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Earth's biggest 'whodunnit': unravelling the clues in the case of the end-Permian mass extinction

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The mass extinction that occurred at the end of the Permian period, 250 million years ago, was the most devastating loss of life that Earth has ever experienced. It is estimated that *ca.* 96% of marine species were wiped out and land plants, reptiles, amphibians and insects also suffered. The causes of this catastrophic event are currently a topic of intense debate. The geological record points to significant environmental disturbances, for example, global warming and stagnation of ocean water.

A key issue is whether the Earth's feedback mechanisms can become unstable on their own, or whether some forcing is required to precipitate a catastrophe of this magnitude. A prime suspect for pushing Earth's systems into a critical condition is massive end-Permian Siberian volcanism, which would have pumped large quantities of carbon dioxide and toxic gases into the atmosphere. Recently, it has been postulated that Earth was also the victim of a bolide impact at this time. If further research substantiates this claim, it raises some intriguing questions. The Cretaceous–Tertiary mass extinction, 65 million years ago, was contemporaneous with both an impact and massive volcanism. Are both types of calamity necessary to drive Earth to the brink of faunal cataclysm? We do not presently have enough pieces of the jigsaw to solve the mystery of the end-Permian extinction, but the forensic work continues.

Keywords: mass extinction; large igneous provinces; oceanic anoxia; global warming; methane hydrate

1. Introduction

The vast majority of species that have ever inhabited the Earth are now extinct. Extinction is part of the natural order, and has been identified throughout the fossil-bearing part of the geological record (the last 600 million years (Myr)). The rate at which extinctions occur, however, varies. 'Background extinctions' occur regularly, as newly evolving species replace older species, but there have also been periods of 'mass extinction', defined as the extinction of a significant proportion of the world's biota in a geologically insignificant period of time (Hallam & Wignall 1997). In this context, 'insignificant' equates to time-scales that cannot easily be resolved in the geological record: a few tens or hundreds of thousands of years, or perhaps much less.

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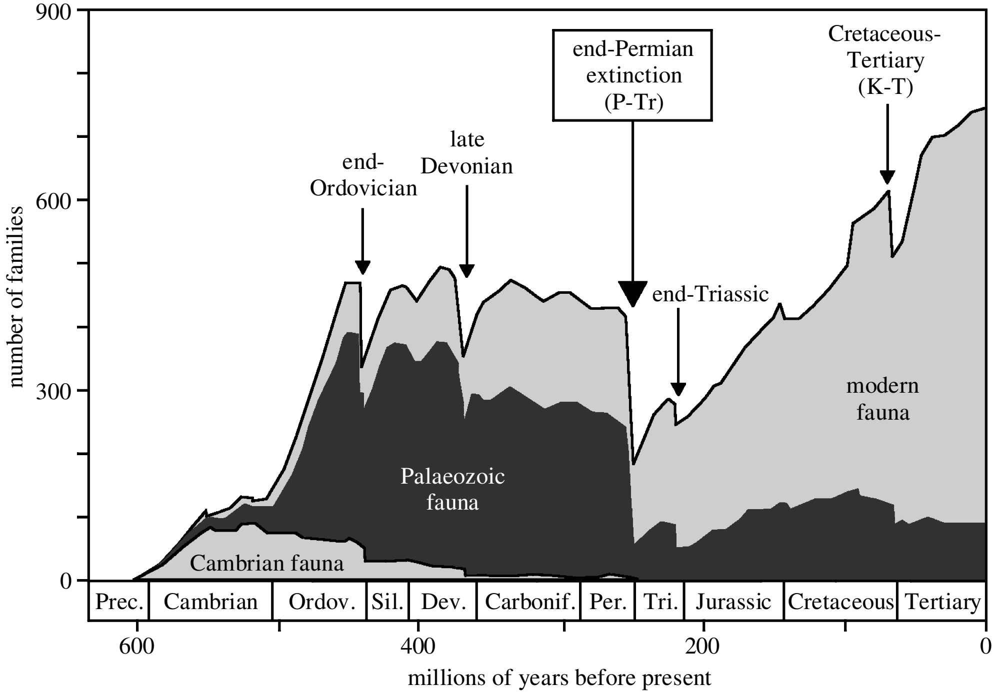

Figure 1. Plot of diversity versus time for the last 600 million years, showing the five main mass extinctions (after Sepkoski 1984). The Palaeozoic 'evolutionary fauna' that dominated during the Permian consisted primarily of filter feeders with a fixed mode of life, whereas the Modern fauna that became dominant after the P–Tr extinction generally had a more mobile mode of life.

Five major mass extinctions during the last 500 Myr have been recognized (figure 1; Raup & Sepkoski 1982). Despite the high public profile of the Cretaceous–Tertiary (K–T) extinction, the most significant extinction by far was that which occurred at *ca.* 250 Ma, between the Permian and Triassic periods. Proof of the causes of this extinction remains elusive, and the hunt for an explanation is truly multidisciplinary, involving collection of evidence from many branches of the Earth sciences. The approach taken is to build up as complete a picture as possible of late-Permian times, including information about the victims, their deaths, the environments in which they lived, how those environments changed at the Permo–Triassic (P–Tr) boundary, and what could have caused those environments to change.

2. The victims (and the survivors)

The death toll at the end of the Permian was unprecedented: it is estimated that 96% of marine species vanished (Raup 1979). The extinctions were not restricted to organisms living in marine environments—land animals and plants were also affected.

The worst hit groups were those that were attached to the sea floor, nourished by filtering organic material from seawater. Rugose and tabulate corals were completely wiped out, and crinoids, bryozoans and brachiopods also suffered. Some mobile organisms were also devastated, including echinoids, ammonoids, foraminifera (microfossils), and the last remaining trilobites. The extinction amongst foraminifera was selective: the complex tropical foraminifera were hardest hit, but the detrital feeders fared better, as did those whose modern-day relatives live in low-oxygen (dysaerobic) environments.

On land, more than two-thirds of terrestrial reptile and amphibian familes, notably the large herbivores, became extinct (Maxwell 1992). The end-Permian is the only known mass extinction of insects (Labandeira & Sepkoski 1993), and terrestrial plants also experienced substantial losses (Retallack 1995).

Given the breadth of the extinctions, it may be more informative to mention those organisms that coped better with the worsening situation. In the marine realm, microfossils that were well adapted to life with low oxygen, such as some ostracods and foraminifera, continued to exist. Stressed conditions are also indicated by large numbers of acritarchs: unicellular microfossils typically associated with poorly oxygenated waters. Free-swimming animals such as fish and conodont animals (marine chordates) also survived relatively unscathed. In the terrestrial environment, the P–Tr boundary is marked by an abundance of microfossils that have been interpreted as fungal spores (Eshet *et al.* 1995). This 'fungal spike' is thought to represent the successful colonization by fungi of large amounts of dead vegetation, without having to share their food source with numerous insects. Recent geochemical evidence of Foster *et al.* (2002), however, suggests that these microfossils may have an algal, rather than fungal, origin.

3. The circumstances and the evidence

Investigations into events of this magnitude rely on finding out as much as possible about the circumstances surrounding the deaths, then putting together the pieces of that puzzle to find what really happened. Our search for evidence is hindered by the fact that the oceanic part (*ca.* 70%) of the Earth's Permian crust has been subducted back into the mantle. Nevertheless, several P–Tr sedimentary sections from continental margins have been documented and more are still coming to light. Unfortunately, there are, and will always be, many pieces of this particular jigsaw missing.

A map of the world in Permian times would have looked very different from today (figure 2). The majority of the continents was arranged in one large supercontinent called Pangaea. The Panthalassa Ocean covered one hemisphere, and the Tethys Ocean occupied a position between Pangaea and some minor continental fragments. Most of the sedimentary successions studied come from the margins of the Tethys Ocean.

(*a*) *Establishing the cause of death*

Establishing the cause of death for organisms that died at 250 Ma is problematic. Fossilization is an inherently improbable process and, even when it occurs, generally only the hard parts of organisms are preserved, so post-mortems would be uninformative. Instead, we must use our general knowledge of death to infer its likely causes. Surprisingly, there are only a handful of ways to die: old age, direct physical trauma, starvation, suffocation or poisoning. Other deaths tend to be variations on these themes. As soon as some deaths occur, the food chain is affected. Any hypothesis proposed for the cause of the end-Permian extinctions must be capable of killing life via one or more of these mechanisms.

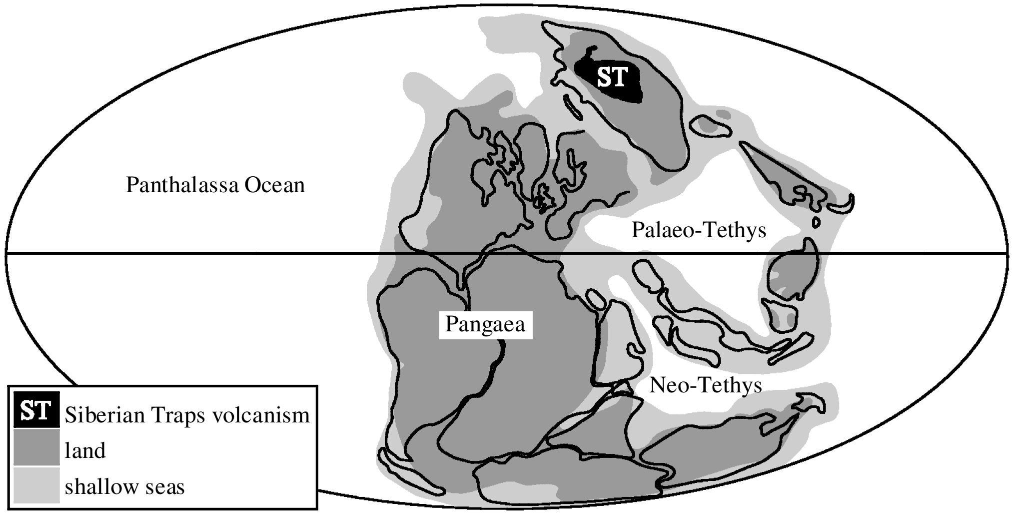

Figure 2. Reconstruction of Earth's landmasses 250 million years ago (compiled from Scotese *et al.* (1979) and Scotese & McKerrow (1990); Mollweide projection).

(*b*) *Establishing the age of the extinction*

The ecological reorganization and change in fossil populations that occurred as a result of the mass extinction has been used as a fundamental boundary in geology: it separates the Permian from the Triassic period and also demarcates the end of the Palaeozoic era and the start of the Mesozoic era. The faunal changes allow relative ages to be determined, and thus enable correlation of fossiliferous rock layers of the same age from all over the world. The P–Tr boundary is defined palaeontologically by the first appearance of a Triassic conodont, *Hindeodus parvus* (Ding 1992; Wignall *et al.* 1996; Yin *et al.* 1996). However, in order to compare fossiliferous sections with non-fossiliferous rocks (e.g. volcanic rocks; see § 4 *c*), it is also necessary to assign an absolute numerical age to the P–Tr boundary.

Absolute dating of the end-Permian extinction is facilitated by the presence of a volcanic-ash layer lying immediately above the last appearance of many fossil species in sedimentary rocks at Meishan, southern China. This layer lies just below the palaeontological P–Tr boundary. The ash contains zircon and feldspar, minerals that can be dated radiometrically. U–Pb ion-microprobe dating of zircon gave ages of 251.2 ± 3.4 Ma (Claoué-Long *et al.* 1991). Another radiometric technique, ^{40}Ar–^{39}Ar dating, gave an age of 249.9 ± 1.5 Ma for feldspar from the same ash layer (Renne *et al.* 1995). Later studies using a more precise U–Pb technique (isotope dilution) yielded ages for the P–Tr boundary of 251.4 ± 0.3 Ma (Bowring *et al.* 1998), and even more recently, Mundil *et al.* (2001) concluded that the P–Tr boundary must be slightly older than 252.5 ± 0.3 Ma.

This list of slightly differing results for the age of the P–Tr boundary demonstrates that these dating techniques cannot yet answer all of our questions. In particular, there are problems tying together 'absolute' ages determined by U–Pb and ^{40}Ar–^{39}Ar methods, due to small uncertainties in the potassium decay constant and ages of the standards used for ^{40}Ar–^{39}Ar dating. Recent results suggest that commonly quoted ^{40}Ar–^{39}Ar dates are 1–2% younger than U–Pb dates from the same rock (Schmitz &

Bowring 2001). This uncertainty is of sufficient magnitude to explain the apparent discrepancy between U–Pb and ^{40}Ar–^{39}Ar ages of minerals from the same ash layer.

(c) *Establishing the duration of the extinction*

In order to develop hypotheses for the cause of the extinctions, it is important to find out how long the decline in diversity took. This is not straightforward. Palaeontology has intrinsic sampling problems: it is improbable that the last individual of a species will have been preserved and even more unlikely that a collector will find it, and thus the species will appear to have become extinct earlier than it really did (Signor & Lipps 1982). The rarer the fossil type, the larger the potential interval between the youngest known specimen and the true extinction age. This means that even an instantaneous mass extinction could appear to be gradual. Estimates for the duration of the extinction vary, therefore, according to different inclinations in attaching importance to particular fossil groups or sampling locations. Holser & Magaritz (1992), for example, suggest a duration of 5–10 Myr, whereas Hallam & Wignall (1997) prefer a 'rapid but not instantaneous' mass extinction.

Assigning an actual duration for the extinction depends on a knowledge of sediment accumulation rates at particular locations. At Meishan, Bowring *et al.* (1998) obtained ages that differed by 0.7 ± 0.3 Myr for two ash layers (27 cm apart) that bracket the extinction period. Other studies using reasonable estimates of sedimentation rates suggest even more rapid rates of ecosystem collapse: Twitchett *et al.* (2001) report a duration of just 10–30 kyr for marine extinctions recorded in sediments in Greenland, similar to that of a statistical analysis of foraminifera by Rampino & Adler (1998).

(d) *Clues from the sedimentological record*

(i) *Widespread oceanic anoxia*

Marine sediments deposited at the end of the Permian record a change from oxic to anoxic conditions. In a number of locations, the end-Permian extinctions coincide with a change from burrowed layers to undisturbed strata, indicating that the sea bed had lost its normal complement of bottom-dwelling organisms. Well-preserved (i.e. non-scavenged) fish fossils may be present (e.g. Wignall & Twitchett 1996). Elsewhere, sediments rich in organic matter (e.g. black shales) were deposited and, at most marine P–Tr boundary sections, pyrite (FeS_2) is present. In well-oxygenated circumstances, most organic matter is oxidized or eaten by scavengers before it has chance to become preserved in sediments on the sea floor, and there is too much oxygen for pyrite to form. In contrast, the end-Permian sediments demonstrate that the bottom waters had little or no oxygen and may have experienced reducing conditions and free H_2S in the water column, rather like the present-day Black Sea. As well as being geographically widespread, there is evidence that the anoxia was not restricted to deep-sea environments and encroached onto the continental shelves (Wignall *et al.* 1998).

The amount of oxygen dissolved in the oceans depends primarily on temperature, efficiency of ocean circulation and biological demand for oxygen. At higher temperatures, less oxygen dissolves in sea water; additionally, higher global temperatures tend to reduce the temperature gradient between the Equator and the poles, and thus restrict convection-driven circulation. An ocean depleted in oxygen is clearly an unfavourable situation for most animals, and the presence of anoxic waters provides an eminently credible kill mechanism. This fits in with the observation that the marine creatures that fared best were those that were either free swimming or those that were adapted to low-oxygen environments.

(ii) *Sea-level changes*

Studies of sedimentary rocks that were deposited in shallow seas can give us information about relative sea-level changes. During the Permian period, sea level reached an extremely low level, a remarkable situation considering that there is no evidence for water being locked-up in polar ice caps at this time (Erwin 1993). Much of the early literature correlated this sea-level lowstand with the end of the Permian period (e.g. Hallam 1989), and the consequent loss of habitat on the shallow continental shelves was commonly blamed for the end-Permian mass extinction of shelf-dwelling creatures. As more P–Tr boundary sections have been discovered, however, it has emerged that some sedimentary rocks actually record a rapid sea-level rise (transgression) at the time of the extinctions (Wu *et al.* 1993; Wignall & Hallam 1992, 1993). The Permian sea-level lowstand, therefore, actually happened significantly *before* the extinctions and could not have been responsible for causing them, although the spread of anoxic bottom waters into the shallow marine habitat during the early stages of transgression may have played a part (Hallam 1989).

(iii) *Global warming*

Various pieces of evidence in the P–Tr sedimentological and palaeontological record hint at significant shifts in temperatures and/or climate patterns. Rocks from Spitsbergen suggest a migration of warm-water algae to high latitudes by the Early Triassic (Wignall *et al.* 1998). In the terrestrial record, peat deposits formed at high latitudes were replaced by warm, temperate soils (Retallack 1996), and the peat-forming glossopterid flora at high southern latitudes were suddenly replaced by a conifer-lycopod assemblage (Retallack 1995). At lower palaeolatitudes, sedimentary rocks indicate a change from a humid, temperate climate to a hot, semi-arid climate (Smith 1995).

Supporting evidence for an increased global temperature comes from the measurement of oxygen isotopes ($^{18}O/^{16}O$) in marine carbonates. At higher temperatures, carbonate-producing organisms incorporate proportionately more ^{16}O than ^{18}O into their shells. The oxygen-isotope record of tropical carbonates at the end of the Permian shows a major shift of seven parts per thousand (7‰) towards lighter oxygen, consistent with a global temperature increase of *ca.* 6 °C (Holser *et al.* 1991; figure 3).

Changes in climate are recorded indirectly by other isotopic systems. Oceanic Sr-isotope ratios ($^{87}Sr/^{86}Sr$) were at a very low value towards the end of the Permian period (Martin & Macdougall 1995), but were rising rapidly by the time of the P–Tr boundary (figure 3). Sr isotopes in the oceans are controlled by the balance of two main inputs: low $^{87}Sr/^{86}Sr$ from hydrothermal circulation at mid-ocean ridges and high $^{87}Sr/^{86}Sr$ from weathering of continental rocks. Rapid increases are generally accepted to be due to increased continental input. Increased continental erosion because of low sea level is unlikely to be the cause, because the $^{87}Sr/^{86}Sr$ increase

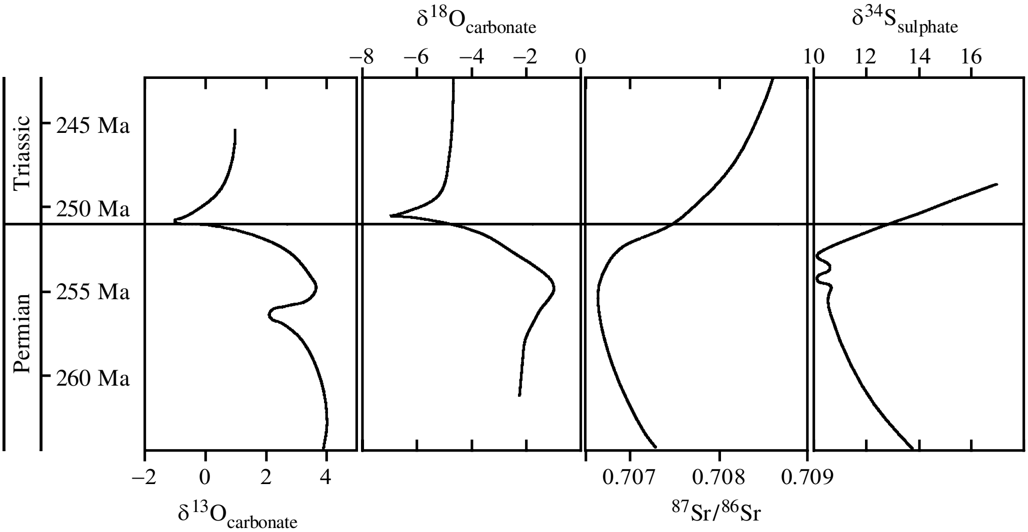

Figure 3. Changes in isotope ratios at the P–Tr boundary. Carbon data are from Baud *et al.* (1989), oxygen data from Holser *et al.* (1991), strontium data from Martin & Macdougall (1995) and sulphur data from Claypool *et al.* (1980) and Kramm & Wedepohl (1991). The absolute age of the boundary is taken from Claoué-Long *et al.* (1991), but see § 3 *b* for alternative views.

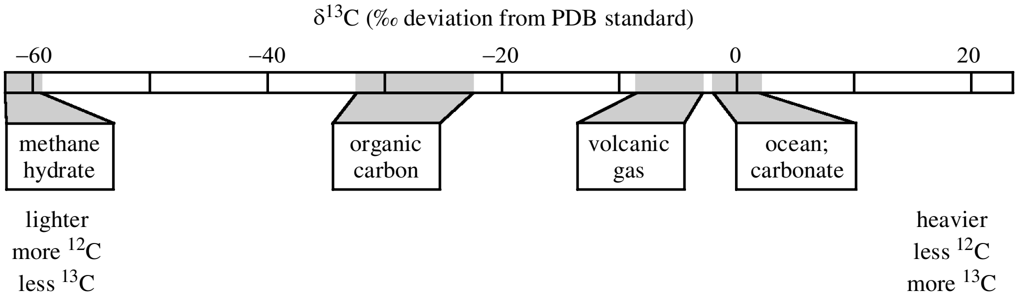

Figure 4. Ranges in $\delta^{13}C$ values associated with the major carbon reservoirs of the Earth.

occurred at a time when the sea level was rising rather than falling, so increased weathering rates due to increased humidity and atmospheric CO_2 levels have been proposed instead (Erwin 1993).

Global warming alone, however, struggles to explain an extinction of the magnitude observed. While the effects on land could have been sufficiently devastating to explain the terrestrial extinctions in terms of loss of habitat and breakdown in the food chain, in the oceans the increased temperatures might be expected to favour an increase in diversity, especially at high latitudes.

(iv) *Carbon-isotope record*

One of the most significant pieces of evidence for a profound event at the P–Tr boundary comes from measurements of carbon isotopes. The ratio of stable carbon isotopes, $^{13}C/^{12}C$, is usually expressed as $\delta^{13}C$, the deviation (in parts per thousand) from a standard value (figure 4). Photosynthesis preferentially concentrates lighter, faster-moving, more reactive ^{12}C, so organic matter has a lighter carbon-isotope signature (negative $\delta^{13}C$) than marine carbonate and sea water. Reduction of organic matter to methane further concentrates light-carbon. The mantle/volcanic value of −7‰ is the weighted average of 'heavier' sea water and carbonate and 'lighter' organic matter and methane.

At the end of the Permian, falls in $\delta^{13}C$ of 5–6‰ are recorded (figure 3; see also Baud *et al.* 1989; Holser *et al.* 1991), with the lowest point at the P–Tr boundary. This shift seems to be ubiquitous, having been recorded in marine carbonates *and* organic matter from the Tethys Ocean, as well as terrestrial plant and animal fossils in both hemispheres (e.g. Thackeray *et al.* 1990; Morante *et al.* 1994). The timing of the shift is less straightforward, with some studies showing a gradual decline prior to the extinctions and many additionally showing a rapid acceleration of the shift at the P–Tr boundary. Bowring *et al.* (1998) estimate that the duration of the carbon-isotope shift at the P–Tr boundary is only *ca.* 165 kyr, whereas Rampino *et al.* (2000) report a duration of less than 30 kyr.

A drop in the $\delta^{13}C_{\mathrm{carbonate}}$ values implies either that more 'light' carbon was being added to the ocean or that a smaller quantity of 'light' carbon was being removed and stored. A decrease in light-carbon removal can be achieved by a decrease in the productivity of marine organisms, leading to less organic matter becoming buried in sediments. Supporting evidence for lower primary productivity comes from the absence of siliceous radiolarian microfossils at this time (Isozaki 1994). Rapid isotope shifts could also be caused by changes in ocean circulation, for example, from a well-mixed to a stratified water column, where the different layers have different isotopic compositions.

In addition to mechanisms that can cause isotope shifts by altering the carbon cycle within the oceans, there are a number of hypotheses involving the addition of isotopically light carbon. These include returning previously stored organic carbon to the active system, e.g. via uplift, erosion and oxidation of coal and peat deposits on land (Faure *et al.* 1995). Although this mechanism could have contributed to the gradual decrease in $\delta^{13}C$ throughout the last few million years of the Permian, the rates at which erosion occurs are insufficient to explain the rapid $\delta^{13}C$ shift at the P–Tr boundary, and other more catastrophic mechanisms for light-carbon addition have been proposed (see §§ 4 *b*, *c* and *d*).

(v) *Sulphur-isotope record*

At the same time as the carbon-isotope negative shift, the sulphur-isotope record shows an increase in the proportion of the heavier S isotope, ^{34}S, in marine sulphates (figure 3). Sulphur isotopes work in an analogous way to carbon isotopes, in that bacterially mediated sulphate-reduction reactions preferentially involve the lighter isotope, ^{32}S. Pyrite formation from the resulting sulphide further enriches ^{32}S relative to ^{34}S, and pyrite consequently has low $\delta^{34}S$.

Claypool *et al.* (1980) and Kramm & Wedepohl (1991) show a decline to low $\delta^{34}S$ values near the end of the Permian, but by the time of the extinction, $\delta^{34}S$ in sulphates was rising rapidly. This could have been achieved by widespread removal of low-$\delta^{34}S$ material, for example, formation and burial of pyrite. This fits with the geological observation of pyrite preserved in many P–Tr boundary sections.

4. The perpetrators?

The question about this extinction that most arouses our curiosity is whether such an event could happen again, and if so, what might initiate it? We are familiar with the concept of negative-feedback loops that dampen the effects of perturbations to Earth's system and thus promote the relative stability of our environment. The geological record, on the other hand, demonstrates occasions when these feedback loops fail. We need to know whether the resulting calamities arise from the *intrinsic* failure of the feedback mechanisms or whether something else, possibly something catastrophic, is needed to push the system into a critical condition.

(*a*) *Bad luck at a vulnerable time*

The environmental changes discussed previously imply that Earth's regulatory system of feedback loops was not operating efficiently (figure 5). Global warming led to lower oxygen solubility in surface waters and to decreased ocean circulation. The resulting stagnation and decline in nutrients caused a productivity drop, which limited the efficiency of the negative part of this feedback loop: the removal of CO_2 from the atmosphere via incorporation into the skeletons of marine photosynthetic organisms. Ultimately, the poor circulation and stagnation resulted in anoxic oceans and extinctions. At this point, carbon was buried in organic-rich black shales but, by this time, it was too late for those organisms that did not make it through the anoxic event.

The Earth may have been particularly vulnerable at the end of the Permian because of the arrangement of the continents (figure 2). Competition between organisms living on or around the same large landmass would have led to reduced biodiversity, and the relatively small continental shelf would have limited carbonate sedimentation, restricting CO_2 drawdown. Additionally, many of the marine photosynthesizing plankton responsible for much of the present-day CO_2 drawdown had not yet evolved.

(*b*) *Methane hydrate release*

The significant and rapid drop in δ^{13}C at the P–Tr boundary has led to proposals that this period was marked by dissociation of methane hydrate (Erwin 1994). Methane hydrate is a white crystalline substance consisting of a 'guest' molecule (methane) trapped in a cage of H_2O molecules. Hydrates form in conditions of low temperature and/or high pressure (figure 6) in locations where methane is abundant. The methane is generated by anaerobic bacteria and is characterized by very light carbon (δ^{13}C of -65‰). The stability conditions for hydrate formation correspond to those currently found in permafrost and within the sediments on continental shelves. Kvenvolden (1998) estimates that the amount of carbon presently stored in these potential energy reserves is 10 000 gigatonnes (Gt, where 1 Gt $= 10^{12}$ kg).

Methane hydrates are prone to dissociation if pressure decreases or sediment temperature increases (figure 6). The end-Permian sea-level rise implies that depressurization was not the release mechanism, but global temperature increases at this time could have liberated significant quantities, particularly if changes in ocean circulation resulted in warmer bottom waters. The primary effect of methane hydrate

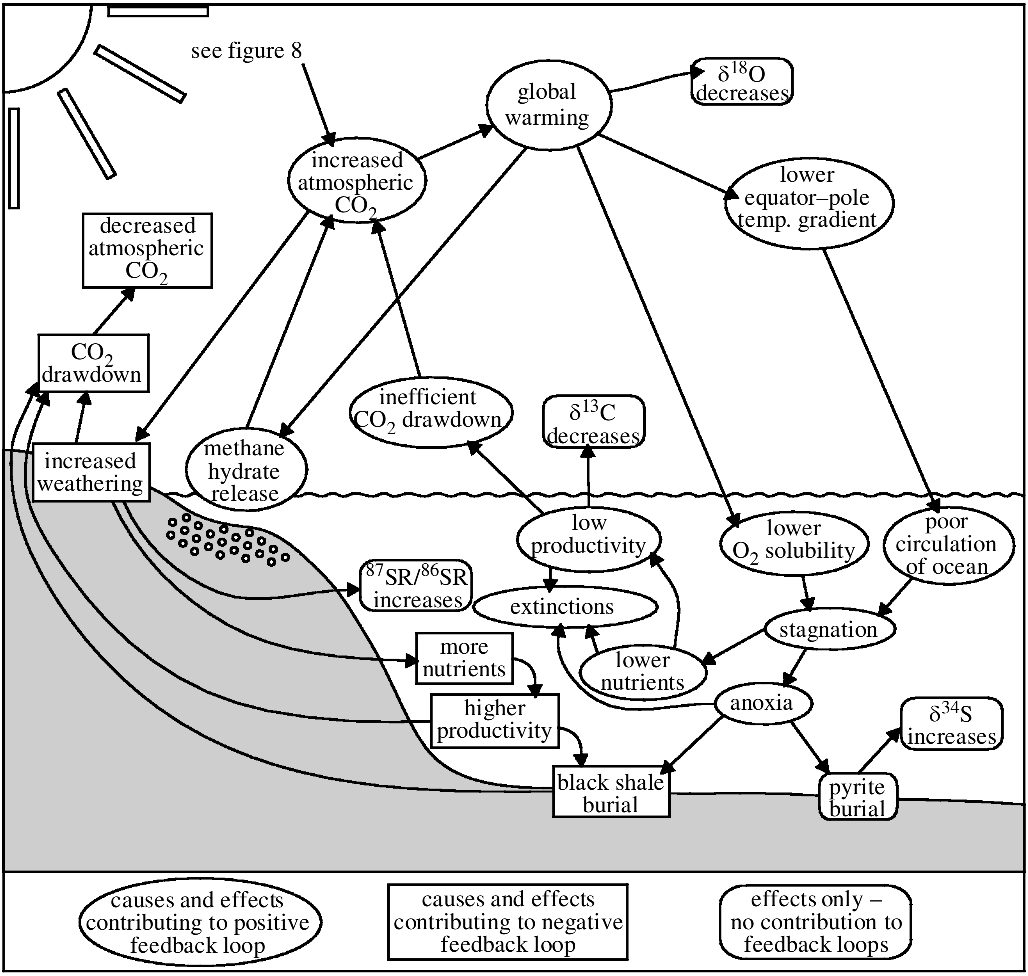

Figure 5. Feedback loops in the ocean–atmosphere system. Outcomes in ellipses are part of a positive-feedback loop in which a 'runaway greenhouse' develops. Rectangles illustrate negative-feedback processes, which could damp the positive feedback and provide an escape route from this runaway greenhouse. A scenario like this explains many of the characteristics of the isotope record (cf. figure 3).

dissociation would be to elevate atmospheric CO_2 values and further increase temperatures. This positive-feedback loop (figure 5) would exacerbate existing instabilities in the carbon cycle and potentially contribute to the extinctions. However, methane hydrate cannot have instigated the global warming, as its release required an earlier global-warming event of sufficient magnitude to counter the stabilization afforded by the sea-level rise. Furthermore, timing constraints from Greenland indicate that whatever caused the δ^{13}C shift occurred *after* the ecosystem collapse (Twitchett *et al*. 2001).

If the observed carbon-isotope excursion was caused entirely by methane hydrates, mass-balance constraints demand that *ca.* 3000 gigatonnes of carbon (GtC) were released. Liberated instantaneously, this would have elevated atmospheric CO_2 by

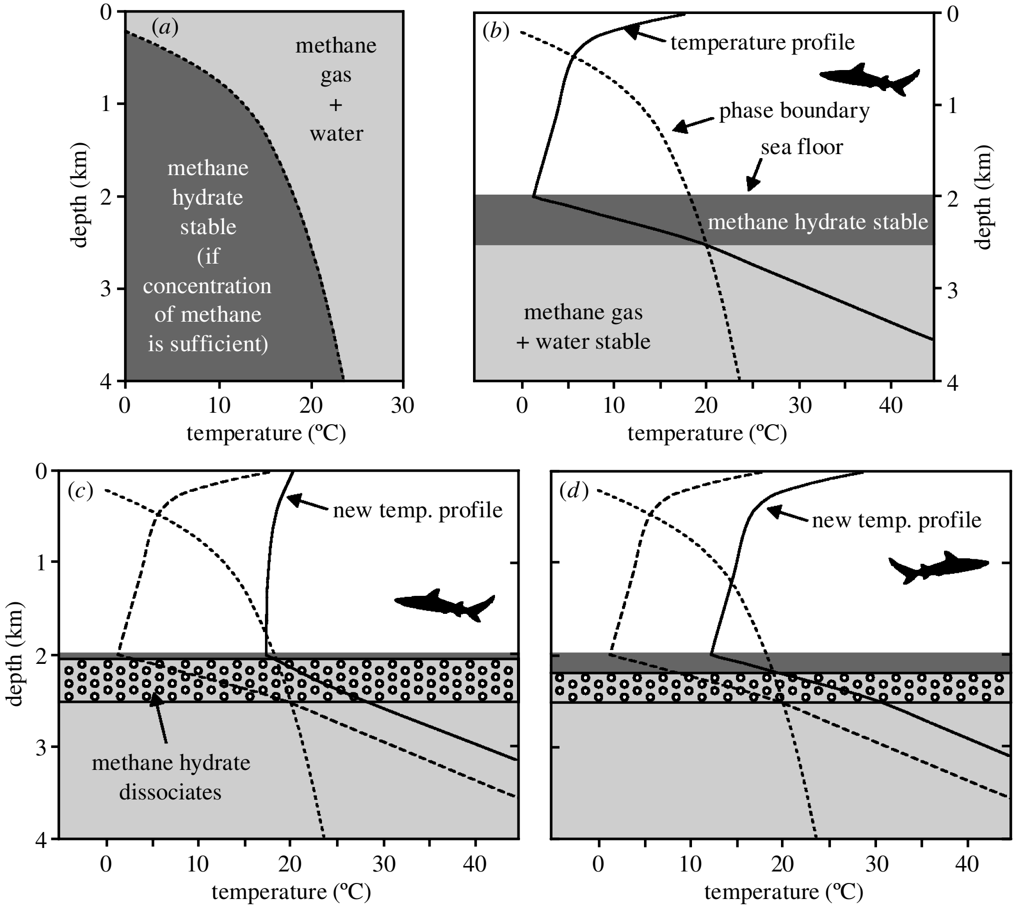

Figure 6. (*a*) Methane hydrate stability as a function of pressure (depth of sea water) and temperature. (*b*) Section through typical modern ocean with warm surface water and cold bottom water. The increase in temperature within the sediment is controlled by the geothermal gradient. Methane hydrate is stable within the dark-grey field, but will only form there if the concentration of methane in the sediment is sufficient, which is not usually the case for the uppermost sediments adjacent to well-oxygenated sea water. (*c*) Hypothetical ocean with limited temperature gradient between surface and bottom waters. The increased bottom-water temperature results in dissociation of any methane hydrate present in the zone indicated by the arrow. (*d*) Hypothetical ocean with increased overall temperature, but retaining thermal gradient between surface and bottom waters. The increased temperature results in methane hydrate dissociation, but this situation does not destabilize as much methane hydrate as in (*c*).

ca. 1400 ppm (cf. modern-day value of 370 ppm). Instant release of methane hydrate, however, is clearly unrealistic; Rampino *et al.* (2000) estimate a duration of less than 30 kyr for the isotope shift, leading to an estimated flux of *ca.* 0.1 GtC yr^{-1}. To put this into context, human activity releases *ca.* 7 GtC yr^{-1}, of which *ca.* 4 Gt is absorbed by the ocean and biosphere and *ca.* 3 Gt remains in the atmosphere. For this extra 0.1 GtC yr^{-1} to have significantly affected global warming, end-Permian CO_2-drawdown mechanisms must have been very severely retarded and certainly much less efficient than at present.

(*c*) *Large-scale volcanism*

A primary suspect for destabilizing the end-Permian environment is the eruption of a large basaltic volcanic province in Siberia. Large volcanic provinces are generally regarded to form via decompression melting in anomalously hot upwelling 'mantle plumes' and are a conspicuous feature of the geological record, with 12 having been erupted onto continents since 300 Ma (figure 7), and several more in the oceans. Three continental flood-basalt provinces coincide with significant mass extinctions: the Deccan Traps with the Cretaceous–Tertiary (K–T) extinction, the Central Atlantic Magmatic Province with the Triassic–Jurassic (Tr–J) extinction, and the Siberian Traps with the P–Tr extinction. Other flood basalts appear to correlate with lesser extinctions (figure 7), and inferences of a causal relationship between volcanism and extinction have been made (e.g. Rampino & Stothers 1988; Courtillot 1994; Wignall 2001).

(i) *The Siberian Traps*

The Siberian flood-basalt province, comprising the exposed 'Siberian Traps' as well as buried sequences in the West Siberian Basin, covers an area of *ca.* 3.9×10^6 km^2 (Reichow *et al.* 2002). This is roughly 15 times the area of Britain. Three main rock types are present: basalts formed from cooling of lava flows, pyroclastic rocks formed during explosive eruptions and intrusive rocks that cooled underground. The sequence is up to 3.5 km thick, and estimates of the total magma volume are 1.2×10^6–2.5×10^6 km^3 (Renne & Basu 1991; Renne *et al.* 1995; Reichow *et al.* 2002).

^{40}Ar–^{39}Ar ages of the Siberian Traps are 250 ± 1.6 Ma (^{40}Ar–^{39}Ar method; Renne *et al.* 1995), and samples from boreholes in the adjacent West Siberian Basin average 249.4 ± 0.8 Ma (Reichow *et al.* 2002), confirming the wide extent of contemporaneous volcanism. These ages are indistinguishable from ^{40}Ar–^{39}Ar ages of the P–Tr boundary (Renne *et al.* 1995), supporting the hypothesis of a causal link between volcanism and extinction. Estimates for the duration of volcanism range from 0.6 Myr (Campbell *et al.* 1992) to 1 Myr (Renne *et al.* 1995).

(ii) *Effects of volcanism on life*

The biosphere can be disrupted by volcanism in a number of different ways (figure 8). For a volcanic province to cause a mass extinction, its effects must be global and must be capable of affecting life in the sea as well as on land.

Links between volcanism and short-term climate changes are well established, e.g. Mount Pinatubo's explosive 1991 eruption caused a drop in global temperatures due to increased stratospheric concentrations of fine volcanic ash and sulphuric acid aerosols absorbing incoming radiation. Other toxic gases released by volcanoes include chlorine and fluorine, which can cause devastation on local scales; chlorine may also contribute to ozone depletion if advected into the stratosphere. These effects last only until the ash or gas-derived acid is rained out of the atmosphere, on timescales of months or years. Volcanoes also release large quantities of CO_2. This affects the CO_2 and global-warming feedback system (figure 5), and, because CO_2 has a longer residence time in the atmosphere than the other volcanic gases, its effects are longer lived.

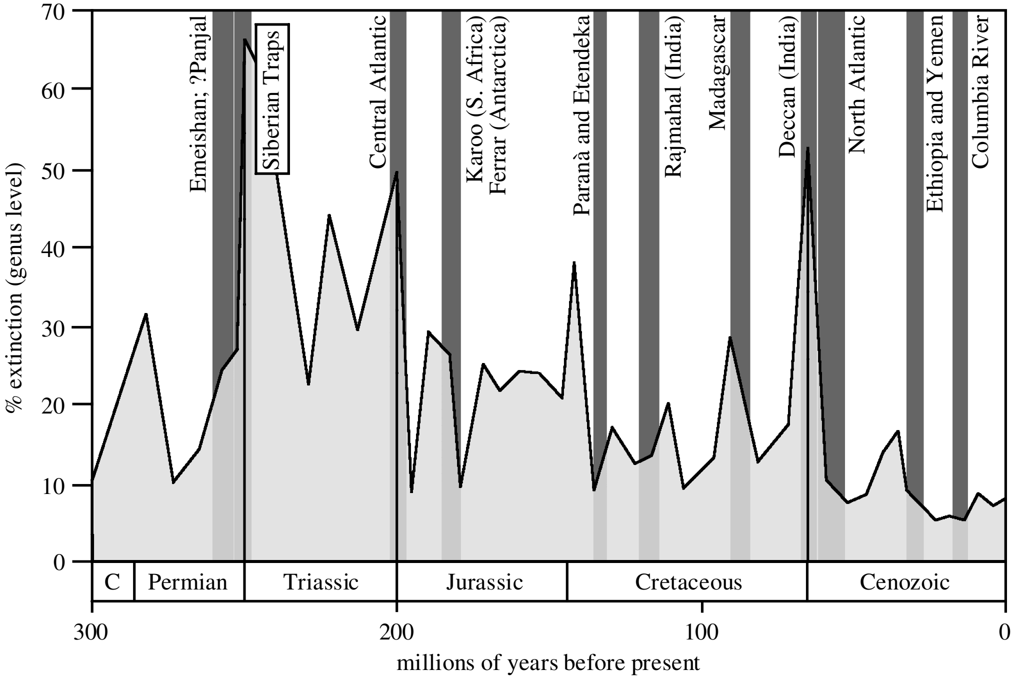

Figure 7. Extinction rate versus time (Sepkoski 1996) compared with eruption ages of continental flood-basalt provinces (taken from Rampino & Stothers (1988), Courtillot (1994), Wignall (2001), and references therein). The three most severe extinctions, the P–Tr, the K–T, and the Tr–J, correspond with eruption of the Siberian Traps, Deccan Traps and Central Atlantic Magmatic Province, respectively. Some lesser extinctions also correlate with eruption of flood basalts, although there are also examples of eruptions without extinctions and extinctions without eruptions. This diagram is not definitive: future revision is inevitable as more precise dates for the volcanism become available, and as correlation between radiometric and stratigraphic time-scales improves.

The effects described above rely on evidence from recent eruptions, but flood-basalt eruptions like those in Siberia were orders of magnitude larger than anything known from the historical record. In the 16 Ma Columbia River Province (USA), Thordarson & Self (1996) record single basaltic eruptive episodes with volumes of up to 1300 km^3 and estimate that each eruption lasted approximately a decade.

It is necessary at this point to make a distinction between different types of volcanism. Basaltic volcanism (e.g. Siberian Traps) is characterized by large-volume eruptions of hot, effusive, runny, low-silica lava. Explosive behaviour is limited to ‘fire-fountains’ at the vent, or eruptions where magmas interact with ground water. Conversely, viscous high-silica magmas commonly erupt explosively, although the total erupted volume is generally smaller. For kill mechanisms that rely on world-wide dispersal of volcanic products, eruptions must be violent enough to introduce material into the stratosphere (the base of which is currently *ca.* 9 km high at the poles and *ca.* 16 km at the Equator). Moreover, for a global (rather than hemispheric) distribution of products, the eruption should happen at low latitudes.

At the end of the Permian, Siberia was located in high northern latitudes (figure 2). Some of the eruptions were probably violent enough to disperse ash and gases into

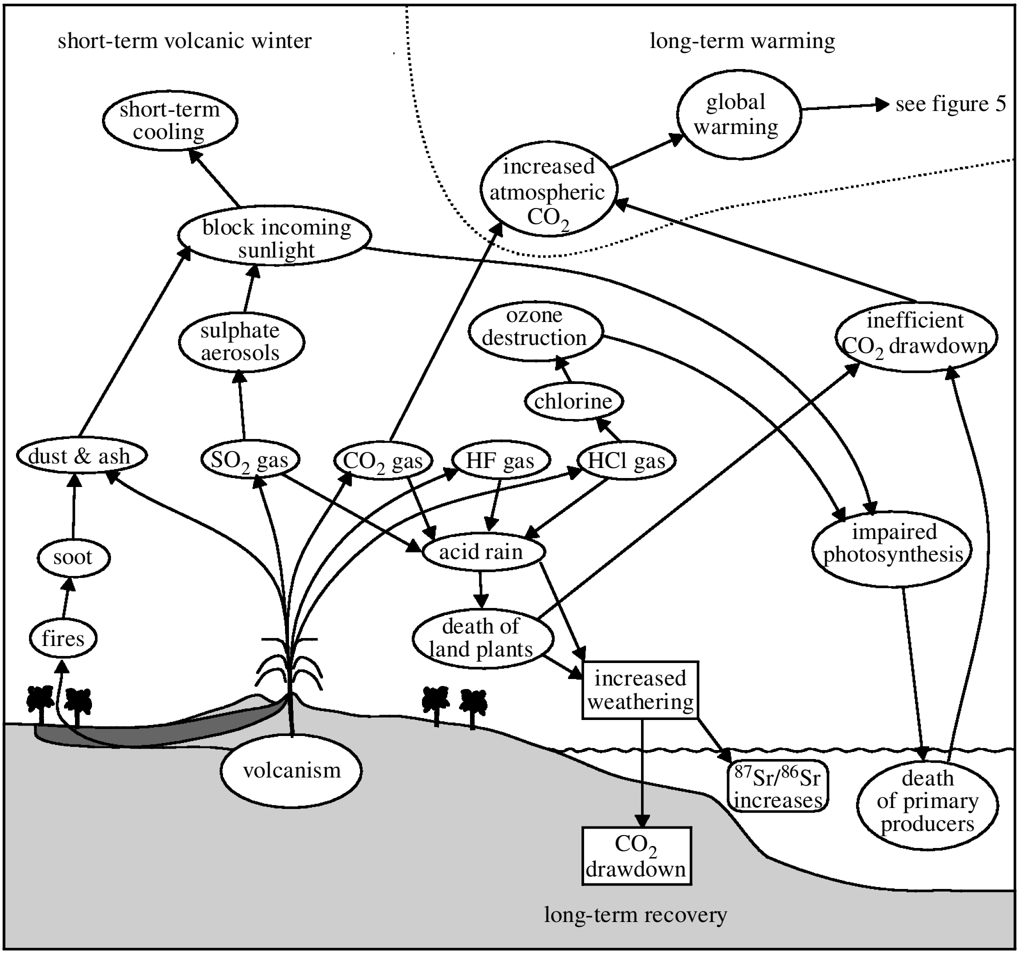

Figure 8. Effects of volcanism on the atmosphere and biosphere. Short-term volcanic winters following each eruption would be combined with long-term global warming as atmospheric CO_2 increased. The effects of an impact are potentially similar, depending on where the impactor lands, but with a single severe 'winter' rather than several cooling events spaced over thousands of years.

the stratosphere at this latitude, but their circulation would not have been global. Nevertheless, a bleak picture is painted for the Northern Hemisphere, with a short-term 'volcanic winter' occurring during and after each eruption: reduced incoming solar radiation, increased toxic fumes and acid rain and problematic photosynthesis and associated breakdowns in the food chain. Every few hundred years, just as the environment was beginning to recover from the previous decade-long eruption, another would begin.

Whether this was sufficient to cause a mass extinction directly is questionable, but these short-term effects were superimposed on a long-term trend of global warming, caused by, or exacerbated by, the volcanism. The CO_2 contributed to the atmosphere by this type of volcanism is significant: a 400 km^3 flow would degas *ca.* 7 $GtCO_2$ (*ca.* 2 GtC) over a decade or so. Over the entire eruptive period, up to 11 000 Gt of carbon was released by the Siberian Traps (assuming a volume of 2.3×10^6 km^3 and degassing of 0.6 wt% CO_2). The total CO_2 released is equivalent to addition of *ca.* 5000 ppm CO_2 to the atmosphere (cf. modern-day value of 370 ppm), although the protracted period of release and the activity of CO_2-drawdown mechanisms means that the volcanism probably led to an approximate doubling of atmospheric CO_2 (this assumes release over only 200 kyr, see Berner (2002)). Doubling of atmospheric CO_2 is thought to lead to global temperature increases of 1.5–4.5 °C (Houghton *et al.* 2001). However, we know that volcanism was not the only factor perturbing Earth's carbon cycle at this time, because volcanic CO_2, which has $\delta^{13}C \approx -7‰$, is not sufficiently 'light' to have been primarily responsible for the end-Permian carbon-isotope shift.

(iii) *Other Permo–Triassic volcanism*

The Siberian Traps were not the only volcanoes that were active towards the end of the Permian. In South China, the Emeishan flood-basalt province (*ca.* 2.5×10^5 km^2; Chung & Jahn 1995) preceded the Siberian Traps by a few million years. At Meishan, the ash layers in the P–Tr boundary section attest to the activity of silicic volcanoes at this time, although the locations of the eruptions have not yet been established. Much thicker ash layers in a P–Tr boundary section in SE Siberia suggest that this area lay closer to an eruptive centre (Kozur 1998); silicic volcanic rocks in southern Siberia are currently under investigation. In addition to these large-scale volcanic provinces, 'background' volcanism would have also added CO_2 to the atmosphere and contributed to the global-warming situation.

(*d*) *Bolide impact*

Ever since the K–T extinction was found to coincide with the impact of a large meteorite at Chicxulub in Mexico (Alvarez *et al.* 1980), there has been a search for evidence of impact coinciding with other mass extinctions, especially the end-Permian extinction. In 2001, the British national newspapers proclaimed, 'Comet killed life before dinosaurs' (*The Guardian*, 23 February 2001), and the debate about an impact at the end of the Permian recommenced.

The attraction of attributing the end-Permian extinction to an impact results from the potential for total devastation. An impact on land would globally disperse rock particles and soot from burning vegetation, reducing incoming solar radiation. If the underlying rock was made of gypsum ($CaSO_4$), rock salt (NaCl) or limestone ($CaCO_3$), volatiles could be injected into the atmosphere and acid rain would ensue. Depending on the size of the impactor, the resulting 'impact winter' could be more severe than any 'volcanic winter'. If the impact occurred in the ocean, less gas and dust would be released, but giant tidal waves (tsunami) could be expected instead.

The newspaper reports in 2001 arose from the publication of a paper by Becker *et al.* (2001) that reported fullerenes (carbon 'buckyballs') in P–Tr boundary sediments; the fullerenes contain trapped noble gases with isotopic ratios indicative of an extraterrestrial source. These results are controversial: attempts to replicate them have so far been unsuccessful (Farley & Mukhopadhyay 2001), and the experimental details of the original work have also been questioned (Braun *et al.* 2001). Other claims for an impact have also been disputed, e.g. sulphur-isotope variations (Kaiho *et al.* 2001) that could also be explained by routine terrestrial processes (Koeberl *et al.* 2002), and P–Tr iridium anomalies (Xu *et al.* 1985) that were subsequently found to be insignificant or non-existent (Zhou & Kyte 1988). Iridium is a siderophile ('iron-loving') metal, and the significant iridium anomaly at the K–T boundary is thought to be derived from an iron-rich meteorite. If an impactor was iron-poor, however, no iridium anomaly would be expected, so the lack of an anomaly at the P–Tr boundary cannot exclude the possibility of an impact.

Other evidence supporting an impact at the K–T boundary includes brecciated (fragmental) rocks, shocked quartz, tsunami-affected sediments and spherules (once-molten droplets ejected from impact sites or during volcanic eruptions). In contrast, these features have been searched for at the P–Tr boundary and not found at all, or not found in sufficient quantities to support the hypothesis of a large, ecosystem-threatening impact (Retallack *et al.* 1998). Spherules present in P–Tr boundary sediments have compositions consistent with a volcanic origin (Yin *et al.* 1992).

In summary, attempts to prove that an impact occurred at the end-Permian are not yet convincing. This does not rule out the possibility of an impact: the evidence for a K–T impact was amassed over a number of years, and there was much healthy scepticism throughout this period, which effectively continued until the discovery of the Chicxulub crater. So far, impact craters proposed for the end of the Permian have turned out to be the wrong age (Mory *et al.* 2000; Uysal *et al.* 2001) or are too small to account for a mass extinction. The 'scent' of an impact detected at the P–Tr boundary may result from an impact too small to have caused the extinction. Alternatively, if a larger impact crater did exist, it may have been subsequently destroyed by subduction, erosion or mountain building.

(i) *Do impacts cause mass extinctions?*

There is no doubt that a large impact would be devastating, and it seems likely that the Chicxulub impact contributed to the K–T extinctions. Proposals that all mass extinctions were caused by impacts are, however, contentious. Many impact structures preserved in the geological record do not appear to have had any notable effect on contemporaneous biota (Hallam & Wignall 1997, p. 245). Thus far, the consensus is that only one major extinction event (the K–T) shows evidence for a strong link with bolide impact, and the contemporaneous eruption of the Deccan Traps makes it difficult to determine objectively which event was the most to blame for the extinction.

Statistical examination of craters on the Earth and Moon demonstrates that Earth should receive a crater at least as big as Chicxulub (180 km in diameter) on average every *ca.* 31 Myr (Hughes 1998). This implies that approximately eight such events 'should' have occurred since the end of the Permian, yet we have only found good evidence for one. This apparent mismatch can be interpreted in a number of ways: either the cratering statistics are flawed, or the Earth has been unexpectedly lucky, or some large impacts remain undetected, possibly because they did not cause significant extinctions and their deposits occur within unremarkable and thus poorly sampled horizons in the sedimentary record.

(ii) *Do impacts cause volcanism?*

The contemporaneity of volcanism and impact at the K–T boundary resulted in suggestions that impact somehow causes the eruption of large igneous provinces

(Rampino 1987). This idea seems to have little basis in observation. The Chicxulub impact did cause melting, but on a very local scale. Suggestions that the Deccan flood basalts formed via focusing of impact-generated seismic waves are incorrect: the Deccan Traps were not located directly opposite the Chicxulub impact, and models involving melting due to seismic focusing of impact energy at the antipode are energetically unviable (Melosh 2000). Furthermore, the location of the iridium anomaly *between* two Deccan lava flows demonstrates that volcanism began *before* the impact (Bhandari *et al.* 1995), excluding the possibility of a causal relationship. Accordingly, similar statements that end-Permian volcanism was caused by impact should be regarded with scepticism.

(*e*) *Volcanism* and *bolide impact*

If the cratering statistics are correct, and Earth has received its quota of large impacts over the last 300 Myr, the implication is that large bolide impacts do not routinely cause major mass extinctions. Similarly, not all flood-basalt provinces coincide with extinctions. Nevertheless, the fact remains that the three largest mass extinctions have coincided with flood-basalt eruptions (figure 7), and at least one of these extinctions (the K–T) was contemporaneous with a large impact. One possible conclusion is that both impact *and* volcanism are required to cause mass extinctions of this magnitude.

My numerical simulations suggest that the conjunction of impacts and flood-basalt volcanism is more probable than it may seem. Assuming 12 flood basalts (each lasting 1 Myr) and 10 randomly occurring Chicxulub-sized impacts over the last 300 Myr, a coincidence between volcanism and at least one impact has a probability of 34%, a coincidence with at least two impacts has a probability of 6%, and with at least three impacts, 0.6%. If the duration of each flood basalt is 2 Myr, the probabilities increase to 57%, 19% and 4%, respectively. The threshold crater size for catastrophic global effects is thought to be *ca.* 100 km (Poag 1997); if this size of crater is used and the average flood-basalt duration is maintained at 2 Myr, the probabilities increase further, to 92%, 72% and 46%, for at least one, two or three coincidences, respectively.

These calculations demonstrate that, over geological time, random conjunctions of flood basalts and significant (crater diameter greater than 100 km) impacts are not only possible but actually probable. However, the proposition that both impact and volcanism are needed to cause the largest mass extinctions requires rigorous testing on several fronts. Firstly, the debate on whether or not an impact occurred at the end of the Permian needs to be resolved via collection of good quality, unequivocal data that can be replicated by independent researchers. Secondly, more research is needed to determine the characteristics and sizes of any impact events that did not coincide with extinctions. Finally, the ages and durations of individual flood-basalt provinces require refinement in order to unambiguously resolve the question of which flood basalts really did coincide with extinctions.

5. Summary and implications

The Earth is a complex system that we do not fully understand. Cause and effect are difficult to unravel, even for the present day, when we are able to make all the observations and measurements we need to. For the end-Permian, the key to unlocking the mystery lies in determining the relative timing of events: this will not necessarily prove causal relationships, but may be able to rule out some options. Detailed studies of sedimentary successions have made substantial progress in recent years, but more comprehensive multidisciplinary studies are needed to work out the relative positions of the extinctions with respect to carbon, sulphur and oxygen isotope shifts and any volcanogenic or impact-derived material.

This paper has outlined the main theories and controversies surrounding the end-Permian extinction. A number of likely kill mechanisms has been discussed, including stagnation and anoxia in the oceans, and volcanic-induced environmental stresses on land. The uniting theme for both marine and terrestrial extinctions seems to be global warming, exacerbated by volcanism, methane hydrate release, and the relative inefficiency of global carbon sinks. A bolide impact may have aggravated matters and, if further research supports these claims, it implies that both volcanism and impact are required to force Earth into such a critical state. The overriding conclusion is that sweeping statements such as 'volcanoes [or whatever] caused the mass extinction' should be treated with extreme caution; the geological record contains strong evidence for a range of disadvantageous conditions at this time, and it is probably the combination of these factors that ultimately caused such a severe extinction. Take just one of these parts out of the equation and things could have taken a very different course.

On a happier note, it should be remembered that life did recover, albeit slowly. The reappearance of so-called 'Lazarus taxa' after an absence of 10 Myr from the geological record suggests that there were refuges that enabled some communities to survive. After the extinction, the old Palaeozoic fauna (figure 1) were largely replaced by modern fauna: things like dinosaurs and, ultimately, things like us.

One issue to contemplate is whether the present Earth is liable to undergo a similar series of events, leading to extinction of modern biota. Several factors point to our relative safety for the immediate future: no massive-scale volcanism, effective oceanic circulation and efficient carbon sinks. Nonetheless, this stability cannot be guaranteed, and although the chances of us as individuals experiencing this sort of trauma are vanishingly small, in geological time, the destruction of *Homo sapiens* is a near certainty.

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Born in Burton-on-Trent, Staffordshire, Rosalind White developed an early passion for geology, owing to numerous childhood holidays in mountainous areas. In 1995, she graduated from the University of Cambridge with first-class honours in geological sciences, and continued to the University of Leicester to study continental crust formation in the Caribbean region for her PhD. After a year as a research fellow with the Geological Survey of Denmark and Greenland, she returned to Leicester to take up her current post, a Royal Society Dorothy Hodgkin Research Fellowship. Her research interests centre upon mantle plumes and how they have influenced the development of our planet. Aged 28, she is an enthusiastic French hornist, and also enjoys hill walking and tending the frogs and newts in her wildlife pond.