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Part V, Second Revision, Chapter 23: Suborder Axonophora, Infraorder Diplograptina II (Climacograptidae, Dicranograptidae): Introduction, Morphology, and Systematic Descriptions

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PART V, SECOND REVISION, CHAPTER 23: SUBORDER AXONOPHORA, INFRAORDER DIPLOGRAPTINA II (CLIMACOGRAPTIDAE, DICRANOGRAPTIDAE): INTRODUCTION, MORPHOLOGY, AND SYSTEMATIC DESCRIPTIONS

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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 development of 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 often twisted longitudinally; thecae with distinct geniculum; intrathecal folds externally expressed through crossbars and often 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, but also 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, while Štorch and others (2011), in the latest revision, referred the climacograptids to the superfamily Climacograptoidea.

A recent cladistic analysis of the Climacograptidae does not exist and the analysis of Cone (2004) was discussed in Štorch and others (2011), but has never been published. The family Climacograptidae (Fig. 1) includes a well-defined group of derived Darriwilian to Ashgillian (Upper Ordovician) taxa united by a number of synapomorphies, but the early members are less easily defined and analyzed. Mitchell and others (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, while Maletz (2011,

Maletz, Jörg. 2020. Part V, Second Revision, Chapter 23: Suborder Axonophora, Infraorder Diplograptina II (Climacograptidae, Dicranograptidae): Introduction, morphology, and systematic descriptions. Treatise Online 129:1–20, 10 fig.

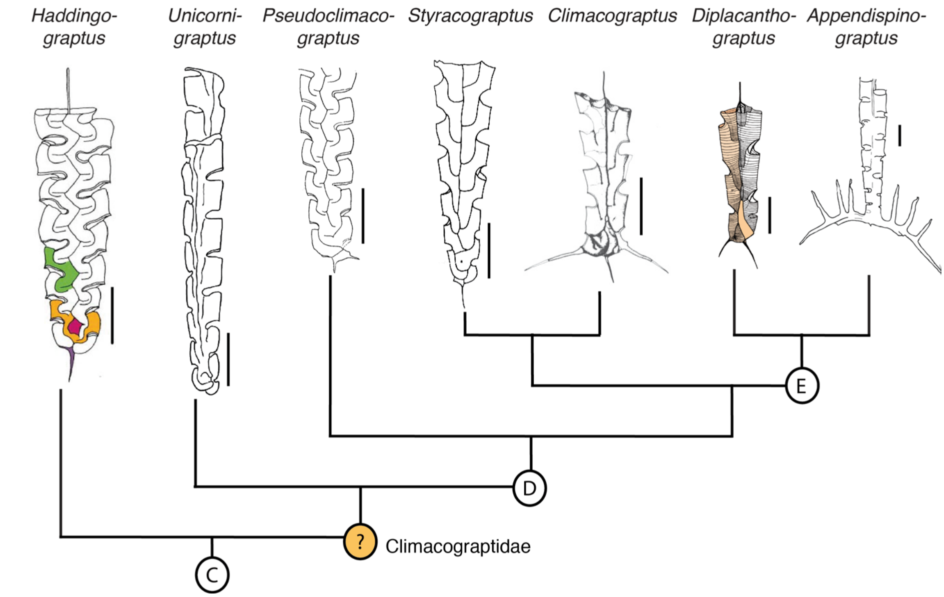

FIG. 1. Interpretation of the evolutionary relationships of the Climacograptidae, showing presence of the proximal development patterns C–E, scale bars, 1 mm (new; based on data from CONE, 2004; MITCHELL & others, 2007; MALETZ, 2011).

fig. 3) and MALETZ (2014) regarded the genera *Undulograptus*, *Oelandograptus,* and *Proclimacograptus* as early member of the Climacograptidae. MALETZ (2011) suggested a derivation of *Pseudoclimacograptus* and its descendants from an ancestor such as *Haddingograptus* (Fig. 1). 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 have to be originating 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 show 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, 1876) 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. 1).

MORPHOLOGY

SICULAR DEVELOPMENT

The sicula of the Climacograptidae is short (less than 1.5 mm long) and widens quickly in all members of the clade from which the sicula is known in isolated specimens. It is straight in early members, but has a distinct curvature and twisting in the genus *Diplacanthograptus* (Fig. 2.1) and related taxa. *Climacograptus* and *Appendispinograptus* may show a short virgella curved or bent across the sicular aperture, but the sicula is not curved noticeably in these cases. The prosicula is often poorly or incompletely preserved in 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. 2.2). These rods are homologous to the longitudinal rods in completely formed prosiculae of other Axonophora. Additional longitudinal rods on the prosicula are not found in Climacograptidae. WILLIAMS and CLARKE

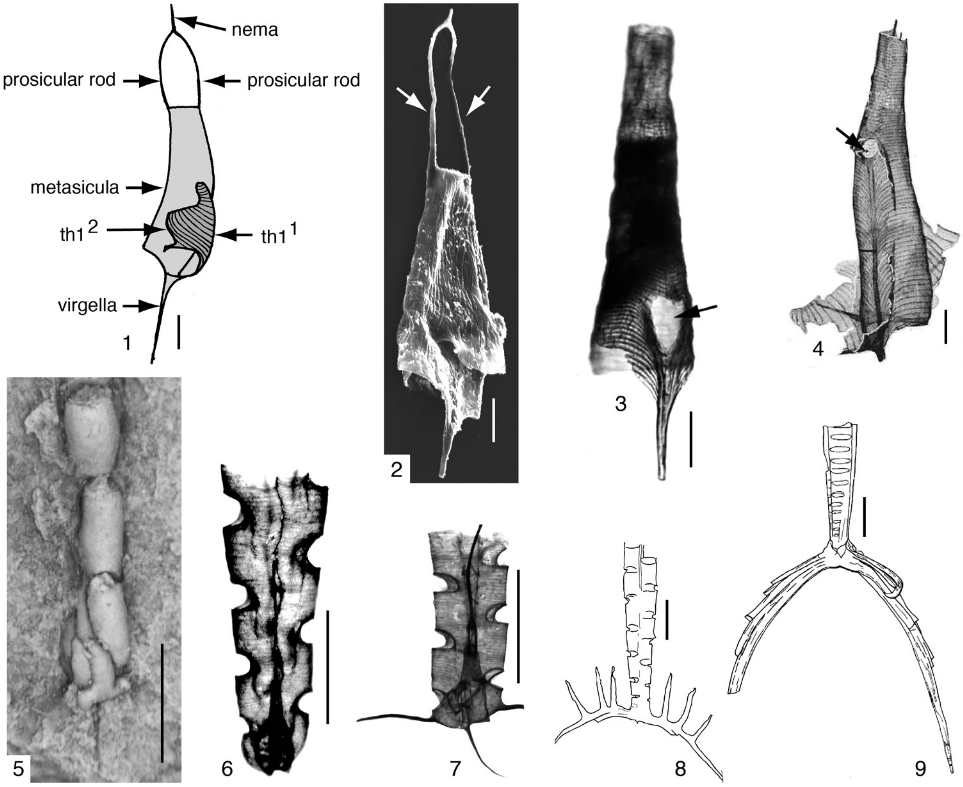

FIG. 2. The sicula and proximal development in the Climacograptidae. *1, Diplacanthograptus spiniferus* (RUEDEMANN, 1912), sicula showing curvature and initial parts of th1[1] and th 1[2] (Mitchell, 1987, fig. 7E); *2, Diplacanthograptus spiniferus*, SMF 75834, SEM photo, sicula showing two rods instead 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, 1876), proximal end showing only the presence of a virgellar spine (Goldman & others, 2011, fig. 1G); *7, Climacograptus crucifer* VANDENBERG, 1990, showing mesial spines on first thecal pair, Viola Limestone (Maletz, 2017, fig. 11,*13F*); *8, Appendispinograptus venustus* (HSÜ, 1959), AFA 84 (NIGP material), Wangjiawan section, Wufeng Formation (Mitchell, Chen, & Finney, 2007, fig. 1,*4*); *9, Appendispinograptus longispinus* (HALL, 1902), AMNH 29267, Toquima Range, Nevada, USA (Riva, 1974b, fig. 4c). All scale bars, 1 mm.

(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 is found 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. 2.3). The origination of virgella occurs late in this taxon and is 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* (Bulman, 1947) (Fig. 2.4).

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. 3.5, Fig. 3.8). 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. 3.8–3.9) 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. 1; Fig. 3.7) 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. 3.1) is unknown. The pattern D astogeny is based on a robust, short and wide sicula with massive crossing canals. The crossing canal of th2^1 is aborted at an early stage and forms a list leaving a characteristic list scar on the ventral surface, easily visible in specimens of *Pseudoclimacograptus* (Fig. 3.8) and derived taxa with pattern D astogeny. The distal development of th2^1 and 2^2 starts with an upward-growing flange on the dorsal side of the early part of th1^2 (Fig. 3.9). This flange grows as a wide construction upward across the aborted crossing canal of th$2^1$and distally differentiates into the thecal tubes of th2^1 and th2^2 (Fig. 3.10). In the pattern E astogeny, a further reduction of the crossing canals can be seen. The development of a flange as the last remains of the crossing canal of th1^2 is abandoned at an early stage. A new flange is secreted at the point where th1^1 starts to grow upward and forms into the upward-growing th1^2 (Fig. 3.12). The differentiation of th2^1 is in the distal, upward-growing part of th1^2.

The Climacograptidae possess 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* (Fig. 1), but often are present only on th1^1 as in *Diplacanthograptus* (Fig. 1), or may be lacking altogether as in *Styracograptus* (Fig. 1). The spines are outward- or downward-directed, depending on their position in the colony and can reach a considerable length (VandenBerg, 1990).

TORSION

The tubaria of many climacograptids (e.g., *Diplacanthograptus*, *Appendispinograptus*) appear to show considerable torsion (VandenBerg, 1990) that might be related to the torsion already visible in the sicular curvature (Fig. 2.1). A moderate torsion of the colonies may already be seen 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, as 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

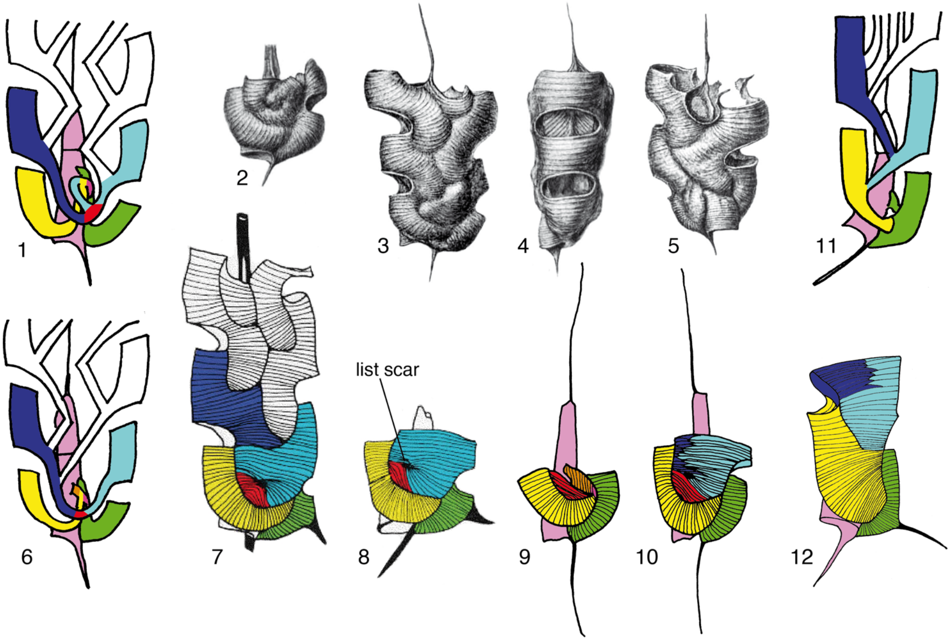

FIG. 3. Proximal development types in *Haddingograptus* MALETZ, 1997 and the Climacograptidae. *1, 6, 11,* pattern C, D, E astogenies (based on Mitchell, 1987); *2–5, Haddingograptus eurystoma* (JAANUSSON, 1960), pattern C astogeny (Bulman, 1932, pl. 1); *7–8, Pseudoclimacograptus scharenbergi* (LAPWORTH, 1876), pattern D astogeny, reconstructions (adapted from Mitchell, 1987, fig. 6F, I); *9–10, Styracograptus tubuliferus* (LAPWORTH, 1876) 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.

visible in specimens of *Appendispinograptus longispinus* (HALL, 1902) from Nevada (USA), showing the proximal spines in a symmetrical position, while the distal part of the colony attains a scalariform view (see RIVA, 1974b).

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. 4,*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. 4,*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; see 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), 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. 4,*2*. **A. venustus* (HSÜ), holotype, No 519, Wufeng Shale, Hubei Province, China, scale bar, 1 mm (adapted from Hsü, 1959).

Climacograptus HALL, 1865, p. 111 [**Graptolithus bicornis* HALL, 1847, p. 268; OD] [=*Mendograptus* RUSCONI, 1948, p. 247 (type, *M. inversus*, M), TORO & BRUSSA, 2007, p. 233; =*Euclimacograptus* RIVA & KETNER, 1989, p. 82 (type, *Climacograptus hastata* HALL, 1902, p. 54, OD), ŠTORCH & others, 2011, p. 354]. Climacograptids with pattern D proximal astogeny; thecae sharply geniculate, with straight supragenicular walls, simple deep semicircular 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. 4,*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. 4,*1e*. *Climacograptus hastatus* (HALL, 1902), lectotype, AMF46104, *Dicellograptus ornatus* Biozone, Stockyard Flat Creek, New South Wales, Australia, scale bar, 1 mm (Riva & Ketner, 1989, fig. 9a).

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, 1876, OD), 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 about 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 $th1^2$ bears small mesial spine as well. *Upper Ordovician (Katian,* Diplacanthograptus caudatus–Pleurograptus linearis *Biozones):* worldwide.——FIG. 4,*4a–c*. **D. spiniferus* (RUEDEMANN); *4a–b,* lectotype, AMNH 1041/5a, Utica Shale, Balston Spa, New York, USA (Riva, 1974a, fig. 4); *4c,* NRM, Holm 1480, juvenile showing position of spines on proximal end and the two rods of the prosicula, Kurland, Estonia (Bulman, 1932, pl. 3). Scale bars, 1 mm.

Pseudoclimacograptus PŘIBYL, 1947, p. 5 [**Climacograptus scharenbergi* LAPWORTH, 1876, 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. 5,*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, 1876, p. 6; OD] [?=*Notograptus* RUSCONI, 1948, p. 248 (type, *N. lanceolatus*, M), TORO & BRUSSA, 2001, p. 362, *nom. nud.,* 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 often 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. 4,*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.

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 often 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. 5,*1a*. **U. xinjiangensis*, holotype, NIGP 157509, reverse view, scale bar, 1 mm (Chen & others, 2016, fig. 6-97N).——FIG. 5,*1b*. *U. ambiguus* (MALETZ, 2011), GSC 81805, flattened, isolated specimen, *Levisograptus dentatus* Biozone, St. Pauls Inlet, western Newfoundland, Canada, scale bar, 1 mm (Maletz, 2011, fig. 4K).——FIG. 5,*1c–d*. *U. pungens* (RUEDEMANN, 1904), GSC 133528, isolated specimen in obverse (*c*) and reverse (*d*) views, scale bars, 1 mm (Maletz, 2011, fig. 4I,J).——FIG. 5,*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).

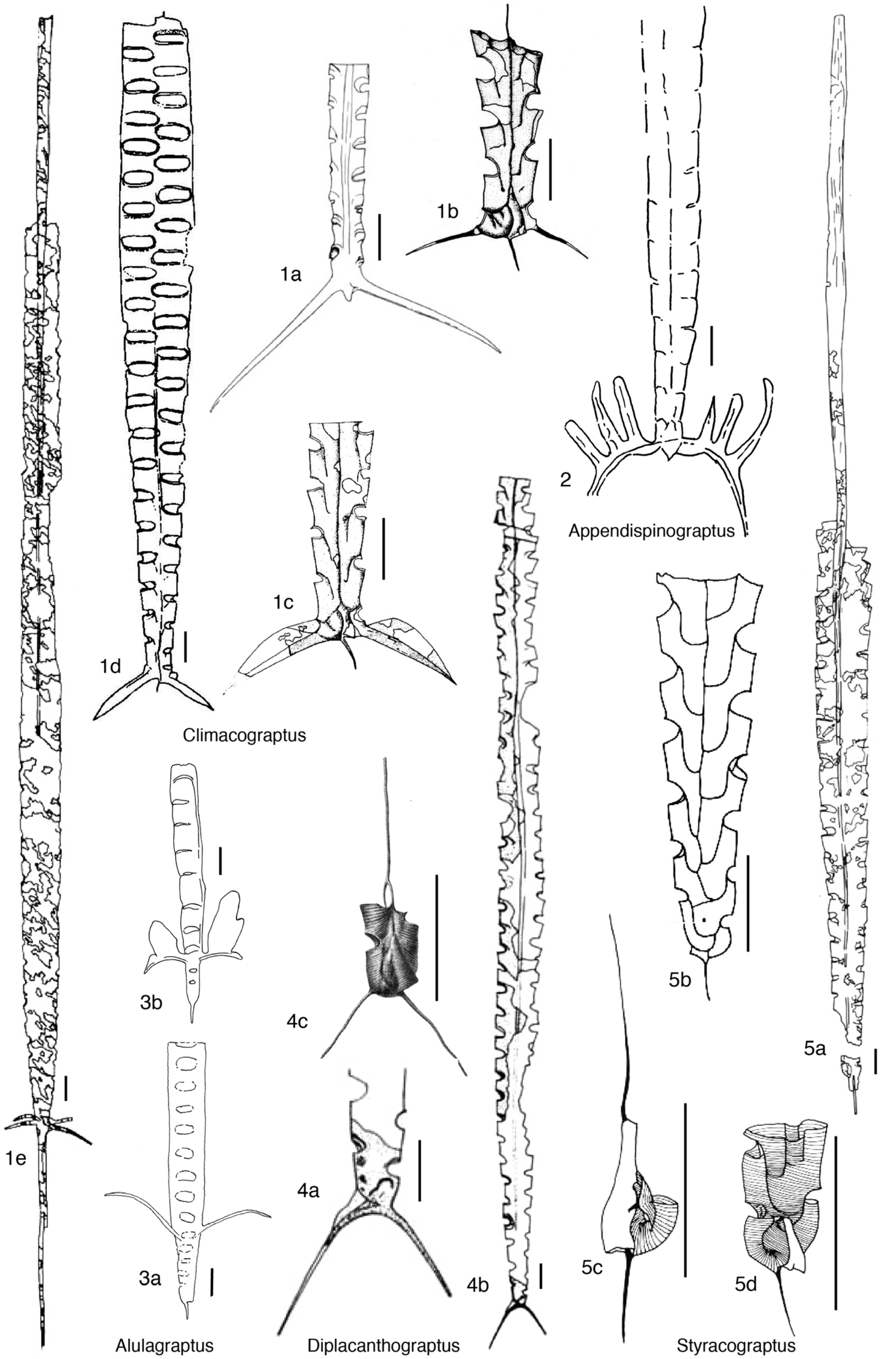

FIG. 4. Climacograptidae (p. 5–6).

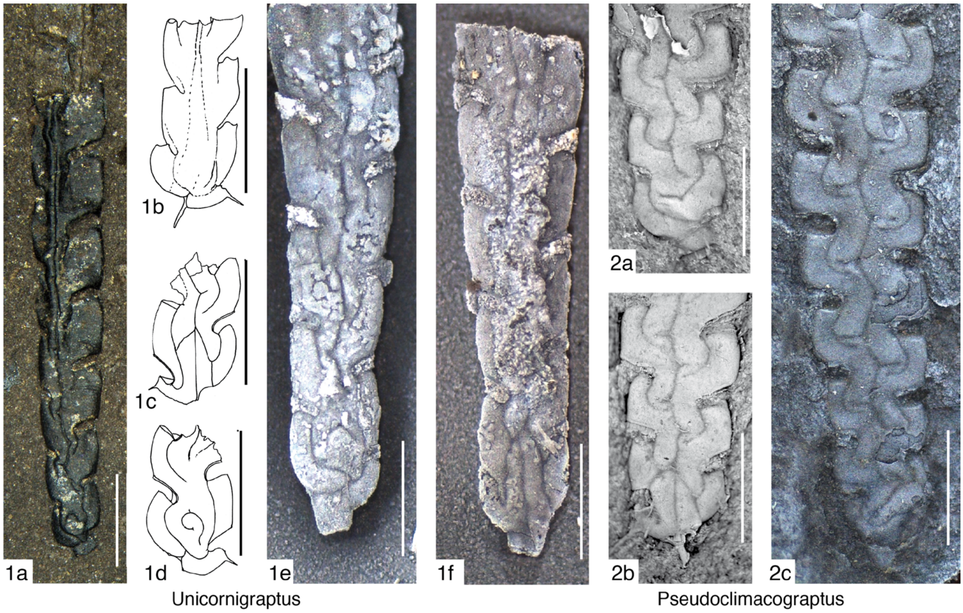

FIG. 5. Climacograptidae (p. 6).

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, 1879, 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 showing a quite variable colony shape from multiramous to one-stiped. The cladistic analysis of MITCHELL and others (2007, fig. 1) indicated that *Dicaulograptus* with a pattern C astogeny shows 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, 1932) as derived from an archiclimacograptid ancestor. The interpretation gets more problematical with the recognition of two-stiped axonophorans with a generally dicellograptid tubarium construction in the early Darriwilian. MALETZ (1998, 2014) 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, 1998) and *Undulograptus* sp. (KRAFT & KRAFT, 2003) in the lower Darriwilian (MALETZ, 2014). These taxa with a possible pattern U astogeny (Fig. 6.8), however, differ from the thecal construction in the younger species of *Dicellograptus* and a considerable biostratigraphic gap in the presence of dicellograptid colony shapes in the Darriwilian renders the interpretation questionable.

PROXIMAL DEVELOPMENT

MITCHELL (1987) analyzed the proximal development of the Dicranograptidae in some detail and recognized several distinct astogenetic patterns (Fig. 6). MITCHELL and others (2007) identified the biserial axonophoran *Dicaulograptus* with a typical pattern C astogeny (Fig. 2.1) 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. 6.5–6.6). MITCHELL (1987) interpreted this development as pattern A′ (Fig. 6.2) in his analysis of the proximal development of Ordovician biserials. It differs from a pattern A astogeny (Fig. 6.1) only through the presence of the lateral clefts at the virgella and a dorsal notch on the sicular aperture (Fig. 6.7). Derived dicranograptids show 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. 6.3) can be separated through the development of two separate stipes (the dicellograptid condition). Pattern N of MITCHELL (1987, fig. 1), the nemagraptid pattern (Fig. 6.5), 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 orientaion of the sicula (e.g., MU & others, 2002; CHEN & others, 2016). While *Dicellograptus* bears a J-shaped first theca ($th1^1$) (Fig. 6.10–6.11), $th1^1$ is more U-shaped in *Jiangxigraptus* with its sicula usually leaning at least partly on stipe 2 (Fig. 6.9).

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, showing the lateral branches originating 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 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, 1881 (SKWARKO, 1974; MALETZ, 1994).

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 appears 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

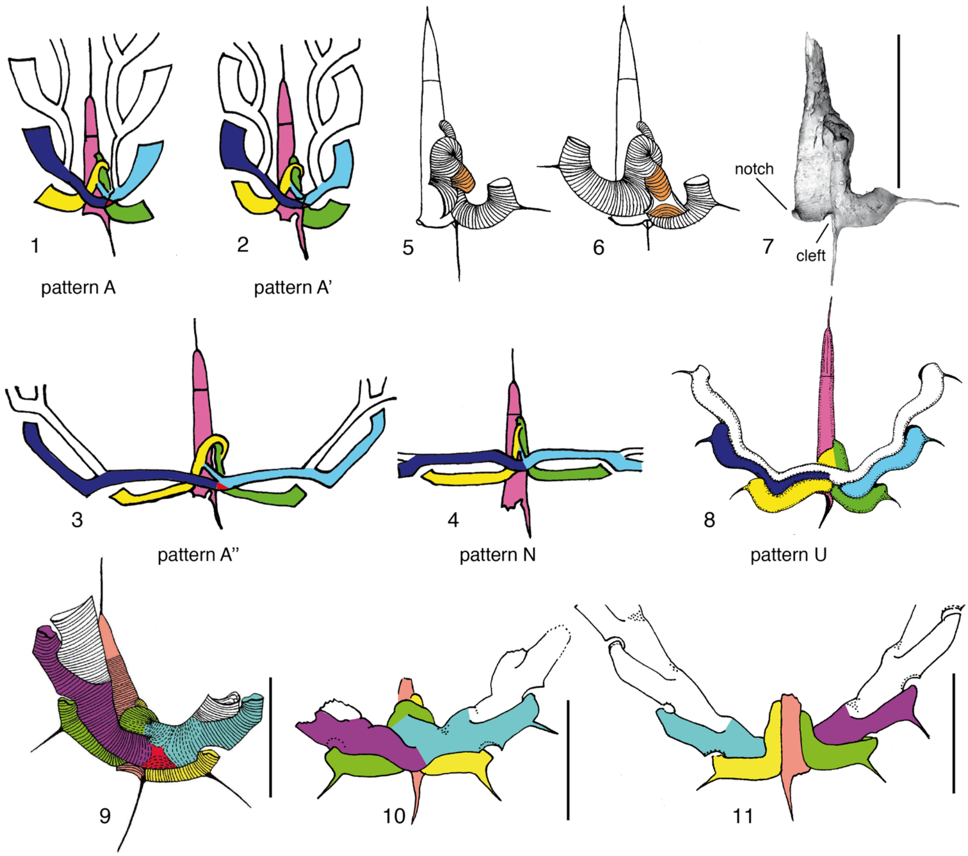

FIG. 6. Proximal development in the Dicranograptidae. *1–4,* Proximal development types (adapted from Mitchell, 1987, fig. 1). *5–6, Dicranograptus nicholsoni* HOPKINSON, 1870, initial part of th2[1] and upward-growing flange on th1[1] highlighted (adapted from Bulman, 1955, fig. 43); *7, Dicranograptus nicholsoni,* SMF 75811, juvenile, showing development of sicular aperture (new); *8,* inferred pattern U astogeny in *Levisograptus dicellograptoides* MALETZ, 1998, reconstruction (adapted from Maletz, 1998, 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, 1880 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.

multiramous and fairly large colonies of the genera *Amphigraptus* and *Pleurograptus* (see HALL, 1859; NICHOLSON, 1867) 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, 1950, p. 181; =Tangyagraptinae, MU, 1963, 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 here 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 in 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.

Dicaulograptus RICKARDS & BULMAN, 1965, p. 278 [**Lasiograptus hystrix* BULMAN, 1932, p. 29; OD]. Biserial dicranograptid with complex thecae showing 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–Jiangxigraptus vagus *Biozones):* China, Sweden, Norway, Canada, USA.——FIG. 7,*1a–c*. **D. hystrix* (BULMAN); *1a,* holotype, NRM Holm 48, reverse view (Bulman, 1932, pl. 9,*5*); *b–c,* paratypes, NRM Cn 59951, 59952, juveniles showing proximal development (Mitchell, 1988, fig. 11,*4,6*).——FIG. 7,*1d–e*. *Dicaulograptus 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, *nom. correct.* LAPWORTH, 1873a, p. 501, *pro Dicellograpsus* HOPKINSON, 1871, spelling changed in ICZN Opinion 650, 1963] [**Didymograpsus elegans* CARRUTHERS, 1867, p. 369; SD GURLEY, 1896, p. 70] [=*Huayinograptus* YU & FANG, 1981; *nom. nud.* (type, *Dicellograptus szechuanensis* MU, 1950, OD), herein] [=*Leptograptus* LAPWORTH, 1873b, p. 558 (type, *Graptolithus flaccidus* HALL, 1865, p. 143, OD), 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. 7,*2a*. **D. elegans* (CARRUTHERS), holotype, NHMUK Q850, Lower Hartfell Shale, *Pleurograptus linearis* Zone, Dob's Linn, Scotland, UK (Elles & Wood, 1904, pl. 23,*2a*).——FIG. 7,*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. 7,*2c–e*. *Dicellograptus complanatus* (LAPWORTH, 1880); *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, 1963, 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. 7,*3*. **D. mirus*, syntype, top of Wufeng Shale, Tangya, Yichang, China, scale bar, 1 mm (Mu, 1963, fig. 13b).

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, often 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 (late Darriwilian,* Jiangxigraptus vagus *Biozone)–Upper Ordovician (Katian,* Paraorthograptus pacificus *Biozone):* worldwide.——FIG. 7,*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.

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), herein] [=*Aclistograptus* GE

FIG. 7. Dicranograptinae without cladia (p. 11–13).

in MU & others, 2002, p. 439 (type, *Graptolithus divaricatus* HALL, 1859, p. 513, OD), herein]. Two-stiped dicranograptids with reclined, often 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. 7,*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. 7,*6b*. *J. inculus* (Ge in Ge, Zheng, & Li, 1990), holotype, NIGP 106213, proximal end, showing strong tectonic deformation, *Nemagraptus gracilis* Biozone, China, scale bar, 1 mm (new; photo by Zhang Yuandong).——Fig. 7,*6c*. *J. divaricatus* (Hall, 1859), 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), herein]. Two-stiped dicranograptid with reclined stipes showing 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–Climacograptus bicornis *Biozones):* China, North America.——Fig. 7,*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. 7,*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 often with genicular hoods; apertures with slight lateral lobes or straight. *Middle Ordovician (Darriwilian,* Jiangxigraptus vagus *Biozone)–Upper Ordovician (Sandbian,* Nemagraptus gracilis *Biozone):* worldwide.——Fig. 7,*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, 1859, p. 509; M] [=*Clematograptus* Hopkinson in Hopkinson & Lapworth, 1875, p. 652 (type, *Graptolithus multifasciatus* Hall, 1859, p. 508, SD Gurley, 1896, p. 93), 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. 8,*1a–b*. **A. divergens* (Hall); *1a, A. multifasciatus*, holotype, NYSM 6840, *Nemagraptus gracilis* Biozone, Normanskill Shale, Kenwood, New York, USA (Ruedemann, 1908, pl. 15,*4)*; *1b,* holotype, *Nemagraptus gracilis* Biozone, Normanskill Shale, Kenwood, New York, USA (Hall, 1859, fig. 9).

Pleurograptus Nicholson, 1867, p. 257, *nom. correct. pro Pleurograpsus* Nicholson, 1867, spelling 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–Paraorthograptus pacificus *Biozones):* UK, Canada, China, USA.——Fig. 8,*2a–b*. **P. linearis* (Carruthers); *2a,* NHMUK PM Q848, large specimen, Hartfell Shale, Scotland, UK (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–Climacograptus bicornis *Biozones):* China, USA.——Fig. 8,*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, 1963, 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, 1963 in Finney, 1985a, p. 1104.] *Upper Ordovician* (*Katian,* Paraorthograptus pacificus *Biozone):* China.——Fig. 8,*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, 1963, fig. 10).

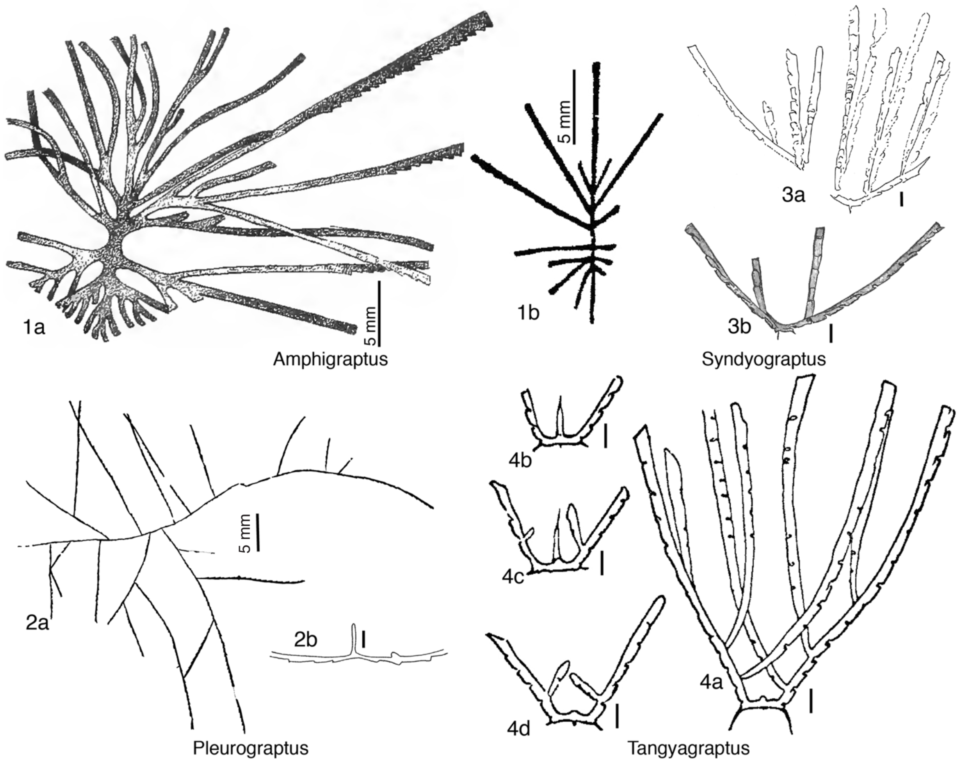

FIG. 8. Dicranograptinae with cladia (p. 13).

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, often 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.

The Nemagraptidae is a traditional name already 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, e.g. 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 (2014, p. 515) revised the family and also included *Pleurograptus*, unaware of the dicellograptid proximal end of this genus illustrated in WILLIAMS (1982, pl. 2).

Nemagraptidae has commonly been used as a taxonomic unit of the family level (e.g. BULMAN, 1970; MU & others, 2002), but is here 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

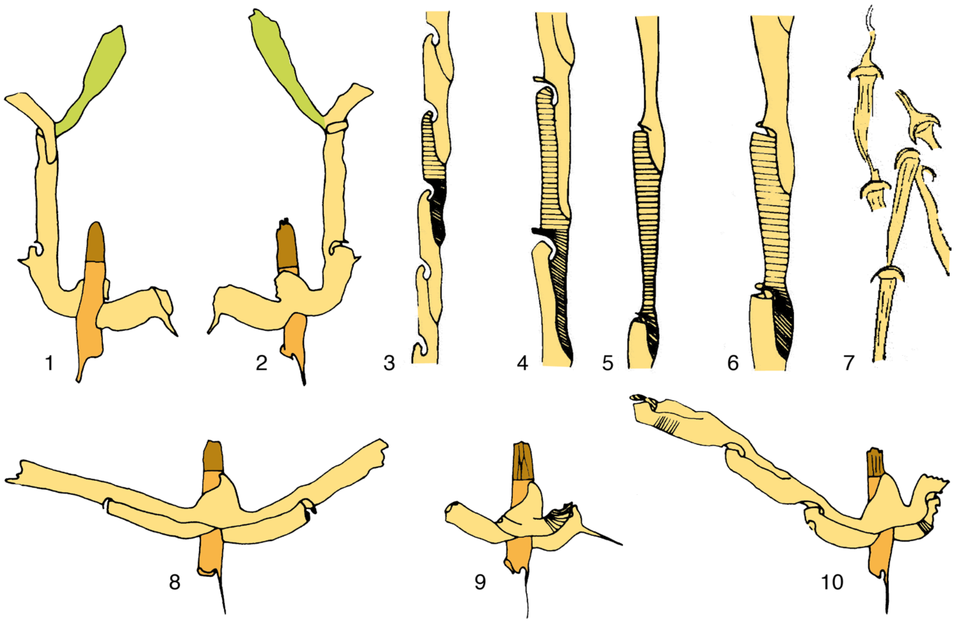

FIG. 9. Tubarium construction in *Nemagraptus*. *1–2, 5–6, 8, Nemagraptus gracilis* (HALL, 1847); *1–2,* proximal end showing cladium (Finney, 1985a, fig. 11–12); *5–6,* proximal *(5)* and distal *(6)* thecal style (Finney, 1985a, fig. 4,*6*–4,*7*); *7,* ventral view of stipes, holotype of *Ordosograptus 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.

& 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 shows the isolated metasicula (Fig. 9) as the main synapomorphy of the nemagraptids (FINNEY, 1985a, fig. 23,*1*). As the genera *Amphigraptus, Pleurograptus,* and *Tangyagraptus* are now included in the Dicranograptinae, the Nemagraptinae includes a single genus with a number of taxa showing variable development of cladia. FINNEY (1985a) illustrated the development of cladia in *Nemagraptus* from chemically isolated material (Fig. 9.1–9.2). The thecae show considerable overlap and indications of intrathecal folds in *Nemagraptus linmassiae* (Fig. 9.3–9.4), while in *Nemagraptus gracilis* the thecae are shorter and lack the introverted thecal apertures and lateral lappets (Fig. 9.5–9.6). Strong genicular lobes or flanges have been used to differentiate the genus *Ordosograptus* LIN, 1980 (Fig. 9.7), 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. 10,*1c–e*).

Nemagraptus EMMONS, 1855, p. 109 [*nom. correct.* HALL, 1859, *pro Nemagrapsus* EMMONS, 1855, spelling 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] [=*Geitonograptus* OBUT & ZUBTZOV, 1965, p. 24 (type, *G. suni,* OD), BULMAN, 1970, p. 120] [=*Helicograpsus* NICHOLSON, 1868, p. 23 (type, *Grapolithus gracilis* HALL, 1847, p. 274, OD)] [=*Ordosograptus* LIN, 1980, p. 477 (type, *O. delicatus,* OD), FINNEY, 1985a, p. 1111] [=*Stephanograptus* GEINITZ, 1866, p. 124 (type,

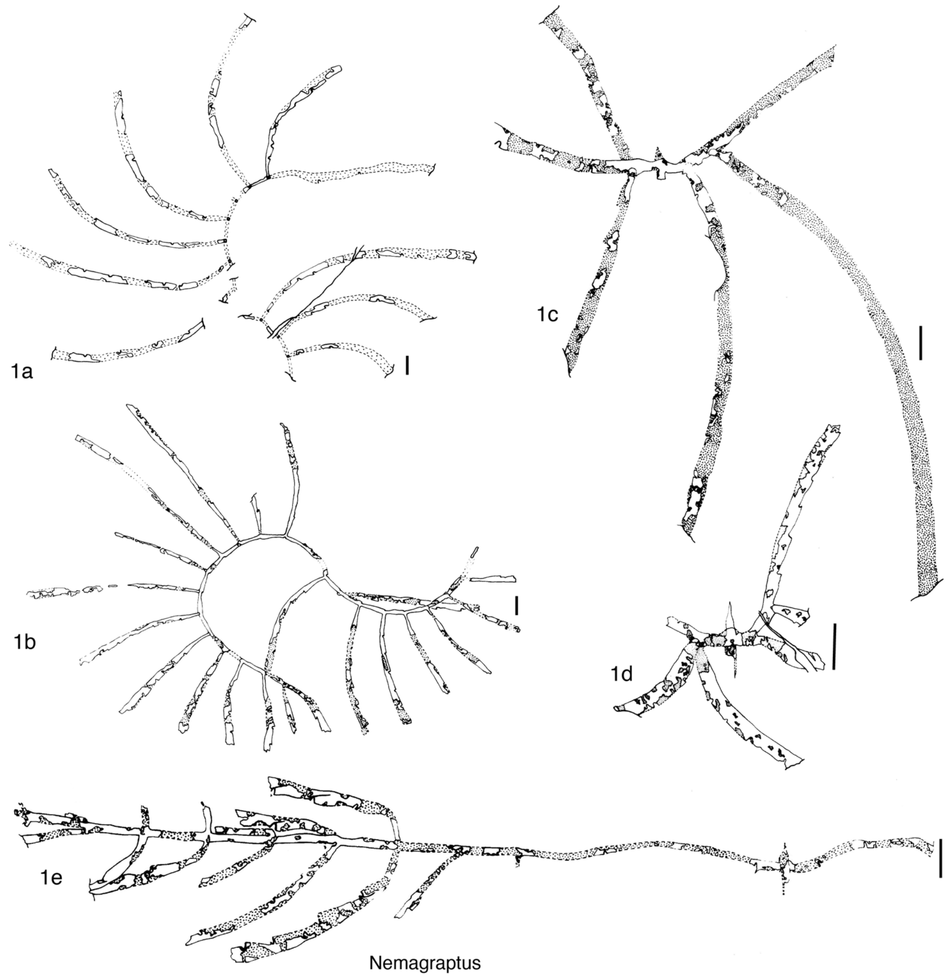

FIG. 10. Nemagraptinae (p. 15–16).

Graptolithus gracilis HALL, 1847, p. 274, OD)]. 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, often 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. 10,*1a–b. *N. gracilis* (HALL); *1a*, AMNH 30458, lectotype, Normans Kill Shales, Kenwood, New York, USA, scale bar, 1 mm; *1b,* AMNH 36766, more complete specimen, Normans Kill Shales, Kenwood, New York, USA; scale bars, 1 mm (Finney, 1985a, fig. 10,*1–2*).——FIG. 10,*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. 10,*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).

ABBREVIATIONS FOR MUSEUM REPOSITORIES

AMF: Australian Museum, Sydney, Australia
AMNH: American Museum of Natural History, New York City, New York, USA

BU: Lapworth Museum, Birmingham University, UK
GSC: Geological Survey of Canada, Ottawa, Canada
LO: Lunds Originale, Department of Geology, Lund University, Sweden
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
NYSM: New York State Museum, Albany, New York, USA
NMV: Museums Victoria, Melbourne, Australia
NRM: Naturhistoriska Riksmuseet Stockholm, Sweden
OSU: Orton Geological Museum, Ohio State University, Columbus, Ohio, USA
PMO: Natural History Museum, Paleontological Type collections, University of Oslo, Norway
PMU: Palaeontological Collections, Museum of Evolution, Uppsala University, Sweden
SM: Sedgwick Museum of Earth Sciences, Cambridge, UK
SMF: Senckenberg Institute, Frankfurt/Main, Germany

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