Ammonoid Extinction Events [and Discussion]
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Ammonoid extinction events

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The ammonoid cephalopods range from the early Devonian to the late Cretaceous, a period of some 320 Ma. Because of their importance for biostratigraphic discrimination and their use in practical age dating for this period they have been intensively studied. Major extinctions at the close of the Devonian, end Permian, end Triassic and end Cretaceous have long been recognized and linked with regressional palaeogeographical events. The recognition of smaller-scale extinction events is relatively new and is especially well shown in the Palaeozoic, when there was a simpler distribution of land and sea pathways than in later periods when the influence of latitudinal distributions and local provinces was more severe. Extinction events in the Devonian show the nature of the process. Usually a gradual decline in diversity is followed by extinction; then there is a period of low diversity but often individual abundance. Then novelty appears and is seen in new characters of the early stages; elaboration and diversification follow. These fluctuations can often be correlated with changes in other groups and also with sedimentological and palaeogeographical changes. Usually a regression–transgression couplet is involved with evidence of ocean turnover indicated by anoxic or low-oxygen events. A new family, Sobolewiidae, is diagnosed.

A new analysis of diversity, appearances and extinctions is made at the family level for 2 Ma time units throughout the history of the Ammonoidea. This record is compared with modern attempts to portray sea-level fluctuations and onlap and offlap movements of marine seas. The correlation, even in detail, is impressive and gives support for the species/area theory. But it is argued that temperature, as well as sea-level factors, is important.

The evidence, on both large and small scales, shows an association of evolutionary change with palaeogeographical change. The new evidence does not suggest a role for periodicity above the Milankovitch Band level. Whether or not periodicity is involved, such factors seem more readily explained in endogenic earth causations and for the present these provide the most parsimonious explanations.

1. INTRODUCTION

The coiled ammonoids first appear in the late Lower Devonian, perhaps about 390 Ma BP on the radiometric scale. They became extinct at the close of the Cretaceous about 66 million years ago, near the end of the Maastrichtian. Although similar in basic morphology to other chambered cephalopods the group is characterized by a distinctive globular to egg-shaped protoconch and in all but the very oldest forms by a distinctive coiled nepionic stage, the ornament of which differs from later coils. Their origin is thought to be from straight orthoconic and ectocochleate bactritids, which had already adopted the distinctive protoconch. Their evolution is characterized by the production of an incredible variety of small forms, which can vary in degree of coiling, in the shape of whorls and the degree and nature of shell ornament. Characteristic also is the great variety in the pattern of folding of the septa that separate the shell chambers: when found fossilized as internal moulds these give the distinctive suture lines of the group.

For as long as they have been studied, the ammonoids have proved very useful to the geologist because the detailed changes of their evolution have enabled a timescale of zones and subzones to be established that is the most precise age-dating tool available for that period. As a result their history is probably as well or better documented through time than any other group.

This contribution is concerned with extinction periods in the Ammonoidea. During the compilation of the latest review of the group (House & Senior 1981) the contributors to the forthcoming revision of the *Treatise on invertebrate paleontology* volume on the Ammonoidea provided detailed ranges of families that enabled the accompanying evolutionary tree for the group to be constructed (figure 1). The data here are that of M. R. House (Devonian), J. Kullmann (Carboniferous), B. F. Glenister and W. M. Furnish (Permian), E. T. Tozer

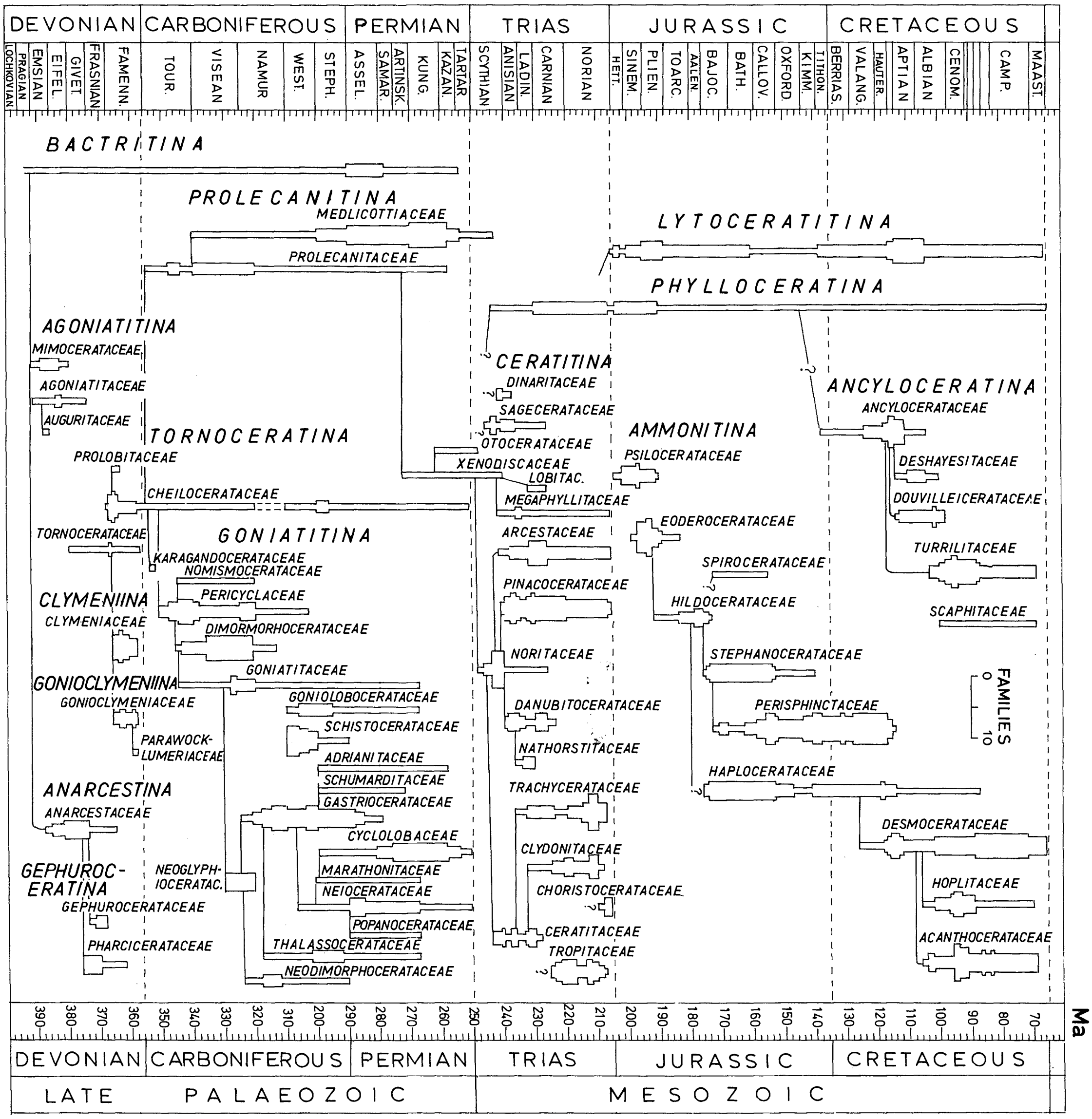

Figure 1. The evolutionary tree of the Ammonoidea from their appearance in the early Devonian to their extinction at the end of the Cretaceous. Based on House & Senior (1981).

(Triassic), D. T. Donovan, J. H. Callomon and M. K. Howarth (Jurassic) and C. W. Wright (Cretaceous), who have given details of the classification used. I was responsible for eliciting agreement over boundary problems. Thus this review is of a snap-shot of the available data at that time and there has been no attempt at a wholesale revision in the light of more recent data.

For this review the detailed manuscript ranges provided by the authorities have been

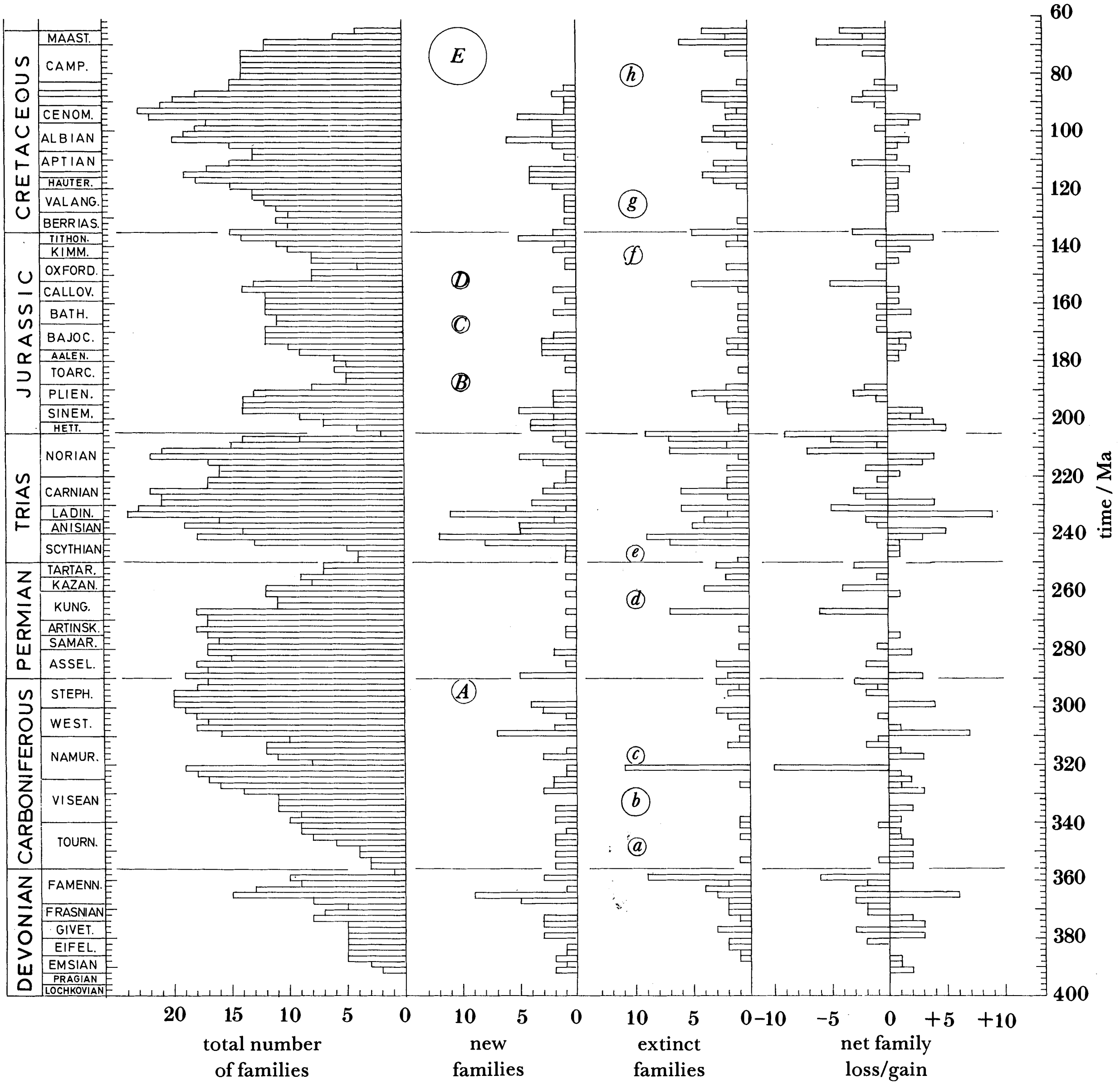

FIGURE 2. Data on family diversity through time of the Ammonoidea (excluding Bactritina) from the early Devonian to the end Cretaceous. Based on data from House & Senior (1981). Time units of two-million-year intervals largely based on Snelling (1985). Total number of families, which is an indication of morphological diversity at particular times, is taken as an indication of success or failure in exploiting a wide range of ecological niches. Totals of new families appearing within a two-million-year unit are an indication of degree of innovation and high values suggest ecological relaxation and exploitation; periods particularly noteworthy for a continued period lacking innovation are marked by circles (*A–E*). Totals of extinct families within a unit show families lost and high values are taken to indicate times of ecological stress; circles (*a–h*) mark continued periods when no families became extinct. More informative is the net family loss–gain plot, which indicates periods when innovation exceeds or is less than extinction.

analysed to give a review of the fortunes of the group at 2 Ma intervals for the time of known existence of the group (figures 2 and 4). The main concern is diversity, as indicated by the number of families at any 21 Ma unit, the number of new families appearing, and families lost and various aspects of the ratio of change and its relation to longevity of taxa involved (figure 4). Division of appropriate scales by two gives the rate for these factors in millions of years. This collation is used as the basis of a discussion on the extinctions but it should be stressed that the main concern is in loss of diversity, by which is inferred loss of niche occupancy through time. Thus whether or not families may be paraphyletic, and whether other

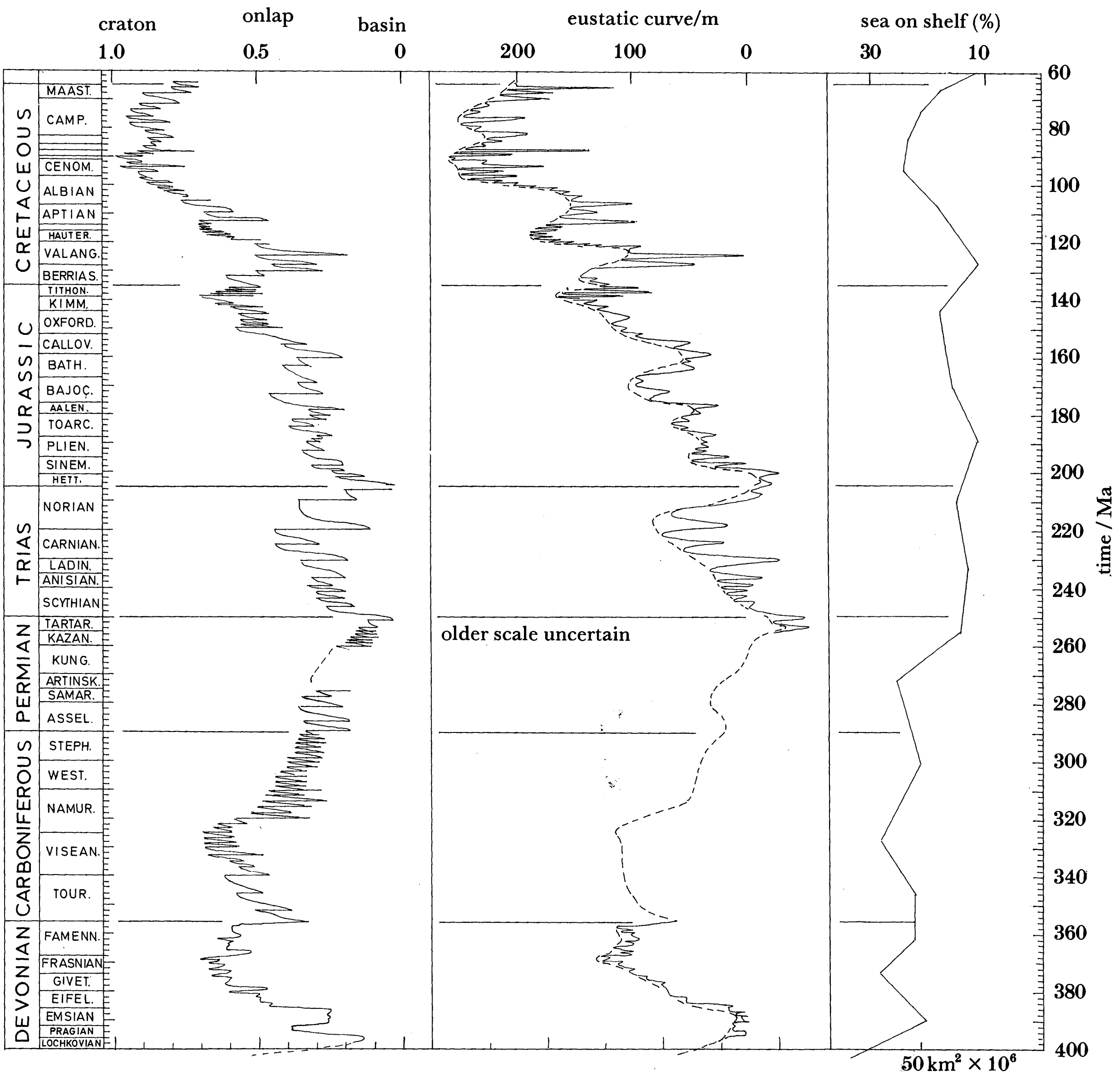

FIGURE 3. Data on changes in sea level through time plotted to enable comparison with the ammonoid evolutionary analysis. Onlap and eustatic data based as follows: Devonian, House (1983, Johnson *et al.* (1985, 1986), Krebs (1979); Carboniferous and Permian, Ramsbottom (1979), Saunders & Ramsbottom (1985), Ross & Ross (1985), Smith *et al.* (1974); Triassic, Holser & Magaritz (1987); Triassic to end Cretaceous, Haq *et al.* (1987). Total sea on continental shelf estimates based on Wise (1974).

interpretations of taxonomic procedure may be possible, are not of concern. The biological effects considered refer to the actual change in standing diversity. The aspects of what this meant in numerical abundance and 'success' can only be approached in a rigorous way by the known geographical distribution of faunas and, far more speculatively, as indicated by their fossilization record, interpreting common occurrence as indicating former abundance. Whereas with ranges reasonable objectiveness is possible, on other matters judgement and experience

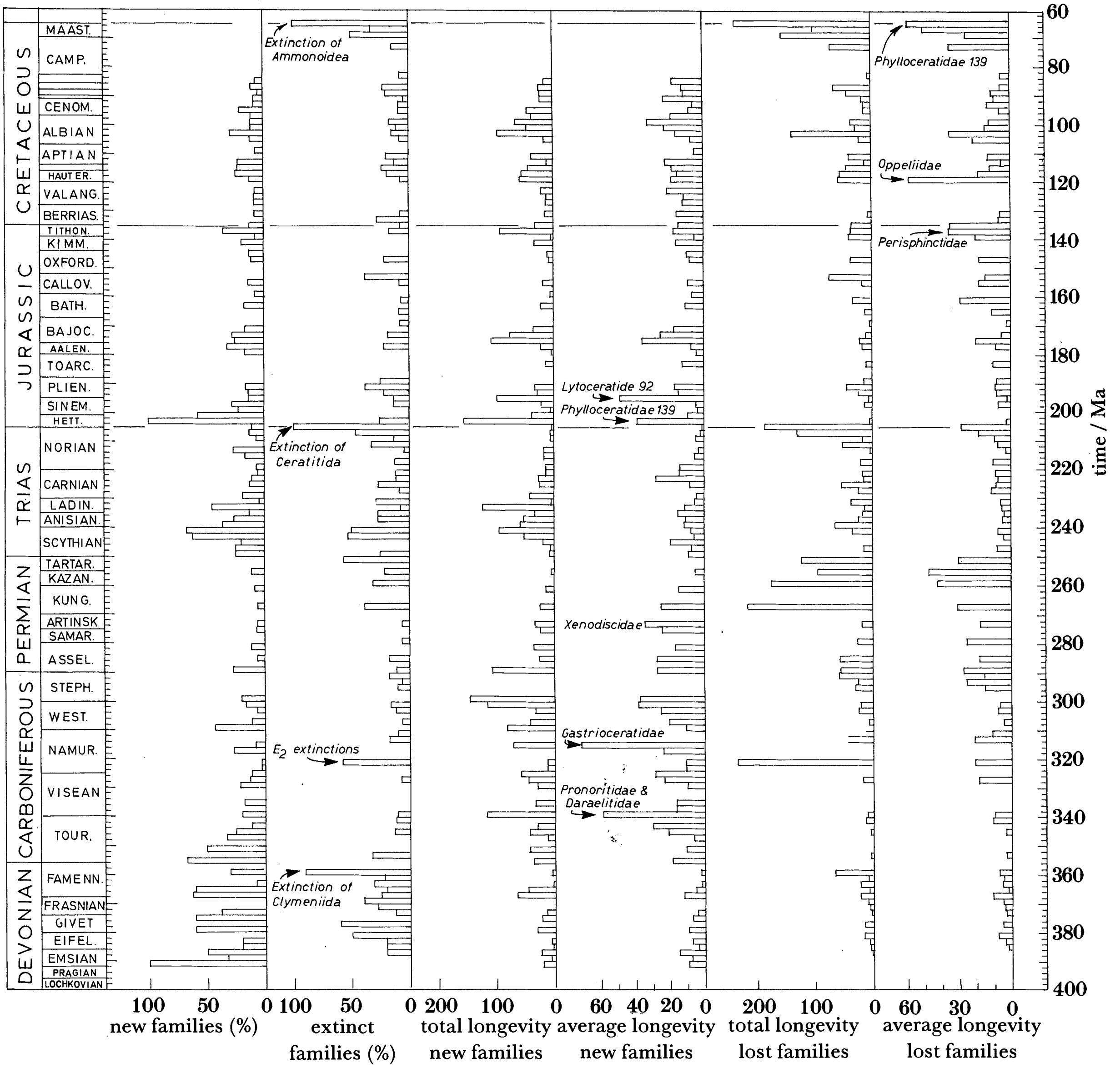

FIGURE 4. Further data on family diversity through time of the Ammonoidea (excluding Bactritina) from the early Devonian to the end Cretaceous (data as for figure 2). Plots of new/total and extinct/total give the ratios as a percentage for each of the two-million-year units used. The longevity, or time range, of families of Ammonoidea is plotted in relation to both the total longevity and the average longevity of families involved in appearance and extinction. Families are named in significant cases where a single family either gives the signal or is responsible for more of it. The loss of groups that have survived long periods of the vicissitudes of life is probably more significant than the loss of short-range taxa.

enter. At present, a similar review would not be possible at the generic level because for some time periods the data have not been published.

Those working on ammonoids have long seen a relation between palaeogeographical changes and periods of extinction and radiation (House 1963). This is analysed in more detail by using a compilation of data on marine transgressions and regressions, and sea-level changes thought to be worldwide and eustatic (figure 3). But several other hypotheses have been suggested as causes of extinction and diversification periods, so some of the important events are discussed in stratigraphic order so that evidence relating to particular events can be separated. The time scale used is largely that of Snelling (1985) and it will be apparent that for the Palaeozoic, if not so much for the Mesozoic, considerable inaccuracy results and variations in interpretation are possible. Nevertheless it seems worthwhile to attempt to assemble the data on a consistent time base so that rates and tempo can be compared, even if it is to be understood that refinements will be inevitable. It should be noted that figure 3 is not based on such rigorous correlation with the biostratigraphic scale as figures 2 and 4, and very detailed correlation of events should not be inferred.

Because my special interests lie with the older Ammonoidea, I shall discuss these in more detail. This will illustrate how, when even more detailed biostratigraphic data are taken into account, the interpretation of crudely totted and clumped data even at the 2 Ma level may be misleading. This will also illustrate that attempts at interpretation at an even cruder level of stages or series is subject to even more suspicion.

Much of the content of this contribution has been discussed with R. Thomas Becker and I also acknowledge the comments he made on the initial draft.

2. The ammonoid record

At several stages in their history the Ammonoidea almost became extinct. In the late Devonian, at the Frasnian–Famennian boundary, only a small group of tornoceratids and *Archoceras* survived. At the very close of the Devonian following the extinction of the clymeniids, at the Famennian–Tournaisian boundary, only restricted group of prionoceratids survived. The major mid-Carboniferous E_2 extinction, the second largest family extinction in the ammonoid record (figures 2 and 4), was not near to a total loss as eight superfamilies survived. The major extinctions by the close of the Permian witness to a gradual attrition through much of the period but with enough survivors to give cause for debate on the origin of Triassic groups. The end-Triassic extinctions come out in the present compilation (figure 2) as the largest family extinction event and perhaps only two or three genera survived it. The final demise of the Ammonoidea is the product of the longest attrition period in the history of the group and for some 18 Ma preceding it no new family-level taxa are reported.

The broad correlation of these events with regressional occasions (figure 3) has been much commented upon. The nature of the process, however, is less clear. What is clear is that any stock that did survive soon developed a wide range of diversifications. Conservatism appears to be a feature of survivors.

Devonian

In the Devonian diversification was largely a matter of inovation in patterns of folding of the septa. As sutural ontogeny has generally been held to be of great importance, and because sutures can readily be used to distinguish groups, high taxon grades have been assigned to such forms. Thus high-taxon extinction is highest in the Devonian with five suborders becoming extinct. This does not, of course, imply that these extinctions are in any way more 'significant' than others, but in that they led to the disappearance of certain special sutural possibilities they served to constrain later evolution.

The major extinction events during the Devonian number about eight and have been named in relation to localities or lithological units showing sedimentary perturbations with which they are associated (House 1985*a*). There is no implication that these are the only such events, but the experience of many years suggests that they may be the most significant. The relation between extinction events and environmental changes has been long recognized but only recently codified in this way. The first records of the coiled Ammonoidea are in the conodont *dehiscens* Zone, which the Devonian Subcommission is likely to use to define the base of the Emsian stage. Goniatites of the *dehiscens* Zone seem known in Alaska and the Yukon, probably Morocco, the Montagne Noire and Australia. This appearance is associated with a Zlichovian (approximately Lower Emsian) transgressive event that has recently been recognized even in Australia and Siberia (Talent & Yolkin 1987). By the following *gronbergi* Zone there was a considerable international distribution of goniatites. During this time loosely coiled and eventually tightly coiled and convolute forms are known, mostly members of the very simple-sutured Mimosphinctidae; but bizarre sutures are shown, by the Auguritidae, for example.

Daleje Event

The Zlichov Formation of Czechoslovakia represents a gradual deepening phase (Chlupáč & Kukal 1986) even reaching black calcareous shale facies in the upper part. This followed a regression at the base of the Zlichovian. The change to the deeper facies of the Daleje Formation is in detail gradual and initiated in the late *gronbergeri* Zone. Facies changes at this level are documented in Europe, North Africa, U.S.S.R., and eastern and western North America (House 1985*a*; Chlupáč & Kukal 1986). It appears to be an international event. In several areas, but especially in Europe, pyritic preservation indicates anoxic sea floors so an ocean overturning, spreading oxygen-low waters over shelves, seems a likely scenario. The loss of the main group of mimosphinctids and the auguritids is associated with this. Higher in the Dalejian two groups of great later significance appear, the Agoniatitidae and the Anarcestacea. Both soon show a closure of the primitive imperforate umbilicus and the latter shows a distinctive sutural pattern in which, in many, there is a lateral migration of an early subumbilical lobe into a more lateral position in the adult. However, it will be noticed that this event is not easy to resolve by using the crude 2 Ma unit plots of figure 2. This is because overall diversity is low and the quick rise of new groups masks the extinctions. Plotted in more detail, with generic range shown, the reality is rather more clearly seen (figure 5*a*). Similarly, the sea-level fluctuation corresponding to this is not well shown on figure 3, where high resolution is not possible, but it corresponds to deepening within Cycle 1*b* shown by Johnson *et al.* (1985). Other faunas show a decrease in provincialism associated with the transgressive event.

Basal Chotec Event

Chlupáč & Kukal (1986) have distinguished a Basal Chotec Event close to the new boundary between the Lower and Middle Devonian. Not marked explicitly on figure 5*a*, the event is indicated by the extinction of the Mimagoniatitidae (which in reality range higher in reduced importance) and of the Mimoceratidae. This event has been recognized as the *jugleri*

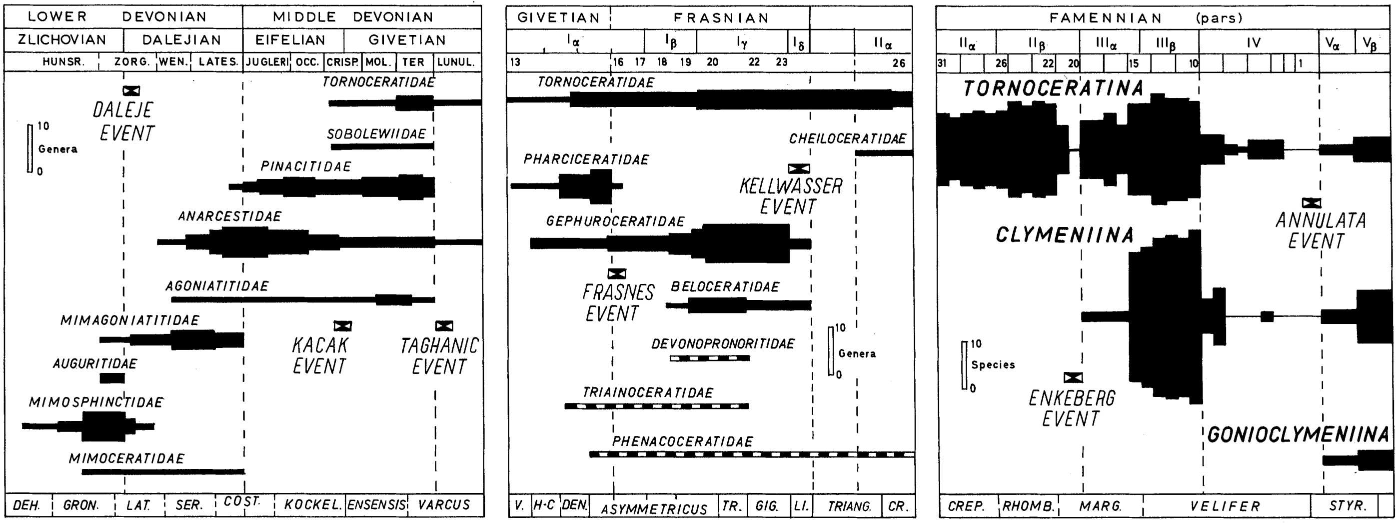

Figure 5. Family and generic data for certain groups of Devonian ammonoids (especially goniatites), illustrating particular extinction events discussed in the text. Modified from House (1985*a*).

event by Walliser (1985), referring to the goniatite *Pinacites jugleri*, which appears following the break. The genus *Pinacites* is not common but is highly distinctive and easily recognized. It is widespread in North Africa and Europe and has recently been found in Alaska. That there is an environmental and palaeogeographical effect here is suggested by the close relation with the great changes in spore floras known close to this level (Riegel 1974). In Europe it corresponds rather closely to the deepening following the Emsian near-shore clastic facies and in North America to the progressive transgression of the Onondaga Limestone, one of the two most significant onlap events in the North American Devonian.

Kačak Event

In the late Eifelian (as now defined), there is a distinct break when *Pinacites* disappears and *Cabrieroceras* becomes internationally abundant. Again this is connected with a sedimentary perturbation. The names *otomari* Event, after the common tentaculite, *Nowakia otomari*, or *rouvillei* Event, after one species of *Cabrieroceras*, have been applied to it (Walliser 1984, 1985). At this event goniatites with perforate umbilici appear to be lost. The distribution of *Cabrieroceras* (House 1978) is considerable in Europe, North Africa and eastern North America but it also occurs in western North America. In Morocco there is a pyritic level with the name-bearer indicating local sea-floor anoxia, and the event is recognized in the Odershausen Limestone in deeper-water facies. In New York State, U.S.A., it is seen as the Werneroceras Bed associated with black shales. However, it is only recently that the environmental effects at this level have been well documented in more shallow facies, and in particular K. Weddige and W. Struve of the F.R.G. have recognized a regressional gap at this level in the Eifel succession between the Giesdorf and Freilingen levels.

Taghanic Event

The extinction of the *Sobolewia* group (named on figure 5 as the Sobolweiidae *fam. nov.*, diagnosed by the simple sutured, involute goniatites with convex lines of the genus), Agoniatitidae, Maenioceratidae and 'Pinacitidae' (forms such as *Foordites* and *Wedekindella*), used to define the end of the Middle Devonian for Devonian workers (as almost universally in Oswald (1967), but the boundary is now taken higher. These earlier groups are shortly replaced by the distinctive multilobed Pharciceratidae and the globally widespread Gephuroceratidae. The new forms are associated with transgressions almost internationally but the North America sub-Taghanic regression is the main clue to the extinctions. The later extinction of most of the Pharciceratidae has been named the Frasnes Event.

Kellwasser Events

The upper of the two late Frasnian black limestones, known in the Schiefergebirge as the Lower and Upper Kellwasser Kalk, marks the extinction of the Gephuroceratidae and Beloceratidae. Only the anarcestid *Archoceras* and a small group of tornoceratids survive. There is an anomaly here, as the anoxic Upper Kellwasserkalk level is where the last gephuroceratids (especially *Crickites*) are seen abundantly. The anoxia itself seems unlikely to have been an immediate cause of extinction but there are several lines of evidence suggesting shallowing, or at least a spread of shallow seas, especially the increase in the conodont *Icriodus* (Sandberg *et al.* 1988). Bolide impact is another favoured theory (McLaren 1982, 1983) although disparate ages for iridium anomalies (Playford *et al.* 1984; McLaren 1985), or absence of any anomaly at critical points (McGhee *et al.* 1984, 1986), is making this increasingly unlikely. The sedimentological perturbations (Sandberg *et al.* 1988) and regressional lag deposits (Geldsetzer *et al.* 1987) interpreted as indicating bolide impact seem equally explained as epeirogenic or eustatic changes linked with a primary cause in tectonism associated with plate movement (Johnson 1988).

When studied in detail (Becker 1986; House 1985*a*), goniatite diversity shows a decline approaching the Frasnian–Famennian boundary and the base of the Lower *triangularis* Zone (figure 5*b*). The extinction is similar to those already documented here for which no extraterrestrial cause is invoked. In a general analysis of all faunas around this boundary (House 1975) it was argued that extinctions are spread around the boundary and sea-level fluctuations were thought to be a cause. Only corals (Pedder 1982), atrypids (Copper 1984, 1986), conodonts (Sandberg *et al.* 1988) and stromatoporoids (Stearn 1987) have been looked at in any detail and the records suggest a staged or gradual extinction rather than a sudden event. Copper (1986) prefers a cold-water cause; Stanley (1988) also prefers this, but by spreading of deeper anoxic water over a shelf by changes in the level of the pycnocline. This might be caused tectonically by epeirogenetic or eustatic changes as readily as by global climatic change. There is now no convincing evidence for Devonian glaciation anywhere, even in the Famennian of South America close to the supposed pole, so it is not possible to invoke glacial events.

Hangenberg Event

There are other extinction events within the Famennian (House 1985*a*; Korn 1986) but that at the close, just below the Devonian–Carboniferous boundary, is the most significant. Details have been published elsewhere (Price & House 1984; House 1985*a*; Becker 1988). In the uppermost Famennian the Tornoceratidae, Posttornoceratidae and Sporadoceratidae, as well as eleven families, become extinct as do the bizarre clymeniids, the only group of ammonoids with a dorsal siphuncle. During the diversity low only a limited group of Prionoceratidae are known, but early stages are quite diverse and they are usually abundant in the black and anoxic shales equivalent to the Hangenberg Shales in several parts of the world. Diversification leading to the major new groups, Prolecanitina and Goniatitina, follows gradually in the early Lower Carboniferous.

These selected extinction events in the Devonian are characterized by an association with sedimentary perturbations, especially in the form of anoxia. They share a common pattern of gradual decline, minimum of diversity and gradual diversification. These suggest a common cause. One of the reasons why I have favoured terrestrial explanations for such extinctions is that ocean upwelling associated with sea-level changes triggered by tectonic events and/or plate tectonic activity seems a reasonable cause. The events vary slightly among themselves, and this too would be expected from terrestrial events. It has been argued that the triggering of the Kellwasser Event specifically is extraterrestrial (McLaren 1983; Sandberg *et al.* 1988) and by bolide impact. However, the pattern of the Kellwasser Event, as has been shown, differs only in degree from the other events discussed, and unified and parsimonious interpretation is to be preferred. That is sought here in terrestrial causations.

When the detail known on Devonian extinction events is looked for in compilations such as figure 2 it is clear that the specialist biostratigrapher has at his or her command far more detailed information than is available to a compiler. The events in subsequent ammonoid history which will be discussed will be based largely on the compilation that has been attempted (figures 2 and 4) and not on such detailed knowledge.

Carboniferous

Carboniferous ammonoid evolution indicates an initially progressive radiation, arising from survivors of the Hangenberg Event, into a great proliferation in Goniatitina and in the less diverse but highly distinctive Prolecanitina, which show elaboration on umbilical lobation. The steady and consistent rise in total diversity during the Tournaisian and Visean is remarkably systematic (figure 2). Also noteworthy are the periods (352–346, and especially 338–328 on the units of figure 2) when no families became extinct at all. The Visean period is the largest timespan known in the Palaeozoic when this occurs for so long and this is equalled only once in the later history in the early Cretaceous. A relation with the widespread early Carboniferous transgression, giving broad shallow seas combined with indications of equable climates, may be the cause.

The major extinction event is in the early Namurian at the end of E_2. The data on the accompanying diagram are from Kullmann (1981) but he has published more specific accounts of changes in evolutionary rates during the period (Kullmann 1983, 1985) based on an analysis of genera at approximately genus-zone divisions rather than zonal level or the attempt at standardized time units adopted here. Generic diversity is at its maximum at about the Visean–Namurian boundary which is second in importance on the family plot (figure 2). The last occurrence of genera is at its peak in E_2 and this does correspond with the family data (figure 2); it is the Palaeozoic extinction peak for total families but not the ratio of extinct to total present. However, E_2 is clearly the major extinction event for the period.

Palaeogeographical correlation with evolutionary diversity increase or reduction is less clearly established. The long-known North America regression between the Kaskaskia and Absaroka cratonic sequences (Sloss 1963) closely corresponds to this and the result emphasizes the Mississippian–Pennsylvanian boundary. In Europe the H genus zone corresponds to a significant influx of Millstone Grit clastics as the prelude to Coal Measure deltaic facies. So in general a palaeogeographical change is likely to be a significant cause of the extinctions.

But in detail it is clear that there are many small-scale transgression/regression couplets through the whole Carboniferous (see Ramsbottom 1979; Heckel 1986; Ross & Ross 1985). Comparison of these between Europe and North America has been attempted by Saunders *et al.* (1979) and the British succession, which is the most detailed, indicates maxima around E_{2c} to H_{1ab} and H_{2a} to H_{2c} suggesting confirmation of the correlation. But the data do not give really precise plots for figure 3 and, of course, no palaeogeographic maps of this detail have been constructed to allow precise estimates of onlap.

The relation between cyclothemic pulses and the entry of goniatite shales with distinctive faunas is the basis for much European Carboniferous zonation, but the data refer to internationally restricted taxa and would not show on a plot such as figure 2. A much more detailed study of the British data by Holdsworth & Collinson (1988) is more helpful in indicating the intimate relation between goniatite faunas and facies changes but international correlation is not advanced enough for this to be documented on a larger scale. Part of the reason this is possible for the Devonian data is the existence of a parallel conodont biostratigraphy.

For the later Carboniferous there is an interesting conflict of evidence. Kullmann's (1985) generic analysis shows a progressive and asymptotic decline in total number of genera from R_1 to the end of the period. The family data (figure 2) on the other hand, show a steady increase to the mid-Stephanian, then a final 8 Ma period (298–290) when no new families appear. This is the only period of such a standstill in the Palaeozoic record and it is equalled only by that preceding the extinction of the ammonoids at the end of the Cretaceous. With the already established glaciation in the Southern Hemisphere, and Coal Measure or terrestrial environments in much of Laurussia, probably rather special conditions characterized the areas of goniatite colonization. Although early collisions between Gondwanaland and Laurussia were initiated in the Devonian with the Acadian orogeny, similar effects were long continued, culminating in the late Visean with widespread European olistostromes and thrusting and later in the main paroxysms of the Variscan orogeny. These events will have been the major cause of the sea level fluctuations which, like a bioseimograph, are reflected in ammonoid evolution, but the detailed correlation is not established. Tectonic and sea-floor spreading effects may also cause the prominent sedimentary rhythmicity at a smaller scale but by the early Namurian the increasing effects of the growth of the Gondwanaland ice cap give also the probability of additional climatically forced sea-level changes.

Permian

The transition between the Carboniferous and Permian is not marked by a major extinction event. Rather, the introduction of the new families Shikhanitidae, Perrinitidae, Metalegoceratidae, Paragastrioceratidae and Popanoceratidae gives a distinctive defining element, although work on the international definition of the actual system boundary is still proceeding. The family data show a gradual decline to the end of the Permian (figure 2), with a significant fall away only after the mid-Kungurian where there is the major extinction event for the system, seven families being lost, corresponding to the late Wolfcamp. Although in general this corresponds to a regression (figure 2) the data are far from clear and international definition and correlation leave much to be desired.

The Permian–Triassic boundary represents a low point in ammonoid family diversity, only surpassed by those at the end of the Devonian, Triassic and Cretaceous. At this point the helpful onlap–offlap and eustatic curves of Haq *et al.* (1987) give evidence of possible causation because the boundary represents the lowest point for both offlap and sea-level lowering in the whole period from the latest Permian to the end Cretaceous. Again a relation between decrease in area of shallow seas and decrease in diversity seems an inescapable conclusion. Holzer & Magaritz (1987) have summarized other changes associated with the boundary regression/transgression couplet, particularly perturbations in $^{87/86}$Sr, δ^{34}S and δ^{13}C. This has been recognized for a long time as the most significant extinction event for marine animal taxa (see Newell 1952, 1963, 1967; Raup & Sepkoski 1984).

It is of particular interest that the end Permian also saw the extinction of the Tornoceratina, the range of which has now been extended into the latest Permian with *Qinglongites* (Zheng 1981). This group alone had survived all the earlier extinction events from the Middle Devonian. For the Devonian there is evidence that the group may have favoured colder or deeper waters (House 1985a).

Triassic

The Permo-Triassic boundary extinctions for the ammonoids are sufficiently severe for there to have been differences of opinion on the relationship of succeeding groups. The evolution has been reviewed by Tozer ((1971*a*) and in House & Senior (1981)) and he has also given a splendidly readable review of the major revisions resulting upon new views of the sequences in the Alps (Tozer 1984), which starts with a quotation at the beginning: 'Were it not for fossils geology would be mere vulgar engineering'.

From the detailed zonal data of Tozer, the evolution of superfamilies of Triassic ammonoids are illustrated here (figure 5) by plots giving total number of genera in each zone. This illustrates a phased pattern of innovation. The earliest Triassic appears to have been a period of standstill (shown as '*e*' on figure 2). The Noritaceae diversify in the Nammalian (Na. on figure 5), followed by six superfamilies appearing in the Spathian (Sp.), a further four in the Ladinian and a final one in the late Norian (or Rhaetian). This shows also how the dominant period or acme for a group is usually markedly later than its first appearance. The decline is also initiated long before the extinction of a group and the extinctions indicated by generic data may differ from those at family or superfamily level. There is also a relay-like replacement of faunal 'packets'; these are probably replacing each other in a similar ecological niche, but it is too early to quantify this. Noticeable also are the high rates in the production of new and extinction of old families. This flourishing evolution emphasizes why the period has been called the 'Age of ammonites'.

The new sea-level curves (figure 3) start to suggest a striking correlation of radiation periods for the Triassic ammonoids with transgressive pulses and of extinctions with regressive periods. Thus it would appear that there are several extinction periods (Benton 1986).

The extinction at the close of the Triassic is, in terms of number of families becoming extinct, the greatest in the history of the Ammonoidea (figure 2). So profound was the effect that it has resulted in great uncertainties in finding the ancestors for Jurassic groups (see Tozer (1971) and Wiedmann (1973)).

Jurassic

Post-Triassic ammonoid evolution is set in a palaeogeography showing the effects of the fracture and break-up of Laurussia and in stages of Gondwanaland. The easterly expanding

Tethys Ocean was mostly near-tropical and led to the development of specialist warmer Tethyan faunas. In higher latitudes the proto-Atlantic and associated fractures, and geographically contained polar areas, lent themselves to the development of colder Boreal faunas and of local provincial evolution in restricted basins.

The two longest-surviving Jurassic and Cretaceous groups, the Phylloceratina and Lytoceratina (figure 1), appear to have characterized deeper levels of more equatorial waters. Formerly it was thought that these groups gave off stocks of coarsely ribbed Ammonitina in evolutionary waves that reiteratively colonized boreal waters, but this simplicity is not now accepted. The current view is that the Ammonitina are independently derived from the Triassic, but this includes groups colonizing Tethyan as well as Boreal shallow waters. Evolution resulted from the success or failure of these related to migrations driven by sea-level changes (eustatic or epeirogenic) and by climatic changes. Because the palaeogeography was complex, so was the resulting evolution. But beginnings are being made in relating evolution to environmental changes.

For the earliest Jurassic evolution Donovan (1988) has suggested that the Arietitidae originated in low latitudes to colonize other areas. He notes significant extinctions within and at the end of the Sinemurian, the former possibly being linked to a regression and the latter corresponding to a switchover in dominance of psiloceratacean by eoderoceratacean (figure 6).

The end Pliensbachian is a marked extinction event for marine groups (see Raup & Sepkoski 1984) and this has been documented in detail for the bivalves and other groups by Hallam (1986) who considers that the main extinction falls within the early Toarcian (Hallam 1987*a*). This event shows in the international ammonoid record by the loss of the Eoderoceratacea (figure 6), especially the amaltheids. This Hallam links with regression.

The Toarcian *falciferum* Zone represents a widespread deepening of facies in Europe associated with anoxia, giving the famous exotic preservation in the Lagerstätten of Holzmaden in Germany and the Jet Rock facies of Yorkshire. This is thought to be related to a global rise in sea level and climatic cooling cannot be ruled out as an additional factor. It corresponds to the second-lowest count of total familes on figure 2 and the first of the significant periods when no new families were produced (shown as B on figure 2). Tethyan phylloceratids extended far to the north at this time, and with them extended an evolutionary radiation of Tethyan derived dactylioceratids and hildoceratids giving rise to dominance in the later Toarcian of the Hildocerataceae (figures 1 and 5).

The Aalenian transgression, and transgressive events within the Bajocian and Bathonian (figure 3) are associated with the rise of Stephanocerataceae, Perisphinctaceae and Haplocerataceae (figure 1), which then dominate the later Jurassic. The first proliferated especially in Boreal waters. However, this is not a period of great family diversity. Ager (1981) has suggested this was a Jurassic warm period. In this interval Bayer & McGhee (1984) have documented iterative morphological sequences linked with sedimentological rhythms.

The celebrated Callovian transgression was a staged event but at its peak it probably deserves much greater emphasis than given to it by Haq *et al.* (1987) and shown on figure 3. Again in Europe there is an anoxic event and after this, at the close of the stage, the extinction of the warmer-water reineckiids and cooler-water kosmoceratids give the marker taken to define the Middle/Upper Jurassic boundary.

An early Oxfordian global deepening shows by the extension of Boreal stephanocerataceans

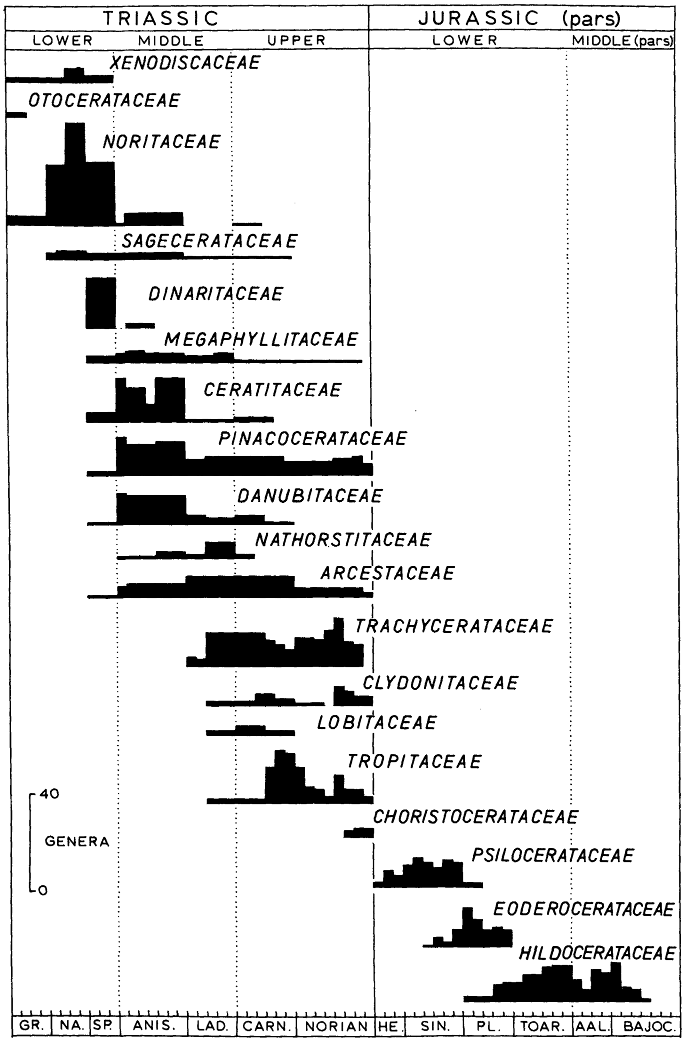

FIGURE 6. Diversity in ammonoid superfamilies for the Triassic and early Jurassic based on data of Tozer (1981) and Donovan *et al.* (1981). The time units are the zonal divisions of stages. This illustrates how evolution of certain morphologically defined clades often shows a slow growth of diversity, a peak and then a decline. It is the decline rather than the extinction that may be the more indicative of selection stress for the group. Noticeable is the 'packet' type evolution in which, relay-style, one group may replace another, possibly in the same ecological niche. From House (1985*b*).

southward in Europe and especially southward through the western interior of North America, with sufficient sea-floor anoxia to give the famous pyritic ammonites of both areas. The later Oxfordian has shallower environments and probably climatic amelioration.

Progressive deepening through the Kimeridgian appears to be having a control because just before the maximum in anoxia is the extinction of the cardioceratids (and with them the Stephanoceratacea), a level that is taken as the boundary between the Kimmeridgian and Tithonian. The large rise in families in the late Tithonian corresponds to a blooming of the perisphinctacians, which include many giants. This culmination would link with another period of warming recognized by Ager (1981). There is an extremely good correlation between late Jurassic regression and the decline in diversity near the Jurassic/Cretaceous boundary (figures 2–4) (Hallam 1986).

Cretaceous

The broad analysis of family diversity (figure 2) shows a maximum in the Upper Cretaceous. This shows a close correspondence with the encroachment of marine waters over cratonic shelves (figure 3) and by the Cenomanian/Turonian interval both reach their maximum for the whole period of existence of the Ammonoidea (figures 2 and 3). Subsequent regressive phases led to the extinction of the group at the close of the Maastrichtian. The novel feature of the early Cretaceous is the rise of the Ancyloceratina, which include the heteromorphic ammonites so distinctive of the period. Otherwise Ammonitina evolution results from Jurassic derivative stocks of the Haploceratacea and the declining Perisphinctaceae (figure 1). A revised family tree for Cretaceous ammonoids has been published by Kennedy & Wright (1985).

The Berriasian faunas comprise holdover stocks from the Jurassic without the type of inovative radiation that might have been expected after the Tithonian extinctions. The sea-level data (figure 3) suggest a cause in continued pulses of regression. Nevertheless, the Valanginian is one of the significant periods when few families become extinct (marked as *g* on figure 2).

It is with the late Lower Cretaceous transgressions that renewed evolution is seen and this reaches a maximum in the Albian interrupted by late Aptian regressions. The Haq *et al.* (1987) curve here owes much to European data where the relation between sedimentary perturbations and ammonoid evolution has been well documented. Early Albian deepening may be the cause of the demise of the Douvilleiceratacea, Deshayesitaceae and Ancycloceratacea.

The Cenomanian transgression is generally considered to represent the greatest onlap of marine waters over continental shelves in the Phanerozoic (Hallam 1977) (figure 3) but the term is used in a general way. Hancock & Kauffman (1979) found a Turonian sea-level high-point for the western interior of the U.S.A. and a Campanian–Maastrichtian maximum for northern Europe. Much of the late Cenomanian peak for ammonoid families (figure 2) comprises families that had their origin in the Albian.

After the Coniacian the ammonoid history is one of progressive family decline (figure 2) and generic decline. No new families were produced during this period and the interval, perhaps of 19 Ma, represents the longest such period in the whole history of the Ammonoidea (marked *E* on figure 2). The evidence of increasing selection pressures that this indicates, together with the associated palaeogeographic changes, are the reasons why palaeontologists do not concede that meteorite impact can be the only cause of the end-Cretaceous extinction (views summarized by Hallam 1987*b*).

The actual documentation of the final demise of the Ammonoidea shows a progressive geographical and diversity restriction (Hancock & Kennedy 1981; Ward 1983, 1988; Wiedmann 1988*a*, *b*). The latest evidence suggests a cutoff of several genera in the last 10 m of the best-documented sections along the Bay of Biscay coast. It is, however, impressive that the very last ammonite known at Zumaya, *Neophylloceras ramosum*, is a member of the Phylloceratitina, the one stock that survived all the earlier extinction events of the Mesozoic. Was this because of evolutionary robustness of the stock or because it lived in an environment that was least subject to rigorous change? If the latter it may hold this in common with the Tornoceratina, the longest-surviving group of the Palaeozoic.

MISGIVINGS

No palaeontologist can be happy about the premises of using taxonomic categories for numerical analysis, as there is no consistency or standard in the definition of such grades nor any likelihood of that being achieved. As the Devonian and Triassic analysis shows, when generic-level data are available a more useful precision results but for the Ammonoidea a comprehensive survey of the whole group at such a level is not yet possible. There are also problems related to the radiometric time units used, for these become vague in the extreme by the Palaeozoic and the scheme used here is but one of many possible. For evolutionary analysis undoubtedly the record of actual successive beds is better than that of subzones, which is better than that of zones, which is considerably better than that of stages. The attempt here at 2 Ma time units is again probably the best that can be done at present for the group as a whole. Parts of the record are known, by contrast, in very great detail but a review at that level could not be attempted by a single individual or for the whole group.

GENERAL CONCLUSIONS

The correlation demonstrated above between the detailed diversity record of the Ammonoidea, onlap–offlap and eustatic curves shows a vivid confirmation of the long-recognized species–area relation in evolution. Indeed, it may well be that the bioseismograph of the ammonoid record, and that of other groups, will provide a key to environmental controls of evolution in this way. This differs from views expressed by Stanley (1984) and Wilde & Berry (1984).

It has been argued throughout this paper that, when studied in detail, most evolutionary perturbations seem to be related to environmental and palaeogeographical changes and that terrestrial causations seem the most parsimonious to explain the record. Furthermore, in the Palaeozoic, a relation between certain sea-level changes and often anoxic events is increasingly being recognized to be related to specific tectonic events. Yolkin & Talent (1988) have demonstrated this for parts of the early Devonian. The effects of the Acadian and Antler orogenies seem part of this and there is considerable evidence of tensional tectonics associated with the Frasnian–Famennian Kellwasser Event. The next stage will be a more precise analysis of sea-level changes as a means of estimating these effects. It is singularly unfortunate that international agreement on stratigraphic units and their correlation is at such an early stage that the production of palaeogeographical maps is at best piecemeal and cannot contribute yet to the more accurate calculation of land/sea area which is required.

There is also a climatic factor more generally involved. It is at present impossible to quantify this effect and it is clearly an important factor, but not the only factor as some would argue. Climatic control of sea level and of sediment types adds a complication to a simplistic consideration of area/species effects. This is also true of anoxic levels, which are here interpreted as more likely caused by ocean upwelling that is tectonically driven than by climatic 'greenhouse' effects.

There is an impression from the data in figure 2 that extinctions are rather more spasmodic and irregular than innovation, which has been steadier. This has been tested by assembling histograms of the numbers of families known to appear ('new') and become extinct in the 2 Ma class intervals used (figure 7). The 'new' plot is the more regularly asymptotic. A similar

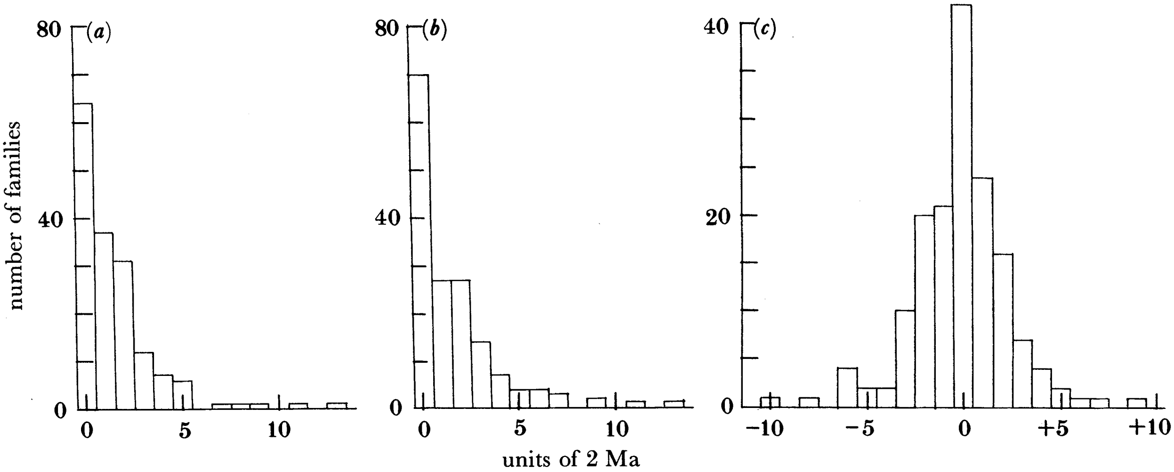

Figure 7. Histograms illustrating the frequency of (*a*) 'new', (*b*) 'extinct' and (*c*) 'gain/loss classes of total families, based on data shown in figure 2. The more regularly Gaussian nature of the 'new' and 'gain' plots is taken to indicate that the character of extinction and loss events is more spasmodic and irregular.

plot for loss–gain also shows the 'gain' plot to be more asymptotic. This suggests that appearances are more regularly programmed and losses more disjunct and irregular.

As for periodicity, there is little doubt that at the smallest scale Milankovitch Band orbital forcing and consequent climatic control is one of the factors important in detailed evolutionary change. This has also been argued for large-scale patterns. The great weakness here is that the actual radiometric timescales available, especially for the Palaeozoic, are far too inaccurate to show whether these really are periodic. The same is probably true of periodicity at the 26 Ma level and no evidence of that periodicity can be traced in the data assembled here (figures 2–4), notwithstanding the importance of certain extinction events that have long been known. Perhaps the advent of a timescale based on Milankovitch cycles will be the only way ahead here.

Finally, I must express the view that it is only by the detailed accumulation of factual data that improvements can be made. It behoves every scientist who wishes to be called a palaeontologist to add as much as possible to this body of knowledge. For this alone will lay a firm foundation for future advances.

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Discussion

W. A. Kerr (*The Thatched Cottage, Whitchurch Hill, U.K.*). The decapod *Spirula* has an internal skeleton, as do the belemnites. Might not the ammonoids have the same? *Spirula* was the subject of research given to Professor J. Graham Kerr by the Danish Government.

M. R. House. The ammonoids are ectocochleate. The shells sometimes show colour banding and periostracum, with no evidence of tissues outside the shell as shown on the guard of some belemnites, which are endocochleate. Nevertheless there are suggestions that there may have been tissue outside the aperture in some cases. There are many ammonoids with a very constricted aperture in the adult, often caused by periodic apertural constriction during growth. In some of the heteromorphs the shell aperture closely abuts earlier whorls, giving very little space for tentacles and the food-gathering facility. Although both radulae and jaw structures are now known in ammonoids, for forms with constricted apertures it is difficult to envisage a 'normal' feeding pattern for them and it may be they developed some type of filter feeding or techniques enabling them to live on small organisms; in this case extra-apertural tissues may well have been involved.