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Title	The End-Permian Crisis, Aftermath and Subsequent Recovery
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Description	International Symposium, "The Origin and Evolution of Natural Diversity". 1-5 October 2007. Sapporo, Japan.
Relation	Edited by Hisatake Okada, Shunsuke F. Mawatari, Noriyuki Suzuki, Pitambar Gautam. ISBN: 978-4-9903990-0-9
Citation	Origin and Evolution of Natural Diversity : Proceedings of the International Symposium, The Origin and Evolution of Natural Diversity, held from 1-5 October 2007 in Sapporo, Japan, 43-48
Issue Date	2008
Doc URL	https://hdl.handle.net/2115/38434
Type	conference paper
File Information	43-48-origin08.pdf



The End-Permian Crisis, Aftermath and Subsequent Recovery

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ABSTRACT

Improvements in biostratigraphic and radiometric dating, combined with palynological and palaeo-ecological studies of the same sections, have allowed the relative timing of ecosystem destruction during the end-Permian crisis to be determined in the past few years. The extinction is revealed to be neither synchronous nor instantaneous but instead reveals a protracted crisis. This is especially the case for terrestrial floral communities that show the onset of floral changes prior to the marine mass extinction, but a final extinction after the marine event making a total duration for the terrestrial extinctions of a few hundred thousand years. In the oceans the radiolarians provide the only detailed record of the fate of planktonic communities and these undergo a phase of stress and final extinction before the marine benthos. The initial phase of the aftermath is characterized by a globally-distributed, low diversity biota and, in shallow, equatorial settings, by the precipitation of Precambrian-like anachronistic carbonates. These are well developed during low points in the $\delta^{13}\text{C}$ record and may be related to super-saturated anoxic waters. Few groups radiate in the Early Triassic and those that did suffered a second mass extinction event late in the Smithian Stage, around 2 million years after the end-Permian event. Only during the ensuing Spathian are there clear signs of uninterrupted recovery.

Keywords: Mass Extinction, End-Permian, Smithian, Carbon isotopes

INTRODUCTION

The end-Permian mass extinction has become the subject of intense scrutiny in the past decade and several valuable reviews of this crisis have recently appeared [1, 2]. This ongoing work has particularly seen an increased focus on the intriguing nature of the Early Triassic aftermath interval when global biodiversity was persistently low [3], the carbon isotope record was extraordinarily unstable [4] and curious anachronistic facies were widespread [5, 6]. New radiometric dates from the Early Triassic [7] have also provided a dramatic improvement in the absolute timing of the recovery within considerable

implications for the timing of recovery [8]. Thus, the long-repeated mantra of an unusually long delay in the onset of recovery now appears to over-state the case. Recovery began with two million years of the mass extinction, a comparable duration to the delay seen after other mass extinction events. This work focuses on the most recent advances and how they are helping our understanding of this entire interval.

THE EXTINCTION RECORD

It has been claimed that the end-Permian mass extinction was abrupt and that consequently a bo-

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Information for use in citing this article: Okada, H., Mawatari, S.F., Suzuki, N. and Gautam, P. (eds.), *Origin and Evolution of Natural Diversity*, Proceedings of International Symposium "The Origin and Evolution of Natural Diversity", 1–5 October 2007, Sapporo, pp. 43–48.

lide-impact extinction mechanism could be considered [9, 10]. However, recent studies have made it clear that the extinction event was neither a simultaneous nor an instantaneous collapse of global ecosystems. Instead, distinct diachronism is discernible. In the marine realm the oncoming crisis is first seen in the surface waters where radiolarians underwent a major extinction event. Thus, in the deep-water chert sections of British Columbia the radiolarian mass extinction preceded the loss of benthic invertebrates by a short interval represented by a few decimetres of chert accumulation [11]. The radiolarian extinction event is best known from Japanese accreted chert terranes but unfortunately they lack a benthic fossil record although they do reveal a protracted radiolarian extinction event. The main phase of extinction occurs at the top of the *A. yaoi* radiolarian zone with the survivors, an impoverished fauna of mutated forms, struggling on to the top of the *A. simplex* zone [12]. Correlation of the Japanese sections with the well-known global stratotype at Meishan in South China reveals that the initial radiolarian extinction occurs at the top of the *C. changxingensis*–*C. deflecta* zone [12]. This level is below the benthic extinction level which occurs in the latest part of the *C. yini* Zone [12, 13]. The final coup de grâce of the radiolarians was after the main phase of benthic extinctions within the final conodont zone of the Permian [12]. A protracted phase of radiolarian extinctions is also seen in the deep-water chert sections of South China where their sequential losses culminate in an impoverished assemblage of Entactinaria and Spumellaria [14].

As noted above, the extinction level of marine invertebrates is best known from the Meishan stratotype where a diverse fauna, dominated by brachiopods and foraminifera, is almost totally eradicated at the top of the Changxing Formation [10]. However, a distinct “transition fauna” or “mixed fauna” consisting of Permian brachiopods and Triassic bivalves persists into the basal centimeters of the overlying Yinkeng Formation. The Permian component of this fauna disappears in a second, minor pulse of extinction at the top of the basal Triassic *H. parvus* zone [15].

Interestingly, the two pulses of marine extinctions are closely associated with two negative C isotope spikes. The first of these has long been known [16] and has been a key line of evidence in many extinction scenarios. The younger spike was also identified in the early studies of Holser and his colleagues [16], although it has only been appreciated recently that it was global phenomenon [17]. These record

major changes in the cycling of carbon within the ocean and atmosphere and are a key component in our understanding of this crisis.

The timing of the terrestrial floral extinction crisis, probably a unique, and certainly the most severe crisis in the history of terrestrial ecosystems, has been revealed from study of the palynological record [18]. The initial hint that all was not well on land comes from the marine sections in East Greenland where fungal remains begin to become an important component of palynological assemblages [18]. There has been considerable debate about the affinity of this material in recent years with several groups favouring a freshwater algal origin for the “fungal spores” [19]. Whatever their identity, their global proliferation immediately prior to the marine extinctions suggests distinctive, crisis conditions in terrestrial settings. The next stage in the crisis was a major dieback of gymnosperm woodland, although without any major extinction losses, to be replaced by a shrubby flora dominated by mosses, ferns, clubmosses and quillworts. In the Greenland sections this event coincides with the marine extinctions but the extinction losses of the gymnosperms occurred at a higher level around the Permian-Triassic boundary (Fig. 1). In SW China this second, true plant extinction phase may have occurred later because the last elements of the distinctive *Gigantopteris* flora survived into the earliest Triassic [20]. Two extinction phases are also seen in the terrestrial record of Antarctica where, like the marine record, they coincide with two negative C isotope spikes [21].

Precise correlation of the tetrapod extinction losses with the floral crises has yet to be achieved, but Ward et al’s [22] observations in the Karoo Basin, South Africa that there was a diversity decline followed by a coup de grace at the Permian/Triassic boundary is clearly comparable to the stressed interval and final extinction seen in the palynological record.

EXTINCTION CAUSES

For over a decade now the finger of blame for the end-Permian extinctions has been pointed at the Siberian Traps. This is one of the most voluminous flood basalt provinces on Earth [23], and the causal mechanism has been variously attributed to either the cooling effect of sulphate aerosols or the warming effect of volcanogenic CO₂ (see Wignall [24] for a review of proposed extinction mechanisms up to that date). Global warming has been linked to a

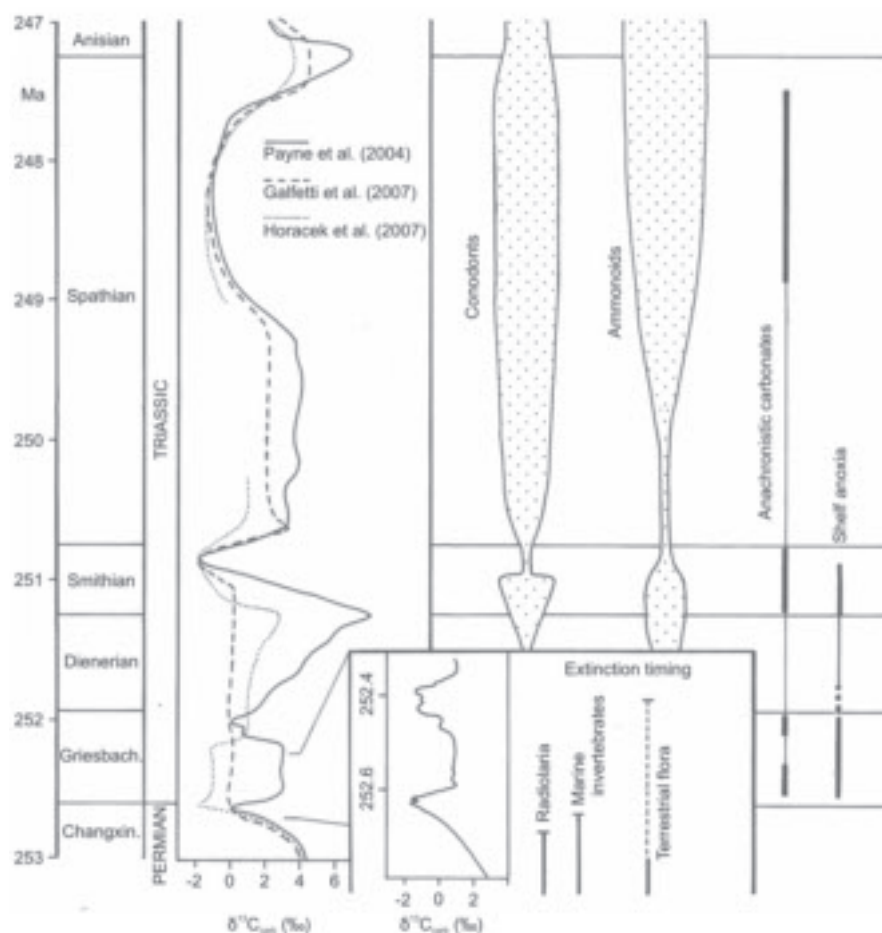


Fig. 1 Summary of palaeoenvironmental and geochemical events in the latest Permian–Early Triassic interval plotted against the absolute age scale of Ovtcharova *et al.* [7]. Published C isotopic curves are very similar for the latest Permian and Spathian intervals but show considerable variation at other times, particularly during the Griesbachian Stage. The detailed onset of the Permian–Triassic boundary interval shows the high resolution $\delta^{13}\text{C}$ record of the Meishan stratotype [17]. The fortunes of conodonts during the Early Triassic are from Orchard [36] and the ammonoid record is from Brayard *et al.* [37]. The distinct phases of anachronistic carbonate development are proposed by Baud *et al.* [6] and the phases of global shelf anoxia are from Wignall and Twitchett [26], with a possible youngest phase during the Smithian suggested by Galfetti *et al.* [8].

slow-down in ocean circulation and development of the most widespread and intensive oceanic anoxic events of the Phanerozoic [25, 26]. The role of volcanogenic CO_2 has been modified in many extinction scenarios because calculations suggest the amount of carbon dioxide released would only be enough to trigger a minor warming event [24]. This is now regarded to have triggered the release of methane from hydrate reservoirs thereby driving a runaway greenhouse scenario [27]. The negative shift in the $\delta^{13}\text{C}$ record provides potential evidence for the release of isotopically-light methane. Increasingly sophisticated computer modeling has been able to replicate these conditions [28, 29]. However, until very recently the cause of the terrestrial extinc-

tions has remained something of an enigma.

To cause a global extinction of terrestrial plants suggests that we should look to the atmosphere. Climatic effects, such as severe global warming, can have regional significance but are not obviously capable of devastating all plant communities. High latitude warming for example will not favour polar plant communities but it will provide new habitats for lower latitude plants. Thus, damage to the ozone layer and the consequent increase of UV-B radiation has become an especially popular, terrestrial extinction cause in the past few years, albeit with different proposed origins [21, 30–33]. In a model that neatly links the oceanic crisis with atmospheric changes, Kump *et al.* [32] suggested that oceanic

anoxia may have become sufficiently severe that hydrogen sulphide began to leak into the atmosphere. The postulated consequences were direct poisoning of the terrestrial biota and also damage to the ozone layer due to the suppression of OH and O radicals in the atmosphere. The latter effect would also prolong the lifespan of methane in the atmosphere and thus increase global warming [32]. Subsequent modeling of the effects of hydrogen sulphide release into the atmosphere has shown that this gas is unlikely to have reached lethal concentrations [34]. The oxidizing capacity of the atmosphere is such that H₂S cannot last more than a decade in the atmosphere, even under conditions of exceptional flux from the oceans, and consequently it cannot penetrate the stratosphere and damage the ozone shield. However, an indirect effect of the presence of H₂S in the troposphere is to decrease the concentration of the hydroxyl radical. This is involved in the oxidation of atmospheric methane and Lamarque et al. [34] have shown that its residence time in the atmosphere can increase tenfold if H₂S suppresses OH levels. Methane is also involved in the destruction of ozone and thus a “double whammy” of both H₂S release, from a euxinic ocean, and methane release from hydrate reservoirs, has the potential to cause substantial damage to the ozone layer.

AFTERMATH

The most immediate effect of the end-Permian mass extinction was to produce the most pandemic communities known from the fossil record [3]. In the oceans a low diversity assemblage dominated by molluscs, especially the bivalve *Claraia*, is found in all basal Triassic marine sections in every region of the world. On land the medium-sized tetrapod *Lystrosaurus* is similarly pandemic, as is the floral assemblage dominated by a few plants, notably the quillwort *Isoetes* [35]. This extraordinary situation partly reflects the severity of the extinction, with so few survivors it is inevitable that the same ones show up in many different areas but it presumably also reflects globally uniform climatic conditions. The first 3 stages of the Early Triassic also mark the most moribund evolutionary interval of the Phanerozoic. Few benthic invertebrate lineages radiate at this time, although the nektonic ammonoids and conodonts were the exception to this rule. The conodonts began to radiate immediately after their modest end-Permian extinctions [36], whilst the ammonoids only began significant radiation in the Smithian Stage when their provinciality also in-

creased [37].

Another characteristic feature of the post-extinction fauna, undoubtedly related to high stress conditions, is their small size relative. This is typified by the common occurrence of microgastropods in marine sections. Twitchett [38] has called this the Lilliput effect and has suggested within lineage size reduction caused by productivity fall. However, recent studies of the supposedly quintessential Lilliput taxa of the Early Triassic, the microgastropods have shown that they mostly belong to new lineages and so do not represent a size reduction of former Permian species. They rather indicate that evolutionary factors favouring small size, such as opportunistic life strategy, were operating at this time [39].

Extending the detailed carbon isotope studies, from the Permo-Triassic boundary into the Early Triassic in sections from South China, has shown that the interval witnessed a remarkable series of high magnitude oscillations and only returned to more stable values in the Middle Triassic (Fig. 1). More recent studies in other sections have partially replicated these results (Fig. 1), especially in the younger Early Triassic interval (mid Smithian to end Spathian stages). Thus, a major negative shift in the later Smithian is followed by a partial “rebound” and period of stability in the early Spathian. This oscillation has an impressive 10‰ magnitude in the data of Payne et al. [4], making it one of the largest (and most rapid) C isotope perturbations in Earth’s history. However, in other records from the Dolomites of northern Italy [40] and from South China [8] this excursion is much subdued or absent. This is probably a more realistic reflection of the global signal (Fig. 1). The Galfetti et al. [8] record is derived from sections only 100 km distant from those sampled by Payne et al. [4], providing a cogent warning of the degree of lateral variability that can be seen in $\delta^{13}\text{C}$ records even over such relatively short distances. The isotopic record earlier in the Triassic also shows little consistency between datasets. After the large negative excursion seen in all Late Permian records, the subsequent Griesbachian Stage either saw the establishment of stable, low values [8, 40] or a partial recovery to positive values followed by a negative excursion at the Griesbachian-Dienerian boundary [4].

Despite the uncertainty over the global C isotope signature of the Early Triassic, the oscillations coincide with some fascinating changes in both the sedimentary and fossil record. The presence of anachronistic carbonate facies in the interval after the end-Permian mass extinction has long been known [41]. This

includes a range of microbial and inorganic carbonates typical of those encountered in Precambrian rather than Phanerozoic sections and include open-shelf stromatolites, microbial carbonates such as thrombolites and, most extraordinary, radial fans of crystals that were originally aragonite. As studies have progressed it has become apparent that there are distinct intervals within the Early Triassic when these anachronistic carbonates were especially prevalent (Fig. 1). The first two of these phases, within the Griesbachian Stage, coincide with a global oceanic anoxic event [26] and it may be that their development records carbonate supersaturation due to the widespread development of bicarbonate-rich, anoxic waters [42]. The third phase of anachronistic carbonate development in the Smithian Stage occurs after the shelf anoxia had waned, although such conditions may still have been regionally important [8]. It remains to be seen if the final phase of anachronistic carbonates, in the later Spathian Stage, is also related to widespread anoxia. Interestingly, all these carbonate phases coincide with negative intervals of the Payne et al. [4] $\delta^{13}\text{C}$ carbonate record (Fig. 1), and it is tempting to relate these two observations to a model in which direct carbonate precipitation was triggered by the appearance of isotopically-light, bicarbonate-rich water masses in shallow shelf settings. Alternatively, Payne and Kump [43] explain the negative excursions in a model that sees the release of light C from the Siberian Traps. This is envisaged to have temporarily depressed oceanic carbonate saturation states before triggering a phase of oceanic anoxia, widespread organic C burial and a positive shift in the $\delta^{13}\text{C}$ carbonate record.

There is clearly much to discover about the global perturbations in the Early Triassic, but a clear signal is seen around the Smithian-Spathian boundary interval. In 1997 Hallam and Wignall [3] highlighted the big losses of conodonts, ammonoids and bivalves at this boundary and suggested that this “extinction event presents a major challenge for future research” Subsequent discoveries have confirmed the severity of the losses at this time [36, 37]. Indeed, were it not for the fact that global diversity had yet to recover from the end-Permian culling (there was not much to kill), this event may have been of much greater magnitude and therefore more apparent in the fossil record compilations. The $\delta^{13}\text{C}$ perturbations at this time are also similar to those seen at other major extinction events, such as the end-Permian extinction, with a positive shift rapidly followed by a negative spike (Fig. 1). The

Horacek et al. [40] data in particular show a close correspondence with the fossil losses. Thus, a late Spathian negative excursion of 2‰ coincides with a major conodont extinction event [36]. Range data for other fossil groups is not known with the same precision but future work, for example on the bivalve record, may yet reveal that this was a late Smithian rather than a Smithian-Spathian boundary crisis. The cause of this crisis has yet to be investigated. Twitchett and Wignall [44] noted a climatic change to humid conditions in the Italian record at this time, and elsewhere shelf anoxia once again becomes prevalent [8]. Clearly there were regional climatic and oceanic changes but a survey of global changes at this time remains to be undertaken. Only with the waning of the late Smithian crisis, was the global biota finally able to radiate, 2 million years after the end-Permian disaster.

ACKNOWLEDGMENTS

David Bond is thanked for help with the preparation of this work.

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