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The tempo of mass extinction and recovery: The end-Permian example

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Mass extinctions are brief episodes of greatly increased extinction, commonly affecting both marine and terrestrial species. Since the origin of animals some 600 million years ago, there have been at least six major mass extinctions. The disappearance of the dinosaurs during the end-Cretaceous mass extinction 65 million years ago is perhaps the best known event, but the end-Permian (*ca.* 251 million years ago) extinction was, without question, the most profound. Although extinctions (often called background extinctions) have occurred throughout Phanerozoic history, they are distinct from mass extinctions. Mass extinctions and recoveries have played a fundamental role in animal evolution, comparable to natural selection, because they may trigger the demise of dominant species and massive reorganization of entire ecosystems. Thus understanding mass extinctions and their recoveries is critical for further developing models of evolutionary process. In particular, we seek to answer the following questions: (*i*) How rapidly do these extinction events occur? (*ii*) What caused them, and is there a single mechanism for all extinctions? (*iii*) What became extinct, what survived, and why? (*iv*) How did life recover in the aftermath of these events?

We have chosen to concentrate on the end-Permian extinction because it eliminated at least twice as many species, over 85% of species in the oceans, as the next largest extinction. This event triggered the most widespread reorganization of ecosystems and animal diversity in the past 500 million years and is largely responsible for much of the structure marine ecosystems today. Out of the devastation of the extinction, the Paleozoic marine communities dominated by sessile filter-feeding clades such as brachiopods and stalked echinoderms were replaced by a new suite of communities. These new communities included more mobile and burrowing groups and a higher percentage of predators. In addition, after the postextinction recovery, we see the rise of both dinosaurs and mammals. The basic facts that must be explained are (1): (*i*) Extinction of 85% or more of all species in the oceans, approximately 70% of land vertebrates, and significant extinctions of plants and insects; (*ii*) widespread evidence for low oxygen levels (anoxia) in both deep and shallow levels of the oceans before, during, and after the extinction interval; (*iii*) dramatic shifts in the carbon cycle of the atmosphere and oceans indicating sequestration of organic carbon in the deep ocean before the extinction and a rapid change in the isotopic composition of carbon in carbonate rocks during the extinction; (*iv*) the extinction occurs during a rise in sea level; (*v*) the extinction is contemporaneous with the eruption of a large-volume (3–5 million km^3) flood basalt province in Siberia; (*vi*) there is evidence for significant global warming after the extinction; and (*vii*) the pattern of extinction of species in the oceans is consistent with a drop in the percentage of atmospheric oxygen, which favors groups with active metabolisms. A better understanding of the end-Permian extinction and its recovery should allow for new insights into the role of mass extinctions in evolution.

How Rapid Was the End-Permian Extinction and Its Subsequent Recovery? Mass extinctions are recognized in the fossil record by the abrupt disappearance of taxa, sometimes associated with a discrete "boundary bed," which in the case of the end-Cretaceous extinction is a layer rich in impact ejecta. Determining the abruptness of any extinction requires a careful statistical analysis of the stratigraphic and fossil record (2). Differences in sediment accumulation rate and preservation potential of organisms can lead to an artificially abrupt and/or drawn-out extinction signal, especially if the extinction is of short duration (i.e., less than 1 million years). The biggest problem in determining how much time is represented by a particular stratigraphic interval is that time is not linearly distributed in the rock record and thus stratigraphic thickness cannot be converted to time. An ultimate goal for understanding an extinction is to constrain its tempo by combining high-precision geochronology with paleontological studies. In south China, the Permo/Triassic boundary is well preserved at many localities, including a classic section near the town of Meishan. Interlayered with the fossil-bearing rocks are a series of thin volcanic ash beds that have been precisely dated by using the U-Pb zircon technique (1). U-Pb zircon geochronology allows the age of individual ash beds to be determined with uncertainties of less than 500,000 years. The technique and error assessment can be independently evaluated by dating a sequence of ash beds in stratigraphic order.

At the Meishan section, the extinction occurs across a 4-cm-thick interval of limestone and volcanic ash. On the basis of interpolations between dated ash beds, we estimate that the extinction at Meishan took place in less than 100,000 years. This result effectively eliminates a variety of proposed causes that operate over several to tens of millions of years. Any mechanism proposed for the extinction must explain its catastrophic nature. The extinction interval is similar to the amount of time estimated for the end-Cretaceous extinction (3). The timing of the postextinction recovery is not well constrained, although on the basis of unpublished data, we prefer an estimate of approximately 5 million years, which is similar to the estimate of more than 3 million years for the recovery of marine ecosystems after the end-Cretaceous extinction (ref. 4; see also ref. 5).

One of the most curious aspects of the end-Permian extinction is the prolonged recovery (5, 6). A few clades began to recover immediately after the extinction, and geochemical proxies suggest relatively rapid recovery. However, diverse

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ecosystems do not reappear for at least 5 million years, which suggests that environmental perturbations may have continued for millions of years after the extinction.

What Causes Mass Extinctions and Is There a Single Mechanism for All? As with the end-Cretaceous event that eliminated the dinosaurs, many different hypotheses have been proposed to explain the end-Permian extinction including: bolide impact, massive outpourings of flood basalts, overturn of density-stratified oceans and poisoning of shelf waters with CO_2, movement of anoxic waters into shelf regions, and long-term climate change (cooling) and drop in sea level related to supercontinent aggregation and dispersal (7). In fact, a single mechanism may not be sufficient, and the extinction may have been caused by a combination of factors (6).

Since the proposal that a meteorite impact played an important role in the end-Cretaceous extinction, several authors have suggested that the impact of extraterrestrial objects may be a general way of driving mass extinctions. However, to date, compelling evidence to support an impact for the end-Permian extinction such as an ejecta layer, elevated iridium concentrations, or shocked quartz have not been discovered. Hallam and Wignall (8) have made the case that every mass extinction is characterized by evidence for transgression (increase in sea level) and onshore movement of a layer of dysoxic and anoxic waters. Marine anoxia is generally recognized as a feature of the deep ocean. In the case of the end-Permian extinction, Isosaki (9) has shown that a few remnants of latest Permian to earliest Triassic deep-sea sedimentary rocks do exhibit evidence for a protracted period of anoxia (*ca*. 20 million years). However, how anoxic water suddenly floods the shallow marine environment to trigger the mass extinction is not clear. A related proposal for overturn of deep anoxic waters resulting in CO_2 poisoning (10) is consistent with patterns of extinction and survival of marine groups, but there is no evidence of latest Permian glaciation, proposed as a trigger for the oceanic overturn. Additionally, long-term sequestration of high levels of CO_2 in the deep sea appear to be implausible.

Renne and others (11) first demonstrated that the 3–5 million km^3 eruption of the Siberian traps occurred in a short period of time that coincided, within error, with the Permo–Triassic boundary. They proposed a model in which sulfur-rich aerosols from the Siberian volcanism led to a brief episode of cooling followed by global warming.

Yet each of these proposed mechanisms has occurred throughout earth history but did not result in mass extinctions. What is it about that end-Permian extinction that led to the demise of greater than 85% of the animals in the ocean? We still don't know the answer to that question, in part because several important questions remain unresolved.

Outstanding Questions. (*i*) Did the extinction occur at exactly the same time in both marine and terrestrial environments? (*ii*) Did the extinction occur simultaneously across the planet? (*iii*) Is the commonly observed negative shift in the carbon isotopic composition of seawater the result of extinction (collapse of primary productivity), the signature of upwelling CO_2-charged bottom water, the melting of methane hydrates, or the result of a cometary impact? (*iv*) What is the magnitude of the carbon isotopic shift and does it always coincide with the extinction? (*v*) Is the main pulse of the Siberian trap eruptions exactly coincident with the extinction? Evaluating the variety of hypotheses and determining the cause of the extinction will require resolution of these issues through combined paleontological, geochemical, and geochronological studies of a variety of depositional settings (terrestrial, shallow marine, and deep marine). Such studies will require additional enhancements to statistical analysis of the fossil record, new and more refined geochemical proxies for environmental change (both marine and terrestrial), and even more accurate methods of geochronology.

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