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PART V, SECOND REVISION, CHAPTER 21: SUBORDER GLOSSOGRAPTINA: INTRODUCTION, MORPHOLOGY, AND SYSTEMATIC DESCRIPTIONS

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Suborder GLOSSOGRAPTINA Jaanusson, 1960

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

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

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

INTRODUCTION TO THE GLOSSOGRAPTINA

Numerous, well-preserved relief specimens and even chemically isolated specimens of the Glossograptina provide the basis for a detailed understanding of colony construction. The main uniting synapomorphic character of the Isograptidae as the basal Glossograptina is the isograptid symmetry, in which the line of symmetry passes between the sicula and th1[1] (Fig. 1.2–1.3). This differs considerably from the maeandrograptid symmetry in earlier dichograptids (Fig. 1.1). In the maeandrograptid symmetry, the line of symmetry passes through the sicula, with th1[1] and th1[2] positioned symmetrically on both sides of the sicula. The maeandrograptid symmetry occurs in early Tremadocian anisograptids, and variations may be due to the orientation of the sicula, which can be vertical or inclined.

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

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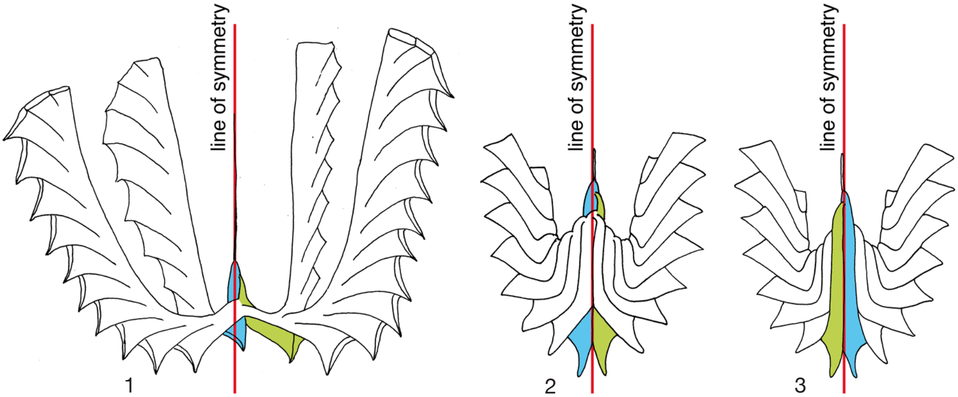

FIG. 1. The proximal symmetry of the Glossograptina. *1, Tetragraptus askerensis* (MONSEN, 1937), maeandrograptid proximal symmetry of a dichograptid in reverse view (adapted from MALETZ, 2011, fig. 2); 2–3, *Arienigraptus dumosus* (HARRIS, 1933), isograptid symmetry in reverse (*2*) and obverse (*3*)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

and the stem isograptids of the superorder Pan-Bireclinata of MALETZ, CARLUCCI, and MITCHELL (2009).

EVOLUTION

The Isograptidae, as the basal Glossograptina, differ from the derived, monopleural Glossograptina, mainly in that the stipes do not have monopleural arrangement. Differences in thecal style and proximal development are minor. COOPER (1973) suggested a reclined didymograptid, similar to *Didymograptus eocaduceus* HARRIS, 1933, as the ancestor to the Isograptidae. However, MALETZ and MITCHELL (1996); MALETZ, CARLUCCI, and MITCHELL (2009); and MALETZ (2010) identified the Tetragraptidae as ancestral to the Isograptidae. The abundant three- and two-stiped reclined tetragraptids of the upper Floian (Lower Ordovician) would have required only the loss of the distal dicalycal thecae, followed by a change to isograptid symmetry, to be transformed into an isograptid without an intermediate didymograptid or expansograptid ancestor. MALETZ (2011) illustrated a number of three- and two-stiped reclined tetragraptids that may represent the transitional forms in the transformation of the reclined tetragraptids to the isograptids.

Cladistic analyses (MALETZ & MITCHELL, 1996; MALETZ, CARLUCCI, & MITCHELL, 2009) have provided insights into the evolutionary relationships of the Glossograptina that indicate that the Glossograptidae and the Axonophora evolved independently from the Isograptidae (Fig. 2). The Isograptidae lead to the scandent, monopleural Glossograptidae through the partial monopleural genera *Skiagraptus* and *Bergstroemograptus* (MALETZ & MITCHELL, 1996), but the differentiation of the two groups is difficult as the new synapomorphies are not recognizable in flattened material. A second independent lineage leads from the derived arienigraptids to the axonophoran graptolites (e.g., *Exigraptus;* Fig. 2). The members of the family Isograptidae provide a number of important biostratigraphic marker species for the Dapingian to Darriwilian (Ordovician) time interval (HARRIS, 1933; COOPER, 1973).

Family ISOGRAPTIDAE Harris, 1933

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

Two-stiped, reclined to scandent or proximally scandent (dipleural) Glossograptina with isograptid or derived maeandrograptid symmetry, with or without manubrium; sicula conical, often elongated, widening slowly towards aperture, with small prosicula; origin of th1^1 in lower part of prosicula; proximal development type isograptid, dextral; thecae simple, widening tubes,

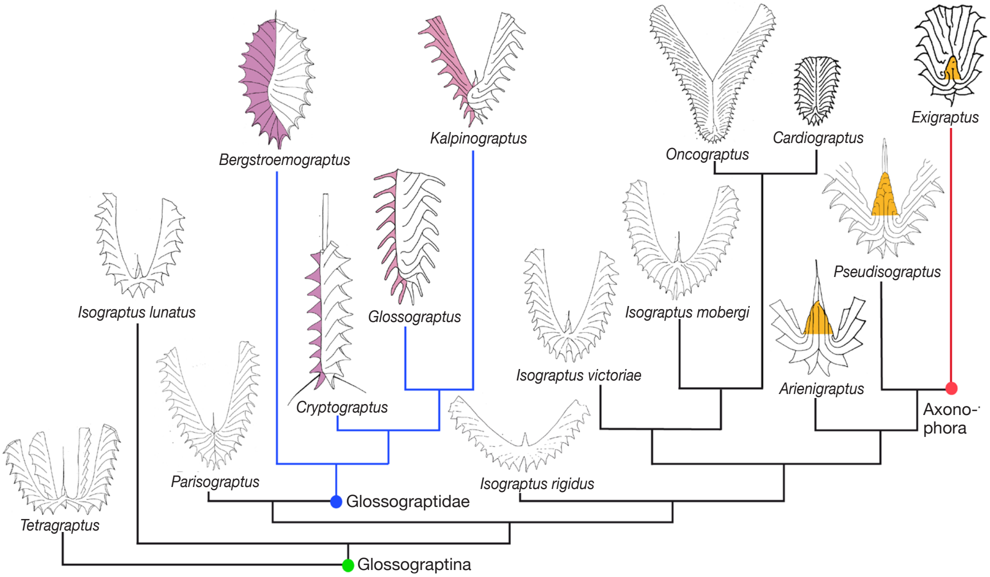

FIG. 2. Evolutionary relationships of the Glossograptina (new).

often with distinct rutella. *Middle Ordovician (Dapingian–Darriwilian):* worldwide.

The family Isograptidae is the paraphyletic partial clade based on the reclined, two-stiped colony with the isograptid symmetry as defining synapomorphy (Maletz & Mitchell, 1996). As discussed above, it excludes the monophyletic Glossograptidae with the monopleural colony shape and the virgellate Axonophora with the biserial, dipleural development of the colonies (Fig. 2). The Axonophora and the Glossograptidae originated independently from the Isograptidae, but the details of the transformations are not yet clear.

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

The family Isograptidae includes several other family group taxa. Mu and Zhan (1966) established the Cardiograptidae for biserial, dipleural taxa and included *Cardiograptus*, *Paracardiograptus,* and *Skiagraptus*, of which *Skiagraptus* is now referred to the Glossograptidae, due to its partly monopleural arrangement of the stipes. Yu and Fang (1981) originally defined the Arienigraptinae as a subfamily of the Kalpinograptidae Jiao, 1977 (listed as Qiao, 1977, in Mu & others, 2002, p. 369). Maletz and Mitchell (1996) elevated the subfamily to family rank and recognized the genus *Arienigraptus* as a pseudisograptid, while *Kalpinograptus* is now

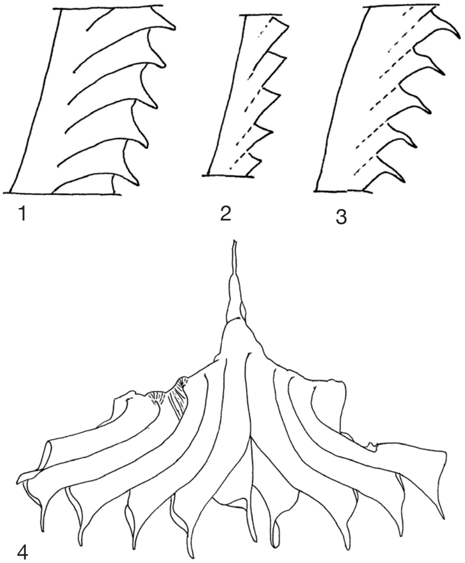

FIG. 3. Thecal style in the Isograptidae. *1,* Isograptid thecal style; *2,* simple manubriate thecal style; *3,* advanced manubriate thecal style (*1–3,* adapted from Cooper & Ni, 1986, fig. 3); *4, Arienigraptus geniculatus* (SKEVINGTON, 1965), PMU Öl 1209, holotype showing advanced manubriate thecal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

regarded as a secondarily two-stiped glossograptid (MALETZ & MITCHELL, 1996). Following HARRIS (1933), the arienigraptid genera *Arienigraptus* and *Pseudisograptus* are included herein in the Isograptidae and interpreted as a paraphyletic group from which the Axonophora (the biserial, dipleural graptolites) originate (MITCHELL, MALETZ, & ZHANG, 1995; FORTEY, ZHANG, & MELLISH, 2005; MALETZ, 2010).

Defining the precise boundary between the Isograptidae and the Axonophora has been problematic. Because of the scarcity of well-preserved and isolated specimens, it is difficult to observe the important synapomorphic characters in this transition. The taxonomy adopted in this revision places the biserial, dipleural taxa with a distinct manubrium (*Exigraptus*, *Apiograptus*) and derived from the genus *Pseudisograptus* in the Axonophora (MALETZ, 2014). This serves as a simple distinction of the latter group from the Isograptidae.

MORPHOLOGY

The tubaria and thecal styles of the Isograptidae are fairly simple and show little morphological variation. In addition to their characteristic isograptid symmetry, the species of the Isograptidae generally possess a dextral mode of growth (Fig. 1). Very few specimens with a sinistral development have been discovered, even though this development is common in earlier graptoloids (HUTT, 1974). COOPER and FORTEY (1982, fig. 54C–D) illustrated a single sinistral specimen of *Isograptus imitatus* HARRIS, 1933. A sinistral proximal development is also present in a number of specimens of *I. spjeldnaesi* MALETZ, 2011, from Norway (MALETZ, 2011, fig. 6A).

The thecae of the Isograptidae are simple tubes, slender and widening slowly towards the aperture in most taxa. Apertures have a pronounced ventral rutellum in most isograptids but show no additional elaboration (Fig. 3.1). In contrast, the manubriate taxa *Arienigraptus* and *Pseudisograptus* possess more variation in their thecal style. The thecae are simple tubes, slowly widening towards the aperture and without a rutellum in early taxa. COOPER and NI (1986) termed this thecal style the simple manubriate thecal style (Fig. 3.2). In derived taxa, the distal thecae often show long and strongly differentiated rutella of the advanced manubriate thecal style (Fig. 3.3). These thecal apertures are more similar to the lamelliform rutellum of the monopleural glossograptids (see, by way of comparison, MALETZ, 2010). Paired lateral lappets appear frequently on the thecal apertures of the arienigraptids and have been illustrated from chemically isolated material in *Arienigraptus geniculatus* (SKEVINGTON, 1965) (Fig. 3.4).

In the Isograptidae, the proximal development is of the isograptid type (COOPER & FORTEY, 1983), and its basic construction is identical to the development in the Anisograptidae (MALETZ, 1994). The development essentially describes the presence of two crossing canals and a dicalycal $th1^2$ on the reverse side of the tubarium. The thecal

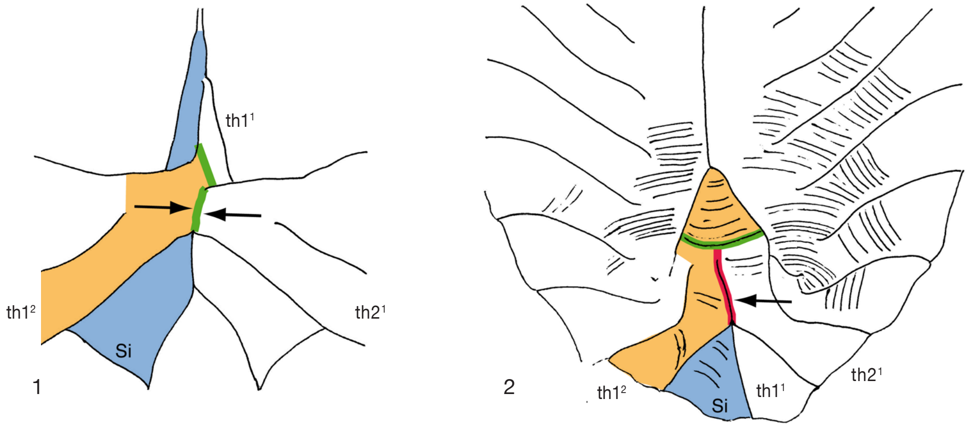

Fig. 4. Isograptid development in the Isograptidae, with thecal notation. *1, Isograptus rigidus* Maletz, 2011, showing successive origins of th1^2 and th2^1 (*green lines*) in a normal isograptid-type proximal development; *2, Cardiograptus amplus* Hsü, 1947, showing paired origin of th1^2 and th2^1 (*green line*) from a downward growing flange and suture between th1^2 and th2^1 (*red line*); *Si,* sicula (new; adapted from photograph in Fortey, Zhang, & Mellish, 2005, fig. 10a).

origins of th1^2 and th2^1 are seen in close succession as nearly vertical openings (Fig. 4.1). The crossing canals are subhorizontally oriented, growing in opposite directions, and have different dimensions, with crossing canal 1 wider than crossing canal 2 (Fig. 4.1). This branching also shows the origins of the two daughter thecae of the dicalycal theca th1^2 at different positions along the mother theca.

In a number of derived isograptids, the development of the proximal end is modified: the two asymmetrical crossing canals are replaced by a much more symmetrical construction without changing the position of the dicalycal theca (Fig. 4.2). In these taxa, the ventral wall of th1^1 grows vertically downwards as a widening flange along the sicula for some distance before it begins to produce a small lip, from which a strip of fusellar material is formed, dividing the temporary opening of the downward-growing thecal tube into two large, lateral openings. From there, the tubes of th1^2 and th2^1 grow as a symmetrical pair. Later thecae are formed in the normal way. This development produces a feature that recalls the arienigraptid suture in relief specimens (Fig. 4.2), but it does not include the parallel downward growth of th2^1 and th2^2. This feature can be found in a number of *Isograptus* species (e.g., *I. maximodivergens* and *I. mobergi*) and is present in *Oncograptus* and *Cardiograptus.*

The reclined arrangement of the stipes in the Glossograptina is the result of a shortening of the distance between thecal origins and the increase in width of the thecal foramina in the early thecae of the isograptids of the *I. victoriae* lineage. A number of proximal thecae produce this arrangement, while the distal thecae all possess approximately equal origination distances. The complex proximal development of the genus *Parisograptus* is known from a few specimens only (Maletz & Zhang, 2003). It includes an upward stacking of thecal origins in the proximal end and an initially biserial, dipleural stipe arrangement (Fig. 5).

The arienigraptids increase the complexity of the proximal development by the formation of a manubrium and the insertion of intrathecal folds in most taxa. In these, the thecal overlap may be more complex with the second thecal pair (th1^2 and th2^2) covering most of the sicula and th1^1 on the reverse side (Fig. 5). Due to this development, the obverse and reverse sides of the tubaria look quite different: on the obverse side, the sicula and th1^1 are freely visible

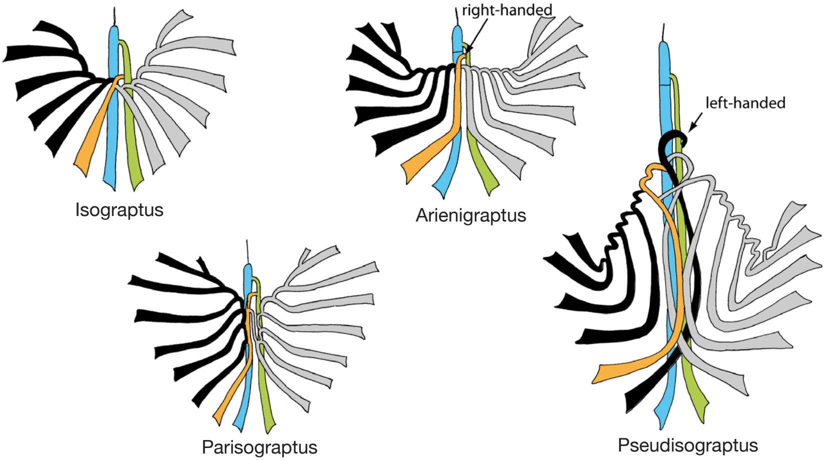

FIG. 5. Growth directions of proximal thecae in the Isograptidae. *Green,* th1^1; *gray,* stipe one; *black,* stipe two; all diagrams in reverse view; note that th2^2 is the dicalycal theca in *Pseudisograptus* (adapted from Maletz & Mitchell, 1996, and Maletz & Zhang, 2003).

along their full lengths (e.g., *Pseudisograptus manubriatus janus* COOPER & NI, 1986).

The manubrium, a massive and complex structure, dominates the proximal end of the isograptids of the genera *Arienigraptus* and *Pseudisograptus* (Fig. 6). The second thecal pair (th1^2 and th2^1) forms the crossing canals but instantly grows downwards along the sicula and th1^1 on the reverse side of the tubarium, forming the characteristic arienigraptid suture. The paired sicula and th1^1 are completely exposed on the obverse side of the colony (Fig. 6.3), but they are covered on the reverse side for most of their length by the second thecal pair (Fig. 6.2). In *Pseudisograptus*, the more complex overlap of the proximal thecae covers the arienigraptid suture (Fig. 6.1).

The thecal length determines the growth patterns and development of the manubrium. The thecae are parallel sided in taxa with a large manubrium (Fig. 7.1) but widen more quickly in taxa with a reduced manubrium (Fig. 7.5–7.6). The arienigraptid proximal structure consists of parallel-downward and distally outward-growing proximal thecae, the manubrium wedge (Fig. 1.3, Fig. 6.1). This is a complex and difficult-to-decipher construction of unknown use in all arienigraptids. The massive structure of the manubrium is a completely new development in a few derived taxa of the isograptids. In some taxa, this structure is modified by a complex of overlapping distal thecae (Fig. 6.1, Fig. 7.3). All thecal origins are dorsal and are characterized by the development of intrathecal folds in most arienigraptids (Fig. 7.5,7). Other taxa clearly develop prothecal folds at the origins of the thecae (Fig. 7.1). The connection between these two types of thecal modification is unclear.

The shape of the manubrium is quite variable (Fig. 7). In *Pseudisograptus*, the manubrium form a massive triangular feature around the sicula positioned above the base of the stipes (Fig. 1.3, Fig. 7.3). The manubrium has long, sloping shoulders with variable inclination. In Darriwilian species of *Arienigraptus*, the manubrium shoulders are often horizontal (or nearly horizontal) and the downward growth of the initial thecae is reduced (Fig. 7.1,5).

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

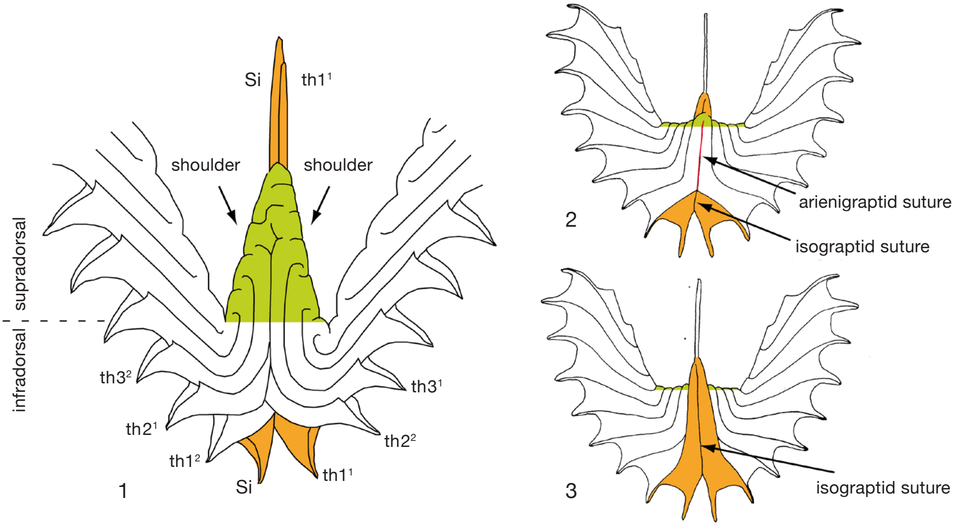

Fig. 6. The arienigraptid manubrium. *1, Pseudisograptus manubriatus* subsp., showing large manubrium with sloping manubrium shoulders, thecal notation, and division of supradorsal and infradorsal; *2–3, Arienigraptus zhejiangensis* Yu & Fang, 1981; *2,* reverse view, small manubrium wedge and nearly horizonal manubrium shoulders, arienigraptid suture (*red*) between th1^2 and th2^1, isograptid suture visible below; *3,* obverse view, showing isograptid suture; *green*, manubrium wedge or supradorsal part of manubrium; *orange*, first thecal pair; *Si*, sicula (new).

Subfamily ISOGRAPTINAE Harris, 1933

[Harris, 1933, p. 85]

Two-stiped, reclined to scandent or proximally scandent, dipleural Glossograptina with isograptid symmetry; sicula conical, often elongated, widening slowly towards the aperture, with small prosicula; origin of th1^1 in lower part of prosicula; proximal development type isograptid, dextral; thecae simple, widening tubes, often with distinct rutellum. *Middle Ordovician (Dapingian,* Isograptus lunatus *Biozone–Darriwilian,* Nicholsonograptus fasciculatus *Biozone):* worldwide.

Isograptus Moberg, 1892, p. 345 [**Didymograptus gibberulus* Nicholson 1875, p. 271; M]. Reclined, two-stiped isograptids; thecae simple with rutellate apertures, shorter and wider in earlier species, with thecal length increasing in later species; proximal development type isograptid, dextral, with low prosicular origin of th1^1, rarely sinistral. *Middle Ordovician (lower Dapingian*, Isograptus lunatus *Biozone–Darriwilian,* Levisograptus austrodentatus *Biozone):* worldwide.——Fig. 8,*1a. *I. gibberulus* (Nicholson), lectotype, SM A17779, Randal Craig, Skiddaw, English Lake District, UK (Rushton, 2000).——Fig. 8,*1b. I. spjeldnaesi* Maletz, 2011, holotype, T878-1, left-handed specimen (Maletz, 2011, fig. 6A).——Fig. 8,*1c. I. mobergi* Maletz, 2011, holotype, SGU 5249 (Maletz, 2011, fig. 6).

Parisograptus Chen & Zhang, 1996, p. 86 [**Isograptus curvithecatus* Hsü, 1959, p. 168; OD; =*Isograptus forcipiformis* Ruedemann, 1904, p. 699; Maletz & Zhang, 2003, p. 301]. Reclined, two-stiped isograptids; crowded and dorsally stacked origins of early thecae with upward and downward early growth on reverse side; colony initially biserial, dipleural; proximal development type isograptid, dextral, with origin of th1^1 in lower part of prosicula; thecae of uniform length and overlapping, with rutella elongated proximally and rutella of sicula and th1^1 united in some species; fusellum attenuated in most species. *Middle Ordovician (Dapingian,* Isograptus maximus [=Arienigraptus hastatus] *Biozone)–Darriwilian,* Nicholsonograptus fasciculatus *Biozone):* Australia, New Zealand, China, UK, Sweden, Norway, USA, Canada, Argentina.——Fig. 8,*2a.* **P. curvithecatus* (Hsü), holotype (Hsü, 1959, fig. 2).——Fig. 8,*2b. P. forcipiformis* (Ruedemann, 1904), lectotype, NYSM 5881, Ash Hill Quarry, Mount Merino, Hudson, New York, USA (new).——Fig. 8,*2c. P. caduceus* (Salter in Bigsbyi, 1853), NIGP 12523, reverse view (Maletz & Zhang, 2003, fig. 1A).

Procardiograptus Xiao, Xia, & Wang, 1985, p. 435 [**Cardiograptus* (*Procardiograptus*) *uniformis*; OD]. Scandent, biserial isograptid with conspicuous, heart-shaped axial cavity in proximal portion; stipes with increasing thecal length and overlap;

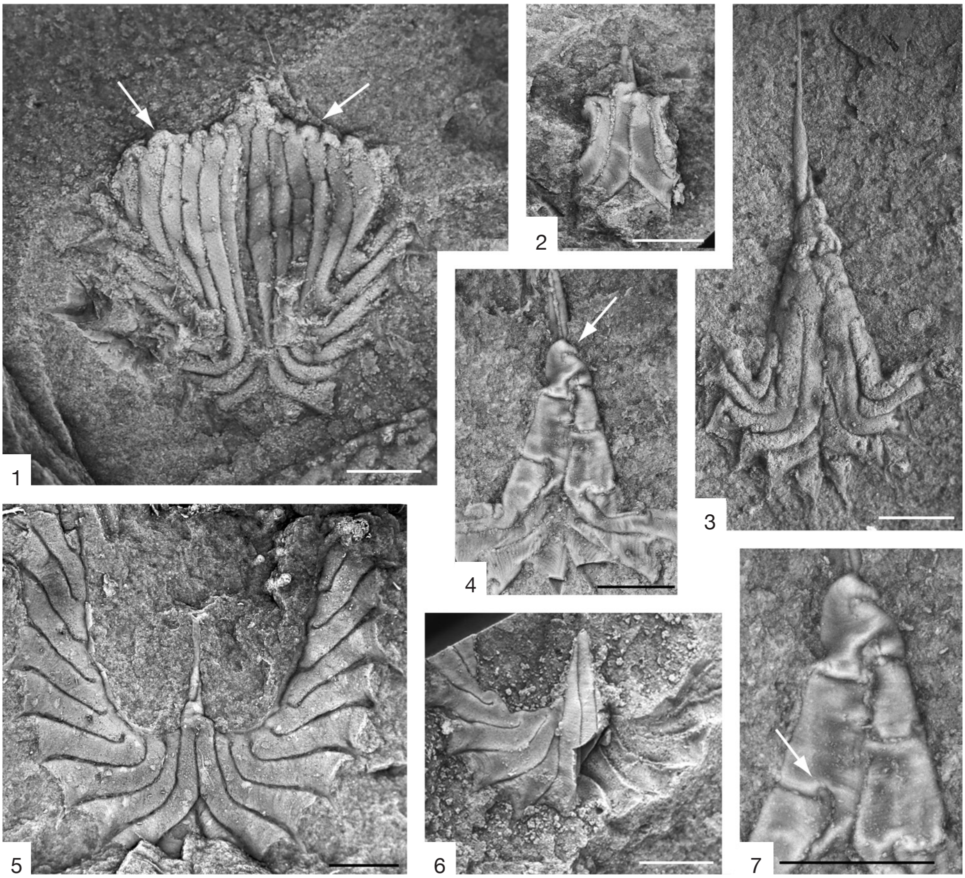

FIG. 7. Examples of manubrium construction. *1, Arienigraptus* sp., LO 12244, Krapperup drill core, Scania, Sweden, specimen with low supradorsal part and long infradorsal part of manubrium, showing prothecal folds (*arrows*); *2, A. zhejiangensis* YU & FANG 1981, PMU 29983, juvenile, Krapperup drill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

thecae simple tubes with distinct rutella; proximal development derived-isograptid type, dextral, with origin of th1^1 low in the prosicula. *Middle Ordovician (upper Dapingian,* Oncograptus magnus–Cardiograptus amplus *Biozones):* China.——FIG. 8,*3a–b*. **P. uniformis; 3a*, NIGP 124849, Hengtang, Zhejiang Province; *3b*, NIGP 124851 Chenjiawu, Zhejiang Province (adapted from Chen, Zhang, & Mitchell, 1995, fig. 26B,D).

Proncograptus XIAO, XIA, & WANG, 1985, p. 434 [**Oncograptus* (*Proncograptus*) *forcatus*; OD]. Initially scandent, biserial isograptid with conspicuous, heart-shaped axial cavity in the proximal portion; two diverging stipes with distally increasing thecal length; thecae simple tubes with distinct rutella; proximal development of derived-isograptid type, dextral with origin of th1^1 low in the prosicula. *Middle Ordovician (upper Dapingian,* Oncograptus magnus *Biozone):* China.——FIG. 8,*4*. *P. robustus* (XIAO, XIA, & WANG, 1985), holotype, Jiangxi Province (adapted from Xiao, Xia, & Wang, 1985, fig. 3).

Cardiograptus HARRIS & KEBLE in HARRIS, 1916, p. 66 [**C. morsus;* M] [=*Paracardiograptus* MU & LEE, 1958, p. 399 (type, *P. hsui;* OD)]. Scandent, biserial isograptids with increasing thecal length distally; thecae simple with distinct rutella; proximal development derived-isograptid type, dextral, with origin of th1^1 low in the prosicula. *Middle Ordovician* (*upper Dapingian,* Cardiograptus morsus

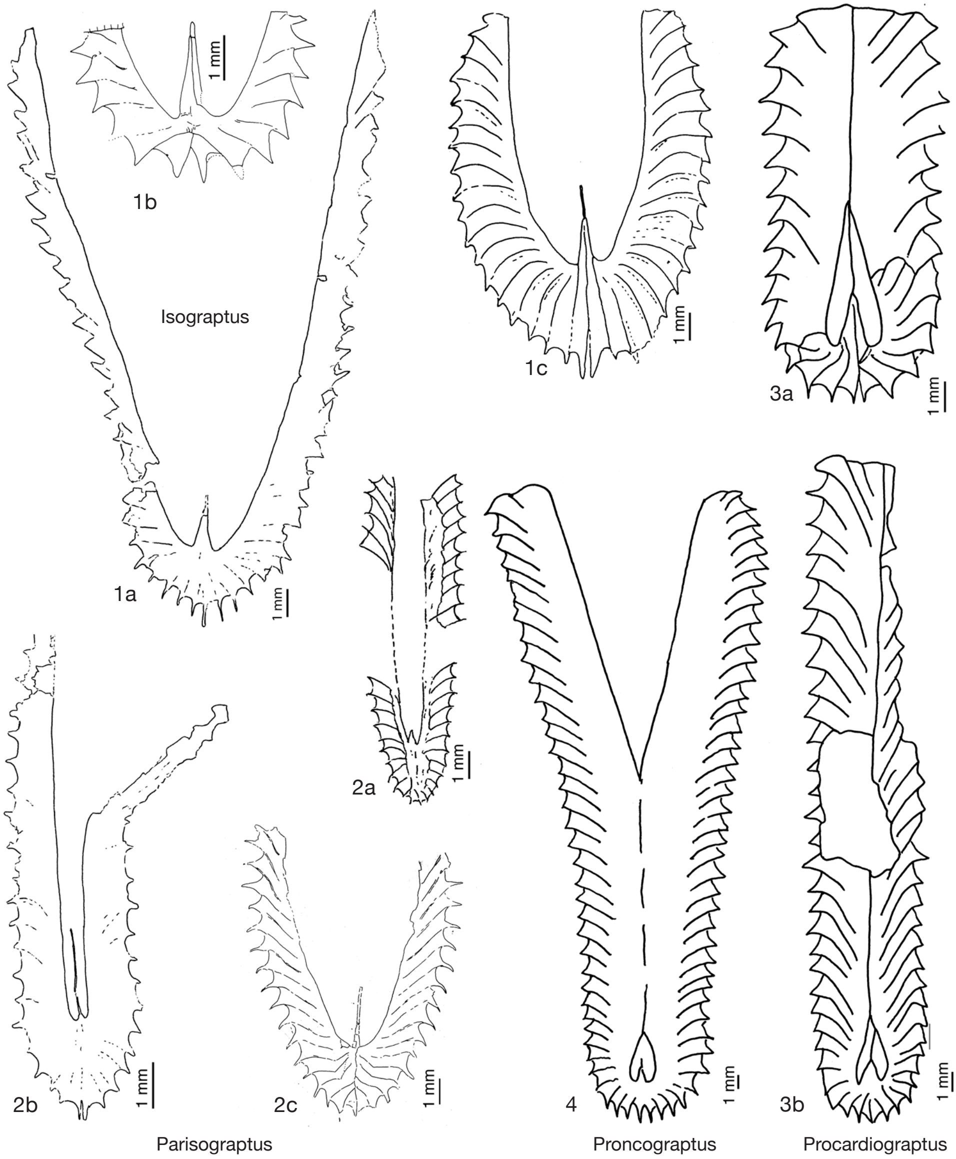

Fig. 8. Isograptidae (p. 7–8)

*Biozone–lower Darriwilian,*Levisograptus austrodentatus *Biozone):* Australia, New Zealand, China, USA, Canada, Argentina——Fig. 9,*2a*. **C. morsus,* NMVP 32148, Chinaman's Creek, Yapeenian 2, Victoria, Australia, (new).——Fig. 9,*2b*. *C. amplus* Hsü, 1947, NIGP 136152, SEM photograph, reverse view (Fortey, Zhang, & Mellish, 2005, fig. 10A).——Fig. 9,*2c–d*. *C. hsui*, Ningkuo Shale, Western Chekiang, China; *2c,* holotype, NIGP 9733, proximal end in reverse view; *2d,* paratype, NIGP 9734, proximal end in obverse view; scale bars, 1 mm (Mu & Lee, 1958, pl. 1,*14*).

Oncograptus Hall, 1914, p. 109 [**O. upsilon;* M]. Initially scandent, biserial isograptid; two distally diverging stipes showing increasing thecal length and overlap; thecae simple tubes with distinct rutella; proximal development of derived-isograptid type, dextral, with origin of th1^1 low in prosicula. *Middle Ordovician (upper Dapingian,* Oncograptus Biozone–*lower Darriwilian,*

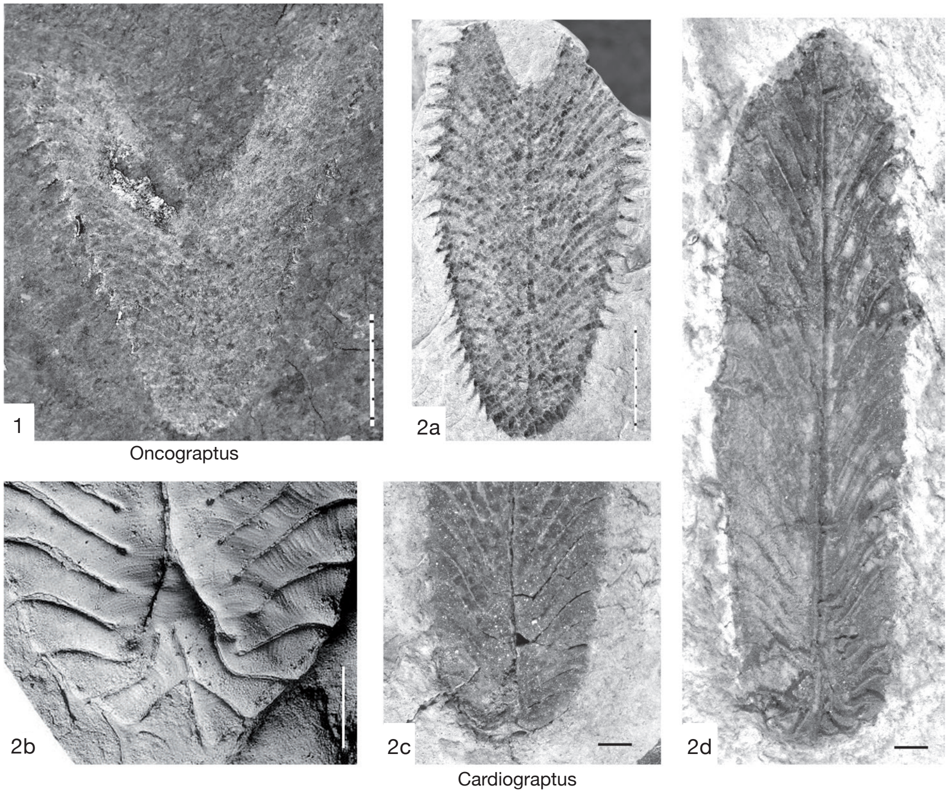

FIG. 9. Isograptidae (p. 8–10)

Levisograptus austrodentatus *Biozone):* Australia, New Zealand, China, USA, Canada, Argentina, Ireland.——FIG. 9,*1.* **O. upsilon,* holotype, NMVP 31177, Victoria, Australia, scale bar 5 mm (new).

Subfamily ARIENIGRAPTINAE Yu & Fang, 1981

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

Two-stiped, reclined glossograptids with isograptid or maeandrograptid symmetry, manubrium invariably present; sicula conical, elongated, largely parallel sided, with short or elongated, conical prosicula; origin of th1^1 in lower part of prosicula; proximal development isograptid type, dextral; origin of th1^2 right- or left-handed or with delayed dicalycal theca; thecae simple, ranging from parallel sided to slightly widening tubes, often with distinct rutella, but some lacking lateral apertural elaborations or with low lateral lappets. *Middle Ordovician (Dapingian,* Isograptus maximus [=Arienigraptus hastatus] *Biozone–Darriwilian,* Levisograptus dentatus *Biozone):* worldwide.

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

COOPER and NI (1986) erected the subfamily Pseudisograptinae, in which they also included the closely related biserial, dipleural genera *Exigraptus* and *Apiograptus.* Following MALETZ (2014), the latter are interpreted in this revision as the earliest

Axonophora, based on the presence of a biserial, dipleural colony retaining the manubrium, and, thus, are separated from the Arienigraptinae.

The subfamily Arienigraptinae, including *Arienigraptus* and *Pseudisograptus,* can be defined as the paraphyletic partial clade, based on a reclined, two-stiped isograptid with the presence of a manubrium as the defining synapomorphy (Maletz & Mitchell, 1996). It excludes the biserial, dipleural Axonophora. The synapomorphies of the Arienigraptinae include (1) a manubrium with the arienigraptid suture between th1^{2} and th2^{1} on the reverse side (Fig. 6.2); (2) an elongated, slender thecae; and (3) a simple, distal thecal apertures lacking the extended rutella of most Isograptidae. The proximal development type is isograptid, dextral with a low prosicular origin of th1^{1}. The derived genus *Pseudisograptus* bears thecae of the advanced manubriate type (Fig. 3.3), often with slight lateral lappets (Fig. 3.4) and a delayed dicalycal theca at th2^{1} or a later one. It also shows a left-handed origin of th1^{2} (Fig. 5.4), a character that Mitchell (1987, p. 355) considered a synapomorphy of the Diplograptina, even though it was present already in the isograptid genus *Pseudisograptus.*

Arienigraptus Yu & Fang, 1981, p. 29 [**A. jiangxiensis;* OD]. Two-stiped, reclined manubriate isograptids with simple arienigraptid proximal structure and isograptid symmetry; th1^{2} and th2^{1} cover sicula and th1^{1} in reverse view, showing arienigraptid suture; proximal development type isograptid, dextral; manubrium wedge of highly variable dimensions; th1^{2} with right-handed origin; thecae simple to advanced manubriate; stipes often poorly developed. *Middle Ordovician (Dapingian,* Isograptus maximus [=Arienigraptus hastatus] *Biozone–Darriwilian,* Holmograptus lentus *Biozone):* Australia, New Zealand, China, UK, Sweden, Norway, USA, Canada, Russia, Argentina, Peru.——Fig. 10,*1a–b.* **A. jiangxiensis; 1a,* drawing of holotype, NIGP 50011 (adapted from Ni, Xiao, & Chen, 1991, fig. 4g); *1b*, photograph of holotype (new, provided by Ni Yunan, 1994).

Pseudisograptus Beavis, 1972, p. 202 [**Didymograptus caduceus* var. *manubriatus* Hall, 1914, p. 108; OD] [=*Xiushuigraptus* Yu & Fang in Yang & others, 1983, p. 406 (type, *X. songxiensis*; M)]. Two-stiped, reclined, manubriate isograptids with complex arienigraptid proximal structure and isograptid to maeandrograptid symmetry; arienigraptid suture between th1^{2} and th2^{1} usually covered by overlap of later thecae; manubrium wedge of highly variable dimensions; proximal development type isograptid, dextral, with delayed dicalycal theca; sicula strongly elongated; th1^{2} with left-handed origin; thecae of advanced manubriate style; stipes sometimes poorly developed; intrathecal folds present. *Middle Ordovician (upper Dapingian,* Oncograptus upsilon *Biozone*–lower Darriwilian, Levisograptus austrodentatus *Biozone):* Australia, New Zealand, China, Russia, UK, Norway, Sweden, USA, Canada, Argentina.——Fig. 10,*2a.* **P. manubriatus manubriatus* (T. S. Hall), holotype, NMVP 31176 (new).——Fig. 10,*2b. P. manubriatus janus* Cooper & Ni, 1986, reverse view (Cooper & Ni, 1986, fig. 17B).——Fig. 10,*2c. P. songxiensis* (Yu & Fang), holotype NIGP 50021 (adapted from Yang & others, 1983, fig. 1).

Family GLOSSOGRAPTIDAE Lapworth, 1873

[Glossograptidae Lapworth, 1873, table 1, facing p. 555] [=Corynoideae Ruedemann, 1908, p. 233; Cryptograptidae Hadding, 1915, p. 332; Corynoididae Bulman, 1945, p. 22, *nom. correct. pro* Corynograptidae Hopkinson & Lapworth, 1875, p. 633; Kalpinograptidae Jiao, 1977, p. 289]

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

The family Glossograptidae is the monophyletic clade based on the scandent, monopleural colony shape as defining synapomorphy (Maletz & Mitchell, 1996). It includes a small group of biserial, monopleural taxa with a simple isograptid proximal development that is covered by the later growth of the colony. Thus, in this group, proximal development and thecal growth patterns are hard to verify and have long been a matter of debate (Bulman, 1945; Strachan, 1985; Maletz & Mitchell, 1996). Some of the younger members (e.g.,

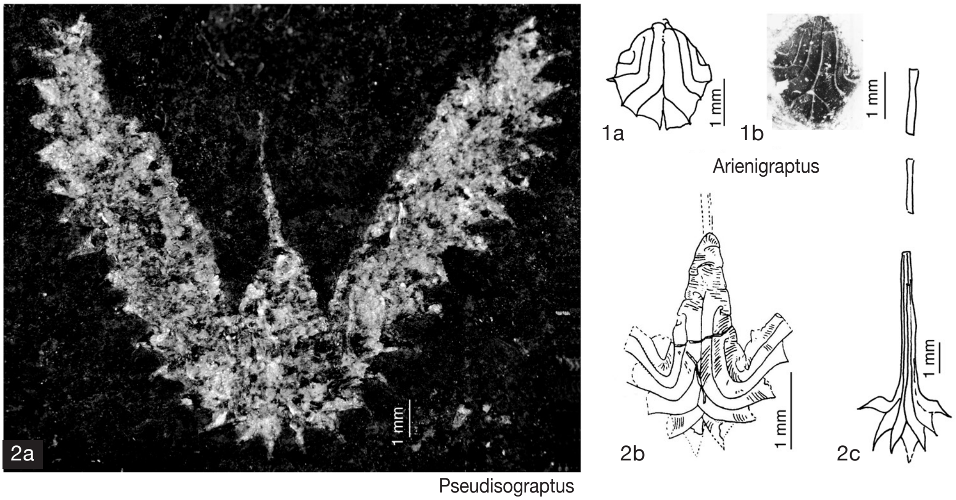

FIG. 10. Isograptidae (p. 11)

Corynoides, Corynites) are included herein, even though their colony development is so reduced that they lack important characteristics for an analysis. MALETZ, CARLUCCI, and MITCHELL (2009, p. 14) defined the taxon as "the common ancestor of *Glossograptus acanthus* ELLES & WOOD, 1908 and the first species to have a monopleural arrangement of the stipes."

MORPHOLOGY

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

The proximal development in all Glossograptidae appears to be of the isograptid-dextral type, with th1^2 as the dicalycal theca. The proximal development type of the Glossograptidae is known from a number of flattened juveniles and is difficult to interpret, with some details remaining conjectural (FINNEY, 1978; MALETZ & MITCHELL, 1996). Relief specimens and isolated juveniles of *Glossograptus* show the sicula and th1^1 as a symmetrical pair (NI & COOPER, 1994, fig. 1–2; MALETZ & MITCHELL, 1996). The origin of th1^1 is variably placed in the prosicula (*Paraglossograptus*, *Corynoides*, *Corynites*) or in the metasicula (*Cryptograptus*). The high prosicular origin of th1^1 in *Paraglossograptus* is unusual, as it occurs in the lower part of the prosicula in most dichograptids and in the ancestral Isograptidae. A higher prosicular origin of th1^1 is also seen in members of the Anisograptidae (HUTT, 1974). In *Paraglossograptus*, th1^1 grows downwards from a point high on the prosicula along the ventral side of the sicula before it gives rise to a dextral development of th1^2 (Fig. 11.3). The sicula and th1^1 form a symmetrical pair, surrounded by dextral coiling of the two scandent stipes. The initial thecae form a considerable glossograptid bulge through the curved overlap of these elongated proximal thecae before shorter, distal thecae grow immediately upwards from their beginning (NI & COOPER, 1994; MALETZ & MITCHELL, 1996). The proximal development of *Cryptograptus* is more difficult to understand, but it appears to follow a similar path. The origin of th1^1 is in the metasicula, and th1^2 initially grows upwards, forming a large loop, and then across the sicula and downwards. As with the other genera, the sicula and th1^1 form a symmetrical pair, but the glossograptid bulge is not developed, as the proximal thecae are short and thecal overlap is low (Fig. 12).

The thecal growth that produces the biserial, monopleural colony shape of the Glossograptidae is initiated by the dextral torsion of the two stipes around the sicula (Fig. 13), as is seen in the partial monopleural development of *Bergstroemograptus crawfordi* (Fig. 13.2–13.3). WHITTINGTON and RICKARDS (1969) described chemically isolated material of *B. crawfordi* under the name *Skiagraptus* sp., while KELLER (1956, pl. 1, *4–5*) identified the species as *Phyllograptus anna* J. HALL, 1865. In completely monopleural colonies of the genus *Glossograptus* (Fig. 13.1), the sicula is fully enveloped by the two stipes, with only the aperture visible, and the colonies look identical in obverse and reverse views.

The proximal development of the genus *Cryptograptus*, as mentioned above, has been difficult to interpret (Fig. 14). In derived taxa of the genus, the fusellum of the initial thecae, including the sicula, is reduced and preserved as a framework of lists only (Fig. 14.2). Different interpretations have been proposed to understand the construction. BULMAN (1945) and STRACHAN (1985) preferred the presence of a centrally positioned sicula (Fig. 14.1) as an explanation. However, MALETZ and MITCHELL (1996) suggested isograptid symmetry of the proximal end with the sicula and th1^1 as a symmetrical pair (Fig. 14.3), based on isolated specimens of *C. schaeferi* from the Table Head Group of western Newfoundland. These specimens clearly show the isograptid symmetry of the sicula and th1^1 (MALETZ & MITCHELL, 1996, fig. 5), thus strengthening the case for its descent from an isograptid ancestor.

The Glossograptidae are characterized by paired lateral apertural spines on the sicula and often also on later thecae. They may not be present on each thecal pair, but they are regularly distributed and form the basis for the four ladder-like strings of mesh, the lacinia, in the genus *Paraglossograptus* (Fig. 15.6). The development of the lacinia is variable, and the spines usually protrude from the meshwork (Fig. 15.3–15.4).

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

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

BULMAN (1945, 1947) was first to describe isolated specimens of *Corynoides* from the Caradoc of Laggan Burn, Scotland (Fig. 16); these showed an elongated, slender prosicula and a long metasicula with a high prosicular origin of the first theca (th1^1), suggesting a relationship with *Glossograptus*. Another typical glossograptid character in *Corynoides* is the development of the lamelliform rutellum,

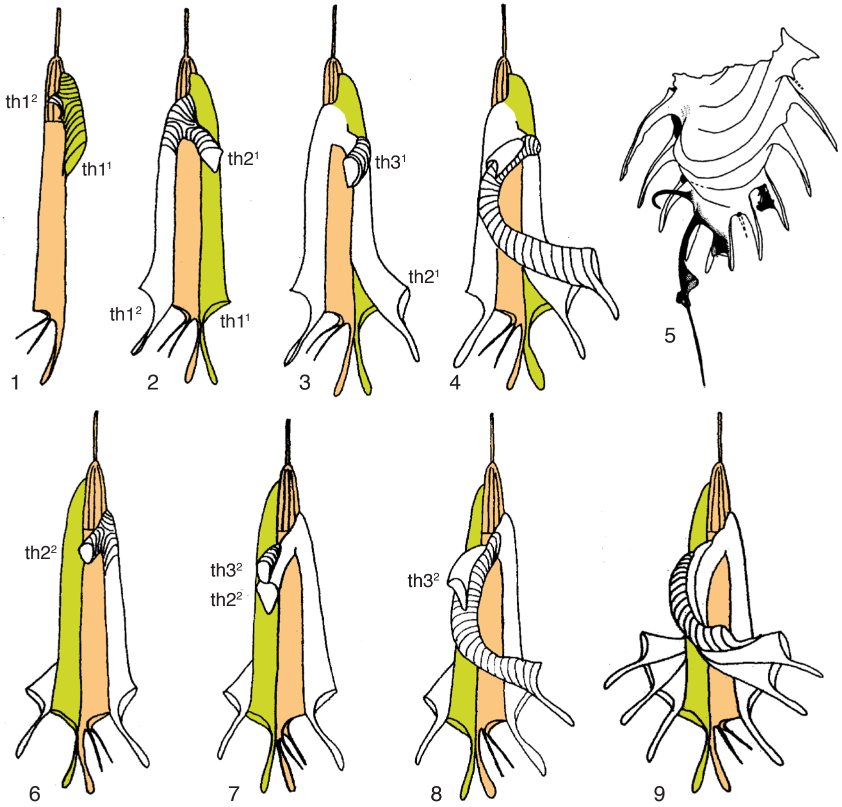

FIG. 11. Early ontogeny of *Paraglossograptus*. *1–4,* reverse view; *6–9,* obverse view; *8–9,* showing development of glossograptid bulge (adapted from Maletz & Mitchell, 1996, fig. 4); *5, P. holmi* (BULMAN, 1931), isolated specimen, western Newfoundland, showing glossograptid bulge (adapted from WHITTINGTON & RICKARDS, 1969, fig. 2C).

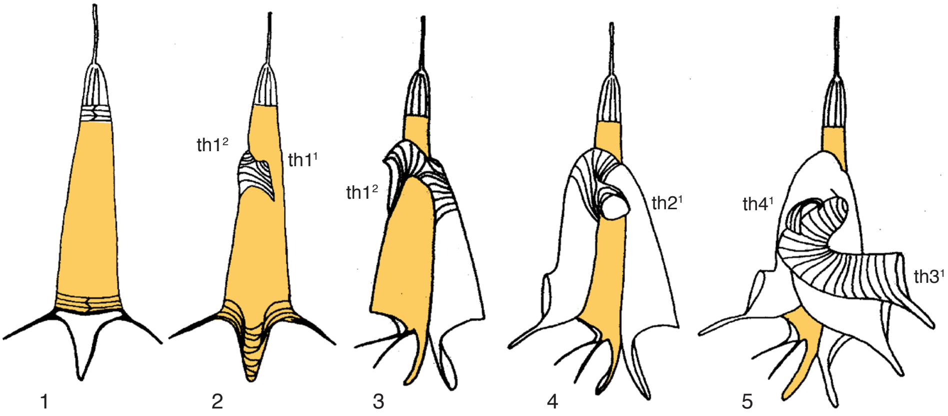

FIG. 12. Early ontogeny of *Cryptograptus schaeferi* LAPWORTH, 1880. *1,* Sicula, dorsal view; *2,* sicula, ventral view; *3,* proximal end with sicula and th1^1, obverse view, showing initial upwards growth of th1^2; *4,* proximal end with sicula and first thecal pair, obverse view; *5,* proximal end with fully developed th3^1 and origin of th4^1; *light brown,* metasicula; reconstructions based on flattened, chemically isolated specimens from western Newfoundland (adapted from Maletz & Mitchell, 1996, fig. 4).

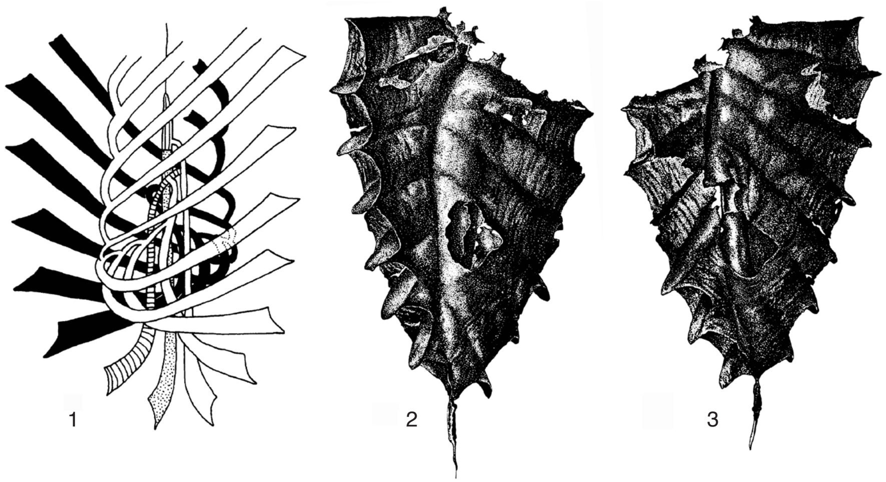

FIG. 13. Monopleural development of the Glossograptidae. *1,* Thecal diagram of *Glossograptus* sp. (adapted from MALETZ & MITCHELL, 1996, fig. 1); *2–3, Bergstroemograptus crawfordi* (HARRIS, 1926), isolated specimen in obverse and reverse views showing the dextral (clockwise) torsion of the stipes (Whittington & Rickards, 1969, fig. 9: illustrated as *Skiagraptus* sp.).

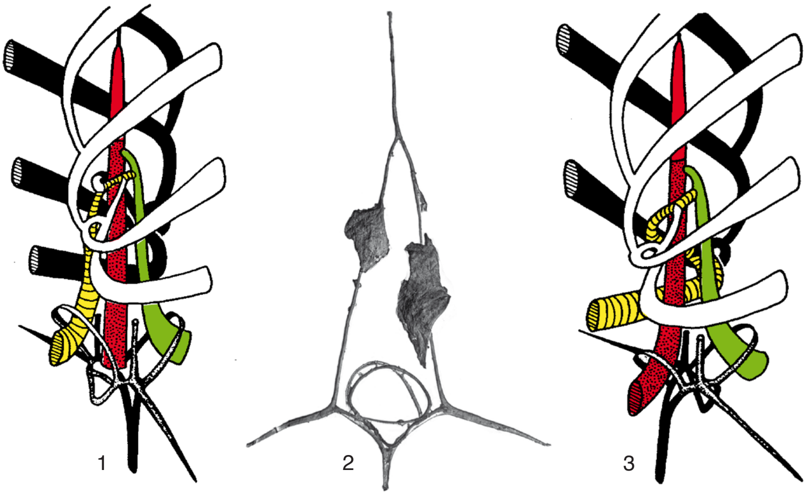

FIG. 14. *Cryptograptus* proximal development. *1,* Interpretation of STRACHAN (1985); *2, Cryptograptus* sp., (new; photograph by Denis Bates); *3,* interpretation of MALETZ & MITCHELL (1996); *red,* sicula; *green,* th1^1; *yellow,* th1^2 (*1, 3,* adapted from Maletz & Mitchell, 1996, fig. 7).

identified as a lamelliform virgella by BULMAN (1945, 1947).

EVOLUTION

A detailed cladistic analysis of the Glossograptidae has not been attempted, and the classification herein is based on data provided by MALETZ and MITCHELL (1996) and MALETZ, CARLUCCI, and MITCHELL (2009). The simple thecae and isograptid symmetry of the Glossograptidae indicates a close relationship to the Isograptidae (FINNEY, 1978; MALETZ & MITCHELL, 1996), as does the proximal development.

The earliest Glossograptidae, from the basal Darriwilian, already possess the biserial,

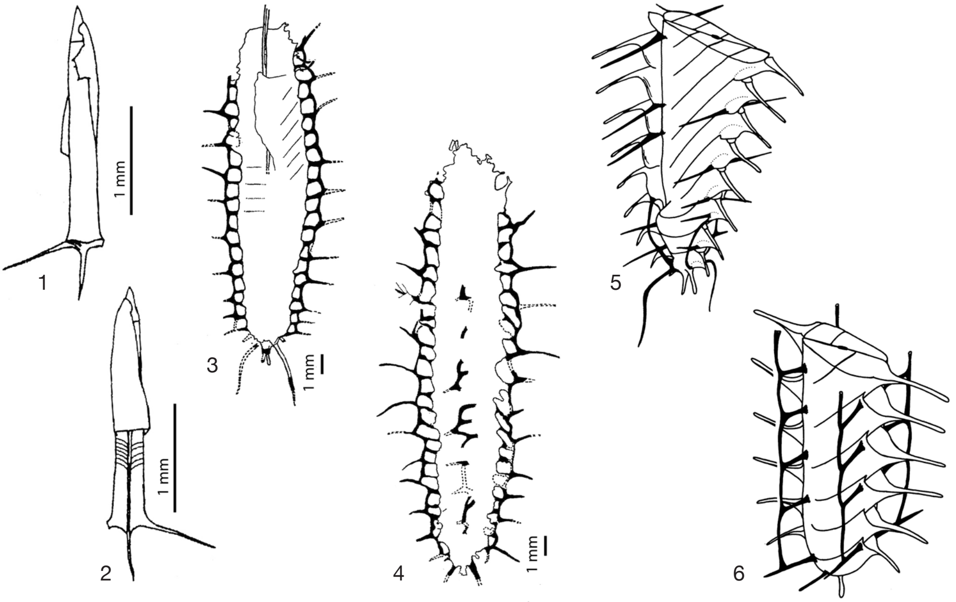

Fig. 15. Thecal spines and lacinia. *1–2, Glossograptus ciliatus* Emmons, 1855, OSU 33142, sicula with lateral apertural spines, pointed rutellum and early growth of th1^1 and th1^2 (adapted from Finney, 1978, fig. 3); *3, Paraglossograptus tentaculatus* (J. Hall, 1865), GSC 950b, syntype showing lacinia development and connection to lateral apertural thecal spines (Rickards, 1972, fig. 1a); *4, Paraglossograptus tentaculatus* (J. Hall, 1865), NMVP 14406, holotype of *Lasiograptus etheridgei* Harris, 1924, showing lacinia (Rickards, 1972, fig. 1b); *5, Paraglossograptus holmi* (Bulman, 1931), reconstruction showing position of lateral apertural spines and prominent glossograptid bulge (adapted from Whittington & Rickards, 1969, fig. 6a); *6, Paraglossograptus proteus* (Harris & Thomas, 1935), reconstruction showing lacinia, lateral apertural spines on sicula and th1^1 not shown (adapted from Whittington & Rickards, 1969, fig. 6b).

monopleural colony development, and transitional taxa have not been recognized in older strata. The genus *Bergstroemograptus*, shown at the base of the clade by Maletz and Mitchell (1996) and Maletz, Carlucci, and Mitchell (2009), possesses the partial monopleural development of a glossograptid, but the taxon is unlikely to represent the base of the clade, as it has been found only in the middle Darriwilian. Nevertheless, *Bergstroemograptus* can be taken as a guide to understanding the early evolution of the clade. The genus *Cryptograptus*, with its metasicular origin of th1^1, separated at an early stage in the evolution of the group, while the remaining taxa maintained a prosicular origin of th1^1.

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

Skiagraptus Harris, 1933, p. 108 [**Diplograptus gnomonicus* Harris & Keble in Harris, 1916, p. 66; OD]. Small, slender, scandent, dipleural(?) glossograptid with rutella of sicula and th1^1 united; thecae short; fusellum attenuated. *Middle Ordovician (upper Dapingian,* Oncograptus upsilon *Biozone–lower Darriwilian,* Levisograptus austrodentatus *Biozone):* New Zealand, Australia, China, Norway, USA, Canada, Argentina.——Fig. 17,*1*. **S. gnomonicus,* NMVP 73118 (Finney & Chen, 1984, fig. 3A).

Bergstroemograptus Finney & Chen, 1984, p. 1198 [**Cardiograptus crawfordi* Harris, 1926, p. 57;

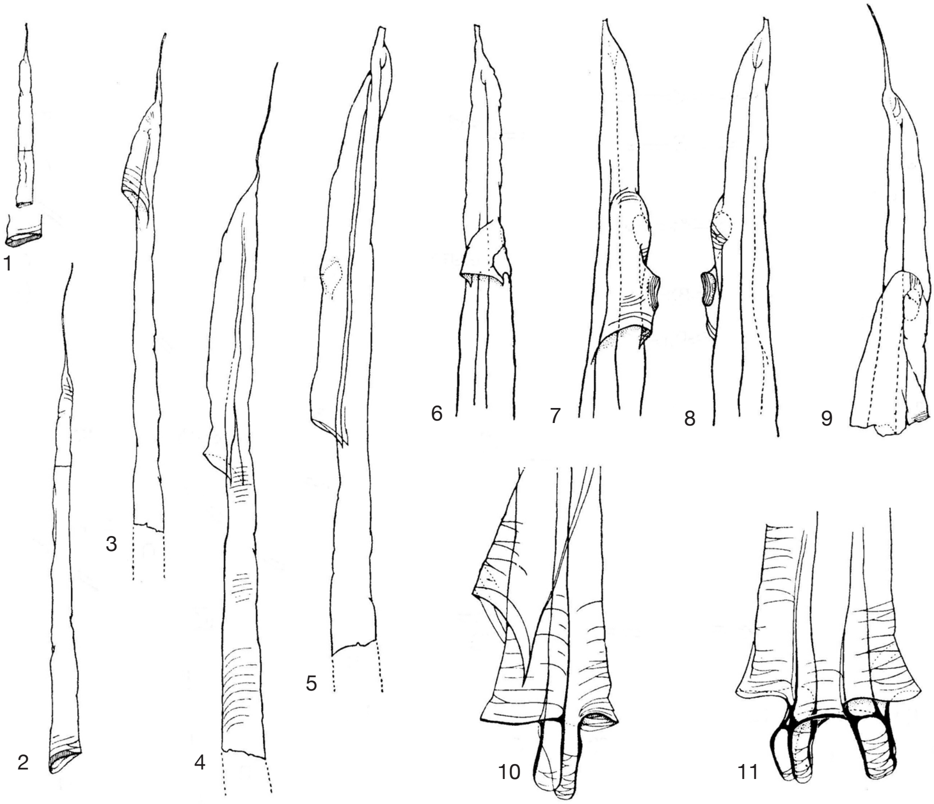

Fig. 16. Ontogeny of the genus *Corynoides*. *1–2,* Sicula development, showing length of prosicula; *3–5,* initial growth of th1; *6–9,* growth of th2; *10–11,* apertures of sicula, th1, and th2 (Bulman, 1947, fig. 39–40).

OD]. Leaf-shaped, dipleural glossograptid with initial monopleural development covering sicula completely on both sides; rutella of sicula and th1^1 united; distal thecae distinctly widening, short. *Middle Ordovician (Darriwilian,* Holmograptus lentus–Nicholsonograptus fasciculatus *Biozones):* Australia, China, UK, Sweden, USA, Canada, Russia, Argentina.——Fig. 17,*2a–b*. **B. crawfordi* (Harris), paratypes; *2a*, NMVP 13360; *2b*, NMVP 13359 (Finney & Chen, 1984, fig. 3C–D).

Cryptograptus Lapworth, 1880, p. 174 [**Diplograpsus tricornis* Carruthers, 1859, p. 468; OD] [=*Tonograptus* Williams, 1992, p. 1727, pl. 3 (type, *T. subulatus;* OD)]. Monopleural, scandent glossograptid formed through dextral torsion of stipes around sicula; paired lateral apertural spines restricted to sicula; origin of th1^1 through resorption foramen in metasicula; th1^2 initially growing upwards and across reverse side of sicula; proximal development type isograptid, dextral; sicula and early thecae reduced to several bars and lists in biostratigraphically younger species. *Middle Ordovician (lower Darriwilian,* Undulograptus austrodentatus *Biozone)–Upper Ordovician (Katian,* Dicranograptus kirki *Biozone):* worldwide.——Fig. 18,*1a*. **C. tricornis*, lectotype, BMHM Q1299, Hartfell Spa, Hartfell Shales, Scotland (Elles & Wood, 1908, pl. 32, fig. 12A).——Fig. 18,*1b*. *C. insectiformis* Ruedemann, 1908, juvenile, MCZ 106835, showing reduction of fusellum, Viola Springs Limestone, Arbuckle Mountains, Oklahoma, USA (Maletz & Mitchell, 1996, fig. 6.5).——Fig. 18,*1c*. *C. schaeferi* Lapworth, 1880, GSC 87720, nematularium, holotype of *T. subulatus* Williams, 1992, western Newfoundland (new).

Glossograptus Emmons, 1855, p. 108 [*nom. correct.* J. Hall, 1865, p. 59 (pro *Glossograpsus* Emmons, 1855), ICZN Opinion 650, 1963] [**G. ciliatus;* SD Lapworth, 1873, table opposite p. 555] [=*Lonchograptus* Tullberg, 1880, p. 313 (type, *L. ovatus;* M)]. Monopleural, scandent glossograptid formed through dextral torsion of stipes around sicula, often with considerable glossograptid bulge; paired lateral apertural spines on sicula and variably developed on later thecae; thecal rutella extended and often modified; origin of th1^1 through resorption

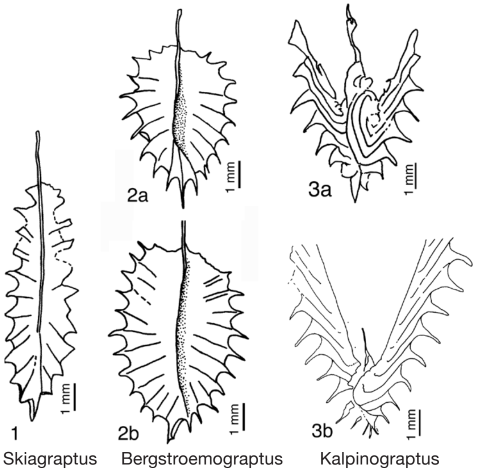

Fig. 17. Glossograptidae (p. 16–18)

foramen in middle to lower part of prosicula; proximal development type isograptid, dextral. [The genus *Lonchograptus* Tullberg, 1880, from the *Didymograptus geminus* (=*Pterograptus elegans*) Biozone of southern Sweden (Ekström, 1937), is regarded as a synonym of *Glossograptus*; however, the type is extremely poorly preserved and lacks features to differentiate it from *Glossograptus*.] *Middle Ordovician (Darriwilian,* Levisograptus austrodentatus *Biozone)–Upper Ordovician (Katian,* Dicellograptus ornatus *Biozone):* worldwide.——Fig. 18,*2a*. **G. ciliatus,* NYSM 7202, Normanskill Shale, Glenmont, New York (Ruedemann, 1908, pl. 27,*1*).——Fig. 18,*2b*. *G. acanthus* Elles & Wood, 1908, NIGP 116481, specimen showing glossograptid bulge, Chenjiawu, Jiangxi, China (Ni & Cooper, 1994, fig. 1).——Fig. 18,*2c*. *G. ovatus* (Tullberg, 1880), holotype, LO 408T (Tullberg, 1880, pl. 11,*1*).

Kalpinograptus Jiao, 1977, p. 290 [**K. spiroptenus;* OD] [=*Apoglossograptus* Finney, 1978, p. 489, *nom. nud*.]. Initially monopleural glossograptid formed through dextral torsion of stipes around sicula; two, distally diverging stipes; glossograptid bulge conspicuous; origin of th1^1 through resorption foramen in initial part of prosicula; proximal development type isograptid, dextral. *Middle Ordovician (upper Darriwilian,* Nicholsonograptus fasciculatus *Biozone)–Upper Ordovician (Sandbian,* Nemagraptus gracilis *Biozone):* Australia, China, Sweden, Norway, Canada, USA, Argentina, Peru.——Fig. 17,*3a*. **K. spiroptenus*, syntype (adapted from Jiao, 1977, fig. 4–5).——Fig. 17,*3b*. *Kalpinograptus* sp., GSC 113324, Table Head Group, western Newfoundland (Maletz & Mitchell, 1996, fig. 2,*1*).

Paraglossograptus Mu in Mu & others, 1962, p. 97 [**P. typicalis*; OD]. Monopleural, scandent glossograptid with conspicuous development of simple lacinia with ladder-like structure; lacinia only present in the proximal part in certain species. [Ganis (2005, p. 803) discussed the availability of the genus name *Paraglossograptus* that appeared first in Hsü, 1959]. *Middle Ordovician (Darriwilian,* Levisograptus austrodentatus–Pterograptus elegans *Biozones):* Australia, New Zealand, China, Norway, USA, Canada, Argentina.——Fig. 18,*3a*. **P. typicalis*, holotype, NIGP 10635 (Mu & Lee, 1960, fig. 127).——Fig. 18,*3b*. *P. tentaculatus* (J. Hall, 1865), GSC 138686, isolated, flattened specimen, Cow Head Group, western Newfoundland (new).——Fig. 18,*3c*. *P. proteus* (Harris & Thomas, 1935), GSC 23949, Daniels Harbour, western Newfoundland (adapted from Whittington & Rickards, 1969, fig. 7).

Nanograptus Hadding, 1915, p. 328 [**N. lapworthi;* SD Bulman, 1929, p. 179] [=*Rogercooperia* Sherwin & Rickards, 2000, p. 162 (type, *Petalograptus? phylloides* Elles & Wood, 1908, p. 284; OD)]. Glossograptid with rounded, finite colony consisting of ~8–10 thecae; sicula with metasicular origin of first theca; glossograptid bulge reduced and restricted to two thecal pairs; slender lateral apertural spines on sicula. *Upper Ordovician (Sandbian,* Nemagraptus gracilis *Biozone):* Australia (New South Wales), Sweden, Scotland.——Fig. 19,*1a–b*. **N. lapworthi; 1a*, lectotype (selected herein), LO 2746t (new); *1b*, paratype, LO 2743t (on slab), previously unfigured specimen showing long, dorsally projecting sicula, origin of th1^1 not visible (new).——Fig. 19,*1c–d*. *N. phylloides* (Elles & Wood); *1c*, paratype, flattened juvenile (new); *1d*, lectotype (selected by Sherwin & Rickards, 2000, p. 162), GSE 5495, flattened specimen (new).

Sinoretiograptus Mu & others, 1974, p. 164 [**S. mirabilis;* OD; =*Rogercooperia paucispinosus* Sherwin & Rickards, 2000, p. 163]. Glossograptid with slender, elongated, probably finite colony consisting of ~8–10 thecal pairs; sicula with metasicular origin of first theca; glossograptid bulge reduced and restricted to two thecal pairs; slender spinelike rutella on all thecae; development unknown. *Upper Ordovician (Katian*, Dicellograptus complexus [=?Dicellograptus ornatus] *Biozone):* China, Australia.——Fig. 19,*2a–d*. **S. mirabilis*; *2a*, NMVP 63643, Warbisco Shale, eastern Victoria, Australia (VandenBerg, 2003, fig. 2a); *2b–c*, holotype, NIGP 21406, late Katian, Wufeng Shale, Wangjiawan, Yichang, South China (new; drawing by Charles Mitchell); *2d*, AMF 103320, Keenan's Bridge, New South Wales (Sherwin & Rickards, 2000, fig. 2a).

Corynites Kozłowski, 1956, p. 260 [**C. wyszogradensis;* OD]. Strongly reduced colony consisting of elongated sicula with single adnate theca and vestigial, coiled second theca; sicular aperture with elaborate apertural flanges; origin of th1^1 in upper part of prosicula. *Upper Ordovician (?Sandbian):* Poland, Germany (glacial erratic boulder).——Fig. 20,*1a*. **C. wyszogradensis,* reconstruction of holotype (Kozłowski, 1956, fig. 1).——Fig. 20,*1b*. *C. divnoviensis,* reconstruction of holotype (Kozłowski, 1953, fig. 1).

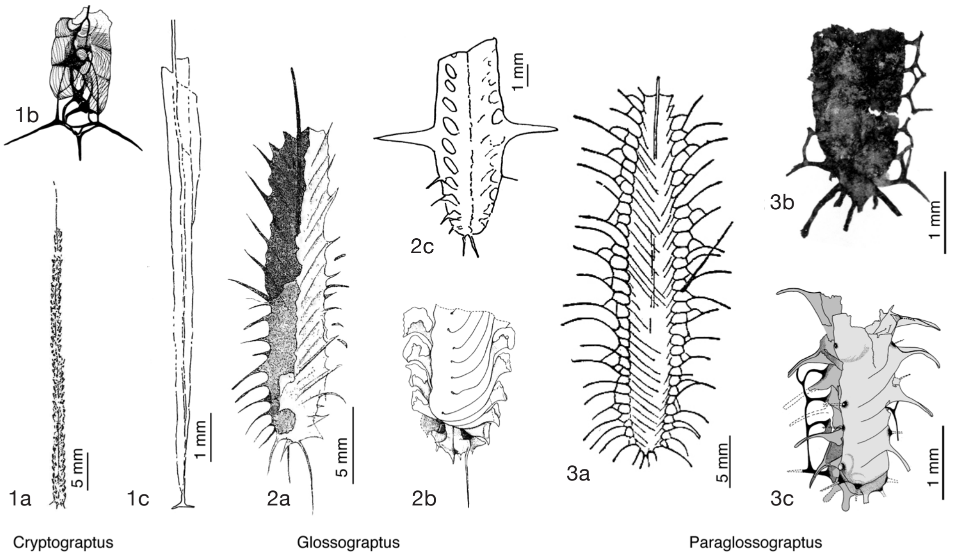

FIG. 18. Glossograptidae (p. 17–18)

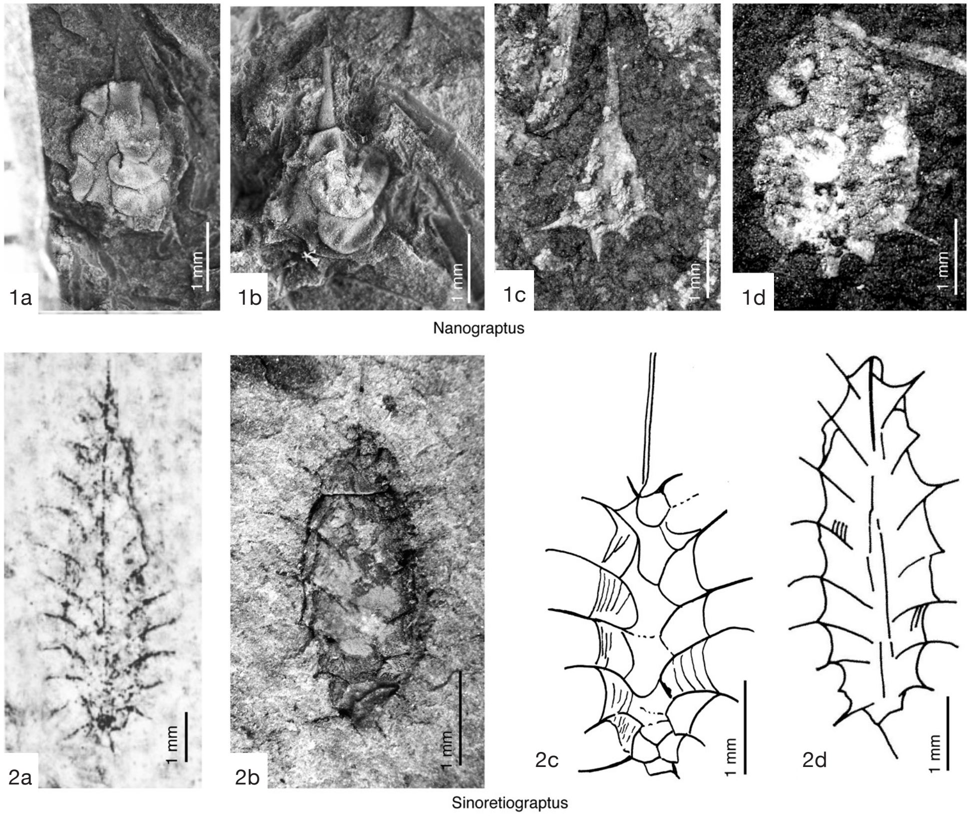

FIG. 19. Glossograptidae (p. 18)

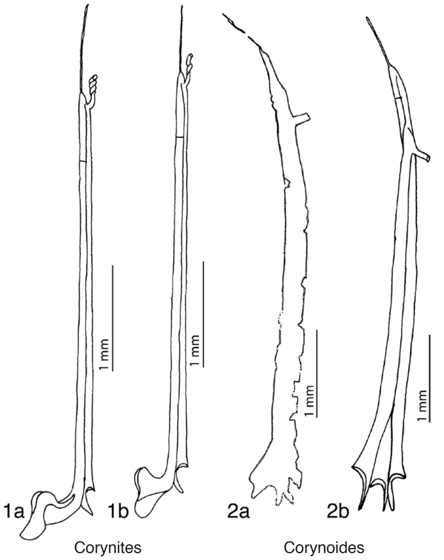

FIG. 20. Glossograptidae (p. 18–20)

Corynoides NICHOLSON, 1867, p. 108 [**C. calicularis*; M] [=*Corynograptus* NICHOLSON in HOPKINSON & LAPWORTH, 1875, p. 633]. Strongly reduced colony consisting of elongated sicula and two adnate thecae with extended rutella; a fourth vestigial theca may be present; origin of th1^1 in the upper part of prosicula. *Upper Ordovician (Sandbian,* Nemagraptus gracilis *Biozone–Katian,* Diplacanthograptus spiniferus *Biozone):* worldwide.——FIG. 20,*2a–b*. **C. calicularis*; *2a,* BMHM Q62, lectotype (Zalasiewicz, 2000); *2b,* reconstruction (new).

ABBREVIATIONS FOR MUSEUM REPOSITORIES

AMF: Australian Museum, Sydney, Australia
BMNH: The Natural History Museum, London, UK
GSC: Geological Survey of Canada, Ottawa
GSE: Geological Survey Museum (British Geological Survey), UK
LO: Lunds Originale, Department of Geology, Lund University, Sweden
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
NIGP: Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China
NMVP: Museum Victoria, Melbourne, Australia
NYSM: New York State Museum, Albany, New York, USA
OSU: Ohio State University, Orton Geological Musuem, Columbus, Ohio, USA
PMU: Palaeontological Collections, Museum of Evolution, Uppsala University, Sweden
SM: Sedgwick Museum of Earth Sciences, Cambridge, UK
T: West Bohemian Museum, Pilsen, Czech Republic

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