Extinction: End-Triassic Mass Extinction

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One of the five greatest mass extinction events in Earth's history occurred at the end of the Triassic, *c.* 200 million years ago. This event ultimately eliminated conodonts and nearly annihilated corals, sphinctozoan sponges and ammonoids. Other strongly affected marine taxa include brachiopods, bivalves, gastropods and foraminifers. On the land, there is evidence for a temporal disturbance of plant communities but only few plant taxa finally disappeared. Terrestrial vertebrates also suffered but timing and extent of this extinction remains equivocal. The cause of the end-Triassic mass extinction was probably linked to the contemporary activity of the Central Atlantic Magmatic Province, which heralded the breakup of the supercontinent Pangaea. Possible kill mechanisms associated with magmatic activity include sea-level changes, marina anoxia, climatic changes, release of toxic compounds and acidification of seawater. Remarkably, long-term effects on marine biota were rather different between ecological groups: a nearly instantaneous recovery of level-bottom communities is contrasted by the virtual absence of reef systems for nearly 10 million years after the extinction event.

Introduction

Although the study of mass extinction events has been a key topic of palaeontological research since the seminal work of Alvarez *et al.* (1980) on the end-Cretaceous catastrophe, the mass extinction event at the end of the Triassic held its attribute as 'the least well understood of the major diversity depletions' (Bambach *et al.*, 2004) until recently. In the past years, however, research progress was immense, and today the end-Triassic biotic crisis is actually among the best-understood events of sudden diversity decline in the geological past. One reason for this progress in knowledge is the documentation of an unexpectedly large volume of magmatic rocks genetically related to the Central Atlantic Magmatic Province (CAMP) and an exact determination of their radiometric ages, which indicate a sudden onset of massive volcanic extrusions synchronous with the disappearance of many taxa and ecosystems at the end of the Triassic. Additionally, detailed work on sedimentology, geochemistry and extinction patterns in Triassic–Jurassic (T–J) boundary sections worldwide has provided palaeontological data that are in accordance with predictions of volcanogenic extinction scenarios. Consequently, discussion today nearly exclusively concentrates on volcanogenically induced kill mechanisms. Because associated changes of many environmental parameters can be estimated relatively precisely and are in a similar order of magnitude than projected environmental changes caused by human activity, the study of the end-Triassic mass extinction event provides a unique test-case for predicting future changes in biosphere. **See also**: Diversity of Life

The Last Days of Pangaea

The transition from the Triassic to the Jurassic period is marked by a pivotal plate tectonic change: The supercontinent Pangaea, which had persisted for nearly 150 Ma, was affected by strong rift tectonics, finally leading to the opening of the central Atlantic in the middle Jurassic. Concomitant with rift tectonics was violent magmatic activity in an area in excess of $10\,000\,000\,km^2$ on either side of the rift zone (Marzoli *et al.*, 2011). Estimates of the erupted volcanic rocks of this CAMP indicate a volume of $2\,300\,000\,km^3$ (McHone, 2003), making the CAMP one of the largest igneous provinces in Earth's history. Magmatic activity probably took place already in the Rhaetian (Late Triassic) with sill and dyke emplacement (Ruhl and Kürschner, 2011), followed by massive extrusive volcanism that started near-synchronously in the circum-Atlantic basins. Critically, the peak activity of the initial lava flows was at $201.8 \pm 0.7\,Ma$, which within error limits is indistinguishable from radiometric ages of the T–J boundary (201.21 Ma; Schoene *et al.*, 2010; Marzoli *et al.*, 2011).

Subsequent magmatic pulses have been recorded up to 10 Ma after the T–J boundary, but these were minor in comparison with the initial eruptions (Nomade *et al.*, 2007; Marzoli *et al.*, 2011). Although volcanism has already earlier been identified as a possible cause for the end-Triassic mass extinction (e.g. Courtillot, 1994; Wignall, 2001), it was only after documentation of the large extent and exact radiometric ages of the volcanic rocks that volcanogenic extinction scenarios have become dominant. **See also**: Continental Drift

Stratigraphy and Sedimentological Record across the T–J Boundary

Continuous marine sections across the T–J boundary are notoriously rare (e.g. Morante and Hallam, 1996), and their correlation has long been complicated by the lack of a global boundary stratotype section and point (GSSP). Recently, however, the Kuhjoch section in the Karwendel Mountains (Northern Calcareous Alps, Austria; **Figure 1**) has been chosen as the GSSP for the base of the Jurassic and hence for the definition of the T–J boundary (Morton, 2008). The index fossil defining the base of the Jurassic in this section is *Psiloceras spelae tirolicum* (Hillebrandt and Krystyn, 2009; **Figure 2**), which first occurs *c.* 6 m above the lithological boundary between the Rhaetian Kössen

Formation and the Tiefengraben Member of the Kendl-bach Formation (Hillebrandt and Krystyn, 2009). This definition places the T–J boundary stratigraphically well above main extinction horizon that is located just above the Kössen Formation, but this is merely a technical aspect.

Figure 2 Holotype of *Psiloceras spelae tirolicum* (Hillebrandt and Krystyn, 2009), the index fossil for the base of the Jurassic. Scale bar represents 1 cm. Photo courtesy of A. von Hillebrandt, Berlin.

Figure 1 Global boundary stratotype section and point (GSSP) for the base of the Jurassic, Kuhjoch section (Karwendel Mountains, Austria), illustrating the abrupt interruption of carbonate sedimentation on top of the late Triassic Kössen Formation. Note that strata are overturned, that is, Late Triassic limestones are above the claystones of the Triassic–Jurassic transition. The first occurrence of *Psiloceras spelae* and thus the base of the Jurassic is stratigraphically *c.* 6 m above the top of the Kössen Formation close to the lower limit of the photograph, notably postdating the extinction event. K. Kment (Bad Tölz) for scale. Photo by the author.

Correlation of the GSSP section with other T–J boundary sections is facilitated by a negative carbon isotope excursion of global extent, which in the GSSP section occurs at the very base of the Tiefengraben Member (Ruhl *et al.*, 2010). In combination with the last appearance datum of the late Rhaetian index fossil *Choristoceras marshi* at the top of the Kössen beds (Hillebrandt and Krystyn, 2009), an easily applicable stratigraphical framework is provided, allowing correlation of the GSSP with palaeogeographically distant sections. An intriguing aspect emerging from interregional correlation of marine sections is the coincidence of the initial negative carbon isotope excursion with a gap in carbonate sedimentation just above the extinction horizon (**Figure 3**). It has been proposed that extinction, negative carbon isotope excursion and interruption of carbonate sedimentation have a common cause: the injection of huge amounts of isotopically light carbon dioxide (CO_2) from the magmatic activity of the CAMP, possibly added by release from thermally dissociated marine gas hydrates (Hautmann, 2004). Predicted environmental consequences of increased atmospheric CO_2 include global warming (possibly following an initial cooling event due to volcanogenic sulfur dioxide (SO_2) emission) and ocean acidification due to the hydrolysis of CO_2 and SO_2, temporarily depressing the saturation state of seawater with respect to calcium carbonate minerals (see later discussion). **See also**: Geological Time: Principles

In continental settings, stratigraphically well-constrained sections spanning the T–J transition are even rarer than in their marine counterparts. Possibly the best-studied sections are from the north-eastern United States (Newark and Hartfort Rift Basins), which combine the record of continental sediments and intercalated volcanic rocks. On the basis of sections from this area and their chemostratigraphic correlation with marine sediments, Whiteside *et al.* (2010) suggested that the end-Triassic mass extinction event began synchronous on land and in the sea and simultaneous with the oldest CAMP eruptions. A sudden perturbation of plant communities (although not leading to significant extinction of taxa) has also been described from east Greenland, possibly taking place synchronously with the marine extinction (McElwain *et al.*, 2009). A contrary view was put forward by
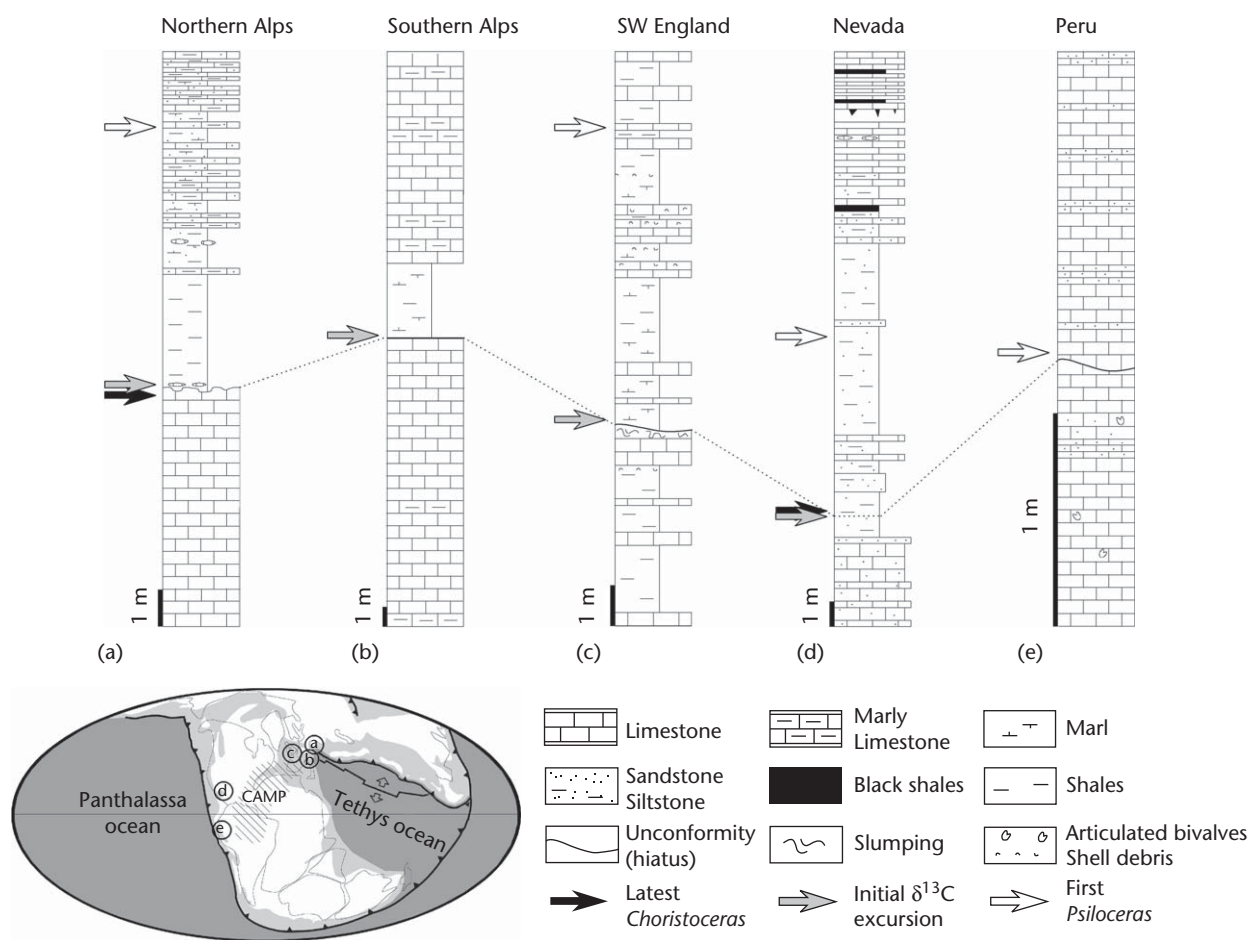

Figure 3 Triassic–Jurassic boundary sections from Europe, North America and South America, showing sedimentology, onset of negative $\delta^{13}C$ excursion, and biostratigraphically important ammonoid occurrences (*Choristoceras* and *Psiloceras*). Note synchronous interruption of carbonate sedimentation, indicated by stippled line. Reproduced from Hautmann *et al.* (2008a) by permission of Schweizerbart'sche Varlagsbuchhandlung.

Lucas *et al.* (2011), who found that extinction of terrestrial vertebrates in continental sediments of the southern Colorado Plateau preceded marine extinction.

Extinction Patterns

The end-Triassic mass extinction event is best documented in the marine record. On the basis of Sepkoski's 2002 compilation of marine animal genera, Bambach *et al.* (2004) calculated that 46.8% of Rhaetian genera did not survive into the Hettangian. Yet, extinction was not evenly distributed among clades (**Figure 4**). Most severely affected were the conodonts, which failed to survive the end of the Triassic. In ammonoids, all Triassic groups became extinct with two exceptions: (1) Choristoceratidae, which may have locally survived in the Hettangian before they finally disappeared and (2) Phylloceratina, which finally gave rise to the Jurassic diversification of ammonids (Guex *et al.*, 2004; Hillebrandt and Krystyn, 2009).

Other prominent victims of the end-Triassic extinction event were reef-building taxa (**Figure 5**). Although coral reefs locally reappeared already during the Hettangian (Kiessling *et al.*, 2009), it was not after a lag phase of 8–10 Ma that reef systems fully re-established (Stanley, 2006). Flügel (2002) indicated an extinction of 96% of all genera of scleractinian corals (74/77 genera) and 91% of sphinctozoan sponges (53/58 genera), the two most prominent groups of Rhaetian reef builders. However, Kiessling *et al.* (2009) criticised that these high values may partly reflect sampling failure and the lack of taxonomic standardisation. On the basis of a sample-standardised approach using the Paleobiology Database (http://paleodb.org/cgi-bin/bridge.pl), Kiessling *et al.* (2009) estimated an extinction of 45% of scleractinian genera across the T–J boundary, but these authors also noted that this value still represents the highest extinction in the geological history of the clade.

With a 71% loss of genera, articulated brachiopods were also among the most severely affected groups, yet the sole two genera of inarticulated bachiopods survived the crisis (Hautmann *et al.*, 2008a). **See also**: Brachiopoda

Bivalves suffered a 40% loss of marine genera (Hautmann *et al.*, 2008a) and thus slightly less than the average of marine genera. Infaunal taxa suffered more than epifaunal taxa (McRoberts and Newton, 1995), but this might be an epiphenomenon of an increased extinction of taxa with completely aragonitic shells in comparison with taxa that had calcitic outer shell layers (50% versus 30% extinction; Hautmann *et al.*, 2008a), because infaunal bivalves are invariably aragonitic, whereas epifaunal bivalves have predominantly calcitic outer shell layers.

Gastropod extinction is difficult to estimate because taxonomically important characters such as the protoconch are seldom preserved, but it has been suggested that the end-Triassic crisis might have been an even more important caesura in the history of this class than the end-Permian mass extinction (Batten, 1973).

The comprehensive compendium of Loeblich and Tappan (1988) suggest extinction of *c.* 35% of Foraminifera genera, which is below the average of marine extinction but still notably high (cf. Bambach *et al.*, 2004). In a thorough regional study, Clémence *et al.* (2010) documented ecological changes in foraminifer communities across the T–J boundary, showing a decreasing abundance and diversity of calcareous taxa and a corresponding increase of agglutinated forms, and a change in feeding strategies from deposit to detritus feeders and bacterial scavengers. **See also**: Foraminifera

Data on the extinction of Radiolaria across the T–J boundary remains controversial. On the basis of local studies, a severe mass extinction of this group has been proposed (e.g. O'Dogherty *et al.*, 2010), which, however, does not appear on the global scale. On the basis of revised data, Kiessling and Danelian (2011) calculated merely a 17% loss of radiolarian genera at the end of the Triassic, which increases to still moderate 29% if short-term survivors were counted as victims. Moreover, Kiessling and Danelian (2011) demonstrated that this moderate extinction is even lower than Triassic background extinction in the Radiolaria, and that extinction rates of Radiolaria actually declined from the Triassic to the Jurassic. **See also**: Radiolaria

Marine reptiles suffered extinction of thalattosaurs, nonplesiosaurian sauropterygians (e.g. Placodontia and Nothosauria) and nonparvipelvian ichthyosaurs near the end of the Triassic, but some of these taxa have their last appearance datum already in the Norian, suggesting some temporal offset in comparison to the end-Rhaetian main extinction event (Benson and Butler, 2011). In contrast, fishes probably passed the T–J transition without major faunal changes (McCune and Schaeffer, 1986).

On the land, plant communities suffered temporal ecosystem perturbations across the T–J boundary (McElwain *et al.*, 2009), but only few taxa became finally lost (Ash, 1986; Kelber, 1998). In fact, Rhaetian and Early Jurassic (Liassic) floras are extremely similar in their taxonomic composition and have traditionally been subsumed as 'Rhaetoliassic floras'.

Although it is generally agreed that Jurassic tetrapod communities differed significantly from their Triassic precursors, it is debated whether the principal change occurred already at the end of the Carnian (Benton, 1993), near the end of the Triassic but preceding marine extinction (Lucas *et al.*, 2011), or synchronous with the extinction of other groups around the T–J boundary (Olsen *et al.*, 2002).

Postulated Causes of Extinction

Overview

Before consensus was reached that the principal cause of the end-Triassic mass extinction was linked with CAMP-volcanism (e.g. Whiteside *et al.*, 2010), a variety of other scenarios has been proposed, including the impact of an
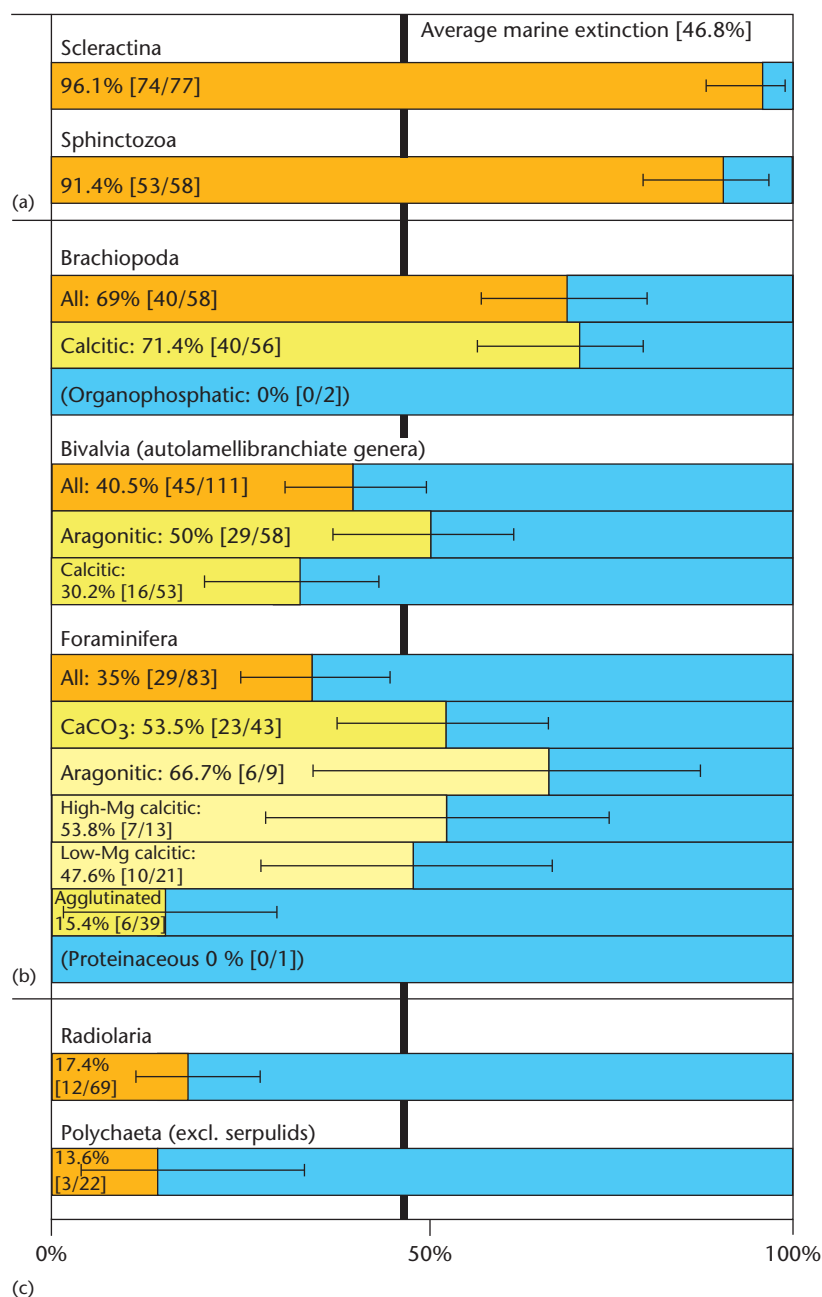
Figure 4 Extinction of genera in taxa with different skeletal physiology. (a) Hypercalcifying taxa with aragonitic and/or high-Mg calcitic skeletal mineralogy and little physiological control of biomineralisation. (b) Extinction in groups with variance in skeletal material, demonstrating increasing extinction risk from noncalcareous skeletons to low-Mg calcitic, high-Mg calcitic and aragonitic skeletal material. (c) Extinction of taxa with noncalcareous skeletons. Error bars indicate 95% binomial confidence intervals. Reproduced with slight modifications from Hautmann et al. (2008a) by permission of Schweizerbart'sche Varlagsbuchhandlung.

extraterrestrial body (Olsen et al., 2002), climatic changes (Fabricius et al., 1970), sea-level changes (Hallam, 1981) and marine anoxia (Hallam, 1981; Hallam and Wignall, 2000). Whereas evidence for an asteroid impact synchronous with the end-Triassic mass extinction rests chiefly on a modest Iridium anomaly from a single locality with poor age control, climatic changes, fluctuation of sea-level

and marine anoxia can all been incorporated in volcanogenic extinction scenarios (e.g. Pálfy, 2003). Additional kill mechanisms resulting from extraordinary magmatic activity include acid rain (Pálfy, 2003), emission or generation of toxic gases (McHone, 2003; van de Schootbrugge et al., 2009) and ocean acidification (Hautmann, 2004; Hautmann et al., 2008a, b). In spite of the wide acceptance

Figure 5 Dendroid scleractinian corals (*Retiophyllia* sp.) in Rhaetian reef limestone (Parvadeh, Lut Desert, east-central Iran). Photo by the author.

of volcanism as the ultimate cause of the end-Triassic mass extinction, there is a lively discussion on which of these possible kill mechanisms had the largest impact on the latest Triassic biota.

Apart from sea-level changes, which possibly reflect a lithosphere bulging-collapse couplet in response to magmatic activity (Pálfy, 2003), all currently discussed kill mechanisms are directly or indirectly related to volcanic gas emissions. The well-known chemical composition of basaltic lavas including the content of volatiles allows direct calculation of absolute volatile emissions from the volume of magmatic rocks (**Table 1**; McHone, 2003). However, these values do not directly translate into atmospheric concentrations, because atmospheric lifetimes for most of these gases are much shorter than the total interval of volcanic degassing. Nevertheless, the short-lived nature and large extent of the main extrusion events concentrated at the T–J boundary (Marzoli *et al.*, 2011) suggest a significant atmospheric build-up of each of these gases. For CO_2, additional release from thermally dissociated marine gas hydrates has been postulated in order to explain changes in the carbon isotope record (Beerling and Berner, 2002). Actual CO_2 palaeoconcentrations in the atmosphere have been inferred from changes in the stomatal density of land plants and on the basis of geochemical methods. A recent palaeobotanic estimate suggests a maximum CO_2 concentration of 2750 ppmv (Bonis *et al.*, 2010), whereas maximum concentrations between 4400 (Schaller *et al.*, 2011) and nearly 6000 ppmv (Yapp and Poth, 1996) have been suggested based on carbon isotope compositions of the $Fe(CO_3)OH$ component in pedogenic oolithic goethites. **See also**: Global Carbon Cycle

Sea-level changes

The idea that sea-level falls might have caused marine extinction events goes back to Newell (1967), who noted a repeated coincidence between sea-level lowstands and marine mass extinctions. The rationale behind this model is

Table 1 Estimation of volatile emission from CAMP-volcanism

Gas	Total emission from CAMP (tons)
CO_2	5.19E + 12
SO_2	2.31E + 12
F	1.11E + 12
Cl	1.58E + 12
H_2O	3.65E + 13

Source: McHone (2003).

that regressions reduce the area of shallow marine habitats where marine biodiversity is concentred, and thus the number of marine taxa according to the well-known species–area relationship. However, it has been doubted whether the effect of reduced shelf areas was sufficient to explain the magnitude of mass extinction events, not the last because many regressions in Earth's history were not associated with significant marine extinctions (see review in Hallam and Wignall, 1997). A regression–transgression couplet during the T–J transition has been described for many palaeogeographically distant areas and first been proposed as a possible cause of the T–J extinction event by Hallam (1981) and Hallam and Goodfellow (1990). However, Hallam (1981) added that the spread of anoxic bottom waters during the Hettangian transgression might have had a bigger impact on marine extinction than the preceding, relatively modest regression (see later discussion). **See also**: Sea Level Change

Marine anoxia

In the 1990s, scenarios of widespread marine anoxia as the ultimate kill mechanism in many of the big Phanerozoic mass extinction event replaced the prevalence of sea-level-related extinction scenarios. For the end-Triassic mass extinction, Hallam and Wignall (1997) summarised evidence for the spread of anoxic bottom waters during the basal most Jurassic as a possible cause of this event. Wignall (2001) later incorporated the anoxia model in volcanogenic extinction scenarios by suggesting that global warming in response to volcanogenic CO_2 exhalations caused a decrease in the equator-to-pole temperature gradient and thus in oceanic circulation, ultimately leading to oxygen deficient bottom waters. However, detailed stratigraphic analyses have shown that early Jurassic black shales in the western United States notably postdate the extinction event (Guex *et al.*, 2004). In the Northern Calcareous Alps, laminated shales near the extinction horizon are superficially suggestive for anoxic–dysoxic conditions but actually contain assemblages of epifaunal and shallow burrowing bivalves that indicate well-oxygenated conditions (McRoberts *et al.*, in press). Moreover, Ruhl *et al.* (2010) have shown that increased organic matter in these shales was from terrestrial rather than marine sources. Thus, whereas marine anoxia may have locally contributed

to marine mass extinction, it is unlikely that they were the main or sole cause of the end-Triassic crisis.

Toxic elements and compounds

Fluorine (F) is highly poisonous and may directly kill organisms around the volcanically active areas (McHone, 2003). Moreover, large ejections of halogens (Cl and F) can lead to ozone depletion (Sigurdsson, 1990) and, by reaction with H_2O, make rainfall acidic, thus attaining interregional to global environmental impact. **Table 1** shows the amounts of F and Cl presumable released to the atmosphere by CAMP, which are clearly high enough for harming life if released within a short time interval. Moreover, van de Schootbrugge *et al.* (2009) found an enrichment of poly-cyclic aromatic hydrocarbons near the T–J boundary in terrestrial settings of north-western Europe, which they interpreted as the result of incomplete combustion of organic matter by ascending magma. They suggested that these toxic compounds in addition to SO_2 have contributed to the extinction event. However, the actual role of toxic elements and compounds in the end-Triassic extinction event is hard to test because no particular selectivity in extinction pattern can be predicted.

Short-term cooling

Although SO_2 is a greenhouse gas, it rapidly forms sulfate aerosols in the atmosphere that absorb or backscatter sunlight (e.g. Wignall, 2001). The net effect is that SO_2 causes pronounced climatic cooling, provided that SO_2 was ejected high enough into the atmosphere for allowing glo-bal dispersion. Although the residence time of sulfur-based aerosols in the atmosphere is short (Pyle *et al.*, 1996), the enormous amount of sulfur ejections form CAMP (**Table 1**) suggest that it might have played an important role in the end-Triassic mass extinction (McHone, 2003; Guex *et al.*, 2004). In support of the cooling hypothesis, Kiessling *et al.* (2007) found a somewhat higher extinction quota for tropical genera, although they concluded that latitudinal preferences were not a dominant factor in the end-Triassic mass extinction.

Global warming

The well-known greenhouse effect of CO_2 is diametrically opposed to the cooling effect of sulfur-based aerosols. Because both effects operate over very different timescales due to the much longer atmospheric residence time of CO_2 in comparison to sulfate aerosols, it is predicted that long-term global warming followed initial cooling after major volcanic events (Wignall, 2001). Surprisingly, little effort has been undertaken to quantify temperature changes across the T–J boundary by means of oxygen isotopes except for the studies of Hallam and Goodfellow (1990) and Morante and Hallam (1996), which however used oxygen data from carbonates that were probably diag-enetically altered, as stated by these authors. Evidence for increased temperatures, therefore, rests chiefly on the quantification of palaeo-CO_2 concentrations in the atmosphere, which suggest a sharp increase up to several thousand ppmv (see earlier discussion). However, no spread of tropical taxa into high latitudes in the wake of the extinction event has been documented so far. Thus, although global warming currently is a likely hypothesis, it still awaits confirmation by geochemical and palaeonto-logical data.

Ocean acidification

Increasing atmospheric CO_2 concentrations are partly counterbalanced by increased hydrolysis of this gas in the seawater. In the present-day global carbon cycle, *c*. 40% of the industrial CO_2 release is taken up by the oceans (Zeebe *et al.*, 2008). This uptake changes seawater chemistry by enhancing the hydrogen ion concentration of seawater, a process known as ocean acidification (Caldeira and Wickett, 2003). A direct effect of ocean acidification is a decrease in the concentration of the carbonate ion and consequently a decrease in the saturation state of seawater with respect to calcium carbonate minerals. Present-day seawater would become undersaturated with respect to aragonite at CO_2 concentrations between 1200 and 1700 ppmv and additionally with respect to calcite between 1900 and 2800 ppmv (Feely *et al.*, 2004). Clarifying the potential harm of decreased carbonate saturation on bio-calcifying organisms is an ongoing research agenda in experimental biology and oceanography (e.g. Orr *et al.*, 2009), but relatively few studies have dealt with examples from the palaeorecord. Of these the end-Triassic event is probably the best understood. Palaeobotanical proxies suggest atmospheric CO_2 maxima of up to 2750 ppmv near the T–J boundary (see earlier discussion), which are in an order of magnitude that suffice complete undersaturation of seawater with respect to both aragonite and calcite (Feely *et al.*, 2004). Berner and Beerling (2007) calculated the effect of CAMP-related CO_2 and SO_2 emissions on $CaCO_3$ saturation of seawater, concluding that complete $CaCO_3$ undersaturation of the world's oceans over a period of 20–40 ka was possible, provided that the emissions were short-lived. In support of strongly decreased $CaCO_3$ sat-uration of palaeo-seawater are observations of a global carbonate gap above the extinction horizon in marine strata worldwide (**Figure 3**). Critically, this gap coincides with a negative $\delta^{13}C$ excursion (**Figure 3**) that indicates the injection of isotopically light carbon from volcanism, with a possible addition from dissociated gas hydrates (Beerling and Berner, 2002; Hautmann *et al.*, 2008a; Črne *et al.*, 2011).

A biocalcification crisis in response to ocean acidifi-cation has been demonstrated for marine phytoplankton (van de Schootbrugge *et al.*, 2007) and foraminifers (Clémence *et al.*, 2010). In both groups, calcareous-walled taxa declined during the crisis in favour of organic-walled and agglutinated species, respectively. The extinction pat-tern of marine invertebrates with respect to their skeletal physiology was analysed by Hautmann *et al.* (2008a),

confirming the prediction that taxa with calcareous skeletons were at a higher extinction risk than taxa with non-calcareous skeletons, and that within the calcareous group aragonite as a skeletal mineral was disadvantageous in comparison to the less soluble calcite (**Figure 4**). Other factors identified as determinants for increased extinction risk include hypercalcification and little biological control on biocalcification, providing an explanation for the high extinction quota of reef-forming corals and sphinctozoan sponges (Hautmann *et al.*, 2008a). The selectivity against hypercalcifying taxa suggests that increased energetic costs for biomineralisation during times of reduced $CaCO_3$ saturation were the principal agent of extinction in macroinvertebrates with calcareous skeletons, rather than increased susceptibility for dissolution. Reduction of skeleton/shell size and replacement of skeletal aragonite by calcite therefore appear plausible as evolutionary responses of marine biocalcifiers to ocean acidification. This prediction has been confirmed in several groups of preadapted epifaunal bivalves (Hautmann, 2006), but it has not yet been described from other clades straddling the T–J boundary.

Recovery from the End-Triassic Mass Extinction

Hallam (1996) reported a relatively slow recovery of the marine fauna in Europe, which he attributed to the prevalence of oxygen-deficient facies. This European pattern is contrasted by a nearly instantaneous recovery of level-bottom communities in southern Tibet (Hautmann *et al.*, 2008b), where no signs of environmental stress have been found. However, the ad hoc explanation that environmental stress was the sole determinant for the onset of recovery is probably not the complete account, because reef communities recovered only after a lag phase of 8–10 Ma (Stanley, 2006). It rather appears that apart from the presence/absence of environmental stress there is also a critical threshold of the extinction quota that poses limits on ecosystem recovery, and that this limit was exceeded in the case of reef-forming organisms during the end-Triassic crisis (see **Figure 4a** versus **Figure 4b** for a comparison between reef-organisms and typical level-bottom fauna). Additionally, Hautmann *et al.* (2008b) suggested that the more co-evolved ecological structure of reef communities in comparison to level-bottom communities was another determinant of the pace of recovery. **See also**: Biotic Recoveries after Extinction

The importance of palaeorecord data like that from the end-Triassic crisis for global change scenarios becomes obvious by their comparison with results from experimental biology. On the basis of a tank experiment, Fine and Tchernov (2007, p. 1811) demonstrated that scleractinian corals can survive and recover from decalcification after acidification of the surrounding water, implying that 'corals might survive large-scale environmental change,

such as that expected for the following century'. However, this provoking conclusion does not account for the natural ecological context of corals, where a lack of calcification would corals not only make more susceptible for predation but also disable them to maintain a growing reef structure, undoubtedly the principal basis of their present biodiversity. The lesson from the end-Triassic mass extinction that recovery of reefs from ocean acidification may take up to 10 Ma is thus probably the more realistic prediction. **See also**: Global Change – Contemporary Concerns

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