# EVOLUTIONARY HISTORY

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The interpretation of evolutionary relationships is one of the most important aspects of modern biology and also connects biology and paleontology in the genealogical interpretation of extant and extinct organisms, combined in a unified biological system comparable to the family trees of humans. The taxonomical concept of Linnaeus (1735, 1758) combined organisms based on shared characters, as does modern cladistics (Hennig, 1950, 1965, 1999). Shared homologies or synapomorphies are employed to understand evolutionary relationships, and early on, characters were often used in a kind of trial-and-error method before a better understanding of evolutionary connections was established. Clearly, the concentration on extant organisms can only produce an unfocused and biased view, but often this is all we have. The inclusion of the fossil record may provide much-needed additional information for evolutionary interpretation, and luckily some fossil material of the Hemichordata is available to help demonstrate the origin and early evolution of this group in the deep time of the early Paleozoic (Maletz, 2019a).

Investigation of the evolutionary history of the Hemichordata, based on the fossil record, highlights the dilemma faced when combining extant and extinct groups of organisms. Bateson (1885a) introduced the Hemichordata to science and suggested that they were closely related to the Chordata due to the presence of a notochord, the precursor of the backbone of the vertebrates. The Hemichordata are now regarded as a sister group to the Echinodermata, and some of the early interpretations have been revised considerably (e.g., Halanych, 1995; Cannon & others, 2009; Philippe & others, 2011; Maletz, 2014a).

The Enteropneusta is a group with an extremely poor fossil record. Only in recent years has it been possible to relate a few of the fossil enteropneusts to the four extant families (Cameron, 2016, 2018). A stem-group taxon from the Burgess Shale of British Columbia, Canada apparently produced a possible housing construction (Nanglu & others, 2016) that has been linked to the pterobranch tubarium formation. However, the crown group Enteropneusta has been verified only from the late Paleozoic onward; and except for five taxa, all known species are extant.

Due to the lack of information on the Enteropneusta, the discussion on the evolutionary history of the Hemichordata will herein be focused on the Pterobranchia. The pterobranch tubaria form extremely important fossil remains for geological research and render them ideal for evolutionary studies. However, these housing constructions provide only a limited insight into the evolutionary history of the clade. The soft-bodied zooids did not leave an interpretable fossil record, and we do not know how much evolutionary change has been involved in the organization of these animals since their first fossil appearance during the early Palaeozoic. It is unknown when and how the pterobranchs started to develop their typical clonal reproduction method and why they became the leading planktic organisms in the early Palaeozoic but then largely disappeared during the late Paleozoic.

Because graptolites (fossil Pterobranchia) are thought to be common and widely distributed, it may be reasonable to assume that their evolutionary history is well known. However, only the general picture is outlined from the fossil record, and numerous questions still remain. The story began with the origin of this fascinating group of organisms, probably somewhere during the early Cambrian time interval and led to the few members that are still around today.

## EVOLUTIONARY INTERPRETATIONS

The differences in the tubarium construction have been used to interpret evolutionary relationships of the graptolites, and early discussions go back to Nicholson and Marr (1895) and Elles (1898), who were clearly aware of the polyphyletic concept of many of the established genera at their time. They understood that many characters used to define taxa evolved independently in unrelated lineages, even though they did not yet use the term convergent evolution as did Lenz and Melchin (2008) when comparing the Silurian monograptids *Cochlograptus* Obut, 1987 and *Testograptus* Přibyl, 1967a. However, Nicholson (1868**c**) had already discussed the zoological position of the graptolites and looked for homologous characters to connect the group with other organisms.

Elles (1922, p. 174) discussed proximal end development types and a number of trends leading to her "lines of evolution in the Graptoloidea," which provided a fairly simplified concept. A later version of this discussion appeared in Jaeger (1978c). It was also clear to him that the evolution of the graptolites was based on numerous lineages with parallel and convergent evolution due to the constructional limitation of the bausteine [building blocks] of their tubaria. Jaeger discussed eight trends in the evolution of the graptolites and stated (Jaeger, 1978c, p. 8), that "Diese Trends wirken gleichzeitig nebeneinander oder abwechselnd und nacheinander; sie sind miteinander korreliert oder voneinander unabhängig. Sie sind nicht gleichwertig. Die Reihenfolge ihrer Behandlung ergibt sich aus Zweckmässigkeitsgründen der Darstellung. Diese ist kein Kriterium für die Wertigkeit des einzelnen Trends." [These trends act simultaneously and parallel to each other, or after one another. They are not equal. Herein, the succession in their discussion is based on practicality of the demonstration. It does not provide a criterion for the value of the individual trends.]

Thus, patterns of parallel and convergent evolution appear to be a fundamental feature in the evolution of the Graptolithina, implied by the constructional limitations of a tubarium formed from fusellar half rings as branching tubes (see Maletz, 2017a, p. 121). Graptolite evolution can thus be regarded as strongly directional (see Mitchell, 1990).

A large number of studies discussed various aspects of graptolite evolution (e.g., Urbanek, 1966, 1970, 1987; Rickards, 1977; Koren' & Sujarkova, 2004; Urbanek & others, 2012; and many others), generally focusing on individual, short-lived anagenetic lineages, typically expressed by the example of the evolution of the *Demirastrites triangulatus* group (Sudbury, 1958; Štorch & Melchin, 2019) and rarely considering a larger picture (see Rickards, Hutt, & Berry, 1977; Mitchell, 1990; Fortey & Cooper, 1986; Mitchell & others, 2013; Crampton & others, 2016, 2018). These individual studies provide puzzle pieces of important information, and fitted together give us an idea on the way evolution through time modified the tubaria of the graptolites.

Bulman (1958), in a classic study, revised the ideas of Elles (1922) and defined a sequence of four overlapping subfaunas (Fig. 88). These were based on several major characteristics. The anisograptid, dichograptid, diplograptid, and monograptid faunas can easily be recognized by their typical tubarium shapes. However, other tubarium developments of these faunas render differentiation difficult at a closer view. Even in the most recent interpretations of graptolite diversity and evolution (see Sadler, Cooper, & Melchin, 2011; Cooper & others, 2014), these four subfaunas are recognizable and have been defined in a seemingly identical way as high-level taxonomic units (Fig. 88). However, Elles (1922), Bulman (1933b, 1958) and Jaeger (1978c) understood these groups as grades of organization that were progressively replaced as the various lineages evolved nearly parallel to each other through time. Modern cladistic interpretations view the patterns as a number of independently

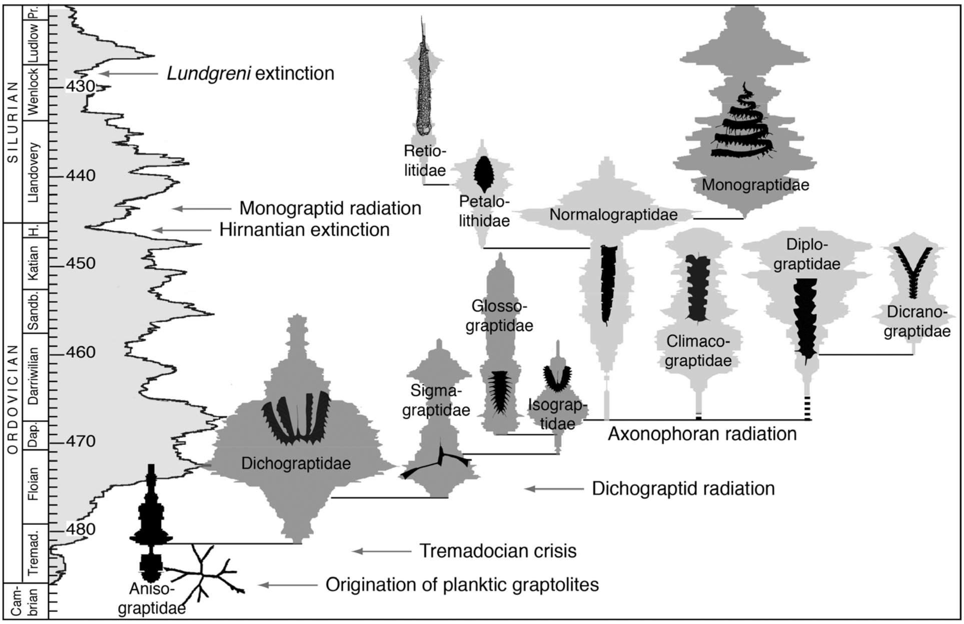


FIG. 88. Graptoloid diversity and the main groups of graptoloids. The anisograptid (*black*), dichograptid (*dark gray*), diplograptid (*light gray*), and monograptid (*dark gray*) faunas can easily be recognized (based on data in Sadler, Cooper, & Melchin, 2011; adapted from Maletz, 2017c, fig. 9). Note: Only some of the events in graptoloid history are marked on the diagram. Pr. = Pridoli; H. = Hirnantian; Sandb. = Sandbian; Dap. = Dapingian; Tremad. = Tremadocian.

evolving clades, but the general picture remains the same.

Detailed information on the evolution of benthic graptolite faunas is not available. Thus, they do not appear in any diversity studies of graptolites. BOUČEK (1957, fig. 75) and CHAPMAN, DURMAN, and RICKARDS (1996) provided some suggestions on the basic evolutionary relationships of the dendroid graptolites. ANDRES (1977, 1980) compared the fusellar construction of Ordovician graptolites and extant pterobranchs and concluded a possible closer relationship of these two groups. MITCHELL and others (2013), in a cladistic analysis, included the modern pterobranchs in their concept of the graptolites but did not analyze the various groups of the dendroids in detail.

More recently, cladistic methods were used to interpret graptolite taxonomy and evolution and to attain information on origination and extinction events that may have shaped the evolutionary history of the group (e.g., FORTEY & COOPER, 1986; MITCHELL, 1987; MELCHIN, 1998; FORTEY, ZHANG, & MELLISH, 2005; MALETZ, CARLUCCI, & MITCHELL, 2009; MELCHIN & others, 2011; MITCHELL & others, 2013; MELCHIN, LENZ, & KOZŁOWSKA, 2017). These cladistic analyses support the main taxonomical concepts of the Graptolithina but cover only some of the recognized clades. A stratocladistic attempt to provide a better understanding of graptolite evolution of a number of Silurian monograptid taxa indicated the need for more detailed morphological investigation for support (WITTINGHAM, RADZEVIČIUS, & SPIRIDONOV, 2020).

SADLER, COOPER, and MELCHIN (2011) noted that the tempo of evolutionary change may have been slower during the Ordovician and faster during the Silurian. Clearly, the data indicate an interconnection to climatic changes; and during colder periods, extinction events may have reduced the diversity of the graptoloids considerably by influencing the equatorial or warm-water faunas more strongly. Over time, a general understanding of graptolite evolution has been achieved from the origin of the planktonic graptoloids near the base of the Ordovician to their final extinction during the Early Devonian. However, major gaps still exist in the evolutionary understanding of the benthic groups, as their fossil record is relatively poor and incomplete.

## ORIGINATION, EXTINCTION, AND DIVERSITY

The macroevolutionary trends in this directional evolution of graptolites have been the focus of diversity studies, indicating a number of extinction, origination, and diversification intervals during the Paleozoic (Fig. 88). A considerable number of extinction events have been established for the graptoloid clade (e.g., Štorch, 1995; Sadler, Cooper, & Melchin, 2011; Bapst & others, 2012; Maletz, 2017a), leading to its near extinction and also to distinct episodes of radiation after a particular extinction event. Various extrinsic factors have been connected to the evolutionary rates of the Ordovician and Silurian planktic graptolites, including climatic conditions and even Milankovitch cycles (Cooper & others, 2014; Crampton & others, 2016, 2018, 2020). Because graptolites are most commonly preserved in black shales, these lithological intervals may have led to an overinterpretation of graptolite diversity due to the better preservation of the specimens in anoxic environments (Maletz, 2018, 2020a). Graptolites are poorly represented in other sediment types, and these faunas are underrepresented, an aspect in graptolite diversity in need of further investigation.

Quantitative methods have recently been employed to understand biostratigraphic distributions and interpret evolutionary relationships and events in the geological history of the graptolites. Foote and others (2019) discussed the completeness of the graptoloid record based on a mathematical model, and Crampton and others (2020) discussed the possibility of sampling bias for the macroevolutionary interpretation of graptolite evolution. Even though sampling is a major factor in the interpretation (see also Boyle & others, 2017), a connection to the sediment type and graptolite taphonomy has rarely been made (Maletz, 2020a).

The Hirnantian event close to the end of the Ordovician (Fig. 89) was one of the largest and best investigated events in graptoloid history (Koren', 1979, 1991; Chen & others, 2003, Chen, Fan, & others, 2005; Štorch & others, 2011). Chen, Melchin, and others (2005) and Finnegan and others (2011) describe the event as a two-step extinction starting with the first step near the Katian/Hirnantian boundary and a second one at the end of the Hirnantian. Also, Bapst and others (2012) discussed two separate extinction episodes during the Hirnantian, associated with the initiation and termination of a global cooling period, located at the base and the top of the Hirnantian interval. Bond and Grasby (2020) recently suggested an early cooling phase and a second phase of warming and anoxia development for the Hirnantian mass extinction, which supports this idea.

During the Hirnantian extinction event, most warm-water graptolite faunas were severely affected, and the Diplograptina went extinct in the second phase, while at the same time, the Neograptina experienced an enormous radiation, suggesting the demise of most warm-water faunal elements (Melchin & Mitchell, 1991; Štorch & others, 2011; Bapst & others, 2012).

A distinct replacement of the Diplograptina faunas by the Neograptina faunas can be demonstrated (Fig. 89). Sadler, Cooper, and Melchin (2011, fig. 13) estimated a diversity of less than 20 species during the Ka4-Hirnantian crisis (circa *Metabolograptus persculptus* Biozone?), but Bapst and others (2012) indicated approximately 25 species in the *Metabolograptus persculptus* Biozone. Goldman and others (2011) listed 39 species of normalograptids from the *Metabolograptus persculptus* Biozone alone (his zone 13, Bo5), but the list does not include the diplograptine faunal elements.

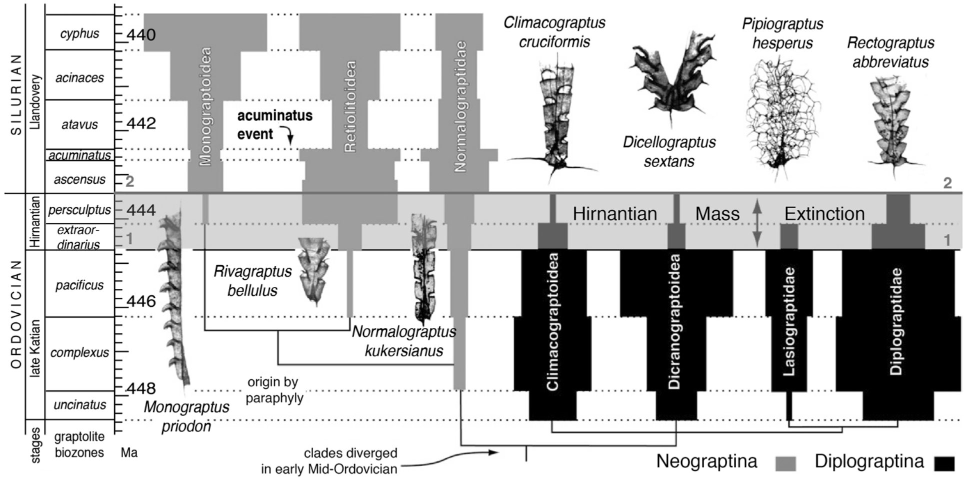


FIG. 89. Interpretation of the Hirnantian extinction and replacement of the Diplograptina (*black*) by the Neograptina (*gray*) (adapted from Bapst & others, 2012, fig. 1).

ŠTORCH and others (2011, fig. 3) regarded a number of the Hirnantian Diplograptina as Lazarus taxa—taxa experiencing an apparent extinction but reappearing later on. As the authors indicated the ranges of these taxa through the supposed extinction interval, the record would not represent a real extinction, and the diversity in the extinction interval may be considerably exaggerated. The faunal change may better be interpreted as a turnover and successive replacement that does not need to be connected to an intense extinction event, as in the *Lundgreni* Event (KOREN', 1987; JAEGER, 1991) in which the diversity of graptolites was extremely reduced. Still, the selectivity of the event suggests that certain graptolite groups were more vulnerable to extinction than others. CRAMPTON and others (2016, p. 1498) suggested that "old species were selectively removed" during the Late Ordovician mass extinction, but SHEETS and others (2016, p. 8380) recognized a "preferential decline in abundance of dysaerobic zone specialist species." The high diversity in the *Metabolograptus persculptus* Biozone could also be based on the increased international attention of the interval due to its being defined as a Global Stratotype Section and Point (GSSP) at the base of the Silurian and the supposed extinction interval in the Hirnantian. This attention led to an extreme splitting of specimens into numerous local graptolite species (SOBOLEVSKAYA, 1974; CHEN & LIN, 1978; NI, 1978; MU & NI, 1983; FANG & others, 1990; LEGRAND, 2001, 2009; MU & others, 1993; CHEN, FAN, & others, 2005; CHEN & others 2007, 2020), possibly masking the real impact of the event on graptolite diversity. However, this suggestion should not downplay the real extinction event that can be recognized in the Late Ordovician and is not restricted to the graptolites.

As earlier discussed, the term Lazarus effect (see FLESSA & JABLONSKI, 1983; WIGNALL & BENTON, 1999), used to describe the cryptic appearance of members of lineages disappearing at an extinction event and reappearing later on (URBANEK, 1993, 1998; RICKARDS & WRIGHT, 2002; ŠTORCH & others, 2011), should not be confused with a genuine extinction. Adding these species to the diversity diagram (ŠTORCH & others, 2011, fig. 5) would lead to a somewhat different interpretation: very few species of the Diplograptina fauna went extinct at the base of the *Metabolograptus extraordinarius* Biozone.

The reappearance of species of the genus *Cyrtograptus* CARRUTHERS in MURCHISON, 1867a as relic elements in the Ludlow of New South Wales (Rickards & others, 1995) could be interpreted as a Lazarus effect. Alternately, they may be based on parallel evolution of main tubarium features, thus needs reinvestigation. This reappearance may not represent a genuine record of the genus *Cyrtograptus* but the emergence of the genus *Formosograptus* Bouček, Mihajlovic, & Vaselinovic, 1976, generally lacking cladia (see Urbanek, 1997a).

The largest extinction event influencing graptolite evolution may have been the Silurian *Lundgreni* Event (e.g., Koren', 1987; Lenz & others, 2006; Crampton & others, 2016) or the Great Crisis of Jaeger (1991) during the early Homerian (Wenlock) (see Fig. 88). During this event, nearly all monograptids and retiolitids disappeared, and the two groups rediversified after a short interval in which only two graptoloid taxa, *Pristiograptus* Eisel, 1912 and *Gothograptus* Frech, 1897, have been recognized as the sole survivors of the previously dominating Silurian neograptine and monograptid clades. Urbanek (1997a, 1998) identified this bottleneck effect of near extinction or survival and recovery with the term oligophyly.

Cooper and others (2014) suggested different causal linkages for the graptolite diversity patterns during the Ordovician and Silurian. They postulated relatively stable marine environments for the Ordovician, but the Silurian appeared to be characterized by more volatile climatic changes leading to a number of distinct extinction events. Cooper and Sadler (2010) discussed the extinction risk of graptolite faunas and came to the conclusion that the facies preference of graptolites predicted their extinction risk. They suggested that species restricted to the deep-water classical graptolite facies (deep-water black shales) had a distinctly lower mean duration than faunal elements also found in shallow-water or platform regions. The analysis, however, does not include the notion that the anoxic black shale facies favors preservation of organic material and thus, superior preservation of graptolite tubaria.

## EVOLUTIONARY TRENDS

Evolutionary studies of graptolites can be used to differentiate micro- and macroevolutionary patterns, but the differentiation is not easy, as the fossil record is typically quite patchy, with micro-evolutionary steps nearly impossible to trace. Tracing the change of single species into a different, derived species may be termed micro-evolution. This is exemplified by the work of Sudbury (1958) and Štorch and Melchin (2019), who demonstrated anagenetic change in the genus *Demirastrites* Eisel, 1912. They documented the stepwise generation of changes in faunal populations until differences became large enough to indicate a speciation event. Numerous further examples are discussed in the scientific literature (see an overview for Silurian monograptids in Rickards, Hutt, & Berry, 1977).

Urbanek (1995) discussed the *Wolynograptus spineus* lineage in some detail from chemically isolated material and was able to trace anagenetic changes in the construction of the thecal apertures through a number of species. *Wolynograptus acer* Tsegelnjuk, 1976 evolved through the apertural addition of new characters to the intermediate *Wolynograptus protospineus* (Urbanek, 1995) and finally to *Wolynograptus spineus* (Tsegelnjuk, 1976) (Fig. 90). The paired apertural spines of *Wolynograptus spineus* are reminiscent of the much older *Monograptus priodon* group, but the species cannot be identified as a cryptogenic faunal element or interpreted as a Lazarus taxon. It was a newly evolved taxon with a homoplastic character indicative of parallel or convergent evolution. Thus, tracing the micro-evolutionary changes in a single lineage was used to understand macroevolution in monograptids and to determine characters as homoplastic and not homologous.

### DIRECTIONAL EVOLUTION AND HOMOPLASY

Larger-scale differentiations or macroevolutionary patterns occurred in the evolution of groups such as the Dichograptina, Axonophora, or Neograptina, and eventually

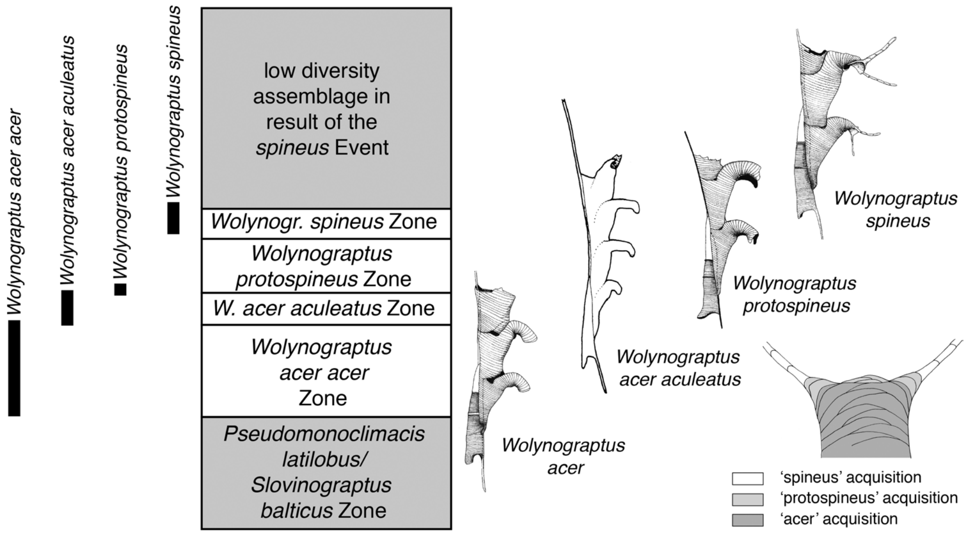


FIG. 90. Phyletic evolution in the *Wolynograptus spineus* (TSEGELNJUK, 1976) lineage based on URBANEK (1995) (adapted from Maletz, 2017a, fig. 7.7).

the Monograptidae, and correspond to the trends in graptolite evolution as suggested by ELLES (1922). These trends have invariably been understood as polyphyletic and not strictly interpretable in a phylogenetic way.

Due to the constructional limitations imposed by the formation of thecal tubes by fusellar half rings, "many tubarium features evolved again and again independently during the evolutionary history of the graptolites" (MALETZ, 2017a, p. 121), a factor identified as directional evolution and discussed for Ordovician axonophorans by MITCHELL (1990). Numerous characters of graptolite colonies cannot be used to simply postulate phylogenetic relationships and explain evolutionary lineages. These characters should be interpreted as homoplastic, and morphological similarities are based on convergent evolution (see LANKESTER, 1870). Thus, real homologies are difficult to detect in graptolites, and a detailed morphological analysis is needed to trace them (Fig. 91).

Excellent examples of this directional evolution and convergence occur in a large number of groups (MITCHELL, 1990). The decrease of the number of stipes was regarded as of prime importance initially, but NICHOLSON and MARR (1895, p. 531) had already stated, that "the number of stipes in the polypary is a character of minor importance." Thus, translated into modern terms, the number of stipes is not a homologous character (Fig. 91.1–91.2). This statement may be supported by the modern inclusion of single-stiped tubaria into several unrelated clades (e.g. *Azygograptus* NICHOLSON & LAPWORTH in NICHOLSON, 1875 in Sigmagraptidae; *Nicholsonograptus* BOUČEK & PŘIBYL, 1952a in Sinograptidae; Monograptidae as a Silurian clade). MALETZ (2017a, fig. 7.6) illustrated the situation as a prime example of convergent evolution (Fig. 91.3–91.4). It is also supported by the recognition of cladia forming secondarily multiramous tubaria (Fig. 91.1–91.2) in various clades of the Graptolithina. As we now know, cladia evolved independently in the Pterograptidae (SKWARKO, 1974; MALETZ, 1994a), the Dicranograptidae (MALETZ, 2020b), the Nemagraptinae (FINNEY, 1985a), and in a number of monograptid genera (STRACHAN, 1952; URBANEK, 1963).

The repeated origination of retiolitid-type developments in the graptolites may be one of the most stunning and easily recognizable examples of convergent evolution. The retiolitid-type development is characterized

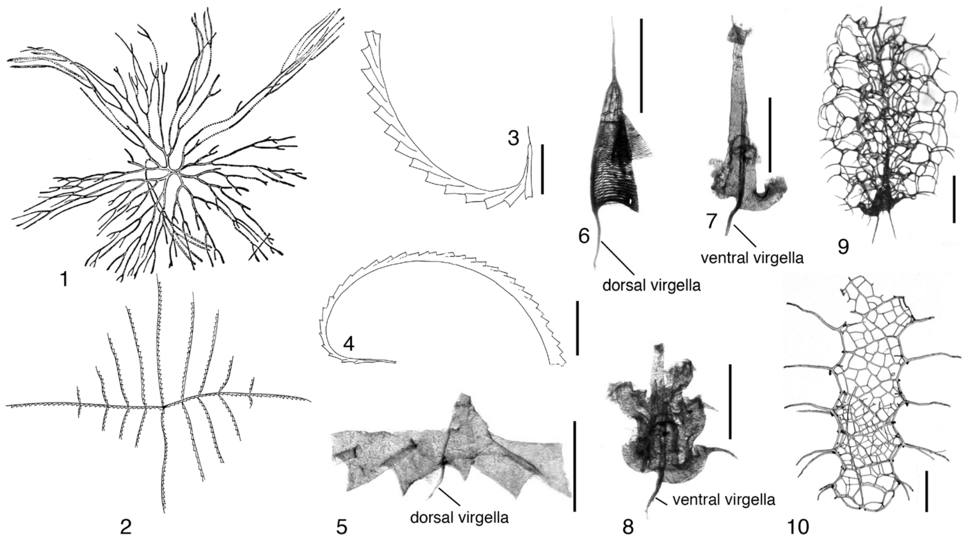


FIG. 91. Examples of directional evolution and homoplasy. *1*, *Clonograptus flexilis* (HALL, 1865), multiramous tubarium with dichotomous branching (Hall, 1865, fig. 8); *2*, *Abiesgraptus multiramosus* HUNDT, 1935a, multiramous tubarium with cladial branching (adapted from Jaeger, 1959, fig. 25); *3*, *Cymatograptus validus* (TÖRNQUIST, 1904), strongly curved taxon with single stipe (reconstructed from Beckly & Maletz, 1991, fig. 19B); *4*, *Coronograptus cyphus* (LAPWORTH, 1876b), strongly curved single stiped monograptid (reconstructed from Zalasiewicz, Williams, & Akhurst, 2003, fig. 2A); *5*, *Xiphograptus lofuensis* (LEE, 1961), showing dorsal virgella (Maletz, 2010a, fig. 8C); *6*, *Phyllograptus typus* HALL, 1865, dorsal virgella (Maletz, 2010a, fig. 6C); *7–8*, *Levisograptus sinicus*, ventral virgella (Maletz, 2010a, fig. 5); *9*, *Pipiograptus* sp. showing meshwork of external bars (Maletz, 2017a, fig. 11.8J); *10*, *Spinograptus spinosus* (WOOD, 1900), retiolitid graptolite with meshwork of ancora sleeve (Maletz, 2010b, fig. 5A). *1, 3, 5–8:* Ordovician; *2:* Devonian; *4, 9–10:* Silurian. Scale bars, 1 mm, with the exception of *4,* which is 5 mm.

by the independent extrathecal development of a meshwork of lists as in the Ordovician Lasiograptidae (Fig. 91.9) and especially in the Silurian Retiolitidae (Fig. 91.10), in which the precise development had a very different origin of comparable features (LENZ & others, 2018).

Another prime example of directional and convergent evolution involves the formation of the virgella spine (Fig. 91.5–91.8), initially regarded as a character used to define the Virgellina as a monophyletic group (FORTEY & COOPER, 1986). At least three instances of independent origin and evolution of a virgellar spine have been identified, and MALETZ (2010a) differentiated a dorsal and a ventral virgellar spine in the Graptolithina. The loss of bithecae in the late Tremadocian appeared even more complex than expected to FORTEY and COOPER (1986). A polyphyletic loss of the bithecae has been suggested by a number of authors (BULMAN, 1960; ERDTMANN, 1982a; LINDHOLM, 1991) and can be supported by the presence of at least a sicular bitheca in the sigmagraptine *Paradelograptus* ERDTMANN, MALETZ & GUTIÉRREZ-MARCO, 1987 (see MALETZ, ZHANG, & VANDENBERG, 2018).

Numerous further characters may be identified as independently evolved in widely separate clades, making cladistic interpretations difficult without the detailed morphological knowledge of the tubarium construction of the graptolites. The instances of homoplasy in the Pterobranchia discussed herein can also be described in the terms of convergence and parallel evolution in various graptolite groups.

RIGBY and MILSOM (1996) suggested neoteny or paedomorphosis as the motor for the evolution of planktic graptolites. It is, however, difficult to use the concept for the development of the colonial astogeny of the graptolite colonies or, in fact, for

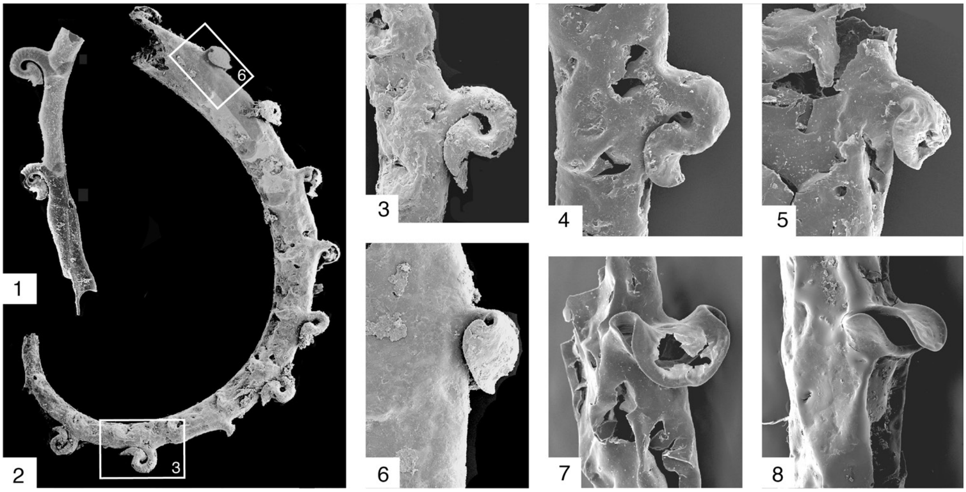


FIG. 92. *Paramonoclimacis sidjachenkoi* (OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA & BONDAREV, 1965) showing thecal gradients. *1*, proximal end with two thecae; *2*, strongly curved proximal fragment lacking sicula; *3–4*, proximal thecae; *5–6*, median thecae with wide hood; *7*, thecal hood reduced in width; *8*, slender thecal hood and lateral lobes of distal theca (new; details of specimens in MALETZ & others, 2019). Not to scale.

colonial organisms in general. RICKARDS (1977) discussed a number of cases that may indicate paedomorphosis, including the evolutionary change from *Petalolithus* SUESS, 1851 to *Cephalograptus* HOPKINSON, 1869. In this example, RICKARDS (1977) interpreted the elongation and reduction of the number of thecae in the tubarium as a possible example of neoteny. There is no change in the size and development of the sicula in these forms. He also regarded the Ordovician genus *Corynoides* NICHOLSON, 1867a as a possible paedomorphic derivative of the isograptids, achieved through the loss of the unrestricted growth of the graptolite colony.

In the Dichograptina, the first few thecal pairs are typically fairly slender as are the stipes. Through the astogeny, the stipes widen considerably distally as in *Tetragraptus* SALTER, 1863a or in *Didymograptellus* COOPER & FORTEY, 1982 (see WILLIAMS & STEVENS, 1988, fig. 44) but also in many other taxa. This can be regarded as a simple expression of morphological gradients in graptolite colonies, even though changes in thecal construction are minimal. Morphological gradients are most commonly described from Silurian monograptids (e.g., BULMAN, 1958; HUTT, 1974b) and are often easily visible even in flattened shale material. MALETZ and others (2019) described the dramatic change of the thecal style in *Paramonoclimacis sidjachenkoi* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVSKAYA, & BONDAREV, 1965 from chemically isolated material (Fig. 92). The proximal thecae of this taxon bear strongly coiled thecae with a streptograptid nozzle (Fig. 92.3–92.4), changing distally to dorsal hooks associated with two lateral lobes (Fig. 92.8) through a number of intermediate thecal stages (Fig. 92.5–92.7). Similar thecal gradients are present in genera such as *Torquigraptus* LOYDELL, 1993, *Pernerograptus* PŘIBYL, 1941, *Pribylograptus* OBUT & SOBOLEVSKAYA, 1966, and to a lesser degree in *Coronograptus* OBUT & SOBOLEVSKAYA in OBUT, SOBOLEVESKAYA, & MERKUREVA, 1968 (HUTT, 1974b; LUKASIK & MELCHIN, 1997).

BULMAN (1958) and URBANEK (1960) discussed and illustrated thecal gradients of a number of examples of Silurian monograptids. They explained the development of *Cyrtograptus* in which cladial branches have initial thecae that are quite different from the thecae of the main stipe at which the

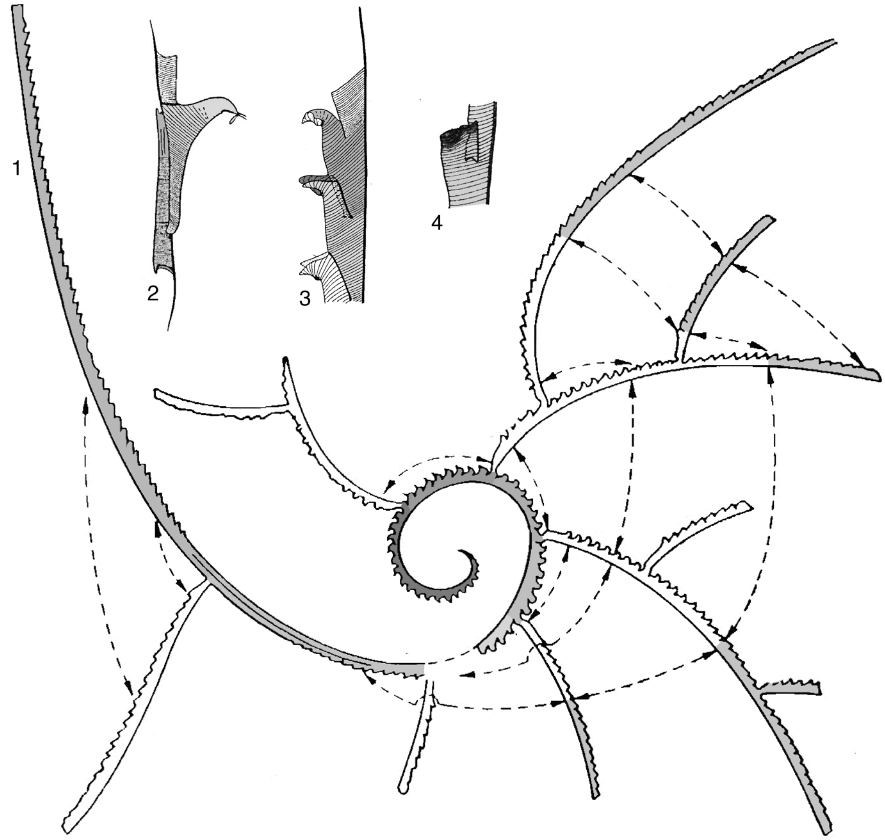


FIG. 93. Thecal gradients in cladial stipes. *1, Cyrtograptus murchisoni* CARRUTHERS, 1867a (new; based on Bulman, 1958, fig. 7 and URBANEK, 1960, fig. 10); *2–3, Cyrtograptus perneri* BOUČEK, 1933, proximal end and thecae from median part of colony (adapted from Thorsteinsson, 1955, fig. 1–2); *4, Cyrtograptus hamatus* (BAILY, 1862), distal theca (Teller, 1976, fig. 12). Illustrations not to scale.

cladium is developed but can be compared to much more distal thecae (Fig. 93). In this example, a thecal gradient is combined with cladial branching, allowing recognition of the exact point during astogeny of initiation of the growth of the cladial branch. They interpreted a delay in the initiation of the growth of cladial branches following the suggestion of THORSTEINSSON (1955), who first described this delay in *Cyrtograptus perneri* BOUČEK, 1933 (see revision of taxon in LENZ & others, 2012, p. 32). However, BULMAN (1958) and URBANEK (1960) illustrated a specimen of *Cyrtograptus murchisoni* CARRUTHERS IN MURCHISON, 1867a as an example in which the thecal gradient has not yet been described in detail (Fig. 93.1). Information of the thecal differentiation can be taken from other taxa of the genus (Fig. 93.2–93.4). The phenomenon was called retardation and was explained by the observation that "before the first signs of the growth of the first cladial theca, some 3–4 next thecae have appeared on the main stipe" (URBANEK, 1960, p. 158). URBANEK (1963, p. 230) suggested that this delay may be described by the "law of morphological equivalence of simultaneously budding thecae, established by THORSTEINSSON (1955)." The "distribution of suitable morphogenetic substances" produced by the oozoid (siculozooid) may be the mechanism behind this delay and lead to the different thecal styles (URBANEK, 1963,

p. 230). It could also help to understand bipolar stipes as the regeneration of stipe fragments, in which the theca growing to one side is often different in size and shape to the one on the other side. Oldest bipolar tubaria without the presence of a sicula were recognized in the Middle Ordovician and described as *Janograptus* TULLBERG, 1880a, but are more common in Silurian monograptids (see RICKARDS, HUTT, & BERRY, 1977). ALBANI and others (2001) illustrated a Darriwilian (Middle Ordovician) janograptid specimen with the first thecal apertures on the two stipes of the bipolar tubarium distinctly different in size. JAANUSSON (1973) discussed morphological discontinuities in the evolution of graptolites and the possible presence of polymorphic populations. He suggested that this was commonly involved in the change of number of stipes in graptolite colonies and provided a number of examples, including the three- and four-stiped specimens of *Tshallograptus fruticosus* (HALL, 1858) (see VANDENBERG, 2017, for a modern taxonomic approach). He expected that, in these cases, both morphological types would coexist for some time as genetic polymorphs. SKEVINGTON (1966, 1967) elaborated on the concept of genetic polymorphism in the case of *Holmograptus* KOZŁOWSKI, 1954 and *Nicholsonograptus,* suggesting that both were likely to be intraspecific variants of a single species. However, both genera are now regarded as separate members of the Sinograptidae (MALETZ, ZHANG, & VANDENBERG, 2018), and the concept of evolutionary change through polymorphy has not been proven for graptolites.

Biogeography was also involved in the evolutionary differentiation of graptolite faunas and was important for the formation of biogeographically distinct regions (see *Paleogeography of the Hemichordata,* p. 119–126).

# GRAPTOLITE PREPARATION AND ILLUSTRATION TECHNIQUES

Denis E. B. Bates, Jörg Maletz, and Jan Zalasiewicz

## INTRODUCTION

The collection, preparation, and illustration techniques for graptolites—as for all fossils—have changed considerably during the last 150 years to enable increased precision in collection and documentation of scientific material, and it will undoubtedly continue to change during the coming decades. Nonetheless, certain basics are still followed and have remained unchanged. New discoveries may be made in museum collections, but the most important source of material remains the tireless fieldwork of geologists and paleontologists. The value of collections is enhanced if their exact origins are carefully noted prior to deposition in public repositories of national museums and geological surveys.

With the change in collection methods, documentation of the material in scientific publications has also changed dramatically. In earlier publications, woodcuts and line drawings were the common method of illustration. The photographic illustration of fossil specimens in scientific books and other publications was rare at the time of Joachim Barrande, James Hall, Hanns Bruno Geinitz, Charles Lapworth, Sven Leonhard Törnquist, Gerhard Holm, and others, because graptolites were just too small to photograph with existing technology. The eventual use of camera lucida (see p. 157) greatly improved the accuracy of drawings. The quality of the scientific illustrations, therefore, is quite variable in earlier publications and can be unreliable, hampered by lack of understanding of the fossils investigated and their construction and preservation (see, for example, *Nautilus veles* Richter, 1871, now *Cochlograptus veles* in Maletz, 2001a). This situation has sometimes resulted in uncertain identification of type specimens and subsequent taxonomic attribution. Techniques such as scanning electron microscopy (SEM) and transmission electron microscopy (TEM) investigation as well as computer techniques, e.g., computer tomography (CT) and X-ray imaging have provided new insights into graptolite research and will likely provide some unique perspectives on these enigmatic fossils.

## COLLECTING GRAPTOLITES

Collecting graptolites does not require any special techniques that are not common to most paleontological collecting. Care should be taken to collect with a precise knowledge of the individual horizons and to document the faunal assemblages. Faunas can change considerably from horizon to horizon, not just in terms of biostratigraphical changes, but also in terms of ecological influences. All available data (e.g., enclosing lithology) concerning these factors should be collected.

Detecting graptolites in rock may require astute attention. Although the classic graptolitic facies is marine black shale, the fossils can occur in various rock types, such as greywackes, sandstones, or carbonates in which the tubaria may not be orientated parallel to bedding planes. Graptolites may be more apparent on weathered surfaces than on fresh rock where they may appear whitish from clay coatings or reddish from iron oxide formation. Graptolites that are clearly visible in newly broken fresh rock may become less visible as the inherent moisture dissipates from the surface. Wetting surfaces with alcohol (isopropyl is recommended) usually enhances graptolite definition on both fresh and weathered rock and sometimes reveals otherwise undetected specimens.

Where possible, counterpart pieces should be collected. These can include fragments of

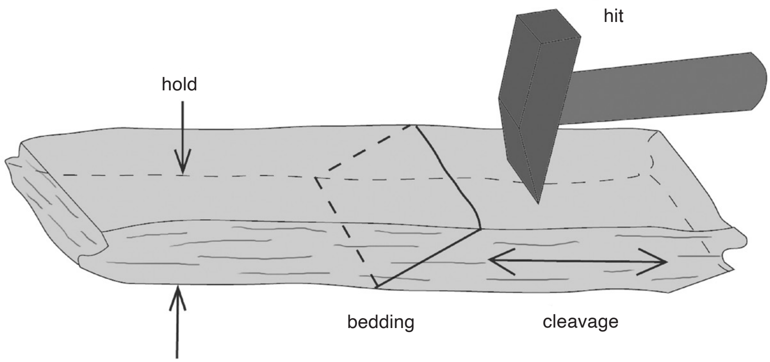


FIG. 94. Splitting tectonized rock slabs to gain fossil specimens (new).

the tubarium material on both parts, as well as molds. Material in friable shales should be particularly protected from abrasion of the surface. Wrapping is best done using pliable paper, such as newspaper or paper towels. Packages of specimens can be held together using tape and put into bags that are labeled with indelible pens. The orientation of material may be recorded; for example, where there appears to be an alignment of specimens. Bulk material, collected for subsequent splitting or acid digestion, is usually more robust. If appropriate, the geologic sections from which specimens are collected should be carefully logged. Both local and national rules on collecting should be obeyed and appropriate permissions obtained to access private property and other sites.

Splitting shale samples with a bladed hammer or with the help of a chisel is usually easily achieved. In tectonized areas, however, it can be difficult to split the rock along bedding rather than cleavage planes. After extracting a piece of rock, one needs to identify a bedding plane going through it, which may have graptolites on it. A good technique would be to hold the rock in one hand, with the bedding plane dipping toward the hand (Fig. 94) and hit the other end of the rock with the chisel end of a hammer, with the chisel held parallel to the bedding (PALMER & RICKARDS, 1991, p. 61).

The immediate marking or labeling of the rock slabs collected is very important. In the past, much care was exercised and scientists labeled each individual slab with the name of the locality and a mark to recognize the important fossil specimens (Fig. 95). Proper labeling is often neglected, and samples are sometimes just placed in boxes with paper notes. Misplacement of these samples in the wrong boxes can easily go unnoticed and may lead to misinterpretations. In Germany, many samples were rendered useless during World War II, when samples and labels were separated and partly lost, leaving the curated material without essential locality data.

## PHYSICAL PREPARATION OF GRAPTOLITES

Developing is the term given to the physical excavation of graptolites by removing rock matrix that overlies and obscures the fossil. Such work is not always necessary. If graptolite-bearing rocks split cleanly along the bedding, the graptolites (particularly when flattened in fine-grained and well-laminated shales) can emerge more or less entirely visible, and no further work is needed. However, when graptolites occur in more massive lithologies or, particularly, in tectonically cleaved rocks that do not split easily along the bedding, then all that may initially be seen is the fractured end of a graptolite that seems to disappear into the rock (Fig. 97.1, Fig. 97.5). In such cases, a good deal of work must follow to reveal the remainder of the fossil.

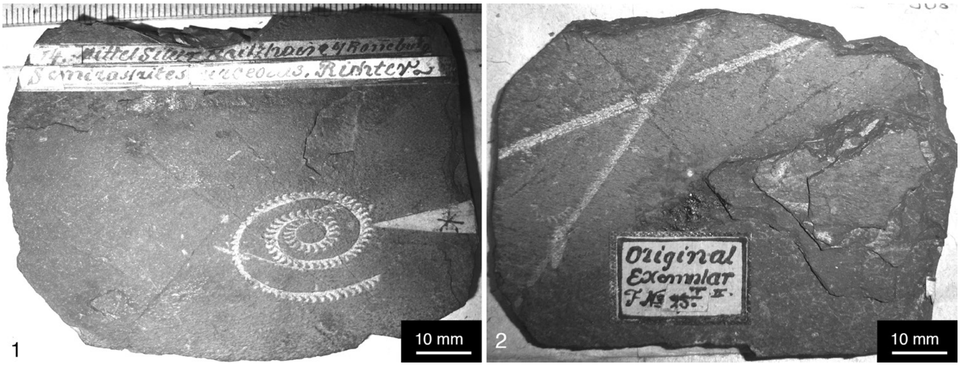


FIG. 95. Labeled fossil slab, with specimen of *Demirastrites urceolus* (RICHTER, 1853), NMG 10015; labels indicate the locality (14. Mittelsilur Raitzhain/Ronneburg) and identification (*Demirastrites urceolus* RICHTER) of specimen (marked with red arrow) on upper side (*1*) of slab, as well as its scientific value (Original Exemplar) on back side (*2*) of slab, indicating that the specimen was illustrated in a scientific publication (Eisel, 1912, pl. 2,25).

The typical implement used to develop these fossils is a strong needle mounted in a handle such as a pin vice (available from some hardware stores) or an engineer's scribe. A typical sewing needle is usually too flexible to be effective. An old-fashioned steel gramophone needle (admittedly hard to find) or something similar is nearer to the ideal. The needle point is best kept very sharp (using an emery stick), though some workers also shape them into tiny, very sharp chisel ends. One may also use a small mechanical drill with a grinding wheel or an electric engraver (vibro-tool)—particularly for graptolites encased in very hard rock such as chert (although the approach here is a little different to that described below).

Some workers prefer to use a scalpel or a razor blade for preparation. A scalpel is best, because it is easier to handle than a razor blade that has to be mounted for this purpose. These tools work well for softer rocks, such as shales that are not overly tectonized or thermally altered. Very precise excavation work can be done with a scalpel, and even larger specimens are easily and cleanly prepared.

Preparation should invariably be carefully done while using a binocular microscope under good light to follow the work exactly. The specimen should be comfortably and firmly held in place, either simply by hand or with the help of wooden blocks or small sandbags.

Many graptolites are far more delicate than the enclosing rock, although this varies, depending on the nature of the rock and the type of preservation of the graptolite (e.g., a pyrite-filled, weathered, flattened film of organic material). The technique, however, remains essentially the same in all cases (Fig. 96). Where the rock matrix cover is thin, the needle is simply pressed down—firmly but carefully—vertically into the rock above, or just adjacent to, the graptolite; scraping laterally is not recommended. This should

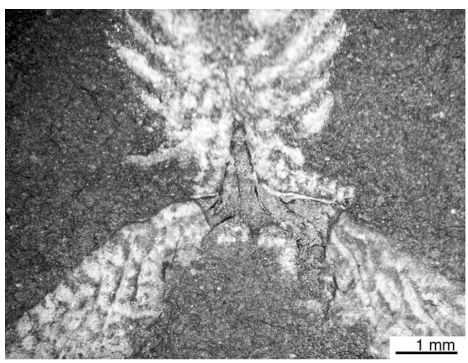


FIG. 96. *Baltograptus jacksoni* RUSHTON, 2011, holotype, BGS Ht 1260a; proximal end excavated from rock matrix with the help of a preparation needle; proximal end with preserved fusellum (dark gray), distal stipes preserved as imprint outlined with orange-colored pressure shadow minerals. Color image available in *Treatise Online* 65.

free a small flake of matrix from the graptolite, exploiting the plane of weakness that almost always exists between graptolite and matrix. One then works progressively along the graptolite, theca by theca (Fig. 96). If the rock matrix above the graptolite is thick, then one can more quickly excavate a small quarry-like hollow area above the graptolite before proceeding more carefully to break through its floor to the graptolite beneath. Careful work is slow, with many breaks to blow or wash away (using alcohol) the dust and rock chips produced from the graptolite; excavating a single graptolite may take a couple of hours or more.

Accidents do happen and many museum specimens, including type specimens, have all too obviously been severely damaged by hasty and careless excavation; it is all too easy to push the needle through the rock into the graptolite itself. Even in these instances where the fossil is accidentally damaged, the organic material of the graptolite almost invariably breaks away, leaving an impression or a pyrite internal cast (that is still taxonomically useful) beneath. Graptolites are often coated with pale phyllosilicates, commonly regarded as pressure shadow minerals formed during the tectonic deformation of the surrounding rocks (Underwood, 1992). One may aim to retain this coating (for example, in the case of flattened, white graptolites on black shale, this essentially represents the graptolite itself) or remove it (as in the case of the so-called chlorite sheath around pyritic Welsh graptolites, although the surface of this coating typically mimics the external outline of the graptolite).

Practice is essential to graptolite preparation, and best done on spare graptolite fragments. Repairs are sometimes possible. A fragment of an accidentally broken graptolite may be put back in place with a drop of glue, carefully applied from the tip of a fine brush or needle (for this, it is best to use water-soluble glue, strongly diluted with water to make it very runny). However, it may be better to keep specimens flaked off a slab in a separate container (glass bottle, etc.) in glycerin or dry on a slide, so they can be viewed from both sides (Fig. 97.3–97.4).

One can almost never entirely free the graptolite from its matrix—and should not try. The idea is to expose as much of the graptolite as possible, and as needed for identification of relevant characters, while leaving it firmly bound into the rock slab. The needle technique works for most graptolites and is mostly done dry, though occasionally it may be best done under alcohol, which necessitates frequent washing of the specimen with the same fluid.

Mechanical drills are best used on very hard rocks, too tough to yield to pressure from a hand-held mounted needle. These drills require care, as it is more difficult to have the same fine control as in the hand-held excavation. It is important to use ear protection, as most such drills are painfully loud. Typically, the most effective drill bit is the sharpest and finest one, which is used to slowly excavate through enclosing matrix, with special care at the interface with the graptolite (at which point, it may be advisable to revert to using the hand-held mounted needle).

Although friable material has often been fixed by varnishing the surface, varnish is difficult to remove, may darken, and invariably cracks with age, so this method is not recommended. An alternative is gum tragacanth. Another material, which can be removed using acetone, is an ethyl methacrylate copolymer, Paraloid/Acraloid B72, diluted to a 20% w/v concentration. Removing specimens that are in the state of separating from the shale surface (Fig. 97.2) is recommended, and they can be kept in separate bottles or on slides. In these instances, latex casts can be taken from the imprint left in the shale if the shale is hard enough. A small glass bottle can be used to keep the separated specimens in glycerin, as it prevents them from being broken on transport. Loose, shifting specimens on slides may easily be damaged, as evidenced by the isolated specimens in the Holm collection, Naturhistoriska Riksmuseet

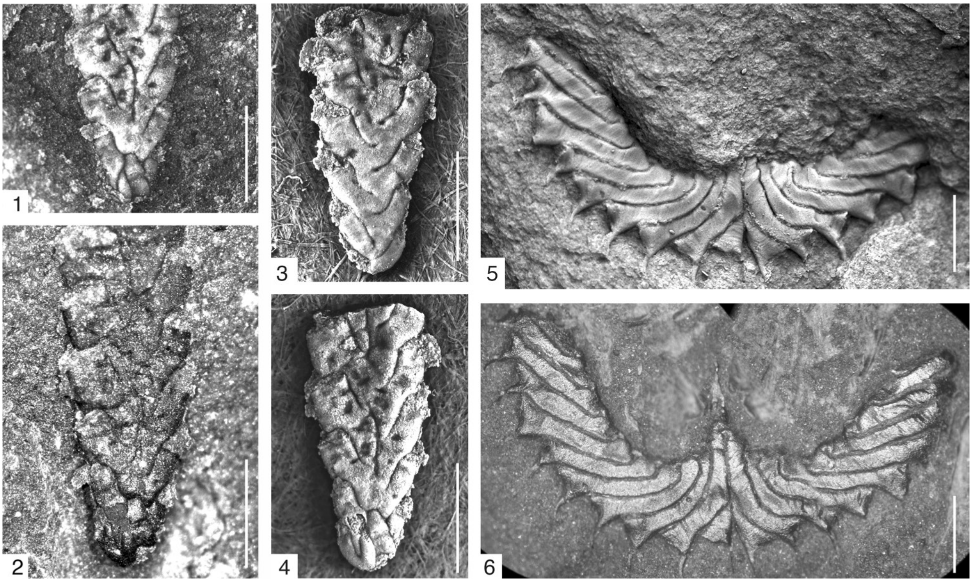


FIG. 97. Preparation of graptolites; specimens from the Lerhamn and Krapperup drill cores of Scania, Sweden. *1–4, Skanegraptus janus* MALETZ, 2011b, LO 11196T, holotype (Maletz, 2011b); *1,* unprepared specimen, coated for photography; *2,* prepared specimen becoming loosened on slab (see shadow on lower left side); *3–4,* specimen separated from slab and coated for photography to show reverse (*3*) and obverse (*4*) views of the same individual; *5–6, Arienigraptus geniculatus* (SKEVINGTON, 1965), LO 10601t; *5,* unprepared, coated specimen (new); *6,* prepared, uncoated specimen (Maletz & Ahlberg, 2011a, fig. 6L). All scale bars, 1 mm.

(Natural History Museum) in Stockholm, Sweden. Many weathered slabs with graptolites from Victoria, Australia, have been completely destroyed by covering the specimens with varnish, which later cracked and started to flake off, as the shale is very soft and deeply weathered.

Serial sectioning (cutting original specimens into very thin slices) has long been used to reconstruct the internal structure of isolated three-dimensional material. Pioneered during the nineteenth century by HOLM (1890, 1895) and WIMAN (1895, 1897a, 1897b, 1901), it was used to great effect during the twentieth century by BULMAN (1944–1947) and KOZŁOWSKI (1949). HOLM used paraffin wax, and BULMAN used collodion and paraffin wax. However, a low-viscosity epoxy resin, such as that used to embed material for TEM sectioning, is a better material. The serial sections are now commonly reasembled using computer programs. Although sectioning has, to some extent, been superseded by SEM examination of isolated specimens, it is still a useful, if time-consuming, technique (see DUMICAN & RICKARDS, 1985). Modern techniques include the use of computer programs to reconstruct the sections (SUTTON & others, 2001). However, a disadvantage of the method is the destruction of the original specimen, which can be avoided using CT scans, as was done by WANG and others (2020) for Upper Ordovician climacograptids.

TÖRNQUIST (1893, p. 2) described a simpler, but highly effective, method for the preparation of sections for graptolite specimens filled with pyrite in hard shales. He ground the slabs down on a slab of sandstone to the desired level and subsequently polished it. The results are beautiful sections of pyritic graptolites showing the internal features (Fig. 98). LOYDELL and MALETZ (2009) used a similar method to investigate the internal features of *Normalograptus scalaris* (HISINGER, 1837) (see Fig. 106.2, 106.3). Chemically isolated specimens were embedded in epoxy resin, ground down on one side, mounted

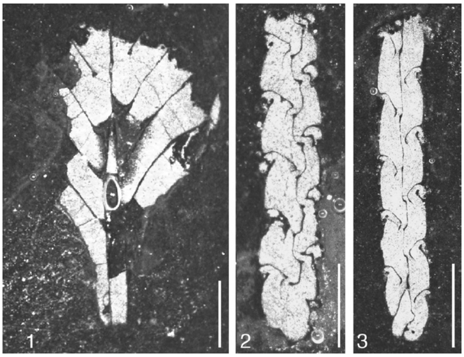


FIG. 98. Specimens from Tommarp, Scania, Sweden, preserved as polished sections on dark shale slabs; sections prepared and illustrated as drawings by TÖRNQUIST (1893). *1, Petalolithus palmeus* (BARRANDE, 1850), LO 1119t, obverse view (Törnquist, 1893, fig. 35); *2, Metaclimacograptus internexus* (TÖRNQUIST, 1890), LO 1111t, reverse view (Törnquist, 1893, fig. 27); *3, Metaclimacograptus internexus* (TÖRNQUIST, 1890), LO 1110t reverse view (Törnquist, 1893, fig. 26). Scale bars, 1 mm.

on a glass slide, and ground down from the other side to get sections of the specimens.

Natural molds of graptolites (Fig. 99.1, Fig. 99.3), commonly the result of pyrite oxidation or weathering, can be studied by making latex replicas to improve the visibility of important features (Fig. 99.2). These latex replicas are sometimes good enough to be examined by SEM. Because latex dries clear, a few drops of Indian Ink can be added to the latex before applying. This will produce a matt black peel that, after whitening, photographs well. The application of liquid latex must be preceded by wetting the slab. This lowers the surface tension of the latex and allows it to seep into every small surface feature to form a perfect cast without producing air bubbles.

Latex can also be used to clean weathered surface areas of shales and make graptolites more easily visible. A first latex cast can be used for cleaning of the shale surface, while a second one provides the useful casts of specimens.

In some instances, the latex (dyed black) slightly dyes the specimens, but not the surrounding shales, and enhances the contrast of the graptolite specimens. Conversely, it may dye the shale and not the smooth surface of the graptolite imprints. Thus, applying latex typically makes the specimens more easily visible on the shale surfaces.

Loss of paleontological specimens by pyrite oxidation is common in geological collections. It may be a serious problem for fossil collections that include pyritic specimens and considerable effort is necessary to preserve these (NEWMAN, 1998). Pyritic internal molds of graptolites often suffer from mineral decomposition and can easily be lost completely (BIRKER & KAYLOR, 1986). Pyritic specimens in shale should be kept in dry conditions; in the presence of oxygen they break down to ferrous sulfate ($FeSO_4$) and sulfur dioxide ($SO_2$). If water is present, sulfuric acid ($H_2SO_4$) is also produced, which can cause damage to labeling and storage containers. The most effective method of preventing rapid decay from pyrite oxidation is to store specimens within a moisture and oxygen barrier containing an oxygen scavenger. Further oxidation can be reduced or eliminated by storing specimens in an environment with a humidity level below 30%. Ammonium gas and ethanolamine thioglycollate treatments neutralize sulfuric acid and remove ferrous sulfate, and they are reportedly effective in partly or completely removing oxidation reaction products (SHINYA & BERGWALL, 2007). HUTT and RICKARDS (1967) suggested a transfer method to preserve pyritic graptolite specimens in polyester resin.

## CHEMICAL ISOLATION OF GRAPTOLITES

Detailed information about the structure and development of graptolites is obtained almost entirely from specimens that have been isolated (dissolved) from their matrix and, in some cases, rendered more or less transparent by the use of various oxidizing agents (Fig. 100). The actual processes and reagents employed depend, of course, on the degree of carbonization of the fossil. Not only is it possible to isolate three-dimensionally

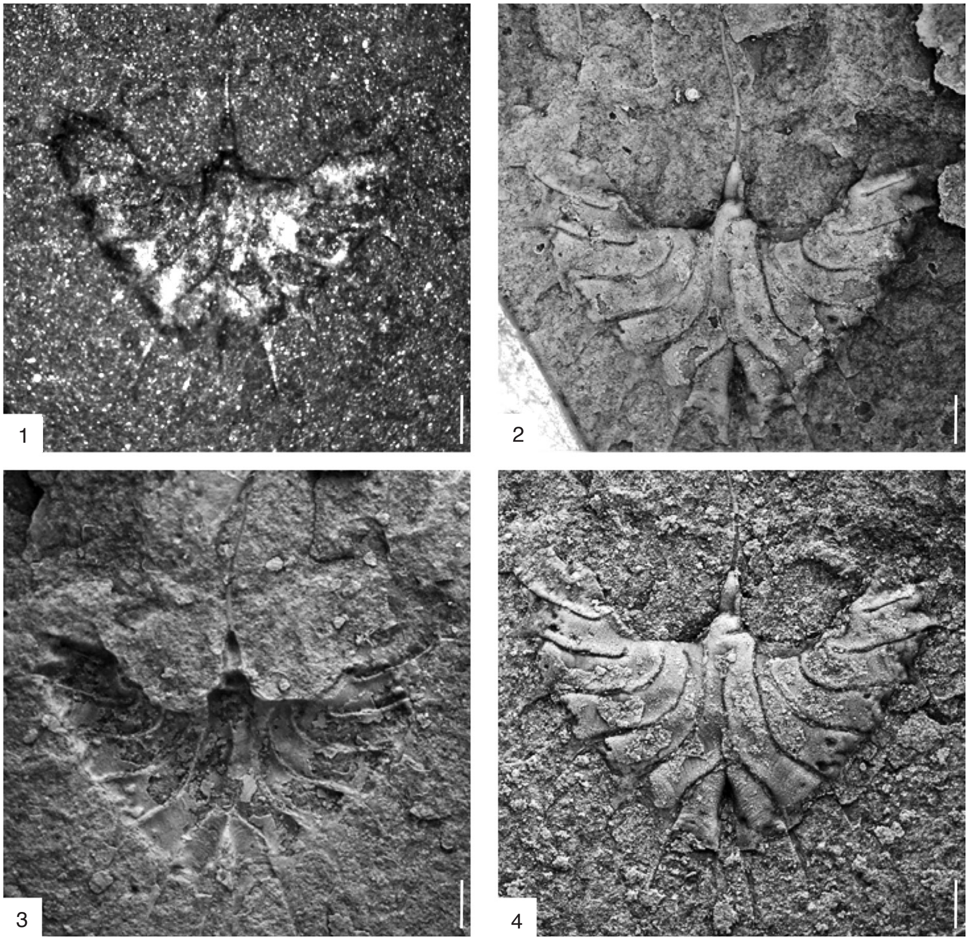


FIG. 99. *Arienigraptus zhejiangensis* YU & FANG, 1981a, Krapperup drillcore, 59.30–59.35 m, LO 12247t. *1,* mold of specimen; *2,* latex cast of mold; *3,* coated mold; *4,* counterpart, relief specimen for comparison. Specimens in *2–4* lightly coated with ammonium chloride to enhance visibility of features; scale bars, 1 mm (new).

preserved specimens, but also flattened ones, as, for example, from shales using hydrofluoric acid (HF); see, for example, ALBANI and others, 2001. Chemical isolation produces the best and most complete assemblages, allowing for recovery of small specimens and delicate forms not easily recognizable on rock surfaces. GÜMBEL (1878) first attempted the chemical isolation of graptolites, but HOLM (1890, 1895) deserves much credit for successfully isolating numerous graptolites and describing them in great detail. Pure limestone matrix containing graptolites can be readily dissolved with hydrochloric acid (HCl) or acetic acid (Fig. 100.1). For fragile material, acetic acid is preferable because of its more gentle action. Dolomite can only be dissolved using HCl, and the concentration should be adjusted so that effervescence is very gentle and is maintained by the repeated addition of drops of concentrated acid. If the concentration of acid becomes too dilute, there could be access to the container and a danger of fungal growth occurring and entangling with the specimens. This can be counteracted by adding thymol.

The physical preservation of the graptolite's organic material is an important factor.

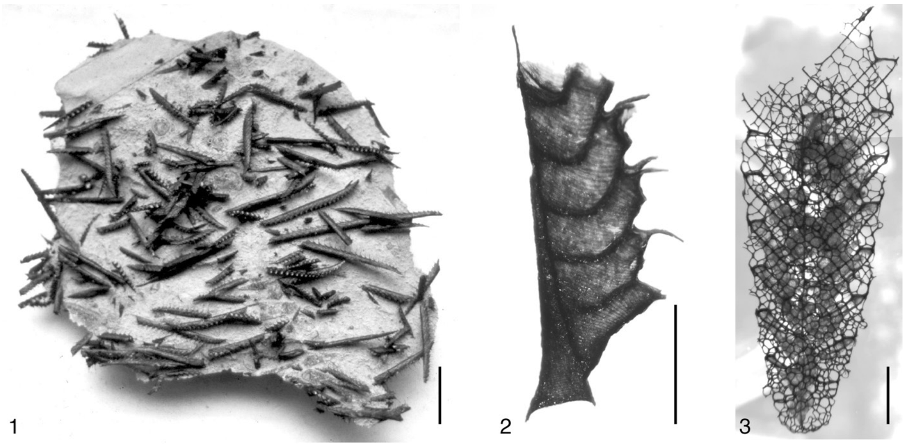


FIG. 100. Chemical isolation of graptolites. *1–2, Saetograptus leintwardinensis* (HOPKINSON in LAPWORTH, 1880a). *1,* numerous specimens partially isolated from limestone, glacial boulder, northern Germany, FGWG 125, scale bar, 10 mm (new); *2,* SMF 68 294, individual specimen from the sample, scale bar, 1 mm (Maletz, 1997d, fig. 4,*12*); *3, Retiolites geinitzianus* (BARRANDE, 1850), isolated specimen, SMF XXIV450, scale bar, 1 mm (Maletz, 2008, fig. 1a).

Some limestone material, otherwise seemingly suitable, should not be subjected to chemical isolation if the graptolite remains are too highly carbonized. Moreover, some graptolites are so brittle that they crumble to a powder when freed from matrix. It is often impossible to know this in advance, and a trial is invariably useful. Before examination by SEM, it is advisable to treat already isolated specimens with hydrofluoric acid (HF), which can remove any fine clay or siliceous material adhering to them. Some graptolite material, however, is surrounded by diagenetic silica and dissolution of this mineral growth will destroy the specimens, as the silica helps to keep the broken graptolite fragments in place (see MALETZ, 2009); in these instances, it is advisable to check whether the specimens show broken tubarium walls or are well preserved.

Impure limestone generally requires a double treatment, involving the solution of the calcareous matter first and then, after washing out all trace of HCl, the solution or disintegration of the arenaceous or argillaceous remainder with HF. Non-calcareous material, such as shale or chert, can be treated directly with HF. Repeated washing and decanting is necessary to remove all HF before the graptolite remains can be picked out with a pipette or a small brush under a low-power binocular microscope. Much of the fine mud can be removed by elutriation. Some workers wash the insoluble residue through one or a series of sieves, although this risks greater breakage of specimens.

JAROCHOWSKA and others (2013) described a new, acid-free method of extraction of graptolites and other fossils from clay-rich sediments. The surfactant Rewoquat® can be used to disintegrate samples and to isolate fossils from sediments with little damage. It is a very gentle method that can produce excellent results and even preserve features, such as the delicate membranes in retiolitids.

A bleaching agent can be used to render material more or less transparent (Fig 101.1, 101.3). Graptolites that have been dissolved out of calcareous rocks may contain bubbles of $CO_2$, which should be removed in a vacuum dessicator before further treatment. Clearing is most usually done in a watch-glass with potassium chlorate and concentrated nitric acid, though bleaching agents (e.g., eau de Javelle) have been used. The treatment time varies with the thickness of the fusellum and the degree of carbonization and can only be judged individually by

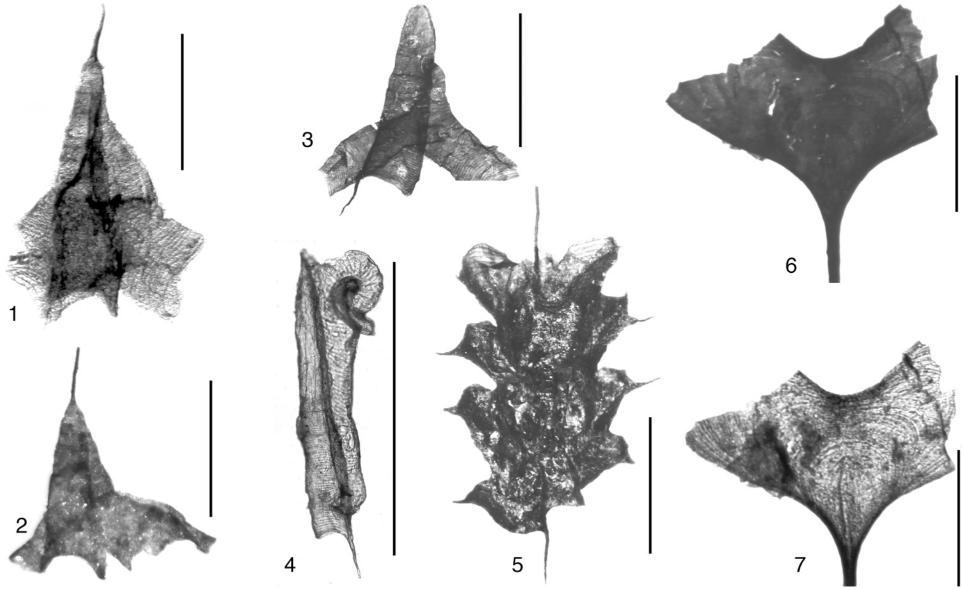


FIG. 101. Photography of isolated specimens (new). *1, Tetragraptus* sp., chemically bleached flattened specimen, showing some fusellar construction; *2, Tetragraptus* sp., unbleached, flattened, not showing fuselli; *3, Xiphograptus primus* MALETZ, 2010a, bleached, flattened specimen, showing well-preserved fuselli; *4, Streptograptus* sp., 3D specimen, IR-photo; *5, Oepikograptus bekkeri* (ÖPIK, 1927), isolated 3D specimen, fuselli visible on distal thecae, unbleached; *6–7, Archiclimacograptus decoratus* (HARRIS & THOMAS, 1935), nematularium, transmitted light photo (6) and IR-photo (7) of same specimen. All scale bars, 1 mm.

constant observation through a low-power binocular microscope. In general, the treatment cannot be prolonged much beyond 20–30 minutes without the specimens becoming too brittle to handle; however, some workers use a much lower concentration of bleaching agent and a correspondingly greater period of time. After bleaching, clove oil can be used to neutralize the acids. Quite a high proportion of material successfully dissolved from its matrix proves unsuitable for further treatment of this kind. The process of bleaching has now been largely superseded by Infrared (IR) photography (Fig. 101.4, Fig. 101.7). If IR photographs do not reveal details such as growth lines, bleaching will not help.

All chemical treatments should be carried out in controlled conditions, with due regard for safety. These activities should be done in appropriately ventilated spaces equipped with fume hoods; protective clothing and eye goggles should be worn; and all written safety instructions consulted and followed.

Long-term preservation of chemically isolated specimens is problematic, because the specimens are generally fragile and can easily break during handling if kept dry. Various methods have been used in the past to ensure their preservation. Robust specimens can be mounted dry, because surface features are more easily seen than when mounted in a relatively high-refractive index medium. Gerhard HOLM mounted specimens between glass slides so they could be observed from both sides. He left enough space between the two slides so the specimens were not damaged (Fig. 102.1). Specimens can be affixed between two glass slides with a minute drop of gum Arabic. These specimens are generally in good shape, even after more than 100 years of museum storage. Roland SKOGLUND used a similar method for flattened graptolite specimens

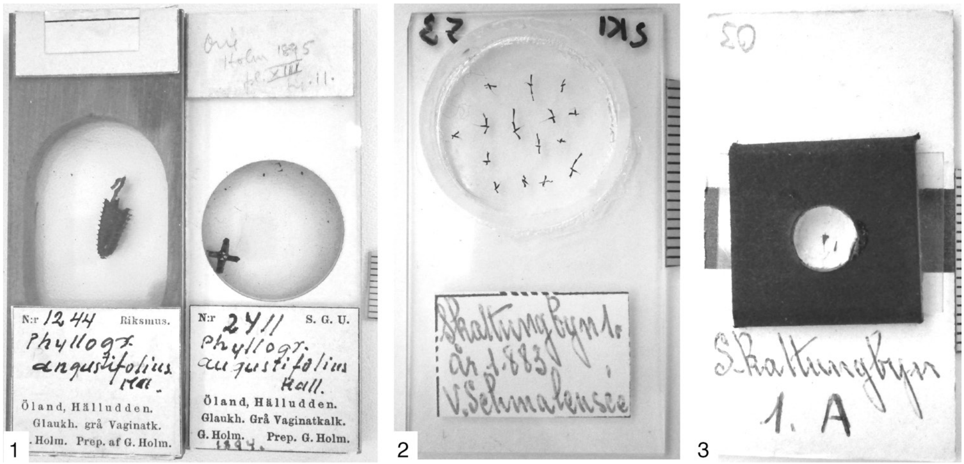


FIG. 102. Isolated and dry-mounted graptolites. *1, Pseudophyllograptus angustifolius* (HALL, 1865), NRM Holm Nr. 1244 and SGU Holm 2411, both specimens mounted by Gerhard HOLM (new, possibly originals for HOLM, 1895, pl. 13–14); *2, Acrograptus* sp. specimens, SGU-SK 1.23, originally mounted by Roland Skoglund in liquid (alcohol or glycerin), which has now evaporated; *3, Pseudophyllograptus* sp., juvenile, SGU-SK 1A.03, mounted dry by Roland SKOGLUND (Skoglund material is unpublished).

from Dalarna. He mounted individual dry specimens on cardboard, covered with a thin glass slide (Fig. 102.3). More problematic is the preservation of his numerous specimens in small containers glued on glass slides (Fig. 102.2). As the liquid in the containers dried out over time, the specimens started to break apart and acquire considerable damage (see also MALETZ & SLOVACEK, 2013, fig. 1).

Transparent specimens may be mounted in Canada balsam. Euparal is an alternative to Canada balsam, which has the advantage of not requiring perfect desiccation in absolute alcohol, thus eliminating processes in which damage to the specimen may occur.

Most specialists agree that graptolites are best kept in glycerin (glycerol) for long-term storage, which allows the specimens to be moved and viewed from all sides. They can also be removed from the glycerin and washed with warm water prior to SEM photography of the dry specimens; thorough removal of the glycerin is necessary, as surface features may be covered by residual fluid. However, ALLINGTON (2006) provided a warning and suggests the use of silicone oil instead.

Graptolites in the Natural History Museum (formerly the British Museum [Natural History]) that were stored in glycerin to prevent pyrite decay apparently allowed pyrite oxidation and deterioration of the material. The containers with graptolite specimens should invariably be tightly closed to prevent absorption of water from the atmosphere by the hygroscopic medium.

Other liquids, such as alcohol, formalin and thymol, can be used for long-term storage. However, long-term preservation in alcohol requires special care because the alcohol needs to be refilled from time to time due to evaporation, even in the most tightly sealed containers.

Special care is also necessary to preserve the delicate and fragile graptolite specimens on SEM stubs. These have to be kept in a dry place and need to be protected from dust. Plastic boxes in which the SEM stubs are mounted securely is one option.

## ILLUSTRATIONS

During the nineteenth century, graptolites, like other groups of fossils, were originally illustrated with drawings or paintings. Even with the advent of light photography, there was no major change to illustration methods—the nature of preservation of most material did not lend itself to photography. As a result, freehand drawing or painting has continued to be a standard method of illustration to the present day.

The illustrations by the Scandinavian authors HOLM and WIMAN and the British authors ELLES, WOOD, and BULMAN mark the high point in freehand graptolite illustration. In HOLM's publications, the illustrations were by Georg Gideon LILJEVALL (1848–1928) (Fig. 103.1). However, such standards are impossible to achieve for most people, and many papers are illustrated with outline drawings, often with use of a camera lucida.

Illustrations should be at as large a scale as possible to show all necessary information. Overall illustrations of most graptolites should be at a smaller scale, whereas details should be shown at greater magnifications. Early scientific works typically have small illustrations at original size that are inadequate in detail for modern use, considering the amount of available detail in many specimens that is necessary for modern identifications (e.g., LAPWORTH, 1876c; ELLES & WOOD, 1901–1918). However, even some earlier authors (e.g., WIMAN, 1893a) provided incredible insight from drawings of highly magnified specimens (Fig. 103.4–103.5). The drawings by Ethel Wood (in ELLES & WOOD, 1901–1918), finely reproduced on the plates (at original scale), remain useful today to understand colony shapes, though they often lack the detail necessary for a proper taxonomic identification.

## DRAWINGS

Most non-isolated and matrix-bound graptolites can be drawn using a binocular microscope with a camera lucida attachment, essentially a drawing mirror. The image of the specimen under the microscope is superimposed by a split screen onto a sheet of paper on the side under a mirror, and the fossil outline can be traced directly (see Fig. 104). The results obtained can give a clearer and cleaner image of the graptolite than can be obtained even by careful close-up photography. This is because the photograph (if not heavily retouched) will have every visible feature, petrological as well as paleontological, regardless of its taxonomic significance. In drawing a graptolite, the illustrator should focus on the morphology of the graptolite, although it is useful to include such features as fractures and compactional or tectonic crumples that are deemed significant. Thus, the drawing is an interpretation, albeit one that is tightly constrained by the physical evidence and dimensionally accurate.

It is best to draw at as high a magnification as is practically possible—considerably higher than is intended for the final published figure. To start, one needs to balance the lighting on both the graptolite and on the sheet of paper (the latter provided by a separate lamp), so that both graptolite and paper (and the moving pencil point) can be clearly seen. For some makes of camera lucida, there is some distortion near the edge of the field of view; therefore, it is best to work in the middle three-fourths or so of the field of view.

A scale must be added to each drawing. This can be done at the time of drawing by placing a scale (e.g., a ruler with millimeter divisions) against the graptolite and then drawing a few of the millimeter divisions using the camera lucida.

For final publication, most illustrators (and publishers) now use computer programs that can assist a rendering of the original pencil or ink drawing by digital means. Digital drawings can be made from a photograph that itself might be unusable. BULMAN's early line drawings were produced from photos (STRACHAN & others, 1991, p. 66), a method still used by some workers. The lines were inked on a highly magnified photo and the photo was subsequently bleached. That process can now be easily achieved digitally.

## VISIBLE LIGHT, ULTRA-VIOLET, AND INFRA-RED PHOTOGRAPHY

Flattened specimens can be very difficult to photograph, unless there is a good

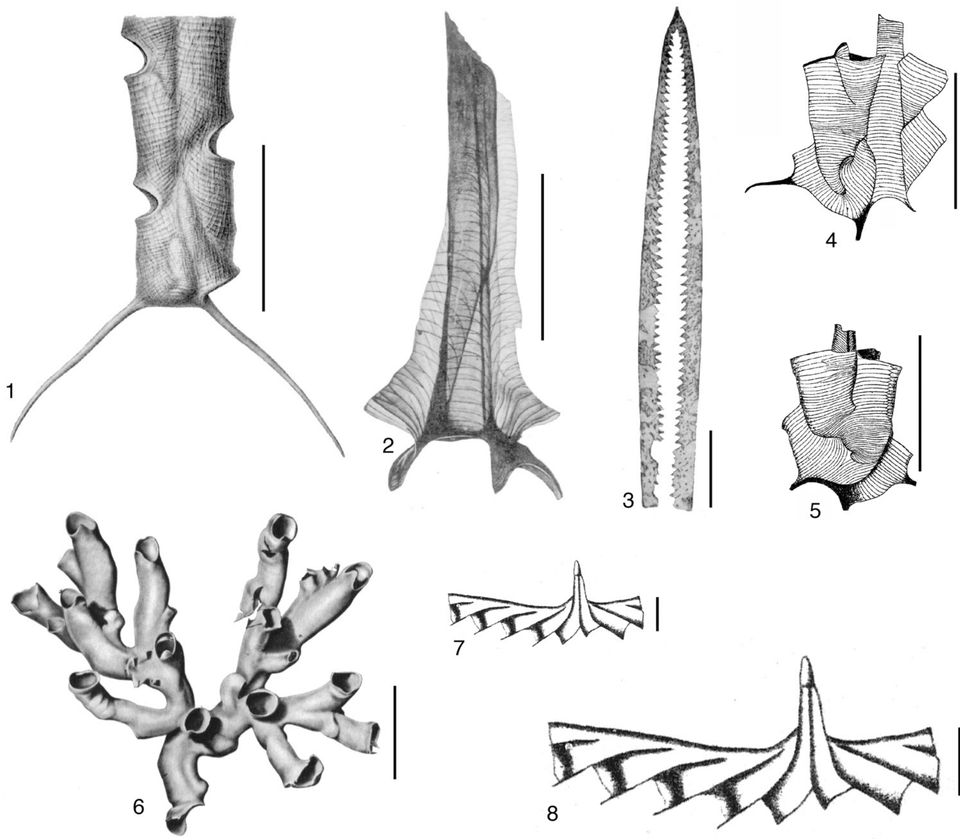


FIG. 103. Illustrations of hand-drawn graptolites with fine detail. *1, Diplacanthograptus spiniferus* (RUEDEMANN, 1912), drawn by G. Liljevall, note even the presence of cortical bandages on the surface of the thecae is drawn, scale bar, 1 mm (Bulman, 1932a, pl. i,*7*); *2, Corynoides* cf. *calicularis* NICHOLSON, 1867a, drawn by O. M. B. Bulman, scale bar, 1 mm (Bulman, 1945 in 1945–1949, pl. *ii,12*); *3, Didymograptus murchisoni* BECK, drawn by E. M. R. Wood, scale bar, 10 mm (Elles & Wood, 1901, pl. iii,*1f*); *4–5, Rectograptus gracilis* (ROEMER, 1861), line drawings of specimen showing growth lines and proximal development in all available detail in obverse (*4*) and reverse (*5*) views (identified as *Diplograptus* sp. in WIMAN, 1893a, fig. 7), corrected from WIMAN's (1893a, p. 104) originals, as he stated that the plate was accidentally prepared as a mirror image of the original drawings, scale bars for *4* and *5,* 1 mm (adapted from Wiman, 1893a, fig. 7); *6, Rhiphidodendrum samsonowiczi* KOZŁOWSKI, 1949, scale bar, 1 mm (Kozłowski, 1949, pl. 10,*1*); *7–8, Expansograptus latus constrictus* (HALL, 1865), originally magnified ×4.5, even showing the differentiation of the prosicula in a relief specimen in black shale, scale bars, 1 mm (Törnquist, 1901, pl. 2,*15*).

contrast between specimen and matrix. Flooding by alcohol, commonly isopropyl alcohol or industrial methylated spirits, can increase contrast, and also reduce unwanted reflections, although it evaporates quickly. An alternative is a mixture of 50% alcohol and 50% glycerin (Loven's reagent). This can be washed off using alcohol. Wetting the surface can improve the contrast between matrix and graptolite, but it may cause the clay minerals to swell and the organic material of the graptolite to flake off.

For specimens in relief, including latex peels and even isolated pyritic specimens, the material can be whitened using either MgO ribbon burning or ammonium chloride, applied as a sublimate. This method improves the visibility of structural details in relief specimens (Fig. 105). Great care must be used for the process.

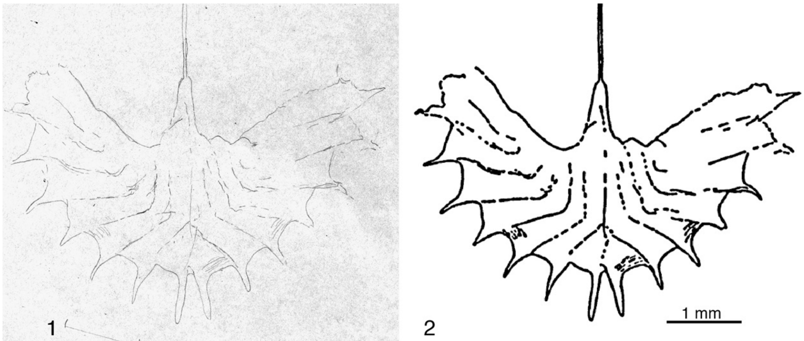


FIG. 104. Example of camera lucida pencil drawing (*1*) and ink drawing (*2*) of *Arienigraptus angulatus* (GEH & YIN in MU & others, 1962), reverse view, from *Levisograptus dentatus* Biozone, Côte Fréchette, Québec, Canada, GSC 102702a (new).

The documentation of internal details of the graptolite colonies has always been difficult, and a number of methods have been used, including various measures of preparation and photographic experimentations (Fig. 105). Good results are achieved by using infrared (IR) photography of chemically isolated graptolites. Infrared photography was explored by EISENACK (1935) to investigate graptolites, though it presented too many difficulties to be a successful method at that time; it was reintroduced by MELCHIN and ANDERSON (1988) using a modern IR-video camera (Fig. 105.1). Infrared video microscopy (IVM) uses a relatively inexpensive video camera that is sensitive through the visible and near IR range, up to wavelengths of 1300 nm. This camera can be connected to a normal biological or petrographic microscope. The best results are obtained when visible light is filtered with a 1000 nm, long-pass filter, although the crossed polarizers on a petrographic microscope can serve a similar function. The images obtained can be viewed on a video monitor, printed by direct connection to a video printer or electronically stored using a computer video image capture system. The stored images can then be analyzed using image analysis software.

Provided the specimens are not of high thermal alteration or very thickly covered in cortical tissues, and are not covered or infilled with IR-opaque mineral material, the resulting images reveal surface morphology, fusellar banding (and occasionally cortical bandages), as well as all internal walls and structures (Fig. 106.1). Optimum image quality requires that the specimens be immersed in a very high refractive index liquid, preferably 1.76, the refractive index of the graptolite fusellum. The best visualization of internal structures can be achieved using stereo-pairs of prints of the video images. These can be obtained

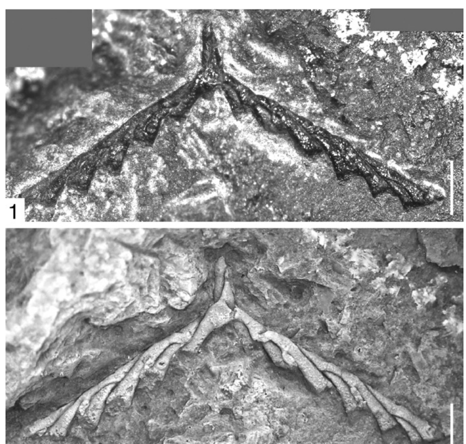


FIG. 105. *Kiaerograptus* (?) *supremus* LINDHOLM, 1991, LO 5970T, holotype; scale bars, 1 mm. *1,* original specimen showing traces of preparation on rock (light color); *2,* same specimen coated with ammonium chloride for photography, showing the tubarium construction more clearly.

by using a universal stage and tilting the specimens approximately 8° between prints. Stereo-pairs are useful for relief material, but flattened specimens can also be examined with IR light and provide useful data (MALETZ, 2010a). Cross-polarized light has recently been used as an imaging technique for graptolites showing low contrast on shale surfaces (MUIR, MCCOBB, & ZHANG, 2021).

With the advent of digital photography and the use of computers, it has become much simpler to improve the quality of images. Contrast can even be improved selectively, for example in the darker areas of the image. Unwanted backgrounds can be removed electronically, instead of physically. This is particularly effective for SEM photographs. Tectonic distortion can be removed easily using an appropriate computer program.

## SCANNING ELECTRON MICROSCOPY

Scanning electron microscopy (SEM) has become, since the early 1970s, a widely used method for illustrating complete tubaria and revealing ultrastructure in three dimensions (see examples, Fig. 107). It is applicable to isolated material and to fossils on rock surfaces where there is relief present or where the graptolite wall material is still preserved. SEM can even be used on artificial molds or casts. The SEM reveals only surface features (Fig. 107), not internal details, unless the specimens are broken open. SEM photography is especially important to show the delicate and complex meshwork of the retiolitids (Fig. 107.3).

In preparation for SEM photography, isolated material, which may be stored in glycerin, water and formalin, or dilute acid, should first be transferred to a small container and then washed in several changes of distilled water. This is best done using a pipette to draw off the liquid and then add distilled water. After washing, the specimens can either be directly placed on the stub or coated in liquids, either pure alcohol—industrial methylated spirits (IMS) is satisfactory—or acetone before placing on the stub. Because these liquids have a lower surface tension than water, they may cause less damage to the specimens when being transferred to the stub. If the specimens are small, they can be lifted and transferred in a pipette: it may be possible to manipulate a specimen on the stub surface, before the liquid evaporates.

A fine artist's brush may also be used to lift a specimen. The specimen will adhere to the brush while the liquid evaporates (holding it above an electric bulb will speed up evaporation), and it can then be gently lowered onto the stub. For very large specimens, it is possible to submerge the stub in the container of liquid and specimen, manipulate the specimen onto the stub with a brush, and then pipette off the liquid until the stub emerges from it.

Specimens may also be completely dried before mounting on SEM stubs. Specimens originally preserved in glycerin can be cleaned using warm water and then dried. A small brush with very few hairs can be used to transfer the specimens to an SEM stub. Rubbing the brush slightly on one's skin provides enough moisture for the specimen to stick to the brush.

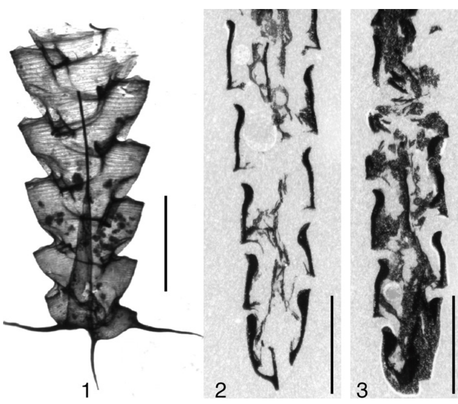


FIG. 106. Documenting internal details of graptolite colonies. *1, Rectograptus intermedius* (ELLES & WOOD, 1907), USNM 542831, infrared photo of relief specimen with internal structures (Štorch & others, 2011, fig. 17C); *2–3, Normalograptus scalaris* (HISINGER, 1837), showing internal thickenings close to the thecal apertures in sectioned specimens (Loydell & Maletz, 2009, fig. 2). All scale bars, 1 mm.

A variety of adhesive surfaces can be used to attach the specimens to the stub. Double-sided tape is clean and efficient, and can be cut from a roll. However, it can release vapor under vacuum, which may affect the working of the instrument. Alternatively, circular patches of tape are specially made to apply to the stubs. Other liquid glues can be used, such as fingernail polish, spread on the stub and allowed to become tacky before mounting the specimens. In this case, check that the glue used will not react with any liquid remaining on, or in, the specimens.

The standard stub for most instruments has a diameter of about 12 mm, and this will suffice for much material. Indeed, a great number of siculae can be attached to a single stub. If the specimen is larger, bigger stubs can be bought or made using a lathe. An alternative method is to glue a piece of thin sheet metal, such as brass or nickel silver, to a standard stub, using an epoxy glue. Conductive paint should be applied to the underside of the metal to ensure good electrical contact with the stub.

To view a specimen from as wide a range of directions as possible, it may be possible to mount it on a wire, which is glued to the stub. It is not possible to use double-sided tape, but the wire can be smeared with a suitable glue, and the specimen stuck to it.

Material on rock can easily be glued to a stub using epoxy resin, after trimming to size. BATES (1996) used a pair of carpenter's nail pincers to break up pieces of the Viola Limestone from Oklahoma, USA, fracturing it along bedding planes to give counterpart specimens, and also trimming the pieces to size.

Material that was fossilized in anaerobic conditions is commonly infilled with and/or coated in pyrite. In these conditions, the actual wall material of the tubarium may still be present, showing up as a thin brown-to-black coating on the surface of the pyrite. Where the tubarium wall is not present, the pyrite surface may bear the extremely fine mold of the internal surface, including that of the cortical fibrils.

For most work, specimens will be coated, usually with a gold-palladium target in the coater. Occasionally (e.g., where it desired to remove the specimen from a stub, and return it for storage in glycerin), it may be better to view the specimen uncoated, with a low accelerating voltage. Some field emission microscopes can also be used with uncoated material.

The SEM can be used to take stereopair photographs, particularly useful in illustrating retiolite graptoloids (e.g., BATES, 1996; LENZ & KOZŁOWSKA, 2006). The specimen can be rotated by about 5° between photographs. The resulting stereopair is

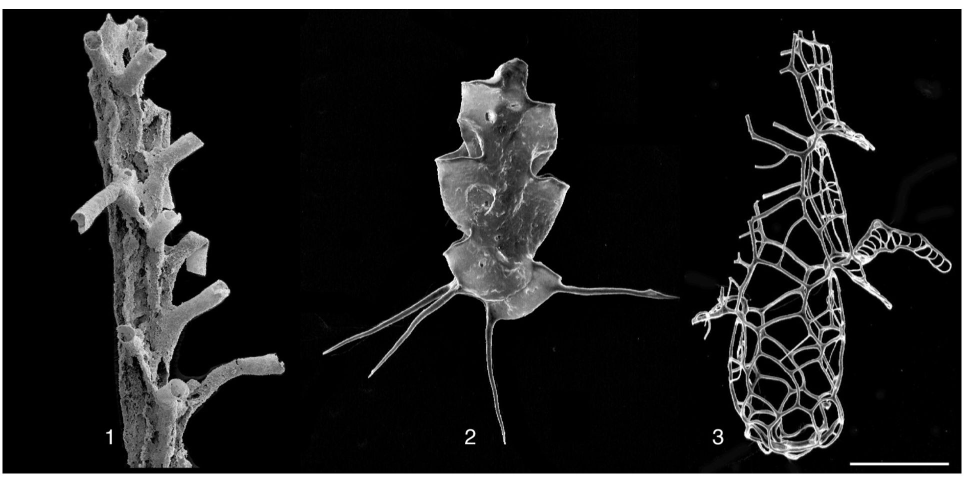


FIG. 107. SEM photos of specimens. *1, Acanthograptus* sp. in obverse view. Öland, Sweden, LO 11412t (new); *2, Rectograptus* sp., Viola Limestone, SMF 75824 (new); *3, Neogothograptus ornatus* MALETZ, 2008, glacial boulder, northern Germany, MB.G. 1079.4; scale bar (applies to all), 600 µm (Maletz, 2008, fig. 10M).

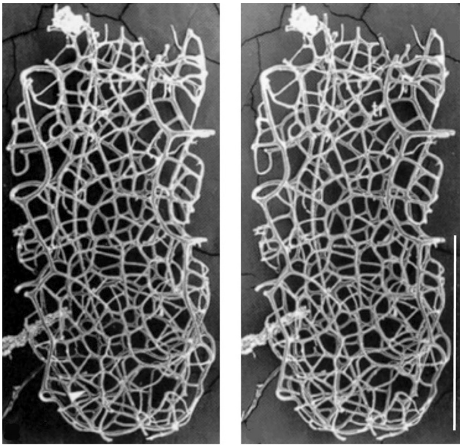

FIG. 108. Stereopair photographs of retiolitid *Sagenograptoides arctos* (LENZ & KOZŁOWSKA-DAWIDZIUK, 2001), scale bar, 1 mm (Lenz & Kozłowska-Dawidziuk, 2001, pl. 8). Color image available in *Treatise Online* 65.


FIG. 109. SEM back-scatter image of *Desmograptus micronematodes* (SPENCER, 1884), FMNH PE60371; *A,* limestone matrix, *B*, pyrite coating of the tubarium, *C,* graptolite; scale bar, 100 µm (Saunders & others, 2009, fig. 3).

normally illustrated using two small prints, with a separation of 60 mm between the images (Fig. 108). It can be viewed through a pocket stereoscope. An alternative method of reproduction uses anaglyph images, typically red and green for the left and right images, the printed image being viewed with green and red spectacles (see color image in *Treatise Online* 65, p. 16, fig. 15.1).

Although the SEM normally shows surface detail, the electron beam does penetrate beneath the surface: the amount of penetration depends on the nature of the specimen, the angle of tilt in the microscope, and the accelerating voltage. In particular, if the fusellum is particularly thin, it may be possible to see such features as fuselli, bandages and even stolons (e.g., BATES & KIRK, 1997, fig. 99a,d).

To obtain SEM images at a higher power than normal, specimens can be examined using a transmission electron microscope in scanning mode. Material, however, must be very small (about 4 mm wide by 3 mm thick by 13 mm long), and it can be tilted to about 60°.

If the back-scattered electron signal is used, an image with mean atomic number contrast is produced. Michael STEINER (described in MALETZ, STEINER, & FATKA, 2005) first used the method for graptolites. MALETZ, STEINER, and FATKA (2005, p. 78) stated that the method worked best with wall thicknesses of less than 5 µm. Thicker wall material did not produce sufficient information and fuselli were not visible. ZHANG and ERDTMANN (2004a) have also applied the back-scattered electron microscopy (BSEM) technique to study graptolites. BSEM images illustrate both the chemical compositional differences on the surface layer and the surface morphology of the sample. On the BSEM pictures of *Psigraptus jacksoni* RICKARDS & STRAIT, 1984 (ZHANG & ERDTMANN, 2004a, fig. 11), the carbonized fuselli are marked as dark lines, whereas the rock matrix is brighter because of the dominance of silicon and heavy elements. The surface morphology of those areas, where the fusellum has broken off and only films have remained, has also been illustrated in the BSEM images. The method also shows the composition of the surrounding sediment and of the pyrite growth (Fig. 109).

## TRANSMISSION ELECTRON MICROSCOPY

The use of TEM started with the work of Wetzel (1958) and Kraatz (1964, 1968), though the seminal work in this field comprises the two monographs by Urbanek and Towe (1974, 1975). Standard TEM techniques have been described in a number of papers and books in the biological field (e.g., Hunter, 1993) and can be readily applied to graptolites (Fig. 110). However, graptolite wall material is harder than most biological tissue, so that a diamond knife is essential for good results. In general, a high degree of skill is needed in cutting the sections.

Isolated material is needed for production of sections, using the techniques described above. Unbleached specimens are embedded in a resin such as Durcupan. Blocks are then sectioned using an ultramicrotome provided with a diamond knife. Sections of ~900 Å are suitable. They are then placed on copper grids, which have been coated with a film of paralodion and carbon.

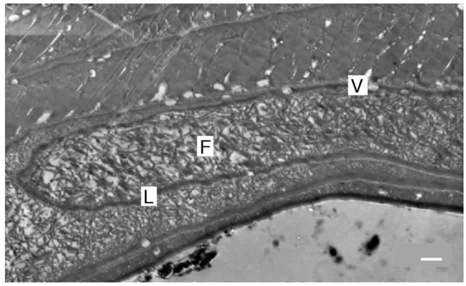


Fig. 110. ?*Dendrograptus* sp., TEM longitudinal section of the closure of a fusellus; parallel fibrils *(F)* of the cortical fabric of the lamella bounding the fusellus are seen as elliptical cross sections that are thicker than the fusellar fibrils but thinner than those of the cortex itself; *L,* basal granular fabric; *V,* vesicles; scale bar, 1 µm (adapted from Bates, 1997, pl. 5).

The TEM work provides ultrastructural details of the tubarium material, showing the development of fibrils in the fusellum and cortex. It offers information on very fine details and helps to compare fossil tubarium material with the tubaria of extant pterobranch specimens.

# GLOSSARY OF THE HEMICHORDATA

Jörg Maletz, Denis E. B. Bates, Edsel D. Brussa, Roger A. Cooper, Alfred C. Lenz, John F. Riva, Blanca A. Toro, and Yuandong Zhang

## PREFACE

The terminology of the Hemichordata used herein differs considerably from the terminology in the previous versions of the two Graptolite *Treatises* (Bulman, 1955, 1970), which were focused entirely on the fossil members of the Graptolithina and the few known tube-bearing extant and extinct Pterobranchia. Both classes were regarded as independent groups of the Hemichordata, but they are now included as a single taxon, the Pterobranchia, with the Graptolithina and the Cephalodiscida as two subclades (Mitchell & others, 2013). A number of terms are changed herein due to better understanding of the construction of the graptolite tubarium and the phylogenetic relationships within the Pterobranchia, the main group of fossilized hemichordates. These changes reflect an attempt to homogenize the terminology of these previously separated groups.

The term tubarium, for example, is reintroduced to the pterobranch terminology to describe the organic housing or domicile of all Pterobranchia, instead of using the term rhabdosome for the fossil Pterobranchia (Graptolithina in Bulman, 1955, 1970) and the coenecium for the extant members (Pterobranchia *sensu* Bulman, 1955, 1970). Lankester (1884) initially introduced the term tubarium to describe the housing of the extant Pterobranchia, as he considered the terms coenecium or zooecium inappropriate because they described the housing construction of bryozoans, to which the Pterobranchia were referred initially. Tubarium describes the housing construction of extant and extinct Pterobranchia more independently; it also describes it more precisely as being formed by glandular secretions and can easily be used for all members. It is therefore extended herein to include the homologous glandular constructions of the domiciles of fossil graptolite taxa, as was already suggested by Urbanek (1994, p. 324).

Other terms, such as the periderm, have been eliminated due to constructional considerations. The term periderm, introduced by Törnquist (1894), suggests a dermal construction of the tubarium, which is now known to be incorrect. The tubarium is formed from glands on the head shield of the zooids and is not a dermal construction as is the coenecium of a bryozoan. The tubarium can perhaps be compared with the formation of a hornet's nest, though a hornet's nest is largely constructed with foreign material. A comparison with hydrozoan colonies also falls short, as these are often covered by an organic exoskeleton, the perisarc (also identified as the periderm in Hyman, 1940, p. 400), which is secreted by the epidermis of the advancing stolon (e.g., Berking, 2006).

Early graptolite literature is written in a number of languages, including Chinese, Czech, English, French, German, Latin, Norwegian, Spanish, and Swedish. Thus, paleontological terms describing graptolite features were created in a variety of languages. Many terms originally proposed in other languages were translated into English before they became the standard, although a few kept their original form. Reference is given herein to the various terms translated from other languages to indicate the historical origin and evolution of the hemichordate terminology.

A number of papers were entirely dedicated to terminology (e.g., Törnquist, 1894; Wiman, 1893a, 1896c) or included chapters on terminology (e.g., Ruedemann, 1904; Jaanusson, 1960; Cooper & Fortey, 1982). However, the authors am not aware of any glossary for graptolite or pterobranch terminology, except for a German one (Kraatz, 1978), providing a compilation of graptolite terms in languages other than the English in the former versions of the Graptolite *Treatise* (Bulman, 1955, 1970). The German glossary (Kraatz, 1978) provided some translations of the terms of the English terminology, but no additional original useful terminology has been proposed and, in general, the terms are not included herein.

References are provided for all morphological terms listed in cases in which the terms were originally created for graptolites. The most recent revision is quoted and discussed. General paleontological or biological terms not restricted to graptolites are not referenced. Terms related to Enteropneusta are not included herein unless they are used in the various chapters dealing with taxonomy. However, they are defined and illustrated on p. 5–7.

Precise terminology can have considerable effect on the taxonomic and evolutionary understanding of graptolite phylogenies and evolution. A good example is the use of the term virgella, long considered to be important for graptolite taxonomy and identified as a homologous character in all later graptoloids (Cooper & Fortey, 1982: Virgellina). However, as Bulman (1963a, p. 404) stated, "it is likely that the virgella spine has evolved more than once," a statement that was supported by the analysis of the dorsal and ventral virgellar spines by Maletz (2010a). Therefore, a differentiation of types of virgellar spines is necessary for the understanding of graptolite taxonomy and evolution and should be reflected in the terminology.

General descriptive terms that have been used in the past to describe thecal form (dichograptid, glyptograptid, climacograptid) are not included herein and should no longer be used. These terms should be replaced by a more precise constructional terminology. The climacograptid thecal style, for example, is based on a geniculate theca, but many apertural features in these thecae are not considered in this terminology (e.g., genicular additions, thecal apertural features, thecal overlap, local thickenings). Climacograptid thecae, in a very generalized sense, are present in *Archiclimacograptus, Climacograptus, Amplexograptus, Monoclimacis, Pseudomonoclimacis,* and other taxa and do not indicate a precisely defined term. These features are clearly developed independently in the listed genera.

Terms describing proximal development types (e.g., dichograptid, isograptid, diplograptid, and monograptid) are not included here as they are generalizations, initially used to describe the precise development of certain genera. They are now known to consist of numerous independently changing characters and are quite variable. Proximal development types, as long as they are used in graptolite taxonomy, are described in the individual chapters dealing with taxonomy.

Terms in bold type are recommended for use. Terms combining italic with nonbold type are not recommended for use.

## MORPHOLOGICAL TERMS

**Abapertural ring** (Urbanek, 1959, p. 287). Thickened rim around the primary opening for a new emerging theca. The abapertural ring may be reduced to a crossbar (see Goldman & others 2011) or lacking completely.

*abiesgraptid budding* (Urbanek, 1963, p. 148). Mode of budding of thecal cladia in monograptids producing two daughter thecae symmetrically placed on either side of the mother theca and producing paired cladia.

*abiesgraptid stage* (Urbanek, 1963, p. 148). Stage of phylogenetic modifications in the development of a monograptid colony in which the procladium and the sicular cladium have acquired the ability to generate cladia.

**aboral list** (Bates, Kozłowska, & Lenz, 2005, p. 710). Thickened dorsal list at the base of the interthecal septum in axonophoran graptolites. Homologous with the transverse list of the Retiolitinae.

**adapertural plate** (Urbanek, 1963, p. 147). The expanded base of the first theca of the second and subsequent sicular cladia in *Linograptus,* shaped as a subtriangular platform with the true thecal tubule rising on it.

**anastomosis.** A biological term used in pterobranch terminology to describe the temporary fusion of adjacent branches to form an ovoid mesh. Bulman

(1945, p. 8) differentiated true anastomosis as a mere touching of stipes. Anastomosis that includes a thecal transfer is defined as pseudanastomosis by RICKARDS and LANE (1997, p. 173).

**ancora** (pl., ancorae) (BOUČEK & MÜNCH, 1952, p. 4, fig. 1; BATES, KOZŁOWSKA, & LENZ, 2005, p. 706). Structure of four-branched lists formed at the end of the virgella in the Retiolitidae (EISENACK, 1951, p. 134). It includes the initial part of the ancora umbrella and the ancora sleeve.

*ancora stage* (EISENACK, 1951, p. 134). Development of the ancora as the first stage in the growth of the ancora sleeve.

**ancora sleeve** (BATES, KOZŁOWSKA, & LENZ, 2005, p. 706). Prolongation of the ancora umbrella of the Retiolitida to enclose the thecae on both the obverse and reverse sides of the tubarium, formed of a fusellar wall (usually not preserved) with bandaged lists secreted on one or both sides. Contact with the thecal framework is only along the lateral apertural list (septal bar) portions of the apertural lists of the thecae.

**ancora umbrella** (BATES, KOZŁOWSKA, & LENZ, 2005, p. 706). Umbrella-shaped structure of lists developed from the ancora that comprises fusellar walls (not usually preserved), initially forking lists and subsequent spiral or polygonal lists, and, in some taxa, a circular rim with or without further looping lists.

**ancora umbrella hub** (BATES & KIRK, 1992, p. 6). Initial part of the ancora umbrella, formed from the two first branching divisions of the virgella, before dividing again to form four secondary ribs which extend to the rim of the ancora umbrella.

**angle of divergence** (HERRMANN, 1885, p. 43; ELLES & WOOD, 1901, p. 5, fig. 3); originally Divergenzwinkel (German). The angle between the ventral sides of the dorsal walls of the stipes, one of the features used to describe the tubarium shape.

**annulus** (pl., annuli) (KOZŁOWSKI, 1949, p. 55); originally *bande annulaire* (French). Internal bands on the sicula and early thecae of some monograptids, comprised of fine, irregularly laminated cortical tissue forming thickened bands as secondary additions on the inside walls of siculae and thecae. KRAFT (1926, p. 234) first misleadingly described this structure as Stillstandsgürtel (growth interruptions). Possible sicular annuli have also been described in dichograptids (WILLIAMS & STEVENS, 1988).

*Antisiculaseite* (WIMAN, 1895, p. 263; HOLM, 1895, p. 436). Side of the graptoloid tubarium where the sicula is partly concealed by the crossing canal(s). See reverse.

**antivirgellar spines** Spines opposite to the virgella of diplograptacean graptolites, usually paired, rarely single or multiple.

**apertural apparatus** (KOZŁOWSKI, 1962, fig. 3; URBANEK, 1966, p. 305); originally l'appareil apertural (French) of KOZŁOWSKI (1949, p. 28). All derivatives of the apertural segment of metatheca, which may consist of an apertural lobe (or lobes), rostral processes, gorget, gular plate, and apertural lip.

**apertural list** (LENZ, 1994a, p. 1345). List around the thecal apertures, originally described for Retiolitidae, but also useful for other graptolites. The term selvage has been used for the same feature.

**apertural spine.** Projection in form of a spine originating on the ventral or lateral margin of the thecal aperture, single or paired.

*Aperturalteil.* See prosicula.

**aperture.** The opening of the thecal tubes. In the older literature (e.g., BARRANDE, 1850), the term orifice was used, but is now restricted to the secondary openings in the Retiolitidae; *ostium* (pl., *ostia*) is found in older literature for the apertures or openings of the housing of *Cephalodiscus.*

**appendix** (BOUČEK & MÜNCH, 1952, p. 3). Reticulate tubular structure at distal end of the tubarium in the Retiolitinae, sometimes incorporating the nema and interpreted as a terminal theca by BATES, KOZŁOWSKA, and LENZ (2005, p. 709).

**apron** (LOYDELL & MALETZ, 2004, p. 69). Hoodlike growth over the central portion of the thecal aperture, formed from normal fuselli, generally covering the proximal and lateral apertural margins of the thecal aperture; present in some streptograptids (Monograptidae).

**arienigraptid suture** (MALETZ & MITCHELL, 1996, p. 642). Visible line of contact between the ventral walls of $th1^2$ and $th2^1$ on the reverse side in certain Isograptidae (*Arienigraptus*, *Pseudisograptus*).

**arms.** Paired extensions of the collar in pterobranch zooids. Previously the term *lophophore* (see LANKESTER, 1884, p. 630) has been used for the arms of extant pterobranchs, but it is inappropriate as it suggests a homology to the Bryozoa.

**aseptate.** Biserial, dipleural tubarium lacking a median septum.

**astogenetic patterns** (MITCHELL, 1987, p. 354). Sequence of budding at the initial dichotomy of the tubarium, giving rise to the first order stipes. See proximal development types.

**astogeny.** General biological term for the combined growth of individuals of a colonial organism; the growth of a graptolite colony describes the combined ontogenies of the zooids of a single colony (URBANEK, 1963, p. 148). See ontogeny.

**auricula** (pl., auriculae) (KOZŁOWSKI, 1962, p. 34). Expanded, earlike lateral lobes of highly modified thecae such as the cucullograptids (Monograptacea) and the Crustoide; also used for the lateral lobes in *Gothograptus auriculatus* KOZŁOWSKA & others (2019).

*autocortex* (URBANEK & TOWE, 1974, p. 13; URBANEK & MIERZEJEWSKI, 1984, p. 76). The individual cortical envelope of a theca, especially an autotheca. See ectocortex.

**autotheca** (KOZŁOWSKI, 1949, p. 24). The larger type of regularly developed graptolite thecae. Name proposed by KOZŁOWSKI (1949) in lieu of the term hydrotheca of earlier workers, which related the graptolites to the hydrozoans. See theca.

*axial cord* (SARS, 1872, p. 11). See pectocaulus.

**axil** (HOPKINSON, 1871, p. 20). Base of V-shaped bifurcation of dichotomously branched tubaria and especially the bifurcation of *Dicranograptus*, *Dicellograptus,* and *Oncograptus*.

**axillary angle** (Elles & Wood, 1904, p. 137). Angle between the dorsal sides of reclined stipes in uni-biserial and two-stiped reclined graptolites. See axil.

*axonolipous* (Frech, 1897, p. 556). Term used in multiramous to pauciramous uniserial graptoloids. Frech (1897) believed that the nema was lacking in these forms.

**axonophorous** (Frech, 1897, p. 555). Term used in scandent biserial and uniserial graptoloids in which the nema is enclosed in the tubarium or embedded in the dorsal wall of the stipes (see *Suborder Axonophora,* p. 329).

*bande annulaire* (French). See annulus.

**bandages** (Crowther & Rickards, 1977, p. 11). Parallel-sided deposits of aligned fibrils, usually covered by sheet fabric; mainly external; originally described as Chitinverdickungs-Bänder by Kraft (1926, p. 231, pl. 7). See cortical bandages, cortex. Kraft (1926, p. 231) described and illustrated the cortical bandages from isolated material, misinterpreting them as indications of the zooid anatomy (evidence of internal organs) due to his understanding of them being deposited on the inside of the sicula and thecae.

**basal disk.** Discoidal to irregular development originating from apex of the sicula for attachment of benthic graptolites; sometimes identified as a holdfast (see Bates & Urbanek, 2002).

*basal membrane* (Kozłowski, 1962, p. 10); originally *membrane interthécale* (French). Lower layer of the creeping tubes in encrusting graptolites and pterobranchs.

**basal notch.** (Urbanek, 1963, p. 147). Incision in the margin of the ventral wall of the basal part of the first theca of the sicular cladia in *Neodiversograptus beklemiskhevi* and *Linograptus posthumus*.

**biform** (Elles & Wood, 1911, p. 361). Graptoloid tubarium with proximal and distal thecae of different form showing gradual or abrupt change along the length of the stipes of the tubarium; originally proposed for monograptids with at least two different types of thecae, but it can also be used for other graptolites with a thecal gradient.

**bilateral symmetry.** General biological term; symmetrical disposition of the stipes of the graptolite tubarium around the sicula. See also isograptid symmetry and maeandrograptid symmetry.

**bipolar** (Urbanek, 1963, p. 137; Rickards, 1973a). Bilateral graptoloid tubarium formed as 1) a regeneration of a broken uniserial stipe through a pseudocladium or 2) a siculate monograptid with a sicular cladium; originally defined by Urbanek (1963, p. 137) exclusively for monograptids. Albani and others (2001, p. 390) identified janograptid proximal ends in dichograptids as regenerated uniserial stipes. The janograptid condition (genus *Janograptus*) in the Middle Ordovician is essentially an identical development to the bipolar regeneration with the formation of a pseudocladium in a monograptid.

**biradiate** (Bulman, 1950a, p. 68). Proximal development with two first-order stipes originating from the sicula through a single dicalycal theca; translated from bilateral; revised by Maletz (1992, p. 299). See triradiate, quadriradiate.

**biserial.** Scandent graptolitid tubarium with two series of thecae enclosing the nema; the thecal series can be arranged back to back (dipleural) or side by side (monopleural; also called duplex species by Lapworth (1873a, p. 501) and diprionid in older literature. See uniserial, triserial, quadriserial.

**bitheca** (pl., bithecae) (Holm, 1890, p. 10). Smaller type of regular graptolite theca, usually developed alternately on the right and left sides of the stipes; corresponds to the *gonangium* (pl., *gonangia*) of early workers (see Wiman, 1895, 1896c).

**black stolon** (Schepotieff, 1906, p. 465). The sclerotized, inflexible organic rod, usually embedded in the ventral wall of the mature tubes in the Pterobranchia. See pectocaulus.

**blastocrypt** (Urbanek, Mierzejewski, & Rickards, 1986, p. 101). Secondary dark inner layer of the graptoblast.

**blastotheca** (Urbanek, Mierzejewski, & Rickards, 1986, p. 99). Terminal portion of a stolotheca and housed by a zooid that never functioned as an autozooid, having been arrested in development at an early growth stage. See graptoblast, blastocrypt.

*blastozooid* (Kozłowski, 1971, p. 314). Term for the zooids of a graptolite colony formed through asexual budding.

**branch.** Single part of a branched graptolite tubarium, sometimes used for the entire colony; in its strict sense it refers to the segment between dichotomies in multiramous forms (Cooper & Fortey, 1982, p. 177). Earlier workers used the term *frond* (e.g., Hall, 1865). See stipe, which can be used interchangeably for branch.

branchial arms. See arm.

*branchial plumes* (M'Intosh, 1887, p. 10). Early term for the paired arms of pterobranch zooids; also *branchial arms*.

**branching.** Division of stipes. See dichotomous and cladial branching.

*buccal disk* (Lankester, 1884). See cephalic disk.

*buccal shield* (M'Intosh, 1887, p. 8). See cephalic disk.

**budding.** Development of daughter zooids from the mother zooids in the Pterobranchia; also used for the branching of stipes.

*budding individual* (see Bulman, 1932b, p. 26). Term used by earlier workers for the stolotheca or protheca.

*calycle* (Hall, 1865, p. 24). An early term for theca; see also *denticle, cellule, cell, cup,* and *denticle* (*Zahn* in German).

**camara** (pl., camarae) (Kozłowski, 1949, p. 170). Inflated proximal portion of autotheca in certain benthic, encrusting graptolites (camaroids, crustoids).

**canaliculus** (pl., **canaliculi**) (Urbanek, Mierzejewski, & Rickards, 1986, p. 103). System of parallel, fine canals perpendicular to the surface of the blastocrypt; first described but not named in Urbanek and Rickards (1974).

**cauda** (pl., caudae) (Hutt, 1974a, p. 80). Parallel-sided, tube-shaped part of the prosicula, closed at the apex and provided with a spiral thread; identical to the *nema prosiculae* of Kraft (1926, p. 222).

*caulotheca* (Lankester, 1884, p. 634). Thick, hard rim or cuticle formed on the gymnocaulus during transformation into the pectocaulus.

*cell* (pl., *cellule*). Term used by earlier workers for theca (see BARRANDE, 1850, p. 5; HALL, 1865).

**central disk** (HALL, 1865, p. 20). Web of sclerotized tissue uniting the proximal ends of stipes in some graptoloid tubaria, mostly Dichograptidae; interpreted to be formed by addition of cortical bandages or cortex, but not known from isolated material.

**cephalic disk**, **cephalic shield.** The frontal part of the pterobranch zooid with the glands secreting the tubarium; identical to the *buccal disk* or *buccal shield* of M'INTOSH (1887, p. 8), the buccal shield and praeoral lobe of LANKESTER (1884), the proboscis of HARMER (1905, p. 26).

*cephalic plumes* (M'INTOSH, 1887, p. 10; RIDEWOOD, 1907, p. 221). Early term for the arms of the pterobranch zooids; also termed *branchial plumes, lophophore arms* or *branchial arms.*

*Chitinverdickungs-Bänder* (German) KRAFT (1926, p. 231). See cortical bandages.

**cladial branching** (ELLES & WOOD, 1914, p. 505). Division of stipe where the branches originate from a thecal aperture or the sicular aperture. See dichotomous branching.

**cladium** (pl., cladia) (ELLES & WOOD, 1914, p. 505). Stipe developed from a mature thecal aperture through cladial branching. URBANEK (1963, p. 147) used the term cladium for any graptolite stipe, but it is suggested herein that the term be used in the restricted sense of ELLES and WOOD (1914), as it is generally used in the literature for a secondary branching from a thecal (or sicular) aperture. See *procladium, metacladium, pseudocladium*.

**cladogeny** (see URBANEK, 1963, p. 148). Describes 1) the growth of a colony or tubarium (BEKLEMISHEV, 1952); or 2) the branching of evolutionary lineages (RENSCH, 1947).

**clathrium** (pl., clathria) (ELLES & WOOD, 1908, p. 306; BATES, KOZŁOWSKA, & LENZ, 2005, p. 709). Skeletal framework of lists forming the preservable part of the retiolitid tubarium; supporting the reticulum or an attenuated fusellum. Included in this definition are lists of both the thecal framework and the ancora sleeve (Retiolitidae). See reticulum.

**clathriate.** Possessing a clathrium.

*coenoecium (*pl., *coenoecia*) (ALLMAN, 1856, p. 8). Describes the common dermal system of the Bryozoa [Polyzoa], consisting of ectocyst and endocyst; introduced for the tubarium of *Rhabdopleura* by ALLMAN (in NORMAN, 1869a, p. 312) and commonly used for extant Pterobranchia; equivalent to the terms *rhabdosome* and tubarium in the description of the Graptolithina.

**collar.** 1) Part of the pterobranch zooid on which the arms are positioned behind the cephalic shield; term originates from the homologization of the tripartite body development with the Enteropneusta (*Balanoglossus*) (HARMER, 1905, p. 30). 2) Externally protruding part of fusellar rings in erect full rings of *Rhabdopleura* tubaria (KULICKI, 1969, p. 539). (3) Wide genicular rim or hood in *Lithuanograptus* (=*Metaclimacograptus*) described by PAŠKEVIČIUS (1976, p. 140); formed from microfusellar tissues (MALETZ, 1997a, p. 21). See fusellar collar.

**collum** (pl., colla) (KOZŁOWSKI, 1949, p. 170). Erect distal tubular portion of the autotheca in some early benthic graptolites (camaroids); not homologous to erect tubes of *Rhabdopleura.*

**colony.** Biological term to describe close associations of individuals of one species living together in some degree of interdependence; In Graptolithina, describes the association of pterobranch individuals or zooids in constant organic contact with one other for mutual benefit and for secreting a common extracellular tubarium

**columella** (COOPER & FORTEY, 1982, p. 282). Thickened column in the center of *Phyllograptus* colonies.

**common canal** (BARRANDE, 1850, p. 5; HALL, 1865, p. 23); originally *canal commun* (French). Continuous tubular cavity collectively formed by the prothecae of graptoloids connecting the individual thecae.

*connecting canal* (TÖRNQUIST, 1893, p. 5). Term used by earlier workers for the crossing canal.

**connecting list** (BATES, KOZŁOWSKA, & LENZ, 2005, p. 709). List linking transverse list and nema in Retiolitidae.

**consecutive dichotomy** (COOPER & FORTEY, 1982, p. 176, fig. 6). Branching pattern in dichograptids in which only a single theca separates successive dichotomies, as in *Goniograptus.* See delayed dichotomy.

**conotheca** (pl., conothecae) (BULMAN & RICKARDS, 1966, p. 50). Relatively large, conical theca with a small circular aperture; irregularly developed in tubaria of some Callograptidae.

*contractile cord* (SARS, 1872, p. 10). See gymnocaulus.

*contractile stalk* (SCHEPOTIEFF, 1907b, p. 199). The unsclerotized, contractile stalk of the pterobranch zooid; identical to the contractile cord of SARS (1872, p. 10), the funiculus of ALLMAN (1869b) and homologous to the pedicle or peduncle of *Cephalodiscus* (M'INTOSH, 1887, p. 20). Originally *kontraktiver Stiel* (German). See gymnocaulus and zooidal stalk.

**conus** (pl., coni) (HUTT, 1974a, p. 80). Distal, cone-shaped part of the prosicula, separated from the cauda by an internal diaphragm.

**corona** (pl., coronae) (EISENACK, 1951, p. 134; BOUČEK & MÜNCH, 1952, p. 5). Initial proximal part of the ancora sleeve in the Retiolitidae. As used by BOUČEK & MÜNCH (1952), it comprises the ancora, ancora umbrella, and lists to the base of the first thecal pair.

*corona stage.* See ancora umbrella.

**cortex, cortical tissue** (KOZŁOWSKI, 1938, p. 190). The outer layer of the graptolite housing construction, formed by slender, parallel-sided bandages; the cortex produces the secondary thickening of the tubarium walls; the secondary lamellae of HARMER (1905, p. 10) in extant Pterobranchia. See fusellum.

**cortical bandages** (CROWTHER & RICKARDS, 1977, p. 11). Formation of cortical layers from thin bandages, crisscrossing the fusellar construction of the tubarium, first described in detail by CROWTHER (1978, 1981). KRAFT (1926, p. 231) described cortical bandages as *Chitinverdickungs-Bänder* (German) and misinterpreted them as internal features. BULMAN (1932a, pl. 3, fig. 7–8: *Climacograptus diplacanthus*) illustrated cortical bandages in *Diplacantograptus spiniferus.* See cortex.

**crassal fabric** (URBANEK & TOWE, 1974, p. 4). Electron dense and homogeneous material, sometimes with indistinct layering but usually lacking a pattern, producing a compact wall of considerable thickness forming the stolons.

**crossing canal** (ELLES & WOOD, 1901, p. 6). Proximal (prothecal or initial) portion of the primordial graptoloid thecae growing across the axis of the sicula on the reverse side of the sicula to develop fully on the opposite side. Earlier workers used the term *connecting canal* (see TÖRNQUIST, 1893, p. 5).

**cryptopyle** (KOZŁOWSKI, 1962, p. 19). Single or paired opening at the distal end of a graptoblast, opposite to the filum.

**cryptoseptate** (URBANEK, 1959, p. 290). Biserial tubaria in which the median septum is comprised of cortical listrs arranged as in septate forms but lacking a fusellar septal membrane.

**cupula** (pl., cupulae) (LOYDELL & MALETZ, 2004, p. 68). Paired bulbous protuberances on the dorsal side of some monograptoid graptolites, flanking the nema. Cupulae are believed to represent prothecal folds at the base of the thecae. Cupulae occur in *Streptograptus* and related taxa (Monograptidae).

*cyrtograptid budding* (URBANEK, 1963, p. 148). Budding of a theca directly from the aperture of the mother theca. See cladial branching.

*cyrtograptid stage* (URBANEK, 1963, p. 148). Stage of phylogenetic modifications in the development of a colony, during which the process of astogeny produces a procladium and at least one thecal cladium that is generated by *cyrtograptid budding*. See cladial branching.

**cyst.** Common biological term. 1) Vesicles of varying size and shape occurring in autothecal cavities of crustoids. 2) Surface features in graptolites that may represent parasitic organisms.

**declined** (ELLES & WOOD, 1901, p. 5, fig. 3). Describes graptoloid tubaria with branches hanging below the sicula, subtending an angle of less than 180° but not parallel to each other (pendent).

**deflexed** (ELLES & WOOD, 1901, p. 5, fig. 3). Similar to declined but with distal extremities of stipes tending to become horizontal.

**delayed dichotomy** (COOPER & FORTEY, 1982, p. 176, fig. 6). Branching pattern in dichograptids in which two or more thecae separate successive dichotomies after the first dichotomy, as, for example, in *Laxograptus*. See consecutive dichotomy.

**dendroid, dendroidal.** 1) Belonging to the order Dendroidea. 2) Descriptive term for tubarium growth showing irregular, bushy colony shapes in benthic graptolites.

*denticle.* Term used by earlier workers to describe the thecae of graptolites and later by English workers for the ventral extension of the prosicula of dendroids along the zigzagging line of suture; considered imprecise by KOZŁOWSKI (1949, p. 20), who replaced it by the term *languette*. See rutellum.

**denticulate.** Pointed sicular and thecal apertures provided with a short spine or rutellum.

**development type.** See proximal development type.

**dextral** (COOPER & FORTEY, 1982, p. 174). Clockwise direction of growth of tubarium. See sinistral.

**diad budding** (KOZŁOWSKI, 1949, p. 141). Mode of budding in pterobranchs resulting in two zooids at each nodal division, lacking regularity of thecal succession. See also triad budding.

**diaphragm** (HUTT, 1974a, p. 80). Membrane stretching across the initial part of the prosicula and separating the conus from the cauda; identified first by KRAFT (1926) as a membrane. See also stolonal diaphragm (URBANEK & DILLY, 2000).

**diaphragm complex** (URBANEK & DILLY, 2000, p. 214). Complex structure developed at the apex of the initial stolon of *Rhabdopleura* inside the mother theca.

**dicalycal theca** (JAANUSSON, 1960, p. 303). Graptoloid theca giving rise to two daughter thecae, resulting in branching of multiramous graptolites. See monocalycal theca.

**dichotomous branching.** Stipe division where two branches diverge symmetrically from the parent stipe; see lateral branching, cladial branching. In a more restricted sense, also used for branching at the distal end of the graptolite.

**dichotomy.** Branching division with two stipes originating at the same point. The direction of growth of the parent stipe is abandoned, with the two stipes growing at identical angles away from it. See lateral branching.

**dipleural** (JAANUSSON, 1960, p. 303). Biserial graptoloid tubaria in which two stipes are in back-to-back contact, resulting in two external lateral walls. See monopleural.

*diprionid.* Early term for biserial (BARRANDE, 1850; TULLBERG, 1883, p. 13).

**discophorous** (KOZŁOWSKI, 1971, p. 314). Possessing a sicula with an attachment disk, but lacking a free nema; taken as indication of a benthic life style. See nematophorous.

**discoidal preservation.** Disklike view of the (multiramous) tubarium with the sicula roughly perpendicular to the stratification. See lateral preservation.

**dissepiment.** Strand of cortical tissue connecting adjacent branches or stipes in graptolite tubaria. HARMER (1905, p. 16) discusses numerous bridges connecting adjacent branches in *Cephalodiscus dodecalophus*. These may be constructionally homologous to the dissepiments in the Graptolithina. In botany, the term is used differently to denote a partition dividing an organ into chambers. See thecal bridge.

**distal.** Last-formed part of tubarium, stipe, or theca; farthest from the point of origin.

**distal lobe** (LOYDELL & MALETZ, 2004, p. 69). Rounded or elongated, broadly triangular processes on the lateral apertural margins of streptograptids (Monograptidae).

*diversograptid budding* (URBANEK, 1963, p. 148). The budding of a theca directly from the aperture of sicula, producing only one sicular cladium and not capable of producing more cladia. See cladial branching.

*diversograptid stage* (URBANEK, 1963, p. 148). Stage of phylogenetic modifications in the development of a colony, in which astogeny results in the formation of a bipolar tubarium consisting of a *procladium* and sicular cladium and also of the thecal cladia budding from them.

**dormant buds** (STEBBING, 1970, p. 210). Large, closed, vesicular bodies; interpreted as enclosing hibernating zooids and also identified as sterile buds by SCHEPOTIEFF (1907b, p. 198; sterile Knospen). See hybernacula, *statoblast*.

**dorsal.** Term denoting the side of the stipe opposite to the thecal apertures or a comparable side of the thecal aperture; not necessarily related to direction of growth but, presumably, to the dorsal side of the zooids.

**dorsal apertural tongue** JAEGER (1959, fig. 14); originally dorsales Zünglein (German). Term for the extension of the dorsal rim of the sicula into a rutellum-like construction in many Monograptidae. The dorsal tongue may be adorned with spines or other elaborations and should be differentiated from the ventral position of the rutellum in the Dichograptina and Sinograptina (MALETZ, 1997d, p. 248).

*duplex species* (LAPWORTH, 1873a, p. 501). See biserial.

**ectocortex** (CROWTHER, 1981, p. 13; URBANEK & MIERZEJEWSKI, 1984, p. 76). The cortical material deposited on the outer surface of the thecal walls or, generally, on the outer surface of the tubarium. URBANEK and TOWE (1974) differentiated the ectocortex into autocortex and rhabdocortex. See endocortex.

**end bulbs** (M'INTOSH, 1887, p. 11). Bulbous structures at the tips of the arms of *Cephalodiscus* zooids. M'INTOSH (1887, p. 11) described the end bulbs as glandular, but HARMER (1905, p. 39) stated that there is no evidence for a function of the end bulbs.

**endocortex** (URBANEK & MIERZEJEWSKI, 1984, p. 76). The cortical material deposited on the inner surface of the thecal walls or, generally, within the cavities of the tubarium. See ectocortex.

**eucortex** (URBANEK & MIERZEJEWSKI, 1984, p. 76). The secondary component made of the typical cortical tissue, including sheets, well-defined straight, parallel, fibrils and some ground substance.

**everted.** Outward-facing thecal aperture.

*exoskeleton.* Term often used for the coenecium or tubarium (rhabdosome) of graptolites. The graptolite tubarium is not an exoskeleton but a housing structure or domicile, secreted by the organism. See tubarium.

**extensiform** (ELLES & WOOD, 1901, p. 5, fig. 3). Term denoting stipes growing more or less horizontally away from the vertical sicula.

**external common canal** (BATES & KIRK, 1992, p. 127). See outer common canal.

*external orifice* (BARRANDE, 1850, p. 6). Term used by BARRANDE for the thecal aperture.

**extroverted.** Thecae turned back on themselves by the exaggerated growth of the dorsal margin of the aperture.

**fibrils, fibrillar structure** (DILLY, 1971, p. 502). Ultrastructural features of the graptolite fusellum; the fine elements forming the collageneous material of the graptolite and pterobranch fusellum. The term fibrils was also used for the surface patterns of cortical bandages in the Retiolitinae by BATES and KIRK (1978, pl. 4), now described as longitudinal striations (LENZ & MELCHIN, 1987, p. 162).

*filum* (pl., *fila*) (KOZŁOWSKI, 1949, p. 207). Remains of the stolon in graptoblasts.

**finite.** Graptolite tubarium with limited growth, forming terminal thecae of reduced size or special shape; present in some Retiolitidae, but also in the Axonophora, such as the genera *Brevigraptus* and *Corynoides.*

**flabellate.** Fan-shaped tubarium form with stipes spreading out in a single plane; used for benthic graptolites.

*float.* A membrane at the proximal or distal end of a tubarium that is interpreted as supporting a stable orientation of the tubarium in the water column or as a float or flotation device. See nematularium.

**foramen** (pl., foramina). Opening in the sicula for the development of the bud of th$1^1$. See primary porus, resorption foramen.

**fornical foramen** (COOPER & FORTEY, 1982, p. 180). The wide openings between thecal series in *Phyllograptus,* representing the remains of the median septum between the four scandent thecal series.

**fornix** (COOPER & FORTEY, 1982, p. 180). The arched strut standing in place of the median septum in the axial region of the quadriserial *Phyllograptus.*

**free ventral wall.** The portion of the ventral thecal margin that extends beyond the aperture of the preceeding theca.

*frond.* Term used by earlier workers (e.g., HALL, 1865) for the stipes of graptolites.

**funicle** (from the Latin funiculus, funiculi) (HALL, 1865, p. 19; LINDHOLM & MALETZ, 1989, p. 713). The combined first-order stipes in the multiramous graptoloids. Originally proposed by HALL (1865) for non-thecate intial parts of dichograptids connecting thecate stipes. It is now known that thecae are present throughout the proximal area in graptolite colonies, but that they may be obscured by secondary overgrowth.

*funiculus* (ALLMAN, 1869b, p. 58). See gymnocaulus.

**fusellar collar.** Externally protruding part of fusellar ring in erect full rings of *Rhabdopleura* tubaria (KULICKI, 1969, p. 539); called ribs, Rippen, or Kragen in ANDRES (1977, p. 57). See collar.

**fusellar tissue** (KOZŁOWSKI, 1938, p. 190). Inner organic layer of the tubarium, generally comprised of alternating L and R bands of fuselli. See fusellum.

**fusellum** (pl., fusella) (KÜHNE, 1955, p. 363; URBANEK & TOWE, 1974, p. 4; URBANEK & MIERZEJEWSKI, 1984, p. 74). Primary skeletal material of graptolites and pterobranchs, formed from fuselli. See cortex.

**fusellus** (pl., fuselli) (KOZŁOWSKI, 1949, p. 20). Individual half rings or full rings of scleroproteic material secreted by the cephalic disk of the graptolite and pterobranch zooids, forming the tubarium laid down sequentially. Fuselli were first described as *Querrunzeln* by RICHTER (1871, p. 233), who stated that they form a zigzag suture on the dorsal and ventral sides of the cells; recognized as growth lines by LAPWORTH (1873a). HARMER (1905, p. 10) identified fuselli as the primary lamellae in extant Pterobranchia. See growth lines.

**geniculum** (JAANUSSON, 1960, p. 304). Angular bend in the upward ventral direction of growth of the graptoloid theca. It may be adorned with a thickened rim, spines, or other genicular processes.

**genicular process** (JAANUSSON, 1960; BATES, KOZŁOWSKA, & LENZ, 2005, p. 709). Processes formed at the geniculum of a graptolite theca.

**glossograptid bulge** (MALETZ & MITCHELL, 1996, p. 643). Conspicuous proximal bulge formed by a variable number of proximal thecae growing in a spiral pattern and covering the sicula and th1[1] on both the obverse and reverse sides of the Glossograptidae; first illustrated from isolated material by WHITTINGTON and RICKARDS (1969).

*gonangium* (pl., *gonangia*). Term used by earlier workers for the bithecae (e.g., WIMAN, 1895, 1896c). RUEDEMANN (1895) also used the term to describe the oval disk to which synrhabdosomes are attached.

**graptoblast** (KOZŁOWSKI, 1949, p. 206). Ovoid-shaped chambers present in crustoids; interpreted as rejuvenated zooidal chambers by URBANEK and MIERZEJEWSKI (1984) and MIERZEJEWSKI (2000a).

**graptolite.** General term for the tubaria of the Graptolithina; derived from the genus *Graptolithus* LINNAEUS, 1735; originally interpreted as inorganic markings by LINNAEUS (1735).

*grapto-gonophore* (NICHOLSON, 1866, p. 489). Fossils identified as ovarian vesicles or grapto-gonophores, but representing various non-graptolitic taxa (PAGE & others, 2009).

**growth lines.** Expression of the fusellar structure (see fuselli) on the surface of the graptolite tubarium; first described by BARRANDE (1850, p. 8; striae), but not recognized as such. LAPWORTH (1873a) was the first to describe the striae on the surface of many graptolites as growth lines. RICHTER (1871, p. 233) described growth lines of graptolites with the term Querrunzeln and remarked that they form a zigzag suture (Zickzacknaht) on the upper and lower side of the thecae (Zellen, cells).

**gymnocaulus** (LANKESTER, 1884, p. 629). Unsclerotized stolon situated behind the permanent terminal zooid in *Rhabdopleura* from which the zooids proliferate. LANKESTER (1884) used the term in a wider sense, including the zooidal stalks; identical to the contractile cord of SARS (1872, p. 10), the funiculus of ALLMAN in NORMAN (1869a, p. 312) and homologous to the pedicle or peduncle of *Cephalodiscus* (M'INTOSH 1887, p. 20). The term is also used for the homologous unsclerotized stolon in graptolites (HUTT, 1974*a*, p. 81).

**heart-shaped axial cavity** (XIAO & CHEN, 1990, 1994). Cavity enclosed by the two reclined and subsequently scandent stipes in *Proncograptus, Procardiograptus,* and *Diceratograptus.*

**helical line** (KOZŁOWSKI, 1949, p. 56); originally ligne hélicoïdale (French). See also spiral thread or spiral line. Identical to the Schraubenlinie of KRAFT (1926).

**helicotheca** (KOZŁOWSKI, 1949, p. 163); originally *hélicothèque* (French). Type of autotheca in Cyclograptidae with coiled initial part.

*Höckerchen* (EISENACK, 1951, fig. 11). See pustules.

**horizontal.** Graptoloid tubarium with stipes growing at a right angle to the axis of the sicula. See extensiform.

**hybernacula** (LANKESTER, 1884, p. 639). Large, closed, vesicular bodies; interpreted as enclosing hibernating zooids, also identified as statoblasts (LANKESTER, 1884, p. 639) and sterile buds by SCHEPOTIEFF (1907b, p. 198: sterile Knospen). See dormant buds.

*hydrorhabd* (FRECH, 1897, p. 549). See tubarium.

*hydrosome*. Term used by earlier workers for the graptolite tubarium, suggesting a relationship to the Hydrozoa. RUEDEMANN (1895, p. 224) used the term for synrhabdosomes.

*hydrotheca* (e.g.,NICHOLSON & MARR, 1895, p. 529). Term used by earlier workers for the autothecae of the Dendroidea and other benthic graptolite groups and for the thecae of the Graptoloidea, suggesting a relationship to the Hydrozoa.

*hypoblastic* (LEGRAND, 1987, p. 61). Term for a certain proximal development type.

**infragenicular wall** (JAANUSSON, 1960, p. 304). Thecal wall between the geniculum and the preceeding theca in geniculate graptolites.

**initial bud.** Outgrowth formed by the first post-sicular zooid through a foramen in the sicular wall, producing the first theca of the tubarium.

**initial foramen.** Opening for the first post-sicular zooid of a graptolite colony.

*Initialteil* (WIMAN, 1895, p. 263). See prosicula.

*internal orifice* (BARRANDE, 1850, p. 7). Primary opening in the mother theca from which the daughter theca originates.

*interpleural list* (LENZ, 1993a, p. 12). Medially placed ventral list connecting the upper apertural list of one theca with the lower apertural list of the succeeding thecal aperture of a retiolitid tubarium. See mid-ventral list.

**interthecal septum** (TÖRNQUIST, 1893). Membrane separating the overlapping thecal cavities in graptoloids. It comprises the dorsal wall of a theca and part of the ventral wall of the succeeding theca.

**introverted.** Inward-facing thecal aperture resulting from the exaggerated growth of the ventral wall of the thecae; usually accompanied by the sigmoidal curvature of the thecal axis.

**introtorted.** Refers to the change in direction of growth of the metatheca toward, rather than away from, the dorsal stipe margin, as in *Dicranograptus.*

**isograptid arch** (COOPER & FORTEY, 1982, p. 180). The arch formed by the ventral walls of the dicalycal theca and its first daughter theca. The structure helps distinguish development types in dichograptids; in species with artus-type proximal development, there is a single thecal aperture showing beneath the arch (that of the sicula), whereas in isograptid-type proximal development, there are two apertures showing beneath the arch (those of the sicula and th1[1]).

**isograptid suture** (MALETZ, 1994b, p. 28). Line of contact between the sicula and th1[1], which is visible in reverse view below the isograptid arch in many dichograptids. It gives a measure of the position of the crossing canals on the sicula.

**isograptid symmetry** (COOPER, 1973, p. 56; COOPER & FORTEY, 1982, p. 180). Sicula and th1[1] forming a symmetrical pair. See maeandrograptid symmetry.

*keroblastic* (LEGRAND, 1987, p. 61). Term for a certain proximal development type in Llandovery axonophorans.

*Kuppel* (EISENACK, 1951, p. 156). See corona.

**labia** (pl., labiae) (Lenz & Kozłowska-Dawidziuk, 2004, p. 17). Thickened apertural lip with distinctive paired structures in Retiolitidae (*Neogothograptus*).

**lacinia** (Elles & Wood, 1908, p. 319; revised by Bates, 1990, p. 717). A three-dimensional network of unseamed lists, thickened by concentric growth of bandages. The lists are attached to ventral apertural spines, to paired obverse and reverse spines branching from the nema, and also to the virgella and paired dorsal sicular apertural spines. A lacinia is present in the Archiretiolitidae and in *Paraglossograptus* (Glossograptidae). Originally termed *marginal meshes* by Lapworth (in Hopkinson & Lapworth, 1875, p. 641).

**lacuna stage** (Eisenack, 1942, p. 31); originally Lacuna-Stadium (German). Second stage in the development of the initial foramen of the growth of the first theca in the Monograptacea. The primary foramen is surrounded by fusellar growth bands. See sinus stage, porus stage.

*Längsverstärkungsleisten* (Kraft, 1926, p. 224). See longitudinal strengthening rods.

*languette* (Kozłowski, 1949, p. 20, 22, and 33). The apertural ventral and dorsal terminal extensions of the thecae in dendroid graptolites along the zigzag suture line of the fuselli. It replaced the less-precise denticle of English workers, which had been originally used for the thecae of graptolites. Kozłowski (1949, p. 22) differentiates a dorsal languette and a ventral languette. The ventral languette is homologous to the rutellum of Williams and Stevens (1988).

**lappet.** Rounded lateral apertural processes of thecae or the sicula; mistakenly also used for ventral apertural lappets, now called rutelli.

**lateral apertural list** (Bates, Kozłowska, & Lenz, 2005, p. 709). The part of the apertural list in Retiolitidae that connects with the lists of the ancora sleeve.

**lateral branching.** A special case of dichotomous branching in which one of the stipes diverges at an angle to the parent stipe, which continues its original direction of growth (e.g., *Holograptus*).

**lateral preservation.** 1) Tubarium showing only one side (see discoidal preservation). 2) Lateral preservation in stipes indicated by the typical sawtooth appearance, showing thecal rutelli.

**lateral proximal orifices** (Bates, Kozłowska, & Lenz, 2005, p. 720). Openings on the lateral wall between the rim of the ancora umbrella and base of ancora sleeve.

**left-handed** (origin of thecae) (Stubblefield, 1929, p. 274; revised by Cooper & Fortey, 1982, p. 173). Refers to thecae originating on the (biologically) left side of the theca viewed from the dorsal side.

**lenticular porus** (Dawson & Melchin, 2007, p. 91). An opening for the emergence of the first post-sicular istal direction onto the virgellar spine. One or two truncated or incompletely formed fuselli may be present. The post-porus fuselli are deflected in the opposite direction but resume their original direction close to the virgellar spine, forming a lenticular primary opening for the th1 bud. See primary porus, resorption foramen.

**line of symmetry.** The line of symmetry passes through the sicula (see maeandrograptid symmetry) or between the sicula and the first theca (see isograptid symmetry).

*linea* (Lapworth, 1897, p. 251). See nema.

*linograptid budding* (Urbanek, 1963, p. 148). Term used to denote multiple sicular cladia.

*linograptid stage* (Urbanek, 1963, p. 148). A stage of phylogenetic modification in the development of a colony, in which a procladium and numerous sicular cladia are produced in astogeny; restricted to the genus *Linograptus.*

**list** (pl., lists) (revised by Bates, Kozłowska, & Lenz, 2005, p. 709). Skeletal list in Retiolitidae that strengthens the fusellar walls with localized cortical bandages.

**longitudinal strengthening rods** (Kraft, 1926, p. 224); originally Längsverstärkungsleisten (German). Cortical ridges on the outside of the prosicula, formed before the growth of the metasicula.

*lophophore* (Lankester, 1884, p. 630). Paired arms or groups of arms in the zooids of pterobranchs, provided with ciliated tentacles and situated adjacent to the mouth of the zooid; originally lophophore arms or branchial arms (Lankester, 1884, p. 630), but also branchial or cephalic plumes (M'Intosh, 1887, p. 10; Ridewood, 1907, p. 221). A lophophore is typically present in Brachiopoda, Bryozoa, and Phoronida; thus, the term should not be used for the Pterobranchia. See arms.

**maeandrograptid symmetry** (Cooper, 1973, p. 56; Cooper & Ni, 1986, p. 316). Used to describe $th1^1$ and $th1^2$ forming a symmetrical pair on both sides of the sicula. See isograptid symmetry.

**manubrium** (Cooper, 1973, p. 54; Maletz & Mitchell, 1996, p. 642). A complex and prominently shouldered structure on the reverse side of arienigraptid graptolites (Isograptidae), which is formed by the strong downward growth of the initial part of $th1^2$ and $th2^1$ and their descendant thecae. It always involves the formation of an arienigraptid suture. The sicula and the early thecae extend downward at least as far as their descendant thecae.

**manubrium shoulders** (Cooper & Ni, 1986, p. 315). Dorsal margin of the manubrium, from the origin of the stipes at the sicula to the sharp dorsal flexure in the dorsal stipe margin.

**manubriate** (Cooper, 1973, p. 56). Tubaria having a manubrium.

*marginal meshes* (Lapworth in Hopkinson & Lapworth, 1875, p. 641). See lacinia.

**median plane** (Cooper & Fortey, 1982, p. 178, fig. 8). The plane of symmetry of branching tubaria, containing the tubarium midline and the two first-order stipes.

**median septum**. Membrane in quadriserial, triserial, and biserial dipleural graptoloids, separating the thecal series, originating at various levels in the tubarium. In some biserial dipleural forms, a partial median septum occurs on the obverse side only.

*membrane interthécale.* See basal membrane.

**mesial.** 1) The middle part of the tubarium. 2) The middle part of the free ventral wall (supragenicular wall) of a theca.

*metacladium* (URBANEK, 1963, p. 147). Thecal or sicular cladium as opposed to *procladium* or main stipe. See cladium.

**metasicula** (KRAFT, 1926, p. 225). Distal part of sicula comprised of fusellar growth bands or fuselli; named the *Aperturalteil* by WIMAN (1895). See prosicula.

**metatheca.** The growth of the metatheca commences at the base/origin of the interthecal septum of the succeeding theca. In taxa lacking an interthecal septum, the metatheca can be defined as commencing its growth at the origin of the ventral wall of the succeeding theca. See protheca.

**microfusellar tissue** (URBANEK, 1966, p. 306). Fusellar substance comprised of extremely fine and somewhat irregular growth bands.

**microtheca** (KOZŁOWSKI, 1949, p. 163); originally microthèque (French). Type of autotheca occurring in Cyclograptidae, characterized by a narrow terminal portion and differently oriented apertures.

**mid-ventral list** (BATES, KOZŁOWSKA, & LENZ, 2005, p. 709). Centrally placed longitudinal list running from the transverse list or from the genicular list to the thecal lip (Retiolitidae). Identical to *interpleural list* of LENZ (1993a, p.12).

**monocalycal theca** (JAANUSSON, 1960, p. 303). Graptoloid thecae giving rise to only one subsequent thecae. See dicalycal theca.

**monofusellar tissue** (URBANEK, 1958, p. 19). Fusellar substance deposited in single and not alternating series of growth bands, forming full fusellar rings (e.g., the erect tubes of *Rhabdopleura*) or in lateral lobes of thecal apertures.

*monograptid budding* (URBANEK, 1963, p. 148). Subapertural, nonperforational budding of theca from an initial, primary opening, subaperturally placed in relation to the definite aperture of the respective mother theca. See cladial branching.

*monograptid stage* (URBANEK, 1963, p. 148). Stage of phylogenetic modification in the development of a colony, in which the process of astogeny produces only a procladium by monograptid budding.

**monopleural** (JAANUSSON, 1960, p. 303). Biserial graptoloid tubarium in which two stipes are in contact laterally, each stipe having only one lateral external wall (Glossograptidae). See dipleural.

**monopodial growth.** Type of colonial growth with permanent terminal zooid behind which new zooids arise as the stem elongates; known exclusively in *Rhabdopleura*. See sympodial growth.

**monoprogressive branching** (COOPER & FORTEY, 1982, p. 177, fig. 6). Branching pattern in which only one of the two daughter stipes formed at a dichotomy divides again, with the other daughter stipe remaining unbranched, as in *Goniograptus,* after the first dichotomy. See progressive branching.

*mouth-spine* (WIMAN, 1896c, p. 188). See virgella.

**multiramous.** Having numerous branches or many branches.

**nema** (pl., nemata or nemas) (LAPWORTH, 1897, p. 251). Filiform process or extension at the apex of the prosicula; originally defined by LAPWORTH (1897) as the flexuous primordial filiform process from which the sicula is suspended. The secretion of the nema starts at the tip of the cauda. The nema may be free (Dichograptina), incorporated in the tubarium (Diplograptina, Glossograptina), or fully visible on the dorsal side of the stipe (Monograptidae). The nema in the Diplograptina and Monograptidae is commonly called the virgula. RICHTER (1850, p. 201) mistook the nema as a siphon, based on the belief that graptolites are related to nautiloids. See pseudovirgula.

*nema prosiculae* (KRAFT, 1926, p. 225). See cauda.

*nemacaulus* (RUEDEMANN, 1904, p. 487). Term proposed by RUEDEMANN (1904) in lieu of nema.

**nematophorous** (KOZŁOWSKI, 1971, p. 314). The possession of a free nema in the graptolite sicula, which is taken as indication of a planktic life style. See discophorous.

**nematularium** (MÜLLER, 1975, p. 330; BATES, KOZŁOWSKA, & LENZ, 2005, p. 709: for retiolitids). Distal development of a vane or spiral structure of the nema.

**nozzle** (LOYDELL & MALETZ, 2004, p. 69). The elongated arch on the dorsal side of the thecal aperture in streptograptids (*Streptograptus, Pseudostreptograptus, Mediograptus*).

**obverse** (TÖRNQUIST, 1893, p. 3). Refers to the side of the graptoloid tubarium on which the sicula is most completely visible and the crossing canals are covered; similar to Siculaseite of WIMAN (1895) and others. See reverse.

**occlusion.** Sealing of the thecal aperture by sclerotized film, possibly made up of cortical material.

**ontogeny.** General biological term for the growth of organisms, used herein for the growth of an individual, a zooid; previously used by KOZŁOWSKI (1971, p. 314) only to describe the ontogeny of the sicular zooid, but it is applicable to all derived zooids. The combined ontogenies of all zooids of a colony represent the astogeny of the colony. See astogeny.

*oozooid* (KOZŁOWSKI, 1971, p. 314). Term for the sicular zooid.

**order** (**of branching**) or **order of stipes.** Successive divisions of dichotomous branches or successive generations of cladia. MALETZ (1992, p. 298) preferred to use the term 1st to nth order of stipes in the Dichograptina instead of the terms primary and secondary stipes.

**orifice** (LOYDELL, STORCH, & BATES, 1997, p. 748). An opening of the tubarium that is partially or entirely rimmed by lists of the ancora sleeve in Retiolitidae. Includes thecal orifices, proximal ventral orifices, proximal lateral orifices, and stomata. The term was used by earlier workers for thecal apertures (e.g., BARRANDE, 1850: internal and external orifices).

*ostium* (pl., *ostiae*). Term used in earlier graptolite literature for thecal apertures.

**outer ancora** (BATES, KOZŁOWSKA, & LENZ, 2005, p. 710). Structure formed by lists on the outside of the ancora umbrella in some Retiolitidae.

**outer common canal** (BATES & KIRK, 1992, p. 127). Initially identified as as external common canal. Development of a common canal between the lateral thecal sides and the ancora sleeve on both sides of the retiolitine tubarium, often with regular or irregularly developed stomata. See common canal.

**outer lamella** (URBANEK & TOWE, 1974, p. 5). Fabric of parallel fibrils in a fusellus immediately beneath the bounding pellicle of sheet fabric.

**pachythecae** (KOZŁOWSKI, 1970, p. 405). Large thecae in *Acanthograptus* with amorphous wall structure and no fuselli; interpreted as possibly parasitic in origin, like the tubothecae.

**paracortex** (URBANEK & MIERZEJEWSKI, 1984, p. 76). Secondary component of cortex made by multiple deposition of sheets separated by an intersheet material, lacking well-defined, individualized cortical fibrils; produced by a tightly packed, condensed meshwork of fibrous material.

**parasicula** (VANDENBERG, 1990, p. 40). Tubular downgrowth of the sicular aperture in biserial graptolites. The term parasicula was first introduced by EISENACK (1938a, p. 156) for the misinterpreted metasicula of a dendroid graptolite, later identified as *Epigraptus bidens* (EISENACK, 1941a).

**paratheca** (pl., parathecae) (MITCHELL, CHEN, & FINNEY, 2007, p. 1123). Tubular outgrowths from the thecal apertures in the proximal part of some biserial graptolites (*Appendispinograptus*).

**parietal list** (KOZŁOWSKA-DAWIDZIUK, 1990, p. 194). Major oblique to horizontal lists on the obverse and reverse ancora sleeve panels, linking the vertical pleural lists. The parietal lists also form the obverse and reverse zigzag struture of many derived retiolitines (e.g., *Plectograptus, Holoretiolites*).

**patagium** (KOZŁOWSKA & URBANEK, 2013, p. 19). Fan-shaped membrane originating from a repeatedly branching rod on the sides of the tubarium in *Bohemograptus*.

**pauciramous.** Planktic pterobranch colony consisting of few branches.

**pectocaulus** (LANKESTER, 1884, p. 634). The sclerotized, inflexible black stolon, usually embedded in the ventral wall of mature tubes in the Pterobranchia; identical to the axial cord of SARS (1872, p. 11) and the chitinous rod of ALLMAN (1869b). The stolon is presumably free in the tubarium of planktic graptolites but is rarely present in the fossil record. The terms pectocaulus and stolon can be used interchangeably, but the latter is more widely distributed.

*pedicle* (M'INTOSH, 1887, p. 20). Thin, flexible, cylindrical stalk at the rear end of the *Cephalodiscus* zooids, provided with a sucker for attachment; new buds originate from the base of the pedicle; term borrowed from the terminology of the Brachiopoda. See gymnocaulus.

*peduncle* (M'INTOSH, 1887, p. 6). Thin, flexible, cylindrical stalk at the rear end of the *Cephalodiscus* zooids, provided with a sucker for attachment; new buds originate from the base of the pedicle; M'INTOSH (1887) used both pedicle and peduncle for the gymnocaulus of *Cephalodiscus*. The term is homologous to the gymnocaulus of *Rhabdopleura* and should not be used. See gymnocaulus. Term also used for pelecypods.

**pendent** (ELLES & WOOD, 1901, p. 5, fig. 3; COOPER, 1973, p. 52, text-fig. 5). Denotes a downward direction of growth of stipes or of thecae when the tubarium is oriented so that the apex of the sicula points vertically upward.

**pericalycal** (BULMAN, 1968, p. 214; MALETZ & MITCHELL, 1996, p. 643). Taxa with an isograpid- or artus-type development, with the enclosure of the obverse side of the sicula by th$2^2$ (or th$1^2$ in some derived species), with resulting initial monopleural growth of the two thecal series such that the tubarium acquires a secondary rotational symmetry normal to the plane of isograptid symmetry. See platycalycal.

*periderm* (TÖRNQUIST, 1894, p. 377). Scleroproteic substance forming the tubarium of the Pterobranchia, comprised of an inner layer of alternating fusellar bands (fuselli) with growth lines and an outer (cortical) layer of finely laminated tissue from thin bandages. The term should not be used any more, as the name suggests a dermal origin, which is incorrect (MITCHELL & others, 2013, p. 51). As there is no definite replacement term, the "material can simply be referred to as tubarium or wall material depending on the specific context" (MITCHELL & others, 2013, p. 51).

**plaited overlap, plaited arrangement** (COOPER & NI, 1986, p. 314; LINDHOLM, 1991, p. 289; MALETZ & MITCHELL, 1996, p. 642). 1) Parallel growth and overlap of several thecae, as in the manubrium of pseudisograptids. 2) The overlapping of thecae in bithecate and nonbithecate tubaria with lateral thecal origins (LINDHOLM, 1991). Both constructional features are developed independently but have similar results in their typical development of multiple parallel-oriented thecae.

**platform** (LOYDELL & MALETZ, 2004, p. 69). Smooth concavity, usually with a distinct genicular rim, in which the coiled metatheca with its aperture sits. Common to streptograptids but occurring also in other monograptids.

*platycalycal* (BULMAN, 1968, p. 214; MALETZ & MITCHELL, 1996, p. 643). Descriptive term used in biserial graptolites (Axonophora) to denote a concentration of budding on the reverse side of the tubarium with a largely free sicula on the obverse side. It largely describes a dipleural development. See pericalycal.

**pleural disk** (FINNEY, 1985b, p. 361). Paired disk structures growing from the pleural list of the thecae in a non-retiolitid axonophoran in a horizontal to subhorizontal fashion. Known only in *Dicaulograptus cumdiscus.*

**pleural list** (BATES, KOZŁOWSKA, & LENZ, 2005, p. 710). Side lists; lateral longitudinal lists of the ancora sleeve, connected to successive lateral apertural lists (septal bars). The pleural lists in *Dicaulograptus cumdiscus* (FINNEY, 1985b) are thecal lists and not homologous to the pleural lists of the Retiolitidae.

*plumes*. See arms.

**polymorphic.** Pterobranch colony comprising more than one kind of zooid or tubarium with more than one type of theca (autothecae, bithecae) or gradational thecal developments along the stipes, as in many monograptids.

*polypary* (SCHARENBERG, 1851, p. 5); originally polypenartige Geschöpfe (German for polyp-like organisms).

Term used by earlier workers for the tubarium (see ELLES & WOOD, 1902, p. xxvi ).

*polypide* (SARS, 1872, p. 8). Early term for pterobranch zooid, suggesting a bryozoan relationship.

*polypidum* (HARKNESS, 1851, p. 60). Old term for tubarium.

*polyzoarium* (SARS, 1874, p. 24). Old term for the tubarium of *Rhabdopleura.*

**porus stage** (EISENACK, 1942, p. 29); originally *Porus-Stadium* (German). First stage in the development of the initial foramen for the growth of the first theca in many graptolites, except for derived monograptids. A hole is formed in the ventral side of the sicula for the emergence of the first post-sicular zooid. See sinus stage, lacuna stage.

**post-coronal orifices** (LENZ, 1993a, p. 12). Openings in the ancora sleeve above the ancora umbrella in the Retiolitida; they can be described as ventral orifices.

**preoral lobe** (LANKESTER, 1884, p. 625). Anterior glandular lobe or disk in the zooids of the pterobranchs secreting the tubarium. See also cephalic shield.

*primary lamellae* (HARMER, 1905, p. 10). Term introduced for the fuselli of extant Pterobranchia.

**primary porus** (EISENACK 1942, p. 31). Pores left as an initial opening during the growth of the sicula through the sinus and lacuna stages. See resorption foramen.

*primary stipe.* MONSEN (1925, p. 160) already differentiated between primary and secondary stipes (Hauptzweige and Nebenzweige). The term was to describe the stipes originating from the sicula. See order of stipes.

*primordial astogeny* (MITCHELL, 1987, p. 354). The initial part of a graptolite colony exhibiting specialized ontogenies with thecae determining the proximal development type. See proximal development type.

*primordial series* (of thecae) (ELLES, 1897, p. 189). The thecal series starting with $th1^1$ in a biserial dipleural colony. See *second series.*

**primordial thecae** (HOLM, 1895, p. 437; MITCHELL, 1987, p. 354). The initial thecae of a graptolite colony exhibiting specialized ontogenies. See primordial astogeny.

**proboscis.** Term for the head part of enteropneusts, homologous to the cephalic shield of the pterobranchs. Generally used as a biological term for the tubular feeding and sucking organs of invertebrates, but also for the trunk of elephants.

*procladium* (URBANEK, 1963, p. 147; BULMAN, 1970). Term proposed for main stipe of cladia-bearing tubarium, with normal cladia being distinguished as metacladia. The term procladium could in theory be used for any graptoloid stipe, but the name would imply a cladial origin which is misleading. See cladium.

**progressive branching** (COOPER & FORTEY, 1982, p. 177, fig. 6). Branching pattern in which each of the two new branches formed at a dichotomy divide again, as in *Clonograptus, Etagraptus,* forming a multiramous colony. See monoprogressive branching.

**prosicula** (KRAFT, 1926, p. 222). The initial part of sicula, secreted as a cone with faintly marked spiral thread to which longitudinal fibers are added; called the *Initialteil* by WIMAN (1895).

**prosicular ring** (BATES & KIRK, 1992, p. 57). The sclerotized remains of the prosicula, preserved as a ring defining the prosicular aperture in many Retiolitidae.

**prosoblastic** (BULMAN, 1963b, p. 671; MITCHELL, 1987, p. 354). Type of diplograptid proximal development in which $th2^1$, and ultimately $th1^2$, grew upward and forward from their origin; $th1^2$ is roughly J-shaped with a downward-growing initial part. See streptoblastic.

**protheca.** Initial part of graptoloid theca before differentiation of succeeding theca (insertion of the median septum). In taxa without an interthecal septum, the point at which the theca becomes a complete tube, e.g., when the foramen of the daughter theca is closed, can be defined as the start of the metatheca. See metatheca.

**prothecal fold** (MU, 1957, p. 412 [English text]). Inverted U-shaped curvature of part of protheca (usually initial portion) giving a nodded appearance to the dorsal margin of the stipe.

**proximal.** First-formed part of the tubarium, nearest to the point of origin of the colony, the sicula.

**proximal development type** (ELLES, 1922, p. 170; COOPER & FORTEY, 1982, p. 171; MITCHELL, 1987, p. 354). Initial budding sequence of the tubarium. Proximal development types are commonly used to identify evolutionary relationships within the graptolites. Individual types are variably named and are not listed here. See astogenetic patterns.

**proximal structure** (COOPER & FORTEY, 1982, p. 173). The proximal structure refers to the orientation, attitude, and arrangement of proximal thecae.

**pseudanastomosis** (RICKARDS & LANE, 1997, p. 173). Temporary fusion of adjacent branches to form an ovoid mesh including the transfer of thecae between stipes. See anastomosis.

*pseudocladium* (URBANEK, 1963, p. 147). The regenerated stipe of a bipolar tubarium lacking a sicula. A pseudocladium is a regenerated stipe and not formed through cladial branching; thus, the term is inappropriate. See cladium.

**pseudocortex** (URBANEK & MIERZEJEWSKI, 1984, p. 76). Secondary component of cortical tissue produced by accumulation of sheets with an extremely scarce and poorly defined intersheet material devoid of any fibrous elements.

*pseudopericalycal* (COOPER & NI, 1986, p. 317). Term used to describe the proximal development in glossograptids. See pericalycal.

**pseudovirgula** (URBANEK, 1963, p. 147). Dorsal rod in the cladia of some Monograptidae, originating as a thecal or sicular apertural spines. Term used by LOYDELL and CAVE (1994) for a secondary nema in *Cochlograptus veles*. See virgula.

**pustule** (BATES, KOZŁOWSKA, & LENZ, 2005, p. 710). Regular protuberances on the sheet fabric bounding bandages of lists in Plectograptinae (Retiolitidae); first recognized by EISENACK (1951, fig. 11; Höckerchen [German]).

**quadriradiate** (BULMAN, 1950a, p. 68). Proximal development with four first-order stipes originating from the sicula through three successive dicalycal thecae; originally quadri-radiate in BULMAN (1950a, p. 68) and revised by MALETZ (1992, p. 303). See biradiate, triradiate.

**quadriserial.** Scandent graptoloid tubarium comprised of four rows of thecae in back-to-back contact as in *Phyllograptus*. See biserial, monoserial.

*Querrunzeln* (RICHTER, 1871, p. 233). RICHTER (1871) erroneously described growth lines of graptolites with this term and remarked that they form a zigzag suture (*Zickzacknaht*) on the upper and lower side of the thecae (Zellen). See growth lines, fuselli.

*radicle* (HALL, 1865, p. 19). Term used by earlier workers to identify the point of origin of the stipes or the "initial point" in graptolite tubaria; vague reference to the unrecognized sicula in dichograptids.

**reclined** (ELLES & WOOD, 1901, p. 5, fig. 3). Graptoloid tubarium with branches growing upward, subtending an angle of less than 180° between their dorsal sides.

**reflexed** (ELLES & WOOD, 1901, p. 5, fig. 3). Graptoloid tubarium with branches growing upward, similar to reclined, but with distal extremities of the stipes tending to be horizontal.

*regenerative virgula* (URBANEK, 1963, p. 147). Thickened cortical fiber, secondarily formed as an axis of the pseudocladium (regenerated stipe), as the result of regeneration in the Monograptidae. This feature is a secondarily grown nema.

**resorption foramen** (KOZŁOWSKI, 1949, p. 22); originally bourgonnement perforant (French). Opening in the sicula, formed by resorption by the initial bud of the first theca ($th1^1$ zooid). KOZŁOWSKI (1949, p. 23) called the primary opening for later thecae the bourgonnement apertural. See porus.

**reticulum** (pl., reticula) (ELLES & WOOD, 1908, p. 333; BATES, KOZŁOWSKA, & LENZ, 2005, p. 710). Delicate irregular network of secondary lists on the ancora sleeve and the thecal walls of the Retiolitidae.

**retroverted.** Thecal apertures facing proximally as the result of the hooked or reflexed shape of the metatheca, following excessive growth of the dorsal wall of the theca.

**reverse** (TÖRNQUIST, 1893, p. 3). Side of the graptoloid tubarium in which the sicula is partly concealed by the crossing canal(s); Antisiculaseite of WIMAN (1895, p. 263), HOLM (1895, p. 436), and others. See obverse.

*rhabdocortex* (URBANEK & TOWE, 1974, p. 13; URBANEK & MIERZEJEWSKI, 1984, p. 76). The common cortical envelope of a tubarium or of a group of thecae. See ectocortex.

*rhabdosome* (TÖRNQUIST, 1890, p. 6). Housing or domicile of graptolites; hydrosome, polypary, polypier, polypariet, and stock (listed in RUEDEMANN, 1904, p. 483) are comparable terms used in earlier literature (e.g., TULLBERG, 1883: *hydrosoma*). See tubarium.

*rhabdosome midline* (COOPER & FORTEY, 1982, p. 178, fig. 8). The primary axis of symmetry of the tubarium, which passes medially through the tubarium, from top to bottom. See tubarium midline.

**right-handed** (origin of thecae) (STUBBLEFIELD, 1929, p. 274; revised by COOPER & FORTEY, 1982, p. 173). Origin on the (biologically) right side of the sicula or later theca when viewed from dorsal side of the stipe.

*root.* Irregular branching structure made from cortical tissue, developed from apex of the sicula and serving for the attachment of benthic graptolites. The term is not recommended as the anchoring construction is not a root system (as in modern plants), but a development for firm attachment on a surface only.

**rutellum** (pl., rutella) (WILLIAMS & STEVENS, 1988, p. 20; MALETZ & MITCHELL, 1996, p. 644). Rounded, ventral, outward apertural elaboration on graptolite thecae. Initially intended for the sicula only. Homologous with the languette of the Dendroidea.

*saccoid* (ELLES & WOOD, 1914, p. 505). "Sac-like expansion" forming the initial part of the cladial thecae in *Cyrtograptus*.

**scalariform.** Preservational view presenting ventral (thecal) aspect of the graptoloid tubarium, mostly used for biserial taxa, but applicable also for other graptolites.

**scandent** (ELLES & WOOD, 1901, p. 5, fig. 3). Graptoloid tubarium with stipes growing erect distally and enclosing or including the nema.

*Schraubenlinie* (KRAFT, 1926, p. 222). German term translated as helical line, spiral thread or spiral line; identical to ligne hélicoïdale of KOZŁOWSKI (1949, p. 56).

**sclerotized.** Hardening of the tubarium walls after the secretion of scleroproteic substances by zooid(s).

**scopulae** (ELLES & WOOD, 1908, p. 319; referred to HOPKINSON & LAPWORTH, 1875). Peculiar ramifying fibrous development from edges of median septum (in lasiograptids); identified as reproductive processes in HALL (1865).

**seam** (BATES & KIRK, 1978, p. 429). Feature in retiolitid graptolites indicating the presence of unpreserved fusellar walls.

*secondary lamella* (HARMER, 1905, p. 10). Early term for the cortical tissue in extant Pterobranchia.

*secondary lists* (LENZ, 1994a, p. 1345). See reticulum.

*secondary stipes*. See order of stipes, primary stipes.

*second series* (of thecae) (ELLES, 1897, p. 189). The thecal series starting with $th1^2$ in a biserial, dipleural colony. See primordial series.

**selvage.** Thickened margin or rim, especially of the aperture of thecae with cortical bandages. See apertural list.

*septal bar* (BATES & KIRK, 1978, p. 437). See lateral apertural list.

**septum.** Membrane separating thecal series or thecae. See interthecal septum; median septum.

**sheet fabric** (URBANEK & TOWE, 1974, p. 4). Electron-dense, homogeneous, or very densely reticulated pellicle delimiting particular fuselli or layers.

**sicula** (LAPWORTH, 1873a, p. 501). Housing of the initial zooid of a graptolite colony, formed by the prosicula and metasicula. RICHTER (1871, p. 236) first recognized the role of the sicula and described it as the foot (Fuß in German) or attachment

(Haftorgan) in *Monograptus priodon;* radicle and initial part are similar terms used in earlier literature.

**sicular bitheca** (BULMAN, 1927b, p. 18; STUBBLEFIELD, 1929, p. 272). First bitheca of graptolite colony, associated with the sicula and visible on the obverse side of the proximal end.

*sicula side* (*Siculaseite*) (HOLM, 1895, p. 436; WIMAN, 1895, p. 263). Side of the graptoloid tubarium in which the sicula is usually partly visible and the crossing canals are covered. See obverse.

**sicular zooid.** The first zooid of a colony, secreting the sicula. It is the only zooid of a colony produced by sexual reproduction.

**sigmoidal structure** (LENZ, 1993a, p. 12, pl. 18,*5*). Solidly sclerotized, sigmoidally curved, bladelike mid-ventral structure in some Retiolitinae, running from the transverse list to the genicular list.

**sinistral** (COOPER & FORTEY 1982, p. 174). Anticlockwise growth direction of proximal thecae. See dextral.

**sinus stage** (EISENACK, 1942, p. 31); originally Sinus-Stadium (German). First stage in the development of the initial foramen for the growth of the first theca in monograptids. A deep notch is formed at the ventral side of the temporal aperture of the sicula. See lacuna stage, porus stage.

*solid axis* (BARRANDE, 1850, p. 4; HALL, 1865, p. 21); originally *axe solide* (French). Term used by earlier workers for the virgella and nema of the graptolite tubarium.

**spinoreticuli** (LENZ, 1993a, p. 15). Reticular lappets of fusellar material attached to the genicular lists at the upper apertural lists of some Retiolitidae, common in *Spinograptus, Agastograptus;* can be branched or replaced by simple spines.

**spiral thread** or **spiral line** (KRAFT, 1926, p. 222); originally Schraubenlinie (German). Spiral line of single fusellus forming the prosicula; also ligne hélicoïdale of KOZŁOWSKI (1949, p. 56). See helical line.

*stalk.* See zooidal stalk.

*statoblast.* Large, closed vesicular bodies, interpreted as enclosing hibernating zooids; also identified as sterile buds by SCHEPOTIEFF (1907b, p. 198). ALLMAN (1869b, p. 61) described what appear to be arrested buds that have not burst through the wall of the axial tubarian chamber as statoblasts. Statoblasts were originally described for bryozoans (Polyzoa) by ALLMAN (1856, p. 37). See dormant buds.

*sterile buds* (SCHEPOTIEFF, 1907b, p. 198); originally *sterile Knospen* (German). Large, closed vesicular bodies, interpreted as enclosing hibernating zooids; see dormant buds, hybernacula (SCHEPOTIEFF, 1907b, p. 200).

*Stillstandsgürtel* (KRAFT, 1926, p. 234). See annulus.

**stipe** (JAANUSSON, 1960, p. 303; BULMAN, 1970, p. 11). Single branch of a branched graptolite tubarium, sometimes used for the entire colony (in monograptids); in its strict sense it refers to the segment between successive dichotomies in multiramous forms (COOPER & FORTEY, 1982, p. 177). Earlier workers used the term frond (e.g., HALL, 1865). See branch, which is used interchangeably for stipe.

**stoloblast** (URBANEK & DILLY, 2000, p. 218). The soft tissues of the stolon and its organic sheath, including the buds in Rhabdopleuridae.

**stolon** (SCHEPOTIEFF, 1906, p. 514); originally black stolon (schwarzer Stolo in German). Thin, sclerotized sheath surrounding the unsclerotized thread of soft tissue, from which pterobranch buds originate; identical to the pectocaulus of LANKESTER (1884, p. 634).

*stolotheca* (KOZŁOWSKI, 1949, p. 24; COOPER & FORTEY, 1983, p. 212). Originally one of the three principal types of thecae in dendroid graptolites (autotheca, bitheca, stolotheca); according to COOPER and FORTEY (1983, p. 212), stolotheca and autotheca form a single continuous unit, the autotheca.

**stoma** (pl., stomata) (BATES, KOZŁOWSKA, & LENZ, 2005, p. 710). Lateral (obverse and reverse) orifices in the ancora sleeve, sometimes bounded by a chimney-like reticular wall in Retiolitidae.

*striae* (BARRANDE, 1850, p. 8). See growth lines.

**strengthening rods** (KRAFT, 1926, p. 224). See longitudinal strengthening rods.

**streptoblastic** (BULMAN, 1963b, p. 671; MITCHELL, 1987, p. 354). Type of diplograptid development in which th$1^2$, th$2^1$, and even th$2^2$ grow essentially downward, with th$1^2$ being S-shaped and growing initially upward from its origin. See prosoblastic.

**supradorsal** (COOPER, 1973, p. 52, fig. 5) In horizontal and reclined dichograptids, that portion of the sicula and theca $1^1$ that projects above the line of the dorsal margin of the diverging stipes.

**supragenicular wall** (JAANUSSON, 1960, p. 304). Thecal wall above the geniculum.

**suture.** Boundary between fuselli (zigzag suture) or in cases between thecae (arienigraptid suture).

**sympodial growth.** Type of colonial growth in which each zooid is in turn a terminal zooid of its branch. See monopodial growth.

**synrhabdosome** (RUEDEMANN, 1904, p. 483; GUTIERREZ-MARCO & LENZ, 1998). Originally defined as a colony of colonies, but now interpreted as an association of graptoloid tubaria, normally of one species (with rare exceptions), attached distally by their long, thin nemata to a particle or enmeshed in a tangle of thin nemata; rarely are tubaria of a synrhabdosome attached by the virgellae. RUEDEMANN (1895, p. 224) used the term hydrosome for the synrhabdosomes and the term rhabdosome for single tubaria.

**taeniocortex** (URBANEK & MIERZEJEWSKA, 1978, p. 639). A secondary component produced by the accumulation of well-defined, ribbonlike units, bundles of cortical fibrils, or made of a different material and sealed by a sheet or free of it.

**terminal theca.** Last theca developed in a finite tubarium, often reduced in size. See appendix.

*test* (BARRANDE, 1850). Term used by earlier workers for the tubarium of graptolites.

**theca** (pl., thecae) (LAPWORTH, 1873a, p. 502). Sclerotized tube or housing of the individual zooids of a graptolite colony. LAPWORTH (1873a) identified the theca as a chamber in which the organism sits. The term cell or cellule was often used in the earlier literature (see ELLES & WOOD, 1902, p. XVII).

**thecal aperture.** Distal opening of the thecae; earlier workers used the term orifice (and *ostia*), which is now restricted to the openings in the ancora sleeve of the Retiolitidae (Bates, Kozłowska, & Lenz, 2005, p. 709).

**thecal bridge** (Maletz, 2019c, p. 152). Development of lateral connections between adjacent stipes through thecal tubes, while stipes retain their consistent lateral distance. Thecal bridges can be formed from a single thecal tube or be complex and include more than one tube. (see dissepiments).

**thecal framework** (Bates, 1990, p. 717; Bates, Kozłowska, & Lenz, 2005, p. 710). Regular network of lists, of thecal origin (i.e., excluding the lists of the ancora sleeve) in retiolitids. It comprises the nema, virga, virgella, transverse lists, lateral apertural lists, lips, and connecting lists. It is part of the clathrium of the Retiolitidae.

**thecal gradient.** Change in thecal style along a stipe. see biform.

**thecal notation** (Elles, 1897, p. 189–190). Scheme used in the naming of thecae, which was introduced by Elles (1897) and revised most recently by Cooper and Fortey (1982, p. 175–175).

**thecorhiza** (Kozłowski, 1949, p. 141); originally thécorhize (French). Encrusting basal disk in Cyclograptidae, comprised principally of prothecae, from which metathecae and bithecae arise singly, in clusters, or as branches.

**transverse list** (Bates, Kozłowska, & Lenz, 2005, p. 710). List at the base of a thecal wall. Homologous with the aboral list of non-retiolitid graptoloids, but because the retiolitids have no interthecal septum, the tranverse list forms the distal part of the thecal aperture. Originally identified as transverse rod.

**triad (budding)** (Kozłowski, 1949, p. 23). Process of budding resulting in regularly alternating triads of autothecae and bithecae; one autotheca and one bitheca originate on alternate sides from a mother-autotheca. See Wiman rule (Kozłowski, 1949, p. 17: règle de Wiman).

**triradiate** (Bulman, 1950a, p. 68). Proximal development with three first-order stipes originating from the sicula through two successive dicalycal thecae; originally triradiate (Bulman, 1950a, p. 68); revised by Maletz (1992, p. 303). See biradiate, quadriradiate.

**triserial.** Stipes or tubaria bearing three rows of serially arranged thecae, arranged back to back. See uniserial, biserial, quadriserial.

**tubarium** (Lankester, 1884, p. 624). Dwelling or housing of the Pterobranchia, secreted from a glandular region on the cephalic shield of the pterobranch zooid; originally proposed for *Rhabdopleura* as a replacement for the inappropriate term coenoecium. Sars (1874) introduced the term polyzoarium for the genus *Rhabdopleura.* The term rhabdosome has long been used for the tubarium of extinct graptolite taxa (see Bulman, 1955, 1970). Mitchell and others (2013) reintroduced the term tubarum for extinct and extant Pterobranchia.

**tubarium midline** (Cooper & Fortey, 1982, p. 178, fig. 8; rhabdosome midline). The primary axis of symmetry of the tubarium, which passes medially through the tubarium from top to bottom. The tubarium is normally oriented, for descriptive purposes, with the sicula vertical, apex uppermost, and the tubarium midline vertical. In biserial graptolites, the midline lies along the median septum and the nema.

**tubotheca** (Kozłowski, 1970a, p. 394). Tubular structures without fuselli, on the tubaria of some Cyclograptidea and Dendroidea; interpreted as the tubes of other animals living in association with graptolite colonies.

**twig** (Wiman, 1895, p. 301); originally Zweig (German). Compound branches in some dendroid graptolites (callograptids). Wiman (1895) differentiated between Ast (branch or stipe) and Zweig (twig).

**two thecae repeat distance (2TRD)** (Howe, 1983, p. 635). Measuring unit for the thecal spacing, used most commonly for Monograptidae, but more recently introduced to diplograptid and dichograptid graptolites.

**umbellate theca** (Bulman, 1970, p. 12). Type of autotheca in some Cyclograptidae, characterized by enlarged, reflexed, umbrella-shaped hood extending back over the aperture of preceeding autotheca; initially called umbrella-like thecae (Bulman & Rickards, 1966, p. 62).

**uniserial.** Stipes or tubaria bearing a single row of serially arranged thecae. See biserial, triserial, quadriserial.

**ventral** (Kozłowski, 1949, p. 22). 1) The side of the metasicula giving rise to the rutellum and on which $th1^1$ originates (see Maletz, 1992). 2) Side of the stipe on which the thecal apertures are located; not necessarily related to position of growth of tubarium but assumed to be related to ventral side of the zooid.

**vesicular diaphragm** (Urbanek & Dilly, 2000, p. 222). Globular swelling on main stolon coinciding with the nodes or points of origin of daughter stolons in *Rhabdopleura.*

**virga** (Bates & Kirk, 1992, p. 57; Bates, Kozłowska, & Lenz, 2005, p. 710). List formed of cortical bandages laid down on the outer surface of the prosicula, which connects the nema and the virgella in Retiolitidae.

**virgella** (pl., virgellae) (Törnquist, 1897, p. 4; Kozłowski, 1949, p. 54, fig. 7F and footnote 2). Structure formed by the growth of the fuselli on the metasicula extending distally from the sicular aperture to form a spine; first described correctly by Kozłowski (1949); called the mouth-spine by Wiman (1896, p. 188). Maletz (2010a) described the evolutionary development and differentiated dorsal and ventral virgellae.

**virgellarium** (Urbanek, 1963, 175). Umbrella-shaped structure developed at the tip of the virgella in linograptids (Monograptidae); also used to describe other secondary secretions related to the virgella.

*virgellar tape* (Chen, 1986, p. 127 [English text]). Structure on the virgella, poorly defined, unclear.

*virgula* (Wiman, 1896c, p. 188). Term originally proposed for a hollow rod extending from the prosicula. Wiman (1896c, fig. 2 and 5) used the term even for the part of the virgella incorporated into the sicula in his illustrations of monograptids and diplograptids (including retiolitids). The virgula is the older term and is often used for the nema in monograptids but not for dichograptids (see Rickards, 1996). See nema, pseudovirgula.

*web structure*. See membrane.

**Wiman rule** (Kozłowski, 1949, p. 17); originally règle de Wiman (French). Process of budding resulting in regularly alternating triads of autotheca, bitheca, and stolotheca. See triad budding.

**zigzag list** (Bates, Kozłowska, & Lenz, 2005, p. 710). The zigzag list is made of clathrial lists or ancora sleeve lists.

**zigzag suture** (Richter, 1871, p. 233; Kraft, 1926, p. 227); originally Zickzacknaht, Zick-Zacknaht, Wechselzeilennaht (German). Regular connection of the fusellar half rings on the dorsal and ventral sides of the thecae.

*zooecium* (pl., *zooecia*) (Harmer, 1905, p. 10). The individual housing tubes of *Cephalodiscus* zooids; term adopted from Bryozoa terminology. See tubarium.

**zooid.** Soft-bodied individual inhabiting the theca or the tubarium (thecal zooid, sicular zooid).

**zooidal stalk** (Fowler, 1904, p. 25). Flexible connection of trunk of pterobranch zooid to stolon system; initially including the gymnocaulus.

# THE HISTORY OF GRAPTOLITE CLASSIFICATION

Jörg Maletz

Graptolite classification has experienced highs and lows during more than 250 years of research, beginning with a lot of misunderstanding and a trial-and-error method of searching to find a useful taxonomy for the graptolites. Its path has included many wrong directions along the way. From our modern perspective and understanding of fossils, this haphazard search for improvement may seem puzzling, but we need to bear in mind that scientific improvement is a natural development that comes only with the increase of data. Elles and Wood (1902, p. i–xxviii) discussed in detail the history of graptolite research up to the early twentieth century, providing important insight into the early beginnings of classification.

## THE EARLY YEARS

From the first notice of a possible graptolite published in the 1700s (von Bromell, 1727, as discussed in Tullberg, 1882b) until the 1850s, when early monographic works on graptolites began appearing, very little was written on these fossils. Linnaeus (1735) coined the term *Graptolithus* in his first edition of *Systema Naturae*. However, he did not regard *Graptolithus* as a fossil, later stating, "a fossil, properly speaking is not a graptolite" (Linnaeus, 1768, p. 173), but he intended its use for possible inorganic markings on shales. He provided an illustration of a "*Graptolitus*" in *Skånska resa* (Linnaeus, 1751), that can easily be recognized as the depiction of a graptolite (Fig. 111.1). It later became the term for all graptolites and still survives today in some form in the name for the subclass Graptolithina Bronn, 1849, even though the genus names *Graptolithus* Linnaeus, 1758 and *Graptolites* M'Coy, 1850 are now unfamiliar to us. Tullberg (1882b, p. 5) discussed the identity of the Linnaeus (1751) material and named the locality as a gravel hill near Östra Herrestad in Scania, Sweden. He identified the graptolite specimens as *Climacograptus scalaris* L. and *Monograptus triangulatus* Harkn., based on later records of graptolites from this locality, but the current whereabouts of this material is unknown. *Climacograptus scalaris* L. is recognized as *Normalograptus scalaris* (Hisinger, 1837) today (e.g., Loydell & Maletz, 2009) and provides the term for the scalariform view (ventral or apertural view) of biserial graptolites (Maletz, Bates, & others, 2014). *Demirastrites triangulatus* (Harkness, 1851) is an important index fossil for the *Demirastrites triangulatus* Biozone of the basal Aeronian, Llandovery age (Loydell, 2012).

Very little was written on graptolites during the early years of the 1800s, perhaps not surprisingly, until Wahlenberg (1821) realized that some of the Linnaeus material actually represented fossils. However, Wahlenberg accepted the Walch (1771, suppl. IVc) opinion referring the graptolites to the orthoceratites. In the following years, this was a common practice (e.g., Bronn, 1835; Geinitz, 1842). Other authors preferred to identify graptolites as polyps in a general sense (Murchison, 1839; Hisinger, 1837; Portlock, 1843). Quenstedt (1840, p. 274–276) discussed what he called 'Graptolithi Linn' under the heading Nautileen, but he suggested including these graptolites with the foraminiferans.

Brongniart (1828) described *Fucoides dentatus,* now *Levisograptus dentatus,* (see Maletz, 2011c) and *Fucoides serra*, now *Tetragraptus serra* (see Cooper & Fortey, 1982) as plants. In general, the research of graptolites was in its infancy, and paleontologists voiced quite diverse opinions on the taxonomical relationship due to the lack of sufficient data. Graptolites were related to hydroids, corals, even foraminiferans, and, not surprisingly, to plants. One can still expect that fossils described as early

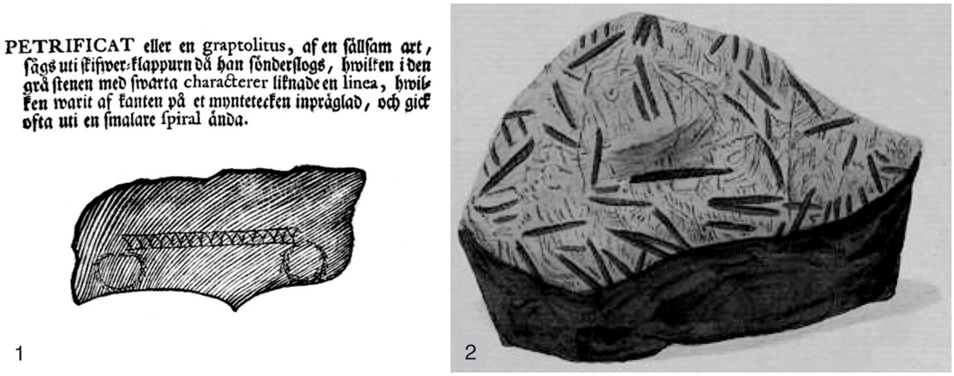


FIG. 111. Early graptolite illustrations. *1,* First illustration of *Graptolitus* (Linnaeus, 1751, p. 147); *2,* possible glacial boulder with graptolites, Stargard, Mecklenburg (Walch, 1771, pl. suppl. 4c,*5*).

land plants may turn out to represent pterobranchs, as demonstrated by the example of the Middle Ordovician *Boiophyton* from the Prague Basin (KENRICK, KVACEK, & BENGTSON, 1999).

Some confusion arose over the naming of graptolites with the introduction of the genus name *Priodon,* apparently suggested but not published by S. NILSSON (see TULLBERG, 1882b, p. 7; cited also in ELLES & WOOD, 1902, p. vii). The name was first used by BRONN (1835, p. 56), who indicated the homonymy with the genus *Priodon* CUVIER in QUOY & GAIMARD, 1825 and introduced the genus name *Lomatoceras* instead. HISINGER (1837) replaced the name *Priodon* with *Prionotus* HISINGER, 1837, which, unfortunately, is a homonym of *Prionotus* LACÉPÈDE, 1801 (Osteichtyes, Triglidae). The classification confusion finally ended with the suppression of *Lomatoceras* through ICZN Opinion 198 (1954b). In the following years, a number of additional genus name taxa were erected, but the need for an upper-level taxonomy was not evident.

## 1850–1865

Joachim BARRANDE (1850) and James HALL (1847, 1865) laid the scientific foundation of graptolite research by describing their faunas with astonishing detail and insight and developed a first taxonomic system (RUEDEMANN, 1904, p. 469). The mid-nineteenth century was the time during which geologists in many regions of the world began to describe graptolite faunas (e.g., HARKNESS, 1851; SUESS, 1851; GEINITZ, 1852; SALTER, 1852; ROEMER, 1855). Thus, knowledge increased immensely and rapidly, and the graptolites settled into their place within the Anthozoa.

M'COY (1850, p. 270) established the family Graptolitidae of the Silurian Radiata (Zoophyta) as the first family group taxon of the Graptolithina. He differentiated the uniserial taxa under the genus name *Graptolites* from the biserial ones for which he proposed the new name *Diplograpsis,* now *Diplograptus* (see MITCHELL, MALETZ, & GOLDMAN, 2009). This may be viewed as the first step in the differentiation of genus-level taxa and the starting point of graptolite taxonomy. It also demonstrated that the differentiation of uni- and biserial taxa and later, the differentiation based on the number of stipes was becoming the basic concept of graptolite classification.

BARRANDE (1850) provided a terminology for the structural features he observed and recognized two subgenera, *Monoprion* and *Diprion*, based on the number of thecal rows. Additional genera were based on the characteristic isolation of the long thecae (*Rastrites* BARRANDE, 1850) and the ancora sleeve meshes of the retiolitids (*Gladiolites* BARRANDE, 1850; *Retiolites* BARRANDE, 1850).

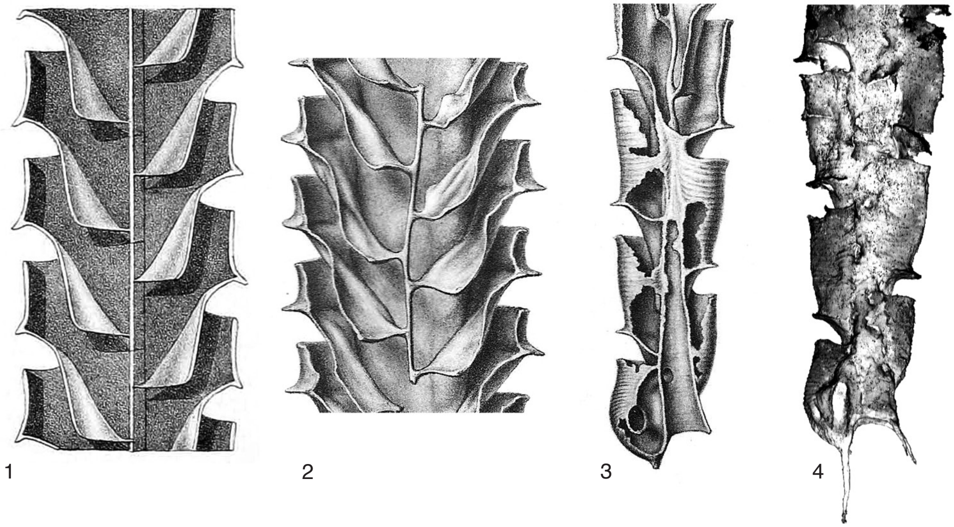


FIG. 112. Comparison of illustrations of *Geniculograptus typicalis* (HALL, 1865). *1,* Reconstruction of internal development (Hall, 1865, pl. A*9*); *2,* internal development, illustration by G. Liljevall for HOLM (Bulman, 1932c, pl. 5,*40a*); *3,* proximal end in obverse view, showing internal structure (Bulman, 1932c, pl. 5,*43*); *4,* proximal end in obverse view, SEM photo, reversed (new). Illustrations not to scale.

By the 1850s, GEINITZ (1852, p. 19) had already recognized five different genera of graptolites (*Diplograpsus, Nereograpsus, Cladograpsus, Monograpsus,* and *Retiolites*). He suggested abandoning the name *Graptolithus* because it was being used for all graptolites (in the same way that the term trilobite or ammonite was used) as an informal label for a group of organisms, an idea also advocated by GURLEY (1896). The genus *Graptolithus* was finally suppressed through ICZN Opinion 197 (1954a).

James HALL (e.g., 1847, 1865) was the second of the great observers of graptolite details. His illustrations (largely done by R. P. Whitfield) are highly accurate (Fig. 112.1), as can be confirmed from the preserved specimens in various museum collections. The illustrations, in part, are comparable to the illustrations of G. Liljevall for HOLM (Fig. 112.2–112.3) and even surpass modern SEM illustrations in clarity (Fig. 112.4). However, not even James HALL was immune to the inclusion of trace fossils as graptolites. For instance, he included *Oldhamia* FORBES, 1848 as a possible graptolite genus (HALL, 1865, p. 51), demonstrating that the scientific understanding of graptolites was not yet settled.

## 1866–1880

ELLES and WOOD (1902) described the years between 1866 and 1880 as a period in which British workers dominated graptolite research. The interval also saw the beginning of a more comprehensive biostratigraphic use of graptolite faunas. The increasing number of described genera and a better understanding of them led to the addition of higher-level taxa by NICHOLSON (1872a, 1872b) and LAPWORTH (1873a, 1873b), but the general structure of the taxonomic tree of the graptolites remained fairly simple (Fig. 113). The construction of the stipes from one, two, or more rows of thecae became the main character used for differentiation of groups within the graptolites. NICHOLSON (1872b, p. 101) used the Graptolitidae at the level of a subclass of the Hydrozoa and differentiated the sections Monoprionidae, Diprionidae, and Tetraprionidae based on the number of back-to-back attached stipes (uniserial, biserial, and quadriserial in modern terms). LAPWORTH (1873a, 1873b)

| Nicholson, 1872 | Lapworth, 1873a |
|---|---|
| Class Hydrozoa | Hydroida |
| sub-class Graptolitidae | Rhabdophora Allman, 1872 |
| | Section I Graptolitidae |
| section Monoprionidae | Monoprionidae Hopkinson |
| *Graptolithus, Didymograpsus, Tetragrapsus, Dichograpsus, Loganograpsus, Pleurograpsus, Coenograpsus (=Helicograpsus), Cyrtograpsus, Rastrites* | Families |
| | Monograptidae<br>Nemagraptidae<br>Dichograptidae |
| | Mono-di-prionidae |
| | Family |
| | Dicranograptidae |
| section Diprionidae | Diprionidae Hopkinson |
| *Diplograpsus, Climacograpsus, Dicranograpsus, Retiolites, Trigonograpsus, Retiograpsus* | Family |
| | Diplograptidae |
| section Tetraprionidae | Tetraprionidae Hopkinson |
| | Family |
| *Phyllograpsus* | Phyllograptidae |
| incertae sedis | Section II Retioloidea |
| *Thamnograpsus, Buthograpsus, Inocaulis, Corynoides* | Families |
| | Glossograptidae |
| | Retiolitidae |

FIG. 113. Comparison of the graptolite taxonomy of LAPWORTH (1873a, 1873b) and NICHOLSON (1872b) (new).

assembled the graptolites under the term Rhabdophora ALLMAN, 1872 and differentiated the Graptolitidae M'COY, 1850 and the Retioloidea LAPWORTH, 1873b as two sections, each with a number of families (Fig. 113). The main difference between the two was LAPWORTH'S addition of the Mono-diprionidae (family Dicranograptidae) and the section II Retioloidea (which included Glossograptidae and Retiolitidae), taxa not considered by NICHOLSON (1872b). NICHOLSON (1872a) and ALLMAN (1872) discussed the relationships of the graptolites and the extant pterobranchs (known only from *Rhabdopleura* at the time) and came to the conclusion that the graptolites were highly aberrant hydrozoans.

The classifications of LAPWORTH and NICHOLSON are not too different from TULLBERG'S (1883) classification, but TULLBERG (1883, p. 12) introduced a number of new taxa with the Monophyontes, Monoamphiphyontes, and Amphiphyontes, which were not accepted by the community and quickly fell into disuse.

The most important aspect of graptolite research in this era became the demonstration of the biostratigraphical use of the graptolite faunas (LAPWORTH, 1878, 1879b, 1879c, 1879d, 1879e, 1880b, 1880c, 1880d, 1880e, 1880f), even though graptolites had been used for biostratigraphic purposes earlier (HALL, 1850; NICHOLSON, 1868b). A decade later, LAPWORTH'S (1878) demonstration of the use of graptolite faunas in the thick greywacke succession of the Moffat Series was a milestone in stratigraphic and paleontological research (see FORTEY, 1993, fig. 1). During the nearly 150 years since, our biostratigraphic resolution has increased considerably (LOYDELL, 2012), yet the basic succession of LAPWORTH is still recognizable and has changed very little. Today, graptolite biostratigraphy is a standard for working

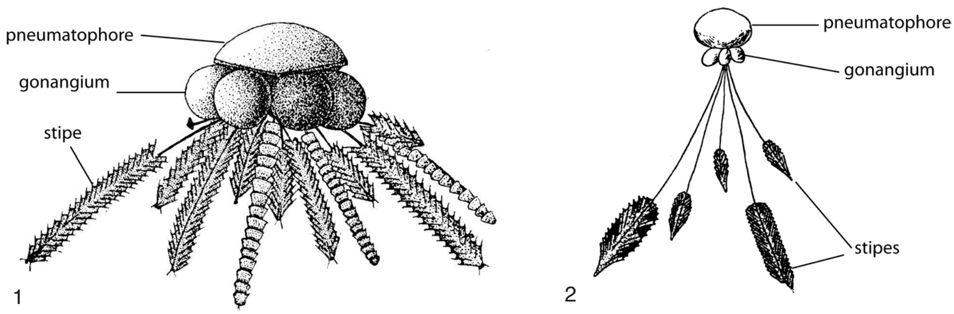


FIG. 114. Historical graptolite reconstructions. *1, Diplograptus pristis* HALL, 1865 (non HISINGER, 1837) (now *Orthograptus quadrimucronatus* (HALL, 1865) (adapted from Ruedemann, 1895, pl. 2); *2, Petalolithus folium* (HISINGER, 1837) (adapted from Frech, 1897, fig. 193). It should be noted that the gonangia and the pneumatophore have never been verified from fossil material and may not exist (Maletz, 2015).

with Paleozoic sedimentary successions and has become an important tool for geological exploration (e.g., PODHALAŃSKA, 2013).

## 1880–1918

In the years from 1880 to 1918, graptolite research was so dominated by the Scandinavian authors HOLM, MOBERG, TÖRNQUIST, and TULLBERG, that the period may be termed the Scandinavian Period. It is characterized by the detailed taxonomic and biostratigraphic description of very well preserved Ordovician and Silurian graptolite faunas of Scandinavia. The work of HOLM (1895) on chemically isolated, three-dimensionally preserved graptolites is a milestone in graptolite research, even though GÜMBEL (1878) was the first to observe graptolites chemically isolated from the surrounding rocks. This method provided much better information on the tubarium construction than the usual flattened shale material or the strongly tectonized specimens available to most researchers.

Much of HOLM's material of chemically isolated Ordovician graptolites from Scandinavian limestones was published posthumously by BULMAN (e.g., 1932c, 1933a, 1936a). The specimens possess fine details up to the presence of cortical bandages on the tubarium surface and provide, for the first time, detailed information on the proximal development of the graptolites. HOLM also worked with serial sections to understand the development of material trapped in the sediments.

FRECH (1897) introduced the differentiation into the Axonophora and the Axonolipa, based on whether the graptolite had development of the nema as a leading rod of the colony or lacked an extended nema. He identified the nema as an axis to which the thecae were attached in the Axonophora. According to FRECH (1897, p. 568), this axis was lacking in the Axonolipa. Even though he misinterpreted part of the graptolite colonies and their development (see Fig. 114.2), following the interpretation of the synrhabdosomes of RUEDEMANN (1895), the Axonophora were reintroduced into the graptolite classification by MALETZ, CARLUCCI, and MITCHELL (2009).

RUEDEMANN (1895) probably wrote the most influential paper of the period. His reconstruction of *Orthograptus quadrimucronatus* (HALL, 1865) under the name *Diplograptus pristis* presented a so-called supercolony with basal cyst or pneumatophore, gonangia, and numerous stipes. He also provided a dorsal and lateral view of a similarly reconstructed supercolony of *Diplograptus ruedemanni* (GURLEY, 1896). This interpretation (Fig. 114.1) may be regarded as the most discussed and most copied graptolite illustration ever. It still appears in modern paleontology textbooks (e.g., Prothero, 2013), even though the gonangia and pneumatophore have not been verified from fossil material (Maletz, 2015).

## THE TWENTIETH CENTURY

The twentieth century was dominated by detailed research on graptolite taxonomy and biostratigraphy and the recognition of the worldwide distribution of graptolite faunas. Graptolites are now known from all continents except Antarctica. The use of graptolite biostratigraphy in economical geology often led to increased research. The Bendigo and Castlemain goldfields of Victoria, Australia (see Hall, 1895; Phillips & Hughes, 1996) are the reason for the detailed Ordovician graptolite biostratigraphy established for the region (Harris & Thomas, 1938a; VandenBerg & Cooper, 1992). Research centers developed with a high number of scientists concentrating on graptolite research in Australia (T. S. Hall, Harris, Thomas); China (Hsü, Mu); Europe (Bouček, Bulman, Eisel, Jaeger, Kozłowski, Rickards); North America (Clark, Decker, Ruedemann); Russia (Obut, Sobolevskaya, Tzaj); and many other regions. The increasingly detailed work and mounting data led to two editions on graptolites published by the *Treatise on Invertebrate Paleontology* (Bulman, 1955, 1970), but taxonomic understanding diverged due to language barriers, lack of communication, and incompatible taxonomic concepts (see Rigby, 1986; Maletz, 2014b).

The constructional morphology of graptolites became important after the recognition of proximal-end development as a key to classification. This was possible with the availability of increasing amounts of chemically isolated graptolites and relief material. Kozłowski (1938, 1949) became one of the leading-edge scientists, describing numerous benthic graptolite taxa from material chemically isolated from cherts. Graptolites were now routinely identified based on their proximal-end construction, and numerous proximal-end development types were established (e.g., Fortey & Cooper, 1986; Mitchell, 1987; Melchin, 1998). Understanding of the distribution patterns of graptolite faunas along with the recognition that not all faunal elements are distributed worldwide, led to the development of the concept of graptolite biogeography (e.g. Skevington, 1969; Goldman & others, 2013).

## CLADISTICS

In recent years, graptolite taxonomy and evolution have received a much-needed boost as cladistic methods became increasingly popular (e.g., Fortey & Cooper, 1986; Mitchell, 1987; Lenz & Melchin, 1997; Maletz, Carlucci, & Mitchell, 2009; Melchin & others, 2011; Štorch & others, 2011; Melchin, Lenz, & Kozłowska, 2017). This new method of analyzing graptolite construction and attaining information for a phylogenetic interpretation has dramatically changed our understanding of graptolite taxonomy and evolution. The concept centers around homologous characters and the monophyly of clades (Hennig, 1950, 1965). In the end, it is not really a new concept (see, for instance, Gegenbaur, 1870, p. 78–81), but the idea has never before been promoted so vehemently. Any taxonomic approach searches for homologous characters for classification but does not necessarily state this explicitly. Certainly, even Linnaeus (1758) thought about meaningful characters. Thus, early graptolite taxonomies used easily recognizable characters such as the number of stipes as sorting features. The Monoprionidae and Diprionidae were established as early as the nineteenth century (Hopkinson, 1869), and even now we use these in a modified sense as the Monograptidae and Diplograptidae. In general, they were correct and precise at the time and were based on useful characters, but "the devil is in the details," as the saying goes.

Apart from the latest compilations of the *Treatise* (Bulman, 1970), a comprehensive modern analysis of all graptolites does not exist. Mu and others (2002) provided the latest overview on current graptolite taxonomy in their compilation of all graptolite faunas from China. They modified the taxonomic system slightly by adding and rejecting a number of family-level taxa. The latest classification (MALETZ, 2014b) provides a combination of cladistic and conservative phenetic taxonomy, keeping up with the established taxonomic groups but placing them on firmer ground through cladistic analyses when possible, while also accepting analyses from constructional morphology on the graptolite tubaria. See *Classification of the Hemichordata,* which follows on page 188.

# CLASSIFICATION OF THE HEMICHORDATA

Phylum Hemichordata Bateson, 1885a, p. 111
?Class Planctosphaeroidea, van der Horst, 1936, p. 612
Class Enteropneusta Gegenbaur, 1870, p. 158
Stem group taxa (no family assignment)
Crown group taxa
Family Harrimaniidae Spengel, 1901, p. 215
Family Spengelidae Willey, 1899, p. 239
Family Ptychoderidae Spengel, 1893, p. 359
Family Torquaratoridae Holland & others, 2005, p. 374
Class Pterobranchia Lankester, 1877, p. 448
Subclass Cephalodiscida Fowler, 1892b, p. 297
Family Cephalodiscidae Harmer, 1905, p. 5
Subclass Graptolithina Bronn, 1849, p. 149
Family Rhabdopleuridae Harmer, 1905, p. 5
Family Cysticamaridae Bulman, 1955, p. 42
Family Wimanicrustidae Bulman, 1970, p. 52
Family Dithecodendridae Obut, 1964, p. 306
Family Cyclograptidae Bulman, 1938, p. 22
Order Dendroidea Nicholson, 1872b, p. 101
Family Dendrograptidae Roemer in Frech, 1897, p. 568
Family Callograptidae Hopkinson, in Hopkinson & Lapworth, 1875, p. 663
Family Mastigograptidae Obut & Sobolevskaya, 1967, p. 58
Order Graptoloidea Lapworth in Hopkinson & Lapworth, 1875, p. 633
Suborder Graptodendroidina Mu & Lin in Lin, 1981, p. 244
Family Anisograptidae Bulman, 1950, p. 79
Suborder Sinograptina Mu, 1957, p. 387
Family Sigmagraptidae Cooper & Fortey, 1982, p. 259
Family Sinograptidae Mu, 1957, p. 387
Family Abrograptidae Mu, 1958, p. 261
Suborder Dichograptina Lapworth, 1873b, table 1 facing p. 555
Family Dichograptidae Lapworth, 1873b, table 1 facing p. 555
Family Didymograptidae Mu, 1950, p. 180
Family Pterograptidae Mu, 1950, p. 180
Family Phyllograptidae Lapworth, 1873b, table 1 facing p. 555
Suborder Glossograptina Jaanusson, 1960, p. 319
Family Isograptidae Harris, 1933, p. 85
Family Glossograptidae Lapworth, 1873b, table 1 facing p. 555
Suborder Axonophora Frech, 1897, p. 607
Infraorder Diplograptina Lapworth, 1880e, p. 191
Family Diplograptidae Lapworth, 1873b, table 1 facing p. 555
Family Lasiograptidae Lapworth, 1879c, p. 454
Family Dicranograptidae Lapworth, 1873b, table 1 facing p. 555
Family Climacograptidae Frech, 1897, p. 607
Infraorder Neograptina Štorch & others, 2011, p. 368
Family Normalograptidae Štorch & Serpagli, 1993, p. 14
Superfamily Retioloidea Lapworth, 1873b, table 1 facing p. 555
Family Neodiplograptidae Melchin & others, 2011, p. 296
Family Retiolitidae Lapworth, 1873b, table 1 facing p. 555
Superfamily Monograptoidea Lapworth, 1873b, table 1 facing p. 555
Family Dimorphograptidae Elles & Wood, 1908, p. 347
Family Monograptidae Lapworth, 1873b, table 1 facing p. 555

# PHYLUM HEMICHORDATA

JÖRG MALETZ and CHRISTOPHER B. CAMERON

## Phylum HEMICHORDATA Bateson, 1885

[Hemichordata BATESON, 1885a, p. 111; *nom. transl. ex* class Hemichordata BATESON, 1885a, p. 111, HYMAN, 1959, p. 74] [=Klasse Helminthomorpha GROBBEN, 1908, p. 505, *non* Helminthomorpha POCOCK, 1887 (Diplopoda, millipedes); =subphylum Stomochordata DAWYDOFF, 1948, p. 367]

Hemichordate synapomorphies include a tripartite body; a muscular-secretory-locomotory preoral organ (enteropneust proboscis or pterobranch cephalic shield) that encloses a heart-kidney coelomic complex, including a stomochord; a collar with paired valved mesocoel ducts and pores; and a trunk that includes a ventral postanal extension of the metacoels (enteropneust juvenile tail or pterobranch stalk). *Cambrian, Terreneuvian* (*Fortunian*)–*Holocene* (extant): worldwide.

## ?Class PLANCTOSPHAEROIDEA van der Horst, 1936

[Planctosphaeroidea VAN DER HORST, 1936, p. 612]

The species *Planctosphaera pelagica* SPENGEL, 1932 is based on a large, spherical larva that may exceed 25 mm in diameter and is the sole member of the monotypic class Planktospharoidea. The surface is laced with paired and ramified food grooves lined by two continuous ciliated bands used in filter feeding (HART, MILLER, & MADIN, 1994). The viscera are clearly visible through the jelly interior and include a mouth that is located internal to paired stomodeal canals, followed by an esophagus, stomach, and intestine with a terminal anus. It has a triangular-shaped protocoel with a posterior extending duct and pore. A muscle strand connects the protocoel with an apical nerve plate, and from the other two corners paired horns extend anteriorly along the stomach. Paired mesocoels and metacoels are located on either side of the intestine. Except for the paired stomodeal canals to the mouth and the horns of the protocoel, all of these features are present in enteropneust tornaria. Other apomorphies include a ventral depression that extends into the larva as paired boot-shaped diverticula positioned on either side of the intestine and posterior stomach.

**Planctosphaera** SPENGEL, 1932, p. 4 [**P. pelagica;* OD]. Hypertrophied, spherical tornaria-type larva with bilateral symmetry; gut system U-shaped; mouth and anus close together on ventral side; surface covered by a complex ciliated band; internal organs occupy only a small part of the whole sphere. *Holocene* (extant): Atlantic Ocean, Pacific Ocean (no known fossil record).——FIG. 115. **P. pelagica* SPENGEL, Bermuda, western Atlantic Ocean, scale bar, 5 mm (Hart, Miller, & Madin, 1994, fig. 1B).

The taxonomic and phylogenetic affinities of *Planctosphaera pelagica* are not clear but its morphology is similar to that of enteropneust tornaria (SPENGEL, 1932; VAN DER HORST, 1936) and its deep-water collection localities suggest that it may be a hypertrophied tornaria that has not undergone metamorphosis due to absence of a settlement cue (HADFIELD & YOUNG, 1983). HADFIELD (1975) and HALANYCH, TASSIA, and CANNON (2019) regarded the taxon as the giant larva of a deep-water enteropneust, thus, probably of the Torquaratoridae.

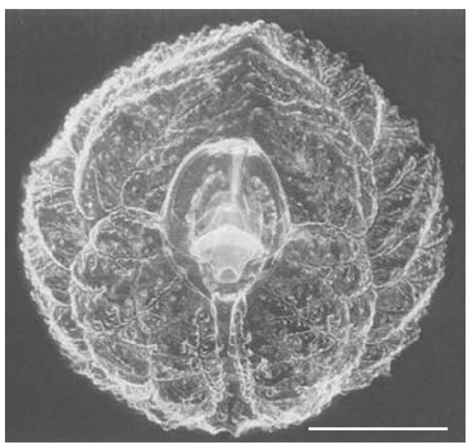

FIG. 115. Class Planctosphaeroidea (p. 189).

A few specimens of *Planctosphaera pelagica* were collected from deep-water trawls in the Bay of Biscay (Spengel, 1932; Damas & Stiasny, 1961) and other regions of the Atlantic Ocean (see Scheltema, 1970, fig. 1), but it is also known from shallow water adjacent to Bermuda (Hart, Miller, & Madin, 1994). Specimens from the Pacific Ocean are from a depth of 75–500 m near O'ahu in the Hawaiian islands (Hadfield & Young, 1983). Scheltema (1970) suggested this was a warm-water species due to the biogeographic distribution of the few known specimens. Hadfield and Young (1983) suggested a worldwide distribution of this organism probably originating from abyssal depths. Hart, Miller, and Madin (1994) described suspension feeding of a single living larva from surface waters near Bermuda in the western Atlantic Ocean.

# CLASS ENTEROPNEUSTA

Christopher B. Cameron

## Class ENTEROPNEUSTA Gegenbaur, 1870

[*nom. correct.* Haeckel, 1879, p. 469 *pro* Enteropneusti Gegenbaur, 1870, p. 158]

Free living, solitary worms ranging from lengths of less than a millimeter to 1.5 meters; entirely marine; body tripartite, with proboscis, collar, and trunk; proboscis coelom contains heart-kidney-stomochord complex; preoral ciliary organ posterior-ventral; collagenous Y-shaped nuchal skeleton extends from proboscis through neck before bifurcating into paired horns in collar; paired dorsal perihaemal coeloms associated with collar dorsal blood vessel; anterior trunk pharynx perforated with paired gill slits that connect via atria to external gill pores; mesocoel ducts connect collar coeloms to first pair of gill pores atria; larvae possess locomotory ciliated band (telotroch), and when tornaria present, apical plate retractor muscle. *Cambrian* (*Miaolingian, Wuliuan*)*–Holocene* (extant): worldwide.

The class Enteropneusta is differentiated among four living families: the Harrimaniidae, Spengelidae, Ptychoderidae, and Torquaratoridae, based in large part on the structure of the heart-kidney coelomic complex, gills, gonads, liver sacs, and diverticula of the coelomic compartments. The modern families are a crown group clade with respect to the Cambrian fossil stem group, which includes *Oesia disjuncta* Walcott, 1911 and *Spartobranchus tenuis* (Walcott, 1911).

The following systematic descriptions are limited to eight genera with fossil evidence—three from the stem group, and five from the crown group. Excluded genera are only known from extant species. What we understand at this point, based on the pattern of appearance of these seven fossil acorn worm species, is: 1) the evolution of acorn worms is characterized by an evolutionary stasis—the harrimaniid body plan of *Spartobranchus tenuis* appears in the Cambrian and persists to this day in the Harrimaniidae, including *Saccoglossus* (Fig. 117); 2) this body plan was followed by that of a spengelid in *Mazoglossus ramsdelli* from the Pennsylvanian (Bardack, 1997) and then by a torquaratorid, characterized by collar lips, in a Lower Triassic trace fossil (Twitchett, 1996); and 3) the complex ptychoderid body plan appeared last in *Ptychodera callovianum* from the Upper Jurassic (Alessandrello, Bracchi, & Riou, 2004; Cameron, 2016) (Fig. 117).

## STEM GROUP TAXA

The stem group enteropneusts include tube-dwelling taxa with a vermiform body that consists of a proboscis, a collar, and a trunk with a pharynx framed by multiple, paired, circumferential gill bars and slits.

**Gyaltsenglossus** Nanglu, Caron, & Cameron, 2020, p. 4238 [**G. senis;* OD]. Vermiform with a maximum length of ~2 cm; body consists of an elongate, ovoid proboscis, a crown of six feeding arms, a cylindrical trunk, and a round posterior structure; feeding arms possess roughly 15 pairs of symmetrical tentacles; gut is straight; anus terminates immediately before the posterior structure. *Cambrian* (*Miaolingian, Wuliuan, Bathyuriscus* Biozone–*Elrathia* Biozone): Canada.——Fig. 116,*3. *G. senis,* holotype, ROMIP 65606, scale bar, 2 mm (Nanglu, Caron & Cameron, 2020, fig. 1).

**Oesia** Walcott, 1911, p. 132 [**O. disjuncta;* OD [=*Margaretia* Walcott, 1931, p. 2 (type, *M. dorus,* OD), Nanglu & others, 2016, p. 2] Tripartite body with proboscis, collar, and trunk; trunk unusual, possessing extensive pharynx and lacking esophagus and intestine; posterior grasping appendage; tubes, fibrous with spirally arranged openings. *Cambrian* (*Miaolingian, Wuliuan, Bathyuriscus* Biozone–*Elrathia* Biozone): Canada.——Fig. 116,*2.* **O. disjunta,* USNM 57630, lectotype (selected by Szaniawski, 2005, p. 2), one of three specimens illustrated by Walcott (1911), Burgess Shale, Walcott Quarry, British Columbia, Canada, scale bar, 10 mm (new, photo by J.-B. Caron).

**Spartobranchus** Caron, Conway Morris, & Cameron, 2013, p. 503 [**Ottoia tenuis* Walcott, 1911, p. 130; OD]. Vermiform, maximum length 10 cm; body comprised of short proboscis, collar, pharyngeal area with as many as 40 pairs of gill and tongue bars; elongate posterior trunk ending in bulbous unit; gut straight, anus terminal; approximately one-quarter of specimens associated with tube of organic walls; tube varies from straight, completely circular, to helicoidal, and sometimes branching; no more than one individual per tube has been observed. *Cambrian* (*Miaolingian, Wuliuan, Bathyuriscus* Biozone–*Elrathia* Biozone): Canada.——Fig. 116,*1a–b.* **S. tenuis* (Walcott); *1a,* USNM 108494, lectotype (selected by Caron, Conway Morris, & Cameron, 2013, supplement 1, from a small number of specimens supposedly collected by Walcott [1911], who described but never illustrated *Ottoia tenuis,* and the whereabouts of his material is unknown), specimen missing proboscis and terminal portion of trunk, polarized light; *1b,* complete specimen, ROM 62123; scale bars, 3 mm in 1*a,* 2 mm in *1b* (Caron, Conway Morris, & Cameron, 2013, fig. 1).

## CROWN GROUP TAXA

### Family HARRIMANIIDAE Spengel, 1901

[Harrimaniidae Spengel, 1901, p. 215]

Simple morphology, largely characterized by features it lacks; no dorsal collar nerve roots arising from the collar nerve cord; gills lack synaptaculae that bridge primary and secondary gill bars; trunk lacks hepatic sacs, circular muscle fibers, and lateral septa, only dorsal and ventral septa present; intestinal pores only rarely present; posterior projecting horns of Y-shaped proboscis skeleton extend at least to middle of collar; longitudinal proboscis musculature may be arranged diffusely, in radial plates, or in

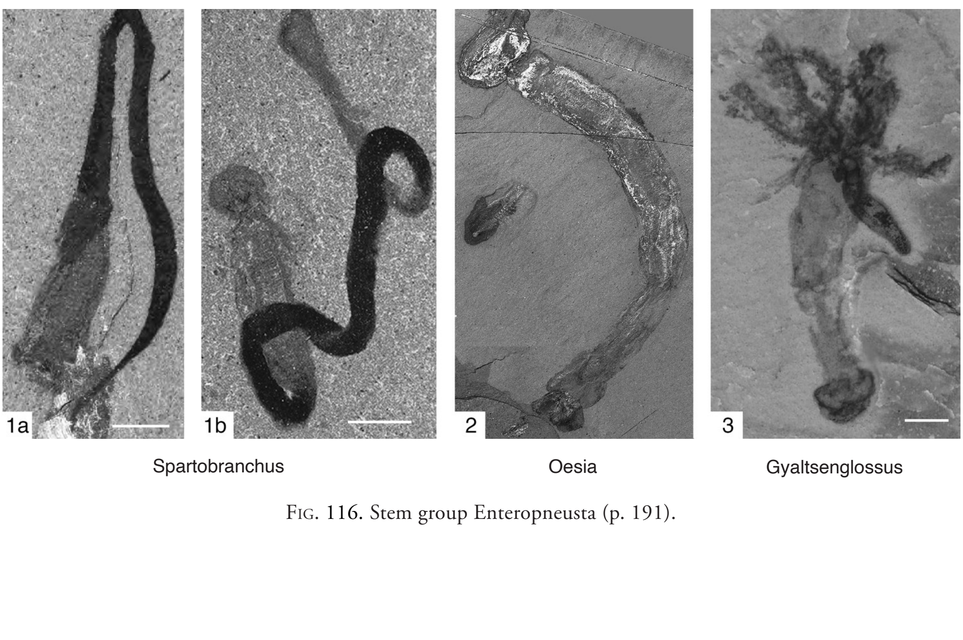


Fig. 116. Stem group Enteropneusta (p. 191).

concentric rings; development via short-lived, non-feeding larvae that become juveniles with adhesive post-anal tail. *Carboniferous* (*Pennsylvanian, Moscovian*)–*Holocene* (extant): worldwide.

The Harrimanidae comprises ten living genera, including one (*Saxipendium* WOODWICK & SENSENBAUGH, 1985) that was previously assigned to its own family (DELAND & others, 2010; WORSAAE & others, 2012). *Saccoglossus* is the most speciose and familiar genus (CAMERON, DELAND, & BULLOCK, 2010). Its longitudinal proboscis musculature is arranged in concentric rings, whereas other genera may be arranged diffusely (e.g., *Mesoglossus*) or in radial plates (e.g., *Protoglossus* VAN DER HORST, 1939).

**Saccoglossus** SCHIMKEWITSCH, 1892, p. 2 [**Balanoglossus mereschkowskii* WAGNER, 1885, p. 46; OD] [=*Balanoglossus* (*Dolichoglossus*) SPENGEL, 1893, p. 360 (type, *D. kowalewskii* AGASSIZ, 1873, SD SPENGEL, 1901, p. 215)]. Proboscis long; longitudinal muscle fibers of proboscis arranged in several concentric rings; middorsal longitudinal groove may be present; collar usually very short compared to proboscis; dorsal interbranchial genital ridges and dorsal gonads absent but lateral extrabranchial genital ridges may be present; intestinal pores typically present; perihaemal cavities always present; peribuccal cavities usually present. [Many species favor quiet muddy-sandy flats not far from the mouth of a bay, living in semi-permanent and helical-shaped burrows and throwing up low conical mounds of quasi-spiral fecal castings. See CAMERON, DELAND, and BULLOCK, 2010; also see Fig 4.2.] *Carboniferous* (*Pennsylvanian, Moscovian*)–*Holocene* (extant): worldwide.——FIG. 117,*1. S. testa* CAMERON, 2016, holotype, FMNH PE 45216, one of two counterparts, scale bar, 1 cm (new).

**Megaderaion** ARDUINI, PINNA, & TERUZZI, 1981, p. 105 [**M. sinemuriense;* OD]. Elongate worm divided into elongate, rounded, and ogival proboscis; collar wider than long, tapering trunk; single specimen small (2 cm) lacking gonadal wings, hepatic sacs, and enlarged branchial region, characteristic of family Harrimaniidae; resembles *Mesoglossus,* with medium-long proboscis. [See DELAND & others, 2010.] *Lower Jurassic* (*Sinemurian, Coroniceras bucklandi* Biozone): Italy.——FIG. 117,*2. *M. sinemuriense,* holotype, i751, Museo Civico di Storia Naturale di Milano, scale bar, 2 mm (Arduini, Pinna, & Teruzzi, 1981, fig. 1).

## Family SPENGELIDAE Willey, 1899

[Spengelidae WILLEY, 1899, p. 239] [=Glandicipitidae SPENGEL, 1901, p. 215]

Anterior vermiform process of stomochord present in all members; skeletal horns usually extend over whole length of collar; dorsal nerve roots arising from collar nerve cord rare; lateral septum absent; hepatic caeca and synapticula may or may not be present; circular muscle fiber layer positioned inside longitudinal muscle layer in trunk. *Carboniferous* (*Pennsylvanian, Moscovian*)–*Holocene* (extant): worldwide.

In the cases where development has been documented, Spengelidae species have a tornaria larva (CAMERON & PEREZ, 2012). The family includes four living genera (see VAN DER HORST, 1939; CAMERON & PEREZ, 2012). CAMERON (2016) referred *Mazoglossus ramsdelli* to the family Spengelidae, thus, extending an extant enteropneust family to include a Carboniferous fossil species.

**Mazoglossus** BARDACK, 1997, p. 89 [**M. ramsdelli;* OD]. Small (specimens less than 10 cm total length); recognizable as an enteropneust by outline shape of proboscis, collar, and trunk. *Carboniferous* (*Pennsylvanian, Moscovian*): USA (Illinois).——FIG. 117,*3. *M. ramsdelli,* FMNH PE 23053, one of two counterparts, complete specimen, scale bar, 1 cm (adapted from Cameron, 2016, fig. 2C).

## Family PTYCHODERIDAE Spengel, 1893

[Ptychoderidae SPENGEL, 1893, p. 359] [=Balanoglossidae WILLEY, 1899, p. 239]

Lateral septa in trunk; invariable absence of abdominal pores; lack of vermiform process of stomochord; dorsal nerve roots in collar present; skeletal horns rarely reach beyond anterior half of collar; synapticulae form bridges between primary and secondary gill bars in pharynx, hepatic caeca usually present; dorsolateral ciliated grooves in abdominal part of alimentary canal; circular muscle fibers in trunk, usually outside the longitudinal fibers; development occurs through typical tornaria larva. [CAMERON & OSTIGUY, 2013, p. 144.] *Middle Jurassic* (*Callovian*)–*Holocene* (extant): worldwide.

Ptychoderidae includes four extant genera, including the familiar *Balanoglossus*. *Mesobalanoglossus* is herein included in the Ptychoderidae. CAMERON (2016) referred the Middle Jurassic *Megaderaion callovianum*

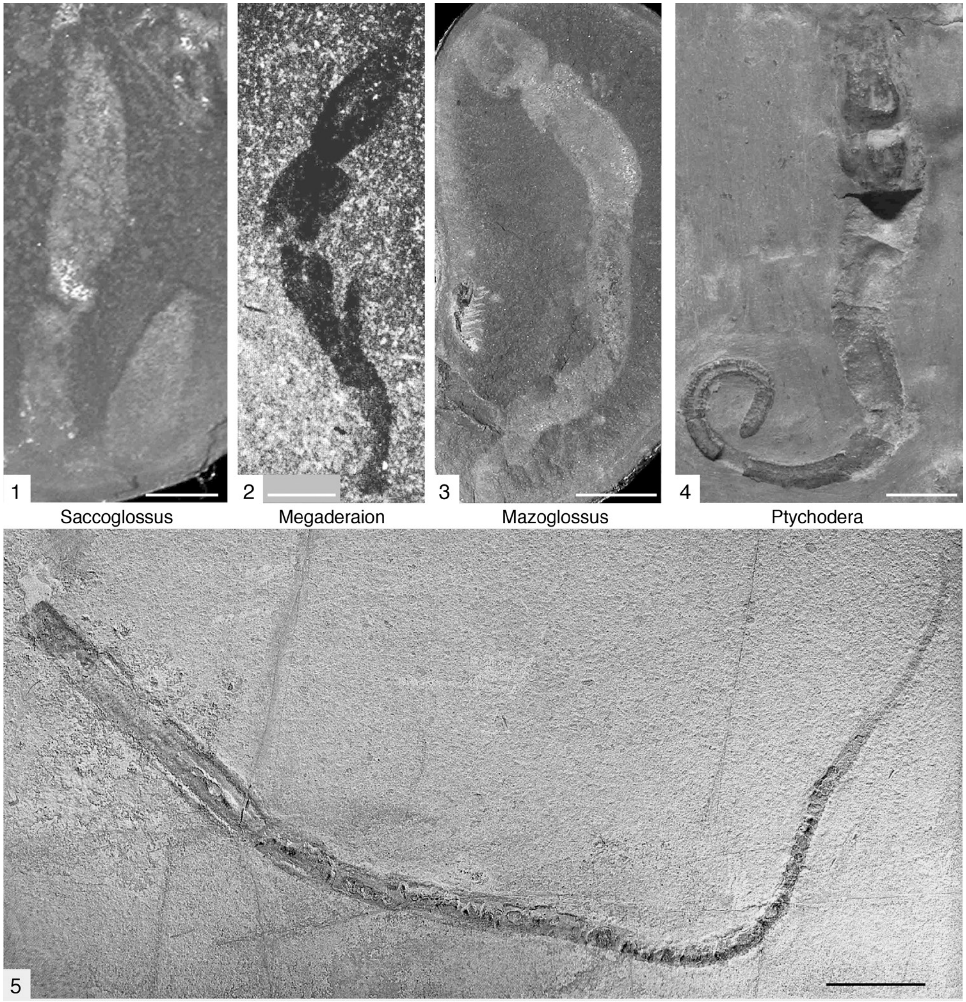


FIG. 117. Harrimaniidae (*1–2*), Spengelidae (*3*), Ptychoderidae (*4–5*) (p. 192–193).

ALESSANDERELLO, BRACCHI, & RIOU, 2004 to the Ptychoderidae. The species is herein included in the genus *Ptychodera*.

**Ptychodera** ESCHSCHOLTZ, 1825, p. 740 [**P. flava;* M]. As for family, except gill pores open by long slits, whereas those of *Balanoglossus* open by small pores. Middle Jurassic (Callovian)–Holocene (extant). ——FIG. 117,*4. P. callovianum,* (ALESSANDRELLO, BRACCHI & RIOU, 2004), holotype, MNHN L.P.M.-B. 48352, scale bar, 5 mm.

**Mesobalanoglossus** BECHLY & FRICKHINGER in FRICKHINGER, 1999, p. 77 [**M. buergeri;* OD] Single specimen, 68.8 cm long, with diminutive proboscis, collar, and long trunk with bristles interpreted as gill bars; trunk tapers posteriorly, anterior wide part interpreted as gonadal wings. *Upper Jurassic* (*lower Tithonian, Hybonoticeras hybonotum* Biozone): Germany.——FIG. 117,*5. *M. buergeri,* holotype, scale bar, 5 cm (Bechly & Frickhinger in Frickhinger, 1999, fig. 144).

## Family TORQUARATORIDAE Holland & others, 2005

[Torquaratoridae HOLLAND & others, 2005, p. 374]

Proboscis broad, short, dome shaped; collar wide, usually embellished with lateral lips; body semi-transparent, frequently brightly colored; muscular system poorly developed; collagenous proboscis skeleton

and gill bars greatly reduced; proboscis skeletal horns absent from all species but *Torquarator bullocki* (HOLLAND & others, 2005). *Lower Triassic* (*upper Olenekian*)–*Holocene* (extant): worldwide.

The family Torquaratoridae is exclusive to the deep sea (HOLLAND & others, 2005, 2009; HOLLAND, KUHNZ, & OSBORN, 2012). There are seven genera (JABR, ARCHAMBAULT, & CAMERON, 2018; Ezhova, 2021).

Fossil specimens of the Torquaratoridae are unknown, but a single resting trace from the Lower Triassic (Olenekian) Werfen Formation of northern Italy (TWITCHETT, 1996) suggests, through its characteristic shape, the presence of the family in the Mesozoic (Fig. 118).

FIG. 118. Resting trace of torquaratorid enteropneust, scale bar, 1 mm (Twitchett, 1996, fig. 2.1).

# PTEROBRANCHIA

JÖRG MALETZ and CHRISTOPHER B. CAMERON

## Class PTEROBRANCHIA Lankester, 1877

[Pterobranchia LANKESTER, 1877, p. 448]

Fixed, sedentary to planktic organisms with communal or colonial zooids divided into three regions: preoral lobe (cephalic shield), collar, and trunk; collar extends to form one or more pairs of arms, each bearing double row of ciliated tentacles; trunk elongated posteriorly to form a zooidal stalk that extends to pectocaulus as interconnection between zooids in colonial forms; soft gymnocaulus connects developing buds and permanent terminal zooid in *Rhabdopleura* ALLMAN, 1869; external organic (?collagen, keratin, or chitin) housing or domicile (tubarium) compried of a series of tubes built from sequential addition of rings or half rings of organic material (fusellum) in most taxa. Cambrian (Series 2, Stage 3–4, *Olenellus* Zone)–*Holocene* (extant): worldwide in marine environments.

### PTEROBRANCHIA *incertae sedis*

MALETZ and STEINER (2015) included the genus *Yuknessia* WALCOTT, 1919 as *incertae sedis* in the Pterobranchia, as they were not able to recognize details supporting an inclusion in the Cephalodiscida or Graptolithina, even though they provided definite evidence of fusellar construction (see also LoDuca & others, 2015).

**Yuknessia** Walcott, 1919, p. 235 [**Y. simplex;* M]. Organisms with long, slender thecal tubes formed from organic material and bearing evidence of fusellar construction; thecal tubes may widen toward the aperture; circular attachment structures at base of tubes; no interconnection between individual tubes recognizable. *Cambrian* (*Miaolingian, Wuliuan, Bathyuriscus/Elrathina–Ptychagnostus punctuosus* Zones): Canada, USA.——Fig. 119. **Y. simplex* Walcott, 1919, USNM 35406, holotype, scale bar, 5 mm (Maletz & Steiner, 2015, fig. 15).

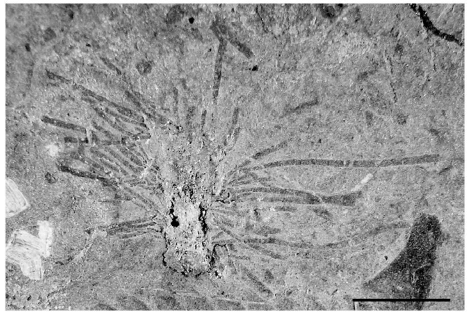

Fig. 119. Pterobranchia *incertae sedis* (p. 195).