The End-Permian Mass Extinction: Nature's Revolution

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Abstract

Several localities around the world expose successions of rocks that straddle the Permian–Triassic boundary documenting a common pattern of environmental change. This change testifies to a large-scale event that led to the extinction of a significant portion of biodiversity, the most severe mass extinction of all times. This event is called the End-Permian Mass Extinction (EPME) or the Permian–Triassic Mass Extinction and was likely triggered by extensive volcanism. It not only affected the biodiversity of the marine realm, but also the terrestrial environments where faunas showed a marked reduction in diversity, whereas evidence for a mass extinction among plants is less robust. Even if the synchronicity of the extinctions in terrestrial and marine environments is still controversial, it seems clear that the event itself was rather fast, and that it took several million years for life to recover completely from the crisis. In fact, it seems likely that massive volcanic eruptions not only caused a chain of reactions that led to the extinction but also hindered the recovery of most of the surviving taxa. The EPME changed life forever, and the following recovery saw the evolution and radiation of many modern taxa that still characterize our planet today.

10.1 Introduction

The End-Permian Mass Extinction (EPME) (also known as Permian–Triassic Mass Extinction, PTME) is one of the most studied geobiological events of the past. It is the most severe mass extinction of all life—"the mother of all extinctions"—and promoted the evolution of modern ecosystems (e.g., Raup and Sepkoski 1982; Erwin 1993, 2006). Hundreds of scientific papers have been written on the topic (see Fig. 1 in Twitchett 2006), and the conclusions of these studies have been summarized in popular books with apocalyptic titles like "When life nearly ended: The greatest mass extinction of all time" (Benton 2005) and "Extinction: How life on Earth nearly ended 250 million years ago" (Erwin 2006). Popular books and TV documentaries are a clear sign that this topic is not only the "intellectual exercise" for a large group of scientists, but that it conveys so many deep implications about our world today that it has the potential of attracting the general public. This is especially true in a time of global warming and, hopefully, increasing environmental awareness.

*The asterisk designates terms explained in the Glossary.

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The vast amount of data available for the EPME and the numerous congruent hypotheses developed in the last decades to explain its dynamics provide us today with an excellent model to describe what happened when a global ecosystem crisis pushed life close to complete annihilation, about 252 million years ago (Chen and Benton 2012). In an excellent overview, still broadly valid even if written about 15 years ago (Benton and Twitchett 2003), three aspects were highlighted as key for understanding the EPME: the scale and pattern of species loss, what combination of environmental changes could possibly have had such a devastating effect, and the pattern of the recovery. Here, we will provide an updated account of such key event for the evolution of life as currently known.

10.2   The Magnitude of Species Loss

The rate and the pattern of species loss is one of the main questions about this event. This is not an easy question to answer actually, because it is time-dependent and, therefore,

needs precise dating of the rocks and fossil associations preserved therein. According to the most recent version of the International Chronostratigraphic Chart (v2019/5; Cohen et al. 2018), the boundary between the late Permian and the Early Triassic is set at a CA-ID-TIMS Uranium-Lead derived age of 251.902 ± 0.024 million years ago. Such CA-ID-TIMS analyses of a population of single-crystal zircons from a horizon or bed provide the highest resolution age estimate for its emplacement. The age of the end-Permian event has been determined in China, at the reference locality for the Permian–Triassic Boundary (PTB). The locality is called Meishan and is placed in Changxing County, Zhejiang Province (Fig. 10.1). It is one of several Global Stratotype Sections and Points (GSSP), where a "golden spike" was literally fixed into the sedimentary succession to mark the exact position of the boundary. In Meishan, each of the limestone and mudstone beds in the succession has been given a number in ascending stratigraphic order. In this succession, the PTB is placed at the base of Bed 27c, which records a deep marine environment from where the first occurrence of the conodont species *Hindeodus parvus* is documented (Yin et al. 2001). However,

Fig. 10.1 The Global Stratotype Section and Point (GSSP) of the Permian–Triassic boundary is located at Meishan (Changxing County, Zhejiang Province) where a monumental garden has been created to celebrate the relevance of the outcrop in Earth history. Photo by Robert A Gastaldo

the extinction is not a one-time or one-level event. It has a sort of a prelude at the base of Bed 24e, a main episode corresponding to Bed 25, and an epilogue at Bed 28 (Yin et al. 2007a). Thanks to the extremely precise dating available in these rocks, we now know that the extinction peak occurred about 40,000 years before the horizon marking the PTB (Burgess et al. 2014; Burgess and Bowring 2015). The whole event was extremely fast in geological terms, with a duration of about 60,000 years (e.g., Brand et al. 2012; Burgess et al. 2014; Shen et al. 2018). Data from other sections, as in the Dolomites of northeast Italy, indicate that the event could have been even more rapid, with a duration of a few millennia (see Brand et al. 2012; Posenato 2019). According to the interpretations of various results of different studies, the extinction events in continental ecosystems occurred over a time span as short as 10,000 years or across a much longer interval of up to 200,000 years (Smith and Botha-Brink 2014, and literature therein). In any case, the rock record clearly indicates that sedimentary strata, in which marine or terrestrial organisms are preserved, are rich in fossils. These fossil assemblages testify to the presence of well-structured communities for most of the late Permian (Lopingian) (Erwin 1993; Bernardi et al. 2017) when the action of marine communities that lived on and in the sediment is registered by intense bioturbation of the ocean floor, indicating oxic conditions (Benton and Twitchett 2003). However, close to the end of the Permian, the oceans around the world record sediments that reflect dysoxic∗ or anoxic∗ conditions. These resulted in the production of non-bioturbated, laminated∗, dark, and pyrite-rich sediments that are scarcely fossiliferous in the marine realm (Wignall and Twitchett 2002; Benton and Twitchett 2003). Degraded terrestrial environments from the same time interval testify to erosion following the reported loss of vegetation (Benton and Newell 2014). Such rocks indicate that, before the PTB, the environmental conditions began to deteriorate, resulting in increasing stress in the biotic communities. Was the end-Permian event limited to the marine realm or did it affect also continental organisms?

According to some research (e.g., Smith and Botha-Brink 2014; Cascales-Miñana et al. 2016), the EPME is the only one of the five major extinction events in the marine realm that "coincided" with a clear and abrupt decrease in continental biodiversity. It is also the only mass extinction thought to have had devastating effects on vegetation at a global scale (but see Nowak et al. 2019). In fact, peat-accumulating wetlands (see Gastaldo et al., Chap. 12) were absent on the landscape for more than ten million years; and, therefore, Early Triassic coals are unknown, except in western China (Thomas et al. 2011), and Middle Triassic coals are rare and thin. Their absence has been termed the "coal gap" by Retallack et al. (1996). But is the concept of coincident diversity loss in the oceans and on land accurate?

The terrestrial vertebrate-fossil record in the Karoo Basin, South Africa (Fig. 10.2), has acted as the cornerstone on which the end-Permian extinction event is recognized on land. Having been considered the standard for understanding the end-Permian turnover in terrestrial ecosystems, any new data that can be used to constrain "time" on land in the Karoo Basin helps to tie together global events. Smith and Botha-Brink (Smith and Botha-Brink 2014; but see also Gastaldo and Neveling 2016) proposed that there were three phases of drought-induced extinctions lasting, respectively (from the oldest), 21,000, 33,000, and 8000 years, separated by periods of 7000 and 50,000 years, over a timeframe equivalent, and coincident with, the marine event (see Fig. 12 in Smith and Botha-Brink 2014). The model has been extrapolated to other parts of the globe (e.g., Benton and Newell 2014) where this polyphased extinction resulted in the decimation of most vertebrate taxa. In the Karoo Basin, the most recognizable vertebrates that went extinct are probably the medium-sized dicynodont therapsid *Dicynodon* and the large gorgonopsid therapsid *Rubidgea* (see also, among others, Retallak et al. 2003; Ward et al. 2005). But, the term "coincident" loss may not be appropriate because, as remarked by Padian (2018) and Fielding et al. (2019), there is growing evidence for a series of events on land that are not synchronous with those that occurred in the oceans. For example, Gastaldo et al. (2015, p. 939) presented the first high precision age on strata close to the inferred PTB in the Karoo Basin, South Africa. These authors concluded that the turnover in vertebrate taxa at this biozone boundary is older than the marine extinction event and "probably does not represent the biological expression of the terrestrial end-Permian mass extinction". Additionally, a more recent analysis in the Karoo Basin likewise concluded that the turnover from the *Daptocephalus* (formerly *Dicynodon*) to *Lystrosaurus* Assemblage Zones (Fig. 10.3), once used to define the PTB on land, is not coincident with the end-Permian marine event (Gastaldo et al. 2018, 2019a). Recently, Gastaldo et al. (2020) published a CA-ID-TIMS Uranium-Lead age date from a pristine ashfall bed in the base of the *Lystrosaurus* Assemblage Zone that is more than 300,000 years prior to the marine crisis. Because of these and other reasons, the expression "the terrestrial Permian–Triassic boundary event [bed] is a nonevent" recently appeared in the literature (Gastaldo et al. 2009; Gastaldo and Neveling 2012, 2016; Ward et al. 2012).

Due to scarce and impoverished fossil megafloras from the earliest Triassic on the different continents, the common perception has been that land plants suffered a mass extinction like the terrestrial and marine animals, but doubts always remained (Nowak et al. 2019). Early Triassic megafloras are, indeed, often markedly impoverished and dominated by opportunistic taxa such as the iconic lycophyte *Pleuromeia* (Box 10.1; Looy et al. 1999; Grauvogel-Stamm and Ash 2005; McElwain and Punyasena 2007), although some megafloras were more diverse and gymnosperm-dominated (Feng et al. 2018). This apparent loss in species is probably based on a strong taphonomic bias (Gastaldo et al.

Fig. 10.2 The Karoo Basin, South Africa, has provided a key fossil record for evaluating the impact of the EPME on terrestrial vertebrate communities. This photo by Robert A. Gastaldo shows the Bethel Farm in Bethulie Valley

Fig. 10.3 Several medium-sized dicynodontian therapsids went extinct in the Karoo Basin at the end of the Permian. In this artistic interpretation by Fabrizio Lavezzi, the body of *Dicynodon* is covered with hair as possibly indicated by bone histology and tentatively suggested in a recent study of Permian coprolites (Bajdek et al. 2016)

2005) and/or on the fact that the macrofossil record (especially the gymnosperm one) is considerably undersampled for the Early Triassic, giving the impression of an increased gymnosperm extinction during the latest Permian (Nowak

et al. 2019). The recent discovery of nearly all major post-extinction plant groups, including bona fides Cycadales, Corystospermales, Bennettitales, Czekanowskiales, Podocarpales, and Araucariaceae in the Permian (e.g. DiMichele et al. 2001; Abu Hamad et al. 2008; Blomenkemper et al. 2018; Kustatscher et al. 2019) and the presence of "mixed" floras (e.g. *Glossopteris-*

Box 10.1: *Pleuromeia sternbergii*
Pleuromeia sternbergii (Fig. 10.4) is the most characteristic plant of the biotic recovery during the Early Triassic. The first megafossil was discovered in 1836 at the Magdeburger cathedral, when weathered sandstone fell down from the tower during repair works, burst, and released an impression of a yet-unknown fossil plant. During the same year, the specimen was brought to Georg Graf zu Münster (1776–1844), also a famous paleobotanist living in the city. He described it in 1839 as *Sigillaria sternbergii* in honor of paleobotanist Kaspar Maria Graf von Sternberg (1761–1844), one of the founders of paleobotany. Later, the species

Fig. 10.4 *Pleuromeia sternbergii* (Münster) Corda is the most characteristic plant megafossil of the biotic recovery during the Early Triassic. (**a**) Fossil from Sollingen, Germany (BSC445, 10 × 14 cm; picture courtesy Léa Grauvogel-Stamm); (**b**) artistic rendering of the live plant by Fabrizio Lavezzi
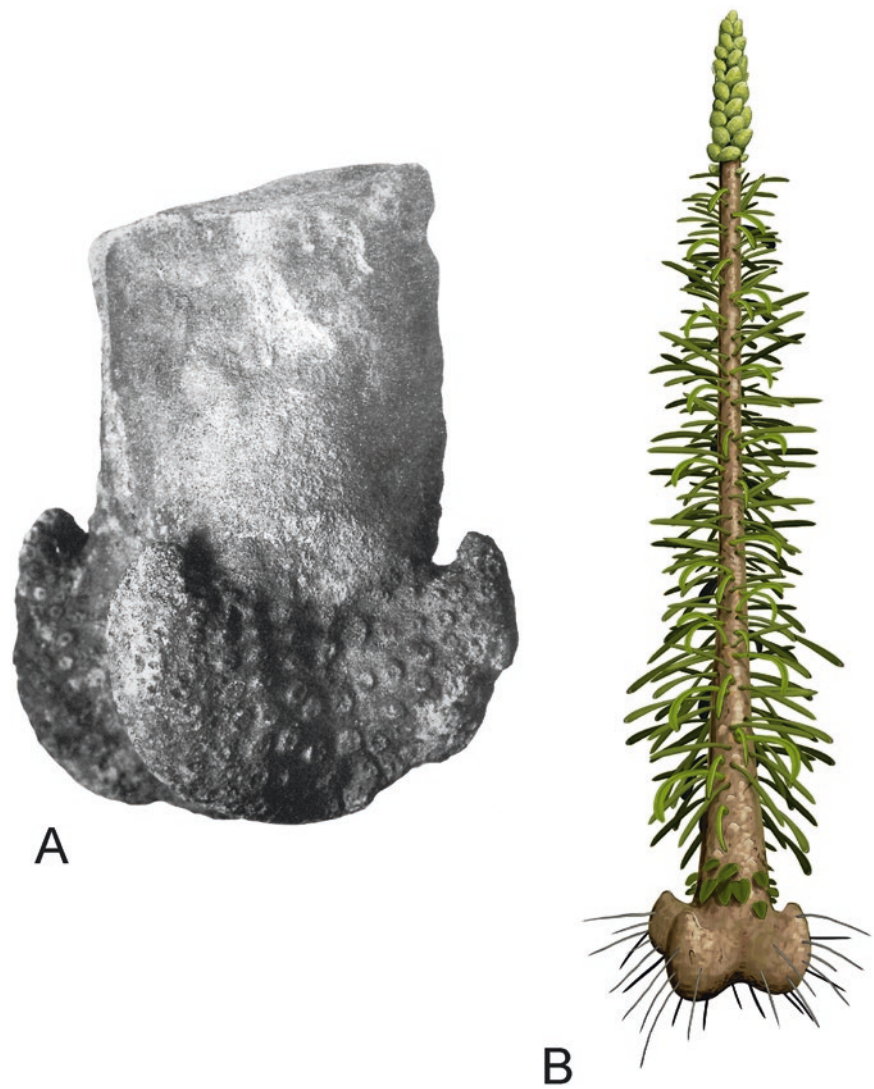
was transferred by Corda to the new genus *Pleuromeia* (originally spelled *Pleuromeya*).

The individual plants have an undivided stem with a maximum height of two meters and a terminal, heterosporous∗ cone-like structure composed of oval sporophylls∗. The four-lobed plant base (rhizophore) shows a typical sequence of root scars. The structure of the rhizophores and the ultrastructure of the micro- and megaspores∗ indicate a strong relationship of this genus with the extant lycophyte *Isoetes*. Several species of *Pleuromeia* colonized all continents during the Early Triassic. *Pleuromeia* is considered a highly adaptive pioneering plant. It experienced a quick radiation during the earliest Triassic where it formed monotypic stands or was part of low-diversity communities that were subsequently replaced by more complex communities in the Anisian.

Dicroidium floras; Schneebeli-Hermann et al. 2015) indicates that these groups did not "evolve" in response to the EPME, but rather had their major radiation after it.

Although the palynological record (Fig. 10.5) reflects a series of ecological disturbances and climatic changes around the PTB (Hochuli et al. 2010, 2016), the microscopic plant remains show less apparent changes during the extinction event than the macroscopic ones. This is possibly because of the higher preservation potential of pollen and spores (Fig. 10.6; Nowak et al. 2019). Nonetheless, the magnitude of the extinction among plants is still a matter of harsh debate (see Nowak et al. 2019).

The estimate of loss in the marine ecosystem, on the other hand, has been calculated several times. As we have seen earlier (Romano in Chap. 7), "fishes" were not too severely affected. However, estimates vary according to which database is used and the methods applied to analyze the data. Most studies agree that up to 49% of marine animal families went extinct, with foraminifers, bryozoans, and brachiopods

Fig. 10.5 *Kraeuselisporites apiculatus*, a spore from the Permian–Triassic boundary interval of the Finnmark platform (Norway)
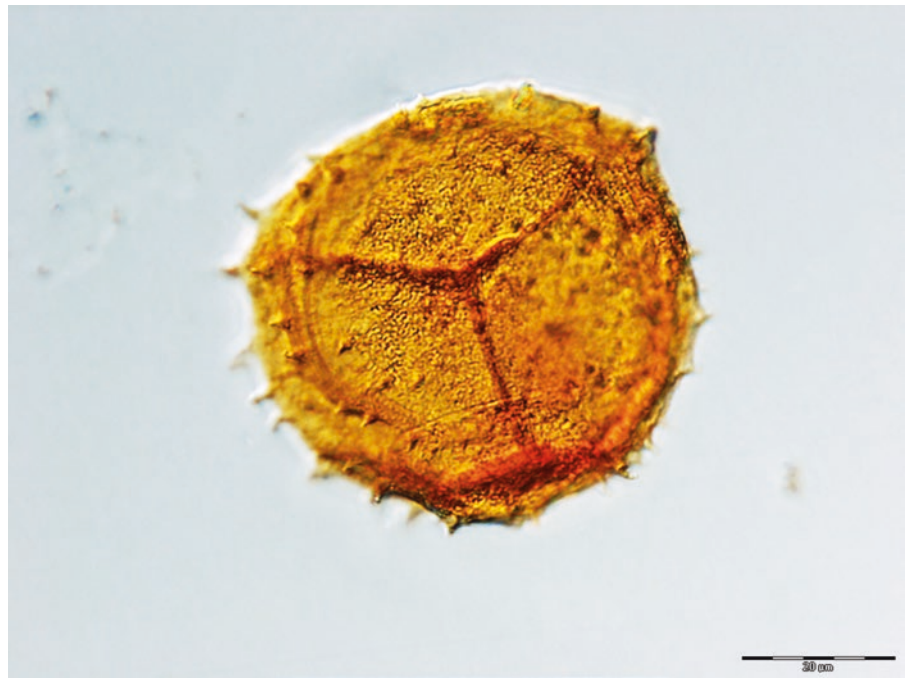
experiencing severe bottlenecks in diversity. Extinctions at the marine-species level have been estimated up to 96% by Raup (1979), but something between 80% (Benton and Twitchett 2003) and 85% (Stanley 2016) is now considered to be a more reliable estimate. On land, about 70% of terrestrial vertebrates experienced extinction, as well (see details in Benton and Newell 2014). Several large groups including fusulinid foraminifera, rugose and tabulate corals, the last trilobites and eurypterids, as well as blastoid echinoderms, are among the groups that completely disappeared during the EPME (Benton and Twitchett 2003).

The end-Permian biological crisis not only resulted in the largest mass extinction of all times but also influenced the biogeographic range and the body size of the lineages that survived on both land and in the oceans (as we have seen in neopterygians; Romano in Chap. 7). Bernardi et al. (2018), for example, found evidence for forced range expansion among tetrapods that moved to higher-latitudinal, cooler regions, in an attempt to escape from the superhot climate that developed in the equatorial belt in the earliest Triassic (see below; Sun et al. 2012). Schaal et al. (2016) recorded the maximum size of 11,224 mostly invertebrate specimens belonging to 2743 species of gastropods, bivalves, calcitic and phosphatic brachiopods, ammonoids, ostracods, conodonts, and foraminiferans, spanning the late Permian through the Middle to Late Triassic. They concluded that the EPME induced more size reduction (the so-called "Lilliput effect"; Urbanek 1993) among species than any other interval in Earth history. The decrease of size in specific lineages not only resulted from the extinction of larger taxa, but also because of the evolution of smaller sizes in the surviving lin-

eages. It is thought that the post-extinction world must have favored organisms with small body sizes in ecologically and physiologically different clades. But what caused such biogeographic changes, size reduction, and the disappearance of about 80% of late Permian biodiversity?

10.3 Looking for the Smoking Gun

Several lines of evidence have been presented in the last decades to explain the EPME. They include a bolide impact, similar to that experienced at the end of the Cretaceous, and extensive volcanism. The role of a bolide impact for the EPME has been thoroughly discussed in several papers (Benton and Twitchett 2003 and references therein). But, remarkably, data from the GSSP at Meishan, as well as other sections in south China and in central and western Tethyan, do not support an instantaneous calamity. The classical impact-related features (such as bolide ejecta or the crater itself) have never been found in any area. The evidence in these localities indicate that the marine biotic crisis started approximately 50,000 years before the possible impact of any bolide (Yin et al. 2007a, b; see also Bottjer et al. 2008). Therefore, as concluded by Twitchett (2006, p. 199), most of the evidence for the bolide impact "is seriously flawed and impact is not favored as a cause for this event" (see also Benton and Twitchett 2003). However, volcanism might have played a major role in the crisis.

The onset of the extensive volcanism that resulted in the emplacement of the Siberian traps (Fig. 10.7), a Large Igneous Province (LIP) in Russia, is now considered as the
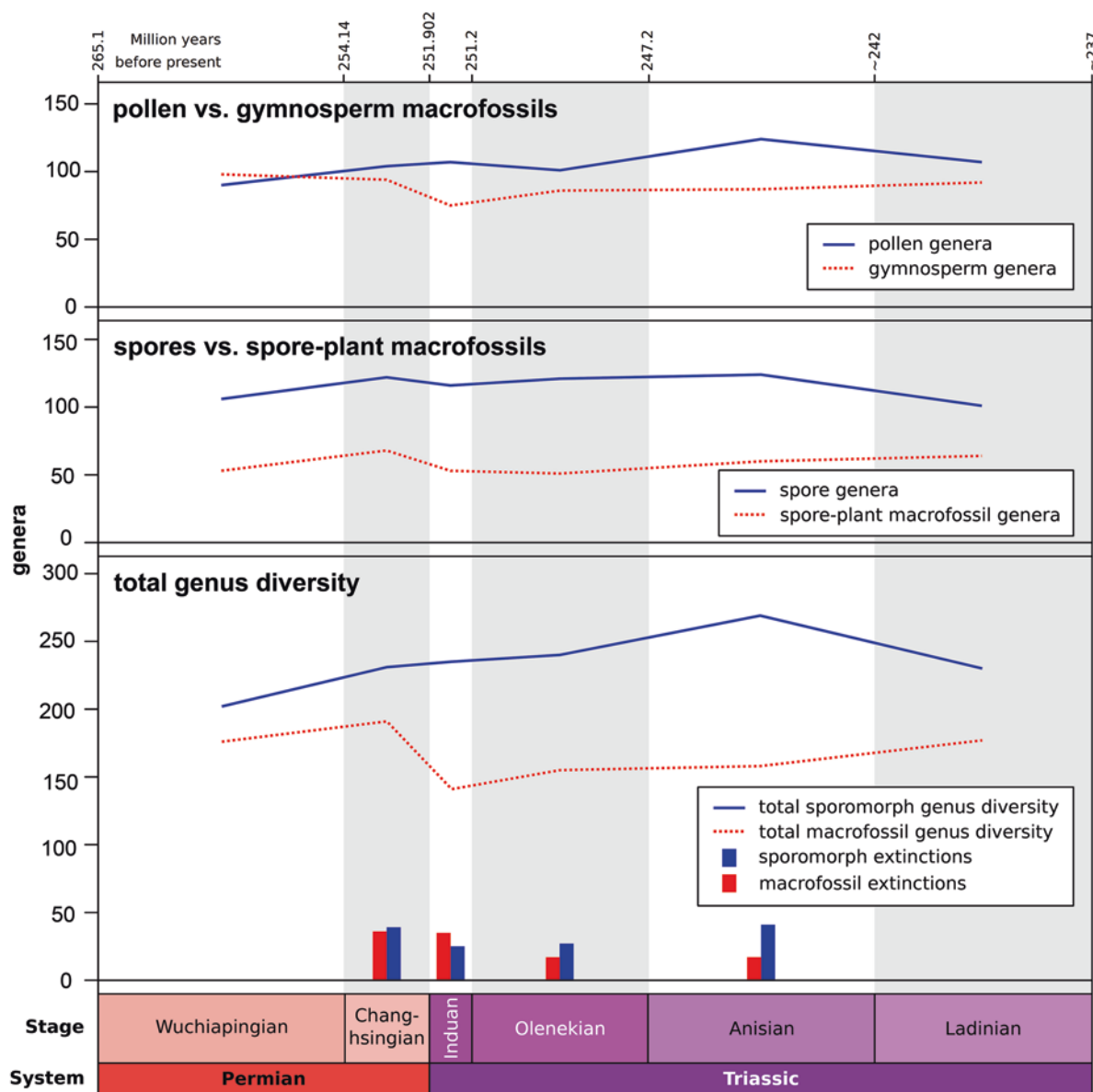
Fig. 10.6 Genus-level diversity curves for land-plant macrofossils and sporomorphs (spores and pollen) from the late Permian to the Middle Triassic (after Nowak et al. 2019). Macrofossil diversity decreases between the late Permian and the Early Triassic, but only less than 20% of the genera go extinct – significantly less than among animals. Sporomorph diversity even increases across the Permian–Triassic boundary and during the Early Triassic, showing no signs of a mass extinction. Interestingly, the diversity trends for spores and macrofossils of spore-producing plants (mosses, club mosses, ferns, horsetails) are quite similar, whereas those for pollen and macrofossils of gymnosperms (the seed plants that produced the pollen) are very different. This is probably because pollen and gymnosperm remains had different limitations affecting transport and preservation. Courtesy Hendrik Nowak

most likely trigger of the EPME (among others, Svensen et al. 2009; Chen and Benton 2012). This prolonged, multi-phase volcanic activity, which started in the latest Permian and continued for about five million years through most of the Early Triassic, produced immense volumes of effusive volcanic rocks over an extensive area of what is now Siberia. Estimates of the volume of basalts, tuffs, and intrusive igneous rock injected into the crust are up to four million km^3 and activated the cascade of events that produced the so-called "lethal triade": extreme global warming, ocean anoxia, and acidification (e.g., Wignall and Hallam 1992; Saunders and Reichow 2009). The magmatic event was characterized by multiple episodes of CO_2 and CH_4 release. The events leading up to, and following, the extinction crisis are associated with a negative excursion in stable-carbon isotope values, indicating the addition of "light" carbon to the planet. The isotopic signature locked in these rocks of −4 to −6‰ is thought to be the evidence that explains the negative excursion of $\delta^{13}C$ across the PTB (Wignall 2001; Payne and Kump 2007; Bond and Wignall 2014 and literature therein).

Fig. 10.7 Siberian Traps cropping out in the area of Talnakh (the Red Stones locality, Krasnoyarsk Krai, Russia). Photo by Cindy Looy

Because the basalt floods were recurrent over time, they impacted the host rock exposed on the surface and deeper in the crust. Those rocks included both coals and limestone (carbonates). Contact between the igneous magma and the host rock resulted in the thermal metamorphism of coal and carbonates of the Siberian craton. Heating of the sedimentary rocks released additional carbon into the atmosphere, which had repercussions in both terrestrial and marine environments. These multiple episodes of lava flood and carbon-rich gas release lasted into the Triassic and are, at least, partly related to the Early Triassic negative and positive $\delta^{13}C$ excursions recorded in these rocks (Benton and Twitchett 2003; Benton 2005; Erwin 2006 and literature therein). However, the magnitude of the negative excursions of $\delta^{13}C$ is so conspicuous that the volcanic CO_2 and CH_4 release, even if coupled with a decrease in biological productivity, cannot explain the phenomenon in its entirety. There must be additional factors or reasons.

It is likely that as a consequence of the rapid global warming (Sun et al. 2012; but see also Goudemand et al. 2013), methane clathrates trapped on shallow oceanic floors and/or high latitude permafrost melted and released light methane (with a $\delta^{13}C$ signature of −65‰) into the atmosphere (Benton and Twitchett 2003; Twitchett 2006). A similar scenario might have happened at the end of Paleocene, during another event of global warming we visited earlier on our journey (Dickens et al. 1995; see also Chap. 4). The amount of CO_2 and CH_4 released in a sort of "runaway greenhouse", with a

positive-feedback loop established between clathrate melting and temperature increase triggered by Siberian volcanism, determined the extent of global warming. The average global increase in temperature has been calculated to be 8–10 °C, and geochemical data indicate that the warming was very rapid (see the summary and Fig. 2 in Lai et al. 2018). The rate of increase is estimated to have occurred over about 2000 years and resulted in ocean temperatures in the intertropical belt of about 39–42 °C (Brand et al. 2012; Sun et al. 2012). The direct release of large quantities of hydrochloric acid (HCl) and chloromethane (CH_3Cl) into the atmosphere, as a result of venting and basin-scale metamorphism, resulted in significant stratospheric ozone depletion. And this modification of the stratosphere increased the incidence of harmful ultraviolet-B radiation to an extent that significantly affected life (Beerling et al. 2007; Benca et al. 2018). It is thought that increasing concentrations of greenhouse gasses resulted in increasing aridity, as well as a short-term production of acid rains that negatively affected terrestrial vegetation (but see Li et al. 2017, Fielding et al. 2019, and Gastaldo et al. 2019b for evidence against abrupt aridification in Australia and South Africa). A loss in plants, due to the disturbance of the terrestrial ecosystems across the land, may have increased soil erosion and, in this model, resulted in a higher sedimentation rate in both freshwater and saltwater basins (Chen and Benton 2012). Shortly after the extreme warming phase, ocean basins experienced widespread anoxic/dysoxic and euxinic (anoxia in waters rich of

hydrogen sulfide) conditions: ocean waters soon became stratified and increasingly acid (e.g. Isozaki 1997; Clarkson et al. 2015). It is the interaction of these factors across Earth Systems that likely explains the marine ecological and environmental turmoil that eclipsed the end-Permian ecosystems (Erwin 1993, 2006; Benton and Newell 2014). And if the establishment of hostile conditions had been a geologically rapid phenomenon, a cascade of geochemical events determined their persistence for a long time thereafter. These conditions shaped the prolonged recovery that followed the most catastrophic mass extinction in Earth history.

10.4 The Recovery

The pattern of recovery is attracting more and more interest of researchers, because it may serve as a model for today's crisis, similar to the Paleocene-Eocene Thermal Maximum (see DeVore and Pigg, Chap. 4). The paleoenvironments and fossil assemblages recorded in the post-extinction strata represent an excellent laboratory for studying evolutionary trajectories and the origin of modern ecosystems. This is because many of the lineages that characterize the life on our planet, today, date back to the Triassic recovery (Chen and Benton 2012). Many new families, genera, and species, in fact, appeared or rapidly diversified in the Early and Middle Triassic. As such, they are technically not part of a real "recovery", if the term "recovery" is thought of as a return to a previous state (Chen and Benton 2012). But these groups are interesting proxies of how ecosystems and trophic levels are restructured as the biosphere returned to a higher level of complexity.

The post-extinction recovery was a slow process for many of the animal groups that survived. This is because hostile conditions prevailed for a few million years. Among other things, hostile conditions across the globe are evidenced by: (1) the presence of multiple stable-carbon isotopic excursions that followed the one found at the PTB (Payne et al. 2004); (2) peaks in temperature (Sun et al. 2012); and (3) changes in the biogeochemical sulfur cycle, which resulted in widespread euxinic conditions and posed a sustained threat to marine life (Schobben et al. 2017; see also Benton et al. 2013). Early Triassic ecosystems were highly unstable (Roopnarine et al. 2007; Roopnarine and Angielczyk 2015), and it has been repeatedly suggested that the aftermath of the crisis extended into the Middle Triassic, about ten million years after the EPME (e.g., Lau et al. 2016; Martindale et al. 2018).

The change of the reef ecosystems before and after the PTB is particularly interesting. Reefs of the late Permian, constructed by sponges, algae, bryozoans, large foramin-ifera, microbes, and rugose corals, hosted benthic invertebrates, including brachiopods, mollusks, foraminifera, sponges, and bryozoans (Martindale et al. 2018). Most of these reef-forming groups never made it past the crisis. After the mass extinction, stromatolites (layered cyanobacterial structures), calcimicrobes (calcareous colonial microfossils), and thrombolites (clotted, cyanobacteria mats) were common at relatively low latitudes. Microbial mats filled the ecological niche previously occupied by metazoan reefs (Heindel et al. 2018). Recent evidence indicates that these microbialites were associated with small-sized, oxygen-dependent metazoans, including ostracods, microconchids, brachiopods, gastropods, bivalves, crinoids, echinoids, and conodonts but no corals (e.g., Martindale et al. 2018). The concept of a "reef gap" has been modified into "reef eclipse" because microbial reefs were present, although severely altered, in the aftermath of the extinction. The first metazoan biostromes (horizontally bedded fossil assemblages) from the Early Triassic (Olenekian) are relatively small structures devoid of corals. These assemblages were made by bivalves and sponges in association with stromatolitic and thrombolitic microbialites. Therefore, a long coral reef eclipse characterized the aftermath of the EPME (Martindale et al. 2018).

In the depauperate Early Triassic marine ecosystems, the presence of some disaster taxa, especially among brachiopods and mollusks, is remarkable (Fig. 10.8). The inarticulate brachiopod *Lingula*, rare in pre-extinction sediments, is an example of a very common and globally widespread taxon in subtidal environments immediately after the crisis (Twitchett 2006). Bivalve disaster taxa are also widespread and numerically abundant in Early Triassic sediments and include well-known taxa like *Claraia*, *Eumorphotis*, *Promyalina*, and *Unionites* (e.g., Bottjer et al. 2008).

The rate of recovery varied in different groups. Both slow and delayed recovery rates are recorded for benthic groups such as bivalves and gastropods (with an initial opportunistic proliferation of microgastropods). In contrast, explosive and rapid recovery is found in ammonoid cephalopods (in less than 2 My after the PTB, diversity levels were higher than in the Permian), conodonts, and some groups of foraminifera (Bottjer et al. 2008; Brayard et al. 2009; Stanley 2009; Song et al. 2011). Rapid diversification also occurred in marine vertebrates. According to Benton et al. (2013), bony (actinopterygian) fishes explosively diversified in the Early Triassic (but see Friedman and Sallan 2012 and Romano in Chap. 7), while the diversification of marine reptiles only occurred in the latest Early–Middle Triassic (Motani 2009). This latter diversification involved ichthyosaurs, thalattosaurs, pachypleurosaurs, nothosaurs, and placodonts (Chen and Benton 2012; Benton et al. 2013).
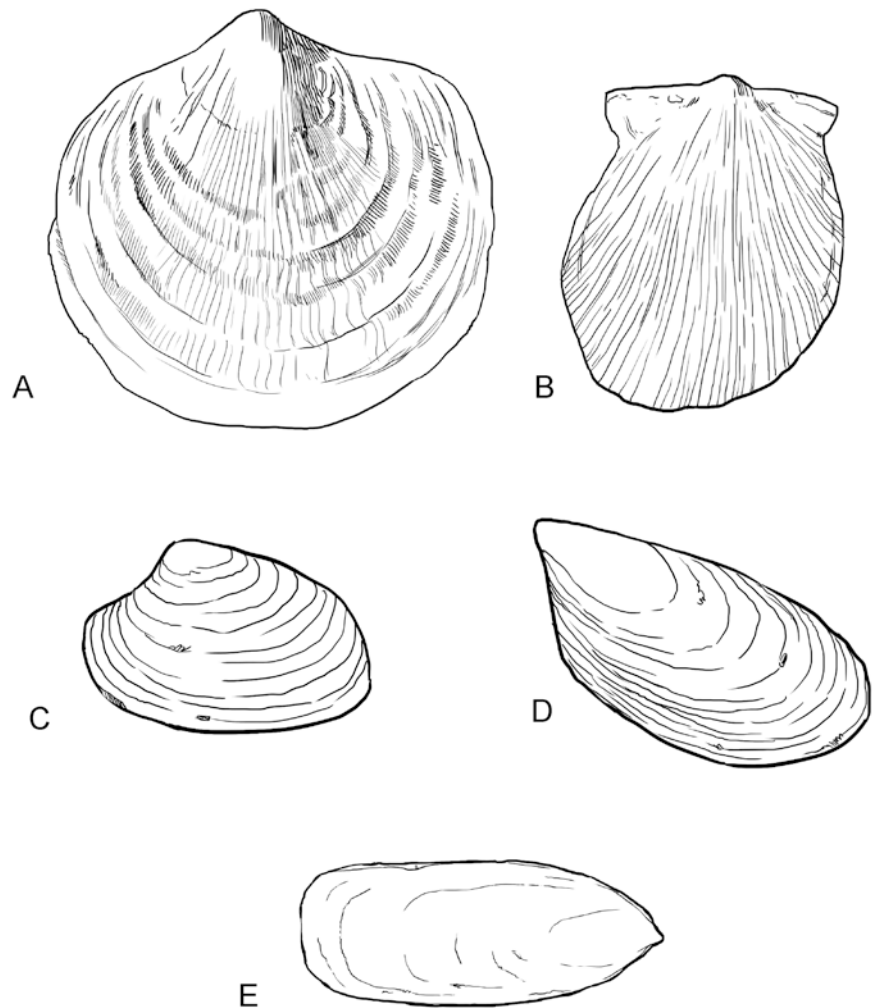
Following the lingering effects of the EPME, when environmental conditions became favorable again for the development of well-structured communities, new groups radiated. For example, Dai et al. (2018) reported high levels of benthic and nektonic faunas in the late Induan, soon after the last carbon-cycle perturbations, with the appearance of 26 new species of mollusks, brachiopods, foraminifers, conodonts, ostracods, and echinoderms. The most dramatic Early Triassic marine radiations are found in the scleractinian corals, bivalves, and crinoids (e.g., Martindale et al. 2018, and literature therein). On land, several groups of ferns and conifers appear for the first time (Cascales-Miñana et al. 2016), and insects are represented by an evolutionary modern fauna with derived clades of orthopteroids and hemipteroids and, especially, holometabolous taxa that replaced the previous Paleozoic faunas (Labandeira 2005). Among terrestrial vertebrates, several tetrapods including lissamphibians (frogs, salamanders) (Ascarrunz et al. 2016), squamate reptiles (lizards, snakes) (Simões et al. 2018), and several archosauriforms, comprising the dinosaurs (Brusatte et al. 2011; Ezcurra and Butler 2018), appear (Box 10.2).

Box 10.2: Archosauromorph Diversity and the EPME

A recent analysis studied archosauromorph diversity from the middle Permian to the early Late Triassic (Ezcurra and Butler 2018). This clade of reptiles likely originated in the middle Permian and may not have been affected by the EPME. The morphological disparity (variation) in the group, depending on the analytical method used, does not change significantly into the earliest Triassic (Induan). In fact, morphological disparity in this group increased significantly in the Olenekian or in the Anisian. Peaks of phylogenetic diversity in both the Induan and Olenekian correspond to very high evolutionary rates. The Induan forms are characterized by a low disparity of a sort considered to characterize a disaster fauna, dominated by proterosuchids and other lineages that were rather homogeneous in terms of their morphology. These forms underwent a major phylogenetic radiation in the Olenekian, which led to the origin or diversification of major clades. These clades include

Fig. 10.9 The archosauriforms *Chasmatosuchus* (**a**), *Erythrosuchus* (**b**), and *Tanystropheus* (**c**) are among the taxa that underwent a major phylogenetic radiation after the EPME in the Triassic. Artwork by Fabrizio Lavezzi
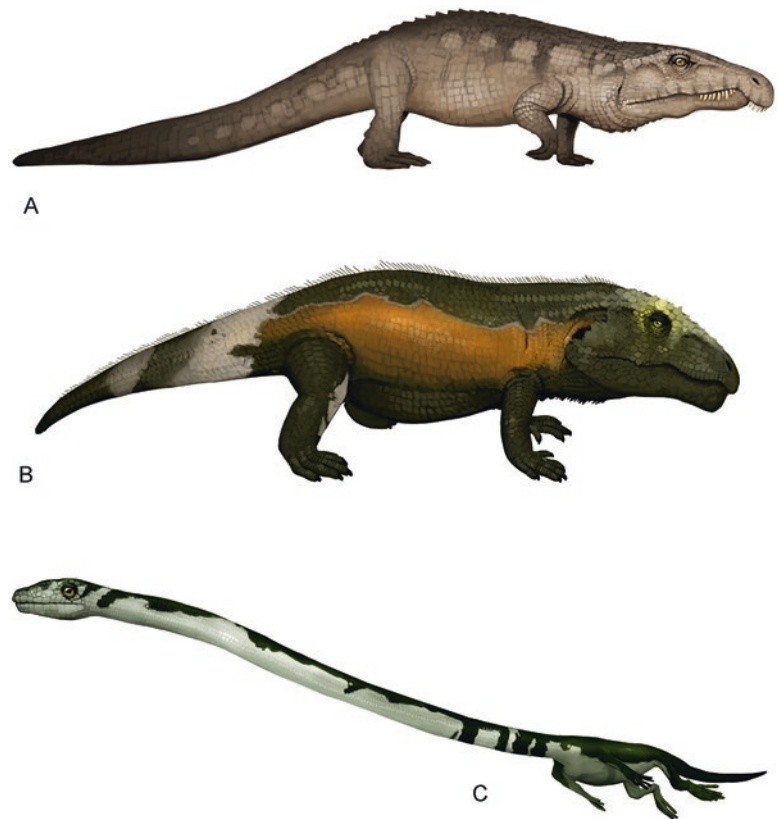
the rhynchosaurs, archosaurs, erythrosuchids, and tanystropheids (Fig. 10.9). During the Anisian, the archosauromorphs underwent an increase in terms of the number of species, abundance, ecomorphological disparity, and also size. In fact, the first part of the Middle Triassic witnessed the appearance of large hypercarnivore taxa, bizarre and highly specialized herbivores, long-necked marine predators, and gracile and agile dinosauromorphs (Ezcurra and Butler 2018). Their appearance corresponds with the return to stable ecosystems, as indicated by the end of the carbon-isotope excursions and the structuring of conifer-dominated forests (Sun et al. 2012). According to Bernardi et al. (2018), the emergence and the radiation of entirely new vertebrate groups, such as the archosaurs (including the dinosaurs) and others, might have been prompted by the forced biogeographic shift induced by the rapidly changing conditions (e.g., global warming) that characterized the aftermath of the EPME.

10.5 Conclusions

As shown above and summarized in Fig. 10.10, the end of the Permian is a drastic moment in Earth history with the most severe mass extinction of all life. This was most impact-

ful among the marine biota, although the various groups were affected differently depending on their life style (our knowledge is biased by their skeletal type and, therefore, the probability of retrieving information). Among the marine organisms, nektonic groups including the ammonoids and fishes were less affected than benthic forms such as bivalves, brachiopods, or reef-building organisms. On land, tetrapods and insects were more affected by either a loss in plant diversity or ecological turnover, although the composition and richness of the communities changed in the latter group as well. The prolonged unstable climatic conditions in the aftermath of the mass extinction affected the biotic recovery of the groups that were affected by the EPME. But, at the same time, it was a cradle for the evolution and especially radiation of a series of animals (archosaurs, squamates) and plants (corystosperms, Cycadales) that became important elements of Triassic ecosystems. Although the latest Permian and the earliest Triassic are among the most studied periods of time in Earth history, the dynamics and timeline of the extinction, biotic recovery, and radiation are still incompletely understood and further studies in the next tens of years will likely shed more light on "the mother of all extinctions".

For Deeper Learning

- Early, general works dealing with the EPME: Newell (1973); Raup (1979); Gould and Calloway (1980); Sepkoski (1981).

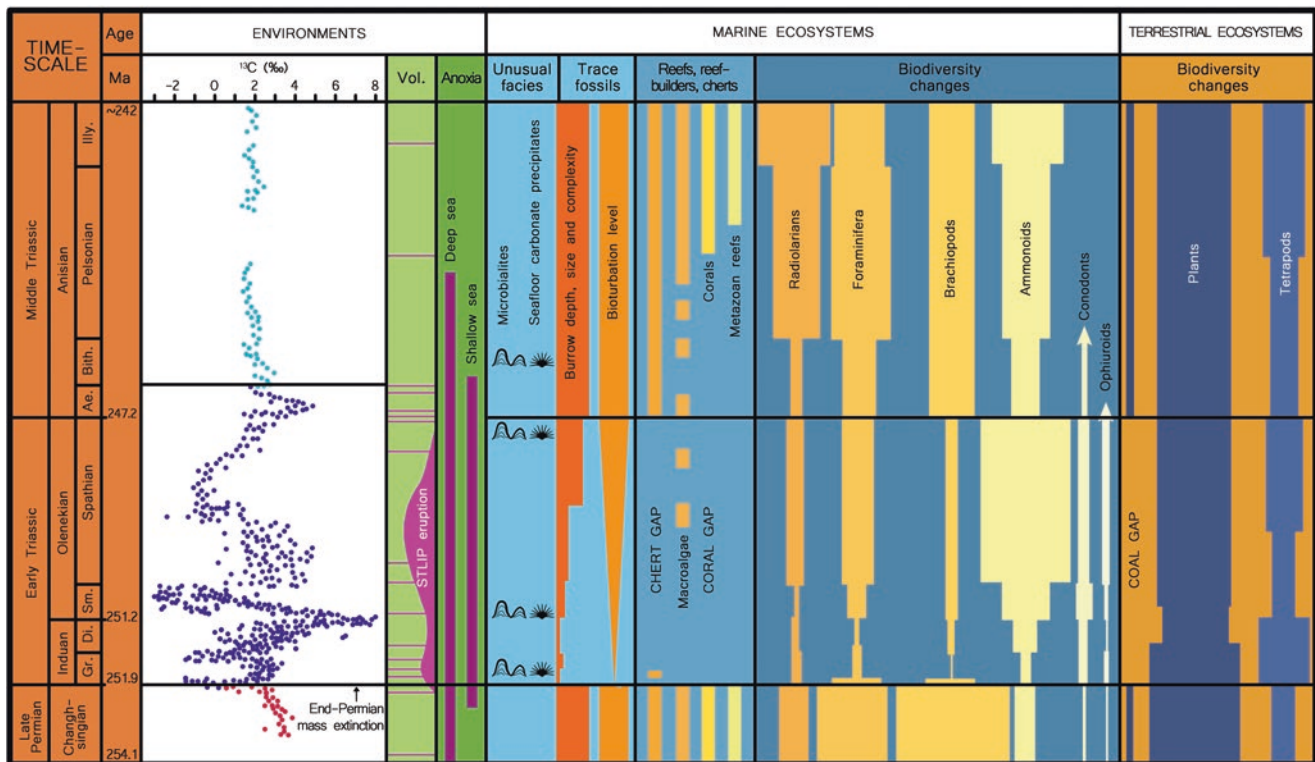**Fig. 10.10** A graphic summary of the environmental changes (oscillation of δ13C, volcanism = Vol., and anoxia), coupled with peculiar events in marine ("unusual" facies, trace fossils, reefs, reef-builders, chert, biodiversity changes in radiolarians, foraminiferans, brachiopods, ammonoids, conodonts, and ophiuroids) and terrestrial (coal gap and biodiversity changes in plants and vertebrates) ecosystems. *Ae.* Aegean, *Bith.* Bithynian, *Di.* Dienerian, *Gr.* Griesbachian, *Illy.* Illyrian, *Sm.* Smithian. Modified from Chen and Benton (2012; Fig. 1) after Nowak et al. (2019) by Fabrizio Lavezzi

- Siberian traps and the "lethal triade" (global warming, ocean anoxia, acidification): Wignall (2001); Algeo and Twitchett (2010); Algeo et al. (2011); Clapham and Payne (2011); Brand et al. (2012); Sun et al. (2012); Clarkson et al. (2015).
- Ocean waters stratification and acidification: Wignall and Hallam (1992); Wignall (2001); Wignall and Twitchett (2002); Algeo and Twitchett (2010); Clapham and Payne (2011); Brand et al. (2012); Winguth and Winguth (2012); Silva Tamayo et al. (2018); Shen et al. (2018).
- Stromatolites, microbialites, and trace fossils across the Permian–Triassic boundary: Schubert and Bottjer (1992); Twitchett and Wignall (1996); Kershaw et al. (2012).
- Plant evolution across the EPME: DiMichele et al. (2001); Hochuli et al. (2010, 2016); Blomenkemper et al. (2018); Nowak et al. (2019).
- Insect evolution across the EPME: Shcherbakov (2008); Labandeira (2005); Ponomarenko (2016).
- Vertebrate evolution across the EPME: Friedman and Sallan (2012); Viglietti et al. (2016).

Questions

1. Why is the EPME considered the worst of the Big Five mass extinctions over geologic time?
2. Which groups of organisms were particularly affected, and which ones suffered relatively low extinction rates?
3. Over what duration of time has the EPME been estimated to have lasted in the oceans and on land? How might you explain the disparity in these estimates?
4. What evidence exists in marine sediments for reduced oxygen (dysoxia/anoxia) at the sea floor during the EMPE?
5. How might a non-synchronous series of events, between the events on land and those in the oceans, be explained?
6. What is the "Lilliput effect" and in which groups of Early Triassic organisms is it found?
7. The emplacement of the Siberian Traps is considered a possible "smoking gun" that pushed ecosystem instability. What are the Siberian Traps, how might their emplacement have resulted in a lethal triade, and what lines of evidence are used to support this concept?

8. What evidence exists for a hostile planet in the aftermath of the EPME?

9. Why might different marine invertebrate groups have undergone different rates of recovery in the Early Triassic?

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