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PART V, SECOND REVISION, CHAPTER 16: ORDER GRAPTOLITHINA, UNCERTAIN FAMILIES: INTRODUCTION, MORPHOLOGY, AND SYSTEMATIC DESCRIPTIONS

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GRAPTOLITHINA BRONN, 1849 UNCERTAIN FAMILIES

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 Stolonidea KOZŁOWSKI, 1938. These are not used by MALETZ (2014), as 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* (Stolonidea) 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 Chau-

nograptidae BULMAN, 1955. OBUT (1974) added the order Archaeodendrida. All these taxa are based on highly fragmented material and here included in the family Dithecodendridae OBUT, 1964 until better known.

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 composed of autothecae and bithecae produced in triads; autothecae usually with inflated proximal portion and erect distal neck, often provided with elaborated apertural lobes; bithecae cylindrical, adnate throughout their length; stolon system usually showing 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. 1), as most other details

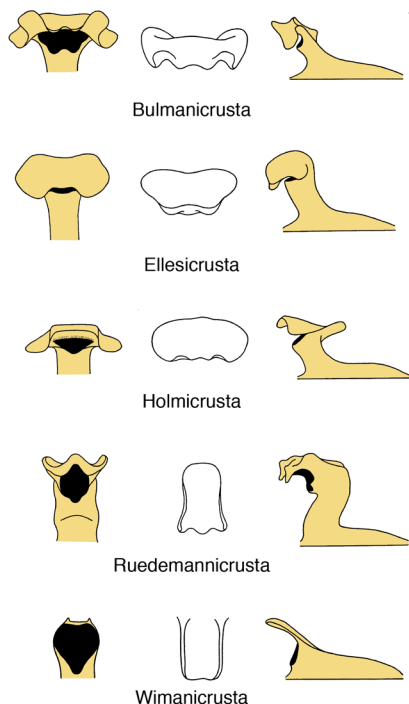


FIG. 1. The apertural modifications of thecae in the Wimanicrustidae in apertural, dorsal, and lateral views (from left to right). The apertural openings are shown in black (Kozłowski, 1962, fig. 13, color added).

of the colonies were unknown. The genus *Hormograptus* may be considered to represent a wimanicrustid preserved in sediment and not being chemically isolated from the sediment, thus, providing a better idea on the tubarium shape and construction. MIERZEJEWSKI (2000b), however, 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.

MORPHOLOGY

The precise morphology of the wimanicrustid colonies is unknown, as 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 metascula, which he tentatively assigned to the crustoids (Fig. 2.1–2.3). The prosicula is an ovoid vesicle (dome), proximally attached to the substrate by a concave and rough surface, surrounded by a marginal membrane. Distally, the dome produces an elongated neck-like part. The metascula consists of a number of annular fuselli, probably lacking an oblique suture. This scula in many ways resembles the dome of the Rhabdopleuridae, but differs by the presence of the neck-like 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. 2). Bifurcation through triads was described by KOZŁOWSKI (1962) and can be seen in MITCHELL, WILSON, and ST. JOHN (1993). The *in situ* colonies of *Bulmanicrusta?* sp. (Fig. 2.4) 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. exhibits 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. 2.7). They developed 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 can be seen clearly in the preserved stolon system. The autothecae are the dominant element in construction of the wimanicrustid colony and are

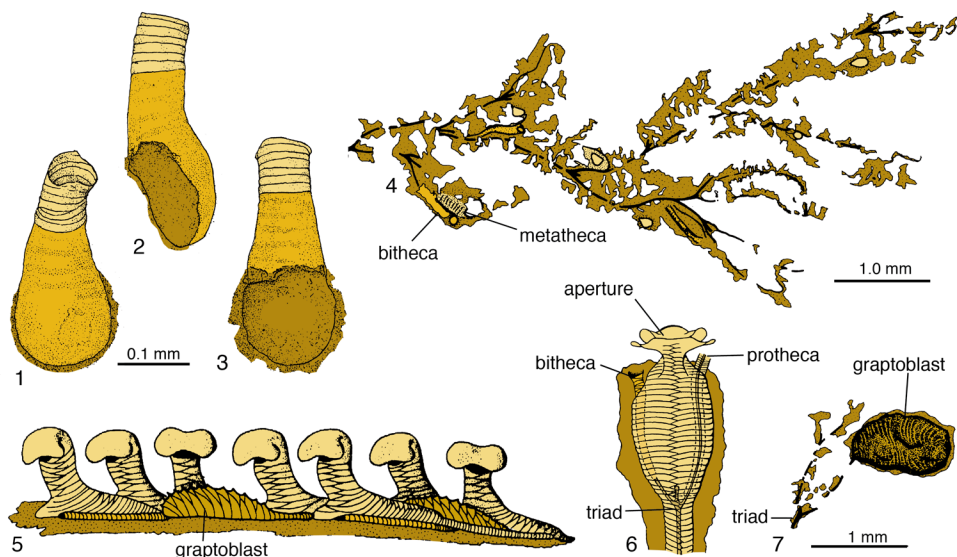


FIG. 2. The tubarium of the Wimanicrustidae. 1–3, possible wimanicrustid sicula in different views, Vistula River Valley, Poland (Kozłowski, 1971, fig. 4, color added); 4, *Bulmanicrusta*? KOZŁOWSKI, 1962, part of colony showing largely basal membranes, stolon system, and some parts of autothecae (Mitchell, Wilson, & St. John, 1993, fig. 3, 6, color added); 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, color added); 7, *Bulmanicrusta*? KOZŁOWSKI, 1962, fragment with graptoblast (Mitchell, Wilson, & St. John, 1993, fig. 3, 7, color added).

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 hood-like process, straight or curved over the aperture. The bithecae are slender, parallel-sided tubes, with their lower wall flat, and upper more or less convex. The apertures of the bithecae are devoid of any elaborations. (Fig. 2.6). The bithecae are usually growing 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 shows distinct zigzag sutures on the dorsal side in both portions of the autothecae (Fig. 2.6), but the basal layer of the autothecae is devoid of any recognizable sutures. Bithecae show 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 TEM investigation to differentiate cortex and fusellum, but this investigation was unable to show whether cortical tissues developed as bandages, as it was based on thin sections and did not provide an impression of surface features.

The stolon system shows 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. 3). The well-sclerotized stolons, 20 to 35 microns in diameter, display a characteristic annulation not seen in other graptolites (Fig. 3.7–3.8). The annulations proved to

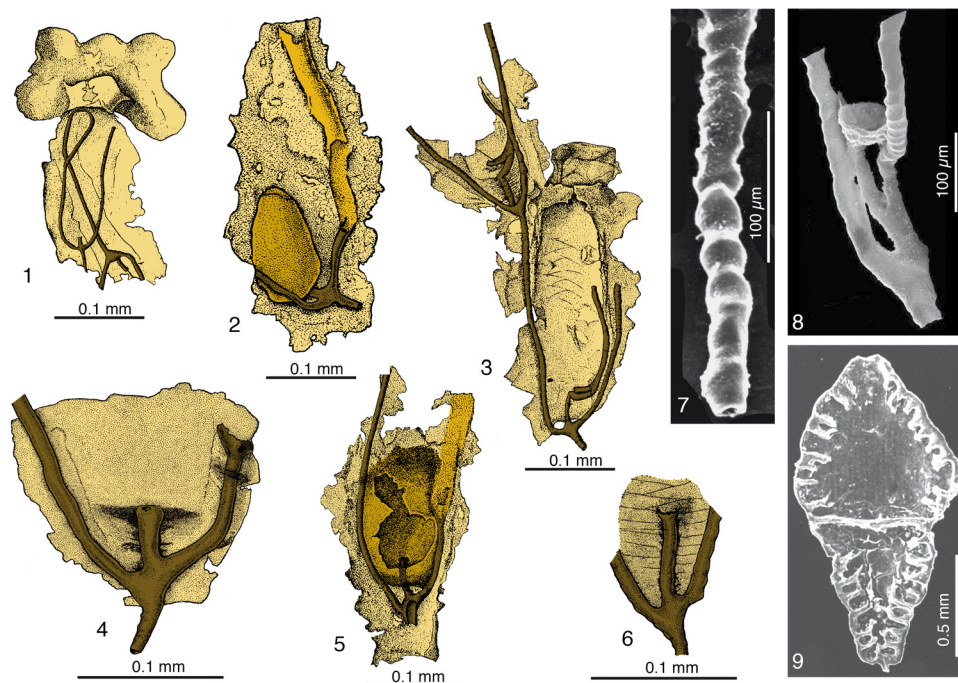


FIG. 3. The stolon system in Wimanicrustidae. 1, *Bulmanicrusta modesta* KOZŁOWSKI, 1962, ventral view showing stolon system with triad budding; 2, 5, triad budding with cyst and bitheca; 3, *Bulmanicrusta modesta* KOZŁOWSKI, 1962, ventral view showing stolon system with triad budding; 4, 6, *Wimanicrusta urbaneki* KOZŁOWSKI, 1962, details of triad budding (1–6, Kozłowski, 1962, fig. 2–3, color added); 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).

be distinct in certain portions and much less pronounced in other parts of the stolon, which at places are almost smooth. Transverse sections of the stolon in *Bulmanicrusta latialata* KOZŁOWSKI, 1962 examined with TEM show a thick wall (about 6 µm) made of homogenous, electron-dense material and a thin inner layer composed 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, were recognized inside many autothecae (Fig. 3.2,5). 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 here interpreted as comparable to the dormant buds of *Rhabdopleura* (see MALETZ & BELI, 2018).

GRAPTOBLASTS

Graptoblasts (Fig. 4) 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,

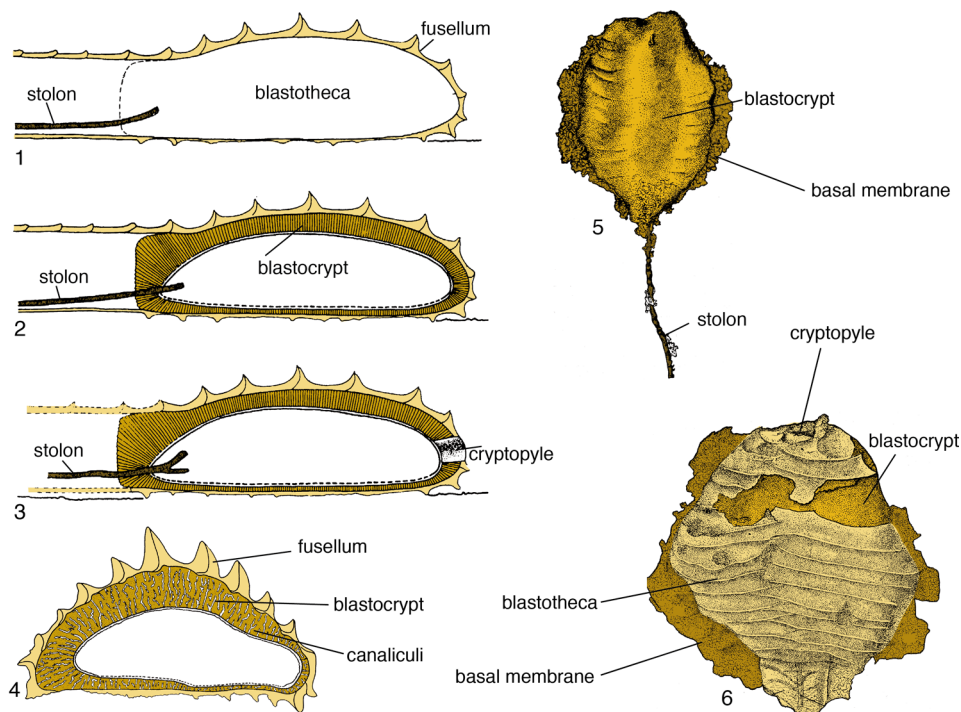


FIG. 4. Construction of the graptoblast. 1–3, development of graptoblast (adapted from Urbanek, 1983, fig. 2); 4, cross section of graptoblast showing canaliculi (adapted from Urbanek, Mierzejewski, & Rickards, 1986, fig. 2A); 5, graptoblast showing basal membrane and chamber, fusellum not preserved (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).

was formed secondarily by resorption of the distal graptoblast wall by the encysted individual or individuals (Fig. 4.3).

The graptoblast displays a two-layered construction formed from fusellar tissue outside and electron-dense crassal tissue inside (Fig. 4.1–4.3). The outer, primary layer is called the blastotheca (Fig. 4.1). The inner component corresponds to KOZŁOWSKI's non-transparent blackish layer and was named the blastocrypt (URBANEK & RICKARDS, 1974; URBANEK, MIERZEJEWSKI, & RICKARDS, 1986), showing numerous and characteristic, vertically oriented and frequently branching canaliculi (Fig. 4.4). Their diameter usually 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 showing traces of layering. In some graptoblasts, the inner cavity become subdivided by the transverse septum (Fig. 3.9) into an anterior and posterior chamber (i.e., genus *Graptoblastus* KOZŁOWSKI, 1949). MIERZEJEWSKI (2000b) used SEM technique to show 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. 4.1–4.4). Their role in the life cycle of crustoid graptolites may be best compared with hibernaculae of ctenostomate bryozoans. MIERZEJEWSKI (2000b) recognized in one of his early Silurian graptoblasts numerous incomplete

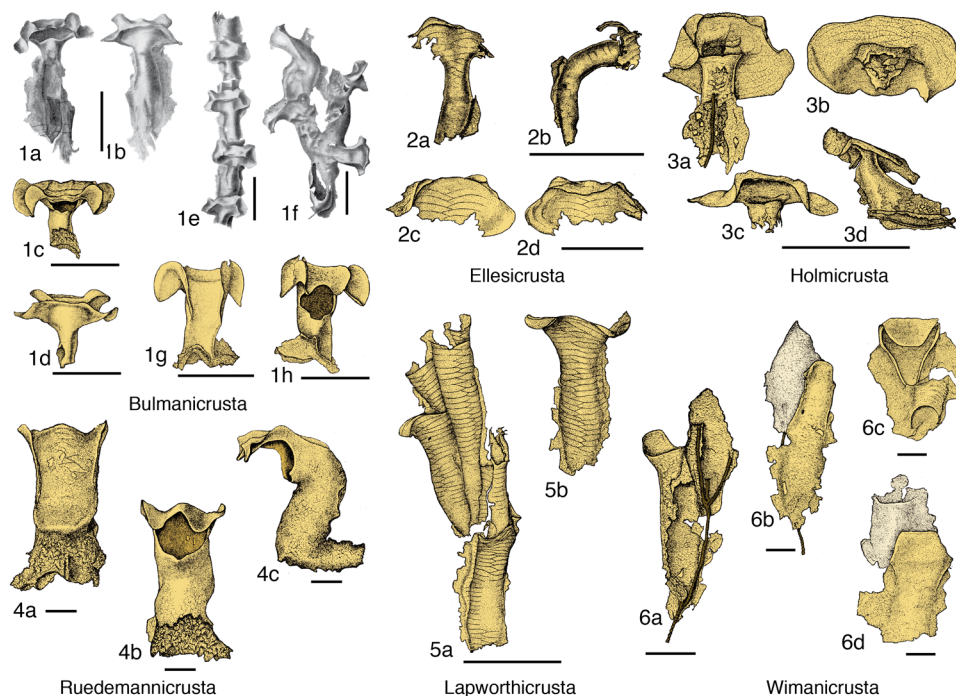


FIG. 5. Wimanicrustidae (p. 6–7).

septae (called hemiseptae by him), produced by folds of the inner lining and spread more or less evenly in both chambers (Fig. 3.9). On the basis of this finding, one cannot conclude whether hemiseptae are normal structures or rare abnormalities.

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. 5, 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, color added).—FIG. 5, 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 (c) and adapertural (d) views, scale bars, 0.5 mm (Kozłowski, 1962, 16A–B, color added).

Ellesicrusta KOZŁOWSKI, 1962, p. 38 [**E. longicollis*; OD]. Apertural lobe with slight lateral folds; long neck; details of colony unknown. *Lower–Middle Ordovician*: Estonia (glacial erratic boulders).—FIG. 5, 2a–d. **E. longicollis*, holotype in various views, scale bars, 0.5 mm (Kozłowski, 1962, fig. 21, color added).

Holmicrusta KOZŁOWSKI, 1962, p. 41 [**H. sombrero*; OD]. Apertural lobe large, flattened; neck long; details of colony unknown. *Lower–Middle Ordovician*: Poland (glacial erratic boulders).—FIG. 5, 3a–d. **H. sombrero*, holotype in various views, scale bars, 0.5 mm (Kozłowski, 1962, fig. 23, color added).

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. 5, 5a–b. **L. aenigmatica*, holotype, two fragments of a single colony, scale bar, 0.5 mm (Kozłowski, 1962, fig. 26, color added).

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. *Lower–Middle Ordovician*: Poland, Estonia (glacial erratic boulders).—FIG. 5, 4a–c. **R. geniculata*, holotype, scale bars, 0.1 mm (Kozłowski, 1962, fig. 22, color added).

Wimanicrusta KOZŁOWSKI, 1962, p. 43 [**W. cristaelingulata*; OD]. Apertural lobe linguiform; neck short or absent; triad budding; other details of colony unknown. *Lower–Middle Ordovician*: Estonia, Poland, Sweden (Öland) (glacial erratic boulders).—FIG. 5, 6a–d. **W. cristaelingulata*, holotype (a–b) and fragment (c–d) in dorsal and

ventral views, scale bars, 0.1 mm (Kozłowski, 1962, fig. 24A–B, color added).

Hormograptus ÖPIK, 1930, p. 8, pro *Thallograptus* ÖPIK, 1928, p. 35, non *Thallograptus* RUEDEMANN, 1925, p. 35 [**Thallograptus sphaericola*; OD]. Runner-type encrusting colony; tubarium details unknown. *Upper Ordovician (Sandbian, Nemagraptus gracilis Biozone)*: Estonia.—FIG. 6, 1a–b. **H. sphaericola*, TUG 1317, holotype and enlargement of part, scale bars, 1 mm (new; provided by Ursula Toom).

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, 1962; URBANEK, 1983), but are listed here for completeness. 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 often distinct zigzag suture visible; formed from electron-dense material showing 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. 6, 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 often visible; formed from electron-dense material showing 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. 6, 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 showing the inner rings and spiral thickenings may have been mistaken for tracheid-like tubes characteristic of land plants.] *?Ordovician*: Poland (glacial erratic boulder).—FIG. 6, 2a–b. **M. ursulae*, fragments of holotype, scale bar, 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 showing triad budding.] *Silurian (Wenlock)*: Poland, Sweden (glacial erratic boulders).—FIG. 6, 3a–b. **U. reversa*, holotype, scale bars, 1 mm (Mierzejewski, 1985, pl. 5).

Xenocyathus EISENACK, 1982, p. 630, *nom. dub.* [**X. stolonifer*; M]. [This taxon is represented as stolon fragments showing triad budding and may be identified as a wimanicrustid (Mierzejewski, 1984). 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. 6, 4a–b. **X. stolonifer*, Upper Ordovician, Estonia; 4a, holotype, scale bars, 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 extracameral 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 collected from a few localities in Scandinavia (e.g., SKEVINGTON, 1963; MIERZEJEWSKI,

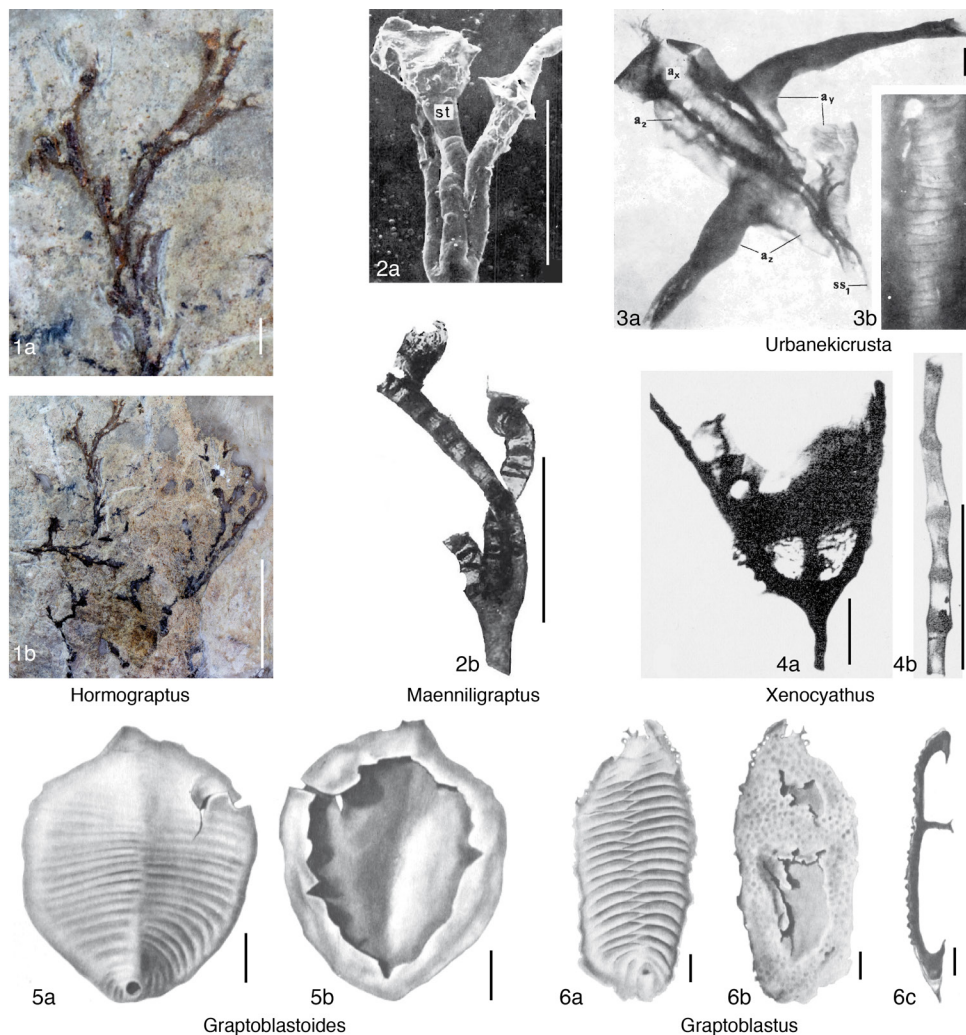


FIG. 6. Wimanicrustidae, uncertain genera (p. 7).

2003). Very little is known about their colony construction and evolutionary relationships, as 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. 7). The basal layer is smooth and does not show any constructional details. The collum is fairly slender as compared to the inflated camara, but both show conspicuous zigzag

sutures. A considerable elongation of the collum has been recognized in a couple of fragments (Figs. 7.4–7.5). The development of the thecal apertures is uncertain in most taxa due to preservational aspects, but may be quite simple. Often the apertures indicate fragmentation and loss of the actual apertural margins through the presence of irregular rims.

Cross sections of *Cysticamara accollis* KOZŁOWSKI, 1949 (Fig. 7.2–7.3) and *Bithecocamara gladiator* KOZŁOWSKI, 1949 show the presence of a stolon system. The stolon

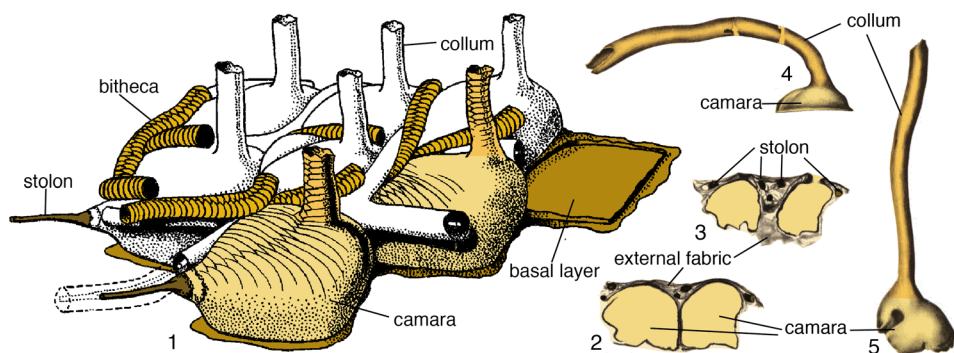


FIG. 7. Morphology of the Cysticamaridae. 1, *Bithecocamara* KOZŁOWSKI, 1949, reconstruction (adapted from Bulman, 1955, fig. 26); 2–3, Sections through the thecae of *Cysticamara accollis* KOZŁOWSKI, 1949 showing the presence of a stolon system (adapted from Kozłowski, 1949, pl. 29; 4–5, two isolated cysticamarid fragments with long collum (adapted from Kozłowski, 1949, pl. 31).

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 usually based on small colony fragments, often 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, as the development of the stolon system has not been described. BULMAN (1955) erected the Bithecocaridae 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.

URBANÉK and MIERZEJEWSKI (1991) described the ultrastructure of *Tubicamara coriacea* KOZŁOWSKI, 1949. TEM studies show fusellum and endo- and ectocortex to be present. The endocortex is thought to

be underdeveloped and may be missing in many cysticamarids. MIERZEJEWSKI (2000a) 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, even 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 extracameral fabric above camarae; differentiated into two types of thecae, of which smaller one, which lacks collum, is termed bitheca. *Lower Ordovician (Tremadocian)*: Poland.—FIG. 8.1. **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] [= *Syringataenia* Obut, 1953, p. 54 (type, *S. bystrovi*, M), see BULMAN, 1970, p. 50]. Thigmophilic tubarium with densely arranged camarae; autothecae with slightly elevated, thickened rim, but without collum; indications of stolon system inside extracameral fabric above camarae. *Lower Ordovician (Tremadocian)–Middle Ordovician (Darriwilian)*: Poland, Sweden, Russia.—FIG. 8, 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 subconical 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. *Upper Ordovician (Sandbian?)*: Poland (glacial erratic boulder).—FIG. 8,4. **E. maennili*, holotype, ZPAL G/XXIV/5, isolated theca, scale bar, 0.1 mm (Mierzejewski, 2000c, fig. 1e).

Flexicoliccamara 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. 8,5. **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), 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. 8,3a–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. 8,6a–b. **T. coriacea*, holotype in two views, ZPAL GI/1-290, scale bars, 0.5 mm (Kozłowski, 1949, pl. 30,1a–b).

Xenotheca EISENACK, 1938, p. 239, [**Xenotheca klinostoma*; OD] [= *Xenokalymma* EISENACK, 1968, p. 306 (type, *X. trematophora*, OD), herein; non *Xenotheca* ARBER & GOODE, 1915, p. 96, Devonian plant]. 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. 8,7a–c. **Xenotheca klinostoma*; 7a, holotype (Eisenack, 1938, fig. 21); 7b, paratype (Eisenack, 1938, 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, showing multiple dichotomous branchings; thin-walled metathecae isolated, tubular, or slightly widening towards aper-

ture; 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. 9). They possess isolated metathecae with thin fusellum and a robust stem (Fig. 9.1), 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 indication of an attachment. Similarities can be seen to the Mastigograptidae, from which stolon systems with triad budding and isolated, thin-walled thecae are known (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 *Archaeolafloea* CHAPMAN, 1919 (included in the Rhabdopleuridae) (see MALETZ & BELI, 2018). BULMAN (1970) listed most of the genera included here in the Dithecodendridae under the category, “taxonomic position uncertain.”

JOHNSTON, JOHNSTON, & POWELL (2009) described larger, complexly branched dithecodendrids from the *Bolaspidella* Zone (Drumian to lower Guzhangian; PENG,

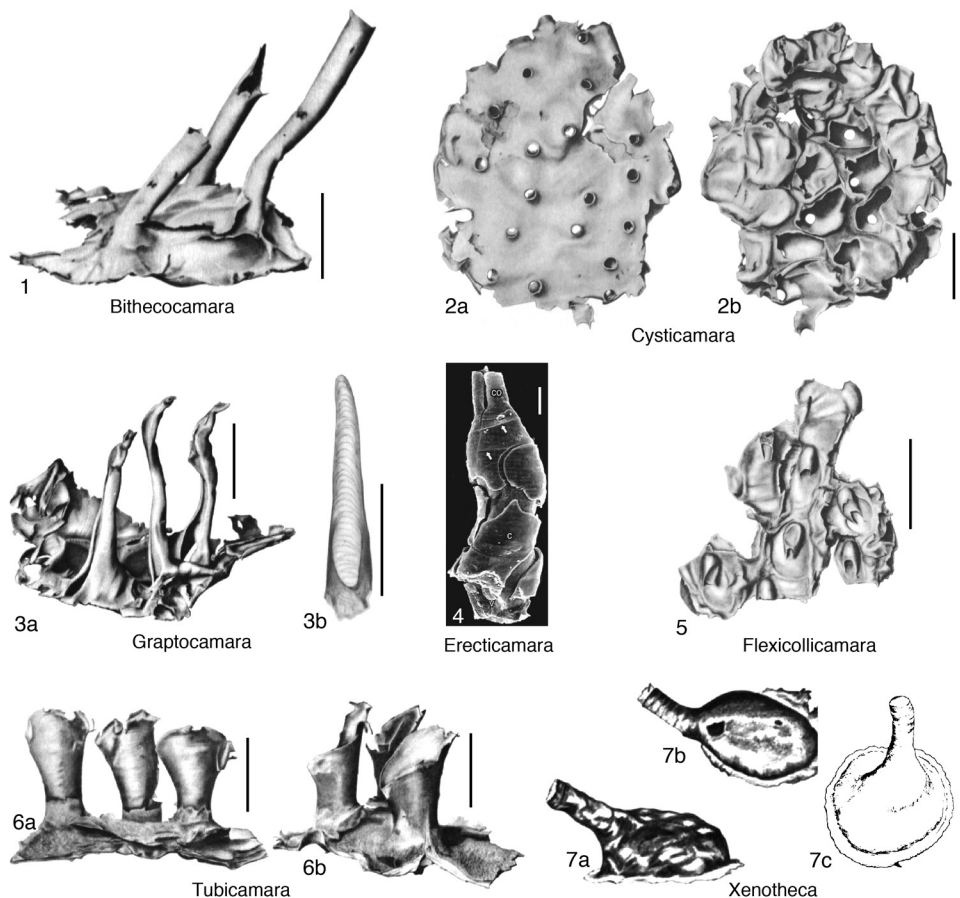


FIG. 8. Cysticamaridae (p. 9–10).

BABCOCK, & COOPER, 2012) of the Chancellor Basin, British Columbia, Canada, and documented fusellar construction in the material (Fig. 9.5–9.6). The specimens represent some of the oldest and best-preserved Middle Cambrian graptolites known so far.

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 graptolitic nature of this genus is uncertain.)] *Middle Cambrian (Miaolingian, Drumian)* Russia (Siberia).—FIG. 10.1. **B. magnificum*, holotype, IGiG 592/5 (Rickards & Durman, 2006, fig. 55).

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. 10.2. **D. sibiricum*, IGiG 960, holotype (Rickards & Durman, 2006, fig. 58c).

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. 10.6. **K. aspidograptoides*, holotype (Sennikov, 1998, pl. 1,3).

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 dithecod. Assignment was based only on age].—FIG. 10.5a–b. **P. paniculiformis*, holotype (Sennikov, 1998, pl. 1,1–2).

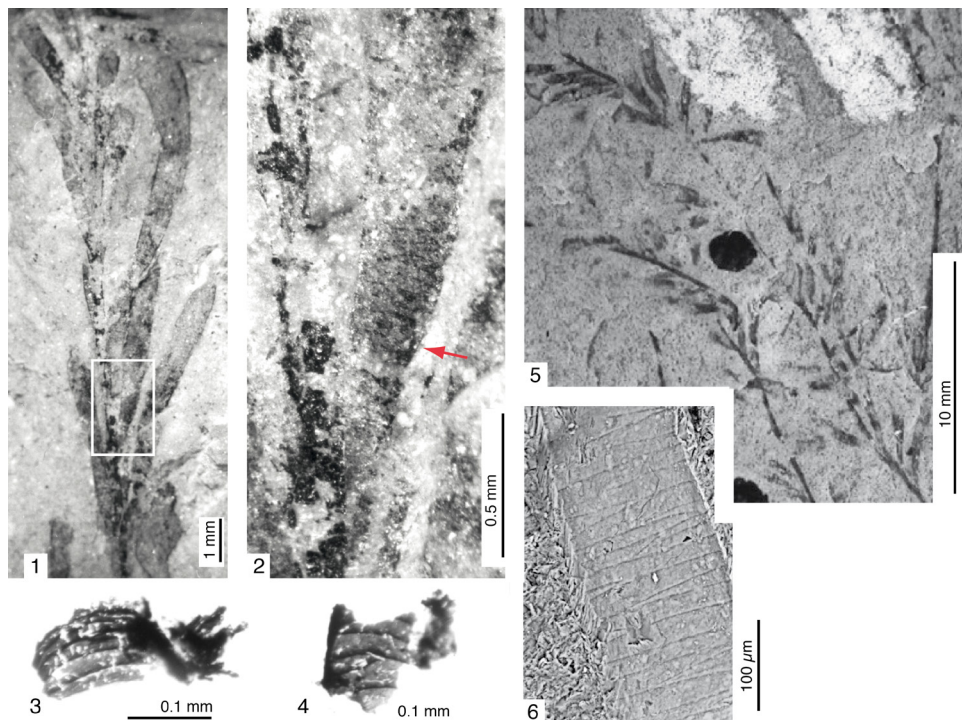


FIG. 9. Tubarium details of the Dithecodendridae. 1–2, *Tarnagraptus cristatus* SDZUY, 1974, SMF 30021; 1, part of holotype showing thin-walled metathecae and indications of robust stem; 2, magnified part of (1) showing indications of fusellar construction (arrow); 3–4, chemically isolated fragments 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).

Siberiodendrum OBUT, 1964, p. 306 [**S. robustum*; OD]. Robust dithecodendrid fragment with densely spaced, wide, probably parallel-sided thecae; thecae probably arranged biserially; tubarium shape unknown. *Late middle Cambrian–early 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. 10.4. **S. robustum*, IGI 960, holotype (Rickards & Durman, 2006, fig. 62).

Siberiograptus OBUT, 1964, p. 306 (there cited as OBUT, 1963) [**S. kotujensis*; OD]. Tubarium slender, with large, distally isolate thecae; thecae arranged biserially. *Upper Cambrian*: Russia (Siberia).—FIG. 10.3. **S. kotujensis*, IGI 960, holotype (Rickards & Durman, 2006, fig. 39).

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. 10.7. **O. gracilis*, holotype, SMF 30028 (new).

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. 10.8. **S. flexilis*, holotype, SMF 30026 (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. 10.9a–b. **T. palma*, holotype, SMF 30023, specimen and detail showing preservation of robust stipes and thin-walled metathecae (new).

Family CYCLOGRAPTIDAE Bulman, 1938

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

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

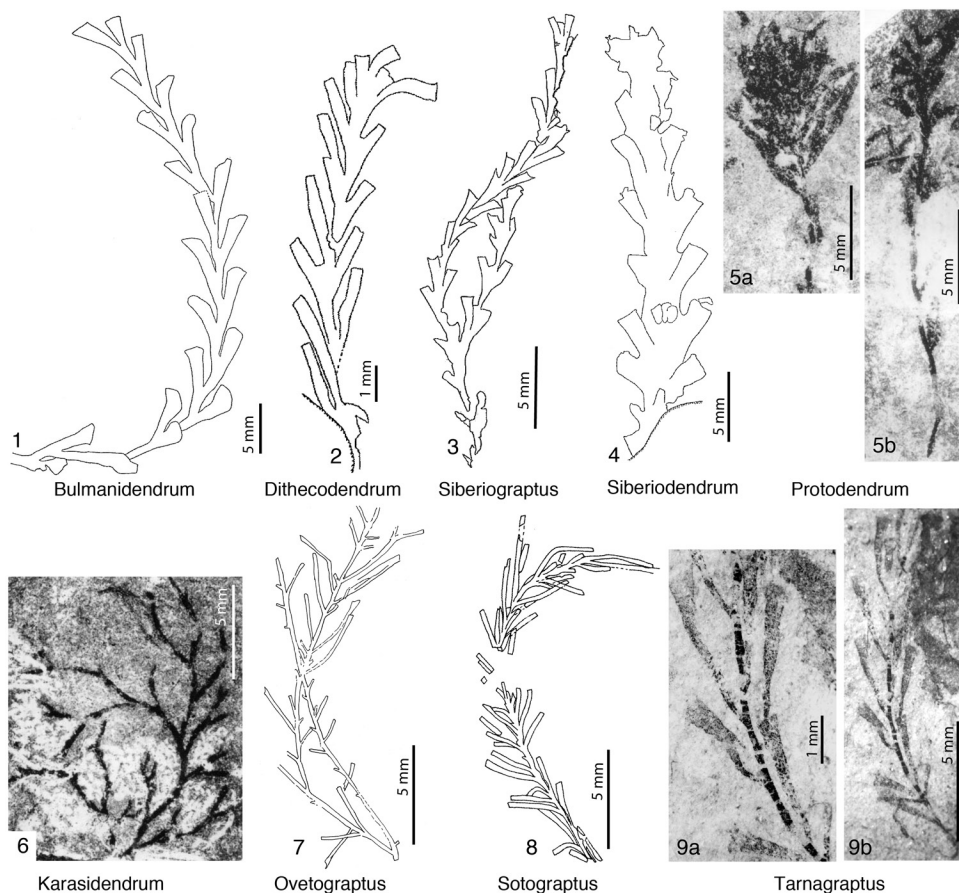


FIG. 10. Dithecodendridae (p. 11–12).

be 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 disc and numerous erect stipes, but BULMAN (1950) considered the family Cyclograptidae as a synonym of the Idiotubidae and BULMAN (1955, 1970) did not even mention the Cyclograptidae. 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 usually 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 grow 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 show one or two branching divisions and the stipes stay relatively short. *Galeograptus* has conothecae and bithecae concentrated in the thecorhiza, while these are not present in the erect stipes (BULMAN & RICKARDS, 1966).

KOZŁOWSKI (1949) illustrates 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. 11.7) 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. 11.5–11.6).

According to BULMAN (1938), the tubaria of the Cyclograptidae are differentiated into autothecae and bithecae with highly irregular distribution and a high amount of bithecae. The identification of the bithecae is made solely on the size of the thecal tubes and the simple straight apertures, while the autothecae often 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. 11.1–11.4; 11.8–11.9). This development may include a variable number of coils, but is not found 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. Dimor-

phic thecae are also present in *Galeograptus*, where 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 wannersteni* 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 *Kozłowskitubus* (Fig. 12,7a), in which the initial thecae grow 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.

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 erratic boulder).—FIG. 12,1a–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. siculooides*; OD]. Slowly 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 *Sphe-noecium* CHAPMAN & THOMAS, 1936]. *Lower Ordovician (Tremadocian)*: Poland.—FIG. 12,2a–c. **C. siculooides*; 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 often serially arranged; proximal portions of thecae commonly coiled into helical spiral. *Lower Ordovician (Tremadocian)*: Poland.—FIG. 12,3. **D. wimani*, holotype,

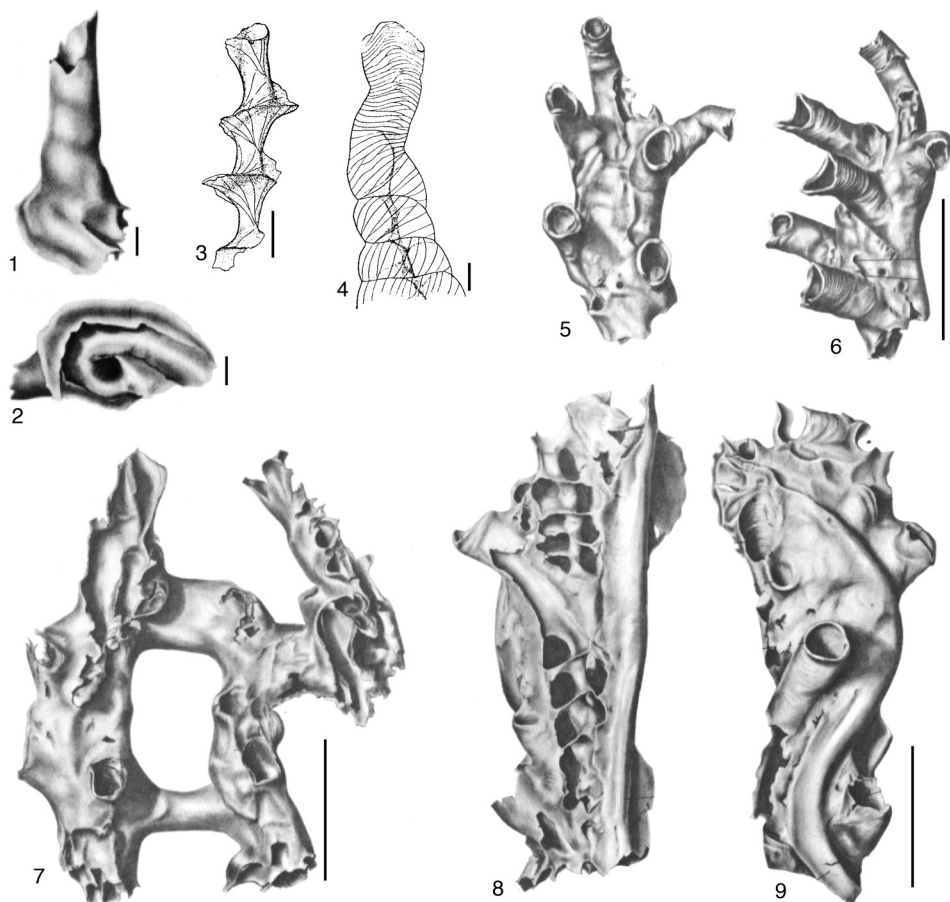


FIG. 11. Morphology of the Cyclograptidae. 1–2, *Dendrotubus wimani* KOZŁOWSKI, 1949, details of coiled median part of thecae; 3–9, *Tubidendrium bulmani* KOZŁOWSKI, 1949; 3, internal helicoidal structure; 4, coiled median part of theca; 5–6, fragment showing thecal orientation; 7, bridges connecting 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).

ZPAL GI/1-290, scale bar, 0.5 mm (Kozłowski, 1949, pl. 16,8).

Cyclograptus SPENCER, 1883, p. 365 [*C. rotadentatus* SPENCER, 1884, p. 592; M] [= *Rodonograptus* POČTA, 1894, p. 204 (type, *R. astericus*, M), BULMAN, 1970, p. 48]. Tubarium discoidal, erect portions of autothecae grouped into 20 to 30 peripheral sheaves bifurcating at mid-length; thecae tubular, elongated; thecal differentiation and stolon system unknown. *Middle Silurian (Wenlock)*: Canada, Czech Republic.—FIG. 12, 4a. **C. rotadentatus*, lectotype, ROM 21623, scale bar, 1 mm (Bulman, 1970, fig. 29,3).—FIG. 12, 4b. *C. astericus*, ?lectotype, scale bar, 1 mm (Počta, 1894, pl. 8,11).

Discograptus WIMAN, 1901, p. 191 [**D. schmidtii*; OD]. Tubarium discoidal, erect portions of autothecae in more or less radially arranged groups on upper surface of thecorhiza; thecae tubular, elong-

ated; 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. 12, 5a–b. **D. schmidtii*; 5a, lectotype, PMU G 786, scale bar, 1 mm (Bulman, 1970, fig. 29,2); 5b, stipe fragment, 0.5 mm (Bulman & Rickards, 1966, fig. 46B).

Galeograptus WIMAN, 1901, p. 189 [**G. wannersteni*; 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

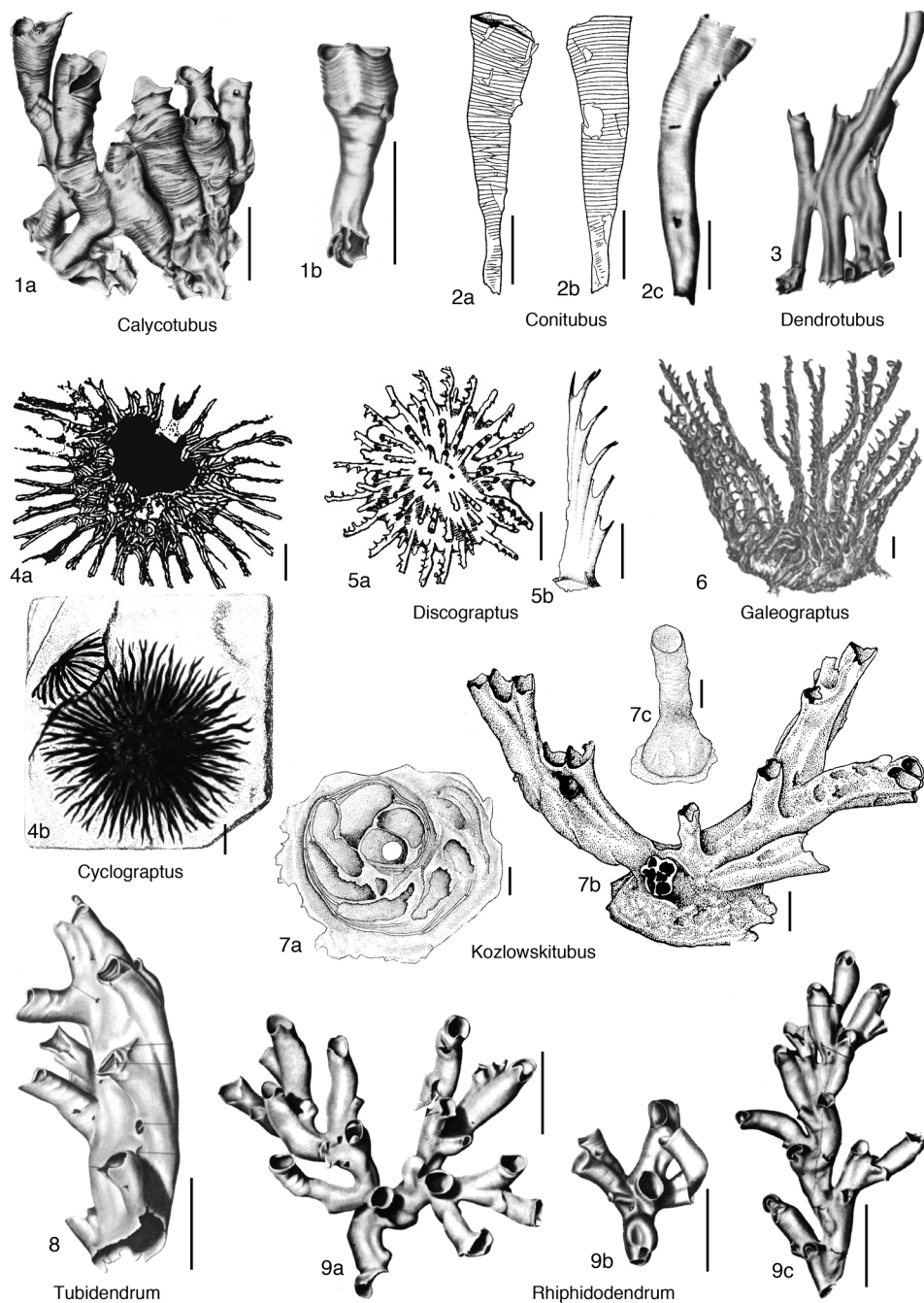


FIG. 12. Cyclograptidae (p. 14–17).

- apertural modifications; BULMAN and RICKARDS, 1966, p. 61].—FIG. 12,6. **G. wennnersteni*, holotype, PMU G 93, specimen preserved as serial sections, scale bar, 1 mm (Wiman, 1901, pl. 8,8).
- Kozłowski** *tubus* MIERZEJEWSKI, 1978, p. 571 [**Dendrotubus erraticus* KOZŁOWSKI, 1963, p. 104; OD]. Encrusting and erect-growing taxa with simple, tube-shaped thecae without apertural elaborations; sícula bottle-shaped, erect, in distal part with spiral line; proximal thecae spirally coiled around sícula; irregularly developed branches comprise thecal bundles arising from theorhiza and thecae formed on branches. *Upper Ordovician (Katian)–Silurian (Ludlow)*: Poland (glacial erratic boulder).—FIG. 12,7a–c. **K. erraticus*, scale bars, 0.1 mm; 7a–7b, holotype in different views (Kozłowski, 1963, fig. 4,9); 7c, sícula (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. 12,9a–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) present, formed possibly through diad budding; tubular thecae with ventral apertural lip (rutellum); autothecae helically coiled in median part. *Lower Ordovician (Tremadocian)*: Poland.—FIG. 12,8. **T. bulmani*, holotype, ZPAL GI/1-290, scale bar, 1 mm (Kozłowski, 1949, pl. 21,1).
- ABBREVIATIONS FOR MUSEUM REPOSITORIES**
- GPIT: Paläontologische Sammlung der Universität Tübingen, Germany
- IGiG: Central Siberian Geological Museum, Novosibirsk, Russia (CSGM)
- MZ: Museum of the Earth, Polish Academy of Sciences, Warsaw, Poland
- PMU: Palaeontological Collections, Museum of Evolution, Uppsala University, Sweden
- ROM: Royal Ontario Museum, Toronto, Canada
- SMF: Senckenberg, Frankfurt/Main, Germany
- TUG: Geological collections at the Institute of Geology at Tallinn University of Technology, Tallinn, Estonia
- ZPAL G.: Institute for Paleobiology, Polish Academy of Sciences, Warsaw, Poland
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