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Virtually all plant and animal species that have ever lived on the earth are extinct. For this reason alone, extinction must play an important role in the evolution of life. The five largest mass extinctions of the past 600 million years are of greatest interest, but there is also a spectrum of smaller events, many of which indicate biological systems in profound stress. Extinction may be episodic at all scales, with relatively long periods of stability alternating with short-lived extinction events. Most extinction episodes are biologically selective, and further analysis of the victims and survivors offers the greatest chance of deducing the proximal causes of extinction. A drop in sea level and climatic change are most frequently invoked to explain mass extinctions, but new theories of collisions with extraterrestrial bodies are gaining favor. Extinction may be constructive in a Darwinian sense or it may only perturb the system by eliminating those organisms that happen to be susceptible to geologically rare stresses.

I N 1980, ALVAREZ ET AL. PROPOSED THAT THE MASS EXTINCtion at the end of the Cretaceous was caused by the impact of a 10-kilometer meteorite (asteroid or comet) (1). This proposal has created a storm of controversy, but it has also stimulated valuable research on the detailed geology, geochemistry, and paleontology of the terminal Cretaceous sequence. Some geologists and paleobiologists see these developments as heralding major shifts in the way we look at earth history and organic evolution. To others, the past 5 years have seen a science gone mad.

Up to 4 billion species of plants and animals are estimated to have lived at some time in the geologic past (2), most of these in the last 600 million years (Phanerozoic time). Yet there are only a few million species living today. Thus, extinction of species has been almost as common as origination.

The data base for extinction analysis is the distribution in space and time of about 250,000 known fossil species (3), an extremely small sample of past life because of the negligible probability of preservation and discovery of any given species. Nevertheless, it is a superb data base when compared with that available for many other aspects of Earth history. When the fossil record is viewed at higher taxonomic levels (genera, families, and orders), the quality of sampling is substantially better because the probability of finding a record of a multispecies group is higher than for a single species.

Extinctions are clustered in time. Not only are there several profound mass extinctions like that at the end of the Cretaceous, but relatively sudden and rapid turnovers occur at lesser scales as well. Both large and small extinctions were used by 19th-century geologists to define boundaries in the time scale. It is thus no accident that most major extinctions fall at important boundaries in the time scale. The clustering of extinctions may have made it possible for the geologic time scale to be established on several continents within just a few decades in the mid-19th century.

The Cretaceous-Tertiary (K-T) mass extinction is of interest not only because of its possible relation to comet or asteroid impact, but also because it is the best documented of the larger extinction events. It is celebrated especially because it included the demise of the dinosaurs, which, in turn, probably made possible the early Tertiary evolutionary radiation of mammals, leading ultimately to human evolution. But the dinosaur extinction was actually a small part of the total K-T event: there may have been as few as 20 coexisting dinosaur species in the latest Cretaceous (4) with a total biomass that was trivial in comparison with the rest of the global biota.

Large numbers of species in a variety of habitats died out sometime near the end of the Cretaceous. In terrestrial habitats, marsupial mammals were hard hit, but many of them, along with most other mammalian groups, managed to survive. Other groups, such as the amphibians and many aquatic reptiles, were relatively unaffected, and land plants suffered only moderate extinction. This sort of selectivity characterizes all major extinctions, although the details are not consistent from one event to the next.

In the marine realm, approximately 13 percent of marine families and about 50 percent of marine genera died out completely in the Maestrichtian, the final stage of the Cretaceous (5). These figures underestimate the actual biological cost because they do not include genera and families that lost many species but still managed to survive with at least one species. An interpolation based on average numbers of species per higher taxon leads to the estimate that somewhere between 60 and 75 percent of the marine species existing in the latest Cretaceous became extinct (6). Losses included some of the most abundant species, particularly among marine plankton. Thus, mortality measured in biomass was probably higher.

A key question is the length of time over which the late Cretaceous extinctions occurred. This question is important to the ultimate understanding of the causes of mass extinction and also influences the format of any statistical analysis. The percentages given above are based on global compilations of the time ranges of families and genera (5, 7). For the terminal Cretaceous, extinction times are grouped into the Maestrichtian stage, the last unit of the Cretaceous that can be recognized easily on a worldwide basis. Because this interval lasted about 8 million years, the global data do not distinguish between instantaneous and protracted events. It is often possible to define the timing of extinctions more precisely.

Variation in Extinction Intensity

Commonly used measures of the intensity of extinction include (i) total taxa becoming extinct in a selected unit of time (a geologic stage), (ii) extinctions in a time unit as a percentage of standing diversity, (iii) number of extinctions per million years, and (iv) percentage of extinctions per million years. All are subject to

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sampling problems and persistent biases, and the proper selection of a measure is rarely obvious. Although the percentage of extinction per million years should be the most appropriate because it normalizes both for standing diversity (taxa available for extinction) and for absolute time, it has two serious problems. First, the time dimension is an estimated duration of a stage or other conventional time unit, and stage durations are uncertain, based as they are on interpolations between widely separated calibration points. Second, the fully normalized metric carries the tacit assumption that extinction is a continuous process. If some major extinction events are effectively instantaneous, normalizing for the duration of some arbitrary time unit (such as the Maestrichtian) obscures the real rate. There is no statistically significant correlation between stage duration and number of extinctions per stage for the Phanerozoic; this may be because of errors in stage durations or because the extinction process is indeed dominated by widely spaced, point events.

In spite of these problems, five extinctions stand out consistently as the largest and they are conventionally labeled mass extinctions. The five are terminal Ordovician (~440 million years ago), late Devonian (~365 million years ago), terminal or late Permian (~250 million years ago), terminal Triassic (~215 million years ago), and terminal Cretaceous (65 million years ago). The ranking of the five depends somewhat on database and metric, but the Permian event usually emerges as the largest, with published estimates of species kill ranging as high as 96 percent (6).

At the other extreme is "background" extinction, seen as the normal or spontaneous rate of replacement of one species by another. Although names may imply that qualitatively different processes are operating, this may not be the case. A plot of varying intensity of extinction for the 79 generally recognized stages of the Phanerozoic (Fig. 1) shows a spectrum of variation and suggests that the simple binary classification of extinction is not warranted. This does not deny the possibility that extinctions are qualitatively different from each other, but it does emphasize that variation is continuous. The problem resembles that faced in the classification of floods or severe storms, with mass extinction being analogous to the 100-year flood or the hurricane.

Episodic Versus Continuous Extinction

Figure 2A shows a survivorship curve for species of marine planktonic foraminifera that is based on census data at intervals of approximately 5 million years over the past 30 million years. The point on the upper left represents the group of species found in the fossil record 30 million years ago. The fate of this group, or "pseudocohort," is monitored through geologic time to show the decay of the group by extinction of its constituent species (8). Origination of new species plays no role.

A logarithmic ordinate is used in Fig. 2A so that the decay will be linear if extinction is a continuous, stochastic process with constant probability of extinction. The array of seven points appears to be linear and can be described by the equation

$$S_t = S_0 e^{-qt}$$

where S_0 and S_t are the numbers of survivors at some initial time and at time t, respectively, and q is the probability of extinction of a species per million years. A best-fit line in this case yields $q = 0.13$, the reciprocal of which is an estimate of mean species duration (7.7 million years) for the pseudocohort.

Figure 2A and its linear interpretation are completely compatible with the model of continuous background extinction known as Van Valen's law (9). This model is attractive because it makes the extinction process mathematically tractable and predictable (10).

Fig. 1. Distribution of extinction intensities for the 79 generally recognized geologic stages of Phanerozoic time, based on recorded times of extinction of 2316 marine animal families (7). Extinction intensity for the last stage of the Cretaceous (Maestrichtian) is indicated for comparison.
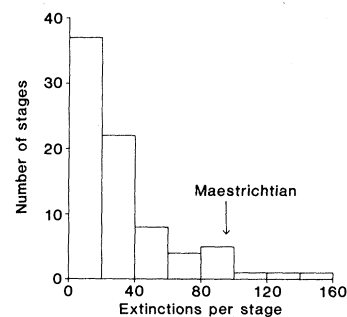
However, foraminiferal extinction in the Tertiary can be viewed differently. Figure 2B shows pseudocohort decay for a fuller data set: more cohorts are considered, and each is monitored with higher temporal resolution. In Fig. 2B, each line represents a pseudocohort starting at a different time, and the data points are connected by straight lines rather than used only as guides for a generalized fit. The steplike pattern indicates a discontinuous process. The tendency for horizontal "treads" and vertical "risers" suggests a series of point events separated by intervals of stability (little or no extinction). An especially marked drop in survivorship 13 million years ago corresponds to a recognized extinction event near the end of the middle Miocene (11).

Figure 3 shows pseudocohort survivorship curves at a different scale. Survivorship is graphed for the entire Phanerozoic, from a stage-level time scale and records of 2316 extinct families of marine animals. The steplike pattern is still seen, with the major extinction events indicated by sharp drops. The pattern is most evident in the right third of the figure, where taxonomic data and radiometric dating are most robust. Comparison of the species and family plots (Figs. 2B and 3) suggests that the patterns have a fractal quality of self-similarity with changing scale, although this possibility has not been confirmed.

Is the extinction process fundamentally continuous or episodic? The foregoing discussion implies that it is episodic, but this has not been demonstrated in the general case. The question remains important and bears on other questions of the mechanisms of extinction.

Dating Extinction Events

Although global data locate extinctions only to the nearest geologic stage, the situation is not quite as bad as this would imply. Stage boundaries have traditionally been defined at points of evolutionary turnover, and, in a number of cases, there is independent evidence that this is true. It is often possible to date extinctions on a local or regional scale with considerable precision.

Figure 4 shows the occurrences of 50 brachiopod species in the few meters above and below the K-T boundary at one locality in Denmark. In this section, the K-T boundary is marked by a distinctive clay layer ("marl"), within 1 meter of which 20 brachiopod species disappear. This fits the episodic model and suggests a sudden environmental or other perturbation. However, species 21 to 26 in Fig. 4 disappear from the record near the K-T boundary only to reappear four or more meters higher. Clearly, these six species did not actually die out. This represents a common situation which has been called the Lazarus effect by Jablonski (12). All 26 species may have lived during all or part of the barren interval but were not preserved because of changes in the depositional regime, postdepositional chemical solution, or greatly reduced population sizes. It is also possible that these species simply migrated away from
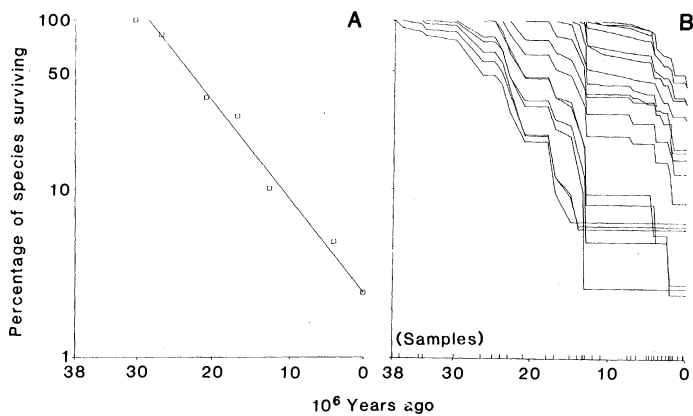
Fig. 2. Survivorship of species of planktonic foraminifera. (A) Survivorship of a cohort monitored at approximately 5-million-year intervals, suggesting constant probability of extinction in a purely stochastic system [data from (33)]. (B) More complete survivorship pattern for cohorts of planktonic foraminifera, suggesting an irregular and distinctly episodic survivorship pattern; sample points are shown inside the horizontal scale [redrawn from figure 9C in (33)].

the site. In any event, the significance of the "extinctions" noted at the beginning of the interval is jeopardized.

The Lazarus effect is known to occur on a large scale after the Permian extinctions: several million years of the succeeding Triassic record show excellent fossil preservation but lack all traces of several major groups of marine organisms (Lazarus taxa) known to have survived the Permian extinction.

Figure 5 shows detailed records of planktonic foraminiferal species through about 15 million years of the Eocene and Oligocene epochs of the Tertiary. Again, there is evidence of steplike extinction, but there are alternative explanations. In this case, there is independent evidence for hiatuses in sedimentary deposition (wavy lines at three horizons). Such hiatuses truncate ranges of species and thus enhance the impression of simultaneous extinction. The termination of the first four species in Fig. 5 falls just below a gap in sampling.

Even if a hiatus is known to occur at an apparent extinction point, simultaneous extinction can occasionally be demonstrated. Hiatuses in the geologic record are commonly associated with true (independently verified) extinction events. Especially in deep-sea situations,

environmental changes (sudden or gradual) that cause hiatuses in sedimentation may also cause biological extinction. This is true for the anoxic events associated with extinctions at the base of the Silurian, in the late Devonian, at the top of the Triassic, and at the tops of the Pliensbachian (Jurassic), Cenomanian (Cretaceous), and Maestrichtian (Cretaceous) stages (13).

In the examples just described, extinction events may appear to be sharper than they actually are, but there is another set of conditions that has the opposite effect. For most organisms, it is unlikely that the true last occurrence of an extinct species or family will be recorded. Therefore, almost all observed time ranges are truncated. This causes a "smearing" of the record of an extinction event backward in time and is called the Signor-Lipps effect (14). The fact that the highest known dinosaur bone in the K-T section in eastern Montana is 3 meters below the iridium anomaly is attributed by some to the Signor-Lipps effect. On a larger scale, extinction of families in the late Permian appears to extend over the last several stages of the Permian, but this may just be a result of range truncation during a long interval of lowered sea level and incomplete sedimentary sections. The Signor-Lipps effect is difficult to prove unless Lazarus taxa are available to evaluate the probability of nonpreservation.

The dating of extinction events requires much more work. Because of the problems and ambiguities found throughout the record, capable geologists and paleontologists differ sharply on interpretations of observations.

Selectivity of Extinction

Major extinction events are selective—that is, the victims and survivors are not random samples of the pre-extinction biota. This opens the way to careful analysis of the physiological, ecological, and biogeographic common denominators of the surviving or nonsurviving species. With this information, a fuller understanding of the causes of extinction should be straightforward.

Some aspects of organismal biology appear to be related to resistance to extinction. Large population size, broad geographic distribution, and high dispersal potential should help protect species and higher taxa from extinction, and this appears to be the case for periods of background extinction. Jablonski has shown that for most of the last third of the Cretaceous, mollusks with high dispersal and
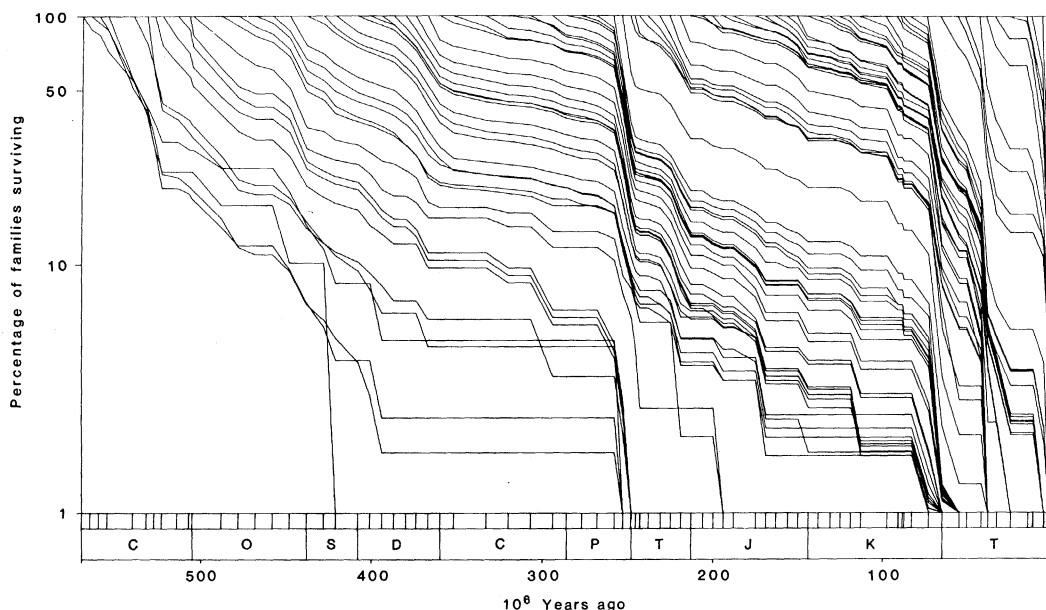

Fig. 3. Survivorship of 2316 families of marine animals over the past 600 million years (7). Each line is a "pseudocohort" which starts (upper left) with the families present in the fossil record at a point in time. Decay of the cohorts is monitored for all recognized geologic stages (indicated by the small boxes along the base of the graph). Mass extinctions appear as sharp drops in survivorship. Because the sample lacks families still living today, the intensity of extinction events is exaggerated toward the right.
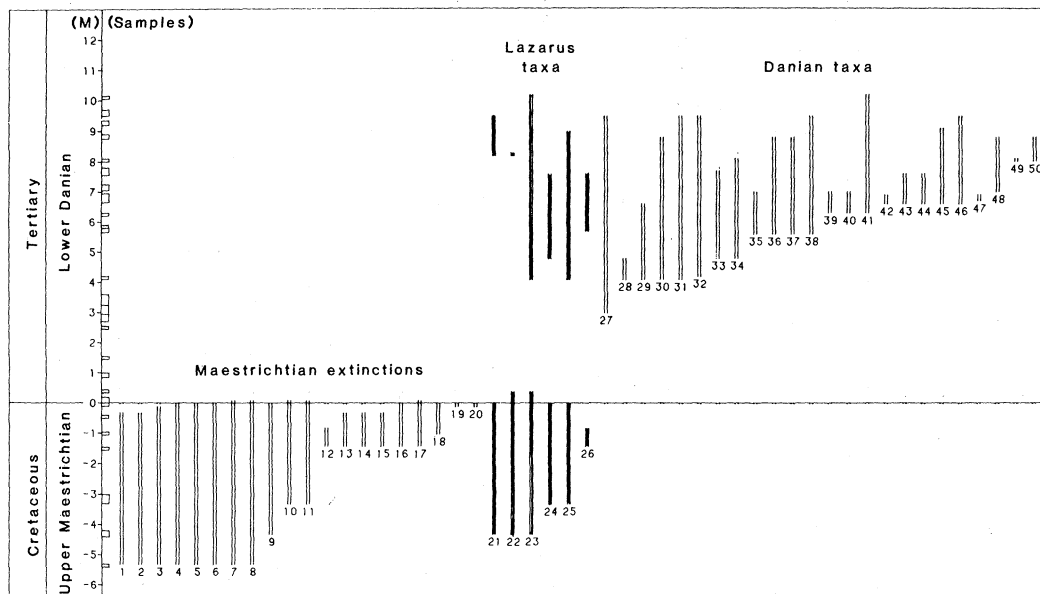
Fig. 4. Ranges of brachiopod species in about 15 meters of the sedimentary sequence near the Cretaceous-Tertiary boundary at Nye Kløv, Denmark (34). Sample points are shown inside the left scale.

broad geographic range survived longer, but Jablonski has also shown that this can break down at mass extinctions (15). Gastropods and bivalves with long-lived larvae and wide geographic distributions have no higher survival rates at the K-T event than other groups. Also, ironically, highly species-rich groups do not appear to have an advantage at this mass extinction.

A few other tentative generalizations apply to one or more of the big mass extinctions. Large body size appears to be a disadvantage, at least among terrestrial animals. Tropical biotas seem to be prone to extinction, and biological groups that consistently show high background rates of speciation and extinction are most likely to be eliminated at mass extinction events.

In general, however, biological selectivity in extinction is poorly studied and little understood. This is perhaps the most crucial area for future research, with rigorous comparisons among extinction events having the highest priority. A full understanding of selectivity is the most promising route to discovering the environmental stresses that cause extinction.

Causes of Extinction

Paleontology and geology have adhered to a strong conventional wisdom, perhaps a dogma, since the days of Lyell and Darwin. The basic tenets are as follows: (i) extinction is a gradual process driven by the intricacies of interactions among species and between species and their physical environment; (ii) because of the complexities of multiple, independent causes, major extinction events are randomly distributed in time; and (iii) all major extinctions are different, and a search for a single, unifying cause is futile. It is implicit in the foregoing that the causes of extinction are not to be found in the alien world of cosmic collisions. Lyell put it this way in 1833:

In our attempt to unravel these difficult questions, we shall [restrict] ourselves to the known or possible operations of existing causes; feeling assured that we have not yet exhausted the resources which the study of the present course of nature may provide, and therefore, that we are not authorized in the infancy of our science, to recur to extraordinary agents. We shall adhere to this plan . . . because . . . history informs us that this method has always put geologists on the road that leads to truth (16, pp. 4 and 5).

It is not surprising that the hypothesis of mass extinction by meteorite impact is anathema to many paleontologists and geologists.

The two most commonly cited causes of mass extinction are change in sea level and climatic deterioriation. Strong evidence exists for an association of extinction with times of lowering sea level, with loss of habitable area on the marine continental shelves being suggested as the primary cause of extinction (17). Climatic deterioration has been claimed as the proximal cause in a number of cases, most notably in recent studies by Stanley of a regional extinction event in the Pliocene (18).

The main problem with these explanations is that both kinds of change are common in earth history. There are many documented times of sea level lowering, some apparently caused by glaciation and others not, and many indications of long-term climatic change independent of sea level. There are also many extinction events. Thus, to establish cause and effect is difficult and requires rigorous assessment of probabilities in a complex time series. The K-T extinction event was preceded by several million years of global cooling and substantial sea-level lowering. But the association of physical and biological events by itself does not prove cause and effect.

Comet or asteroid scenarios have a long but not very distinguished history. As long as comets have been known, claims have been made that their collisions with the earth have caused devastation and destruction. But no empirical evidence was offered until recently. In 1973, Urey presented a reasonable statistical argument, based on ages of tektites and extinctions, for comets as a cause of several of the lesser extinction events in the Tertiary (19).

The first hard evidence came with the report of Alvarez et al. in 1980 of the iridium anomaly at the K-T boundary (1). The main arguments in favor of the Alvarez scenario are embodied in interpretations of iridium enrichment (1, 20), osmium isotope ratios (21), shocked quartz (22), and spherules interpreted to be microtektites (23). The case for impact is strong but has its detractors (24).

The more important question in the present context is whether the impact caused the terminal Cretaceous extinctions. This, again, comes down to questions of the probability of co-occurrence of events. Mass extinctions of the magnitude of the K-T event are relatively rare in Phanerozoic time (perhaps five in 600 million years). Similarly, collisions with 10-kilometer objects are also rare: perhaps ten such events in the last 600 million years (25). It should be simple to compute the appropriate probabilities if the timing of both could be tied down precisely, but the problem is complex because of uncertainties in the actual timing of the terminal Creta-

Fig. 5. Ranges of planktonic foraminiferal species from Deep Sea Drilling Project site 253 in the southern Indian Ocean (35). Wavy lines at three levels indicate hiatuses in the sedimentary record. Sample points are shown inside the left scale.
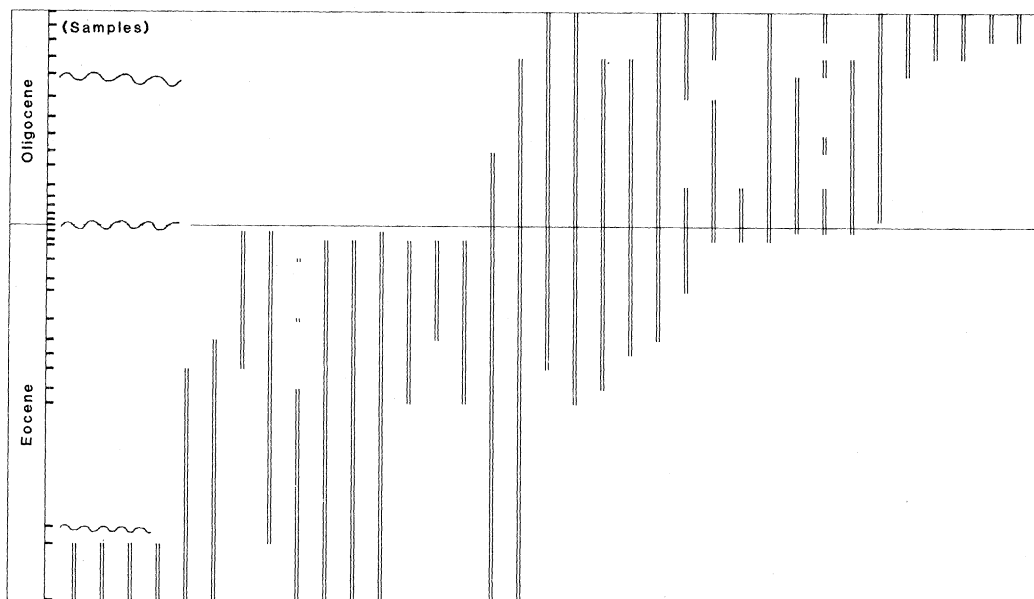
ceous extinctions on a global basis. If all extinctions are assumed to coincide with those in the microplankton at Gubbio, Italy, the probability of chance co-occurrence is negligible (26), but this assumption is difficult to prove. This uncertainty, more than anything else, has led competent researchers to conflicting conclusions on the likelihood that the impact of a large body caused a mass extinction.

Broadly based studies of impact craters and of geophysical and geochemical indicators of impact are needed before it is possible to construct a fuller chronology of the earth's impact history for comparison with the biological record. Only then can the uncertainties inherent in the interpretation of a single event be accommodated. To date, there are reports of five impact-extinction pairs other than the K-T event, but each raises substantial questions. All five are based on evidence of iridium enrichment, and some have other features suggesting extraterrestrial input (27). It is too early to say definitely whether impacts of large bodies caused these extinctions. It may even turn out that impacts cause mass extinctions but only when biological systems are already strained by other kinds of environmental stress, such as a change in sea level or climate.

Periodicity of Extinction

According to a number of analyses, major extinction events are regularly spaced in geologic time (11, 28, 29)—a further departure from the conventional wisdom of Lyell. The periods claimed range from 26 to 32 million years, and most studies have been limited to the last 250 million years of the Phanerozoic, which permits relatively high resolution. If periodicity can be established, a common cause is virtually required.

After Sepkoski and I proposed a 26-million-year stationary extinction periodicity (11), several astrophysical explanations were proposed (30). Most suggested that perturbations of comets in the Oort Cloud raise the probability of comet impact on the earth. Thus, a link is suggested between the claimed periodicity of extinction and the impact theory of Alvarez et al. (1). This link has been supported by two studies suggesting that impact craters on the earth show a periodicity compatible with that for extinction (29, 31).

Periodicity and extinction by impact are not necessarily linked, however. The flux of large comets and asteroids has been sufficient to make the extinction-by-impact proposals plausible, with or without periodicity. By the same token, periodicity need not require impact by a large body. The recent success in relating Milankovich cycles to the history of the younger terrestrial glaciations demonstrates that solar system processes can have recognizable effects on the earth (32). Thus, periodicity and impact should be viewed as separate, although possibly linked, phenomena.

Evolutionary Significance of Extinction

Because the half-life of a biological species in geologic time is very short (generally less than 10 million years), turnover rates are high. Extinction must therefore be important to the total evolutionary process; to ignore it would be as inappropriate as for a population biologist to ignore mortality or a sedimentologist to ignore erosion.

It has been conventional to view extinction as a constructive force by which less well-adapted organisms are eliminated, leading to improvement in the mean adaptive level of the total biota. For example, it has been assumed that Cretaceous mammals were better adapted than the large reptiles. In general, however, it has been impossible to verify the constructive aspect of extinction.

It may be that extinction, although selective, is not constructive. If mass extinctions are the result of environmental stresses so rare as to be beyond the "experience" of the organisms, extinction may be just a matter of the chance susceptibility of the organisms to these rare stresses. Consider, as a hypothetical example, the effects that large doses of ionizing radiation would have on present-day biota. In terrestrial habitats, one can imagine radiation levels that would kill all exposed mammals but have negligible effects on most insects and plants. The result would be a highly selective extinction, but one having no constructive effect in terms of the general success of organisms in normal times. Only if such crises were common in geologic time would the evolutionary system be able to cope through natural selection.

This model provides for profound effects on evolving systems, but the effects are not constructive in the usual Darwinian sense. It is conceivable that something like this model was operating among land vertebrates in the late Cretaceous. Mammals and dinosaurs had coexisted for more than 100 million years. After the large reptiles became extinct, mammals underwent an explosive evolutionary

radiation made possible by the absence of the dinosaurs. But the dinosaurs may not have done anything "wrong" in a Darwinian sense.

The nonconstructive role of extinction is only hypothesis, just as the conventional Darwinian role is hypothesis. With the recent renewal of interest in extinction, thanks to new theories of mass extinction, we may expect that this and other significant questions can be investigated fruitfully.

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