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What, If Anything, are Mass Extinctions? [and Discussion]

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What, if anything, are mass extinctions?

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Many phenomena that have traditionally been called 'mass extinctions' are in fact clusters of extinction episodes roughly associated in geological time. This is the case with the latest Ordovician, late Devonian, mid-Cretaceous, latest Cretaceous and Late Eocene–Oligocene extinctions. Several of these clusters are caused, each episode by a different causal factor. Such mass extinctions are then due to the coincidence of various processes in the environment, and they can hardly be considered as individual events. The latest Permian mass extinction, however, is caused by a single process that affected the global ocean–atmosphere system. In the late Permian, the world ocean was full of deposits rich in organic matter, which enhanced nutrient recycling. After oxygen was brought to the sea floor (by whatever process), nutrients began to sink to the sea-bottom, and the resulting nutrient deficiency must have caused mass extinction in the sea. Oxidation of huge amounts of organic matter and associated sediments at the sea bottom must have drawn oxygen from the atmosphere, and the resulting fall in atmospheric oxygen must have contributed to extinctions on land.

1. A historical perspective

'Mass extinctions' is the term traditionally used in geology and palaeontology to denote those relatively short intervals of geological time when rather large and diverse segments of the world's biota underwent extinction. Historically, five mass extinctions have been distinguished: the latest Ordovician, late Devonian, latest Permian, latest Triassic and latest Cretaceous; but several other time intervals often are also interpreted as mass extinction phenomena, especially the Eocene–Oligocene (in the Tertiary) and Cenomanian–Turonian (in the mid-Cretaceous) transitions.

The problem of mass extinctions has only very recently (in the 1980's) become one of the most studied topics in historical geology and biology. The main factors for this are the spectacular and provocative hypotheses that, first, the latest Cretaceous mass extinction was caused by the impact of a huge bolide (Alvarez *et al.* 1980); second, that mass extinctions are periodic (Raup & Sepkoski 1984) and caused by comet showers triggered by an unseen solar companion (Davis *et al.* 1984; Whitmire & Jackson 1984); and third, that the biotic effects of mass extinctions are qualitatively different from all other phenomena in the history of life on Earth (Jablonski 1986*a*). All these exciting hypotheses have become the subject of intense debates and, perhaps more importantly, have stimulated much new and very productive empirical and theoretical research. The problem of mass extinctions, however, is not at all new, and the current controversies fit very well into a history that extends well back into the 19th century.

Ever since Georges Curvier had, in the early 19th century, observed several faunal breaks in the geological strata exposed in the Paris Basin, more or less dramatic changes of the fossil contents in the stratigraphic column were widely regarded as indications of mass extinctions.

This view was particularly developed by Alcide d'Orbigny, who established a whole time-series of such biotic catastrophes punctuating the history of life on Earth. On the other hand, Charles Lyell professed a more gradualist view of species extinction, which he interpreted as a result of individual species sooner or later encountering the conditions to which they could not adapt. In this perceptive, there was no room for mass-extinction phenomena. Charles Darwin adopted a more pluralist viewpoint, and although he suggested that the latest Permian and latest Cretaceous mass extinctions were in reality artefacts of large gaps in the fossil record, he also allowed for profound environmental changes leading to protracted but roughly simultaneous extinction of a large variety of species.

Lyell's view became untenable in the 20th century because the existence of mass-extinction phenomena in the fossil record could no longer be denied and demanded a causal explanation. The opposition was between the concept of each mass extinction being a real catastrophe brought upon life by whatever extraordinary environmental factor, and the notion of mass-extinction phenomena reflecting periods of considerably accelerated extinction rate, perhaps additionally amplified by some gaps in the record. Both these viewpoints were strongly advocated by several scientists. For example, Marshall (1928), Hennig (1932) and Krasovskiy & Shklovskiy (1957) regarded the latest Cretaceous mass extinction as geologically instantaneous and attributed it to a wave of cosmic radiation, whereas Pavlova (1924), Sobolev (1928) and Newell (1967) interpreted it as a prolonged side-effect of the diastrophic cycle. Similarly, Schindewolf (1954) considered the latest Permian mass extinction as an abrupt catastrophe caused perhaps by the explosion of a supernova, whereas Schopf (1974) viewed this biotic phenomenon as extending over several million years in parallel to major changes in geographical distribution of the continental plates.

Such opposition between the catastrophic and the more gradualist interpretations of mass-extinction phenomena has persisted until today, and many of the current debates on mass extinctions can indeed be presented in these terms (see reviews by Jablonski (1986*b*); Hoffman (1989*a*)). This is, however, only one set of contrasting viewpoints on mass extinctions. In a sense, these two interpretations resemble each other in that they both regard mass-extinction phenomena as each being caused by one single factor, most commonly, though not necessarily, all of them by the same factor. The causal agent invoked to explain mass extinctions may be an extraterrestrial impact, or an extraordinary volcanic eruption, or a major palaeogeographical, oceanographic or climatic change, but it is always just one single driving force that is conceived as being the ultimate cause of all extinctions during the time interval interpreted as a mass extinction. I have recently proposed a contrasting perspective, however (Hoffman 1989*a*). I suggested that many mass-extinction phenomena in fact represent clusters of extinction episodes, each of them triggered by another casual factor or set of factors and accidentally aggregated within time periods of a few million years. This would imply that they are not natural phenomena at all, but rather mental constructs of the geologist or palaeontologist. In this view, then, there is no ultimate cause, no process of overwhelming physical environmental or biotic change responsible for many apparent mass extinctions, but merely coincidence on the geological timescale that makes them look like single events in the history of the biosphere.

2. MASS EXTINCTIONS AS CLUSTERS OF EVENTS

There are in fact several examples that clearly demonstrate that what has been traditionally considered as mass-extinction events are actually clusters of minor episodes of extinction. For the late Devonian extinctions, the stratigraphic data collected by Buggisch (1972) show that, although the stromatoporoid-coral reef structures disappeared with the onset of an anoxic régime (Kellwasser Limestone) in the late Frasnian, the pelagic biota survived this crisis and underwent extinction only a couple of conodont zones later. House (1985) demonstrated several extinction pulses among ammonoids. Farsan's (1986) detailed studies on continuous sections of strata deposited in the late Devonian indicate a series of pulses of extinction among shallow-water benthic animals that are spread throughout the entire Frasnian rather than limited solely to its terminal portion. Moreover, Stearn (1987) shows that although the late Devonian reef structures largely disappeared toward the end of the Frasnian, the extinction of reef-building stromatoporoids actually took place only during the early Famennian. The view that unrelated causes triggered two separate pulses of extinction in the late Frasnian is also strongly supported by Sandberg *et al.* (1988).

For the latest Ordovician extinctions, Brenchley (1984) observes that they almost certainly include two separate waves of extinction: one at the latest Caradocian – earliest Ashgillian transition when many trilobite and brachiopod taxa disappeared, and another one several million years later, during the very latest Ashgillian. This second wave of extinction, in turn, extended over a period of some two million years and encompassed several pulses that separately affected graptolites, trilobites and cystoids, brachiopods and rugose corals, once again brachiopods and corals, and finally (perhaps as late as in the earliest Silurian) conodonts.

Also well documented is the aggregate nature of extinctions at the Cenomanian–Turonian and Eocene–Oligocene transitions. For the mid-Cretaceous events, much – though perhaps not yet compelling – evidence has been presented by Kauffman (1984) and Elder (1987) based on very detailed studied on strata deposited in a broad epicontinental sea in North America. For the Eocene–Oligocene extinctions, evidence for a series of minor pulses extending over several million years comes from the open ocean (Corliss *et al.* 1984) as well as from shallow-water benthic biota (Hansen 1987) and terrestrial ecosystems (Prothero 1985).

By now, there is also little doubt that the latest Cretaceous extinctions were not confined to a single holocaust at the very end of the Cretaceous. The catastrophist scheme for this mass extinction holds, at the minimum, that the pelagic plankton and much of terrestrial flora and large vertebrate fauna underwent a tremendous and exactly simultaneous extinction. This claim is debatable, to say the least, because there is clearly a temporal structure to the plankton extinctions (Smit & Romein, 1985; Keller 1987; Lindinger & Keller 1987) and there is no compelling evidence for their simultaneity with the dinosaur extinction in North America (Fastovsky 1987; Rigby *et al.* 1987; Smit *et al.* 1987). Even taking this part of the scheme for granted, however, there is unequivocal evidence for an earlier extinction step that exterminated the rudistid reefs, many ammonites and other marine macroinvertebrates; two further pulses of extinction in the marine realm seem to have taken place still before the terminal Cretaceous episode (Kauffman 1986; Mount *et al.* 1986; Ward *et al.* 1986).

That many mass extinctions are series of extinction episodes does not, of course, prove the point that they are sets of separate events accidentally aggregated in time. Each series of episodes might also be caused by one agent, whose action was extended in time. This is indeed the concept advocated by Stanley (1984, 1988) who argues for global climatic cooling as the main cause of all mass extinctions. On the other hand, it is also put forth by Hut *et al.* (1987) who maintain that because (i) the mid-Cretaceous, latest Cretaceous, and Eocene–Oligocene extinctions have composite nature, (ii) evidence exists for several bolide impacts at the Eocene–Oligocene transition, and (iii) impact causation has been demonstrated for the terminal Cretaceous extinction episode, these three mass extinctions, and most probably also the others, are caused by comet showers. In my opinion, however, a more comprehensive analysis of historical geological data on events associated in time with some mass extinctions suggests coincidence of independent processes as a more, or at least equally, likely explanation.

There is indeed evidence for several impacts at the Eocene–Oligocene transition (microtektite fields, iridium anomalies), but their association with extinction episodes is at best tenuous. As clearly visible in the diagrams provided by Hut *et al.* (1987), some impacts are not associated with extinction and some extinction episodes are not associated with impact fingerprints. On the other hand, evidence for global climatic cooling appears fully convincing (Keller 1983; Stanely 1984; Prothero 1985; Hansen 1987). Moreover, extraordinary volcanic activity took place during this time interval (Kennett *et al.* 1985). There is no reason to believe that all these extraterrestrial, climatic and geodynamic events were causally related to each other rather than that they merely coincided within the same several-million-year-long time interval.

The case for the terminal Cretaceous impact is by now very strong. The inference made originally from the iridium anomaly and corroborated later by osmium isotopes, shocked quartz, and possible soot enrichment (see reviews by Jablonski (1986*b*); Hoffman (1989*a*)) is currently supported by new lines of evidence. Rhodium isotope data clearly indicate extraterrestrial, rather than crustal, origin of this element in the Cretaceous–Tertiary boundary clay (Bekov *et al.* 1988), cathodoluminescence analysis of the shocked quartz grains in this clay corroborates the postulate of their non-volcanic nature (Owen & Anders 1988), possible tsunami deposits occur as predicted at the iridium-enriched Cretaceous–Tertiary boundary horizon (Bourgeois *et al.* 1988), and the concentration of apparent soot is much greater than previously estimated and seems to reach a maximum exactly at the iridium peak (Wolbach *et al.* 1988). On the other hand, however, Deccan-trap volcanism – which has also been implicated as the ultimate cause of the terminal Cretaceous extinctions (Officer *et al.* 1987; Hallam 1987) – is now known to have antedated the impact and lasted no more than a million years (see Courtillot *et al.* 1988; Duncan & Pyle 1988). Thus it could not be caused by the impact but its environmental effects could contribute to the extinctions. Neither impact nor volcanic eruptions, however, could have been responsible for destruction of the rudistid reefs, which had begun a couple of million years earlier. The Cretaceous–Tertiary transition, moreover, is the time of a major sea-level fall (Hallam 1984; Haq *et al.* 1987). This process, again, does not seem to be causally related to either impact or volcanic activity.

Historical geological data are much worse for the other clusters of extinction episodes that are traditionally called mass extinctions, but the very existence of empirical evidence to support several different causal explanations in each case suggests that they also might represent coincidence on the geological timescale of a variety of processes. Such coincidence, in fact, is not at all extraordinary or unlikely. Consider the number of various types of physical environmental event that might lead to substantial, though not necessarily mass, extinctions. At least five types of event immediately come to the mind: large bolide impacts, sustained and unusually intense volcanic activity, global climatic change, major sea-level fluctuations, and oceanic anoxic events. Provided that events of each kind occur at random in geological time and with the average frequency of one event per 50 Ma – which seems to be a reasonable estimate – there is a greater than 50% chance that, within a period of 100 Ma, two or more different events will roughly coincide in time (that is, will occur during a 2 Ma time interval); and there is almost certainty that coincidence during a 4 Ma time interval will take place within a period of 250 Ma (Hoffman 1989*b*).

I submit that many mass extinctions may actually be caused each by a variety of factors that by pure chance happened to roughly coincide within time intervals of 2–4 Ma. Should this hypothesis withstand the scrutiny of empirical testing, these mass extinctions could not be rightly called mass extinctions at all, for they would then represent artificial collections of causally independent phenomena instead of causally coherent events. The latest Cretaceous extinctions, for example, may perhaps include a mass-extinction phenomenon – if the terminal Cretaceous event is indeed attributable to one environmental process (but even this assertion is far from being firmly established) – the preceding steps of extinction, however, may only by chance appear related to this phenomenon. The Eocene–Oligocene extinctions may not include any mass extinction at all, but only a set of minor episodes of extinction.

3. A TRUE MASS EXTINCTION

This is not to say, however, that all the traditionally recognized mass extinctions comprise several independent but accidentally aggregated events. The latest Permian extinctions among marine animals that could be fossilized were undoubtedly the most severe in the Phanerozoic. Because of a huge marine regression and consequent extraordinarily intense erosion, however, the geological record at the Permo-Triassic transition is so poor that the temporal pattern of extinctions cannot be firmly established. This record nevertheless bears strong evidence for a change in the world ocean–atmosphere system, which appears to have been much more dramatic than any other in the Phanerozoic. If our current causal interpretation of this phenomenon is correct, then the latest Permian biotic change fully deserves to be called 'mass extinction' because the record seems to indicate a process which must have caused a true mass extinction.

The evidence comes from studies of stable carbon and oxygen isotopic changes in seawater composition during the latest Permian (Gruszczyński *et al.* 1989; Małkowski *et al.* 1989). Carbon isotopic composition (that is, the ratio between the light and the heavy isotopes of carbon, which is usually shown in 'delta' (δ) notation, as deviations from a certain standard) varies between major carbon reservoirs in the Earth's system: organic carbon in the biosphere and its products, carbonate sediments, the ocean, and the atmosphere. Therefore a change in the oceanic carbon isotopic composition must indicate either a change in fluxes between the reservoirs or a change in juvenile carbon input to the system controlled by degassing of the Earth's mantle. Because of the very rapid cycling of carbon both within and between the ocean and the atmosphere, major changes in stable carbon isotopic composition of seawater must be recorded everywhere in the ocean, unless we deal with a very extreme and unusual environment where some local processes overwhelm the global ones. As indicated by analysis of carbon isotopes in the calcite of productacean brachiopod shells from uppermost Permian outer shelf deposits of west Spitsbergen, which had at the time free and wide connections with the world ocean, seawater was relatively enriched in the heavy isotope of carbon during the late Permian (δ^{13}C of approximately +4‰). Subsequently, however, its carbon isotopic composition rapidly shifted towards still heavier values (δ^{13}C of more than +7‰) and then declined down to very light values (δ^{13}C of less than −3‰). This dramatic drop in the oceanic carbon isotopic values took place within no more, but very likely less, than a few million years. It is roughly paralleled by a similar decline in the oxygen isotopic composition of seawater. This pattern is generally consistent with observations made in other geological sections (Holser & Magaritz 1987) and represents the most spectacular change observed thus far in the geological record.

Because of the nature of the isotope fractionation processes, which cause differences in carbon isotopic composition between the reservoirs, this change must be explained by shifts of carbon masses enriched in the light isotope (cf. Hoefs 1987). Knowing the initial δ^{13}C values of the late Permian ocean and assuming its total carbon contents to have been comparable to the current value, one can easily calculate that the observed decline in δ^{13}C can only be plausibly explained by rapid input to seawater of huge amounts of oxidized organic carbon; these amounts are approximately equal to the total carbon contents in the ocean and almost two orders of magnitude greater than the present standing crop of the entire biosphere. This interpretation is indeed consistent also with the parallel decline in oxygen isotope values because such a massive oxidation would preferentially involve the light isotope of oxygen and cause its disproportionate enrichment in dissolved carbonates in seawater. The shape of the δ^{13}C curve in the preceding times, in turn, implies removal of great amounts of organic carbon from the ocean–atmosphere system.

The best explanation for the whole pattern is that deposits rich in organic matter accumulated in the Permian at the sea floor, and the rate of this accumulation rapidly increased in the late Permian. This is possible solely under strongly reducing conditions in the absence of such deepwater circulation as it exists today in the ocean, for it would bring oxygen down to the bottom and prevent organic matter from accumulating. Thus the oceanographic situation must have been fundamentally different from the one observed today. In the latest Permian, however, some geodynamic process brought oxygen down to the sea bottom and hence the amassed organic carbon underwent rapid oxidation and uptake by seawater (Gruszczyński *et al.* 1989).

This process must have had tremendous and detrimental consequences for the marine biosphere (Małkowski *et al.* 1989). Under reducing conditions, phosphorus and nitrogen recycling is enhanced because they are liberated from decaying organic matter and return to seawater; this is why upwelling waters are so rich in these nutrients. Thus the main limiting factors on the growth of the marine biosphere were relaxed during the late Permian. The subsequent development of oxidizing conditions at the sea bottom dramatically changed the situation because under such conditions both phosphorus and nitrogen sink at the sea floor, as it is observed presently. Thus the massive oxidation of organic matter that accumulated previously at the sea bottom removed large amounts of nutrients from seawater. The resulting nutrient deficiency must have led to a collapse of the marine ecosystem and hence to a mass extinction in the sea. At the same time, massive oxidation of organic carbon and the associated chemical compounds (primarily iron and manganese sulphides) must have drawn oxygen from the atmosphere. The resulting drop in atmospheric oxygen levels most likely led to extinctions among land biotas.

Thus the latest Permian was the time of a change in the Earth's system that must have caused a mass extinction. Given the poor stratigraphic resolution at the Permo-Triassic transition, it is not known whether or not all the extinctions occurred simultaneously with the observed carbon and oxygen isotopic event; nor is it known what happened during the earliest Triassic, in the aftermath of the latest Permian paleoceanographic change. The Permo-Triassic mass extinction, however, differs from the latest Cretaceous one because we know that various processes were at work during the latter time interval. And it dramatically differs from events during the latest Ordovician, late Devonian, mid-Cretaceous and Eocene–Oligocene transition because it is known that all of these phenomena were in fact clusters of episodes.

4. Conclusions

Many phenomena that have been traditionally called 'mass extinctions' are in fact sets of lesser episodes of extinction. These lesser episodes, moreover, often seem to be each caused by another environmental factor. The causal plexus of such mass extinctions involves, then, coincidence of various processes in the physical environment of life, these processes happening to co-occur roughly in time (on the geological timescale). The Permo-Triassic mass extinction, however, seems to be different from the others in that it may indeed be caused by one, although not truly catastrophic, process of environmental change that affected the global ocean–atmosphere system.

References

Alvarez, L. W., Asaro, F., Michel, H. V. & Alvarez, W. 1980 Extraterrestrial cause for the Cretaceous–Tertiary extinction. *Science, Wash.* **208**, 1095–1108.

Bekov, G. I., Letokhov, V. S., Radaev, V. N., Badyukov, D. D. & Nazarov, M. A. 1988 Rhodium distribution at the Cretaceous/Tertiary boundary analysed by ultrasensitive laser photoionization. *Nature, Lond.* **332**, 146–148.

Bourgeois, J., Hansen, T. A., Wiberg, P. L. & Kauffman, E. G. 1988 A tsunami deposit at the Cretaceous–Tertiary boundary in Texas. *Science, Wash.* **241**, 567–570.

Brenchley, P. J. 1984 Late Ordovician extinctions and their relationship to the Gondwana glaciation. In *Fossils and climate* (ed. P. J. Brenchley), pp. 291–316. Chichester: Wiley.

Buggisch, W. 1972 Zur Geologie und Geochemie der Kellwasserkalke und ihrer begleitenden Sedimente (unteres Oberdevon). *Abh. hess. Landesamt Bodenforsch.* **62**, 1–68.

Corliss, B. H., Aubry, M. P., Berggren, W. A., Fenner, J. M., Keigwin, L. D. & Keller, G. 1984 The Eocene/Oligocene boundary event in the deep sea. *Science, Wash.* **226**, 806–810.

Courtillot, V., Feraud, G., Maluski, H., Vandamme, G., Moreau, M. G. & Besse, J. 1988 Deccan flood basalts and the Cretaceous/Tertiary boundary. *Nature, Lond.* **333**, 843–846.

Davis, M., Hut, P. & Muller, R. A. 1984 Extinction of species by periodic comet showers. *Nature, Lond.* **308**, 715–718.

Duncan, R. A. & Pyle, D. G. 1988 Rapid eruption of the Deccan flood basalts at the Cretaceous/Tertiary boundary. *Nature, Lond.* **333**, 841–843.

Elder, W. P. 1987 The paleoecology of the Cenomanian–Turonian (Cretaceous) stage boundary extinctions at Black Mesa, Arizona. *Palaios* **2**, 24–40.

Farsan, N. M. 1986 Faunenwandel oder Faunenkrise? Faunistische Untersuchung der Grenze Frasnium–Famennium im mittleren Südasien. *Newsl. Stratigr.* **16**, 113–131.

Fastovsky, D. 1987 Paleoenvironments of vertebrate-bearing strata during the Cretaceous–Paleogene transition, eastern Montana and western North Dakota. *Palaios* **2**, 282–295.

Gruszczyński, M., Hałas, S., Hoffman, A. & Małkowski, K. 1989 A brachiopod calcite record of the oceanic carbon and oxygen isotopic shifts at the Permo/Triassic transition. *Nature, Lond.* **337**, 64–68.

Hallam, A. 1984 Pre-Quaternary sea-level changes. *A. Rev. Earth planet. Sci.* **12**, 205–243.

Hallam, A. 1987 End-Cretaceous mass extinction event: argument for terrestrial causation. *Science, Wash.* **238**, 1237–1242.

Hansen, T. A. 1987 Extinction of Late Eocene to Oligocene molluscs: relationship to shelf area, temperature changes, and impact events. *Palaios* **2**, 69–75.

Haq, B. U., Hardenbol, J. & Vail, P. R. 1987 Chronology of fluctuating sea levels since the Triassic. *Science, Wash.* **235**, 1156–1167.

Hennig, E. 1932 *Wege und Wesen der Paläontologie*. Berlin: Borntraeger.

Hoefs, J. 1987 *Stable isotope geochemistry*, 3rd edn. Berlin: Springer.

Hoffman, A. 1989*a* Mass extinctions: the view of a sceptic. *J. geol. Soc. Lond.* **146**, 21–35.

Hoffman, A. 1989*b* Changing paleontological views on mass extinction phenomena. In *Mass extinctions: processes and evidence* (ed. S. K. Donovan). London: Belhaven Press. (In the press.)

Holser, W. T. & Magaritz, M. 1987 Events near the Permian–Triassic boundary. *Mod. Geol.* **11**, 155–179.

House, M. R. 1985 Correlation of mid-Palaeozoic ammonoid evolutionary events with global evolutionary perturbations. *Nature, Lond.* **313**, 17–22.

Hut, P., Alvarez, W., Elder, W. P., Hansen, T., Kauffman, E. G., Keller, G., Shoemaker, E. M. & Weissman, P. R. 1987 Comet showers as a cause of mass extinctions. *Nature, Lond.* **329**, 118–126.

Jablonski, D. 1986*a* Background and mass extinctions: the alternation of macroevolutionary regimes. *Science, Wash.* **231**, 129–133.

Jablonski, D. 1986*b* Causes and consequences of mass extinctions: a comparative approach. In *Dynamics of extinction* (ed. D. K. Elliott), pp. 183–230. New York: Wiley.

Kauffman, E. G. 1984 The fabric of Cretaceous marine extinctions. In *Catastrophes and Earth history* (ed. W. A. Berggren & J. A. Van Couvering), pp. 151–246. Princeton University Press.

Kauffman, E. G. 1986 High-resolution event stratigraphy: regional and global Cretaceous bio-events. In *Global bio-events* (ed. O. H. Walliser), pp. 279–335. Berlin: Springer.

Keller, G. 1983 Biochronology and paleoclimatic implications of middle Eocene to Oligocene planktic foraminiferal faunas. *Mar. Micropaleont.* **7**, 463–486.

Keller, G. 1987 Prolonged biotic stress and species survivorship across the Cretaceous–Tertiary boundary. *Abstr. Progm. geol. Soc. Am.* **19**, 724.

Kennett, J. P., Borch, C. van der, Baker, P. A., Barton, C. E., Boersma, A., Cauler, J. P., Dudley, W. C., Gardner, J. V., Jenkins, D. G., Lohman, W. H., Martini, E., Merrill, R. B., Morin, R., Nelson, C. S., Robert, C., Srinivasan, M. S., Stein, R., Takeuchi, A. & Murphy, M. G. 1985 Paleotectonic implications of increased late Eocene–early Oligocene volcanism from South Pacific DSDP sites. *Nature, Lond.* **316**, 507–511.

Krasovskiy, V. I. & Shklovskiy, I. S. 1957 The possible influence of explosions of supernovae on the evolution of life on Earth. (In Russian.) *Dokl. Akad. Nauk SSSR* **116** (2), 197–199.

Lindinger, M. & Keller, G. 1987 Stable isotope stratigraphy across the Cretaceous/Tertiary boundary in Tunisia: evidence for a multiple extinction mechanism? *Abstr. Progm. geol. Soc. Am.* **19**, 747.

Małkowski, K., Gruszczyński, M., Hoffman, A. & Hałas, S. 1989 Oceanic stable isotope composition and a scenario for the Permo-Triassic crisis. *Hist. Biol.* **2**. (In the press.)

Marshall, H. T. 1928 Ultra-violet and extinction. *Am. Nat.* **62**, 165–187.

Mount, J. F., Margolis, S. V., Showers, W., Ward, P. & Doehne, E. 1986 Carbon and oxygen isotope stratigraphy of the Upper Maastrichtian, Zumaya, Spain: a record of oceanographic and biologic changes at the end of the Cretaceous Period. *Palaios* **1**, 87–91.

Newell, N. D. 1967 Revolutions in the history of life. *Spec. Pap. geol. Soc. Am.* **89**, 63–91.

Officer, C. B., Hallam, A., Drake, C. L. & Devine, J. D. 1987 Late Cretaceous and paroxysmal Cretaceous/Tertiary extinctions. *Nature, Lond.* **326**, 143–149.

Owen, M. R. & Anders, M. H. 1988 Evidence from cathodoluminescence for non-volcanic origin of shocked quartz at the Cretaceous/Tertiary boundary. *Nature, Lond.* **334**, 145–147.

Pavlova, M. V. 1924 *The causes of extinctions of animals in the last geological period*. (In Russian.) Moscow: Nauka.

Prothero, D. R. 1985 North American mammalian diversity and Eocene–Oligocene extinctions. *Paleobiology* **11**, 363–388.

Raup, D. M. & Sepkoski, J. J. 1984 Periodicity of extinctions in the geological past. *Proc. natn. Acad. Sci. U.S.A.* **81**, 801–805.

Rigby, J. K. Jr., Newman, K. R., Smit, J., Kaars, S. van der, Sloan, R. E. & Rigby, J. K. 1987 Dinosaurs from the Paleocene part of the Hell Creek Formation, McCone County, Montana. *Palaios* **2**, 296–302.

Sandberg, C. A., Ziegler, W., Dreesen, R. & Butler, J. L. 1988 Late Frasnian mass extinction: conodont event stratigraphy, global changes, and possible causes. *Courier Forschungsinst. Senckenberg* **102**, 263–307.

Schindewolf, O. H. 1954 Über die möglichen Ursachen der grossen erdgeschichtlichen Faunenschnitte. *Neues Jb. Geol. Paläont. Mh.* **1954**, 457–465.

Schopf, T. J. M. 1974 Permo-Triassic extinctions: relation to seafloor spreading. *J. Geol.* **82**, 129–143.

Smit, J., Kaars, W. A. van der & Rigby, J. K. Jr. 1987 Stratigraphic aspects of the Cretaceous–Tertiary boundary in the Bug Creek area of eastern Montana, USA. *Mém. Soc. géol. Fr.* (N.S.) **150**, 53–74.

Smit, J. & Romein, A. J. T. 1985 A sequence of events across the Cretaceous–Tertiary boundary. *Earth planet. Sci. Lett.* **74**, 155–170.

Sobolev, D. N. 1928 Earth and life. On the causes of extinction of organisms. (In Russian.) Kiev.

Stanley, S. M. 1984 Marine mass extinctions: a dominant role for temperature. In *Extinctions* (ed. M. H. Nitecki), pp. 69–117. Chicago University Press.

Stanley, S. M. 1988 Paleozoic mass extinctions: shared patterns suggest global cooling as a common cause. *Am. J. Sci.* **288**, 334–352.

Stearn, C. W. 1987 Effect of the Frasnian–Famennian extinction event on the stromatoporoids. *Geology* **15**, 677–679.

Ward, P., Wiedmann, J. & Mount, J. F. 1986 Maastrichtian molluscan biostratigraphy and extinction patterns in a Cretaceous/Tertiary boundary section exposed at Zumaya, Spain. *Geology* **14**, 899–903.

Whitmire, D. P. & Jackson, A. A. 1984 Are periodic mass extinctions driven by a distant solar companion? *Nature, Lond.* **308**, 713–715.

Wolbach, W. S., Gilmour, I., Anders, E., Orth, C. J. & Brooks, R. R. 1988 Global fire at the Cretaceous–Tertiary boundary. *Nature, Lond.* **334**, 665–669.

Discussion

P. W. King (*Department of Biology, University College London, U.K.*). Would it not be much better in plotting a graph of last appearance against time to use a natural genetic unit, i.e. the species, rather than the family, because the amount of difference between species in a family may differ considerably from one taxonomic group to another, and because different families are not equal to each other as they include very different numbers of species?

A. Hoffman. Yes, it would be much better to employ species as the unit of quantitative analysis of extinction patterns. This is often done in studies of local-scale patterns. In global-scale studies, however, the use of species-level data must be very seriously hampered by the notorious vagaries of the fossil record, which make such data extremely biased and unreliable. Family-level data have therefore been customarily accepted as a compromise between biological meaningfulness and palaeontological reliability.