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Graptolites: An Introduction

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What are graptolites? To many geologists, they are somewhat scratch mark-like markings on rocks that represent one of the more strange fossil groups, lacking the ferocity of the dinosaurs, the smooth elegance of the ammonites or the charisma of the trilobites. And yet, observed closely, they represent one of the most beautiful, mysterious and useful of all of the fossil groups.

Their beauty is often concealed by the unkindness of geological preservation, all too many specimens being crushed by the weight of overlying strata, or distorted by the tectonic forces that raise mountains. They are also, simply, too small for casual human observation. Many are smaller than a matchstick, and their tiny shapes can appear as mere scratch-like markings on the rocks. Others are quite large, with some umbrella-shaped colonies in the Ordovician measuring about 1 m in diameter, and some stick-like straight Silurian monograptids measuring more than 1 m in length.

But there are – more commonly than one might think – those specimens that have managed to resist the twin pressures of burial and tectonics, perhaps because a rigid mass of pyrite (fool's gold) crystallized within their remains, or because they were encased in chemically precipitated calcium carbonate or silica before they were deeply buried. These, when looked at through a hand lens, or, better, a stereo microscope, reveal a rich diversity of extraordinary, other-worldly geometric patterns, finely engineered for purposes that we still, for the most part, can only guess at. The precision of their construction, and the distinct architectures shown by different species are, of course, key to their identification (Figure 1.1) and hence to their use by geologists.

The exquisite morphological detail can, in some specimens, extend to the finest scale of observation, where minute parts of these fossils, magnified

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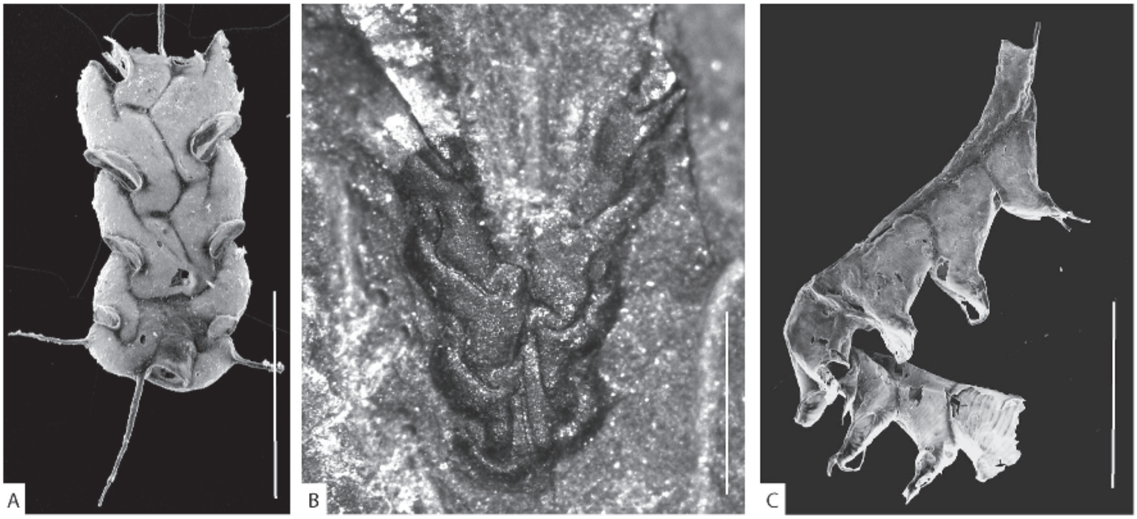
Figure 1.1 Images of well-preserved graptolites, showing the complexity and beauty of their construction. (A) *Archiclimacograptus* sp., obverse view, SEM photo, Table Head Group, western Newfoundland, Canada. (B) *Dicranograptus irregularis*, obverse view, relief specimen, Scania, Sweden. (C) *Spirograptus turriculatus* (Barrande, 1850), proximal end, SEM photo, Kallholn Shale, Llandovery, Dalarna, Sweden. Scale indicated by 1 mm long bar in each photo.



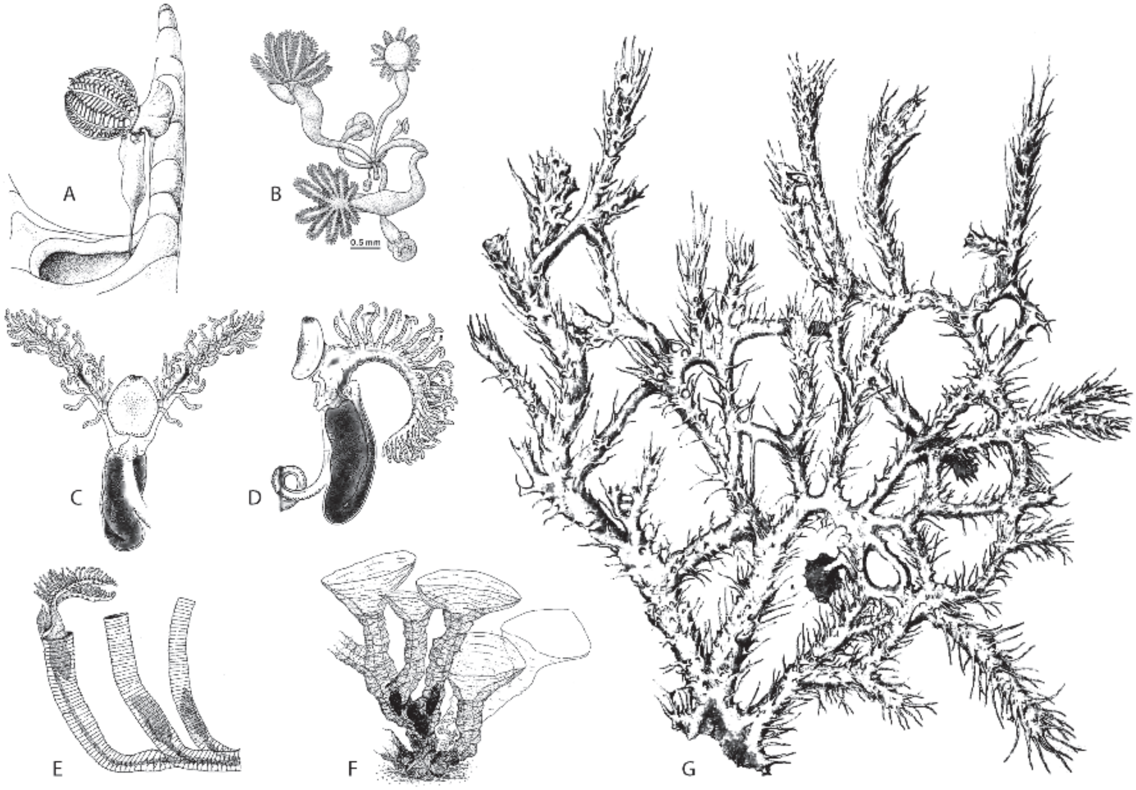
hundreds of thousands of times by an electron microscope, show traces of their original molecular architecture, relics of the biological processes that built the entire fossils but also remain largely mysterious.

Biology

Graptolites are biological enigmas of the first order. They were all colonial, and seemingly obliged to be so. A few colonies went down to just a handful of individuals, while some had thousands. They are represented today by the colonial pterobranch hemichordate *Rhabdopleura*, which, through modern taxonomic analyses, is now regarded as lying within the graptolite clade (Chapter 2). *Rhabdopleura* comprises bottom-living colonies (Figure 1.2E) that share a pattern of behaviour with corals and bryozoans. They are animal architects constructing the "homes", the collagenous tubes, in which they live. One of the major differences, however, is that their housing constructions are formed from an organic compound, not from minerals like the calcium carbonate used by the corals. *Rhabdopleura* is most closely related to the cephalodiscids (order Cephalodiscida), a second, less well organized and not truly colonial group of pterobranchs forming their tubaria from organic material in a very similar fashion (Figure 1.2 F, G).

Thus, graptolites built the robust, easily fossilizable constructions, or more precisely their tubaria, while the architects themselves, the delicate and perishable zooids of the colony, were almost never preserved in the fossil record, and we know of them only through their living representatives. The discovery of that evidence, in the 1980s (Chapter 2), in the form of the "fuselli" and "cortical bandages" with which the graptolites, quite literally, wrapped their homes, is one of the classic paradigm shifts in the whole of paleontology. Moreover, in the intricacy, complexity and integration of these homes, which were not skeletons, the planktic graptolites far surpassed the

Figure 1.2 Pterobranchs and their housing constructions (tubaria). Extant *Cephalodiscus* (A, B, F, G) and *Rhabdopleura* (C–E) to show the zooids (A–D) and their tubaria. Illustrations after Sars 1874 (C, D), Lester 1985 (B), Dilly et al. 1986 (A), Emig 1977 (F), and M'Intosh 1887 (G). Illustrations not to scale. [(A) adapted from Dilly et al. (1986) with permission from John Wiley & Sons. (B) adapted from Lester (1985) with permission from Springer Science + Business Media.]



often crude and untidy constructions of the living, benthic taxa (Chapter 8), especially those of the encrusting forms.

Analysis of the command-and-control systems by which the graptolite zooids, acting cooperatively, carried out these scarcely believable constructional feats is in its infancy, while the implications for graptolite evolution, and, more widely, for understanding the evolution of animal behaviour, have scarcely been examined at all. There must be implications here, too, for the extremely rapid evolution shown by the graptolites, or, to be specific, by the planktic graptoloids (Chapter 9). Again, these implications have yet to be seriously examined. We are, in a very real sense, at the beginning – we trust – of a new phase of graptolite research.

Evolution

The planktic graptolites in particular provide splendid examples of evolution (Chapter 7). Their evolutionary changes can be followed, often stratum by stratum, through the geological column. In Darwin's concept of "descent with modification", they show clear changes in graptolite species assemblages and morphology through successions of strata and also, importantly, provide the basis for biostratigraphy.

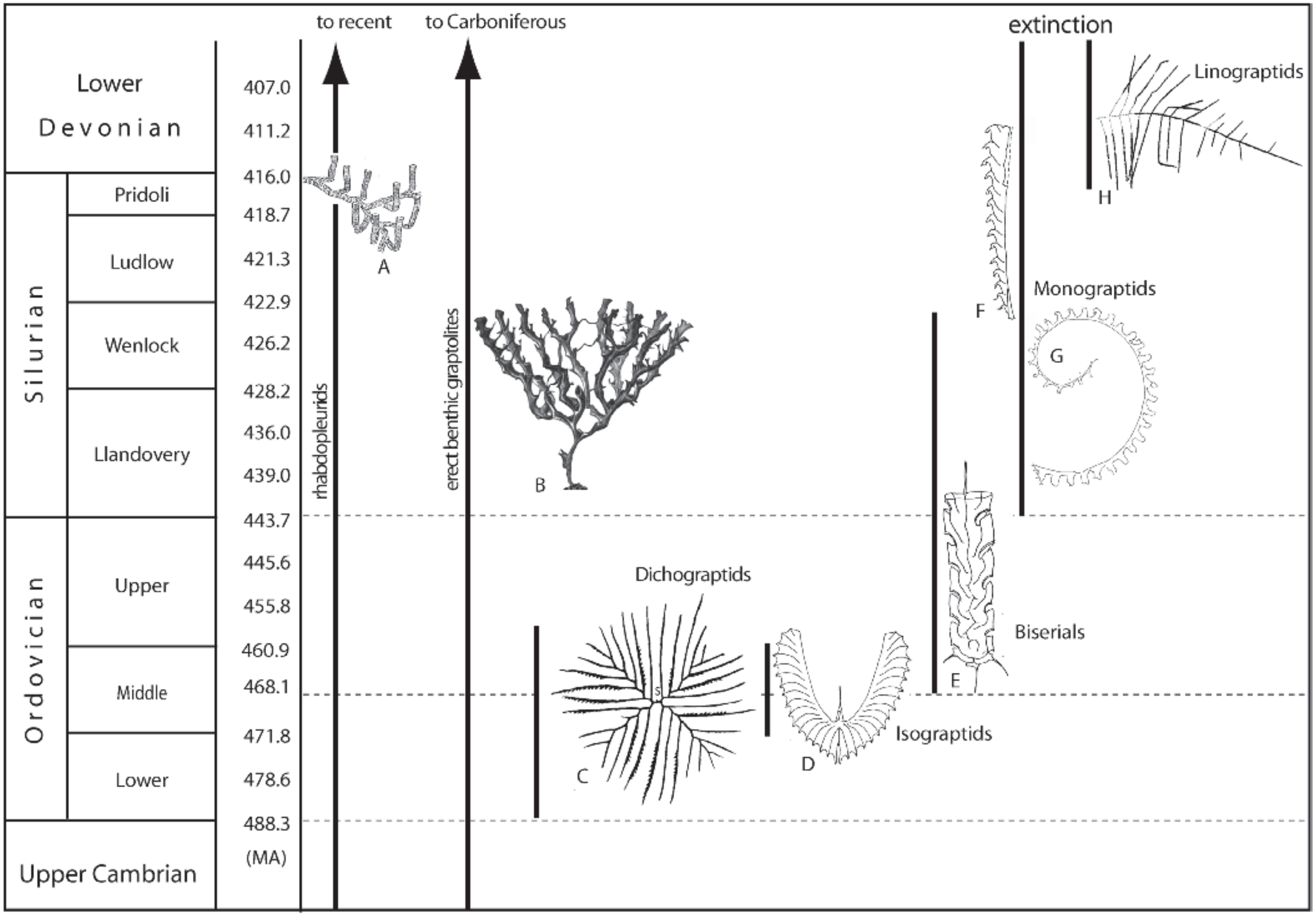


Figure 1.3 Large-scale evolutionary changes in graptoloids. (A) Encrusting benthic graptolite, *Rhabdopleura normani* Allman, 1869. (B) Benthic dendroid, *Dictyonema cavernosum* Wiman, 1896. (C) Multiramous *Goniograptus thureaui* (M'Coy, 1876). (D) Two-stiped, reclined *Isograptus mobergi* Maletz, 2011d. (E) Biserial graptolite, *Archiclimacograptus* sp. (F) Straight monograptid *Monograptus priodon* (Bronn, 1834). (G) Coiled monograptid *Demirastrites* sp. (H) Secondarily multiramous *Abiesgraptus* sp. Graptolite illustrations not to scale.

The overall pattern of change (Figure 1.3) has been clear since Lapworth's day: the change from the many-branched early forms that, already by the Lower Ordovician, settled into myriad forms of two- to four-branched dichograptids, including the classic "tuning-fork" species or pendent didymograptids (Chapter 10). Early in the Ordovician there was the development of graptolites with two "back-to-back" branches, the biserial graptolites that dominated faunas from then on, and into the early Silurian, with some then reverting wholly or partly to a uniserial state, such as the V-shaped dicellograptids or the Y-shaped dicranograptids (Chapter 11). Following the end-Ordovician crisis when graptolites nearly became extinct, the monograptid graptolites arose. It is somewhat counterintuitive that this morphology, seemingly so simple, took so long to appear. Single-stiped graptoloids, though, had been around since early Ordovician times and evolved several times independently, as can be seen in the Lower Ordovician genus *Azygograptus* (see Beckly & Maletz 1991) and the Upper Ordovician *Pseudazygograptus* (see Mu et al. 1960). The monograptids, liberated of the need to involve another stipe in their construction, rapidly evolved a dazzling – and often highly complex – range of overall forms and thecal shapes, including many variations on the spiral theme, and developed secondary branches in some cases.

There were many other innovations. At least twice in their history, graptolites found means to largely replace their solid-walled living chambers with elaborate, delicate meshworks: the archiretiolitids of the Ordovician (Chapter 11) and the retiolitids of the Silurian (Chapter 12). The latter represent the peak of graptolite complexity, at least as far as the architecture of their living chambers is concerned, and their study is a highly specialized endeavour, even within the specialist world of graptolite paleontology.

The evidence that is preserved is that of the graptolite tubaria, collected from various levels in strata in various parts of the world. Sampling by paleontologists reflects only tiny fragments of the ancient world of the Early Paleozoic. These fragments may be more or less representative of that world, but much evolution must have taken place in regions where strata were not preserved, or have not yet been recovered. Given this, what can be said about the patterns of evolution, when looking more closely?

One can look, most simply, for micro-evolutionary species lineages. Those that we recognize, of course, are all inferred, by linking morphological resemblance across successive stratigraphic levels. There are a number of seemingly clear examples, particularly well seen in those lineages where morphological change seems more or less unidirectional, and where ancestor–descendant relationships seem clear. One example is the evolution of the triangulate monograptids (genus *Demirastrites*) by elongation of the thecae, a tendency that found yet greater expression in the bizarre rastritids (genus *Rastrites*) that evolved from the triangulates (Chapter 13). There are a number of such examples, and some of these show remarkably rapid rates of morphological change when placed against a numerical timescale. The selective pressures that led to such morphological changes, and the biochemical mechanisms that controlled them, remain largely unknown.

At a larger scale, the origins of the major groups of graptolites and the architecture of the evolutionary tree have been the focus of much recent attention. In particular, there have been serious attempts at cladistic analysis (Chapter 7) that seeks to compare morphological characteristics between different groups, without reference to stratigraphic level, in order to extract information on evolutionary relationships. Advances have been made, and the origins of a number of the major graptolite groups have been traced by these means. There remain outstanding questions, but the outlines have become clearer. This is despite the patchiness of the sampling in time and space, and despite the fact that many of the key evolutionary steps involved subtle changes to the earliest-formed parts of the colony – parts that are only rarely preserved in sufficient detail to extract useful information. There is still much work to do to solve the remaining mysteries.

Stratigraphy

In a practical sense, the mechanisms that drove and shaped graptoloid evolution might be thought immaterial. The graptoloids, through the ~100 Ma of their existence, from the beginning of the Ordovician to midway through the Devonian, provide to geologists a biostratigraphical zonation that is among the best in the stratigraphic column (Chapter 6). This zonation continues to be refined, by the ever-more-precise characterization of individual graptolite taxa, by better constraints on their stratigraphic ranges, and by improved correlation between the graptolite successions in different parts of the world.

The graptolites continue to underpin much of the geological timescale of the Early Paleozoic. The fine time resolution that they provide complements and, arguably, still overshadows such well-established biozonations as those provided by benthic macrofossils such as brachiopods, and by the conodonts, the acritarchs and, more recently, by the chitinozoans.

Graptolite biostratigraphy remains highly effective (Figure 1.4) despite the fact that graptolites were, for the most part, restricted to offshore/deepwater settings, being rare, poorly diverse or absent in shallow shelf environments (Chapter 4). Furthermore, even within these deeper water settings, they occur almost exclusively in the "graptolite shale" facies that accumulated under anoxic conditions, being generally absent from the intervening "barren beds" that accumulated when oxygen (and a burrowing biota) reached the deep sea floor. This may reflect a preservational bias, as graptolites probably flourished in general under normal marine conditions, when the sea floor as well as the sea surface was oxygenated. In these conditions the organic tubaria have much less chance of preservation because of scavenging by bottom-dwelling organisms (see Chapter 5).

Major advantages of the graptolites as biostratigraphical index fossils include their size relative to microfossils, such that preliminary identifications may be made in the field, and the distribution of the living (and dead) colonies through transport by marine currents into regions where they may not have lived, but which enhance their value to the biostratigrapher, particularly in rock successions where no other fossils can be found.

Furthermore, biostratigraphical assignments in practice are often made on the basis of a small amount of material, perhaps only a handful of incomplete specimens. Indeed, in some cases a single fragment may be enough to establish the presence of a biozone. This reflects the extraordinary morphological complexity and diversity of these fossils, which can make even fragments commonly distinctive and identifiable to species level. It also helps that the graptolites, unlike palynomorphs, were only very rarely reworked into younger strata, because they rapidly became brittle and friable after burial.

Hence graptolites have been key to the unravelling of the geological structure of many regions where strata of Early Paleozoic age dominate (Chapter 6). For instance, the Southern Uplands of Scotland were famously interpreted by Charles Lapworth in the mid-19th century as comprising multiple repetitions of strata, and with more refinement from the 1970s on as one of the best examples in the world of a fossilized accretionary prism. The structures of the Welsh Basin, too, and of parts of the Appalachians and other mountain ranges around the world, have been deciphered with the help of graptolites.

Going beyond "abstract" regional studies, graptolites have been key to resolving major economic deposits hosted within strata of Early Paleozoic age, such as the Bendigo goldfields of Australia. Today, they are key to working out the structure of some of the world's most important oil source rocks (in the Middle East and north Africa, for example) and more recently in the identification of shale gas horizons.

The material of which graptolite tubaria were made, formerly termed periderm, a term that is no longer used by a number of graptolite workers because it is not a "skin", also has its uses. Originally transparent, it progressively changed its colour on progressive deep burial and heating, from straw-yellow to orange to brown and finally to black, which becomes "shinier" (i.e. has progressively greater reflectance) on further burial and heating (see Chapter 5). In this way, graptolites can be used as a kind of geothermometer, to determine the highest temperatures that buried rock strata once reached, and therefore to determine the history of the hydrocarbons that they contained.

Ecology

In exploring the ecology of the graptolites (Chapter 4), there is much still to study. The benthic graptolites have clear analogies with such filter-feeding organisms as sponges, bryozoans and others, and indeed the ecology of the living pterobranchs themselves may be studied.

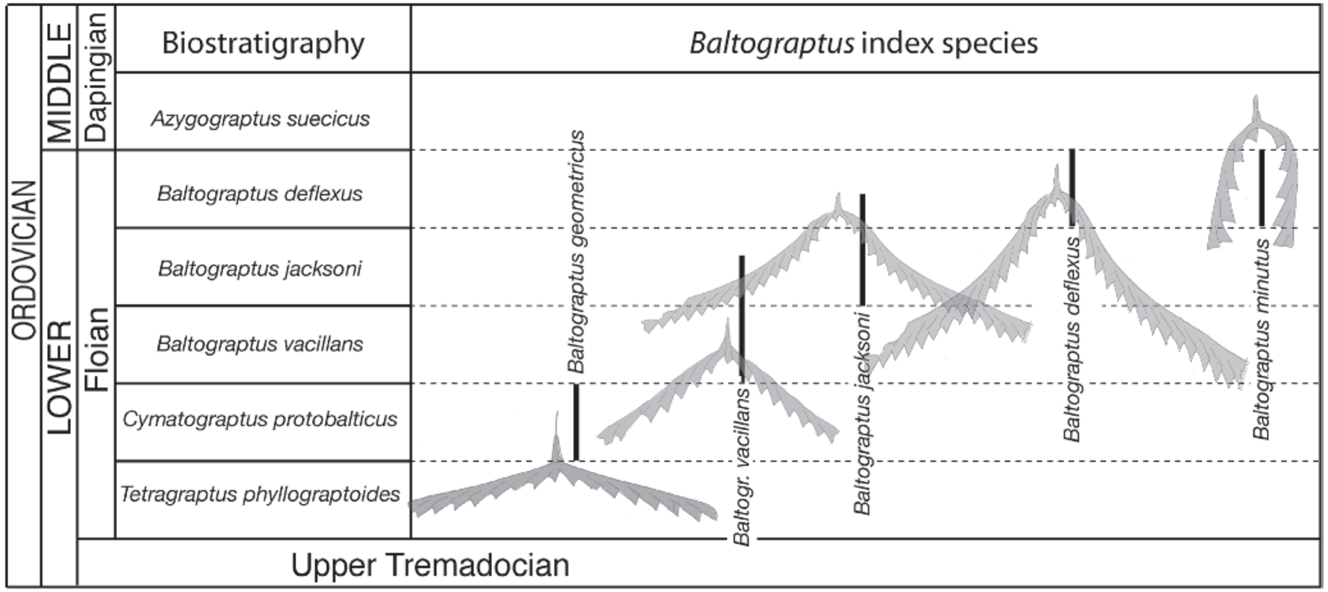


Figure 1.4 Graptolite biostratigraphy of the Floian, Lower Ordovician of Scandinavia, based on the evolution of *Baltograptus* species with subhorizontal *(B. geometricus)* to pendent *(B. minutus)* habit, as an example of biostratigraphical subdivision of an evolutionary lineage. Graptolite illustrations not to scale.

However, the planktic graptolites have no close analogues in the modern plankton, and it helps little here that virtually all of the evidence that we have of them is that of their robust homes or housing constructions, the tubaria, with no evidence left of the animals themselves. Because of this, there have arisen great differences in opinion on how the planktic graptolites may have swam, fed, reproduced, and so on. There have been ingenious attempts at reconstructing the life mode of graptolites, both physically, for instance by the use of model graptolites placed in wind tunnels to simulate ocean currents, or by computer models placing "electronic graptolites" in "electronic water".

Exploration of the world of the planktic graptolites is hindered because so little of the other zooplankton, with which they would have shared the water column and competed, and which they would likely have preyed upon and been the prey of, have not been preserved. Graptolites are the only consistently preserved macro-zooplankton from the early Paleozoic, although accompanied by various microfossils (Figure 1.5): chitinozoans (possibly the eggs of some as yet unknown creature), acritarchs, radiolarians, conodonts, scolecodonts and, in places, some of the more robust planktic arthropods and scattered problematica. Almost nothing has remained of a likely host of jellyfish, arrow-worms, comb-jellies, and delicate euphasiid-style arthropods that would clearly have influenced the life of graptolites. Even the benthic graptolites are poorly known in this respect, as many of their remains are preserved after they were transported from the shallow sea floors on which they lived into deeper water strata.

These other planktic organisms almost certainly played some part in the rollercoaster, "boom-and-bust" evolutionary history of the graptolites, where rapid changes in morphology, disparity and diversity were punctuated by periodic crashes in species numbers, followed by re-radiation from surviving stocks (Chapter 7). These changes were clearly linked to oceanographic changes, and perhaps with the supply of oxygen to deep waters. Counterintuitively, graptolite diversity typically decreased with increases in oxygenation, suggesting that these organisms might have adapted to, or preferred, low-oxygen conditions. When the low-oxygen waters shrank, then graptolites commonly became more prone to extinction. But this general link of graptolite diversity patterns to ocean oxygenation may not have been mediated through such direct cause and effect. Levels of ocean oxygenation broadly reflected global climate, then as subsequently, and the graptolites may have been sensitive to other parameters, as yet unknown, that were more directly linked to climate. A major factor affecting the evidence is that, as noted above, graptolites are much more easily preserved in black shales formed on oxygen-starved and hence scavenger-free sea floors (Chapter 5); nevertheless, some of the most notable reductions in graptolite species diversity seem to be clearly associated with major changes in climate and ocean chemistry.

The last of the bursts in graptolite diversity in the Lower Devonian was the final one, and the planktic graptolites disappeared forever, while the benthic dendroids persisted until the Carboniferous, and a few encrusting pterobranchs remain with us today (Figure 1.3) although these last have left very few traces of their long existence in the stratigraphic record. The disappearance of these extraordinary organisms from the sea has bequeathed to us a magnificent fossil record, and some of the greatest puzzles in paleontology.

Paleogeography

While graptolites are often cited as ideal zone fossils because of their wide geographical distribution, a more nuanced analysis shows that they, like modern zooplankton assemblages, can be resolved into assemblages controlled by oceanographic setting, water temperature and other factors (Chapter 4). Thus there has been, for instance, the recognition of continental (Laurentian) and oceanic assemblages around the North American continent (Figure 1.6A), and of low-latitude and high-latitude faunas (Figure 1.6B), while development of the latter concept has helped refine paleoclimate reconstructions of the late Ordovician, in indicating the shifting location of such features as the Arctic Front.

A continuing debate among graptolite paleontologists has been the relative importance of depth control versus control by lateral separation of water masses of different properties. Because planktic graptolites as fossils are, by definition,

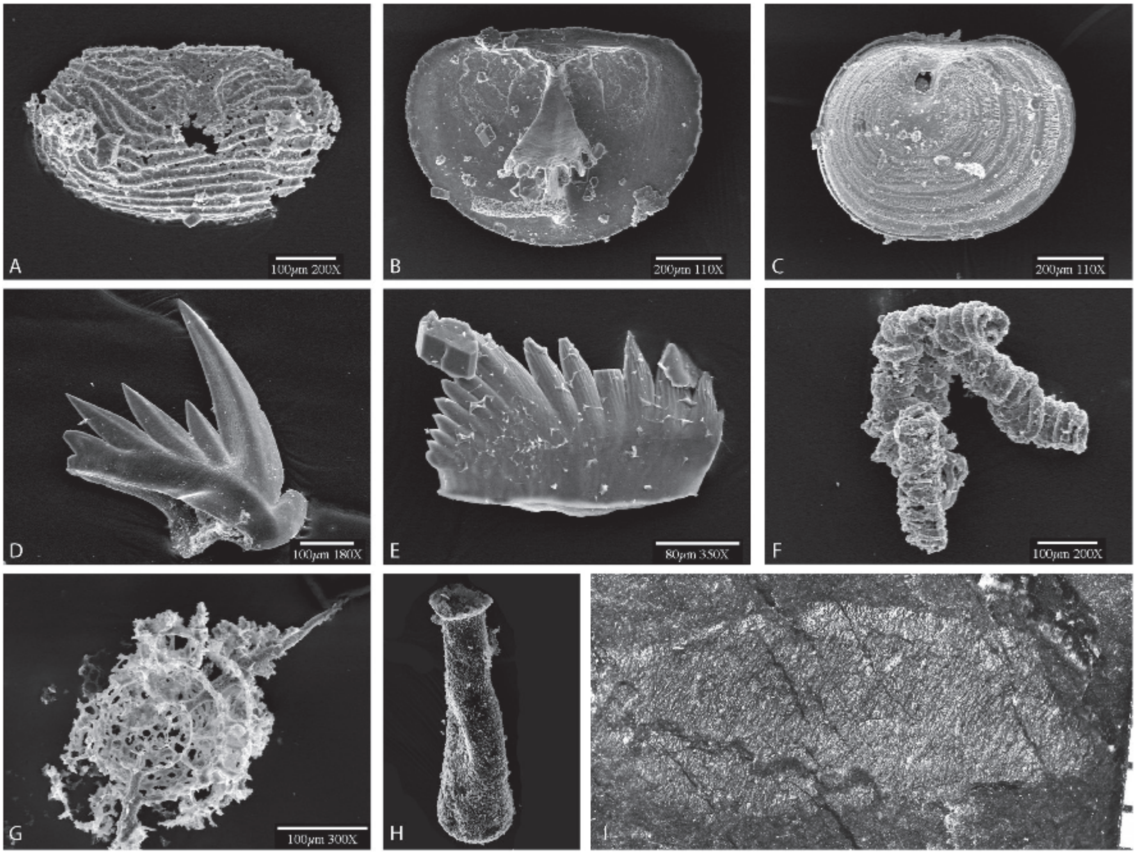


Figure 1.5 Organisms associated with graptolites. (A) Silicified ostracod carapace. (B–C) Phosphatic brachiopods. (D–E) Conodont elements. (F) *Obruchevella*, silicified microbial organism. (G) Radiolarian. (H) Chitinozoan. (I) Phyllocarid fragment in shale. Specimens from the Middle Ordovician of eastern Canada.

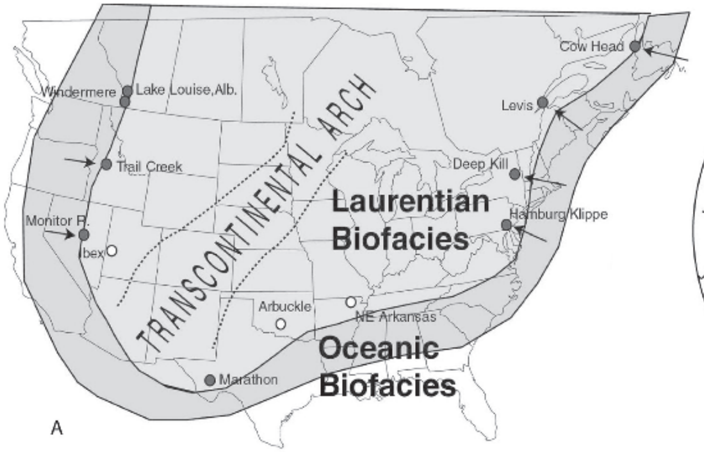
never found in their life habitat, but have fallen through the water column to rest, in death, on the sea floor, this has been a difficult question to resolve, with interpretations favouring both models, or variations of them, having been suggested in recent years.

Colony Shapes

The planktic graptoloids, in particular, developed an enormous diversity in colony shapes (Chapters 9–13), far outcompeting the benthic taxa, which had stricter constructional limitations on their tubaria imposed by life on the sea floor. Benthic graptolites either encrusted the sediment surface in various ways or reached upwards into the water column, their stipes and branches forming erect, bushy or fan-shaped colonies (Chapter 8). Throughout their development they were more affected by the local environmental conditions of currents and sediment input than were their planktic cousins. Thus, their shapes tended to be irregular as is seen in recent bryozoan colonies and even in corals, growing towards the light, but being unable to overcome their limitations. These two groups in some ways provide the closest living analogues to the numerous fossil benthic graptolite taxa of the Paleozoic.

With the emergence of the planktic graptoloids, a new chapter of graptolite colony design and construction was opened. Their intricate thecae and

Figure 1.6 Paleogeography of graptolites. (A) Biogeography of Laurentia showing oceanic and shallow water, epicratonic (Laurentian) biofacies (based on Maletz et al. 2005a, Fig. 4). (B) Biogeographical distribution of the Floian dichograptid *Baltograptus* in high latitudes (from Goldman et al. 2013). The areas in grey show the distribution of *Baltograptus* species. (Map based on Egenhoff & Maletz 2007, Fig. 2.)



elaborate branched colonies are only understandable in terms of their free-swimming lifestyle. This was a true revolution in many aspects and brought about a fundamental change in the organization of graptolite colonies. The graptolites threw off the limitations imposed by their old benthic lifestyle and evolved a freestyle architecture unrivalled by any other organisms (Chapter 9). The colony shapes became more regular and typically highly symmetrical, since maintaining themselves in the water column was much more easily achieved with a more symmetrical and balanced design. This was acquired through close integration and coordination of the individual zooids and the thecae forming the individual stipes, so that no single stipe could grow faster than another. Initially, there arose umbrella-shaped swimming colonies like that of *Rhabdinopora*, the closest relative of the benthic *Dictyonema*.

Slightly later in the evolution of the group, still in early Ordovician times, a great reduction in the number of stipes took place and led to many additional changes in colony design. Four-, two- and even single-branched designs quickly evolved in the Early to Mid Ordovician, with a variety of branching patterns developing in the colonies. While the thecal development became simplified in one respect, losing some of the more complex developmental aspects of the early dendroid graptolites (see Chapter 10), at the same time the thecae became morphologically more complex, with the development of a wide range of modifications of the thecal apertures.

Seemingly small constructional changes may have led to enormous modifications of the colonies, as shown by the example of the development of cladial (secondary) branching. Such many-branched colonies evolved many new designs: for example, xiphograptids of the genus *Pterograptus* (Chapter 10), the beautifully curved *Nemagraptus* (Chapter 11), and the spectacular cyrtograptids (Chapter 13) with their regularly developing single cladia (Figure 1.7A).

One of the greatest evolutionary breakthroughs in the transformation of their colonies was the construction of the biserial colony of the Axonophora (Chapter 11). Complex growth patterns within the proximal thecae enabled development into a biserial colony with two stipes growing parallel to each other in a back-to-back fashion (Figures 1.7F, G). This design dominated the Ordovician and early Silurian graptolite communities, with the emergence of a multitude of new genera and species. This seemingly simple scheme became elaborated by spines, flanges,

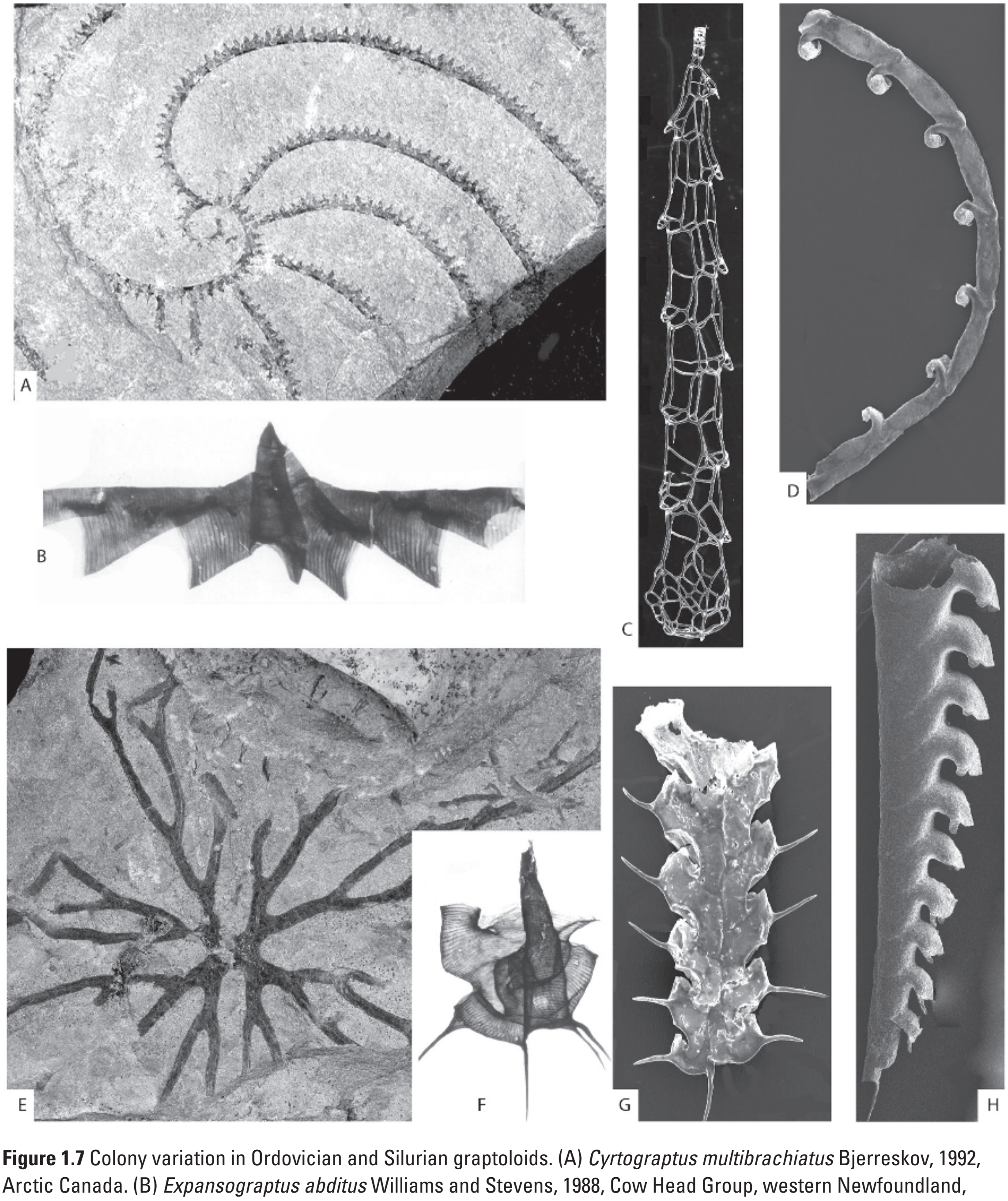


Figure 1.7 Colony variation in Ordovician and Silurian graptoloids. (A) *Cyrtograptus multibrachiatus* Bjerreskov, 1992, Arctic Canada. (B) *Expansograptus abditus* Williams and Stevens, 1988, Cow Head Group, western Newfoundland, Canada. (C) *Neogothograptus balticus* (Eisenack, 1951), glacial boulder, Northern Germany. (D) *Streptograptus galeus* Lenz & Kozłowska, 2006. (E) *Paradelograptus norvegicus* (Monsen, 1937), Fezouata Biota, Morocco. (F) *Amplexograptus maxwelli* (Decker, 1935). (G) *Dicranograptus nicholsoni* Hopkinson, 1870, Viola Limestone. (H) *Monograptus priodon* (Bronn, 1835), Arctic Canada. Illustrations not to scale. Photos by A.C. Lenz, J.C. Gutiérrez-Marco and J. Maletz.

genicular rims, and modifications of the thecal shape – there is an astonishing range of such variations. But still, this was not the end, as external complex systems of bars forming "fences" around the colonies were explored by the archiretiolitids. Later, and independently, the Silurian retiolitid graptolites evolved a way of simultaneously lightening and strengthening their tubaria with the help of a system of fine meshes laid down on very thin fusellar layers (Figure 1.7C).

During the Silurian the monograptids (Figures 1.7D, H), with a single stipe growing straight up from the sicula, started to dominate the faunas (Chapter 13). The biserial Axonophora diminished and eventually vanished in the mid-Silurian. Another complete reorganization of the construction of the colonies of planktic graptolites happened, but this time in a less dramatic fashion. The new design had appeared already in the basal Silurian, but tracing its origins has proved difficult. Initially, the monograptids were inconspicuous elements in the basal Silurian graptolite faunas and their evolution only slowly gained speed, before they rapidly became the overwhelmingly dominant component of graptolite faunas, with new colony and thecal designs.

The end of the reign of planktic graptolites in the world's oceans came not unexpectedly. After many smaller and larger extinction events in the Silurian, the diversity of the planktic graptolites reduced and their colony designs became severely limited and generally conservative. Only a few straight monograptids survived into the Lower Devonian, even though a short-lived bloom of multiramous taxa (*Abiesgraptus*, *Linograptus*) briefly recreated a diversity that had long been lost. Thus, the end came slowly and was barely noticeable: the world's oceans lost a group of organisms that long represented a major player in the ecosystem, while other groups positioned themselves and became ready to take over.

While unsurprising, the end of the planktic graptolites, their final extinction, is still not explained in detail. The main problem in understanding the interconnections between fossil groups remains the lack of sufficient data. Many groups of organisms do not leave fossil remains and are thus untraceable in the fossil record. The main players in the marine ecosystems of the Paleozoic likely have not been discovered and, without knowledge of these, our explanations are incomplete and questionable. However, we may reasonably postulate that the graptolites, after major blooms in the Ordovician and Silurian, had competitors in their marine ecosystem that eventually outcompeted them and led to their demise. With such little understanding even of the graptolites' lifestyle, it is hard to gain a better insight into their interactions with other groups of organisms, to reconstruct the environment in which they flourished and from which they were finally expelled. However, one intriguing point to note is that, since the disappearance of the planktic graptolites, no other marine group of organisms has evolved into a similar type of macro-zooplankton that was able to leave evidence of its presence. Modern planktic organisms are usually small, grow extremely fast and are present in large numbers but do not sacrifice either time or energy to construct a preservable housing system.

What remains of the graptolites, and their cousins within the pterobranchs, the cephalodiscids, are a number of small colonial and pseudocolonial, benthic organisms. Their origin can be traced back to the Mid Cambrian, when colonial pterobranchs were already a common component of the ecosystem. Thus, the benthic pterobranchs were either more successful or just lucky to survive into our modern days. They had a very successful time during the Late Cambrian to Carboniferous, but then their diversity diminished and most taxa extinguished, leaving the modern cephalodiscids and rhabdopleurids as the sole survivors. During their early days the benthic graptolites were one of only a few known groups of colonial organisms inhabiting the shallow water marine environments. They flourished in these shallow waters, but competition, probably with the bryozoans, which developed a similar lifestyle, may have been too strong for them in the end. Pterobranchs can be found in many environments today, from coastal sandy beaches to deep-water Arctic and Antarctic regions, but they are usually only a small, inconspicuous component of the faunas. It is said that rhabdopleurids can only be found close to marine research stations, but this may be regarded as an inside joke, as this is the only place where scientists search for them. Looking back, we can say that graptolites have been around for the last 500 million years, much longer than mankind will ever last on this planet, and have accompanied the evolution of life until today. They had their heyday long ago, but, if left undisturbed, may quietly last another 500 million years – a symbol of hope for the future of our planet.

History of Research

As is the case with many fossil groups, misunderstanding and incomplete knowledge of graptolite anatomy and comparison with unrelated taxa led scientists to many unusual interpretations about graptolites (Figure 1.8A, B, E). The example of the synrhabdosome interpretation of Ruedemann, with the – as it turned out – nonexistent "floats" and other hypothesized structures of these "supercolonies", is only one example of such misunderstanding, but certainly will not be the last. It all started with the genus *Graptolithus* erected by Linnæus (1735), a term used for supposedly inorganic markings on rocks. We now recognize the *Writing in the Rocks* – the title, later, of a popular book on graptolites (Palmer & Rickards 1991) – as paleontological reality, and we can now understand this kind of "writing" and interpret it in a paleobiological sense. However, it took more than 250 years for scientists to gather the information we have at hand today, and to relate the fossil graptolites to the living pterobranchs.

Many scientists have devoted their time to the enigmatic and elusive graptolites and provided us with their insights and interpretations (Chapter 15). What counts at the end is the result, while the many blind alleys that were pursued along the way ultimately helped set us on the path to our modern understanding. Even what we now perceive as errors along the way were useful and even important, as the example of Nancy Kirk and her extrathecal tissue model of graptolites shows. Here a suggestion that was shown to be wrong in hindsight produced enormous amounts of discussion, new research and fruitful ideas. The recent understanding of graptolites as a largely fossil group of pterobranch hemichordates would not

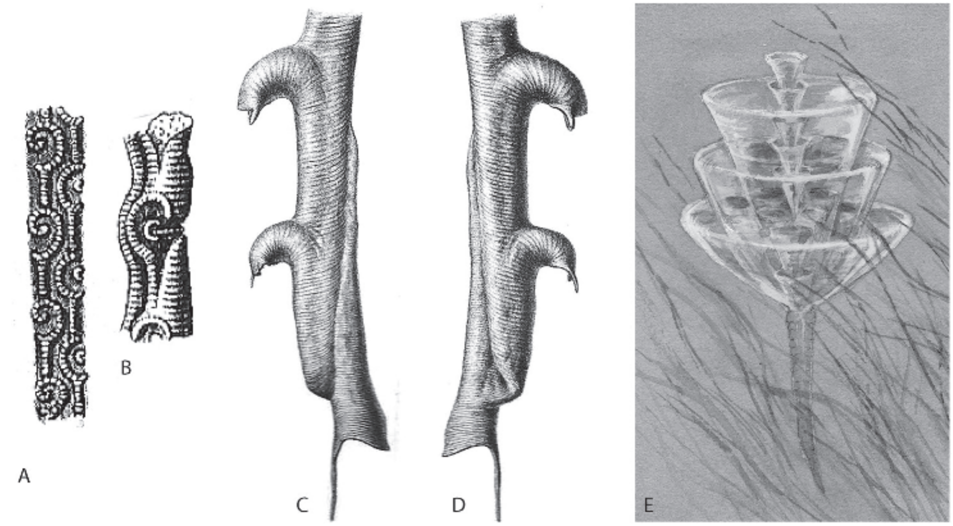


Figure 1.8 (A, B) Reconstruction and interpretation of indeterminable biserial graptolite fragment from Richter (1853, pl. 12, Figs 12, 13). (C, D) Excellent illustration by Georg Liljevall (ca. 1895) for Gerhard Holm, *Monograptus priodon* (Bronn, 1835), proximal end in obverse (C) and reverse (D) views (published in Bulman 1932a, pl. 1, Figs 10, 11). (E) Erroneous reconstruction of biserial graptolite with complex float structure by Franziska Zörner-Bertina (ca. 1950) for Rudolf Hundt, unpublished (original at Naturkundemuseum Gera, Germany; provided by Frank Hrouda, Gera).

have been possible without her provocative and thoughtful suggestions.

Outlook

As a short overview of graptolites and their development, this chapter is just the starting point for the reader to explore an unusual but fascinating group of organisms. Generally thought to be extinct, graptolites are recently recognized to include a few extant living members and provide deep insight into more than 500 million years of biological evolution on our planet. Surprisingly little change happened during this long time interval to the benthic taxa that represent the graptolites, and their closest ancestors from the Ordovician times have apparently not changed much at all. However, this is an inference from their tubaria, the housing construction, since information on the soft-body anatomy of the fossil taxa is not available. Will it be possible in the future to find fossilized graptolite zooids? Perhaps this is destined to be forever a vain hope, but graptolite workers will go on searching for direct clues to the architect and builder of some of the most remarkable constructions in the history of life on this planet.