Who Profits From Ecological Disaster?

Paleontologists studying ancient mass extinctions are finding that mere survival rarely guarantees evolutionary success; the post-extinction recovery process seems to hold the key

PLYMOUTH, ENGLAND—Two hundred and fifty-one million years ago, the lowly bellerophonts had it made—or at least seemed to. These primitive, coiled-shell sea creatures had been around for the preceding quarter-billion years and had just come through the worst mass extinction in the history of life in better shape than almost any other group of surviving mollusks. But it wasn't enough. Surviving "didn't do them any good," says paleontologist Douglas Erwin of the Smithsonian's National Museum of Natural History. Other groups came on strong, "and the bellerophonts were history. They win the extinction but lose the recovery." Within 5 million years after the Permo-Triassic mass extinction, the bellerophonts had succumbed.

The fate of creatures that died off—or flourished unexpectedly—in the aftermath of mass extinctions was much on the minds of the paleontologists who gathered here last month.* Until recently, most paleontologists studying the five mass extinctions of the last 500 million years concentrated on the die-offs, looking for clues to the cause—gradual environmental change or a swift catastrophe, such as a meteorite impact—and the traits that enabled some creatures to survive. But as results reported at the meeting showed, the first few million years after a mass extinction leave their own powerful stamp on the history of life.

In the immediate aftermath of an extinction, some taxa—groups of animals such as species or genera—flourish, then gradually fade. Others that had apparently vanished can reappear, Lazarus-like. In the turmoil, new groups may gain ascendancy, filling ecological niches left empty by the extinction and displacing other survivors to create a new ecological order (see box on p. 29). The next step—still a long way off—is understanding how nature sorts winners from losers among the survivors. Why, for example, did the bellerophonts bomb? And why, conversely, did the mammals emerge as big winners after the mass extinction 65 million years ago that killed off the dinosaurs?

Spurring this focus on recoveries is the realization that, as paleontologist George McGhee of Rutgers University put it, "just because you survive [an extinction] doesn't mean you're going to do well in the future." David Jablonski of the University of Chicago, for example, was stunned when he compared the fate of mollusks in Europe and

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In search of lost crinoids. The barren terrain of northwest China *(top)* yielded fossils *(left)* indicating that the region was once a refuge for sea creatures such as crinoids, which survived a mass extinction and repopulated the oceans *(right)*.

on the Gulf Coast of North America following the mass extinction 65 million years ago. Both areas were hard-hit during the extinction, which wiped out perhaps 75% of marine species worldwide, says Jablonski. The patterns of extinction—which mollusk groups became extinct and which survived—were similar as well. Jablonski says he expected that the recoveries would be similar, too.

Far from it. Some surviving groups, such as the turritellid snails, flourished in North America, blossoming into a myriad of new species, while languishing in Europe. Other taxa diversified steadily though not explosively in Europe but stagnated in North America. McGhee saw equally varied outcomes when he studied the fate of brachiopods—stalked, clamlike creatures—that survived the moderate Givetian extinction 377 million years ago.

What separates winners from losers in the post-extinction sweepstakes isn't just fecundity. Take the stromatolites—pillars or reefs of blue-green algae and cemented sediment. These ancient life-forms had long been in decline by the time of the Permo-Triassic extinction 251 million years ago, when oxygen-poor water may have risen from the deep ocean and suffocated many marine life-forms. The meteoric rise of the multicellular metazoans—snails, nematodes, and other creatures—550 million years ago had sealed the stromatolites' fate as they became prey for these voracious newcomers. The stromatolites hung on only in severe environments, such as hypersaline lagoons, where their predators couldn't survive.

But the mass extinction that wiped out 80% or more of other marine species made the world safe for stromatolites. As Jennifer Schubert of the University of Miami and David Bottjer of the University of Southern California found, stromatolites suddenly appeared in normal marine environments in Nevada, where the two paleontologists studied them, as well as elsewhere in North America, Europe, and Asia. Schubert and Bottjer view stromatolites as a "disaster form," a taxonomic group that takes the disruption wreaked by a mass extinction as an opportunity to multiply and invade environments normally closed to it. The interlude didn't last, though; in time, the marine communities recovered, predation stepped up, and the still-defenseless stromatolites had to retreat to harsh environments, where they remain.

Back from the dead

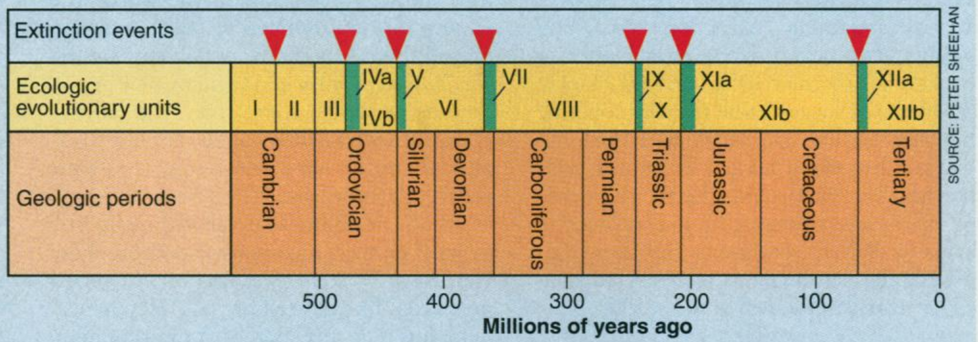
In contrast to the stromatolites, which flourished right after the ecological catastrophe, many life-forms that did better in the long run—including some of the marine snails that eventually drove out the stromatolites—were nowhere to be seen right after the Permo-Triassic extinction. Apparently extinct, they reappeared millions of years

*Meeting of International Geologic Correlation Project 335, Biotic Recovery From Mass Extinction Events; Plymouth, England, 4 to 12 September; Douglas Erwin and Erle Kauffman, co-conveners.

Between Extinctions, Evolutionary Stasis

More and more, paleontologists are learning that the full measure of a mass extinction can't be found in its immediate toll. Just as important is the wholesale reorganization of living communities that takes place afterward (see main text). And those brief recovery periods, lasting just a few million years, are all the more important because during the tens or hundreds of millions of years that follow, until the next mass extinction, not much may happen.

The idea that the history of life alternates fits of rapid change and long periods of stasis when the dominant kinds of organisms don't change much isn't new. But a new analysis by paleontologist Peter Sheehan of the Milwaukee Public Museum ties that pattern explicitly to mass extinctions and recoveries. Sheehan subdivides the last 460 million years into six "Ecologic Evolutionary Units" (EEUs) lasting 35 million to 142 million years apiece. Each is terminated by a mass extinction; the subsequent EEU begins after a recovery lasting 3 million to 8 million years.



Chapters in the history of life. Mass extinctions and recoveries usher in long periods when ecological patterns remain stable. These often subsume several traditional geologic periods.

Traditionally, paleontologists and geologists have subdivided the history of life according to the appearance and disappearance of a few indicator species. But Sheehan, building on work by Arthur Boucot of Oregon State University, took a different tack. He focused not on individual species but on ecological patterns, identifying which kinds of animals occupied the key niches in ancient ecosystems.

The two most familiar EEUs are the most recent. For 180 million years, dinosaurs played all the major roles in terrestrial ecosystems; other animals lived on the fringe. The dinosaurs were the herbivores, carnivores, and omnivores, large and small, while the latecomers, the mammals, mostly had to settle for restricted roles as very small-bodied insectivores. Then, 65 million years ago, a mass extinction took out the major players, and their top-dog status was up for grabs. The ensuing few million years of ecological rebuilding saw a scramble among mammals, birds, and lizards for supremacy. The mammals, of course, won.

The story of the dinosaurs and the mammals has been repeated with other players five times in the past 460 million years, according to Sheehan's analysis. Before the dinosaurs, the mammallike reptiles occupied the key niches. Before them came the amphibian-dominated community that first colonized the land. Earlier still, a succession of various sorts of marine organisms such as the crinoids, brachiopods, and trilobites held sway.

Even on shorter time scales, Carlton Brett of the University of Rochester and his colleagues have found, the same pattern prevails. Studying the record of marine organisms that lived around 400 million years ago in what is now upstate New York and Pennsylvania, they found that communities persisted for 5 million to 7 million years, with only about 20% turnover in their species. Each time, the status quo ended when the community lost perhaps 90% of its species over about 100,000 years, possibly because of a change in climate or sea level. A community rebuilt by survivors and invaders from other areas then rose from the ashes to prevail for another 6 million years or so. Sheehan sees these intervals as analogous to his longer, global EEUs, reaffirming that stability—as boring as it may be—is the evolutionary norm.

–R.A.K.

later to compete for dominance. Such resurrections prompted Jablonski, who was among the first to describe this behavior, to name them "Lazarus taxa."

In some cases, the apparent resurrection may actually be a case of mistaken identity. Erwin and Mary Droser of the University of California, Riverside, pointed out last year that some supposed Lazarus taxa may be imitators of taxa that truly became extinct. One example they cited is some reef organisms that disappeared in the Permo-Triassic extinction and reappeared—in apparently identical forms—5 million years later. After taking a close look at the second coming of the reef organisms, Erik Flügel of the University of Erlangen recently decided that many were new taxa unrelated to those that perished in the extinction.

But although their close resemblance to earlier forms was not a matter of ancestry, says Erwin, it wasn't accidental either. Instead, it was a response to common physical problems, which are inherent in building a reef. "For ecological or physical reasons, there may be only a couple of solutions to a particular problem that nature can come upon," he says. Erwin and Droser propose the name "Elvis taxa" for these fakers, "in recognition of the many Elvis impersonators who have appeared since the death of The King."

But many other Lazarus taxa do stand up to inspection. Putting no stock in resurrection, paleontologists have always assumed that these taxa survived the extinctions and any lingering hard times early in the recovery by taking refuge in some out-of-the-way, congenial place. But no one could identify such a refuge in the fossil record.

At the Plymouth meeting, however, Paul Wignall of the University of Leeds presented some clues from fieldwork in China indicating that shallow, near-shore environments beyond the reach of lethal anoxic water could have served as refuges from the Permo-Triassic extinction. Few of these environments are preserved in the fossil record of the extinction, but Wignall found thin beds of shells that had apparently been washed by storms from the shallows into deeper waters, where the native mollusks had been killed off by anoxia. And Erwin found that a disproportionate number of Permo-Triassic Lazarus taxa first reappeared in Japan and China, suggesting that the refuge was in Asia.

But it's the aftermath of the Frasnian-Famennian mass extinction of 367 million years ago that has yielded the biggest break in the search for refuges, as Christopher Maples of the Kansas Geological Survey and Johnny A. Waters of West Georgia College reported. That episode has its own mystery disappearance and resurrection: The echinoderms—including sea urchins, starfish, crinoids, and sea cucumbers—nearly disappeared from the fossil record after the extinction, only to come back strong more than 5 million years later in the Carboniferous. The first clue came when Hou Hong-Fei of the Institute of Geological Sciences in Beijing sent Maples and Waters two well-preserved echinoderm fossils dating from just after the extinction.

When Maples and Waters journeyed to far northwest China to investigate, they struck it rich, uncovering more Famennian echinoderm fossils than have ever been collected before. Their finds quadruple the number of known Famennian echinoderm taxa, and together they bear a strong resemblance to the later Carboniferous fauna, said Maples. The evidence suggests that the seas covering that part of China could have been the long-sought echinoderm refuge. There, the creatures were somehow spared the anoxia sweeping other parts of the world and continued to diversify. When conditions elsewhere improved, the echinoderms reconquered their old territories in the rest of the world.

Sorting winners from losers

Identification of refuges can solve only one mystery of recovery periods, however. Another, deeper problem is what enables a group to flourish in the long run, as many Lazarus taxa do, while others bow out for good. As Erle Kauffman of the University of Colorado pointed out at the meeting, the key characteristics might depend on the nature of the extinction. If an extinction is abrupt, as a number of paleontologists believe the Cretaceous-Tertiary extinction was, the ability to evolve rapidly might be a boon. In the wake of the extinction, plenty of ecological niches would suddenly be vacant. The prize would go to the group able to diversify rapidly and fill those niches; more slowly evolving groups would be left in the dust.

Erwin thinks his bellerophonts may be a case in point. Their history until the mass extinction shows they never produced new species or genera very quickly; it took them hundreds of millions of years to diversify into species spread around the world in a variety of environments. That ubiquity helped them survive the extinction, says Erwin, but afterward, when so many new opportunities presented themselves, the bellerophonts couldn't evolve rapidly enough to exploit them. Perhaps as a result, they were eclipsed by other groups.

Still, the ability to diversify rapidly isn't in itself enough to guarantee success. Thor Hansen of Western Washington University noted that four of what he calls "bloom taxa" of mollusks greatly increased their numbers of species per family following the Cretaceous-Tertiary extinction but then, within 5 million years, fell back to the diversity levels at which they had started.

The failure of a quickly evolving species to take firm hold makes sense to Kauffman. For him, a quick evolutionary response may not always be as important as a running start—which is only possible if mass extinctions are gradual affairs. Kauffman thinks all extinctions—including the Cretaceous-Tertiary—were driven by environmental change spanning at least 1 million or 2 million years. Given that much time, some species will be able to adapt to environmental stresses such as changing climate, says Kauffman. As a result, they will have an edge over their rivals in the early recovery period, while those stresses still linger.

Kauffman has found that some seemingly abrupt "explosive radiations" that were assumed to have taken place during the recovery actually began earlier, during the extinction episode itself. The diversification of the bivalve mollusk *Mytiloides* after the Cenomanian-Turonian extinction 90 million years ago, for example, seems to have begun with a "progenitor taxon" that evolved under high environmental stresses late in the extinction.

But meeting attendees agreed that testing these ideas will take a much more detailed view of recoveries than paleontologists have usually had. One way to get the needed detail is to apply the same scrutiny to the fossil record of recoveries that paleontologists have lately given to the extinction episodes. Kauffman, for example, helped pioneer the technique of sampling outcrops every centimeter or so instead of at intervals of meters for studying deposits from extinction intervals; he's now applying it to recoveries. He and others are also attacking the record with geochemical and isotopic techniques for deciphering environmental change and correlating records at different sites. As these efforts start to yield results, paleontologists may finally learn what it takes for a survivor to become a winner.

–Richard A. Kerr

ASTRONOMY

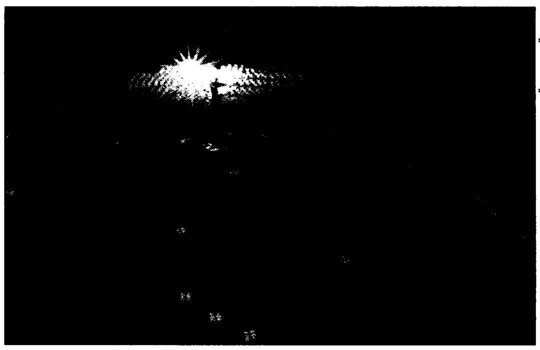
Solar Farms May Reap Gamma Rays

The sun, leisurely crossing the sky each day above Barstow, California, shines its light down on 1800 mirrors belonging to the world's largest solar "farm." In response, the farm does—absolutely nothing. The $140-million experimental facility, designed to convert the sun's energy into electricity, was built during the Carter years when alternative energy was a hot topic. Officially known as the Solar One Solar Power Pilot Plant, it was eventually shut down in the late 1980s.

In an ironic twist, this facility built for the sun may be resurrected by operating at night. A small group of astronomers confirmed recently that Solar One's mirrors, or heliostats, can be used to detect the faint bursts of light produced when gamma rays from deep space crash into Earth's atmosphere. These researchers hope that, if more elaborate tests support this finding, Solar One could explore a part of the gamma ray spectrum to which present detectors are blind and which Iowa State University astronomer Richard Lamb calls "terra incognita." That ability, in turn, would allow astronomers to study some of the most energetic objects in the universe, such as the monstrous black holes thought to lie at the centers of galaxies.

Exploring this untouched territory with Solar One could be not only a productive journey but a relatively cheap one. O. Tümay Tümer of the University of California, Riverside, who first proposed the conversion in 1991, estimates that the solar plant could be turned into a gamma ray detector for the bargain price of $1 million. The only alternative may be to build a new detector at a cost of hundreds of millions. "The good thing about Solar One is it's $140 million lying on the ground there. You can't beat that," Tümer says. But skeptics argue that Solar One, among other limitations, is at a less-than-ideal site and has low-quality mirrors that would reduce its effectiveness.

Boosters and detractors agree, however, that something is sorely needed to fill in a blind spot marring the vision of gamma ray astronomers. In space, instruments such as the EGRET detector on the Compton Gamma Ray Observatory have been able to scan the sky for gamma rays with energies up to 30 gigaelectron volts (GeV). In contrast, ground-based detectors, such as a collecting mirror at Whipple Observatory in Arizona that's 10 meters in diameter, can only catch gamma rays with energies of 200 GeV and higher. "There's this window where we have no observations, and we know exciting physics occurs there," says Michael Salamon of the University of Utah.



O. TÜMAY TÜMER

Solar astronomy. This abandoned solar power plant might provide a new look at the gamma ray spectrum.