



# MASS EXTINCTIONS, CONCEPT OF

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## GLOSSARY

- benthos** Organisms living on or in sediment, below the water.
- extinction** The disappearance of a species upon death of its last surviving individual. In the fossil record, this is treated as the last fossil occurrence of individuals of a species.
- foraminifera** An order of animal-like protists, many of which secrete calcareous skeletons (“tests”).
- mass extinction** The simultaneous extinction of a disproportionate number of species over timescales of  $10^0$  to  $10^6$  years resulting in loss of biodiversity.
- phanerozoic** The geological interval of abundant animal fossils, beginning approximately 545 years ago.
- stratigraphic section** An outcrop of rock (with fossils

in this case) or a drilled core. The term can also refer to a composite for a region in which fossil ranges and stratigraphic events have been summarized into a synthesized rock column.

**tetrapod vertebrates** Vertebrate animals with four limbs (or vertebrates that have evolved from such animals, such as snakes).

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**MASS EXTINCTION** refers to the disappearance of large numbers of organisms over relatively short geologic spans of time. The result is diminished biodiversity, which can take millions of years to recover, depending on the magnitude of the extinction event. This chapter presents topics related to this concept, including its history, current measurements of the magnitude and timing of mass extinctions, and consequences for the recovering biota.

## I. HISTORY OF THE CONCEPT

The concept of extinction of species goes back at least several centuries. The extirpation of aurochs (wild relatives of cattle) and disappearance of lions from Europe were well known in the era of enlightenment and ascribed to human interference. The fact that species could become extinct from nonhuman causes was promoted by Cuvier at the end of the 18th century through his exquisitely detailed studies of mammalian fossils of the Paris Basin. His arguments were not accepted by

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all intellectuals at the time, and, in fact, Thomas Jefferson, the third president of the United States, doubted species could disappear before humans; he assigned Lewis and Clark a secondary mission in their explorations of the American northwest to search for living mammoths and mastodons.

The division of sequences of sedimentary rock into geologic systems by British geologists and paleontologists in the first half of the 19th century reflected a concept of major changes in marine faunas between these still-used time periods. But the first quantitative depiction of mass extinctions—major declines in biodiversity followed by recovery—appears to be Phillips's (1860) count of known numbers of fossil species and interpretive graphing of massive drops in diversity between the Paleozoic and Mesozoic eras and the Mesozoic and Cenozoic eras (terms he coined; see Fig. 1).

The study of mass extinctions rested largely in limbo from Phillips's pioneering work into the mid-20th century. This was perhaps because of emphasis on documenting evolutionary continuity in the fossil record and an assumption of substantive uniformitarianism, inherited from Lyell. However, with accumulation of paleontological data, the greatest of all Phanerozoic mass extinctions—the end-Permian, or “Permo-Triassic,” event—could not remain unnoticed. Schindewolf (1963) wrote a seminal paper discussing this event and invoking lethal radiation from an extraterrestrial catastrophe of a nearby supernova explosion. In response, Newell (1967) carefully counted fossil taxa (mostly described families) and argued that there were at least five events of mass extinction in addition to the Permo-Triassic. These papers set the stage for modern studies: examining detailed biostratigraphic data on local species disappearance and global compilations of taxonomic ranges.

Despite the contributions of Schindewolf and Newell, work on mass extinctions remained largely a “cottage industry” among paleontologists until 1980. Workers would examine one of Newell's events (usually in isolation of others) and posit some associated physical event as the cause, such as fall of sea level, or invent ad hoc hypotheses, such as heavy metal poisoning in the oceans as a result of mountain building.

Maturation of the study of mass extinction came with the bold hypothesis of Alvarez *et al.* (1980) that the Mesozoic-Cenozoic event, recognized 120 years before by Phillips, was caused by impact of a 10-km meteorite. The initial evidence of Alvarez and coworkers was concentration of the rare terrestrial element, iridium, at solar-system abundances in a clay layer at the Cretaceous-Tertiary boundary. But the hypothesis implied

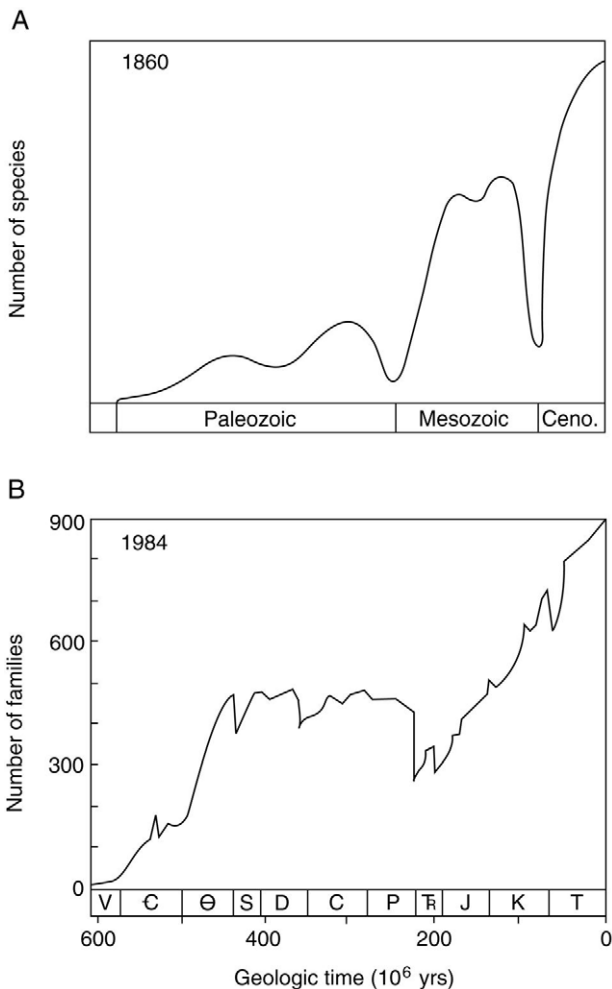


FIGURE 1 The first diversity curve for fossil organisms (a) compiled by Phillips (1860) compared to a late-20th century diversity curve for fossil marine animals (b). While Phillips' curve was generalized and based on comparatively few described taxa, the end-Permian mass extinction (between the Paleozoic and Mesozoic eras) and end-Cretaceous mass extinction (between the Mesozoic and Cenozoic ["Ceno"] eras) were recognized. The lower graph illustrates three additional mass extinctions among those recognized by Newell (1967): the end Ordovician, Late Devonian, and end-Triassic. Abbreviations along the abscissa for geologic time in (b) and in other figures are V = Vendian; C = Cambrian; O = Ordovician; S = Silurian; D = Devonian; C = Carboniferous; P = Permian; Tr = Triassic; J = Jurassic; K = Cretaceous; T = Tertiary. From Sepkoski and Schopf (1992).

other testable questions: (a) Is there additional physical evidence of an impact at the Cretaceous-Tertiary boundary and (b) Is the abruptness of biological extinctions at the event consistent with a catastrophe induced by meteorite impact? Impressive evidence affirming the first question has been assembled, including global identification of the iridium-rich clay layer (in both

marine and terrestrial stratigraphic sections); presence of shocked mineral grains (e.g., quartz), microspherules of shock-melted minerals, and abundant soot in the global clay layer; and the presence at 65 Ma of the largest impact crater known from the Phanerozoic in the Yucatan, Mexico. Answers to the second question have proved more difficult and will be considered later.

The recognition of extinction events in the geologic past demands comparison to modern extinctions, from the auroch to the myriad other species documented to have disappeared from human interference. Questions include not only how modern rates of extinction compare to those in the fossil record but also the consequences of extinction: What kinds of organisms are most susceptible to extinction and what are the patterns of biotic recovery after the pressure of extinction has been removed? These questions will be considered further later in this discussion.

## II. MODELS OF MASS EXTINCTION

A variety of patterns of extinction have been observed in the fossil record around events, ranging from abrupt termination of species at an extinction level to gradual disappearance up to it, and perhaps beyond, the extinction level. Three scenarios for mass extinction have been proposed based on empirical observations: abrupt extinction, gradual extinction, and stepwise extinction.

### A. Abrupt Extinction

This is the pattern hypothesized by Alvarez *et al.* (1980) of species disappearing in a geologic instant (which could in fact be  $10^1$  to  $10^3$  years). Observed declines in diversity before the event (such as seen in detailed records of foraminifera or broader records of dinosaurs before the Cretaceous-Tertiary) are a result of the Signor-Lipps sampling effect (discussed later).

### B. Gradual Extinction

The fossil record is taken on face value, especially if there has been extensive sampling around the horizon of extinction. Slow attrition of species up to the end of a mass extinction has been claimed for extensively sampled foraminifers around the Cretaceous-Tertiary event, where several large, but rare foraminifers seem to disappear below the stratigraphic boundary and some small, generalized foraminifers occur above the boundary.

### C. Stepwise Extinction

The fossil record is again taken at face value but exhibits a series of pulses of species terminations. This pattern has been hypothesized for situations such as the Late Devonian mass extinction ("upper Kellwasser Event") where intensively sampled taxa of different groups appear to disappear in small pulses separated by  $10^4$  to  $10^5$  years. The model can be expanded to intervals such as the end Ordovician (the second largest marine mass extinction of the Phanerozoic) when many trilobites and other marine animals of tropical areas appear to become extinct at the onset of major glaciation, and then, perhaps  $10^6$  years later, surviving deep-shelf benthos disappear as normal conditions of low oxygen return with the end of glaciation. (In this case, each pulse of extinction could be dissected to determine if it had been abrupt, gradual, or stepwise at finer timescales.)

These scenarios need to be distinguished from the low levels of extinction that are observed in all geologic intervals. These levels are normally termed "background extinction" to distinguish them from events of mass extinction. Background extinction for marine animals appears to decline through Phanerozoic time. Thus, smaller extinction events are more obvious in Newell-type data over the Mesozoic and Cenozoic eras than during the early Paleozoic when background rates were high.

## III. INTERPRETING DATA FROM THE FOSSIL RECORD

The fossil record provides direct evidence of previous mass extinction but only an incomplete accounting because of differences in preservability of organisms (e.g., bivalve mollusks versus polychaete worms) and in scientific sampling (e.g., Europe and North America versus Antarctica). With an incomplete record, observed last occurrences of fossil species are only a minimum estimate of actual times of extinction. This consideration was formalized for mass extinction by Signor and Lipps (1982) who modeled how observed terminations of species would appear around an abrupt extinction (Fig. 2). With less intensive sampling or less complete preservation, the expectation is a pattern of gradual disappearance of fossil species up to a boundary of abrupt mass extinction. This sampling pattern holds true whether one is examining detailed stratigraphic sections of fossils or analyzing compilations of fossil taxa, like those of Newell.

Raup presented a very intuitive example of the Sig-

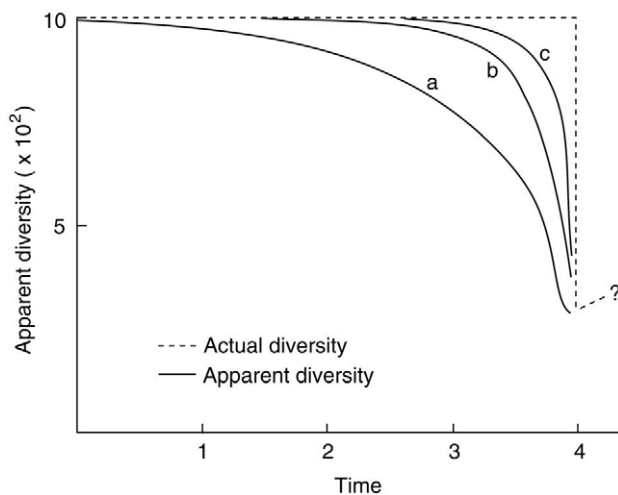


FIGURE 2 Hypothetical and calculated diversity curves reflecting the “Signor-Lipps effect”—that is, imperfect sampling around a catastrophic mass extinction. The dashed curve represents true diversity, which is treated as constant until time unit 4 at which there is a catastrophic mass extinction reducing diversity by three-quarters. If fossil taxa are not sampled up to the times of their true extinctions, declines in diversity will appear more or less gradual, depending on the intensity of sampling. Curve a represents the poorest sampling, and curve c the best (three times better than a). From Signor and Lipps (1982 with permission from the Geological Society of America).

nor-Lipps effect (Fig. 3). He used data collected for ammonites below the Cretaceous-Tertiary boundary to investigate how the fossil record of extinction would have appeared if the mass extinction had occurred at an interval 100 m lower in the stratigraphic section. (A meteorite impact or other unpredictable catastrophe potentially could occur anywhere in a stratigraphic section.) The decline in observed diversity up to the artificial event does not appear substantially different from the gradual decline of diversity actually observed below the true Cretaceous-Tertiary boundary. This suggests that problems of variable preservation and incomplete sampling of fossils can indeed influence empirical patterns of species disappearance around extinction events, hindering discrimination among the three models of mass extinction.

More powerful statistical methods have been developed to investigate how apparent last occurrences of fossil species may relate to actual times of extinction. These methods involve calculating “confidence intervals” on the time of last sampled occurrence of a species (Fig. 4). The basic concept is that the last fossil occurrence of a species that is rarely sampled is a poorer predictor of actual time of extinction than the last occurrence of a species that is densely sampled. Using various

models of the density distribution of sampling of a fossil species, probability statements can be made about how far true extinction lies above the last observation of a species.

## IV. MAGNITUDES OF MASS EXTINCTION

Questions of abrupt, gradual, or stepwise extinction involve patterns in the fossil record resolved over  $10^3$  to  $10^5$  years (encompassing the range from the late Pleistocene extinctions of large mammals to the historical extirpation of species). On larger timescales, general magnitudes of mass extinction can be measured from global fossil data. These data are best for the marine record of animals from continental shelves and seas and fall into roughly three classes of magnitude (Fig. 5).

### A. The End-Permian Mass Extinction

This class of magnitude stands alone in its effects on the biota (Erwin, 1993). Compilations of taxa lost indicate that more than 50% of animal families and 80% of genera in the oceans became extinct. Extrapolations of species loss have been attempted, using ecological rarefaction (how many species would be lost given measured declines in genera or families, assuming some distribution of species within higher taxa); results range from 90 to 96% loss of marine species. This loss of marine biodiversity at the end-Permian is unprecedented. Recent work suggests that on land important groups, including insects, tetrapod vertebrates, and plants, also experienced substantial declines in diversity.

### B. Four Other Events of Marine Mass Extinction

This class of magnitude eliminated substantial proportions of marine animals and seem to have had nearly equal magnitudes: the end-Ordovician, Late Devonian, end-Triassic, and end-Cretaceous events. (The occurrence of these events at or near the end of geologic periods reflects the use of faunal change to define intervals of geologic time.) The four events have measured family extinction in the oceans of 15 to 25% and extrapolated species extinctions of 64 to 85%.

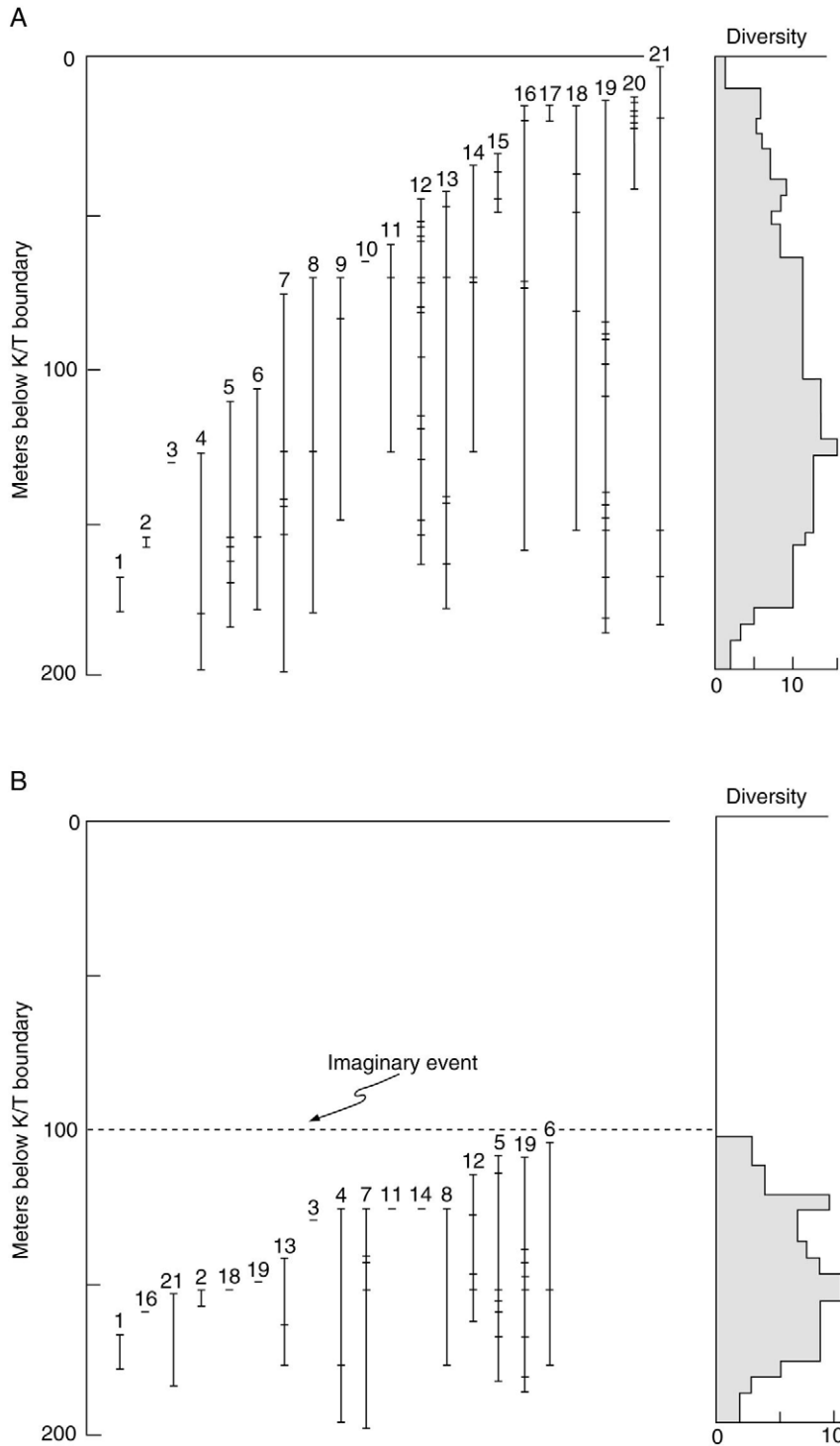


FIGURE 3 Apparent gradual extinction at an imaginary sudden extinction event. (a) Actual observed geologic ranges of 20 fossil species. The y-axis is stratigraphic position, in meters, below the Cretaceous/Tertiary boundary. Vertical lines show the total observed ranges of the species and horizontal ticks indicate horizons at which they were actually sampled. The curve at the right, labeled "Diversity," is the sum of the ranges of the species. (b) Resultant ranges if an imaginary catastrophic extinction were imposed at 100 m. Apparent last occurrences of species again are graded below the mass extinction and diversity appears to decline, both as a result of species being irregularly sampled through the geologic interval. (Note that the species in b have been reordered based on their highest geologic occurrence.) From Sepkoski and Koch (1996), based on Raup.

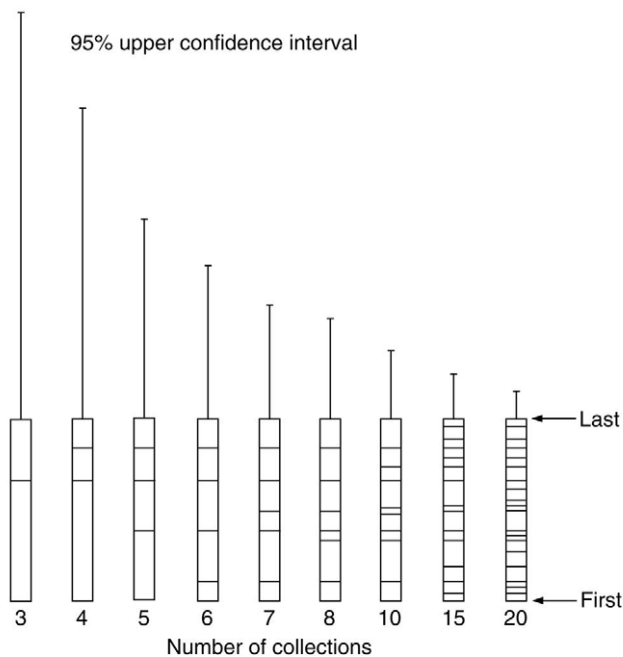


FIGURE 4 Confidence intervals on times of extinction based on the density of sampling of fossil species. The bars represent observed ranges of fossil species with horizontal ticks (including bottom and top of the bars) representing samples of the species. Vertical lines capped by ticks are calculated relative intervals during which there is a 95% probability that extinction actually occurred (thus allowing a 5% probability that real extinction actually occurred higher). The probable position of true extinction is closest to the position of last observation when species are densely sampled, but true extinction can still be expected to be somewhere above the position of last observation. From Sepkoski and Koch (1996) after Strauss and Sadler, with permission from the Geological Society of America.

### C. Other Intervals of Unusual Amounts of Extinction

This class of magnitude is now termed “extinction events” (Fig. 6). These appear in more detailed compilations of the kind Newell made as well as in precise biostratigraphic and paleogeographic analyses. Paleogeographic analyses suggest that many of these third-order events were not global in extent or taxonomic effects, unlike the two previous categories. Examples include the Cambrian bioturbation events, marked by nearly complete extinction of North American trilobites but with uncertain effects in other parts of the world or on other taxa (although some events are recognized in Australia, China, Siberia, and Europe); the lower Toarcian event affecting mollusks in Europe but not around the Pacific basin; and the Pliocene event, again documented for mollusks, in the south temperate Northern

Atlantic Ocean and Mediterranean Sea but not evident in the tropics or in the Pacific.

There are extinction events that could be classified at lower ranks. For example, it has been demonstrated that marine animal communities persist on order of  $10^6$  years during the middle Paleozoic, punctuated by rapid changes in faunal composition (Miller, 1997). This raises the question of Raup (1991a) as to whether extinction events represent a continuum between rare major events and frequent small events (discussed later).

## V. HYPOTHESIS OF PERIODICITY

Given the varying magnitudes and geographic extents of extinction events, one would expect differing forcing agents. With a plethora of forcings acting independently over geologic time, it would be expected that extinction events would be distributed at random through the fossil record. Thus, it came as a surprise when Fischer and Arthur (1977) and Raup and Sepkoski (1984) observed that extinction events of first through third rank appeared regularly distributed through time. Raup and Sepkoski performed extensive statistical analyses of Newell-type data and concluded there was a strong periodicity of 26 myr for events during the Mesozoic and Cenozoic eras (Fig. 7). This suggested some sort of clocklike mechanism behind mass extinction with a periodicity unknown in terrestrial processes. Because one of the periodic events was the end-Cretaceous mass extinction, Raup and Sepkoski speculated that the clocklike mechanism might be extraterrestrial.

This speculation engendered both intriguing hypotheses from astronomers and geologists and critical scrutiny of data and statistical methods from paleontologists, geologists, and statisticians (Raup, 1991b; Sepkoski, 1989). The best-known hypothesis is Nemesis, sometimes called “Shiva”; this is an hypothesized small binary companion to the sun with a large and eccentric orbit that brings it through the Oort Cloud of comets beyond the planets every 26 myr. Nemesis’ gravitational perturbation scatters up to  $10^9$  comets of which  $10^1$  to  $10^2$  might impact the earth, disrupting climate and causing mass extinction.

Nemesis has not been observed, and astronomical models cast doubt on the possibility that a small star could maintain a stable orbit at large distance from the sun through the 4.6 billion-year history of the solar system. Also, there is direct evidence of extraterrestrial impact for only a few of the periodic extinctions, despite intensive investigation: Shocked quartz has been found

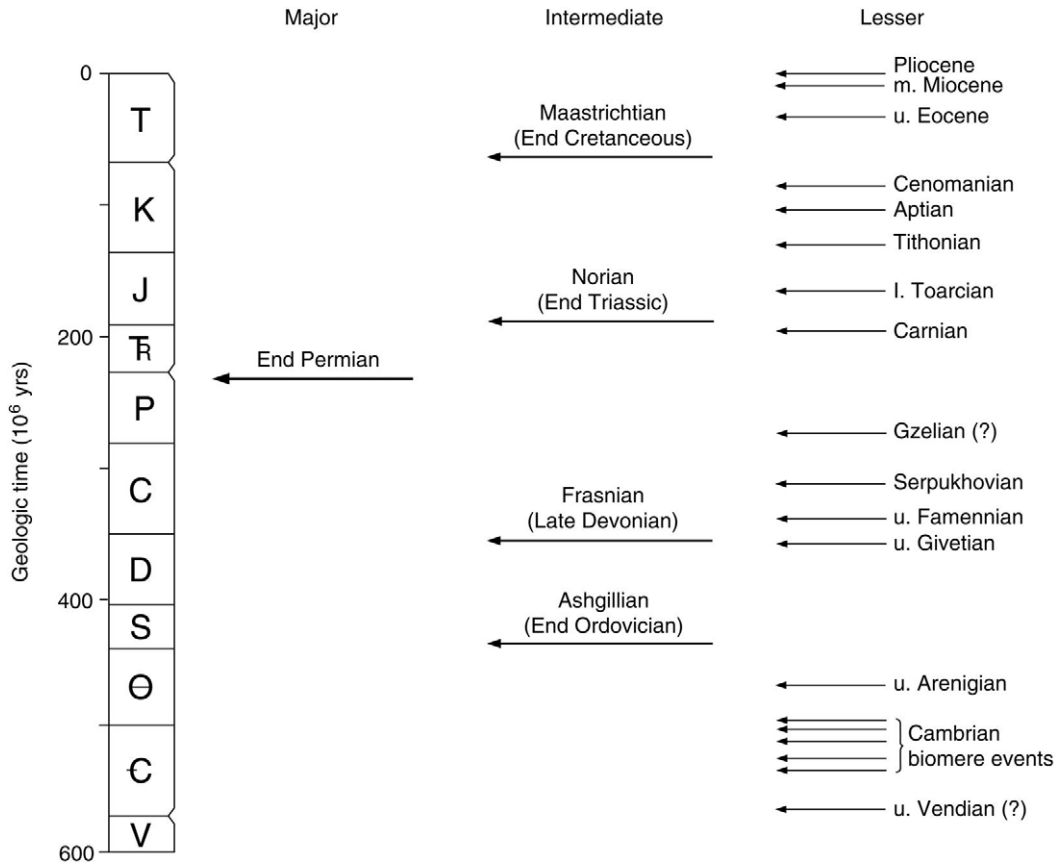


FIGURE 5 Time distribution of notable extinction events in the marine fossil record, classified as major (“first order”), intermediate (“second order”), and lesser (“third order”) events. Only major and intermediate events are normally referred to as “mass extinctions.” Abbreviations are mostly as in Figure 1; l = lower, u = upper. Names refer to stratigraphic intervals (mostly form stages). (?) indicates an event that has not been well documented. From Sepkoski (1992).

at several end-Triassic localities, and concentrated iridium, microtektites (annealed globules of impact melt), and a crater have been found in the Late Eocene, although their temporal correspondence to extinctions remains unclear. Searches of this nature are difficult and time consuming, and one should not be surprised if more discoveries are made.

Questions about data and analyses with respect to the hypothesis of periodicity have been largely technical (Sepkoski, 1989). Questions of data concern the veracity of fossil families and genera as indicators of extinction in the geological past and the accuracy of geochronological dating of intervals of extinction. Statistical questions involve problems of analyzing data that are not sampled evenly through time (geologic intervals vary in duration; Fig. 7) and problems of significance when performing multiple tests when searching for periodicities of best fit. Some of these questions entered

new analytic ground, leading to new kinds of analyses, but not all analytical issues have yet been resolved.

Thus, a nonrandom, periodic distribution of extinction events remains a hypothesis on the table, with neither a clear forcing mechanism nor a definitive analytical test.

## VI. THE KILL CURVE AND SELF-ORGANIZED CRITICALITY

Raup (1991a) treated extinction in the fossil past not as a hierarchy of events but as a continuum, in which the obvious events of large magnitude are rare relative to less obvious events of small magnitude. An analogy is to the historical record of river floods, in which the 1000-year event stands out but is really part of a spec-

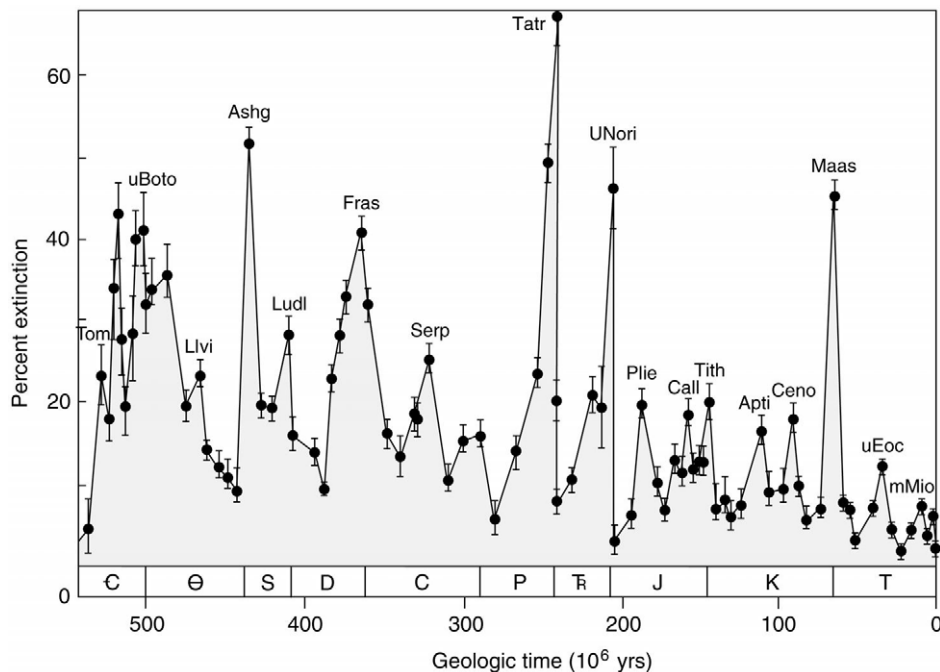


FIGURE 6 Extinction intensities for marine animal genera through the Phanerozoic. Intensity is measured as percent extinction ( $= 100 \times \text{number of extinctions/observed diversity}$ ) in geologic intervals averaging about 5.5 myr in duration. Estimated errors of estimate are indicated by error bars ( $\pm 1$  standard deviation). Significant events are labeled: Tom = Tommotian; uBoto = upper Botomian; Llvi = Llanvirnian; Ashg = Ashgillian (end-Ordovician mass extinction); Ludl = Ludlovian; Fras = Frasnian (Late Devonian mass extinction); Serp = Serpukhovian; Tatr = Tatarian (end-Permian mass extinction); uNori = upper Norian (= end-Triassic mass extinction); Plie = Pliensbachian; Call = Callovian; Tith = Tithonian; Apts = Aptian; Ceno = Cenomanian; Maas = Maastrichtian (end-Cretaceous mass extinction); uEoc = upper Eocene; mMio = middle Miocene. From Sepkoski (1996) with permission.

trum with smaller decadal or even yearly events. The 1000-year event does not occur regularly but rather has a chance of 0.001 of occurring during any given year. Raup used a standard function for these kinds of events to analyze probabilities of species extinction of a given magnitude during some duration of geologic time (Fig. 8): the longer the duration, or “waiting time,” the larger a pulse of extinction that can be expected. The limitation of Raup’s analysis is that it was based on generalized geological intervals, the same as illustrated in Figs. 6 and 7, and cannot distinguish between sudden events, such as observed at the end of the Cretaceous, and cumulative small events, such as may also have occurred during the last stratigraphic stage of the Cretaceous during the 9 million years prior to the impact-induced mass extinction.

Raup’s analysis was posited on an assumption that external perturbations of varying magnitude caused most extinction through geologic time, and he in fact demonstrated a linear relationship between his empiri-

cally based kill curve and the similar curve established for the flux of meteorites of varying magnitude (Raup, 1992). Other approaches have posited extinction to be a result of internal dynamics of the biota over time. Solé *et al.* (1997), for example, analyzed Phanerozoic time series of extinction and diversity fluctuation to determine if there was evidence of “self-organized criticality.” The prediction was that a power series from fourier transforms of the data would exhibit a linear  $1/f^x$  relationship when power was plotted logarithmically against the logarithm of frequency,  $f$ . The exponent,  $x$ , is expected to be between 1 and 2, which is indeed what was found.

Self-organized criticality refers to systems of interactive components that grow to a degree of complexity that leads to cascades into chaos or collapse. The standard analogy is to a pile of sand onto which one grain is added at a time: As the pile approaches critical size, one more grain can cause a small shuffle of sand while, far less frequently, another grain can cause a major



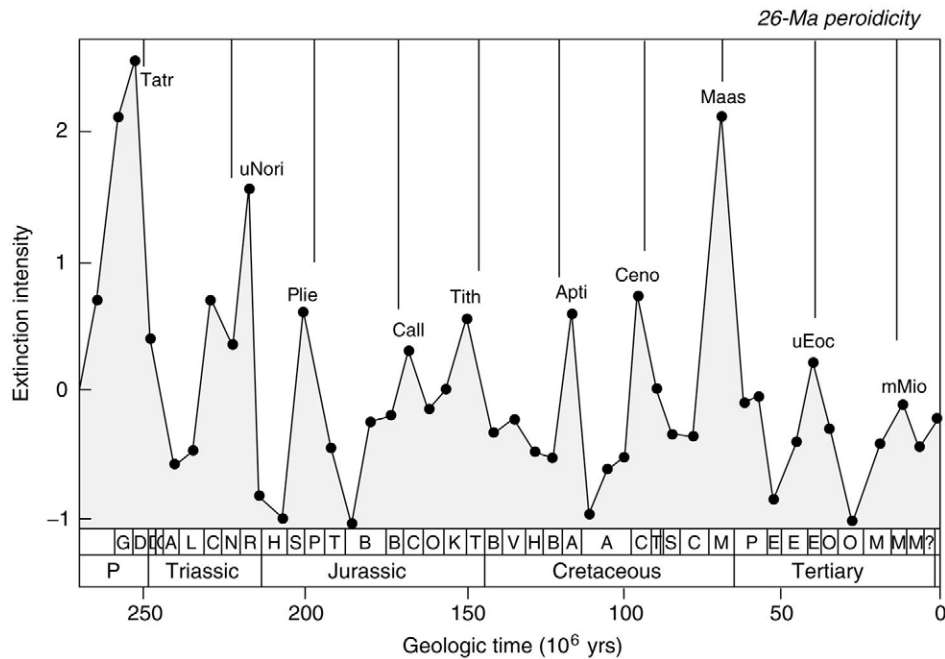


FIGURE 7 Time series for extinction intensity of marine animal genera through the Mesozoic and Cenozoic showing the putative 26-my periodicity of mass extinction (vertical bars). The abbreviations are as in Fig. 6. Extinction intensity here is measured as an average of percent extinction in major taxa that have been standardized to zero means and unit standard deviations. From Sepkoski (1990).

avalanche. The sizes of the avalanches follow the  $1/f$  power law. For species, one more new population packed into an interacting community might lead to extinction of a variable number of species if the community were self-critical; usually, extinction numbers would be small, but occasionally there would be a major avalanche of extinction.

There are three criticisms of this argument. First, some mass extinctions are clearly associated with physical disturbances, such as the meteorite impact at the end of the Cretaceous. Second, many other processes can produce  $1/f$  power laws when analyzed in the way organized self-criticality is; for example, the secular decline in background extinction over time, perhaps induced by changing taxa with different characteristic rates of extinction (Sepkoski, 1984), can cause power series to decline relative to increasing frequency. Finally, there is no independent evidence that species within marine communities, for which data have normally been analyzed, are as interactive as posited.

There still may be some interesting avenues of inquiry to pursue. The state of the biota is not constant, given variations in the earth's climates, changing positions of continents, and varying tectonic events and their effects on environments and the time over which

the biota evolves to these varying conditions. A perturbation at one stage of the earth's conditions and the biota's development could have very different effects than an identical perturbation at a different time (Sepkoski, 1989). Thus, an expectation of some chaotic element in the record of extinction cannot be ruled out.

## VII. SELECTIVITY OF MASS EXTINCTION: VICTIMS AND SURVIVORS

An obvious effect of the end-Cretaceous mass extinction is that all (nonavian) dinosaurs disappeared whereas some mammals survived. At other mass extinctions there are also cases of major taxonomic groups disappearing and others surviving. This observation has led to a search for rules as to what makes some kinds of organisms more vulnerable to mass extinction than others. Patterns that have been found are largely probabilistic, and all seem to have unexplained exceptions:

1. Taxa that have high rates of extinction during times of background extinction suffer disproportion-

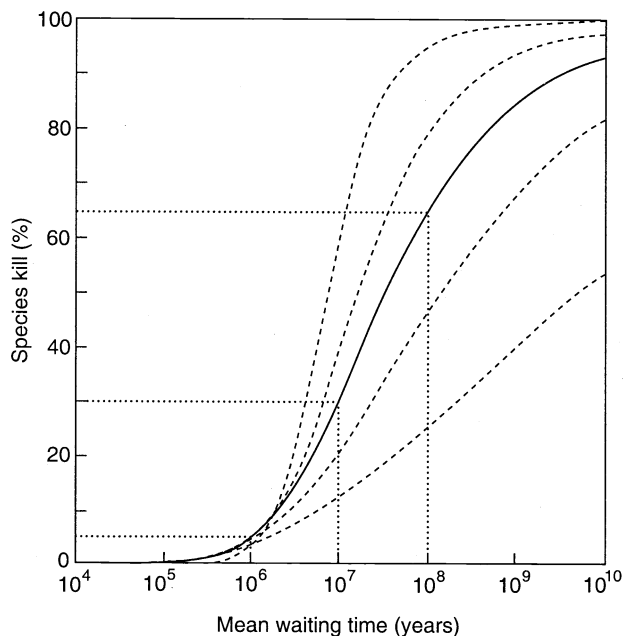


FIGURE 8 Raup's "kill curve" showing the expected extinction of marine species, as a percentage of standing diversity, over intervals of time ("mean waiting time"). During intervals of less than  $10^6$  years, percent of diversity expected to become extinct is low, but over longer intervals, especially greater than  $10^8$  years, extinction events of large magnitude become quite probable. The solid line is the best fit curve to fossil data; the dotted curves fall at bounds of uncertainty for empirical data. From Raup (1991a).

ately at mass extinctions. Rates of extinction measured for higher taxa (e.g., classes) during background times tend to be good predictors of magnitudes of extinction at major events. Thus, trilobites, with higher rates of background extinction than articulate brachiopods, suffered more loss at the end-Ordovician, and brachiopods, with higher characteristic rates of extinction than bivalves, suffered greater proportional declines at the end-Permian and even the end-Cretaceous, when brachiopods were relatively marginalized (Sepkoski, 1984). It remains a major question as to why major taxonomic groups have different characteristic rates of extinction during background times and why these rates are conserved over vast stretches of macroevolutionary history and species turnover.

2. Animals, particularly terrestrial vertebrates, with large body size seem to be particularly prone to extinction. Dinosaurs perished at the end of the Cretaceous whereas many of the small mammals survived; many large mammals and birds that had evolved by the Eocene disappeared during the Eocene-Oligocene transition; and the late to end-Pleistocene extinctions that

afflicted all continents other than Africa (and Antarctica) are often referred to as the "Pleistocene large mammal extinctions." Explanations for this selectivity involve (a) lower absolute population numbers of large animals, exposing them to greater chance of all individuals perishing during perturbations and (b) longer gestation times of large mammals, lengthening the time to restoration of pre-perturbation population numbers. Size-selectivity may not apply to marine invertebrates. Jablonski (1996) examined marine mollusks (gastropods and bivalves) for size-selectivity at the end-Cretaceous and found no differential extinction among large-sized species. On the other hand, Fischer and Arthur (1977) argued that marine vertebrate "megacarnivores" were very vulnerable to smaller extinction events.

3. It is often claimed that tropical plants and animals in the fossil past have been more susceptible to extinction than organisms living at higher latitudes. This is based in part on the observation that tropical reef communities disappear at several of the major mass extinctions, including the Late Devonian, end-Permian, and end-Cretaceous events, and millions to tens of millions of years intervene before diverse reefs re-evolve. The pattern for level bottom marine communities is not so clear: Jablonski and Raup (1995) analyzed the biogeography of bivalve extinction at the end of the Cretaceous and found no difference in extinction between tropical and temperate genera that were not associated with reefs.

4. Taxa with restricted geographic ranges appear to have been more prone to extinction than widespread taxa. Jablonski (1995) documented this for Late Cretaceous molluscan species during normal times of background extinction. At the end of the Cretaceous, however, the geographic range of individual species did not seem to be a factor, with widespread species suffering as much extinction as restricted species. At the rank of the genus, however, genera with geographically dispersed species tended to survive preferentially relative to genera with species restricted to one or a few biogeographic provinces. Similar results have been obtained for Cambrian trilobites at various extinction events.

5. Environment seems to have played only a minor role in selectivity of extinction among marine animals at mass extinctions. Rates of extinction among Paleozoic marine animals tended to increase toward shallower waters during background times but to be equal across continental shelves at mass extinctions. There is some suggestion, however, that deep-water animals fared better: Marine shelves seem to have been repopulated by descendants of deep-water trilobites after Cambrian extinction events; shelf communities contained dispro-

portionate numbers of deep-water sponges and corals after the Late Devonian mass extinction (McGhee, 1996); and descendants of mollusks typical of low-oxygen deep-water communities of the late Paleozoic are common after the end-Permian mass extinction (Erwin, 1993).

These reports of taxonomic selectivity at mass extinctions are largely confined to analyses around a few events of extinction, and much larger comparative studies need to be conducted across all mass extinctions for both marine and terrestrial organisms. However, if there are consistent probabilistic biases in terms of the properties of species and higher taxa that survive mass extinctions, then extinction events on frequencies of  $2.6 \times 10^7$  years, eliminating 30 to 90% of the biota, could be a major factor in the history of life.

## VIII. RECOVERIES FROM MASS EXTINCTIONS

Global data on mass extinctions exhibit not only the geologically rapid declines of the biota at mass extinctions but also subsequent recoveries of biodiversity in the aftermaths. With modern data, these recoveries are seen to encompass longer intervals of time than the extinction events, ranging up to about 5 myr for third-order extinction events to around 10 to 15 myr for second-order mass extinctions; recovery from the great end-Permian mass extinction took even longer but was interrupted by the end-Triassic event, some 30 myr later.

On long geologic timescales, recoveries from mass extinctions follow simple patterns expected for a diversifying biota. At more detailed scales, there is great complexity, with some patterns repeated after every mass extinction.

### A. Large-Scale Rebound of Diversity

To a first approximation, diversification in the oceans can be described as a system with equilibrium constraints imposed by limitations of resources and their utilization (Sepkoski, 1984, 1992). This is most obvious in the long plateau of diversity during the Paleozoic era, spanning approximately one-quarter billion years. This interval witnessed two second-order mass extinctions, the end-Ordovician and Late Devonian. Significantly, after each, animal diversity rebounded to previous, unperturbed levels and then continued the

Paleozoic plateau (Fig. 1b). Also, the rate of rediversification after these mass extinctions was approximately the same as during the Ordovician radiations that established the Paleozoic plateau of global marine diversity.

Such a system can be modeled if it is assumed that Paleozoic animals were constrained by an equilibrium diversity, conditioned on the environment and the way these animals subdivided resources (Fig. 9). The simplest mathematical description of diversification is a logistic model, assuming decreasing rates of origination as diversity increases. A mass extinction is a perturbation to the environment that increases extinction rates (Fig. 9b). Following the perturbation, when extinction rates return to background levels, taxa rediversify to the normative level (Fig. 9c).

Patterns are more complex through the quarter-billion years after the Paleozoic era, as diversity in the oceans generally increased. The increase reflects expansion of the modern marine fauna, which may have subdivided resources in ways different from the fauna of the Paleozoic era. Nonetheless, rebounds after mass extinctions during the Mesozoic and Cenozoic eras were much more rapid than the long-term increase in marine diversity when measured over millions of years and were congruent with initial rates of diversification of the taxonomic groups involved (cf. Miller and Sepkoski, 1989).

### B. Delayed Diversification

When rebounds from mass extinction are analyzed at finer timescales, many complications become apparent (Erwin, 1998). One is delayed recovery: rediversification does not commence immediately after perturbations. For example, there are only slow rates of rediversification for  $10^5$  years after the end-Cretaceous event among planktonic foraminifers (actually, fast at first and then slow for some four myr; D'Hondt *et al.*, 1996), benthic mollusks (Jablonski, 1998), and terrestrial mammals (Maas and Krause, 1994). Recovery seems to be delayed for nearly 5 myr after the much larger end-Permian event, with only depauperate faunas in the oceans and on land (Erwin, 1998).

Explanations for this pattern have varied. Some workers have suggested that the extended post-extinction intervals of low diversity reflect lingering effects of the external perturbation—that is, continued environmental stress or instability. Others have hypothesized that substantial amounts of time are required for the evolution of new species that can reestablish normal ecosystem function which, in turn, can support high diversity. An example is the evolution of planktonic

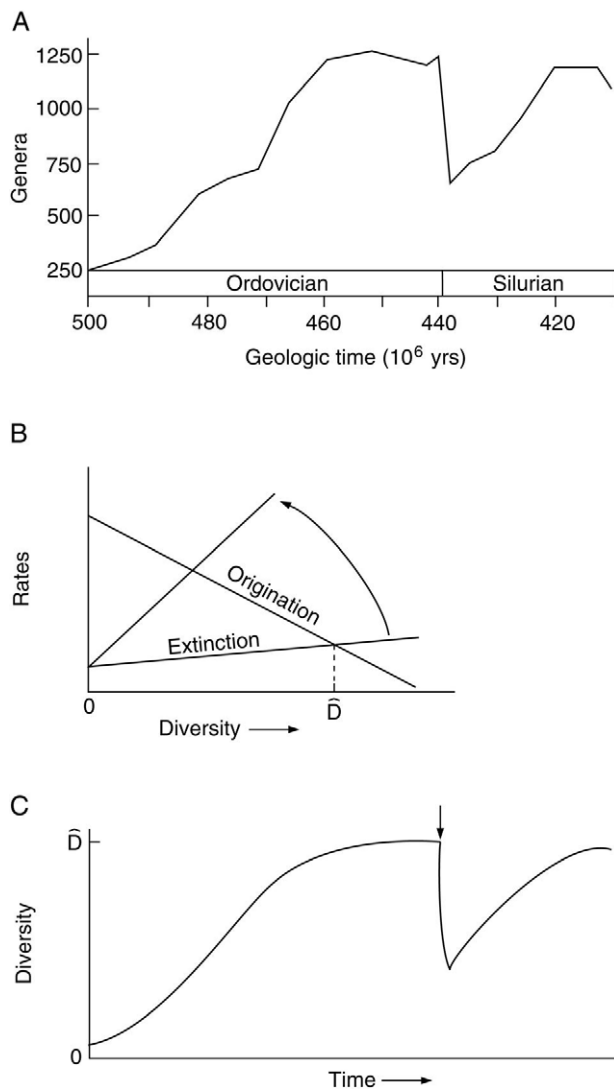


FIGURE 9 Observed and modeled loss and recovery of diversity around a mass extinction. (a) Observed numbers of genera through the Ordovician and Silurian periods, illustrating the major decline in diversity at the end of the Ordovician and subsequent recovery during the Silurian. Note that the rate of recovery is not very different from the rate of radiation during the Ordovician (cf. Fig. 1) and that diversity during the Silurian recovers to the same level as during the late Ordovician. (b) Structure of a logistic model to describe diversification, mass extinction, and recovery. It is assumed that diversity increases multiplicatively and that per capita rates of origination decrease with increasing diversity, leading to sigmoidal growth of diversification. A mass extinction is a temporary steepening of the extinction function (or, alternatively, increasing of its elevation).  $\bar{D}$  signifies the diversity at which origination rate equals extinction rate during normal times and diversity no longer grows. (c) A solution to the logistic model using rates measured from Ordovician marine animals, with a perturbation (arrow) applied at a model time corresponding to the observed end-Ordovician mass extinction. Diversity declines precipitously when extinction rate is increased, but then rebounds when extinction is returned to normal. Diversity in the model solution rebounds at the same rate as the Ordovician radiations and equilibrates at the same level as previously. From Sepkoski (1992).

microherbivores after the end-Cretaceous mass extinction (D'Hondt *et al.*, 1998). The delayed interval of recovery after the severe end-Permian event could even be conceived as a long lag in a logistic system after diversity had been reduced by an order of magnitude.

### C. "Disaster Species" and "Lazarus Taxa"

A feature that appears consistent during early phases of recovery from mass extinction is the appearance of "disaster species." These are remarkably abundant and geographically widespread species that appear in the waning stages or aftermaths of mass extinctions. Examples include the small foraminifer, *Guembelitra*, that spread out from marginal environments to form nearly monospecific assemblages immediately after the end-Cretaceous extinction and the terrestrial "fern spike" observed at the same time on land. Another example is the terrestrial synapsid ("mammal-like reptile"), *Lystrosaurus*, that produced monospecific assemblages in Gondwanaland following the end-Permian mass extinction.

Disaster species are characterized by not only great abundance in fossil deposits but also short geologic durations. Marine disaster species seem to flourish for around  $10^5$  years and then disappear, often to be replaced by another "disaster species" with similarly short duration. This appears like an evolutionary "boom and bust" cycle. Thus, the earliest Tertiary foraminifer, *Guembelitra*, declined and was replaced in dominance by a succession of bursts of *Paravularugoglobigerina*, "*Eoglobigerina*," and finally *Woodringina* over timescales of  $10^5$  years as the planktonic ecosystem seemed to regain stability.

Perhaps the antithesis of disaster species are "Lazarus taxa." These are lineages that disappear around mass extinctions—seemingly to have died—only to reappear in the fossil record some  $10^6$  to  $10^7$  years later (Erwin, 1998; Jablonski, 1986). These can be conspicuous but usually never dominant members of the biota prior to a mass extinction. Presumably, these taxa survived in some environmental or geographical refugium until the ecosystem regained sufficient function so that their dispersal—and recovery of sufficient abundance to be encountered by paleontologists—was possible.

## IX. THE MODERN BIODIVERSITY CRISIS

The collapses of ecosystems in the fossil past can inform thinking and actions with respect to the contemporary

loss of biodiversity. The fossil record is incompletely known, but the data seem little worse than estimates of living biodiversity and current rates of species extinction. Estimates of modern global biodiversity range over more than an order of magnitude, from 5 to  $100 \times 10^6$  species. Estimates of present-day loss of species range over nearly two orders of magnitude, from 5 to 150 species extinction *per day*. Most of these extinctions are terrestrial animals (largely insects), whereas the best data from the fossil record are for marine species. Still, in the geologic past, mass extinctions appear to have occurred largely contemporaneously both on land and in the seas (except for the end-Pleistocene event), so some simple calculations can be made.

If a median contemporary extinction rate of 41 species per day is assumed and species attrition is treated as a negative exponential, then it would take only about 16,000 years for 96% of the modern biota to become extinct (Sepkoski, 1997). This is a long time by human standards, but it is beyond the limits of geologic resolution at 250 Ma (the end-Permian), the only other time when 96% of Earth's biota disappeared.

This discussion has been largely in terms of fossil diversity. Another variable that can be measured in the geologic record is ratios of stable carbon isotopes. Because organisms tend to utilize  $^{12}\text{C}$  in slight bias over the heavier  $^{13}\text{C}$ , the ratio of the two isotopes preserved in the rock record can indicate, among other things, the activity of primary producers. For example, after the end of the Cretaceous, there was no difference in isotopic ratios of carbon in the skeletons of surface planktonic foraminifers and deep-sea benthic foraminifers. This indicates that organic carbon stopped sinking to the deep ocean. This change must have resulted from either (a) a major decline in oceanic productivity or (b) a major collapse of community structure in marine producers or consumers (D'Hondt *et al.*, 1998).

## X. SUMMARY

Exploration of the fossil record has demonstrated that the earth's biota is fragile at timescales of  $10^7$  years, suffering numerous declines in diversity. The magnitudes of these declines have been variable, but at least five times in the last 500 myr animal diversity was reduced by more than 50%, with the most severe event, at the end of the Permian, eliminating more than 90% of animal diversity. Recoveries from these events have been slower than the mass extinctions, often taking 5 to 10 myr or more. Although the long-term rebounds of biodiversity are predictable, the detailed patterns of recovery are complex, involving outbreaks of disaster

species and considerable ecological instability over timescales of  $10^5$  to  $10^6$  years. Current rates of species extinction could eliminate as many species as seen in past mass extinctions in a geologically short interval, and biotic recovery could be long and unpredictable.

## See Also the Following Articles

DINOSAURS, EXTINCTION THEORIES FOR • EXTINCTIONS, CAUSES OF • EXTINCTIONS, MODERN EXAMPLES OF • FOSSIL RECORD • MARINE MAMMALS, EXTINCTIONS OF • MASS EXTINCTIONS, NOTABLE EXAMPLES OF

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