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PART V, SECOND REVISION, CHAPTER 17: ORDER DENDROIDEA: INTRODUCTION, MORPHOLOGY, AND SYSTEMATIC DESCRIPTIONS

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Order DENDROIDEA Nicholson, 1872

[Dendroidea NICHOLSON, 1872, p. 101; *ex* section Dendroidea NICHOLSON, 1872, p. 101] [=Cladophora HOPKINSON in HOPKINSON & LAPWORTH, 1875, p. 634; *non* Inocaulida BOUČEK, 1957, p. 145, herein (dasycladacean algae); =Mastigograptida BATES & URBANEK, 2002, p. 458, herein]

Benthic graptoloids with erect, bushy, cone- or fan-shaped tubarium; thecae often serially arranged along stipes with regularly placed bithecae based on triad budding system; thecal development variable from tube shaped and aperturally isolated to distinctly widening and with ventral rutellum; anastomosis, dissepiments, or thecal bridges may connect stipes laterally; sicula possibly tubular with helical line but development unknown in most taxa. *Cambrian (Miaolingian)–Carboniferous, Serpukhovian (Arnsbergian):* worldwide.

Dendroidea includes most of the benthic graptoloids with an erect tubarium, possessing a triad-budding system with distinct thecal differentiation. The families Dendrograptidae, Callograptidae, and Mastigograptidae are separated due to the shape and organization of their autothecae. Bushy growth, however, also appears in some Cyclograptidae (see MALETZ, 2019c), in which the encrusting part may be reduced in size, but the included species do not show triad budding. The genera of the dendroid families are typically defined from tubarium fragments, based on general constructional features, and the final shape of their tubaria remains unknown. The differentiation into various genera and families varied considerably through time, and the attribution of the hundreds of described species to a certain genus and family is often arbitrary and in need of re-evaluation. Proximal ends and siculae are rarely known in enough detail to understand the real phylogenetic relationships of the taxa. The thecal development is unknown in most species, and the inclusion into a certain genus is based on the tubarium shape, thus remains tentative. Therefore, also the precise biostratigraphic ranges of most genera cannot be evaluated.

HOPKINSON in HOPKINSON and LAPWORTH (1875) differentiated the family Callograptidae (genera *Dendrograptus, Callograptus, Dictyograptus, Desmograptus*) from the family Ptilograptidae (*Ptilograptus*) among the Dendroidea. The family name Callograptidae has rarely been used afterwards (e.g., BOUČEK, 1957), but MU (1953) defined a subfamily Callograptinae within the family Dendrograptidae. MU and others (2002) used the subfamily Callograptinae for the genera *Callograptus, Aspidograptus, Desmograptus,* and *Syrrhipidograptus*.

CHAPMAN, RICKARDS, and GRAYSON (1993) and CHAPMAN, DURMAN, and RICKARDS (1996) used the thecal style and tubarium shape to differentiate and sort the genera into a number of families, but little information on the important initial colony development exists to support these taxa as phylogenetically meaningful. MITCHELL and others (2013) did not provide any indication or opinion on the differentiation

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of the dendroid benthic graptolites. The authors differentiated the Eugraptolithina as a holophyletic group, united by the presence of a helical line in the erect prosicula, excluding the benthic, encrusting taxa. The term should not be confused with the Eugraptoloida of MALETZ, CARLUCCI, and MITCHELL (2009), referring to the traditional Graptoloidea lacking bithecae, excluding the planktic Anisograptidae.

MORPHOLOGY

All Dendroidea produce erect-growing colonies starting from a disk-like proximal attachment site, called a basal disk or holdfast, which is known only from a few taxa. WIMAN (1896) illustrated the proximal end of *Dictyonema cavernosum* WIMAN, 1896 with an irregularly formed attachment disk (Fig. 1.3) and BATES and URBANEK (2002) showed the basal disk of *Mastigograptus* sp. cf. *M. tenuiramosus* (WALCOTT, 1883), indicating the growth on a ridged underground, possibly a brachiopod shell.

The sicula is known from very few taxa and may be tubular in form with an upward-directed aperture (Fig. 1.1), possessing a helical line in the prosicula and distinct fusellar half rings in the metasicula. Initially, the flat base of the prosicula is attached to a surface and in later stages is covered by cortical material forming the basal disk. The dendroid colonies then may either develop a bushy form through a number of proximal branching divisions, forming the main stipes of the colony or, alternately, a single stem that branches only at some distance from the proximal end, forming a more treelike shape (Fig. 1.4). During the later growth of the colony, various shapes can develop. The stipes are either oriented in a single plane in fan-shaped or cone-shaped tubaria or the branches develop more irregularly in three-dimensional bushy or treelike colonies (Fig. 1.3–1.7). The diagenetic flattening of the colonies in the sediments and fragmentation due to postmortem transport often make these shapes difficult to recognize and distinguish.

The development and differentiation of thecae is recognized mainly from chemically isolated material and shows a triad budding system (WIMAN, 1895, 1896; BULMAN, 1927a; KOZŁOWSKI, 1949) in which each autotheca is associated with a bitheca (Fig. 2.3a–b, Fig. 2.4). The bithecae originate on alternating sides on their mother thecae (MALETZ, LENZ, & BATES, 2016). Triad budding has been demonstrated from chemically isolated material in the Mastigograptidae by ANDRES (1961, 1977) (Fig. 2.1b), but a morphological differentiation of autothecae and bithecae is not present. BATES and URBANEK (2002) described important details of the construction of the stolon system in stem fragments of *Mastigograptus* sp. and verified the presence of triad budding in this taxon. Triad budding in the Callograptidae has only been verified in *Desmograptus micronematodes* (SPENCER, 1884) (see SAUNDERS & others, 2009). Three-dimensionally preserved isolated material of *Koremagraptus* shows triad budding, but the differentiation of autothecae and bithecae is nearly impossible in the ropy stipes with strongly elongated thecae (BULMAN, 1945).

The thecal style varies considerably between the various groups of the Dendroidea. The thecae are parallel sided and typically elongated in the Callograptidae (Fig. 2.2), forming a ropy appearance of the stipes of the tubarium. Thecal apertures are typically raised above the stipes and form isolated tubes and compound twigs. The thecal apertures may be oriented either to all sides or toward one side, identified as the ventral side of the stipe. In the Mastigograptidae (Fig. 2.1), the delicate and thin-walled metathecae originate from slender to robust branches and appear to be largely isolate, gradually widening toward their apertures. It is unclear whether the thecal apertures show a preferred orientation. The Dendrograptidae (Fig. 2.3) have serially arranged thecae, in which all metathecal apertures are ventrally oriented in one single row. The thecae gradually widen toward their apertures and commonly show a ventral apertural lip or rutellum. The

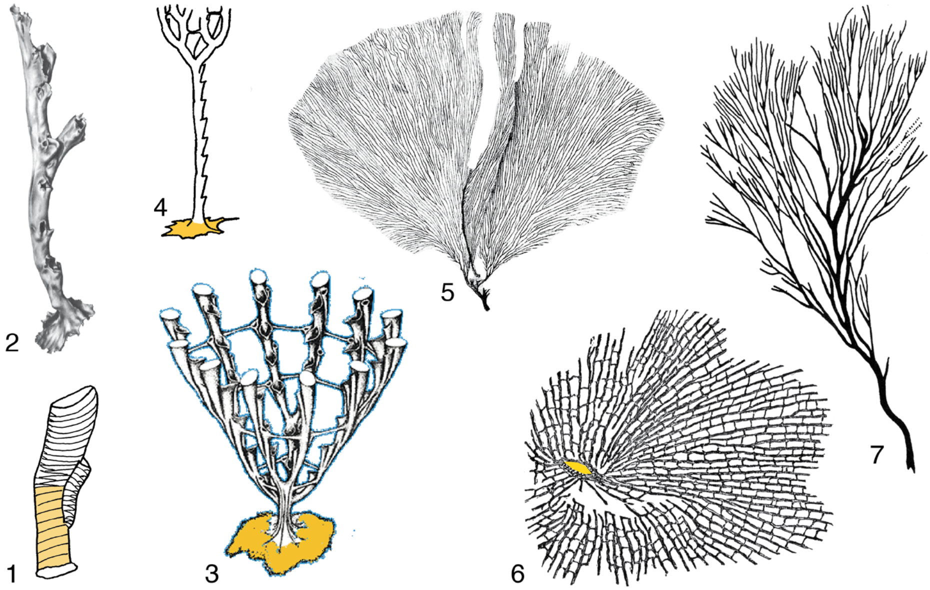

Fig. 1. Astogeny and tubarium shape of the Dendroidea. *1–2, Dendrograptus communis* Kozłowski, 1949; *1,* sicula with bud of th1 (adapted from Kozłowski, 1949, fig. 1); *2,* stem with part of attachment disc and one distal branching (Kozłowski, 1949, pl. 6,*5*); *3, Dictyonema cavernosum* Wiman, 1896, reconstruction of cone-shaped colony (from Mierzejewski website); *4, Dictyonema* sp. with long stem (adapted from Bulman, 1928, fig. 2F); *5, Callograptus elegans* Hall, 1865, fan-shaped colony (Hall, 1865, pl. 19,*2*); *6, Dictyonema retiforme* (Hall, 1843), holotype, cone-shaped benthic colony, attachment site marked in color (Hall, 1865, fig. 10); *7, Dendrograptus fruticosus* Hall, 1865, bushy colony (Bulman, 1970, fig. 16,*1a*). Illustrations not to scale.

rutellum may be modified into a complex apertural construction. The thecal development is largely identical to the development in the bithecate Anisograptidae (Fig. 2.4) with a distinct difference in thecal size between autothecae and bithecae.

EVOLUTION

Very little is known about the evolutionary patterns of the Dendroidea. Chapman, Durman, and Rickards (1996) discussed a general middle Cambrian origin of the main groups of the Graptolithina. Rickards and Durman (2006) provided an overview on the Cambrian graptolites known at the time, indicating that a number of taxa were already present in the Miaolingian (Cambrian). Many taxa were only identified by their general tubarium shape as they were poor and fragmentary in preservation. Maletz (2019a) indicated the presence of the Dithecodendridae in Cambrian, Series 2 (Stage 4) and the appearance of the Dendrograptidae in the Miaolingian. A considerable diversification of the Dendrograptidae and Callograptidae might have taken place during the late Cambrian. During the Ordovician and Silurian time intervals, the diversity of the Dendroidea remained high, but few groups survived into the Devonian and only the Callograptidae have been recognized with certainty from the Carboniferous (Chapman, Durman, & Rickards, 1996; Maletz & others, 2020).

Family DENDROGRAPTIDAE
Roemer in Frech, 1897

[Dendrograptidae Roemer in Frech, 1897, p. 568; *ex* Dendrograptidi Roemer in Frech, 1897, p. 568] [Family Dendroidea Hopkinson, 1872, p. 503]

Benthic graptoloids with variable colony shape; erect, bushy or fan-shaped tubarium; thecae serially arranged along stipes with

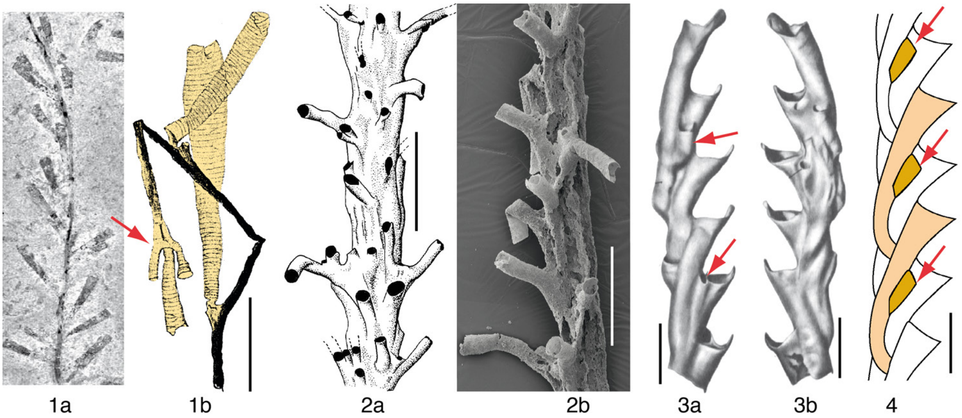

FIG. 2. Thecal style in the Dendroidea. *1a, ?Mastigograptus* sp., Marjum Formation, Utah, Miaolingian, Cambrian (LoDuca & Kramer, 2014, fig. 2,*2*); *1b, Mastigograptus* sp., *arrow* points to triad budding, glacial boulder, Ostseekalk, Upper Ordovician, Germany (Andres, 1977, fig. 13, color added); *2a, Acanthograptus musciformis* (WIMAN, 1901), Upper Ordovician, Gotland, Sweden (Bulman & Rickards, 1966, fig. 20); *2b, Acanthograptus divergens* SKEVINGTON, 1963, LO 11412t, Middle Ordovician, Öland, Sweden (new); *3a–b, Dendrograptus communis* KOZŁOWSKI, 1949, Lower Ordovician, Tremadocian, Poland, specimen shown from both sides, *arrows* (*a*) show bitheacae (adapted from Kozłowski, 1949, pl. 6,*8*, 6,*8a*); *4,* Anisograptidae, thecal style showing bithecae (*arrows*) (adapted from Maletz, Lenz, & Bates, 2016, fig. 16,*1*). Scale bars, 1 mm in all figures.

regularly placed bithecae based on a triad budding concept; anastomosis or dissepiments present in some taxa; sicular and proximal development largely unknown; autothecae widening toward the apertures, possessing a ventral lip or rutellum, sometimes with complex apertural modifications. *Cambrian (Miaolingian)–Lower Devonian (uppermost Emsian to lowermost Eifelian, possibly* Nowakia maureri–Novakia sulcata sulcata *biozones):* worldwide.

Dendrograptidae represent a paraphyletic taxon from which the derived planktic graptoloids originated. ALLMAN (1872, p. 380) suggested the term Rhabdophora for the taxa "by the possession of a solid supporting rod," later identified as the nema by LAPWORTH (1873) (e.g., the planktic graptolites), while HOPKINSON in HOPKINSON and LAPWORTH (1875) separated the benthic taxa as the Cladophora. At the time, encrusting taxa were unknown to science, and all benthic taxa were supposed to be erect in growth. HOPKINSON in HOPKINSON and LAPWORTH, 1875 erected the new family Ptilograptidae for the genus *Ptilograptus* and referred *Dendrograptus* to the Callograptidae. MITCHELL and others (2013, fig 6) showed the dendroids as a paraphyletic unit including a number of genus level taxa that are here informally referred to a variety of family level taxa (e.g., Callograptidae, Dendrograptidae, Mastigograptidae).

Most taxa of the Dendrograptidae are poorly known from flattened shale material or isolated fragments, usually preserved as current-transported specimens. The proximal end development and sicular construction are unknown in most taxa. The erect growth of the colonies with the relatively simple aperturally widening thecae may be regarded as defining characters of Dendrograptidae. The thecae are invariably serially arranged on the stipes and possess the typical triad budding with bithecae on alternate sides of the stipes. Branching is often irregular and secondary connections between stipes through dissepiments and anastomosis are common.

Planktic dendroids (Fig. 3) have been described from a number of occurrences (RICKARDS, HAMEDI, & WRIGHT, 1994; KRAFT & KRAFT, 2007). They may be referred to the genus *Calyxdendrum* KOZŁOWSKI, 1960, a genus that Bulman (1970) identified as a member of the planktic Anisograptidae. *Pseudocallograptus* cf. *salteri* (Skevington, 1963) from the Middle Ordovician of Öland possesses a sicula with a free nema, indicating a possibly planktic taxon but might be unrelated to *Calyxdendrum*. These planktic taxa should not be placed in the planktic Graptoloidea, as they likely represent a secondary, independent origination of a planktic life style (see Kraft & Kraft, 2007). It is preferred here to keep them with the benthic Dendrograptidae, as they do not possess the defining characters of the planktic Anisograptidae.

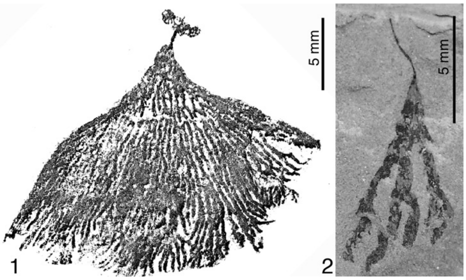

Fig. 3. Planktic Dendrograptidae. *1, Calyxdendrum ghodsiae* (Rickards, Hamedi, & Wright, 1994), holotype, Dapingian, Iran (Rickards, Hamedi, & Wright, 1994, fig. 2); *2, Calyxdendrum titanus* (Kraft, 1990) note the long nema, Dapingian, *Tetragraptus abbreviatus* Biozone, Czech Republic (Kraft & Kraft, 2007, fig. 1).

MORPHOLOGY

The morphology of the tubaria of the Dendrograptidae is largely related to ecological influences of the attached colonies and their environmental conditions. The basic shape of the dendrograptid tubarium depends on the branching mode and direction of growth of the stipes. Three main types can be differentiated: the disorderly developed bushy shape, the fan shape, and the conical shape (Fig. 1). In all these shapes, taxa with and without a thickened stem are known. The colony shape may be influenced considerably by the late-stage addition of cortical material and thecal style may be considerably masked to the extent that the original thecal shape is not recognizable (see Bates & others, 2011).

A proximal development of the Dendrograptidae is known from a few juvenile specimens of the genus *Dendrograptus* and *Graptolodendrum*. The sicula is tubular with a flat base for attachment (Fig. 1.1). The prosicula can be differentiated through the spiral line, while the metasicula has fusellar half rings and regularly placed oblique sutures on the dorsal and ventral sides in *Dendrograptus communis* Kozłowski, 1949, but in *Graptolodendrum,* full fusellar rings are present and the sutures are irregularly placed. A very irregular development of fusellar rings can also be noted in the more triangular sicula of *Calyxdendrum* in which a free nema is also present. The origin of th1^1 is variable and may be in the prosicula (*Dendrograptus communis, Calyxdendrum*) or in the metasicula (*Graptolodendrum*). The first dicalycal theca may be th1^2 or a later one in specimens with a stem. The details are not available for most species and genera.

One of the characteristic features of many Dendrograptidae is the secondary connection between stipes. These connections are regarded as a means of keeping the stipes at a certain distance to prevent competition for the zooids. Dissepiments are variably developed rods formed initially from fusellar tissue overlain by cortical material (Urbanek & Mierzejewski, 2009). They are sometimes very thin and delicate but can also be fairly robust and then appear similar to the bridges in the Callograptidae. Dissepiments form straight, perpendicular connections between stipes, but obliquely developed dissepiments are also common. Dissepiments are characteristic for dendroids previously included in the genus *Dictyonema* (see Bulman, 1970; Erdtmann, 1982). The material described by Urbanek and Mierzejewski (2009) consists of Middle to Upper Ordovician fragments and a specific identification of the material is difficult. Dissepiments are also typical for the planktic anisograptid *Rhabdinopora* (see Erdtmann, 1982; Cooper & others, 1998). A second way of connecting stipes is the growth of thecal tubes as bridges,

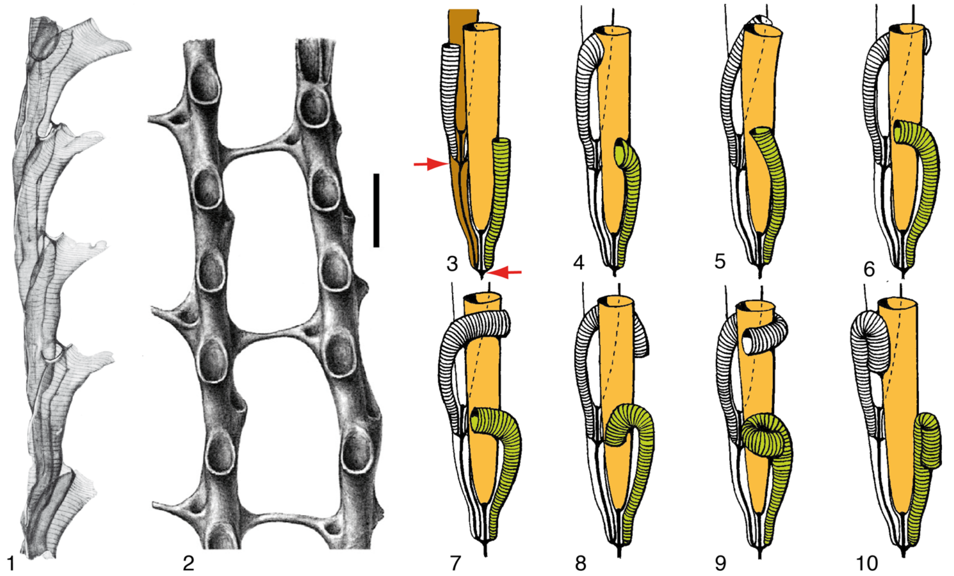

FIG. 4. The stipe and thecal development in the Dendrograptidae. *1,* ?*Dictyonema* aff. *estlandicum* BULMAN, 1933, GSM 71879, stipe fragment showing thecal style and fusellar construction, Katian, Laggan Burn, Girvan, UK. Scale bar, 1 mm (Bulman, 1945, pl. 1,*1*); *2, Rhabdinopora flabelliformis* (EICHWALD, 1840), stipe fragment with dissepiments (Bulman, 1933, pl. 1,*6*); *3–10,* reconstructions to show bithecal growth; *3, Rhabdinopora flabelliformis* (EICHWALD, 1840), *arrows* indicate the presence of triad budding, which is present in all taxa; *4, Dictyonema peltatum* WIMAN, 1895; *5, Dictyonema cotyledon* BULMAN, 1933; *6, Dictyonema rarum* WIMAN, 1895; *7, Callograptus infrabithecalis* KOZŁOWSKI; *8, Dictyonema inconstans* BULMAN, 1933; *9, Dendrograptus cofeatus* KOZŁOWSKI, 1949; *10, Dictyonema wysoczkianum* KOZŁOWSKI, 1949 (*3–10,* Bulman, 1955, fig. 10).

common in the Callograptidae (identified as Acanthograptidae in MALETZ, 2019b). These may easily be mistaken as dissepiments when flattened. A different way of stipe interaction is the temporary fusion of adjacent stipes or the transfer of thecae, called anastomosis and pseudanastomosis (RICKARDS & LANE, 1997).

The stipes are constructed by parallel-sided, slender bithecae and aperturally widening autothecae with or without apertural modifications. There appears to be considerable variation in the development of the bithecae (Fig. 4.3–4.10); but for most taxa, the precise development of the bithecae is uncertain.

THECAL DEVELOPMENT

The thecal development is unknown in many Dendrograptidae, but well-preserved fragments have been found during the last hundred years. BULMAN (1933) described a number of taxa from chemically isolated Scandinavian material and provided the best information on the three-dimensional construction of dendroid thecae. The thecae develop with a typical triad budding system of autothecae and alternately originating daughter thecae and bithecae. The largely parallel-sided bithecae usually open at the aperture of the previous autotheca (Fig. 2). The autothecae widen distinctly toward the aperture and are usually connected with their dorsal side to the ventral side of the next theca of the stipe. The ventral side of the aperture is provided with a rutellum of variable dimension and shape. In some species, the apertural part of the thecae is isolated (e.g., *Dictyonema wimani* BULMAN, 1933), but the typical shape of the autothecae of the Dendrograptidae is retained. The bithecae are either simple tubes, opening adjacent to the autothecal apertures, or they are growing in various shapes around the autothecae (Fig.

4). Little is known on the patterns of distribution of certain styles of bithecae, but the early planktic Anisograptidae, derived from the Dendrograptidae, possess fairly simple, straight bithecae (Fig. 2.4).

EVOLUTION

Even though hundreds of species have been referred to the various genera of the Dendrograptidae, ranging from the upper Cambrian to at least the Devonian, little is known of the phylogeny of the family. It appears reasonable that the clade produced the stem leading to the planktic Graptoloidea (see Erdtmann, 1982), but further information on evolutionary pattern and changes in the Dendrograptidae is not available.

Dendrograptus Hall, 1858, p. 143 [**Graptolithus hallianus* Prout, 1851, p. 189; SD Hall, 1862, p. 21] [=*Odontocaulis* Lapworth, 1881, p. 175 (type, *O. keepingii,* OD), herein; =*Ophiograptus* Poulsen, 1937, p. 24 (type, *O. inexpectans,* OD), Bulman, 1970, p. 38]. Erect, bushy dendrograptid with loosely branching stipes; stem of variable length may be present; tubular sicula with spiral line in prosicula known from one species; origin of first theca in pro- or metasicula. *Cambrian, Furongian (Jiangshanian)–?Devonian:* worldwide.——Fig. 5,*1a*. **D. hallianus* (Prout), CMC IP83197, Potsdam Sandstone, Afton, Minnesota, USA (Bulman, 1970, fig. 16.*1b*).——Fig. 5,*1b. D. inexpectans* (Poulsen, 1937), holotype (Poulsen, 1937, fig. 11).——Fig. 5,*1c. D. keepingii* (Lapworth, 1881), holotype, Llandovery, Aberystwyth, Wales, UK (Bulman, 1928, fig. 1; specimen not identified).

Airograptus Ruedemann, 1916, p. 20 [**Dictyonema furciferum* Ruedemann, 1904, p. 606; OD]. Flabellate or shrub-like dendrograptid tubarium; thecae with low inclination and furcate or peltate ventral apertural processes; proximal development unknown; circular attachment disk known from juveniles; bithecae regularly developed, inconspicuous to strongly bulbous; dissepiments slender, irregularly developed. *Cambrian (Furongian)–Middle Ordovician (Dapingian,* Didymograptellus bifidus *Biozone):* China, Sweden, Canada, USA.——Fig. 5,*2a–b*. **A. furciferus* (Ruedemann); *2a,* NYSM 6838, small specimen with attachment disk, Bellefonte, Pennsylvania, USA (Ruedemann, 1916, fig. 7); *2b,* holotype, fragment, Deep Kill, New York, USA (Ruedemann, 1904, fig. 28).——Fig. 5,*2c*. **A.* aff. *furciferus* (Ruedemann), NIGP 134654, Dayangcha, Jilin Province, northeast China, specimen showing colony shape (Zhang & Erdtmann, 2004, fig. 5a).

Aspidograptus Bulman, 1934, p. 70 [**Clematograptus implicatus* Hopkinson in Hopkinson & Lapworth, 1875, p. 652; OD]. Cone-shaped to fan-shaped dendrograptid branching laterally from ?4 curved principal stipes; lateral branches close-set, irregularly produced, bifurcating repeatedly. *Cambrian, Furongian (Paibian)–Lower Devonian (Lochkovian,* Uncinatograptus uniformis *Biozone):* Britain, Argentina, Czech Republic, China, Tasmania.——Fig. 5,*4a–c*. **A. implicatus* (Hopkinson in Hopkinson & Lapworth); *4a,* SM A5325, lectotype, Whitesand Bay, St. David's, Wales (selected by Bulman, 1934, p. 71) (Hopkinson in Hopkinson & Lapworth, 1875, pl. 34,*1*); *4b,* SM A5326, Shelve, Shropshire, UK (Bulman, 1970, fig. 16,*5*); *4c,* SM A5319, stipe fragment possibly belonging to the species, Shelve, Shropshire, UK (Bulman, 1934, fig. 37).

Calyxdendrum Kozłowski, 1960, p. 109 [**C. graptoloides;* M]. Possibly biradiate, multiramous dendrograptid with thick free nema; autothecae conical, bithecae opening into autothecal cavities. *Upper Ordovician (Sandbian,* Nemagraptus gracilis *Zone):* Poland (glacial boulder), Czech Republic, Iran.——Fig. 5,*3a–d*. **C. graptoloides*, glacial erratic boulder, Poland; *3a,* prosicula and early part of metasicula; *3b,* holotype, proximal end in reverse view; *3c,* stipe fragment showing triad budding; *3d,* stipe fragment with several branchings (Kozłowski, 1960, fig. 1,3,10,11, respectively).

Capillograptus Bouček, 1957, p. 42; *ex Callograptus (Capillograptus)* Bouček, 1957, p. 42 [*?*Callograptus dichotomous* Počta, 1894, p. 182; M]. Fan-shaped to conical dendrograptid with slender stipes; thecae simple with low inclination and prominent ventral apertural spines; few thin dissepiments irregularly distributed in colony. *Silurian (Wenlock,* Cyrtograptus radians *Biozone–Pridoli,* Monograptus ultimus *Biozone):* Czech Republic.——Fig. 5,*5a*. **C. dichotomous* (Počta), paratype (Bouček, 1957, fig. 16a).——Fig. 5,*5b–c*. *C. pilosus* Bouček, 1957, fragments showing dissepiments and ventral apertural spines (Bouček, 1957, fig. 16c–d).

Graptolodendrum Kozłowski, 1966, p. 4 [**G. mutabile;* OD]. Erect, multiramous dendrograptid with metasicular origin of th1^1; metasicula with irregular development of fuselli and without dorsal and ventral zigzag suture; regular triad budding with bithecae of branching divisions on same side, position changing at branching points. *Middle Ordovician (upper Darriwilian or Sandbian,* Dicellograptus vagus *or* Nemagraptus gracilis *Biozone):* Poland (glacial boulder only).——Fig. 5,*8a–d*. **G. mutabile; 8a,* holotype (Kozłowski, 1966, fig. 1.*1*); *8b–c*, sicula with first theca and first triad, th2^1 covered behind th1^1 in *5b* (Kozłowski, 1966, fig. 13a–b, color added); *8d,* prosicula and initial part of metasicula (Kozłowski, 1966, fig. 10, color added).

Licnograptus Ruedemann, 1947, p. 196 [**L. elegans;* OD]. Robust erect dendrograptid with short thickened stem and several main branches bearing groups of subparallel fanlike extended stipes; thecae with low inclination and long apertural spines. *Lower Ordovician (Tremadocian–Floian):* Canada.——Fig. 5,*6a*. **L. elegans; 6a,* holotype

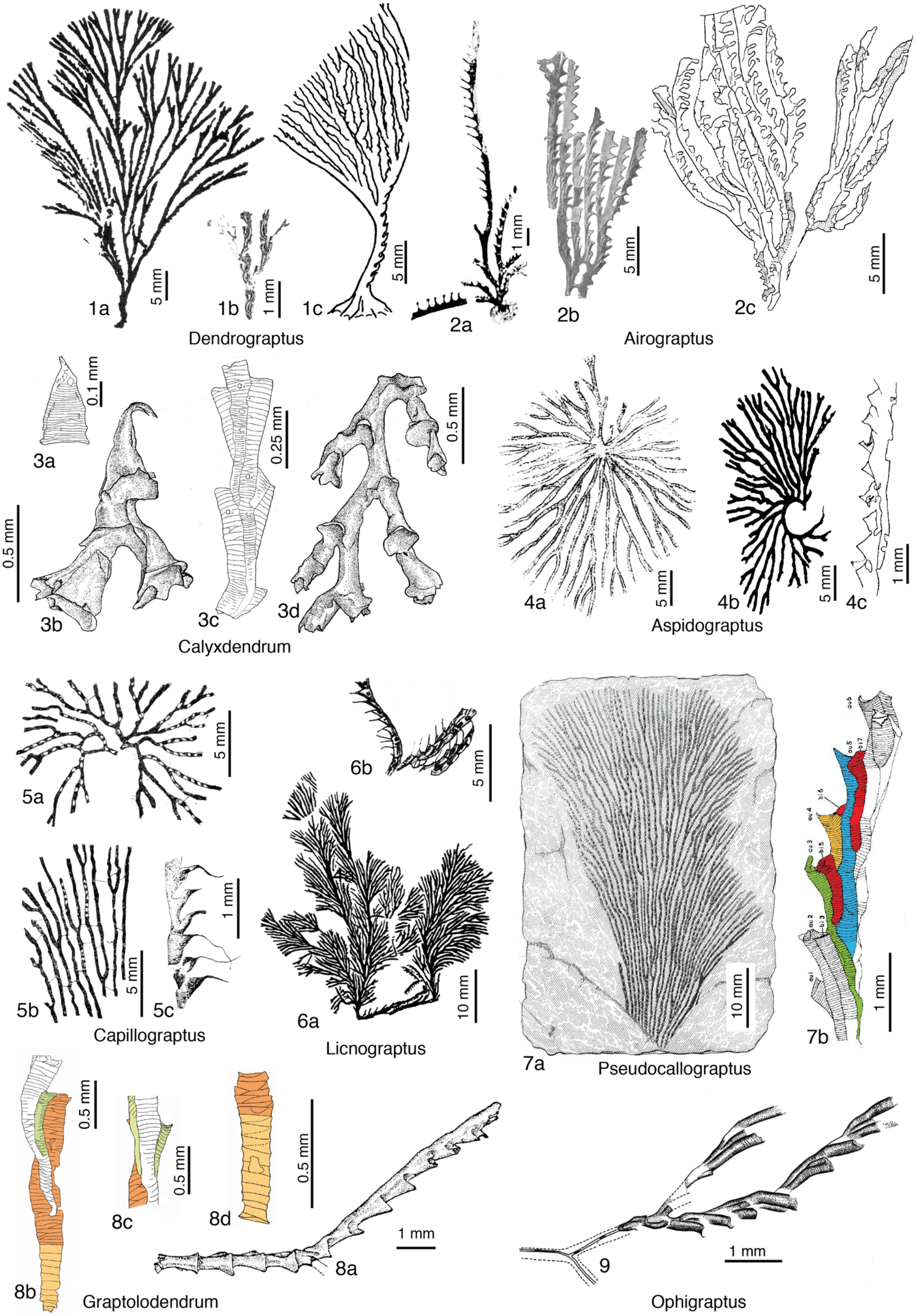

FIG. 5. Dendrograptidae (p. 7–9).

(Bulman, 1970, fig. 16.7); *6b,* detail showing spined thecal apertures (Ruedemann, 1947, pl. 16,*5*).

Ophigraptus Jaeger, 1992, p. 125 [**O. hercyniae* Jaeger, 1992, p. 125; OD]. Erect, slender dendrograptid with monoprogressive branching forming several zigzag shaped main branches; some of the lateral branches also with monoprogressive branching divisions; distances between branchings regular, probably consisting of two or three autothecae each; proximal end unknown; thecae simple with low inclination and straight apertures; bithecae small and tubular. *Lower Devonian (uppermost Emsian to lowermost Eifelian, possibly* Nowakia maureri *to* Novakia sulcata sulcata *biozones;* see Alberti & others, 1996, p. 275): Germany.——Fig. 5,*9*. **O. hercyniae*, MBg 811, detail of holotype, Buntenbock, Harz, Germany (Jaeger, 1992, fig. 1).

Pseudocallograptus Skevington, 1963, p. 19 [**Callograptus salteri* Hall, 1865, p. 135; OD]. Fan-shaped robust dendrograptid; autothecae and bithecae possibly slender, elongate, with increased overlap and low inclination; producing ropy appearance of stipe and unusual association of thecal apertures; autothecae generally denticulate. [The diagnosis is based on chemically isolated fragments from Sweden and the relationship to *Callograptus salteri* from Canada remains uncertain (see Skevington, 1963, p. 25).] *Lower Ordovician (Floian* Didymograptellus bifidus *Biozone)–Middle Ordovician (Darriwilian,* Didymograptus murchisoni *Biozone):* Sweden, Canada, Argentina.——Fig. 5,*7a*. **P. salteri* (Hall), GSC 955a, syntype, larger colony fragment, Gros Maule, Québec, Canada (probably in error for Lévis, Québec, Canada) (Hall, 1865, pl. 19,*5*).——Fig. 5,*7b*. *Pseudocallograptus* sp. cf. *P. salteri* showing thecal overlap and development of bithecae, Öland, Sweden (adapted from Skevington, 1963, fig. 23a).

Family CALLOGRAPTIDAE Hopkinson, in Hopkinson & Lapworth, 1875

[Callograptidae Hopkinson, in Hopkinson & Lapworth, 1875, p. 663] [=Acanthograptidae Bulman, 1938, p. 20; =Pseudodictyonemidae Chapman, Rickards, & Grayson, 1993, p. 308; =Stelechocladiidae Chapman, Rickards, & Grayson, 1993, p. 307; =?Ptilograptidae Hopkinson in Hopkinson & Lapworth, 1875 p. 633; ?=Nephelograptidae Bouček, 1957, p. 83 (misspelled Nephellograptidae in Bouček, 1957, p. 5); *non* Inocaulidae Ruedemann, 1947, p. 230, Mierzejewski, 1986, p. 165]

Benthic graptoloids with variable shape of colonies, from erect, bushy, cone-, or fan-shaped; commonly complex stipe development of ropy appearance; anastomosis, dissepiments or thecal bridges may connect stipes; thecae tube shaped, with isolated autothecal apertures; development of twigs common; regularly placed bithecae based on a triad budding concept, but no size differentiation of bithecae; proximal development and details of fusellar construction unknown. *Cambrian (Miaolingian)–Carboniferous, Serpukhovian (Arnsbergian):* worldwide.

The Callograptidae include a characteristic group of multiramous benthic graptolites with a typically complex development of their stipes from slender tubular thecae. Rickards and Durman (2006, fig. 18, 20) described the Callograptidae (as Acanthograptidae) as a monophyletic group in their study. They regarded the presence of multiserial stipes as the defining synapomorphy of the group. This character is here regarded as a feature of derived callograptids; earlier taxa (e.g., *Callograptus* Hall, 1865) show less complex development but share the simple parallel-sided thecae with isolated apertures. The proximal development and sicula are unknown for all included taxa. Triad budding indicates the presence of thecal differentiation, but the recognition of bithecae is not possible through size differences as it is in the Dendrograptidae.

A number of taxa previously included in the Inocaulidae Ruedemann, 1947 may turn out to represent callograptids. The type species of the genus *Inocaulis*—*Inocaulis plumulosa* Hall, 1865—may represent a dasycladacean alga or at least not a graptolite (Mierzejewski, 1986). *Thallograptus succulentus* (Ruedemann, 1904), the type species of *Thallograptus* Ruedemann, 1925, is regarded as a dasycladacean alga, while many other taxa included in this genus (e.g., Bouček, 1957; Chapman, Durman, & Rickards 1996) have to be referred to other callograptid genera. *Thallograptus phycoides* (Spencer, 1884) was illustrated by Bulman (1970, fig. 22,*2*) as characteristic of the genus *Thallograptus* but identified as *Thallograptus cervicornis* (Spencer, 1884).

Specimens of the Callograptidae are easily misidentified as land plants in poor, flattened material, as was convincingly demonstrated by Kenrick, Kvaček, and Bengtson (1999), who recognized the graptolitic relationships of *Boiophyton* Obrehl, 1959, and is indicated for the genus *Saxonia* Roselt, 1962 herein. Lundblad (1972) redescribed *Psilophyton*? *hedei* Halle, 1920 from the Gorstian (Silurian) of Gotland as a dendroid graptolite. The species can be regarded as a member of the Callograptidae based on the isolated tubular thecal apertures visible in the material and may belong to *Boiophyton* (see Kenrick, Kvaček, & Bengtson, 1999).

MORPHOLOGY

The Callograptidae include mostly robust, erect-growing graptoloids with a variably fan-shaped to cone-shaped tubarium reaching a considerable size. Typical bushy forms may appear but are rare. Specimens may be as much as 30 cm or more in diameter in cone-shaped colonies, but mostly small colonies or fragments are found as preserved specimens. These have generally been transported, and few specimens have been found *in situ.* Fragments may be difficult to identify to species level, as features of proximal and distal pieces may differ considerably in dimensions. In all callograptids, dorsal and ventral sides of the stipes can be differentiated, as even in complexly developed taxa, thecal apertures may be oriented ventrally and laterally but never dorsally.

Large differences can be seen in the complexity of the development of the stipes and their connections. Taxa may develop large colonies without even connecting adjacent stipes (e.g., *Callograptus*), but more commonly, dissepiments or thecal bridges connect the individual stipes (e.g., *Dictyonema*). Maletz (2019b) recognized the growth of thecae crossing the gap to an adjacent stipe as thecal bridges. There may be bridges constructed by a single thecal tube, but also multiple thecae may cross at a point. Urbanek and Mierzejewski (2009) quoted the presence of dissepiments in *Ptiograptus,* for example, but it is clear now that the stipe connections in *Ptiograptus* are formed as thecal bridges (Maletz, 2019b, p. 152).

Anastomosis has been described in a few taxa (Fig. 6.2,4), but may be difficult to separate from accidental connections of the stipes of the colonies in the sediment. Bulman (1945, pl. 1,*2*) illustrated the anastomosis in an isolated fragment of *Koremagraptus kozlowskii* Bulman, 1945. Rickards and Lane (1997) described the transfer of thecae from one stipe to another as pseudanastomosis.

Twigs can be regarded as an important character of the Callograptidae. However, many taxa only show isolated apertural parts of the thecae, and twigs are lacking (Fig. 6.2). Through the evolution of the Callograptidae, more thecae have joined the laterally growing isolated autothecal apertures; these became elongated and the twigs (Fig. 6.5) formed as short and complex extensions or lateral stipes. The colony shapes appear more similar to those of the Dendrograptidae in these forms without twigs (Fig. 6.1). Maletz and Kozłowska (2013) illustrated partial relief specimens of *Acanthograptus sinensis* Hsü and Ma, 1948 with slender and parallel-sided, tubelike thecae, typical of Callograptidae. The specimens show paired thecal origins, indicating the presence of triad budding (Fig. 6.5). A differentiation of potential autothecae and bithecae is impossible in this material as there is no obvious size difference in the thecae. Thecae are generally straight and curve outward only toward their apertures, but a number of thecae have irregular curved paths (Fig. 6.6). The development of the thecae in more slender stipes with fewer overlapping thecae and a more regular development is evident in *Callograptus elegans* (Hall, 1865) (Fig. 6.4).

EVOLUTIONARY RELATIONSHIPS

Little is known about the evolutionary relationships of the Callograptidae. Chapman, Durman, and Rickards (1996) concluded that *Thallograptus* (now identified as a dasycladacean alga) might have been the earliest taxon of the Callograptidae and originated in the upper Cambrian but also stated that the early forms of the Callograptidae are poorly known. Rickards and

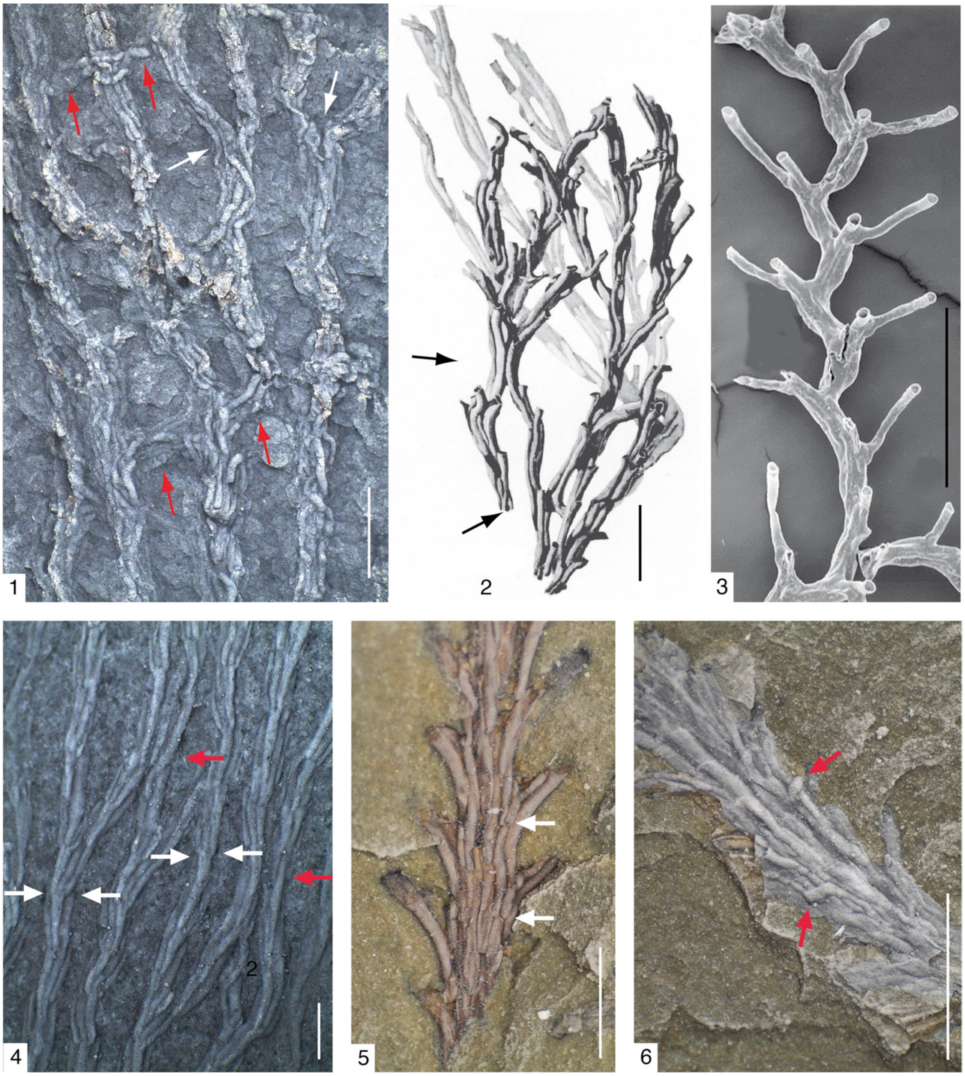

Fig. 6. Stipe development and connections in the Callograptidae. *1, Dictyonema fournieri* (Ubaghs, 1941), fragment in dorsal view, latex cast showing bridges (*red arrows*) and branching (*white arrows*), scale bar, 1 mm (new); *2, Koremagraptus kozlowskii* Bulman, 1945, arrows indicate anastomosis, scale bar, 1 mm (adapted from Bulman, 1945, pl. 1,*2*); *3, Ptilograptus* sp., GSC 119695, ventral view, showing alternating growth of long autothecae, Wenlock, Snowblind Creek, Cornwallis Island, Arctic Canada (Lenz & Kozłowska-Dawidziuk, 2001, pl.1,*12: Acanthograptus*); *4, Callograptus elegans* Hall, 1865, GSC 955a, lectotype, latex cast showing dorsal view of stipes with triad budding (*white arrows*) and anastomosis (*red arrows*), Lévis, Quebec (new); *5–6, Acanthograptus sinensis* Hsü & Ma, 1948, PKUM02-0627, 0629, specimens showing twigs and irregular growth (*red arrows* in *6)* of thecal tubes (*white arrows* indicate triad budding in *5*) Tianjianling, Hubei Province, China (Maletz & Kozłowska, 2013, fig. 5b,d). Scale bar, 1 mm for all photos.

Durman (2006) listed the biostratigraphic ranges of Cambrian graptolites and listed the first occurrence of *Acanthograptus* (thus, the Callograptidae) from the *Goniagnostus nathorsti* Biozone of the Drumian (Miaolingian), based on *Acanthograptus banksi* Quilty, 1971 from Tasmania. Mitchell and others (2013) suggested a sister group relationship to the Dendrograptidae and Mastigograptidae, but their analysis showed only a low resolution, as it was not aimed at differentiating clades within the Dendroidea.

Acanthograptus Spencer, 1878, p. 461, *pro Acanthograpsus* Spencer, 1878, ICZN Opinion 650, 1963 [**Acanthograpsus granti;* M] [=*Xylonograptus* Sennikov, 1976, p. 108 (type, *X. regularis,* M), herein; =*Paracanthograptus* Wang in Wang & others, 1987, p. 365 (English text, p. 548–549) (type, *P. sanxianensis,* OD), herein (synonym of *Thallograptus* in Mu & others, 2002, p. 104)]. Erect, possibly bushy or fan-shaped callograptid with complex development of stipes; apertural parts of slender isolated autothecal tubes, inclined to main stipes. ?*Cambrian (Miaolingian, Drumian,* Goniagnostus nathorsti *Biozone)–Silurian, Ludlow (Gorstian,* Saetograptus chimaera *Biozone):* worldwide.——Fig. 7,*1a.* **A. granti,* Hamilton, Ontario, Canada, type specimen whereabouts unknown (Ruedemann, 1908, pl. 6,*4*).——Fig. 7,*1b. A. arborescens* (Bouček, 1957), specimen showing branching pattern (Bull, 1987, fig. 10b).——Fig. 7,*1c. A. musciformis* (Wiman, 1901), reconstruction of distal part of stipe showing thecal growth (Bulman, 1970, fig. 21,*1b*).

Alternograptus Bouček, 1956, p. 131 *ex Callograptus* (*Alternograptus*) Bouček, 1956, p. 131 [**C.* (*A.*) *holubi;* OD]. Bushy callograptid with slender, possibly monoprogressive stipes showing isolated thecal apertures; proximal development unknown. *Lower Ordovician (Dapingian,* Tetragraptus reclinatus abbreviatus *Biozone):* Czech Republic.——Fig. 7,*2a–b.* **A. holubi; 2a,* holotype, proximal end (Bouček, 1956, fig. 2a); *2b,* fragment showing thecal apertures (Bouček, 1956, fig. 2c).

Callograptus Hall, 1865, p. 133 [**C. elegans,* SD Miller, 1889, p. 175]. Tubarium conical, flabellate or irregular with or without a thecate stem; stipes branching dichotomously, attaining a subparallel to parallel orientation quickly; autothecae tubular, slightly to strongly isolate aperturally; bithecae indistinct, tubular. *Cambrian (Furongian)–Carboniferous:* worldwide.——Fig. 7.3. **C. elegans,* GSC 956a, lectotype, Lévis, Quebec, Canada (Hall, 1865, pl. 19,*2*).

Callodendrograptus Decker, 1945, p. 28 [**C. sellardsii;* OD]. Callograptid with bushy tubarium; compound stipes and tubular thecae with isolated, ventrally oriented apertures; details unknown. *Cambrian (Furongian, Jiangshanian,* Ellipsocephaloides–Idahoia *Biozone)–Ordovician:* USA.——Fig. 7,*5.* **C. sellardsii,* cotype, Point Peak Member, Wilberns Formation, Texas, USA (Decker, 1945, pl. 4,*5*).

Desmograptus Hopkinson in Hopkinson & Lapworth, 1875, p. 668; *ex Dictyograptus (Desmograptus)* Hopkinson in Hopkinson & Lapworth, 1875, p. 668 [**D.* (*D.*) *cancellatus;* M] [=*Rhizograptus* Spencer, 1878, p. 460, *pro Rhizograpsus* Spencer, 1878, ICZN Opinion 650, 1963, Ruedemann, 1947, p. 224 (type, *R. bulbosus,* M), Bulman, 1970, p. 38; =*Syrrhipidograptus* Poulsen, 1924, p. 4 (type, *S. nathorsti,* M), Bulman, 1970, p. 38]. Tubarium may be conical or fan-shaped; simple to compound stipes; regular, dominant anastomosis; dissepiments rare; autothecae tubular, denticulate to isolate aperturally; bithecae much smaller. *Lower Ordovician (Tremadocian)–?Devonian:* worldwide.——Fig. 8,*1a,* **D. cancellatus*, holotype, SMA17507 (Bulman, 1970, fig. 16,*2*).——Fig. 8,*1b, D. bulbosus* (Spencer, 1878), holotype, Silurian, Niagara Limestone, Hamilton, Ontario, Canada (Spencer, 1884, pl. 4,*4*)——Fig. 8,*1c–d. D. nathorsti* (Poulsen, 1924), holotype, Katian, Bornholm, Denmark (Poulsen, 1924, fig. 2a–b).

Dictyonema Hall, 1851, p. 401 [**Gorgonia*? *retiformis* Hall, 1843, p. 115; SD Miller, 1889, p. 185]; [=*Dictyograptus* Hopkinson in Hopkinson & Lapworth, 1875, p. 667 (type not designated), herein; =*Dictyonema* (*Pseudodictyonema*) Bouček, 1957, p. 69 (type, *Dictyonema graptolithorum* Počta, 1894, p. 196, OD), Maletz, 2019b, p. 152; *non Dictyonema* Adgardh in Kunth, 1822, p. 1 (lichens, Agaricales, family Hygrophoraceae), see Parmasto, 1978; Dal-Forno & others, 2013; Lücking & others, 2013]. Tubarium conical to fan-shaped; conical tubaria varying from almost cylindrical to almost discoidal; stipes straight, subparallel to parallel, branching dichotomously; stipes united by regularly or irregularly produced thecal bridges formed from single or multiple thecal tubes; stipes compound, formed from complexly overlapping slender, tubular thecae; thecal apertures isolate, openings oriented ventrally; sicular and proximal development unknown. [A number of species currently referred to *Dictyonema* (e.g., *D. peltatum, D. cotylodon, D. rarum,* and others) will need to be moved to a genus of the family Dendrograptidae due to their thecal development that is unlike that of the callograptid *Dictyonema*.] *Cambrian (Miaolingian)–?Carboniferous:* worldwide.——Fig. 7,*4a–b.* **D. retiformis* (Hall); *4a*, holotype, AMNH 1671 (Hall, 1865, fig. 10); *4b*, NYSM 7112, detail of stipe fragment showing complex thecal overlap and bridge development (Ruedemann, 1908, fig. 64).——Fig. 7,*4c. D. graptolithorum* Počta, 1894, fragment with complex stipes (Bouček, 1957, fig. 27b).

Koremagraptus Bulman, 1927b, p. 345 [**K. onniensis* Bulman, 1927b, p. 345; M] [=*Coremagraptus* Bulman, 1942, p. 285 (misspelling); =*Archaeodictyota* Obut & Sobolevskaya, 1967, p. 55 (type,

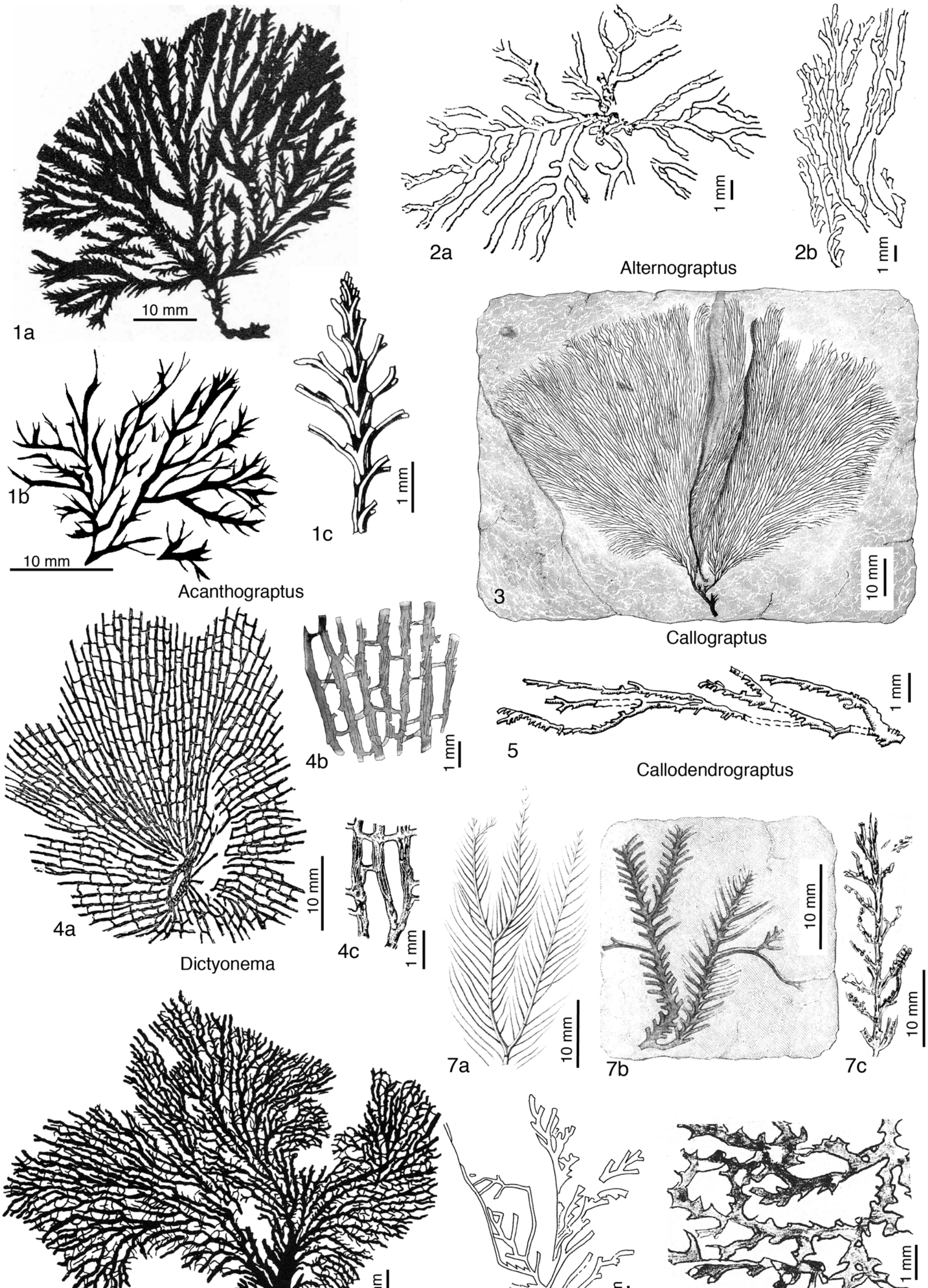

FIG. 7. Callograptidae (p. 12–14).

A. draguovi, OD); Bulman, 1970, p. 43; =*Dyadograptus* Obut, 1960, p. 147 (type, *D. praecursor,* OD), Bulman, 1970, p. 43]. Tubarium conical or flabellate; branches complex, with several stolonal chains; branches and twigs anastomosing irregularly; thecae very long, tubular, usually adnate for much of their length but isolated at the apertures. ?*Cambrian (Furongian)–Lower Devonian (Lochkovian):* worldwide.——Fig. 8,*3a*. **K. onniensis*, holotype (Bulman, 1927b, fig. 1).——Fig. 8,*3b*. *K. fibratus* Bulman, 1927b, holotype, SMF XXIV C 115a, fragment showing complex stipes (Bulman, 1927b, fig. 2,*1*).

Palaeodictyota Whitfield, 1902, p. 399 [**Inocaulis ramulosus* Whitfield, 1902, p. 399 (*non* Spencer, 1884); =*Inocaulis anastomotica* Ringueberg, 1888, p. 131; SD Ruedemann, 1908, p. 200]. Resembling *Koremagraptus* but without projecting thecae and twigs; branches probably composite but stolonal system unknown. *Silurian–Middle Devonian;* Canada,USA, Europe.——Fig. 8,*2*. *P. anastomotica* (Ringueberg), typical colony, Rochester Shale, Silurian, Lockport, New York, USA (Ruedemann, 1908, pl. 6,*4*).

Ptilograptus Hall, 1865, p. 139 [**P. plumosus;* SD Miller, 1889, p. 201, misspelled *Ptylograptus* in Spencer, 1878, p. 462] [=*Stelechograptus* Ruedemann, 1908, p. 279 (type, *S. rectus,* OD), herein]; =*Denticulograptus* Schmidt, 1940, p. 122, *ex Ptilograptus* (*Denticulograptus*) Schmidt, 1940, p. 122 (type, *Ptilograptus acutus* Hopkinson & Lapworth, 1875, p. 662, OD), herein; =*Zigzagigraptus* Yu, 1962, p. 49 (type, *Z. yunnanensis,* OD), Zhang & others, 2009, p. 311]. Tubarium with several orders of monoprogressive branches; isolated metathecae to complex twigs and stipes form later order extensions; thecal details and development unknown. *Middle Ordovician (Dapingian,* Didymograptellus bifidus *Biozone)–Silurian (Wenlock,* Cyrtograptus radians *Biozone):* Australia, Czech Republic, Canada, USA.——Fig. 7,*7a*. **P. plumosus,* lectotype (herein) (Hall, 1865, pl. 21,*1*).——Fig. 7,*7b*. *P. geinitzianus* Hall, 1865, GSC 561b (Hall, 1865, pl. 21,*6*).——Fig. 7,*7c*. *P. rectus* (Ruedemann, 1908), holotype (Ruedemann, 1947, pl. 42,*9*).——Fig. 7,*7d*. *P. yunnanensis* (Yu), holotype (adapted from Yu, 1962, pl. 1,*2*).

Ptiograptus Ruedemann, 1908, p. 175 [**P. percorrugatus;* OD]. Fan-shaped tubarium with robust, compound stipes; attachment and stem development unclear; dichotomously branched stipes connected through numerous bridges; bridges may form secondary stipes. Possibly *Middle Devonian (Eifelian,* Paraspirifer acuminatus *Biozone):* USA.——Fig. 7,*6*. **P. percorrugatus*, NYSM 7348, holotype, waterlime at Louisville, Kentucky, USA (Bulman, 1970, fig. 16,*6*) [The limestone looks like Louisville Limestone and the specimen may be of Silurian age.]

Reticulograptus Wiman, 1901, p. 189 [**R. tuberosus;* OD] [=*Marsipograptus* Ruedemann, 1936, p. 385 (type, *M. bullatus,* OD), Bulman, 1970, p. 47]. Callograptid with probably fan-shaped tubarium, showing anastomosis; thecal details unknown; conothecae may be present. *Lower Ordovician (Tremadocian)–Silurian (Wenlock):* Sweden, Canada, USA.——Fig. 8,*4a–c*. **R. tuberosus; 4a,* holotype (Wiman, 1895, pl. 12,*9*); *4b*, stipe fragment (Wiman, 1895, pl. 12,*12*).——Fig. 8,*4c*. *R. thorsteinssoni* Bulman & Rickards, 1966, GSC 20322, fragment showing conothecae (Bulman & Rickards, 1966, fig. 38B).

Ruedemannograptus Termier & Termier, 1948, p. 174; *pro Streptograptus* Ruedemann, 1947, p. 197; *non Streptograptus* Yin, 1937 (Monograptidae) [**Streptograptus tenuis* Ruedemann, 1947, p. 198; SD Bulman, 1970, p. 57]. Irregularly branched dendroid tubarium with projecting thecae alternately opening to the sides of the stipes. *Ordovician (Sandbian)–?Middle Devonian (Givetian,* middle Polygnathus varcus *Biozone):* Morocco, Czech Republic, Germany, USA.——Fig. 7,*8*. **R. tenuis* (Ruedemann), part of holotype (Ruedemann, 1947, pl. 14,*9*).

TAXA PREVIOUSLY IDENTIFIED AS EARLY LAND PLANTS

These taxa are here separated, as they are described from small, largely unbranched fragments originally referred to as land plant remains. They clearly show complex stipe and isolated tubular extensions that may represent thecal tubes. So far, there is no evidence of fusellar construction in this material to support the inclusion in the Graptolithina.

Boiophyton Obrhel, 1959, p. 536 [**B. pragense;* OD]. Large, bushy, erect callograptid with complex development of stipes; long and slender autothecal apertures inclined to main stipes, not forming compound twigs. *Middle Ordovician (Darriwilian,* Corymbograptus retroflexus *Biozone)–Silurian, Ludlow (Gorstian):* Czech Republic, Sweden. ——9,*3a–c*. *B. aculeatus* (Počta, 1894), *3a,* pyritic stipe fragment showing thecal details, Lodenice, *Cyrtograptus radians* Zone (Bouček, 1957, pl. 15,*7*); *3b, s*pecimen showing isolated thecal tubes, Kopanina beds, Silurian (Ludlow) (Bouček, 1957, pl. 15,*5*); *3c,* holotype of *Psilophyton hedei* (Halle, 1920) now identified as a specimen of *B. aculeatus,* S-010022, Hemse Marl (Silurian, Ludlow), southeast of Petesviken, parish of Hablingbo, Gotland, Sweden (Kenrick, Kvaček & Bengtson, 1999, fig. 3D).——Fig. 9,*3d–e*. **B. pragense,* holotype, NM-D418, specimen (*e*) and enlargement (*d*), Praha-Vokovice, Czech Republic, Darriwilian (Kenrick, Kvaček & Bengtson, 1999, fig. 3a–b).

Bowerophylloides Edwards, Morel, Poiré, & Cingolani, 2001, p. 7 [**B. mendozaensis;* OD]. Unbranched stipe fragments with radiating tubular extensions. [The taxon was originally described as

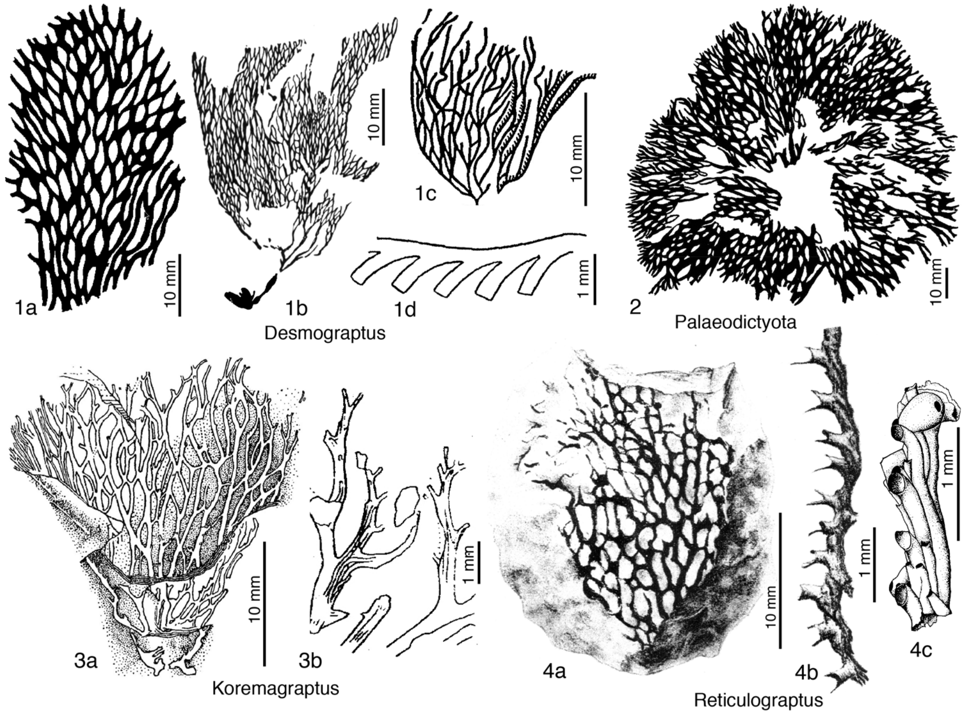

Fig. 8. Callograptidae (p.12–14).

a plant fossil, but Kraft & Kvaček (2017, p. 185) suggested it to be a possible animal.] *Devonian (possibly Lochkovian):* Argentina.——Fig. 9,*1*. **B. mendozaensis,* holotype, Devonian, Argentina (Edwards, & others, 2011, pl. 1,*16*).

Saxonia Roselt, 1962, p. 323 [**S. microphylla;* OD]. Robust, dichotomously branching stems of considerable length reaching 0.5–0.7 cm in width; slender projecting tubes. *Silurian (Ludlow):* Germany.——Fig. 9,*2*. **S. microphyla*, holotype, Ölsnitz, Vogtland, Germany (Roselt, 1962, pl. 1,*1*).

Family MASTIGOGRAPTIDAE
Bates & Urbanek, 2002

[Family Mastigograptidae Bates & Urbanek, 2002, p. 458]

Bushy dendroid colonies with slender stipes formed from stolonal strands; metathecae arranged in pairs, distinctly widening; fuselli formed as complete fusellar rings with irregularly placed sutures; triad budding present; auto- and bithecae not differentiated by size; sicular development poorly known. *Middle Ordovician (Darriwilian)–Upper Ordovician (Katian):* worldwide.

Mastigograptidae is likely a monophyletic clade differing from all other graptolites through their slender stems with a tightly adhering tube covering the stolon system and the thin-walled, distinctly widening and completely isolated metathecal tubes. Rickards and Durman (2006) included *Mastigograptus* in Dithecoidea (Dithecodendridae), but this relationship cannot be supported without the knowledge on the thecal origin and development the members of the Dithecodendridae. Unfortunately, this group is known exclusively from flattened shale material and details are not available. All records of the Mastigograptidae from the Cambrian have to be questioned and may represent members of the Dithecodendridae.

The family Mastigograptidae is based on two closely related genera with a typical triad budding system. The taxa are known from isolated three-dimensionally preserved specimens found in glacial boulders in northern Germany and Poland. Their origin and phylogenetic relationships are uncertain, but the development of a typical triad budding system demands an inclusion in Dendroidea.

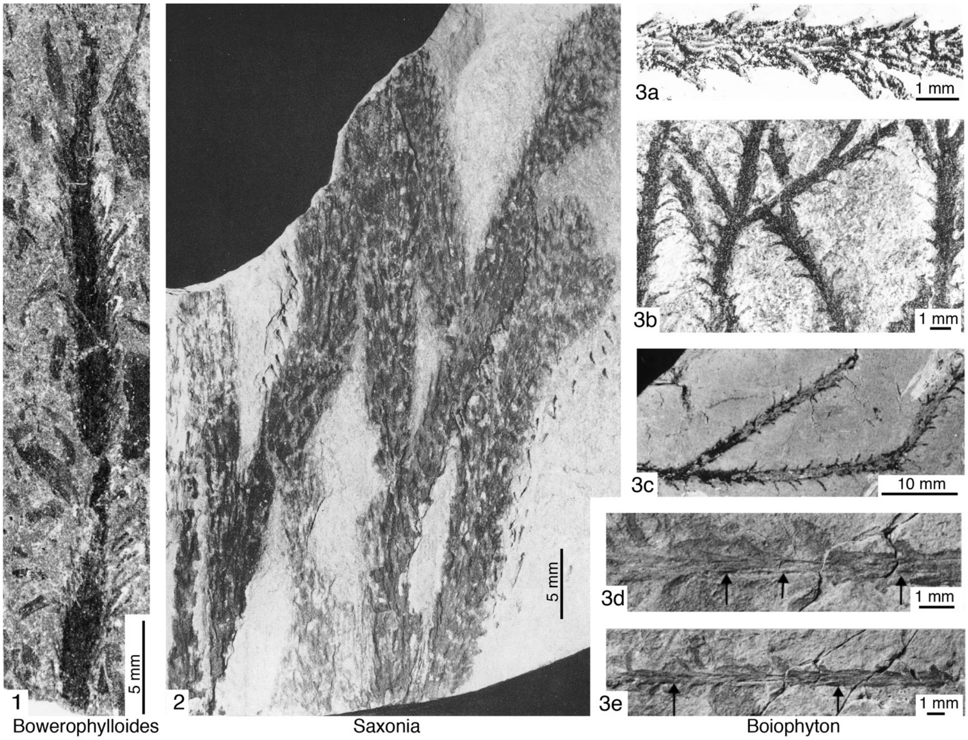

FIG. 9. Possible Callograptidae, previously identified as plants (p. 14–15).

RUEDEMANN (1908) for the first time recognized the conical thecae in *Mastigograptus tenuiramosus* (WALCOTT, 1883) in material from the Eden Shale of Kentucky, USA, not visible in the type of WALCOTT (1883). The identification of this material with *M. tenuiramosus* is uncertain and the inclusion of the material from Ordovician glacial erratics of Europe in *Mastigograptus* has been questioned by OBUT and SOBOLEVSKAYA (1967). Cambrian taxa with isolated metathecae are generally included in the Dithecodendridae (MALETZ, 2019c), based on the assumed diad budding (OBUT, 1960), which has not been verified.

MORPHOLOGY

Specimens of the Mastigograptidae indicate a loosely branching bushy shape with widely spaced paired autothecae. The stipes are robust and strongly thickened with extrathecal cortical material. The colonies are anchored to the sediment surface or fossil shells by a distinct attachment disk developed from cortical material (Fig. 10.4), in which the erect sicula is hidden. The holdfast of a number of specimens of *Mastigograptus* shows an ornamentation indicating that the specimens were attached to ribbed brachiopods (e.g., EISENACK, 1934; BATES & URBANEK, 2002).

BATES and URBANEK (2002) provided some general information on the initial segment of the *Mastigograptus* colonies, which they presumed to represent the sicula. However, important details of the sicular development are not available due to the strong cortical overgrowth of the proximal ends. The authors interpreted the structure as a cylindrical sicula similar to the sicula of the dendroid graptolites but different from the embryonic vesicle of *Rhabdopleura* or the conical sicula of *Dendrotubus*. The sicula opens upward as in Dendrograptidae, and a possible origin of th1 appears in the lower to middle part of the sicula. Later development is unknown, even though the general triad budding has been documented (Bates & Urbanek, 2002).

The thecae are formed from thin-walled fusellar rings (Fig. 10.1–2). They are conical, widening distinctly toward their simple straight apertures. The fusellar rings show full-ring development with irregularly placed sutures. The prothecal parts may show swollen initial parts (Fig. 10.3) but are simple in other species.

Mastigograptus Ruedemann, 1908, p. 210 [**Dendrograptus tenuiramosus* Walcott, 1883, p. 21; OD]. Bushy dendroid colonies with slender, elongated stipes formed from stolonal strands; isolated metathecae arranged in pairs, distinctly widening; thecae formed from complete fusellar rings with irregularly placed sutures; triad budding present; auto- and bithecae not differentiated by size; sicular development poorly known. *Upper Ordovician (Sandbian–Katian):* USA, Germany, Poland (glacial boulder).——Fig. 11,*1a–b*. **M. tenuiramosus* (Walcott)*; 1a,* holotype, Utica Slate, Trenton, New York, USA, scale bar, 10 mm (Walcott, 1883, pl. 1,*4*); *1b,* specimens showing conical thecae; scale bar, 1 mm (part of Ruedemann, 1908, pl. 11,*1*).

Micrograptus Eisenack, 1974, p. 665 [* *M. fragilis;* OD]. Bushy dendroid colonies with slender, elongated stipes formed from stolonal strands; isolated metathecae arranged in pairs, distinctly widening; thecae formed from complete fusellar rings with irregularly placed sutures; triad budding present; auto- and bithecae probably not differentiated by size. *Middle Ordovician (Darriwilian)–Upper Ordovician (Sandbian):* Estonia, Finland.——Fig.11,*2a–c*. **M. fragilis, 2a,* holotype, glacial boulder, southern Finland; *2b,* specimen with thecal bud; *2c,* specimen possibly belonging to the species, showing re-growth of theca, Estonia (Eisenack, 1974, fig. 1,*3–4*). Scale bars, 0.1 mm.

DENDROIDEA INDET

The following taxa most likely belong to the Dendroidea. They are based on highly incomplete fragments and show little detail of their development. The genus *Archaeoantennularia* was initially described as a hydrozoan, but Muscente, Allmon, and Xiao (2016) recognized fusellar construction in the taxon, supporting a graptolitic nature of the material. The available material has a quite special tubarium shape, not recognized in other dendroids. The denticulate or rutellate nature of the thecae in the erect tubarium may indicate an inclusion with the Dendroidea and possibly the Dendrograptidae when more details of its development are available.

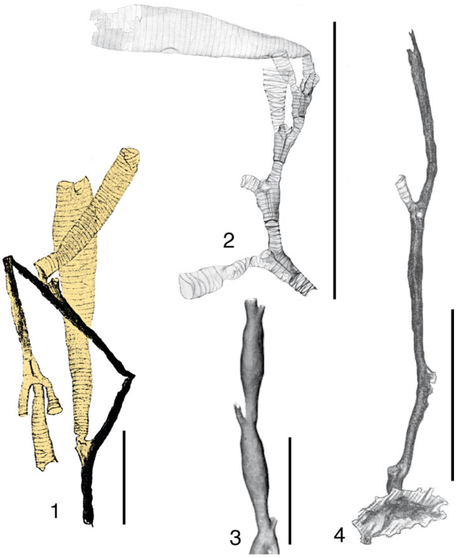

Fig. 10. Morphology of Mastigograptidae. *1,3–4, Mastigograptus* sp. *1,* stipe fragment with triad (Andres, 1977, fig. 13); *3,* stolon with swollen central part (inverted photo, Bates & Urbanek, 2002, fig. 3G); *4,* proximal end with attachment and short stipe showing bases of thecae (Andres, 1961, fig. 2a); *2, Micrograptus* sp., stipe fragment showing four closely spaced branching divisions (Andres, 1977, fig. 21). Scale bars, 1 mm.

The genus *Multitubus* is based on a few small stipe fragments with an apparently unusual development, and Skevington (1963) even referred the genus to his new family Multitubidae. Bulman and Rickards (1966) synonymized the genus with *Reticulograptus*, a suggestion that is without true evidence.

Archaeoantennularia Decker, 1952, p. 656 [**A. byersi;* M]. Cylindrical tubarium with a central axis from which branches radiate in all directions; thecae appear to be denticular and not isolate aperturally; thecal differentiation and stolon system not recognized; details of colony unknown. *Middle Devonian:* USA (Michigan).——Fig.12,*1a–c*. **A. byersi,* Silvania Sandstone, Wayne County, Michigan, USA; *1a,* holotype, UMMP material, specimen strongly retouched, scale bar, 10 mm (Decker 1952, fig. 1); *1b–c,* metatype, SNOMNH OU622, fragments showing thecal style (new; provided by A. D. Muscente). Scale bars, 1 mm.

Cactograptus Ruedemann, 1908, p. 196 [**C. crassus;* OD]. Dichotomously branching, elongate stipes;

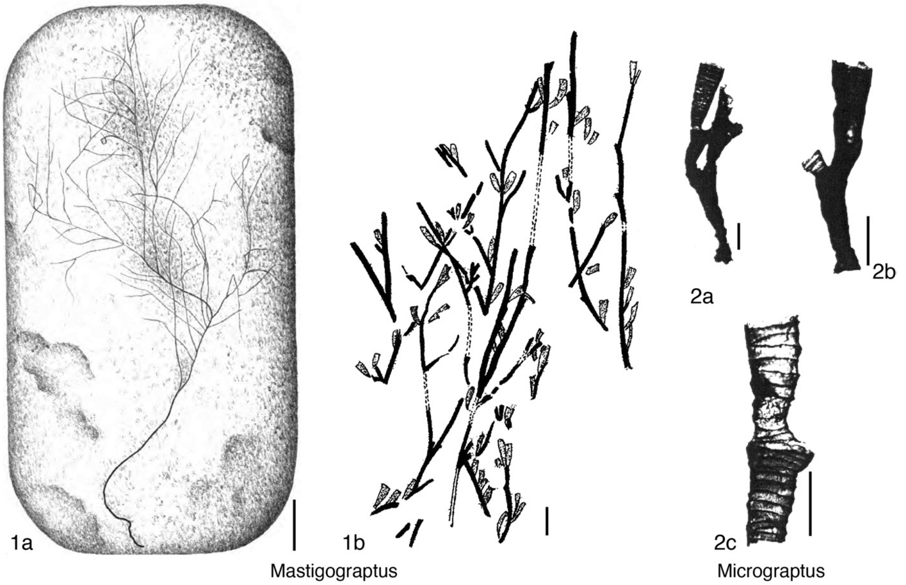

FIG. 11. Mastigograptidae (p. 17).

prominent thecae projecting to both sides. *Cambrian, Miaolingian (Wuliuan,* Ptychagnostus gibbus *Biozone)–Silurian (Llandovery,* Streptograptus crispus–Cyrtograptus centrifugus *Biozone):* Kazachstan, Australia, USA.——Fig. 12,*2a–b*. **C. crassus*, holotype, NYSM 6860, specimen (*a*) and detail (*b*), Williamson Shale Formation, New York, USA (*a,* Ruedemann, 1908, pl. 8,*1; b,* Ruedemann, 1908, fig. *99*). Scale bar, 10 mm in *2a,* 1 mm in *2b.*

Multitubus Skevington, 1963, p. 51 [**M. spinosus;* OD] Stipe fragments with serially arranged, spinose or rutellate autothecae and multiple capriciously distributed bithecae. *Middle Ordovician (Darriwilian):* Sweden.——Fig.12,*3a–c*. **M. spinosus,* holotype, fragments, Darriwilian, Öland, Sweden (Skevington, 1963, fig. 73–74). Scale bars, 1 mm.

Nephelograptus Ruedemann, 1947 p. 196 [**N. rectibrachiatus;* OD]. Fan-shaped tubarium with delicate dissepiments; thecae probably denticulate, oriented alternately to both sides; details of development unknown due to poor preservation. *Ordovician (Katian?):* USA (Tennessee).——Fig. 12,*4*. **N. rectibrachiatus*, holotype, Ottosee Shale, Knoxville, Tennessee, USA. scale bar, 1 mm (Ruedemann, 1947, pl. 14,*26*).

Parvitubus Skevington, 1963, p. 47 [**Azygograptus*? *oelandicus* Bulman, 1936, p. 46; OD] Colony erect; branches with serially arranged autothecae, possibly with triad budding; bithecae restricted to one side of the stipe; opening into autothecae. *Middle Ordovician (Darriwilian):* Sweden.——Fig.12,*6a–c*. **P. oelandicus* (Bulman), Öland, Sweden; *6a–b*, holotype from both sides (Bulman, 1936, pl. 2,*23–24*); *6c,* paratype, long specimen (Bulman, 1936, pl. 2,*16*). Scale bars, 1 mm.

Stelechiocladia Počta, 1894, p. 206 [**S. fruticosa* Počta, 1894, p. 207; SD Bouček, 1957, p. 35 as *Dendrograptus* (*Stelechocladia*) *suffruticosus* Bouček, 1957, p. 36]. Bushy tubarium with strongly compound stipes; thecae elongate and in ropy bundles. *Ordovician, Sandbian–?Middle Devonian (Givetian,* middle Polygnathus varcus *Biozone):* Czech Republic.——Fig. 12,*7*. **S. fruticosa,* holotype, Silurian, Bohemia, scale bar, 10 mm (Bouček, 1957, pl. 2,*1*).

Trimerohydra Kozłowski, 1959, p. 217 [**T. glabra;* OD]. Stolon system with distinct nodes, showing triad budding. *Ordovician:* Poland (glacial boulder). [Bulman, 1970, p. 43, suggested a synonymy with *Koremagraptus*].——Fig. 12,*5*. **T. glabra,* holotype, scale bar, 0.5 mm (Kozłowski, 1959, fig. 1).

ABBREVIATIONS FOR MUSEUM REPOSITORIES

AMNH: American Museum of Natural History, New York City, New York, USA

CMC: Cincinnati Museum Center, Cincinnati, Ohio, USA (collection formerly at University of Minnesota)

GSC: Geological Survey of Canada, Ottawa, Canada

LO: Lunds Originale, Department of Geology, Lund University, Sweden

MB.G.: Museum für Naturkunde, Berlin, Germany

NIGP: Nanjing Institute of Geology and Paleontology, Academia Sinica, Nanjing, China

NM: Department of Palaeontology, National Museum, Prague, Czech Republic

NYSM: New York State Museum, Albany, New York, USA

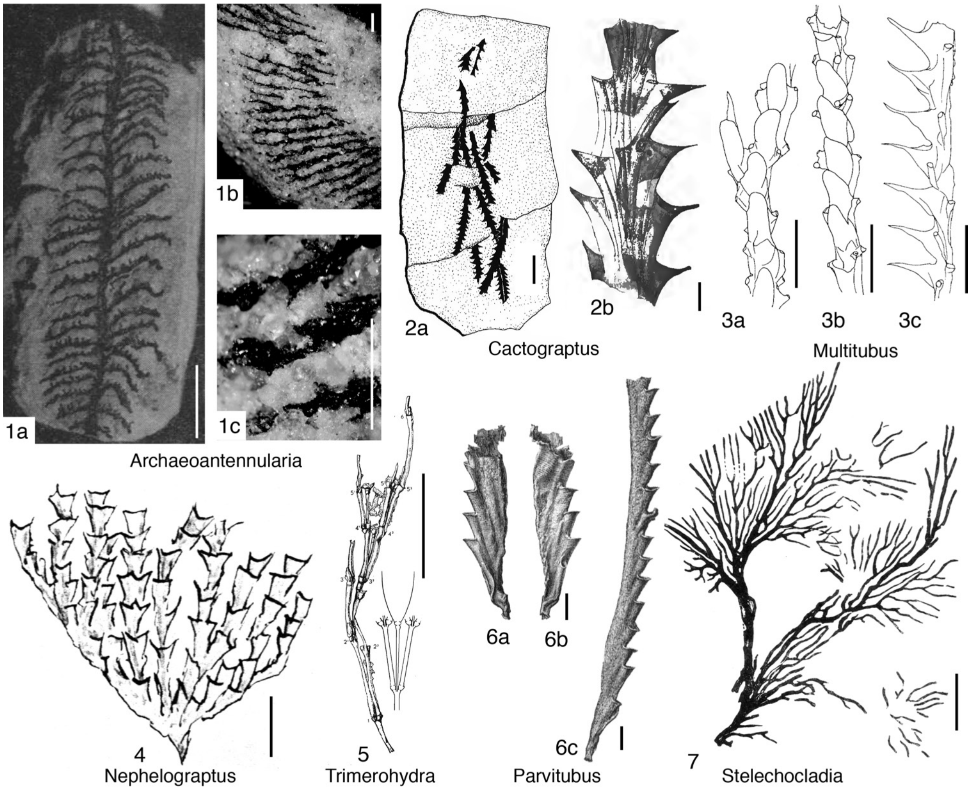

FIG. 12. Dendroidea indet (p. 17–18).

PKUM: Geological Museum of Peking University, Beijing, China
S: Department of Palaeobotany, Swedish Museum of Natural History, Stockholm, Sweden
SM: Segwick Museum of Earth Sciences, Cambridge, UK
SMF: Naturmuseum Senckenberg, Frankfurt am Main, Germany
SNOMNH: Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA
UMMP: University of Michigan, Museum of Paleontology, Ann Arbor, Michigan, USA

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