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Population structure of graptolite assemblages

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Graptolite rhabdosomes display a diverse suite of morphologies. The range of morphotypes present within most moderate to high diversity assemblages from the Ordovician and Silurian is similar, despite the different taxonomic composition of the faunas at different times. Survivorship analyses of graptolite faunas from the Ordovician and Silurian demonstrate strong similarities in the mortality rates of unrelated graptolites of similar functional morphology. It also shows a strong correlation of decreasing mortality rates amongst more mature colonies with increasing rhabdosome complexity. This similarity in both functional morphology and life history of graptolites suggests that they lived within a very stable planktic community structure.

□ *Graptolites, ontogeny, palaeoecology, populations, survivorship.*

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Planktic graptolites comprise the best known of the faunal elements present within Ordovician and Silurian open marine ecosystems (Bulman 1964; Williams & Rickards 1984; Underwood 1993a). Although their precise mode of life is to some degree problematic (compare Bulman 1970 and Kirk 1990), it is evident that they filled a wide range of niches within the planktic realm. Analysis of their specific ecogroups has centred on rhabdosome functional morphology (Kirk 1969,1990; Rigby 1991; 1992; Rigby & Rickards 1989; Underwood 1993a), and has demonstrated the convergent nature of several of these morphologies within unrelated taxa. Despite this acknowledgement that the autecological strategies of many graptolites are repeated over time, the similarities in community structure within graptolite faunas of differing taxonomic composition are poorly known.

Changes in assemblage structure over time

For much of their period of dominance of the plankton, graptolite faunas were diverse both taxonomically and in the range of morphotypes shown by the rhabdosomes. Although the taxonomic turnover of graptolites was high, the basic rhabdosome morphotypes recurred within unrelated groups (e.g. Underwood 1993a). The means by which these morphotypes were achieved, however, varied at different times depending on the mode of rhabdosome structure of the taxa present. For example, an overall rhabdosome curvature of up to 180° could be achieved in biramous taxa by having a proximal stipe divergence angle, whereas in monoramous monograptids, the same form could only be achieved by having stipe curvature. At periods of high species diversity (Arenig, basal Caradoc, upper Caradoc-lower Ashgill, mid to upper Llandovery, lower Ludlow) a wide range of morphotypes were present within assemblages, with most of the main morphotypes being represented at any time (Fig. 1). These morphotypes were almost certainly related to specific hydrodynamic functions and thus directly related to the ecological niche of the taxon (Kirk 1969,1990; Rigby 1991; 1992; Rigby & Rickards 1989; Underwood 1993a).

At several periods within the Ordovician and Silurian, graptolites were severely affected by extinction events. These events had a filtering effect on the graptolite faunas present, selectively removing taxa with larger and more complex rhabdosome morphologies (e.g. Rigby 1991; Fig. 1). The most severe graptolite extinction event occurred during the Hirnantian (e.g. Melchin & Mitchell 1991), coincident with the uppermost Ordovician glacial episode (e.g. Brenchley *et al.* 1994). This event saw the extinction of many graptoloids, leaving only about three genera. These survivors all possessed a single morphotype, that of straight biserial colonies with unornamented thecae. A second major extinction event within the upper Wenlock had a rather lesser effect, seen more at species than generic level (e.g. Urbanek 1993). This did, however, have the effect of removing genera with curved and multiramous rhabdosome morphotypes. After each extinction event lost morphotypes are rapidly replaced through adaptive radiation of surviving taxa. This rapid niche replacement is also seen at periods of rapid faunal turnover, such as in the lower Caradoc and around the Aeronian-Telychian boundary.

Graptolite survivorship strategies

There are few methods which allow for a quantitative study of elements of community structure of extinct organisms such as graptolites. Probably the most readily used method which does allow for direct quantitative investigation is the analysis of survivorship patterns. Used extensively on modern organisms (e.g. Deevey 1947), this produces an age spectrum for either living or dead individuals of a species, with different curves being characteristic of different ecological strategies.

There have been few attempts to analyse the population structure of graptolites. The work that has been done (e.g. Palmer 1986; Rigby 1993) has focused on faunas on individual bedding planes, with results probably being more relevant to taxonomic and taphonomic studies than palaeoecology. Among other fossil organisms, studies of population dynamics have been more extensive, but have generally concentrated on community analysis or variations within a population for purely taxonomic ends. These studies of fossil populations have concentrated on shelly groups such as brachiopods (Cate & Evans 1992), foraminifera (Kaesler & Fisher 1969), ostracods (Kurten 1964) and bivalves (Snyder & Bretsky 1971). These are all benthic and either sedentary or poorly mobile, thus being subject to very different ecological controls to graptolites. Population structures of these organisms are thus not directly comparable to those of graptolites. It should be noted that the term survivorship has also been used to refer to taxonomic extinction rates (e.g. Pearson 1992). Although using similar techniques, species level survivorship cannot readily be compared to the survivorship of individuals within a species.

Methods.

The population structures of three graptolite assemblages were analysed. These represent material from periods of moderate to high diversity, one before and two after the Hirnantian extinction event.

Studies of populations of fossil organisms are hindered by the integral biases imposed on the perceived population by predation, pre- and post-burial taphonomy and sampling technique. Sampling methods were therefore chosen to lessen these effects as much as possible. The vast majority of graptolite fossils studied are exposed on shale bedding surfaces, such as those described in the only previous survivorship analysis of graptolites by Rigby (1993). Observations on bedding surfaces may, however, allow for several sources of error. Firstly, bedding plane assemblages are by their nature 'instantaneous' events, at least as far as burial is concerned, and as such represent a single death assemblage as opposed to a time-averaged consensus. Where bedding planes chosen are particularly rich in graptolites, they are likely to have been subject to significant taphonomic concentration. The assemblages present will therefore be either winnowed to some extent, possibly removing small elements, or have developed at hiatus horizons with the continual or episodic addition of new material. This may allow ample sea-floor exposure time for the biological or mechanical destruction of small or fragile specimens. Secondly, even when the

colour contrast between rock and fossil is high, it is frequently difficult to recognise the smallest elements, both due to their size and the rarity with which mudstones split evenly on bedding planes (splitting often being concentrated along planes of weakness, especially larger fossils). Prosiculae therefore appear rare or absent in many bedding assemblages.

An alternative to counting from bedding planes is to extract an entire graptolite fauna by acid digestion of the rock. This produces a time-averaged consensus death assemblage (Kidwell & Bosence 1991). The material used for such a study has to fit a number of criteria. The rock must be abundantly graptolitic but lack obvious signs of taphonomic concentration effects, be readily soluble in acid and contain graptolites which are well enough preserved to be extracted largely intact. Worldwide there are few localities which yield material which fulfils all these criteria, dramatically limiting the scope of such studies. Two samples which were found to be particularly suitable were from the Caradoc Viola Limestone of Oklahoma and the Wenlock Cape Phillips Formation of Arctic Canada. Llandovery material from Osmundsberg in Sweden was also used, but the fragility of the graptolites and the poorly calcareous matrix made this less suitable. All samples were from between 200 and 500 grammes of rock, with about 5cm stratigraphic thickness represented within each sample. The samples all lacked discrete bedding concentrations of graptolites, and as such contain material deposited over a prolonged period of time recording a continual input of graptolite material. This is likely to have had the effect of averaging out any unrecognised biostratinomic effects. This time averaging of the fauna gives a consensus of graptolite faunas through the depositional period of the rock sampled, but does not allow for the reconstruction of a community structure of any specific point in time. This is advantageous as it allows the analysis of the ecological strategy a species as a whole, and not that of a temporally isolated sub-population of individuals which may, for reasons of ephemeral environmental change, be unrepresentative. There is no evidence for any of the breakage being due to primary taphonomic processes; indeed, examples of pre-burial breakage of graptolites are extremely rare. For example, in a study of graptolite taphonomy, Underwood (1993b) records only two bedding surfaces bearing biostratinomically broken graptolites.

Removal of the graptolites from a fine mud residue allowed for the recognition of almost all the graptolites present, including the prosiculae. As the amount of rock sampled was fairly small (due to the abundance of graptolites), many of the larger colonies were broken at the edges of the rock sample or during extraction. For this reason, sampling only complete rhabdosomes would result in an underrepresentation of larger colonies. These breakages are considered to have occurred at entirely random intervals. To, at least in part, counter these problems, all of the broken pieces were recorded and randomly re-assembled. Reassembly was carried out by sorting all stipe fragments to identify those with a complete proximal end (with preserved sicula), distal end (with undamaged growing surface parallel to fusellae) or neither. Specimens in each category were then numbered. A broken proximal or distal end, whichever was less common for the taxon, was selected and then other sections of either a mid or opposite end section were randomly picked (by use of a simple random number generation program) and added to the end section. On selection of a mid section the process is repeated until the opposite end is encountered, at which point the

colony was considered complete and its size recorded. With cladia-bearing forms which may possess several distal ends, the process was similar, starting with a distal end but randomly adding distal, mid and proximal fragments, only stopping when a proximal end was encountered. For simplicity, the few remaining sections were considered as complete. This method of random reconstruction may give a somewhat smoothed rhabdosome size distribution, not allowing the recognition of polymodal size distributions. The small sample size and time averaging of these largest rhabdosomes, however, would make recognition of these subtleties difficult even if only complete specimens were considered. Random reconstruction of rhabdosomes results in an approximate normal distribution of the number of fragments within each rhabdosome. However, the average number of fragments in each reconstructed specimen is very low (e.g. 2.4 fragments per reconstructed *Geniculograptus*; only *Amphigraptus* averaging above 3) whilst the thecal counts are generally high (*Geniculograptus* being the lowest at an average of 5.8 thecae per reconstructed rhabdosome). The overall size distribution of reconstructed rhabdosomes does not therefore follow a normal distribution, and gives a size distribution that is in continuity with that of unbroken colonies (see Table 1).

The growth stages of graptolite rhabdosomes are readily identifiable without the need for measurement. Juvenile growth stages are represented by the prosicula, metasicula, and up to the completion of theca 1, adult growth stages are identified by the number of completed thecae. In monograptids the stage is determined by a total thecal count. In diplograptids, retiolitids and dichograptids, thecae were counted along a single stipe, as this was considered to be more analogous as far as thecal spacing is concerned with monograptid thecal counts than total numbers of thecae. These growth stages, both observed and reconstructed, were plotted as cumulative survivorship curves. The survivorship curves constructed are therefore relative to growth stage of the rhabdosome, which would only be equivalent to age if the growth rate of the colony remained constant. In all of the samples studied, the earlier growth stages vastly outnumber successive growth stages. This is normal among the majority of organisms and reflects the higher mortality rate amongst juveniles. For this reason, the cumulative numbers of specimens in the survivorship curves were plotted on a logarithmic scale. Although a number of graptoloid taxa have pre-determined maximum rhabdosome sizes, all of the taxa considered here have been figured or described at far greater thecal counts than any observed or reconstructed here. It is therefore evident that if any of these taxa do possess a defined maximum rhabdosome size, it is not likely to effect the results of this study.

Material.

Cape Phillips Formation.- The Cape Phillips Formation is a pelitic offshore deposit ranging from Upper Ordovician to Lower Devonian in age, well known at outcrop on Cornwallis Island, Arctic Canada (e.g. Thorsteinsson 1958). Graptolite-bearing carbonate nodules are present from the Llandovery to lower Ludlow. The material studied consists of a piece of a dark, microspar nodule from 196 metres above the base of the type section. This is Wenlock in age, and is

probably from the upper *instrenuus/kolobus* Zone (Lenz & Melchin 1991). The sediment within the nodule was seen to be a laminated silty hemipelagite (*sensu* Kemp 1991), cemented prior to any significant compaction. The graptoloid fauna is abundant and scattered evenly throughout the nodule, including both monograptids and retiolitids. Monograptids are represented by *Monoclimacis flumendosae*, *Monograptus instrenuus* and *Cyrtoagraptus cf. multiramis* (but with relatively few cladia) together with rare *Monoclimacis cf. linnarssoni* and a single specimen of *Monograptus priodon*. The retiolitids comprise *Paraplectograptus praemacilentus*, and an unidentified retiolitid with a complete sicula. Other planktic elements include numerous radiolarians, whilst the benthos contains dendroids (?*Acanthograptus*), tuboid fragments, brachiopod spat, scolecodonts and numerous sponge spicules.

The siculae of *Monograptus*, *Monoclimacis* and *Cyrtoagraptus* proved inseparable, and counts of the monograptid siculae were therefore combined. The two species of *Monograptus* and the two species of *Monoclimacis* were also combined, as early growth stages are difficult to differentiate in imperfectly preserved material. Although it is acknowledged that the closely related species within these two genera may have had somewhat different niches, their functional morphology would probably have been very similar. The relative rarity of *Monograptus priodon* and *Monoclimacis cf. linnarssoni* would make any errors they induce for the genera as a whole negligible. The poorly sclerotised and fragile nature of the sicula of the plectograptids allowed them to be separated, although recognition of the small and delicate early growth stages was difficult. The irregular form of the dendroids made recognition of individual colonies impractical.

Osmundsberg.- The Osmundsberg limestones consist of a sequence of Llandovery nodular limestones and shales from the Dalarna area, Sweden. The area has yielded isolatable graptolites from a number of horizons (e.g. Hutt 1970; Loydell 1991). The sample was recovered from a small piece of a micritic limestone nodule from the Upper Llandovery *geurichi* Zone. The sediments are very similar to those from Cape Phillips, differing primarily in the lower carbonate content of the nodule and syn-compactional lithification. The quantity of material recovered was far smaller than from the other two localities, representing less than 150 individuals. The graptolites recovered were fragile and often highly fractured, preventing the recovery of any large, intact colonies. Despite this small sample and paucity of well preserved material, a fairly diverse fauna was identified. The graptolites are dominated by *Torquigraptus planus*, *Monograptus marri*, and *Rastrites ?linnaei*. Also present were early growth stages of *Petalolithus sp.* and fragments of a small species of *Rastrites*. A single reticulum fragment of ?*Pseudoplegmatorgraptus* was the only indication of retiolitids. The only other fossils present were a range of scolecodonts. Most of the graptolite siculae could not be identified, although larger metasiculae of *Torquigraptus* and *Rastrites* are fairly distinct. The low carbonate content of the rock resulted in a residue of clay pellets. As these were large enough to conceal siculae, and it is likely that a number were missed whilst picking the residue. The graptolites also proved very fragile; slender proximal ends of *Torquigraptus* being completely broken up into individual thecae.

Viola Limestone.- These carbonate mudstones are essentially Caradoc in age, outcropping throughout much of the Ouachita and Arbuckle Ranges, Oklahoma. The material analysed consisted of a sample of pale, bedded micrite from the *americanus* Subzone (Finney 1986) from Howe Ranch, Arbuckle Mountains. On the thin section scale, the sample used shows only weakly defined lamination, although this is due to lack of fine-scale sediment heterogeneity rather than subsequent homogenisation. Graptolites are abundant and evenly distributed throughout the sample. The sediments are here considered to represent a carbonate mud hemipelagite. There is little or no evidence of biostratigraphic sorting or reworking. The fauna is dominated numerically by *Geniculograptus typicalis*, although large, multiramous colonies of *Amphigraptus* sp. constitute a far higher bulk of graptolite material. Abundant *Cryptograptus insectiformis* are also present, with small numbers of both *Corynoides americanus* and *Orthoretiolites hami*. Rare or single specimens of *Ensigraptus caudatus*, *Orthograptus quadrimucronatus*, *Phormograptus sooneri* and '*Climacograptus*' sp. were also recorded. Benthic organisms are represented by occasional disarticulated trinucleid trilobites (?*Cryptolithus*) and a range of scolecodonts.

It proved impractical to separate the siculae of *Geniculograptus*, *Ensigraptus*, *Orthograptus*, *Phormograptus* and *Amphigraptus*, and so the colonies of these taxa were summed. The few *Orthoretiolites* were identified by their characteristic metasacula and frequent absence of a prosacula. The relatively abundant *Cryptograptus* were not counted because their thin and unusual periderm (Underwood 1995) resulted in poor preservation, especially of the siculae, well preserved examples of which were not seen. Reconstruction of the colonies of *Amphigraptus* was not attempted due to the extremely large number of fragments (over one thousand), often with cladia. It was therefore assumed that most of the broken proximal ends of *Amphigraptus* belonged to very large, mature colonies, several of which were seen on the surfaces of the sample prior to dissolution.

Results (See Table 1)

Cape Phillips Formation.- Plots of the survivorship data of the four genera give a range of subtly different survivorship curves suggesting somewhat differing population structures. Survivorship curves of the monograptid taxa are all somewhat concave (Fig. 2), indicating that the mortality rate is not constant throughout life, but is higher amongst juveniles than amongst more mature colonies. The survivorship curves for *Monograptus* and *Cyrtograptus* appear very similar, although the small sample size of *Cyrtograptus* may allow for unrepresentative data. The smooth profile of the *Monograptus* survivorship curve demonstrates that the rate of mortality per growth stage gradually decreased from the start of growth of the first theca to the completion of about theca seven, thereafter the mortality rate appears to have remained low. The survivorship curve of *Monoclimacis* shows a somewhat different pattern, with far less evidence for a progressive decrease in adult mortality rate. At the growth stage where theca one is developing, there are about three times as many specimens of *Monoclimacis* as *Monograptus*. The steep gradient of the survivorship curve of these juvenile *Monoclimacis*, up to the completion of theca two, suggests

that the mortality rate was high, but after this point the gradient lessens and forms a near logarithmic curve, implying that the mortality of these more mature colonies is lesser, but thereafter remains fairly constant. This mortality rate remains rather higher than that of *Monograptus*, which is the commoner graptolite at large colony size.

As the sicula of *Paraplectograptus* is only rarely preserved, only rhabdosomes from the development of the first theca onwards are preserved consistently enough to be considered here. These 'adult' stages show a logarithmic survivorship curve (Fig. 3) indicating a constant death rate throughout ontogeny. This constant mortality rate shown by *Paraplectograptus* demonstrates a rather different ecological strategy from the monograptids, which have a higher juvenile mortality rate but a lower mortality rate amongst mature colonies.

Osmundsberg.- The low carbonate content of the nodule studied meant that only a small sample of graptolites (130 specimens) were recovered. The extreme fragility of these prevented any meaningful reconstruction of their survivorship as growth stages were not readily reconstructed. The low numbers of prosiculae may be due largely to the difficulty in recognising prosiculae within the pelletal residue, a sampling effect that would also seriously bias any results.

Viola Limestone.- As with the Cape Phillips sample, the taxa present within this sample show rather different survivorship curves (Fig.4). Fragments of *Amphigraptus* dominated the sampled residue. As well as a number of intact young growth stages, 28 broken proximal ends were found. This compares with huge numbers of distal fragments containing several thousand thecae. Although it proved impractical to reconstruct these large colonies, it is obvious that these few adult colonies must have averaged a very large size, with bedding surfaces of the rock from the same locality as the sample studied revealing multiramous colonies over ten centimetres across. To consistently attain these large sizes, the mortality rate per theca must have been extremely low, allowing the assumption that there was very little mortality between the 1 and 16 theca stages. The survivorship curve therefore shows a high rate of mortality up to theca 1 stage, but after this point the mortality rate was dramatically reduced. The survivorship of *Geniculograptus* follows a logarithmic curve indicative of a constant mortality rate through ontogeny.

Discussion

Growth and Coloniality.- Although graptoloids were colonial organisms, the high degree of coloniality they showed is unmatched amongst other animal groups, and each rhabdosome is probably better considered a 'superindividual' than a clonal collection of separate individuals within a colony (Underwood 1993; Urbanek 1986). The change in colony form with increasing number of thecae of many graptoloids and the presence of a predetermined 'mature' size of others (such as *Corynoides* and many species of *Cephalograptus*, *Petalolithus* and members of the plectograptinae) suggests that although the addition of new zooids is biologically adding to a

colony (astogeny), it is functionally allowing the colony to develop as a single entity (ontogeny). As this study treats rhabdosomes as discrete individual entities, their growth is here considered to be through ontogeny, although it is acknowledged that this is not correct terminology in the strictly developmental sense. Possibilities for direct comparisons between graptoloid growth and survivorship and the astogeny on non-morphologically predetermined colonial organisms or ontogeny *s.s.* of non-colonial organisms are therefore likely to be limited.

Graptoloid Survivorship.- The growth rate of graptolites is unknown, although analogy with modern hemichordates gives some idea of possible growth rates (Rigby 1993). There is therefore no suggestion that the rate of thecal production is constant, either between taxa or between different growth stages of the same species. Despite this, within all three faunas analysed there is a remarkable consistency in the net survivorship curves for the graptolite fauna. Where the taxa within the assemblage can be separated, the graptolites appear to fall into one of two general survival strategies and hence ecological groupings.

The survivorship curves for *Geniculograptus* and *Paraplectograptus* indicate that they followed very similar life strategies resulting in a mortality rate that remained constant throughout their life (the type 2 survivorship curve of Deevey (1947)). The general morphology of these taxa is similar, consisting of small, biserial colonies. It therefore seems likely that these distantly related and structurally dissimilar taxa occupied a similar ecological niche. A second survivorship strategy is shown by the monograptids and *Amphigraptus*. A concave survivorship curve (nearing the type 3 curve of Deevey (1947)) is characteristic of organisms with a high rate of reproduction and high juvenile mortality. In these taxa, a high mortality rate of siculae is followed by lower relative mortality rate within the mature growth stages, the change in rates occurring at about the theca 1 stage. This 'adult' mortality rate may either be relatively constant (as in *Monograptus*) or gradually decrease with increasing rhabdosome size (as in *Monoclimacis*). There are several reasons for a decrease in relative mortality rate coincident with this 'metamorphosis'. An ecological separation of siculae and adults at this stage could remove the maturing colonies from areas of greatest physiological or predator stress. The increase in physical size of the colony may also make it unavailable to a certain suite of predators (e.g. Underwood 1993a), removing one of the main causes of death. Additionally, it is possible that the presence of 'adult' zooids may have conveyed an immediate survival advantage, by means such as allowing storage of nutrients, aiding avoidance of predators etc. Equally, the taxa could show a variable growth rate, with a rapid increase in growth after the first theca, with interspecific variations in graptolite growth rate being evident. In this case, even if the mortality rate remained constant with time, the mortality rate per unit of growth will be reduced.

There appears to be a strong link between the overall morphology of a graptolite colony and its survivorship strategy. This is to be expected, as more growth would have been needed to construct the larger and more complex graptolite rhabdosome morphologies. Conversely, simpler rhabdosome morphologies probably reached their optimum efficiency, and hence presumably reproductive maturity, after only moderate growth. Within the graptolite taxa whose survivorship

curves are well constrained, there is a progressive tendency towards lower mortality rates of post theca 1 growth stages with increasing colony size and complexity. Thus, post theca 1 mortality rates are highest in *Geniculograptus* and *Paraplectograptus*, lower in *Monoclimacis*, lower still in *Monograptus* and *Cyrtograptus* and lowest in *Amphigraptus*, where the bulk of post theca 1 rhabdosomes appear to be of very large size.

None of these samples produced the rather convex survivorship curves obtained from 'diplograptid' assemblages from bedding surfaces by Rigby (1993). These populations contained very few juvenile stages, and it is probable that, as Rigby suggests, there has been some degree of taphonomic modification of the faunas.

Studies of both the range of graptolite morphotypes present within Ordovician and Silurian sediments and the population ecology shown by specific assemblages show a consistency of graptolite ecogroups. It is therefore evident that the graptolites possessed a very stable community structure, with well defined ecological niches. After periods of extinction radiation within surviving taxa was rapid, very quickly filling any niches left empty by the extinction of the graptolites that previously inhabited them. This niche separation within the plankton allowed for the coexistence of a number of closely related taxa within the same environment and hence the wide taxonomic variety of graptolites present within many assemblages.

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FIGURE CAPTIONS.

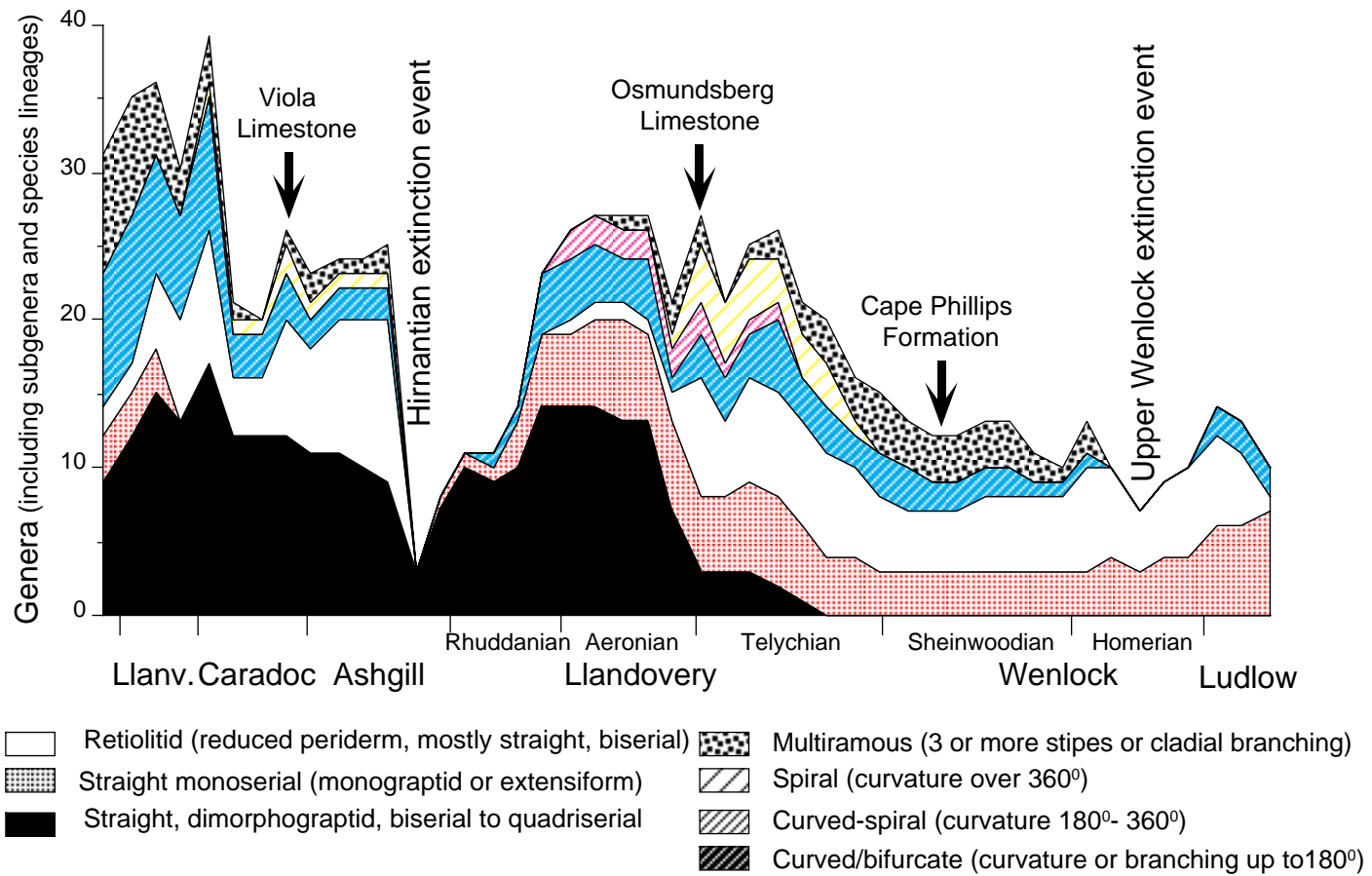
Fig. 1. Distribution of the main graptolite morphotypes from the mid Ordovician to late Silurian. From the distribution of graptoloid morphotypes it is evident that the ecology of graptolite assemblages within the Ordovician and Silurian would have been similar, and direct comparisons between them is possible. The stratigraphic positions of the three samples are shown, as are the two largest graptolite extinction events within this time period. Note that some genera may contain more than one morphotype in which case they are represented more than once, and many of the boundaries between morphotypes are gradational. Rhabdosome form is classified purely on morphological grounds, irrespective of thecal orientation, and no attempt has been made to separate forms according to 'standard orientations' or assumed life position. In some cases genera have been subdivided where they are seen to contain several discrete species groups or lineages. Constructed from range charts compiled from diverse primary sources.

Fig. 2. Survivorship curves for the monograptids from the Cape Phillips sample.

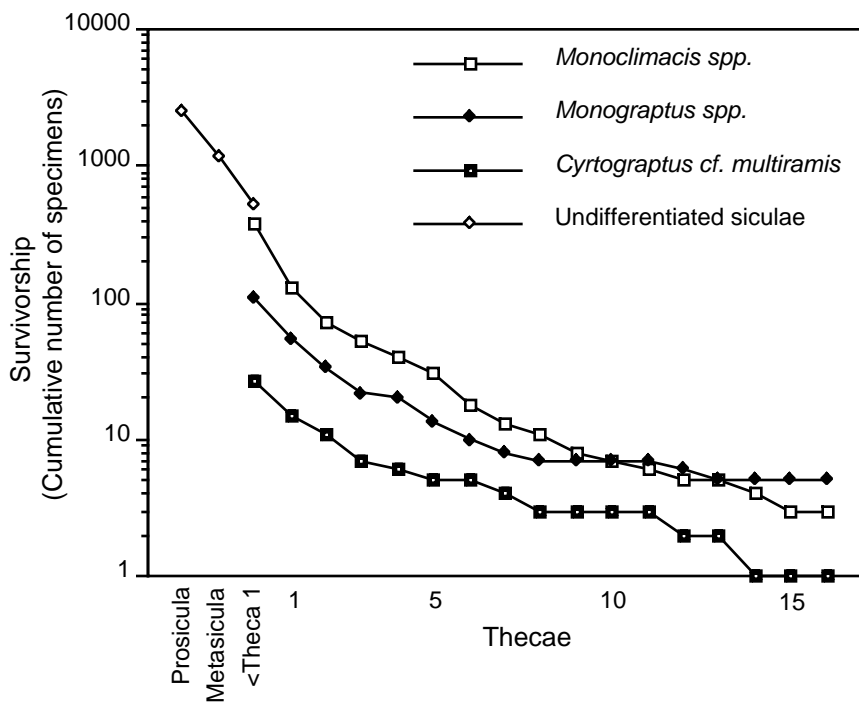
Fig. 3. Survivorship curve for *Paraplectograptus* and a composite survivorship curve of the monograptids from the Cape Phillips sample.

Fig. 4. Survivorship curves for the graptolites from the Viola Limestone sample. Note that the mortality rate of the larger colonies of *Amphigraptus* is predicted from the indirect observation of the very large average size of the colonies, with it likely that most of the broken proximal ends belonging to colonies of over 16 thecae.

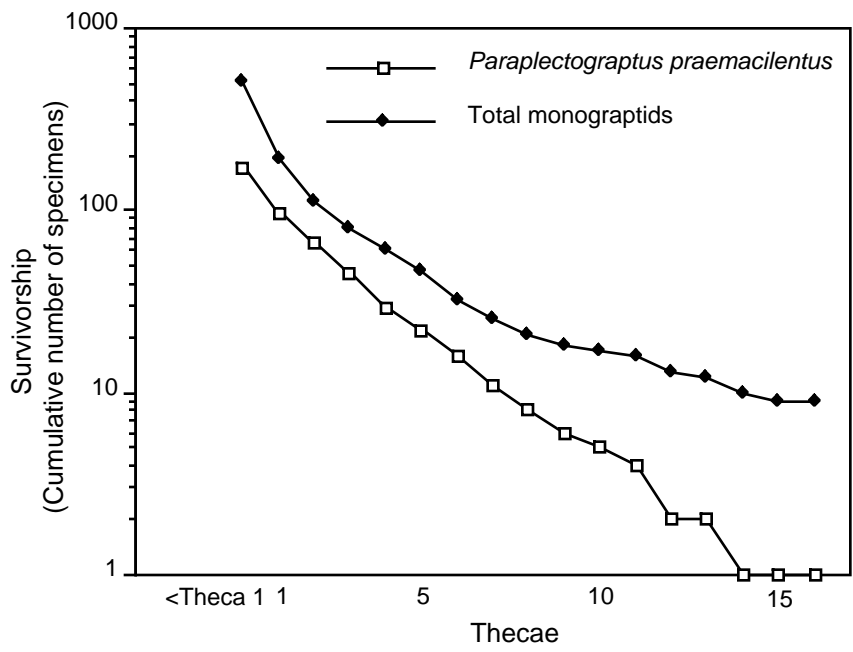
Table 1. Table showing the numbers of specimens per growth stage, both intact and reconstructed, and cumulative survivorship counts of the main taxa from the three samples studied.



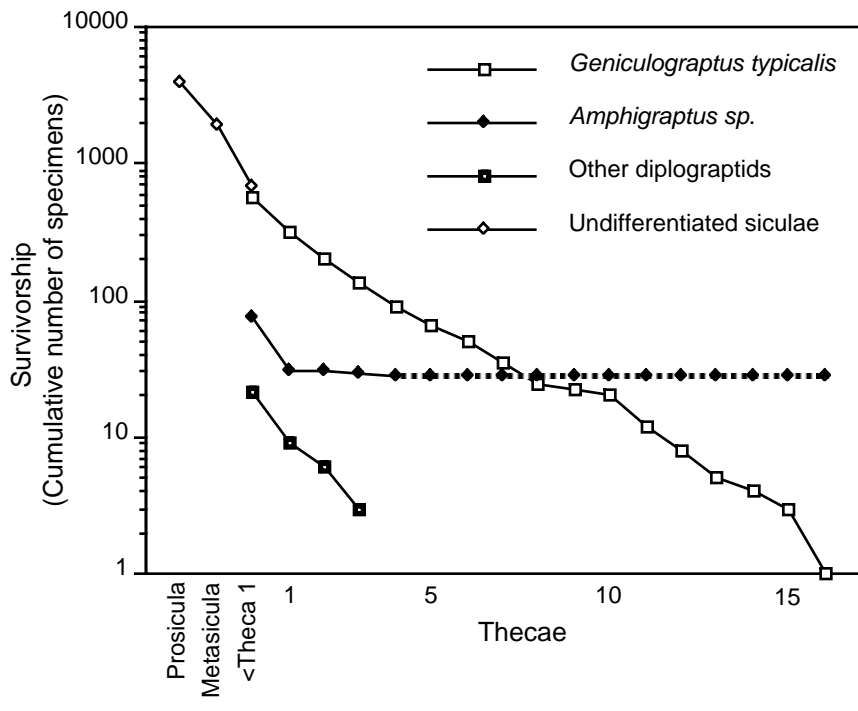
Underwood Fig. 1



Underwood Fig.2



Underwood Fig.3



Underwood Fig. 4

Cape Phillips	pro-sicula	meta-sicula	<1 theca	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	>15
Undifferentiated monograptid	1256	673																	
monograptid, cumulative	2438	1179	506																
<i>Monoclimacis</i> , whole			244	44	15	4	4	2											
<i>Monoclimacis</i> , reconstructed				10	4	9	6	10	5	2	3	1	1	1	0	1	1	0	3
<i>Monoclimacis</i> , cumulative			370	126	72	53	40	30	18	13	11	8	7	6	5	5	4	3	3
<i>Monograptus</i> , whole			52	19	14	0	1	3	2										
<i>Monograptus</i> , reconstructed				2	1	1	6	0	0	1	0	0	0	1	1	0	0	0	5
<i>Monograptus</i> , cumulative			109	57	36	21	20	13	10	8	7	7	7	7	6	5	5	5	5
<i>Cyrtograptus</i> , whole			12	2															
<i>Cyrtograptus</i> , reconstructed				2	4	1	1	0	1	1	0	0	0	1	0	1	0	0	1
<i>Cyrtograptus</i> , cumulative			27	13	11	7	6	5	5	4	3	3	3	3	2	2	1	1	1
<i>Paraplectograptus</i> , whole			75	27	16	15	6	3	1	1									
<i>Paraplectograptus</i> , reconstructed				1	1	1	2	1	5	2	2	1	1	2	0	1	0	0	1
<i>Paraplectograptus</i> , cumulative			168	93	65	45	29	21	17	11	8	6	5	4	2	2	1	1	1
Osmundsberg	pro-sicula	meta-sicula	<1 theca	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	>15
Undifferentiated sicalae	49	57																	
Cumulative	130	81	35																
<i>Torquigraptus</i> , whole			9	1															
<i>Torquigraptus</i> , reconstructed				0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	3
<i>Monograptus</i> , whole			4	3															
<i>Monograptus</i> , reconstructed				0	0	0	0	1	0	0	0	0	0	0	0	1			
<i>Petalolithus</i> , whole			4	1															
<i>Rastrites</i> , whole			2	1															
<i>Rastrites</i> , reconstructed				0	1	0	1	0	0	1									
Viola Limestone	pro-sicula	meta-sicula	<1 theca	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	>15
Undifferentiated sicalae	1966	1274																	
Cumulative	3902	1936	662																
<i>Geniculograptus</i> , whole			257	102	62	22	14	7	3										
<i>Geniculograptus</i> , reconstructed				6	9	22	11	9	11	11	2	2	8	4	3	1	1	2	1
<i>Geniculograptus</i> , cumulative			566	308	205	134	90	65	49	35	24	22	20	12	8	5	4	3	1
'diplograptids' other, whole			12	3	3	3													
'diplograptids' other, cumulative			21	9	6	3													
<i>Amphigraptus</i> , whole			44	1	1	1													
<i>Amphigraptus</i> , proximal ends			13	12	1	1	0	1											
<i>Amphigraptus</i> , cumulative			75	31	30	29	28												

Underwood Table 1