TREATISE ONLINE

Number 156

Part V, Second Revision, Chapter 28: Family Monograptidae: Introduction, Morphology, and Systematic Descriptions

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2021

KU PALEONTOLOGICAL INSTITUTE
The University of Kansas

Lawrence, Kansas, USA
ISSN 2153-4012
paleo.ku.edu/treatiseonline

PART V, SECOND REVISION, CHAPTER 28: FAMILY MONOGRAPTIDAE: INTRODUCTION, MORPHOLOGY, AND SYSTEMATIC DESCRIPTIONS

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AUTHOR CONTRIBUTIONS

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

TERMINOLOGY AND TAXONOMIC NOTE

MITCHELL and others (2013) suggested use of the term tubarium (LANKESTER, 1884), initially used exclusively for extant Pterobranchia, for the housing construction of all Pterobranchia including fossil and extant taxa and suggested replacing the term rhabdosome previously used for the graptolites. Not all researchers have accepted this replacement and several (e.g. ŠTORCH, ROQUÉ BERNAL, & GUTIÉRREZ-MARCO, 2019; LOYDELL, 2020), including one of the authors of this chapter, much prefer to use the term rhabdosome. The term tubarium is used herein for consistency with other chapters in the *Treatise*.

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

Family MONOGRAPTIDAE Lapworth, 1873

[Monograptidae LAPWORTH, 1873, table 1, facing p. 555] [=Pristiograptidae GÜRICH, 1908, p. 32; =Rastritidae GÜRICH, 1908, p. 35; =Cyrtograptidae AVERIANOW, 1929, p. 103; =Demirastritidae HUNDT, 1943, p. 263; =Diversograptidae HUNDT, 1943, p. 263; =Dibranchiograptidae HUNDT, 1949a, p. 20; =Gangliograptidae HUNDT, 1949a, p. 21; =Linograptidae OBUT, 1957, p. 18; =Wolynograptidae TSEGELNJUK, 1976, p. 110; =Tirassograptidae TSEGELNJUK, 1976, p. 118]

Maletz, Jörg, & David K. Loydell. 2021. Part V, Second Revision, Chapter 28: Family Monograptidae: Introduction, morphology, and systematic descriptions. Treatise Online 156:1–43, 19 fig.

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

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

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

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

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

MORPHOLOGY

SICULAR DEVELOPMENT

All Monograptidae initially grew a single stipe from a sicula of variable (conical) shape and dimensions, and the definition of the family Monograptidae is essentially that of Lapworth (1873). Little is known about the development of a conus and cauda in the prosicula, even though numerous chemically isolated monograptids have been described. Kraft (1926) discussed the nema prosiculae (cauda) in a species of *Monograptus* (Fig. 1.1) and described the spiral line and the

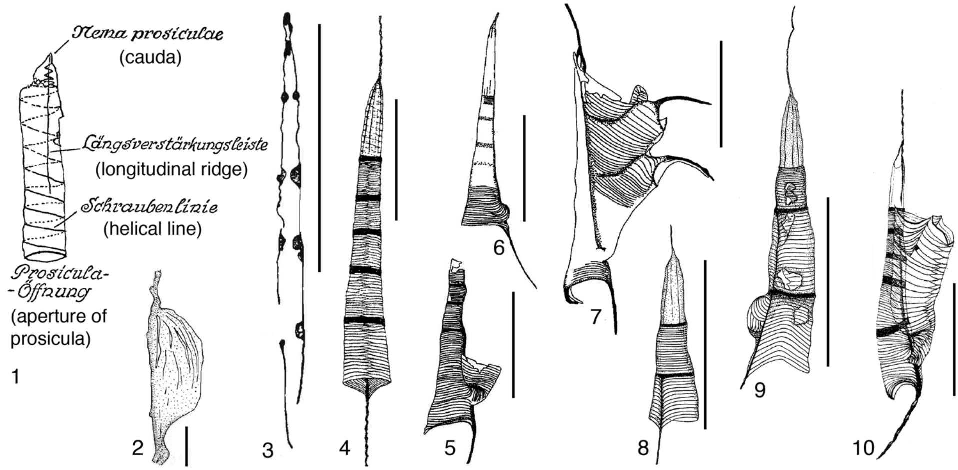

FIG. 1. The sicular development of the uniserial Axonophora (Monograptidae). *1*, monograptid prosicula, schematic (Kraft, 1926, fig. 2); *2–3,* cross section of sicula (*3*) and enlargement of sicular annulus (*2*) (Urbanek, 1958, fig. 5A, 6C); *4*, *Pristiograptus frequens* (JAEKEL, 1889)?, sicular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

longitudinal rods of the conus (prosicula proper). A cauda has not been mentioned in later descriptions of chemically isolated monograptids. The shape of the sicula ranges from very slender and long (e.g., in *Coronograptus*), short and straight (e.g., in *Streptograptus*), or variably curved (e.g., in *Spirograptus*). Siculae with a broad triangular outline and a considerably widened aperture appear in several groups independently (Fig. 1.5–1.7). These features were initially described from the Wenlock species *Colonograptus deubeli* (JAEGER, 1959) but appear independently in the early Wenlock species *Monograptus riccartonensis* LAPWORTH, 1876b (see LOYDELL & LARGE, 2019); in the Ludlow species *Saetograptus leintwardinensis* (LAPWORTH, 1880) (see MALETZ, 1997; ŠTORCH, MANDA, & LOYDELL, 2014); and in the Devonian *Uncinatograptus hercynicus* (PERNER, 1899) and may be present in other genera as well.

Longitudinal ridges (see KRAFT, 1926) are present on the prosicula of many graptoloids, but their origin and further evolution has not been investigated. It is unclear whether these ridges are formed in constant numbers in the graptoloids or are formed randomly. They first appeared as paired ridges in Floian taxa (WILLIAMS & CLARKE, 1999) and are present in latest Silurian monograptids (Fig. 1.8-1.9). KOREN', KIM, and WALLISER (2007) described longitudinal rods in the early Devonian *Uncinatograptus falcarius* (KOREN', 1969).

Sicular annuli occur in many monograptids (Fig. 1.2–1.6, 1.8–1.10). The origin and constructional purpose of the sicular annuli are unknown. Sectioned material clearly shows the secretion of the annuli to be cortical additions on the inside of the sicula (WALKER, 1953; URBANEK, 1958) (Fig. 1.2–1.3). They are typically present in many Homerian (late Wenlock, Silurian) and younger monograptids (LENZ & KOZŁOWSKA-DAWIDZIUK, 1998). Very little is known about sicular annuli in older taxa because these have rarely been investigated in detail. Sicular annuli appear to have formed in fixed positions in most monograptids (URBANEK, 1997a). MALETZ (1997) recognized a variable number of sicular annuli in *Saetograptus leintwardinensis* (Fig. 1.5–1.7), ranging from two to six, with most speci-

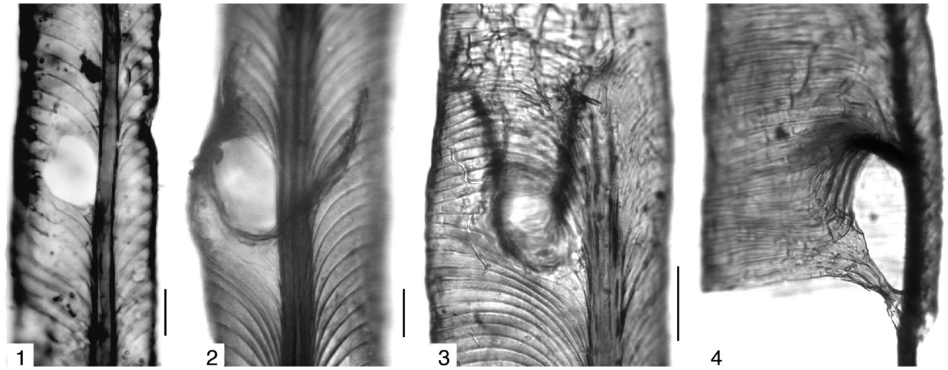

FIG. 2. The porus type in the Monograptidae. *1*, *Coronograptus gregarius* (LAPWORTH, 1876a), resorption foramen in metasicula, GSC 116236; *2*, *Monoclimacis*? *galeritus* MELCHIN & KOREN', 2001, modified resorption foramen, GSC 118589; *3*, *Monograptus* cf. *Monograptus arciformis* CHEN & LIN, 1978,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

mens possessing four to six annuli. The first of the sicular annuli appears at the boundary between the prosicula and metasicula. The later ones are more indistinct and indicate their successive construction as the metasicula grew (MALETZ, 1997). PORĘBSKA (1984) recognized sicular annuli in many latest Silurian to early Devonian monograptids but was unable to confirm their presence in all specimens of the taxa because she had only shale material at hand.

The development of the foramen for the origin of th1 changes considerably throughout the evolution of the Monograptidae (MALETZ & others, 2019). Initially, a resorption foramen (Fig. 2.1) was present, in species of the genera *Atavograptus*, *Coronograptus*, *Lagarograptus*, *Pernerograptus*, and probably in early *Monoclimacis* (LUKASIK & MELCHIN, 1994, 1997; MELCHIN & KOREN', 2001). Most details are unknown for the contemporary *Pribylograptus* because very few siculae have been attributed to this genus, and they are not known in enough detail (see KOREN' & BJERRESKOV, 1997, fig. 22L regarding ?*Pribylograptus* sp.; and RUSSEL-HOUSTON, 2001, pl. 5e regarding *Pribylograptus leptotheca* LAPWORTH, 1876b). MELCHIN and KOREN' (2001) discussed a modified resorption foramen in specimens of *Monoclimacis* (Fig. 2.2), in which the fuselli involved in the formation of the foramen are slightly deflected with the sicula bulging outward at this point. A lenticular porus (Fig. 2.3) is present as a third type in early monograptids (DAWSON & MELCHIN, 2007). In this type, a number of pre-porus fuselli are deflected proximally and a few truncated fuselli can be seen. The post-porus fuselli are deflected in the opposite direction, forming the lenticular porus in *Paramonoclimacis* and *Streptograptus*. Derived monograptids may have a primary porus formed through the typical sinus and lacuna stage of development described by EISENACK (1942) for *Pristiograptus frequens*. This porus type was considered to be typical of all monograptids (e.g., BULMAN, 1970). DAWSON and MELCHIN (2007) illustrated this primary porus for *Monograptus priodon* from the mid-Sheinwoodian, representing the stratigraphically earliest known record of this character.

TUBARIUM SHAPE

The tubarium shape is highly variable in monograptids and/or ranges from straight to dorsally and ventrally curved uniserial stipes to multiramous taxa with numerous cladial branches. The shape appears to be characteristic for certain groups and also for certain stratigraphical intervals, but particular shapes appear to also have evolved inde-

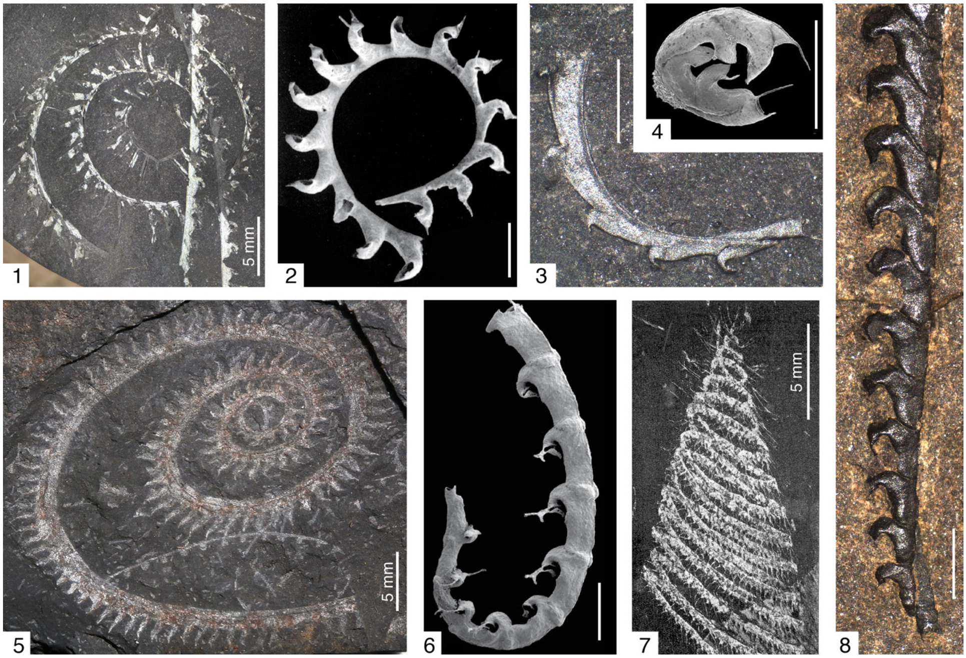

FIG. 3. The tubarium shape. *1*, *Lituigraptus convolutus* (HISINGER, 1837), dorsally coiled tubarium, NIGP 168325, Yangtze platform, China (Maletz, Wang, & Wang, 2021, fig. 11E); *2*, *Cyrtograptus* sp. cf. *C. laqueus* JACKSON & ETHERINGTON, 1969, dorsally curved proximal end lacking the sicula, Cape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

pendently in separate groups. Spirally coiled tubaria are common in a number of taxa and may be planispiral or trochospiral. However, in many taxa, the precise mode of coiling is difficult to recognize. Large specimens of *Oktavites spiralis* (GEINITZ, 1842) may appear to be planispiral (Fig. 3.5), but the astogeny derived from early growth stages indicates a trochospiral development when seen in lateral preservation (SCHAUER, 1971). High trochospiral development is typical of *Spirograptus turriculatus* (BARRANDE, 1850) (Fig. 3.7), a species usually preserved in lateral view. Also, many specimens of *Cyrtograptus* (Fig. 3.2) are coiled in a trochospiral fashion, even though larger specimens appear to have a planispiral shape when preserved on shale surfaces (BOUČEK, 1933; LENZ & others, 2012). The shape of colonies of *Cyrtograptus* has been modeled as a logarithmic spiral forming planispiral colonies and this has been suggested as a character useful for the discrimination of taxa (e.g., HUO, FU, & SHU, 1986; DENG, 1986).

It is important to differentiate dorsally (Fig. 3.1–3.3) and ventrally (Fig. 3.4) curved taxa. Dorsally coiled tubaria were particularly common during the Telychian Age (e.g., Pernerograptinae, Monograptinae), whereas ventrally curved taxa proliferated during Gorstian and early Ludfordian times (e.g., Linograptinae), but details need to be investigated. A high degree of variation of dorsally, dorso-ventrally, and ventrally curved tubaria occur especially in streptograptines, in which both types appear. Many of the slender taxa are quite variable in shape, but a distinct dorsal curvature may be present along the first few thecae in *Streptograptus*. Distally, the curvature changes to ventral or the stipe is straight (as is shown in an overview of the biostratigraphical ranges of streptograptine genera by MALETZ & others, 2019, fig. 4). This is also seen in the straight to slightly dorsally curved proximal end and strong ventral curvature of the distal part in *Pseudostreptograptus* (Fig. 3.6) and the *Streptograptus exiguus* group, with their fish-hook-shaped tubaria (LOYDELL & MALETZ, 2004).

CLADIA

Cladia are a way of secondary branching (MALETZ, LENZ, & BATES, 2016), first developed by the Dichograptina (e.g., *Pterograptus,* see SKWARKO, 1974) and the Diplograptina (e.g., *Nemagraptus,* see FINNEY, 1985) during the Ordovician. For a number of monograptid taxa, cladial branching was used as an option to form multiramous colonies. Cladia were the only way in which monograptids added new stipes to their tubaria. In this way, they differed from the earlier Dichograptina, in which dichotomous branching was the main mode of producing additional stipes (see MALETZ, LENZ, & BATES, 2016). The cladia in monograptids invariably included the formation of a secondary nema along which the cladial stipe grew (THORSTEINSSON, 1955). URBANEK (1963) differentiated the procladium (the main stipe) and the metacladia (sicular and thecal cladia) and recognized that cladia of several orders may be developed in some taxa. The term procladium for the main stipe should not be used as it might be misleading (see MALETZ & others, 2014). An analysis of the appearance of cladial branching has never been attempted, but it appears certain that cladia originated independently in several clades of monograptids. Thus, the family Cyrtograptidae of earlier workers, represents a highly polyphyletic taxonomic unit and should not be used. The genus *Cyrtograptus* is the most prominent taxon in which cladial branching has been investigated from chemically isolated material (THORSTEINSSON, 1955; TELLER, 1976), but cladial development has also been described in great detail for the linograptines (URBANEK, 1963, 1997b).

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

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

Subfamily PERNEROGRAPTINAE Hundt, 1943

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

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

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

The proximal end and thecal style of early monograptids appear to be quite variable but can be reduced to a few fundamental features. Melchin and others (2011) considered the species *Atavograptus ceryx* (Rickards & Hutt, 1970) from the *Akidograptus ascensus/Parakidograptus acuminatus* Biozone to be the earliest monograptid. The sicula is about 1.5–1.8 mm long, slowly widening toward the aperture (Fig. 4.1). The origin of th1 is in the lower third of the metasicula. The thecae widen from the origin, forming a rounded geniculum, after which they are parallel-sided, nearly parallel to the dorsal line of the stipe. They have low thecal overlap and apparently no or only a slight increase of this feature distally. *Atavograptus ceryx* has considerable dorsal curvature (Fig. 4.2), reminiscent of the tubarium shape in the genus *Coronograptus*. An early thecal differentiation in *Atavograptus atavus* (Zalasiewicz, 2000a) has very slender proximal thecae and a conspicuous but gradual distal widening of the stipes.

Distinct elongation of the slender metasicula is present in *Coronograptus* (Fig. 4.4) and also in a few other genera (Rickards, Hutt, & Berry, 1977) as well as an enhancement of the geniculum with the formation of genicular flanges (Fig. 4.6, 4.8). A differentiation of the thecal apertures with the formation of lateral apertural flanges and lobes also occurs (Fig. 4.5–4.8). The precise evolutionary relationship of these features has not been studied.

GENERA WITH SHORT SICULAE

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

Atavograptus Rickards, 1974, p. 141 [**Monograptus atavus* Jones, 1909, p. 531; OD]. Straight to somewhat dorsally curved tubarium that becomes straight distally; sicula 1.2–1.8 mm long; first theca arises from middle part of metasicula via a resorption porus; thecae simple overlapping tubes, commonly with rounded genicula; thecal apertures simple, straight. *Silurian, Llandovery* (*Rhuddanian, Akidograptus ascensus/Parakidograptus acuminatus* Biozone–*Aeronian, Neodiplograptus magnus* Biozone): worldwide.——Fig. 5,*1a–c*. **A. atavus* (Jones); *1a,* lectotype, GSM 23710, stipe fragment (Zalasiewicz, 2000a, Atlas 1.6); *1b,* latex cast of topotype, proximal end with sicula, GSM 95254 (Zalasiewicz, 2000a, Atlas 1.6); *1c,* proximal end, PŠ 3521, Czech Republic (Štorch, 2015, fig. 10M). Scale bars, 1 mm.

Euroclimacis Štorch, 1998a, p. 120 [**Monograptus aduncus* Bouček, 1931, p. 295; OD]. Tubarium dorsally curved proximally and ventrally curved or almost straight distally; sicula short; thecae with sharp geniculum, narrow aperture, and, particularly in proximal thecae, pronounced apertural hoods formed by elongated dorsal thecal wall. [Štorch (1994) discussed the strong intraspecific variation in the development of the genicular hoods of *E. adunca*]. *Silurian, Llandovery* (*Telychian,*

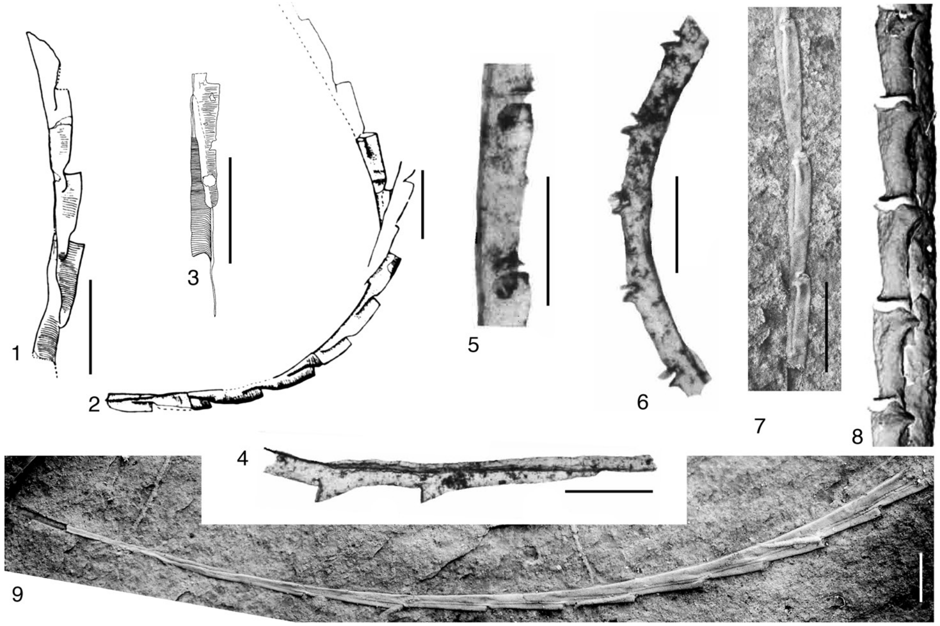

FIG. 4. The proximal end and thecal development of early monograptids. *1–2, Atavograptus ceryx* (RICKARDS & HUTT, 1970); *1,* SM A67088, complete proximal end of longer specimen (Rickards & Hutt, 1970, fig. 1D), *2,* holotype, SM A67087, pyritic internal mold (Rickards & Hutt, 1970, fig. 2A); *3, Atavograptus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

Monoclimacis crenulata Biozone)–*Wenlock,* (*Homerian, Cyrtograptus lundgreni* Biozone): Spain, Czech Republic, UK, Estonia, Latvia, Morocco, Arctic Canada.——FIG. 5,*2a–c*. **E. adunca* (BOUČEK); *2a,* ?lectotype (selected by PŘIBYL, 1940b, p. 8), NMP L30665, showing the shape of the colony, Vyskočilka, Czech Republic (Zalasiewicz & Williams, 2000, Atlas 1.43); *2b,* proximal end from type slab NMP L30665 (Zalasiewicz & Williams, 2000, Atlas 1.43); *2c,* PŠ 475, *Cyrtograptus murchisoni* Biozone, Velká Ohrada, Czech Republic (ŠTORCH, 1994, fig. 5,*20c*). Scale bars, 1 mm.

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

Pernerograptus PŘIBYL, 1941, p. 9 [**Graptolites argenteus* NICHOLSON, 1869, p. 239; OD] [=*Pernerograptus* (*Quasipernerograptus*) ZHAO, 1984, p. 105 (type, *P.* (*Q.*) *leptotheca,* OD), syn. by LOYDELL, herein; =*Pseudopernerograptus* WANG in WANG & others, 1987, p. 380 (type *Monograptus revolutus*

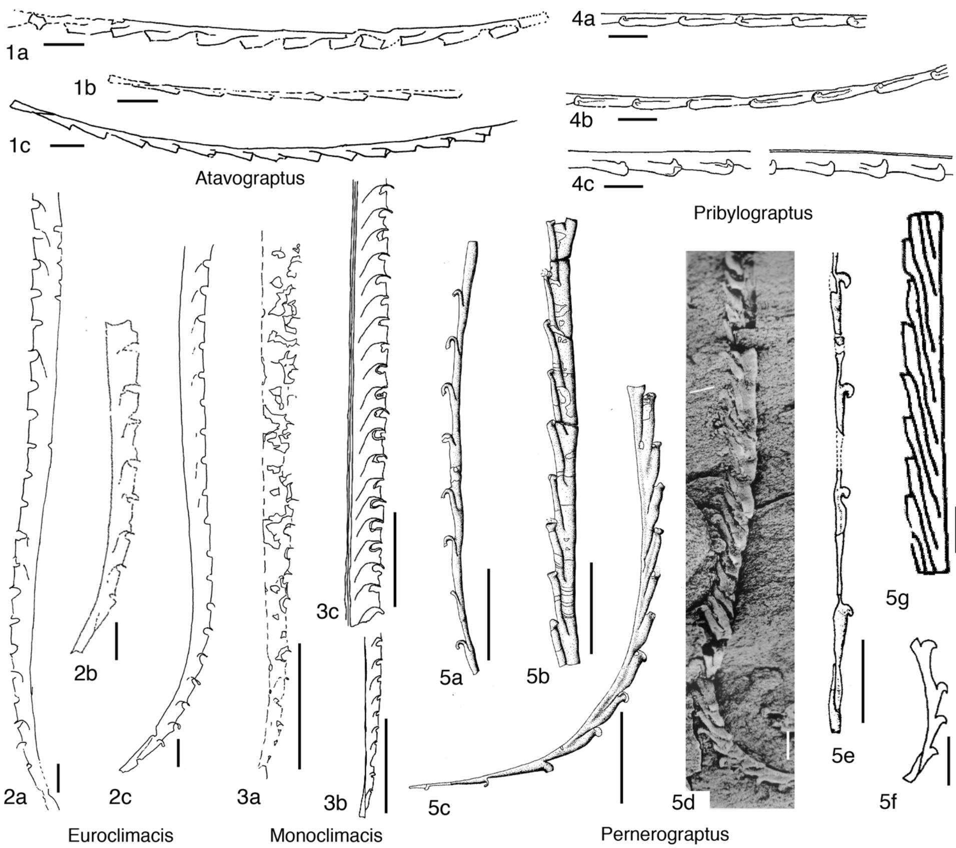

FIG. 5. Pernerograptinae (short siculae) (p. 7–9).

KURCK, 1882, p. 299, OD), syn. by LOYDELL, herein]. Straight to dorsally curved proximal part of tubarium with straight distal part; dorsal curvature accentuated in mesial part of colony; biform thecae; sicula small, apex not reaching to first metatheca; proximal thecae slender, axially elongated without overlap, terminated by apertural hoods that are either simple or transversely expanded; apertural hoods retreat in mesial thecae leaving only lateral lappets and dorsal apertural hoods which also subsequently retreat resulting in simple cylindrical, greatly overlapping distal thecae. *Silurian, Llandovery* (*Rhuddanian, Pernerograptus revolutus/Coronograptus cyphus* Biozone–*Aeronian, Lituigraptus convolutus* Biozone): worldwide.——FIG. 5,*5a–b*. *P. revolutus* (KURCK), syntype, LO 475t, Bollerup, Scania, Sweden, scale bars, 1 mm (Hutt, 1974, fig. 1a–b).——FIG. 5,*5c*. *P. sudburiae* (HUTT, 1974), holotype, LO 4454T, Tommarp, Sweden, scale bar, 1 mm (Hutt, 1974, fig. 1d).——FIG. 5,*5d–e*. **P. argenteus* (NICHOLSON); *5d,* lectotype, NHMUK Q3148, Skelgill, Lake District, England (Hutt, 1975, pl. 17,*3*); *5e*, proximal end with sicula, SM A85016, Yewdale Beck, England (Hutt, 1975, fig. 17,*2*). Scale bars, 1 mm.——FIG. 5,*5f–g*. *P. leptotheca* (ZHAO, 1984), proximal and distal fragments (Zhao, 1984, fig. 4A,C). Scale bars, 1 mm.

Pribylograptus OBUT & SOBOLEVSKAYA, 1966, p. 33 [**Monograptus incommodus* TÖRNQUIST, 1899, p. 11; OD]. Tubarium long, variably and gently curved proximally, straight distally; sicula rarely recorded but usually 1.8–2.0 mm long; thecae simple, gradually widening tubes proximally, often with increasing overlap distally; transitions between thecal morphologies gradual; thecal apertures flanked by lateral lappets throughout colony; geniculate thecae have flanges or hoods overhanging thecal apertures; unpaired genicular or supragenicular spines may be present. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone–*Aeronian, Stimulograptus sedgwickii* Biozone): worldwide.——FIG. 5,*4a–c*. **P. incommodus* (TÖRNQUIST), Röstånga, Scania, Sweden; *4a–b,* holotype, LO 1456T, thecal style (Koren'

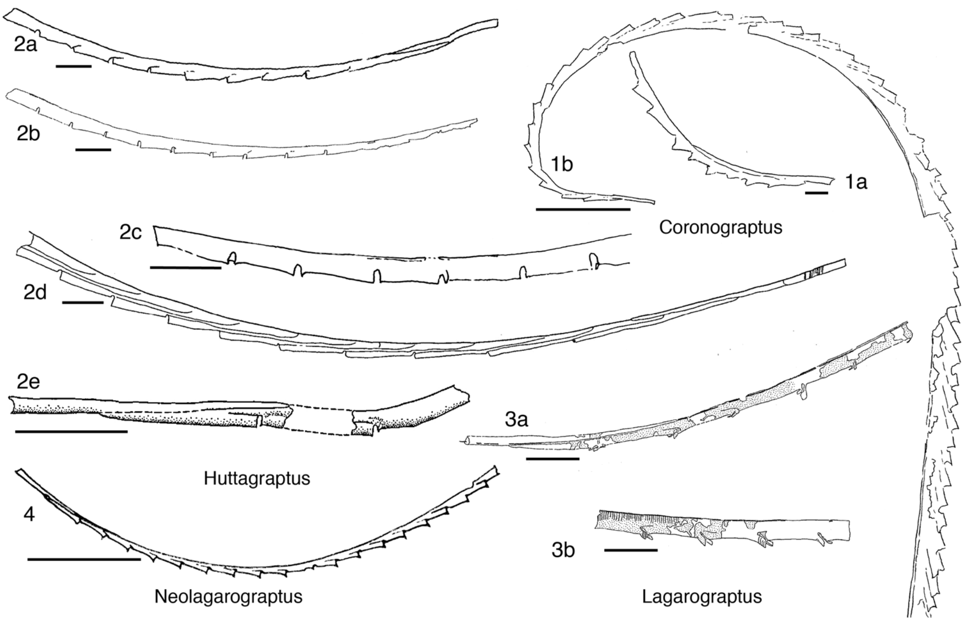

FIG. 6. Pernerograptinae (long siculae) (p. 10–11).

& Bjerreskov, 1997, fig. 21A); *4c,* paratype, LO 1457t, fragment (Koren' & Bjerreskov, 1997, fig. 21B). Scale bars, 0.1 mm.

GENERA WITH LONG SICULAE

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

Coronograptus OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVESKAYA, & MERKUREVA, 1968, p. 92 [**Monograptus gregarius* LAPWORTH, 1876a, p. 317; OD]. Strongly dorsally curved tubarium that may become straight distally; sicula long (2.5–16 mm), with majority of length contributed by metasicula, which possesses a resorption porus; first theca emerges high on metasicula; thecae long overlapping tubes; geniculate immediately above or below thecal apertures, with concave free ventral thecal walls subaperturally at least in proximal thecae; flared, unornamented thecal apertures; genicular hoods may be developed proximally or throughout tubarium but are absent in most species. *Silurian, Llandovery* (*Rhuddanian, Coronograptus cyphus* Biozone–*Aeronian, Lituigraptus convolutus* Biozone): worldwide.——FIG. 6,*1a.* **C. gregarius* (LAPWORTH), syntype, BU 1435, Dob's Linn, Scotland, scale bar, 1 mm (Zalasiewicz, 2000b, Atlas 1.13).——FIG. 6,*1b. C. cyphus* (LAPWORTH, 1876b), typical specimen BU 1430, Dob's Linn, Scotland, scale bar, 5 mm (Zalasiewicz, Williams, & Akhurst, 2003, fig. 2A).

Huttagraptus KOREN' & BJERRESKOV, 1997, p. 13 [**Atavograptus praestrachani* HUTT & RICKARDS in RICKARDS, HUTT, & BERRY, 1977, p. 102; OD]. Long, slender, slightly to strongly dorsally curved tubarium; sicula long (2–7 mm); first theca originates high on metasicula via resorption foramen; typically long overlapping thecae with free ventral walls at very low angle or parallel to tubarium axis and with pronounced angular geniculum proximally, creating marked thecal excavation, and in some species these features are retained mesially or throughout entire tubarium; genicular flanges may overhang thecal apertures forming distinct hoods; in some species geniculum retreats gradually and thecae become simple tubes with increased inclination of free ventral wall to the tubarium axis in species with thecae lacking genicula mesially or distally. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone–*Aeronian, Demirastrites triangulatus* Biozone): worldwide.——FIG. 6,*2a–c,e.* **H. praestrachani* (HUTT & RICKARDS in RICKARDS, HUTT, & BERRY), holotype, SM A60415a–b, Keisley, northern England, scale bars, 1 mm (Hutt & Rickards, 1970, fig. 3C; Zalasiewicz, 2008a, Atlas 2.73); *2e,* MGUH 24205, proximal end, Kos-Istek region, southern Urals, Russia, scale bars, 1 mm (Koren' & Bjerreskov, 1997, fig. 10B).——FIG. 6,*2d. H. acinaces* (TÖRNQUIST, 1899), holotype, LO 1436T, scale bar, 1 mm (Koren'& Bjerreskov, 1997, fig. 12H).

Lagarograptus OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVESKAYA, & MERKUREVA, 1968, p. 90 [**L. inexpeditus;* OD]. Narrow, dorsally curved tubarium; long sicula (1.9–4.35 mm); first theca originates via a resorption porus; overlapping, sharply geniculate thecae with free ventral walls subparallel to tubarium axis; shallow and narrow apertural excavations; tonguelike ventral apertural process and dorsal apertural hood present on all thecae. *Silurian, Llandovery* (*Rhuddanian, Coronograptus cyphus* Biozone–*Aeronian, Campograptus curtus* Biozone): Siberia, Kazakhstan, northern and Arctic Canada, China.——FIG. 6,*3a–b*. **L. inexpeditus* OBUT & SOBOLEVSKAYA; *3a,* proximal end, MGUH 24347, Kos-Istek region, southern Urals, Russia (Koren' & Bjerreskov, 1997, fig. 23H); *3b,* distal fragment, MGUH 24343, Kos-Istek region, southern Urals, Russia (Koren' & Bjerreskov, 1997, fig. 23B). Scale bars, 1 mm.

Neolagarograptus ŠTORCH, 1998b, p. 228 [**Lagarograptus helenae* ŠTORCH, 1988, p. 24; OD]. Tubarium arcuately dorsally curved, slowly expanding in dorso-ventral width, with tendency to be parallel sided; sicula long (3.5–5.1 mm); long, overlapping, geniculate thecae with simple, slightly widened apertures, shallow apertural excavations and, in some species, a single ventral apertural process. *Silurian, Llandovery* (*Aeronian, Pribylograptus leptotheca* Biozone–*Stimulograptus sedgwickii* Biozone): Czech Republic, Great Britain, Latvia, Myanmar, Iran, Saudi Arabia.——FIG. 6,*4*. **N. helenae* (ŠTORCH), holotype, PŠ 274, Tmaň, Czech Republic, scale bars, 5 mm (Štorch, 1988, fig. 4D).

'STREPTOGRAPTINES'

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

BOUČEK and PŘIBYL (1943, 1951) and BOUČEK and PŘIBYL in PŘIBYL, 1948) discussed *Streptograptus* and *Mediograptus* as characterized by their special thecal apertures, but identified them as subgenera of *Monograptus*. The authors differentiated several distinct groups in the two taxa. MALETZ and others (2019) used the term streptograptid to describe the characteristic thecal construction of the genus *Streptograptus* and of related genera, here included in the informal group referred to as the 'streptograptines.' The streptograptines may be identified as a subfamily if the constructional details prove to be phylogenetically meaningful. They can be viewed as related through their complex thecal apertures bearing conspicuous distal (lateral) lobes and the proximally directed nozzle (Fig. 7.3, Fig. 8.4). The tubarium shape is highly variable, ranging from dorsally curved in *Paramonoclimacis* (Fig. 7.1) to fish-hook-shaped, with initial dorsal curvature and distal ventral curvature. Many slender forms are more variable in shape but are only slightly sinuously curved. The isolated hooked distal metathecae may be of a variable length, but are often conspicuous. The apertures are strongly introverted and open into the ventral metathecal sides, typically into a platform with thickened rim (Fig. 8.10) (LOYDELL & MALETZ, 2004). Earlier taxa without cupulae usually possess metathecae with a relatively long, isolated hook (Fig. 8.1) before the development of the thecal aperture.

Specimens of the genus *Paramonoclimacis* may easily be misidentified as *Pernerograptus* species with simple apertural hoods when flattened. A thecal gradient comparable to that of *Pernerograptus* is also visible in *Paramonoclimacis* (see Fig. 7.1, displacement of cupulae) but not in other genera of the group and may indicate the phylogenetic relationship of the streptograptines to the earlier pernerograptines.

Important characters such as the characteristic cupulae (Fig. 8) of derived streptograptines or the increasing thecal overlap of earlier forms (Fig. 7.1) are typically not recognizable in flattened material. Therefore, the generic assignment of many species is difficult. Chemically isolated material clearly shows remains of cupulae in *Mediograptus* species and also the characteristic thecal

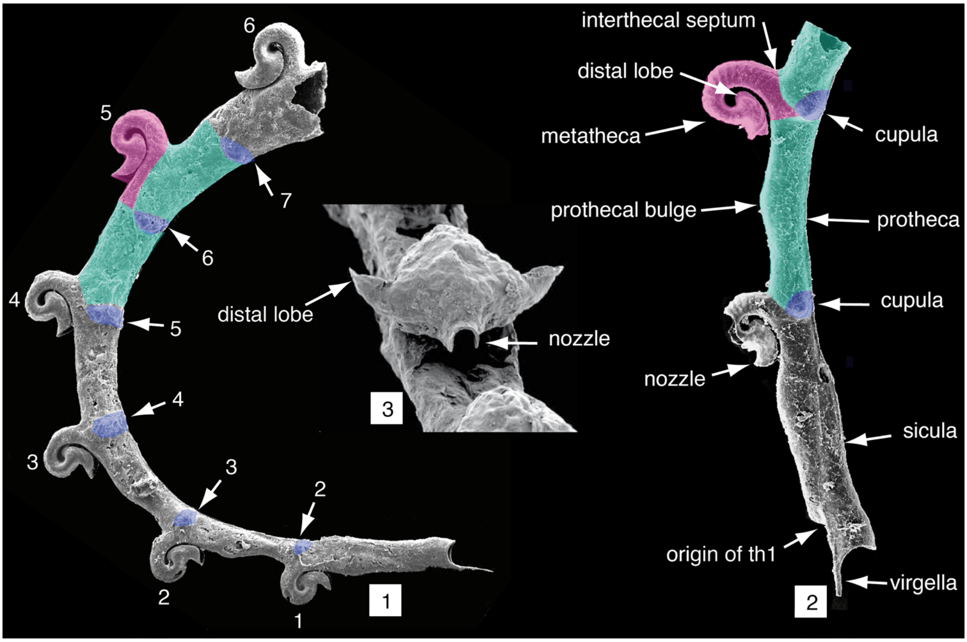

FIG. 7. Streptograptine proximal ends and colony construction. *1–2, Paramonoclimacis sidjachenkoi* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & BONDAREV, 1965); *1*, thecal apertures and associated cupulae (*blue*) are labeled; *2*, proximal end illustrating important tubarium features (based on Maletz & others, 2019, fig. 1); *3, Streptograptus dalecarlicus* LOYDELL & MALETZ, 2004, thecal aperture showing distinct nozzle and outward-directed distal lobes on thecal aperture. Prothecae (*green*) and metathecae (*purple*) are color coded (new).

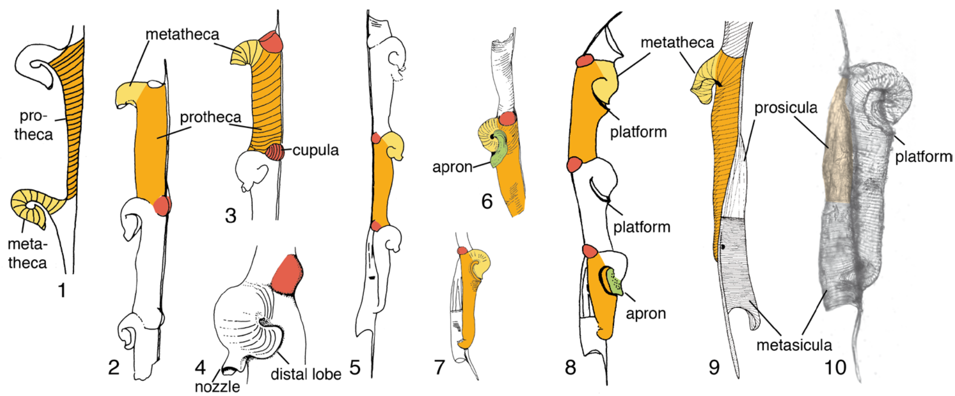

FIG. 8. Tubarium character of streptograptines. *1, Streptograptus ansulosus* (TÖRNQUIST, 1892), thecal style with long isolated part, lacking cupulae and platform; *2–5, Streptograptus dalecarlicus* LOYDELL & MALETZ, 2004, showing cupulae and laterally extended distal lobes; *6–7, Streptograptus sartorius*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

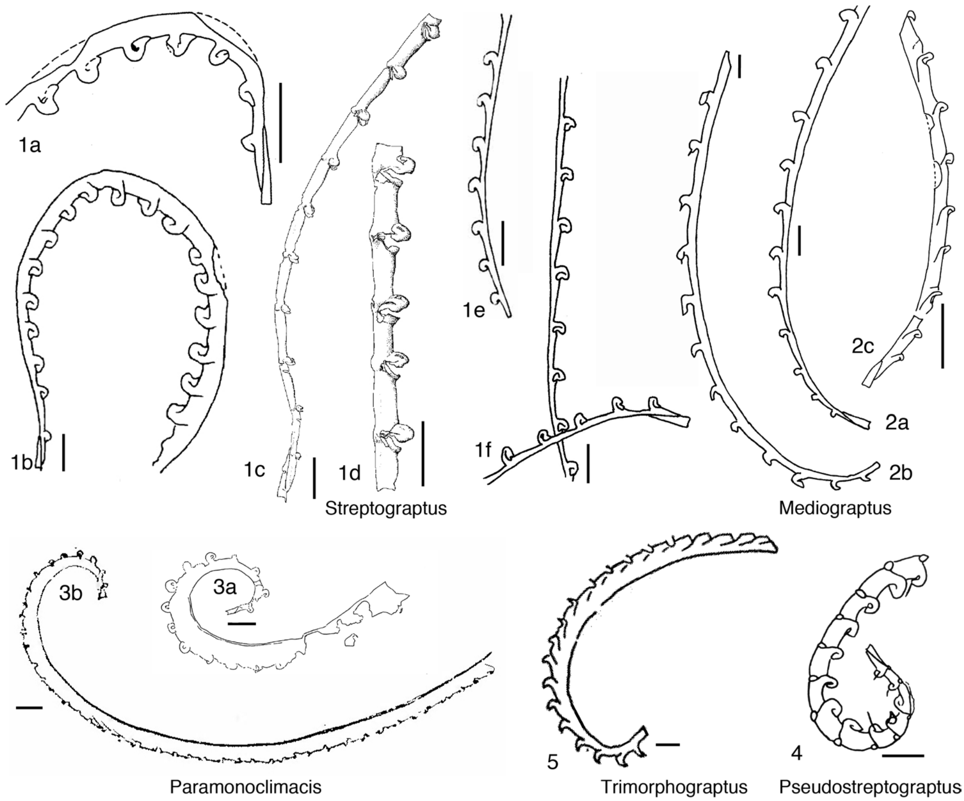

FIG. 9. Streptograptines (p.13–14).

apertural nozzle. The cupulae may be reduced in size. TELLER (1986) described isolated specimens of *Mediograptus antennularius* (MENEGHINI, 1857) and *Mediograptus flexuosus* (TULLBERG, 1883) from the *Monograptus flexilis* Biozone (Sheinwoodian, Wenlock) of Poland. *Mediograptus flexuosus* appears to have cupulae (TELLER, 1986, pl. 6.11). The illustrations are partly simplified (Fig. 8.*9*) but show the main characters of the tubaria. JAEGER (1991) described *Streptograptus serexiguus* (JAEGER, 1991) from the Homerian *Testograptus testis* Biozone (equivalent to the *Cyrtograptus lundgreni* Biozone) of Nevada as the youngest form within the *Streptograptus exiguus* group.

Streptograptus YIN, 1937, p. 297 [**Graptolithus plumosus* BAILY, 1871, p. 22; SD ICZN, 1993, p. 90 (replacement of *Monograptus nodifer* TÖRNQUIST, 1881, *sensu* ELLES & WOOD, 1913, pl. 46,*2a–d;* YIN, 1937, p. 297; proposed to ICZN by LOYDELL & CHEN, 1991)] [=*Globosograptus* BOUČEK & PŘIBYL in PŘIBYL, 1948, p. 37 (type, *Monograptus wimani* BOUČEK 1932, p. 153, OD), syn. by LOYDELL, 1996, p. 891; =*Awarograptus* ZALASIEWICZ & HOWE, 2003, p. 45 (type, *Monograptus nodifer* TÖRNQUIST, 1881, OD), syn. by LOYDELL & NESTOR, 2006, p. 590]. Tubarium straight, dorsally, ventrally or dorsoventrally curved; sicula small; first theca originates via a lenticular porus; metathecae coiled; thecal apertures with central, proximo-ventrally directed nozzle, in some taxa developed only in the apron. *Silurian, Llandovery* (*Aeronian, Pribylograptus leptotheca* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——FIG. 9,*1a–b*. **S. plumosus* (BAILY); *1a,* neotype, BELUM K12274d, Tieveshilly, County Down, Northern Ireland, scale bar, 1 mm (Loydell, 1990b, fig. 1); *1b,* larger specimen showing tubarium shape, MGM6646-0, El Pintado reservoir, Seville Province, Spain, scale bar, 1 mm (Loydell, Frýda, & Gutiérrez-Marco, 2015, fig. 21AQ).——FIG. 9,*1c–d. S. nodifer* (TÖRNQUIST), neotype (ZALASIEWICZ & HOWE, 2003, p. 46), proximal end and distal thecal style, LO 6465t, Nitsjö, Dalarna, Sweden (Zalasiewicz & Howe, 2003, fig. 1). Scale bars, 1 mm.——Fig. 9,*1e–f. S. wimani* (Bouček, 1932); *1e,* lectotype (Bouček & Přibyl in Přibyl, 1948, p. 38), Vyskočilka, Czech Republic (Bouček, 1932, fig. 1i); *1f,* proximal end showing sicula, MGM 142-S, Jabalón River section, central Spain (Loydell & others, 2009, fig. 4F). Scale bars, 1 mm.

Mediograptus Bouček & Přibyl in Přibyl, 1948, p. 39 [**Monograptus kolihai* Bouček, 1931; OD]. Slender, dorsally or dorso-ventrally curved tubarium; sicula short, apex reaching no higher than top of first theca; long, narrow prothecae in some species with cupulae at base; metathecae complex, the aperture comprising central, more or less well defined, proximal-facing portion, and two laterally curved parts, which may face laterally, dorsally, ventrally, proximally, distally, or a combination of the above depending on degree of twisting of horn-like lateral regions of metatheca; thecae exhibit overlap throughout tubarium. *Silurian, Llandovery* (*Telychian, Cyrtograptus insectus* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——Fig. 9,*2a–b.* **M. kolihai* (Bouček); *2a,* lectotype (Přibyl, 1948, p. 39), NMP L30671 Motol Formation, Vyskočilka near Malá Chuchle, Prague, Czech Republic (Bouček, 1931, fig. 8A); *2b,* proximal end, PŠ 481.11 (Štorch, 1994, fig. 5.*6*) Scale bars, 1 mm.——Fig. 9,*2c. M. flittoni* Loydell & Cave, 1996, holotype, BGS RCV3587, Banwy River section, Powys, Wales, scale bar, 1 mm (Loydell & Cave, 1996, fig. 13B).

Paramonoclimacis Wang & Ma in Wang & others, 1977, p. 360 [**P. typicalis;* OD; =*Pernerograptus sidjachenkoi;* Obut & Sobolevskaya in Obut, Sobolevskaya, & Bondarev, 1965; syn. by Mu & others, 2002, p. 896]. Initially dorsally planispirally coiled, distally straight distinctly widening tubarium; small sicula; cupulae at base of prothecae; proximal thecae lack overlap and have coiled metathecae with lateral apertural lobes and nozzle; thecal overlap increases distally; distally coiling of metathecae becomes steadily less pronounced and distalmost thecae have a thecal apertural excavation and overhanging hood. *Silurian, Llandovery* (*Aeronian, Lituigraptus convolutus* Biozone): China, Russia, Canada, USA (Alaska).——Fig. 9,*3a–b. P. sidjachenkoi* (Obut & Sobolevskaya); *3a,* holotype, proximal end, CNIGR 8783/89, Taimyr (Maletz & others, 2019, fig. 2A); *3b,* **P. typicalis,* holotype, large specimen (Wang & others, 1977, fig. 47). Scale bars, 1 mm.

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

Trimorphograptus Zhao, 1984, p. 102 [**Pernerograptus qijiangensis* Ye, 1978, p. 478; OD]. Tubarium dorsally curved considerably near proximal end, straight distally; proximal end unknown; proximal thecae hooked; mesial thecae with geniculum, apertural excavation and thecal hoods; distal thecae with rounded geniculum or straight ventral walls; thecal details unknown. *Silurian* (*Aeronian*): China.——Fig. 9,*5. T. minor* Zhao, 1984, nearly complete specimen, scale bar, 1 mm (Zhao, 1984, fig. 3).

Subfamily MONOGRAPTINAE Lapworth, 1873

[Monograptinae Lapworth, 1873, table 1, facing p. 555, *ex* Monograptidae Lapworth, 1873, table 1, facing p. 555] [=Rastritinae Gürich, 1908, p. 35, *ex* Rastritidae Gürich, 1908, p. 35, Přibyl, 1946, p. 276; =Demirastritinae Hundt, 1943, p. 263, *ex* Demirastritidae Hundt, 1943, p. 263, Přibyl, 1946, p. 276; =Diversograptinae Hundt, 1943, p. 263, *ex* Diversograptidae Hundt, 1943, p. 263, Přibyl, 1946, p. 276; =Spirograptinae Obut, 1950, p. 265; =Cyrtograptinae Averianow, 1929, p. 103, *ex* Cyrtograptidae Averianow, 1929, p. 103, Yin, 1937, p. 296]

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

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

MORPHOLOGY

Most taxa of the Monograptinae have a variably developed dorsal curvature, either planispiral or trochospiral. Distally, the stipes may be straight. The relationships to the ventrally curved genera *Cochlograptus* and *Testograptus* with similar thecal style have been uncertain in the past. Lenz and Melchin (2008) analysed the two genera

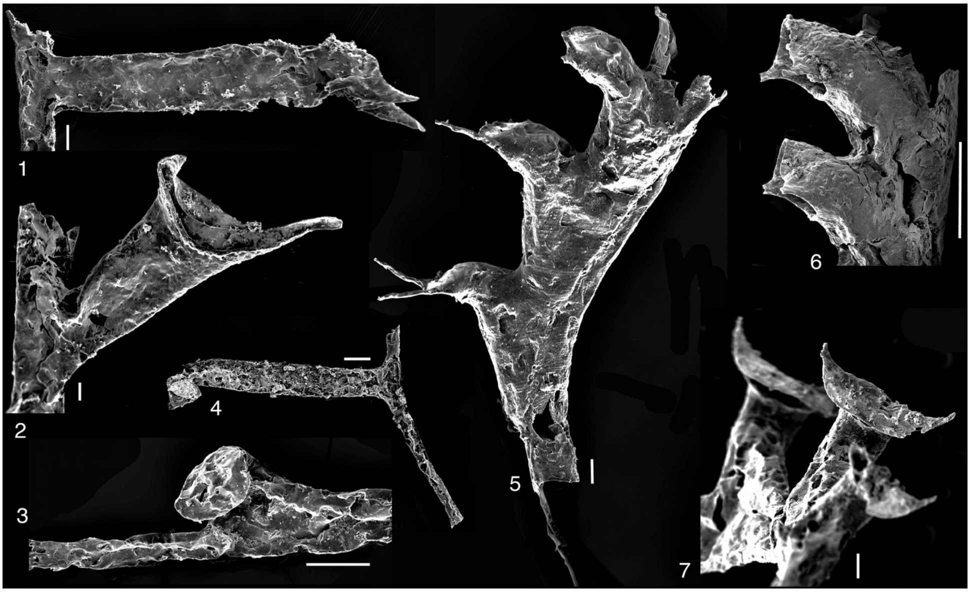

FIG. 10. Thecal style in the Monograptinae. *1–2, Lituigraptus convolutus* (HISINGER, 1837), isolated thecae in lateral (*1*) and ventral (*2*) views; *3, Torquigraptus* sp., isolated theca with torsion and laterally widened aperture; *4, Rastrites* sp., single theca; *5, Spirograptus turriculatus* (BARRANDE, 1850), juvenile; *6, Stimulograptus sedgwickii* (PORTLOCK, 1843), two thecae with paired spines; *7, Oktavites contortus* (PERNER, 1897), thecal apertures with pointed lateral extensions and wide hood (new). All specimens Kalholn Shale, Dalarna. Scale bars, 1 mm in 6; all others 0.1 mm.

and concluded that both originated independently from monograptid ancestors as a result of convergent evolution. *Cochlograptus* may be related to *Stimulograptus* or *Monograptus* and *Testograptus* could have its origin in a *Monograptus flemingii* type ancestor.

The thecae in the Monograptinae (Fig. 10) are quite variable at first sight, but have certain commonalities. They are variably elongated with an apertural hood or hook, thus an opening that is proximally or ventrally directed. The shape may change gradually along the stipes in a typical biform fashion. In general, it is triangular with an isolated apertural part, however, parallel-sided isolated prothecae are also common. Metathecae may be completely isolated and parallel sided as in *Rastrites* or in the proximal thecae of *Lituigraptus* (Fig. 10.1–10.2, 10.4) and early *Torquigraptus,* such as *Torquigraptus decipiens* (TÖRNQUIST, 1899). In *Lituigraptus,* the thecae bear paired laterally directed hornlike extensions in distal thecae. The thecal aperture is directed proximally or ventrally and bears a wide dorsal hood (Fig. 10.2). Distally, the thecae are more robust and the prothecae widen considerably (LOYDELL & MALETZ, 2009). The apertural hood may be strongly laterally extended as in *Oktavites contortus* (Fig. 10.7). Thecal overlap may be close to none, as in *Spirograptus* and *Oktavites,* but is absolutely none in *Rastrites,* with its very slender parallel-sided prothecae (Fig. 10.4). Considerable thecal overlap is present in many species of *Monograptus. Campograptus harpago* (TÖRNQUIST, 1899) and *Campograptus lobiferus* (M'COY, 1850) have proximal thecae with hooked apertures and distinct paired spines as do species of the genus *Monograptus,* for example, as in *Monograptus priodon* (BRONN, 1835). The spines diminish distally and the thecal apertures curve and aperturally grow back on themselves as they also do in *Lapworthograptus grayae* (CHOPEY-JONES, WILLIAMS, & ZALASIEWICZ, 2003). In *Stimulograptus sedgwickii*, the thecal apertures bear paired lateral spines, but a dorsal hood is lacking. The central part of the thecal aperture is

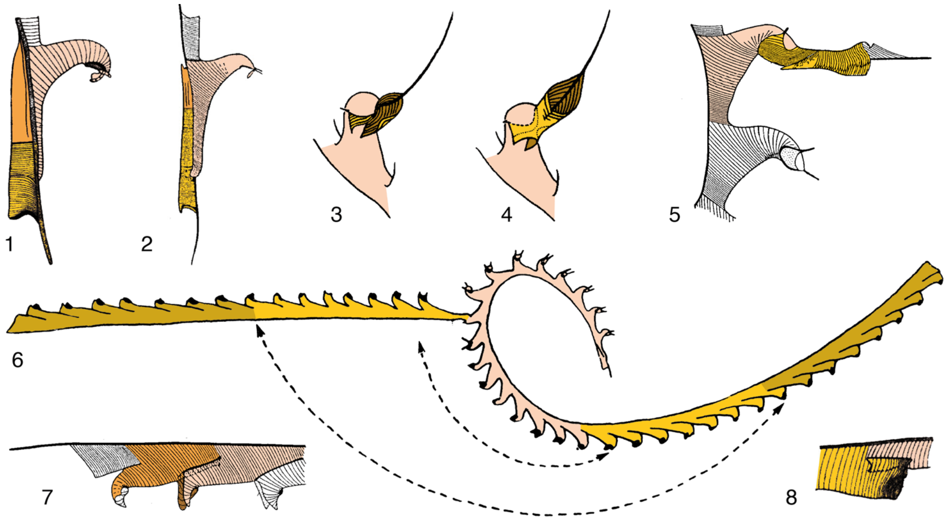

FIG. 11. Tubarium development in *Cyrtograptus*. *1* and *8*, *Cyrtograptus hamatus* (BAILY, 1862) (adapted from Teller, 1976, fig. 11–12); *2–7, Cyrtograptus perneri* BOUČEK, 1933 (*2,5,7;* adapted from Thorsteinsson, 1955, fig. 1–4 as *Cyrtograptus rigidus* n. ssp.; LENZ & others, 2012, p. 32); 3–*4*,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

directed ventrally with the paired spines in a proximal position (Fig. 10.6), producing a wide and much more open aperture in distal thecae. Proximal thecae clearly show the apertural hood and paired lateral spines, indicating a considerable transformation of thecal shapes along the stipes in the Monograptinae, leading to the development of biform thecal styles.

Torsion of the metathecae can be seen in *Torquigraptus,* in which the thecal apertures are twisted to the reverse side of the tubarium, and the thecal hood may be somewhat laterally expanded (Fig. 10.3). Asymmetry without torsion is visible in the thecae of *Spirograptus turriculatus* (Fig. 10.5), in which the second apertural spine is missing in most thecae, and the aperture becomes tear-shaped (MELCHIN & LENZ, 1986).

Triangulate thecae with a distinct hood or hook and a proximally oriented aperture bearing paired spines, along with a strong dorsal hood or lobe (Fig. 11.1, 11.2), are also present in many *Cyrtograptus* species (see TELLER, 1976), while their cladial stipes often bear more simple thecae with some thecal overlap and distally directed, paired apertural lobes (Fig. 11.7). These hooked apertures and apertural spines are either symmetrical or asymmetrical in species of *Cyrtograptus* (LENZ & MELCHIN 1989). A distinct thecal gradient from triangulate thecae proximally to those with low inclination may also occur. Increased thecal overlap also signals changes in the apertural development (Fig. 11.6). Simple apertural development, without any hooks, hoods, or lobes, is present in *Cyrtograptus hamatus* (Fig. 11.8) and some other species of the genus *Cyrtograptus*. The genus has been suggested to be polyphyletic (e.g., RICKARDS, HUTT, & BERRY, 1977; FU, 1994; WILLIAMS & ZALASIEWICZ, 2004; URBANEK & TELLER, 1997), and LENZ and others (2012) decided not to use the family Cyrtograptidae but include the genus *Cyrtograptus* in Monograptidae instead.

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

NON-CLADIA BEARING TAXA

RICKARDS, HUTT, and BERRY (1977; fig. 1) provided the only available interpretation of early monograptids, suggesting the origination of several independent lineages from the genus *Atavograptus* and of the *Monograptus priodon* group from *Monoclimacis*. The non-cladia bearing taxa of the Monograptinae form a paraphyletic taxon and gave rise to cladia-bearing taxa multiple times.

Campograptus OBUT, 1949, p. 24 [**Monograptus convolutus* var. *communis* LAPWORTH, 1876b, p. 358; SD OBUT, 1964, p. 328]. Tubarium gently to strongly dorsally curved proximally, becoming almost straight distally; thecae triangular with no overlap; prothecal bases broad; simply hooked metathecae, thecal hook proximally involving primarily dorsal and, to much lesser extent, ventral thecal wall, and mesially and distally probably dorsal wall only; thecal apertures of proximal, mesial and, in some species, even distal thecae possess paired ventro-laterally or proximo-laterally directed spines; proximal thecae may be axially elongated. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone–*Stimulograptus sedgwickii* Biozone): worldwide.——FIG. 12,*1a–c*. **C. communis* (LAPWORTH); *1a,* lectotype (PŘIBYL, 1948, p. 48), BU 1684a, proximal end not shown (Lapworth, 1876b, fig. 4a); *1b,* proximal end in relief, internal mould, SM A24487, C horizon (*Demirastrites triangulatus* Biozone), Rheidol Gorge (Sudbury, 1958, fig. 20). Scale bars, 1 mm.

Cochlograptus OBUT, 1987, p. 142 [**Nautilus veles* RICHTER, 1871, p. 243, fig. 1; OD]. Disk-shaped, ventrally and continuously planispirally coiled tubarium with sharp ventral deflection near apex of sicula; tubarium development by means of pseudovirgula; sicula moderately to strongly ventrally curved; prominent triangular dorsal tongue on sicular aperture; thecae hooked, with well-developed, paired lateral spines. *Silurian, Llandovery* (*Telychian, Streptograptus crispus* Biozone–*Oktavites spiralis* Biozone): worldwide.——FIG. 12,*2a–b*. **C. veles* (RICHTER); *2a,* lectotype, BGR X11901a, Thuringia, Germany (precise locality unknown) (Maletz, 2001, fig. 3a); *2b,* holotype of *Monograptus discus* TÖRNQUIST, 1883, LO 1071T, Kallholn, Dalarna, Sweden (Maletz, 2017a, fig. 6D). Scale bars, 1 mm.

Cultellograptus LOYDELL & NESTOR, 2006, p. 602 [**Monograptus cultellus* TÖRNQUIST, 1881, p. 434; OD]. Tubarium straight, except for initial ventral curvature that involves the sicula; thecae with extremely wide metathecae, hooked, nonspinose, lacking overlap; common canal narrow. *Silurian, Llandovery* (*Telychian, Oktavites spiralis* Biozone)–*Wenlock* (*Sheinwoodian, Cyrtograptus murchisoni* Biozone): UK, Czech Republic, Germany, Romania, Baltic States, Sweden, Morocco.——FIG. 12,*9a–b*. **C. cultellus; 9a,* MGUH 31.681, Sommerodde-1 core, Bornholm, Denmark, (Loydell & others, 2017, fig. 16I); *9b,* isolated proximal end, Ventspils D-3 drill core, Latvia (adapted from Loydell & Nestor, 2006, fig. 9E). Scale bars, 1 mm.

Demirastrites EISEL, 1912, p. 27 [**Rastrites triangulatus* HARKNESS, 1851, p. 59; SD BULMAN, 1929, p. 175]. Tubarium with proximally accentuated dorsal curvature; sicula small, apex reaching to about level of first metatheca at maximum; metathecae isolated, inclined at high angle to the tubarium axis; thecal apertural hoods or hooks may be extended transversely into pair of lateral horns; mesial and distal thecae are more or less high-triangular in profile; first theca rastritid or triangular, axially elongated; up to several succeeding proximal thecae may have very slender elongated prothecae, slightly widening toward the base of widely separated, parallel-sided rastritiform metathecae. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone–*Demirastrites pectinatus* Biozone): worldwide.——FIG. 12,*3a–c*. **D. triangulatus* (HARKNESS); *3a,* lectotype (PŘIBYL & MÜNCH, 1941, p. 5), strongly distorted specimen, BGS 6941, Birkhill Shales, Frenchland Burn, Scotland (Zalasiewicz, 2008b, Atlas 2.92); *3b,* specimen missing proximal end, PŠ 3517, Všeradice, Czech Republic (Štorch, 2015, fig. 17f); *3c,* proximal end, PŠ 3643, Všeradice, Czech Republic (Štorch, 2015, fig. 17m). Scale bars, 1 mm.

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

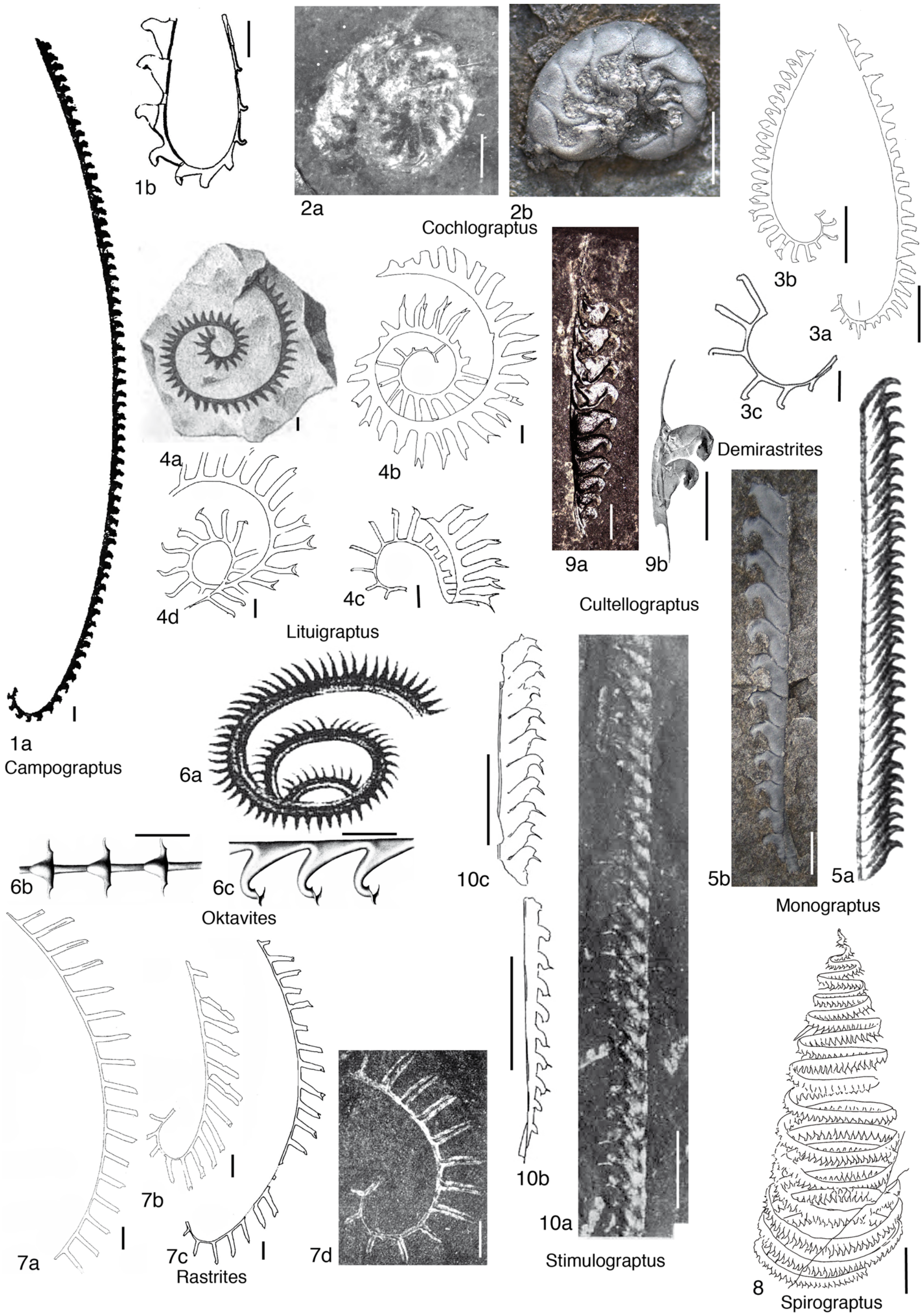

FIG. 12. Monograptinae (p. 17–20).

Lituigraptus Ni, 1978, p. 412, *ex Rastrites* (*Lituigraptus*) Ni, 1978, p. 412, Štorch, 1998b, p. 248 [**Rastrites* (*Lituigraptus*) *glomeratus;* OD; =*Prionotus convolutus* Hisinger, 1837, syn. by Štorch, 1998b, p. 248] [=*Corymbites* Obut & Sobolevskaya in Obut, Soboleveskaya, & Nikolaev, 1967, p. 132 (type, *C. sigmoidalis,* OD) syn. by Loydell, herein; *non Corymbites* Linnaeus, 1758 (Coleoptera, Elateridae, modern beetle)]. Dorsally enrolled spiral tubarium; distally tubarium axis may gradually twist and thecae may be situated ventrally or perpendicular to spiral plane; proximal thecae rastritiform, with threadlike prothecae and straight, tubular metathecae with hooded apertures; mesially thecae gradually become high triangular; apertural hoods gradually retreat being substituted by prominent paired, ventrally to ventro-proximally directed, lateral processes. *Silurian, Llandovery* (*Aeronian, Demirastrites simulans* Biozone–*Telychian*, *Spirograptus guerichi* Biozone): worldwide.——Fig. 12,*4a–d*. *P. convolutus* (Hisinger); *4a,* holotype, NRM Cn 68951, Furudal, Dalarna, Sweden (Hisinger, 1837, pl. 35.*7*); *4b,* medium-sized specimen with thecal apertures, BB 697, Tmaň, Czech Republic (Štorch, 1998b, fig. 11.*7B*); *4c,* proximal end with sicula, PŠ 724, Tmaň, Czech Republic (Štorch, 1998b, fig. 11,*7D*); *4d*, holotype of **L. glomeratus* Ni, 1978, NIGP 45401 (Ni, 1978, fig. 7.*7*). Scale bars, 1 mm.

Monograptus Geinitz, 1852, p. 32, *nom. correct. pro Monograpsus* Geinitz, 1852, p. 32; ICZN, Opinion 198, 1954; *pro Lomatoceras* Bronn, 1835, p. 56; *pro Monoprion* Barrande, 1850, p. 36, ICZN, Opinion 198, 1954 [**Lomatoceras priodon* Bronn, 1835; SD Bassler, 1915, p. 822] [=*Pomatograptus* Jaekel, 1889, p. 677 (type, *Lomatoceras priodon* Bronn, 1835, SD Bulman, 1929, p. 180) obj.; =*Priodon* Nilsson cited in Bronn, 1835, p. 56; =*Ancylograptus* Obut & Morozova in Obut & others, 1988, p. 62; *ex Monograptus* (*Ancylograptus*) Obut & Morozova in Obut & others, 1988, p. 62 (type, *Monograptus flexilis* Elles, 1900, p. 407; OD; =*Graptolithus* (*Monograpsus*) *belophorus* Meneghini, 1857, p. 165, syn. by Štorch & Manda, 2019, p. 53), syn. herein]. Tubarium straight or dorsally curved proximally and then straight; thecae hooked with or without paired apertural spines or processes; thecal apertures face proximally or proximo-dorsally; thecae overlap, typically for half their length or more distally. *Silurian, Llandovery* (*Telychian, Spirograptus guerichi* Biozone)–*Wenlock* (*Homerian, Colonograptus praedeubeli-deubeli* Biozone): worldwide.——Fig. 12,*5a–b*. **M. priodon* (Bronn); *5a,* holotype, fragment (Bronn, 1835, pl. 1.*13;* not found in the Bronn collection at the Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (personal communication, Jessica D. Cundiff, 2014), scale unknown; *5b,* proximal end in relief, SMF 75780, glacial boulder, scale bar, 1 mm (Maletz, 2017b, pl. 15B).

Oktavites Levina, 1928, p. 10 [**Graptolithus spiralis* Geinitz, 1842, p. 700; SD Obut, 1964, p. 328] [=*Obutograptus* Mu, 1955, p. 10 (type, *Graptolithus spiralis* Geinitz, 1842, p. 700, OD, obj.)]. Dorsally curved or spirally coiled tubarium; metathecae triangular, sometimes almost rastritiform proximally, with little or no overlap; thecal apertures laterally expanded, sometimes asymmetrically; torsion, affecting the entirety of metatheca, developed distally; extension of metathecal dorsal wall over central portion of aperture causes this to face dorsally. *Silurian, Llandovery* (*Aeronian, Stimulograptus sedgwickii* Biozone–*Telychian, Cyrtograptus lapworthi* Biozone): worldwide.——Fig. 12,*6a*. **O. spiralis* (Geinitz), syntype (not preserved, see Maletz, 2001, p. 171) (Geinitz, 1842, pl. 10.*26*); *6b–c,* stipe fragments showing thecal style, Dalarna, Sweden (Bulman, 1932, pl. 6,*15–16*). Scale unknown.

Rastrites Barrande, 1850, p. 64 [**R. peregrinus;* SD Hopkinson, 1869, p. 158] [=*Rastrograptus* Hopkinson & Lapworth, 1875, p. 633 *pro Rastrites* Barrande, 1850; =*Stavrites* Obut & Sobolevskaya in Obut, Sobolevskaya, & Merkureva, 1968, p. 111 (type, *S. rossicus,* OD), syn. by Loydell, herein]. Tubarium straight or dorsally curved proximally to various degrees, straight distally; threadlike prothecae; straight, isolated metathecae, inclined at high angle to tubarium axis throughout length of colony; thecal apertures slightly hooked or hooded, sometimes with small paired apertural spines or lateral extensions. [Rickards, Hutt, and Berry (1977) and Štorch and Loydell (1992) discussed a possibly polyphyletic concept of the genus]. *Silurian, Llandovery* (*Aeronian, Demirastrites triangulatus* Biozone–*Telychian, Monoclimacis griestoniensis* Biozone): worldwide.——Fig. 12,*7a–c*. **R. peregrinus; 7a,* lectotype, fragment, NMP L27954, Libomyšl, Czech Republic (Štorch, 2000a, Atlas 1.87); *7b,* complete specimen, NMP L30073, Bykoš, Czech Republic (Štorch, 2000a); *7c,* long specimen with complete sicula, PŠ 724, Tmaň, Czech Republic (Štorch, 1998b, fig. 11,*3B*).——Fig. 12,*7d. R. rossicus* (Obut & Sobolevskaya in Obut, Sobolevskaya, & Merkureva, 1968) holotype, CNIGR 270/9765 (Obut & Sobolevskaya in Obut, Sobolevskaya, & Merkureva, 1968, pl. 31,*6*). Scale bars, 1 mm.

Spirograptus Gürich, 1908, p. 34 [**Graptolithus turriculatus* Barrande, 1850, p. 56; SD Bulman, 1929, p. 182] [=*Tyrsograptus* Obut, 1949, p. 24 (type, *Graptolithus turriculatus* Barrande, 1850, p. 56, SD Obut, 1964, p. 328), obj.]. Tubarium trochospirally coiled; sicula small (<1.5 mm) and dorsally curved, and in one species at least also exhibits dextral torsion; thecae hooked in manner of those of *Stimulograptus*, and bearing one or two apertural spines; thecal apertures may be symmetrical or asymmetrical resulting from differential development of the apertural margin, but without significant torsion; thecal overlap is negligible; common canal wide. *Silurian, Llandovery* (*Aeronian, Stimulograptus halli* Biozone–*Telychian, Streptograptus sartorius* Biozone): worldwide.——

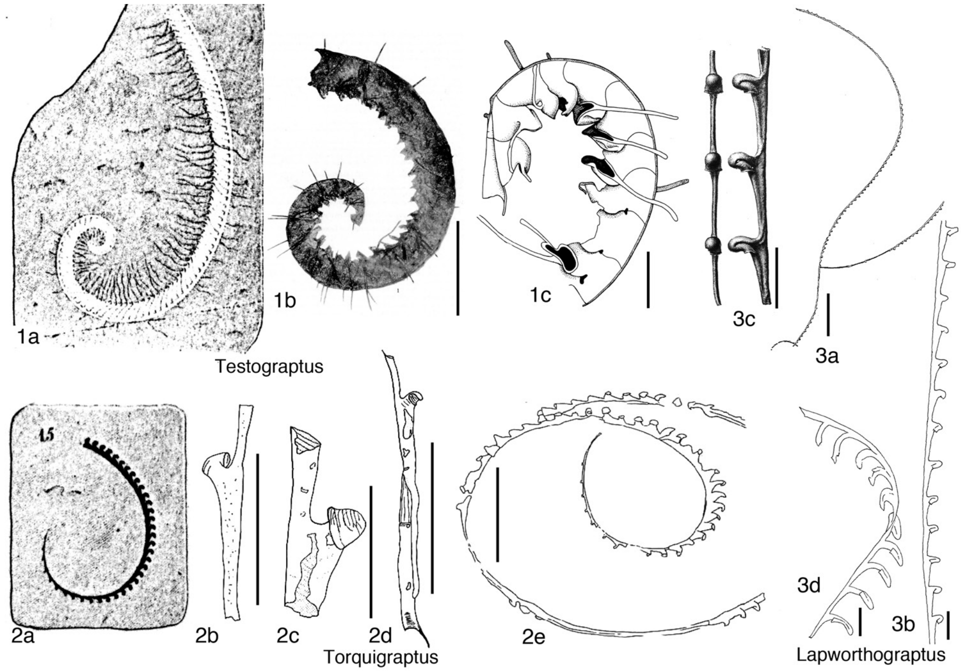

FIG. 13. Monograptinae (p. 17–20).

FIG. 12,*8*. **S. turriculatus* (BARRANDE), lectotype, NMP L27597, Litohlavy, Czech Republic, scale bar, 5 mm (Štorch, 2000b, Atlas 1.92).

Stimulograptus PŘIBYL & ŠTORCH, 1983, p. 221, *ex Monograptus* (*Stimulograptus*) PŘIBYL & ŠTORCH, 1983, p. 221[**Graptolithus halli* BARRANDE, 1850, p. 48; OD] Tubarium straight, dorso-ventrally curved, or dorsally curved proximally then straight distally; sicula less than 2 mm long; hooked, triangular thecae bear paired latero-ventrally directed spines; thecal overlap insignificant; distal thecae may be ventrally directed and without hook. *Silurian, Llandovery* (*Aeronian, Lituigraptus convolutus* Biozone–*Telychian, Oktavites spiralis* Biozone): worldwide.——FIG. 12,*10a–c*. **S. halli* (BARRANDE); *10a,* lectotype, NMP L20322, *Rastrites linnaei* Biozone, Želkovice, Czech Republic (Přibyl & Štorch, 1983, pl. 2.*1*); *10b,* proximal end, PŠ 106b, Hlásná Třebaň, Czech Republic (Přibyl & Štorch, 1983, fig. 2A); *10c,* distal fragment, PŠ 108/3, Hlásná Třebaň, Czech Republic (Přibyl & Štorch, 1983, fig. 2B).

Testograptus PŘIBYL, 1967b, p. 49, *ex Monograptus* (*Testograptus*) PŘIBYL, 1967b, p. 49; LOYDELL & CAVE, 1994, p. 612 [**Graptolithus testis* BARRANDE, 1850; OD]. Tubarium planispirally and ventrally coiled through up to 450°, curvature strongest proximally with abrupt ventral flexure immediately distal of sicular apex; sicula weakly ventrally curved; tubarium development occasionally by means of pseudovirgula; thecae biform, with long, paired, laterally directed spines; proximalmost thecae with strongly hooked metatheca, distal thecae with lesser hook; thecal overlap about 50–75%. *Silurian, Wenlock* (*Homerian*, *Cyrtograptus lundgreni* Biozone): worldwide.——FIG. 13,*1a–c*. **T. testis* (BARRANDE); *1a,* ?lectotype, scale unknown (Barrande, 1850, pl. 3.*19*); *1b,* isolated specimen, scale bar, 5 mm (Urbanek & Teller, 1974, pl. 24); *1c,* small isolated specimen showing tubarium details, scale bar, 1 mm (Urbanek & Teller, 1974, fig. 1).

Torquigraptus LOYDELL, 1993, p. 112 [**Graptolithus proteus* var. *plana* BARRANDE, 1850, p. 58; OD]. Tubarium curved, or coiled, bearing thecae that exhibit torsion only of apertural part of the metatheca, toward reverse side of tubarium, in most cases throughout length of the colony, in some species only mesially and distally; thecal apertures simple, with no marked asymmetry or lateral expansion; early thecae may be axially elongate or rastritiform; distal thecae triangulate. *Silurian, Llandovery* (*Aeronian, Pribylograptus leptotheca* Biozone–*Telychian, Oktavites spiralis* Biozone): worldwide.——FIG. 13,*2a–d*. **T. planus* (BARRANDE); *2a,* ?holotype, Czech Republic (Barrande, 1850, pl. 4.*15*); *2b–d,* isolated specimens, Dalarna, Sweden (Hutt, Rickards, & Skevington, 1970, pl. 3,*51–52,54,* as *Monograptus proteus*); *2e,* large specimen, Wales, UK, scale bar, 5 mm (Loydell, 1993, fig. 21,*19*).

CLADIA BEARING TAXA

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

Cyrtograptus CARRUTHERS, in MURCHISON, 1867, p. 540, *nom. correct.* LAPWORTH, 1873 *pro Cyrtograpsus* CARRUTHERS in MURCHISON, 1867; ICZN, Opinion 650, 1963; *non Cyrtograpsus* DANA, 1851, p. 288 (Decapoda) [**C. murchisoni;* OD] [=*Pleurograptoides* AVERIANOW, 1931, p. 21 (type, *P. erectus,* OD), syn. herein; =*Averianowograptus* OBUT, 1949, p. 29 (type, *Cyrtograptus magnificus* AVERIANOW, 1931, p. 9, OD), syn. herein; =*Damosiograptus* OBUT, 1950, p. 270 (type, *Cyrtograptus spiralis* AVERIANOW, 1931, OD), syn. by RICKARDS, HUTT, & BERRY, 1977, p. 76; =*Uralograptus* KOREN', 1962, p. 724 (type, *U. insuetus* KOREN', 1962, p. 724, OD), syn. by BULMAN, 1970, p. 135; =*Kurganakograptus* GOLIKOV, 1969, p. 515 (type, *K. primus,* OD), syn. herein]. Dorsally curved, low helically spiralled or dorsally curved then straight tubarium bearing at least one thecal cladium; thecae of main stipe hooked throughout, often laterally expanded and spinose, or hooked proximally then with hooks retreating distally, becoming hooded initially and then simple tubes with lateral lappets flanking aperture; thecae of thecal cladia hooked, hooded, simple adnate or isolated tubes in some cases with lateral lappets flanking aperture; secondary and tertiary cladia may develop from cladial thecae. [The genus has been considered polyphyletic, e.g., RICKARDS, HUTT, and BERRY (1977), and needs re-investigation]. *Silurian, Llandovery* (*Telychian, Cyrtograptus lapworthi* Biozone)–*Wenlock* (*Homerian, Cyrtograptus lundgreni* Biozone): worldwide.——FIG. 14,*1a–c*. **C. murchisoni,* Builth District, Wales; *1a,* counterpart of holotype, GSM 10718; *1b,* topotype, proximal end, GSM 10716; *1c,* topotype, proximal end with sicula, GSM 10716, scale bars, 5 mm, 1 mm in *1b* (*a–c,* Zalasiewicz & Williams, 2008, Atlas 2.60).——FIG. 14,*1d. C. insuetus* (KOREN'), holotype, scale bar, 5 mm (Rickards, Hutt, & Berry, 1977, fig. 39).——FIG. 14,*1e. C. magnificus* (AVERIANOW), holotype, scale bar, 5 mm (Obut, 1950, fig. 6).

Barrandeograptus BOUČEK, 1933, p. 62, *ex Monograptus* (*Barrandeograptus*) BOUČEK, 1933, p. 62; MÜNCH, 1938, p. 53][**Cyrtograptus pulchellus* TULLBERG, 1883, p. 36; OD]. Slender tubarium, strongly dorsally and/or ventrally curved proximally, less strongly curved distally; up to at least three orders of thecal cladia may be developed; thecae slender and axially elongated; proximally appearing hooked; distal thecae triangular tubes typically with pronounced notch between dorsal wall and ventral wall of succeeding protheca; apertures of distal thecae may be furnished with lateral lappets. *Silurian, Llandovery* (*Telychian, Oktavites spiralis* Biozone)–*Wenlock* (*Sheinwoodian, Monograptus riccartonensis* Biozone): worldwide.——FIG. 14,*2a–c, d*?. **B. pulchellus* (TULLBERG); *2a,* holotype, SGU 5684, complete specimen showing sicula, Röstånga, Scania, Sweden (Tullberg, 1883, pl. 3.*12*); *2b–c,* MGUH (MMH) 13497, fragments showing distal thecal style (Bjerreskov, 1975, fig. 27C–D); *2d,* proximal theca tentatively referred to *B. pulchellus,* inverted SEM photo (Loydell & Nestor, 2006, fig. 13C). Scale bars, 1 mm; 0.2 mm in *2d.*

Diversograptus MANCK, 1923, p. 283 [**D. ramosus;* SD BULMAN, 1929, p. 176] [=*Dibranchiograptus* HUNDT, 1949a, p. 19 (type, *D. bibrachiatus,* OD), syn. herein]. Narrow tubarium comprising main stipe and one sicular cladium with or (usually) without thecal cladia; stipes straight or gently curved; thecae hooked, with retroflexed apertures flanked by small lateral lappets. *Silurian, Llandovery* (*Telychian, Oktavites spiralis* Biozone–*Cyrtograptus lapworthi* Biozone): Germany, UK (Wales, Scotland), Estonia, Latvia, Czech Republic, Turkey, Morocco.——FIG. 14,*3a–c*. **D. ramosus; 3a,* lectotype (selected by BOUČEK & PRIBYL, 1953, p. 489), repository unknown, scale bar, 5 mm (reconstruction from Bulman, 1970, fig. 102,*3a*); *3b,* specimen showing bipolar growth, MGM 146-S, Jabalón River section, central Spain, scale bar, 1 mm (Loydell & others, 2009, fig. 4J); *3c*, stipe fragment, MGM 419-52, Aizpute-1 drill core, Latvia, scale bar, 1 mm (Loydell & Nestor, 2006, fig. 11C).——FIG. 14,*3d–e. D.*? *pergracilis* (BOUČEK, 1931, p. 302), fragments showing thecal style, Ventspils D-3 drill core, 826.7 m, Latvia (Loydell & Nestor, 2006, fig. 12A–B). Scale bars, 1 mm (*d*); 0.1 mm (*e*).

Paradiversograptus SENNIKOV, 1976, p. 225, *ex Monograptus* (*Paradiversograptus*) SENNIKOV, 1976, p. 225; LOYDELL, 1993, p. 143 [**Rastrites capillaris* CARRUTHERS, 1867b, p. 368; OD]. Gently ventrally or dorso-ventrally curved tubarium; sicular cladium; metathecae simply hooked; no thecal overlap. *Silurian, Llandovery* (*Aeronian, Lituigraptus*

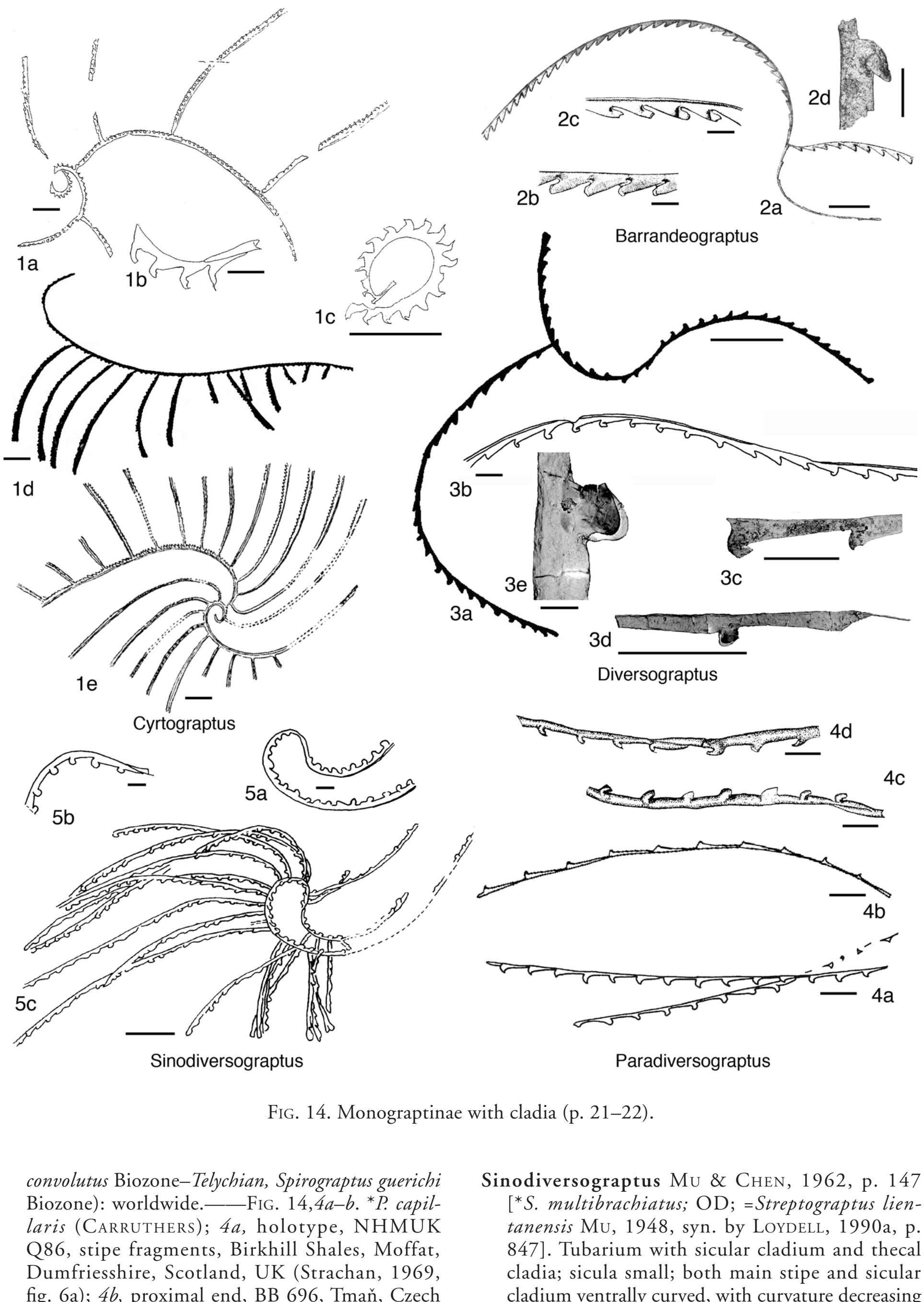

FIG. 14. Monograptinae with cladia (p. 21–22).

convolutus Biozone–*Telychian, Spirograptus guerichi* Biozone): worldwide.——FIG. 14,*4a–b*. **P. capillaris* (CARRUTHERS); *4a,* holotype, NHMUK Q86, stipe fragments, Birkhill Shales, Moffat, Dumfriesshire, Scotland, UK (Strachan, 1969, fig. 6a); *4b,* proximal end, BB 696, Tmaň, Czech Republic (Štorch, 1998b, fig. 8,*3*). Scale bars, 1 mm.——FIG. 14,*4c–d*. *P. runcinatus* (LAPWORTH, 1876d), Glenkiln Burn, Dumfriesshire, Scotland, UK; *4c*, proximal end in relief; *4d,* specimen with sicular cladium (Strachan, 1952, fig. 1B–C). Scale bars, 1 mm.

Sinodiversograptus MU & CHEN, 1962, p. 147 [**S. multibrachiatus;* OD; =*Streptograptus lientanensis* MU, 1948, syn. by LOYDELL, 1990a, p. 847]. Tubarium with sicular cladium and thecal cladia; sicula small; both main stipe and sicular cladium ventrally curved, with curvature decreasing distally; tubarium develops through three stages: monograptid, diversograptid (with sicular cladium), and sinodiversograptid (with thecal cladia); metathecae hooked; gently ventrally curved cladia originate from almost all proximal and mesial thecae. *Silurian, Llandovery* (*Telychian*, *Spirograptus* *guerichi* Biozone): Australia, Canada, China.——FIG. 14,*5a–c*. *S. lientanensis* (MU); *5a,* holotype, specimen with sicular cladium, Lientan, Guandong Province, China, scale bar, 5 mm (Loydell, 1990a, fig. 2.*5*); *5b,* small proximal end, Lientan, Guandong Province, China, scale bar, 1 mm (Loydell, 1990a, fig. 2.*1*); *5c.* holotype of **S. multibrachiatus* (MU & CHEN), mature specimen with numerous cladia, NIGP 11580a, Qiaoting, Nanjiang District, Sichuan Province, China, scale bar, 5 mm (Loydell, 1990a, fig. 1).

Subfamily PRISTIOGRAPTINAE Gürich, 1908

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

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

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

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

MORPHOLOGY

The morphology of early Pristiograptinae is fairly simple, with basically straight tubarium shapes and simple thecae having an angular, straight aperture, typically adorned only with a thickened rim (Fig. 15.1–15.2). Dorsal curvature is present in *Formosograptus*, *Slovinograptus,* and *Wolynograptus*, associated with thecal elongation and isolation of metathecae. Distally, the thecae possess increasing overlap in these taxa. Ventral curvature may be present and affects the sicula and very few proximal thecae. Regular ventral curvature is typical for *Pristiograptus paradoxus* LOYDELL & WALASEK, 2019 and *Pristiograptus macrodon* ŠTORCH, 1992, both of which exhibit only slight dorso-ventral curvature. Further examples of this are *Pseudomonoclimacis tetlitensis* LENZ, 1988 and *Monograptus banksi* RICKARDS & others, 1995.

The sicula is straight to somewhat curved ventrally and in many species bears a variable number of sicular annuli (Fig. 15.4). The number and position of the sicular annuli appears to have become stabilized during the uppermost Silurian in which most taxa

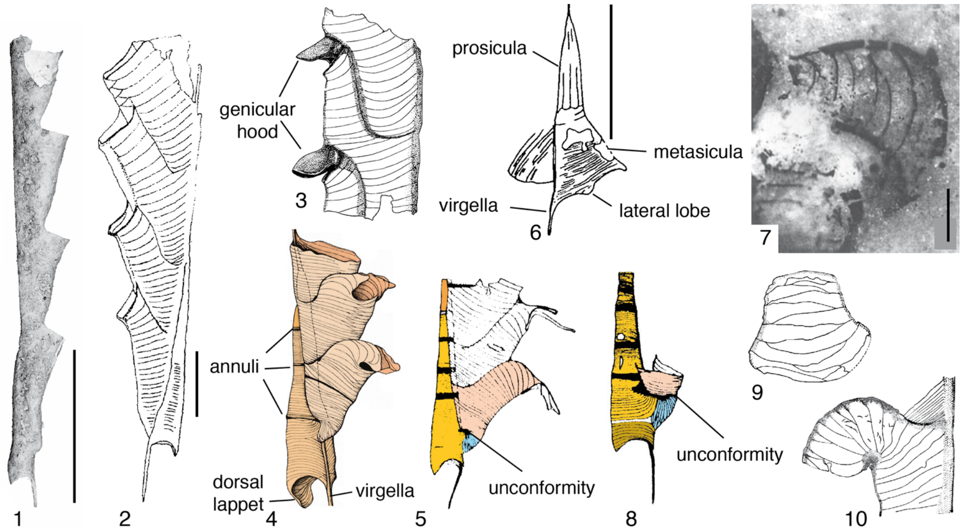

FIG. 15. Morphology of Pristiograptinae. *1, Pristiograptus* sp. cf. *Pristiograptus regularis* (TÖRNQUIST, 1899) (SEM photo inverted from Russel-Houston, 2001, pl. 12C); *2, Pristiograptus frequens* (JAEKEL, 1889), proximal end in obverse view showing thecal shape (Maletz, 1999, fig. 2R); *3, Heisograptus micropoma* (JAEKEL, 1889), development of microfusellar hoods (Urbanek, 1958, fig. 67); *4, Skalograptus lochkovensis* (PŘIBYL, 1940a), proximal end (adapted from Urbanek, 1997a, fig. 49); *5, Saetograptus chimaera* (BARRANDE, 1850), proximal end (adapted from Walker 1953, fig. 4G); *6–7, Uncinatograptus falcarius* (KOREN', 1969), showing sicular development and formation of dorsal hood (Koren', Kim & Walliser, 2007, fig. 4R, pl. 1.*9*); *8, Pristiograptus dubius* (SUESS, 1851), juvenile in reverse view, showing prothecal unconformity (Walker, 1953, fig. 2B); *9–10, Uncinatograptus uncinatus* (TULLBERG, 1883), development of thecal hood (Urbanek, 1958, fig. 21). Scale bars, 1 mm; reconstructions, no scale.

possessed three or fewer annuli (URBANEK, 1997a).

The prosicula is small and slender and bears a small number of longitudinal rods (Fig. 15.6). The metasicula widens slowly, except in taxa with trumpetlike siculae such as *Colonograptus deubeli* (JAEGER, 1959) and a number of other taxa, including some early Devonian forms (see JAEGER, 1988). Apertural modifications of the sicula are rare, but dorsal lappets are present in a number of taxa (Fig. 15.4), and slight lateral lappets or lobes appear to be present in *Uncinatograptus falcarius* (Fig. 15.6) and probably in other related taxa.

The origin of th1 may be through a sinus and lacuna development in all Pristiograptinae but has been verified from only a few taxa. It has been described in *Pristiograptus frequens* (EISENACK, 1942), *Heisograptus micropoma* (MALETZ, 1999), *Wolynograptus acer* (URBANEK, 1997a), *Formosograptus* (URBANEK, 1997a) and *Skalograptus* (URBANEK, 1997a). LUKASIK and MELCHIN (1994) illustrated a possible primary porus in *Pristiograptus* sp. cf. *Pristiograptus regularis* from Arctic Canada. WALKER (1953) described in great detail the early growth of th1 in *Pristiograptus* and *Saetograptus* from glacial boulders found in northern Germany. The specimens show a distinct unconformity in the early growth on the reverse side but not on the obverse side in *Pristiograptus* (Fig. 15.8) and to a lesser extent in *Saetograptus* (Fig. 15.5).

Many taxa have a gradient in the development of thecal apertures, from low lateral lobes or spines to simple straight apertures distally. Geniculae are present in some taxa, rounded in *Heisograptus* but also angular as in *Uncinatograptus*. The details of the development of thecal hoods in the Pristiograptinae are known from a number of taxa (URBANEK, 1958, 1997a; KOREN', KIM, & WALLISER, 2007). *Heisograptus* has hoods formed from microfusellar material as secondary additions at the genicula (Fig. 15.3). In *Unci-*

natograptus, apertural hoods are present at least on the proximal thecae but may be lacking in distal thecae. These hoods look similar to genicular developments but are true hoods formed as extensions of the dorsal thecal wall. In *Uncinatograptus falcarius* and related early Devonian taxa, the initial part of the thecal hood is reduced in width, but distally a considerable lateral extension is visible forming a spatulate process (Fig. 15.7) and not a thecal hood as in *Uncinatograptus uncinatus* (Fig. 15.9–15.10). The thecal hood, thus, does not cover the thecal aperture.

Colonograptus PŘIBYL, 1943, p. 2, *ex Pristiograptus* (*Colonograptus*) PŘIBYL, 1943, p. 2 [**Graptolithus colonus* BARRANDE, 1850; OD] [=*Ludensograptus* TSEGELNJUK, 1978, p. 88 (type, *Graptolithus Ludensis* MURCHISON, 1839, OD), syn. herein] [=*Conomograptus*, misspelling in PŘIBYL, 1983, p. 149]. Tubarium gently ventrally curved throughout or only proximally, being straight distally; sicula ventrally curved; biform thecae; proximal two or three thecae with ventrally projecting broad fusellar lappets; distal thecae simple tubes. *Silurian, Wenlock* (*Homerian, Colonograptus praedeubeli/deubeli* Biozone)*–Ludlow* (*Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide.——FIG. 16,*1a–b*. **C. colonus* (BARRANDE), lectotype, NMP L19771, Butovice-Nová-Ves, Czech Republic, *Neodiversograptus nilssoni* Biozone, proximal end and distal part of specimen preserved in relief, scale bars, 1 mm (new; drawing by Štorch, & Strossova, 2021).

Dulebograptus TSEGELNJUK, 1976, p. 98 [**D. bresticus* TSEGELNJUK, 1976, p. 98; OD]. Tubarium straight or ventrally curved proximally and straight distally; proximal one to three thecae with complete fusellar hoods formed of dorsal walls of thecae; succeeding thecae have apertures with symmetrical lateral lobes which retreat distally; distal thecae becoming simple with straight margins, similar to those in *Pristiograptus*. *Silurian, Pridoli* (*Skalograptus lochkovensis* Biozone): Ukraine, Belarus, Poland.——FIG. 16,*2a–c*. *D. trimorphus* TSEGELNJUK, 1976; *2a,* specimen in ventral view; *2b,* sicula with first bud, showing presence of sicular annuli; *2c,* fragment showing style of thecal apertures (Urbanek, 1997a, pl. 14.A; text-fig. 42). Scale bars, 1 mm.

Formosograptus BOUČEK, MIHAJLOVIC, & VASELINOVIC, 1976, p. 84 [**Monograptus formosus* BOUČEK, 1931, p. 300; OD] [=*Tamplograptus* TSEGELNJUK, 1976, p. 114 (type, *Monograptus* (*?Spirograptus*) *convexus* PŘIBYL, 1940a, p. 73; OD), syn. by PŘIBYL, 1983, p. 150]. Dorsally curved tubarium; sicula straight or very gently ventrally curved, with dorsal process; proximal thecae non-overlapping, subtriangular with distinctly isolated apertural part; distal thecae overlap for approximately half their length with metathecae that are more adnate; thecal aperture overhung by laterally expanded lobe, with semitubular lateral processes terminating in auriculum. *Silurian, Ludlow* (*Ludfordian, Pseudomonoclimacis latilobus* Biozone)*–Pridoli* (*Neocolonograptus ultimus* Biozone): worldwide.——FIG. 16,*3a–c*. **F. formosus* (BOUČEK), Mielnik drill core, Poland; *3a,* proximal end showing shape of tubarium (adapted from Urbanek, 1997a, fig. 19B); *3b–c,* distal fragment showing increase of thecal overlap (Urbanek, 1997a, fig. 21). Scale bars, 1 mm.

Heisograptus TSEGELNJUK, 1976, p. 103 [**Pomatograptus micropoma* JAEKEL, 1889, p. 682; OD]. Tubarium straight or nearly so; sicula ventrally curved, with dorsal tongue; thecae with sharp geniculae and supragenicular walls that are parallel to tubarium axis; apertural excavations semi-circular or semi-elliptical; aperture may be overhung by hood of microfusellar tissue. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone*–Lobograptus scanicus* Biozone): worldwide.——FIG. 16,*4a–d*. **H. micropoma* (JAEKEL); *4a,* lectotype (selected by JAEGER, 1959, pl. 6,*7*), MB.G 470d, glacial boulder, Zölling bei Neusalz an der Oder, now Nowa Sól, Poland (Wilkinson, 2018a, Atlas 3.52); *4b–c,* juveniles in reverse (*4b*) and obverse (*4c*) views, showing presence of sicular annuli (Maletz, 1999, fig. 2C,E); *4d,* specimen showing apertural hoods (Jaeger, 1959, fig. 20D). Scale bars, 1 mm.

Neomonograptus MU & NI, 1975, p. 18 [**N. himalayensis;* OD; =*Monograptus atopus* BOUČEK, 1966, syn. by JAEGER 1983, p. 250]. Tubarium straight throughout or with dorsal curvature proximally; first theca robust and strongly hooked, concealing aperture; subsequent thecae with dorsal hoods above semi-circular or semi-elliptical apertures, these becoming much less pronounced in mesial and distal thecae; thecae are strongly geniculate throughout. *Lower Devonian* (*Lochkovian, Uncinatograptus uniformis* Biozone)*–Emsian*, *Uncinatograptus yukonensis* Biozone): worldwide.——FIG. 16,*5a–b*. *N. atopus* (BOUČEK), holotype, proximal end (*5a*) and distal thecae (*5b*), scale bars, 1 mm (Bouček, 1966, fig. 1C); *5c,* holotype of **N. himalayensis,* scale bar, 1 mm (Chen & others, 2021, fig. 5F).

Pristiograptus JAEKEL, 1889, p. 667 [**P. frequens;* OD]. Tubarium straight or gently dorsally or ventrally curved; thecal length increasing over first few thecae, later constant; sicula of medium length with low origin of th1; thecae straight, cylindrical, with straight or nearly straight ventral wall; thecal aperture without any supplementary structures except thickened apertural rim. *Silurian, Llandovery* (*Rhuddanian, Cystograptus vesiculosus* Biozone)*–Pridoli* (*Skalograptus perneri* Biozone): worldwide.——FIG. 16,*8a–d*. **P. frequens* (JAEKEL); *8a*, neotype, MB.G 458.3.1, selected by ŠTORCH, MANDA, & LOYDELL, 2014, p. 1016 (Jaeger, 1991, fig. 26.*9*); *8b–d, P. dubius* (SUESS, 1851), isolated specimens, glacial boulder, note the lack of sicular annuli (Maletz, 1999, fig. 2Q-S). Scale bars, 1 mm.

Proteograptus LENZ, SENIOR, KOZŁOWSKA, & MELCHIN, 2012, p. 26 [**Monograptus opimus* LENZ & MELCHIN, 1991, p. 230; OD]. Gently ventrally curved tubarium that widens rapidly proximally; sicula straight with dorsal tongue; thecae appear hooked in profile view, but this hook is formed from paired lateral lappets that may fuse centrally, particularly in proximal part of tubarium to produce a pseudohood, the dorsal side of which has a consistently present laterally ovate opening onto the protheca. *Silurian, Wenlock* (*Sheinwoodian*, *Proteograptus opimus–Cyrtograptus perneri* Biozone): Arctic Canada.——FIG. 16,*6a–d*. **P. opimus* (LENZ & MELCHIN), GSC 134694, Cape Phillips, Arctic Canada; *6a–b,* reverse (*6a*) and ventral (*6b*) views of colony showing thecal style, (Lenz & others, 2012, pl. 12,*1–2*); *6c,* change in thecal style over first four thecae (Lenz & others, 2012, pl. 12,*3*); *6d,* development of distal thecae (Lenz & others, 2012, pl. 12.*6*). Scale bars, 1 mm.

Pseudomonoclimacis MIKHAILOVA, 1975, p. 156 [**P. elegans*; OD]. Tubarium gently ventrally curved proximally and mesially, straight distally; sicula ventrally curved, with dorsal process; thecae moderately to strongly geniculate, generating a thecal excavation. *Silurian, Ludlow* (*Gorstian, Lobograptus progenitor* Biozone)–*Pridoli* (*Skalograptus perneri* Biozone): worldwide.——FIG. 16,*7a*. **P. elegans,* CNIGR 20/10290, holotype, scale bar, 1 mm (Mikhailova, 1975, pl. 38,*3*).——FIG. 16,*7b*. *P. dalejensis* (BOUČEK, 1936), specimen showing curvature of sicula, Všeradice section, Prague syncline, Czech Republic, scale bar, 1 mm (Štorch, Manda, & Loydell, 2014, fig. 6F).——FIG. 16,*7c–e*. *P. antiqua* ŠTORCH, MANDA, & LOYDELL, 2014; *7c*, slender specimen, Všeradice section, Prague syncline, Czech Republic (Štorch, Manda, & Loydell, 2014, fig. 6Q); *7d–e*. juvenile specimens in reverse (*7d*) and obverse (*7e*) view, glacial boulder, Bramsche, northern Germany (Maletz, 1999, fig. 2M–N; identified as *Heisograptus* sp.). Scale bars, 1 mm.

Saetograptus PŘIBYL, 1943, p. 11 [**Graptolithus chimaera*, BARRANDE, 1850, p. 52; OD]. Straight or dorsally curved tubarium; sicula with variably developed dorsal apertural tongue; tubular thecae terminated by paired apertural spines developed on all or only proximal thecae; aperture of first theca has broad, triangular, spine like lateral lappets; other thecal apertures have ventral notch and laterally to dorso-laterally situated spines separated by trough from ventral wall of next theca. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone–*Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide.——FIG. 16,*10a–b*. **S. chimaera* (BARRANDE); *10a,* holotype, NMP L19973 (new; drawing by P. Štorch, 2021); *10b,* chemically isolated specimen (Přibyl, 1943, fig. 1, redrawn from original illustration in Münch, 1938, pl. 5,*1a*). Scale bars, 1 mm.

Skalograptus TSEGELNJUK, 1976, p. 100 [**Skalograptus vetus;* OD; =*Monograptus ultimus* PERNER, 1899; KŘÍŽ & others, 1986, p. 322; KOREN' & SUJARKOVA 1997, p. 87] [=*Istrograptus* TSEGELNJUK, 1988, p. 85 (type species not selected; illustrated as *Is*(*tr*)*ograptus transgrediens* (PERNER, 1899) and *Istrograptus ultimus* (PERNER, 1899); =*Neocolonograptus* URBANEK, 1997a, p. 165 (type, *Monograptus lochkovensis* PŘIBYL, 1940a, Urbanek 1997a, p. 128, table 1, OD), syn. herein].Tubarium gently ventrally curved, gently dorso-ventrally curved or straight; sicula moderately to strongly ventrally curved; thecae with bilobate apertural elaborations, ranging from gentle undulations to strong lappets oriented antero-laterally; apertures of distal thecae may lack these elaborations; ventral walls of thecae sigmoidal or straight. *Silurian, Pridoli* (*Skalograptus parultimus* Biozone–*Skalograptus transgrediens* Biozone): worldwide.——FIG. 16,*9a–b*. *S. ultimus* (PERNER); *9a*, lectotype (selected by PŘIBYL, 1948, p. 77) Praha-Dvorce (formerly Dworetz), Czech Republic (Perner, 1899, fig. 14a); *9b,* chemically isolated specimen, Kosov Quarry, Czech Republic, *Skalograptus ultimus* Biozone, ~4 m above base of Pridoli (adapted from Kříž & others, 1986, fig. 36a). Scale bars, 1 mm.

Slovinograptus URBANEK, 1997a, p. 129 [**Monograptus balticus* TELLER, 1966, p. 556; OD; URBANEK, 1997a, p. 128; =*Monograptus kallimorphus* KRAATZ, 1958, p. 48, syn. by JAEGER 1978, p. 514]. Tubarium slender and dorsally curved proximally, straight distally; sicula ventrally curved; thecal apertures provided with globose hoods, adnate to the ventral wall; substantial thecal overlap, especially distally. *Silurian, Ludlow* (*Ludfordian, Pseudomonoclimacis latilobus/Slovinograptus balticus* Biozone)–*Lower Devonian* (*Lochkovian, Uncinatograptus uniformis* Biozone): worldwide.——FIG. 16,*11a–e*. *S. kallimorphus* (KRAATZ); *11a,* holotype of **Monograptus balticus* (Koren' & Suyarkova, 1997, fig. 9G); *11b–d, S. kallimorphus* (KRAATZ); *11b,* CGM 26/12879, Peshkaut Valley, southern Tien Shan (Koren' & Suyarkova, 1997, fig. 9A); *11c,* proximal end, KR 58d, Mollenberg, Harz Mountains, Germany (new); *11d,* distal fragment, KR 58A, Mollenberg, Harz Mountains (new). Scale bars, 1 mm.

Uncinatograptus TSEGELNJUK, 1976, p. 96 [**Monograptus uncinatus* TULLBERG, 1883, p. 30; OD] [=*Tirassograptus* TSEGELNJUK, 1976, p. 119 (type, *Monograptus* (*Pomatograptus*) *uncinatus* var. *uniformis* PŘIBYL, 1940a, p. 71; OD), syn. herein; =*Metamonograptus* WANG, 1977, p. 198 (type *Monograptus* (*Metamonograptus*) *qinzhouensis* WANG, 1977, p. 198; OD), syn. herein]. Tubarium straight or dorsally curved proximally and mesially, becoming straight distally; sicula straight or ventrally curved, aperture flaring with or without distal curving lappet; thecae with dorsal hoods, often best developed in proximal thecae but present throughout the tubarium; ventrolateral margin of aperture may be lobate and also spinose; thecal overlap increases distally. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone)–*Lower Devonian* (*Pragian, Uncinatograptus yukonensis* Biozone): worldwide.——*FIG. 16,12a–c. *U. uncinatus* (TULLBERG); *12a,* lectotype, selected by Přibyl, 1948, p. 35 (Tullberg, 1883, pl. 1,*25;*

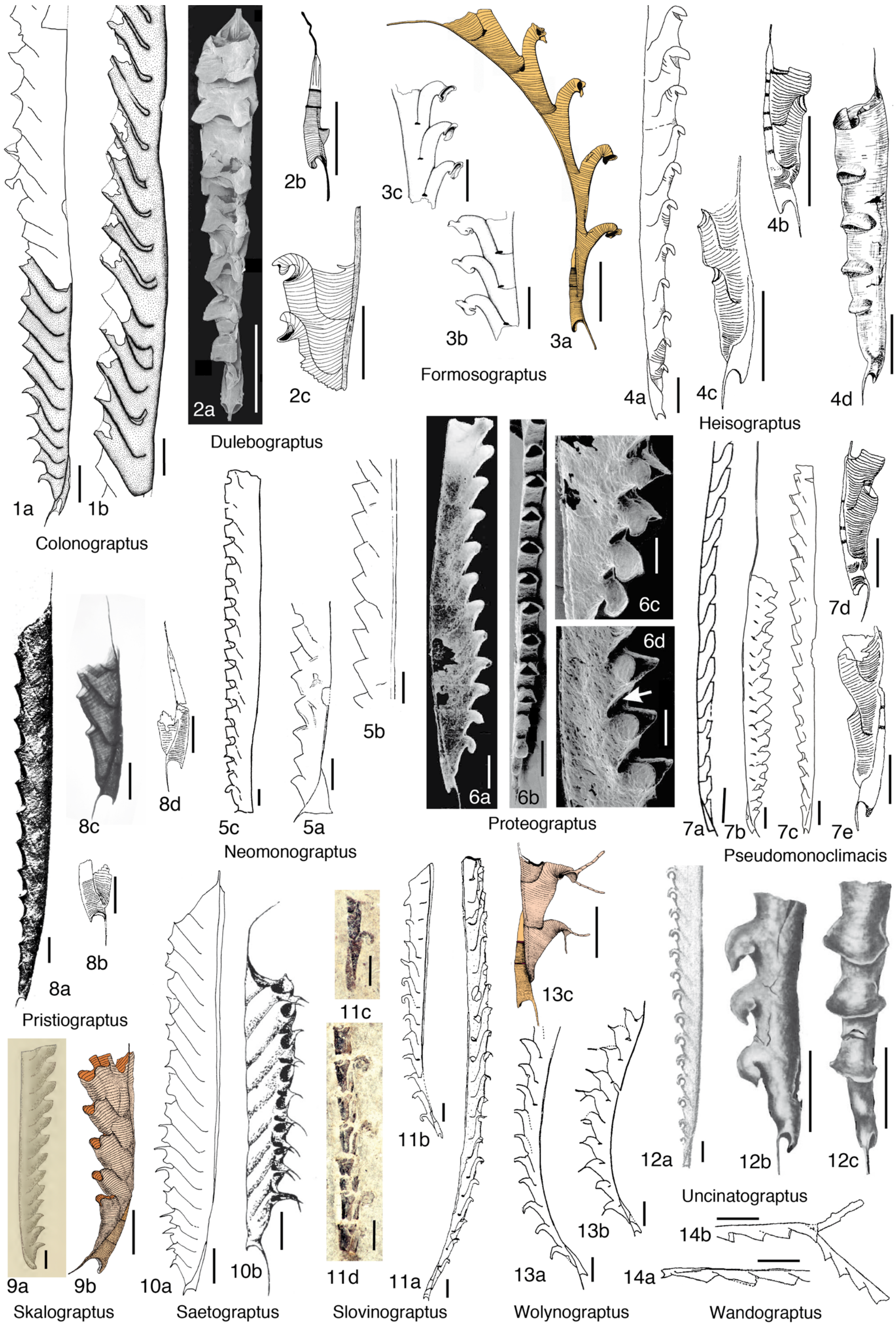

FIG. 16. Pristiograptinae (p. 25–28).

?LO collection, specimen not identified); *12b–c,* proximal end in lateral (*3b*) and ventral (*3c*) views (Urbanek, 1958, pl. 1,*3a–3b*). Scale bars, 1 mm.

Wandograptus Rickards & Jell, 2002, p. 118 [**W. wandovalensis;* OD]. *Pristograptus*-like tubarium but with more frequent and irregular curvature and development of thecal cladia. [The taxonomic position of the genus is uncertain. Rickards and Jell (2002) described it as related to *Pristiograptus,* but bearing cladia. The proximal end and thecae are very similar to those of early *Pristiograptus* and *Atavograptus*.] *Silurian, Llandovery* (*Telychian, Spirograptus turriculatus* Biozone–*Streptograptus crispus* Biozone): Australia (Queensland).——Fig. 16,*14a–b*. **W. wandovalensis,* fragments from the holotype slab, UQ 35968, Queensland, Australia; (Rickards & Jell, 2002, fig. 4I–J, L–M). Scale bars, 1 mm.

Wolynograptus Tsegelnjuk, 1976, p. 110 [**W. valleculosus;* OD) [=*Acanthograptus* Tsegelnjuk, 1976, p. 113 (type *A. spineus;* OD), syn. by Přibyl, 1983, p. 150, homonym of *Acanthograptus* Spencer, 1878 [Dendroidea]); =*Bugograptus* Tsegelnjuk, 1998, p. 272 (type, *A. spineus* Tsegelnjuk, 1976, OD), syn. herein]. Tubarium dorsally curved proximally and mesially, becoming straight distally; sicula straight or ventrally curved, bearing two annuli; thecae with extensive dorsal hoods; anterolateral margin of aperture may be lobate and also spinose; thecal overlap increases distally. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone–*Ludfordian, Wolynograptus spineus* Biozone): worldwide.——Fig. 16,*13a*. *W. aculeatus* Tsegelnjuk, 1976, proximal end, scale bar, 1 mm (Koren' & Suyarkova, 1997, fig. 8A).——Fig. 16,*13b–c*. *W. spineus* Tsegelnjuk, 1976; *13b*, proximal end (Koren' & Suyarkova, 1997, fig. 14H); *13c*, proximal end (Urbanek, 1995, fig. 1D). Scale bars, 1 mm.

Subfamily LINOGRAPTINAE Obut, 1957

[Subfamily Linograptinae Obut, 1957, p. 18; *nom. transl.* Teller, 1962, p. 153, *ex* Linograptidae Obut, 1957, p. 18] [=Cucullograptinae Urbanek, 1958, p. 62; herein; =Neocucullograptinae Urbanek, 1970, p. 265; herein; =Neolobograptinae Tsegelnjuk, 1976, p. 120; herein]

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

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

MORPHOLOGY

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

The thecal apertures vary from simple (Fig. 17.3) to complex, often including a considerable asymmetry of the two lateral lobes (Fig. 17.12–17.17), but lacking torsion of the metathecae. The complex thecal apertures are formed either from normal fusellar development (Fig. 17.12–17.13) or from microfusellar additions (Fig. 17.16–17.17). The simple thecal apertures have a straight aperture, inclined to the ventral side of the tubarium. Lateral lobes are barely recognizable in some taxa (Fig. 17.6–17.8) but may be quite extensive in others. They may have

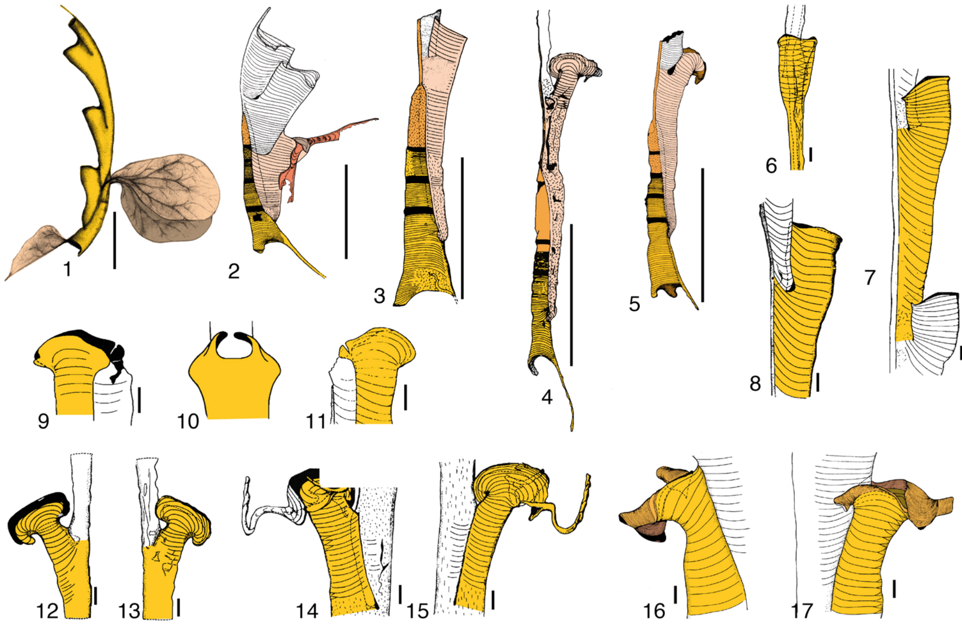

FIG. 17. Thecal morphology of the Linograptinae. *1, Bohemograptus papilio* KOZŁOWSKA & URBANEK, 2013, reconstruction showing patagia (Kozłowska & Urbanek, 2013, fig. 5); *2, Bohemograptus cornutus* URBANEK, 1970 with partly preserved lateral apertural processes (Urbanek, 1970, pl. 25); *3, 8, Lobograptus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

strong lateral extensions and may be curved or coiled.

Bohemograptus cornutus (URBANEK, 1970) shows an extreme development of lateral additions in the form of paired spatulate extensions formed from fusellar material (Fig. 17.2), and membranes with an internal branching system of rods have been documented in *Bohemograptus papilio* KOZŁOWSKA & URBANEK, 2013 (Fig. 17.1). A characteristic virgellarium ending with four finger-like extensions can be found in *Linograptus* and probably in *Abiesgraptus* (URBANEK, 1997b).

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

Bohemograptus PŘIBYL, 1967a, p. 134 [**Graptolithus bohemicus* BARRANDE, 1850, p. 40; OD] [=*Pterograptus* TSEGELNJUK, 1976, p. 131 (type, *F. torsivus,* OD), syn. by Loydell, herein]. Tubarium ventrally curved; thecae tubular, with straight or gently elevated lateral apertural margins, either devoid of or provided with microfusellar additions forming broadly lobate, annular or tape-like apertural structures. *Silurian, Wenlock* (*Homerian, Colonograptus ludensis* Biozone)–*Ludlow* (*Ludfordian, Neocucullograptus kozlowskii* Biozone): worldwide.——FIG. 18,*1a–c*. **B. bohemicus* (BARRANDE, 1850); *1a–b,* NMP L17762, lectotype (Přibyl, 1948, p. 68) and associated specimen with sicula (Štorch, 2000c, Atlas 1.9); *1c,* proximal end with sicular annuli, Mielnik drill core, 957.90 m, Poland (Urbanek, 1970, fig. 10B). Scale bars, 1 mm.

Crinitograptus Rickards, 1995, p. 1107 [**Monograptus crinitus* Wood, 1900, p. 480; OD]. Slender tubarium, straight or irregularly flexed; short sicula with annuli; simple tubular thecae, parallel to or inclined to tubarium axis at less than 10°; thecae increasing in lateral width toward aperture; only slight thecal overlap; thecal aperture simple, with overhanging hood formed by extension of dorsal wall of theca. *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone)–*Pridoli* (*Neocolonograptus parultimus* Biozone): UK, Germany (erratics), Bulgaria, Arctic Canada, Australia, Russia.——Fig. 18,*2a–c*. **C. crinitus* (Wood), Long Mountain, Shropshire, UK; *2a,* BU 1615, part of holotype (Rickards, 1995, fig. 4.*1*); *2b,* BU 1618, syntype, proximal end showing sicular annuli (Rickards, 1995, fig. 1). *2c*, BU 1616, bipolar fragment (Rickards, 1995, fig. 4,*3*). Scale bars, 1 mm.

Cucullograptus Urbanek, 1954, p. 291 [**C. pazdroi;* OD]. Narrow, straight, or gently ventrally curved tubarium; small sicula; first theca originates via a primary porus; thecae long, with elongate protheca and short metatheca; thecal aperture slit-like, with complex auriculate lateral apertural lobes, with increasing asymmetry distally; the left apertural lobe overlaps right lobe, restricting thecal aperture. *Silurian*, *Ludlow* (*Gorstian, Lobograptus parascanicus* Biozone–*Ludfordian, Cucullograptus rostratus/lower Bohemograptus tenuis* Biozone): Poland, Czech Republic, Germany, China (Yunnan).——Fig. 18,*3a–c*. **C. pazdroi; 3a–c,* three different views of holotype, glacial boulder, Gdansk-Wrzeszcz, Poland (Urbanek, 1954, fig. 2). Scale bars, 1 mm.

Egregiograptus Rickards & Wright, 1997b, p. 222 [*'*Monograptus*' *egregius* Urbanek, 1970, p. 367; OD]. Tubarium strongly ventrally curved, almost circular; short sicula (usually less than 1.5 mm long); thecae adnate, tubular; proximal thecae extremely elongated and inclined at a very low angle to the tubarium axis; distal thecae with considerable overlap; thecal apertures straight or with paired lateral lobes. *Silurian, Ludlow* (*Gorstian, Lobograptus scanicus* Biozone–*Ludfordian, Saetograptus chimaera–Neocucullograptus kozlowskii* Biozone): Poland, Czech Republic, Kyrgyzstan, Canada (Yukon), Australia.——Fig. 18,*4a–c*. **E. egregius; 4a,* holotype (Urbanek, 1970, pl. 43D1); *4b,* proximal end showing sicular annuli (Urbanek, 1970, p. 42A); *4c,* proximal end, th1 reconstructed (Urbanek, 1970, pl. 42F). Scale bars, 1 mm.——Fig. 18,*4d. E. dimitrii* (Koren' & Suyarkova, 2004), CNIGR 13107/63, holotype, Tien Shan, Kyrgyzstan, scale bar, 1 mm.

Enigmagraptus Rickards & Wright, 2004, p. 192 [**Neocucullograptus*? *yassensis* Rickards & Wright, 1999a, p. 200; OD]. Very slender tubarium (up to 0.25 mm wide), straight or irregularly flexed; small sicula with virgella and dorsal apertural process; axially elongate prothecae usually developed from threadlike origin; metatheca up to half tubarium width comprising hood derived by retroversion of the dorsal metathecal wall, and variously enrolled ventrally to enclose simple ventral thecal margin. *Silurian* (*Pridoli, Neocolonograptus parultimus* Biozone): Australia (New South Wales).——Fig. 18,*5a–b*. **E. yassensis; 5a,* AMF 92343, holotype, proximal end; *5b,* AMF 92346, stipe fragment (Rickards & Wright, 2004, fig. 4B–C). Scale bars, 1 mm.

Korenea Rickards, Packham, Wright, & Williamson, 1995, p. 54 [**K. sherwini;* OD]. Tubarium ventrally curved, hook-shaped; sicula small; uniform overlapping tubular thecae with strongly developed paired symmetrical lateral apertural lappets resembling retroverted hooks in profile. *Silurian* (*Ludlow*): Australia.——Fig. 18,*6a–b*. **K. sherwini,* New South Wales, Australia; *6a*, holotype, AMF 89624 (Rickards & others, 1995, fig. 33B); *6b*, thecal detail (Rickards & others, 1995, fig. 38E). Scale bars, 1 mm.

Lobograptus Urbanek, 1958, p. 12 [**Monograptus scanicus* Tullberg, 1883, p. 26; OD] [=*Falcatograptus* Hundt, 1965, p. 48 (type *F. rarus,* M), syn. herein]. Narrow, straight, dorso-ventrally or gently ventrally curved tubarium, widening distally; thecae long, with elongate protheca and increasing distal overlap; thecal aperture with asymmetrical or symmetrical lateral lobes that may curve over central part of aperture. *Silurian, Wenlock* (*Homerian, Colonograptus praedeubeli* Biozone)–*Ludlow* (*Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide.——Fig. 18,*7a–b*. **L. scanicus* (Tullberg), *7a,* syntype, specimen not identified (Tullberg, 1883, pl. 2.*42*); *7b,* proximal end (Urbanek, 1966, fig. 11). Scale bars, 1 mm.

Neocucullograptus Urbanek, 1970, p. 329 [**N. kozlowskii;* OD]. Tubarium strongly ventrally curved proximally, less strongly curved or nearly straight distally; sicula with dorsal apertural process and late astogenetic paired symmetrical lobes of microfusellar tissue situated on reverse and obverse apertural margins; first theca originates via a primary porus; complex metathecae, consisting of smaller right and larger left lobe, sometimes provided with gular, rostral, and lateral processes. *Silurian, Ludlow* (*Ludfordian, Neocucullograptus inexpectatus* Biozone–*Neocucullograptus kozlowskii* Biozone): Poland, Czech Republic, Kyrgyzstan, Kazakhstan.——Fig. 18,*8a–d*. *N. kozlowskii,* Mielnik drill core, Poland; *8a–b,* holotype in lateral (*8a*) and ventral (*8b*) views (Urbanek, 1970, fig. 20A); *8c*, distal theca (Urbanek, 1970, pl. 38A); *8d,* reconstruction (Urbanek, 1970, pl. 7C). Scale bars, 1 mm.

Neolobograptus Urbanek, 1970, p. 321 [**N. auriculatus;* OD]. Ventrally curved tubarium; straight sicula with prominent dorsal process; thecae slender and elongate; thecal apertures with lateral elevations and dorso-lateral incisions. *Silurian, Ludlow* (*Ludfordian, Saetograptus leintwardinensis* Biozone–*Neocucullograptus inexpectatus* Biozone): Poland, Kyrgyzstan.——Fig. 18,*9a–b*. **N. auriculatus,* Mielnik drill core, Poland; *9a,* holotype, sicula with incomplete first theca (Urbanek, 1970, pl. 29B); *9b,*

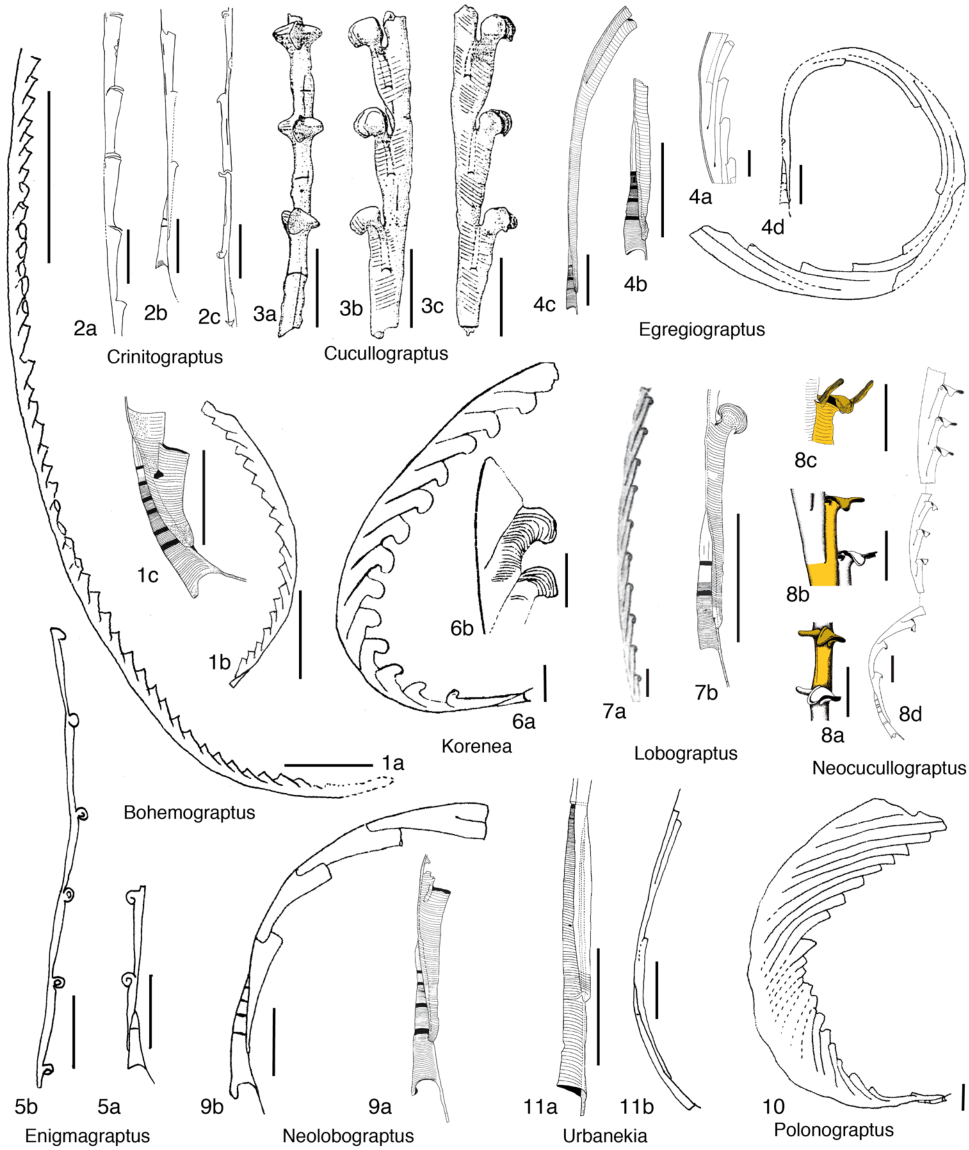

Fig. 18. Linograptinae (p. 29–31).

reconstruction (Rickards & Wright, 1999b, fig. 3F, based on Urbanek, 1970, pl. 7A). Scale bars, 1 mm.

Polonograptus Tsegelnjuk, 1976, p. 124 [**P. podoliensis* Přibyl, 1983, p. 158; SD ICZN 2003; Riva, Koren', & Rickards (2001) applied to the ICZN to change the type species from *Monograptus butovicensis* Bouček, 1936 to *Polonograptus podoliensis*, approved as Opinion 2023 (ICZN, 2003)]. Tubarium ventrally curved with proximally accentuated curvature; sicula small and straight; thecae subsequent to the short first theca exhibit considerable elongation and overlap; all thecae are simple tubes; apertures have lateral elevations. *Silurian, Ludlow* (*Ludfordian*, *Neocucullograptus inexpectatus* Biozone–*Neocucullograptus kozlowskii* Biozone): Czech Republic, Austria, Australia, Kyrgyzstan.——Fig. 18,*10*. **P. podoliensis,* CNIGR 13107/104, southern Tien Shan, Kyrgyzstan (Koren' & Sujarkova, 2004, fig. 28B). Scale bar, 1 mm.

Urbanekia Rickards & Wright, 1999b, p. 319 [*'*Monograptus*' *proegregius* Urbanek, 1970, p. 364;

OD]. Tubarium known from fragments only, but appears narrow (less than 0.3 mm) and ventrally curved; sicula elongated (more than 3 mm long) and ventrally curved; sicular aperture lacks dorsal process; thecae very long (at least 7 mm), narrow and tubular, with ventral walls subparallel to the tubarium axis; thecal apertures simple, perpendicular to thecal axis and with slight lateral elevations. *Silurian, Ludlow* (*Gorstian, Lobograptus parascanicus* Biozone): Poland.——FIG. 18,*11a–b*. **U. proegregius* (URBANEK); *11a,* paratype, sicula with part of first theca (Urbanek, 1970, pl. 41.*C*); *11b,* reconstruction (Rickards & Wright, 1999b, fig. 2L). Scale bar, 1 mm.

CLADIA-BEARING LINOGRAPTINAE

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

Abiesgraptus HUNDT, 1935, p. 3 [**A. multiramosus;* SD BULMAN, 1938, p. 84] [=*Didymograptoides* HUNDT, 1953, p. 40 (type, *D. liebei,* M), syn. herein; =*Gangliograptus* HUNDT, 1939, p. 119 (type, *G. hoppeianus,* SD MÜLLER, 1969, p. 919), syn. herein]. Tubarium complex, comprising the main stipe and three sicular cladia; the main stipe and central sicular cladium bear paired thecal cladia; thecae simple, without apertural modifications. *Lower Devonian* (*Lochkovian, Uncinatograptus uniformis* Biozone–*Pragian, Uncinatograptus fanicus* Biozone): worldwide.——FIG. 19,*1a–b.* **A. multiramosus* HUNDT, *1a*, lectotype, selected by Müller, 1965, p. 5, BAF 73/H4151, Ramstal bei Creunitz, Thuringia, Germany (Müller, 1965, fig. 1); *1b*, reconstruction, scale bars, 10 mm (Jaeger, 1959, fig. 25).

Lenzograptus LOYDELL, 2021, p. 205 [**Lenzia lenzi* RICKARDS & WRIGHT, 1999b, p. 319; OD] [*pro Lenzia* RICKARDS & WRIGHT, 1999b; homonym of *Lenzia* PERRY, BOUCOT, & GABRIELSE 1981 (Devonian brachiopod)]. Cladia-bearing linograptid, with tubarium largely ventrally curved but twisting around its axis; thecae simple or with slight lateral apertural lobes, generating cladia every one or two thecae, directed to the dorsal side of main stipe. *Silurian* (*Ludlow*): Canada (Yukon).——FIG. 19,*2*. **L. lenzi,* holotype, UWO 2664, Richardson Mountains, Yukon, Canada, scale bar, 5 mm (Lenz, 1984, fig. 1a).

Linograptus FRECH, 1897, p. 662 [**Dicranograptus posthumus* RICHTER, 1875, p. 267; OD; =*Linograptus nilssoni* FRECH, 1897, p. 662; JAEGER, 1959, p. 143] [=*Thuringiograptus* HUNDT, 1939, p. 121 (type, *T. voigtii,* M), syn. herein]. Tubarium with narrow stipes comprising main stipe and, late in astogeny, several sicular cladia; main stipe and sicular cladia may be straight or more usually gently ventrally curved; virgella with virgellarium, a terminal four-pronged membranous structure; sicula with a long dorsal apertural spine which forms secondary nema for first sicular cladium; further cladia develop from reverse and obverse margins of the sicula; first theca of main stipe originates close to boundary of prosicula and metasicula; thecae simple tubes, apertures with lateral elevations which are more pronounced in distal thecae, which may be somewhat introverted. *Silurian, Ludlow* (*Ludfordian, Bohemograptus tenuis* Biozone)–*Lower Devonian* (*Lochkovian, Uncinatograptus hercynicus* Biozone): worldwide.——FIG. 19,*3a–c.* **L. posthumus; 3a,* lectotype, BGR 10370 (Richter, 1875, pl. 8.*3*); *3b,* specimen from Herzogswalde bei Silberberg, Schlesien (Frech, 1897, pl. A7); *3c,* isolated proximal end with virgellarium and one sicular cladium (adapted from Urbanek, 1997a, fig. 5D). Scale bars, 1 mm.

Neodiversograptus URBANEK, 1963, p. 149 [**Monograptus nilssoni* LAPWORTH, 1876a, p. 315; *sensu* URBANEK, 1954, p. 300; OD]. Proximally gently dorsally curved monograptid stipe, distally straight or dorso-ventrally curved, forming bipolar tubarium in mature specimens; sicula with long dorsal apertural spine, with its further prolongation producing secondary nema for sicular cladium; thecae tubular, with apertures either straight or with slightly elevated margins; ventral thecal wall at low angle to tubarium axis. [The problems of the identification of *N. nilssoni* were discussed in PALMER (1971a, 1971b) and STRACHAN (1973).] *Silurian, Ludlow* (*Gorstian, Neodiversograptus nilssoni* Biozone–*Ludfordian, Saetograptus leintwardinensis* Biozone): worldwide (although only questionably from Arctic Canada).——FIG. 19,*4a–c.* **N. nilssoni* (LAPWORTH); *4a,* neotype (PALMER 1971b, p. 97), Long Mountain Shales, Welsh Borderlands, UK (Wilkinson, 2018b, Atlas 3.58); *4b–c,* proximal ends without (*4b*) and with (*4c*) sicular cladium, Silurian, Ludlow, Poland (Urbanek, 1997b, fig. 2A–B). Scale bars, 1 mm.

Prolinograptus RICKARDS & WRIGHT, 1997b, p. 225 [**P. packhami;* OD]. Very slender tubarium with numerous sicular cladia; stipes straight or gently ventrally curved; sicula small; sicular cladia with secondary nemata; thecae with simple everted apertures. *Silurian, Ludlow* (*Gorstian, Neodiversograptus*

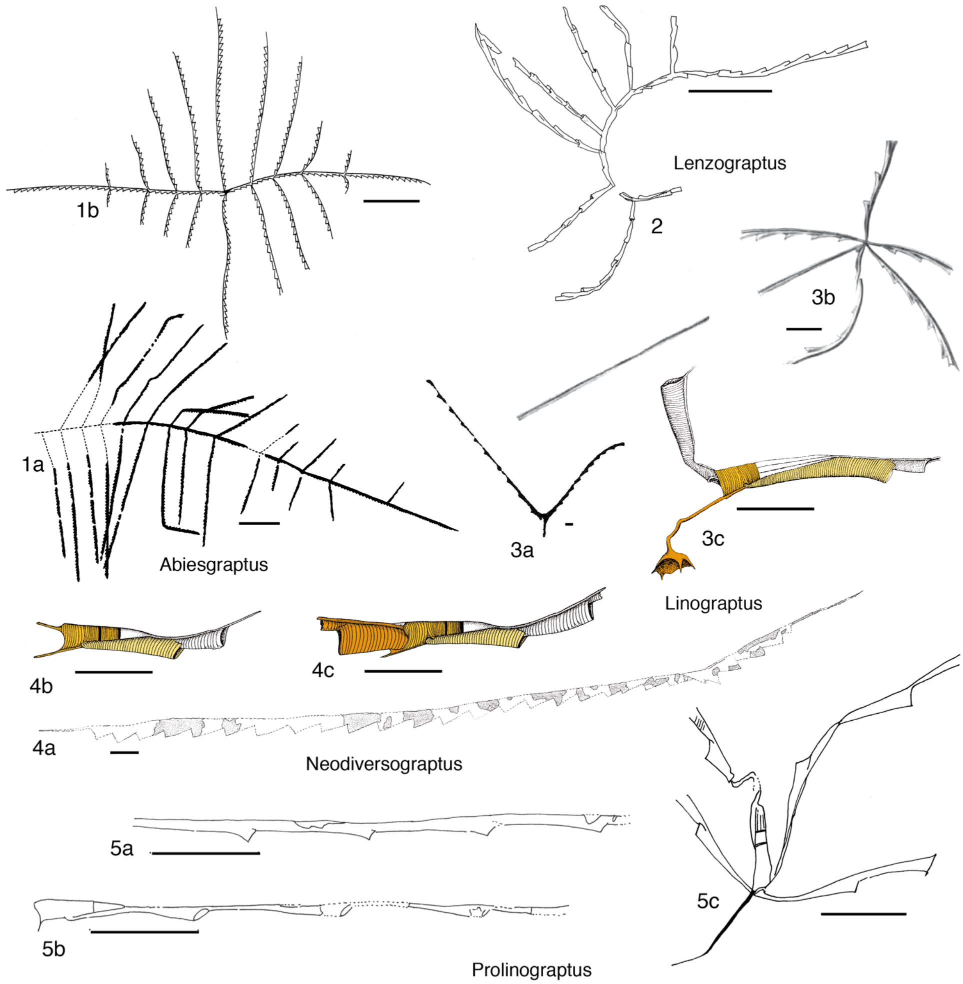

FIG. 19. Linograptinae (cladia-bearing) (p. 32).

nilssoni Biozone–*Ludfordian, Neocucullograptus inexpectatus/kozlowskii* Biozone): Australia, Poland, Arctic Canada.——FIG. 19,*5a–b*. **P. packhami; 5a,* AMF 81773a, distal thecae of holotype (Rickards & Wright, 1997b, fig. 9L); *5b,* AMF 91956b, proximal end with sicula (Rickards & Wright, 1997b, fig. 9K). Scale bars, 1 mm.——FIG. 19,*5c*. *P. orangensis* (RICKARDS & others,1995); AMF 81650, holotype (Rickards & others, 1995, fig. 35d). Scale bar, 1 mm.

ABBREVIATION FOR MUSEUM REPOSITORIES

AMF: Australian Museum, Sydney, Australia
BAF: Palaeontological collection, Department of Geology, TU Bergakademie Freiberg, Germany
BB: Bedřich Bouček collection, Czech Geological Survey, Prague, Czech Republic.
BELUM: Ulster Museum, Belfast, Northern Ireland
BGR: Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin, Germany.
BGS: British Geological Survey, Keyworth, UK
BU: Lapworth Museum, University of Birmingham, UK
CGM: Central Geological Museum named after F. N. Tchernyshev, St. Petersburg, Russia
CNIGR: A. P. Karpinsky All-Union Geological Research Institute (VSEGEI), St. Petersburg, Russia
GSC: Geological Survey of Canada, Ottawa, Canada
GSM: Geological Survey Museum, London, UK
KR: TU Clausthal, Institut für Geologie und Paläontologie, Clausthal-Zellerfeld, Germany
LO: Lunds Originale, Department of Geology, Lund University, Sweden
MB.G: Museum für Naturkunde, Berlin, Germany
MGM: Museo Geominero, Spanish Geological Survey (IGME), Madrid, Spain

MGUH: Geological Museum of the University of Copenhagen, Denmark
MMH: Mineralogical and Geological Museum of the University of Copenhagen, Denmark
NHMUK: The Natural History Museum, London, UK (formerly BMNH)
NIGP: Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China
NMW: National Museum of Wales, Cardiff, UK
NMP L: National Museum, Prague, Czech Republic
NRM: Naturhistoriska Riksmuseet Stockholm, Sweden
PŠ: Petr Štorch collection, Czech Geological Survey, Prague, Czech Republic
SGU: Sveriges Geologiska Undersökning, Uppsala, Sweden
SM: Sedgwick Museum of Earth Sciences, Cambridge, UK
SMF: Naturmuseum Senckenberg, Frankfurt am Main, Germany
UQ: Queensland Museum, South Brisbane, Queensland, Australia
UWO: University of Western Ontario, London, Ontario, Canada

REFERENCES

Averianow, B. N. 1929. Graptoloidea der obersilurischen Schiefer aus Ost-Turkestan. Izvestiia, Bulletins du Comité Géologique 48:101–124, pl. 34–35. [Spelled Averyanov in Sennikov & others, 2008.]

Averianow, B. N. 1931. Graptoloidea from the shales of the Ura-Tuibe region and the Zeravshan Valley, Turkestan. Transactions of the Geological and Prospecting Service of the USSR 101*:*1–29, 5 pl.

Baily, W. H. 1862. Graptolites from Co. Meath. Journal of the Geological Society of Dublin 9:300–306.

Baily, W. H. 1871 Palaeontological remarks. *In* W. A. Traill & F. W. Egan, eds., Explanatory memoir to accompany Sheets 49, 50 and part of 61 of the maps of the Geological Survey of Ireland including the country around Downpatrick, and the shores of Dundrum Bay and Strangford Lough, County of Down. Alexander Thom. Dublin & London. p. 22–23.

Barrande, Joachim. 1850. Graptolites de Bohême. Théophile Haase Fils. Prague. 74 p., 4 pl. Published by the author.

Bassler, R. S. 1915. Bibliographic index of American Ordovician and Silurian fossils, volume 2. United States National Museum Bulletin 92:719–1521.

Bjerreskov, Merete. 1975. Llandoverian and Wenlockian graptolites from Bornholm. Fossils and Strata 8:1–93.

Bouček, Bedřich. 1931. Předběžná zpráva o některých nových druzích graptolitů z českého Gotlandienu [Communication préliminaire sur quelques nouvelles speèces de graptolites provenant du Gothlandien de la Bohême]. Věstník státního geologicického ústavu Československé republiky 7:293–306, 307–313; French text. Reprint with different pagination also available.

Bouček, Bedřich. 1932. Předběžná zpráva o některých nových druzích graptolitů z českého Gotlandienu (Část II.) [Preliminary report on some new species of graptolites from the Gothlandian of Bohemia]. Věstník státního geologicického ústavu Československé republiky 8:150–155. Reprint with different pagination. p. 1–5.

Bouček, Bedřich. 1933. Monographie der obersilurischen Graptolithen aus der Familie Cyrtograptidae. Práce geologicko-paleontologického ústavu Karlovy university v Praze 1*:*1–84, 7 pl.

Bouček, Bedřich. 1936. Graptolitová fauna českého spodního ludlowu. Rozpravy II, Třidy České Akademie 46 (16):1–26, 2 pl.

Bouček, Bedřich. 1966. Eine neue und bisher jüngste Graptolithen-Fauna aus dem böhmischen Devon. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1966:161–168.

Bouček, Bedřich, & Alois Přibyl. 1943. Über böhmische Monograpten aus der Untergattung *Streptograptus* Yin. Mitteilungen der Tschechischen Akademie der Wissenschaften 43:1–23.

Bouček, Bedřich, & Alois Přibyl. 1951. On some slender species of the genus *Monograptus* Geinitz, especially of the subgenera *Mediograptus* and *Globosograptus*. Bulletin International de l'Académie Tcheque des Sciences 52:1–32.

Bouček, Bedřich, & Alois Přibyl. 1952. Contribution to our knowledge of the cyrtograptids from the Silurian of Bohemia and on their stratigraphical importance. Rozpravy České akademie Věd, Řada matematicko-přírodovědných Věd 62(9):1–24.

Bouček, Bedřich, & Alois Přibyl, 1953. On the genus *Diversograptus* Manck from the Silurian of Bohemia. Sborník Ústředního ústavu geologického, oddil paleontologicky 20:485–576, 3 pl.

Bouček, Bedřich, Milena Mihajlovic, & Miroslav Veselinovic. 1976. Graptolites of Upper Silurian and Lower Devonian of Zvonačka Banja (Eastern Yugoslavia). Classe de l'Académie serbe des sciences et des arts, Classe des sciences mathematiques et naturelles 39:79–114.

Bronn, H. G. 1835. Lethaea Geognostica, Erster Band, das Übergangs-, bis Oolithen-Gebirge enthaltend. Schweizerbart. Stuttgart. 768 p.

Bulman, O. M. B. 1929. The Genotypes of the Genera of Graptolites. Annals and Magazine of Natural History 4(20):169–185.

Bulman, O. M. B. 1932. On the graptolites prepared by Holm 2-5. Arkiv för Zoologi 24A(9):1–29.

Bulman, O. M. B. 1938. Graptolithina. *In* O. H. Schindewolf, ed., Handbuch der Paläozoologie, Vol. 2D. Borntraeger. Berlin. 92 p.

Bulman, O. M. B. 1955. Graptolithina. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part V. Geological Society of America & University of Kansas Press. New York & Lawrence. xvii + 101 p.

Bulman, O. M. B. 1970. Graptolithina. *In* Curt Teichert, ed., Treatise on Invertebrate Paleontology, Part V, Second Edition. Geological Society of America and University of Kansas Press. New York & Lawrence. xxxii + 163 p.

Bulman, O. M. B., & R. B. Rickards. 1970. Addendum. Classification of the graptolite family Monograptidae Lapworth, 1873. *In* Curt Teichert, ed., Treatise on Invertebrate Paleontology, Part V, Second Edition. Geological Society of America and University of Kansas Press, New York & Lawrence. xxxii + 163 p.

Carruthers, William. 1867a. On Graptolites. Appendix D. *In* R. I. Murchison, Siluria. 4th Edition. John Murray. London. p. 538–541.

Carruthers, William. 1867b. Graptolites: their structure and systematic position. Part II. Intellectual Observer 11(4):64, 365–374, pl. 2.

Chen, Qing, Xu Chen, Linna Zhang, & L. A. Muir. 2021. A restudy of Early Devonian graptolites from the Himalayan Mountains, southern Xizang, China. Geological Journal 2021:1–16 [doi: 10.1002/gj.4246].

Chen, Xu, & Yaokun Lin. 1978. Lower Silurian graptolites from Tongzi, northern Guizhou. Memoir of the Nanjing Institute of Geology and Palaeontology, Academia Sinica 12:1–106, 19 pl. In Chinese, English summary.

Chopey-Jones, Anna, Mark Williams, & Jan Zalasiewicz. 2003. Biostratigraphy, palaeobiogeography and morphology of the Llandovery (Silurian) graptolites *Campograptus lobiferus* (M'Coy) and *Campograptus harpago* (Törnquist). Scottish Journal of Geology 39:71–85.

Dana, J. D. 1851. On the classification of the Crustacea Grapsoidea. The American Journal of Science and Arts 12:283–290.

Dawson, D. H., & M. J. Melchin. 2007. A possible transitional stage between the resorption porus and the primary porus in early monograptid graptolites. Acta Palaeontologica Sinica 46 (Suppl.):89–94.

Deng, Bao. 1986. On the morphological characteristics of the *spiralis* group and the stratigraphic significance of the appearance of *Cyrtograptus*. Geological Society Special Publication 20:191–195.

Eisel, Robert. 1912. Über zonenweise Entwicklung der Rastriten und Demirastriten. 53./54.Jahresbericht der Gesellschaft von Freunden der Naturwissenschaften Gera. p. 27–43, 3 pl. [different pagination in reprint, p. 1–17, 3 pl.]

Eisenack, Alfred. 1942. Über einige Funde von Graptolithen aus ostpreußischen Silurgeschieben. Zeitschrift für Geschiebeforschung und Flachlandsgeologie 18:29–42.

Elles, G. L. 1900. The zonal classification of the Wenlock shales of the Welsh Borderland. Quarterly Journal of the Geological Society of London 56: 370–414.

Elles, G. L., & E. M. R. Wood. 1913. British graptolites, Part 9. Monograph of the Palaeontographical Society London 66(323):415–486, pl. 42–49.

Finney, S. C. 1985. Nemagraptid graptolites from the Middle Ordovician Athens Shale, Alabama. Journal of Paleontology 59:1100–1137.

Frech, Fritz. 1897. Lethaea Geognostica oder Beschreibung und Abbildung für die Gebirgs-Formationen bezeichnendsten Versteinerungen, Herausgegeben von einer Vereinigung von Palaeontologen, 1. Theil, Lethaea Palaeozoica. E. Schweizerbart'sche Verlagshandlung. Stuttgart. p. 544–684.

Fu, Lipu. 1994. Four evolutionary lineages of cyrtograptids from late Llandovery to early Wenlock. *In* Xu Chen, B.-D. Erdtmann, & Yunan Ni, eds., Graptolite Research Today. Nanjing University Press. Nanjing. p. 256–262.

Geinitz, H. B. 1842. Über Graptolithen. Neues Jahrbuch Mineralogie, Geognosie, Geologie und Petrefakten-Kunde, Jahrgang 1842:697–701, pl. 10.

Geinitz, H. B. 1852. Die Versteinerungen der Grauwackenformation in Sachsen und den angrenzenden Länder-Abtheilungen. Heft 1. Die Silurische Formation. Die Graptolithen, ein monographischer Versuch zur Beurtheilung der Grauwackenformation in Sachsen und den angrenzenden Länderabtheilungen sowie der Silurischen Formation überhaupt. Verlag von Wilhelm Engelmann. Leipzig. 58 p., 6 pl.

Golikov, A. N. 1969. Novyye rannevenlokskiye graptolity semeystva Cyrtograptidae na yugo-zapade Tyan'-Shanya. Paleontologicheskiy Zhurnal 4:64–75. [English translation: Golikov, A. N. 1969. New early Wenlockian graptolites of the family Cyrtograptidae from southwestern Tien Shan. Paleontological Journal 3(4):506–519.]

Gürich, Georg. 1908. Leitfossilien. Ein Hilfsbuch zum Bestimmen von Versteinerungen bei geologischen Arbeiten in der Sammlung und im Felde. Erste Lieferung: Kambrium und Silur. (Bogen 1–6, Tafel 1–28 nebst Erklärungen). Verlag Gebrüder Bornträger, Berlin. p. 1–95, pl. 1–28.

Harkness, Robert. 1851. Description of the graptolites found in the Black Shales of Dumfriesshire. Quarterly Journal of the Geological Society of London 7:58–65, pl. 1.

Hisinger, Wilhelm. 1837. Lethaea Suecica seu Petrifacta Suecica. Supplementum 1. D. A. Norstedt et filii, Stockholm. p. 1–124.

Hopkinson, John. 1869. On British graptolites. Journal of the Quekett Microscopical Club 1:151–166, pl. 8.

Hopkinson, John, & Charles Lapworth. 1875. Descriptions of the graptolites of the Arenig and Llandeilo rocks of St. David`s. Quarterly Journal of the Geological Society of London 31:631–672, pl. 33–37.

Hundt, Rudolf. 1935. Die Graptolithenfauna des obersten Obersilurs Thüringens (mit einem Beitrag über Graptolithen in Roteisensteinknollen). Zeitschrift für Naturwissenschaften 91(1):1–34.

Hundt, Rudolf. 1939. Das mitteldeutsche Graptolithenmeer. Martin Bornträger-Verlag, Halle. Saale. 395 p.

Hundt, Rudolf. 1943. Bau und Leben der Graptolithen. Beiträge zur Geologie von Thüringen 6:260-269.

Hundt, Rudolf. 1949a. 2. Neue Graptolithenfunde aus dem Gotlandium Osthüringens.. *In* Hundt, Rudolf, ed., Zur Erforschung des Silurs Ostthüringens. Thüringer Volksverlag, Weimar, Zweigniederlassung Gera, Geologischer Verein von Gera und Umgebung. 48 p. p. 18–23.

Hundt, Rudolf. 1949b. Die Welt der Graptolithen. Prisma: Illustrierte Monatsschrift für Natur, Forschung und Technik 4(7):327–333.

Hundt, Rudolf. 1953. Graptolithen. Neue Erkenntnisse über die Leitversteinerungen der Silurformation. Die Neue Brehm-Bücherei. Heft 103. Akademische Verlagsgesellschaft Geest & Portig K.-G., Leipzig. 48 p.

Hundt, Rudolf. 1965. Aus der Welt der Graptolithen, Commercia Verlag, Berlin & Bonn. 208 p.

Huo, Shicheng, Lipu Fu, & Degan Shu. 1986. A mathematical study of the *Cyrtograptus sakmaricus* lineage with discussions of the evolutionary trends in this lineage. Geological Society Special Publication 20:197–205.

Hutt, J. E. 1974. A new group of Llandovery biform monograptids. Special Papers in Palaeontology 13:189–203.

Hutt, J. E. 1975. The Llandovery graptolites of the English Lake District. Part 2. Palaeontographical Society Monograph 129(542):1–137, 26 pl.

Hutt, J. E., & R. B. Rickards. 1970. The evolution of the earliest Llandovery monograptids. Geological Magazine 107(1):67–77.

Hutt, J. E., R. B. Rickards, & David Skevington. 1970. Isolated Silurian graptolites from the Bollerup and Klubbudden Stages of Dalarna, Sweden. Geologica et Palaeontologica 4:1–23.

ICZN (International Commission on Zoological Nomenclature). 1954. Opinion 198. Suppression, under the plenary powers, of the generic names ‚*Lomatoceras*' Bronn, 1834, and '*Monoprion*' Barrande, 1850 (Class Graptolithina) and validation of the generic name '*Monograptus*' Geinitz, 1852. Bulletin of Zoological Nomenclature 3(16):219–228.

ICZN (International Commission on Zoological Nomenclature). 1963. Opinion 650. Graptolite generic names: Validation of certain emendations under the plenary powers. Bulletin of Zoological Nomenclature 20:105–110.

ICZN (International Commission on Zoological Nomenclature). 1993. Opinion 1714. *Streptograptus* Yin, 1937 (Graptolithina): *Graptolithus plumosus* Baily, 1871 designated as the type species. Bulletin of Zoological Nomenclature 50(1):90–91.

ICZN (International Commission on Zoological Nomenclature). 2003. Opinion 2023 (Case 3195). *Polonograptus* Tsegelnjuk, 1976 (Graptolithina): *P. podoliensis* Přibyl, 1983 designated as the type species. Bulletin of Zoological Nomenclature 60(1): 74–75.

Jackson, D. E., & J. E. Etherington. 1969. New Silurian cyrtograptid graptolites from northwestern Canada and northern Greenland. Journal of Paleontology 43:1114–1121.

Jaeger, Hermann. 1959. Graptolithen und Stratigraphie des jüngsten Thüringer Silurs. Abhandlungen der deutschen Akademie der Wissenschaften zu Berlin, Klasse für Chemie, Geologie und Biologie 1959(2):1–197, 14 pl.

Jaeger, Hermann. 1978. Late graptoloid faunas and the problem of graptoloid extinction. Acta Palaeontologica Polonica 23(4):497–521.

Jaeger, Hermann. 1983. Unterdevonische Graptolithen aus Burma. Jahrbuch der Geologischen Bundes-Anstalt 126(2):245–257.

Jaeger, Hermann. 1988. Devonian Graptoloidea. Canadian Society of Petroleum Geologists Memoir 14:431–438.

Jaeger, Hermann. 1991. Neue Standard-Graptolithenzonenfolge nach der "Großen Krise" an der Wenlock/Ludlow-Grenze (Silur). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 182(3): 303–354.

Jaekel, Otto. 1889. Über das Alter des sog. Graptolithengesteins mit besonderer Berücksichtigung der in demselben enthaltenen Graptolithen. Zeitschrift der Deutschen Geologischen Gesellschaft 41:653–716.

Jones, O. T. 1909. The Hartfell-Valentian succession in the District around Plynlimon and Pont Erwyd, North Cardiganshire. Quarterly Journal of the Geological Society London 65:463–537.

Koren', T. N. 1962. Novyi siluriiskii rod *Uralograptus.* Paleontologicheskiy Zhurnal 3:137–138. [English translation: Koren', T. N. 1964. International Geological Review 6 (4):724–725.]

Koren', T. N. 1969. The upper boundary of the *Monograptus hercynicus* Zone in Pai Khoi and its paleontological definition. Doklady Akad. Nauk SSSR, Geologia 189:1325–1328. In Russian.

Koren', T. N. 1983. New late Silurian monograptids from Kazakhstan. Palaeontology 26 (2):407–434, pl. 49–53.

Koren', T. N., & Merete Bjerreskov. 1997. Early Llandovery monograptids from Bornholm and the southern Urals: taxonomy and evolution. Bulletin of the Geological Society of Denmark 44:1–43.

Koren', T. N., A. I. Kim, & O. H. Walliser. 2007. Contribution to the biostratigraphy around the Lochkovian-Pragian boundary in Central Asia (graptolites, tentaculites, conodonts). Senckenbergiana lethaea 87(2):187–219.

Koren', T. N., & A. A. Sujarkova. (also Suyarkova). 1997. Late Ludlow and Pridoli monograptids from the Turkestan-Alai Mountains, South Tien Shan. Palaeontographica A247(1–4):59–90, 8 pl.

Koren', T. N., & A. A. Sujarkova. 2004. The Ludlow (Late Silurian) neocucullograptid fauna from the southern Tien Shan, Kyrghizstan. Alcheringa 28:333–387.

Kozłowska, Anna, & Adam Urbanek. 2013. *Bohemograptus papilio* sp. nov. three-dimensionally preserved monograptid (Graptolithina) with an adaptation to retard sinking, from the Upper Silurian Poland. Comptes Rendus Palevol 12:13–21.

Kraatz, Reinhard. 1958. Stratigraphische und palaontologische Untersuchungen (besonders im Gotlandium) im Gebiet zwischen Wieda und Zorge (südl. Westharz). Zeitschrift der Deutschen Geologischen Gesellschaft 110:22–70.

Kraft, Paul. 1926. Ontogenetische Entwicklung und Biologie von *Diplograptus* und *Monograptus*. Paläontologische Zeitschrift 7:207–249, fig.1–4, pl. 1–15.

Kříž, Jiří, Hermann Jaeger, Florentin Paris, & H. P. Schönlaub. 1986. Přídolí: the fourth subdivision of the Silurian. Jahrbuch der geologischen Bundesanstalt Wien 129(2):291–360.

Kurck, Claes. 1882. Några nya graptolitarter från Skåne. Geologiska Föreningens i Stockholm Förhandlingar 6:294–304, pl. 14.

Lankester, E. R. 1884. A contribution to the knowledge of *Rhabdopleura*. Quarterly Journal of Microscopical Science 24:622–647.

Lapworth, Charles. 1873. Notes on the British graptolites and their allies. 1. On an improved classification of the Rhabdophora, part 2. Geological Magazine 10:555–560 + table facing p. 555.

Lapworth, Charles. 1876a. On Scottish Monograptidae. I. Introduction. Geological Magazine (decade II, vol. III) 13:308–321, pl. 10–11.

Lapworth, Charles. 1876b. On Scottish Monograptidae (continued from page 321). Geological Magazine (decade II, vol. III) 13:350–360, pl. 12–13.

Lapworth, Charles. 1876c. On Scottish Monograptidae (concluded from page 507). Geological Magazine (decade II, vol. III) 13:544–552.

Lapworth, Charles. 1876d. On Scottish Monograptidae (continued from page 360). Geological Magazine (decade II, vol. III) 13:499–507, pl. 20.

Lapworth, Charles. 1880. On new British graptolites. Annals and Magazine of Natural History 5:149–177.

Lenz, A. C. 1984. A new mid Ludlow faunule from northern Yukon, Canada. Canadian Journal of Earth Sciences 21:969–972.

Lenz, A. C. 1988. Upper Silurian and Lower Devonian graptolites and biostratigraphy, northern Yukon, Canada. Canadian Journal of Earth Sciences 25(3):355–369.

Lenz, A. C. 2013. Early Devonian graptolites and graptolite biostratigraphy, Arctic Islands, Canada. Canadian Journal of Earth Sciences 50:1097–1115.

Lenz, A. C., & Anna Kozłowska-Davidziuk 1998. Sicular annuli and thickened interthecal septa in Silurian graptolites: new information. Temas Geológico-Mineros ITGE 23:212–214.

Lenz, A. C., & M. J. Melchin. 1989. *Monograptus spiralis* and its phylogenetic relationship to early cyrtograptids. Journal of Paleontology 63(3):341–348.

Lenz, A. C., & M. J. Melchin. 1991. Wenlock (Silurian) graptolites, Cape Phillips Formation, Canadian Arctic Islands. Transactions of the Royal Society of Edinburgh: Earth Sciences 82(3):211–237.

Lenz, A. C., & M. J. Melchin. 2008. Convergent evolution of two Silurian graptolites. Acta Palaeontologica Polonica 53(3):449–460.

Lenz, A. C., Sherill Senior, Anna Kozłowska, & M. J. Melchin. 2012. Graptolites from the mid Wenlock (Silurian), Middle and Upper Sheinwoodian, Arctic Canada. Palaeontographica Canadiana 32:1–93.

Levina, E. F. 1928. Graptolitit iz Aq-Tengi v Turkestanskom chrebte. Trudy Sredie-Aziatskogo Gosydarstvennogo Universiteta, Series 7a, Geologiya 5:1–18.

Li, Jijin. 1995. Lower Silurian graptolites from the Yangtze Gorge district. Palaeontologica Cathayana 6:215–344.

Linnæus, Carolus. 1758. Systema naturæ, per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Laurentius Salvius. Holmiæ. 842 p. [http://reader.digitale-sammlungen.de/resolve/display/bsb10076014.html; http://www.biodiversitylibrary.org/item/10277].

Loydell, D. K. 1990a. *Sinodiversograptus*: Its occurrence in Australia and northern Canada. Journal of Paleontology 64(5):847–849.

Loydell, D. K. 1990b. On the graptolites described by Baily (1871) from the Silurian of Northern Ireland and the genus *Streptograptus* Yin. Palaeontology 33(4):937–943.

Loydell, D. K. 1991. The biostratigraphy and formational relationships of the upper Aeronian and lower Telychian (Llandovery, Silurian) formations of western mid-Wales. Geological Journal 26:209–244.

Loydell, D. K. 1993. Upper Aeronian and Lower Telychian (Llandovery) graptolites from western Mid-Wales, Part 2. Monograph of the Palaeontographical Society 147(592):56–180, pl. 2–5.

Loydell, D. K. 1996. *Globosograptus* Bouček and Přibyl *in* Přibyl, 1948 (Silurian; Graptoloidea) is a synonym of *Streptograptus* Yin, 1937. Journal of Paleontology 70(5):891–892.

Loydell, D. K. 2020. Middle Telychian (Llandovery, Silurian) graptolites and biostratigraphy of the Howgill Fells, England, based upon the collections of D. W. R. Wilson housed in the Lapworth Museum of Geology, University of Birmingham. Proceedings of the Yorkshire Geological Society 63(1):33–42.

Loydell. D. K. 2021. *Lenzograptus*, a new name for the graptolite *Lenzia* Rickards and Wright, 1999. Journal of Paleontology 95(1):205.

Loydell, D. K., & Richard Cave. 1993. The Telychian (Upper Llandovery) stratigraphy of Buttington Pit, Wales. Newsletters on Stratigraphy 29(2):91–103.

Loydell, D. K., & Richard Cave. 1994. Pseudovirgular development in the Llandovery graptolite *Cochlograptus veles*. Geobios 27(5):609–613.

Loydell, D. K., & Richard Cave 1996. The Llandovery-Wenlock boundary and related stratigraphy in eastern mid-Wales with special reference to the Banwy River section. Newsletters on Stratigraphy 34(1):39–64.

Loydell, D. K., & Xu Chen. 1991. *Streptograptus* Yin, 1937 (Graptolithina): proposed designation of *Graptolithus plumosus* Baily, 1871 as the type species. Bulletin of Zoological Nomenclature 48:236–237.

Loydell, D. K., Jiří Frýda, & J. C. Gutiérrez-Marco. 2015. The Aeronian/Telychian (Llandovery, Silurian) boundary, with particular reference to sections around the El Pintado reservoir, Seville Province, Spain. Bulletin of Geosciences 90(4):743–794.

Loydell, D. K., & R. R. Large. 2019. Biotic, geochemical and environmental changes through the early Sheinwoodian (Wenlock, Silurian) carbon isotope excursion (ESCIE), Buttington Quarry, Wales. Palaeogeography, Palaeoclimatology, Palaeoecology 514:305–325.

Loydell, D. K., & Jörg Maletz. 2004. The Silurian graptolite genera *Streptograptus* and *Pseudostreptograptus*. Journal of Systematic Palaeontology 2(2):65–93.

Loydell, D. K., & Jörg Maletz. 2009. Isolated graptolites of the *Lituigraptus convolutus* Biozone (Silurian, Llandovery) of Dalarna, Sweden. Palaeontology 52(2):273–296.

Loydell, D. K., & Viiu Nestor. 2006. Isolated graptolites from the Telychian (Upper Llandovery, Silurian) of Latvia and Estonia. Palaeontology 49(3):585–619.

Loydell, D. K., G. N. Sarmiento, Petr Štorch, & J. C. Gutiérrez-Marco. 2009. Graptolite and conodont biostratigraphy of the upper Telychian-lower Sheinwoodian (Llandovery–Wenlock) strata, Jabalón River section, Corral de Calatrava, central Spain. Geological Magazine 146(2):187–198.

Loydell, D. K., Petr Štorch, & M. J. Melchin. 1993. Taxonomy, evolution and biostratigraphical importance of the Llandovery graptolite *Spirograptus*. Palaeontology 36(4):909–926.

Loydell, D. K., & Natalia Walasek. 2019. Two new species of graptolite from the Telychian (upper Llandovery, Silurian) of Kallholn, Dalarna, Sweden. GFF 142(2):154–157.

Loydell, D. K., Natalia Walasek, N. H. Schovsbo, & A. T. Nielsen. 2017. Graptolite biostratigraphy of the lower Silurian of the Sommerodde-1 core, Bornholm, Denmark. Bulletin of the Geological Society of Denmark 65:135–160.

Lukasik, J. J., & M. J. Melchin. 1994. *Atavograptus primitivus* (Li) from the earliest Silurian of Arctic Canada: Implications for monograptid evolution. Journal of Paleontology 68(5):1159–1163.

Lukasik, J. J., & M. J. Melchin. 1997. Morphology and classification of some early Silurian monograptids (Graptoloidea) from the Cape Phillips Formation, Canadian Arctic Islands. Canadian Journal of Earth Sciences 34(8):1128–1149.

Maletz, Jörg. 1997. The rhabdosome structure of a *Saetograptus* species (Graptoloidea, Monograptacea) from a North German glacial boulder. Paläontologische Zeitschrift 71(3/4):247–255.

Maletz, Jörg. 1999. *Heisograptus micropoma* (Jaekel 1889) (Graptoloidea, Monograptidae) in a north German glacial erratic boulder. Greifswalder Geowissenschaftliche Beiträge 6:279–290.

Maletz, Jörg. 2001. Graptolite Research in Germany. Geologica Saxonica, Abhandlungen des Staatlichen Museums für Mineralogie und Geologie Dresden 46/47:169–180.

Maletz, Jörg. 2017a. Fossils explained 70. Graptolites: fossil and living. Geology Today 33(6):237–244.

Maletz, Jörg. 2017b. Graptolite Paleobiology. Topics in Palaeobiology (Series Editor Mike Benton, Bristol, UK). Wiley–Blackwell. 323 p., 16 pl.

Maletz, Jörg, A. C. Lenz, & D. E. B. Bates. 2016. Treatise on Invertebrate Paleontology, Part V, Second Revision, Chapter 4: Morphology of the Pterobranch Tubarium. Treatise Online 76:1–63.

Maletz, Jörg, M. J. Melchin, Peter Bullock, T. N. Koren', & Jennifer Russel-Houston. 2019. *Paramonoclimacis sidjachenkoi* (Obut & Sobolevskaya, 1968) and the origin of the streptograptid thecal aperture. Papers in Palaeontology 5(3):499–520.

Maletz, Jörg, Chuanshang Wang, & Xiaofeng Wang. 2021. Katian (Ordovician) to Aeronian (Silurian, Llandovery) graptolite biostratigraphy of the YD-1 drill core, Yuanan County, Hubei Province, China. Papers in Palaeontology 7(1):163–194.

Manck, Elfried. 1923. Untersilurische Graptolithenarten der Zone 10 des Obersilurs, ferner *Diversograptus* gen. nov. sowie einige neue Arten anderer Gattungen. Natur (Leipzig) 14:282–289.

M'Coy, Frederick. 1850. On Some New Genera and Species of Silurian Radiata in the Collection of the University of Cambridge. Annals and Magazine of Natural History Series 2(6):270–290.

Melchin, M. J., & T. N. & Koren'. 2001. Morphology and phylogeny of some early Silurian (mid-Rhuddanian) monograptid graptolites from the South Urals of Russia. Journal of Paleontology 75(1):165–185.

Melchin, M. J., & A. C. Lenz. 1986. Uncompressed specimens of *Monograptus turriculatus* (Barrande, 1850) from Cornwallis Island, Arctic Canada. Canadian Journal of Earth Sciences 23(4):579–582.

Melchin, M. J., C. E. Mitchell, Amanda Naczk-Cameron, J. X. Fan, & Jason Loxton. 2011. Phylogeny and adaptive radiation of the Neograptina (Graptoloidea) during the Hirnantian mass extinction and Silurian recovery. Proceedings of the Yorkshire Geological Society 58(4):281–309.

Meneghini, Guiseppe. 1857. Paleontologie de L'Ile de Sardaigne. La Marmora, Voyage en Sardaigne. 3. In *Voiage en Sardaigne,* cur. A. La Marmora. Turin-Paris: Imprimaire royal. p. 53–144.

Mikhailova, N. F. 1975. Graptolity. *In* V. V. Menner, ed., Kharacteristika fauny progranichnych sloev silura i devona tsentralnogo Kazakhstana. Nedra Moskva. p. 151–158. In Russian.

Mitchell, C. E., M. J. Melchin, C. B. Cameron, & Jörg Maletz. 2013. Phylogenetic analysis reveals that *Rhabdopleura* is an extant graptolite. Lethaia 46:34–56.

Mu, Antze. 1948. Silurian succession and graptolite fauna of Lientan. Bulletin of the Geological Society of China 28:207–231.

Mu, Antze. 1950. On the evolution and classification of graptolites. Geological Review 15:171–183.

Mu, Antze. 1955. On *Spirograptus* Gürich. Acta Palaeontologica Sinica 3:1–10.

Mu, Antze, & Xu Chen. 1962. *Sinodiversograptus multibrachiatus* gen. et sp. nov. and its developmental stages. Acta Palaeontologica Sinica 10:143–154.

Mu, Enzhi, Jijin Li, Meiyu Ge, Yaokun Lin, & Yunan Ni. 2002. Fossil graptolites of China. Nanjing Institute of Geology and Palaeontology, Academia Sinica. 1205 p. Nanjing, China [In Chinese].

Mu, Enzhi, Jijin Li, Meiyu Ge, Xu Chen, Yunan Ni, Yaokun Lin, & Xu Mu. 1974. Graptolites. *In* NIGPAS, eds., A Handbook of the Stratigraphy and Palaeontology of Southwest China. Nanjing Institute of Geology and Palaeontology, Science Press. Nanjing. p. 154–164, pl. 67–70 (Ordovician); p. 211–220, pl. 98–101 (Silurian).

Mu, Enzhi, & Yunan Ni. 1975. Silurian and Devonian graptolites from the Qomolangma Feng Region. *In* Tu Sheng Wu, ed., A Report of Scientific investigation in the Qomolangma Feng Region (Palaeontology 1) 1966–1968: Scientific Press. Beijing. p. 5–29, pl. 1–8.

Müller, A. H. 1965. Über *Abiesgraptus* und Verwandte (Graptoloidea) aus dem mitteldeutschen Obersilur. Freiberger Forschungshefte C182:5–18.

Müller, H. A. 1969. Monograptiden (Graptoloidea) mit Nebenzweigen 2. Ordnung aus dem Unterdevon von Thüringen. Monatsberichte der deutschen Akademie der Wissenschaften, Berlin 11:913–921, 3 pl.

Münch, Arthur. 1938. Einige grundlegende Fragen über Bau und Struktur von *Monograptus* GEIN. und *Barrandeograptus* BOUC. (mit 4 Abb. und Tafel 5-9). Zeitschrift für Geschiebekunde und Flachlandsgeologie 14(1):31–70.

Muir, L. A. 1999. A cladistic analysis of some Llandovery (Silurian) Monograptidae (Graptolithina). Dissertation, University of Bristol. 64 p. [Supervised by Dr P. Pearson, Bristol and Dr S. Rigby, Edinburgh.]

Murchison, R. I. 1839. The Silurian System. London. i-xxxii + 768 p.

Murchison, R. I. 1867. Siluria. Fourth Edition. John Murray. London. p. 566. (Carruthers, William. On Graptolites. Appendix D. p. 538-541.)

Ni, Yunan. 1978. Lower Silurian graptolites from Yichang, western Hubei. Acta Palaeontologica Sinica 17(4):387–416.

Nicholson, H. A. 1869. On some new species of graptolites. Annals and Magazine of Natural History, London Series 4(4):231–242.

Nicholson, H. A. 1872. A monograph of the British Graptolitidae. Part 1. Blackwood & Sons. Edinburgh & London. 133 p.

Obut, A. M. 1949. Polevoi atlas rukovodyashchikh graptolitov verkhnego silura Kirgizskoi SSR. [Field Atlas of leading graptolites of the Upper Silurian of Kirgiz SSR.] Akademia. Nauk SSSR, Kirgiz. Filial, Geologii Institut. Frunze. 56 p. 7 pl. In Russian.

Obut, A. M. 1950. Semeistva i nekotorye nody odnoryadnykh graptolitov. [Families and some genera of uniserial graptolites.] Voprosy Paleontologii 1:264–272. In Russian.

Obut, A. M. 1957. Klassifikatsiya i ukazatel rodov graptolitov. [Classification and ordering of the genera of graptolites]. Vsesoyuznogo Paleontologicheckogo Obsehchectva Ezhegodnik 16:11–47. In Russian.

Obut, A. M. 1964. Podtip Stomochordata. Stomokhordovye. Osnovy paleontogii: Echinodermata, Hemichordata, Pogonophora, Chaetognatha. Y. A. Orlov. Nedra Press. Moscow. p. 279–337. In Russian.

Obut, A. M. 1987. *Cochlograptus*: novyi rod siluriiskich graptolitov [*Cochlograptus:* A new genus of the Silurian graptolites.] Akademia Nauk SSSR Sibirskoe otdelenie, Institut Geologii i Geofiziki Trudy 688:140–144. In Russian.

Obut A. M., F. I. Morozova, T. A. Moskalenko, & P. D. Chegodayev. 1988. Graptolites, conodonts and stratigraphy of the Silurian, Lower Devonian North Caucasus. Works of the Institute of Geology and Geophysics for the 60th anniversary of the Soviet Union of Soviet Socialist Republics 698. Novosibirsk. 221 p. In Russian.

Obut, A. M., & R. F. Sobolevskaya. 1966. Graptoliti rannego silura v Kazachstane. [Lower Silurian grapotlites of Kazakhstan.] Akademiya Nauk SSSR, Sibirskoe Otdelenie Instituta Geologii Geofiziki, Ministerstvo Geologii SSSR, Nauchno-issledovatelskie Institut Geologii Arktiki. p. 1–56. In Russian.

Obut, A. M., R. F. Sobolevskaya, & V. I. Bondarev. 1965. Silurian graptolites of Taimyr. Moscow, Akademiya Nauk SSSR, 120 p. In Russian.

Obut, A. M., R. F. Sobolevskaya, & A. P. Merkureva. 1968. Graptolity llandoveri v kernakh burovykh skvazhin Noril'skogo rayona. [Llandovery graptolites from drill cores in the Noril'sk region.] Nauka, Moskva. 137 p. In Russian.

Obut, A. M., R. F. Sobolevskaya, & A. A. Nikolaev. 1967. Graptoliti y stratigrafiya nizhnego silura okainnykh podnyatii kolymskogo massifa. [Graptolites and stratigraphy of the early Silurian Period in the Kolyma Formation (northeast of the USSR).] Akademii Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii i Geofiziki, Ministerstvo Geiologii, SSSR, Nauchno-issledovatelskie Institut Geologii Arktiki. p. 1–162, pl. 1–20. In Russian.

Palmer, Douglas. 1971a. The Ludlow graptolites *Neodiversograptus nilssoni* and *Cucullograptus* (*Lobograptus*) *progenitor*. Lethaia 4(4):357–384.

Palmer, Douglas. 1971b. The graptolite species *Graptolithus nilssoni* Barrande, 1850; proposed use of the plenary powers to designate a neotype. Bulletin of Zoological Nomenclature 28(3–4):94–99.

Perner, Jaroslav. 1897. Études sur les graptolites de Bohême, Part 3a. Palaeontographica Bohemiae. Prague. p. 1–25, pl. 9–13.

Perner, Jaroslav. 1899. Études sur les graptolites de Bohême, Part 3b. Palaeontographica Bohemiae. Prague. p. 1–24, pl. 14–17.

Perry, D. G., A. J. Boucot, & Hubert Gabrielse. 1981. Late Early Devonian brachiopods from the Mount Lloyd area, northern British Columbia. Geological Survey of Canada Bulletin 300:15–40.

Porębska, Elżbieta. 1984. Latest Silurian and early Devonian graptolites from Żdanów section, Bardo Mts. (Sudetes). Annales Societatis Geologorum Poloniae 52(1–4):69–209.

Portlock, J. E. 1843. Report on the Geology of the county of Londonderry, and of parts of Tyrone and Fermanagh. A-H. Alexander Thom. Dublin, UK. p. 1–784, 38 pl.

Přibyl, Alois. 1940a. Die Graptolithenfauna des Mittleren Ludlows von Böhmen (oberes e β). Vestnik der Geologischen Landesanstalt für Böhmen und Mähren 16(2–3):63–73, 1 pl. Includes German and Czech versions.

Přibyl, Alois. 1940b. Revise českých graptolitů rodu *Monoclimacis*, Frech. Rozpravy II, Třídy České Akademie 50(23):1–19, 3 pl. [German Version: Revision der böhmischen Vertreter der Monograptidengattung *Monoclimacis* Frech. Mitteilungen der Tschechischen Akademie der Wissenschaften 1940:1–16, 3 pl.]

Přibyl, Alois. 1941. *Pernerograptus* nov. gen. a jeho zástupci z českého a cizího siluru. [*Pernerograptus* nov. gen. und seine Vertreter aus dem böhmischen und ausländischen Silur]. Věstník Královské České Společnosti Nauk. Třída Matemat.-Přírodověd. Ročník 1941:1–19 [1–7, 15–18: Czech text; 8–14: German Text].

Přibyl, Alois. 1943. Revise Pristiograptu z podrodu *Colonograptus* nov. subg. a *Saetograptus* nov. subg. Rozpravy II. Třídy České Akademie 52(15):1–24.

[German Text: Přibyl, A. 1943. Revision der Pristiograpten aus den Untergattungen *Colonograptus* n. subg. und *Saetograptus* n. subg. Mitteilungen der tschechischen Akademie der Wissenschaften 43:161–184.]

Přibyl, Alois. 1946. Contribution to a new systematic of the Graptolites of the family Monograptidae. Státního geologického ústavu Československé republiky 21:274–285. [In Czech with English and Russian summaries]

Přibyl, Alois. 1948. Bibliographic index of Bohemian Silurian graptolites. Knihovna Státního Geologického ústavu Republiky Československé 22:1–97.

Přibyl, Alois. 1967a. O rodu *Bohemograptus* gen. nov. (Graptoloidea) z českého a ciziho ludlowu. Zur Gattung *Bohemograptus* gen. nov. (Graptolitoidea) aus dem böhmischen und fremden Ludlovium. Časopis Národniho Muzea 3:133–136.

Přibyl, Alois. 1967b. *Monograptus* (*Testograptus*) subg. n. aus dem böhmischen und europäischen Silur. Věstník Ústředního ústavu geologického 42:49–52.

Přibyl, Alois. 1981. New graptolites of the family Monograptidae from the Upper Silurian of Bohemia. Věstník Ústředního ústavu geologického 56: 371–375.

Přibyl, Alois. 1983. Graptolite biozones of the Kopanina and Pridoli Formations in the Upper Silurian of central Bohemia. Časopis pro mineralogii a geologii 28(2):149–168, 4 pl.

Přibyl, Alois, & Arthur Münch. 1941. Revize středoevropských zástupců rodu *Demirastrites* Eisel. RozpravyII. Třídy České akademie věd a umění 51(31):1–29. [German Version: Revision der mitteleuropäischen Vertreter der Gattung *Demirastrites* Eisel. Rozpravy II. Třídy České Akademie věd a umění 52(30):1–26, 3 pl.]

Přibyl, Alois, & Petr Štorch. 1983. *Monograptus* (*Stimulograptus*) subgen. n. (Graptolites) from the Lower Silurian of Bohemia. Věstník Ústředního ústavu geologického 58(4):221–225.

Přibyl, Alois, & Petr Štorch, 1985. *Prochnygraptus* gen. n. (Graptolithina, Monograptidae) from the middle and upper Llandovery of Europe. Věstník Ústředního ústavu geologického 60(2):159–164.

Richter, Reinhard. 1871. Aus dem thüringische Schiefergebirge. Zeitschrift der Deutschen Geologischen Gesellschaft 23:231–256.

Richter, Reinhard. 1875. Aus dem Thüringischen Schiefergebirge. Zeitschrift der Deutschen Geologischen Gesellschaft 27:261–273, pl. 8.

Rickards, R. B. 1974. A new monograptid genus and the origin of the main monograptid genera. Special Papers in Palaeontology 13:141–147.

Rickards, R. B. 1995. *Crinitograptus*, a new genus of Ludlow (Silurian) graptoloid. Journal of Paleontology 69(6):1107–1111.

Rickards, R. B., & J. E. Hutt. 1970. The earliest monograptid. Proceedings of the Geological Society of London 1663:115–119.

Rickards, R. B., J. E. Hutt, & W. B. N. Berry. 1977. Evolution of the Silurian and Devonian graptoloids. Bulletin of the British Museum (Natural History) Geology 28(1):120 p.

Rickards, R. B., & J. S. Jell. 2002. New graptolite faunas from the Llandovery, lower Silurian of the Graveyard Creek Subprovince, Broken River region, Queensland, Australia. Proceedings of the Geologists' Association 113:111–120.

Rickards, R. B., G. H. Packham, A. J. Wright, & P. L. Williamson. 1995. Wenlock and Ludlow graptolite faunas and biostratigraphy of the Quarry Creek district, New South Wales. Association of Australasian Paleontologists, Memoir 17:1–68.

Rickards, R. B., & A. J. Wright. 1997a. Graptolite zonation in the late Wenlock (early Silurian), with a new graptolite-brachiopod fauna from New South Wales. Records of the Australian Museum 49:229–248.

Rickards, R. B., & A. J. Wright. 1997b. Graptolites of the Barnby Hills Shale (Silurian, Ludlow) New South Wales, Australia. Proceedings of the Yorkshire Geological Society 51(3):209–227.

Rickards, R. B., & A. J. Wright. 1999a. Systematics, biostratigraphy and evolution of the Late Ludlow and Pridoli (Late Silurian) graptolites of the Yass district, New South Wales, Australia. Records of the Australian Museum 51:187–214.

Rickards, R. B., & A. J. Wright. 1999b. Evolution of the Ludlow (Silurian) graptolite genus *Bohemograptus* Přibyl 1936. Proceedings of the Yorkshire Geological Society 52(3):313–320.

Rickards, R. B., & A. J. Wright. 2004. *Enigmagraptus* n. gen., a new graptoloid (Pridoli, Silurian, New South Wales, Australia). Paläontologische Zeitschrift 78(1):189–194.

Rigby, John. 1986. A critique of graptolite classification, and a revision of the suborders Diplograptina and Monograptina. Geological Society Special Publication 20:1–12.

Riva, J. F. V., T. N. Koren', & R. B. Rickards, 2001. Case 3195. *Polonograptus* Tsegelnjuk, 1976 (Graptolithina): proposed designation of *P. podoliensis* Přibyl, 1983 as the type species. Bulletin of Zoological Nomenclature 58(4):291–293.

Russel-Houston, Jennifer. 2001. Taphonomy and paleosynecology of the Lower Silurian graptoloid fauna, Cape Phillips Formation, Nunavut, Canada. PhD thesis, Dalhousie University, Halifax, Nova Scotia, Canada. 518 p.

Schauer, Manfred. 1971. Biostratigraphie und Taxionomie der Graptolithen des tieferen Silurs unter besonderer Berücksichtigung der tektonischen Deformation. Freiberger Forschungshefte C 273:1–185.

Sennikov, N. V. 1976. Graptolity i stratigrafiya nizhnego silura Altaya [Graptolites and stratigraphy of the Lower Silurian of the Altai]. Akademiya Nauk SSSR, Sibirskoe otdelenie, Trudy Insituta Geologii i Geofiziki 304:1–230. In Russian.

Skwarko, S. K. 1974. Some Ordovician graptolites from the Canning Basin, western Australia. 2: Graptolites from the Goldwyer No. 2 well. Bulletin of the Bureau of Mineral Resources, Geology and Geophysics of Australia 150:43–56.

Spencer, J. W. 1878. Graptolites of the Niagara Formation. Canadian Naturalist and Geologist 8: 457–463.

Štorch, Petr. 1988. Earliest Monograptidae (Graptolithina) in the lower Llandovery sequence of the

Prague Basin. Sbornik Geologických Věd Paleontologie 29:9–48.

Štorch, Petr. 1992. Some new and little known graptolites from the Lower Silurian of Bohemia (Prague Basin, Barrandian Area). Časopis pro mineralogii a geologii 37:193–201.

Štorch, Petr. 1994. Llandovery–Wenlock boundary beds in the graptolite-rich sequence of the Barrandian area (Bohemia). Journal of the Czech Geological Society 39:163–82.

Štorch, Petr. 1998a. New data on Telychian (Upper Llandovery, Silurian) graptolites from Spain. Journal of the Czech Geological Society 43:113–142.

Štorch, Petr. 1998b. Graptolites of the *Pribylograptus leptotheca* and *Lituigraptus convolutus* biozones of Tmaň (Silurian, Czech Republic). Journal of the Czech Geological Society 43(3):209–272, 20 pl.

Štorch, Petr. 2000a. *Rastrites peregrinus* (Barrande, 1850). Atlas of Graptolite Type Specimens 1.87.

Štorch, Petr. 2000b. *Spirograptus turriculatus* (Barrande, 1850). Atlas of Graptolite Type Specimens 1.92.

Štorch, Petr. 2000c. *Bohemograptus bohemicus* (Barrande, 1850). Atlas of Graptolite Type Specimens 1.9.

Štorch, Petr. 2015. Graptolites from the Rhuddanian–Aeronian boundary interval (Silurian), Prague Synform, Czech Republic. Bulletin of Geosciences 90(4):841–891.

Štorch, Petr, & D. K. Loydell. 1992. Graptolites of the *Rastrites linnei* Group from the European Llandovery (Lower Silurian). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 184(1):63–86.

Štorch, Petr & Štěpán Manda. 2019. Little known Homerian (Lower Silurian) graptolites form Kosov quarry near Beroun, the Czech Republic. Fossil Imprint 75:44–58.

Štorch, Petr, Štěpán Manda, & D. K. Loydell. 2014. The early Ludfordian *leintwardinensis* graptolite event and the Gorstian-Ludfordian boundary in Bohemia (Silurian, Czech Republic). Palaeontology 57(5):1003–1043.

Štorch, Petr, Štěpán Manda, Ladislav Slavík, & Zuzana Tasáryová. 2016. Wenlock-Ludlow boundary interval revisited: New insights from the offshore facies of the Prague synform, Czech Republic. Canadian Journal of Earth Sciences 53:666–673.

Štorch, Petr, Štěpán Manda, Zuzana Tasáryová, Jiří Frýda, Leona Chadimová, & M. J. Melchin. 2018. A proposed new global stratotype for Aeronian Stage of the Silurian System: Hlásná Třebaň section, Czech Republic. Lethaia 51:357–388.

Štorch, Petr, Josep Roqué Bernal, & J. C. Gutiérrez-Marco. 2019. A graptolite-rich Ordovician–Silurian boundary section in the south-central Pyrenees, Spain: stratigraphical and palaeobiogeographical significance. Geological Magazine 156(6):1069–1091.

Strachan, Isles. 1952. The development of *Diversograptus* Manck. Geological Magazine 89(5):365–368.

Strachan, Isles. 1969. A redescription of W. Carruthers' type graptolites. Bulletin of the British Museum of Natural History, Geology 17(4):183–206.

Strachan, Isles. 1971. A synoptic supplement of 'A monograph of British Graptolites by Miss G. L: Elles and Miss E. M. R. Wood'. Palaeontographical Society Monograph 125(529):1–130.

Strachan, Isles. 1973. Comment on the proposed neotype of the graptolite species *Graptolithus nilssoni* Barrande, 1850. Bulletin of Zoological Nomenclature 30(1):7–8.

Sudbury, Margaret. 1958. Triangulate monograptids from the *Monograptus gregarius* zone (Lower Llandovery) of the Rheidol Gorge (Cardiganshire). Philosophical Transactions of the Royal Society of London, Series B. Geological Sciences 241(685):485–555.

Suess, Eduard. 1851. Über böhmische Graptolithen. Naturwissenschaftliche Abhandlungen von W. Haidinger 4(4):87–134.

Teller, Lech. 1962. Linograptinae, a new subfamily of Monograptids (Graptoloidea). Bulletin de l'Académie Polonaise des Sciences, Série des sciences géologiques et géographiques 10(3):153–154.

Teller, Lech. 1966. Two new species of Monograptidae from the Upper Ludlowian of Poland. Bulletin de L'Académie Polonaise des Sciences, Série des Sciences Biologiques 14:553–558.

Teller, Lech. 1976. Morphology of some Upper Wenlockian Cyrtograptinae from Zawada 1 profile (NE Poland). Acta Geologica Polonica 26(4):469–484.

Teller, Lech. 1986. Morphology of selected Monograptidae from the Wenlock of NE Poland. Palaeontographica A192:51–73.

Thorsteinsson, Raymond. 1955. The mode of cladial generation in *Cyrtograptus*. Geological Magazine 92(1):37–49.

Törnquist, S. L. 1881. Om några graptolitarter från Dalarne. Geologiska Föreningens i Stockholm Förhandlingar 5:434–445.

Törnquist, S. L. 1883. Öfversigt ofver bergbygnaden inom Siljansomradets i Dalarna. Sveriges Geologiska Undersökning. Afhandlingar och uppsatser C57:1–59, 1 map.

Törnquist, S. L. 1892. Undersökningar öfver Siljanområdets graptoliter 2. Lunds Universitets Årsskrift 28:1–47, 3 pl.

Törnquist, S. L. 1899. Researches into the Monograptidae of the Scanian Rastrites Beds. Lunds Universitets Årsskrift 35(1):1–25.

Tsegelnjuk, P. D. 1976. Late Silurian and early Devonian monograptids from the south-western margin of the East European Platform (in Russian). *In* P. L. Shulga, ed., Palaeontology and Stratigraphy of the Upper Precambrian and Lower Paleozoic of the South-West part of the east European Platform. Naukova Dumka. Kiev. p. 91–133.

Tsegelnjuk, P. D. 1978. On the evolution of late Silurian Monograptidae Lapw. 1873 (Graptolithina) (In Russian). Geologicheskii zhurnal 38:88–98.

Tsegelniuk, P. D. 1988. Graptolity gruppy *Monograptus ultimus* Perner, 1889 i nektorye nerodstvekhnye monograptidy. [Graptolites of the *Monograptus ultimus* Perner, 1899 group and some unrelated monograptids]. *In* Graptolites in the Earth History. Abstracts 5th Symposium on investigation of graptolites in USSR. October 26–28, 1988. Vilnius, 1988. p. 84–87.

Tsegelnjuk, P. D. 1998. Problems in the evolution of the Silurian Uncinatograptinae and their stratigraphic value. Temas Geologico-Mineros ITGE 23:271–273.

Tullberg, S. A. 1883. Skånes Graptoliter II. Graptolitfaunorna i Cardiolaskiffern och Cyrtograptusskiffern. Sveriges Geologiska Undersökning, Serie C. Afhandlingar och Upsatser 55:1–43, 4 pl.

Urbanek, Adam. 1954. Some observations on the morphology of Monograptidae. Acta Geologica Polonica 4:291–306.

Urbanek, Adam. 1958. Monograptidae from erratic boulders of Poland. Acta Palaeontologica Polonica 9:1–105.

Urbanek, Adam. 1960. An attempt at biological interpretation of evolutionary changes in graptolite colonies. Acta Palaeontologica Polonica 5(2):127–234.

Urbanek, Adam. 1963. On generation and regeneration of cladia in some Upper Silurian monograptids. Acta Palaeontologica Polonica 8(2):135–254.

Urbanek, Adam. 1966. On the morphology and evolution of the Cucullograptinae (Monograptidae, Graptolithina). Acta Palaeontologica Polonica 11(3–4):291–544, pl. 1–47.

Urbanek, Adam. 1970. Neocucullograptinae n. subfam. (Graptolithina) their evolutionary and stratigraphic bearing. Acta Palaeontologica Polonica 15(2–3):163–388, pl. 1–45.

Urbanek, Adam. 1995. Phyletic evolution of the latest Ludlow spinose monograptids. Acta Palaeontologica Polonica 40(1):1–17.

Urbanek, Adam. 1997a. Late Ludfordian and early Pridoli monograptids from the Polish lowland. Palaeontologia Polonica 56:87–231.

Urbanek, Adam. 1997b. The emergence and evolution of linograptids. Palaeontologia Polonica 56:233–269.

Urbanek, Adam, Sigitas Radzevičius, Anna Kozłowska, & Lech Teller. 2012. Phyletic evolution and iterative speciation in the persistent *Pristiograptus dubius* lineage. Acta Palaeontologica Polonica 57 (3):589–611.

Urbanek, Adam, & Lech Teller. 1974. Sicula and thecae in *Monograptus* (*Testograptus*) *testis*. Special Papers in Palaeontology 13:237–248.

Urbanek, Adam, & Lech Teller. 1997. Graptolites and stratigraphy of the Wenlock and Ludlow Series in the East European Platform. Palaeontologia Polonica 56:23–57.

Walker, Margaret. 1953. The development of *Monograptus dubius* and *Monograptus chimaera*. Geological Magazine 90(5):362–373.

Wang, Xiaofeng. 1977. The discovery of the latest Silurian and Early Devonian monograptids from Qinzhou, Guangxi and its significance. Acta Geologica Sinica 2:190–205. In Chinese with English summary.

Wang, Xiaofeng, Yuqin Jin, Zhaofong Wu, Hanying Fu, Zuocong Li, & Guoqian Ma. eds., 1977. Graptolites of Central-South China. *In* Handbook to Palaeontology of Central-South China. Part 1. Early Palaeozoic Era. Geological Publishing House. Beijing. p. 266-371, pls. 82-116.

Wang, Xiaofeng, Shizhao Ni, Qinglan Zhen, Guanghong Xu, Zhihong, Liwen Xiang, & Caigeng Lai. 1987. Biostratigraphy of the Yangtze Gorge Area (2). Early Palaeozoic Era. Geological Publishing House, Beijing, China. 641 p., 72 pl. In Chinese with English summary, p. 548–549.

Whittingham, Misha, Sigitas Radzevičius, & Andrej Spiridonov. 2020. Moving towards a better understanding of iterative evolution: An example from the late Silurian Monograptidae (Graptolithina) of the Baltic Basin. Palaeontology 63(4):629–649.

Wilkinson, James. 2018a. *Monoclimacis micropoma* (Jaekel, 1889). Atlas of Graptolite Type Specimens 3.52.

Wilkinson, James. 2018b. *Neodiversograptus nilssoni* (Barrande, 1850). Atlas of Graptolite Type Specimens 3.58.

Williams, Mark, & Jan Zalasiewicz 2004. The Wenlock *Cyrtograptus* species of the Builth Wells District, central Wales. Palaeontology 47(2):223–263.

Williams, S. H., & L. C. Clarke. 1999. Structure and secretion of the graptolite prosicula, and its application for biostratigraphical and evolutionary studies. Palaeontology 42:1003–1015.

Wood, E. M. R. 1900. The Lower Ludlow Formation and its graptolite fauna. Quarterly Journal of the Geological Society of London 56:415–492.

Yang, Daquan, Yunan Ni, Jijin Li, Xu Chen, Yaokun Lin, Jianhua Yu, Guangsheng Xia, Shiding Jiao, Yiting Fang, Meiyu Ge, & Enzhi Mu. 1983. Hemichordata. *In* Nanjing Institute of Geology and Mineral resources, ed., Palaeontology Atlas of East China Area (Part 1). Early Palaeozoic volume. Geological Publishing House, Beijing, China. p. 353–508.

Ye, S.-H. 1978. Class Graptolithina. *In* Atlas of Fossils of Southwest China, Sichuan volume, Part 1: Sinian to Devonian. Chengdu Institute of Geology and Mineral Resources, eds., Geological Publishing House, Beijing, China, 617 p. p. 431–686.

Yin, T. H. 1937. Brief description of the Ordovician and Silurian fossils of Shihtien. Bulletin of the Geological Society of China 16:281–302, 2 pl.

Zalasiewicz, J. A. 1995. The structure and affinities of *Lapworthograptus grayae* (Lapworth, 1876). Scottish Journal of Geology 31(1):29–36.

Zalasiewicz, J. A. 2000a. *Atavograptus atavus* (Jones, 1909). Atlas of Graptolite Type specimens 1.6.

Zalasiewicz, J. A. 2000b. *Coronograptus gregarius gregarius* (Lapworth, 1876). Atlas of Graptolite Type specimens 1.13.

Zalasiewicz, J. A. 2000c. *Monoclimacis vomerina vomerina* (Nicholson, 1872). Atlas of Graptolite Type specimens 1.48.

Zalasiewicz, J. A. 2008a. *Huttagraptus praestrachani* Rickards, Hutt & Berry, 1977. Atlas of Graptolite Type Specimens 2.73.

Zalasiewicz, J. A. 2008b. *Monograptus triangulatus triangulatus* (Harkness, 1851). Atlas of Graptolite Type specimens 2.92.

Zalasiewicz, J. A., & Michael Howe. 2003. A case of profound astogenetic metamorphosis: The structure and affinities of *Awarograptus nodifer* (Törnquist, 1881). Scottish Journal of Geology 39(1):45–49.

Zalasiewicz, J. A., & D. K. Loydell. 2008. *Lapworthograptus grayae* (Lapworth, 1876). Atlas of Graptolite Type Specimens 2.33.

Zalasiewicz, J. A., & Mark Williams. 2000. *Monoclimacis adunca* (Bouček, 1931). Atlas of Graptolite Type specimens 1.43.

Zalasiewicz, J. A., & Mark Williams. 2008. *Cyrtograptus murchisoni* Carruthers, 1867. Atlas of Graptolite Type Specimens 2.60.

Zalasiewicz, Jan, Mark Williams, & Maxine Akhurst. 2003. An unlikely evolutionary lineage: the Rhuddanian (Silurian, Llandovery) graptolites *Huttagraptus*? *praematurus* and *Coronograptus cyphus* re-examined. Scottish Journal of Geology 39(1):89–96.

Zhao, Yuting. 1984. On the evolution of monograptids based on the contraction of the thecal apertural margin. Acta Geologica Sinica 58(2):97–105.