# The complexity of mass extinction

**Hermann W. Pfefferkorn***

*Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, PA 19104-6316*

Major mass extinctions are among the most troublesome and puzzling events in Earth's history (Fig. 1). Rapid progress has been made in the understanding of duration, extent, causes, and consequences of these events. One important insight has been the recognition that each event was different and very complex in itself. In this issue of PNAS, Visscher *et al.* (1) add an astonishing insight into effects on the genetic material of plants during the most devastating of all mass extinctions 251 million years ago (2). The results of Visscher *et al.* (1) document a complex chain of cause and effect relationships that occurred not as a single pulse but over a significant time span. The forests of gymnosperms that covered large areas of most climate zones of the late Permian Period disappeared and were replaced by herbaceous lycopsids (mostly relatives of quillworts) represented frequently only by the genus *Pleuromeia* covering the landscape with a rather monotonous vegetation (Fig. 2). These plants were 1.5–2 m (≈6 ft) tall. Although these plants often formed denser stands than shown in Fig. 2*b*, they depended on water and represented vegetation that was certainly much less dense and had a lower biomass than the forests they replaced. Visscher *et al.* (1) report that a significant percentage of microspores of these plants occurs as tetrads, which means that the four microspores that originate from one mother cell do not separate and are clumped together in the very place that opens during spore germination, indicating that they were not viable. It has been established in living plants that specific genetic changes are required to achieve this effect (3, 4). Thus, a morphological feature that can be readily observed in microscopic preparations of fossil spores or pollen is the indicator for genetic changes occurring in these plants. Visscher *et al.* (1) suggest a convincing scenario of the cause and effect relationship between the geologic occurrences of volcanism over large areas of Siberia that released organohalogens from hydrocarbons widely present in the rocks of that area. The resulting destruction of atmospheric ozone lead to an increase of UV-B radiation that triggered the mutations in the plants. The question arises immediately how a plant group could dominate the landscape that was severely impacted by mutations with negative consequences for propagation. The answer comes from previous research that pointed out that these lycopsids could employ asexual reproduction during times of unfavorable environmental conditions (5). The discovery and explanation of this chain of interrelated consequences represents a new insight into the level of complexity of physical and biological processes during a mass extinction.

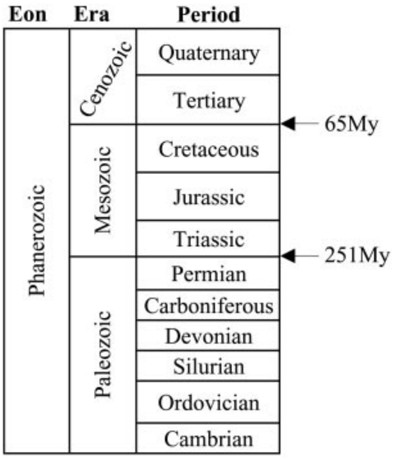

**Fig. 1.** Chart of the subdivisions of the last 545 million years (My) of Earth history showing the position of the two largest mass extinctions at the Permian–Triassic and Cretaceous–Tertiary boundaries. The one at 251 million years is discussed here and in the companion article (1). Vertical axis not to scale.

Early in the history of geology, it was recognized that there were two levels in the geologic column of sedimentary rocks (Fig. 1) where the composition of faunas and floras changed dramatically. Therefore, these levels were used not only as boundaries between periods (Permian–Triassic and Cretaceous–Tertiary) but also as boundaries between the three eras that were named Paleozoic ("old life"), Mesozoic ("middle life"), and Cenozoic ("new life") in Greek-derived terminology. Other boundaries between periods also show changes, albeit less drastic ones.

At first, all these boundaries and other levels of changes were seen as the expression of catastrophes. However, even before 1800, it was realized that most geological processes are slow and achieve their results through the accumulation of small effects over long periods of time. Uniformitarianism replaced catastrophism as the leading theory of the Earth sciences. Today, uniformitarianism is defined as the constancy of physical and chemical laws over time, while the rates and areal extent of any given process can be variable. In addition, there are processes that happen so rarely that humans have never observed them during the exceedingly short span of written history. Thus, catastrophes are now part of our uniformitarian understanding of Earth processes.

Mass extinctions certainly can be seen as catastrophes, and the careful observational and quantitative work of the last decades has shed new light on the complexity of these events. Ultimately, we want to understand the cause(s) and mechanism(s) behind these momentous changes. At first, potential causes that were well understood by geologists were considered. There have been times in Earth's history when volcanism was much more extensive than it is today and huge areas were covered by volcanoes. Timewise, two of these major volcanic events coincide with the two largest mass extinctions. Secondly, both major mass extinctions coincide with large sea-level low-stands. Thus, the biggest crises of life on Earth coincide with exceptional conditions in two major geological processes (6, 7). The second process also contributed to a difficulty in studying these two time intervals. As sea-level fell, deposition of sediments ceased and erosion began in most of those areas no longer covered by the sea. Thus, resulting sedimentary rocks that form the record of these times are rare and difficult to find. Visscher *et al.* (1) studied a section of terrestrial rocks that spans this time interval in Greenland.

The debate about mass extinctions changed dramatically when an iridium anomaly was discovered at the Cretaceous–Tertiary boundary and later when the Chicxulub Crater in Yucatan of the same age was discovered (6, 7). These two findings, together with additional work elsewhere, indicated that the actual boundary and major parts of this mass extinction had a direct connection with a meteorite impact. An impact presented an easily understandable and dramatic event that made it easier to grasp the cause of a mass extinction.

---

See companion article on page 12952.

*E-mail: hpfeffer@sas.upenn.edu.

www.pnas.org/cgi/doi/10.1073/pnas.0404933101

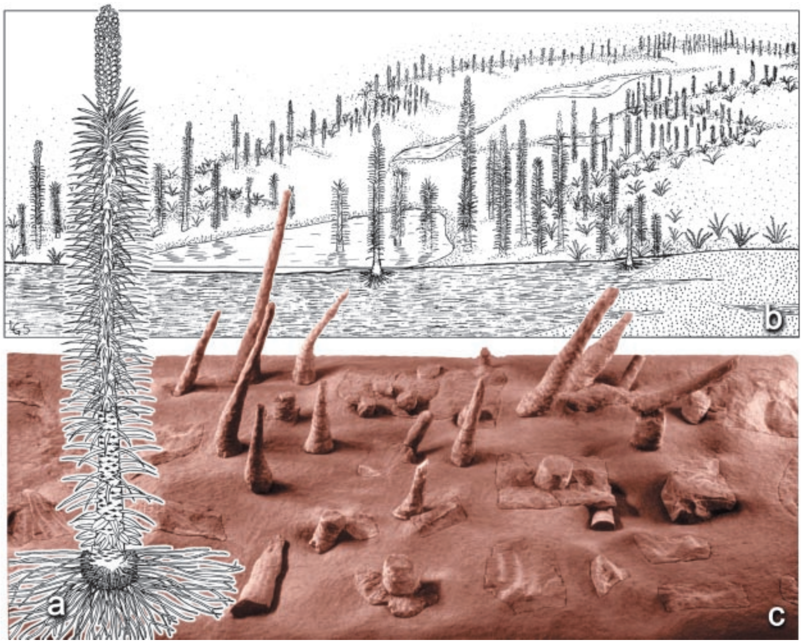

**Fig. 2.** During the mass extinction at the Permian–Triassic boundary, forests were replaced by herbaceous vegetation of spore-bearing plants in large areas. This figure shows reconstructions of one of the larger representatives of the herbaceous lycopsids, *Pleuromeia*, which was 1.5–2 m (≈6 ft) tall (*a*), a landscape with this plant and a fern species (*b*), and the *in situ* occurrence of casts of stems of this species in a red sandstone of the early Triassic Period, Eifel area, Germany (*c*) (10). This montage of specimens in life position (*c*) is on exhibit in the Staatliche Museum für Naturkunde, Karlsruhe, Germany. [*a–c* are reproduced with permission from ref. 10 (Copyright 1991, E. Schweizerbart'sche Verlagsbuchhandlung, www.schweizerbart.de). Compound figure is reproduced with permission from ref. 11 (Copyright 2003, Städtische Museen Heilbronn).]

However, it was often forgotten that there were other processes happening at the same time, some of which that started well before the impact and others that continued afterward. It appears that there were several trends of considerable magnitude occurring simultaneously, which were then topped by a specific event. The article by Visscher *et al.* (1) demonstrates a specific part of complexity for the Permian–Triassic crisis.

Recently, Becker *et al.* (8) reported a possible end-Permian impact crater offshore in northwestern Australia, and it is clear that they see this find as a parallel to the Cretaceous–Tertiary impact. The view of Becker *et al.* (8) is supported by earlier evidence of such an impact in rocks deposited across the Permian–Triassic boundary. The question arises as to how the different processes were related? It is undisputed that the Permian–Triassic boundary extinction was not a single-step event and that the crisis lasted for 5–8 million years (9). Visscher *et al.* (1) do not even consider an impact because they are describing a multiphase event that extended over a significant amount of time at the end of the Permian Period. Their explanation lies in the volcanism that occurred in a part of the globe that is opposite the impact but not antipodal. Becker *et al.* (8) discuss and speculate on this matter and point out that the connection between the impact and the volcanism is uncertain and has to be further investigated, and they also suggest that an impact could have increased the intensity of an already ongoing major volcanic event.

Today, we are living through another mass extinction. We will be better able to assess this problem if we understand the details of previous ones. Paleontology and geology with their subspecialties are the only way to elucidate the very complex histories of mass extinctions. The basis is still systematic paleontology that collects qualitative and quantitative data that have to be combined with biological knowledge to see fossils as remnants of living organisms and ecosystems as expressed in the transformation of paleontology into paleobiology that started 30 years ago. Currently, we see its further development into geobiology, the study of the interaction of physical and biological systems. It should be clear that one cannot study Earth systems without considering both the physical and the biological systems and their interaction in deep time.

1. Visscher, H., Looy, C. V., Collinson, M. E., Brinkhuis, H., van Konijnenburg-van Cittert, J. H. A., Kürschner, W. M. & Sephton, M. A. (2004) *Proc. Natl. Acad. Sci. USA* **101,** 12952–12956.
2. Erwin, D. H. (1993) *The Great Paleozoic Crisis* (Columbia Univ. Press, New York).
3. Preuss, D., Rhee, S. Y. & Davis, R. W. (1994) *Science* **264,** 1458–1460.
4. Rhee, S. Y. & Sommerville, C. R. (1998) *Plant J.* **15,** 79–88.
5. DiMichele, W. A., Davis, J. I. & Olmstead, R. G. (1989) *Taxon* **38,** 1–11.
6. Prothero, D. R. & Dott, R. H., Jr. (2002) *Evolution of the Earth* (McGraw Hill, New York).
7. Stanley, S. M. (1999) *Earth System History* (W.H. Freeman, New York).
8. Becker, L., Poreda, R. J., Basu, A. R., Pope, K. O., Harrison, T. M., Nicholson, C. & Iasky, R. (2004) *Science* **304,** 1469–1476.
9. Payne, J. L., Lehrmann, D. J., Wei, J., Orchard, M. J., Schrag, D. P. & Knoll, A. H. (2004) *Science* **305,** 506–509.
10. Fuchs, G., Grauvogel-Stamm, L. & Mader, D. (1991) *Palaeontographica B* **222,** 89–120.
11. Kelber, K.-P. (2003) *Museo* **19,** 38–59.