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**Douglas H. Erwin: Extinction**

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## CHAPTER 1

### Introduction

#### *San Rafael Swell, Near Green River, Utah*

Early Triassic rocks are boring. It doesn't matter where you are, China, Europe or here in Utah; there is a certain similarity to them, and a dreadful monotony. A kind of austere beauty, but monotonous nonetheless. This great swath of sandstones and limestones flows across hundreds of square miles from Nevada up through Utah into Idaho and Montana, remnants of a shallow sea 250 million years old. In Idaho and Montana these rocks are buried by rock debris along the slopes of wonderful mountain valleys, or pine forests swallow them up (plants are no friend to the field geologist, except at lunch when you need some shade).

In Utah the Triassic is laid out for anyone who cares to look, although few do. The dry mesas of the San Rafael Swell west of Green River are home to rattlesnakes and lizards and visited by archeologists seeking the rock art of the ancient Fremont culture. Fossils are few and far between: a few species of fossil clams, the occasional snail or two, and the odd coiled ammonite, a distant relative of today's nautilus. Today the starfish, sea anemones, crabs, and snails in a tide pool at Santa Barbara, California, are very different from those in Baja California, much less Maine or Japan. These fossils in Utah are almost identical to those in rocks

of the same age in northern Italy, Iran, and southern China. Farther north, clams are incredibly abundant: great pavements of the scalloplike clam *Claraia* cover the surface in their thousands or tens of thousands. Not dinosaurs perhaps, but to me far more valuable. Occasionally a few narrow bands of rock yield a richer trove of fossils. Rich is relative, of course, for there may be only nine or ten species of snails, but they pose an enigma far more compelling than the end of the dinosaurs.

To understand this enigma we need to travel farther back in time, to rocks 20 million years older in the Guadalupe Mountains of west Texas (figure 1.1). Instead of the scattered species of the Early Triassic of Utah, hundreds of species of snails have been found here. But these were dwarfed by a myriad of other marine animals. The Guadalupe Mountains stretch from Carlsbad Caverns southwestward to Guadalupe Mountains National Park. This 265-million-year-old fossilized reef once flourished across west Texas along the margins of what was then a warm, nourishing equatorial sea. The reef rivaled today's Great Barrier Reef of Australia in size and biotic diversity.

Today the canyons and caves of the Guadalupe Mountains dissect the reef for all to explore. There are few places in the world, of any age, where one can explore the inside of a reef, see how it was formed, and how it evolved over millions of years. Not surprisingly, geologists have been making pilgrimages to the Guadalupe Mountains for decades because erosion has exhumed the reef intact. At the base of the steep escarpment at McKittrick Creek one is standing on the ancient sea bottom of the Permian Basin looking up toward the reef some 1,200 feet above, just as one could today off the Bahamas or some other modern reef if all the water was removed. Hiking up the Permian Reef Trail in McKittrick Canyon is just like walking (or better, swimming) up the face of the reef as it was millions of years ago. The trail twists between juniper trees and across fine-grained limestones, then, climbing a bit more steeply, the trail dodges huge blocks of limestone. Turning to look across to the opposite side of the canyon, hikers can see the outline of avalanches of the reef into deep water clearly preserved. One huge block of limestone, a chunk of reef two hundred feet long and forty feet high, lies where it slid toward the basin 270



Figure 1.1 A view of the Guadalupe Mountains from the south. The massive cliff is limestone, part of the reef complex that grew here and throughout west Texas during the Permian. The older of the two pulses of extinction ended the deposition of the Permian reef.

million years ago. Then the trail climbs steeply, switching back and forth until the massive limestones of the reef finally appear some three miles and eight hundred feet above the parking lot.<sup>1</sup>

Entombed here is the world of the Permian, the very last profusion of life before the extinction. Water is always precious in west Texas but whenever I climb the Reef Trail I take enough to pour on the rocks. A splash of water and the fossils spring out of the whitish-gray limestone, opening a window into a world of animals far different than we find in modern oceans. Some rocks seem to consist of nothing but half-inch-long grains of rice: the skeletons of single-celled organisms known as foraminifera. Forams were abundant and evolved rapidly, providing a rough clock to the age of these rocks. Brachiopods are common too. With two valves they look superficially like clams, but brachiopods on the half-shell would be hard to swallow. In place of the muscular and tasty foot of a clam, the shell enclosed a looping curtain of filaments that filtered food from the water. Distant cousins to clams and other molluscs, the hundreds of brachiopod species helped build much of the reef. Their cousins the bryozoans share the filamentous filter-feeding structure of brachiopods, but formed tightly packed colonies growing as lacy fronds, massive stony buttresses, and intricate fans (figures 1.2, 1.3).

Today sea urchins, sand dollars, and starfish move easily, and many of them are happy carnivores. But the five living groups of echinoderms (starfish, brittle stars, sea urchins, crinoids, and holothuroidians, or sea cucumbers) provide a restricted view of the evolutionary history of the group. Starfish and sea urchins were uncommon during the Permian, while echinoderms that lived attached to the sea bottom were abundant. A long stack of circular calcite plates formed a stalk that attached crinoids to the sea floor. The body of the animal sat atop the stalk, encased by a network of plates and surrounded by a circle of arms forming an effective net for filtering organic material out of the water.

Brachiopods, bryozoans, and crinoids had dominated the world's oceans for 250 million years, attached to the sea bottom and placidly filtering small animals out of the ocean water. None of them were active predators, could move as adults, or had much



Figure 1.2 A reconstruction of the Permian reef of west Texas based on over forty years of research at the National Museum of Natural History. A school of nautiloids with a straight shell are passing in front of the reef. Most of the animals are various brachiopods, along with some bryozoans, sponges, and clams. Corals, one of the major modern reef builders, were almost absent from this Permian reef. Smithsonian Institution photograph.

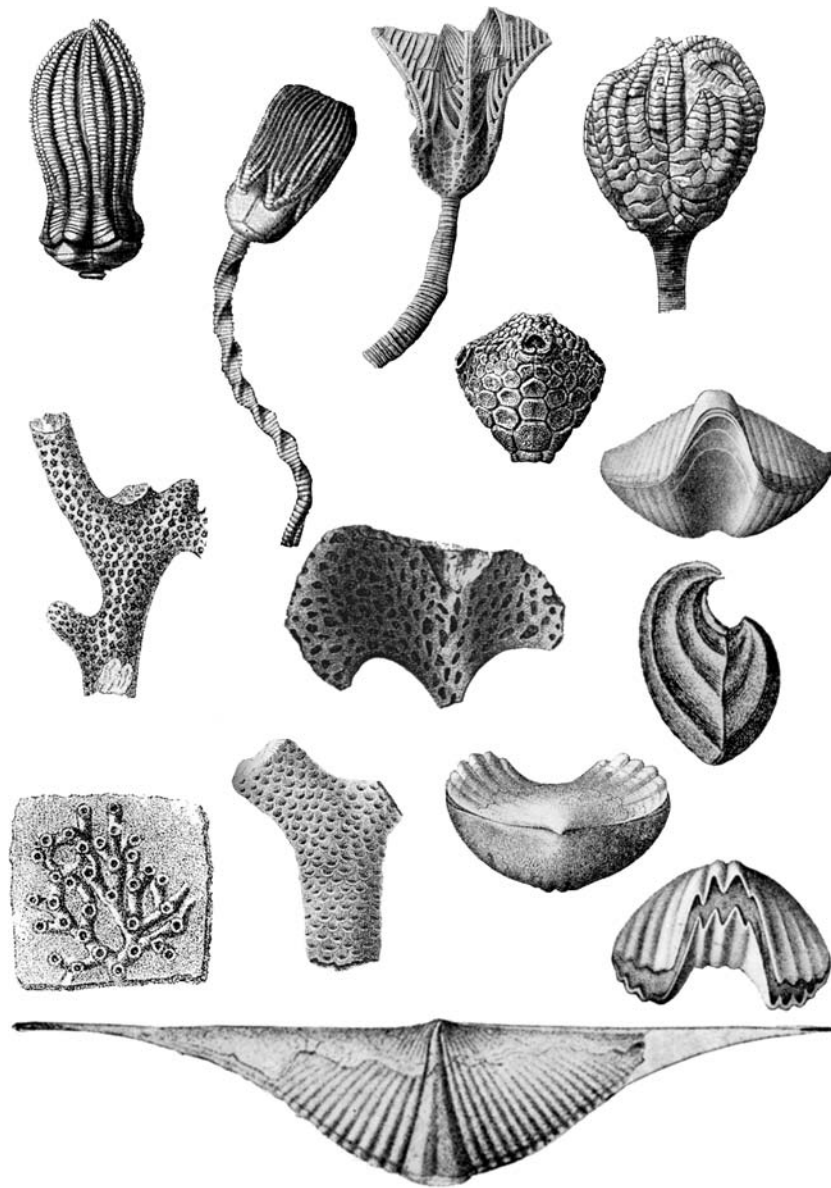


Figure 1.3 The dominant invertebrate marine animals of Paleozoic oceans were crinoids (upper four figures), colonial bryozoans (the stick and lacy fronds on the left) and brachiopods (the four bivalved shells in lower right). Grabau (1904), Wanner (1930, 1931).

meat to them. The *Joy of Permian Cooking* would have been a short book indeed. Their world was about to end.

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This book is about what had happened in the 20 million years separating the rich faunas preserved in West Texas and the scrappy, grubby fossils of the Early Triassic of Utah. Between the reefs of Texas, teeming with fossils and rivaling modern reefs in the number of species, and the barren deposits in Utah lies the greatest biodiversity crisis in the history of life—a far greater crisis than the extinction of dinosaurs 65 million years ago. What so turned the world upside down that biodiversity plunged from hundreds or even thousands of species at a single locality, with thousands of individuals, to perhaps only a dozen species?

Between the rocks in Texas and Utah the Earth experienced two great crises some 10 million years apart. These twin disasters extinguished at least nine of every ten species in the oceans. Moving up the taxonomic hierarchy to more inclusive groups, about 82% of genera and fully half of all marine families disappeared, a level of extinction that dwarfs any of the other great mass extinctions. As many marine families were wiped out during this event as the next two largest mass extinctions combined. Each of these Permian events alone was greater than the extinction that killed off the dinosaurs. Together the twin crises form the greatest biotic catastrophes of the past 543 million years (figure 1.4).

On land, plants and animals came closer to complete elimination than at any point since they first evolved, and yet they rebounded in a few tens of millions of years. These crises at the end of the Permian Period were so extreme, and the animals on either side of the events so different, that John Phillips and other mid-nineteenth century geologists took them as evidence for separate creations of life. Today geologists recognize the Permo-Triassic boundary as a fundamental turning point in the history of life, bringing the world of the Paleozoic to a close, and, in the aftermath of the extinction, constructing the world of today. Despite all the evolution of the past 251 million years, today's oceans still reflect the winners and losers of events at the close of the Permian.

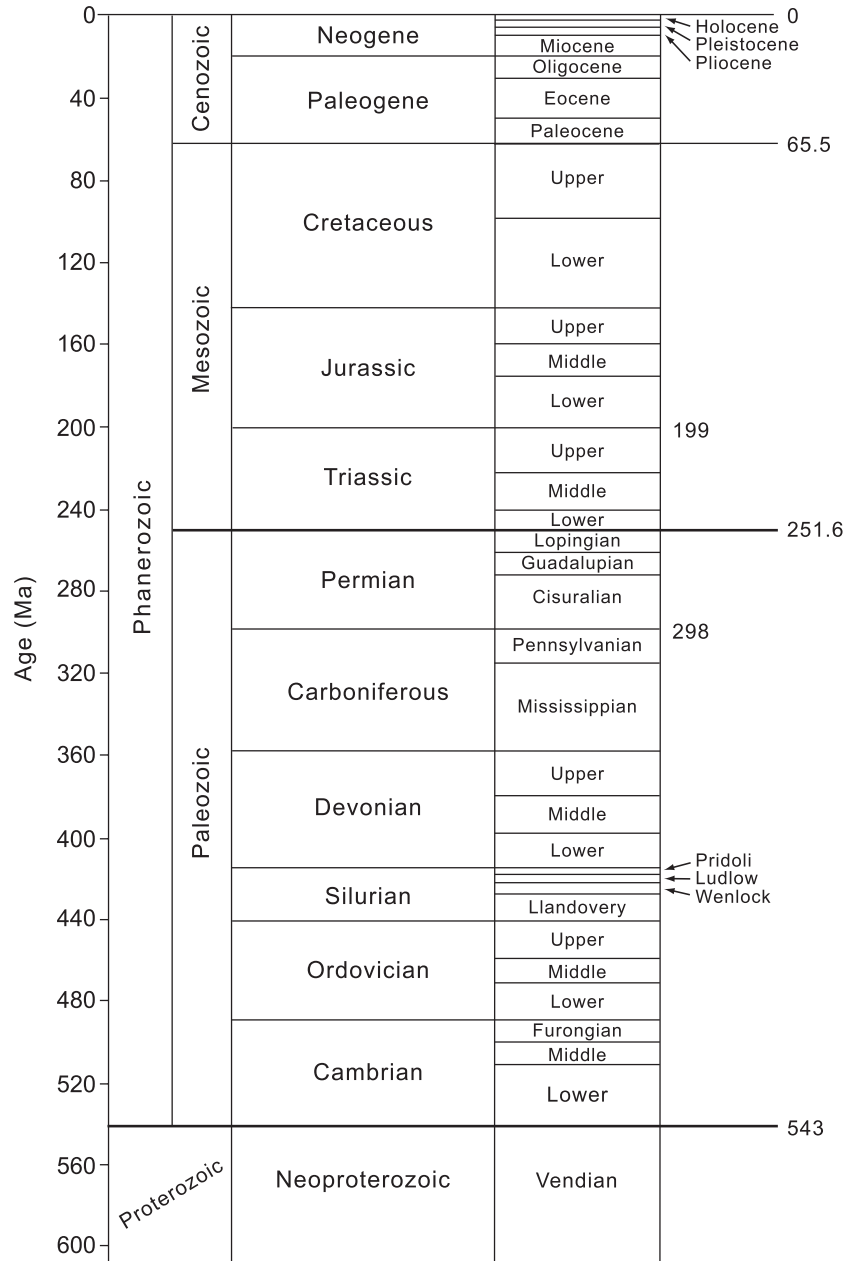


Figure 1.4 The Geologic Time Scale as of 2004, showing the eras and periods of the Phanerozoic (the past 543 million years) and the current ages assigned to the boundaries between the periods.

What could have triggered such a massive loss of life? Geologists are endlessly creative so there is no lack of suggestions, some of which are even plausible. Not wanting to feel left out of the mother of mass extinctions, physicists, evolutionary biologists, and complexity theorists have all offered their solutions to the mystery. And it is a mystery. Over the past several decades, dozens of different hypotheses have been proposed, ranging from the movement of the continents, the warming of the seas, and the impact of an extraterrestrial object to the eruption of massive volcanoes or the suggestion that ecosystems had become too complex and collapsed with no physical trigger at all. Unlike other mass extinctions where the number of physical events is relatively few and causality is easy to establish, so many things occurred during the Permo-Triassic interval that establishing what caused the extinction is very difficult.

The simple truth is that we do not know what caused these twin extinctions. Or at least I don't know. Some of my colleagues are less reticent (or more confident) but there is certainly no agreement yet. None of the extinction models fits all the evidence and some hypotheses require data that despite every effort have not been found. Ten years ago the end-Permian extinction appeared to be a prolonged, drawn-out event over millions of years. Better data on fossil occurrences through the Permian have revealed two discrete episodes of extinction in the sea: one at the end of the Middle Permian, and the second at the very end of the Permian. Although I will touch on the older crisis at several points, particularly in chapters 5 and 8, we know relatively little about it. This first extinction pulse killed a vast number of species in the oceans, probably occurred during a sudden drop in sea level, and coincides with a sharp shift in the cycling of carbon through the oceans and atmosphere. Beyond this we do not even know if plants and animals on land also suffered extinction. This first extinction pulse seems to have had little long-term impact on life, for many Late Permian fossil assemblages look much like those before the extinction.

The greater enigma is the second, catastrophic extinction at the end of the Permian. This shattered Paleozoic ecosystems so

thoroughly that they never recovered, and this is the problem to which I have devoted the past twenty years of my research. Unless I specifically mention the earlier extinction when I discuss the Permian extinction, I am referring to this latter episode. Among the myriad suggestions, four stand out as possible causes: the impact of a meteorite or comet; climatic destruction from massive volcanism in Siberia; the oceans losing their oxygen (becoming anoxic) and snuffing out the animals that require it; and a combination of several interacting and mutually reinforcing events.

Almost everything we know is consistent with an extinction caused by the collision of an extraterrestrial object at the very end of the Permian: a very rapid extinction, a dramatic shift in the flow of carbon through the oceans and atmosphere, and extinctions on land and ocean. We will discuss the evidence for the impact of a meteorite triggering the end of the dinosaurs in the next chapter, but in contrast to this end-Cretaceous event, there is only suggestive evidence for impact in the Permian. Permo-Triassic sediments do not contain a blanket of debris that rained out from the dust cloud of an impact. There is no sign of characteristic extraterrestrial elements such as iridium. Some geologists have offered tantalizing suggestions of impact, but so far these have failed to convince most scientists.

The end-Permian mass extinction coincides with one of the most massive volcanic eruptions of the past 600 million years. It is hard to believe this is a coincidence, but just how volcanism triggers a mass extinction is unclear. Global cooling from erupted dust, followed by global warming from clouds of carbon dioxide and acid rain from billowing sulfur are commonly proposed links between volcanism and extinction, but are very difficult to test. A number of scientists, largely physicists but including some geologists who should know better, have proposed that an impact triggered the volcanism. While I admire the broad sweep of such generalizations, there is little geological support for it.

Geologists have uncovered considerable evidence for anoxic waters in both the deep sea and shallow water near the Permo-Triassic boundary, and this has led to the third leading hypothesis: the spread of low-oxygen, or anoxic, waters. What has never been clear

is how low-oxygen waters cause widespread extinctions of land plants, insects, and vertebrates. If anoxia was a major cause of extinction, it must have been linked to some other process responsible for extinctions on land.

The final possibility is that this event, like much of history, was messy and lacked a single cause. In 1993 I termed this the *Murder on the Orient Express* hypothesis in honor of the wonderful Agatha Christie mystery where the solution is that *all* the suspects participated in the crime. Some of my scientific colleagues tend to dislike this idea. Not because it may not be true, but because science is about testing ideas and rejecting those that fail the test. Single causes are much easier to test than multiple causes and thus, to some, seem more “scientific.”

Ten years ago I was opposed to the first three possibilities because they seemed inconsistent with our evidence for the speed of the end-Permian mass extinction and with the timing of other geological events. Despite much effort since 1980, no evidence for impact had been found at any Permo-Triassic boundary site, and the pattern of extinction appeared to be too prolonged to be due to an impact. The volcanism model bothered me because I could not see a causal link to the extinction. It also appeared that volcanism could not explain the well-documented shift in the carbon cycle associated with the extinction. Then as now, the various anoxia hypotheses (there are at least three) suffer from an inability to explain the terrestrial extinction. There was a difficulty with causality too: was the apparent evidence for anoxia better explained as a consequence of the mass extinction?

I have changed my mind as our research has dramatically shortened the duration of the extinction. I confess my hope that the cause turns out not to be an impact for an aesthetic reason. The Permo-Triassic and Cretaceous-Tertiary mass extinctions look increasingly similar. Since we already (believe we) know that impact can cause mass extinction, we would learn more about life’s susceptibility to catastrophe if a very different, essentially earth-bound process produced the end-Permian crisis. The physicists, seeking generality, hope for impact while the historians, celebrating diversity, yearn for more intrinsic events.

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This book is frankly written as a mystery story. Chapter 2 introduces the suite of possible perpetrators of the mass extinction and outlines the type of evidence geologists and paleontologists need to evaluate each hypothesis. Chapters 3 to 7 detail the actual evidence we have to test the hypotheses presented in chapter 2, in essence providing the clues needed to eliminate some suspects. By the end of chapter 7 most readers will probably have their own ideas as to the cause of the extinction. Had I wanted, I could have skewed the material to favor one hypothesis or another (and I expect some of my colleagues will claim I have). As far as possible, I have attempted to put the best light on each of the potential miscreants in chapter 2, and have provided all the relevant clues in chapters 3 to 7. The denouement occurs in chapter 8 where we return to the hypotheses and address the cause of the extinction. I present my views of the cause, but since at the moment it is not clear what caused the extinction, no doubt some readers will arrive at very different conclusions. The final section, chapters 9 and 10, discuss the recovery following the mass extinction and its impact on the history of life.

Science is not simply about developing plausible ideas and telling a good story, but about developing ideas that are congruent with the facts as we know them, then critically testing them by collecting new information. Chapter 2, *A Cacophony of Causes*, sketches the leading causes for the end-Permian mass extinction and identifies the kind of data required to evaluate them. Since some understanding of the other mass extinctions is useful to place these hypotheses in context, this chapter begins with a brief précis of these other events.

The keys to understanding the end-Permian mass extinction lie in China. There are more marine rocks spanning the Permo-Triassic here than in the rest of the world combined and Chinese geologists have been at the forefront of establishing our new understanding of the Permian. I have been fortunate to collaborate over the past decade with an excellent group of Chinese geologists at the Nanjing Institute of Geology and Palaeontology. Rocks at Meishan, just south of the Yangtze River between Shanghai and Nan-

jing, are the global reference point for the Permo-Triassic, and an account of our fieldwork there and elsewhere in China forms the basis of South China Interlude, chapter 3. This chapter also introduces the complexity of the fossil record. One of the most useful pieces of geological evidence at the Permo-Triassic boundary is the abrupt shift in the carbon cycle. This is such a useful tool that I introduce it in chapter 3, employ it to correlate to other regions in chapter 4, and then discuss the causes and interpretation of the signal in chapter 7.

Evaluating the various proposed causes of the extinction depends upon knowing how rapidly the mass extinction occurred: no dates, no rates, as a colleague of mine is fond of saying. A mass extinction drawn out over millions of years demands a much different explanation than an extinction lasting only a few hundred thousand years, or less. Establishing the duration of the extinction is critical. Together with my good friends Jin Yugan and his colleagues from Nanjing, and Sam Bowring and his group from Massachusetts Institute of Technology (MIT), we have scoured south China in search of volcanic ash beds bracketing the extinction interval. Chapter 4, *It's a Matter of Time*, introduces the tools used to date volcanic eruptions. We have shown that the end-Permian destruction occurred in less than 500,000 years and probably less than 160,000 years. We cannot yet say how much less than this, but nothing excludes the possibility that the extinction was as abrupt as the end-Cretaceous mass extinction. But this only tells us how fast the extinction was in South China. This chapter concludes with a look at how we can extend these results to other regions by integrating them into correlation schemes based on fossils and the distinctive shifts in the carbon cycle.

Chapter 5, *Filter Feeding Fails*, chronicles the shift in perspective over the past decade from a lengthy event to the twin crises, and the patterns of extinction and survival in the oceans. Not all groups suffered to the same extent, and these differences provide important clues to the causes of the extinction. The varying patterns of extinction and survival between different groups are another important clue in determining the causes of the extinction.

South African Eden, chapter 6, focuses on the extraordinary fossil animals of the Karoo Desert of South Africa, one of my favor-

ite places. Here a magnificent record of vertebrates preserves documentation of extinctions near the Permo-Triassic boundary. This chapter also discusses extinctions among plants and other animals, providing critical clues to whether life on land was as severely affected as life in the oceans. Absent such information we cannot distinguish between proposed causes that only affect the oceans, and those with more global impacts. Insects are remarkably resistant to extinction, and as far as we know, the only mass extinction insects ever suffered occurred during the Permo-Triassic. Other major disappearances occurred among land vertebrates and some plants, although it is not entirely clear whether the events on land and in the oceans occurred at the same time.

Life depends on the flow of carbon through the oceans and atmosphere, and its burial as organic debris, oil, and limestone. Consequently, geochemists have developed very sensitive tools to follow perturbations to this cycle. The problem is that there are often too many ways to generate these shifts, as discussed in chapter 7, *The Perils of Permian Seas*. We know that a massive volume of carbon from organic matter was added to the atmosphere and oceans at the Permo-Triassic boundary. Where did the carbon come from? The simplest solution is that it came from all the organisms that died during the extinction, but it turns out that if every living thing were vaporized today the resulting carbon is not enough to cause the shift seen at the Permo-Triassic boundary. So some of the carbon must have come from some other source, such as coal beds, methane trapped in deep-sea sediments, or carbon dioxide from volcanoes. In addition, there appears to have been a longer-term shift in the amount of carbon buried in rocks from the Permian into the Triassic. The elements sulfur, oxygen, and strontium each have a cycle that was perturbed during the Permo-Triassic transition. In chapter 8 we return to the various hypotheses discussed in chapter 2 and evaluate them.

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The aftermath of the extinction may be as puzzling as the mass extinctions, and from the standpoint of the history of life, they are at least as important. After the other mass extinctions, new species

begin to proliferate within a few hundred thousand years. Chapter 9, *Resurrection and Recovery*, charts the cryptic patterns and processes of the end-Permian aftermath. Despite the nine species of gastropod I could collect beneath the brush and scrubby piñon pine of that Utah hillside, I know of two dozen snail lineages that survived the end-Permian extinction, but that simply cannot be found anywhere in the world during the first 5 million years of the Triassic. These lineages clearly survived the extinction, but are missing until they reappear, phoenixlike, from the ashes of the crisis. Such seemingly miraculous rebirths were christened Lazarus taxa by David Jablonski, a paleontologist from the University of Chicago (and normally not the most religious of men). The number of Lazarus lineages among gastropods and other taxa tell us that many fossils simply were not preserved in the fossil record. But something else was also happening. Lazarus taxa do not reappear in the fossil record until the pace of diversification, or origination of new species, begins to pick up. This suggests some connection between the recovery and the reemergence of the Lazarus taxa. What? There are two explanations: The first is that environmental perturbations continued for millions of years after the extinction, retarding the recovery. The alternative is that the extinction so disrupted the ecology of communities that a slow convalescence was required before ecological communities could begin to function, new species appear, and Lazarus taxa emerge.

To grasp the significance of the extinction for the history of life, we need to understand why those hillsides in Utah have so few fossils, and why rocks all over the world have the same grubby fossils. Out of such scrappy remains and the return of the Lazarus taxa, evolution molded the world of today. Many environmentally minded people view extinction as tragic, even intolerable, an assault upon the integrity of the ecosystems that sustain us, and likely to produce a world we would not want to pass on to our children's children. At the rapidity of our current, human-induced biodiversity crisis, extinction is intolerable. But as discussed in the final chapter, *The Paradox of the Permo-Triassic*, mass extinction is a powerful creative force. From the wreckage of mass extinctions the survivors are freed for bursts of evolutionary creativity, chang-

ing the dominant members of ecological communities and enabling life to move off in new and unexpected directions.

Before anyone rushes out to proclaim that mass extinction is a good idea, remember how long the recovery lasted. The 5 million years after the end-Permian mass extinction were a pretty lousy time to be alive (even for snails), and the diversity of life in the seas did not begin to approach preextinction levels for tens of millions of years. A long time to wait.