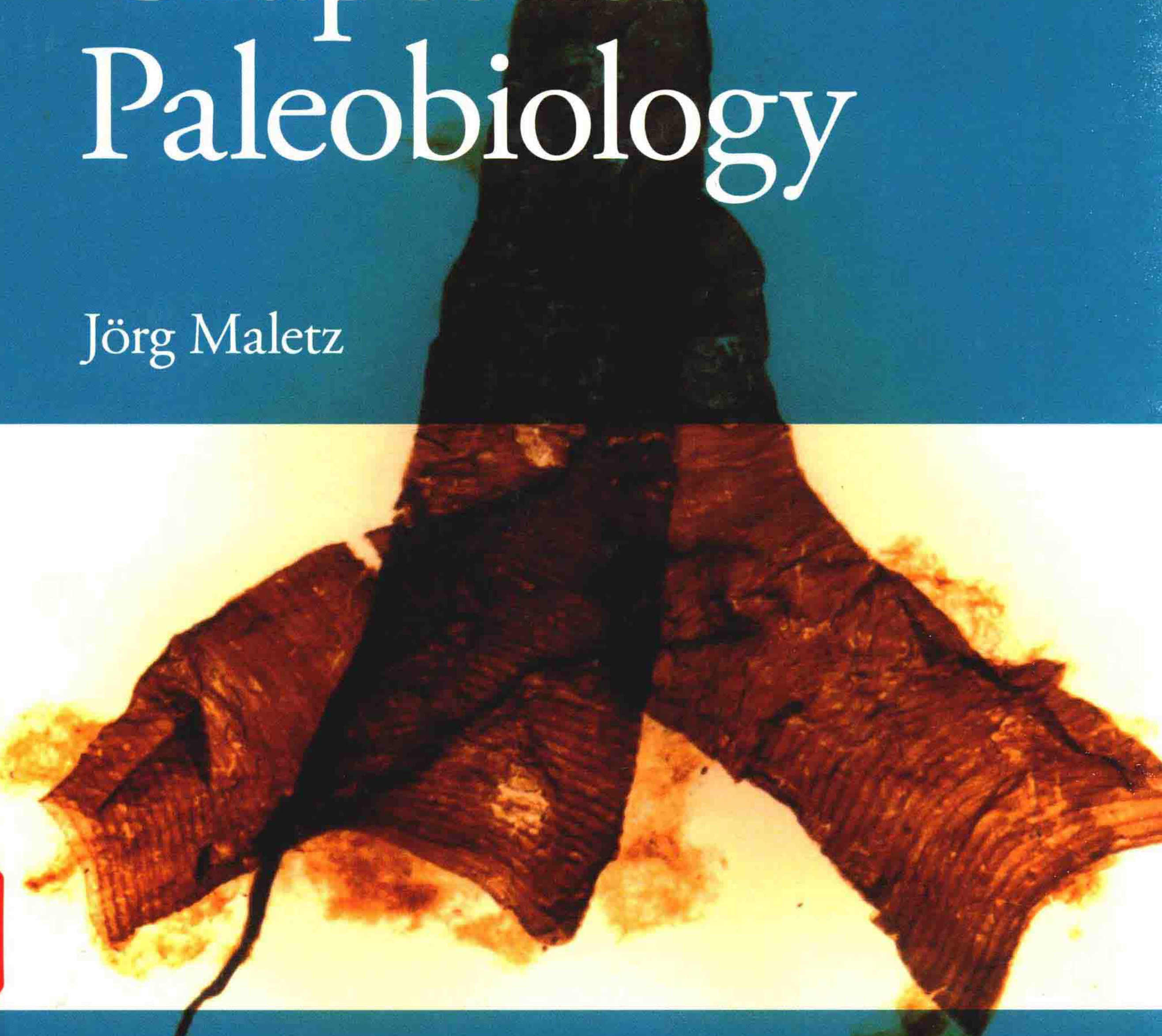
Topics in Paleobiology

Graptolite Paleobiology

Jörg Maletz



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Preface

Graptolite specialists would certainly regard their fossils as the most "sexy" fossils of the world, even though they may not be the most popular ones in the view of the general public. However, graptolites are among the most useful fossils found in the geological record, as every geologist and paleontologist working in the Paleozoic time interval would tell you. Our research cannot compete with the public attention that the dinosaurs generate, and not even with the trilobites or ammonites – favourites among the fossil collectors. We do not look for the big fossils or produce the reconstructions that Hollywood uses for its movies to scare, but also fascinate, its audiences. The general public looks at fossils and paleontologists in a more Indiana Jones fashion, or, if you will, compare us with Dr Alan Grant, the paleontologist of the *Jurassic Park* movies. Nothing could be further from reality, as most paleontologists are not working with the prehistoric beasts that stimulate the fantasies of the moviegoers. Paleontology is more commonly a detailed investigation of tiny objects, fossils that most people will never look at or even recognize as such. It is the microfossils, often less than 1 mm in size and barely visible to the naked eye, that earn us our life and reputation in the scientific world, and also in companies using geological information in their exploration of natural resources.

Fossil graptolites early on earned themselves the reputation of being extremely useful for dating purposes and thus important for geological exploration. Even James Hall in the 1840s recognized this potential when he prepared one of the earliest monographic works on graptolites. Graptolite research is not a hobby for specialists, for people sitting in their offices, identifying fossils and putting them into small boxes. Our research has been motivated by the need for a biostratigraphical framework for rock successions, as exemplified by the graptolite biostratigraphy established for the Australasian Bendigo and Castlemaine goldfields by Thomas Sergeant Hall in the 1890s, and extended and revised by William John Harris and David Evan Thomas in the 1930s. At the time the Australian state of Victoria was one of the major regions of the world for gold production, and the precious gold was hosted in the Paleozoic rocks in which our favourite fossils, the graptolites, were also found. Ballerat, Bendigo and Castlemaine, among others, became famous names as the most productive goldfields of Australia and of the whole world, even though we as paleontologists know these names mainly from the modern regional Australasian chronostratigraphy (the Bendigonian and Castlemainian Stages of the Ordovician System) and the fossil faunas we investigate.

Hydrocarbon source rocks, particularly "hot shales", are a more recent area of interest, since our modern world relies upon hydrocarbons as an energy source and much more. Without hydrocarbons our world would be quite different, with no gas for our cars or heating systems, or plastic for so many purposes. In particular the Silurian hot shales in Iraq, Saudi Arabia and North Africa, but also in China, North America and Europe, are the source of the hydrocarbons that modern petroleum companies exploit at the moment. Here, as graptolite specialists, we are asked to help with exploration and provide expertise to search for the most productive layers.

Our work as specialists is not restricted to the scientific "ivory tower", but has important implications for the modern world. We are not working isolated in our research offices and labs, but are integrated into a larger world. Personally, we may see ourselves as the scientists and we may not be interested in the commercial application of our research, but this we cannot ignore entirely.

Our input in biological aspects and the evolution of life on our planet should also not be ignored. Graptolites are now known to be one of the longest-living groups of organisms, and the extant genus *Rhabdopleura* is often regarded as a living fossil. This term – introduced by Charles Darwin – should not be taken too literally, as it is wrong in every case. Fossils are remains of dead animals, even though we may be able to refer some fossils (e.g. Pleistocene organisms) to extant species. However, we are not able to identify a fossil graptolite specimen and refer it without doubt to an extant species. Still, with our fossils, we connect the modern world to a time lost in the mist of the geological past. More than 500 million years of evolution and our favourite organisms are still around. They survived extinction events and ecological catastrophes of many kinds. What does this tell us about their ways of life? What was their origin? Where will it end? The questions of complexity of life, of the evolution of coloniality as a means of communication among individuals and of help in the survival of a group instead of an individual – all this can be and needs to be explored. More than 150 years of research on graptolites lies behind us as graptolite specialists, and many important questions have been answered, but much is still to be learned from them. Graptolites have not yet provided answers to all our questions, but hopefully they will give us a few more hints in the future.

Jörg Maletz
Berlin, Germany
August 2016

Acknowledgments

When I was first asked by Mike Benton and Jan Zalasiewicz to write a book on graptolites, I was very uncertain and reluctant, as this would be a major and risky undertaking. Would anybody be interested in reading a book on graptolites? There are not too many books on this topic, and the last one I remembered was the Palmer and Rickards volume with its beautiful photo plates, for which I also provided a few photos, but this was a long time ago and much has happened in our scientific field since that time. I know of very few books for a more general audience, except for the ones in German by Rudolf Hundt, arguably one of the most strange and unusual people who worked on graptolites. As a self-made man with a geological background, Hundt was the most published person in German graptolite research, but the scientific community did not accept him or his work for a long time. However, his aim was to educate the general public and to show scientific work in an understandable and relatable way. Thus, Hundt – and many others working at the time, when graptolite research was not popular in Germany – should be thanked as they kept the torch alight, and now much scientific material can be found in German museum collections that otherwise would never have been collected.

From a practical point of view, graptolite collections in natural history museums and geological institutions guided my way, and for many years the curators provided the material upon which my research is based. Thus, many people need to be mentioned here: Per Ahlberg, Mats Eriksson, Kent Larsson, Anita Löfgren (Lund University, Sweden), Tom Bolton, Jean Dougherty, Michelle Coyne, Ann Thériault (GSC, Ottawa, Ontario, Canada), David. L. Bruton, Franz-Joseph Lindemann, Elisabeth Sunding (Natural History Museum [PMO], Oslo, Norway), Douglas H. Erwin, Mark Florence (Smithsonian Institution, Washington, USA), Una C. Farrell (University of Kansas Museum of Invertebrate Paleontology, Lawrence, Kansas, USA), Christina Franzén, Jonas Hagström (Naturhistoriska Risksmuseet, Stockholm, Sweden), Birgit Gaitzsch (TU Bergakademie Freiberg, Germany), Michael Howe, Paul Shepherd (British Geological Survey, Nottingham, UK), Frank Hrouda (Museum für Naturkunde, Gera, Germany), Ed Landing (New York State Museum, Albany, New York, USA), Paul Meyer (Field Museum, Chicago, USA), Hermann Jaeger, Christian Neumann (Museum für Naturkunde, Berlin, Germany), Bernard Mottequin (Royal Belgian Institute of Natural Sciences, Bruxelles, Belgium), Michael Ricker, Eberhard Schindler (Senckenberg, Frankfurt/Main, Germany), Matthew Riley (Sedgwick Museum of Earth Sciences, Cambridge, UK), Andrew Sandford, Rolf Schmidt (National Museum of Victoria, Australia), and Linda Wickström (SGU Uppsala, Sweden). A special mention goes also to the German Science Foundation (DFG) for the support of my research over the years.

I should not forget the many graptolite specialists, without whom a book like this would not have been possible: Denis E.B. Bates (Aberystwyth, UK), Christopher B. Cameron (Montreal, Canada), Chen Xu (Nanjing, China), Roger A. Cooper (Lower Hutt, New Zealand), Robert Ganis (Southern Pines, North Carolina, USA), Dan Goldman (Dayton, Ohio, USA), Juan Carlos Gutiérrez-Marco (Madrid, Spain), Anna Kozłowska (Warszaw, Poland), Alfred C. Lenz (London, Ontario, Canada), Kristina Lindholm (Kävlinge, Sweden), David K. Loydell (Portsmouth, UK), Michael J. Melchin (Antigonish, Nova Scotia, Canada), Charles E. Mitchell (Buffalo, New York, USA), John F. Riva (Québec, Canada), Michael Steiner (Berlin, Germany), Anna Suyarkova (St. Petersburg, Russia), Blanca A. Toro (Cordoba, Argentina), Petr Štorch (Praha, Czech Republic), Alfons H.M. VandenBerg (Melbourne, Australia), Wang Xiaofeng (Wuhan, China), Jan Zalasiewicz (Leicester, UK), and Zhang Yuandong (Nanjing, China). You all provided me with photos, information, discussions on many subjects, and in the preparation of the various chapters of this book, not necessarily supporting my personal views, but always willing to help me. I know many of you since I gave a talk at the 3rd International Conference of the Graptolite Working Group of the IPA in Copenhagen, Denmark, organized by Merete Bjerreskov (Kopenhagen, Denmark) in 1985. I was just a diploma student from Germany at the time, trying to make the best of it and finding friends and colleagues for life. I will never forget the situation when Prof. En-Zhi Mu, one of the greatest graptolite specialists of all time, shook my hand and said: "See you at the next graptolite conference in Nanjing". Graptolites have been part of my life ever since and I am deeply grateful that this research gave me so much pleasure and enjoyment.

Obviously, my family have supported all my efforts for so many years, and helped me to survive in the sometimes difficult "science environment" that I choose to live in. Especially, I must not forget to thank my friend Ralf Kubitz, who has dealt with me for decades now, and without whom I might not have been able to finish this project.

Contents

1 Graptolites: An Introduction

Jan Zalasiewicz and Jörg Maletz

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.

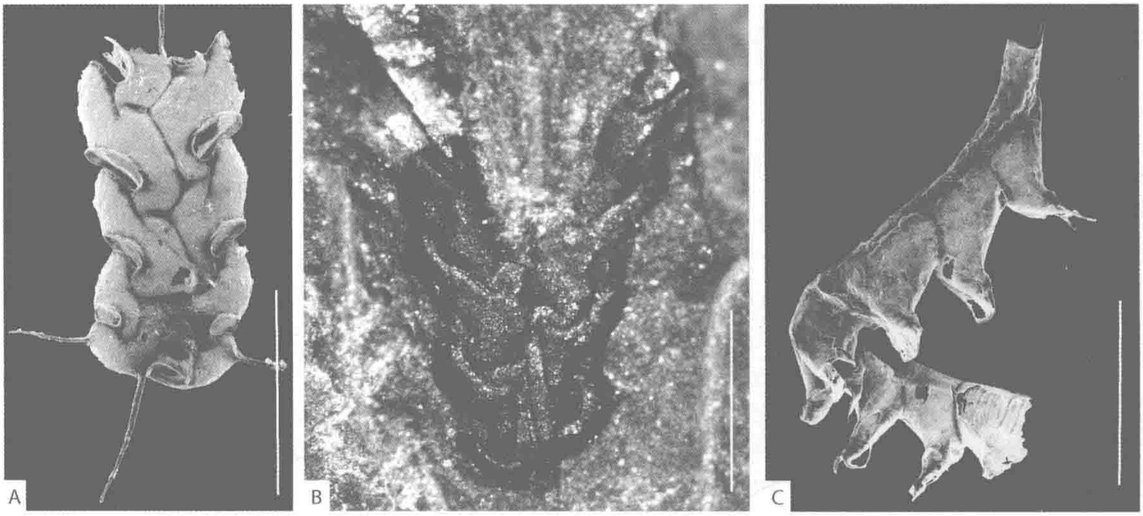
Their beauty is often concealed by the unkindness of geological preservation, all too many specimens being crushed by the weight of overlying strata, or distorted by the tectonic forces that raise mountains. They are also, simply, too small for casual human observation. Many are smaller than a matchstick, 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

Graptolite Paleobiology, First Edition. Jörg Maletz.

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.



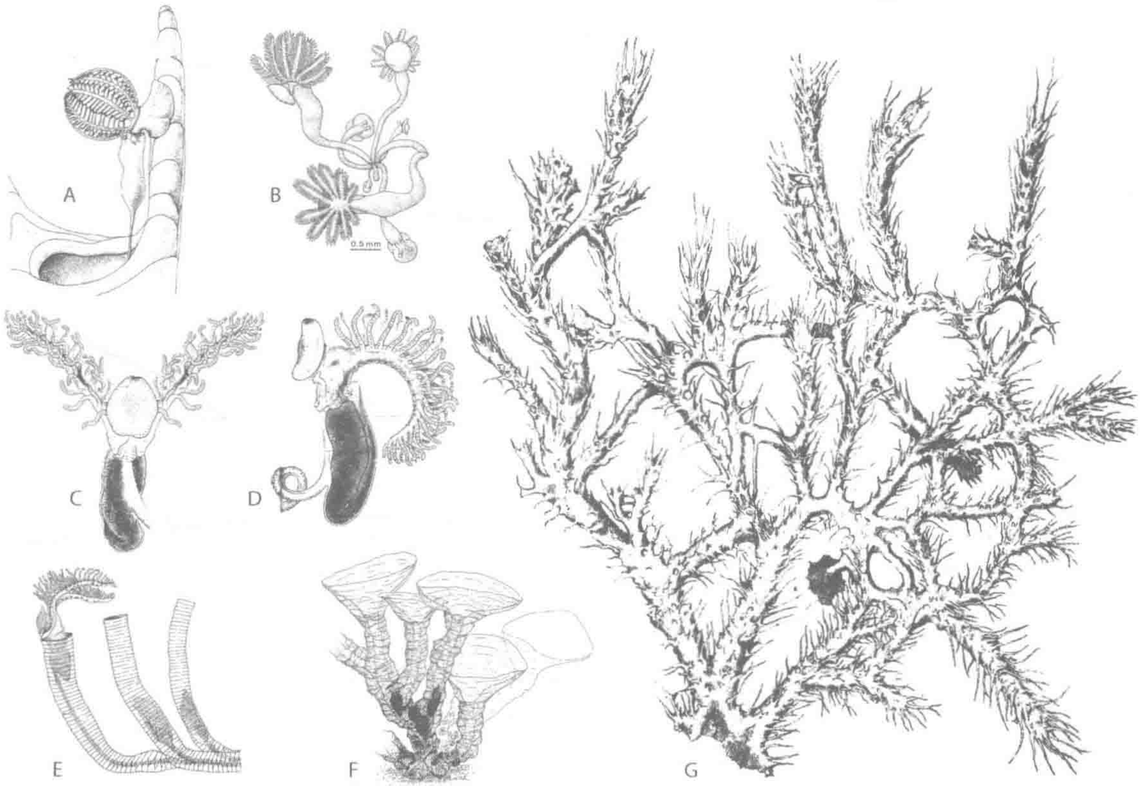
hundreds of thousands of times by an electron microscope, show traces of their original molecular architecture, relics of the biological processes that built the entire fossils but also remain largely mysterious.

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.

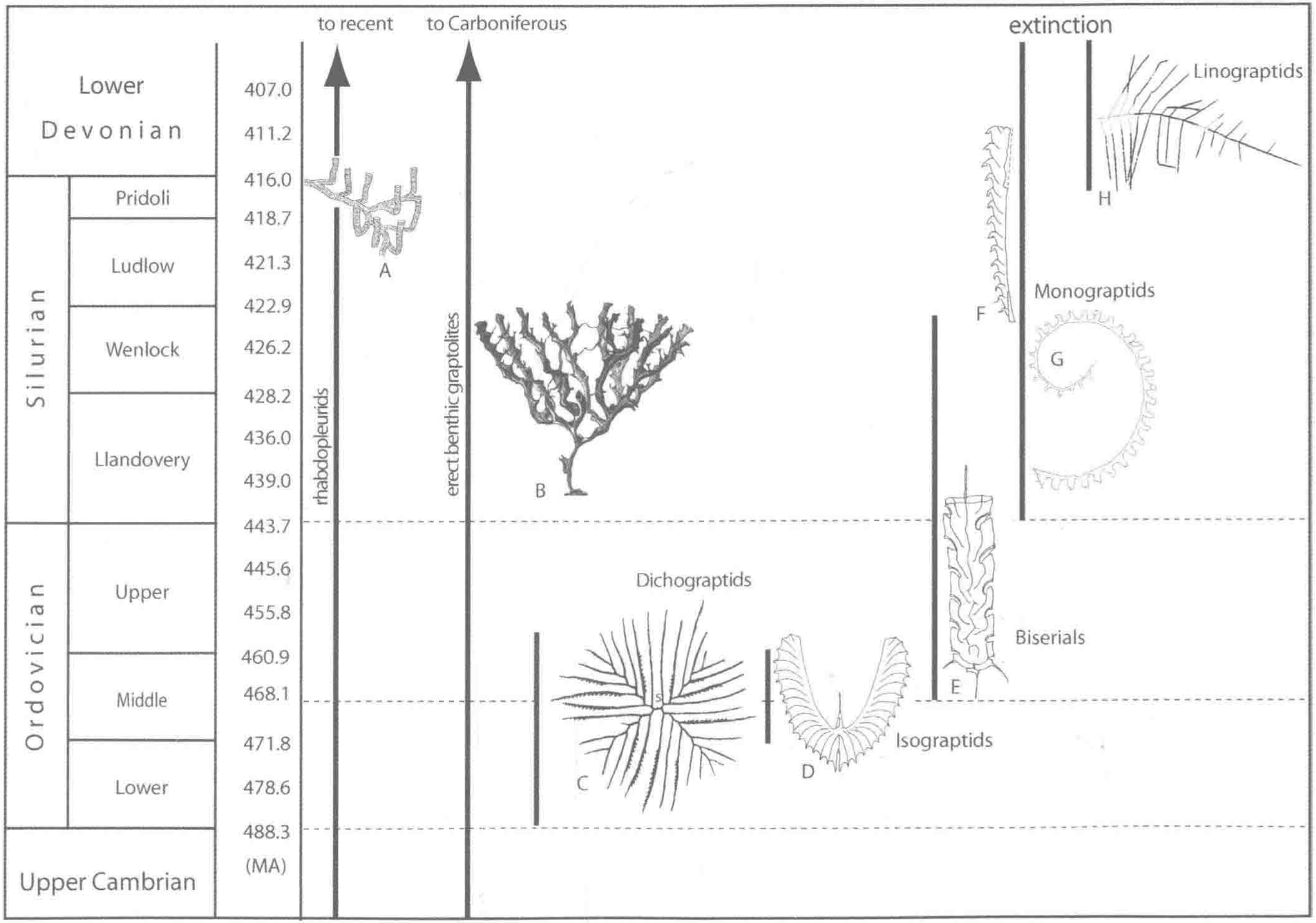


Figure 1.3 Large-scale evolutionary changes in graptoloids. (A) Encrusting benthic graptolite, *Rhabdopleura normani* Allman, 1869. (B) Benthic dendroid, *Dictyonema cavernosum* Wiman, 1896. (C) Multiramous *Goniograptus thureaui* (M'Coy, 1876). (D) Two-stiped, reclined *Isograptus mobergi* Maletz, 2011d. (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.