

invertebrates promise deep insights into both the diversity and general concepts of stem cell biology beyond the classical model organisms.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Palaeobiology: Rapid succession during mass extinction

Michael J. Benton

School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol BS8 1TQ, UK

Correspondence: mike.benton@bristol.ac.uk

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The mass extinction at the end of the Permian period was a time of considerable ecological upheaval. A new study shows that in Southern Africa top predators replaced each other in succession across the end-Permian interval, suggesting that ecological crisis preceded the mass extinction.

There is a conundrum with mass extinctions: it is sometimes easier to reconstruct the physical aspects of an environmental crisis than its biological aspects. We read about impact craters, global darkness, volcanic eruptions, carbon isotopes or ocean acidification;

and yet, the reason we care about mass extinctions is because of their dire effects on life. Direst of all was the Permian-Triassic mass extinction (PTME) 252 million years ago, which wiped out about 95% of species^{1–3}. Did everything die at once, or were there a series of crises over

months, years or thousands of years? As ecosystems collapsed, which species went first, top predators or primary consumers? Did the crisis proceed equally across the world, from equator to poles? Life came so close to complete annihilation during the PTME that we



require detailed information on ecosystem collapse. Frustratingly, such information on terrestrial ecosystems has been sparse, limited mainly to localities in South Africa, Russia and China, which are hard to date. Despite this, individual faunas may be well documented, represented by hundreds or thousands of specimens.

As an example, the Vyatikian community from the latest Permian of European Russia^{4,5} has yielded dozens of skeletons of a wide variety of tetrapods and fishes, allowing a reasonable reconstruction of one of the last ecosystems before the PTME (Figure 1). The anatomy and adaptations of each of the species have been studied in detail, and food webs can be constructed and tested, but the conundrum is how to link this to the next such fauna and infer what occurred between these snapshots of ancient life. Work on the Permian and Triassic rock sequences in the Karoo Basin of South Africa, however, is beginning to address these problems. In a new study, in this issue of *Current Biology*, Christian Kammerer, Jennifer Botha and colleagues⁶ identify a large sabre-toothed predator from South Africa as *Inostrancevia*, a genus well known already from the terminal Permian of Russia, providing a strong link across the world.

That an animal known from Russia should crop up in South Africa is an unexpected finding because in those times, South Africa lay far south, as it does today, and Russia in the northern hemisphere, but there were substantial arid zones and mountains across the equatorial belt that inhibited biotic interchange between both areas.

Inostrancevia is particularly interesting, because it was a large, sabre-toothed predator, belonging to the clade Gorgonopsia, at the top of the food chains in both territories. In Russia, *Inostrancevia* has been known for a long time from the terminal Permian faunas (Figure 1), preying upon the one-tonne pareiasaurs, such as *Scutosaurus*.

The second key aspect of the new paper by Kammerer and colleagues⁶ is that they identify a four-step replacement process among the top predators, from rubidgeine gorgonopsians to *Inostrancevia*, then to therocephalians, and, following the mass extinction, proterosuchids. These four taxa represent

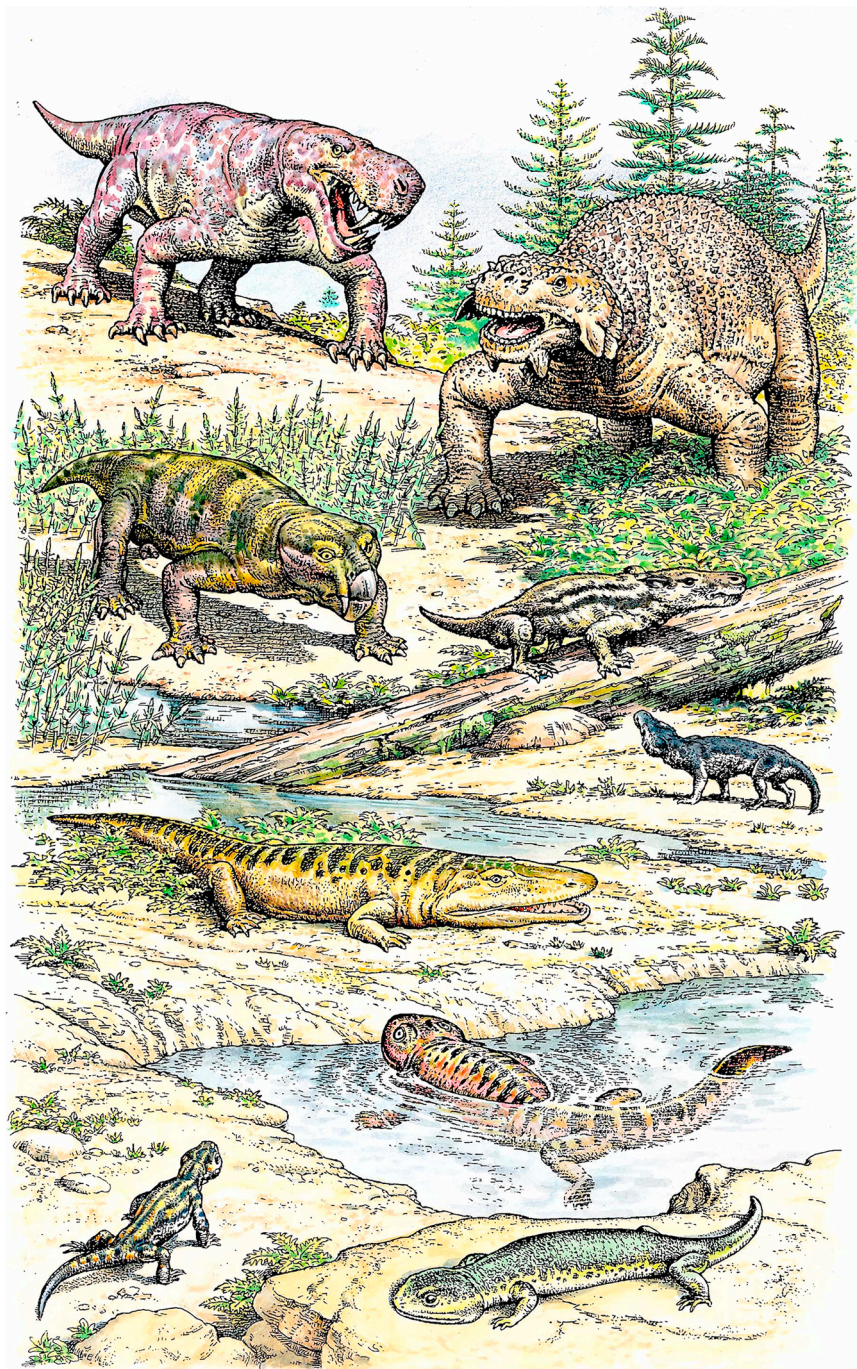


Figure 1. The latest Permian Vyatikian fauna from Russia.

At the back, the gorgonopsian *Inostrancevia* looks speculatively at the one-tonne, plant-eating pareiasaur *Scutosaurus*. A dicynodont stands at the water's edge, while the flesh-eating therocephalian *Annatherapsidus* sits on a log, with the cynodont *Dvinia* below. The temnospondyl *Chroniosuchus* sits on a sand bank, with the reptiliomorph *Kotlassia* in the water. In the foreground, the little procolophonid *Microphon* is to the left, and the temnospondyl *Raphanodon* to the right (artwork: © John Sibbick, reproduced with permission).

a close-up view of the turmoil of those crisis days, and a major switch from synapsids — the large tetrapod group that

led to mammals (gorgonopsians, therocephalians) — to archosauromorphs, which led to birds

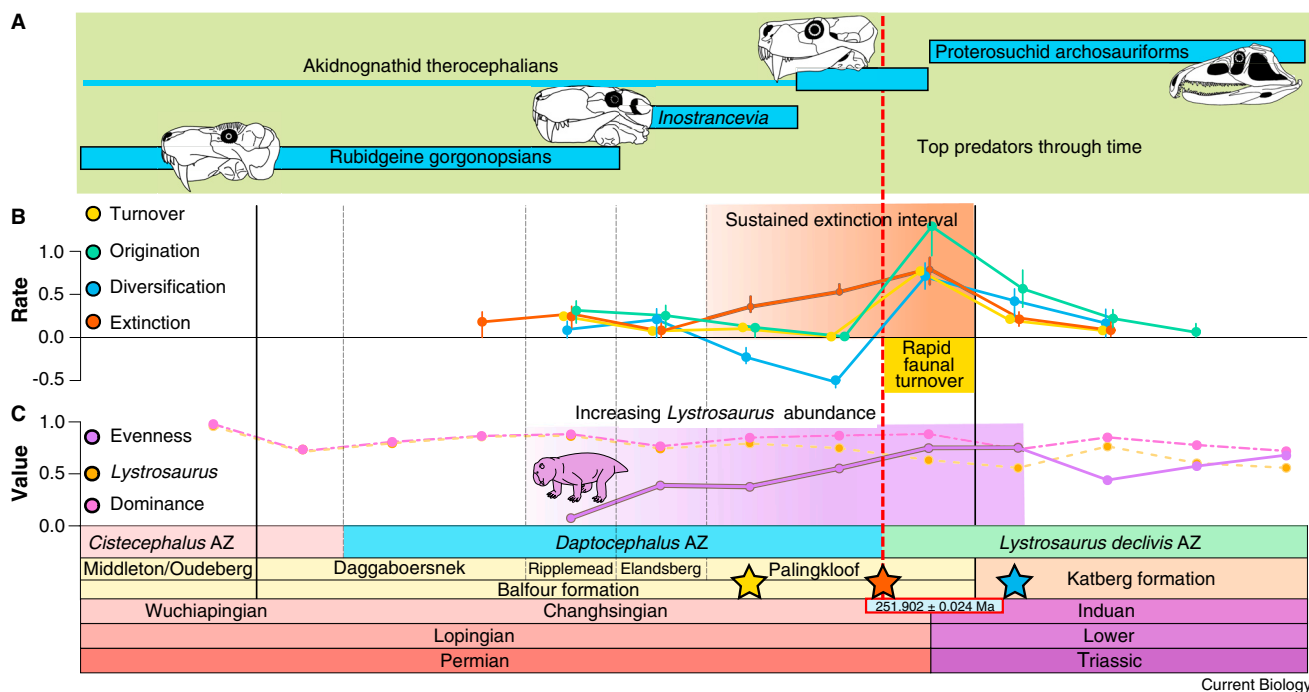


Figure 2. Diversity dynamics of tetrapods through the latest Permian and earliest Triassic of the Karoo basin, South Africa.

(A) Relay-like replacement of the top predator through the latest Permian and earliest Triassic. (B) Evidence for rising extinction rates in the latest Permian, and high turnover of species at the beginning of the Triassic. (C) Ecological evenness, a measure of the distribution of relative abundances of all species in the faunas, shown as remaining relatively steady at species and genus levels, together with the relative abundance of species of the genus *Lystrosaurus*, rising from low levels in the middle *Daptocephalus* Assemblage Zone (AZ) to 70% of faunal abundance in the earliest Triassic. The exact position of the Permian–Triassic boundary is disputed by different authors, shown by coloured stars: Jennifer Botha (yellow), traditional (red) and Robert Gastaldo (blue). Source: Pia Viglietti and Christian Kammerer.

and crocodylians (proteosuchid). All the gorgonopsians were large predators, mostly armed with sabre teeth, and yet victims in the end of the PTME. Their replacements, the proterosuchids, were long-snouted, faintly crocodylian-like reptiles that may have been partly aquatic, hunting fish and smaller tetrapod prey.

Kammerer and colleagues⁶ note that there are two surprising aspects about their new discovery, not only that there was a Russian interloper, but also that faunal turnovers began well before the PTME itself. This suggests that some perturbation of environments may have occurred before the crisis, and that top predators were turning over and the functional guild continued into the Triassic, whereas ecological theory might suggest that top predators would have disappeared entirely during the crisis. Admittedly though, the earliest Triassic predator, the proterosuchid, might have fed on fish or at best *Lystrosaurus*, rather than being a sabre-toothed predator on 1-tonne prey, so it

could be debated whether the top predator guild was untouched or not. This whole relay of top predators (Figure 2A) spans an interval of 3–4 million years; still not the kind of time scale ecologists would like, but a massive improvement on what was possible.

This relay replacement of top predators can be related to wider research on ecological dynamics. Even though the exact position of the Permian–Triassic boundary in the Karoo beds is debated (Figure 2B,C), the large collections of fossils have enabled a tracking of speciation dynamics⁷. Extinction rates remained high over an interval of up to one million years, beginning some time before the Permian–Triassic boundary and continuing high into the earliest Triassic. At this point, origination rates of tetrapods also increased, corresponding to a time of rapid faunal turnover immediately after the peak of extinction. Measures of faunal evenness and dominance were relatively constant through the Permian, but dropped through the PTME, reflecting

perturbation and loss of ecosystem stability.

There were several ‘disaster taxa’ in the immediate aftermath of the PTME, species that evolved fast and went extinct fast. The one-metre long herbivorous synapsid *Lystrosaurus* was famously one of these (Figure 2C), present in South Africa in the latest Permian, surviving the crisis and diversifying worldwide in the earliest Triassic. It was successful for a while but disappeared without contributing descendants to the subsequent Triassic faunas.

How long life took to recover after the PTME has been much debated: there is evidence for a long process⁸, as well as for an early recovery of ecosystems, even within one million years after the crisis^{9,10}. Certainly, physical environments were hugely perturbed by repeated heating crises, and conditions did not return to normal until six million years after the extinction crisis^{11,12}. It was hard for plant and animal species to become established and for ecosystems to rebuild

and stabilise. The debate on the timing of recovery is resolved by accepting that both sides are right; life could recover fast and quite complex ecosystems became established, but these were hit hard by the next heating crisis. The fast-evolving species of foraminifera, ammonoids, conodonts, fishes and reptiles crashed to extinction, then the ecosystem was rebuilt and crashed again. But can these early-recovery ecosystems be regarded as stable or merely transient and part of the disaster aftermath?

In fact, extinct ecosystems can be assessed for stability just as modern examples. Computational network analyses can be applied, especially a method called ‘cascading extinction on graphs’ (CEG)^{13,14}. CEG is based on the observation that if one species is knocked out of a food web, there is a cascade effect on other species up and down the food chain. In normal situations, that local species extinction or removal might be only temporary, and neighbouring species expand their functions, or a new species emerges to plug the gap. By modelling hypothetical species removals from a food web model, ecosystem stability can be tested. An ecosystem is stable if it can be stressed by the removal of many species, but its general structure remains, whereas an unstable ecosystem collapses after removal of just a few species.

In studies of the PTME and its effect on terrestrial ecosystems, food webs for seven Karoo faunas through the Late Permian to Middle Triassic were reconstructed^{15,16}, including all the plants, insects, fishes, and tetrapods. The network shows who eats whom and includes estimates of the relative biomass represented by each component of the ecosystem. Through application of the CEG dynamic food web model Late Permian ecosystems were found to be stable, even though species died out and were replaced, and these ecosystems were also characterized by numerous relatively long-lived species. Everything changed in the earliest Triassic ecosystems, dominated by *Lystrosaurus*. Here, although there were nearly as many species as before the PTME, these were short-lived, ‘disaster taxa’, and the whole ecosystem was unstable to any perturbation. Only by the early Middle Triassic a stable ecosystem arose, where

species were longer-lived again, and the system was robust to perturbation. Likewise, marine ecosystems before and after the PTME in South China showed a two-step process of extinction, where biodiversity dropped dramatically during the two pulses of extinction in the PTME crisis, separated by 61,000 years, but ecosystems collapsed only on the second hit¹⁷.

Recovery from the PTME can also be documented in geographic terms. In the immediate aftermath of the crisis, tetrapod faunas became cosmopolitan, with a small number of species, notably *Lystrosaurus*, occurring worldwide. After this episode of disaster taxa, faunas became more endemic, at least in Gondwana¹⁸. A network analysis, measuring the relative degree of connectedness between terrestrial tetrapod faunas by the proportions of shared species revealed¹⁹ that tetrapod faunas generally had low connectedness values, meaning faunas were highly endemic. However, connectedness values rose after the PTME to four times the pre-extinction level (cosmopolitanism) and did not recover to normal levels until the early Late Triassic. Therefore, cosmopolitanism of Triassic tetrapod faunas on land remained high for the first 15 million years of the Triassic.

The new work by Kammerer and colleagues⁶ on succession of top predators adds detail to our understanding of ecosystem collapse and rebuilding through the greatest of all mass extinctions. Palaeontologists are concerned to document their data carefully, in terms of the taxonomy and phylogeny, and functional and ecological inferences about fossil taxa, as well as their exact temporal and spatial occurrences. Importantly, the new work, and other studies mentioned here, are beginning to allow us a view of the impacts on life of these past environmental crises, but with some levels of confidence. Because of heterogeneity in the fossil record, the comparative methods have been chosen to work with the strengths of the fossil record and avoid the weaknesses.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Social conflict: Illuminating the great resignation

Elim Hong

INSERM, CNRS, Neurosciences Paris Seine - Institut de Biologie Paris Seine (NPS - IBPS), Sorbonne Université, 75005 Paris, France

Correspondence: elim.hong@inserm.fr

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Social conflict between conspecifics results in the establishment of a hierarchy composed of a winner and loser. A recent study elucidates the molecular mechanism that may underlie the behavioral switch between winner and loser states.

The establishment of hierarchies by social conflict in conspecifics is deemed necessary to create a stable environment. The idea that higher levels of aggression correlate with dominance is widely accepted as evidenced by the ubiquitous use of the expression ‘alpha male’ or ‘pecking order’ to describe dominance in humans. As such, studies have identified various factors that regulate aggression levels including hormones (glucocorticoids, testosterone), neurotransmitters (serotonin) and brain regions, including the ventromedial hypothalamus and prefrontal cortex¹. However, the relationship between aggression, dominance and social hierarchies is far from clear. Wolves in a pack follow the leader because he is the eldest and usually the father of the pack²; pecking order in chicks is established based on their age³. Multiple studies show that aggressiveness is not necessarily an indicator of dominance^{4,5} and may even reduce social influence during complex group behavioral tasks⁶. Once a hierarchy is established, dominant or submissive animals tend to maintain their social status when regrouped with naive animals¹. However, ethology studies in many species including fish, rodents and primates^{7,8} also show that behavioral and physiological changes associated with

the ascent or descent in a hierarchy can occur in a short period, suggesting that the behavioral states are readily reversible. Neither the causes for the switch between the behavioral states nor the brain area that is responsible for this switch are well understood. A new study by Kinoshita and Okamoto⁹ reported in this issue of *Current Biology* elucidates a molecular mechanism that may underlie the switch in behavior.

As in many fish species, when two adult male zebrafish are placed in a confined tank, they resort to circling and biting attacks until one surrenders and displays a fleeing behavior, at which point the conflict is resolved¹⁰ (Figure 1A). The biting fish is referred to as the winner and the fleeing fish as the loser. A previous study by Okamoto’s lab identified a key role for an evolutionarily conserved region of the brain, the dorsal habenula-interpeduncular nucleus (Hb-IPN) pathway, in regulating the outcome of the social conflict paradigm¹¹. The Hb-IPN pathway consists of two distinct circuits that co-release different neurotransmitters in addition to the neurotransmitter glutamate: the lateral subnucleus (dHbL) contains peptidergic (Substance P) neurons that project to the dorsal/intermediate IPN (d/iIPN) and the medial subnucleus (dHbM) contains cholinergic (acetylcholine) neurons projecting to the intermediate/ventral IPN

(i/vIPN)¹² (Figure 1B). Fish with silenced dHbL or dHbM outputs exhibit a decreased or increased probability to win in the social conflict paradigm, respectively. Furthermore, the experience of losing results in the potentiation of dHbM-i/vIPN neurotransmission (Figure 1B)^{10,13}. For simplicity’s sake, we will henceforth refer to the dHbM-i/vIPN circuit as the loser circuit.

Neuronal potentiation refers to a long-term change in synaptic plasticity leading to learning and memory¹⁴. The mechanisms that drive neuronal potentiation are not fully understood. One emerging idea is that neuromodulators recruit specific glutamatergic AMPA receptors in the postsynaptic neurons leading to the strengthening of the synaptic weight. In the new study by Kinoshita and Okamoto⁹, they first elucidated the neuromodulator and corresponding receptor type that promotes the potentiation of the loser circuit. As this circuit contains neurons that co-release the neuromodulator acetylcholine, it was the primary candidate for circuit potentiation.

Nicotinic acetylcholine receptors (nAChRs), named due to their high affinity to the compound, represent a main receptor class for acetylcholine. They are composed of homomeric or heteromeric combinations of 12 different subunits in