

The position of graptolites within Lower Palaeozoic planktic ecosystems

Charlie J. Underwood

An integrated approach has been used to assess the palaeoecology of graptolites both as a discrete group and also as a part of the biota present within Ordovician and Silurian planktic realms. Study of the functional morphology of graptolites and comparisons with recent ecological analogues demonstrates that graptolites most probably filled a variety of niches as primary consumers, with modes of life related to the colony morphotype. Graptolite coloniality was extremely ordered, lacking any close morphological analogues in Recent faunas. To obtain maximum functional efficiency, graptolites would have needed varying degrees of coordinated automobility. A change in lifestyle related to ontogenetic changes was prevalent within many graptolite groups. Differing lifestyle was reflected by differing reproductive strategies, with synrhabdosomes most likely being a method for rapid asexual reproduction. Direct evidence in the form of graptolithophage 'coprolitic' bodies, as well as indirect evidence in the form of probable defensive adaptations, indicate that graptolites comprised a food item for a variety of predators. Graptolites were also hosts to a variety of parasitic organisms and provided an important nutrient source for scavenging organisms. **KEY WORDS;** *Feeding, graptolites, hydrodynamics, ontogeny, parasitism, palaeoecology, plankton, predation.*

*Charlie.J. Underwood, Department of Geology, University of Bristol, Wills Memorial Building,
Queens Road, Bristol, BS81RJ, England. May 27, 1992.*

Graptolitic ecogroups.

Within Ordovician and Silurian rocks the benthic ecogroups or assemblages which characterize shelf sediments are well documented (e.g. Cocks & McKerrow 1978a, b; Ziegler *et al.* 1968) allowing at least some picture of the organism interactions to be built up. Within more distal environments with a fauna largely of planktic and nektonic elements the assemblages tend to be 'unclassified' or referred to simply as 'graptolitic' (e.g. Brenchley 1990; Cocks & McKerrow 1978a, b; Williams & Rickards, 1984). Graptolites are dominant, in terms of both diversity and biomass, among groups of non-benthic organisms preserved in these environments.

Many graptolitic assemblages are accompanied by an insignificant and low diversity benthos, largely of small and thin shelled inarticulate brachiopods (Williams & Lockley 1983), hyoliths and trilobites, with specialist articulate brachiopods (Sheehan 1977) and praecardioid bivalves appearing in the Silurian. Sponge spicules may be present in large numbers (Bulman, 1964; Rickards 1990) indicating rich faunas of low-oxygen tolerant sponges. In many deposits, especially in the Silurian, orthoconic cephalopods may dominate these low diversity benthic assemblages. Within some deposits crinoids or benthic dendroid graptoloids may also be present. A non-shelly benthos is proved by the frequent presence of the burrow network *Chondrites*. These burrows are often present within graptolitic sediments even in the absence of any other benthos and must thus represent the behaviour of highly tolerant organisms (Bromley & Ekdale 1984; Ekdale & Mason 1988). Within other graptolite-dominated sequences, planktic elements such as radiolaria, acritarchs (Rickards 1990) and, from the mid-Silurian, myodocopid ostracodes (Siveter 1989), may all be present without any associated benthos. Less common but important elements within such biotas include conodont elements (Williams & Barnes 1988), scolecodonts and phyllocarids (Rolfe 1969: R316; Størmer 1937) and specialist trilobites (Fortey 1985; Fortey & Owens 1987). Within such assemblages, orthoconic cephalopods are generally rare or absent, indicating a probable nektobenthic habit for many species as opposed to a truly nektonic habit, and hence being subject both to benthic oxygen levels and to water pressure (Wells *et al.* 1992).

Within most ecosystems, and especially those within the planktic realm, there are a variety of non-skeletonised and non-trace making organisms for which fossil evidence is, at best, conjectural and, at worst, hypothetical. As a result, no fossil assemblages can be relied on to produce a full consensus of the original biota, and more indirect approaches must be used to evaluate the entire fauna.

Lower Palaeozoic oceanic conditions

Reviews of oceanic conditions within the Lower Palaeozoic (e.g. Cloud 1983; Holland 1984; Wilde & Berry 1984) have generally identified a rise in atmospheric oxygen through the Palaeozoic, with initial low oxygen levels being linked to the abundance of early Palaeozoic anoxic mudstones. The characteristic 'anoxic black shale' facies within which graptolites are frequently abundant are not, however, restricted to the Lower Palaeozoic, but are found periodically from Cambrian to Carboniferous, and again within the Mesozoic (Leggett *et al.*, 1981; Wilde & Berry 1984). Even

within these 'anoxia rich' periods, the existence of oxygen poor basinal conditions was not continuous, with several aerated phases being recorded, such as within the Ashgill (Berry 1989; Leggett *et al.*, 1981), upper Llandovery and uppermost Wenlock (Kemp 1991). There thus appears to be little fundamental difference between lower Palaeozoic and Post-Silurian oceanic conditions, with atmospheric oxygen levels not integrally linked to that within oceanic systems, which appear to be far more dependant on transgressive/regressive cycles and the presence of glacial episodes (Wilde & Berry 1984).

The graptolite as a living organism

Coloniality.- A graptolite rhabdosome represents a colony, which, as in other colonial organisms, consisted of a collection of separate clonal individuals in stolonal continuity, with all of the individuals of the same genotype. Individual planktic graptolite colonies show a far lower degree of morphological plasticity than any other colonial organisms, with a highly ordered growth plan, and therefore possessing a phenotypically constant set of modifications to the basic pattern (such as cladia, where present). The highly constrained colony morphology allows the geometrical growth forms of stipes (Fortey 1983), branching colonies (Fortey & Bell 1987) and spiral colonies (Shi-cheng *et al* 1986) to be modelled mathematically. Graptolites also show an extremely low rate of morphological reiteration in response to trauma compared to other colonial organisms (Rosen 1990).

Graptolites show a high degree of division of labour between zooids. This tends to be slight within most colonial organisms and modern hemichordates such as *Rhabdopleura* show only slight differentiation between sexual and feeding zooids (Hutt 1991). The siculazoid in graptolites, however, almost certainly played a different role in the development and behaviour of the colony to that of subsequent 'adult' zooids. Despite the strong coloniality, the ability of individual zooids to leave the theca to apply cortical material (Crowther 1978, 1981), indicates that they were not restricted entirely to coordinated behaviour. Within rhabdosomes with restricted apertures in the fully developed form, as in many monograptids, the zooid would have been unable to leave the confines of the theca, and so the developing, most distal zooid must have applied external cortical bandages and secreted the nema. The developing zooid therefore changed function during growth from that of a 'free roving' builder to a sedentary feeder. The combination of the division of labour, the extreme symmetry of the rhabdosome, and the far higher degree of coloniality than modern pterobranchs or other comparable organisms (Urbanek 1986) suggest that the graptolite colony should be treated more as a 'super individual' than as a set of separate entities. The rhabdosome must have functioned as a single, coordinated entity rather than as a loose collection of functionally independent individuals. Anatomically, the presence of a 'common canal' within graptolite rhabdosomes allows for a considerable amount of stolonal connection between zooids, and hence close communication would be more readily achieved than in most colonial organisms.

Diet.- The apertures of even large graptolite thecae with simple openings rarely exceed 2mm across, severely restricting the maximum size for food particles, assuming that external comminution of food did not precede internal digestion. Most graptolites have even smaller apertures, and in a large

number of species these are reduced by lobes, lappets or spines, restricting the maximum size of particle uptake even further. Thus larger food particles such as many radiolarians and chitinozoans could not have been consumed. In modern Antarctic oceanic systems, for example, the largest proportion of zooplankton biomass (*Euphausia spp.*) feeds largely on phytoplankton (Hopkins, 1985). By direct comparison it seems likely that graptolites grazed on floating phytoplankton and were thus primary consumers (Berry & Wilde, 1990; Bulman, 1964). The model of graptolites as the main primary consumer would allow for Lower Palaeozoic planktic ecosystems to possess a similar trophic structure to that in modern systems. Because of the short nature of planktic food chains, there is a discontinuous variation of biomass with size, with peaks relating to bacteria, microphytoplankton, miozooplankton (euphausiids, copepods etc.) and megazooplankton (scyphozoans etc.) (Parsons & Takahashi, 1973). This size distribution would compare favourably to a Palaeozoic system of bacteria, phytoplankton, graptolites and large predators. Between 10% and 90% of carbon within the production zone in modern oceans is in the form of dead particulate debris (Steele 1974). The presence of this material may help buffer planktic ecosystems from the effects of reduced photosynthetic productivity during winter. The association of graptolites with symbiotic algae has been suggested (Kirk 1990), but the presence of a largely opaque periderm in most species makes this highly unlikely.

Grazing on phytoplankton is very heavy compared with that on terrestrial plants, leading to frequent 'overgrazing' of areas of productivity and a very patchy phytoplankton distribution. The spread of phytoplankton outwards from these patches tends to be by passive biodiffusion. Patchy distribution of zooplankton on the other hand is due more to active swarming (Okubo, 1978). Some modern zooplankton species, such as *Euphausia superba*, form extremely dense swarms with a monospecific biomass of 1.5 to 15kg/m³ (Everson, 1977). Similar behaviour in graptolites may, at least in part, allow for the formation of the common monospecific concentrations of graptolites on certain bedding planes. These would appear to be analogous with some of the death assemblage swarms noted for other non-benthic organisms such as fish, crustaceans and belemnites (Boucot 1990, pp.142-149).

Mobility.- The feeding methods of a planktic organism are largely dependant on how motile it is. Poorly motile forms have to rely on a passive 'drift netting' mode of food capture, whilst those with some degree of self motility may use a variety of techniques varying from undirected movement until a food-rich area is located to systematic 'trawling' for food particles.

Immotile organisms can only acquire free floating food and oxygen where they are carried at a different speed to the water flow (Rigby & Rickards, 1989). Passive drifters move at the same rate as the surrounding water body making feeding from lateral currents (as suggested by Rickards, 1975) impossible. The few immotile members of the modern macrozooplankton, such as the cystonectid siphonophoran *Physalia*, get round this problem by the use of air currents as a source of propulsion. For an animal trapped within the water column, however, some form of motility is necessary.

Within a colonial organism two basic forms of motility are possible. Motility of the colony as a whole is generally uncommon among Recent colonial organisms, and is present only in specialised forms such as some siphonophorans. Even when the colony as a whole is sessile, individual zooids may be capable of degrees of movement ranging from the production of feeding currents to almost free movement within the confines of the colony as seen in the hemichordate *Cephalodiscus*. Within some colonies the movement of zooids may be highly coordinated, as in feeding and waste removal in a number of bryozoans such as *Cauloramphus* (Winston, 1979). Within a free living planktic colony any movement of individual zooids will have some effect on the behaviour of the colony within the water column. Hence some form of automobility in graptolites (Kirk, 1969, 1972a,b, 1978, 1990) need not invoke fully coordinated zooidal activity (Williams, 1987). However, given the extremely high degree of coloniality demonstrated by graptolite morphology, it is likely that the zooids were capable of some coordinated movement, as in some bryozoans.

The most pervasive use of motility within modern zooplankton is that of diurnal vertical migration, of often up to several hundred metres. This migration may function in avoiding predators or toxic photosynthetic byproducts of phytoplankton, or it may reduce competition between species or allow for the organism to take advantage of deep currents to move the organism to a different water mass each day (Marshall, 1979).

Interpretations of the mode of life of graptolites have tended to polarise, some authors regarding them as actively automobile (Erdtmann, 1971a; Kirk, 1969, 1972a,b, 1978, 1990; Lenz, 1974; Rigby, 1991b, 1992), others as passive drifters (Bulman, 1964, 1970; Rickards 1975). Both experimental (Rigby 1991b; Rigby & Rickards, 1989) and mathematical (Rigby 1992) modelling have shown that most graptolite colony forms showed a tendency to spiral through the water column, an action imposed purely passively due to the colony morphotype and a density variation between between the rhabdosome and surrounding water. Although descent may have been passive (a tactic favoured by many recent planktic organisms)(Rigby, 1991a; Rigby & Rickards, 1989), coordinated automobility would still have been needed to restore the colony to its original position prior to another feeding spiral (Rigby 1992). Within euphausiids such as *Meganycitiphanes norvegica* (Mauchline & Fisher, 1969), for example, the diurnal descent is entirely passive, whilst the slower rise is carried out by active swimming.

It has been suggested that least some graptolites possessed vacuolated tissues supported by nemal vanes (Bulman, 1964; Bulman & Størmer, 1971). Vertical movement may then have been controlled by varying the tissue density, either by altering the quantity of gas (as in the cephalopod *Spirula*), or low density fluids (as in the radiolarian *Thalassicola* (Jacobs, 1935)). In the latter case at least, large amounts of extrathecal tissue would be needed. This would be at odds with microstructural evidence for a general lack of extrathecal tissue (Crowther, 1978, 1981), and it is unlikely that organisms showing such a range of probable defensive adaptations would possess a large body of unprotected tissue.

Feeding methods-. Graptolite colonies occur in a number of morphotypes presumably related to feeding strategies (Rigby, 1991a,b, 1992), which can be classified into five main groups on the basis of their functional morphology, although there is a continuous gradation between them. Niches available in the Lower Palaeozoic are difficult to reconstruct, but it is reasonable to assume that nutrient flow, at least at lower trophic levels, has changed little since the formation of a planktic ecosystem. Within deeper marine environments, several different faunules may be present within a water column, and hence vertical superimposition of surfacial and deep water forms will occur within the fossil assemblage (Erdtmann, 1976).

The type 1 'trawl net' morphotype (Fig. 1,1) occurs in the relatively few taxa of graptolite in which the stipe arrangement creates an open-ended cone. Taxa demonstrating this morphotype include *Rhabdinopora* and conically spiral monograptids such as *Monograptus proteus* and *M. turriculatus*. This morphotype would have functioned as a food trawl with a flow of water passing in through the open end of the cone and passing out past the feeding zooids (as in Kirk, 1990). Food gathering would be most effective in a continually moving colony. Within the monograptids where this morphotype is produced by a single coiled stipe, a strong spiral motion would have been imparted into the colony.

The type 2 or 'drift net' morphotype (Fig. 1,2) is a recurrent feature of graptolite evolution. This comprises of a range of taxa producing multi-stiped flat or weakly conical rhabdosomes, often of large size. This morphotype includes such taxa as multiramous dichograptids, *Nemagraptus*, *Pleurograptus*, planar spiral monograptids, *Cyrtograptus* and multiramous diversograptids. A number of these forms possess proximal structures of large surface area to retard and help control movement. Web-like sheets of thin periderm are not uncommon in multiramous dichograptids (Bulman 1970; Rigby & Rickards, 1989), and large, delicate flanges have been observed in *Cyrtograptus* (Lenz 1974). Slow rates of vertical movement (Kirk, 1990; Rigby & Rickards, 1989) and a wide variation in spiral feeding pattern indicate energy efficient, slow moving methods of feeding. Increased rates of rotation would have enabled a high degree of nutrient extraction per unit of water passed through (Rigby 1992), but higher rotation rates would have also reduced the overall velocity of the colony, allowing smaller units of water to be sampled. These feeding techniques would have allowed the extraction of a high proportion of the available food in nutrient poor, quiet waters (Bates & Kirk, 1984; Fortey & Bell, 1987; Kirk, 1990; Rigby 1991b). The occurrence of these morphotypes in deeper water sediments (Bates & Kirk, 1984; Cooper *et al*, 1991) is additional evidence for this strategy. These large, branched graptolites may have filled a benthopelagic niche (as suggested for *Amphigraptus* by Kirk (1990) and numerous Ordovician forms by Erdtmann (1976)), which is occupied today by a wide range of fish, cephalopods and arthropods (Marshall 1979).

The type 3 morphotype (Fig. 1,3) includes any uniserial biramous forms in which the stipes are not bilaterally symmetrical due either to a spiral stipe form (as in *Dicellograptus complexus*), thecal offset (as in *D. complanatus*) (Williams 1987), or asymmetrical proximal structures (as in *Isograptus manubriatus* (Kirk 1972a)), as well as any curved uniramous forms (such as *Azygograptus* and many monograptids). These taxa would have rotated to different degrees during vertical movement as even the smallest amount of curvature or offset would have created some

rotational movement (Rigby & Rickards, 1989). Each zooid would have harvested food from a different, spiral, path through the water column (Rigby 1992). Proximal spines or webs in forms such as *Dicellograptus* may have acted as ballast or balancing organs to maintain a constant orientation (Williams 1987).

In biform monograptids, such as *Monograptus argenteus*, a sudden change in the degree of stipe curvature occurred during ontogeny. This is probably related to a more specialist mode of feeding or a change in feeding strategy related to such a change in stipe symmetry.

The type 4 morphotype (Fig. 1,4) is characterised by uniserial, bilaterally symmetrical stipes. It was prevalent during the Ordovician, occurring in many dichograptids, isograptids and dicranograptids. There may have been too little asymmetry in the rhabdosome to create significant rotation. Even in the absence of significant rotation, however, movement of the rhabdosome would have allowed each zooid to pass through a different unit of water from any other due to the divergence angle of the stipes. During non-rotational movement, each zooid would have passed through a smaller column of water per unit of vertical movement than in colonies where spiral movement occurred, giving a less efficient feeding technique.

The type 5 morphotype (Fig. 1,5) includes straight uni-, bi- or multiseriate scandent forms and is common in taxa from Arenig to Devonian. Asymmetry is uncommon, involving either thecal asymmetry as in glossograptids and *Cucullograptus*, or asymmetry of nemal vanes as in *Pseudoclimacograptus scharenbergi* (Rigby & Rickards, 1989) and species of *Petalograptus* (Bulman, 1964).

Examples of this morphotype are generally assumed to have been orientated vertically in the water, with the sicula opening upwards (Kirk 1969, 1972a,b, 1990) or downwards (as in Bulman, 1970; Rigby 1992)(the vertical 'standard orientation' of Rigby (1991b)). Several reasons have been suggested for assuming the latter 'standard' orientation, but none are based on particularly compelling biological reasoning. Evidence includes the vertical orientation of stipes containing gas bubbles upon release from matrix during acid etching of carbonates (Rickards & Crowther, 1979), but this need not reflect the orientation of living organisms. The slight curvature of the uniserial portion of some dimorphograptids has also been interpreted as an adaptation for vertical stability (Rickards 1975). This curved portion would also have stabilised the colony in other orientations, however, and may have been simply a developmental feature caused by the loss of thecae on one side of an otherwise biserial stipe, as suggested for the curvature of *Atavograptus ceryx* compared to *Glyptograptus* (Rickards & Hutt, 1970). Equally, this curvature is not present in all dimorphograptids (Rickards *et al* 1977). As cortical tissue is applied to thecae as they mature, the older, proximal end of a graptolite would be expected to have thicker, heavier periderm giving weighting of one end of the rhabdosome. However, as the optimum thickness of cortex was probably rapidly reached (especially in forms with restricted apertures)(Crowther 1981), only in very small or juvenile rhabdosomes would any significant lengthwise density contrast exist. Within these rhabdosomes there would have been less intrazooidal competition due to the small numbers of zooids present, as well as a lesser overall energy requirement, and so retention of an optimum feeding orientation would have been less critical. Planar nemal vanes would only have kept the

rhabdosome vertical if heavy enough to act as a keel or light enough to act as a float. Otherwise, the large surface area of these projections would have aided the graptolite maintain any constant orientation. Long nemal and virgellar spines would have served a similar function in many, especially small or juvenile, diplograptids and monograptids.

If members of this group were vertically inclined (Rigby 1992; Rigby & Rickards 1989), whether they rotated or not, the volume of the cylinder of water passed through during vertical movement would have been small and rapidly depleted in nutrients. If movement were sicula first, proximal thecae would have had best access to nutrient whilst the larger, growing, distal zooids would have access to the least nutrient. For a higher efficiency of nutrient gathering, therefore, the colony must have moved sideways in relation to the water. As the resistance of water on the side of a colony during sideways movement would be far greater than that on the end (especially the tapered sicular end), the most efficient use of energy would be to swim upwards sicula first and then turn before sinking sideways (Fig. 1,5). If vacuolated tissues were present over the surface of the nemal vanes, the movement of only small amounts of liquid or gas would be sufficient to 'fine tune' the orientation of the colony. As there would have been some variation in the density or resistance to sinking along the length of the rhabdosome, some amount of active buoyancy control or coordinated zooidal activity may have been needed to maintain a stable position in the water.

These colonies would, however, have extracted only a small proportion of the nutrients from the cylinder of water through which they pass, making this strategy most efficient in areas of high nutrient presence such as within the neritic or surface photosynthetic production zone. Many of the suggested inshore (Finney 1986) and near surface (Bates and Kirk 1984; Cooper *et al.*, 1991; Erdtmann 1976) graptolites consist of this, and the type 4 morphotype. Existence within this preferred habitat has been suggested as the reason for the far higher survivorship of small type 5 morphologies during regressive episodes than any other graptolite forms (Berry & Wilde 1990).

The main production zone in modern oceans usually lies between 10 and 125 m of the surface, and tends to be deeper in the tropics and shallower in neritic areas, with a general downward increase in the size of individual phytoplanktic organisms (Semina 1979). A second concentration of nutrient is at or near the sea bed (as fallout), with little midwater nutrient. Due to this uneven distribution, oceanic biotas tend to be concentrated near the primary production zone or near the sea floor. A comparison has been made between modern zooplankton and graptolites in a preference for a high nitrogen/ low oxygen environment, often related to oxygen minimum zones in areas of upwelling (Berry *et al.*, 1987; Berry & Wilde 1990) Planktonic faunas also show an increase in diversity, but decrease in biomass towards the equator. The variations between density and depth of available nutrient with latitude may explain some of the biogeographical variation of graptolite morphotype (as in Cooper *et al.* 1991).

Ontogeny and the siculazooid.

Many marine organisms undergo an ontogenetic shift in lifestyle, frequently associated with metamorphosis. Graptolites could be said to undergo two stages of gradual metamorphosis, from prosicula to metasicula and from metasicula to adult colony. Both pro and metasiculae were

presumably solitary zooplankton (except when incorporated into a synrhabdosome), possibly resembling pteropods in habit. A benthic habit has, however, been suggested for siculae (Kirk 1990), but this appears to be based on very little evidence. Within some paedomorphic taxa, such as *Corynoides*, this pteropod-like lifestyle was probably retained throughout life. Within, what appear to be ecologically comparable modern planktic euphausiids, after an initial migration to the surface, the larval stages live there and do not undergo a diurnal migration, but gradually descend and undergo larger vertical migrations as maturity is reached (Baker 1959). A similar pattern would have separated siculae and adult graptolites, resulting, as in modern plankton, in less intraspecific competition. The common occurrence of bedding assemblages of either siculae or adults suggests a spatial or behavioural separation. The initial budding of 'adult' zooids introduced an asymmetry into the colony, which became more extreme in bi- and multiramous forms as the first zooids started to feed, setting up asymmetrical water currents. At this point activity of the sicular zooid may have helped stabilise the colony, as would the presence of nemal and virgellar spines. As the adult stipes grew, the stabilising function of the sicula and spines may have been no longer needed, and this may explain the sicular resorption recognised in *Dicellograptus elegans* (Williams 1982) and in 'janograptid' dichograptids, and the covering of the sicula (and proximal thecae) by peridermal 'sheets' noted in many multiramous dichograptids (Rigby & Rickards 1989). The proximal (juvenile) uniserial section in dimorphograptids and scandant portion of *Dicranograptus* may confer hydrodynamic stability during the initial budding of adult zooids by keeping the actively feeding zooids nearer to the centre of gravity of the rhabdosome.

Graptolite reproductive strategies.

The large, frequently branched, graptolites of morphotypes 1 and 2 represent the investment of considerable time and energy in the production of a large number of zooids and a complex and highly ordered rhabdosome. This would have necessitated a long life span in a reasonably stable environment. Some taxa show evidence of reaching a distinct level of maturity: for example at stages of cladial development or thecal dimorphism in *Monograptus argenteus* (Bulman 1970) and *Thamnograptus capillaris* (Finney 1980). Presumably this indicates a regular and 'pre-set' rate of sexual reproduction; there is no evidence of reproduction to take advantage of ephemeral nutrient sources for example. The growth of a large colony in species of *Monograptus*, *Expansograptus* and *Dicranograptus* for example, may have been related to a similar reproductive strategy.

Smaller graptolite taxa from within the higher, more nutrient rich parts of the water column would be expected to show an altogether different reproductive style. These taxa, usually of morphotypes 4 or 5, reached hydrodynamic equilibrium after the budding of only small numbers of 'adult' thecae. The rapid attainment of maturity, and rapid reproduction, either sexual or asexual, would have allowed for the utilization of ephemeral food sources. Taxa such as *Corynoides* and *Holoretiolites simplex* (Kirk 1978) rapidly attained a maximum but small number of thecae, allowing any surplus energy to be used for reproduction instead of growth.

Synrhabdosomes consist of clusters of rhabdosomes attached centrally by the nemata, which may be tangled distally (Rickards 1975; Zalasiewicz 1984), or held together by soft tissue, such as

stolonial threads (Kirk 1978). Some synrhabdosomes may also be attached proximally (Bjerreskov, 1976). A range of unrelated graptolite taxa formed synrhabdosomes (Zalasiewicz 1984), and hence this could be a recurrent, convergent characteristic. Synrhabdosomes occur in several morphotypes, but usually in small colonies such as simple dichograptids (Beckly & Maletz, 1991; Zalasiewicz 1984), various diplograptids and *Saetograptus* (Siveter *et al* 1989), as well as in *Rhabdinopora flabelliforme*. Complex central structures of floats have been recorded (Ruedemann 1947; Kozłowski 1949; Bulman 1970), but restudy of the original material has shown them to consist of nothing but abiogenic preservational artifacts (Rickards 1975; Walters 1977). Synrhabdosomes have been associated with both sexual (Zalasiewicz 1984) and asexual (Bulman 1970; Kozłowski 1949) reproduction of graptolites.

Synrhabdosomes may show a series of developmental stages (Beckly & Maletz 1991; Bulman 1970; Kozłowski 1949; Ruedemann 1947), from a single or small number of siculae, with gradual appearance of new siculae as those already present develop into mature colonies. The successive appearance of associated siculae suggests that the synrhabdosome represented a site of asexual reproduction through parthenogenesis or self fertilisation by a sexually mature, (?paedogenetic,) hermaphroditic sicolazoid, rather than a sexual congregation of developed adults (as suggested by Kirk 1978; Zalasiewicz 1984). The result would have been genetically identical, cloned colonies, which may have separated from the synrhabdosome at a particular stage of ontogeny giving rise to a series of sister colonies, each consisting of clonal, zooids. Three discrete levels of individuality may thus have been present in graptolites - at the level of the zooid, the colony, and possibly the genotype (as expressed in a series of cloned colonies). Synrhabdosomes could only readily have formed in areas of very high nutrient concentration, as the movement of each colony within the water column would have been severely restricted, and there was a large concentration of feeding zooids within a reduced area. This may explain the rarity and sporadic occurrence of synrhabdosomes. Some organisms undergo asexual reproduction under stressful conditions, but the restrictions the synrhabdosome placed on graptolite feeding mechanisms would make this situation highly unlikely in graptolites. There is possible evidence of a benthic habit of some synrhabdosomes (Kirk 1978), and indeed, many are found within sediments of ample bottom water oxygenation (Kirk 1978; Bates *pers. comm.*).

Many colonial organisms can regenerate from broken portions of colony, asexually creating new colonies by fragmentation. This ability appears rare in graptolites, where it is restricted to a small number of taxa presumably reflecting the high degree of organisation of the colony. Within Ordovician taxa, regeneration has only been reported in the janograptid state in '*Didymograptus*' and in *Thamnograptus capillaris* (Finney 1980), although at least some of the occurrences of regenerative structures in 'janograptids' have been rejected on the grounds of their restricted stratigraphic occurrence (Erdtmann 1971b), and may instead be due to the resorption of the sicula in certain taxa. Among Silurian taxa regeneration occurs rarely, and only within straight colonies where it has little effect on their hydrodynamics, such as in *Neodiversograptus nilssoni* (Bulman 1970; Palmer 1971), *Pristograptus* and *Monograptus lobiferus* (Rickards 1973), and very rarely at the proximal end of triangulate monograptids (Rickards 1973).

Predation on graptolites

Graptolites were among the most important macrozooplankton during the Lower Palaeozoic. As such they constituted a large reserve of accessible energy within the water column, and hence a major utilisable source for pelagic or nectic predators. A diverse fauna of benthic and free swimming predators existed within the Cambrian (Conway Morris 1986) but as they lacked mineralized tissue, they are known almost exclusively in a small number of *Konservat-Lagerstätten*. After the Cambrian, however, such exceptional preservations are rarer (Allison & Briggs 1991), resulting in the lack of direct evidence of many of the potential predators of graptolites.

The only evidence for predation on graptolites is indirect, including, for example, damage to colonies and the occurrence of rhabdosome features which could be interpreted as means of defence. Swarming is the most common mode of defence among planktic organisms, and this strategy would allow for the formation of dense monospecific bedding assemblages .

Several forms of predation on the colony were possible (Fig. 2). Within the Lower Palaeozoic graptolite predation by filter feeding can be discounted due to the lack of suitable large organisms.

Modern pelagic realms contain a wealth of moderate to large predators which feed by the process of enveloping individual food organisms entire, digesting any readily accessible organic matter and expelling any waste undigestible material. This method of feeding is largely restricted to unskeletonised forms with a relatively simple body plan, such as scyphozoans, siphonophores and ctenophores. Fossils of such organisms are rare; ctenophores have been recorded from Cambrian and Devonian *Konservat-Lagerstätten* (Conway Morris 1985) and a variety of medusoid forms from the Precambrian and sparingly throughout the Phanerozoic (Nudds & Sepkoski *in press*). Thus such predators were present in the Ordovician and Silurian oceans. Food organisms are usually trapped by tentacles, before being dragged into the body chamber for digestion. Graptolite zooids would have been consumed rapidly, whilst the robust collagen-like material (Crowther 1981; Towe and Urbanek 1974) of the periderm may have remained undigested, in much the same way that collagenous worm jaws can pass undamaged through a fish's gut (Colbath 1986). Evidence of this form of predation would be expected to be scarce, even when the frequency of predation is high, due to its having little or no physical effect on the periderm. When heavily buckled rhabdosomes of robust morphotypes such as diplograptids occur, with little or no other evidence of hydrological sorting, damage or destruction, it may be the result of ingestion by a predator (Fig. 4B,C). If rhabdosomes were egested in a mucus sheath, this would bind colonies if several were expelled together, resulting in faecal packages of rhabdosomes (Figs. 3A-C, 4A). Where only a single species is present, these coprolitic clusters could easily be mistaken for synrhabdosomes, but where several species are present the origin would be more obvious. Feeding within a swarm of siculae could give rise to coprolitic sicular masses such as that figured as an 'egg mass' by Jeager (1986b). Defence from this form of predation would take the form of a large overall colony size, the presence of spinose processes, and possibly rapid automobility.

A second form of predation would have been the removal of individual zooids from the colony. Predation of this type on modern corals and bryozoans is common but is rarely fatal to the colony as a whole. Likely predators for this mode of attack on graptolites are diverse and include a variety of arthropods, planktic polychaetes and conodontophorids. Evidence is likely to be rare as little damage would be done to the periderm except perhaps around the apertures. Some of the healed apertural damage recognised on isolated graptolites (eg. Herr 1971; Kozłowski 1949) may be due to attacks of this sort. Apertural modifications affording protection from such attacks may include recessed 'climacograptid' thecae, hooked thecae, thecal spines and lappets and most dramatically the partial closure of mature thecae in many monograptid groups such as triangulate monograptids, *Rastrites* (Sudbury 1958), *Streptograptus* and *Cucullograptus* (Rickards *et al.*, 1977).

Where zooids were covered by a rigid periderm, a predator may gain access to zooidal material by breaking open the rhabdosome to 'liberate' the contents. Carnivorous taxa with mineralized skeletons known from the Ordovician and Silurian either lacked the ability to destroy graptolites, or were largely absent from graptolitic environments, and the existence of suitable large, poorly skeletonised, predators is largely conjecture. Powerful predators such as *Anomalocaris* are well known in the Cambrian (Whittington & Briggs 1985), and these were almost certainly able to bite through the calcite skeletons of trilobites (Conway Morris & Jenkins 1985; Whittington & Briggs 1985). Such organisms, if present in the Ordovician and Silurian, would have made competent predators on graptolites, but there appears to be no large comparable organisms within the succeeding Lower Devonian Hunsrück Slate (Bergström 1990). Other powerful predators included cephalopods, many modern forms of which actively seek out tough food items (Tsudy *et al.*, 1989), eurypterids, and (in the Silurian) jawed fish. These organisms generally show a more inshore distribution than graptolites (Koren *et al.*, 1989) and are likely to have been major predators only rarely. The evidence for this type of predation would be in the form of unexpectedly broken stipes (as in Fig. 4.D), but this may be difficult to tell from breakage as a result of normal decay, transport, and uneven splitting of the rock. Graptolite fragments within coprolitic masses would be a more reliable form of evidence. These appear to be rare, with only a single probable example recorded during this study (Fig. 4.E). Although this 9mm long pellet is superficially similar to phyllocarids and 'algae' (of Williams & Rickards 1984), SEM study has shown it to consist of comminuted, curved fragments identical to graptolite periderm. Defence against such attack could be the reason for the thick layers of cortical bandaging in many taxa (Crowther 1981), added weight otherwise generally undesirable to a planktic organism, and the existence of the highly robust, ancora-derived retiolite structure, as in *Retiolites*, gaining the maximum strength for the minimum of energy outlay (Bates 1989).

Parasitism

Parasites are ubiquitous elements of all modern ecosystems, and were likely therefore to have been present within graptolitic ecogroups. Most parasitic infestations leave little or no trace on skeletal material. However, some forms of parasitic organism produce galls and cysts on the surface of or inside the host's skeleton, and as such are fairly well represented in the fossil record (Boucot 1990,

pp. 59-125; Conway Morris 1981). A number of very rare structures on benthic graptolites have been attributed to parasites. These include expanding, loosely coiled tubular structures or tubothecae (Conway Morris, 1981, 1990; Koslowski, 1970) with a composition and texture identical to normal graptolite cortical tissue (Crowther *pers. comm*). These occur on a number of benthic graptolite taxa either issuing from thecal openings, or from the dorsal wall of the rhabdosome. Tubothecae appear to be the dwellings of parasites or commensals using the host's own tendency to envelop foreign material to produce a dwelling chamber. Flask-like objects of unknown affinity, bearing a resemblance to cephalopod eggs, have been observed attached to *Mastigograptus* (Koslowski, 1959, 1965). Elongate, spiral, bifurcate tubes (*Helicorynx*) which, unlike tubothecae, do not appear to originate from within the host rhabdosome (Koslowski 1967) have also been noted encrusting *Mastigograptus*, although, again, their affinity is unknown.

Parasitic outgrowths would have had a detrimental effect on the hydrodynamics of pelagic graptoloids. Evidence for parasite infestations among planktic graptolites is therefore represented by more discrete outgrowths. These more subtle parasitic features may therefore be difficult to tell from deformities caused by growth defects and damage sustained during ontogeny, and much of the recorded parasite damage is more readily interpreted as growth defects or damage to the sicula, virgella or nema. Small rings recorded on isolated diplograptids (Jackson 1971; Loydell 1991) and monograptids (Fig. 4.F) may be genuine evidence for parasitism. These appear to consist of cortical tissue, with the obviously broken edges of the rings indicating the original presence of a more complete flask or cyst such as those recognised on *Monoclimacis* (Urbanek 1958). There is no connection between the inside of the capsule and the interior of the periderm. It is likely, therefore, that the organism was more of a commensal than a parasite, using the graptolite's ability to lay down external cortical tissue as a means of obtaining a rigid dwelling or egg chamber.

It has long been recognised that 'oval bodies' occur in association with graptolite rhabdosomes (Nicholson 1866). These are frequently no more than chance associations of graptolites with phyllocarids and inarticulate brachiopods, but in some cases the bodies appear to be part of the graptolite. They are generally known only in a flattened condition, although a flask-like body of uncertain affinity has been figured protruding from a theca of a chemically isolated *Testograptus* (Urbanek and Teller 1974). These have been interpreted as various types of graptolite brood pouches or egg cases (Elles 1940), but the possibility that they are parasitic outgrowths cannot be ruled out.

Utilization of dead rhabdosomes

Within many deep sea environments one of the main limiting factors to sea floor colonisation is the lack of firm substrates. For this reason skeletal parautochthonous material from plankton and nekton, as well as allochthonous material such as wood and uprooted algae, is readily colonised (Allison *et al.*, 1991; Sheehan 1977). In the Lower Palaeozoic such material was rare, and even objects as small as graptolite rhabdosomes may have been used as attachment sites. Indeed, some graptolite 'oval bodies' or 'goniothecae' may be small inarticulate brachiopods or phyllocarids (Gürich 1928) making use of the graptolite as a rigid attachment site on a soft sediment surface. The

association of tentaculitids with dead graptolite rhabdosomes may represent a similar situation (Jaeger 1986a).

Scavenging and recycling

The bulk of primary production in oceanic systems is consumed, either dead or alive, within or near the production zone (Steele 1974). The bulk of seafloor decay is therefore of animal waste products and remains. A similar situation presumably prevailed during the Lower Palaeozoic.

After the death of a graptolite colony, the breakdown of the more volatile zooid material within the rhabdosome would start immediately, at first largely by the actions of autolysis and internal bacteria (Briggs and Kear *in press*) and later by action of saprophytic organisms within the water column. Free swimming scavengers such as polychaetes and arthropods would also have consumed material from the sinking colony. In some cases all trace of smaller, surface dwelling or neritic rhabdosomes may have undergone biological or chemical destruction during sinking (Erdtmann 1976).

Within the classic 'graptolitic black shale' facies, a quantity of organic material (up to over 2% (Kemp 1991)) frequently occurs, indicating that the decay of carbonaceous biogenic material was not complete. Decay was anaerobic, with little or no activity of metazoan scavengers. The preservation of periderm may indicate that the periderm protein, like lignin (Hedges *et al.*, 1985), was comparatively resistant to anaerobic decay.

Within mudstones bearing a mixed fauna of graptolites and specialist shelly forms, graptolite periderm also can be observed to be well preserved, even when there is a high rate of bioturbation. The low rate of utilization of periderm protein demonstrates that the energy yield in breaking its structure down was low compared to that gained from other organic material in the sediment. Any graptolites containing zooid material reaching the sea floor would have been extensively scavenged. If rhabdosomes containing zooidal material were rapidly buried, scavenging would have been carried out by burrowing organisms adapted to dysaerobic conditions such as those producing *Chondrites*.

'Barren grey mudstone' facies frequently alternate with darker graptolitic rocks. These sediments are heavily oxidised and often bioturbated. Although graptolites are not readily visible, comminuted fragments are often present, indicating taphonomic loss under these conditions (Berry 1989). The periderm material was therefore, at least to some extent, metabolisable under highly oxic conditions, either undergoing total destruction, or being degraded so as to allow comminution by bioturbation. Graptolite preservation is frequently far better in much higher energy sediments, and so purely hydrological mechanical destruction seems unlikely.

Conclusions and implications

The lack of *morphological* analogies to graptolites within modern faunas presents a problem in their ecological reconstruction, however *functional* analogies do exist, and using these it is possible to deduce the most efficient survival strategies (in terms of obtaining nutrient, avoiding predation and optimum modes of reproduction) available to graptolites of differing morphologies. This evidence

can, at least to some degree, be compared with evidence gained from temporal and spatial distributions of taxa across differing palaeoenvironments.

The low preservation potential of a large proportion of a community will only rarely allow their occurrence within a fossil biota, however within many environments, occasional 'taphonomic windows' (*sensu* Allison & Briggs 1991) may allow a record of a higher proportion of the assemblage. Under more 'normal' conditions, when this part of a biota is not preserved, taxa of a single trophic level with a high preservation potential, as with graptolites, will give an indication of the gross trophic structure of the ecosystem. Comparisons of these 'normal' fossil assemblages with the temporally and environmentally closest *Konservat Lagerstätten* will give some idea as to the 'missing' taxa of this ecosystem.

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FIGURE CAPTIONS

Fig. 1. Cartoon of the main graptolite morphotypes and their relation to the most likely feeding strategies. For convenience the feeding motion of all rhabdosomes is drawn as a vertical descent. Colonies of groups 3 and 4 are figured in the most hydrodynamically stable position, although other orientations would also have been possible. *Graptolites drawn from various sources.*

1. Graptolites with a conical colony morphotype, either consisting of a single spiral stipe (1a, *Monograptus turriculatus*) or a conical reticular net (1b, *Rhadinopora*) imposing either spiral or linear motion on the colony.
2. Flat (2a, multiramous dichograptid) or slightly conical (2b, *Cyrtograptus*) colony morphotypes characterised by slow movement with a variable spiral component.
3. Mono or biramous morphotypes with a spiral motion imposed by proximal asymmetry (3a, *Isograptus manubriatus*), spiral stipes (3b, *Dicellograptus complexus*) or proximal curvature (3c, curved monograptid).
4. Graptolite morphotypes with a linear motion with high (3a, *Expansograptus*) or low (3b, *Didymograptus*) angles separating the stipes.
5. Straight rhabdosomes with a linear, horizontal feeding descent (5a, 5b), with either a spiral (5a", *Petalograptus*) or linear (5b", straight monograptid) ascent.

Fig. 2.

Cartoon showing the three major classes of graptolite predation .

Fig. 3.

Camera lucida drawings of graptolites showing evidence of predation or scavenging. All specimens from laminated hemipelagite facies of the Lower Wenlock, *centrifugus* Zone.

A. Faecal accumulation of broken monograptids of various sizes. Ross Formation, Kirkudbright Bay, Southern Scotland. Other than when in such accumulations, graptolites in the Ross Formation very rarely show any signs of pre-burial damage.

B. Faecal accumulation of similar sized broken stipes of *Monograptus priodon*. Ross Formation, Ross Bay, Southern Scotland.

C. Faecal accumulation of broken rhabdosomes of *Retiolites geinitzianus* (pieces of broken reticulum omitted for clarity). Ross Formation, Ross Bay, Southern Scotland.

D. Possible evidence of scavenging, with a *Chondrites* burrow (stippled) apparently entering the distal end of a retiolitid. Black areas are pyrite nodules. Brathay Flags Formation, Ecker Secker Beck, Howgill Fells, Northern England.

Fig. 4.

A. Multispecific faecal accumulation of at least seven unbroken rhabdosomes of *Orthograptus ex. gr. calcaratus* and three of *Climacograptus ?tubuliferous*. Note the superficial resemblance to a

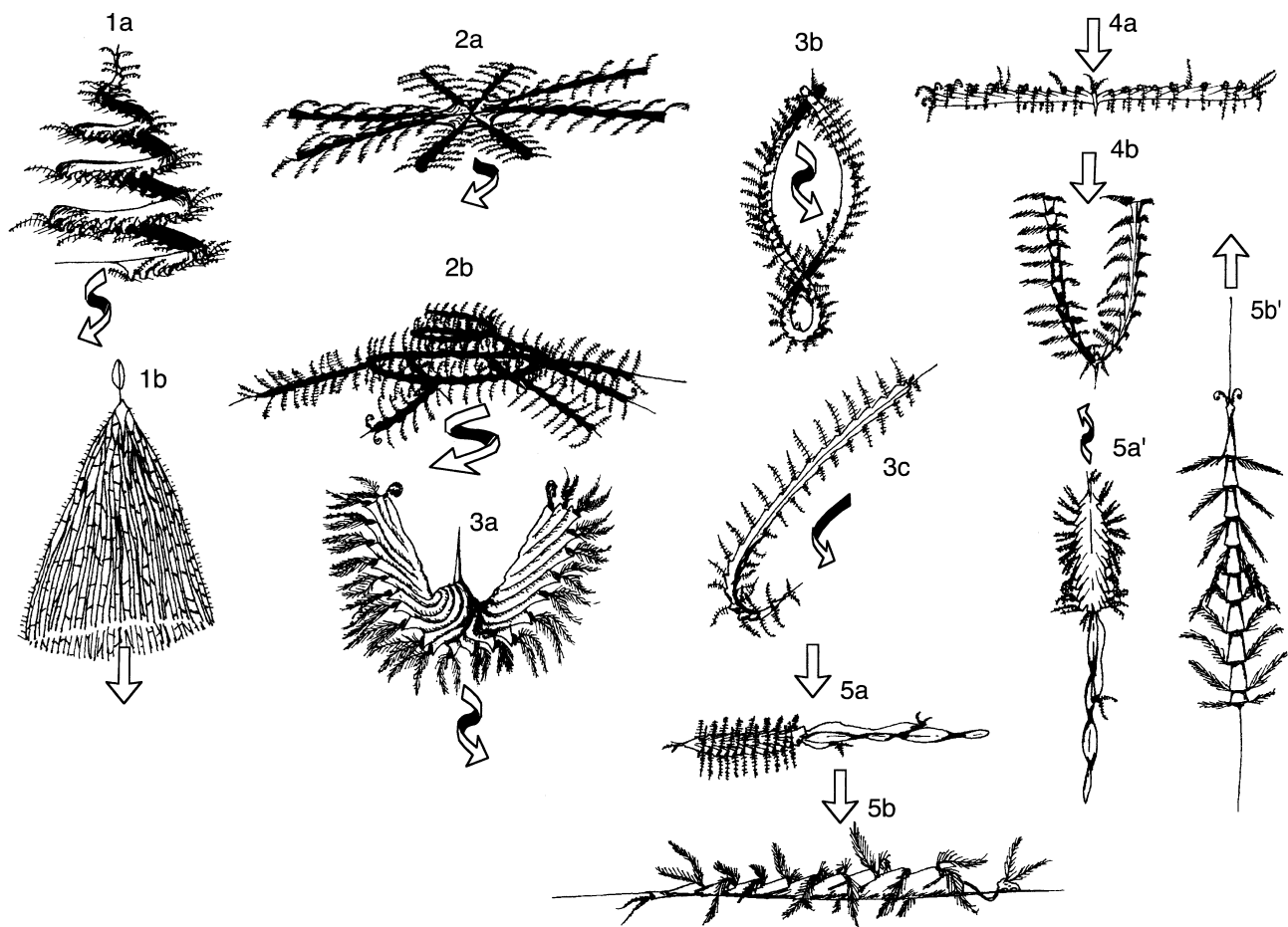
synrhabdosome. Lower Hartfell Shale, Caradoc, *linearis* Zone, Dobb's Linn, Southern Scotland. X 1.2

B and C. Two severely buckled robust diplograptids (*Orthograptus calcaratus basilicus* and *Climacograptus ?styloideus* respectively) from quiet water assemblages of otherwise undamaged graptolites. Lower Hartfell Shale, Caradoc, *linearis* Zone, Dobb's Linn and Hartfell Spa, Southern Scotland. X 2.2 and X 2.

D. Small ?predator damaged rhabdosome of *Climacograptus Sp.*. The periderm is damaged around a thecal aperture allowing one half of the rhabdosome to be rotated through 90° in relation to the other. There is no sign of physical damage within the associated fauna. Birkhill Shale, Llandovery, ?*magnus* Zone, Dobb's Linn, Southern Scotland. X 12

E. Well defined 'teardrop' shaped mass of carbonaceous fragments, probably representing a faecal pellet of comminuted graptolite debris. Note that this is structurally different from either phyllocarid valves or 'algae', despite the superficial resemblance. Browgill Beds, Llandovery, *crispus* Zone, Ashgill Beck, Coniston, Northern England. X.3.5

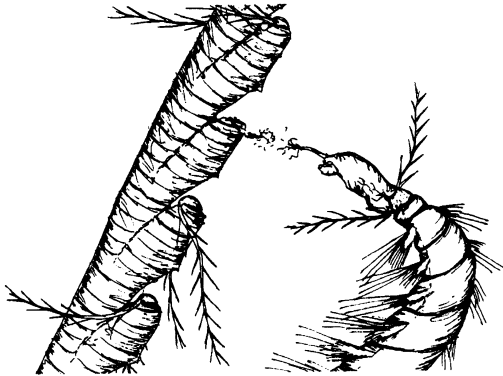
F. Two ring-like attachment areas of ?parasite induced vesicular bodies on a proximal portion of *Monograptus cf. riccartonensis*. The rings are composed of cortical tissue and are seen to overgrow both metasicula and protheca. An band of thickened tissue on the inside of the ring gives the appearance of a fainter, inner ring. Cape Phillips Formation, Wenlock, ?*rigidus* Zone, Cornwallis Island, Arctic Canada. X 100.





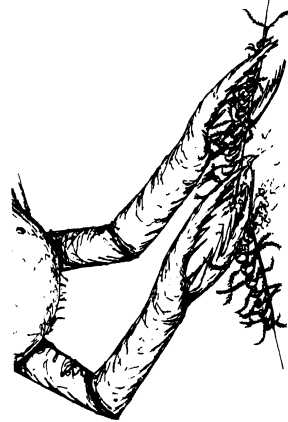
Absorption: Entire rhabdosome taken in and zooids digested

Probability: Moderate to high
Predators: Ctenophores, scyphozoans, siphonophorans
Evidence: Very little; some buckling, agglutinated groups
Defence: large size, spinose form, ?automobility



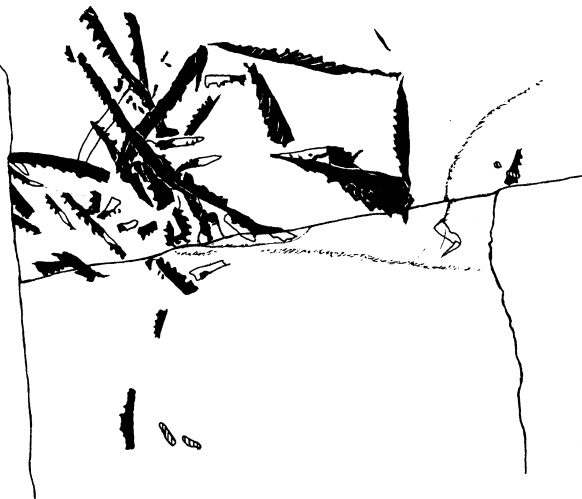
Crunching: Rhabdosome broken open

Probability: Variable
Predators: Arthropods, cephalopods, ?fish, ?conodontophorids
Evidence: Unexpectedly broken rhabdosomes, coprolites
Defence: Thick cortical bandaging, spines, framework of lists

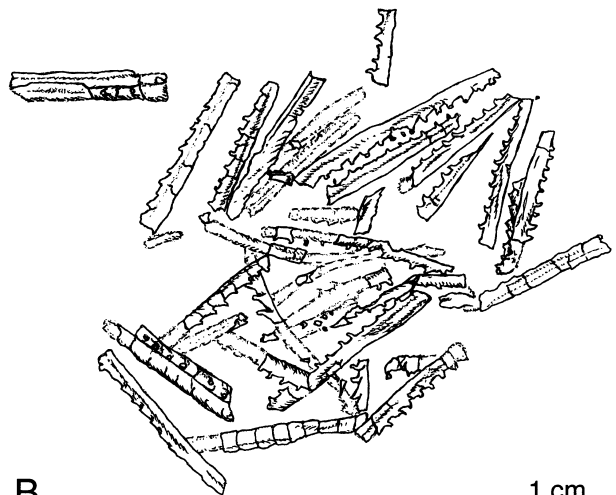


Plucking: Zooids removed individually

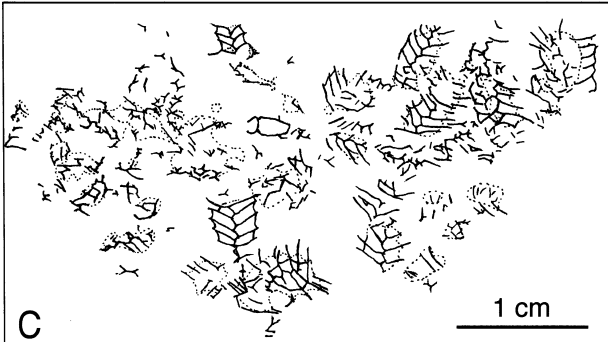
Probability: High to very high
Predators: Various arthropods, polychaetes, conodontophorids
Evidence: Little or none; maybe damaged apertures
Defence: Apertural spines, reduced apertures, hooked thecae



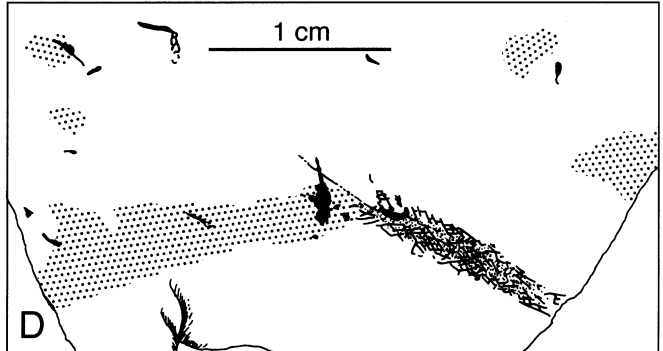
A 1 cm



B 1 cm



C 1 cm



D 1 cm

