Presidential Address 2007: The end-Permian mass extinction – events on land in Russia

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BENTON, M. J. 2008. The end-Permian mass extinction – events on land in Russia. Proceedings of the Geologists’ Association, 119, 119–136. The mass extinction of life in the sea and on land 251 million years ago, at the Permian–Triassic boundary, was undoubtedly the largest mass extinction of all time. Sedimentological and geochemical evidence show that global temperatures rose, that there was extensive oceanic anoxia, and that there was massive erosion of sediment, especially soils, from the land. These phenomena might have been a consequence of the massive eruptions of the Siberian Traps, which produced carbon dioxide – a greenhouse gas – as well as acid rain, which killed plants and led to stripping of soils. Field work in Russia over the past decade has shown evidence for massive erosion at the boundary, and for the nature of ecosystem collapse and slow recovery after the event.

Key words: Permian, Triassic, mass extinction, Russia

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1. INTRODUCTION

I have been interested in mass extinctions for many years, particularly in their effects on life, especially the backboned animals on land. So, I was intrigued, many years ago, to read a statement by Bob Carroll (1988), in his standard textbook Vertebrate paleontology and evolution:

The most dramatic extinction in the marine environment occurred at the end of the Permian, wiping out 95 percent of the nonvertebrate species and more than half the families. Surprisingly, there was not a correspondingly large extinction of either terrestrial or aquatic vertebrates.

It seemed unlikely that a mass extinction that acted so severely on life in the sea would be so limited in its effects on life on land. I was intrigued to try to establish why the data seemed to be so contradictory.

The end-Permian mass extinction, or Permo-Triassic boundary (PTB) event, dated at 251 million years (Ma) ago, was the largest of all time, with the extinction of some 90–95% of all species on land and sea. Knowledge of the event has changed remarkably since 1990. Up to that point, most attention had focused on the Cretaceous–Tertiary (KT) event, 65 Ma ago, and it was clear by then that the Earth had been hit by an asteroid which led to catastrophic environmental changes, causing the extinction of 50% of species. Surprisingly, perhaps, the even larger PT event was somewhat shrouded in mystery.

When Doug Erwin reviewed the PT event, in both a book and a review article (Erwin, 1993, 1994), he reflected the uncertainties of the time, not only about precisely what went extinct, but also about the timing of the event, and the possible causes. A comparison with the present state of affairs shows the changes in evidence. Where Erwin cites a duration of up to 8 Ma, the event is now known to have taken much less than 1 Ma. Where Erwin presents a general contrast of pre-extinction and post-extinction faunas in the sea, field studies have now provided millimetre-by-millimetre precision in several parts of the world. Where Erwin talks about a combination of possible environmental triggers, linked in part to long-term continental accretion, as well as to the eruptions, the current models look to the Siberian basalts plus explosive gas hydrate release. Where Erwin could say little about the nature of events on land, strong evidence now shows soil wash-off, extinction of most green plants, flushing of terrestrial debris into the oceans, and collapse of complex ecosystems. The changed views about the PT mass extinction are reflected in more recent books (Benton, 2003; Erwin, 2006).

In this article I shall review work carried out in Russia since the early 1990s, and how it is adding to understanding of the PT event. I shall also talk a little about the challenge and the fun of field work in Russia.

2. FIRST FORAYS INTO RUSSIA

We first visited Russia in 1993, as part of a jointly funded research programme between the Royal Society in London and the Russian Academy of Sciences in Moscow. In those heady days, shortly after perestroika, there was enormous political will to engage
with Russia and help the country to recover from Soviet times. The Royal Society even opened an office in Moscow to help British scientists to visit and to supply tickets and money for Russian scientists to come to England.

During our first visit, my colleague Glenn Storrs and I met Russian palaeontologists and saw the remarkable collections in the Palaeontological Institute Museum in Moscow. We were also taken in the field to see an Early Triassic locality on the River Volga, near the city of Rybinsk, site of some discoveries of remarkably well-preserved skulls and skeletons of amphibians that had survived the mass extinction.

On our second visit, in 1994, Glenn and I spent a short time in Moscow, but our main purpose was to go in the field and see the Permo-Triassic first hand. We travelled by train to Orenburg at the foot of the Ural Mountains, a 36-hour train journey east from Moscow. Our colleagues from Moscow, Mikhail Shishkin and Andrey Sennikov, accompanied us on the train and we met our field leaders, Valentin Tverdokhlebov and Vitaly Ochev, in Orenburg. These two scientists shared a vast knowledge of the rocks and fossils around Orenburg. Ochev was a distinguished palaeontologist; sadly he died in 2004. He had worked on the fossil amphibians and reptiles of the Permo-Triassic of the Urals since the late 1950s and had published many descriptive papers. Tverdokhlebov is a field geologist, specializing in sedimentology and the interpretation of ancient environments and climates. He has worked for the Geological Survey of the USSR, and now of Russia, for decades, producing geological maps and identifying economically valuable minerals.

The 1994 expedition was for a mere two weeks but, during that time, we saw dozens of localities in the Late Permian and Early Triassic, many of them the sites of discovery of fossil amphibians and reptiles. It was relatively easy to find rather scrappy fossil teeth and bones in some of the channel deposits, especially in the earliest Triassic, but more substantial finds were rarer, partly because the fossils can be found only in the ravines that cut through the steppe lands, and these erode at a slow rate, and partly because Ochev and his colleagues had removed many excellent specimens during the 1950s and 1960s by the use of bulldozers. He would proudly point to vast hollows in the ground that had yielded single skeletons of large reptiles, sometimes even whole graveyards of skeletons in close association.

We planned a larger expedition for July 1995, this one to have clear research aims. Glenn Storrs and I went, together with other colleagues who specialized in field sedimentology (Andy Newell) or fossil reptiles (Patrick Spencer, David Gower, Darren Partridge). We divided into two teams and, this time, made a point of logging every sedimentary succession we could. We revisited sites we had seen in 1994 and saw others. We were able to collect a great deal of information that led to a publication about the major sedimentary changes at the PTB (Newell et al., 1999) and, later on, the pattern of the PT mass extinction among the Russian amphibians and reptiles (Benton et al., 2004). I return to these topics below; fuller accounts of earlier Russian expeditions may be found in Benton (2003).

3. THE 2004 EXPEDITION

Logistics

Earlier field work had shown the potential of the Orenburg Permo-Triassic red bed successions and we bid for more funding. We received support from the National Geographic Society for a major summer field season of a month or so, as well as further money from the Royal Society to pay for exchange visits between scientists in Bristol and Saratov. In July 2004, a team of five of us set off: Richard Twitchett, then a postdoctoral researcher in Tokyo; Andy Newell, a former graduate student in Bristol who had been our sedimentologist on the 1995 expedition and was now a geologist with the British Geological Survey; and Cindy Looy, a Dutch palaeobotanist and palynologist who had worked with Twitchett on the PTB in Greenland; my son Donald, who was 14 then; and myself. By adding the sedimentologists Twitchett and Newell, and palaeobotanist Looy, we hoped to be able to carry out more formal analysis of the rock successions and their fossil contents. Our Russian collaborators were, as always, Valentin Tverdokhlebov, the leader of the expedition, and Misha Surkov, our palaeontological collaborator and translator, as well as two of his students, drivers, cooks and others.

As ever, Misha met us at Sheremetyevo Airport in Moscow, a rather forbidding and frustrating place. We travelled by bus and metro to Pavaletsksiy Station for our evening train to Saratov. After our overnight journey, we were delivered to a remarkable hotel in the midst of an abandoned aircraft factory. The hotel had evidently been built in the 1960s as a showplace to welcome apparatchiks and factory managers from around the Soviet Union. The factory was one of several in Saratov that produced high-tech planes for the Russian airforce and was the reason that Saratov was a closed city in Soviet times. Now, this has all changed: the factory is derelict, as is the hotel, more or less. Anyone can visit Saratov and the secret factories all appear to have gone. Indeed, the once-proud hotel is falling apart: the elaborate paths and stone-lined ponds and flower beds are full of weeds, the pond is dry and the front of the hotel looks forlorn. We appeared to be the sole guests, so great care was lavished on us by the startling red-haired lady at reception, the cleaning personnel and the team of giggling female students who served the meals. The elaborately arranged veneer of marble over the walls of public areas, designed perhaps to give an air of Mediterranean opulence, had fallen away. Our rooms were mini-apartments, each with a bedroom and sitting room with a large refrigerator of ‘Saratov’ brand, made locally and still popular in Russia. Donald was...
eaten alive by mosquitoes in the two days we were resident in the aircraft factory hotel; the rest of us did not suffer so much.

We spent a damp two days in Saratov having our visas counterstamped. There had been heavy rain for a day and the roads were awash with water up to 20 cm deep in places; people and cars pushed doggedly through the torrents. Misha told us that money intended for repairs to the roads and drainage had been siphoned away by corrupt local politicians. The visa-stamping place is a special police station that serves both Russians and foreigners. Russians have never been entirely free to move about their own country and they must receive documents and visas for travel and work outside their registered region. We entered the incredible mêlée of people, all jostling to get through to the tiny windows in the wall behind which officials dealt calmly with the passports and documents. With profuse apologies for the scenes of madness and bureaucracy, we were eventually shown through to a small office where an official with a large green hat swiftly counterstamped our visas and entry papers and we were free to go.

We took the train from Saratov to Orenburg – again an overnight trip where we slept in the normal four-berth second-class cabins. Valentin Tverdokhlebov had already been there for a week or two and the camp was established on the banks of the River Sakmara, our old spot where we had spent most of the 1995 expedition (Fig. 1). There was a cookhouse, with a full-sized domestic gas cooker run from large propane tanks, a cook, one dog, two drivers (one had also brought his 14-year-old son Dmitry) and two students, Edvard Mamzurin and Alexander (‘Sasha’) Butyrin. Comfortable, modern tents had been set up for us, equipped with camp beds. Valentin is a skilled camper and must have spent more than twenty years of his life under canvas: in the heyday of the Soviet Geological Survey, he spent three months in the field every summer, camping like this, in charge of twenty or more geologists and helpers, as he mapped vast swaths of the Soviet Union for his masters in Moscow.

Donald and Dmitry raced around on Dmitry’s smart new bicycle and went swimming and fishing in the river. The fish were rather pathetic little tiddlers, but we made sure the boys gutted them and cooked them over the bonfire. Wading in the river, we felt sharp edges in the soft sand bottom with our bare feet. These were large river clams, Unio, whose broken shells were often washed up on the shore. We pulled up several dozen of these and Donald cooked perhaps the first French-style moules marinières à la russe on the banks of the River Tok, our later campsite. During our 1995 field trip, Andrew Newell and David Gower had done a remarkably detailed piece of aktuopalaeontological study on the Unio shells of the River Sakmara, mapping out hundreds of specimens over sand bars, and observing how the empty shells are transported and how they act as indicators of water movement and velocity (Newell et al., 2007).

We had three campsites: on the banks of the Sakmara for two weeks; then nearly one week in the Korolki Ravine beside the Elshanka River on the Asiatic side of the Ural River, near Sol-Iletsk; and, finally, on the banks of the Tok, near Buzuluk, halfway between Orenburg and Samara. Our purpose in visiting all these locations was to see as many good rock sections that spanned the PTB as we could, to produce sedimentary logs through these and to collect fossils and samples for isotopic study.

The sedimentary shift: massive run-off

From our camp on the banks of the Sakmara, we went forth to localities nearby to study the PTB, most notably the high crag Sambulla (Fig. 2a). This had been logged in 1995, but Andy Newell and Richard Twitchett made fresh and much more detailed sedimentary logs, and collected samples of carbonate rocks for isotope analysis. Sambulla lies about 5 km from the
campsite and we were driven there around farm fields and over open steppe grasslands. From the top, one can see a huge distance, across to the town of Saraktash, perhaps 20 km away in one direction, along the meandering wooded valley of the Sakmara, a broad tributary of the River Ural. The crest of Sambulla Hill is composed of 10 m or more of well-cemented, hard conglomerate (Fig. 2b), dipping at 10° or so to the east. Walking 1 km along the crest of the ridge takes you from the highest point in the vicinity gently down to the riverside. The same conglomerate can be picked out in neighbouring ranges of hills and it clearly extends some distance, forming part of the base of a vast alluvial fan measuring at least 20 km across, even at this distance of some 50 km west of the Ural Mountains.

Earlier logging had shown that the Sambulla succession below the conglomerate consists of repeated fining-upward cycles (Fig. 3a). Each cycle begins with a coarse cross-bedded sandstone, fines upwards to siltstones and mudstones and ends with a palaeosol (Fig. 3b). The palaeosols are sometimes associated with plant remains and are nearly always invested with carbonate. The broad interpretation is that these are the deposits of cyclical lakes, with occasional influx of sediment (the coarser sands), then finer lake deposits and finally a palaeosol when the lake dried out – all perhaps the result of a broadly monsoonal climate. The Russians had clear biostratigraphic evidence that these finer lake beds were latest Permian in age, belonging to the upper part of the Tatarian, the

Fig. 2. The basal Triassic conglomerate on Sambulla Hill, on the banks of the River Sakmara. (a) Walking up the slope of Late Permian age towards the massive conglomerate unit. (b) Richard Twitchett gets his nose on the Permo-Triassic boundary at Sambulla.

Fig. 3. Sediments from the uppermost Permian Vyatskian Gorizont in the Vyazovka ravine. (a) Numerous fining-upward cycles in lake sediments, with Cindy Looy. (b) Close-up of a carbonate-rich palaeosol from the top of a fining-upward cycle, showing mottling and root traces.
Vyatskian. They dated the overlying conglomerate as lowermost Triassic, Vokhmian, based partly on mapping evidence and partly on finds of ostracods and of the aquatic tetrapod *Tupilakosaurus* in associated channel lags. These age assignments are probably correct, but must still be assessed with respect to other units in Russia, more particularly by comparison with the international (marine) time-scale.

Andy Newell had interpreted the PT successions in Russia previously as evidence for a major change in fluvial style (Newell *et al*., 1999). Below the boundary, in the uppermost Permian, the clastic sediments indicated relatively low-energy styles of deposition and meandering streams. Above the boundary, the sediments pointed to much higher-energy flow regimes, with deposition of conglomerates close to the Ural Mountains, and coarse sands at greater distances.

Valentin Tverdokhlebov had studied these great outpourings of coarse sediment at the beginning of the Triassic and he attributed them to renewed uplift of the Ural Mountains. The Urals had been uplifted primarily in the late Carboniferous and early Permian as the separate Eurasian and Siberian continental plates came into contact. Plate movement more or less ceased, but it would be no surprise if the deep suture zone between the two former continents was still tectonically active.

Tverdokhlebov (1971) had shown, in his PhD work, that the coarse sediments were in the form of vast alluvial fans (Fig. 4) that spewed westwards from the west side of the Ural Mountains, each fan spreading for a length of 100–150 km over the low-lying Permian lakes and meandering rivers on the great plain. He had identified all the boulders in the different basal Triassic alluvial fans and found that each fan had its own petrological signature, indicating subtly different sources of the rocks from deep within the Ural Mountains. The conglomerate boulders include blocks of Devonian or Carboniferous limestones, often with fossils, and metamorphic and igneous rocks.

Independently, Roger Smith — a sedimentologist working in South Africa — and his collaborator Peter Ward from the University of Washington in Seattle, had reached a similar conclusion. The famous Permian-Triassic succession of the Karoo Basin showed a similar sedimentary switch from a low-energy flow regime with meandering streams in the Late Permian to a high-energy flow regime with braided streams and alluvial fans in the Early Triassic (Ward *et al*., 2000). Since then, a similar shift in fluvial style has been noted across the PTB in Australia (Michaelsen, 2002), India (Sarkar *et al*., 2003) and Spain (Arche & López-Gómez, 2005). Such a shift does not occur everywhere: in numerous PT sections in Antarctica, for example, there is some evidence of coarsening of the sandstones above the boundary in some sections, but braided streams set in during the latest Permian, and the main change is from sandstones dominated by volcanic clasts in the Permian to sandstones with quartz clasts in the earliest Triassic (Collinson *et al*., 2006). Studies of soils and their chemical signatures (Retallack, 2005; Sephton *et al*., 2005) confirm that there was a soil erosion crisis, where soil and organic matter from the land was washed into the sea. If this was a world-wide phenomenon, local-scale tectonism cannot be the cause – but what then?

Perhaps there were global-scale upheavals, with mountains being uplifted in several parts of the world. So far, independent evidence for such global activity has not been found. Perhaps there was a massive
increase in rainfall world-wide? Again, there is no clear evidence for such a phenomenon, nor a suggestion of how it might have come about. If anything, the evidence suggests reduced rainfall. Andy Newell (Newell et al. 1999) argued that the abrupt increase in channel size associated with a major influx of gravel around the PTB could be related to climate change. There was a well-documented switch worldwide from a semi-arid/sub-humid climate in the latest Permian toward one of greater aridity in the earliest Triassic, and this can increase sediment yield by reducing vegetation cover. If vegetation is stripped from the surface of the land, rates of erosion can increase perhaps tenfold. This fits with other evidence that the normal green plants had been temporarily killed off and replaced by an unusual horizon at the boundary, dominated by strands produced either by fungi or algae. Below this horizon, the sediment samples contain spores of ferns, seed ferns, horsetails and other plants that grew at low, medium and tree-like levels. Such plants soon return in higher units in the Early Triassic. But the fungal/ algal boundary bed perhaps indicates a dramatic loss of normal vegetation. We know the devastating erosion that can follow the removal of plants today, such as in Bangladesh, where the rate of runoff and erosion has increased hugely after logging higher in the foothills of the Himalayas.

Isotopes and climate change

Our second major objective on the 2004 expedition was to take samples for isotopic analysis. The key isotopes are those of oxygen and carbon. At the PTB, there is a dramatic shift in oxygen isotope values of marine carbonates, a decrease in the value of the δ¹⁸O ratio of about six parts per thousand (ppt), corresponding to a global temperature rise of about 6°C. Climate modellers have shown how global warming can reduce ocean circulation and the amount of dissolved oxygen, creating anoxia in the oceans; this is seen in marine sediments from around the world. The marine evidence for anoxia nearly worldwide is dramatic and convincing, and this episode of superanoxia, which surely killed much of the life on the sea bottom (Wignall & Twitchett, 1996), must form part of any model for events at the PTB.

Carbon isotopes have been hugely important in determining models for the PT mass extinction. Geochemists measure the ratio of the stable isotopes ¹³C and ¹²C in limestones and fossil shells, and even in carbonate palaeosols. In nature, most carbon occurs as ¹²C, with minor, but measurable, amounts of ¹³C. The ratio of these two isotopes in the atmosphere is the same as in the surface waters of the oceans. During photosynthesis, plants preferentially take up ¹²C to produce organic matter. If this organic matter is buried, rather than returned to the atmosphere–ocean system, then the atmosphere–ocean ¹³C/¹²C ratio will shift in favour of the heavier isotope. Conventionally, this ratio is expressed as δ¹³C, which is the difference between the ¹³C/¹²C ratios in the sample being tested and in a known standard.

In the ocean system, during times 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 ¹³C. Shallow-water carbonate deposits are precipitated from this seawater, and record the seawater ¹³C/¹²C ratio without any preferential uptake of one or other isotope. Therefore, during times of high surface productivity, shallow-water carbonates record a positive shift in δ¹³C (i.e. towards the heavier isotope).

The PTB is characterized by a negative shift in δ¹³C, which is recorded in the carbonate deposits of all geological sections studied so far (e.g. Magaritz et al., 1988; (Sephton et al., 2002), including terrestrial ones (Retallack, 1995; MacLeod et al., 2000). 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 (Fig. 5). There is an initial short, sharp negative shift in δ¹³C, almost synchronous with the extinction horizon itself. The amount of negative swing varies between sections, but is typically 4–6‰ (Magaritz et al., 1988; MacLeod et al., 2000; Twitchett et al., 2001; Sephton et al., 2002). In most sections, a swing back towards the heavier end of the scale then follows. However, the δ¹³C 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 (Erwin, 1993; Wignall, 2001). An additional input of light carbon to the ocean–atmosphere system is required. The CO₂ emitted by volcanoes has a δ¹³C signature of −5‰, but calculations show that even the output from the Siberian Traps could not cause the observed shift in δ¹³C. Even if all life was killed in an instant and the resulting biomass was 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 δ¹³C signature of −65‰ (Erwin, 1993; Dickens et al., 1997; Wignall, 2001; Berner, 2002). If these gas hydrates can be made to melt, enough methane would be released to cause the observed shift.

Kenneth MacLeod and colleagues (2000) had managed to extract carbon and oxygen isotope signals from carbonate palaeosols and from reptile bones at points through the Karoo successions. These showed the same pattern on land through the PTB in the Karoo as had been detected in so many marine successions before. But their task had been technically difficult because the entire Permo-Triassic succession of the
Karoo has been lightly baked by the overlying Drakensberg volcanics of Early Jurassic age. This meant that the oxygen and carbon isotope signals could have been distorted or reset by the later heating, and the samples had to be treated repeatedly in acid to remove later-formed diagenetic calcite. We are fortunate with the Russian successions that they have not been metamorphosed by any later volcanics or tectonic activity. This means the carbonate samples should be easier to process. Initial results show the expected shifts in both carbon and oxygen isotopes at the PTB, but we await analysis of the more thoroughly sampled materials from the 2006 expedition before drawing conclusions regarding atmospheric and climatic changes.

4. THE EXTINCTION OF TETRAPODS IN THE PERMO-TRIASSIC MASS EXTINCTION

The Russian faunas

Skeletons of amphibians and reptiles are found throughout the Late Permian rock sequence around the South Urals. The latest Permian fauna of Russia, the Vyatskian assemblage (Fig. 6), known from the North Dvina river and from the south Urals, was rich and diverse. Herbivores include the large pareiasaur *Scutosaurus*, a formidable hippo-sized animal covered in bony excrescences, and the large, smooth-skinned dicynodont *Dicynodon*, with its two expanded canine teeth and otherwise toothless jaws. Carnivores include four species of gorgonopsians, including *Inostrancevia*, a great sabre-toothed reptile that presumably preyed on *Scutosaurus* and *Dicynodon*, as well as two smaller carnivores, a therocephalian and a cynodont. In other localities, latest Permian reptiles include *Archosaurus*, a 1 m-long slender fish-eating reptile, oldest member of the Archosauria, or ‘ruling reptiles’ (the group that includes crocodiles and dinosaurs) and procolophonids, small triangular-skulled reptiles, related to pareiasaurs, but superficially looking somewhat like fat lizards. At the water’s edge were three or four species of amphibians.

This was a rich and complex ecosystem, with as many animals as in any modern terrestrial community. There were herbivores specializing in plants of different kinds, fish-eating amphibians, insect-eating synapsids, carnivores feeding on small prey, and the gorgonopsians, so-called top predators, feeding on the largest of the herbivores. These animals were all wiped out by the end-Permian crisis.

The amphibians and reptiles that survived the crisis into the earliest Triassic in Russia are a poor assemblage, the so-called Lower Vetluga (Vokhmian) Community. The only reasonably sized herbivore was *Lystrosaurus*; other tetrapods include one species of procolophonid, and some rare therocephalians and diapsids that fed on insects and smaller reptiles, as well as fish-eating, broad-headed amphibians.

Big foot

Throughout the expedition, we kept ever-alert in our search for fossil amphibians and reptiles, but found very little. Isolated teeth and dermal plates are relatively common in channel lag deposits, especially in the earliest Triassic rock units, but more complete material is rarer. Our only reasonable fossil find had been on the 1995 expedition, when Andrey Sennikov spotted a procolophonid skull, an example of *Kapes*, in some Early Triassic sandstone, a specimen later described by Novikov & Sues (2004). So, we expected little, but were astonished by a find we made in the Korolki ravine (Fig. 7a).

One day during our five days at the site, Richard Twitchett spotted a discarded block in the ravine that appeared to have three rather pointed impressions radiating from the centre. The block was perhaps 30 cm across. Then, just behind it, in the face of a step
in the bottom of the ravine, he saw a curved depression at the base of a sandstone bed (Fig. 7b). This could have been a small channel or a load cast, but we decided to investigate further. We took the loose block back to camp, and showed it to our Russian colleagues. At first, they were unimpressed, but agreed to walk down to the site. Richard was convinced the two blocks were fossilized footprints of some large animal. Valentin Tverdokhlebov instructed Sasha and Edvard to work at the sandstone bed, and they turned over slab after slab, which we fitted together on the step above (Fig. 8a). The impressions were so huge, from 50 cm to 1 m across, and so mixed up that it was hard to make out what we had found. After ten minutes of hard work, everyone present agreed that we had, indeed, found some massive footprints of a five-toed animal, and that there were several intersecting tracks criss-crossing the area we had exposed (Fig. 8b). Valentin immediately christened the beast who had made the tracks ‘big foot’.

Careful logging by the Russian and British geologists showed that the footprints were part of the Vyatskian zone, some 50 m below the PTB (Fig. 9). The footprints were emplaced in a reddish-brown mudstone deposited from suspension beneath shallow ponded water in a floodplain environment. The footprints were subsequently cast by the base of the overlying fine-grained sandstone, which was deposited from a sheet flood event. Seventeen prints in all were observed. We could have gone on turning slabs for some time, but there would have been no point. Our Russian colleagues loaded up the best examples to add to the museum collection at Saratov State University. But who was ‘big foot’?

Fossil tracks are remarkably rare in the Late Permian of both Russia and South Africa. In Russia, as far as we know, we had reported the first finds in 1997 (Tverdokhlebov et al., 1997), tracks of a small reptile that Valentin Tverdokhlebov had found some years before near our campsite on the Sakmara at a site called Kulchomovo. A second find of larger tracks of a pareiasaur from the Sukhona river in the northern part of Russia was reported by Gubin et al. (2003). So this was apparently only the third find ever. But it was important to determine the track-maker.

We first compared the tracks with other specimens that had been described from other parts of the world. It seemed clear that our tracks were not a new form, but were more or less identical with Brontopus giganteus described by Heyler & Lessertisseur (1963) from the latest Permian of France. The name was chosen by the French authors to indicate that the maker was ponderous and huge – it means literally ‘gigantic thunder foot’. The prints indicate that the animal was plantigrade or semi-plantigrade (placed the soles of its feet flat on the ground. The hand print has five short stumpy fingers of similar length, while the foot also has five toes, but decreasing in length from the second toe to the fifth. The fingers and toes are broad and end in pointed claw marks. The fact that hands and feet each have five digits shows that the maker was almost certainly a reptile, and not an amphibian (nearly all amphibians had, and have, four fingers on the hand). Among Late Permian

Fig. 6. The latest Permian Vyatskian fauna from Russia. At the back, the gorgonopsian Inostrancevia looks speculatively at the plant-eating pareiasaur, Scutosaurus. A dicynodont stands at the water’s edge, while the flesh-eating synapsid Annatherapsidus sits on a log, with Drinia below. The temnospondyl amphibian Chroniosuchus sits on a sand bank, with Kotlassia in the water. In the foreground, the little procolophonid Microphon is to the left, the temnospondyl Raphanodon to the right. (Drawing by John Sibbick.)
Reptiles there are three possible candidates: pareiasaurs, dinocephalians or dicynodonts. Heyler & Lesertisseur (1963) were clear that *Brontopus* was made by a pareiasaur, whereas other authors assigned the track to a ‘pelycosaur’. The latter proposal seems unlikely because the ‘pelycosaurs’ were basal synapsids (‘mammal-like reptiles’) known from the Late Carboniferous and Early and Middle Permian. They had been extinct for at least 10 Ma before the Vyatskian. Pareiasaurs are also ruled out because of the inferred posture of big foot. Pareiasaurs had sprawling fore and hind limbs, with their elbows and knees sticking out sideways, whereas the *Brontopus* tracks indicate an only partially sprawling stance. That leaves dinocephalians and dicynodonts as possible track-makers. Both groups included some members large enough to have made the *Brontopus* tracks.

The largest Russian herbivorous dinocephalians that could have produced *Brontopus*-sized footprints are *Ulemosaurus* and *Deuterosaurus*, but their skeletal remains are too old, being known only from the upper part of the Urzhumian (Tverdokhlebov et al., 2005). World-wide, dinocephalians had largely disappeared by the end of the Tatarian and mostly by the mid to late Tatarian (Kemp, 2005). Dinocephalians are thus rejected from consideration as potential track-makers for the Russian material on stratigraphic grounds. That leaves dicynodonts. Some of these synapsids with 0.5 m skulls (*Rhachiocephalus, Aulacephalodon*) are known from the uppermost beds of the Upper Permian in South Africa (Rubidge, 1995). Although such truly giant dicynodonts have not been reported from Russia, the genus *Vivaxosaurus* (Kalandadze & Kurkin, 2000) has nearly the same skull size (0.4 m) and is known from the Vyatskian of Russia (Fig. 6). As an experiment, we scaled a dicynodont foot skeleton to ‘big foot’ size and found that this fitted more or less perfectly within a *Brontopus* footprint (Fig. 11). Further, dicynodonts had a kind of dual mode of locomotion in which the hind limbs were held in an erect or semi-erect position, and the forelimbs sprawled somewhat, expressed memorably by Kemp (1980), who described the locomotion as akin to a man pushing a wheelbarrow: the hind limbs striding in erect, parasagittal posture and the sprawling forelimbs scrabbling along in front.

So, even though giant skeletons of dicynodonts are not known from the terminal Permian in Russia, the...
tracks of ‘big foot’ appear to confirm their presence. The track-maker was then a massive herbivore, about the size of a hippopotamus, that scraped up plant material with a pair of massive tusks in its upper jaws and sliced the vegetable matter with horn-covered jaw margins. The footprints are so huge that they cannot be regarded as particularly beautiful fossils, but they have added considerably to knowledge of life just before the PT mass extinction (Surkov et al., 2007).

Patterns of extinction

One of our key aims is, of course, to determine how life went extinct at the PTB. Practically, we cannot hope to collect enough specimens of amphibians and reptiles ourselves from the Russian PT succession. However, Valentin Tverdokhlebov has kept an elaborate card index file of every tetrapod specimen – whether complete skeletons or skulls, or isolated bones – over the past fifty years of his work in the Orenburg area. In this, he documents 675 specimens from 289 localities in the entire PT red-bed area of exposure from Buzuluk to Saraktash, some 400 km from west to east and 200 km from north to south. The locality records are each assigned to one or other of the 13 stratigraphic divisions into which the Late Permian and Early to Middle Triassic succession is divided (Fig. 12).

We were first shown the card index in 1995, and we discussed the possibilities of extracting valuable statistical data then. Eventually, after careful checking, we were able to publish the thorough documentation as two papers, one on the Early to Middle Triassic localities and faunas (Tverdokhlebov et al., 2003) and one on the Late Permian localities and faunas (Tverdokhlebov et al., 2005). These papers provide the first thorough account of the Russian terrestrial Permo-Triassic red-bed succession in any language, whether Russian or English, and they should set right a major omission in the literature. Hitherto, the equivalent successions in the Karoo basins in South Africa have been extensively documented over the years, and yet the Russian rocks and fossils have been reported sporadically, partly because the field geological data were considered a part of the mapping programme by the Soviet authorities, and so top secret.

Our statistical analysis of the data showed some of the complexity of the extinction event (Fig. 12). There were seven families of amphibians and 15 families of reptiles in the Late Permian of Russia, some of them rather short-lived, and others extending through the entire time span. In each of the six Middle and Late Permian faunas, in the rivers and lakes, four to seven genera of small, medium and large aquatic tetrapods (‘amphibians’) fed on the abundant thick-scaled bony fishes and rarer freshwater sharks and lungfishes. On the wooded banks were five to eleven genera of terrestrial tetrapods (‘reptiles’), ranging in size from tiny insect-eaters to rhino-sized plant-eating pareiasaurs and the wolf- to bear-sized, sabre-toothed gorgonopodians that fed on them.

Twenty of the 22 Middle and Late Permian families went extinct at, or before, the PTB, and only two – the
small, mainly herbivorous procolophonids and the larger herbivorous dicynodonts – survived through the mass extinction. Of the 22 families, 11 were present at the end of the Vyatskian interval, the terminal Russian Permian time unit, and the extinction of nine of these corresponds to a family-level extinction rate of 82%. This is high when compared with the global family-level extinction rate of 55% or so for marine families (Sepkoski, 1997) and it scales, of course, to a much higher rate of extinction at generic or specific levels.

The pattern of familial and generic extinction in Russia is similar to that already known from other PT sections, in South Africa and South America, for example. However, the pattern of extinction and origination before the boundary was a little surprising. Indeed, the families and genera showed seemingly erratic behaviour, with repeated peaks in extinction and origination. As a supposedly stable Late Permian ecosystem, it might have been assumed that there would have been relatively little turnover of families and genera. But, of course, no genus or species lasts for ever, and it is quite expected that a mature and stable ecosystem would show such turnover patterns through a time span of 10–15 Ma.

Recovery

As expected, the earliest Triassic faunas, after the PT event, were unusual and seemingly ecologically unbalanced. As well as the two surviving reptile families, the procolophonids and dicynodonts, faunas were dominated by amphibians. In the basal Triassic (Kopanskaya Svita (‘formation’); Induan), there were only medium-sized and large fish-eaters in the rivers and lakes (Tupilakosauridae, Capitosauridae, Benthosuchidae) and medium-sized insect/tetrapod-eaters (Prolacertidae, Proterosuchidae). Dicynodonts must have been present, but are known from fossils only from later in the Early Triassic in the South Urals, but from the basal mostly Triassic elsewhere in Russia.

Only one family (Tupilakosauridae) could be identified as a ‘disaster taxon’, present for a short time immediately after the crisis. Other families present in the Kopanskaya Svita persisted through the Early Triassic. New taxa were added through the 15 Ma of the Early and Mid Triassic; further medium-sized and large fish-eaters in the fresh waters, and further medium-sized herbivores and large carnivores on land. The Early and Mid Triassic are characterized by the steady addition of taxa, and slow loss of existing families: turnover was much less volatile than in the Late Permian (Fig. 13).

Our evidence suggests rather slow recovery of tetrapod faunas in the Russian sections, with ecosystems seemingly still unbalanced at the end of the sampling period, some 15 Ma after the mass extinction, in the Ladinian (late Middle Triassic). Donguz and Bukobay ecosystems were again complex, but small fish-eaters and small insect-eaters were still absent, as were large
herbivores and specialist top carnivores to feed on them (Fig. 12). These gaps presumably reflect incomplete ecosystems and delayed recovery, rather than that the ecosystem had reached equilibrium at a lower level of complexity than is observed in the Late Permian. Evidence for this is that Late Triassic faunas from other parts of the world show all the families seen in the Mid Triassic Russian faunas, as well as taxa that plug the ecological gaps – various amphibians as small fish-eaters, small diapsids as insect-eaters, ever-larger dicynodonts as large herbivores, and rauisuchians as large carnivores.

**Sampling**

The continental fossil record of vertebrates is notoriously patchy and there is a risk that studies such as this reflect little more than poor sampling. It could be argued, for example, that the range chart (Fig. 12) and the plots of extinction and origination metrics (Fig. 13) merely document fluctuations in the quality of preservation of the fossils, variations in the environments represented, or in the number of localities and specimens recorded for each time division. Such problems with sampling could reflect human efforts – perhaps geologists and palaeontologists have worked with different degrees of vigour on different rock units, and so their collecting efforts might then bias the apparent patterns of diversity through time. On the other hand, sampling might more probably reflect the nature of the rock record. Terrestrial sediments in such red-bed successions reflect sporadic deposition in rivers, lakes and dune fields. A great deal of deposited rock could well be eroded by subsequent sediment movements.
**Fig. 12.** The end-Permian mass extinction of tetrapods in the South Urals Basin, Russia. Solid lines indicate the family is known from the time bin in question; dashed lines indicate gaps in the distribution. Families are plotted by broad-scale ecological categories, based on major habitat (freshwater or terrestrial), diet (fish, browsing, insects, tetrapods) and size (small, medium, large). Completeness of the record is documented to the right by numbers of localities and specimens from each svita (‘formation’) and quality of the fossils is divided into four classes (1, isolated bone; 2, several associated bones; 3, complete or near-complete skull; 4, complete or near-complete skeleton). The time-scales of svitas (based on field criteria) and horizons (based on fossil assemblages) are the Russian standards for the South Urals Basin (Tverdokhlebov et al., 2003, 2005) and these are correlated with the international time-scale (Gradstein et al., 2004). The approximate positions of the South African tetrapod assemblage zones are indicated. Boundaries for which good radiometric dates exist are indicated with black blobs (●). Abbreviations: Br, browsers; Chang., Changhsingian; In, insect-eaters; Kung., Kungurian; Loc, localities; Nos, numbers; Spec, specimens; Tet, tetrapod-eaters. (Reproduced from Benton et al. (2004), with permission.)
under water or air. So, how can palaeontologists attempt to rule out such sampling problems?

In our paper (Benton et al., 2004), we presented three tests for sampling that sought to determine whether we were looking at a geological or a biological signal.

- First, we plotted the numbers of genera and families against numbers of localities and specimens. If sampling intensity drove apparent diversity, then stratigraphic intervals that are well sampled (lots of specimens, lots of localities) might very well show higher diversity than more poorly sampled stratigraphic intervals (few specimens, few localities). Our plot (Fig. 14a, b) shows no correlation: if anything, time bins with large numbers of localities and specimens are associated with low-diversity faunas and vice versa. Further, when the distributions of generic and familial diversity through time are compared with the distributions of numbers of sites and numbers of specimens per time bin (Fig. 14c), there is no apparent tracking. Peaks and troughs in the diversity data do not match peaks and troughs in richness of the fossil record. And, crucially, the time of diversity decline across the PTB corresponds to a rising trend in numbers of sites and specimens.

- Secondly, we looked at sample sizes. Five of the 13 stratigraphic units are represented by small

Fig. 13. Turnover of tetrapod families through the Late Permian and Early Triassic in the South Urals Basin, Russia. Rates of origination and extinction are percentage metrics based on all taxa (including Lazarus taxa, but excluding singleton families – families known from a single species or single locality) known from a time bin. Stratigraphic units are the successive svitas of the Upper Permian (1, Osnovskaya; 2, Belebey; 3, Bolshekinelskaya; 4, Amanakskaya; 5, Malokinelskaya/Vyakovskaya; 6, Kutulukskaya/Kulemova, Lower Triassic (7, Kopanskaya; 8, Staritskaya; 9, Kyzlasinskaya; 10, Gostevskaya; 11, Petropavlovskaya) and Middle Triassic (12, Donguz; 13, Bukobay). Binomial 95% confidence intervals are shown for the percentage extinction metrics (confidence intervals are of similar magnitude for the percentage origination metrics, but are omitted for clarity). (Reproduced from Benton et al. (2004), with permission.)

Fig. 14. The data on tetrapod distributions from the South Urals are probably reliable and cannot be accounted for simply by sampling (the patchiness of the rock and fossil record). Numbers of genera and families are not related to (a) numbers of localities or (b) numbers of specimens. (c) The distributions of generic and familial diversity through time (left-hand y-axis) follow similar curves, but these do not appear to relate to measures of sampling (numbers of localities and specimens per time bin – which themselves are correlated; right-hand y-axis). Stratigraphic units are as in Figure 13. (Reproduced from Benton et al. (2004), with permission.)
Thirdly, we applied a statistical technique called rarefraction analysis, which is designed to adjust sample sizes to the lowest common level. The question is asked: what result would we find if we drew a subsample of a particular size from the overall samples. The idea is to pick a subsample size that matches the smallest actual sample, and to use the rarefaction analysis to determine how much of the pattern might be generated by variation in sample sizes through the 13 stratigraphic units. Our rarefaction analysis showed that the better-sampled time units – the Kopanskaya, K-oldsaiiskaya and Staritskaya svitas (Fig. 12) – may overestimate diversity by one, or at most, two families, in comparison to the other time bins. Normalizing all time bin sizes to the range of 49–63 specimens, cuts diversity of the first three Triassic horizons by one or two families and, hence, makes the PTB extinction seem larger (91% instead of 82% extinction rate) and depresses earliest Triassic diversity even more than has been indicated from the raw figures.

Our conclusion is then that the patterns we see in the Russian sections are more biological than geological. Sampling effects are not ruled out completely, of course, but the pattern of data (Figs. 12–14) cannot be passed off simply as a geologically driven signal. It seems reasonable for the present to read the patterns as evolutionary and then to compare them with other areas.

Patterns of PT extinction and recovery

Our most striking finding has been that the high-diversity and complex latest Permian terrestrial ecosystems in Russia were volatile in terms of generic and familial turnover, but that when these ecosystems were largely destroyed by the PT crisis the volatility disappeared, and recovery from low diversity was a slow process, with longer survivorship of genera and families and less turnover. Within the 15 Ma post-event window, full recovery of the ecosystems had not taken place. This contrasts with conclusions from elsewhere. Smith & Botha (2005) reported a 69% generic extinction rate, based on collection of 225 specimens, across the PTB in South Africa. Only four genera, Lystrosaurus, Tetracynodon, Moschorhinus and Ictidosuchoides, survived the PTB. But, within 37 m of the boundary, Smith & Botha (2005) reported a total of ten genera, compared to 13 just below the PTB, and interpreted this to mean that recovery was relatively fast, really within a few hundred thousand years of the mass extinction event.

Of course, it is important to define what is meant by ‘recovery’. To some, recovery would mean simply the recovery of species numbers in faunas – when post-extinction generic diversity of faunas matches the pre-extinction diversity. In the Russian faunas, this was achieved in the Early Triassic, at the time of the Gostevskaya Sand Petropavlovskaya Svitas, when there were again ten or eleven families, as in the terminal Permian Vyatskian Svita. However, that probably does not represent full recovery in the sense of recovery of the species numbers and ecological roles in faunas. In other words, during Gostevskaya and Petropavlovskaya Svita times, the families present did not include any small insectivores or large herbivores. In that sense, the ecosystems were incomplete and large herbivores at least did not come on the scene until latest Middle Triassic or early Late Triassic, some 20 Ma after the PT mass extinction.

A third definition of recovery could be the recovery of higher-taxon diversity on a global scale. On this count, terrestrial tetrapod faunas worldwide had not recovered the Late Permian global patterns until the Late Triassic and the time of origin of the dinosaurs and other groups, again some 20 Ma after the PT mass extinction. For marine families, the global recovery period was even longer, extending into the Early Cretaceous, when global marine family numbers recovered their Late Permian levels, some 125 Ma after the PT mass extinction. In this regard, the global recovery of marine family numbers was set back further by the end-Triassic mass extinction.

So, the Russian evidence suggests a rather slow ecosystem recovery lasting for more than 20 Ma, whereas Smith & Botha (2005) proposed a rapid recovery in South Africa over a time span of less than 1 Ma. The difference in findings reflects partly a difference in definition, whether recovery indicates overall ecosystem recovery (Russian example) or species diversity in faunas (South Africa). Sampling might play a role, but so too might the sedimentary environments represented. The apparent relative abundance of amphibians in the Early Triassic of both South Africa and Russia has long been noted (e.g. Milner, 1990) and could reflect, to some extent, a bias relating to the kinds of rock facies preserved. Ironically, while the earliest Triassic was a time of increasing aridity in Russia (Newell et al., 1999) and South Africa (Smith & Botha, 2005), the wet-adapted amphibians predominated in some localities. Smith & Botha (2005) noted specific evidence in the Karoo of drought-induced deaths of Lystrosaurus and other taxa and, in both regions, overall drought might have been associated with rare monsoonal rainfall that produced massive floods and coarse river deposits, as well as skeletons of...
short-lived amphibians that flourished during the weeks of wet conditions.

A possible bias in comparing the two regions is the relative abundance of the famous dicynodont *Lythrosaurus* in South Africa, and its complete absence from the Orenburg region (although the genus is known elsewhere in the Russian Early Triassic (Surkov et al., 2005). Further, although truly large herbivores are not known in the Early Triassic units of the Karoo, as in Russia, there were insect-eating reptiles among the cynodonts that are not known in the Early and Mid Triassic of Orenburg, and only rarely from elsewhere in the Russian successions (Battail & Surkov, 2000). The absence of dicynodonts and cynodonts in the Early Triassic of the Russian South Urals area, and their relative rarity elsewhere in Russia, might indicate a palaeobiogeographical difference between South Africa and Russia, but further consideration of the distribution of sedimentary facies and sampling controls must be considered.

Among other terrestrial groups, plants seem to show a slow recovery, lasting until the end of the Middle Triassic (Grauvogel-Stamm & Ash, 2005). Indeed, in several parts of the world, including Russia and South Africa, the recovery did not really start until the end of the Early Triassic: after the extinction of Permian floras, the lycopsid *Pleuromeia* proliferated worldwide. Then, conifers re-established themselves in the early Anisian, and new groups – cycadophytes andpteridosperms – appeared in the late Anisian. The timing of floral recovery world-wide is more in line with the slow recovery of tetrapod faunas seen in Russia than with the rather more rapid recovery of tetrapods suggested from South Africa.

### 5. THE RUNAWAY GREENHOUSE: A KILLING MODEL

Our work in Russia is consistent so far with the most widely accepted model for the PT mass extinction. A small minority have argued for an extraterrestrial impact at this time, but the evidence is limited (Wignall, 2001; Benton, 2003; Benton & Twitchett, 2004). More consistent with the evidence, but by no means proved, is an earth-bound model that stems from the combination of the geological and palaeontological data already described, together with the fact that there were massive volcanic eruptions in Siberia at the same time.

At the end of the Permian, giant volcanic eruptions occurred in Siberia, spewing out some $2 \times 10^6$ km$^3$ of basalt lava, and covering $1.6 \times 10^5$ km$^3$ of eastern Russia to a depth of 400–3000 m. It was first suggested in the 1980s that this massive volcanic activity might be linked to the PT mass extinction. The Siberian Traps are composed of flood basalts that built up over thousands of years to considerable thicknesses. Early efforts at dating the Siberian Traps produced a huge array of dates, from 160 Ma to 280 Ma, with a particular cluster between 260 Ma and 230 Ma. More recent dating, using newer radiometric methods, yielded dates exactly on the boundary, with a total range of 600 000 years. Further work has to be done to determine exactly how many major phases of eruption there were and their precise dates. These can then be keyed to dated ash layers in sedimentary sequences as far away as southern China.

Since 1990, attempts have been made to provide a coherent killing model by linking the geological evidence for oceanic anoxia, global warming, a catastrophic reduction in the diversity and abundance of life with the eruption of the Siberian eruptions. The sharp negative excursion in carbon isotope values, dropping from a value of $+2$ ppt to $+4$ ppt to $-2$ ppt at the mass extinction level, implies a dramatic increase in the light carbon isotope ($^{12}C$). Geologists and atmospheric modellers have tussled over trying to identify a source. Neither the instantaneous destruction of all life on Earth, and subsequent flushing of the $^{12}C$ into the oceans, nor the amount of $^{12}C$ estimated to have reached the atmosphere from the carbon dioxide ($CO_2$) released by the Siberian Trap eruptions are enough to explain the observed shift. Something else is required, and that ‘something else’ has been identified as methane released from gas hydrates (Wignall, 2001; Berner, 2002; Corsetti et al., 2005).

The assumption is that initial global warming at the PTB, triggered by the huge Siberian eruptions, melted frozen gas hydrate bodies. Massive volumes of methane (rich in $^{12}C$) 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. So the process continued in a positive feedback spiral, termed the ‘runaway greenhouse’ phenomenon. Some sort of threshold was probably reached, beyond which the natural systems that normally reduce carbon dioxide levels could not operate. The system spiralled out of control, leading to the biggest crash in the history of life.

The duration of the crisis is worth investigating. We have seen that some evidence from the record of plants and tetrapods suggests that recovery took a long time. Indeed, the carbon isotope record also suggests that crisis conditions might have existed for the whole 5 Ma or so of the Early Triassic. Corsetti et al. (2005), in reviewing geochemical evidence from around the world, noted that the initial negative carbon isotope shift at the PTB is followed by three or four further negative anomalies of similar magnitude right to the end of the Olenekian/Spathian (end of the Early Triassic). Carbon isotope values then move back close to their pre-extinction mean in the Anisian (Middle Triassic). As Corsetti et al. (2005) noted, this long-term pattern of negative anomalies in $^{13}C$ implies a long-term cause, and they suggested this could be either ocean stratification/turnover or reorganization of the carbon cycle. There is evidence for the former in the world-wide anoxia of the earliest Triassic, which implies some stratification (no mixing and oxygenation of bottom waters). It is harder, however, to
demonstrate that overturn occurred, mixing isotopically light organic matter from the lower waters back to surface waters from time to time. Reorganization of the carbon cycle implies that burial of terrestrially derived organic matter was severely cut back, and this is supported by the implied massive loss of vegetation owing to acid rain and aridification at the PTB, and by the subsequent ‘coal gap’, when it has been suggested forests were absent and plant material was not being produced or buried in normal quantities. Marine organic matter produces an isotopically lighter carbon signal than terrestrial organic matter, or mixed terrestrial and marine, because of the difference in δ13C (about 7–8‰) between dissolved organic carbon in the sea versus CO2 in the atmosphere. This difference provides a useful marker for determining animal diets, but also for detecting sudden influxes of terrestrially derived organic matter into the sea.

Could it be then that the post-extinction crisis can be divided into two parts? (1) The immediate aftermath that lasted for perhaps a few hundred thousand years, as the Siberian Traps continued to erupt (Jin et al., 2000). (2) A longer episode, perhaps encompassing all 5 Ma or so of the Early Triassic, when plants on land were sparse and forests had not become re-established, and when tetrapod communities consisted of generally small to medium-sized animals occupying a restricted range of niches, and not yet including larger herbivores or carnivores. More precise dating of Early Triassic rock sequences and closer study of the fossils are required.

6. CONCLUSION

In the study of the PT mass extinction, much attention so far has focused on marine sections, and such studies must be continued and multiplied so the true geographical extent of each phase of the mass extinction and the post-extinction recovery may be assessed. We believe that terrestrial sections will also be of value. They offer an important view of the other half of life and the other half of the carbon cycle. The classic view has been that terrestrial sections are very hard to date and that they can yield only rather poor information about faunal and floral changes. We believe, however, that the potential is good for meaningful biological studies, but would stress the need for good independent stratigraphic schemes and a thorough understanding of sedimentology and sampling issues.

If the runaway greenhouse model is correct and explains perhaps the biggest crisis on Earth in the last 500 Ma, it is a model worth exploring further. It appears to represent a breakdown in global environmental mechanisms, where normal systems that would equilibrate atmospheric gases and temperatures took hundreds of thousands of years to come into play.

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 can be sustained and at what level the runaway greenhouse comes into play.

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