



# How to kill (almost) all life: the end-Permian extinction event

Michael J. Benton and Richard J. Twitchett

Department of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK

**The biggest mass extinction of the past 600 million years (My), the end-Permian event (251 My ago), witnessed the loss of as much as 95% of all species on Earth. Key questions for biologists concern what combination of environmental changes could possibly have had such a devastating effect, the scale and pattern of species loss, and the nature of the recovery. New studies on dating the event, contemporary volcanic activity, and the anatomy of the environmental crisis have changed our perspectives dramatically in the past five years. Evidence on causation is equivocal, with support for either an asteroid impact or mass volcanism, but the latter seems most probable. The extinction model involves global warming by 6°C and huge input of light carbon into the ocean-atmosphere system from the eruptions, but especially from gas hydrates, leading to an ever-worsening positive-feedback loop, the 'runaway greenhouse'.**

When Doug Erwin wrote a review for *TREE* in 1989 about the end-Permian event [1], he presented evidence for what had died out and reviewed a range of killing scenarios (i.e. models of environmental crisis that would lead to the levels of extinction observed, and that were supported by available geological and geochemical evidence). At that time, it was unclear whether the cause of the mass extinction had been major continental movements, sea-level fall, salinity changes, volcanic eruption, extraterrestrial impact, or some combination of these. Oceanic anoxia and global warming models were suggested later. Indeed, even the timescale of the event was uncertain: had it happened essentially overnight or had it dragged on for as long as 10 million years (My)?

Since then, and especially since 1995, the whole story has become clearer. Four main parallel themes have arisen, noted here not necessarily in chronological order. First, the Permo–Triassic (PTr) boundary has been dated precisely to 251 My ago (Mya). Second, the Siberian traps, vast volumes of volcanic lavas, have also been dated more precisely than had been possible before, and the peak of their eruption history matches the PTr boundary. Third, extensive study of rock sections that straddle the PTr boundary, and the discovery of new sections, began to show a common pattern of environmental changes through the latest Permian and earliest Triassic (~253–249 Mya). Fourth, studies of stable isotopes (oxygen and carbon) in

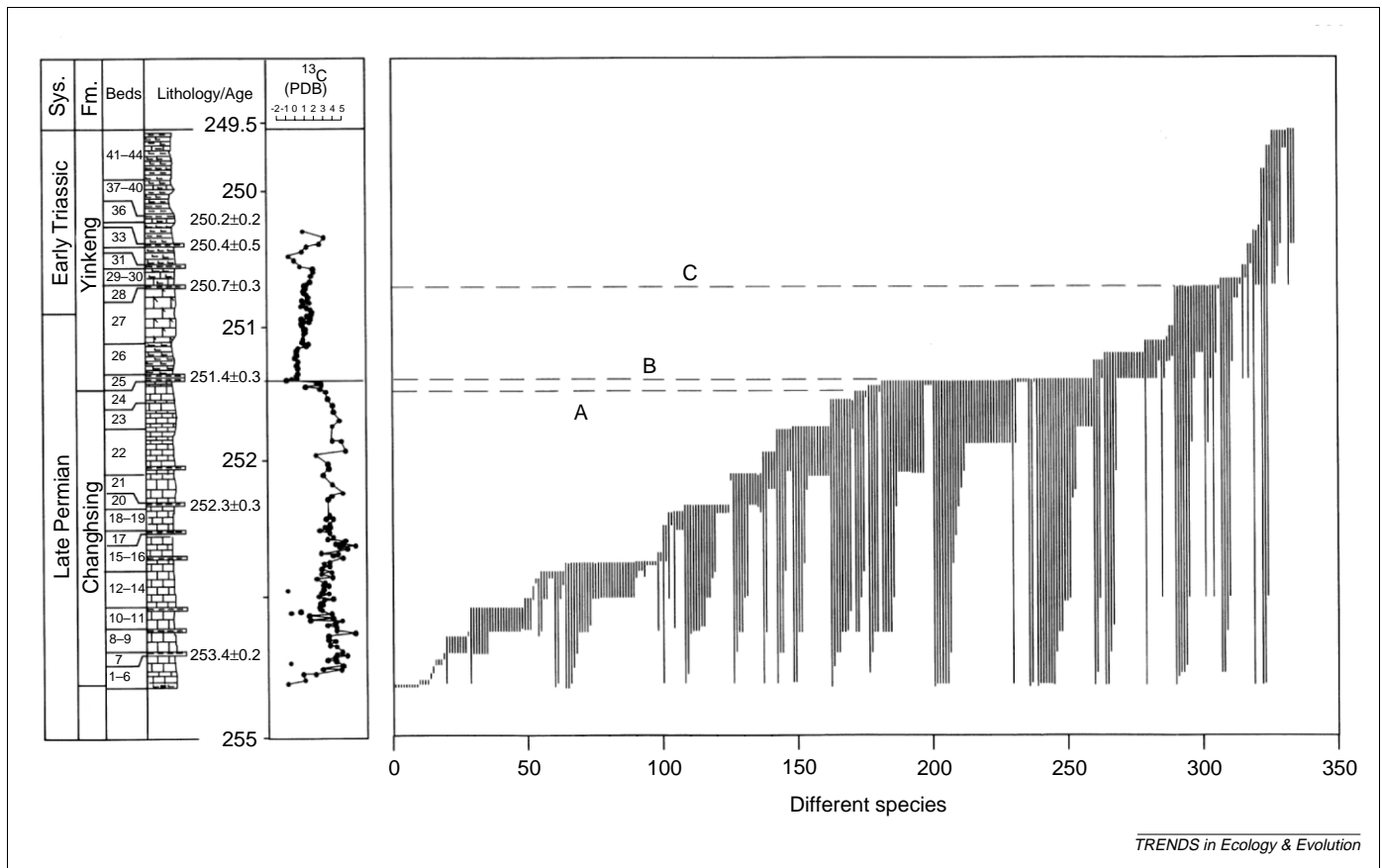
those rock sections revealed a common story of environmental turmoil. Together, these themes seemed to point to a model of change in which normal feedback processes could not cope, and the chemical and temperature balance of the atmosphere and oceans went into catastrophic breakdown. Here, we shall present the current geological and palaeontological thinking by reviewing these four recent advances.

## Dating and timing

In spite of being long recognized as the biggest mass extinction of all time, and far more significant than the better-known event at the end of the Cretaceous period (the KT event; 65 Mya) when the dinosaurs succumbed, the end-Permian mass extinction was, until recently, hard to define. Timing was a key problem. Standard dates of 225, 245, or 250 Mya were often quoted for the PTr boundary, but these were based on interpolation from more precisely dated rocks well above and well below the boundary. This lack of precise dating meant that palaeontologists could not demonstrate whether the decline of life on Earth at this time had been a long process or had been instantaneous. However, new rock sections and new radiometric dating methods enabled Sam Bowring and his group [2] to date volcanic ash bands in Chinese sections using the uranium/lead method [2], and to assign a date of 251 Mya to the PTr boundary.

Dating the boundary was only one problem. Dating the shape of the extinction was another. The classic Meishan section in southern China, the global stratotype for the PTr boundary [3], provided the means to do this because it is rich in fossils and there are several datable ash bands scattered through the succession. In a recent study, Jin Yugan and colleagues [4] identified 333 species belonging to 15 marine fossil groups (including microscopic foraminifera, fusulinids, and radiolarians; rugose corals, bryozoans, brachiopods, bivalves, cephalopods, gastropods, trilobites, conodonts, fish, and algae). In all, 161 species became extinct below the boundary beds (Fig. 1) during the 4 My years before the end of the Permian. Extinction rates in particular beds amounted to 33% or less. Then, just below the PTr boundary, at the contact of beds 24 and 25, most of the remaining species disappeared, giving a rate of loss of 94% at that level. Three extinction levels were identified, labelled A, B and C (Fig. 1). Jin and colleagues argued that the six species that apparently died out at level A are probably artefactual records, really pertaining to level B (examples of the Signor-Lipps Effect, the axiom

Corresponding author: Michael J. Benton (mike.benton@bris.ac.uk).



**Fig. 1.** The extinction of life at the end of the Permian in southern China, showing rock systems (Sys.), geological formations (Fm.), radiometric ages and carbon isotope values (measured to the Pee Dee Belemnite standard, PDB; see Box 3 for explanation). Three extinction levels, A, B and C, are identified. Vertical lines indicate stratigraphic ranges of marine species in the sections and show that more than 90% of species died out in the interval from A to C. Numbers on x-axis indicate species names. Reprinted with permission from [4].

that palaeontologists will rarely find the very last fossil of a species). But Level C might be real, and this suggests that, after the huge catastrophe at level B, some species survived through the 1 My to level C, but most disappeared step-by-step during that interval. Scaling up from local rock sections to establish the global pattern is tricky, but the figures from other sections, such as northern Italy [5] and East Greenland [6,7], seem to agree both in magnitude and rate of extinction (Box 1).

The suddenness and magnitude of the mass extinction suggest a dramatic cause, perhaps asteroid impact or volcanism. Traditionally, earth scientists have been slow to accept such catastrophic models [8]. For example, until 1960, many geologists were reluctant to accept that Meteor Crater in Arizona had been produced by an impact, and they were also slow to accept the impact model for the KT mass extinction after its announcement in 1980 [9]. However, both views are now the standard, and geologists have looked hard for evidence that the end-Permian mass extinction was also the result of an extraterrestrial impact.

#### Evidence for an impact?

Three key pieces of evidence for the KT impact [10] are the candidate crater in Mexico, the iridium spike (massive enrichment of the rare metallic element iridium, which generally reaches the surface of the earth only from space), and shocked quartz (a form of the commonest mineral in

rocks that has been subjected to intense pressure). All three phenomena were reported from PTR beds in the 1980s and 1990s, and all three have been either rejected or greeted with lukewarm enthusiasm at best [8,10].

Early in 2001, Luann Becker and colleagues [11] reported the presence of extraterrestrial noble gases (helium and argon) trapped in the cage-like molecular structure of fullerenes at the PTR boundary in China and Japan. Fullerenes are large molecules of carbon, comprising 60–200 carbon atoms arranged as regular hexagons around a hollow ball. Fullerenes, called buckyballs, are named after Richard Buckminster Fuller (1895–1983), inventor of the geodesic dome, because their natural structure mimics what he had invented. Fullerenes can form in meteorites, in forest fires, and even within the mass spectrometers that are used to study them.

Because the helium and argon in the PTR boundary fullerenes was identical isotopically to helium and argon derived from meteorites, it was argued that they must have come from the impact of a meteorite. These results have been criticized soundly. Farley and Mukhopadhyay [12] reported that they had reanalyzed samples from exactly the same sites in China using exactly the same laboratory procedures, and yet they had failed to replicate the results of Becker and her team. Furthermore, Isozaki [13] argued that the PTR boundary is missing in the Japanese section studied by Becker and colleagues, and

### Box 1. Extinction magnitude

Many animal groups suffered major losses during the Late Permian (Fig. 1). Fusulinid foraminifera disappeared completely, although other foram groups suffered much lower levels of extinction. Palaeozoic corals (Rugosa and Tabulata) also vanished. Stenolaemate bryozoans and articulate brachiopods suffered near-complete extinction. The extant echinoderm groups all experienced severe bottlenecks at this time: only two lineages of crinoids and echinoids made it into the Mesozoic. Several echinoderm groups (e.g. Blastoidea) suffered complete extinction. Major losses of previously dominant and ecologically important groups caused the collapse of many biological communities. It took several million years for complex communities to reappear, both in the oceans and on land [6,7].

Estimating the severity of past extinction events is not easy. Palaeontologists focus on genera or families when discussing long-term, global changes in biodiversity because preservation becomes patchier at the species level and true biological species are hard to recognize from fossil remains. Based on two databases of family

diversity through time [34,40], estimates of losses during the Permo–Triassic event are 49% [41] or 48.6% [42] of marine animal families, 62.9% of families of continental organisms [42], and 60.9% of all life [42].

The level of extinction at lower taxonomic levels was then estimated by Raup [32] using a reverse rarefaction technique [43]. This is founded on the intuitive idea that the loss of 50% of families must equate to the loss of a much higher proportion of species: for a family to go extinct, every species in it must die out. The loss of 50% of families must mean that the other, surviving families are also hit hard, but if only one out of 100 species in a family survive, that family is deemed to survive. From this method, it is estimated that 96% of marine species were lost during the end-Permian extinction event [32]. However, this calculation assumes random species extinction across all families (i.e. no selectivity against certain groups), which is not true [43]. The rarefaction technique might overestimate species extinction levels by 10–15%, so the real magnitude of the end-Permian event might be closer to 80% species loss.

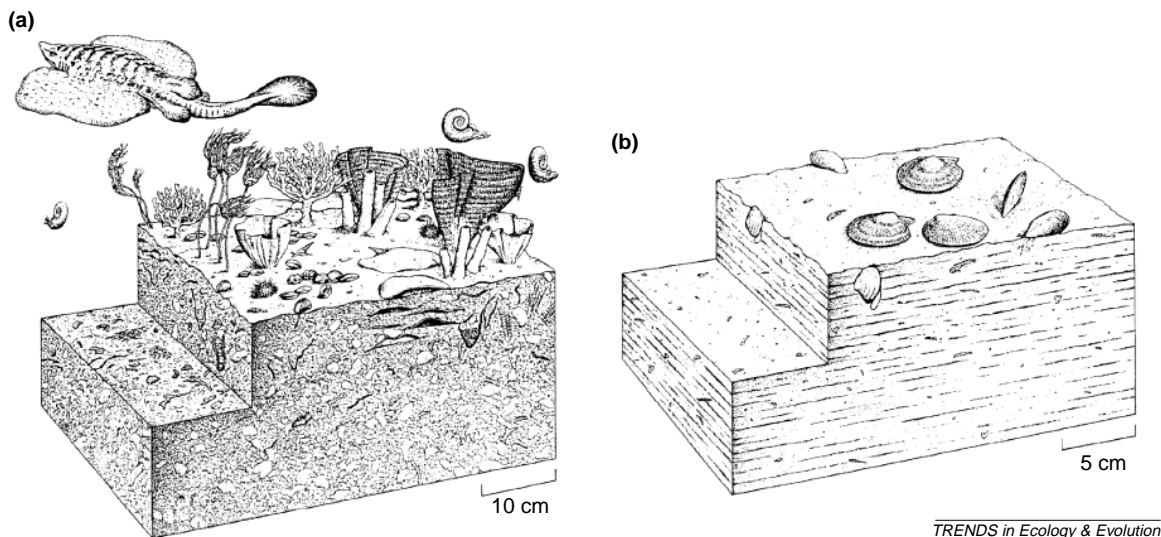


Fig. 1. Block-diagram reconstructions of the ancient seabed in southern China immediately before (a) and after (b) the Permo–Triassic mass extinction. Note the richness of reef life and the burrowing infauna before the crisis, and the absence of such species after. A marine fauna of 100 or more species is reduced to four or five. Original artwork by John Sibbick.

that their samples came from at least 80 cm below the boundary. Indeed, the helium and argon reported by Becker and colleagues did come from rocks containing fullerenes, but it was never demonstrated that those noble gases were actually trapped in the fullerenes, a key claim.

More recently, Kaiho and colleagues [14] have reported sediment grains that supposedly show evidence of compression by impact, as well as geochemical shifts that they interpret as indicating the impact of a huge asteroid. However, their data are far from conclusive and have also been criticized severely by other geochemists [15]. Although the evidence for impact at the PTr boundary has been promoted vigorously recently [16], we regard it as tenuous. The evidence is far weaker and more limited than for impact at the KT boundary and it would be premature to construct a killing scenario founded on such evidence.

#### Evidence for an eruption?

At the end of the Permian, giant volcanic eruptions occurred in Siberia, spewing out some 2 million km<sup>3</sup> [17] of basalt lava, and covering 1.6 million km<sup>2</sup> of eastern

Russia to a depth of 400–3000 metres, equivalent to the area of the European Community. It is now accepted widely that these massive eruptions, confined to a time span of <1 My, were a significant factor in the end-Permian crisis.

The suggestion to this effect was first made in the 1980s. Russian geologists had explored the Siberian Traps long before then, but were unsure of their age. The Siberian Traps are composed of basalt, a dark-coloured igneous rock, which is generally not erupted explosively from classic conical volcanoes, but usually emerges more sluggishly from long fissures in the ground (as seen in Iceland). Flood basalts typically form many layers and can build up over thousands of years to considerable thicknesses. They produce a characteristic landscape, called trap scenery, where the different lava flows erode back through time, producing a layered, stepped appearance to the hills (the word ‘trap’ comes from the old Swedish word *trapp*, meaning a staircase).

Early efforts at dating the Siberian Traps produced a huge array of dates, from 160 to 280 Mya, with a particular

cluster between 230 and 260 Mya. According to these ranges, geologists in 1990 could conclude only that the basalts might be anything from Early Permian to Late Jurassic in age, but probably spanned the PTr boundary. More recent dating [2,18,19] using newer radiometric methods, yielded dates exactly on the boundary, and the range from bottom to top of the lava pile was ~600 000 years, highlighting that the event occurred, geologically speaking, overnight. In addition, this kind of time duration for the eruptions matches the evidence from China of a rapid extinction (Fig. 1).

Consequently, with increasingly precise dating, the Siberian Trap eruptions have moved from having been allotted a relatively minor role in the PTr crisis as part of a complex web of interacting processes [20], to being the most probable trigger for the catastrophe [2,4,21]. However, there are still unresolved debates concerning the accuracy of the new dates [19]. Some scientists have even suggested recently that the massive flood basalts were actually themselves caused by a giant extraterrestrial impact, which tore deep into the continental crust of that part of present-day Siberia [22]. However, the nature of the eruptions casts doubt on such a model, and there is no evidence that any volcanism on the Earth, or indeed on any other planet, was triggered by an impact [23,24].

### Reading the environmental changes

To investigate the faunal, floral and environmental changes in more detail, continuous fossiliferous rock sections through the PTr crisis need to be studied. In the late 1980s, few such sections were thought to exist and those that had been studied previously were thought to contain significant gaps right at the crucial extinction interval. Reanalysis of these sections by Tony Hallam and Paul Wignall, among others, in the early 1990s [10,25–27] led to the realization that the records through the extinction event were much more complete than was believed previously.

The rocks contain a huge diversity of fossil shells and skeletons, showing that the latest Permian seas teemed with life. In particular, the Permian sediments are intensely bioturbated, full of burrows made by a plethora of benthic animals living, feeding and moving through the sediment. The communities were diverse and ecologically complex. By contrast, sediments deposited immediately after the extinction event, in the earliest Triassic, are dark-coloured, often black and full of pyrite. They largely lack burrows, and those that do occur are very small, and fossils of marine benthic invertebrates are extremely rare. These observations, in association with geochemical evidence, suggest a dramatic change in oceanic conditions from well-oxygenated bottom waters to widespread benthic anoxia [26,27]. Before the catastrophe, the ocean fauna was differentiated into recognizably distinct biogeographical provinces. After the event, a cosmopolitan, opportunistic fauna of thin-shelled bivalves, such as the 'paper pecten' *Claraia* and the inarticulate brachiopod *Lingula* spread around the world.

On land too, life was hugely diverse in the latest Permian. Terrestrial tetrapod (amphibian and reptile) faunas had reached high levels of complexity, arguably as

complex as modern mammalian communities [8,28], with four or five trophic levels among carnivorous forms. For example, the sabre-toothed gorgonopsians fed on thick-skinned, rhinoceros-sized herbivores, whereas several ranks of smaller flesh-eaters fed on smaller prey. Numerous groups of plants [28] provided a diversity of habitats, and some floras were endemic, indicating geographical differentiation relating to climatic zones. The decline and loss of tetrapods has been documented in some detail in South Africa [29], where the disappearance of taxa is indicated to be rapid. Comparison of the timings of species loss on land and in the sea suggests that they were coincident [6,7]. In many places, it seems that soils were washed off the land completely, and the only organisms to survive appear to have been fungi (Box 2).

Geochemistry gives additional clues about the nature of the environmental changes. Exactly at the PTr boundary, there is a dramatic shift in oxygen isotope values: a decrease in the value of the  $\delta^{18}\text{O}$  ratio of about six parts per thousand (ppt), which corresponds to a global temperature rise of ~6°C. Climate modellers have shown how global warming can reduce ocean circulation and the amount of dissolved oxygen to create benthic anoxia [30]. A dramatic global rise in temperature is also reflected in the types of sediment and ancient soil deposited on land [28].

### Box 2. The fungal spike

Immediately after the end-Cretaceous impact event, terrestrial sediments from North America contained fern spores and little else [44]. This 'fern spike' is interpreted as representing the initial stages of colonization of a barren land surface stripped of vegetation by the asteroid impact and subsequent wildfires. Similar pioneering fern communities are found in the aftermath of present day volcanic eruptions, colonizing the freshly deposited lava and ash.

A similar 'spike' has been reported at the Permo–Triassic (PTr) boundary: not a fern spike, but a fungal spike [45]. A study by Eshet and colleagues [46] on sections in northern Italy and Israel showed that fungal remains account for 10% of the pollen and spores just below and just above the extinction horizon, but increase to nearly 100% of the assemblage right at the extinction level. These fungi were interpreted as terrestrial forms and were said to represent the survivors of the catastrophic die-back of standing vegetation and sudden surge in decomposers in response to the piles of dead plant material left behind by the catastrophic killing.

This interpretation is not accepted universally. Some authors question whether the fungi were truly terrestrial because they are encountered only in shallow marine deposits [47]. Others have suggested that the apparent abundance of fungi could be an artefact of preservation because fungal hyphae are tougher than other plant tissues and are likely to survive longer in the environment [20].

In a detailed study of terrestrial vegetation through a complete and very well preserved PTr section in East Greenland, Looy and colleagues [7] failed to detect a fungal spike. Fungi were certainly present, but always in low abundance. However, there were 'spikes' in other vegetation types. Spores of heterosporous lycopsids (especially Selaginellales) increased briefly in abundance right after the collapse of the diverse woody gymnosperms of the Late Permian. Minor fern and bryophyte spikes were also detected. These groups were opportunistic pioneers, much like the ferns after the end-Cretaceous event. The PTr floral response is more complicated than this, however, with different groups (fungi and lycopsids) responding differently in different regions.

## The runaway greenhouse

Can the evidence for oceanic anoxia, global warming, a catastrophic reduction in the diversity and abundance of life be linked to the co-occurrence of the Siberian eruptions in a coherent killing model? The key might come from further study of carbon isotopes (Box 3). Values of  $\delta^{13}\text{C}$  show a sharp negative excursion during the PTr interval, dropping from a value of +2 to +4 ppt to -2 ppt at the mass extinction level [10,21,23,26,27]. This drop implies a dramatic increase in the light carbon isotope ( $^{12}\text{C}$ ), and geologists and atmospheric modellers have tussled over trying to identify its source. Neither the instantaneous destruction of all life on Earth and subsequent flushing of the  $^{12}\text{C}$  into the oceans, nor the amount of  $^{12}\text{C}$  estimated to have reached the atmosphere from the carbon dioxide released by the Siberian Trap eruptions are sufficient to explain the observed shift (Box 3). Something else is required.

Not only must this new source of  $^{12}\text{C}$  be identified, but that source must also be capable of overwhelming normal atmospheric feedback systems. The only option so far identified is the methane released from gas hydrates (Box 3), an idea that has been accepted with alacrity [12,23,24,31].

The assumption is that initial global warming at the PTr boundary, triggered by the huge Siberian eruptions, melted frozen gas hydrate bodies, and massive volumes of methane rich in  $^{12}\text{C}$  rose to the surface of the oceans in huge bubbles. This vast input of methane into the atmosphere caused more warming, which could have melted further gas hydrate reservoirs. The process continued in a positive feedback spiral that has been termed the 'runaway greenhouse' phenomenon. Some sort of threshold was probably reached, which was beyond where the natural systems that normally reduce carbon dioxide levels could operate effectively. The system spiralled out of control, leading to the biggest crash in the history of life.

## Conclusions and perspectives

Life came close to complete annihilation 251 Mya. A fortunate 5% of species did, however, survive and understanding how these few taxa recovered from the severest of evolutionary bottlenecks [32] is crucial to understanding the subsequent evolution of the biosphere. It took 100 My for global biodiversity at the family level to return to pre-extinction levels [10]. However, ecological recovery was somewhat quicker, with complex communities such as reefs becoming re-established by the Middle Triassic (some 10 My after the PTr boundary).

Details of the recovery of the marine ecosystem in the aftermath of the extinction are known only from two sites, northern Italy [33] and the western USA [34], both of which were located in tropical regions during the Early Triassic. Initial benthic low-diversity communities were composed of small-sized, epifaunal suspension-feeding opportunists, which were living under suboptimal environmental conditions of low oxygen and low food supply. Microbial mats covered much of the sea floor. A scarce infauna of small, deposit-feeding vermiform animals burrowed feebly just below the sediment surface. This

lasted for maybe a million years. With the disappearance of benthic oxygen restriction and the increase in food supply, larger and more diverse communities reappeared slowly. Epifaunal communities increased in complexity as crinoids and bryozoans returned and began to reach up into the overlying water column [33,35]. Infaunal communities saw the return of suspension feeders and finally crustaceans, and the size and depth of burrowing returned to pre-crisis levels by the Middle Triassic [33].

Little is known currently of the recovery pattern from elsewhere in the oceans, although work is ongoing. On land, for millions of years, virtually the only tetrapod was the plant-eating *Lystrosaurus*, subsisting on the few surviving herbaceous plants. Forest communities were absent until the Middle Triassic [7]. Life was clearly tough in the 'post-apocalyptic greenhouse' [28].

### Box 3. Carbon isotope shifts

Measuring the ratio of the stable isotopes  $^{13}\text{C}$  and  $^{12}\text{C}$  in geological specimens (e.g. limestones and fossil shells) is an important tool in the study of mass extinction events. In nature, most carbon occurs as  $^{12}\text{C}$ , with minor, but measurable, amounts of  $^{13}\text{C}$ . The ratio of these two isotopes in the atmosphere is the same as in the surface waters of the oceans. During photosynthesis, plants take up  $^{12}\text{C}$  preferentially to produce organic matter. If this organic matter is buried rather than returned to the atmosphere-ocean system, then the  $^{13}\text{C}:^{12}\text{C}$  ratio will shift in favour of the heavier isotope. Conventionally, this ratio is expressed as  $\delta^{13}\text{C}$ , which is the difference between the  $^{13}\text{C}:^{12}\text{C}$  ratios in the sample being tested and in a known standard (a belemnite fossil from the Cretaceous Pee Dee Formation in South Carolina).

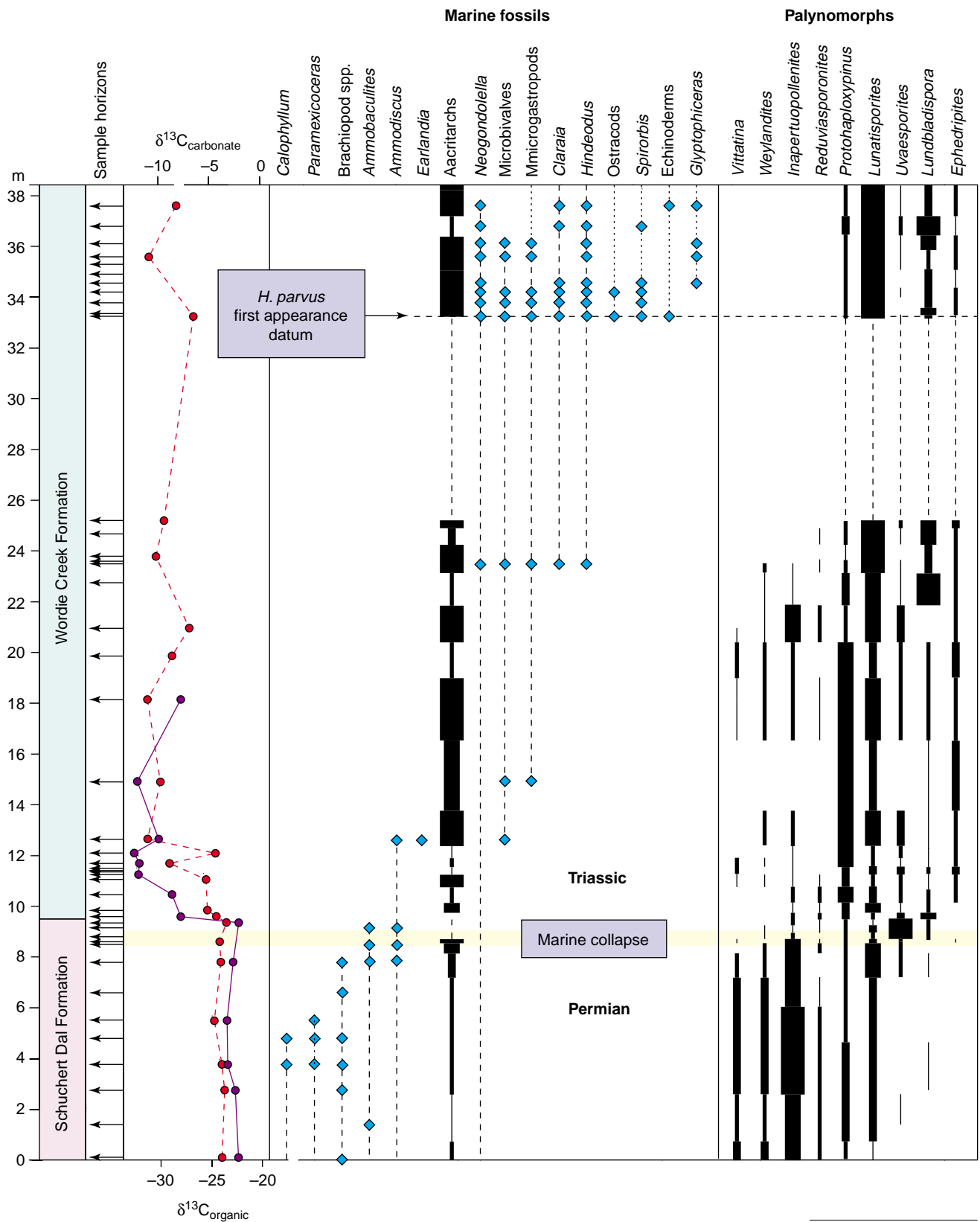
Consider the ocean system. During periods of high surface productivity, large amounts of organic matter are fixed at the surface and the surface waters of the ocean become relatively enriched in  $^{13}\text{C}$ . Shallow-water carbonate deposits are precipitated from this seawater and record the seawater  $^{13}\text{C}:^{12}\text{C}$  ratio without any preferential uptake of either isotope. Therefore, during times of high surface productivity, shallow-water carbonates record a positive shift in  $\delta^{13}\text{C}$  (i.e. towards the heavier isotope).

The Permo-Triassic interval is characterized by a negative shift in  $\delta^{13}\text{C}$  (Fig. 1), which is recorded in the carbonate deposits of all geological sections studied thus far [48,49], including terrestrial ones [50,51]. On the face of it, this should imply a massive decrease in biological production and rate of burial of organic matter.

However, the picture is more complicated than this. There is an initial short, sharp negative shift in  $\delta^{13}\text{C}$  that is nearly synchronous with the extinction horizon itself. The amount of negative swing varies between sections, but is typically 4–6‰ [6,48–51]. In most sections, a swing back towards the heavier end of the scale then follows. However, the  $\delta^{13}\text{C}$  values never swing right back to pre-extinction values, but remain lighter by some 0.5–1.5‰. This relatively small difference can be explained by low productivity in the extinction aftermath. The initial shorter, sharper swing needs another explanation.

Calculations have shown that the amount of negative swing (4–6‰) is too great to be explained solely by a lack of biological production [21]. An additional input of light carbon to the ocean-atmosphere system is required. The carbon dioxide emitted by volcanoes has a  $\delta^{13}\text{C}$  signature of -5‰, but calculations show that even the output from the Siberian Traps could not cause the observed shift in  $\delta^{13}\text{C}$  [21]. Even if all life were killed in an instant and the resulting biomass were incorporated into sediments, this would produce only 20% of the required isotope shift. The only viable source of light carbon is the methane trapped in gas hydrate deposits, which has a  $\delta^{13}\text{C}$  signature of -65‰ [52]. If these gas hydrates can be made to melt, enough methane would be released to cause the observed shift.

*Continued on the next page*



TRENDS in Ecology &amp; Evolution

**Fig. 1.** Changes in carbon isotope values across the Permo–Triassic boundary in shallow marine (coastal) sediments from Jameson Land, East Greenland. The diagram shows rock thickness in metres (left-hand side), the names of the geological formations, horizons at which sediment samples were collected for geochemical analysis, and the carbon isotope ratios based on measurements from marine limestones ( $\delta^{13}\text{C}_{\text{carbonate}}$ ) and from terrestrially derived organic matter ( $\delta^{13}\text{C}_{\text{organic}}$ ). These isotope measurements show very similar signals in the marine and terrestrially derived material. In the middle and to the right are range plots for marine species and palynomorphs (pollen and spores blown in from the nearby land). Known ranges are indicated by solid vertical bars (width indicates relative abundance) and dashed lines are interpolated ranges. Reproduced, with permission, from [6].

If the runaway greenhouse model is correct and explains perhaps the biggest crisis on Earth in the past 500 My, it is a model worth exploring further. It appears to indicate a breakdown in global environmental mechanisms, where normal systems that equilibrate atmospheric gases and temperatures took hundreds of thousands of years to come into play. Perhaps the combination of global warming and anoxia from gas hydrate release was a cause of other extinction events. This scenario certainly has been postulated recently for the end-Triassic mass extinction [36] and for smaller events in the early Jurassic [37], Cretaceous [38], and Tertiary [39].

Models for ancient extinction events affect the current debate about global warming and its possible medium-term consequences. Some scientists and politicians look to the sky for approaching asteroids that will wipe out humanity. Perhaps we should also consider how much global warming could be sustained, and at what level the runaway greenhouse comes into play.

Future research on the end-Permian event will focus on exploring more geological sections that span the P-Tr boundary to assess which aspects of the patterns are local and which are global. Such studies will provide ever-finer resolution of issues of dating and timing of the event, what died out and where, and how the physical environmental crisis unfolded.

#### Acknowledgements

Many thanks for Christian Sidor, Stuart Sumida, and Paul Wignall for thorough reviewing of this article and for many helpful comments.

#### References

- Erwin, D.H. (1989) The end-Permian mass extinction – what really happened and did it matter? *Trends Ecol. Evol.* 4, 225–229
- Bowring, S.A. *et al.* (1998) U/Pb zircon geochronology and tempo of the end-Permian mass extinction. *Science* 280, 1039–1045
- Yang, Z.Y. *et al.* (1995) The Permian–Triassic boundary – the global stratotype section and point (GSSP). *Episodes* 18, 49–53
- Jin, Y.G. *et al.* (2000) Pattern of marine mass extinction near the Permian Triassic boundary in South China. *Science* 289, 432–436
- Rampino, M.R. and Adler, A.C. (1998) Evidence for abrupt latest Permian mass extinction of foraminifera: results of tests for the Signor-Lipps effect. *Geology* 26, 415–418
- Twitchett, R.J. *et al.* (2001) Rapid and synchronous collapse of marine and terrestrial ecosystems during the end-Permian biotic crisis. *Geology* 29, 351–354
- Looy, C.V. *et al.* (2001) Life in the end-Permian dead zone. *Proc. Natl. Acad. Sci. U. S. A.* 98, 7879–7883
- Benton, M.J. (2003) *When Life nearly Died: The Greatest Mass Extinction of all Time*, Thames & Hudson
- Alvarez, L.W. *et al.* (1980) Extraterrestrial cause for the Cretaceous–Tertiary extinction. *Science* 208, 1095–1108
- Hallam, A. and Wignall, P.B. (1997) *Mass Extinctions and their Aftermath*, Oxford University Press
- Becker, L. *et al.* (2001) Impact event at the Permian–Triassic boundary: evidence from extraterrestrial noble gases in fullerene. *Science* 291, 1530–1533
- Farley, K.A. and Mukhopadhyay, S. (2001) An extraterrestrial impact at the Permian–Triassic boundary? *Science* 293, U1–U3
- Isozaki, Y. (2001) An extraterrestrial impact at the Permian–Triassic boundary? *Science* 293, 2343
- Kaiho, K. *et al.* (2001) End-Permian catastrophe by a bolide impact: evidence of a gigantic release of sulfur from the mantle. *Geology* 29, 815–818
- Koerberl, C. *et al.* (2002) End-Permian catastrophe by bolide impact: evidence of a gigantic release of sulfur from the mantle: Comment. *Geology* 30, 855–856
- Becker, L. (2002) Repeated blows. *Sci. Am.* 286, 62–69
- Reichow, M.K. *et al.* (2002)  $^{40}\text{Ar}/^{39}\text{Ar}$  dates form the West Siberian Basin: Siberian flood basalt province doubled. *Science* 296, 1846–1849
- Renne, P.R. *et al.* (1995) Synchrony and causal relations between Permian–Triassic boundary crises and Siberian flood volcanism. *Science* 269, 1413–1416
- Mundil, R. *et al.* (2001) Timing of the Permian–Triassic biotic crisis: implications from new zircon U/Pb age data (and their limitations). *Earth Planet. Sci. Lett.* 187, 131–145
- Erwin, D.H. (1993) *The Great Paleozoic Crisis: Life and Death in the Permian*, Columbia University Press
- Wignall, P.B. (2001) Large igneous provinces and mass extinctions. *Annu. Rev. Earth Planet. Sci.* 53, 1–33
- Jones, A.P. *et al.* (2002) Impact induced melting and the development of large igneous provinces. *Earth Planet. Sci. Lett.* 202, 551–561
- Erwin, D.H. *et al.* (2002) End-Permian mass extinctions: a review. *Geol. Soc. Am. Spec. Pap.* 356, 363–383
- White, R.V. (2002) Earth's biggest 'whodunnit': unravelling the clues in the case of the end-Permian mass extinction. *Philos. Trans. R. Soc. London Ser. B* 360, 2963–2985
- Wignall, P.B. and Hallam, A. (1992) Anoxia as a cause of the Permian/Triassic extinction: facies as evidence from northern Italy and the western United States. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 93, 21–46
- Wignall, P.B. and Twitchett, R.J. (1996) Oceanic anoxia and the end Permian mass extinction. *Science* 272, 1155–1158
- Wignall, P.B. and Twitchett, R.J. (2002) Extent, duration, and nature of the Permian–Triassic superanoxic event. *Geol. Soc. Am. Spec. Pap.* 356, 395–413
- Retallack, G.J. (1999) Postapocalyptic greenhouse paleoclimate revealed by earliest Triassic paleosoils in the Sydney Basin, Australia. *Geol. Soc. Am. Bull.* 111, 52–70
- Smith, R.M.H. and Ward, P.D. (2001) Pattern of vertebrate extinctions across an event bed at the Permian–Triassic boundary in the Karoo Basin of South Africa. *Geology* 29, 1147–1150
- Hotinski, R.M. *et al.* (2001) Ocean stagnation and end-Permian anoxia. *Geology* 29, 7–10
- Berner, R.A. (2002) Examination of hypotheses for the Permo–Triassic boundary extinction by carbon cycle modeling. *Proc. Natl. Acad. Sci. U. S. A.* 99, 4172–4177
- Raup, D.M. (1979) Size of the Permo–Triassic bottleneck and its evolutionary implications. *Science* 206, 217–218
- Twitchett, R.J. (1999) Palaeoenvironments and faunal recovery after the end-Permian mass extinction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 154, 27–37
- Sepkoski, J.J. Jr (1992) *A Compendium of Fossil Marine Animal Families*, 2nd edn, Milwaukee Public Museum
- Schubert, J.K. and Bottjer, D.J. (1995) Aftermath of the Permian–Triassic mass extinction event – paleoecology of Lower Triassic carbonates in the western U.S.A. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 116, 1–39
- Sephton, M.A. (2002) Carbon and nitrogen isotope disturbances and an end-Norian (Late Triassic) extinction event. *Geology* 30, 1119–1122
- Hesselbo, S.P. *et al.* (2000) Massive dissociation of gas hydrate during a Jurassic oceanic anoxic event. *Nature* 406, 392–395
- Jahren, A.H. and Arens, N.C. (1998) Methane hydrate dissociation implicated in Aptian OAE events. *Geol. Soc. Am. Abs. Progs.* 30, 53
- Dickens, G.R. *et al.* (1995) Dissociation of oceanic methane hydrate as a cause of the carbon isotope excursion at the end of the Paleocene. *Paleoceanography* 10, 965–971
- Benton, M.J. (1993) *The Fossil Record 2*, Chapman & Hall
- Sepkoski, J.J. Jr (1996) Patterns of Phanerozoic extinction: a perspective from global data bases. In *Global Events and Event Stratigraphy* (Walliser, O.H., ed.), pp. 35–51, Springer
- Benton, M.J. (1995) Diversification and extinction in the history of life. *Science* 268, 52–58
- McKinney, M.L. (1995) Extinction selectivity among lower taxa – gradational patterns and rarefaction error in extinction estimates. *Paleobiology* 21, 300–313
- Vajda, V. *et al.* (2001) Indication of global deforestation at the Cretaceous–Tertiary boundary by New Zealand fern spike. *Science* 294, 1700–1702
- Visscher, H. and Brugman, W.A. (1988) The Permian–Triassic

- boundary in the southern Alps: a palynological approach. *Mem. Soc. Geol. Ital.* 34, 121–128
- 46 Eshet, Y. *et al.* (1995) Fungal event and palynological record of ecological crisis and recovery across the Permian–Triassic boundary. *Geology* 23, 967–970
- 47 Wignall, P.B. *et al.* (1996) The timing of palaeoenvironmental changes at the Permo–Triassic (P/Tr) boundary using conodont biostratigraphy. *Hist. Biol.* 12, 39–62
- 48 Magaritz, M. *et al.* (1988) The carbon-isotope shift at the Permian–Triassic boundary in the southern Alps is gradual. *Nature* 331, 337–339
- 49 Sephton, M.A. *et al.* (2002) Synchronous record of  $\delta^{13}\text{C}$  shifts in the oceans and atmosphere at the end of the Permian. *Geol. Soc. Am. Spec. Pap.* 356, 455–462
- 50 Retallack, G.J. (1995) Permian–Triassic life crisis on land. *Science* 267, 77–80
- 51 MacLeod, K.G. *et al.* (2000) Timing of mammal-like reptile extinctions across the Permian–Triassic boundary in South Africa. *Geology* 28, 227–230
- 52 Dickens, G.R. *et al.* (1997) Direct measurement of *in situ* methane quantities in a large gas-hydrate reservoir. *Nature* 385, 426–428

## Articles of interest BioMedNet News

Access these News stories and more at <http://news.bmn.com>

### So you think you know the double helix story?

by Henry Nicholls

So you think you know the story of how the structure of DNA was discovered? Think again, say New York science historians. Single-handedly, James Watson has massaged our understanding of the events of 1953, and now, in 2003, is dictating how we celebrate the 50th anniversary of the discovery, they allege.

### Food for the future

by Damaris Christensen

The health benefits of food may soon owe almost as much to biotech companies as to Mother Nature, predict agricultural biotechnologists. But early optimism for marketable products may have been misplaced, warn some.

### Immunologists unearth HIV archive

by Julie Clayton

Reservoirs of HIV that can persist in the body even in the face of powerful anti-retroviral drugs are only poorly understood. But new data reveal that follicular dendritic cells are one such repository, carrying virus particles that are more genetically diverse than in any other tissue in the body.

### Commercial norms and population genomics

by J C. Louis

Policies governing benefit-sharing following the exploitation of genomic data have not kept pace with commercialization, especially in the USA, says a leading US bioethicist.

### The rise and rise of the humble sea sponge

by Jacqueline Ali

One of the world's most primitive multi-cellular organisms, which lives underwater and evolved over 500 million years ago, looks set to become a key player in the fight against cancer.

### Double helix photo not taken by Franklin

by Henry Nicholls

Rosalind Franklin's famous 'photograph 51' of DNA, which James Watson claims led him and Francis Crick directly to the discovery of the double helix, was not, after all, taken by her.