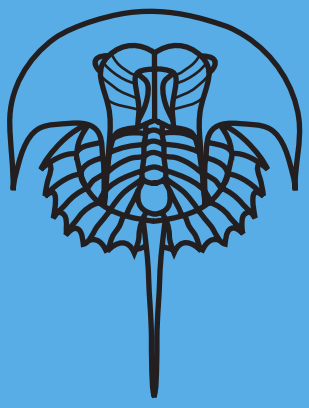

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Part V, Second Revision, Chapter 24: Infraorder Neograptina and Family Normalograptidae: Introduction, Morphology, and Systematic Descriptions

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PART V, SECOND REVISION, CHAPTER 24: INFRAORDER NEOGRAPTINA AND FAMILY NORMALOGRAPTIDAE: INTRODUCTION, MORPHOLOGY, AND SYSTEMATIC DESCRIPTIONS

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

[Neograptina ŠTORCH, MITCHELL, FINNEY, & MELCHIN, 2011, p. 368]
[=family Monograptidae LAPWORTH, 1873 *sensu* MITCHELL, 1987, p. 390; =suborder Monograptina of MITCHELL & others, 2007]

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

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

ŠTORCH and others (2011, p. 368) erected the monophyletic taxon Neograptina as a sister taxon to the Diplograptina, using the results of an analysis by MITCHELL and others (2007) and identified *Undulograptus formosus* MU & LEE, 1958 as the earliest member of the clade. MELCHIN and others (2011, fig. 3) separated three groups in the Neograptina (Fig. 1), the Normalograptidae, the Monograptoidea, and the Retiolitoidea and regarded the genus *Hirsutograptus* as *incertae sedis*. The authors considerably extended the concept of the Retiolitoidea and included a number of non-ancorate taxa.

Maletz, Jörg. 2019. Part V, Second Revision, Chapter 24: Infraorder Neograptina and family Normalograptidae: Introduction, morphology, and systematic descriptions. Treatise Online 116:1–15, 8 fig.

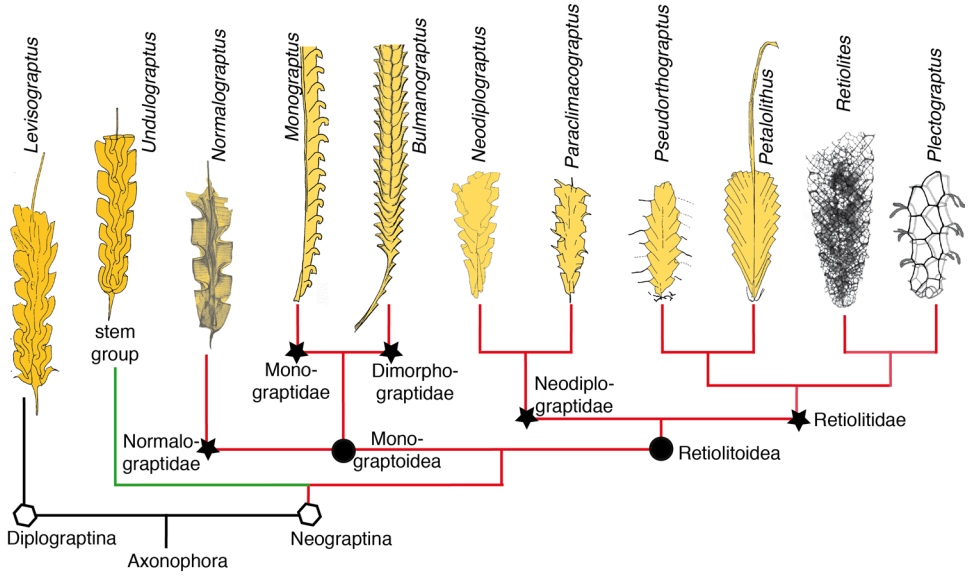

FIG. 1. Cladistic interpretation of origin of the Neograptina (new, based on data in MELCHIN & others, 2011, fig. 2 and ŠTORCH & others, 2011, fig. 6).

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

MORPHOLOGY

The description of the tubarium morphology focuses on the early taxa and their development (stem group taxa and Normalograptidae). Derived taxa (Retiolitoidea, Monograptoidea) will be covered in later chapters. The proximal development types of early Neograptina are poorly understood. MITCHELL (1987) stated a pattern A astogeny (Fig. 2.2) for *Oelandograptus oelandicus* BULMAN, 1963 (Fig. 2.3–2.5) and a pattern B astogeny for the genus *Undulograptus* (Fig. 2.1). The pattern B astogeny of *Undulograptus* was based on *Proclimacograptus angustatus* (EKSTRÖM, 1937), as described by MALETZ (1997). The species was erroneously regarded as the type species of *Undulograptus* by MITCHELL (1987, p. 397). The type of *Undulograptus*, however, is *Pseudoclimacograptus formosus* MU & LEE, 1958, a species for which the proximal development was unknown at the time, but MITCHELL (1992) identified a pattern C astogeny in *Undulograptus formosus* (Fig. 2.8) and some other species referred to *Undulograptus*. MALETZ and AHLBERG (2011) discussed a group of *Undulograptus* species from the Krapperup drill core showing a pattern C astogeny. A pattern C astogeny can also be seen in *Haddingograptus* species. MALETZ (2011b) discussed a possible origin of the derived climacograptids from these. Thus, a pattern C astogeny may be found in basal Neograptina, but the development of *Oelandograptus* and its inclusion in the Neograptina remains uncertain.

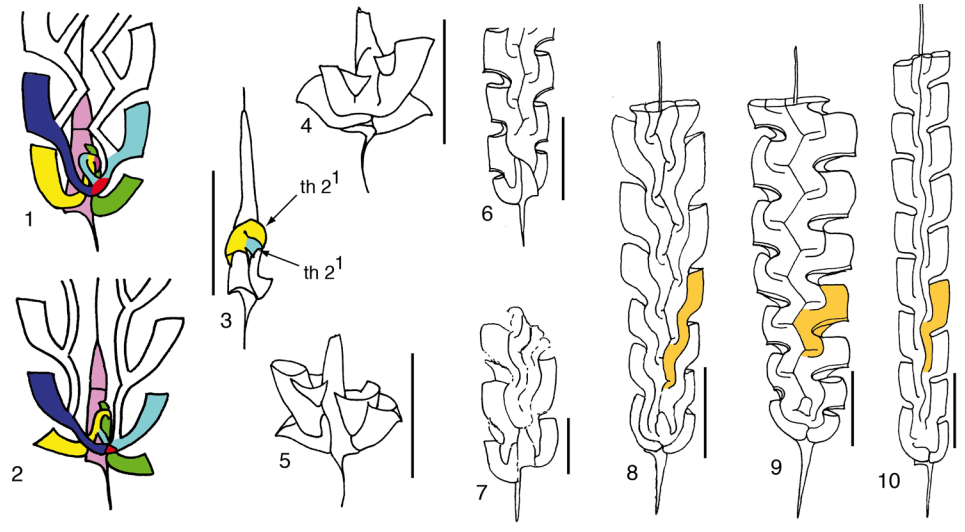

FIG. 2. Proximal development and tubarium shape of early Neograptina. *1,* Pattern C astogeny; *2,* pattern A astogeny; *3–5, Oelandograptus oelandicus* (BULMAN, 1963), juveniles in reverse (*3–4*) and obverse (*5*) views; *6, Haddingograptus* MALETZ, 1997 sp., proximal end in obverse view, reconstruction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

The proximal end of early Neograptina is evenly rounded to strongly asymmetrical. The first thecal pair is strongly upturned (Fig. 2) and the thecal apertures are oriented horizontally, but in *Oelandograptus* the apertures are outward inclined. The proximal development of pattern A astogeny in this taxon needs to be revised and verified. Depending on the position of the dicalycal theca, the proximal development of pattern C astogeny can be differentiated into two slightly different types. In taxa with a dicalycal theca th3[1], the obverse side shows an arch connecting th2[2] and th3[1]. This development is found in *Haddingograptus eurystoma* (JAANUSSON, 1960) and other *Haddingograptus* species (Fig. 2.6). In *Haddingograptus oliveri* (BOUČEK, 1973) with a dicalycal theca th2[1], the median septum is complete on both the obverse and reverse sides (see MALETZ, 1997, fig. 7I–J).

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

The thecal style varies considerably in the early Neograptina (Fig. 2.8–2.10) from simple straight tubes to strongly geniculate ones. The geniculum may be provided with a genicular flange or can be rounded without elaborations. The suprageniculum wall may be vertical, inward or outward sloping, or convexly curved. The thecal apertures also can vary in their orientation from introverted through horizontal to everted. In biostratigraphically earlier taxa, the thecal overlap is high, and the thecae show a double

sigmoidal curvature and the conspicuous presence of intrathecal septa and folds (Fig. 2.8), but the thecal overlap is subsequently reduced and thecae may be short and show little curvature. In these, the intrathecal septa are missing and intrathecal folding does not exist (Fig. 2.10).

STEM GROUP NEOGRAPTINA

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

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

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

Haddingograptus MALETZ, 1997, p. 63 [**Pseudoclimacograptus* (*Pseudoclimacograptus*) *oliveri* BOUČEK, 1973, p. 121; OD]. Neograptines with broadly rounded, often somewhat asymmetrical proximal end of pattern C astogeny; median septum usually sharply zigzag shaped; intrathecal folding conspicuous; strong genicular flanges or collar structures common, often with distinct ventral genicular notch; thecal apertures slit-like, horizontal. *Middle Ordovician (Darriwilian,* Nicholsonograptus fasciculatus–Dicellograptus vagus *Biozones):* China, Sweden, Norway, Spain, Canada, USA, Argentina.——FIG. 3,*6a–b*. **H. oliveri* (BOUČEK); *6a,* paratype, RM Cn 2541, reverse view; *6b,* holotype, RM Cn 2539, obverse view; Elnes Formation Rigshospitalet, Oslo, Norway, scale bars, 1 mm (adapted from Bulman, 1953, fig.1).——FIG. 3,*6c*. *Haddingograptus*. sp. nov., obverse view, reconstruction based on PMO 138.400, scale bar, 1 mm (see Maletz, 1997, fig. 31g) (new).——FIG. 3,*6d–e*. *H. eurystoma* (JAANUSSON, 1960), RM Holm 2345, 2352, juvenile specimens in reverse (*d*) and obverse (*e*) views; scale bars, 1 mm (Bulman, 1932, pl. 1,*12* and 1,*14*, respectively).

Oelandograptus MITCHELL, 1987, p. 383 [**Glyptograptus austrodentatus oelandicus* BULMAN, 1963, p. 682; M]. Neograptines with undulatory median septum; thecae weakly sigmoidal with long, outwardly inclined infragenicular wall, sharply rounded geniculum, short, nearly vertical supragenicular wall; thecal apertures slightly everted, undulatory with concave ventral margin; proximal development of pattern A astogeny with evenly rounded to somewhat blunt, nearly symmetrical proximal end. *Middle Ordovician (Darriwilian,* Holmograptus lentus–Nicholsonograptus fasciculatus *Biozones):* Norway, Sweden.——FIG. 3,*1a–b*.

Proclimacograptus Maletz, 1997, p. 68 [**P. bulmani;* OD]. Neograptines with slender tubarium; th1[1] and th1[2] strongly upturned with horizontal apertures; median septum straight to moderately undulate; thecae short with straight, horizontal apertures; proximal development of pattern B astogeny. *Middle Ordovician (Darriwilian,* Nicholsonograptus fasciculatus–Pterograptus elegans *Biozones):* Czech Republic, Norway, Sweden, China.——Fig. 3,*5a.* **P. bulmani,* holotype, PMO 138.711, reverse view, Almedalsveien, Slemmestad, Norway, scale bar, 1 mm (Maletz, 1997, fig. 34C).——Fig. 3,*5b. P. angustatus* (Ekström, 1937), PMO 138.809, proximal end in obverse view, scale bar, 1 mm (Maletz, 1997, fig. 33K).

Prolasiograptus Lee, 1963, p. 564 (p. 574, English text) [**Lasiograptus retusus* Lapworth, 1880, p. 175; OD]. Neograptines with widely rounded proximal end, virgella as single proximal end spine; thecae with distinct geniculum, short, inward-inclined supragenicular walls; proximal development of pattern C astogeny. *Middle Ordovician (Darriwilian*, Pseudamplexograptus distichus *Biozone):* Britain, Germany, Norway, Sweden, China.——Fig. 3,*7a–c.* **P. retusus* (Lapworth); *7a,* RM Cn 226 (Holm collection), Gärslösa, Öland, Sweden (illustrated as *Climacograptus scharenbergi* in Bulman, 1932, pl. 1,*25–26*); *7b,* RM No 213 (Holm collection), Gärslösa, Öland, Sweden (Maletz, 1997, fig. 29G); *7c,* holotype, BU 1349, Llandrindod Wells, Llandeilo, Wales, UK (new, drawing by C. E. Mitchell). Scale bars, 1 mm.

Reteograptus Hall, 1859, p. 518 [**R. geinitzianus;* OD] [=*Retiograptus* Hall, 1865, p. 115 *nom. null.;* =*Clathrograptus* Lapworth, 1873, table facing p. 555, see Elles & Wood, 1908, p. 315 (type, *C. cuneiformis,* OD)]. Proximally rounded, robust neograptines; fusellum strongly reduced, lacking in biostratigraphically younger taxa; preserved often as clathrial framework outlining tubarium; internal construction and proximal development unclear; sicula small, with complete prosicula, widening considerably towards aperture. *Middle Ordovician (Upper Darriwilian,* Pterograptus elegans *Biozone)–Upper Ordovician (Sandbian,* Climacograptus bicornis *Biozone):* worldwide.——Fig. 3,*2a–b. R. speciosus* Harris, 1924, Darriwilian, Slemmestad, Oslo Region, Norway; *2a,* PMO 138.440, reverse view; *2b,* PMO 138.436, obverse view; scale bars, 1 mm (Maletz, 1997, pl. 7l and pl. 6i, respectively).——Fig. 3,*2c–e.* **R. geinitzianus; 2c,* lectotype, AMNH 37757, Austin Glen Graywacke (Normanskill Shale), Kenwood near Albany, New York, USA, scale bar, 1 mm; *2d,* OSU 32915, chemically isolated proximal end in reverse view, Pratt's Syncline, Athens Shale, Alabama, USA, scale bar, 1 mm; *2e,* OSU 32918, juvenile showing origin of th1[1] (*arrow*), Pratt's Syncline, Athens Shale, Alabama, USA, scale bar, 0.5 mm (*2c–e,* Finney, 1980, fig. 12c, 13f, and 14, respectively).

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

Family NORMALOGRAPTIDAE Štorch & Serpagli, 1993

[Normalograptidae Štorch & Serpagli, 1993, p. 14] [=superfamily Normalograptacea Mitchell & others, 2007, p. 337] [=Metaclimacograptidae Koren' & Rickards, 1996, p. 94]

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

Štorch and others (2011) discussed the family Normalograptidae as a paraphyletic taxon and extended it to include the basal Neograptina. The authors erroneously included all post-Hirnantian graptolites in the Normalograptidae in their cladistic diagram (Štorch & others, 2011, fig. 6),

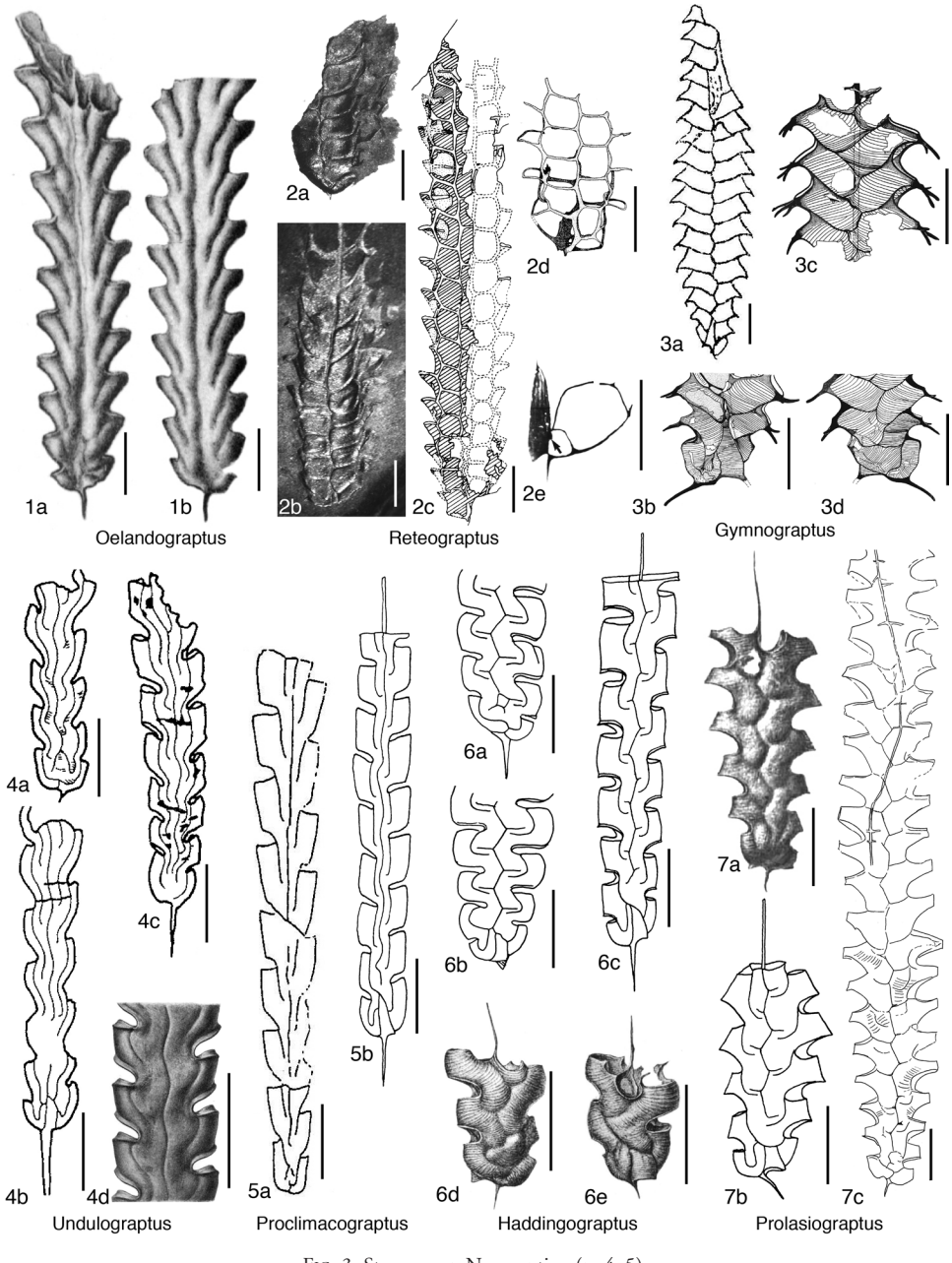

FIG. 3. Stem group Neograptina (p. 4–5).

even though they explicitly excluded them in the accompanying text. MELCHIN and others (2011, p. 293) stated that "As a consequence of the variety of proximal and thecal morphologies found among taxa within this stem group, it is not currently possible to identify any morphologic criteria that can be used to uniquely characterize this taxon." The Normalograptidae represents a family with roots in the lower Darriwilian (Middle Ordovician). Both the precise origin of the Normalograptidae from a taxon of the early

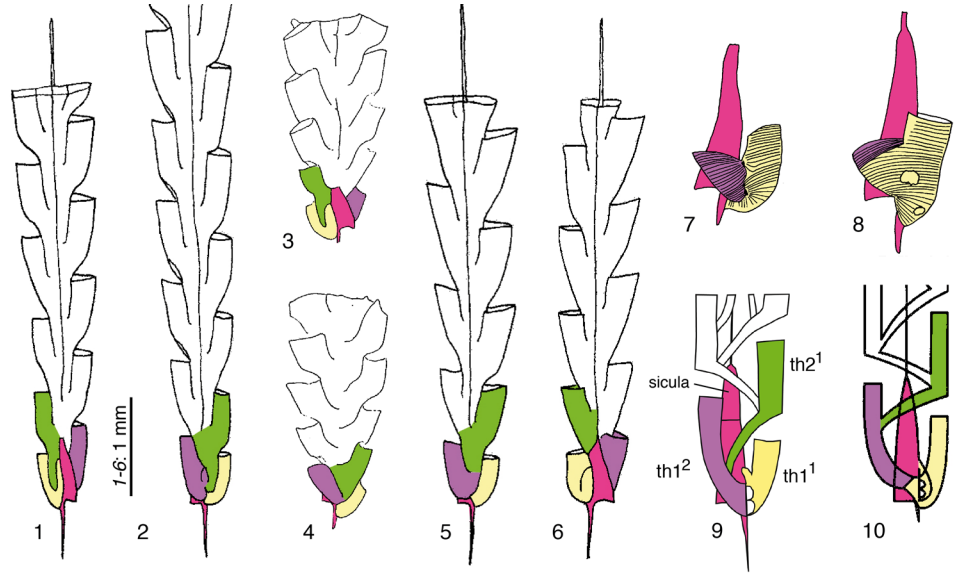

FIG. 4. Proximal development and colony shape of biserial Neograptina. *1–2*, *Proclimacograptus bulmani* MALETZ, 1997 in reverse (*2*) and obverse (*1*) views (new); *3–4, Skanegraptus janus* MALETZ, 2011c, in reverse (*4*) and obverse (*3*) views (adapted from Maletz, 2011c, fig. 2); *5–6, Pronormalograptus antiquus* (GE in GE, ZHENG, & LI, 1990) in reverse (*5*) and obverse (*6*) view (adapted from Maletz, 2011c, fig. 2); *7, Metaclimacograptus orientalis* (OBUT & SOBOLEVSKAYA, 1966), GSC 104912 (adapted from Melchin, 1998, fig. 4A); *8, Korenograptus nikolayevi* (OBUT, 1965), a neodiplograptid, GSC 104823, pattern H′ astogeny (adapted from Melchin, 1998, fig. 4B); *9*, diagram showing pattern H astogeny (adapted from Mitchell, 1987, fig. 1H); *10*, diagram showing pattern H′ astogeny (adapted from Melchin, 1998, fig. 2H). Sicula and thecae color coded for easy comparison (see *9*); *1–6,* scale bar, 1 mm.

Neograptina *incertae sedis* and the relationship to the Climacograptidae are unclear (MALETZ, 2011c). The origin and subsequent differentiation of the Normalograptidae may have to be reevaluated, and it is here preferred to base them on the origin of a pattern H astogeny for now instead of including (1) taxa with pattern A to pattern C astogenies and (2) lack of proximal spines except for the virgella (e.g., the taxa included in the stem group Neograptina). The first taxon with a proximal end pattern similar to proximal development type H is the genus *Skanegraptus*, but this taxon still has a number of characters similar to taxa with a pattern C astogeny (MALETZ, 2011c).

MORPHOLOGY

Normalograptidae contains a number of biserial, dipleural graptoloids with a rounded to pointed proximal end and a single proximal end spine, the virgella (Fig. 4.3–4.7). Their thecal style is simple—thecae with straight, outward-inclined to strongly geniculate ventral thecal walls. Geniculate thecae are prevalent and genicular elaborations are common. The thecal apertures are horizontal to everted and in geniculate taxa generally slit-like. A long nema is typical of many species and may be modified into an elongated nematularium.

MITCHELL (1987) introduced the proximal development pattern H based on the investigation of *Normalograptus brevis* (ELLES & WOOD, 1906) and *Normalograptus kukersianus* (WIMAN, 1895), a pattern that is considered characteristic of most Normalograptidae. In *Skanegraptus,* th1[1] grows downward along the ventral side of the sicula to a point below the sicular aperture and upward again in a U-shaped loop and leaves a space between the downward- and upward-growing parts on the obverse side (Fig. 4.3), in which the early part of th2[1]

is visible. In derived taxa, the metathecal part of th1[1] grows attached to the dorsal side of its protheca (Fig. 4.6). There are two separate openings at the base of the downward growth of th1[1], one for the metatheca of th1[1] and the second for the origin of th1[2] (Fig. 4.9). An unconformity can be seen at the point of origin of th1[2] (Fig. 4.7) on the reverse side of the tubarium in pattern H species. In taxa of the derived pattern H′, found in neodiplograptids, the unconformity is delayed (Fig. 4.8,10), but otherwise the development is identical.

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

The thecae (Fig. 4) show a short, straight, or slightly curved interthecal septum. An abrupt widening of the metatheca can be seen in many taxa at the aperture of the mother theca, after which the thecal tubes are nearly parallel sided (e.g., *Metaclimacograptus*). Apertural spines, except for the virgella, are extremely rare in the Normalograptidae, and chemically isolated material of such features does not exist. The genus *Hirsutograptus* bears multiple antivirgellar spines and paired genicular spines on the thecae. These spines often branch distally. Elongated basal spines appear in *Normalograptus trifilis* (MANCK, 1923) and *Normalograptus longifilis* (MANCK, 1924) and may be more common in the normalograptids.

The development of the median septum is quite variable in the Normalograptidae. The median septum appears to be lacking in part on the obverse side and is not developed on the reverse side in the only available relief specimen of *Skanegraptus janus* (Fig. 4.3–4.4). Early members of the Normalograptidae may bear a complete median septum on the obverse side, as in *Pronormalograptus antiquus* (Fig. 4.5–4.6). The median septum starts approximately at the base of th3[1] on the reverse side, and the first four thecae appear to be alternating in origin. In derived species, the median septum may be delayed considerably. The median septum is straight to considerably undulate, but intrathecal folding has not been recognized. It does not show the characteristic crossbars of the derived climacograptids (GOLDMAN & others, 2011).

BIOGEOGRAPHY AND EXTINCTION

The Ordovician Normalograptidae are often difficult to differentiate from the Climacograptidae. A number of constructional differences, however, can be noted and GOLDMAN and others (2011) used these to recognize a distinct pattern of extinction and reinvasion of Upper Ordovician normalograptids in the palaeotropical regions (Fig. 5). The normalograptids apparently originated in high latitude regions during the early to middle Darriwilian and from there spread to the palaeotropics. During the early Katian, the clade suddenly disappeared from low paleolatitudes, but reinvaded the regions in the late Katian to early Hirnantian. The Normalograptidae formed one of the few axonophoran groups surviving the Hirnantian extinction and then quickly rediversified during the Llandovery. Actually,

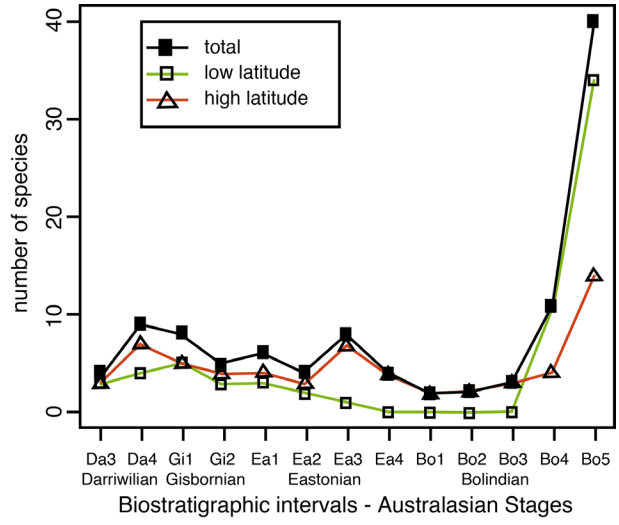

FIG. 5. Normalograptid diversity in the Upper Ordovician (redrawn from Goldman & others, 2011).

the Monograptoidea, Retiolitoidea, and Normalograptidae started to diversify during the upper Ordovician (Katian to Hirnantian) time interval, while the Diplograptina went extinct at the end of the Hirnantian (BAPST & others, 2012). The Neograptina, especially the Monograptidae, apparently saw one of the largest diversification events in graptolite history during the Llandovery, early Silurian (MELCHIN & others, 2011; SADLER, COOPER, & MELCHIN, 2011). However, a comparison of the diversity studies is difficult due to varying taxonomic concepts at the family level and higher taxonomical units in the analyses (see Retiolitoidea in BAPST & others, 2012; Retiolitidae + Petalolithidae in SADLER, COOPER, & MELCHIN, 2011). While GOLDMAN and others (2011) indicated a total diversity of the Normalograptidae with 39 taxa in the Bo5 (upper Hirnantian *Metabolograptus persculptus* Biozone), BAPST and others (2012) indicated the presence of only five species in the interval.

After the Hirnantian extinction event, the normalograptids rediversified and evolved in the Silurian to produce the Monograptidae as one of the most successful groups of the planktic graptoloids. A number of diversity peaks and minor to major extinction events (e.g., ŠTORCH, 1995; SADLER, COOPER, & MELCHIN, 2011) also constituted the evolutionary pattern of the Silurian graptoloids and led to a bloom of the Normalograptidae, the Petalolithinae, and the Retiolitinae until the complete extinction of the biserial axonophorans in the late Silurian.

Normalograptus LEGRAND, 1987, p. 62 [**Climacograptus scalaris normalis* LAPWORTH, 1877, p. 138; OD] [=*Scalarigraptus* RIVA, 1988, p. 230 (type, *Climacograptus scalaris normalis* LAPWORTH, 1877, p. 138, OD), obj.]. Normalograptids with pattern H astogeny; unornamented geniculate thecae with straight or concave interthecal septa throughout tubarium; complete median septum, slightly undulate to straight, may be delayed; genicular hoods common. *Middle Ordovician (Upper Darriwilian,* Pterograptus elegans *Biozone)–Silurian, Llandovery (Telychian,* Spirograptus turriculatus *Biozone):* worldwide.——FIG. 6,*1a–b*. **N. normalis* (LAPWORTH); holotype, BU 1136, *Parakidograptus acuminatus* Biozone, Dob's Linn, Southern Uplands, Scotland, UK, scale bars, 1 mm (Blackett & Zalasiewicz, 2008).

Clinoclimacograptus BULMAN & RICKARDS, 1968, p. 8 [**Pseudoclimacograptus* (*Clinoclimacograptus*) *retroversus;* OD] [=*Pseudoglyptograptus* BULMAN & RICKARDS, 1968, p. 13 (type, *P. vas*, OD), herein]. Normalograptid with proximally convex and distally concave supragenicular walls; thecal apertures strongly everted; median septum gently undulating proximally, distally straight; interthecal septae one-half the length of the supragenicular thecal walls proximally, ~two-thirds to three-fourths

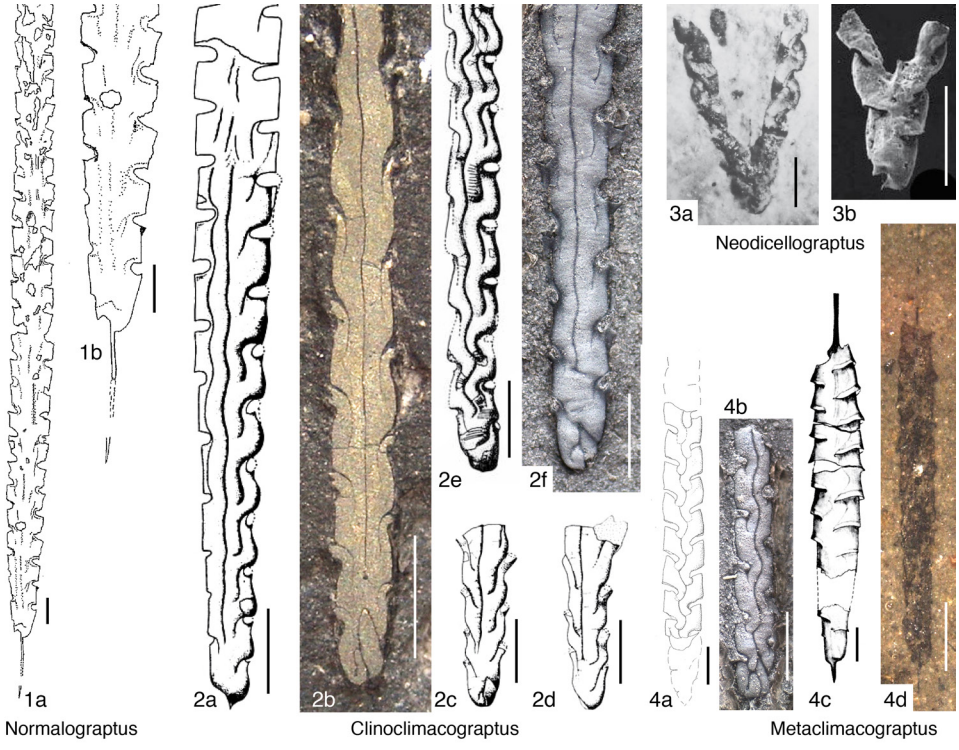

FIG. 6. Normalograptidae (p. 9–11).

distally. [*Pseudoglyptograptus* is based on internal casts of *Clinoclimacograptus* as can be shown from the sectioned pyrite-filled material of TÖRNQUIST (see Fig. 6,*2b*)]. *Silurian, Llandovery (Aeronian,* Demirastrites triangulatus–Stimulograptus sedgwickii *Biozones):* UK, Sweden, China.——FIG. 6,*2a–f*. **C. retroversus* (BULMAN & RICKARDS); *2a,* holotype, SMA 52951, reverse view, ?*Stimulograptus sedgwickii* Biozone, Tomarp, Scania, Sweden (Bulman & Rickards, 1968, fig. 4b); *2b,* LO 1097t (identified as *Climacograptus scalaris* HISINGER, 1837 by TÖRNQUIST, 1893, pl. 1,*7–8*), Tomarp, Scania, Sweden (new); *2c–d,* GSM WEG 4058, holotype of *Pseudoglyptograptus vas* (BULMAN & RICKARDS) proximal end in obverse (*c*) and reverse (*d*) views, *Neodiplograptus magnus* Biozone, Cross Fell, northern England, UK (Bulman & Rickards, 1968, fig. 1K–L); *2e*, SM A23951, *Stimulograptus sedgwicki* Biozone, Spengill, Westmorland, UK (Bulman & Rickards, 1968, fig. 4a); *2f,* LO 11860t, obverse view, Röstånga drill core, 35.40–35.30 m, Scania, Sweden (Maletz & others, 2014, fig. 1K). Scale bars, 1 mm.

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

Metaclimacograptus BULMAN & RICKARDS 1968, p. 3 [**Diplograpsus hughesi* NICHOLSON 1869, p. 235; OD] [=*Lithuanograptus* PAŠKEVIČIUS, 1976, p. 141 (type, *L. fusiformis*, OD); LOYDELL, 1993, p. 55; =*Retioclimacis* Nanjing Institute of Geology and Palaeontology in MU & others, 1974, p. 215 (type, *R. typica,* OD, =*Metaclimacograptus undulatus* [KURCK, 1882], LOYDELL, 1993, p. 55)]. Normalograptid with pattern H astogeny and an undulose to zigzag median septum; convex or concavo-convex subapertural thecal walls and apertural introversion; very short thecal overlap; genicular thecal hoods formed from dorsal thecal wall, not as secondary genicular additions. *Silurian,*

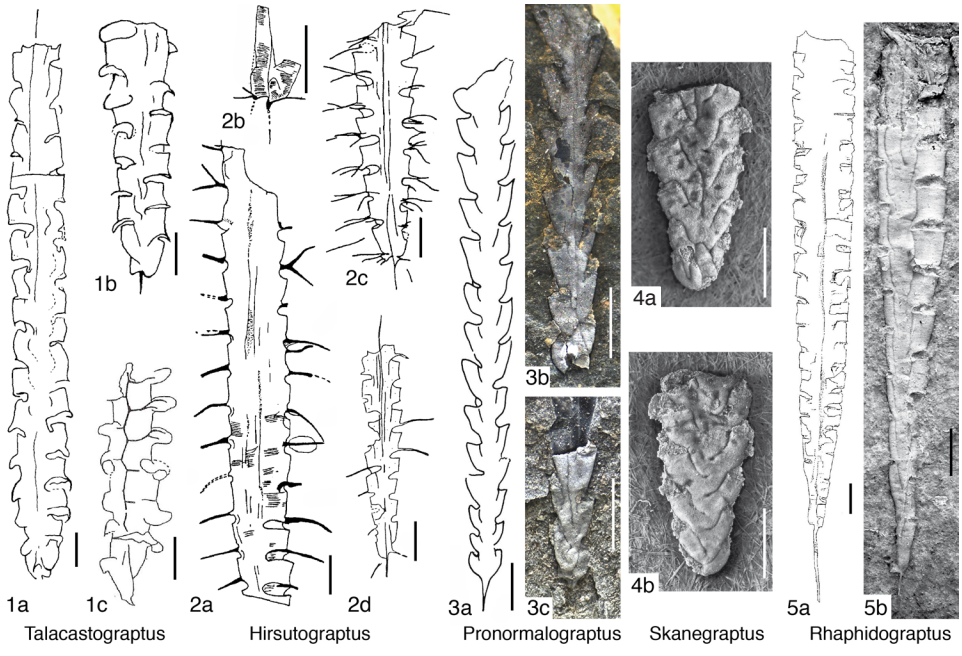

FIG. 7. Normalograptidae (p. 10–12).

Llandovery (Rhuddanian, Akidograptus ascensus *Biozone–Telychian,* Monoclimacis crenulata *Biozone):* worldwide.——FIG. 6,*4a–b*. **M. hughesi* (NICHOLSON); *4a*, neotype (designated by PŘIBYL, 1948, p. 18), NHM Q1360, *Pribylograptus* ?*leptotheca* Biozone, Skelgill beds, Ambleside, England, UK (Zalasiewicz, 2000); *4b,* PMU 34438, obverse view, Röstånga drill core, 36.70–36.60 m, Scania, Sweden, scale bars, 1 mm (new).——FIG. 6,*4c*. *M. fusiformis* (PAŠKEVIČIUS, 1976), holotype, *Coronograptus cyphus* Biozone, Paroveja drill core, 721 m, Lithuania, scale bar, 1 mm (Paškevičius, 1979, pl. 2,*5*).——FIG. 6,*4d*. *M. undulatus* (KURCK, 1882), NIGP 45344, illustrated as *Retioclimacis typica* MU & LI, 1974 by NI (1978, pl. 2,*15*), scale bar, 1 mm (new).

Neodicellograptus MU & WANG, 1977, p. 313 [**N. dicranograptoides;* OD; ='*Dicellograptus*' *siluricus* MU & LI, 1974, p. 211; herein]. Normalograptid with pattern H astogeny; stipes diverging distally; thecae geniculate with introverted apertures; undulose dorsal stipe walls. *Silurian, Llandovery (*?*upper Rhuddanian,* Cystograptus vesiculosus *Biozone–Aeronian,* Lituigraptus convolutus *Biozone):* China, Canada.——FIG. 6,*3a–b*. **N. siluricus* (MU & LI); *3a*, syntype, repository unknown, scale bar, 1 mm (Mu & Li, 1974, pl. 99,*2;* photo provided by Wang Xiao-feng); *3b*, GSC 104837, Cape Manning section, Cornwallis Island, Arctic Canada, scale bar, 1 mm (Melchin, 1998, pl. 2,*12*).

Pronormalograptus CHEN in CHEN & others, 2017, p. 325 [**P. acicularis;* OD]. Normalograptids with pattern H proximal development; proximal end narrow, rounded, asymmetrical with short sicula; thecae with low angle of inclination to tubarium axis; thecae biform, often geniculate proximally, showing curved to straight ventral thecal walls distally; medium septum complete or incomplete. *Middle Ordovician (Darriwilian,* Pterograptus elegans *Biozone)–Upper Ordovician (Sandbian,* Nemagraptus gracilis *Biozone):* worldwide.——FIG. 7,*3a*. **P. acicularis;* holotype, NIGP 157666, Dashimen section, Wuhai, Inner Mongolia, China, scale bar, 1 mm (Chen & others, 2017, fig. 6-102H).——FIG. 7,*3b–c*. *P. antiquus* GE in GE, ZHENG, & LI, 1990, *Pterograptus elegans* Biozone, Elnes Formation, Slemmestad, Norway; *3b*, PMO 234.255, obverse view; *3c*, PMO 234.061; scale bars, 1 mm (new).

Rhaphidograptus BULMAN, 1936a, p. 25 [**Climacograptus toernquisti* ELLES & WOOD, 1906, p. 190; OD]. Normalograptids with pattern H astogeny modified by presence of uniserial theca one, produced by truncation of growth of th1[2]; thecae geniculate with genicular flanges, straight supragenicular walls; median septum complete on obverse side, considerably delayed on reverse side. *Silurian, Llandovery (Rhuddanian,* Cystograptus vesiculosus *Biozone–Aeronian,* Lituigraptus convolutus *Biozone):* UK, Czech Republic, Sweden, Germany, Poland, ?Canada.——FIG. 7,*5a–b*. **R. toernquisti* (ELLES & WOOD); *5a*, lectotype (designated by PŘIBYL, 1948, p. 20), BU 1155, Birkhill Shale, Dob's Linn, Southern Uplands,

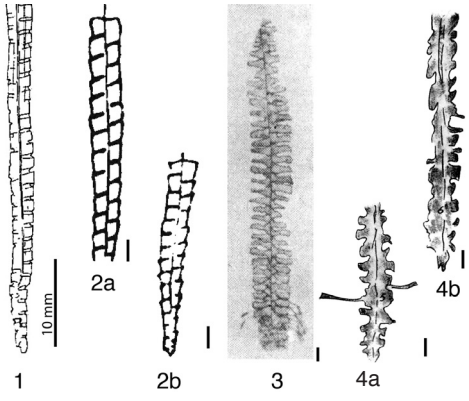

FIG. 8. Normalograptidae indet. (p. 12).

Scotland, UK, scale bar, 1 mm (Zalasiewicz, 2008); *5b*, LO 1456t, latex cast in reverse view showing delay of median septum, specimen on slab with holotype of *Monograptus incommodus* TÖRNQUIST, 1899, scale bar, 1 mm (new).

Skanegraptus Maletz, 2011c, p. 53 [* *S. janus;* OD]. Normalograptid with pointed, asymmetrical proximal end, lacking apertural spines on first thecal pair; proximal end with U-shaped th1[1]; paired early differentiation of th1[2] and th2[1] on reverse side; thecae with short overlap, straight outward-inclined apertures, lacking geniculum; median septum incomplete; thecal origins alternate. *Middle Ordovician, Darriwilian* (Holmograptus lentus *Biozone):* Sweden.——FIG. 7,*4a–b*. **S. janus,* holotype, LO 11196T, in obverse (*a*) and reverse (*b*) views, Krapperup drill core, Scania, Sweden, scale bars, 1 mm (Maletz, 2011c, fig. 1d and 1g, respectively).

Talacastograptus CUERDA, RICKARDS, & CINGOLANI, 1988, p. 753 [**T. leanzai;* OD] [=*Songxigraptus* FANG & others, 1990, p. 87 (English text, p. 135) (type, *S. elongatus*, OD); herein]. Normalograptid with pronounced genicular hoods which in profile views of tubarium give thecae strongly hooked appearance, especially at proximal end; thecae strongly geniculate; ventral thecal margins introverted, strongly overgrown by genicular hoods; supragenicular wall convex; median septum complete, gently undulating to straight. *Lower Silurian (Llandovery, Rhuddanian,* Atavograptus atavus *Biozone):* Argentina, China.——FIG. 7,*1a–c*. **T. leanzai; 1a*, holotype, DPI 21883; *1b*, paratype, DPI 21884, proximal end in reverse view; both from La Chilca Formation, 16 km WNW of Talacasto station, San Juan Province, Argentina, scale bars, 1 mm (Cuerda, Rickards, & Cingolani, 1988, fig. 4a–b); *1c*, SM X. 28480, Lipéon Formation, Argentina, scale bar, 1 mm (Rickards & others, 2002, fig. 4e).

UNCERTAIN STATUS

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

Hedrograptus OBUT, 1949, p. 13 [**H. janischewskyi;* OD]. *Silurian, Llandovery (Rhuddanian–?Aeronian):* Russia. [According to RIVA (1988, p. 225), "OBUT (1949) erected the genus *Hedrograptus* for early Silurian climacograptids with insignificant or incomplete apertural excavations on one side of the rhabdosome and complete on the other." RIVA (1988) provided a drawing of a latex cast of the type *H. janischewskyi*. According to this, the taxon does not bear any proximal spines except for the virgella and has a pointed proximal end, indicating a normalograptid relationship. The specimen is preserved in scalariform view and is indeterminate at the genus and species level.]——FIG. 8,*1. *H. janischewskyi*, holotype, I.G.G.-COAH-SSSP No. 278/5, 1945, drawing from latex cast, scale bar, 10 mm (Riva, 1988, fig. 6).

Limpidograptus KHALETZKAYA, 1962, p. 72 [**L. posohovae;* OD]. *Silurian (Llandovery):* Uzbekistan (Tian-Shan). [This genus might be based on a scalariform biserial and is indeterminable at the genus and species level.]——FIG. 8,*2a–b*. **L. posohovae*, scale bars, 1 mm (Khaletzkaya, 1962, pl. 9,*11a–b*).

Sichuanograptus ZHAO in YE, 1978, p. 474 [**S. pennatus;* OD]. Axonophorans with biserial tubarium; proximally the periderm normal, but thecae largely isolated, with common dissepiments, apertural spines and floating vesicles, whereas distally the thecal walls are reduced and form clathria and reticula (diagnosis translated by Yuandong Zhang, 2017). *Silurian, Llandovery (Telychian,* Spirograptus turriculatus *Biozone):* China. [The taxon appears to be an indeterminable, strongly decayed or weathered normalograptid with thickened apertural rims.]——FIG. 8.*3*. **S. pennatus*, holotype, Qiaotang, Nanjiang, Sichuan Province, China, scale bar, 1 mm (Mu & others, 2002, p. 799, pl. 211,*3*).

Heterograptus HERNÁNDEZ SAMPELAYO, 1960, p. 33, *nom. dub.,* type not designated; non *Heterograptus* ZHAO & ZHANG in LIN, 1986, p. 241; syn. of *Rhabdinopora*, Anisograptidae]. *Silurian, Llandovery (Telychian):* Spain (Almadén). [Taxon is characterized by prolonged mesial spines and thecae, giving them an aspect of *Glossograptus;* possibly based on specimens of *Metaclimacograptus flamandi* (LEGRAND, 1993). Information provided by Juan Carlos Gutiérrez Marco.]——FIG. 8,*4a–b. Heterograptus* examples, scale bars 1 mm (Hernández Sampelayo, 1960, pl. 15,*5–6*).

ABBREVIATIONS FOR MUSEUM REPOSITORIES

AMF: Australian Museum, Sydney, Australia
BU: Lapworth Museum, Birmingham University, UK
CNIGR: Museum of the A. P. Karpinsky All-Union Geological Research Institute (VSEGEI), St. Petersburg, Russia
DPI: La Plata Museum, La Plata, Argentina
GSC: Geological Survey of Canada, Ottawa, Canada
GSM: Geological Survey Museum, London, United Kingdom
LO: Lunds Originale, Department of Geology, Lund University, Sweden
NHMUK PM: The Natural History Museum, London, UK
NIGP: Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China
OMR: B. Horák Museum, Rokycany, Czech Republic
PMO: Natural History Museum, University of Oslo, Paleontological Type collections, Norway
PMU: Palaeontological Collections, Museum of Evolution, Uppsala University, Sweden
RM: Naturhistoriska Riksmuseet, Stockholm, Sweden
SM: Sedgwick Museum of Earth Sciences, Cambridge, UK

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