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THE SEARCH FOR EVIDENCE OF MASS EXTINCTION

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A QUARTER OF A BILLION YEARS AGO THE "GREAT DYING" CHANGED EARTH'S ECOLOGICAL RULES. DO CURRENT GLOBAL EVENTS SIGNAL A SIMILAR REVOLUTION?

CHARLES DARWIN FAMOUSLY CONCLUDED On the Origin of Species by Means of Natural Selection with upbeat reassurance: "There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that...from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved." But the subtitle of his work--The Preservation of Favoured Races in the Struggle for Life--is a reminder that nearly all of those "endless forms" are extinct. Moreover, we now know that both evolution and extinction are not always the gradual, incremental processes that Darwin envisioned. The escalating impact of the human population on Earth is even billed as a "sixth mass extinction." With extinction the rule rather than the exception, however, disentangling the mechanisms and outcomes of a "mass" extinction turns out to be anything but easy.





Marine sedimentary rocks, exposed in Tibet as a result of mountain building, record the end of the Permian period and beginning of the Triassic, about 251 million years ago. The mass extinction at that juncture also marks the transition from the Paleozoic era to the Mesozoic. Opposite page: Silurian- or Devonian-period fossils of crinoids, about 410 million to 420 million years old, were collected in Morocco. Crinoids were among the many sedentary, filter-feeding animals of the Paleozoic era.

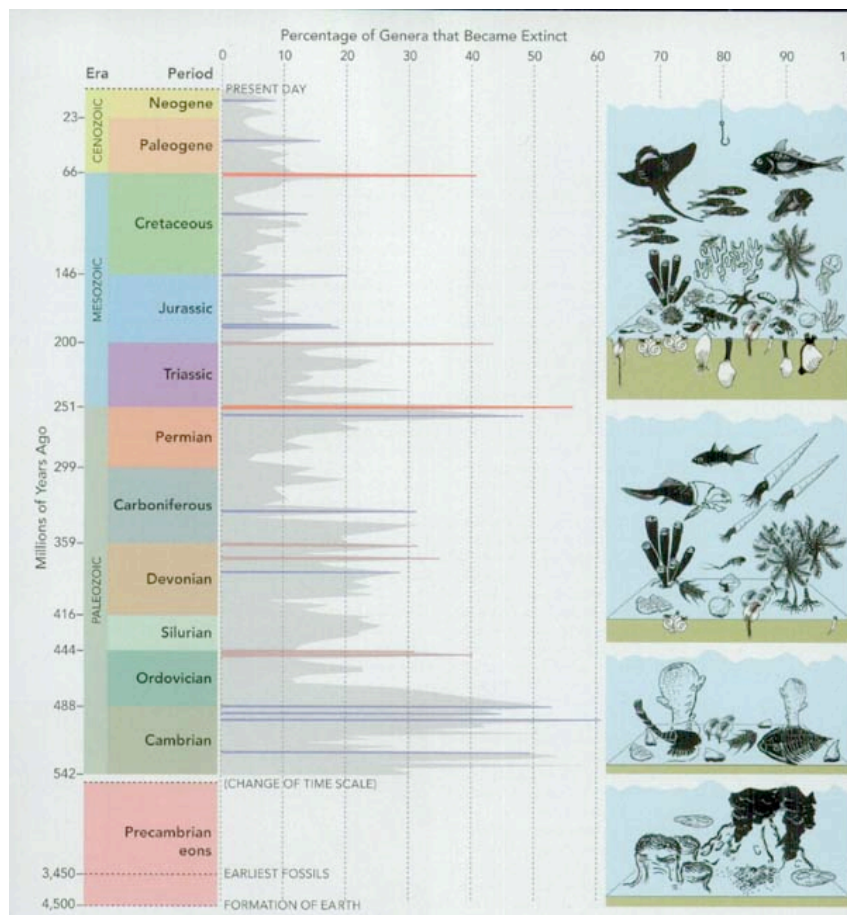
Darwin and the geologist Charles Lyell took the fossil record to be incomplete and were skeptical that it could reveal much about patterns of extinction and diversity. But in 1860, only a year after Origin's publication, the geologist John Phillips begged to differ in a groundbreaking lecture at Cambridge, published as *Life on the Earth, Its Origin and Succession*. "Surely this imperfection of the geological record is overrated," he wrote. "With the exceptions of the two great breaks at the close of the Palaeozoic and Mesozoic periods, the series of strata is nearly if not quite complete, the series of life almost equally so." Looking back in time, Phillips saw that the fossil faunas of Britain during the Paleozoic, Mesozoic, and Cenozoic were distinct from one another (we now call those great successive stretches of time eras, using the term period for shorter subdivisions). He also showed that drastic reductions in the variety of fossil life at the ends of those eras were followed by radiations of new forms.

Such mass extinctions and subsequent radiations appeared to differ from the gradual turnover of life forms typical of most of the fossil record. Naturally, scientists were tempted to hypothesize causes. In 2006, Richard K. Bambach, a professor emeritus of paleontology at Virginia Tech, reviewed the historical highlights of that quest. In 1952, for example, geologist Norman D. Newell proposed that mass extinctions might best be accounted for by a drastic drop in sea level that would have devastated ocean life in all the broad shallow zones. Soon thereafter, the paleontologist Otto H. Schindewolf suggested that catastrophic bursts of cosmic radiation from supernovae could have caused some faunal changeovers. And in 1980, evidence of an asteroid impact at the end of the Cretaceous period captured the popular imagination, not only because the evidence was concrete but also because the event affected two charismatic groups of animals, with the so-called Age of Dinosaurs giving way to the Age of Mammals.

Before addressing why a mass extinction occurred, however, scientists need to determine what counts as an abnormally large extinction event. The problem is akin to identifying a great athlete. We would not label an athlete "great" after a few good games: any good athlete can have winning streak or a successful career. But only a great athlete will set new records and have a major impact on the history of a sport. By the same token, the label "mass extinction" should be invoked only for an event that kills off an unusually high number of species over a relatively short geologic interval, over a broad geographic range, and among many ecologic and taxonomic groups.

For much of Earth's history, marine fossils preserve the only evidence of life's evolution, and they provide the most complete record even after plants and animals took to the land. In 1982, the University of Chicago paleontologist J. John (Jack) Sepkoski drew up a compendium of fossil marine families and, with David

M. Raup, then of Chicago's Field Museum of Natural History, demonstrated that beginning in the Paleozoic, 542 million years ago, five candidates for mass extinction stood out particularly starkly from background extinction levels. Subsequently, Sepkoski compiled a database of global marine diversity that records the times of origination and extinction for some 36,000 genera (a computerized version was published posthumously in 2002). On that basis, eighteen statistically respectable candidates for mass extinction have been identified [see chart on opposite page]. Other analyses have suggested, however, that many of those eighteen are merely artifacts of missing fossil records. But in everybody's book, two events stand out: one ended the Cretaceous period and Mesozoic era, 65 million years ago, and the greatest mass extinction of all ended the Permian period and Paleozoic era, about 251 million years ago.



Geological time line of Earth, from Precambrian eons (bottom) to the present (top): Beginning with the Cambrian period, fluctuations in the percentage of marine genera becoming extinct are represented by the shaded graph, based on 165 evolutionary intervals tabulated by the paleontologist J. John (Jack) Sepkoski. The extinction peaks at the end of the Permian and end of the Cretaceous (red bars) are universally considered mass extinctions. Some paleontologists think one other peak and two pairs of peaks (brown bars) may reflect three more mass extinctions. Other peaks (blue bars) most likely reflect distortions in collected data, not catastrophic events. The vignettes of life (right) portray the increasing ecological complexity of marine communities over time.

Such catastrophic intervals do much more than just sweep some of the players off the global playing field. They change the game. Back in 1860, Phillips perceived a trend of increasing complexity, writing that "the variety of life, estimated by the

marine tribes existing in a given period, is greater in the more recent periods." He realized more was involved than the abundance of life, or the number of individuals. Phillips's insight has since been reinforced, in part from refinements in correlating geological strata from different parts of the world and in assembling more comprehensive lists of the players and their evolutionary appearances and disappearances.

But the biggest surprises in the past few years have come from comparisons of fossil assemblages in a cooperative venture known as the Paleobiology Database, an electronic repository of information about thousands of fossil communities. Our own analyses in that regard led us to an unexpected conclusion: the end-Permian event not only eliminated large numbers of species; it also set the stage for reorganizing marine ecosystems.

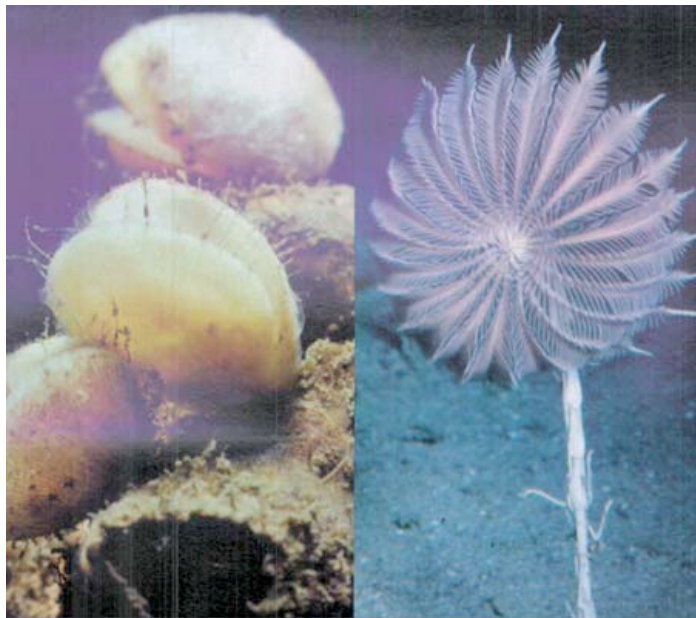
OFTEN CALLED THE GREAT DYING, the end-Permian mass extinction killed off at least 50 to 60 percent of all marine genera, embracing perhaps 90 percent of marine species, in a geologically short span of time. Immense shallow-water reefs died off completely. Among bottom-dwelling organisms, sedentary animals may have suffered the most, such as filter-feeding corals, brachiopods, and single-celled fusulinids. Filter-feeding crinoids that in earlier periods blanketed many shallow continental shelves did not diversify again for tens of millions of years. The trilobites, mobile detritus-feeding arthropods dominant through the Paleozoic, already in decline, now finally met their end.

Earth itself apparently unleashed this disaster--an asteroid impact like the one that wiped out the dinosaurs seems much less likely. David J. Bottjer of the University of Southern California, along with several of his collaborators, and Douglas H. Erwin of the Smithsonian Institution independently reviewed and critiqued the many proposed causes. Both empirical evidence and climate modeling indicate that buildup of carbon dioxide and other greenhouse gases, global warming, and reduced circulation or even stagnation of the world oceans were all on the march during the Late Permian. Those already stressful conditions were punctuated by a continental-scale volcanic eruption of lava in what is now Siberia, the largest known instance in Earth history of what is called flood basalt deposition. The present-day landscape that testifies to that event, known as the Siberian Traps, extends some 750,000 square miles, but the lava may have originally covered three and a half times that area, in places to a depth of a mile or more.

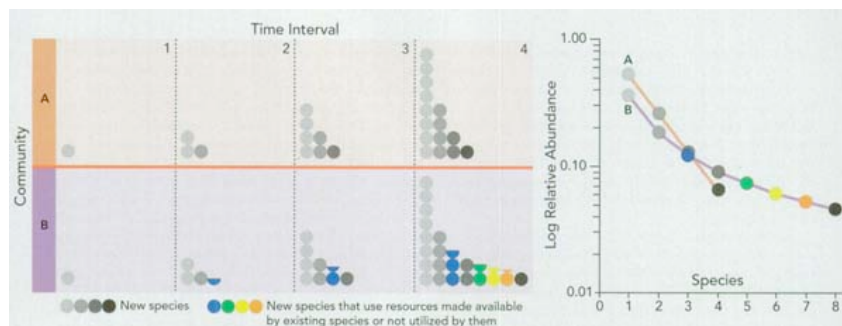
As it flowed up to the surface the magma vaporized minerals and organic matter, adding to the outpouring of volcanic gases--carbon dioxide, sulfur dioxide, hydrogen sulfide, methane, and halocarbons. Like pure halogens, halocarbons may have degraded the protective ozone layer, though some researchers believe that was more than offset by an ozone buildup. Climate fluctuations probably increased following eruptions, and photosynthesis on land and in oceans was likely disrupted; both those consequences are known on regional scales following major eruptions in historical time. Carbon dioxide and (to a much lesser extent) methane would have diminished the proportion of oxygen in the atmosphere and accelerated global warming. Elevated carbon dioxide levels probably also acidified most ocean waters, impairing the ability of many organisms to secrete carbonate skeletons.

Hydrogen sulfide may have reached toxic levels, in part because lower ocean layers containing the gas in dissolved form rose onto the continental shelves, possibly even breaching the surface. The resultant dilution of oxygen and poisoning of shallow waters would have wiped out nearly all but the anaerobic

organisms living there. Sulfide-reducing bacteria, for instance, likely thrived, and that could explain the large-scale bacterial blooms and mats that overran some shallow parts of the ocean. Such marine changes may have been exacerbated by runoff and decomposition of terrestrial detritus.



Brachiopods of the species Terebratulina unguicula, left, and the crinoid Neocrinus decorus, right, are living descendants of two groups of sedentary, filter-feeding marine animals that dominated in Paleozoic seas. Brachiopods, once very diverse and abundant on typical ocean bottoms, have been largely replaced by such mollusks as clams and snails. Crinoids, which were once attached to vast areas of the seafloor, are echinoderms related to free-living sea stars and urchins. Modern crinoids are either restricted to deep, dark waters or are able to swim or crawl, making them mobile enough to hide from predators during the day.



In two theoretical models of ecological communities (left), each shade or color of dot represents one species; the number of dots for each species indicates the relative abundance of that species in the total population of its community. In community A, grayscale dots represent new species as they make their appearance at regular time intervals and compete for the same resources. The model assumes that species present longer are more abundant relative to newcomers because of their "head start" in exploiting those resources. When graphed mathematically as a log scale (right), this results in a simple, straight-line relation between the number of different species and their relative abundance. In community B, colored dots represent additional species that are able to eke out a living by exploiting new-resources unused or produced by the preexisting species (including the older species themselves, which might become prey). The graph of that community now shows a variety of newcomers, though relatively rare,

"bending the curve" in their favor. The authors' research showed that simple ecological models, such as A, often suffice to characterize fossil communities before the end-Permian extinction. Thereafter, complex models are needed far more often.

In sum, the massive volcanism unleashed a rapid cascade of kill mechanisms, concentrating the end-Permian extinctions in tens of thousands of years. Direct evidence of precisely which mechanisms caused the extinctions may be elusive. But as Bambach observed in his review of all the reputed mass extinctions, "Fossils were once alive, and death is a biological, not geological, phenomenon." He emphasized the power of evaluating the physiologies and life habits of both victims and survivors to determine the physical nature of the catastrophes.

The fossil evidence for several million years after the Great Dying shows that only simple communities of small marine animals survived, along with widespread bacterial mounds, evidence that dire conditions persisted. But gradually during the Mesozoic, newly diversifying groups of burrowing bivalves exploited food resources and refuges deep beneath the sediment surface--much more so than during the Paleozoic, which was characterized by filter-feeding, sedentary animals that lived on the sea bottom. Although trilobites and other mobile, detritus-feeding animals were common in the Paleozoic, and mobile predators such as nautiloid mollusks existed, beginning in the Mesozoic highly mobile, shell-crushing or shell-boring predators underwent dramatic radiations. Their descendants included many arthropods such as lobsters and crabs, neogastropods, marine reptiles, and ray-finned fishes. At the same time many prey animals evolved greater skeletal defenses. The product of that evolutionary arms race is widely known as the "Mesozoic Marine Revolution."

OUR OWN RESEARCH did not set out to highlight the end-Permian or any other mass extinction, but to test a more general hypothesis: that the complexity of marine communities increases through geologic time. How to measure ecological complexity is a controversial question even for modern ecologists, because complexity has many meanings. Three indices are often used: taxonomic richness, a tabulation of the different kinds of organisms that live in a given place; abundance, the number of individuals; and evenness, the relative commonness or rarity of the different kinds of organisms. On average, for example, the number of genera in late Cenozoic communities of skeletonized, bottom-dwelling animals is 2.5 to 3.7 times greater than in mid-Paleozoic communities. There is also a trend toward greater evenness, implying a change from dominance by one or a few groups of organisms to more equal abundance. Comparisons of living communities show that those with greater evenness often have a hierarchy of different niche types.

An even more powerful way of examining these communities is rooted in ecological theory, which holds that the ways organisms partition resources will strongly affect the "relative abundance distributions" (RADs) of species in a community. Model RADs summarize elements of all three indices of ecological complexity mentioned above in one quantitative measurement representing all the fundamental diversity information in a community. In communities alive now, different RADs are typically associated with different types of ecological structuring. In the simplest models, for example, all individuals from all species compete for the same set of resources. The relative abundance of species is determined by the order and frequency with which species appear, and how those that have been around longer use up available resources. The exact pattern depends on whether new species arrive regularly (either like clockwork, say one

each year, or probabilistically, on average one each year), and also on whether there is a finite limit to resources.

Alternatively, consider a community where species do not all compete for the same resources. Consider further that some resources become available only after particular species have colonized a community. The predator-prey relationship offers an obvious, example, because predators can consume prey only after prey species appear. There are many other ways in which members of one species take advantage of resources that are created (or made accessible) by members of another species. In such cases, the available niches expand as diversity increases. A new species can add to the resources available, or leave some resources completely, untouched, thus boosting the opportunities for future species. [See diagram on opposite page.]

While we couldn't directly observe vanished ecological communities in action, we could determine the most likely statistical fit of various model RADs to fossil assemblages. We did this for each of 1,176 fossil communities drawn from the Paleobiology Database. Our samples spanned the past 542 million years--from the Cambrian period, when animal life underwent its first major diversification, to the present. Among our strategies was to focus on marine genera or families with better chances of discovery when looking at fossils on a global scale, as opposed to tabulating all known species. As expected, despite intervals of decline that could represent mass extinctions, as well as intervals without much net change, marine genera increased overall from the Cambrian period onward. With more kinds of organisms comes the prospect of more complex interactions among them.



Weathered basaltic rock in the mountainous region known as the Siberian Traps is the remains of a gigantic outpouring of lava about 251 million years ago. The volcanism coincided with the end-Permian mass extinction and may have been the precipitating cause, on top of underlying trends in climate change.

What we discovered, looking at the data as ecologists, is that prior to the end-Permian mass extinction, our simpler RAD models fit fossil communities slightly more frequently than complex models. For the post-Paleozoic, however, complex RADs predominate. Not only did that mass extinction decimate the global variety of life, it permanently altered the typical complexity of marine communities. This was not just a trend, it was some kind of abrupt shift. No other extinction event had

that profound effect.

At first we couldn't believe our results, or more precisely, one of us said, "It has to be an artifact." But it wasn't. We had already taken into account different sample sizes among the communities. We tested to see if our results' were tied to different sediment types, global richness levels, worker bias in compilation of the original data, or alternate timing of events. None of those variables could explain away our finding.

GOING FROM THEORY to biological reality, one notable characteristic of typical Paleozoic communities is the dominance of animals that lived sedentary lives on top of or attached to the ocean bottom, filtering organic particles suspended in the seawater. Although such organisms are still abundant in modern marine ecosystems, they are now joined by a great diversity of mobile predators and detritivores. Whereas a large proportion of the Paleozoic organisms were competing for much the same resource, namely particulate matter floating in the water column, in the post-Paleozoic there is an increased richness and abundance of organisms competing for other resources.

Other lines of evidence seem to be consistent with this change in ecological complexity. The end-Permian extinction more adversely affected groups of animals with relatively low metabolic rates. Perhaps those that had higher metabolic rates could also exert better control over the diffusion of gases dissolved in seawater, enabling them to gain essential oxygen while excluding harmful toxins. Separately, taxa that formed skeletons from material other than calcium carbonate proved less vulnerable compared with those that were heavily calcified, most likely because they were less affected by acidification of seawater. This pruning of the evolutionary tree through the selectivity of mass extinction possibly opened the door to subsequent diversification of taxa whose ancestors had been present in the Paleozoic, but neither as diverse nor abundant as other groups that had a stronger foothold. Still, the reasons why this one mass extinction seems to have been such a game changer remain to be unraveled, as do the synergistic events that caused it.

THAT A "SIXTH MASS EXTINCTION" is currently underway is not hyperbole. In an assessment of the ecological health of the modern oceans, Jeremy Jackson at Scripps Institution of Oceanography describes a combination of greenhouse-gas buildup, ocean warming, increased acidification, massive nutrient runoff, pollution, and habitat destruction that has eerie similarities to our emerging picture of the end-Permian environment. The ocean contains large "dead zones" depleted in oxygen. Enormous coral reefs are dying. Reduced rates of calcification have been measured in a number of organisms. Assaulted as well by bacterial and toxic algal blooms and disease, diverse, complex marine communities and food chains are degrading into simpler ones. Overfishing by humans has disrupted marine communities, destroying their structural balance by removing the larger regulators of those systems.

The causes of the Great Dying and the current extinction event are not the same--humans were not a factor then, eruptions of flood basalts are not a factor now. Climatic conditions are different as well. We live in a cool interglacial period of geological history, not a hot, arid one. Atmospheric carbon dioxide levels during the end-Permian crisis may have been three to six times higher than the preindustrial levels of 200 years ago. What is staggering is the pace of modern environmental degradation, which is occurring in hundreds of years rather than over tens of thousands or more.

Many species will fail to adjust to this pace. It is too soon to say which ones. But a glance far back in time does tell us that the survivors, no matter how decimated, will eventually evolve new complex communities, as unfamiliar as we might find them.

All three have been involved with development of the Paleobiology Database, organized by an international community of scholars.

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PHOTO (COLOR): Marine life in the Late Permian period, far left, depicted in a former diorama at the Field Museum in Chicago, is dominated by sedentary, filter-feeding animals, such as the tubular yellow sponges and light-colored brachiopods (on mound at left). Near Left: A diorama of life late in the Triassic, the period that followed the Permian, shows many free-swimming organisms. Among them are a large coiled ammonite (center) and long nautiloids (both animals with tentacles like modern squids), as well as clams and snails.

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By Scott Lidgard; Peter J. Wagner and Matthew A. Kosnik

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Matthew A. Kosnik holds a PhD in paleobiology from the University of Chicago. His postdoctoral research has taken him to the NMNH and to James Cook University in Townsville, Australia. His research focuses on ecological and evolutionary processes in shallow marine environments.

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