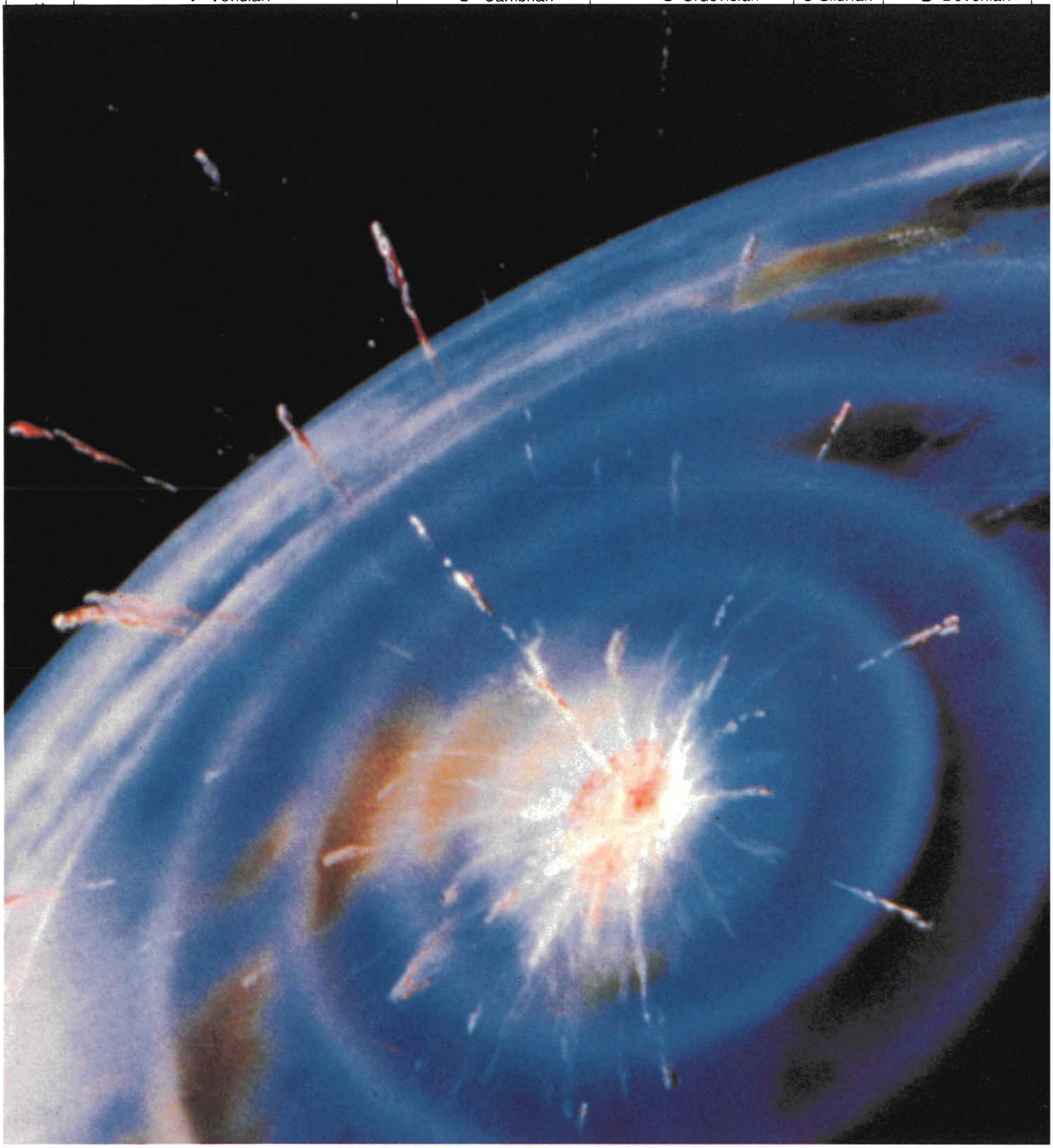
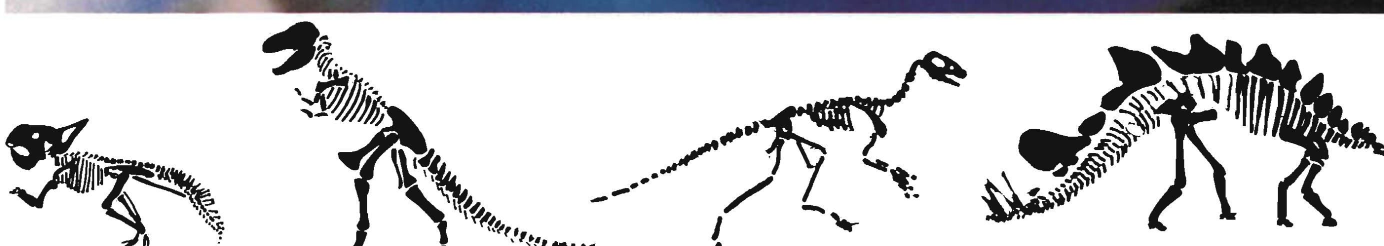
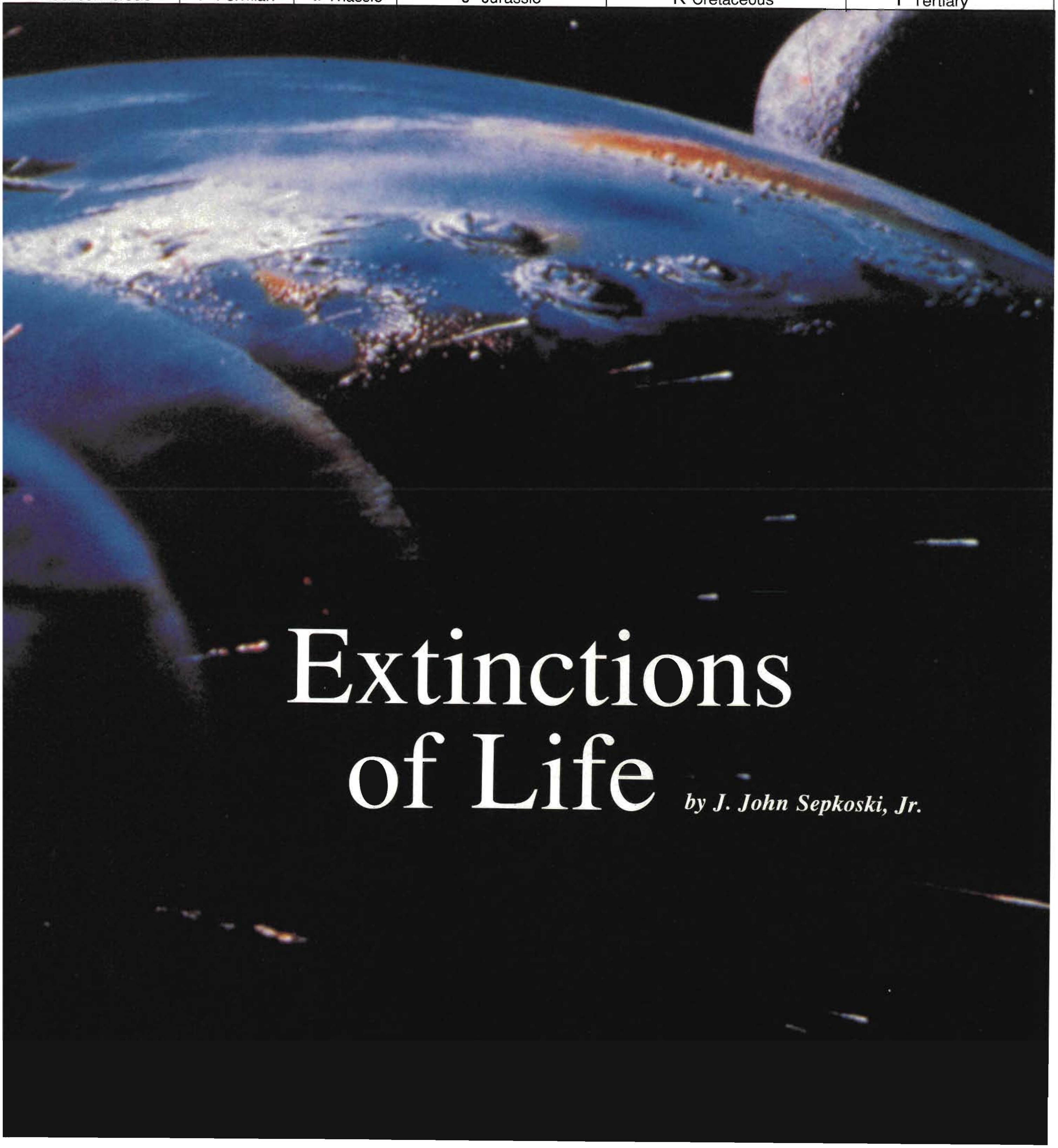
Precambrian		Paleozoic				
	V Vendian	Є Cambrian	O Ordovician	S Silurian	D Devonian	





		Mesozoic			Cenozoic
C Carboniferous	P Permian	Ꞧ Triassic	J Jurassic	K Cretaceous	T Tertiary



Extinctions of Life

by J. John Sepkoski, Jr.

It is a delight to be here and to talk about extinctions of life, although some of you might find that title incongruous. We usually use the word *life* to refer to the collective properties of living organisms. So *extinction of life* suggests perhaps annihilation of *all* life. However, the study of extinctions is in its infancy, and in new fields, where there is much more ignorance than understanding, we often use order-of-magnitude estimates, ballpark guesses, and first approximations. Given that, the title is okay, since, to a first approximation, life *is* extinct. Probably more than 99 percent of all species that have ever lived on this planet have disappeared. The richness of the biota around us reflects only a slight excess of speciation over extinction.

Despite its magnitude and its apparent importance in the evolution of life, we know very, very little about what extinction is, as either a phenomenon or a process. How does a particular species become extinct? What array of processes are operative during an extinction? How frequently are extinctions catastrophic? How can we predict what species or what kinds of species will become extinct in a given situation? And, how can we manage the biota to control extinction in the present and future world? These are some questions that we are not sure how to answer. But they are certainly of vital contemporary importance. As more and more of the earth's surface is altered and re-engineered, we are facing unprecedented levels of extinction, unprecedented at least in historical time. And as we face the possibility of nuclear winter, we need to know what that might do to the biota. Finally, from the standpoint of pure science, we want to understand how extinction has influenced the history of life on this planet and perhaps be able to make statements concerning the evolution of living systems elsewhere in the universe. So we need to know something about extinction—how it operates and what results it produces.

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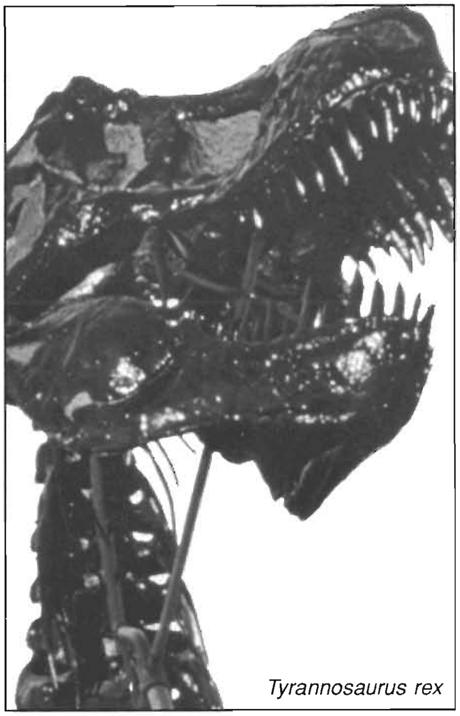


Tyrannosaurus rex

When we think about extinction, the image that immediately comes to mind is the dinosaur. Dinosaurs have been known for well over a century now, the first fossils having been recognized in the 1820s. The early conceptions about dinosaurs were that they were a strange group of animals. They were very large animals, thought perhaps to be too big for terrestrial ecosystems. They were thought to be cold-blooded, like most modern reptiles, and therefore too slow. They were thought to have too small brains and therefore to be too dumb. In a nutshell, dinosaurs were thought to have all of the characteristics that an extinct group of animals ought to have, and their disappearance seemed perfectly understandable. That of course led to the use of the epithet *dinosaur* for anything that is beyond its time and ought to be gone. I hope my students never refer to me as a dinosaur.

Many of the old ideas about dinosaurs have changed radically through research of the last few decades. We now know that not all dinosaurs were large, although the average size was fairly great. Some dinosaurs were the size of birds, and, in fact, some dinosaurs were the ancestors of birds. (Some people make the statement that dinosaurs are not extinct; they have simply taken to the trees.) We know from their morphology that some dinosaurs were very active and were probably not cold-blooded. They may have been as homeothermic as you and I are. From studies of trackways of dinosaurs as well as some of their morphological features, people have argued that dinosaurs weren't incredibly dumb animals. Some of them traveled in organized herds and probably showed some fairly complex behaviors.

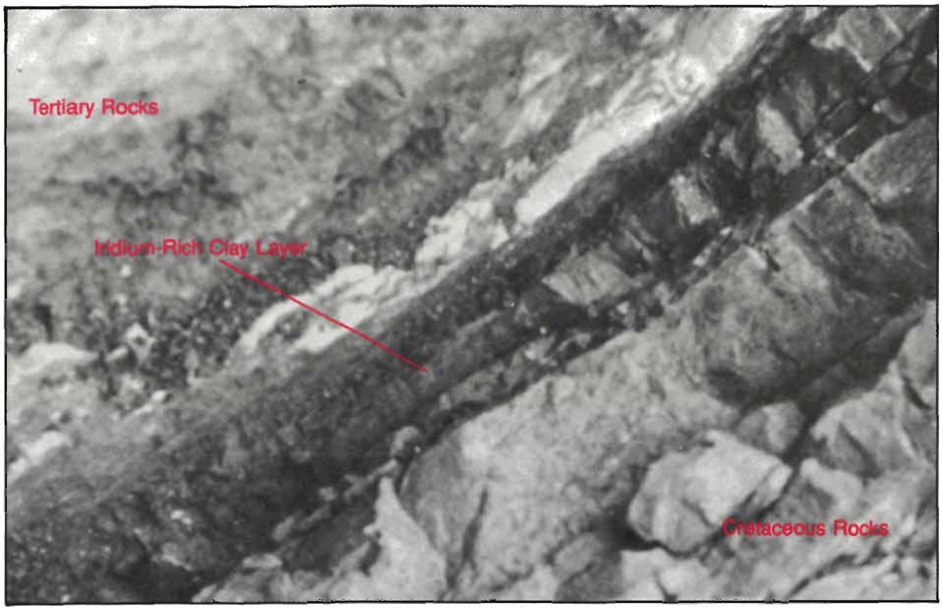
Finally, we know that dinosaurs were the dominant large animals on land for about 150 million years, twice the span during which mammals have held that position. Dinosaurs arose in the late Triassic, at about the same time that mammals appeared. They then dominated the large-animal adaptive zone until they became extinct rather rapidly at the end of the Cretaceous.

The research of the last few decades turned the disappearance of this very symbol of extinction into very much of an enigma. Many speculations were

← Phanerozoic →

Era	Precambrian		Paleozoic							Mesozoic			Cenozoic
Period		V	Є	O	S	D	C	P	Ћ	J	K	T	
4600	670	570	505	438	408	360	286	248	213	144	65	2	

Millions of Years before the Present



IRIDIUM-RICH DEPOSIT AT CRETACEOUS-TERTIARY BOUNDARY

Fig. 1. Close-up of the iridium-rich clay layer at the boundary between Cretaceous and Tertiary rocks in a stratigraphic section near Gubbio, Italy. The high iridium content of the clay (see Fig. 2) is attributed to the impact with the earth of an extraterrestrial body. Since discovery of the Gubbio anomaly in 1978, deposits similarly rich in iridium have been found at Cretaceous-Tertiary boundaries worldwide. (Photo courtesy of Alessandro Montanari, Department of Geology and Geophysics, University of California, Berkeley.) ◀

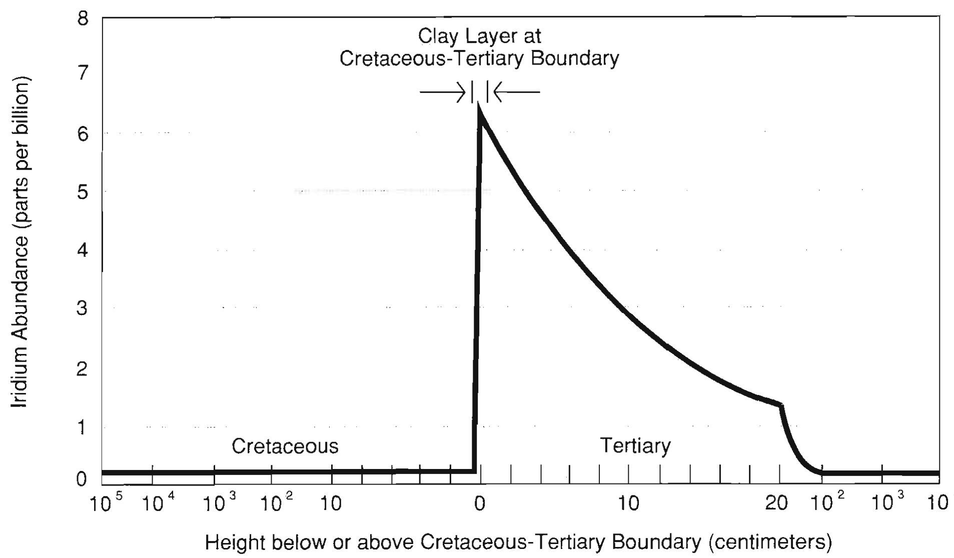
published on what circumstances might have caused dinosaurs to become extinct, but none seemed very satisfying, at least not until a discovery by Luis and Walter Alvarez in 1979.

Most of you are probably familiar with that discovery. Walter Alvarez was looking at some stratigraphic sections, near Gubbio in central Italy, that span the Cretaceous-Tertiary boundary. He saw a peculiar clay layer, 1 to 2 centimeters thick, sandwiched between older Cretaceous rocks and younger Tertiary rocks (Fig. 1). Walter was curious about the clay and sent it back to his father for analysis. Luis, Frank Asaro, and Helen Michel performed a number of geochemical analyses of the clay and found that it contained an excess of iridium (Fig. 2). The excess was far too large to explain on the basis of terrestrial surface sources, which are highly depleted in iridium. They hypothesized that the excess iridium was due to the impact of a large—perhaps 10 kilometers in diameter—extraterrestrial object on the last day of the Cretaceous.

Now an impact by a 10-kilometer-diameter object would wreak havoc on the earth. Various scenarios, which differ quantitatively but agree qualitatively, suggest that huge amounts of dust were thrown into the atmosphere, blocking out sunlight for perhaps three months. The impact may have first heated the atmosphere and then cooled it. It may have produced large amounts of nitrogen oxides, which would rain down as nitric acid. The list of damages can go on and on.

THE ALVAREZ IRIDIUM ANOMALY

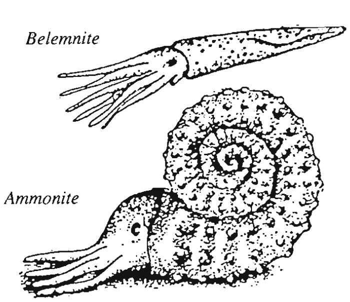
Fig. 2. A plot, versus height above or below the Cretaceous-Tertiary boundary, of iridium abundance in various stratigraphic sections from the vicinity of Gubbio, Italy. The abundance rises abruptly at the end of the Cretaceous to a value some twenty-five times greater than the background level and then falls back to that level within approximately 15,000 years. (Figure adapted from "Current status of the impact theory for the terminal Cretaceous extinction" by Walter Alvarez, Luis W. Alvarez, Frank Asaro, and Helen V. Michel. In Silver and Schultz 1982, 305–315.) ▼



Precambrian		Paleozoic			
	V Vendian	Є Cambrian	O Ordovician	S Silurian	D Devonian

Various climatic and chemical models suggest that the earth wouldn't have been a very pleasant place on the last night of the Cretaceous, that is, the three-month night that followed the impact. Photosynthesis by green plants would have been shut down, and large herbivores that fed upon them would have starved, as would the carnivores that stalked the plant eaters. The expected result would be extinctions. We don't have an equation relating the species that would become extinct to the size of the impacting body. The one thing we do know is that if things got as bad as the models predict, more kinds of animals than just dinosaurs should have become extinct. And indeed that is what the fossil record shows. The flying reptiles, which had a long history in the Mesozoic, vanished at the end of the Cretaceous. In the oceans the large marine reptiles, such as the plesiosaurs, disappeared. So did a large number of marine invertebrates, including the ammonites (well-known marine fossils of the Mesozoic), almost all of the belemnites, and a large variety of clams, snails, crabs, bryozoans, and brachiopods.

Thus a whole suite of organisms became extinct at the same time that the dinosaurs did. From the fossil record we can estimate that about 45 percent of marine animal genera became extinct at the end of the Cretaceous. Extrapolating down to the species level leads to estimates that 60 to 75 percent of marine species became extinct in the last 2 million years or less of the Cretaceous period. So whatever happened was indeed quite devastating to the marine biota.



How do we know what became extinct? How do we make quantitative estimates of the magnitudes of mass extinctions? Paleontologists use two basic methods to study mass extinctions and other events in geologic history. The traditional method is to collect information about the types and numbers of fossils in the various strata of outcrops or core samples and then to determine the times when the various fossil taxa first appeared, flourished, and then disappeared. Such data are then used to assess patterns of origination and extinction and perhaps to test hypotheses concerning those phenomena.

This "normal" methodology gives many details about extinction, such as the abundance of an organism before its disappearance and the time scale of its disappearance. But usually such data are available only for a single group—a single order or class or even phylum—in a rather local region of the earth. And amassing the data is very labor-intensive. Despite a century and a half of work by paleontologists worldwide, we still have detailed data on patterns of extinction for only a small number of localities, a small number of time intervals, and a small number of taxa.

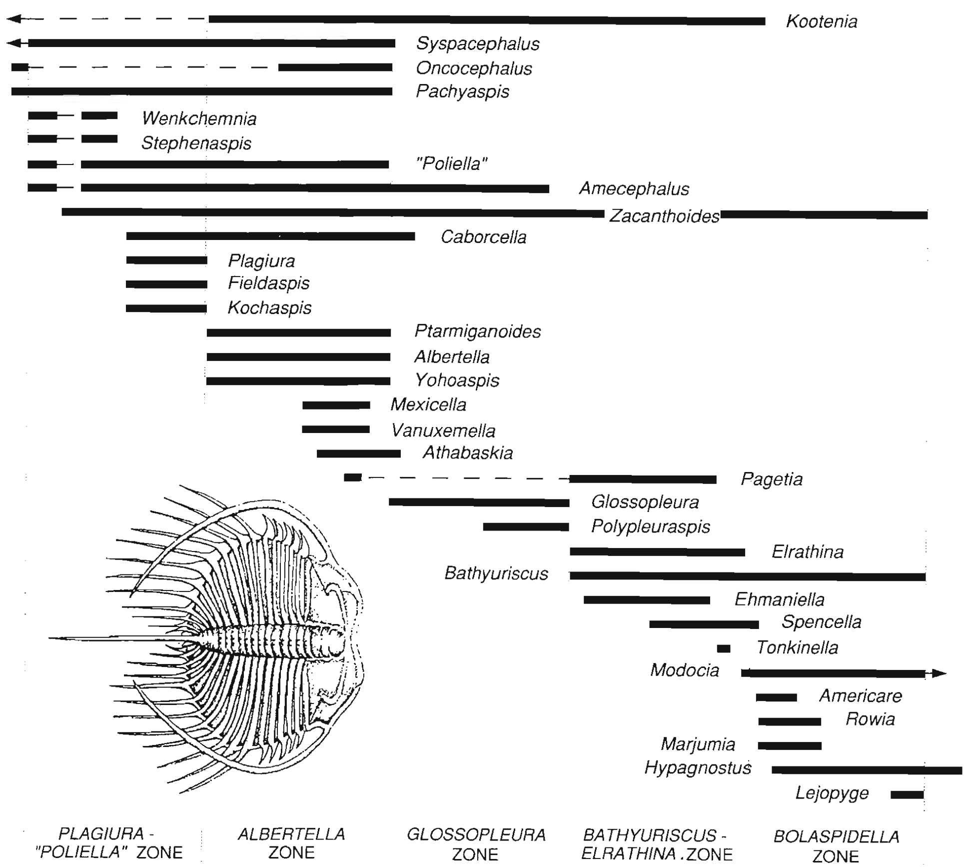
To sidestep the gaps in the detailed paleontological data—and to supplement them—a second way of studying mass extinctions has been developed. This second way has been the subject of my work. Rather than studying detailed information on local patterns of extinction over relatively short time intervals, I am trying to discern global patterns over longer time intervals. My approach is analogous to deducing the population demographics of ancient peoples from the spotty records available. What records have been unearthed are assembled and correlated, as well as possible considering the many records that are missing. The focus is not on individuals but on some higher group—families, perhaps, or tribes.

Like historical census data, the fossil record is incomplete, covering only a small sample of the earth's biota. Still, it contains a huge number of species from all parts of the world—too much data to assess well. We therefore usually work at higher taxonomic levels, such as the genus or the family. We lose resolution doing that but sometimes get a better overall picture, because a genus, say, is included in our data set even if all but one of its species are missing from the fossil record.

I have attempted to obtain data on all animals but have concentrated most of my attention on marine organisms. The reason for doing so is that, although terrestrial organisms, such as dinosaurs, flying reptiles, and giant mammals, are certainly more spectacular, our fossil record for them is far poorer than that for marine organisms. After all, land is an area of net erosion, as you can certainly see in the environs of Los Alamos. The oceans are areas of net sedimentation. They end up with a larger and more complete fossil record that, for various historic and economic reasons, has been far better explored and far better studied.

The detailed data collected by paleontologists are usually presented as "biostratigraphic range charts." Figure 3 is an example showing data for the occurrence of trilobite genera in Middle Cambrian strata in western North America. Note that even this study dealt not with species but with genera. Note also that the geologic zones are not plotted according to scale. That is, the time interval spanned by each zone is not the same, although each is allotted an equal space on the chart. We don't have good estimates of the duration of those geologic time intervals since our methods for determining time in the Cambrian are not accurate enough. Furthermore,

		Mesozoic			Cenozoic
C Carboniferous	P Permian	Tr Triassic	J Jurassic	K Cretaceous	T Tertiary



BIOSTRATIGRAPHIC RANGE CHART

Fig. 3. This chart presents paleontologic data for the time ranges of trilobite genera through the stratigraphic zones of the Middle Cambrian period in western North America. Dashed lines indicate lack of field data. (Figure adapted from *The Cambrian System in the Southern Canadian Rocky Mountains, Alberta and British Columbia (Second International Symposium on the Cambrian System, Guidebook for Field Trip 2)*, compiled by James D. Aiken, edited by Michael E. Taylor, 31. Denver, Colorado: U.S. Geological Survey, International Union of Geological Sciences, Geological Survey of Canada, 1981.) ▶

geologic time intervals usually can be accurately characterized only over local areas.

Putting together data for all fossil marine taxa from all over the world, we come up with something like a small telephone book. Figure 4 is a page from such a compilation giving first and last appearances in the fossil record for Cambrian and Ordovician trilobite families. The data set I have assembled covers about 3500 marine families and about 30,000 marine genera.

To develop some picture of extinction patterns from such a data set, the simplest thing to do is to count the number of families or genera that are present in each time interval. In the case of families, 77 standard geologic time intervals compose the last 600 million

EXTINCTION DATA FOR TRILOBITE FAMILIES

Fig. 4. A page from a summary of data on the appearance and disappearance worldwide of marine families. The data shown are those for trilobites. The abbreviations in parentheses denote subdivisions of the Cambrian and Ordovician geologic periods. (Figure adapted from *A Compendium of Fossil Marine Families* by J. John Sepkoski, Jr. Milwaukee Public Museum Contributions in Biology and Geology Number 51. Milwaukee, Wisconsin: Milwaukee Public Museum Press, 1982.) ◀

Class Trilobita	
Order Agnostida (= Miomera)	
Agnostidae	Ꞓ (Boto) — O (Ashg)
Clavagnostidae	Ꞓ (uMid) — Ꞓ (Dres)
Condylopygidae	Ꞓ (Boto) — Ꞓ (uMid)
Diplagnostidae	Ꞓ (mMid) — O (Trem)
Discagnostidae	Ꞓ (Dres)
Eodiscidae	Ꞓ (Atda) — Ꞓ (uMid)
Pagetiidae	Ꞓ (Atda) — Ꞓ (mMid)
Phalacromidae	Ꞓ (uMid) — Ꞓ (Dres)
Sphaeragnostidae	O (Ashg)
Trinodidae	Ꞓ (Dres) — O (Ashg)
Order Redlichiida	
Abadiellidae	Ꞓ (Atda) — Ꞓ (lMid)
Bathynotidae	Ꞓ (Boto) — Ꞓ (lMid)
Chengkouiidae	Ꞓ (Boto)
Daguinaspididae	Ꞓ (Atda)
Despujolsiidae	Ꞓ (Atda)
Dolerolenidae	Ꞓ (Atda) — Ꞓ (Boto)
?Ellipsocephalidae	Ꞓ (Atda) — Ꞓ (mMid)
Emuellidae	Ꞓ (lMid)
Gigantopygidae	Ꞓ (Boto)
Hicksiidae	Ꞓ (Boto)
Kueichowiidae	Ꞓ (Boto)
Longduiidae	Ꞓ (Boto)
Mayiellidae	Ꞓ (Boto)
Neoredlichiidae	Ꞓ (Atda) — Ꞓ (Boto)
Olenellidae	Ꞓ (Atda) — Ꞓ (mMid)
Paradoxididae	Ꞓ (Atda) — Ꞓ (uMid)
Protolenidae	Ꞓ (lTom) — Ꞓ (mMid)
Redlichiidae	Ꞓ (Atda) — Ꞓ (mMid)
Saukiandidae	Ꞓ (Boto)
Yinitidae	Ꞓ (Atda) — Ꞓ (Boto)
Yunnanocephalidae	Ꞓ (Atda)

Precambrian		Paleozoic			
V Vendian		Є Cambrian	O Ordovician	S Silurian	D Devonian

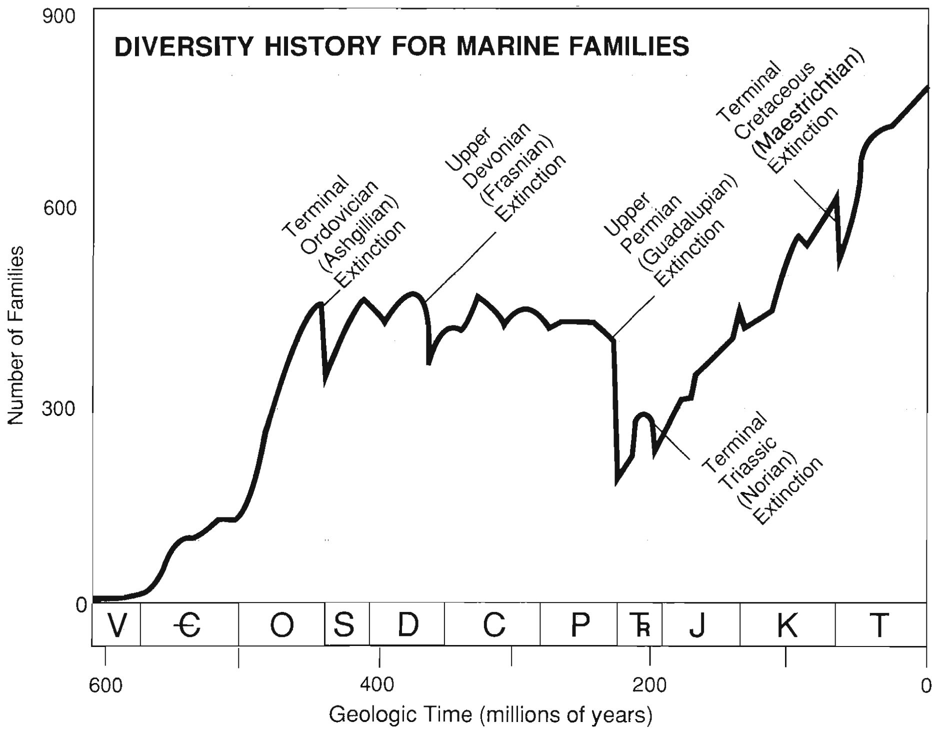
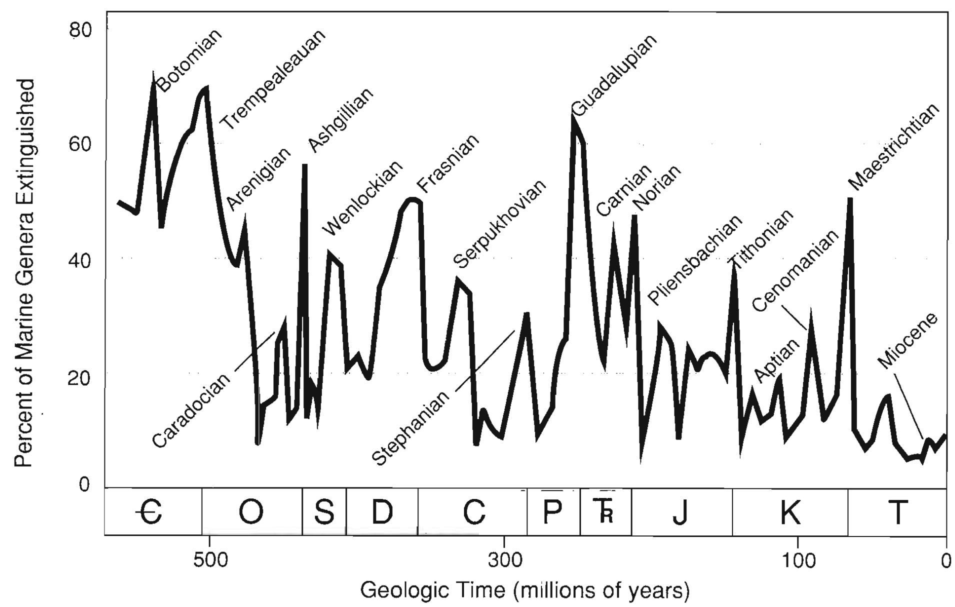


Fig. 5. This history of marine animal diversity reveals five principal mass extinctions, of which the upper Permian, or Guadalupian, was by far the most devastating. Lesser extinction events are also visible. (Figure adapted from "Mass extinctions in the Phanerozoic oceans: A review" by J. John Sepkoski, Jr. In Silver and Schultz 1982, 283–289.) ◀

EXTINCTION RATE HISTORY FOR MARINE GENERA

Fig. 6. This history of extinction rates shows more clearly than the diversity curve (Fig. 5) the many extinction events experienced by marine fauna. (Figure adapted from "Phanerozoic overview of mass extinction" by J. J. Sepkoski, Jr. In *Patterns and Processes in the History of Life (Report of the Dahlem Workshop on Patterns and Processes in the History of Life, Berlin 1985, June16–21)*, edited by D. M. Raup and D. Jablonski, 277–295. Berlin: Springer-Verlag, 1986.) ▼



years, which is often referred to as the Phanerozoic, the eras of geologic time for which evidence of animal life on the earth is abundant. For genera the data base I have is a little better, composed of about 100 time intervals (attained by carefully subdividing some of the longer standard intervals).

Figure 5 is a plot of the number of marine animal families versus time interval. The big mass extinctions show up as large and rapid drops in the number of families. As you can see, the terminal Cretaceous, or Maestrichtian, extinction, the one that led to the demise of the dinosaurs on land, was fairly rapid but not excessively large. About 17 percent of marine animal families disappeared in that time interval. Because the disappearance of a family requires the disappearance of every genera and species within the family, a family kill of about 17 percent corresponds to a genus kill of about 45 percent and a species kill of around 60 to 75 percent.

The terminal Cretaceous event certainly isn't the only large mass extinction we see in Fig. 5. And it certainly isn't the largest. The largest was the Guadalupian at the end of the Permian, when about 55 percent of marine families became extinct. Virtually every order and class of marine organisms lost an extensive number of families. Going through the same sort of extrapolation,

			Mesozoic			Cenozoic
C Carboniferous	P Permian	₸ Triassic	J Jurassic		K Cretaceous	T Tertiary

we find that about 80 percent of marine genera and perhaps more than 95 percent of marine species disappeared at the end of the Permian period. Other major events visible in Fig. 5 include one at the end of the Ordovician, which is probably the second largest extinction of marine animal fauna. But it is not that much larger than the one at the end of the Cretaceous. Another extinction occurred in the late Devonian, and another in the late Triassic, right on the tail of the Guadalupian extinction.

In addition to the large mass extinctions, many smaller extinction events have occurred—in fact, around two dozen. Simple diversity data don't reveal the smaller extinctions, but other metrics of extinction intensity do.

Figure 6 shows one such metric, a plot of the extinction rate for marine genera in each of the hundred or so sampling intervals spanning the Phanerozoic. Most of the spikes, or local maxima, correspond to extinction events. The larger spikes—the Maestrichtian, the Norian, the Guadalupian, the Frasnian, and the Ashgillian—are the same major mass extinctions that we see in the familial diversity data (Fig. 5). Many of the other spikes have been recognized by paleontologists in detailed field data on localized regions and restricted groups of organisms.

TIMING OF MARINE GENERA EXTINCTIONS

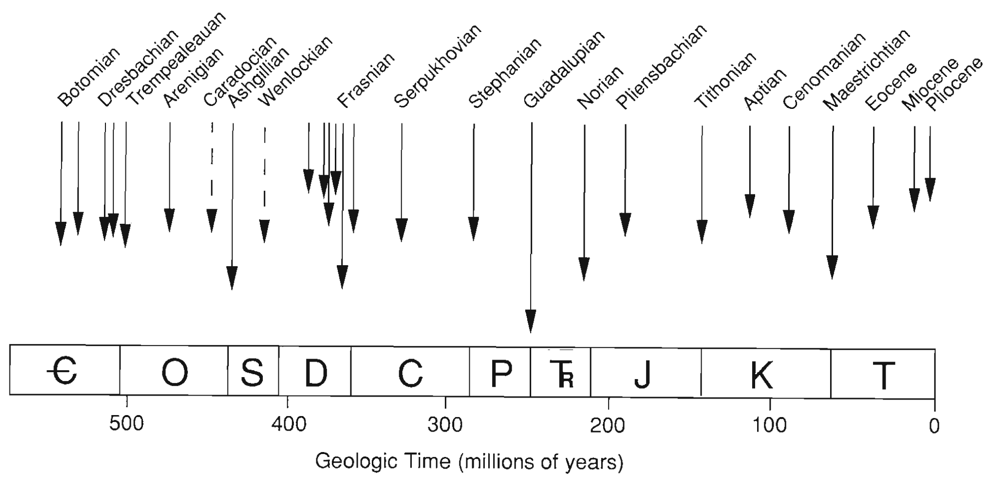


Fig. 7. At least during the most recent 300 million years of geologic time, extinctions have occurred with considerable regularity, as this display of the data of Fig. 6 reveals. The lengths of the arrows indicate the magnitudes of the extinction rates. (Figure adapted from "Phanerozoic overview of mass extinction" by J. J. Sepkoski, Jr. In *Patterns and Processes in the History of Life (Report of the Dahlem Workshop on Patterns and Processes in the History of Life, Berlin 1985, June 16–21)*, edited by D. M. Raup and D. Jablonski, 277–295. Berlin: Springer-Verlag, 1986.)

The data of Fig. 6, particularly when displayed as in Fig. 7, reveal a very interesting feature of extinctions—a remarkable regularity in their timing during the past 300 million years. That observation was first made by Al Fisher in the late seventies and was then rediscovered by my colleague David Raup and me about five years ago when we were looking at the family data.

Figure 8 is another attempt to portray the regularity. Here I have simply assigned a cycle number to extinction events during the last 250 million years and plotted the cycle numbers against the estimated times of the events. Note the good fit of the data points to a straight line, which indicates a constant, or stationary, periodicity. Dave Raup and I have performed a variety of analyses and have found that the probability of such a periodic extinction pattern occurring at random is extremely low. A stationary periodicity describes the extinction events far better than any sort of random or semi-random model we can conceive of. I am quite convinced that, at least over the last 250 million years of the earth's history, extinctions have occurred with a stationary periodicity of 26 million years.

That observation, however, does not agree with traditional views of mass extinctions, which implicitly assume that each extinction event was produced independently by some random environmental perturbation or perhaps by a random coincidence of several environmental variables. And, since each extinction event was independent of the others, it therefore could be studied independently. But if the extinction events recur regularly, they cannot be independent of one another, at least not in terms of their timing. Perhaps we are dealing with a series of events caused by a single, ultimate forcing agent that has clock-like behavior.

When Dave Raup and I published that speculation, we didn't know what the agent was. However, one event, the terminal Cretaceous mass extinction, was known to be associated with the impact of a large extraterrestrial object with the earth. If an impact caused one mass extinction in the periodic sequence, perhaps impacts caused all the others as well.

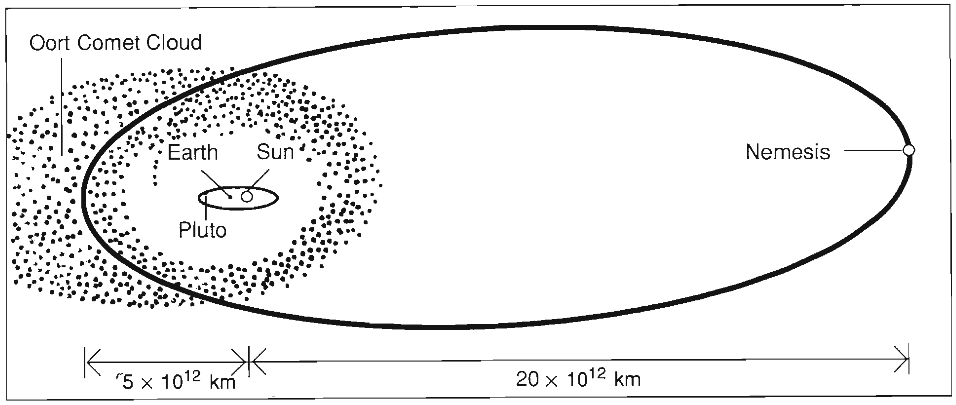
The idea that most mass extinctions, at least over the last 250 million years, are the result of impacts of one or more extraterrestrial bodies leads of course to the next question: What could be the cause of regularly periodic impacts? Several hypotheses have been offered;

Precambrian		Paleozoic			
	V Vendian	Є Cambrian	O Ordovician	S Silurian	D Devonian

the best known is the Nemesis, or so-called death-star, hypothesis (Fig. 9), which was put forward independently by several groups. The idea is that the sun is not alone, that it is accompanied by a small companion star in a highly elliptic orbit with an orbital periodicity of 26 million years or so. That companion, Nemesis, is usually far from the sun, but during the small portion of its period when it is passing through the Oort Cloud, it scatters up to a billion comets into the inner solar system. Jack Hills has calculated that, out of that billion or so comets, perhaps an average of about two dozen of various masses hit the earth, wreaking havoc and causing extinction of many species on land and in the ocean.

Several years ago we were all very excited about such ideas, but time has tempered our excitement somewhat. Some of the predictions of the models are now looking a little cloudy, if you will permit me. Carl Orth, Frank Kyte, and others have failed to find iridium or other geochemical anomalies appearing consistently with the various periodic extinctions. Although an iridium anomaly and microtektites are associated with the Eocene extinction event, the one that occurred about 26 million years after the end of the Cretaceous, there is no good evidence of impact signatures at many of the others. Also, Nemesis has not yet been found, and there are some unresolved theoretical problems with the death-star hypothesis, expecially about the stability of the companion star's orbit.

The only thing that I think has survived is the regular periodicity of the extinctions. To me that still looks good, especially now that some of the gaps in the periodic series have been filled in. But some better data have also led to new observations and new questions.

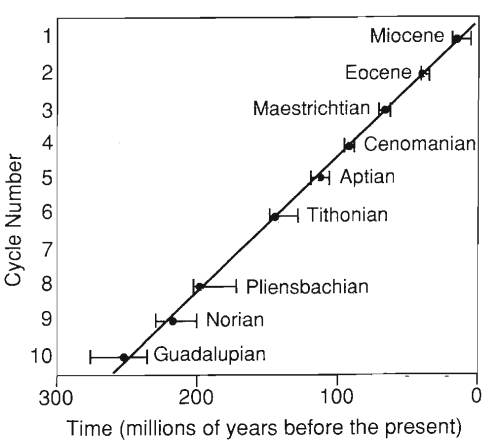


THE NEMESIS HYPOTHESIS

Fig. 9. The Nemesis hypothesis has been proposed as an explanation for the apparent regular periodicity of extinctions. According to that hypothesis, Nemesis, a companion star of the sun, scatters comets into the inner solar system when it passes through the Oort Cloud every 26 million years. The impacts of a small number of the scattered comets with the earth cause the observed extinctions.

REGULAR PERIODICITY OF MESOZOIC EXTINCTIONS

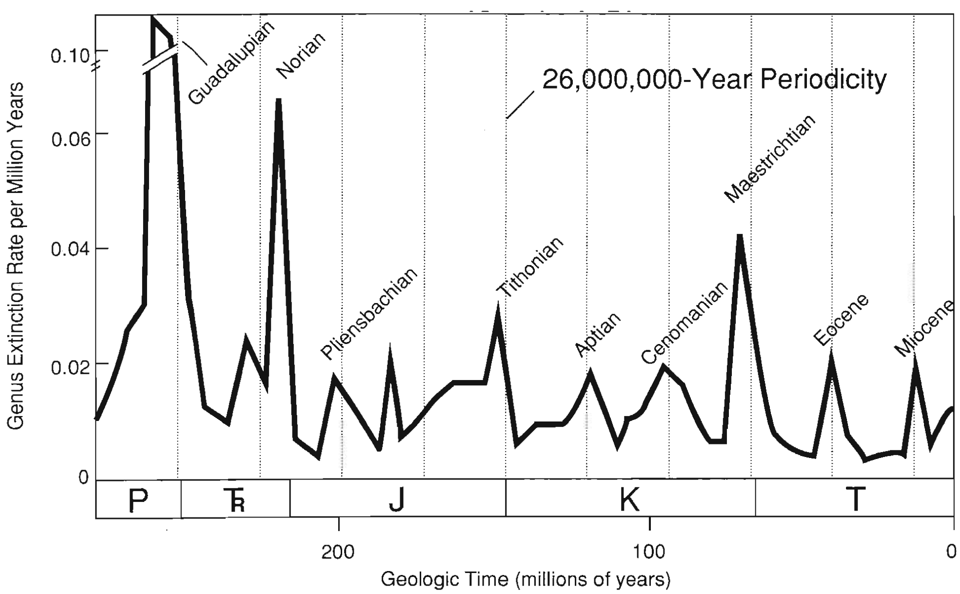
Fig. 8. The data points in this graph consist of "cycle numbers" assigned to the Mesozoic and Cenozoic extinction events and the times of their occurrence. The good fit of the points to a straight line indicates that the extinctions are regularly periodic. (Figure adapted from "Periodicity in marine extinction events" by J. John Sepkoski, Jr., and David M. Raup. In *Dynamics of Extinction*, edited by David K. Elliott, 3–36. New York: John Wiley & Sons, 1986.)



One of the more remarkable observations that come from the latest generation of data is shown in Fig. 10, a plot of the per genus extinction rate per million years. That metric is essentially the probability of extinction per time interval. Figure 10 seems to show a remarkable uniformity not only in the timing but also in the magnitude of the smaller extinction events. Within the resolution of the data, the smaller events are identical in amplitude. In addition to the smaller, constant-amplitude events, we have a few outliers, particularly the Maestrichtian, Norian, and Guadalupian events. Perhaps—and this is pure speculation now—the impact or whatever it was that happened at the end of the Cretaceous, say, was simply coincidental with a peak of extinction produced by an independent periodic forcing agent, and the combination of the two caused absolute havoc. But if the impact had occurred in a trough between periodic events, it would have caused a much smaller, aperiodic extinction event.

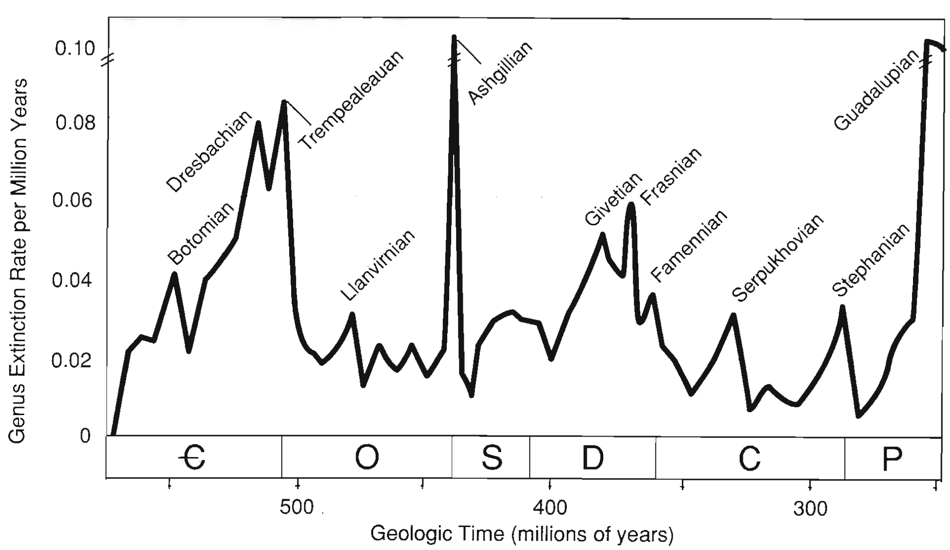
Figure 11 is a similar plot for the Paleozoic era. The extinction peaks in the Permian and Carboniferous periods still give an impression of some regularity in their timing. There is a little more vari-

		Mesozoic			Cenozoic
C Carboniferous	P Permian	Ꞧ Triassic	J Jurassic	K Cretaceous	T Tertiary



COMPARISON OF 26,000,000-YEAR PERIODICITY AND MESOZOIC EXTINCTION PEAKS

Fig. 10. This superposition of a 26,000,000-year periodicity on data for genus extinction rates during the Mesozoic shows how closely such a regular periodicity fits the extinction peaks. Note also the similarity in magnitude among most of the extinction rate peaks. (Figure adapted from Sepkoski 1986.)

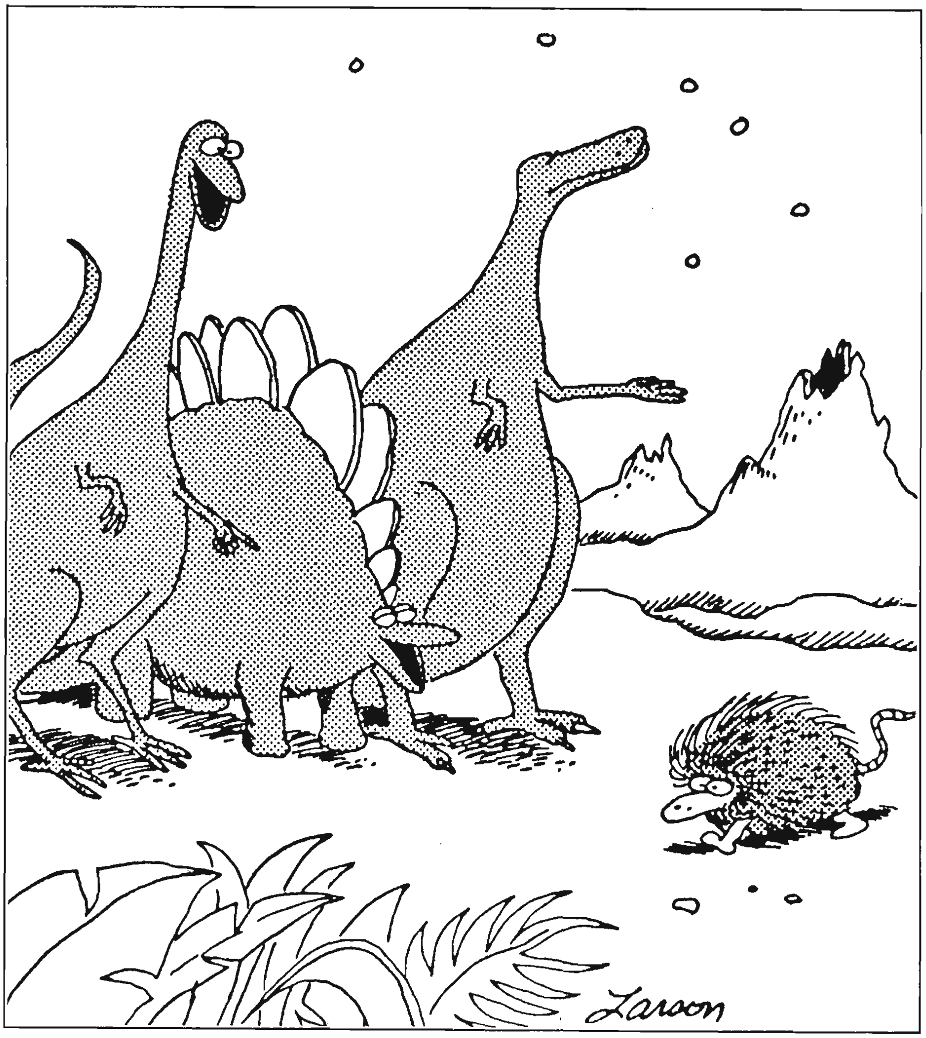


PALEOZOIC EXTINCTION PEAKS

Fig. 11. During the Permian and Carboniferous periods of the Paleozoic era the peaks of the genus extinction rate history exhibit a fairly regular periodicity but one closer to 30 to 35 million rather than 26 million years. In contrast, the earlier extinction peaks (during the Devonian, Silurian, Ordovician, and Cambrian periods) seem to lack any periodicity. (Figure adapted from Sepkoski 1986.)

ation in the timing, but then our ability to estimate geologic time during that era isn't so good. However, our best estimates suggest that the spacing between the Permian and Carboniferous events is on the order of 30 to 35 million years, somewhat longer than the 26-million-year spacing between the Mesozoic events. Perhaps that indicates a variable periodicity. Back beyond the Carboniferous the pattern seems to break down into chaos. It is not clear whether the lack of pattern, or at least of periodic pattern, represents problems with the fossil data or with our ability to tell geologic time accurately. It is also possible that the apparently chaotic pattern reflects a combination of periodic and aperiodic events. And it is eminently possible that there is no periodicity at all in the Paleozoic.

Despite the many unanswered questions about extinction, one thing is clear: Many extinction events have occurred, some of them rather large. And that fact raises a question that's not easy to answer: What are the effects of those frequent extinction events on the course of evolution, on the history of the earth's biota? Our feeling is that the effects were more profound than the simple elimination of various



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taxa, such as the "outmoded" dinosaurs. Indeed, the extinction events may have had some very constructive effects.

Looking back at Fig. 5, we see that the number of marine families rises rapidly to a sort of equilibrium during the Paleozoic era. That equilibrium is punctuated by extinction events of various amplitudes but the system seems to rebound and to fill up again rather quickly. Then the great Permian mass extinction seems to destabilize the system, and the subsequent number of families rises above the former equilibrium value. But, in fact, arguments can be made that diversity was already increasing before that event, and what appears to be a great increase in the number of families during the Mesozoic and early Cenozoic eras is a combination of rebound from the Permian event and a natural rise that would eventually have moved asymptotically toward a greater equilibrium value.

The reason the system fills up is that the whole-ocean ecosystem is finite in terms of habitat space and other resources. Therefore it can hold only a limited number of kinds of animals. And the reason the system rebounds very quickly after an extinction event is that ecospace has been opened up, which leads to a very rapid radiation into specialized taxa. Even during the long-term rise in diversity during the Mesozoic and Cenozoic, we see rapid rebounds after the Norian and Maestrichtian mass extinctions. So those large mass extinctions are opening up ecospace and promoting very rapid evolution in their wake.

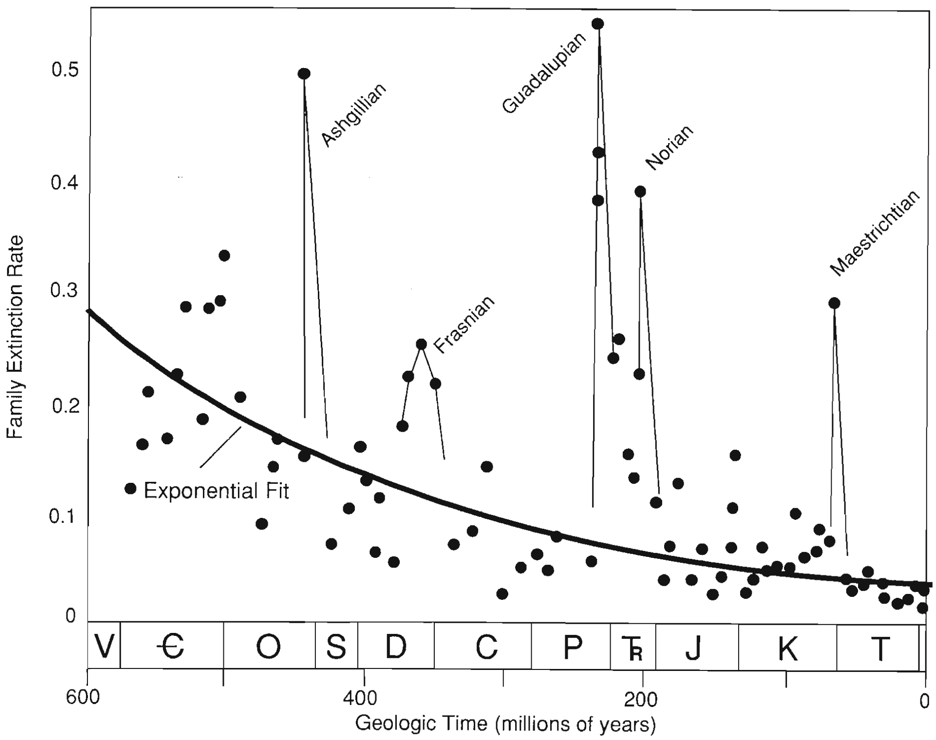
Let's look at evolutionary innovation, that is, at the appearance of new kinds of animals, in the marine system. We find that after the Ordovician period nearly two-thirds of the new taxonomic orders that appeared in the oceans originated during the rebounds that followed extinction events. Those rebounds, though, constitute only one-third of the time span. So mass extinctions increase evolutionary innovation by a factor of about 2 and in that sense seem to be filling a creative, constructive role. However, the best example of this by far is seen not in the oceans but on land.

Did you know that your ancestors were vermin? During most of its history, the mammal class consisted of tiny quivering vermin living in the interstices of a dinosaurian world. Mammals have been pre-eminent only for the last 65 million years, that is, only following the rapid extinction of dinosaurs. Within approximately a dozen million years of the early Tertiary, virtually every modern order of mammal—from mice to whales, from bats to elephants—appeared in terrestrial ecosystems. It was as if an inhibiting force on innovative mammalian evolution had been lifted with elimination of the dinosaurs.

This constructive role of mass extinction might be absolutely necessary in the earth's evolutionary system and perhaps in evolutionary systems elsewhere in the universe, as George Wald certainly argued and I'm sure Frank Drake will argue.

Another feature of extinction in general that increases the evolutionary importance of the large mass extinctions is the following. In some of the graphs shown previously, you may have noticed a secular decline in the "background" extinction rate through the Phanerozoic. (Background extinction is total extinction minus that occurring during the big mass extinctions.) The rates tend to be very high early in the Cambrian and decline through the later Phanerozoic. Figure 12 shows how a simple exponential fits that decline for marine families. The decline suggests that marine taxa are becoming more and more resistant to whatever processes cause extinction, at least at the family

		Mesozoic			Cenozoic
C Carboniferous	P Permian	Ꞁ Triassic	J Jurassic	K Cretaceous	T Tertiary



DECLINE OF BACKGROUND EXTINCTION

Fig. 12. Extinction is an ever-present feature of geologic history. The background extinction (that is, total extinction minus the large peaks of extinction) shows a decline throughout the Phanerozoic that is fitted quite well by a simple exponential. Such a decline has implications for evolutionary innovation. (Figure adapted from "Some implications of mass extinction for the evolution of complex life" by J. John Sepkoski, Jr. In *The Search for Extraterrestrial Life: Recent Developments (Proceedings of the 112th Symposium of the International Astronomical Union held at Boston University, Boston, Mass., U.S.A., June 18–21, 1984)*, edited by Michael D. Papagiannis, 223–232. Dordrecht, Holland: D. Reidel Publishing Company, 1985.)

level. We might speculate that background extinction will asymptotically grind to a halt. If that should happen and if no more mass extinctions occur, there would be very little potential for evolutionary innovation or for further evolutionary development of the ecosystem. The evolutionary machine might not halt completely, but it would certainly slow down without major mass extinctions to reset it. Thus extinctions may be a necessary force in the development of complex life and, from what we see of patterns at the end of the Cretaceous, perhaps even for the appearance of consciousness in an evolutionary system.

I hope I have shown that our understanding of extinction is still very limited and that this aspect of the science of life presents numerous unsolved problems. ■

Questions and Answers

Question: Has anybody tried to correlate the dates of large craters with those of extinction events? Also, a lot of meteors are carbonaceous chondrites, which probably wouldn't be expected to contain much iridium. So wouldn't it be a mistake to say that if you don't find iridium there was no impact?

Sepkoski: In 1982 Greeve published a compendium of the best estimates of crater ages at that time. An analysis by Walter Alvarez and Rich Muller suggested a periodicity in those crater ages that wasn't too different from the periodicity we see in extinction events. Since then a lot of the crater dates were cleaned up, and on reanalysis the periodicity didn't look as good. But several manuscripts now in press or review [and subsequently published] indicate that a periodicity in crater ages has been essentially refound. If it is assumed that maybe 50 to 65 percent of the craters are due to random cratering events, perhaps impacts of Apollo asteroids or something of that nature, the timing of the rest of the craters looks quite periodic statistically. However, the periodicity is about 30 million years, which isn't the same as 26 million years. Also, over at least the most recent part of the extinction time series, the crater dates are out of phase by about 9 million years.

Your second question would best be answered by an expert on meteorites, which I am not. But it is my understanding that virtually all meteorites, except eucrites, are enriched in iridium relative to earth crustal rocks, often by several orders of magnitude.

Question: Is the type of extinction due to humans the same as that of the older extinctions?

Sepkoski: I think that the advent of humans has probably caused two mass extinctions. There was certainly a major extinction on land—but not in the oceans—about twelve thousand years ago. The Holarctic continents, South America, and Australia lost their large mammal fauna then. According to some pretty good arguments, now coupled with some pretty good evidence, that extinction event was related to the appearance of fairly efficient hunting bands at the end of the last ice age. Of course, the extinction was an aperiodic event, and so I would expect some extraordinary agent, such as human predation, to have been responsible. Like many earlier mass extinctions, the event twelve thousand years ago affected large terrestrial animals but not marine fauna. There are also good arguments that in historical times we have entered a second mass extinction that is much more extensive in terms of the kinds of organisms that are being affected. It is difficult as yet to get good information on what kinds of organisms are being affected at present, so comparisons with older events are tenuous.

The closing statements I made about the beneficial effects of extinction may need a litttle clarification. As a paleontologist, an evolutionary paleobiologist, I am looking at how the whole evolutionary system behaves over vast spans of time—tens of millions of years. That is very different from processes that happen over human time scales of days, weeks, and years. I fear that some of the animals and plants disappearing right now may be very useful for a variety of purposes. We shouldn't be too relaxed to see them disappear before we can characterize them better and know what the short-term ramifications of their extinction are. The rebounds from mass extinctions, which take place over 10 million years or so, may be good from the standpoint of a large-scale evolutionary system such as the entire biosphere of the earth. But, from the human standpoint, the first few decades or centuries after the initiation of an extinction event may in fact be quite catastrophic. Thus, my comments about the constructive aspects of extinction are meant to give solace.

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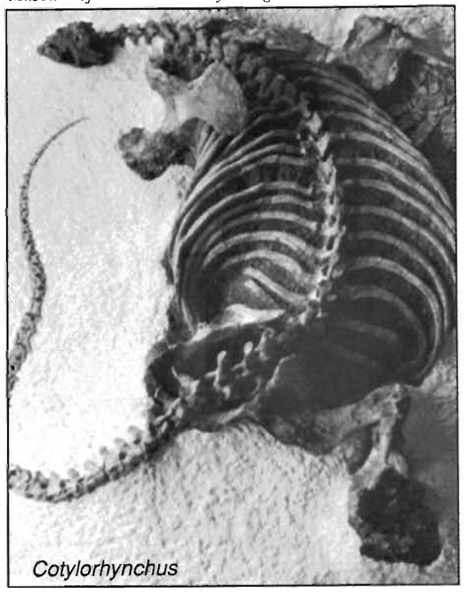

Cotylorhynchus

Question: Are there correlations between the changes in the earth's magnetic field and the extinction events?
Sepkoski: Work by David Raup and several others suggests that the reversals of the earth's magnetic field over the last 200 or 250 million years show a periodicity. But there is some question as to whether that periodicity is stationary or nonstationary. Also the purported periodicity isn't the same as that of the extinction events. It is about 30 million years, more in tune in both frequency and phase with the cratering periodicity than with the extinction periodicity.

Question: The effects of an impact that creates a crater a couple hundred kilometers in diameter are obviously horrendous—far worse than those of a nuclear war. So how can it be that an extinction is not associated with every large crater?
Sepkoski: An extinction of some magnitude could well be associated with every large crater, but that doesn't mean we would see such a correlation in the data. I could, for instance, sweep that whole question under the rug by simply saying that our ability to date craters is still rudimentary, not nearly approaching even our ability to date fossils. The problem may also lie in the loss of resolution we incur by dealing with higher taxonomic levels. Remember that even the impact at the end of the Cretaceous, which spread a 1-centimeter dust layer over the entire face of the earth, eliminated only about 17 percent of the animal families in the oceans, and on land it eliminated only about 10 percent of the vertebrate families. So at the family level the biosphere seems rather insensitive to perturbation. The combination of a small response and imperfections in the data for higher taxonomic levels could obliterate any observable response. Alternatively, absence of a marked response in association with an impact or the like could mean that the impact was completely out of phase with the periodic extinction force. We are trying to use statistical models to sort out these problems and to learn how to start attacking when we see associations, but we are really just beginning.

Question: Are there any explanations for the rebound phenomenon, and does the nature of the animals that survive an extinction provide information about the nature of the extinction force?
Sepkoski: That is a very good question. One thing that we know from looking at radiations, including rebounds, is that evolution can go on extraordinarily rapidly, at least on geologic time scales. If the rate of evolution across the Precambrian-Cambrian boundary had continued to the present, the oceans would now contain on the order of 10^{27} families, in contrast to the about 3×10^3 that in fact they do contain. (We would essentially have bouillabaisse from New York to London.) What we

		Mesozoic			Cenozoic
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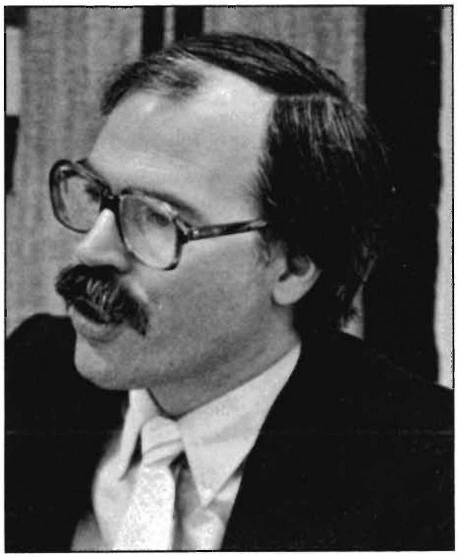
see as normal rates of evolution through most of the fossil record seem to be very, very damped, which I suspect is just a crowding effect. The clearing of ecospace by the extinction of a lot of species may take the brakes off evolution, so that the initial, unconstrained evolutionary rates are again in effect, rapidly refilling the open ecospace. The evolutionary rates during the rebounds can be of about the same magnitude as that across the Precambrian-Cambrian boundary, when animals were first appearing in large numbers in the marine system.

At this time only a few systematic studies of victims and survivors of mass extinctions exist, and so little can be deduced from them about the nature of extinctive forces. At the end of the Cretaceous, small animals and animals in detritus-based food chains preferentially survived, which seems consistent with impact scenarios. On the other hand, warm-blooded, high-energy birds also survived, which seems problematic. Whatever the forces, David Jablonski recently completed a study for the Cretaceous that suggests the rules of the game change during mass extinctions: Victims of those events do not have the same sort of properties as species that are vulnerable to extinction during normal "background" times. Thus, mass extinctions represent more than simply intensification of extinction; they represent real changes in the nature of extinctive forces.



J. John Sepkoski, Jr., received a B.S. in geology from the University of Notre Dame in 1970 and a Ph.D. in geological sciences from Harvard University in 1977. After serving from 1974 to 1978 as an Instructor and then Assistant Professor in the Department of Geological Sciences at the University of Rochester, he moved to the Department of the Geophysical Sciences at the University of Chicago, where he is now a Professor of Paleontology. He is also a Research Associate at the Field Museum of Natural History. In 1983 he received the Charles Schuchert Award from the Paleontological Society. He has served as coeditor of *Paleobiology* and is a consulting editor for McGraw-Hill's *Encyclopedia of Science and Technology*. He is a member of the American Association for the Advancement of Science, the Paleontological Society, the Society of Sigma Xi, and the Society for the Study of Evolution.

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