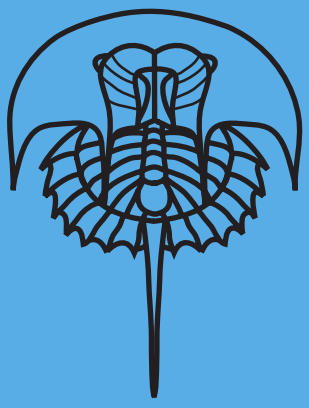

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Part V, Second Revision, Chapter 15: Subclass Graptolithina and *Incertae Sedis* Family Rhabdopleuridae: Introduction and Systematic Descriptions

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PART V, SECOND REVISION, CHAPTER 15: SUBCLASS GRAPTOLITHINA AND *INCERTAE SEDIS* FAMILY RHABDOPLEURIDAE: INTRODUCTION AND SYSTEMATIC DESCRIPTIONS

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Subclass GRAPTOLITHINA Bronn, 1849

[Graptolithina Bronn, 1849, p. 149] [=Rhabdophora Allman, 1872, p. 380] [incl. order Rhabdopleurida Fowler, 1892, 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 (2014).

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 have often not been recognized as pterobranch remains. Several authors (e.g., Mierzejewski, 1986; Urbanek & Dilly, 2000; Maletz, 2014) 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, 1937) (stolon with cysts) and *Eorhabdopleura urbaneki* Kozłowski, 1970 (tubes of fusellar construction) into a single rhabdopleurid taxon.

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 (Series 3, Stage 5*, Ptychagnostus praecurrens *Biozone):* Canada.——Fig. 1,*1*. **D. racemata,* lectotype, USNM 354117, Burgess Shale, loc. 35K, British

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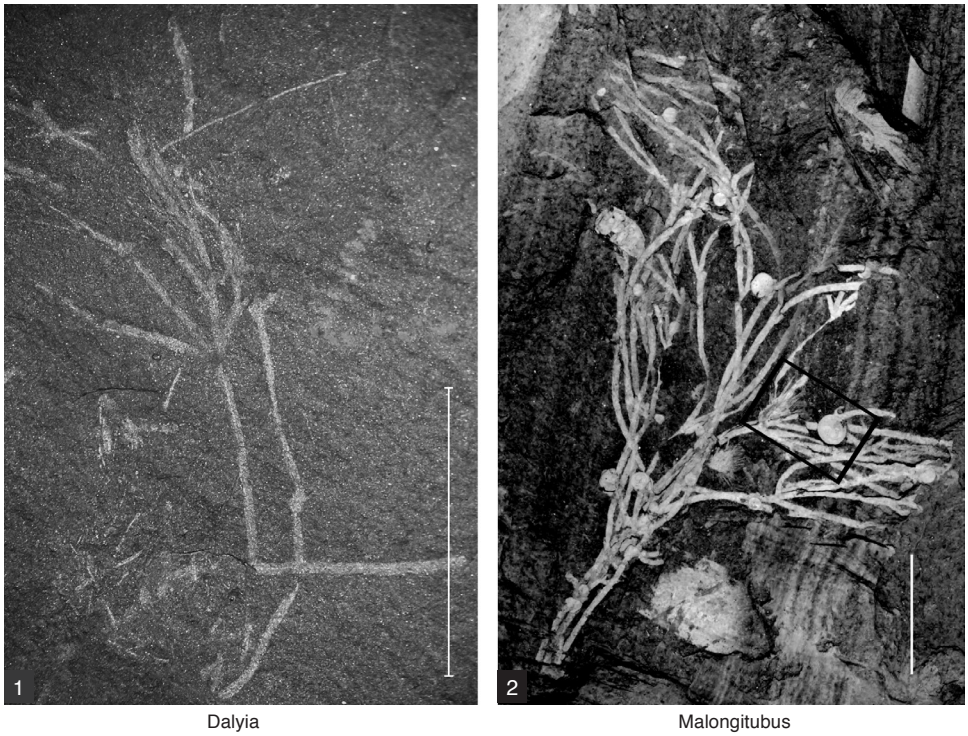

FIG. 1. Graptolithina? *incertae sedis* (p. 1–2).

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)]. 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. 1,*2*. **M. kuangshanensis,* holotype, NIGP 165032, Kuangshan, Yunnan Province, China, scale bar, 10 mm (Hu, 2005, pl. 18).

GRAPTOLITHINA FAMILIES *INCERTAE SEDIS*

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

Incertae Sedis 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, showing 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 slowly widening, with simple or ornamented apertures; zooids connected through robust stolon system showing diad budding with diaphragm complexes and dormant bud capsules (cysts); sicular zooid secretes featureless dome. *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, 1869, but details of fossil taxa are difficult to interpret, as they are often 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 (1907) described the early colony development in *Rhabdopleura normani* Allman in Norman, 1869. His description shows 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 (1907) 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, 1880 is largely comparable in its construction (see Hincks, 1880; 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 found in other pterobranchs. Early 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, 2015) from the middle Cambrian of Siberia already shows 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 (1907, 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, 1907, p. 213) at the sides of this stem. The permanent terminal zooid (Fig. 2.1) produces fusellar half rings and increases the length of the stipe. At regular

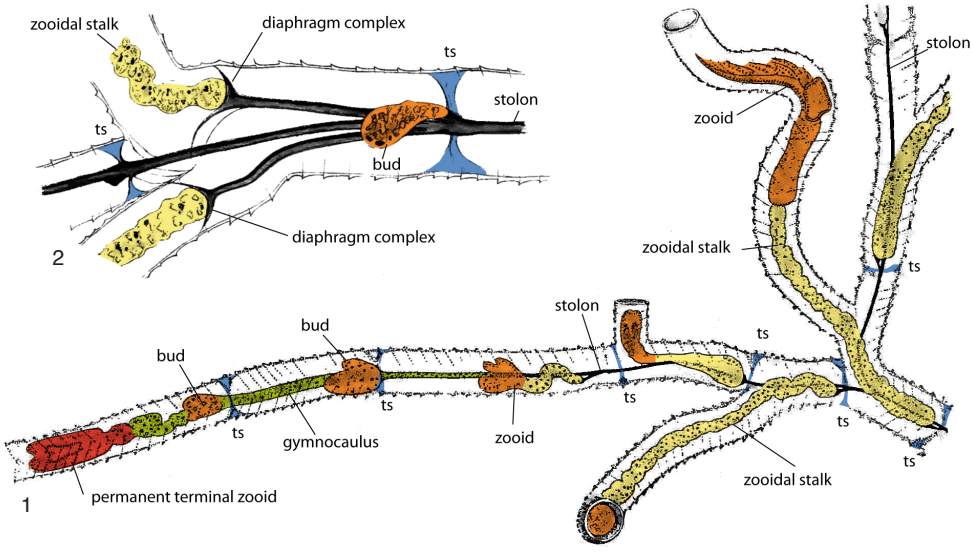

FIG. 2. *Rhabdopleura normani* ALLMAN in NORMAN, 1869, monopodial growth and stolon system with diaphragm complexes. *1,* Growing end of colony showing monopodial growth with permanent terminal zooid (adapted from Ridewood, 1907, fig. 7); *2,* branching point; *ts*, transverse septum (adapted from Lankester,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

or irregular distances, transverse septa are formed to separate individual segments of the stem into compartments for the developing zooids (LANKESTER, 1884; SCHEPOTIEFF, 1907; URBANEK & DILLY, 2000). The development of the transverse septa starts from the inner wall of the tubes, as incompletely developed septa indicate (SCHEPOTIEFF, 1907, p. 220).

The zooids resorb an opening into one side of the main stem, invariably at the distal end of the compartment (see SCHEPOTIEFF, 1907, 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. While the main stem invariably bears a dorsal zigzag suture in *Rhabdopleura*, the thecal tubes show full fusellar rings with a single oblique suture. A distinct collar is often 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 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. 3.1). 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

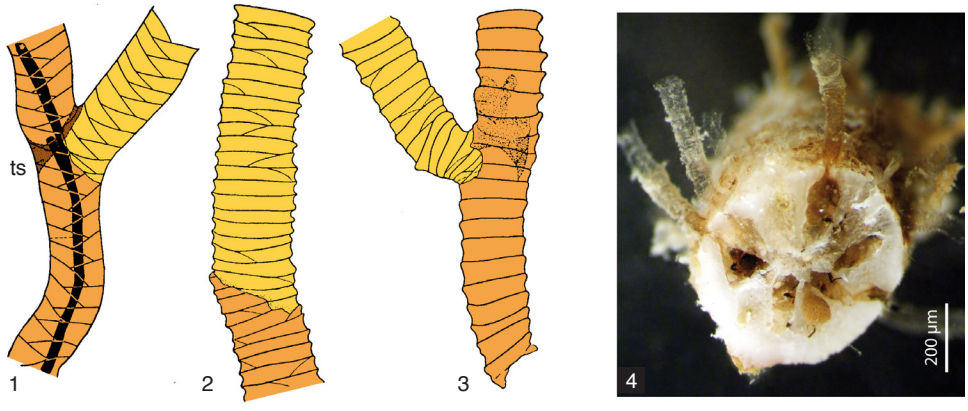

FIG. 3. Branching of tubarium. *1,* Main stem with branching, see stolon and transverse septum (*ts*); *2,* part of erect thecal tube with regeneration; *3,* erect tube with unusual lateral branching. (adapted from Kozłowski, 1949, fig. 14); *4, Rhabdopleura recondita* BELI & others, 2018 finds shelter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

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. 3.3). Regeneration of thecal tubes is more common (Fig. 3.2) and can be seen by the irregular break across a tube and the subsequent addition of fusellar full rings (RIGBY, 1994). Often, 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. 2.1). 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).

A short branch of the stolon connects to the zooidal stalk of the zooids (Fig. 2.1). At the tip of the zooidal stolon, a diaphragm complex (URBANEK & DILLY, 2000) develops (Fig. 4), 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) as "hibernacula." Later, SCHEPOTIEFF (1907) referred to them as "sterile Knospen" (sterile buds). STEBBING (1970a) showed 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 can be seen as 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 can be seen from retracted zooids with a coiled zooidal stalk in the terminal diaphragm complex (URBANEK & DILLY, 2000, fig. 9).

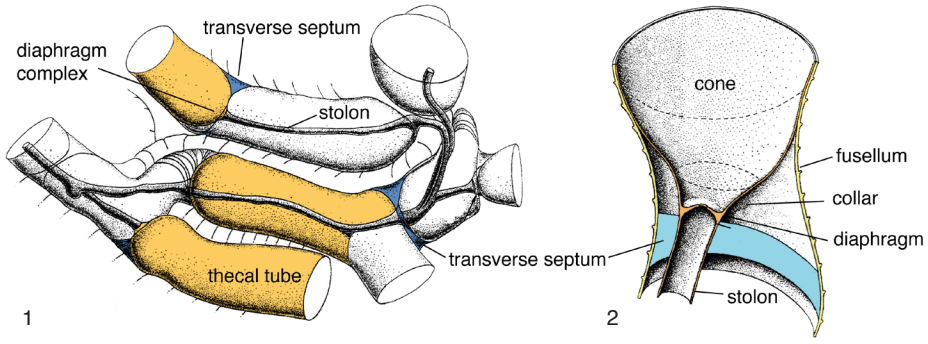

FIG. 4. The stolon system. *1,* stolon and inner lining (cone) of thecal tubes; *2,* diaphragm complex and connection to the fusellar tube (adapted from Urbanek & Dilly, 2000).

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, showing 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 originate from the middle Cambrian and may be referred to the genus *Sphenoecium* (MALETZ & STEINER, 2015). They 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 in 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 shows 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), while older rhabdopleurids can be referred to the genus *Kystodendron*

Kozłowski 1959 (see Mierzejewski & Kulicki, 2001, 2002, 2003).

Chapman, Durman, and Rickards (1995) identified fragmentary material from the Ordovician (upper Darriwilian) of China as *Rhabdopleura sinica* Kozłowski, 1959, fig. 10. *Rhabdopleura graysoni* Chapman, Durman, & Rickards, 1995 from the Asbian (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 (1956) described *Rhabdopleura vistulae* Kozłowski, 1956 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, 1869, 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 show 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. 5,*1. *R. normani,* part of tubarium, Shetland Sea, ~165 m depth, scale bar, ~1 mm (Allman, 1869, pl. 8,*1*).

Archaeolafoea Chapman, 1919, p. 390 [** A. longicornis;* M] [=*Archaeocryptolaria* Chapman, 1919, p. 392 (type, *A. skeatsi;* SD Bulman, 1970, p. 55): 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 (Series 3)–?Ordovician:* Australia (Victoria).——Fig. 5,*2a. *A. longicornis,* holotype, NMVP 13112, scale bar, 1 mm (new).——Fig. 5,*2b. Archaeocryptolaria skeatsi* Chapman, 1919, holotype, NMVP 13114, scale bar, 1 mm (new).

Chaunograptus Hall, 1882, p. 225 [**Dendrograptus* (*Chaunograptus*) *novellus;* M] [=*Desmohydra* Kozłowski, 1959, p. 227 (type, *D. flexuosa;* OD): Mierzejewski, 1986, p. 163] [=*Epallohydra* Kozłowski, 1959, p. 230 (type, *E. adhaerensis;* OD): 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 (Series 3, Stage 5,* Ptychagnostus praecurrens *Biozone)–Silurian (Wenlock):* Poland, USA.——Fig. 5,*4a–b. *C. novellus* Hall, 1882; *4a,* syntype, NYSM 3170/1, specimens attached to *Spirifera radiata,* scale bar, 10 mm (Hall, 1882, pl. 1); *4b,* syntype, UC 11989, specimen attached to *Eucalyptocrinus,* scale bar, 1 mm (new).——Fig. 5,*4c. C. flexuosus* (Kozłowski, 1959), holotype, ZPAL material, Poland, glacial boulder, scale bar, 1 mm (Kozłowski, 1959, fig. 10).——Fig. 5,*4d. C. adhaerensis* (Kozłowski, 1959), holotype, ZPAL material, Poland, glacial boulder, scale bar, 1 mm (Kozłowski, 1959, fig. 10).

Sokoloviina Kirjanov, 1968, p. 22 [**S. costata;* OD]. Small- to medium-sized tubes of black color with collars in the form of sharp-pointed or circular annular growths. *Lower Cambrian (Terreneuvian, Fortunian):* Ukraine (Podolia).——Fig. 5,*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*).

Epigraptus Eisenack, 1941, p. 25 [**E. bidens;* M] [=*Idiotubus* Kozłowski, 1949, p. 144 (type, *I. typicalis;* OD): Mierzejewski, 1978, p. 566]. Encrusting thecoriza 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)–Upper Ordovician:* Estonia, Germany, Poland, Sweden (glacial boulder).——Fig. 6,*1a–b. *E. bidens. 1a,* neotype, GPIT S.G. 158, Nr. (Eisenack, 1974, p. 671); *1b,* holotype (not preserved), Wesenberg D1, Estonia (Eisenack, 1941, fig. 1). Scale bars, 1 mm.——Fig. 6,*1c. Epigraptus* sp., small colony with part of dome, whereabouts unknown, scale bar, 1 mm (Andres, 1977, fig. 27).——Fig. 6,*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. 6,*2a–c. *G. spiralis. 2a–b,*

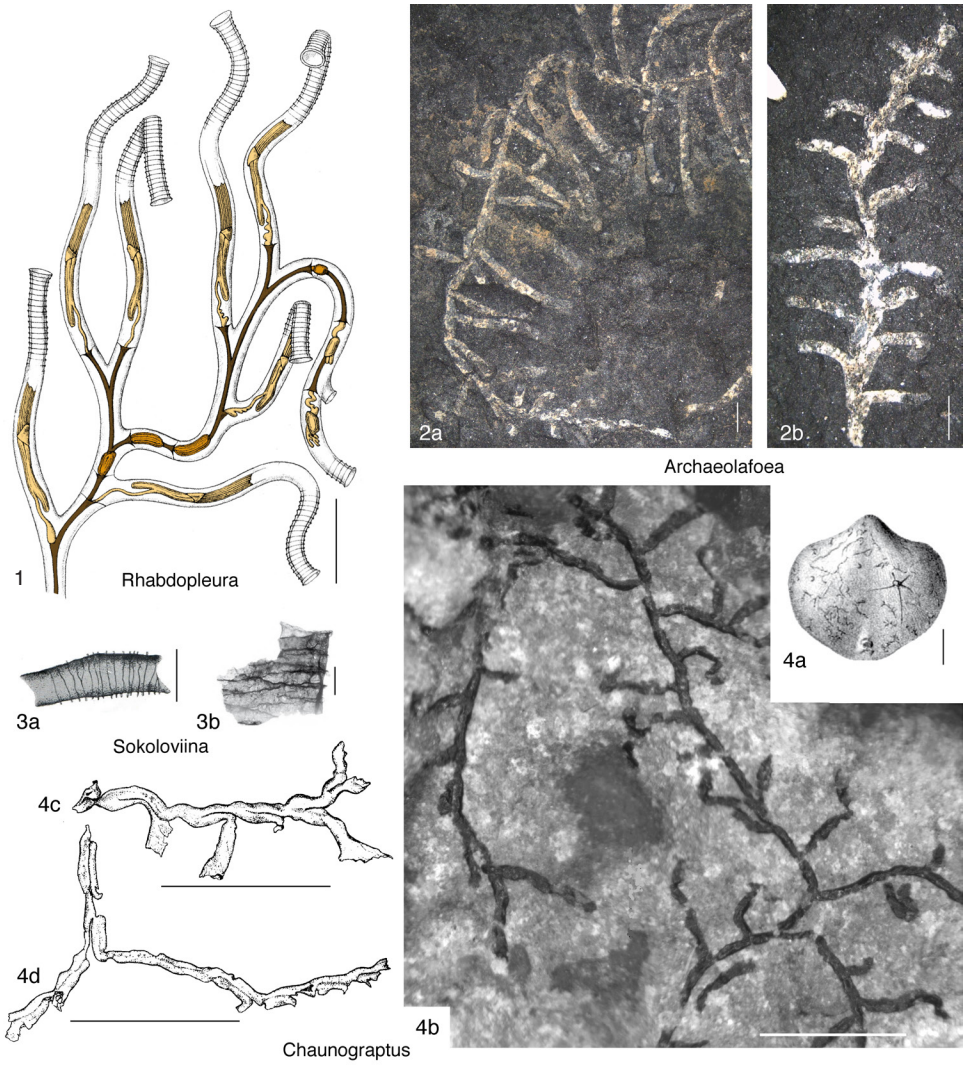

FIG. 5. Rhabdopleuridae (p. 7).

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. 36).——FIG. 6,*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. 6,*4*. **H. wisconsinensis* RUEDEMANN, 1933, holotype. repository unknown. scale bar, 1 mm (Ruedemann, 1947, pl. 40,*6*).

Kystodendron KOZŁOWSKI, 1959, p. 252 [**Chitinodendron longicarpus* EISENACK, 1937, 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. 7,*2a*. **K. longicarpus,*

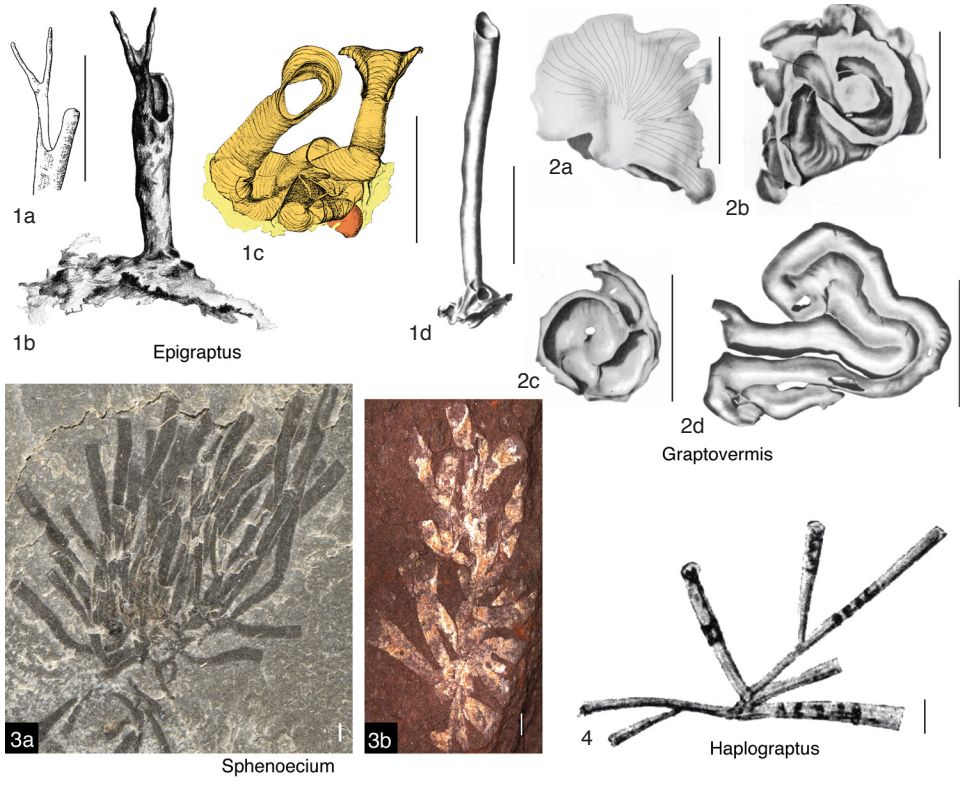

FIG. 6. Rhabdopleuridae (p. 7–10).

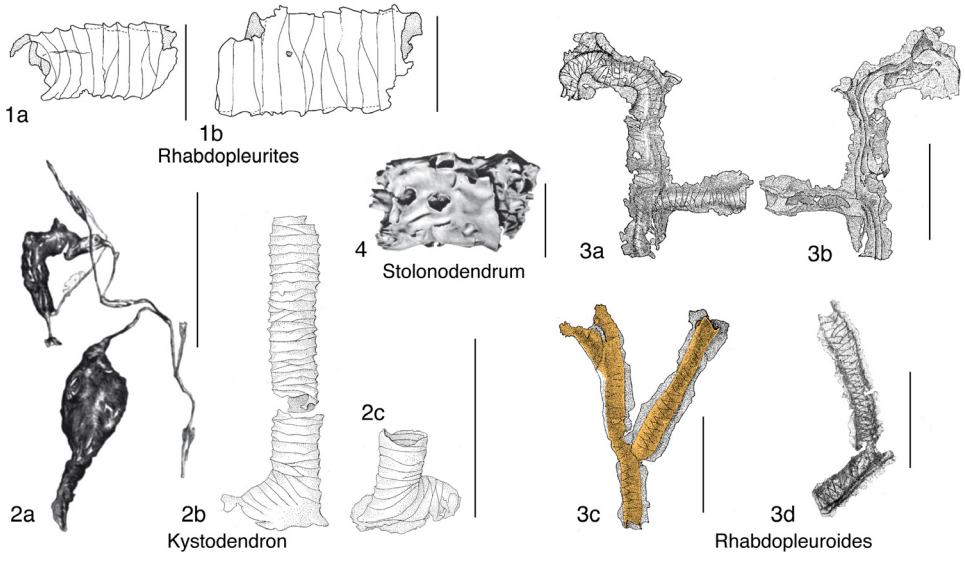

FIG. 7. Rhabdopleuridae (p. 8–10).

holotype, ZPAL material, stolon with cysts, scale bar, 1 mm (Eisenack, 1937, fig. 18).——Fig. 7,*2b–c, Eorhabdopleura urbaneki* Kozłowski, 1970, holotype, ZPAL material, thecal tube, scale bar, 0.1 mm (Kozłowski, 1970, fig. 1).

Rhabdopleurites Kozłowski, 1967, p. 126. [**R. primaevus;* OD]. Colony encrusting, with dendroidal part underdeveloped, composed of stolonal and zooidal tubes; fusellar tubes varying from 0.3 to 0.6 mm in width and fuselli 60 to 100 μm wide; fusellar 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. 7,*1a–b. *R. primaevus. 1a,* syntype, ZPAL material, thecal tube; *1b,* syntype, ZPAL material, thecal tube, scale bars, 0.5 mm (Kozłowski, 1961, fig. 13).

Rhabdopleuroides Kozłowski, 1961, p. 4 [**R. expectatus;* M]. Tubarium exclusively composed of creeping stolonal and zooidal tubes; stolons without cysts of sterile buds. *Middle Ordovician (Darriwilian)–Upper Ordovician (Sandbian):* Poland (glacial boulder).——Fig. 7,*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.

Sphenoecium Chapman & Thomas, 1936, p. 205 [**Sphenothallus filicoides* Chapman, 1917, p. 92; SD Bulman, 1970, p. 57] [pro *Sphenothallus* Chapman, 1917; non J. Hall, 1847, p. 261 (type, *Sphenothallus angustifolius* Hall, 1847, p. 261; SD Moore & Harrington 1956, p. 65); =*Cnidaria* van Iten, Cox, & Mapes (1992, p. 143)] [=*Rhabdotubus* Bengtson & Urbanek, 1986 (type, *R. johannssoni;* OD): Maletz & Steiner, 2015, p.1098] [=*Fasciculitubus* Obut & Sobolevskaya, 1967, p. 56 (type, *F. tubularis;* OD): 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 (Series 3, Stage 5)–Ordovician:* worldwide.——Fig. 6,*3a. S. wheel-erensis* Maletz & Steiner, 2015, Spence Shale, Wellsville Mountains, Utah, USA, scale bar, 1 mm (photo, Maletz & Steiner, 2015, fig. 17C).——Fig. 6,*3b. *S. filicoides,* NMVP 47737, well-preserved specimen, scale bar, 1 mm (photo, 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; interpreted as creeping tubes of Rhabdopleuridae (Bengtson & Urbanek 1986, p. 294). *Ordovician (Tremadocian):* Poland (glacial boulder).——Fig. 7,*4. *S. uniramosum,* holotype, ZPAL material, scale bar, 1mm (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 showing distinct branching patterns—have been found in the Paleozoic and have often been identified as hydroid remains (e.g., Kozłowski, 1959). Mierzejewski (1986) erected the family Rhabdohydridae for the genera *Rhabdohydra* Kozłowski, 1959 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, 2014). 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 or as alumosilicate "films" (pressure shadow minerals, see Underwood, 1992; Maletz & Steiner, 2015), while 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, 1959, p. 221 [**C. gemellithecata;* OD; =rhabdopleurid stolon, Mierzejewski, 1986, p. 168]. Branching system with more or less regular dichotomous diversions; terminal branches with conical tubes; no diaphragms. *Ordovician:* Poland (glacial boulder).——Fig. 8,*1. *C. gemellithecata,* holotype, ZPAL material, scale bar, 0.5 mm (Kozłowski, 1959, fig. 3).

Chitinodendron Eisenack, 1937, p. 236 [**C. bacciferum;* SD Kozłowski, 1959, p. 251; =?rhabdopleurid stolon, herein]. Branched stolon system with irregularly placed oval cysts. *Ordovician–Silurian:* Estonia, Poland.——Fig. 8,*6. *C. bacciferum,* holotype, ZPAL material, scale bar, 0.5 mm (Eisenack, 1937 fig. 13).

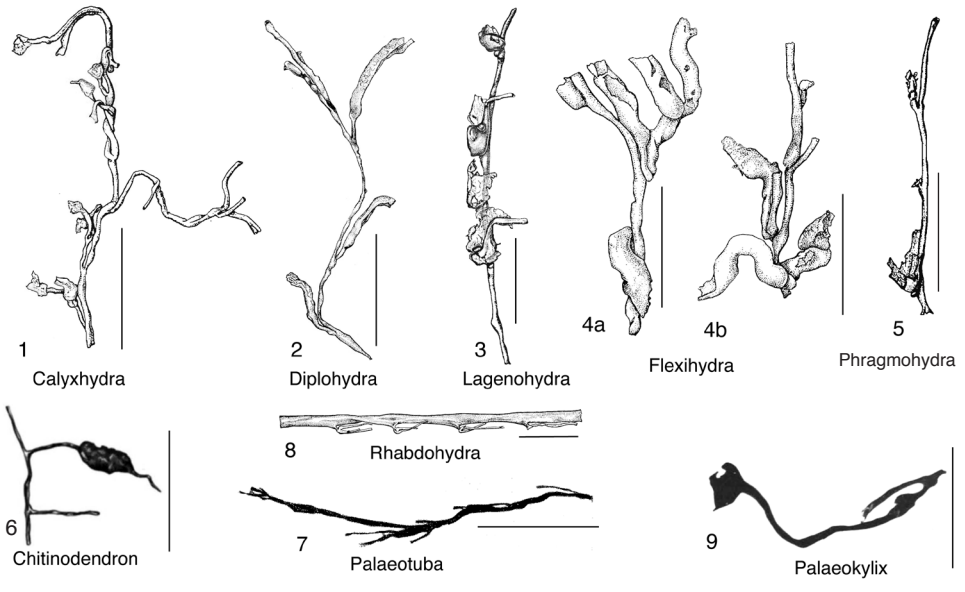

FIG. 8. Rhabdopleurid stolons (p. 10–11).

Diplohydra KOZŁOWSKI, 1959, p. 240 [**D. longithecata;* OD; =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 composed 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. 8,*2. *D. longithecata,* holotype, ZPAL material, scale bar, 1 mm (Kozłowski, 1959, fig. 16).

Flexihydra KOZŁOWSKI, 1959, p. 225 [**F. undulata;* OD; =?rhabdopleurid remains, herein]. Short stolons with elongated, flexible thecal cups; fusellum unknown. *Ordovician:* Poland (glacial boulder).——FIG. 8,*4a–b, *F. undulata,* syntype, ZPAL material, scale bar, 0.5 mm (Kozłowski, 1959, fig. 7).

Lagenohydra KOZŁOWSKI, 1959, 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. 8,*3. *L. phragmata,* holotype (specimen not preserved, see Mierzejewski, 1986, p. 194), scale bar, 0.5 mm (Kozłowski, 1959, fig. 22A).

Palaeokylix EISENACK, 1932, p. 266 [**P. chitinosus;* OD; *nom. dub.,* herein]. Simple branched stolon with thecal cup; fusellum unknown. *Ordovician–Silurian?:* Oblast Kaliningrad (formerly Samland), Russia (glacial boulder).——FIG. 8,*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. 8,*7. *P. polycephala,* holotype, repository unknown, scale bar, 1 mm (Eisenack, 1934, pl. 4,*5*).

Phragmohydra KOZŁOWSKI, 1959, p. 238 [**P. articulata;* OD; =?rhabdopleurid remains, herein]. Stolon system with complex peduncular diaphragms; fusellum unknown. *Ordovician:* Poland (glacial boulder).——FIG. 8,*5. *P. articulata,* holotype, ZPAL material, scale bar, 0.5 mm (Kozłowski, 1959, fig. 15a).

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

ABBREVIATIONS FOR MUSEUM REPOSITORIES

GPIT: Geologisch-Paläontologisches Institut der Universität Tübingen, Germany

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

NMVP: Museum Victoria, Melbourne, Australia

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

UC: Field Museum of Natural History, Chicago, Illinois, USA
USNM: US National Museum of Natural History, Washington, DC, USA
ZPAL: Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland (older ZPAL materials do not have type numbers)

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