Synchronology, Taxonomy and Reality [and Discussion]

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Synchronology, taxonomy and reality

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Geochronometry is only of limited help in establishing the timing of evolutionary events. Biostratigraphy and the establishment of a global standard stratigraphic scale are essential. These must be handled sensibly. Suggested periodicity of extinctions is dismissed. So called 'mass extinctions' are assessed by reference to the Ordovician–Silurian, Frasnian–Famennian and Cretaceous–Tertiary examples. Too ready use of the term 'mass extinction' tends to over-dramatize the patterns truly obtainable from the fossil record. It is easier to play with secondary data than to collect primary data.

Limitations of geochronometry

The present symposium is concerned largely with extinction rather than with evolution in general. Extinction is, of course, a limiting case of evolutionary rate, before which come all the problems of punctuation versus stasis, of macroevolution compared with microevolution, of tempo and mode. All these questions are time related. One wants to know when an evolutionary event took place; one wants to know the rate of an evolutionary change. It is still not sufficiently recognized that geochronometry – the science of dating rocks in years – is singularly insensitive in providing answers to these questions. The past 40 years have seen the advent of additional and improved methods for the radiometric dating of rocks and an increase in the number of laboratories where this work continues. Yet, as I have previously stated: 'The point is seldom explicitly made that the broadly consistent, but ever changing, geochronometric scale is somewhat loosely attached to the stratigraphic scale within ranges of dates in years' (Holland 1986). The point is illustrated in figure 1, where dates for the beginning and end, and hence the duration, of three Palaeozoic periods (Ordovician, Silurian and Devonian) are given from several well-known and authoritative compilations of the radiometric timescale. It is not perhaps impossible that at some future time a new and magical 'black box' will be invented that can date rocks of many kinds expeditiously and very accurately. For the foreseeable future, however, investment in improved radiometric dating, in the expansion of the database, and in the efficient dissemination of data should be encouraged and will be to our benefit.

There is, of course, an additional snag: the persistent problem of relating radiometric dates to the stratigraphic scale. To take an example relevant to our present purpose, McKerrow *et al.* (1985) have constructed a timescale for the Ordovician, Silurian and Devonian of which the most accurate points are listed as five in number. Stratigraphic interpolation between these points provides their summary scale. Thus the Ordovician–Silurian boundary must be interpolated between an accurate point of 450 ± 7 Ma in the early Cardoc and one at 431 ± 6 Ma at the end of the early Llandovery. Their fully plotted graph crosses only one additional relevant point within this interval, which can be placed only as somewhere between the beginning of the *bicornis* graptolite biozone, through the *wilsoni* biozone, to the middle of the *clingani* biozone, whereas the two accurate points already mentioned are confined respectively

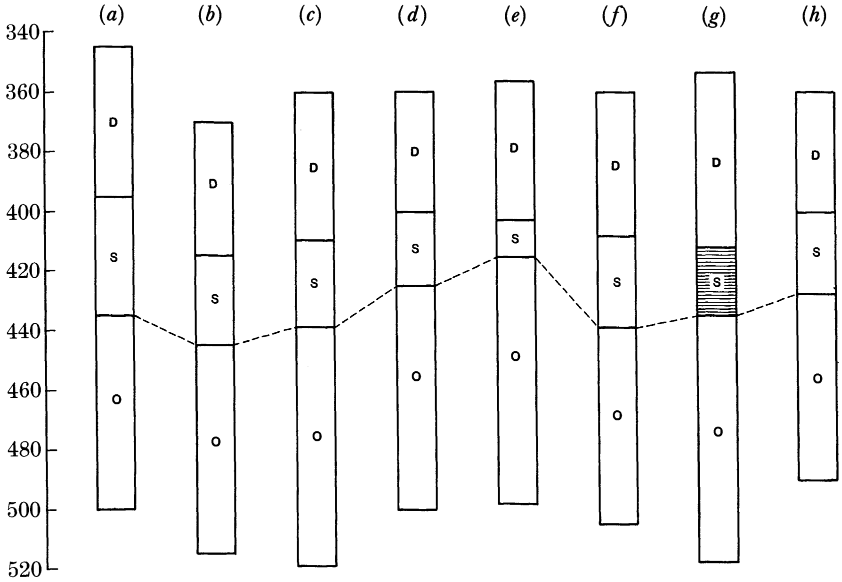

FIGURE 1. Age ranges of the Ordovician, Silurian and Devonian Systems according to (*a*) Geological Society (1964), (*b*) Lambert (1971), (*c*) McKerrow *et al.* (1980), (*d*) Gale *et al.* (1980), (*e*) Odin *et al.* (1982), (*f*) Harland *et al.* (1982), (*g*) McKerrow *et al.* (1985) and (*h*) Gale (1985). Column (*g*) is divided into 20 equal parts representing the standard graptolite biozones of Koren (1984).

to the *clingani* and *cyphus* Biozones. Thus, in terms strictly of radiometric dating, the Ordovician–Silurian boundary lies within an interval of about 20 Ma.

This is not, of course, to detract from the tremendous philosophical value of the sense of scale provided by radiometric dating: the vastness of geological time, the vast length of Precambrian time which is now known to have passed between the origin of life and the Cambrian explosion of invertebrate evolution.

But here I am concerned with the recognition of isochronous evolutionary and evolutionary related events, and with knowledge of the temporal spacing of these, and consequently of evolutionary rates. Things are simpler in the Cainozoic, when so many different strands of evidence may be brought to bear. I confine my comments to the Palaeozoic and Mesozoic, where much of the recent discussion has centred.

Let it be said at once that there are certain situations in which an immensely detailed event stratigraphy is achievable. One thinks immediately of the work of E. G. Kauffman and his colleagues in the Western Interior Cretaceous Basin of North America (Kauffman 1970, 1977), where a sequence containing abundant ammonites and bivalves also includes over 400 bentonites or other layers of volcanic material which provide record of isochronous events within the basin. The sequence has been subjected to a programme of K–Ar dating such that each biozone may represent even as little as 0.25 Ma. But let us accept that this kind of opportunity is very rare and is most likely to remain rare.

What can be more readily done is to subject a stratigraphical sequence simply to a rigorous biostratigraphic subdivision. Thus if one takes the figure of 27 Ma for the length of the Silurian Period (McKerrow *et al.* 1985), this can presently, under the usual scheme, be divided into about 41 graptolite biozones. If we employ the more widely applicable set of standard graptolite biozones which Koren (1984) has been developing, there are still 20 of these, their rocks representing an average figure of only about 1.35 Ma each. I have made this point in a previous figure (Holland 1986, fig. 1) and do so again on one column of figure 1 of the present paper.

Biostratigraphy and the global standard stratigraphic scale

This is not the place to discuss the whole topic of methods and resolution in stratigraphy, but there are several points that deserve emphasis. The first is that the work of the Commission on Stratigraphy of the International Union of Geological Sciences, and of its various subsidiary Subcommissions and Boundary Working Groups, should be encouraged, supported and accelerated. This work is not some luxury to be savoured at leisure. It is to provide an agreed international standard of stratigraphic language, such that our research can continue against a stable and understood background. This procedure is not helped by stratigraphic nationalism, which has certainly been in evidence in recent years.

Secondly, it is important that as soon as possible this work should be carried down to the level of the chronozone: the lowest category in the Global Standard Stratigraphical hierarchy, which comes below the stage. In the Lower Palaeozoic, Koren (1984) has shown the way ahead with her first attempt at a set of Silurian Standard Graptolite Biozones, already mentioned above. Eventually such divisions should be related to boundary stratotype sections. In the Mesozoic, the standardization of biozonal schemes is further advanced. T. P. Poulton writes in a recent letter to the Chairman of the International Subcommission on Stratigraphical Classification: '...as correlations become more and more confident, the finest useful worldwide biostratigraphic unit is coming, in Mesozoic circles anyway, to be called the Standard Zone or Chronozone...'. 'Insofar as the zones are subunits of stages, and systems, they require stratotypes, in which the base of each is clearly defined.' I emphasized this coming together of the once very different approaches of Mesozoic and Palaeozoic stratigraphy in a previous paper (Holland 1986, see fig. 9).

Thirdly, in discussing the primary evidence for stasis, Schopf (1981) has very usefully reviewed the limitations associated with the plotting of species durations through stages, series and systems. His first limitation is expressed as follows: 'In sum, the largest amount of direct stratigraphic evidence for stasis over millions of years comes from macroscopic taxa which occur discontinuously in a few localities and to which one has extrapolated over millions of years a polytypic model of species variation designed for the modern world.' A second limitation, which has frequently been mentioned elsewhere, is that when a species is found within a stage it is usually assumed to have the total duration of that stage. I remember the late Professor Lecompte graphically declaiming how such plots showed taxa halting at stratigraphic boundaries like battalions of soldiers. A small part of a range chart of brachiopods compiled by Amsden & Barrick (1988) illustrates a more helpful approach (figure 2). A third limitation worth recording is that short-ranged, rare species are less likely to be preserved, found and described than more abundant forms of longer duration.

To this we may add the advantage of assessing a biozonal scheme based upon one group of fossils against that provided by another. For example, Sevastopulo & Nudds (1987) compared the coral and conodont biozones of the Courceyan Stage (lower Dinantian) of the British Isles. These rocks have been extensively investigated. A modification of the coral biozonal scheme of Ramsbottom & Mitchell (1980) was plotted for several well-known sections against an

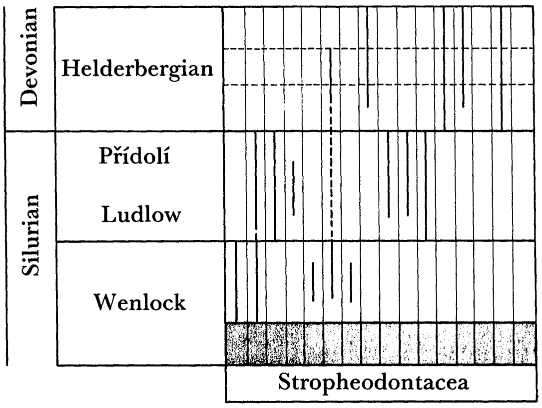

FIGURE 2. A small part of a range chart of brachiopod genera from plate 4 of Amsden & Barrick (1988). The grey area in the Wenlock and the divisions within the Devonian separated by broken lines are individual members.

integrated set of conodont biozones and sub-biozones. As shown in figure 3, the bases of the coral biozones do not appear consistently at the same level relative to the conodont biozonation. Most of the conodont biozones are based upon lineages, whereas the coral biozones are based upon cryptogenic taxa, although this does not automatically imply that the former are isochronous. Analysis suggested that the conodont biozones are not facies controlled; they may occur in different lithologies. Sevastopulo & Nudds conclude from their analysis that the corals, on the other hand, represent ecologically controlled assemblages.

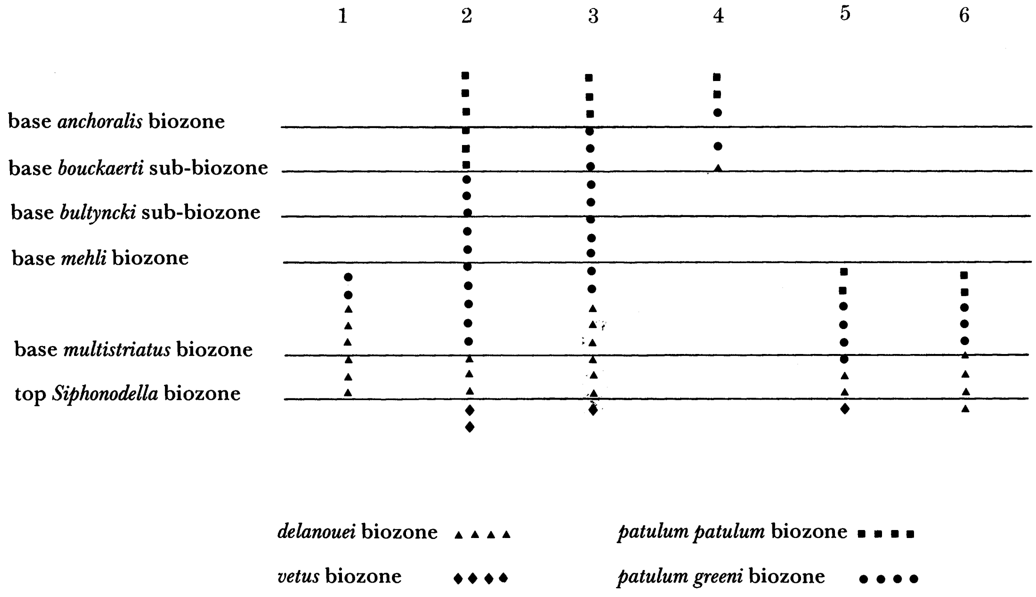

FIGURE 3. Courceyan coral biozones plotted against conodont biozones and sub-biozones for six localities in south Wales, southwest England and Ireland. After Sevastopulo & Nudds (1987), who give names and positions of the localities.

Horowitz *et al.* (1979) compared a Lower Carboniferous subsurface section in Tennessee with one in the Illinois Basin and with the classic section in Belgium, using algae, conodonts, foraminiferans and spores. The last of their conclusions is that 'The combined efforts of several paleontologists working on different groups of fossils is both necessary and important if chronological correlations are to transcend problems associated with different rock types (facies).'

May I suggest, then, in this first part of the paper in which I am simply looking in general ways at the acquisition of primary data, that one always try to say what is meant by the various kinds of biozones that are used; that one is as rigorous as possible in taxonomy (and I can return to this point later); that, in plotting ranges of fossils, one tries to indicate the beginnings and endings of these as closely as possible; that if one is connecting two occurrences through a significant stretch of barren strata one indicate this to be the case; and that if records are thought to be doubtful it is made clear that this is so. It is immensely important that there should be continuing support for taxonomic and biostratigraphic research and that the notion should be dispelled that it is more significant to theorize about palaeobiology by playing with secondary data.

There is increasing preoccupation with quantitative stratigraphy, which is obviously very useful in borehole and offshore work. It has been thoroughly reviewed by Agterberg & Gradstein (1988) and Thomas *et al.* (1988) have provided a useful bibliography of 637 items. The methods may be too laborious for widespread and worldwide use, though carefully designed experiments at particular levels and in chosen places may prove to be of interest. We have one such project in hand, *Transhemisphere Telychian* (Holland 1988), which is designed to test the limits of precision in correlation between rocks of the uppermost stage of the Llandovery Series in the British Isles and in China, and to investigate such matters as palaeobiogeography and coevolution at this level.

In what follows, I can myself, of course, be accused of dwelling on secondary data. The literature on cases of extinction (and particularly the so called mass extinctions) and their explanation is now so vast that I can also be accused (as one so often is) of providing information that is simply anecdotal. But in this paper I make no apology for being selective about selected cases.

Supposed periodicity of extinctions

It seems to me that periodicity of extinctions, rather then their irregular occurrence at irregular intervals is unlikely. Suggested causes of an astronomical nature are highly speculative. Worse still, as Teichert (1988*a*) notes, the discussion 'is increasingly being dominated by geophysicists, astronomers, statisticians, and others (even psychologists have joined the fun) who have little or no first hand knowledge of the fossil record which provides the only data base for all speculations and statistics'. Of course, this does not mean that a scientific investigation should not be undertaken. The question involves taxonomy as well as timing. We find that the approximately 26 Ma periodicity suggested by Raup & Sepkosi (1982, 1984) has, I believe, been disposed of by the work of Patterson & Smith (1987). These authors, experienced respectively in working with fish and echinoderms, checked the families within these two groups, which formed about one fifth of Raup & Sepkosi's original data. All the extinctions recorded by these last two authors were treated as occurring at the end of the stage in which each taxon was recorded. Patterson & Smith note that with acceptance of the cladistic approach there is understanding of monophyletic groups (which can become extinct) and non-monophyletic groups (which cannot become extinct). The latter are artificially circumscribed and so their ending does not 'directly reflect extinction of a lineage'. Patterson & Smith recognize seven categories of taxa in Raup & Sepkosi's data:

(1) the acceptable cases of monophyletic families with two or more species whose extinction is attributed to the correct stage;

(2) monophyletic families whose disappearance is attributed to the wrong stage;

(3) paraphyletic 'ancestral groups' that do not become extinct in a biological sense;

(4) polyphyletic families united by convergent features, which, being artificial, again cannot become extinct;

(5) families which may be either paraphyletic or polyphyletic;

(6) monotypic families whose real distribution in time and space is poorly known;

(7) non-marine families.

In terms of their own records, the one valid category expressed as (1) above provides components of only 27% in the echinoderms and 23% in the fishes. The remaining 'noise' component in Raup & Sepkosi's data comes mainly from paraphyletic groups in the echinoderms and from monotypic families in the fishes. Mistaken dating ((2) above) makes a significant contribution in both cases. The families do show five of the eight extinction peaks that Raup & Sepkosi had recognized, but it is the 'noise' that provides these peaks. Patterson & Smith speculate that the cause of the peaks in 'noise' may be taphonomic or monographic.

In a recent consideration of arthropod extinctions, Briggs *et al.* (1988) have also made the distinction 'between the true extinction of major clades and "taxonomic pseudoextinction", where the "termination" of a group is a reflection of taxonomic practice, such as the acceptance of paraphyletic groups.'

Teichert (1988*a*) reminds us that families are of very different sizes. 'Obviously, the extinction of a monogeneric family is an event of vastly different importance from that of the extinction of a family with 50 genera.'

There have been other criticisms of proposed periodicity in the extinction of marine families, notably that of Quinn's (1987) statistical analysis.

On the other hand, it is surely likely that there were times of conspicuous extinction in some groups (to avoid for now use of the expression 'mass extinction') related to times of major change in the tectonic evolution of the earth.

There is a possible explanation of major cycles in plate tectonic evolution as one convection system switches over to another, with considerable consequences for continental distribution, climatic change and above all for sea level. Such events would necessarily have their effects upon living things, variously of course, according to the type of organism in question, and over an extended period.

So-called mass extinctions

The so-called mass extinctions, in which large proportions, or even all, of the members of many different groups of living things disappeared, presumably rapidly in terms of geological time, are now the subject of a vast literature. Teichert (1988*a*) referred to them as 'still fashionably described as global catastrophies that wiped out up to 90 percent of the biomass on earth'. As Benton (1985*a*) put it: 'It is becoming clear that the history of life has been punctuated by a series of events during which, typically, an apparently random selection of organisms died out. These mass extinction events can be seen to have "re-set" the evolutionary clock....'

Benton (1985*b*) attempted a survey of non-marine tetrapods on the lines of those developed for marine invertebrates. He found several mass extinctions but none of these associated with a statistically high extinction rate. 'The extinction events, including the famous terminal Cretaceous extinction, were the result of a slightly elevated extinction rate combined with a depressed origination rate, and the present evidence does not support the view that mass extinctions are statistically distinguishable from background extinctions.' Benton (1985*b*) does warn us (and this cannot be said too often) that the time resolution in his studies is very coarse which 'could minimize the true size of a sudden event by averaging it out over several million years'.

But each case should really be taken on its merits and the literature now covers various individual cases of supposed mass extinction and, naturally, with attempts to relate these to particular events. Three examples, taken in turn, will illustrate different aspects of the problem.

THE ORDOVICIAN–SILURIAN BOUNDARY EVENT

The boundary between the Ordovician and Silurian systems was the subject of investigation by a Working Group of the Commission on Stratigraphy of the International Union of Geological Sciences between 1974 and 1985. Its achievements have been summarized by Cocks (1985, 1988) and by Cocks & Rickards (1988). The recent volume edited by Cocks & Rickards (1988) provides abundant data on sections about the world and on the behaviour of selected fossil groups across the boundary. In this case a significant event, namely the glaciation centred upon Gondwana, was already recognized and had been well described (Beuff *et al.* 1971; Allen 1975; Spjeldnaes 1981; Brenchley 1984, 1988). Spjeldnaes (1981, plate 2) provided a striking illustration of glacial striations from the Upper Ordovician of southern Algeria, but there are many other convincing features of the glaciation in the central Sahara and its extension to South Africa and North Africa (figure 4). Evidence from South America may indicate a separate ice sheet and there are glaciofluvial deposits in Europe. In the present context, the dating of this event must be of concern. Spjeldnaes (1981) referred to studies by Destombes in Morocco as giving a precise date of Upper Asgill for the glacial beds. He concluded, however,

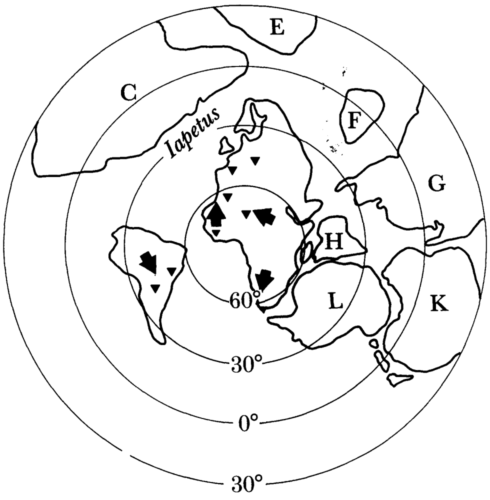

FIGURE 4. After a reconstruction of palaeogeography and climatic zonation in the Ordovician by Spjeldnaes (1981), but with data here confined to evidence for the late Ordovician glaciation. Triangles show glacial beds, arrows glacial striations. C, North America; E, northeast Asia; F, Kazakhstan; G, Southeast Asia; K, Australia; L, Antartica.

that the dating of the Ordovician glaciation as a whole is 'still somewhat doubtful'. He noted that time resolution in the Ordovician is normally not better than ± 1 Ma and that within this margin there may have been more than one glacial episode. In summary, he concluded that the evidence suggests a polar ice cap present from the Arenig onwards and that this 'expanded drastically' in the Upper Ordovician.

One of the most recent assessments of the age of the glaciation is by Brenchley (1988), who concerns himself with the regression–transgression phase in the late Ordovician and early Silurian, which is of the same age on different Lower Palaeozoic plates, thus indicating eustatic change. The fall in sea level started at the beginning of the Hirnatian stage and the subsequent rise in level was largely completed by the end of Hirnatian time, that is within the Ordovician period, though, of course, close to its end. Such radiometric dates as are available can be used in different ways to suggest a duration for the Hirnatian. Brenchley suggests that a figure between 1 and 2 Ma is probable.

Barnes's (1986) review of the Ordovician–Silurian boundary event mentions 'three or four major glacial phases' in North Africa, dated imprecisely from late Caradoc through Ashgill. He refers to the maximum glaciation as in the Hirnantian 'but with significant fluctuations even within this interval'. The Hirnantian is estimated as covering 2 Ma and the subsequent earliest Silurian deglaciation is thought to have been rapid. He considers the influence of plate motions through this brief time to have been minimal. Indeed one can agree in suggesting that over an interval of 2 Ma a figure of only 40 km of lateral movement is reasonable and for the Ashgill as a whole a figure of 200 km. Barnes (1986) argues that draining of warm seas on low-latitude platforms, combined with widespread cooling, would destroy endemic faunas. The more cosmopolitan faunas of the slope and oceanic environments were modified during the Ashgill. The main turnover of both was in the Hirnatian.

Cocks & Rickards (1988) suggest that the maximum glacio-eustatic drop in sea level was probably about half-way through the (top Ordovician) *persculptus* Biozone, on the basis of well-dated *persculptus* bearing post-glacial transgressive beds in North Africa. Incidentally, the international agreement to move the Ordovician–Silurian boundary from the base of the *persculptus* biozone to the base of the succeeding *acuminatus* biozone is obviously something to beware of in assessing older and modern literature together. They consider that the glacial episode varied from place to place, commencing even in late Caradoc times in parts of Gondwana.

It is to be expected that such changes in environment would have affected different groups of organisms in different ways in different parts of the world. Analysis of faunal distributions suggests that this is indeed the case. Particularly striking in this context is the so-called *Hirnantia* fauna, which is diachronous through three pre-*persculptus* biozones in China (Rong 1984) but extends into the *persculptus* biozone in Kazakhstan (Apollonov *et al.* 1988; Koren *et al.* 1988), in Quebec (Lespérance 1985), and in the English Lake District (Cocks 1988).

Some major groups of fossils are now briefly considered. Scrutton (1988), in his general review of patterns of extinction and survival in Palaeozoic corals finds a 'significant end Ordovician extinction event' followed by an increased percentage of new genera. This applies to both rugose corals and tabulates, but in neither case is the extinction shown as nearly complete.

According to Taylor & Larwood (1988), the Bryozoa at neither family nor generic level reach a high level of extinction at the time of the end-Ordovician 'mass extinction'.

In his review of brachiopods across the boundary, Cocks (1988) considers that 'in general, however, the degree of extinction across the boundary appears to have been less than previously reported...'. The extinctions at the end of the Hirnantian do not appear to be greater than at the end Caradoc or end Rawtheyan.'

Briggs *et al.* (1988), on the other hand, see the end-Ordovician event as significant in the extinction of major clades of trilobites. The associated reduction in trilobite diversity may be attributed to the extension of cold-water regions. The low diversity cool-water faunas themselves are typified by the widespread occurrence of the *Mucronaspis* fauna. 'With such an important glacial event recognised from independent evidence there seems to be no good reason to look further for the cause of the Hirnantian decline. However, it is not obvious that the same cause was necessarily responsible for the extinction of families at the *end* of the Hirnantian.' Possibly widespread anoxia in the oceans at the transgression may have caused the selective extinctions there.

Lespérance (1988) refers to the distinctive and impoverished trilobite fauna of the Hirnantian Stage, but notes that the degree and nature of the impoverishment varied from region to region. He considers that the major extinction of the trilobites came near the boundary between the Rawtheyan and Hirnatian Stages, rather than at the base of the Silurian System.

Dr A. W. Owen's view of patterns of extinction at this level (expressed in an abstract prepared for the Annual Conference of the Palaeontological Association at the University of Aston in December 1988) suggests that they 'were disproportionately concentrated in deeper water trilobite assemblages. This indicates that although draining of the shelves and migration of the thermocline in response to the end Ordovician glaciation may have been contributory factors, many extinctions may have been caused by the chemical effects of oceanic overturn.'

The history of the nautiloid cephalopods as a whole has been reviewed by Teichert (1988*b*) and Holland (1987). There are some losses, such as the almost complete disappearance of the Endoceratida; but most groups decline from their middle Ordovician acme on through the Ordovician–Silurian boundary.

Eckhert's (1988) analysis of the crinoids reveals a diversity peak in the Caradoc, a descent to a minimum in the early Ashgill, and a major extinction in the late Ashgill. Glacio-eustatic lowering of sea level is blamed for this. The Silurian radiation of crinoids originated from assemblages of Hirnantian crinoids.

Aldridge (1988) sees conodont evolution as follows: 'The Caradoc was punctuated by an interval in which extinction rates exceeded origination rates,.... Following a brief late Caradoc – early Ashgill recovery, the latest Ordovician saw severe faunal changes, with extinctions reaching a rate of seven genera per Ma, the highest in conodont history.' The survivors led to little innovation in the earliest Silurian. Barnes & Bergstrom (1988), in their elaborate consideration of conodonts at this level, consider this perhaps the most striking faunal turnover in the whole history of the group.

The graptolites (Rickards 1988), so important themselves in dating these horizons, show a gradual change between the *persculptus* and *atavus* biozones. The widespread fauna of the *acuminatus* biozone, between them, 'represents a distinctive stage in the evolution of Silurian graptoloids reflecting a very advanced stage of post-glacial marine transgression and the development of widespread anaerobic black shales and the re-establishment of a rich, marine, tropical plankton'. There is a pronounced increase in diversity at this level, though this had begun even before the *persculptus* biozone.

To conclude, there is a clear evidence of a significant event in the latest Ordovician, the timing of the associated changes, although imprecise, does appear to involve a period of only a few million years. In terms of extinction, one sees, as might be expected, different effects in different groups. To call this a mass extinction is to dramatize unduly.

The Frasnian–Famennian extinctions

According to McLaren (1982), at the Frasnian–Famennian boundary there was a 'huge disappearance of biomass in tropical and sub-tropical shallow seas with an almost total change in fauna which occurred within one conodont sub-zone of less; that is in 0.5–1 Ma. Pedder (1982) presented detailed documentation on the rugose corals at this level. Only 4% of the 148 shallow water species survived, compared with 3 or 4 out of the 10 deeper-water forms.

An attempt was made to locate an iridium anomaly at the boundary in the now well-known and beautifully displayed sections of Upper Devonian rocks in the Canning Basin, Western Australia (Playford *et al.* 1984). One such was found in the Virgin Hills formation on the McWhae Ridge. In a verbal discussion at the International Geological Congress in Moscow in 1984, I suggested, as Ager (1988) has since done, that perhaps iridium anomalies should be looked for in places where it would be regarded as not so useful to find them. In the event, McLaren's (1985) well-balanced account of the matter suggested that sedimentation here was very slow. The iridium anomaly occurs in a 12 cm stromatolitic bed, containing the cyanobacterium *Frutexites* and showing enrichment in iron oxide minerals. One of the possibilities here is therefore that the *Frutexites* not only fixed iron but also concentrated other elements from seawater.

Sandberg *et al.* (1988) have provided a long discussion of the 'Late Frasnian Mass Extinction', with particular reference to conodont stratigraphy. Documentation is provided (with reference to sea-level curves) that a rapid eustatic rise followed by an abrupt fall in sea level immediately preceded the extinction and that this continued into the early Famennian, though the extinction event was clearly over. The mass extinction is deduced to be very short because of the thinness of sediments involved and the lack of significant evolutionary change in the surviving conodonts. A duration of some 12500 to 21500 years is estimated. These figures are decided by the quantification of conodont biozones within a known radiometric time span. The extinction mechanism, it is suggested, was caused by a variety of interrelated factors including sea-level changes and changes in ocean currents. The authors 'theorize' that a large bolide impact was ultimately responsible.

The Systematics Association's Special Volume on *Extinction and survival in the fossil record* (Larwood 1988) is a useful source on the behaviour of different groups at this (and other) levels. Brasier (1988) here reminds us of the extinction of reef faunas at the end of the Frasnian, associated with major transgressive pulses and anoxic black shales, especially of the 'Kelwasser Event' (House 1975, 1985). This event affected the foraminiferans, eliminating 'faunas of relatively advanced architecture...while those of primitive to intermediate architecture survived. Even these suffered a setback in the number of species.'

On the Bryozoa, Taylor & Larwood (1988) note that 'The mid–late Devonian falls within a general trough of low bryozoan family diversity and it is not possible to distinguish any times of outstanding reduction in diversity.'

In their survey of the arthropods, Briggs *et al.* (1988) give particular attention to patterns of trilobite diversity across this boundary. They conclude that 'Extinctions of major clades coinciding exactly with the end of the Frasnian are relatively few...'. The clades terminating at the boundary had already become reduced. 'The Frasnian–Famennian drop is much less than that between the Eifelian and Givetian.'

Stratigraphic control at this level is already good. There were certainly changes of sea level and climate (the drop-off in well-developed reefs of Frasnian times alone would suggest this); but it does not seem very satisfactory to speak of mass extinction when the behaviour of different groups is so variable.

HAPPENINGS AT THE CRETACEOUS–TERTIARY BOUNDARY

One hesitates to penetrate the jungle of this matter. The literature is now enormous and in some cases emotive. In any case, Hallam (1987) has provided an excellent review of the case for a terrestrial explanation of the supposed mass extinction at the close of the Cretaceous. For my part, I have already referred to Benton's (1985*b*) views on the quantitative aspect of the extinction of terrestrial vertebrates. My own interest in the cephalopods, though largely older ones, has led to concern with the Upper Cretaceous record of the ammonites.

Professor J. M. Hancock has kindly provided fuel, both from his own wide experience of the Cretaceous ammonites and by drawing attention to references. He writes that the ammonites did not fade away quite so gradually as he used to think, in particular because of more accurate stratigraphical assignment of rocks from the Southern Hemisphere. Nevertheless, the decrease in the number of families still shows a pattern similar to that he recorded in *The fossil record* (Harland *et al.* 1967). Hancock provides a more recent graph (figure 5), in which the stages are given a more nearly correct proportion of time. He notes that even this diagram is now some seven years old. The numbers of families are derived from the new edition of the relevant volume of the *Treatise on invertebrate paleontology*, not yet published.

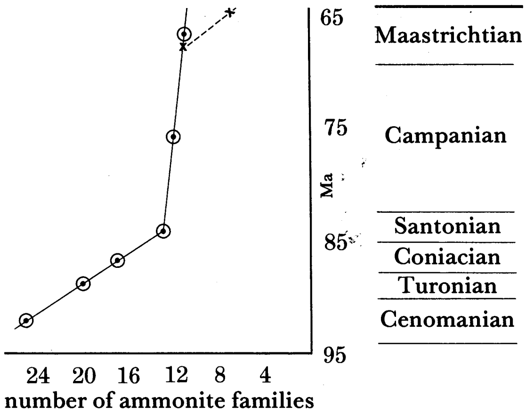

FIGURE 5. Numbers of Upper Cretaceous ammonite families. Numbers for each stage placed at the middle point of the stage. The broken lines shows the reduction in ammonite families during the Maastrichtian. (Original kindly provided by Professor J. M. Hancock).

Professor Hancock notes that there are only two places presently available where the ammonite succession close to the top of the Cretaceous is even potentially known, respectively in Denmark and northern Spain. Birkelund (1979) demonstrated the reduction of ammonite genera within the Maastrichtian of Denmark from 34 to about half that number. He saw this as part of a general decline through the Cretaceous. Seven genera were recorded in the 'topmost layer of the Upper Maastrichtian'. There are large numbers of juveniles at the top and regression of the sea is suggested as the cause.

In an abstract by Ward & Wiedman (1983), reference was made to poorly preserved ammonites from northern Spain. The highest ammonites here came from strata 12 m below the boundary clay with its iridium enrichment. Abundance and diversity had dropped off long before the close of the Cretaceous. Wiedmann (1986), in an extended review, places emphasis on sea-level changes. He observes that the Bryozoa and ostracods, both sensitive to water quality, actually reached their peak density at the time of the 'mass extinction'. The point was made verbally at this Discussion Meeting that Ward has now collected additional ammonites from other sections in northern Spain, taking the record to very close to the boundary, but not altering the picture of an earlier established decline.

Kennedy (1984), too, noted that the ammonites declined throughout the late Cretaceous and that most of the decline was pre-Santonian. He pointed out that the diversity of ammonites during the Maastrichtian was no lower than during the Berriasian.

In consideration of a very different group of animals, Whalley (1988), writing about evolutionary changes in the insects over the Cretaceous–Tertiary boundary, notes that they 'provide no evidence of abrupt or catastrophic changes'. I am indebted to Dr D. C. G. Briggs for this reference.

Once again, at this level, stratigraphic control is possible, but there is always room for improvement; and, once again, different groups may have been affected in different ways, as one would expect if changes in sea level, continental distribution and climate were involved. Even here it seems that the term 'mass extinction' may be over dramatic. One must continue to work at biostratigraphy, at radiometric dating and at taxonomy seen to some extent at least with a cladistic eye. From such acquisition of primary data better models can perhaps be built.

The sociologists of science will make much of the story of theorizing about the Cretaceous–Tertiary boundary event. One of them (Elizabeth S. Clemens) has already suggested that the Alvarez hypothesis owes much of its support to its relative simplicity and a favourable press. 'It offered an elegant and parsimonious solution to a question firmly embedded in popular culture' (quoted by Malcolm W. Browne in the *New York Times* for 19 January 1988).

I have not mentioned as such the end-Cretaceous bolide. I simply do not believe in it. Unseen bolides dropping into an unseen sea are not for me. It must be said, though, that things reach a low level when palaeontologists, who after all alone can provide the necessary data, are described by a proponent as 'not very good scientists', 'more like stamp collectors' (quoted by M. W. Browne, reference cited above). I leave some of the last words to two exceedingly experienced palaeontologists who are certainly not 'stamp collectors'.

Teichert (1988*b*) contrived to say many important things in a paper only one page long. It includes the following statement: 'There has been since early days, a tendency to search for a unified theory of the causes of extinction, preferably the same cause for all extinctions of all ages. These attempts are, in my opinion, simplistic and misguided.' He continues later: '...I believe on the contrary that no single cause is sufficient to explain mass extinctions and "partial extinctions", and that the explanation must be sought, in each case, in random combinations of a number of factors that ordinarily and continuously influence the course of organic evolution and its record in the rocks.'

Ager (1988) has this to say: 'The most publicized mass extinction in the whole fossil record is that at the end of the Cretaceous. All that I can say about it here is that no-one told the brachiopods.'

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Discussion

L. B. Halstead (*Department of Geology, University of Reading, U.K.*). Over two decades ago during the compilation *The Fossil Record* (Geological Society of London), which listed first and last occurrences or most major taxa of the animal and plant kingdoms, the arbitrary decision was made to mark each last record as terminating at the end of the stage in which it was last deemed to have been present. This convention was for ease of drafting.

It is important to recognize the limitations of such ranges of fossils and their apparent extinction at exact geological boundaries. I was responsible for the chapter on the Agnatha (the jawless vertebrates). All the major groups finally became extinct at the end of the Frasnian stage of the Upper Devonian; one of the five major mass extinctions recognized in the fossil record. It is certainly the case that the last examples of, say, the cephalaspids and anaspids are from the Frasnian of Nova Scotia. But this is quite misleading. The mass of cephalaspids died out at the end of the Lower Devonian, one genus is known from the Middle Devonian of the Orcadian Basin of Scotland and two isolated forms are known from the Upper Devonian of Nova Scotia. These were essentially 'living fossils' just hanging on in isolated regions, they were not part of the mainstream and their final demise is hardly significant.

To all intents and purposes the more streamlined anaspids also died out at the end of the Lower Devonian, but once again a couple of genera managed to hang on in Nova Scotia until the Frasnian.

With the thelodonts the story is somewhat different. The main extinction was at the end of the Lower Devonian but a few forms continued into the lower part of the Middle Devonian of Spitsbergen. Recently further Middle Devonian thelodonts have been found in Iran, Thailand and Australia and in Australia (and perhaps Antarctica) they flourished into the Upper Devonian, finally disappearing during the Frasnian. In this case the thelodonts lived on in Australia long after they had died out throughout the rest of the world.

It is important to determine whether the extinctions being discussed are regional or global; and whether they involve the main faunas or merely just the last few stragglers.