SUBORDER GLOSSOGRAPTINA

Jörg Maletz and Yuandong Zhang

Suborder GLOSSOGRAPTINA Jaanusson, 1960

[Glossograptina Jaanusson, 1960, p. 319] [=Pan-Glossograpta Maletz, Carlucci, & Mitchell, 2009, p. 14] =Pan-Bireclinata Maletz, Carlucci, & Mitchell, 2009, p. 13, *partim*]

Two-stiped, reclined to scandent graptoloids with isograptid symmetry; scandent taxa monopleural or dipleural; sicula tubular, commonly elongated, slightly widening toward Faperture, with small prosicula less than one-third of sicular length; proximal development type isograptid, dextral, with prosicular origin of th1[1] or, in a few cases, a derived pattern; thecae simple, gradually widening tubes, typically with distinct rutella; apertural thecal spines and lacinia present in derived taxa; attenuation of fusellum common. *Middle Ordovician* (*Dapingian*)–*Upper Ordovician* (*Katian*): worldwide.

The paraphyletic taxon Glossograptina includes the partial clade identified by the isograptid symmetry of the colony as the defining synapomorphy (see Maletz & Mitchell, 1996, fig. 8; Maletz, Carlucci, & Mitchell, 2009, fig. 2). However, it excludes the Axonophora (biserial, dipleural graptoloids).

INTRODUCTION

Numerous, well-preserved relief specimens and even chemically isolated specimens of the Glossograptina provide the basis for a detailed understanding of colony construction. The main uniting synapomorphic character of the Isograptidae as the basal Glossograptina is the isograptid symmetry, in which the line of symmetry passes between the sicula and th1[1] (Fig. 202.2–202.3). This differs considerably from the maeandrograptid symmetry in earlier dichograptids (Fig. 202.1). In the maeandrograptid symmetry, the line of symmetry passes through the sicula, with th1[1] and th1[2] positioned symmetrically on both sides of the sicula. The maeandrograptid symmetry occurs in early Tremadocian anisograptids, and variations may be due to the orientation of the sicula, which can be vertical or inclined.

Jaanusson (1960) originally included only the family Glossograptidae in the Glossograptina because the phylogenetic relationships with the ancestral Isograptidae were unknown. Maletz and Mitchell (1996, p. 651) expanded the family to include the isograptids and the glossograptids, to acknowledge their close phylogenetic relationships, stating that it is not possible to define a taxon as a monophyletic unit without including both the traditional glossograptids and the isograptids. In contrast, in the taxonomy adopted herein, the Glossograptina are not monophyletic but represent a paraphyletic unit from which the Axonophora originated through the manubriate isograptids (Mitchell, Maletz, & Zhang, 1995; Fortey, Zhang, & Mellish, 2005; Maletz, 2010a). The suborder Glossograptina includes the suborder Pan-Glossograpta and the stem isograptids of the superorder Pan-Bireclinata of Maletz, Carlucci, and Mitchell (2009).

EVOLUTION

The Isograptidae, as the basal Glossograptina, differ from the derived, monopleural Glossograptina, mainly in that the stipes do not have monopleural arrangement. Differences in thecal style and proximal development are minor. Cooper (1973) suggested a reclined didymograptid, similar to *Didymograptus eocaduceus* Harris, 1933, as the ancestor to the Isograptidae. However, Maletz and Mitchell (1996); Maletz, Carlucci, and Mitchell (2009); and Maletz (2010a) identified the Tetragraptidae as ancestral to the Isograptidae. The abundant three- and two-stiped reclined

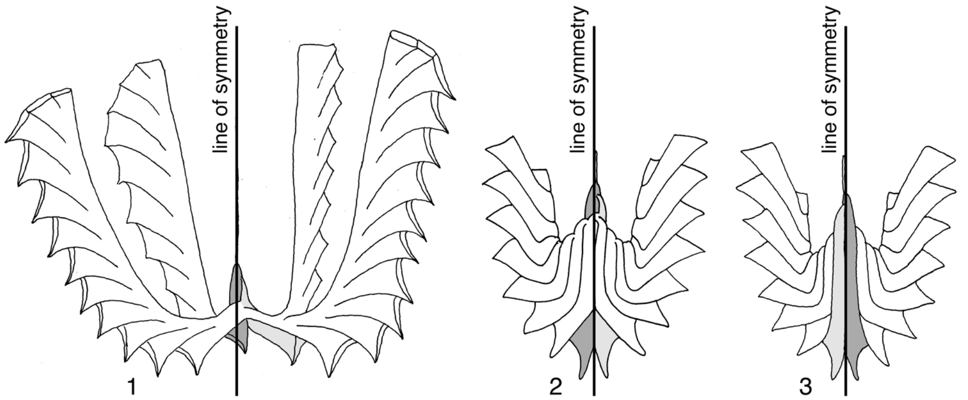

FIG. 202. The proximal symmetry of the Glossograptina. *1, Tetragraptus askerensis* (MONSEN, 1937), maeandrograptid proximal symmetry of a dichograptid in reverse view (adapted from MALETZ, 2011a, fig. 2); 2–3, *Arienigraptus dumosus* (HARRIS, 1933), isograptid symmetry in reverse (*2*) and obverse (*3*) views; sicula in *dark gray,* th1[1] in *light gray* (new).

tetragraptids of the upper Floian (Lower Ordovician) would have required only the loss of the distal dicalycal thecae, followed by a change to isograptid symmetry, to be transformed into an isograptid without an intermediate didymograptid or expansograptid ancestor. MALETZ (2011a) illustrated a number of three- and two-stiped reclined tetragraptids that may represent the transitional forms in the transformation of the reclined tetragraptids to the isograptids.

Cladistic analyses (MALETZ & MITCHELL, 1996; MALETZ, CARLUCCI, & MITCHELL, 2009) have provided insights into the evolutionary relationships of the Glossograptina that indicate that the Glossograptidae and the Axonophora evolved independently from the Isograptidae (Fig. 203). The Isograptidae lead to the scandent, monopleural Glossograptidae through the partial monopleural genera *Skiagraptus* and *Bergstroemograptus* (MALETZ & MITCHELL, 1996), but the differentiation of the two groups is difficult as the new synapomorphies are not recognizable in flattened material. A second independent lineage leads from the derived arienigraptids to the axonophoran graptolites (e.g., *Apiograptus,* COOPER & MCLAURIN, 1974) (Fig. 203). The members of the family Isograptidae provide a number of important biostratigraphic marker species for the Dapingian to Darriwilian (Ordovician) time interval (HARRIS, 1933; COOPER, 1973).

Family ISOGRAPTIDAE Harris, 1933

[Family Isograptidae HARRIS, 1933, p. 85] [incl. Cardiograptidae MU & ZHAN, 1966, p. 96]

Two-stiped, reclined to scandent or proximally scandent (dipleural) Glossograptina with isograptid or derived maeandrograptid symmetry, with or without manubrium; sicula conical, commonly elongated, widening gradually toward aperture, with small prosicula; origin of th1[1] in lower part of prosicula; proximal development type isograptid, dextral; thecae simple, widening tubes, typically with distinct rutella. *Middle Ordovician* (*Dapingian–Darriwilian*): worldwide.

The family Isograptidae is the paraphyletic partial clade based on the reclined, two-stiped colony with the isograptid symmetry as defining synapomorphy (MALETZ & MITCHELL, 1996). As discussed earlier, it excludes the monophyletic Glossograptidae with the monopleural colony shape and the virgellate Axonophora with the biserial, dipleural development of the colonies (Fig. 203). The Axonophora and the Glossograptidae originated independently from the Isograptidae, but the details of the transformations are not yet clear.

HARRIS (1933) established the Isograptidae as a separate family from the Dichograp-

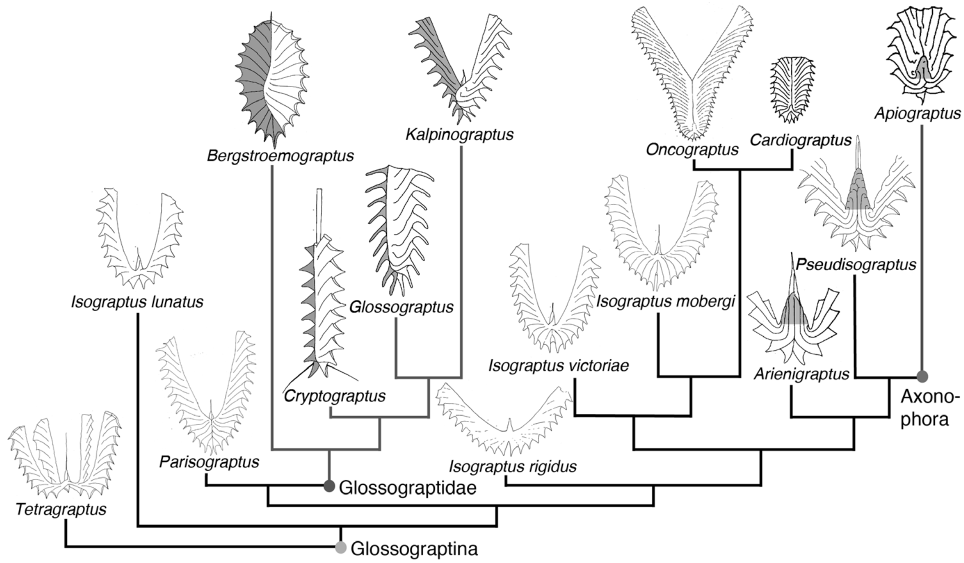

FIG. 203. Evolutionary relationships of the Glossograptina (new).

tidae, which is distinguished by having a two-stiped tubarium with reclined stipes. He included the genus *Maeandrograptus* MOBERG, 1892a, but this genus is now transferred to the Sigmagraptidae, though some species included in *Maeandrograptus* by HARRIS (1933) are now placed in the genus *Pseudisograptus* (COOPER, 1973; COOPER & NI, 1986). COOPER (1973) recognized isograptid symmetry as a more important character, and the definition of the family is now based upon this symmetry and the reclined arrangement of the two stipes. Isograptids are generally easily recognized and useful for biostratigraphic and paleogeographic purposes. They evolved quickly during the Dapingian to early Darriwilian into a number of short-lived species that are regarded as important biostratigraphic index species (HARRIS, 1933; COOPER, 1973). The Isograptidae represent the stem group of the superorder Pan-Bireclinata MALETZ, CARLUCCI, and MITCHELL, 2009.

The family Isograptidae includes several other family group taxa. MU and ZHAN (1966) established the Cardiograptidae for biserial, dipleural taxa and included *Cardiograptus, Paracardiograptus,* and *Skiagraptus,* of which *Skiagraptus* is now referred to the Glossograptidae, due to its partly monopleural arrangement of the stipes. YU and FANG (1981a) originally defined the Arienigraptinae as a subfamily of the Kalpinograptidae JIAO, 1977 (listed as QIAO, 1977 in MU & others, 2002, p. 369). MALETZ and MITCHELL (1996) elevated the subfamily to family rank and recognized the genus *Arienigraptus* as a pseudisograptid, but *Kalpinograptus* is now regarded as a secondarily two-stiped glossograptid (MALETZ & MITCHELL, 1996). Following HARRIS (1933), the arienigraptid genera *Arienigraptus* and *Pseudisograptus* are included in the Isograptidae herein and interpreted as a paraphyletic group from which the Axonophora (the biserial, dipleural graptolites) originated (MITCHELL, MALETZ, & ZHANG, 1995; FORTEY, ZHANG, & MELLISH, 2005; MALETZ, 2010a).

Defining the precise boundary between the Isograptidae and the Axonophora has been problematic. Because of the scarcity of well-preserved and isolated specimens, it is difficult to observe the important synapomorphic characters in this transition. The taxonomy adopted in this revision places the biserial, dipleural taxa with a distinct

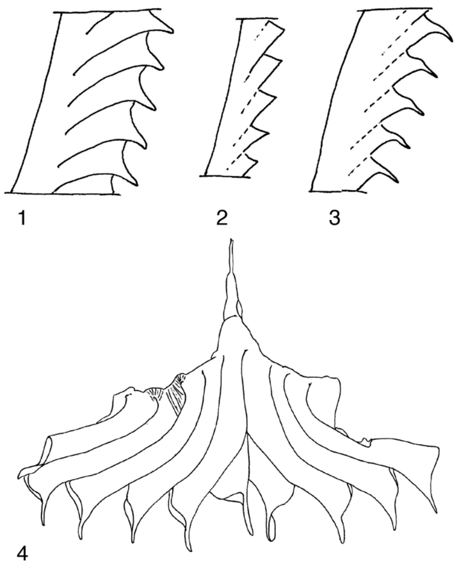

FIG. 204. Thecal style in the Isograptidae. *1,* Isograptid thecal style; *2,* simple manubriate thecal style; *3,* advanced manubriate thecal style (*1–3,* adapted from Cooper & Ni, 1986, fig. 3); *4, Arienigraptus geniculatus* (SKEVINGTON, 1965), PMU Öl 1209, holotype showing advanced manubriate thecal style with lateral lappets on all thecae (adapted from Skevington, 1965, fig. 54D).

manubrium (*Apiograptus*) and derived from the genus *Pseudisograptus* in the Axonophora (MALETZ, 2014b). This serves as a simple distinction of the latter group from the Isograptidae.

MORPHOLOGY

The tubaria and thecal styles of the Isograptidae are fairly simple and show little morphological variation. In addition to their characteristic isograptid symmetry, the species of the Isograptidae generally possess a dextral mode of growth (Fig. 202). Very few specimens with a sinistral development have been discovered, even though this development is common in earlier graptoloids (HUTT, 1974a). COOPER and FORTEY (1982, fig. 54C–D) illustrated a single sinistral specimen of *Isograptus imitatus* HARRIS, 1933. A sinistral proximal development is also present in a number of specimens of *I. spjeldnaesi* MALETZ, 2011a from Norway (MALETZ, 2011a, fig. 6A).

The thecae of the Isograptidae are simple tubes, slender and widening slowly towards the aperture in most taxa. Apertures have a pronounced ventral rutellum in most isograptids but possess no additional elaboration (Fig. 204.1). In contrast, the manubriate taxa *Arienigraptus* and *Pseudisograptus* possess more variation in their thecal style. The thecae are simple tubes, slowly widening towards the aperture and without a rutellum in early taxa. COOPER and NI (1986) termed this thecal style the simple manubriate thecal style (Fig. 204.2). In derived taxa, the distal thecae commonly have long and strongly differentiated rutella of the advanced manubriate thecal style (Fig. 204.3). These thecal apertures are more similar to the lamelliform rutellum of the monopleural glossograptids (see MALETZ, 2010a). Paired lateral lappets appear frequently on the thecal apertures of the arienigraptids and have been illustrated from chemically isolated material in *Arienigraptus geniculatus* (SKEVINGTON, 1965) (Fig. 204.4).

In the Isograptidae, the proximal development is of the isograptid type (COOPER & FORTEY, 1983), and its basic construction is identical to the development in the Anisograptidae (MALETZ, 1994b). The development essentially describes the presence of two crossing canals and a dicalycal th1^2 on the reverse side of the tubarium. The thecal origins of th1^2 and th2^1 are seen in close succession as nearly vertical openings (Fig. 205.1). The crossing canals are subhorizontally oriented, growing in opposite directions, and have different dimensions, with crossing canal 1 wider than crossing canal 2 (Fig. 205.1). This branching also reveals the origins of the two daughters of the dicalycal theca th1^2 at different positions along the mother theca.

In a number of derived isograptids, the development of the proximal end is modified: the two asymmetrical crossing canals are replaced by a much more symmetrical construction without changing the position of the dicalycal theca (Fig. 205.2). In these taxa, the ventral wall of th1^1 grows

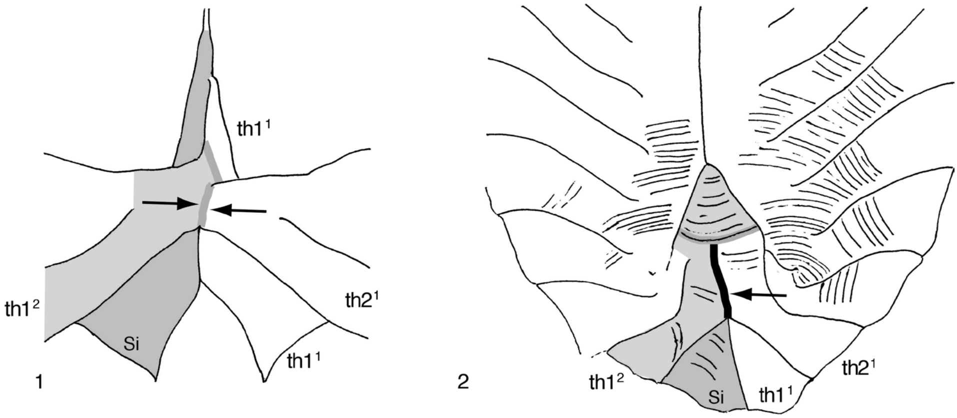

FIG. 205. Isograptid development in the Isograptidae, with thecal notation. *1, Isograptus rigidus* MALETZ, 2011a, showing successive origins of th1^2 and th2^1 (*gray lines*) in a normal isograptid-type proximal development; *2, Cardiograptus amplus* HSÜ, 1947, showing paired origin of th1^2 and th2^1 (*gray line*) from a downward growing flange and suture between th1^2 and th2^1 (*black line*); *Si,* sicula (new; adapted from photograph in Fortey, Zhang, & Mellish, 2005, fig. 10a).

vertically downward as a widening flange along the sicula for some distance before it begins to produce a small lip, from which a strip of fusellar material is formed, dividing the temporary opening of the downward-growing thecal tube into two large, lateral openings. From there, the tubes of th1^2 and th2^1 grow as a symmetrical pair. Later thecae are formed in the normal way. This development produces a feature that recalls the arienigraptid suture in relief specimens (Fig. 205.2), but it does not include the parallel downward growth of th2^1 and th2^2. This feature is present in a number of *Isograptus* species (e.g., *I. maximodivergens* and *I. mobergi*) and is present in *Oncograptus* and *Cardiograptus*.

The reclined arrangement of the stipes in the Glossograptina is the result of a shortening of the distance between thecal origins and the increase in width of the thecal foramina in the early thecae of the isograptids of the *I. victoriae* lineage. A number of proximal thecae produce this arrangement, whereas the distal thecae all possess approximately equal origination distances. The complex proximal development of the genus *Parisograptus* is known from only a few specimens (MALETZ & ZHANG, 2003). It includes an upward stacking of thecal origins in the proximal end and an initially biserial, dipleural stipe arrangement (Fig. 206).

The arienigraptids increase the complexity of the proximal development by the formation of a manubrium and the insertion of intrathecal folds in most taxa. In these, the thecal overlap may be more complex with the second thecal pair (th1^2 and th2^2) covering most of the sicula and th1^1 on the reverse side (Fig. 206). Due to this development, the obverse and reverse sides of the tubaria look quite different: on the obverse side, the sicula and th1^1 are freely visible along their full lengths (e.g., *Pseudisograptus manubriatus janus* COOPER & NI, 1986).

The manubrium, a massive and complex structure, dominates the proximal end of the isograptids of the genera *Arienigraptus* and *Pseudisograptus* (Fig. 207). The second thecal pair (th1^2 and th2^1) formed the crossing canals but instantly grew downward along the sicula and th1^1 on the reverse side of the tubarium, forming the characteristic arienigraptid suture. The paired sicula and th1^1 are completely exposed on the obverse side of the colony (Fig. 207.3), but they are covered on the reverse side for most of their length by the second thecal pair (Fig. 207.2). In *Pseudisograptus*, the more complex overlap of the proximal thecae covers the arienigraptid suture (Fig. 207.1).

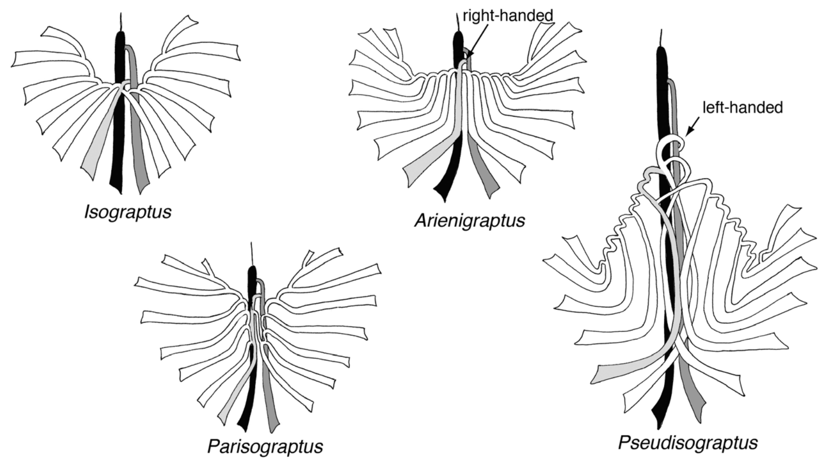

FIG. 206. Growth directions of proximal thecae in the Isograptidae. Sicula in *black,* th1[1] in *dark gray,* dicalycal theca in *light gray;* all diagrams in reverse view; note that th2[2] is the dicalycal theca in *Pseudisograptus* (adapted from Maletz & Mitchell, 1996, and Maletz & Zhang, 2003).

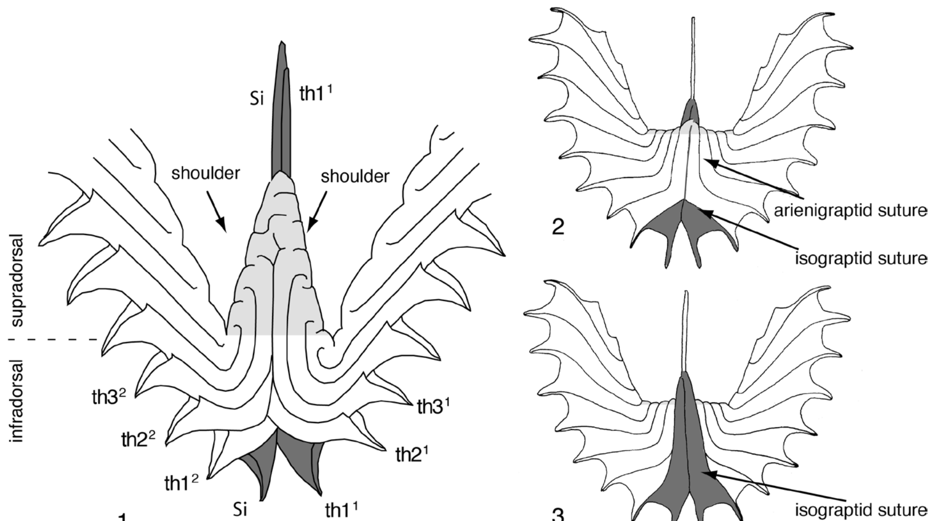

FIG. 207. The arienigraptid manubrium. *1, Pseudisograptus manubriatus* subsp., showing large manubrium with sloping manubrium shoulders, thecal notation, and division of supradorsal and infradorsal; *2–3, Arienigraptus zhejiangensis* YU & FANG, 1981a; *2,* reverse view, small manubrium wedge and nearly horizonal manubrium shoulders, arienigraptid suture between th1[2] and th2[1], isograptid suture visible below; *3,* obverse view, showing isograptid suture; manubrium wedge or supradorsal part of manubrium (*light gray*); first thecal pair (*dark gray*); *Si*, sicula (new).

The thecal length determines the growth patterns and development of the manubrium. The thecae are parallel sided in taxa with a large manubrium (Fig. 208.1) but widen more quickly in taxa with a reduced manubrium (Fig. 208.5–208.6). The arienigraptid proximal structure consists of parallel-downward and distally outward-growing proximal thecae, the manubrium wedge (Fig. 202.3, Fig. 207.1). This is a complex and difficult-to-decipher construction of unknown use in all arienigraptids.

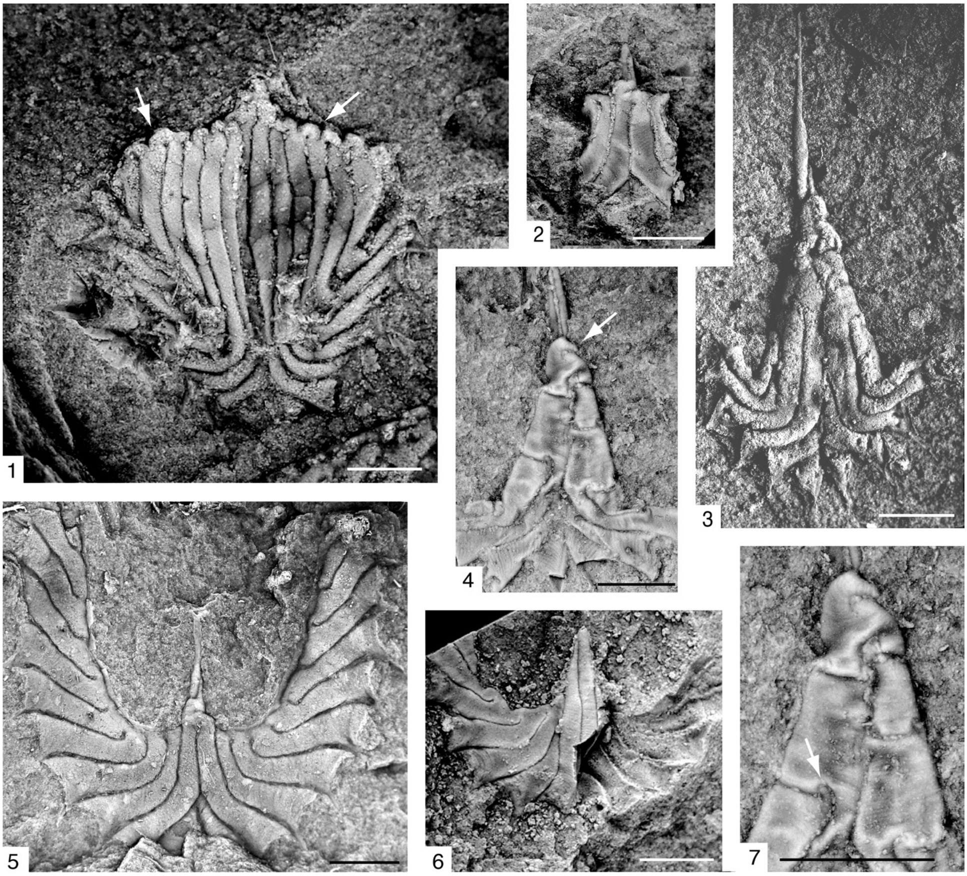

FIG. 208. Examples of manubrium construction. *1, Arienigraptus* sp., LO 12244, Krapperup drill core, Scania, Sweden, specimen with low supradorsal part and long infradorsal part of manubrium, showing prothecal folds (*arrows*); *2, A. zhejiangensis* YU & FANG 1981a, PMU 29983, juvenile, Krapperup drill core at 59.30–59.35 m; *3, Pseudisograptus manubriatus* ssp., PMU 28978, latex cast; *4, 7, Pseudisograptus* sp., PMU 29984, coated, Krapperup drill core at 60.67–60.68 m, showing left-handed origin of th1^2 (*arrow* in *4*) and construction of manubrium with intrathecal folds (*arrow* in *7*); *5, A. zhejiangensis* YU & FANG, 1981a, PMU 29985, coated, Lovisefred drill core, Scania, Sweden, 472.58–472.59 m; *6, Arienigraptus* sp. with strongly reduced manubrium, PMU 29986, coated, Krapperup drill core at 58.75–58.77 m; all specimens in reverse view, except (*6*), which shows the obverse view; scale bars, 1 mm (new).

The massive structure of the manubrium is a completely new development in a few derived taxa of the isograptids. In some taxa, this structure is modified by a complex of overlapping distal thecae (Fig. 207.1, Fig. 208.3). All thecal origins are dorsal and are characterized by the development of intrathecal folds in most arienigraptids (Fig. 208.4, Fig. 208.7). Other taxa clearly develop prothecal folds at the origins of the thecae (Fig. 208.1). The connection between these two types of thecal modification is unclear.

The shape of the manubrium is quite variable (Fig. 208). In *Pseudisograptus,* the manubrium form a massive triangular feature around the sicula positioned above the base of the stipes (Fig. 202.3, Fig. 208.3). The manubrium has long, sloping shoulders with variable inclination. In Darriwilian species of *Arienigraptus,* the manubrium shoulders are typically horizontal (or nearly horizontal) and the downward growth of the initial thecae is reduced (Fig. 208.1, Fig. 206).

As the stratigraphically oldest arienigraptid species, *Arienigraptus hastatus* HARRIS, 1933 already has a conspicuous and highly complex manubrium; however, the exact evolutionary origin of the structure is unknown. Cooper and Ni (1986) first described the construction of the manubrium from three-dimensionally preserved material of a number of *Pseudisograptus manubriatus* specimens.

Subfamily ISOGRAPTINAE Harris, 1933

[Harris, 1933, p. 85]

Two-stiped, reclined to scandent or proximally scandent, dipleural Glossograptina with isograptid symmetry; sicula conical, commonly elongated, widening gradually toward the aperture, with small prosicula; origin of th1¹ in lower part of prosicula; proximal development type isograptid, dextral; thecae simple, widening tubes, typically with distinct rutellum. *Middle Ordovician* (*Dapingian, Isograptus lunatus* Biozone–*Darriwilian, Nicholsonograptus fasciculatus* Biozone): worldwide.

Isograptus Moberg, 1892a, p. 345 [**Didymograptus gibberulus* Nicholson 1875, p. 271; M]. Reclined, two-stiped isograptids; thecae simple with rutellate apertures, shorter and wider in earlier species, with thecal length increasing in later species; proximal development type isograptid, dextral, with low prosicular origin of th1¹, rarely sinistral. *Middle Ordovician* (*lower Dapingian, Isograptus lunatus* Biozone–*Darriwilian, Levisograptus austrodentatus* Biozone): worldwide.——Fig. 209,*1a*. **I. gibberulus* (Nicholson), lectotype, SM A17779, Randal Craig, Skiddaw, Cumbria (English Lake District), UK, scale bar, 1 mm (Rushton, 2000c, Atlas, Folio 1.34).——Fig. 209,*1b*. *I. spjeldnaesi* Maletz, 2011a, holotype, T878-1, left-handed specimen, scale bar, 1 mm (Maletz, 2011a, fig. 6A).——Fig. 209,*1c*. *I. mobergi* Maletz, 2011a, holotype, SGU 5249, scale bar, 1 mm (Maletz, 2011a, fig. 6).

Cardiograptus Harris & Keble in Harris, 1916, p. 66 [**C. morsus;* M] [=*Paracardiograptus* Mu & Lee, 1958, p. 399 (type, *P. hsui,* OD), syn. by Maletz & Mitchell, 1996, p. 650]. Scandent, biserial isograptids with increasing thecal length distally; thecae simple with distinct rutella; proximal development derived-isograptid type, dextral, with origin of th1¹ low in the prosicula. *Middle Ordovician* (*upper Dapingian, Cardiograptus morsus* Biozone–*lower Darriwilian, Levisograptus austrodentatus* Biozone): Australia, New Zealand, China, USA, Canada, Argentina——Fig. 210,*2a*. **C. morsus,* NMV P32148, Chinaman's Creek, Yapeenian 2, Victoria, Australia, scale bar, 5 mm (new).——Fig. 210,*2b*. *C. amplus* Hsü, 1947, NIGP 136152, SEM photograph, reverse view, scale bar, 1 mm (Fortey, Zhang, & Mellish, 2005, fig. 10A).——Fig. 210,*2c–d*. *C. hsui* (Mu & Lee), Ningkuo Shale, Western Chekiang, China; *2c,* holotype, NIGP 9733, proximal end in reverse view; *2d,* paratype, NIGP 9734, proximal end in obverse view; scale bars, 1 mm (Mu & Lee, 1958, pl. 1,*14*).

Oncograptus T. S. Hall, 1914, p. 109 [**O. upsilon;* M] [=*Otricograptus* Percival, Quinn, & Glen, 2011, fig. 4; *nomen nullum;* misspelling]. Initially scandent, biserial isograptid; two distally diverging stipes with increasing thecal length and overlap; thecae simple tubes with distinct rutella; proximal development of derived-isograptid type, dextral, with origin of th1¹ low in prosicula. *Middle Ordovician* (*upper Dapingian, Oncograptus* Biozone–*lower Darriwilian, Levisograptus austrodentatus* Biozone): Australia, New Zealand, China, USA, Canada, Argentina, Ireland.——Fig. 210,*1*. **O. upsilon,* holotype, NMV P31177, Victoria, Australia, scale bar 5 mm (new).

Parisograptus Chen & Zhang, 1996, p. 86 [**Isograptus curvithecatus* Hsü, 1959b, p. 168; OD; =*Isograptus forcipiformis* Ruedemann, 1904, p. 699, syn. by Maletz & Zhang, 2003, p. 301]. Reclined, two-stiped isograptids; crowded and dorsally stacked origins of early thecae with upward and downward early growth on reverse side; colony initially biserial, dipleural; proximal development type isograptid, dextral, with origin of th1¹ in lower part of prosicula; thecae of uniform length and overlapping, with rutella elongated proximally and rutella of sicula and th1¹ united in some species; fusellum attenuated in most species. *Middle Ordovician* (*Dapingian, Isograptus maximus* [=*Arienigraptus hastatus*] Biozone)–*Darriwilian, Nicholsonograptus fasciculatus* Biozone): Australia, New Zealand, China, UK, Sweden, Norway, USA, Canada, Argentina.——Fig. 209,*2a*. **P. curvithecatus* (Hsü), holotype, scale bar, 1 mm (Hsü, 1959b, fig. 2).——Fig. 209,*2b*. *P. forcipiformis* (Ruedemann, 1904), lectotype, NYSM 5881, Ash Hill Quarry, Mount Merino, Hudson, New York, USA, scale bar, 1 mm (new).——Fig. 209,*2c*. *P. caduceus* (Salter in Bigsbyi, 1853), NIGP 12523, reverse view, scale bar, 1 mm (Maletz & Zhang, 2003, fig. 1A).

Procardiograptus Xiao, Xia, & Wang, 1985, p. 435 [**Cardiograptus* (*Procardiograptus*) *uniformis;* OD]. Scandent, biserial isograptid with conspicuous, heart-shaped axial cavity in proximal portion; stipes with increasing thecal length and overlap; thecae simple tubes with distinct rutella; proximal development derived-isograptid type, dextral, with origin of th1¹ low in the prosicula. *Middle Ordovician* (*upper Dapingian, Oncograptus magnus* Biozone–*Cardiograptus amplus* Biozone): China.——Fig. 209,*3a–b*. **P. uniformis; 3a*, NIGP 124849, Hengtang, Zhejiang Province, China; *3b*, NIGP 124851 Chenjiawu, Zhejiang Province, China; scale bars, 1 mm (adapted from Chen, Zhang, & Mitchell, 1995, fig. 26B,D, respectively).

Proncograptus Xiao, Xia, & Wang, 1985, p. 434 [**Oncograptus* (*Proncograptus*) *forcatus;* OD].

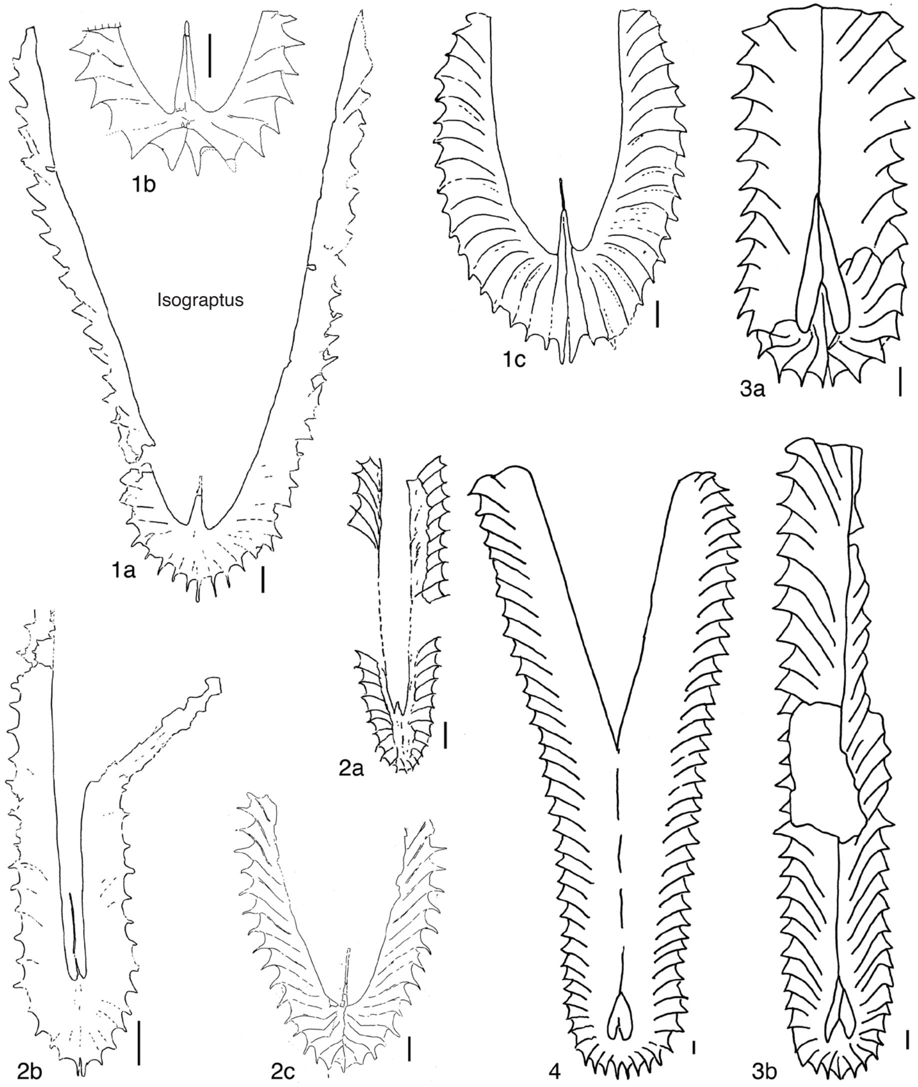

FIG. 209. Isograptidae (Isograptinae) (p. 316–317).

Initially scandent, biserial isograptid with conspicuous, heart-shaped axial cavity in the proximal portion; two diverging stipes with distally increasing thecal length; thecae simple tubes with distinct rutella; proximal development of derived-isograptid type, dextral with origin of th1[1] low in the prosicula. *Middle Ordovician* (*upper Dapingian*, *Oncograptus magnus* Biozone): China.——FIG. 209,*4*. *P. robustus* (XIAO, XIA, & WANG, 1985), holotype, Jiangxi Province, scale bar, 1 mm (adapted from Xiao, Xia, & Wang, 1985, fig. 3).

Subfamily ARIENIGRAPTINAE Yu & Fang, 1981

[Arienigraptinae YU & FANG, 1981a, p. 29] [=Pseudisograptinae COOPER & NI, 1986, p. 323]

Two-stiped, reclined glossograptids with isograptid or maeandrograptid symmetry, manubrium invariably present; sicula conical, elongated, largely parallel sided, with short or elongated, conical prosicula;

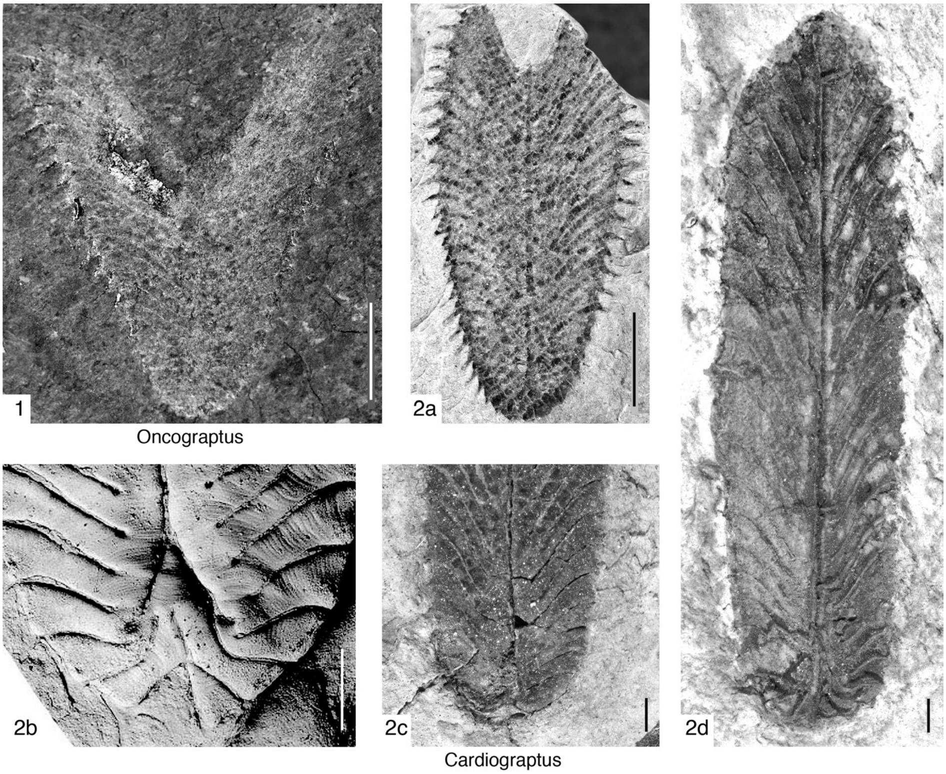

FIG. 210. Isograptidae (Isograptinae) (p. 316).

origin of th1[1] in lower part of prosicula; proximal development isograptid type, dextral; origin of th1[2] right- or left-handed or with delayed dicalycal theca; thecae simple, ranging from parallel sided to slightly widening tubes, commonly with distinct rutella, but some lacking lateral apertural elaborations or with low lateral lappets. *Middle Ordovician* (*Dapingian, Isograptus maximus* [=*Arienigraptus hastatus*] Biozone–*Darriwilian, Levisograptus dentatus* Biozone): worldwide.

YU and FANG (1981a, fig. 2) referred the Arienigraptinae to the family Kalpinograptidae based on their interpretation that *Kalpinograptus* derived from *Pseudisograptus*. The genus *Kalpinograptus* can be referred to the Glossograptidae based on the development of its sicula and the proximal end construction with a monopleural development (FINNEY, 1978). The development is very different from the proximal development of the manubriate *Arienigraptus*.

COOPER and NI (1986) erected the subfamily Pseudisograptinae, in which they also included the closely related biserial, dipleural genera *Exigraptus* and *Apiograptus*. Following MALETZ (2014b), the latter are interpreted in this revision as the earliest Axonophora, based on the presence of a biserial, dipleural colony retaining the manubrium, and, thus, are separated from the Arienigraptinae.

The subfamily Arienigraptinae, including *Arienigraptus* and *Pseudisograptus,* can be defined as the paraphyletic partial clade, based on a reclined, two-stiped isograptid with the presence of a manubrium as the defining synapomorphy (MALETZ & MITCHELL, 1996). It excludes the biserial, dipleural Axonophora. The synapomorphies of the Arienigraptinae include 1) a manubrium with the arienigraptid suture between

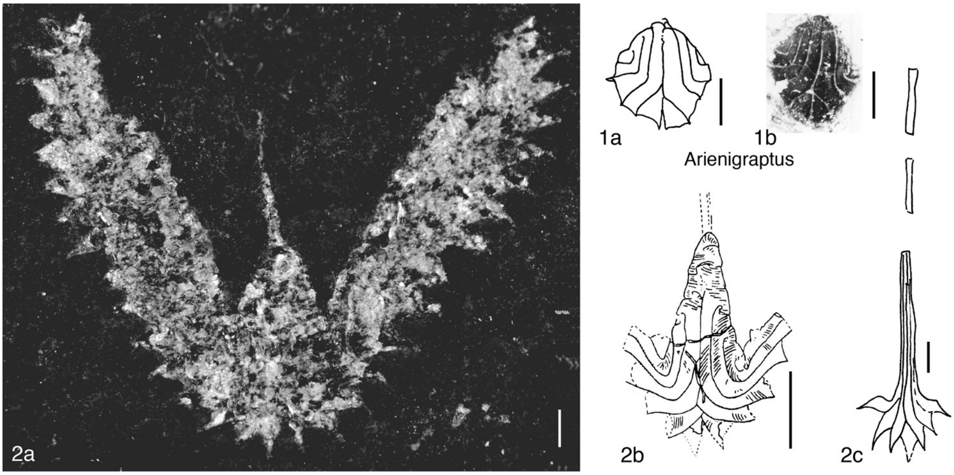

FIG. 211. Isograptidae (Arienigraptinae) (p. 319).

th1[2] and th2[1] on the reverse side (Fig. 207.2); 2) an elongated, slender thecae; and 3) a simple, distal thecal apertures lacking the extended rutella of most Isograptidae. The proximal development type is isograptid, dextral with a low prosicular origin of th1[1]. The derived genus *Pseudisograptus* bears thecae of the advanced manubriate type (Fig. 204.3), typically with slight lateral lappets (Fig. 204.4) and a delayed dicalycal theca at th2[1] or a later one. It also shows a left-handed origin of th1[2] (Fig. 206), a character that MITCHELL (1987, p. 355) considered a synapomorphy of the Diplograptina, even though it was present already in the isograptid genus *Pseudisograptus*.

Arienigraptus YU & FANG, 1981a, p. 29 [**A. jiangxiensis;* OD]. Two-stiped, reclined manubriate isograptids with simple arienigraptid proximal structure and isograptid symmetry; th1[2] and th2[1] cover sicula and th1[1] in reverse view, showing arienigraptid suture; proximal development type isograptid, dextral; manubrium wedge of highly variable dimensions; th1[2] with right-handed origin; thecae simple to advanced manubriate; stipes typically poorly developed. *Middle Ordovician* (*Dapingian, Isograptus maximus* [=*Arienigraptus hastatus*] Biozone–*Darriwilian, Holmograptus lentus* Biozone): Australia, New Zealand, China, UK, Sweden, Norway, USA, Canada, Russia, Argentina, Peru.——FIG. 211,*1a–b*. **A. jiangxiensis; 1a*, drawing of holotype, NIGP 50011 (adapted from Ni, Xiao, & Chen, 1991, fig. 4g); *1b*, photograph of holotype (new; provided by Ni Yunan, 1994). Scale bars, 1 mm.

Pseudisograptus BEAVIS, 1972, p. 202 [**Didymograptus caduceus* var. *manubriatus* T. S HALL, 1914, p. 108; OD] [=*Xiushuigraptus* YU & FANG in YANG & others, 1983, p. 406 (type, *X. songxiensis;* M), syn. by MALETZ & MITCHELL, 1996, p. 653]. Two-stiped, reclined, manubriate isograptids with complex arienigraptid proximal structure and isograptid to maeandrograptid symmetry; arienigraptid suture between th1[2] and th2[1] usually covered by overlap of later thecae; manubrium wedge of highly variable dimensions; proximal development type isograptid, dextral, with delayed dicalycal theca; sicula strongly elongated; th1[2] with left-handed origin; thecae of advanced manubriate style; stipes sometimes poorly developed; intrathecal folds present. *Middle Ordovician* (*upper Dapingian, Oncograptus upsilon* Biozone–*lower Darriwilian, Levisograptus austrodentatus* Biozone): Australia, New Zealand, China, Russia, UK, Norway, Sweden, USA, Canada, Argentina.——FIG. 211,*2a*. **P. manubriatus manubriatus* (T. S. HALL), holotype, NMV P31176 scale bar, 1 mm (VandenBerg & Maletz, 2016, fig. 1A).——FIG. 211,*2b*. *P. manubriatus janus* COOPER & NI, 1986, reverse view, scale bar, 1 mm (Cooper & Ni, 1986, fig. 17B).——FIG. 211,*2c*. *P. songxiensis* (YU & FANG), holotype NIGP 50021, scale bar, 1 mm (adapted from Yang & others, 1983, fig. 1).

Family GLOSSOGRAPTIDAE Lapworth, 1873

[Glossograptidae LAPWORTH, 1873b, table 1, facing p. 555] [=Corynoideae RUEDEMANN, 1908, p. 233; Cryptograptidae HADDING, 1915b, p. 332; Corynoididae BULMAN, 1945, p. 22, *nom. correct. pro* Corynograptidae HOPKINSON & LAPWORTH, 1875, p. 633; =Kalpinograptidae JIAO, 1977, p. 289]

Two-stiped, scandent graptoloids with isograptid symmetry and monopleural development based on dextral torsion of the stipes around sicula; proximal development type isograptid, dextral; prosicular and occasional metasicular origin of th1[1]; sicula tubular, widening toward the aperture, with small prosicula; thecae simple, widening tubes with distinct rutella; lateral apertural thecal spines common; lacinia in a few taxa, attached to the lateral apertural spines; attenuation of fusellum and reduction of number of thecae in colony common. *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone)–*Upper Ordovician* (*Katian, Dicellograptus complexus* Biozone): worldwide.

The family Glossograptidae is the monophyletic clade based on the scandent, monopleural colony shape as defining synapomorphy (MALETZ & MITCHELL, 1996). It includes a small group of biserial, monopleural taxa with a simple isograptid proximal development that is covered by the later growth of the colony. Thus, in this group, proximal development and thecal growth patterns are hard to verify and have long been a matter of debate (BULMAN, 1945; STRACHAN, 1985; MALETZ & MITCHELL, 1996). Some of the younger members (e.g., *Corynoides, Corynites*) are included herein, even though their colony development is so reduced that they lack important characteristics for an analysis. MALETZ, CARLUCCI, and MITCHELL (2009, p. 14) defined the taxon as "the common ancestor of *Glossograptus acanthus* ELLES & WOOD, 1908 and the first species to have a monopleural arrangement of the stipes."

MORPHOLOGY

In well-preserved specimens, Glossograptidae can be distinguished from other biserial taxa by the presence of pronounced ventral rutella and the characteristic paired proximal spines. For most members, details of the early development of tubaria are unknown because they were enclosed by the two scandent stipes.

The proximal development in all Glossograptidae appears to be of the isograptid, dextral type, with th1[2] as the dicalycal theca. The proximal development type of the Glossograptidae is known from a number of flattened juveniles and is difficult to interpret, with some details remaining conjectural (FINNEY, 1978; MALETZ & MITCHELL, 1996). Relief specimens and isolated juveniles of *Glossograptus* show the sicula and th1[1] as a symmetrical pair (NI & COOPER, 1994, fig. 1–2; MALETZ & MITCHELL, 1996). The origin of th1[1] is variably placed in the prosicula (*Paraglossograptus*, *Corynoides*, *Corynites*) or in the metasicula (*Cryptograptus*). The high prosicular origin of th1[1] in *Paraglossograptus* is unusual because it occurs in the lower part of the prosicula in most dichograptids and in the ancestral Isograptidae. A higher prosicular origin of th1[1] is also present in members of the Anisograptidae (HUTT, 1974a).

In *Paraglossograptus*, th1[1] grew downward from a point high on the prosicula along the ventral side of the sicula before it gave rise to a dextral development of th1[2] (Fig. 212.3). The sicula and th1[1] formed a symmetrical pair, surrounded by dextral coiling of the two scandent stipes. The initial thecae formed a considerable glossograptid bulge through the curved overlap of these elongated proximal thecae before shorter, distal thecae grew immediately upward from their beginning (NI & COOPER, 1994; MALETZ & MITCHELL, 1996). The proximal development of *Cryptograptus* is more difficult to understand, but it appears to follow a similar path. The origin of th1[1] is in the metasicula, and th1[2] initially grew upward, forming a large loop, and then across the sicula and downward. As with the other genera, the sicula and th1[1] formed a symmetrical pair, but the glossograptid bulge was not developed, because the proximal thecae were short and thecal overlap was low (Fig. 213).

The thecal growth that produced the biserial, monopleural colony shape of the Glossograptidae was initiated by the dextral torsion of the two stipes around the sicula (Fig. 214), as was demonstrated in the partial monopleural development of *Bergstroemograptus crawfordi* (Fig. 214.2–214.3). WHITTINGTON and RICKARDS (1969) described chemically isolated material of *B. crawfordi* under the name *Skiagraptus* sp., but KELLER (1956, pl. 1, *4–5*) identified the

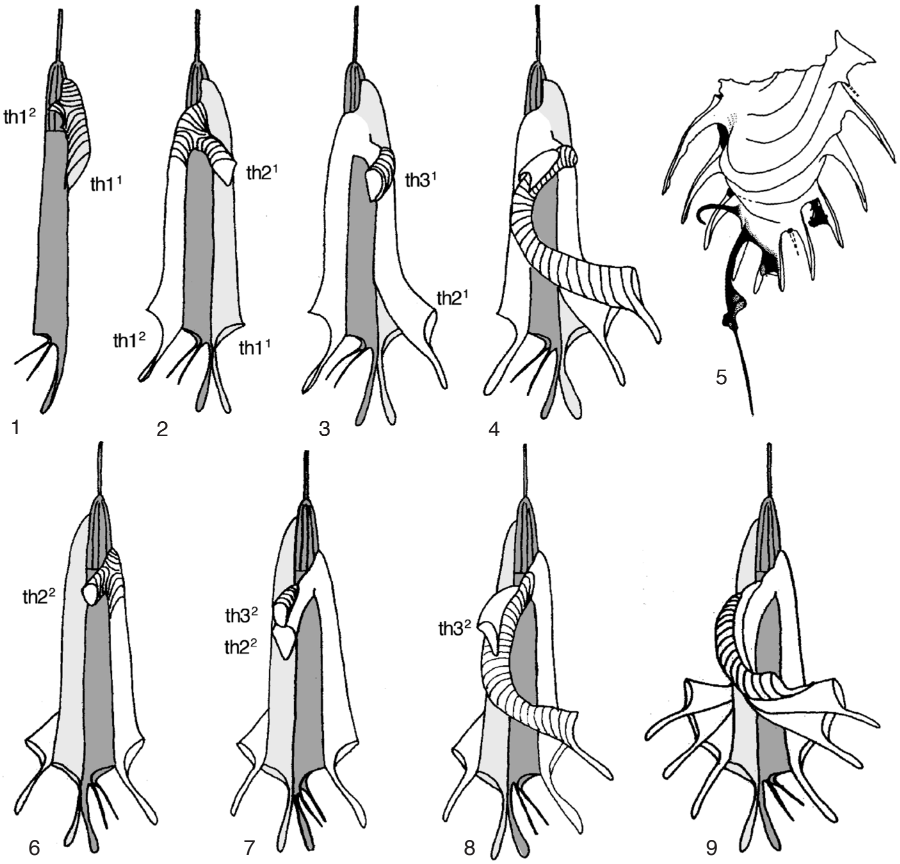

FIG. 212. Early ontogeny of *Paraglossograptus*. *1–4,* reverse view; *6–9,* obverse view; *8–9,* showing development of glossograptid bulge (adapted from Maletz & Mitchell, 1996, fig. 4); *5, P. holmi* (BULMAN, 1931), isolated specimen, western Newfoundland, showing glossograptid bulge (adapted from WHITTINGTON & RICKARDS, 1969, fig. 2C).

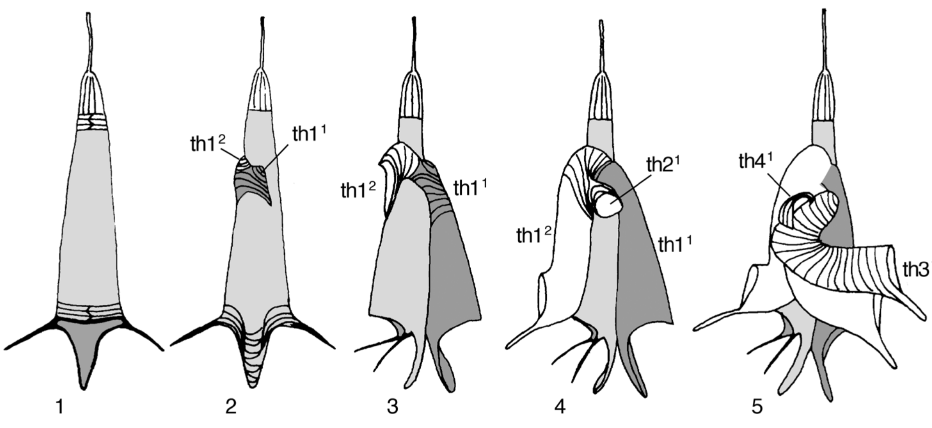

FIG. 213. Early ontogeny of *Cryptograptus schaeferi* LAPWORTH, 1880a. *1,* Sicula, dorsal view; *2,* sicula in ventral view with origin of th1¹ and upward-growing initial part of th1²; *3,* proximal end in reverse view, showing upward initial growth from th1¹ and arch of th1²; *4,* proximal end in reverse view, showing initial growth of th2¹; *5,* proximal end with fully developed th3¹ and origin of th4¹; *light gray,* metasicula, *dark gray,* th1¹; reconstructions based on flattened, chemically isolated specimens from western Newfoundland (adapted from Maletz & Mitchell, 1996, fig. 4).

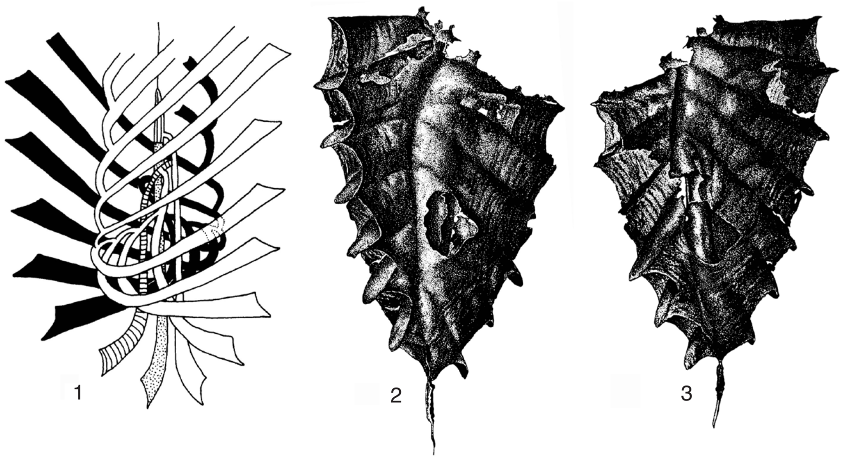

FIG. 214. Monopleural development of the Glossograptidae. *1,* Thecal diagram of *Glossograptus* sp. (adapted from MALETZ & MITCHELL, 1996, fig. 1); *2–3, Bergstroemograptus crawfordi* (HARRIS, 1926), isolated specimen in obverse and reverse views showing the dextral (clockwise) torsion of the stipes (Whittington & Rickards, 1969, fig. 9: illustrated as *Skiagraptus* sp.).

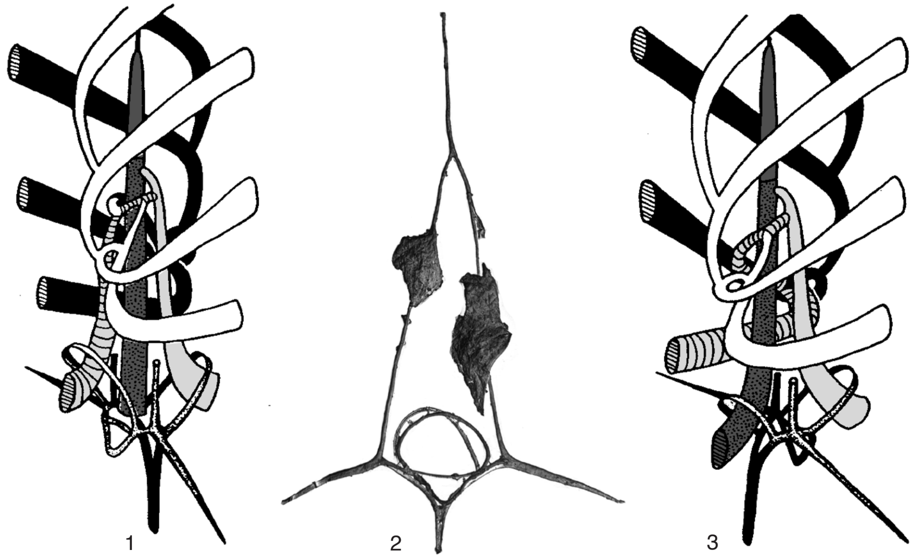

FIG. 215. *Cryptograptus* proximal development. *1,* Interpretation of STRACHAN (1985); *2, Cryptograptus* sp., (new; photo by Denis Bates); *3,* interpretation of MALETZ & MITCHELL (1996); *dark gray,* sicula; *light gray,* th1^1; *light gray with stripes,* th1^2 (*1, 3,* adapted from Maletz & Mitchell, 1996, fig. 7).

species as *Phyllograptus anna* HALL, 1865. In completely monopleural colonies of the genus *Glossograptus* (Fig. 214.1), the sicula is fully enveloped by the two stipes, with only the aperture visible, and the colonies look identical in obverse and reverse views.

The proximal development of the genus *Cryptograptus*, as mentioned earlier, has been difficult to interpret (Fig. 215). In derived taxa of the genus, the fusellum of the initial thecae, including the sicula, is reduced and preserved as a framework of

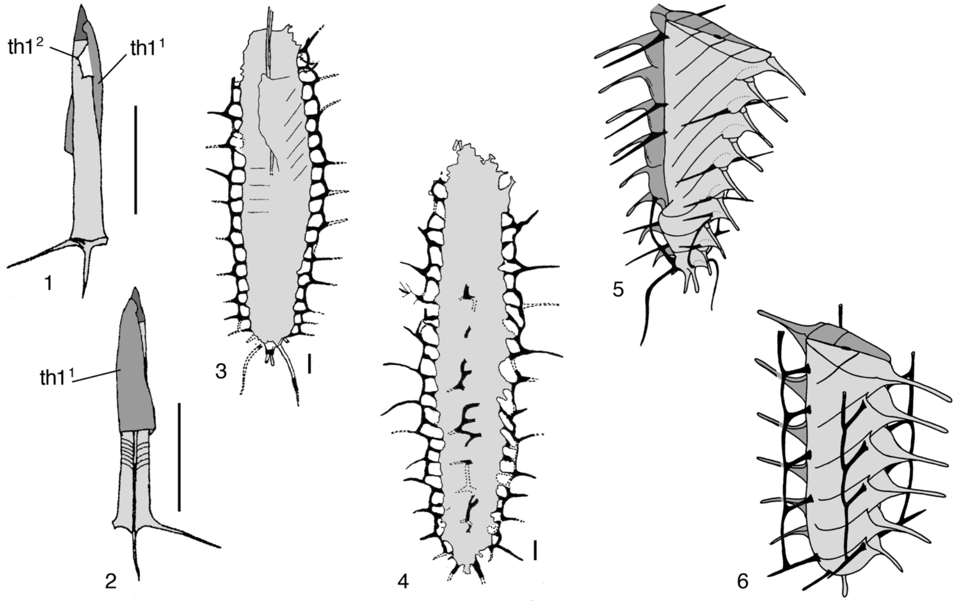

FIG. 216. Thecal spines and lacinia. *1–2, Glossograptus ciliatus* EMMONS, 1855, OSU 33142, sicula with lateral apertural spines, pointed rutellum and early growth of th1¹ and th1² (adapted from Finney, 1978, fig. 3); *3, Paraglossograptus tentaculatus* (HALL, 1865), GSC 950b, syntype showing lacinia development and connection to lateral apertural thecal spines (Rickards, 1972, fig. 1a); *4, Paraglossograptus tentaculatus* (HALL, 1865), NMVP 14406, holotype of *Lasiograptus etheridgei* HARRIS, 1924, showing lacinia (Rickards, 1972, fig. 1b); *5, Paraglossograptus holmi* (BULMAN, 1931), reconstruction showing position of lateral apertural spines and prominent glossograptid bulge (adapted from Whittington & Rickards, 1969, fig. 6a); *6, Paraglossograptus proteus* (HARRIS & THOMAS, 1935), reconstruction showing lacinia, lateral apertural spines on sicula and th1¹ not shown (adapted from Whittington & Rickards, 1969, fig. 6b). Scales bars, 1 mm in *1–4*.

lists only (Fig. 215.2). Different interpretations have been proposed to understand the construction. BULMAN (1945) and STRACHAN (1985) preferred the presence of a centrally positioned sicula (Fig. 215.1) as an explanation. However, MALETZ and MITCHELL (1996) suggested isograptid symmetry of the proximal end with the sicula and th1¹ as a symmetrical pair (Fig. 215.3), based on isolated specimens of *C. schaeferi* from the Table Head Group of western Newfoundland. These specimens clearly demonstrate the isograptid symmetry of the sicula and th1¹ (MALETZ & MITCHELL, 1996, fig. 5), thus strengthening the case for its descent from an isograptid ancestor.

The Glossograptidae are characterized by paired lateral apertural spines on the sicula and typically also on later thecae. They may not be present on each thecal pair, but they are regularly distributed and form the basis for the four ladderlike strings of mesh (the lacinia) in the genus *Paraglossograptus* (Fig. 216.6). The development of the lacinia is variable, and the spines usually protrude from the meshwork (Fig. 216.3–216.4).

A reduction in the colony size occurred in a number of taxa of the Glossograptidae. In early taxa, mature colonies reached considerable size; stipe length could be several centimeters in the isograptids and more than 3 cm in *Glossograptus* and *Cryptograptus*. However, a decrease in colony size was already apparent in the genera *Nanograptus* and *Sinoretiograptus*, with *Nanograptus* having colonies only 3–4 mm long, comprising only about five or six thecae. The diminution in these taxa is not associated with other changes in the colony development; it appears that their growth was suddenly arrested.

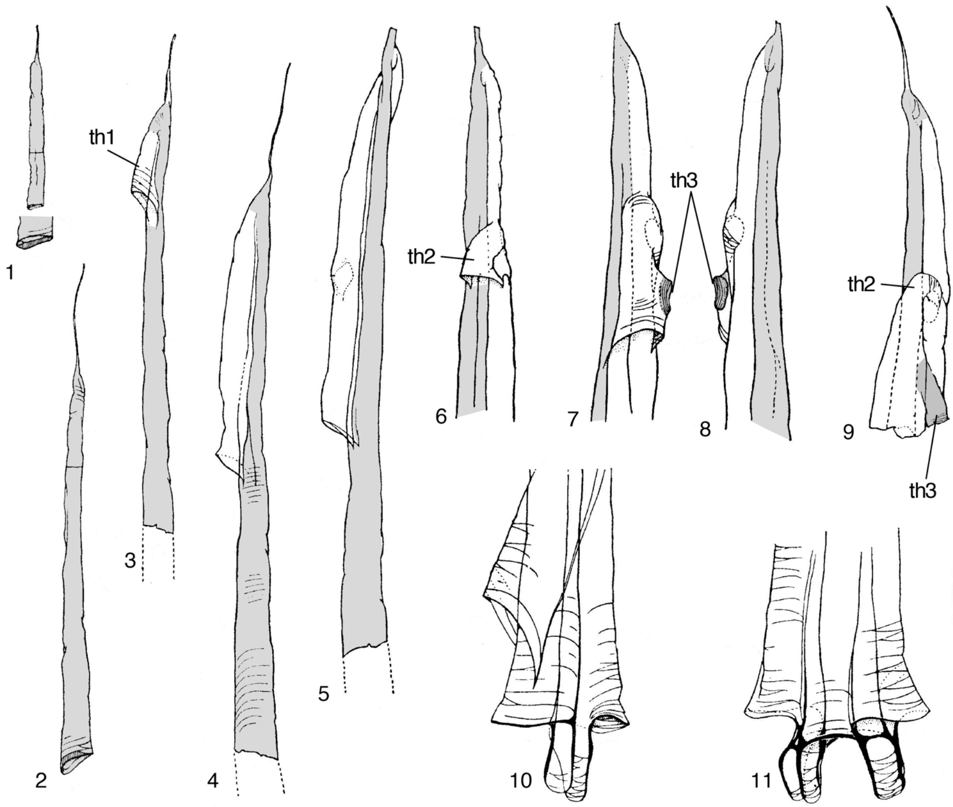

FIG. 217. Ontogeny of the genus *Corynoides*. *1–2,* Sicula development, showing length of prosicula; *3–5,* initial growth of th1; *6–9,* growth of th2; *10–11,* apertures of sicula, th1, and th2 (Bulman, 1947, fig. 39–40).

An even more drastic diminution is apparent in the colonies of *Corynoides* and *Corynites*, which have tiny tubaria consisting of only two or three thecae. However, the most important character that distinguishes these taxa from other Glossograptidae is the extreme elongation and attenuation of the thecae, with lengths up to 12 mm but widths generally not exceeding 0.2 mm. The most distal theca, usually th2[1], is reduced to a small appendage that bends away from the colony in *Corynoides* and is coiled in *Corynites*. BULMAN (1955, p. 81; 1970, p. 119) included these genera in a separate family, the Corynoididae, which he later placed in the Didymograptina (BULMAN 1970). FINNEY (1978) suggested that the Corynoididae be included as a separate family in the Glossograptina. MALETZ and MITCHELL (1996) advocated the inclusion of *Corynoides* and *Corynites* in the Glossograptidae, instead of the Corynoididae.

BULMAN (1945, 1947) was first to describe isolated specimens of *Corynoides* from the Caradoc of Laggan Burn, Scotland (Fig. 217); these possess an elongated, slender prosicula and a long metasicula with a high prosicular origin of the first theca (th1[1]), suggesting a relationship with *Glossograptus*. Another typical glossograptid character in *Corynoides* is the development of the lamelliform rutellum, identified as a lamelliform virgella by BULMAN (1945, 1947).

EVOLUTION

A detailed cladistic analysis of the Glossograptidae has not been attempted, and the classification herein is based on data provided by MALETZ and MITCHELL (1996) and MALETZ, CARLUCCI, and MITCHELL

(2009). The simple thecae and isograptid symmetry of the Glossograptidae indicates a close relationship to the Isograptidae (FINNEY, 1978; MALETZ & MITCHELL, 1996), as does the proximal development.

The earliest Glossograptidae, from the basal Darriwilian, already possessed the biserial, monopleural colony development, and transitional taxa have not been recognized in older strata. The genus *Bergstroemograptus*, shown at the base of the clade by MALETZ and MITCHELL (1996) and MALETZ, CARLUCCI, and MITCHELL (2009), possesses the partial monopleural development of a glossograptid, but the taxon is unlikely to represent the base of the clade, given that it is only known from the middle Darriwilian. Nevertheless, *Bergstroemograptus* can be taken as a guide to understanding the early evolution of the clade. The genus *Cryptograptus,* with its metasicular origin of th1[1], separated at an early stage in the evolution of the group, but the remaining taxa maintained a prosicular origin of th1[1].

As discussed earlier, *Corynoides* and *Corynites* have extremely reduced colonies and are difficult to relate to other taxa, as many indicative characters may be missing. However, the prosicular origin of th1[1] indicates a relationship with *Glossograptus* or *Kalpinograptus*. This relationship is also supported by the elongation of the sicula, which is present, for example, in *Kalpinograptus spiroptenus* JIAO, 1977. These genera might be related to the Dichograptina, but this seems unlikely, given the long gap between the extinction of the Dichograptina and the appearance of *Corynoides* and *Corynites*.

Glossograptus EMMONS, 1855, p. 108, *nom. correct.* HALL, 1865, p. 59, original spelling as *Glossograpsus* changed in ICZN Opinion 650, 1963 [**G. ciliatus;* SD LAPWORTH, 1873b, table opposite p. 555] [=*Lonchograptus* TULLBERG, 1880a, p. 313 (type, *L. ovatus,* M), syn. herein]. Monopleural, scandent glossograptid formed through dextral torsion of stipes around sicula, typically with considerable glossograptid bulge; paired lateral apertural spines on sicula and variably developed on later thecae; thecal rutella extended and commonly modified; origin of th1[1] through resorption foramen in middle to lower part of prosicula; proximal development type isograptid, dextral. [The genus *Lonchograptus* TULLBERG, 1880a, from the *Didymograptus geminus* (=*Pterograptus elegans*) Biozone of southern Sweden (EKSTRÖM, 1937), is regarded as a synonym of *Glossograptus;* however, the type is extremely poorly preserved and lacks features to differentiate it from *Glossograptus*.] *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone)–*Upper Ordovician* (*Katian, Dicellograptus ornatus* Biozone): worldwide.——FIG. 220,*2a*. **G. ciliatus,* NYSM 7202, Normanskill Shale, Glenmont, New York, scale bar, 5 mm (Ruedemann, 1908, pl. 27,*1*).——FIG. 220,*2b*. *G. acanthus* ELLES & WOOD, 1908, NIGP 116481, specimen showing glossograptid bulge, Chenjiawu, Jiangxi, China, scale bar, 1 mm (Ni & Cooper, 1994, fig. 1).——FIG. 220,*2c*. *G. ovatus* (TULLBERG, 1880a), holotype, LO 408T, scale bar, 1 mm (Tullberg, 1880a, pl. 11,*1*).

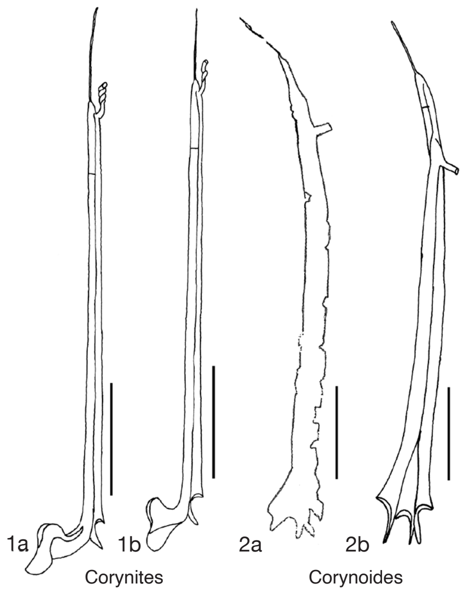

FIG. 218. Glossograptidae (p. 325–326).

Bergstroemograptus FINNEY & CHEN, 1984, p. 1198 [**Cardiograptus crawfordi* HARRIS, 1926, p. 57; OD]. Leaf-shaped, dipleural glossograptid with initial monopleural development covering sicula completely on both sides; rutella of sicula and th1[1] united; distal thecae distinctly widening, short. *Middle Ordovician* (*Darriwilian, Holmograptus lentus* Biozone–*Nicholsonograptus fasciculatus* Biozone): Australia, China, UK, Sweden, USA, Canada, Russia, Argentina.——FIG. 219,*2a–b*. **B. crawfordi* (HARRIS), paratypes; *2a*, NMV P13360; *2b*, NMV P13359; scale bars, 1 mm (Finney & Chen, 1984, fig. 3C–D).

Corynites KOZŁOWSKI, 1956b, p. 260 [**C. wyszogradensis;* OD]. Strongly reduced colony consisting of elongated sicula with single adnate theca and vestigial, coiled second theca; sicular aperture with elaborate apertural flanges; origin of th1[1] in upper

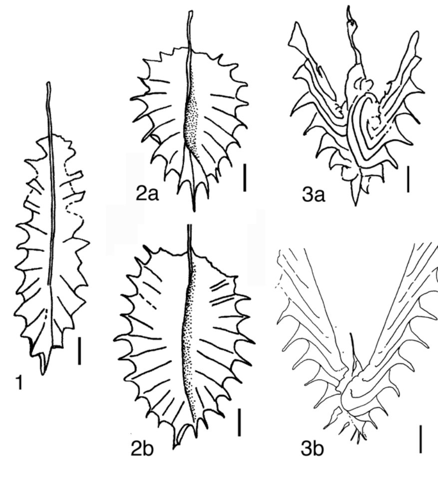

FIG. 219. Glossograptidae (p. 325–328).

part of prosicula. *Upper Ordovician* (?*Sandbian*): Poland, Germany (glacial erratic boulder).——FIG. 218,*1a*. **C. wyszogradensis,* reconstruction of holotype, scale bar, 1 mm (Kozłowski, 1956b, fig. 1).——FIG. 218,*1b. C. divnoviensis,* reconstruction of holotype, scale bar, 1 mm (Kozłowski, 1953, fig. 1).

Corynoides NICHOLSON, 1867a, p. 108 [**C. calicularis;* M] [=*Corynograptus* NICHOLSON in HOPKINSON & LAPWORTH, 1875, p. 633]. Strongly reduced colony consisting of elongated sicula and two adnate thecae with extended rutella; a fourth vestigial theca may be present; origin of th1[1] in the upper part of prosicula. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone–*Katian, Diplacanthograptus spiniferus* Biozone): worldwide.——FIG. 218,*2a–b*. **C. calicularis; 2a,* BMHM Q62, lectotype (Zalasiewicz, 2000a, Atlas, Folio 1.14); *2b,* reconstruction; scale bars, 1 mm (new).

Cryptograptus LAPWORTH, 1880a, p. 174 [**Diplograpsus tricornis* CARRUTHERS, 1858, p. 468; OD] [=*Tonograptus* WILLIAMS, 1992, p. 1727, pl. 3 (type, *T. subulatus,* OD), syn. by MALETZ & MITCHELL, 1996, p. 653]. Monopleural, scandent glossograptid formed through dextral torsion of stipes around sicula; paired lateral apertural spines restricted to sicula; origin of th1[1] through resorption foramen in metasicula; th1[2] initially growing upward and across reverse side of sicula; proximal development type isograptid, dextral; sicula and early thecae reduced to several bars and lists in biostratigraphically younger species. *Middle Ordovician* (*lower Darriwilian, Undulograptus austrodentatus* Biozone)–*Upper Ordovician* (*Katian, Dicranograptus kirki* Biozone): worldwide.——FIG. 220,*1a*. **C. tricornis* (CARRUTHERS), lectotype, NHMUK Q1299, Hartfell Spa, Hartfell Shales, Scotland, scale bar, 5 mm (Elles & Wood, 1908, pl. 32, fig. 12A).——FIG. 220,*1b. C. insectiformis* RUEDEMANN, 1908, juvenile, MCZ 106835, showing reduction of fusellum, Viola Springs Limestone, Arbuckle Mountains, Oklahoma, USA, scale bar, 1 mm (Maletz & Mitchell, 1996, fig. 6.5).——FIG. 220,*1c. C. schaeferi* LAPWORTH, 1880a, GSC 87720, nematularium, holotype of *T. subulatus* WILLIAMS, 1992, western Newfoundland, Canada, scale bar, 1 mm (new).

Kalpinograptus JIAO, 1977, p. 290 [**K. spiroptenus;* OD] [=*Apoglossograptus* FINNEY, 1978, p. 489, *nom. nud.*]. Initially monopleural glossograptid formed through dextral torsion of stipes around sicula; two distally diverging stipes; glossograptid bulge conspicuous; origin of th1[1] through resorption foramen in initial part of prosicula; proximal development type isograptid, dextral. *Middle Ordovician* (*upper Darriwilian, Nicholsonograptus fasciculatus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): Australia, China, Sweden, Norway, Canada, USA, Argentina, Peru.——FIG. 219,*3a*. **K. spiroptenus,* syntype, scale bar, 1 mm (adapted from Jiao, 1977, fig. 4–5).——FIG. 219,*3b. Kalpinograptus* sp., GSC 113324, Table Head Group, western Newfoundland, Canada, scale bar, 1 mm (Maletz & Mitchell, 1996, fig. 2*,1*).

Nanograptus HADDING, 1915b, p. 328 [**N. lapworthi;* SD BULMAN, 1929, p. 179] [=*Rogercooperia* SHERWIN & RICKARDS, 2000, p. 162 (type, *Petalograptus? phylloides* ELLES & WOOD, 1908, p. 284, OD), syn. herein]. Glossograptid with rounded, finite colony consisting of ~8–10 thecae; sicula with metasicular origin of first theca; glossograptid bulge reduced and restricted to two thecal pairs; slender lateral apertural spines on sicula. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): Australia (New South Wales), Sweden, Scotland.——FIG. 221,*1a–b*. **N. lapworthi; 1a*, lectotype (selected herein), LO 2746t (new); *1b*, paratype, LO 2743t (on slab), previously unfigured specimen showing long, dorsally projecting sicula, origin of th1[1] not visible; scale bars, 1 mm (new).——FIG. 221,*1c–d. N. phylloides* (ELLES & WOOD); *1c*, paratype, flattened juvenile (new); *1d*, lectotype (selected by SHERWIN & RICKARDS, 2000, p. 162), GSE 5495, flattened specimen; scale bars, 1 mm (new).

Paraglossograptus MU in MU & others, 1962, p. 97 [**P. typicalis;* OD]. Monopleural, scandent glossograptid with conspicuous development of simple lacinia with ladderlike structure; lacinia only present in the proximal part in certain species. [GANIS (2005, p. 803) discussed the availability of the genus name *Paraglossograptus* that appeared first in Hsü, 1959b]. *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone–*Pterograptus elegans* Biozone): Australia, New Zealand, China, Norway, USA, Canada, Argentina.——FIG. 220,*3a*. **P. typicalis*, holotype, NIGP 10635, scale bar, 5 mm (Mu & Lee, 1960, fig. 127).——FIG. 220,*3b. P. tentaculatus* (HALL, 1865), GSC 138686, isolated, flattened specimen, Cow Head Group, western

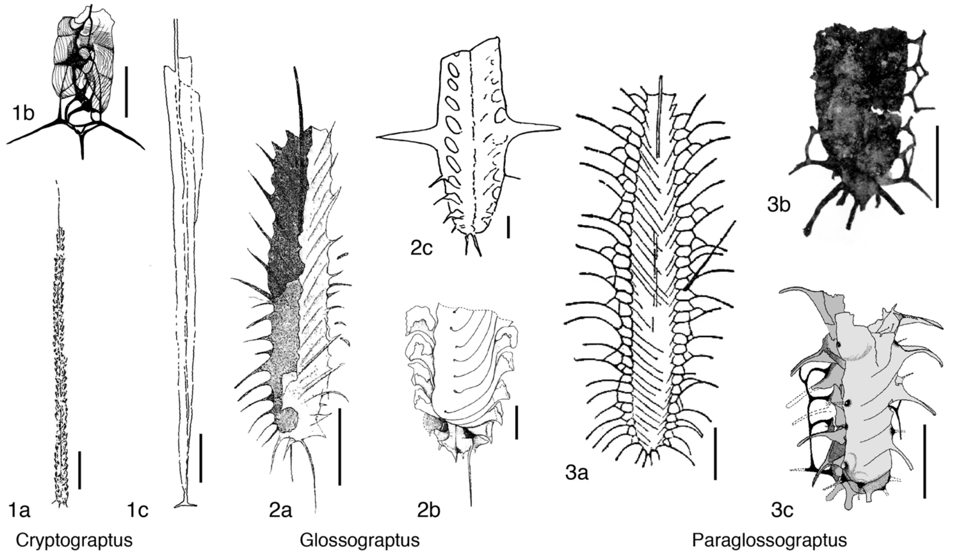

FIG. 220. Glossograptidae (p. 325–328).

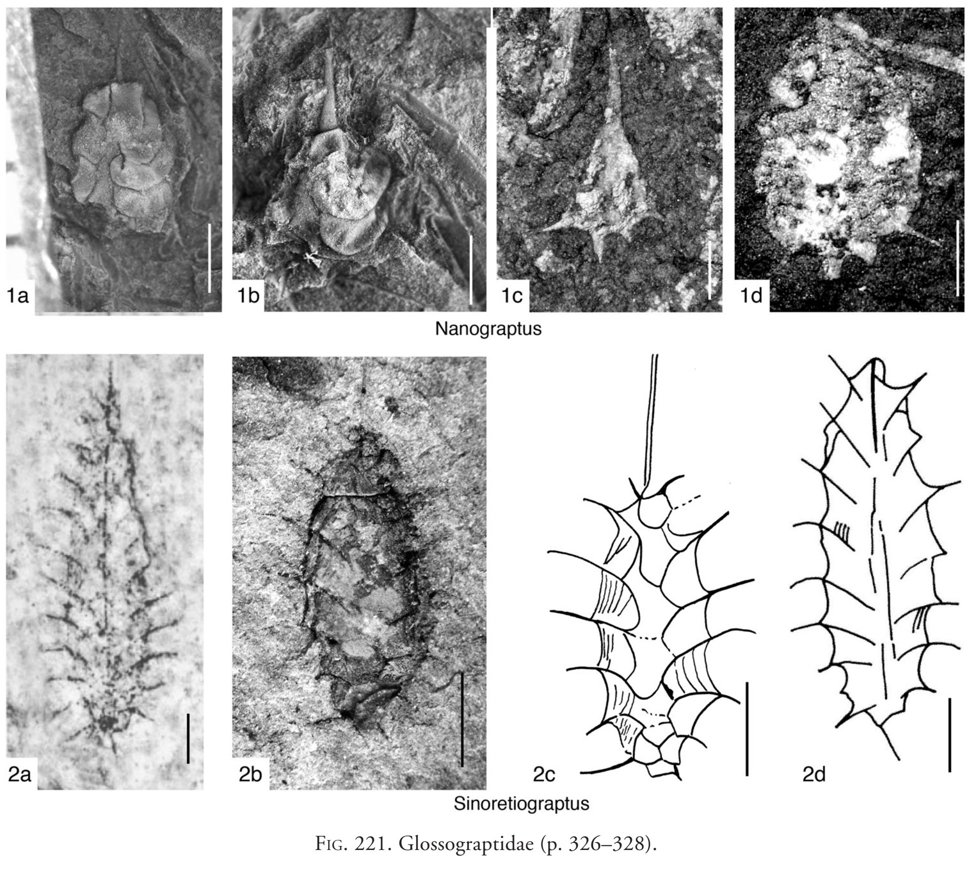

FIG. 221. Glossograptidae (p. 326–328).

Newfoundland, Canada, scale bar, 1 mm (new).——Fig. 220,*3c. P. proteus* (Harris & Thomas, 1935), GSC 23949, Daniels Harbour, western Newfoundland, Canada, scale bar, 1 mm (adapted from Whittington & Rickards, 1969, fig. 7).

Sinoretiograptus Mu & others, 1974, p. 164 [**S. mirabilis;* OD; =*Rogercooperia paucispinosus* Sherwin & Rickards, 2000, p. 163, herein]. Glossograptid with slender, elongated, probably finite colony consisting of ~8–10 thecal pairs; sicula with metasicular origin of first theca; glossograptid bulge reduced and restricted to two thecal pairs; slender spine-like rutella on all thecae; development unknown. *Upper Ordovician* (*Katian, Dicellograptus complexus* [=?*Dicellograptus ornatus*] Biozone): China, Australia.——Fig. 221,*2a–d. *S. mirabilis; 2a,* NMV P63643, Warbisco Shale, eastern Victoria, Australia (VandenBerg, 2003, fig. 2a); *2b–c,* holotype, NIGP 21406, late Katian, Wufeng Shale, Wangjiawan, Yichang, South China (new; drawing by Charles Mitchell); *2d,* AMF 103320, Keenan's Bridge, New South Wales, Australia (Sherwin & Rickards, 2000, fig. 2a). All scale bars, 1 mm.

Skiagraptus Harris, 1933, p. 108 [**Diplograptus gnomonicus* Harris & Keble in Harris, 1916, p. 66; OD]. Small, slender, scandent, dipleural(?) glossograptid with rutella of sicula and $th1^1$ united; thecae short; fusellum attenuated. *Middle Ordovician* (*upper Dapingian, Oncograptus upsilon* Biozone–*lower Darriwilian, Levisograptus austrodentatus* Biozone): New Zealand, Australia, China, Norway, USA, Canada, Argentina.——Fig. 219,*1. *S. gnomonicus* (Harris & Keble), NMV P73118, scale bar, 1 mm (Finney & Chen, 1984, fig. 3A).

SUBORDER AXONOPHORA

JÖRG MALETZ

Suborder AXONOPHORA Frech, 1897

[Axonophora FRECH, 1897, p. 607] [=Virgellina FORTEY & COOPER, 1986, p. 639, *partim* (see MALETZ, 2010a, p. 416); =suborder Diplograptacea LAPWORTH in MITCHELL, 1987, p. 367; =order Diplograptoidea in MITCHELL & others, 2007, p. 332]

Graptoloids with nema as leading rod followed by or engulfed in growth of thecal rows; colonies either biserial, dipleural, or uniserial; proximal development complex, with pro- or metasicular origin of $th1^1$, dicalycal theca delayed from position at $th1^2$ or lacking altogether; characteristic cross bars connect interthecal septa to nema in many taxa and form ring with aboral lists at base of interthecal septa. *Middle Ordovician* (*Dapingian, Oncograptus upsilon* Biozone)–*Lower Devonian* (*Pragian, Uncinatograptus yukonensis* Biozone): worldwide.

FRECH (1897) introduced the name Axonophora for uniserial and biserial graptolites with a nema leading the growth of the stipe. The term has been accepted by some scientists, especially in Russian and Chinese literature (e.g., OBUT, 1964; MU, 1974), but it fell into disuse in western taxonomy (BULMAN 1955, 1970; RIGBY, 1986) and was only reintroduced by MALETZ, CARLUCCI, and MITCHELL (2009). FRECH (1897) largely misinterpreted the colony development, following RUEDEMANN'S (1895) reconstructions of synrhabdosomes. However, Frech recognized the central position of the nema in the growth of the graptolite colony. In discussing the early evolution of the axonophorans, FORTEY, ZHANG, and MELLISH (2005, p. 1255) preferred the name Virgellina for this clade. MITCHELL and others (2007) called the same clade Diplograptoidea. MALETZ, CARLUCCI, and MITCHELL (2009, fig. 6) separated the early biserials of the *Levisograptus austrodentatus* (HARRIS & KEBLE, 1932) group (see MALETZ, 2011c) as stem axonophorans and even included the Arienigraptidae *sensu* MALETZ and MITCHELL (1996) in their Pan-Axonophora. This definition separates the *Levisograptus austrodentatus* group—which, in the past, has generally been accepted as the earliest biserials or axonophorans—from the remaining axonophorans.

The concept used herein (Fig. 222) identifies all biserial, dipleural graptolites as axonophorans. The defining synapomorphy of the Axonophora, then, is the biserial, dipleural colony construction engulfing a central nema between the dorsal sides of the two stipes. The Axonophora comprise all biserial, dipleural taxa derived from the two-stiped genus *Pseudisograptus* and the derived uniserial Monograptidae. The stem group is formed by *Apiograptus* and *Levisograptus,* bearing a pattern U astogeny. However, a trichotomy within the Diplograptina indicates remaining problems with this interpretation (see MITCHELL & others, 2007). Based on a number of tubarium features, MALETZ (2011d, fig. 3) preferred the origin of the Climacograptidae from a neograptine ancestor close to *Undulograptus,* thus, independent from the genus *Archiclimacograptus* and the Diplograptina. As a solution has not been proposed, the Climacograptidae are here retained in the Diplograptina. Further research is necessary to document the precise relationships of the three clades.

MORPHOLOGY

In the Axonophora, the nema gained a new importance and was used as the rod along which the stipes grew, while in non-axonophoran graptoloids the stipes did not need a leading rod and the nema was free and commonly relatively short and inconspicuous (Fig. 223.1). A long nema engulfed between the two laterally connected stipes is visible in biserial, monopleural Glossograptidae specimens (MALETZ & ZHANG,

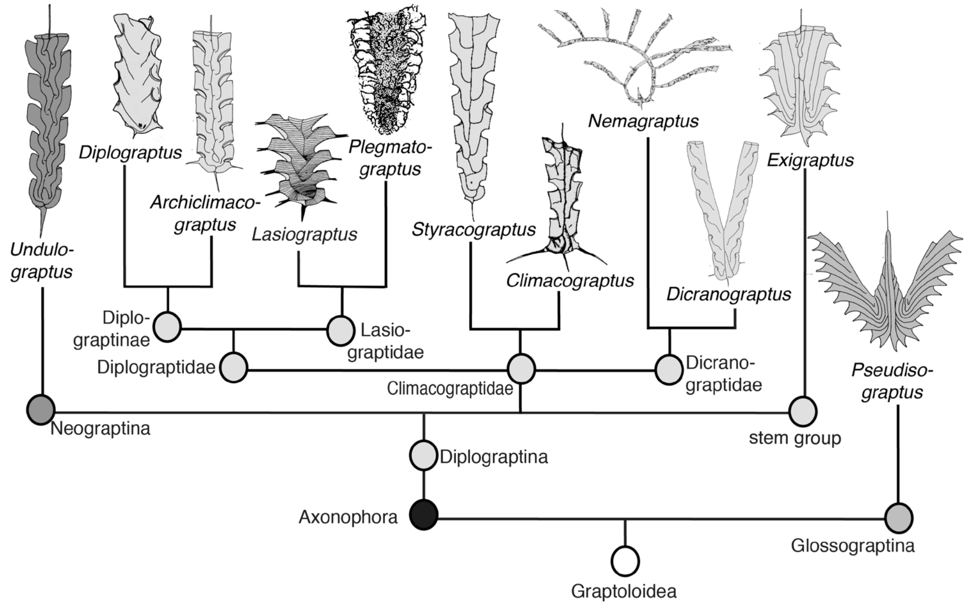

FIG. 222. Diagram of the Axonophora, showing the unresolved trichotomy within the Diplograptina leading to the Diplograptidae, Climacograptidae, and Dicranograptidae. Specimens not to scale (new).

2016). Early Axonophora were invariably biserial, dipleural (Fig. 223.2) but the biserial tubarium shape was lost in the Silurian monograptids (Fig. 223.3). In specimens of both groups, the nema extends distally beyond the thecate part of the tubarium.

The prosicula with the typical spiral line and the metasicula formed from fuselli is recognizable in the Axonophora. KRAFT (1926) differentiated the nema prosiculae (cauda) from the conus in *Rectograptus gracilis* (ROEMER, 1861) and in an indeterminate monograptid, ?*Heisograptus micropoma* (JAEKEL, 1889). He stated that the cauda is very short in monograptids but does not differ otherwise from the development in *Rectograptus*. The cauda has not been differentiated in later descriptions of isolated materials of axonophorans. Information on the number and development of the longitudinal rods on the prosicula is not available for most axonophoran taxa. The prosicula appears to be reduced in some climacograptids, where it is preserved in the form of a single rod or two rods united distally to form a normal nema (MITCHELL, 1987).

The nema was secreted in fusellar increments as a spine from the cauda of the prosicula (BATES, 1987a). The differentiation of the nema and virgula (RICKARDS, 1996) cannot be upheld, and the virgula in older literature should be regarded as identical to the nema. Nematularia are common in the Axonophora and may have various shapes (MÜLLER & SCHAUER, 1969; MÜLLER, 1975). Few nematularia are known from chemically isolated material of the Diplograptina, and many details of their development and use are still uncertain. They may have formed as two- and three-vaned structures (Fig. 223.5–223.6), as is seen in a number of examples (e.g., BULMAN, 1947; URBANEK, KOREN', & MIERZEJEWSKI, 1982; MITCHELL & CARLE, 1986). MALETZ and others (2011) illustrated the heart-shaped nematularium of *Archiclimacograptus decoratus* (HARRIS & THOMAS, 1935) from western Newfoundland produced from fusellar or microfusellar material. In the Lasiograptidae, paired lateral spines or scopulae with variably formed vanes with fusellar construction are present in a number of species (Fig. 223.4), but are

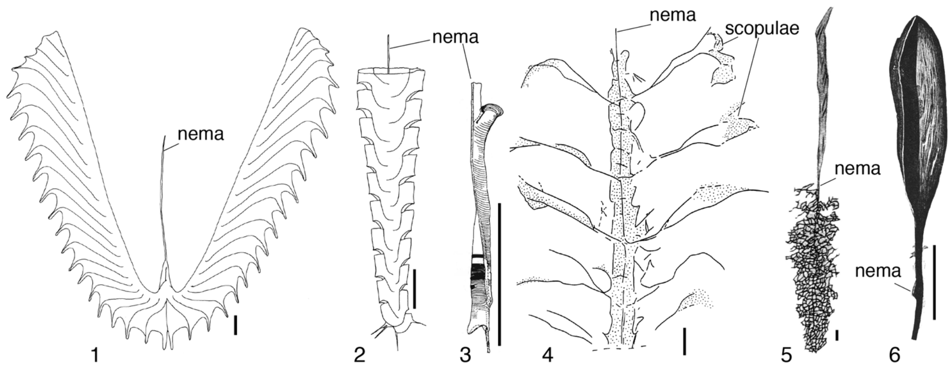

FIG. 223. Nema and nematularium development in the Graptolithina. *1, Isograptus divergens* HARRIS, 1933, completely free nema between two reclined stipes (new); *2, Amplexograptus praetypicalis* RIVA, 1987, nema incorporated in colony, visible at distal end (new); *3, Lobograptus imitator* URBANEK, 1966, nema visible on dorsal side of stipe (Urbanek, 1966, pl. 28D); *4, Neurograptus fibratus* (LAPWORTH, 1876a), NIGP 127015, part of colony showing paired scopulae, Kalpin, China (Chen & others, 2000, fig. 6); *5, Phormograptus laqueus* (ROSS & BERRY, 1963), holotype showing long nematularium (Ruedemann, 1934, pl. 15,*10*); *6, Pseudoclimacograptus scharenbergi* (LAPWORTH, 1876a), three-vaned nematularium (Bulman, 1947, pl. 9). Scale bars, 1 mm.

best known in chemically isolated material of *Orthoretiolites hami* (BATES & KIRK, 1991).

The origin of the ventral virgella of the Axonophora from a rutellum can be documented in all steps leading to the final apertural virgellar spine (MALETZ, 2010a; MALETZ, LENZ, & BATES, 2016). It occurred in the glossograptid *Isograptus* MOBERG, 1892a, in which the rutellum is often considerably extended, leading to the lamelliform rutellum of *Arienigraptus* and the Glossograptidae. A lanceolate virgella has been recognized in chemically isolated material of the genus *Levisograptus* (Fig. 224.1–224.4). The genus *Apiograptus* may still have possessed a lamelliform rutellum, but isolated material is not available.

PROXIMAL DEVELOPMENT

The proximal development and structure is quite complex in axonophorans and becomes successively simpler. Quite a number of proximal development types have been described for biserial graptolites, based on the origins and growth directions of proximal thecae (MITCHELL 1987, 1990; MELCHIN & MITCHELL, 1991; MELCHIN, 1998; MELCHIN & others, 2011). The development of relief specimens of the oldest axonophorans (*Apiograptus*, *Levisograptus*) can easily be related to the manubriate isograptids, because the remains of the manubrium are still present, even though often considerably reduced in size (Fig. 225.1). Relief specimens of *Apiograptus* have a low prosicular origin of $th1^1$ (ZHANG, 1993; MITCHELL & MALETZ, 1995, fig. 3N) as a symplesiomorphic character and not the typical metasicular origin of $th1^1$ of derived axonophorans. The manubrium is reduced but retains the initial parallel-sided downward growth of the proximal thecae (Fig. 225.2). The proximal development is comparable to the pattern U astogeny in all other features. The manubrium is lost in the genus *Levisograptus,* and the last remains of the manubrium exist only as an exposed patch of thecal origins on the reverse side of the colony (Fig. 225.3–225.4). The dicalycal theca appears to be $th2^2$, but apart from a few relief specimens, isolated juveniles are not available to confirm this construction. The delayed dicalycal theca $th2^2$ is also present in the genus *Pseudisograptus* (see COOPER & NI, 1986). *Levisograptus primus* (LEGG, 1976) and *Levisograptus austrodentatus* bear a pattern U astogeny, the most complex type described from axonophorans (MITCHELL, 1990).

Initially, the two stipes of the axonophorans were folded over the apex of the sicula

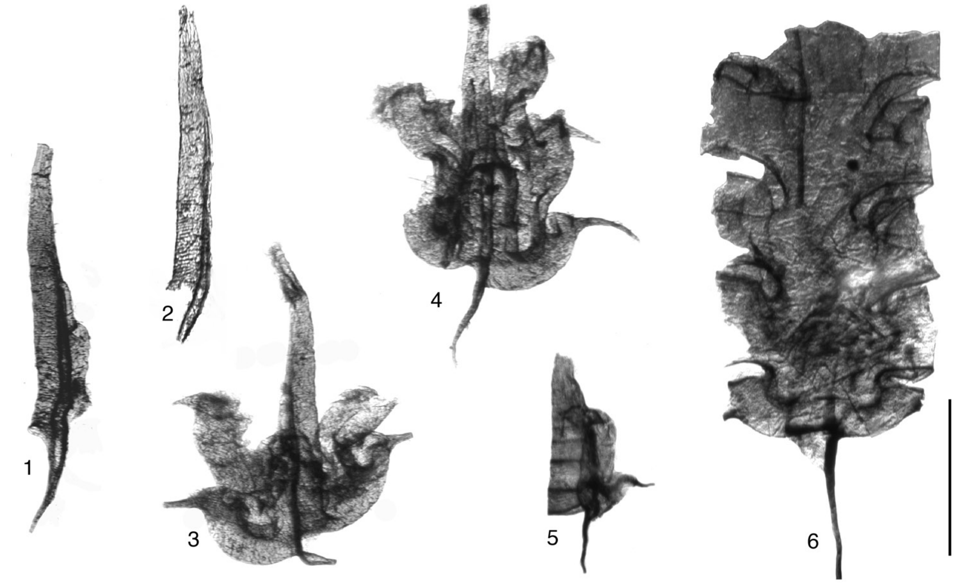

FIG. 224. The virgellar spine development in early Axonophora, infrared photos. *1–4, Levisograptus sinicus* (MU & LEE, 1958), Cow Head Group, western Newfoundland; *1,* GSC 133381, nearly complete sicula with lanceolate virgella and part of first theca; *2,* GSC 133380, juvenile sicula with tip of lanceolate virgella broken, showing thickened rims; *3,* GSC 133386, small specimen with five thecae and strongly bent lanceolate virgella; *4,* GSC 133378, specimen with three thecal pairs, some parts broken (*1–4,* Maletz, 2010a, fig. 5,*b,a,g,h,* respectively); *5–6, Archiclimacograptus* MITCHELL, 1987, West Bay Centre Quarry, western Newfoundland; *5,* GSC 140112, juvenile, showing virgellar spine and dark banding on sicula (new); *6,* GSC 140113 (new). All specimens are flattened, chemically isolated from shales. Scale bar, 1 mm for all specimens.

and grew parallel to each other, forming the median septum with the nema integrated in the layer. The precise construction of the median septum is far from being understood, and the reconstruction of BULMAN (1970, fig. 46), as well as the interpretation of GOLDMAN and others (2011) in climacograptids, suggest a single layered construction. The median septum varies considerably in shape due to the thecal style of the colony. Due to the presence of intrathecal folding (MALETZ, LENZ, & BATES, 2016), the median septum may be undulating or even zigzag shaped (Fig. 226.2).

Intrathecal folds are common in earlier axonophorans but easily overlooked because the short bars connected to the median septum are only recognizable in well-preserved relief material (Fig. 226.1). The intrathecal folds represent a temporary stop and change in growth direction at the base of the metathecae and the introduction of the median septum. A short lateral bar is commonly visible, around which the interthecal septum bends. The position of this part of the cross bar is clearly marked in *Urbanekograptus retioloides* (URBANEK, 1959, pl. 2) to be above the origin of the prothecae and can be recognized as the cross bars connected to the median septum in taxa with intrathecal folding (Fig. 226.3). The ventral parts of these cross bars (Fig. 226.2) anchor the nema and stabilize the median septum. The robust strengthening cross bars connect the nema with the lateral walls in many taxa and are connected to the thickened bases of the interthecal septae, the aboral lists (Fig. 226.2). BULMAN (1932a) illustrated the thickened cross bars from chemically isolated material in *Archiclimacograptus* (?) *skagensis* (JAANUSSON & SKOGLUND, 1963) and *Haddingograptus eurystoma* (JAANUSSON, 1960) (Fig. 226.4–226.5), showing that they are part of the median septum construction.

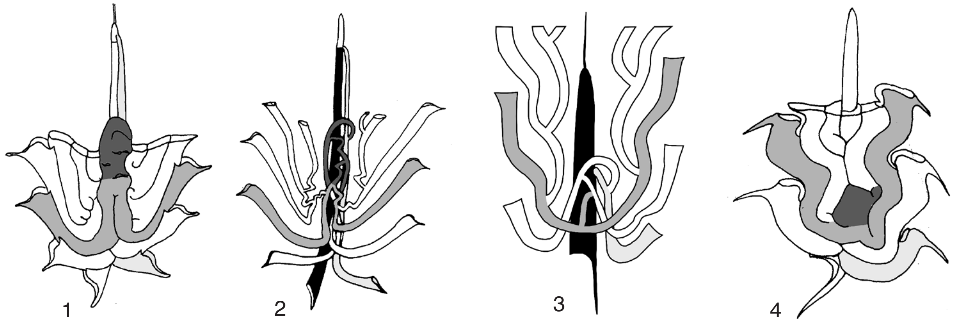

FIG. 225. Proximal development, pattern U astogeny. *1, Apiograptus uniformis* (MU in MU & others, 1979), reverse view, reconstruction (new drawing, adapted from Mitchell & Maletz, 1995, fig. 3N); *2,* pattern U astogeny of *Apiograptus* COOPER & MCLAURIN, 1974 with conspicuous downward growth of proximal thecae (manubrium in *light and dark gray*) and prosicular origin of th1[1] (new); *3,* pattern U astogeny (adapted from Mitchell, 1990, fig. 11,*1C*); *4, Levisograptus sinicus* (MU & LEE, 1958), reverse view showing remains of manubrium, reconstruction (new).

In derived axonophorans, a median septum may be absent, and the thecae grow alternately to form a unistipular, biserial colony (MELCHIN, NACZK-CAMERON, & KOREN', 2003). These either have an unconnected nema freely wandering through the colony, or the nema is attached to the center of the interthecal septae through a short central bar. BULMAN (1932c) described the development of the unistipular colony of *Geniculograptus typicalis* (HALL, 1865) in some detail and illustrated the connection of the interthecal septae to the nema (Fig. 226.6–226.7). The aboral list is modified into a V-shaped form with the tip connected to the nema. The median septum may also be delayed and not present in the proximal end in many diplograptines (i.e., *Amplexograptus*, *Hustedograptus, Orthograptus;* see MITCHELL, 1987).

THECAL STYLES

In the literature, the thecal shapes of biserial axonophorans are frequently described by referring to typical genera. The terminology ranges from dichograptid, glyptograptid, and orthograptid to climacograptid and lasiograptid thecal styles (BULMAN, 1970, fig. 41–42). These styles are not used herein; it is preferred to describe the thecal features independent of any named genera, following MALETZ, BATES, and others (2014). Thus, the thecal descriptions are based on constructional features, the shape, presence/absence or style of the geniculum, genicular additions and also of apertural modifications. The profile of the ventral thecal wall may be straight or nearly so (Fig. 227.1) or may have a geniculum that is rounded (Fig. 227.2) or angular (Fig. 227.3–227.4). The position of the geniculum may vary considerably and can be close to the underlying thecal aperture or close to the overlying aperture. In cases in which the geniculum is close to the thecal aperture above, the term pseudogeniculum has been used (see MITCHELL, MALETZ, & GOLDMAN, 2009).

Thecal apertures can be quite variably adorned with lappets, spines, or other features. These can be restricted to the sides of the thecal apertures or to the ventral apertural margins. In the Peiragraptinae, for example, lateral apertural lobes or lappets can be modified into horns (Fig. 227.1) and eventually into paired apertual spines, as in the *Orthograptus quadrimucronatus* (HALL, 1865) group (GOLDMAN, 1995). Geniculate thecae often bear conspicuous flanges or collars (Fig. 227.4a), sometimes completely surrounding the thecal aperture. A ventral notch (Fig. 227.4b) in the aperture is commonly formed, supporting the paired lateral lobes of many species. In addition, a genicular notch (Fig. 227.3b) may also be present. Thecal apertures may be

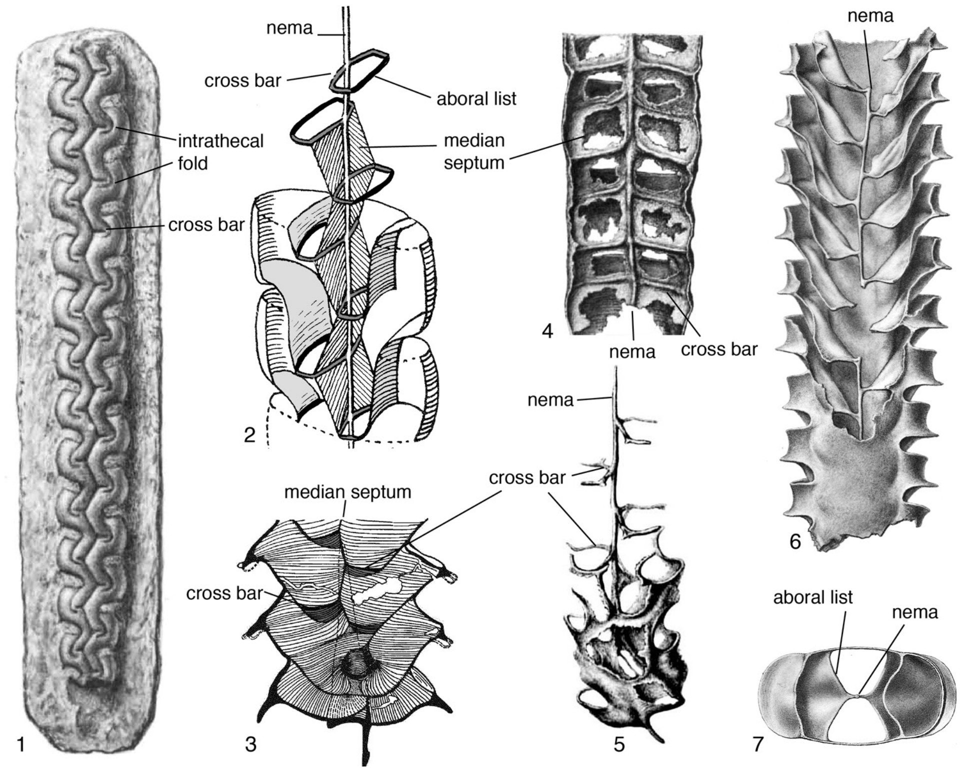

FIG. 226. Median septum development. *1,* Climacograptid indet., relief specimen showing zigzag median septum and intrathecal folding (Bulman, 1932a, pl. 3,*34*); *2,* part of colony showing integration of median septum, nema, crossbars, and aboral list (adapted from Bulman, 1970, fig. 46); *3, Urbanekograptus retioloides* (WIMAN, 1895), reconstruction showing the cross bars and intrathecal folding, prothecal parts of third and fourth thecal pair in *gray,* note change of growth direction at this point (Urbanek, 1959, pl. 5A); *4–5, Haddingograptus oliveri* (BOUČEK, 1973); *4,* fragment showing cross bars from inside, fusellum of median septum largely preserved (Bulman, 1932a, pl. 1); *5,* proximal end in lateral view, showing connecting bars in distal part of colony where fusellum is missing (Bulman, 1932a, pl. 2); *6–7, Geniculograptus typicalis* (HALL, 1865), unistipular colony; *6,* distal colony fragment with partially preserved nema and V-shaped attachment to base of interthecal septa; *7,* cross section of a colony showing connection of interthecal septa to nema in center (*6–7,* adapted from Bulman, 1932b, pl. 4,*5*).

introverted, horizontal, or everted, but these features are often modified by preservational aspects or the development of lateral lobes and horns (Fig. 227.1) and, thus, may be unreliable. All these thecal features can be modified independently and do not provide a useful guide for taxonomy.

Infraorder DIPLOGRAPTINA Lapworth, 1880

[*nom. correct.* OBUT, 1957, p. 17, *ex* Diplograpta LAPWORTH, 1880f, p. 191, *non* order Diplograptoidea in MITCHELL & others 2007; *non* superfamily Diplograptoidea, ŠTORCH & others 2011, fig. 6] [=Diplograptina, JAANUSSON, 1960, p. 321, *partim,* excl. Monograptidae]

Biserial axonophorans with pattern U astogeny or derived one, excluding taxa of the Neograptina; early taxa with manubrium and prosicular origin of $th1^1$, but metasicular origin of $th1^1$ in derived taxa; proximal end wide and rounded to highly asymmetrical, generally provided with virgellar spine and additional apertural spines, at least on first thecal pair; tubarium may be secondarily multiramous to single stiped; fusellum attenuated in some taxa, in which also reticulum and sometimes a lacinia develop (Lasiograptidae); thecae geniculate or non-geniculate with intrathecal folds and

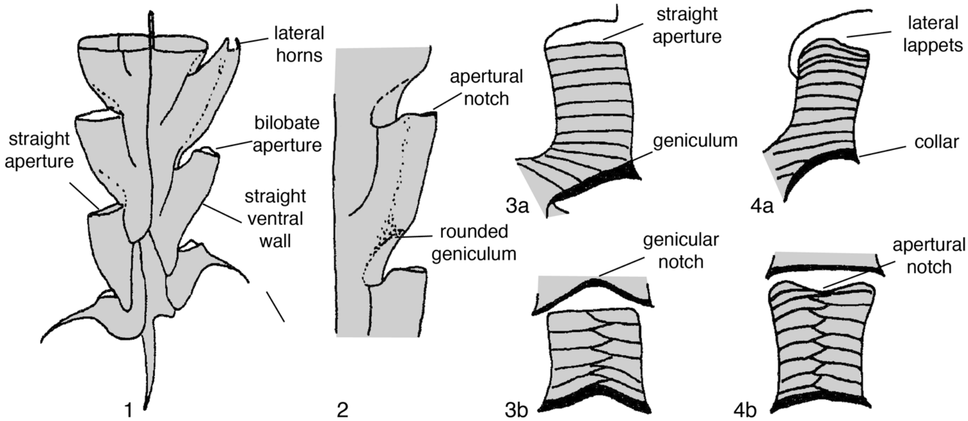

FIG. 227. The thecal morphology in biserial axonophorans (adapted from Maletz, 1997a, fig. 7).

complete median septum in earlier taxa; interthecal septa long and undulating in early taxa, becoming successively shorter in later ones; characteristic cross bars connect interthecal septa to nema in many taxa and form ring with aboral lists at base of interthecal septa. *Middle Ordovician* (*Dapingian, Exigraptus clavus* Biozone)–*Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

MALETZ, CARLUCCI, and MITCHELL (2009) and ŠTORCH and others (2011) differentiated two major clades in the Axonophora, which ŠTORCH and others (2011, p. 368) identified as the Diplograptina and the Neograptina and recognized the earliest taxon of the Neograptina as *Undulograptus formosus* (MU & LEE, 1958), a typical axonophoran with a pattern C astogeny (see MITCHELL & others, 2007, fig. 1), most probably derived from a diplograptine ancestor. Whereas MITCHELL and others (2007) and MALETZ, CARLUCCI, and MITCHELL (2009) suggested separating a paraphyletic stem group to define the Diplograptina and Neograptina as two monophyletic taxa, it is preferred herein to include their stem group in the Diplograptina, generating a paraphyletic taxon from which the Neograptina originated.

The concept used here for the Diplograptina is nearly identical to the order Diplograptoidea of MITCHELL and others (2007, fig. 1A), but includes the genus *Apiograptus* COOPER & MCLAURIN, 1974 and thus follows the opinion of HARRIS and THOMAS (1935, p. 303) who identified *Apiograptus crudus* (HARRIS & THOMAS, 1935) as the earliest biserial graptolite and suggested a relationship to the genus *Isograptus* MOBERG, 1892a. ŠTORCH and others (2011) included the superfamilies Dicranograptoidea, Diplograptoidea, and Climacograptoidea in the Diplograptina, interpreted here as family level taxa (Fig. 222). The detailed relationships of the Diplograptina and Neograptina are still uncertain, because the early evolution of the axonophorans is poorly known (MALETZ, 2011c).

STEM GROUP DIPLOGRAPTINA

The early axonophorans having the remains of the pseudisograptid manubrium are herein referred to an unnamed stem group taxon. This stem group is characterized by a pattern U astogeny, lost in the Diplograptidae, in which early taxa have a pattern C astogeny. A pattern A to pattern C astogeny occurs in the basal members of the Neograptina. The genus *Apiograptus* retains a prosicular origin of th1^1, a remnant of the origin through a pseudisograptid ancestor, lost in *Levisograptus*.

Apiograptus COOPER & MCLAURIN, 1974, p. 80 [*(?) *Glossograptus crudus* HARRIS & THOMAS, 1935, p. 303; OD] [=*Exigraptus* MU in MU & others, 1979, p. 128 (type, *E. clavus,* OD), syn. by NI &

XIAO, 1994, p. 15]. Diplograptina with strongly developed manubrium and pattern U astogeny; proximal end rounded, with maeandrograptid to isograptid symmetry; thecae elongated, tube-like, with widening apertures, long rutella, and sometimes with low lateral apertural lappets; sicula probably with lamelliform rutellum and low prosicular origin of th1[1]; proximal development of pattern U astogeny. *Middle Ordovician* (*upper Dapingian, Cardiograptus morsus* Biozone–*lower Darriwilian, Levisograptus austrodentatus* Biozone): Australia, New Zealand, China, Sweden.——FIG. 229,*1a–c*. **A. crudus* (HARRIS & THOMAS)*; 1a,* lectotype, NMV P31960 (new; provided by A. H. M. VandenBerg); *1b,* topotype, NMV P27485, Chinaman's Creek, Muckleford, Victoria, Australia (Cooper & McLaurin, 1974, fig. 2h); *1c,* topotype, NMV P30515, juvenile showing large manubrium (new). Scale bars, 1 mm.

Levisograptus MALETZ, 2011c, p. 856 [**Fucoides dentatus* BRONGNIART, 1828, p. 70; OD]. Diplograptina with pattern U astogeny; tubarium parallel sided to distally widening; proximal end broad, fairly symmetrical; manubrium structure reduced, lacking downward growth of thecae or manubrium lacking altogether; thecae long and doubly sigmoidal in shape; supragenicular thecal walls vertical to outwardly inclined; apertural spines at least on first thecal pair, rarely on distal thecae; thecae bear rounded or flowing geniculum and incipient to well-developed lateral apertural lappets. *Middle Ordovician* (*upper Dapingian, Exigraptus clavus* Biozone–*Darriwilian, Holmograptus lentus* Biozone): worldwide.——FIG. 229,*4a–c*. **L. dentatus; 4a,* neotype (selected by BULMAN, 1963b, p. 672), GSC 943, distal end omitted; *4b,* GSC 134280, associated with neotype; *4c,* GSC 134266, reverse view in low relief; Lévis, Québec, Canada (Maletz, 2011c, fig. 3A–B, 5G, respectively). Scale bars, 1 mm.——FIG. 229,*4d*. *L. austrodentatus* (HARRIS & KEBLE, 1932), GSC 102618, Begins Hill, Lévis, Québec, obverse view, scale bar, 1 mm (Maletz, 1997b, fig. 7C).

Family DIPLOGRAPTIDAE Lapworth, 1873

[Diplograptidae LAPWORTH, 1873b, table 1 facing p. 555; =superfamily Diplograptoidea LAPWORTH in ŠTORCH & others, 2011]

Diplograptina with pattern C astogeny or derived one, excluding derived Lasiograptidae; proximal end without manubrium; metasicular origin of th1[1]; proximal end wide and rounded to highly asymmetrical, generally provided with virgellar spine and additional apertural spines on at least first thecal pair; thecae variable, typically with complex apertural or genicular additions; long, double sigmoid thecae with intrathecal folds and complete median septum in earlier taxa; tubarium with attenuated fusellum in some taxa. *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone)–*Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

The Diplograptidae is a paraphyletic family from which the Lasiograptidae originated (Fig. 222). The precise origin and differentiation of the Climacograptidae (see discussion in MALETZ, 2011d) and the Dicranograptidae (see MALETZ, 1998b) remains unclear. In their cladistic interpretation, MITCHELL and others (2007) placed them at the base of an unresolved trichotomy within the Diplograptina.

The concept of the family Diplograptidae has changed considerably during the time of its use. LAPWORTH (1873b) introduced the taxon for all biserial, dipleural graptolites, but stated that this arrangement was provisional and essentially artificial. As used by MITCHELL and others (2007), it includes most of the Orthograptidae of MITCHELL (1987), except for the Lasiograptinae, now recognized as the family Lasiograptidae (MITCHELL & others, 2007). Even though a number of taxa are well known from isolated material, many questions still remain open on the internal structure of the tubarium in members of the clade.

MITCHELL, MALETZ, and GOLDMAN (2009) revised the genus *Diplograptus* (the name giver of the Diplograptidae) and considered it as nesting among the main plexus of the Orthograptidae of MITCHELL (1987), a clade of biserials with a pattern G or a derived astogeny and possessing paired antivirgellar spines. As the authors stated, except for the proximal end pattern, the genus might better fit with the archiclimacograptids. ŠTORCH and others (2011) defined their superfamily Diplograptoidea as the clade including a stem lineage with the genera *Eoglyptograptus* and *Pseudamplexograptus* and the two families Diplograptidae and Lasiograptidae.

Subfamily DIPLOGRAPTINAE Lapworth, 1873

[Diplograptinae LAPWORTH, 1873b, table 1 facing p. 555, *ex* Diplograptidae LAPWORTH, 1873b]

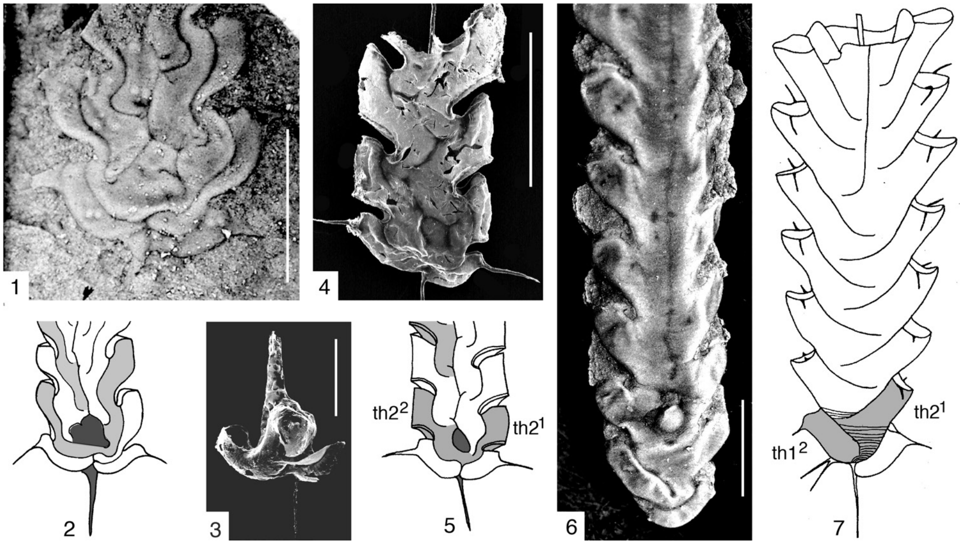

FIG. 228. Proximal development in the Diplograptina. *1, Levisograptus sinicus* (MU & LEE, 1958), PMU 31733, pattern U astogeny, latex cast, coated, Fågelsång-3 drill core at 56.28–56.30 m, Scania, Sweden (Maletz & Ahlberg, 2018, fig. 6G); *2, Levisograptus austrodentatus* (HARRIS & KEBLE, 1932), reverse view, pattern U astogeny, reconstruction (new); *3–5, Archiclimacograptus decoratus* (HARRIS & THOMAS, 1935); *3,* GSC 139286a, reverse view, showing upward-growing flange, Daniels Harbour, Table Head Group, western Newfoundland (new); *4,* GSC 139286b, small specimen in reverse view, Daniels Harbour, western Newfoundland (new); *5,* reconstruction of pattern C astogeny (new); *6, Diplograptus pristis* (HISINGER, 1837), LO 2354t, reverse view (new); *7, Orthograptus quadrimucronatus* (HALL, 1865), reverse view, reconstruction, showing pattern G astogeny (based on Maletz, 2011b, fig. 2B). Scale bar 0.5 in 3, all other scale bars, 1 mm.

Biserial diplograptids with pattern C or derived astogeny, excluding taxa of the Lasiograptidae; proximal end with metasicular origin of th1^1; proximal end square to highly asymmetrical, generally provided with virgellar spine and additional apertural spines on first thecal pair; thecae variable, commonly with complex apertural or genicular additions; intrathecal folds and complete median septum in earlier taxa. *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone)*–Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

The early evolution of the Diplograptinae is unclear because detailed information on the proximal development and thecal construction of most basal axonophorans—and thus, the connection to the stem group taxa—is not available. The proximal development of the Diplograptinae varies considerably. Whereas taxa of the stem group had a pattern U astogeny (Fig. 228.1–228.2), early Diplograptinae possessed a pattern C astogeny (Fig. 228.3–228.5), and younger taxa may have had a derived pattern G astogeny (Fig. 228.6–228.7). Species with pattern C or derived astogeny usually had an upward-growing flange (Fig. 228.3) uniting with the downward-growing initial part of th2^1, forming the paired openings for the growth of th2^1 and th2^2 (Fig. 228.5). In derived taxa, th1^2 and th2^1 may have formed a conspicuous arch in the pattern G astogeny (Fig. 228.7). The evolutionary origin of the upward-growing flange is uncertain as it has not been detected in any species with a pattern U astogeny and appears to be lacking in species with the derived pattern B astogeny (see MITCHELL, 1987).

Diplograptus M'COY, 1850, p. 270, *nom. correct.* HALL, 1865, p. 109, original spelling as *Diplograpsis* changed in ICZN Opinion 650, 1963] [**Prionotus pristis* HISINGER, 1837, p. 114; SD GURLEY, 1896, p. 78]. Diplograptines with bluntly rounded proximal end; th1[1] and th1[2] with subapertural or apertural spines; tubarium with or without median septum and alternating thecal origin; thecal gradient with proximally geniculate to distally straight, outward-inclined ventral sides and everted thecal apertures; proximal development probably of pattern G astogeny. *Upper Ordovician* (*upper Katian, Pleurograptus linearis* Biozone–*Hirnantian, Normalograptus extraordinarius* Biozone): China, Europe, UK, Estonia, Sweden, Canada, USA, Russia (Siberia).——FIG. 229,*9a–c*. **D. pristis* (HISINGER); *9a*, holotype, NRM-PZ Cn 59728, Draggabro, Dalarna, Sweden (new; drawing by John F. Riva); *9b,* GIT 708-1, infrared photo, obverse view, showing sicular length; *9c*, GIT 708-1, reverse view, Paasvere drill core, Estonia (*b–c,* Mitchell, Maletz, & Goldman, 2009, fig. 1E–2E). Scale bars, 1 mm.

Archiclimacograptus MITCHELL, 1987, p. 387; *ex* subgenus *Pseudoclimacograptus* (*Archiclimacograptus*) MITCHELL, 1987, p. 387, MALETZ, 1997a, p. 52 [**Pseudoclimacograptus angulatus sebyensis* JAANUSSON, 1960, p. 330; OD]. Diplograptines with a pattern C astogeny; square proximal end with apertural to subapertural spines on first thecal pair, an arch connecting th1[2] and th2[1], and early origin of th3[1] on reverse side; exposed part of the crossing canal of th1[2] small; dicalycal theca is th2[1] or later one; thecae with distinct geniculae, variably developed lateral apertural lappets and variably long thecal overlap; intrathecal septa originate from median septum, indicating intrathecal folds; gradual shape change common in development of geniculae, lateral apertural lappets, and shape and length of septa along tubarium. *Middle Ordovician* (*Darriwilian, Holmograptus lentus* Biozone)–*Upper Ordovician* (*Sandbian, Climacograptus bicornis* Biozone): worldwide.——FIG. 229,*8a–b*. **A. sebyensis* (JAANUSSON); *8a,* obverse view, reconstruction of holotype (Jaanusson, 1960, fig. 7D); *8b,* PMO 138.785, proximal end in reverse view (Maletz, 2011d, fig. 2). Scale bars, 1 mm.

Mesograptus ELLES & WOOD, 1907, p. 258 [**Graptolithus foliaceus* MURCHISON, 1839, p. 694; OD (type based on distal fragment), =*Diplograptus* (*Mesograptus*) *multidens* ELLES & WOOD, 1907, p. 261, HUGHES, 1989, p. 54]. Diplograptines with robust, parallel-sided to distally distinctly widening tubarium; thecae geniculate throughout or geniculum lost distally; thecal excavations deep and semicircular to somewhat restricted; apertures horizontal to everted; supragenicular wall short and commonly of similar height to that of thecal excavations; proximal development and median septum unknown, but possibly pattern C astogeny; first thecal pair with subapertural to median spines. *Upper Ordovician* (*Sandbian, Climacograptus bicornis* Biozone): UK, Sweden, China, Russia. [The distribution of the genus may indicate a high latitude faunal element.]——FIG. 229,*7a–b*. **M. foliaceus* (MURCHISON); *7a,* NHMUK PM 1288, proximal part of lectotype of *Diplograptus* (*Mesograptus*) *multidens* ELLES & WOOD; *7b*, second specimen on NHMUK PM 1288, obverse view; scale bars, 1 mm (new; drawings by John F. Riva).

Oepikograptus OBUT & SENNIKOV, 1984b, p. 110 [**Diplograptus bekkeri* ÖPIK, 1927, p. 28; OD] [=*Fenhsiangograptus* HONG, 1957, p. 495 (type, *F. fenhsianensis,* OD), syn. herein]. Diplograptines with distinctly biform thecae; proximal thecae spined, distal ones geniculate; median septum complete without indications of intrathecal folds; proximal end of pattern G astogeny, with apertural spines on variable number of proximal thecal pairs; thecal apertures provided with lateral lappets; sicula extensively exposed on the obverse side of the tubarium. *Middle Ordovician* (*Darriwilian, Jiangxigraptus vagus* Biozone or *Sandbian, Nemagraptus gracilis* Biozone): China, Estonia, Latvia, Spain, Sweden, Syria. [The distribution of the genus may indicate a high latitude faunal element.]——FIG. 229,*5a*. **O. bekkeri* (ÖPIK), holotype, TUG 1087-8, Kohtla, Estonia, scale bar, 1 mm (new; provided by Ursula Toom).——FIG. 229,*5b. O. fenshiangensis* (HONG, 1957), holotype, scale bar, 1 mm (Hong, 1957, pl. 5,*7*).

Prorectograptus LI, 1994, p. 66 [**Cryptograptus uniformis* CHEN in MU & others, 1979, p. 132; M]. Diplograptines with square proximal end and parallel-sided colony; thecae with straight, everted ventral thecal sides and everted apertural margins, possessing strong rutella or apertural spines; proximal development unknown. *Middle Ordovician* (*lower Darriwilian, Levisograptus austrodentatus* Biozone): China.——FIG. 229,*3*. **P. uniformis* (CHEN in MU & others), lectotype (selected herein), NIGP 32333, scale bar, 1 mm (new).

Pseudamplexograptus MITCHELL, 1987, p. 389 [**Lomatoceras distichum* EICHWALD, 1840, p. 101; OD (lectotype illustrated by JAANUSSON, 1960, pl. 5,*5*)]. Diplograptines with broad and nearly parallel-sided tubarium; thecae geniculate throughout or geniculum lost distally; thecal excavations deep and semicircular to somewhat restricted; apertures horizontal to introverted; supragenicular wall short and commonly of similar height to that of thecal excavations; pattern C astogeny with early origin of th3[1]; dicalycal theca th2[1] with complete median septum and intrathecal folding; first thecal pair with apertural or subapertural spines. [Taxon may be synonymous to *Mesograptus.*] *Middle Ordovician* (*upper Darriwilian, Pseudamplexograptus distichus* Biozone): UK, Estonia, Latvia, Sweden, Norway, China, Russia. [The distribution of the genus may indicate a high latitude faunal element].——FIG. 229,*6a–c*. **P. distichus* (EICHWALD) isolated specimens, Öland, Sweden; *6a*, NRM-PZ Cn 2355; *6b–c*, NRM-PZ 111 (Holm collection), juvenile in reverse (*b*) and obverse (*c*) views, showing pattern C astogeny (Bulman, 1932a, pl. 4,*19–20,* pl. 5,*1*, respectively). Scale bars, 1 mm.

Urbanekograptus MITCHELL, 1987, p. 389 [**Climacograptus retioloides* WIMAN, 1895, p. 276;

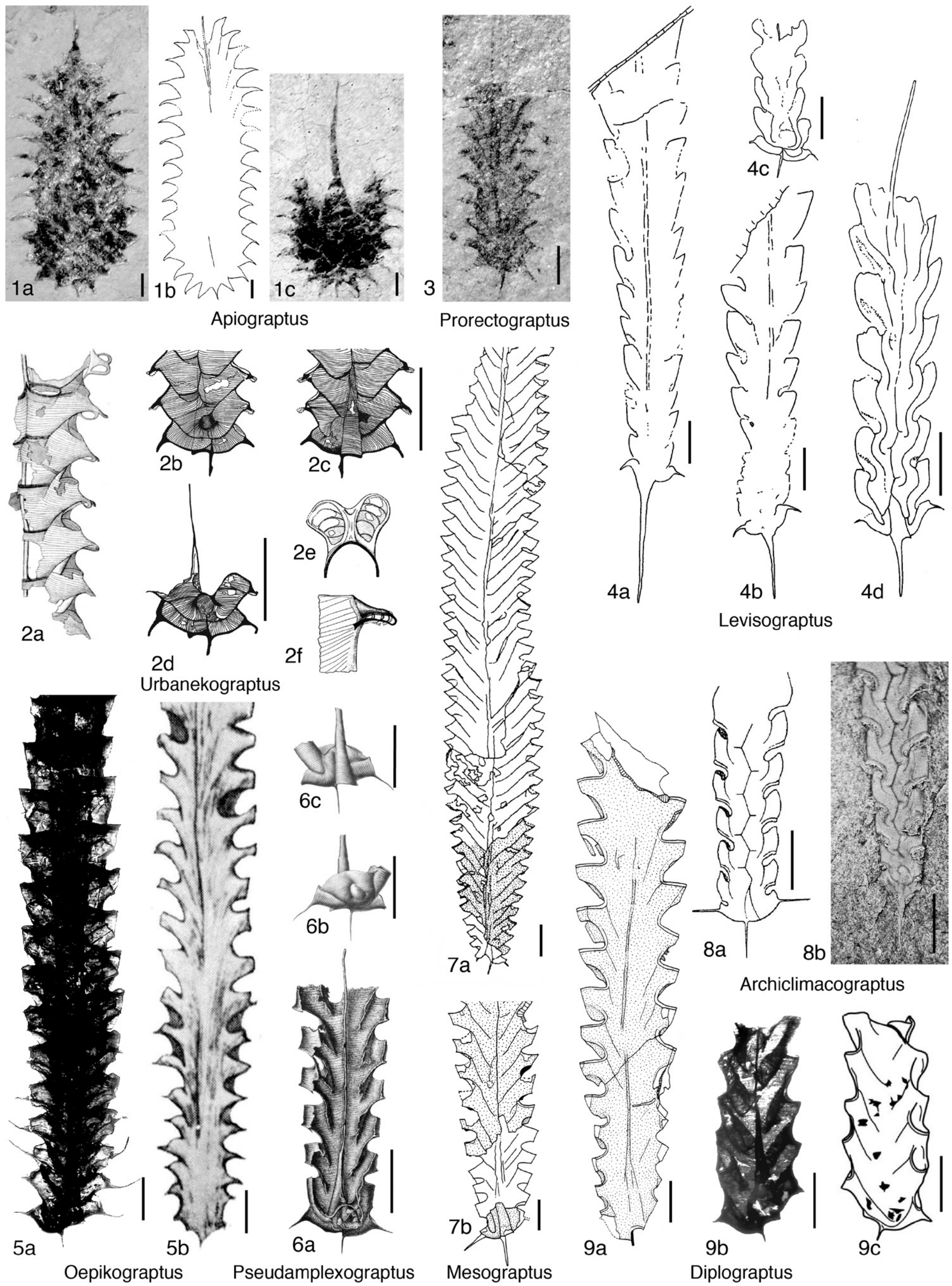

FIG. 229. Stem group Diplograptina and Diplograptinae (p. 335–340).

OD]. Diplograptines with nearly symmetrical, square proximal end and pattern C astogeny with th2[2] as the dicalycal theca; aperturtal spines on first thecal pair; later thecae with prominent paired subapertural lobes; intrathecal folds present; median septum undulating. *Middle Ordovician* (*upper Darriwilian, Dicellograptus vagus* Biozone) or *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): Poland, Sweden (glacial boulders).——FIG. 229,*2a–f.* **U. retioloides* (WIMAN) *2a,* holotype, fragment, Grisslehamn, Wäddö, northeast of Stockholm, Sweden, glacial boulder (Wiman, 1895, pl. 9,*4*); *2b–c,* proximal end in reverse (*b*) and obverse (*c*) views, glacial boulder 0.31, Poznan Czerwonak, Poland; *2d,* juvenile with complete sicula, proximal development in reverse view; *2e–f,* detail of apertural lobes from the side (*f*) and above (*e*) (*2b–2f,* Urbanek, 1959, from text-pl. 4, 5, and 7, respectively). Scale bars, 1 mm.

Subfamily PEIRAGRAPTINAE Jaanusson, 1960

[Peiragraptinae JAANUSSON, 1960, p. 322] [=Orthograptinae MITCHELL, 1987, p. 380] [=Eoglyptograptinae MITCHELL, 1987, p. 396; revised from misspelling as Eoglyptograptidae subfamily *nov.*]

Septate to aseptate diplograptids with straight median septum; onset of median septum often considerably delayed; interthecal septae in aseptate taxa attached to nema by central bar, but contact may be lost in younger taxa, in which nema is free; proximal development of pattern A astogeny or derived one (patterns B, G, F, K); often strongly asymmetrical proximal end with sicula extensively exposed on obverse side in younger taxa; sicula bearing paired antivirgellar spines in younger taxa; thecae variable, with straight to strongly geniculate ventral wall; apertures frequently with paired processes, lobes, horns, or spines; genicular modifications common; fusellum reduced in some taxa. *Middle Ordovician* (*Darriwilian,* ?*Holmograptus lentus* Biozone)*–Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

JAANUSSON (1960) based his subfamily Peiragraptinae on the genus *Peiragraptus,* which is now regarded as an abnormal taxon or population of distally uniserial axonophorans of general diplograptid relationships. MITCHELL (1987) emended the subfamily and referred a number of additional genera to the subfamily, based on the strongly geniculate thecae and the derived proximal development with a pattern G astogeny. MITCHELL (1987) separated the genera *Orthograptus* and *Hustedograptus* in the subfamily Orthograptinae. MITCHELL and others (2007) and ŠTORCH and others (2011) eliminated the subfamilies Orthograptinae and Peiragraptinae and referred all genera to the Diplograptidae instead. MALETZ (2014b) differentiated the Diplograptinae and the Orthograptinae in the family Diplograptidae.

Early peiragraptines bear a pattern A astogeny (Fig. 230.1a–c), but during the evolution of the group, patterns G and K became the standard, and the dicalycal theca was delayed or even eliminated in species without a median septum. Another important change occurred in the development and shape of $th1^1$. A typical U-shaped $th1^1$ with a space between the downward- and upward-growing parts of the theca was present in species with a pattern G astogeny on the obverse side of the colony (Fig. 230.2a–c). This gap was filled by the initial part of $th2^1$. In pattern K astogeny species (Fig. 230.4a–c), $th1^1$ filled this gap by reversing its growth direction, growing vertically upward. Pattern F astogeny species tightened the loop so that the dorsal part of the $th1^1$ aperture became attached to the ventral side of the sicula (Fig. 230.3a–c). In flattened material, these proximal development patterns may be impossible to tell apart.

Peiragraptus STRACHAN, 1954, p. 509 [**P. fallax;* OD]. Peiragraptines with square proximal end; subsequently slightly curved uniserial tubarium based on stipe 1; prominent antivirgellar spines and subapertural spine on $th1^1$ but not on $th1^2$; thecae with outward-inclined ventral thecal walls, rounded geniculum and everted apertures possessing paired apertural horns; proximal development comparable to pattern G astogeny. *Upper Ordovician* (*Katian*): Canada (Anticosti Island, boulder).——FIG. 232,*4a–c.* **P. fallax,* Observation Cliff, Anticosti Island, probably from Vaureal Formation, Canada; *4a,* holotype, BU 682, reverse view; *4b,* paratype, BU 679, juvenile, obverse view; *4c,* paratype, BU 680, juvenile, reverse view; scale bars, 1 mm (*a–c,* Strachan, 1954, fig. 2).

Amplexograptus ELLES & WOOD, 1907, p. 267 [**Diplograptus perexcavatus* LAPWORTH, 1876a, pl. 2,*38;* OD]. Peiragraptines with square proximal end, prominent antivirgellar spines and subapertural spine on $th1^1$, but not on $th1^2$; thecae geniculate, often with short, outward-inclined supragenicular walls; median septum delayed or lacking; pattern G astogeny; thecal apertures horizontal, with lateral apertural lappets. *Upper Ordovician* (*Sandbian, Climacograptus bicornis* Biozone*–Katian, Diplacanthograptus caudatus* Biozone): worldwide.——FIG. 231,*1a–b.* **A. perexcavatus* (LAPWORTH); *1a,* neotype, BU 1297a; *1b*, BU 1297b, proximal end of unfigured specimen from neotype slab; scale bars, 1 mm (new; drawings by John F. Riva).——

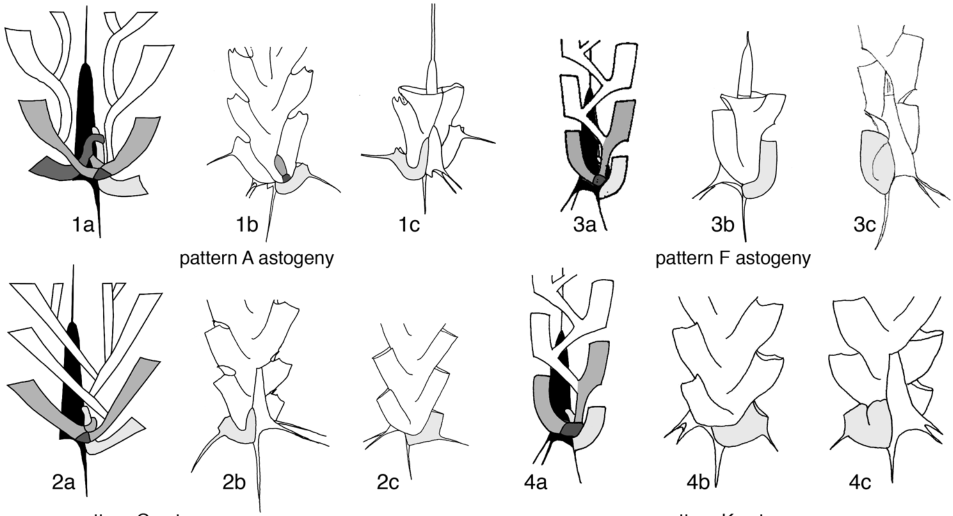

FIG. 230. Proximal development in the Peiragraptinae. *1,* pattern A astogeny (*a*), *Hustedograptus uplandicus* (WIMAN, 1895) in reverse (*b*) and obverse (*c*) views, showing exposed patch of crossing canal of $th1^2$, note the paired antivirgellar spines; *2,* pattern G astogeny (*a*), *Rectograptus* (PŘIBYL, 1949) in reverse (*b*) and obverse (*c*) views; *3,* pattern F astogeny (*a*), *Geniculograptus pygmaeus* (RUEDEMANN, 1925c) in reverse (*b*) and obverse (*c*) views; *4,* pattern K astogeny (*a*), *Anticostia hudsoni* (JACKSON, 1971) in reverse (*b*) and obverse (*c*) views. All specimen illustrations are reconstructions, not to scale. Proximal details shaded for easier access (new).

FIG. 231,*1c. A. leptotheca* BULMAN, 1946, BU 1299, holotype of *A. fallax* BULMAN, 1962; scale bar, 1 mm (new; drawing by John F. Riva).——FIG. 231,*1d. A. maxwelli* DECKER, 1935b, MCZ 115921, isolated specimen, note distal origin of median septum, Bromide Formation, Oklahoma, USA, scale bar, 1 mm (Goldman, Campbell, & Rahl, 2002, fig. 2,*11*).

Anticostia STEWART & MITCHELL, 1997, p. 219 [**A. macgregorae;* OD]. Peiragraptines with rounded, asymmetrical proximal end, distally widening tubarium, prominent antivirgellar spines and subapertural spine on $th1^1$ but not on $th1^2$; thecae with straight, outward-inclined ventral wall to strongly geniculate with vertical supragenicular wall; median septum lacking; proximal development of pattern K astogeny; thecal apertures horizontal to introverted, often with lateral lappets. *Upper Ordovician* (*Katian, Dicellograptus ornatus* Biozone–*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.——FIG. 231,*2a–b.* **A. macgregorae;* holotype, GSC 115740, reverse (*a*) and obverse (*b*) views, Vaureal Formation, Anticosti Island, Quebec, Canada, scale bar, 1 mm (Stewart & Mitchell, 1997, fig. 5a–b).

Arnheimograptus MITCHELL, 1987, p. 382 [**Glyptograptus lorrainensis anacanthus* MITCHELL & BERGSTRÖM, 1977, p. 262; OD]. Peiragraptines with rounded, asymmetrical proximal end, parallel-sided to distally widening aseptate tubarium; prominent antivirgellar spines, but lacking apertural spines on first thecal pair; thecae with straight outward-inclined to strongly geniculate ventral wall with vertical supragenicular walls; proximal development of pattern F astogeny; thecal apertures horizontal to introverted. *Upper Ordovician* (*Katian, Paraorthograptus manitoulinensis* Biozone [=*Pleurograptus linearis* Biozone, see GOLDMAN, BERGSTRÖM & MITCHELL,1995]): USA. [The distribution of the genus indicates a low latitude endemic faunal element.]——FIG. 231,*5a–c.* **A. anacanthus* (MITCHELL & BERGSTRÖM) Cincinnati region, Ohio, USA; *5a,* OSU 31663, holotype (Mitchell & Bergström, 1977, fig. 4); *5b,* SMF 75832, broken proximal end in reverse view; *5c,* SMF 75833, obverse view (new). Scale bars, 1 mm.

Eoglyptograptus MITCHELL, 1987, p. 396 [**Fucoides dentatus* BRONGNIART, 1828, *sensu* BULMAN, 1963b (=*E. gerhardi* MALETZ, 2011c, p. 859); OD]. Robust peiragraptines with distinctly asymmetrical proximal end and distally widening colony; apart from a typically elongated virgella, proximal end bears single apertural spine on $th1^1$; proximal development of pattern B astogeny; thecae with rounded to angular geniculum and outward-inclined apertures, commonly with slight lateral lobes, median septum straight to undulating; interthecal septae short, no intrathecal folds. *Middle Ordovician, Darriwilian* (*Holmograptus lentus* Biozone–*Jiangxigraptus vagus* Biozone): China, UK, Norway, Sweden.——FIG. 231,*4a–b.* **E. gerhardi* (MALETZ), NRM-PZ Cn 1280, holotype, Öland, Sweden, scale bars, 1 mm (Bulman, 1936a, pl. 3,*1–2*).

Geniculograptus MITCHELL, 1987, p. 381 [**Climacograptus typicalis* HALL, 1865, p. 57; OD] [=*Uticagraptus* RIVA, 1987, p. 932, obj.]. Peiragraptines with

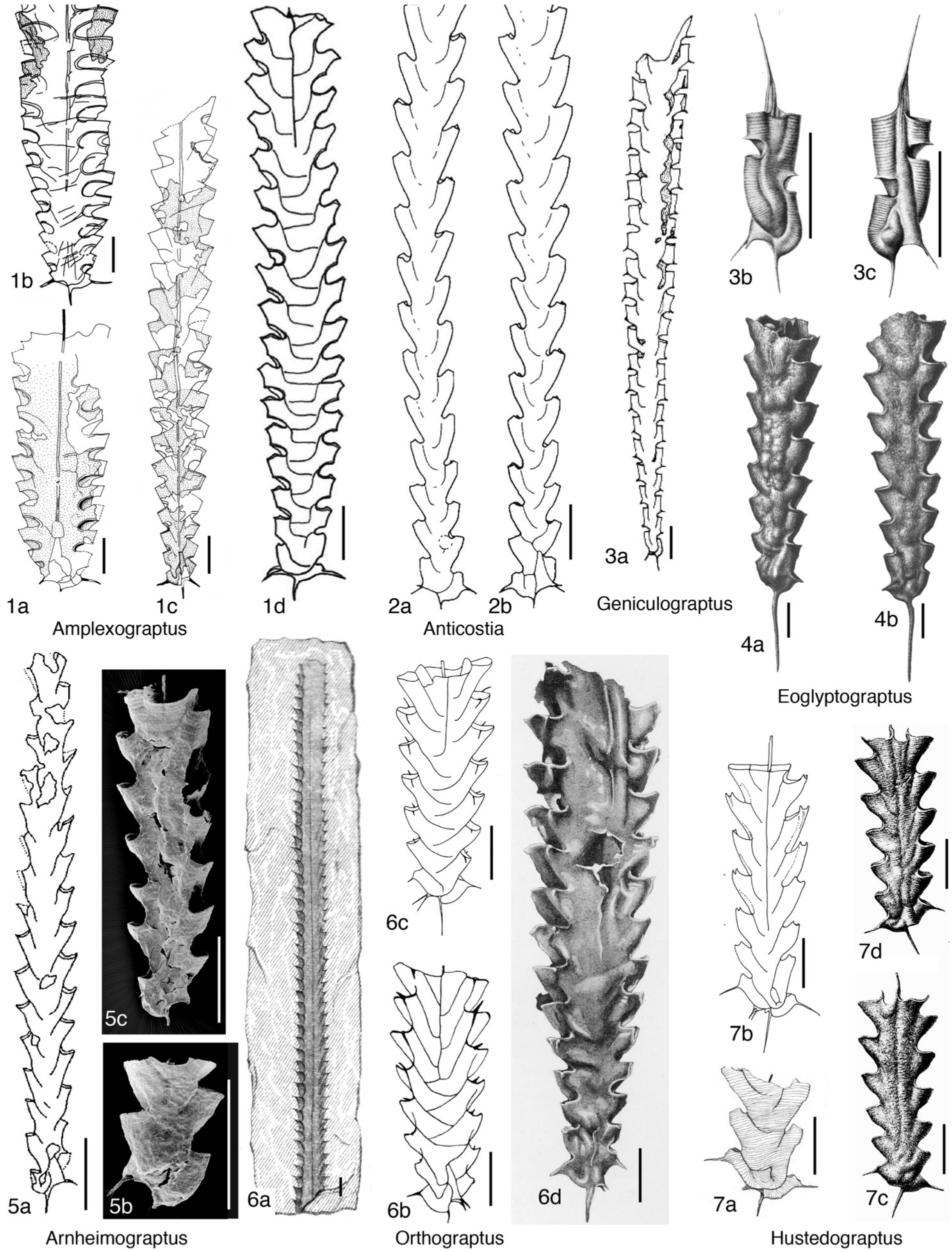

FIG. 231. Peiragraptinae (p. 340–343).

aseptate, gradually widening to nearly parallel-sided tubarium and narrow, pointed proximal end, bearing the virgella and two antivirgellar spines; geniculate thecae with slightly outwardly inclined supragenicular walls, bearing a variably prominent genicular flange; proximal development of pattern F astogeny; thecae with straight aperture, generally with low lateral apertural lobes. *Upper Ordovician* (*Katian, Diplacanthograptus caudatus* Biozone–*Climacograptus tubuliferus* Biozone): USA (Eastern), Canada (Eastern).——FIG. 231,*3a–c*. **G. typicalis* (HALL); *3a,* lectotype, AMNH 39957, Eden Shale, Cincinnati, Ohio, scale bar, 1 mm (Riva, 1987, fig. 7b); *3b–c,* reverse (*b*) and obverse (*c*) views of chemically isolated specimen, Cincinnati, Ohio, USA, scale bars, 1 mm (Bulman, 1932c, pl. 2,*22a–b*).

Hustedograptus Mitchell, 1987, p. 380 [**Diplograptus uplandicus* Wiman, 1895, p. 274; OD). Slender to robust peiragraptines with square, symmetrical to strongly asymmetrical proximal end, bearing apertural spines on sicula and first thecal pair; paired antivirgellar spines in stratigraphically younger species; median septum straight, commonly delayed; thecae regularly with rounded geniculum, distally with straight ventral wall; apertures simple or with paired lateral lappets; proximal development of pattern A astogeny. *Middle Ordovician* (*Darriwilian, Holmograptus lentus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.——Fig. 231,*7a–b*. **H. uplandicus* (Wiman); *7a,* holotype, reverse view (Wiman, 1895, pl. 9,*1*); *7b,* reconstruction in reverse view based on isolated material in Mitchell collection, Buffalo, New York, USA (new); scale bars, 1 mm.——Fig. 231,*7c–d. H. bulmani* Mitchell, Brussa, & Maletz, 2008, holotype, NRM-PZ Cn 59946, reverse (*c*) and obverse (*d*) views, scale bars, 1 mm (Bulman, 1936a, pl. 3,*10–11*).

Orthograptus Lapworth, 1873b, table 1, opposite p. 555, *ex* subgenus *Diplograptus* (*Orthograptus*) Lapworth, 1873b, table 1, opposite p. 555 [**Graptolithus quadrimucronatus* Hall 1865, p. 144; OD]. Peiragraptines with proximally rounded to strongly asymmetrical tubarium and apertural spines on the first thecal pair; median septum delayed; proximal development of pattern G astogeny; thecae with straight to slightly sigmoidal ventral walls; thecal apertures generally bearing paired spines or horns, rarely unadorned; fusellum may be attenuated. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone–*Katian, Pleurograptus linearis* Biozone): worldwide.——Fig. 231,*6a–c*. **O. quadrimucronatus* (Hall); *6a,* syntype, GSC 1898a, Lake St. John, Quebec, Canada (Hall, 1865, pl. 13,*1*); *6b–c,* MCZ 9472/5, isolated specimen in reverse (*c*) and obverse (*b*) views showing delay of median septum (adapted from Mitchell, 1987, fig. 9G–H). Scale bars, 1 mm.——Fig. 231,*6d. O. apiculatus* (Elles & Wood, 1907), Laggan Burn, Scotland, scale bar, 1 mm (Bulman, 1946, pl. 6,*2*).

Paraorthograptus Mu & others, 1974, p. 160 [**P. typicus;* OD; =*Climacograptus innotatus* var. *pacificus* Ruedemann, 1947, p. 429, see Williams, 1982a, p. 41] [=*Pacificograptus* Koren', 1979, p. 70, obj.]. Peiragraptines with square proximal end, prominent antivirgellar spines and subapertural spine on th1^1, but not on th1^2; thecae geniculate, with outward-inclined supragenicular walls; median septum lacking; proximal development of pattern G astogeny; thecal apertures horizontal or outward inclined with or without apertural cusps; geniculum adorned with paired spines, lobes, or collar. *Upper Ordovician* (*Katian, Paraorthograptus pacificus* Biozone–*Hirnantian, Normalograptus persculptus* Biozone): Australia, China, UK, Czech Republic, Canada, USA.——Fig. 232,*1a–c*. **P. typicus; 1a*, counterpart of holotype, NIGP 21418a, associated with specimen of *Appendispinograptus supernus* (Elles & Wood, 1906) (Riva, 1988, fig. 5a); *1b,* holotype of *P. pacificus* (Ruedemann), USNM 102838, Phi Kappa Formation, Idaho, USA (Riva, 1974c, fig. 2f); *1c,* GSC 104924, infrared photo, Cape Phillips Formation, Cornwallis Island, Arctic Canada (Melchin & Anderson, 1998, fig. 1,*1*). Scale bars, 1 mm.——Fig. 232,*1d. P. manitoulinensis* (Caley, 1936), GSC 56900, reverse view, Manitoulin Island, Ontario, Canada, scale bar, 1 mm (Riva, 1988, fig. 5i).

Pararetiograptus Mu in Mu & others, 1974, p. 163 [**P. sinensis;* OD] [=*Orthoretiograptus* Mu in Wang & others, 1977, p. 345 (type *O. denticulatus,* OD), syn. by Štorch & others, 2011, p. 342; =*Pseudoreteograptus* Mu in Mu & others, 1993, p. 231 (type, *P. nanus,* OD), syn. by Štorch & others, 2011, p. 343]. Peiragraptines with square proximal end, prominent antivirgellar spines and subapertural spine on th1^1, but not on th1^2; fusellum attenuated and may be lacking distally, where represented by thickened lists; thecae with outward-inclined ventral walls; incipient geniculum only in proximal thecae; lateral apertural lappets on proximal thecae; median septum lacking; proximal development possibly of pattern K astogeny (Štorch & others, 2011, p. 341); thecal apertures horizontal. [Genus name was misspelled as *Parareteograptus* in Mu, 1974, p. 233 and Štorch & others, 2011, p. 341.] *Upper Ordovician, Katian* (*Dicellograptus ornatus* Biozone–*Paraorthograptus pacificus* Biozone): China, USA).——Fig. 232,*3a–b*. **P. sinensis;* 3a, NIGP 83257, Wufeng Shale, China; *3b,* USNM 542746, long specimen, Nevada, USA (Štorch & others, 2011, fig. 18b and 14s, respectively). Scale bars, 1 mm.——Fig. 232,*3c–d. P. denticulatus* (Mu in Wang & others, 1977); *3c*, NIGP 57854, holotype; *3d,* NIGP 57807; scale bars, 1 mm (Mu & others, 1993, fig. 39a–b).——Fig. 232,*3e. P. nanus* (Mu in Mu & others, 1993), NIGP 57734, paratype, scale bar, 1 mm (Mu in Mu & others, 1993, fig. 38).

Rectograptus Přibyl, 1949, p. 25 [**Diplograptus pristis* var. *truncatus* Lapworth, 1877, p. 133; OD]. Peiragraptines with square proximal end, distally widening or largely parallel-sided tubarium, prominent antivirgellar spines and subapertural spine on th1^1 but not on th1^2; thecae with or without geniculum on proximal thecae or straight, outward-inclined ventral thecal walls and straight, everted apertures; sometimes with low lateral lappets on thecal apertures that may be lost distally; median septum lacking; proximal development of pattern G astogeny. *Upper Ordovician* (*Sandbian, Climacograptus bicornis* Biozone–*Hirnantian, Paraorthograptus pacificus* Biozone): worldwide.——Fig. 232,*2a*. **R. truncatus* (Lapworth) holotype (Lapworth, 1877, pl. 6,*17a* [specimen not identified, see Strachan, 1997, p. 72]).——Fig. 232,*2b–d. R. gracilis* (Roemer, 1861); *2b*, neotype, GPIT 1056/3, infrared photo, scale bar, 1 mm (Eisenack 1959, fig. 1); *2c–d*, NRM-PZ Cn 654, 885, isolated specimens, glacial boulder, Sweden, scale bars, 1 mm (Bulman, 1932a, pl. 7,*11* and 7,*10,* respectively).

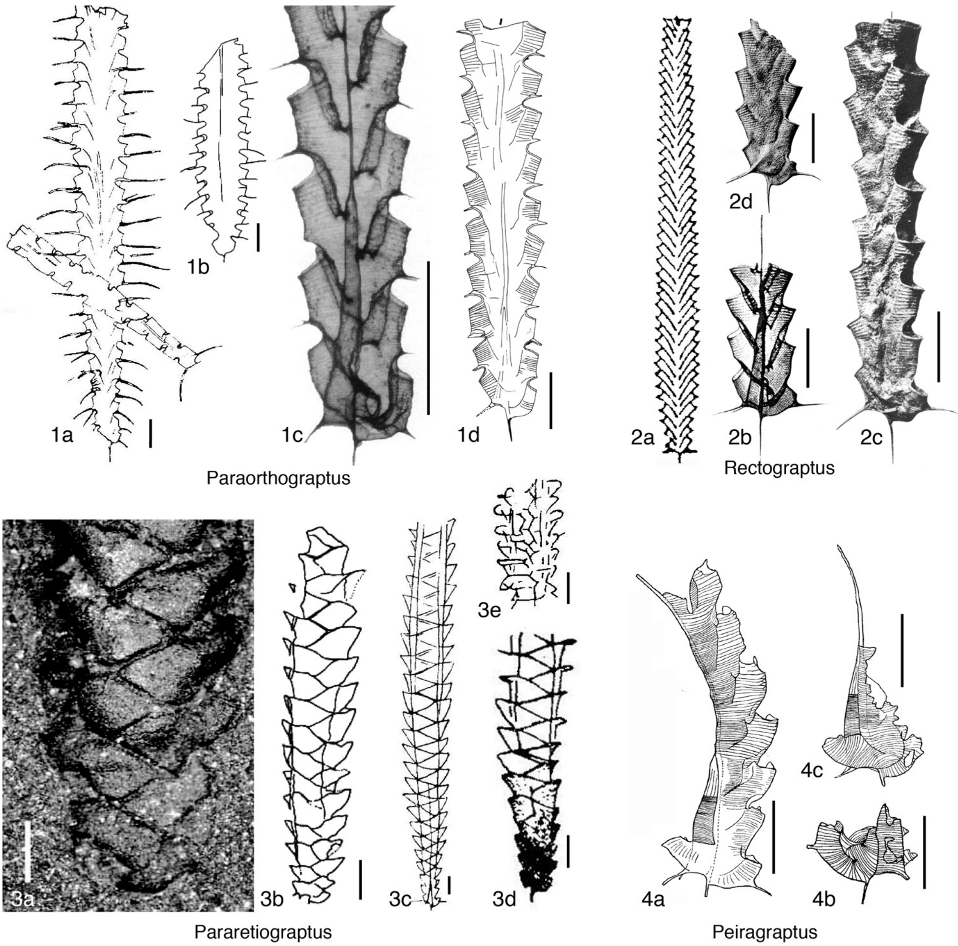

FIG. 232. Peiragraptinae (p. 340–344).

Family LASIOGRAPTIDAE Lapworth, 1879

[Lasiograptidae LAPWORTH, 1879c, p. 454] [=Hallograptidae MU, 1950b, p. 182; =Archiretiolitinae BULMAN, 1955, p. 88]

Biserial axonophorans with proximal development of pattern A astogeny or derived one (pattern L of MITCHELL and others, 2007); median septum complete to variable to lacking; thecal fusellum attenuated to absent; thecae with prominent lists (clathrium) and commonly bearing lacinia derived from genicular and lateral nemal spines or scopulae; thecae geniculate to highly stylized; polygonal reticulum may be present. *Upper Ordovician* (*Sandbian,* ?*Nemagraptus gracilis* Biozone–*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

MITCHELL, (1987, p. 382) defined the Lasiograptidae at the subfamily level and emended the diagnosis of LAPWORTH (1879c). MITCHELL and others (2007) and ŠTORCH and others (2011, p. 346) discussed the Lasiograptidae, based on a cladistic analysis. The taxon incorporates the genera previously included in the Archiretiolitinae as possible relatives of the Silurian Retiolitidae (see BULMAN, 1955).

BATES (1990) indicated that *Orthoretiolites*, *Phormograptus,* and *Pipiograptus* may not be closely related due to differences in their colony construction. Along with differently shaped thecae, *Orthoretiolites* has the nema embedded into the obverse side of the tubarium and lacks a lacinia. BATES and KIRK (1986) suggested that *Pipiograptus* may have

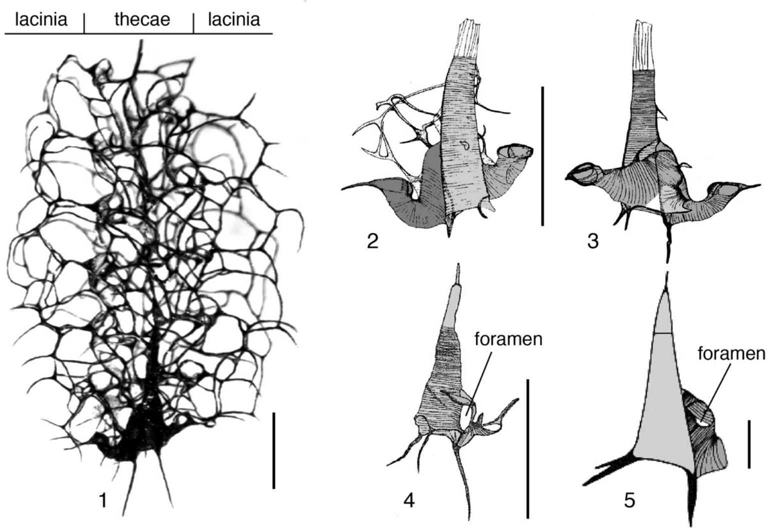

FIG. 233. Tubarium development in Lasiograptidae. *1–3,* Fusellum reduction and lacinia in *Pipiograptus hesperus* WHITTINGTON, 1955; *1,* photo of larger specimen, vaguely showing the thecal outline remains of the fusellum (Maletz, 2017a, fig. 11,8J); *2–3,* isolated paratype specimens showing part of proximal development, specimens from Viola Limestone, Oklahoma, USA (Whittington, 1955, fig. 12–13); *4, Orthoretiolites hami* WHITTINGTON, 1954, showing foramen for th1^2 (Whittington, 1954, fig. 5); *5, Lasiograptus harknessi* (NICHOLSON, 1867b), juvenile, showing foramen for th1^2 (Rickards & Bulman, 1965, fig. 3B). Scale bars, 0.5 mm.

been derived from a form such as *Dicaulograptus hystrix* (BULMAN, 1932a) based on the thecal construction, whereas MITCHELL (1988) discussed the constructional details in *Brevigraptus* and *Dicaulograptus* as indicating convergent evolution.

The proximal development is unknown in most Lasiograptidae due to the reduction of the fusellum. MITCHELL and others (2007) noted a pattern L astogeny in the Lasiograptidae, but this pattern has never been described. The proximal development in *Orthoretiolites, Brevigraptus,* and *Pipiograptus* is characterized by the lack of a reverse wall of th1^1 separating the foramen for th1^2 from the sicula (Fig. 233.3), thus differing from the development in taxa with a pattern G or pattern L astogeny (Fig. 233.5) (MITCHELL, 1987).

FUSELLUM REDUCTION

In many graptolites that are not phylogenetically closely related, the fusellum is reduced independently and is seldom preservable in fossils, e.g., in the Silurian Retiolitidae (LENZ & others, 2018), in the Abrograptidae (MALETZ, ZHANG, & VANDENBERG, 2018), or in some Glossograptina (see *Cryptograptus* in MALETZ & ZHANG, 2016). A reduction of the fusellum is also visible, for example, in some climacograptids (MITCHELL, 1987) in the lack of a preservable prosicula in a number of genera (e.g., *Diplacanthograptus* MITCHELL, 1987).

A reduction of the thickness of the thecal walls is common in members of the Lasiograptidae (Fig. 233.1) but should not be confused with the presence of the lacinia, a secondary development formed from branching lists outside the original tubarium construction (BATES & KIRK, 1991). In the early lasiograptids (e.g., *Hallograptus, Lasiograptus*), the fusellum is attenuated but is preservable in the fossil record, and it is possible to easily recognize the proximal development and thecal style. Other taxa show an extreme reduction of the fusellum, with the thecae visible only as an outline of thecal lists (clathrium), associated in some with the development of a variably formed reticulum. This development should not be confused with the lacinia developed from thecal spines and surrounding at least parts of the colonies. In *Pipiograptus* (Fig. 233.1–233.3), the sicula and the first thecal pair preserve the fusellum, but the later thecae do not. A further reduction leads to the complete loss of preservable fusellum of the colonies; and as a result, the proximal development is not easy to discern. Only the sicula is completely preserved in all taxa of the clade.

THE LACINIA

The lacinia is a development of a meshwork of lists outside the fusellar walls of the tubarium. The presence of a lacinia (Fig. 233.1) is well known from chemically isolated material of a number of lasiograptids (e.g., Whittington, 1955; Mitchell & others, 2007), but the details of the construction of the lacinia are unknown. Bates and Kirk (1991) demonstrated the development of the lacinia surrounding the colonies on all sides in the genera *Pipiograptus* and *Phormograptus*. The lacinia is attached to the tubarium by lateral apertural spines and spines originating from the sides of the colonies, often termed scopulae. There appears to be no membrane associated with the lacinia in the manner of the ancora sleeve of the retiolitids (Lenz & others, 2018), and the rods of the lacinia have circular cross sections (Bates, 1987a; Bates & Kirk, 1987). Most lacinate taxa are known only from flattened shale specimens, which makes the interpretation of the construction difficult and unreliable, leaving details of their evolutionary relationships unexplained.

Lasiograptus Lapworth, 1873b, p. 559 [**L. costatus;* OD] [=*Thysanograptus* Elles & Wood, 1908, p. 325 (type, *Diplograptus harknessi* Nicholson, 1867b, p. 262), syn. by Bulman, 1970, p. 126]. Lasiograptids with proximally widening, distally parallel-sided tubarium and rounded proximal end; median septum complete; proximal development of pattern G astogeny; thecae showing inwardly inclined supragenicular wall and single or paired genicular or mesial spines; clathria weakly developed in some taxa; possibly paired septal processes or scopulae visible in scalariform view in some taxa. *Middle Ordovician* (*upper Darriwilian, Jiangxigraptus vagus* Biozone)–*Upper Ordovician* (*Katian, Climacograptus bicornis* Biozone): worldwide(?).——Fig. 234,*3a*. **L. costatus*, BU 1341, lectotype, Dob's Linn, Scotland (adapted from Hughes, 2000, Atlas, Folio 1.35).——Fig. 234,*3b–c*. *L. harknessi; 3b,* isolated specimen, reverse view, Laggan Burn, Ayrshire, UK (Bulman, 1947, pl. 8,*11*); *3c,* reconstruction in reverse view (Rickards & Bulman, 1965, fig. 3). Scale bars, 1 mm.

Archiretiolites Eisenack, 1935, p. 74 [**A. regimontanus;* M]. Lasiograptids with highly asymmetrical proximal end; proximal end astogeny unknown; sicula with single antivirgellar spine; tubarium reduced to clathrial lists and coarse reticulum with the sicula and the initial part of th1^1 preserved as complete fusellum; presence of lacinia uncertain; central virgella attached to clathrial thecal lists. *Upper Ordovician* (*Sandbian,* ?*Nemagraptus gracilis* Biozone): Estonia, Germany, Sweden (glacial boulder).——Fig. 234,*1a–d*. **A. regimontanus; 1a–c,* holotype, proximal end in reverse (*a*) and obverse (*b*) views, complete specimen in obverse view (*c*); *1d,* juvenile, showing development of thecal lists in th1^1; scale bars, 1 mm (Eisenack, 1935, pl. 6).

Brevigraptus Mitchell, 1988, p. 450 [**B. quadrithecatus;* OD). Small lasiograptids with finite growth, bearing maximum of five to six thecae; fusellum attenuated and clathria well developed; sicula with single antivirgellar spine; proximal development probably of pattern G astogeny; thecae with birds-head construction of the apertures, bearing branched subapertural or mesial spines; lateral spines present on reverse and obverse side of tubarium; lacinia lacking. *Upper Ordovician* (*Katian, Diplacanthograptus caudatus* Biozone): USA.——Fig. 234,*7a–c*. **B. quadrithecatus; 7a–b,* holotype, MCZ 9437, in obverse (*a*) and reverse (*b*) views; *7c,* MCZ 9438, reverse view; Carter County, Oklahoma, USA; scale bars, 1 mm (adapted from Mitchell, 1988, fig. 5,*11–13*).

Hallograptus Lapworth, 1876a, p. 7 [**Diplograptus bimucronatus* Nicholson, 1869, p. 236]. Lasiograptids with proximally widening, distally parallel-sided tubarium and square proximal end; proximal development possibly of pattern A astogeny; thecae with short, inwardly inclined supragenicular walls and single or paired genicular spines; clathria weakly developed; paired septal processes or scopulae visible in scalariform view. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide(?).——Fig. 234,*2a*. **H. bimucronatus* (Nicholson) Glenkiln Shale, Scotland, scale bar, 1 mm (Bulman, 1970, fig.93,*2a*).——Fig. 234,*2b–d*. *H. mucronatus* (Hall, 1847); *2b*, Glenkiln Shale, Scotland (Bulman, 1970, fig. 93,*2b*); *2c–d,* isolated specimens in reverse view, showing possible pattern A astogeny, Dalby Limestone, Skövde, Västergötland, Sweden, scale bars, 1 mm (new; drawings by C. E. Mitchell).

Neurograptus Elles & Wood, 1908, p. 320, =*Neurograptus* Lapworth in Hopkinson & Lapworth, 1875, p. 641, *nom. nud.* [**Retiolites fibratus* Lapworth, 1876a, fig. 62]. Lasiograptids

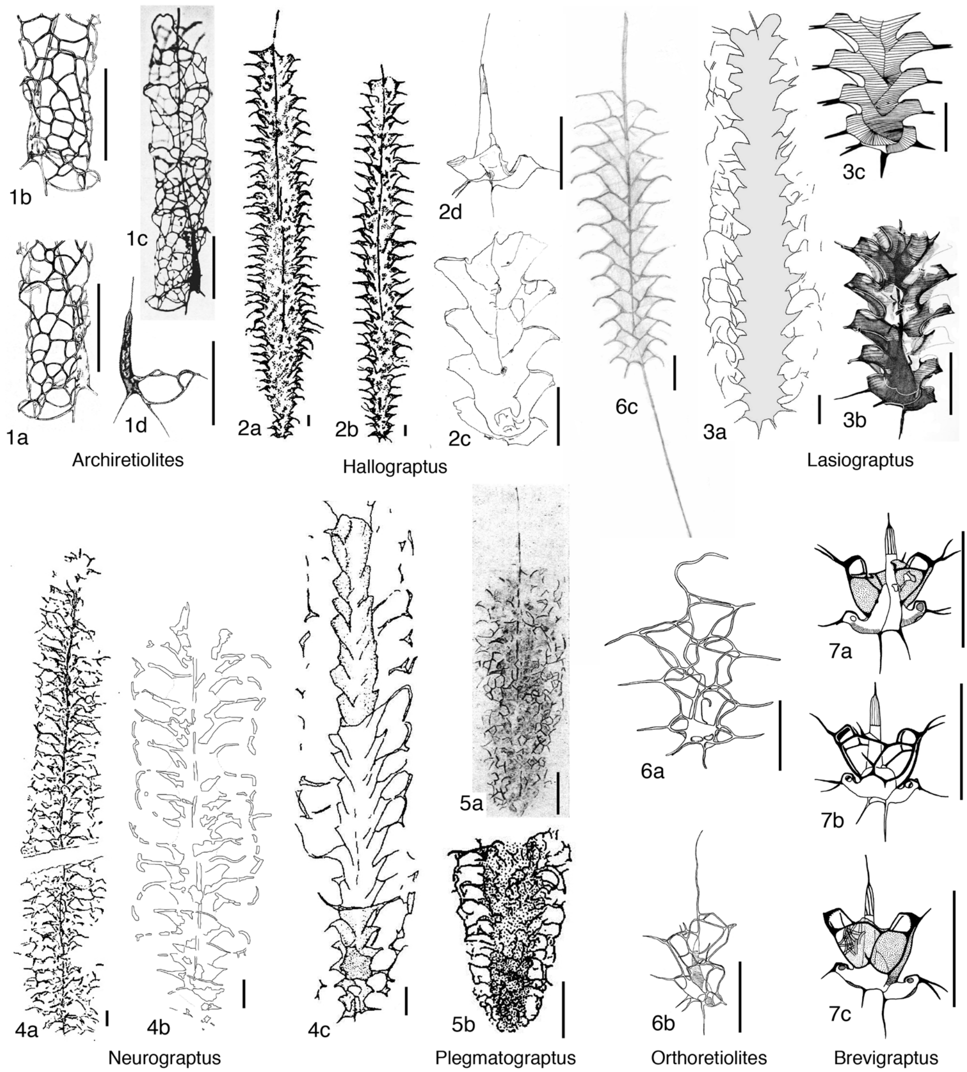

FIG. 234. Lasiograptidae (p. 346–349).

with proximally widening, distally parallel-sided tubarium and square proximal end; proximal development probably of pattern G astogeny; thecae with single or paired apertural spines as the base of a simple lacinia development on the ventral tubarium sides; septal processes or scopulae visible in scalariform view. [BULMAN (1929, p. 179) selected *Lasiograptus margaritatus* LAPWORTH, 1876a (pl. 2,*60*) as genolectotype of *Neurograptus* in consent with G. ELLES. The species may be a synonym of *N. fibratus* (VANDENBERG & COOPER, 1992, p. 82).] *Upper Ordovician* (*Katian, Dicranograptus clingani* Biozone): Australia, China, UK, Norway, Canada, USA.——FIG. 234,*4a–c*. **N. margaritatus* (LAPWORTH); *4a,* BU 1351, holotype of *Retiolites fibratus* LAPWORTH, 1876a (Elles & Wood, 1908, pl. 34,*5a*); *4b,* lectotype, BU 1353a, Dob's Linn, Scotland (Wilkinson, 2018a); *4c,* PMO 108.905, obverse view, Oslo Region, Norway (Williams & Bruton, 1983, fig. 24c). Scale bars, 1 mm.

Nymphograptus ELLES & WOOD, 1908, p. 320, *ex* subgenus *Lasiograptus* (*Nymphograptus*) ELLES & WOOD, 1908, p. 320 [**L.* (*N.*) *velatus;* OD] [=*Yangzigraptus* MU in YANG & others, 1983, p. 492 (type, *Y. yangziensis,* OD), syn. herein]. Lasiograptids with strongly developed lacinia on reverse and obverse sides formed from septal bars (scopulae) extending far outward and upward from

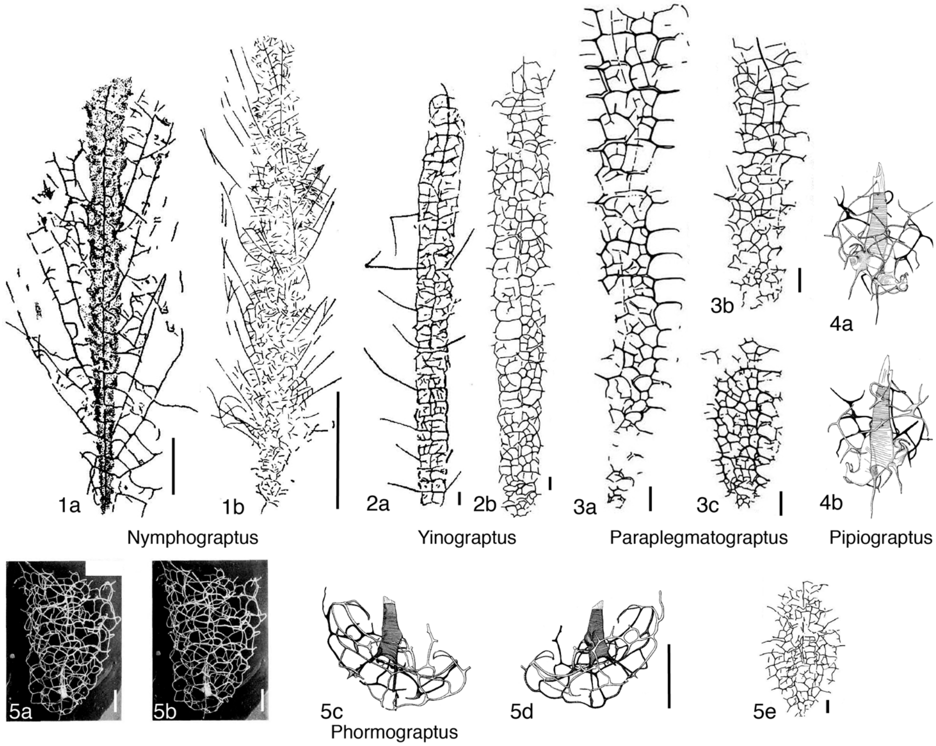

FIG. 235. Lasiograptidae (p. 348–349).

thecate part of the tubarium; fusellum strongly attenuated; thecal style and proximal development unknown. *Upper Ordovician* (*Katian, Dicellograptus anceps* Biozone): Kazakhstan, China, UK.——FIG. 235,*1a*. **N. velatus* (ELLES & WOOD), BGS GSE 10856, lectotype (selected by KOREN', TZAI, & MIKHAILOVA, 1980, p. 164), Ettrickbridge End, Scotland, UK, scale bar, 10 mm (Bulman, 1970, fig. 93,*4*).——FIG. 235,*1b*. *N. yangziensis* (MU & others, 1993), holotype, NIGP 57843, scale bar, 10 mm (Mu & others, 1993, fig. 59).

Orthoretiolites WHITTINGTON, 1954, p. 613 [**O. hami;* OD]. Lasiograptids with strongly reduced fusellum and thickened clathrial lists outlining colony; nema embedded into obverse wall of colony; proximal development unknown; thecal apertures simple, outward inclined with centrally positioned single apertural spine which may be branched distally; paired nemal spines or scopulae present at regular distances along nema. *Upper Ordovician* (*Katian, Diplacanthograptus caudatus* Biozone): Australia, Canada, USA.——FIG. 234,*6a–b*. **O. hami,* Oklahoma, USA; *6a,* holotype, MCZ 511; *6b,* paratype, MCZ 512h; scale bars, 1 mm (Whittington, 1954, fig. 4,*12*).——FIG. 234,*6c*. *Orthoretiolites* sp., GSC 141089a, flattened specimen with long virgella, Bald Mountain core, Quebec, Canada, scale bar, 1 mm (new, original drawing by John F. Riva).

Paraplegmatograptus MU & LIN, 1984, p. 66 [*non Paraplegmatograptus* MU, 1963b, p. 365, *nom. nud.*, ŠTORCH & others, 2011, p. 348] [**P. uniformis* MU in WANG, 1978, p. 210; OD]. Lasiograptids with obverse and reverse walls reduced to irregular clathrium consisting of lateral lists, indistinct dorsal lists, and well-defined reticulum; prominent lacinia that surrounds sicular aperture and is confined to apertural margins of colony; nema possibly unconnected. *Upper Ordovician* (*Katian, Dicellograptus ornatus* Biozone–*Hirnantian, Metabolograptus extraordinarius* Biozone): China, USA.——FIG. 235,*3a–c*. **P. uniformis*, Vinini Formation, Nevada, USA. *3a,* USNM 542769, long fragment in lateral view; *3b,* USNM 542705, proximal end; *3c,* USNM 542766; scale bars, 1 mm (Štorch & others, 2011, fig. 16,*a,c,q,* respectively).

Phormograptus WHITTINGTON, 1955, p. 846 [**P. sooneri;* OD] [=*Arachniograptus* ROSS & BERRY, 1963, p. 159 (type, *A. laqueus,* M), syn. by ŠTORCH & others, 2011, p. 348]. Lasiograptids with thecal framework consisting of lightly thickened dorsal lists, apertural lists, and aboral lists; dorsal lists linked to nema by scopular spines; ventral lists absent; lacinia encloses entire tubarium forming complex, and usually dense, three-dimensional mesh along obverse and reverse side of colony and with regular apertural openings along pleural margin of colony; proximal development unknown as only sicula is fully sclerotized. *Upper Ordovician* (*Katian, Diplacanthograptus caudatus* Biozone–*Metabolograptus persculptus* Biozone): China, Czech Republic, USA.——FIG. 235,*5a–d*. **P. sooneri; 5a–b,* stereopair of small specimen (Bates & Kirk, 1987, fig. 4a); *5c–d,* holotype in reverse (*c*) and obverse (*d*) views, Oklahoma, USA (Whittington, 1955, fig. 17–18). Scale bars, 1 mm.——FIG. 235,*5e. P. connectus* (MU in WANG & others, 1977), USNM 542742, small specimen showing colony shape, Vinini Formation, Nevada, USA, scale bar, 1 mm (Štorch & others, 2011, fig. 16b).

Pipiograptus WHITTINGTON, 1955, p. 839 [**P. hesperus;* OD]. Lasiograptids with sicula, much of th1^1 and th 1^2 and initial part of th2^1 sclerotized; later thecae coarsely reticulate, clathrium not clearly differentiated from extensive development of lacinia; thecal characters imperfectly known, but th2^1 with initial downward direction of growth; proximal development type probably of pattern G astogeny. *Upper Ordovician, Katian* (*Diplacanthograptus caudatus* Biozone): USA.——FIG.235,*4a–b*. **P. hesperus,* holotype, MCZ 521, in reverse (*a*) and obverse (*b*) views, Oklahoma, USA, scale bars, 1 mm (Whittington, 1955, fig. 12–13).

Plegmatograptus ELLES & WOOD, 1908, p. 340, *ex* subgenus *Retiolites* (*Plegmatograptus*) ELLES & WOOD, 1908, p. 340 [**Retiolites* (*Plegmatograptus*) *nebula* ELLES & WOOD, 1908, p. 337, 340; OD]. Lasiograptids with reticulum and well-developed lacinia; fusellum strongly attenuated or lacking; details of development unknown. *Upper Ordovician* (*Katian, Dicranograptus clingani* Biozone–*Pleurograptus linearis* Biozone): Australia, China, UK, USA.——FIG. 234,*5a–b*. **P. nebula; 5a,* lectotype (selected by WILLIAMS, 1982b, p. 253), BGS GSE 5615, Hartfell Shale, Scotland, UK (Elles & Wood, 1908, fig. 222b); *5b,* BGS GSE 5539, Hartfell Shale, Scotland (Bulman, 1970, fig. 95,*4*). Scale bars, 1 mm.

Yinograptus MU in MU & CHEN, 1962b, p. 112 [**Gothograptus*? *disjunctus* YIN & MU, 1945, p. 216; OD] [=?*Sunigraptus* MU in MU & others, 1993, p. 247 (type, *S. regularis,* OD), syn. herein; based on poor, indeterminable fragments]. Lasiograptids with obverse and reverse walls reduced to regular clathrium consisting of lateral lists and dorsal lists; sparse planar reticulum linked to nema by prominent spines or scopulae; scopulae project outward from lateral walls at regular intervals, generally at every fourth thecal pair; somewhat delicate lacinia surrounds the sicular region and is confined to apertural margins of colony more distally; proximal development unknown. *Upper Ordovician* (*upper Katian, Dicellograptus ornatus* Biozone–*Paraorthograptus pacificus* Biozone): China; USA.——FIG. 235,*2a–b*. **Y. disjunctus; 2a,* holotype, NIGP 57816, apertural view showing scopular spines (Mu & others, 1993, fig. 53a); *2b,* USNM 542767, lateral view, Roberts Mountains, Nevada, USA (Štorch & others, 2011, fig. 16o). Scale bars, 1 mm.

Family CLIMACOGRAPTIDAE Frech, 1897

[Climacograptidae FRECH, 1897, p 607, *nom. transl. ex.* Familie Climacograptidi FRECH, 1897, p. 607] [=superfamily Climacograptoidea FRECH *sensu* ŠTORCH & others, 2011, p. 353; =Pseudoclimacograptidae MITCHELL, 1987 (in press version), FORTEY & COOPER, 1986, p. 652, *nom. nud.*]

Biserial, dipleural axonophorans; metasicular origin of th1^1; proximal end square to highly asymmetrical, generally provided with virgellar spine as only proximal end spine, but secondarily developed thecal spines on first thecal pair or only on th1^1 may be present; proximal development type of pattern C astogeny or progressively more derived pattern; tubarium commonly twisted longitudinally; thecae with distinct geniculum; intrathecal folds externally expressed through crossbars and with strongly zigzag-shaped median septum in early taxa; straight median septum and straight, short thecae with crossbars in derived taxa; median septum may be delayed or lacking altogether; parasiculae and parathecae common. *Middle Ordovician* (*lower Darriwilian, Levisograptus dentatus* Biozone)–*Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

The family Climacograptidae originally included the genus *Climacograptus,* the Dicranograptidae, and Glossograptidae. It also included the monograptid genus *Monoclimacis* and was based entirely on the climacograptid (geniculate) thecal outline (see FRECH, 1897). BULMAN (1955, 1970) included the genus *Climacograptus* in the Diplograptidae, whereas ŠTORCH and others (2011), in their latest revision, referred the climacograptids to the superfamily Climacograptoidea.

A recent cladistic analysis of the Climacograptidae does not exist. The analysis of CONE (2004) was discussed in ŠTORCH and others (2011) but has never been published. The family Climacograptidae (Fig. 236) includes a well-defined group of derived Darriwilian to Hirnantian (Upper Ordovician) taxa united by a number of synapomorphies, but the early members are less easily defined and analyzed. MITCHELL and others

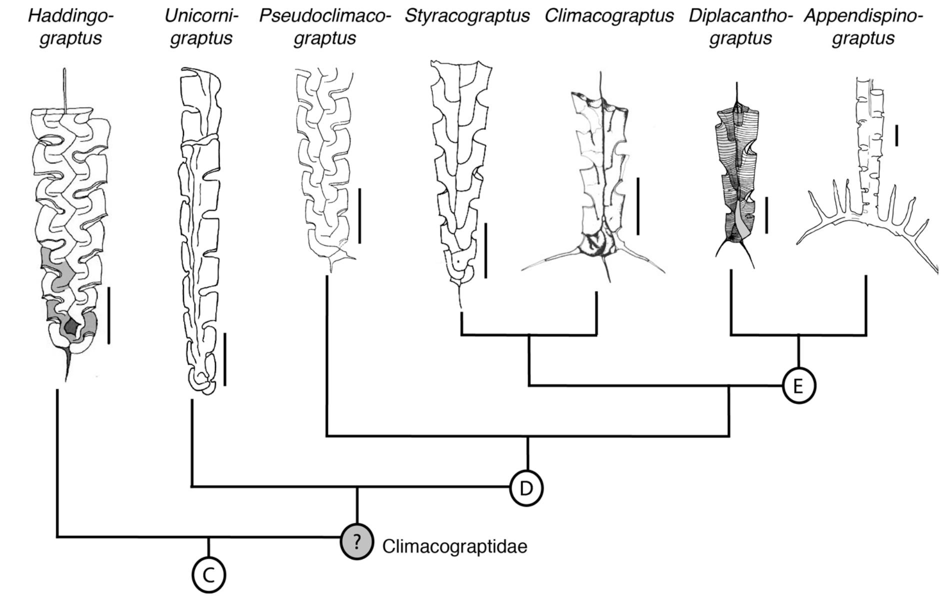

FIG. 236. Interpretation of the evolutionary relationships of the Climacograptidae, showing presence of the proximal development patterns C–E, scale bars, 1 mm (new; based on data from CONE, 2004; MITCHELL & others, 2007; MALETZ, 2011b).

(2007) performed a cladistic analysis of the Axonophora but did not publish any data supporting the analysis and did not provide a definition of the family Climacograptidae. ŠTORCH and others (2011, fig. 6) modified the cladistic tree of MITCHELL and others (2007) to define the Neograptina but also did not include data to support the diagram. Thus, the basis for the differentiation of the Diplograptina and Neograptina is unclear, as is the inclusion of early taxa referred to the Neograptina by ŠTORCH and others (2011) and the position of the Climacograptidae.

ŠTORCH and others (2011, fig. 6) discussed *Undulograptus formosus* (MU & LEE, 1958) as the earliest member of the Neograptina and, thus, of the Normalograptidae; whereas MALETZ (2011d, fig. 3) and MALETZ (2014b) regarded the genera *Undulograptus, Oelandograptus,* and *Proclimacograptus* as early member of the Climacograptidae. MALETZ (2011d) suggested a derivation of *Pseudoclimacograptus* and its descendants from an ancestor such as *Haddingograptus* (Fig. 236). Instead of an inclusion with the Diplograptina, the Climacograptidae then may alternatively be referred to the Neograptina. In this interpretation, the mesial to subapertural spines on the derived Climacograptidae would have originated secondarily from a spineless ancestor.

CHEN and GOLDMAN (in CHEN & others, 2016) referred the genus *Unicornigraptus* with its pattern C astogeny to the Climacograptidae. The species of this genus has a virgellar spine and a spine on th1^1 but not on th1^2 and represent the earliest climacograptids. Their development resembles the development in *Pseudoclimacograptus scharenbergi* (LAPWORTH, 1876a), with its pattern D astogeny, but still bears an exposed patch of the crossing canal of th1^2, indicating a typical pattern C astogeny (Fig. 236).

MORPHOLOGY

Sicular Development

The sicula of the Climacograptidae is short (less than 1.5 mm long) and widens rapidly in all members of the clade from which the sicula is known in isolated speci-

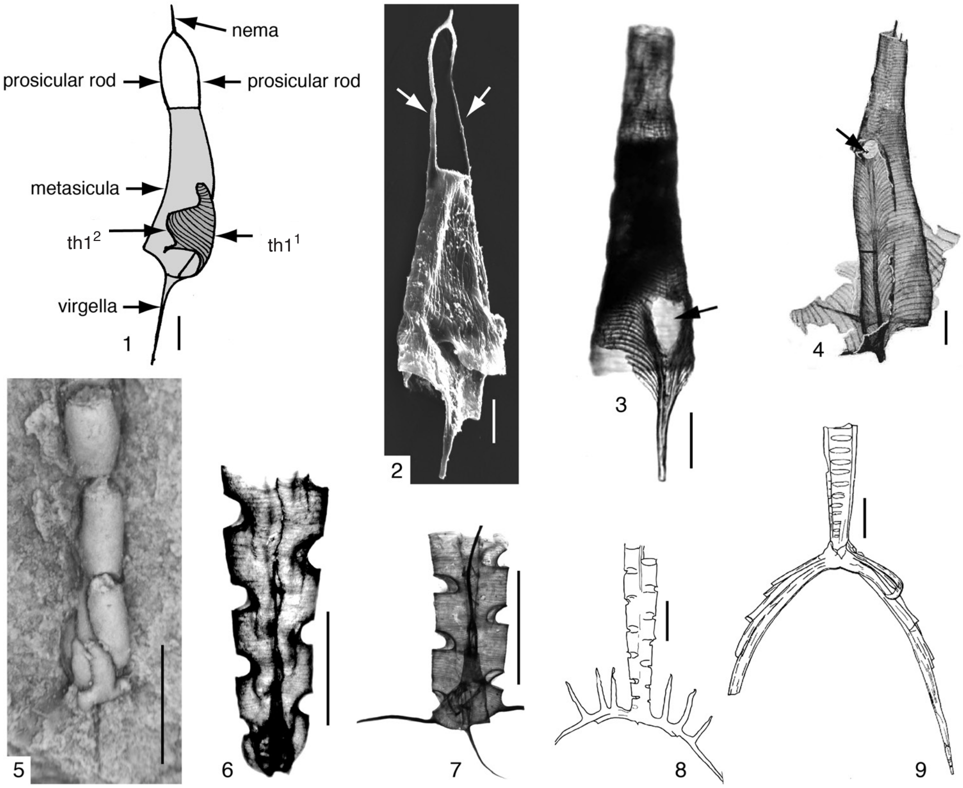

FIG. 237. The sicula and proximal development in the Climacograptidae. *1, Diplacanthograptus spiniferus* (RUEDEMANN, 1912), sicula showing curvature and initial parts of th1^1 and th 1^2 (Mitchell, 1987, fig. 7E); *2, Diplacanthograptus spiniferus*, SMF 75834, SEM photo, sicula showing two rods instead of prosicula, note cortical bandages on metasicula (new); *3, Appendispinograptus supernus* ELLES & WOOD, 1906, sicula showing central origin of th1^1 foramen (Loxton & others, 2011, fig. 1J); *4, ?Pseudoclimacograptus scharenbergi stenostoma* (BULMAN, 1947), juvenile with central position of th1^1 foramen (Bulman, 1947, pl. X,*3*); *5, Appendispinograptus supernus*? (ELLES & WOOD, 1906), proximal end with parasiculae, NIGP 139881, Honghuanyuan section, Tongzi, Guizhou Province, China, *Dicellograptus complanatus* Biozone (new); *6, Styracograptus tubuliferus* (LAPWORTH, 1876a), proximal end showing only the presence of a virgellar spine (Goldman & others, 2011, fig. 1G); *7, Climacograptus cruciformis* VANDENBERG, 1990, showing mesial spines on first thecal pair, Viola Limestone (Maletz, 2017a, fig. 11,13F); *8, Appendispinograptus venustus* (HSÜ, 1959a), AFA 84 (NIGP material), Wangjiawan section, Wufeng Formation (Mitchell, Chen, & Finney, 2007, fig. 1,*4*); *9, Appendispinograptus longispinus* (T. S. HALL, 1902), AMNH 29267, Toquima Range, Nevada, USA (Riva, 1974a, fig. 4c). All scale bars, 1 mm.

mens. It is straight in early members but has a distinct curvature and twisting in the genus *Diplacanthograptus* (Fig. 237.1) and related taxa. *Climacograptus* and *Appendispinograptus* may have a short virgella curved or bent across the sicular aperture, but the sicula is not curved noticeably in these cases. The prosicula is poorly or incompletely preserved in many early members of the Climacograptidae (MITCHELL, 1987). In derived taxa, the prosicula is not preserved as a membrane but as one or two cortical rods, forming the outline of the prosicula (Fig. 237.2). These rods are homologous to the longitudinal rods in completely formed prosiculae of other Axonophora. Additional longitudinal rods on the prosicula are not present in the Climacograptidae. WILLIAMS and CLARKE (1999) described the rods in *Diplacanthograptus spiniferus* (RUEDEMANN, 1912) as secondary longitudinal ridges attached to the metasicula by radiating cortical bandages.

Mitchell (1987, fig. 6A–B) figured specimens identified as *Pseudoclimacograptus scharenbergi* from the Balclatchie beds of Scotland lacking the prosicula, which is replaced by a single rod and possessing a distinctly twisted metasicula.

The position and exact development of the primary porus is unknown in most taxa of the Climacograptidae but is assumed to be of the resorption style, positioned on the right side of the virgella, as in *Diplacanthograptus spiniferus* (Mitchell, 1987, fig. 7E–F). However, the resorption porus in *Appendispinograptus* is formed in a position directly on the virgellar axis (Fig. 237.3). The origination of virgella occurred late in this taxon and formed only at a point after the development of the porus (see Loxton & others, 2011). Bulman (1947) described a similar development in a juvenile of *Pseudoclimacograptus scharenbergi stenostoma* (Fig. 237.4).

A parasicula is commonly present in the Climacograptidae and can reach a considerable length. Some species of the genus *Appendispinograptus* developed a candle-like complex of secondary tubes on the proximal end, called parathecae (Fig. 237.5, Fig. 237.8). These have been identified as tubes only through the record of a single three-dimensionally preserved specimen of *Appendispinograptus supernus*? (Elles & Wood, 1906) (Mitchell, Chen, & Finney, 2007). The development of parasiculae and parathecae in *Appendispinograptus* is highly variable (Fig. 237.8–237.9) and unreliable for taxonomic identification (see Loxton & others, 2011, p. 259). Parathecae are present in some mature specimens of *Climacograptus bicornis* (Hall, 1847) (Bulman, 1947, fig. 30).

Thecal Development

All thecae, except for the first thecal pair, possess a distinct geniculum in the Climacograptidae. The geniculum may be provided with a genicular flange or be rounded without elaborations. The supragenicular wall may be vertical, inward- or outward-sloping or convexly curved. Also, the thecal apertures vary in their orientation from introverted through horizontal to everted. The strong zigzag shape of the median septum of *Pseudoclimacograptus scharenbergi* (Fig. 236; Fig. 238.7) has been regarded as typical of climacograptids, but is now known to be restricted to earlier taxa in which intrathecal folding is pronounced and strong crossbars are present.

The derivation of a pattern D astogeny from a pattern C astogeny (Fig. 238.1) is unknown. The pattern D astogeny is based on the presence of a robust, short and wide sicula with massive crossing canals. Most probably the crossing canal of $th2^1$ was aborted at an early stage and formed a list leaving a characteristic list scar on the ventral surface, easily visible in specimens of *Pseudoclimacograptus* (Fig. 238.8) and derived taxa with pattern D astogeny. The distal development of $th2^1$ and 2^2 started with an upward-growing flange on the dorsal side of the early part of $th1^2$ (Fig. 238.9). This flange grew as a wide construction upward across the aborted crossing canal of $th2^1$ and distally differentiated into the thecal tubes of $th2^1$ and $th2^2$ (Fig. 238.10). In the pattern E astogeny, a further reduction of the crossing canals occurred. The development of a flange as the last remains of the crossing canal of $th1^2$ was abandoned at an early stage. A new flange was secreted at the point where $th1^1$ began to grow upward and formed into the upward-growing $th1^2$ (Fig. 238.12). The differentiation of $th2^1$ is in the distal, upward-growing part of $th1^2$.

The Climacograptidae possessed a variable number of proximal end spines, and the virgella is the only consistent presence of a spine in the colonies. Subapertural to mesial spines can be present on $th1^1$ and $th1^2$ as in *Climacograptus,* but they often are present only on $th1^1$ as in *Diplacanthograptus* or may be lacking altogether as in *Styracograptus* (see Fig. 236). The spines are outward- or downward-directed, depending on their position in the colony and can reach a considerable length (VandenBerg, 1990).

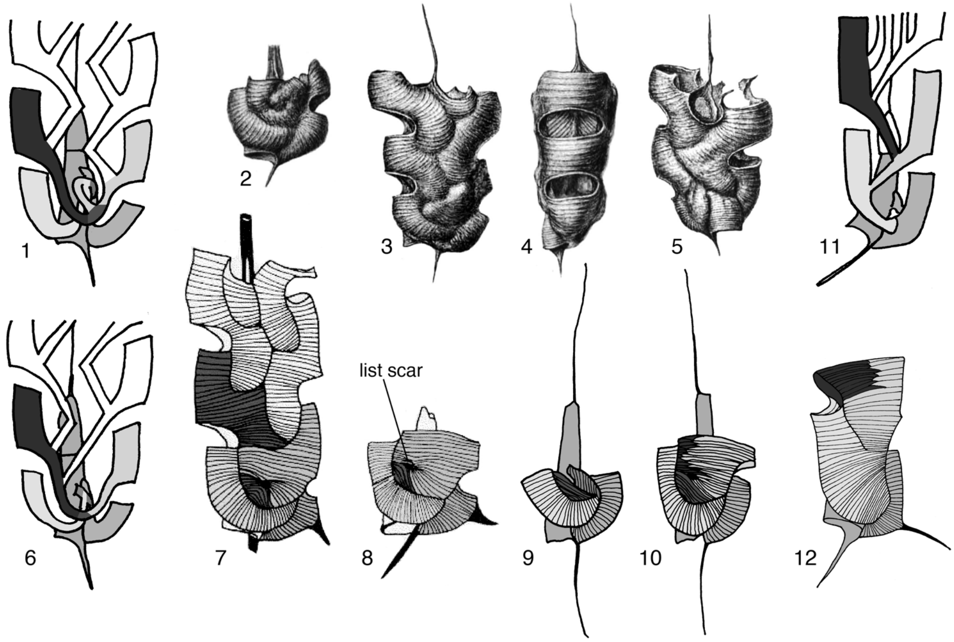

FIG. 238. Proximal development types in *Haddingograptus* MALETZ, 1997a and the Climacograptidae. *1, 6, 11,* pattern C, D, E astogenies (based on Mitchell, 1987); *2–5, Haddingograptus eurystoma* (JAANUSSON, 1960), pattern C astogeny (Bulman, 1932a, pl. 1); *7–8, Pseudoclimacograptus scharenbergi* (LAPWORTH, 1876), pattern D astogeny, reconstructions (adapted from Mitchell, 1987, fig. 6F, I); *9–10, Styracograptus tubuliferus* (LAPWORTH, 1876a) pattern D astogeny (specimens identified as *Climacograptus* (*Climacograptus*) sp. cf. *C.* (*C.*) *caudatus* by MITCHELL, 1987; GOLDMAN & WRIGHT, 2003); *12, Diplacanthograptus spiniferus* (RUEDEMANN, 1912), reverse view (adapted from Mitchell, 1987, fig. 7L). Specimens not to scale.

Torsion

The tubaria of many climacograptids (e.g., *Diplacanthograptus*, *Appendispinograptus*) appear to possess considerable torsion (VANDENBERG, 1990) that might be related to the torsion already visible in the sicular curvature (Fig. 237.1). A moderate torsion of the colonies may already be present in *Climacograptus bicornis, Climacograptus cruciformis* (VANDENBERG, 1990), and *Diplacanthograptus lanceolatus* (VANDENBERG, 1990), as described by VANDENBERG (1990). LOXTON and others (2011) suggested that the torsion is a taphonomic consequence of the presence of parasiculae and not an independent character of the colonies because torsion appears to be absent in specimens of *Appendispinograptus supernus* without parasiculae. However, the authors noted that the mesial spine on th1[1] in *A. supernus* is off-profile (LOXTON & others, 2011, p. 254). The strong torsion is also visible in specimens of *Appendispinograptus longispinus* (T. S. HALL, 1902) from Nevada (USA), which show the proximal spines in a symmetrical position, whereas the distal part of the colony attains a scalariform view (see RIVA, 1974a).

Climacograptus HALL, 1865, p. 111 [**Graptolithus bicornis* HALL, 1847, p. 268; OD] [=*Mendograptus* RUSCONI, 1948, p. 247 (type, *M. inversus*, M), syn. by TORO & BRUSSA, 2007, p. 233; =*Euclimacograptus* RIVA & KETNER, 1989, p. 82 (type, *Climacograptus hastata* T. S. HALL, 1902, p. 54, OD), syn. by ŠTORCH & others, 2011, p. 354]. Climacograptids with pattern D proximal astogeny; thecae sharply geniculate, with straight supragenicular walls, simple deep semi-circular thecal excavations, and short thecal overlap; complete median septum weakly undulose to straight; subapertural to mesial spines on first pair of thecae; proximal membranes and parasiculae in mature specimens. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone–*Katian, Paraorthograptus pacificus* Biozone):

worldwide.——FIG. 239,*1a–d*. **C. bicornis* (HALL), *1a,* lectotype, AMNH 1030a, Austin Glen Greywacke, left bank of Normans Kill, Kenwood, New York, USA (Riva, 1974a, pl. 1,*1*); *1b,* topotype, AMNH 29386, small specimen in obverse view (Riva, 1974a, fig. 1a); *1c,* topotype, AMNH 29390, proximal end with membranes (Riva, 1976, fig. 5f); *1d,* NMV P63487, showing torsion of tubarium, Warbisco Shale, east Gippsland, Victoria, Australia (VandenBerg, 1990, fig. 3a). Scale bars, 1 mm.——FIG. 239,*1e*. *Climacograptus hastatus* (T. S. HALL, 1902), lectotype, AMF46104, *Dicellograptus ornatus* Biozone, Stockyard Flat Creek, New South Wales, Australia, scale bar, 1 mm (Riva & Ketner, 1989, fig. 9a).

Alulagraptus CHEN, CHEN, MITCHELL, CHEN, & ZHANG, 2019, p. 1189 [**Climacograptus uncinatus* KEBLE & HARRIS, 1934; OD]. Climacograptid with complete median septum; proximal development pattern unknown; proximal end rounded with virgella as only proximal end spine; single pair of scopuli branching from nema; scopuli may bear vane-like appendages. *Upper Ordovician* (*Katian, Dicellograptus complanatus* Biozone): Australia, China, North America.——FIG. 239,*3a*. **A. uncinatus* (KEBLE & HARRIS), lectotype, NMV P 14401A, Bolindian, *Alulagraptus uncinatus* Biozone, Yarra Track, between Matlock and Oaks, Victoria, Australia, scale bar, 1 mm (new; drawing by Jörg Maletz, based on photo provided by F. VandenBerg).——FIG. 239,*3b*. *A. ensiformis* (MU & ZHANG in MU & others, 1963), holotype, NIGP 11749, *Appendispinograptus longispinus* Biozone, Xiehao Formation, East Qiqiaogou section, Chilianshan, northwest China, scale bar, 1 mm (new, redrawn from Chen & others, 2019, fig. 10,*4*).

Appendispinograptus LI & LI, 1985, p. 36, *ex Climacograptus* (*Appendispinograptus*) LI & LI, 1985, p. 36, RIVA & KETNER, 1989, p. 77 [**Climacograptus venustus* HSÜ, 1959, p. 346; OD] [=*Leptothecalograptus* LI in MU & others, 2002, p. 677 (type, *Climacograptus leptothecalis* MU & GEH in FU, 1982, p. 456, OD), syn. herein]. Septate to aseptate climacograptids with distinct torsion of the tubarium and pattern E astogeny; th2^2 or later theca dicalycal in septate species; mesial spines arise from first thecal pair; secondary thecal parasicular outgrowths or webs common. *Upper Ordovician* (*Katian, Dicellograptus ornatus* Biozone–*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.——FIG. 239,*2*. **A. venustus* (HSÜ), holotype, No 519, Wufeng Shale, Hubei Province, China, scale bar, 1 mm (adapted from Hsü, 1959a).

Diplacanthograptus MITCHELL, 1987, p. 388 [**Climacograptus spiniferus* RUEDEMANN, 1912, p. 84; OD (=*Climacograptus typicalis* mut. *spinifer* RUEDEMANN, 1908, p. 411)] [=*Ensigraptus* Riva in RIVA & KETTNER, 1989, p. 89 (type, *Climacograptus caudatus* LAPWORTH, 1876a, OD), syn. by GOLDMAN & WRIGHT, 2003, p. 37]. Climacograptids with pattern E astogeny and narrow, asymmetrical proximal end with sicula lying almost entirely to right of tubarium midline in obverse view; sicular aperture oriented at ~70° from axis and bearing stout (but not necessarily long) virgella deflected across sicular aperture; virgella commonly matched by mesial spine on th1^1, such that they form pair which, in undeformed state, is symmetrical around tubarium axis; more rarely th1^2 also bears small mesial spine. *Upper Ordovician* (*Katian, Diplacanthograptus caudatus* Biozone–*Pleurograptus linearis* Biozone): worldwide.——FIG. 239,*4a–c*. **D. spiniferus* (RUEDEMANN); *4a–b,* lectotype, AMNH 1041/5a, Utica Shale, Balston Spa, New York, USA (Riva, 1974a, fig. 4); *4c,* NRM 1480 (Holm Collection), juvenile showing position of spines on proximal end and the two rods of the prosicula, Kurland, Estonia (Bulman, 1932a, pl. 3). Scale bars, 1 mm.

Pseudoclimacograptus PŘIBYL, 1947, p. 5 [**Climacograptus scharenbergi* LAPWORTH, 1876a, p. 6; OD]. Climacograptids with wide, rounded proximal end, strong zigzag median septum and distinct intrathecal folds; proximal end with virgellar spine and with or without subapertural spine on th1^1; thecal apertures straight, horizontal; three-vaned nematularium in mature specimens; proximal end of pattern D astogeny. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone–*Katian, Pleurograptus linearis* Biozone): China, Russia, Belgium, UK, Norway, Sweden, USA, Canada.——FIG. 240,*2a–c*. **P. scharenbergi* (LAPWORTH); *2a–b,* specimen in reverse (*a*) and obverse (*b*) views, PMO 118.047a,b, latex casts, Arnestad Formation, Oslo Region, Norway; *2c,* topotype, SM A19704, reverse view, Lower Hartfell Formation, Scotland, UK (see Williams, 1994, fig. 7g); scale bars, 1 mm (new).

Styracograptus ŠTORCH & others, 2011, p. 356 [**Climacograptus tubuliferus* LAPWORTH, 1876a, p. 6; OD] [?=*Notograptus* RUSCONI, 1948, p. 248 (type, *N. lanceolatus*, M), *nom. nud.,* TORO & BRUSSA, 2001, p. 362, based on scalariform climacograptid indet. with long nema, virgella, and parasicula, see RUSCONI, 1950, fig. 46; TORO & BRUSSA, 2001 identified the type as *Climacograptus* sp. cf. *C. caudatus*]. Climacograptids with rounded proximal end and Pattern D proximal development that lacks spines on proximal thecae; prosicula represented by single prominent rod that is continuous with nema; virgella normally elongated; long nematularium may be present; tubarium septate or aseptate with median septum delayed in some septate species; thickened nemal crossbars at base of interthecal septum. *Upper Ordovician* (*Katian, Dicellograptus ornatus* Biozone–*Hirnantian, Normalograptus extraordinarius* Biozone): worldwide.——FIG. 239,*5a–d*. **S. tubuliferus* (LAPWORTH); *5a,* lectotype, BU 1193g, *Pleurograptus linearis* Biozone, Hartfell Spa, Scotland, UK (Riva & Kettner, 1989, fig. 10H); *5b,* MCZ 9463/11, reverse view, somewhat reconstructed, showing origin of median septum; *5c,* MCZ 9463/10, juvenile showing single rod of prosicula grading into nema; *5d,* proximal end in obverse view (Mitchell, 1987, fig. 5R,K,Q; identified therein as *Climacograptus* sp. cf. *C. caudatus*). Scale bars, 1 mm.

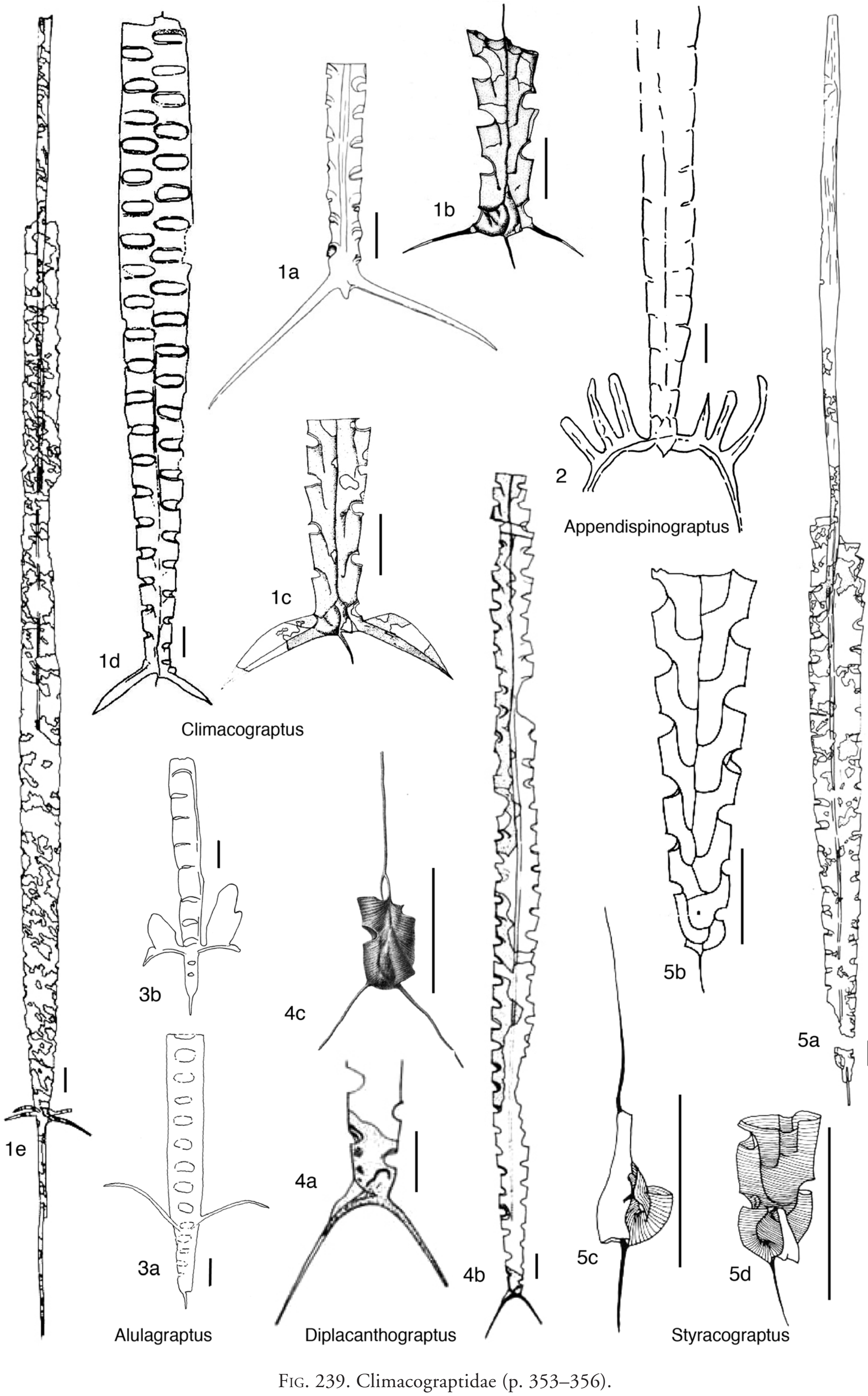

FIG. 239. Climacograptidae (p. 353–356).

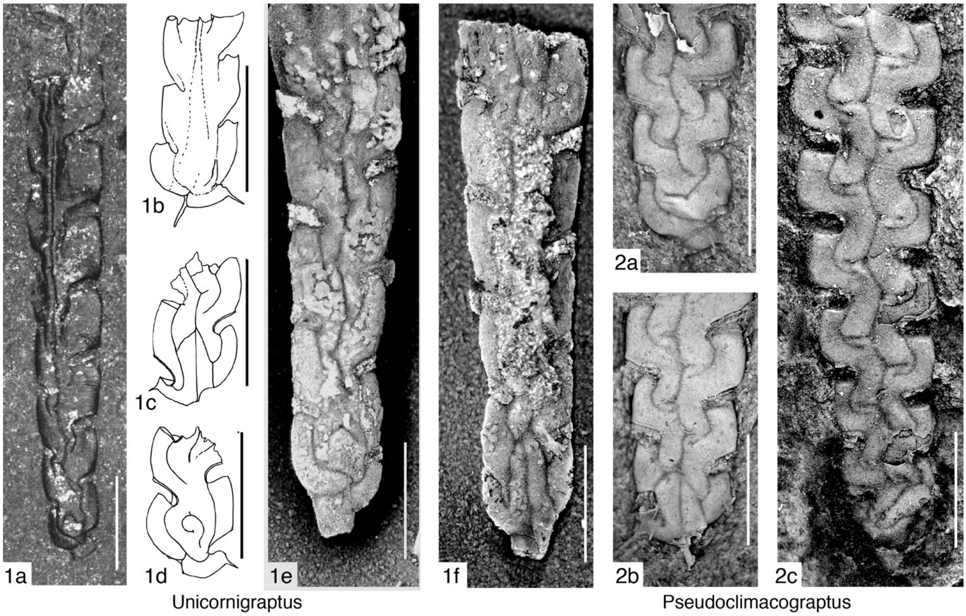

FIG. 240. Climacograptidae (p. 354–356).

Unicornigraptus CHEN & GOLDMAN, in CHEN & others, 2016, p. 311 [**U. xinjiangensis;* OD]. Proximal end of tubarium asymmetric with short first theca; th1^2 much longer than th1^1; subapertural spine on th1^1 only; pattern C astogeny; virgella usually elongated; parasicula may be present; median septum complete, undulating, and with intrathecal folding; thecae with long and straight ventral side; with or without geniculum; thecal apertures with paired lobes or straight. *Middle Ordovician* (*Darriwilian, Levisograptus dentatus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.——FIG. 240,*1a*. **U. xinjiangensis,* holotype, NIGP 157509, reverse view, scale bar, 1 mm (Chen & others, 2016, fig. 6-97N).——FIG. 240,*1b*. *U. ambiguus* (MALETZ, 2011d), GSC 81805, flattened, isolated specimen, *Levisograptus dentatus* Biozone, St. Pauls Inlet, western Newfoundland, Canada, scale bar, 1 mm (Maletz, 2011d, fig. 4K).——FIG. 240,*1c–d*. *U. pungens* (RUEDEMANN, 1904), GSC 133528, isolated specimen in obverse (*c*) and reverse (*d*) views, scale bars, 1 mm (Maletz, 2011d, fig. 4I,fig. 4J).——FIG. 240,*1e–f*. *U. scandinavicus* CHEN & GOLDMAN, in CHEN & others, 2016, holotype, LO 2410t, in reverse (*e*) and obverse (*f*) views (specimen flaked out of slab, imprint bears a very long virgella and parasicula), Almelund Shale, Fågelsång, Scania, Sweden; scale bars, 1 mm (new).

Family DICRANOGRAPTIDAE Lapworth, 1873

[Dicranograptidae LAPWORTH, 1873b, table facing p. 555] [=superfamily Dicranograptacea LAPWORTH, 1873b, MITCHELL & others, 2007 (misspelled Dicranograptacae in fig. 1); =superfamily Dicranograptoidea LAPWORTH, 1873b, ŠTORCH & others, 2011); =Leptograptidae LAPWORTH, 1879c, p. 454; =Incumbograptidae GE in MU & others, 2002, p. 437; =Ningxiagraptidae GE in MU & others, 2002, p. 331; =Ordosograptidae LIN, 1980, p. 477]

Biserial, dipleural axonophorans, secondarily two-stiped or partly two-stiped, reclined, uniserial, or with cladial branching; proximal end with metasicular origin of th1^1; proximal end provided with virgellar spine and additional apertural spines on at least first thecal pair; proximal development type dextral; pattern C astogeny or derived one; thecae variable, geniculate and with isolated, introverted apertures or simplified in derived taxa; intrathecal folds with crossbars present; complete median septum in biserial taxa; intrathecal folds lost in younger taxa with shortened thecal overlap and thecal simplification. *Middle Ordovician* (*Darriwilian, Nicholsonograptus fasciculatus* Biozone)–*Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

MITCHELL (1987) and MITCHELL and others (2007) considered the Dicranograptidae to be a monophyletic clade with its members possessing quite variable colony shapes from multiramous to one-stiped. The cladistic analysis of MITCHELL and others (2007, fig. 1) indicated that *Dicaulograptus* with a pattern C astogeny is the ancestral condition of the dicranograptid colony with all derived taxa possessing a pattern A astogeny or a derived one. MITCHELL (1987, fig. 17) interpreted the biserial, dipleural *Dicaulograptus hystrix* (BULMAN, 1932a) as derived from an archiclimacograptid ancestor. The interpretation gets more problematical with the recognition of two-stiped axonophorans with a generally dicellograptid tubarium construction during the early Darriwilian. MALETZ (1998b, 2014b) suggested a possible origin of the dicranograptids through *Levisograptus sinicus* (MU & LEE, 1958), based on the evidence from the earliest two-stiped taxa *Levisograptus dicellograptoides* (MALETZ, 1998b) and *Undulograptus* sp. (KRAFT & KRAFT, 2003) in the lower Darriwilian (MALETZ, 2014b). However, these taxa with a possible pattern U astogeny (Fig. 241.8) differ from the thecal construction in the younger species of *Dicellograptus,* and a considerable biostratigraphic gap in the presence of dicellograptid colony shapes during the Darriwilian renders the interpretation questionable.

MORPHOLOGY

Proximal Development

MITCHELL (1987) analyzed the proximal development of the Dicranograptidae in some detail and recognized several distinct astogenetic patterns (Fig. 241). MITCHELL and others (2007) identified the biserial axonophoran *Dicaulograptus* with a typical pattern C astogeny as the basal member of the Dicranograptidae. *Dicaulograptus hystrix* bears a simple sicula with multiple antivirgellar spines, but antivirgellar spines are lacking in *Dicaulograptus cumdiscus* FINNEY, 1985b.

BULMAN (1945) described the proximal development of *Dicranograptus nicholsoni* HOPKINSON, 1870 from isolated material and recognized the upward-growing flange connecting the initial part of $th2^1$ and forming the foramina for $th2^1$ and $th2^2$ and originating from the horizontally growing median part of $th1^1$ (Fig. 241.5–241.6). MITCHELL (1987) interpreted this development as pattern A′ (Fig. 241.2) in his analysis of the proximal development of Ordovician biserials. It differs from pattern A astogeny (Fig. 241.1) only through the presence of the lateral clefts at the virgella and a dorsal notch on the sicular aperture (Fig. 241.7). Derived dicranograptids have a dorsal notch and paired clefts on the side of the virgella, but these features are quite variable in the expression and may be lost in some taxa. Pattern A″ (Fig. 241.3) differs through the development of two separate stipes (the dicellograptid condition). Pattern N of MITCHELL (1987, fig. 1), the nemagraptid pattern (Fig. 241.4), bears a sicula that extends below the ventral sides of the stipes and should not be confused with the pattern N astogeny of MELCHIN and others (2011), referring to the development of a group of Silurian axonophorans. Recently, the genus *Dicellograptus* has been differentiated into a number of closely related genera, based on the growth direction of the proximal thecae and the orientation of the sicula (e.g., MU & others, 2002; CHEN & others, 2016). *Dicellograptus* bears a J-shaped first theca ($th1^1$) (Fig. 241.10–241.11), but it is more U-shaped in *Jiangxigraptus,* with its sicula usually leaning at least partly on stipe 2 (Fig. 241.9).

Cladia

BULMAN (1970, p. 106) expected that branching in the nemagraptids is cladial, and FINNEY (1985a) confirmed this based on isolated fragments of *Nemagraptus gracilis* (HALL, 1847) from the Athens Shale of Alabama, USA, in which the lateral branches originated from the thecal apertures of mature thecae. BATES and others (2011) described and illustrated the proximal end of a species of *Amphigraptus* with paired cladial branches originating from the apertures of the mother theca. The development of cladia in other Dicranograptidae has not been described in detail from isolated material, and details on the fusellar construction of these cladia are unknown. A dorsal rod

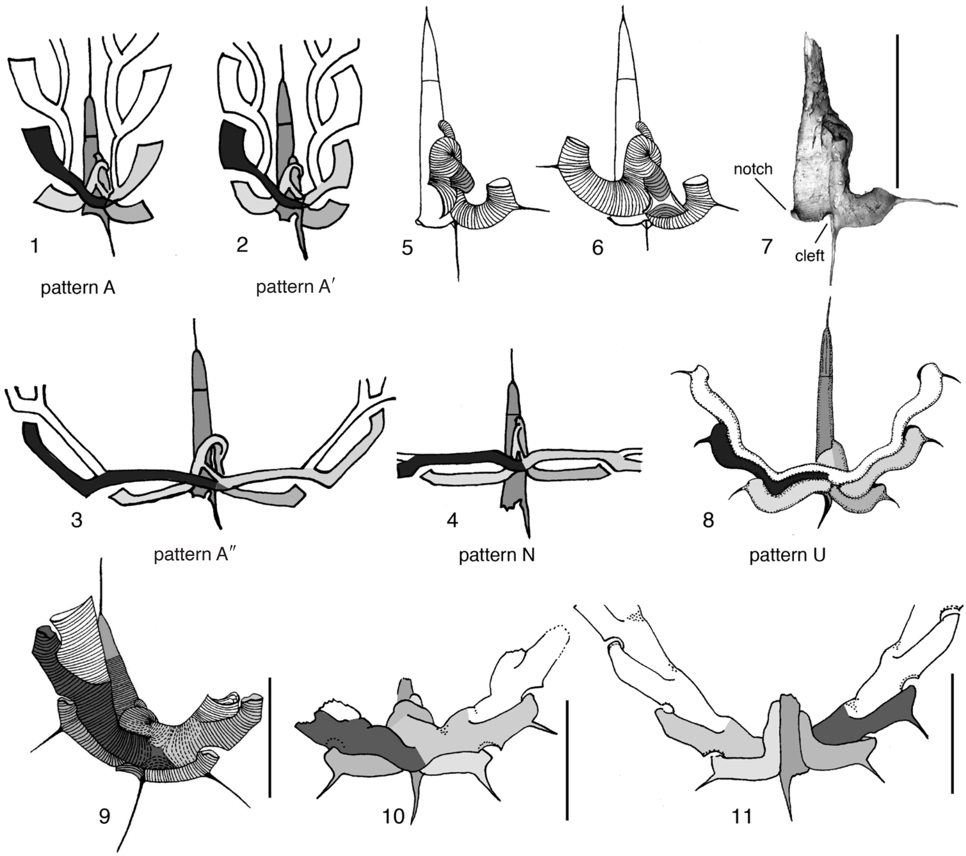

FIG. 241. Proximal development in the Dicranograptidae. *1–4,* Proximal development types (adapted from Mitchell, 1987, fig. 1). *5–6, Dicranograptus nicholsoni* HOPKINSON, 1870, initial part of th2[1] and upward-growing flange on th1[1] highlighted (adapted from Bulman, 1955, fig. 43); *7, Dicranograptus nicholsoni,* SMF 75811, juvenile, showing development of sicular aperture (new); *8,* inferred pattern U astogeny in *Levisograptus dicellograptoides* (MALETZ, 1998b), reconstruction (adapted from Maletz, 1998b, fig. 1A); *9, Jiangxigraptus salopiensis* (ELLES & WOOD, 1906) (adapted from reconstruction in Bulman, 1955, fig. 40; original specimen in STRACHAN, 1959, fig. 1); *10–11, Dicellograptus complanatus* LAPWORTH, 1880a in reverse (*10*) and obverse (*11*) views, PMU 35692, PMU 35691a, Koängen drill core, Scania, Sweden (new). Scale bars in *7, 9–11,* 1 mm.

similar to the secondary nema or pseudovirgula as in the monograptids (for example, *Cyrtograptus,* see THORSTEINSSON, 1955; URBANEK, 1963) has not been discovered in any dicranograptid, suggesting that the development is similar to that in the dichograptinid *Pterograptus* HOLM, 1881a (SKWARKO, 1974; MALETZ, 1994a).

The development of a colony with cladial distal branchings is considered a secondarily multiramous condition of the dicranograptid tubaria. Cladial branching appears in several genera and constructionally, most probably, these genera represent independent lineages. It is quite likely that the cladia-bearing nemagraptids (FINNEY, 1985a) are independently derived from a two-stiped nemagraptid such as *Nemagraptus subtilis* HADDING, 1913. Single cladia and even secondary cladia occur in the horizontal multiramous and fairly large colonies of *Amphigraptus* and *Pleurograptus* (see HALL, 1859c; NICHOLSON, 1867b) but also occur in the reclined *Tangyagraptus*.

Subfamily DICRANOGRAPTINAE Lapworth, 1873

[Dicranograptinae LAPWORTH, 1873b, table 1, facing p. 555] [=Dicellograptinae GE in MU & others, 2002, p. 412; =Leptograptinae MU, 1950b, p. 181; =Tangyagraptinae MU, 1963a, p. 368]

Biserial, dipleural axonophorans; secondarily two-stiped or partly two-stiped, reclined, uniserial, or with cladial branching; proximal end provided with virgellar spine and additional apertural to mesial spines on at least first thecal pair; proximal development type dextral; pattern C astogeny or derived one, excluding the Nemagraptinae with pattern N astogeny; thecae geniculate and with isolated, introverted apertures or simplified in derived taxa; complete median septum in biserial taxa; intrathecal folds and crossbars lost in younger taxa with shortened thecal overlap and apertural simplification. *Middle Ordovician* (*Darriwilian, Nicholsonograptus fasciculatus* Biozone)*–Upper Ordovician (Hirnantian, Metabolograptus persculptus* Biozone): worldwide.

The subfamily Dicranograptinae is herein regarded as a paraphyletic group of taxa from which the Nemagraptinae originated through a number of changes in the proximal end of the colony. The biserial-uniserial tubarium shape of *Dicranograptus* could be interpreted as a secondary development due to the early appearance of the dicellograptids during the late Darriwilian. However, if the relationship to the genus *Dicaulograptus* can be substantiated, the two-stiped dicellograptid-type tubarium must be interpreted as the derived type.

TAXA WITHOUT CLADIAL BRANCHING

The grouping of the Dicranograptinae into taxa with and without cladia used herein is informal and does not suggest any taxonomic relevance. Cladial branching may have originated separately and independently in a number of lineages.

Dicranograptus HALL, 1865, p. 112 [**Graptolithus ramosus* HALL, 1847, p. 270; OD] [=*Cladograpsus* EMMONS, 1855, p. 107 (type, *Cladograpsus dissimilaris* EMMONS, 1855, pl. 1,*15*), SD BULMAN, 1929, p. 173 (misspelled as *C. dissimilis*); *non Cladograpsus* GEINITZ, 1852, syn. of *Didymograptus*]. Initiallly biserial and distally two-stiped dicranograptid with reclined, commonly spirally coiled stipes; proximal end of pattern A′ astogeny; thecae with intrathecal folds and geniculum; thecal apertures introverted and with apertural isolation; thecae with mesial to subapertural spines, at least in proximal end. *Middle Ordovician* (*upper Darriwilian, Jiangxigraptus vagus* Biozone)*–Upper Ordovician* (*Katian, Paraorthograptus pacificus* Biozone): worldwide.——FIG. 242,*5a–b*. **D. ramosus* (HALL), *5a,* AMNH 30440, syntype (new; photo by Dan Goldman); *5b,* AMNH 30440, proximal end of syntype showing spines (new; drawing by John F. Riva). Scale bars, 1 mm.

Dicaulograptus RICKARDS & BULMAN, 1965, p. 278 [**Lasiograptus hystrix* BULMAN, 1932a, p. 29; OD]. Biserial dicranograptid with complex thecae with apertural introversion and mesial spines; thecae geniculate with strongly curved prothecae and metathecae, very convex free ventral wall, pleural spines, or pleural disks may be present; apertural excavations alternating and situated deep in tubarium, close to median septum; median septum slightly zigzag; proximal development of pattern A or pattern C astogeny. *Middle Ordovician* (*upper Darriwilian, Nicholsonograptus fasciculatus* Biozone*–Jiangxigraptus vagus* Biozone): China, Sweden, Norway, Canada, USA.——FIG. 242,*1a–c*. **D. hystrix* (BULMAN); *1a,* holotype, NRM 48 (Holm collection), reverse view, scale bar 5 mm (Bulman, 1932a, pl. 9,*5*); *b–c,* paratypes, NRM Cn 59951, 59952, juveniles showing proximal development (Mitchell, 1988, fig. 11,*4,6*).——FIG. 242,*1d–e*. *D. cumdiscus* FINNEY, 1985b, holotype, USNM 377408, proximal (*d*) and distal (*e*) fragments of specimen, *Hustedograptus teretiusculus* Biozone, Pratts Ferry, Alabama, USA, scale bars, 1 mm (Finney, 1985b, fig. 2).

Dicellograptus HOPKINSON, 1871, p. 20, original spelling as *Dicellograpsus* changed in ICZN Opinion 650, 1963][**Didymograpsus elegans* CARRUTHERS, 1867b, p. 369; SD GURLEY, 1896, p. 70] [=*Huayinograptus* YU & FANG, 1981b; *nom. nud.,* herein (type, *Dicellograptus szechuanensis* MU, 1950b, OD)] [=*Leptograptus* LAPWORTH, 1873b, p. 558 (type, *Graptolithus flaccidus* HALL, 1865, p. 143, OD), syn. by CHEN & others, 2016, p. 162] [=*Leptograpsus* RUEDEMANN, 1908, p. 253 (misspelling of *Leptograptus*] [*non Leptograpsus* MILNE EDWARDS, 1853, p. 171 (Crustacea, Decapoda, Grapsidae)]. Two-stiped dicranograptids with reclined, straight to spirally coiled stipes; proximal end of pattern A′ astogeny with sicula vertical and free between stipes; geniculate thecae with or without intrathecal folds and introverted and isolated apertures; at least first thecal pair with mesial to subapertural spines; J-shaped $th1^1$ and $th1^2$. *Middle Ordovician* (*upper Darriwilian, Jiangxigraptus vagus* Biozone)*–Upper*

Ordovician (*Hirnantian, Metabolograptus persculptus* Biozone): worldwide.——FIG. 242,*2a*. **D. elegans* (CARRUTHERS), holotype, NHMUK Q850, Lower Hartfell Shale, *Pleurograptus linearis* Zone, Dob's Linn, Scotland, UK, scale bar, 10 mm (Elles & Wood, 1904, pl. 23,*2a*).——FIG. 242,*2b*. *D. flaccidus* (HALL), GSC 1957b, proximal end, Lake St. John's, east from Blue Point, Utica Shale, Canada, scale bar, 1 mm (new; drawing by John F. Riva).——FIG. 242,*2c–e*. *Dicellograptus complanatus* (LAPWORTH, 1880a); *2c,* PMU 22496, proximal end in reverse view; *2d,* PMU 22498, proximal thecae; *2e,* PMU 22499, distal thecae; Fjäcka Shale, Bestorp, Västergötland, Sweden, scale bars, 1 mm (Skoglund, 1963, fig. 10B–D).

Diceratograptus MU, 1963a, p. 367 (p. 377, English text) [**D. mirus;* OD]. Two-stiped dicranograptids with heart-shaped axial cavity and distally separate stipes; supradorsal part of sicula visible between stipes; thecae strongly geniculate; number of spined proximal thecae and proximal development uncertain. *Upper Ordovician* (*Katian, Diceratograptus mirus* subzone of *Paraorthograptus pacificus* Biozone): China, Canada, USA.——FIG. 242,*3*. **D. mirus*, syntype, top of Wufeng Shale, Tangya, Yichang, China, scale bar, 1 mm (Mu, 1963a, fig. 13b).

Jiangxigraptus YU & FANG, 1966, p. 93 [**J. mui;* OD] [=*Incumbograptus* GE in MU & others, 2002, p. 437 (type, *Jiangxigraptus inculus* GE in GE, ZHENG, & LI, 1990, p. 89, OD), syn. herein] [=*Aclistograptus* GE in MU & others, 2002, p. 439 (type, *Graptolithus divaricatus* HALL, 1859c, p. 513, OD), syn. herein]. Two-stiped dicranograptids with reclined, commonly spirally coiled stipes; proximal end of pattern A′ astogeny with sicula partly or completely attached laterally to stipe two; thecae with strong prothecal folds; geniculum in proximal thecae; thecal apertures introverted and with apertural isolation; at least first thecal pair with mesial to subapertural spines; $th1^1$ and $th1^2$ generally U-shaped with upward-turned apertures. *Middle Ordovician* (*upper Darriwilian, Jiangxigraptus vagus* Biozone)–*Upper Ordovician* (*Sandbian, Climacograptus bicornis* Biozone): worldwide.——FIG. 242,*6a*. **J. mui,* holotype, *Nemagraptus gracilis* Biozone, Hulo Formation, Xiushui drainage basin, Jiangxi Province, China, scale bar, 1 mm (Yu & Fang, 1966, fig. 2).——FIG. 242,*6b*. *J. inculus* (GE in GE, ZHENG, & LI, 1990), holotype, NIGP 106213, proximal end, with strong tectonic deformation, *Nemagraptus gracilis* Biozone, China, scale bar, 1mm (new; photo by Zhang Yuandong).——FIG. 242,*6c*. *J. divaricatus* (HALL, 1859c), syntype, AMNH 35193, Kenwood, Normanskill, New York, USA, scale bar, 1 mm (new; photo by Dan Goldman).

Ningxiagraptus GE in MU & others, 2002, p. 331 [**Janograptus reclinatus* GE in GE, ZHENG, & LI, 1990, p. 71; =*Ningxiagraptus yangtzensis* (MU in GEH, 1963); CHEN & others, 2016, p. 204; OD] [=*Deflexigraptus* GE in MU & others, 2002, p. 443 (type, *Leptograptus declinatus* GE in GE, ZHENG, & LI, 1990, p. 81, OD), syn. herein]. Two-stiped dicranograptid with reclined stipes having wide angle of divergence; proximal end probably of pattern A′ astogeny; sicula connected laterally to stipe two; thecae with or without geniculum; apertures introverted or with straight apertures; mesial to subapertural spines on at least first thecal pair. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone–*Climacograptus bicornis* Biozone): China, North America.——FIG. 242,*7a–b*. *N. yangtzensis; 7a,* syntype, NIGP 13010 (Geh, 1963, fig. 2d); *7b,* **N. reclinatus* (GE in GE, ZHENG, & LI), holotype, NIGP 106102 (Mu & others, 2002, pl. 101,*6*). Scale bars, 1 mm.——FIG. 242,*7c*. *N. mensurans* (RUEDEMANN, 1908), AMNH 36147, proximal end, reverse view, J. Hall collection, Kenwood, New York, USA, scale bar, 1 mm (new; drawing by John F. Riva).

Pseudazygograptus MU, LEE, & GEH, 1960, p. 37 [**Azygograptus incurvus* EKSTRÖM, 1937, p. 33; OD]. Single-stiped dicranograptid with variously oriented stipe, from horizontal to strongly reflexed; thecae slender, geniculate and frequently with genicular hoods; apertures with slight lateral lobes or straight. *Middle Ordovician* (*Darriwilian, Jiangxigraptus vagus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.——FIG. 242,*4a–b*. **P. incurvus* (EKSTRÖM); *4a*, syntype, LO 3322T, fragment, Scania, Sweden (new); *4b,* OSU 32911, proximal end, Athens Shale, Alabama, USA (Finney, 1980, fig. 9B). Scale bars, 1 mm.

TAXA WITH CLADIAL BRANCHING

Taxa with single cladia, paired cladia, and even secondary cladia exist. The taxa may also be differentiated by their proximal developments. It is likely that the cladial-bearing taxa of the Dicranograptinae are not a monophyletic group. They are here assembled for easy access only.

Amphigraptus LAPWORTH, 1873b, p. 559 [**Graptolithus divergens* HALL, 1859c, p. 509; M] [=*Clematograptus* HOPKINSON in HOPKINSON & LAPWORTH, 1875, p. 652 (type, *Graptolithus multifasciatus* HALL, 1859c, p. 508, SD GURLEY, 1896, p. 93), syn. by BULMAN, 1970, p. 121]. Multiramous dicranograptids with paired primary cladia; secondary cladia may be present in mature specimens; stipes subhorizontal to moderately reclined; thecae geniculate and introverted; subapertural to mesial spines at least on first thecal pair; sicula slender and free or resorbed in larger specimens. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone–*Katian, Dicranograptus clingani* Biozone): China, UK, USA.——FIG. 243,*1a–b*. **A. divergens* (HALL); *1a, A. multifasciatus,* holotype, NYSM 6840, *Nemagraptus gracilis* Biozone, Normanskill Shale, Kenwood, New York, USA, scale bar, 5 mm (Ruedemann, 1908, pl. 15,*4*); *1b,* holotype,

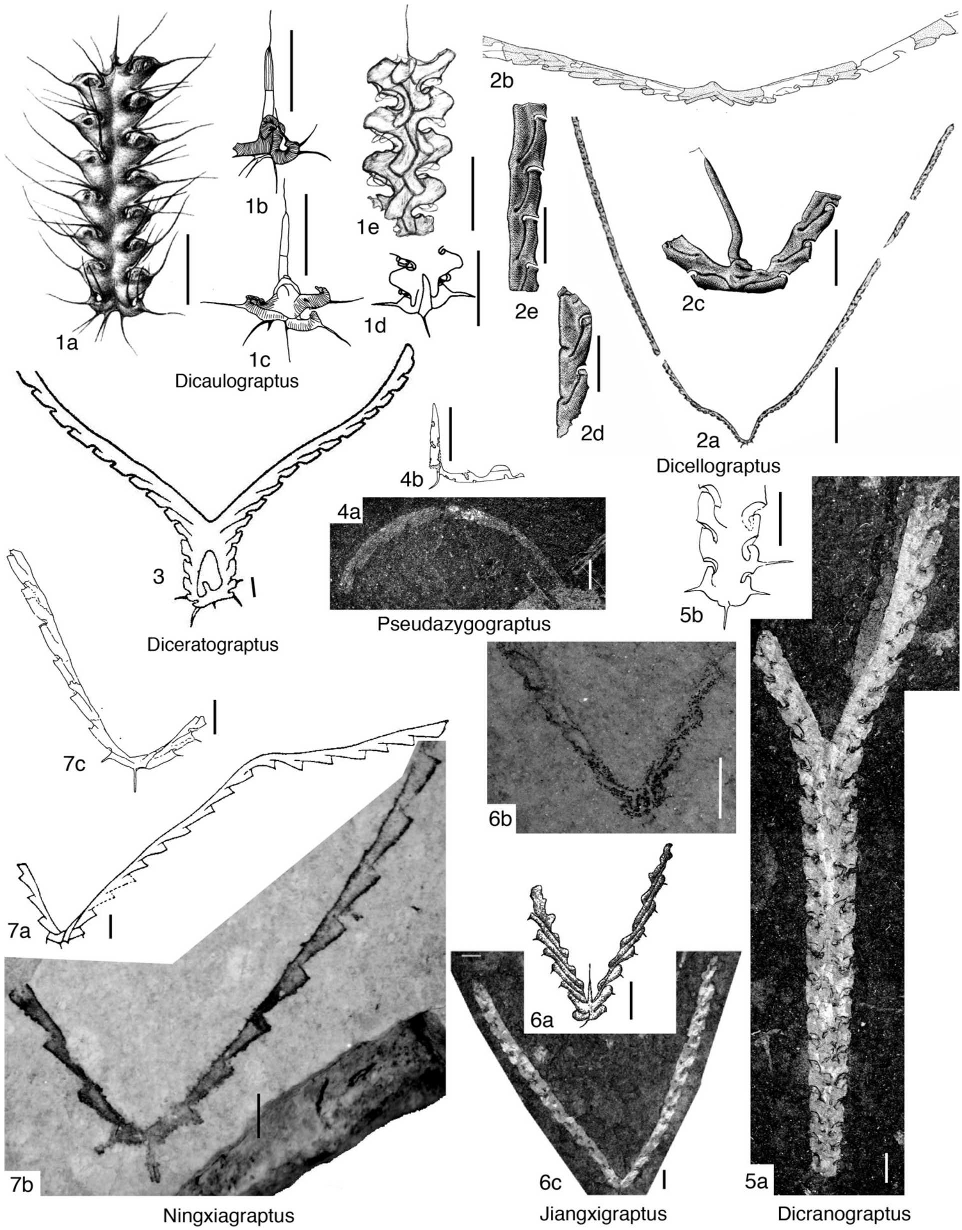

FIG. 242. Dicranograptinae without cladia (p. 359–360).

Nemagraptus gracilis Biozone, Normanskill Shale, Kenwood, New York, USA, scale bar, 5 mm (Hall, 1859c, fig. 9).

Pleurograptus NICHOLSON, 1867b, p. 257, original spelling as *Pleurograpsus* changed in ICZN Opinion 650, 1963 [**Cladograpsus linearis* CARRUTHERS, 1858, p. 467; OD]. Dicranograptid with cladial stipes of several orders; proximal development uncertain; sicula very slender and long, may be resorbed in mature specimens; thecae slender, ventral side parallel to dorsal side, with distinct geniculum. *Upper Ordovician* (*Katian, Dicellograptus ornatus* Biozone–*Paraorthograptus pacificus* Biozone): UK, Canada, China, USA.——FIG. 243,*2a–b*. **P. linearis* (CARRUTHERS); *2a,* NHMUK PM Q848, large specimen, Hartfell Shale, Scotland, UK, scale

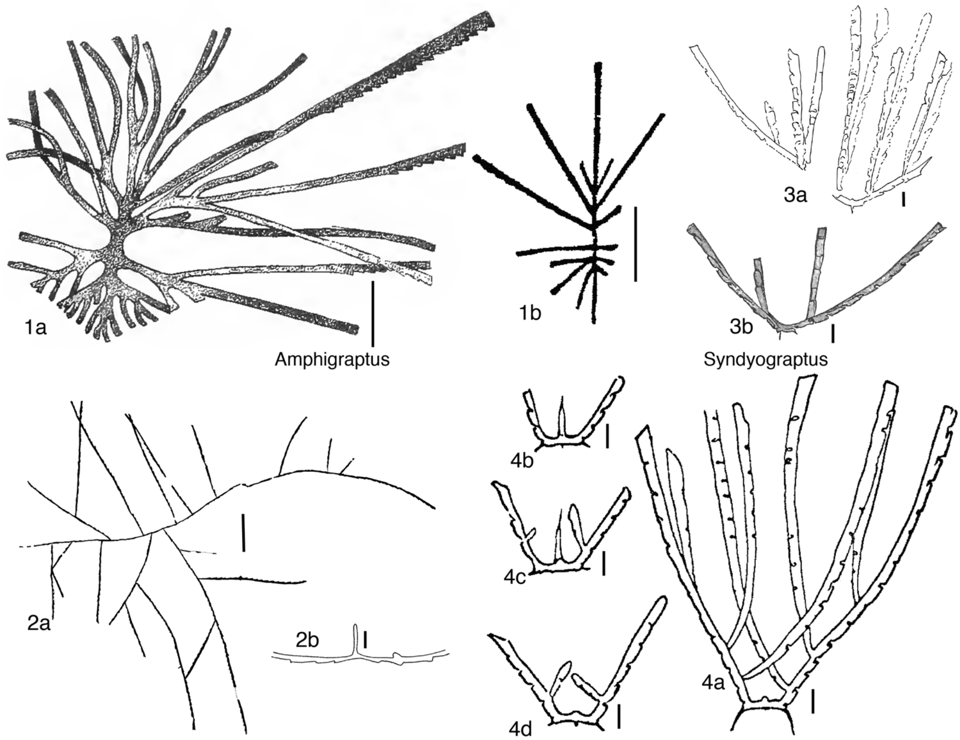

FIG. 243. Dicranograptinae with cladia (p. 360–362).

bar, 5 mm (Bulman, 1970, fig. 87,*1*); *2b,* NHMUK PM Q848, proximal end, scale bar, 1 mm (Strachan, 1969, fig. 1C).

Syndyograptus RUEDEMANN, 1908, p. 266 [**S. pecten;* OD]. Multiramous dicranograptids with paired primary cladia; stipes moderately reclined; thecae geniculate and introverted, with low inclination of ventral side; subapertural to mesial spines at least on first thecal pair; slender sicula connected laterally to stipe two. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone–*Climacograptus bicornis* Biozone): China, USA.——FIG. 243,*3a–b*. **S. pecten; 3a,* syntype, NYSM 7363 (new); *3b,* syntype, NYSM 7364, proximal end showing inclined sicula; Glenmont, New York, USA (Ruedemann, 1908, fig. 185). Scale bars, 1 mm.

Tangyagraptus MU, 1963a, p. 359 (p. 377, English text)[**T. typicus;* OD]. Reclined, two-stiped dicranograptid with unpaired cladia originating on one side of both stipes; proximal development unknown; proximal end with prominent apertural spines on first thecal pair; prominent sicula may be resorbed in mature specimens. [Genus was misspelled as *Tangyograptus* MU, 1963a in FINNEY, 1985a, p. 1104.] *Upper Ordovician* (*Katian, Paraorthograptus pacificus* Biozone): China.——FIG. 243,*4a–d*. **T. typicus,* top of Wufeng Shale, Tangya, Yichang, China; *4a,* NIGP WM 185, holotype; *4b–d,* paratypes showing astogeny; scale bars, 1 mm (Mu, 1963a, fig. 10).

Subfamily NEMAGRAPTINAE Lapworth, 1873

[Nemagraptinae LAPWORTH, 1873b, p. 556, *ex* family Nemagraptidae LAPWORTH, 1873b]

Two-stiped dicranograptids with or without single or paired cladial branching; proximal end with high metasicular origin of $th1^1$; proximal development type of pattern N astogeny with sicular aperture reaching beyond base of stipes; thecae variable, usually with strong, laterally expanded genicular flanges; apertures isolated and introverted, but simple and with low overlap in derived taxa; intrathecal folds may be present. *Middle Ordovician* (*upper Darriwilian, Jiangxigraptus vagus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.

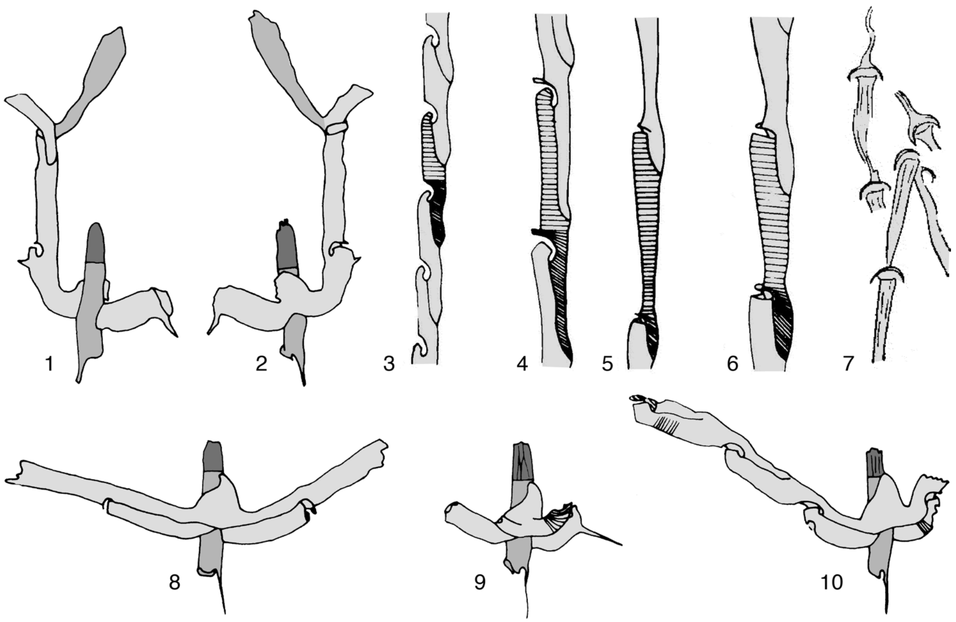

FIG. 244. Tubarium construction in *Nemagraptus*. *1–2, 5–6, 8, Nemagraptus gracilis* (HALL, 1847); *1–2,* proximal end showing cladium (Finney, 1985a, fig. 11–12); *5–6,* proximal (*5*) and distal (*6*) thecal style (Finney, 1985a, fig. 4,*6*–4,*7*); *7,* ventral view of stipes, holotype of *Ordosograptus delicatus* LIN, 1980 (Lin, 1980, fig. 1,*2*); *8,* proximal end in reverse view, slightly reclined stipes, see high metasicular origin of th1[1]; *3–4, 9–10, Nemagraptus linmassiae* FINNEY, 1985a; *3–4,* reconstruction of proximal (*4*) and distal (*3*) thecal style; *9–10,* proximal ends in reverse view (all adapted from Finney, 1985a). Illustrations not to scale.

The Nemagraptidae is a traditional name introduced by LAPWORTH (1873b) and consistently used to differentiate two-stiped to multiramous Upper Ordovician axonophorans. It was restricted by FINNEY (1985a) to taxa with a nemagraptid proximal end, that is to taxa in which the sicula extends downward beyond the stipes, excluding two-stiped to multiramous taxa with a dicellograptid proximal end in which the stipes diverge from close to the sicula (*Amphigraptus, Pleurograptus*). MALETZ (2014b, p. 515) revised the family and also included *Pleurograptus,* unaware of the dicellograptid proximal end of this genus illustrated in WILLIAMS (1982b, pl. 2).

Nemagraptidae has commonly been used as a taxonomic unit at the family level (e.g. BULMAN, 1970; MU & others, 2002), but is herein used as a subfamily to indicate its relationships to the dicranograptids. The Nemagraptinae originate from a dicellograptid ancestor in the late Darriwilian (see MITCHELL, 1987, fig. 13,*17*; MITCHELL & others, 2007), but the transition is poorly documented. *Nemagraptus linmassiae* FINNEY, 1985a still possesses the intrathecal folds (recognized as prothecal folds in FINNEY, 1985a) as a symplesiomorphic character retained from the dicellograptids, but already has the isolated metasicula (Fig. 244) as the main synapomorphy of the nemagraptids (FINNEY, 1985a, fig. 23,*1*). With the genera *Amphigraptus, Pleurograptus,* and *Tangyagraptus* now included in the Dicranograptinae, the Nemagraptinae comprises a single genus with a number of taxa having variable development of cladia. FINNEY (1985a) illustrated the development of cladia in *Nemagraptus* from chemically isolated material (Fig. 244.1–244.2). The thecae possess considerable overlap and indications of intrathecal folds in *Nemagraptus*

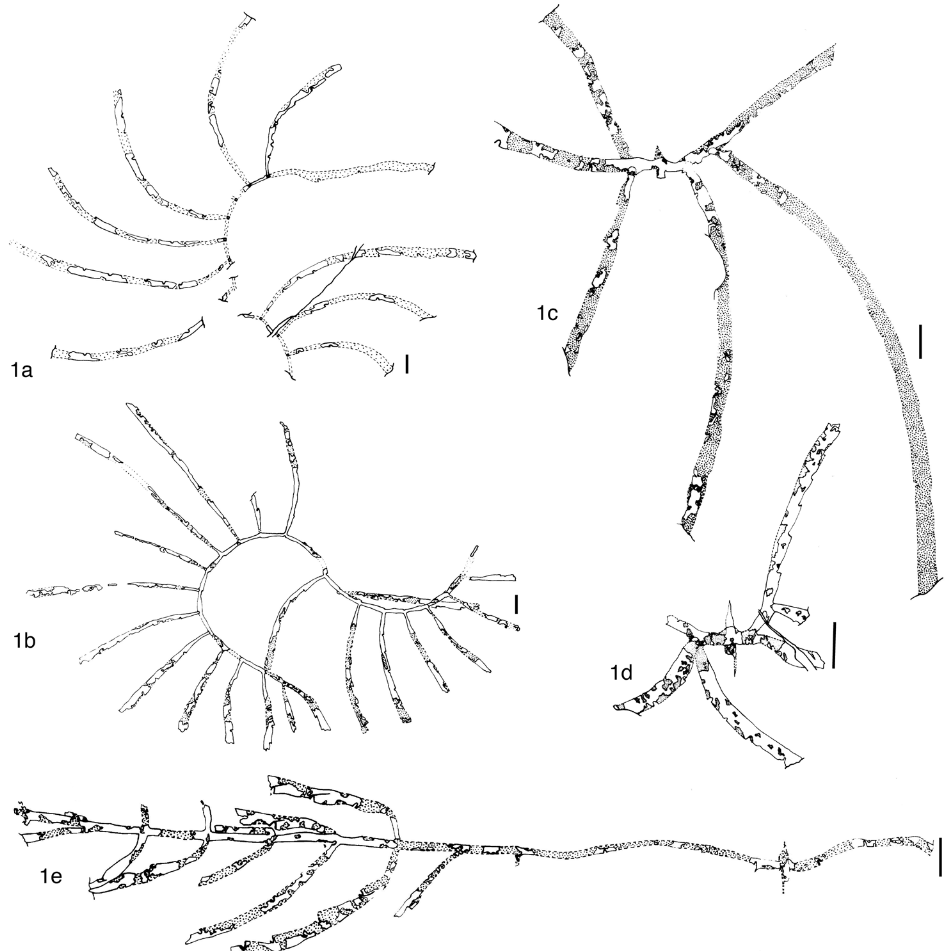

FIG. 245. Nemagraptinae (p. 364–365).

linmassiae (Fig. 244.3–244.4), whereas in *Nemagraptus gracilis* the thecae are shorter and lack introverted thecal apertures and lateral lappets (Fig. 244.5–244.6). Strong genicular lobes or flanges have been used to differentiate the genus *Ordosograptus* LIN, 1980 (Fig. 244.7), but is based on dorso-ventrally preserved *Nemagraptus* stipe fragments. Paired cladia were unknown from *Nemagraptus*, but the proximal ends of specimens described as *Amphigraptus* n. sp. A and *Amphigraptus* n. sp. B in FINNEY (1985a) clearly possess a nemagraptid proximal end and should be included in *Nemagraptus* (Fig. 245,*1c–e*).

Nemagraptus EMMONS, 1855, p. 109, original spelling as *Nemagrapsus* changed in ICZN Opinion 650, 1963 [**Graptolithus gracilis* HALL, 1847, p. 274; =*Nemagraptus elegans* EMMONS, 1855, p. 109; SD HALL, 1868, p. 211] [=*Coenograptus* HALL, 1868, p. 179 (type, *Graptolithus gracilis* HALL, 1847; SD BULMAN, 1929, p. 169, obj.)] [=*Geitonograptus* OBUT & ZUBTZOV, 1965, p. 24 (type, *G. suni,* OD), syn. by BULMAN, 1970, p. 120] [=*Helicograpsus* NICHOLSON, 1868e, p. 23 (type, *Grapolithus gracilis* HALL, 1847, p. 274, OD, obj.)] [=*Ordosograptus* LIN, 1980, p. 477 (type, *O. delicatus,* OD), syn. by FINNEY, 1985a, p. 1111] [=*Stephanograptus* GEINITZ, 1866, p. 124 (type, *Graptolithus gracilis* HALL, 1847, p. 274, OD, obj.)]. Two-stiped dicranograptids with or without single or paired cladial branching; proximal end with high metasicular origin of th1^1; proximal development type pattern N astogeny with sicular aperture reaching beyond base of stipes; thecae variable, usually with strong, laterally expanded genicular flanges; apertures isolated and introverted, but simple and with low overlap in derived taxa; intrathecal folds may be present. *Middle Ordovician* (*upper Darriwilian, Jiangxigraptus vagus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.——FIG. 245,*1a–b*. **N. gracilis* (HALL); *1a,* AMNH 30458, lectotype; *1b,* AMNH 36766, more complete specimen; Normans Kill Shales, Kenwood, New York, USA; scale bars, 1 mm (Finney, 1985a, fig. 10,*1–2*).——FIG. 245,*1c–d*. *Nemagraptus* sp. B, Athens Shale, Calera, Alabama, USA; *1c,* OSU 32976, paired cladia on left stipe, scale bar, 1 mm; *1d,* OSU 32975, showing *Nemagraptus*-type proximal end; scale bar, 1 mm (Finney, 1985a, fig. 27,*1,3*; as *Amphigraptus* sp. B).——FIG. 245,*1e*. *Nemagraptus* sp. A, OSU 32973, paired cladia on distal part of stipe, Athens Shale, Pratt's syncline section, Alabama, USA, scale bar, 1 mm (Finney, 1985a, fig. 273; as *Amphigraptus* sp. A).

INFRAORDER NEOGRAPTINA

Jörg Maletz

Infraorder NEOGRAPTINA Štorch, Mitchell, Finney, & Melchin, 2011

[Neograptina Štorch, Mitchell, Finney, & Melchin, 2011, p. 368] [=family Monograptidae Lapworth, 1873b *sensu* Mitchell, 1987, p. 390; =suborder Monograptina of Mitchell & others, 2007]

Biserial, uni-biserial, and uniserial graptoloids lacking proximal spines except for the virgellar spine; proximal end in biserial taxa slender and usually pointed, asymmetrical; pattern A astogeny in early members and variable derived patterns in derived taxa; thecal style variable, from simple tubes with straight aperture to taxa with complex thecal apertures adorned with lappets, flanges, apertural and genicular hoods or hooks, or single or paired spines. *Middle Ordovician* (*Darriwilian, Holmograptus lentus* Biozone)–*Lower Devonian* (*Pragian, Uncinatograptus yukonensis* Biozone): worldwide.

Mitchell (1987) emended the family Monograptidae to include all taxa that are now included in the Neograptina, thus extending the familiar term Monograptidae considerably. Mitchell and others (2007) used the name Monograptina for the same unit, but excluded the *Undulograptus* (now *Levisograptus*, see Maletz, 2011c) *austrodentatus* group as a stem group. The resulting confusion led Štorch and others (2011, p. 314) to introduce the term Neograptina for the same clade. Štorch and others (2011, p. 368) provided a cladistic definition (not a diagnosis; corrected in Melchin & others, 2011, p. 291) of the Neograptina, stating that "the Neograptina is the total clade comprising all species sharing a more recent common ancestor with *Monograptus priodon* than with *Diplograptus pristis* (i.e., the species on the branches arising from the right side of node 1 in fig. 6 [of Štorch & others, 2011] and all their descendents)." The definition was based on a specific diagram, but the authors noted that it would be difficult to provide a diagnosis due to the high variation of the included taxa. Typical biserial axonophorans and the derived uniserial taxa can be included in the Neograptina, following a similar concept to the one advocated first by Mitchell (1987) when redefining the Monograptidae.

Štorch and others (2011, p. 368) erected the monophyletic taxon Neograptina as a sister taxon to the Diplograptina, using the results of an analysis by Mitchell and others (2007) and identified *Undulograptus formosus* Mu & Lee, 1958 as the earliest member of the clade. Melchin and others (2011, fig. 3) separated three groups in the Neograptina (Fig. 246), the Normalograptidae, the Monograptoidea, and the Retiolitoidea and regarded the genus *Hirsutograptus* as *incertae sedis*. The authors considerably extended the concept of the Retiolitoidea and included a number of non-ancorate taxa.

The early (biserial) Neograptina possess a rounded to pointed proximal end without spines, except for the virgella, and a pattern A astogeny in the early members, modified to a pattern H astogeny or a derived one in later ones. According to Maletz (2011d), the precise phylogenetic relationship of the genus *Undulograptus* at the roots of the Climacograptidae and Normalograptidae (see Mitchell & others, 2007; Štorch & others, 2011) is uncertain, as the origin and early evolution of proximally spineless (except for the virgella) axonophorans is completely unresolved. Thus, a number of early Neograptina are herein regarded as stem group taxa and not included in the family Normalograptidae.

MORPHOLOGY

The description of the tubarium morphology focuses on the early taxa and their development (stem group taxa and Normalograptidae). Derived taxa (Retiolitoidea,

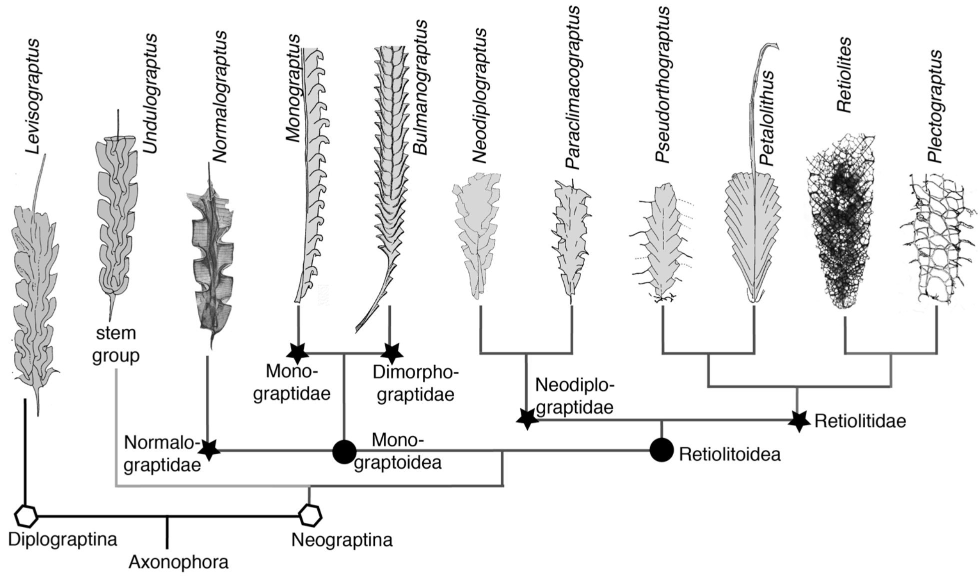

FIG. 246. Cladistic interpretation of origin of the Neograptina (new, based on data in MELCHIN & others, 2011, fig. 2 and ŠTORCH & others, 2011, fig. 6).

Monograptoidea) are covered in the following sections.

The proximal development types of early Neograptina are poorly understood. MITCHELL (1987) stated a pattern A astogeny (Fig. 247.2) for *Oelandograptus oelandicus* (BULMAN, 1963b) (Fig. 247.3–247.5) and a pattern B astogeny for the genus *Undulograptus* (Fig. 247.1). The pattern B astogeny of *Undulograptus* was based on *Proclimacograptus angustatus* (EKSTRÖM, 1937), as described by MALETZ (1997a). The species was erroneously regarded as the type species of *Undulograptus* by MITCHELL (1987, p. 397). The type of *Undulograptus*, however, is *Pseudoclimacograptus formosus* MU & LEE, 1958, a species for which the proximal development was unknown at the time, but MITCHELL (1992) identified a pattern C astogeny in *Undulograptus formosus* (Fig. 247.8) and some other species referred to *Undulograptus*. MALETZ and AHLBERG (2011b) discussed a group of *Undulograptus* species from the Krapperup drill core having a pattern C astogeny. A pattern C astogeny also appears in *Haddingograptus* species. MALETZ (2011d) discussed a possible origin of the derived climacograptids from these. Thus, a pattern C astogeny may be found in basal Neograptina, but the development of *Oelandograptus* and its inclusion in the Neograptina remains uncertain.

The proximal end of early Neograptina is evenly rounded to strongly asymmetrical. The first thecal pair is strongly upturned (Fig. 247) and the thecal apertures are oriented horizontally, but in *Oelandograptus* the apertures are outward inclined. The proximal development of pattern A astogeny in this taxon needs to be revised and verified. Depending on the position of the dicalycal theca, the proximal development of pattern C astogeny can be differentiated into two slightly different types. In taxa with a dicalycal theca $th3^1$, the obverse side has an arch connecting $th2^2$ and $th3^1$. This development appears in *Haddingograptus eurystoma* (JAANUSSON, 1960) and other *Haddingograptus* species (Fig. 247.6). In *Haddingograptus oliveri* (BOUČEK, 1973), with a dicalycal theca $th2^1$, the median septum is complete on both the obverse and reverse sides (see MALETZ, 1997a, fig. 7I–7J).

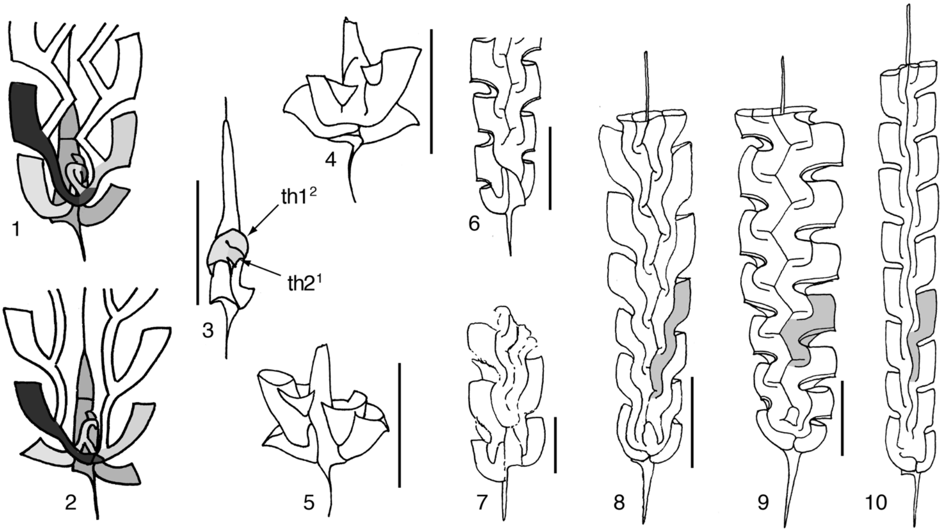

FIG. 247. Proximal development and tubarium shape of early Neograptina. *1,* Pattern B astogeny; *2,* pattern A astogeny; *3–5, Oelandograptus oelandicus* (BULMAN, 1963b), juveniles in reverse (*3–4*) and obverse (*5*) views; *6, Haddingograptus* MALETZ, 1997a sp., proximal end in obverse view, reconstruction (new); *7, Undulograptus novaki* (PERNER, 1895), OMR 54977, Drahous, Czech Republic, obverse view (new); *8, Undulograptus formosus* (MU & LEE, 1958), reconstruction of holotype, reverse view, showing long double sigmoidal thecae (adapted from Maletz, 2011c, fig. 1a); *9, Haddingograptus oliveri* (BOUČEK, 1973), short thecae with strong intrathecal folds (Maletz, 1997a, fig. 29c); *10, Proclimacograptus angustatus* (EKSTRÖM, 1937), short thecae, no intrathecal folds; (*1-5* adapted from Mitchell, 1987). All scale bars, 1 mm.

The sicula of most early Neograptina is short (less than 1.5 mm long) and widens rapidly in most members in which the sicula is known in isolated specimens, but elongated siculae exist in a number of derived taxa (e.g., *Cystograptus*, some *Petalolithus*, the monograptid *Lagarograptus* OBUT & SOBOLEVSKAYA in OBUT, SOLBOLEVSKAYA, & MERKUREVA, 1968, and *Coronograptus*). A number of members of the genera *Prolasiograptus* and *Haddingograptus* may have a short virgella curved or bent across the sicular aperture, but the sicula is not curved noticeably in these cases.

The thecal style varies considerably in the early Neograptina (Fig. 247.8–247.10) from simple straight tubes to strongly geniculate ones. The geniculum may be provided with a genicular flange or can be rounded without elaborations. The supragenicular wall may be vertical, inward or outward sloping, or convexly curved. The thecal apertures also can vary in their orientation from introverted through horizontal to everted. In biostratigraphically earlier taxa, the thecal overlap is high, and the thecae have a double sigmoidal curvature and a conspicuous presence of intrathecal septa and folds (Fig. 247.8). Subsequently, thecal overlap is reduced, and thecae may be short and show little curvature. In these, the intrathecal septa are missing and intrathecal folding does not exist (Fig. 247.10).

STEM GROUP NEOGRAPTINA

Biserial tubaria with rounded to pointed proximal end; primordial astogeny of pattern A (see MITCHELL, 1987) or a derived pattern; first two thecae generally U-shaped, initially closely adpressed to the sicula, lacking apertural spines; thecae with straight to undulate or geniculate ventral thecal walls; median septum straight to strongly sigmoidal, sometimes angular; intrathecal folding in many taxa. *Middle Ordovician* (*Darriwilian, Corymbograptus retroflexus* Biozone)*–Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.

The taxa discussed herein as stem group Neograptina are not included in any family group taxon herein. They may be combined by considering 1) their rounded proximal ends without apertural spines on the first thecal pair and 2) their initially long and doubly sigmoid thecae. In these taxa, the geniculum is rounded to strongly angular and may possess considerable genicular flanges or other modifications. The ventral thecal walls are either outward inclined or parallel to the tubarium midline. The unusual genus *Gymnograptus* may be related to the group, as it shares the proximal end lacking apertural spines on the first thecal pair and the short wide thecae comparable to those of *Haddingograptus* species. The proximal development, however, is derived and similar to a pattern H astogeny with th1[1] growing downward and upward again on its own protheca. Thecae widen rapidly, the supragenicular walls are reduced, and intrathecal folds are lacking. The genus *Reteograptus* is herein included due to the lack of proximal end spines and the thecal style of the early *Reteograptus speciosus* HARRIS, 1924, in which the fusellum is completely preserved (see MALETZ, 1997a, pl. 6,*7*).

Gymnograptus BULMAN, 1953 (*ex* TULLBERG, manuscript), p. 514 [**Diplograptus linnarssoni* MOBERG, 1896, p. 17; OD] [?=*Diplograptus* (*Idiograptus*) LAPWORTH, 1880a, p. 169 (type, *I.* (*Diplograptus*) *aculeatus* LAPWORTH, 1880a, p. 170, OD, *nom. dub.,* STRACHAN, 1996, p. 10)]. Neograptines with attenuated fusellum and thickened thecal lists; proximal end of pattern G astogeny; single antivirgellar spine and virgella bending outward from sicular aperture; distinct geniculum with short supragenicular wall and variably developed extensions developed as paired or multiple spines; median septum complete. *Middle Ordovician* (*upper Darriwilian, Jiangxigraptus vagus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): China, Sweden, Norway, Spain.——FIG. 248,*3a–d*. **G. linnarssoni* (MOBERG); *3a*, syntype, Fågelsång, Scania, Sweden (Moberg, 1896, fig. b); *3b–3d,* isolated specimens in reverse (*d*) and obverse (*b*) views, distal fragment (*c*), glacial boulder, Poland (Urbanek, 1959, fig. 4, 5, and 9, respectively). Scale bars, 1 mm.

Ekstroemograptus MALETZ & AHLBERG, 2021, p. 377 (**E. inexpectatus;* OD). Robust neograptine with long overlapping, double sigmoid thecae with outward-inclined ventral thecal walls; proximal development similar to pattern B astogeny with strongly upturned thecal apertures of th1[1] and th1[2]; proximal end rounded with the virgella as the only proximal end spine; unusual U-shaped th1[2] seen in obverse view, whereas downward-growth of th1[1] is covered. *Middle Ordovician* (*middle Darriwilian, Holmograptus lentus–lower Nicholsonograptus fasciculatus* Biozone): Sweden, Belgium.——FIG. 249. **E. inexpectatus,* Krapperup drill core, Scania, Sweden; *a,* holotype, obverse view, LO 11201T; *b,* juvenile, obverse view, PMU 37430/1; *c,* PMU 37430/2, reverse view; *d–e,* PMU 37431, relief specimen in obverse (*d*) and reverse (*e*) views. Scale bars, 1 mm.

Haddingograptus MALETZ, 1997a, p. 63 [**Pseudoclimacograptus* (*Pseudoclimacograptus*) *oliveri* BOUČEK, 1973, p. 121; OD]. Neograptines with broadly rounded, normally somewhat asymmetrical proximal end of pattern C astogeny; median septum usually sharply zigzag shaped; intrathecal folding conspicuous; strong genicular flanges or collar structures commonly with distinct ventral genicular notch; thecal apertures slit-like, horizontal. *Middle Ordovician* (*Darriwilian, Nicholsonograptus fasciculatus* Biozone–*Jiangxigraptus vagus* Biozone): China, Sweden, Norway, Spain, Canada, USA, Argentina.——FIG. 248,*6a–b*. **H. oliveri* (BOUČEK); *6a,* paratype, NRM Cn 2541, reverse view; *6b,* holotype, NRM Cn 2539, obverse view; Elnes Formation Rigshospitalet, Oslo, Norway; scale bars, 1 mm (adapted from Bulman, 1953, fig.1).——FIG. 248,*6c. Haddingograptus tarimensis* CHEN in CHEN & others, 2017, obverse view, reconstruction based on PMO 138.400, scale bar, 1 mm (based on Maletz, 1997a, fig. 31g).——FIG. 248,*6d–e. H. eurystoma* (JAANUSSON, 1960), NRM 2345, 2352 (Holm collection), juvenile specimens in reverse (*d*) and obverse (*e*) views; scale bars, 1 mm (Bulman, 1932a, pl. 1,*12* and 1,*14*, respectively).

Oelandograptus MITCHELL, 1987, p. 383 [**Glyptograptus austrodentatus oelandicus* BULMAN, 1963b, p. 682; M]. Neograptines with undulatory median septum; thecae weakly sigmoidal with long, outwardly inclined infragenicular wall, sharply rounded geniculum, short, nearly vertical supragenicular wall; thecal apertures slightly everted, undulatory with concave ventral margin; proximal development of pattern A astogeny with evenly rounded to somewhat blunt, nearly symmetrical proximal end. *Middle Ordovician* (*Darriwilian, Holmograptus lentus* Biozone–*Nicholsonograptus fasciculatus* Biozone): Norway, Sweden.——FIG. 248,*1a–b*. **O. oelandicus* (BULMAN), holotype, NRM Cn 307 (Holm collection) in obverse (*a*) and reverse (*b*) views, lower Darriwilian, ?*Holmograptus lentus* Biozone, glauconithåltig grå Vaginatumkalk, Hälludden, Öland, Sweden, scale bars, 1 mm (Bulman, 1936a, pl. 3,*5–6*).

Proclimacograptus MALETZ, 1997a, p. 68 [**P. bulmani;* OD]. Neograptines with slender tubarium; th1[1] and th1[2] strongly upturned with horizontal apertures; median septum straight to moderately undulate; thecae short with straight, horizontal apertures; proximal development of pattern B astogeny. *Middle Ordovician* (*Darriwilian, Nicholsonograptus*

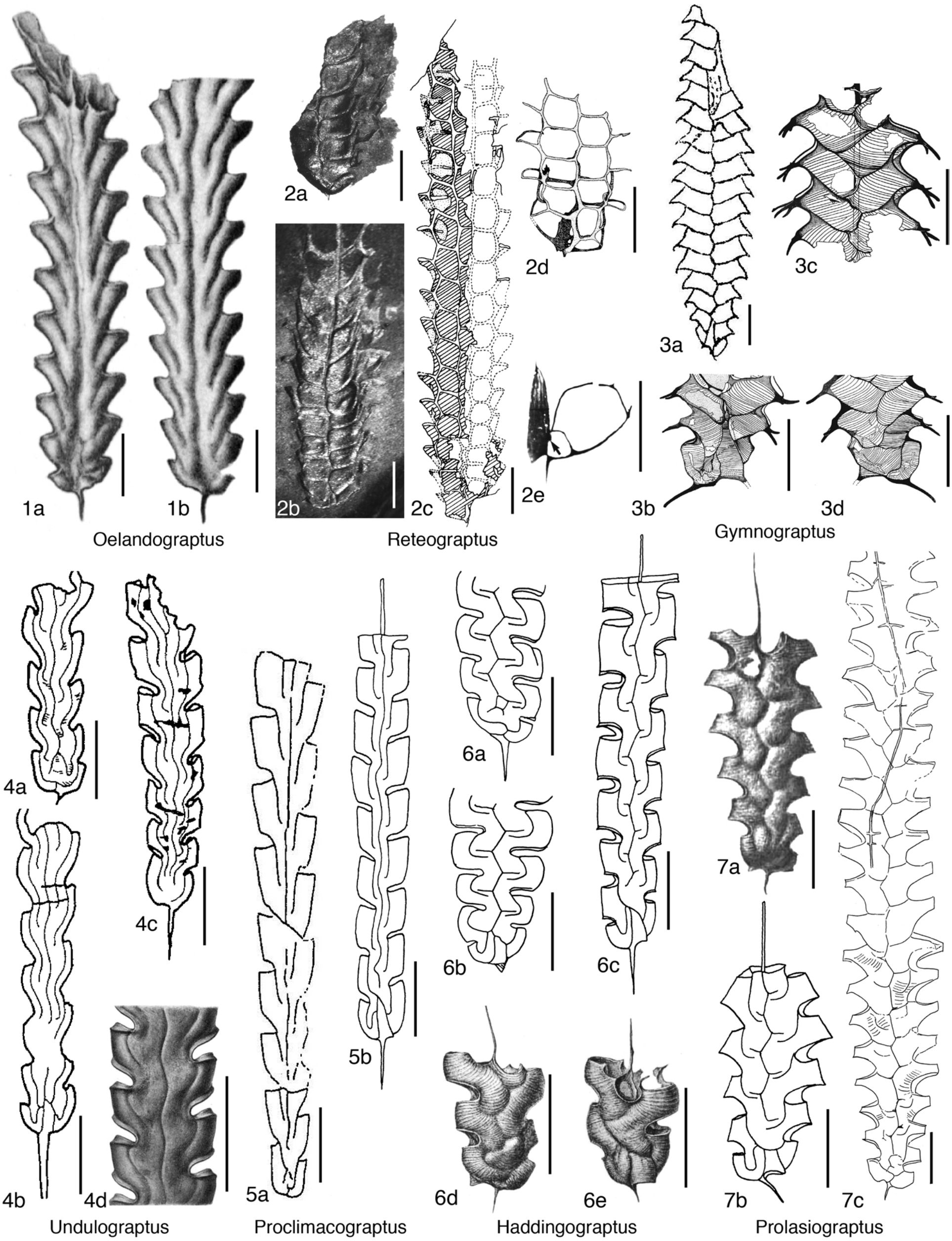

FIG. 248. Stem group Neograptina (p. 370–372).

fasciculatus Biozone–*Pterograptus elegans* Biozone): Czech Republic, Norway, Sweden, China.——FIG. 248,*5a*. **P. bulmani,* holotype, PMO 138.711, reverse view, Almedalsveien, Slemmestad, Norway, scale bar, 1 mm (Maletz, 1997a, fig. 34C).——FIG. 248,*5b*. *P. angustatus* (EKSTRÖM, 1937), PMO 138.810, proximal end in obverse view, scale bar, 1 mm (Maletz, 1997a, fig. 33K).

Prolasiograptus LEE, 1963, p. 564 (p. 574, English text) [**Lasiograptus retusus* LAPWORTH, 1880a, p. 175; OD]. Neograptines with widely rounded proximal end, virgella as single proximal end spine; thecae with distinct geniculum, short, inward-inclined supragenicular walls; proximal development of pattern C astogeny. *Middle Ordovician* (*Darriwilian*, *Pseudamplexograptus distichus* Biozone):

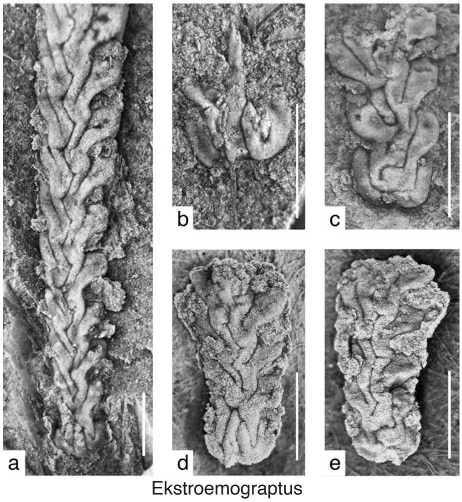

FIG. 249. Stem group Neograptina (p. 370).

Britain, Germany, Norway, Sweden, China.——FIG. 248,*7a–c*. **P. retusus* (LAPWORTH); *7a,* NRM Cn 226 (Holm collection), Gärslösa, Öland, Sweden (illustrated as *Climacograptus scharenbergi* in Bulman, 1932a, pl. 1,*25–26*); *7b,* NRM 213 (Holm collection), Gärslösa, Öland, Sweden (Maletz, 1997a, fig. 29G); *7c,* holotype, BU 1349, Llandrindod Wells, Llandeilo, Wales, UK (new, drawing by C. E. Mitchell). Scale bars, 1 mm.

Reteograptus HALL, 1859b, p. 518 [**R. geinitzianus;* OD] [=*Retiograptus* HALL, 1865, p. 115 *nom. null.;* =*Clathrograptus* LAPWORTH, 1873b, table facing p. 555 (type, *C. cuneiformis,* OD), syn. by ELLES & WOOD, 1908, p. 315]. Proximally rounded, robust neograptines; fusellum strongly reduced, lacking in biostratigraphically younger taxa; preserved frequently as clathrial framework outlining tubarium; internal construction and proximal development unclear; sicula small, with complete prosicula, widening considerably toward aperture. *Middle Ordovician* (*upper Darriwilian, Pterograptus elegans* Biozone)–*Upper Ordovician* (*Sandbian, Climacograptus bicornis* Biozone): worldwide.——FIG. 248,*2a–b*. *R. speciosus* HARRIS, 1924, Darriwilian, Slemmestad, Oslo Region, Norway; *2a,* PMO 138.440, reverse view; *2b,* PMO 138.436, obverse view; scale bars, 1 mm (Maletz, 1997a, pl. 7l and pl. 6i, respectively).——FIG. 248,*2c–e*. **R. geinitzianus; 2c,* lectotype, AMNH 37757, Austin Glen Graywacke (Normanskill Shale), Kenwood near Albany, New York, USA, scale bar, 1 mm; *2d,* OSU 32915, chemically isolated proximal end in reverse view, Pratt's Syncline, Athens Shale, Alabama, USA, scale bar, 1 mm; *2e,* OSU 32918, juvenile showing origin of th1[1] (*arrow*), Pratt's Syncline, Athens Shale, Alabama, USA, scale bar, 0.5 mm (*2c–e,* Finney, 1980, fig. 12c, 13f, and 14, respectively).

Undulograptus BOUČEK, 1973, p. 121 [**Pseudoclimacograptus formosus* MU & LEE, 1958, p. 406; OD; ?=*Climacograptus novaki* PERNER, 1895, pl. 7,*12a* (holotype, NM-L-7546, designated by BOUČEK, 1973, p. 114); ?=*Pseudoclimacograptus klabavensis* BOUČEK, 1973, p. 119, syn. by KRAFT & KRAFT, 2003, p. 136]. Neograptines with slender tubarium, with wide, rounded proximal end lacking spines except for commonly elongated virgella; geniculum rounded; proximal development of pattern C astogeny; median septum strongly undulate; thecae long, with double sigmoidal shape, without intrathecal folds, and with straight horizontal apertures. *Middle Ordovician* (*Darriwilian, Levisograptus dentatus* Biozone): Czech Republic, Sweden, Germany, Turkey, China.——FIG. 248,*4a–b*. **U. formosus* (MU & LEE); *4a,* NIGP 9771b, specimen on slab with holotype, reverse view; *4b,* holotype, NIGP 9771, obverse view; scale bars, 1 mm (Mitchell, 1992, fig. 2c, 2e).——FIG. 248,*4c–d. U. camptochilus* (SKEVINGTON, 1965); *4c,* NRM Cn 59945, isolated specimen, scale bar, 1 mm (Mitchell, 1992, fig. 2a); *4d,* NRM Cn 59944, note unusual apertural flanges, scale bar, 1 mm (Bulman, 1936a, pl. 3,*30*).

Family NORMALOGRAPTIDAE Štorch & Serpagli, 1993

[Normalograptidae ŠTORCH & SERPAGLI, 1993, p. 14] [=superfamily Normalograptacea MITCHELL & others, 2007, p. 337] [=Metaclimacograptidae KOREN' & RICKARDS, 1996, p. 94]

Biserial tubaria with asymmetrical, usually narrow, rounded to pointed proximal end and short sicula; primordial astogeny of pattern H (see MITCHELL, 1987) or derived pattern; first two thecae closely adpressed to sicula, lacking spines; thecae with straight to undulate or geniculate ventral thecal walls; median septum straight to strongly sigmoidal, sometimes angular; median septum formed intermittently or lacking in some taxa. *Middle Ordovician* (*Darriwilian, Holmograptus lentus* Biozone)–*Silurian* (*upper Telychian,* ?*Oktavites spiralis* Biozone): worldwide.

ŠTORCH and others (2011) discussed the family Normalograptidae as a paraphyletic taxon and extended it to include the basal Neograptina. The authors erroneously included all post-Hirnantian graptolites in the Normalograptidae in their cladistic diagram (ŠTORCH & others, 2011, fig. 6), even though they explicitly excluded them in the accompanying text. MELCHIN and others (2011, p. 293)

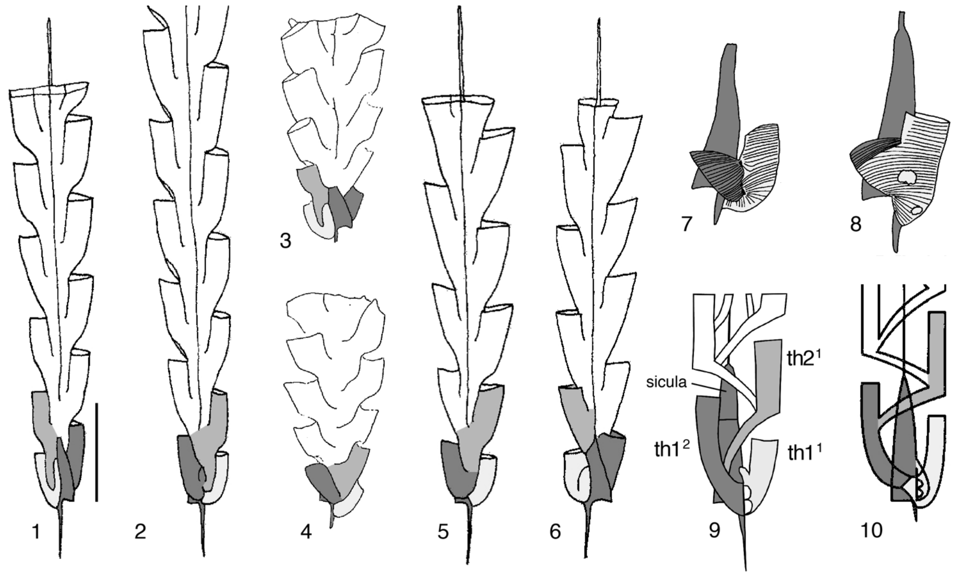

FIG. 250. Proximal development and colony shape of biserial Neograptina. *1–2*, *Proclimacograptus bulmani* MALETZ, 1997a in reverse (*2*) and obverse (*1*) views (new); *3–4, Skanegraptus janus* MALETZ, 2011b, in reverse (*4*) and obverse (*3*) views (adapted from Maletz, 2011b, fig. 2); *5–6, Pronormalograptus antiquus* (GE in GE, ZHENG, & LI, 1990) in reverse (*5*) and obverse (*6*) view (adapted from Maletz, 2011b, fig. 2); *7, Metaclimacograptus orientalis* (OBUT & SOBOLEVSKAYA, 1966), GSC 104912 (adapted from Melchin, 1998, fig. 4A); *8, Korenograptus nikolayevi* (OBUT, 1965), a neodiplograptid, GSC 104823, pattern H′ astogeny (adapted from Melchin, 1998, fig. 4B); *9*, diagram showing pattern H astogeny (adapted from Mitchell, 1987, fig. 1H); *10*, diagram showing pattern H′ astogeny (adapted from Melchin, 1998, fig. 2H). Sicula and thecae shading coded for easy comparison (*9*); scale bar, 1 mm (bar for *1* applies to *1–6*); *7–10* not to scale).

stated that "As a consequence of the variety of proximal and thecal morphologies found among taxa within this stem group, it is not currently possible to identify any morphologic criteria that can be used to uniquely characterize this taxon." The Normalograptidae represents a family with roots in the lower Darriwilian (Middle Ordovician). Both the precise origin of the Normalograptidae from a taxon of the early Neograptina *incertae sedis* and the relationship to the Climacograptidae are unclear (MALETZ, 2011b). The origin and subsequent differentiation of the Normalograptidae may need to be reevaluated, and it is herein preferred to base them on the origin of a pattern H astogeny instead of including 1) taxa with pattern A to pattern C astogenies and 2) lack of proximal spines except for the virgella (e.g., the taxa included in the stem group Neograptina). The first taxon with a proximal end pattern similar to proximal development type H is the genus *Skanegraptus,* but this taxon still has a number of characters similar to taxa with a pattern C astogeny (MALETZ, 2011b).

MORPHOLOGY

Normalograptidae contains a number of biserial, dipleural graptoloids with a rounded to pointed proximal end and a single proximal end spine, the virgella (Fig. 250.3–250.7). Their thecal style is simple—thecae with straight, outward-inclined to strongly geniculate ventral thecal walls. Geniculate thecae are prevalent and genicular elaborations are common. The thecal apertures are horizontal to everted and in geniculate taxa generally slit-like. A long nema is typical of many species and may be modified into an elongated nematularium.

MITCHELL (1987) introduced the proximal development pattern H based on the investigation of *Normalograptus brevis* (Elles & Wood, 1906) and *Normalograptus kukersianus* (Wiman, 1895), a pattern that is considered characteristic of most Normalograptidae. In *Skanegraptus,* $th1^1$ grew downward along the ventral side of the sicula to a point below the sicular aperture and upward again in a U-shaped loop that left a space between the downward- and upward-growing parts on the obverse side (Fig. 250.3), in which the early part of $th2^1$ is visible. In derived taxa, the metathecal part of $th1^1$ grew attached to the dorsal side of its protheca (Fig. 250.6). There are two separate openings at the base of the downward growth of $th1^1$, one for the metatheca of $th1^1$ and the second for the origin of $th1^2$ (Fig. 250.9). An unconformity appears at the point of origin of $th1^2$ (Fig. 250.7) on the reverse side of the tubarium in pattern H species. In taxa of the derived pattern H′ in neodiplograptids, the unconformity was delayed (Fig. 250.8, Fig. 250.10), but otherwise the development was identical.

The thecae are fairly simple tubes in the Normalograptidae. The earliest known species, *Skanegraptus janus* Maletz, 2011b, has thecae with slightly convex ventral walls and moderate thecal overlap. The thecal apertures are straight and slightly everted. Most species, however, possess strongly geniculate thecae with a quite variable degree of genicular modification, mostly in the form of thickened genicular rims, but genicular flanges and even spines may exist. A considerable thickening may also be present around the thecal apertures, but other modifications have not been noted. Considerable genicular hoods developed in several *Metaclimacograptus* species. These were formed from the dorsal wall of the theca (not the ventral wall as stated by Loydell & Maletz, 2009, p. 279) before much of the succeeding theca was formed above it. These hoods display a distinct unconformity and, thus, may not be homologous to the genicular flanges in the diplograptids (e.g., *Archiclimacograptus*) and many neograptines in which the flanges or hoods are secondary constructions at the thecal geniculum.

The thecae (Fig. 250) have a short, straight, or slightly curved interthecal septum. An abrupt widening of the metatheca exists in many taxa at the aperture of the mother theca, after which the thecal tubes are nearly parallel sided (e.g., *Metaclimacograptus*). Apertural spines, except for the virgella, are extremely rare in the Normalograptidae, and chemically isolated material of such features does not exist. The genus *Hirsutograptus* bears multiple antivirgellar spines and paired genicular spines on the thecae. These spines may branch distally. Elongated basal spines appear in *Normalograptus trifilis* (Manck, 1923) and *Normalograptus longifilis* (Manck, 1924) and may be more common in the normalograptids.

The development of the median septum is quite variable in the Normalograptidae. The median septum appears to be lacking in part on the obverse side and is not developed on the reverse side in the only available relief specimen of *Skanegraptus janus* (Fig. 250.3–250.4). Early members of the Normalograptidae may bear a complete median septum on the obverse side, as in *Pronormalograptus antiquus* (Fig. 250.5–250.6). The median septum starts approximately at the base of $th3^1$ on the reverse side, and the first four thecae appear to be alternating in origin. In derived species, the median septum may be delayed considerably. The median septum is straight to considerably undulate, but intrathecal folding has not been recognized. It does not have the characteristic crossbars of the derived climacograptids (Goldman & others, 2011).

BIOGEOGRAPHY AND EXTINCTION

The Ordovician Normalograptidae are difficult to differentiate from the Climacograptidae. However, a number of constructional differences can be noted, and Goldman and others (2011) used these to recognize a distinct pattern of extinction and reinvasion of Upper Ordovician normalograptids in the palaeotropical regions (Fig. 251). The normalograptids apparently

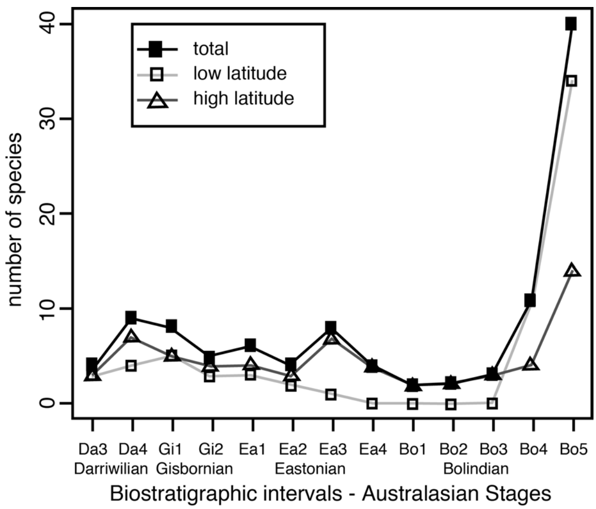

FIG. 251. Normalograptid diversity in the Upper Ordovician (redrawn from Goldman & others, 2011).

originated in high latitude regions during the early to middle Darriwilian and from there spread to the paleotropics. During the early Katian, the clade suddenly disappeared from low paleolatitudes, but reinvaded the regions during the late Katian to early Hirnantian.

The Normalograptidae formed one of the few axonophoran groups surviving the Hirnantian extinction and then quickly rediversified during the Llandovery. Actually, the Monograptoidea, Retiolitoidea, and Normalograptidae started to diversify during the Upper Ordovician (Katian to Hirnantian) time interval, while the Diplograptina went extinct at the end of the Hirnantian (BAPST & others, 2012). The Neograptina, especially the Monograptidae, apparently experienced one of the largest diversification events in graptolite history during the Llandovery, early Silurian (MELCHIN & others, 2011; SADLER, COOPER, & MELCHIN, 2011). However, a comparison of the diversity studies is difficult due to varying taxonomic concepts at the family level and higher taxonomical units in the analyses (see Retiolitoidea in BAPST & others, 2012; Retiolitidae and Petalolithidae in SADLER, COOPER, & MELCHIN, 2011). GOLDMAN and others (2011) indicated a total diversity of the Normalograptidae with 39 taxa in the Bo5 (upper Hirnantian, *Metabolograptus persculptus* Biozone), but BAPST and others (2012) indicated the presence of only five species in the interval. After the Hirnantian extinction event, the normalograptids rediversified and evolved during the Silurian to produce the Monograptidae as one of the most successful groups of planktic graptoloids. A number of diversity peaks and minor to major extinction events (e.g., ŠTORCH, 1995; SADLER, COOPER, & MELCHIN, 2011) also constituted the evolutionary pattern of the Silurian graptoloids and led to a bloom of the Normalograptidae, Petalolithinae, and Retiolitinae until the complete extinction of the biserial axonophorans in the late Silurian.

Normalograptus LEGRAND, 1987, p. 62 [**Climacograptus scalaris normalis* LAPWORTH, 1877, p. 138; OD] [=*Scalarigraptus* RIVA, 1988, p. 230 (type, *Climacograptus scalaris normalis* LAPWORTH, 1877, p. 138, OD), obj.]. Normalograptids with pattern H astogeny; unornamented geniculate thecae with straight or concave interthecal septa throughout tubarium; complete median septum, slightly undulate to straight, may be delayed; genicular hoods common. *Middle Ordovician* (*upper Darriwilian, Pterograptus elegans* Biozone)*–Silurian, Llandovery (Telychian, Spirograptus turriculatus* Biozone): worldwide.——FIG. 252,*1a–b*. **N. normalis* (LAPWORTH); holotype, BU 1136, *Parakidograptus acuminatus* Biozone, Dob's Linn, Southern Uplands, Scotland, UK, scale bars, 1 mm (Blackett & Zalasiewicz, 2008, Atlas, Folio 2.61).

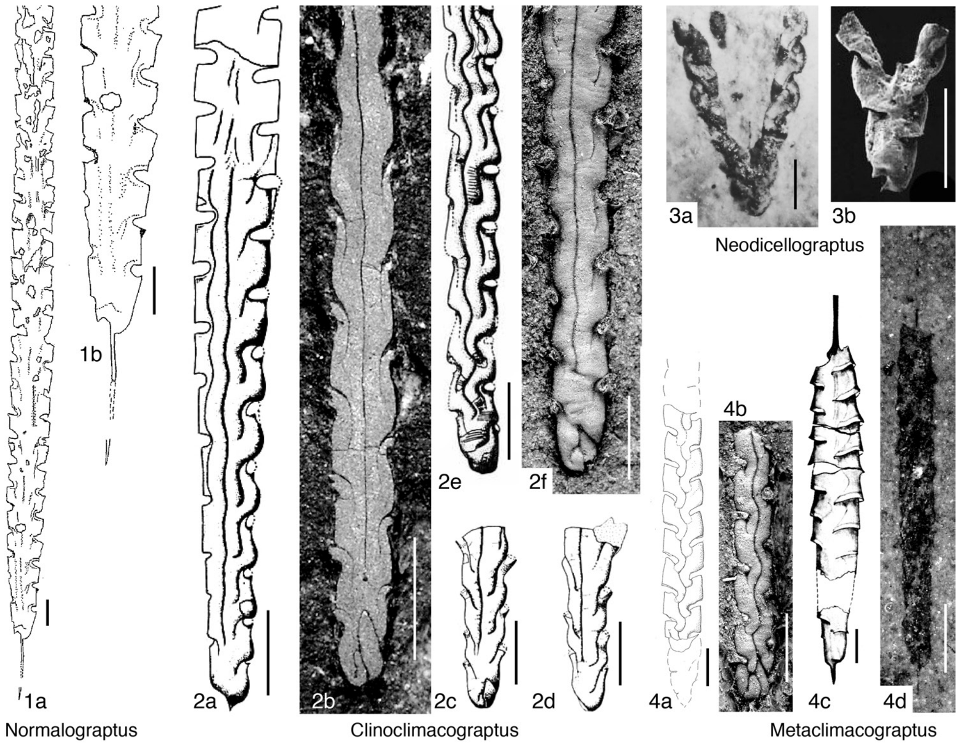

FIG. 252. Normalograptidae (p. 375–377).

Clinoclimacograptus BULMAN & RICKARDS, 1968, p. 8 [**Pseudoclimacograptus* (*Clinoclimacograptus*) *retroversus;* OD] [=*Pseudoglyptograptus* BULMAN & RICKARDS, 1968, p. 13 (type, *Pseudoglyptograptus vas* BULMAN & RICKARDS, 1968, p. 13, OD), syn. herein]. Normalograptid with proximally convex and distally concave supragenicular walls; thecal apertures strongly everted; median septum gently undulating proximally, distally straight; interthecal septae one-half the length of the supragenicular thecal walls proximally, ~two-thirds to three-fourths distally. [*Pseudoglyptograptus* is based on internal casts of *Clinoclimacograptus* as can be shown from the sectioned pyrite-filled material of TÖRNQUIST (see Fig. 252,*2b*)]. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone–*Stimulograptus sedgwickii* Biozone): UK, Sweden, China.——FIG. 252,*2a–f*. **C. retroversus* (BULMAN & RICKARDS); *2a,* holotype, SM A52951, reverse view, ?*Stimulograptus sedgwickii* Biozone, Tomarp, Scania, Sweden (Bulman & Rickards, 1968, fig. 4b); *2b,* LO 1097t (identified as *Climacograptus scalaris* HISINGER, 1837 by TÖRNQUIST, 1893, pl. 1,*7–8*), Tomarp, Scania, Sweden (new); *2c–d,* GSM WEG 4058, holotype of *Pseudoglyptograptus vas* (BULMAN & RICKARDS) proximal end in obverse (*c*) and reverse (*d*) views, *Neodiplograptus magnus* Biozone, Cross Fell, northern England, UK (Bulman & Rickards, 1968, fig. 1K–L); *2e*, SM A23951, *Stimulograptus sedgwicki* Biozone, Spengill, Westmorland, UK (Bulman & Rickards, 1968, fig. 4a); *2f,* LO 11860t, obverse view, Röstånga drill core, 35.40–35.30 m, Scania, Sweden (Maletz, Ahlberg, & others, 2014, fig. 1K). Scale bars, 1 mm.

Hirsutograptus KOREN' & RICKARDS, 1996, p. 38 [**H. longispinosus;* OD]. Normalograptids with pattern H astogeny; geniculate thecae bearing laterally and ventrally directed genicular hoods, genicular spines, or both; full median septum. *Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus*/*Parakidograptus acuminatus* Biozone): Kazakhstan, Canada, China, UK (Scotland).——FIG. 253,*2a*. **H. longispinosus,* holotype, CNIGR 103/12879, Zhaksy-Kargala Valley, Kazakhstan, scale bar, 1 mm (Koren' & Rickards, 1996, fig. 8A).——FIG. 253,*2b–c*. *H. villosus* KOREN' & RICKARDS, 1996, Kos-Istek region, Kazakhstan; *2b,* juvenile, CNIGR 93A/12879 (Koren' & Rickards, 1996, fig. 7C); *2c,* holotype, CNIGR 90/12879, (Koren' & RICKARDS, 1996, fig. 8C). Scale bars, 1 mm.——FIG. 253,*2d*. *H. sinitzini* (KHALETZKAYA, 1960), Kurama Range, Uzbekistan, GSC 118401, scale bar, 1 mm (Koren' & Melchin, 2000, fig. 8,*16*).

Metaclimacograptus BULMAN & RICKARDS 1968, p. 3 [**Diplograpsus hughesi* NICHOLSON 1869, p. 235; OD] [=*Lithuanograptus* PAŠKEVIČIUS, 1976,

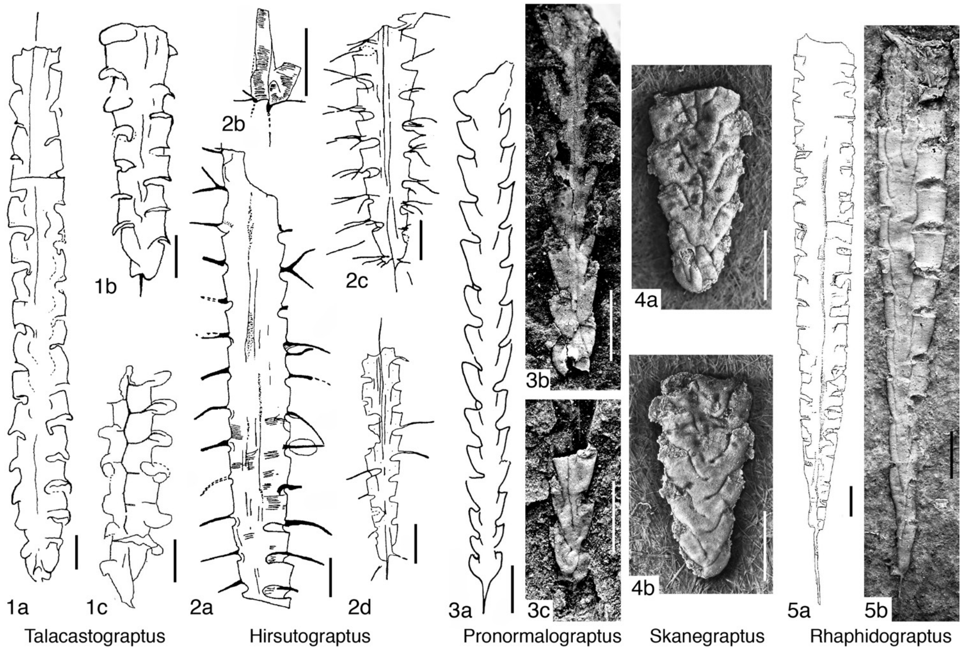

FIG. 253. Normalograptidae (p. 376–378).

p. 141 (type, *L. fusiformis* PAŠKEVIČIUS, 1976, p. 142, OD); syn. by LOYDELL, 1993, p. 55; =*Retioclimacis* Nanjing Institute of Geology and Palaeontology in MU & others, 1974, p. 215 (type, *R. typica,* OD, =*Metaclimacograptus undulatus* [KURCK, 1882]), *syn. by* LOYDELL, 1993, p. 55]. Normalograptid with pattern H astogeny and an undulose to zigzag median septum; convex or concavo-convex subapertural thecal walls and apertural introversion; very short thecal overlap; genicular thecal hoods formed from dorsal thecal wall, not as secondary genicular additions. *Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus* Biozone–*Telychian, Monoclimacis crenulata* Biozone): worldwide.——FIG. 252,*4a–b*. **M. hughesi* (NICHOLSON); *4a*, neotype (designated by PŘIBYL, 1948a, p. 18), NHMUK Q1360, ?*leptotheca* Biozone, Skelgill beds, Ambleside, England, UK (Zalasiewicz, 2000b, Atlas, Folio 1.42); *4b,* PMU 34438, obverse view, Röstånga drill core, 36.70–36.60 m, Scania, Sweden, scale bars, 1 mm (new).——FIG. 252,*4c. M. fusiformis* (PAŠKEVIČIUS, 1976), holotype, *Coronograptus cyphus* Biozone, Paroveja drill core, 721 m, Lithuania, scale bar, 1 mm (Paškevičius, 1979, pl. 2,*5*).——FIG. 252,*4d. M. undulatus* (KURCK, 1882), NIGP 45344, illustrated as *Retioclimacis typica* MU & LI, 1974 by NI (1978, pl. 2,*15*), scale bar, 1 mm (new).

Neodicellograptus MU & WANG, 1977, p. 313 [**N. dicranograptoides;* OD; =‘*Dicellograptus*’ *siluricus* MU & others, 1974, p. 211; syn. herein]. Normalograptid with pattern H astogeny; stipes diverging distally; thecae geniculate with introverted apertures; undulose dorsal stipe walls. *Silurian, Llandovery* (?*upper Rhuddanian, Cystograptus vesiculosus* Biozone–*Aeronian, Lituigraptus convolutus* Biozone): China, Canada.——FIG. 252,*3a–b*. **N. siluricus* (MU & LI); *3a,* syntype, repository unknown, scale bar, 1 mm (Mu & others, 1974, pl. 99,*2;* photo provided by Xiao-feng Wang); *3b*, GSC 104837, Cape Manning section, Cornwallis Island, Arctic Canada, scale bar, 1 mm (Melchin, 1998, pl. 2,*12*).

Pronormalograptus CHEN in CHEN & others, 2017, p. 325 [**P. acicularis;* OD]. Normalograptids with pattern H proximal development; proximal end narrow, rounded, asymmetrical with short sicula; thecae with low angle of inclination to tubarium axis; thecae biform, commonly geniculate proximally, with curved to straight ventral thecal walls distally; medium septum complete or incomplete. *Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.——FIG. 253,*3a*. **P. acicularis;* holotype, NIGP 157666, Dashimen section, Wuhai, Inner Mongolia, China, scale bar, 1 mm (Chen & others, 2017, fig. 6-102H).——FIG. 253,*3b–c. P. antiquus* GE in GE, ZHENG, & LI, 1990, *Pterograptus elegans* Biozone, Elnes Formation, Slemmestad, Norway; *3b,* PMO 234.255, obverse view; *3c,* PMO 234.061; scale bars, 1 mm (new).

Rhaphidograptus BULMAN, 1936b, p. 25 [**Climacograptus toernquisti* ELLES & WOOD, 1906, p.

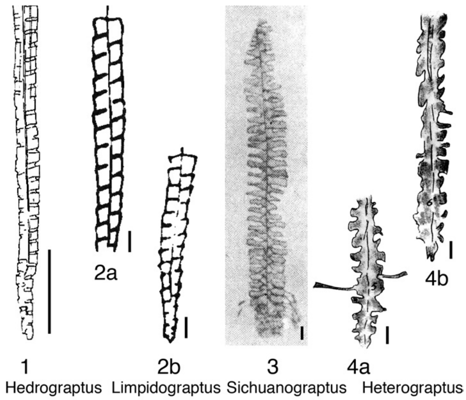

FIG. 254. Normalograptidae indet. (p. 378–379).

190; OD]. Normalograptids with pattern H astogeny modified by the presence of uniserial theca 1, produced by truncation of growth of th1²; thecae geniculate with genicular flanges, straight supragenicular walls; median septum complete on obverse side, considerably delayed on reverse side. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone–*Aeronian, Lituigraptus convolutus* Biozone): UK, Czech Republic, Sweden, Germany, Poland, ?Canada.——FIG. 253,*5a–b*. **R. toernquisti* (ELLES & WOOD); *5a,* lectotype (designated by PŘIBYL, 1948a, p. 20), BU 1155, Birkhill Shale, Dob's Linn, Southern Uplands, Scotland, UK, scale bar, 1 mm (Zalasiewicz, 2008a, Atlas, Folio 2.91); *5b,* LO 1456t, latex cast in reverse view showing delay of median septum, specimen on slab with holotype of *Monograptus incommodus* TÖRNQUIST, 1899, scale bar, 1 mm (new).

Skanegraptus MALETZ, 2011b, p. 53 [* *S. janus;* OD]. Normalograptid with pointed, asymmetrical proximal end, lacking apertural spines on first thecal pair; proximal end with U-shaped th1¹; paired early differentiation of th1² and th2¹ on reverse side; thecae with short overlap, straight outward-inclined apertures, lacking geniculum; median septum incomplete; thecal origins alternate. *Middle Ordovician, Darriwilian* (*Holmograptus lentus* Biozone): Sweden.——FIG. 253,*4a–b*. **S. janus,* holotype, LO 11196T, in obverse (*a*) and reverse (*b*) views, Krapperup drill core, Scania, Sweden, scale bars, 1 mm (Maletz, 2011b, fig. 1d and 1g).

Talacastograptus CUERDA, RICKARDS, & CINGOLANI, 1988, p. 753 [**T. leanzai;* OD] [=*Songxigraptus* FANG & others, 1990, p. 87 (English text, p. 135) (type, *S. elongatus*, OD); syn. herein]. Normalograptid with pronounced genicular hoods, which in profile views of tubarium, give thecae strongly hooked appearance, especially at proximal end; thecae strongly geniculate; ventral thecal margins introverted, strongly overgrown by genicular hoods; supragenicular wall convex; median septum complete, gently undulating to straight. *Lower Silurian* (*Llandovery, Rhuddanian, Atavograptus atavus* Biozone): Argentina, China.——FIG. 253,*1a–c*. **T. leanzai; 1a,* holotype, DPI 21883; *1b,* paratype, DPI 21884, proximal end in reverse view; both from La Chilca Formation, 16 km WNW of Talacasto station, San Juan Province, Argentina, scale bars, 1 mm (Cuerda, Rickards, & Cingolani, 1988, fig. 4a–b); *1c,* SM X. 28480, Lipéon Formation, Argentina, scale bar, 1 mm (Rickards & others, 2002, fig. 4e).

UNCERTAIN TAXA

A number of taxa listed here may be normalograptids, but are too poorly preserved or lack the proximal end for a more specific identification. They are listed and illustrated here in the interest of being complete, but these genera should not be considered available for further taxonomic purposes.

Hedrograptus OBUT, 1949, p. 13 [**H. janischewskyi;* OD]. *Silurian, Llandovery* (*Rhuddanian–?Aeronian*): Russia. [According to RIVA (1988, p. 225), "OBUT (1949) erected the genus *Hedrograptus* for early Silurian climacograptids with insignificant or incomplete apertural excavations on one side of the rhabdosome and complete on the other." RIVA (1988) provided a drawing of a latex cast of the type *H. janischewskyi*. According to this, the taxon does not bear any proximal spines except for the virgella and has a pointed proximal end, indicating a normalograptid relationship. The specimen is preserved in scalariform view and is indeterminate at the genus and species level.]——FIG. 254,*1*. **H. janischewskyi*, holotype, I.G.G.-COAH-SSSP No. 278/5, 1945, drawing from latex cast, scale bar, 10 mm (Riva, 1988, fig. 6).

Heterograptus HERNÁNDEZ SAMPELAYO, 1960, p. 33, *nom. dub.* [*type not designated]; *non Heterograptus* ZHAO & ZHANG in LIN, 1986, p. 241 (syn. of *Rhabdinopora*, Anisograptidae)]. *Silurian, Llandovery* (*Telychian*): Spain (Almadén). [Taxon is characterized by prolonged mesial spines and thecae, giving them an aspect of *Glossograptus;* possibly based on specimens of *Metaclimacograptus flamandi* (LEGRAND, 1993). Information provided by Juan Carlos Gutiérrez Marco.]——FIG. 254,*4a–b*. *Heterograptus* examples, scale bars 1 mm (Hernández Sampelayo, 1960, pl. 15,*5–6*).

Limpidograptus KHALETZKAYA, 1962, p. 72 [**L. posohovae;* OD]. *Silurian* (*Llandovery*): Uzbekistan (Tian-Shan). [This genus might be based on a scalariform biserial and is indeterminable at the genus and species level.]——FIG. 254,*2a–b*. **L. posohovae*, scale bars, 1 mm (Khaletzkaya, 1962, pl. 9,*11a–b*).

Sichuanograptus ZHAO in YE, 1978, p. 474 [**S. pennatus;* OD]. Axonophorans with biserial tubarium; proximally the periderm normal, but thecae largely isolated, with common dissepiments, apertural spines, and floating vesicles, whereas distally the thecal walls are reduced and form clathria and reticula (diagnosis translated by Yuandong Zhang, 2017). *Silurian, Llandovery* (*Telychian, Spirograptus turriculatus* Biozone): China. [The taxon appears to be an indeterminable, strongly decayed or weathered normalograptid with thickened apertural rims.]——FIG. 254,*3*. **S. pennatus*, holotype, Qiaotang, Nanjiang, Sichuan Province, China, scale bar, 1 mm (Mu & others, 2002, p. 799, pl. 211,*3*).

SUPERFAMILY RETIOLITOIDEA

Jörg Maletz

Superfamily RETIOLITOIDEA Lapworth, 1873

[Retiolitoidea Lapworth, 1873b, table 1, facing p. 555, *nom. correct.* Kozłowska-Dawidziuk, Lenz, & Bates, 2003, p. 51, *ex* Retioloidea Lapworth, 1873b, table 1, facing p. 555] [=order Retiolitina Mikhaylova, 1970, p. 103, *partim*]

Neograptine axonophorans with scandent, biserial, dipleural, bistipular to unistipular tubarium; proximal development pattern supposedly of pattern H astogeny or a derived pattern, but development unknown in many taxa; thecae with straight to curved ventral walls; distinct geniculum present in some, with or without genicular additions; ancora, ancora umbrella, and ancora sleeve in derived Retiolitidae. *Upper Ordovician* (*Katian, Paraorthograptus pacificus* Biozone)–*Silurian, Ludlow* (*Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide.

Kozłowska-Dawidziuk, Lenz, and Bates (2003) regarded the presence of the ancora umbrella as the defining character for the Retiolitoidea and included the ancorate petalolithines in the clade. Melchin and others (2011) extended the concept of the Retiolitoidea by including the Neodiplograptidae (Fig. 255). No morphological diagnosis was provided for the taxon, but it was defined as "the most recent common ancestor of *Metabolograptus ojsuensis* and *Retiolites geinitzianus* and all of its descendants (Melchin & others, 2011, node 3, fig. 2–3)." The authors expanded the concept of the Retiolitoidea considerably from what was generally understood to be a retiolitid by adding a number of taxa that bear no indications of a true ancora. Melchin and others (2011, p. 296, node 3 in fig. 3) considered the presence of inclined, distal apertural thecal walls and inclined, interthecal septa as important synapomorphies of the Retiolitoidea, although there are no interthecal septa present in the derived retiolitines. The base of node 3 is collapsed into a polytomy in their figure 3, indicating the low bootstrap support of the nodes in this region of their cladogram (Melchin & others, 2011, fig. 2).

EVOLUTION

The Retiolitoidea originated in the Upper Ordovician through a normalograptid ancestor, but the precise biostratigraphic timing of the origin of the clade is uncertain (see Melchin & others, 2011, fig. 7). The oldest members of the Retiolitoidea appear to be *Neodiplograptus charis* (Mu & Ni, 1983) and *Metabolograptus ojsuensis* (Koren' & Mikhaylova in Koren', Mikhaylova, & Tzai, 1980) from the late Katian (Melchin & others, 2011).

The Retiolitoidea includes a basal paraphyletic family Neodiplograptidae with a number of very similar genera having an initial low disparity and low diversity in the uppermost Ordovician to lowermost Silurian. In the Llandovery, however, the diversification increased considerably with the evolution of the ancora sleeve and the following radiation of the Retiolitidae (see Lenz & others, 2018).

Family NEODIPLOGRAPTIDAE Melchin & others, 2011

[Neodiplograptidae Melchin, Mitchell, Naczk-Cameron, Fan, & Loxton, 2011, p. 296] [incl. Cameragraptidae Hundt, 1953b, p. 3, *nom. dub.*]

Biserial, dipleural neograptines with pattern H proximal development type or derived one; first thecal pair with outward-inclined apertures forming lip in derived taxa; thecae in many taxa having considerable biform development; ventral side of thecae rounded to geniculate, distally straight with outward-inclined straight apertures; medium septum complete, partial or lacking; interthecal septae outward inclined. *Upper Ordovician* (*upper Katian, Paraorthograptus pacificus* Biozone)–*Silurian, Llandovery* (*Telychian, Monoclimacis griestoniensis* Biozone): worldwide.

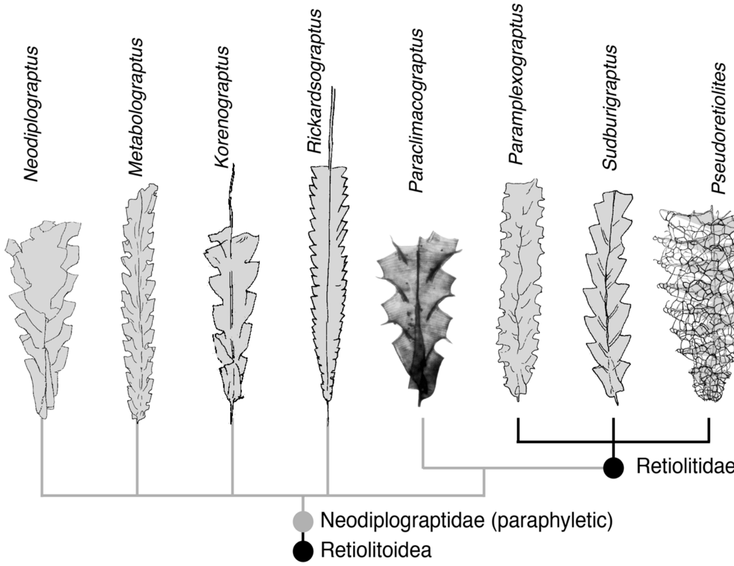

FIG. 255. Cladogram explaining the concept of the Retiolitoidea and the paraphyletic Neodiplograptidae; specimens from various sources, not to scale (new; based on data in MELCHIN & others, 2011).

MELCHIN and others (2011, p. 296) analyzed the early Silurian biserial axonophorans and erected the family Neodiplograptidae as "the partial clade that includes the most recent common ancestor of *Metabolograptus ojsuensis* and *Retiolites geinitzianus,*" and referred quite a number of taxa to the Retiolitoidea. MALETZ (2014b), however, identified only taxa with an ancora sleeve meshwork as the Retiolitoidea and preferred to include the non-ancorate Petalolithinae in the Neodiplograptidae.

The Neodiplograptidae, as defined by MELCHIN and others (2011), represents a poorly resolved clade with a basal polytomy (Fig. 255), indicating the difficulty of differentiating the individual taxa based on the largely flattened material available for investigation. As a paraphyletic taxon, the Neodiplograptidae led to the monophyletic Retiolitidae through a number of steps in the development of the ancora umbrella and ancora sleeve as an external, secondary development around the biserial tubarium. MELCHIN and others (2011) separated the retiolitid *Paramplexograptus* MELCHIN & others, 2011 from the neodiplograptid *Paraclimacograptus* through the lack of a median septum in *Paramplexograptus*. Otherwise the two genera are basically inseparable (Fig. 255).

MORPHOLOGY

The proximal development (Fig. 256) of the Neodiplograptidae ranges from a pattern H astogeny to a pattern H′ astogeny. The details of the proximal development of many of the taxa included in the analysis of MELCHIN and others (2011, Appendix 1) were listed as based on unpublished information. Thus, the proximal development types have to be regarded as uncertain until further material is published. The proximal development of *Neodiplograptus* and *Metabolograptus* has not been demonstrated from chemically isolated material or relief specimens showing growth lines. The proximal development of *Rickardsograptus tcherskyi* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & NIKOLAEV, 1967) is known from isolated material (MELCHIN 1998; MELCHIN & others, 2011). The species has a distal origin of $th1^2$ from a wide flange of $th1^1$ (Fig. 256.1–256.2), indicating a pattern H′ astogeny. A pattern H′ astogeny (Fig. 256.6) is also present in *Korenograptus*

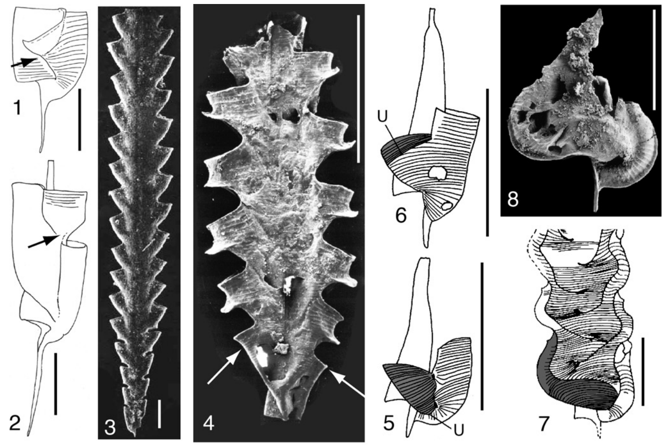

FIG. 256. Morphology and proximal development of the Neodiplograptidae. *1–3, Rickardsograptus tcherskyi* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & NIKOLAEV, 1967); *1,* juvenile showing late origin of th1^2 from large flange (new); *2,* origin of th2^1 from distal part of th1^2 (new); *3,* SEM photo of large specimen in relief showing geniculate proximal thecae and non-geniculate distal thecae (Melchin & others, 2011, fig. 4G); *4, Paraclimacograptus innotatus* (NICHOLSON, 1869), showing outward-inclined apertures with lip (*arrows*) on proximal end and geniculate thecae with strong genicular flanges (Koren' & Rickards, 2004, fig. 29); *5,* pattern H astogeny in the normalograptid *Metaclimacograptus orientalis* (OBUT & SOBOLEVSKAYA, 1966) showing unconformity (*u*) at origin of th1^2 tube; *6,* pattern H′ astogeny in *Korenograptus nikolayevi* (OBUT, 1965) with delayed unconformity (*5-6,* adapted from Melchin, 1998, fig. 4a–b) *7, Cystograptus penna* (HOPKINSON, 1869), reverse view (adapted from Jones & Rickards, 1967, fig. 2D); *8, Cystograptus vesiculosus* (NICHOLSON, 1868c), juvenile, obverse view (Koren' & Rickards, 2004, fig. 12). Scale bars, 1 mm.

nikolayevi (OBUT, 1965) as demonstrated by MELCHIN (1998, pl. 1,*4–9*) and LOYDELL and MALETZ (2009). The genus *Cystograptus,* with its extremely elongated sicula and long undulating thecae, is included preliminarily in the Neodiplograptidae following ŠTORCH (1985) and MELCHIN and others (2011, p. 296), who suggested a derivation from a species of *Neodiplograptus* or *Metabolograptus*. JONES and RICKARDS (1967) illustrated a possible pattern H astogeny for *Cystograptus penna* (HOPKINSON, 1869), which can also be supported by a single specimen of *Cystograptus vesiculosus* (NICHOLSON, 1868c) illustrated by KOREN' and RICKARDS (2004). In both taxa, the origin of th1^2 appears to be very low on the th1^1 at the point of change from downward to upward growth (Figs. 256.7–256.8) and not from an upward-growing flange on th1^1. Details of the number and position of proximal foramina are not available.

The thecal style of the Neodiplograptidae ranges from simple outward-inclined thecae with straight ventral wall and aperture to strongly geniculate thecae with ventral thecal walls parallel to the tubarium midline. Many taxa are biform with the thecal style changing considerably from the proximal to the distal end. A number of geniculate proximal thecae are present in *Rickardsograptus* but the colony quite abruptly changes to nongeniculate thecae distally (Fig. 256.3). In other genera, the change in thecal style is more gradual and imperceptible and is difficult to see in poorly preserved, flattened specimens. MELCHIN and others (2011, p. 296) indicated that the most characteristic synapomorphies of their Neodiplograptidae include the presence of inclined distal thecal subapertural walls and inclined interthecal septa. Genicular elaborations largely include flanges (Fig. 256.4), but these may appear similar to spines in the typical lateral preservation of the tubaria.

Neodiplograptus LEGRAND, 1987, p. 62 [**Diplograptus magnus* LAPWORTH, 1900, p. 132; OD]. Neodiplograptids with pattern H proximal development type with rapidly widening proximal end; thecae sharply geniculate proximally and with slightly rounded, non-geniculate ventral side in distal

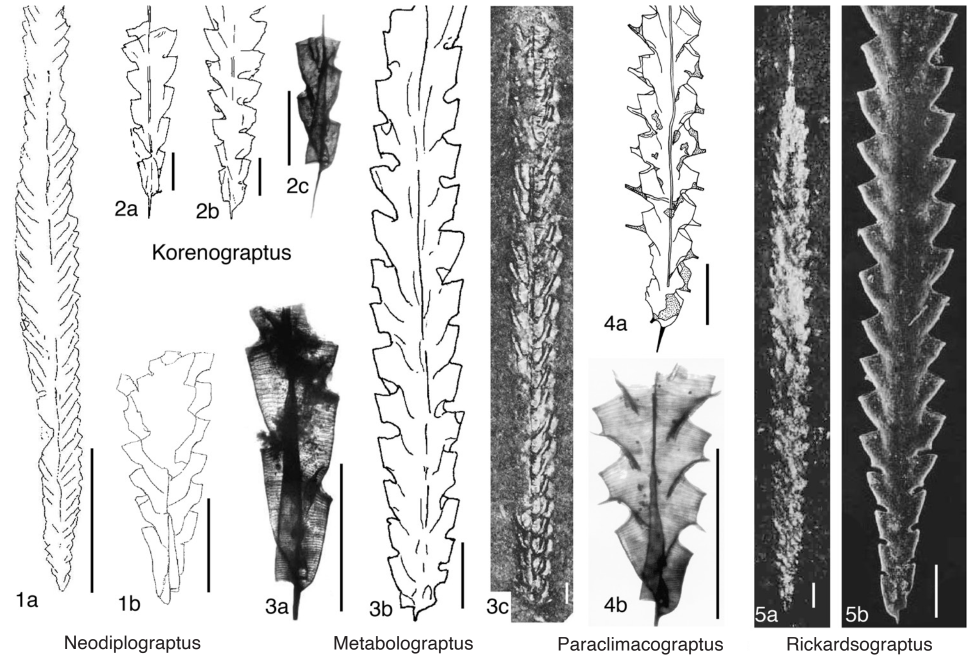

FIG. 257. Neodiplograptidae (p. 383–385).

thecae; thecal inclination increasing significantly through the proximal to mesial regions; full median septum distally. *Upper Ordovician* (*upper Katian, Paraorthograptus pacificus* Biozone)–*Silurian, Llandovery* (*Aeronian, Neodiplograptus magnus* Biozone): worldwide.——FIG. 257,*1a–b*. **N. magnus* (LAPWORTH), River Wye, Rhayader, Wales, UK; *1a,* lectotype, BU 1295, poor external mold, scale bar 10 mm; *1b,* topotype, BU 1296, obverse view, scale bar, 1 mm (Zalasiewicz, 2000c, Atlas, Folio 1.68).

Korenograptus MELCHIN & others, 2011, p. 297 [**Glyptograptus gnomus* CHURKIN & CARTER, 1970, p. 24; OD]. Neodiplograptids with a pattern H proximal development type or derived type; colony parallel sided or widening slowly from the proximal end; thecae with slightly rounded to straight, non-geniculate ventral side; full median septum distally. *Upper Ordovician* (?*upper Katian, Paraorthograptus pacificus* Biozone)–*Silurian, Llandovery* (*Rhuddanian, Neodiplograptus magnus* Biozone): worldwide.——FIG. 257, *2a–b*. **K. gnomus (*CHURKIN & CARTER), Alaska, USA; *2a,* USNM 161727; *2b,* holotype, USNM 161644; scale bars, 1 mm (Churkin & Carter, 1970, fig. 11f and 11e, respectively).——FIG. 257,*2c*. *K. magnus* (CHURKIN & CARTER, 1970), GSC 135126, Cape Manning, Nunavut, Canada, scale bar, 1 mm (Melchin & others, 2011, fig. 5i).

Metabolograptus OBUT & SENNIKOV, 1985, p. 55 [**Diplograptus modestus siberica* OBUT, 1955, p. 138; OD] [=*Persculptograptus* KOREN' & RICKARDS, 1996, p. 32 (type, *Diplograpsus persculptus* SALTER, 1873, p. 28, OD); syn. by MELCHIN & others, 2011, p. 296]. Neodiplograptids with pattern H proximal development type; colony parallel sided or widening gradually from proximal end; thecae with sharp to bluntly rounded genicula; full median septum, gently sinuous proximally; sinuous interthecal septa; subapertural walls parallel to moderately inclined. *Upper Ordovician* (?*upper Katian, Paraorthograptus pacificus* Biozone)–*Silurian, Llandovery (Rhuddanian, Huttagraptus acinaces* Biozone): worldwide.——FIG. 257,*3a*. Possibly *Metabolograptus praecursor* (KOREN' & RICKARDS, 2004), GSC 135121, topotype (species unrecognizable, as based on distal fragments), scale bar, 1 mm (Melchin & others, 2011, fig. 5a).——FIG. 257,*3b*. **M. sibericus* (OBUT), holotype, CSGM211/6a, scale bar, 1 mm (Melchin & others, 2011, fig. 6a).——FIG. 257,*3c*. *M. persculptus* (ELLES & WOOD, 1907), lectotype, GSM 11782, scale bar, 1 mm (Williams, 1983, pl. 66,*3*).

Paraclimacograptus PŘIBYL, 1947, p. 4 [**Climacograpsus innotatus* NICHOLSON, 1869, p. 238; OD]. Neodiplograptids with a pattern H´ proximal development type; colony parallel sided or widening slowly from the proximal end; thecae with sharp to bluntly rounded genicula; genicula with ventrally projecting hood; thecae with wide apertural excavations, everted apertures, and slightly to moderately inclined supragenicular walls; median septum partial in proximal end, complete distally. *Upper Ordovician* (*Hirnantian, Metabolograptus persculptus*

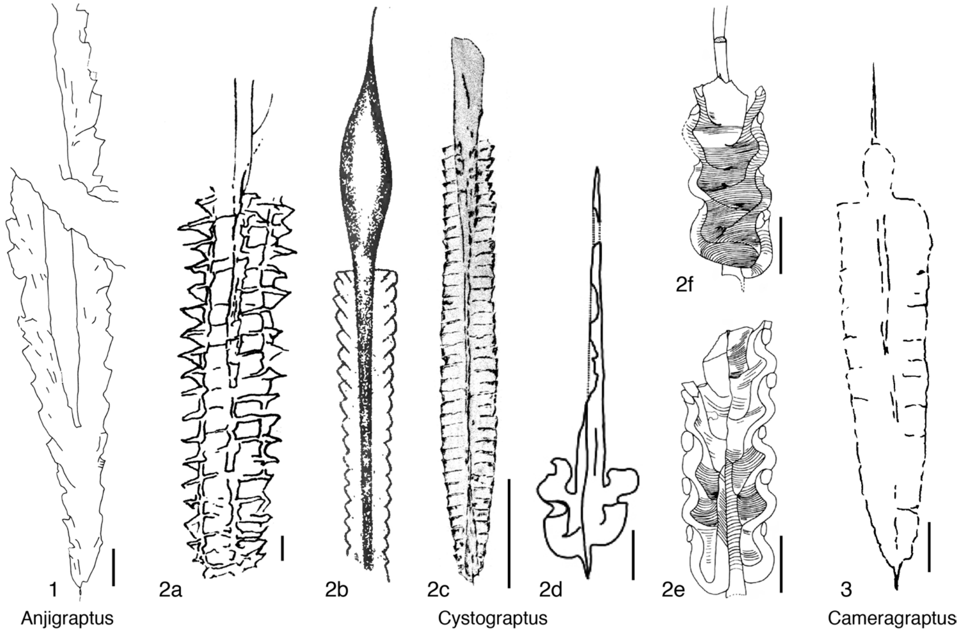

FIG. 258. Neodiplograptidae, uncertain status (p. 386).

Biozone)–*Silurian, Llandovery* (*Rhuddanian, Coronograptus cyphus* Biozone): worldwide.——FIG. 257,*4a–b*. **P. innotatus* (NICHOLSON); *4a,* SM A20222, Dob's Linn, Scotland, topotype, 'typical specimen' of ELLES & WOOD (1906, pl. 27,*10a*) (Riva, 1988, fig. 5L); *4b,* GSC 104929, isolated specimen, Sakmara Formation, southern Urals, Russia (Russel, Melchin, & Koren' 2000, fig. 1,*9*). Scale bars, 1 mm.

Rickardsogratus MELCHIN & others, 2011, p. 297 [**Diplograptus* (?) *tcherskyi* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & NIKOLAEV, 1967, p. 59; OD]. Neodiplograptids with a pattern H´proximal development, or possibly pattern H astogeny in earlier taxa; thecae have pronounced widening mesially, which corresponds to change to more inclined and more gently sigmoidal to straight thecae. *Silurian, Llandovery* (*Rhuddanian, Atavograptus atavus* Biozone–*Neodiplograptus magnus* Biozone): worldwide.——FIG. 257,*5a–b*. **R. tcherskyi* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & NIKOLAEV); *5a,* holotype, flattened specimen, (Obut, Sobolevskaya, & Nikolaev, 1967, pl. 3,*1*); *5b,* isolated specimen in obverse view, GSC 135120, Arctic Canada (Melchin & others, 2011, fig. 4g). Scale bars, 1 mm.

UNCERTAIN STATUS

Genera listed here are either difficult to interpret and uncertain as to whether they belong to the family Neodiplograptidae, or poorly characterized and unrecognizable as valid. The genus *Cystograptus* has been considered to be related to *Neodiplograptus* (see ŠTORCH, 1985; MELCHIN & others, 2011); but because it possesses features not known from any other genus of the Neodiplograptidae, it cannot be reliably included here. The genus has an elongated sicula unlike any other neodiplograptid. The U-shaped initial thecae of the colony and the long sigmoidally curved thecae are reminiscent of an *Undulograptus* BOUČEK, 1973 species from the Middle Ordovician. A closer relationship, however, is unlikely. The proximal development type of *Cystograptus* appears to be a pattern H astogeny with a delayed dicalycal theca, indicated by the distal origin of the median septum. *Cystograptus* bears a conspicuously extended three-vaned nematularium that is overgrown by the advancing stipes in mature specimens (URBANEK, KOREN', & MIERZEJEWSKI, 1982).

Cameragraptus HUNDT, 1953b has been erected validly but is based on unrecognizable scalariform biserials. HUNDT (1953b) included a number of species in this genus, all based on the form of the nematularium.

SCHAUER (1971, p. 35) indicated that most specimens identified as *Cameragraptus* by HUNDT (1953b) may belong to *Neodiplograptus thuringiacus* (KIRSTE, 1919), but this cannot be verified.

Anjigraptus MUIR, ZHANG, BOTTING, & MA, 2021, p. 396 [**Anjigraptus wangi;* OD] Proximally biserial neodiplograptid with two uniserial stipes distally; proximal development probably of pattern H astogeny; proximal thecae geniculate, distally with straight, outwards inclined ventral sides, lacking a geniculum; apertures slightly extroverted. *Upper Ordovician* (*Hirnantian, Metabolograptus persculptus* Biozone): South China (Zhejiang Province).——FIG. 258,*1*. **A. wangi,* holotype, scale bar, 1 mm (Muir & others, 2021, fig. 2B).

Cystograptus HUNDT, 1942, p. 205 [**C. speciosus;* SD JONES & RICKARDS, 1967, p. 181–182; =*Diplograpsus vesiculosus* NICHOLSON, 1868c, p. 61, syn. by JONES & RICKARDS, 1967, p. 181]. Neodiplograptids with elongated sicula and long, doubly sigmoid thecae; proximal development of modified pattern H astogeny; median septum straight to slightly undulate, delayed; robust three-vaned nematularium proximally overgrown in mature colonies. *Silurian, Llandovery* (*Rhuddanian, Parakidograptus acuminatus Biozone–Aeronian, Coronograptus cyphus* Biozone): Britain, Czech Republic, Denmark, Germany, Sweden, Kazakhstan, Canada, USA.——FIG. 258,*2a–d*. **C. vesiculosus* (NICHOLSON)*; 2a,* holotype of *C. speciosus,* repository unknown, scale bar, 1 mm (Münch, 1952, pl. 10,*8*); *2b,* holotype, original illustration, possibly NHMUK PM P.1880 (see BENTON, 1979; STRACHAN, 1997), magnification unknown (Nicholson, 1868c, pl. 3,*11*); *2c,* BU 1231, typical specimen with nematularium, Dob's Linn, Scotland, UK, scale bar, 10 mm (Elles & Wood, 1907, pl. 28,8c); *2d,* juvenile showing long sicula, scale bar, 1 mm (Štorch, 2015, fig. 4g).——FIG. 258,*2e–f*. *C. penna* (HOPKINSON, 1869), *Lagarograptus acinaces* Biozone, Rheidol Gorge, UK; *2e,* SM A57550, proximal end, reverse view; *2f,* SM A23952, proximal end, obverse view; scale bars, 1 mm (Jones & Rickards, 1967, fig. 1–2).

Cameragraptus HUNDT, 1953b, p. 3 (no pagination in paper) [**C. cuneatus,* HUNDT, 1953b, p. 4, fig. 7 (not fig. 4 as stated in the text); SD herein]. [Figure is a scalariform view of a biserial.] *Silurian, Llandovery* (*Rhuddanian–Aeronian*): Germany.——FIG. 258,*3*. *C. cuneatus,* holotype, BAF 186/4211, scale bar, 1 mm (Blumenstengel & others, 2006, pl. 1,*1B*).