Middle Phanerozoic mass extinctions and a tribute to the work of Professor Tony Hallam

PAUL B. WIGNALL*† & BAS VAN DE SCHOOTBRUGGE‡

*School of Earth and Environment, University of Leeds, Leeds LS2 9JT, UK
‡Institute of Earth Sciences, Utrecht University, Utrecht, Budapestlaan 4, 3584CD, The Netherlands

Abstract – Tony Hallam's contributions to mass extinction studies span more than 50 years and this thematic issue provides an opportunity to pay tribute to the many pioneering contributions he has made to this field. Early work (1961) on the Jurassic in Europe revealed a link, during the Toarcian Stage, between extinction and the spread of anoxic waters during transgression – the first time such a common leitmotif had been identified. He also identified substantial sea-level changes during other mass extinction intervals with either regression (end-Triassic) or early transgression (end-Permian) coinciding with the extinction phases. Hallam's (1981) study on bivalves was also the first to elevate the status of the end-Triassic crisis and place it amongst true mass extinctions, changing previous perceptions that it was a part of a protracted period of turnover, although debates on the duration of this crisis continue (Hallam, 2002). Conflicting views on the nature of recovery from mass extinctions have also developed, especially for the aftermath of the end-Permian mass extinction. These discussions can be traced to Hallam's seminal 1991 paper that noted the considerable delay in benthic recovery during Early Triassic time and attributed it to the persistence of the harmful, high-stress conditions responsible for the extinction itself. This idea now forms the cornerstone of one of the more favoured explanations for this ultra-low diversity interval.

Keywords: mass extinction, Hallam, anoxia, sea level.

1. Introduction

The 125th Anniversary Meeting of the Geological Society of America was held in Denver in late October 2013. Amongst the many sessions were no less then three devoted to mass extinctions and their aftermath. This research area has been a topical subject of enquiry for over 30 years ever since publication of Alvarez *et al.* (1980), and most large geological meetings now have at least one mass-extinction-themed session. The Denver topical sessions specifically focused on the aftermath of the end-Permian and end-Triassic mass extinctions and the nature of the intervening interval:

> T167. The Road to Recovery—The Nature of Biotic and Geochemical Cycles During the Early Triassic. Organised by Stephen Grasby and Benoit Beauchamp.
>
> T227. Into the Frying Pan: The Early Triassic Hothouse of Pangea and Panthalassa. Organised by Tom Algeo, Arne Winguth and Dave Bottjer.
>
> T238. New Insights into Triassic–Jurassic Transition Events and End-Triassic Mass Extinction. Organised by Rowan Martindale, Morgan Schaller and Jessica Whiteside

This thematic volume gathers together some of the research from these sessions together with overviews

†Author for correspondence: p.wignall@see.leeds.ac.uk

of the current state-of-art in the highly dynamic field of mass extinction studies. Following the initial focus on the dinosaur-killing, end-Cretaceous mass extinction in the 1980s there has been a gradual shift of attention to earlier mass extinctions, with the two mid-Phanerozoic examples, at the end of the Permian and the Triassic periods, being especially topical. Alongside these studies, the extraordinary nature of the aftermath interval in Early Triassic time has also become a subject of intense scrutiny – and this field too has its initiation paper: Hallam (1991).

Hallam's articles feature in many of the debates on middle Phanerozoic extinctions, and this thematic volume provides us with an opportunity to acknowledge his substantial and frequently pioneering contributions. Indeed, many of the current concepts and ideas relating to mass extinctions derive from Hallam's earliest papers; some pre-date the Alvarez *et al.* (1980) starting pistol by nearly 20 years. Here we highlight Hallam's earliest works and show how they have influenced the current and ongoing debates on mass extinctions and their causation. It is worth noting that this review of Hallam's extinction studies just gives a flavour of his enormous and diverse research output that includes themes such as evolution, sea-level change, palaeobiogeography, petroleum source rock origins, palaeoclimatology and the history of science. It would take a much longer contribution than this to evaluate the influence of this impressive oeuvre.

The treatment here is in chronological order of Hallam's mass extinction studies (rather than stratigraphic order) because this allows the evolution of key ideas to be explored and to see their subsequent contribution to the debates in burgeoning fields. So, we begin (at the end!) with the Toarcian crisis of the Early Jurassic.

2. Toarcian extinction

Hallam's earliest studies were on the Liassic strata in and around the United Kingdom, and these allowed him to pioneer the investigation of topics such as trace fossils, facies analysis and sea-level change. Hallam's (1961) paper on sea-level and faunal change in the Early Jurassic Epoch of Europe is especially important because it contains a species-level range chart for marine invertebrates constructed at the level of ammonite zones – a temporal resolution that has rarely been bettered even today. The chart reveals the loss of 64 of 66 benthic species at the base of the Toarcian Stage at a point where black shales, such as the Jet Rock in the UK, become widespread. The link between the two phenomena was immediately apparent, and Hallam concluded that there was a 'mass disappearance followed by a complete renewal of forms [and] It can hardly be a coincidence that this striking change is intimately correlated with the widespread development of finely laminated bituminous shales, signifying bottom conditions unfavourable to benthic organisms.' (Hallam, 1961, p. 154). Thus, was born the idea of a mass extinction linked with the spread of marine anoxia, decades before such ideas became commonplace.

Hallam's subsequent studies have added detail to the timing and nature of the Early Jurassic extinction losses. Thus, extinctions amongst the nektonic ammonites and belemnites were found to occur at the Pliensbachian–Toarcian boundary whilst the benthic losses were a little later, in earliest Toarcian time, at the point at which black shales become extensive (Hallam, 1967, 1976). Amongst a plethora of cogent observations, Hallam noted that the benthic bivalves show little evidence for ecological selectivity amongst the losses (Hallam, 1986). This discovery provides an interesting contrast with extinction selectivity during other crises such as the end-Triassic mass extinction discussed in Section 3 below.

As well as their temporal complexity, the Toarcian extinction losses also show geographic variation, with the timing of the extinction varying from region to region as first shown in Hallam's (1972) study of the Iberian record. Black shales are weakly developed in this region, and some extinction losses in Portugal occur considerably after those in northern Europe. The Lower Jurassic of South America similarly has a dearth of black shales, and this region too shows an extinction history somewhat nonsynchronous with that of northern Europe (Hallam, 1986). Despite this temporal variation, the observation that transgression, anoxia and

marine extinction went hand-in-hand in Early Jurassic time has been shown to be a generally recurring theme during other mass extinctions (Hallam, 1986, 1987, 1989; Hallam & Wignall, 1999) and in some regards can be considered a 'rule' in global biodiversity studies (e.g. Hannisdal & Peters, 2011).

Much current research effort continues to be expended on the Toarcian extinction, with many workers especially concerned with the interpretation given to the substantial carbon isotope oscillations of early Toarcian time and in particular the sharp negative excursion at the same time that black shale deposition became widespread (Hesselbo et al. 2000; Wignall et al. 2006; Harazim et al. 2013). Oxygen isotope data have also shown that the interval was a period of warming (Bailey et al. 2003), and radiometric dating reveals that the crisis coincides with the eruption of a large igneous province (LIP), the Karoo-Ferrar Traps of the Gondwanan continent (Pálfy & Smith, 2000; Svensen et al. 2007).

The Toarcian crisis, thus, has many of the hallmarks of most Phanerozoic mass extinctions: LIP eruption, global warming and $\delta^{13}C$ negative excursions (Hallam & Wignall, 1997), together with transgression and marine anoxia – the two facets that were first identified by Hallam in 1961. The recognition of a temporal complexity to extinction losses also continues to feature as a key issue in understanding this event (e.g. Wignall, Newton & Little, 2005) and especially its relationship with basaltic eruptions (Caruthers, Smith & Gröcke, 2013).

3. End-Triassic mass extinction

Was there a mass extinction at the end of the Triassic Period? Prior to the seminal work of Alvarez et al. (1980) and its catastrophist message, the idea of an abrupt end-Triassic mass extinction had little currency. A major Triassic–Jurassic turnover of terrestrial vertebrates had been identified by the mid-twentieth century but it was thought to be a protracted affair rather than a short-lived crisis. The losses were viewed as 'only a part of a large and extended sequence of events that makes the Triassic period a time span of great significance' (Colbert, 1958, p. 973). In contrast, Newell (1967) considered the end-Triassic to be one of several Phanerozoic mass extinction events that were marked by the rapid loss of many diverse groups. In this case, Newell especially highlighted the coincident loss of numerous ammonoids and reptiles at the end of the Triassic Period, pointing to a crisis on both land and sea. Today Newell's claims are uncontroversial, but at the time they were distinctly at odds with prevailing ideas and had little or no influence on contemporary studies. The idea of gradual change was deeply entrenched: 'the transition from the Triassic to the Jurassic was not marked by sudden, simultaneous extinctions of large numbers of higher order taxa of vertebrates, but instead was a time of gradual faunal replacement' (Olsen & Galton, 1977, p. 985). Indeed, the main changes amongst

tetrapods were placed tens of millions of years earlier, within the Carnian Stage (e.g. Bakker, 1977).

This appreciation profoundly changed with Hallam's evaluation of the marine fossil record (Hallam, 1981), and saw the end-Triassic crisis gain a mass extinction status. Hallam demonstrated that European bivalves show major losses in a geologically brief interval of latest Triassic time. Interestingly, unlike the Toarcian crisis, Hallam showed the extinction was clearly selective, with epifaunal groups showing much greater extinction losses compared with the sediment-dwelling infaunal groups (Hallam, 1981).

Hallam's paper provided clear data that showed the severity of the marine losses and invigorated the debate on the end-Triassic's mass extinction status. The main questions that developed in the 1980s and continue to be addressed to this day are: (1) How severe was this crisis, especially on land? (2) How quickly did it occur? (3) Was it in fact just a minor event in comparison with a much more intense Carnian extinction?

Within a few years of Hallam's 1981 paper, the end-Triassic mass extinction crisis was being ranked alongside the end-Cretaceous event and it even had its own meteorite-impact crater at Manicouagan in Quebec Province (Olsen, Shubin & Anders, 1987). However, the crater is now known to be much too old to be implicated in an end-Triassic extinction, and for many palaeontologists the key extinction happened earlier. Thus, Benton has argued that both marine and terrestrial extinctions were at their most severe within the Carnian Age whereas the end-Triassic losses were both less intense and less sudden – very much a second-rate crisis compared with the earlier event (Benton, 1986, 1991). Late Carnian extinctions removed many taxa from species-rich tetrapod families (e.g. the kannemeyerids and the rhynchosaurs) but the end-Triassic event only removed species-poor families. Thus, Benton concluded that 'The Carnian event unequivocally had greater impact than the end-Triassic event among terrestrial vertebrates' (Benton, 1991, p. 270) and 'the end-Triassic extinction was a whimper' (Benton, 1991, p. 263). These views were very much in keeping with pre-1981 views and have echoes in the earlier opinions of Colbert (1958) and Bakker (1977). More recent reviews have tended to acquiesce with Benton's (e.g. Tanner, Lucas & Chapman, 2004).

Despite these attempts of vertebrate palaeontologists to downgrade or dismiss the status of the end-Triassic terrestrial mass extinction, the marine record clearly shows substantial losses, albeit potentially spread over the last few million years of the Triassic (Hallam, 2002). More recent studies also suggest that the tetrapod extinction may indeed have been a severe but selective one. The diverse and successful pseudosuchians suffered severe end-Triassic losses leaving only crocodylomorphs, which radiated rapidly in Early Jurassic time (Toljagić & Butler, 2013). In contrast dinosaur extinctions were minor (Brusatte *et al.* 2010).

As well as exploring the nature of the marine extinctions, Hallam has also pioneered palaeoenvironmental studies of the Triassic–Jurassic transition interval. The end-Triassic crisis coincided with the onset of a phase of long-term sea-level rise that saw the flooding of extensive low-lying areas in central Pangaea (now western Europe). By the end of Early Jurassic time extensive epicontinental seas had developed, but in the latest Triassic Rhaetian Age this flooding had only just begun, and it is within Rhaetian strata that the extinction record is preserved. Thus, the relationship between sea-level change and extinction at the end of the Triassic Period is enigmatic. Hallam (1981) considered Rhaetian eustasy to be the culmination of a first-order lowstand with a superimposed second-order transgressive–regressive couplet. The terminal Rhaetian regression is mostly clearly manifest as a karst surface developed atop reefs in the Austrian Alps (Satterley, Marshall & Fairchild, 2006).

There is, thus, a temporal link between regression and extinction at the end of the Triassic Period and the notion that the two phenomena are causally linked has a long pedigree. It was first explicitly proposed by Newell (1967). The idea derives from MacArthur and Wilson's species-area effect and it suggests that, as shallow seas retreat and shallow-marine habitat areas are lost, marine extinction rates increase (although the concept clearly cannot be invoked to cause terrestrial losses). The general link between sea level and diversity is a recurrent and disputed theme in biodiversity studies (e.g. Hallam, 1977; Hallam & Wignall, 1999; Hannisdal & Peters, 2011; Smith, 2007). The link at the end of the Triassic Period is complicated because the terminal Rhaetian regression was swiftly followed by the rapid spread of anoxic bottom waters, a phenomenon that could have been also bound up in the extinction and its aftermath (Hallam, 1981, 1995; Richoz *et al.* 2012). Summing up the difficulties of disentangling the key factor, Hallam noted that: 'Because such transgressions normally follow quickly after major regressions, it is not always clear from analysis of extinction events what the critical causal factor was, although in both cases [regression and transgression-with-anoxia] there would have been a reduction in benthic and nektobenthic habitable area.' (Hallam, 1989, p. 443).

Subsequent studies by Hallam and other workers have added to, and to some extent, clarified the possible culprits for the end-Triassic mass extinction. Analysis of the rate and regional variation of sea-level change has provided further, indirect evidence of a potential smoking gun. The Rhaetian sea-level changes seen in Europe, with their regressive–transgressive couplet around the end of the Triassic Period are only weakly manifest in North America (Hallam & Wignall, 2000) and are not seen at all in South America (Hallam, 1989) nor in the Perigondwanan sections of southern Tibet (Hallam *et al.* 2000) where the story is one of gradual sea-level rise across the Triassic–Jurassic boundary (Hallam & Wignall, 1999).

Rates of sea-level change across the Triassic–Jurassic boundary in western and central Europe (but not further afield) are too fast to be attributed to

normal eustatic drivers such as changes in mid-ocean ridge spreading rates (Hallam, 1997). Instead, they can be linked with North Atlantic tensional tectonic activity 'where it is associated with substantial basaltic activity' (Hallam, 1997 p. 777) and widespread deformed horizons that probably formed as a consequence of this activity (Hallam & Wignall, 2004).

Studies of the fragments of a flood basalt province now found in Morocco, Spain, Brazil and the United States have borne out Hallam's claim of 'substantial basaltic activity'. This volcanism is now recognized as the Central Atlantic Magmatic Province, or CAMP, and it is one of the largest of all LIPs with an eruption onset that appears to closely coincide with the mass extinction (Marzoli *et al.* 1999; Wignall, 2005; van de Schootbrugge *et al.* 2009; Pálfy & Kocsis, 2014; Bachan & Payne, 2015, this issue).

4. End-Permian mass extinction and its aftermath

Whilst the role of widespread marine anoxia during the end-Triassic crisis is enigmatic, there is a much more clear-cut link between anoxia and the end-Permian mass extinction. Hallam's work in collaboration with one of us (PBW) was the first to show the close synchrony between the spread of marine anoxia and the marine extinction losses (Wignall & Hallam, 1992, 1993). There are, however, close parallels between Triassic–Jurassic and Permian–Triassic events: sea-level changes for both show a regression–transgression couplet (Hallam & Wignall, 1999). The contrast is that whilst the end-Permian losses occurred during the transgressive–anoxic phase of the sea-level cycle, the end-Triassic losses were during the preceding regression. Summing up, Wignall & Hallam (1992, p. 43) concluded that, 'the disappearance of Permian faunas at the end of the period is abrupt, taking place not at the level of regression but shortly above, associated with a major transgression [and] dysaerobic to anaerobic conditions'.

The concept of an 'abrupt' end-Permian mass extinction was, in the early 1990s, counter to the widely held view of a protracted extinction spanning several million years (e.g. Teichert, 1990). It has subsequently proved to be a rather non-controversial claim. It is certainly less contentious than the notion that there was an abrupt end-Triassic extinction. Most studies of the past 20 years have viewed the end-Permian crisis to have taken place in a geologically short period of time, probably only a few tens of thousands of years at most (e.g. Kaiho *et al.* 2006): the latest radiometric dates suggest 60 ka (Burgess, Bowring & Shen, 2014). However, detailed study of marine sections has revealed that the crisis in South China can be resolved into two separate extinction events straddling the Permian–Triassic boundary (Song *et al.* 2013). It may be that the discrete extinction intervals were much shorter than this (a few thousand years?) and it is their spacing that is measured in tens of thousands of years.

The parallels between the end-Permian and the end-Triassic and Toarcian extinctions are manifold, but it is the aftermath of the crisis that marks the end-Permian crisis out as a uniquely severe event. Hallam investigated the fortunes of bivalves with Miller and revealed the peculiar nature of the Early Triassic aftermath fauna. Rather than marking a recovery and diversification phase, there was instead a prolonged phase of low diversity throughout Early Triassic time followed by the reappearance of many bivalves in Middle Triassic time that had not been seen since Permian time (Hallam & Miller, 1988). Hallam returned to this theme in 1991 in a short but influential paper in which he suggested that the long-delayed recovery was caused by the prolonged duration of the harsh conditions (such as marine anoxia) that had triggered the mass extinction (Hallam, 1991). Subsequent study has confirmed that the Early Triassic Epoch was indeed marked by one of the most prolonged and intense phases of Phanerozoic oceanic anoxia (Isozaki, 1997; Wignall *et al.* 2010, 2015, this issue).

As with all major topics, the nature of the Early Triassic world, its biota and the role of environmental constraints on radiation have been the subject of intense debate. There are currently three distinct viewpoints:

(1) The Early Triassic world was a harsh one that inhibited the recovery of all but a few hardy groups (Hallam's original idea). The recognition of extremely hot conditions at this time (Sun *et al.* 2012), alongside the widespread anoxia, adds credence to this stance as do studies of the recovery record in South China (Song *et al.* 2015, this issue).

(2) The Early Triassic world was normal but the preceding extinction had caused such devastation that it took a long time for the biota to even start to recover. This viewpoint can be traced back to a highly influential paper by Schubert & Bottjer (1992). They identified the extraordinary abundance of stromatolites in Early Triassic time and argued that the dearth of grazers, such as gastropods, following the mass extinction allowed cyanobacteria to flourish.

(3) The Early Triassic world was normal as was the recovery, which proceeded untrammelled. For this 'nothing unusual' view see the recent study of Hofman *et al.* (2013) on the post-extinction record in the US Rockies.

Clearly these are all discordant views and the debates continue, but it was Hallam's characteristically perceptive thoughts that sparked this research field. To some extent, the most recent studies suggest some compromise between these alternatives with an initial early harsh environmental phase followed by the first hints of recovery in early Olenekian time only to be pegged back by a resultant crisis around the Smithian–Spathian boundary (e.g. Song *et al.* 2011). But the original observation of Hallam remains pertinent – alpha diversity in Early Triassic environments was exceptionally low. It remains to be seen if a consensus develops or whether, like the end-Triassic extinction, the same themes are still being debated in the decades to come.

References

ALVAREZ, L., ALVAREZ, W., ASARO, F. & MICHEL, H. V. 1980. Extraterrestrial cause for the Cretaceous–Tertiary extinction – experimental results and theoretical implications. *Science* **208**, 1095–108.

BACHAN, A. & PAYNE, J. 2015. Modelling the impact of pulsed CAMP volcanism on pCO$_2$ and δ^{13}C across the Triassic–Jurassic transition. *Geological Magazine*.

BAILEY, T. R., ROSENTHAL, Y., MCARTHUR, J. M., VAN DE SCHOOTBRUGGE, B. & THIRLWALL, M. F. 2003. Paleoceanographic changes of the Late Pliensbachian–Early Toarcian interval: a possible link to the genesis of an Oceanic Anoxic Event. *Earth and Planetary Science Letters* **212**, 307–20.

BAKKER, R. T. 1977. Tetrapod mass extinctions – a model of the regulation of speciation rates and immigration by cycles of topographic diversity. In *Patterns of Evolution as Illustrated in the Fossil Record* (ed. A. Hallam), pp. 439–68. Amsterdam: Elsevier.

BENTON, M. J. 1986. More than one event in the late Triassic mass extinction. *Nature* **321**, 857–61.

BENTON, M. J. 1991. What really happened in the Late Triassic? *Historical Biology* **5**, 263–78.

BRUSATTE, S. L., NESBITT, S. J., IRMIS, R. B., BUTLER, R. J., BENTON, M. J. & NORELL, M. A. 2010. The origin and early radiation of dinosaurs. *Earth-Science Reviews* **101**, 68–100.

BURGESS, S. D., BOWRING, S. & SHEN, S.-Z. 2014. High-precision timeline for Earth's most severe extinction. *Proceedings of the National Academy of Sciences* **111**, 3316–21.

CARUTHERS, A. H., SMITH, P. L. & GRÖCKE, D. R. 2013. The Pliensbachian–Toarcian (Early Jurassic) extinction, a global multi-phased event. *Palaeogeography, Palaeoclimatology, Palaeoecology* **386**, 104–18.

COLBERT, E. H. 1958. Tetrapod extinctions at the end of the Triassic Period. *Proceedings of the National Academy of Sciences* **44**, 973–7.

HALLAM, A. 1961. Cyclothems, transgressions and faunal change in the Lias of north-west Europe. *Transactions of the Edinburgh Geological Society* **18**, 124–74.

HALLAM, A. 1967. An environmental study of the Upper Domerian and Lower Toarcian in Great Britain. *Philosophical Transactions of the Royal Society* **B 252**, 393–455.

HALLAM, A. 1972. Diversity and density characteristics of Pliensbachian–Toarcian molluscan and brachiopod faunas of the North Atlantic. *Lethaia* **5**, 389–412.

HALLAM, A. 1976. Stratigraphic distribution and ecology of European Jurassic bivalves. *Lethaia* **9**, 245–59.

HALLAM, A. 1977. Jurassic bivalve biogeography. *Paleobiology* **3**, 58–73.

HALLAM, A. 1981. The end-Triassic bivalve extinction event. *Palaeogeography, Palaeoclimatology, Palaeoecology* **35**, 1–44.

HALLAM, A. 1986. The Pliensbachian and Tithonian extinction events. *Nature* **319**, 765–8.

HALLAM, A. 1987. Radiations and extinctions in relation to environmental change in the marine Lower Jurassic of north-west Europe. *Paleobiology* **13**, 152–68.

HALLAM, A. 1989. The case for sea level as a dominant causal factor in mass extinction of marine invertebrates. *Philosophical Transactions of the Royal Society* **B 325**, 437–55.

HALLAM, A. 1991. Why was there a delayed radiation after the end-Palaeozoic crisis? *Historical Biology* **5**, 257–62.

HALLAM, A. 1995. Oxygen-restricted facies of the basal Jurassic of north west Europe. *Historical Biology* **10**, 247–57.

HALLAM, A. 1997. Estimates of the amount and rate of sea-level change across the Rhaetian–Hettangian and Pliensbachian–Toarcian boundaries (latest Triassic to earliest Jurassic). *Journal of the Geological Society, London* **154**, 773–9.

HALLAM, A. 2002. How catastrophic was the end-Triassic mass extinction? *Lethaia* **35**, 147–57.

HALLAM, A. & MILLER, A. I. 1988. Extinction and survival in the Bivalvia. In *Extinction and Survival in the Fossil Record* (ed. G. P. Larwood), pp. 121–38. Systematics Association Special Volume **34**. Oxford: Clarendon Press.

HALLAM, A. & WIGNALL, P. B. 1997. *Mass Extinctions and their Aftermath*. Oxford: Oxford University Press, 320 pp.

HALLAM, A. & WIGNALL, P. B. 1999. Mass extinctions and sea-level changes. *Earth-Science Reviews* **48**, 217–50.

HALLAM, A. & WIGNALL, P. B. 2000. Facies change across the Triassic–Jurassic boundary in Nevada, USA. *Journal of the Geological Society, London* **156**, 453–6.

HALLAM, A. & WIGNALL, P. B. 2004. Discussion on sea-level change and facies development across potential Triassic–Jurassic boundary horizons, SW Britain. *Journal of the Geological Society, London* **161**, 1–4.

HALLAM, A., WIGNALL, P. B., YIN, J. & RIDING, R. 2000. An investigation into possible facies changes across the Triassic–Jurassic boundary in southern Tibet. *Sedimentary Geology* **137**, 101–6.

HANNISDAL, B. & PETERS, S. E. 2011. Phanerozoic Earth system evolution and marine biodiversity. *Science* **334**, 1121–4.

HARAZIM, D., VAN DE SCHOOTBRUGGE, B., SORICHTER, K., FIEBIG, J., WEUG, A., SUAN, G. & OSCHMANN, W. 2013. Spatial variability of watermass conditions within the European Epicontinental Seaway during the Early Jurassic (Pliensbachian–Toarcian). *Sedimentology* **60**, 359–90.

HESSELBO, S. P., GRÖCKE, D. R., JENKYNS, H. C., BJERRUM, C. J., FARRIMOND, P., MORGANS BELL, H. S. & GREEN, O. R. 2000. Massive dissociation of gas hydrate during a Jurassic oceanic anoxic event. *Nature* **406**, 392–5.

HOFMAN, R., HAUTMANN, M., WASMER, M. & BUCHER, H. 2013. Palaeoecology of the Spathian Virgin Formation (Utah, USA) and its implications for the Early Triassic recovery. *Acta Palaeontologica Polonica* **58**, 149–73.

ISOZAKI, Y. 1997. Permo-Triassic boundary superanoxia and stratified superocean: records from lost deep sea. *Science* **276**, 235–8.

KAIHO, K., CHEN, Z.-Q., KAWAHATA, H., KAJIWARA, Y. & SATO, H. 2006. Close-up of the end-Permian mass extinction recorded in the Meishan section, South China: sedimentary, elemental, and biotic characterization and a negative shift of sulfate sulfur isotope ratio. *Palaeogeography, Palaeoclimatology, Palaeoecology* **239**, 396–405.

MARZOLI, A., RENNE, P. R., PICCIRILLO, E. M., ERNESTO, A., BELLIENI, G. & DE MIN, A. 1999. Extensive 200-million-year-old continental flood basalts of the Central Atlantic Magmatic Province. *Science* **284**, 616–8.

NEWELL, N. D. 1967. Revolutions in the history of life. In *Uniformity and Simplicity: A Symposium on the Principle of the Uniformity of Nature* (ed. C.C. Albritton), pp. 63–91. Geological Society of America, Special Papers 89.

OLSEN, P. E. & GALTON, P. M. 1977. Triassic–Jurassic tetrapod extinctions: are they real? *Science* **197**, 983–6.

OLSEN, P. E., SHUBIN, N. H. & ANDERS, M. H. 1987. New Early Jurassic tetrapod assemblages constrain Triassic–Jurassic tetrapod extinction event. *Science* **237**, 1025–9.

PÁLFY, J. & KOCSIS, A. T. 2014. Volcanism of the Central Atlantic magmatic province as the trigger of environmental and biotic changes around the Triassic–Jurassic boundary. In *Volcanism, Impacts, and Mass Extinctions: Causes and Effects* (eds G. Keller & A. C. Kerr), pp. 245–61. Geological Society of America, Special Papers 505.

PÁLFY, J. & SMITH, P. L. 2000. Synchrony between Early Jurassic extinction, oceanic anoxic event, and the Karoo-Ferrar flood basalt volcanism. *Geology* **28**, 747–50.

RICHOZ, S., VAN DE SCHOOTBRUGGE, B., PROSS, J., PÜTTMAN, W., QUAN, T. M., LINDSTRÖM, S., HEUNISCH, C., FIEBIG, J., MAQUIL, R., SCHOUTEN, S., HAUZENBERGER, C. A. & WIGNALL, P. B. 2012. Hydrogen sulphide poisoning of shallow seas following the end-Triassic extinction. *Nature Geoscience* **5**, 662–7.

SATTERLEY, A. K., MARSHALL, J. D. & FAIRCHILD, I. J. 2006. Diagenesis of an Upper Triassic reef complex, Wilde Kirche, Northern Calcareous Alps, Austria. *Sedimentology* **41**, 935–50.

SCHUBERT, J. K. & BOTTJER, D. J. 1992. Early Triassic stromatolites as post-mass extinction disaster forms. *Geology* **20**, 883–6.

SMITH, A. B. 2007. Marine diversity through the Phanerozoic: problems and prospects. *Journal of the Geological Society, London* **164**, 731–45.

SONG, H.-J., TONG, J.-N., WIGNALL, P. B., LUO, M., TIAN, L., SONG, H.-Y., HUANG, Y.-F. & CHU, D.-L. 2015. Early Triassic disaster and opportunistic foraminifers in South China. *Geological Magazine*.

SONG, H.-J., WIGNALL, P. B., CHEN, Z.-Q., TONG, J.-N., BOND, D. P. G., LAI, X.-L., ZHAO, X.-M., JIANG, H.-S., YAN, C.-B., NIN, Z.-J., CHEN, J., YANG, H. & WANG, Y.-B. 2011. Recovery tempo and pattern of marine ecosystems after the end-Permian mass extinction. *Geology* **39**, 739–42.

SONG, H.-J., WIGNALL, P. B., TONG, J.-N. & YIN, H.-F. 2013. Two pulses of extinction during the Permian–Triassic crisis. *Nature Geoscience* **6**, 52–6

SUN, Y.-D., JOACHIMSKI, M. M., WIGNALL, P. B., YAN, C.-B., CHEN, Y.-L., JIANG, H.-S., WANG, L.-N. & LAI, X.-L., 2012. Lethally hot temperatures during the Early Triassic greenhouse. *Science* **388**, 366–70.

SVENSEN, H., PLANKE, S., CHEVALLIER, L., MALTHE-SØRENSSEN, A., CORFU, F. & JAMTVEIT, B. 2007. Hydrothermal venting of greenhouse gases triggering Early Jurassic global warming. *Earth and Planetary Science Letters* **256**, 554–66.

TANNER, L. H., LUCAS, S. G. & CHAPMAN, M. G. 2004. Assessing the record and causes of Late Triassic extinctions. *Earth-Science Reviews* **65**, 103–39.

TEICHERT, C. 1990. The Permian–Triassic boundary revisited. In *Extinction Events in Earth History* (eds E. G. Kauffman & O. H. Walliser), pp. 199–238. Berlin: Springer-Verlag.

TOLJAGIĆ, O. & BUTLER, R. J. 2013. Triassic-Jurassic mass extinction as a trigger for the Mesozoic radiation of crocodylomorphs. *Biological Letters* **9**, doi: 10.1098/rsbl.2013.0095.

VAN DE SCHOOTBRUGGE, B., QUAN, T. M., LINDSTRM, S., PTTMANN, W., HEUNISCH, C., PROSS, J., FIEBIG, J., PETCHICK, R., RHLING, H.-G., RICHOZ, S., ROSENTHAL, Y. & FALKOWSKI, P. G. 2009. Floral change across the Triassic/Jurassic boundary linked to flood basalt volcanism. *Nature Geoscience* **2**, 589–94.

WIGNALL, P. B. 2005. The link between large igneous province eruptions and mass extinctions. *Elements* **1**, 293–7.

WIGNALL, P. B., BOND, D. P. G., KUWAHARA, K., KAKUWA, K., NEWTON, R. J. & POULTON, S. W. 2010. An 80 million year oceanic redox history from Permian to Jurassic pelagic sediments of the Mino-Tamba terrane, SW Japan, and the origin of four mass extinctions. *Global and Planetary Change* **71**, 109–23.

WIGNALL, P. B., BOND, D. P. G., SUN, Y. D., GRASBY, S. E., BEAUCHAMP, B., JOACHIMSKI, M. M. & BLOMEIR, D. P. G. 2015. Ultra-shallow marine anoxia in an Early Triassic storm-dominated clastic ramp (Spitsbergen) and the suppression of benthic radiation. *Geological Magazine*.

WIGNALL, P. B. & HALLAM, A. 1992. Anoxia as a cause of the Permian/Triassic extinction: facies evidence from northern Italy and the western United States. *Palaeogeography, Palaeoclimatology, Palaeoecology* **93**, 21–46.

WIGNALL, P. B. & HALLAM, A. 1993. Griesbachian (Earliest Triassic) palaeoenvironmental changes in the Salt Range, Pakistan and south-east China and their bearing on the Permo-Triassic mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* **102**, 215–37.

WIGNALL, P. B., HALLAM, A., NEWTON, R. J., SHA, J.-G., REEVES, E., MATTIOLI, E. & CROWLEY, S. 2006. An eastern Tethyan (Tibetan) record of the Early Jurassic (Toarcian) mass extinction event. *Geobiology* **4**, 179–90.

WIGNALL, P. B., NEWTON, R. A. & LITTLE, C. T. S. 2005. The timing of paleoenvironmental change and cause-and-effect relationships during the Early Jurassic mass extinction in Europe. *American Journal of Sciences* **305**, 1014–32.