Impacts and marine invertebrate extinctions

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Abstract: The Phanerozoic history of life has been interrupted by at least 17 different stage-level episodes of elevated extinction intensity. These range from major turnovers that affected the majority of the Earth's extant biota (e.g. the Tatarian, Ashgill, and Maastrichtian events) to much smaller and perhaps more geographically localized disruptions. Review of available stage-level stratigraphic evidence suggests that bolide impacts do not exhibit a compelling correspondence to the Phanerozoic record of marine invertebrate extinctions. A much stronger case can be made for the repeated association of extinction events and episodes of long-term eustatic sea-level fall and/or major episodes of continental flood basalt volcanism. Moreover, during the last 250 Ma particularly severe extinction events have occurred during times of simultaneous continental flood basalt eruption and eustatic sea-level fall (e.g. Tatarian, Norian, Maastrichtian). Attempts to employ patterns of extinction selectivity to infer the physical cause of extinction events have foundered on the non-specificity of biological predictions as well as the seemingly unique biotic nature of each event. Although a few high-resolution biostratigraphic analyses have demonstrated that largely progressive patterns of faunal turnovers are consistent with co-extinction models under certain assumptions, this does not constitute a strong confirmation of the co-extinction model as a necessary or sufficient general explanation for Phanerozoic extinction events. In all likelihood, the nature of the fossil record precludes precise identification of extinction causal mechanisms. Nevertheless, comparative studies are able to evaluate the role both large and small extinction events have played in altering the long-term course of Earth's biological history.

Two hundred years ago Georges Cuvier astonished a public audience at the National Institute of Arts in Paris by presenting 'detailed and almost irrefutable evidence' for the idea that animals could become extinct (Rudwick 1972, p. 101). In doing this, Cuvier initiated a debate over the reality and causes of extinction that greatly influenced the zeitgeist of his time and led to a surge of interest in the topic of extinction that lasted well into the eighteenth century. Cuvier's preferred extinction mechanism was environmental change, but environmental change of a particular kind. Under his model, extremes of typical environmental variation would be met by species either toughing out the bad seasons (perhaps with some local extinction of populations on the periphery of the species' geographical range) or migrating to more favourable regions. In Cuvier's opinion, only some sudden and catastrophic environmental change could decimate a widespread and successful species so completely as to render it extinct.

Today, arguments similar to Cuvier's are being proposed to account for the extinctions of many fossil groups and, in particular, for episodes of mass extinction. Some theories would go so far as to claim that the overwhelming majority of all extinctions have resulted from very short term catastrophic mechanisms such as bolide impact (e.g. Alvarez *et al.* 1980; McLaren 1989; Raup 1991*a*, *b*; Alvarez 1997). Others have proposed that catastrophic extinctions have been visited upon the planet with a Newtonian regularity (e.g. Raup & Sepkoski 1984; Sepkoski & Raup 1986*a*, *b*; Raup 1989).

In Cuvier's time the evidence for seemingly violent upheavals in the recent geological past were coming to be appreciated through studies of Quaternary geomorphology and stratigraphy. In our own time the existence of such exotica as iridium anomalies, tsunami deposits, and spherule layers is often cited as evidence for a causal link between catastrophic mechanisms and mass extinctions (Alvarez 1997). At the extreme end of this spectrum we find scenarios in which the existence of certain extinction events themselves is regarded as sufficient grounds on which to infer the existence of the catastrophic mechanism(s) that *must* have produced them (e.g. McLaren 1970, 1989, 1996).

Despite the popularity of this 'new catastrophism' (Ager 1993) longer-term physical processes continue to be advanced as alternative extinction mechanisms. The two most consistently cited alternative mechanisms are flood basalt volcanism (e.g. Vogt 1972; McLean 1978, 1985*a*, *b*; Courtillot *et al.* 1986, 1988, 1996; Courtillot 1990) and eustatic sea-level change (e.g. Newell 1967, Hallam 1984, 1989). All three

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mechanisms are thought to bring about organismal extinctions via climate changes, especially temperature fluctuations and the destruction of particular habitats (e.g. marine planktonic habitats).

To evaluate the degree to which these alternative extinction mechanisms account for the observed marine invertebrate fossil record direct evaluations must be undertaken in which the specific and reasonable predictions following from the various hypotheses are tested against the fossil record as it is currently known. It is important to remember that the debate over extinction mechanisms is not about the physico-chemical evidence for impacts, volcanism, and/or sea-level rise *per se*. The existence of these processes and their ability to disrupt the Earth's climate and ecosystems are well established. Much less well understood is their relation (if any) to the historical record of life on Earth. Consequently, a detailed consideration of the fossil record in light of predictions based on specific causal mechanisms is unavoidable (Archibald 1996a).

Gross temporal correlations between mass extinctions and causal event classes

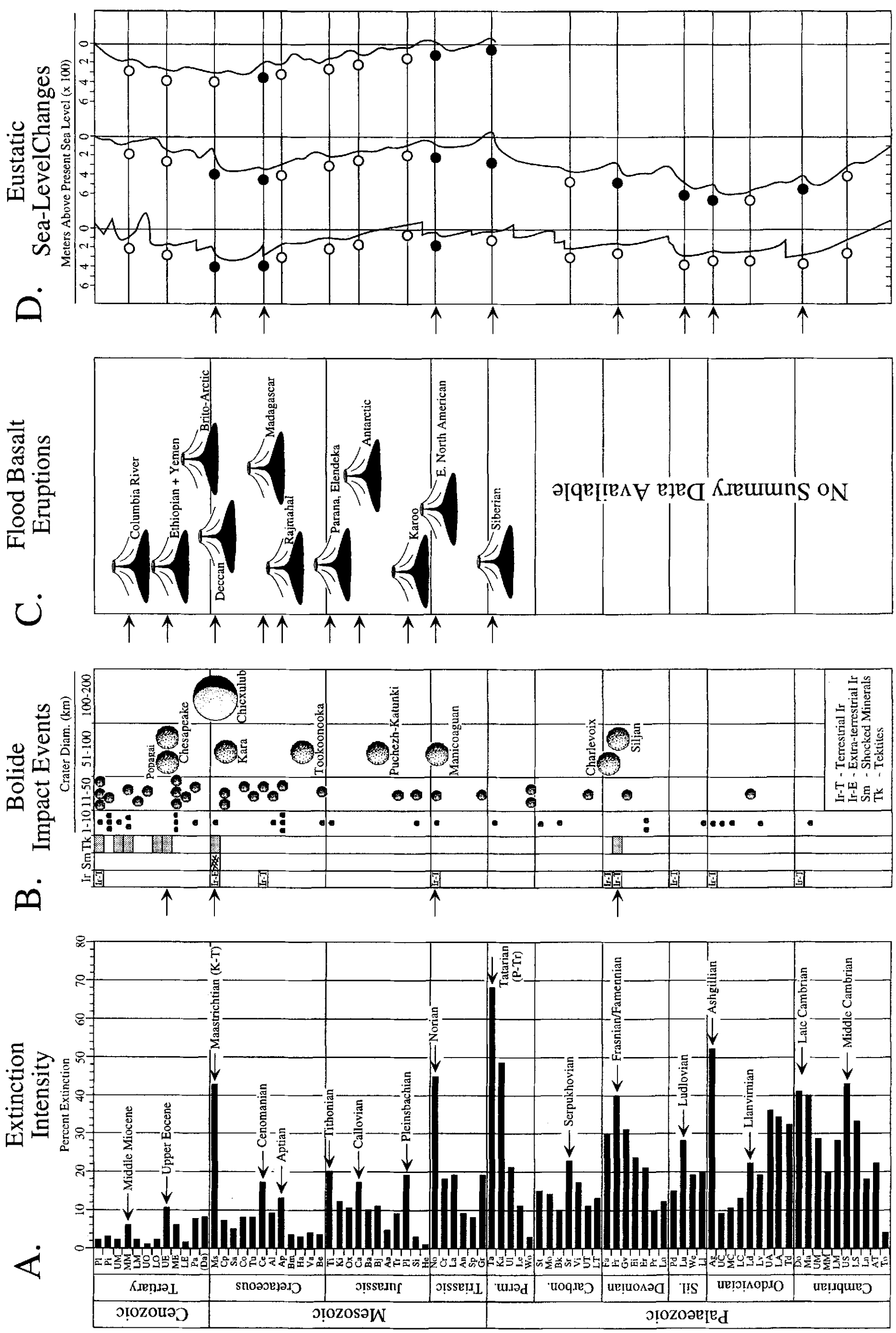
The most obvious test of a relation between bolide impacts and marine invertebrate extinctions is to determine whether there is a consistent correlation between their respective time series. The extinction patterns of most invertebrate fossil families and genera can be regarded as being known to the level of the stratigraphic stage (Sepkoski 1982, 1990, 1994; Sepkoski & Raup 1986*a*, *b*; Benton 1993). Detailed species-level biostratigraphies resolved to the level of the biozone are available for some marine invertebrate groups (see below), but these are the exception rather than the rule.

Lack of detailed knowledge of phylogenetic relations within biotic groups can bias the observed fossil record, especially in the case of recognizing mass extinction survivor species or lineages. This source of bias has been discussed by Archibald (1984), Patterson & Smith (1987, 1989), Smith & Patterson (1988), Carlson (1991), Norell (1992), Smith (1994), MacLeod (1996*a*), and MacLeod *et al.* (1997). Fisher (1991) and Foote (1996) have presented the case for retaining the traditional (i.e. non-phylogenetic) approach to taxic analyses, at least for certain types of studies. But even these researchers acknowledge that in many, if not most, instances phylogenetic data contribute a unique and important source of information and should be taken into consideration whenever possible. Unfortunately, the current state of marine invertebrate phylogenetic research is such that corrections to stratigraphic ranges based on phylogenetic relations are not possible for most invertebrate groups. Accordingly, the taxonomic summary presented below represents a compendium of stage-level observations that have not been corrected for phylogenetic relationship.

Several graphical summaries of taxonomic compendia are available for comparison with the physical record of Phanerozoic extinction events. The most detailed of these is Sepkoski's (1994) Phanerozoic generic compendia (Fig. 1(A)). As with all such compendia, taxa whose last appearance is recorded to fall within a particular stage (e.g. Maastrichtian) are listed as having ranged through the entire time interval. Under this convention all taxa become extinct at stage boundaries irrespective of where the taxon's last appearance was actually observed. Although this range-through convention is widely acknowledged to overestimate the number of extinctions that actually occur at stage boundaries (e.g. Raup 1994; MacLeod & Keller 1996), given the current state of stratigraphic knowledge for Phanerozoic marine invertebrate taxa this represents the most accurate overall summary of extinction intensity.

Inspection of Fig. 1(A) shows that extinction intensity has undergone substantial and repeated fluctuations during the past 600 Ma. Seventeen separate extinction peaks are shown in this summary, ranging from the Tatarian event

Fig. 1. Stage-level correlation between the Phanerozoic marine invertebrate extinction intensity (**A**, based on Sepkoski (1994)), the physical record of Phanerozoic bolide impact events (**B**, data from Grieve *et al.* (1996); (crater ages and sizes), Orth *et al.* (1990; iridium anomalies), Hut *et al.* (1987; tektite horizons), the Permian–Recent record of major flood basalt events (**C**, data from Courtillot (1996)), and the Phanerozoic record of eustatic sea-level change (**D**, based on Vail *et al.* (1977), Hallam (1984) and Haq *et al.* (1987)). Arrows mark: stages in which extinction events occur (**A**) (this diagram does not show the internal structure of these events, only a stage-level summary). Arrows mark large bolide impact events (**B**); flood basalt eruption events (**C**); and eustatic sea-level falls (**D**) that exhibit stage-level correlations with marine invertebrate extinction events. Filled circles beside each eustatic sea-level curve mark a correlation between a stage-level extinction peak and a long-term fall in eustatic sea level for the specific curve.



A. Extinction Intensity
Percent Extinction
B. Bolide Impact Events
Crater Diam. (km)
C. Flood Basalt Eruptions
D. Eustatic Sea-Level Changes
Meters Above Present Sea Level (x 100)
No Summary Data Available
Ir-T - Terrestrial Ir
Ir-E - Extra-terrestrial Ir
Sm - Shocked Minerals
Tk - Tektites
Cenozoic
Mesozoic
Palaeozoic
Tertiary
Cretaceous
Jurassic
Triassic
Perm.
Carbon.
Devonian
Sil.
Ordovician
Cambrian
Middle Miocene
Upper Eocene
Maastrichtian (K-T)
Cenomanian
Aptian
Tithonian
Callovian
Pleinsbachian
Norian
Tatarian (P-Tr)
Serpukhovian
Frasnian/Famennian
Ludlovian
Ashgillian
Llanvirnian
Late Cambrian
Middle Cambrian
Popagai
Chesapeake
Chicxulub
Kara
Tookoonooka
Puchezh-Katunki
Manicouaguan
Charlevoix
Siljan
Columbia River
Ethiopian + Yemen
Brito-Arctic
Deccan
Madagascar
Rajmahal
Parana, Elendeka
Antarctic
Karoo
E. North American
Siberian

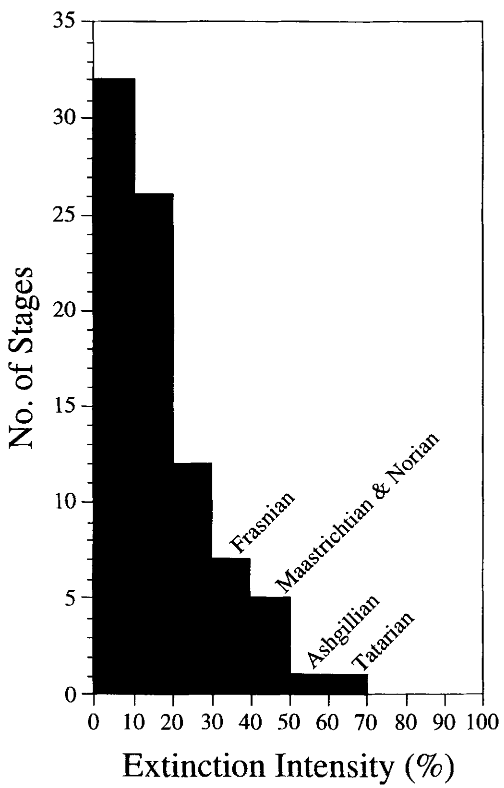


Fig. 2. Histogram of extinction intensities from Fig. 1(**A**). The shape of this distribution suggests that extinction intensity is distributed as a continuous series throughout the Phanerozoic, with the larger or 'mass' extinction events forming one tail of this distribution. The possible existence of biodiversity thresholds makes it possible (in theory) to accommodate a qualitative classification of extinction events in spite of the continuous nature of the extinction intensity distribution (see Van Valen 1994). However, the manner in which patterns of extinction selectivity differ among large and intermediate-sized extinction events has not been investigated in detail. It is likely that extinction events of differing intensity are capable of disrupting different types of ecological–evolutionary patterns in a quasi-continuous manner (see Jablonski 1996).

(*c.* 68% generic extinction) to the Middle Eocene event (*c.* 6% generic extinction). A histogram of extinction intensities for all Phanerozoic stages (Fig. 2) exhibits the topology of a 'decay curve', with large numbers of small events and a small number of larger or 'mass' extinctions. McKinney (1987), Steigler (1987), Raup & Boyajian (1988) and Raup (1991*a*, *b*, 1994) have pointed out that various extinction data point to the existence of a continuous range of extinction intensities within the fossil record. Jablonski (1986*a*, *b*, 1989; see also Kitchell 1990; Van Valen 1994) argued that despite the shape of the extinction intensity distribution different extinction classes could be recognized based on the presence (background extinction) or lack (mass extinctions) of ecological–geographical structure among the event's victims or survivors. These data imply the existence of 'threshold factors' that qualitatively subdivide the extinction intensity continuum. However, Jablonski (1996) found it likely that these threshold effects are themselves distributed in a more or less continuous manner throughout the various extinction events. Irrespective of this controversy, most palaeontologists continue to recognize a binary classification of extinction events, with 'mass extinctions' occupying the distribution's right-hand tail and 'background extinctions' occupying the left-hand tail. Although many of the intermediate extinction peaks (e.g. Upper Eocene, Cenomanian, Tithonian) are often referred to as 'mass extinctions', their ontological status with respect to the end-member categories remains uncertain.

Bolide impacts

The stratigraphic record of Phanerozoic bolide impacts can be derived from several sources, including crater age estimates, iridium anomalies, micro- and macrotektite horizons, and shocked mineral horizons. Of these, impact craters offer the most information in that the timing and size of the impact event can be directly measured within stated accuracy limits and subject to the smallest number of assumptions. However, like any physical record, impact craters, iridium anomalies, microtektite horizons, etc. can be removed by erosion, covered by sediments, destroyed via subduction, or fail to be discovered owing to limited outcrop area. These processes should conspire to render the physical record of bolide impacts less accurate as a function of the impact's age. In addition, some bolide impact proxies (e.g. local iridium anomalies) have been challenged as providing unambiguous evidence of impact occurrence and/or timing (Jablonski 1986*a*; Orth *et al.* 1990; Wang *et al.* 1993). Although these deficiencies in the stratigraphic record of bolide impacts are acknowledged, any claim that a general relation exists between bolide impacts and mass extinctions must be based on the known impact record. Indeed, this record has already been the subject of several extinction-related studies (e.g. Shoemaker 1983; Alvarez & Muller 1984; Rampino & Stothers 1984; Sepkoski & Raup 1986; Raup & Trefil 1987). The stage-level Phanerozoic bolide impact record is summarized in Fig. 1(**B**).

Interestingly, Fig. 1(**B**) shows that the most detailed record of impact activity is the record of impact craters. Although great effort has gone into the search for and analysis of impact proxies, this effort has not produced evidence of impact activity for stages within which impact craters are unknown. This reflects the relative frequency of large impact craters in the stratigraphic record, the expensive and time-consuming nature of impact proxy studies, the fact that some types of bolide impacts (e.g. comets) would not be expected to produce widespread impact proxy deposits, and the controversial nature of some data bearing on the interpretation of impact proxy deposits (see above). Regardless, although the stratigraphic record of impact proxies provides additional evidence in support of the impact crater record, it does not substantially modify that record.

Comparing Figs 1(A) and 1(**B**), the relation between marine invertebrate extinction intensity and the bolide impact record appears complex. The Pleistocene–Quaternary interval exhibits the greatest number of craters, most of these below 10 km in diameter. Failure of any other stratigraphic interval to record as many craters as the relatively short Pleistocene–Quaternary interval suggests that bolide impacts are far more common than would be suspected on the basis of the pre-Pleistocene stratigraphic record. The tailing off in impact frequency with age also supports this inference. Nevertheless, the fact that the impact-ridden Pleistocene–Quaternary interval fails to exhibit an extinction intensity peak suggests that the large number of smaller impacts whose records have been lost from the pre-Pleistocene stratigraphic record do not make a significant contribution to impact-mediated extinction patterns.

Within the remainder of the stratigraphic record there does not appear to be a strong correlation between impact frequency and extinction intensity, either for the Phanerozoic as a whole or for the last 250 Ma, where temporal control is much better (Fig. 3(**A**)). The Spearman correlation coefficient for these data is −0.219, which is not significant at the 95% confidence level. Some intervals of elevated extinction intensity (e.g. Norian, Aptian, Middle Miocene) are associated with local increases in the frequency of large impacts, whereas others (e.g. Cenomanian, Tithonian, Callovian) are not. On the whole, it would seem that the known record of impact frequency is a relatively poor predictor of marine invertebrate extinction intensity peaks.

Similarly, the relative size of impacting bodies does not seem to be deterministically associated with extinction intensity (Fig. 3(**B**)). An obvious exception to this is the Maastrichtian interval in which the fifth largest Phanerozoic mass

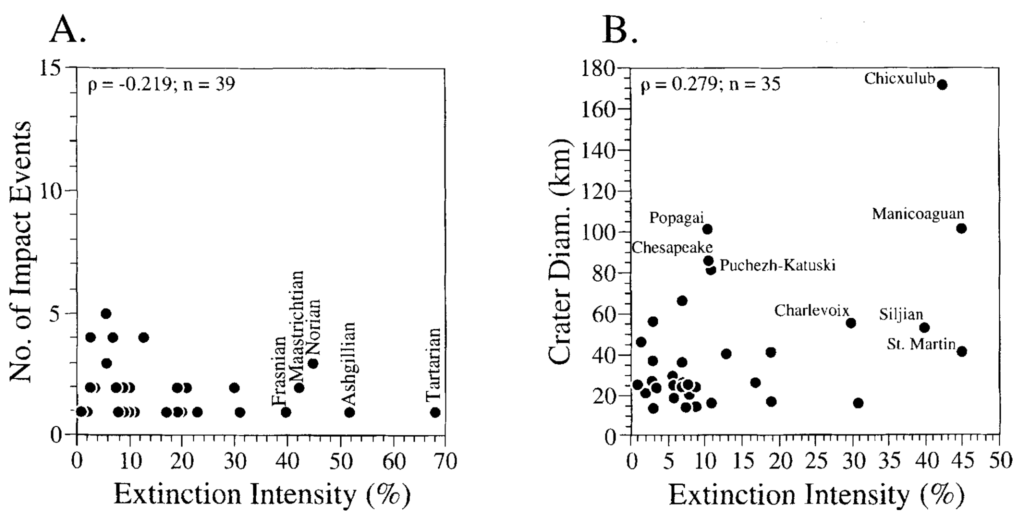


Fig. 3. Quantitative relation between extinction intensity and bolide impact history as inferred from (**A**) number of impact events per stage, and (**B**) size of impact events per stage. Spearman rank-order correlation coefficients (ρ-values) for these data are not significant at the 95% confidence level, indicating that these data conform to the expectations of a null model.

extinction (as measured by per cent extinction) is associated at the stage level with the largest Phanerozoic bolide impact crater (Chicxulub). (Note: Chicxulub is only the third largest crater known in all of Earth history.) Below this level, however, the relationship breaks down. Of the eight stages containing 51–100 km diameter impact craters, only four are associated with extinction intensity peaks. Moreover, large impacts appear to be associated with small extinction intensity values as often as with large. For example, the Upper Eocene interval has long been associated with unambiguous evidence for multiple impact events (see Prothero 1994) and recent investigations (e.g. Grieve *et al.* 1996; Bottomley *et al.* 1997) suggest that two sizeable impact events (Chesapeake Bay and Popagai) may have occurred within the space of as little as 3.0 Ma. Nevertheless, the Late Eocene interval is characterized by one of the smallest increases in genus-level extinction intensity in the entire Phanerozoic. The Spearman correlation coefficient for the data shown in Fig. 2(**B**) (including the Chicxulub event) is 0.279, which is not significant at the 95% confidence level. Together, these results suggest that given present data, neither impact number nor impact size exhibits a consistent association with extinction intensity.

Flood basalt eruptions

Flood basalt eruptions or (as they are sometimes called) large igneous provinces are massive crustal emplacements of mostly mafic extrusive and intrusive rock that originate through processes other than normal sea-floor spreading (Courtillot *et al.* 1996). Flood basalt eruptions are typically associated with mantle plumes or 'hot spots' (Coffin & Eldholm 1994) and are many orders of magnitude larger than any eruption recorded during human history. The stratigraphic association between flood basalts and increases in extinction intensity has been commented on by a number of researchers (e.g. Vogt 1972; Officer & Drake 1983, 1985; McLean 1985*a*, *b*; Morgan 1988; Courtillot *et al.* 1986, 1996; Stothers & Rampino 1990; Stothers 1993). Rampino & Stothers (1988) proposed that such eruptions may be a by-product of bolide impacts, but this has been directly challenged by White (1989) and is inconsistent with the widely accepted hypothesis that flood basalt events involve the lower mantle (e.g. Richards *et al.* 1989; Coffin & Eldholm 1994). Flood basalt eruptions may take place on the continents (where they form geomorphological features called 'traps') or on the ocean floor (where they form large subsurface plateaux). Of these two classes, continental flood basalt eruptions are thought to be the more climatically influential because erupted gases, particulate material and heat flow are injected directly into the atmosphere. The most recent compilation of Permian–Recent continental flood basalt ages (Courtillot *et al.* 1996) was used to produce Fig. 1(**C**).

Figure 4 shows a plot of estimated continental flood basalt ages compared with the durations of stages containing the nearest extinction peak. All major continental flood basalt eruptions in the last 250 Ma. have been associated with extinction peaks, with the exception of the Antarctic event (176.0 ± 1.8 Ma). Of the 11 remaining continental flood basalt events listed by Courtillot *et al.* (1996), six take place within or very close to the stages containing elevated per cent extinction frequencies. Levels of discordance within the events that do not fall within the predicted stage (according to age estimates given by Gradstein & Ogg (1996)) range from 3.5 Ma (Madagascar eruption–Cenomanian extinction) to 11.2 Ma (Serra Geral eruption–Tithonian extinction). To some extent, these discrepancies may be accounted for by intrinsic uncertainties associated with the isotopic methods used to date the continental flood basalt eruptions themselves and/or differences between competing geological time scales. However, the overall association between continental flood basalt eruption events and marine invertebrate extinction peaks over the last 250 Ma is both striking and statistically significant (Spearman correlation coefficient is 0.998). In this instance, available data suggest that over the last 250 Ma the temporal distribution of continental flood basalt eruptions is an excellent predictor of extinction intensity peaks at the stage level.

Eustatic sea-level change

Secular variations in eustatic sea level have long been suspected to play an important role in marine invertebrate mass extinctions (e.g. Moore 1954; Newell 1967; Schopf 1974; Hallam 1989). Owing to the use of sequence stratigraphy as an overarching conceptual framework for much contemporary stratigraphic research (especially in the hydrocarbon industry) eustatic sea-level curves have been determined for the entire Phanerozoic. The most widely used sets of sea-level curves are those of the Exxon research group (Vail *et al.* 1977; Haq *et al.* 1987)

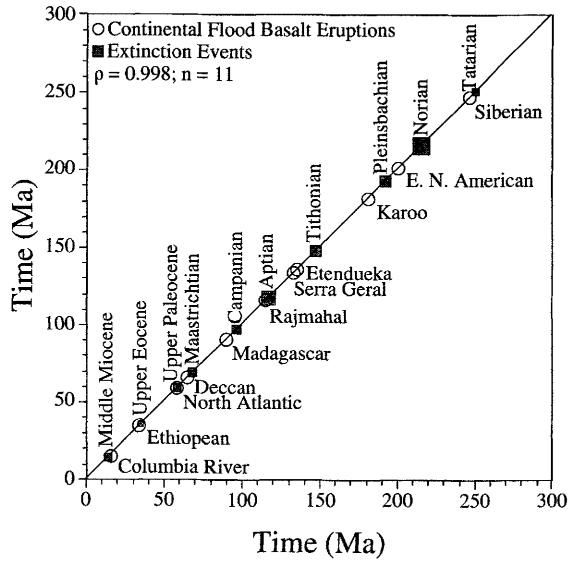


Fig. 4. Quantitative relation between the age of large continental flood basalt eruptions and stages containing extinction intensity peaks over the last 250 Ma (flood basalt age dates from Courtillot *et al.* (1996), geological time scale of Gradstein & Ogg (1996)). Spearman rank-order correlation for these data is 0.998, which is significant at the 95% confidence level.

and those of Hallam (1984). All three curves have been used as the basis for a large number of stratigraphic studies.

Figure 1(**D**) shows the long-term eustatic sea-level curves from Vail *et al.* (1977), Hallam (1984) and Haq *et al.* (1987). All three curves reflect long-term estimates of eustatic sea-level fluctuation. Although the use of long-term curves is preferable for gross trend analysis, it does underestimate the magnitude of short-term fluctuations in eustatic sea level (e.g. Pleistocene sea-level fluctuations) that may have been important at basinal and regional scales. As with the stratigraphic record of bolide impacts and continental flood events, the accuracy of the eustatic sea-level curve estimates is expected to decrease with increasing age.

The Exxon and Hallam curves show similar overall trends, but differ in the magnitude of eustatic sea-level change attributed to individual events. These differences arise because of differences in the methods used to construct the curves. The Mesozoic and Cenozoic portions of the Vail *et al.* (1977) and Haq *et al.* (1987) curves are based on Exxon seismic stratigraphic interpretations, augmented (in the case of Haq *et al.* (1987)) with data from selected marine sections exposed on continental platforms. The Palaeozoic portion of the Vail *et al.* (1977) curve was based on Sloss' (1963) interpretation of North American cratonic sequences. Hallam's (1984) sea-level curve is based on a combination of seismic stratigraphic results and palaeogeographical reconstructions of marine sediment coverage at various time intervals in the Phanerozoic calibrated against the hypsometric curve. Both methods of eustatic sea-level curve reconstruction have their advantages and disadvantages (see Hallam (1992) for a review), and their general pattern-level concordance, if not their estimates of sea-level change magnitudes, provides a measure of confidence in the results.

Comparison of these long-term trends with the marine invertebrate extinction record (Figs 1(**A**) and 1(**D**) suggests that although there is a general correlation between intervals of eustatic sea-level fall and mass extinctions at the stage level (e.g. Tatarian, Ashgill, Maastrichtian, Norian), many intermediate–smaller extinction events (e.g. Middle Miocene, Aptian, Pleinsbachian) appear to have taken place during eustatic sea-level rises. Hallam (1984, 1989) suggested that all six of Newell's (1967) mass extinction events are correlated with major eustatic sea-level regressions. The revised Phanerozoic marine extinction record of Sepkoski (1994) preserves all of Hallam's (1984, 1989) correlations and adds relatively minor events in the Cenomanian and Ludlow to this list. Associations between eustatic sea-level change and extinctions are not as frequent in the Vail *et al.* (1977) and Haq *et al.* (1987) compilations. It should be noted, however, that the short-term Haq *et al.* (1987) curve does show a sharp eustatic sea-level fall occurring just before the Cretaceous–Tertiary (K–T) boundary. Traditionally, the end Maastrichtian eustatic sea-level fall has been assigned a greater magnitude than that given by Haq *et al.* (1987). Some of the discrepancy between the Hallam (1984) and Haq *et al.* (1987) curves for this event may be attributable to the latter's use of the Braggs, Alabama, K–T section, which is incomplete across the uppermost Maastrichtian–lowermost Danian interval (Bryan & Jones 1989), as the basis for their reconstruction (see Hallam (1992) for an extended discussion). Because of discrepancies between the eustatic sea-level curve, and the high degree of 'guesstimation' (see Hallam 1992) in the specification of the long-term curve's slope, no formal statistical tests of the association between sea-level regressions and extinction intensity peaks are possible. However, many workers have commented that, of all geological phenomena, eustatic sea-level fall exhibits the most consistent correlation with large extinction events (see Jablonski (1986*a*) and Hallam (1989) and references therein).

Selectivity as a criterion to identify extinction event causes

Although the stage-level associations between bolide impact numbers and size and sea-level regression do not appear to be significant given present data, there are many problems with the stratigraphic record of these events that might bias coarse-grained analyses against finding the predicted relations. Moreover, these physical events could figure as a sole or contributory cause for certain extinction events, but not others. To explore these alternatives it is necessary to switch from a coarser to a finer analytical scale and ask the question: 'Do the predictions of biotic effects derived from the various extinction event scenarios (e.g. bolide impacts, flood basalt volcanism, sea-level regression) match the patterns observed in the marine invertebrate extinction record?'

This is the traditional scale at which mass extinction studies have been pursued. It is also the scale at which the greatest number of complications arise. The scientific enigma of extinction events is not that they have taken place (this was convincingly demonstrated by Cuvier in 1796), but turns on the question of the mechanisms by which such events are brought about. To provide precise answers to this question for specific extinction events we would like to know the predicted physical effects of the proposed extinction mechanisms on the global environment, the susceptibilities of particular biotic groups to these environmental–ecological factors, and the consistency with which physical predictions match biotic patterns for extinctions associated with known and/or suspected bolide impact events.

Table 1 lists the major killing mechanisms associated with bolide impact, volcanism, and sea-level regression. In terms of the type of mechanisms predicted to be in operation, there is little difference between bolide impact and volcanism scenarios. Both are regarded as events in which large amounts of gas and particulate matter are emplaced in either the troposphere (small events) or stratosphere (large events). Residence times of these materials range up to several months for large events (Alvarez *et al.* 1980; Toon *et al.* 1982; Pollack *et al.* 1983; Barron & Moore 1994) and would be expected to result in reduced light levels, acidification of rainwater, global cooling as a result of increased albedo, and increased irradiation of the Earth's surface because of ozone destruction. Longer-term effects may also involve global warming caused by increased concentration of greenhouse gases; principally CO_2 (O'Keefe & Ahrens 1982). Bolide impacts have been additionally associated with an initial very short term shock heating (Croft 1982), and the ignition of 'global' wildfires (Wolbach *et al.* 1985, 1990).

It is important to note that in many cases the calamitous effects predicted for bolide impact events are only predictions. There are no independent physical data confirming or refuting the thermal pulse, ozone depletion, or short-term global cooling. Retallack (1994, 1996) has interpreted geochemical and soils evidence from K–T sections in the western USA as being consistent with acid rain fallout, but his interpretations have been challenged by Archibald (1996*a*; see also Archibald and Retallack (1996)). Similarly, Archibald (1996*a*, *b*) has used sedimentological data to challenge the Wolbach *et al.* (1990) global wildfire scenario (see also Hallam and Wignall (1997)). On the other hand, there is abundant empirical support for the climatic and environmental effects of volcanism based on studies of historical eruptions (Officer & Drake 1983, 1985; McLean 1985*a*, *b*; Officer *et al.* 1987). Nevertheless, many aspects of the terrestrial and marine biotic records are plainly inconsistent with more extreme variants of bolide impact and volcanic eruption scenarios (see Jablonski (1986*a*) and Archibald (1996*a*, *b*) and references therein) and there is ample reason to suspect that some of these predicted effects

Table 1. *Effects of proposed extinction event causal mechanism*

Effect	Reference
Large bolide impact	
Reduced light penetration	Gerstl & Zardecki (1982), Toon *et al.* (1982), Pollack *et al.* (1983)
Lowered levels of photosynthesis	
Increased atmospheric particulates	O'Keefe & Ahrens (1982), Toon *et al.* (1982), Pollack *et al.* (1983)
Increased albedo	
Global cooling	
Global warming	
Greenhouse warming	
Increased cloud cover	Croft (1982), Jones & Kodis (1982), O'Keefe & Ahrens (1982)
Increased albedo	
Global cooling	
Global warming	
Increased atmospheric water vapour and CO_2	Emiliani *et al.* (1981), Toon *et al.* (1982)
Greenhouse warming	
Ozone depletion	Lewis *et al.* (1982)
Increased irradiation of surface	
Increased abundance of trace elements	Alvarez *et al.* (1980), Hsü *et al.* (1982)
Interference with biochemical processes	
Acid rain	Park (1978), Park & Menees (1978), Prinn & Fegley (1987)
Habitat destruction	
Interference with biochemical processes	
'Global' wildfires	Wolback *et al.* (1985, 1990)
Increased atmospheric particulates (see above)	
Increased cloud cover (see above)	
Increased CO_2 (see above)	
Habitat destruction	
Shock heating	Croft (1982)
Flood basalt volcanism	
Reduced light penetration	Deirmendijan (1973)
Lowered levels of photosynthesis	
Increased atmospheric particulates	Toon *et al.* (1982), Pollack *et al.* (1983)
Increased albedo	
Global cooling	
Global warming	
Greenhouse warming	
Increased cloud cover	McLean (1985)
Increased albedo	
Global cooling	
Global warming	
Increased CO_2	McLean (1985)
Greenhouse warming	
Ozone depletion	Stolarski & Butler (1979), Keith (1980, 1982)
Increased irradiation of surface	
Increased abundance of trace elements	Hansen (1991)
Interference with biochemical processes	
Eustatic sea-level fall	
Reduced shelf area	Schopf (1974), Simberloff (1974), Hallam (1989)
Species-area effect	
Habitat destruction	
Intensification of climatic gradients	Barron & Moore (1994)
Heating of continental interiors	

Table 1. (*continued*)

Effect	Reference
Eustatic sea-level fall (continued)	
Increased seasonality	Barron & Moore (1994)
Increased albedo	
Global cooling	
Reduced atmospheric CO_2	Barron & Moore (1994)
Global cooling	
Bottom-water anoxia	Hallam (1989)

may have been less intense than currently advocated by some research groups.

With respect to perturbations of the marine environment resulting from eustatic sea-level change, as eustatic sea-level changes of varying magnitudes have occurred repeatedly throughout the Phanerozoic (see Fig. 1(**D**), their effects on the marine ecosystem and marine invertebrate communities have been the subject of intense study (see, e.g. Schopf (1980) and Barron & Moore (1994) and references therein). In some cases the weight attributed to secondary biotic-effect predictions has changed in light of new data (e.g. Jablonski 1985, 1986*a*). Nevertheless, the predicted climatic perturbations associated with sea-level fall listed in Table 1 are supported by abundant empirical and theoretical evidence. It is disturbing to note, however, that in many cases these effects are identical to those produced under the bolide impact and large volcanic eruption scenarios (e.g. global warming, collapse of primary productivity) albeit as responses to different mechanisms.

The following example illustrates the complexities, and to a large extent the failures, of attempts to use patterns of extinction selectivity to infer extinction event causes. Sheehan & Hansen (1986; see also Arthur *et al.* (1987), Hansen *et al.* (1987*a*), Roy *et al.* (1990) and McGhee (1996)) suggested that invertebrate species whose feeding requirements tie them to primary production (e.g. suspension feeders, carnivores) suffer differentially intense extinction rates relative to detritus feeders across the K–T boundary and, by implication, other extinction horizons where bolide impact is thought to have been a driving force. The original study (Sheehan & Hansen 1986) was based in part on a literature review of Late Cretaceous and Early Tertiary marine invertebrate studies, but linked to the K–T impact event on the basis of molluscan data from the Brazos River K–T section (Hansen *et al.* 1984, 1987*a*). Sheehan & Hansen (1986) concluded that this pattern resulted from a collapse in primary productivity at the K–T boundary brought about by 1–2 months impact-generated darkness (the 'Strangelove Ocean' of Hsü & MacKenzie (1985, 1990)). (Note: To the extent that large volcanic eruptions can affect global marine productivity via attenuation of light intensities, alteration of circulation patterns, increase in atmospheric concentrations of greenhouse gases, etc., the same predictions would apply.)

Sheehan & Hanson's deposit feeder = survivorship model was challenged in marine settings by Bryan & Jones (1989), who reported the opposite trend (an increase in suspension feeders in the lowermost Danian) from the Braggs, Alabama, K–T section, and later by Archibald (1996*a*, *b*) for terrestrial stream communities. Rhodes & Thayer (1991) confirmed the bias toward deposit-feeding and sessile bivalves over suspension-feeding and active species using a Maastrichtian–Danian stage-level dataset consisting of 424 generic records. Owing to the stage-level resolution afforded by these data, however, Rhodes & Thayer (1991) concluded that their results were only consistent with the hypothesis of reduced primary productivity and declined to associate the productivity drop with any specific causal mechanism. Paul & Mitchell (1994) further challenged the association of productivity collapse with bolide impact by pointing out that a very similar pattern was present at the Cenomanian–Turonian event (which is not a major extinction event and not felt to be impact related). Paul & Mitchell (1994) suggested that a drop in primary productivity was a general feature of marine extinction events and could be generated by rapid eustatic sea-level fall in addition to bolide impact.

In 1993, Hansen *et al.* published new molluscan data from Brazos River K–T sections. This report concluded that in the lowermost Danian virtually all the deposit-feeding bivalves recovered from Brazos River were not K–T survivors themselves, but new species that originated in the Danian. Of the three bivalve species reported to survive the K–T boundary event in this new study, two were suspension feeders! These data suggested (in contrast to the results of Sheehan & Hansen (1986)) that deposit-feeding and suspension-feeding bivalves exhibited comparable extinction rates in the Brazos River section. This alternative interpretation was also supported by Jablonski & Raup (1995) (see also Jablonski (1996)), who used a global database to show that K–T extinction resistance was not a uniform property of all deposit-feeding molluscs, but varied between taxonomic groups, with some deposit feeders (e.g. Tellinidae, Aporrhaidae) suffering extinction rates as high as those of suspension-feeding molluscs. In addition, much recent ecological research has shown that the deposit-feeding life mode tracks changes in marine primary productivity to a much greater extent than was previously supposed (Lambshead & Gooday 1990; Rex *et al.* 1993; Levinton 1996).

These studies represent convincing challenges to Sheehan & Hansen's (1986) model for preferential survivorship of short-term extinction events by deposit feeders or scavengers and question any unique relation between these patterns and bolide impact events. Although Sheehan *et al.* (1996) made a large number of references to the possibility that marine invertebrate K–T survivors had switched from suspension feeding to deposit feeding, these speculations remain unsupported by any empirical data. Indeed, Jablonski (1996) pointed out that tellinid bivalves, modern representatives of which are known to be able to switch facultatively from suspension feeding to deposit feeding (Levinton 1991; Kamermans 1994; Lin & Hines 1994), suffered some of the highest K–T extinction intensities of any molluscan group.

Patterns of extinction selectivity are present for the K–T event (see MacLeod *et al.* 1997), as they are for the Frasnian (McGhee 1996), Tatarian (Erwin 1993) and Late Eocene (Prothero & Berggren 1992; Prothero 1994) events. The problem lies in the fact that each extinction event has so many unique attributes, and each attribute is consistent with so many possible causes, that no generalizations are possible (Van Valen 1994). Table 2 provides a rough taxonomic list of victims and survivors for the four best-studied extinction events. There is little in the way of a consistent taxonomic signal in these data that could be used to subdivide them into impact-associated (Maastrichtian, Eocene), non-impact associated (Tatarian), or equivocal (Frasnian) groups even if one were willing to specify the proximate extinction mechanisms *post hoc*. Moreover, such tables hide the fact that within each extinction a wide variety of adaptive types, intrinsic diversities, and extinction modes exist. When common factors are found (e.g. the decline of reef ecosystems during the Frasnian, Tatarian, and Maastrichtian events; see Jablonski (1989)), they fail to subdivide the extinction spectrum in any meaningful way other than to separate large events from smaller ones. This frustrating randomness in the biotic extinction signal also pervades finer-scale analyses. Indeed, the most generally accepted result of this research effort is that mass extinction events differ from background extinction intervals in their *lack* of statistically significant within-group structure (Jablonski 1986*a*, *b*, 1989).

This failure, despite intense efforts spanning decades, to uncover a consistent biotic–ecological–distributional signal that unequivocally groups extinction events into separate classes has serious implications for the study of extinction causes. As pointed out by Raup (1991*b*), the only way to establish cause and effect in historical data is to document patterns of coincidence. If every extinction event is unique (as increasingly seems the case) it will be logically unjustified to prefer one causal scenario over another on biotic grounds, and hence impossible to develop an overarching explanation for groups of individual extinction events.

There is little doubt that environmental variation exhibits a stochastic pattern of random fluctuation about a mean value (Elton 1958; Ehrlich & Birch 1967; May 1974; Pimm 1991). Departures from this characteristic environmental mean will take place at a variety of scales, from normal seasonal variation through 'once in a decade', 'once in a century', 'once in a millennium', type perturbations to 'once in a geological period' perturbations and beyond. Bolide impact, massive flood basalt volcanism, and long-term eustatic sea-level change all belong to the latter tail of this environmental change distribution. Although there is ample evidence that all these mechanisms can produce extinction events, it is reasonable to expect that fortuitous conjunctions in the time series of each of these mechanisms would lead to anomalously large extinction events. The correlations shown in Fig. 1 suggest that this has been the case for the three largest extinction events of the last 250 Ma (Tatarian, Norian, Maastrichtian) in that each took place during a conjunction between large continental flood basalt eruptions and a relatively rapid drop in long-term eustatic sea level. Raup (1991*b*) criticized the connection

Table 2. *Taxonomic victims and survivors for the four best-studied extinction events*

	Extinction event			
Taxonomic group	Frasnian	Tatarian	Maastrichtian	Mid–Upper Eocene
Phytoplankton	●	○	○	○
Coccolithophores	–	–	●	●
Dinoflagellates	–	–	○	○
Diatoms	–	–	○	○
Zooplankton				
Planktonic Foraminifera			●	●
Benthic Foraminifera	●	○*	○	○
Radiolaria	○	○	○	○
Arthropods				
Ostracods	●	●	○	○
Trilobites	●	●	–	–
Sponges	○	○†	○	○
Cnidaria	●	●	○	○
Bryozoans	○	●	○	○
Brachiopods	●	●	○	○
Molluscs				
Gastropods	○	○	○	●
Bivalves	○	⊙	⊙	●
Cephalopods	●	●	●	○
Echinoderms				
Asteroids	?	?	○	○
Crinoids	●	●	○	○
Echinoids	?	?	⊙	●

●, Event victim; ⊙, selective extinctions; ○, event survivor.
* Excluding fusulinids.
† Excluding reef sponges.
Data from Erwin (1993), Prothero (1994), McGhee (1996), MacLeod *et al.* (1997).

between sea-level fluctuations and extinctions by arguing that the dramatic short-term Pleistocene glacio-eustatic sea-level fluctuations did not produce sizeable extinction events. However, long-term eustatic sea level was already low during the Pleistocene (resulting in much less flooding of the continental platforms than in the Late Permian, Late Triassic and Late Cretaceous; see Fig. 1(**D**)), and Jackson (1995) has shown that the Late Pliocene onset of glaciation did result in dramatic extinctions among tropical molluscs, corals, and planktonic Foraminifera. The fact that biotas which have recently been stressed by particular perturbations often show ecological resistance to subsequent perturbations of the same types has widespread empirical (Pimm *et al.* (1995) and Greuter (1995) and references therein) and theoretical (Nee & May 1992; May *et al.* 1995; Tilman *et al.* 1996) support. These results adequately account for the so-called Pleistocene extinction anomaly. In addition, this same model can be used to form a general understanding of why extinction events resulting from the fortuitous conjunction of different causal mechanisms have such dramatic effects on the global biota.

This type of stochastic system constitutes a null hypothesis for the biotic interpretation of extinctions. To prefer the identification of a particular overriding causal process, it is not only necessary to show that a large proportion of accidents or extinctions took place during the suspect time interval, but that they also occur for reasons directly attributable to the proposed cause, and occur in comparable frequencies every time the proposed cause is active. These are admittedly stringent requirements, but they are the minimum necessary to establish the pattern of coincidences required to test extinction models using biotic data within a cause–effect framework. Thus far, biotic data from Phanerozoic marine invertebrate extinction events have proven to be too generalized to be used to conduct such tests. Present patterns strongly suggest that each major Phanerozoic environmental perturbation was itself multicausal and operated on a metastable biotic system whose initial conditions largely determined the extent of the corresponding biotic extinction (Jablonski 1996). Within such a system, and given the coarse levels of biotic resolution provided by the fossil record, it may well be impossible to use the contingent pattern of extinction selectivity to uniquely identify specific causal factors.

Ambiguities in high-resolution biostratigraphical data

Given the generalized and ambiguous nature of biotic predictions following from the various extinction causal event scenarios, most palaeontologists have turned to the biostratigraphic record to provide criteria that can be used to distinguish between alternative causal models. However, like the extinction selectivity research programme (see above), tests involving the time interval over which extinctions take place are bedevilled by similarities in the predictions of various causal models and by ambiguities in the nature of the data on which they are based.

As mentioned above, the maximum estimated time interval over which the proximate effects of individual bolide impacts would be expected to last range from 2 to 24 months (Toon *et al.* 1982; Pollack *et al.* 1983). Longer-term effects (e.g. greenhouse warming) cannot be ruled out (e.g. Ryder 1996), but the time scale over which these effects would be predicted to last has never been specified because the environmental feedbacks controlling these durations are not well understood. In most instances, though, the demonstration of 'rapid' extinction rates has been used as evidence favouring bolide impact causal models (e.g. Smit 1982, 1990; Pospichal 1993, 1994; Ward 1995; Marshall & Ward 1996). Flood basalt volcanic events are known to occur over time scales ranging from <1 Ma (Deccan, Parana–Serra Ceral) to 8 Ma (Siberian; see Courtillot *et al.* (1996) and references therein), but these estimates refer to the aggregate period over which a number of genetically related, yet distinct eruptions occur. Individual eruptions take place over much shorter time scales (10^0–10^1) and their proximate environmental effects would be expected to be most pronounced over these intervals. Eustatic sea-level changes occur over a large range of time scales from parasequences (10^4–10^5 years) to supercycles (10^7–10^8 years) (Vail *et al.* 1977; Hallam 1984; Haq *et al.* 1987). These data suggest that under the best of circumstances the duration of an extinction event is only likely to be diagnostic at the extreme lower end of the scale (months to years).

The stage-level resolution of most biostratigraphic data effectively prevents them from being used to examine hypotheses that specify very short extinction durations. Stages' time-spans vary widely, but they are on average several million years long. Therefore, to assess the question of extinction duration palaeontologists must turn to studies of individual stratigraphic sections and/or cores. Stratigraphic sections and cores, however, present their own complications. Prominent among these are the following.

Effect of hiatuses

Hiatuses are intervals of time missing in the stratigraphic record. In fossiliferous sedimentary sequences hiatuses most often form as a result of non-deposition or active erosion. They are present at all temporal and many spatial scales. From a historical perspective the major faunal changes used to subdivide the Phanerozoic (e.g. Permo-Triassic boundary, Cretaceous–Tertiary boundary) were often (inadvertently) placed at hiatuses because they accentuate faunal turnover patterns.

The significance of hiatuses with respect to extinction studies was first discussed by Birkelund & Hakansson (1982) and has been subsequently mentioned by many workers (e.g. Jablonski 1986*a*; MacLeod 1996*a*). MacLeod & Keller (1991) reviewed the biostratigraphy–chronostratigraphy of all major K–T boundary sections or cores and found that the majority contained boundary hiatuses as inferred by the absence of entire biozones. These included such well-known sections as Stvens Klint, Denmark (no evidence for the presence of the lowermost two Tertiary planktonic foraminiferal biozones, see also Hakansson & Hansen (1979), Perch-Nielsen *et al.* (1982) and Ekdale & Bromley (1984)), Gubbio, Italy (no evidence for the presence of the lowermost Tertiary planktonic foraminiferal biozone; see also Luterbacher & Premoli-Silva (1964)), and Zumaya, Spain (no evidence for the presence of the lowermost Tertiary planktonic foraminiferal biozone (Herm 1965; Smit & Ten Kate 1982); see also Ward & Kennedy (1993)). The fact that each of these sections contains a well-developed iridium anomaly is not inconsistent with a boundary hiatus, but can be accounted for under a variety of geochemical models (e.g. Goldschmidt 1954;

Keith 1982; Rucklidge *et al.*, 1982; Hansen *et al.* 1987*b*; Crockett *et al.* 1988; Tredoux *et al.* 1988; Colodner 1992; Sawlowicz 1993; Burns *et al.* 1996). Comparably detailed stratigraphic studies have not been carried out for other extinction event horizons–intervals. However, if an extinction event horizon coincides with a stratigraphic hiatus, the character of biotic change across that horizon is unknowable.

Circular arguments for dating

The highest temporal resolutions available for the majority of Phanerozoic extinction events come from biostratigraphic, as opposed to isotopic, dating. As a result, the location of physical event horizons (e.g. iridium anomalies, tektite horizons) with respect to faunal or floral event horizons is of critical importance. For example, the observation of an 18 m section of bedded, undisturbed marls containing a diverse assemblage of upper Maastrichtian planktonic Foraminifera overlying the Chicxulub breccia deposits in the Chicxulub 1 well (Ward *et al.* 1995, see also Löpez Ramos (1973), Jéhanno *et al.* (1992) and Leroux *et al.* (1995)) suggests that either the Chicxulub impact event did not take place at the K–T boundary (as defined by biostratigraphic criteria), or that survivorship among late Maastrichtian planktonic Foraminifera is much greater than previously thought. Inconsistencies between data of different types must be reconciled on the basis of external criteria, as differences of opinion exist on the priority of biotic and physical data for the proposed K–T boundary definition (compare Smit *et al.* (1992), with Keller *et al.* (1993)). In such cases analytical approaches that encompass all available data to achieve an internally consistent consensus should be preferred (e.g. MacLeod & Keller 1991; MacLeod 1995*a–c*, 1996*b*, *c*).

Arbitrary interpretations of biotic disappearances or appearances

The disappearance or appearance of species from local sections is an inherently ambiguous observation that may result from a variety of different processes. In addition to the obvious global extinction or global origination interpretation, disappearances or appearances may also result from emigration or immigration events caused by local facies shifts and speciation events (usually coupled with hiatuses and/or facies shifts) in which descendants are assigned a different taxonomic name and so counted as a different unit in statistical summaries of biotic turnover patterns. An example of the former includes the benthic foraminiferal study of Speijer (1994) and Speijer & Van der Zwann (1996), who argued for an 'abrupt extinction' of this group at the K–T boundary in the southern Tethys. Inspection of the data upon which this study is based (Speijer 1994, table 1) shows that of 51 listed taxa 28 (54.9%) disappear within ±5 cm of the El Kef K–T boundary. Nevertheless, of these 28 taxa all but six (11.8%) reappear higher in the section. The 22 taxa that undergo temporary disappearances are formally classified as Lazarus taxa (Jablonski 1986*a*) and should not be counted in estimates of global or regional extinction intensity. Miller (1982), Keller (1988*a*, 1992), Thomas (1990*a*, *b*), Widmark & Malmgren (1992) and Coccioni & Galeotti (1994) concluded that benthic foraminiferal faunas did not undergo significant extinction across the K–T boundary. As an example of the latter phenomenon among K–T echinoids, Andrew Smith (pers. comm. 1997) noted that the genus *Actinophyma* Cotteau & Gauthier (Campanian–Maastrichtian) is morphologically identical to the late Thanetian genus *Acanthechinus* Duncan & Sladen, suggesting that these two taxa actually constitute a single K–T survivor lineage. Similarly, Carlson (1991) has shown that Permo-Triassic extinction patterns among brachiopods are strongly attenuated by consideration of phylogenetic data (see also general discussion of Permo-Triassic extinction intensity estimates by Erwin (1993)).

The Signor–Lipps effect

The Signor–Lipps effect (Signor & Lipps 1982; see also Shaw (1964), Raup (1989), Archibald (1996*a*) and MacLeod (1996*a–c*), suggested that interactions between sample size, relative abundance, susceptibility to diagenesis, and environmental tolerance can conspire to distort the last appearance pattern of taxa that disappear during an extinction event. Consequently, 'if the distribution of fossil last occurrences is random with respect to actual biotic extinction, then apparent extinction will begin well before a mass extinction and will gradually increase in frequency until the mass extinction event, thus giving appearance of a gradual extinction' (Signor & Lipps 1982, p. 291). As such, the Signor–Lipps effect is a special case of the Lazarus effect and changes the geometry of apparent faunal turnover patterns in a manner opposite to that of the hiatus effect.

Several researchers have used the Signor–Lipps effect to argue that gradual faunal turnover patterns are consistent with catastrophic extinction mechanisms (Jablonski 1986*a*; Raup 1986*b*; 1989, 1991; Marshall & Ward 1996; Smit & Nederbragt 1997). Although this conclusion is correct in a strict sense, it represents a half-truth that substantially distorts the intention of Signor & Lipps (1982). The Signor–Lipps effect is a statement of fundamental uncertainty that is best understood to state that the true geometry of fossil species' first or last appearances can only be inferred within fairly broad stratigraphic limits. With respect to the question of extinction studies Signor & Lipps (1982, p. 295) explicitly stated that 'our arguments should not be interpreted as support for the impact hypothesis or any other theory invoking a catastrophe as the extinction mechanism. The evidence at hand is as compatible with a gradual extinction as a catastrophic one.' (Note: this ambiguity is also present in Jablonski's (1986*a*) use of Lazarus taxa to evaluate apparent faunal turnover patterns.) Several statistical tests and data analytical strategies designed to evaluate the conformance of the observed fossil record with the predictions of the Signor–Lipps effect have been developed (Koch & Morgan 1988; Marshall 1995; MacLeod 1996*b*, *c*), but thus far these have only been applied to the extinction event records of a few groups in local stratigraphic successions.

The Zombie effect

Just as the Lazarus and Signor–Lipps effects bias the extinction record by under-representing local stratigraphic ranges, the Zombie effect (Archibald 1996*a*; see also Barrera & Keller (1990) and MacLeod & Keller (1994)) postulates that local stratigraphic ranges may be artificially extended by the reworking of fossils from underlying sediments. The Zombie effect has been used to argue that seemingly anomalous occurrences of 'Cretaceous' nannoplankton (Pospichal 1993, 1994, 1996) and planktonic Foraminifera (Liu & Olsson 1992, 1994; Olsson & Liu 1993) represent reworked Cretaceous specimens. However, Archibald (1996*a*) pointed out that reworking cannot be assumed to only be confined to time intervals following mass extinction events. It is far more likely to be a common factor throughout the fossil record.

Several recent studies have lent empirical support to this inference by demonstrating that 'modern' surface assemblages of molluscs and benthic Foraminifera represent time-averaged assemblages on the order of 10^3–10^4 years (Broecker *et al.* 1990; Flessa 1993; Martin 1993; Flessa & Kowalewski 1994). If these estimates are valid for marine invertebrate taxa as a whole it would seem that time intervals of this order might represent the maximum resolution available in the fossil record. With respect to extinction event horizons, the Zombie effect would also operate to artificially extend the ranges of taxa that actually became extinct before the event (and so accentuate the magnitude of the apparent extinction) as well as extending the ranges of taxa that became extinct at the event horizon itself. Under favourable circumstances the Zombie effect can be tested for individual species (e.g. Barrera & Keller 1990; Huber 1996) and entire faunas (e.g. MacLeod & Keller 1994; MacLeod 1996*b*, *c*).

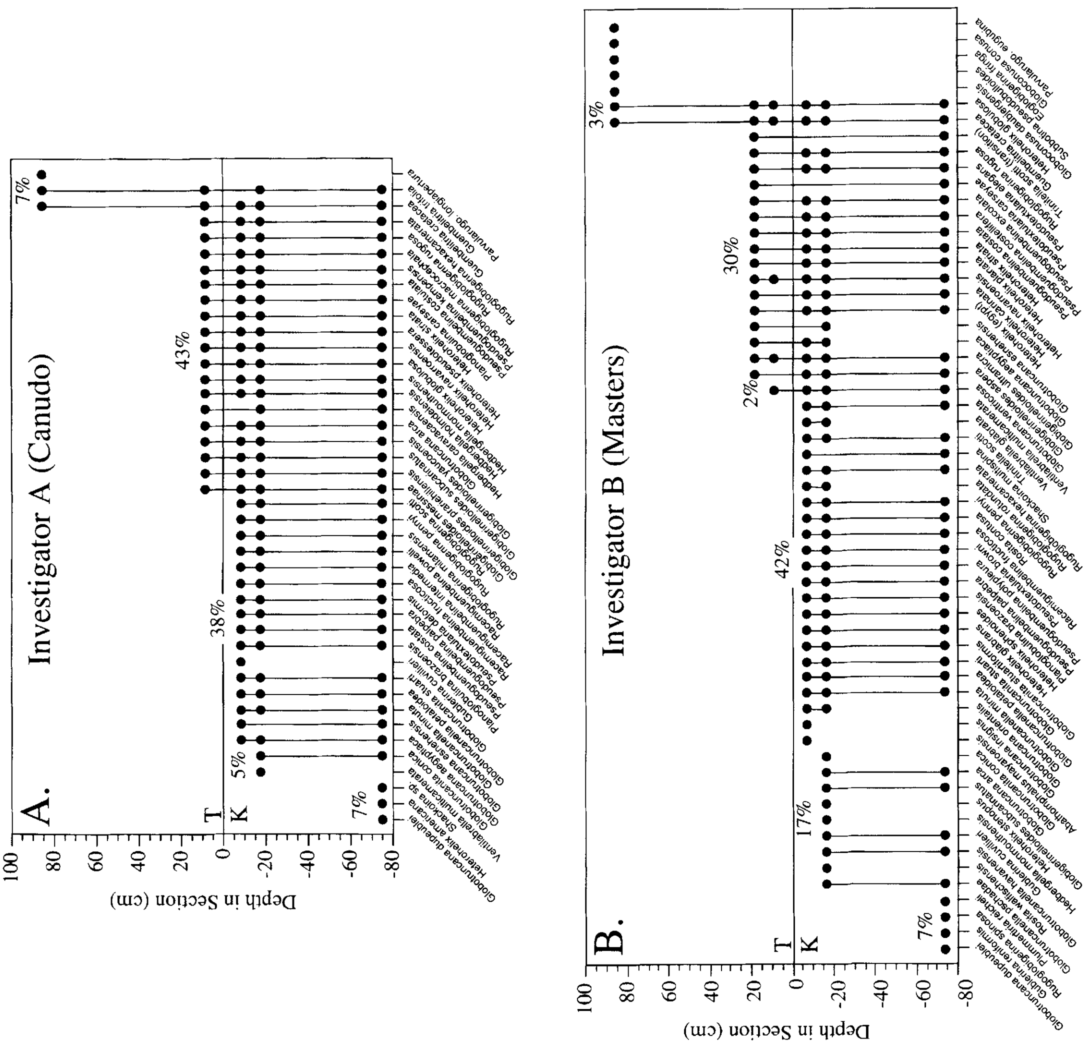
Case studies

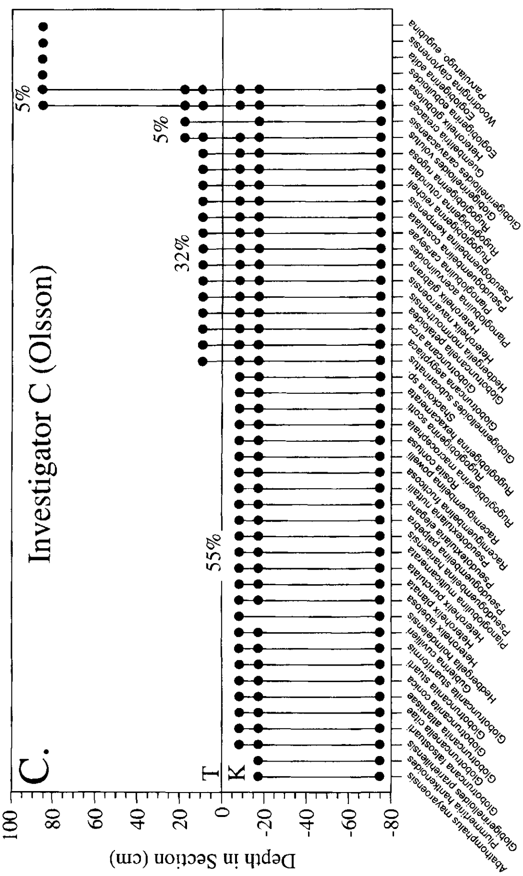
To illustrate the strategies used and complications encountered in studying marine invertebrate extinction events in local sections, controversies over the K–T records of planktonic Foraminifera and ammonites are briefly reviewed below.

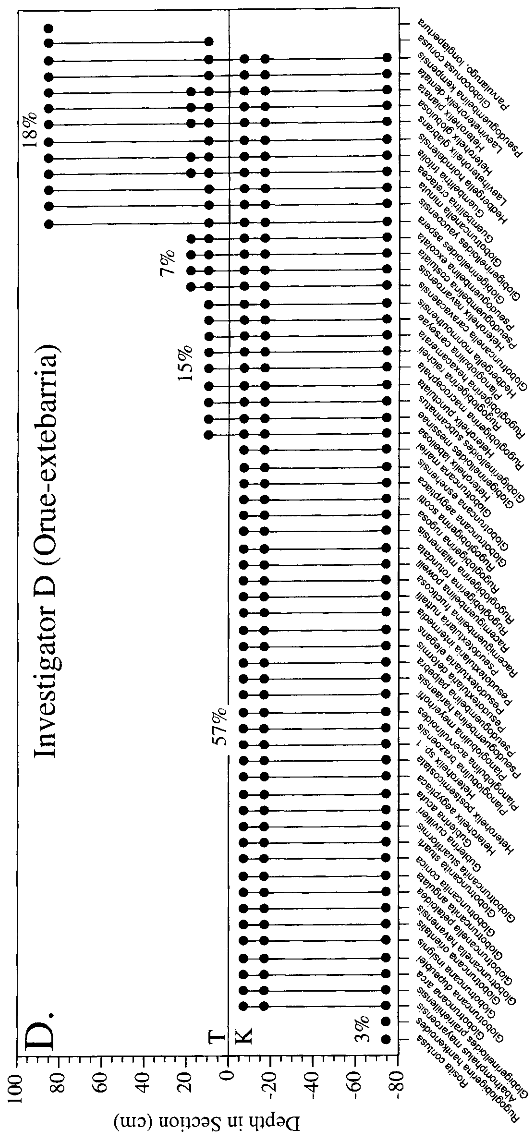
The K–T planktonic foraminiferal controversy

More is known about the K–T record of planktonic Foraminifera than that of any other organismal group across any major extinction interval. Thanks to the efforts of Gerta Keller, Jan Smit and their colleagues, an extremely detailed, high-resolution, global record of upper Maastrichtian–lower Danian planktonic foraminiferal faunas is available for study (see Smit 1977, 1981, 1982, 1990; Keller 1988*b*, 1989*a*, *b*, 1993; Smit *et al.* 1988; Canudo *et al.* 1990; Keller & Benjamini 1991; Keller *et al.* 1994, 1995). In addition, this record has been extensively evaluated for bias related to the hiatus–facies effect, the Zombie effect, and the Signor–Lipps effect (Keller & MacLeod 1994; MacLeod 1996*b*, *c*).

Although planktonic Foraminifera have long been known as one of the primary victims of the K–T mass extinction (Newell 1967), the actual nature of their K–T turnover pattern across this interval has been controversial. Bramlette (1965) argued that the K–T planktonic foraminiferal turnover was abrupt ($\ll$1.0 Ma), though he acknowledged that the deep-sea sections upon which he based his conclusions contained a


A.
Investigator A (Canudo)
Depth in Section (cm)
B.
Investigator B (Masters)
Depth in Section (cm)


C.
Investigator C (Olsson)
Depth in Section (cm)
5%
5%
32%
55%
T
K


D.
Investigator D (Orue-extebarria)
Depth in Section (cm)
18%
7%
15%
57%
3%
T
K

boundary hiatus. Smit (1981, 1982, 1990; see also Smit *et al.* (1988)) also argued that a virtually complete replacement of Cretaceous planktonic foraminiferal species (with one or two exceptions) took place coincident with the K–T boundary and in the space of less than 50 years. On the other hand, Keller and colleagues have documented progressive patterns of planktonic foraminiferal extinction and replacement, beginning below the K–T boundary and continuing into the lowermost Danian in all biostratigraphically complete K–T successions, including many of those studied by Smit (see references above).

To determine the true pattern of planktonic foraminiferal turnover in the K–T boundary stratotype section (El Kef, Tunisia), this succession was recently the subject of a 'blind-test' (Ginsburg 1997) in which four independent investigators examined Cretaceous and Tertiary planktonic foraminiferal samples from the El Kef section that were identified to them only by number (Canudo 1997; Masters 1997; Olsson 1997; Orue-extebarria 1997). Results showed that each investigator identified varying numbers of Cretaceous species disappearing from the section before the K–T boundary as well as reporting other 'Cretaceous' species above the K–T boundary in lowermost Danian sediments (Fig. 5).

Several commentators have concluded that the variability exhibited by the blind test investigators' results precludes resolution of the Smit–Keller controversy (e.g. Ginsburg 1997; Lipps 1997), or that they support the Smit model of catastrophic extinction (e.g. Smit 1994; Ward 1995*a*, *b*). Certainly these results are more variable than the organizers of the blind test expected. They are not, however, without precedent. Zachariasse *et al.* (1978) conducted and published the results of a similar blind test based on samples collected from a Sicilian lower Pliocene section for the purpose of assessing the reproducibility of micropalaeontological data. Although planktonic Foraminifera were not considered in the Zachariasse *et al.* (1978) study, benthic Foraminiferal analyses (organized by M. J. Brolsma) returned results fully consistent with those of the El Kef blind test. These data suggest that much higher degrees of variability between the results of different systematists are present in micropalaeontological (and probably in macropalaeontological) biostratigraphic data than is commonly assumed (see also Smith & Buzas (1986) and Funnell & Swallow (1997)).

As the El Kef blind test results appear consistent with results from comparable reproducibility studies it seems fair to ask how consistent these results are with the original El Kef studies of Keller (1988*a*, *b*; see also Keller (1992)) and Smit (1982; see also Smit *et al.* (1988)). Unfortunately, Smit has not published tables of his species-level biostratigraphic observations. The studies reported by Keller (1988*b*) and Keller *et al.* (1995) contain such tables. (Note: the studies reported by Keller *et al.* (1995) were conducted using an separate suite of samples from those employed in the El Kef blind test.) Table 3 presents the results of a rank-order correlation analysis among the El Kef blind test participants. The rank-order correlation coefficient is insensitive to variations in the faunal lists of different investigators, but does not correct for differences in species concept or nomenclature (e.g. referring to the same morphotype by different names).

Rank-order correlations among the blind test investigators' results range from 0.748 (Orue-extebarria–Canudo) to 0.271 (Masters–Olsson) with a mean of 0.473 (Table 3). Although this mean is slightly larger than the mean correlation between the blind test investigators' results and those of Keller (1988*b*, $\rho = 0.416$), it is decidedly smaller than the mean correlation with the Keller *et al.* (1995) biostratigraphy ($\rho = 0.539$). This discrepancy between Keller's two studies is probably due to differences in the species concepts employed in the two studies as well as variations induced by picking specimens from different samples. These results indicate that Keller's El Kef biostratigraphies are either comparable with that of Keller (1988*a*, *b*) or more similar to those of the blind test investigators' biostratigraphies that those biostratigraphies are among themselves.

In interpreting the El Kef blind test results Smit & Nederbragt (1997) proposed that aggregation of the blind test results would more faithfully represent the true turnover pattern. This is a slight diversion of the purpose of the blind test, which was organized to test the reproducibility of the Smit v. Keller results. A consensus biostratigraphy can be constructed from the blind test investigators' results by representing each species' stratigraphic range to the highest level at which all investigators' results agree (i.e. strict consensus, Fig. 6(**A**)). The consensus biostratigraphy estimates the pattern any individual investigator would be expected to reproduce and, as shown in Fig. 6(**A**), it indicates that local species disappearances are typically observed before, at, and after the El Kef K–T boundary.

The aggregate result of the four El Kef blind test biostratigraphies is shown in Fig. 6(**B**). This

Table 3. *Spearman rank-order correlations among the positions of common taxa in various El Kef blind test biostratigraphies*

	Investigator					
Investigator	Canudo	Masters	Olsson	Orue-extebarria	Keller (1988)	Keller *et al.* (1995)
Canudo	1.000					
Masters	0.301	1.000				
Olsson	0.600**	0.271	1.000			
Orue-etxebarria	0.748**	0.337*	0.460**	1.000		
Keller (1988)	0.441*	0.308*	0.521**	0.392**	1.000	
Keller & Li (1994)	0.758**	0.362*	0.390*	0.644**	0.466**	1.000
Summary statistics:	Mean correlation among blind test participants: 0.453 Mean correlation with Keller (1988): 0.416 Mean correlation with Keller *et al.* (1995): 0.539					

* Significant at $p = 0.05$.
** Significant at $p = 0.01$.

representation is analogous to the results that would be expected if collecting efforts (in this case sample size) were increased four-fold. As expected, Fig. 6(**B**) shows that with increased collecting effort most species' last appearance datum rises; a pattern that is consistent with expectations of the Signor–Lipps effect. Smit & Nederbragt (1997) argued that these results were consistent with recognition of a mass extinction coincident with the K–T boundary. This seems inconsistent with the interpretation by Signor & Lipps' (1982) of their effect. Figure 6(**B**) shows that a minority of the El Kef planktonic foraminiferal fauna disappear at the last Cretaceous sample, and the Signor–Lipps effect predicts that further increases in sample efforts would result in further reductions of observed last appearance datum levels coinciding with the local K–T boundary.

Smit & Nederbragt (1997) also interpreted all but two Cretaceous genera found in the lowermost Tertiary interval in the El Kef section to be 'zombies' reworked from underlying Cretaceous sediments (see also Smit (1982) and Smit *et al.* (1988)). Keller (1997) dissented from this interpretation, preferring to regard this fauna as the remains of K–T survivor populations. Keller's (1997) interpretation is consistent with standard biostratigraphical practice. Indeed, even the critics of Keller's interpretations argue that the observation of planktonic foraminiferal species *below* the K–T boundary provides sufficient evidence to infer their presence as living populations (rather than reworked zombies) throughout the upper Maastrichtian.

Among the blind test participants Olsson (1997) concurred with Smit & Nederbragt (1997), with regard to *Guembelitria cretacea* (Hofker), but also listed *Hedbergella monmouthensis* Olsson and *Hedbergella holmdelensis* Olsson as K–T survivor species. This interpretation is consistent with Liu & Olsson (1992), who argued that these two *Hedbergella* species must be regarded as survivor taxa because all Tertiary planktonic Foraminifera are phylogenetically derived from these species. Berggren & Norris (1997) have recently reviewed the phylogenetics of Tertiary trochospiral taxa and, although these workers accept the hypothesis of derivation from *Hedbergella*, they were unable to demonstrate the existence of any synapomorphies linking the Paleocene planktonic foraminiferal fauna when multiple Cretaceous taxa were used as the outgroup. Most practitioners of phylogenetic analysis (e.g. Nixon & Carpenter 1993; Smith, 1994; P. Forey, pers. comm. 1997) would regard these results as indicating that Paleocene planktonic Foraminifera are neither monophyletic nor uniquely derived from *Hedbergella*. Among the remainder of the blind test participants, Canudo (1997) and Orue-extebarria (1997) agreed with Keller (1997) that their results were consistent with the presence of an expanded K–T planktonic foraminiferal survivor fauna, whereas Masters (1997) felt that the reworking–survivorship question could not be resolved without recourse to intra-specific stable isotopic data (which cannot be obtained from the El Kef planktonic foraminiferal faunas owing to diagenesis).

The K–T ammonite controversy

The best studied K–T ammonite successions are the Bay of Biscay sequences of northern Spain

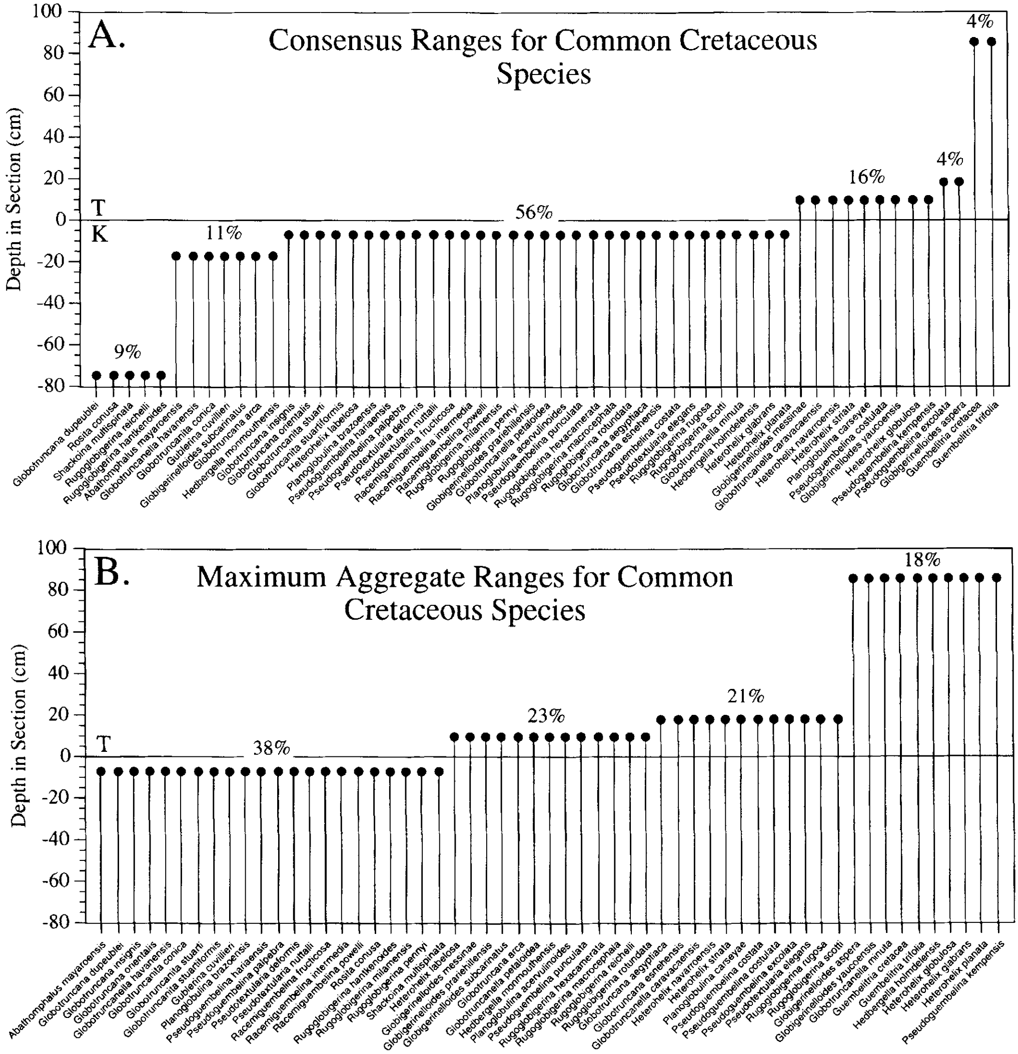


Fig. 6. Alternative summaries of the El Kef blind text data for common species (i.e. those found by two or more of the participants. (**A**) Consensus biostratigraphy. (**B**) Maximum aggregate biostratigraphy. It should be noted that although the maximum aggregate biostratigraphy shows that all Cretaceous species rise at least to the last Cretaceous sample, a distinct minority of these species disappear at this end-Cretaceous horizon. Moreover, the Signor–Lipps effect predicts that this already small percentage will decrease further with additional scrutiny of the blind test samples. (See text for discussion.)

(especially the Zumaya section). Intensive sampling by Ward and coworkers (Ward *et al.* 1986, 1991; Ward 1990; Ward & Kennedy 1993; Marshall & Ward 1996) has shown that 21 ammonite species approach to within 120 m of the local K–T boundary and that five of these rise to the last 30 m of the Maastrichtian interval. These five uppermost Maastrichtian species represent three families; a figure that should be contrasted with the 14, 16, 17, 24, 23, and 27 ammonite families or subfamilies present at the beginning of the Maastrichtian, Campanian, Santonian, Coniacian, Turonian, and Cenomanian stages, respectively (Kennedy 1989; Ward & Kennedy 1993). Chronostratigraphic resolution in the Bay of Biscay successions is such that these final ammonite records are placed 'a few thousand years prior to the K–T boundary event itself *if sedimentation had been continuous*. The latter, unfortunately cannot be determined at this time' (Ward & Kennedy 1993, p. 14, italics in the original). As mentioned above, planktonic foraminiferal faunas from the Zumaya section yield no evidence of the lowermost Danian planktonic foraminiferal biozone.

Marshall & Ward (1996) used stratigraphic confidence intervals (Paul 1982; Strauss & Sadler 1989; Marshall 1991, 1994) to determine whether the observed gradual ammonite extinction pattern in the Zumaya section was consistent with a catastrophic or co-extinction model. Ward and Marshall's test (originally based on Springer (1990); see also Marshall (1995)) postulates that if ammonite extinctions were catastrophic the 50% confidence intervals on each species' last appearance datum should be distributed uniformly about the actual extinction horizon (Marshall 1995, fig. 1). This results in the definition of an interval within which a co-extinction horizon may be placed. If this interval includes the observed stratigraphic range of any species used in the analysis the co-extinction hypothesis is rejected. Provided the co-extinction hypothesis is not rejected the binomial distribution can then be used to contour the indicated interval in an effort to determine the strength of support for particular stratigraphic horizons being consistent with observed data under the co-extinction model. Marshall & Ward's (1996) results indicate that, for the 21 youngest Maastrichtian species the most likely co-extinction horizon lies 8 m below the K–T boundary, and for the five youngest species the most likely co-extinction horizon band includes the K–T boundary. These workers have interpreted their results to suggest a 'sudden and complete catastrophe' (Ward, quoted by Kerr (1996)) and that 'any gradual disappearance must have been on the order of 1000 years' (Marshall paraphrased by Kerr (1996)).

Although the results of the Marshall & Ward (1996) study are interesting, they do not shut the door on alternative interpretations for the ammonite extinction. Springer (1990, p. 515) pointed out that whereas the 50% test is a necessary condition of the co-extinction model, 'it does not constitute proof for simultaneous local extinction'. In interpreting the results of a similar study, Marshall (1995) observed that they were compatible with both simultaneous and gradual extinction models within the interval defined by the 50% test.

Assumptions inherent in the calculation of stratigraphic confidence intervals are also a matter of some concern. Marshall (1994) pointed out that the distribution-free method of confidence interval determination (which was used in the Marshall and Ward (1996) study) assumes uniform collecting effort throughout the sampled interval. However, Ward & Kennedy (1993) noted that a much greater effort was expended in searching for ammonites in the upper 10 m of the Zumaya section than elsewhere. In addition, Marshall (1994) discussed the need for the gap size distribution to be determined to estimate distribution-free confidence intervals. If this gap size distribution is based on the physical separation between fossil occurrence horizons (as in the Marshall & Ward (1996) study), the analysis assumes continuous sediment accumulation at a constant rate throughout the sampled interval and within the zone of range extension defined by the confidence intervals. The many changes in lithology (especially at the K–T boundary; see Ward & Kennedy (1993)) along with biostratigraphic evidence for a substantial (>40 ka) boundary hiatus contradict this assumption.

The best that can be said for the Zumaya ammonite data, which is one of the most thoroughly documented and completely analysed K–T fossil records available, is that if one is prepared to accept some aspects of the local stratigraphic situation at face value (e.g. continuity of sediment accumulation, constancy of sediment accumulation rate), and is willing to assume a co-extinction model, a non-exclusively consistent case can be made for the simultaneous extinction of five ammonite species at the K–T boundary horizon. With respect to the remainder of ammonite evolutionary history, however, associations between ammonite diversity and eustatic sea-level changes show a much more compelling correspondence than those between ammonite extinctions and bolide impacts (House 1989, 1993, fig. 2.4; Wiedemann & Kullman 1996, fig. 5).

Summary

The mass extinction debate has long been seen as a clash between catastrophist and uniformitarian world views. This is unfortunate because, by their very nature, all extinctions represent interruptions in the continuity of evolutionary processes. Thus, all extinctions represent biological catastrophes of a sort. The significance of the Alvarez *et al.* (1980) bolide impact extinction hypothesis is not that it made catastrophism a respectable subject for scientific debate or that it 'solved' the mystery of the dinosaur extinction, but that it provided an illustration of how independent physical evidence for the operation and timing of an extraterrestrial process could be recovered from the stratigraphic record and used to both formulate and test a novel extinction model. In doing this Alvarez *et al.* (1980) moved the question of extraterrestrial forcing out of the non-scientific realm of unconstrained speculation and into the hypothetico-deductive realm of mainstream, actualistic science.

This having been said, it does not necessarily follow that extraterrestrial processes must have played a dominant role in shaping the Earth's physical or biotic environment through the Phanerozoic. The data presented above fail to make a compelling case for such an association as a consistent feature of Earth history. With the possible exception of the Maastrichtian event it seems as though the stage-level extinction record bears little correspondence to the record of bolide impacts. Stage-level correspondences between the extinction record and those of continental flood basalt events and eustatic sea-level changes are much more convincing. Yet all three of these causal mechanisms have thus far failed to provide any unique prior predictions with respect to the nature of species sorting, and patterns of extinction selectivity have failed to reveal the retrospective biotic patterns necessary to make a case for similarity between events known to be associated with similar non-biotic perturbations (e.g. large bolide impacts during the Frasnian, Maastrichtian, and Upper Eocene events, continental flood basalt eruptions during the Tatarian and Norian events). These data suggest that extinction events result from complex multi-causal perturbations, the effects of which are sensitive to the state of the biosphere at the time of the event (see Van Valen 1994; Jablonski 1996; MacLeod 1996*a*; Hallam & Wignall 1997). Consequently, the most likely causal hypothesis supported by these data is that the environmental–biotic effects of a bolide impact (or a major flood basalt eruption) may be magnified or diminished depending on the relative height of eustatic sea-level, distribution and/or size of continents, composition of the atmosphere, temporal proximity to other unrelated environmental perturbations, etc.

In seeking to test various extinction-related hypotheses the nature of palaeontological data must be kept in mind. All of the leading extinction event causal mechanisms make essentially the same predictions not only with regard to their secondary and tertiary environmental effects, but also with respect to the time scales over which these perturbations would be expected to operate. In the overwhelming majority of cases the data from the fossil record are limited in terms of their ability to record short-term biotic and environmental signals as well as the degree to which specific time horizons can be recognized in different stratigraphic successions. Even the inherent time averaging of all fossiliferous deposits operates to make temporal resolutions of less than 10^3–10^4 years all but impossible to achieve using palaeontological data. On the environmental side, the factors that actually limit the geographical or environmental distributions for most modern marine invertebrate species (much less fossil forms, many of which have no close modern analogue) are almost wholly unknown. Archibald (1996*a*, *b*) has had some success formulating biotic tests of specific extinction scenarios using the terrestrial record, but this will be very difficult to duplicate using data from the marine invertebrate fossil record because of our comparative ignorance of the marine environment and its inhabitants.

Owing to this lack of strong, predictive biotic tests or even consistent biotic patterns that might be used to group extinction events into putative causal classes, many palaeontologists have opted for the weaker alternative of demonstrating that under certain assumptions observed data are consistent with predictions of different causal scenarios. However, as Jablonski (1996) correctly argued, the list of secondary and tertiary effects proceeding from the three leading extinction event causal alternatives is so extensive and generalized that virtually any conceivable extinction pattern can be accommodated by each hypothesis. This feature of the extinction debates brings into question exactly what constitutes an 'explanation' for extinction-related phenomena. Extinction tests based on general consistency, as opposed to hypothetico-deductive tests based on unique sets of predictions, can do no more than formulate a list of equally plausible alternatives. If such hypothetico-deductive tests cannot be formulated, or if the data required to apply these tests cannot be collected (or cannot be collected without making assumptions that are not independently verifiable), the question of extinction causal mechanisms will remain unanswered.

If palaeontological data cannot be used to make distinctions between alternative extinction event causal models, what is the appropriate subject for palaeontologists who wish to study the phenomenon of extinction? Palaeontology is inherently about the study of long term biotic patterns, and the effects of extinction (regardless of their cause) are inherently long-term. From an evolutionary perspective the significance of extinction events lies in their effects on subsequent diversification patterns. These effects are manifest at all scales within the phylogenetic–ecological plexus and are now recognized as being integral to our understanding of macroevolutionary phenomena from the level of the individual clade to the level of the entire biosphere. Moreover, different groups appear to respond to extinction events in different ways. Jablonski (1986*a*, *b*) showed that mollusc extinction–survivorship patterns differed during background and mass extinction events. Planktonic Foraminifera, on the other hand, appear to undergo similar morphological–ecological responses to major short-term (K–T), major long-term (Late Eocene) and minor events (Cifelli 1969; Stanley *et al.* 1988; MacLeod 1996*b*; MacLeod *et al.* 1998). In the realm of biogeography, the differing legacies of the K–T extinction for the faunas and floras of different continental platforms are only beginning to be explored (e.g. Wolfe 1987; Jablonski 1995). Given the limitations of palaeontological data, it seems unlikely that the specific causes of most large marine invertebrate extinction events will ever be known in detail. However, by combining the temporal, geographical, and ecological scope of the marine invertebrate fossil record with a new appreciation of the extraordinary diversity of roles extinction events play in mediating evolutionary process, palaeontologists stand at the threshold of an exciting new research programme in which extinction events are used to understand biological, rather than physical, processes. It is this programme that will constitute the most important legacy of the mass extinction debates.

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