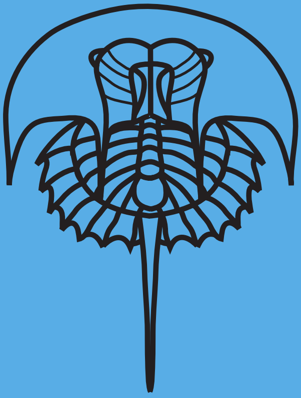

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Part V, Second Revision, Chapter 22: Suborder Axonophora, Infraorder Diplograptina I (Diplograptidae, Lasiograptidae): Introduction, Morphology, and Systematic Descriptions

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PART V, SECOND REVISION, CHAPTER 22: SUBORDER AXONOPHORA, INFRAORDER DIPLOGRAPTINA I (DIPLOGRAPTIDAE, LASIOGRAPTIDAE): INTRODUCTION, MORPHOLOGY, AND SYSTEMATIC DESCRIPTIONS

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Suborder AXONOPHORA Frech, 1897

[Axonophora Frech, 1897, p. 607] [=*partim* Virgellina Fortey & Cooper, 1986, p. 639 (see Maletz, 2010, 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), while 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 in his understanding. 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 the Diplograptoidea. Maletz, Carlucci, and Mitchell (2009, fig. 6) separated the early biserials of the *Levisograptus austrodentatus* (Harris & Keble, 1932) group (see Maletz, 2011a) 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. 1) 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 is seen as indicating remaining problems of this interpretation (see Mitchell & others, 2007). Based on a number of tubarium features, Maletz (2011b, fig. 3) preferred

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Maletz, Jörg. 2019. Part V, Second Revision, Chapter 22: Suborder Axonophora, Infraorder Diplograptina I (Diplograptidae, Lasiograptidae): Introduction, morphology, and systematic descriptions. Treatise Online 127:1–26, 14 fig.

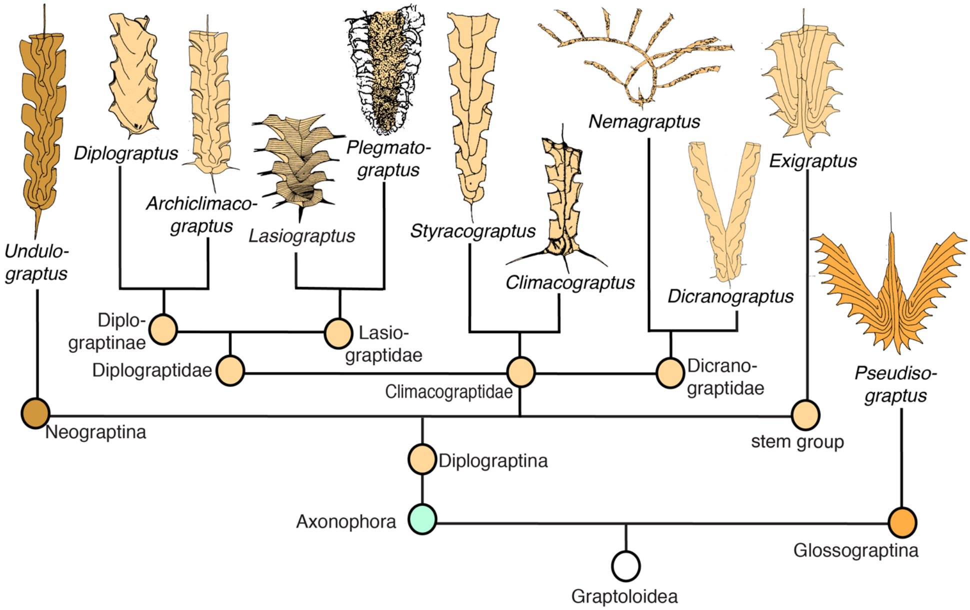

FIG. 1. Diagram of the Axonophora, showing the unresolved trichotomy within the Diplograptina leading to the Diplograptidae, Climacograptidae, and Dicranograptidae. Specimens not to scale (new).

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 often relatively short and inconspicuous (Fig. 2.1). A long nema engulfed between the two laterally connected stipes can be seen in biserial, monopleural Glossograptidae (MALETZ & ZHANG, 2016). Early Axonophora were invariably biserial, dipleural (Fig. 2.2), but the biserial tubarium shape was lost in the Silurian monograptids (Fig. 2.3). In both groups, the nema can be seen extending distally beyond the thecate part of the tubarium.

The prosicula with the typical spiral line and the metasicula formed from fuselli can be recognized 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, 1987). The differentiation of the nema and virgula (RICKARDS, 1996) cannot be upheld and the virgula in older literature has to be regarded as identical to

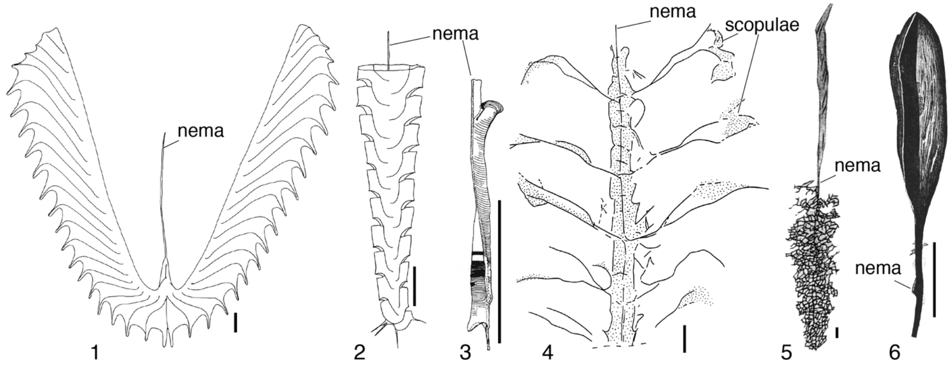

Fig. 2. Nema and nematularium development in the Graptolithina. *1, Isograptus divergens* Harris, 1933, completely free nema between two reclined stipes (new); *2, Amplexograptus praetypicalis* Riva, 1987, nema incorporated in colony, visible at distal end (new); *3, Lobograptus imitator* Urbanek, 1966, nema visible on dorsal side of stipe (Urbanek, 1966, pl. 28D); *4, Neurograptus fibratus* (Lapworth, 1876), 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, 1876), three-vaned nematularium (Bulman, 1947, pl. 9). Scale bars, 1 mm.

the nema. Nematularia are common in the Axonophora and may show 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 be formed as two- and three-vaned structures (Fig. 2.5–2.6), 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 can be found in a number of species (Fig. 2.4), but are 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, 2010; Maletz, Lenz, & Bates, 2016). The origin can be found in the glossograptid *Isograptus* Moberg, 1892, 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. 3.1–3.4). 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, as the remains of the manubrium are still present, even though often strongly reduced in size (Fig. 4.1). Relief specimens of *Apiograptus* show 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.

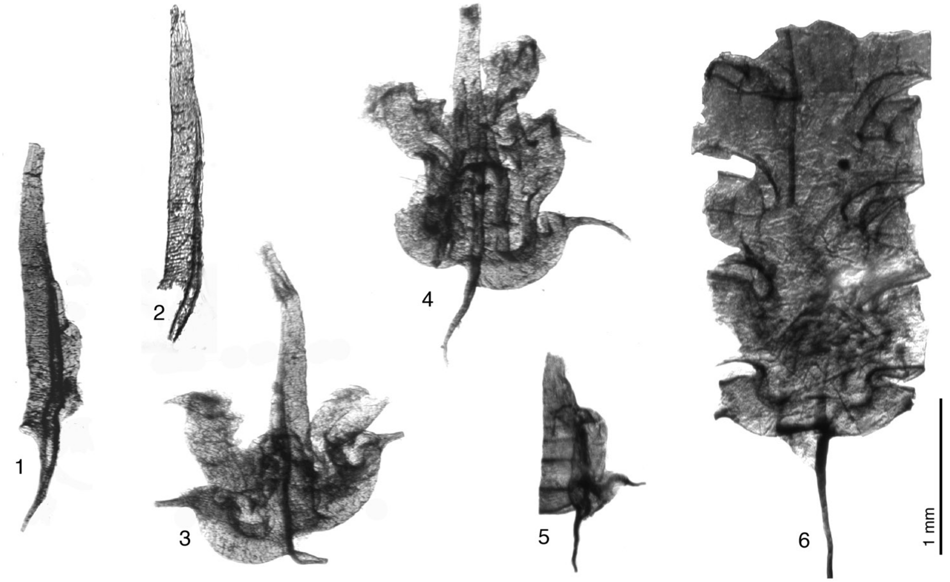

FIG. 3. The virgellar spine development in early Axonophora, infrared photos. *1–4, Levisograptus sinicus* (MU & LEE, 1958), Cow Head Group, western Newfoundland; *1,* GSC 133381, nearly complete sicula with lanceolate virgella and part of first theca; *2,* GSC 133380, juvenile sicula with tip of lanceolate 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, 2010, 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.

The manubrium is reduced, but retains the initial parallel-sided downward growth of the proximal thecae (Fig. 4.2). 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 can be recognized as an exposed patch of thecal origins on the reverse side of the colony (Fig. 4.3–4.4). 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 are folded over the apex of the sicula and grow 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. 5.2).

Intrathecal folds are common in earlier axonophorans, but easily overlooked as the short bars connected to the median septum are only recognizable in well-preserved relief material (Fig. 5.1). The intrathecal folds represent a temporary stop and change in growth direction at the base of

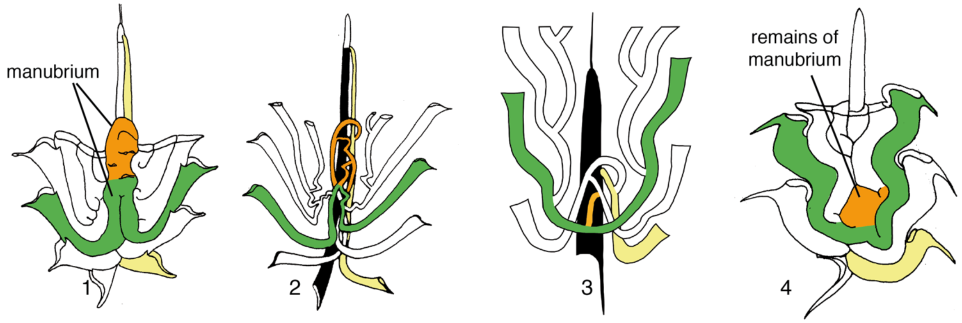

FIG. 4. Proximal development, pattern U astogeny. *1, Apiograptus uniformis* (MU in MU & others, 1979), reverse view, reconstruction (new drawing, adapted from Mitchell & Maletz, 1995, fig. 3N); *2,* pattern U astogeny of *Apiograptus* COOPER & MCLAURIN, 1974 with conspicuous downward growth of proximal thecae (manubrium in *orange* and *green*) 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).

the metathecae and the introduction of the median septum. A short lateral bar is often 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 representing the cross bars connected to the median septum in taxa with intrathecal folding (Fig. 5.3). The ventral parts of these cross bars (Fig. 5.2) 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 often thickened bases of the interthecal septae, the aboral lists (Fig. 5.2). BULMAN (1932a) illustrated the thickened cross bars from chemically isolated material in *Archiclimacograptus* (?) *skagensis* (JAANUSSON & SKOGLUND, 1963) and *Haddingograptus eurystoma* (JAANUSSON, 1960) (Fig. 5.4–5.5), showing that they are part of the median septum construction.

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 (1932b) 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. 5.6–5.7). 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 often 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 here as it is preferred to describe the thecal features independent of any named genera, following MALETZ 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. 6.1) or may have a geniculum that is rounded (Fig. 6.2) or angular (6.3–6.4). The position of the geniculum may vary considerably and can be close to the underlying thecal

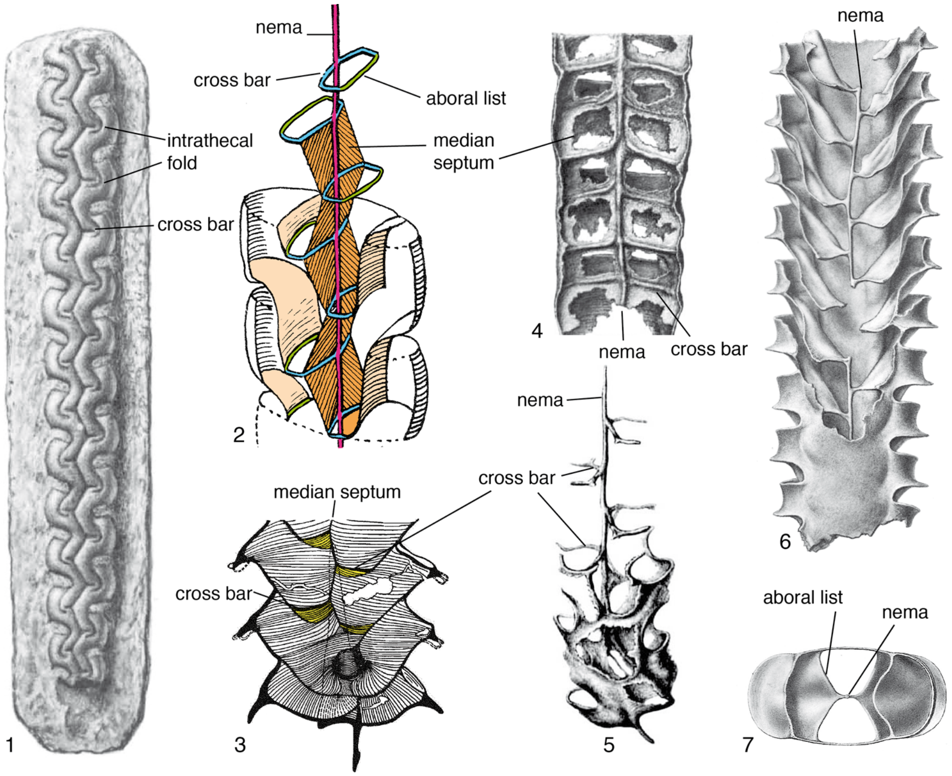

FIG. 5. Median septum development. *1,* Climacograptid indet., relief specimen showing zigzag median septum and intrathecal folding (Bulman, 1932a, pl. 3,*34*); *2,* part of colony showing integration of median septum, nema, crossbars, and aboral list (adapted from Bulman, 1970, fig. 46); *3, Urbanekograptus retioloides* (WIMAN, 1895), reconstruction showing the cross bars and intrathecal folding, prothecal parts of third and fourth thecal pair in *yellow,* 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*).

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. 6.1) 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. 6.4a), sometimes completely surrounding the thecal aperture. A ventral notch (Fig. 6.4b) in the aperture is commonly formed, supporting the paired lateral lobes of many species. In addition, a genicular notch (Fig. 6.3b) may also be present. Thecal apertures may be introverted, horizontal, or everted, but these features are often modified by preservational aspects or the development of lateral lobes and horns (Fig. 6.1) and thus may be unreliable. All these thecal features can be

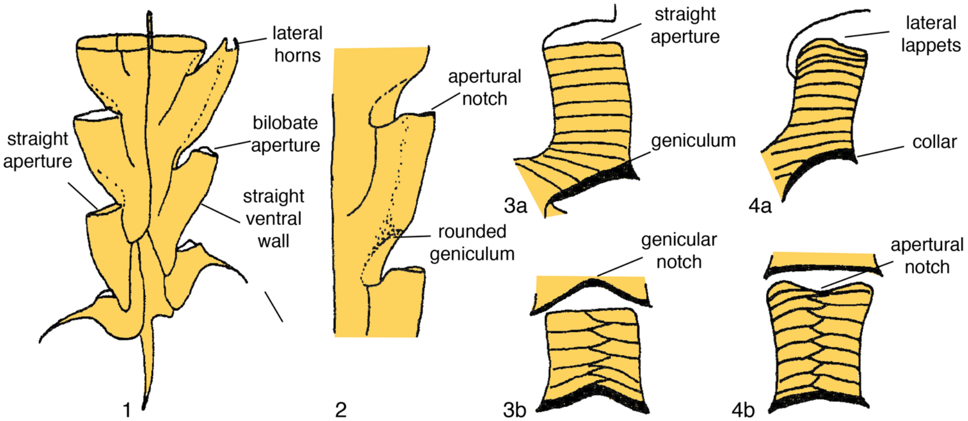

FIG. 6. The thecal morphology in biserial axonophorans (adapted from Maletz, 1997, fig. 7).

modified independently and do not provide a useful guide for taxonomy.

Infraorder DIPLOGRAPTINA Lapworth, 1880

[=*nom. correct.* Obut, 1957, p. 17, *ex* Diplograpta Lapworth, 1880, p. 191, *non* order Diplograptoidea in Mitchell & others 2007; *non* superfamily Diplograptoidea, Štorch & others 2011, fig. 6] [=*partim* Diplograptina, Jaanusson, 1960, p. 321, 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 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. While 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 here preferred 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, 1892. Štorch and others (2011) included the superfamilies Dicranograptoidea, Diplograptoidea, and

Climacograptoidea in the Diplograptina, interpreted here as family level taxa (Fig. 1). The detailed relationships of the Diplograptina and Neograptina are still uncertain, as the early evolution of the axonophorans is poorly known (MALETZ, 2011c).

STEM GROUP DIPLOGRAPTINA

The early axonophorans showing the remains of the pseudisograptid manubrium are here referred to an unnamed stem group taxon. The stem group is characterized by a pattern U astogeny, lost in the Diplograptidae, in which early taxa show a pattern C astogeny. A pattern A to pattern C astogeny can be seen 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), NI & XIAO, 1994, p. 15]. Diplograptina with strongly developed manubrium and pattern U astogeny; proximal end rounded, with maeandrograptid to isograptid symmetry; thecae elongated, tubelike, 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. 8,*1a–c.* **A. crudus; 1a,* lectotype, NMVP 31960 (new, provided by A. H. M. VandenBerg); *1b,* topotype, NMVP 27485, Chinaman's Creek, Muckleford, Victoria, Australia (Cooper & McLaurin, 1974, fig. 2h); *1c,* topotype, NMVP 30515, juvenile showing large manubrium (new). Scale bars, 1 mm.

Levisograptus MALETZ, 2011a, 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. 8,*4a–c.* **L. dentatus; 4a,* neotype (selected by BULMAN, 1963, 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, 2011a, fig. 3A–B,5G, respectively). Scale bars, 1 mm.——FIG. 8,*4d. L. austrodentatus* (HARRIS & KEBLE, 1932), GSC 102618, Begins Hill, Lévis, Québec, obverse view, scale bar, 1 mm (Maletz, 1997, fig. 7C).

Family DIPLOGRAPTIDAE
Lapworth, 1873

[Diplograptidae LAPWORTH, 1873, 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, often 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. 1). The precise origin and differentiation of the Climacograptidae (see discussion in MALETZ, 2011b) and the Dicranograptidae (see MALETZ, 1998) remains unclear. In their cladistic interpretation, MITCHELL and others (2007) showed 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 (1873) introduced the taxon for all biserial, dipleural graptolites, but stated that this arrangement was provisionally 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 showed it to nest among the main plexus of the Orthograptidae of MITCHELL (1987), a clade of biserials with a pattern G astogeny or a derived one 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, 1873, table 1 facing p. 555, *ex* Diplograptidae LAPWORTH, 1873]

Biserial diplograptids with pattern C astogeny or derived one, 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, often with complex apertural or genicular additions; intrathecal folds and complete median septum in earlier taxa. *Middle Ordovician (Dapingian,* Oncograptus upsilon *Biozone)–Upper Ordovician (Hirnantian,* Metabolograptus persculptus *Biozone):* worldwide.

The early evolution of the Diplograptinae is unclear as 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. While taxa of the stem group have a pattern U astogeny (Fig. 7.1–7.2), early Diplograptinae possess a pattern C astogeny (Fig. 7.3–7.5) and younger taxa may show the derived pattern G astogeny (Fig. 7.6–7.7). Species with pattern C astogeny or derived one usually show an upward-growing flange (Fig. 7.3) uniting with the downward-growing initial part of th2^1, forming the paired openings for the growth of th2^1 and th2^2 (Fig. 7.5). In derived taxa, th1^2 and th2^1 may form a conspicuous arch in the pattern G astogeny (Fig. 7.7). 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, *non. correct.* HALL, 1865, p. 109, original spelling as *Diplograpsis* M'Coy, 1850 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. 8,*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 [**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. 8,*8a–b*. **A. sebyensis* (JAANUSSON); *8a,* obverse view, reconstruction of holotype (Jaanusson, 1960, fig. 7D); *8b,* PMO

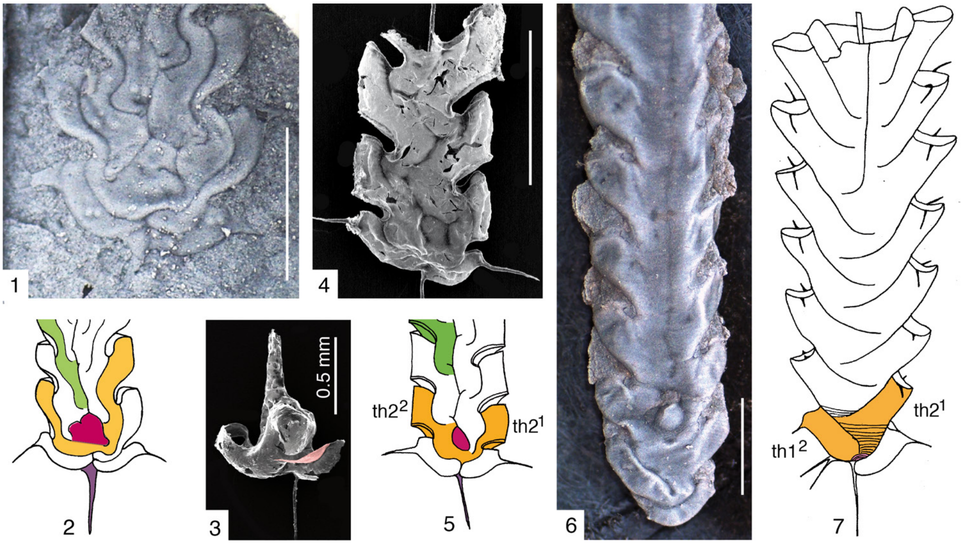

FIG. 7. Proximal development in the Diplograptina. *1, Levisograptus sinicus* (Mu & Lee, 1958), PMU 31733, pattern U astogeny, latex cast, coated, Fågelsång-3 drill core at 56.28–56.30 m, Scania, Sweden (Maletz & Ahlberg, 2018, fig. 6G); *2, Levisograptus austrodentatus* (Harris & Keble, 1932), reverse view, pattern U astogeny, reconstruction (new); *3–5, Archiclimacograptus decoratus* (Harris & Thomas, 1935); *3,* GSC 139286a, reverse view, showing upward-growing flange in red, 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, 2011c, fig. 2B). Scale bars, 1 mm, unless otherwise stated.

138.785, proximal end in reverse view (Maletz, 2011b, 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. 8,*7a–b*. **M. foliaceus* (Murchison); *7a*, NHMUK PM 1288, proximal part of lectotype of *Diplograptus* (*Mesograptus*) *multidens* Elles & Wood; *7b*, second specimen on BU 1288, obverse view; scale bars, 1 mm (new; drawings by John F. Riva).

Oepikograptus Obut & Sennikov, 1984, p. 110 [**Diplograptus bekkeri* Öpik, 1927, p. 28; OD] [=*Fenhsiangograptus* Hong, 1957, p. 495 (type, *F. fenhsianensis,* OD), 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,* Dicellograptus 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. 8,*5a*. **O. bekkeri* (Öpik), holotype, TUG 1087-8, Kohtla, Estonia, scale bar, 1 mm (new; provided by Ursula Toom).——Fig. 8,*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. 8,*3*. **P. uniformis* (Chen in Mu & others), lectotype (selected herein), NIGP 32333, scale bar, 1 mm (new).

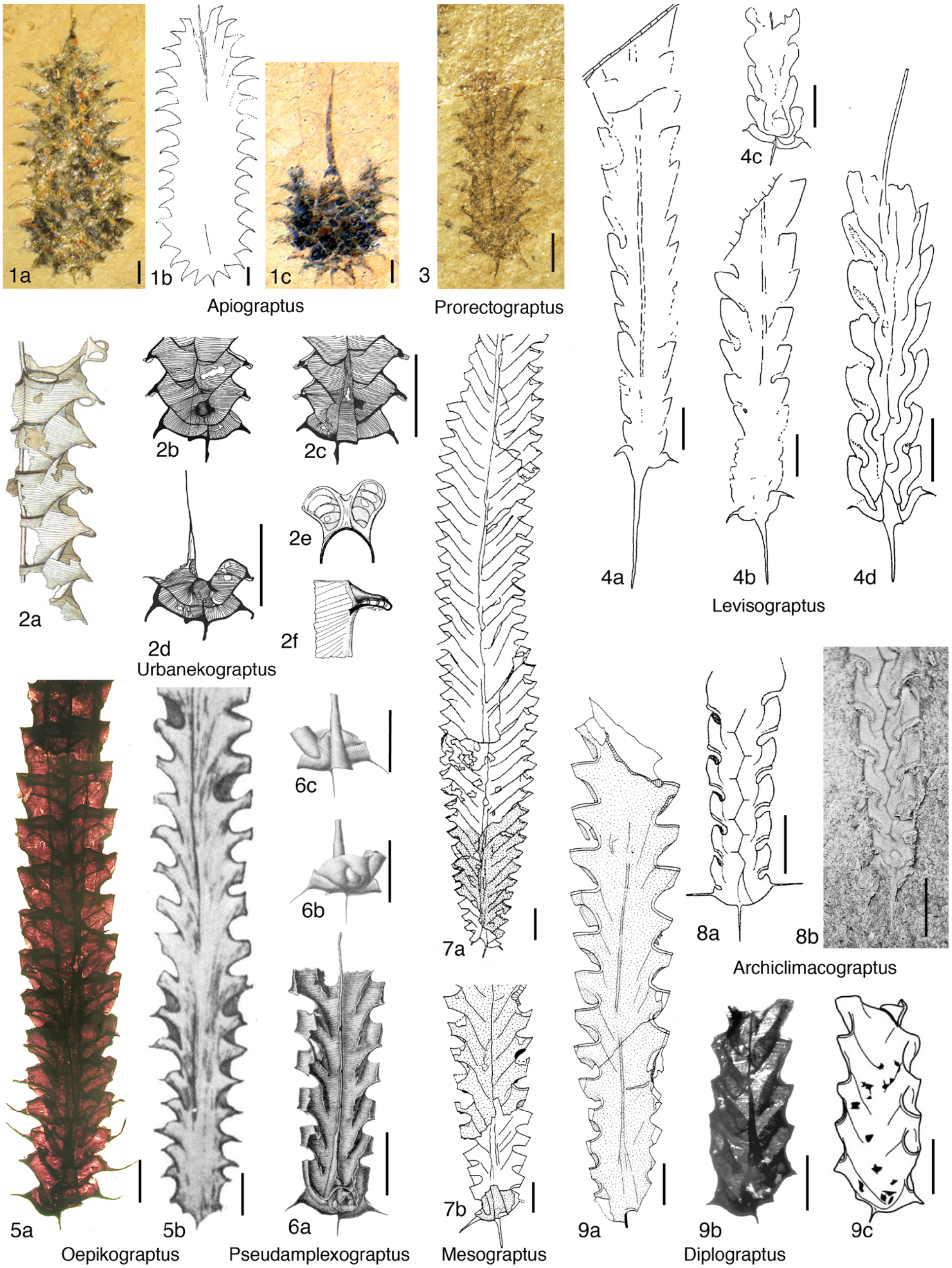

FIG. 8. Stem group Diplograptina and Diplograptinae (p. 8–12).

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. 8,*6a–c.* **P. distichus* (EICHWALD) isolated specimen, Öland, Sweden; *6a*, NRM-PZ Cn 2355; *6b–c*, NRM-PZ Holm 111, juvenile in reverse (*b*) and obverse (*c*) views, showing pattern C astogeny (Bulman, 1932a, pl. 4,*19–20,* 5,*1*, respectively). Scale bars, 1 mm.

Urbanekograptus MITCHELL, 1987, p. 389 [**Climacograptus retioloides* WIMAN, 1895, p. 276; 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. 8,*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. 4,5,7, 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 the 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 often 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 (2014) differentiated the Diplograptinae and the Orthograptinae in the family Diplograptidae.

Early peiragraptines bear a pattern A astogeny (Fig. 9.1a–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. 9.2a–c). This gap was filled by the initial part of th2^1. In pattern K astogeny species (Fig. 9.4a–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. 9.3a–c). In flattened material, these proximal development patterns may be impossible to tell apart.

Amplexograptus ELLES & WOOD, 1907, p. 267 [**Diplograptus perexcavatus* LAPWORTH, 1876, 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

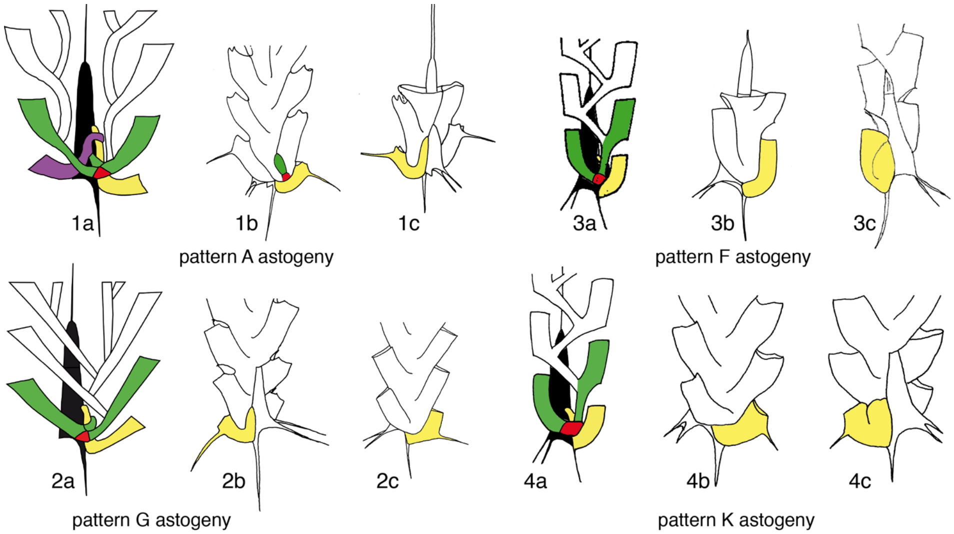

Fig. 9. Proximal development in the Peiragraptinae. *1,* pattern A astogeny (*a*), *Hustedograptus uplandicus* (Wiman, 1895) in reverse (*b*) and obverse (*c*) views, showing exposed patch of crossing canal of th1^2, note the paired antivirgellar spines; *2,* pattern G astogeny (*a*), *Rectograptus* (Přibyl, 1949) in reverse (*b*) and obverse (*c*) views; *3,* pattern F astogeny (*a*), *Geniculograptus pygmaeus* (Ruedemann, 1925) 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 color coded for easier access (new).

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. 10,*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. 10,*1c. A. leptotheca* Bulman, 1946, BU 1299, holotype of *A. fallax* Bulman, 1962; scale bar, 1 mm (new; drawing by John F. Riva).——Fig. 10,*1d. A. maxwelli* Decker, 1935, 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. 10,*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. 10,*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, 1963 (=*E. gerhardi* Maletz, 2011a, p. 859); OD]. Robust peiragraptines with distinctly asymmetrical proximal end and distally widening colony; apart from an often 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,

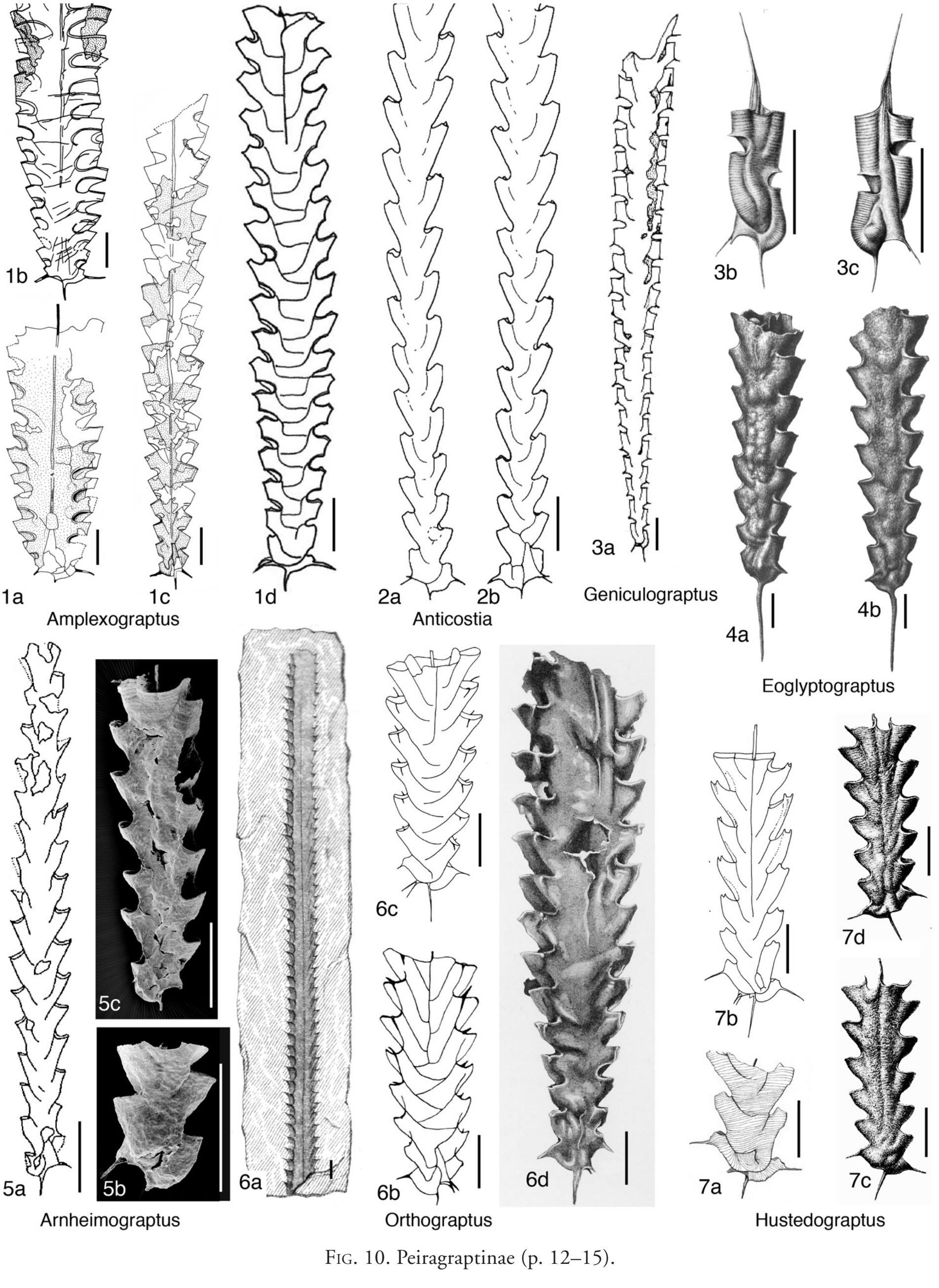

FIG. 10. Peiragraptinae (p. 12–15).

often with slight lateral lobes, median septum straight to undulating; interthecal septae short, no intrathecal folds. *Middle Ordovician, Darriwilian* (Holmograptus lentus–Dicellograptus vagus *Biozones):* China, UK, Norway, Sweden.——FIG. 10,*4a–b*. **E. gerhardi* (MALETZ), NRM-PZ Cn 1280, holotype, Öland, Sweden, scale bars, 1 mm (Bulman, 1936, pl. 3,*1–2*).

Geniculograptus MITCHELL, 1987, p. 381 [**Climacograptus typicalis* HALL, 1865, p. 57; OD] [=*Uticagraptus* RIVA, 1987, p. 932, obj.]. Peiragraptines with 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–Climacograptus tubuliferus *Biozones):* USA (Eastern), Canada (Eastern). ——Fig. 10,*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, 1932b, 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, often delayed; thecae often 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. 10,*7a–b*. **H. uplandicus* (Wiman); *7a,* holotype, reverse view (Wiman, 1895, pl. 9,*1*); *7b,* reconstruction in reverse view after isolated material in Mitchell collection, Buffalo, New York, USA (new); scale bars, 1 mm.——Fig. 10,*7c–d. H. bulmani* Mitchell, Brussa, & Maletz, 2008, holotype, NRM-PZ Cn 59946, reverse (*c*) and obverse (*d*) views, scale bars, 1 mm (Bulman, 1936, pl. 3,*10–11*).

Orthograptus Lapworth, 1873, table 1, opposite p. 555, *ex* subgenus *Diplograptus* (*Orthograptus*) Lapworth, 1873, 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. 10,*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. 10,*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, 1982b, 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. 11,*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, 1974, 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. 11,*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, Jin, & Wu, 1978, p. 345 (type *O. denticulatus;* OD), Štorch & others, 2011, p. 342; =*Pseudoreteograptus* Mu in Mu & others, 1993, p. 231 (type, *P. nanus,* OD), 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; Štorch & others, 2011, p. 341.] *Upper Ordovician, Katian* (Dicellograptus ornatus–Paraorthograptus pacificus *Biozones):* China, USA).——Fig. 11,*3a–b*. **P. sinensis;* 3a, NIGP 83257, Wufeng Shale, China (Štorch & others, 2011, fig. 18); *3b,* USNM 542746, long specimen, Nevada, USA (Štorch & others, 2011, fig. 14s). Scale bars, 1 mm.——Fig. 11,*3c–d. P. denticulatus* (Mu in Wang, Jin, & Wu, 1978); *3c*, NIGP 57854, holotype; *3d,* NIGP 57807; scale bars, 1 mm (Mu & others, 1993, fig. 39a–b).——Fig. 11,*3e. P. nanus* (Mu in Mu & others, 1993), NIGP 57734, paratype, scale bar, 1 mm (Mu in Mu & others, 1993, fig. 38).

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. 11,*4a–c*. **P. fallax,* Observation Cliff, Anticosti Island, probably from Vaureal Formation;

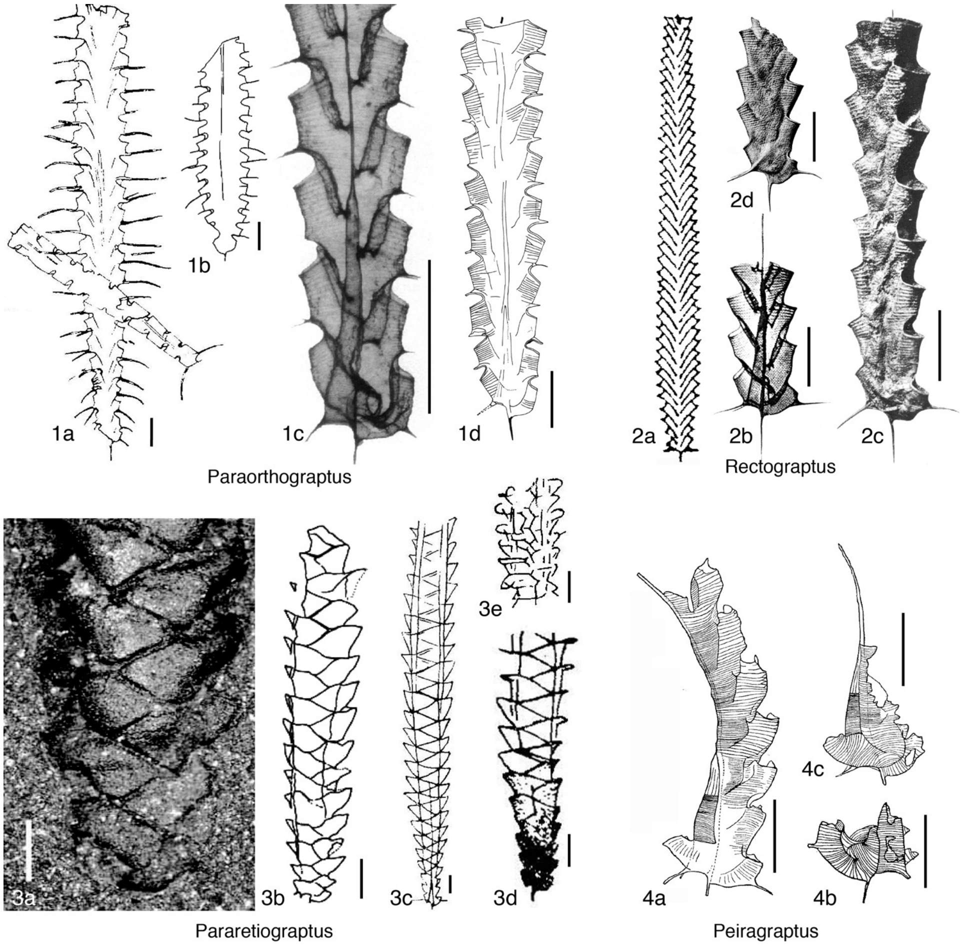

FIG. 11. Peiragraptinae (p. 15–16).

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).

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; often 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. 11,*2a*. **R. truncatus* (LAPWORTH) holotype (Lapworth, 1877, pl. 6,*17a* [specimen not identified, see STRACHAN, 1997, p. 72]).——FIG. 11,*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,*11,10,* respectively).

Family LASIOGRAPTIDAE Lapworth, 1879

[Lasiograptidae LAPWORTH, 1879, p. 454] [=Hallograptidae MU, 1950, 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 (1879). 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 been derived from a form such as *Dicaulograptus hystrix* (Bulman, 1932a) based on the thecal construction, while 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. 12.3), thus differing from the development in taxa with a pattern G or pattern L astogeny (Fig. 12.5) (Mitchell, 1987).

FUSELLUM REDUCTION

In many phylogenetically not closely related graptolites, the fusellum is reduced independently and is often not 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), but mainly 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 commonly seen in members of the Lasiograptidae (Fig. 12.1), 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 recognize the proximal development and thecal style easily. Other taxa show an extreme reduction of the fusellum and the thecae are shown 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. 12.1–12.3), 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. 12.1) 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

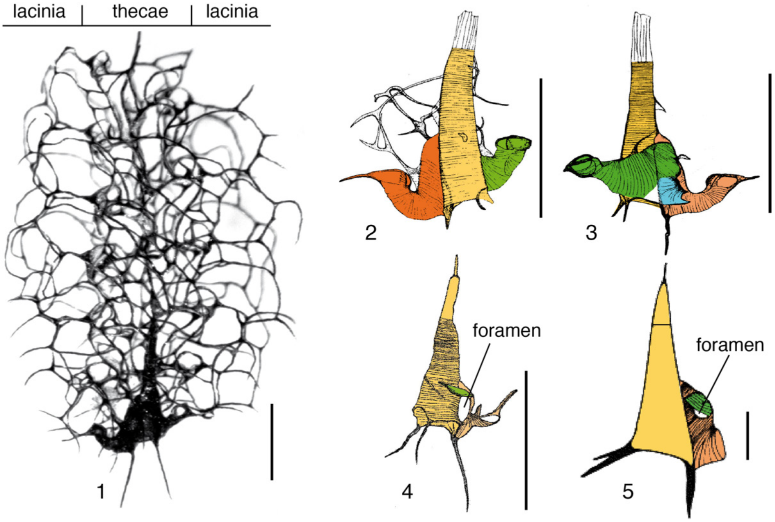

FIG. 12. Tubarium development in Lasiograptidae. *1–3,* Fusellum reduction and lacinia in *Pipiograptus hesperus* WHITTINGTON, 1955; *1,* photo of larger specimen, vaguely showing the thecal outline remains of the fusellum (Maletz, 2017, fig. 11,*8J*); *2–3,* isolated paratype specimens showing part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

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, 1987; 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.

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. 13,*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. 13,*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, 1876, 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 showing 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. 13,*2a*. **H. bimucronatus* (Nicholson) Glenkiln Shale, Scotland, scale bar, 1 mm (Bulman, 1970, fig.93,*2a*).——Fig. 13,*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).

Lasiograptus Lapworth, 1873, p. 559 [**L. costatus;* OD] [=*Thysanograptus* Elles & Wood, 1908, p. 325 (type, *Diplograptus harknessi* Nicholson, 1867, p. 262), 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 inward-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,* Dicellograptus vagus *Biozone)–Upper Ordovician (Katian,* Climacograptus bicornis *Biozone):* worldwide(?).——Fig. 13,*3a*. **L. costatus*, BU 1341, lectotype, Dob's Linn, Scotland (adapted from Hughes, 2000).——Fig. 13,*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.

Neurograptus Elles & Wood, 1908, p. 320, =*Neurograptus* Lapworth in Hopkinson & Lapworth, 1875, p. 641, *nom. nud.* [**Retiolites fibratus* Lapworth, 1876, fig. 62].Lasiograptids 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, 1876 (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. 13,*4a–c*. **N. margaritatus* (Lapworth); *4a,* BU 1351, holotype of *Retiolites fibratus* Lapworth, 1876 (Elles & Wood, 1908, pl. 34,*5a*); *4b,* lectotype, BU 1353a, Dob's Linn, Scotland (Wilkinson, 2018); *4c,* PMO 108905, 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), herein]. Lasiograptids with strongly developed lacinia on reverse and obverse sides formed from septal bars (scopulae) extending far outward and upward from thecate part of the tubarium; fusellum strongly attenuated; thecal style and proximal development unknown. *Upper Ordovician* (*Katian,* Dicellograptus anceps *Biozone):* Kazakhstan, China, UK.——Fig. 14,*1a*. **N. velatus* (Elles & Wood), BGS GSE 10856, lectotype (selected by Koren', Tzai, & Mikhailova, 1980, p. 164), Ettrickbridge End, Scotland, UK (Bulman, 1970, fig. 93,*4*).——Fig. 14,*1b. N. yangziensis* (Mu & others, 1993), holotype, NIGP 57843 (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. 13,*6a–b*. **O. hami*, Oklahoma, USA; *6a,* holotype, MCZ 511; *6b,* paratype, MCZ 512h; scale bars, 1 mm (Whittington, 1954, fig. 4,*12*).——Fig. 13,*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 in Mu, 1963, p. 365, *nom. nud.*, see Štorch & others, 2011, p. 348] [**P. uniformis* Mu in Wang, Jin, & Wu, 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. 14,*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), 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 often 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–Metabolograptus

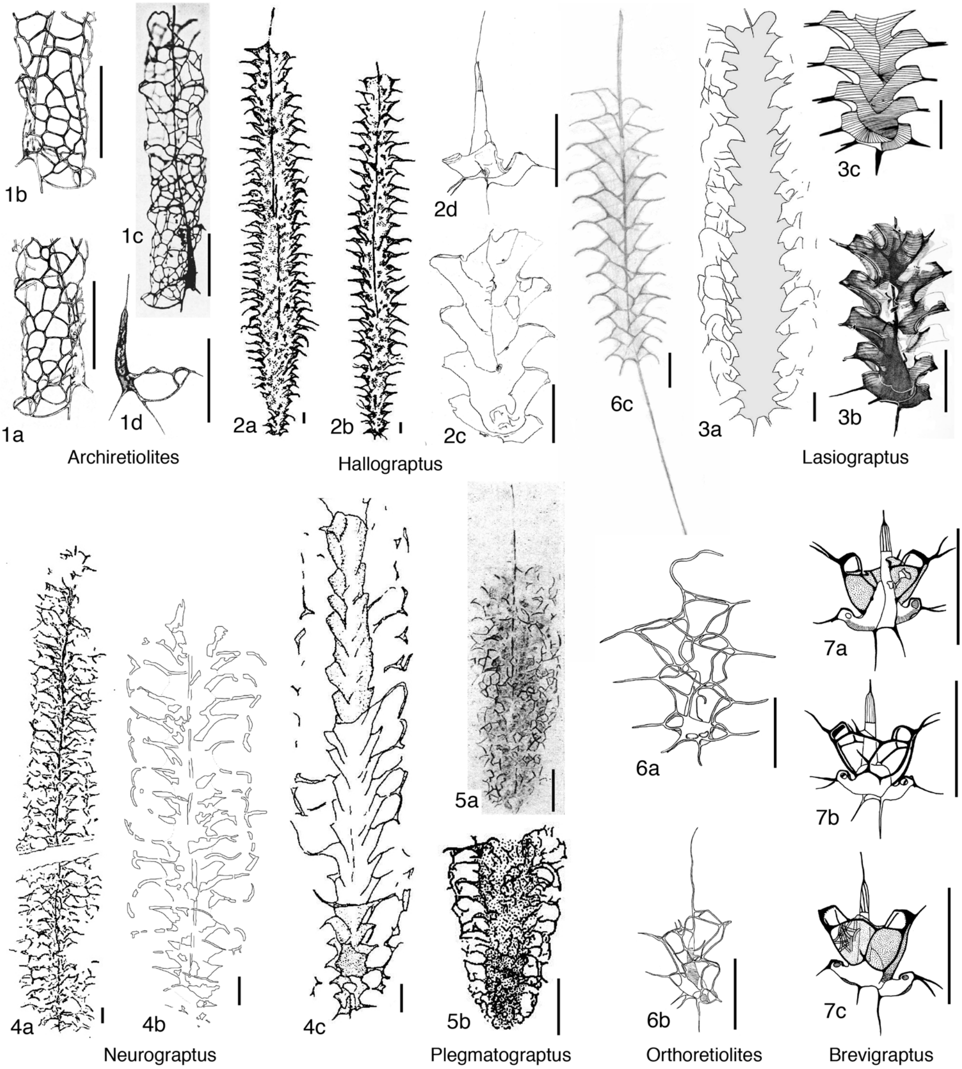

FIG. 13. Lasiograptidae (p. 18–21).

persculptus *Biozones):* China, Czech Republic, USA.——FIG. 14,*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. 14,*5e. P. connectus* (Mu in Wang, Jin, & Wu, 1978), 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.14,*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

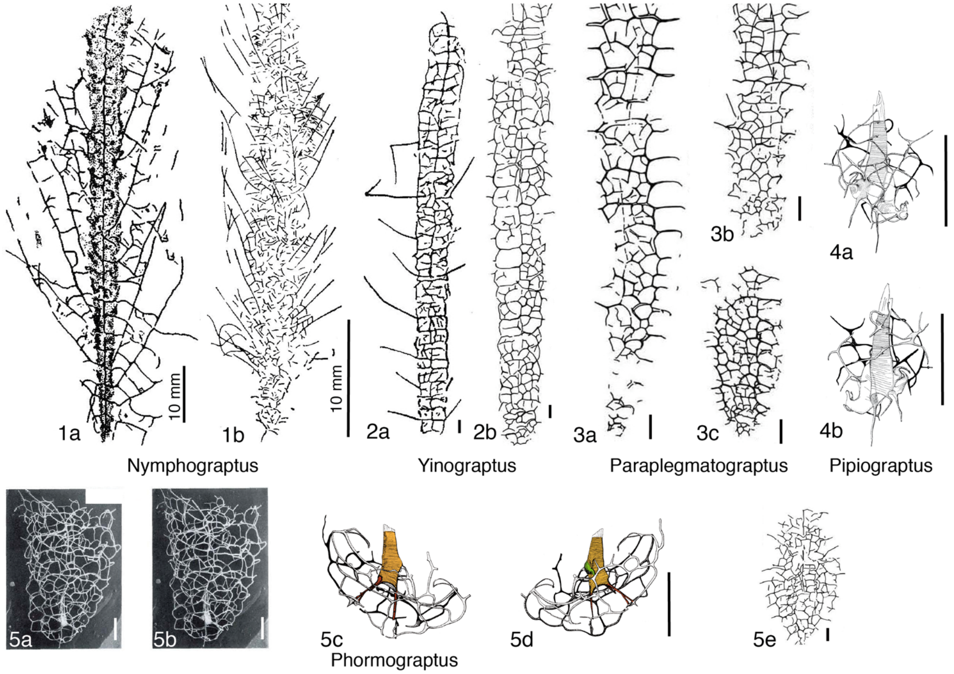

Fig. 14. Lasiograptidae (p. 19–21).

lacinia; fusellum strongly attenuated or lacking; details of development unknown. *Upper Ordovician (Katian,* Dicranograptus clingani–Pleurograptus linearis *Biozones):* Australia, China, UK, USA.——Fig. 13,*5a–b*. **P. nebula; 5a,* lectotype (selected by Williams, 1982a, p. 253), BGS GSE 5615, Hartfell Shale, Scotland, UK, scale bar, 1 mm (Elles & Wood, 1908, fig. 222b); *5b,* BGS GSE 5539, Hartfell Shale, Scotland, scale bar, 1 mm (Bulman, 1970, fig. 95,*4*).

Yinograptus Mu in Mu & Chen, 1962, p. 112 [**Gothograptus*? *disjunctus* Yin & Mu, 1945, p. 216; OD] [=?*Sunigraptus* Mu in Mu & others, 1993, p. 247 (type, *S. regularis,* OD), 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–Paraorth-ograptus pacificus *Biozones):* China; USA.——Fig. 14,*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

ABBREVIATIONS FOR MUSEUM REPOSITORIES

AMNH: American Museum of Natural History, New York City, New York, USA
BGS GSE: British Geological Survey, Geological Survey Museum, Keyworth, Nottingham, UK
BU: Lapworth Museum, Birmingham University, UK
GPIT: Paläontologische Sammlungen, Universität Tübingen, Germany
GSC: Geological Survey of Canada, Ottawa, Canada
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
NHMUK: The Natural History Museum, London, UK
NIGP: Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China
NMVP: Museums Victoria, Melbourne, Australia
NRM-PZ: Naturhistoriska Riksmuseet Stockholm, Sweden
OSU: Orton Geological Museum, Ohio State University, Columbus, Ohio, USA
PMO: Natural History Museum, Paleontological Type collections, University of Oslo, Sweden
SMF: Naturmuseum Senckenberg, Frankfurt am Main, Germany
TUG: University of Tartu, Natural History Museum, Tartu, Estonia
USNM: US National Museum of Natural History, Washington DC, USA

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