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There are extinctions and extinctions: examples from the Lower Palaeozoic

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The extinction events at the Cambrian–Ordovician and Ordovician–Silurian boundaries are compared and contrasted. A simple theoretical model shows that times of increased cladogenesis produce elevated rates of taxonomic pseudo-extinctions, according to the recognition of paraphyletic groups. Taxonomists have traditionally placed stratigraphically early and morphologically primitive members of clades into paraphyletic groups. The Cambrian–Ordovician boundary coincided with such a period of cladogenesis. Extinctions occurred among shelf taxa: deeper-water taxa were mostly unaffected. The various explanations that have been proposed to explain Cambrian–Ordovician extinctions are evaluated. The Cambrian–Ordovician boundary event was probably similar to 'biomere-type' events that preceded it in the Cambrian and followed in the Ordovician. However, the rapid, but apparently staggered appearance of major new taxa at this time elevated taxonomic pseudoextinctions. In contrast, the Ordovician–Silurian extinction event terminated many major clades. An important 'oceanic' event (or events) profoundly affected outer- to off-shelf taxa (including plankton), some having had long and stable histories. The late Ordovician glaciation produced changes in shelf taxa, but changes in brachiopod faunal composition were spread over a long time compared with that for oceanic events. The likely role of anoxia in explaining deeper water end-Ordovician extinctions at the time of deglaciation is discussed.

1. Introduction

When Newell (1967) identified major extinction events, those at the Cambrian–Ordovician and Ordovician–Silurian boundaries were regarded as of major consequence. However, these intervals have not attracted the same amount of attention as events later in the geological column, particularly those associated with supposed catastrophic extinction (Raup & Sepkoski 1982, 1986; Jablonski 1986). If Sepkoski's (1981, 1984) account of the fossil record is correct, the Cambrian–Ordovician boundary marks the onset of expansion of the Palaeozoic evolutionary fauna, whereas the Ordovician–Silurian boundary marks both the decline of the Cambrian evolutionary fauna and a relative rise in importance of the Modern evolutionary fauna. It might be claimed that events in the early Palaeozoic set the course of subsequent evolution in the marine realm, notwithstanding the major extinction events that were to follow. It has also been claimed that the Cambrian soft-bodied biota, such as those represented in the Burgess Shale, reveal a phase of evolutionary 'experiment' (Conway Morris 1979), even with distinct phyla; most did not survive the Cambrian Period. If all, or any, of these conjectures are true, it is clear that the extinction events at the Ordovician–Silurian and Cambrian–Ordovician boundaries are of some interest. There have been many recent papers on the Ordovician–Silurian extinction events; usually from the perspective of a single group (e.g. brachiopods (Sheehan 1975, 1986), graptolites (Koren 1988; Melchin & Mitchell 1988)). The pattern of arthropod extinctions through both boundaries was described by Briggs *et al.* (1988). The factors that might have been involved at the Cambrian–Ordovician boundary have mostly been discussed in relation to trilobite evidence (Fortey 1983; Westrop & Ludvigsen 1987). This paper reviews some of the problems special to these extinction horizons, and examines the mechanisms that might have brought about the extinctions themselves.

2. Problems peculiar to lower palaeozoic extinction horizons

There are some problems with the Cambrian–Ordovician and Ordovician–Silurian extinction events that should be stated at the outset. Not least is the problem that in many cases stratigraphic knowledge is still at the descriptive stage. For example, the detailed Ordovician–Silurian stratigraphy of the Oslo region, Norway (Brenchley & Cocks 1985), or the Eastern Great Basin, U.S.A., has only been fully described recently; there are still parts of the world where stratigraphic knowledge is lacking or incomplete. Some of the most important sections for studying the Cambrian–Ordovician boundary have only been closely studied in the past decade, and some have only just been described (Chen *et al.* 1985). None the less much new knowledge has become available over the past few years (Cocks 1988; Norford 1988). The stratigraphic emphasis has been the result of the need to define the bases of the Ordovician and Silurian Systems; information directly pertaining to extinctions has mostly been derived as a by-product.

Correlation problems

Although the international correlation of the Cambrian–Ordovician and Ordovician–Silurian boundaries is much more precise than before, many problems remain. International agreement has been reached on the base of the Silurian (at the base of the *Akidograptus acuminatus* biozone), but the base of the Ordovician has yet to be defined formally, and any discussion of the Cambro–Ordovician event has to take an arbitrary decision on the matter. The problems can be summarized in two categories.

(i) Correlation between different biofacies and lithofacies. This has always been a problem in the Ordovician with regard to the graptolitic and shelly facies. Much of the discussion on fixing the base of the Silurian centred on such problems. Graptolites give a very refined stratigraphy in some facies through the critical late Ordovician to early Silurian interval. Sequences in conodont faunas that might be used to effect correlation into shelf carbonate sequences are less refined. The regressive sequences at the top of the Ordovician are usually lacking in graptolites, and correlation of such rocks with the graptolitic facies is difficult. Furthermore, the Hirnantian-style shelf faunas are typical facies faunas, and as such are subject to problems of diachronism (Rong 1984). All these problems combine to give a simplified view of the chronology of the late Ordovician glaciation, and it may be the case that a polyphase glacial episode will be recognised when some of these stratigraphic problems are resolved. There are comparable but less acute biofacies problems in the late Cambrian to early Ordovician (Fortey *et al.* 1982; Shergold 1988) with contrasting platform and off-shelf faunas.

(ii) International correlation. Discussion of a supposed event requires a reliable basis for correlation between what were separate continents in the early Palaeozoic. Particularly in the Cambro–Ordovician interval there was a high degree of provincialism in inshore faunas as a result of relatively dispersed continental masses at that time (Ziegler *et al.* 1979), coupled with a comparatively strong climatic gradient. This means that certain events (like the early history of cephalopods – most fully known from China) are manifest only in confined areas, and that it is not easy to establish synchroneity of events without circular argument. The recent discovery of a magnetic reversal at this horizon could be a useful adjunct to biostratigraphy, if it is confirmed in other sections. None the less, conodonts (Miller 1988), graptolites and trilobites are a reasonable control internationally, even if there are still arguments about the exact level appropriate for the definition of the base of the Ordovician.

3. Systematics, paraphyletic groups, and extinction events

Systematics and the study of extinctions are inextricably connected. If extinction is the termination of lineages, the meaning of the taxa concerned defines the nature of the event. The problems involved are not trivial ones. For example, Briggs *et al.* (1988) identified several cases where taxonomic practice itself could give rise to spurious extinctions (taxonomic pseudo-extinctions). This applied where a particular horizon served to separate the specializations of different taxonomists who became disposed to apply different names on either side of a boundary. A supposed extinction may merely record the disappearance of a paraphyletic taxon, which is a consequence of the inadequacy of phylogenetic resolution, and not the termination of a clade. Similar criticisms by Patterson & Smith (1988) were applied to family level data used by Raup & Sepkoski (1986). These systematic problems may have a major influence on the kind of extinction pattern, or even call its reality into question. Similar problems have some influence on the differences between the Cambrian–Ordovician and Ordovician–Silurian boundary events as discussed below.

Paraphyletic groups and extinction horizons

Patterson & Smith (1988) noted that a significant part of the family-level data used by Raup & Sepkoski (1986) was flawed. Some of these limitations, such as the use of monospecific families, which are simply those for which relationships have not been determined, are obvious. But the observation that many of the family taxa were paraphyletic groups is much more interesting. Is a cyclicity of extinction actually a cyclicity of paraphyletic groups?

Patterson & Smith's approach to the systematics of these families was cladistic, and correctly so, for such methods of analysis 'permit the sensible marriage of history with models involving process' (Levinton 1988, p. 492). It is the meaning of paraphyletic groups that is important in the context of extinction events (Smith 1988). From a cladistic taxonomic standpoint, paraphyletic groups are meaningless in the sense that they are based on shared primitive characters (symplesiomorphies) rather than synapomorphies, which define 'good' groups (Wiley 1981). However, this does not mean that their appearance is historically meaningless. Why, after all, should paraphyletic taxa be concentrated at certain horizons in the geological record? The employment of paraphyletic groups by palaeontologists has usually been based on shared general resemblance, regardless of whether the characters were primitive or derived. Paraphyletic groups of this kind share one or more characters that link them with derived groups, but their overwhelming plexus of primitive characters often makes it impossible to decide to what derived taxon any member of the paraphyletic group is related. They are 'bags' to which primitive members of a clade are consigned. Although this makes them difficult to deal with from a cladistic point of view (meaningless, even) the presence of such groups is not without meaning historically.

I have attempted to model a possible explanation for the presence of paraphyletic groups in association with extinction events in figure 1.

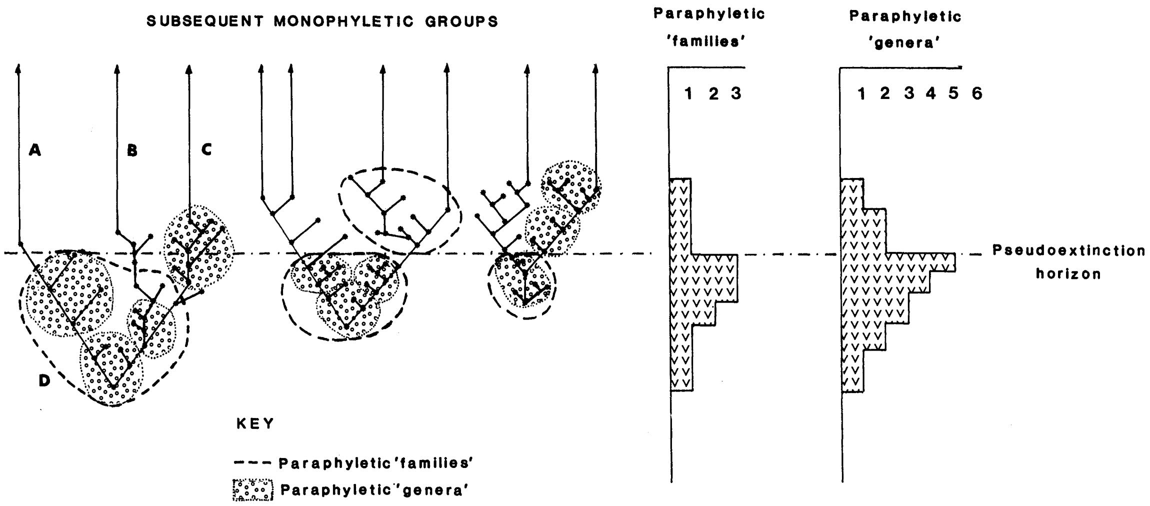

FIGURE 1. Early phases of cladogenesis, if concentrated in a short time interval, produce a temporal concentration of paraphyletic groups as recognized in traditional taxonomy and a taxonomic pseudoextinction of some magnitude. Points represent hypothetical species, arrows signify groups that would have had a long subsequent history and be recognized as clades by most taxonomists.

It has been widely claimed that periods of cladogenesis follow extinction events, and hence that the early history of clades will be recorded in the rock sequences immediately overlying horizons of extinction. The early species may retain characters from their immediate ancestors, and phyletic divergence may not have proceeded far enough to be certain to what (if any) derived taxon any given species should be assigned. These are precisely the circumstances when early representatives are grouped together as paraphyletic taxa. Even with the added precision provided by cladistics it may not be possible to dismantle the constituents of such taxa into derived clades, simply because character complexes defining subsequent clades may not have been fully assembled. A cluster of early species may differ only in the most trivial characters; ornament or size. A taxonomist may have placed such species within a single genus regardless of whether that genus may subsequently prove paraphyletic. Even if the phylogenetic relationships of derived taxa are known it may be that any one of the early species may substitute for any other as the sister group of the derived clades; they may not show characters that enable their relationships to be resolved more finely. The more complete the fossil record, the more likely it becomes that such early stem species will be discovered, and the more likely it is that there will be numbers of such species that may be grouped together in a larger paraphyletic taxon. This implies that later taxa will be identified into monophyletic clades (A, B, C, in figure 1), and that the paraphyletic taxon (D) will include those ancestral taxa where relationships to the derived groups are not clear. The size of D is limited by the extent that derived taxa can be 'pruned' from it. The disappearance of taxon D (that might be claimed as a family) is a taxonomic pseudoextinction. A repetition of the same argument leads to the conclusion that within the paraphyletic family, the earliest and most primitive members may themselves be congregated into a paraphyletic genus (figure 1) including those species plesiomorphic in all fossilisable respects to the rest of the clade A+B+C+D.

It may be concluded that a period of cladogenesis (e.g. that following an extinction event) may yield a high rate of taxonomic pseudoextinction. Families and genera, at least as presented in tabular summaries of ranges, will 'disappear'. Could some such factor have been responsible for the cyclical appearance of paraphyletic groups in Patterson & Smith's (1988) analysis of Raup & Sepkoski's (1986) data?

Stratigraphic refinement comes into this argument. Most extinction data are derived from rocks representing a given period, usually those of a stage. This is often the most feasible unit for worldwide correlation. An average stage in the Jurassic has a duration of about 7 Ma, but even if it were less than half this figure this would presumably represent enough time to gather together the effects of extinction (genuine termination of clades) and the earlier part of subsequent re-diversification (taxonomic pseudoextinction of paraphyletic clades). In a particular case this would no doubt depend on how and where stage boundaries were drawn. It seems possible that some extinction events were composite, with different groups having terminated at different times, perhaps even staggered over several million years. This might prove to be the case with the Ordovician–Silurian boundary event. If this were so, true extinction and taxonomic pseudoextinction at early cladogenesis could overlap in time. Both would produce an extinction peak.

This is not mere quibbling over taxonomy. The basal Ordovician has long been recognized as a period whence major taxa originate. Many of them are still extant. The same phenomenon would be reflected in the steep climb in Sepkoski's (1984) curve of overall familial diversity at this level. Hence one might expect this time interval to include many paraphyletic taxa (the ancestors of later clades), and a correspondingly high rate of taxonomic pseudoextinctions.

There are few full phylogenetic analyses of taxa at their times of origin, close to the base of the Ordovician. However, some case histories indicate that there is a relative preponderance of paraphyletic taxa early in the history of clades at this time. Figure 2 shows the proportion of paraphyletic taxa within the Graptoloidea during the early Ordovician based on a phylogenetic classification by Fortey & Cooper (1986) and incorporating some further indications of paraphyletic taxa introduced by Erdtmann (1988). The early graptoloids are all placed in an avowedly paraphyletic family, the Anisograptidae. Members of this family have not yet been unequivocally ascribed to any derived clade. Anisograptids retain a primitive characteristic, bithecae, that is lost in later clades. Within the Anisograptidae, the earliest and most primitive genera are themselves considered to be paraphyletic taxa, especially on the basis of Erdtmann's account (1988). Later anisograptids probably include some genera that are true

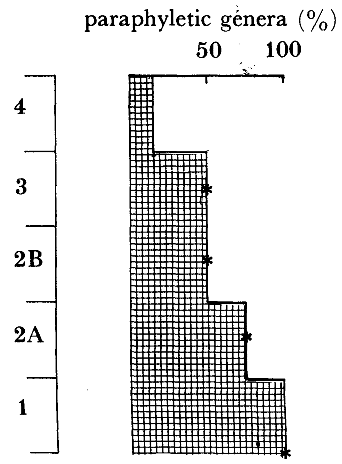

FIGURE 2. Decrease in proportion of paraphyletic genera in the early history of the Graptoloidea through time. The Tremadoc zones of Erdtmann (1988) are shown on the left.

clades. Overall there is a preponderance of paraphyly early in the history of the group. Disappearances of such taxa are pseudoextinctions and these will also be concentrated earlier in the group's history, with another event at the base of the Arenig. Among trilobites too there are more paraphyletic groups in the region of the Cambrian–Ordovician boundary. Subfamily or family level has to be considered because generic relationships are not worked out. The paraphyletic nature of some of these trilobites is not obvious from the current literature. These are mentioned here. For example hystricurids, so characteristic of the early Ordovician in palaeoequatorial regions, were regarded by Fortey & Owens (1975), in a treatment antedating a cladistic viewpoint, as the stock that gave rise to Proetida by more than one phylogenetic line. In other words, they are a paraphyletic group, although they have not formally been described as such. Symphysurinids are typical of early Ordovician platform limestones. In a phylogenetic analysis of Asaphina, Fortey & Chatterton (1988) noted that symphysurinids were not asaphids (as they had been regarded) but exhibited a combination of primitive and advanced characters that made it likely that they were ancestral to both cyclopygids and nileids. Hence symphysurinids probably constitute another paraphyletic taxon. It has been claimed (Ludvigsen & Westrop 1984) that Missisquoiids are ancestral to the scutelluid clade. According to Fortey & Chatterton (1988), jegorovaiids are the trinucleacean equivalent. These taxa all become extinct within a biozone or two of the Cambrian–Ordovician boundary. Many trilobite families passed through the Cambrian–Ordovician boundary unscathed, and hence paraphyletic taxa constitute only a proportion (perhaps 20%) of the whole sample.

This provides some indication that a preponderance of paraphyletic taxa in some parts of the geological column may elevate 'extinction rates' as recorded in faunal lists. Termination of clades must be distinguished from the more arbitrary 'disappearance' of paraphyletic taxa. Species-level extinction may still be a real phenomenon within a paraphyletic taxon of higher rank, but the disappearance of paraphyletic taxa above species rank could be intimately connected with an immediately preceding extinction event, or with a spurt in cladogenesis.

4. THE CAMBRIAN–ORDOVICIAN EVENT – CLADOGENSIS OR EXTINCTION?

Newell (1967) and Sepkoski (1986) have recognized an extinction event of importance at the Cambrian–Ordovician boundary. That there are differences between Ordovician faunas and those of the Cambrian is not in dispute; many of the higher taxa still living (among the bryozoans, cephalopods and bivalves, for example) first appear close to the Ordovician boundary. It is natural to assume that the extinction of a Cambrian fauna predated the origination of 'modern' taxa, and that the boundary between the systems was when this happened.

The boundary between the Cambrian and Ordovician systems is under scrutiny from the International Working Group on the Cambrian–Ordovician boundary; this is seeking to determine at what level the boundary should be drawn, and in what section the boundary horizon should be defined. Although the problem has not yet been resolved, a positive outcome of this interest has been the discovery and investigation of several sections spanning the critical interval (Norford 1988). These include sections in most of the Ordovician palaeogeographical regions. The boundary is now reasonably defined globally. Thanks to detailed studies on conodonts, trilobites and graptolites the international correlation is now on a better footing, although there are still disagreements. For this paper the boundary is taken at the base of the

North American *Parakoldinioidia* (= *Missisquoia*) biozone and its equivalents that marks the appearance of trilobite faunas with an Ordovician cast.

If the Ordovician was a time when many groups with a long subsequent history appeared it is likely that the species that are recovered from the earliest rocks would have included the ancestors of at least some later clades. This makes it likely *a priori* that they will have been placed in paraphyletic groups, especially by palaeontologists basing their classifications on general resemblance. Even with the refinements of cladistic analysis such groups may not be resolved into derived clades because of a paucity of synapomorphies capable of solving their phylogenetic relationships. The question then arises whether the Cambrian–Ordovician event could have been dominated by taxonomic pseudoextinctions as described above. Is it an important event because of the cladogenesis going on at the time, rather than as a result of the extirpation of major clades?

Briggs *et al.* (1988) summarized trilobite data across the boundary. At the family level several of the late Cambrian groups were unsatisfactory, being polyphyletic or paraphyletic taxa. After subtracting these, there was greater family continuity across the boundary than had been supposed. One major group (Dikelocephalacea) did become extinct at or close to the boundary. Extinction was more prevalent at the generic level. This was preceded by a decline. The taxa affected were inhabitants of platform areas; deeper water taxa appeared to be largely unscathed. Some of these deep water taxa had long ranges extending from late Cambrian until well into the Ordovician (figure 6). The Cambrian–Ordovician boundary is thought by many workers to coincide with a eustatic event (Lange Ranch event of Miller (1985)). All workers agree that there was a Tremadoc overstep, although Ludvigsen *et al.* (1988) regard the evidence for a Cambrian regression preceding it as inadequate.

The late Cambrian genera that became extinct were much less likely to represent paraphyletic taxa; data on trilobite distribution support an extinction event – but how major an event? The Lower Palaeozoic has other, minor, extinction events, such as the Cambrian 'biomere' events (Palmer 1984). Similar events probably delimit the Ordovician series (Fortey 1984). Shelf trilobites were apparently more vulnerable to extinction at biomere boundaries, and the picture generally drawn of a biomere (Stitt 1975) is one of a radiation on-shelf followed by a stabilization of diversity before a comparatively slow decline, and eventual sudden extinction. One way to examine whether the Cambrian–Ordovician boundary is different from one of these minor events is to compare their extinction patterns. The Cambrian biomere events and their Ordovician equivalents have not been claimed as major extinction events. In figure 3 the trilobite evidence is summarized across the Tremadoc–Arenig boundary. This is the next horizon above the Cambrian–Ordovician boundary at which there appears to be a turnover in genera, and more 'Ordovician families' (trilobites: trinucleids, calymenids *sensu stricto*, for example) appear just above it, so it affords an appropriate comparison. There are difficult correlation problems at this level, however, and my Arenig base is taken at an horizon equivalent to the *Tetragraptus approximatus* graptolite biozone with an attempt at its equivalents elsewhere. This includes a correlation with the base of Zone G2 of the zonal scheme for platform North America of Ross (1951), and the base of the Moridunian (Fortey & Owens 1987) in the Anglo-Welsh area. The correlation problems are discussed in more detail by Bergström (1986), Cooper & Fortey (1982) and Fortey & Owens (1987).

There seems to be considerable similarity between the Cambrian–Ordovician and Tremadoc–Arenig patterns. Last appearances of genera rise at the end of the Tremadoc,

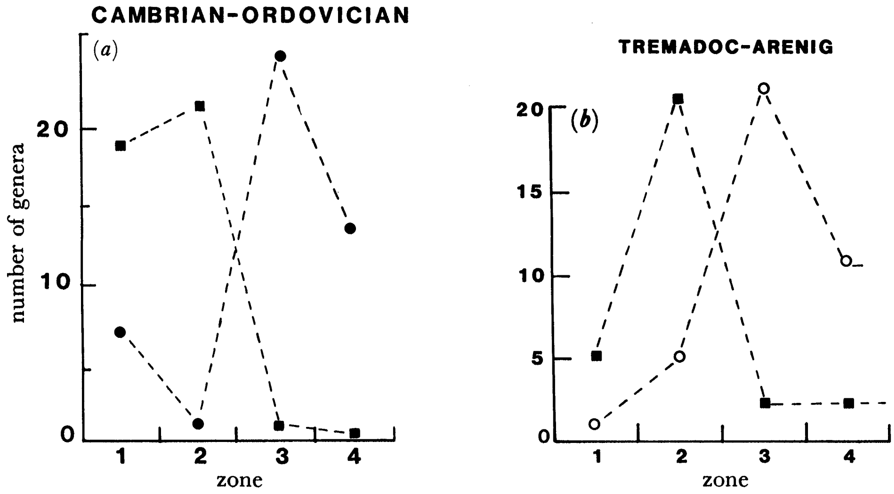

FIGURE 3. The similarity of pattern between last (■) and first (○) appearances of trilobite genera across the Cambrian–Ordovician boundary, and the Tremadoc–Arenig Series boundary within the Ordovician, the former from Briggs *et al.* (1988), the latter a new compilation. In both, an elevation in last appearances just before the boundary is complemented by a great increase in first appearances above the boundary. This has been claimed to correspond with a regressive–transgressive event in both cases.

whereas there is a peak in first appearances of genera at the base of the Arenig. The latest Tremadoc (Lancefield 2 in graptolite terms), like the end of the Cambrian, has been claimed as a regressive interval on the platform (Fortey 1984). The last appearance of the trilobite superfamily Ceratopygacea is in the late Tremadoc, this group has a history extending back to the middle Cambrian. Its disappearance can be compared with the extinction of the Dikelocephalacea close to the base of the Ordovician.

Overall, there is a greater number of families that become extinct at the Cambrian–Ordovician boundary than at the Tremadoc–Arenig boundary. The similarity in the pattern of disappearances and appearances of genera leads one to suspect that this represents a difference in degree rather than in kind. At the Tremadoc–Arenig boundary the graptolite family Anisograptidae probably became 'extinct', but this is a paraphyletic taxon (Fortey & Cooper 1986) and its disappearance is a taxonomic pseudoextinction. It seems that the Cambrian–Ordovician event might be no more than one more, perhaps rather exacerbated, biomere-type boundary. If this were the case, elevated extinction rates at this level may reflect an increased rate of cladogenesis commensurate with the general increase in diversity through the early Ordovician interval (Sepkoski 1984). The apparent extinctions may include taxonomic pseudoextinctions produced by the 'disappearance' of paraphyletic groups in the early history of clades.

The tests of such a theory reside in phylogenetics. Cladistic methods have hardly been applied to phylogenetic studies of the relevant groups through this interval. More traditional taxonomic methods tend to show paraphyletic groups as short-lived 'trunks' from whence various (presumably monophyletic) 'branches' arise. See, for example, Flower's (1964) view of cephalopod phylogeny where most such 'branches' arise from the early Ordovician Ellesmeroceratida. There is already evidence that the times of origin near the Cambrian–Ordovician boundary of such 'rootstocks', like paraphyletic taxa, are not simultaneous. Nor do they necessarily correspond with the Cambrian–Ordovician boundary used here (base *Parakoldinioidia* biozone) that is based on platform North American trilobite faunas (figure 4).

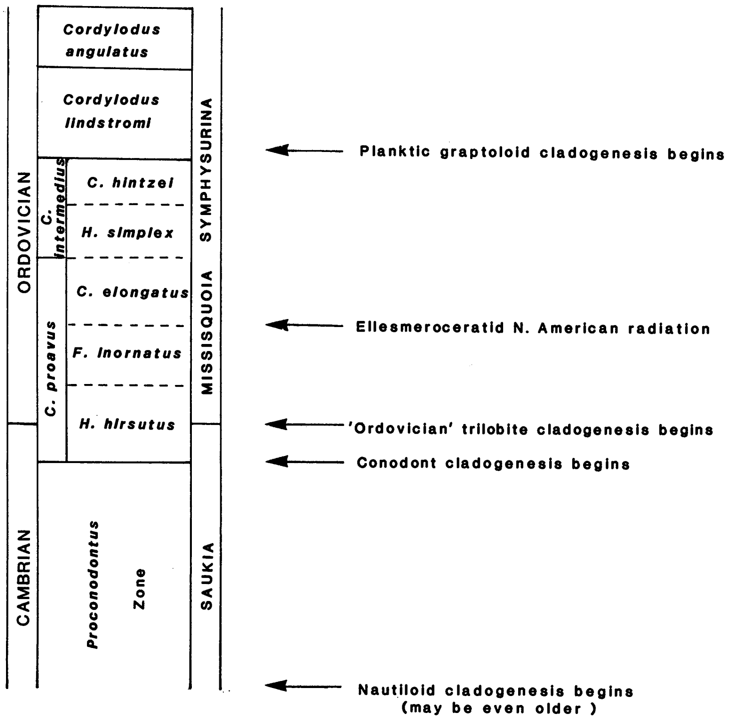

FIGURE 4. Timing of inception of major cladogenesis in different groups through the Cambrian–Ordovician boundary interval, showing that it is not simultaneous in different groups of organisms. Taxonomic pseudoextinction is to be expected; compare with figure 1.

For example, the inception of the radiation of the Graptoloidea began approximately one zone above this (probably within *Symphysurina* biozone equivalent). An initial radiation of the Cephalopoda has recently been discovered in the latest Cambrian of China (Chen *et al.* 1979) with little record elsewhere. The taxa described include ancestors of several derived groups; it is likely that phylogenetic analysis will show such groups to be paraphyletic. Typically, they are accorded high taxonomic rank because their stratigraphic position and characteristics make it awkward to accommodate them within the known phylogeny. The fossil record of other molluscan groups is too discontinuous through the critical interval for comment. The limitations on echinoderm data have recently been discussed by Smith (1988). Where Ordovician-style conodonts begin has not been agreed among conodont workers, but *Cordylodus proavus* and its associates have been regarded as the 'natural' base to the Ordovician (Miller 1988), including taxa ancestral to later Ordovician forms. The base of the *C. proavus* biozone lies below that of the *Parakoldinioidia* biozone. Unless there are major surprises to come in the international correlation, it seems that the onset of cladogenesis was different in different groups, and probably spanned several million years. This does not imply a catastrophic extinction event followed by renewed speciation.

Taking these facts together, we conclude that if cladogenesis was staggered in different groups through a comparatively broad time interval at or below the base of the Ordovician it is likely that a variety of groups ancestral to those typical of the Ordovician and later will have evolved in the latest Cambrian to earliest Ordovician interval. Traditional taxonomic practice will have erected stratigraphically-based and likely paraphyletic groups for such early taxa. The boundary event extinguished shelf taxa, at least at generic level, and is present as an unconformity in many sections. For the same reason this may be a natural 'cut off' for those groups that underwent early cladogenesis below the boundary: that is, taxonomic pseudoextinctions will tend to be concentrated at this horizon. This, combined with the effect of grouping stratigraphically separated events in broad-scale analyses, may account for the elevation in higher level taxon extinction near the Cambrian–Ordovician boundary. Much of it may be taxonomic pseudoextinction reflecting the 'diversity pump' effect at this time, which was probably the most rapid period of cladogenesis in the fossil record.

The extinction event at the Cambrian–Ordovician boundary affected shelf faunas particularly although by no means all of these were exterminated. Trilobite taxa that lived in outer shelf to slope environments were little affected (Fortey 1983, Ludvigsen & Westrop 1987). This is not different from Cambrian biomere events, nor, apparently, from those events at Ordovician series boundaries, such as the Tremadoc–Arenig boundary discussed above. For example, the long-lived trilobite taxa Leiostegiacea and Dikelokephalinidae, both of them shelf taxa and both with histories extending back to the mid Cambrian, were apparently terminated at or near the Llandeilo–Caradoc boundary having weathered earlier perturbations. One could argue that the Llandeilo–Caradoc event, which accompanied one of the greatest marine transgressions in the Phanerozoic (Vail *et al.* 1977), was the equal of the Cambrian–Ordovician event in terms of the elimination of major trilobite clades.

To summarize, the Cambrian–Ordovician boundary marks the inception of many higher taxa. Early phases of cladogenesis multiply paraphyletic groups; many are accorded high taxonomic status because of the difficulties in assigning them to advanced clades. The disappearance of these taxa represents taxonomic pseudoextinction. Such pseudoextinctions were of importance around the Cambrian–Ordovician boundary. The detailed time of inception of new clades was different between groups and a major catastrophic extinction seems improbable. The extinction of genera in platform sites was apparently similar to other events earlier in the Cambrian or later in the Ordovician.

Possible causes of Cambrian–Ordovician extinctions

If the notion of any catastrophic extinction is taken out of consideration, the stratigraphic record can be examined for evidence of possible causes of platform extinctions. If comparison with other Cambrian and Ordovician events is valid it is reasonable to seek common cause.

That biomere boundaries in the Cambrian and the Cambro-Ordovician boundary share common features has been observed by several workers (Stitt 1975, 1977; Ludvigsen 1982). Some biomere boundaries are not accompanied by dramatic facies changes (Palmer 1984). In the majority of Cambrian–Ordovician platform sequences where data is recorded there is a break, or paraconformity, at the boundary (as taken at the base of the *Parakoldinioidia* trilobite biozone) that has been regarded as representing a eustatic regression. The basal Ordovician is transgressive. Although the reality of the late Cambrian regressive event has been challenged locally (Ludvigsen *et al.* 1988) it is a striking fact that apparently identical features occur at exactly the same time in carbonate platform sequences on what were separate plates in the Ordovician (Miller 1984). These features occur widely in the U.S.A., Australia and in the North China platform. I find it difficult to explain this without assuming the existence of eustatic control. However, it is also true that such platform carbonates are generally characterized by small diastems that may be of no more than local significance, and there is the danger of circularity in diagnosing such phenomena as worldwide. Whatever the possible disagreements over the latest Cambrian regression, all authors seem to agree that the early

Ordovician marked a time of transgression. This can produce complicated results locally with biofacies migrations (Ludvigsen & Westrop 1983). One general effect is the shelfward movement of more exterior biofacies, limiting the extent of inshore biofacies (Fortey 1983; Westrop & Ludvigsen 1987). The sudden appearance of offshelf taxa, such as olenid trilobites, within shelf sequences is another consequence. This is analogous to the claimed repopulation of the shelf from offshelf forms that has long been described in biomeres (Palmer 1965). I claimed similar regressive-transgressive cycles in the Ordovician (Fortey 1984) at the Tremadoc–Arenig and Arenig–Llanvirn boundaries, and approximately commensurate with the Llandeilo.

There are several models available to explain how these events could have caused extinction of some platform faunas. They differ significantly, and are summarized in simple form in figure 5.

(i) *With regression, and peripheral refugia*

This model treats a combination of regression and transgression as causing the extinction of platform taxa. The term 'refugia' is used to mean small sites where species may persist during a time of crisis over their formerly widespread habitat area. The regressive phase accounts for the high proportion of last appearances of genera in the latest Cambrian. Some trilobite taxa survive as Lazarus forms (i.e. they reappear later in the Ordovician in shelf facies comparable with those in the late Cambrian, e.g. bynumiids, catillicephalids and lecanopygids). The survival of these is explained by shelf-edge refugia during the regressive interval (Fortey 1983). Subsequent transgression introduced offshelf taxa onto the shelf, and also permitted recolonization of the shelf from the marginal refugia. The implication is that there was greater phylogenetic continuity between Cambrian and Ordovician shelf genera than had been supposed. A rather similar picture can be painted for the Ordovician regressive and transgressive cycles, where there is generally greater taxonomic continuity across boundaries between supposed eustatic events than has been claimed in the Cambrian between biomeres.

(ii) *Transgression and biofacies changes*

Ludvigsen (1982), Ludvigsen & Westrop (1983) and Westrop & Ludvigsen (1987) associate extinctions with a transgressive event alone, producing biofacies shifts and biogeographical changes that are considered sufficient to account for the reduction in habitat variety available for on-shelf trilobites. Extinction was associated with loss of inshore habitats appropriate for particular taxa (especially 'thermophylic and stenogeographic' ones (Ludvigsen 1982, figure 18)) and the shoreward spread of 'eurygeographic and cryophylic' trilobites. The explanation of extinction is thus a combination of the species–area effect, biofacies redistribution and onshore migration of cold-water taxa.

(iii) *Cold-water excursions without necessary transgression*

This appears to be the favoured explanation for Cambrian biomere patterns (Stitt 1977; Palmer 1979, 1984). I do not wish to discuss the problem of where the top of the biomere lies, as opposed to the base of the succeeding biomere (Palmer 1979). Extinctions are associated with change in oceanic structure, especially the upward displacement of the thermocline in the water column such that the more oceanic, long-lived taxa can make their excursion onto the platform, the abrupt change in conditions extirpating its previous inhabitants. Transgressive

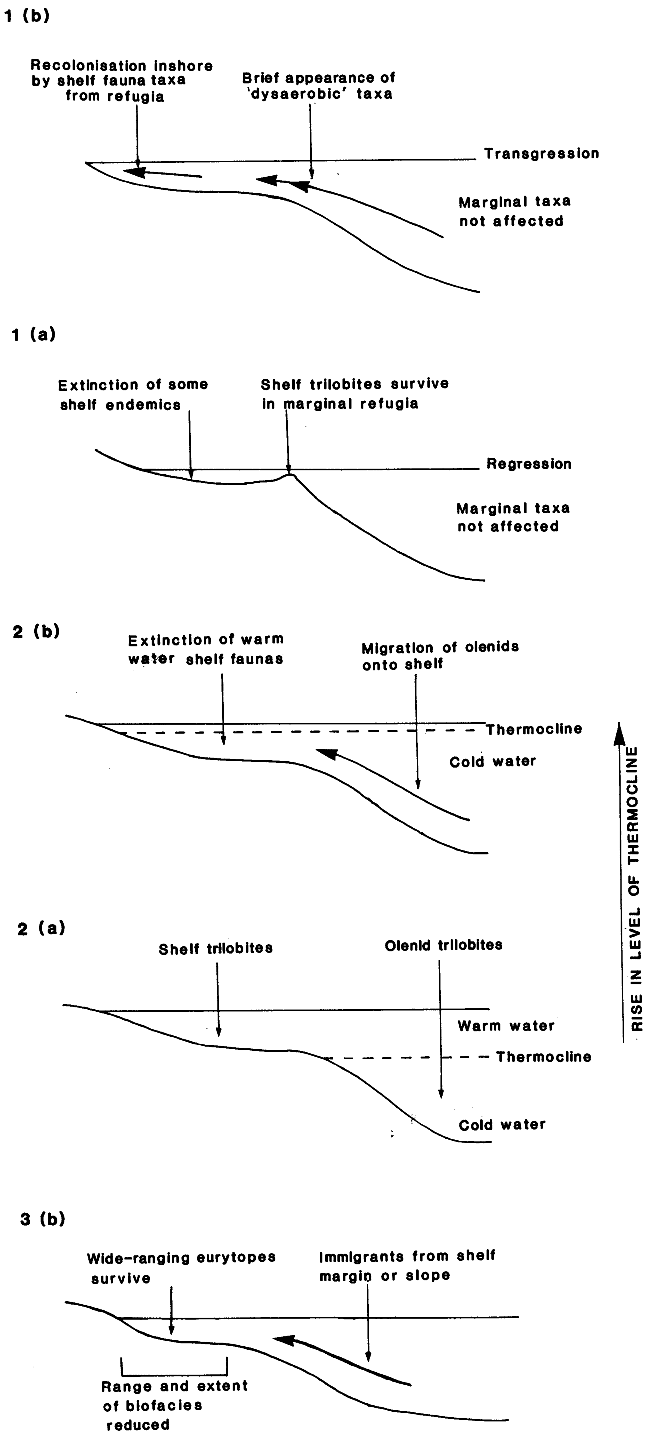

FIGURE 5. Three theories about causes of on-shelf extinction at the Cambrian–Ordovician boundary (a) and (b) represent immediately before and after the boundary interval. (1) Combined regression–transgression, with marginal refugia at regressive maximum to account for continuity of some taxa. (2) Raising of level of thermocline causing platform crisis and appearance thereon of olenid trilobites. (3) Shelfward displacement of exterior biofacies with loss of extent and variety of inshore biofacies; pre-boundary interval much like 2(a).

or regressive events are not necessary for this explanation, and an example of regression within the pterocephaliid biomere, but without major biological effect is cited. Palmer (1984, p. 609) accepts the possibility that the biomere boundaries may record 'widespread anoxic events'.

These models are based on what happened in shelf carbonate sequences, particularly those of North America. A similar pattern may be observed in the Sino-Korean platform (Chen *et al.* 1985). However, contemporary sequences in Scandinavia and Wales record nothing dramatic, and there is undisturbed phyletic continuity among olenid trilobites through the same interval (Henningsmoen 1957). Explanations of the Cambrian–Ordovician events have to take such continuity into account, as well as the observed change.

All the models share one common feature: the shelfward movement of exterior biofacies. This can be accomplished with or without transgression, according to the favoured hypothesis. Is there evidence for more widespread anoxia in the earliest Ordovician accompanying this biofacies shift? It would be true to say that in Norway, the Anglo–Welsh area, and North Africa the early Ordovician *Dictyonema* shales are widespread, and often only yield the planktic graptolite that gives the shales their name. Benthos is often completely lacking (Thickpenny & Leggett 1987). Where present, as in North Wales (Rushton 1982) or Random Island, eastern Newfoundland, the commonest trilobites are often olenids. Olenid trilobites also appear in platform sequences, or become abundant in peripheral platform sequences at the same time. For example, genera such as *Bienvillia*, *Jujuyaspis* and *Parabolinella* make their appearance, occasionally in abundance, in earliest Ordovician sequences (Winston & Nicholls 1967; Ludvigsen 1982). Nobody has suggested that these taxa constitute a 'rootstock' for subsequent platform evolution, in the manner of the biomere model (Palmer 1965). They are interlopers from more peripheral sites.

The olenids are particularly interesting, therefore, in interpreting boundary events. The family has a long history through the later Cambrian to the late Ordovician. Most authors agree that they were a specialized group, but there are different opinions as to what they were specialized for. Their common occurrence with dark shales, lacking other benthos, or with laminated, pyritic limestones or 'stinkstones', has long led to their being associated with dysaerobic environments (Henningsmoen 1957). This has led some authors to suppose that they were pelagic animals, living above a deoxygenated sea floor, but their strict facies association, and many aspects of their functional morphology, make this an unlikely assumption for the major part of the group (Fortey 1985). It is also claimed that one of the main constraints on their distribution was that they lived beneath the thermocline (Taylor & Forrester 1979). This accounts for an unusual interprovincial spread of olenid taxa under these uniform oceanic conditions. Such an explanation would naturally favour upward displacement of the thermocline at the Cambrian–Ordovician boundary. I favour adaptation to the dysaerobic environment as the most plausible explanation for olenid distribution and morphology. Because thermocline and oxygen minimum layer may correspond, it is not perhaps surprising to find the two factors operating together at former continent margins, and the olenid biofacies always represent some of the deepest occupied by trilobites. The Olenid biofacies may, however, become established in marginal basins, at some remove from the continent edge, as in the early Arenig of South Wales (Fortey & Owens 1987). There, the development of a local basin poor in oxygen seems to provide the most plausible explanation of the presence of the biofacies: deep water biofacies in adjacent areas have a different assemblage of trilobites. Truly pelagic trilobites accompany the olenid biofacies in oceanic settings, but may be lacking in sites with restricted access to the open sea, as in South Wales.

If this view of the habits of olenid life is correct, their incursion into platform sites at the Cambrian–Ordovician boundary was probably the result of a shelfward movement of water poor in oxygen, to which the olenids were adapted. This neatly explains the truncation of the ranges of trilobites with normal respiratory requirements that could linger on only in confined inner shelf areas. The majority of deep water taxa already had the necessary physiology to survive the boundary perturbation. Note that there are some sections (such as at Dayangcha, China) where the early Ordovician transgression fails to introduce olenids into the section. Although there is evidence for facies shifts in China compatible with a regressive–transgressive event, the evidence for an oxygen crisis is not clear from the faunas alone. In general, perhaps the shoreward movement of exterior facies with short-lived oxygen reduction, especially at the margins of shelves, provides a more satisfactory explanation of the facts than the elevation of the thermocline. Would it really be possible for cool water to persist on a flooded, shallow platform with tropical insolation for the duration of a trilobite zone? Geochemistry may eventually provide the evidence critical for arbitration between these alternatives. Then there is the question of whether refugia were necessary to explain the persistence of taxa across the Cambrian–Ordovician boundary. The answer will partly depend on confirming or denying the existence of a sub-Ordovician regression. As I discuss below it is clear that there had to be such refugia over the Ordovician–Silurian boundary, even though they are unknown in the fossil record. If there were a major regression across the Cambrian–Ordovician boundary, the record of these sites is likely to be equally poor, although they may be recorded in boulders (derived from sites near the continent edge) in such deposits as the Cow Head Group, western Newfoundland (James & Stevens 1987). I find it difficult to account for the sudden appearance of hystricurid and symphysurinid trilobites in the early Ordovician. There is no phylogenetic hypothesis to suggest that they originated from the outer shelf invaders as the biomere model supposes. It seems far more likely that their sister taxa were Cambrian, and inhabitants of the same kind of in-shelf biofacies. In general, trilobites appear to have remained in their preferred habitats for long periods of time (Robison 1972; Fortey 1980). It is not possible to produce shelf genera with characteristic autapomorphies without plausible antecedents. Simply invoking a vague 'radiation' is not good enough. In some cases the phylogenetic connections are known, at least in a general way, between Cambrian and Ordovician forms. For example, leiostegiids are typical trilobites of Ordovician zone C–D interval in Nevada and Utah. Probably related leiostegiaceans occur in the Upper Cambrian. This leads me to ask where they were in the earliest Ordovician. The Lazarus effect is even more pronounced with the lecanopygid *Benthamaspis* (Briggs *et al.* 1980). Refugia are one possibility. This could be proved by further search in sites marginal to former continents.

5. ORDOVICIAN–SILURIAN EXTINCTION EVENTS

The Ordovician–Silurian boundary is now internationally defined as lying between the Ashgill Series and the Llandovery Series. The Ashgill, and in particular its final stage, the Hirnantian, is known to coincide with a major glacial episode centred on the African part of Gondwana (see Brenchley (1984) for literature). For trilobites, graptolites, echinoderms, molluscs and other groups the late Ordovician marks the last appearance of several major clades. The groups that disappear are good clades and hence taxonomic pseudoextinction was not a major problem in elevating higher taxon extinction rates. The Llandovery was a time of uniform faunas with low diversity. Therefore, at least as far as the fossil record allows us to see it, there was not a period of rapid cladogenesis early in the Silurian. To this extent the reality of the Ordovician–Silurian event is uncontroversial.

Necessity for early Silurian faunal refugia

An important point with regard to the Ordovician–Silurian event is that the known poverty of early Llandovery faunas does not fully record the history of several animal groups. This is because there are many Lazarus taxa that disappear in the later Ordovician only to reappear in the Silurian after a gap of several million years. I can find examples from most groups. The brachiopod subfamily Leptellininae is abundant in the mid-Ordovician, but disappears approximately in the middle of the Ashgill not to reappear, again widespread, until the late Llandovery. Cocks (1988) notes the temporary absence of the superfamilies Craniacea and Eichwaldiacea from the early Llandovery (Rhuddanian). Paul (1982) records only one cystoid family with a Llandovery record, out of eight families that survive the Ordovician–Silurian event. Five more reappear in the Wenlock, whereas there is an even longer gap before the remaining two reappear. There are certain well-defined trilobite genera known from the late Ordovician that disappear through the Llandovery, or only appear in the latest Llandovery. Examples include: the only surviving member of Asaphina, *Raphiophorus*; proetides such as *Scharyia*, *Panarchaeogonus* and *Xenocybe*; the cheirurids *Sphaerocoryphe* and *Staurocephalus* (P. D. Lane, personal communication). The family Brachymetopidae is known from the Caradoc and Ashgill, and again from the Wenlock, but has no Llandovery record. I do not believe that there is any risk of the resemblance between Ordovician forms and their Silurian congeners being homoplasy. Of trilobite families that survived the Ordovician, harpetids and illaenids are absent from the early Llandovery. If one accepts the view of Destombes and Henry (1987) of calmoniid phylogenetics, we have an even longer gap between their Ashgillian Gondwanan ancestors and Devonian descendants. Only in the graptoloids has the record been claimed to be complete enough to read continuously through this interval.

The implication is clear: there have to be refugia for many taxa through the early Silurian. We have no fossil record of these refugia. The early Llandovery record is highly imperfect. This means that one cannot be certain of the sharp termination of clades at the Ordovician–Silurian boundary. After all, if we know that certain taxa must have endured, despite the lack of evidence for this at the moment, how can we be sure that the same refugia did not include the last representatives of taxa known at the present, no later than Ashgill? In the account that follows the assumption is made that what we know from the fossil record accurately records the timing of extinction. This is a working assumption, and probably not an unreasonable one for those groups, like trilobites, with a prolific record. However, until some fossil record is found for the refugia that must have existed in the Llandovery there remains the possibility that extinction was staggered over a longer time period than current opinion allows.

The late Ordovician glacial episode

The glaciogenic rocks at the end of the Ordovician coincide, on the whole, with the extinction events. The evidence can be summarized, briefly. Glaciogenic sediments in North Africa have their counterparts elsewhere in regressive sequences of Hirnantian age that are dominated by clastics and the development of karst surfaces on limestones deposited in inshore Ordovician tropical environments. Few places, other than some deep water graptolitic sites, pass through the glacial interval without its leaving an obvious lithological signature. A eustatic sea-level drop of up to 100 m has been claimed (Brenchley & Newall 1984). The biotas of the Hirnantian are dominated by the so-called *Hirnantia* fauna, named from the characteristic brachiopod. An almost invariable associate is the trilobite *Mucronaspis*. This fauna, widespread in the Hirnantian, extended from higher towards lower latitudes accompanying the glacial episode (Jaanusson 1979; Rong 1984). In detail there is more than one brachiopod community grouped within the Hirnantia fauna as loosely applied in the past (Rong & Harper 1988). The implication would seem to be that this fauna was associated with a latitudinal expansion of the cool water 'province' during the glacial episode, extending into temperate or even subtropical palaeolatitudes, although Rong (1984) seems to prefer the idea that the Hirnantia fauna was eurythermal. The tropical belt did survive, although much compressed latitudinally, in a few sites such as Anticosti Island. There is some evidence of a double glacial pulse (Brenchley 1984), but so far not much evidence to suggest a polyphase glaciation like that of the Pleistocene.

The regressive nature of the Hirnantian must produce a taphonomic bias towards comparatively inshore faunas. The Hirnantia fauna has now been subdivided into a number of benthic community types (Rong & Harper 1988) but the equivalents of deeper-water assemblages typical of the earlier Ordovician are hard to recognize. The critical intervals as far as extinctions are concerned are the Hirnantian and the underlying Rawtheyan stage of the Angle-Welsh area, that equates approximately with the Gamachian interval recognized on the eastern side of North America. The Hirnantian is considered to be a short time interval, 2 Ma, or even less. At species level at least, extinctions were probably scattered through this Rawtheyan–Hirnantian interval; correlation problems make for difficulties in summarizing timing of extinctions on single diagrams for the world. Inevitably this results in grouping of data within intervals, particularly the Hirnantian. With the definition of the base of the Silurian at the *Akidograptus acuminatus* biozone the Hirnantian now includes a short, post-glacial interval rather than coinciding closely with the glacial interval itself.

Patterns of faunal change

The number of Lazarus taxa indicated above impose a limitation on what can be read directly from the rocks through this interval. Groups with a continuous record include graptolites, brachiopods, trilobites and conodonts, and these provide the most informative basis for looking for patterns. Only one superfamily of brachiopods, the Gonambonitacea, becomes extinct within, or at the end of, the Hirnantian. Cocks (1988) comments that the degree of brachiopod extinction 'across the boundary appears to have been far less than previously reported', whereas 'extinctions at the late Hirnantian do not appear to have been greater than at the end Caradoc or end Rawtheyan'. The Hirnantian sees 34 genera make their last appearance compared with some 57 others that continue into the Silurian. Sheehan & Coorough (1989) comment that the most cosmopolitan of brachiopod genera were those that persisted from Ashgill to Silurian. In general the effects of the Ashgill glaciation on brachiopod extinction were spread over the whole of the last Ashgill to earliest Silurian interval (figure 7) rather than concentrated at one specific horizon. Briggs *et al.* (1988) showed that maximum 'last appearances' of genera of trilobites was within, or at the end of, the Rawtheyan or its equivalents. Although Brenchley (1984) claimed that the mortality of most trilobite families coincided with the Rawtheyan extinction event, and with the onset of profound glaciation, a recent study of Owen (1986) showed that, although rare, examples of most of the Ordovician trilobite families persisted into the Hirnantian (Briggs *et al.* 1988) (figures 6 and 8). Their rarity may partly be the result of the facies changes in this interval. The pattern of generic extinction can be compared with a typical series boundary event such as the Tremadoc–Arenig boundary (figure 3) or even with the Cambrian–Ordovician boundary discussed above. The general patterns are remarkably similar, the main point of difference being a low rate of originations early in the Silurian. If this is so, in what feature does the identification of the Ordovician–Silurian boundary coinciding with one of the more important extinction events in the record reside?

As far as the trilobites are concerned the answer has to be the termination of so many major

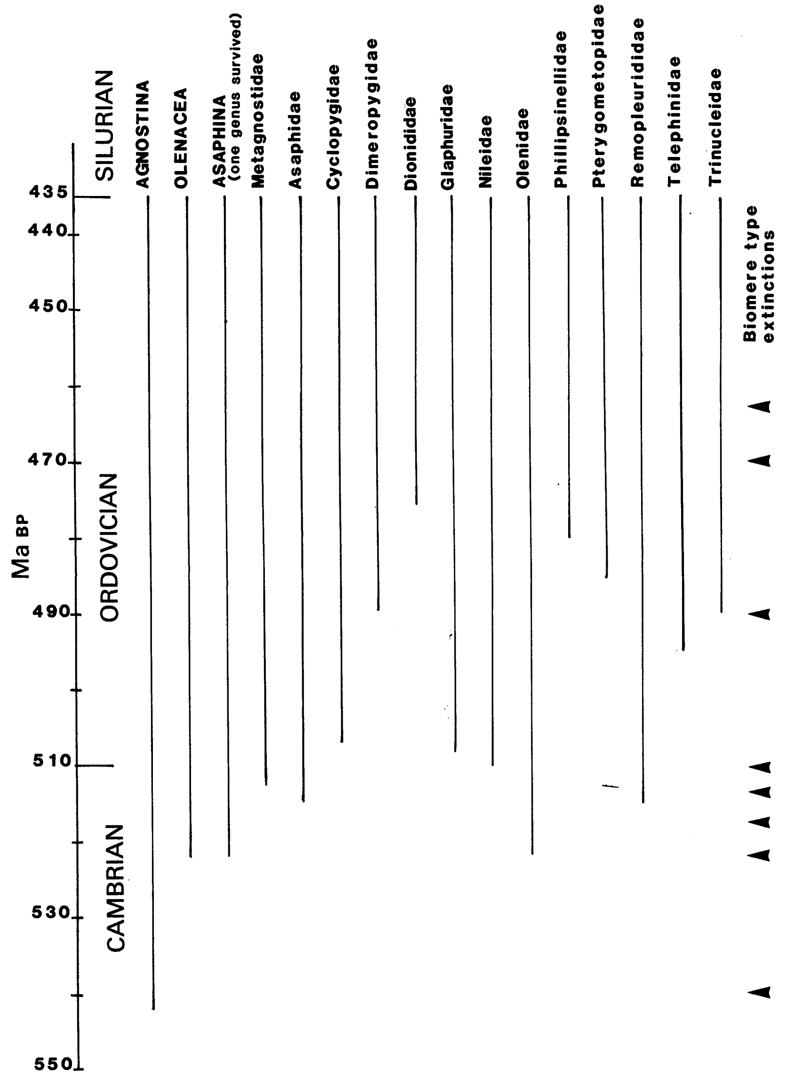

FIGURE 6. Range of higher trilobite taxa that become extinct at the Ordovician–Silurian boundary. Arrows on right mark some of the more important biomere-type events that affect platform taxa, showing how the families affected at the end of the Ordovician have passed through these.

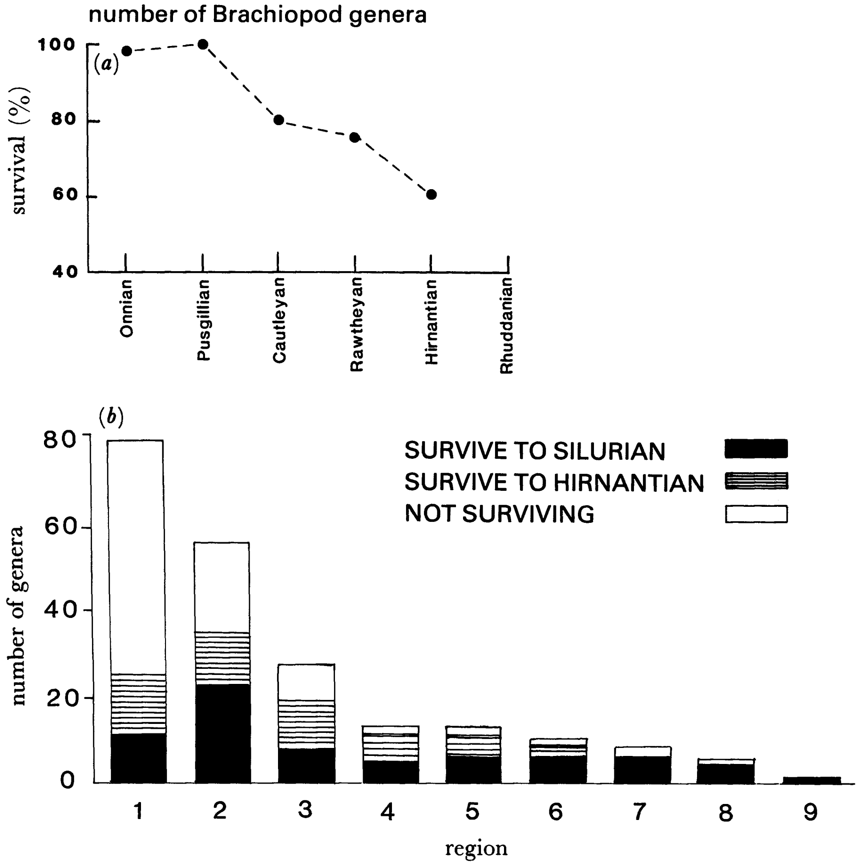

Figure 7. Brachiopods through the Ordovician–Silurian boundary, showing continuous high turnover rather than catastrophic extinction. (*a*). Percentage of genera surviving from one stage to the next through the late Ordovician early Silurian period, after Brenchley (1984). (*b*). Brachiopods divided according to their occurrence in one or more biogeographic regions (1–9) by Sheehan & Coorough (1989) showing how those most widely distributed in the Ashgill were also the strongest survivors.

clades after a history of tens of millions of years, and in some cases more than 100 Ma (figure 6). These include groups that passed through the Cambrian–Ordovician boundary, such as Agnostida and Olenacea. The extinction event seems to be different in kind from other events (including biomere-like events, or those connected with regressive–transgressive events) that are characteristic of the lower Palaeozoic, as mentioned above. Because many of these major clades persist into the Hirnantian, the event in question is not that producing generic mortality within or at the end of the Rawtheyan, but one that is likely to have occurred at or towards the end of the glacial episode. The onset of major glaciation did not terminate the clades. It could be argued that previous extinctions coincident with the glaciation rendered a remnant trilobite fauna more vulnerable to extinction later on. Given the taphonomic bias against finding deeper water trilobite faunas through the regressive Hirnantian interval, this kind of argument would be difficult to prove; there are other intervals within the Ordovician (for example at the Tremadoc–Arenig boundary) where deeper faunas are equally elusive. There has been no success in finding widespread iridium anomalies associated with the Ordovician–Silurian boundary event, and so at the moment there are no grounds for suspecting the involvement of extra-terrestrial agents in the extinction.

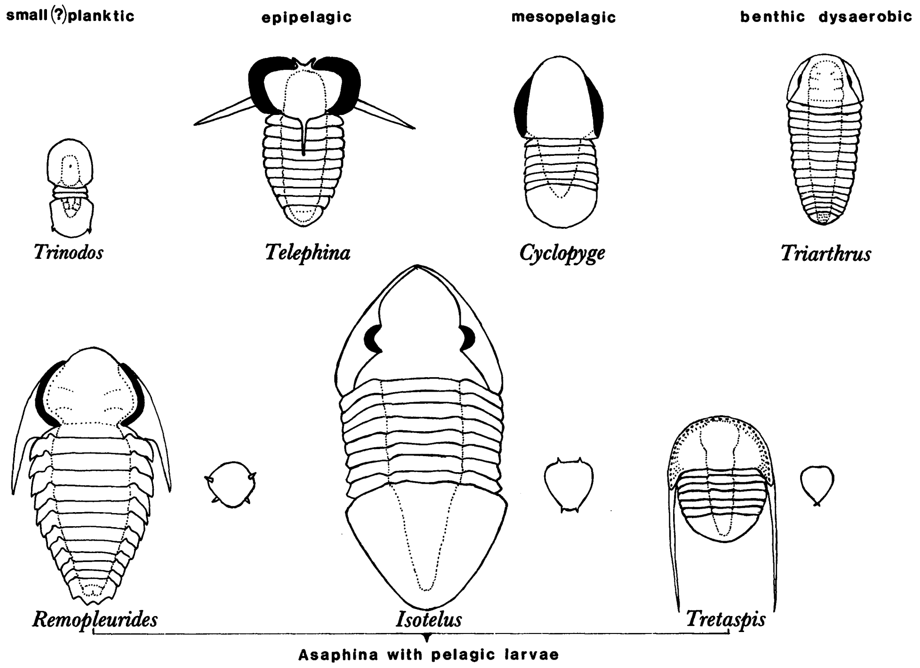

FIGURE 8. The morphological range and life habits of trilobites belonging to clades that became extinct at the Ordovician–Silurian boundary. Bottom row shows planktic asaphoid larvae of mostly benthic Asaphina with very disparate adult morphologies.

Trilobite extinctions: oceanic crisis?

Assuming that I am looking for a terrestrial cause for trilobite extinctions, it is informative to see whether there are any common features between the families that became extinct. Considering the life habits of trilobites, the common factors appear to be that nearly all of the trilobites were deeper shelf forms, or had a phase in their life cycle as part of the oceanic plankton (figure 8).

(i) Asaphina

This suborder of trilobites was the largest group in terms of numbers of constituent families extinguished at the Ordovician–Silurian boundary. As reclassified by Fortey & Chatterton (1988) it includes such typical Ordovician families as Trinucleidae, Nileidae, Asaphidae, Cylopygidae and Remopleurididae, which do not survive into the Silurian. One member of the family Raphiophoridae, *Raphiophorus*, is the lone asaphine survivor, surviving until late in the Silurian. Asaphina include a great range of morphology, and presumably a matching range of life habits. The life habits of Cyclopygidae are the best known (Fortey 1985). These generally eschew shallow shelf environments, and were probably mostly mesopelagic. They persisted from the Arenig to the Ashgill with remarkably little morphological change. This may be attributed to the general persistence and stability of the environment they occupied at the edge of Ordovician continents. This stability was upset by the Ordovician–Silurian extinction. Most of the remainder of the group were benthic. Some Asaphina occupied shelf habitats (some Asaphidae) and the group can be found on all the palaeocontinents in the late Ordovician, including relatively high palaeolatitudes around Gondwana and low palaeolatitudes in Laurentia. What can unite such a disparate selection of trilobites to make them vulnerable to extinction? The only conspicuous unifying feature is the possession of a globular and inflated larval stage termed the asaphoid protaspis, (Fortey & Chatterton 1988). Chatterton & Speyer, (1989) maintain that this larval type was specially adapted for a planktonic existence. Some of these larvae grew to several millimetres in length. Their change into benthic adults was accompanied by something akin to a metamorphosis. Unlike the cyclopygids, which spent all of their lives in the water column, the asaphoid larvae settled at some intermediate growth stage. None the less this great group were obligate inhabitants of the oceanic column at one stage in their lives. Hence it is reasonable to conclude that disruption of oceanic structure is implied in their demise.

(ii) *Other groups*

Non-asaphine groups that did not survive the Ordovician include the following (Briggs *et al.* 1988, fig. 9.5).

(i) Agnostidae. The last of a great group ranging from the early Cambrian, agnostids were particularly associated with oceanic settings throughout their history, and may have been pelagic (Robison 1972). Their end might be explained by oceanic disruption.

(ii) Olenidae. As discussed above, olenids are associated with deeper water and dysaerobic palaeoenvironments.

(iii) Telephinidae. This group included activity swimming pelagic animals of frequent occurrence in oceanic biofacies.

(iv) Nileidae. Nileids are mostly found in outer shelf habitats; Dionididae had similar habits and habitats.

(v) Pterygometopidae, Glaphuridae and Dimeropygidae. These groups are the only major trilobite clades that become extinct that are characteristic of more inshore facies. Pterygometopidae may be paraphyletic.

Overall, there is a striking dominance of trilobites that either lived habitually in deeper water facies or had a prolonged planktic larval stage, or pelagic adult stage. Survivors (cheirurids, illaenids, homalonotids, harpids, scutelluids, encrinurids, many proetides, lichids, dalmanitids, odontopleurids and calymenids) are either well known as inhabitants of reef-like calcareous habitats, or were common in inshore clastics around Ordovician Gondwana. It was these habitats and their occupants that seemed to have survived the end Ordovician event. The necessity for the existence of early Silurian refugia has been stated. Although there seems to be no problem about the persistence of clastic facies, which dominate boundary sequences, there is a scarcity of early Llandovery carbonates. They must have persisted somewhere in the equatorial region: the only examples known to me are in Estonia.

Hence it can be concluded that the Ordovician–Silurian event was quite different from the Cambro–Ordovician event (or indeed any of the intra-Ordovician or Cambrian biomere events) as far as the trilobites were concerned. The long-lived clades, the deep-water taxa, or those with specialized planktic larvae, were greatly affected. This is not to deny that the end Ordovician glaciation had an important effect on shelf taxa. Like the brachiopods (Sheehan 1975, 1982), which were less profoundly affected at high taxonomic level than the trilobites (Brenchley 1984; Cocks 1988), shelf trilobites had a high rate of generic extinction, coinciding with the onset of major glaciation, but the major phylogenetic continuity was not broken. The major event was in exterior and oceanic sites. In that the ranges of the last representatives of the affected families extend into the Hirnantian, it is likely that this event occurred at or near the end of that stage (faunas are too rare to say whether extinctions were exactly synchronous). In that pelagic larvae and adults, and benthic adults were all affected it seems likely that a substantial breakdown in oceanic structure was involved. This implies major anoxia.

Graptolites through the Ordovician–Silurian interval

Many graptolitic rocks accumulated in oceanic sites, producing a record of nearly continuous sedimentation through the later Ordovician and into the Silurian. That the passage from Ordovician into Silurian produced a profound change in the graptolite fauna has been recognized for a long time (Elles 1922; Bulman 1958). Recent studies through boundary sequences have provided more detailed narrative accounts of the changes in the graptolite faunas through the critical interval than are available for any other group (Williams 1983, 1987; Koren 1988; Melchin & Mitchell 1988). The question of which taxa survived the extinction events has been clarified by recent studies of the phylogenetics of graptolites (Cooper & Fortey 1986; Mitchell 1987). It is now clear, for example, that biserial graptolites in the Llandovery are closely related to very few of those in the Ashgill, although this is not necessarily reflected in the current taxonomy (Melchin & Mitchell 1988). The main extinction event for the graptolites probably occurred well below the end of the Hirnantian, within or at the end of the *pacificus* biozone (sometimes considered as a subzone of the *anceps* biozone). This horizon marks the end of the dicellograptids, and the bulk of the Ordovician biserials and retiolitimorphs; all of these are good clades. Where graptolitic and non-graptolitic facies occur together, as in China, the end of the *pacificus* biozone or its local equivalent marks the widest spread of the Hirnantia fauna (Mu 1988), and it can be concluded that the graptolite extinction coincides not with the onset of glaciation but with its maximum extent. The interval succeeding the *pacificus* biozone is marked by a generally barren mudstone in the Dob's Linn stratotype, but this contains within it the *extraordinarius* band, the only British occurrence of the biozone of *Climacograptus extraordinarius*, which represents a low point in graptoloid diversity wherever it has been recognized. A few biserial graptoloids are present. It is believed that these comprise the stock that all the spectacular radiation of the Silurian graptoloids was derived from. Although the fauna of the succeeding *persculptus* biozone is also limited in variety, the sister groups of most of the Silurian graptoloids are probably present therein, including the earliest monograptid, *Atavograptus ceryx* (Rickards & Hutt 1970). The base of the succeeding *acuminatus* biozone, with a slightly more diverse fauna, is taken as the conventional base for the Ordovician–Silurian boundary. At Dob's Linn, Scotland, typical graptolitic black shale deposition is resumed in the *persculptus* biozone, having been almost entirely absent during the *extraordinarius* interval. The early Llandovery marks a very widespread extension of organic-rich graptolitic shale over platform areas in general (Cocks & Mackerrow 1973, fig. 1; Thickpenny & Leggett 1988).

This summary suggests that the record of the graptolites is unusually complete through the Ordovician–Silurian boundary interval, probably more complete than that of any other group. Because graptolites were planktonic animals it is clear that, whatever the nature of their extinction crisis, it has to be one that affected the oceanic water column. Skevington (1974, p. 67) suggested that there was a reduction in the overall distribution of graptolite faunas in the late Ordovician that could be implicated in the extinction event: 'in the late Ordovician all graptolite faunas, with rare exceptions, were confined to the tropical zone'. The subsequent description by Legrand (1981, 1988) of extensive graptolitic formations crossing the

Ordovician–Silurian boundary in the Algerian Sahara, which was close to the glaciated area of the late Ordovician, makes this explanation untenable. Graptolites were capable of living at all palaeolatitudes beyond the end of the Ordovician into the Silurian. So the explanation of their crisis has to encompass a worldwide oceanographic change. It will be recalled that much the same was said above about the trilobite extinctions. To a large extent, the nature of this change depends on the interpretation of graptolite life habits; to what kind of change would they be vulnerable?

Berry *et al.* (1987) have recently proposed the challenging theory that graptolites lived within the early Palaeozoic low-oxygen zone. This may be contrasted with a traditional view that they had a 'superficial drifting mode of life' (Bulman 1970). If they were inhabitants of a low oxygen zone this would make them peculiarly vulnerable to any change that destroyed the stratified structure of the ocean, producing a greater short-term mixing and general oxygenation (Wilde & Berry 1984). Such an event could have accompanied the melting of the Gondwana ice sheet. Could this correspond with the curious facies change in the barren mudstones (hardly a typical black graptolite shale) in the *extraordinarius* interval at Dob's Linn? On the other hand, if the more conventional notion of graptolite life habits were accepted, with some depth stratification accounting for the variety of species, then perhaps most species would be regarded as having had a normal oxygen tolerance, and, barring catastrophes, they would have been vulnerable to anoxia.

Conodonts through the Ordovician–Silurian boundary interval

The conodont record is not as complete as the graptolite record, if only because of a shortage of suitable calcareous successions to record their history. Barnes & Bergström (1988) have summarized this history. The most completely known succession is that on Anticosti Island, Canada. Only 8 out of 32 genera listed in their figure 5 pass between Ordovician and Silurian worldwide, and the change is as profound as that in other groups. Taxonomic pseudoextinction does not appear to present a difficulty. The correlation with graptolitic facies presents something of a problem, but Barnes & Bergström comment that the main extinction event is 'likely to be in the upper part of the *persculptus* zone'. If so, this is slightly later than the graptolite event. An important observation relates to the phylogenetics of the Silurian survivors. Barnes & Bergström that 'where the origin of the Llandovery stocks is known or can be postulated, they appear to be derived, in almost all cases, from stocks that inhabited the tropical waters of the Midcontinent province during the Ordovician'. The Midcontinent province had a long history in the shallow, tropical seas of the Ordovician. This implies that those clades that became extinct were those that tended to inhabit deeper shelf sites in the Ordovician, including North Atlantic province taxa. As with the trilobites it was oceanward taxa that were particularly affected.

Attempt at a synthesis of the Ordovician–Silurian extinctions

I have attempted to gather together the most important facts concerning the groups that have the most complete records across this boundary. A synthetic explanation has to account for all of these facts, regardless of a preferred explanation for one kind of organism.

(i) Timing (figure 7). The timing of major events does not correspond precisely between different groups, even though all are concentrated within the period of the late Ordovician glaciation and its immediate aftermath. The graptolite event apparently preceded the conodont event. We do not know precisely when the deeper water trilobites became extinct because of their rarity in the Hirnantian but, given the similarity in extinction patterns, it is not unreasonable to assume that they were affected by the same event as the conodonts.

(ii) The regressive event and climatic deterioration associated with the glaciation produced extinctions in the shallow platform faunas, especially at generic level, but the extinction of major clades particularly affected deeper-water forms. Brachiopods, which are characteristic of shelf habitats, had a rather protracted history of extinction through the later Ordovician associated with climatic deterioration, and many Hirnantian genera survived into the Llandovery. The factors possibly involved with extinguishing platform taxa have been described by Brenchley (1984), Jablonski (1986) and Sheehan & Coorough (1989), and include: the spread of cold climate; the reduction in area of certain, especially tropical, habitats ('species–area effect'); and the dominance of the clastic Hirnantia–Dalmanitina biofacies and lithofacies. Legislating between these factors is probably impossible.

(iii) Many groups have a Lazarus interval through the Llandovery, or the Hirnantian plus Llandovery (in some cases even longer). Refugia for these taxa must have existed. The wide spread of monotonous Llandovery muds, often anoxic, readily accounts for the taphonomic bias against Llandovery records of such taxa. Taxa within groups such as echinoderms that are liable to exhibit such Lazarus effects may not have died out precisely at the end of the Ordovician.

(iv) An interesting observation is that the major extinction events, as recorded by the termination of clades in the trilobites and conodonts, particularly affected deeper water taxa. In this respect the Ordovician–Silurian event differs from most others in the Lower Palaeozoic, where deeper-water taxonomic continuity is claimed as the norm. Planktic graptolites were also profoundly affected. It can be concluded that major extinction involved an oceanic crisis.

If all four points hold, a scenario to explain them is not easy to find. Saying that the late Ordovician extinction was caused by the glaciation is unsatisfactorily vague, because it does not account for the different timing of events, nor for the different effects on different groups of organisms. Presumably brachiopod extinction is primarily related to their comparatively inshore history through this interval, and hence directly to glacial influence. Diverse Lower Palaeozoic brachiopod faunas are generally more characteristic of inshore environments. One can find rather conflicting accounts of the extent of the brachiopod crisis. For example, Sheehan (1982) stresses a dramatic turnover in brachiopod faunas between late Ordovician and Silurian, whereas Cocks (1988) indicates a greater degree of continuity than had been supposed. Because Sheehan also emphasizes the early history of brachiopod radiation in the Silurian (a different matter from extinction, as I discussed above) it is possible that these differences are a matter of taxonomy. When Sheehan (1982, p. 477) remarks, for example: 'some of these Silurian groups had well-known ancestors in the Ashgill' this implies that the phylogenetic continuity was not broken by the Hirnantian glaciation, merely that subsequent cladogenesis occurred in the Silurian. The group in question is not Silurian at all, in a phylogenetic sense. However, there was clearly a high rate of generic last appearances among brachiopods throughout the Rawtheyan–Hirnantian interval, and this was probably related to a combination of climatic and glacioeustatic causes, as discussed by many authors.

The most interesting question relates to the oceanic change. To summarize briefly: trilobites that became extinct included benthic forms with a long history in exterior sites, Asaphina with distinctive pelagic larval phases, and pelagic trilobites; conodonts (nektobenthic and pelagic animals according to most authorities) of North Atlantic province type that also included oceanic forms: graptolites with planktic habits, well-known for their wide distribution even at specific level. The deepest-water late Ordovician brachiopod community type, the *Foliomena* community (Sheehan 1973), also failed to survive into the Silurian. The graptolite event predated the conodont event, so far as the stratigraphic correlation allows us to tell.

I can only identify one common cause that is likely to have exterminated the range of trilobites affected, and that is a period of complete anoxia in some niches. Some other options may be eliminated as follows. Spread of cool water accompanying the glaciation is an unlikely factor because some of the trilobites were well-adapted to cool waters anyway. For example, the cyclopygids had a long prior history peripheral to Gondwana in boreal palaeolatitudes. The glacioeustatic regression *per se* cannot account for the change because at least some of the trilobites lived in the water column, and many endured beyond the main Hirnantian regression. The fact that both trilobites that lived in the water column as adults (cyclopygids, telephinids), or as juveniles (Asaphina), and those with benthic adults (olenids, most non-cyclopygid Asaphina) were equally vulnerable, indicates that the causative agency had a considerable bathymetric span. A widespread anoxic event seems to be the only mechanism available to do this. The same event accounted for the conodont extinctions. The degree of anoxia would have to be exceptional to account for the disappearance even of some taxa, like olenids, that may have been able to tolerate reduced oxygen tension (see above). Because of the rarity of Hirnantian deep-water trilobites we cannot be precise about the timing, but of the conodonts were affected by the same event, which is probable given the similarity in extinction pattern, then we can do no better than suggesting that it happened in 'an interval in the upper *persculptus* zone' (Barnes & Bergström 1988). This is at, or very close to, the end of the Ordovician glaciation.

The Hirnantia faunas representing the glacial interval underlie *persculptus* graptolite faunas in China, but elsewhere in the world, Britain for example, they extend into at least the lower part of the *persculptus* interval. The sharp lithological change into dark shale occurs either towards the end of this zone or at the base of the succeeding *acuminatus* biozone; at present further refinement is not possible because of the limits of stratigraphic resolution. But it is likely that the faunal change in trilobites and conodonts coincides closely with the post-glacial 'rebound' that was within the *persculptus* or basal *acuminatus*, or both biozones. If this were so it should be possible to relate the anoxic event to the ensuing transgression, by one of the mechanisms outlined by Hallam (this symposium). One among several obvious possibilities was the sudden release of nutrient-rich water stimulating massive plankton blooms, and concomitant consumption of free oxygen. Whatever the cause, an anoxic event should leave some distinctive geochemical signatures. A variety of such signatures has been recognized 'no older than the base of the *persculptus* zone' (Nowlan *et al.* 1988) in northwestern Canada, and this is consistent with more general studies of widespread reducing conditions in the early Llandovery (Thickpenny & Leggett 1988). The anoxic event is likely to have been the cause of the major extinction in the oceanic realm.

Could the same event have been the cause of the graptolite extinctions? On the evidence currently available this does not seem probable, but stratigraphic correlation problems leave room for manoeuvre. If the graptolite event occurred before the conodont event, as indicated on figure 9, then the two extinctions should have been decoupled, because they are separated by the *C. extraordinarius* range zone in several sections, including Dob's Linn (Williams 1988).

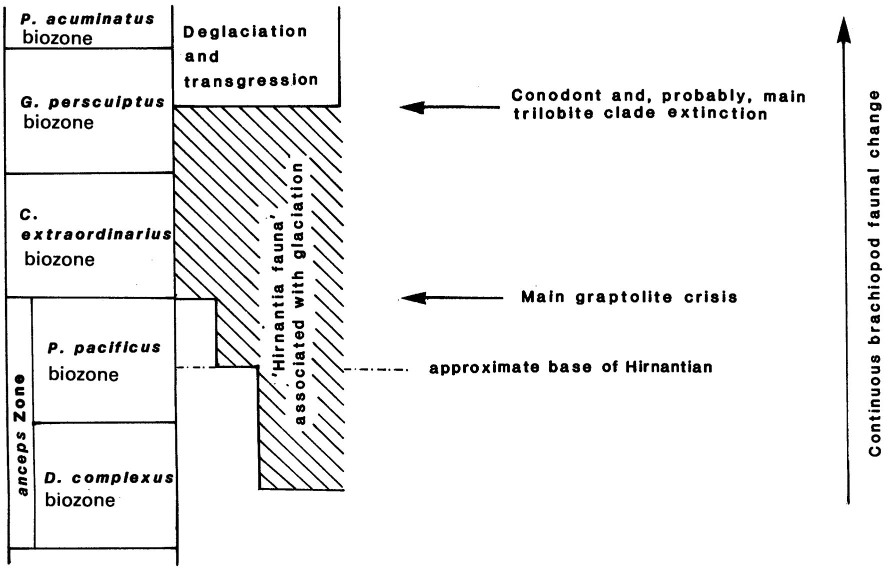

FIGURE 9. Approximate timing of the extinction events affecting higher level taxa of groups with a more or less continuous record through the Ordovician–Silurian boundary interval.

It will be recalled that this interval represented the nadir of graptolite diversity. However, there are parts of the world where the *extraordinarius* biozone is not recognized, for example in China. This pushes the graptolite and other events together in these regions (although there could still be an hiatus). It is possible that the *extraordinarius* interval was very short; the barren mudstone lithology at this interval at Dob's Linn could have accumulated rapidly. Interestingly, a similar barren mudstone interval has been observed to equate with biomere boundaries in the Cambrian (Conway Morris & Rushton 1988). If one accepts the Berry *et al.* (1987) version of graptolite life habits (above), the lethal event for the graptoloids should have been a period of exceptional ventilation, not anoxia, to which one presumes the conodonts and trilobites would have been immune. This view would favour a separate, earlier horizon as the ventilation event; the surviving graptolites would have been the least affected by the anoxic event, and indeed, did go on to proliferate greatly in the Llandovery whereas benthic diversity continued to be rather low. The alternative account of events might be as follows: the apparently different extinction horizons could be explained either by the brevity of the *extraordinarius* interval, perhaps exacerbated by correlation problems, or by the diachronous, shelfward spread of anoxic water from oceanic environments. Gross anoxia caused crises in the graptolite and deeper water groups. Only those species (all apparently diplograptids) that lived in some safe environment could survive; they may have been extreme epiplanktics or shelf taxa. The choice between these hypotheses depends on more refined correlation, independent geochemical evidence, and better ecological understanding of the animals involved. I am reluctant to arbitrate between them here, except to note that the simple explanation is the second, only requiring a single event. However, investigating the problems should afford a fruitful line of further research.

The demise of deeper-shelf trilobites at the end of the Ordovician seems to have had an effect which lasted well into, if not throughout the Silurian. There were no replacements for pelagic trilobites. I can find no convincing Silurian records of the kind of trilobites with reduced or atrophied eyes (atheloptic assemblage) that were characteristic of deep water sites from the mid-Cambrian onwards. None of the trilobite associations from the Wenlock listed by Thomas (1980) seem to be of this kind, and even the lone Ordovician asaphine survivor *Raphiophorus* reappears in an on-shelf basinal facies. By the early Devonian, trilobites with reduced eyes are well-known again, mostly of phacopoid origin. Although the possibility of taphonomic factors being responsible for the Silurian absences cannot be ruled out, it seems as likely that the absence of such morphs indicates a long time-lag in repopulating the full environmental range available to the group. This is particularly interesting in view of hypotheses (see, for example, Jablonski *et al.* (1983)) relating the recruitment of deep water faunas to migrations from shelf environments over a period of time. Could the Ordovician–Silurian boundary have been a major crisis in deep-sea faunas, one that took much of the Silurian to recover from?

6. Anoxia and transgression

There is an association between marine transgression and extinction that has been recognized for some time, and Hallam (this symposium) has claimed the pattern as being general. As discussed above, there is some faunal evidence at the Cambrian–Ordovician boundary, and much at the Ordovician–Silurian boundary, for associated anoxic intervals at times of transgression. In detail an increased rate of last appearances of genera appears to be associated with a regressive phase predating the transgression. Relatively minor biomere events through the Cambrian have been associated with anoxia, if not transgression (Palmer 1984), whereas faunal changes at series boundaries in the Ordovician have been associated with regression and subsequent transgression, if not anoxia (Fortey 1984). In general the idea of an association of extinction with anoxia-eustatic cyles is supported, although different authors stress one or the other, and there is a great deal of disagreement as to how these factors might be involved in causing extinction. The Ordovician–Silurian event seems to have been the one wherein the influence on oceanic faunas was most profound. The kind of animals that survived earlier events were vulnerable at this horizon. If anoxia is sought as common cause, it can be concluded that its effectiveness as an agent of extinction must have varied from one event to another.

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