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PART V, SECOND REVISION, CHAPTER 18: ORDER GRAPTOLOIDEA AND FAMILY ANISOGRAPTIDAE: INTRODUCTION, MORPHOLOGY, AND SYSTEMATIC DESCRIPTIONS

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Order GRAPTOLOIDEA Lapworth, 1875

[Graptoloidea Lapworth in Hopkinson & Lapworth, 1875, p. 633, *nom. transl.* Ruedemann, 1904, p. 573, *ex* section Graptoloidea] [=suborder Rhabdophora Allman, 1872, p. 380; =division Graptoloida Mitchell, Melchin, Cameron, & Maletz, 2013, p. 53]

Graptolites united by the retention of the nematophorous sicula in the adult stage as the defining synapomorphy. *Ordovician (Tremadocian,* Rhabdinopora flabelliformis praeparabola *Biozone)–Devonian* (*lower Emsian*, Monograptus yukonensis *Biozone):* worldwide.

In the past, all bithecae-bearing planktic taxa (family Anisograptidae) were included in the Dendroidea (Bulman, 1955, 1970) or in the Graptodendroidina (Mu & Lin in Lin, 1981) as they show close similarities to the construction of the benthic graptolites due to the presence of a typical triad budding system with development of bithecae along the stipes. Fortey and Cooper (1986) differentiated the Graptoloidea on a cladistic interpretation and based it on the presence of a free nema in the adult stage as the defining synapomorphy. These authors promoted the inclusion of all nematophorous graptolites in a single order and indicated that the loss of bithecae is polyphyletic within the Graptoloidea (Fig. 1), a notion supported by the analysis of Li and others (2007). Maletz, Carlucci, and Mitchell (2009) provided an analysis of the derived graptoloids but did not include enough taxa of the Anisograptidae to be able to shed light on the early divergence of the graptoloids. Mitchell and others (2013, p. 53) defined the Graptoloidea (as the division Graptoloida) as the taxon including all graptolites retaining a nematophorous sicula in the adult stage, and thus provided a definition based on an easily recognizable synapomorphy, but otherwise followed the interpretations of Fortey and Cooper (1986).

Early Graptoloidea share numerous tubarium characters with the Dendroidea, especially the stipe structure formed by triad budding (Wiman rule), in which each autotheca produces two daughter thecae—an autotheca and a bitheca (see Cooper & Fortey, 1983). Dicalycal thecae are inserted at various distances to produce branching of the stipes. The most obvious difference the Graptoloidea has from the benthic taxa is the development of a free nema and the differentiation of the conus and cauda of the prosicula (Hutt, 1974).

A number of planktic dendroids have been described (Rickards, Hamedi, & Wright, 1994; Kraft & Kraft, 2007), among which *Calyxdendrum graptoloides* (Kozłowski, 1960) from the *Nemagraptus gracilis* Biozone is the best known and the only one available from chemically isolated material. These are not considered to be

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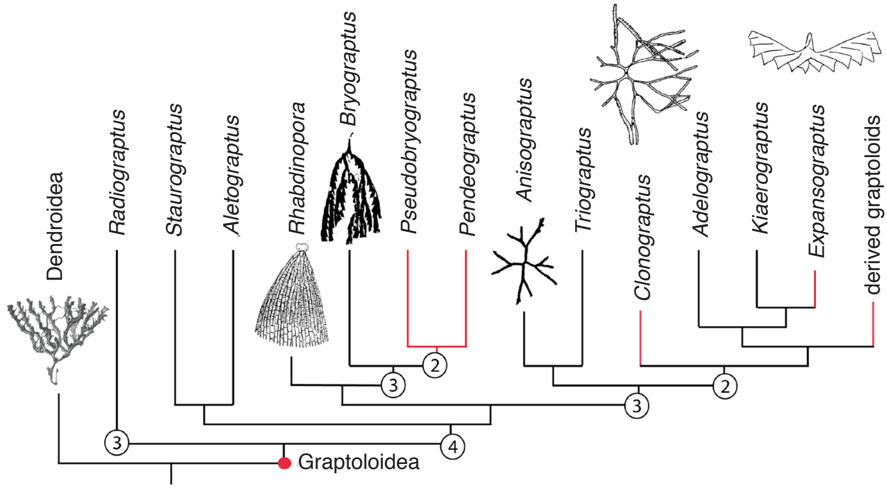

FIG. 1. Cladistic interpretation of early Graptoloidea by FORTEY and COOPER (1986), showing possible polyphyletic origin of non-bithecate graptoloids (*red* lines); circled numbers indicate origins of quadriradiate (*4*), triradiate (*3*), and biradiate (*2*) proximal development (new).

graptoloids, but are regarded as examples of dendroids independently developing a planktic life style.

Suborder GRAPTODENDROIDINA Mu & Lin, 1981

[Graptodendroidina MU & LIN in LIN, 1981, p. 244]

Quadriradiate to biradiate planktic, nematophorous graptolites with a triad budding system of the thecae; bithecae reduced or even lost in stratigraphically younger taxa; colonies multiramous to biramous, pendent to reclined; dissepiments present in some taxa; autothecae simple, widening tubes with or without short ventral rutellum; thecal apertures may be isolated; prosicula with distinct differentiation of conus and cauda; origin of $th1^1$ in the middle part of the conus; proximal end may possess one to three successive (proximal) dicalycal thecae with $th1^2$ as the first dicalycal theca; later dicalycal thecae adventitiously or regularly distributed. *Lower Ordovician (Tremadocian,* Rhabdinopora flabelliformis praeparabola *Biozone–Floian*, Sagenograptus murrayi *Biozone):* worldwide.

The Graptodendroidina is a paraphyletic taxon from which all younger groups of the Graptoloidea originated. The group and its biostratigraphic range is poorly known, as few horizons in the upper Tremadocian time interval provide faunas bearing the younger members of the Graptodendroidina. Thus, the transition to the derived suborders of the order Graptoloidea (e.g., Dichograptina, Sinograpta) is only vaguely defined.

Family ANISOGRAPTIDAE Bulman, 1950

[Anisograptidae BULMAN, 1950, p. 79] [incl. Adelograptinae MU, 1974, p. 231; Rhabdinoporinae ERDTMANN, 1982, p. 128; Psigraptidae LIN, 1981, p. 244; Muenzhigraptidae ZHAO & ZHANG, 1985, p. 16; Staurograptinae MU, 1974, p. 230]

Planktic nematophorous, multiramous graptoloids with a triad budding system; colony shape ranges from reclined through horizontal to declined and bell-shaped or pendent; bithecae distinctly smaller than autothecae; bithecae initially regular, but in later taxa irregular and often reduced or absent; autothecae simple, widening tubes, sometimes aperturally isolated; ventral rutella common; dissepiments present in a few taxa; proximal development type isograptid, quadriradiate to biradiate, variably dextral and sinistral; maeandrograptid type proximal symmetry with inclined sicula; prosicula with distinct differentiation of conus and cauda; origin of first theca in median part of the conus; th1^2 is first dicalycal thecae, later dicalycal thecae adventitiously or regularly distributed. *Lower Ordovician (Tremadocian,* Rhabdinopora flabelliformis praeparabola *Biozone–Floian,* Sagenograptus murrayi *Biozone):* worldwide.

The Anisograptidae form a paraphyletic stem group of the Graptoloidea (see Fig. 1). The Dichograptina and Sinograpta originated from this stem independently, but the details of the divergence of both groups have not been explored. MALETZ, CARLUCCI, and MITCHELL (2009) defined the supercohort Eugraptoloida as a monophyletic group through the defining synapomorphy, loss of bithecae along stipes, and indicated a monophyletic origin of the derived graptoloids. Their results are in direct conflict with the interpretation of FORTEY and COOPER (1986) and LINDHOLM (1991) concerning the multiple independent loss of bithecae in the Anisograptidae.

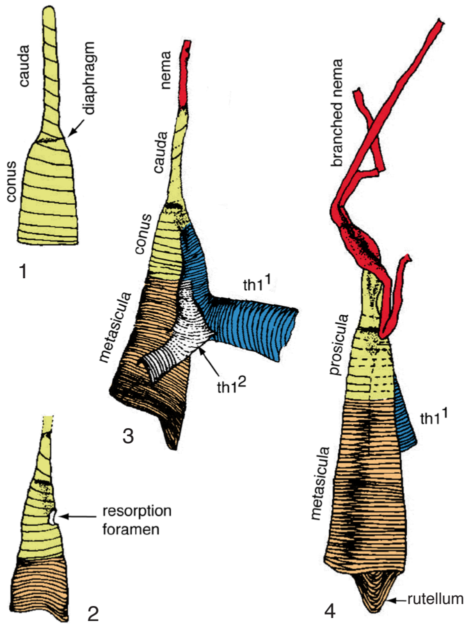

FIG. 2. Sicular development in Anisograptidae. *1,* prosicula showing conus and cauda, *arrow* indicates diaphragm; *2,* prosicula (*yellow*) with early metasicula (*brown*), resorption foramen for th1^1 indicated by *arrow; 3,* juvenile with complete sicula, part of th1^1 and crossing canal of th1^2, reverse view; *4,* sicula with complex nema (adapted from Hutt, 1974).

MORPHOLOGY

The tubarium shape of the Anisograptidae is quite variable and ranges from pendent to horizontal and reclined. The stratigraphically earliest taxa (*Rhabdinopora*, *Staurograptus*) recall the multiramous, dissepimentous tubaria of the benthic *Dictyonema*. The stipes are connected by irregularly or regularly distributed dissepiments to keep them at a certain distance, most probably to prevent interaction and feeding competition of zooids from adjacent stipes (FORTEY & BELL, 1987).

All Anisograptidae possess a free nema (Fig. 2), indicating that the colonies are not attached to any object. Nemata can be branched or replaced by various features interpreted as float structures or described simply as nematularia with unknown function. The nematularia are not known from isolated material and their precise construction is uncertain. HUTT (1974) described the distal end of the nema in *Adelograptus tenellus* (LINNARSSON, 1871) as open and interpreted it as a growing end of the colony. BATES (1987) considered the growth to be similar to that of other spines of the colonies and suggested an incremental growth from fusellar or cortical components. RICKARDS (1975, 1996) discussed the construction of the nema and claimed that it is a hollow tube (actually referring to the cauda of HUTT, 1974), later overgrown by the addition of fusellar tissue in the form of a spine. He identified this addition as the virgula. The virgula is here regarded as a synonym of the nema. Early developments on the nema include various vanes or possibly vesicular bodies of uncertain construction (e.g., nematularia).

The sicula of the Anisograptidae is conical, slowly widening from the prosicula

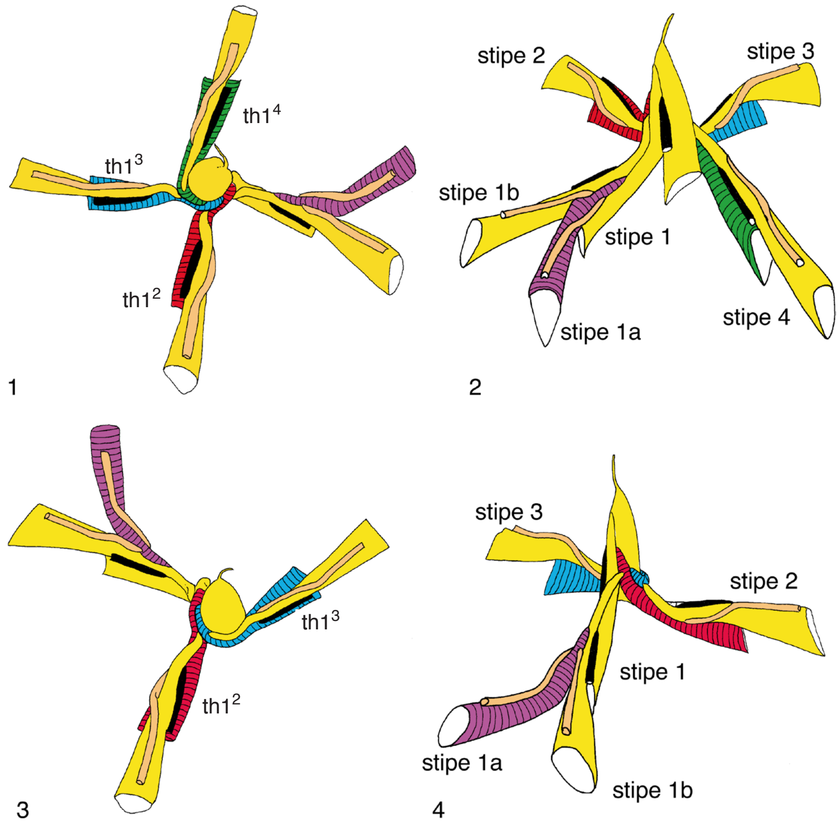

FIG. 3. Quadriradiate and triradiate proximal development. *1,* quadriradiate development, dorsal view, showing successive, clockwise (dextral) origins of dicalyal thecae (th1^2, th1^3, th1^4) around the sicula; *2,* quadriradiate development, obverse view, showing sicular bitheca; *3,* triradiate development, dorsal view, showing two successive dicalycal thecae (th1^2, th1^3) originating in anticlockwise (sinistral) fashion; *4,* triradiate development, reverse view. Dicalycal thecae are striped and color-coded: bithecae, *black*, first distal dicalycal theca, *purple* (adapted from Maletz, 1992, fig. 3).

and often bearing a short rutellum (Fig. 2.4). The prosicula is differentiated into two parts of approximately equal length, the conus and cauda (HUTT, 1974), separated by a diaphragm (Fig. 2.1). A highly regular development of fuselli with a dorsal and a ventral zigzag suture characterizes the metasicula of the Anisograptidae and of all derived Graptoloidea. The origin of the tube of th1^1 is through a resorption foramen in the upper half of the conus on the ventral side of the prosicula (Fig. 2.2). The length of the prosicula may be reduced, and the origin of th1^1 is close to the apex of the sicula (*Choristograptus* LEGRAND, 1964a).

The position of the dicalycal thecae defines the branching geometry of the graptoloid colonies. Dicalycal thecae are most densely distributed in the proximal end and more widely dispersed distally in most multiramous taxa. MALETZ (1992) described the proximal development of the Anisograptidae and provided a model for their construction. Dicalycal thecae can be differentiated into proximal dicalycal thecae and distal ones. The first dicalycal theca is th1^2, defining an isograptid proximal development as the basic constructional unit of the proximal end of all Anisograptidae. Dicalycal thecae may be consecutive, but a dicalycal theca can only generate a single further dicalycal theca.

The successive dicalycal thecae, starting from the first dicalycal theca (th1^2), are identified as proximal dicalycal thecae, while distal dicalycal thecae are separated from proximal ones by at least one monocalycal theca. Earliest anisograptids (*Staurograptus*, *Rhabdinopora*) possess three successive (proximal) dicalycal thecae and therefore develop a quadriradiate proximal end (Fig. 3.1–3.2). The successive dicalycal thecae all form on one side of the growing stipe, growing in a circular fashion around the sicula, either clockwise or anticlockwise. During the evolution of the Anisograptidae, the number of proximal dicalycal thecae is reduced to two (triradiate development) and finally to one (biradiate development).

A biradiate proximal development is the standard in younger anisograptids and is present in non-bithecate multiramous to biramous graptoloids. The position of distal dicalycal thecae may be highly variable. Those closest to the proximal dicalycal thecae are $th3^1$ and $th3^2$. This proximal construction has been termed the tetragraptid foundation (Maletz, 1992, p. 299). It is typically developed in the multiramous dichograptids, especially in *Clonograptus* (see Lindholm & Maletz, 1989) and derived taxa. A tetragraptid foundation also appears to be present in the anisograptid *Psigraptus* and in some adelograptids.

Bulman (1925, 1927) and Stubblefield (1929) first described bithecae in planktic graptolites. In earlier Anisograptidae, the bithecae were found to be alternating along the stipes, with the first bitheca associated with the sicula, termed the sicular bitheca (Fig. 4.1). Bithecae are more irregularly placed along the stipes in some late taxa such as *Kiaerograptus kiaeri* (Spjeldnaes, 1963), and the typical alternation is lost (Fig. 4.2). Lindholm (1991) and Williams and Stevens (1991) discussed the loss of bithecae in upper Tremadocian anisograptids. Lateral budding of the thecae, typical of the Dendroidea, is preserved in most members of the Anisograptidae, even when bithecae along the stipes are lost (Fig. 4.3). The sicular bitheca is the last remaining bitheca according to Williams and Stevens (1991) and is present in *Hunnegraptus copiosus* Lindholm, 1991 (Fig. 4.4).

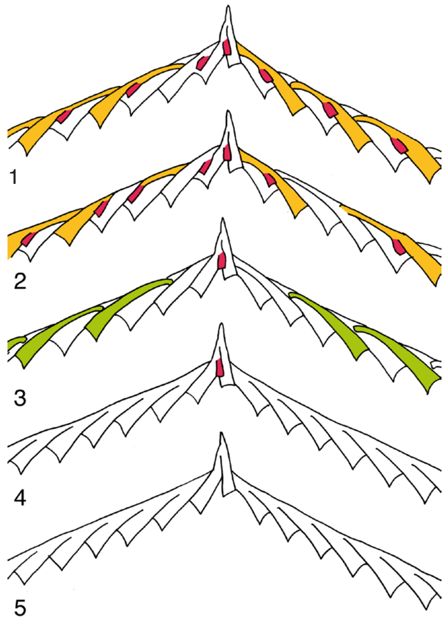

Fig. 4. Diagram illustrating the loss of bithecae in the Anisograptidae in obverse view to show presence/absence of sicular bitheca, proximal ends hypothetical. *1,* stipes based on *Kiaerograptus? supremus* Lindholm, 1991; *2,* stipes based on fragment of *Kiaerograptus kiaeri* Monson, 1925, with successive bithecae on one side; *3,* stipes based on fragment of ?*Clonograptus* sp. aff. *Clonograptus multiplex* (Nicholson, 1868); *4,* stipes based on *Hunnegraptus copiosus* Lindholm, 1991, with sicular bitheca as the only remaining bitheca; *5,* stipes based on *Clonograptus multiplex* (Nicholson,1868) (adapted from Lindholm, 1991, fig. 4).

EVOLUTION

The Anisograptidae represent the initial step in graptolites becoming successful planktic organisms. The earliest planktic form, *Rhabdinopora praeparabola* (Erdtmann, 1982), appears close to the base of the Tremadocian Stage, and species of *Rhabdinopora* have commonly been used to indicate the base of the Ordovician System. The genus *Rhabdinopora* quickly diversified and represents one of the most compelling examples of evolutionary conservatism in early Ordovician graptolites (see Cooper & others, 1998).

A clear trend in evolutionary simplification can be seen in the successive loss of first-order stipes. The Anisograptidae evolved from initially quadriradiate to triradiate and finally to biradiate forms until a stabilization point was reached in the upper Tremadocian. All subsequently appearing graptoloids possess two first-order stipes and one single, proximal dicalycal theca, which is the typical biradiate development (see MALETZ, 1992). The exact points of change from a quadriradiate to triradiate and from triradiate to biradiate development have not been documented, and the trends appear to be polyphyletic, according to the interpretation of FORTEY and COOPER (1986) and LI and others (2007) (see Fig. 1).

Upper Tremadocian faunas from the *Hunnegraptus copiosus* Biozone of Scandinavia (LINDHOLM, 1991) and the *Aorograptus victoriae* Biozone of western Newfoundland (WILLIAMS & STEVENS, 1991) indicate a breakdown of the typical dendroid triad budding structure along several lineages. Specimens of the sigmagraptine *Paradelograptus* initially still possess a sicular bitheca with a dorsal origin of all thecae along the stipes (MALETZ, 2014, fig. 10), a condition similar to that in the dichograptine genus *Hunnegraptus* LINDHOLM, 1991. The genus *Paratemnograptus* shows the plaited thecal overlap of the Anisograptidae and possibly bears a sicular bitheca, but bithecae along the stipes are not present. Thus, it may be possible to demonstrate the loss of bithecae and plaited overlap of thecae independently in the sinograptids and dichograptids.

The genus *Rhabdinopora* EICHWALD, 1855 and its type species *Rhabdinopora flabelliformis* (EICHWALD, 1840) are among the most controversial taxa of the planktic graptolites. For a long time, benthic and planktic graptolites with the typical mesh of *Rhabdinopora flabelliformis* have been included in the genus *Dictyonema*, before ERDTMANN (1982) reestablished the genus *Rhabdinopora* for planktic taxa and separated the benthic species under the genus name *Dictyonema* HALL, 1851. HOPKINSON and LAPWORTH (1875, p. 667) changed *Dictyonema* to *Dictyograptus*, based on the notion that *Dictyonema* was "an old-established name for a genus of plants." The name was actually based on a group of lichens described as *Dictyonema* by ADGARTH (in KUNTH, 1822) (see PARMASTO, 1978). Graptolite material now referred to the genera *Dictyonema* and *Rhabdinopora* had originally been identified as *Gorgonia* LINNAEUS, 1758, due to their similarity to gorgonian soft corals. The bryozoan *Fenestella* LONSDALE in MURCHISON, 1839, is another fossil easily misidentified as a graptolite, but is constructed from calcite instead of the organic material found in the graptolites. SALTER (1858) described the genus *Graptopora* and referred to the species *Fenestella socialis* as the type, a taxon now identified as *Rhabdinopora flabelliformis socialis* (SALTER, 1858). At the time, the species was only known from a yet-unpublished manuscript and was first described and illustrated in SALTER (1866).

Rhabdinopora EICHWALD, 1855, p. 454. [**Gorgonia flabelliformis* EICHWALD, 1840, p. 207; SD BULMAN, 1970, p. 38] [=*Phyllograpta* ANGELIN, 1854, p. 4 (type, *Gorgonia flabelliformis* EICHWALD, 1840, p. 207, M); =*Graptopora* SALTER, 1858, p. 65 (type, *G. socialis,* OD, illustrated in SALTER, 1866, p. 331, pl. 4,*1*); =*Dictyograptus* HOPKINSON in HOPKINSON & LAPWORTH, 1875, p. 667, *pro Dictyonema* HALL, 1851 (type species not defined); =*?Damesograptus* JAHN, 1892, p. 645 (type, *Dictyonema* sp., DAMES, 1873, p. 383, OD); =*Dictyodendron* WESTERGÅRD, 1909, p. 62 (type, *Gorgonia flabelliformis* EICHWALD, 1840, p. 207, OD); =*Heterograptus* ZHAO & ZHANG in LIN, 1986, p. 241 (type, *H. radiatus,* OD)]. Pendent, multiramous anisograptid with irregularly to regularly distributed dissepiments; proximal development quadriradiate. *Lower Ordovician (lower Tremadocian,* Rhabdinopora flabelliformis praeparabola–Adelograptus *Biozones):* worldwide.——FIG. 5,*1a–b*. **R. flabelliformis; 1a,* neotype (BULMAN, 1966, p. 408, BULMAN, 1967), NHMUK PM Q 1392, Pakerort, north of Paldiski, Estonia (Bulman, 1966, fig. 1); *1b,* LO 4144t, proximal end, Paldiski, Estonia (Bulman, 1966, fig. 2a).——FIG. 5,*1c. Heterograptus radiatus* ZHAO & ZHANG in LIN, 1986, holotype, CCG G8456, Dayangcha, Jilin, China (Lin, 1986, fig. 96,*1*).

Staurograptus EMMONS, 1855, p. 108, original spelling as *Staurograpsus* changed in ICZN, Opinion 650, 1963 [**S. dichotomus;* M] [=*Aletograptus* OBUT & SOBOLEVSKAYA, 1962, p. 76 (type, *A. hyperboreus* COOPER & others, 1998, p. 21, M)]. Quadriradiate anisograptid with horizontal to subhorizontal, multiramous to pauciramous tubarium; distal dichotomies irregularly spaced; dissepiments rare and scattered distally in some mature and gerontic specimens of early species, otherwise lacking altogether. *Lower Ordovician (lower Tremadocian,* Rhabdinopora flabelliformis praeparabola–

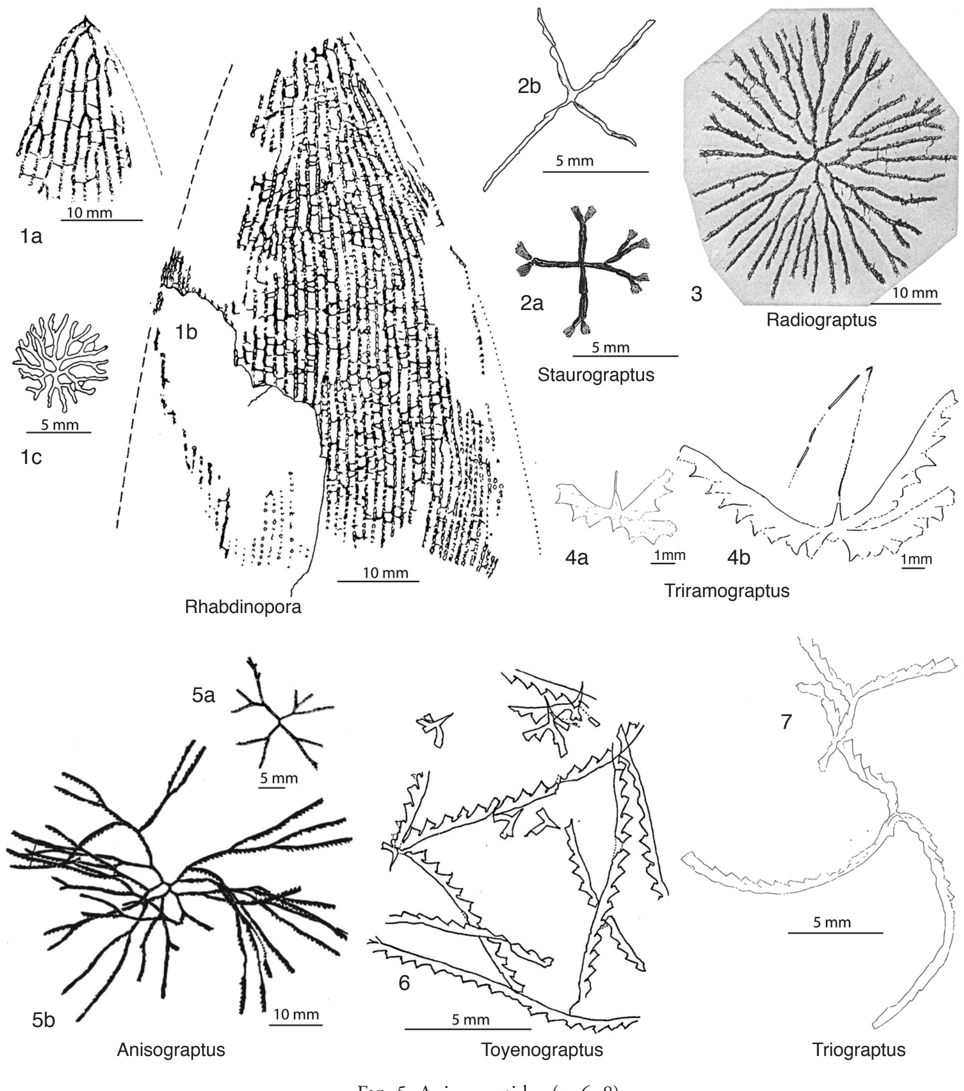

FIG. 5. Anisograptidae (p. 6–8)

Rhabdinopora flabelliformis parabola *Biozones):* worldwide.——FIG. 5,*2a*. **S. dichotomous*, type specimen whereabouts unknown (Feng, Erdtmann, & Zhang, 2005, p. 1013).——FIG. 5,*2b*. *S. hyperboreus* (OBUT & SOBOLEVSKAYA, 1962)*,* holotype, CGMSP 8310/11(Feng, Erdtmann, & Zhang, 2005, fig. 11C).

Anisograptus RUEDEMANN, 1937, p. 61 [**A. matanensis;* OD]. Triradiate anisograptid with horizontal to subhorizontal tubarium; distal dichotomies irregularly spaced. *Lower Ordovician (lower Tremadocian,* Anisograptus matanensis–Rhabdinopora flabelliformis anglica *Biozones):* worldwide.——FIG. 5,*5a*. **A. matanensis*, holotype, NYSM 6841, Matane, Quebec, Canada (Ruedemann, 1937, fig. 6).——FIG. 5,*5b*. *A. flexuosus* BULMAN, 1950, GSC 9861, Matane, Quebec (Bulman, 1950, fig. 6a).

Toyenograptus LI 1984, p. 579 (English text p. 584) [**Anisograptus isolatus* BULMAN, 1954, p. 32; OD]. Triradiate anisograptid with horizontal to subhorizontal tubarium; distal dichotomies irregularly spaced; thecal apertures isolated. *Lower Ordovician (lower Tremadocian,* Anisograptus matanensis *Biozone):* Norway.——FIG. 5,*6*. **T. isolatus*, holotype, PMO 61876, Tøyen, Oslo, Norway (Bulman, 1954, fig. 13).

Triograptus MONSEN 1925, p. 169 [**T. osloensis;* OD]. Triradiate anisograptid; tubarium composed of three horizontal, undivided stipes, showing distinct lateral curvature; details of thecae unknown. *Lower*

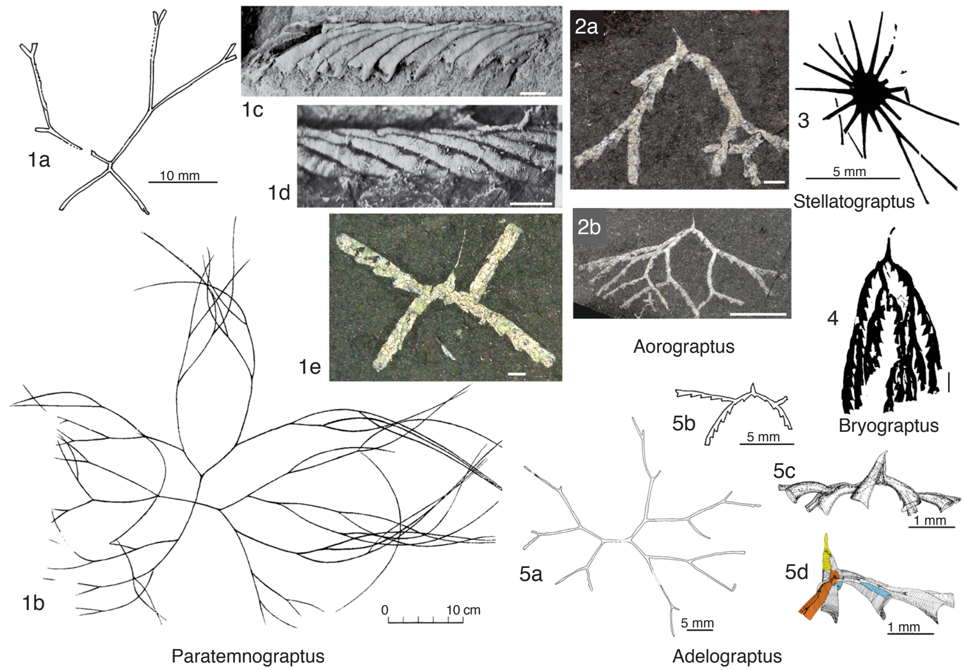

FIG. 6. Anisograptidae (p. 8–10)

Ordovician (upper Tremadocian, Kiaerograptus kiaeri *Biozone):* Norway, ?Argentina.——FIG. 5,*7*. **T. osloensis*, lectotype (selected herein), PMO 60232 (Monsen, 1925, pl. 4,*2*).

Triramograptus ERDTMANN in COOPER & others 1998, p. 27 [**T. atavus;* OD]. Robust, triradiate, reclined anisograptid with three stipes; mature specimens often with long nema. *Lower Ordovician (lower Tremadocian,* Rhabdinopora flabelliformis parabola *Biozone):* Canada (western Newfoundland).——FIG. 5,*4a–b*. **T. atavus; 4a,* holotype, GSC 115854 (Cooper & others, 1998, fig. 23a); *4b,* GSC 115857, large specimen (Cooper & others, 1998, fig. 23d).

Radiograptus BULMAN 1950, p. 89 [**R. rosieranus*; OD]. Triradiate anisograptid with horizontal to subhorizontal tubarium; distal dichotomies irregularly spaced; dissepiments present. [Taxon may be synonymous to *Rhabdinopora*] *Lower Ordovician (lower Tremadocian,* ?Anisograptus matanensis *Biozone):* Canada. .——FIG. 5,*3*. **R. rosieranus*, holotype, GSC 9871, Cap de Rosier, Gaspe Peninsula, Quebec, Canada (Bulman, 1950, pl. 6).

Adelograptus BULMAN, 1941, p. 114 [**Bryograptus*? *hunnebergensis* MOBERG, 1892, p. 92; OD; =*Dichograptus? tenellus* LINNARSSON, 1871, p. 794, MALETZ & ERDTMANN, 1987, p. 180] [=*Clonograptus* (*Paraclonograptus*) ZHAO & ZHANG, 1985, p. 15, *nom. nud.,* herein]. Biradiate anisograptid with horizontal to subhorizontal tubarium; distal dichotomies irregularly spaced; cortical overgrowth of proximal part of stipes in gerontic specimens; bithecae on alternate sides of stipes; slender, slowly widening thecae, often with short rutellum. *Lower Ordovician (upper Tremadocian,* Adelograptus tenellus–Hunnegraptus copiosus *Biozones):* Algeria, ?Australia, China, Sweden, Norway, UK, Canada, USA, Argentina, Bolivia.——FIG. 6,*5a–b, d*. *A. tenellus* (LINNARSSON, 1871); *5a*, neotype, SGU 4497a–b (Maletz & Erdtmann, 1987, pl. 1A); *5b*, SGU 4506, lectotype of **Bryograptus? hunnebergensis* (selected herein) (Maletz & Erdtmann, 1987, p 188); *5d,* SM A82770, showing prosicula, bithecae, and initial dicalycal theca (th1^2) in color, Shineton Shale, Shropshire, UK (adapted from Hutt, 1974, fig. 6C).——FIG. 6,*5c*. *A. messaoudi* LEGRAND, 1964b, proximal end, obverse view showing sicular bitheca (adapted from Legrand, 1964b, fig. 3a).

Paratemnograptus WILLIAMS & STEVENS, 1991, p. 19 [**P. isolatus;* M; =*Temnograptus magnificus* PRITCHARD, 1892, p. 56, herein]. Horizontal to subhorizontal, multiramous tubarium with biradiate development and tetragraptid foundation; sicular bitheca present; stipes with plaited overlap of thecae, but without bithecae. *Lower Ordovician (upper Tremadocian,* Aorograptus victoriae–Tetragraptus phyllograptoides *Biozones):* Australia, Norway, Sweden, Canada, Argentina, Bolivia.——FIG. 6,*1a*. **P. isolatus,* holotype, GSC 87284 (Williams & Stevens, 1991, fig. 10L).——6,*1b–d*. *P. magnificus* (PRITCHARD, 1892). *1b,* holotype, NMVP 134000, Lancefield, Victoria, Australia (Pritchard, 1892, pl. 6); *1c,* MG1968, stipe

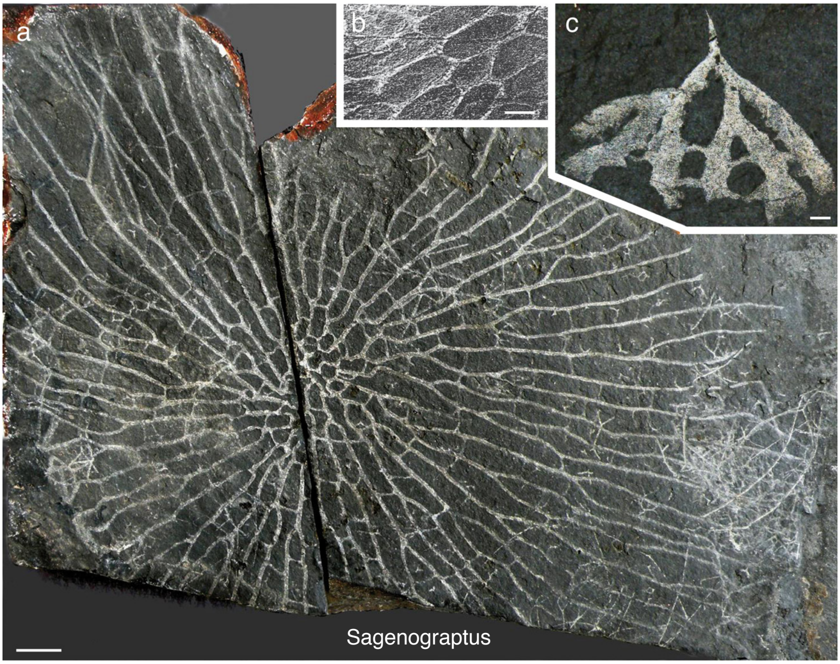

FIG. 7. Anisograptidae (p. 9)

fragment showing plaited overlap and lack of bithecae, Fezouata Lagerstätte, Morocco, scale bar, 1 mm (new, photo provided by J. C. Gutiérrez-Marco); *1d,* PMO 108.558, latex cast showing plaited overlap and lack of bithecae, Slemmestad, Norway, scale bar, 1 mm (Lindholm & Maletz, 1989, pl. 83,*7*).——6,*1e. Tetragraptus decipiens* HALL, 1899, lectotype, NMVP 14368, proximal end, scale bar, 1 mm (new, photo provided by F. VandenBerg).

Stellatograptus ERDTMANN, 1967, p. 343 [**S. stellatus;* M]. Multiramous ?anisograptid with proximally concentrated dichotomies; distal stipes long and rarely branching; proximal development and thecal style unknown; strong cortical overgrowth of proximal end. *Lower Ordovician (upper Tremadocian,* ?Aorograptus victoriae *Biozone):* Canada (Quebec).——FIG. 6,*3*. **S. stellatus,* holotype, 1341 at Laval University, Quebec City, material now at Geological Survey of Canada, but no GSC numbers given (personal communication, Michelle Coyne, GSC, Ottawa, March 2014), 1.2 miles downstream from the wharf at St. Michelle de Bellechasse, Quebec, Canada (Erdtmann, 1967, p. 344, fig. 4).

Aorograptus WILLIAMS & STEVENS, 1991, p. 23 [**Bryograptus victoriae* HALL, 1899, p. 165; OD]. Declined to pendent, multiramous anisograptid with biradiate proximal development; distal dichotomies irregularly distributed. *Lower Ordovician (upper Tremadocian,* Aorograptus victoriae *Biozone):* Australia, New Zealand, Norway, Canada, USA, Argentina, Bolivia.——FIG. 6,*2a–b*. **A. victoriae; 2a*, holotype, NMVP 14240, scale bar, 1 mm (new); *2b,* NMVP 318 132A, large specimen, Victoria, Australia, scale bar, 5 mm (new).

Sagenograptus OBUT & SOBOLEVSKAYA, 1962, p. 74 [**S. gagarini;* OD] [=*Araneograptus* ERDTMANN & VANDENBERG, 1985, p. 53 (type, *Dictyonema macgillivrayi* T. S. HALL, 1897, p. 15, OD)]. Robust, possibly biradiate, multiramous tubarium with subhorizontal to pendent habit; stipes connected with dissepiments; presence of bithecae uncertain. *Lower Ordovician (upper Tremadocian,* Sagenograptus murrayi *Biozone–lower Floian,* Tetragraptus approximatus *Biozone):* Morocco, Australia, New Zealand, UK, Germany, Norway, Sweden, Canada, Russia, Bolivia, Argentina.——FIG. 7*a,c*. *S. macgillivrayi* (HALL, 1897); *a,* NMVP 13126, lectotype (selected by ERDTMANN & VANDENBERG, 1985, p. 54), Lancefield Quarry near Lancefield, Victoria, Australia, scale bar, 10 mm; *c,* NMVP 73461, proximal end in lateral view, scale bar, 1 mm (new, photos provided by A. VandenBerg).——FIG. *7b*. **S. gagarini*, holotype, 5/8310, scale bar, 5 mm (Sobolevskaya, 2011, pl. 2,*5*).

Bryograptus LAPWORTH, 1880, p. 164 [**B. kjerulfi;* SD GURLEY, 1896, p. 64]. Declined to pendent anisograptid with triradiate proximal development and unlimited branching capacity; bithecae alternate along the stipes; sicula elongated, often with long and thickened nema. *Lower Ordovician (upper Tremadocian,* Bryograptus ramosus *Biozone):* UK, Norway, Sweden, Argentina, Bolivia.——FIG. 6,*4*. **B. kjerulfi*, lectotype, PMO 71284, Vaekkero, Oslo

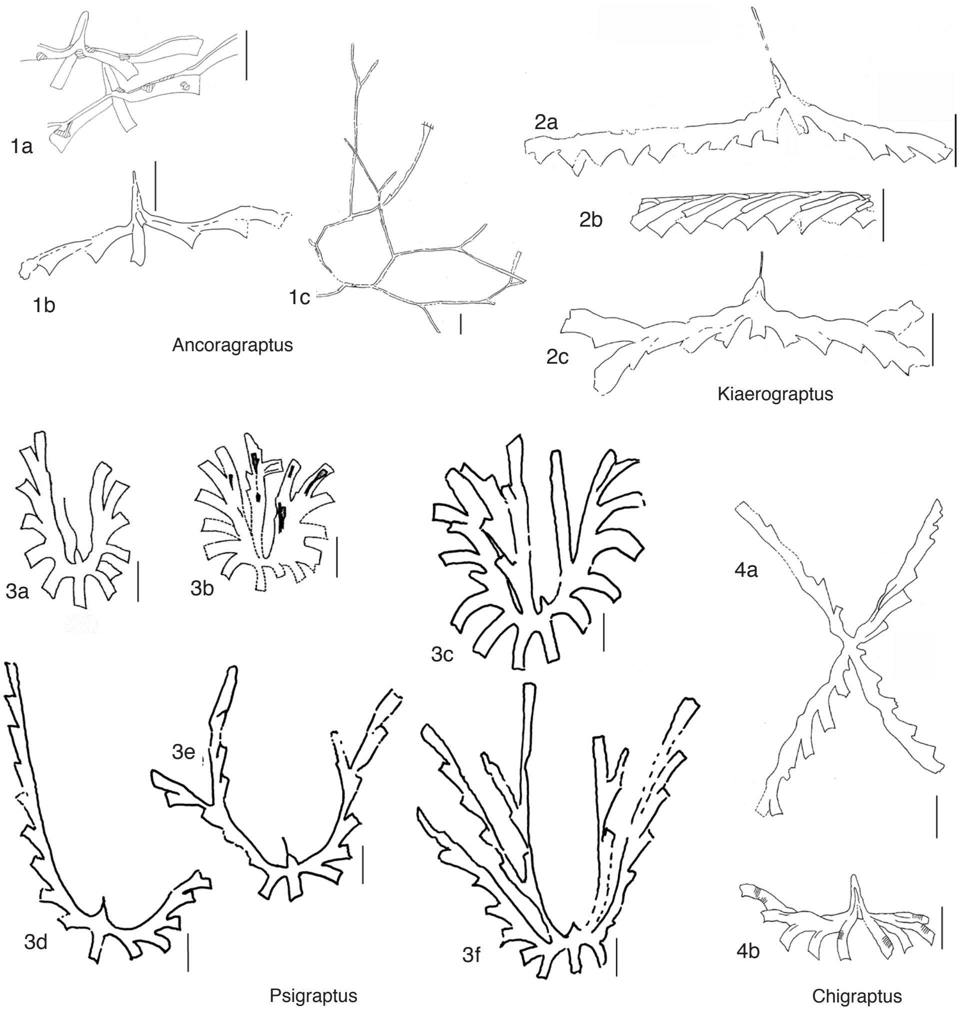

Fig. 8. Anisograptidae (p. 10–11)

Region, Norway, scale bar, 1 mm (Bulman, 1971, p. 363, fig. 1a).

Ancoragraptus Jackson & Lenz, 2003, p. 141 [**Adelograptus*? *bulmani* Spjeldnaes, 1963, p. 127; OD]. Biradiate anisograptid with horizontal to subhorizontal tubarium; distal dichotomies irregularly spaced; short bithecae on alternate sides of stipes; slender, slowly widening thecae often with short rutellum; tubular sicula and often a number of proximal thecae isolated aperturally; bithecae may be reduced or missing along the stipes. *Lower Ordovician (upper Tremadocian,* Aorograptus victoriae *Biozone):* China, South Korea, Norway, Canada, Argentina.——Fig. 8,*1a–c*. **A. bulmani; 1a,* holotype, PMO 72835a, Slemmestad, Norway; *1b,* PMO 214.032, proximal end in obverse view showing sicular bitheca; *1c,* PMO 214.028, multiramous colony; scale bars, 1 mm (new).

Choristograptus Legrand, 1964a, p. 52 [**C. louhai;* OD]. Biradiate anisograptid with declined tubarium; prosicula strongly reduced or lacking, with origin of th1[1] on prosicular apex; distal dichotomies irregularly spaced; short bithecae on alternate sides of stipes; slender, slowly widening thecae without rutellum; tubular sicula and often a number of proximal thecae isolated aperturally. *Lower Ordovician (upper Tremadocian,* ?Aorograptus victoriae *Biozone):* Algeria, Morocco.——Fig. 9*a–d*. **C. louhai; a,* proximal end with reduced prosicula and nema; *b,* proximal fragment showing isolated thecal apertures and bitheca; *c,* distal fragment showing bitheca; *d,* apex of sicula with nema and origin

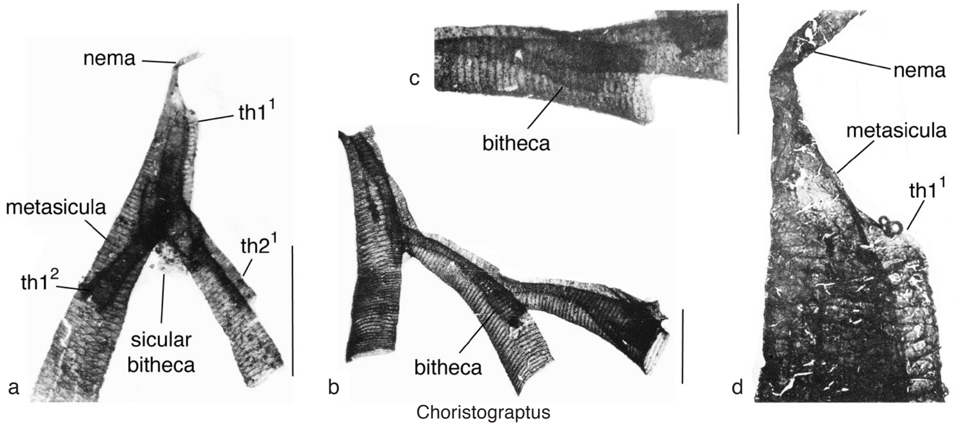

Fig. 9. Anisograptidae (p. 10–11)

of th1^1; scale bars, 0.5 mm for *a–c;* 0.1 mm for *d* (Legrand, 1964a, *pl. 3–4*).

Kiaerograptus Spjeldnaes, 1963, p. 123 [**Didymograptus kiaeri* Monsen, 1925, p. 172; OD]. Horizontal to declined, multiramous to two-stiped, robust anisograptid; relatively long bithecae present, but often irregularly placed; apertural part of sicula freely pending; thecal apertures, at least in proximal parts, often isolated. *Lower Ordovician (upper Tremadocian,* Aorograptus victoriae *Biozone):* Algeria, China, Norway, Sweden, Canada, Argentina.——Fig. 8,*2a–b.* **K. kiaeri; 2a,* lectotype, PMO 60212a, scale bar, 1 mm (Monsen, 1925, pl. 2,*10;* Spjeldnaes, 1963, pl. 17,*5*); *2b,* PMO 72 833, fragment with bithecae, scale bar, 1 mm (Spjeldnaes, 1963, pl. 2,*1*).——Fig. 8,*2c. K. lauzonensis* (Erdtmann, 1966), GSC 122 714, showing distal branching, scale bar, 1 mm (Maletz & Egenhoff, 2001, fig. 4a).

Psigraptus Jackson, 1967, p. 314 [**P. arcticus;* OD] [=*Yukonograptus* Lin, 1981, p. 244, English text p. 261 (type, *P. lenzi* Jackson, 1967, p. 319; OD); =*Muenzhigraptus* Zhao & Zhang, 1985, p. 16 (type, *M. sinicus;* OD); =*Diphygraptus* Zhao & Zhang, 1985, p. 19, (type, *D. reclinatus;* OD); =*Hunjiangograptus* Zhao & Zhang, 1985, p. 20, (type, *H. typicus;* OD); =*Holopsigraptus* Zhao & Zhang, 1985, p. 20 (type, *H. hunjiangensis;* OD); =*Clonograptus* (*Neoclonograptus*) Zhao & Zhang, 1985, p. 21, *nom. nud.,* herein]. Reclined multiramous to pauciramous anisograptid with partly isolated metasicula and metathecae; proximal end biradiate with short, first-order stipes; bithecae present, but variably developed; autothecae tubular, without rutellum, considerably curved when aperturally isolated. *Lower Ordovician (upper Tremadocian,* Psigraptus *Biozone):* Australia, China, South Korea, Canada.——Fig. 8,*3a.* **P. arcticus,* holotype, GSC 21248, scale bar, 1 mm (new).——Fig. 8,*3b. P. lenzi* Jackson, 1967, holotype, GSC 21253, scale bars, 1 mm (new).——Fig. 8,*3c. P. hunjiangensis* (Zhao & Zhang, 1985), holotype, scale bar, 1 mm (new).——Fig. 8,*3d. P. reclinatus* (Zhao & Zhang, 1985), holotype, scale bar, 1 mm (new).——Fig. 8,*3e. P. typicus* (Zhao & Zhang, 1985), holotype, scale bar, 1 mm (new).——Fig. 8,*3f. P. sinicus* (Zhao & Zhang, 1985), holotype, scale bar, 1 mm (new).

Chigraptus Jackson & Lenz, 1999, p. 155 [**C. supinus;* OD]. Small quadriradiate tubarium with four, unbranched, first-order stipes disposed horizontally to slightly reclined; autothecae biform, comprising long, curved, downwardly directed, isolate autothecae proximally, grading to tubes with low angle of inclination and slightly isolate distally; sicular bitheca and bithecae present throughout the colony. *Lower Ordovician (Tremadocian–?*basal Staurograptus dichotomous *Biozone):* Canada.——Fig. 8,*4a–b.* **C. supinus; 4a,* holotype, GSC 117664, dorso-ventral preservation; *4b,* GSC 117666, small specimen in lateral preservation; scale bars, 1 mm (Jackson & Lenz, 1999, p. 156, fig. 4).

ABBREVIATIONS FOR MUSEUM REPOSITORIES

CCG: Changchun College of Geology, Changchun, Jilin Province, China
CGMSP: St. Petersburg, Russia
GSC: Geological Survey of Canada, Ottawa
LO: Lunds Originale, Department of Geology, Lund University, Sweden
NHMUK PM: The Natural History Museum, London, UK (formerly BMNH)
NMVP: Museum Victoria, Melbourne, Australia
NYSM: New York State Museum, Albany, New York, USA
PMO: Natural History Museum, University of Oslo, Paleontological Type collections, Norway
SGU: Sveriges Geologiska Undersökning, Uppsala, Sweden
SM: Sedgwick Museum of Earth Sciences, Cambridge, UK

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