

INTERSTIPE WEBBING IN THE SILURIAN GRAPTOLITE *CYRTOGRAPTUS MURCHISONI*

by C. J. UNDERWOOD

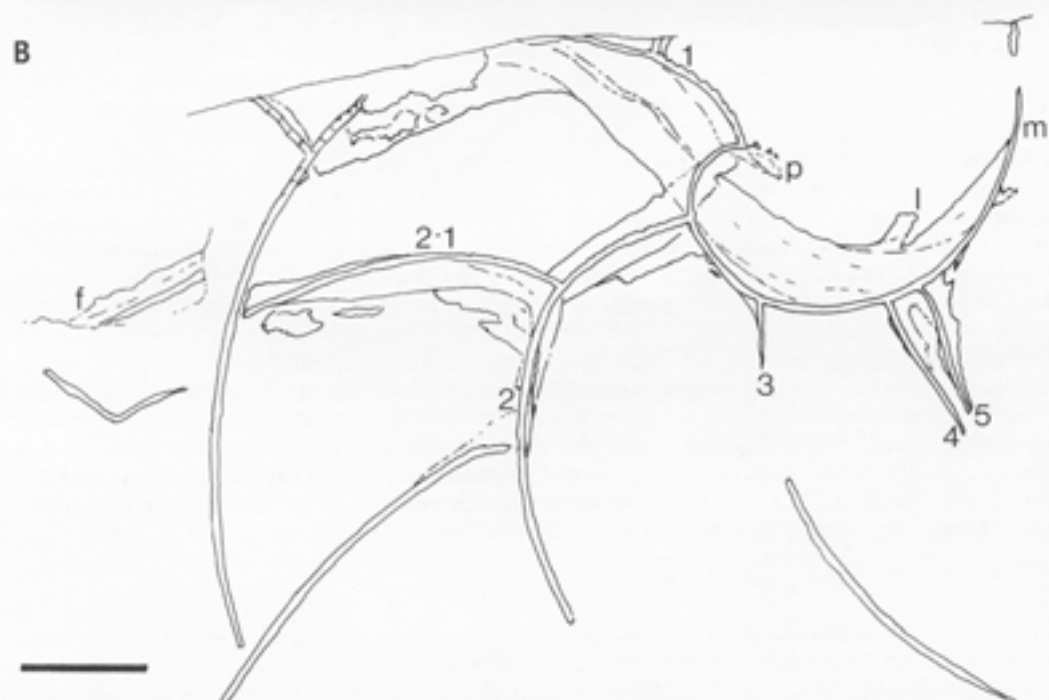
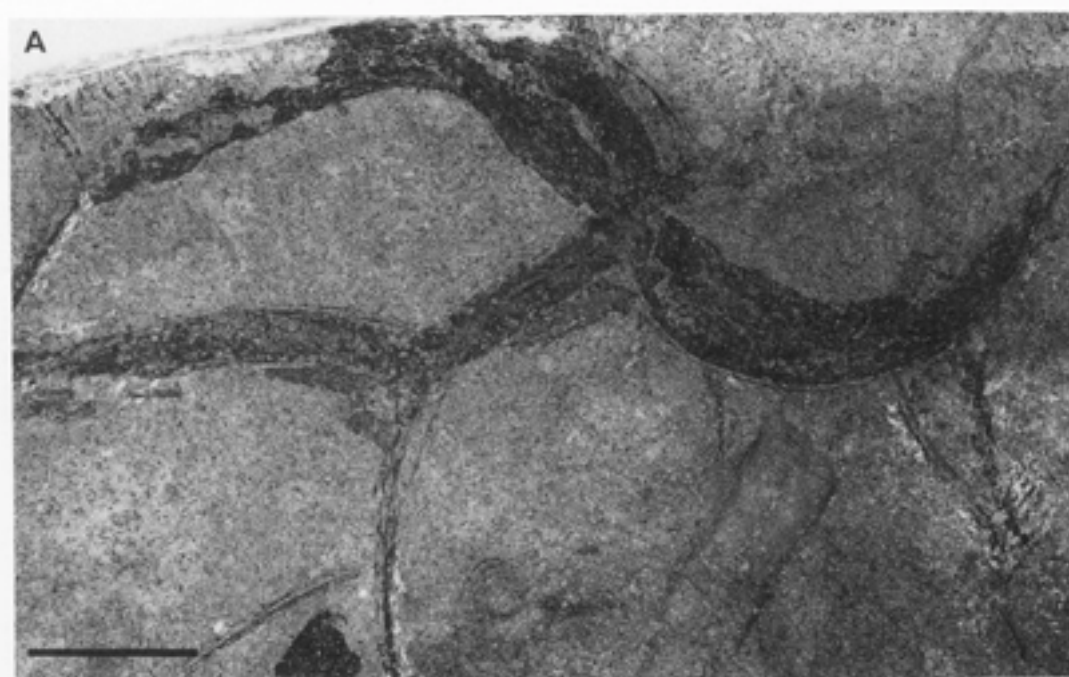
ABSTRACT. Although it has long been recognized that the Graptoloidea constituted a diverse group of planktic organisms, the precise hydrodynamics of the various colony morphotypes has been a source of debate. Recent discoveries of specimens of *Cyrtograptus murchisoni* with a complex suite of webs or vanes between the central coiled stipe and the cladial branches have shown that the hydrodynamic modifications of at least this taxon were considerably more complex than previously thought. These webs are composed of very thin peridermal tissue and stretch between the first or second order cladial branches and the main stipe, the webs overlapping to give a screw-like morphology to the rhabdosome. The form of the webbing also has implications for the mode of life and mobility of individual zooids within the colony, as the main areas of web construction are in regions in which the zooids were enclosed within restricted thecal apertures.

AFTER many years of acceptance of graptolites as passive drifters (e.g. Bulman 1970), it has become evident that graptolites were to some extent motile (e.g. Kirk 1990; Rigby 1991; Underwood 1993). The degree and form of this motility is controlled by the hydrodynamic properties of the living rhabdosome (Rigby 1991), which may not necessarily be the same as those of the dead colony as preserved owing to the influence of zooidal and other 'unpreserved' tissues (Underwood 1993). Although no preserved hydrodynamically important parts of zooids (such as lophophores) are known, a number of rarely preserved semi-sclerotized tissues have been recorded. These include proximal webbing in several taxa of anisograptids (Bulman 1970), ancoral periderm in retiolitids (Lenz and Melchin 1987; Bates and Kirk 1992) and a single example of a proximal web in *Cyrtograptus* (Lenz 1974). Such structures are of fundamental importance to the interpretation of the functional morphology of these taxa.

The discovery of three specimens of *Cyrtograptus murchisoni* Carruthers, 1867 with complex interstipe webbing has important implications for graptolite functional morphology and lifestyle. They were found by Mr Brian Beveridge in the *murchisoni* Biozone (Silurian, Wenlock Series) of Buttington Brick Pit, near Welshpool, Powys, Wales (see Cave and Dixon 1993 for locality details). They are preserved as periderm compressions in a grey mudstone, associated with a rich fauna of other *C. murchisoni*, *Monograptus priodon* (Bronn) and *Monoclimacis* sp., along with occasional pelmatozoan material, bivalves and trilobites. None of the specimens has a counterpart. The presence of web-bearing stipe fragments of other individuals of *Cyrtograptus* on two of the slabs suggests that interstipe webbing was normal, but is preserved only under particularly favourable taphonomic conditions. All three specimens are exposed with the sicular or apical surface uppermost, but with the sicula itself missing, and all show sinistral coiling, but it is unclear whether this is characteristic of the taxon. The specimens are deposited in the collection of the Bristol City Museum and Art Gallery, registered as BRSMG Cd2548-2550.

WEB MORPHOLOGY

A proximal web was described from a specimen of *Cyrtograptus* by Lenz (1974) as a simple sheet of periderm stretched between the main stipe and the first two cladial branches. The far larger and more mature rhabdosomes of *C. murchisoni*, however, show that the web in this species was not a single sheet draped between branches, but a complex series of sheets showing varying degrees of overlap.



TEXT-FIG. 1. For caption see opposite.

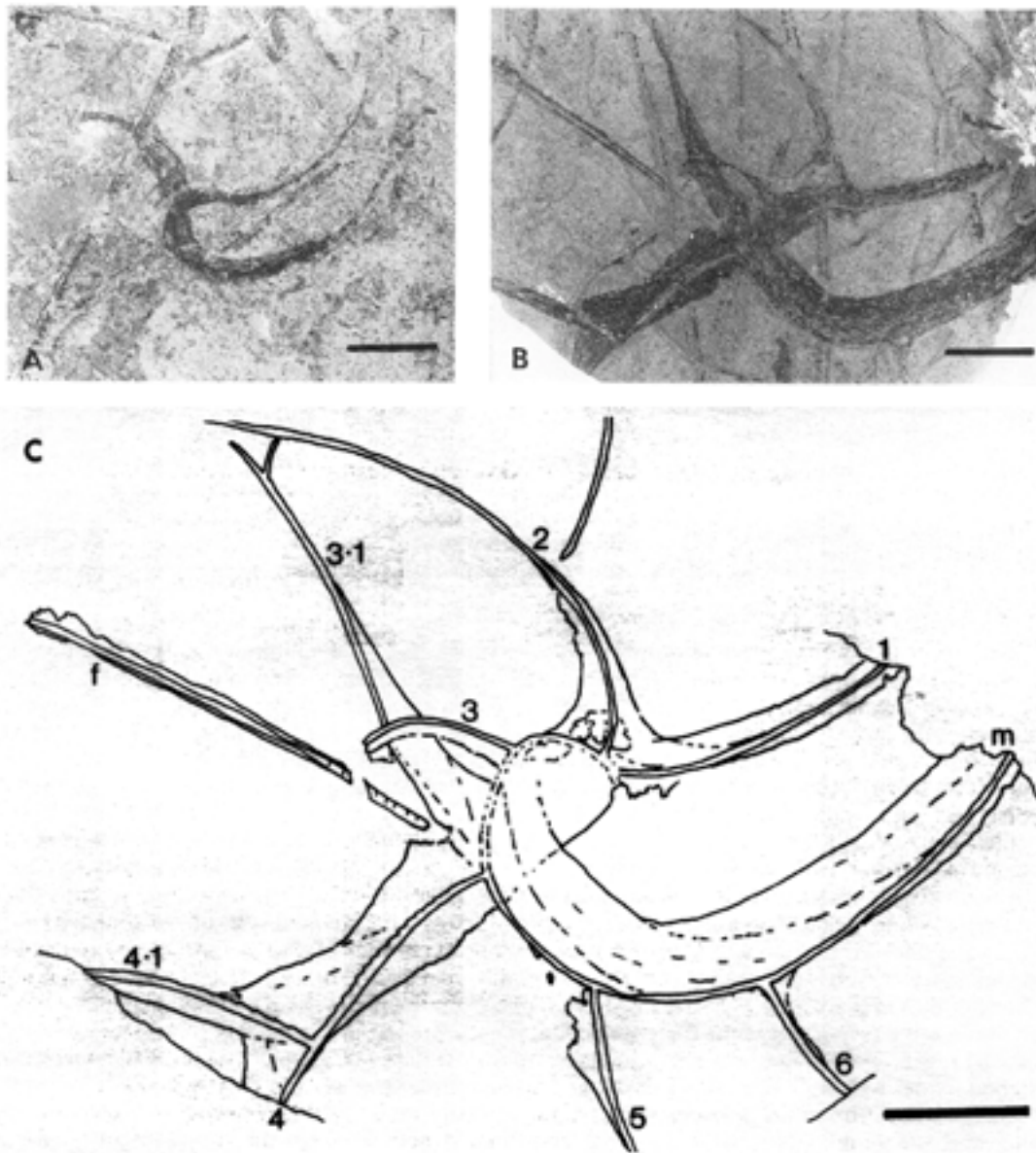
Specimen Cd2550 represents a mature rhabdosome, and possesses the most readily recognizable web structure (Text-fig. 1A–B). The webs are present as a series of overlapping sheets, which generally become more extensive towards the central part of the rhabdosome. Many of the webs grade distally from a wide sheet to a narrow flange which becomes difficult to differentiate from the ‘normal’ stipe, with some suggestion of these flanges being present along almost all of the stipes of the graptolites studied.

Although very poorly preserved, there is evidence of a small web at the extreme proximal end, stretching probably from the sicula to the first cladium. The webbing over the rest of the primary stipe is broad and extends along its concave edge until the origination of at least the fifth cladium. It appears to be in three distinct overlapping layers, with the more distal layers being overlapped by the more proximal (Text-fig. 3); the most distal of these has a large lobe or irregularity on its trailing edge. The webs along the first cladial stipe are more extensive than along the primary stipe, but also appear to be composed of three overlapping sheets stretched along the concave edge. It appears that these are, at least in part, continuous with webs along the primary stipe. The third major area of webbing is along the second cladial stipe and its second order branches. Less easily interpreted than the other two areas of webs, this appears to consist of two main layers. The better preserved of these is present along the concave and convex sides of the main cladial stipe, as well as forming an extensive web along the second order branch 2·1. This is probably continuous with the second web along the primary stipe. A second, much wider web is also evident along branch 2·1, behind (abscicular to) the aforementioned web. Small webs are also present along the proximal parts of cladial stipes 3, 4 and 5, as well as forming a small process which may mark the position of stipe 6, which is not seen.

The smallest of the specimens, Cd2549, shows the simplest web structure (Text-fig. 2A). There appear to be two webs along the primary stipe, each of which is in continuity with webs along the first two cladial stipes. The longer of these is seen to stretch from 13 mm along the cladial stipe 1, passes over the adscicular (‘upper’) surface of the primary stipe before extending 35 mm along its concave edge, whilst the second, wider, web extends from the concave edge of cladial stipe 2, passes over the adscicular surface of the earlier web and continues as a wider second web along the primary stipe. A further small area of similar material may indicate an incipient web along the poorly preserved third cladium.

Specimen Cd2548 is the most mature and complex rhabdosome (Text-fig. 2B–C). Although the webs are generally well preserved, the proximal end of the primary stipe has been largely lost with the counterpart, making interpretation difficult. The most proximal webs extend along both sides of cladial stipes 1 and 2 and are then seen to pass across the proximal part of the primary stipe. Although unclear, this then appears to continue along both sides of cladial stipe 4 and branch 4·1. A small area of web is also visible at the base of third order cladial branch 2·1·1 (not seen in figures), showing that in places the web extends over 70 mm from the primary stipe. Cladial stipe 3 appears to provide the origin of two or three webs. One web is present along the concave edge of the first order branch, extending along the primary stipe to just past the origination of cladial stipe 5. A second, wider web is present along the edge of second order branch 3·1. This appears to pass over the asicular surface of all of the previous webs, extending along the concave edge of the primary stipe and attaching to its convex edge close to the origination of cladial stipe 4. It also appears that the main web, which extends along the concave side of the primary stipe, itself probably consisting of two overlapping sheets, may originate in the area of stipe 3. A small web is also present between the convex edges of the primary stipe and cladial stipes 5 and possibly 6.

TEXT-FIG. 1. *Cyrtograptus purchisoni*, Wenlock Series, Buttington, Powys. BRSMG Cd2550. A, central portion showing the wrinkled and overlapping nature of the dark interstipe webs. B, drawing interpreting the full extent of the webs along the proximal parts of the stipes. Note the small proximal web (p) and the lobe of web material (l). The main stipe (m) is labelled, as are the cladial branches 1–5 and second order branch 2·1. The webbed stipe fragment (f) belongs to another specimen at a lower level in the rock. Scale bars represent 10 mm.



TEXT-FIG. 2. *Cyrtograptus murchisoni*, Wenlock Series, Buttington, Powys. A, BRSMG Cd2549, small rhabdosome, with only two webs visible. B, BRSMG Cd 2548, large and complex rhabdosome. C, drawing of BRSMG Cd2548, showing the complex nature of the multiple, overlapping interstipe webs. The main stipe (m) is labelled, as are the cladia 1-6 and second order branches 3-1 and 4-1. The webbed stipe upper left (f) probably belongs to a second specimen. Scale bars represent 10 mm.

A straight stipe fragment with some webbing between cladial stipes 3 and 4 appears to be on a lower lamella in the rock and belongs to a separate specimen.

WEB STRUCTURE

The webs appear as dark, vaguely striated films. In places, pyrite polyframboids are present, but these are surface encrustations rather than infills of some hollow structure. The dark material appears to be normal periderm, but is seen to be far thinner than periderm from the stipes and cladia. The striations could represent original structure, but their irregular form makes them more likely to be the manifestation of a wrinkled surface texture. Otherwise there is no evidence for the microstructural composition of the webs. However, as structures obviously post-dating the formation of the thecae, it is likely that they are composed largely or totally of cortical tissue (see Crowther 1981).

The hydrodynamic properties of the web periderm would have been strongly influenced by its rigidity in life. Normal graptolite periderm in life was a rigid material, but far more likely to deform in a ductile than brittle manner (as evidenced by the extreme predominance of buckled over broken stipes in fossil assemblages). The probable wrinkled surface texture of the webs suggests that they were composed of a far more flexible material. This suggestion is supported up by the ease with which the webs twist as they pass from the convex edges of the cladial branches to primary stipe. It is unclear whether the webs represented a loose, flexible sheet or an elastic membrane. Small-scale scalloping along some of the trailing edges of webs could either be a result of contraction of a flexible web or reflect original irregularities in the edge. In specimen Cd 2550 these form a small loose lobe, showing that some original irregularities are present.

IMPLICATIONS FOR PERIDERM CONSTRUCTION

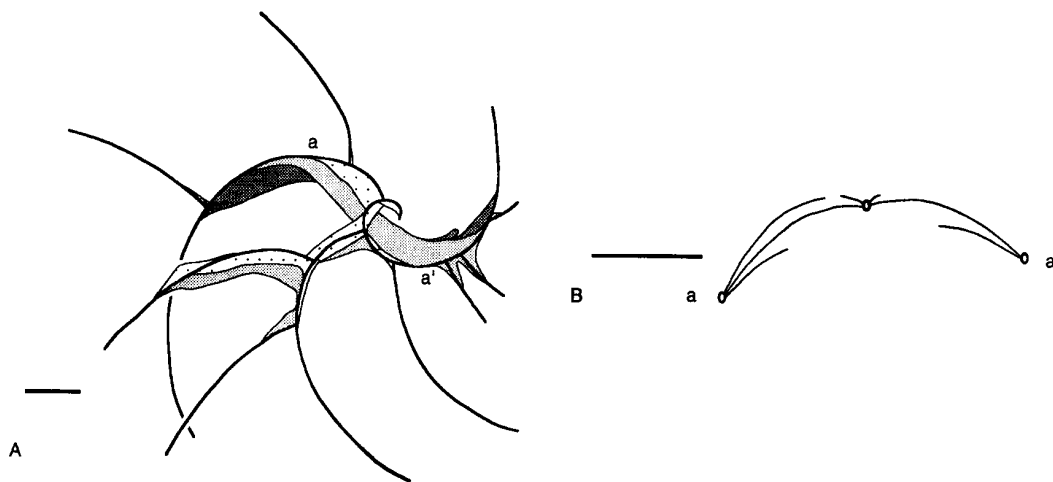
The presence of wide peridermal webs has considerable implications for the manner by which periderm was laid down. The general manner of periderm secretion was for the thecae to be built up by the zooids secreting fusellar tissue, with the subsequent addition of cortical bandages to both outer and inner surfaces (Crowther 1981). Structures such as nemal vanes were built in a similar manner, being constructed by the most mobile, distal, zooids (Urbanek 1973). In all cases, it was probably only the more distal zooids which carried out the construction. The webs in *C. purchisoni*, however, are concentrated at the proximal ends of mature rhabdosomes and must thus have been constructed at a considerable distance from developing zooids. This is shown by an increase in colony size and complexity in the series of specimens Cd2549–2550–2548, with a corresponding increase in area and complexity of the webs. The size of these webs, extending up to 8 mm from the closest zooid, would suggest highly mobile proximal zooids. However, this is not suggested by the thecal morphology. The thecae of *Cyrtograptus*, especially at the proximal end, are hooked with restricted apertures. This modification was almost certainly defensive (Underwood 1993), preventing access by predators, but also probably restricted zooid mobility. Each web also stretches across many thecae, and would have required coordinated activity from all zooids involved for its construction. There are thus three options for the mode of web secretion. (1) The morphology of the webs could easily be accommodated by secretion within a body of extrathecal tissue (e.g. Kirk 1972). This, however, would contradict the need for restricted thecal apertures, and the body of tissue would detract from the hydrodynamic advantage given by the webs, and therefore seems unlikely. (2) Zooids were both considerably more mobile than previously thought, and showed extremely highly coordinated behaviour. They were also small enough to fit through the restricted proximal thecal apertures. (3) It is possible that the unrestricted distal zooids carried out the construction. This would involve high mobility, with zooids needing to have travelled over 100 mm from the growing stipe ends. This mechanism would also have been possible if the thecae below the webs were empty or occupied by non-mobile zooids.

IMPLICATIONS FOR HYDRODYNAMICS AND FEEDING

It is obvious from the general form of the rhabdosome that the hydrodynamics of *Cyrtograptus* were both complex and closely constrained. It has long been realized that the spiral of the main stipe forms a low, open cone (e.g. Bulman 1970), with it now being evident, owing to the manner in which stipes overlie each other, that the cladial branches diverge at a steeper angle, emphasizing the general conical form. The spiral pattern of the *Cyrtograptus* rhabdosome is itself closely constrained, following a set geometric pattern within each taxon (Huo *et al.* 1986). Within this controlled pattern, the morphology of the interstipe sheets is closely constrained by the spiral geometry of the rhabdosome. Although this was suggested by Lenz (1974) from his observations on a webbed specimen, the small and broken nature of that specimen prevented any firm conclusions.

Physical modelling of the mode of movement of graptolites by Rigby and Rickards (1989) included work on large *Cyrtograptus*, but no allowance was made for the presence of interstipe webbing. The effects of interstipe webs on the hydrodynamics of large multiramose dichograptids were modelled, as the presence of these webs is well known within a range of taxa (Bulman 1970). Dichograptid webs are not, however, directly functionally analogous with the webs of *Cyrtograptus*, as they formed a simple drape between the symmetrical stipes of a planar rhabdosome. This symmetrical webbing in dichograptids would thus have acted simply to increase surface area and reduce the rate of movement, whilst the complex screw morphology of *Cyrtograptus* webs would have controlled the rate of movement, degree of rotation and probably the rhabdosome orientation.

The overlapping nature of the webbing suggests that the hydrodynamic structure was not so much a planar screw controlling water flow over a single curved surface, but more a series of (probably flexible) 'wings' or 'sails' acting to direct water through distinct channels between the stipes (see Text-fig. 3). Along the leading edge of each of these wings was a stipe filled with zooids.



TEXT-FIG. 3. *Cyrtograptus murchisoni*, Wenlock Series, Buttington, Powys. A, diagrammatic reconstruction of BRSMG Cd2550 showing the various layers of interstipe webbing recognized. There is no suggestion that all the webs of the same generation are laterally continuous with each other. B, hypothetical life cross section along line a-a' in A showing the overlapping relationships of the webs. Scale bars represent 10 mm.

Any water through which the central area of the rhabdosome passed thus had to pass through the lophophores of the zooids and the channels between the webs. It is therefore likely that although the webs controlled the flow of water in a purely passive manner, the water flowing over the webs could have been controlled by the zooids.

As filter feeders, the flow of water over the zooids would have controlled the quantity of food

available to the colony. The webs would thus have directly (by directing water over the zooids) and indirectly (by helping control the mobility of the rhabdosome) increased the feeding efficiency of the colony. This would support the idea that *Cyrtograptus* was adapted for highly efficient feeding (Rigby 1991) within deeper, more nutrient-poor waters (e.g. Kirk 1990; Underwood 1993).

The direction of movement of *Cyrtograptus* was assumed by Underwood (1993) to be open end first, the colony acting as an open 'trawl net'. In all three specimens examined, however, narrower webs are present on the adscicular surface of wider ones. To get a hydrodynamic benefit from these narrower webs the colony would have had to move adscicular (closed) end first. This style of orientation with the point of the cone up-current has been noted within other groups of filter feeders, particularly crinoids (Prof. C. R. C. Paul, pers. comm. 1994). On the largest specimen (Cd 2548), however, one narrow web is seen to pass over the abscicular surface of a wider one. It may be therefore, the movement of *Cyrtograptus* was not simply unidirectional, and the colony may have been able to move in a variety of orientations.

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REFERENCES

- BATES, D. E. B. and KIRK, N. H. 1992. The ultrastructure, mode of construction and functioning of a number of Llandovery ancorate diplograptid and retiolitid graptolites. *Modern Geology*, **17**, 1–270.
- BULMAN, O. M. B. 1970. Graptolithina, with sections on Enteropneusta and Pterobranchia. VI–V163. In TIECHERT, C. (ed.). *Treatise on Invertebrate Paleontology. Part V* (2nd Edition). Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, i–xxxii + 163 pp.
- CARRUTHERS, W. 1867. On Graptolites. 538–541. In MURCHISON, R. I. *Siluria*. 4th Edition. London
- CAVE, R. and DIXON, R. J. 1993. The Ordovician and Silurian of the Welshpool area. 51–84. In WOODCOCK, N. H. and BASSETT, M. G. (eds). *Geological excursions in Powys, Central Wales*. University of Wales Press, Cardiff, 366 pp.
- CROWTHER, P. R. 1981. The fine structure of graptolite periderm. *Special Papers in Palaeontology*, **26**, 1–119.
- HUO SHI-CHENG, FU LI-PU and SHU DE-GAN. 1986. A mathematical study of the *Cyrtograptus sakmaricus* lineage with discussions of the evolutionary trends in this lineage. 197–205. In HUGHES, C. P. and RICKARDS, R. B. (eds). *Palaeoecology and biostratigraphy of graptolites*. Geological Society Special Publication No. 20, Oxford, 277 pp.
- KIRK, N. H. 1972. Some thoughts on the construction of the rhabdosomes in the Graptolithina, with special reference to extrathecal tissue and its bearing on the theory of automobility. *University College of Wales, Aberystwyth. Department of Geology Publication*, **1**, 21 pp.
- 1990. Juvenile sessility, vertical automobility and passive lateral transport as factors in graptoloid evolution. *Modern Geology*, **14**, 153–187.
- LENZ, A. C. 1974. A membrane-bearing *Cyrtograptus* and the interpretation of the hydrodynamics of cyrtograptids. *Special Papers in Palaeontology*, **13**, 205–214.
- and MELCHIN, M. J. 1987. Peridermal and interthecal tissue in Silurian retiolitid graptolites: with examples from Sweden and Arctic Canada. *Lethaia*, **20**, 353–359.
- RIGBY, S. 1991. Feeding strategies of graptolites. *Palaeontology*, **34**, 797–815.
- and RICKARDS, R. B. 1989. New evidence for the life habits of graptoloids from physical modelling. *Paleobiology*, **15**, 402–413.
- UNDERWOOD, C. J. 1993. The position of graptolites within Lower Palaeozoic planktic ecosystems. *Lethaia*, **26**, 189–202.
- URBANEK, A. 1973. Organization and evolution of graptolite colonies. 414–441. In BOARDMAN, R. S., CHEETHAM, A. H. and OLIVER, W. A. (eds). *Animal colonies through time*. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.

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