Fossils explained 70

Graptolites: fossil and living

Every student of palaeontology will stumble upon the term 'graptolite' at some point and will wonder what these strange little fossils mean. Thought to be long extinct, the few living graptolites and their extinct relatives have been united quite recently by palaeontologists through cladistic analysis. Not that the extant graptolites were overlooked, but the connection has never been made between the fossil graptolites and their modern descendants. We now have a much better scientific basis for our interpretation and understanding of these fossils and graptolites are recognized as part of a living clade of small and inconspicuous marine organisms, the Pterobranchia. They have been around since the Cambrian Period (*c.* 520–510 Ma) and, thus, they may represent one of the longest-existing groups of organisms. Not that they should be termed 'living fossils', but their perseverance is remarkable in its own way and may lead to the question as to how they were able to achieve this success and survive for all these eons. May they be able to show us a key to survival in the future?

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Graptolites often look like scratches or engravings on shale surfaces (Fig. 1) and may not be recognized as once living organisms; but when well preserved they reveal an incredible beauty in the detail of their tubarium development, outcompeting many much better known groups of fossil organisms. These fossils range from millimetre scale tiny beasts to colonies a metre and more in length for straight monograptids, or even in diameter for multiramous tubaria. Graptolites are visible with the naked eye or under a hand lens in the field, but often hide important taxonomic features of their delicate organic construction. The slender stipes of the graptolites with their tiny thecal tubes, originally housing the small animals called zooids, are thus difficult to investigate with the unaided eye. Details can only be recognized under a high-powered microscope, and sometimes even an electron microscope is necessary to reveal their hidden beauty and constructional complications.

As nearly invisible constituents of the Cambrian Explosion and the ensuing Ordovician diversification, graptolites survived quite a number of extinctions that shattered the surface of our planet and erased numerous groups of organisms. Graptolites must have done something right to succeed, even though their greatest achievements and success were limited to the Early Palaeozoic, where they were dominant creatures in the world's oceans. Afterwards, they retreated into the background to lead a little disturbed life as benthic organisms until today, and left us very little Mesozoic and Cenozoic fossils.

The invention of a colonial organization in the early Cambrian and of a planktic life style at the base of the Ordovician transformed them into a group both famous and extremely useful for palaeontologists and geologists. Thus, they are not forgotten and have successfully defended their special place in our scientific world.

For more than 500 million years graptolites have populated the worlds' oceans, but undoubtedly their heyday was in the Early Palaeozoic, when they suddenly bloomed and formed the most important (at least for palaeontologists) plankton group of their time. For the following more than 100 million years of Earth's history, graptolites were a quickly evolving group of organisms that today provide the key to age dating and biostratigraphical interpretations by palaeontologists and geologists. Numerous species evolved and quickly disappeared after a short bloom, being replaced by other species, but leaving their

Fig. 1. Bridging the time gap: a modern dragonfly (*Aeshna eremita*) on a piece of shale with basal Ordovician *Rhabdinopora flabelliformis* from western Newfoundland. A delicate organic fossil, it appears as though etched into the rock by a skilled engraver, but actually represents a fossil that is about 485 million years old and documents the origin of the planktic graptolites.

housing constructions for us to investigate and admire.

Graptolites—fossil and alive

Where and when did the graptolites originate, and what are their closest relatives? The origin of the graptolites is still shrouded in mystery, as very few early graptolite fossils exist to identify their oldest members. However, one of the most difficult questions about graptolites was answered recently, when the extant *Rhabdopleura* (Fig. 2a–d) was recognized as the only graptolite surviving into the modern world. *Rhabdopleura* and its close cousins *Cephalodiscus* and *Atubaria* were long included in the Pterobranchia, a sister group of the Enteropneusta or acorn worms (Fig. 2e), and thus, previously seen as members of the Hemichordata. For a long time palaeontologists recognized graptolites as a special group of fossils, and regarded their phylogenetic relationships as unknown. They were, thus, referred to the hydroids, the corals, the cephalopods and even the foraminiferans in the past. Now we understand graptolites as a nearly extinct group of the Hemichordata, the sister group of the more widely distributed Enteropneusta, found in all marine environments.

All graptolites secrete a housing construction, the tubarium (Fig. 2a,d) from glands on their cephalic shield. This housing construction (formerly identified as the rhabdosome in fossil taxa) is what we find in the fossil record, but we basically have no clue of the anatomical features of the little animals (called zooids) that inhabited and constructed these elegant tubaria. We can only look at the zooids of the modern *Rhabdopleura* to get some general ideas (Fig. 2b,c). However, the colonies of the planktic graptolites are so different to the extant *Rhabdopleura* that we have to assume that their zooids were also strongly modified from the basic *Rhabdopleura* zooid concept. Unfortunately, there is no reasonable fossil record of graptolite zooids, as these small organic remains would have decayed within a few days after death. Thus, it is unlikely that they left any fossil remains under normal circumstances. All we can estimate is that the zooids were secreting their own housing, in which they fairly freely moved around, even though they were connected with the stolon system to each other, forming a truly colonial organism (Fig. 2a). The zooids must have been bilaterally symmetrical with a single pair or more of arms with tentacles, extending from the thecal apertures for feeding as *Rhabdopleura* does today. Here, the speculations end.

Some anatomical peculiarities

As mentioned before, our knowledge of graptolite zooids is limited to the zooids of the extant *Rhabdopleura* and its pterobranch relatives *Cephalodiscus* and *Atubaria*. The zooids of extant pterobranchs are differentiated

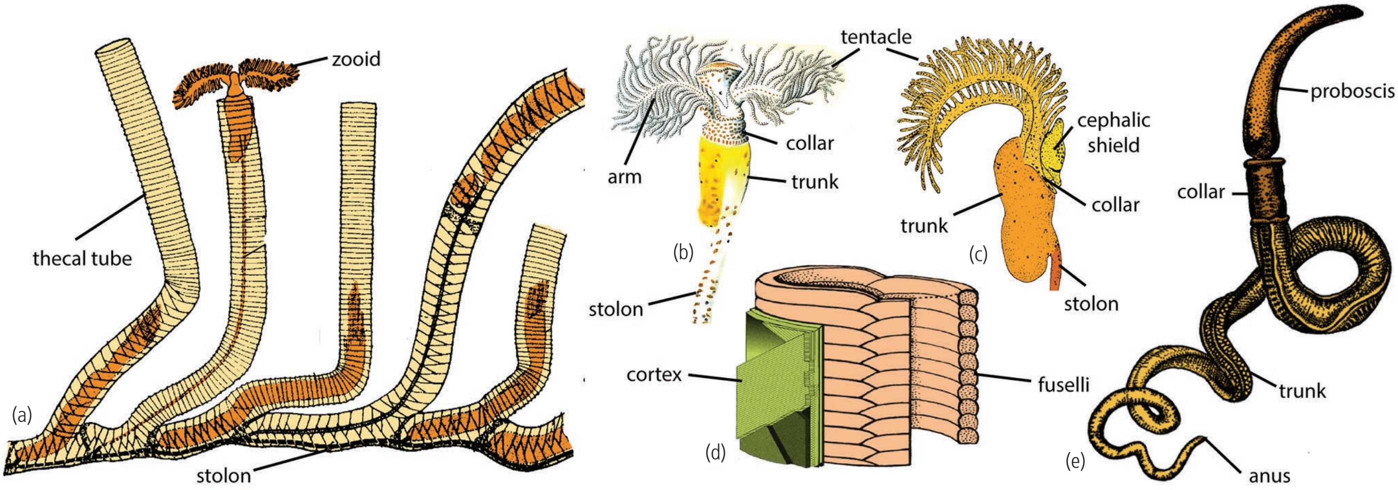

Fig. 2. a–d, *Rhabdopleura*, zooids and housing construction (tubarium). **e.** *Saccoglossus pusillus* (Enteropneusta). Illustrations not to scale.

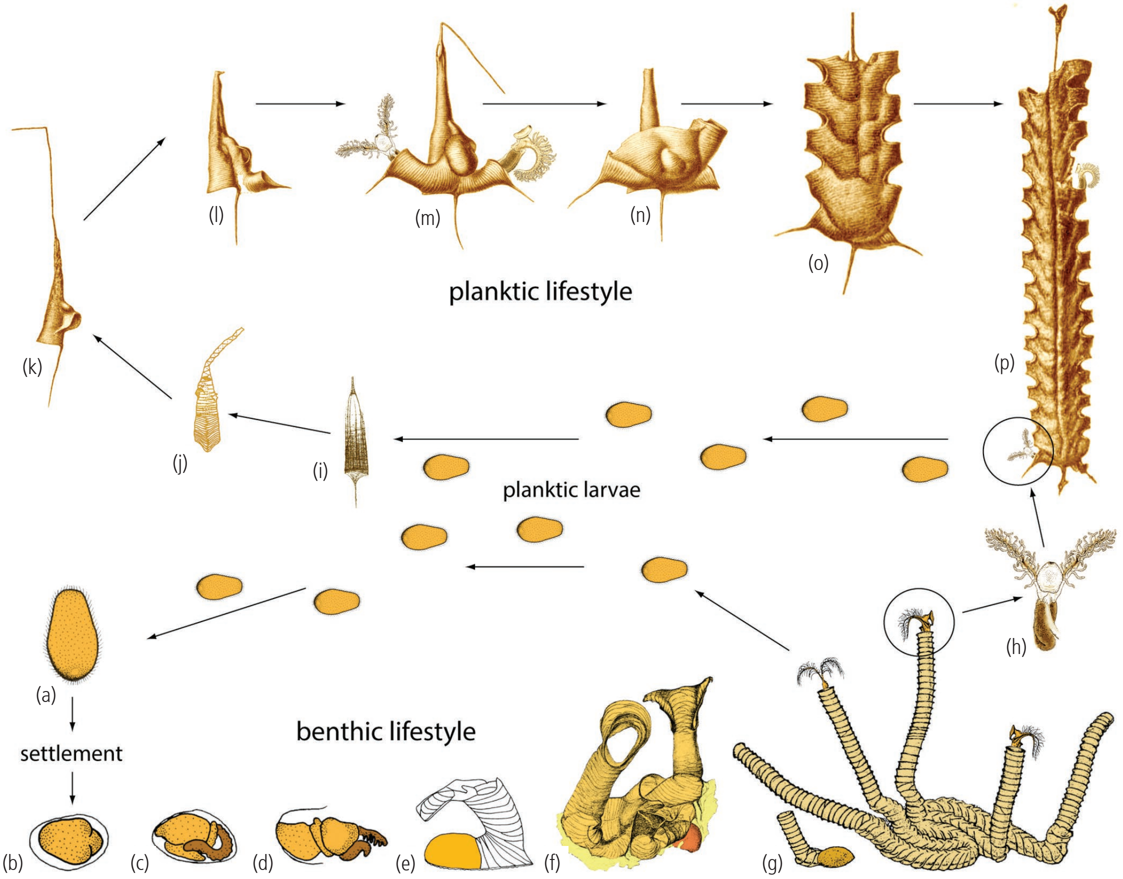

Fig. 3. Ontogeny and astogeny of the graptolites. **a–d, g, h,** *Rhabdopleura compacta*, benthic, extant. **E, F,** *Epigraptus* sp., benthic, Ordovician. **i–p,** *Pseudamplexograptus distichus*, planktic, Middle Ordovician. Illustrations not to scale.

into three parts, the cephalic shield or proboscis, the collar with the arms and the trunk regions (Fig. 2b,c). This differentiation into three parts is shared with the acorn worms or Enteropneusta, their sister group in the Hemichordata. (Fig. 2d) However, the pterobranch zooids do not share the elongated worm-like body shape with the mouth at one end and the anus at the other end. They all possess a U-shaped intestine with the anus opening close to the collar on the opposite side of the mouth, which could be handy if you live in a tube with only one opening (Fig. 2a). The living zooids sit at the opening of their individual tubes for feeding, with the help of their arms and tentacles generating a stream of water to skim for food particles and at the same time disperse the waste they produce.

Graptolite ecology and life cycle

All graptolites, both fossil and extant, have been colonial organisms that share the development of a complex reproduction and growth style. There is the classical sexual reproduction through eggs and sperm, forming individual larvae growing into the founding zooids of a new colony. The larvae are mobile and swim for a short period of their life, after which they settle down and start secreting their tubarium (Fig. 3a–g). All subsequent zooids of a single colony are formed by asexual budding from the stolon system, initiated by the first zooid. The colony grows by the addition of modules, zooids formed by asexual budding on the stolon system, and the secretion of the thecal tubes by these zooids (Fig. 3i–p). Therefore, we differentiate the ontogeny or growth of the individual little zooids from the astogeny or colony growth of the compound organisms, which may be called a superindividual. The individual zooids of a colony appear to be unable to survive as independent organisms and have never been found in such a state. The dual cycle of reproduction through ontogeny and astogeny can be inferred for the fossil graptolites through the interpretation of the tubaria, but is known in some detail only from extant *Rhabdopleura* species.

Benthic graptolites

Graptolites originated as benthic organisms, probably from a worm-like hemichordate without the typical tentaculate arms, but all interpretations are speculative, as the fossil record is scanty. Their origin may be inferred from the presence of the cephalodiscids, non-colonial pterobranchs with a homologous zooidal anatomy. The cephalodiscids also secrete a tubarium from the organic material in which the zooids live. The individual thecal tubes, however, are separate and not interconnected as are

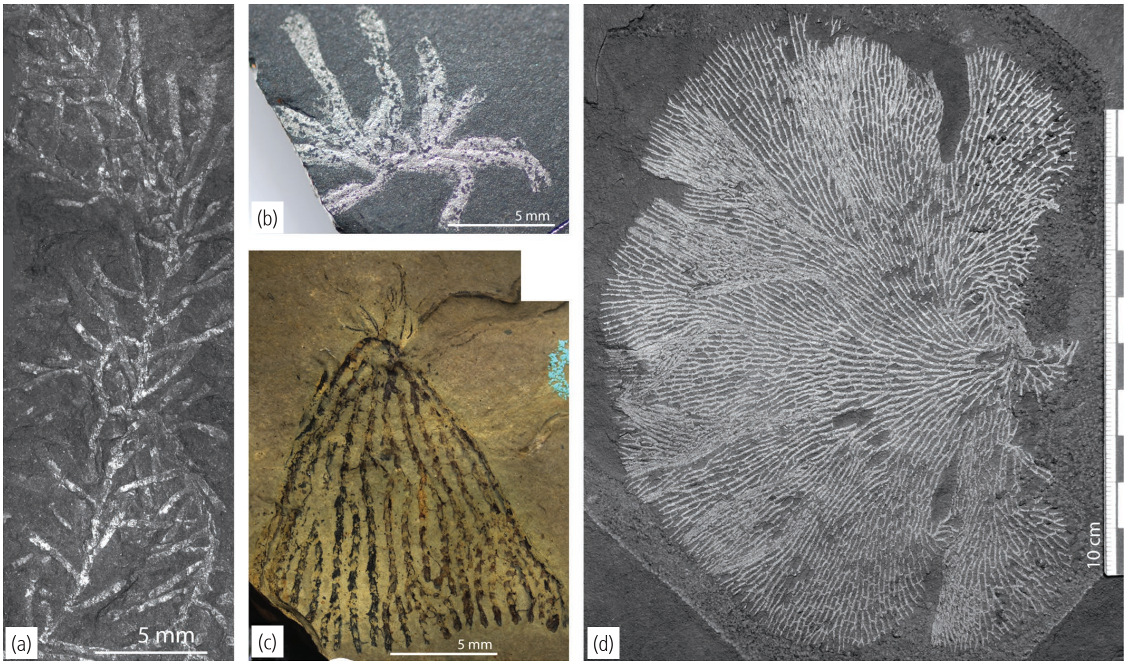

Fig. 4. Early benthic and planktic graptolites. **a.** *Archaeolafoea longicornis* Chapman, 1919, Cambrian Series 3, Victoria, Australia. **b.** *Sphenoecium mesocambricus* (Öpik, 1933), Cambrian Series 3, Krekling Norway (Mark Wolvers collection). **c.** *Rhabdinopora flabelliformis parabola* (Bulman, 1954), basal Ordovician, Dayangcha, Jilin Province, China. **d.** *Ptiograptus fournieri* Ubaghs, 1941, Carboniferous, Visean, Denée, Belgium. (Image: B. Mottequin.)

the thecal tubes of graptolite tubaria. The mature zooids of *Cephalodiscus* also live as individuals, but after the development of a sexually produced zooid, additional zooids may be formed asexually through budding. These budded zooids separate from their mother zooid when mature.

Early graptolites from the Early and Middle Cambrian show fairly simple colony styles (Fig. 4a,b) with erect tubes reaching into the water column, formed from irregularly developed fuselli or growth increments (Fig. 2d). Their growth starts from an initial attachment of the sicular zooid (the first and sexually produced zooid) with the addition of an irregular branching 'rhizomal construction' from which the zooidal tubes originate. From this organization of an encrusting organism it is easy to evolve into complex colonies with erect stipes forming bush-like, tree-like or even fan-shaped colonies (Fig. 4d), as do modern bryozoans.

These benthic graptolite forms survived unchanged for about 170 million years (from the Early Cambrian Series 2, stage 4 to the Visean, Early Carboniferous), where their evolution apparently came to a sudden halt, as the presence of still quite diverse faunas of the early Visean age demonstrates.

Since this time, only a few records of rhabdopleurid fossils indicate the presence of this once so dominant fossil group. It is not clear why the benthic graptolites were more or less out-competed during the Carboniferous by other organisms, but a hint may be seen in the slow growth of the colonies, related to the tedious secretion of the individual fuselli of the thecal tubes, one at a time. Even in modern *Rhabdopleura*, it takes a few hours to secrete a single half-ring and weeks to form a complete thecal tube. Larger colonies may need years to grow. Other colonial organisms like corals and bryozoans can achieve this much faster and, thus, have a clear advantage. A similar advantage may also be seen in modern planktic organisms. These are characterized by fast growth and short life cycles, being able to quickly react to environmental changes or changes in predation. The planktic Graptoloidea did not have the chance to survive this competition and went extinct.

Graptolites as plankton

The evolution of the planktonic graptolites marks one of the most dramatic changes in the evolution of the marine ecosystem. The earliest known species was *Rhabdinopora flabelliformis parabola* (Fig. 4c), a form still very similar to many of the multi-branched benthic taxa. The planktic graptolites were probably one of the first major groups of organisms to venture into the open oceans and explore the water column for a new lifestyle. Until then, only small microplanktonic organisms (e.g. acritarchs, planktic arthropod larvae) were found in the water column, as the food availability was still quite low and the world's oceans appeared nearly empty and unexploitable. Organisms were restricted to the bottom of the seas where the food also was, leaving the water column largely uninhabited. No food–no life can be said of the planktic realm of the early Palaeozoic. Today the former void is filled with numerous small planktic organisms and yields food for many larger animals as the food chain has evolved, but we have little evidence that this was also the case in the early Palaeozoic. The exploration of the planktic realm led to the first major diversification of the graptolites in the basal

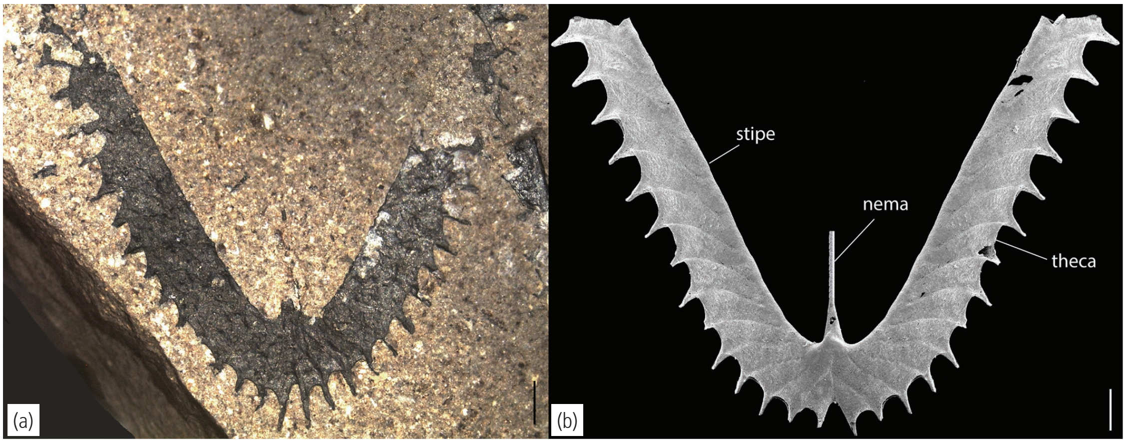

Fig. 5. The symmetry of the Isograptids. *Isograptus imitatus* (Cooper, 1973) from the Cow Head Group of western Newfoundland. **a.** Flattened shale specimen. **b.** Chemically isolated specimen preserved in full relief, SEM photo (partly reconstructed). Scale bar = 1 mm.

Ordovician. This revolutionary development now forms the base of our biostratigraphical framework and was only possible through the endless possibilities of the construction of graptolite colonies from clonally formed modules. The population of the numerous ecological niches of the world's oceans began with the explosive diversification of the graptolites during the Great Ordovician Biodiversification.

One of the most obvious changes in the colony design of the now planktic graptolites was a reduction of the number of stipes and the change to a more symmetrical shape of the colonies (Fig. 5). Certainly, this is related to the new environment in which the graptolites flourished. Instead of being influenced by environmental effects such as currents and competition with adjacent organisms, the planktic graptolites enjoyed the freedom of the water column and developed the symmetry and balance that characterizes planktic organisms. Damage is rare, and the growth of the colonies is not disturbed as much. Numerous new colony shapes were explored. These characterize the planktic graptolites and now make the work of palaeontologists and biostratigraphers easier due to the quick changes and incredible variation found in the graptolites, as they can be used for biostratigraphy.

Axonophoran graptolites

During the Middle Ordovician, the planktic graptolites produced another innovative new design that characterizes all later graptolites. The nema, free in earlier planktic taxa (Fig. 5b), became engulfed by the two stipes of the biserial colony (Fig. 6a,b) and is not visible any longer, except if it extended beyond the distal end. The nema was used as a central rod along which the stipes of the colonies grew, in a way guiding and supporting the growth. The nema often developed into a long rod, sometimes longer than the rest of the colony, but also additional features,

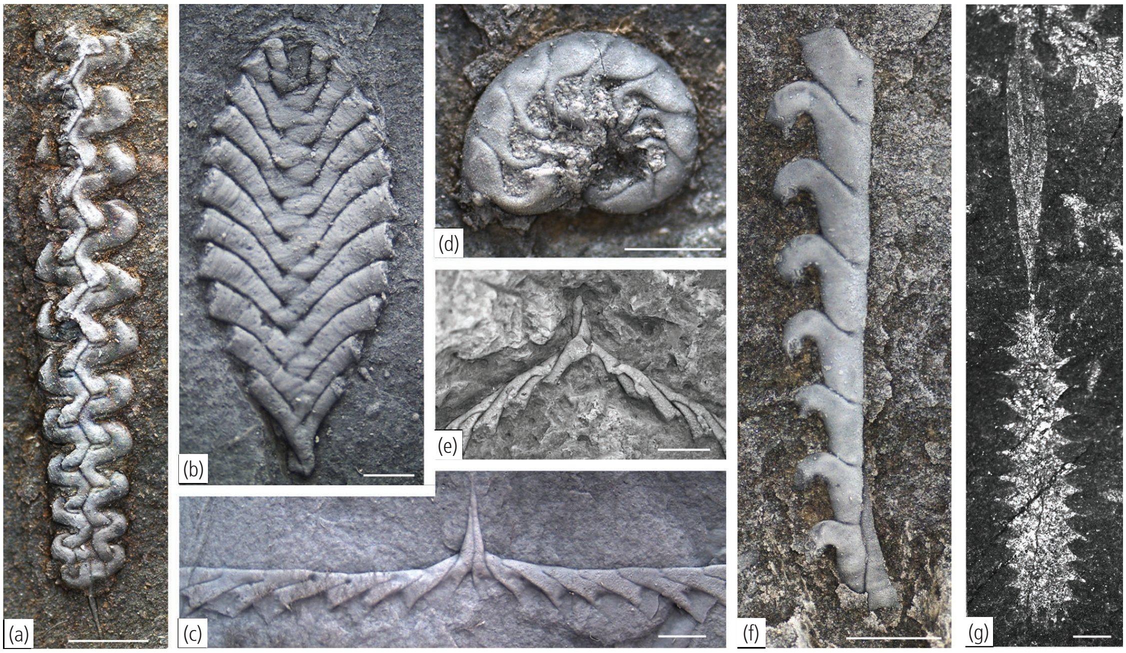

Fig. 6. Examples showing variation of the tubaria of planktic graptolites. **a.** *Haddingograptus*. **b.** *Petalolithus minor* (Elles, 1898). **c.** *Expansograptus holmi* (Törnquist, 1901). **d.** *Cochlograptus veles* (Richter, 1853). **e.** *Kiaerograptus supremus* Lindholm, 1991. **f.** *Monograptus priodon* (Bronn, 1835). **g.** *Cryptograptus schaeferi* (Lapworth, 1880), specimen showing nematularium. Scale bar = 1 mm in each photo.

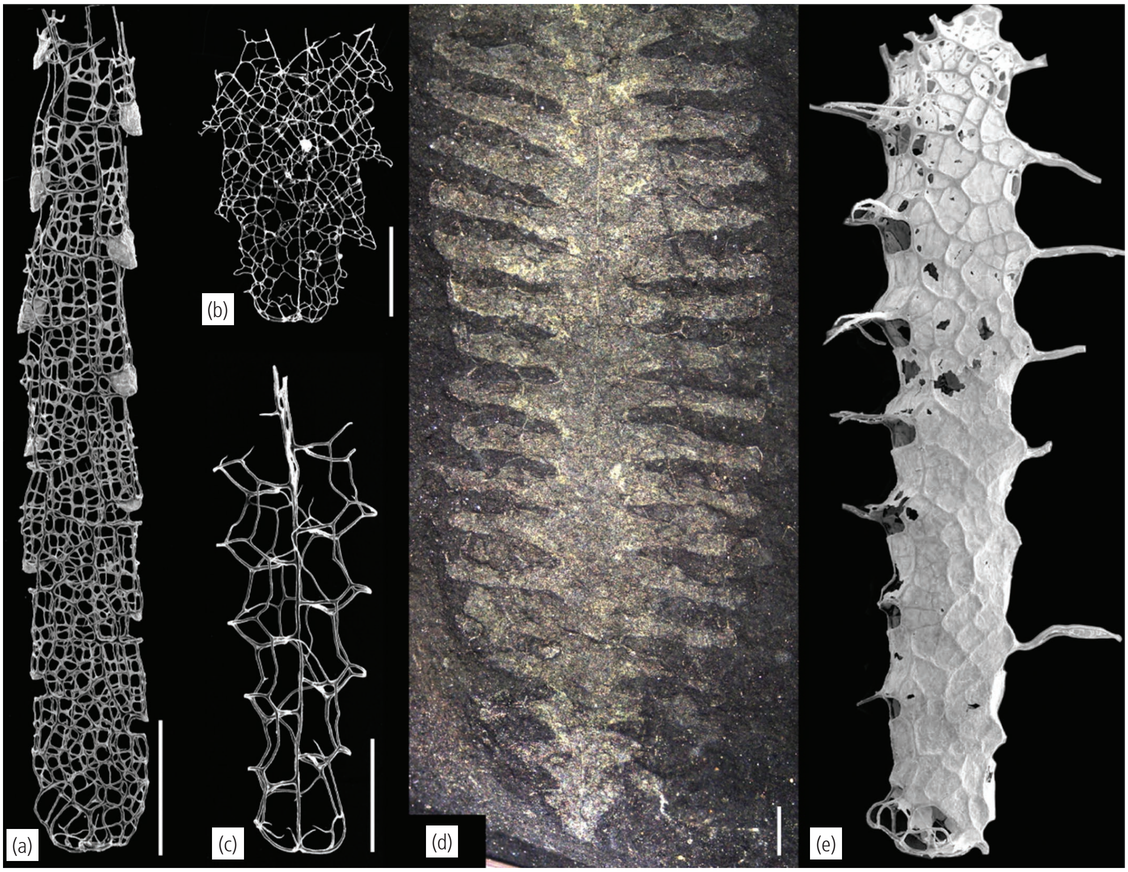

Fig. 7. Retiolitidae. **a.** *Gothograptus nassa* Holm, 1890, glacial boulder, northern Germany. **b.** *Retiolites geinitzianus* Barrande, 1850, proximal end, glacial boulder, northern Germany. **c.** *Paraplectograptus* sp., Silurian, glacial boulder, northern Germany. **d.** *Pseudoretiolites perlatus* (Nicholson, 1868), Yesanguan, Badong County, Hubei, China, showing preservation of thecae overlain by lists of the ancora sleeve reticulum. **e.** *Spinograptus clathrospinosus* (Eisenack, 1951), Arctic Canada, showing complete ancora sleeve walls. Scale bar = 1 mm in each photo. (**a–c, e** are SEM photos).

the nematularia, were formed. These take their name from the position in the colony, but the use of the nematularia remains elusive (Fig. 6g). The main differences in biserial, axonophoran taxa can be seen in the extensive variation of the thecal styles, especially in the development of the thecal apertures. Very good preservation is needed to observe these details and the taxonomic identification of the graptolites became more difficult.

In a last step, the colonies lost their second stipe and the uniserial monograptids (Fig. 6f) were born. The monograptids, however, kept the nema as a guiding rod on the dorsal side of the tubarium, extending over the growing end at the tip of the colony. The thecal styles were even more elaborate that those of the biserials and a new bloom of graptolites provided the data for a continued biostratigraphical use of the graptolites. In the Llandovery, early Silurian, the planktic graptolites reached the highest diversity ever and their subsequent history became that of a slow demise and final extinction through a million cuts.

Retiolitidae—the strangest of graptolites

The Retiolitidae remain one of the strangest and most fascinating groups of the graptolites. Many of their mysteries were only resolved after the invention of the scanning electron microscope, which enabled the minute details of their elaborate colonies to be seen (Fig. 7a–c). Initially, the retiolitids were regarded as graptolites formed from a meshwork of regularly or irregularly produced bars without the secretion of normal thecal tubes. However, more precise observations indicated that they had a two-layered construction with an inner layer formed from thecal tubes and an outer layer, the meshwork of the reticulum and clathrium (Fig. 7d), but the story does not end here. Specimens chemically isolated from limestones provide us with the best information and show that even the outer meshwork appears to be formed on an outer membrane (the ancora sleeve membrane), that is rarely preserved. The impression of the retiolitids given by the meshwork provides only an incomplete and inaccurate picture and we are still far away from really comprehending these strange beasts. It is impossible to understand the evolution from the simple *Rhabdopleura*-like benthic graptolites to the complex Retiolitidae and to describe these within the limitations of our knowledge of the anatomy of the zooids of the extant graptolites.

Graptolite biostratigraphy and exploration

Graptolites have been used for at least 150 years to provide information on the age of rock successions and to date geological strata. The short biostratigraphical range of many graptolite taxa enables them to be used for very precise dating. Some graptolite biozones

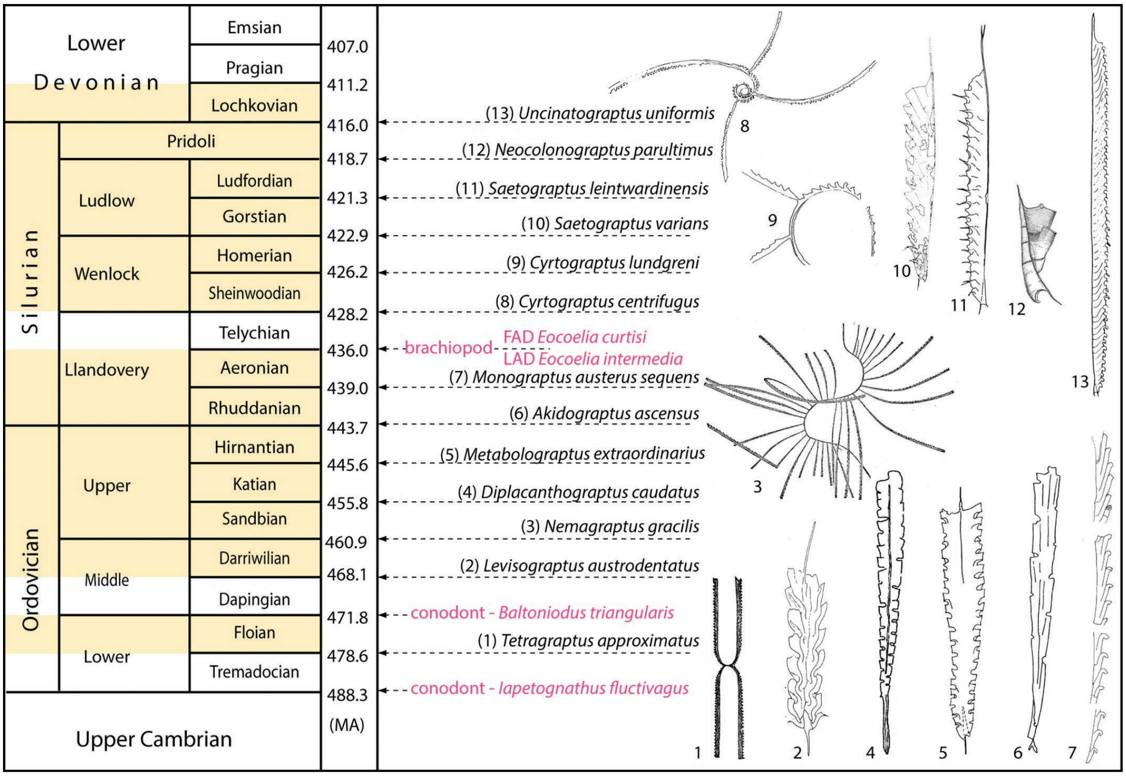

Fig. 8. Graptolite index species for chronostratigraphy (GSSP—Global Stratotype Section and Point) of the International Commission on Stratigraphy (ICS). Graptolite specimens represent the index species, illustrations not to scale.

and subzones span a mere 100000 years, but in general individual graptolite biozones may be one to three million years in length, still considerably below the uncertainties of most radiometric dating methods. Thus, graptolite biostratigraphy is the prime option for dating early Palaeozoic marine successions, but it only works when graptolites are present in the rocks. The importance of graptolites can easily be seen in their use for the determination of chronostratigraphical units. 13 of 16 GSSPs (Global Stratotype Section and Points) at the stage level in the interval from the base of the Ordovician System to the base of the Devonian System are based on the first appearance (FAD) of graptolite species (Fig. 8).

Much is known about biodiversity, origination and extinction events during the 150 million years of the existence of planktic graptolites (Fig. 9), while little evidence has been collected on the patterns of their benthic ancestors and relatives. A number of origination and extinction events can be documented through the diversity patterns of the planktic graptolites in the Ordovician and Silurian, some of them quite severe. The patterns differ from group to group and often one group disappears and another one takes over and flourishes in a complex and unpredictable connection and interaction. At least during the late Hirnantian (HiEE) in the uppermost Ordovician and the *Lundgreni* Extinction event (HomEE) in the Homerian (late Wenlock, Upper Silurian), the planktic graptolites were close to a final extinction. It is said that only two species, a monograptid and a retiolitid, survived the *Lundgreni* extinction event.

The use of graptolites for dating purposes and even for the interpretation of structural geology was first established by the famous British geologist Charles Lapworth during the investigation of the Moffat Series of the Southern Uplands, UK. His work still remains a milestone in graptolite research. It demonstrated the enormous importance of graptolites and graptolite research for geological exploration, as did the application of graptolite biostratigraphy to follow strata-bound gold deposits in Victoria, Australia, in the late nineteenth and early twentieth centuries. The gold deposits of the Bendigo and Castlemaine goldfields generated an enormous increase in graptolite research to understand the structural geology of the region. The economic exploration of the (at the time) largest gold reserves of the world would have been impossible without an investigation of the graptolite faunas in the encasing successions. The names of these goldfields are still found in the regional Bendigonian and Castlemainian stages of the Australasian chronostratigraphy, based on the biostratigraphical ranges of characteristic graptolite species.

Graptolite reflectance data have been compared with the Colour Alteration Index (CAI) of conodonts, as the graptolite fusellum preserves information on the burial history of the entombing sediments. The fusellum changes in colour from brown to silvery, as the coalification of the organic material increases. Thermal alteration and metamorphism of sediments

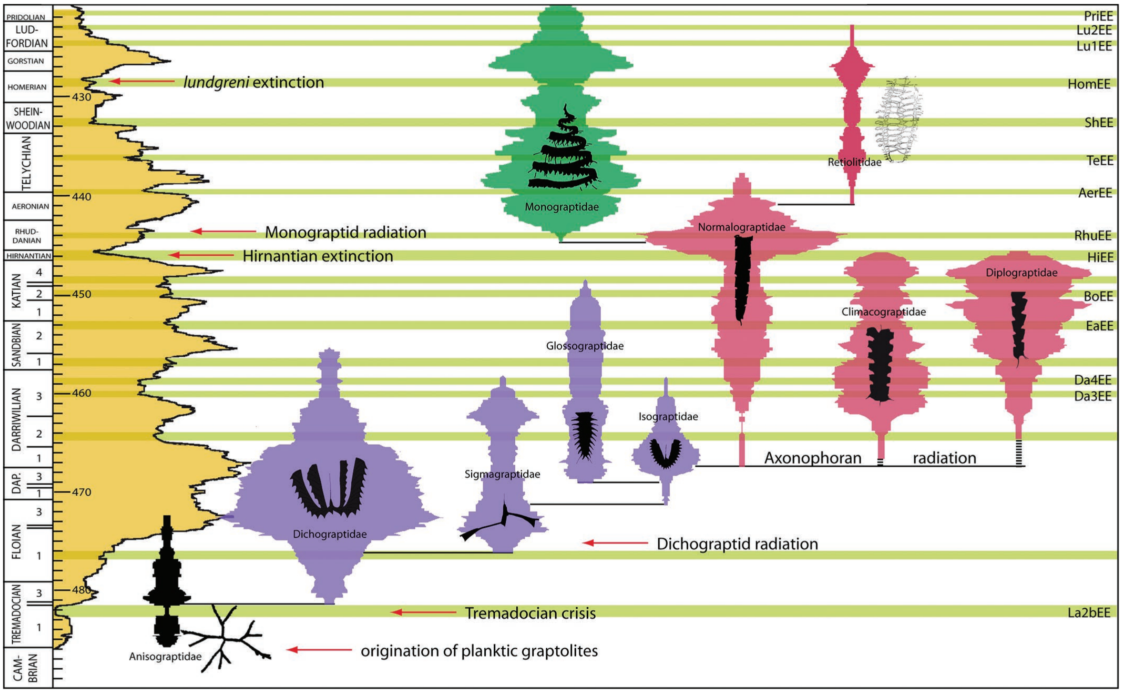

Fig. 9. Graptolite diversity and extinction in the Ordovician and Silurian. The curve on the left represents general diversity. Diversities of selected graptolite groups are shown as balloons. Green horizontal intervals indicate major extinction events.

can be estimated with this observation. This is especially important, as the Palaeozoic graptolite shales of many regions are now regarded as important source rocks for hydrocarbons. Graptolites thus became an instrument for examining potential source rocks for hydrocarbon exploration, including shale gas. It led to the enormous increase of investigations of the Upper Ordovician to Lower Silurian graptolite successions of the Wufeng to Longmaxi formations in the Sichuan Basin of South China over the last few years. A recent assessment of the 'Hot Shales' of North Africa and Arabia through the petroleum industry also shows the importance of Silurian shale basins for economic use. The lower Silurian shales are important hydrocarbon source rocks and are the origin for 80–90 percent of the hydrocarbons of Palaeozoic age in these regions.

There is enormous potential for future geological exploration and exploitation of graptolites and they remain one of the most successful and useful fossil groups in geological research.

Suggestions for further reading

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