

since protonation gives the ring a net positive charge. The higher histidyl imidazole pK values of Hb are a consequence of more negative microenvironments around Hb's histidyls. These more negative microenvironments stabilize the binding of protons to the imidazole rings.

These data have several interesting messages for the student of molecular evolution. First, they indicate that pH changes of around one-half pH unit are a strong selective factor leading to adaptive changes in protein amino acid sequence. Thus, as in the case of temperature and pressure, we can begin to understand more precisely what are the thresholds of perturbation that lead to adaptive evolution in proteins. Second, the comparisons of Hb and Mb show that many sites along the protein sequence can be important in establishing the correct microenvironment for residues that are critical to function, e.g. imidazole residues. It bears noting, in fact, that the adaptive adjustment in pK values that is possible by modification of the microenvironments of key amino acid residues is a mechanism

not only of importance in protein evolution, but one that is coming to be employed by 'protein engineers' in their efforts to adapt proteins better for particular technological feats¹⁷. Without an appreciation of the effects that subtle alterations in protein surface charge and polarity can have on the key amino acid residues involved in binding, catalysis or buffering, one might fail to comprehend the adaptive significance of amino acid substitutions that occur at other loci in the protein molecule. The discovery that several amino acid substitutions may be needed to adjust the pK value of a single amino acid residue shows that protein evolution is a concerted process in which substitutions that at first glance might seem to have no apparent significance may, in fact, play critical albeit subtle roles in fine-tuning function for particular conditions of pH, temperature or pressure.

References

- 1 McDonald, J.F. (1983) *Annu. Rev. Ecol. Syst.* 14, 77-102
- 2 Koehn, R.K., Zera, A.J. and Hall, J.G. (1983) in *Evolution of Genes and Proteins* (Koehn, R.K. and Nei, M., eds), pp. 115-136. Sinauer
- 3 Jaenicke, R. (1981) *Annu. Rev. Biophys. Bioeng.* 10, 1-67
- 4 Hochachka, P.W. and Somero, G.N. (1983) *Biochemical Adaptation*, Princeton
- 5 Place, A.R. and Powers, D.A. (1979) *Proc. Natl Acad. Sci. USA* 76, 2354-2358
- 6 Yancey, P.H. and Somero, G.N. (1978) *J. Comp. Physiol.* 125, 129-134
- 7 Swezey, R.R. and Somero, G.N. (1982) *Biochemistry* 21, 4496-4503
- 8 Swezey, R.R. and Somero, G.N. (1985) *Biochemistry* 24, 852-860
- 9 Siebenaller, J.F. and Somero, G.N. (1978) *Science* 201, 255-257
- 10 Seibenaller, J.F. and Somero, G.N. (1979) *J. Comp. Physiol.* 129, 295-300
- 11 Siebenaller, J.F. (1984) *J. Comp. Physiol.* 154, 443-448
- 12 Graves, J.E. and Somero, G.N. (1982) *Evolution* 36, 97-106
- 13 Siebenaller, J.F. (1984) *Biochim. Biophys. Acta* 786, 161-169
- 14 Matthew, J.C., Hanania, G.I.H. and Gurd, F.R.N. (1979) *Biochemistry* 18, 1919-1928
- 15 Matthew, J.C., Hanania, G.I.H. and Gurd, F.R.N. (1979) *Biochemistry* 18, 1928-1936
- 16 Somero, G.N. (1986) *Am. J. Physiol.* 251, R197-R213
- 17 Thomas, P., Russell, A.J. and Fersht, A.R. (1985). *Nature* 318, 375-376
- 18 Somero, G.N. (1983) *Comp. Biochem. Physiol.* 76A, 621-633
- 19 Graves, J.E., Rosenblatt, R.H. and Somero, G.N. (1983) *Evolution* 37, 30-37

Local extinctions of populations, species or groups of species in a particular area are commonly observed by biologists. There are also historical records of the total extinction of single species such as the Dodo, the Great Auk and the Tasmanian Wolf. Mass extinctions are on a much larger scale, and their study is based on the fossil record. The aims of this review are to explore the nature of mass extinctions and their evolutionary significance. The key questions are: what is mass extinction, what are the causes of mass extinctions, do mass extinctions follow a regular pattern, and how do mass extinctions affect our understanding of evolutionary processes?

A mass extinction is said to have occurred if an excessively large number of taxa became extinct within a geologically short interval of time. Some mass extinction events have gained notoriety because of the particular groups that became extinct, such as the event

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The Evolutionary Significance of Mass Extinctions

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at the boundary between the Cretaceous and Tertiary periods (the 'K-T event'), 65 million years ago, when the dinosaurs disappeared. In fact, the extinction of the dinosaurs was probably less remarkable, in terms of the numbers or diversity of species disappearing, than the extinctions at that time amongst the marine plankton.

Various suggestions have been made about how the occurrence and magnitude of mass extinctions can be quantified. A first impression can be obtained simply by plotting the numbers of species, genera or families of a fossil group against a time axis. In general, the total numbers of extant taxa have risen through time. Mass extinctions have often been identified as

times when there was a drop in total numbers (Fig. 1).

A simple statistical test for mass extinctions was proposed by Raup and Sepkoski¹, who calculated 'extinction rates' for each segment of geological time. The extinction rate is simply the numbers of species, or families, that died out every million years. Raup and Sepkoski assumed a constant rate of 'background extinction', punctuated by occasional high 'mass extinction' rates. The mass extinctions were defined as those extinction rate values that were much higher than the overall trend (in statistical terms, 'outliers' from the trend). The outliers were identified by calculating a linear regression of extinction rate versus time, and ident-

Table 1. Major animal groups affected (total extinction or severe reduction in diversity) by the five principal mass extinction events.

Late Ordovician
trilobites
articulate brachiopods
nautiloid cephalopods
crinoids
Late Devonian
trilobites
articulate brachiopods
cephalopods
stromatoporoids
ostracodes
rugose and tabulate corals
crinoids
placoderm fishes
End of Permian
rostronch†
trilobites†
blastoids†
brachiopods
cephalopods
corals
crinoids
terrestrial reptiles
Late Triassic
brachiopods
cephalopods
gastropods
bivalves
sponges
marine reptiles
terrestrial reptiles
freshwater fish
insects
Cretaceous–Tertiary boundary
foraminifera
acritarchs
coccolithophorids
bryozoans
sponges
corals
crinoids
gastropods
bottom-living bivalves
echinoids
ammonites†
belemnites†
plesiosaurs†
mosasaurs†
pterosaurs†
dinosaurs†
marsupials

† Groups which became totally extinct.

ifying those points that lay outside the 95% confidence envelope of the regression line (Fig. 2). There are problems with this approach, in particular since there is not a complete normal distribution of extinction rates – negative rates are impossible². Adjustments to produce a normal distribution, by logarithm and square root transformations, then failed to show up the mass extinction outliers².

In general however, it is agreed that a mass extinction should have three characteristics³. It should be brief (the whole event should last for a short time in geological terms),

it should have considerable breadth (in terms of the groups of plants and animals that die out, and in terms of the environments affected), and it should be associated with elevated extinction rates.

The major mass extinctions

The largest mass extinction occurred 245 million years ago, at the end of the Permian period. Many major groups disappeared both in the sea and on land (Table 1), and it has been estimated that up to 95% of all species died out^{1,3–6}. There were four other smaller mass extinctions spaced over 500 million years or so (Fig. 2)^{1,3–6}. At the end of the Ordovician (440 million years ago), and near the end of the Devonian (370 million years ago), two events of similar magnitude each saw the extinction of about 100 families of marine organisms. At the end of the Triassic (210 million years ago), further marine groups as well as insects, freshwater fish and reptiles on land disappeared in a mass extinction that equalled in magnitude the K–T event^{3–7}.

The K–T event was the most recent of the five major mass extinctions. On land, only certain groups seem to have been affected, and in general, land plants show very little change in abundance and diversity at this time. Likewise, snails, bivalves, insects, freshwater fish, frogs, salamanders, lizards, snakes, birds and mammals show no particular drop in diversity or elevated extinction rate at the K–T boundary^{6,8,9}. Amongst mammals, only the marsupials were really affected, with two of the three families that existed in the latest Cretaceous dying out². Nineteen families of dinosaurs and two families of pterosaurs are known from the Maastrichtian (the last geological stage of the Cretaceous), and these all disappeared. However, it has been suggested^{8,10} that many of these families died out before the K–T boundary, during the 8–9 million years of the Maastrichtian. In the sea, many major groups of animals died out at the end of the Cretaceous, including the swimming molluscs and the large marine reptiles, and family diversity of other marine groups was much decreased (Table 1)^{6,9}. There were also major extinctions and reduc-

tions of diversity in the microplankton¹¹; for instance, forams declined from 36 species in the latest Maastrichtian to only one in the succeeding Danian.

These five events are the best known mass extinctions. Many other smaller ones have been identified in the Cambrian, Jurassic, Cretaceous and Tertiary, but most of these affected only restricted groups of plants and animals, or were limited geographically. In general, at any mass extinction certain groups are heavily affected and others are relatively unaffected. However, it is very hard to discern simple ecological or physiological reasons for the disappearance of some groups and the persistence of others.

What causes mass extinctions?

Most suggested causes for mass extinctions have applied to the K–T event alone. The two main current explanations for the K–T event (including the extinction of the dinosaurs) are the 'gradualist' ecological succession model of Leigh Van Valen and others^{10,12–14} and the 'catastrophist' extraterrestrial impact model of Luis Alvarez and others^{15–18}. The gradualist viewpoint proposes that the extinction of the dinosaurs, and the radiation of the mammals at the K–T boundary, was the result of gradual climatic change, and of competition between dinosaurs and mammals. The catastrophist models generally call for the impact of a giant asteroid, or a shower of comets, that triggers the spread of a huge dust cloud or the emission of poisonous gases.

There is considerable evidence^{3,8–18} for both explanations: mainly palaeontological and geological for the ecological succession model, and mainly geochemical and astrophysical for the extraterrestrial impact model. A catastrophist would envisage that the main extinction event lasted less than, say, a year, while a gradualist would regard the time-span as somewhat more than, say, 1000 years. At present, the dating of rocks by radiometric means, and the record of magnetic changes in the earth's crust, cannot approach the kind of resolution needed to distinguish these time-spans: although very different on a biological time-scale,

they are both still geologically 'instantaneous'. Nevertheless, in future it may be possible to determine short time-spans like these by means of, say, the use of annual bands in cyclic sedimentation.

Do mass extinctions occur in cycles?

One of the most important recent suggestions about mass extinctions is that their occurrence may be cyclical. They may or may not have a regular periodicity, and the ultimate causes may be terrestrial or extraterrestrial. Cyclicity raises the possibility of identifying one kind of explanation for all mass extinctions through time.

Although geologists had proposed in the 1960s that certain earth processes followed regular or irregular cycles, the idea of cyclicity in mass extinctions gained widespread attention amongst biologists only in 1984 when Raup and Sepkoski¹⁹ published a new analysis of the mass extinctions of marine animals, which apparently showed a periodic pattern (Fig. 3). Every 26–30 million years, there was a mass extinction event. This study involved time series analysis of extinction rate data to seek temporal regularities in the fluctuations, and the testing of the identified peaks of extinction against the predicted timings of peaks. The suggestion of periodicity in the history of life^{6,19–21} excited wide interest, since such a high-order pattern would most probably be controlled by some extraterrestrial factor.

Several authors immediately took up Raup and Sepkoski's suggestion that the ultimate cause might be extraterrestrial, and three main ideas arose. One is that a hypothetical companion star of the Sun (called Nemesis) follows a highly eccentric orbit with a periodicity of 30 million years and disturbs the Oort cloud (inner comet cloud), sending a shower of comets hurtling towards the Earth every 30 million years^{22,23}. The second is that the Solar System oscillates through the galactic plane with a semi-period of 30 million years and scatters Oort cloud comets into the terrestrial zone^{20,24,25}. The third is that there is an as yet undiscovered 'planet' lying beyond Pluto in the outer reaches of the solar system²⁶; it follows a vast eccentric orbit, and

every 30 million years it enters the Oort cloud, thus triggering a comet shower towards the Earth. These and other striking astronomical theories are still controversial²⁷.

There have been strong criticisms of the idea of periodic mass extinctions. There are problems with the data, both in terms of the accuracy of the stratigraphic record and of the exact set of fossil distribution data that is used for analysis. More accurate identification of the distributions in time of each group is needed, and more accurate dating of the rocks is also necessary²⁸. Some have argued that the cyclicity does not even exist, that it is an artefact of the mathematical treatment and that the 'cycles' are really random and independent of each other^{29,30}. Much more work is needed before any consensus can be reached^{6,7,31}.

Mass extinctions and evolution

In evolutionary terms, extinction is not a remarkable aberration – species disappear continually and new species appear throughout the record of the history of life. One common interpretation of mass extinction periods is that they are just intensified versions of the normal rate of 'background' extinction^{2,7,8,10–14,24–31,33}. Another interpretation is that mass extinctions are essentially random, produced by some freak catastrophe, and the species that die out are simply unlucky^{9,15–18}.

Jablonski has outlined a third view^{3,32}. He argues that mass extinctions are both quantitatively and qualitatively different from background extinctions, and also that they are not entirely random in their effects. His evidence is from the fossil records of marine bivalves and gastropods from North America during the last 16 million years of the Cretaceous before the K–T event.

Jablonski compared the relationships between the probability of extinction for different groups of shellfish during background times and at the time of the mass extinction. For example, in the late Cretaceous certain groups of bivalves and gastropods persisted longer than others because of their particular characteristics, such as having larvae that fed on plankton, or having a large number of closely

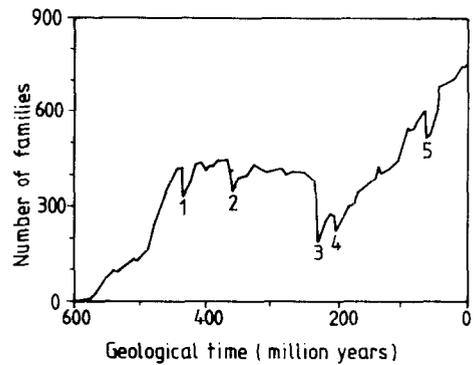


Fig. 1. The total diversity of families of marine animals during the last 500 million years. There have been five major mass extinctions: 1, Late Ordovician; 2, Late Devonian; 3, end-Permian; 4, Late Triassic; and, 5, end-Cretaceous. (After Ref. 2.)

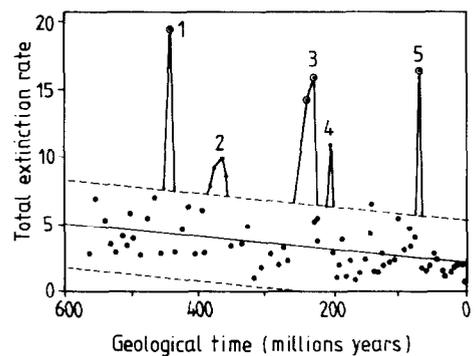


Fig. 2 A statistical test for mass extinctions. The total extinction rate (extinctions per million years) is plotted against geological time. Most extinction rates plot around a sloping line ('background' extinction rates), but there are several statistically very high rates ('mass' extinction rates) that correspond to the five mass extinctions shown in Fig. 1. (After Ref. 2.)

related species. However, at the time of the K–T event, these features counted for nothing: all forms became extinct with an equal probability.

There was only one characteristic that seemed to buffer certain groups of bivalves and gastropods against the effects of the K–T event,

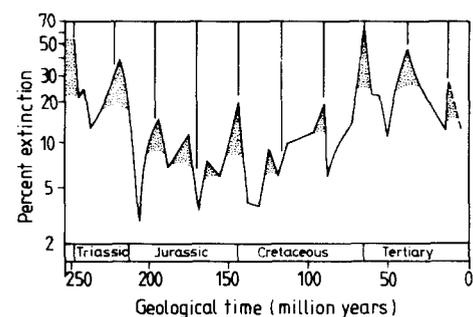


Fig. 3 Relative extinction rates seem to have shown a regular cyclical pattern over the past 250 million years. The peaks (mass extinctions) are shaded, and the best-fit 26 million year cycle is indicated by vertical lines. Note that the fit is not perfect, and this idea is still highly controversial. (After Ref. 15.)

and that was the geographic extent of the whole group. Widely distributed families with species in several oceans survived the mass extinction much better than endemic groups that were restricted to a single basin. This effect was independent of the individual geographic ranges of the constituent species within the group.

Jablonski concludes^{3,32} that mass extinctions constitute an important component of macroevolution. They are not random, but do appear to have selective effects. However, selection during mass extinctions is quite distinctive because 'it is apparently indifferent to many adaptations that had arisen or flourished during the background regime'.

If this view is correct, then another mode of selection in evolution would be added to those that operate during normal (background extinction) times. The new mode, a kind of 'rare-event selection', would operate on adaptations that were not necessarily of value in normal times, independently of Darwinian natural selection.

This new suggestion deserves serious consideration. First of all, the accuracy and breadth of the fossil record will have to be explored: how precisely can fossil assemblages be dated, how accurately do they reflect living floras and faunas, what biases exist, and can these factors be improved upon? Secondly, answerable ques-

tions will have to be framed, questions to do with the duration and magnitude of the events, and the adaptations of the survivors and those that died out. Do Jablonski's findings reflect what happened, or are they based on inadequacies of the fossil record? Do his findings from molluscs apply to other taxa as well? Do major differences in response to mass extinctions exist in the marine and non-marine habitats? Hoffmann has found recently³³ that speciose and widespread taxa may in fact be likely to weather a mass extinction, and he argues that there is no qualitative difference between background and mass extinctions. There are clearly large numbers of biological questions that have to be explored. Mass extinctions may yet lead to a revolution in our views of evolution.

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References

- 1 Raup, D.M. and Sepkoski, J.J., Jr (1982) *Science* 215, 1501-1503
- 2 Quinn, J.F. (1983) *Science* 219, 1239-1240
- 3 Jablonski, D. (1986) in *Dynamics of Extinction* (Elliott, D.K., ed.), pp. 183-229, Wiley
- 4 Sepkoski, J.J., Jr (1982) *Geol. Soc. Am. Spec. Pap.* 190, 283-289
- 5 Raup, D.M. (1986) *Science* 231, 1528-1533
- 6 Sepkoski, J.J., Jr and Raup, D.M. (1986) in *Dynamics of Extinction* (Elliott, D.K., ed.), pp. 3-36, Wiley
- 7 Benton, M.J. (1986) *Nature* 321, 857-861
- 8 Clemens, W.A. (1986) in *Dynamics of Extinction* (Elliott, D.K., ed.), pp. 63-85, Wiley
- 9 Russell, D.A. (1979) *Annu. Rev. Earth Planet. Sci.* 7, 163-182
- 10 Sloan, R.E., Rigby, J.K., Van Valen, L.M. and Gabriel, D. (1986) *Science* 232, 629-633
- 11 Lipps, J.H. (1986) in *Dynamics of Extinction* (Elliott, D.K., ed.), pp. 87-104, Wiley
- 12 Van Valen, L.M. and Sloan, R.E. (1977) *Evol. Theory* 2, 37-64
- 13 Archibald, J.D. and Clemens, W.A. (1982) *Am. Sci.* 70, 377-385
- 14 Van Valen, L.M. (1984) *Paleobiology* 10, 121-137
- 15 Alvarez, L.W., Alvarez, W., Asaro, F. and Michel, H.V. (1980) *Science* 208, 1095-1108
- 16 Alvarez, L.W. (1983) *Proc. Natl. Acad. Sci. USA* 80, 627-642
- 17 Alvarez, W., Kauffman, E.G., Surlyk, F., Alvarez, L.W., Asaro, F. and Michel, H.V. (1984) *Science* 223, 1135-1141
- 18 Hsü, K.J., He, O., et al. (1982) *Science* 216, 249-256
- 19 Raup, D.M. and Sepkoski, J.J., Jr (1984) *Proc. Natl. Acad. Sci. USA* 81, 801-805
- 20 Rampino, M.R. and Stothers, R.B. (1984) *Nature* 308, 709-712
- 21 Raup, D.M. and Sepkoski, J.J., Jr (1984) *Science* 231, 833-836
- 22 Whitmire, D.P. and Jackson, A.A. (1984) *Nature* 308, 713-715
- 23 Davis, M., Hut, P. and Muller, R.A. (1984) *Nature* 308, 715-717
- 24 Schwartz, R.D. and James, P.B. (1984) *Nature* 308, 712-713
- 25 Clube, S.V.M. and Napier, W.M. (1984) *Nature* 308, 635-636
- 26 Whitmire, D.P. and Matese, J.J. (1985) *Nature* 313, 36-38
- 27 Weismann, P.R. (1985) *Nature* 314, 517-518
- 28 Hallam, A. (1984) *Nature* 308, 686-687
- 29 Kitchell, J.A. and Pena, D. (1984) *Science* 226, 689-691
- 30 Hoffmann, A. (1985) *Nature* 315, 659-662
- 31 Benton, M.J. (1985) *Nature* 314, 496-497
- 32 Jablonski, D. (1986) *Science* 231, 129-133
- 33 Hoffmann, A. (1986) *Neues Jahrb. Geol. Palaeontol. Abh.* 172, 219-244
- 34 Surlyk, F. and Johansen, M.B. (1984) *Science* 223, 1174-1177