SUBCLASS CEPHALODISCIDA

JÖRG MALETZ and PAUL GONZALEZ

Subclass CEPHALODISCIDA Fowler, 1892

[Cephalodiscida FOWLER, 1892b, p. 297] [=Cephalodiscoidea BEKLEMISHEV, 1951]

Fixed, sedentary marine organisms with communal zooids divided into three regions, preoral lobe (cephalic shield), collar, and trunk; collar extends to form several pairs of arms, each bearing double row of ciliated tentacles; trunk elongated posteriorly to form stalk with sucker at base from which new zooids are generated asexually; external proteinaceous housing or domicile (the tubarium) comprised of series of tubes built from sequential addition of full rings or half rings of organic material in most taxa; tubaria with separate zooidal tubes to communal dwellings; housing construction unknown in one genus. *Cambrian* (*Miaolingian,* ?*Wuliuan*)–*Holocene* (extant): worldwide in marine environments.

INTRODUCTION

The Cephalodiscida is a group of pseudocolonial, benthic organisms, typically living in large communities and known largely from extant members. The 18 described extant species belong to a single genus, *Cephalodiscus,* which is divided into four subgenera: *C.* (*Orthoecus*), *C.* (*Idiothecia*), *C.* (*Cephalodiscus*), and *C.* (*Acoelothecia*). These species are present in waters from the Antarctic to the tropics. See Table 1 for the geographical ranges.

Most species were described from fixed specimens acquired at great depths during expeditions of the late nineteenth and early twentieth centuries and have not been studied since. Most recent observations of living colonies were of a shallow water population of *C.* (*C.*) *gracilis* from Bermuda.

Zooid morphology is fairly homogenous across species (see p. 5–7). Individual zooids are small (1–10 mm) and exhibit the tripartite body plan characteristic of the phylum Hemichordata. The anterior body region (prosome) consists of a ciliated cephalic shield used for locomotion and secretion of the tubarium. The mesosome, or collar region, extends into two to nine pairs of arms (depending on species and developmental stage) used in filter feeding. Ciliated tentacles on each arm capture food particles, and cilia on the arms transport it toward the mouth. The trunk contains the U-shaped digestive tract and extends into an extensible stalk. The stalk ends in an adhesive disk, from which asexually budded individuals originate. Unlike rhabdopleurid pterobranchs, cephalodiscids possess gill slits, a defining feature of Deuterostomia. In enteropneust hemichordates and filter-feeding chordates, the pharynx is perforated with tens to hundreds of gill slits used in pumping water. In cephalodiscids, only one pair of gill slits is present. This reduction may be associated with the evolution of external filter feeding with arms and tentacles in the pterobranch lineage.

TABLE 1. Geographical range of *Cephalodiscus*

Region	Species
Antarctic waters	*C.* (*C.*) *hodgsoni* RIDEWOOD, 1907 [=*C.* (*C.*) *aequatus* ANDERSSON, 1907] *C.* (*C.*) *inaequatus* ANDERSSON, 1907 *C.* (*I.*) *nigrescens* HARMER, 1905 *C.* (*O.*) *densus* ANDERSON, 1907 *C.* (*O.*) *solidus* ANDERSSON, 1907
Subantarctic waters	*C.* (*C.*) *dodecalophus* M'INTOSH, 1887
Temperate regions	*C.* (*I.*) *levinseni* HARMER, 1905 *C.* (*I.*) *evansii* RIDEWOOD, 1918 *C.* (*O.*) *australiensis* JOHNSTON & MUIRHEAD, 1951 *C.* (*I.*) *gilchristi* (RIDEWOOD, 1906)
Tropical regions	*C.* (*C.*) *gracilis* HARMER, 1905 *C.* (*C.*) *sibogae* HARMER, 1905 *C.* (*C.*) *indicus* SCHEPOTIEFF, 1909 *C.* (*C.*) *graptolitoides* DILLY, 1993

Cephalodiscid communities appear to originate from a single, sexually produced founder zooid, comparable to the sicular zooid of the Graptolithina (see 7–9). Subsequently formed members of the pseudocolony are produced asexually through budding from the base of the stalk. Mature zooids may separate from the stalk of the mother zooid and lead an independent life but stay in the community. Thus, in many tubaria, a number of interconnected zooids (as many as 20 in some species) at various stages of development are attached to the base of the stalk of the mother individual, and entirely separate individuals may be rare (see Lester, 1985; Dilly, 2014). Mature zooids formed through asexual budding appear to be able to reproduce asexually. This method of asexual reproduction differs from rhabdopleurid pterobranchs, in which asexually budded individuals remain connected by a stolon system. In this regard, cephalodiscids represent an intermediate strategy between solitary enteropneusts and fully colonial rhabdopleurid pterobranchs.

TUBARIUM CONSTRUCTION

The Cephalodiscida secrete a housing construction, the tubarium, from fuselli and cortical material (with the possible exception of *Atubaria* Sato, 1936, in which zooids appear to be living as naked individuals on corals). Contrasting with their highly conserved zooidal morphology, the tubaria of the Cephalodiscida are very diverse and form the basis of their taxonomy. Because the tubarium is the only feature that can be compared with graptolites, observations on tube building and behavior in extant cephalodiscids may provide insights into the morphology and behavior of extinct species.

The tubaria can be encrusting, compact, or even branched, dendroid in shape, and replicating many shapes, as seen in colonial Graptolithina. In many taxa, the individual dwelling tubes of the zooids are completely separate, forming pseudocolonies where large masses of tubes are connected by or enclosed in extrathecal (cortical?) material. However, in some taxa, a communal dwelling of interconnected tubes or other three-dimensional constructions is formed for the protection of the zooids. Apertural openings may be smooth and straight or bear a variety of elaborations, from robust rutelli to strong apertural spines.

There are three major types of tubarium organization in *Cephalodiscus:* 1) In *Cephalodiscus* (*Orthoecus*), the tubarium is comprised of discrete, nearly straight and parallel-sided tubes (Fig. 120.5). The individual tubes originate from a basal surface, a hardground or rock surface, and create a meadow. Tubes are built of somewhat annular growth increments resembling the fuselli of graptolites and are cemented together by secondary deposits that contain large amounts of embedded foreign material (sand, debris). 2) In *Cephalodiscus* (*Idiothecia*), the individual tubes are partly enclosed in a thick development of cortical tissue and form erect structures, commonly with branching stipes. These tubes are closed at the base and have straight to rutellate openings oriented in every direction (Fig. 120.1). Observations in *C.* (*Idiothecia*) *nigrescens* indicate that more than one adult and its buds may share a single tube (Dilly, 2014). 3) In the subgenus *C.* (*Cephalodiscus*), discrete cylindrical tubes are lacking, and the tubarium consists of an interconnected network of irregularly shaped cavities. The openings in the communal tubaria (generally termed ostia) are either simple or adorned with single or multiple spines (Fig. 120.2–120.3, Fig. 120.6) on which zooids perch to feed (Lester, 1985). Addition of material between preexisting spines is common, and spines are commonly embedded into the walls of the tubarium. Most species form erect branching tubaria, with lateral connections resembling the dissepiments and anastomosis of the Graptolithina. Encrusting forms also occur, for example, *Cephalodiscus* (*C.*) *graptolitoides*. Thecal apertures of the *Cephalodiscus* (*C.*) *calciformis* Emig, 1977 have a very unusual shape—a wide, funnel-shaped structure not found in any

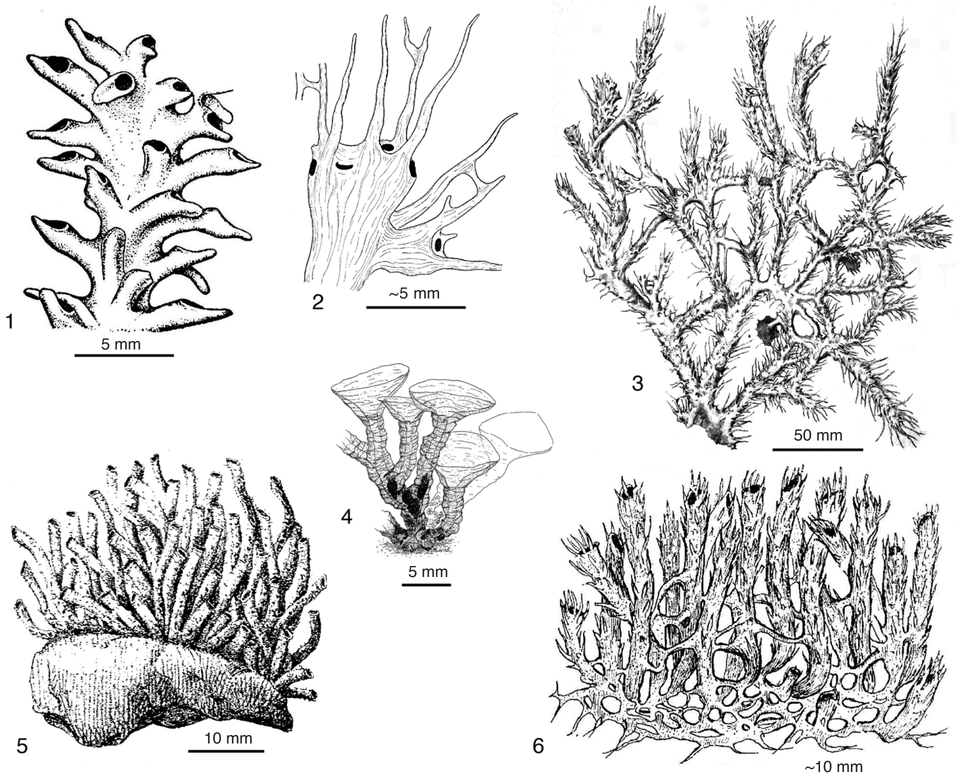

FIG. 120. Tubarium shape in the Cephalodiscidae. *1, Cephalodiscus* (*Idiothecia*) *levinseni* HARMER, 1905 (Kozłowski, 1949, fig. 9c); *2, Cephalodiscus* (*Cephalodiscus*) *hodgsoni* RIDEWOOD, 1907, fragment showing apertures with multiple spines (John, 1931, fig. 1); *3, Cephalodiscus* (*Cephalodiscus*) *dodecalophus* M'INTOSH, 1887 (M'Intosh, 1887, pl. 1); *4, Cephalodiscus* (*Cephalodiscus*) *calciformis* EMIG, 1977 (Emig, 1977, fig. 1); *5, Cephalodiscus* (*Orthoecus*) *rarus* ANDERSSON, 1907 (Andersson, 1907, pl. 2,*6*); *6, Cephalodiscus* (*Cephalodiscus*) sp. (Dawydoff, 1948, fig. 82).

other pterobranch (Fig. 120.4). The tubes of the tubarium are interconnected and inhabited by the zooids and their attached asexually developing buds. These zooids are comparable to those in other species of *Cephalodiscus* (*Cephalodiscus*), but little detail is known about their development and interconnection. In the monospecific subgenus *Acoelothecia,* the tubarium is dissolved into a complex mesh of spines and bars in which the zooids roam freely.

The phylogeny of the extant subgenera of *Cephalodiscus* is unresolved, and as a result, the relationships of the constructional features of their tubaria are unknown. The complete individual tubes of *Cephalodiscus* (*Idiothecia*) RIDEWOOD, 1906 and *Cephalodiscus* (*Orthoecus*) ANDERSSON, 1907 may represent the plesiomorphic mode of tubarium construction, as their features are shared with those of the closely related Graptolithina.

In many aspects, the tubarium construction of the Cephalodiscidae has features also apparent in the construction of the tubaria of the Graptolithina. Erect tubaria have branching and lateral connection of stipes, even though the zooids do not work in a colony but are separate as individuals. GONZALEZ and CAMERON (2012) investigated the ultrastructure of *Cephalodiscus* tubaria in the subgenera *Cephalodiscus, Idiothecia,* and *Orthoecus* and noted a continuum in thickness and development of fusellar-like and cortical-like layers but were unable to recognize clearly differentiated cortical bandages. The investigation indicated that fibril type and arrangement may be evolving independently from larger scale features of the pterobranch tubaria. The interpretation of cortical material in *Cephalodiscus* (see Kozłowski, 1967; Dilly, 1993) may be misleading, as the material is not differentiated into the distinct bandages of the Graptolithina (see, for instance, Crowther & Rickards, 1977; Crowther, 1978, p. 474). Thus, the evolutionary origin of the cortical bandages might not be traced back to the cephalodiscids.

THE FOSSIL RECORD

The Cephalodiscida are mainly known from modern, extant taxa, but a few possible fossil cephalodiscid taxa have been described. These are preserved only in the form of their tubaria, and their zooids are absent from the fossil record. As a result, differentiating fossil cephalodiscids from closely related Graptolithina can be difficult because interconnected housing constructions are present in both taxa. The oldest possible cephalodiscid taxon may be a fragment found in the Kaili Formation of China (Harvey & others, 2012), but the poor preservation precludes the identification as a cephalodiscid or graptolitid (Maletz, 2014a).

Rickards and Durman (2006) referred the upper Cambrian genus *Aellograptus* Obut, 1964 and its type species *A. savitskyi* Obut, 1964 to *Cephalodiscus,* thus synonymyzing *Aellograptus* with *Cephalodiscus*. The genus is here kept as a separate cephalodiscid genus, as details of the tubarium construction are not available. The size difference from *Cephalodiscus* (*I.*) *levinseni* tubaria quoted by Rickards and Durman (2006) may be regarded as a species-specific character. Other potential cephalodiscid genera are the Ordovician taxa *Eocephalodiscus* Kozłowski, 1949, *Melanostrophus* Öpik, 1930, and *Pterobranchites* Kozłowski, 1967. Of these, only *Eocephalodiscus* has unanimously been referred to the cephalodiscids, and to its own family Eocephalodiscidae (see Kozłowski, 1949). The affinity of the genus *Melanostrophus* has been the focus of a long debate. The genus was known from very fragmentary and poor material, in which Eisenack (1937) first recognized fusellar construction. Zessin and Puttkamer (1994) discussed new material of *Melanostrophus* and erected the family Melanostrophidae for this taxon. Mierzejewski and Urbanek (2004) referred to *Melanostrophus* as a *Cephalodiscus*-like taxon based on their investigation of isolated fragments. *Pterobranchites* is known from small fragments, and its tubarium construction is unknown. Similarities to the encrusting *Cephalodiscus* (*C.*) *graptolitoides* may exist. Schweigert and Dietl (2013) described *Cephalodiscus*? *nusplingensis* as a possible cephalodiscid pterobranch from the Upper Jurassic Nusplingen lithographic limestone of Germany but were unable to verify the presence of fusellar construction.

Family CEPHALODISCIDAE Harmer, 1905

[Cephalodiscidae Harmer, 1905, p. 5] [incl. Eocephalodiscidae Kozłowski, 1949, p. 194; Melanostrophidae Zessin & Puttkamer, 1994 p. 564; Atubaridae, *nom. dub.,* herein]

Fixed, sedentary marine organisms with communal zooids divided into three regions, preoral lobe (cephalic shield), collar, and trunk; collar extends to form several pairs of arms, each bearing a double row of ciliated tentacles; trunk elongated posteriorly to form stalk with sucker at base, from which new zooids are generated asexually; external proteinaceous housing or domicile (the tubarium) comprised of a series of tubes built from sequential addition of full rings or half rings of organic material in most taxa; tubaria with separate zooidal tubes to communal dwellings, unknown in one genus. *Cambrian* (*Miaolingian,* ?*Wuliuan*)*–Holocene:* worldwide in marine environments.

The Cephalodiscida include a single family, the Cephalodiscidae Harmer, 1905. A differentiation of the Eocephalodiscidae Kozłowski, 1949 for fossil members appears unnecessary, as is the introduction of the Melanostrophidae Zessin and Puttkamer,

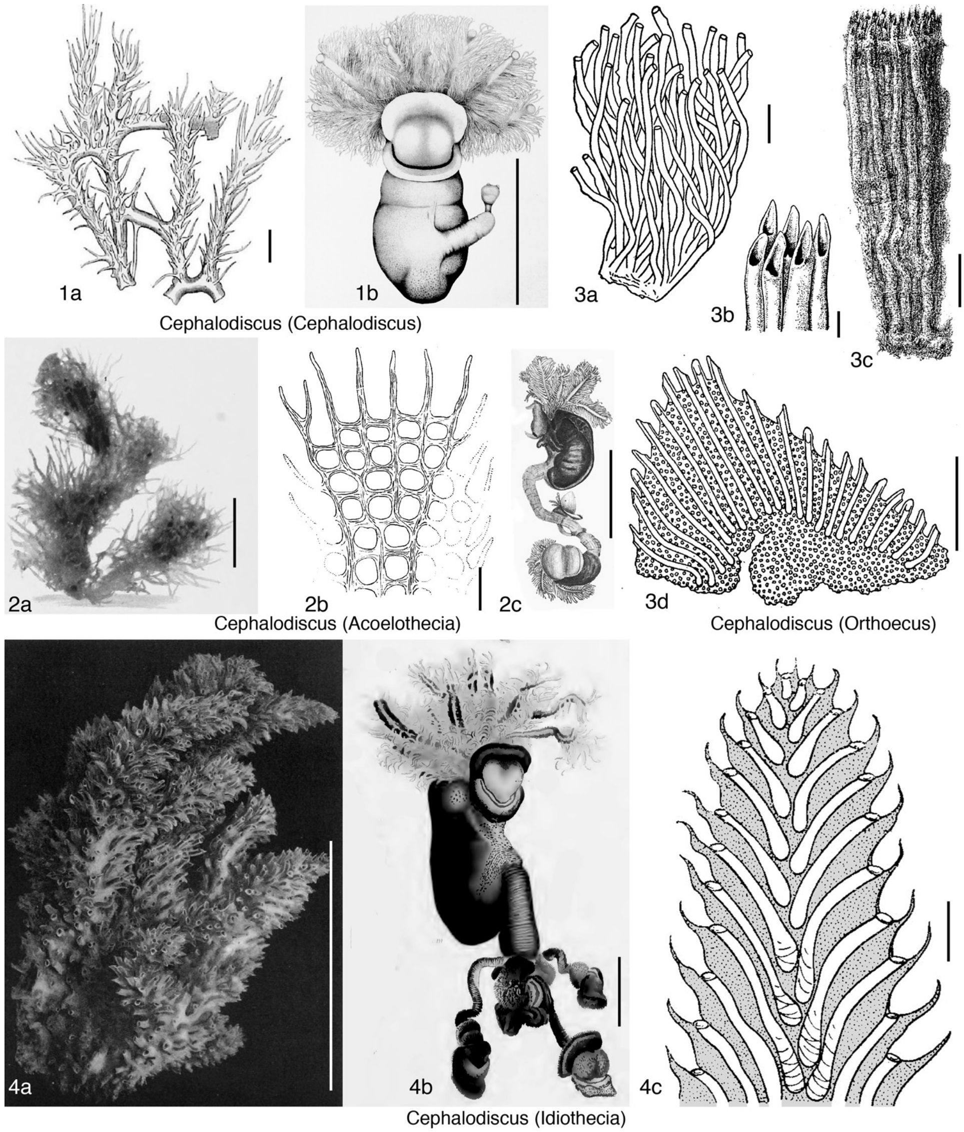

FIG. 121. Cephalodiscidae (extant) (p. 202–203).

1994, based on the taxon *Melanostrophus,* recently recognized as a possible cephalodiscid pterobranch (MIERZEJEWSKI & URBANEK, 2004). The latter authors rejected the genus *Stolonofolliculus* ZESSIN & PUTTKAMER, 1994 with its type *Melanostrophus signum* ÖPIK, 1930 and, thus, viewed the Stolonofolliculidae ZESSIN and PUTTKAMER, 1994 as a *nomen dubium* (MIERZEJEWSKI & URBANEK, 2004, p. 521–522). The name Atubaridae has been used in the Encyclopedia of Life and Catalogue of Life (online at eol.org), but appears to be a *nomen dubium,* as a published diagnosis and description is not available.

A number of subgenera have been erected in the genus *Cephalodiscus* based on the tubarium construction but not on the anatomy of the zooids. If known from the

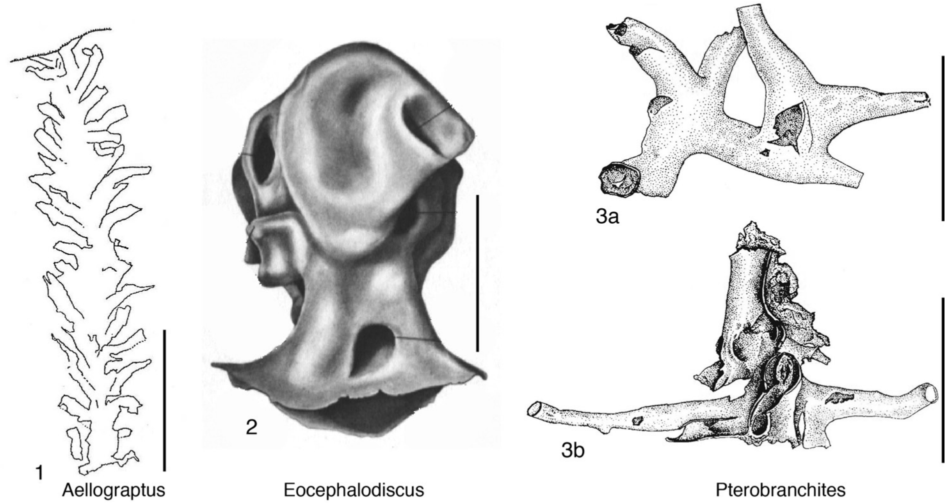

FIG. 122. Cephalodiscidae (fossil) (p. 203).

fossil record only, these subgenera would certainly have been treated as separate genera.

Cephalodiscus M'INTOSH, 1882, p. 348 [**C. dodecalophus;* OD]. Tubarium comprised of series of tubes secreted from the sequential addition of full rings or half rings of organic material in most taxa; tubarium with separate zooidal tubes to communal dwellings and may be reduced to a meshwork of bars; tubarium shape varies from encrusting to erect and branching; with or without spines at apertures. *Cambrian* (*Miaolingian, ?Wuliuan*)–*Holocene:* worldwide in marine environments.

C. (**Cephalodiscus**) M'INTOSH, 1882, p. 348, *non Cephalodiscus* BERLESE, 1918, p. 12, =*Capitodiscus* VITZTHUM, 1931, p. 144 (Arachnida) [**C. dodecalophus;* OD] [=*Demiothecia* RIDEWOOD, 1906, p. 191 (type species never selected)]. Encrusting to erect branched tubarium with communal cavity open to all zooids; apertures with single or multiple long spines. *Cenozoic* (*Eocene*)–*Holocene* (extant): worldwide.——FIG. 121,*1a–b*. **C.* (*C.*) *dodecalophus* (type specimen not designated by M'INTOSH, 1882); *1a,* fragment of tubarium showing branches and bridges, long apertural spines common; *1b,* zooid with attached bud (M'Intosh, 1887, pl. 2). Scale bars, 10 mm (*1a*); 1 mm (*1b*).

C. (**Acoelothecia**) JOHN, 1931, p. 241 [**C.* (*A.*) *kempi;* M]. Tubarium consists of meshwork of spines and bars; no true communal cavity present; spaces between meshwork irregular and occupied by zooids and their buds. *Holocene* (extant): Antarctic Ocean (Ross Sea, Victoria Land, McMurdo Sound, Ross Island, Cape Royds).——FIG. 121,*2a–c*. *C.* (*A.*) *kempi* (type specimen not designated by JOHN, 1931); *2a,* part of tubarium, scale bar, ~10 mm (John, 1931, pl. 34,*2*); *2b*, small piece showing spines and bars, scale bar, 1 mm (John, 1931, fig. 4); *2c,* zooid with buds, scale bar, 1 mm (John, 1931, pl. 35,*2*).

C. (**Idiothecia**) RIDEWOOD, 1906, p. 191 [**C. nigrescens* LANKESTER, 1905, p. 400; SD BULMAN, 1970, p. 17)]. Tubaria with individual tubes for each mature zooid; tubarium erect, with complex stipes or without branching; apertures with blunt lips or rutelli; individual tubes enclosed in masses of spongy material forming bulk of tubarium; in longer tubes lower part may be closed off; zooids lack end swellings or refractive beads on arms (JOHN, 1931, p. 233–235). *Holocene* (extant): worldwide.——FIG. 121,*4a–c*. *C.* (*I.*) *nigrescens; 4a,* holotype, tubarium, scale bar, ~10 cm (Lankester, 1905, pl. 8); *4b,* zooid with several buds, scale bar, ~1 mm (Ridewood, 1907, pl. 3,*8*); *4c,* section through tubarium, scale bar, ~5 mm (Dawydoff, 1948, fig. 83; Ridewood, 1907, pl. 4,*10*).

C. (**Orthoecus**) ANDERSSON, 1907, p. 11 [**C. solidus;* SD BULMAN, 1970, p. 17)]. Encrusting tubaria with individual tubes for each mature zooid; basal parts of tubes may be connected by extratubarial spongy material; individual tubes laterally connected to each other or distally free and isolated; apertures simple, straight, or with short rutellum. *Holocene* (extant): worldwide.——FIG. 121,*3a*. *C.* (*O.*) *densus* ANDERSSON, 1907, small tubarium; see RIDEWOOD, 1918, p. 40 for synonymy of *C. rarus,* scale bar, 10 mm (Kozłowski, 1949, fig. 9A).——FIG. 121,*3b–d*. **C.* (*O.*) *solidus;* thecal apertures (*3b*) and fragment (*3c*) of tubarium (Kozłowski, 1949, fig. 9); *3d*, specimen showing sand grains in the tissue surrounding the zooidal tubes (Ridewood, 1918, fig. 2). Scale bars, 2 mm (*3b*); 10 mm (*3c–3d*).

Atubaria SATO, 1936, p. 105 [**A. heterolopha;* OD]. Cephalodiscid zooids without known tubarium. *Holocene* (extant): Asia (Japan, Dyogasima, Sagami-Bay, east side of Honshu).——FIG. 123, *a–c*. **A. heterolopha. a,* mature zooid (Komai, 1949, fig. 1); *b,* immature zooid (Hyman, 1959, fig. 66D); *c,* characteristic granule-covered antero-internal arm (Sato, 1936, fig. 5a). Scale bars, 0.5 mm.

Aellograptus OBUT, 1964, p. 306 [**A. savitskyi;* M]. Elongate, unbranched, or sparsely divided tubarium with numerous short, projecting, cylindrical thecae. *Cambrian* (*Furongian, Paibian*): Russia (Siberia), Australia (Tasmania).——FIG. 122,*1*. **A. savitskyi,* paratype, SM A79058, Siberia, scale bar, 10 mm (Rickards & Durman, 2006, fig. 23B).

Eocephalodiscus KOZŁOWSKI, 1949, p. 195 [**E. polonicus;* OD]. Compact tubarium with isolated chambers for zooids; chambers with large circular openings; no apertural elaborations. *Lower Ordovician* (*Tremadocian*): Poland.——FIG. 122,*2*. **E. polonicus,* holotype, scale bar, 5 mm (Kozłowski, 1949, pl. 33,*1b*).

Melanostrophus ÖPIK, 1930, p. 10 [**M. fokini;* OD]. Tubarium comprised of long, slender, circular, subcircular, or subpolygonal erect zooidal tubes, rarely branched; zooidal tube wall made of thin fusellar layer and very thick outer and inner cortical deposits; tubes fused by their walls to form a cuplike colony. *Middle Ordovician* (*upper Darriwilian*)–*Upper Ordovician* (*Sandbian,* Kukruse Stage): Estonia, Germany (glacial boulder).——FIG. 124, *a–b*. **M. fokini, a,* holotype, TUG 11053-19, Ubja, Estonia, scale bar, 10 mm; *b,* northern Germany, scale unknown (Zessin & Puttkamer, 1994, fig. 2).

Pterobranchites KOZŁOWSKI, 1967, p. 123 [**P. antiquus;* OD]. Tubarium of irregularly aggregated tubes and elongated vesicles; no apertural elaborations. *Lower Ordovician* (*Tremadocian*): Poland (glacial boulder).——FIG. 122,*3a–b*. **P. antiquus,* syntypes, two fragments of a single colony, scale bars, 1 mm (Kozłowski, 1967, fig. 11).

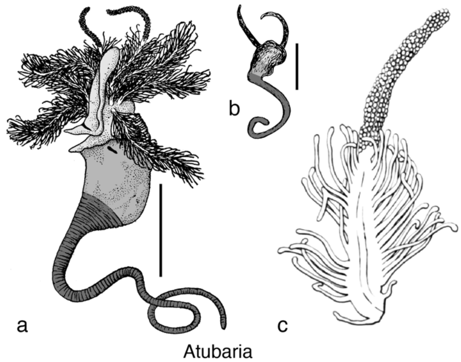

FIG. 123. Cephalodiscidae (extant) (p. 203).

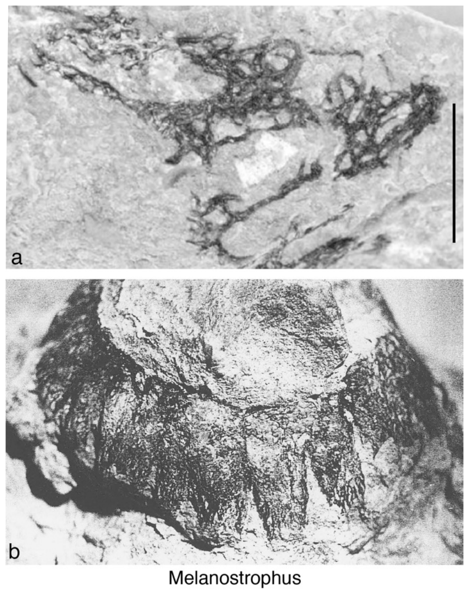

FIG. 124. Cephalodiscidae (fossil) (p. 203).

SUBCLASS GRAPTOLITHINA AND BENTHIC FAMILIES OF UNCERTAIN RELATIONSHIPS

Jörg Maletz and Elena Beli

Subclass GRAPTOLITHINA Bronn, 1849

[Graptolithina Bronn, 1849, p. 149] [=Rhabdophora Allman, 1872, p. 380] [incl. order Rhabdopleurida Fowler, 1892b, p. 297; order Rhabdopleuroidea Beklemishev, 1951, p. 414; order Graptovermida Kozłowski, 1949, p. 204, herein]

Pterobranchs with a colonial habit, building a tubarium from individual fusellar rings and half rings or, in some instances, featureless membranes; rigid stolon system (black stolon) connects the individual, clonally produced zooids attached to stolon by highly flexible and extendable zooidal stalk. *Cambrian* (*Terreneuvian, Fortunian*)–*Holocene* (extant): worldwide.

Mitchell and others (2013) defined the taxon based on a detailed cladistic analysis of Paleozoic benthic graptolites and extant pterobranchs and regarded serial budding from an interconnected stolon system as the defining synapomorphy. The Graptolithina can be characterized as pterobranchs with a clonal, colonial development, secreting a tubarium from individual fusellar rings and half rings, as was described by Mitchell and others (2013) and Maletz (2014b).

Fossil taxa can be recognized through the preservation of the tubarium. More rarely, the black stolon and the diaphragm complexes are preserved. These are not formed from fusellar tissue and generally have not been recognized as pterobranch remains. Several authors (e.g., Mierzejewski, 1986; Urbanek & Dilly, 2000; Maletz, 2014b) identified stolonal remains, initially identified as hydroids, as putative stolonal fragments of Graptolithina. Mierzejewski (1986) was able to convincingly combine the remains of *Kystrodendron longicarpus* (Eisenack, 1938b) (stolon with cysts) and *Eorhabdopleura urbaneki* Kozłowski, 1970b (tubes of fusellar construction) into a single rhabdopleurid taxon.

The precise status of the families of the benthic graptolites within the subclass Graptolithina has not yet been established. Thus, they are considered to represent preliminary taxonomic units of uncertain value. Their diagnoses are based on strongly limited features of fragmentary material.

Kozłowski was against the use of the family rank as a taxonomic unit (Mierzejewski, 1986, p. 174) and used the order level to differentiate his graptolite taxa. Thus, he erected the orders Camaroidea Kozłowski, 1938; Crustoidea Kozłowski, 1962; Graptovermida Kozłowski, 1949; Tuboidea Kozłowski, 1938; and Stolonoidea Kozłowski, 1938. These are not used by this author (see Maletz, 2014b) because the included taxa are impossible to relate precisely to other groups of the Graptolithina and are largely considered as taxa *incertae sedis,* based on a strongly limited number of fragmentary specimens of unknown relationships. Bengtson and Urbanek (1986) identified *Stolonodendrum* (Stolonoidea) as creeping tubes of Rhabdopleuridae. Maletz and Beli (2018) included the genus *Graptovermis* Kozłowski, 1949 (Graptovermida) in the Rhabdopleuridae. The remaining taxa are listed here as the family level taxa Wimanicrustidae Bulman, 1970; Cysticamaridae Bulman, 1955; and Cyclograptidae Bulman, 1938.

Obut (1960) erected the order Dithecoidea for erect growing dendroids with diad budding, dimorphism of the thecae, but lacking bithecae; and he included the families Dithecodendridae Obut, 1957; Siberiograptidae Obut, 1957; and Chaunograptidae Bulman, 1955. Obut (1974) added the order Archaeodendrida. All these taxa are based on highly fragmented material and herein included in the family

Dithecodendridae OBUT, 1964 until better known.

Family RHABDOPLEURIDAE Harmer, 1905

[Rhabdopleuridae HARMER, 1905, p. 5] [incl. Chaunograptidae BULMAN, 1955, p. 36, *partim;* Idiotubidae KOZŁOWSKI, 1949, p. 144, *partim;* Stolonodendridae BULMAN, 1955, p. 43; Rhabdopleuroididae MIERZEJEWSKI, 1986, p. 176; Rhabdopleuritidae MIERZEJEWSKI, 1986, p. 177; ?Rhabdohydridae MIERZEJEWSKI, 1986, p. 151]

Colonial pterobranchs with encrusting tubarium, having irregular fusellar rings or regular zigzag sutures in creeping and erect tubes; resorption foramen for the origination of new tubes; erect thecal tubes parallel sided or gradually widening, with simple or ornamented apertures; zooids connected through robust stolon system having diad budding with diaphragm complexes and dormant bud capsules (cysts); featureless dome secreted by sicular zooid. *Cambrian* (*Terreneuvian, Fortunian*)–*Holocene* (extant): worldwide.

The Rhabdopleuridae represent a group of encrusting benthic organisms, restricted to the marine environment. They possess a complex life cycle with a planktic, swimming larval stage and a benthic stage, growing through asexual production of clonal zooids and forming encrusting colonies with various structures, known only from extant taxa. Rhabdopleurids occur from the shallow intertidal zone to the deep marine regions, from the tropical equatorial regions to Arctic and Antarctic regions. The fossil remains of their tubaria can easily be compared to the tubaria of a number of extant species. The modern taxa provide the only information of the soft body anatomy of the rhabdopleurids.

MORPHOLOGY

The complexities of the tubarium of the Rhabdopleuridae are known in some detail from the extant genus *Rhabdopleura* ALLMAN in NORMAN, 1869a, but details of fossil taxa are difficult to interpret, as they are usually based on highly fragmented material. Two main features have to be differentiated: 1) the tubarium secreted from fusellar rings and half rings by the zooids; and 2) the stolon system (pectocaulus) formed as a dermal construction on the surface of the living tissues of the gymnocaulus with all its additional developments in the form of thecal cones, dormant bud capsules, cysts, and diaphragm complexes. SCHEPOTIEFF (1907b) described early colony development in *Rhabdopleura normani* ALLMAN in NORMAN, 1869a. His description includes the presence of the Embryonalblase (dome) and an Embryonalring (initial circular part of the stolon), formed from the stolon. The rhabdopleurid tubarium starts with the dome, sometimes homologized with the prosicula of the Graptoloidea (see MALETZ, STEINER, & FATKA, 2005; MITCHELL & others, 2013). The dome is secreted by the sicular zooid as a featureless membrane in which the larva morphs into the mature zooid. It generally has an ovoid shape and is attached to the substrate on one side. The zooid emerges from one side of the dome by resorbing a foramen into the membrane and starts to secrete the first fusellar rings. In most *Rhabdopleura,* even the earliest fuselli form half rings and a dorsal zigzag suture on the developing metasicular tube (DILLY, 1986). The sicular zooid produces a horizontal, encrusting thecal tube with a distinct dorsal zigzag suture and a flat basal surface, with which it is attached to the substrate. In other (fossil) taxa, the initial fuselli may be irregularly formed, but details are available from few specimens.

SARS (1872), LANKESTER (1884), and SCHEPOTIEFF (1907b) described and illustrated the tubarium of the extant *Rhabdopleura normani* in some detail and provided the most complete understanding of any rhabdopleurid tubarium. The tubarium of *Rhabdopleura compacta* HINCKS, 1880a is largely comparable in its construction (see HINCKS, 1880a; STEBBING, 1970a, 1970b), but the presence of a permanent terminal zooid is not confirmed. All rhabdopleurids produce a tubarium in the shape of interconnected tubes for the individual zooids. These tubaria possess a number of characteristics not present in other pterobranchs. Early

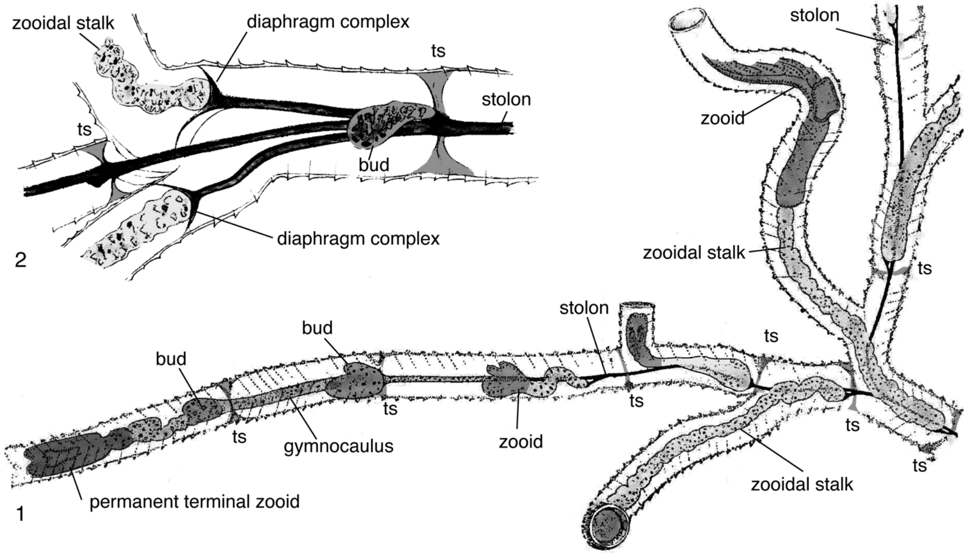

FIG. 125. *Rhabdopleura normani* ALLMAN in NORMAN, 1869a, monopodial growth and stolon system with diaphragm complexes. *1,* Growing end of colony showing monopodial growth with permanent terminal zooid (adapted from Ridewood, 1907, fig. 7); *2,* branching point; *ts*, transverse septum (adapted from Lankester, 1884, pl. 41,*7*). Color version available in *Treatise Online,* 101.

rhabdopleurids appear to possess irregularly placed fusellar sutures, for example, *Sphenoecium wheelerensis* MALETZ & STEINER, 2015 (see MALETZ & STEINER, 2015), but details are only available from a few specimens. *Sphenoecium obuti* (DURMAN & SENNIKOV, 1993) (see DURMAN & SENNIKOV, 1993; SENNIKOV, 2016a, 2016b) from the middle Cambrian of Siberia already has a relatively regular development of the sutures closely resembling the zigzag suture of extant *Rhabdopleura*.

The most remarkable character of the *Rhabdopleura normani* tubarium is the monopodial development of the main stem, the branching axis (LANKESTER, 1884, p. 625) or "Hauptröhre" of SCHEPOTIEFF (1907b, p. 213), but a comparable feature is not known in most other *Rhabdopleura* taxa. Colony growth is achieved through the increasing length of the main stem and the addition of new thecal tubes ("Wohnröhren" in SCHEPOTIEFF, 1907b, p. 213) at the sides of this stem. The permanent terminal zooid (Fig. 125.1) produces fusellar half rings and increases the length of the stipe. At regular or irregular distances, transverse septa are formed to separate individual segments of the stem into compartments for the developing zooids (LANKESTER, 1884; SCHEPOTIEFF, 1907b; URBANEK & DILLY, 2000). The development of the transverse septa starts from the inner wall of the tubes, as incompletely developed septa indicate (SCHEPOTIEFF, 1907b, p. 220).

The zooids resorb an opening into one side of the main stem, invariably at the distal end of the compartment (see SCHEPOTIEFF, 1907b, p. 220; KOZŁOWSKI, 1949, fig. 14E) and start to build erect thecal tubes from fusellar full rings. These tubes can reach considerable lengths and are inhabited by a single zooid attached to the stolon system with a highly flexible gymnocaulus. The main stem invariably bears a dorsal zigzag suture in *Rhabdopleura*, but the thecal tubes have full fusellar rings with a single oblique suture. A distinct collar is typically also present in the fuselli of the thecal tubes but in fossil material may be difficult to recognize.

The interconnection between the zooidal development and the tubarium construction

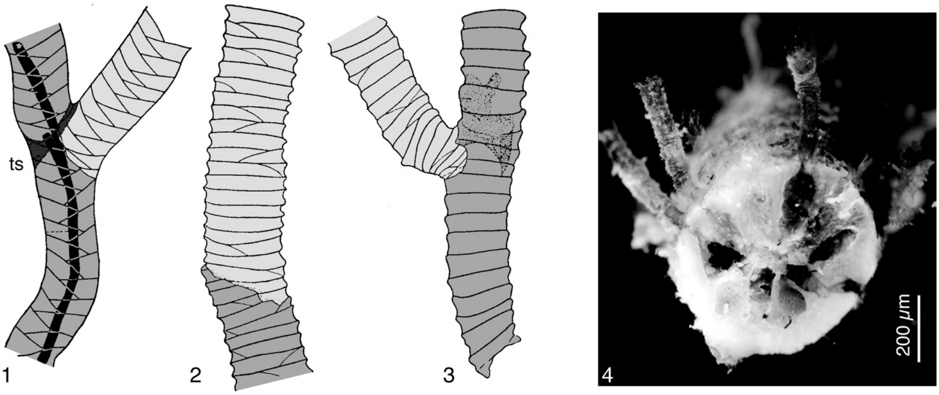

FIG. 126. Branching of tubarium. *1,* Main stem with branching, see stolon and transverse septum (*ts*); *2,* part of erect thecal tube with regeneration; *3,* erect tube with unusual lateral branching. (adapted from Kozłowski, 1949, fig. 14); *4, Rhabdopleura recondita* BELI & others, 2018 finds shelter inside the dead branches of bryozoan hosts, erect tubes project from the pores (new; photo courtesy of Stefano Piraino). Color images available in *Treatise Online,* 101.

in *Rhabdopleura normani* and possibly in other members of the genus is an important observation. LANKESTER (1884, p. 627) noted that the creeping (recumbent) tubes with their characteristic zigzag sutures are invariably secreted by immature zooids before arms have developed. The mature zooids with their two, fully formed arms secrete the full rings of the erect thecal tubes. Thus, the zooids morph in their initial compartments into fully grown organisms before they break through the tube wall and start secreting the thecal tubes. The permanent terminal zooid represents the model of an immature zooid before the maturation process is finished.

Branching of the main stem can be produced irregularly and appears to be through a resorption foramen and the immediate development of a dorsal zigzag suture of the new branch (Fig. 126.1). An illustration of KOZŁOWSKI (1949, fig. 14A) shows the original branch and the laterally originating secondary branch, at the base of which truncated fuselli of the previous branch can be seen. A transverse septum separates the continuing part of the main branch. Branching of the thecal tubes is generally not noted, but KOZŁOWSKI (1949, fig. 14C) illustrated a fragment that appears to show an unusual resorption foramen and the growth of a secondary thecal tube (Fig. 126.3). Regeneration of thecal tubes is more common (Fig. 126.2) and can be seen by the irregular break across a tube and the subsequent addition of fusellar full rings (RIGBY, 1994a). Typically, the new addition is also less strongly colored than the older part of the tubarium.

One of the most conspicuous features of the Rhabdopleuridae is the stolon system connecting the individual zooids. The fully developed stolon system is a black rod either lying free within the main tube or attached to the ventral tube wall, which develops as the gymnocaulus hardens to form the stolon system (black stolon) and is surrounded by denser, dark material (LANKESTER, 1884, p. 636). This dark stolonal material is formed from dense crassal fabric, as is the stolon system of other graptolites (URBANEK & TOWE, 1974; BATES & URBANEK, 2002; SAUNDERS & others, 2009). In extant rhabdopleurids, the stolon is often easily visible through the translucent tubarium (see URBANEK & DILLY, 2000).

Initially, the stolon (gymnocaulus) is naked and flexible and begins to lengthen behind the terminal zooid and its developing buds (Fig. 125.1). When a number of buds are formed and separated into their individual chambers, the gymnocaulus within these chambers subsequently and slowly thickens and hardens, attaining a dark coloration and losing its original flexibility (LANKESTER, 1884).

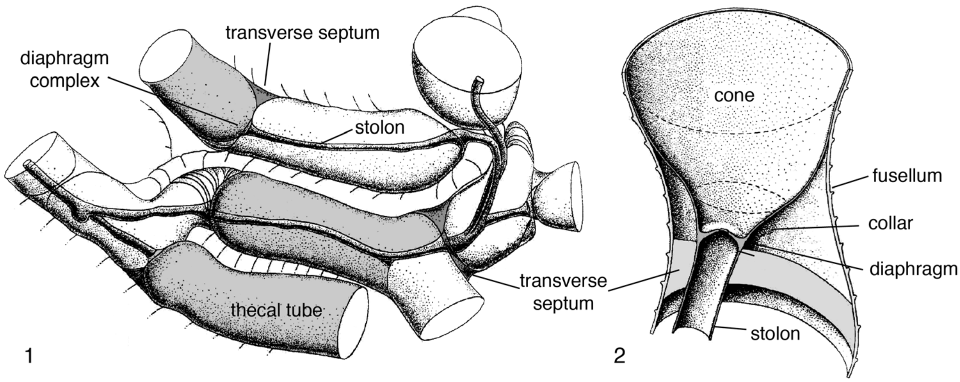

FIG. 127. The stolon system. *1,* stolon and inner lining (cone) of thecal tubes; *2,* diaphragm complex and connection to the fusellar tube (adapted from Urbanek & Dilly, 2000).

A short branch of the stolon connects to the zooidal stalk of the zooids (Fig. 125.1). At the tip of the zooidal stolon, a diaphragm complex (URBANEK & DILLY, 2000) develops (Fig. 127), representing the encysting shell of a dormant bud or a resting stage of the developing zooid, also called the pigmented peridermal capsule (URBANEK & DILLY, 2000, p. 210). These capsules were first recognized by LANKESTER (1884) who termed them hibernacula. Later, SCHEPOTIEFF (1907b) referred to them as sterile Knospen (sterile buds). STEBBING (1970a) concluded that these buds were able to develop into zooids and introduced the term dormant buds. In thecal tubes of active zooids, these capsules are open distally and appear to be an inner lining of the tube over considerable distances, adhering closely to the fusellar wall (URBANEK & DILLY, 2000, p. 214). The zooid is independent of this thecal lining, as indicated from retracted zooids with a coiled zooidal stalk in the terminal diaphragm complex (URBANEK & DILLY, 2000, fig. 9).

When KOZŁOWSKI (1949) introduced the order Graptovermida, he described them as tubes of unknown origin, possessing a flat basal surface indicating an encrusting habit. He documented the presence of fuselli in some specimens. The Graptovermida can be included in the Rhabdopleuridae as they are easily interpreted as remains of a sigmophyllic *Rhabdopleura*-like species. KOZŁOWSKI (1949, p. 206) indicated the presence of an ovoid initial part or dome in *Graptovermis spiralis* KOZŁOWSKI 1949, termed a cul-du-sac ovale. The vermiform tubes represent the creeping tubes of the tubarium, with zigzag suture lines on the upper surface of the tubes. The erect tubes with their collared full fusellar rings may not be preserved. MIERZEJEWSKI (1988) discussed the graptovermids in some detail based on chemically isolated material from Öland, Sweden. The material consisted of stolonal developments with strongly elongated cysts or buds, similar to the diaphragm complexes of extant rhabdopleurids. MIERZEJEWSKI (1988) interpreted them as resting stolothecae of encrusting graptolites. However, the ultrastructure of the graptovermids has not yet been investigated.

EVOLUTION

The evolutionary origin of the Rhabdopleuridae is uncertain, but a number of observations have led to some understanding. Earliest rhabdopleurid fossils originated during the middle Cambrian and may be referred to the genus *Sphenoecium* (MALETZ & STEINER, 2015). Specimens clearly show the clonal, colonial development through the presence of interconnected thecal tubes in encrusting colonies with erect, unbranched distal thecal tubes.

Sphenoecium wheelerensis and *Sphenoecium mesocambricus* (Öpik, 1933) belong to the oldest members of the group. However, *Sphenoecium obuti* appears to be the oldest well-preserved rhabdopleurid. Very little is known about the diversification of the Graptolithina in the upper Cambrian, and even the cladistic analysis (Mitchell & others, 2013) did not provide sufficient evidence for an evolutionary interpretation of the early origins of the group. Rhabdopleurids with numerous modern tubarium features are present during the Ordovician (Skevington, 1965; Mierzejewski, 1986) but may not be referred to the genus *Rhabdopleura*. Chemically isolated material of *Sokoloviina* Kirjanov, 1968 may represent the oldest rhabdopleurid record in the lower Cambrian (Fortunian), as it has fusellar construction and collars on the tubes.

The earliest taxon referable to the extant genus *Rhabdopleura* may be *Rhabdopleura hollandi* Rickards, Chapman, & Temple, 1984 from the Silurian *Spirograptus turriculatus* Biozone of Wales (Rickards, Chapman, & Temple, 1984), and older rhabdopleurids can be referred to the genus *Kystodendron* Kozłowski 1959a (see Mierzejewski & Kulicki, 2001, 2002, 2003a).

Chapman, Durman, and Rickards (1995) identified fragmentary material from the Ordovician (upper Darriwilian) of China as *Rhabdopleura sinica* Kozłowski, 1959a, fig. 10. *Rhabdopleura graysoni* Chapman, Durman, & Rickards, 1995 from the Visean (Carboniferous) resembles the extant *Rhabdopleura compacta*, but little detail of the tubarium development is available. Another record from the Carboniferous is *Rhabdopleura delmeri* Mortelmans, 1955 from Belgium. Fossil records of rhabdopleurids from the Mesozoic and Cenozoic are rare, and few specimens have been described. Kozłowski (1956a) described *Rhabdopleura vistulae* Kozłowski, 1956a from the Danian (Cretaceous) of Poland, and Kulicki (1969, 1971) recorded the species *Rhabdopleura kozlowskii* Kulicki, 1969 from the Callovian (Jurassic) of Poland. A single record of *Rhabdopleura* exists from the Eocene of England (Thomas & Davies, 1949a, 1949b, 1950).

Rhabdopleura Allman in Norman, 1869a, p. 311 [**R. normani;* M] [=*Halilophus* Sars, 1868, p. 255 (type, *H. mirabilis*), *nom. nud.,* herein]. Rhabdopleurids with thigmophyllic to thigmophobic tubarium; creeping tubes with fusellar half rings and dorsal zigzag sutures, sutures on ventral sides indistinct or lacking; sicular zooid forms dome from which the metasicula and first autotheca develop; creeping tubes with irregularly to regularly produced partitions; erect tubes with irregularly placed sutures and full fusellar rings; branching occurs only in creeping tubes; apertures simple, straight; fuselli on erect tubes with distinct collar; stolon system with diad budding and complex diaphragm complexes. ?*Silurian* (*Llandovery, Spirograptus turriculatus* Biozone)–*Holocene* (extant): worldwide.——Fig. 128,*1*. **R. normani,* part of tubarium, Shetland Sea, ~165 m depth, scale bar, ~1 mm (Allman, 1869b, pl. 8,*1*).

Archaeolafoea Chapman, 1919, p. 390 [* *A. longicornis;* M] [=*Archaeocryptolaria* Chapman, 1919, p. 392 (type, *A. skeatsi,* SD Bulman, 1970, p. 55), syn. by Maletz & Steiner, 2015, p. 1097]. Tubarium construction of colonial pterobranch formed from organic tubes; creeping and branching, elongated central tube with erect and unbranched lateral tubes bearing simple, straight apertures; parallel-sided lateral tubes formed from fusellar half rings or full rings, possibly with irregularly developed oblique sutures; stolon and zooidal development unknown. *Cambrian* (*Miaolingian*)–?*Ordovician:* Australia (Victoria).——Fig. 128,*2a*. **A. longicornis,* holotype, NMV P 13112, scale bar, 1 mm (new).——Fig. 128,*2b*. *Archaeocryptolaria skeatsi* Chapman, 1919, holotype, NMV P 13114, scale bar, 1 mm (new).

Chaunograptus Hall, 1882, p. 225 [**Dendrograptus* (*Chaunograptus*) *novellus;* M] [=*Desmohydra* Kozłowski, 1959a, p. 227 (type, *D. flexuosa;* OD), syn. by Mierzejewski, 1986, p. 163] [=*Epallohydra* Kozłowski, 1959a, p. 230 (type, *E. adhaerensis,* OD), syn. by Mierzejewski, 1986, p. 163]. Tubarium formed from organic tubes; creeping and branching, elongated central tube with unbranched lateral tubes bearing simple, straight apertures; fusellar construction; stolons and zooidal development unknown. *Cambrian* (*Miaolingian, Wuliuan, Ptychagnostus praecurrens* Biozone)–*Silurian* (*Wenlock*): Poland, USA.——Fig. 128,*4a–b*. **C. novellus* (Hall); *4a,* syntype, NYSM 3170/1, specimens attached to *Eospirifer radiatus* (brachiopod), scale bar, 10 mm (Hall, 1882, pl. 1); *4b,* syntype, FMNH UC 11989, specimen attached to *Eucalyptocrinus* (echinoderm), scale bar, 1 mm (new).——Fig. 128,*4c*. *C. flexuosus* (Kozłowski, 1959a), holotype, ZPAL material, Poland, glacial boulder, scale bar, 1 mm (Kozłowski, 1959a, fig. 10).——Fig. 128,*4d*. *C. adhaerensis* (Kozłowski, 1959a), holotype, ZPAL material, Poland, glacial boulder, scale bar, 1 mm (Kozłowski, 1959a, fig. 10).

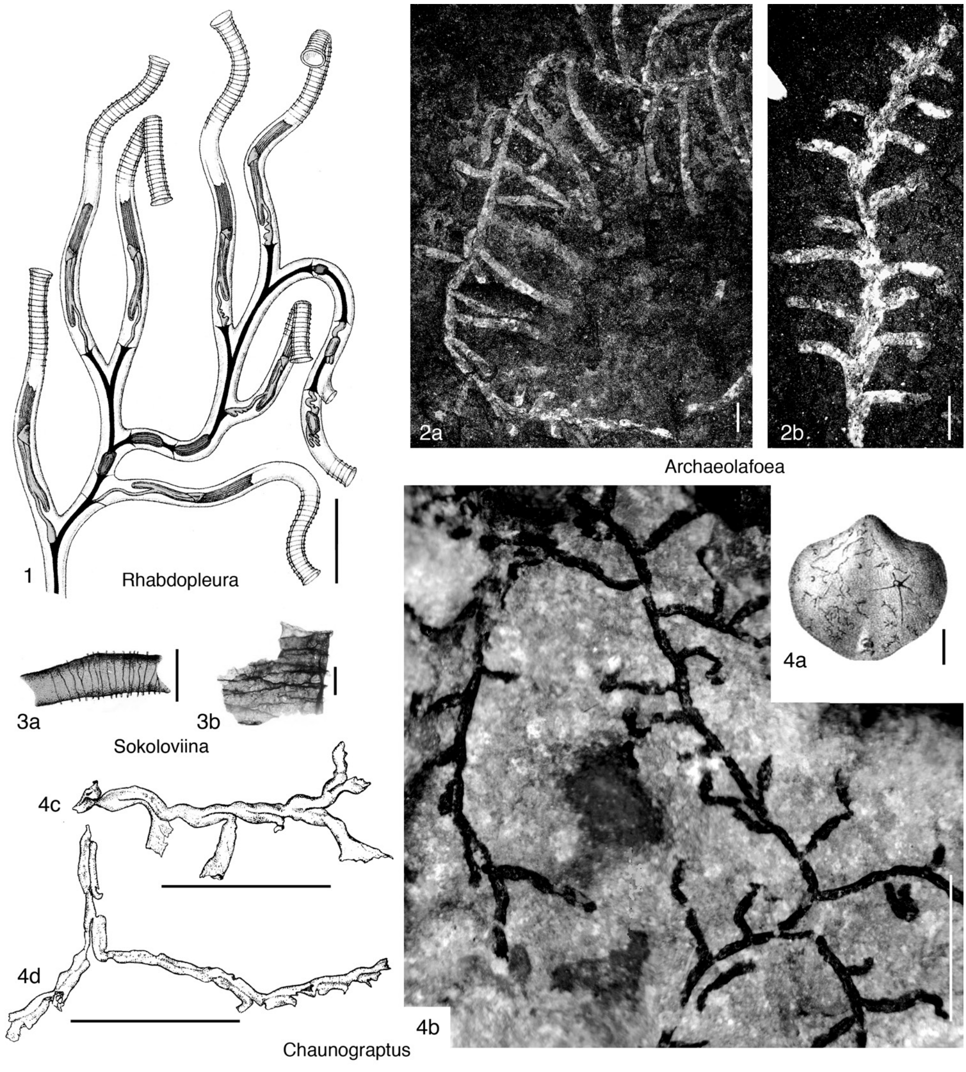

FIG. 128. Rhabdopleuridae (p. 210–213).

Epigraptus EISENACK, 1941a, p. 25 [**E. bidens;* M] [=*Idiotubus* KOZŁOWSKI, 1949, p. 144 (type, *I. typicalis,* OD), syn. by MIERZEJEWSKI, 1978, p. 566]. Encrusting thecorhiza of unknown form; erect portions of autothecae arising directly from surface of thecorhiza; autothecal apertural apparatuses in form of single or two lamelliform or bifurcate process; stolon system unknown. *Lower Ordovician* (*Tremadocian*)*–Silurian, Ludlow:* Estonia, Germany, Poland, Sweden (glacial boulder).——FIG. 129,*1a–b.* **E. bidens; 1a,* neotype, GPIT S.G. 158, Nr. (Eisenack, 1974, p. 671); *1b,* holotype (not preserved), Sandbian, Wesenberg (Rakvere), Estonia (Eisenack, 1941a, fig. 1). Scale bars, 1 mm.——FIG. 129,*1c. Epigraptus* sp., small colony with part of dome, whereabouts unknown, scale bar, 1 mm (Andres, 1977, fig. 27).——FIG. 129,*1d. E. typicalis* (KOZŁOWSKI, 1949), holotype, ZPAL material, Poland, scale bar, 1 mm (Kozłowski, 1949, pl. 13,*1*).

Graptovermis KOZŁOWSKI, 1949, p. 206 [**G. spiralis;* OD]. Rhabdopleurids with thigmophyllic tubarium; creeping tubes with fusellar development; thecal apertures and erect tubes unknown; sicular zooid forms dome; details of tubarium unknown. *Lower Ordovician* (*Tremadocian*): Poland (glacial boulder).——FIG. 129,*2a–c.* **G. spiralis; 2a–b,* holotype, ZPAL material, in dorsal (*a*) and ventral (*b*) views; *2c,* paratype, ZPAL material, showing spiral development from ventral side, scale bars, 1 mm (6,*2a–c,* Kozłowski, 1949, pl.

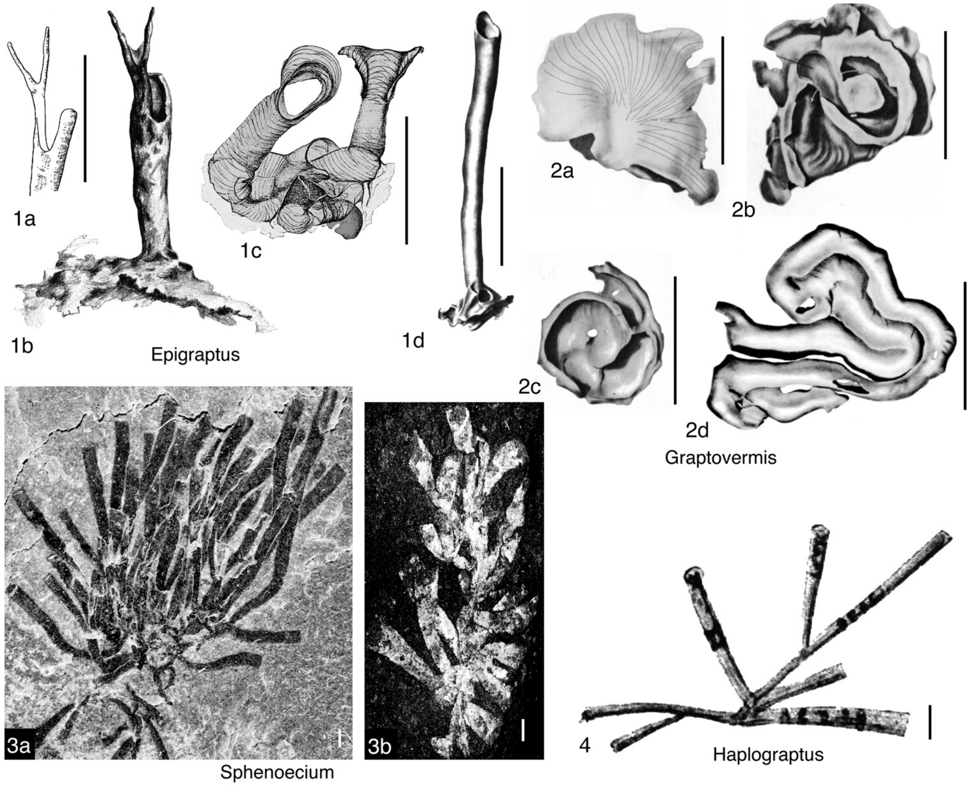

FIG. 129. Rhabdopleuridae (p. 211–213).

36).——FIG. 129,*2d. G. intestinalis* KOZŁOWSKI, 1949, holotype, ZPAL material, scale bar, 1 mm (Kozłowski, 1949, pl. 35,*6*).

Haplograptus RUEDEMANN, 1933, p. 323 [**H. wisconsinensis;* OD]. Branched, encrusting to erect tubes with elongate conical or vermiform, erect theca forming irregularly dendroid tubarium. *Cambrian* (*Furongian*)–*Middle Ordovician* (*Darriwilian*): China, Canada, USA.——FIG. 129,*4*. **H. wisconsinensis* RUEDEMANN, 1933, holotype. repository unknown. scale bar, 1 mm (Ruedemann, 1947, pl. 40,*6*).

Kystodendron KOZŁOWSKI, 1959a, p. 252 [**Chitinodendron longicarpus* EISENACK, 1938b, p. 237; OD] [=*Eorhabdopleura* KOZŁOWSKI, 1970, p. 4 (type, *E. urbaneki,* OD); *nom. dub.,* MIERZEJEWSKI, 1986, p. 184] [=?*Cylindrotheca* EISENACK, 1934, p. 66 (type, *C. profunda,* OD); *nom. dub.,* MIERZEJEWSKI, 1986, p. 183]. Zooidal and stolonal tubes similarly developed as in *Rhabdopleura;* major stolon and peduncular stolons of cysts of sterile buds without diaphragms; sterile bud cysts circular in cross section, simple or composite. *Ordovician:* Poland (glacial boulder).——FIG. 130,*2a*. **K. longicarpus* (EISENACK), holotype, ZPAL material, stolon with cysts, scale bar, 1 mm (Eisenack, 1938b, fig. 18).——FIG. 130,*2b–c*. *Kystodendron urbaneki (*KOZŁOWSKI, 1970), holotype, ZPAL material, thecal tube fragments, scale bar, 0.1 mm (Kozłowski, 1970, fig. 1).

Rhabdopleurites KOZŁOWSKI, 1967, p. 126. [**R. primaevus;* OD]. Colony encrusting, with dendroidal part underdeveloped, comprised of stolonal and zooidal tubes; fuseIlar tubes varying from 0.3 to 0.6 mm in width and fuselli 60 to 100 µm wide; fuseIlar collars varying in size, sometimes very large; some stolonal tubes nonfusellar; stolons without diaphragms; sterile bud cysts missing. *Ordovician* (*Darriwilian*): Germany, Poland, Sweden (glacial boulder).——Fig. 130,*1a–b*. **R. primaevus;* syntypes, ZPAL material, thecal tubes; scale bars, 0.5 mm (Kozłowski, 1961, fig. 13).

Rhabdopleuroides KOZŁOWSKI, 1961, p. 4 [**R. expectatus;* M]. Tubarium exclusively comprised of creeping stolonal and zooidal tubes; stolons without cysts of sterile buds. *Middle Ordovician* (*Darriwilian*)–*Upper Ordovician* (*Sandbian*): Poland (glacial boulder).——FIG. 130,*3a–d*. **R. expectatus; 3a–b,* holotype, not preserved (Mierzejewski, 1986, p. 177); *3c,* paratype, ZPAL material; *3d,* lectotype (designated by MIERZEJEWSKI, 1986, p. 177), ZPAL material (Kozłowski*,* 1961, 1970, fig. 2). Scale bars, 0.5 mm.

Sokoloviina KIRJANOV, 1968, p. 22 [**S. costata;* OD]. Small- to medium-sized tubes of black color with

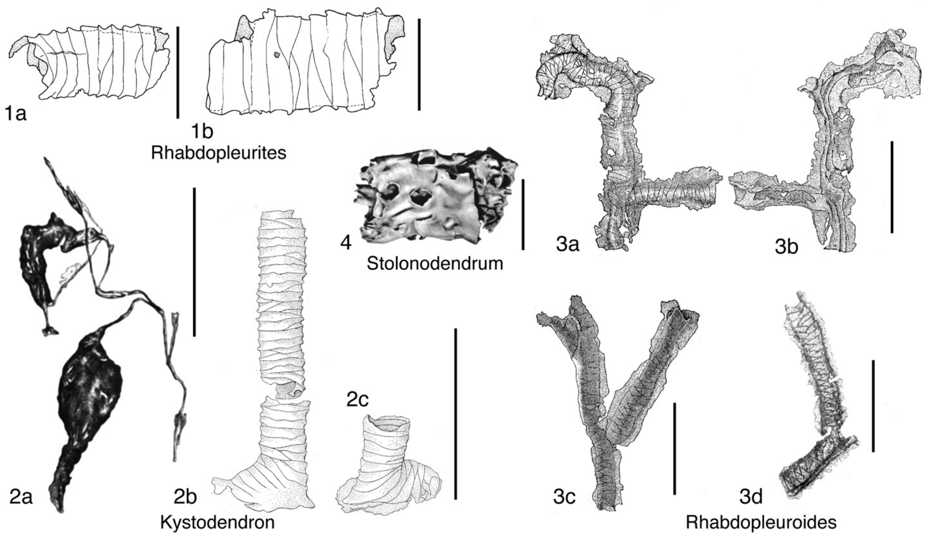

FIG. 130. Rhabdopleuridae (p. 212–213).

collars in the form of sharp-pointed or circular annular growths. *Cambrian* (*Terreneuvian, Fortunian*): Estonia, Ukraine (Podolia).——FIG. 128,*3a-b*. **S. costata; 3a,* syntype, tube fragment, scale bar, 1 mm (Kirjanov, 1968, pl. 3,*8*); *3b,* chemically isolated fragment, scale bar, 10 µm (Sokolov, 1997, pl. 9,*4*).

Sphenoecium CHAPMAN & THOMAS, 1936, p. 205 [**Sphenothallus filicoides* CHAPMAN, 1917, p. 92; SD BULMAN, 1970, p. 57, *pro Sphenothallus* CHAPMAN, 1917, *non* HALL, 1847, p. 261 [=phylum Cnidaria VAN ITEN, COX, & MAPES, (1992, p. 143); =*Rhabdotubus* BENGTSON & URBANEK, 1986 (type, *R. johannssoni,* OD), syn. by MALETZ & STEINER, 2015, p.1098; =*Fasciculitubus* OBUT & SOBOLEVSKAYA, 1967, p. 56 (type, *F. tubularis,* OD), syn. by MALETZ & STEINER, 2015, p. 1098]. Tubarium construction of colonial pterobranchs formed from organic tubes; short creeping and branching tubes with distally erect and unbranched, slowly widening tubes with simple, straight apertures; tubes formed from fusellar half rings or full rings with irregularly developed oblique sutures; colony shapes often dependent on the availability of suitable surface for attachment, from small and circular to elongate or with multiple branchings covering larger areas. *Cambrian* (*Miaolingian, Wuliuan*)–*Ordovician:* worldwide.——FIG. 129,*3a. S. wheelerensis* MALETZ & STEINER, 2015, Spence Shale, Wellsville Mountains, Utah, USA, scale bar, 1 mm (Maletz & Steiner, 2015, fig. 17C).——FIG. 129,*3b.* **S. filicoides* (CHAPMAN), NMV P 47737, well-preserved specimen, scale bar, 1 mm (Maletz & Steiner, 2015, fig. 12C).

Stolonodendrum KOZŁOWSKI, 1949, p. 194 [**S. uniramosum;* OD]. Branched stolonal tubes with cysts and elongated thecal tubes with fusellum showing irregular sutures. [These were interpreted as creeping tubes of Rhabdopleuridae by BENGTSON & URBANEK 1986, p. 294.] *Ordovician* (*Tremadocian*): Poland (glacial boulder).——FIG. 130,*4*. **S. uniramosum,* holotype, ZPAL material, scale bar, 1 mm (Kozłowski, 1949, pl. 32,*2*).

POSSIBLE RHABDOPLEURID STOLONS

Numerous fragments of strings or slender tubes of organic material—sometimes with attached rounded or elongated bodies and distinct branching patterns—have been found from the Paleozoic and have generally been identified as hydroid remains (e.g., KOZŁOWSKI, 1959a). MIERZEJEWSKI (1986) erected the family Rhabdohydridae for the genera *Rhabdohydra* KOZŁOWSKI, 1959a and *Palaeotuba* EISENACK, 1934 and regarded it as an extinct group related to the hydrozoan suborder Athecata HINCKS, 1868. A number of taxa originally described as possible hydroids have subsequently been referred to the Pterobranchia (see MIERZEJEWKSI, 1986; BATES & URBANEK, 2002; MALETZ, 2014b). MUSCENTE, ALLMON, and XIAO (2015, p. 79) especially questioned the hydroid fossil record in the Paleozoic and suggested a hemichordate origin for many remains. They recognized that lower Paleozoic putative hydroid fossils are either preserved as carbonaceous microfossils

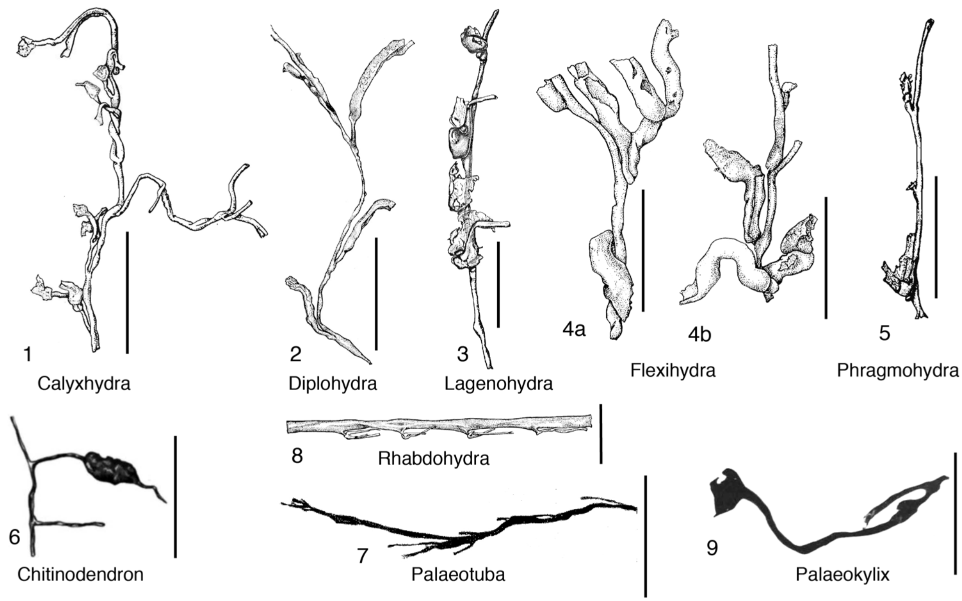

FIG. 131. Rhabdopleurid stolons (p. 214–215).

or as alumosilicate films (pressure shadow minerals, see UNDERWOOD, 1992; MALETZ & STEINER, 2015), but younger taxa are commonly preserved as bioimmured fossils. KEUPP, DOPPELSTEIN, and MALETZ (2016) described the rare occurrence of the stolon system of a rhabdopleurid preserved *in situ* on a Lower Jurassic hardground.

Calyxhydra KOZŁOWSKI, 1959a, p. 221 [**C. gemellithecata;* OD; =rhabdopleurid stolon, MIERZEJEWSKI, 1986, p. 168]. Branching system with more or less regular dichotomous divisions; terminal branches with conical tubes; no diaphragms. *Ordovician:* Poland (glacial boulder).——FIG. 131,*1*. **C. gemellithecata,* holotype, ZPAL material, scale bar, 0.5 mm (Kozłowski, 1959a, fig. 3).

Chitinodendron EISENACK, 1938b, p. 236 [**C. bacciferum;* SD KOZŁOWSKI, 1959a, p. 251; =?rhabdopleurid stolon, herein]. Branched stolon system with irregularly placed oval cysts. *Ordovician–Silurian:* Estonia, Poland.——FIG. 131,*6*. **C. bacciferum,* holotype, ZPAL material, scale bar, 0.5 mm (Eisenack, 1938b, fig. 13).

Diplohydra KOZŁOWSKI, 1959a, p. 240 [**D. longithecata;* OD] [=order Rhabdopleuroidea BEKLEMISHEV, 1951, p. 19, MIERZEJEWSKI & KULICKI, 2002, p. 171]. Stolon system devoid of diaphragms, peduncular stolons, and true capsules of the dormant buds; major stolon with irregularly arranged lateral offshoots; lateral offshoots form diads comprised of the two daughter stolons; as a rule, one of the daughter stolons is strongly inflated and sometimes forms an imperfect composite cyst. *Ordovician–Permian* (*Roadian*): Norway (Barents Shelf), Poland (glacial boulder).——FIG. 131,*2*. **D. longithecata,* holotype, ZPAL material, scale bar, 1 mm (Kozłowski, 1959a, fig. 16).

Flexihydra KOZŁOWSKI, 1959a, p. 225 [**F. undulata;* OD; =?rhabdopleurid remains, herein]. Short stolons with elongated, flexible thecal cups; fusellum unknown. *Ordovician:* Poland (glacial boulder).——FIG. 131,*4a–b*. **F. undulata,* syntype, ZPAL material, scale bars, 0.5 mm (Kozłowski, 1959a, fig. 7).

Lagenohydra KOZŁOWSKI, 1959a, p. 245 [**L. phragmata;* OD; =rhabdopleurid stolon, MIERZEJEWSKI, 1986, p. 193]. Stolon system with distinct thecal dimorphism; each node bears two differently shaped thecae; fusellum unknown. *Ordovician:* Poland (glacial boulder).——FIG. 131,*3*. **L. phragmata,* holotype (specimen not preserved, see MIERZEJEWSKI, 1986, p. 194), scale bar, 0.5 mm (Kozłowski, 1959a, fig. 22A).

Palaeokylix EISENACK, 1932, p. 266 [**P. chitinosus;* OD; *nom. dub.,* herein]. Simple branched stolon with thecal cup; fusellum unknown. *Ordovician–?Silurian*: Russia (Oblast Kaliningrad, formerly Samland) (glacial boulder).——FIG. 131,*9*. **P. chitinosus*, holotype, ZPAL material, scale bar, 0.1 mm (Eisenack, 1932, pl. 11,*22*).

Palaeotuba EISENACK, 1934, p. 54 [**P. polycephala;* OD; =?rhabdopleurid stolon, MIERZEJEWSKI, 1986, p. 179]. Stolon system with multiple branchings. *Upper Ordovician* (*lower Sandbian,* Kukruse Stage):

Estonia, Poland (glacial boulder).——FIG. 131,*7*. **P. polycephala,* holotype, repository unknown, scale bar, 1 mm (Eisenack, 1934, pl. 4,*5*).

Phragmohydra KOZŁOWSKI, 1959a, p. 238 [**P. articulata;* OD; =?rhabdopleurid remains, herein]. Stolon system with complex peduncular diaphragms; fusellum unknown. *Ordovician:* Poland (glacial boulder).——FIG. 131,*5*. **P. articulata,* holotype, ZPAL material, scale bar, 0.5 mm (Kozłowski, 1959a, fig. 15a).

Rhabdohydra KOZŁOWSKI, 1959a, p. 235 [**R. tridens;* OD; =?rhabdopleurid remains, herein]. Stolon system with multiple peduncular diaphragms; fusellum unknown. *Ordovician:* Poland (glacial boulder), Sweden.——FIG. 131,*8*. **R. tridens,* ZPAL material, holotype, scale bar, 0.5 mm (Kozłowski, 1959a, fig. 14A).

Family WIMANICRUSTIDAE Bulman, 1970

[Wimanicrustidae BULMAN, 1970, p. 52] [incl. Hormograptidae BULMAN, 1970, p. 52]

Encrusting Graptolithina with irregularly branching colonies made of creeping stipes; segments of stipes comprised of autothecae and bithecae produced in triads; autothecae usually with inflated proximal portion and erect distal neck, typically provided with elaborated apertural lobes; bithecae cylindrical, adnate throughout their length; stolon system usually having distinct annulation; graptoblasts routinely produced as resting bodies, which morphologically form normal part of colony (synapomorphic feature of the Wimanicrustidae); cortical deposits spurious, cortical bandages not observed. *Ordovician* (*Tremadocian, Drepanoistodus deltifer* Conodont Biozone)–*Silurian* (*Ludlow,* ?*Ludfordian, Saetograptus leinwardinensis*/*Cucullograptus aversus* Biozone): worldwide.

KOZŁOWSKI (1962) based the systematic classification of his order Crustoidea almost exclusively on the evidence of chemically isolated distal parts of autothecae, especially on the morphology of their apertural apparatuses (Fig. 132), because most other details of the colonies were unknown. The genus *Hormograptus* may be considered to represent a wimanicrustid preserved in sediment and is not chemically isolated from the sediment, thus, providing a better idea on the tubarium shape and construction. However, MIERZEJEWSKI (2000a) regarded the material of *Hormograptus* as completely useless for generic and specific identification of crustoid genera and species. All crustoids have beaded stolons, i.e., stolons provided with fine transverse annulations (KOZŁOWSKI, 1962; see also URBANEK & MIERZEJEWSKI 1984; MIERZEJEWSKI, KULICKI, & URBANEK, 2005) and an apertural apparatus created through dorsal autothecal processes.

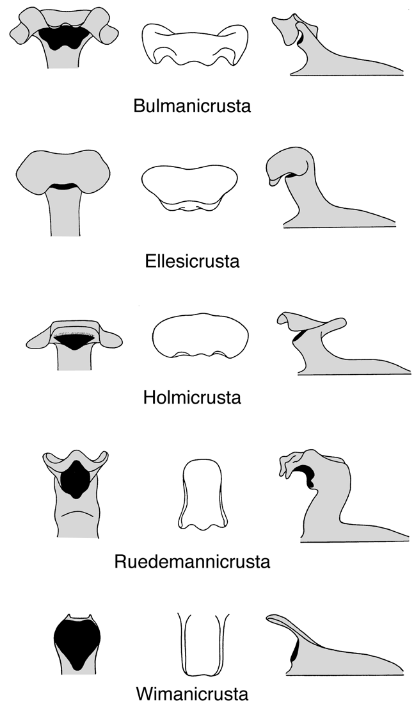

FIG. 132. The apertural modifications of thecae in the Wimanicrustidae in apertural, dorsal, and lateral views (from left to right). The apertural openings are shown in black (Kozłowski, 1962, fig. 13).

MORPHOLOGY

The precise morphology of the wimanicrustid colonies is unknown because most taxa have been described from minute fragments, usually isolated autothecae. KOZŁOWSKI (1971) described a single isolated specimen consisting of the prosicula and an incipient metasicula, which he tentatively assigned to the crustoids (Fig. 133.1–133.3). The prosicula is an ovoid vesicle (dome), proximally attached to the substrate by a

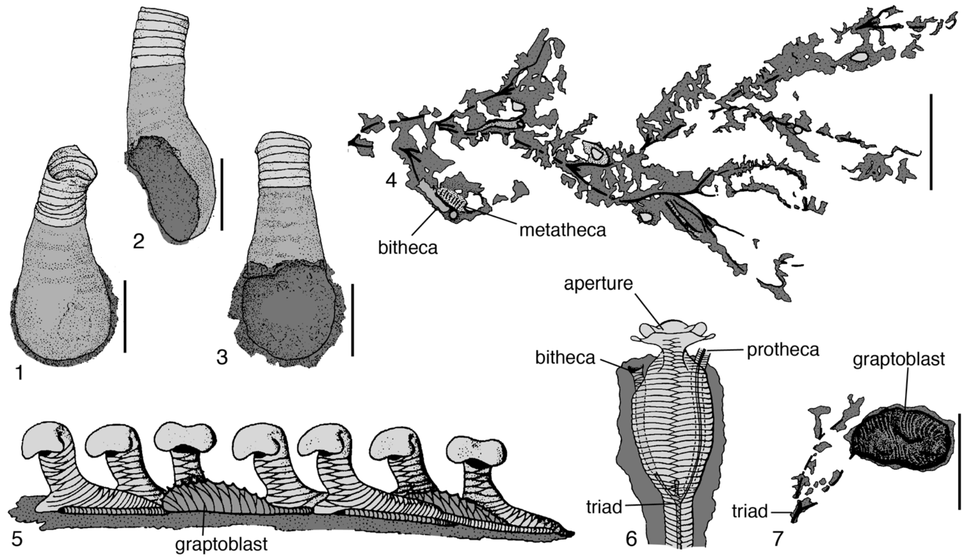

FIG. 133. The tubarium of the Wimanicrustidae. *1–3,* possible wimanicrustid sicula in different views, Vistula River Valley, Poland, scale bars, 0.1 mm (Kozłowski, 1971, fig. 4); *4, Bulmanicrusta*? KOZŁOWSKI, 1962, part of colony showing largely basal membranes, stolon system, and some parts of autothecae, scale bar, 1 mm (Mitchell, Wilson, & St. John, 1993, fig. 3,*6*); *5,* reconstruction of colony in lateral view, not to scale (adapted from Urbanek, 1983, fig. 4); *6,* reconstruction of thecal triad from above, not to scale (Kozłowski, 1962, fig. 1); *7,* ?*Bulmanicrusta* KOZŁOWSKI, 1962, fragment with graptoblast, scale bar, 1 mm (Mitchell, Wilson, & St. John, 1993, fig. 3,*7*).

concave and rough surface, surrounded by a marginal membrane. Distally, the dome produces an elongated necklike part. The metasicula consists of a number of annular fuselli, probably lacking an oblique suture. This sicula in many ways resembles the dome of the Rhabdopleuridae but differs by the presence of the necklike part raised above the substratum. It is unknown whether this specimen can be related to the Wimanicrustidae or represents a rhabdopleurid taxon. The specimen originated from glacial boulder O.544, Vistula River Valley, Poland, from which MIERZEJEWSKI (1986, p. 136) noted the presence of *Dictyonema* sp. and others, including specimens of *Rhabdopleurites primaevus* KOZŁOWSKI, 1967.

Later astogeny proceeded through triad formation to produce larger colonies (Fig. 133). Bifurcation through triads was described by KOZŁOWSKI (1962) and also by MITCHELL, WILSON, and ST. JOHN (1993). The *in situ* colonies of *Bulmanicrusta*? sp. (Fig. 133.4) encrusting the surface of a hardground from the Upper Ordovician of Ohio provide most of the available information concerning the colony shape and growth habits. *Bulmanicrusta*? sp. exhibit runner-type colonies made of radiating and irregularly branching stipes in which successive autothecae grow to alternate sides. The graptoblasts are situated mainly near the periphery of the colony at branch tips (Fig. 133.7). They develop as distal terminations of a stolotheca and appear to be associated with cessation of branch growth.

Wimanicrustid colonies are comprised of autothecae and bithecae, which are produced in triads, as is clearly visible in the preserved stolon system. The autothecae are the dominant element in construction of the wimanicrustid colony and are distinctly larger than the bithecae. The autothecae are made of a proximally more or less inflated portion and an erect distal portion producing a neck and an apertural apparatus. In its simplest form, the apertural apparatus is made of a hoodlike process, straight or curved over the aperture. The bithecae are slender, parallel-sided tubes, with their lower wall flat and

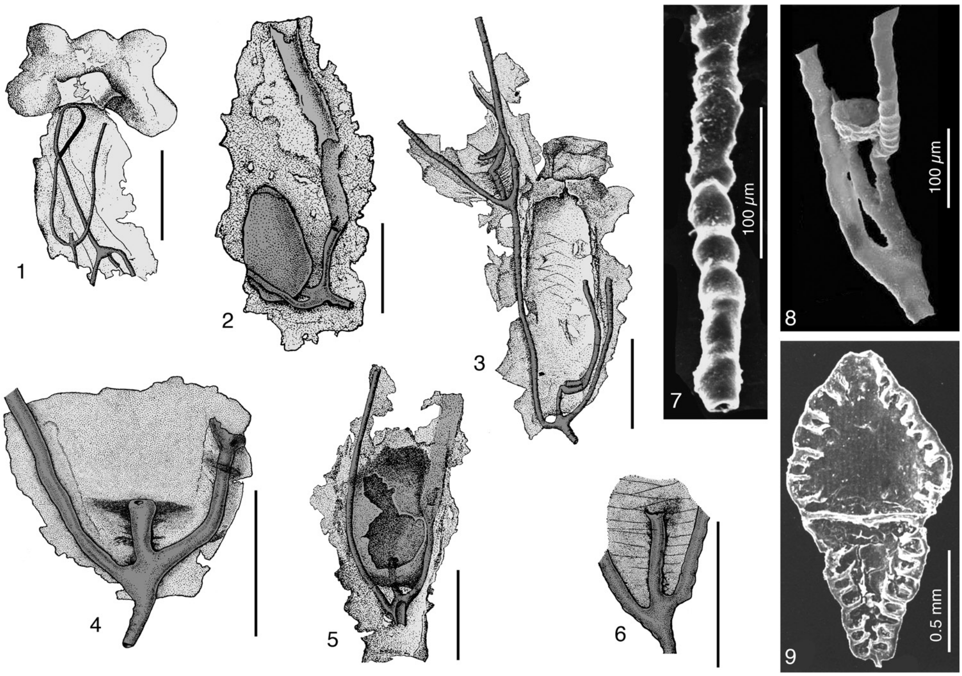

FIG. 134. The stolon system in Wimanicrustidae. *1, Bulmanicrusta modesta* KOZŁOWSKI, 1962, ventral view showing stolon system with triad budding; *2, 5,* triad budding with cyst and bitheca; *3*, *Bulmanicrusta modesta* KOZŁOWSKI, 1962, ventral view showing stolon system with triad budding; *4, 6, Wimanicrusta urbaneki* KOZŁOWSKI, 1962, details of triad budding (*1–6,* Kozłowski, 1962, fig. 2–3); *7–8, Bulmanicrusta latialata* KOZŁOWSKI, 1962, beaded stolon system (Mierzejewski, Kulicki, & Urbanek, 2005, fig. 2H); *9,* Inner cavity of graptoblast with transverse septum and hemiseptae (Mierzejewski, 2000b, fig. 2A). Scale bars, 0.1 mm in *1–6*; *7–9* as marked.

upper more or less convex. The apertures of the bithecae are devoid of any elaborations. (Fig. 133.6). The bithecae typically grow along the autothecae and open close to their apertures, but because of their great variation in length, these apertures might be an autotheca of the same or the next generation. A tendency toward right- and left-hand alternation of bithecae in successive triads can be observed.

The fusellum has distinct zigzag sutures on the dorsal side in both portions of the autothecae (Fig. 133.6), but the basal layer of the autothecae is devoid of any recognizable sutures. Bithecae have an irregular arrangement of their sutures and do not produce a zigzag suture. The differentiation of the fusellum and the ecto- and endocortex in the Wimanicrustidae has not been investigated in detail. Both types can be observed, but the ectocortex is much more common.

URBANEK and MIERZEJEWSKI (1984) used transmission electron microscopy (TEM) investigation to differentiate cortex and fusellum, but this investigation was unable to determine whether cortical tissues developed as bandages because it was based on thin sections and did not provide an impression of surface features.

The stolon system has a typical triad budding system, in which the centrally placed autothecal stolon is distinctly shorter than the other stolons. As a rule, the triads are less regular than those in other dendroids and may be interpreted as two diads produced in rapid succession (MIERZEJEWSKI, KULICKI, & URBANEK, 2005) (Fig. 134). The well-sclerotized stolons, 20 to 35 µm in diameter, display a characteristic annulation not present in other graptolites (Fig. 134.7–134.8). The annulations have proved to be distinct in certain portions and much less pronounced

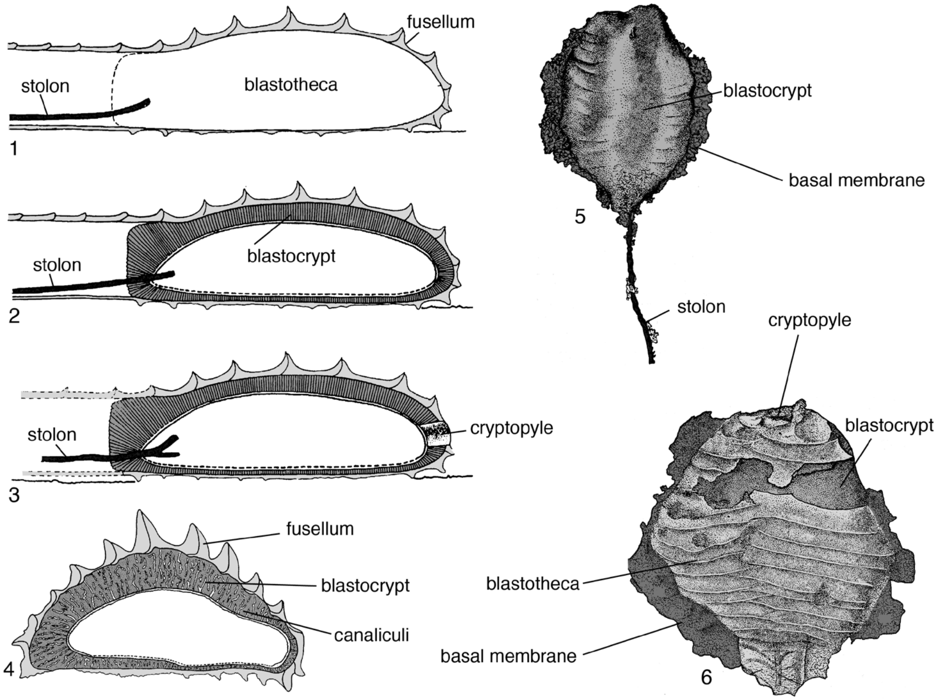

FIG. 135. Construction of the graptoblast. *1–3,* development of graptoblast (adapted from Urbanek, 1983, fig. 2); *4,* cross section of graptoblast showing canaliculi (adapted from Urbanek, Mierzejewski, & Rickards, 1986, fig. 2A); *5,* graptoblast showing basal membrane and chamber, fusellum not preserved (adapted from Kozłowski, 1962, fig. 7); *6,* graptoblast showing basal membrane and part of fusellum with dorsal zigzag suture (adapted from Kozłowski, 1962, fig. 8).

in other parts of the stolon and at places are almost smooth. Transverse sections of the stolon in *Bulmanicrusta latialata* KOZŁOWSKI, 1962 examined with TEM reveal a thick wall (about 6 µm) made of homogenous, electron-dense material and a thin inner layer comprised of loose-layered and granular material (URBANEK & MIERZEJEWSKI, 1984). The lumen of the stolon may contain organic matter in the form of filaments or globular bodies.

Cysts or vesicular bodies, varying greatly in size and shape, have been recognized inside many autothecae (Fig. 134.2, 134.5). In extreme cases, they fill the entire cavity of the autotheca, adhering tightly to its wall, but frequently are much smaller. They possess thick, blackish, and structureless walls. KOZŁOWSKI (1962) suggested they may represent the envelopes of degenerate zooids and are herein interpreted as comparable to the dormant buds of *Rhabdopleura.*

GRAPTOBLASTS

Graptoblasts (Fig. 135) were first described by KOZŁOWSKI (1949) as isolated ovoid bodies bearing traces of fusellar structure, associated with graptolite remains from the late Tremadocian fauna of Wysoczki, Poland. KOZŁOWSKI (1962) was also the first to recognize graptoblasts attached to the distal part of stolons in crustoid colonies, supported by MITCHELL, WILSON, and ST. JOHN (1993). The appendix of graptoblasts was called filum by KOZŁOWSKI (1949), but can be identified as the remnant of the stolon (KOZŁOWSKI, 1962). According to KOZŁOWSKI (1962), an opening, the cryptopyle, was formed secondarily by resorption of the distal graptoblast wall by the encysted individual or individuals (Fig. 135.3).

The graptoblast displays a two-layered construction formed from fusellar tissue outside and electron-dense crassal tissue inside (Fig. 135.1–135.3). The outer, primary layer is called the blastotheca (Fig. 135.1). The inner component corresponds to KOZŁOWSKI's non-transparent blackish layer and was named the blastocrypt (URBANEK & RICKARDS, 1974; URBANEK, MIERZEJEWSKI, & RICKARDS, 1986), It possessed numerous and characteristic, vertically oriented and frequently branching canaliculi (Fig. 135.4). Their diameter typically varies from 0.02 nm to 0.04 nm. Some canaliculi are open to the inner cavity. The stolon may reach deep into the cavity of the graptoblast. The inner surface of the blastocrypt is covered by the inner lining, an essentially homogenous, electron-dense material sometimes with traces of layering. In some graptoblasts, the inner cavity became subdivided by the transverse septum (Fig. 134.9) into an anterior and posterior chamber (i.e., genus *Graptoblastus* KOZŁOWSKI, 1949). MIERZEJEWSKI (2000a) used SEM technique to demonstrate that the transverse septum is two-layered, each layer being the continuation of the inner lining either from the anterior or posterior chamber.

According to URBANEK (1983), graptoblasts may be reinterpreted as closed, resting terminal portions of thecae, housing encysted dormant buds (Fig. 135.1–135.4). Their role in the life cycle of crustoid graptolites may be best compared with hibernaculae of ctenostomate bryozoans. In one of the early Silurian graptoblasts he investigated, MIERZEJEWSKI (2000a) recognized numerous incomplete septae (which he called hemiseptae) produced by folds of the inner lining. These were spread more or less evenly in both chambers (Fig. 134.9). However, on the basis of this finding, one cannot conclude whether hemiseptae are normal structures or rare abnormalities.

Wimanicrusta KOZŁOWSKI, 1962, p. 43 [**W. cristaelingulata;* OD]. Apertural lobe linguiform; neck short or absent; triad budding; other details of colony unknown. *Lower Ordovician–Upper Ordovician:* Estonia, Poland, Sweden (Öland) (glacial erratic boulders).——FIG. 136,*6a–d*. **W. cristaelinguata*, holotype (*a–b*) and fragment (*c–d*) in dorsal and ventral views, scale bars, 0.1 mm (Kozłowski, 1962, fig. 24A–B).

Bulmanicrusta KOZŁOWSKI, 1962, p. 31 [**B. latialata;* OD]. Wimanicrustid with runner-type colony, showing triad budding; large apertural lobes with median and auriculate lateral folds; neck distinct or absent. *Middle Ordovician* (*Darriwilian*)*–Upper Silurian* (*Ludlow*): Baltic Region, ?USA.——FIG. 136,*1a–d*. **B. latialata; 1a–b,* holotype (Kozłowski, 1962, pl. 2A–B); *1c–d,* thecal aperture in apertural (*c*) and adapertural (*d*) views, scale bars, 0.5 mm (Kozłowski, 1962, 15A–B).——FIG. 136,*1e–h. B. latialata scutellifera* KOZŁOWSKI, 1962; *1e–f,* two fragments in dorsal view (Kozłowski, 1962, pl. 4A–B); *1g–h,* holotype, thecal aperture in apertural (*h*) and adapertural (*g*) views, scale bars, 0.5 mm (Kozłowski, 1962, 16A–B).

Ellesicrusta KOZŁOWSKI, 1962, p. 38 [**E. longicollis;* OD]. Apertural lobe with slight lateral folds; long neck; details of colony unknown. *Middle Ordovician–Upper Ordovician:* Estonia (glacial erratic boulders).——FIG. 136,*2a–d*. **E. longicollis,* holotype in various views, scale bars, 0.5 mm (Kozłowski, 1962, fig. 21).

Holmicrusta KOZŁOWSKI, 1962, p. 41 [**H. sombrero;* OD]. Apertual lobe large, flattened; neck long; details of colony unknown. *Lower Ordovician–Middle Ordovician:* Poland (glacial erratic boulders).——FIG. *136,3a–d*. **H. sombrero,* holotype in various views, scale bars, 0.2 mm (Kozłowski, 1962, fig. 23).

Hormograptus ÖPIK, 1930, p. 8, *pro Thallograptus* ÖPIK, 1928, p. 35, *non Thallograptus* RUEDEMANN, 1925b, p. 35 [**Thallograptus sphaericola;* OD]. Runner-type encrusting colony; tubarium details unknown. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): Estonia.——FIG. 137,*1a–b*. **H. sphaericola* (RUEDEMANN), TUG 1317, holotype and enlargement of part, scale bars, 1 mm (new; provided by Ursula Toom).

Lapworthicrusta KOZŁOWSKI, 1962, p. 44 [**L. aenigmatica;* OD]. Apertural lobe small; autothecae slender without interthecal membrane; neck absent; details of colony unknown. *Middle Ordovician* (*Darriwilian*): Poland (glacial erratic boulders).——FIG. 136,*5a–b*. **L. aenigmatica,* holotype, two fragments of a single colony, scale bars, 0.5 mm (Kozłowski, 1962, fig. 26).

Ruedemannicrusta KOZŁOWSKI, 1962, p. 39 [**H. geniculata;* OD]. Apertural lobe distinct with small auriculate lateral folds; neck long, curved, with strong internal ridges; details of colony unknown. *Middle Ordovician–Upper Ordovician:* Poland, Estonia (glacial erratic boulders).——FIG. 136,*4a–c*. **R. geniculata,* holotype, scale bars, 0.1 mm (Kozłowski, 1962, fig. 22).

UNRECOGNIZABLE WIMANICRUSTID TAXA

The following taxa represent unidentifiable preservational forms, too imperfectly known for taxonomic description and placement. The genera *Graptoblastus* KOZŁOWSKI, 1949 and *Graptoblastoides* KOZŁOWSKI, 1949 are now identified as the resting stages of the Wimanicrustidae and not identified as separate graptolite genera (see KOZŁOWSKI,

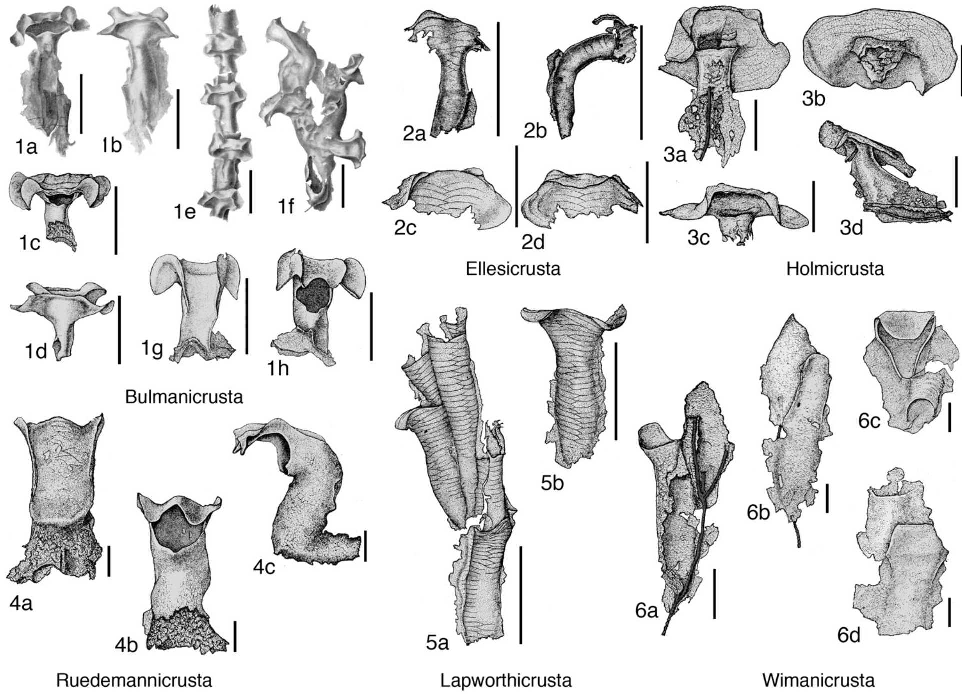

FIG. 136. Wimanicrustidae (p. 219).

1962; URBANEK, 1983) but are listed herein in the interest of being complete. A connection of the known graptoblasts to certain genera of the Wimanicrustidae has not been established; and, thus, these cannot be referred to any genus in particular.

Graptoblastus KOZŁOWSKI, 1949, p. 210 [**G. planus;* OD]. Ovoid to vesicular body with flat base, convex upper wall; dorsally distinct zigzag suture usually visible; formed from electron-dense material having numerous canaliculi; septum separates internal chamber into two partitions; indication of stolon on one end, cryptopyle on other end. [The taxon represents a resting stage or graptoblast in a parataxonomic context and not a valid graptolite genus (see KOZŁOWSKI, 1962, p. 18).]——FIG. 137,*6a–c*. **G. planus,* holotype in dorsal and ventral view, ZPAL G.I/1-290, scale bars, 0.1 mm (Kozłowski, 1949, pl. 37,*3*).

Graptoblastoides KOZŁOWSKI, 1949, p. 216 [**G. nowaki;* OD]. Ovoid to vesicular body with flat base, convex upper wall; dorsally, distinct zigzag suture visible; formed from electron-dense material having numerous canaliculi; single internal chamber; indication of stolon on one end, cryptopyle on other end. [The taxon represents a resting stage or graptoblast in a parataxonomic context and not a valid graptolite genus (see KOZŁOWSKI, 1962, p. 18)].——FIG. 137,*5a–b*. **G. nowaki,* holotype in dorsal and ventral view, ZPAL G.I/1-290, scale bars, 0.1 mm (Kozłowski, 1949, pl. 39,*1*).

Maenniligraptus MIERZEJEWSKI, 1985, p. 196 [**M. ursulae;* OD]. Encrusting taxon with tubular thecae, devoid of erect parts and any apertural apparatus; stolons with diad and triad budding; stolon with annular and helical thickenings; details of colony unknown. [The taxon is very poor and specifically indeterminate. MIERZEJEWSKI (1982) identified this material as a camaroid and suggested that similar organic material from pre-Devonian samples with the inner rings and spiral thickenings may have been mistaken for tracheid-like tubes characteristic of land plants.] ?*Ordovician:* Poland (glacial erratic boulder).——FIG. 137,*2a–b*. **M. ursulae,* fragments of holotype, scale bars, 0.1 mm (Mierzejewski, 1985, pl. 7,*8*).

Urbanekicrusta MIERZEJEWSKI, 1985, p. 194 [**U. reversa;* OD]. Dorsal apertural process long with wide lobe; neck long; bithecae unknown (absent?); details of colony unknown. [The taxon is unrecognizable due to poor preservation and fragmentation, but clearly represents pterobranch remains, possibly with triad budding.] *Silurian* (*Wenlock*): Poland, Sweden (glacial erratic boulders).——FIG. 137,*3a–b*. **U. reversa,* holotype, scale bar for *3a,* 1 mm, *3b,* scale bar, 0.1 mm (Mierzejewski, 1985, pl. 5).

Xenocyathus EISENACK, 1982, p. 630, *nom. dub.* [**X. stolonifer;* M]. [This taxon is represented as stolon fragments with triad budding and may be identified as a wimanicrustid (MIERZEJEWSKI, 1984).

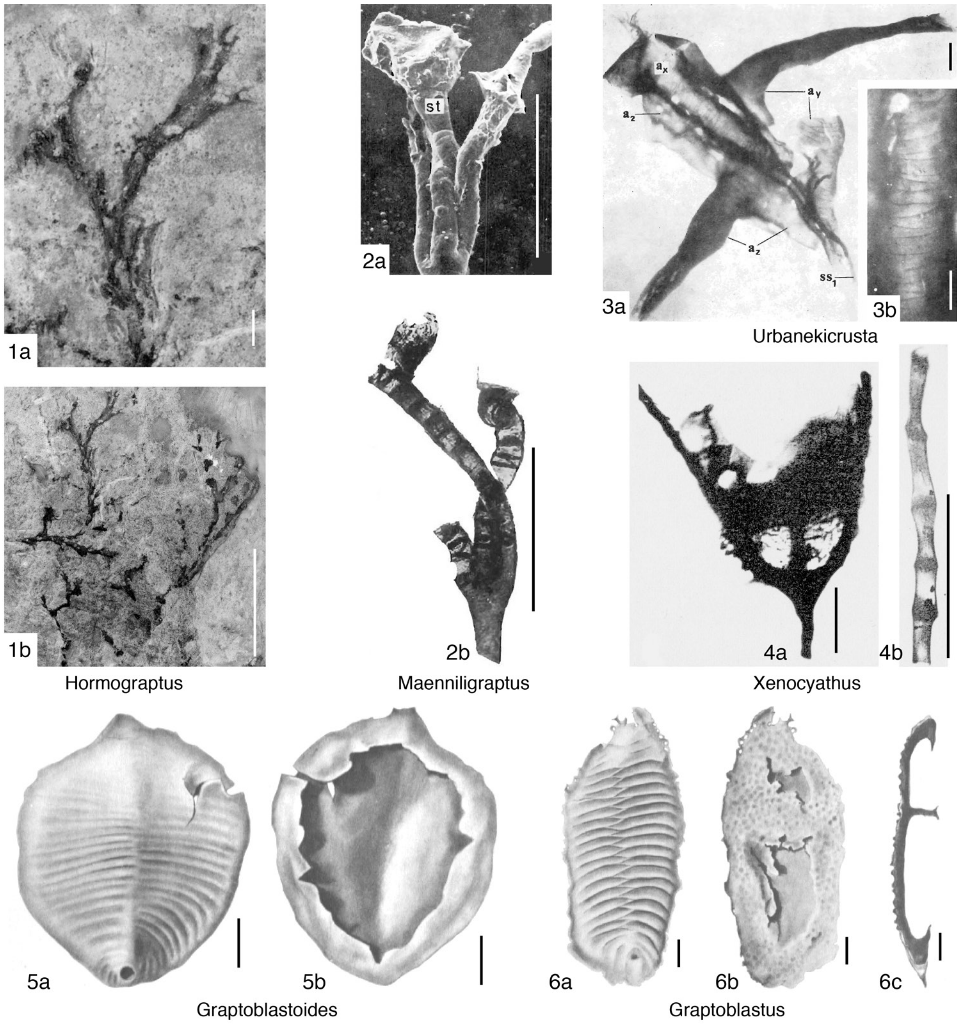

FIG. 137. Wimanicrustidae, uncertain genera (219–221).

The material cannot be related to any identifiable wimanicrustid genus.] *Ordovician* (*Sandbian*)–*Silurian* (*Wenlock*): Estonia, Finland, *Ordovician;* Sweden (Gotland) (glacial erratic boulders), *Silurian* (*Wenlock*).——FIG. 137,*4a–b*. *X. *stolonifer,* Upper Ordovician, Estonia; *4a,* holotype, scale bar, 0.1 mm; *4b,* beaded stolon, scale bar, 0.1 mm (Eisenack, 1982, fig. 2,*4*).

Family CYSTICAMARIDAE Bulman, 1955

[Cysticamaridae BULMAN, 1955, p. 42; incl. Bithecocamaridae BULMAN, 1955, p. 42]

Encrusting, sigmophyllic Graptolithina producing autothecae as characteristic camara with erect neck or collum; stolon usually embedded in extracamaral tissue on surface of camara; bithecae may be present in some. *Lower Ordovician* (*Tremadocian*)–*Upper Ordovician* (*Sandbian*): Finland, Poland (glacial erratic boulders), Russia, Sweden.

The Cysticamaridae represent a small group of benthic, encrusting graptolites. Most of the material originated from the famous locality Wysoczki in the Holy Cross Mountains of Poland, where they are known mainly from glacial boulders (KOZŁOWSKI, 1949), but rare additional specimens were

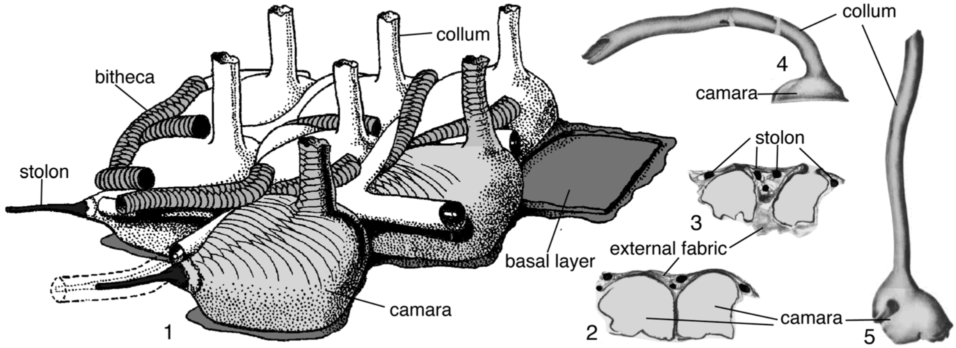

FIG. 138. Morphology of the Cysticamaridae. *1, Bithecocamara* KOZŁOWSKI, 1949, reconstruction (adapted from Bulman, 1955, fig. 26); *2–3,* Sections through the thecae of *Cysticamara accollis* KOZŁOWSKI, 1949 showing the presence of a stolon system (adapted from Kozłowski, 1949, pl. 29; *4–5,* two isolated cysticamarid fragments with long collum (adapted from Kozłowski, 1949, pl. 31).

collected from a few localities in Scandinavia (e.g., SKEVINGTON, 1963a; MIERZEJEWSKI, 2003). Very little is known about their colony construction and evolutionary relationships because the material is based on highly fragmented specimens.

MORPHOLOGY

The Cysticamaridae possess characteristically inflated autothecal tubes, camara with an erect tube, and a collum or neck (Fig. 138). The basal layer is smooth and constructional details are not visible. The collum is fairly slender as compared to the inflated camara, but both have conspicuous zigzag sutures. A considerable elongation of the collum has been recognized in a couple of fragments (Fig. 138.4–138.5). The development of the thecal apertures is uncertain in most taxa due to preservational aspects but may be quite simple. Commonly, the apertures indicate fragmentation and loss of the actual apertural margins through the presence of irregular rims.

Cross sections of *Cysticamara accollis* KOZLOWSKI, 1949 (Fig. 138.2–138.3) and *Bithecocamara gladiator* KOZLOWSKI, 1949 indicate the presence of a stolon system. The stolon system is encased in extrathecal fabric. It is positioned above the camara and is not visible externally. Thus, it has been verified only from thin sections of a few members. There is no information on the development of the stolon system as a diad or triad development as isolated stolon fragments have not been described. The description of bithecae in *Bithecocamara* suggests a thecal differentiation, but this is not known from other taxa, as these are typically based on small colony fragments that are commonly isolated metathecae.

KOZŁOWSKI (1949) differentiated bithecae in *Bithecocamara gladiator* as slender tubes without erect growth from the camarate autothecae with their characteristic colla. The development and differentiation of auto- and bithecae in most Cysticamaridae is uncertain, considering that the development of the stolon system has not been described. BULMAN (1955) erected the Bithecocamaridae based on the presence of bithecae in *Bithecocamara gladiator*. A thecal differentiation is unknown in other taxa of the family, but it may be argued that the preservation and fragmentation is too incomplete to recognize these details.

URBANEK and MIERZEJEWSKI (1991) described the ultrastructure of *Tubicamara coriacea* KOZŁOWSKI, 1949. TEM studies reveal fusellum and endo- and ectocortex to be present. The endocortex is thought to be underdeveloped and may be missing in

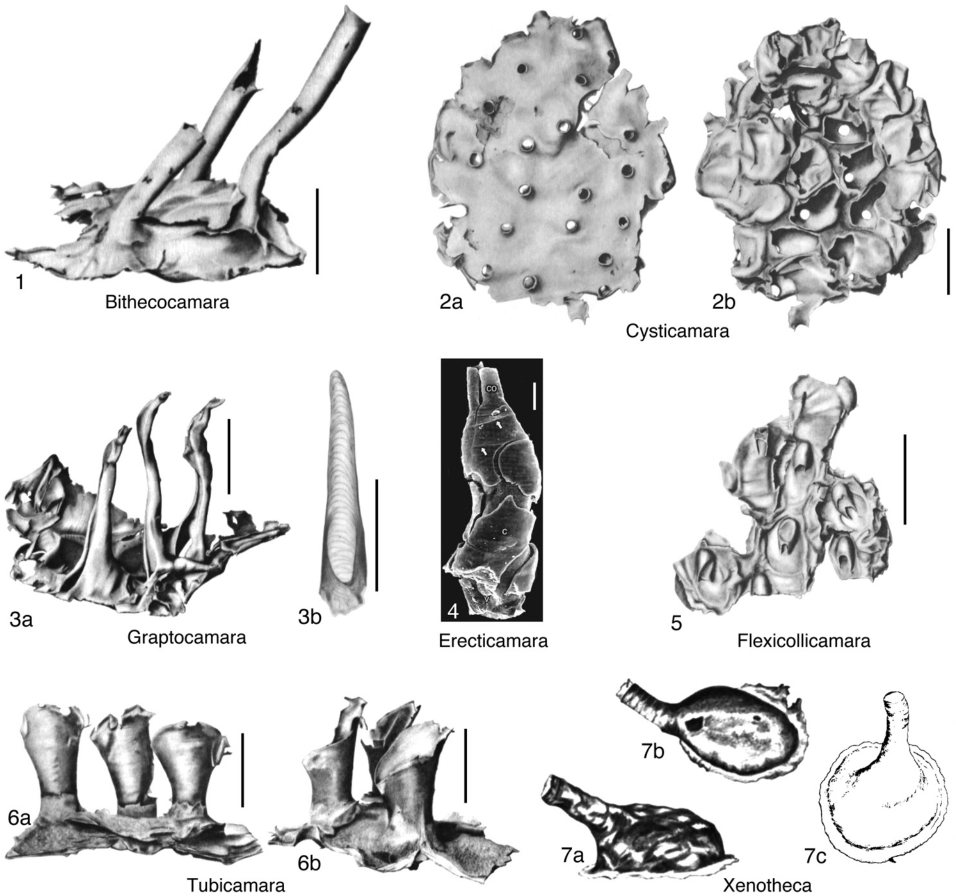

FIG. 139. Cysticamaridae (p. 223–224).

many cysticamarids. MIERZEJEWSKI (2000b) described the wall construction of *Xenotheca* in some detail and described the verrucose fabric as a previously unrecognized material on the outside of the taxon, very likely occluding the thecal apertures (MIERZEJEWSKI, 2003).

Bithecocamara Kozłowski, 1949, p. 176 [*B. gladiator; OD]. Thigmophilic tubarium with densely arranged camarae; autothecae with well-developed collum, but apertural modifications unknown; indications of stolon system inside extracamaral fabric above camarae; differentiated into two types of thecae, of which smaller one, which lacks collum, is termed bitheca. Lower Ordovician (Tremadocian): Poland.——Fig. 139.1. **B. gladiator,* holotype, ZPAL GI/1-290, scale bar, 0.5 mm (Kozłowski, 1949, pl. 24,1a).

Cysticamara KOZŁOWSKI, 1949, p. 183 [**C. accollis;* OD] [=*Syringotaenia* Obut, 1953, p. 54 (type, *S. bystrovi,* M), syn. by BULMAN, 1970, p. 50]. Thigmophilic tubarium with densely arranged camarae; autothecae with slightly elevated, thickened rim, but without collum; indications of stolon system inside extracamaral fabric above camarae. [VISKOVA & IVANTSOV, 1999, p. 25 referred *Syringothenia* (misspelling) to the bryozoan family Alcyonidiidae.] *Lower Ordovician* (*Tremadocian*)*–Middle Ordovician* (*Darriwilian*): Poland, Sweden, Russia.——FIG. 139,*2a–b*. **C. accollis,* holotype in dorsal (*a*) and ventral (*b*) views, ZPAL GI/1-290, scale bar, 0.5 mm (Kozłowski, 1949, pl. 28,*1–1a*).

Erecticamara MIERZEJEWSKI, 2000c, p. 241 [**E. maennili;* OD]. Tubarium unknown; slender, bottle-shaped or subconidal autothecae more or less differentiated into erect, broad proximal part (camara), provided with narrow distal part (collum); aperture devoid of any kind of apertural processes; bottom of camara convex with small camaral processes or in form of small, flat sole; fuselli irregular, no zigzag suture formed; indications of stolon system present.

Middle Ordovician (*Darriwilian*): Poland (glacial erratic boulder).——FIG. 139,*4*. **E. maennili,* holotype, ZPAL G/XXIV/5, isolated theca, scale bar, 0.1 mm (Mierzejewski, 2000c, fig. 1e).

Flexicollicamara KOZŁOWSKI, 1949, p. 182 [**F. bryozoaeformis;* OD]. Thigmophilic tubarium with densely arranged camarae; collum strongly bent back ventrally and fused to upper wall of camara; stolon system unknown. [The taxon is known from two fragments of which only one was ever illustrated.] *Lower Ordovician* (*Tremadocian*): Poland (glacial erratic boulder).——FIG. *139,5*. **F. bryozoaeformis,* holotype, ZPAL GI/1-290, scale bar, 0.5 mm (Kozłowski, 1949, pl. 28,*4*).

Graptocamara KOZŁOWSKI, 1949, p. 187 [**G. hyperlinguata;* OD] [=*Camarotubus* MIERZEJEWSKI, 2001, p. 371 (type, *C. graptocamaraeformis,* OD), syn. herein]. Thigmophilic tubarium with densely arranged camarae; autothecae with elongated rutellate apertural process, lacking collum; stolon system poorly known. *Lower Ordovician* (*Tremadocian*)*–Middle Ordovician* (*Darriwilian*): Poland, Sweden.——FIG. 139,*3a–b*. **G. hyperlinguata; 3a*, holotype, ZPAL GI/1-290, scale bar, 0.5 mm (Kozłowski, 1949, pl. 30,*6*). *3b*, isolated apertural process showing fuselli, scale bar, 0.5 mm (Kozłowski, 1949, pl. 30,*5*).

Tubicamara KOZŁOWSKI, 1949, p. 188 [**T. coriacea;* OD]. Thigmophilic tubarium with densely arranged camarae; funnel-shaped collum with ventral apertural process; abundant cortical tissue; stolon system unknown. *Lower Ordovician* (*Tremadocian*): Poland.——FIG. 139,*6a–b*. **T. coriacea,* holotype in two views, ZPAL GI/1-290, scale bars, 0.5 mm (Kozłowski, 1949, pl. 30,*1a–b*).

Xenotheca EISENACK, 1938b, p. 239, *non Xenotheca* ARBER & GOODE, 1915, p. 96 (Devonian plant) [**X. klinostoma;* OD] [?=*Xenokalymma* EISENACK, 1968, p. 306 (type, *X. trematophora,* OD), syn. herein]. Tubarium shape unknown; tubarium known from isolated metathecae formed as robust camarae with semi-erect collum; indications of stolon system present. *Middle Ordovician* (*Darriwilian*): Finland, Poland (glacial erratic boulder).——FIG. 139,*7a–c*. **X. klinostoma; 7a,* holotype (Eisenack, 1938b, fig. 21); *7b,* paratype (Eisenack, 1938*b*, fig. 22); *7c*, neotype, GPIT Tr. 5, Nr. 17 (Eisenack, 1970, fig. 1). Scale bar, 1 mm for all.

Family DITHECODENDRIDAE Obut, 1964

[Dithecodendridae OBUT, 1964, p. 306 (misquoted as OBUT, 1957); incl. Siberiograptidae OBUT, 1964, p. 306 (misquoted as OBUT, 1957); Bulmanidendridae OBUT, 1974, p. 12]

Graptolithina with erect-growing tubarium, with multiple dichotomous branchings; thin-walled metathecae isolated, tubular, or slightly widening towards aperture; thecae arranged alternately or irregularly on slender to robust stem. *Cambrian* (*Miaolingian–Furongian*): Australia, Canada, USA, Spain, Poland (glacial erratic boulders), Sweden, Russia (Siberia).

The Dithecodendridae OBUT, 1964 is a group of benthic graptolites with an erect growth of the colony and isolated, trumpet-like to parallel-sided, long metathecae. All taxa are formed from an organic material, but only in rare cases has the presence of the fusellum been demonstrated (e.g., *Tarnagraptus;* MALETZ, STEINER, & FATKA, 2005) (Fig. 140). They possess isolated metathecae with thin fusellum and a robust stem (Fig. 140.1), probably thickened with considerable amounts of cortical tissues. Nothing is known about the style of budding, and the presence of a stolon system has not been demonstrated. SDZUY (1974) described and illustrated holdfast structures (termed Basal-Scheibe) in a number of taxa, including *Tarnagraptus palma* SDZUY, 1974 and *Tarnagraptus thomasi* SDZUY, 1974, but most remains are fragmented stipes without of an attachment. Similarities to the Mastigograptidae include the stolon systems with triad budding and isolated, thin-walled thecae (BATES & URBANEK, 2002).

OBUT (1960, p. 149) erected the order Dithecoidea based on the assumed diad budding in the included genera. Most of the genera are known from fragments, and details of their development are not available. OBUT (1974) added the order Archaeodendrida OBUT, 1974 for the genera *Archaeodendrum* OBUT, 1974 (a possible hydroid; RICKARDS & DURMAN, 2006, p. 58) and *Archaeolafoea* CHAPMAN, 1919 (included in the Rhabdopleuridae; see p. 210). BULMAN (1970) listed most of the genera included here in the Dithecodendridae under the category, "taxonomic position uncertain."

JOHNSTON, JOHNSTON, and POWELL (2009) described larger, complexly branched dithecodendrids from the *Bolaspidella* Zone (Drumian to lower Guzhangian; PENG, BABCOCK, & COOPER, 2012) of the Chancellor Basin, British Columbia, Canada, and documented fusellar construction in the material (Fig. 140.5–140.6). The speci-

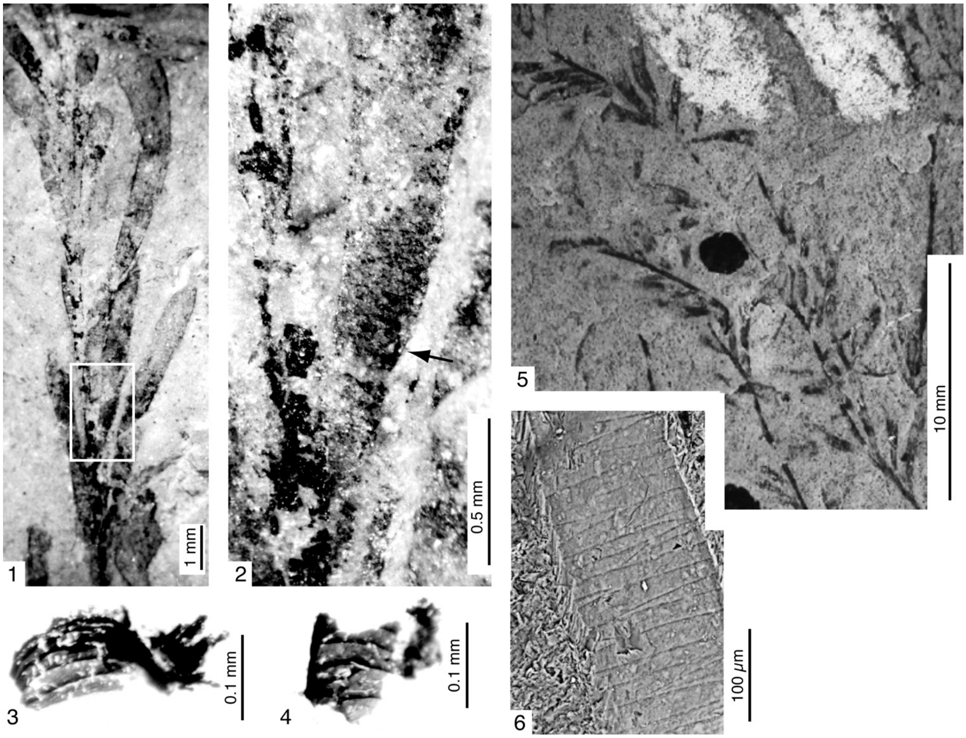

FIG. 140. Tubarium details of the Dithecodendridae. *1–2, Tarnagraptus cristatus* SDZUY, 1974, SMF 30021; *1*, part of holotype showing thin-walled metathecae and indications of robust stem; *2,* magnified part of (*1*) showing indications of fuselllar construction (*arrow*); *3–4,* chemically isolated fragments of *Tarnagraptus palma* SDZUY, 1974, from SMF 30002, showing fuselli (*1–4,* Maletz, Steiner, & Fatka, 2005, fig. 6); *5–6*, Dithecodendridae indet., Duchesnay unit, British Columbia, Canada, part of colony (*5*) and detail showing imprints of fuselli (*6*) (Johnston, Johnston, & Powell, 2009, fig. 7).

mens represent some of the oldest and best-preserved Middle Cambrian graptolites presently known.

Dithecodendrum Obut, 1964, p. 306 [**D. sibiricum;* OD]. Slender, elongate colony with tubular thecae; thecae isolated distally, possibly arranged biserially. *Cambrian* (*Miaolingian, Drumian*): Russia (Siberia). [The genus is based on a single flattened stipe fragment].——FIG. 141,*2*. **D. sibiricum,* IGiG 960, holotype, scale bar, 1 mm (Rickards & Durman, 2006, fig. 58c).

Bulmanidendrum OBUT, 1974, p. 12[**B. magnificum;* OD]. Stipe(s)? flexuous, robust, with long, slightly widening, alternately arranged thecae, proximally adnate and isolate distally. [A fusellar structure is not recognized (RICKARDS & DURMAN, 2006, p. 65), therefore the graptolithic nature of this genus is uncertain.] *Middle Cambrian* (*Miaolingian, Drumian*): Russia (Siberia).——FIG. 141,*1*. **B. magnificum*, holotype, IGiG 592/5, scale bar, 5 mm (Rickards & Durman, 2006, fig. 55).

Karasidendrum SENNIKOV, 1998, p. 17 [**K. aspidograptoides;* OD]. Slender tubarium with regularly and dichotomously branching stipes; details of thecae not available. *Cambrian* (*Miaolingian, Drumian*): Russia (Siberia). [The illustrations are poor and unclear. No fuselli are visible to ascertain the graptolitic nature of the taxon].——FIG. 141,*6*. **K. aspidograptoides*, holotype, scale bar, 5 mm (Sennikov, 1998, pl. 1,*3*).

Ovetograptus SDZUY, 1974, p. 131 [**O. gracilis;* OD]. Dithecodendrids with bushy growth; metathecae parallel sided and widely spaced; stolon system unknown. *Cambrian, Miaolingian* (*Wuliuan–Drumian*): Spain.——FIG. 141,*7*. **O. gracilis,* holotype, SMF 30028, scale bar, 5 mm (new).

Protodendrum SENNIKOV, 1998, p. 16 [**P. paniculiformis;* OD]. Possible dithecodendrid with slender stem and crown of densely spaced tubular thecae; details of tubarium unknown. *Cambrian* (*Miaolingian, Drumian*): Russia (Siberia). [The taxon is based on poor material and could be a dithecoid. Assignment was based only on age].——FIG. 141,*5a–b*. **P. paniculiformis,* holotype, scale bars, 5 mm (Sennikov, 1998, pl. 1,*1–2*).

Siberiodendrum OBUT, 1964, p. 306 [**S. robustum;* OD]. Robust dithecodendrid fragment with densely

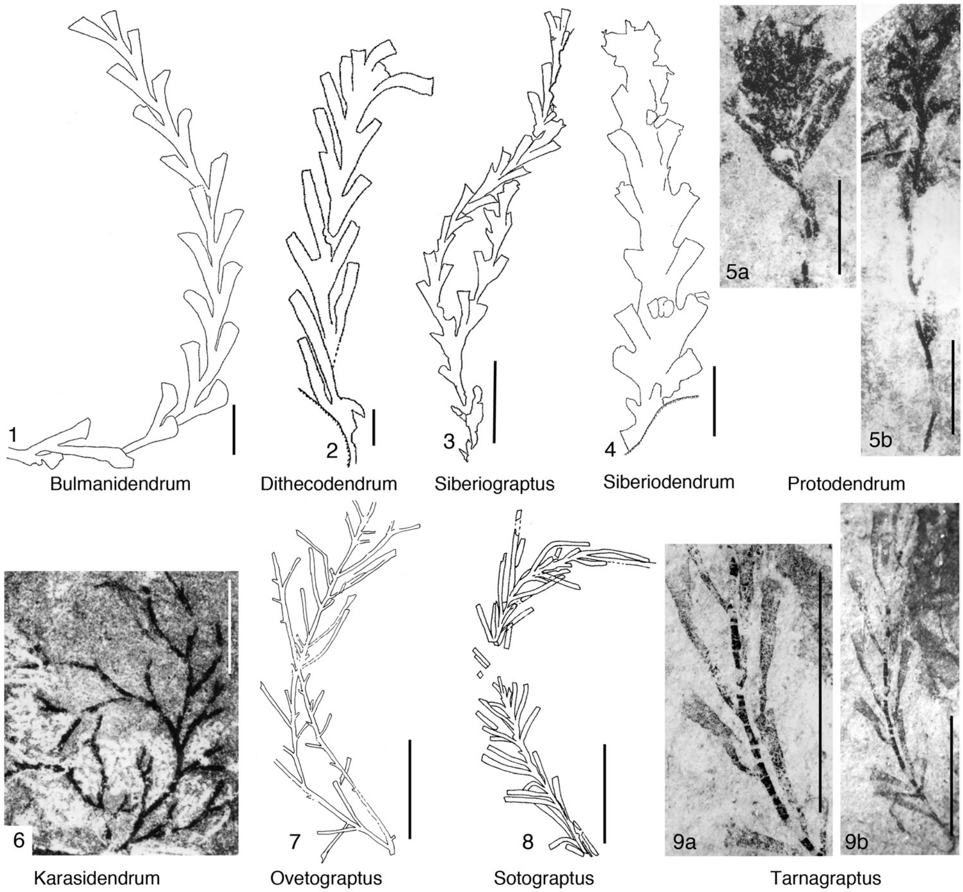

FIG. 141. Dithecodendridae (p. 225–226).

spaced, wide, probably parallel-sided thecae; thecae probably arranged biserially; tubarium shape unknown. *middle Cambrian–upper Cambrian:* Russia (Siberia). [The taxon is known from a single fragment. Its precise locality and age are unknown. RICKARDS & DURMAN (2006, p. 71) referred the taxon to the hydroids.]——FIG. 141,*4*. **S. robustum,* IGiG 960, holotype, scale bar, 5 mm (Rickards & Durman, 2006, fig. 62).

Siberiograptus OBUT, 1964, p. 306 (there cited as OBUT, 1963) [**S. kotujensis;* OD] [=*Palaeodiphasia* SONG, RUTHENSTEINER, LYU, LIU, WANG & HAN, 2021, p. 2 (type, *S. simplex* LIN, 1985), syn. herein]. Tubarium slender, with large, distally isolate thecae; thecae arranged biserially. [The identity of *Palaeodiphasia simplex* as a hydroid relies on a reinterpretation of the poorly preserved type material and remains equivocal.] *upper Cambrian:* Russia (Siberia).——FIG. 141,*3*. **S. kotujensis,* IGiG 960, holotype, scale bar, 5 mm (Rickards & Durman, 2006, fig. 39).

Sotograptus SDZUY, 1974, p. 130 [*S. flexilis;* OD]. Dithecodendrids with bushy growth; metathecae barely widening aperturally; stipes surrounded by initial parts of thecae; stolon system unknown. *Cambrian, Miaolingian* (*Wuliuan–Drumian*): Spain.——FIG. 141,*8*. **S. flexilis,* holotype, SMF 30026, scale bar, 5 mm (Sdzuy, 1974, fig. 17).

Tarnagraptus SDZUY 1974, p. 124 [**T. palma;* OD]. Dithecodendrids with bushy growth; thin-walled metathecae distinctly widening; stolon system unknown. *Cambrian, Miaolingian* (*Wuliuan–Drumian, Paradoxides paradoxissimus* Biozone): Spain.——FIG. 141,*9a–b*. **T. palma,* holotype, SMF 30023, specimen and detail showing preservation of robust stipes and thin-walled metathecae, scale bars, 5 mm (new).

Family CYCLOGRAPTIDAE Bulman, 1938

[Cyclograptidae BULMAN, 1938, p. 22] [=Tubidendridae KOZŁOWSKI, 1949, p. 160; *non* Tubidendridae NUTTING, 1905, p. 940 (a family of Hydrozoa), emend. SCHUCHERT, 2003]

Encrusting Graptolithina with tubular thecae; erect-growing short stipes may form from thecorhiza; thecal differentiation may be

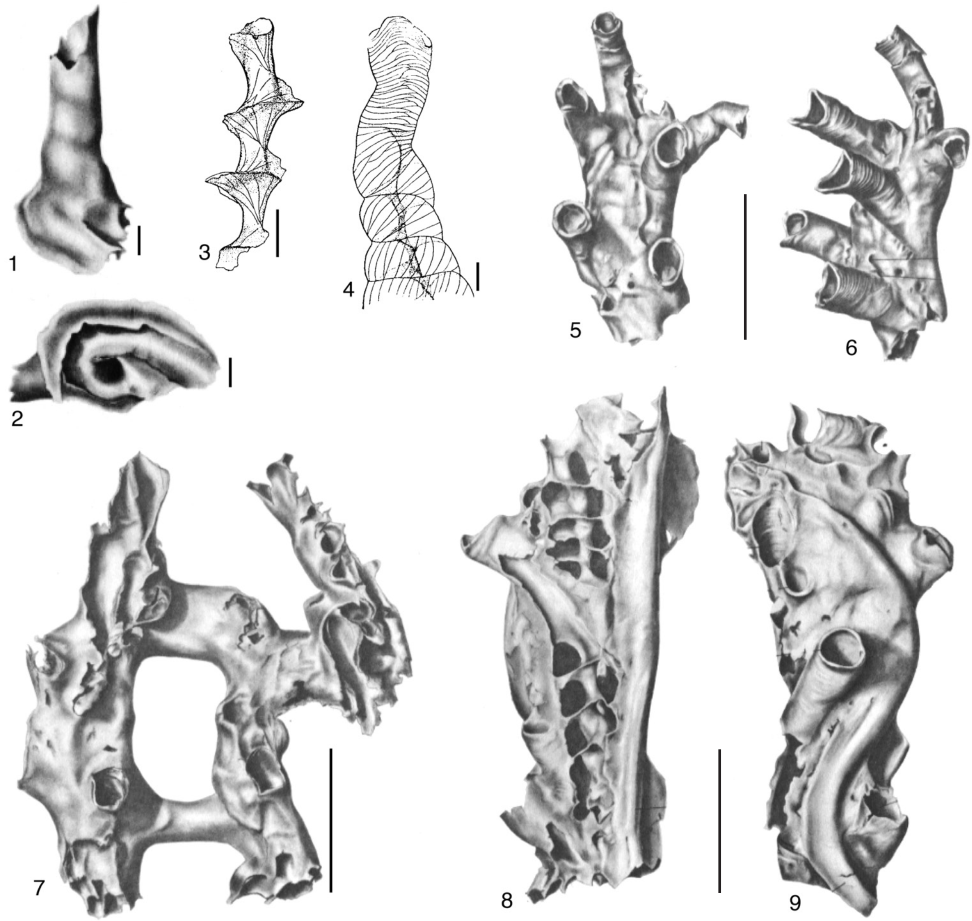

FIG. 142. Morphology of the Cyclograptidae. *1–2*, *Dendrotubus wimani* KOZŁOWSKI, 1949, details of coiled median part of thecae; *3–9*, *Tubidendrum bulmani* KOZŁOWSKI, 1949; *3*, internal helicoidal structure; *4*, coiled median part of theca; *5–6*, fragment showing thecal orientation; *7*, bridges connecting stipes; *8–9*, fragment with coiled thecae and external tubes; *1–4,* scale bars, 0.1 mm; *5–9,* scale bars, 1 mm (*1–9,* Kozłowski, 1949, see fig. 50a–b and pl. 19–20).

present, but rarely expressed through differences in size; stolon system might be quite variable; branching apparently by diads with irregular succession at variable spacing. *Lower Ordovician* (*Tremadocian*)–*Upper Ordovician* (*Sandbian*): Finland, Poland (glacial erratic boulders), Russia, Sweden.

The Cyclograptidae include mostly taxa formerly referred to the order Tuboidea by KOZŁOWSKI (1949). BULMAN (1938) erected the family for benthic taxa with a basal disk and numerous erect stipes, but BULMAN (1950b) considered the family Cyclograptidae as a synonym of Idiotubidae and did not even mention Cyclograptidae in the earlier Treatise volumes (BULMAN, 1955, 1970). MIERZEJEWSKI (1978, p. 562) discussed the validity of the taxon and questioned the monophyly of the family Cyclograptidae, but found it impossible to provide a better solution. The details of the tubarium formation are typically known from small fragments chemically isolated from limestones and cherts. It is quite difficult to relate these fragments with material from shales and to understand their construction.

MORPHOLOGY

The colony shape of most Cyclograptidae is not well established and BULMAN (1970) considered encrusting to flabellate and bushy forms to be represented. The thecae grew upward from the thecorhiza as individuals or in groups, forming complex stems.

The genera *Cyclograptus*, *Galeograptus,* and *Discograptus* are known from larger and more complete colonies. They have a rounded thecorhiza with erect growing groups of thecae and may be closely related. Erect stipes on the thecorhiza may have one or two branching divisions, and the stipes remained relatively short. *Galeograptus* has conothecae and bithecae concentrated in the thecorhiza, but these are not present in the erect stipes (BULMAN & RICKARDS, 1966).

KOZŁOWSKI (1949) illustrated possible bithecae in *Calycotubus*, but these appear to be based on the diameter of the openings on the thecorhiza only. The so-called bithecae may actually be initial parts of aborted or broken thecal tubes. Nothing is known on the presence of a stolon system, budding style, and other tubarium details. Even the origins of individual autothecae and thecal connections are unknown.

Thecae may produce anastomosis and thecal bridges to connect the stipes laterally (Fig. 142.7) through which tubular thecae grow from one stipe to an adjacent one in *Tubidendrum bulmani* KOZŁOWSKI, 1949 and possibly in others. The apertures of the autothecae are commonly oriented to one side of the stipe, interpreted as the ventral side, showing a possible serial arrangement (Fig. 142.5–142.6).

According to BULMAN (1938), the tubaria of the Cyclograptidae are differentiated into autothecae and numerous bithecae with a highly irregular distribution. The identification of the bithecae is made solely on the size of the thecal tubes and the simple straight apertures, whereas the autothecae typically bear short rutella and are larger. A spiral development of the median parts of the thecae has been described for *Tubidendrum bulmani* and *Dendrotubus wimani* KOZŁOWSKI, 1949 (Fig. 142.1–142.4; Fig. 142.8–142.9). This development may include a variable number of coils, but is not present in all taxa referred to the Cyclograptidae.

KOZŁOWSKI (1949) described a thecal dimorphism in *Tubidendrum,* in which special thecae, called microthecae, possess a narrow terminal portion with an oblique aperture facing the opposite side of the stipe from that of normal autothecae. Dimorphic thecae are also present in *Galeograptus* in which umbellate thecae form an umbrella-shaped structure shielding the aperture of the preceding theca (BULMAN & RICKARDS, 1966; BULMAN, 1970). The shields of these umbellate thecae fill the cavity formed by the ring of stipes in the proximal region of the specimens with a vesicular mass of tissue. Umbellate thecae are only known from thin sections of *Galeograptus wennersteni* WIMAN, 1901.

KOZŁOWSKI (1949) described the diad development of the stolon system of *Tubidendrum* from serial sections of the holotype. A diad budding system is known from *Kozlowskitubus* (Fig. 143,*7a*), in which the initial thecae grew in a circle around the erect sicula, and all thecae bud from the left side of the stolon. MIERZEJEWSKI (1978) described similar construction for *Dendrotubus wimani.* BULMAN and RICKARDS (1966) discussed a diad stolon system in *Reticulograptus* WIMAN, 1901 from serial sections, but the taxon is now referred to the Acanthograptidae. The stolon system is poorly known in most Cyclograptidae and is documented largely from serial sections. Thus, important information on its construction is not available.

Cyclograptus SPENCER, 1883, p. 365 [**C. rotadentatus* SPENCER, 1884, p. 592; M] [=*Rodonograptus* POČTA, 1894, p. 204 (type, *R. astericus,* M), syn. by BULMAN, 1970, p. 48]. Tubarium discoidial, erect portions of autothecae grouped into 20 to 30 peripheral sheaves bifurcating at mid-length; thecae tubular, elongated; thecal differentiation and stolon system unknown. *Silurian* (*Wenlock*): Canada, Czech Republic.——FIG. 143,*4a*. **C. rotadentatus,* lectotype, ROM 21623, scale bar, 1 mm (Bulman, 1970, fig. 29,*3*).——FIG. 143,*4b*. *C. astericus*, ?lectotype, scale bar, 1 mm (Počta, 1894, pl. 8,*11*).

Calycotubus KOZŁOWSKI, 1949, p. 156 [**C. infundibulatus;* OD]. Encrusting taxon with strongly widening, robust autothecae, bearing regular zigzag sutures and forming irregular associations; simple, straight apertures or slight development of rutellum on one side; fuselli robust and regular, invariably developed as half rings with two zigzag sutures. *Lower Ordovician* (*Tremadocian*): Poland (glacial

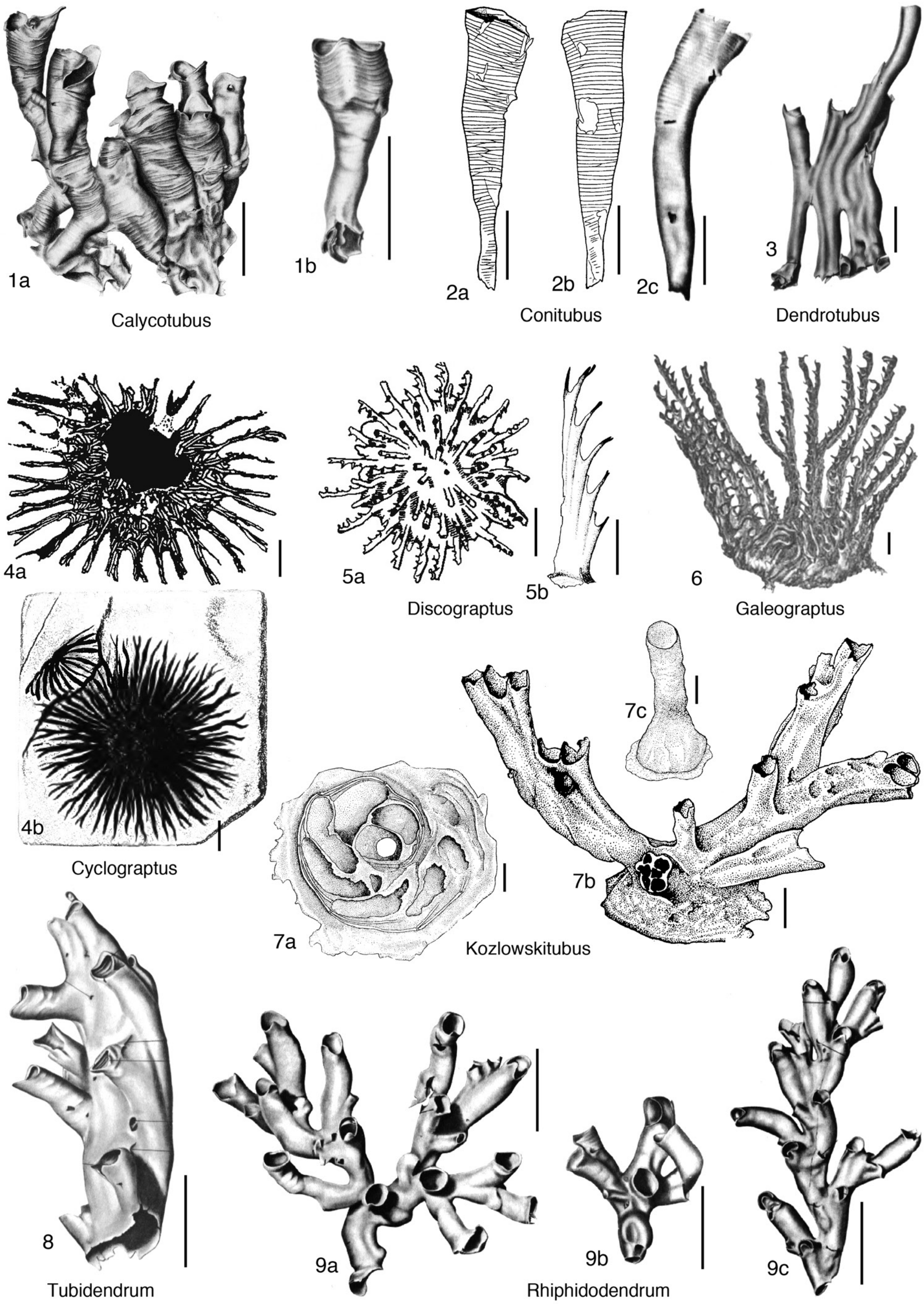

FIG. 143. Cyclograptidae (p. 228–231).

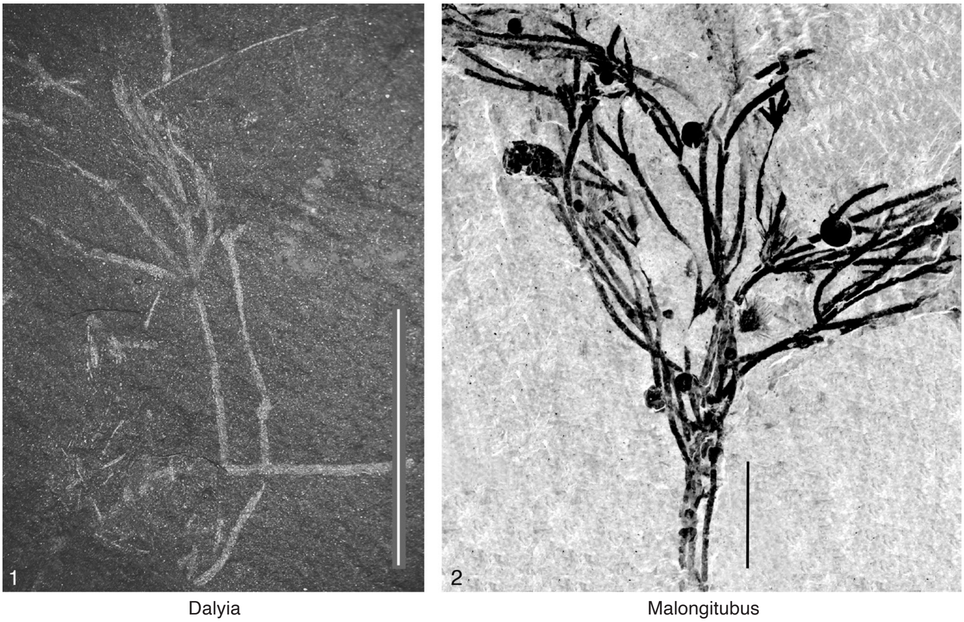

FIG. 144. Graptolithina? *incertae sedis* (p. 231).

erratic boulder).——FIG. 143,*1a–b*. *C. *infundibulatus,* holotype, ZPAL GI/1-290, scale bars, 0.5 mm (Kozłowski, 1949, pl. 18,*1–2*).

Conitubus KOZŁOWSKI, 1949, p. 159 [**C. siculoides;* OD]. Gradually widening autotheca with irregular sutures; colony shape unknown. [The taxon consists of isolated autothecae of uncertain origin, thus, may be useless. It could be identical to *Sphenoecium* CHAPMAN & THOMAS, 1936]. *Lower Ordovician* (*Tremadocian*): Poland.——FIG. 143,*2a–c*. **C. siculoides;* holotype in different views, ZPAL GI/1-290, scale bars, 0.5 mm (Kozłowski, 1949, fig. 46).

Dendrotubus KOZŁOWSKI, 1949, p. 153 [**D. wimani;* OD]. Encrusting tubarium with tubular thecae; erect portions of autothecae forming irregularly distributed groups; thecae typically serially arranged; proximal portions of thecae commonly coiled into helical spiral. *Lower Ordovician* (*Tremadocian*): Poland.——FIG. 143,*3*. **D. wimani,* holotype, ZPAL GI/1-290, scale bar, 0.5 mm (Kozłowski, 1949, pl. 16,*8*).

Discograptus WIMAN, 1901, p. 191 [**D. schmidti;* OD]. Tubarium discoidal, erect portions of autothecae in more or less radially arranged groups on upper surface of thecorhiza; thecae tubular, elongated; bottle-shaped sicula with first thecae growing in circular pattern around it; thecal differentiation and stolon system unknown; thecae with prominent dorsal and ventral rutella; presence of conothecae uncertain. *Upper Ordovician* (*Katian*): Sweden (Gotland).——FIG. 143,*5a–b*. **D. schmidti; 5a,* lectotype, PMU G 786, scale bar, 1 mm (Bulman, 1970, fig. 29.*2*); *5b*, stipe fragment, scale bar, 0.5 mm (Bulman & Rickards, 1966, fig. 46B).

Galeograptus WIMAN, 1901, p. 189 [**G. wennersteni;* OD]. Tubarium encrusting, discoidal, erect portions of autothecae in more or less radially arranged groups on upper surface of thecorhiza; bithecae and conothecae confined to thecorhiza; thecae tubular, with extended dorsal and ventral rutella. *Upper Ordovician* (*Katian*): Sweden. [Lectotype preserved as series of thin sections, also indicating the presence of umbrella-shaped apertural modifications; BULMAN and RICKARDS, 1966, p. 61].——FIG. *143,6*. **G. wennersteni,* holotype, PMU G 93, specimen preserved as serial sections, scale bar, 1 mm (Wiman, 1901, pl. 8,*8*).

Kozlowskitubus MIERZEJEWSKI, 1978, p. 571 [**Dendrotubus erraticus* KOZŁOWSKI, 1963, p. 104; OD]. Encrusting and erect-growing taxa with simple, tube-shaped thecae without apertural elaborations; sicula bottle-shaped, erect, in distal part with spiral line; proximal thecae spirally coiled around sicula; irregularly developed branches comprise thecal bundles arising from thecorhiza and thecae formed on branches. *Upper Ordovician* (*Katian*)–*Silurian* (*Ludlow*): Poland (glacial erratic boulder).——FIG. 143,*7a–c*. **K. erraticus* (KOZŁOWSKI), scale bars, 0.1 mm; *7a–7b,* holotype in different views (Kozłowski, 1963, fig. 4,*9*); *7c,* sicula (Kozłowski, 1963, fig. 3).

Rhiphidodendrum KOZŁOWSKI, 1949, p. 133 [**R. samsonowiczi;* OD]. Multiramous, erect colony with irregular branching from three first order stipes; autothecae and bithecae tubular; stolon system unknown. *Lower Ordovician* (*Tremadocian*): Poland (glacial erratic boulder).——FIG. 143,*9a–c*. **R. samsonowiczi,* ZPAL GI/1-290; *9a,* holotype; *9b,* proximal end; *9c,* stipe fragment; scale bars, 0.5 mm (Kozłowski, 1949, pl. 10).

Tubidendrum KOZŁOWSKI, 1949, p. 160 [**T. bulmani;* M]. Colony erect, conical or flabellate; irregularly developed stipes connected by bridges through single thecal tubes; thecae concentrated on one side of stipe but not serially arranged; two types of thecae, larger (?autothecae) and smaller ones (?bithecae), formed possibly through diad budding; tubular thecae with ventral apertural lip (rutellum); autothecae helically coiled in median part. *Lower Ordovician* (*Tremadocian*): Poland.——FIG. 143,*8*. **T. bulmani,* holotype, ZPAL GI/1-290, scale bar, 1 mm (Kozłowski, 1949, pl. 21,*1*).

GRAPTOLITHINA? *INCERTAE SEDIS*

A few apparently colonial genera are here tentatively identified as Graptolithina? *incertae sedis* following MALETZ and STEINER (2015), even though the final recognition of fusellar construction for their complex fossils is lacking and the material is poorly preserved. They differ considerably in the construction of their tubaria from the remaining taxa of the Graptolithina, as thecal apertures are recognized only at the distal end of the stipes and not at the branching segments. It is impossible to refer the material to the recognized families included in the Graptolithina.

Dalyia WALCOTT, 1919, p. 237 [**D. racemata;* OD]. Colonial organism with long, slender, almost parallel-walled thecal tubes(?) and prominent internal thread; axes both erect and creeping, with whorls of thecal tubes radiating at specific branching points; circular attachment structures at base of branching points. *Cambrian* (*Miaolingian, Wuliuan, Ptychagnostus praecurrens* Biozone): Canada.——FIG. 144,*1*. **D. racemata,* lectotype, USNM 354117, Burgess Shale, loc. 35K, British Columbia, Canada, scale bar, 10 mm (Maletz & Steiner, 2015, fig. 16).

Malongitubus HU, 2005, p. 185 [**M. kuangshanensis;* OD] [=?*Cambrohydra* HU, 2005, p. 188 (type, *C. ercaia,* OD), syn. herein]. Colonial organism(?) formed from parallel-sided tubes(?), branching at irregular distances to form whorls of radiating tubes of next order; number of tubes forming at branching division variable from two to at least six; distal tubes may be open-ended; length of the longest tubular branch measures at least 6 cm. *Cambrian* (*Series 2, Stage 3, upper Eoredlichia–Wutingaspis* Zone): China.——FIG. 144,*2*. **M. kuangshanensis,* holotype, NIGP 165032, Kuangshan, Yunnan Province, China, scale bar, 10 mm (Hu, 2005, cover).

ORDER DENDROIDEA

JÖRG MALETZ

Order DENDROIDEA Nicholson, 1872

[Dendroidea NICHOLSON, 1872a, p. 101; *ex* section Dendroidea NICHOLSON, 1872a, p. 101] [=Cladophora HOPKINSON in HOPKINSON & LAPWORTH, 1875, p. 634; *non* Inocaulida BOUČEK, 1957, p. 145, herein (dasycladacean algae); =Mastigograptida OBUT & SOBOLEVSKAYA, 1967, p. 58, herein]

Benthic graptoloids with erect, bushy, cone- or fan-shaped tubarium; thecae typically 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, 2019d), in which the encrusting part may be reduced in size, but the included species do not have triad budding. The genera of the dendroid families are typically defined from tubarium fragments and are based on general constructional features. However, the final shape of their tubaria remains unknown. The differentiation into various genera and families has 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, 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 afterward (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 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. 145.3), and Bates and Urbanek (2002) illustrated 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. 145.1) 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. 145.4). 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. 145.3–145.7). 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 has a triad budding system (Wiman, 1895, 1896; Bulman, 1927b; Kozłowski, 1949) in which each autotheca is associated with a bitheca (Fig. 146.3a–b, Fig. 146.4). 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. 146.1b), 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* has 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. 146.2), 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. 146.1), 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 have a preferred orientation. The Dendrograptidae (Fig. 146.3) 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 have a ventral apertural lip or rutellum. The rutellum may be modified into a complex apertural construction. The thecal development is largely identical to the development in the bithecate Anisograptidae (Fig. 146.4) 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

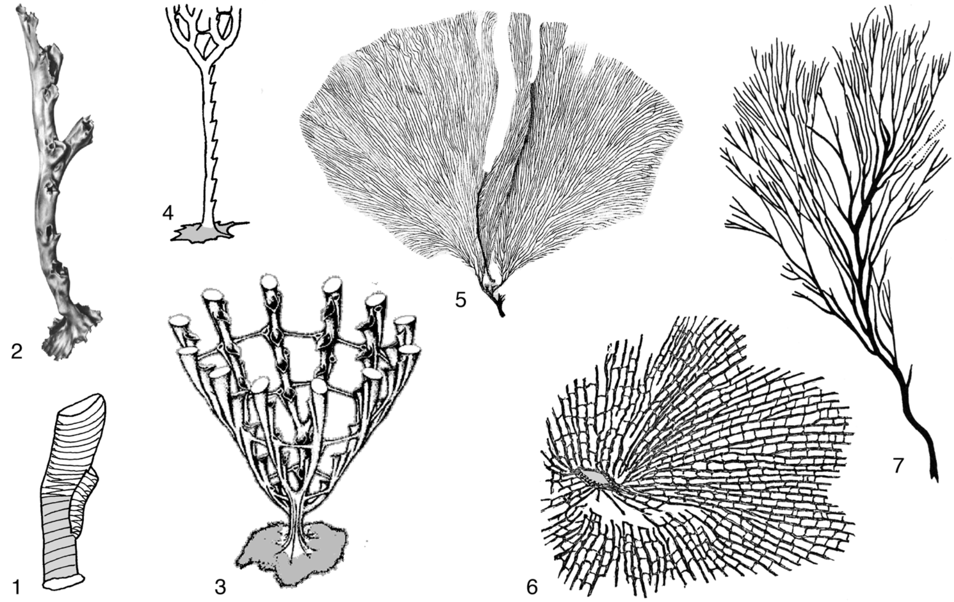

FIG. 145. Astogeny and tubarium shape of the Dendroidea. *1–2, Dendrograptus communis* KOZŁOWSKI, 1949; *1,* sicula with bud of th1 (adapted from Kozłowski, 1949, fig. 1); *2,* stem with part of attachment disk and one distal branching (Kozłowski, 1949, pl. 6,*5*); *3, Dictyonema cavernosum* WIMAN, 1896, 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 gray (Hall, 1865, fig. 10); *7, Dendrograptus fruticosus* HALL, 1865, bushy colony (Bulman, 1970, fig. 16,*1a*). Illustrations not to scale.

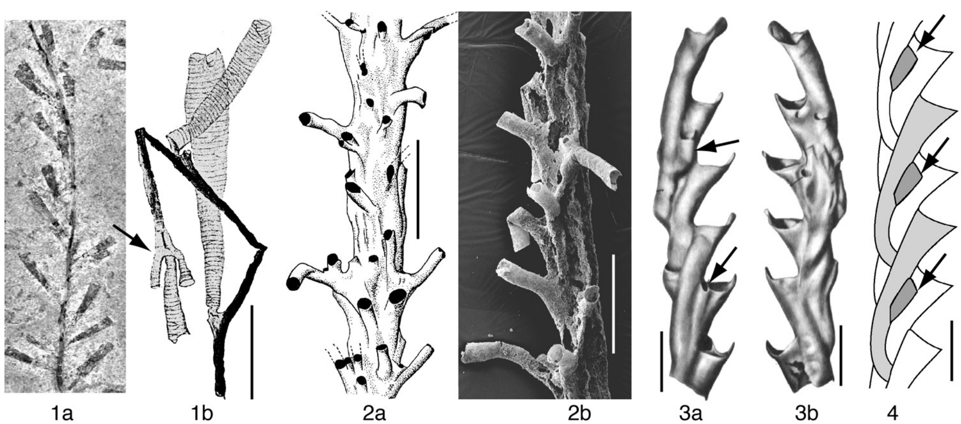

FIG. 146. Thecal style in the Dendroidea. *1a,* ?*Mastigograptus* sp., Marjum Formation, Utah, Miaolingian, Cambrian (LoDuca & Kramer, 2014, fig. 2,*2*); *1b, Mastigograptus* sp., *arrow* points to triad budding, glacial boulder, Ostseekalk, Upper Ordovician, Germany (Andres, 1977, fig. 13); *2a, Acanthograptus musciformis* (WIMAN, 1901), Upper Ordovician, Gotland, Sweden (Bulman & Rickards, 1966, fig. 20); *2b, Acanthograptus divergens* SKEVINGTON, 1963a, 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 bithecae (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.

were already present in the Miaolingian (Cambrian). Many taxa were only identified by their general tubarium shape because they were poor and fragmentary in preservation. MALETZ (2019a) indicated the presence of the Dithecodendridae during the 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 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* Biozone*–Novakia sulcata sulcata* Biozone): 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 (1897) (e.g., the planktic graptolites), and 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) interpreted the dendroids as a paraphyletic group 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. 147) 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, 1963a) from the Middle Ordovician of Öland (Sweden) 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 herein to keep them with the benthic Dendrograptidae, as they do not possess the defining characters of the planktic Anisograptidae.

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 (see Fig. 145). 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. 145.1). The prosicula can be differentiated through the spiral line, and the metasicula has fusellar half rings and regularly placed oblique sutures on the dorsal and ventral sides in *Dendrograptus communis* KOZŁOWSKI, 1949. However, in *Graptolodendrum,* full fusellar rings are present and the sutures are irregularly placed. A very irregular development of fusellar rings also occurs 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

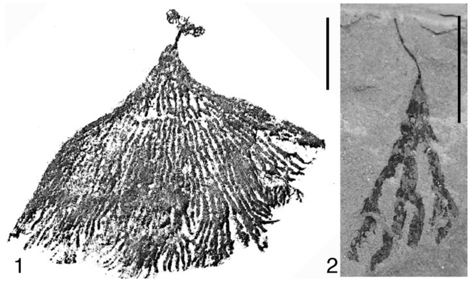

FIG. 147. Planktic Dendrograptidae. *1, Calyxdendrum ghodsiae* (RICKARDS, HAMEDI, & WRIGHT, 1994), holotype, Dapingian, Iran (Rickards, Hamedi, & Wright, 1994, fig. 2); *2, Calyxdendrum titanus* (KRAFT, 1990) note the long nema, Dapingian, *Tetragraptus abbreviatus* Biozone, Czech Republic, scale bars, 5 mm (Kraft & Kraft, 2007, fig. 1).

(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, 1982a). 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, 1982a; COOPER & others, 1998). A second way of connecting stipes is the growth of thecal tubes as bridges, common in the Callograptidae (identified as Acanthograptidae in MALETZ, 2019c). 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

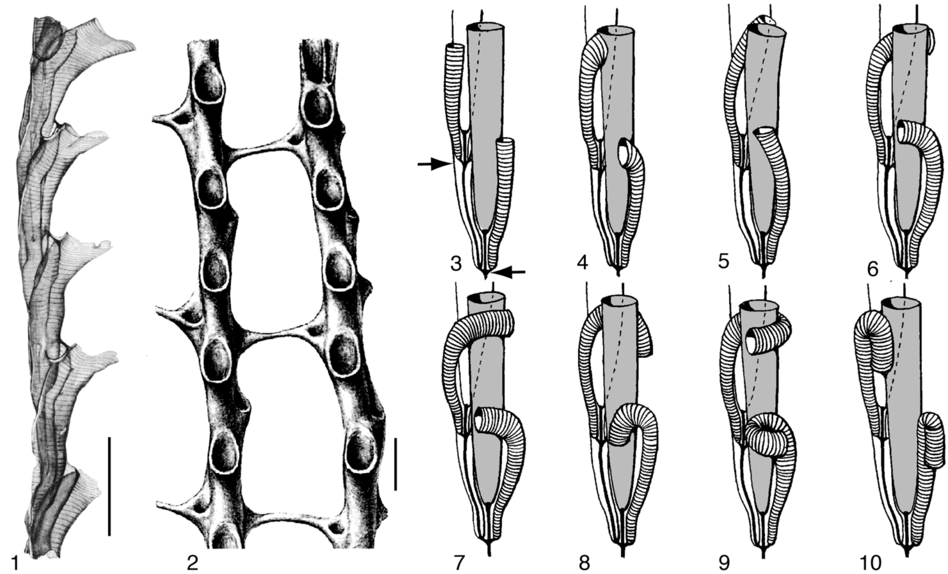

FIG. 148. The stipe and thecal development in the Dendrograptidae. *1,* ?*Dictyonema* aff. *estlandicum* BULMAN, 1933, GSM 71879, stipe fragment showing thecal style and fusellar construction, Katian, Laggan Burn, Girvan, UK, scale bar, 1 mm (Bulman, 1945, pl. 1,*1*); *2, Rhabdinopora flabelliformis* (EICHWALD, 1840), stipe fragment with dissepiments, scale bar, 1 mm (Bulman, 1933, pl. 1,*6*); *3–10,* reconstructions to show bithecal growth, bithecae shown with parallel lines, not representing fusellar construction; *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).

considerable variation in the development of the bithecae (Fig. 148.3–148.10); but for most taxa, the precise development of the bithecae is uncertain.

THECAL DEVELOPMENT

Thecal development is unknown in many Dendrograptidae, but well-preserved fragments have been found during the last hundred years. BULMAN (1933a) 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 typically open at the aperture of the previous autotheca (Fig. 146). The autothecae widen distinctly toward the aperture and are commonly 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. 148). Little is known about the patterns of distribution of certain styles of bithecae, but the early planktic Anisograptidae, derived from the Dendrograptidae, possess fairly simple, straight bithecae (Fig. 146.4).

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, 1982a), 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), syn. herein; =*Ophiograptus* POULSEN, 1937, p. 24 (type, *O. inexpectans,* OD), syn. by 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. 149,*1a.* **D. hallianus* (PROUT), CMC IP83197, Potsdam Sandstone, Afton, Minnesota, USA, scale bar, 5 mm (Bulman, 1970, fig. 16.1b).——FIG. 149,*1b. D. inexpectans* (POULSEN, 1937), holotype, scale bar, 1 mm (Poulsen, 1937, fig. 11).——FIG. 149,*1c. D. keepingii* (LAPWORTH, 1881), holotype, Llandovery, Aberystwyth, Wales, UK, scale bar, 5 mm (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. 149,*2a–b.* **A. furciferus* (RUEDEMANN); *2a,* NYSM 6838, small specimen with attachment disk, Bellefonte, Pennsylvania, USA, scale bar, 1 mm (Ruedemann, 1916, fig. 7); *2b,* holotype, fragment, Deep Kill, New York, USA, scale bar, 5 mm (Ruedemann, 1904, fig. 28).——FIG. 149,*2c. A.* aff. *furciferus* (RUEDEMANN), NIGP 134654, Dayangcha, Jilin Province, northeastern China, specimen showing colony shape, scale bar, 5 mm (Zhang & Erdtmann, 2004b, 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 ?four curved principal stipes; lateral branches close set, irregularly produced, bifurcating repeatedly. *Cambrian, Furongian* (*Paibian*)*–Lower Devonian* (*Lochkovian, Uncinatograptus uniformis* Biozone): UK, Argentina, Czech Republic, China, Tasmania.——FIG. 149,*4a–c.* **A. implicatus* (HOPKINSON IN HOPKINSON & LAPWORTH); *4a,* SM A5325, lectotype, Whitesand Bay, St. David's, Wales, UK, scale bar, 5 mm (selected by BULMAN, 1934, p. 71) (Hopkinson in Hopkinson & Lapworth, 1875, pl. 34,*1*); *4b,* SM A5326, Shelve, Shropshire, UK, scale bar, 5 mm (Bulman, 1970, fig. 16,*5*); *4c,* SM A5319, stipe fragment possibly belonging to the species, Shelve, Shropshire, UK, scale bar, 1 mm (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. *Middle Ordovician* (*Dapingian, Tetragraptus abbreviatus* Biozone)*–Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): Poland (glacial boulder), Czech Republic, Iran.——FIG. 149,*3a–d.* **C. graptoloides*, glacial erratic boulder, Poland; *3a,* prosicula and early part of metasicula, scale bar, 0.1 mm; *3b,* holotype, proximal end in reverse view, scale bar, 0.5 mm; *3c,* stipe fragment showing triad budding, scale bar, 0.5 mm; *3d,* stipe fragment with several branchings, scale bar, 0.5 mm (Kozłowski, 1960, fig. 1, 3, 10, and 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. 149,*5a.* **C. dichotomous* (POČTA), paratype, scale bar, 5 mm (Bouček, 1957, fig. 16a).——FIG. 149,*5b–c. C. pilosus* BOUČEK, 1957, fragments showing dissepiments and ventral apertural spines, scale bars, 5 mm, 1 mm, respectively (Bouček, 1957, fig. 16c–d).

Graptolodendrum KOZŁOWSKI, 1966b, 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. 149,*8a–d.* **G. mutabile; 8a,* holotype, scale bar, 1 mm (Kozłowski, 1966b, fig. 1.*1*); *8b–c*, sicula with first theca and first triad, $th2^1$ covered behind $th1^1$ in *5b,* scale bars, 0.5 mm (Kozłowski, 1966b, fig. 13a–b); *8d,* prosicula and initial part of metasicula. scale bar, 0.5 mm (Kozłowski, 1966b, fig. 10).

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. 149,*6a–b.* **L. elegans; 6a,* holotype, scale bar, 10 mm (Bulman, 1970, fig. 16.7); *6b,* detail showing spined thecal apertures, scale bar, 5 mm (Ruedemann, 1947, pl. 16,*5*).

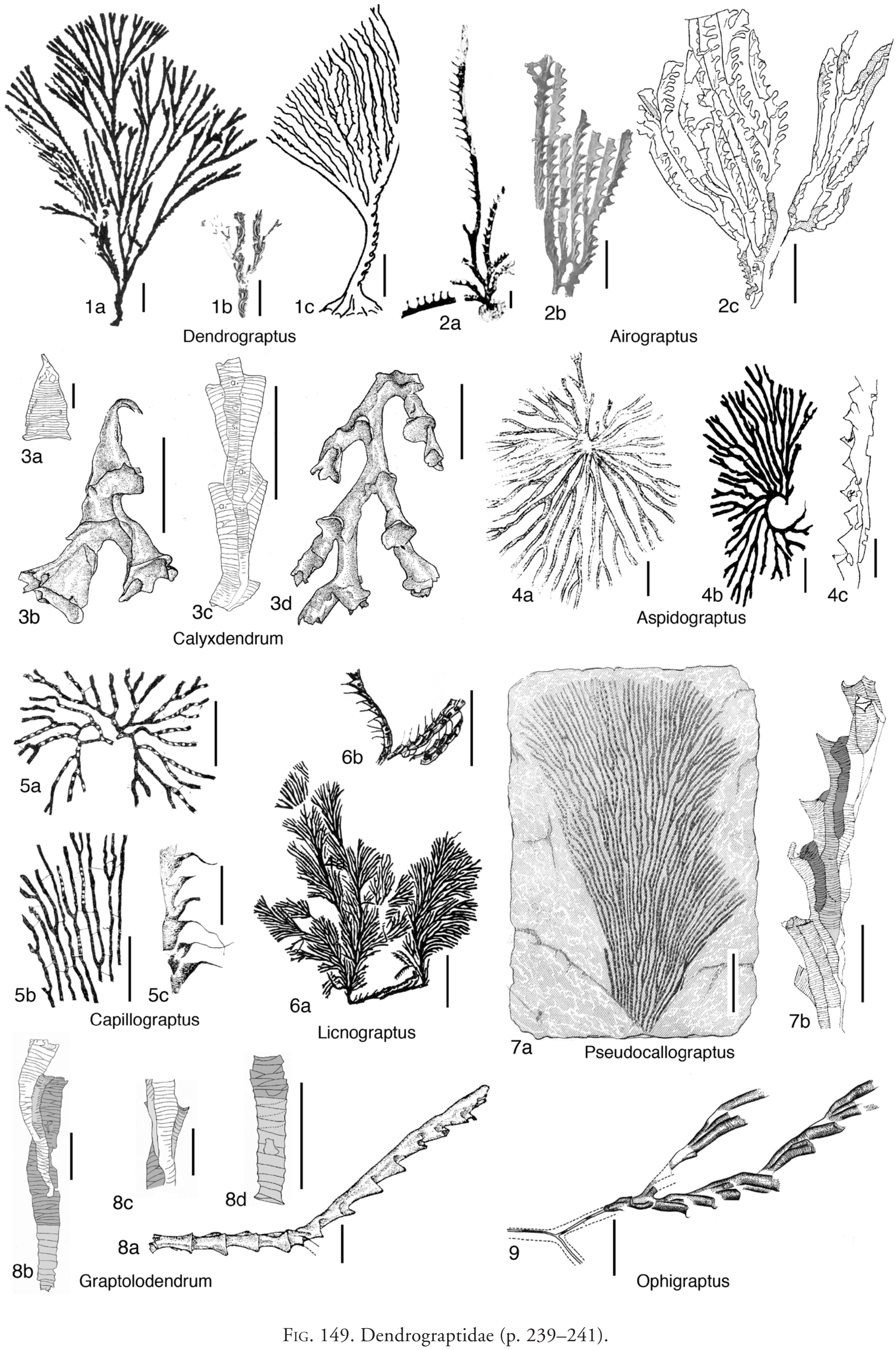

FIG. 149. Dendrograptidae (p. 239–241).

Ophigraptus Jaeger, 1992, p. 125 [**O. hercyniae;* 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. 149,*9*. **O. hercyniae,* MB.G. 811, detail of holotype, Buntenbock, Harz, Germany, scale bar, 1 mm (Jaeger, 1992, fig. 1).

Pseudocallograptus Skevington, 1963**a**, 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, 1963a, p. 25).] *Lower Ordovician* (*Floian, Didymograptellus bifidus* Biozone)–*Middle Ordovician* (*Darriwilian, Didymograptus murchisoni* Biozone): Sweden, Canada, Argentina.——Fig. 149,*7a*. **P. salteri* (Hall), GSC 955a, syntype, larger colony fragment, Gros Maule, Québec, Canada (probably in error for Lévis, Québec, Canada), scale bar, 10 mm (Hall, 1865, pl. 19,*5*).——Fig. 149,*7b*. *Pseudocallograptus* sp. cf. *P. salteri* showing thecal overlap and development of bithecae, Öland, Sweden, scale bar, 1 mm (adapted from Skevington, 1963a, 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* (*Upper Mississippian, 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 herein regarded as a feature of derived callograptids; earlier taxa (e.g., *Callograptus* Hall, 1865) have 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, 1925b, is regarded as a dasycladacean alga, whereas 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. The same is indicated for the genus *Saxonia* Roselt, 1962 herein. LUNDBLAD (1972) redescribed *Psilophyton*? *hedei* HALLE, 1920 from the Gorstian (Silurian) of Gotland (Sweden) 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, because even in complexly developed taxa, thecal apertures may be oriented ventrally and laterally but never dorsally.

Large differences are present 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 (2019c) 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, 2019c, p. 152).

Anastomosis has been described in a few taxa (Fig. 150.2, Fig. 150.4), 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 have isolated apertural parts of the thecae, and twigs are lacking (Fig. 150.3). Through the evolution of the Callograptidae, more thecae have joined the laterally growing isolated autothecal apertures. These became elongated and the twigs (Fig. 150.5) 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. 150.1). 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 have paired thecal origins, indicating the presence of triad budding (Fig. 150.5). 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. 150.6). 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. 150.4).

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

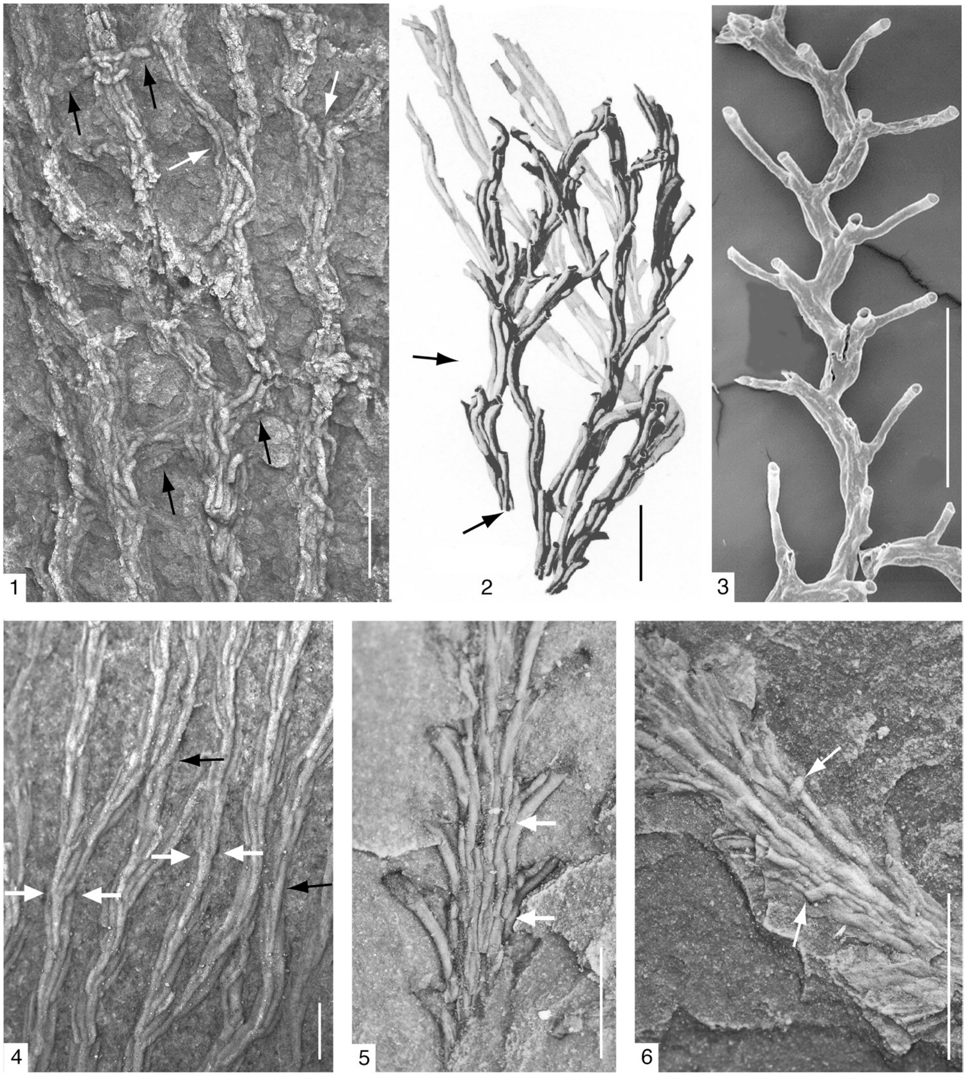

FIG. 150. Stipe development and connections in the Callograptidae. *1, Dictyonema fournieri* (UBAGHS, 1941), fragment in dorsal view, latex cast showing bridges (*black arrows*) and branching (*white arrows*), scale bar, 1 mm (new); *2, Koremagraptus kozlowskii* BULMAN, 1945, arrows indicate anastomosis, 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,* as *Acanthograptus*); *4, Callograptus elegans* HALL, 1865, GSC 955a, lectotype, latex cast showing dorsal view of stipes with triad budding (*white arrows*) and anastomosis (*black arrows*), Lévis, Quebec (new); *5–6, Acanthograptus sinensis* HSÜ & MA, 1948, PKUM02-0627, 0629, specimens showing twigs and irregular growth (*black arrows* in *6*) of thecal tubes (*arrows* indicate triad budding in *5*), Tianjianling, Hubei Province, China (Maletz & Kozłowska, 2013, fig. 5b,d). Scale bars, 1 mm for all images.

early forms of the Callograptidae are poorly known. RICKARDS and 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 was based on a low resolution, as it was not aimed at differentiating clades within the Dendroidea.

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. 151,*3*. **C. elegans,* GSC 956a, lectotype, Lévis, Quebec, Canada, scale bar, 10 mm (Hall, 1865, pl. 19,*2*).

Acanthograptus SPENCER, 1878, p. 461, original spelling as *Acanthograpsus* changed in ICZN Opinion 650, 1963 [**Acanthograpsus granti;* M] [=*Xylonograptus* SENNIKOV, 1976, p. 108 (type, *X. regularis,* M), syn. herein; =*Paracanthograptus* WANG in WANG & others, 1987, p. 365 (English text, p. 548–549) (type, *P. sanxianensis,* OD), syn. 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. 151,*1a*. **A. granti,* Hamilton, Ontario, Canada, type specimen whereabouts unknown, scale bar, 10 mm (Ruedemann, 1908, pl. 6,*4*).——FIG. 151,*1b*. *A. arborescens* (BOUČEK, 1957), specimen showing branching pattern, scale bar, 10 mm (Bull, 1987, fig. 10b).——FIG. 151,*1c*. *A. musciformis* (WIMAN, 1901), reconstruction of distal part of stipe showing thecal growth, scale bar, 1 mm (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. 151,*2a–b*. **A. holubi; 2a,* holotype, proximal end (Bouček, 1956, fig. 2a); *2b,* fragment showing thecal apertures (Bouček, 1956, fig. 2c). Scale bars, 1 mm.

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* Biozone–*Idahoia* Biozone)–*Ordovician:* USA.——FIG. 151,*5*. **C. sellardsii,* cotype, Point Peak Member, Wilberns Formation, Texas, USA, scale bar, 1 mm (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, original spelling as *Rhizograpsus* changed in ICZN Opinion 650, 1963, syn. by RUEDEMANN, 1947, p. 224 (type, *R. bulbosus,* M), BULMAN, 1970, p. 38; =*Syrrhipidograptus* POULSEN, 1924, p. 4 (type, *S. nathorsti,* M), syn. by 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. 152,*1a*. **D. cancellatus*, holotype, SM A17507, scale bar, 10 mm (Bulman, 1970, fig. 16,*2*).——FIG. 152,*1b, D. bulbosus* (SPENCER, 1878), holotype, Silurian, Niagara Limestone, Hamilton, Ontario, Canada, scale bar, 10 mm (Spencer, 1884, pl. 4,*4*).——FIG. 152,*1c–d. D. nathorsti* (POULSEN, 1924), holotype, Katian, Bornholm, Denmark. scale bars, 10 mm, 1 mm, respectively (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), syn. herein; =*Dictyonema* (*Pseudodictyonema*) BOUČEK, 1957, p. 69 (type, *Dictyonema graptolithorum* POČTA, 1894, p. 196, OD), syn. by MALETZ, 2019c, 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. 151,*4a–b*. **D. retiformis* (HALL); *4a*, holotype, AMNH 1671, scale bar, 10 mm (Hall, 1865, fig. 10); *4b*, NYSM 7112, detail of

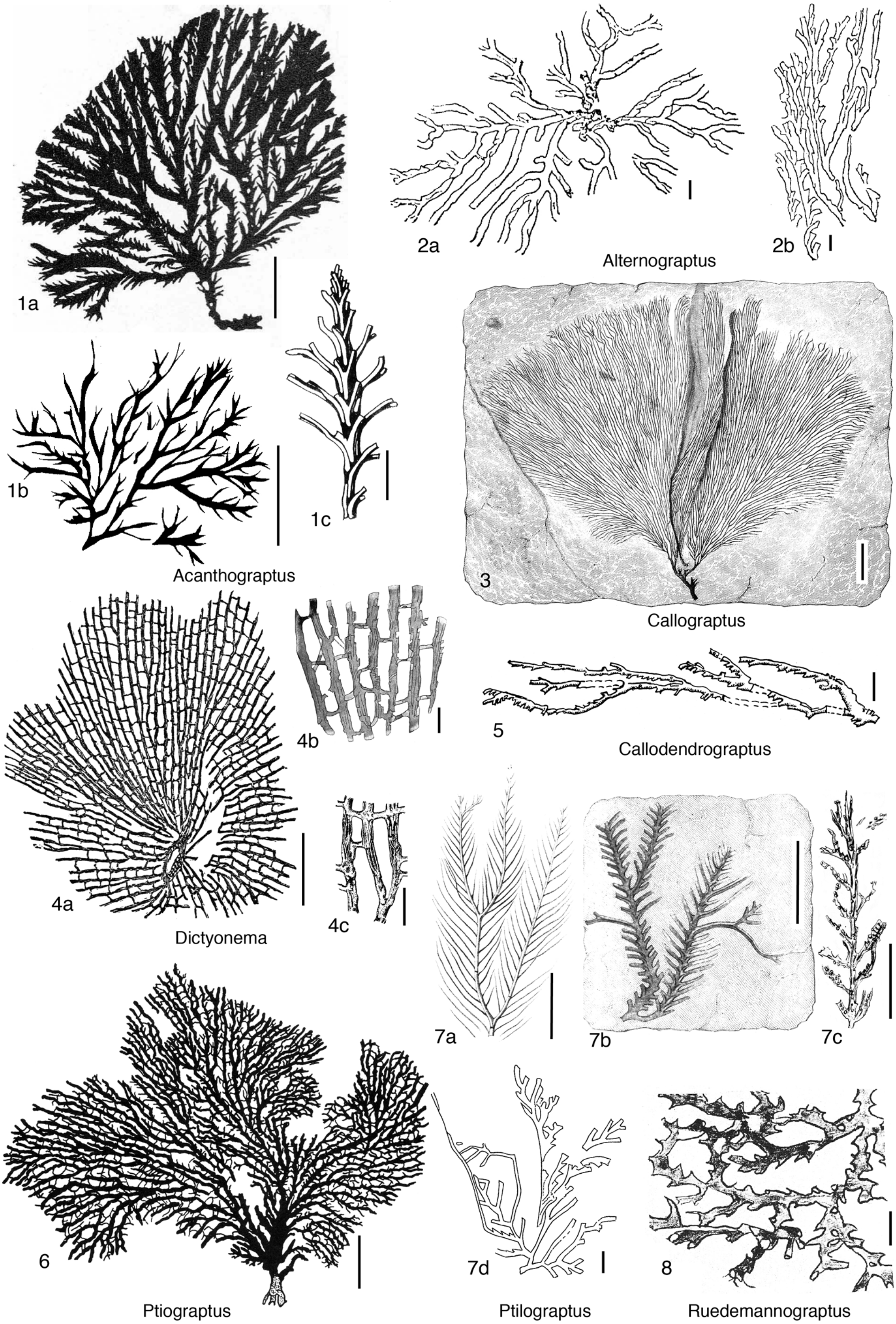

FIG. 151. Callograptidae (p. 244–247).

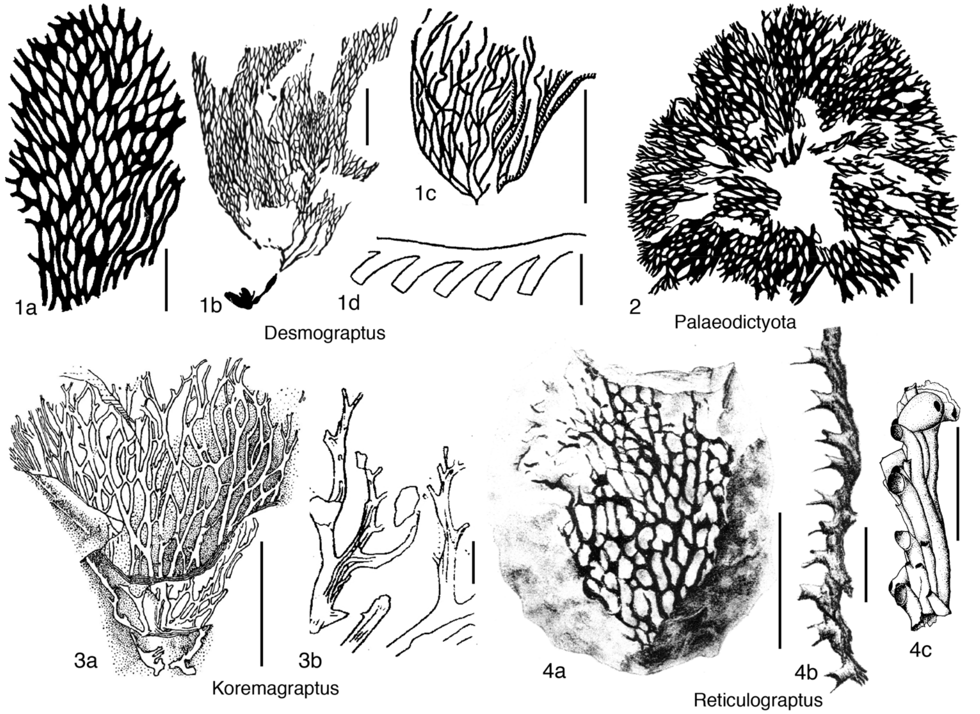

FIG. 152. Callograptidae (p. 244–247).

stipe fragment showing complex thecal overlap and bridge development, scale bar, 1 mm (Ruedemann, 1908, fig. 64).——FIG. 151,*4c. D. graptolithorum* POČTA, 1894, fragment with complex stipes, scale bar, 1 mm (Bouček, 1957, fig. 27b).

Koremagraptus BULMAN, 1927a, p. 345 [**K. onniensis* BULMAN, 1927a, p. 345; M] [=*Coremagraptus* BULMAN, 1942, p. 285 (misspelling); =*Archaeodictyota* OBUT & SOBOLEVSKAYA, 1967, p. 55 (type, *A. draguovi,* OD); syn. by BULMAN, 1970, p. 43; =*Dyadograptus* OBUT, 1960, p. 147 (type, *D. praecursor,* OD), syn. by 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. 152,*3a.* **K. onniensis*, holotype, scale bar, 10 mm (BULMAN, 1927b, fig. 1).——FIG. 152,*3b. K. fibratus* BULMAN, 1927a, holotype, SMF XXIV C 115a, fragment showing complex stipes, scale bar, 1 mm (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. 152,*2. P. anastomotica* (RINGUEBERG), typical colony, Rochester Shale, Silurian, Lockport, New York, USA, scale bar, 10 mm (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), syn. herein]; =*Denticulograptus* SCHMIDT, 1940, p. 122, *ex Ptilograptus* (*Denticulograptus*) SCHMIDT, 1940, p. 122 (type, *Ptilograptus acutus* HOPKINSON & LAPWORTH, 1875, p. 662, OD), syn. herein; =*Zigzagigraptus* YU, 1962, p. 49 (type, *Z. yunnanensis,* OD), syn. by 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. 151,*7a.* **P. plumosus,* lectotype (designated herein), scale bar, 10 mm (Hall, 1865, pl. 21,*1*).——FIG. 151,*7b. P. geinitzianus* HALL, 1865, GSC 561b, scale bar, 10 mm (Hall, 1865, pl. 21,*6*).——FIG. 151,*7c. P. rectus* (RUEDEMANN, 1908), holotype, scale bar, 10 mm (Ruedemann, 1947, pl. 42,*9*).——FIG. 151,*7d*. *P. yunnanensis* (YU), holotype, scale bar, 1 mm (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. 151,*6*. **P. percorrugatus,* NYSM 7348, holotype, waterlime at Louisville, Kentucky, USA, scale bar, 10 mm (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), syn. by 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. 152,*4a–b*. **R. tuberosus; 4a,* holotype, scale bar, 10 mm (Wiman, 1895, pl. 12,*9*); *4b*, stipe fragment, scale bar, 1 mm (Wiman, 1895, pl. 12,*12*).——FIG. 152,*4c*. *R. thorsteinssoni* BULMAN & RICKARDS, 1966, GSC 20322, fragment showing conothecae, scale bar, 1 mm (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. 151,*8*. **R. tenuis* (RUEDEMANN), part of holotype, scale bar, 1 mm (Ruedemann, 1947, pl. 14,*9*).

TAXA PREVIOUSLY IDENTIFIED AS EARLY LAND PLANTS

These taxa are separated herein, as they are described from small, largely unbranched fragments originally referred to as land plant remains. They clearly have complex stipe and isolated tubular extensions that may represent thecal tubes. To date, 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. ——FIG. 153,*3a–c*. *B. aculeatus* (POČTA, 1894), *3a,* pyritic stipe fragment showing thecal details, Lodenice, *Cyrtograptus radians* Zone, scale bar, 1 mm (BOUČEK, 1957, pl. 15,*7*); *3b,* specimen showing isolated thecal tubes, Kopanina beds, Silurian (Ludlow), scale bar, 1 mm (BOUČEK, 1957, pl. 15,*5*); *3c,* holotype of *Psilophyton hedei* (HALLE, 1920) now identified as a specimen of *B. aculeatus,* NRM-S 010022, Hemse Marl (Silurian, Ludlow), southeast of Petesviken, parish of Hablingbo, Gotland, Sweden, scale bar, 10 mm (Kenrick, Kvaček & Bengtson, 1999, fig. 3D).——FIG. 153,*3d–e*. **B. pragense,* holotype, NM-D418, specimen (*e*) and enlargement (*d*), Praha-Vokovice, Czech Republic, Darriwilian, scale bars, 1 mm (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 a plant fossil, but KRAFT & KVAČEK (2017, p. 185) suggested it to be a possible animal.] *Devonian* (possibly *Lochkovian*): Argentina.——FIG. 153,*1*. **B. mendozaensis,* holotype, Devonian, Argentina, scale bar, 1 mm (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. 153,*2*. **S. microphyla*, holotype, Ölsnitz, Vogtland, Germany, scale bar, 5 mm (Roselt, 1962, pl. 1,*1*).

Family MASTIGOGRAPTIDAE Obut & Sobolevskaya, 1967

[Family Mastigograptidae OBUT & SOBOLEVSKAYA, 1967, p. 58]

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*

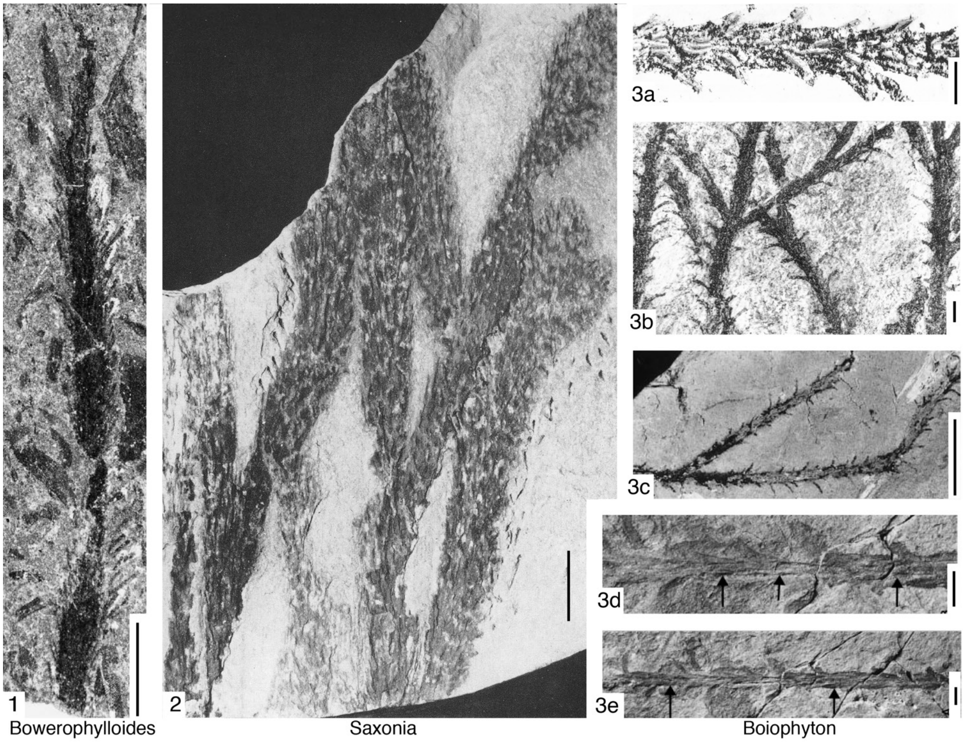

FIG. 153. Possible Callograptidae, previously identified as plants (p. 247).

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 are questionable 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 strongly indicates an inclusion in Dendroidea.

RUEDEMANN (1908) for the first time recognized the conical thecae in *Mastigograptus tenuiramosus* (WALCOTT, 1883) in material from the Eden Shale of Kentucky, USA (now the Kope Formation), 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. 154.4), in which the erect sicula is hidden. The holdfast of a number of specimens of *Mastigograptus* has 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. 154.1–154.2). They are conical, widening distinctly toward their simple straight apertures. The fusellar rings have full-ring development with irregularly placed sutures. The prothecal parts may have swollen initial parts (Fig. 154.3) 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. 155,*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

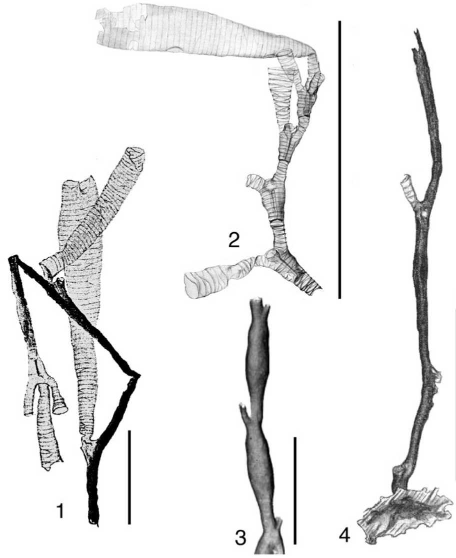

FIG. 154. Morphology of Mastigograptidae. *1,3–4, Mastigograptus* sp. *1,* stipe fragment with triad (Andres, 1977, fig. 13); *3,* stolon with swollen central part (inverted photo, Bates & Urbanek, 2002, fig. 3G); *4,* proximal end with attachment and short stipe showing bases of thecae (Andres, 1961, fig. 2a); *2, Micrograptus* sp., stipe fragment showing four closely spaced branching divisions (Andres, 1977, fig. 21). Scale bars, 1 mm.

irregularly placed sutures; triad budding present; auto- and bithecae probably not differentiated by size. *Middle Ordovician* (*Darriwilian*)*–Upper Ordovician* (*Sandbian*): Estonia, Finland.——FIG.155,*2a–c*. **M. fragilis, 2a,* holotype, glacial boulder, southern Finland; *2b,* specimen with thecal bud; *2c,* specimen possibly belonging to the species, showing regrowth of theca, Estonia; scale bars, 0.1 mm (Eisenack, 1974, fig. 1,*3–4*).

DENDROIDEA INDET

The following taxa most likely belong to the Dendroidea. They are based on highly incomplete fragments and preserve 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

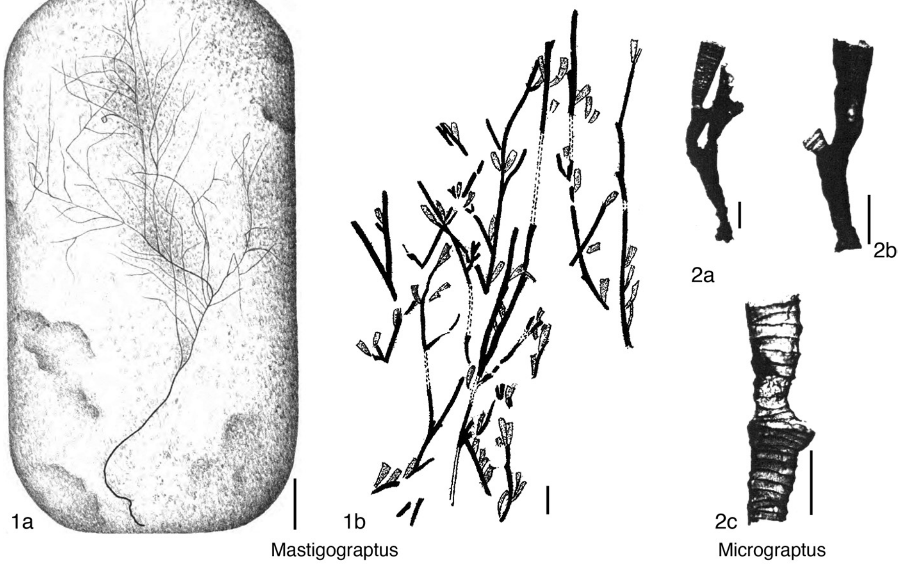

FIG. 155. Mastigograptidae (p. 249).

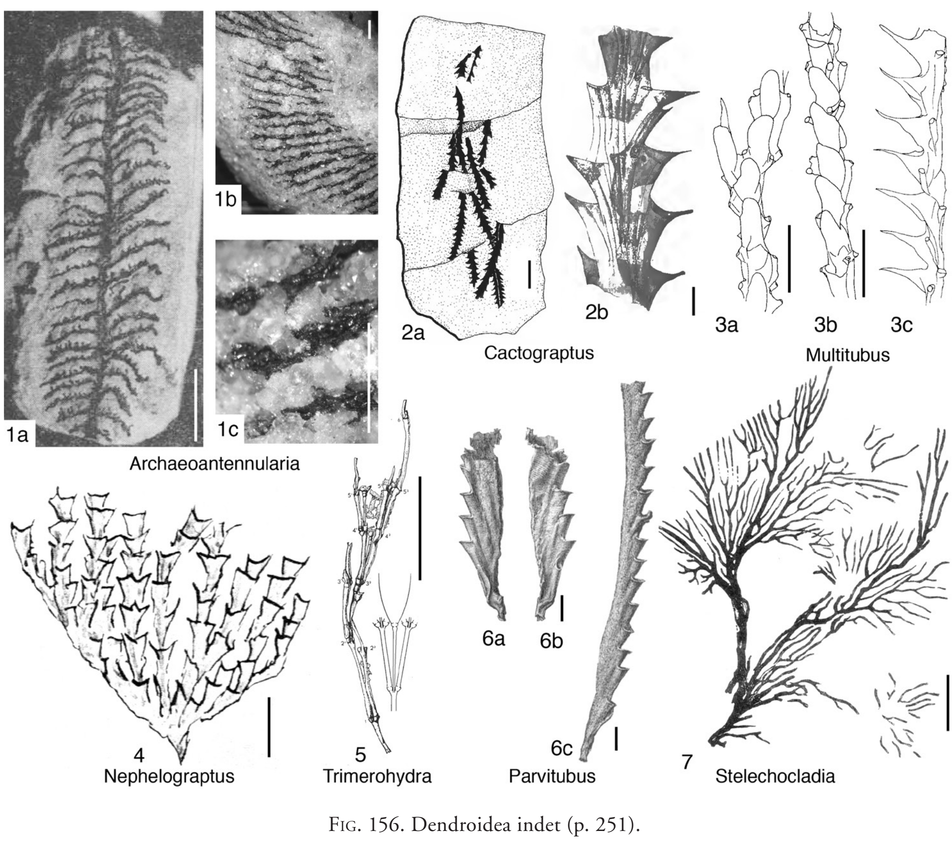

FIG. 156. Dendroidea indet (p. 251).

Dendroidea and possibly the Dendrograptidae when more details of its development are available.

The genus *Multitubus* is based on a few small stipe fragments with an apparently unusual development, and SKEVINGTON (1963a) 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.156,*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; prominent thecae projecting to both sides. *Cambrian, Miaolingian* (*Wuliuan, Ptychagnostus gibbus* Biozone)–*Silurian* (*Llandovery, Streptograptus crispus* Biozone–*Cyrtograptus centrifugus* Biozone): Kazachstan, Australia, USA.——FIG. 156,*2a–b*. **C. crassus,* holotype, NYSM 6860, specimen (*a*) and detail (*b*), Williamson Shale Formation, New York, USA (2*a,* Ruedemann, 1908, pl. 8,*1; 2b,* Ruedemann, 1908, fig. 99). Scale bars, 10 mm, 1 mm, respectively.

Multitubus SKEVINGTON, 1963a, p. 51 [**M. spinosus;* OD] Stipe fragments with serially arranged, spinose or rutellate autothecae and multiple capriciously distributed bithecae. *Middle Ordovician* (*Darriwilian*): Sweden.——FIG.156,*3a–c*. **M. spinosus,* holotype, fragments, Darriwilian, Öland, Sweden, scale bars, 1 mm (Skevington, 1963**a**, fig. 73–74).

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. 156,*4*. **N. rectibrachiatus*, holotype, Ottosee Shale, Knoxville, Tennessee, USA. scale bar, 1 mm (Ruedemann, 1947, pl. 14,*26*).

Parvitubus SKEVINGTON, 1963a, 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.156,*6a–c*. **P. oelandicus* (BULMAN), Öland, Sweden; *6a–b*, holotype viewed 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. 156,*7*. **S. fruticosa,* holotype, Silurian, Bohemia, scale bar, 10 mm (Bouček, 1957, pl. 2,*1*).

Trimerohydra KOZŁOWSKI, 1959a, 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. 156,*5*. **T. glabra,* holotype, scale bar, 0.5 mm (Kozłowski, 1959a, fig. 1).

ORDER GRAPTOLOIDEA

Jörg Maletz, Blanca A. Toro, and Yuandong Zhang

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 proparabola* Biozone)–*Devonian* (*lower Emsian, Uncinatograptus 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) because they have 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 into a single order and indicated that the loss of bithecae was polyphyletic within the Graptoloidea (Fig. 157), 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 they 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, 1974a).

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 graptoloids but are regarded as examples of dendroids that independently developed 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

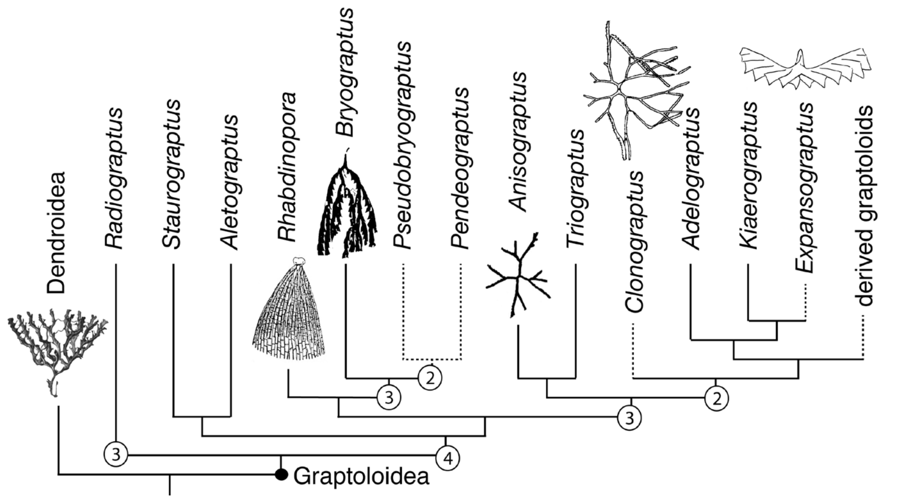

FIG. 157. Cladistic interpretation of early Graptoloidea by FORTEY and COOPER (1986), showing possible polyphyletic origin of non-bithecate graptoloids (*dotted lines*); circled numbers indicate origins of quadriradiate (*4*), triradiate (*3*), and biradiate (*2*) proximal development (new).

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 proparabola* 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, because 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, 1982a, 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 commonly 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 conus; th1^{2} is first dicalycal thecae, later dicalycal thecae adventitiously or regularly distributed. *Lower Ordovician* (*Tremadocian, Rhabdinopora proparabola* Biozone–*Floian, Sagenograptus murrayi* Biozone): worldwide.

The Anisograptidae form a paraphyletic stem group of the Graptoloidea (see Fig. 157). 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.

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 Dendrograptidae. 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. 158), 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 (1974a) 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 (1987a) 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, 1974a), later overgrown by the addition of fusellar tissue in the form of a spine. He identified this addition as the virgula. The virgula is herein 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, gradually widening from the prosicula and typically bearing a short rutellum (Fig. 158.4). The prosicula is differentiated into two parts of approximately equal length,

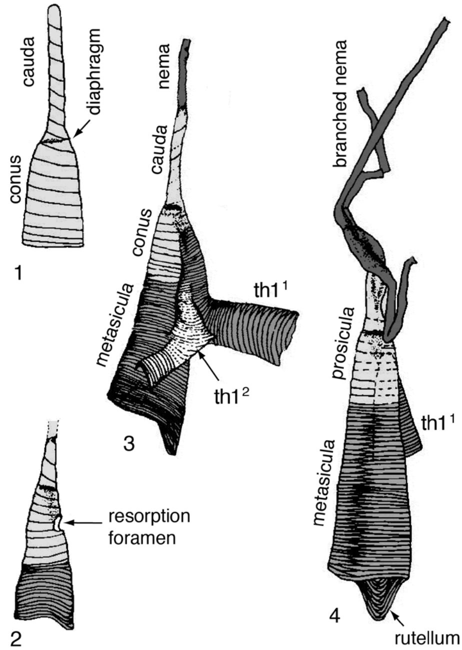

FIG. 158. Sicular development in Anisograptidae. *1,* prosicula showing conus and cauda, *arrow* indicates diaphragm; *2,* prosicula (*light gray*) with early metasicula (*dark gray*), resorption foramen for $th1^1$ indicated by *arrow; 3,* juvenile with complete sicula, part of $th1^1$ and crossing canal of $th1^2$, reverse view; *4,* sicula with complex nema (adapted from Hutt, 1974a).

the conus and cauda (HUTT, 1974a), separated by a diaphragm (Fig. 158.1). 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. 158.2). The length of the prosicula may be reduced, and the origin of $th1^1$ is close to the apex of the sicula (*Choristograptus* LEGRAND, 1964b).

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.

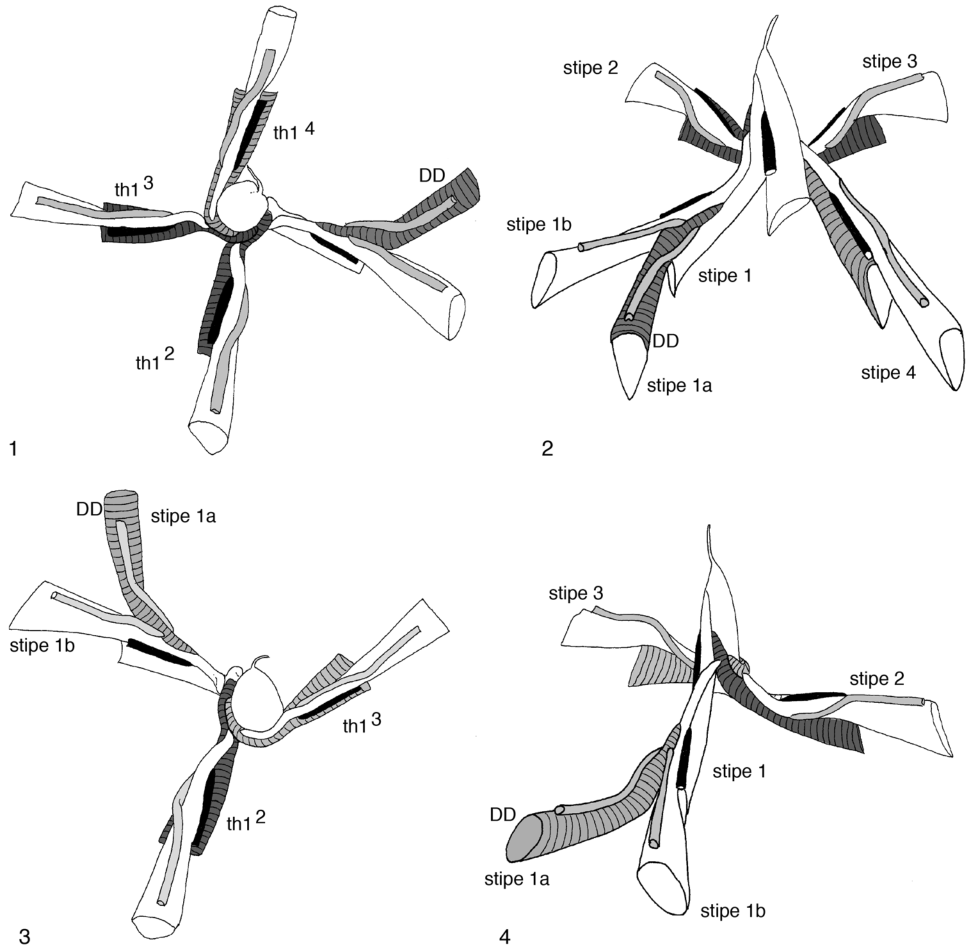

FIG. 159. Quadriradiate and triradiate proximal development. *1,* Quadriradiate development, dorsal view, showing successive, clockwise (dextral) origins of dicalyal thecae ($th1^2$, $th1^3$, $th1^4$) around the sicula; *2,* quadriradiate development, obverse view, showing sicular bitheca; *3,* triradiate 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 show various shades of gray: bithecae, *black*, first distal dicalycal theca, marked *DD* (adapted from Maletz, 1992, fig. 3).

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, whereas distal dicalycal thecae are separated from proximal ones by at least one monocalycal theca. Earliest anisograptids (*Staurograptus*, *Rhabdinopora*) possessed three successive (proximal) dicalycal thecae and, therefore, developed a quadriradiate proximal end (Fig. 159.1–159.2). The successive dicalycal thecae all formed 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 was 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, 1927b) and STUBBLEFIELD (1929) first described bithecae in planktic graptolites. In earlier Anisograptidae, the bithecae alternated along the stipes, with the first bitheca associated with the sicula termed the sicular bitheca (Fig. 160.1). 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. 160.2). 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. 160.3). The sicular bitheca is the last remaining bitheca according to WILLIAMS and STEVENS (1991) and is present in *Hunnegraptus copiosus* LINDHOLM, 1991 (Fig. 160.4).

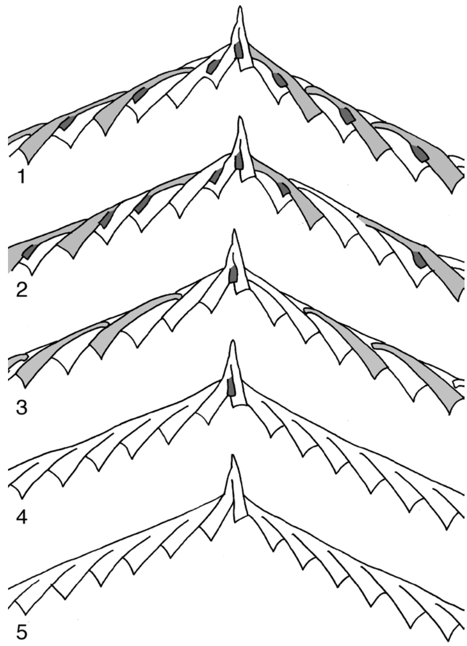

FIG. 160. Diagram illustrating the loss of bithecae in the Anisograptidae in obverse view to show presence/absence of sicular bitheca, proximal ends hypothetical. *1,* Stipes based on *Kiaerograptus*? *supremus* LINDHOLM, 1991; *2,* stipes based on fragment of *Kiaerograptus kiaeri* MONSON, 1925, with successive bithecae on one side; *3,* stipes based on fragment of ?*Clonograptus* sp. aff. *Clonograptus multiplex* (NICHOLSON, 1868d); *4,* stipes based on *Hunnegraptus copiosus* LINDHOLM, 1991, with sicular bitheca as the only remaining bitheca; *5,* stipes based on *Clonograptus multiplex* (NICHOLSON,1868d) (adapted from Lindholm, 1991, fig. 4).

EVOLUTION

The Anisograptidae represent the initial step in graptolites becoming successful planktic organisms. The earliest planktic form, *Rhabdinopora proparabola* (LIN, 1986), appeared close to the base of the Tremadocian, 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 is illustrated by 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 during 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. 157).

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, 2014b, fig. 10), a condition similar to that in the dichograptine genus *Hunnegraptus* LINDHOLM, 1991. The genus *Paratemnograptus* possesses 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 (1982a) 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 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. 453 [**Gorgonia flabelliformis* EICHWALD, 1840, p. 207; SD BASSLER, 1911, p. 348] [=*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); =?*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) non *Heterograptus* HERNÁNDEZ SAMPELAYO, 1960, p. 33; *nomen oblitum*] [*non Graptopora* ULRICH, 1882, p. 148, *nom. nud.*, =*Graptodictya* ULRICH, 1882, p. 165 (type, *Ptilodictya perelegans,* ULRICH 1878, p. 94, SD, BASSLER, 1953, p. 137, Bryozoa); *non Graptopora* LANG, 1916, p. 405 (type, *G. scripta,* OD; =*Graptoporella* BASSLER, 1953, p. 189, Bryozoa)]. Pendent, multiramous anisograptid with irregularly to regularly distributed dissepiments; proximal development quadriradiate. *Lower Ordovician* (*lower Tremadocian, Rhabdinopora proparabola* Biozone–*Adelograptus* Biozone): worldwide.——FIG. 161,*1a–b*. **R. flabelliformis* (EICHWALD); *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). Scale bars, 10 mm.——FIG. 161,*1c. R. proparabola* (LIN, 1986), holotype of *Heterograptus radiatus* ZHAO & ZHANG in LIN, 1986, CCG G8456, Dayangcha, Jilin, China, scale bar, 5 mm (Lin, 1986, fig. 96,*1*).

Adelograptus BULMAN, 1941, p. 114 [**Bryograptus*? *hunnebergensis* MOBERG, 1892b, 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, gradually widening thecae, commonly with short rutellum. *Lower Ordovician* (*upper Tremadocian, Adelograptus tenellus* Biozone–*Hunnegraptus copiosus* Biozone): Algeria, ?Australia, China, Sweden, Norway, UK, Canada, USA, Argentina, Bolivia.——FIG. 162,*5a–b,d. A. tenellus* (LINNARSSON, 1871); *5a,* neotype, SGU 4497a–b,

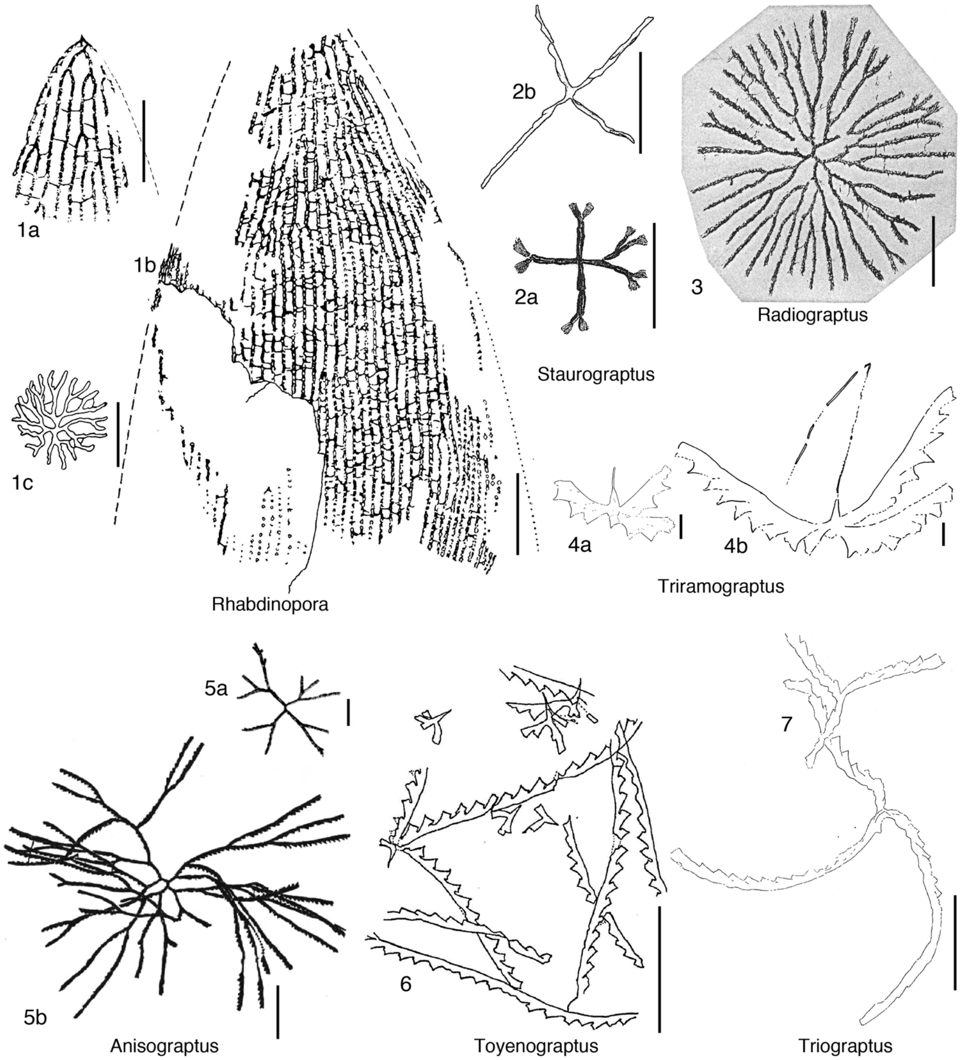

FIG. 161. Anisograptidae (p. 258–263).

scale bar, 5 mm (Maletz & Erdtmann, 1987, pl. 1A); *5b*, SGU 4506, lectotype of **Bryograptus*? *hunnebergensis* (selected herein), scale bar, 5 mm (Maletz & Erdtmann, 1987, p 188); *5d,* SM A82770, Shineton Shale, Shropshire, UK, scale bar, 1 mm (Maletz, 1992, fig. 1F).——FIG. 162,*5c. A. messaoudi* LEGRAND, 1964a, proximal end, obverse view showing sicular bitheca, scale bar, 1 mm (adapted from Legrand, 1964a, fig. 3a).

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, gradually widening thecae commonly with short rutellum; tubular sicula and typically 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. 164,*1a–c.* **A. bulmani* (SPJELDNAES); *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).

Anisograptus RUEDEMANN, 1937, p. 61 [**A. matanensis;* OD]. Triradiate anisograptid with horizontal to subhorizontal tubarium; distal dichotomies irregularly spaced. *Lower Ordovician* (*lower Tremadocian,*

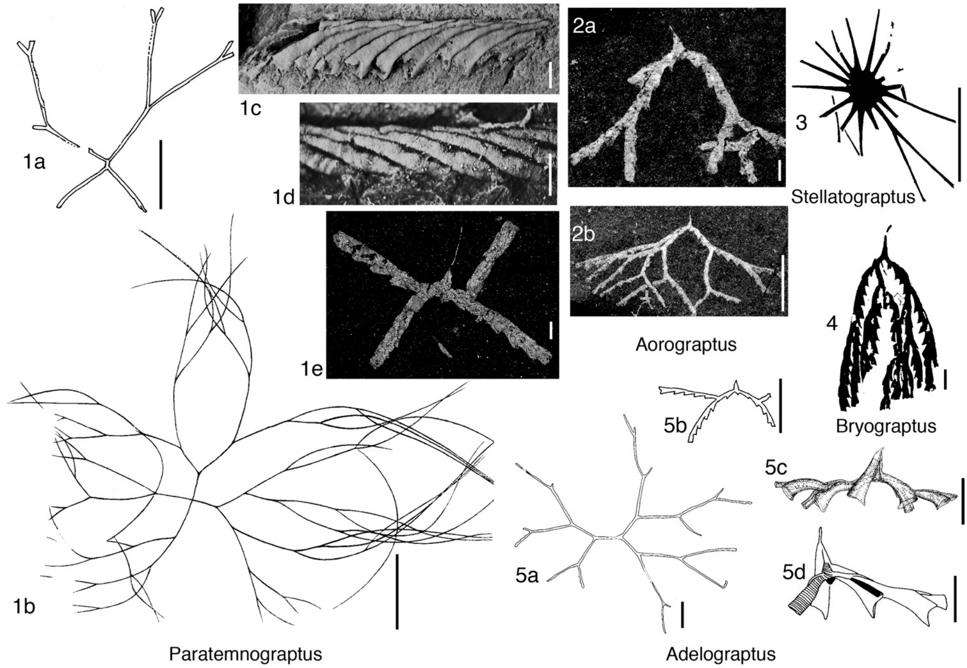

FIG. 162. Anisograptidae (p. 258–263).

Anisograptus matanensis Biozone–*Rhabdinopora flabelliformis anglica* Biozone): worldwide.——FIG. 161,*5a*.**A. matanensis,* holotype, NYSM 6841, Matane, Quebec, Canada, scale bar, 5 mm (Ruedemann, 1937, fig. 6).——FIG. 161,*5b*. *A. flexuosus* BULMAN, 1950, GSC 9861, Matane, Quebec, Canada, scale bar, 10 mm (Bulman, 1950, fig. 6a).

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. 162,*2a–b*. **A. victoriae; 2a*, holotype, NMV P 4240, scale bar, 1 mm (new); *2b,* NMV P318132A, large specimen, Victoria, Australia, scale bar, 5 mm (new).

Bryograptus LAPWORTH, 1880a, 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, commonly with long and thickened nema. *Lower Ordovician* (*upper Tremadocian, Bryograptus ramosus* Biozone): UK, Norway, Sweden, Argentina, Bolivia.——FIG. 162,*4*. **B. kjerulfi,* lectotype, PMO 71284, Vaekkero, Oslo Region, Norway, scale bar, 1 mm (Bulman, 1971b, p. 363, fig. 1a).

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. 164,*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).

Choristograptus LEGRAND, 1964b, 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, gradually widening thecae without rutellum; tubular sicula and typically a number of proximal thecae isolated aperturally. *Lower Ordovician* (*upper Tremadocian,* ?*Aorograptus victoriae* Biozone): Algeria, Morocco.——FIG. 163*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 of tcale bars, 0.5 mm in *a–c,* 0.1 mm in *d* (Legrand, 1964b, *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 typically irregularly placed; apertural

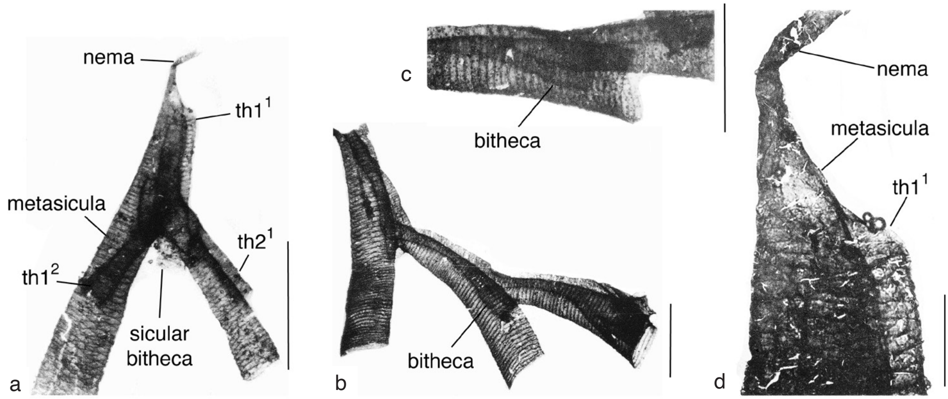

FIG. 163. Anisograptidae (p. 260).

part of sicula freely pendent; thecal apertures, at least in proximal parts, commonly isolated. *Lower Ordovician* (*upper Tremadocian, Aorograptus victoriae* Biozone): Algeria, China, Norway, Sweden, Canada, Argentina.——FIG. 164,*2a–b*. **K. kiaeri* (MONSEN); *2a,* lectotype, PMO 60212a, scale bar, 1 mm (Monsen, 1925, pl. 2,*10;* Spjeldnaes, 1963, pl. 17,*5*); *2b,* PMO 72833, fragment with bithecae, scale bar, 1 mm (Spjeldnaes, 1963, pl. 2,*1*).——FIG. 164,*2c*. *K. lauzonensis* (ERDTMANN, 1966), GSC 122714, showing distal branching, scale bar, 1 mm (Maletz & Egenhoff, 2001, fig. 4a).

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* Biozone–*Tetragraptus phyllograptoides* Biozone): Australia, Norway, Sweden, Canada, Argentina, Bolivia.——FIG. 162,*1a–e*. *T. magnificus; 1a,* holotype of *P. isolatus,* GSC 87284, scale bar, 10 mm (Williams & Stevens, 1991, fig. 10L); *1b,* holotype, NMV P34000, Lancefield, Victoria, Australia, scale bar, 10 cm (Pritchard, 1892, pl. 6); *1c,* MG1968, stipe 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*);*1e,* lectotype of *Tetragraptus decipiens* HALL, 1899, NMV P14368, proximal end, scale bar, 1 mm (new; photo provided by F. VandenBerg).

Psigraptus JACKSON, 1967, p. 314 [**P. arcticus;* OD] [=*Yukonograptus* LIN, 1981, p. 244, English text p. 261 (type, *Psigraptus lenzi* JACKSON, 1967, p. 319, OD), syn. by RICKARDS & others, 1991, p. 249; =*Muenzhigraptus* ZHAO & ZHANG, 1985, p. 16 (type, *M. sinicus,* OD), syn. by RICKARDS & others, 1991, p. 249; =*Diphygraptus* ZHAO & ZHANG, 1985, p. 19, (type, *D. reclinatus,* OD), syn. by RICKARDS & others, 1991, p. 249; =*Hunjiangograptus* ZHAO & ZHANG, 1985, p. 20, (type, *H. typicus,* OD); =*Holopsigraptus* ZHAO & ZHANG, 1985, p. 20 (type, *H. hunjiangensis,* OD), syn. by RICKARDS & others, 1991, p. 249; =*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. 164,*3a*. **P. arcticus,* holotype, GSC 21248, scale bar, 1 mm (new).——FIG. 164,*3b*. *P. lenzi* (JACKSON), holotype, GSC 21253, scale bar, 1 mm (new).——FIG. 164,*3c*. *P. hunjiangensis* (ZHAO & ZHANG), holotype, scale bar, 1 mm (new).——FIG. 164,*3d*. *P. reclinatus* (ZHAO & ZHANG), holotype, scale bar, 1 mm (new).——FIG. 164,*3e*. *P. typicus* (ZHAO & ZHANG), holotype, scale bar, 1 mm (new).——FIG. 164,*3f*. *P. sinicus* (ZHAO & ZHANG), holotype, scale bar, 1 mm (new).

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. 161,*3*. **R. rosieranus,* holotype, GSC 9871, Cap de Rosier, Gaspe Peninsula, Quebec, Canada, scale bar, 10 mm (Bulman, 1950, pl. 6).

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, =*Dictyonema grande* HALL, 1892); =*Nyssenia* SOUGY, 1964, p. 187 (type, *N. zemmourensis,* OD), syn. by GUTIÉRREZ-

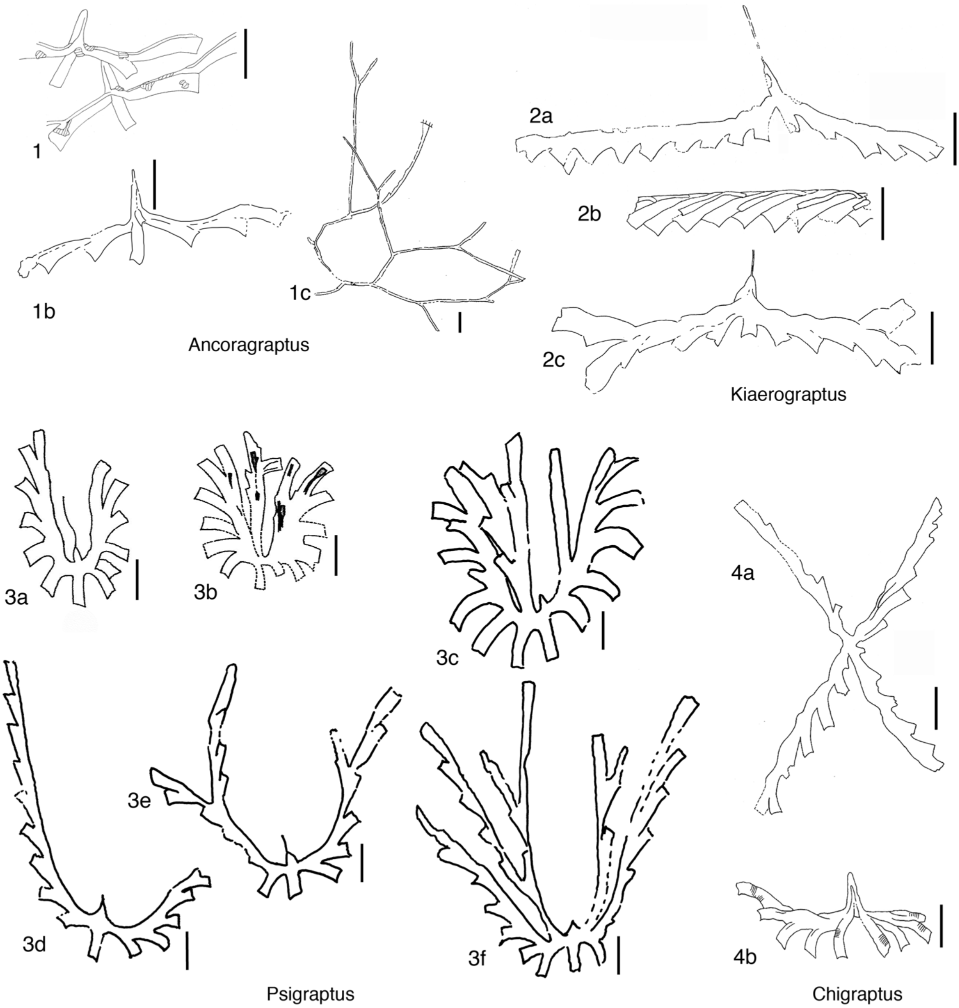

FIG. 164. Anisograptidae (p. 260–261).

MARCO & ACENOLAZA, 1987, p. 325]. 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. 165*a,c–d. S. macgillivrayi* (T. S. HALL); *a,* NMV P13126, Lancefield Quarry near Lancefield, Victoria, Australia, scale bar, 10 mm; *c,* NMV P73461, proximal end in lateral view, scale bar, 1 mm; *d,* NMV P13127, proximal end of lectotype (selected herein); (new; photos provided by A. VandenBerg).——FIG. 165*b.* *S. gagarini,* holotype, 5/8310, scale bar, 5 mm (Sobolevskaya, 2011, pl. 2,*5*).

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,* OD), syn. by COOPER & others, 1998, p. 21]. 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 proparabola* Biozone–*Rhabdinopora campanulatum* Biozone): worldwide.——FIG. 161,*2a.* **S. dichotomous,* type specimen whereabouts unknown, scale bar, 5 mm (Feng, Erdtmann, & Zhang, 2005, p. 1013).——FIG. 161,*2b. S. hyperboreus* (OBUT & SOBOLEVSKAYA,

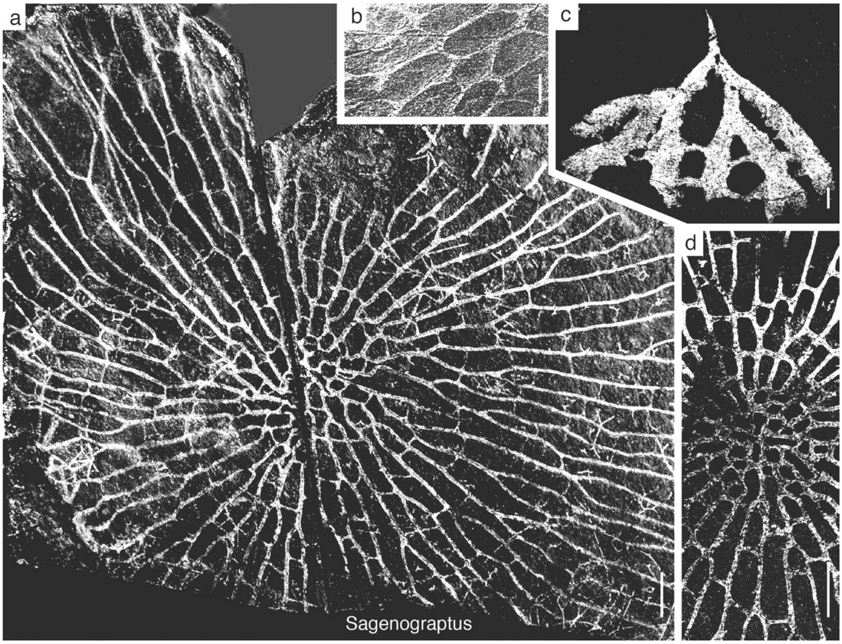

FIG. 165. Anisograptidae (p. 262).

1962), holotype, CGMSP 8310/11, scale bar, 5 mm (Feng, Erdtmann, & Zhang, 2005, fig. 11C).

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. 162,*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. Michel de Bellechasse, Quebec, Canada, scale bar, 5 mm (Erdtmann, 1967, p. 344, fig. 4).

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. 161,*6*. **T. isolatus* (BULMAN), holotype, PMO 61876, Tøyen, Oslo, Norway, scale bar, 5 mm (Bulman, 1954, fig. 13).

Triograptus MONSEN 1925, p. 169 [**T. osloensis;* OD]. Triradiate anisograptid; tubarium comprised of three horizontal, undivided stipes with distinct lateral curvature; details of thecae unknown. *Lower Ordovician* (*upper Tremadocian, Kiaerograptus kiaeri* Biozone): Norway, ?Argentina.——FIG. 161,*7*. **T. osloensis*, lectotype (selected herein), PMO 60232, scale bar, 5 mm (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 typically with long nema. *Lower Ordovician* (*lower Tremadocian, Rhabdinopora flabelliformis parabola* Biozone): Canada (western Newfoundland).——FIG. 161,*4a–b*. **T. atavus; 4a,* holotype, GSC 115854; *4b,* GSC 115857, large specimen; scale bars, 1 mm (Cooper & others, 1998, fig. 23a and 23d, respectively).

SUBORDER SINOGRAPTINA

JÖRG MALETZ, YUANDONG ZHANG, and ALFONS H. M. VANDENBERG

Suborder SINOGRAPTINA Mu, 1957

[Sinograptina MU, 1957, p. 387; *nom. transl.* MALETZ, ZHANG, & VANDENBERG, 2018, p. 1; *ex* Sinograptidae MU, 1957, p. 387] [=cohort Pan-Sinograpta MALETZ, CARLUCCI, & MITCHELL, 2009, p. 11]

Planktonic graptoloids with multiramous to single-stiped, horizontal to subhorizontal tubarium; sicula generally nearly parallel sided and without rutellum, oriented perpendicular to stipes; proximal development isograptid, dextral or sinistral with distinct asymmetry of the crossing canals, lost in derived forms; artus-type development in derived taxa; origin of $th1^1$ in middle part of prosicula in early taxa, but generally in lower part of prosicula, rarely in metasicula; thecal style varies from simple dichograptid with gradually widening thecae to forms with distinctly differentiated pro- and metathecae; thecal elaborations such as prothecal folds, lateral apertural lappets, rutella or spines common; fusellum normal to strongly reduced and possibly lacking in some (Abrograptidae). *Lower Ordovician* (*upper Tremadocian, Sagenograptus murrayi* Biozone)–*Upper Ordovician (Sandbian, Climacograptus bicornis* Biozone): worldwide.

INTRODUCTION

The maeandrograptid proximal symmetry of the Graptodendroidina (Fig. 166.4) is retained in the Sinograptina, but the orientation of the sicula is changed from an oblique position to a vertical position (Fig. 166.1–166.2). The proximal development of the early members of the Sinograptina is characterized by very slender crossing canals and slender prothecal tubes with considerably widening metathecae. It bears some similarity to the features of the Graptodendroidina, with their typical asymmetrical development of the slender crossing canals, but lacks the typical bithecae of the Graptodendroidina. In all taxa, the first crossing canal diverges from the sicula at a point distinctly higher on the metasicula than the second crossing canal. The first crossing canal grows from its origin obliquely downward and across the reverse side of the sicula. Its ventral side touches the dorsal side of the sicular aperture, where it typically bends considerably to form the horizontal stipe (Fig. 166.1). The second crossing canal grows horizontally across the metatheca of $th1^1$ (Fig. 166.2). Both crossing canals are slender and the thecae widen only distally, toward the apertures in *Paradelograptus*.

MALETZ, CARLUCCI, and MITCHELL (2009, p. 11) defined the subcohort Pan-Sinograpta as the group comprising the common ancestor of *Nicholsonograptus fasciculatus* (NICHOLSON, 1869)—the first species with a slender sicula and parallel-sided prosicula—and all its descendants, based on the cladistic diagram they provided. According to the authors, the cohort Pan-Sinograpta is a sister group to the cohort Pan-Reclinata, differing mainly in the development of the sicula and the shape and position of the crossing canals. The internal structure of the clade is not well resolved, but a number of distinct groups are present (MALETZ, CARLUCCI, & MITCHELL, 2009). Derived forms tend to be strongly modified and may be difficult to classify. The Sinograptidae is the only group to appear as distinct in the cladistic analysis of MALETZ, CARLUCCI, and MITCHELL (2009), however it included the genus *Maeandrograptus,* herein referred to the Sigmagraptidae (Fig. 167). The genus *Acrograptus,* which they included in the stem-reclinatids (suborder Dichograptina, herein) as a sister to *Didymograptellus* TZAJ, 1969, is now referred to the Sigmagraptidae, based on the proximal development. The genus *Perissograptus* with its four reclined stipes is considered to be a close relative to *Maeandrograptus.*

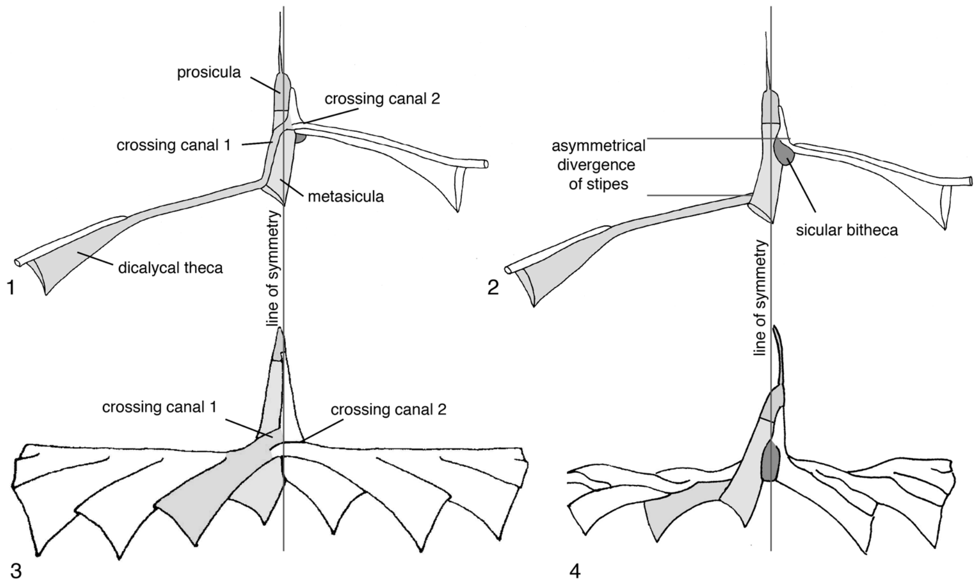

FIG. 166. Sinograptid (*1–2*) and dichograptid (*3–4*) proximal ends. *1–2, Paradelograptus onubensis* ERDTMANN, MALETZ, & GUTIERREZ-MARCO, 1987; *1,* reverse view, dextral; *2,* obverse view, sinistral, showing sicular bitheca; *3, Expansograptus holmi* (TÖRNQUIST, 1901), reverse view, dextral, showing inclination of sicula; *4, Kiaerograptus*? *supremus* LINDHOLM, 1991, obverse view, sinistral, showing strong inclination of sicula (new).

TAXONOMY OF THE SINOGRAPTINA

The differentiation of the Sinograptina into families, as proposed herein, is based mainly on proximal-end features. The older (upper Tremadocian to Darriwilian) Sigmagraptidae have an asymmetrical proximal-end development with fairly simple thecal styles. The younger (largely Darriwilian) Sinograptidae possess a symmetrical development of the crossing canals and a more complex thecal style with prothecal folds, and some may even have metathecal folds. The Abrograptidae is differentiated by the reduction of the fusellum. However, whether it constitutes a monophyletic family is uncertain, because detailed tubarium structures are unknown for most members. The Thamnograptidae are referred to the Sinograptina as *incertae sedis,* as they share similarities in their thecal development. However, the proximal end of the Thamnograptidae is known only from poorly preserved specimens of *Wuninograptus* NI, 1981.

Family SIGMAGRAPTIDAE Cooper & Fortey, 1982

[Sigmagraptidae COOPER & FORTEY, 1982, p. 259] [*nom. transl.* FORTEY & COOPER, 1986, p. 652; *ex* Sigmagraptinae COOPER & FORTEY, 1982, p. 259] [incl. Goniograptidae YU & FANG, 1979, p. 441; Azygograptinae MU, 1950b, p. 176; Kinnegraptidae MU, 1974, p. 231; Prokinnegraptidae YU & FANG, 1979, p. 441]

Multiramous to one-stiped, reclined to horizontal and pendent tubaria; colony biradiate with asymmetrical placing of first-order stipes; sicula parallel sided or nearly parallel sided with parallel-sided prosicula; proximal development isograptid, dextral or sinistral, or of artus-type development in derived taxa; origin of first theca in median part of prosicula in early taxa, in lower part of prosicula in younger ones; crossing canals more slender than in Dichograptina; thecae simple or with complex and elaborate apertures, slender and sometimes elongated. *Lower Ordovician* (*upper Tremadocian, Sagenograptus murrayi* Biozone)*–Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.

COOPER and FORTEY (1982) introduced the subfamily Sigmagraptinae for gracile

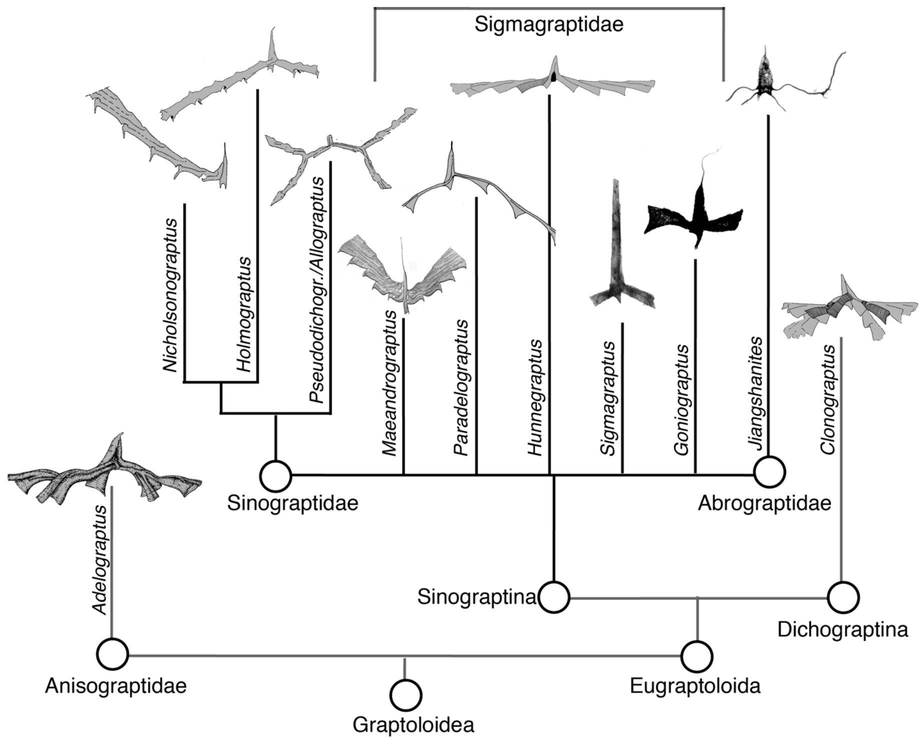

FIG. 167. The Sinograptina (new; based on diagram in MALETZ, CARLUCCI, & MITCHELL, 2009, fig. 2).

dichograptid graptolites with an asymmetrical proximal end and a long and slender sicula. The earliest sigmagraptid in the current interpretation appears to be the genus *Paradelograptus* from the upper Tremadocian *Sagenograptus murrayi* Biozone, representing the first group of graptolites in which the thecae became differentiated into distinct pro- and metathecae. The Sigmagraptidae retain the asymmetrical divergence of the stipes from their ancestors, but change the orientation of the sicula. The widening cone of the sicula of the Graptodendroidina is modified and the metasicula in the Sigmagraptidae is more or less parallel sided with little widening from the aperture of the prosicula. Rutella are lacking in early Sigmagraptidae, but elaborate rutella are present in some derived forms (i.e., *Kinnegraptus*).

MORPHOLOGY

The Sigmagraptidae includes taxa with a single stipe to taxa with numerous branching divisions. Branching appears highly irregular in early taxa, but the genera *Goniograptus* and *Sigmagraptus* possess very regular monoprogressive branching. In general, the colonies are subhorizontal to umbrella-shaped, but reclined taxa also occur, and pendent taxa are rare. All taxa with more than one stipe have $th1^2$ as the only proximal dicalycal theca or lack proximal dicalycal thecae. The position of later dicalycal thecae is adventitious and irregular in many species, and the position of a dicalycal theca cannot be taken as a character of higher taxonomic value.

The sicula is highly variable in the Sigmagraptidae (Fig. 168), but species with a parallel-sided pro- and metasicula prevail (Fig. 168.1). In some genera, the prosicula is relatively large, forming more than half of the length of the sicula. Considerably elongated siculae are present in some *Maeandrograptus* species and in *Sigmagraptus*. *Perissograptus* is a strongly derived genus sharing numerous tubarium characters with

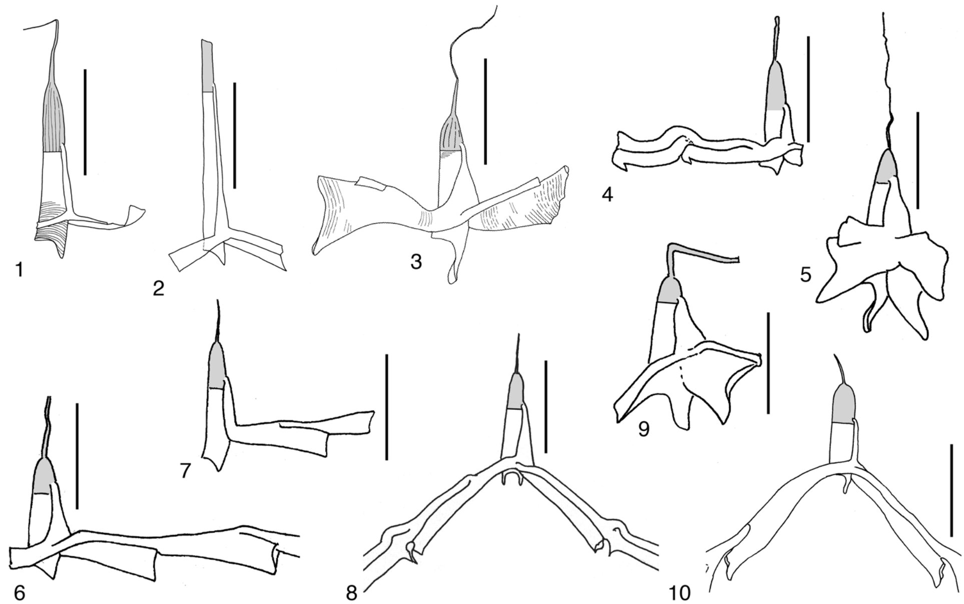

FIG. 168. Sicular and proximal development in the Sinograpta, prosicula shown in *gray*. *1,* Sigmagraptine indet., GSC 81787a, showing long mitre-shaped prosicula with few longitudinal rods and isograptid, dextral development (new); *2, Sigmagraptus praecursor* RUEDEMANN, 1904, GSC 139255, CHN 11.4E, Cow Head Group, western Newfoundland (new); *3, Goniograptus thureaui* (M'COY, 1876), GSC 125786, proximal end with typical rutellate sicula and small prosicula (new); *4, Maeandrograptus sinuosus* MALETZ, 2004, holotype, GSC 125764, Sigmagraptidae (MALETZ, 2004, fig. 5I); *5,* ?*Eotetragraptus* sp. cf. *E. spinosus* (SPJELDNAES, 1953), GSC 125752, Sigmagraptidae (MALETZ, 2004, fig. 2V); *6,* GSC 125806, sigmagraptine sp. indet. (Maletz, 2004, fig. 6K); *7,* GSC 125810, sigmagraptine sp. with one single stipe (Maletz, 2004, fig. 6P); *8, Holmograptus* sp., Sinograptidae, reconstruction (new); *9, Keblograptus geminus* MALETZ, 2004, GSC 125778, Sigmagraptidae (Maletz, 2004: fig. 4C); *10, Anomalograptus reliquus* (CLARK, 1924), Sinograptidae, reconstruction (new). All scale bars, 1 mm.

Maeandrograptus but developing a reclined, four-stiped colony with an aperturally isolated, parallel-sided sicula. Siculae with strongly widening, triangular shapes develop in a number of genera (*Keblograptus, Kinnegraptus,* abrograptids) (Fig. 168.9). The prosicula has numerous longitudinal rods in many taxa, but the exact development in others is unknown. WILLIAMS and CLARKE (1999) illustrated prosiculae of *Goniograptus* sp. with few (~8–10) longitudinal ridges. There is no information on the differentiation of the conus and cauda in the prosicula of the Sigmagraptidae. The helical line is distinctive in chemically isolated specimens and in relief specimens of *Paradelograptus* in which the prosicular fusellar band is wider than the subsequent metasicular fusellar half rings (see *Adelograptus filiformis* WILLIAMS & STEVENS, 1991).

The proximal development type is isograptid, dextral in most forms (Fig. 168–Fig.169), but a sinistral development has been recognized in *Paradelograptus* (see ERDTMANN, MALETZ, & GUTIERREZ-MARCO, 1987) (Fig. 169.1). SKOGLUND (1961) described chemically isolated material of the genus *Kinnegraptus* from the Dapingian of Sweden with an artus-type development and a metasicular origin of $th1^1$. The proximal development is uncertain in many slender sigmagraptines so that the taxonomic interpretation may be questionable. The development in *Acrograptus affinis* (NICHOLSON, 1869) can be interpreted as of artus-type, based on a possible topotype specimen illustrated by RUSHTON (2000a). It has a distal origin of $th2^2$ on $th2^1$, thus the dicalycal theca must be $th1^1$.

The origin of $th1^1$ is in the middle part of the prosicula in some *Paradelograptus* speci-

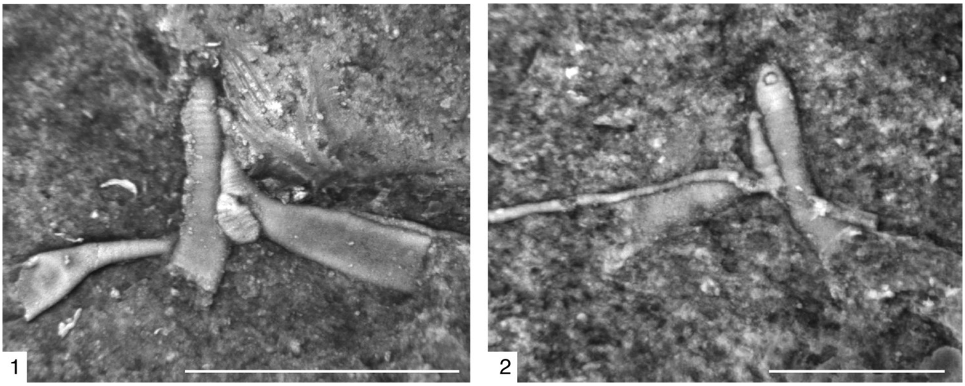

FIG. 169. Proximal development in *Paradelograptus* ERDTMANN, MALETZ, & GUTIERREZ-MARCO, 1987. *1*, specimen on slab with GSC 118739, obverse view showing sicular bitheca, sinistral development (*Adelograptus antiquus* T. S. HALL, 1899 in Jackson & Lenz, 2000, fig. 7A); *2*, GSC 118750, reverse view, sinistral development, crossing canal of $th1^1$ broken off (*P. onubensis* ERDTMANN, MALETZ, & GUTIERREZ-MARCO, 1987 in Jackson & Lenz, 2000, fig. 11A); specimens from Road River Formation, Yukon, Canada; scale bars, 1 mm (new).

mens known from relief material (Fig. 169). In most taxa, however, the origin of $th1^1$ is in the lower part of the prosicula (WILLIAMS & STEVENS, 1988; MALETZ, 2004). SKOGLUND (1961, fig. 5B) described and illustrated a high prosicular origin of $th1^1$ in *Prokinnegraptus multiramosus* (SKOGLUND, 1961), but this is based on fragmentary material and additional specimens are not available. This feature might indicate a secondarily derived condition.

The presence of bithecae is very difficult to verify in early members of the Sigmagraptidae because the stipes are extremely slender and thecal details are difficult to see. A sicular bitheca is present in some early species of the genus *Paradelograptus* (Fig. 166, Fig. 169.1), but not in derived taxa of the genus. The sicular bitheca is short and wide and opens in the crotch between the sicula and $th1^1$ with the aperture directed toward the reverse side of the colony. Thecal bithecae have not been recognized in *Paradelograptus* and are unlikely to be present due to the dorsal origins of the very slender prothecae.

The Sigmagraptidae are characterized by the ability to generate a variety of thecal elaborations. The thecal length may vary considerably along the stipes in a number of taxa. Because the thecae generally have a low overlap and inclination, lengthening of thecae and increase of thecal overlap provides a means of stability and rigidity for the stipes. A cross section of a distal stipe can cut through five or six thecae in mature specimens of *Maeandrograptus*. In *M. leptograptoides* (MONSEN, 1937), thecal overlap increases distally and stipes widen considerably; whereas in the robust *M. schmalenseei*, thecal length remains constant, with overlap remaining at three thecae. The changes in seen in *M. leptograptoides* occur independently in the sinograptid genera *Holmograptus* and *Nicholsonograptus*, in which thecal overlap is low in the proximal portion of the stipe but very high in the extremely robust distal portion. The thecal apertures can be simple as in *Paradelograptus*, but considerable elaborations are present in some younger forms.

Branching in the Sigmagraptidae is either progressive with regular or irregular dichotomous branching (*Paradelograptus*, *Anomalograptus*, *Allograptus*) or monoprogressive as exemplified by the genera *Goniograptus* and *Sigmagraptus*. Dichotomous lateral branching was reported in *Trichograptus,* but no cladial branching has been observed.

The genus *Azygograptus* lost all capacity for branching and bears a single, typically curved, slender stipe. MALETZ (2004) described an unusual sigmagraptine taxon without a proximal dichotomy as sigmagraptine sp. 3. The species has a typical slender sigmagraptine sicula with low prosicular origin of th1[1]. The first dichotomy is formed as a distal dichotomy only after two successive monocalycal thecae have developed from th1[1].

The Sigmagraptidae are herein differentiated into a number of informal groups, but only for easier reference; no taxonomic implications are intended and a taxonomic differentiation of subgroups has to be left to the future when better material is known.

The following are multiramous to single-stiped genera with simple thecae.

Sigmagraptus RUEDEMANN, 1904, p. 701 [**S. praecursor;* OD] [=*Hemigoniograptus* JIN & WANG, 1977, p. 81 (type, *H. declinatus,* OD), syn. by MU & others, 2002, p. 329]. Sigmagraptines with single order of progressive branching followed by monoprogressive branching, forming two main zigzag-shaped stipes and numerous lateral stipes; proximal end isograptid, dextral, with long and slender sicula; thecae simple with low thecal overlap and without apertural elaborations. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone–*Didymograptellus bifidus* Biozone): Australia, New Zealand, China, Canada, USA, Norway.——FIG. 170,*4a–c.* **S. praecursor; 4a,* lectotype, NYSM 16006, Deep Kill, New York, USA (Cooper & Fortey, 1982, fig. 60c); *4b,* holotype of *Hemigoniograptus declinatus* JIN & WANG, 1977, IV75045 (repository unknown), Qiaotingzhe Formation, central Hunan, China (Jin & Wang, 1977, fig. 7,*1*); *4c*, GSC 79889, mature specimen, Cow Head Group, western Newfoundland, Canada (Williams & Stevens, 1988, fig. 75H). All scale bars, 1 mm.

Acrograptus TZAJ 1969, p. 142 [**Didymograptus affinis* NICHOLSON, 1869, p. 240; OD]. Slender sigmagraptine with two horizontal to declined stipes; sicula small, triangular; proximal development artus type; thecae slender and with low thecal overlap or with distally increasing overlap. *Middle Ordovician* (*Darriwilian, ?Levisograptus dentatus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): worldwide.——FIG. 171,*4a–b.* **A. affinis* (NICHOLSON); *4a,* lectotype (selected by ELLES & WOOD, 1901, p. 24), NHMUK PI Q.3108; *4b,* possible topotype, NHMUK PI Q.5858a, low relief showing th2[1] originating on distal end of th1[1] (*arrow*), indicating artus-type development; Llanvirn (Darriwilian), Tarn Moor Formation, Aik Beck, east of Ullswater, Cumbria, UK, scale bars, 1 mm (Rushton, 2000a, Atlas, Folio 1.1).

Azygograptus NICHOLSON & LAPWORTH in NICHOLSON, 1875, p. 269 [**A. lapworthi;* OD] [=*A.* (*Eoazygograptus*) OBUT & SENNIKOV, 1984a, p. 100 (type, *A. coelebs* LAPWORTH, 1880a, p. 159, OD, syn. by BECKLY & MALETZ, 1991, p. 896); =*A.* (*Metazygograptus*) OBUT & SENNIKOV, 1984a, p. 101 (type, *A. suecicus* MOBERG, 1892a, p. 342, OD, syn. by BECKLY & MALETZ, 1991, p. 896)]. Single-stiped tubarium; th1[1] originating from metasicula, growing downward first or immediately outward from lower part of metasicula; stipe either straight or dorsally curved; sicula straight to slightly curved, moderate widening toward aperture; thecae simple, elongate, and inclined at low angle to the dorsal margin and with low thecal overlap; prothecal folds in one species. [The type material of *A. lapworthi*, from Hodgson How Quarry (1 km west of Keswick, UK), has not yet been identified]. *Lower Ordovician* (*upper Floian, Tetragraptus phyllograptoides* Biozone)–*Middle Ordovician* (*lower Darriwilian, Levisograptus austrodentatus* Biozone): China, Czech Republic, UK, Germany, Norway, Spain, Sweden, Canada, Argentina, Bolivia.——FIG. 171,*2a–b. A. suecicus; 2a,* lectotype, SGU 5247; *2b,* paratype, SGU 5248; Killeröd, Scania, Sweden, scale bars, 1 mm (Moberg, 1892a, pl. 8,*1* and 8,*2,* respectively).——Fig. 171,*2c.* **A. lapworthi,* NIGP 32222, southwest China, scale bar, 1 mm (on slab with Mu & others, 1979, pl. 38,*11*).

Catenagraptus VANDENBERG, 2018b, p. 4 [**C. communalis;* OD]. Assemblages of pseudotubaria resembling those of *Azygograptus* but linked by thread-like structures (aulons) of variable length that join fallosiculae to adjacent pseudotubaria. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone): Australia.——FIG. 170,*6.* **C. communalis,* holotype, NMV P318828, Victoria, Australia, scale bar, 1 mm (VandenBerg, 2018b, fig. 2D).

Etagraptus RUEDEMANN, 1904, p. 644 [**Tetragraptus* (*Etagraptus*) *lentus;* M]. Four-stiped to multiramous horizontal sigmagraptines with simple thecae and low thecal inclination; proximal development isograptid, dextral; branching regular. *Lower Ordovician* (*Floian, Didymograptellus bifidus* Biozone)–*Middle Ordovician* (*Dapingian, Isograptus maximodivergens* Biozone): Australia, New Zealand, Norway, Sweden, China, Canada, USA.——FIG. 170,*2a.* **E. lentus,* syntype, NYSM 6064, scale bar, 1 mm (new).——FIG. 170,*2b–c. E. tenuissimus* (HARRIS & THOMAS, 1942), holotype, NMV P32110, along with detail of thecal style (*c*), Chewtonian 2 (Lower Ordovician) Campbelltown, Allotment 41B, Victoria, Australia; scale bars, 1 mm (VandenBerg, 2008a, Atlas, Folio, 2.35). Specimen was subsequently prepared and has much longer distal stipes.

Jiangnanograptus XIAO & CHEN, 1990, p. 99 [**J. undulatus;* OD]. Multiramous sigmagraptines with two declined to reclined first-order stipes and short first and second branching divisions; third- to fifth-order stipes long and slender; branching appears to be triple due to elongated metathecae; proximal development unknown. *Middle Ordovician* (*lower Dapingian, Azygograptus suecicus* Biozone): China (Jiangnan Region).——FIG. 170,*1.* **J. undulatus*, Yc77-333 (repository of material unknown), Yushan, China, scale bar, 1 mm (Xiao & Chen, 1990, fig. 9).

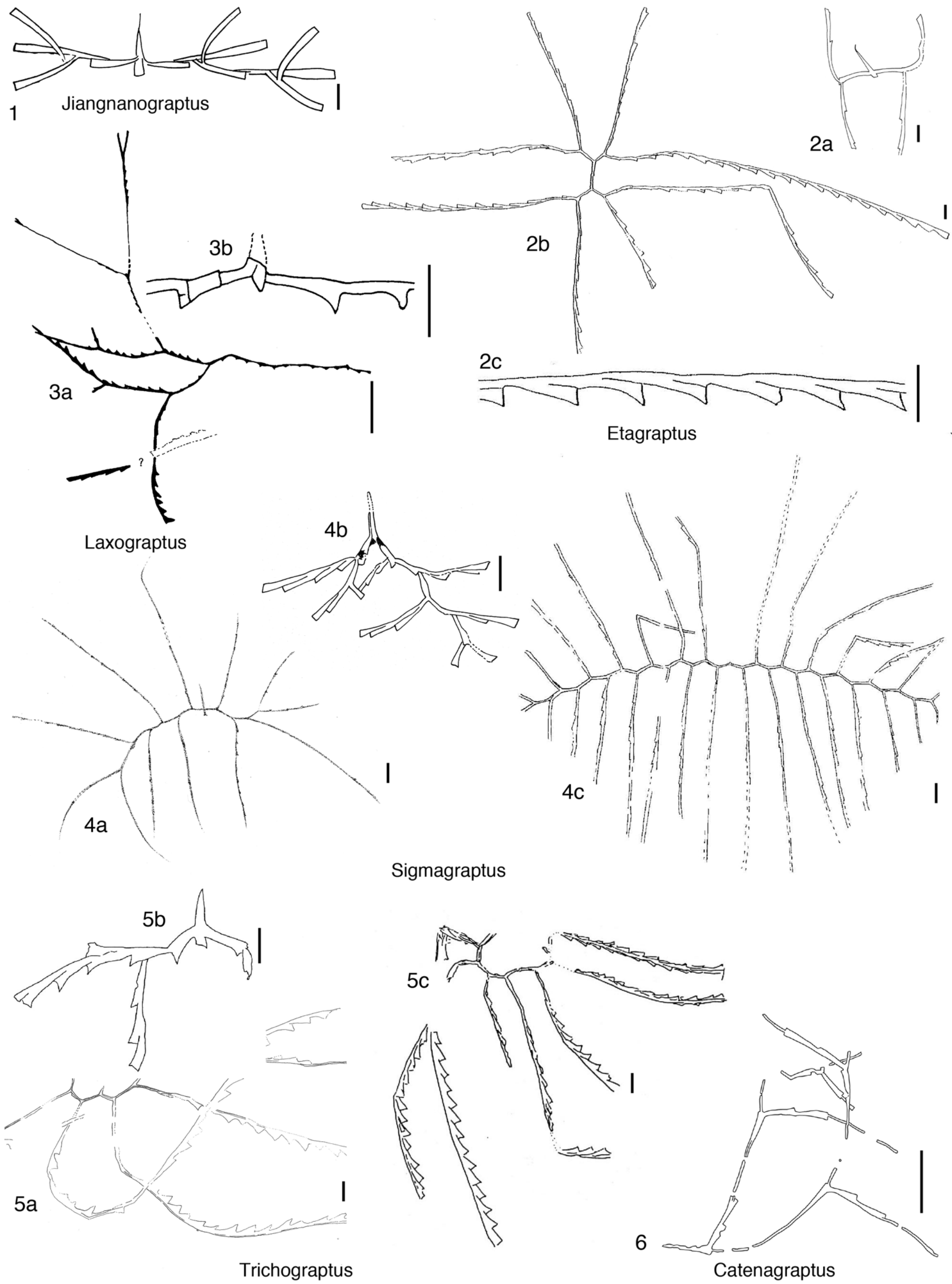

FIG. 170. Sigmagraptidae (p. 270–272).

Laxograptus COOPER & FORTEY, 1982, p. 269 [**Zygograptus irregularis* HARRIS & THOMAS, 1941, p. 310; OD]. Sigmagraptines with stipes of two or more orders in which dichotomies after the first dichotomy are delayed and placed irregularly; progressive branching; thecae simple with low overlap; indistinct rutella in some species. *Lower Ordovician* (*lower Floian, Paratetragraptus approximatus* Biozone)–?*Middle Ordovician* (*Dapingian, Isograptus maximodivergens* Biozone): worldwide.——FIG. 170,*3a–b*. **L. irregularis* (HARRIS & THOMAS), holotype, NMV P32124; *3a,* full

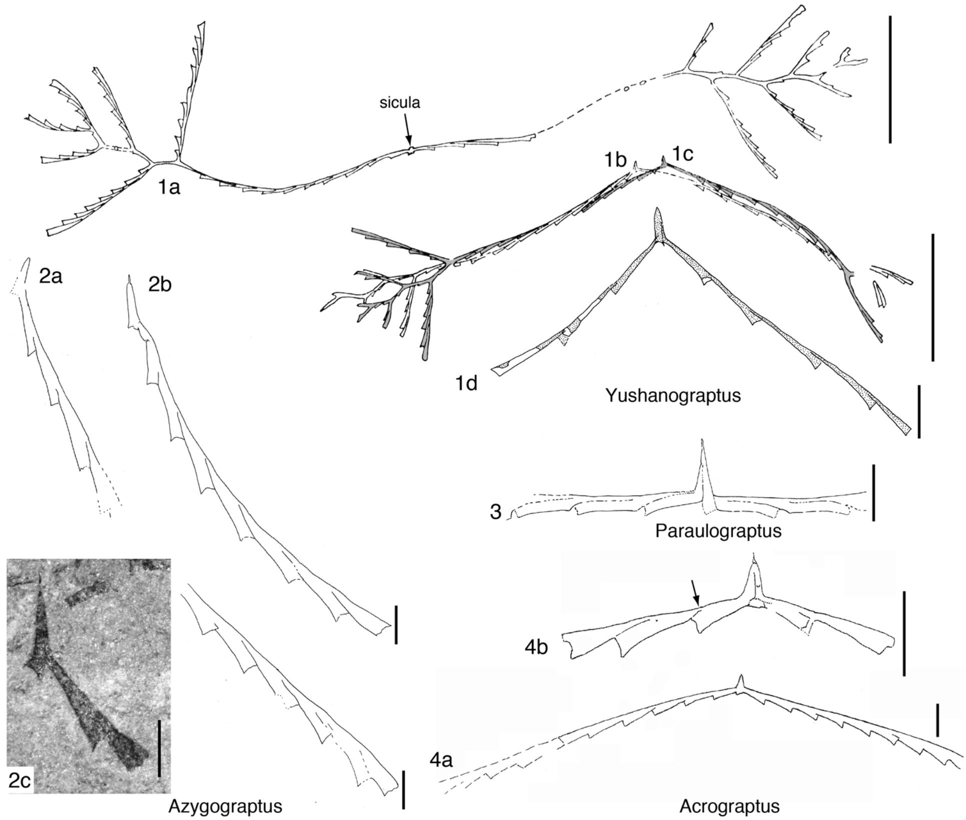

FIG. 171. Sigmagraptidae (p. 270–272).

specimen, scale bar, 5 mm; *3b,* close-up showing proximal end of holotype; Scotts Gully, Castlemaine, Victoria, Australia, scale bar, 1 mm (Rickards & Chapman, 1991, fig. 73 and 61, respectively).

Paraulograptus BOUČEK, 1973, p. 74 [**P. expectatus;* OD]. Two-stiped horizontal sigmagraptines with low-inclined, geniculate thecae and high thecal overlap distally. *Middle Ordovician* (*Darriwilian, Corymbograptus retroflexus* Biozone, *Expansograptus ferrugineus* horizon): Czech Republic.——FIG. 171,*3.* **P. expectatus,* holotype, UUG-BB 85, proximal end, Šarka Formation, Krušná hora, Czech Republic, scale bar, 1 mm (adapted from Bouček, 1973, fig. 23).

Trichograptus NICHOLSON, 1876, p. 248 [**Dichograptus fragilis* NICHOLSON, 1869, p. 232; OD]. Horizontal to subhorizontal sigmagraptine with two curved main stipes; lateral second-order stipes originating on one side of main stipes through normal dichograptid, but lateral branching; proximal development isograptid, dextral, with distinct asymmetry of crossing canals; thecae simple dichograptid, low overlaping tubes. *Lower Ordovician* (*Floian, Baltograptus vacillans* Biozone)–*Middle Ordovician* (*Darriwilian, Didymograptus artus* Biozone): Australia, UK, Ireland, Norway, Argentina.——FIG. 170,*5a.* **T. fragilis* (NICHOLSON), holotype, NHMUK PI Q.1, Tarn Moor Formation, Thornship Beck, Shap, Cumbria (Lake District), UK, scale bar, 1 mm (VandenBerg, 2008b, Atlas, Folio 2.26).——FIG. 170,*5b–c. T. dilaceratus* (HERRMANN, 1885), Diabasbrottet, Hunneberg, Sweden; *5b,* MB.G. DI 894/1301-2, small specimen showing sicular shape; *5c,* MB.G. DI 894/1291-1, large specimen showing lateral branching of curved main stipes; scale bars, 1 mm (new).

Yushanograptus CHEN, SUN, & HAN, 1964, p. 236 [**Y. separatus;* OD] [=*Pendeosalicograptus* JIAO, 1981, p. 65 (type, *P. zhejiangensis,* OD), syn. herein]. Multiramous sigmagraptines with long first-order stipes and monoprogressive distal branching; thecal style simple, dichograptid with low thecal overlap. *Middle Ordovician* (*Dapingian, Didymograptus abnormis* Biozone): China.——FIG. 171,*1a–d.* **Y. separatus; 1a,* paratype, NIGP 14515; *1b,* paratype, NIGP 14516; *1c,* holotype, NIGP 14514; *1d,* NIGP 168219, AEP 27, proximal end in obverse view; scale bars 1 mm (*1a–1c,* Chen, Sun, & Han, 1964, fig. 1; *1d,* new).

The following are multiramous to two-stiped genera with simple thecae, differentiated rutellum on sicula and typically with lateral lobes.

Eotetragraptus BOUČEK & PŘIBYL, 1952a, p. 7 [**Graptolithus quadribrachiatus* HALL, 1858, p. 125; OD]. Four-stiped sigmagraptines with simple, rutellate, commonly considerably curved thecae; stipes pendent to reclined and reflexed, rarely with dorsal spines; short and wide sicula with distinct rutellum and lateral apertural lobes; proximal development isograptid, dextral, with symmetrically placed slender crossing canals; thecal style simple, widening tubes with rutellate apertures, often with slight lateral lobes. *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone–*Pterograptus elegans* Biozone): worldwide.——FIG. 172,*4a–b*. *E. quadribrachiatus* (HALL); *4a,* syntype, GSC 928b, specimen shows the distinct rutellum on the sicula, Lévis, Quebec, Canada, scale bar, 1 mm (new); *4b,* GSC 132327, obverse view of flattened proximal end, Bay Cove, western Newfoundland, Canada, scale bar, 1 mm (new).——FIG. 172,*4c*. *E. acanthonotus* (GURLEY, 1896), scale bar, 1 mm (new; reconstruction based on Maletz, 1997b, fig. 7N).

Goniograptus M'COY, 1876, p. 129 [**Didymograpsus thureaui;* M]. Sigmagraptines with two orders of progressive branching, followed by unlimited monoprogressive branching forming four zigzag main stipes; proximal end isograptid, dextral; extended rutellum on sicula; thecae dichograptid with short rutella; moderate to high thecal overlap; thecal shape variable, from low inclined and considerably widening to high overlap and strong curvature towards aperture. *Lower Ordovician* (*upper Floian, Tshallograptus fruticosus* Biozone)–*Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone): Australia, New Zealand, China, Norway, Sweden, Canada, USA, Argentina.——FIG. 172,*1a–b*. **G. thureaui; 1a*, holotype, NMV P12215; *1b*, GSC 125786, proximal end; scale bars, 1 mm (new).

Harrisgraptus VANDENBERG, 2019a, p. 35 [**Didymograptus eocaduceus* HARRIS, 1933]. Two-stiped tubaria with habit ranging from strongly reclined to horizontal; sicula and proximal thecae adorned with prominent rutella; thecae have curved ventral walls. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone): Australia, New Zealand.[VANDENBERG (2019a) referred the genus to the Phyllograptidae.]——FIG. 172,*5a–c*. **H. eocaduceus* (HARRIS), Victoria, Australia; *5a,* NMV P319254, specimen with distally overlapping stipes; *5b,* ectotype, NMV P13800 l; *5c, Didymograptus hemicyclus* HARRIS, 1933, (syn. of *H. eocaduceus*) lectotype, NMV P13797; scale bars, 1 mm (VandenBerg, 2019a, fig. 2F, 2C, and 2H, respectively).

Keblograptus RIVA, 1992, p. 316 [**Didymograptus bidens* KEBLE, 1927, p. 157; OD]. Sigmagraptines with two slender, declined to pendent stipes; sicula short and triangular; sicular aperture with strong rutellum and often with lateral lobes; thecae curved, distinctly widening aperturally and with gentle prothecal folds in some species. *Lower Ordovician* (*upper Floian, Didymograptellus bifidus* Biozone)–*Middle Ordovician* (*lower Dapingian, Isograptus lunatus* Biozone): Australia, New Zealand, China, Norway, Canada, USA.——FIG. 172,*3a*. **K. bidens* (KEBLE), holotype, OU 2512, Cape Providence, Chalky Inlet, Southland, New Zealand, scale bar, 1 mm (Riva, 1992, fig. 2A).——FIG. 172,*3b*. *K. mendicus* (KEBLE & HARRIS, 1934), GSC 81778, proximal end, western Newfoundland, Canada, scale bar, 1 mm (new).——FIG. 172,*3c*. *K. geminus* MALETZ, 2004, holotype, GSC 125734, Martin Point south, western Newfoundland, Canada, scale bar, 1 mm (Maletz, 2004, fig. 5E).

Praegoniograptus RICKARDS & CHAPMAN, 1991, p. 91 [**Goniograptus thureaui clonograptoides* HARRIS & THOMAS, 1939, p. 55; OD]. Multiramous sigmagraptines with several orders of progressive branching followed by monoprogressive branching; thecae simple with low overlap. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone): Australia (Victoria), Canada (Newfoundland).——FIG. 172,*2*. **P. clonograptoides* (HARRIS & THOMAS), holotype, NMV P32169, Campbelltown, Victoria, Australia, scale bar, 10 mm (new).

The following are genera with long thecal overlap and differentiated apertures, commonly with increasing overlap distally.

Jishougraptus GE, 1988, p. 208 [**J. mui;* OD]. Sigmagraptines with a single deflexed stipe; dorsal stipe margin somewhat undulate but without pronounced prothecal folds; sicula long and slender with $th1^1$ origin in middle part of metasicula or close to sicular aperture; thecae long and slender with high overlap and increasing overlap distally; apertural elaborations indistinct; thecae may be geniculate. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone)–*Middle Ordovician* (*lower Dapingian, Azygograptus suecicus* Biozone or *Baltograptus minutus* Biozone): China, Norway, Sweden.——FIG. 173,*4a–b*. **J. mui; 4a,* juvenile, showing sicula shape; *4b,* holotype, NIGP 104481, fragment showing thecal style; scale bars, 1 mm (new).——FIG. 173,*4c*. *J. novus* BECKLY & MALETZ, 1991, paratype, PMO 118.593, latex cast, Tøyen Shale, Oslo, Norway, scale bar, 1 mm (Beckly & Maletz, 1991, pl. 1,*9*).

Maeandrograptus MOBERG, 1892a, p. 344 [**M. schmalenseei;* M]. Horizontal to subhorizontal and reclined sigmagraptines with two stipes; stipes increased thecal overlap distally; thecae long and slender; sicula with long and parallel-sided prosicula and long metasicula; aperture of metasicula typically but not necessarily isolated; thecae with rutella and sometimes lateral lappets; prothecal folds and undulating thecae in some species. *Lower Ordovician* (*upper Floian, Tshallograptus fruticosus* Biozone)–*Middle Ordovician* (*lower Dapingian, Isograptus maximus* Biozone): China, Norway, Sweden, Canada.——FIG. 173,*3a*. *M. mobergi* (TÖRNQUIST, 1901), holotype, LO 1642T, reverse view, drawing of latex cast, Killeröd, Scania, Sweden, scale bar, 1

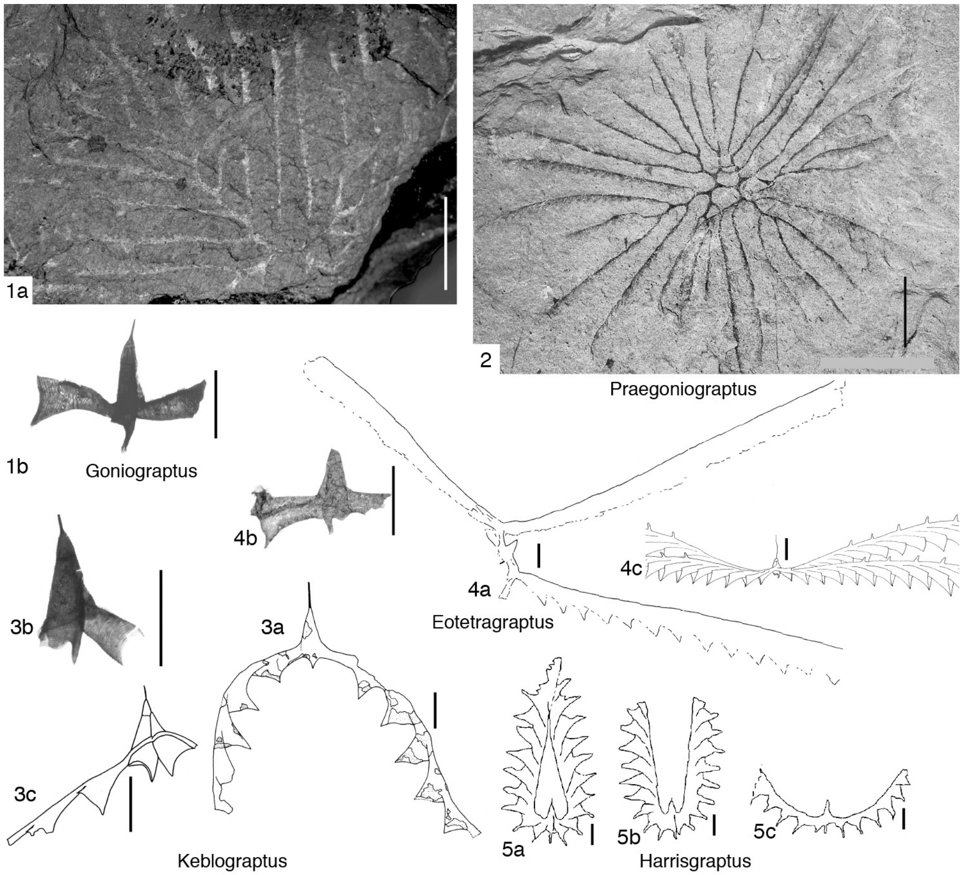

FIG. 172. Sigmagraptidae (p. 273).

mm (new).——FIG. 173,*3b–c*. **M. schmalenseei; 3b,* lectotype, SGU 5255, reverse view; *3c,* paratype, SGU 5257, obverse view, showing long sicula; Killeröd, Scania, Sweden, scale bars, 1 mm (Bulman, 1932c, pl. 9).——FIG. 173,*3d. M. leptograptoides* (MONSEN, 1937), PMU 23165/2, reverse view, drawing of latex cast, Nipan, Jemtland, Sweden, scale bar, 1 mm (new).

Oslograptus JAANUSSON, 1965, p. 427 [**O. peculiaris;* M]. Sigmagraptines with a subhorizontal to pendent tubarium; thecal apertures positioned in distinct excavations formed by thecal folding. *Lower Ordovician* (*upper Floian, Didymograptellus bifidus* Biozone): Norway, Canada.——FIG. 173,*1*. **O. peculiaris,* holotype, PMO 73669, drawing of latex cast, Old Quarry, Slemmestad, Norway, scale bar, 1 mm (new).

Perissograptus WILLIAMS & STEVENS, 1988, p. 88 [**Tetragraptus pygmaeus* RUEDEMANN, 1904, p. 664; M]. Sigmagraptine with four reclined stipes; proximal end with stipes diverging high on sicula, leaving apertural part of sicula free pending; thecae with distinct rutella. *Lower Ordovician* (*upper Floian, Didymograptellus bifidus* Biozone): Australia, ?China, Canada, USA.——FIG. 173,*2a–c*. **P. pygmaeus* (RUEDEMANN); *2a,* lectotype (designated by WILLIAMS & STEVENS, 1988, p. 89), NYSM 6073, Deep Kill, New York, USA, (Ruedemann, 1904, pl. 12,*14*); *2b–c,* GSC 82059, obverse (*b*) and reverse (*c*) views of isolated specimen; all scale bars, 0.5 mm (infrared photos; new).

The following are multiramous to two-stiped genera with distinctly differentiated pro- and metathecae, generally with apertural elaborations (Kinnegraptidae of MU, 1974). VANDENBERG (2019b) referred these taxa to his revised subfamily Kinnegraptinae.

Kinnegraptus SKOGLUND, 1961, p. 391 [**K. kinnekullensis;* OD]. Multiramous to two-stiped sigmagraptines with horizontal to subhorizontal tubarium; proximal end isograptid or artus type, with dextral or sinistral development; origin of $th1^1$ in prosicula or metasicula; thecae with very slender prothecae and distinctly widening metathecae; strong rutella

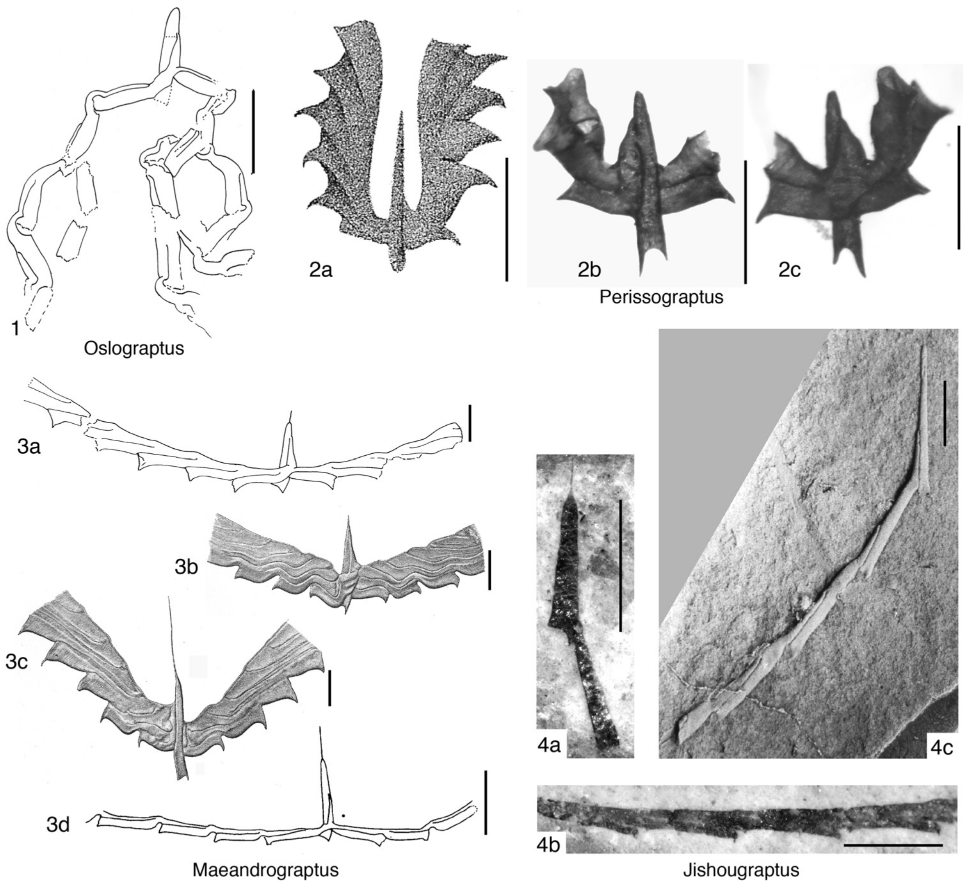

FIG. 173. Sigmagraptidae (p. 273–274).

on all thecae. *Middle Ordovician* (*lower Dapingian, Isograptus victoriae lunatus* Biozone): Norway, Sweden, Canada, Argentina.——FIG. 174,*2a–c*. **K. kinnekullensis; 2a,* PMU 23633; *2b,* PMU 23634; *2c,* holotype PMU 23635; Hällekis, Västergötland, Sweden; scale bars, 0.5 mm (Skoglund, 1961, fig. 1B, 1D, and 2A, respectively).

Lignigraptus VANDENBERG, 2019b, p. 25 [**Tetragraptus chapmani* KEBLE & HARRIS, 1934; OD; =*Paradelograptus mosseboensis* ERDTMANN, MALETZ, & GUTIERREZ-MARCO, 1987, syn. by VANDENBERG, 2019b, p. 27]. Proximal end with characteristic asymmetrical appearance; sicula skewed toward stipe 1; thecae long and slender; metathecal walls may be attenuated, thecal apertures bearing elongate rutellae. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone–*Didymograptellus bifidus* Biozone): Australia, Canada, USA, Sweden, Norway, China.——FIG. 174,*4a–b*. **L. chapmani* (KEBLE & HARRIS); *4a,* holotype, NMV P14378, combination of counterparts, Victoria, Australia (new); *4b,* holotype of *Paradelograptus mosseboensis,* MB.G. Di 614/119; scale bars, 1 mm (new).

Paradelograptus ERDTMANN, MALETZ, & GUTIERREZ-MARCO, 1987, p. 114 [**P. onubensis;* OD]. Multiramous to biramous, horizontal to subhorizontal sigmagraptines with distinct differentiation of thecae; prothecae very slender, metathecae considerably widening; thecal apertures simple and straight to bearing moderate rutellum; bithecae present in earlier species, at least on sicula. *Lower Ordovician* (*upper Tremadocian, Hunnegraptus copiosus* Biozone–*Floian, Tshallograptus fruticosus* Biozone): Australia, New Zealand, China, Sweden, Norway, Scotland, Spain, Canada, USA, Argentina, Bolivia.——FIG. 174,*1a–b*. **P. onubensis;1a,* holotype, DPM 4107, scale bar, 1 mm (Erdtmann, Maletz & Gutierrez Marco, 1987, fig. 5A); *1b,* paratype, DPM 4001, large specimen, scale bar, 5 mm (Erdtmann, Maletz, & Gutierrez-Marco, 1987, fig 7C).

Prokinnegraptus MU, 1974, p. 233 [**Kinnegraptus multiramosus* SKOGLUND, 1961, p. 397; OD]. Multiramous sigmagraptines with horizontal to subhorizontal tubarium; proximal end isograptid type, with dextral or sinistral development; origin of $th1^1$ high in prosicula; thecae with very low thecal

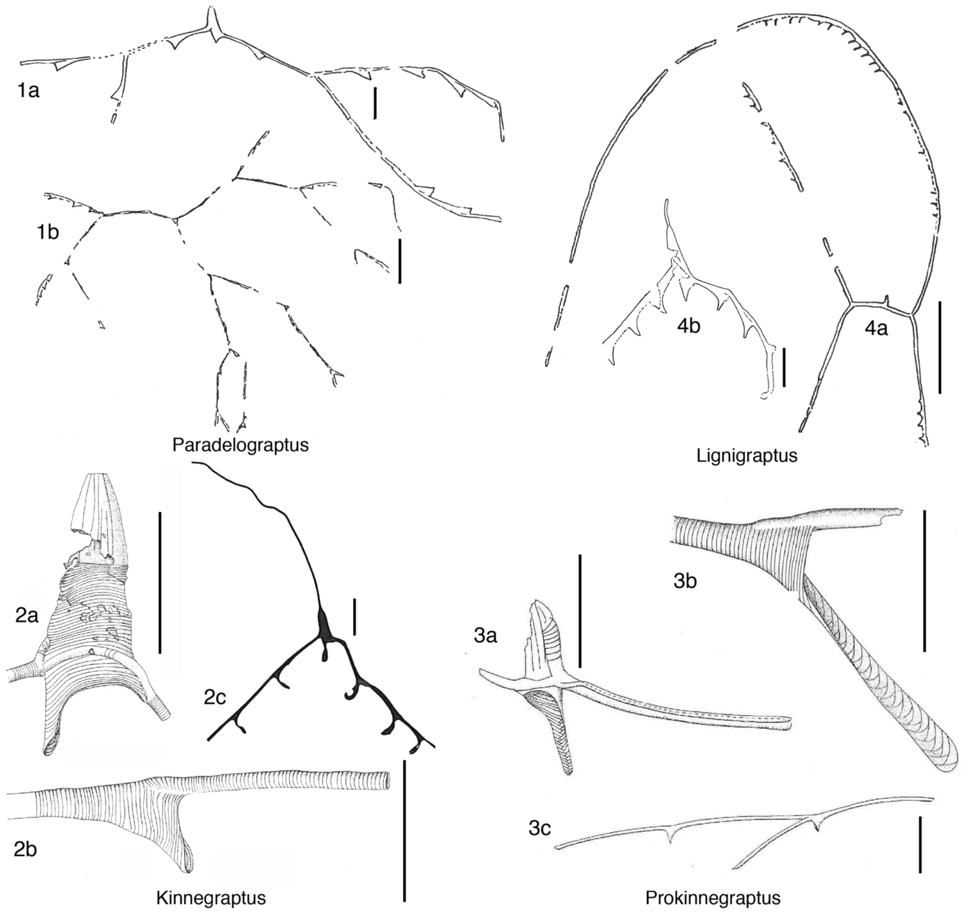

FIG. 174. Sigmagraptidae (p. 274–276).

overlap, very slender prothecae and distinctly widening metathecae; strong rutella on all thecae. *Middle Ordovician* (*lower Dapingian, Isograptus victoriae lunatus* Biozone): Norway, Sweden.——FIG.174,*3a–c*. **P. multiramosus* (SKOGLUND), Norra Skagen drill core near Hällekis, Västergötland, Sweden; *3a,* PMU 23639, Norra Skagen at 61.10 m; *3b,* PMU 23641, Norra Skagen at 62.16 m; *3c,* PMU 23642, Norra Skagen at 62.72 m; scale bars, 0.5 mm (Skoglund, 1961, fig. 5B, 6B, and 7, respectively).

Family SINOGRAPTIDAE Mu, 1957

[Sinograptidae MU, 1957, p. 387] [incl. Paradidymograptidae WANG, 1975, p. 8; Atopograptidae HARRIS, 1926, p. 59; Pseudodichograptinae HSÜ & CHAO, 1976, p. 126; Pseudotetragraptinae HSÜ & CHAO, 1976, p. 129; Holmograptinae HSÜ & CHAO, 1976, p. 132]

Planktic, graptoloid graptolites with multiramous to single-stiped, horizontal to subhorizontal tubaria; sicula parallel sided with straight aperture, perpendicular to the stipes; sicular aperture with ventral rutellum or dorsal and ventral rutellate extensions; proximal development isograptid, dextral, with symmetrically placed crossing canals close to the aperture of the sicula; origin of th1^1 in the lower part of the prosicula; thecal style typically complex with distinctly differentiated pro- and metathecae; thecal elaborations such as prothecal folds, lateral apertural lappets, rutella, or spines common. *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone–*Nicholsonograptus fasciculatus* Biozone): worldwide.

The Sinograptidae includes graptolites with a symmetrical proximal development and distinctly elaborated thecal apertures

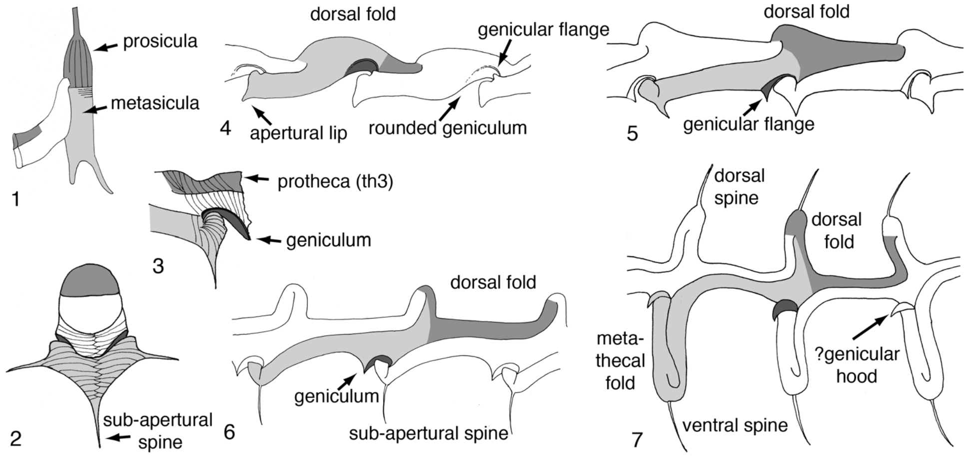

FIG. 175. Thecal development in *Holmograptus* KOZŁOWSKI, 1954 and *Sinograptus* MU, 1957. *1*, *Nicholsonograptus fasciculatus* (NICHOLSON, 1869), sicula and first theca (based on GSC 132333); *2, Holmograptus* sp., reconstruction, apertural view, showing lateral and subapertural thecal spines; *3*, *Holmograptus* sp., lateral view to show geniculum and apertural elaborations, note the lack of lateral spines; *4*, *Anomalograptus reliquus* (CLARK 1924), simple theca with median position of dorsal fold; *5*, *N. fasciculatus* with dorsal fold prior to origin of next theca and elaborated geniculum; *6*, *Holmograptus* sp. with strong dorsal fold and subapertural spine; *7*, *Sinograptus typicalis* MU, 1957 with dorsal and metathecal folds, dorsal and ventral spines (new; based in part on Kozłowski, 1954 and Zhang & Fortey, 2001).

(Fig. 175). The members of the family possess the most elaborate thecal structure known from Lower to Middle Ordovician multiramous graptolites. The thecae are fairly simple in early members, with low thecal inclination. Derived taxa may have considerable prothecal and metathecal folding, forming strongly elongated thecae. The thecal apertures may be complexly formed with introverted apertures and lateral lobes (see KOZŁOWSKI, 1954, fig. 6). Subapertural ventral spines and even paired lateral spines may be present. Dorsal spines are developed on the top of the prothecal folds in some *Holmograptus* species (MALETZ, 2009, fig. 5L–N, fig. 6H) and especially in *Sinograptus* (Fig. 175.7). The details of the thecal constructions are unknown, as fuselli are rarely preserved, even in isolated material. Therefore, the construction of the prothecal and metathecal folds is unclear. The material of KOZŁOWSKI (1954) may indicate a considerable widening of the prothecae before the insertion of a new theca (see Fig. 175.3). In this case, the dorsal prothecal folding may actually represent this widening, and the initial protheca of the succeeding theca is only part of the fold.

Sinograptus MU, 1957, p. 400 [**S. typicalis;* OD]. Two-stiped, declined sinograptids with exagerated prothecal and metathecal folds; prothecal and ventral apertural spines present; proximal development isograptid, dextral, with symmetrically placed crossing canals. *Middle Ordovician, Darriwilian* (*upper Holmograptus lentus* Biozone): China, Canada.——FIG. 177,*2*. **S. typicalis,* holotype, NIGP 8909, scale bar, 1 mm (Zhang, 2008, Atlas, Folio 2.94).

Allograptus MU, 1957, p. 388 [**A. mirus;* OD] [=*Pseudodichograptus* CHU, 1965, p. 97 (type, *P. confertus,* OD), syn. herein; =*Pseudojanograptus* HSÜ & CHAO, 1976, p. 131 (type, *?Allograptus fluitans* MU, 1957, p. 391; OD), syn. herein; =*Pseudotetragraptus* HSÜ & CHAO, 1976, p. 129 (type, *P. corniculiformis,* OD), syn. herein]. Multiramous, horizontal to subhorizontal sinograptids with as many as three orders of stipes; progressive branching, often with delayed dichotomies; thecae with variably developed prothecal folding, often possessing a geniculum and apertural elaborations. *Middle Ordovician* (*lower Darriwilian, Levisograptus austrodentatus* Biozone–*Levisograptus dentatus* Biozone): ?Australia, China, Canada, Norway.——FIG. 176,*3a*. *A. confertus* (CHU, 1965), holotype, repository unknown, scale bar, 5 mm (Chu, 1965, fig. 4).——FIG. 176,*3b*. *Allograptus* sp., GSC 102622, Lévis, Quebec, Canada, scale bar, 1 mm (Maletz, 1997b, fig.

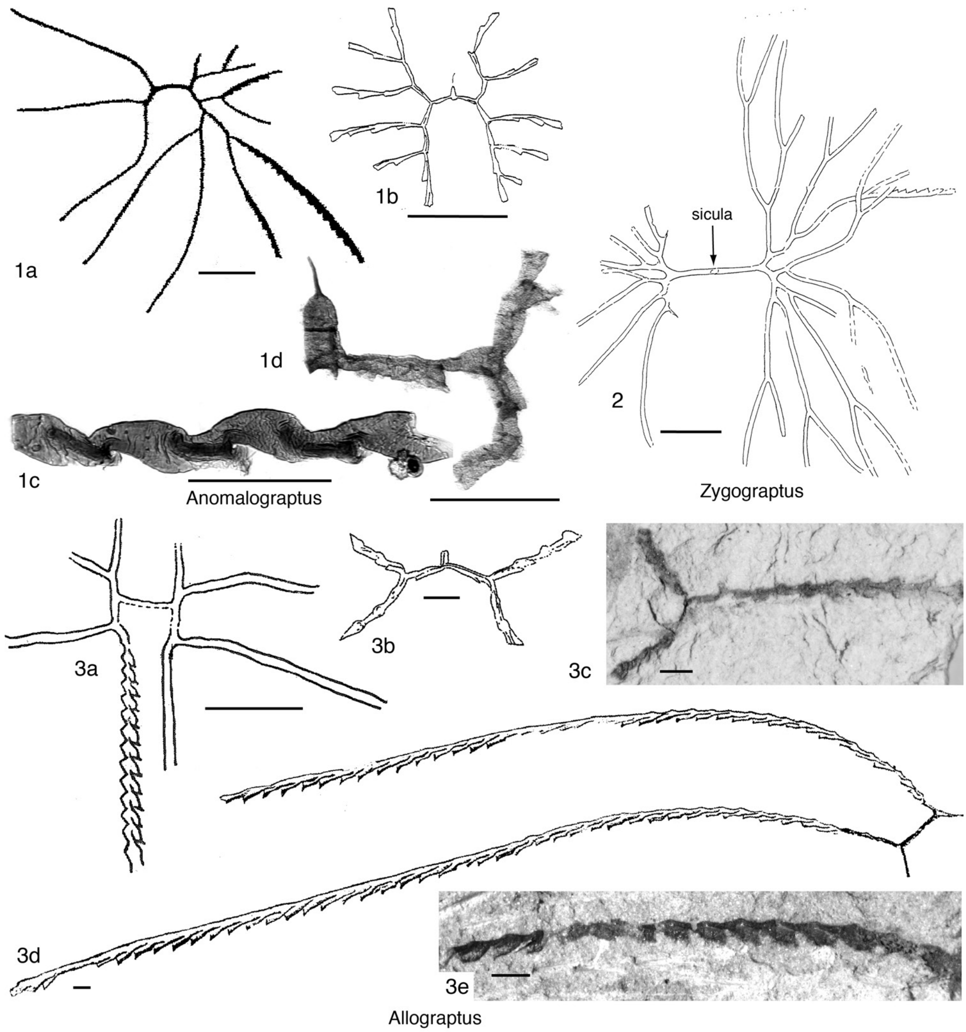

FIG. 176. Sinograptidae (p. 177–180).

8G).——FIG. 176,*3c*. **A. mirus,* holotype, NIGP 8867, internal cast, scale bar, 1 mm (new).——FIG. 176,*3d*. *A. corniculiformis* HSÜ & CHAO, 1976, holotype, No. 1575 (repository unknown), scale bar, 1 mm (Hsü & Chao, 1976, pl. 6,*3e*).——FIG. 176,*3e*. *A. fluitans* MU, 1957, holotype, NIGP 8874, scale bar, 1 mm (new).

Anomalograptus CLARK, 1924, p. 63 [**A. reliquus;* OD] [=*Brachiograptus* HARRIS & KEBLE, 1932, p. 43 (type, *B. etaformis,* OD), syn. herein; =*Pseudologanograptus* HSÜ & CHAO, 1976, p. 126 (type, *P. geniculatus*), syn. herein]. Multiramous, horizontal to subhorizontal sinograptids; first distal dichotomies usually at th3^1 and th3^2; branching crowded proximally with two to four progressive dichotomies; no distal branching; thecae with variably developed prothecal folding, sometimes possessing geniculum and apertural elaborations. *Middle Ordovician* (*lower Darriwilian, Levisograptus austrodentatus* Biozone–*Levisograptus dentatus* Biozone): Australia, New Zealand, China, Canada, USA, Argentina, Bolivia, UK.——FIG. 176,*1a, c–d*. **A. reliquus; 1a,* holotype, MCZ 101403, near Victoria Hotel, Lévis, Quebec, Canada, scale bar, 5 mm (Clark, 1924, pl. 5,*4*); *1c,* GSC 140007, stipe fragment; *1d,* GSC 139257, isolated proximal end; *Levisograptus dentatus* Biozone; *1c–d* from Western Brook Pond, bed 52, Cow Head Group, western Newfoundland, Canada; scale bars, 1 mm (new).——FIG. 176,*1b. A. etaformis* (HARRIS & KEBLE, 1932), paratype, NMV P24109, scale bar, 5 mm (VandenBerg, 2008c, Atlas, Folio 2.22).

Atopograptus HARRIS, 1926, p. 59 [**A. woodwardi;* OD]. Horizontal to declined, two-stiped

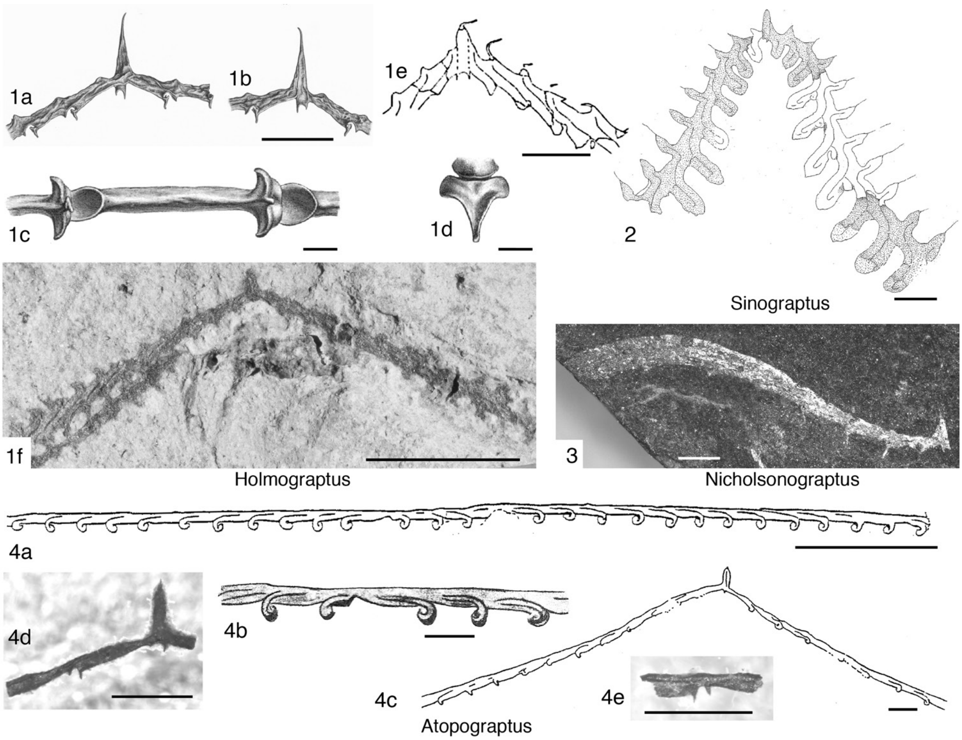

FIG. 177. Sinograptidae (p. 277–280).

sinograptid tubarium; thecae with strong geniculum and apertural hood. *Middle Ordovician, middle Darriwilian* (*Holmograptus lentus* Biozone–*Nicholsonograptus fasciculatus* Biozone): Australia (Victoria), China, Sweden, Canada.——FIG. 177,*4a–b*. **A. woodwardi; 4a,* holotype, NMV P 3352, janograptid specimen, Bendigo east, Victoria, Australia, scale bar 5 mm (VandenBerg, 2008d, Atlas, Folio 2.19); *4b,* enlargement of proximal end, scale bar, 1 mm (Harris, 1926, fig. 14).——FIG. 177,*4c*. *A. dubitatus* (HARRIS & THOMAS, 1935), NMV P31948, Strathfieldsaye, Bendigo, Victoria, Australia, scale bar, 1 mm (VandenBerg, 2008d, Atlas, Folio 2.19).——FIG. 177,*4d–e*. *Atopograptus* sp; *4d,* GSC 133519, proximal end; *4e,* GSC 133519, distal theca; Les Méchins, Quebec, Canada; scale bars, 1 mm (Maletz, 2009, fig. 5).

Holmograptus KOZŁOWSKI, 1954, p. 432 (French translation, p. 124) [**Didymograptus callotheca* BULMAN, 1932c, p. 16; OD] [=*Tylograptus* MU, 1957, p. 393, English translation, p. 428 (type, *T. regularis,* OD), syn. herein; =*Paradidymograptus* MU, GEH & YIN in MU & others, 1962, p. 73 (type, *P. acanthonotus,* OD), syn. herein]. Two-stiped pendent or declined to subhorizontal sinograptids; stipes with high, commonly distally increasing thecal overlap; thecal apertures elaborate, constricted with variously modified ventral and dorsal lips; prothecal folds may be present as well as spines on prothecae or thecal apertures. *Middle Ordovician* (*lower Darriwilian, Levisograptus austrodentatus* Biozone–*Holmograptus lentus* Biozone): worldwide.——FIG. 177,*1a–d*. **H. callotheca* (BULMAN); *1a–b,* holotype, NRM-PZ Cn 71835, in reverse (*a*) and obverse (*b*) views, Grå Vaginatumkalk, Hälludden, Öland, Sweden; scale bar 1 mm (Bulman, 1936a, pl. 2,*1–2*); *1c–d*, NRM-PZ Cn 71836, stipe fragment in ventral view (*c*) showing laterally expanded thecal aperture, and geniculum and apertural view (*d*) showing apertural complexity, scale bars, 0.1 mm (Bulman, 1936a, pl. 2,*10* and 2,*13,* respectively).——FIG. 177,*1e*. *H. spinosus* (RUEDEMANN, 1904), NYSM 5916, lectotype, scale bar, 1 mm (Archer & Skevington, 1973, fig. 1a).——FIG. 177,*1f*. *H. regularis* (MU, 1957), holotype, NIGP 8892, flattened specimen, Ningkuo Shale of Tawu, Changshan, China, scale bar 5 mm (new).

Nicholsonograptus BOUČEK & PŘIBYL, 1952a, p. 14 [**Didymograpsus fasciculatus* NICHOLSON, 1869, p. 241; OD] [=*Sinazygograptus* WANG & WU in WANG & others, 1977, p. 305 (type, *S. spinatus,* OD), syn. herein; =*Hemiholmograptus* HSÜ & CHAO, 1976, p. 137 (type, *Azygograptus falciformis* EKSTRÖM, 1937, p. 32, OD), syn. herein]. Sinograptid with a single, strongly S-shaped stipe; thecae with prothecal folds and distally increasing thecal overlap; thecae with distinct geniculum and introverted apertures; thecal

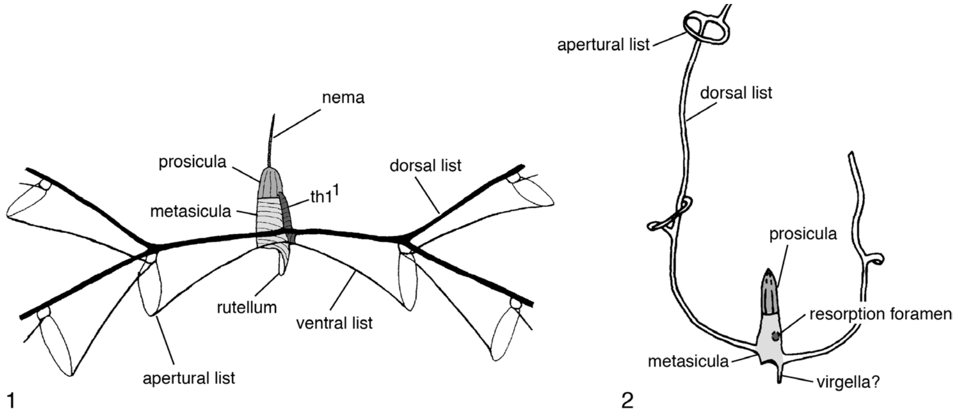

FIG. 178. Morphology of the Abrograptidae. *1, Jiangshanites* (?) *dubius* MALETZ, 1993 with prosicular origin of th1[1] and rutellate sicular aperture (adapted from Maletz, 1993, fig. 1); *2, Dinemagraptus warkae* KOZŁOWSKI, 1951, showing metasicular origin of th1[1] (resorption foramen) and possible presence of virgellar spine (adapted from Finney, 1980, fig. 11).

apertures elaborated as in *Holmograptus*, typically with long ventral spines; sicular aperture with ventral rutellum and even longer dorsal, typically curved rutellum. *Middle Ordovician* (*Darriwilian, Nicholsonograptus fasciculatus* Biozone): worldwide.——Fig. 177,*3*. **N. fasciculatus* (NICHOLSON), LO 3315T, holotype of *Azygograptus falciformis* EKSTRÖM, 1937, Röstånga, Scania, Sweden, scale bar, 1 mm (new).

Zygograptus HARRIS & THOMAS, 1941, p. 308 [**Graptolithus abnormis* HALL, 1858, p. 117; OD]. Multiramous sinograptids with strongly elongated funicle, followed by number of progressive dichotomies at close intervals of 1–3 thecae; thecae low inclined, slightly undulating, with slight apertural elaborations. *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone–*Levisograptus dentatus* Biozone): ?China, Canada.——FIG. 176,*2*. **Z. abnormis* (HALL), holotype, GSC 941, Darriwilian, Lévis, Quebec, scale bar, 5 mm (new).

Family ABROGRAPTIDAE Mu, 1958

[Abrograptidae MU, 1958, p. 261]

Tubarium either multiramous or consisting of two reclined uniserial or biserial stipes, scandent and possibly dipleural; sicula completely sclerotized with strongly developed rutellum; fusellum of stipes reduced, preservable parts consisting of lists outlining thecae; thecal apertures represented by circular lists attached to ventral and dorsal lists; proximal-end development dichograptid, probably isograptid, dextral. *Middle Ordovician* (*lower Darriwilian, Levisograptus austrodentatus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): China, UK, Poland, Canada, USA.

The Abrograptidae are herein regarded as a family closely related to the Sigmagraptidae. The inclusion is based on the shape and development of the sicula and the origin of the first theca in isolated material of *Jiangshanites* (?) *dubius* found in the *Levisograptus austrodentatus* Biozone of western Newfoundland. It is the only abrograptid for which isolated material exists, with the exception of the poorly understood *Dinemagraptus*. It has a small, cone-shaped sicula with a prosicular origin of th1[1] (Fig. 178.1), but the later proximal development is not known from the specimens, because the crossing canals are not sclerotized. The species produces a multiramous tubarium in which the first distal branching occurs after the production of the first thecal pair. *Dinemagraptus warkae* KOZŁOWSKI, 1951 is known from a single proximal end showing a sicula with a possible virgellar spine and a metasicular origin of th1[1], indicated by a resorption foramen in the middle of the metasicula (Fig. 178.2).

The recognition of the abrograptids is generally based on fragmented list structures on shale surfaces, and in many specimens,

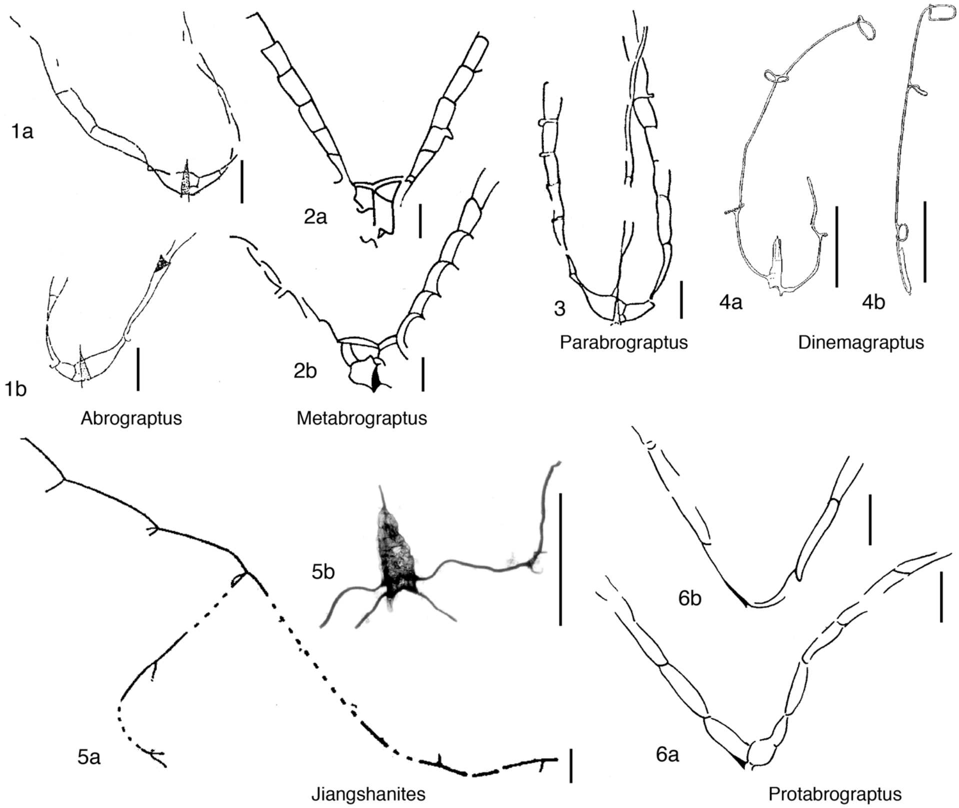

FIG. 179. Abrograptidae (p. 281–282).

the development is uncertain. For example, *Protabrograptus* is very poorly preserved and cannot be recognized as a genuine graptolite.

Abrograptus MU, 1958, p. 261 (English text, p. 264) [**A. formosus;* OD]. Reclined, two-stiped abrograptid; stipes comprised of two longitudinal filaments and apertural rings or crossbars, forming rectangular meshes; sicula with one crossing canal; development probably corresponding to *bifidus* stage of dichograptid type. *Middle Ordovician* (*upper Darriwilian, Hustedograptus teretiusculus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): China, Canada, USA.——FIG. 179,*1a–b*. **A. formosus; 1a,* paratype, NIGP 9402; *1b,* holotype, NIGP 9397 (type material for both missing at NIGP); *Nemagraptus gracilis* Biozone, Kiangshan, Chekiang, China; scale bars, 1 mm (Mu, 1958, pl. 1).

Dinemagraptus KOZŁOWSKI, 1951, p. 292 (French text, p. 87) [**D. warkae;* OD]. Reclined, two-stiped abrograptid; stipes reduced to dorsal and apertural lists; sicula completely sclerotized. *Middle Ordovician* (*upper Darriwilian,* ?*Hustedograptus teretiusculus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): China, Poland.——FIG. 179,*4a–b*. **D. warkae,* glacial boulder, Stara Warka, ~50 km south of Warsaw, Poland, scale bars, 1 mm (Kozłowski, 1951, fig. 1).

Jiangshanites MU & QIAO, 1962, p. 3 (English text, p. 7) [**J. ramosus;* OD]. Multiramous abrograptid; completely sclerotized sicula with sclerotized initial part of first theca; prosicular origin of th1^1; thecae constructed of dorsal, ventral, and apertural lists. [The type material is very incomplete and a sicula is not recognizable in the specimens.] *Middle Ordovician* (*Darriwilian, Levisograptus austrodentatus* Biozone)–*Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): China, Canada.——FIG. 179,*5a*. **J. ramosus,* syntype, NIGP 13240, fragment, scale bar, 1 mm (Mu & Qiao, 1962, pl. 2,*12*).——FIG. 179,*5b*. *J.* (?) *dubius* MALETZ, 1993, GSC 102774, sicula with incomplete first thecal pair, Western Brook Pond, south section, Newfoundland, Canada, scale bar, 1 mm (Maletz, 1993, fig. 2,1).

Metabrograptus STRACHAN, 1990, p. 934 [**M. scoticus;* OD]. Biserial-uniserial abrograptid; uniserial stipes

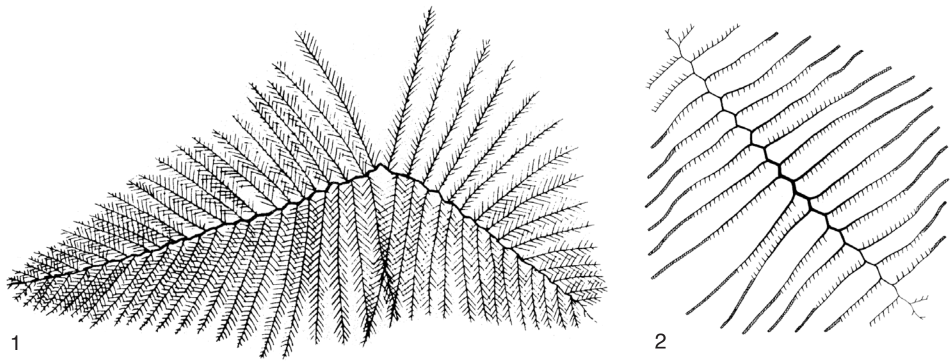

FIG. 180. *Thamnograptus capillaris* (EMMONS, 1855) reconstructions. *1,* RUEDEMANN reconstruction (1947, pl. 43, *7*); *2,* FINNEY reconstruction (1980, fig. 7).

diverge at an angle of 80° to 110°; sicula sclerotized. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): UK (Scotland), USA.——FIG. 179,*2a–b*. **M. scoticus; 2a,* holotype, BU 1336b; *2b,* paratype, BU 2150a; Glenkiln Shale, Birnock, UK, scale bars, 1 mm (Strachan, 1990, fig.1A and 1D, respectively).

Parabrograptus MU & QIAO, 1962, p. 2 [*P. tribrachiatus;* OD]. Scandent, ?biserial abrograptid; two ventrolateral lists connected with horizontal apertural lists on each side; two vertical lists in the center of the tubarium, probably connected to the sicula. *Upper Ordovician* (*Sandbian, Nemagraptus gracilis* Biozone): China.——FIG. 179,*3*. **P. tribrachiatus,* holotype, NIGP 13236, scale bar, 1 mm (Mu & Qiao, 1962, pl. 2.*1*).

Protabrograptus NI, 1981, p. 203 [**P. sinicus;* OD]. Minute tubarium with a generally rounded base, consisting of two reclined stipes, comprised of two longitudinal filaments (ventral and dorsal) and apertural rings or crossbars; sicula fully preserved, merging into the ventral filament of second stipe [This might not be a graptolite. A sicula cannot be recognized in the type material.] *Middle Ordovician* (*upper Darriwilian, Didymograptus jiangxiensis* Biozone): China (Wuning).——FIG. 179,*6a–b*. *P. sinicus; 6a,* paratype, NIGP 57943; *6b,* holotype, NIGP 57941; Wuning, Jiangxi, China, scale bars, 1 mm (Ni, 1981, fig. 1).

Suborder UNCERTAIN

Family THAMNOGRAPTIDAE Hopkinson & Lapworth, 1875

[Thamnograptidae HOPKINSON & LAPWORTH, 1875, p. 633]

Tubarium consisting of straight or flexuous stipes (first-order branches, number unknown) with widely spaced, second-order lateral branches comprised of narrow tubular thecae bearing strongly elongated rutella or hairlike spines; thecae of lateral, second-order branches possibly abruptly changing to dichograptid thecae distally; details of proximal development unknown. *Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone)–*Upper Ordovician* (*Katian, Climacograptus bicornis* Biozone): Australia, China, Sweden, USA.

HOPKINSON and LAPWORTH (1875) established the family Thamnograptidae for the two genera *Thamnograptus* and *Buthograptus* HALL, 1861b. FINNEY (1980) revised the family Thamnograptidae and excluded the genus *Buthograptus* as unrecognizable, following BULMAN (1970, p. 139), thus, incorporating a single genus into the family. Numerous species have been included in the genus *Thamnograptus* (referenced in RUEDEMANN, 1947), but most of them consist of slender indeterminable stipe fragments. In the restricted sense, the genus is used herein for a number of multiramous Middle Ordovician, possibly planktic graptoloids with very slender thecae and unknown tubarium development. Silurian taxa are excluded and may belong to other fossil groups. The genus *Wuninograptus* is herein included in the Thamnograptidae due to a similar development of the thecae during the Middle Ordovician (late Darriwilian) age. It is the only taxon of the family from which a proximal end has been described.

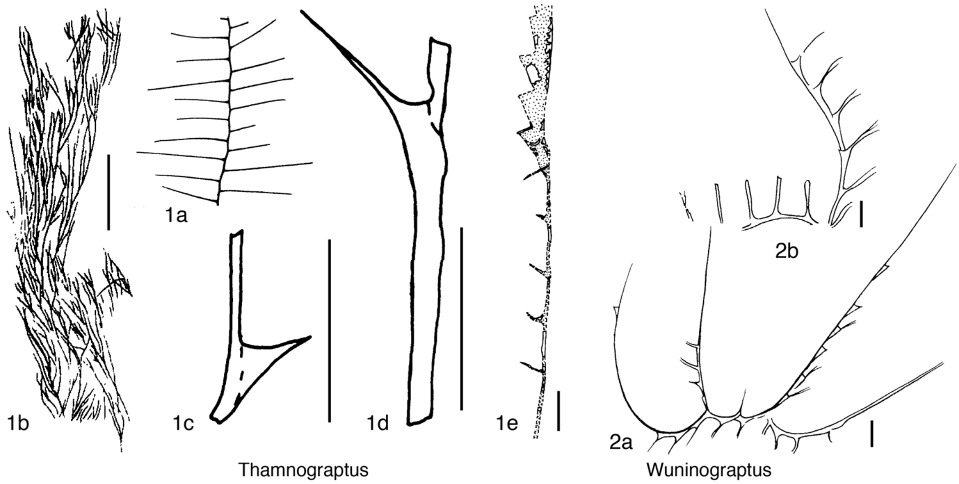

FIG. 181. Thamnograptidae Uncertain (p. 283).

Wuninograptus may otherwise be related to *Kinnegraptus*. If *Thamnograptus* is related to *Wuninograptus*, the genus could be included in the Sigmagraptidae.

MORPHOLOGY

The proximal development of the species of *Thamnograptus* is unknown as is the thecal style of most taxa. FINNEY (1980) described a few chemically isolated thecae and referred them to *T. capillaris* (EMMONS, 1855). The thecae are parallel sided through most of their length and bear a slightly widening aperture with long and slender ventral apertural spines. The thecal overlap is strongly reduced, but details of the fusellar construction are not available. According to FINNEY (1980), the thecae abruptly change to a dichograptid style in the distal parts of the second-order stipes (Fig. 180.2), but this is not confirmed from isolated material, and the illustrated shale specimens could be accidental associations of thamnograptid and acrograptid stipe fragments. The largest preserved colonies have thickened zigzag central stipes with thinner, alternating lateral stipes, similar to the tubarium construction in *Sigmagraptus*. Thus, the style of branching may be described as monoprogressive. Because all known specimens are flattened in shale, no details of the development are available.

Thamnograptus HALL, 1859b, p. 519 [**T. typus*, =*Nemagrapsus capillaris* EMMONS, 1855, p. 109, syn. by RUEDEMANN, 1908, p. 205; SD RUEDEMANN, 1908, p. 206]. Tubarium consisting of straight to slightly zigzag-shaped, flexible stipes (first-order branches, number unknown) with widely spaced, second-order lateral branches comprised of narrow tubular thecae bearing hairlike spines; thecae of lateral, second-order branches abruptly changing to dichograptid thecae distally; proximal development unknown. *Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone)–*Upper Ordovician* (*Katian, Nemagraptus gracilis* Biozone–*Climacograptus bicornis* Biozone): Australia, China, UK, Sweden, USA.——Fig. 181,*1a–e*. **T. capillaris* (EMMONS); *1a,* syntype of *T. typus* HALL, 1859b, whereabouts of specimen unknown, scale information unavailable (Hall, 1859b, fig. 2); *1b,* neotype (selected by FINNEY, 1980, p. 1190), NYSM 7368, Mount Merino, near Hudson, Columbia County, New York, USA, scale bar, 10 mm (Ruedemann, 1908, pl. 10,*5*); *1c–d,* individual thecae of neotype, scale bars, 0.5 mm (Finney, 1980, fig. 3); *1e,* OSU 32903, stipe fragment with abrupt change in thecal style, Athens Shale, Alabama, USA, scale bar, 1 mm (Finney, 1980, fig. 4F).

Wuninograptus NI, 1981, p. 204 [**W. quadribrachiatus;* OD]. Thamnograptid with three to four reclined stipes; sicula and thecae with a long, tongue-shaped apertural process and low thecal overlap; thecal apertures with thickened rim. *Middle Ordovician* (*upper Darriwilian, Didymograptus jiangxiensis* Biozone): China, Argentina.——FIG. 181,*2a–b*. **W. quadribrachiatus; 2a,* holotype, NIGP 54074; *2b,* NIGP 54077, thecal details on fragment

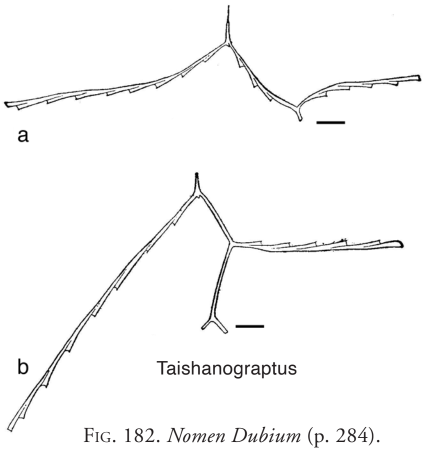

FIG. 182. *Nomen Dubium* (p. 284).

showing extended rutella; Jiangxi Province, China; scale bars, 1 mm (Ni, 1981, fig. 2,*4* and 2,*3,* respectively).

NOMEN DUBIUM

Taishanograptus LI & GE in LI, GE, & CHEN, 1987, p. 102 [**T. graciliramosus;* OD]. Sigmagraptines with slender stipes and widely spaced, irregularly placed dichotomies; thecae simple, low-inclined tubes of dichograptid type. *Middle Ordovician* (*lower Darriwilian, Cardiograptus amplus* Biozone): China. [The types are extremely poor and the presence of a sicula or proximal end is uncertain.]——FIG. 182,*a–b*. **T. graciliramosus; a,* syntype NIGP 76829; *b,* syntype, NIGP 76828; scale bars, 1 mm (Li, Ge, & Chen, 1987, fig. 2).

SUBORDER DICHOGRAPTINA

JÖRG MALETZ, BLANCA A. TORO, YUANDONG ZHANG, and
ALFONS H. M. VANDENBERG

Suborder DICHOGRAPTINA Lapworth, 1873

[Dichograptina LAPWORTH, 1873b, table 1, facing p. 555; *nom. transl.* OBUT, 1957, p. 19; *ex* Dichograptidae LAPWORTH, 1873b] [=suborder Didymograptina LAPWORTH, 1880f, p. 192 *nom. correct.* JAANUSSON, 1960, p. 309; *ex* section Didymograpta LAPWORTH, 1880f]

Multiramous to two-stiped graptoloids with biradiate isograptid proximal development and maeandrograptid proximal symmetry; colony shape scandent to reclined, horizontal, and pendent; prosicula small, with widening and much larger metasicula; thecae simple, widening tubes with or without rutellum; a sicular bitheca may be present in early taxa; branching dichotomous or cladial. *Lower Ordovician* (*upper Tremadocian, Hunnegraptus copiosus* Biozone)–*Middle Ordovician* (*upper Darriwilian, Pterograptus elegans* Biozone): worldwide.

INTRODUCTION

The Dichograptina is one of the two major groups of graptoloids originating from the earliest planktic graptolites of the family Anisograptidae (Fig. 183). According to MALETZ, CARLUCCI, and MITCHELL (2009), the Dichograptina and the Sinograpta (Sinograptina herein) can be regarded as sister groups. However, FORTEY and COOPER (1986) and LINDHOLM (1991) suggested a polyphyletic origin of derived graptoloids (non-bithecate graptoloids) from the Anisograptidae. Thus, the sister group relationship between the Anisograptidae and the supercohort Eugraptoloida (the Graptoloidea of BULMAN, 1970) as shown by MALETZ, CARLUCCI, and MITCHELL (2009) is unlikely to be correct and more research on the transition is needed.

LAPWORTH (1873b) understood the Dichograptidae as the group of genera that includes two-stiped to multiramous taxa with simple thecae and dichotomous bifurcation or lateral branching. He listed the genera *Didymograptus, Tetragraptus, Dichograptus, Loganograptus,* and *Clonograptus*. OBUT (1957) erected the suborder Dichograptina for the families Dichograptidae, Tetragraptidae, Bryograptidae, and Didymograptidae, essentially confirming the classification of LAPWORTH (1873b) for multiramous to pauciramous Lower to Middle Ordovician graptoloids. However, the name Dichograptina must be credited to LAPWORTH under the provisions of ICZN, 1999, Article 36. BULMAN (1970) used the term Didymograptina LAPWORTH, 1880f but included the Nemagraptidae, Dicranograptidae, and Phyllograptidae, taxa that are not closely related. The Didymograptina of BULMAN (1970) thus is a polyphyletic taxon and should not be used.

FORTEY and COOPER (1986) used the Dichograptina LAPWORTH, 1873b for the non-virgellate graptoloids and introduced the new term Virgellina for all virgellate graptoloids. They defined the Dichograptina as "graptoloids lacking bithecae and virgella" (FORTEY & COOPER, 1986, p. 640) and referred the two superfamilies Dichograptacea and Glossograptacea to the taxon. MALETZ, CARLUCCI, and MITCHELL (2009) introduced the supercohort Eugraptoloida as a monophyletic taxon defining all nonbithecate graptoloids. Of these, the stem reclinatids and the Pan-Tetragrapta would be included in the Dichograptina. MALETZ (2014b) referred four families to the Dichograptina: the Dichograptidae, Didymograptidae, Tetragraptidae, and the virgella-bearing Pterograptidae. He discussed the taxon as a paraphyletic unit with poor internal resolution.

MORPHOLOGY

The dichograptid sicula is known from few isolated specimens and details of its

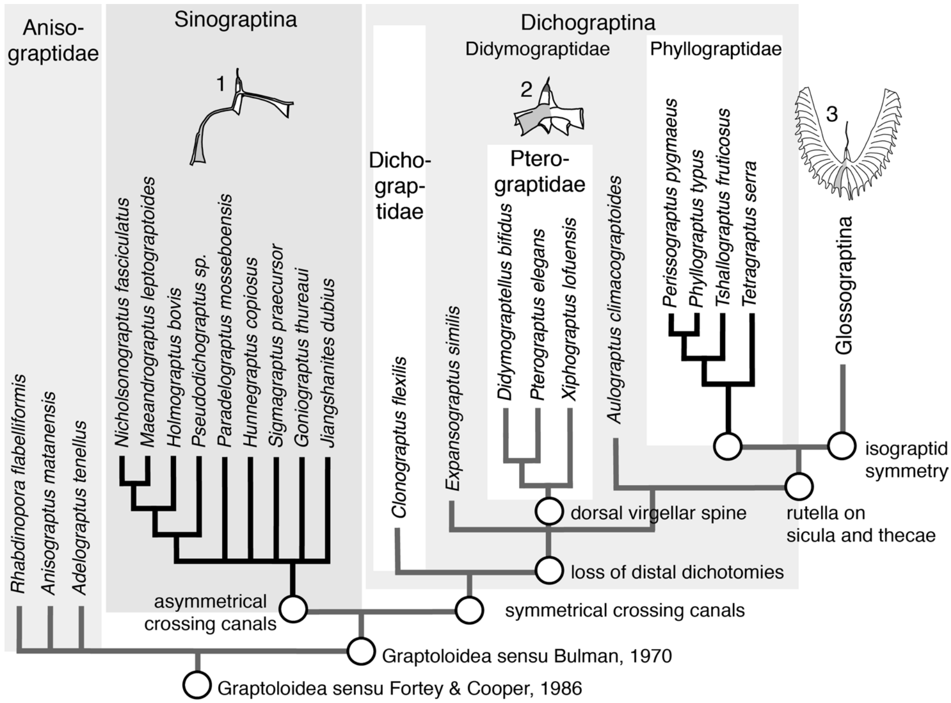

FIG. 183. Cladistic interpretation of the Dichograptina. The diagram also shows the different symmetries of the stipes in the Sinograptina (*1*), Dichograptina (*2*), and the glossograptid *Isograptus* (*3*) (adapted from Maletz, 2014b).

development are unknown for most species. However, a number of general features can be recognized (Fig. 184). It is easily differentiated from the sicula in the Sinograptina through the distinctly widening metasicula. The prosicula usually has less than one-quarter of the length of the sicula and widens gradually toward its aperture, as does the metasicula (Fig. 184.5–184.6).

The Dichograptina possess a distinct nema, which is formed as a slender rod at the tip of the prosicula. The nema is of variable length and may be quite long in some taxa but is rarely modified. It may be thickened considerably as in *Tshallograptus fruticosus* (HALL, 1858), but true nematularia, common in the Glossograptina and derived taxa, have not been described for the Dichograptina. The differentiation of the conus and cauda (Fig. 184) has rarely been discerned in the prosicula of isolated material of the Dichograptina and may not be present in many taxa. WILLIAMS and CLARKE (1999) illustrated dichograptid siculae from a variety of taxa and discussed the reduction of the cauda (not the conus—WILLIAMS and CLARKE, 1999, confused the terms conus and cauda) in early Floian taxa. These authors recognized a number of features modifying the sicula of early dichograptids, such as the differentiation of the pro- and metasicula, the diaphragm, and the development of longitudinal strengthening rods in the prosicula. The prosicula (conus) widens gradually from the apex, usually with a ratio of ~1:2, and commonly forms a long cone. In some derived taxa, however, the prosicula may be wider than long and form a wide, nearly triangular structure (e.g., *Expansograptus abditus* WILLIAMS & STEVENS, 1988). The spiral line is prominent in many specimens, and the spiral may be most dense toward the apex of the prosicula (the cauda).

Typically, the prosicula has a number of longitudinal rods secreted on the outside of the cone. In tubaria from the late Tremado-

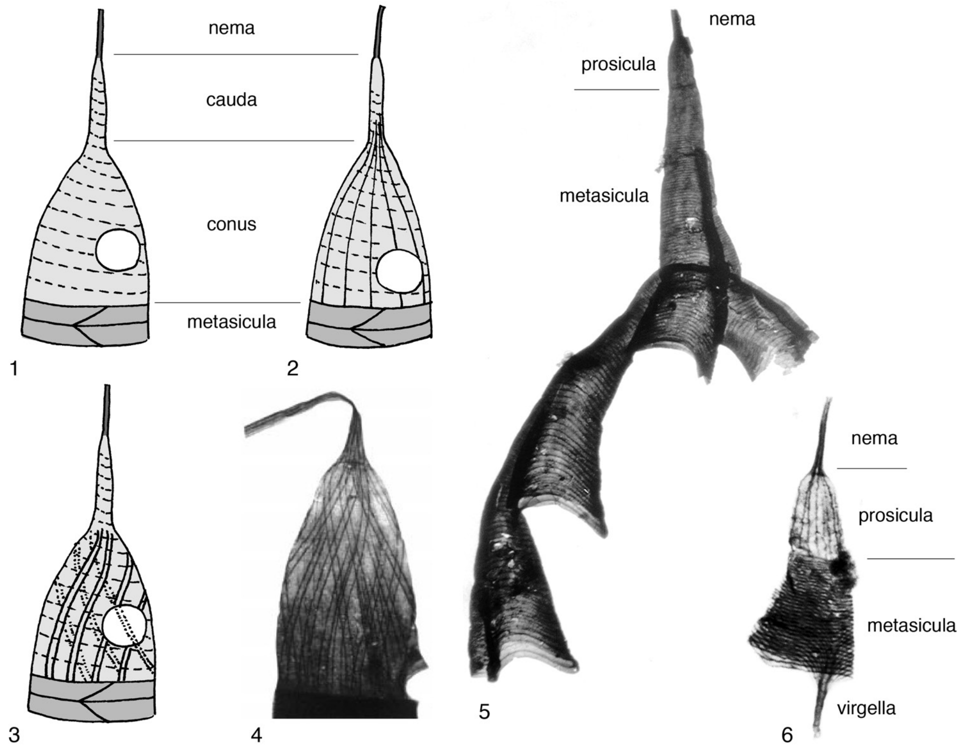

FIG. 184. Development of the sicula in Ordovician graptoloids. *1,* Anisograptidae; *2, Isograptus lunatus* HARRIS 1933; *3, Paratetragraptus approximat*us (NICHOLSON, 1873); *4, P. approximatus* (NICHOLSON,1873), transmitted light photo; *5, Tshallograptus fruticosus* (HALL, 1858), GSC 125727, isolated proximal end showing fuselli, western Newfoundland, Canada; *6, Phyllograptus typus* HALL, 1865, GSC 125754, sicula with virgellar spine and simple longitudinal rods on prosicula, western Newfoundland, Canada (*1–4,* adapted from Williams & Clarke, 1999; *5–6,* Maletz, 2004).

cian to early Floian, the longitudinal rods are paired (Fig. 184.3–184.4) and usually run somewhat obliquely down the prosicula. This is seen in a number of phyllograptids and expansograptids illustrated by WILLIAMS and CLARKE (1999). Individual longitudinal rods are present in isograptids and may be characteristic for axonophorans, e.g., *Rectograpus gracilis* (ROEMER, 1861); see KRAFT (1926).

The metasicula is a simple, gradually widening cone formed from numerous fuselli (Fig. 184.5–184.6). It may be straight or moderately to strongly bent or curved. When present, curvature of the sicula is usually most pronounced close to the aperture and may be enhanced by the development of a rutellum. The sicula is located in the center of the tubarium, and the plane of symmetry (bilateral plane in COOPER & FORTEY, 1982, fig. 8) cuts through it—termed maeandrograptid symmetry. A distinct ventral rutellum may be developed in derived dichograptids, but other apertural modifications of the sicula are rare.

The dorsal virgellar spine developed independently from a simple rutellum in *Phyllograptus* (Fig. 184.6) and in the Pterograptidae. MALETZ (2010a) discussed in detail the origin and evolution of the dorsal virgellar spine in the genus *Xiphograptus* and related taxa. The early xiphograptid *Didymograptellus* is the only member of this group that has an origin of th1^1 in the middle part of the prosicula combined with an unusually large, parallel-sided prosicula. Both are characters present in the early planktic graptoloids of the family

Anisograptidae but have not been recognized in any other Dichograptina. Thus, it may be possible that the pterograptids have an independent origin within the Anisograptidae and are not closely related to the rest of the Dichograptina.

Maletz, Carlucci, and Mitchell (2009) regarded the symmetrical branching (bifurcation) of the two first-order stipes as the defining character of the cohort Pan-Reclinata, a character that separates its members easily from the often highly asymmetrical development in the Sinograptina (Fig. 183). Both crossing canals grow symmetrically and at the same level across the reverse side of the sicula before forming the first stipes. The proximal end symmetry is maeandrograptid, a plesiomorphic character retained from the Anisograptidae, with the plane of symmetry passing through the sicula. $Th1^1$ and $th1^2$ are symmetrically placed flanking the sicula (Fig. 185.1–185.2).

The origin of $th1^1$ is generally in the lower portion of the prosicula, but in a few taxa it may be in the middle portion (e.g., *Didymograptellus*). A metasicular origin of $th1^1$ has been demonstrated for a few taxa of *Tetragraptus* (see Skevington, 1965) and from a population of *Tshallograptus fruticosus* (Fig. 184.5) from the *Didymograptellus bifidus* Biozone of western Newfoundland (Maletz, 2004) but has not been confirmed from other species. It is common in taxa of the Didymograptidae (Fig. 185.3–185.6).

The dichograptinid tubarium is generally based on a biradiate proximal end with $th1^2$ as the first dicalycal theca. However, in a number of taxa, the development may be replaced by an independently derived condition in which the dicalycal theca is $th1^1$ (artus-type development). The change in proximal development type from isograptid (Fig. 185.3–185.4) to artus (Fig. 185.5–185.6) is best known in the genus *Baltograptus*. In the early species *Baltograptus geometricus* (Törnquist, 1901) and *Baltograptus vacillans* (Tullberg, 1880b), the proximal development is isograptid (Maletz, 1994b; Toro & Maletz, 2008), but in some later taxa, it is artus type (Maletz & Ahlberg, 2011a; Maletz & Slovacek, 2013). An isograptid proximal development is present in most expansograptids, whereas *Cymatograptus bidextro* Toro & Maletz, 2008 has an artus-type development.

The first distal dicalycal thecae in the Dichograptina are $th3^1$ and $th3^2$, forming the tetragraptid proximal end with its biradiate development (Maletz, 1992). Later dicalycal thecae are commonly placed irregularly along the stipes to form multiramous colonies and are increasingly delayed distally (Lindholm & Maletz, 1989). Thus, the branching intervals become progressively longer.

The multiramous dichograptids of the family Dichograptidae are the most distinctive graptolites of the Dichograptina. They reached colony diameters of more than 80 cm in *Holograptus deani* Elles & Wood, 1902 specimens, similar to the earlier anisograptid *Paratemnograptus magnificus* (Pritchard, 1892). Colony development started from the sicula with two first-order stipes (biradiate condition). Consecutive dichotomous branching led to a multiramous colony with numerous terminal branches (Fig. 186.1). During the evolution of the Dichograptina, the number of branches became reduced and two-stiped Didymograptidae appeared early in the Floian.

Dichograptina encompasses the full range of colony shapes, ranging from scandent (*Phyllograptus*) through reclined (*Tetragraptus*), horizontal, declined, and deflexed to pendent forms (*Didymograptus*). Pendent and deflexed forms are most common in pauciramous taxa. *Tshallograptus fruticosus* is a typical example of a deflexed two- to four-stiped species. Branching in the Dichograptina in general is dichotomous, through a bifurcation, with the stipe divisions typically Y-shaped. With rare exceptions, it only occurs at the growing tips of stipes. Lateral branching is present in some multiramous taxa (e.g. *Schizograptus*), but the precise method of branching in these has not been determined as no relief material or isolated specimens are available. The

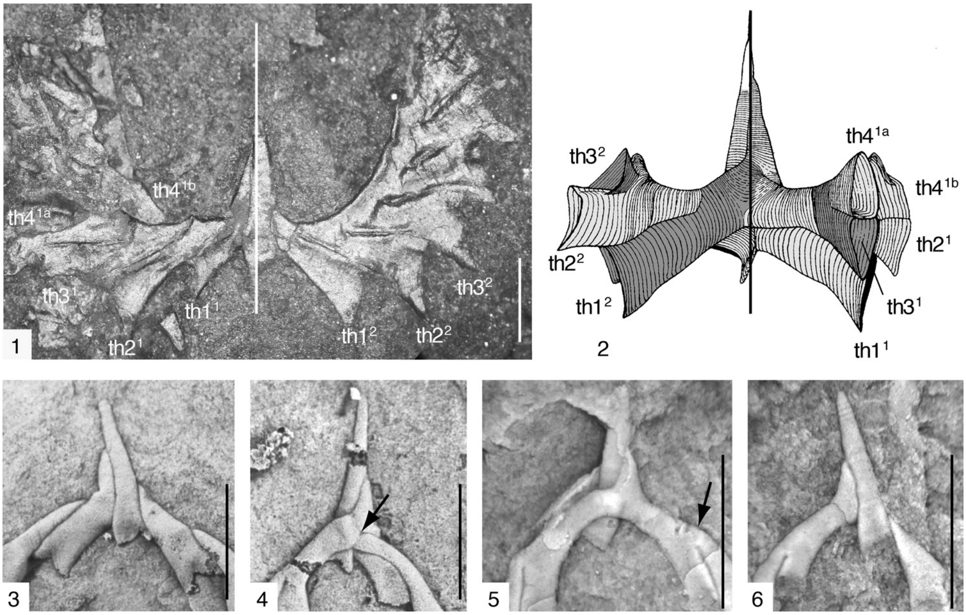

FIG. 185. Proximal development of the Dichograptina. *1, Tetragraptus reclinatus* ELLES & WOOD, 1902, LO 10598t, obverse view, *vertical line* shows line of symmetry, Lerhamn drill core, Sweden (new); *2, Tetragraptus* sp., reconstruction of proximal end in reverse view, *vertical line* shows line of symmetry, dicalycal thecae (th1², th3¹, th3²) in *darker gray* (adapted from Bulman, 1970, fig. 53); *3–4, Baltograptus vacillans* (TULLBERG, 1880b), PMU 23157, isograptid development in obverse (*3*) and reverse (*4*) views; *5–6, Baltograptus minutus* (TÖRNQUIST 1879), artus-type development in reverse (*5*) and obverse (*6*) views, PMU 23165, Nipan, Jemtland, Sweden, *arrows* in *4–5* indicate origin of th2¹; all scale bars, 1 mm (*3–6,* adapted from Maletz, 1994a).

number of terminal stipes has been regarded as important and was used to differentiate genera and species in the past. It is now generally accepted, however, that the number might be variable and a species of *Dichograptus* does not invariably bear eight stipes. A certain intraspecific variation is to be expected, but additional complications may have been introduced by accidental loss of stipes and damage to the colonies during their lifetime.

Lateral branching is typical in *Pterograptus* species, but here the branching occurs in the form of cladial branching (SKWARKO, 1974; MALETZ, 1994a). The origin of the new stipe is from the aperture of the parent theca. Branching in this case is not at the growing tip of the stipe but can occur at later stages in the growth of the colony.

The thecae of the Dichograptina are simple, aperturally widening tubes (Fig. 186.2–186.3). They range from straight to strongly ventrally curved. Apertural modifications are rare and include extended rutella in some taxa. A few taxa (e.g., *Aulograptus*) develop more complex thecal apertures with genicular flanges and thickened apertural rims. Prothecal folding is present in some taxa. The most pronounced prothecal folding is in the genus *Cymatograptus*, but the details of this thecal development are unknown.

In many species with low thecal inclination, the stipes are largely parallel sided and the thecal overlap is low. In other taxa, thecae are larger distally, and the initial parts of the stipes have considerable widening (Fig. 186.3). In some, this widening decreases markedly after the first few thecae, when the zooids apparently reached their maximum size. In others, thecal size increases distally, both in length and apertural width and inclination. This may be due to continued

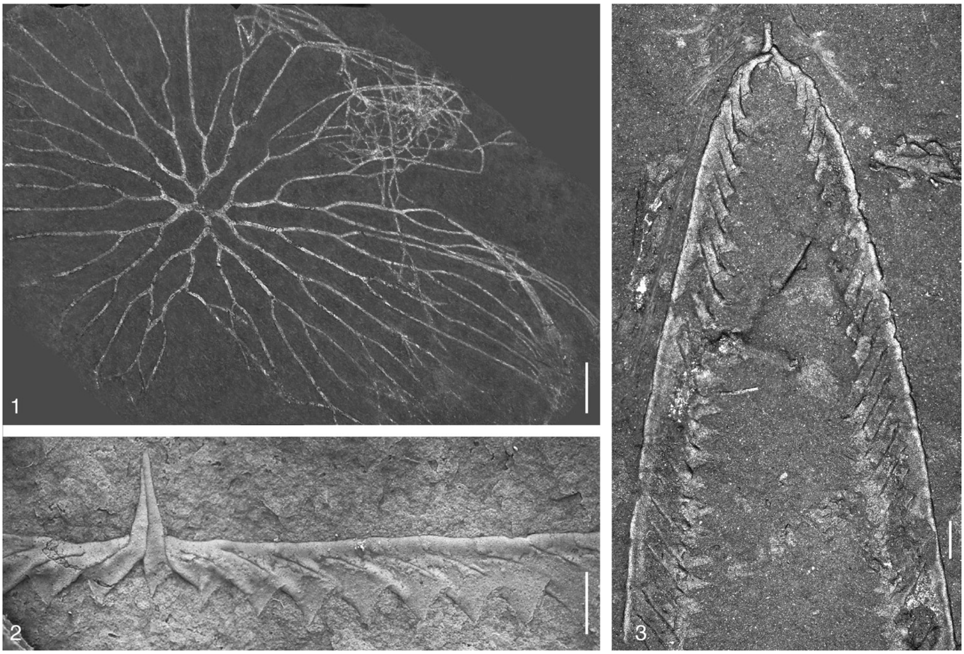

FIG. 186. Main tubarium features of the Dichograptina. *1. Clonograptus flexilis* (HALL, 1865). NMV P309374, large multiramous colony showing dichotomous branching, Lancefield Quarry, Victoria, Australia, specimen originally illustrated in Morris (1988, Ph.D. thesis), scale bar, 10 mm (new); *2, Expansograptus holmi* (TÖRNQUIST, 1904), PMU 23166, latex, obverse view, Diabasbrottet, Västergötland, Sweden, scale bar, 1 mm (new); *3, Didymograptus artus* (ELLES & WOOD, 1901), PMU 31742, reverse view, showing increase of thecal overlap and curvature, Fågelsångsdalen drill core at 22.9 m, Scania, Sweden, scale bar, 1 mm (new).

thecal growth after the growing stipe tip has passed them. Thus, thecae may have reached extreme lengths, as in robust specimens of the *Didymograptus murchisoni* (BECK in MURCHISON, 1839) type (e.g., *Didymograptus clavulus* PERNER, 1895; see BOUČEK, 1973; *Didymograptus obesus* WANG, 1974) or in *Didymograptellus bifidus* (HALL, 1865) and related taxa (WILLIAMS & STEVENS, 1988; MALETZ, 1994b).

Family DICHOGRAPTIDAE Lapworth, 1873

[Dichograptidae LAPWORTH, 1873b, table 1, facing p. 555] [incl. Schizograptinae GE in MU & others, 2002, p. 201; Mimograptinae GE in MU & others, 2002, p. 316]

Biramous to multiramous graptoloids with biradiate isograptid proximal development, symmetrically placed crossing canals and maeandrograptid proximal symmetry; prosicula small, with widening and much larger conical metasicula; sicular bitheca may be present in early taxa; thecae simple, widening tubes with or without rutellum; branching dichotomous to lateral. *Lower Ordovician* (*upper Tremadocian, Hunnegraptus copiosus* Biozone)*–Middle Ordovician* (*Dapingian, Expansograptu hirundo* Biozone).

Characters present in all Dichograptidae are a biradiate proximal end, a multiramous or pauciramous colony, simple thecae, and the absence of bithecae. Important details of the proximal development of many genera of the Dichograptidae are not clear. Thus, the family and the included taxa are largely based on inference and indirect evidence.

The Dichograptidae must be regarded as a paraphyletic taxon because the relationships to the Didymograptidae and Pterograptidae remain unclear. The roots of the Didymograptidae have not been explored due to the lack of sufficient material. The development of the prosicula and proximal development in the early Pterograptidae (e.g., *Didymograptellus*) similarly suggests that this family may have its roots independently in the Anisograptidae.

Dichograptus SALTER, 1863a, p. 136, original spelling as *Dichograpsus* changed in ICZN, Opinion 650, 1963 [**Dichograpsus sedgwickii;* SD GURLEY, 1896, p. 64]. Large multiramous horizontal to subhorizontal tubarium with two to three consecutive bifurcations starting from a tetragraptid proximal end and without distal dichotomies; central disk in some species but not in others; thecae simple with moderate overlap. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone)–*Middle Ordovician* (*Dapingian, Isograptus maximodivergens* Biozone): worldwide.——FIG. 187,*1a*. **D. sedgwickii,* lectotype (selected by ELLES & WOOD, 1902, explanation on pl. 10), BGS GSM 7650, Middle Skiddaw Slates, Braithwaite, Cumbria, UK, *arrow* indicates position of sicula, scale bar, 10 mm (Elles & Wood, 1902, pl. 10,*3a*).——FIG. 187,*1b. D. octobrachiatus* (HALL, 1858), lectotype (selected by WILLIAMS & STEVENS, 1988, p. 24), GSC 931i, Lévis, Quebec, Canada, scale bar, 10 mm (Hall, 1865, pl. 7,*1*).

Clonograptus HALL & NICHOLSON in NICHOLSON, 1873, p. 138, original spelling as *Clonograpsus* changed in ICZN, Opinion 650, 1963 [**Graptolithus rigidus* HALL, 1858, p. 121, SD MILLER, 1889, p. 179] [=*Temnograptus* NICHOLSON, 1876, p. 248 (type, *Dichograpsus multiplex* NICHOLSON, 1868d, p. 129, OD), syn. by LINDHOLM & MALETZ, 1989, p. 718; =*Anthograptus* TÖRNQUIST, 1904, p. 22 (type, *A. nidus,* M), syn. by LINDHOLM & MALETZ, 1989, p. 718]. Multiramous, horizontal to subhorizontal dichograptid with increasing distances of numerous distal, more irregularly placed dichotomies; thecae simple, widening tubes with moderate overlap and without extended rutella; proximal development isograptid, dextral, or sinistral. *Lower Ordovician* (*upper Tremadocian, Hunnegraptus copiosus* Biozone–*Floian, Tshallograptus fruticosus* Biozone): worldwide.——FIG. 187,*3a*. **C. rigidus* (HALL), lectotype, GSC 935b, *arrow* indicates position of sicula, scale bar, 10 mm (Lindholm & Maletz, 1989, p. 719, fig. 2D).——FIG. 187,*3b. C. flexilis* (HALL, 1858), lectotype, GSC 965c, *arrow* indicates position of sicula, scale bar, 10 mm (Lindholm & Maletz, 1989, p. 724, fig. 3A).——FIG. 187,*3c–e. C. multiplex* (NICHOLSON, 1868d); *3c,* lectotype, NHMUK PM Q31, *arrow* indicates position of sicula, scale bar, 10 mm (Lindholm & Maletz, 1989, fig. 7); *3d,* LO 1748T, holotype of *Anthograptus nidus* TÖRNQUIST, 1901, scale bar, 10 mm (Lindholm & Maletz, 1989, fig. 11c); *3e,* reconstruction from latex cast of juvenile, dicalycal theca striped, scale bar, 1 mm (Maletz, 1992, fig. 1e).

Herrmannograptus MONSEN, 1937, p. 186 [**Graptolithus milesi* HALL in HAGER, 1861a, p. 372; OD]. Multiramous dichograptid with a funicle formed by two first-order stipes comprised of two thecae each; up to seven or more orders of dichotomy with second and later dichotomies delayed; proximal end with sicular bitheca; bithecae lacking along stipes; thecae simple with slight rutellum. *Lower Ordovician* (*Floian,* ?*Paratetragraptus approximatus* Biozone): USA.——FIG. 188,*1a–e*. **H. milesi* (HALL in HAGER); *1a,* lectotype, AMNH 433/1, scale bar, 10 mm; *1b–e,* juvenile specimens from type slab, showing astogeny, sicular bitheca visible in *1e,* float, Monkton, Vermont, USA; scale bars, 1 mm (Lindholm & Maletz, 1989, fig. 4).

Holograptus HOLM, 1881b, p. 45 [**H. expansus;* M] [=*Rouvilligraptus* BARROIS, 1893, p. 109 (type, *Graptolithus richardsoni* HALL, 1865, p. 107, OD), syn. by BULMAN, 1970, p. 114]. Multiramous colony based on tetragraptid proximal end; lateral stipes of third and later orders originate at irregular intervals on either side of parent stipes, which follow the growth direction of second-order stipes; lateral stipes can themselves produce further lateral stipes; central web may be present; commonly long second-order stipes before insertion of first lateral stipes. *Lower Ordovician* (*Floian, Paratetragraptus approximatus/Tetragraptus phyllograptoides* Biozone–*Middle Ordovician* (*Darriwilian, Holmograptus lentus* Biozone): Sweden, UK, France, Canada, Bolivia.——FIG. 190,*1a*. **H. expansus,* holotype, NRM-PZ Cn 1500, *Tetragraptus phyllograptoides* Biozone, Diabasbrottet, Hunneberg, Sweden, *arrow* indicates position of sicula, scale bar, 10 mm (Holm, 1881b, pl. 13,*1*).——FIG. 190,*1b. H. deani* ELLES & WOOD, 1902, holotype, BU 1374, *arrow* indicates position of sicula, Skiddaw Slates, Buttermere, Newlands Valley, Cumbria, UK, scale bar, 10 mm (Elles & Wood, 1902, pl. 8,*2a*).——FIG. 190.*1c. H. richardsoni* (HALL, 1865), syntype, GSC 937a, Lévis, Quebec, Canada, scale bar, 10 mm (Hall, 1865, pl. 12,*1*).

Hunnegraptus LINDHOLM, 1991, p. 298 [**H. copiosus;* OD]. Multiramous dichograptids with long first-order stipes of uneven length; thecae slender, dichograptid with moderate overlap; proximal end isograptid, dextral or sinistral with sicular bitheca; sicula parallel sided, obliquely placed between the stipes; thecae along stipes with dorsal origins, lacking bithecae. *Lower Ordovician* (*upper Tremadocian, Hunnegraptus copiosus* Biozone): Australia, ?China, Bulgaria, Norway, Sweden, Canada, USA, Argentina, Bolivia.——FIG. 188,*2a–d*. **H. copiosus; 2a,* holotype, PMO 58969, Galgeberg, Oslo, Norway; *2b,* LO 5978t, Slemmestad, Norway; *2c–d,* LO 5976 and counterpart, Storeklev, Hunneberg, Sweden; scale bars, 5 mm (*2a–b*); 1 mm (*2c–d*) (Lindholm, 1991, fig. 8).

Loganograptus Hall, 1868, p. 237 [**Graptolithus logani* HALL, 1858, p. 115; OD]. Large multiramous horizontal to subhorizontal tubarium with two to three consecutive distal bifurcations starting from a tetragraptid proximal end and without distal dichotomies; central disc present; thecae simple with moderate inclination and overlap. *Lower Ordovician* (*Floian, Baltograptus vacillans* Biozone)–*Middle Ordovician* (*Dapingian, Expansograptus*

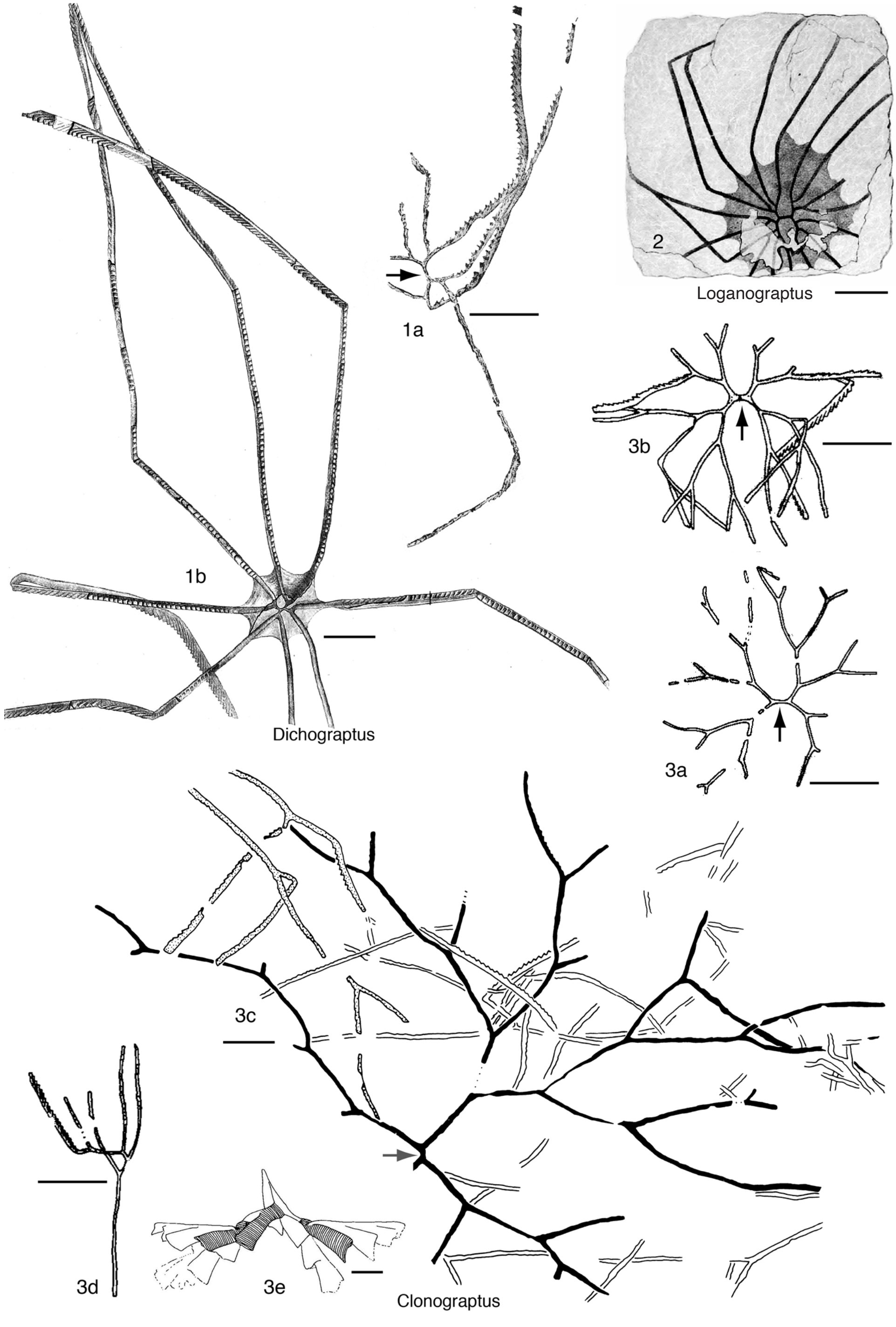

FIG. 187. Dichograptidae (p. 291–293).

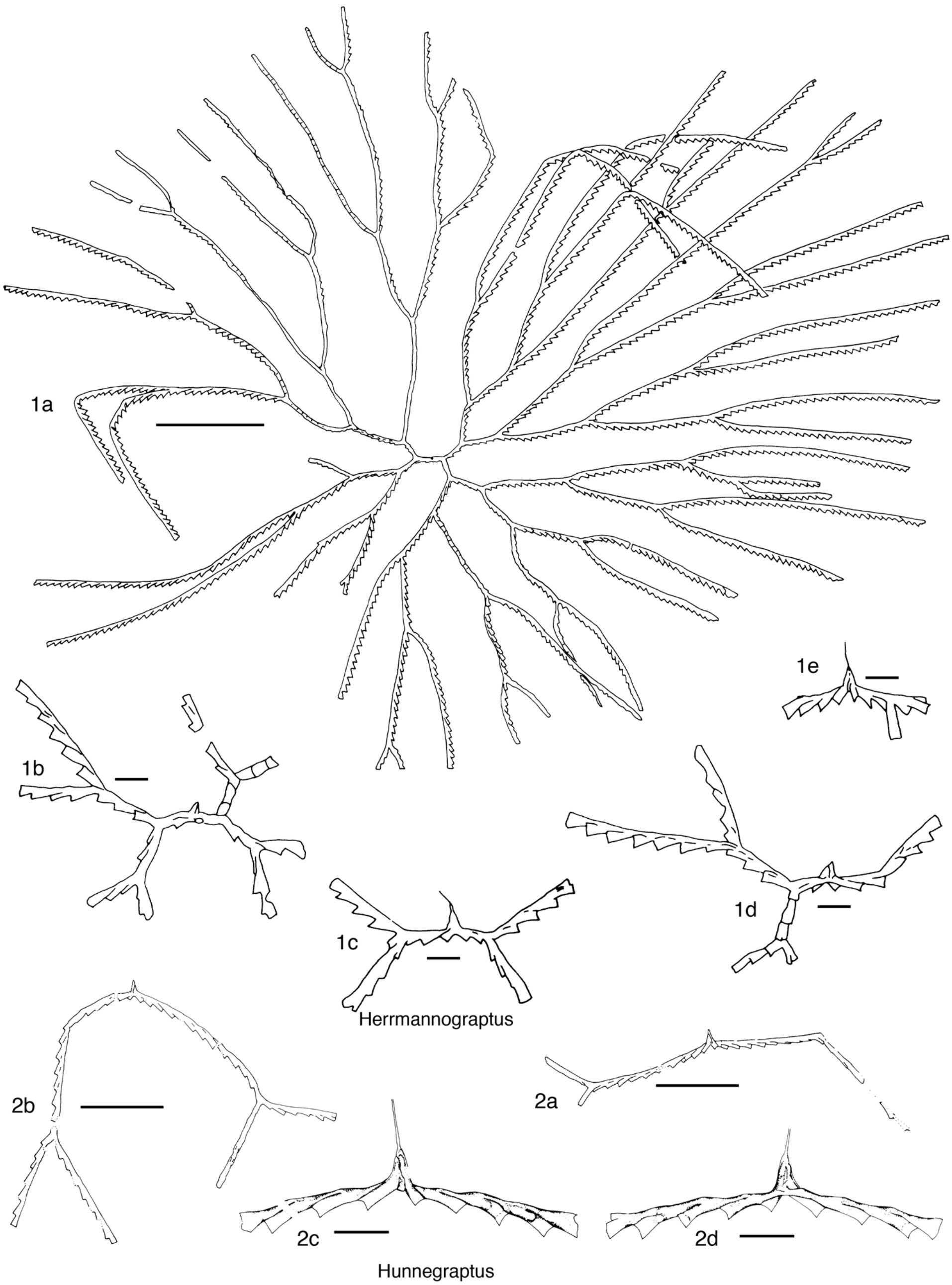

FIG. 188. Dichograptidae (p. 291).

hirundo Biozone): worldwide.——FIG. 187,*2*. **L. logani* (HALL), GSC 932a, Lévis, Quebec, Canada, scale bar, 10 mm (Hall, 1865, pl. 9,*2*).

Mimograptus HARRIS & THOMAS, 1940, p. 197 [**M. mutabilis;* M] [=*Kstaugraptus* TZAJ, 1973, p. 5 (type, *K. obuti,* OD), syn. herein]. Dichograptid based on two subhorizontal to declined main stipes and irregularly placed lateral stipes on both sides of main stipes; proximal end details unknown. *Lower Ordovician* (*upper Floian, Didymograptellus bifidus* Biozone)–?*Middle Ordovician* (*Darriwilian*, ?*Levisograptus austrodentatus* Biozone): China,

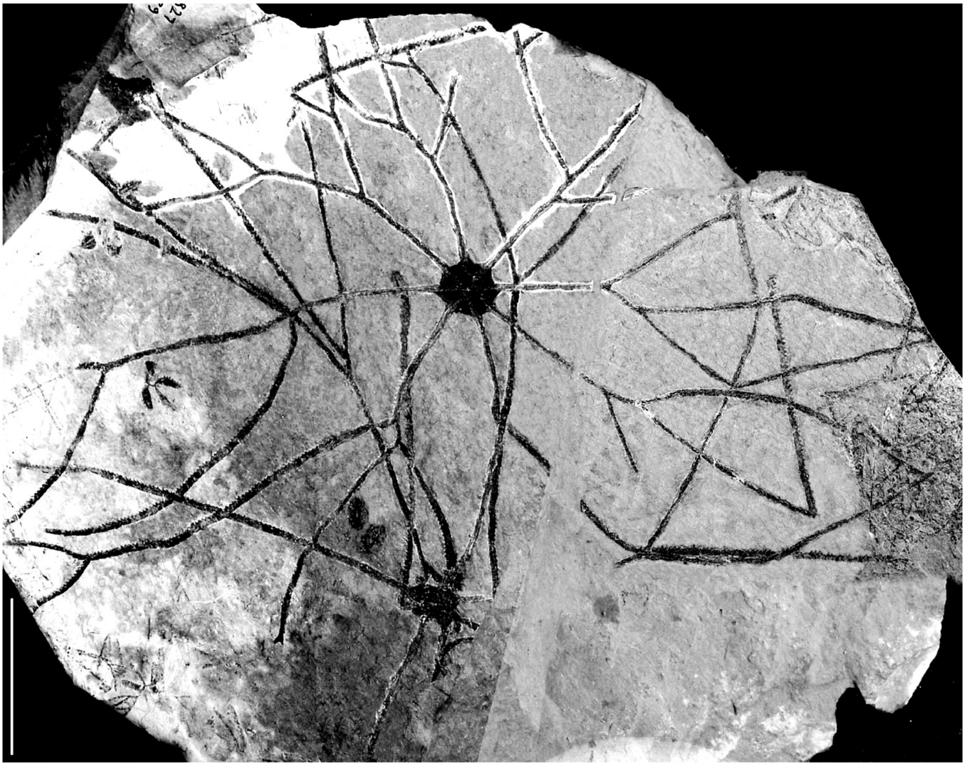

FIG. 189. Dichograptidae (p. 294). Color image available in *Treatise Online* 108.

Kazakhstan, Australia.——FIG. 191,*2a–2c*. **M. mutabilis; 2a,* NMV P34927B, holotype, Allotment 41B, Parish of Campbelltown, Victoria, Australia, *arrows* indicates position of sicula, scale bar, 10 mm (new); *2b–c,* NMV P318805, specimen showing sicula, Victoria, Australia, *arrow* (*2b*) indicates position of sicula, scale bars, 10 mm (*2b*), 1 mm (*2c*) (new).——FIG. 191,*2d, M. obuti* (TZAJ, 1973), holotype, GM 1226/360, *arrow* indicates position of sicula, Chu-Iliy Mountains, southern Kazakhstan, interval is of Darriwilian age as it includes biserials, scale bar, 10 mm (Tzaj, 1973, fig. a).

Orthodichograptus D. E. THOMAS, 1972, p. 529, [**O. robbinsi;* OD]. Large multiramous horizontal to subhorizontal tubarium with two to three consecutive distal bifurcations starting from a tetragraptid proximal end followed by one or more orders of delayed dichotomy; central disc present; thecae simple with moderate overlap. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone): Australia.——FIG. 189. **O. robbinsi,* holotype, NMV P73827 (upper specimen) and paratype, NMV P83089 (lower specimen), Victoria, Australia, scale bar, 50 mm (new).

Schizograptus NICHOLSON, 1876, p. 248 [**Dichograpsus reticulatus* NICHOLSON, 1868d, p. 143; OD] [=*Kellamograptus* RICKARDS & CHAPMAN, 1991, p. 45, (type, *Trochograptus australis* HARRIS & THOMAS, 1938a, OD), syn. herein; =*Trochograptus* HOLM, 1881b, p. 48 (type, *T. diffusus,* M), syn. herein; =*Ctenograptus* NICHOLSON, 1876, p. 248 (type, *Dichograpsus* (?) *annulatus* NICHOLSON, 1869, p. 233, OD), syn. herein]. Multiramous tubarium with two dichotomous bifurcations producing a tetragraptid proximal end, followed by three or more orders of lateral branching produced on one side of parent stipe, which follows the growth direction of second-order stipes; thecal style poorly known. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone)–*Middle Ordovician* (*Dapingian, Expansograptus hirundo* Biozone): worldwide.——FIG. 190,*2a*. **S. reticulatus* (NICHOLSON), lectotype (selected by NICHOLSON, 1876, p. 248), NHMUK PM Q29, *arrow* indicates position of sicula, Skiddaw Slates, Scale Hill, Loweswater Cottages, Cumbria, UK, scale bar, 10 mm (Elles & Wood, 1902, pl. 7).——FIG. 190,*2b. S. australis* (HARRIS & THOMAS, 1938a), holotype, NMV P32081, Allotment 25B, northern boundary, section III, Sandon, Victoria, Australia, *arrow* indicates position of sicula, scale bar, 50 mm (Rickards & Chapman, 1991, fig. 82).

Triaenograptus T. S. HALL, 1914, p. 115 [**T. neglectus;* M] [?=*Tridensigraptus* ZHAO, 1964, p. 638 (type,

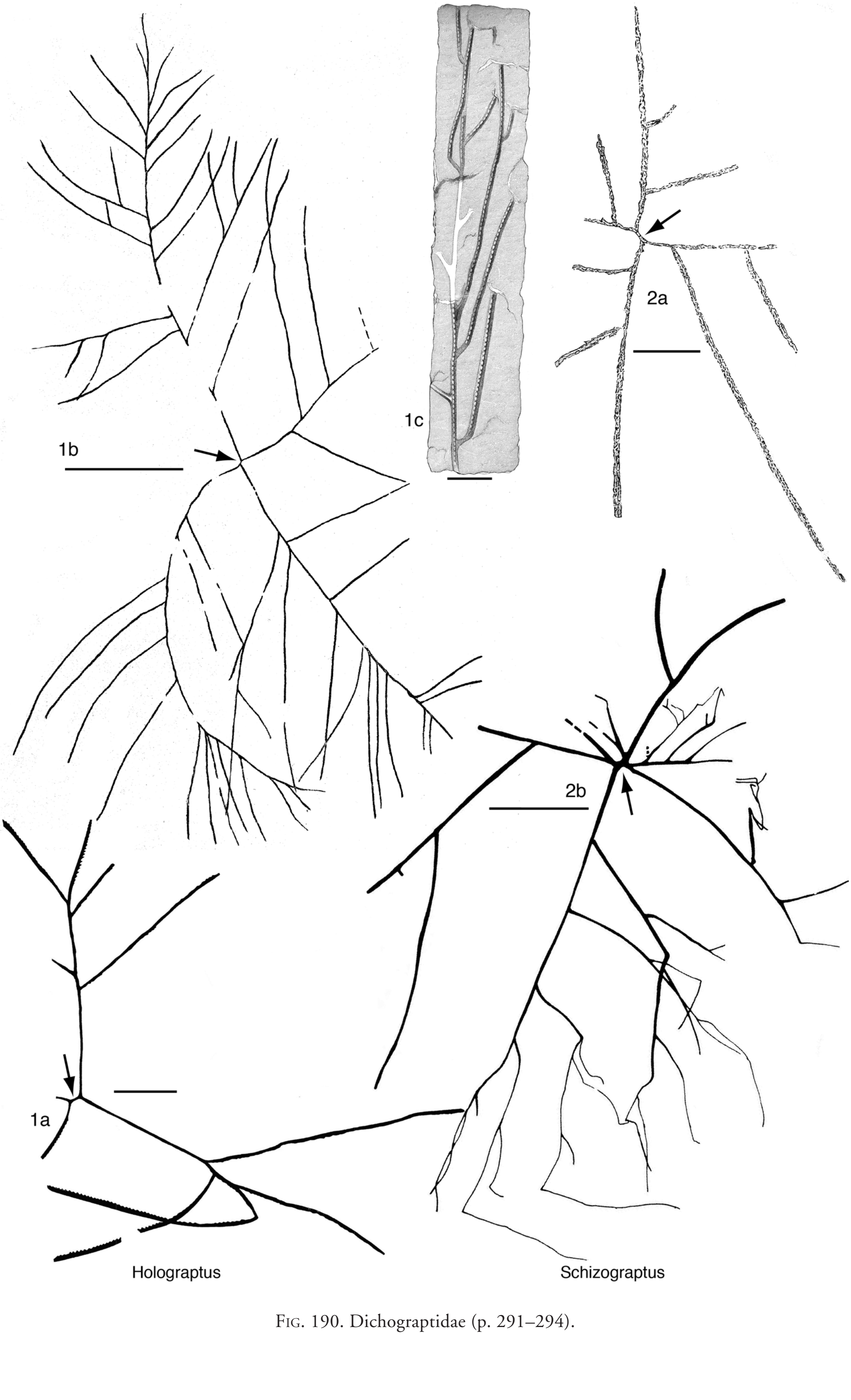

FIG. 190. Dichograptidae (p. 291–294).

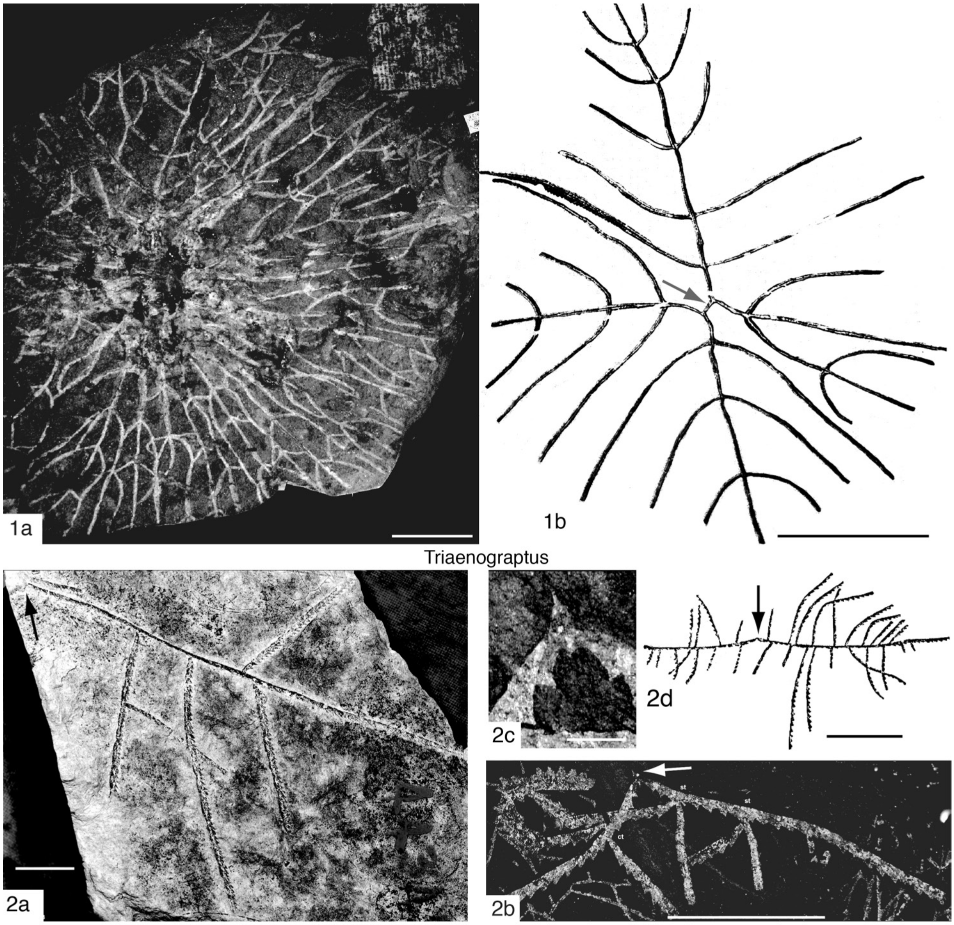

FIG. 191. Dichograptidae (p. 293–296). Color images of specimens available in *Treatise Online* 108.

Tridensigraptus zhejiangensis, OD), syn. herein]. Large umbrella-shaped dichograptid with tetragraptid proximal end; paired lateral branches (tridents) of third and later orders anastomose with adjacent branches in larger specimens; details of proximal end not known. *Lower Ordovician* (*upper Floian, Isograptus lunatus* Biozone)–*Middle Ordovician* (*Dapingian, Expansograptus hirundo* Biozone): Australia, China.——FIG. 191,*1a*. **T. neglectus,* holotype, NMV P132125, Barkers Creek Slate Quarry, north of Castlemaine, Victoria, Australia, scale bar, 50 mm (new).——FIG. 191,*1b*. *T. zhejiangensis* (ZHAO, 1964), holotype, GMCH 1836, Duze, western Zhejiang, China; *arrow* indicates position of sicula, scale bar, 50 mm (Zhao, 1964, pl. 3,*1*).

Family PHYLLOGRAPTIDAE Lapworth, 1873

[Phyllograptidae LAPWORTH, 1873b, table 1, facing p. 555] [=Tetragraptidae FRECH, 1897, p. 593 (*ex* subfamily Tetragraptini FRECH, 1897, p. 593); =Tetragraptidae MU, 1950b, p. 180; =Tetragrapta in MALETZ, CARLUCCI, & MITCHELL, 2009, p. 12; =Pseudotrigonograptidae OBUT & SENNIKOV, 1984a, p. 80]

Four- to two-stiped, pendent to horizontal, reclined, reflexed, and scandent, biradiate graptoloids produced by one proximal dichotomy and with th3^1 and th3^2 as only distal dicalycal theca; sicula conical, widening distinctly toward the aperture, with rutellum and small prosicula; thecae simple, widening tubes commonly with distinct rutellum; proximal end development isograptid, dextral. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone)–*Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone): worldwide.

The Phyllograptidae LAPWORTH, 1873b originally included only the scandent quadriserial dichograptids. It is used herein for the paraphyletic clade identified as the family Tetragraptidae Frech, 1897 by Maletz (2014b). Maletz, Carlucci, and Mitchell (2009, p. 12) defined their crown-clade Tetragrapta as "the common ancestor of *Tetragraptus serra* (Brongniart, 1828)and the first taxon to have distal dicalycal thecae limited to th3[1] and th3[2], forming a quadriramous rhabdosome." They referred to it as the superorder Pan-Tetragrapta but essentially accepted the clade as a monophyletic grouping. Cooper and Fortey (1982) emended Phyllograptidae Lapworth, 1873b to include the genera *Phyllograptus* and *Xiphograptus,* based on the interpretation of the virgellar spine as a synapomorphy of the group. However, Maletz (2010a) considered the origin of the dorsal virgellar spine to be independent in *Phyllograptus* and *Xiphograptus*, based on chemically isolated material.

The members of the Phyllograptidae can be characterized by the presence of only two distal dichotomies, those at th3[1] and th3[2] (see Maletz, 1992, fig. 1e). Stipe reduction by suppression of distal dichotomies is present in some species, such as the two- to four-stiped members of *Tshallograptus fruticosus* (see Harris & Thomas, 1938b; Thomas, 1960). Stipe attitude is quite variable, whereas the proximal development with its compact crossing canals appears to be largely constant. Cooper and Fortey (1982) studied details of the proximal development of *Phyllograptus* and *Pseudophyllograptus* from isolated material and serial sectioning and compared it with the development in *Tetragraptus*. The proximal development of *Pseudotrigonograptus* is known from the investigation of Fortey (1971), who demonstrated that the construction of its tubarium is identical to that of other phyllograptids. The sicula develops a dorsal virgellar spine in the genus *Phyllograptus* (see Cooper & Fortey, 1982; Maletz, 2010a), but the precise evolutionary origin of this feature has not been traced.

The evolutionary relationships of the genera *Tetragraptus* and the scandent phyllograptids were evaluated by Strandmark (1902) and Cooper and Lindholm (1985), among others; and it is clear that taxa such as *Tetragraptus phyllograptoides* Strandmark, 1902 and *Tetragraptus cor* (Strandmark, 1902) can be regarded as good indicators of this transition, even though the precise evolutionary relationships are not known. The appearance of partly scandent *Tetragraptus* species at several levels in the Lower to Middle Ordovician may indicate a complex repetitive evolution of phyllograptid-like species. Cooper and Lindholm (1985) suggested the existence of at least three independent lineages leading to phyllograptoid colonies, interpreted as an example of convergent evolution in graptolites.

Phyllograptus Hall, 1858, p. 137 [**P. typus;* OD] [=*Phyllograpsus* Hall in Nicholson, 1872a, 1872b; non *Phyllograpsus* Angelin in Salter, 1858 (=*Rhabdinopora* Eichwald, 1855)]. Phyllograptid with four stipes united along dorsal margins, producing cruciform cross section; median septa reduced to framework of fornices and central columella with open foramen between thecae of adjacent series; sicula with dorsal virgellar spine, often strongly elongated and thickened, proximal development isograptid, dextral; thecae continuing to grow and elongate as tubarium itself continues to grow. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone)*–Middle Ordovician* (*Dapingian, Isograptus victoriae* Biozone): Canada, USA, Australia, New Zealand, Argentina, China.——Fig. 192,*1a–e*. **P. typus; 1a,* lectotype, GSC 942b, ?G-locality, Lévis, Quebec, Canada; *1b–c,* PMO NF 3312, PMO NF 3314, isolated material in obverse (*b*) and reverse (*c*) views; *1d,* PMO NF3314, distal view of isolated fragment showing interthecal foramina; *1e,* reconstruction to show central columella; *1b–d,* Spitsbergen, Norway; scale bars, 1 mm (Cooper & Fortey, 1982, fig. 67a–b, 71, 71k, and 74, respectively).

Corymbograptus Obut & Sobolevskaya, 1964, p. 27 [**Didymograpsus v-fractus* Salter, 1863a, p. 138; OD]. Deflexed, two-stiped phyllograptid with distally distinctly widening stipes; proximal development isograptid, dextral; low prosicular origin of th1[1]; crossing canals low on sicula; sicula long and slender as in *Tshallograptus* with mitre-shaped prosicula. *Lower Ordovician* (*Floian, Cymatograptus protobalticus* Biozone)*–Middle Ordovician* (*Darriwilian, Corymbograptus retroflexus* Biozone): China, UK, Czech Republic, Norway, Sweden, Canada, USA, Argentina, ?Bolivia.——Fig. 193,*3a–b*. **C. v-fractus* (Salter); *3a,* neotype, BU 1005a, *Baltograptus jacksoni* Biozone, Buttermere, Skiddaw Slates, Cumbria, UK (Rushton, 2011, fig. 1A); *3b,* BU 1005b, proximal end of larger specimen, scale bars, 1 mm (Rushton, 2011, fig. 1D).——Fig. 193,*3c–d. C. v-fractus tullbergi* (Monsen, 1937);

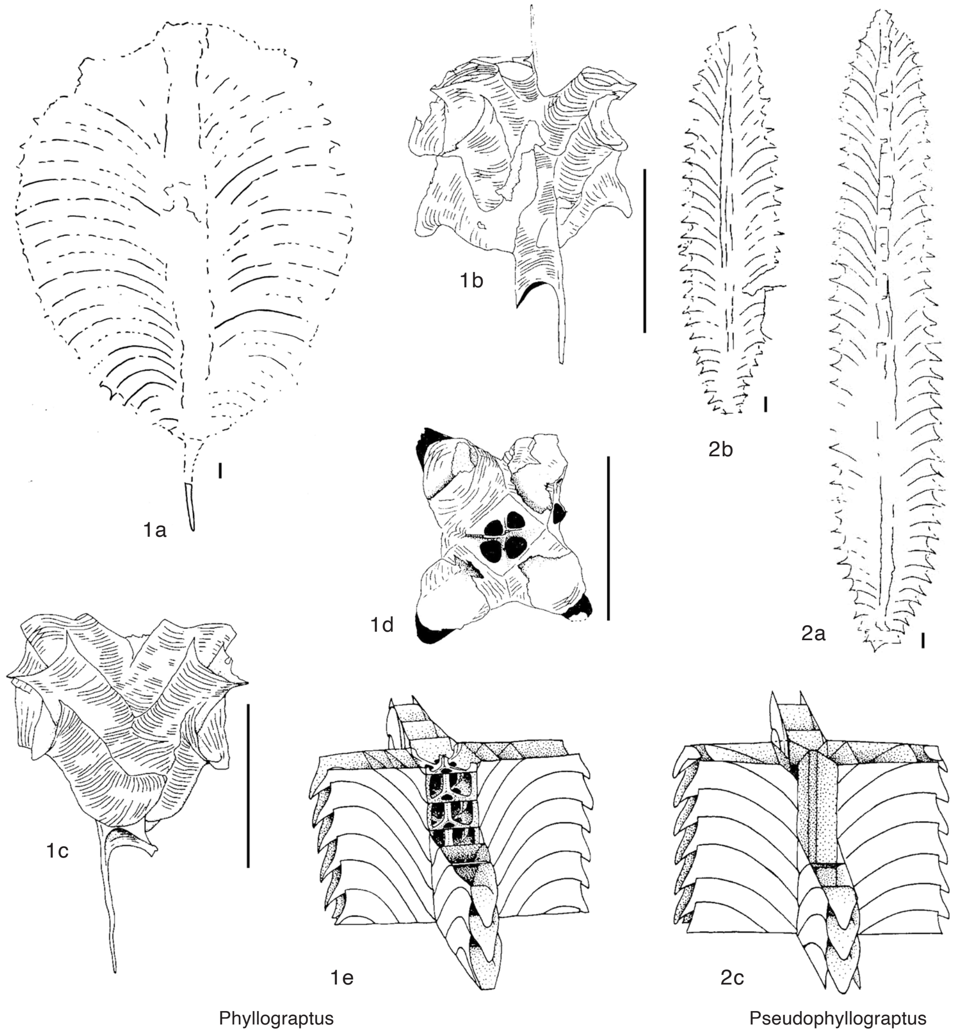

FIG. 192. Phyllograptidae (p. 297–299).

drawings from latex cast, counterpart of holotype, PMO K0484, reverse view (*c*) and PMO 59957 obverse view (*d*); Oslo Region, Norway, scale bars 1 mm (new).——FIG. 193,*3e. C. retroflexus* (PERNER, 1895), OMR 54919, proximal end in reverse view, Drahouš, Czech Republic, scale bar, 1 mm (new).

Paratetragraptus OBUT, 1957, p. 38 [**Tetragraptus approximatus* NICHOLSON, 1873, p. 136; OD]. Phyllograptid with nearly horizontal tubarium; proximal end with slightly deflexed funicle; paired, parallel-oriented second-order stipes; proximal development isograptid, dextral, with robust and wide crossing canals. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone–*Tshallograptus fruticosus* Biozone): worldwide.——FIG. 195,1. **P. approximatus* (NICHOLSON), lectotype, NHMUK PM 1996, Lévis, Quebec, Canada (G-locality, see Maletz, 1997b), scale bar, 1 mm (Nicholson, 1873, fig. 2a).

Pendeograptus BOUČEK & PŘÍBYL, 1952a, p. 12 [**Tetragraptus pendens* ELLES, 1898, p. 491; OD]. Pendent phyllograptid with four stipes; proximal development isograptid, dextral; low prosicular origin of th1[1]; sicula long and slender. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone): worldwide.——FIG. 193,*1*. **P. pendens* (ELLES), lectotype (selected by WILLIAMS & STEVENS, 1988, p. 38), NHMUK PM Q37, Barf, Loweswater Formation, Skiddaw Slates, Cumbria, UK, scale bar, 1 mm (adapted from Elles, 1898, fig. 13).

Pseudophyllograptus COOPER & FORTEY, 1982, p. 241 [**Phyllograptus angustifolius angustifolius* HALL, 1858; OD]. Phyllograptid with four stipes united along dorsal margins, producing cruciform

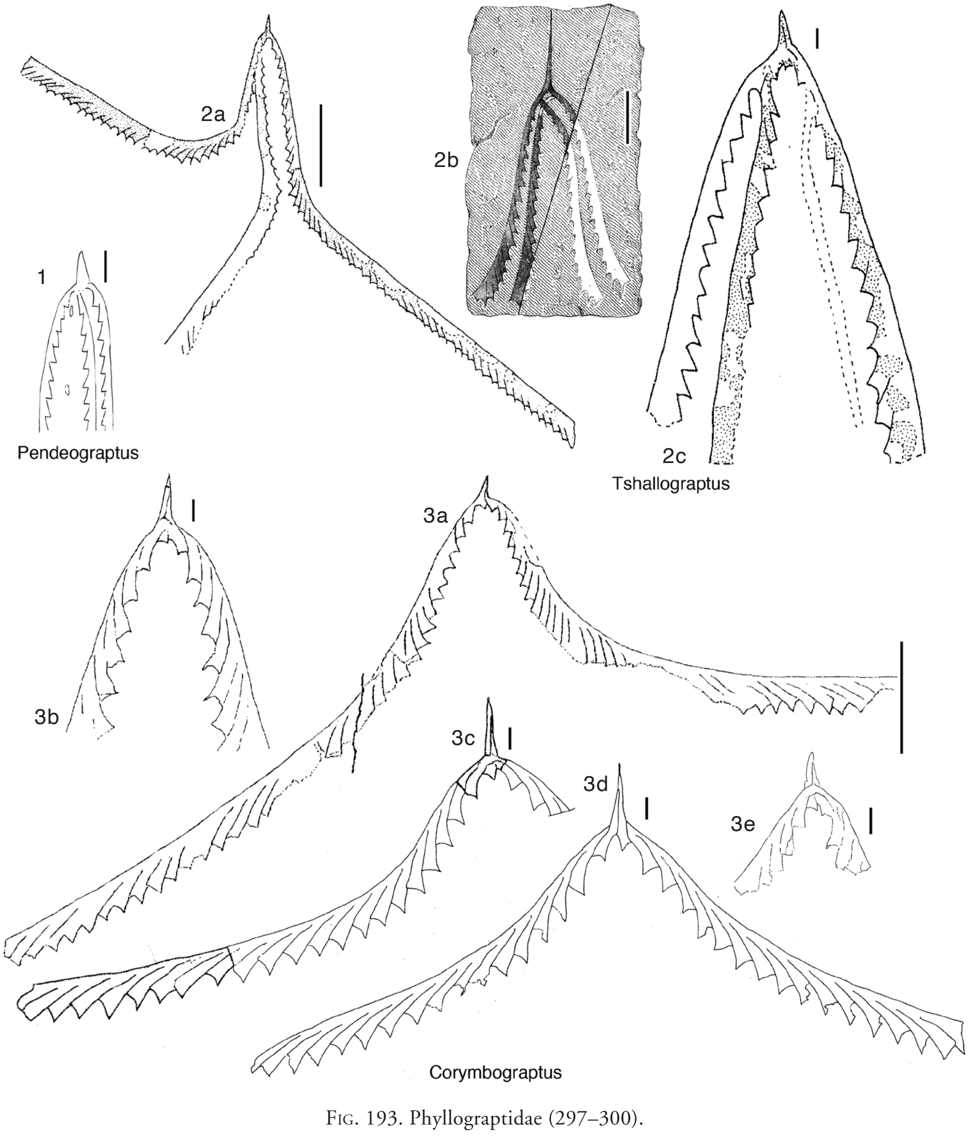

FIG. 193. Phyllograptidae (297–300).

cross section; median septa cruciform, imperforate; proximal development isograptid, dextral. *Lower Ordovician* (*Floian, Tetragraptus akzharensis* Biozone)–*Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone): worldwide.——FIG. 192,*2a–c*. **P. angustifolius* (HALL)*; 2a,* lectotype, GSC 939b; *2b,* paratype, GSC 939; *2c,* reconstruction to show median septum; *Levisograptus dentatus* Biozone Lévis, Quebec, Canada; *2a–b,* scale bars, 1 mm (Cooper & Fortey, 1982, fig. 48f, 48e, and 51, respectively).

Pseudotrigonograptus MU & LEE, 1958, p. 397 (p. 416, English text) [**P. uniformis;* OD] [=*Tristichograptus* JACKSON & BULMAN, 1970, p. 108 (type, *Graptolithus ensiformis* HALL, 1858, p. 133, OD), syn by FORTEY, 1971, p. 192]. Quadriserial or rarely triserial, scandent phyllograptid with stipes not only united along their dorsal margins, but also in lateral contact, elliptical in cross section; median septa cruciform, imperforate; proximal development isograptid, dextral; thecae may have continued growth. *Middle Ordovician* (*Dapingian, Isograptus lunatus* Biozone–*Darriwilian, Holmograptus spinosus* or *Nicholsonograptus fasciculatus* Biozone): worldwide.——FIG. 194,*a–b*. *P. ensiformis* (HALL, 1858); *a,* lectotype (selected by RICKARDS, 1973b, p. 598), GSC 949g, Cote Frechette section, Lévis, Quebec, Canada, scale bar, 1 mm (Hall, 1865, pl. 14,*4*); *b,* cross section diagram Cooper & Fortey, 1982, fig. 53).——FIG.194,*c–d, P. minor* MU & LEE, 1958,

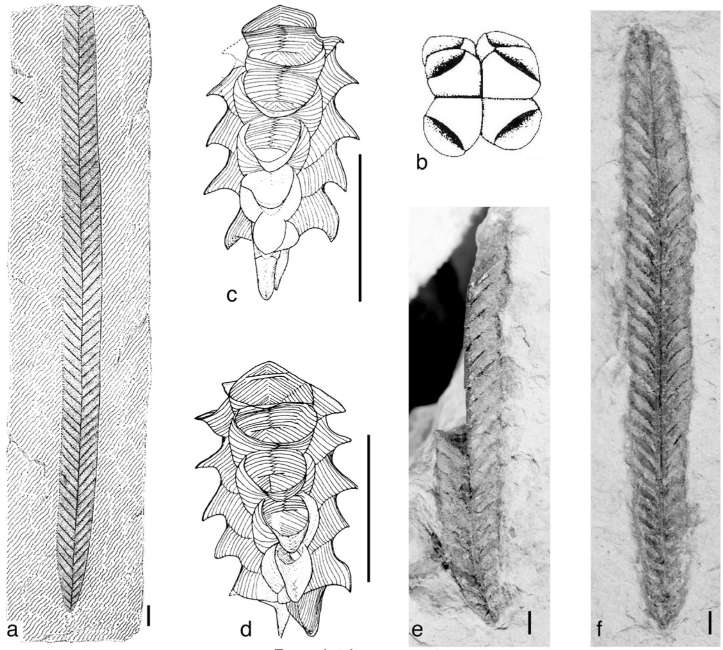

FIG. 194. Phyllograptidae (p. 299–300).

three-stiped taxon in different views (not preserved, see SM A70588 for a similar specimen), Spitsbergen, Norway; scale bars, 1 mm (Fortey, 1971, fig. 3).——FIG.194,*e–f* (on one slab); **P. uniformis; e,* holotype, NIGP 9719, *Exigraptus clavus* Biozone, Ningkuo Shale, Huangnikang, Kiangshan, China (new); *f,* paratype, NIGP 9718; scale bars, 1 mm (new).

Tetragraptus SALTER, 1863a, p. 140, original spelling as *Tetragrapsus* changed in ICZN, Opinion 650, 1963 [**Graptolithus bryonoides* HALL, 1858, p. 126; OD (=*Tetragraptus serra* BRONGNIART, 1828, p. 71, see ELLES & WOOD, 1902, p. 66)] [*non Tetragrapsus* RATHBUN, 1918, p. 273 (Decapoda)]. Phyllograptid with four horizontal to reclined, reflexed, and scandent stipes; proximal end isograptid, dextral, with wide crossing canals and tetragraptid proximal end; thecae with considerable overlap and moderate development of rutellum. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone)*–Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone): worldwide.——FIG. 195,*2a*. **T. serra,* lectotype, NHMUK PM 26995, Lévis, Quebec, Canada, scale bar, 1 mm (Cooper & Fortey, 1982, fig. 14).——FIG. 195,*2b*. *T. bryonoides* (HALL), lectotype, GSC 978, scale bar, 1 mm (Cooper & Fortey, 1982, fig. 16).——FIG. 195,*2c*. *T. cor* (STRANDMARK, 1902), SGU 3844, 1-2 preservation, scale bar, 1 mm (Cooper & Lindholm, 1985, fig. 3g).——FIG. 195,*2d–e*. *T. phyllograptoides* STRANDMARK, 1902; *2d,* LO 5377t, specimen in 1-2 preservation; *2e,* LO 5372t, specimen in a-b preservation; scale bars, 1 mm (Cooper & Lindholm, 1985, fig. 1m and 1c).——FIG. 195,*2f–g*. *T. phyllograptoides triumphans* COOPER & FORTEY, 1982; *2f,* PMO NF3303, juvenile in obverse view; *2g,* PMO NF 3181, proximal end in reverse view showing massive crossing canals; scale bars, 1 mm (Cooper & Fortey, 1982, fig. 22c and 22g, respectively).

Tshallograptus VANDENBERG, 2017, p. 54 [**Graptolithus fruticosus* HALL, 1858, p. 128; OD]. Pendent to deflexed phyllograptid; proximal development isograptid, dextral; low prosicular origin of th1[1]; crossing canals low on sicula; sicula long and slender, with mitre-shaped prosicula. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone–*Didymograptellus kremastus* Biozone): worldwide.——FIG. 193,*2a–c*. **T. fruticosus* (HALL); *2a,* GSC 79584, large, three-stiped specimen, Cow Head Group, western Newfoundland, Canada, scale bar, 10 mm (Williams & Stevens, 1988, fig. 27s); *2b,* paratype, GSC 925, showing deflexed stipe ends, sicula merges into thickened nema, scale bar, 5 mm (Hall, 1865, pl. 6,*1*); *2c,* lectotype, GSC 926, Isle d'Orleans, Quebec, Canada; scale bar, 1 mm (Williams & Stevens, 1988, fig. 27G).

Family DIDYMOGRAPTIDAE Mu, 1950

[Didymograptidae MU, 1950b, p. 180 (*emend.* MU & others, 2002, p. 228)] [incl. Aulograptinae HSÜ & CHAO, 1976, p. 137]

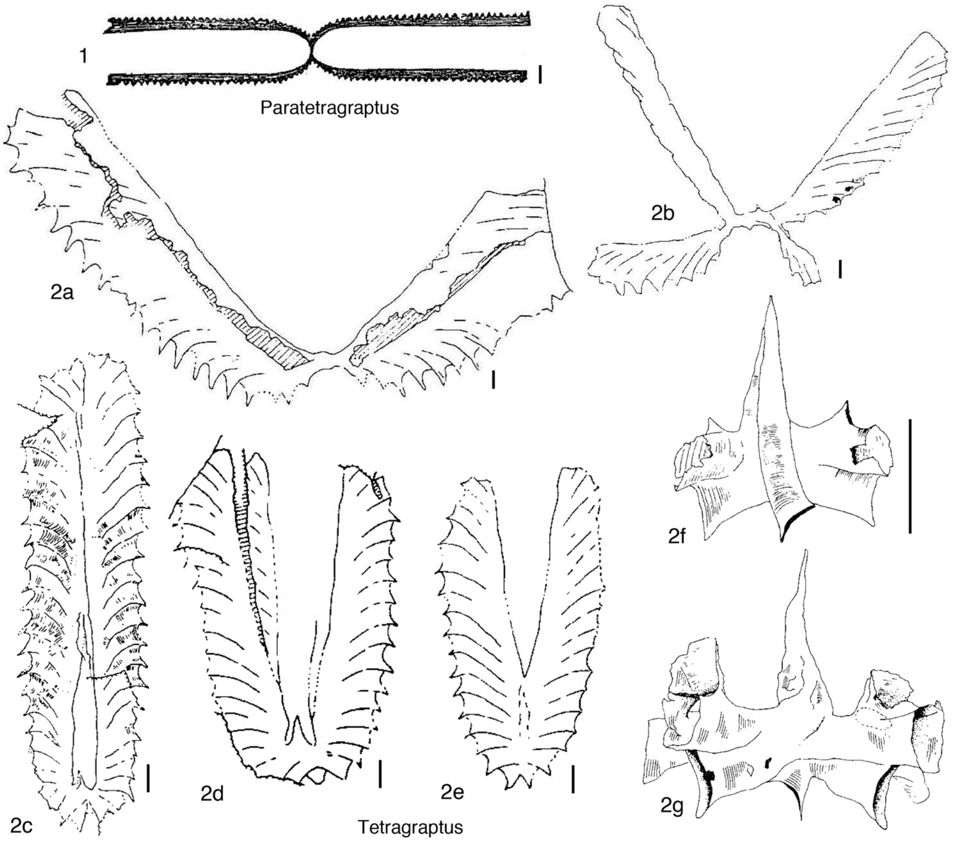

FIG. 195. Phyllograptidae (298–300).

Two-stiped, pendent to horizontal, reclined, reflexed, and deflexed graptoloids; sicula conical, widening distinctly toward aperture, with small prosicula; thecae simple, widening tubes; rutellum present in derived taxa; thecae rarely complex or with prothecal folding; proximal development isograptid, dextral or derived artus type. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone)–*Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone): worldwide.

The Didymograptidae is a poorly defined group of two-stiped taxa with a highly variable tubarium shape, ranging from pendent to reclined. The taxa are united by a conical sicula with a relatively small prosicula. The proximal development is of the isograptid dextral type or the derived artus type with the crossing canals symmetrically placed but typically having distinct differences in width. The position of the foramen for $th1^1$ is in the lower part of the prosicula in early taxa (Fig. 196.1) but may be in the middle part of the metasicula (Fig. 196.2) and even in its lower part in derived forms. GUTIÉRREZ-MARCO (1986) considered the separation of genera or subgenera based on the presence of an isograptid- or artus-type proximal development in the genus *Didymograptus.* He differentiated the subgenus *Jenkinsograptus* with an isograptid-type development from *Didymograptus* with an artus-type development. MALETZ (1994b) and MALETZ and SLOVACEK (2013), however, preferred to keep species with isograptid- and artus-type developments in the genus *Baltograptus,* indicating that the position of the dicalycal theca might be of lesser importance for taxonomic interpretations.

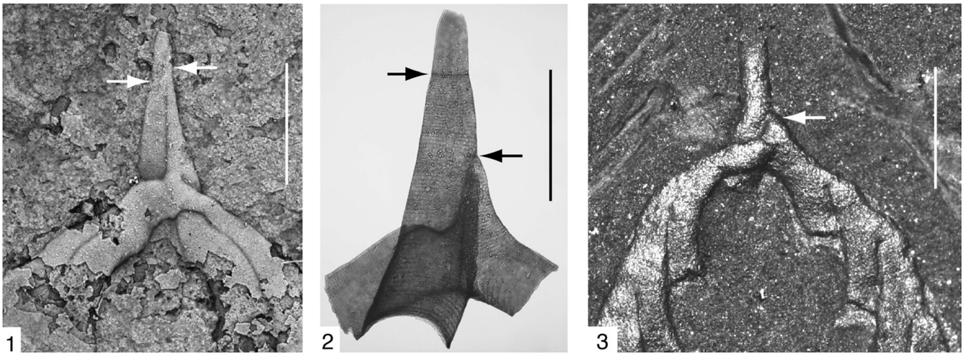

FIG. 196. The proximal development of the Didymograptidae. *1, Expansograptus* sp., PMU 23168, latex cast, low prosicular origin of th1[1], Hunneberg, Västergötland, Sweden (new); *2, Baltograptus kurcki* (TÖRNQUIST, 1901), SGU 9615, isolated specimen showing fuselli, metasicular origin of th1[1], artus-type development, Talubäcken, Dalarna, Sweden (new); *3, Didymograptus artus* (ELLES & WOOD, 1901), PMU 31742, reverse view, Fågelsångsdalen drill core, 22.9m, Scania, Sweden (new). All scale bars, 1 mm.

The distinction of *Norvegiograptus* LI & others, 2014 based on the proximal development is unclear. The authors state an artus-type development with a dicalycal th1[2] in the English translation of the text and show an isograptid, sinistral development (LI & others, 2014, fig. 2B). Further specimens identified as *Norvegiograptus liber* (MONSEN, 1937) have an artus-type development (LI & others, 2014, fig. 4) in dextral and sinistral specimens.

Numerous taxa have been referred to the genus *Didymograptus* in the past (MU & others, 2002), and many have been reassigned to other genera in recent decades due to the recognition of constructional differences in the proximal development and thecal style. The sigmagraptine genus *Acrograptus* TZAJ, 1969 largely includes species with a sigmagraptine parallel-sided sicula and slender, asymmetrically placed stipes. Species with a dorsal virgellar spine are now included in *Didymograptellus*, *Yutagraptus*, and *Xiphograptus*, as revised by MALETZ (2010a), and are referred to the Pterograptidae. Most horizontal and some reclined and declined forms are now referred to *Expansograptus*.

Didymograptus M'COY, 1851 in SEDGWICK & M'COY, 1851–1854, p. 9, original spelling as *Didymograpsus* changed in ICZN Opinion 650, 1963 [**Graptolithus murchisoni* BECK in MURCHISON, 1839, p. 694; SD MILLER, 1889, p. 185] [=*Cladograpsus* GEINITZ, 1852, p. 29 (type, *Graptolithus murchisoni* BECK in MURCHISON, 1839, p. 694, SD BULMAN, 1929, p. 169), obj.; =*Parazygograptus* KOZŁOWSKI, 1954, p. 439 (type, *P. erraticus,* OD), syn. by MALETZ, 1994b, p. 30; =*Trigonograpsus* NICHOLSON, 1869, p. 231 (type, *T. lanceolatus*, M), syn. by JACKSON & BULMAN, 1970, p. 108]. Pendent didymograptid with low metasicular origin of th1[1] and artus-type proximal development; stipes slender or distinctly widening distally; proximal end usually covered by cortical overgrowth in gerontic specimens. *Middle Ordovician* (*Darriwilian, Didymograptus artus* Biozone–*Pseudamplexograptus distichus* Biozone): Belgium, UK, Czech Republic, France, Germany, Norway, Spain, Sweden, China, North Africa, Saudi Arabia, western Australia, Bolivia, Colombia, Peru.——FIG. 197,*1a. D. murchisoni* (BECK in MURCHISON), lectotype (selected by ELLES & WOOD, 1901, p. 40), BGS GSM 6820b, Gelli, near Llandrindod, Wales, UK, scale bar, 1 mm (Strachan & Kashogji, 1984, fig. 7).——FIG.197, *1b–d. D. artus* (ELLES & WOOD, 1901); *1b,* CPC 7010, isolated proximal fragment showing artus-type development, Canning Basin, Willara 1 drill core, Australia, scale bar, 0.5 mm (Skwarko, 1968, fig. 2); *1c–d, D. erraticus*, holotype, ZPAL G./III, complete specimen (*d*) and proximal end (c) showing fuselli, Poland, scale bars 1 mm (*1c*), 0.5 mm (*1d*) (Kozłowski, 1954, fig. 9).——FIG. 197,*1e. Didymograptus* sp., NHMUK PM Q49, holotype of *Trigonograpsus lanceolatus*, scale bar, 1 mm (Jackson & Bulman, 1970, fig. 1).

Aulograptus SKEVINGTON, 1965, p. 25 [**Didymograptus cucullus* BULMAN, 1932c, p. 15; OD (=*Didymograptus climacograptoides* BULMAN, 1931, p. 41, syn. by MALETZ, 1997a, p. 29)]. Pendent didymograptid with metasicular origin of th1[1]; stipes subparallel, gradually widening distally; proximal development of isograptid type; thecae with strongly modified, geniculate thecal apertures. *Middle Ordovician* (*lower Darriwilian, Undulograptus austro-*

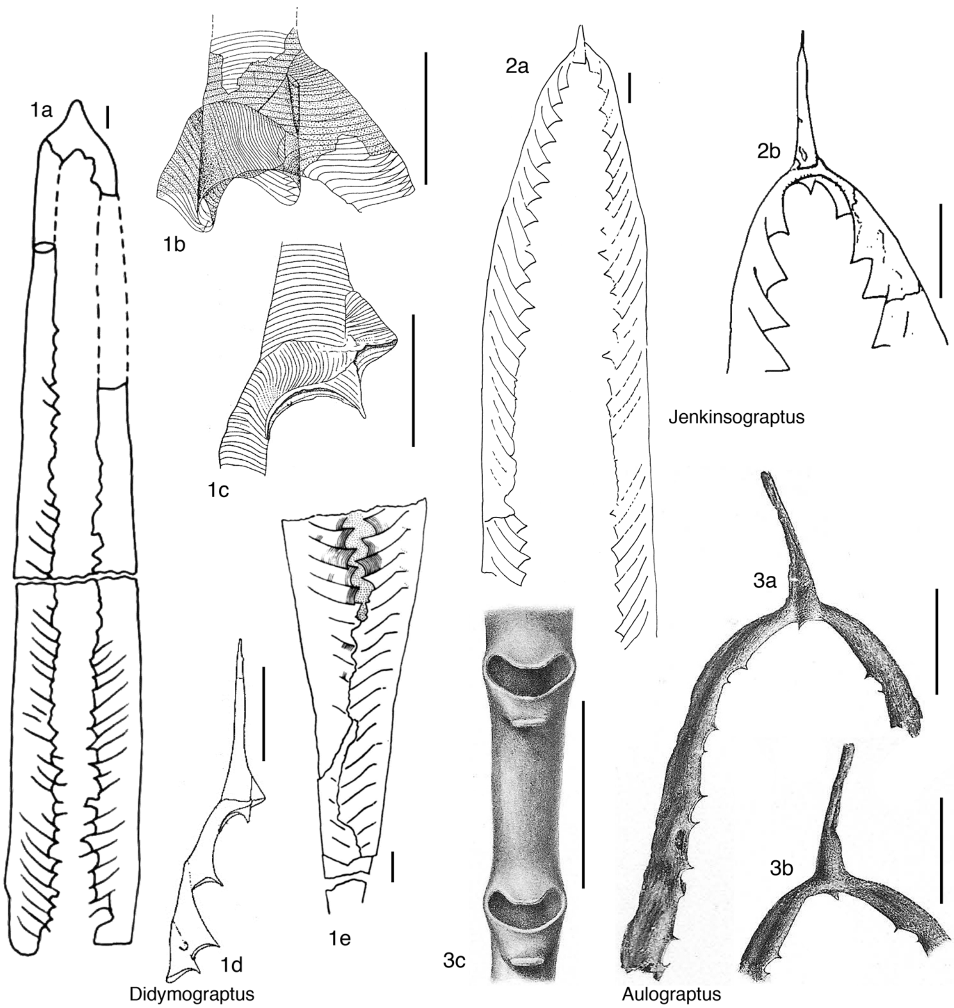

FIG. 197. Didymograptidae (p. 302–305).

dentatus Biozone–*Nicholsonograptus fasciculatus* Biozone): Belgium, UK, Czech Republic, Norway, Spain, Sweden, Canada, Argentina, Bolivia, Peru, China.——FIG. 197,*3a–c*. *A. climacograptoides* (BULMAN, 1931); *3a–3b,* originally described as the holotype of *A. cucullus,* NRM-PZ Cn 1261, obverse (*a*) and reverse (*b*) views, Hälludden, Öland, Sweden, scale bars, 1 mm (Bulman, 1932**c**, pl. 1,*3–4*); *3c,* fragment showing thecal apertures, reconstruction, scale bar, 1 mm (Bulman, 1932**c**, pl. 1,*5*).

Baltograptus MALETZ, 1994b, p. 36 [**Didymograptus vacillans* TULLBERG, 1880b, p. 42; OD] [=*Norvegiograptus* LI & others, 2014, p. 173 (type, *Didymograptus liber* MONSEN, 1937, p. 122, OD, =*D. kurcki* TÖRNQUIST, 1901), syn. herein]. Horizontal to deflexed, declined and pendent didymograptids; sicula slender, with long supradorsal portion; proximal development of isograptid or artus type with moderately low origin of $th1^1$ from metasicula and comparably long ventral free apertural length of sicula; isograptid suture very short or missing. *Lower Ordovician* (*Floian, Cymatograptus protobalticus* Biozone–*Baltograptus minutus* Biozone): UK, Czech Republic, France, Norway, Sweden, Turkey, Argentina, Bolivia, China.——FIG. 198,*2a–c*. **B. vacillans* (TULLBERG); *2a,* lectotype, LO 345t, Kiviks Esperöd, Scania, Sweden (new); *2b–c,* PMU 23157, reverse (*b*), and obverse view (*c*) drawing of latex cast, Diabasbrottet, Hunneberg, Sweden (new). All scale bars, 1 mm.——FIG. 198,*2d–e*. *B. kurcki* (TÖRNQUIST, 1901), *2d*, LO 1633t, proximal end, obverse view; *2e,* lectotype, LO 1632T, reverse view of molds; Tøyen Shale

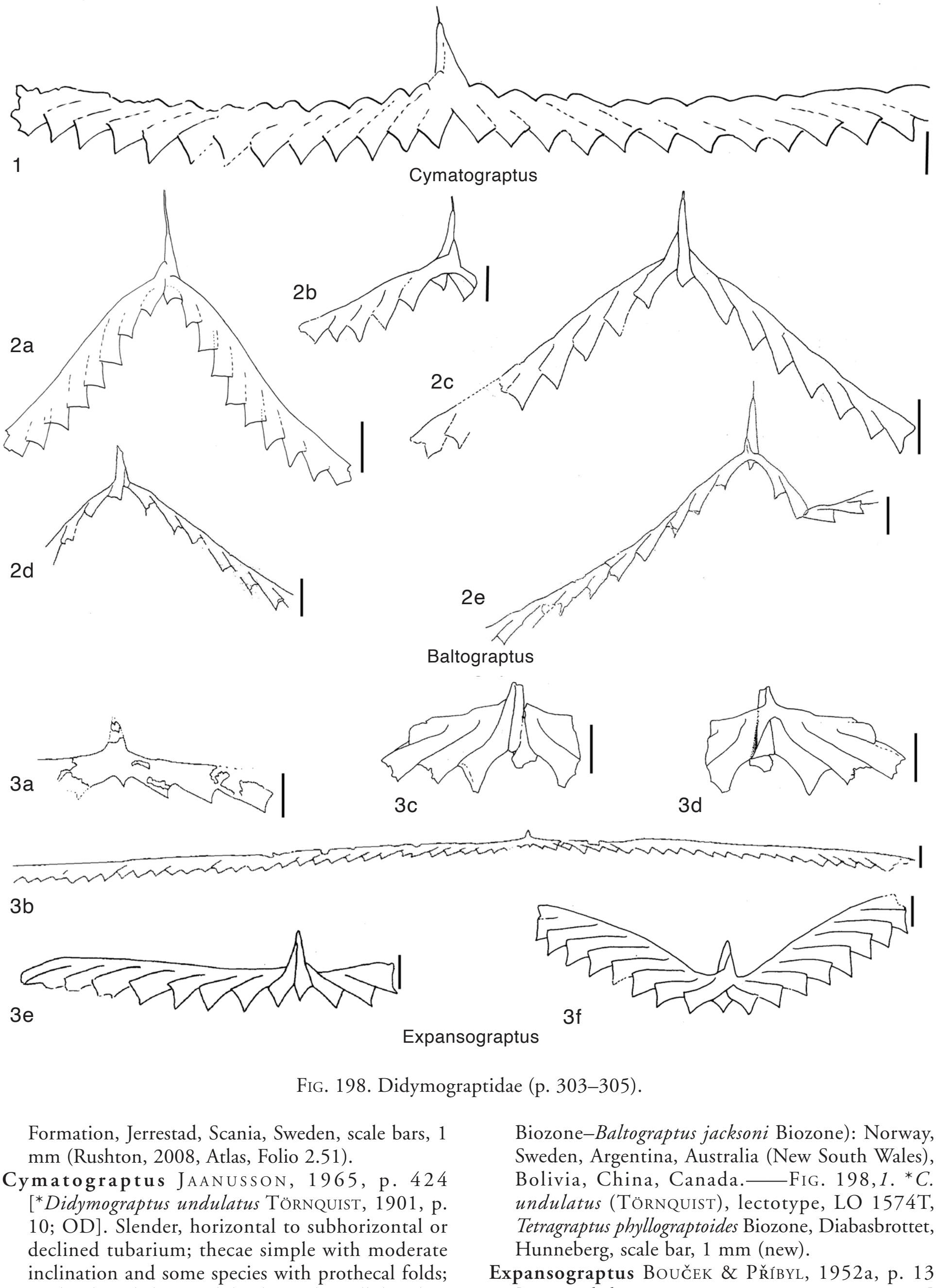

FIG. 198. Didymograptidae (p. 303–305).

Formation, Jerrestad, Scania, Sweden, scale bars, 1 mm (Rushton, 2008, Atlas, Folio 2.51).

Cymatograptus JAANUSSON, 1965, p. 424 [**Didymograptus undulatus* TÖRNQUIST, 1901, p. 10; OD]. Slender, horizontal to subhorizontal or declined tubarium; thecae simple with moderate inclination and some species with prothecal folds; sicula relatively long and slender, with small (less than one-fourth of sicular length) prosicula; supradorsal portion of sicula prominent and with long free ventral side of the aperture; proximal development type isograptid, dextral to artus type, dextral or sinistral; low prosicular origin of th1[1]. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone–*Baltograptus jacksoni* Biozone): Norway, Sweden, Argentina, Australia (New South Wales), Bolivia, China, Canada.——FIG. 198,*1*. **C. undulatus* (TÖRNQUIST), lectotype, LO 1574T, *Tetragraptus phyllograptoides* Biozone, Diabasbrottet, Hunneberg, scale bar, 1 mm (new).

Expansograptus BOUČEK & PŘÍBYL, 1952a, p. 13 [**Graptolithus extensus* HALL, 1858, p. 132; OD] [=*Extensograptus* BOUČEK & PŘÍBYL, 1952a (English abstract), p. 1, misspelling of *Expansograptus*]. More or less horizontal didymograptids with isograptid, dextral proximal development; proximal portion of sicula perpendicular to stipes; sicular and thecal apertures straight, without elaborations; origin of th1[1] low on prosicula; stipe width variable; crossing canals more or less symmetrically placed on sicula; crossing canal 1 is initially much wider than crossing canal 2; length of isograptid suture variable. *Lower Ordovician* (*Floian, Paratetragraptus approximatus* Biozone)–*Middle Ordovician* (*Darriwilian, Undulograptus austrodentatus* Biozone): worldwide.——FIG. 198,*3a–b*. **E. extensus* (HALL), lectotype, GSC 976, proximal end (*a*) and complete specimen (*b*), scale bars, 1 mm (Cooper & Fortey 1982, fig. 40d–e).——FIG. 198,*3c–d*. *E. hirundo* (SALTER, 1863a), obverse (*c*) and reverse (*d*) view, Tøyen Shale, Slemmestad, Oslo, Norway; scale bars, 1 mm (new).——FIG. 198,*3e*. *E. suecicus* (TULLBERG, 1880*b*), T226, Tøyen section, Oslo, Norway, scale bar, 1 mm (new).——FIG. 198,*3f*. *E. urbanus* (MONSEN, 1937), PMU 23152B, drawing of latex cast in reverse view, Diabasbrottet, Hunneberg, Sweden, scale bar, 1 mm (new).

Jenkinsograptus GUTIÉRREZ-MARCO, 1986, p. 199 [**Didymograptus spinulosus* PERNER, 1895, p. 22; OD]. Pendent didymograptid with low metasicular origin of th1[1] and isograptid-type proximal development; stipes slender or distinctly widening distally. *Middle Ordovician* (*Darriwilian, Didymograptus artus* Biozone–*Nicholsonograptus fasciculatus* Biozone): Belgium, UK, Czech Republic, France, Germany, Norway, Spain, Sweden, China, Saudi Arabia.——FIG. 197,*2a–b*. *J. spinulosus* (PERNER); *2a,* holotype, NMP L7564, *Corymbograptus retroflexus* Biozone, Šarka Formation, Osek near Rokycany, scale bar, 1 mm (adapted from Bouček, 1973, fig. 27a); *2b,* NHMUK PM Q5161, proximal end in reverse view, Llanfallteg Formation, South Wales, UK; scale bar, 1 mm (Fortey & Owens, 1987, fig. 112a).

Family PTEROGRAPTIDAE Mu, 1950

[Pterograptidae MU, 1950b, p. 180] [*nom. emend.* MU, 1974, p. 231, *ex* Pterograptinae MU, 1950, p. 180]

Two-stiped, pendent to deflexed, and horizontal graptoloids; cladial branching in some taxa form secondarily multiramous tubaria; sicula conical, widening distinctly toward aperture and with small prosicula, or parallel-sided with wide prosicula; sicula with distinct dorsal virgellar spine and antivirgellar origin of th1[1]; thecae simple, widening tubes with moderate development of rutella; proximal development isograptid or artus type, dextral. *Lower Ordovician* (*Floian, Paratetragraptus akzharensis* Biozone)–*Middle Ordovician* (*upper Darriwilian, Pterograptus elegans* Biozone): worldwide.

All taxa of the Pterograptidae possess a dorsal virgellar spine on the sicula. This spine is regarded as the defining synapomorphy. The family may be monophyletic, but no cladistic analysis of the group has yet been carried out. MALETZ, CARLUCCI, and MITCHELL (2009) included a group of virgellate taxa among the stem reclinatids. The Pterograptidae incorporates the virgellate dichograptids, except for the four-stiped, scandent members of the genus *Phyllograptus* in which the virgellar spine evolved independently (MALETZ, 2010a). The proximal part is quite variable with the dimension of the prosicula changing considerably from a comparably large prosicula in the early taxa (Fig. 199.1, Fig. 199. 3) to a small one in later taxa (Fig. 199.4, Fig. 199.7, Fig. 199.10–11). The proximal development is of the isograptid type, but derived species possess an artus-type development (Fig. 199.10). All taxa have two main stipes with an orientation ranging from pendent to deflexed and horizontal, and, in a few cases, slightly reflexed proximally. The genera *Pterograptus* and *Pseudobryograptus* have a multiramous, pendent colony shape through the addition of thecal cladia.

The Pterograptidae originated during the Floian with the genus *Didymograptellus* bearing primitive, symplesiomorphic characters, such as the origin of th1[1] in the middle part of the prosicula and simple thecae (Fig. 199.1–199.3). The earliest known species *Didymograptellus primus* MALETZ, 2010a from the *Tetragraptus akzharensis* to *Tshallograptus fruticosus* biozones already had a fully developed dorsal virgellar spine. The evolutionary origin of the dorsal virgellar spine is unknown as no morphologically intermediate taxa are available showing its formation. The development of the sicula with the large, parallel-sided prosicula, however, may indicate a close connection to the Anisograptidae, as in this group, the pro- and metasicula generally appear to be parallel sided and do not have a widening from the aperture of the prosicula onward.

Pterograptus HOLM, 1881a, p. 74 [**P. elegans;* M]. Pterograptid with long slender sicula, prosicula expanded, origin of th1[1] on metasicula, th1[1]

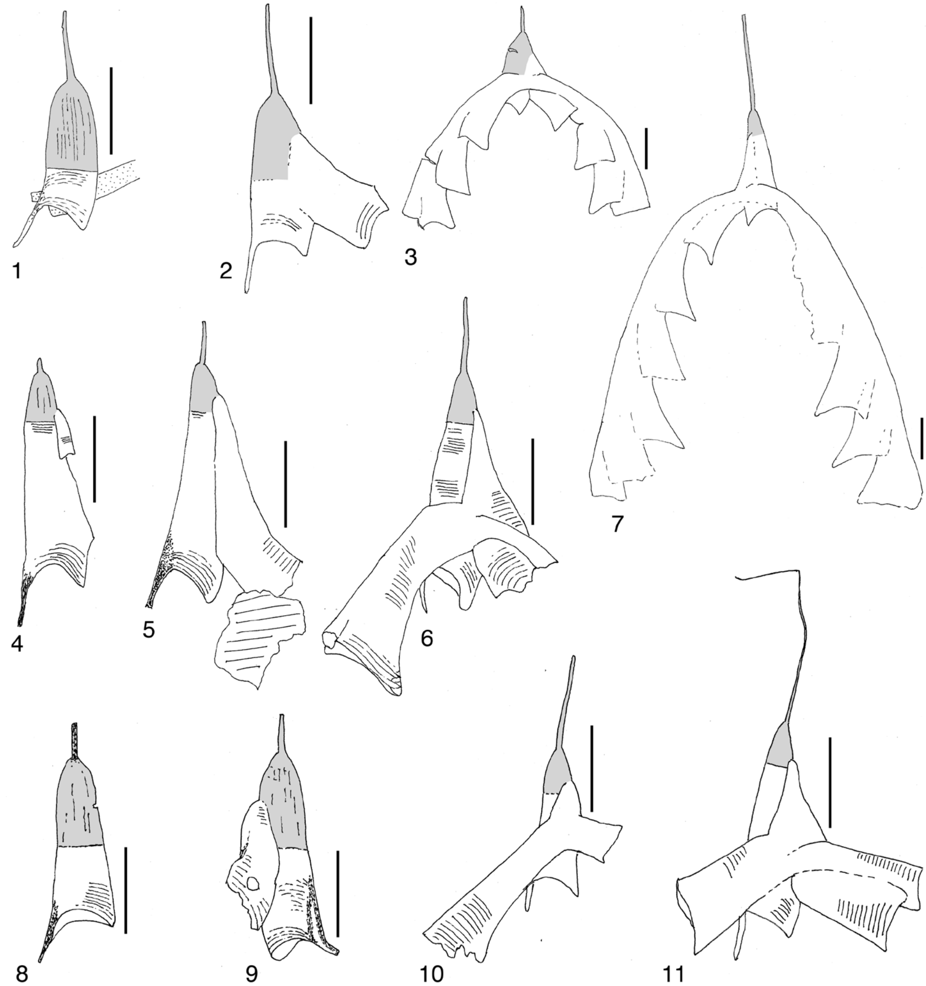

FIG. 199. Proximal ends of isolated pterograptids. *1–3, Didymograptellus bifidus* (HALL, 1865). *1,* Growing sicula, metasicula incomplete; *2,* complete sicula with th1[1]; *3,* proximal end of larger specimen; *4–7, Yutagraptus mantuanus* RIVA, 1994; *4,* sicula with initial part of th1[1]; *5,* sicula with incomplete th1[1]; *6,* proximal end in reverse view, showing virgellar spine; *7,* complete proximal end; *8–9, Didymograptellus primus* MALETZ, 2010a; *8,* incomplete sicula with prominent virgellar spine; *9,* juvenile with incomplete th1[1]; *10, Xiphograptus artus* MALETZ, 2010a, proximal end showing artus-type development; *11, X. lofuensis* (LEE, 1961), proximal end with isograptid development; prosicula in *gray;* all scale bars, 0.5 mm (specimens adapted from Maletz, 2010a).

dicalycal (artus-type development); alternating cladial branches on each theca of the two main stipes; main stipes declined to deflexed. *Middle Ordovician* (*upper Darriwilian, Pterograptus elegans* Biozone): UK, France, Germany, Portugal, Sweden, Norway, Canada, USA, Argentina, China, Australia, New Zealand.——FIG. 200,*1a–c.* **P. elegans; 1a–1b,* holotype, PMO 2697, Oslo Region, Norway, scale bars, 10 mm (Holm, 1881a, fig. 2–3); *1c,* GSC 102784, flattened and bleached proximal end showing artus-type development, scale bar, 0.5 mm (Maletz, 1994a, fig. 1).——FIG. 200,*1d. P. lyricus* KEBLE & HARRIS, 1934, paratype, NMV P13755, showing zigzag pattern of main stipe, Victoria, Australia, scale bar, 1 mm (new).——FIG. 200,*1e. P. scanicus* HOLM, 1881a, reconstruction, scale bar, 10 mm (Bulman, 1970, fig. 77).

Didymograptellus COOPER & FORTEY, 1982, p. 220 [**Graptolithus bifidus* HALL, 1865, p. 73; OD]. Simple, parallel-sided sicula with a nearly straight aperture and prominent dorsal virgellar spine; prosicula large, at least one-third to one-half of sicular length; proximal development isograptid type, dextral, with high origin of th1[1] in prosicula;

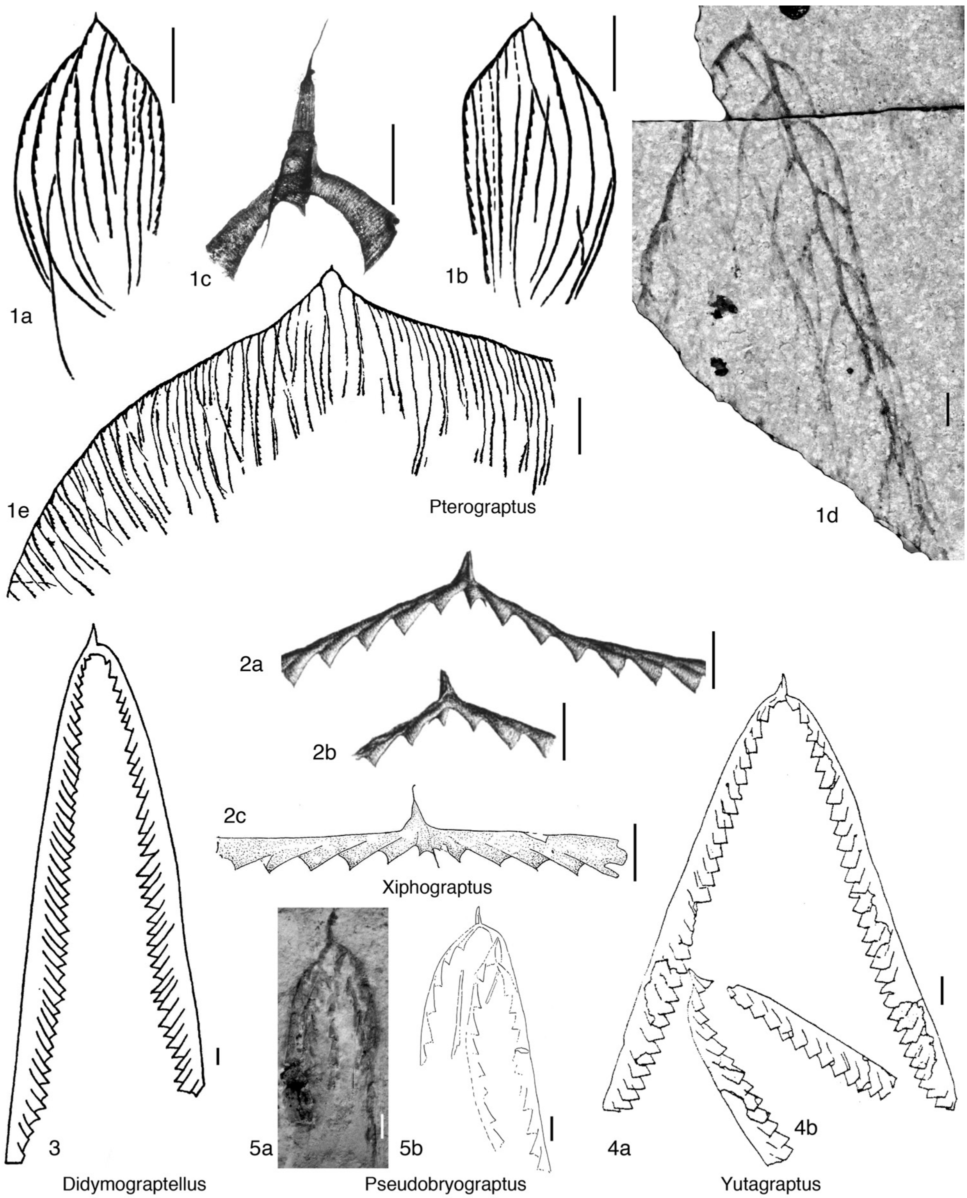

FIG. 200. Pterograptidae (p. 305–308).

crossing canals low on sicula; thecae simple dichograptid with straight apertures; tubarium form pendent. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone)–*Middle Ordovician* (*Dapingian, Arienigraptus gracilis* Biozone): Canada, USA, Argentina, Bolivia, China, Australia, New Zealand.——FIG. 200,*3.* **D. bifidus* (HALL), lectotype, GSC 910a, Lévis, Quebec (possibly Begin's Hill section), scale bar, 1 mm (Berry, 1962b, fig. 2a).

Pseudobryograptus MU, 1957, p. 385 (p. 421, English translation) [**P. parallelus;* OD]. Small, pendent tubarium with five to eight stipes; thecae simple with low inclination and overlap; branching after the initial dichotomy possibly by cladia generation; proximal development likely artus type. *Middle Ordovician* (*Darriwilian,* ?*Holmograptus lentus* Biozone): China, Argentina, Australia, ?Canada.——FIG. 200,*5a–b.* **P. parallelus; 5a,* holotype, NIGP 8863; *5b,* paratype, NIGP 8864;

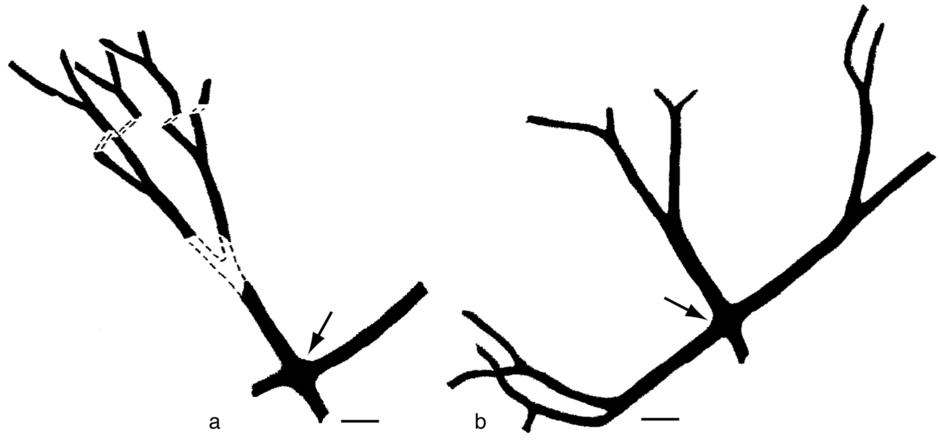

FIG. 201. Suborder Uncertain (p. 308).

possibly *Holmograptus lentus* Biozone (originally cited as *Didymograptus hirundo* Biozone); Changshan, western Chekiang, China, scale bars, 1 mm (new).

Xiphograptus COOPER & FORTEY, 1982, p. 289 [**Didymograptus formosus* BULMAN, 1936a, p. 24; OD]. Simple conical, considerably widening sicula with straight aperture and prominent dorsal virgellar spine (antivirgellar origin of $th1^1$); prosicula small, less than one-fourth of sicular length; proximal development isograptid or artus type, $th1^1$ dextral and originating low in prosicula; crossing canals low on sicula, isograptid suture absent on reverse side; thecae simple dichograptid with straight apertures; tubarium form horizontal, declined, or less commonly, deflexed, with no or little distal widening of the stipes. *Lower Ordovician* (*Floian, Tshallograptus fruticosus* Biozone)–*Middle Ordovician* (*Darriwilian, Pterograptus elegans* Biozone and possibly to *Dicellograptus vagus* Biozone): worldwide.——FIG. 200,*2a–b*. **X. formosus* (BULMAN), lectotype, NRM-PZ Cn1264, obverse (*a*) and reverse (*b*) views, Hälludden, Öland, Sweden, scale bars, 1 mm (Bulman, 1936a, pl. 1,*5–6*).——FIG. 200,*2c*. *X. lofuensis* (LEE, 1961), holotype, NIGP 10541, Dawan Formation, Majiang, Guizhou Province China, scale bar, 1 mm (Ni, 1988, fig. 1a).

Yutagraptus RIVA, 1994, p. 4 [**Y. mantuanus;* OD]. Simple conical, considerably widening sicula with straight aperture and prominent dorsal virgellar spine; prosicula small, less than one-fourth of sicular length; proximal development isograptid type, dextral, with low origin of $th1^1$ in prosicula; crossing canals low on sicula, isograptid suture lacking on reverse side; thecae simple dichograptid with straight apertures; tubarium form pendent with no or little distal widening of the stipes. *Middle Ordovician* (*Dapingian, Didymograptellus bifidus* Biozone–*Darriwilian, Levisograptus austrodentatus* or *Levisograptus primus* Biozone): Australia, Canada, USA, ?Iran.——FIG. 200,*4a–b*. **Y. mantuanus,* RPM 13677, holotype (*a*) and paratype (*b*) as associated on slab, Mantua, Utah, scale bar, 1 mm (Riva, 1994, fig. 3M–N).

Suborder UNCERTAIN

Calamograptus CLARK, 1924, p. 61 [**C. porrectus;* OD]. Multiramous dichograptid with tetragraptid proximal end and long second-order stipes; distal stipe division intervals decreasing in length; thecal style and proximal development unknown. *Lower Ordovician* (*upper Tremadocian*, *Clonograptus* Biozone): Canada. [The taxon is based on two very poor specimens, possibly a senior synonym of *Paratemnograptus.*]——FIG. 201,*a–b*. *C. porrectus* CLARK, 1924; *a,* holotype, MCZ IP 101402; *b,* paratype, MCZ IP 10140; North Ridge, Lévis, Quebec, Canada; scale bars, 10 mm (Clark, 1924, pl. 5,*2* and 5,*1,* respectively).