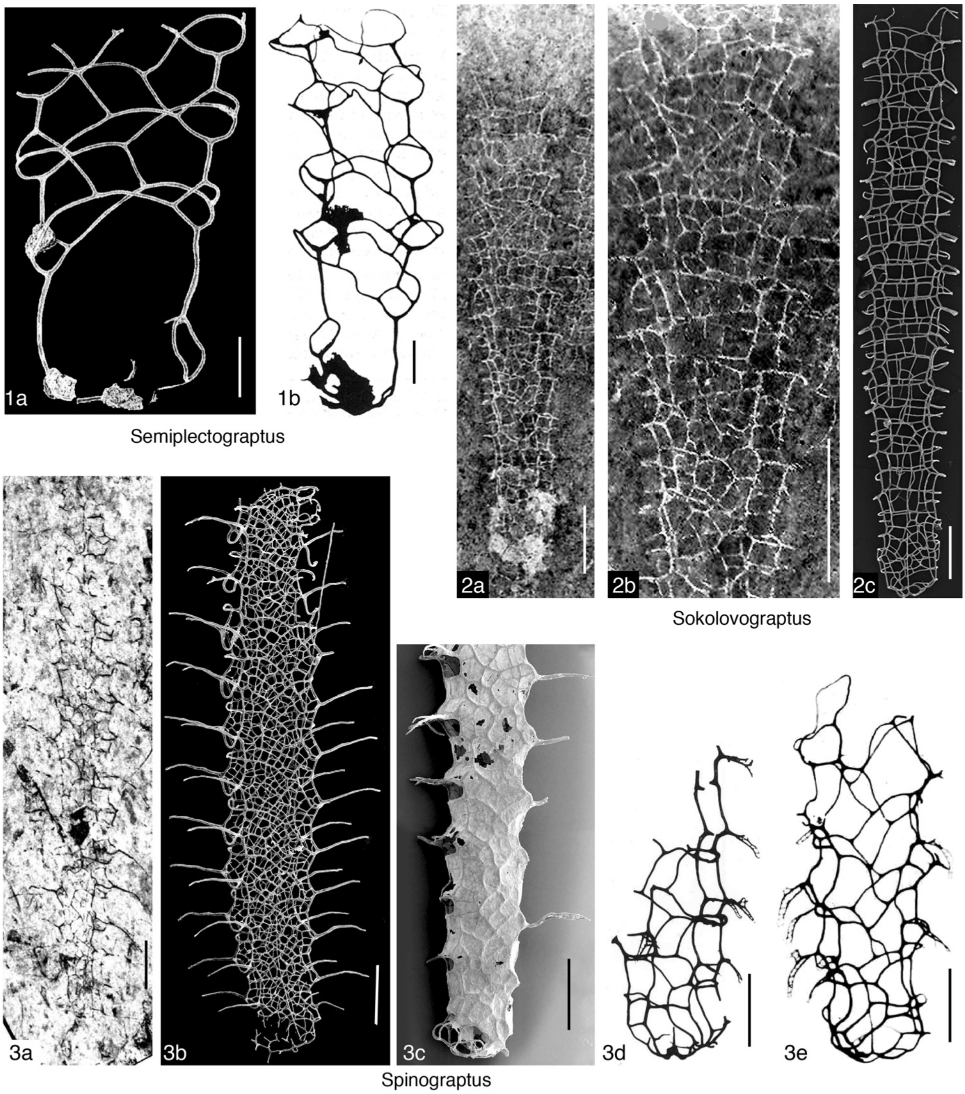


FIG. 280. Retiolitidae (Retiolitinae) (p. 413–414).

## Family UNCERTAIN

A number of genera must 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 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, 1953a, 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,*

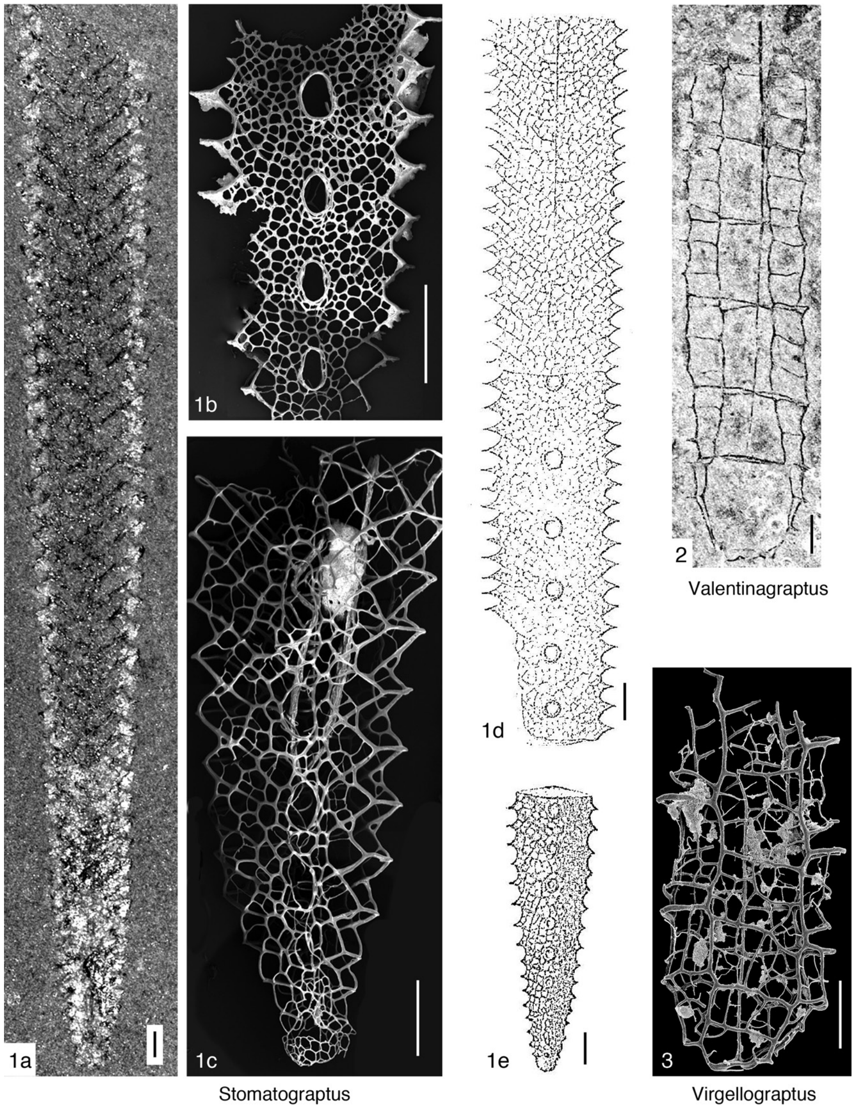


FIG. 281. Retiolitidae (Retiolitinae) (p. 414).

*Lituigraptus convolutus* Biozone): Germany.——FIG. 282,*3*. **D. nindeli*, BAF H4/68/2295, Igelsberg bei Ronneburg, Thuringia, Germany, scale bar, 5 mm (Hundt, 1950, fig. 11).

**Mirorgraptus** LENZ & KOZŁOWSKA, 2007, p. 499 [**M. arcticus;* OD]. Straight nema with some lists similar to connecting lists 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 list, oriented 90°, distally connecting lists 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. 282,*1*. **M. arcticus,* holotype, GSC 38919, oblique view, Silurian, Llandovery, Canada, scale bar, 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 curva-

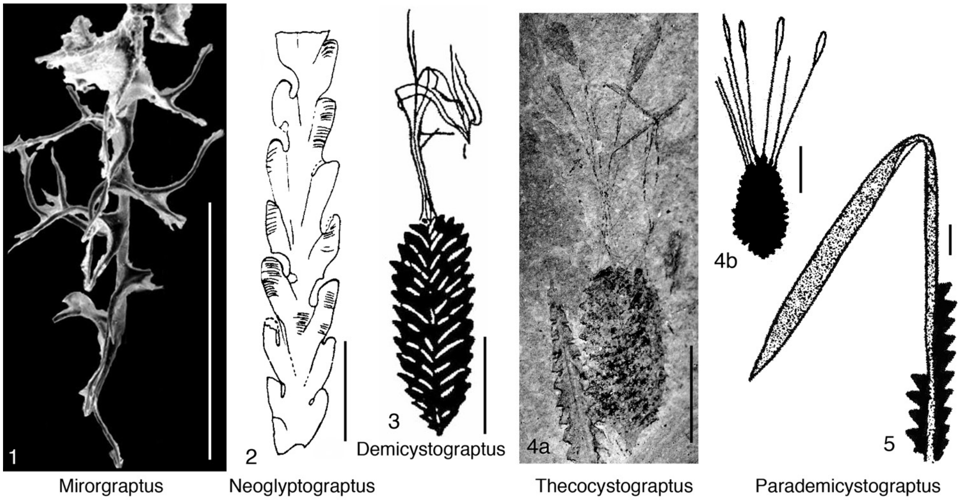


FIG. 282. Retiolitidae *incertae sedis* (p. 415–417).

ture, 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. 282,*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. 282,*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. 282,*4a–b*. **T. polycystus; 4a,* NIGP 170803, Dingjiapo, Hubei Province, China; *4b,* holotype, BAF 186/4707, Wachtelberg/Frankenberg, Thuringia, Germany, scale bars, 5 mm (Hundt, 1950, fig. 14).

# SUPERFAMILY MONOGRAPTOIDEA

JÖRG MALETZ

## Superfamily MONOGRAPTOIDEA Lapworth, 1873

[Monograptoidea LAPWORTH, 1873b, table 1, facing p. 555, *nom. correct.* MELCHIN & others, 2011, p. 294, *pro* Monograptidae LAPWORTH, 1873b] [incl. suborder Monograptina LAPWORTH, 1880f, p. 191, *nom. correct.* OBUT, 1957, p. 18, *pro* Monograpta (Monoprionida) LAPWORTH, 1880f, p. 191]

Biserial to uni-biserial and uniserial graptoloids with pattern J or derived pattern astogenies (patterns J, M, N); colony shape and thecal style highly variable; cladial branching and secondarily multiramous colonies common in taxa with pattern M astogeny. *Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone)–*Lower Devonian* (*Pragian, Uncinatograptus yukonensis* Biozone): worldwide.

MELCHIN (1998, Table 1) referred the families Dimorphograptidae and Monograptidae to the Diplograptoidea and did not differentiate the Monograptoidea, following MITCHELL (1987), who regarded the Monograptinae as a subfamily of the Monograptidae (see Neograptina in MELCHIN & others, 2011).

FORTEY, ZHANG, and MELLISH (2005, p. 1255) introduced the name Monograptoidea but did not discuss the concept. MELCHIN and others (2011, p. 294) defined the Monograptoidea as "the most recent common ancestor of *Avitograptus avitus* and *Monograptus priodon* and all of its descendants" and referred to node 1 in their figures 2 and 3 (2011, p. 284, 286), thus defining the taxon by reference to a cladistic diagram (see Fig. 283). The analysis of MELCHIN and others (2011, fig. 7) showed the Monograptoidea as a monophyletic clade with possible ancestral relationships to the genera *Normalograptus* LEGRAND, 1987 and *Avitograptus* MELCHIN & others, 2011, as an intermediate step to the akidograptids (*Akidograptus* and *Parakidograptus*). The authors recognized the families Dimorphograptidae and Monograptidae as members of the Monograptoidea.

### Family DIMORPHOGRAPTIDAE Elles & Wood, 1908

[Dimorphograptidae ELLES & WOOD, 1908, p. 347] [=Heteroprionidae TULLBERG, 1883, p. 14] [incl. Akidograptinae LI & GE, 1981, p. 227]

Biserial and uni-biserial axonophoran graptoloids with a pattern J astogeny or a derived one; th$1^2$ absent in derived taxa with proximally uniserial tubarium; length of uniserial portion variable; colonies commonly septate with straight median septum, but median septum may be delayed; sicula may bear an ancora. *Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone)–*Silurian* (*Llandovery, Rhuddanian, Coronograptus cyphus* Biozone): China, Russia, Australia (Victoria), Belgium, UK, Denmark, Sweden, Norway, Spain, Canada, USA, Argentina.

ELLES and WOOD (1908) originally defined the Dimorphograptidae as uni-biserial graptolites with a uniserial proximal portion and a biserial distal colony portion, following the original concept of TULLBERG's (1883) Heteroprionidae. ELLES and WOOD (1908, p. 348) suggested the name change with the only argument being "to bring it into harmony with the names of the other families of the Graptoloidea." The change has been universally accepted, and the term Heteroprionidae is no longer used. LI (1987) discussed a possible independent origin of several lineages of dimorphograptids but did not include details of the proximal development. The idea was supported by the cladistic analysis of MELCHIN and others (2011), which included the presence of uni-biserial genera in more than one place in their cladistic interpretation. A uni-biserial development exists independently

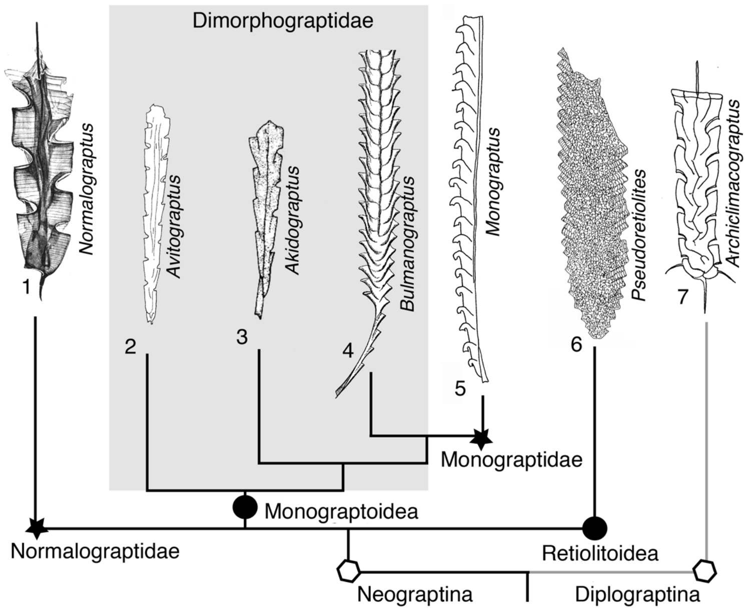


FIG. 283. Diagram showing the concept of the Dimorphograptidae (in gray box), following MELCHIN and others (2011). Specimen examples include: *1, Normalograptus brevis* (ELLES & WOOD, 1906); *2, Avitograptus avitus* (DAVIES, 1929); *3, Akidograptus ascensus* (DAVIES, 1929); *4, Bulmanograptus swanstoni* (LAPWORTH, 1876d); *5, Monograptus priodon* (BRONN, 1835); *6, Pseudoretiolites perlatus* (NICHOLSON, 1868a); *7, Archiclimacograptus* sp. (new, diagram adapted from data in Melchin & others 2011, fig. 2; graptolite specimens from various sources, not to scale).

in *Agetograptus* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968; *Dimorphograptoides* KOREN' & RICKARDS, 1996; and *Rhaphidograptus* BULMAN, 1936b.

ŠTORCH and SERPAGLI (1993) emended the Akidograptinae, originally referred to the Orthograptidae (see LI & GE, 1981), and included the subfamilies Dimorphograptinae and Akidograptinae in the Dimorphograptidae. They changed the original concept of the Dimorphograptidae of TULLBERG (1883) considerably by including normal biserial taxa. KOREN' and RICKARDS (1996) elevated the Akidograptinae to family rank and kept the Dimorphograptidae and Akidograptidae as separate families. MELCHIN (1998, p. 301) provided a detailed diagnosis of the Dimorphograptidae. He indicated a pattern J astogeny with uni-biserial or fully biserial tubarium, a long, fully exposed sicula, variable thecal form, and a fully or partly septate tubarium. MELCHIN and others (2011, p. 295) defined the Dimorphograptidae as the "partial clade that includes the common ancestor of *Avitograptus avitus* and *Monograptus priodon* and all of its descendents, including *Dimorphograptus elongatus* but excluding those taxa included in the family Monograptidae (i.e., excluding the uniserial monograptids)." The taxon is a paraphyletic clade at the base of the traditional monograptids, the Monograptidae *s. str.* (see Fig. 283).

## MORPHOLOGY

The Dimorphograptidae, as defined by MELCHIN and others (2011), include fully biserial to uni-biserial taxa with a variety of thecal shapes, thus differing considerably from the original concept of TULLBERG (1883), who included only taxa with a uniserial proximal end and a biserial distal end but did not consider the importance of details of the thecal construction. The phylogenetic relationships of many taxa are difficult to establish, and the morphological variation of these is extreme.

The colonies of most Dimorphograptidae are slightly dorsally curved at the proximal

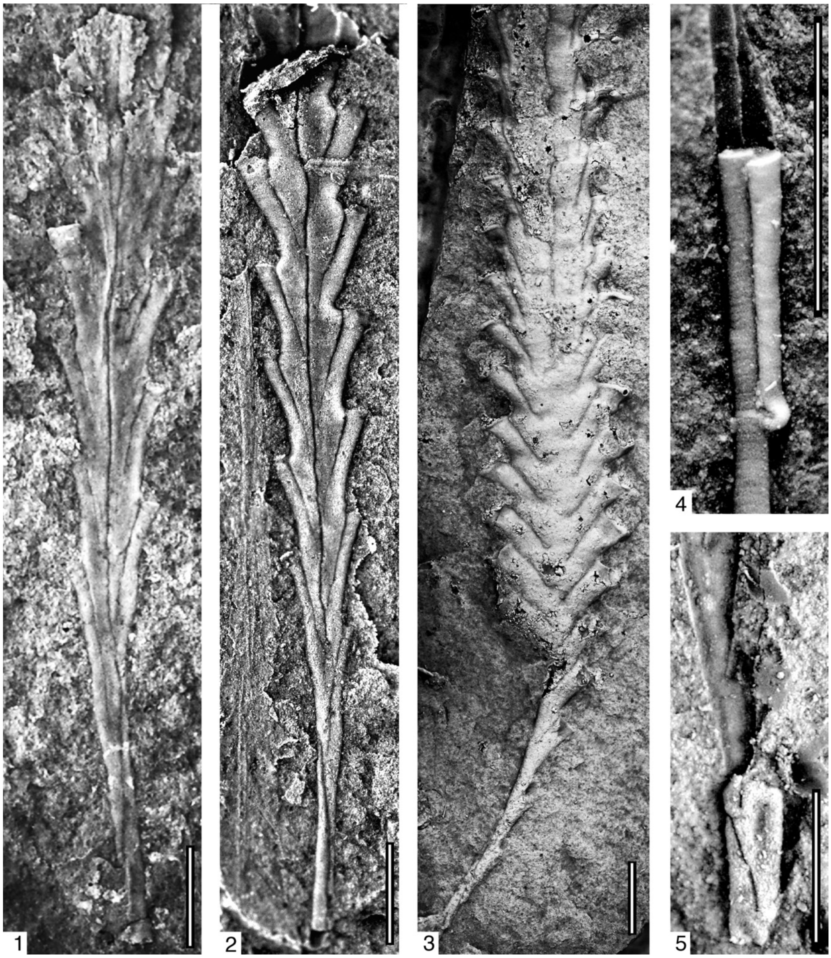


FIG. 284. *1–2, Parakidograptus acuminatus* (NICHOLSON, 1867a); *1,* LO 1283t, obverse view, low relief, latex cast, Tomarp, Scania (new); *2*, LO 1284t, reverse view, low relief, latex cast, Tomarp, Scania (new); *3, Bulmanograptus swanstoni* (LAPWORTH, 1876d), LO 476t, reverse view, latex cast, showing delay of median septum on reverse side, Bollerup, Scania (new); *4, Huttagraptus acinaces* (TÖRNQUIST, 1899), LO 11856t, specimen showing origin and initial growth of th1, Röstånga drill core, Scania (Maletz, Ahlberg, & others, 2014, fig. 1F); *5, Dimorphograptus* sp., reverse view, Röstånga drill core, 33.55–33.62 m (new). Scale bars, 1 mm in all photos.

end, at least in the uniserial part of derived taxa, but this tendency is also present in *Akidograptus* and *Parakidograptus*. The two genera have colonies with strongly protracted proximal ends and long, slender thecae, either with a distinct geniculum and slightly outward-inclined, supragenicular thecal walls or with outward-inclined, ventral thecal walls and without a geniculum (Fig. 284.1–284.2). The thecal overlap is relatively high and the interthecal septa start slightly below the aperture of the previous theca. The straight median septum is complete on the obverse side but slightly delayed on the reverse side, indicating that $th2^1$ is the dicalycal theca.

### Proximal Development

A pattern J or derived pattern J (J′) astogeny is generally assumed for the Dimorphograptidae (MELCHIN & MITCHELL, 1991; MELCHIN, 1998; MELCHIN & others, 2011), but these patterns are unknown from isolated material. Pattern J astogeny (Fig. 285.1) is supposed to have a very short downward-growing part of $th1^1$ and a normal biserial development with a distal origin of $th1^2$ on the upward-growing part of $th1^1$ (see pattern H′ astogeny, MELCHIN, 1998, fig. 4B). A pattern H and H′ have two foramina at the base of the downward-growing part of $th1^1$, but in pattern J, $th1^1$ grows directly upward onto itself, and the foramina are lacking (MELCHIN, 1998, fig. 2). In pattern J′ astogeny (Fig. 285.2), the proximal end is uniserial with a variable number of thecae in the uniserial part of the tubarium, and the growth direction of $th1^2$ is supposedly redirected above the first theca (see MELCHIN & others, 2011, p. 289).

The cladistic implications indicate that *Avitograptus* may be positioned at the base of the Dimorphograptidae and Monograptidae (MELCHIN & others, 2011, fig. 2). Thus, the interpretation of the proximal development of the genus *Avitograptus* is vital for the understanding of the origin of the group. This development is uncertain (MELCHIN & others, 2011, p. 295) because there are no isolated specimens available that indicate the presence of foramina at the termination of the downward growth of $th1^1$. A pattern H or I would therefore be an alternative interpretation for *Avitograptus*, not the pattern J astogeny as indicated by MELCHIN and others (2011).

Pattern J astogeny is observed in *Parakidograptus acuminatus* (NICHOLSON, 1867a) (Fig. 284.1–284.2) in partial relief and appears to be very similar to the development of early Monograptidae (see LUKASIK & MELCHIN, 1994, 1997; DAWSON & MELCHIN, 2007), in which the first theca does not grow downward but immediately outward and upward from its origin (Fig. 284.4). BULMAN (1932b) interpreted the development of the closely related *Akidograptus acuminatus* quite differently. He indicated the presence of an initial downward growth of $th1^1$ and the presence of a reduced $th1^2$ in the proximal end. This construction has not been verified from further specimens.

A pattern J′ astogeny of *Dimorphograptus* (Fig. 285.2) with a distinct initial downward growth of the first theca and delay of the dicalycal theca (Fig. 285.3) was suggested in an illustration in KOREN’ and RICKARDS, 1996 (fig. 22*j*) but is not known from relief specimens.

### Delay and Development of $th1^2$

The earliest members of the Dimorphograptidae can be described as simple biserial axonophoran graptolites with an indeterminate proximal end. However, the name *Dimorphograptus* is generally related to taxa with a uniserial proximal end and a biserial distal end in which the uniserial proximal end is formed through the redirection of $th1^2$ (pattern J′ astogeny). The length of the uniserial proximal end can range from one to numerous thecae and appears to be constant in length within each species. The delay of $th1^2$ development, the “dimorphograptid condition” of MELCHIN (1998, p. 278) may have developed at least four times in the evolution of Silurian axonophorans according to RICKARDS, HUTT, and BERRY (1977) and LI (1987), whereas MITCHELL (1987) thought this pattern arose only once. However, in the absence of isolated material for most taxa, this suggestion has not been verified.

MELCHIN and others (2011) recognized the origin of the aseptate genus *Agetograptus* with a delayed $th1^2$ as being independent from *Rivagraptus* KOREN’ & RICKARDS, 1996 and suggested these genera were derived from a *Glyptograptus*-type ancestor (MELCHIN & others, 2011, fig. 7). These authors did not include the genus *Dimorphograptoides* in the analysis but thought that it might be closely related to *Pseudorthograptus obuti* (RICKARDS & KOREN’, 1974), which has similar development, thereby suggesting another independent origin of an uni-biserial colony development. The proximal end illustrated by BULMAN (1970, fig. 61), thought to show the development of *Dimorphograptus,* was re-identified as representing a specimen of *Agetograptus* (Melchin, 1998, p. 274).

### Median Septum

The genera *Akidograptus* and *Parakidograptus* appear to have a complete median septum on the obverse side and a slight delay on the reverse side, indicating a dicalycal theca th2[1] (Fig. 285.1). The median septum is straight or nearly straight, as is visible from its trace on the lateral tubarium wall. A relief specimen of *Bulmanograptus confertus* (Nicholson, 1868a) from the Röstånga drill core has a complete median septum on the obverse side (Fig. 286.4). A single relief specimen of *Bulmanograptus swanstoni* (Lapworth, 1876d) (Fig. 284.3) has four thecae in the uniserial proximal end, followed by eight pairs of alternating thecae before the median septum starts on the reverse side. However, for most taxa referred to the Dimorphograptidae, the development of the median septum has not been described and considerable variation may be expected.

### Thecal Style

The thecal style of the Dimorphograptidae varies between distinctly geniculate thecae with outwardly inclined, supragenicular, ventral thecal walls, to thecae with straight, outwardly inclined, ventral thecal walls. Details of the thecal development are not documented for most taxa. Genicular flanges appear to be absent or at least not visible in flattened specimens. The thecal apertures are straight and range from outwardly inclined to perpendicular to the length of the colony. In *Bulmanograptus confertus* and related taxa, the thecal apertures appear slightly convex and bear a distinct apertural thickening. Fragments in ventral preservation show a distinct lateral widening of the thecal apertures associated with the thickened rims and the possible presence of paired apertural spines that are not visible in laterally preserved specimens (Fig. 286.2).

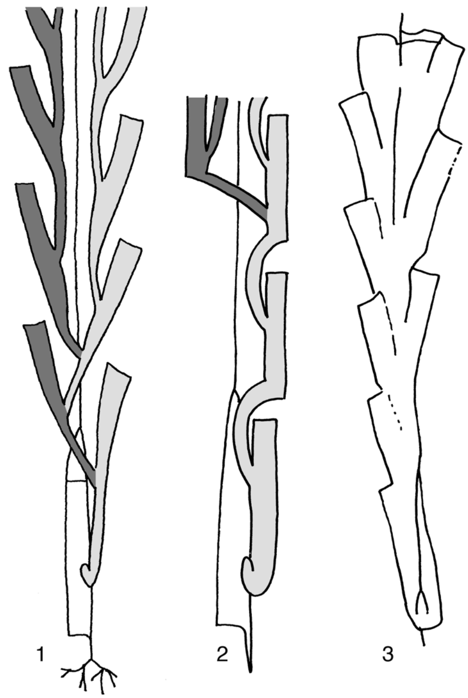


Fig. 285. Proximal development. *1*, *Parakidograptus*, pattern J astogeny (adapted from Štorch & Serpagli, 1993, fig. 4); *2*, *Dimorphograptus,* pattern J′ astogeny, (adapted from Melchin, 1998, fig. 8); *3*, *Dimorphograptus erectus*, showing initial downward growth of th1 in obverse view (adapted from Koren' & Rickards, 1996, fig. 22*j*).

### The Ancora

Specimens of *Akidograptus ascensus* Davies, 1929 and *Parakidograptus acuminatus* typically have a distal branching of the virgella (Stein, 1965; Koren' & Rickards, 1996; Štorch & Feist, 2008) reminiscent of the ancora umbrella of the Retiolitidae. This construction is best seen in juvenile specimens and is not preserved in most mature material. The construction, similar to that of the ancora of the Retiolitidae, is formed from a short virgellar spine that branches into two bars. At least two further dichotomous branching points may occur in the ancora of *Akidograptus ascensus* (Fig. 285.1; Fig. 286.1). A branched virgellar spine is also documented for a single specimen of *Avitograptus*

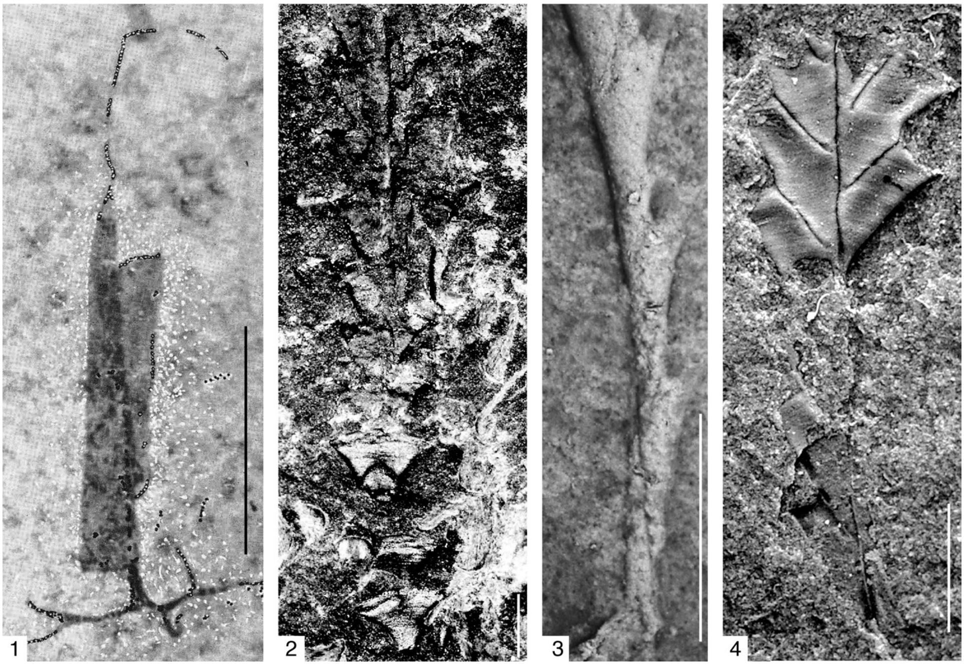


FIG. 286. *1*, *Akidograptus ascensus* (DAVIES, 1929), juvenile specimen showing ancora, Göttingen, 506-48 (Stein, 1965, pl. 15*B*); *2*, *Bulmanograptus* sp., fragment, ventral view, Röstånga drillcore, Scania, 36.40–36.30 m (new); *3*, *Bulmanograptus swanstoni* (LAPWORTH, 1876d), LO 476t, counterpart, latex cast showing origin of th1 (new); *4*, *Bulmanograptus confertus* (NICHOLSON, 1868a), Röstånga drillcore, Scania, 38.80–38.70 m, obverse view of distal end with complete median septum, proximal end preserved as a mold (new). Scale bars, 1 mm.

sp. cf. *Avitograptus avitus* (MELCHIN & others, 2011, fig. 6c) and was shown by STEIN (1965) in *Avitograptus avitus*.

**Dimorphograptus** LAPWORTH, 1876, p. 545 [**D. elongatus* LAPWORTH, 1876, p. 547; SD BASSLER, 1915a, p. 441] [=*Metadimorphograptus* PŘÍBYL, 1948b, p. 39 (Czech text), p. 47 (English text) (type, *D. extenuatus* ELLES & WOOD, 1908, p. 358, OD, herein)]. Straight to proximally curved dimorphograptid with long uniserial part; thecae with distinct geniculum and small, slit-like apertures; proximal development pattern probably of pattern J´ astogeny; biserial portion probably fully septate. *Silurian*, *Llandovery* (*Rhuddanian, upper Cystograptus vesiculosus* Biozone): Morocco, China, ?New Zealand, UK, France, Germany, Denmark, Sweden, Serbia, Canada (Arctic).——FIG. 288,*1a–b*. *D. extenuatus* ELLES & WOOD, 1908; *1a,* lectotype (selected by HUTT, 1974c, p. 55), UM K736 (Elles & Wood, 1908, pl. 35,*10a*); *1b,* SM A20814, proximal end showing sicula (Příbyl, 1948, fig. 4). Scale bars, 1 mm.——FIG. 288,*1c–e*. **D. elongatus; 1c,* BU 1423, curved specimen (Bulman, 1970, fig. 97,*2B*); *1d,* lectotype, BU 1423, straight specimen (Elles & Wood, 1908, pl. 35,*11a*); *1e,* curved specimen, Bornholm, Denmark, (Koren' & Bjerreskov, 1997, fig. 17*B*). Scale bars, 1 mm.

**Akidograptus** DAVIES, 1929, p. 9 [**A. ascensus;* OD] [=*Acidograptus* DAVIES, 1929 (misspelling in BULMAN, 1929, p. 172)]. Biserial monograptoid with protracted proximal end and early upward growth of first two thecae; proximal end probably with pattern J astogeny; thecae slender and elongated, strongly geniculate, with straight apertures lacking genicular flanges. *Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus* Biozone–*Atavograptus atavus* Biozone): China, UK, Germany, Denmark, Norway, Sweden, Canada (Arctic), USA.——FIG. 287,*2a–b*. **A. ascensus; 2a,* holotype, SM A10021 (adapted from Melchin & others, 2011, fig. 6*G*); *2b,* holotype (adapted from Rigby, 2000). Scale bars, 1 mm.

**Avitograptus** MELCHIN & others, 2011, p. 295 [**Glyptograptus* (?) *avitus* DAVIES, 1929, p. 8, fig. 21; OD]. Biserial monograptoid with slender proximal end and possibly pattern J astogeny; $th1^1$ upturned at level of sicular aperture; $th1^2$ arises from point low within upward-grown portion of $th1^1$; thecae geniculate, slightly to moderately inclined; first

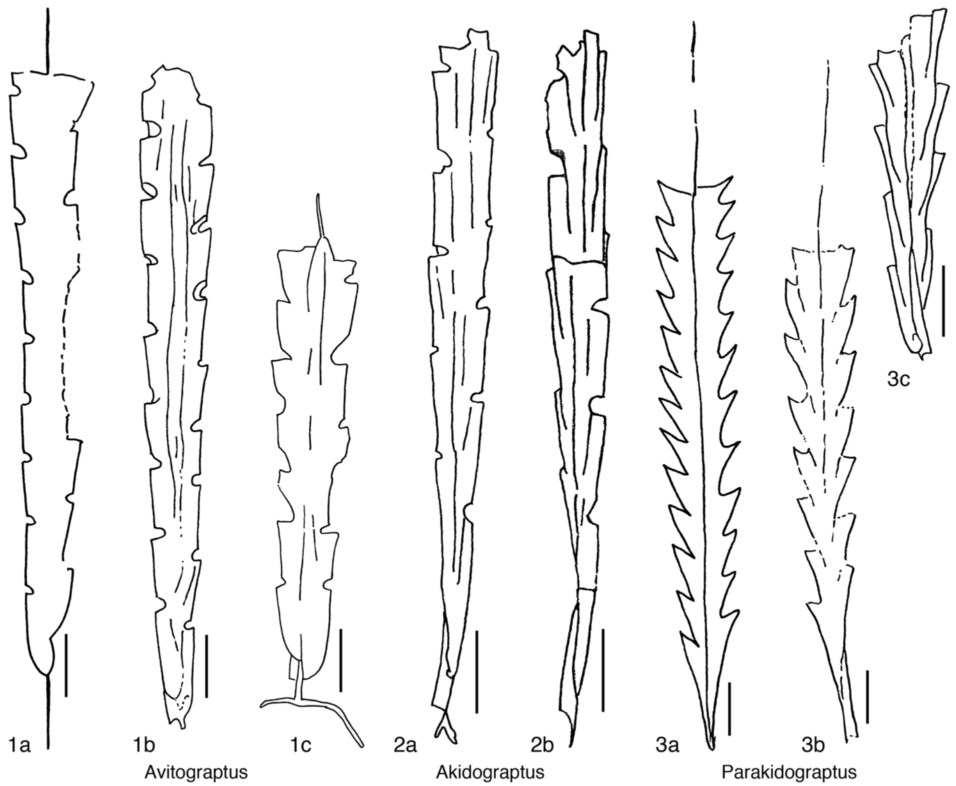


Fig. 287. Dimorphograptidae (p. 424–426).

thecal pair slightly elongated relative to subsequent thecae; complete median septum. *Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone)–*Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus* Biozone): UK, Germany, Canada (Arctic).——Fig. 287,*1a–b*. **A. avitus* (Davies); *1a,* holotype, SM A10019 (adapted from Davies, 1929, fig. 21); *1b,* topotype, GLAHM 131711 (adapted from Melchin & others, 2011, fig. 6*B*). Scale bars, 1 mm.——Fig. 287,*1c*. *Avitograptus* sp. aff. *A. avitus,* GLAHM 131712, showing branched virgella, scale bar, 1 mm (adapted from Melchin & others, 2011, fig. 6C).

**Bulmanograptus** Přibyl, 1948b, p. 39 (Czech text), p. 47 (English text)[**Diplograpsus confertus* Nicholson, 1868a, p. 526; OD] [=*Cardograptus* Hundt, 1965, p. 117 (type, *C. primus,* M, =*Cardograptus elongatus* Hundt, 1959, p. 19, *nom. nud.,* herein), syn. herein]. Robust dimorphograptid with slender, often curved, uniserial proximal end of variable length; thecae proximally slender, with high inclination and straight ventral sides in biserial part; biserial part with or without median septum; thecae typically with considerably thickened apertural rim. *Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus* Biozone–*Atavograptus atavus* Biozone): Morocco, China, Russia, UK, Czech Republic, Germany, Poland, Denmark, Sweden, Serbia, USA (Alaska), Canada (Arctic).——Fig. 288,*2a–b*. **B. confertus* (Nicholson); *2a,* SM A20699, typical specimen (Elles & Wood, 1908, pl. 35,*3a*); *2b,* BU 1368, proximal end (Elles & Wood, 1908, fig. 227a), Scale bars, 1 mm.——Fig. 288,*2c*. *B. primus* (Hundt, 1965), holotype, BAF 186/1715, scale bar, 1 mm (new).

**Parakidograptus** Li & Ge, 1981, p. 229 [**Diplograpsus acuminatus* Nicholson, 1867a, p. 109; OD]. Biserial monograptoid with protracted proximal end and early upward growth of first two thecae; proximal end probably with pattern J astogeny; thecae slender and elongated, tubular, with straight, outward-inclined apertures; median septum complete. *Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone)–*Silurian, Llandovery* (*Rhuddanian, Atavograptus atavus* Biozone): China, Australia (Victoria), UK, Czech Republic, Germany, Poland, Denmark, Sweden, Spain, Canada, USA.——Fig. 287,*3a–b*. **P. acuminatus* (Nicholson); *3a,*

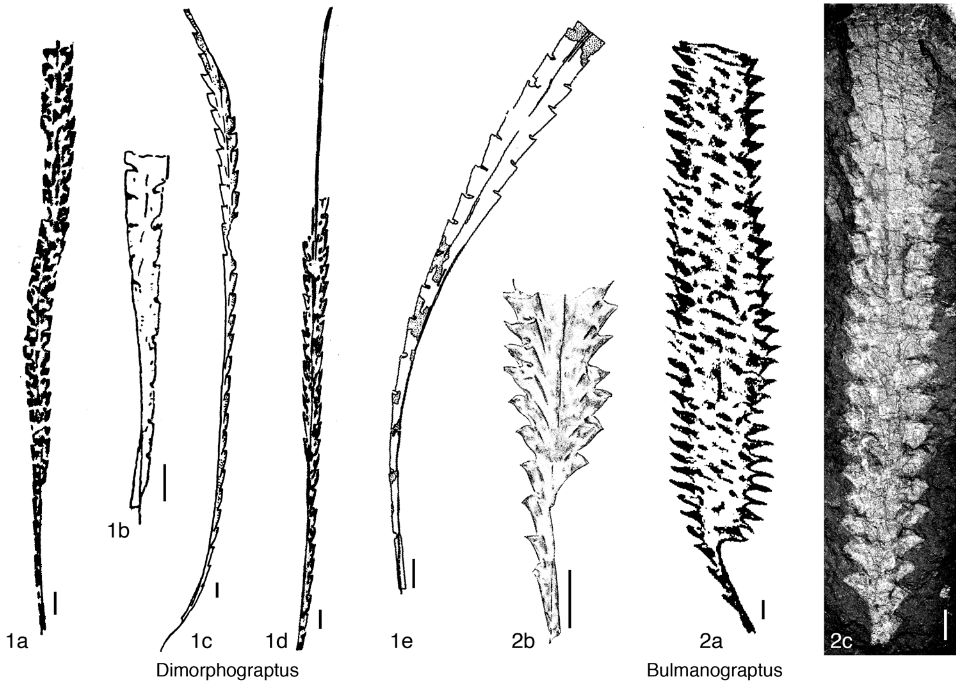


FIG. 288. Dimorphograptidae (p. 424–425).

?NHMUK PM 1310 (adapted from Nicholson, 1867a, fig. 16a); *3b,* SM A20672, small specimen (adapted from Elles & Wood, 1908, fig. 199). Scale bars, 1 mm.——Fig. 287,*3c. P. acuminatus praematurus* (DAVIES, 1929), holotype, SM A10023, specimen showing obverse view and possible downward initial growth of th1, scale bar, 1 mm (adapted from Zalasiewicz, 2008c, Atlas, Folio 2.71).

# FAMILY MONOGRAPTIDAE

Jörg Maletz and David K. Loydell

## AUTHOR CONTRIBUTIONS

David K. Loydell wrote the majority of the generic descriptions and provided almost all of the information regarding type species and their stratigraphical and geographic ranges. Jörg Maletz is responsible for the remainder, including illustrations, suprageneric classification, discussions and descriptions of terminology, family, and subfamily level subdivisions.

## TERMINOLOGY AND TAXONOMIC NOTE

Mitchell and others (2013) suggested use of the term tubarium (Lankester, 1884), initially used exclusively for extant Pterobranchia, for the housing construction of all Pterobranchia including fossil and extant taxa and suggested replacing the term rhabdosome previously used for the graptolites. Not all researchers have accepted this replacement and several (e.g. Štorch, Roqué Bernal, & Gutiérrez-Marco, 2019; Loydell, 2020), including one of the authors of this chapter, much prefer to use the term rhabdosome. The term tubarium is used herein for consistency with other chapters in the *Treatise*.

One remaining problem for the taxonomy and understanding of the Monograptidae is the old and much used genus *Monograptus sensu lato*. Geinitz (1852) used the genus *Monograptus* to include all single-stiped Silurian to Early Devonian graptoloids. Lapworth (1873b) separated the genus *Rastrites* Barrande, 1850, based on its isolated thecae, and the genus *Cyrtograptus* Carruthers in Murchison, 1867a with its compound tubarium. Numerous monograptid species have been included in *Monograptus* over the years due to a lack of understanding of their constructional details and evolutionary relationships. Even though more than 100 genera are now described to subdivide the original genus *Monograptus,* many species are still included in the form genus *Monograptus sensu lato* or '*Monograptus*' (e.g., Bulman, 1970; Koren', 1983; Štorch & others, 2018) as their differentiation is uncertain. Lenz (2013, p. 1101) still employed the genus *Monograptus* as a "form genus for those whose thecae are not fully understood" and included within it a number of Early Devonian taxa. Thus, numerous not necessarily closely related monograptid species have been and continue to be included under this umbrella name. These taxa are not included in the overview or classification herein.

### Family MONOGRAPTIDAE Lapworth, 1873

[Monograptidae Lapworth, 1873b, table 1, facing p. 555] [=Pristiograptidae Gürich, 1908, p. 32; =Rastritidae Gürich, 1908, p. 35; =Cyrtograptidae Averianow, 1929, p. 103; =Demirastritidae Hundt, 1943, p. 263; =Diversograptidae Hundt, 1943, p. 263; =Dibranchiograptidae Hundt, 1949a, p. 20; =Gangliograptidae Hundt, 1949a, p. 21; =Linograptidae Obut, 1957, p. 18; =Wolynograptidae Tsegelnjuk, 1976, p. 110; =Tirassograptidae Tsegelnjuk, 1976, p. 118]

Uniserial Neograptina with and without cladia; thecal apertures on main or primary stipe oriented in opposite direction to sicular aperture. *Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus*/*Parakidograptus acuminatus* Biozone)–*Lower Devonian* (*Emsian, Uncinatograptus yukonensis* Biozone): worldwide.

Monograptidae is regarded as a monophyletic clade (Melchin & others, 2011) forming the Monograptoidea with the paraphyletic stem group, the Dimorphograptidae. Melchin and others (2011) indicated that the loss of the dicalycal theca and the loss of any downward growth of the first theca are the defining synapomorphies of the clade. However, they indicated that a number of biserial Neograptina lack a dicalycal theca; thus, this character may be a plesiomorphic character or was derived independently more than once.

Přibyl (1946) introduced a number of subfamilies, most of them including a single genus, but this was before many monograptid genera were established. Urbanek (1958, p. 6) discussed Přibyl's (1946) approach as a "purely pragmatic rather than a theoretically evidenced taxonomy" and regarded it as a starting point for further discussion. A number of additional family and subfamily groups were introduced subsequently to the monograptid classification and are discussed herein as appropriate in the text. Some of these taxonomic units are used herein as a guide to differentiate particular groups within the Monograptidae. These may or may not represent monophyletic taxa and details are provided where available. Bulman (1955, 1970) did not acknowledge these suprageneric taxa in the previous versions of the *Treatise* and ignored any subdivisions of the Monograptidae, except for the acceptance of the Cyrtograptidae for taxa with cladial branching. Bulman and Rickards (1970), in an addendum to Bulman (1970), discussed some of the available monograptid genera but regarded most of them to be of dubious value. They did not mention or discuss any of the previously introduced subfamilies and families. Rickards, Hutt, and Berry (1977) took the same approach and again none of the monograptid subfamilies was mentioned in their discussions.

There is no cladistic analysis available to differentiate phylogenetically meaningful units within the Monograptidae. However, in the light of the high number of genus-level taxa (more than 100 described genera), it seems reasonable to use previously established taxonomic units or clades herein. These names were introduced to separate morphologically distinctive groups based on characters considered to be phylogenetically meaningful by the original authors.

A differentiation into cladia-bearing and non cladia-bearing taxa was introduced by Yin (1937) and Mu (1950b), who referred all cladia-bearing monograptids to the Cyrtograptinae and all other monograptids to the Monograptinae. This division has been maintained in the last two editions of the Graptolite *Treatise* (Bulman, 1955, 1970) and is included in most classification systems (see overview in Rigby, 1986). The few attempts at a cladistic interpretation of monograptids (Muir, 1999; Melchin & Koren', 2001; Lenz & Melchin, 2008) cover only a very limited number of taxa. Muir (1999, abstract) stated that "at present, many genera are polyphyletic," a statement that still may be true and indicates the need for a thorough investigation of monograptid phylogeny.

## MORPHOLOGY

### Sicular Development

All Monograptidae initially grew a single stipe from a sicula of variable (conical) shape and dimensions, and the definition of the family Monograptidae is essentially that of Lapworth (1873b). Little is known about the development of a conus and cauda in the prosicula, even though numerous chemically isolated monograptids have been described. Kraft (1926) discussed the nema prosiculae (cauda) in a species of *Monograptus* (Fig. 289.1) and described the spiral line and the longitudinal rods of the conus (prosicula proper). A cauda has not been mentioned in later descriptions of chemically isolated monograptids. The shape of the sicula ranges from very slender and long (e.g., in *Coronograptus*), short and straight (e.g., in *Streptograptus*), or variably curved (e.g., in *Spirograptus*). Siculae with a broad triangular outline and a considerably widened aperture appear in several groups independently (Fig. 289.5–289.7). These features were initially described from the Wenlock species *Colonograptus deubeli* (Jaeger, 1959) but appear independently in the early Wenlock species *Monograptus riccartonensis* Lapworth, 1876b (see Loydell & Large, 2019); in the Ludlow species *Saetograptus leintwardinensis* (Lapworth, 1880a) (see Maletz, 1997d; Štorch, Manda, & Loydell, 2014); in the Devonian *Uncinatograptus hercynicus*

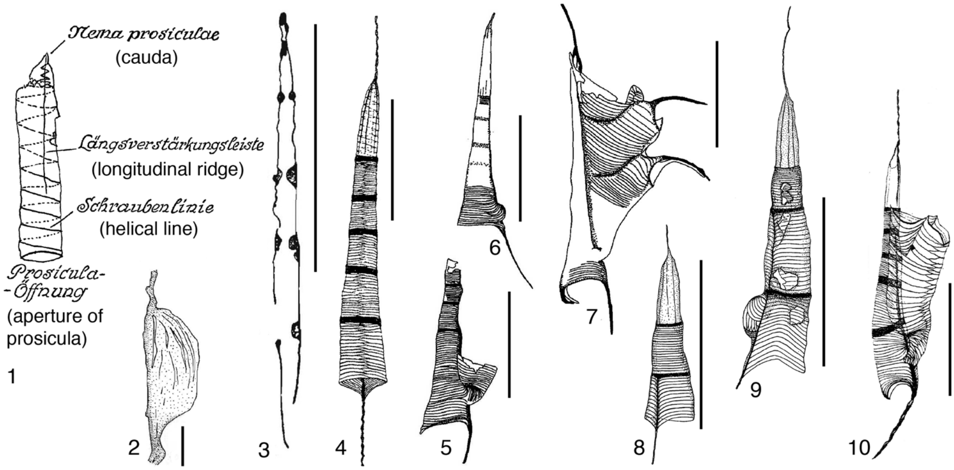


FIG. 289. The sicular development of the uniserial Axonophora (Monograptidae). *1,* monograptid prosicula, schematic (Kraft, 1926, fig. 2); *2–3,* cross section of sicula (*3*) and enlargement of sicular annulus (*2*) (Urbanek, 1958, fig. 5A, 6C); *4, Pristiograptus frequens* JAEKEL, 1889, sicular development (Kraft, 1926, fig. 3); *5–7, Saetograptus leintwardinensis* (LAPWORTH, 1880a), showing sicular shape and annuli (Maletz, 1997d, fig. 1); *8–9, Skalograptus ultimus* (PERNER, 1899), siculae with longitudinal rods, showing origin of virgella at first metasicular annulus (Kříž & others, 1986, fig. 35); *10, Pristiograptus frequens*?, showing sicular annuli (Kraft, 1926, fig. 4). Scale bars, 0.01 mm in *2,* all others, 1 mm.

(PERNER, 1899); and may be present in other genera as well.

Longitudinal ridges (see KRAFT, 1926) are present on the prosicula of many graptoloids, but their origin and further evolution has not been investigated. It is unclear whether these ridges were formed in constant numbers in the graptoloids or were formed randomly. They first appeared as paired ridges in Floian taxa (WILLIAMS & CLARKE, 1999) and are present in latest Silurian monograptids (Fig. 289.8–289.9). KOREN', KIM, and WALLISER (2007) described longitudinal rods in the Early Devonian *Uncinatograptus falcarius* (KOREN', 1969).

Sicular annuli occur in many monograptids (Fig. 289.2–289.6, Fig. 289.8–289.10). The origin and constructional purpose of the sicular annuli are unknown. Sectioned material clearly shows the secretion of the annuli to be cortical additions on the inside of the sicula (WALKER, 1953; URBANEK, 1958) (Fig. 289.2–289.3). They are typically present in many Homerian (late Wenlock, Silurian) and later monograptids (LENZ & KOZŁOWSKA-DAWIDZIUK, 1998). Very little is known about sicular annuli in older taxa because these have rarely been investigated in detail. Sicular annuli appear to have formed in fixed positions in most monograptids (URBANEK, 1997a). MALETZ (1997d) recognized a variable number of sicular annuli in *Saetograptus leintwardinensis* (Fig. 289.5–289.7), ranging from two to six, with most specimens possessing four to six annuli. The first of the sicular annuli appeared at the boundary between the prosicula and metasicula. The later ones were more indistinct and indicate their successive construction as the metasicula grew (MALETZ, 1997d). PORĘBSKA (1984) recognized sicular annuli in many latest Silurian to Early Devonian monograptids but was unable to confirm their presence in all specimens of the taxa because she had only shale material at hand.

The development of the foramen for the origin of th1 changed considerably throughout the evolution of the Monograptidae (MALETZ & others, 2019). Initially, a resorption foramen (Fig. 290.1) was present in species of the genera *Atavograptus*, *Coronograptus*, *Lagarograptus*, *Pernerograptus*, and

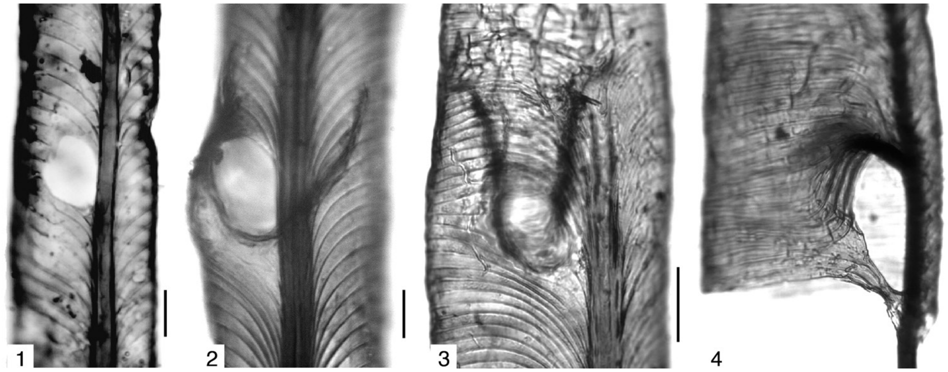


FIG. 290. The porus type in the Monograptidae. *1*, *Coronograptus gregarius* (LAPWORTH, 1876c), resorption foramen in metasicula, GSC 116236; *2*, *Monoclimacis*? *galeritus* MELCHIN & KOREN', 2001, modified resorption foramen, GSC 118589; *3*, *Monograptus* cf. *Monograptus arciformis* CHEN & LIN, 1978, lenticular porus, GSC 130563; *4*, *Monograptus priodon* (BRONN, 1835), primary porus with sinus and lacuna stages, GSC 130558. Scale bars, 0.1 mm (Maletz & others, 2019, fig. 5).

probably in early *Monoclimacis* (LUKASIK & MELCHIN, 1994, 1997; MELCHIN & KOREN', 2001). Most details are unknown for the contemporary *Pribylograptus* because very few siculae have been attributed to this genus, and they are not known in enough detail (see KOREN' & BJERRESKOV, 1997, fig. 22L regarding ?*Pribylograptus* sp.; and RUSSEL-HOUSTON, 2001, pl. 5e regarding *Pribylograptus leptotheca* LAPWORTH, 1876b). MELCHIN and KOREN' (2001) discussed a modified resorption foramen in specimens of *Monoclimacis* (Fig. 290.2), in which the fuselli involved in the formation of the foramen are slightly deflected with the sicula bulging outward at this point. A lenticular porus (Fig. 290.3) is present as a third type in early monograptids (DAWSON & MELCHIN, 2007). In this type, a number of pre-porus fuselli are deflected proximally and a few truncated fuselli are present. The post-porus fuselli are deflected in the opposite direction, forming the lenticular porus in *Paramonoclimacis* and *Streptograptus*. Derived monograptids may have a primary porus (Fig. 290.4) formed through the typical sinus and lacuna stage of development described by EISENACK (1942) for *Pristiograptus frequens* JAEKEL, 1889. This porus type was considered to be typical of all monograptids (e.g., BULMAN, 1970). DAWSON and MELCHIN (2007) illustrated this primary porus for *Monograptus priodon* (BRONN, 1835) from the middle Sheinwoodian, representing the stratigraphically earliest known record of this character.

### Tubarium Shape

The tubarium shape is highly variable in monograptids and/or ranges from straight to dorsally and ventrally curved uniserial stipes to multiramous taxa with numerous cladial branches. The shape appears to be characteristic for certain groups and also for certain stratigraphical intervals. However, particular shapes appear to have also evolved independently in separate groups. Spirally coiled tubaria are common in a number of taxa and may be planispiral or trochospiral. However, in many taxa, the precise mode of coiling is difficult to recognize. Large specimens of *Oktavites spiralis* (GEINITZ, 1842) may appear to be planispiral (Fig. 291.5), but the astogeny derived from early growth stages indicates a trochospiral development if viewed in lateral preservation (SCHAUER, 1971). High trochospiral development is typical of *Spirograptus turriculatus* (BARRANDE, 1850) (Fig. 291.7), a species usually preserved in lateral view. Also, many specimens of *Cyrtograptus* (Fig. 291.2) are coiled in a trochospiral fashion, even though larger specimens appear to have

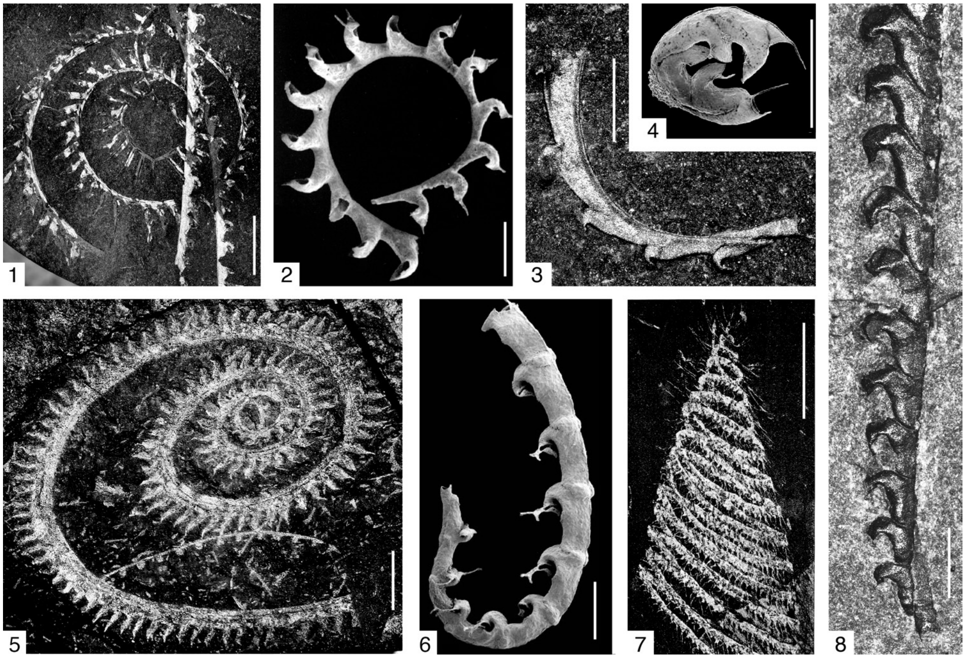


FIG. 291. The tubarium shape. *1*, *Lituigraptus convolutus* (HISINGER, 1837), dorsally coiled tubarium, NIGP 168325, Yangtze platform, China (Maletz, Wang, & Wang, 2021, fig. 11E); *2*, *Cyrtograptus* sp. cf. *C. laqueus* JACKSON & ETHERINGTON, 1969, dorsally curved proximal end lacking the sicula, Cape Phillips Formation, Arctic Canada (Lenz & Melchin, 1989, fig. 3c); *3*, *Pernerograptus variabilis* (NI, 1978), dorsally curved proximal end, NIGP 168346, Yangtze Platform, China (Maletz, Wang, & Wang, 2021, fig. 17A); *4*, *Cochlograptus veles* (RICHTER, 1871), GSC 34909, Devon Island, Arctic Canada (Lenz & Melchin, 2008, fig. 1D); *5*, *Oktavites spiralis* (GEINITZ, 1842), seemingly planispiral colony, dorsally coiled, SMF XXIV 188, Johannesberg, Thuringia, collected by Hemmann, 1942 (new); *6, Pseudostreptograptus williamsi* LOYDELL, 1991a, ventrally curved fish-hook-shape, NMW UCWG935B, Osmundsberget, Dalarna, Sweden (Loydell & Maletz, 2004, fig. 23); *7*, *Spirograptus turriculatus* (BARRANDE, 1850), high spiral, dorsally coiled, BAF 111/H/4135, Hohenleuben, Thuringia (Hundt, 1949b, fig. on p. 330); *8, Monograptus priodon* (BRONN, 1835), nearly straight tubarium, SMF 75780, glacial boulder (new). Scale bars 5 mm in 1, 5, and 7. All others 1 mm.

a planispiral shape when preserved on shale surfaces (BOUČEK, 1933; LENZ & others, 2012). The shape of colonies of *Cyrtograptus* has been modeled as a logarithmic spiral forming planispiral colonies and this has been suggested as a character useful for the discrimination of taxa (e.g., HUO, FU, & SHU, 1986; DENG, 1986).

It is important to differentiate dorsally (Fig. 291.1–291.3) and ventrally (Fig. 291.4) curved taxa. Dorsally coiled tubaria were particularly common during the Telychian (e.g., Pernerograptinae, Monograptinae), whereas ventrally curved taxa proliferated during Gorstian and early Ludfordian times (e.g., Linograptinae), but details need to be investigated. A high degree of variation of dorsally, dorso-ventrally, and ventrally curved tubaria occur especially in streptograptines, in which both types appear. Many of the slender taxa are quite variable in shape, but a distinct dorsal curvature may be present along the first few thecae in *Streptograptus*. Distally, the curvature changes to ventral or the stipe is straight (as is shown in an overview of the biostratigraphical ranges of streptograptine genera by MALETZ & others, 2019, fig. 4). This is also present in the straight to slightly dorsally curved proximal end and strong ventral curvature of the distal part in *Pseudostreptograptus* (Fig. 291.6) and the *Streptograptus exiguus* group, with their fish-hook-shaped tubaria (LOYDELL & MALETZ, 2004).

### CLADIA

Cladia are a way of secondary branching (MALETZ, LENZ, & BATES, 2016), first developed by the Dichograptina (e.g., *Pterograptus,* see SKWARKO, 1974) and the Diplograptina (e.g., *Nemagraptus,* see FINNEY, 1985a) during the Ordovician. For a number of monograptid taxa, cladial branching was used as an option to form multiramous colonies. Cladia were the only way in which monograptids added new stipes to their tubaria. In this way, they differed from the earlier Dichograptina, in which dichotomous branching was the main mode of producing additional stipes (see MALETZ, LENZ, & BATES, 2016). The cladia in monograptids invariably included the formation of a secondary nema along which the cladial stipe grew (THORSTEINSSON, 1955). URBANEK (1963) differentiated the procladium (the main stipe) and the metacladia (sicular and thecal cladia) and recognized that cladia of several orders may be developed in some taxa. The term procladium for the main stipe should no longer be used as it might be misleading (see Glossary, p. 176). An analysis of the appearance of cladial branching has never been attempted, but it appears certain that cladia originated independently in several clades of monograptids. Thus, the family Cyrtograptidae of earlier workers, represents a highly polyphyletic taxonomic unit and should not be used. The genus *Cyrtograptus* is the most prominent taxon in which cladial branching has been investigated from chemically isolated material (THORSTEINSSON, 1955; TELLER, 1976), but cladial development has also been described in great detail for the linograptines (URBANEK, 1963, 1997b).

Early taxa with cladial branching appeared during the upper Aeronian and lower Telychian with the genera *Paradiversograptus* and *Sinodiversograptus* (MANCK, 1923; LOYDELL, 1990a). Little is known about the development of the cladia in these taxa because chemically isolated material does not exist. The genus *Sinodiversograptus* from the *Spirograptus guerichi* Biozone (LOYDELL, 1990a) is the stratigraphically earliest record of regular and frequent thecal cladial branching in a Silurian monograptid. The process began with the formation of a strongly curved bipolar tubarium. It appears that thecal cladia were produced from each theca on the main stipe, but it is uncertain at what stage in the astogeny of the colony the cladial growth was initiated.

An independent origin of cladial branching occurred in Linograptinae. URBANEK (1963) discussed in great detail the development of cladial branching in this clade, indicating that the stratigraphically early taxon *Neodiversograptus* had a bipolar tubarium with a single cladium originating from the sicular aperture. The derived taxa *Linograptus* and *Abiesgraptus* produced numerous cladia, either from the sicula (*Linograptus*) or paired cladia from the sicula and from later thecae (*Abiesgraptus*) (URBANEK, 1997b). In *Abiesgraptus,* a single sicular cladium initially formed a bipolar tubarium from which additional paired thecal cladia were formed at certain distances, producing a multiramous tubarium.

### Subfamily PERNEROGRAPTINAE Hundt, 1943

[Pernerograptinae HUNDT, 1943, p. 263, *ex* Pernerograptidae HUNDT, 1943, p. 263; PŘIBYL, 1946, p. 277]

Uniserial Neograptina without cladia; single stipe straight to strongly dorsally curved, commonly variable; resorption foramen for emergence of th1 or a derived pattern, but development unknown in most species; sicula may be elongated; thecal style highly variable with or without geniculum; various apertural modifications may be present, mainly based on apertural hood or hook. *Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus/Parakidograptus acuminatus* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.

PŘIBYL (1946) discussed the Pernerograptinae as a subfamily, but it was initially listed by HUNDT (1943) as a family. However, this taxonomic unit has not been discussed in detail subsequently and needs considerable attention. Přibyl (1946) differentiated the subfamily from the Monograptinae due to the biform nature of the thecal development in *Pernerograptus*. A differentiation into taxa with short and with long siculae may be useful and has been made herein. Further investigation is necessary to understand the evolutionary relationships of early monograptids. All taxa have a slightly to considerably dorsally curved tubarium, at least proximally. The sicular length is quite variable. The thecae are slender with low overlap or lacking overlap proximally, but overlap may increase considerably distally. A geniculum is commonly present and the thecal apertures are simple, hooded, or provided with lateral lobes. According to Melchin and others (2011, fig. 7), *Atavograptus* and the derived monograptids originated in the early Rhuddanian *Akidograptus ascensus*/*Parakidograptus acuminatus* Biozone as a sister group to the genus *Dimorphograptus*.

The proximal end and thecal style of early monograptids appear to be quite variable but can be reduced to a few fundamental features. Melchin and others (2011) considered the species *Atavograptus ceryx* (Rickards & Hutt, 1970) from the *Akidograptus ascensus*/*Parakidograptus acuminatus* Biozone to be the earliest monograptid. The sicula is approximately 1.5–1.8 mm long, gradually widening toward the aperture (Fig. 292.1). The origin of th1 is in the lower third of the metasicula. The thecae widen from the origin, forming a rounded geniculum, after which they are parallel-sided, nearly parallel to the dorsal line of the stipe. They have low thecal overlap and apparently no or only a slight increase of this feature distally. *Atavograptus ceryx* has considerable dorsal curvature (Fig. 292.2), reminiscent of the tubarium shape in the genus *Coronograptus*. An early thecal differentiation in *Atavograptus atavus* (Zalasiewicz, 2000f) has very slender proximal thecae and a conspicuous but gradual distal widening of the stipes.

Distinct elongation of the slender metasicula is present in *Coronograptus* (Fig. 292.4) and also in a few other genera (Rickards, Hutt, & Berry, 1977) as well as an enhancement of the geniculum with the formation of genicular flanges (Fig. 292.6, 292.8). A differentiation of the thecal apertures with the formation of lateral apertural flanges and lobes also occurs (Fig.292.5–292.8). The precise evolutionary relationship of these features has not been studied.

## GENERA WITH SHORT SICULAE

The sicula is approximately 1–2 mm long in these taxa, but details of the development are rarely available. The dimensions of the prosicula are unknown in most taxa.

**Atavograptus** Rickards, 1974, p. 141 [**Monograptus atavus* Jones, 1909, p. 531; OD]. Straight to somewhat dorsally curved tubarium that becomes straight distally; sicula 1.2–1.8 mm long; first theca arises from middle part of metasicula via a resorption porus; thecae simple overlapping tubes, commonly with rounded genicula; thecal apertures simple, straight. *Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus*/*Parakidograptus acuminatus* Biozone–*Aeronian, Neodiplograptus magnus* Biozone): worldwide.——Fig. 293,*1a–c*. **A. atavus* (Jones); *1a,* lectotype, GSM 23710, stipe fragment (Zalasiewicz, 2000d, Atlas, Folio 1.6); *1b,* latex cast of topotype, proximal end with sicula, GSM 95254 (Zalasiewicz, 2000d, Atlas, Folio 1.6); *1c,* proximal end, PŠ 3521, Czech Republic (Štorch, 2015, fig. 10M). Scale bars, 1 mm.

**Euroclimacis** Štorch, 1998c, p. 120 [**Monograptus aduncus* Bouček, 1931, p. 295; OD]. Tubarium dorsally curved proximally and ventrally curved or almost straight distally; sicula short; thecae with sharp geniculum, narrow aperture, and pronounced apertural hoods formed by elongated dorsal thecal wall, particularly in proximal thecae. [Štorch (1994) discussed the strong intraspecific variation in the development of the genicular hoods of *E. adunca*.] *Silurian, Llandovery* (*Telychian, Monoclimacis crenulata* Biozone)–*Wenlock,* (*Homerian, Cyrtograptus lundgreni* Biozone): Spain, Czech Republic, UK, Estonia, Latvia, Morocco, Arctic Canada.——Fig. 293,*2a–c*. **E. adunca* (Bouček); *2a,* ?lectotype (selected by Přibyl, 1940b, p. 8), NMP L30665, showing the shape of the colony, Vyskočilka, Czech Republic (Zalasiewicz & Williams, 2000, Atlas, Folio 1.43); *2b,* proximal end from type slab NMP L30665 (Zalasiewicz & Williams, 2000, Atlas, Folio 1.43); *2c,* PŠ 475, *Cyrtograptus murchisoni* Biozone, Velká Ohrada, Czech Republic (Štorch, 1994, fig. 5,*20c*). Scale bars, 1 mm.

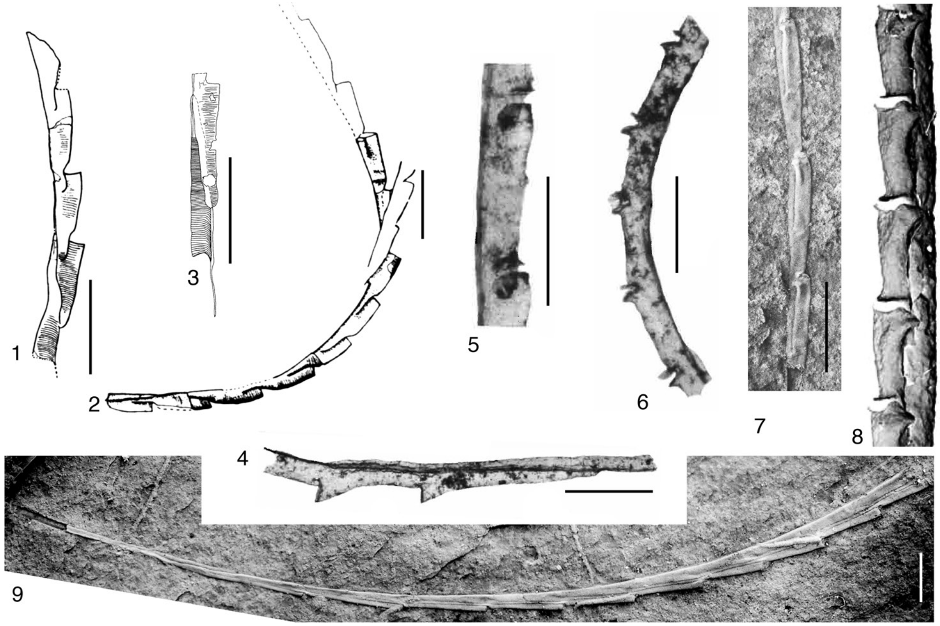


FIG. 292. The proximal end and thecal development of early monograptids. *1–2, Atavograptus ceryx* (RICKARDS & HUTT, 1970); *1,* SM A67088, complete proximal end of longer specimen (Rickards & Hutt, 1970, fig. 1D), *2,* holotype, SM A67087, pyritic internal mold (Rickards & Hutt, 1970, fig. 2A); *3, Atavograptus primitivus* (LI in YANG & others, 1983) proximal end (Lukasik & Melchin, 1994, fig. 1,*1*); *4*, *Coronograptus gregarius* (LAPWORTH, 1876b), proximal end, GSC 116247 (Lukasik & Melchin, 1997, fig. 7I); *5, Pribylograptus pleganopsis* LUKASIK & MELCHIN, 1997, stipe fragment showing genicular hoods and lateral apertural lobes, GSC 116240 (Lukasik & Melchin, 1997, fig. 7B); *6*, *Huttagraptus tholians* LUKASIK & MELCHIN, 1997, stipe fragment showing genicular hoods and flared apertures, note fragment of prosicula, GSC 116254 (Lukasik & Melchin, 1997, fig. 7P); *7*, *Pribylograptus incommodus* (TÖRNQUIST, 1899), fragment, latex cast of part of specimen, LO 1456T (new); *8*, *Pribylograptus argutus* (Lapworth, 1876b), thecal style, NMW 2002/19G.29D (adapted from Loydell & Maletz, 2009, pl. 6,*7*); *9*, *Huttagraptus acinaces* (TÖRNQUIST, 1899), holotype, LO 1436T, latex cast, showing long sicula and increasing thecal overlap (new). Scale bars, 1 mm.

**Monoclimacis** FRECH, 1897, p. 621 [**Graptolites vomerinus* NICHOLSON, 1872a, p. 52; OD] [=*Hemimonograptus* ZHAO, 1984, p. 101 (type, *Monoclimacis opercula* MU & others, 1974, p. 218, OD), syn. by MALETZ, herein] [?=*Hubeigraptus* LI, 1995, p. 268 (type, *H. semilunatus,* OD), syn. by MALETZ, herein]. Tubarium straight or dorsally curved proximally; sicula short; first theca originated via modified resorption porus or derived type; thecae geniculate, with supragenicular wall parallel to or less commonly inclined to axis of tubarium; apertural excavations semi-circular or semi-elliptical, commonly with overhanging hood, outgrowth of the dorsal wall; in some species, small number of proximal thecae hooked. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——FIG. 293,*3a–c*. **M. vomerina* (NICHOLSON); *3a,* neotype (STRACHAN, 1971, p. 91), proximal end only, Riccarton Beds, Elliotsfield, Scotland (Zalasiewicz, 2000f, Atlas, Folio 1.48); *3b–c,* proximal end and distal fragment, BGS RCV2012, BGS RCV236, Buttington quarry, Wales (Loydell & Cave, 1993, fig. 7E–F). Scale bars, 5 mm.

**Pernerograptus** PŘIBYL, 1941, p. 9 [**Graptolites argenteus* NICHOLSON, 1869, p. 239; OD] [=*Pernerograptus* (*Quasipernerograptus*) ZHAO, 1984, p. 105 (type, *P.* (*Q.*) *leptotheca,* OD), syn. by LOYDELL, herein; =*Pseudopernerograptus* WANG in WANG & others, 1987, p. 380 (type *Monograptus revolutus* KURCK, 1882, p. 299, OD), syn. by LOYDELL, herein]. Straight to dorsally curved proximal part of tubarium with straight distal part; dorsal curvature accentuated in mesial part of colony; biform thecae; sicula small, apex not reaching to first metatheca; proximal thecae slender, axially elongated without overlap, terminated by apertural hoods that are either simple or transversely expanded; apertural hoods retreat in mesial thecae leaving only lateral lappets and dorsal apertural hoods that also subsequently retreat, resulting in simple, cylindrical, greatly overlapping distal thecae. *Silurian, Llandovery* (*Rhuddanian, Pernerograptus revolutus/Coro-*

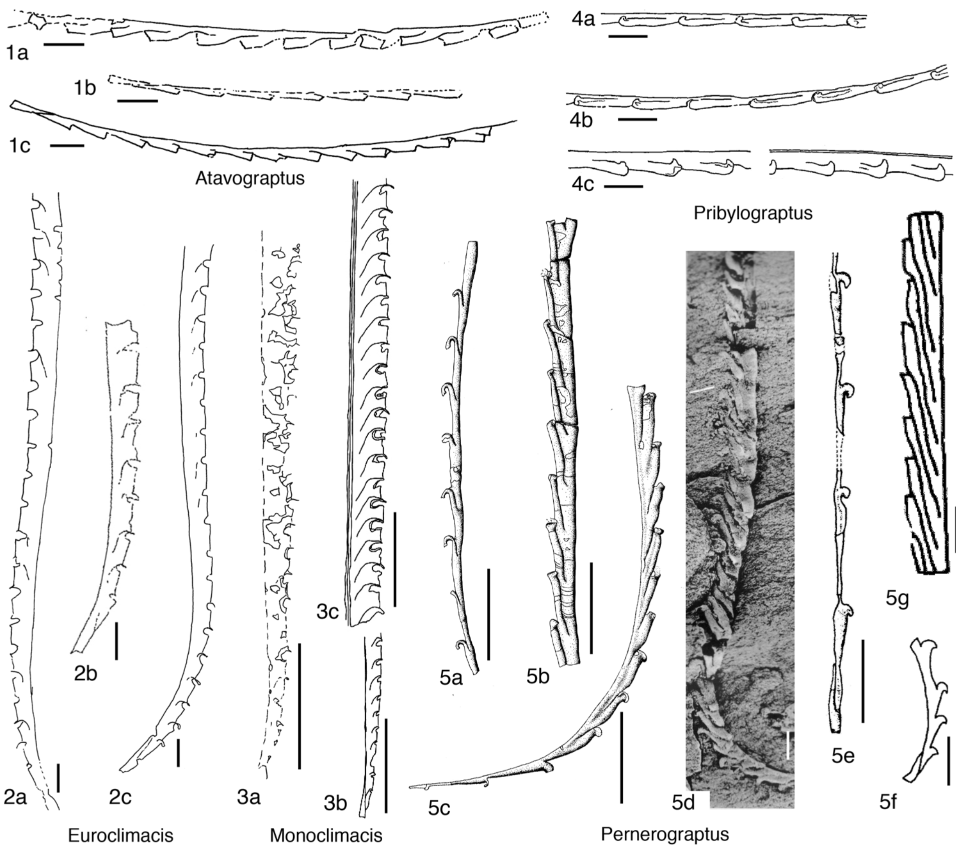


FIG. 293. Pernerograptinae (short siculae) (p. 433–435).

*nograptus cyphus* Biozone–*Aeronian*, *Lituigraptus convolutus* Biozone): worldwide.——FIG. 293,*5a–b*. *P. revolutus* (KURCK), syntype, LO 475t, Bollerup, Scania, Sweden, scale bars, 1 mm (Hutt, 1974b, fig. 1a–b).——FIG. 293,*5c*. *P. sudburiae* (HUTT, 1974b), holotype, LO 4454T, Tommarp, Sweden, scale bar, 1 mm (Hutt, 1974b, fig. 1d).——FIG. 293,*5d–e*. **P. argenteus* (NICHOLSON); *5d,* lectotype, NHMUK Q3148, Skelgill, Lake District, England (Hutt, 1975, pl. 17,*3*); *5e*, proximal end with sicula, SM A85016, Yewdale Beck, England (Hutt, 1975, fig. 17,*2*). Scale bars, 1 mm.——FIG. 293,*5f–g*. *P. leptotheca* (ZHAO, 1984), proximal and distal fragments (Zhao, 1984, fig. 4A,C). Scale bars, 1 mm.

**Pribylograptus** OBUT & SOBOLEVSKAYA, 1966, p. 33 [**Monograptus incommodus* TÖRNQUIST, 1899, p. 11; OD]. Tubarium long, variably and gently curved proximally, straight distally; sicula rarely recorded but usually 1.8–2.0 mm long; thecae simple, gradually widening tubes proximally, commonly with increasing overlap distally; transitions between thecal morphologies gradual; thecal apertures flanked by lateral lappets throughout colony; geniculate thecae with flanges or hoods overhanging thecal apertures; unpaired genicular or supragenicular spines may be present. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone–*Aeronian, Stimulograptus sedgwickii* Biozone): worldwide.——FIG. 293,*4a–c*. **P. incommodus* (TÖRNQUIST), Röstånga, Scania, Sweden; *4a–b,* holotype, LO 1456T, thecal style (Koren' & Bjerreskov, 1997, fig. 21A); *4c,* paratype, LO 1457t, fragment (Koren' & Bjerreskov, 1997, fig. 21B). Scale bars, 0.1 mm.

## GENERA WITH LONG SICULAE

The sicula is more than 2 mm long in all taxa included in this group, and siculae of as much as 16 mm in length have been documented for *Coronograptus maxiculus* ŠTORCH, 1988 (see ŠTORCH, 1988).

**Coronograptus** OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVESKAYA, & MERKUREVA, 1968, p. 92 [**Monograptus gregarius* LAPWORTH, 1876c, p. 317; OD]. Strongly dorsally curved tubarium that may become straight

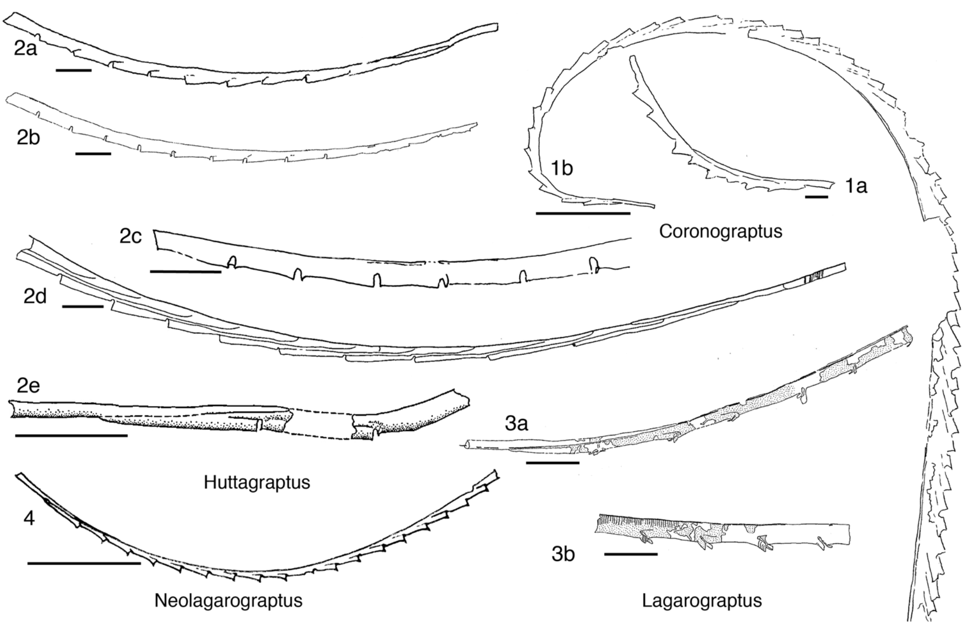


FIG. 294. Pernerograptinae (long siculae) (p. 435–437).

distally; sicula long (2.5–16 mm), with majority of length contributed by metasicula, which possesses a resorption porus; first theca emerges high on metasicula; thecae long overlapping tubes; geniculate immediately above or below thecal apertures, with concave free ventral thecal walls subaperturally at least in proximal thecae; flared, unornamented thecal apertures; genicular hoods may be developed proximally or throughout tubarium but are absent in most species. *Silurian, Llandovery* (*Rhuddanian, Coronograptus cyphus* Biozone–*Aeronian, Lituigraptus convolutus* Biozone): worldwide.——FIG. 294,*1a*. **C. gregarius* (LAPWORTH), syntype, BU 1435, Dob's Linn, Scotland, scale bar, 1 mm (Zalasiewicz, 2000e, Atlas Folio 1.13).——FIG. 294,*1b*. *C. cyphus* (LAPWORTH, 1876b), typical specimen BU 1430, Dob's Linn, Scotland, scale bar, 5 mm (Zalasiewicz, Williams, & Akhurst, 2003, fig. 2A).

**Huttagraptus** KOREN' & BJERRESKOV, 1997, p. 13 [**Atavograptus praestrachani* HUTT & RICKARDS in RICKARDS, HUTT, & BERRY, 1977, p. 102; OD]. Long, slender, slightly to strongly dorsally curved tubarium; sicula long (2–7 mm); first theca originated high on metasicula via resorption foramen; typically long overlapping thecae with free ventral walls at very low angle or parallel to tubarium axis and with pronounced angular geniculum proximally, creating marked thecal excavation, and in some species these features retained mesially or throughout entire tubarium; genicular flanges may overhang thecal apertures forming distinct hoods; geniculum retreats gradually and thecae become simple tubes with increased inclination of free ventral wall to the tubarium axis in species with thecae lacking genicula mesially or distally. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone–*Aeronian, Demirastrites triangulatus* Biozone): worldwide.——FIG. 294,*2a–c,e*. **H. praestrachani* (HUTT & RICKARDS in RICKARDS, HUTT, & BERRY), holotype, SM A60415a–b, Keisley, northern England, scale bars, 1 mm (Hutt & Rickards, 1970, fig. 3C; Zalasiewicz, 2008d, Atlas, Folio 2.73); *2e,* MGUH 24205, proximal end, Kos-Istek region, southern Urals, Russia, scale bars, 1 mm (Koren' & Bjerreskov, 1997, fig. 10B).——FIG. 294,*2d*. *H. acinaces* (TÖRNQUIST, 1899), holotype, LO 1436T, scale bar, 1 mm (Koren'& Bjerreskov, 1997, fig. 12H).

**Lagarograptus** OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVESKAYA, & MERKUREVA, 1968, p. 90 [**L. inexpeditus;* OD]. Narrow, dorsally curved tubarium; long sicula (1.9–4.35 mm); first theca originated via a resorption porus; overlapping, sharply geniculate thecae with free ventral walls subparallel to tubarium axis; shallow and narrow apertural excavations; tonguelike ventral apertural process and dorsal apertural hood present on all thecae. *Silurian, Llandovery* (*Rhuddanian, Coronograptus cyphus* Biozone–*Aeronian, Campograptus curtus* Biozone): Siberia, Kazakhstan, northern and Arctic Canada, China.——FIG. 294,*3a–b*. **L. inexpeditus* OBUT & SOBOLEVSKAYA; *3a,* proximal end, MGUH 24347, Kos-Istek region, southern Urals, Russia (Koren' & Bjerreskov, 1997, fig. 23H); *3b,* distal fragment, MGUH 24343, Kos-Istek region, southern Urals, Russia (Koren' & Bjerreskov, 1997, fig. 23B). Scale bars, 1 mm.

**Neolagarograptus** Štorch, 1998a, p. 228 [**Lagarograptus helenae* Štorch, 1988, p. 24; OD]. Tubarium arcuately dorsally curved, gradually expanding in dorso-ventral width, with tendency to be parallel sided; sicula long (3.5–5.1 mm); long, overlapping, geniculate thecae with simple, slightly widened apertures, shallow apertural excavations and, in some species, a single ventral apertural process. *Silurian, Llandovery* (*Aeronian, Pribylograptus leptotheca* Biozone–*Stimulograptus sedgwickii* Biozone): Czech Republic, Great Britain, Latvia, Myanmar, Iran, Saudi Arabia.——Fig. 294,*4*. **N. helenae* (Štorch), holotype, PŠ 274, Tmaň, Czech Republic, scale bar, 5 mm (Štorch, 1988, fig. 4D).

## 'STREPTOGRAPTINES'

Dorsally or ventrally curved to proximally vaguely S-shaped and distally straight to fish-hook-shaped tubaria; proximal thecae without overlap in earlier taxa bearing thecae with distally increasing overlap; younger taxa lacking thecal overlap; sicula small with comparably large prosicula; origin of th1 from lenticular porus development low in sicula if known (sinus and lacuna stages not described or illustrated for any taxon of the group); isolated metathecae with coiled apertural part, bearing proximo-ventrally directed nozzle; thecae originating through paired cupulae in derived taxa; thecae typically bear genicular platform with longitudinal convexity; uncoiled initial part of thecae widening distally or with bulge, widest part at base in some. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.

Bouček and Přibyl (1943, 1951) and Bouček and Přibyl in Přibyl, 1948a) discussed *Streptograptus* and *Mediograptus* as characterized by their special thecal apertures but identified them as subgenera of *Monograptus*. The authors differentiated several distinct groups in the two taxa. Maletz and others (2019) used the term streptograptid to describe the characteristic thecal construction of the genus *Streptograptus* and of related genera, herein included in an informal group referred herein to as the 'streptograptines.' The streptograptines may be identified as a subfamily if the constructional details prove to be phylogenetically meaningful. They can be viewed as related through their complex thecal apertures bearing conspicuous distal (lateral) lobes and the proximally directed nozzle (Fig. 295.3, Fig. 296.4). The tubarium shape is highly variable, ranging from dorsally curved in *Paramonoclimacis* (Fig. 295.1) to fish-hook-shaped, with initial dorsal curvature and distal ventral curvature. Many slender forms are more variable in shape but are only slightly sinuously curved. The isolated hooked distal metathecae may be of a variable length but are often conspicuous. The apertures are strongly introverted and open into the ventral metathecal sides, typically into a platform with thickened rim (Fig. 296.10) (Loydell & Maletz, 2004). Earlier taxa without cupulae usually possess metathecae with a relatively long, isolated hook (Fig. 296.1) before the development of the thecal aperture.

Specimens of the genus *Paramonoclimacis* may easily be misidentified as *Pernerograptus* species with simple apertural hoods when flattened. A thecal gradient comparable to that of *Pernerograptus* is also visible in *Paramonoclimacis* (see Fig. 295.1, displacement of cupulae) but not in other genera of the group and may indicate the phylogenetic relationship of the streptograptines to the earlier pernerograptines.

Important characters such as the characteristic cupulae (Fig. 296) of derived streptograptines or the increasing thecal overlap of earlier forms (Fig. 295.1) are typically not recognizable in flattened material. Therefore, the generic assignment of many species is difficult. Chemically isolated material clearly has remains of cupulae in *Mediograptus* species and also the characteristic thecal apertural nozzle. The cupulae may be reduced in size. Teller (1986) described isolated specimens of *Mediograptus antennularius* (Meneghini, 1857) and *Mediograptus flexuosus* (Tullberg, 1883) from the *Monograptus flexilis* Biozone (Sheinwoodian, Wenlock) of Poland. *Mediograptus flexuosus* appears to have cupulae (Teller, 1986, pl. 6.11). The illustrations are partly simplified (Fig. 296.9)

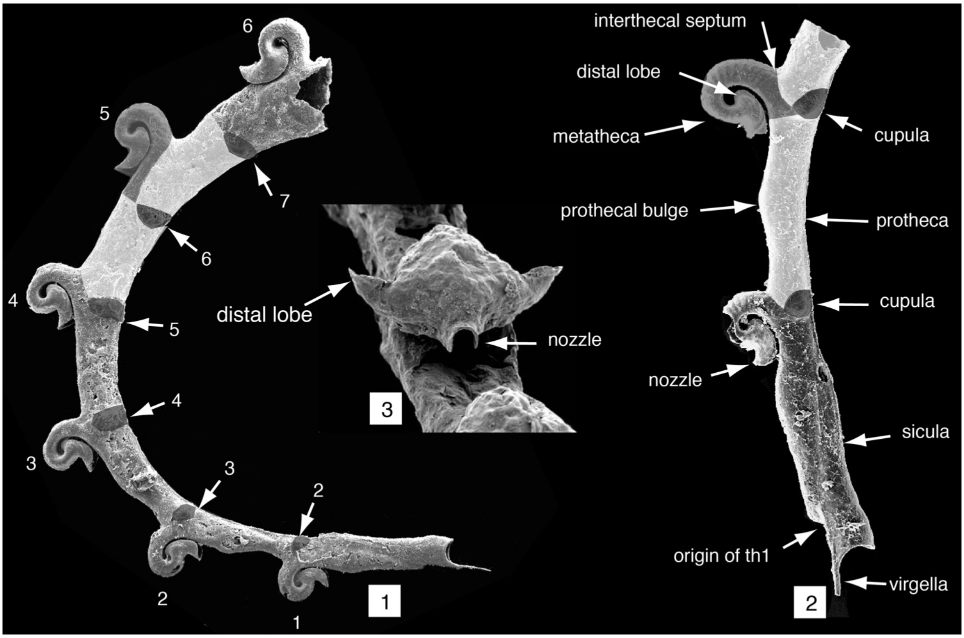


FIG. 295. Streptograptine proximal ends and colony construction. *1–2, Paramonoclimacis sidjachenkoi* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & BONDAREV, 1965); *1*, thecal apertures and associated cupulae are labeled; *2*, proximal end illustrating important tubarium features (based on Maletz & others, 2019, fig. 1); *3, Streptograptus dalecarlicus* LOYDELL & MALETZ, 2004, thecal aperture showing distinct nozzle and outward-directed distal lobes on thecal aperture.

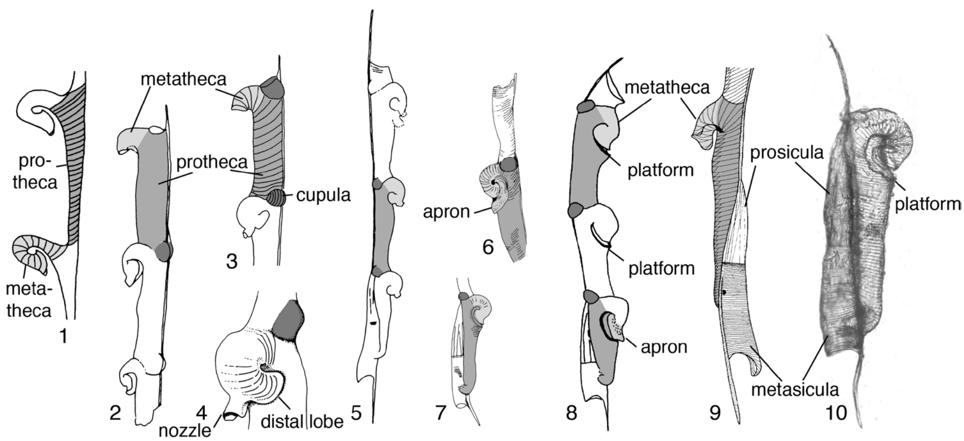


FIG. 296. Tubarium character of streptograptines. *1*, *Streptograptus ansulosus* (TÖRNQUIST, 1892), thecal style with long isolated part, lacking cupulae and platform; *2–5*, *Streptograptus dalecarlicus* LOYDELL & MALETZ, 2004, showing cupulae and laterally extended distal lobes; *6–7, Streptograptus sartorius* (TÖRNQUIST, 1881) with apron covering the platform in mature thecae; *8*, *Streptograptus johnsonae* (LOYDELL, 1991a), proximal end with complete th1 showing apron, th2 and th3 without apron (*1–8,* new); *9, Mediograptus antennularius* (MENEGHINI, 1857), reconstruction of proximal end showing simplified metatheca and origin of th2 (adapted from Teller, 1986, fig. 8); *10, Streptograptus sartorius* specimen, Solberga, Dalarna, Sweden (Maletz & others, 2019, fig. 3L). Illustrations not to scale.

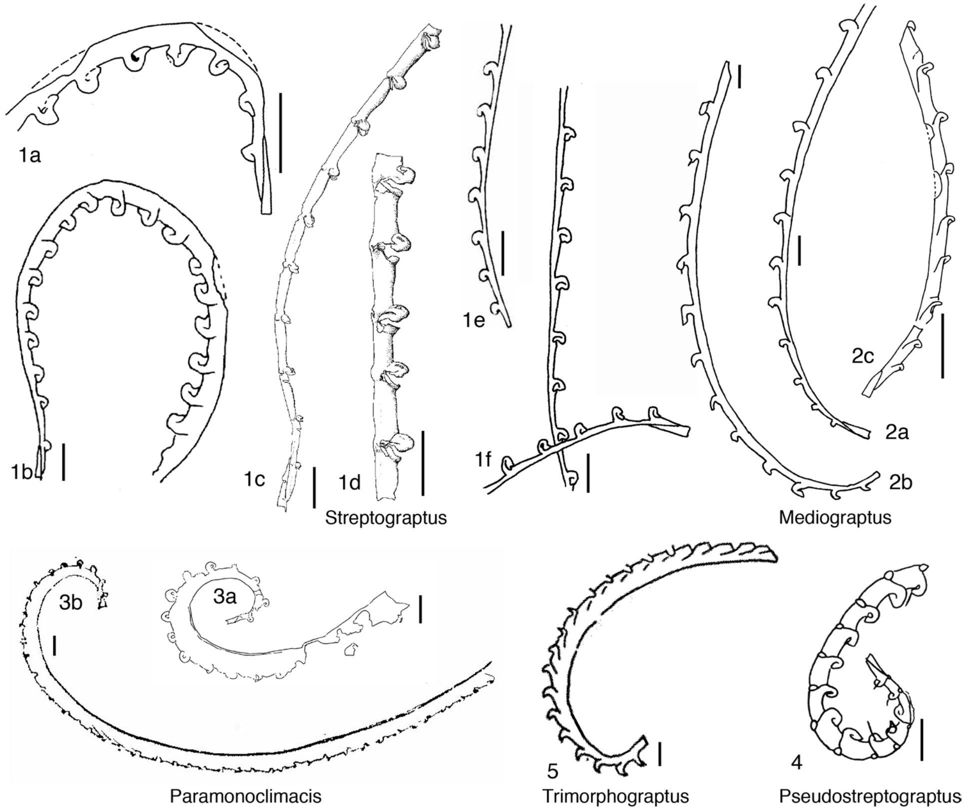


FIG. 297. Streptograptines (p. 439–440).

but show the main characters of the tubaria. JAEGER (1991) described *Streptograptus serexiguus* (JAEGER, 1991) from the Homerian *Testograptus testis* Biozone (equivalent to the *Cyrtograptus lundgreni* Biozone) of Nevada as the youngest form within the *Streptograptus exiguus* group.

**Streptograptus** YIN, 1937, p. 297 [**Graptolithus plumosus* BAILY, 1871, p. 22; SD ICZN, Opinion 1714, 1993, p. 90 (replacement of *Monograptus nodifer* TÖRNQUIST, 1881, *sensu* ELLES & WOOD, 1913, pl. 46,2a–d; YIN, 1937, p. 297; proposed to ICZN by LOYDELL & CHEN, 1991)] [=*Globosograptus* BOUČEK & PŘIBYL in PŘIBYL, 1948a, p. 37 (type, *Monograptus wimani* BOUČEK 1932, p. 153, OD), syn. by LOYDELL, 1996, p. 891; =*Awarograptus* ZALASIEWICZ & HOWE, 2003, p. 45 (type, *Monograptus nodifer* TÖRNQUIST, 1881, OD), syn. by LOYDELL & NESTOR, 2006, p. 590]. Tubarium straight, dorsally, ventrally or dorso-ventrally curved; sicula small; first theca originated via a lenticular porus; metathecae coiled; thecal apertures with central, proximo-ventrally directed nozzle, in some taxa developed only in the apron. *Silurian, Llandovery* (*Aeronian, Pribylograptus leptotheca* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——FIG. 297,*1a–b*. **S. plumosus* (BAILY); *1a,* neotype, BELUM K12274d, Tieveshilly, County Down, Northern Ireland, scale bar, 1 mm (Loydell, 1990b, fig. 1); *1b,* larger specimen showing tubarium shape, MGM6646-0, El Pintado reservoir, Seville Province, Spain, scale bar, 1 mm (Loydell, Frýda, & Gutiérrez-Marco, 2015, fig. 21AQ).——FIG. 297,*1c–d*. *S. nodifer* (TÖRNQUIST), neotype (ZALASIEWICZ & HOWE, 2003, p. 46), proximal end and distal thecal style, LO 6465t, Nitsjö, Dalarna, Sweden (Zalasiewicz & Howe, 2003, fig. 1). Scale bars, 1 mm.——FIG. 297,*1e–f*. *S. wimani* (BOUČEK, 1932); *1e,* lectotype (BOUČEK & PŘIBYL in PŘIBYL, 1948a, p. 38), Vyskočilka, Czech Republic (Bouček, 1932, fig. 1i); *1f,* proximal end showing sicula, MGM 142-S, Jabalón River section, central Spain (Loydell & others, 2009, fig. 4F). Scale bars, 1 mm.

**Mediograptus** BOUČEK & PŘIBYL in PŘIBYL, 1948a, p. 39 [**Monograptus kolihai* BOUČEK, 1931; OD]. Slender, dorsally or dorso-ventrally curved tubarium; sicula short, apex reaching no higher than top of first theca; long, narrow prothecae in some species with cupulae at base; metathecae complex, the aperture comprising central, more or less well defined, proximal-facing portion, and two laterally curved parts, which may face laterally, dorsally, ventrally, proximally, distally, or a combination of the above depending on degree of twisting of horn-like lateral regions of metatheca; thecae exhibit overlap throughout tubarium. *Silurian, Llandovery* (*Telychian, Cyrtograptus insectus* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——FIG. 297,*2a–b*. **M. kolihai* (BOUČEK); *2a,* lectotype (PŘIBYL, 1948a, p. 39), NMP L30671 Motol Formation, Vyskočilka near Malá Chuchle, Prague, Czech Republic (BOUČEK, 1931, fig. 8A); *2b,* proximal end, PŠ 481.11 (Štorch, 1994, fig. 5.*6*) Scale bars, 1 mm.——FIG. 297,*2c. M. flittoni* LOYDELL & CAVE, 1996, holotype, BGS RCV3587, Banwy River section, Powys, Wales, scale bar, 1 mm (Loydell & Cave, 1996, fig. 13B).

**Paramonoclimacis** WANG & MA in WANG & others, 1977, p. 360 [**P. typicalis;* OD; =*Pernerograptus sidjachenkoi;* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & BONDAREV, 1965; syn. by MU & others, 2002, p. 896]. Initially dorsally planispirally coiled, distally straight distinctly widening tubarium; small sicula; cupulae at base of prothecae; proximal thecae lack overlap and have coiled metathecae with lateral apertural lobes and nozzle; thecal overlap increases distally; distally coiling of metathecae becomes steadily less pronounced and distalmost thecae have a thecal apertural excavation and overhanging hood. *Silurian, Llandovery* (*Aeronian, Lituigraptus convolutus* Biozone): China, Russia, Canada, USA (Alaska).——FIG. 297,*3a–b*. *P. sidjachenkoi* (OBUT & SOBOLEVSKAYA); *3a,* holotype, proximal end, CNIGR 8783/89, Taimyr (Maletz & others, 2019, fig. 2A); *3b,* **P. typicalis,* holotype, large specimen (Wang & others, 1977, fig. 47). Scale bars, 1 mm.

**Pseudostreptograptus** LOYDELL, 1991a, p. 236 [**P. williamsi;* OD]. Tubarium strongly ventrally curved; sicula small; prominent cupulae at base of prothecae; retroverted metathecae terminate in upturned lip as in *Streptograptus* but are also laterally expanded and furnished with lateral spines or more distally branching spatulate processes; platform concave. *Silurian, Llandovery* (*Telychian, Spirograptus guerichi* Biozone): Wales, Spain, Sweden, Australia.——FIG. 297,*4*. **P. williamsi,* topotype, BGS DKL 1372, south of Craig-y-Delyn, Aberystwyth, Wales, scale bar, 1 mm (Loydell, 1991a, fig. 9H).

**Trimorphograptus** ZHAO, 1984, p. 102 [**Pernerograptus qijiangensis* YE, 1978, p. 478; OD]. Tubarium dorsally curved considerably near proximal end, straight distally; proximal end unknown; proximal thecae hooked; mesial thecae with geniculum, apertural excavation and thecal hoods; distal thecae with rounded geniculum or straight ventral walls; thecal details unknown. *Silurian* (*Aeronian*): China.——FIG. 297,*5*. *T. minor* ZHAO, 1984, nearly complete specimen, scale bar, 1 mm (Zhao, 1984, fig. 3).

## Subfamily MONOGRAPTINAE Lapworth, 1873

[Monograptinae LAPWORTH, 1873b, table 1, facing p. 555, *ex* Monograptidae LAPWORTH, 1873b, table 1, facing p. 555] [=Rastritinae GÜRICH, 1908, p. 35, *ex* Rastritidae GÜRICH, 1908, p. 35, PŘIBYL, 1946, p. 276; =Demirastritinae HUNDT, 1943, p. 263, *ex* Demirastritidae HUNDT, 1943, p. 263, PŘIBYL, 1946, p. 276; =Diversograptinae HUNDT, 1943, p. 263, *ex* Diversograptidae HUNDT, 1943, p. 263, PŘIBYL, 1946, p. 276; =Spirograptinae OBUT, 1950, p. 265; =Cyrtograptinae AVERIANOW, 1929, p. 103, *ex* Cyrtograptidae AVERIANOW, 1929, p. 103, YIN, 1937, p. 296]

Straight to dorsally coiled, planispiral to trochospiral, S-shaped, or ventrally coiled tubarium with hooked, triangular to rastritid thecae with or without thecal overlap; hooks may be lost and thecal overlap may increase distally; sicula with lenticular porus or derived one; apertures hooked, generally bearing paired apertural spines or lappets. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.

The subfamilies introduced by HUNDT (1943) and PŘIBYL (1946) for taxa here included in the Monograptinae are not considered necessary. OBUT (1950) used the subfamily Spirograptinae in his text, but the taxon was never defined or discussed further. PŘIBYL (1946) included the genus *Spirograptus* in his subfamily Monograptinae, however, OBUT (1957, 1964) did not mention the Spirograptinae.

### MORPHOLOGY

Most taxa of the Monograptinae have a variably developed dorsal curvature, either planispiral or trochospiral. Distally, the stipes may be straight. The relationships to the ventrally curved genera *Cochlograptus* and *Testograptus* with similar thecal style have been uncertain in the past. LENZ and MELCHIN (2008) analysed the two genera and concluded that both originated independently from monograptid ancestors as a result of convergent evolution. *Cochlograptus* may be related to *Stimulograptus* or *Monograptus* and *Testograptus* could have its origin in a *Monograptus flemingii* type ancestor.

The thecae in the Monograptinae (Fig. 298) are quite variable at first sight, but they have certain commonalities. They are

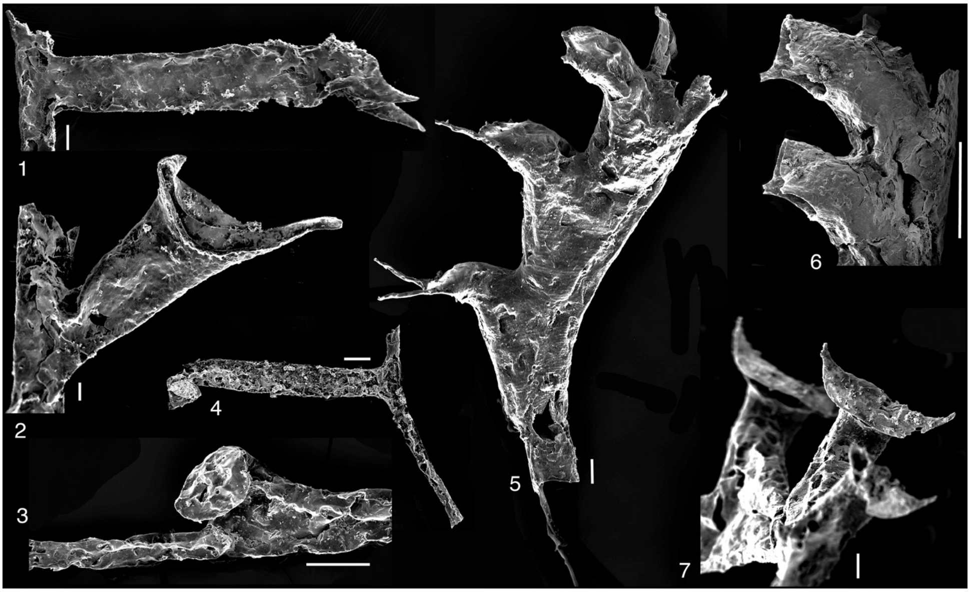


FIG. 298. Thecal style in the Monograptinae. *1–2, Lituigraptus convolutus* (HISINGER, 1837), isolated thecae in lateral (*1*) and ventral (*2*) views; *3*, *Torquigraptus* sp., isolated theca with torsion and laterally widened aperture; *4*, *Rastrites* sp., single theca; *5*, *Spirograptus turriculatus* (BARRANDE, 1850), juvenile; *6*, *Stimulograptus sedgwickii* (PORTLOCK, 1843), two thecae with paired spines; *7*, *Oktavites contortus* (PERNER, 1897), thecal apertures with pointed lateral extensions and wide hood (new). All specimens Kalholn Shale, Dalarna. Scale bars, 1 mm in 6; all others 0.1 mm.

variably elongated with an apertural hood or hook, thus an opening that is proximally or ventrally directed. The shape may change gradually along the stipes in a typical biform fashion. In general, it is triangular with an isolated apertural part, however, parallel-sided isolated prothecae are also common. Metathecae may be completely isolated and parallel sided as in *Rastrites* or in the proximal thecae of *Lituigraptus* (Fig. 298.1–298.2, 298.4) and early *Torquigraptus,* such as *Torquigraptus decipiens* (TÖRNQUIST, 1899). In *Lituigraptus,* the thecae bear paired laterally directed hornlike extensions in distal thecae. The thecal aperture is directed proximally or ventrally and bears a wide dorsal hood (Fig. 298.2). Distally, the thecae are more robust and the prothecae widen considerably (LOYDELL & MALETZ, 2009). The apertural hood may be strongly laterally extended as in *Oktavites contortus* (Fig. 298.7). Thecal overlap may be close to none, as in *Spirograptus* and *Oktavites,* but is absolutely none in *Rastrites,* with its very slender parallel-sided prothecae (Fig. 298.4). Considerable thecal overlap is present in many species of *Monograptus*. *Campograptus harpago* (TÖRNQUIST, 1899) and *Campograptus lobiferus* (M'COY, 1850) have proximal thecae with hooked apertures and distinct paired spines as do species of the genus *Monograptus,* for example, as in *Monograptus priodon.* The spines diminish distally and the thecal apertures curve and grow back on themselves as they also do in *Lapworthograptus grayae* (CHOPEY-JONES, WILLIAMS, & ZALASIEWICZ, 2003). In *Stimulograptus sedgwickii*, the thecal apertures bear paired lateral spines, but a dorsal hood is lacking. The central part of the thecal aperture is directed ventrally with the paired spines in a proximal position (Fig. 298.6), producing a wide and much more open aperture in distal thecae. Proximal thecae clearly possess the apertural hood and paired lateral spines, indicating a considerable transformation of thecal shapes along the stipes in the Monograptinae, leading to the development of biform thecal styles.

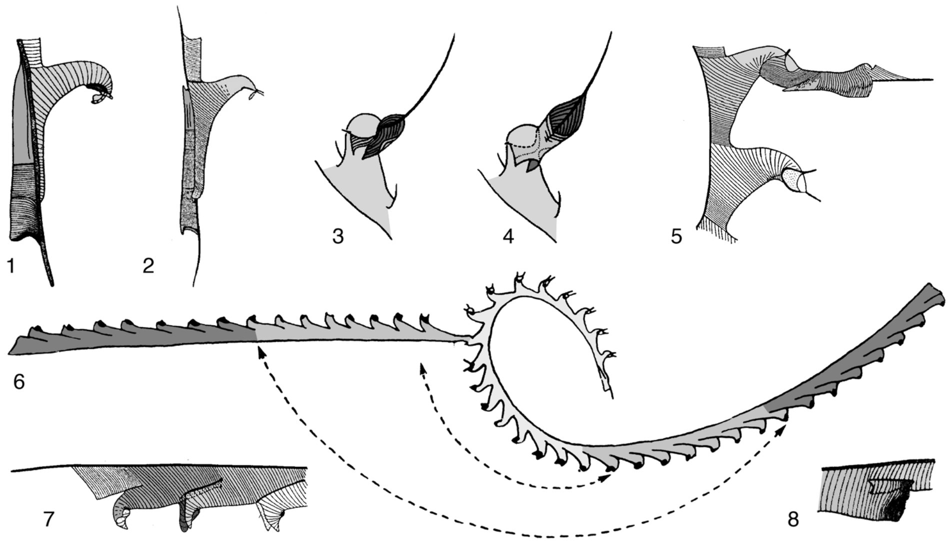


FIG. 299. Tubarium development in *Cyrtograptus*. *1* and *8*, *Cyrtograptus hamatus* (BAILY, 1862) (adapted from Teller, 1976, fig. 11–12); *2–7, Cyrtograptus perneri* BOUČEK, 1933 (*2,5,7;* adapted from Thorsteinsson, 1955, fig. 1–4 as *Cyrtograptus rigidus* n. ssp.; LENZ & others, 2012, p. 32); *3–4*, adapted from Bulman (1955, fig. 47); *6*, adapted from Bulman (1970, fig. 65; correction after Bulman, 1955, fig. 47). Illustrations not to scale.

Torsion of the metathecae occurs in *Torquigraptus,* in which the thecal apertures are twisted to the reverse side of the tubarium, and the thecal hood may be somewhat laterally expanded (Fig. 298.3). Asymmetry without torsion is visible in the thecae of *Spirograptus turriculatus* (Fig. 298.5), in which the second apertural spine is missing in most thecae and the aperture becomes tear-shaped (MELCHIN & LENZ, 1986).

Triangulate thecae with a distinct hood or hook and a proximally oriented aperture bearing paired spines, along with a strong dorsal hood or lobe (Fig. 299.1–299.2), are also present in many *Cyrtograptus* species (see TELLER, 1976). However, their cladial stipes often bear more simple thecae with some thecal overlap and distally directed, paired apertural lobes (Fig. 299.7). These hooked apertures and apertural spines are either symmetrical or asymmetrical in species of *Cyrtograptus* (LENZ & MELCHIN 1989). A distinct thecal gradient from triangulate thecae proximally to those with low inclination may also occur. Increased thecal overlap also signals changes in the apertural development (Fig. 299.6). Simple apertural development, without any hooks, hoods, or lobes, is present in *Cyrtograptus hamatus* (Fig. 299.8) and some other species of the genus *Cyrtograptus*. The genus has been suggested to be polyphyletic (e.g., RICKARDS, HUTT, & BERRY, 1977; FU, 1994; WILLIAMS & ZALASIEWICZ, 2004; URBANEK & TELLER, 1997), and LENZ and others (2012) decided not to use the family Cyrtograptidae but include the genus *Cyrtograptus* in Monograptidae instead.

Taxa with and without cladia are differentiated herein for purely practical reasons. The differentiation does not have any taxonomic implications, and the cladia-bearing taxa may have evolved independently from other taxa of the Monograptinae. The presence or absence of cladia cannot be regarded as a useful taxonomic character but has been used as an important and even defining character for the genus *Cyrtograptus* in the past.

## TAXA WITHOUT CLADIA

RICKARDS, HUTT, and BERRY (1977; fig. 1) provided the only available interpretation of early monograptids, suggesting the origination of several independent lineages from the genus *Atavograptus* and of the *Monograptus priodon* group from *Monoclimacis*. The taxa of the Monograptinae without cladia form a paraphyletic taxon and gave rise to cladia-bearing taxa multiple times.

**Campograptus** Obut, 1949, p. 24 [**Monograptus convolutus* var. *communis* Lapworth, 1876b, p. 358; SD Obut, 1964, p. 328]. Tubarium gently to strongly dorsally curved proximally, becoming almost straight distally; thecae triangular with no overlap; prothecal bases broad; simply hooked metathecae, thecal hook proximally involving primarily dorsal and, to much lesser extent, ventral thecal wall, and mesially and distally probably dorsal wall only; thecal apertures of proximal, mesial and, in some species, even distal thecae possess paired ventro-laterally or proximo-laterally directed spines; proximal thecae may be axially elongated. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone–*Stimulograptus sedgwickii* Biozone): worldwide.——Fig. 300,*1a–b*. **C. communis* (Lapworth); *1a,* lectotype (Přibyl, 1948a, p. 48), BU 1684a, proximal end not shown (Lapworth, 1876b, fig. 4a); *1b,* proximal end in relief, internal mould, SM A24487, C horizon (*Demirastrites triangulatus* Biozone), Rheidol Gorge (Sudbury, 1958, fig. 20). Scale bars, 1 mm.

**Cochlograptus** Obut, 1987, p. 142 [**Nautilus veles* Richter, 1871, p. 243, fig. 1; OD]. Disk-shaped, ventrally and continuously planispirally coiled tubarium with sharp ventral deflection near apex of sicula; tubarium development by means of pseudovirgula; sicula moderately to strongly ventrally curved; prominent triangular dorsal tongue on sicular aperture; thecae hooked, with well-developed, paired lateral spines. *Silurian, Llandovery* (*Telychian, Streptograptus crispus* Biozone–*Oktavites spiralis* Biozone): worldwide.——Fig. 300,*2a–b*. **C. veles* (Richter); *2a,* lectotype, BGR X11901a, Thuringia, Germany (precise locality unknown) (Maletz, 2001a, fig. 3a); *2b,* holotype of *Monograptus discus* Törnquist, 1883, LO 1071T, Kallholn, Dalarna, Sweden (Maletz, 2017c, fig. 6D). Scale bars, 1 mm.

**Cultellograptus** Loydell & Nestor, 2006, p. 602 [**Monograptus cultellus* Törnquist, 1881, p. 434; OD]. Tubarium straight, except for initial ventral curvature that involves the sicula; thecae with extremely wide metathecae, hooked, nonspinose, lacking overlap; common canal narrow. *Silurian, Llandovery* (*Telychian, Oktavites spiralis* Biozone)–*Wenlock* (*Sheinwoodian, Cyrtograptus murchisoni* Biozone): UK, Czech Republic, Germany, Romania, Baltic States, Sweden, Morocco.——Fig. 300,*9a–b*. **C. cultellus; 9a,* MGUH 31.681, Sommerodde-1 core, Bornholm, Denmark, (Loydell & others, 2017, fig. 16I); *9b,* isolated proximal end, Ventspils D-3 drill core, Latvia (adapted from Loydell & Nestor, 2006, fig. 9E). Scale bars, 1 mm.

**Demirastrites** Eisel, 1912, p. 27 [**Rastrites triangulatus* Harkness, 1851, p. 59; SD Bulman, 1929, p. 175]. Tubarium with proximally accentuated dorsal curvature; sicula small, apex reaching to about level of first metatheca at maximum; metathecae isolated, inclined at high angle to the tubarium axis; thecal apertural hoods or hooks may be extended transversely into a pair of lateral horns; mesial and distal thecae are more or less high-triangular in profile; first theca rastritid or triangular, axially elongated; up to several succeeding proximal thecae may have very slender elongated prothecae, slightly widening toward the base of widely separated, parallel-sided rastritiform metathecae. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone–*Demirastrites pectinatus* Biozone): worldwide.——Fig. 300,*3a–c*. **D. triangulatus* (Harkness); *3a,* lectotype (Přibyl & Münch, 1941, p. 5), strongly distorted specimen, BGS 6941, Birkhill Shales, Frenchland Burn, Scotland (Zalasiewicz, 2008e, Atlas, Folio 2.92); *3b,* specimen missing proximal end, PŠ 3517, Všeradice, Czech Republic (Štorch, 2015, fig. 17f); *3c,* proximal end, PŠ 3643, Všeradice, Czech Republic (Štorch, 2015, fig. 17m). Scale bars, 1 mm.

**Lapworthograptus** Bouček & Přibyl, 1952b, p. 13, *ex Monograptus* (*Lapworthograptus*) Bouček & Přibyl, 1952b, p. 13; Zalasiewicz, 1995, p. 30. [**Cyrtograptus Grayi* Lapworth, 1876d, p. 545; OD] [=*Prochnygraptus* Přibyl & Štorch, 1985, p. 159 (type, *Monograptus singularis* Törnquist, 1892, p. 22, OD), syn. by Zalasiewicz, 1995, p. 34]. Tubarium irregularly curved or coiled in loose spiral; prothecae narrow, expanding gradually distally; metathecae initially growing ventrally to dorso-ventrally, then bending sharply through 180 degrees to grow dorsally; thecal apertures face dorsally or proximally. [Possible cladium only known from holotype (Zalasiewicz & Loydell, 2008); needs to be verified.] *Silurian, Llandovery, Telychian* (*Monoclimacis crenulata* Biozone–*Oktavites spiralis* Biozone): UK, Germany, Sweden, Baltic States.——Fig. 301,*3a–c*. **L. grayae* (Lapworth); *3a–b*, holotype, NHMUK Q847, specimen and thecal detail, Penwhapple Glen, Girvan, Scotland, scale bars, 5 mm (Zalasiewicz & Loydell, 2008, Atlas, Folio 2.33); *3c,* isolated thecae, NRM PZ Holm 1352, Stygforsen, Dalarna, Sweden, scale bar, 1 mm (Bulman, 1932c, pl. 6,*13*–6,*14*).——Fig. 301,*3d. L. singularis* (Törnquist, 1892), PŠ 218/1, fragment, Prague-Řepy, Czech Republic, scale bar, 1 mm (Přibyl & Štorch, 1985, fig. 3C).

**Lituigraptus** Ni, 1978, p. 412, *ex Rastrites* (*Lituigraptus*) Ni, 1978, p. 412, Štorch, 1998a, p. 248 [**Rastrites* (*Lituigraptus*) *glomeratus;* OD; =*Prionotus convolutus* Hisinger, 1837, syn. by Štorch, 1998a, p. 248] [=*Corymbites* Obut & Sobolevskaya in Obut, Soboleveskaya, & Nikolaev, 1967, p. 132 (type, *C. sigmoidalis,* OD) syn. by Loydell, herein; *non Corymbites* Linnaeus, 1758 (Coleoptera, Elateridae, modern beetle)]. Dorsally enrolled spiral tubarium; distally tubarium axis may gradually twist and thecae may be situated ventrally or perpendicular to spiral plane; proximal thecae rastritiform, with thread-like prothecae and straight, tubular metathecae

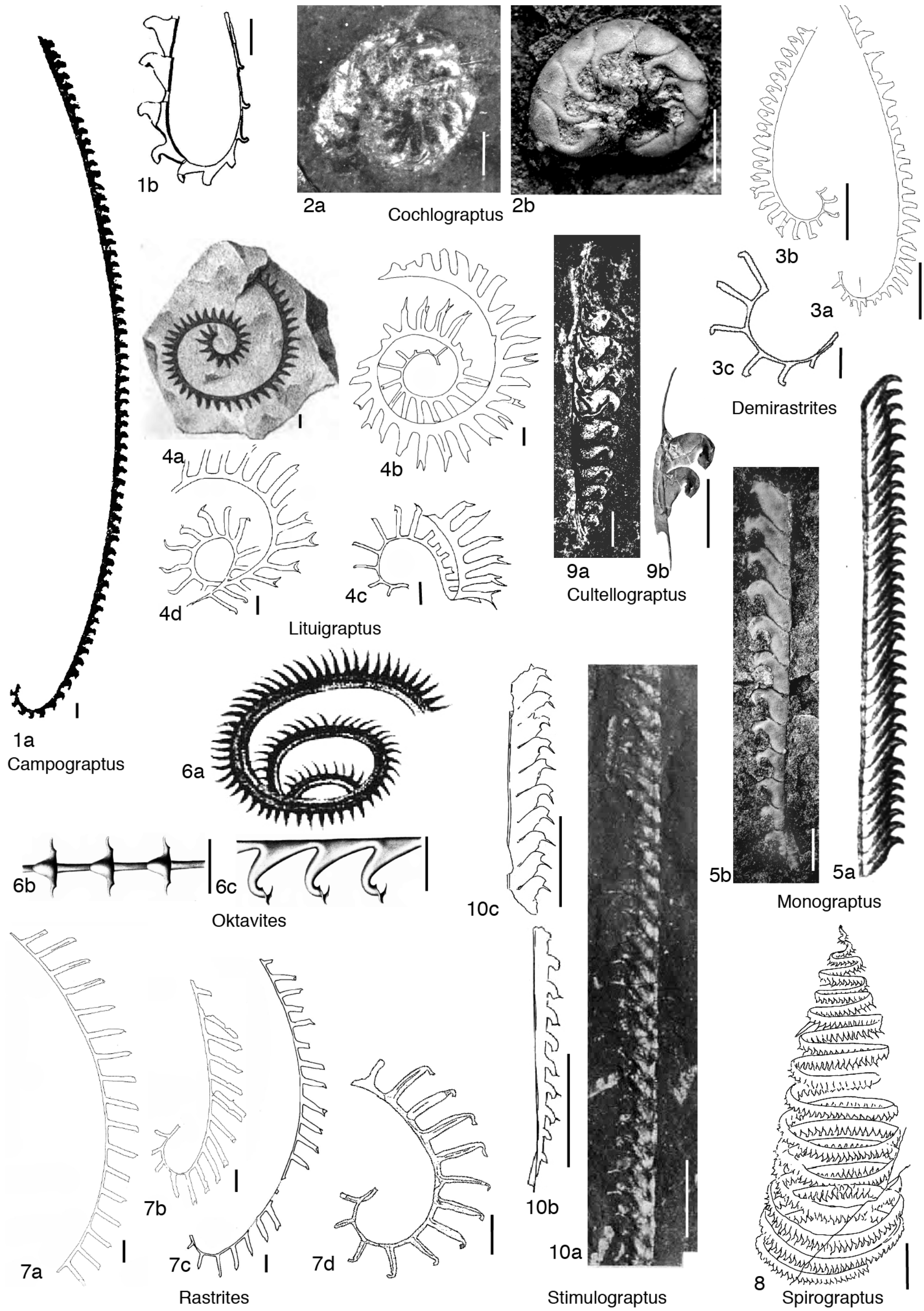


FIG. 300. Monograptinae (p. 443–446).

with hooded apertures; mesially thecae gradually become high triangular; apertural hoods gradually retreat being substituted by prominent paired, ventrally to ventro-proximally directed, lateral processes. *Silurian, Llandovery* (*Aeronian, Demirastrites simulans* Biozone–*Telychian, Spirograptus guerichi* Biozone): worldwide.——FIG. 300,*4a–d*. *P. convolutus* (HISINGER); *4a,* holotype, NRM Cn 68951, Furudal, Dalarna, Sweden (Hisinger, 1837, pl. 35.*7*); *4b,* medium-sized specimen with thecal apertures, BB 697, Tmaň, Czech Republic (Štorch, 1998a, fig. 11.*7B*); *4c,* proximal end with sicula, PŠ 724, Tmaň, Czech Republic (Štorch, 1998a, fig. 11,*7D*); *4d*, holotype of **L. glomeratus* NI, 1978, NIGP 45401 (NI, 1978, fig. 7.*7*). Scale bars, 1 mm.

**Monograptus** GEINITZ, 1852, p. 32, *nom. correct. pro Monograpsus* GEINITZ, 1852, p. 32; ICZN, Opinion 198, 1954b; *pro Lomatoceras* BRONN, 1835, p. 56; *pro Monoprion* BARRANDE, 1850, p. 36, ICZN, Opinion 198, 1954b [**Lomatoceras priodon* BRONN, 1835; SD BASSLER, 1915b, p. 822] [=*Pomatograptus* JAEKEL, 1889, p. 677 (type, *Lomatoceras priodon* BRONN, 1835, SD BULMAN, 1929, p. 180), obj.; =*Priodon* NILSSON cited in BRONN, 1835, p. 56; =*Ancylograptus* OBUT & MOROZOVA in OBUT & others, 1988, p. 62; *ex Monograptus* (*Ancylograptus*) OBUT & MOROZOVA in OBUT & others, 1988, p. 62 (type, *Monograptus flexilis* ELLES, 1900, p. 407; OD; =*Graptolithus* (*Monograpsus*) *belophorus* MENEGHINI, 1857, p. 165, type syn. by ŠTORCH & MANDA, 2019, p. 53), syn. herein]. Tubarium straight or dorsally curved proximally and then straight; thecae hooked with or without paired apertural spines or processes; thecal apertures face proximally or proximo-dorsally; thecae overlap, typically for half their length or more distally. *Silurian, Llandovery* (*Telychian, Spirograptus guerichi* Biozone–*Wenlock, Homerian, Colonograptus praedeubeli-deubeli* Biozone): worldwide.——FIG. 300,*5a–b*. **M. priodon* (BRONN); *5a,* holotype, fragment (Bronn, 1835, pl. 1.*13;* not found in the Bronn collection at the Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (personal communication, Jessica D. Cundiff, 2014), scale unknown; *5b,* proximal end in relief, SMF 75780, glacial boulder, scale bar, 1 mm (Maletz, 2017a, pl. 15B).

**Oktavites** LEVINA, 1928, p. 10 [**Graptolithus spiralis* GEINITZ, 1842, p. 700; SD OBUT, 1964, p. 328] [=*Obutograptus* MU, 1955, p. 10 (type, *Graptolithus spiralis* GEINITZ, 1842, p. 700, OD, obj.)]. Dorsally curved or spirally coiled tubarium; metathecae triangular, sometimes almost rastritiform proximally, with little or no overlap; thecal apertures laterally expanded, sometimes asymmetrically; torsion, affecting the entirety of metatheca, developed distally; extension of metathecal dorsal wall over central portion of aperture causes this to face dorsally. *Silurian, Llandovery* (*Aeronian, Stimulograptus sedgwickii* Biozone–*Telychian, Cyrtograptus lapworthi* Biozone): worldwide.——FIG. 300,*6a–c*. **O. spiralis* (GEINITZ); *6a,* syntype (not preserved, see MALETZ, 2001a, p. 171) (Geinitz, 1842, pl. 10.*26*); *6b–c,* stipe fragments showing thecal style, Dalarna, Sweden (Bulman, 1932c, pl. 6,*15–16*). Scale unknown.

**Rastrites** BARRANDE, 1850, p. 64 [**R. peregrinus;* SD HOPKINSON, 1869, p. 158] [=*Rastrograptus* HOPKINSON & LAPWORTH, 1875, p. 633 *pro Rastrites* BARRANDE, 1850; =*Stavrites* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968, p. 111 (type, *S. rossicus,* OD), syn. by LOYDELL, herein]. Tubarium straight or dorsally curved proximally to various degrees, straight distally; threadlike prothecae; straight, isolated metathecae, inclined at high angle to tubarium axis throughout length of colony; thecal apertures slightly hooked or hooded, sometimes with small paired apertural spines or lateral extensions. [RICKARDS, HUTT, and BERRY (1977) and ŠTORCH and LOYDELL (1992) discussed a possibly polyphyletic concept of the genus]. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone–*Telychian, Monoclimacis griestoniensis* Biozone): worldwide.——FIG. 300,*7a–c*. **R. peregrinus; 7a,* lectotype, fragment, NMP L27954, Libomyšl, Czech Republic (Štorch, 2000b, Atlas, Folio 1.87); *7b,* complete specimen, NMP L30073, Bykoš, Czech Republic (Štorch, 2000b); *7c,* long specimen with complete sicula, PŠ 724, Tmaň, Czech Republic (Štorch, 1998a, fig. 11,*3B*).——FIG. 300,*7d. R. rossicus* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968) holotype, CNIGR 270/9765 (Sun & others, 2022, fig. 12Q). Scale bars, 1 mm.

**Spirograptus** GÜRICH, 1908, p. 34 [**Graptolithus turriculatus* BARRANDE, 1850, p. 56; SD BULMAN, 1929, p. 182] [=*Tyrsograptus* OBUT, 1949, p. 24 (type, *Graptolithus turriculatus* BARRANDE, 1850, p. 56, SD OBUT, 1964, p. 328), obj.]. Tubarium trochospirally coiled; sicula small (<1.5 mm) and dorsally curved, and in one species at least also exhibits dextral torsion; thecae hooked in manner of those of *Stimulograptus,* and bearing one or two apertural spines; thecal apertures may be symmetrical or asymmetrical resulting from differential development of the apertural margin, but without significant torsion; thecal overlap is negligible; common canal wide. *Silurian, Llandovery* (*Aeronian, Stimulograptus halli* Biozone–*Telychian, Streptograptus sartorius* Biozone): worldwide.——FIG. 300,*8*. **S. turriculatus* (BARRANDE), lectotype, NMP L27597, Litohlavy, Czech Republic, scale bar, 5 mm (Štorch, 2000c, Atlas, Folio 1.92).

**Stimulograptus** PŘIBYL & ŠTORCH, 1983, p. 221, *ex Monograptus* (*Stimulograptus*) PŘIBYL & ŠTORCH, 1983, p. 221[**Graptolithus halli* BARRANDE, 1850, p. 48; OD]. Tubarium straight, dorso-ventrally curved, or dorsally curved proximally then straight distally; sicula less than 2 mm long; hooked, triangular thecae bear paired latero-ventrally directed spines; thecal overlap insignificant; distal thecae may be ventrally directed and without hook. *Silurian, Llandovery* (*Aeronian, Lituigraptus convolutus* Biozone–*Telychian, Oktavites spiralis* Biozone): worldwide.——FIG. 300,*10a–c*. **S. halli* (BARRANDE); *10a,* lectotype, NMP L20322, *Rastrites*

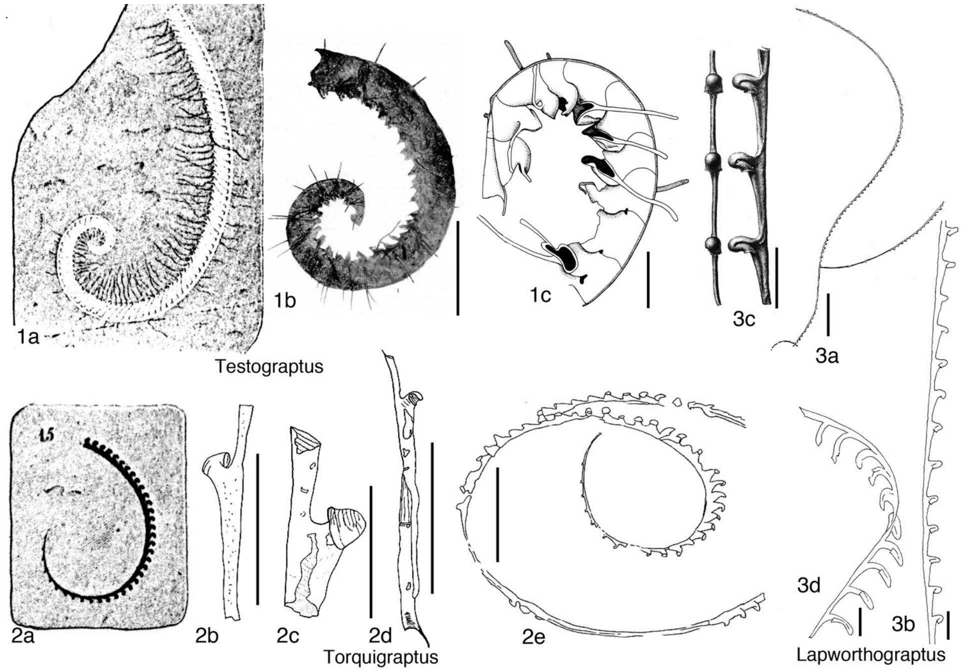


FIG. 301. Monograptinae (p. 443–446).

*linnaei* Biozone, Želkovice, Czech Republic (Přibyl & Štorch, 1983, pl. 2.*1*); *10b,* proximal end, PŠ 106b, Hlásná Třebaň, Czech Republic (Přibyl & Štorch, 1983, fig. 2A); *10c,* distal fragment, PŠ 108/3, Hlásná Třebaň, Czech Republic (Přibyl & Štorch, 1983, fig. 2B). Scale bars, 5 mm.

**Testograptus** PŘIBYL, 1967a, p. 49, *ex Monograptus* (*Testograptus*) PŘIBYL, 1967a, p. 49; LOYDELL & CAVE, 1994, p. 612 [**Graptolithus testis* BARRANDE, 1850; OD]. Tubarium planispirally and ventrally coiled through up to 450°, curvature strongest proximally with abrupt ventral flexure immediately distal of sicular apex; sicula weakly ventrally curved; tubarium development occasionally by means of pseudovirgula; thecae biform, with long, paired, laterally directed spines; proximalmost thecae with strongly hooked metatheca, distal thecae with lesser hook; thecal overlap ~50–75%. *Silurian, Wenlock* (*Homerian*, *Cyrtograptus lundgreni* Biozone): worldwide.——FIG. 301,*1a–c*. **T. testis* (BARRANDE); *1a,* ?lectotype, scale unknown (Barrande, 1850, pl. 3.*19*); *1b,* isolated specimen, scale bar, 5 mm (Urbanek & Teller, 1974, pl. 24); *1c,* small isolated specimen showing tubarium details, scale bar, 1 mm (Urbanek & Teller, 1974, fig. 1).

**Torquigraptus** LOYDELL, 1993, p. 112 [**Graptolithus proteus* var. *plana* BARRANDE, 1850, p. 58; OD]. Tubarium curved, or coiled, bearing thecae that exhibit torsion only of apertural part of the metatheca, toward reverse side of tubarium, in most cases throughout length of the colony, in some species only mesially and distally; thecal apertures simple, with no marked asymmetry or lateral expansion; early thecae may be axially elongate or rastritiform; distal thecae triangulate. *Silurian, Llandovery* (*Aeronian, Pribylograptus leptotheca* Biozone–*Telychian, Oktavites spiralis* Biozone): worldwide.——FIG. 301,*2a–e*. **T. planus* (BARRANDE); *2a,* ?holotype, Czech Republic (Barrande, 1850, pl. 4.*15*); *2b–d,* isolated specimens, Dalarna, Sweden, scale bars 1 mm (Hutt, Rickards, & Skevington, 1970, pl. 3,*51–52,54,* as *Monograptus proteus*); *2e,* large specimen, Wales, UK, scale bar, 5 mm (Loydell, 1993, fig. 21,*19*).

## TAXA WITH CLADIA

The cladia-bearing Monograptinae have previously been included in the family Cyrtograptidae (see AVERIANOW, 1929; BOUČEK, 1933). YIN (1937) defined the subfamily Cyrtograptinae as branched, suggesting the presence of cladia as the sole character to separate the taxon from the rest of the Monograptidae. BULMAN (1955, 1970) separated the Cyrtograptidae, with its two subfamilies Cyrtograptinae and Linograptinae, from the Monograptidae. It is now clear that the Cyrtograptidae is not as useful taxonomically as was originally intended and needs to be abandoned. Cladia appear independently in a number of monograptid lineages. The compilation of the cladia-bearing taxa here is for purely practical reasons and does not imply any phylogenetic relationship.

**Cyrtograptus** CARRUTHERS in MURCHISON, 1867a, p. 540, *nom. correct.* LAPWORTH, 1873b original spelling as *Cyrtograpsus* changed in ICZN Opinion, 650, 1963; *non Cyrtograpsus* DANA, 1851, p. 288 (Decapoda) [**C. murchisoni;* OD] [=*Pleurograptoides* AVERIANOW, 1931, p. 21 (type, *P. erectus,* OD), syn. by LOYDELL, herein; =*Averianowograptus* OBUT, 1949, p. 29 (type, *Cyrtograptus magnificus* AVERIANOW, 1931, p. 9, OD), syn. by LOYDELL, herein; =*Damosiograptus* OBUT, 1950, p. 270 (type, *Cyrtograptus spiralis* AVERIANOW, 1931, OD), syn. by RICKARDS, HUTT, & BERRY, 1977, p. 76; =*Uralograptus* KOREN', 1962, p. 724 (type, *U. insuetus* KOREN', 1962, p. 724, OD), syn. by BULMAN, 1970, p. 135; =*Kurganakograptus* GOLIKOV, 1969, p. 515 (type, *K. primus*, OD), syn. by LOYDELL, herein]. Dorsally curved, low helically spiralled or dorsally curved then straight tubarium bearing at least one thecal cladium; thecae of main stipe hooked throughout, often laterally expanded and spinose, or hooked proximally then with hooks retreating distally, becoming hooded initially and then simple tubes with lateral lappets flanking aperture; thecae of thecal cladia hooked, hooded, simple adnate or isolated tubes in some cases with lateral lappets flanking aperture; secondary and tertiary cladia may develop from cladial thecae. [The genus has been considered polyphyletic, e.g., RICKARDS, HUTT, and BERRY (1977) and needs re-investigation]. *Silurian, Llandovery* (*Telychian, Cyrtograptus lapworthi* Biozone)–*Wenlock* (*Homerian,* Cyrtograptus *lundgreni* Biozone): worldwide.——FIG. 302,*1a–c*. **C. murchisoni,* Builth District, Wales; *1a,* counterpart of holotype, GSM 10718; *1b,* topotype, proximal end, GSM 10716; *1c,* topotype, proximal end with sicula, GSM 10716, scale bars, 5 mm, 1 mm in *1b* (*a–c,* Zalasiewicz & Williams, 2008, Atlas, Folio 2.60).——FIG. 302,*1d. C. insuetus* (KOREN'), holotype, scale bar, 5 mm (Rickards, Hutt, & Berry, 1977, fig. 39).——FIG. 302,*1e. C. magnificus* (AVERIANOW), holotype, scale bar, 5 mm (Obut, 1950, fig. 6).

**Barrandeograptus** BOUČEK, 1933, p. 62, *ex Monograptus* (*Barrandeograptus*) BOUČEK, 1933, p. 62; MÜNCH, 1938, p. 53][**Cyrtograptus pulchellus* TULLBERG, 1883, p. 36; OD]. Slender tubarium, strongly dorsally and/or ventrally curved proximally, less strongly curved distally; up to at least three orders of thecal cladia may be developed; thecae slender and axially elongated; proximally appearing hooked; distal thecae triangular tubes typically with pronounced notch between dorsal wall and ventral wall of succeeding protheca; apertures of distal thecae may be furnished with lateral lappets. *Silurian, Llandovery* (*Telychian, Oktavites spiralis* Biozone)–*Wenlock* (*Sheinwoodian, Monograptus riccartonensis* Biozone): worldwide.——FIG. 302,*2a–c, d*?. **B. pulchellus* (TULLBERG); *2a,* holotype, SGU 5684, complete specimen showing sicula, Röstånga, Scania, Sweden (Tullberg, 1883, pl. 3.*12*); *2b–c,* MGUH (MMH) 13497, fragments showing distal thecal style (Bjerreskov, 1975, fig. 27C–D); *2d,* proximal theca tentatively referred to *B. pulchellus,* inverted SEM photo (Loydell & Nestor, 2006, fig. 13C). Scale bars, 1 mm; 0.2 mm in *2d.*

**Diversograptus** MANCK, 1923, p. 283 [**D. ramosus;* SD BULMAN, 1929, p. 176] [=*Dibranchiograptus* HUNDT, 1949a, p. 19 (type, *D. bibrachiatus,* OD), syn. by LOYDELL, herein]. Narrow tubarium comprising main stipe and one sicular cladium with or (usually) without thecal cladia; stipes straight or gently curved; thecae hooked, with retroflexed apertures flanked by small lateral lappets. *Silurian, Llandovery* (*Telychian, Oktavites spiralis* Biozone–*Cyrtograptus lapworthi* Biozone): Germany, UK (Wales, Scotland), Estonia, Latvia, Czech Republic, Turkey, Morocco.——FIG. 302,*3a–c*. **D. ramosus; 3a,* lectotype (selected by BOUČEK & PRIBYL, 1953, p. 489), repository unknown, scale bar, 5 mm (reconstruction from Bulman, 1970, fig. 102,*3a*); *3b,* specimen showing bipolar growth, MGM 146-S, Jabalón River section, central Spain, scale bar, 1 mm (Loydell & others, 2009, fig. 4J); *3c,* stipe fragment, MGM 419-52, Aizpute-1 drill core, Latvia, scale bar, 1 mm (Loydell & Nestor, 2006, fig. 11C).——FIG. 302,*3d–e. D.*? *pergracilis* (BOUČEK, 1931, p. 302), fragments showing thecal style, Ventspils D-3 drill core, 826.7 m, Latvia (Loydell & Nestor, 2006, fig. 12A–B). Scale bars, 1 mm (*d*); 0.1 mm (*e*).

**Paradiversograptus** SENNIKOV, 1976, p. 225, *ex Monograptus* (*Paradiversograptus*) SENNIKOV, 1976, p. 225; LOYDELL, 1993, p. 143 [**Rastrites capillaris* CARRUTHERS, 1867b, p. 368; OD]. Gently ventrally or dorso-ventrally curved tubarium; sicular cladium; metathecae simply hooked; no thecal overlap. *Silurian, Llandovery* (*Aeronian, Lituigraptus convolutus* Biozone–*Telychian, Spirograptus guerichi* Biozone): worldwide.——FIG. 302,*4a–b*. **P. capillaris* (CARRUTHERS); *4a,* holotype, NHMUK Q86, stipe fragments, Birkhill Shales, Moffat, Dumfriesshire, Scotland, UK (Strachan, 1969, fig. 6a); *4b,* proximal end, BB 696, Tmaň, Czech Republic (Štorch, 1998a, fig. 8,*3*). Scale bars, 1 mm.——FIG. 302,*4c–d. P. runcinatus* (LAPWORTH, 1876e), Glenkiln Burn, Dumfriesshire, Scotland, UK; *4c*, proximal end in relief; *4d,* specimen with sicular cladium (Strachan, 1952, fig. 1B–C). Scale bars, 1 mm.

**Sinodiversograptus** MU & CHEN, 1962a, p. 147 [**S. multibrachiatus;* OD; =*Streptograptus lientanensis* MU, 1948, syn. by LOYDELL, 1990a, p. 847]. Tubarium with sicular cladium and thecal cladia; sicula small; both main stipe and sicular

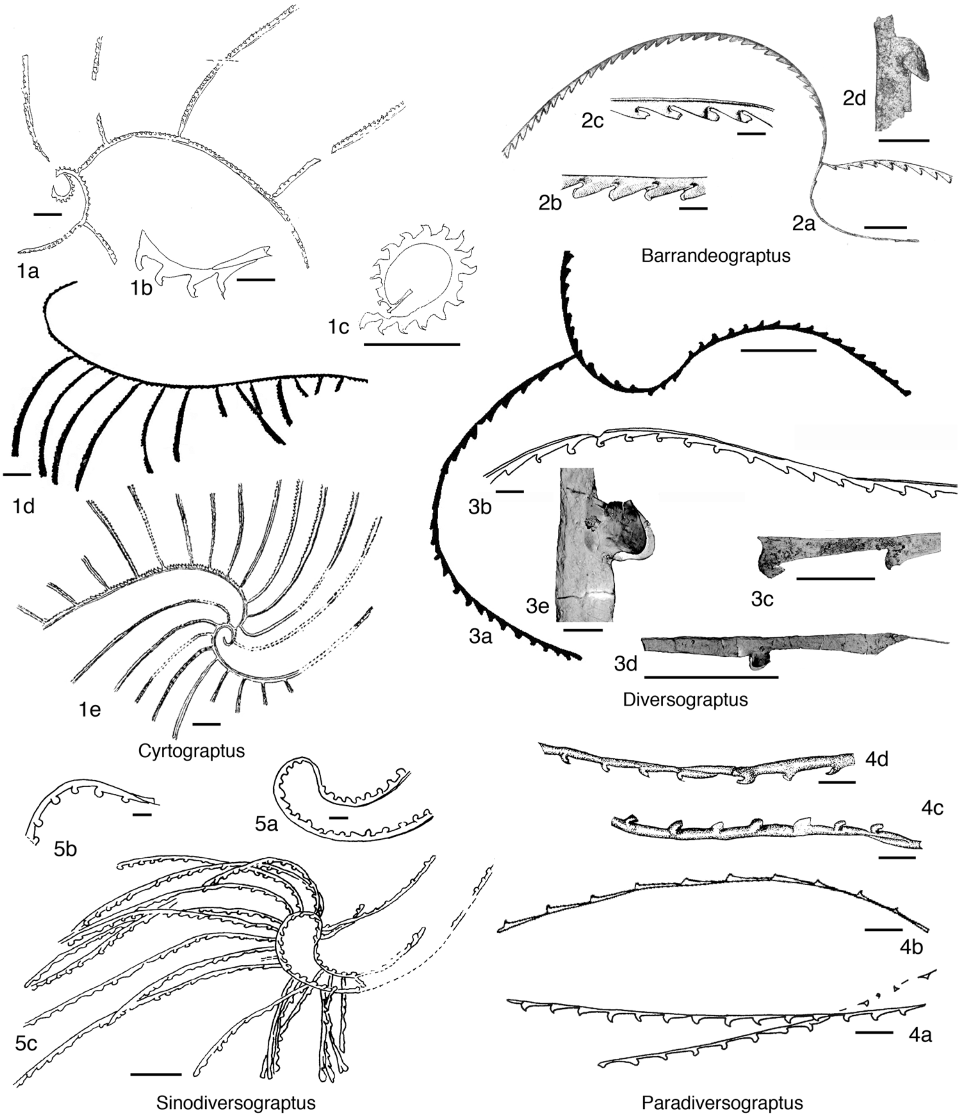


FIG. 302. Monograptinae with cladia (p. 447–448).

cladium ventrally curved, with curvature decreasing distally; tubarium developed through three stages: monograptid, diversograptid (with sicular cladium), and sinodiversograptid (with thecal cladia); metathecae hooked; gently ventrally curved cladia originated from almost all proximal and mesial thecae. *Silurian, Llandovery* (*Telychian*, *Spirograptus guerichi* Biozone): Australia, Canada, China.——FIG. 302,*5a–c*. *S. lientanensis* (MU); *5a,* holotype, specimen with sicular cladium, Lientan, Guandong Province, China, scale bar, 5 mm (LOYDELL, 1990a, fig. 2.*5*); *5b,* small proximal end, Lientan, Guandong Province, China, scale bar, 1 mm (Loydell, 1990a, fig. 2.*1*); *5c.* holotype of **S. multibrachiatus* (MU & CHEN), mature specimen with numerous cladia, NIGP 11580a, Qiaoting, Nanjiang District, Sichuan Province, China, scale bar, 5 mm (Loydell, 1990a, fig. 1).

## Subfamily PRISTIOGRAPTINAE Gürich, 1908

[*nom. correct*. PŘIBYL, 1946, p. 277, *ex* Unterfamilie Pristiograptidi GÜRICH, 1908, p. 32] [=Heisograptinae TSEGELNJUK, 1976, p. 102; =Saetograptinae URBANEK, 1958, p. 50; =Uncinatograptinae TSEGELNJUK, 1976, p. 96; =Wolynograptinae TSEGELNJUK, 1976, p. 110; herein]

Tubarium straight or gently dorsally or ventrally curved proximally; thecal length increasing along first few thecae, later constant in most taxa, but may increase in others; sicula of medium length with low metasicular origin of th1; thecae usually straight, with straight or nearly straight, outward-inclined ventral wall; rarely, proximal thecae with isolation of metathecae; geniculum may be present; thecal aperture straight, outward-inclined to hooked, or provided with lateral lobes or spines; thecal style may be modified considerably in derived taxa. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone)–*Lower Devonian* (*Emsian, Uncinatograptus yukonensis* Biozone): worldwide.

The Pristiograptinae are difficult to define in the light of the numerous species included in the genus *Pristiograptus* and the independently derived lineages from this stem. Rickards, Hutt, and Berry (1977) provided an overview of the then identified taxa and their biostratigraphic ranges. Earliest taxa were considered close to *Atavograptus* by the authors. They differentiated the *Pristiograptus regularis* (Llandovery) and *Pristiograptus dubius* (upper Llandovery *Spirograptus turriculatus* Biozone and upward) lineages as having only short biostratigraphical overlap during the upper Llandovery.

Tsegelnjuk (1976) erected a number of subfamilies that are here referred to the Pristiograptinae. Tsegelnjuk (1998, p. 271) especially discussed the Uncinatograptinae and their stratigraphical value in the upper Silurian. Due to the incomplete knowledge of many tubarium characters, these subfamilies are not differentiated herein, awaiting a detailed phylogenetic analysis based upon well-preserved material. The Pristiograptinae are considered to derive from an ancestor in the genus *Atavograptus* during the Rhuddanian, early Silurian (see Rickards, Hutt, & Berry, 1977; Štorch, 1988). Evolutionary investigations of this clade, however, are largely restricted to the *Pristiograptus dubius* lineage. *Pristiograptus dubius* is a particularly long-ranging taxon from which a number of derived taxa originated, leading to iterative speciation and the evolution of new groups of monograptids (Urbanek & others, 2012; Whittingham, Radzevičius, & Spiridonov, 2020).

## MORPHOLOGY

The morphology of early Pristiograptinae is fairly simple, with basically straight tubarium shapes and simple thecae having an angular, straight aperture, typically adorned only with a thickened rim (Fig. 303.1–303.2). Dorsal curvature is present in *Formosograptus*, *Slovinograptus,* and *Wolynograptus*, associated with thecal elongation and isolation of metathecae. Distally, the thecae possess increasing overlap in these taxa. Ventral curvature may be present and affects the sicula and very few proximal thecae. Regular ventral curvature is typical for *Pristiograptus paradoxus* Loydell & Walasek, 2019 and *Pristiograptus macrodon* Štorch, 1992, both of which exhibit only slight dorso-ventral curvature. Further examples of this are *Pseudomonoclimacis tetlitensis* Lenz, 1988b and *Monograptus banksi* Rickards & others, 1995.

The sicula is straight to somewhat curved ventrally and, in many species, bears a variable number of sicular annuli (Fig. 303.4). The number and position of the sicular annuli appears to have become stabilized during the uppermost Silurian during which most taxa possessed three or fewer annuli (Urbanek, 1997a).

The prosicula is small and slender and bears a small number of longitudinal rods (Fig. 303.6). The metasicula widens gradually, except in taxa with trumpetlike siculae such as *Colonograptus deubeli* (Jaeger, 1959) and a number of other taxa, including some Early Devonian forms (see Jaeger, 1988). Apertural modifications of the sicula are rare, but dorsal lappets are present in a number of taxa (Fig. 303.4), and slight lateral lappets or lobes appear to be present in *Uncinatograptus falcarius* (Fig. 303.6) and probably in other related taxa.

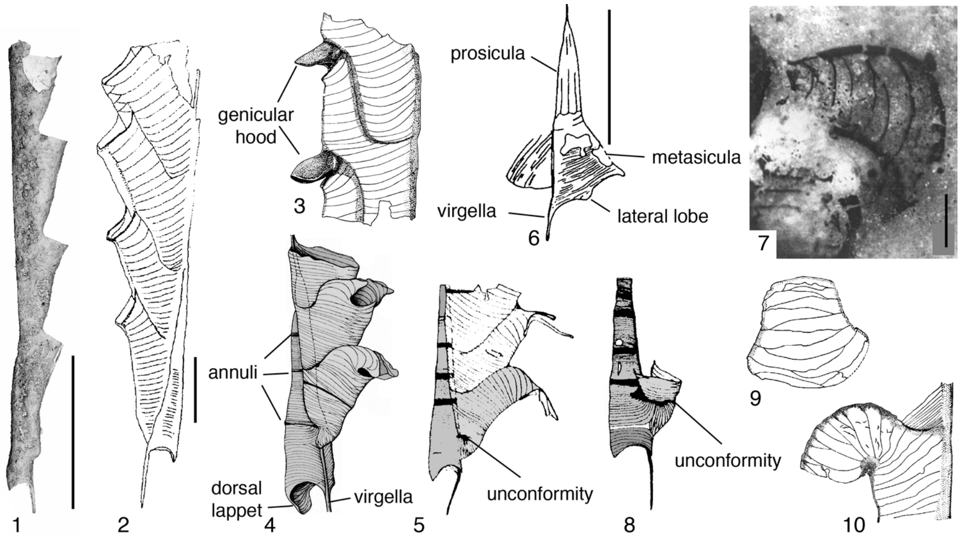


FIG. 303. Morphology of Pristiograptinae. *1, Pristiograptus* sp. cf. *Pristiograptus regularis* (TÖRNQUIST, 1899) (SEM photo inverted from Russel-Houston, 2001, pl. 12C); *2, Pristiograptus frequens* JAEKEL, 1889, proximal end in obverse view showing thecal shape (Maletz, 1999a, fig. 2R); *3, Heisograptus micropoma* (JAEKEL, 1889), development of microfusellar hoods (Urbanek, 1958, fig. 67); *4, Skalograptus lochkovensis* (PŘIBYL, 1940a), proximal end (adapted from Urbanek, 1997a, fig. 49); *5, Saetograptus chimaera* (BARRANDE, 1850), proximal end (adapted from Walker 1953, fig. 4G); *6–7, Uncinatograptus falcarius* (KOREN', 1969), showing sicular development and formation of dorsal hood (Koren', Kim & Walliser, 2007, fig. 4R, pl. 1.*9*); *8, Pristiograptus dubius* (SUESS, 1851), juvenile in reverse view, showing prothecal unconformity (Walker, 1953, fig. 2B); *9–10, Uncinatograptus uncinatus* (TULLBERG, 1883), development of thecal hood (Urbanek, 1958, fig. 21). Scale bars, 1 mm; reconstructions, no scale.

The origin of th1 may be through a sinus and lacuna development in all Pristiograptinae but has been verified from only a few taxa. It has been described in *Pristiograptus frequens* (EISENACK, 1942), *Heisograptus micropoma* (MALETZ, 1999a), *Wolynograptus acer* (URBANEK, 1997a), *Formosograptus* (URBANEK, 1997a), and *Skalograptus* (URBANEK, 1997a). LUKASIK and MELCHIN (1994) illustrated a possible primary porus in *Pristiograptus* sp. cf. *Pristiograptus regularis* from Arctic Canada. WALKER (1953) described in great detail the early growth of th1 in *Pristiograptus* and *Saetograptus* from glacial boulders found in northern Germany. The specimens show a distinct unconformity in the early growth on the reverse side but not on the obverse side in *Pristiograptus* (Fig. 303.8) and to a lesser extent in *Saetograptus* (Fig. 303.5).

Many taxa have a gradient in the development of thecal apertures, from low lateral lobes or spines to simple straight apertures distally. Geniculae are present in some taxa, rounded in *Heisograptus* but also angular as in *Uncinatograptus*. The details of the development of thecal hoods in the Pristiograptinae are known from a number of taxa (URBANEK, 1958, 1997a; KOREN', KIM, & WALLISER, 2007). *Heisograptus* has hoods formed from microfusellar material as secondary additions at the genicula (Fig. 303.3). In *Uncinatograptus*, apertural hoods are present at least on the proximal thecae but may be lacking in distal thecae. These hoods look similar to genicular developments but are true hoods formed as extensions of the dorsal thecal wall. In *Uncinatograptus falcarius* and related Early Devonian taxa, the initial part of the thecal hood is reduced in width, but distally a considerable lateral extension is visible forming a spatulate process (Fig. 303.7) and not a thecal hood as in *Uncinatograptus uncinatus* (Fig. 303.9–303.10). The thecal hood, thus, does not cover the thecal aperture.

**Colonograptus** PŘIBYL, 1943, p. 2, *ex Pristiograptus* (*Colonograptus*) PŘIBYL, 1943, p. 2 [**Graptolithus* *colonus* Barrande, 1850; OD] [=*Ludensograptus* Tsegelnjuk, 1978, p. 88 (type, *Graptolithus Ludensis* Murchison, 1839, OD), syn. by Loydell, herein] [=*Conomograptus*, misspelling in Přibyl, 1983, p. 149]. Tubarium gently ventrally curved throughout or only proximally, being straight distally; sicula ventrally curved; biform thecae; proximal two or three thecae with ventrally projecting broad fusellar lappets; distal thecae simple tubes. *Silurian, Wenlock* (*Homerian, Colonograptus praedeubeli/deubeli* Biozone)–*Ludlow* (*Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide.——Fig. 304,*1a–b*. **C. colonus* (Barrande), lectotype, NMP L19771, Butovice-Nová-Ves, Czech Republic, *Neodiversograptus nilssoni* Biozone, proximal end and distal part of specimen preserved in relief, scale bars, 1 mm (new; drawing by Petr Štorch and Zuzana Strossova, 2021).

**Dulebograptus** Tsegelnjuk, 1976, p. 98 [**D. bresticus* Tsegelnjuk, 1976, p. 98; OD]. Tubarium straight or ventrally curved proximally and straight distally; proximal one to three thecae with complete fusellar hoods formed of dorsal walls of thecae; succeeding thecae have apertures with symmetrical lateral lobes which retreat distally; distal thecae becoming simple with straight margins, similar to those in *Pristiograptus*. *Silurian, Pridoli* (*Skalograptus lochkovensis* Biozone): Ukraine, Belarus, Poland.——Fig. 304,*2a–c*. *D. trimorphus* Tsegelnjuk, 1976; *2a,* specimen in ventral view; *2b,* sicula with first bud, showing presence of sicular annuli; *2c,* fragment showing style of thecal apertures (Urbanek, 1997a, pl. 14.A; text-fig. 42). Scale bars, 1 mm.

**Formosograptus** Bouček, Mihajlovic, & Vaselinovic, 1976, p. 84 [**Monograptus formosus* Bouček, 1931, p. 300; OD] [=*Tamplograptus* Tsegelnjuk, 1976, p. 114 (type, *Monograptus* (?*Spirograptus*) *convexus* Přibyl, 1940a, p. 73, OD), syn. by Přibyl, 1983, p. 150]. Dorsally curved tubarium; sicula straight or very gently ventrally curved, with dorsal process; proximal thecae non-overlapping, subtriangular with distinctly isolated apertural part; distal thecae overlap for approximately half their length with metathecae that are more adnate; thecal aperture overhung by laterally expanded lobe, with semitubular lateral processes terminating in auriculum. *Silurian, Ludlow* (*Ludfordian, Pseudomonoclimacis latilobus* Biozone)–*Pridoli* (*Neocolonograptus ultimus* Biozone): worldwide.——Fig. 304,*3a–c*. **F. formosus* (Bouček), Mielnik drill core, Poland; *3a,* proximal end showing shape of tubarium (adapted from Urbanek, 1997a, fig. 19B); *3b–c,* distal fragment showing increase of thecal overlap (Urbanek, 1997a, fig. 21). Scale bars, 1 mm.

**Heisograptus** Tsegelnjuk, 1976, p. 103 [**Pomatograptus micropoma* Jaekel, 1889, p. 682; OD]. Tubarium straight or nearly so; sicula ventrally curved, with dorsal tongue; thecae with sharp geniculae and supragenicular walls that are parallel to tubarium axis; apertural excavations semi-circular or semi-elliptical; aperture may be overhung by hood of microfusellar tissue. *Silurian, Ludlow* (*Gorstian*, *Neodiversograptus nilssoni* Biozone–*Lobograptus scanicus* Biozone): worldwide.——Fig. 304,*4a–d*. **H. micropoma* (Jaekel); *4a,* lectotype (selected by Jaeger, 1959, pl. 6,*7*), MB.G 470d, glacial boulder, Zölling bei Neusalz an der Oder, now Nowa Sól, Poland (Wilkinson, 2018b, Atlas, Folio 3.52); *4b–c,* juveniles in reverse (*4b*) and obverse (*4c*) views, showing presence of sicular annuli (Maletz, 1999a, fig. 2C,E); *4d,* specimen showing apertural hoods (Jaeger, 1959, fig. 20D). Scale bars, 1 mm.

**Neomonograptus** Mu & Ni, 1975, p. 18 [**N. himalayensis;* OD; =*Monograptus atopus* Bouček, 1966, syn. by Jaeger 1983, p. 250]. Tubarium straight throughout or with dorsal curvature proximally; first theca robust and strongly hooked, concealing aperture; subsequent thecae with dorsal hoods above semi-circular or semi-elliptical apertures, these becoming much less pronounced in mesial and distal thecae; thecae strongly geniculate throughout. *Lower Devonian* (*Lochkovian, Uncinatograptus uniformis* Biozone)–*Emsian, Uncinatograptus yukonensis* Biozone): worldwide.——Fig. 304,*5a–b*. *N. atopus* (Bouček), holotype, proximal end (*5a*) and distal thecae (*5b*), scale bars, 1 mm (Bouček, 1966, fig. 1C); *5c,* holotype of **N. himalayensis,* scale bar, 1 mm (Chen & others, 2021, fig. 5F).

**Pristiograptus** Jaekel, 1889, p. 667 [**P. frequens;* OD]. Tubarium straight or gently dorsally or ventrally curved; thecal length increasing along first few thecae, later constant; sicula of medium length with low origin of th1; thecae straight, cylindrical, with straight or nearly straight ventral wall; thecal aperture without any supplementary structures except thickened apertural rim. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone)–*Pridoli* (*Skalograptus perneri* Biozone): worldwide.——Fig. 304,*8a–d*. **P. frequens; 8a,* neotype, MB.G 458.3.1, selected by Štorch, Manda, & Loydell, 2014, p. 1016 (Jaeger, 1991, fig. 26.*9*); *8b–d, P. dubius* (Suess, 1851), isolated specimens, glacial boulder, note the lack of sicular annuli (Maletz, 1999a, fig. 2Q-S). Scale bars, 1 mm.

**Proteograptus** Lenz, Senior, Kozłowska, & Melchin, 2012, p. 26 [**Monograptus opimus* Lenz & Melchin, 1991, p. 230; OD]. Gently ventrally curved tubarium that widens rapidly proximally; sicula straight with dorsal tongue; thecae appear hooked in profile view, but this hook is formed from paired lateral lappets that may fuse centrally, particularly in proximal part of tubarium to produce a pseudohood, the dorsal side of which has a consistently present laterally ovate opening onto the protheca. *Silurian, Wenlock* (*Sheinwoodian*, *Proteograptus opimus* Biozone–*Cyrtograptus perneri* Biozone): Arctic Canada.——Fig. 304,*6a–d*. **P. opimus* (Lenz & Melchin), GSC 134694, Cape Phillips, Arctic Canada; *6a–b,* reverse (*6a*) and ventral (*6b*) views of colony showing thecal style, (Lenz & others, 2012, pl. 12,*1–2*); *6c,* change in thecal style over first four thecae (Lenz & others, 2012, pl. 12,*3*); *6d,* development of distal thecae (Lenz & others, 2012, pl. 12.*6*). Scale bars, 1 mm.

**Pseudomonoclimacis** MIKHAILOVA, 1975, p. 156 [**P. elegans*; OD]. Tubarium gently ventrally curved proximally and mesially, straight distally; sicula ventrally curved, with dorsal process; thecae moderately to strongly geniculate, generating a thecal excavation. *Silurian, Ludlow* (*Gorstian, Lobograptus progenitor* Biozone)–*Pridoli* (*Skalograptus perneri* Biozone): worldwide.——FIG. 304,*7a*. **P. elegans,* CNIGR 20/10290, holotype, scale bar, 1 mm (Mikhailova, 1975, pl. 38,*3*).——FIG. 304,*7b*. *P. dalejensis* (BOUČEK, 1936), specimen showing curvature of sicula, Všeradice section, Prague syncline, Czech Republic, scale bar, 1 mm (Štorch, Manda, & Loydell, 2014, fig. 6F).——FIG. 304,*7c–e*. *P. antiqua* ŠTORCH, MANDA, & LOYDELL, 2014; *7c*, slender specimen, Všeradice section, Prague syncline, Czech Republic (Štorch, Manda, & Loydell, 2014, fig. 6Q); *7d–e,* juvenile specimens in reverse (*7d*) and obverse (*7e*) view, glacial boulder, Bramsche, northern Germany (Maletz, 1999a, fig. 2M–N; identified as *Heisograptus* sp.). Scale bars, 1 mm.

**Saetograptus** PŘIBYL, 1943, p. 11 [**Graptolithus chimaera*, BARRANDE, 1850, p. 52; OD]. Straight or dorsally curved tubarium; sicula with variably developed dorsal apertural tongue; tubular thecae terminated by paired apertural spines developed on all or only proximal thecae; aperture of first theca has broad, triangular, spine-like lateral lappets; other thecal apertures have ventral notch and laterally to dorso-laterally situated spines separated by trough from ventral wall of next theca. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone–*Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide.——FIG. 304,*10a–b*. **S. chimaera* (BARRANDE); *10a,* holotype, NMP L19973 (new; drawing by P. Štorch, 2021); *10b,* chemically isolated specimen (Přibyl, 1943, fig. 1, redrawn from original illustration in Münch, 1938, pl. 5,*1a*). Scale bars, 1 mm.

**Skalograptus** TSEGELNJUK, 1976, p. 100 [**Skalograptus vetus;* OD; =*Monograptus ultimus* PERNER, 1899; KŘÍŽ & others, 1986, p. 322; KOREN' & SUJARKOVA 1997, p. 87] [=*Istrograptus* TSEGELNJUK, 1988, p. 85 (type species not selected; illustrated as *Is*(*tr*)*ograptus transgrediens* [PERNER, 1899] and *Istrograptus ultimus* [PERNER, 1899]); =*Neocolonograptus* URBANEK, 1997a, p. 165 (type, *Monograptus lochkovensis* PŘIBYL, 1940a, OD, see URBANEK, 1997a, p. 128, table 1), syn. by LOYDELL, herein].Tubarium gently ventrally curved, gently dorso-ventrally curved or straight; sicula moderately to strongly ventrally curved; thecae with bilobate apertural elaborations, ranging from gentle undulations to strong lappets oriented antero-laterally; apertures of distal thecae may lack these elaborations; ventral walls of thecae sigmoidal or straight. *Silurian, Pridoli* (*Skalograptus parultimus* Biozone–*Skalograptus transgrediens* Biozone): worldwide.——FIG. 304,*9a–b*. *S. ultimus* (PERNER); *9a*, lectotype (selected by PŘIBYL, 1948a, p. 77) Praha-Dvorce (formerly Dworetz), Czech Republic (Perner, 1899, fig. 14a); *9b,* chemically isolated specimen, Kosov Quarry, Czech Republic, *Skalograptus ultimus* Biozone, ~4 m above base of Pridoli (adapted from Kříž & others, 1986, fig. 36a). Scale bars, 1 mm.

**Slovinograptus** URBANEK, 1997a, p. 129 [**Monograptus balticus* TELLER, 1966, p. 556; OD; URBANEK, 1997a, p. 128; =*Monograptus kallimorphus* KRAATZ, 1958, p. 48, syn. by JAEGER 1978b, p. 514]. Tubarium slender and dorsally curved proximally, straight distally; sicula ventrally curved; thecal apertures provided with globose hoods, adnate to the ventral wall; substantial thecal overlap, especially distally. *Silurian, Ludlow* (*Ludfordian, Pseudomonoclimacis latilobus/Slovinograptus balticus* Biozone)–*Lower Devonian* (*Lochkovian, Uncinatograptus uniformis* Biozone): worldwide.——FIG. 304,*11a–d*. *S. kallimorphus* (KRAATZ); *11a,* holotype of **Monograptus balticus* (Koren' & Suyarkova, 1997, fig. 9G); *11,b,* CGM 26/12879, Peshkaut Valley, southern Tien Shan (Koren' & Suyarkova, 1997, fig. 9A); *11c,* proximal end, KR 58d, Mollenberg, Harz Mountains, Germany (new); *11d,* distal fragment, KR 58A, Mollenberg, Harz Mountains (new). Scale bars, 1 mm.

**Uncinatograptus** TSEGELNJUK, 1976, p. 96 [**Monograptus uncinatus* TULLBERG, 1883, p. 30; OD] [=*Tirassograptus* TSEGELNJUK, 1976, p. 119 (type, *Monograptus* (*Pomatograptus*) *uncinatus* var. *uniformis* PŘIBYL, 1940a, p. 71; OD), syn. by LOYDELL, herein; =*Metamonograptus* WANG, 1977, p. 198 (type *Monograptus* (*Metamonograptus*) *qinzhouensis* WANG, 1977, p. 198; OD), syn. by LOYDELL, herein]. Tubarium straight or dorsally curved proximally and mesially, becoming straight distally; sicula straight or ventrally curved, aperture flaring with or without distal curving lappet; thecae with dorsal hoods, often best developed in proximal thecae but present throughout the tubarium; ventrolateral margin of aperture may be lobate and also spinose; thecal overlap increases distally. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone)–*Lower Devonian* (*Emsian, Uncinatograptus yukonensis* Biozone): worldwide.——FIG. 304*,12a–c*. **U. uncinatus* (TULLBERG); *12a,* lectotype, selected by Přibyl, 1948a, p. 35 (Tullberg, 1883, pl. 1,*25;* ?LO collection, specimen not identified); *12b–c,* proximal end in lateral (*12b*) and ventral (*12c*) views (Urbanek, 1958, pl. 1,*3a–3b*). Scale bars, 1 mm.

**Wandograptus** RICKARDS & JELL, 2002, p. 118 [**W. wandovalensis;* OD]. *Pristograptus*-like tubarium but with more frequent and irregular curvature and development of thecal cladia. [The taxonomic position of the genus is uncertain. RICKARDS and JELL (2002) described it as related to *Pristiograptus,* but bearing cladia. The proximal end and thecae are very similar to those of early *Pristiograptus* and *Atavograptus*.] *Silurian, Llandovery* (*Telychian, Spirograptus turriculatus* Biozone–*Streptograptus crispus* Biozone): Australia (Queensland).——FIG. 304,*14a–b*. **W. wandovalensis,* fragments from the holotype slab, UQ 35968, Queensland, Australia;

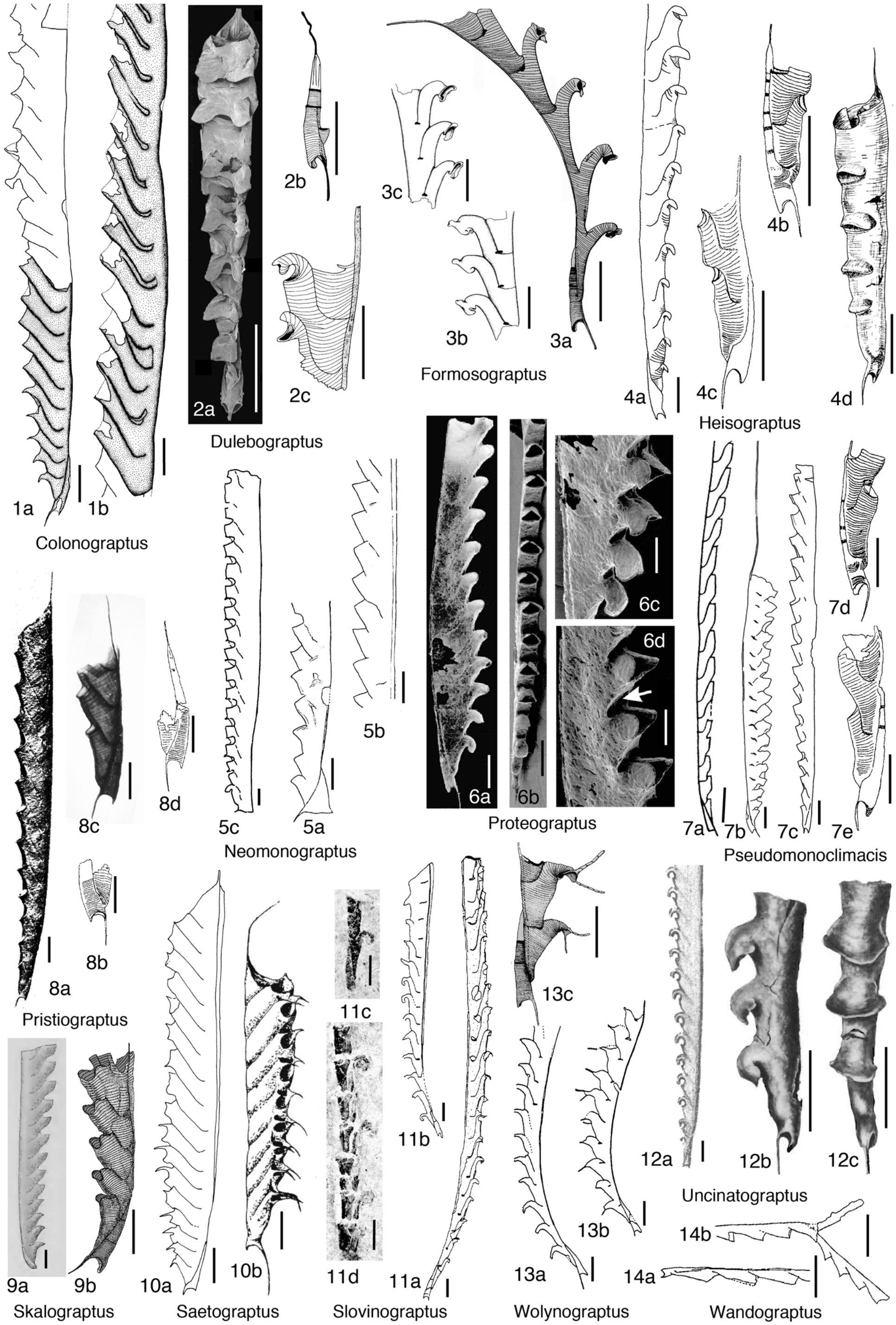


FIG. 304. Pristiograptinae (p. 450–454).

(Rickards & Jell, 2002, fig. 4I–J, L–M). Scale bars, 1 mm.

**Wolynograptus** TSEGELNJUK, 1976, p. 110 [**W. valleculosus;* OD) [=*Acanthograptus* TSEGELNJUK, 1976, p. 113 (type *A. spineus;* OD), syn. by PŘIBYL, 1983, p. 150, homonym of *Acanthograptus* SPENCER, 1878 [Dendroidea]); =*Bugograptus* TSEGELNJUK, 1998, p. 272 (type, *A. spineus* TSEGELNJUK, 1976, OD), syn. by LOYDELL, herein]. Tubarium dorsally curved proximally and mesially, becoming straight distally; sicula straight or ventrally curved, bearing two annuli; thecae with extensive dorsal hoods; anterolateral margin of aperture may be lobate and also spinose; thecal overlap increases distally. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone–*Ludfordian, Wolynograptus spineus* Biozone): worldwide.——FIG. 304,*13a*. *W. aculeatus* TSEGELNJUK, 1976, proximal end, scale bar, 1 mm (Koren' & Suyarkova, 1997, fig. 8A).——FIG. 304,*13b–c*. *W. spineus* TSEGELNJUK, 1976; *13b*, proximal end (Koren' & Suyarkova, 1997, fig. 14H); *13c*, proximal end (Urbanek, 1995, fig. 1D). Scale bars, 1 mm.

## Subfamily LINOGRAPTINAE Obut, 1957

[Subfamily Linograptinae OBUT, 1957, p. 18; *nom. transl.* TELLER, 1962, p. 153, *ex* Linograptidae OBUT, 1957, p. 18] [=Cucullograptinae URBANEK, 1958, p. 62; herein; =Neocucullograptinae URBANEK, 1970, p. 265; herein; =Neolobograptinae TSEGELNJUK, 1976, p. 120; herein]

Variably straight to usually ventrally curved, slender to distally widening monograptids; thecal overlap from very low to extremely high; thecal apertures may be elaborated with paired lateral lobes, commonly with asymmetrical development; sicula slender to aperturally widening (trumpet-shaped), with variable number of annuli. *Silurian, Wenlock* (*Homerian, Colonograptus ludensis* Biozone)–*Lower Devonian* (*Lochkovian, Uncinatograptus hercynicus* Biozone): worldwide.

A number of small subfamilies have been erected for late Wenlock (Homerian) and Ludlow (Gorstian to Ludfordian) monograptids. Small-scale modifications of their thecae have been used to describe the evolutionary transformation of the species. URBANEK (1970, pl. 8) suggested a close phylogenetic relationship between the various groups. URBANEK (1958) did not provide a diagnosis of the Cucullograptinae and his description of the various species is based largely on small fragments. URBANEK (1966) discussed and described a number of additional species of the clade and suggested common roots with the Linograptinae and the '*Pristiograptus*' *bohemicus* group (URBANEK, 1966, pl. 8). WHITTINGHAM, RADZEVIČIUS, and SPIRIDONOV (2020) supported these relationships when they discussed iterative evolution during the late Silurian graptolite faunas and indicated a possible sister-group relationship between the *Colonograptus* and *Lobograptus* clades, based on stratocladistics.

## MORPHOLOGY

Most of the taxa included in the Linograptinae, as used herein, are characterized by a ventrally curved to straight tubarium with thecae having low inclination and often distally increasing thecal overlap. The sicula is small in most taxa and bears a variable number of sicular annuli. An elongated sicula is present in the genus *Urbanekia*. Cladial branching is present in a few taxa forming very large colonies.

The thecal apertures vary from simple (Fig. 305.3) to complex, often including a considerable asymmetry of the two lateral lobes (Fig. 305.12–305.17), but lacking torsion of the metathecae. The complex thecal apertures are formed either from normal fusellar development (Fig. 305.12–305.13) or from microfusellar additions (Fig. 305.16–305.17). The simple thecal apertures have a straight aperture, inclined to the ventral side of the tubarium. Lateral lobes are barely recognizable in some taxa (Fig. 305.6–305.8) but may be quite extensive in others. They may have strong lateral extensions and may be curved or coiled.

*Bohemograptus cornutus* (URBANEK, 1970) has an extreme development of lateral additions in the form of paired spatulate extensions formed from fusellar material (Fig. 305.2), and membranes with an internal branching system of rods have been documented in *Bohemograptus papilio* KOZŁOWSKA & URBANEK, 2013 (Fig. 305.1). A characteristic virgellarium ending with four finger-like extensions occurs in *Linograptus* and probably in *Abiesgraptus* (URBANEK, 1997b).

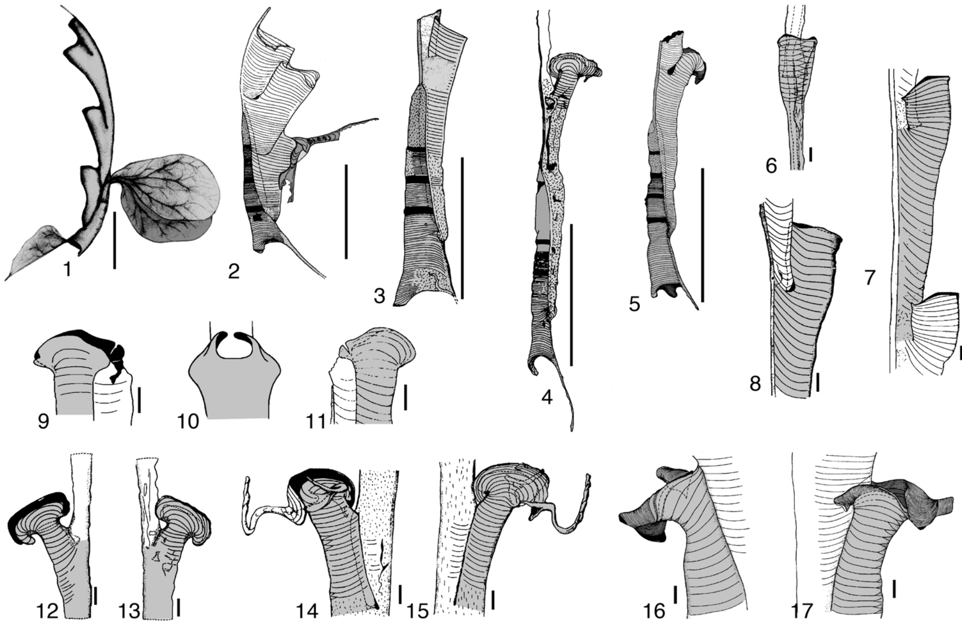


FIG. 305. Thecal morphology of the Linograptinae. *1, Bohemograptus papilio* KOZŁOWSKA & URBANEK, 2013, reconstruction showing patagia (Kozłowska & Urbanek, 2013, fig. 5); *2, Bohemograptus cornutus* URBANEK, 1970 with partly preserved lateral apertural processes (Urbanek, 1970, pl. 25); *3, 8, Lobograptus progenitor* URBANEK, 1966, proximal end (*3*) and thecal style (*8*) (Urbanek, 1966, pl. 14A); *4, 14–15, Lobograptus cirrifer* URBANEK, 1966, proximal end (*4*) and thecal style (*14–15*) (Urbanek, 1966, pl. 34); *5, Neocucullograptus kozlowskii* URBANEK, 1970, proximal end (*5*) and thecal style (*16–17*) (Urbanek, 1970, pl. 38); *6–7, Linograptus posthumus* (RICHTER, 1875), thecal style in ventral (*6*) and lateral (*7*) views (Urbanek, 1963, pl. 9); *9–11, Lobograptus simplex* URBANEK, 1960, thecal style (Urbanek, 1966, pl. 16); *12–13, Lobograptus scanicus* (TULLBERG, 1883), thecal style (Urbanek, 1966, pl. 27). All illustrations are modified from the original illustrations. Scale bars, 1 mm in *1–5;* all others 0.1 mm.

Taxa with cladial branching (URBANEK, 1997b) may possess a sicular cladium to form a bipolar tubarium as in *Neodiversograptus* or thecal cladia as in *Lenzograptus*. More complex tubaria are present in *Linograptus,* in which the sicula may form numerous sicular cladia but no thecal cladia. *Abiesgraptus* bears three sicular cladia and additional thecal cladia along the initial stipe and the first sicular cladium (JAEGER, 1959; URBANEK, 1997b).

**Bohemograptus** PŘIBYL, 1967b, p. 134 [**Graptolithus bohemicus* BARRANDE, 1850, p. 40; OD] [=*Fterograptus* TSEGELNJUK, 1976, p. 131 (type, *F. torsivus,* OD), syn. by LOYDELL, herein]. Tubarium ventrally curved; thecae tubular, with straight or gently elevated lateral apertural margins, either devoid of or provided with microfusellar additions forming broadly lobate, annular or tape-like apertural structures. *Silurian, Wenlock* (*Homerian, Colonograptus ludensis* Biozone)–*Ludlow* (*Ludfordian, Neocucullograptus kozlowskii* Biozone): worldwide.——FIG. 306,*1a–c*. **B. bohemicus* (BARRANDE, 1850); *1a–b,* NMP L17762, lectotype (Přibyl, 1948a, p. 68) and associated specimen with sicula (Štorch, 2000d, Atlas, Folio 1.9); *1c,* proximal end with sicular annuli, Mielnik drill core, 957.90 m, Poland (Urbanek, 1970, fig. 10B). Scale bars, 1 mm.

**Crinitograptus** RICKARDS, 1995b, p. 1107 [**Monograptus crinitus* WOOD, 1900, p. 480; OD]. Slender tubarium, straight or irregularly flexed; short sicula with annuli; simple tubular thecae, parallel to or inclined to tubarium axis at less than 10°; thecae increasing in lateral width toward aperture; only slight thecal overlap; thecal aperture simple, with overhanging hood formed by extension of dorsal wall of theca. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone)–*Pridoli* (*Neocolonograptus parultimus* Biozone): UK, Germany (erratics), Bulgaria, Arctic Canada, Australia, Russia.——FIG. 306,*2a–c*. **C. crinitus* (WOOD), Long Mountain, Shropshire, UK; *2a,* BU 1615, part of holotype (Rickards, 1995b, fig. 4.*1*); *2b,* BU 1618, syntype, proximal end showing sicular annuli (Rickards, 1995b, fig. 1). *2c*, BU 1616, bipolar fragment (Rickards, 1995b, fig. 4,*3*). Scale bars, 1 mm.

**Cucullograptus** URBANEK, 1954, p. 291 [**C. pazdroi;* OD]. Narrow, straight, or gently ventrally curved tubarium; small sicula; first theca originated via a primary porus; thecae long, with elongate protheca and short metatheca; thecal aperture slit-like, with complex auriculate lateral apertural lobes, with increasing asymmetry distally; the left apertural lobe overlaps right lobe, restricting thecal aperture. *Silurian*, *Ludlow* (*Gorstian, Lobograptus parascanicus* Biozone–*Ludfordian, Cucullograptus rostratus/lower Bohemograptus tenuis* Biozone): Poland, Czech Republic, Germany, China (Yunnan).——FIG. 306,*3a–c*. **C. pazdroi;* three different views of holotype, glacial boulder, Gdansk-Wrzeszcz, Poland (Urbanek, 1954, fig. 2). Scale bars, 1 mm.

**Egregiograptus** RICKARDS & WRIGHT, 1997b, p. 222 [*'*Monograptus' egregius* URBANEK, 1970, p. 367; OD]. Tubarium strongly ventrally curved, almost circular; short sicula (usually less than 1.5 mm long); thecae adnate, tubular; proximal thecae extremely elongated and inclined at a very low angle to the tubarium axis; distal thecae with considerable overlap; thecal apertures straight or with paired lateral lobes. *Silurian, Ludlow* (*Gorstian, Lobograptus scanicus* Biozone–*Ludfordian, Saetograptus chimaera* Biozone–*Neocucullograptus kozlowskii* Biozone): Poland, Czech Republic, Kyrgyzstan, Canada (Yukon), Australia.——FIG. 306,*4a–c*. **E. egregius; 4a,* holotype (Urbanek, 1970, pl. 43D1); *4b,* proximal end showing sicular annuli (Urbanek, 1970, p. 42A); *4c,* proximal end, th1 reconstructed (Urbanek, 1970, pl. 42F). Scale bars, 1 mm.——FIG. 306,*4d. E. dimitrii* (KOREN' & SUYARKOVA, 2004), CNIGR 13107/63, holotype, Tien Shan, Kyrgyzstan, scale bar, 1 mm.

**Enigmagraptus** RICKARDS & WRIGHT, 2004, p. 192 [**Neocucullograptus*? *yassensis* RICKARDS & WRIGHT, 1999a, p. 200; OD]. Very slender tubarium (up to 0.25 mm wide), straight or irregularly flexed; small sicula with virgella and dorsal apertural process; axially elongate prothecae usually developed from threadlike origin; metatheca up to half tubarium width comprising hood derived by retroversion of the dorsal metathecal wall, and variously enrolled ventrally to enclose simple ventral thecal margin. *Silurian* (*Pridoli, Neocolonograptus parultimus* Biozone): Australia (New South Wales).——FIG. 306,*5a–b*. **E. yassensis; 5a,* AMF 92343, holotype, proximal end; *5b,* AMF 92346, stipe fragment (Rickards & Wright, 2004, fig. 4B–C). Scale bars, 1 mm.

**Korenea** RICKARDS, PACKHAM, WRIGHT, & WILLIAMSON, 1995, p. 54 [**K. sherwini;* OD]. Tubarium ventrally curved, hook-shaped; sicula small; uniform overlapping tubular thecae with strongly developed paired symmetrical lateral apertural lappets resembling retroverted hooks in profile. *Silurian* (*Ludlow*): Australia.——FIG. 306,*6a–b*. **K. sherwini,* New South Wales, Australia; *6a*, holotype, AMF 89624 (Rickards & others, 1995, fig. 33B); *6b*, thecal detail (Rickards & others, 1995, fig. 38E). Scale bars, 1 mm.

**Lobograptus** URBANEK, 1958, p. 12 [**Monograptus scanicus* TULLBERG, 1883, p. 26; OD] [=*Falcatograptus* HUNDT, 1965, p. 48 (type, *F. rarus,* M), syn. by LOYDELL, herein]. Narrow, straight, dorsoventrally or gently ventrally curved tubarium, widening distally; thecae long, with elongate protheca and increasing distal overlap; thecal aperture with asymmetrical or symmetrical lateral lobes that may curve over central part of aperture. *Silurian, Wenlock* (*Homerian, Colonograptus praedeubeli* Biozone)–*Ludlow* (*Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide.——FIG. 306,*7a–b*. **L. scanicus* (TULLBERG), *7a,* syntype, specimen not identified (Tullberg, 1883, pl. 2.*42*); *7b,* proximal end (Urbanek, 1966, fig. 11). Scale bars, 1 mm.

**Neocucullograptus** URBANEK, 1970, p. 329 [**N. kozlowskii;* OD]. Tubarium strongly ventrally curved proximally, less strongly curved or nearly straight distally; sicula with dorsal apertural process and late astogenetic paired symmetrical lobes of microfusellar tissue situated on reverse and obverse apertural margins; first theca originated via a primary porus; complex metathecae, consisting of smaller right and larger left lobe, sometimes provided with gular, rostral, and lateral processes. *Silurian, Ludlow* (*Ludfordian, Neocucullograptus inexpectatus* Biozone–*Neocucullograptus kozlowskii* Biozone): Poland, Czech Republic, Kyrgyzstan, Kazakhstan.——FIG. 306,*8a–d*. **N. kozlowskii,* Mielnik drill core, Poland; *8a–b,* holotype in lateral (*8a*) and ventral (*8b*) views (Urbanek, 1970, fig. 20A); *8c*, distal theca (Urbanek, 1970, pl. 38A); *8d,* reconstruction (Urbanek, 1970, pl. 7C). Scale bars, 1 mm.

**Neolobograptus** URBANEK, 1970, p. 321 [**N. auriculatus;* OD]. Ventrally curved tubarium; straight sicula with prominent dorsal process; thecae slender and elongate; thecal apertures with lateral elevations and dorso-lateral incisions. *Silurian, Ludlow* (*Ludfordian, Saetograptus leintwardinensis* Biozone–*Neocucullograptus inexpectatus* Biozone): Poland, Kyrgyzstan.——FIG. 306,*9a–b*. **N. auriculatus,* Mielnik drill core, Poland; *9a,* holotype, sicula with incomplete first theca (Urbanek, 1970, pl. 29B); *9b,* reconstruction (Rickards & Wright, 1999b, fig. 3F, based on Urbanek, 1970, pl. 7A). Scale bars, 1 mm.

**Polonograptus** TSEGELNJUK, 1976, p. 124 [**P. podoliensis* PŘIBYL, 1983, p. 158; SD ICZN, Opinion 2023, 2003; RIVA, KOREN', & RICKARDS (2001) applied to the ICZN to change the type species from *Monograptus butovicensis* BOUČEK, 1936 to *Polonograptus podoliensis*, approved as Opinion 2023 (ICZN, 2003)]. Tubarium ventrally curved with proximally accentuated curvature; sicula small and straight; thecae subsequent to the short first theca exhibit considerable elongation and overlap; all thecae simple tubes; apertures have lateral elevations.

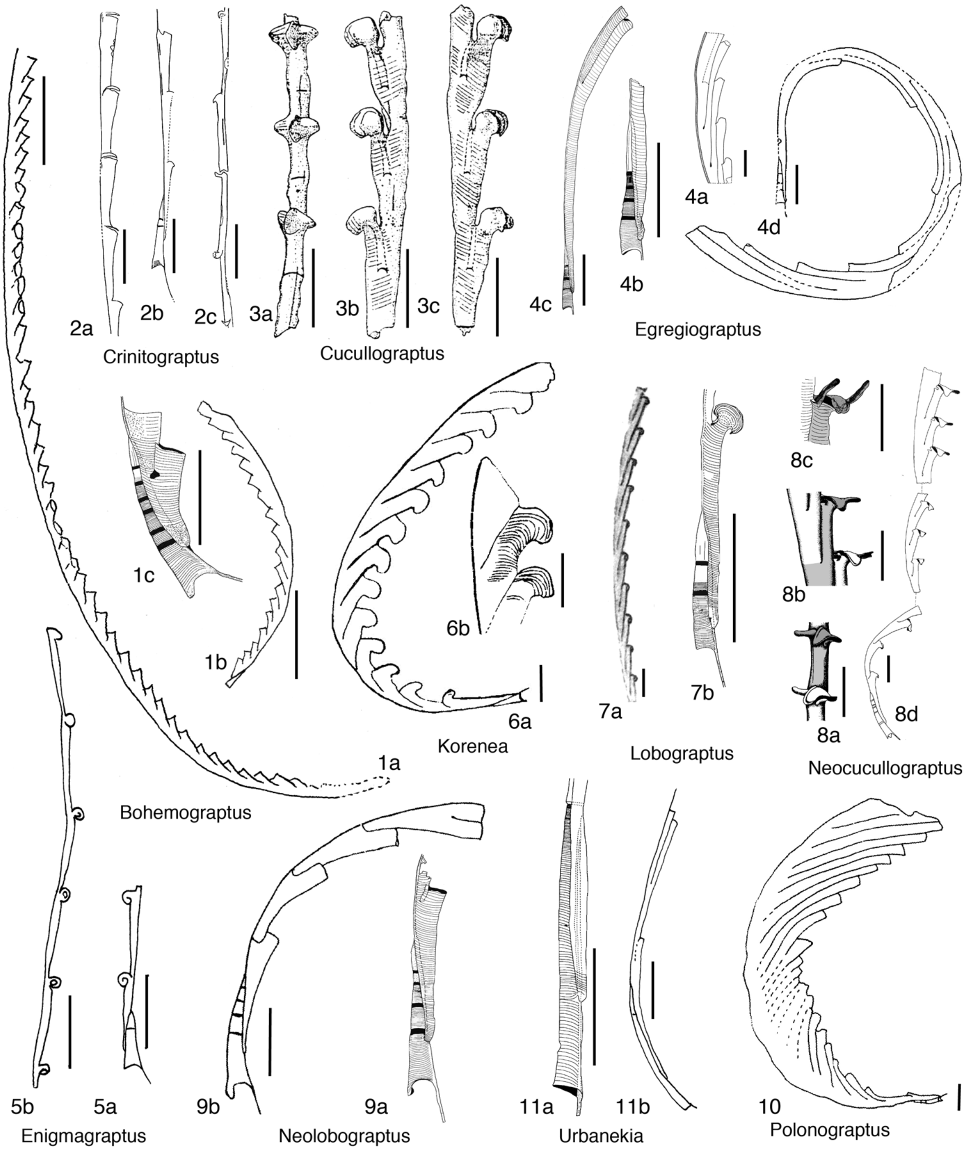


Fig. 306. Linograptinae (p. 455–457).

*Silurian, Ludlow* (*Ludfordian*, *Neocucullograptus inexpectatus* Biozone–*Neocucullograptus kozlowskii* Biozone): Czech Republic, Austria, Australia, Kyrgyzstan.——FIG. 306,*10*. **P. podoliensis,* CNIGR 13107/104, southern Tien Shan, Kyrgyzstan, scale bar, 1 mm (Koren' & Sujarkova, 2004, fig. 28B).

**Urbanekia** RICKARDS & WRIGHT, 1999b, p. 319 [*'*Monograptus*' *proegregius* URBANEK, 1970, p. 364; OD]. Tubarium known from fragments only but appears narrow (less than 0.3 mm) and ventrally curved; sicula elongated (more than 3 mm long) and ventrally curved; sicular aperture lacks dorsal process; thecae very long (at least 7 mm), narrow and tubular, with ventral walls subparallel to the tubarium axis; thecal apertures simple, perpendicular to thecal axis and with slight lateral elevations. *Silurian, Ludlow* (*Gorstian, Lobograptus parascanicus* Biozone): Poland.——FIG. 306,*11a–b*. **U. proegregius* (URBANEK); *11a,* paratype, sicula with part of first theca (Urbanek, 1970, pl. 41.*C*); *11b,* reconstruction (Rickards & Wright, 1999b, fig. 2L). Scale bars, 1 mm.

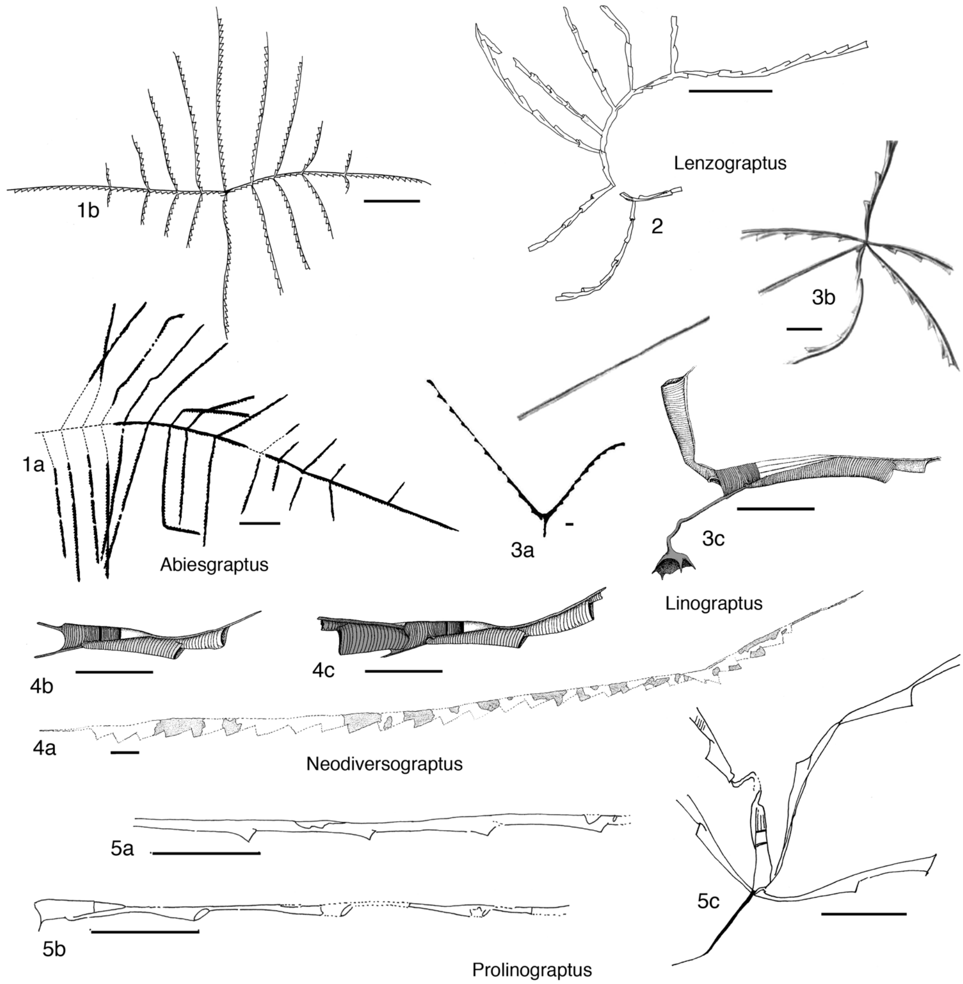


FIG. 307. Linograptinae (cladia-bearing) (p. 458–459).

## LINOGRAPTINAE WITH CLADIA

URBANEK (1997b) discussed in some detail the evolution of the cladia-bearing linograptines from the genus *Lobograptus* (probably *Lobograptus sherrardae*) through the bipolar *Neodiversograptus* and, thus, indicated the independent origin of cladia-bearing taxa from older cladia-bearing forms during the early Silurian. URBANEK (1963, 1997b) included only three genera, *Neodiversograptus, Linograptus,* and *Abiesgraptus* in his subfamily Linograptinae and suggested that they represent an instance of a single line of descent forming sequential chronospecies. The relationship to the genus *Lenzograptus* remains uncertain. Thus, the cladia-bearing taxa, separated here from the other taxa for practical reasons, might not form a phylogenetically definable clade.

**Abiesgraptus** HUNDT, 1935a, p. 3 [**A. multiramosus;* SD BULMAN, 1938, p. 84] [=*Didymograptoides* HUNDT, 1953a, p. 40 (type, *D. liebei,* M), syn. by LOYDELL, herein; =*Gangliograptus* HUNDT, 1939, p. 119 (type, *G. hoppeianus,* SD MÜLLER, 1969, p. 919), syn. by LOYDELL, herein]. Tubarium complex, comprising the main stipe and three sicular cladia; the main stipe and central sicular cladium bear paired thecal cladia; thecae simple, without apertural modifications. *Lower Devonian* (*Lochkovian, Uncinatograptus uniformis* Biozone–*Pragian, Uncinatograptus fanicus* Biozone): worldwide.——FIG.

307,*1a–b*. **A. multiramosus* HUNDT, *1a,* lectotype, selected by Müller, 1965, p. 5, BAF 73/H4151, Ramstal bei Creunitz, Thuringia, Germany (Müller, 1965, fig. 1); *1b,* reconstruction; scale bars, 10 mm (Jaeger, 1959, fig. 25).

**Lenzograptus** LOYDELL, 2021, p. 205 [**Lenzia lenzi* RICKARDS & WRIGHT, 1999b, p. 319; OD] [*pro Lenzia* RICKARDS & WRIGHT, 1999b; homonym of *Lenzia* PERRY, BOUCOT, & GABRIELSE 1981 (Devonian brachiopod)]. Cladia-bearing linograptid, with tubarium largely ventrally curved but twisting around its axis; thecae simple or with slight lateral apertural lobes, generating cladia every one or two thecae, directed to the dorsal side of main stipe. *Silurian* (*Ludlow*): Canada (Yukon).——FIG. 307,*2*. **L. lenzi,* holotype, UWO 2664, Richardson Mountains, Yukon, Canada, scale bar, 5 mm (Lenz, 1984, fig. 1a).

**Linograptus** FRECH, 1897, p. 662 [**Dicranograptus posthumus* RICHTER, 1875, p. 267; OD; =*Linograptus nilssoni* FRECH, 1897, p. 662; syn. by JAEGER, 1959, p. 143] [=*Thuringiograptus* HUNDT, 1939, p. 121 (type, *T. voigtii,* M), syn. by LOYDELL, herein]. Tubarium with narrow stipes comprising main stipe and, late in astogeny, several sicular cladia; main stipe and sicular cladia may be straight or more usually gently ventrally curved; virgella with virgellarium, a terminal four-pronged membranous structure; sicula with a long dorsal apertural spine that forms secondary nema for first sicular cladium; further cladia develop from reverse and obverse margins of the sicula; first theca of main stipe originated close to boundary of prosicula and metasicula; thecae simple tubes, apertures with lateral elevations which are more pronounced in distal thecae and may be somewhat introverted. *Silurian, Ludlow* (*Ludfordian, Bohemograptus tenuis* Biozone)–*Lower Devonian* (*Lochkovian, Uncinatograptus hercynicus* Biozone): worldwide.——FIG. 307,*3a–c*. **L. posthumus; 3a,* lectotype, BGR 10370 (Richter, 1875, pl. 8.*3*); *3b,* specimen from Herzogswalde bei Silberberg, Schlesien (Frech, 1897, pl. A7); *3c,* isolated proximal end with virgellarium and one sicular cladium (adapted from Urbanek, 1997a, fig. 5D). Scale bars, 1 mm.

**Neodiversograptus** URBANEK, 1963, p. 149 [**Monograptus nilssoni* LAPWORTH, 1876c, p. 315; *sensu* URBANEK, 1954, p. 300; OD]. Proximally gently dorsally curved monograptid stipe, distally straight or dorso-ventrally curved, forming bipolar tubarium in mature specimens; sicula with long dorsal apertural spine, with its further prolongation producing secondary nema for sicular cladium; thecae tubular, with apertures either straight or with slightly elevated margins; ventral thecal wall at low angle to tubarium axis. [The problems of the identification of *N. nilssoni* were discussed in PALMER (1971a, 1971b) and STRACHAN (1973).] *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone–*Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide (although only questionably from Arctic Canada).——FIG. 307,*4a–c*. **N. nilssoni* (LAPWORTH); *4a,* neotype (PALMER 1971b, p. 97), Long Mountain Shales, Welsh Borderlands, UK (Wilkinson, 2018c, Atlas, Folio 3.58); *4b–c,* proximal ends without (*4b*) and with (*4c*) sicular cladium, Silurian, Ludlow, Poland (Urbanek, 1997b, fig. 2A–B). Scale bars, 1 mm.

**Prolinograptus** RICKARDS & WRIGHT, 1997b, p. 225 [**P. packhami;* OD]. Very slender tubarium with numerous sicular cladia; stipes straight or gently ventrally curved; sicula small; sicular cladia with secondary nemata; thecae with simple everted apertures. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone–*Ludfordian, Neocucullograptus inexpectatus/kozlowskii* Biozone): Australia, Poland, Arctic Canada.——FIG. 307,*5a–b*. **P. packhami; 5a,* AMF 81773a, distal thecae of holotype (Rickards & Wright, 1997b, fig. 9L); *5b,* AMF 91956b, proximal end with sicula (Rickards & Wright, 1997b, fig. 9K). Scale bars, 1 mm.——FIG. 307,*5c*. *P. orangensis* (RICKARDS & others,1995); AMF 81650, holotype, scale bar, 1 mm (Rickards & others, 1995, fig. 35d).

# UNCERTAIN GENERA

Jörg Maletz and Michael Steiner

## INTRODUCTION

The history of research on graptolites includes quite a number of genus-level taxa that have later been identified as belonging to other groups of organisms, even to trace fossils. Some genera have been described that cannot be identified at all. Bulman (1955, 1970) provided a list of unrecognizable taxa. That list is updated here with additional information to provide a better understanding of the current status of these genus-level names. In the future, some of these taxa will be properly identified and referred to other fossil groups or recognized as genuine graptolite taxa. Organic macrofossils can be very similar in fossil preservation to some graptolites, and differentiation may be difficult or impossible in poorly preserved material. Thus, some Neoproterozoic taxa identified as worms, algae, or other organisms have features that are strongly reminiscent of early graptolites and graptolitic tubaria. The organic-walled taxa of the Sabelliditidae may have distinct tubular structures with wrinkled surface ornamentation (Urbanek & Mierzejewska, 1977) similar to the fusellar construction of the graptolite tubaria. Maletz and Beli, 2018) and Maletz (2019a) identified material of the presumed sabelliditid *Sokoloviina costata* Kirjanov, 1968 as remains of early pterobranchs and referred them preliminarily to the Rhabdopleuridae.

## GRAPTOLITIC (PTEROBRANCH) REMAINS OF UNCERTAIN VALUE

A number of genus-level taxa have been mentioned but never described or are based on inadequate material. These taxa are listed here if a graptolitic identity can be suggested. This possible graptolite identity is generally based on the preservation of organic material in the fossil specimens or in the concept of the described genus. In some cases, it may be that the publications with descriptions of those taxa have not been traced or are not currently identifiable. For example, many of the several hundred publications of Rudolf Hundt were in newspapers or in obscure or difficult-to-obtain local journals and are impossible to trace, especially if references to these are not correct. Other genera listed herein have been referred to a number of fossil groups but can be recognized as graptolitic in nature.

**Alexandrograptus** Přibyl, 1981, p. 373, *nom. dub.*, Urbanek & Teller, 1997, p. 43; rejected and invalid name, ICZN, Opinion 2023, 2003, p. 74 [**Monograptus butovicensis* Bouček, 1936, p. 4; OD]. Přibyl (1981, p. 375) recognized *Alexandrograptus* as a synonym of *Polonograptus,* based on the same types species in a postscript to his paper. Urbanek and Teller (1997) identified the type species *Monograptus butovicensis* as a *nomen dubium* and Riva, Koren', and Rickards (2001) applied to ICZN to replace *Monograptus butovicensis* with *Polonograptus podoliensis* Přibyl, 1983 as the type species of *Polonograptus,* granted, ICZN Opinion 2023 (2003).

**Amansites** Brongniart, 1828, p. 70, *nom. dub.,* herein, *ex Fucoides*, section *Amansites,* Brongniart, 1828, p. 70. The author of the genus *Amansites* is usually listed as Brongniart in d'Orbigny (1849), but it was introduced earlier by Brongniart (1828). The genus was listed as algal remains in d'Orbigny (1849, p. 145), based on the two species: *Amansites serra* Brongniart, 1828 (=*Tetragraptus serra*) and *Amansites dentata* Brongniart, 1828 (=*Levisograptus dentatus*). It was listed in Andrews (1970, p. 16), Burkhardt (2018), and most recently in the Guiry and Guiry (2020) algae database. A type species has never been designated for the genus, and it has never been discussed or revised. If these remains are not plant fossils, the genus *Amansites* would be a senior synonym of *Tetragraptus* Salter, 1863a or *Levisograptus* Maletz, 2011c. [The history of this taxon can be regarded as a good example of an unwarranted resurrection of a long-unused taxon name for recent interpretations (see Guiry & Guiry, 2020) and also of the difficulty of identifying organically preserved fossils.]

**Ascograptus** Ruedemann, 1925b, p. 18, *nom. dub.,* herein [**A. similis;* OD]. Small, conical thecae, arranged spirally along an unbranched axis.

[This taxon could represent a juvenile dendroid graptolite; herein.] *Silurian, Ludlow* (*Gorstian*): North America.——FIG. 308,*1a–b*. **A. similis; 1a,* holotype; *1b*, reconstruction (Ruedemann, 1925b, pl. 6,*6* and 6,*8*). Scale bars, 1 mm.

**Birastrites** GEINITZ, 1866, p. 125, *nom. dub.,* herein. Remarks of GEINITZ (1866) suggest, that he intended to include biserial forms with isolated thecal tubes in the genus, based on a theoretical concept, not on actual material.

**Ceramograptus** HUDSON, 1915, p. 129, *nom. dub.*, herein [**C. ruedemanni;* OD]. The type specimen is preserved on the slab with the holotype of *Urasterella pulchella* (BILLINGS, 1857) as stated by HUDSON (1915, p. 129). The specimen is at the GSC, Ottawa, Canada. It is clearly an indeterminable biserial graptolite fragment. *Upper Ordovician:* Canada.——FIG. 308,*2*. **C. ruedemanni,* magnification unclear (Hudson, 1915, pl. 2).

**Changyangograptus** SHAO, JIA, LIU, FU, ZHANG, QIN, JIANG, TANG, WANG, & HU, 2018, p. 422, *nom. nud.*, herein [**Monograptus changyangensis* SUN, 1933, p. 43; OD]. *Silurian* (*Llandovery*). The taxon was listed in a range chart with a single species from the Aeronian (lower Silurian), here regarded as the type species, but there is no description available. CHEN and LIN (1978) described and illustrated the Llandovery (lower Silurian) *Monograptus changyangensis* on which the genus may be based.

**Coelograptus** RUEDEMANN, 1947, p. 266, *nom. dub.,* herein [**Inocaulis problematicus* SPENCER, 1878; OD]. Multiramously branching, encrusting colony; thecal style and development unknown. [This might be a benthic, encrusting graptolite] *Silurian, Ludlow* (*Gorstian*): Canada.——FIG. 308,*3a–b*. **C. problematica* (SPENCER), Niagara Dolomite, Hamilton, Ontario, Canada. *3a,* holotype, scale bar, 10 mm (Ruedemann, 1947, pl. 91,*3*); *3b,* plesiotype, scale bar, 5 mm (Ruedemann, 1947, pl. 39,*12*).

**Cystoturriculagraptus** HUNDT, 1953a, p. 40, *nom. nud.,* herein. It was cited as *Cystoturriculagraptus* HUNDT, 1952, but a 1952 paper with such a citation has not been identified. The genus was listed under the heading Monograptidae without a description or illustration.

**Demicystifer** HUNDT, 1959, p. 27, *nom. dub.,* herein [**Demicystifer cavernalis;* OD]. No description is included, but there is a single illustration of an unidentifiable distal fragment of a biserial graptolite bearing a nematularium. This is not a misspelling of the petalolithid *Demicystograptus* HUNDT, 1950 (see LENZ & others, originally published in *Treatise Online,* 2018, p. 31). *Silurian, Llandovery* (*Rhuddanian, Parakidograptus acuminatus* Biozone–*Cystograptus vesiculosus* Biozone): Germany.——FIG. 308,*4*. **D. cavernalis,* holotype, Hohenleuben, Thuringia, Germany (Hundt, 1959, pl. 6.*1;* specimen not identified). Scale unclear.

**Furkagraptus** HUNDT, 1959, p. 18, *nom. nud.,* herein [**F. furkatus;* OD]. The taxon was listed but neither described nor illustrated by HUNDT, 1959. *Silurian, Llandovery* (*Telychian, Spirograptus turriculatus* Biozone): Germany.

**Geminograptus** HUNDT, 1953a, p. 40, *nom. nud.,* herein). The taxon was listed in HUNDT (1953a) as having been published in HUNDT (1951), but a paper describing the taxon has not been identified. There is no illustration or description available. HUNDT (1953a) also listed a family Geminograptidae.

**Graptolites** M'COY, 1850, p. 270. M'COY (1850) introduced the name as a genus name for monograptids and compared it to '*Diplograpsis*' (now *Diplograptus*) introduced for biserial graptolites. NICHOLSON (1868b) used the genus name, but it survives only as the common name for the group, as it was already used by BARRANDE (1850) and has never been accepted as a valid genus name.

**Graptolithus** LINNAEUS, 1768, p. 173. LINNAEUS (1768) listed the genus *Graptolithus* with a number of taxa that may have included plants (algae), dendrites, and other inorganic objects (In a note on the bottom of page 173: "Petrificatum, proprie dictum, non est Graptolithus, licet petrificaris communiter annumeretur"). The genus name was originally applied to inorganic marks simulating fossils (LINNAEUS, 1735). LINNAEUS (1751, p. 147) for the first time illustrated a *Graptolitus* (sic) in his account of his Scania visit. This illustration has been copied repeatedly and may remain the earliest illustration of a graptolite (see MALETZ, 2017a, fig. 15,*1*), but a specific identification of the taxon is impossible and the original material is not preserved. LINNAEUS (1768) listed among others *Graptolithus sagittarius* and *Graptolithus scalaris*. ICZN Opinion 197 (1954a) finally suppressed the genus name *Graptolithus* LINNAEUS, 1768 and the species *Graptolithus scalaris* LINNAEUS, 1768.

**Halograptus** HUNDT, 1936, p. 36, *nom. nud.,* herein. HUNDT (1936) stated that *Halograptus* can be compared to *Abiesgraptus* (Lower Devonian), but is from the Ordovician (lower Silurian at that time in Germany). It may be a misspelling of *Holograptus,* but HUNDT never illustrated a specimen under this name in any of his papers.

**Hippurograptus** EHLERS & WILSON MS in EHLERS, 1973, p. 129, *nom. nud.*, herein [**H. ruedemanni;* OD] The name was provided in a faunal list from the Schoolcraft Member of the Manistique Dolomite, Clinton Group (Silurian) of Michigan, USA. A description or illustration is not available.

**Janograptus** TULLBERG, 1880a, p. 314, *nom. dub.,* herein [**J. laxatus;* M]. Regenerated stipe fragments of expansograptid or acrograptid origin; see ALBANI & others, 2001, p. 390. *Lower Ordovician* (*Floian*)–*Middle Ordovician* (*Darriwilian*): worldwide.——FIG. 308,*5a*. **J. laxatus*, LO 413t, syntype, Scania, Sweden, scale bar, 1 mm (Tullberg, 1880a, fig. 5).——FIG. 308,*5b*. Janograptid specimen, GSC 119829, *Pterograptus elegans* Biozone, Mainland, western Newfoundland, Canada, scale bar, 1 mm (Albani & others, 2001, fig. 5D).

**Labrumograptus** HUNDT, 1953a, fig. 122, *nom. dub.,* herein [**L. primigenius;* M]. The illustration shows a robust monograptid fragment preserved as an internal cast in pyrite. It is specifically indeterminable. *Silurian, Ludlow* (Zone 20): Germany.——

FIG. 308,*6*. **L. primigenius,* Ronneburg-Raitzhain, Thuringia, Germany, scale bar, 1 mm (Hundt, 1953a, fig. 122; specimen is not identified).

**Lunatograptus** SHAO, JIA, LIU, FU, ZHANG, QIN, JIANG, TANG, WANG & HU, 2018, p. 422, *nom. nud.,* herein. Three species from the Aeronian (lower Silurian) were listed under this genus name in a range chart, but there is no description available. The species are *Lunatograptus lunata* (CHEN & LIN, 1978), *Lunatograptus variabilis* (NI, 1978), and *Lunatograptus falcata* (CHEN & LIN, 1978).

**Mystiograptus** HUNDT, 1965, p. 45, *nom. dub.,* herein [**M. primus;* OD]. Proximally uniserial and distally biserial colony with triangular to hook-shaped thecae. [The holotype BAF 186/299 (HUNDT, 1965, fig. 36.1) is based on an indeterminate tectonically deformed curved uniserial graptolite fragment. The locality is Arnsbach near Gräfenthal, Thuringia, Germany.] *Silurian, Llandovery* (*Telychian, Spirograptus turriculatus* Biozone): Germany.

**Nereitograptus** HUNDT, 1953a, p. 40, *nom. dub.*, herein [type not selected; ?*N. linearis* HUNDT, 1965; M]. The taxon was listed in HUNDT (1953a) as having been published in HUNDT (1951a), but a paper describing the taxon has not been identified. HUNDT (1965, fig. 36,*2*) illustrated a single specimen as *N. linearis* HUNDT, 1965 (BAF H225?). This is a non-identifiable graptolite fragment. HUNDT (1953a) also used the family name Nereitograptidae.

**Nodosograptus** HUNDT, 1965, p. 46, *nom. dub.,* herein [**N. pensilis* HUNDT, 1965; M]. The genus was spelled *Nodosugraptus* in HUNDT, 1953a, p. 40. The taxon was already listed in HUNDT (1953a) as having been published in HUNDT (1951a), but this paper has not been identified and may not exist. The illustration of *N. pensilis* in HUNDT (1965, fig. 38) may be a dorsoventrally preserved fragment of a *Campograptus* or *Monograptus* specimen from the *Stimulograptus sedgwickii* to *Spirograptus turriculatus* Biozone interval at Steinpöhl, Vogtland, Thuringia, Germany.

**Paradimorphograptus** HUNDT, 1953a, p. 40, *nom. nud.,* herein. The taxon was listed in HUNDT (1953a) as having been published in HUNDT (1951a), but a paper describing the taxon has not been identified.

**Paragraptus** HUNDT, 1965, p. 47 [*P. *rhabdopleuraoides;* OD]. HUNDT (1965, fig. 115, BAF H 2517, Weinberg bei Hohenleuben, Thuringia) compared the taxon with the extant *Rhabdopleura* and with *Rastrites*. Zone 13? (*Monograptus sedgwickii* Biozone?): Germany.

**Phycograptus** GURLEY, 1896, p. 89, *nom. dub.,* herein [**P. brachymera;* OD]. RUEDEMANN (1908, p. 245) considered *P. brachymera* GURLEY, 1896 from the Lower *Dicellograptus* Zone at Stockport, New York as a frontal view (ventral view) of a *Dicellograptus* stipe, based on his material, but he was unable to find the type specimen in the Gurley collection. RUEDEMANN (1908, p. 246) discussed *P. laevis* (HALL, 1847) as an undescribed sponge taxon. The type is from the Utica Shale of Turin, Lewis County, New York, USA, and is preserved at the AMNH.

**Polygonograptus** BOUČEK, 1957, p. 151, *nom. dub.,* herein [**Palaeodictyota sokolovi* OBUT, 1953, p. 54; OD]. Irregular network of mainly pentagonal or hexagonal meshes; thecal structure completely unknown. [The genus is unrecognizable and may represent a fragment of a callograptid or dendrograptid graptolite.] *Upper Ordovician–Silurian* (*Wenlock, Testograptus testis* Biozone): Czech Republic, Russia.——FIG. 308,*7a*. **P. sokolovi* (OBUT), holotype, Leningrad area, Russia, scale bar, 1 mm (Obut, 1953, pl. 11,*4a*).——FIG. 308,*7b*. *P. boncevi* BOUČEK, 1957, holotype, Czech Republic, scale bar, 10 mm (Bouček, 1957, pl. 38,*1*).

**Praerhynia** HUNDT, 1949d, p. 45, *nom. dub.,* herein. HUNDT (1949d) introduced the genus without diagnosis and illustrated two specimens. These can probably be recognized as *Cephalograptus cometa* juveniles (HUNDT, 1949d, fig. 31; *Praerhynia*) and an unidentifiable biserial, most likely a *Normalograptus* fragment (HUNDT, 1949d, fig. 30, identified as "Sporangien von *Praerhynia*"). The material originated from the Llandovery of Thuringia, probably from the *Lituigraptus convolutus* Biozone, but different biostratigraphic levels were given in HUNDT (1949d, 1965) for the same specimen. The specimen initially identified as a sporangium of *Praerhynia* was later re-illustrated under the name *Triplograptus triangulatus* (HUNDT, 1965, fig. 120; BAF 186/2296, Heinrichsruh/Schleiz, Zone 11/12).

**Priodon** NILSSON cited in HISINGER, 1831, p. 29, 37; homonym of *Priodon* (attributed to CUVIER) QUOY & GAIMARD, 1825, p. 377 [**P. annulatus* QUOY & GAIMARD; OD; =*Naso annulatus* (Actinopterygii, Acanthuridae)]. Some confusion arose over the naming of graptolites with the introduction of the genus name *Priodon*, apparently suggested but not published by Sven NILSSON (see TULLBERG, 1882b, p. 7; cited also in ELLES & WOOD, 1902, p. vii) and used first by BRONN (1835, p. 56), who indicated the homonymy with the genus *Priodon* QUOY & GAIMARD, 1825.

**Prionotus** NILSSON, cited in HISINGER, 1837, p. 113; homonym of *Prionotus* LACÉPÈDE, 1801, p. 20 (a fish genus of the family Triglidae, searobins). A note to the preoccupation of the name *Prionotus* is in TULLBERG (1882b) and BULMAN (1929). REGNÉLL (1991) discussed the influence of the Swedish scientist Sven NILSSON on graptolite research in Sweden and explained the reason for the reference of the genus names *Priodon* and *Prionotus* to NILSSON, even though NILSSON never published a single paper on graptolites.

**Procyrtograptus** POULSEN, 1943, p. 304, (*nom. dub.,* BJERRESKOV, 1975, p. 46) [**P. garboei;* OD]. BJERRESKOV demonstrated that this genus consists of a combination of specimens of *Coronograptus gregarius* and *Pernerograptus sudburiae* and is therefore not a valid genus.——FIG. 308,*8*. **P. garboei,* 2943, Bornholm, Denmark, scale bar, 1 mm (Poulsen, 1943, fig. 2).

**Protograptus** MATTHEW, 1886, p. 31, original spelling as *Protograpsus* changed in ICZN Opinion 650, 1963, *nom. dub.,* herein [**P. alatus;* M]. Peculiar

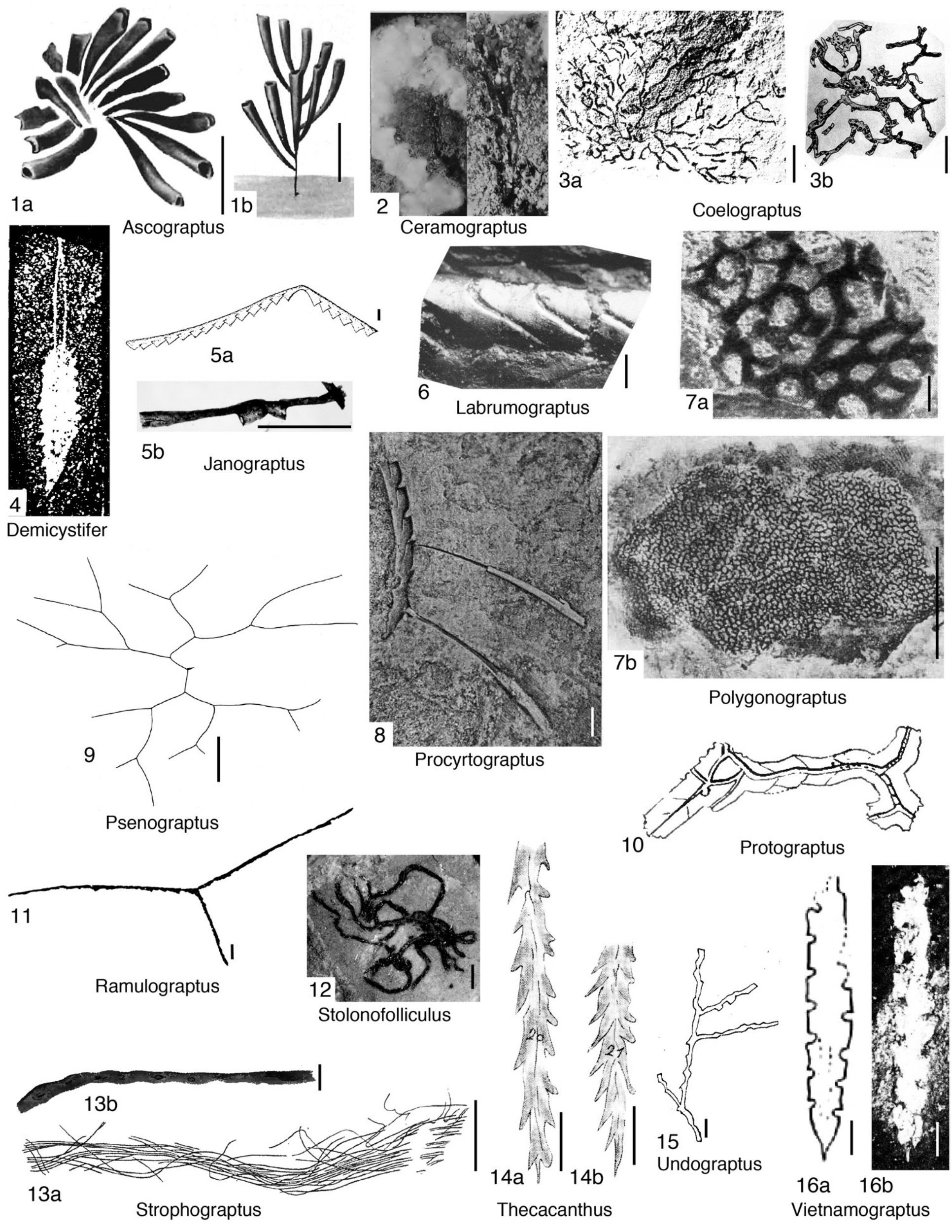


FIG. 308. Uncertain graptolitic remains (p. 461–466).

in its alation, which extends along the axis of the stipe, apparently without bearing cells at the margin. [This fragment looks like a late Tremadocian to Floian adelograptid or clonograptid but is specifically indeterminable. It is associated with *Dendrograptus*(?) *primordialis* MATTHEW, 1886. The material is supposed to come from the "highest *Paradoxides* horizon of the St. John Group" (MATTHEW, 1893a, p. 4), thus the middle Cambrian.] ?*Middle Cambrian:* Canada.——FIG. 308,*10*. **P. alatus,* Porter's Brook, St. Martin's, New Brunswick, Canada (Matthew, 1886, pl. 5,*6*).

**Psenograptus** VANDENBERG, 2019b, p. 47, *nom. dub.,* herein [* *P. costermansi;* OD]. Multiramous species with horizontal funicle, lacking visible thecae. *Lower Ordovician* (*Floian, Paratetragraptus approxi-*

*matus* Biozone): Australia. [The material is poorly preserved, does not show thecae, and therefore is unidentifiable even at the genus level. However, it may represent a multiramous sigmagraptine or dichograptine from the Floian Stage of Australia and is similar to *Clonograptus subtilis* TÖRNQUIST (1904) from the Floian of Sweden, in which low-inclined thecae are visible.]——FIG. 308,*9*. **P. costermani,* holotype, NMV P 327560, Campbelltown, Victoria, Australia, scale bar, 10 mm (new; drawing based on VandenBerg, 2019b, fig. 48).

**Ramulograptus** ROSS & BERRY, 1963, p. 84, *nom. dub.,* herein [**R. surcularis;* OD]. *Middle Ordovician* (*Dapingian–Darriwilian, Isograptus* Zone): USA. The specimen appears to be an indeterminable graptolite fragment of dichograptid or sigmagraptid origin.——FIG. 308,*11*. **R. surcularis,* holotype, USNM 138492, Vinini Formation, Nevada, USA, scale bar, 1 mm (Ross & Berry, 1963, pl. 5,*6*).

**Sinograptus** SHRUBSOLE, 1880 (?), *nom. nud.,* herein. MÜNCH (1931, p. 42) discussed the name, but a paper providing a description or illustration is not currently available. According to MÜNCH (1931), "Mr. Korn initially compared the new species with a graptolite described in American literature under the name *Sinograptus* by SHRUBSOLE (1880), but did not find a match" (MÜNCH, 1931, p. 42, translated by J. MALETZ). It appears that the name *Sinograptus* SHRUBSOLE, 1880 was used to describe a retiolitid graptolite (see discussion in MÜNCH, 1931, p. 42), but it might not have been published officially and has not been found in an unpublished manuscript. The genus cannot be identified with *Sinograptus* MU, 1957 (see p. 277).

**Spinosudiplograptus** HUNDT, 1953a, p. 40, *nom. nud.,* herein. The taxon was listed in HUNDT (1953a) as published in HUNDT (1951a), but a paper describing the taxon has not been identified. HUNDT (1953a) included the genus in the Diplograptidae, but did not provide a diagnosis, description, or illustration.

**Stenograptus** GURLEY, 1896, p. 296, *nom. nud.*, herein. *Lower Ordovician* (*Floian–?Dapingian*): Canada. The name was used in a manuscript sent from Charles LAPWORTH to R. R. GURLEY (see GURLEY, 1896, p. 303) but appears not to have been published by LAPWORTH subsequently. The only record is in a list in GURLEY (1896, p. 296) in which the species *Stenograptus speciosus* "LAPWORTH, MS" is included.

**Stolonofolliculus** ZESSIN & PUTTKAMER, 1994, p. 570, *nom. dub*., MIERZEJEWSKI & URBANEK, 2004, p. 521–522 [**Melanostrophus signum* ÖPIK, 1930; OD]. ZESSIN & PUTTKAMER (1994) even erected a new family, Stolonofolliculidae, for the genus. MIERZEJEWSKI (1988) stated that the type material of *M. signum* was lost but referred the taxon to *Graptovermis intestinalis* KOZŁOWSKI, 1949. *Ordovician.*——Fig. 308,*12*. **S. signum* (ÖPIK), holotype, TUG 1053-17, Kukruse Stage, (lower Sandbian) Kohtla, Estonia, scale bar, 1 mm (new; provided by Ursula Toom).

**Strophograptus** RUEDEMANN, 1904, p. 716, *nom. dub.,* herein [* *S. trichomanes;* OD]. Bundles of long thin flexuous carbonaceous fibers, subparallel and not bifurcating; thecae indistinct, perhaps represented by minute pores along the stipes. [The genus has to be regarded as graptolite indet. at the moment. It is not even clear whether the material represents graptolite remains. The few known specimens were collected from graptolitic shales and are apparently comprised of organic material.] *Middle Ordovician* (*lower Darriwilian, Levisograptus dentatus* Biozone): USA.——Fig. 308,*13a–b*. **S. trichomanes,* holotype (*a*) and enlargement (*b*) of single stipe; scale bar, 10 mm (*a*); 1 mm (*b*) (Ruedemann, 1904, pl. 4,*17,20*).

**Thecacanthus** HERNÁNDEZ SEMPELAYO, 1960, p. 35, *nom. dub.*, herein, *ex Glossograptus* (*Thecacanthus*) HERNÁNDEZ SEMPELAYO, 1960, p. 35 [**Glossograptus* (*Thecacanthus*) *loxos;* OD]. This taxon was introduced for biserial forms where the interthecal septa "are not precisely marked inside the fossil" and whose "thecae are individualized and prolongate to end in spines with proximal inclination" (HERNÁNDEZ SEMPELAYO, 1960, p. 35). The material originated from the Almadén syncline and the Almadén mine and may instead represent distal fragments of *Parapetalolithus* or *Glyptograptus*. (information and translation, J. C. GUTIÉRREZ-MARCO, May, 2020).] *Silurian:* Spain.——FIG. 308,*14a–b*. **T. loxos,* two examples, scale bars, 1 mm (Hernández Sampelayo, 1960, pl. 16,*20–21*).

**Triplograptus** HUNDT, 1965 (listed in HUNDT, 1959, p. 19) *nom. dub.*, herein [*non Triplograptus* RICHTER, 1871, p. 251 (type, *T. nereitarum,* OD, trace fossil *Protovirgularia*, see p. 9)]. Tubaria with three rows of thecae. [HUNDT (1965, in explanation to fig. 39,*1–3*) listed a family Triplograptidae. HUNDT (1965) listed a number of species that may belong to the genera *Cystograptus*, *Petalolithus,* and *Normalograptus*.] *Silurian, Llandovery* (*Aeronian*): Germany.

**Undograptus** NINDEL, 1949, p. 24, *nom. dub.,* herein [**U. nodosus;* OD]. Undulating stipes with ?alternate thecae, branching observable. [This is certainly a strongly tectonized monograptid graptolite but is too poorly preserved for identification. NINDEL (1949, p. 24) indicated that the genus was already described by HUNDT (1946), but this paper is unknown]. *Silurian, Llandovery* (*Telychian*).——FIG. 308,*15*. **U. nodosus,* Raitzhain, Ronneburg, Thuringia, Germany, Zone 15 (*Monograptus exiguus* Zone of EISEL, 1903; =*crispus/griestoniensis* Zone), scale bar, 1 mm (NINDEL, 1949, fig. 21,*4*).

**Vietnamograptus** VAN PHUC, 1998, p. 286, *nom. dub.*, herein [**V. thamhocensis;* OD]. According to the author, the new genus is small and short, slender and undulated. The rhabdosome has two types of thecae: monograptid type on one side, but glyptograptid type with the star thecal apertures on the other side (VAN PHUC, 1998). [No illustrations of Vietnam material are available, but JAEGER (1988) illustrated a single specimen, which is not mentioned in the abstract in which the genus was introduced. It appears to be a secondarily? biserial taxon, originating from a monograptid ancestor (comparable to the abnormal, partly biserial specimen of *Slovinograptus balticus* in URBANEK, 1997a, fig. 10).] *Lower Devonian* (*Lochkovian, Uncinatograptus hercynicus* Biozone): Austria, Vietnam.——FIG.308,*16a–b*. **V. thamocensis,* Obere Bischoffsalm, Carnic Alps, Austria; *16a,* drawing (Jaeger, 1988, fig. 1K); *16b,* photo (Flügel, Mostler, & Schönlaub, 1993). Scale bars, 1 mm.

## TAXA OF UNCERTAIN ORIGIN

The genera listed here do not represent graptolitic remains, but cannot currently be assigned to any fossil group. They were initially described as graptolites.

**Acanthastus** KOZŁOWSKI, 1949, p. 226 [**A. luniewskii;* OD]. BULMAN (1970) included the order Acanthastida KOZŁOWSKI, 1949 with its single genus *Acanthastus* under the heading Graptolithina *incertae sedis*. KOZŁOWSKI (1949) suggested a chitinous composition and a possible secretion of the features as evidence of a possible graptolite relationship, which has not been verified. The complex development of the specimens and the lack of any recognizable pterobranch features may render doubtful the assignment to the Pterobranchia. *Lower Ordovician* (*Tremadoc*): Poland.——FIG. 309,*1a–c*. **A. luniewskii,* holotype, dorsal (*a*), ventral (*b*), and lateral (*c*) views; scale bars, 1 mm (Kozłowski, 1949, pl. 40,*2*).

**Conograptus** RUEDEMANN, 1947, p. 267 [**C. simplex;* OD]. Simple, conical tube that contains bundles of filiform thecae within the outer periderm; thecal apertures circular, scattered on surface of rhabdosome. *Cambrian:* USA (Colorado).——FIG. 309,*2a–b*. **C. simplex,* drawings of two fragmented specimens; scale bars, 1 mm (Ruedemann, 1947, pl. 40,*26–27*).

**Crinisdendrum** DZIK, BALIŃSKI, & SUN, 2016, p. 327 [**C. sinicum;* M]. Mature colony with lateral branches (thecae?) distributed along axis. [DZIK, BALIŃSKI, and SUN (2016) erected the family Crinisdendridae for the genera *Crinisdendrum* and *Webbyites* KRAFT, KRAFT, & PROKOP, 2001 and suggested a pterobranch affinity as the most likely hypothesis. There is no evidence of fusellar construction in these taxa to support a pterobranch affinity.] *Lower Ordovician* (*Floian,* ?*Tetragraptus approximatus* Biozone): China (Hubei Province).——FIG. 309,*10a–b*. **C. sinicum,* Fenxiang Formation, Hubei Province, China; *10a,* juvenile colony, scale bar, 0.5 mm; *10b,* part of mature colony; scale bars 5 mm (DZIK, BALIŃSKI, & SUN, 2016, fig. 5).

**Hunanodendrum** MU, LI, GE, CHEN, NI, LIN & MU, 1974, p. 220 [**H. typicum;* OD]. It is impossible to relate the material to any known graptolite taxon. *Silurian, Llandovery* (*Telychian*): China.——FIG. 309,*3a*. **H. typicum,* syntype, scale bar, 10 mm (Mu & others, 2002, pl. 33,*5*).——FIG. 309,*3b*. *H. irregulare* NI, in LI & NI, 1979, holotype, scale bar, 10 mm (Mu & others, 2002, pl. 33,*9*).

**Protistograptus** MCLEARN, 1915, p. 55 [**Creseis corrugata* MATTHEW, 1892, p. xviii & Errata (listed as *Cyrtotheca* on p. xviii, revised in Errata; no page number); OD; see BULMAN, 1929, p. 181 (referred to *Styliola* by BASSLER, 1915b, p. 1242)]. Arched or straight cone, formed from carbonaceous material; probably representing a sicula comparable to the genus *Corynoides*. [The graptolitic assignment is based on the presence of carbonaceous material and the interpretation as a large sicula, but the identification is uncertain. MATTHEW (1893b, p. 105) described it as "a horny consistency, or of thick chitenous substance." The specimens may be comparable with carbonaceous problematica from the Martinsburg Formation of Pennsylvania (MEYER & others, 2018) (see Fig. 309,*5b*).] *Lower Ordovician* (?*Floian*)–*Upper Ordovician* (*Sandbian*): ?Australia (Tasmania), Canada, USA.——FIG. 309,*5a*. **P. corrugata* (MATTHEW), St. John, New Brunswick, Canada, scale bar, 1 mm (McLearn, 1915, fig. 2).——FIG. 309,*5b*. Carbonaceous problematica, Martinsburg Formation, USA, scale bar, 1 mm (Meyer & others, 2018, fig. 5D).

**Quadruplograptus** HAUPT, 1878, p. 51 [**Q. rhomboidalis;* M]. The identity of this material is uncertain and it might not be a graptolite. Haupt's paleontological collection may be at the University of Wrocław, Poland (formerly Breslau) (SCHÖNWÄLDER, 1882), but the specimen has not been identified. *Silurian* (*Wenlock–Ludlow*).

**Undagraptus** HEMMANN, 1951, p. 75 [**U. stolzenbergensis;* OD]. The identification is based on the undulating shape of the specimen. The original was said to be in the collection of the author. The counterpart is at Paläontologisches Institut, Martin Luther Universität Halle, Germany (Nr. 48015). The available photo is too poor for an identification or re-illustration. *Silurian, Ludlow* (*Gorstian*).

## ARTHROPODS

A few taxa were described initially as graptolites but can be recognized as arthropods. Pieces of phyllocarids, in particular, have been identified as graptolites in the past, either as colonies (rhabdosomes; tubaria), floats, or ovarian capsules due to their representing organically preserved material in graptolitic shales. MANCK (1927) described a number of examples as gonothecae and float structures of graptolites from the Silurian of Germany. GÜRICH (1928) strongly opposed this view and recognized some of the specimens as phyllocarid remains. The most prominent example may be *Megalograptus* MILLER, 1874, now recognized as fragments of an eurypterid.

**Coronagraptus** HUNDT, 1951a, p. 60 [**C. singularis;* OD]. BULMAN (1970) considered the genus as unrecognizable. It is clearly a phyllocarid fragment, possibly belonging to the genus *Peltocaris* SALTER, 1862 as described by SALTER (1862). The species may be common in the Unterer Graptolithenschiefer in Germany. The genus should not be confused with *Coronograptus* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968, a Silurian monograptid. *Silurian, Llandovery* (*Telychian, Spirograptus turriculatus* Biozone): Germany.——FIG. 309,*6*. **C. singularis,* holotype, not identified, Hässlich near Weckersdorf, Thuringia, Germany, scale bar, 5 mm (Hundt, 1951a, fig. 16).

**Dawsonia** NICHOLSON, 1873, p. 139 [**D. campanulata;* SD MILLER, 1889, p. 184] [*non Dawsonia* HARTT in DAWSON, 1868 (Trilobita, Eodiscina); AXHEIMER, 2006]. The genus is a junior homonym to *Dawsonia* HARTT in DAWSON, 1868, thus invalid. ROLFE (1969, p. 316) stated that *Dawsonia* NICHOLSON, 1873 is a junior synonym of *Caryocaris* SALTER, 1862, but PAGE and others (2009) discussed *D. campanulata* as a fossil of uncertain origin, a flat problematicum, but recognized that a number of unrelated fossil remains were described under this name, including linguliform brachiopods and crustacean tail pieces. *Silurian, Llandovery.*——FIG. 309,*7*. **D. campanulata,* lectotype NHMUK Q253, Silurian, Llandovery, Dob's Linn, Scotland, scale bar, 1 mm (Page & others, 2009, fig. 1a).

**Megalograptus** MILLER, 1874, p. 343 [**M. Welchi;* OD]. RUEDEMANN (1908, p. 247) discussed the genus as "fragments of a crustacean" and compared it with *Echinognathus clevelandi* WALCOTT, 1882. CLARKE and RUEDEMANN (1912a, 1912b) referred the material to the Eurypterida. LAMSDELL and others (2015) included it in the family Megalograptidae (see STØRMER, 1955, p. 36) and recognized the members of the family as the oldest known eurypterids. TOLLERTON (1989) elevated the family to the superfamily Megalograptoidea. *Upper Ordovician, Katian.*

## HYDROIDS

Quite a number of dendroid graptolites have been identified as hydroids in the past (see MALETZ & BELI, 2018). Due to their poor preservation, it is often difficult or impossible to determine the true affinity of such taxa. For example, MUSCENTE, ALLMON, and XIAO (2015) recognized the hydroid genus *Archaeoantennularia* DECKER, 1952 as a benthic graptolite, and there might be more such taxa that could be identified as graptolites in the fossil record. Conversely, other taxa regarded as graptolites may belong to the hydroids, as was verified for the genus *Plumalina* (see MUSCENTE & ALLMON, 2013).

**Archaeodendrum** OBUT, 1974, p. 9 [* *A. bulmani;* OD] Colony slender, flexuous, shape unknown; thecae tubular, elongate, isolated distally, slightly widening toward the aperture, arranged in triad groups on alternate sides of stem. [According to RICKARDS & DURMAN (2006, p. 58), this taxon belongs to the Hydroida. It does have an unusual grouping of the thecae and a flexing of the axis. No fusellar features or stolons are known.] *Cambrian, Miaolingian* (*upper Drumian, Anomocaroides* Zone): Russia (Siberian Platform).——FIG. 309,*8a–b*. **A. bulmani,* holotype (*a*) and paratype (*b*), scale bars, 1 mm (Rickards & Durman, 2006, fig. 47).

**Dyadodendrum** SENNIKOV, 1998, p. 18., *ex Archaeodendrum* (*Dyadodendrum*) SENNIKOV, 1998, p. 18, herein [**A.* (*D.*) *obuti;* OD]. According to RICKARDS and DURMAN (2006, p. 58), this taxon belongs to the Hydroida. The authors did not recognize much difference from *Archaeodendrum* but did not synonymize the two taxa, which they regarded as subgenera. *Cambrian, Miaolingian* (*Drumian*).

**Plumalina** HALL, 1858, p. 143 [**P. plumaria;* OD]. HALL (1858) included the taxon in his family Graptolitidae. RUEDEMANN (1916) and BAYER (1956) referred *Plumalina* to the Gorgoniidae (Alcyonaria). SASS and ROCK (1975) suggested a possible inclusion in the Hydrozoa but were uncertain. MUSCENTE and ALLMON (2013) identified the genus *Plumalina* as a hydroid of the superfamily Plumularioidea MCCRADY, 1859. DZIK, BALIŃSKI, and SUN (2016) rejected the hydrozoan affinity of *Plumalina* and suggested an algal relationship. *Silurian* (*Wenlock*)*–Devonian* (*Famennian*).

**Protohalecium** CHAPMAN & THOMAS, 1936, p. 203 [**P. hallianum;* M]. Erect, multiramous tubarium, with isolated tubular thecae, formed in bundles. [RICKARDS and DURMAN (2006) regarded the genus *Protohalecium* from the Middle Cambrian of Australia as a hydroid. However, there is a chance that the taxon belongs to the Dithecodendridae if the presence of fusellar construction can be proven.] *Cambrian, Furongian* (*Paibian, Olenus* Biozone): Australia.——FIG. 309,*9a–c*. **P. hallianum; 9a*, holotype, Victoria, Australia (Rickards & Durman, 2006, fig. 50a); *9b–c*, counterpart specimens from Que River, Tasmania (Rickards & Durman, 2006, fig. 50). Scale bars, 1 mm.

## ECHINODERMS?

**Planctograptus** YAKOVLEV, 1933, p. 979 (misspelled as *Planktograptus* in BULMAN, 1955, 1970) [**P. rastritoides;* M]. Hexagonal central body (also identified as a central disk, 7.3 × 10 mm) and cirrus rays emanating from its corners. [Based on the original illustration, the genus may represent an unusual echinoderm but needs to be re-investigated. It is certainly not a graptolite.] ?*Upper Silurian*——FIG. 309,*11*. **P. rastritoides,* holotype, Kazakhstan, scale unknown (Yakovlev, 1933, pl. 2,*2b*).

## TRACE FOSSILS

Due to an incomplete understanding of graptolites, early researchers often included unrelated fossils in the group. Thus, a number

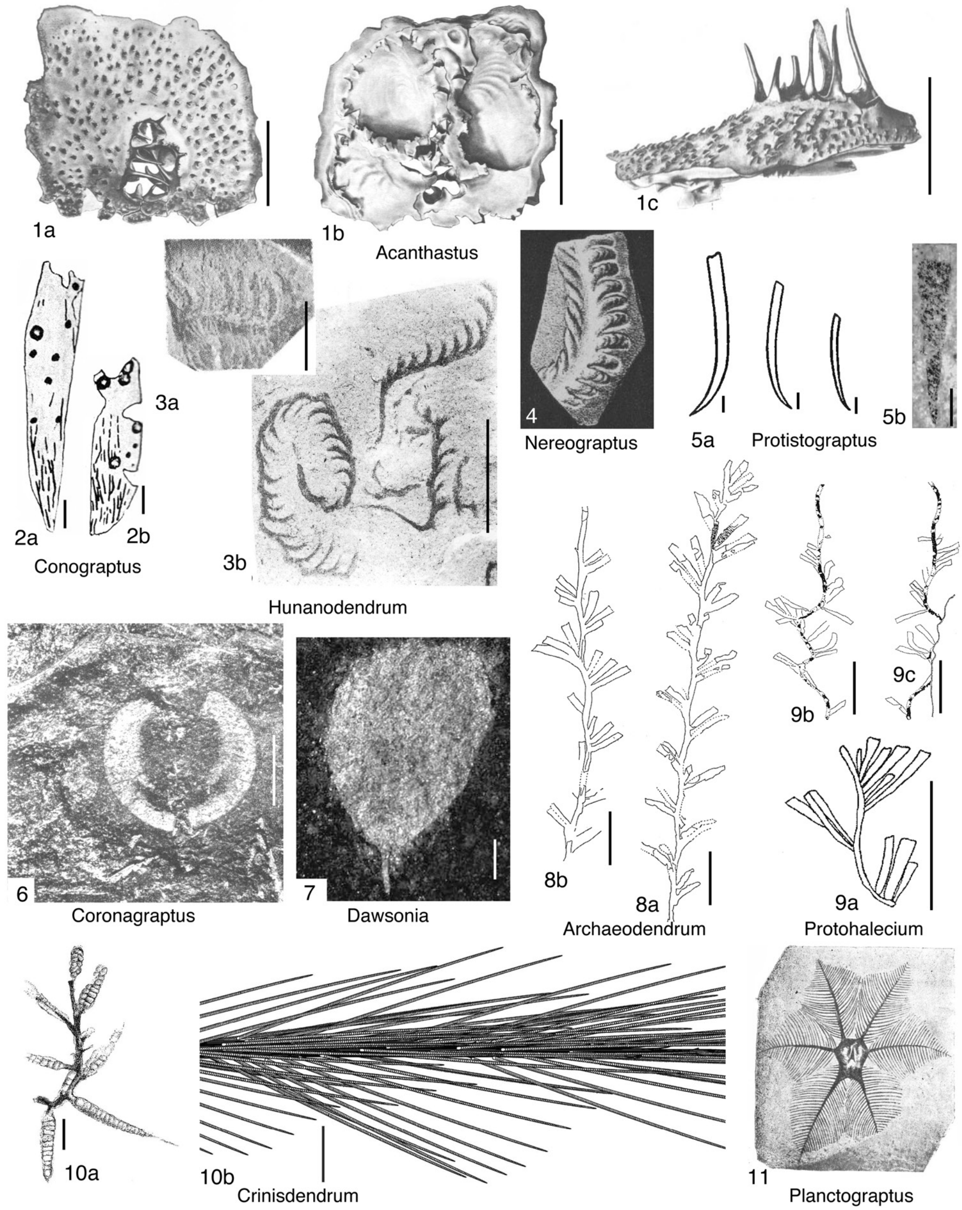


FIG. 309. Genera of uncertain affinity and genera possibly assignable to arthropods, hydroids, echinoderms, or trace fossils (p. 466–469).

of genera were initially described as graptolite remains but later recognized as trace fossils. HALL (1865, p. 51) included—with a question mark—the genus *Oldhamia* FORBES, 1848 in his Graptolitidae and listed the species *Oldhamia fruticosa* HALL 1865 but did not describe or illustrate the species. WHITFIELD (1894) described fossil material as the marine alga *Callithamnopsis fruticosa* (HALL, 1865). The taxon was regarded as a noncalcified dasycladacean alga by LODUCA, KLUESSENDORF, and MIKULIC (2003), who referred to WHITFIELD (1894) as the author of the species. This example illuminates the difficulty of understanding graptolite remains during the early stages of investigation.

**Humiligraptus** HUNDT, 1940, p. 244 [**H. attenuatus;* SD herein]. HUNDT (1940) referred three species from the Phycodes Group (late Tremadocian–Floian) of Thuringia to this new genus. *H. attenuatus* may represent a poorly preserved trace fossil. There are no good illustrations of the specimens referred to this genus available, and the material has never been revised and was not identified in the Hundt collection at FU Bergakademie Freiberg Thuringia, Germany. *Ordovician* (*late Tremadocian–Floian*): Germany (Thuringia).

**Nereograptus** GEINITZ, 1852, p. 27, *nom. correct. pro Nereograpsus* GEINITZ, 1852, p. 27; GEINITZ, 1866, p. 125 [**Nereites cambrensis* MURCHISON, 1839; OD]. GEINITZ (1852) clearly identified *Nereograptus* as giant graptolites (zum Teil gigantische Graptolithinen) from the Ordovician (lower Silurian at the time) of Thuringia, Germany. It seems he wanted to introduce the name *Nereograptus* to demonstrate his interpretation of these fossils as graptolites, because he synonymized the genus *Nereites* with his *Nereograptus*. RICHTER (1849) had previously described *Nereites cambriensis* from Thuringia, even though at the time he did not identify it as a trace fossil but as a kind of fossil worm. There is no doubt that *Nereograptus* GEINITZ, 1852 is a trace fossil and the name is a synonym of *Nereites* MACLEAY, 1839.——FIG. 309,*4*. **Nereograptus cambrensis* (MURCHISON), Ordovician, Saalfeld, Thuringia, Germany, scale uncertain (Geinitz, 1852, pl. 5,*20*).

**Protovirgularia** M'COY, 1850, p. 272 [**P. dichotoma;* M] [=*Triplograptus* RICHTER, 1871, p. 251 (type, *Cladograpsus Nereitarum* RICHTER, 1853, p. 450; M); HAN & PICKERILL, 1994, p. 203]. M'COY (1850) referred the genus *Protovirgularia* to the family Gorgonidae and compared it with some biserial graptolites. HAN and PICKERILL (1994) revised the genus, and SEILACHER and SEILACHER (1994) identified it as a bivalve trace fossil.

## MACROALGAE

The identification of fossil algae as graptolites has been common in the past. The reasons for this may be 1) the preservation as organic remains and 2) the general similarity of algal shapes to the shapes of dendroid graptolite tubaria. The taxonomy of fossil noncalcified macroalgae is very difficult due to the typically poor preservation as thin films of carbonaceous material in shales, siltstones, and limestones. Furthermore, many have been transported and, thus, fragmented and rarely preserved as complete specimens in their original growth position (see LODUCA & BRETT, 1997; LODUCA, MELCHIN, & VERBRUGGEN, 2011).

In a number of genera, the phylogenetic relationships to other macroalgae have been proposed in the literature, but for many forms, an algal origin can only be inferred from the shape of the fossil. The material invariably does not have the typical fusellar structure of the Pterobranchia (graptolites) but is preserved as structureless, dark carbonaceous material. MALETZ and CAMERON (originally published in *Treatise Online,* 2016, p. 12) identified the Cambrian alga *Yuknessia* WALCOTT, 1919 as a pterobranch, based on the presence of fusellar construction (LODUCA & others, 2015). MALETZ and BELI (originally published in *Treatise Online,* 2018, p. 1–2) listed the Cambrian algae *Dalyia* WALCOTT, 1919 and *Malongitubus* HU, 2005 as Graptolithina *incertae sedis* and recognized the presumed hydroids *Archaeolafoea* CHAPMAN, 1919 and *Sphenoecium* CHAPMAN & THOMAS, 1936 as rhabdopleurid pterobranchs.

LODUCA, MELCHIN, and VERBRUGGEN (2011) provided the description of a number of dasycladacean algae associated with graptolites from Cornwallis Island in the Canadian Arctic, explaining the usual preservation of these floras. LODUCA (1990) identified the genus *Medusaegraptus* RUEDEMANN, 1925b from the Silurian of New York State as a noncalcified dasycladacean, based on the type material and additional specimens from a variety of localities in New York State, USA, and Ontario, Canada. This may have been the start of a more cautious approach to some so-called dendroid graptolite remains and the recognition that some genera may better be referred to as algal remains of various types.

LODUCA and BRETT (1997) described the so-called *Medusaegraptus* epibole of the Lockport Group (Silurian) of western New York and southern Ontario, in which thallophytic algae and dendroid, benthic graptolites were a common constituent of the fauna and flora. Many specimens of these were found *in situ* because they had grown on the sea floor, associated with other algae, brachiopods, conularids, corals, mollusks, annelids, and arthropods. The authors suggested a water depth of approximately 10–15 m for the environment in which the *Medusaegraptus* epibole flourished.

No attempt is made to differentiate the discussed genera and refer them to any taxonomic units within the Dasycladales herein; therefore the genera are listed in alphabetical order. Only taxa with uncertain, but possible, algal affinity are illustrated through their type material (Fig. 310). Otherwise, the most current revisions of the taxa are referenced below.

**Boucekocaulis** Obut, 1960, p. 148 [**Acanthograptus jubatus* Obut, 1953, p. 53; OD]. This taxon may represent an alga but needs to be re-investigated.——Fig. 310,*1*. **B. jubatus* (Obut, 1953), fragment, Russia, scale unclear (Obut, 1953, pl. 12,*5a*).

**Buthograptus** Hall, 1861b, p. 18 [**B. laxus;* M]. Hall (1861b) described *Buthograptus* as a benthic graptolite from the Upper Ordovician of Wisconsin, but Whitfield (1894, p. 352) first identified the taxon as an alga. LoDuca (2019) more recently revised the genus and referred it to the green algal order Bryopsidales. *Upper Ordovician:* USA.

**Calyptograptus** Spencer, 1878, p. 459, original spelling as *Calyptograpsus* changed in ICZN, Opinion 650, 1963 [**C. cyathiformis;* OD]. The genus is herein identified as a possible alga. The type may, however, represent a poorly preserved callograptid or dendrograptid, but there is no evidence of thecae or fusellar construction.——Fig. 310,*2*. **C. cyathiformis,* 1878), holotype, scale bar, 10 mm (Bassler, 1909, fig. 48).

**Crinocaulis** Obut, 1960, p. 148 [**C. flosculus;* OD]. The identity of this strange taxon is uncertain, but an algal relationship cannot be excluded.——Fig. 310,*3*. **C. flosculus,* scale unclear (Obut, 1960, pl. 3, fig. 1A).

**Diplospirograptus** Ruedemann, 1925b, p. 34 [**D. goldringae;* OD]. Bulman (1938) expressed doubts about the graptolitic nature of this taxon and suggested an algal affinity. Mierzejewski (1986) discussed *D. goldringae* as a possible alga of the class Chlorophyceae, essentially rejecting an inclusion in the graptolites. This interpretation is supported by the assignment of LoDuca (1990) and LoDuca, Kluessendorf, and Mikulic (2003).

**Estoniocaulis** Obut & Rotsk, 1958, p. 137 [**E. jaervensis*; OD]. Mierzejewski (1991) investigated the type material and recognized solid, roller-like elements that he compared with the melanosclerites and preliminarily referred the taxon to the order Melanoskleritoidea, a clade of possible algae from the lower Silurian.

**Inocaulis** Hall, 1852, p. 176 [**I. plumulosa;* M] ?*Ordovician–Silurian:* worldwide. The genus has long been identified as a dendroid graptolite and in the family Inocaulidae, established by Ruedemann (1947). Furthermore, Bouček (1957) referred to the group as the order Inocaulida Bouček, 1957. Mierzejewski (1986, p. 166) doubted the graptolitic nature of *Inocaulis* and discussed the genus as a hydroid. Maletz (2014b) suggested that *Inocaulis plumulosa* is an alga, but LoDuca and others (2017, p. 599) illustrated *I. plumulosus* as a "hemichordate with an alga-like tubarium." Because fusellar construction has not been identified in the type species of the genus, its inclusion in the graptolites is uncertain, and the preference herein is to keep it as an alga. However, most species referred to *Inocaulis* may represent species of the Callograptidae and should be referred to a number of other genera. Muir, Zhang, and Lin (2013) discussed a single fragment as *Inocaulis* sp., in which fusellar construction was detected.——Fig. 310,*4a–b*. **I. plumulosa; 4a*, illustration of type (Hall, 1865, fig. 26); *4b–c*, commonly illustrated typical specimens; scale bars, 10 mm (Bassler, 1909, fig. 59, 61).

**Leveilleites** Foerste, 1923, p. 62 [**L. hartnageli;* M]. The taxon was originally described as a possible alga but referred to the graptolites by Ruedemann (1947). An alga with similar form has been illustrated in Tinn and others (2009) from the Llandovery (Aeronian) of Estonia, suggesting an algal relationship of *Leveilleites*.

**Medusaegraptus** Ruedemann, 1925b, p. 29 [**M. mirabilis;* OD]. Bulman (1938) already expressed his doubts on this taxon and suggested an algal affinity. Mierzejewski (1991) discussed *Medusaegraptus* as an alga, and LoDuca (1990) referred the taxon to the noncalcified dasycladacean algae.

**Palmatophycus** Bouček, 1941, p. 3 [**P. kettneri;* OD]. *P. kettneri* was originally described as a dendroid graptolite from the Silurian (Wenlock/Ludlow) of the Czech Republic. LoDuca and others (2017) illustrated the taxon from the Eramosa Formation of Canada as a non-calcified marine alga.

**Rhadinograptus** Obut, 1960, p. 151 [**R. jurgensonae;* OD]. Mierzejewski (1991) did not find evidence of a graptolitic relationship and suggested that the taxon should be regarded as a fossil alga.

**Thallograptus** Ruedemann, 1925b, p. 35 [**Dendrograptus? succulentus* Ruedemann, 1904; OD] [*non Thallograptus* Öpik, 1928, p. 35 (type, *T. sphaericola,* OD [Wimanicrustidae, Graptolithina]); =*Hormograptus* Öpik, 1930 (Wimanicrustidae)]. Ruedemann (1925b) discussed a close similarity in shape to marine algae and reported that the thecal apertures appear as pores on the surface. Hewitt and Birker (1986) discussed the type specimens of *Buthotrephis grantii* Dawson, 1890 and *Inocaulis vegetabilis* Gurley in Bassler, 1909 from the Silurian Eramosa Member of the Lockport Dolomite of Ontario, Canada. Both types represent fragments of a single specimen referred now to *Thallograptus grantii* (Dawson, 1890) and interpreted as a possible alga, supporting the algal origin of some but not all taxa referred to the genus *Thallograptus* in the past. Bulman (1970) interpreted *Thallograptus* as a member of the Acanthograptidae

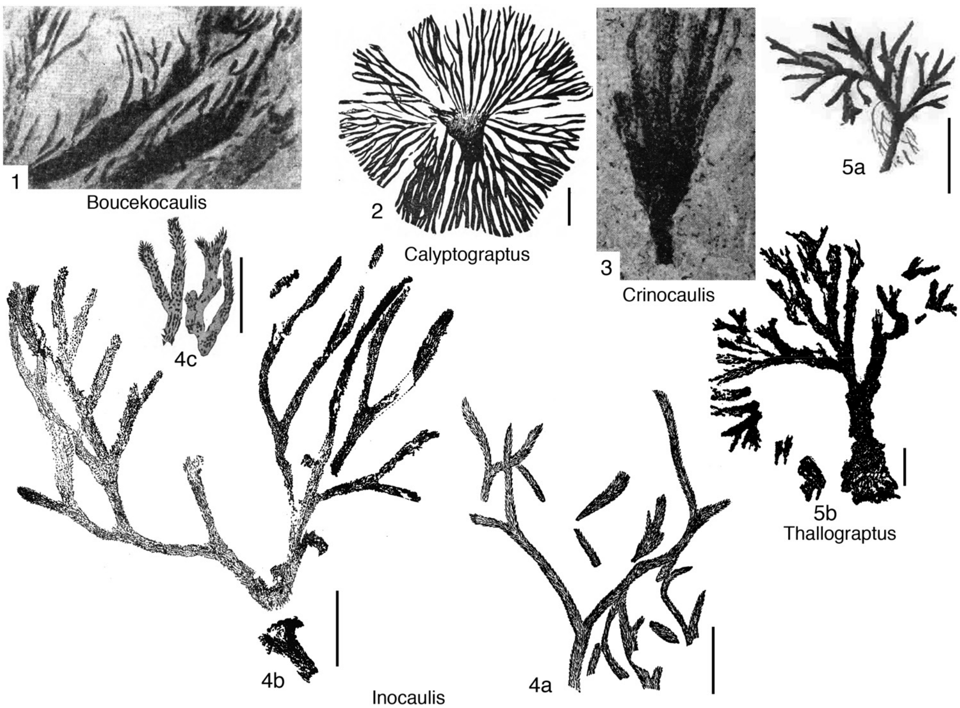


FIG. 310. Possible algae identified as graptolites (p. 470–471).

(now Callograptidae). Many taxa assigned to the genus in the past may need to be re-evaluated and referred to other genera of the Callograptidae.——Fig. 310,*5a*. **T. succulentus* (RUEDEMANN), syntype, scale bar, 10 mm (Ruedemann, 1904, pl. 4,*4*).——FIG. 310,*5b*. *T. phycoides* (SPENCER, 1884), specimen illustrated as *Thallograptus cervicornis* in BULMAN (1970, fig. 22,*2*). RUEDEMANN (1925b, fig. 23) illustrated the specimen as characteristic of the genus *Thallograptus*, scale bar, 10 mm.

## LAND PLANTS

It should not be forgotten, that Rudolf HUNDT identified graptolite remains as early land plants. HUNDT (1949d, fig. 29) illustrated fragments of a biserial graptolite as "*Praerhynia* spec. Sporangien" and re-illustrated the specimen as *Triplograptus triangulatus* HUNDT in HUNDT (1965). Also, material he identified as *Baragwanathia oelheyi* HUNDT, 1952b (HUNDT, 1952b, fig. 30) might represent graptolite fragments. Uncertain fossils are also the "Praepsilophyten mit Sporangien" (HUNDT, 1952a). Unfortunately, the material illustrated by HUNDT in these papers has not been identified in his collection.