

End-Permian Mass Extinction in the Oceans: An Ancient Analog for the Twenty-First Century?

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Abstract

The greatest loss of biodiversity in the history of animal life occurred at the end of the Permian Period (~252 million years ago). This biotic catastrophe coincided with an interval of widespread ocean anoxia and the eruption of one of Earth's largest continental flood basalt provinces, the Siberian Traps. Volatile release from basaltic magma and sedimentary strata during emplacement of the Siberian Traps can account for most end-Permian paleontological and geochemical observations. Climate change and, perhaps, destruction of the ozone layer can explain extinctions on land, whereas changes in ocean oxygen levels, CO₂, pH, and temperature can account for extinction selectivity across marine animals. These emerging insights from geology, geochemistry, and paleobiology suggest that the end-Permian extinction may serve as an important ancient analog for twenty-first century oceans.

INTRODUCTION

Few events in the history of life pose greater challenges or have prompted more varied speculation than the end-Permian mass extinction [~ 252 million years ago (Mya)], the greatest biodiversity crisis in the history of animal life. The mass extinction event permanently altered the taxonomic composition and ecological structure of Earth's biota (e.g., Bambach et al. 2002, Sepkoski 1981). Identifying the causes of the end-Permian catastrophe and the controls on subsequent recovery is therefore critical to understanding the origins of modern global ecosystems.

The Permian-Triassic (P-Tr) transition has long been recognized as the post-Cambrian minimum in marine diversity (Phillips 1860), but the possibility that this decline resulted from a global biotic crisis received little attention until Schindewolf (1954) proposed that it was caused by a burst of extraterrestrial radiation. Early quantitative biodiversity compilations revealed the great severity of the end-Permian extinction, but testing between gradual (Newell 1962) and catastrophic (Schindewolf 1954) hypotheses remained beyond the resolution of existing data.

Demonstrations of rapid biodiversity loss during the latest Permian (Changhsingian) emerged during the 1990s. Jin et al. (1994) and Stanley & Yang (1994) showed that diversity losses at the end of the Middle Permian (Capitanian) were distinct and separated by millions of years from the end-Permian (Changhsingian) crisis. A geologically rapid (i.e., less than a few million years) end-Permian biodiversity crisis ruled out any slow-acting process, such as the assembly of Pangaea, as the primary cause of mass extinction. However, many potential extinction mechanisms remained, leading Erwin (1993) to propose that flood basalt volcanism, methane hydrate release, climate change, ocean anoxia, and sea-level fall combined to cause the mass extinction.

In this review, we address recent paleontological and geochemical findings that place new constraints on the end-Permian extinction. We focus primarily on the better-studied marine record and use a new database of Permian and Early Triassic marine invertebrate occurrences (Clapham et al. 2009), which is freely available in the Paleobiology Database (<http://www.paleodb.org>), to reevaluate marine extinction severity and selectivity. All analyses presented here are based on data downloaded from the Paleobiology Database on July 12, 2011.

PALEONTOLOGY

Severity

Despite the severity of the end-Permian extinction and the recognition of a distinct Capitanian crisis (Jin et al. 1994, Stanley & Yang 1994), the partitioning of taxonomic losses between those extinctions has been less certain. Estimates of Capitanian extinction severity using Sepkoski's (2002) compendium suggested that it was comparable in size with the younger end-Permian extinction (e.g., Knoll et al. 2007, Stanley & Yang 1994). However, recent work shows that Sepkoski's database overestimates Capitanian and underestimates Changhsingian extinction magnitude for a number of reasons (Clapham et al. 2009). Our reevaluation of Permian extinctions using an expanded and revised data set shows that genus extinctions were strongly concentrated in the Changhsingian (79% extinction in the Changhsingian versus 24% in the Capitanian; see **Figure 1**) (see also **Supplemental Sidebar 1**, Measuring Diversity and Extinction; access it by following the Supplemental Materials link from the Annual Reviews home page at <http://www.annualreviews.org>).

No major marine invertebrate or protist group escaped the end-Permian extinction unscathed (**Figure 2**), and many invertebrate clades were eliminated entirely. Trilobites, rugose corals, tabulate corals, goniatites, strophomenate brachiopods, blastoids, and rostroconchs occur for the final time in Changhsingian strata, in many cases immediately below the extinction horizon, or in postextinction mixed faunas. Spiriferid and orthid brachiopods (Class Rhynchonellata) also

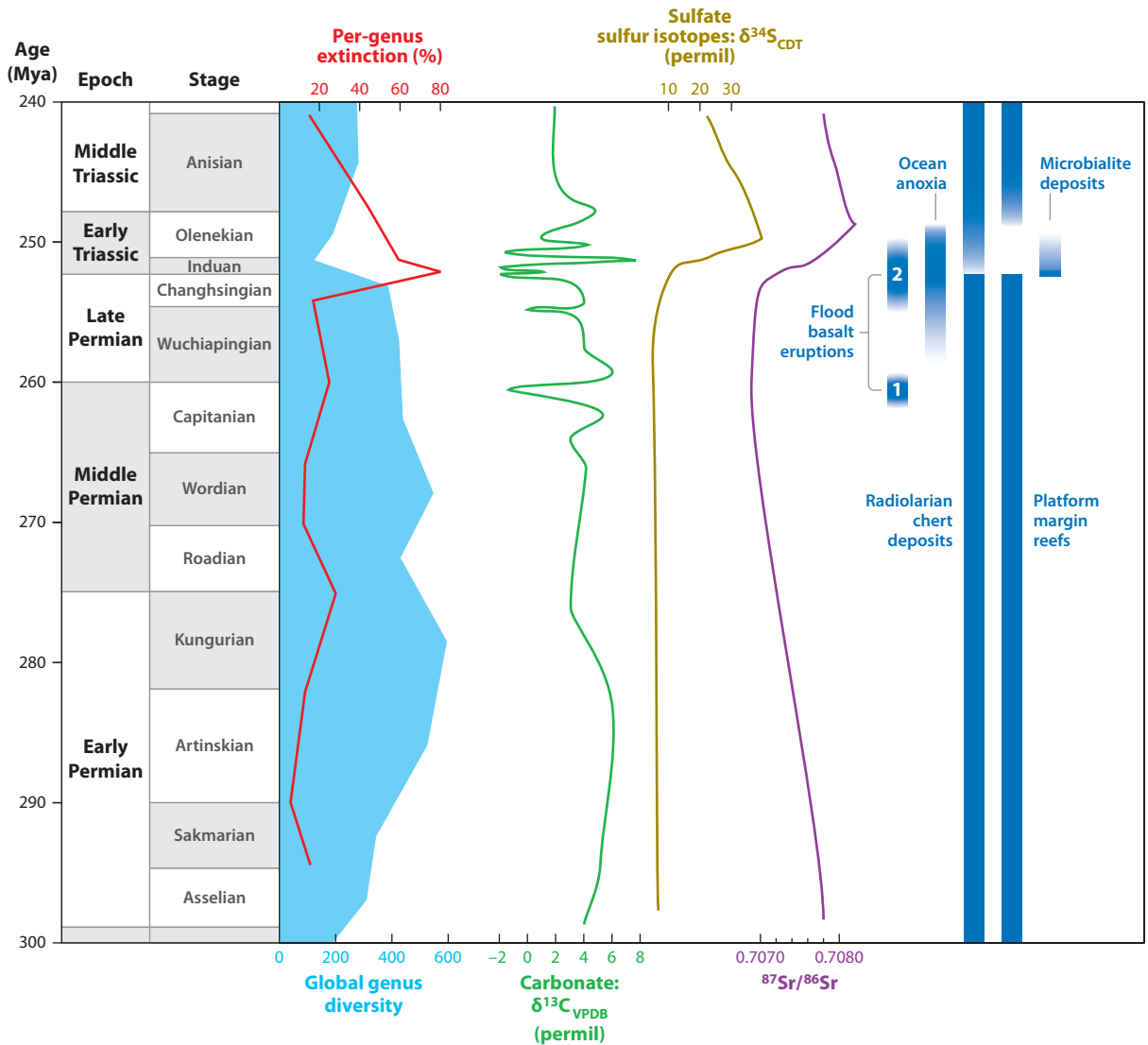


Figure 1

Overview of Early Permian through Middle Triassic Earth history, illustrating the coincidence of biological, geochemical, and sedimentary perturbations near the Permian-Triassic (P-Tr) boundary. Global diversity data and extinction rates calculated from the Paleobiology Database using Alroy's (2010) shareholder quorum subsampling (SQS) method. Carbon isotope record based on data from Grossman et al. (2008), Bond et al. (2010), Shen et al. (2010b), and Payne et al. (2004). Sulfur isotope record based on data from Kampschulte & Strauss (2004) and Horacek et al. (2010). Strontium isotope record based on data from McArthur et al. (2001) and Korte et al. (2004). Flood basalts: 1: Emeshan large igneous province; 2: Siberian Traps large igneous province. Abbreviations: CDT, Canyon Diablo Troilite; permil, parts per thousand (‰); VPDB, Vienna Pee Dee Belemnite.

went extinct. Fenestrate bryozoans were victims as well, but all other bryozoan orders survived (Powers & Pachut 2008). The P-Tr was the time of greatest turnover among crinoid groups; of the five Permian clades (Cladida, Flexibilia, Disparida, Camerata, and Articulata), only the artikulates survived (Twitchett & Oji 2005). The extinction was severe (91% genus loss) for all calcified orders of foraminifera (Lagenida, Miliolida, and Fusulinida), but particularly so for the large and

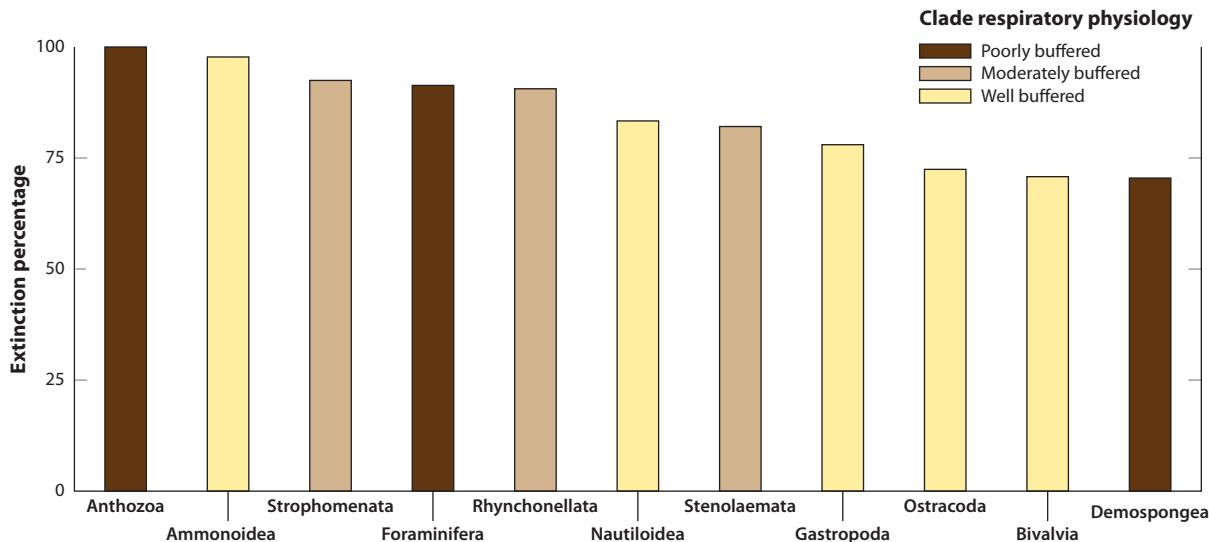


Figure 2

Physiological selectivity of the end-Permian extinction. Clades with poorly buffered respiratory physiology are shaded dark brown, moderately buffered clades are in brown, and well-buffered clades are in light yellow. Invertebrate extinctions are calculated as a raw percentage on the basis of all Changhsingian genera from Paleobiology Database data; foraminiferan extinction is also a raw percentage from Groves & Altiner (2005).

morphologically complex superfamily Fusulinoidea, which suffered complete extinction (Groves & Altiner 2005). Radiolarians also suffered major genus-level extinctions (Feng et al. 2007, Kozur 1998), although Paleozoic holdover taxa occur at many sites (Sano et al. 2010) and members of Triassic genera have been found in the latest Permian faunas (Feng et al. 2007, Sano et al. 2010).

The end-Permian extinction was particularly severe for reef organisms and ecosystems. More than 70% of Changhsingian sponge genera were lost, a number that may be artificially low owing to homeomorphy of unrelated Permian and Triassic taxa (Flügel 2002). The complete extinction of rugose and tabulate corals and the appearance and increasing ecological importance of scleractinian corals in Middle and Late Triassic reefs were other key differences between Permian and Triassic reefs (Flügel 2002). The ecological severity of the extinction was even more pronounced; diverse upper Changhsingian hypercalcified sponge-microbe reef ecosystems collapsed abruptly (Flügel & Kiessling 2002) and were replaced by microbialite reefs in the Early Triassic (Baud et al. 2007, Kershaw et al. 2012, Lehrmann et al. 2003).

Less is known about genus-level extinction severity among algae. The diversity of dasycladacean green algae was notably lower in the Triassic than in the Permian (Aguirre & Riding 2005), but Changhsingian genus-level extinction was only 43% (6/14) (calculated from data compiled by Granier & Grgasovic 2000). The relevance of extinction intensity in algae is unclear, however, because many algal genera are morphologically simple and long ranging. Despite these comparatively low taxonomic losses, the near-complete absence of calcareous algae from the Early Triassic fossil record (Aguirre & Riding 2005) indicates that P-Tr environmental conditions strongly affected these organisms.

Palynological data indicate a rapid terrestrial crisis synchronous with the marine event, including decimation of the gymnosperm flora and replacement by opportunistic lycopods (Hochuli et al. 2010, Shen et al. 2011, Twitchett et al. 2001). Blooms of organic-walled microfossils have

been interpreted as a fungal spike following destruction of plant communities (Visscher et al. 1996, 2011), but the taxonomic position of these fossils has been debated and an algal affinity has also been advocated (Foster et al. 2002).

A discrete, global end-Permian mass extinction event is less clearly demonstrated in the vertebrate and plant macrofossil records (Fröbisch 2008, Maxwell 1992, Rees 2002, Xiong & Wang 2011). Global compilations of terrestrial vertebrate diversity also indicate equally high extinction intensity in earlier or later time intervals (e.g., Maxwell 1992). Sections in Russia and the Karoo basin (South Africa), the best-documented regions, display a major extinction at the P-Tr boundary (Benton et al. 2004, Ward et al. 2005), at least broadly equivalent to the marine crisis, but also show elevated extinction in earlier intervals (Benton et al. 2004). Tetrapod extinctions in the Karoo basin are consistent with an abrupt crisis (Ward et al. 2005), but the precise synchronicity with the marine extinction is still unknown because of problematic lithological correlations (Gastaldo et al. 2009) and the questionable validity of correlations based on organic carbon $\delta^{13}\text{C}$ (Korte & Kozur 2010).

Selectivity

The end-Permian extinction disproportionately affected certain marine animal clades, a distinction that largely defines the differences between members of Sepkoski's (1981) Paleozoic and Modern faunas. Physiological differences between the two faunas, particularly the varying degrees of stenotopy and eurytopy between brachiopods (Paleozoic fauna) and bivalves (Modern fauna), were initially proposed as a potential explanation for the differential severity of the extinction (e.g., Steele-Petrović 1979), although data available at the time did not permit statistical testing. Later, Rhodes & Thayer (1991) found no significant association between trophic mode or locomotor type and extinction risk across bivalve genera during the end-Permian mass extinction, in marked contrast to the corresponding association during the end-Cretaceous extinction. Knoll et al. (1996) used Sepkoski's genus compendium to examine extinction selectivity across marine animals and protists in terms of predicted susceptibility to hypercapnia, finding greatly elevated extinction rates in the taxa most susceptible (e.g., corals, brachiopods, echinoderms). Knoll et al. (2007) further found that heavily skeletonized groups, such as corals, suffered more in the extinction and argued that hypercapnic stress from elevated $p\text{CO}_2$ could best account for extinction selectivity even if anoxia, hydrogen sulfide, and temperature change also contributed to the severity through synergistic effects on respiratory physiology. The same suite of stresses may also account for the ecological structure of Early Triassic marine communities (Fraiser & Bottjer 2007, Knoll et al. 2007). The importance of respiratory physiology has been confirmed in studies of the Paleobiology Database (Clapham & Payne 2011, Kiessling & Simpson 2011), and multiple regression analysis shows that both physiological buffering capacity and shell mineralogy are significant predictors of survivorship, even after accounting for the effects of geographic range, abundance, and life position (Clapham & Payne 2011).

In contrast to the strong influence of individual-level traits such as physiology, population-level traits played only a weak role in end-Permian survivorship. Local or global abundance did not favor survival (Clapham & Payne 2011, Leighton & Schneider 2008), and the effects of wide geographic range, usually a strong predictor of survival, were greatly weakened in the end-Permian extinction (Clapham & Payne 2011, Payne & Finnegan 2007). Extinction severity was remarkably uniform among different regions within Tethys, as well as at high northern and southern latitudes (**Figure 3**). Extinctions in south China deviate slightly from the otherwise spatially homogeneous pattern owing to the short-term survival of the most common brachiopod taxa in postextinction mixed faunas (Chen et al. 2005).

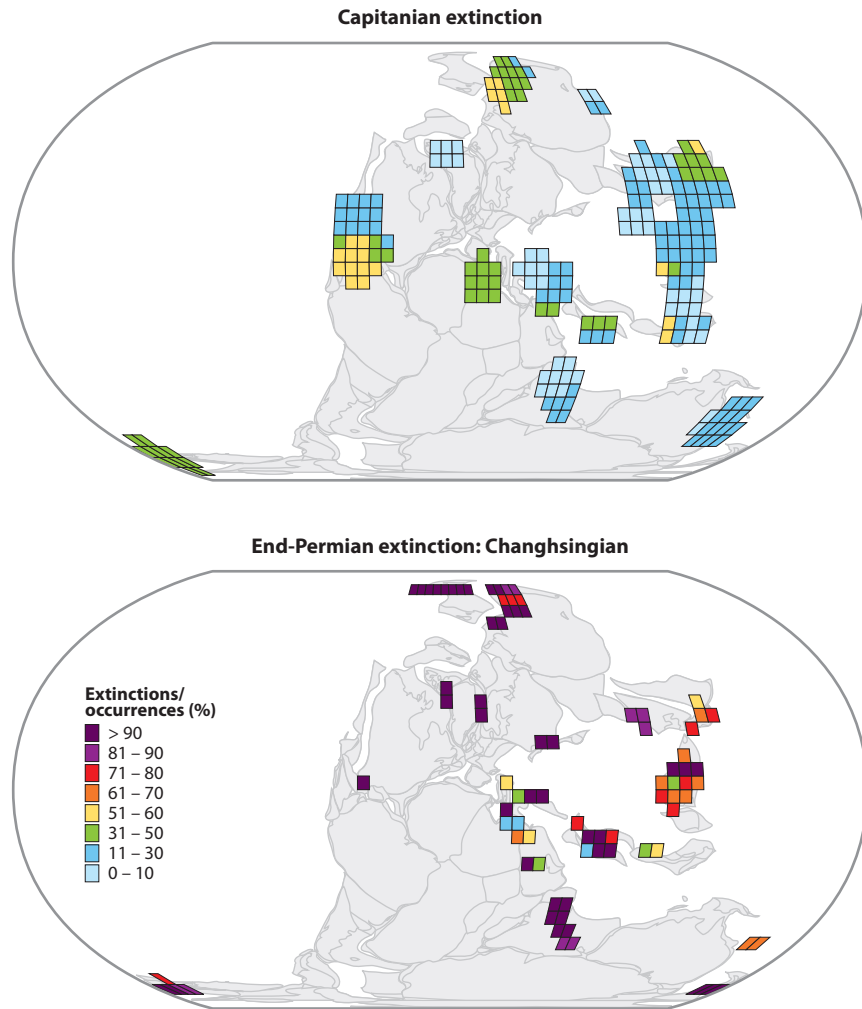


Figure 3

Geographic selectivity of Capitanian and end-Permian extinctions, using a kernel density function that compares the number of occurrences of extinct genera against the total number of occurrences. The end-Permian extinction was extremely severe in all regions, such as Tethys, peri-Gondwana, and at high northern and southern latitudes, in contrast with the Capitanian extinction, which had considerable spatial variability owing to sedimentary record loss (Clapham et al. 2009).

There is no evidence for variation in extinction intensity across environmental gradients. Chen et al. (2011) documented 72–92% extinction among brachiopod genera in six different habitats from nearshore to bathyal regions in south China. Although the 92% genus extinction in the reef habitat was higher than in other habitats, the among-habitat differences are not statistically significant.

Timing and Tempo of Extinction

Studies of classic P-Tr boundary sections in Kashmir, India (Nakazawa et al. 1975), south China (Sheng et al. 1984), and Italy (Broglia Loriga et al. 1986) demonstrated that extinctions

were concentrated in a narrow stratigraphic interval in the latest Changhsingian. Intensified investigation of P-Tr boundary sections in the past decade is beginning to allow detailed comparison across regions to determine whether diversity losses were globally synchronous.

Constraints on the absolute age of the end-Permian extinction derive primarily from the Meishan and Shangsi sections in south China, where volcanic ash layers are intercalated within uppermost Permian and lowermost Triassic carbonates. Improved preparation methods to etch damaged parts of zircons that suffered lead loss and exclusive use of single-crystal analyses yield ages of 252.4 ± 0.3 Mya (Mundil et al. 2004) and 252.28 ± 0.08 Mya (Shen et al. 2011) for Meishan bed 25, which agree within error.

The main pulse of the end-Permian extinction was synchronous across south China, the best-studied region (**Figure 4**), beginning at the top of the *Clarkina yini* zone, before the biostratigraphically defined P-Tr boundary, and extending into the basal Triassic *Hindeodus parvus* zone (J. Chen et al. 2009, Ji et al. 2007, Shen et al. 2011). Combining geochronologic constraints with fossil ranges from well-studied sections in south China shows that biodiversity loss occurred as a single pulse beginning at 252.30 Mya and ending by 252.10 Mya (Shen et al. 2011). These findings are consistent with evidence for abrupt extinction of foraminifera in Italy (Groves et al. 2007, Rampino & Adler 1998) and Turkey (Groves et al. 2005) at approximately the same stratigraphic level as those in China. Although short-lived survivor taxa occur in postextinction strata (Chen et al. 2005, Z.-Q. Chen et al. 2009, Posenato 2009), newly compiled data indicated that an apparent multiphase extinction (Yin et al. 2007) reflects sampling effects rather than truly discrete crises (Shen et al. 2011).

Assessment of synchronicity at wider scales is complicated by facies specificity of important conodont index fossils (Farabegoli et al. 2007) and by the limits of conodont biostratigraphic correlation and resolution (Shen & Mei 2010). In Italy, the main extinction pulse (Groves et al. 2007) occurred within the *H. praeaparus* conodont zone, correlated in part with the *C. meishanensis* zone, potentially implying a slightly diachronous onset of extinction between eastern and western Tethys (Farabegoli et al. 2007, Kozur 2007); however, alternative sequence stratigraphic correlations suggest a synchronous crisis (Posenato 2010). In Iran, the extinction occurred at the top of the *C. hauschkei* zone, most likely correlative to the upper part of the *C. yini* zone at Meishan (Kozur 2007; C. Henderson, personal communication), but it has also been correlated with the younger *meishanensis* zone (Shen & Mei 2010). The timing of the extinction is broadly contemporaneous in peri-Gondwanan localities of Tibet, Spiti, Kashmir, and the Salt Range (Shen et al. 2006); in seamounts in central Neotethys (Shen et al. 2010a); and in the Boreal localities of Greenland and Spitsbergen (Twitchett et al. 2001, Wignall et al. 1998), although precise synchronicity is difficult to prove because conodont occurrences are limited prior to the extinction.

ENVIRONMENTAL CONTEXT

Lithological Evidence

Laminated, pyrite-rich lithofacies in P-Tr boundary sediments provided the first evidence for widespread anoxia in shallow-marine environments during the end-Permian extinction (Wignall & Hallam 1992, 1993; Wignall & Twitchett 1996). Common in boundary interval strata is syngenetic pyrite (Wignall & Hallam 1992), which includes small-sized pyrite framboids that suggest anoxic and euxinic (i.e., H₂S-bearing) seawater was widespread in Tethyan, eastern Panthalassan, and Boreal sections around the time of the extinction (Bond & Wignall 2010, Nielsen et al. 2010, Shen et al. 2007, Wignall et al. 2005). Framboidal pyrite data suggest development of anoxia and

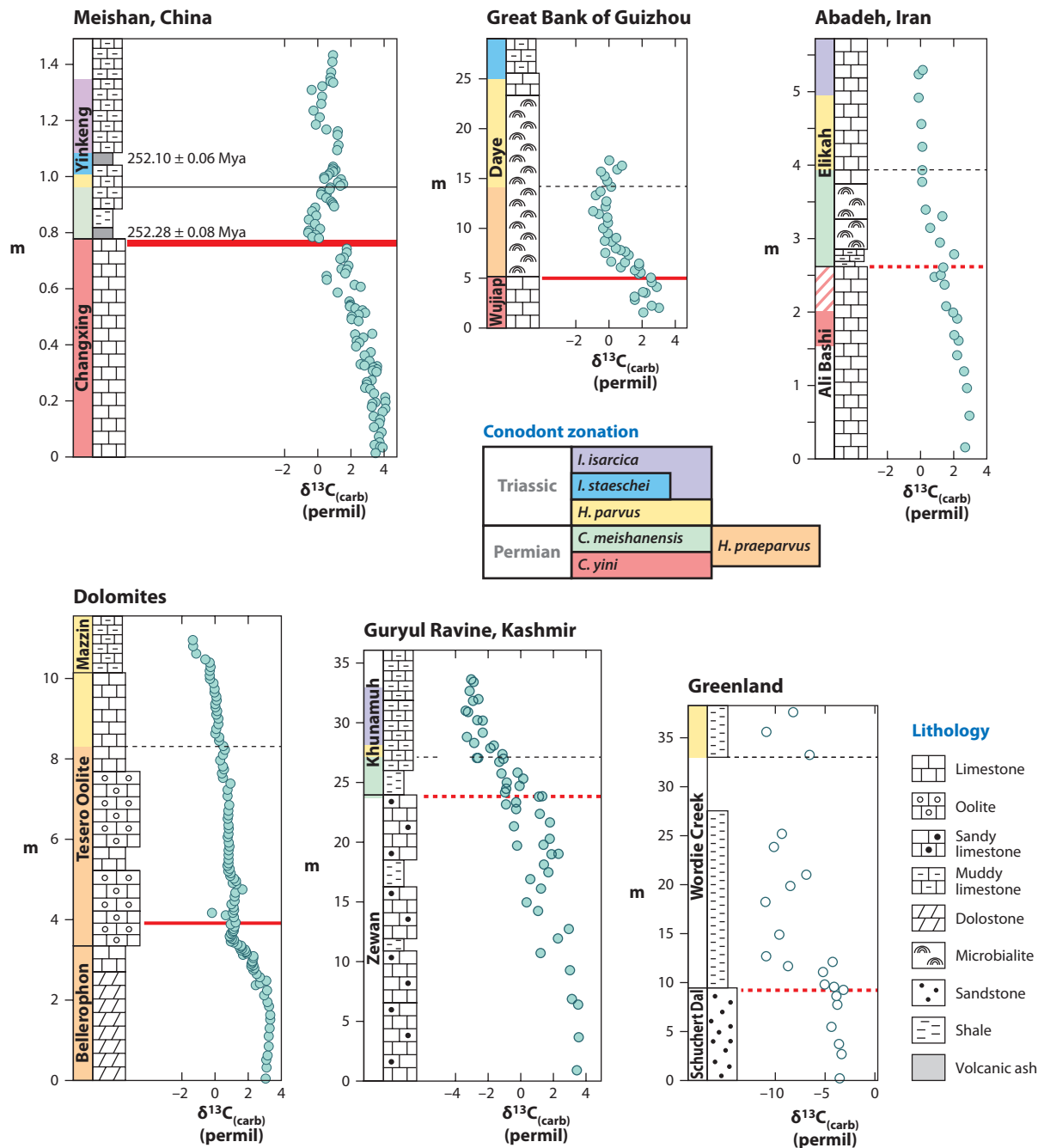


Figure 4

Uppermost Changhsingian to lowermost Triassic stratigraphy of selected Permian-Triassic (P-Tr) boundary sections from eastern Tethys (Meishan, Great Bank of Guizhou), western Tethys (Abadeh, Dolomites), peri-Gondwana (Guryul Ravine), and the Boreal realm (Greenland). All vertical scales are in meters. Main extinction pulses are indicated by red lines: solid when constrained by confidence intervals or other quantitative analyses, and dashed when assessed qualitatively. See the **Supplemental Material** for data sources and further explanation. Abbreviations: (carb), carbonate; permil, parts per thousand (‰).

euxinia was also spatially complex (Bond & Wignall 2010), consistent with the lithofacies evidence for diachronous anoxia in P-Tr boundary sections (Wignall & Hallam 1993).

Sediments immediately overlying the extinction horizon are often dominated by microbial buildups (stomatolites and thrombolites; **Figures 4 and 5**) or feature unusual sedimentary textures such as decimeter-scale crystal fans representing seafloor carbonate precipitates (e.g., Baud et al. 2007, Kershaw et al. 2007). These facies are most widespread within the basal Triassic *H. parvus* conodont zone, occurring in south China, western Tethys, Panthalassa, Greenland, and Australia (reviewed in Kershaw et al. 2012). Crusts and mounds composed of crystal fans are best developed in western Tethys localities (Baud et al. 2007). The development and preservation of microbial facies in the aftermath of the extinction have been attributed to a reduction in metazoan grazing and bioturbation (Lehrmann et al. 2003, Pruss & Bottjer 2004), upwelling of alkaline deep waters supersaturated with calcium carbonate (Kershaw et al. 2007, Lehrmann et al. 2003), and increased carbonate deposition in the aftermath of an ocean acidification event (Payne et al. 2007, 2010).

Carbon Isotopes

One of the first documented geochemical features of P-Tr boundary strata was a perturbation of the global carbon cycle. In the best-studied marine sections with the longest temporal records, $\delta^{13}\text{C}$ values typically exhibit a gradual decline from near +4‰ to closer to +2‰ near the extinction horizon (**Figures 4 and 5**). The $\delta^{13}\text{C}$ excursion has now been documented at more than 100 marine localities and numerous nonmarine sections and has been observed in carbonate sediments, bulk organic matter, and individual organic compounds (reviewed by Korte & Kozur 2010). Near the extinction horizon, values decline more rapidly to a minimum typically near -1‰ or -2‰ before returning to (temporarily) stable values between +1‰ and +2‰. The interval of extremely depleted $\delta^{13}\text{C}$ values coincides approximately with the basal Triassic *H. parvus* conodont zone. There may be two or more cycles between more enriched and more depleted $\delta^{13}\text{C}$ values during the earliest Triassic (Holser et al. 1989, Xie et al. 2007).

Two classes of explanation have been proposed for the $\delta^{13}\text{C}$ excursion: (a) collapse of primary productivity and the resulting isotopic homogenization of the oceans (known as a Strangelove Ocean) (e.g., Erwin et al. 2002, Rampino & Caldeira 2005) and (b) addition of ^{13}C -depleted carbon to the oceans and atmosphere (known as a carbon injection). Carbon depleted in ^{13}C could derive from methane clathrates (e.g., Erwin 1993), methane dissolved in deep ocean waters (Ryskin 2003), dissolved inorganic carbon in the deep waters of a stratified ocean (e.g., Kajiwarra et al. 1994, Knoll et al. 1996), a large dissolved marine organic carbon reservoir (Rothman 2010), or sedimentary organic carbon deposits (e.g., Svensen et al. 2004). In the Strangelove Ocean scenario, the isotope excursion is a consequence of extinction, whereas in the carbon injection scenario it is linked to the cause.

Carbon injection and the Strangelove Ocean are not mutually exclusive, but two lines of evidence suggest carbon injection was the more important control on the carbon isotope record. First, there appears to have been a substantial depth gradient in $\delta^{13}\text{C}$ values shortly following the mass extinction event (Meyer et al. 2011), contrary to the isotopic homogenization predicted under the Strangelove Ocean scenario. Second, the boundary $\delta^{13}\text{C}$ excursion was not an isolated event; rather, it was part of a series of large positive and negative excursions that began during Permian time and persisted through the Early Triassic (**Figure 1**).

Although most authors have interpreted the boundary $\delta^{13}\text{C}$ excursion to result from carbon injection, the magnitude and isotopic composition of the released carbon are unknown because they cannot be uniquely constrained by the magnitude of the $\delta^{13}\text{C}$ excursion alone. Berner (2002) argued that the amount of carbon required from any source isotopically heavier than biogenic

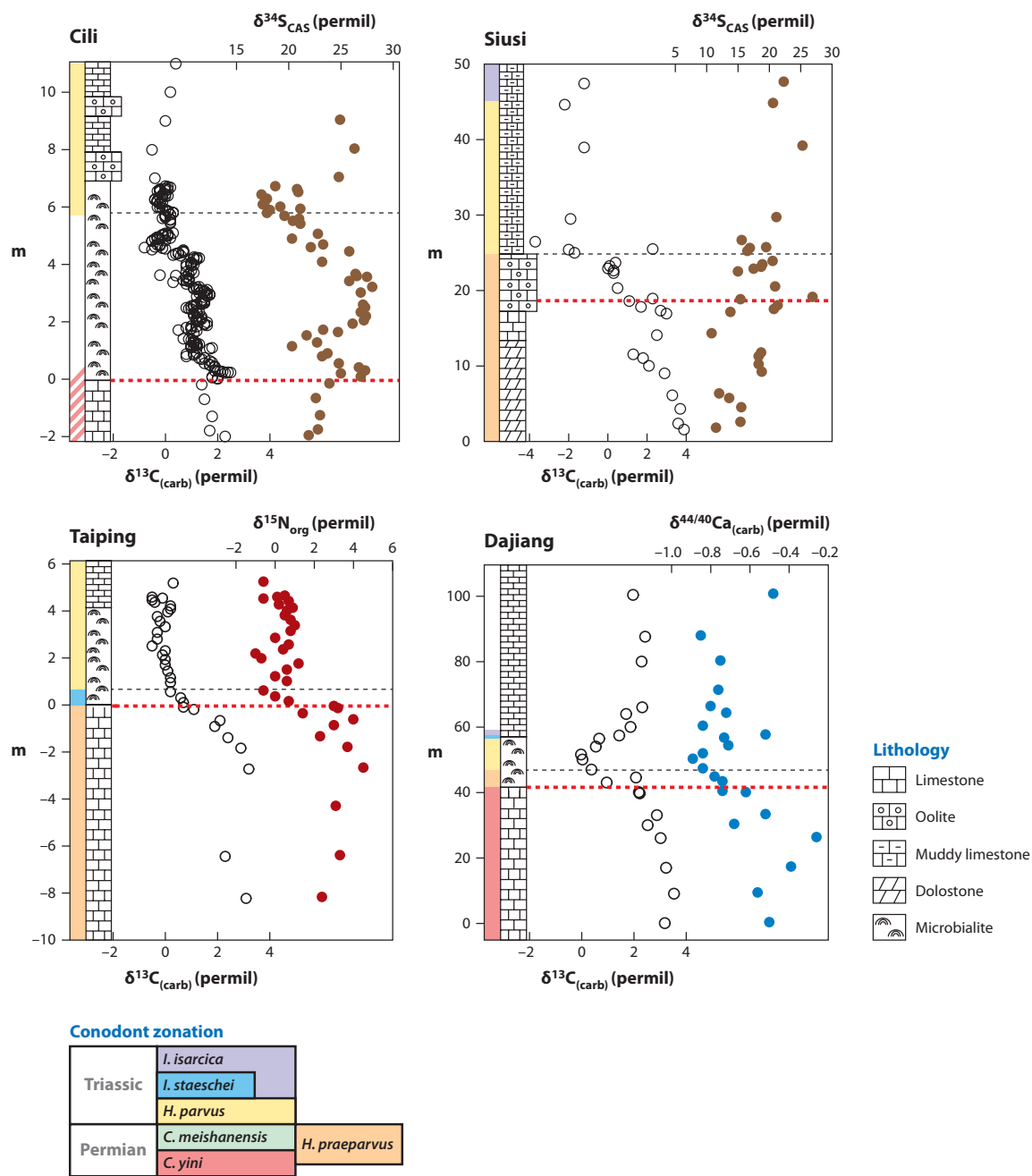


Figure 5

Coupled isotope records from representative Permian-Triassic (P-Tr) boundary sections. Cili section from Luo et al. (2010); Siusi section from Newton et al. (2004); Taiping section from Luo et al. (2011); Dajiang section from Payne et al. (2010). All symbols as in **Figure 4**. Cross-hatched pattern in the conodont zonation for lower Cili section indicates constraints based on foraminifera, and carbon isotopes suggest correlation with the *Clarkina yini* zone. Conodont zonation for Dajiang is based on correlative strata at Heping (Krull et al. 2004) and Dawen (J. Chen et al. 2009), on the same carbonate platform. Error bars on calcium isotope values indicate one standard deviation based on replicate measurements. Abbreviations: (carb), carbonate; CAS, carbonate-associated sulfate; org, organic.

methane (-60%) was implausibly large. However, recent work on volcanic interactions with organic carbon in sedimentary basins suggests that volcanism can induce the volatilization of much larger quantities of carbon from sedimentary strata than had previously been appreciated (e.g., Svensen et al. 2009), opening the possibility that at least some carbon was derived from other pools.

Calcium Isotopes

Calcium isotope ($\delta^{44/40}\text{Ca}$) records have the potential to further constrain interpretations of carbon cycling because the two cycles are linked through the common sink of calcium carbonate burial. The only detailed calcium isotope record across the end-Permian extinction horizon exhibits a negative shift of approximately 0.3% in the micrite fraction of bulk carbonate rock (**Figure 5**). This excursion could reflect either a global shift in the proportion of aragonite versus calcite deposition (because these two polymorphs of CaCO_3 fractionate calcium isotopes differently relative to seawater) or a rapid increase in the calcium concentration of seawater, likely resulting from ocean acidification (Payne et al. 2010). If the latter scenario applies, variation in $\delta^{44/40}\text{Ca}$ values can be used to constrain the isotopic composition of injected carbon. The 0.3% excursion in $\delta^{44/40}\text{Ca}$ values suggests injected carbon $\delta^{13}\text{C}$ values near -15% and no lighter than -30% (see **Supplemental Sidebar 2**, Interpreting the P-Tr Boundary Carbon Isotope Excursion), ruling out biogenic methane as the sole source of injected carbon (Payne et al. 2010). Records from additional localities are required to determine the extent to which this signal is globally reproducible and whether it is likely to reflect a shift in the $\delta^{44/40}\text{Ca}$ of seawater.

Sulfur Isotopes

Similar to carbon isotope records, sulfur isotope records exhibit substantial variations near the end-Permian extinction and through the P-Tr transition more broadly. A long-term positive shift in $\delta^{34}\text{S}$ values of sulfate evaporites from $+12\%$ to $+28\%$ between the Late Permian and the late part of the Early Triassic (**Figure 1**) has been established for several decades (e.g., Cortecchi et al. 1981). More recently, analysis of $\delta^{34}\text{S}$ variation in pyrite and carbonate-associated sulfate has opened the possibility of examining sulfur cycle behavior at high resolution across the P-Tr boundary interval.

High-resolution sulfur isotope records from sedimentary pyrite and carbonate-associated sulfate typically exhibit variation of tens of permil (parts per thousand; ‰), often between stratigraphically adjacent samples (**Figure 5**; see also Algeo et al. 2008, Fenton et al. 2007, Gorjan et al. 2007, Kaiho et al. 2001, Kajiwara et al. 1994, Luo et al. 2010, Newton et al. 2004, Nielsen et al. 2010, Riccardi et al. 2006).

Interpretations of P-Tr boundary sulfur cycle dynamics from isotope records have focused on two possibilities: mixing of isotopically distinct and physically separated reservoirs and variation in the isotopic composition of the entire ocean sulfur reservoir. The rapidity and magnitude of the sulfur isotope excursions have led many authors to favor the former possibility. Kajiwara et al. (1994) and many subsequent authors (e.g., Algeo et al. 2008, Newton et al. 2004, Riccardi et al. 2006) proposed that isotopically distinct sulfur pools were segregated vertically in a stratified ocean, with negative isotope excursions in shallow-marine sections reflecting upwelling of waters from below the chemocline. In contrast, Luo et al. (2010) interpreted the excursions to reflect variation in the proportional burial of pyrite versus sulfate in an ocean with low sulfate concentrations ($<1\text{ mM}$). Kaiho et al. (2001) suggested that the negative shift resulted from a massive addition of ^{34}S -depleted sulfur from the mantle, which was released during a massive bolide impact.

The implications of the impact scenario (Kaiho et al. 2001) are implausible, requiring an asteroid of 30–60 km in diameter or a comet of 15–30 km in diameter, a resulting crater of 600–1,200 km, and a postimpact ocean pH of 1.5–2.5, the latter of which would likely have killed nearly all invertebrate animals. Oxidation of the sulfur would have consumed as much as 40% of the atmospheric O₂ reservoir.

Distinguishing between the upwelling and low-sulfate scenarios remains a challenge, as both explain large-amplitude, short-term variation in $\delta^{34}\text{S}$ values as well as correlation between the $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ records (Algeo et al. 2008, Luo et al. 2010). Because the upwelling scenario is inherently of local-to-regional scale, the demonstration of correlative excursions at a global scale would point toward the low-sulfate scenario. However, determining whether features of the $\delta^{34}\text{S}$ record are indeed correlative across widely separated sections is challenging because many occur on timescales shorter than those resolved by biostratigraphy.

Nitrogen Isotopes

Decrease in the nitrogen isotopic ($\delta^{15}\text{N}$) composition of organic carbon across the end-Permian extinction horizon suggests an increased proportional contribution of nitrogen fixers (e.g., cyanobacteria) to preserved organic matter. $\delta^{15}\text{N}$ values exhibit a negative shift of approximately 3‰ at Meishan (Cao et al. 2009) and in two shallow-marine sections from the Nanpanjiang Basin of south China (Luo et al. 2011) (**Figure 5**). In contrast, $\delta^{15}\text{N}$ values show little variation across the boundary interval at the Guryul Ravine section of Kashmir (Algeo et al. 2007). Decreases in $\delta^{15}\text{N}$ values and enhanced nitrogen fixation are predicted under conditions of widespread marine anoxia and consistent with many other lines of evidence (e.g., Isozaki 1997, Wignall & Twitchett 2002).

Organic Geochemistry

Organic geochemical analysis has provided important confirmation of shallow-marine anoxia. Isorenieratane and aryl isoprenoids (molecular fossils derived from isorenieratene, a photosynthetic pigment produced by green sulfur bacteria) occur in P-Tr boundary sediments at Meishan and in the Hovea-3 core (Grice et al. 2005). Because green sulfur bacteria require sunlight and hydrogen sulfide to conduct photosynthesis, this finding supports interpretations of shallow-marine anoxia and euxinia around the time of the main extinction pulse. Cao et al. (2009) recovered isorenieratane at many stratigraphic levels within Changhsingian strata at Meishan, suggesting that photic-zone euxinia developed at least intermittently through Changhsingian time, long prior to the main extinction event. Thus, if anoxia was a cause of extinction, it must have surpassed a threshold of biological tolerance during the latest Changhsingian. However, the co-occurrence of abundant isorenieratane with diverse benthic invertebrate assemblages suggests that green sulfur bacteria may have thrived during intervals, perhaps seasonal, of photic-zone euxinia that were neither extensive nor prolonged enough to significantly impact animal communities. Alternatively, the occurrence of seafloor microbialites in the boundary interval at Meishan (Cao & Zheng 2009) and in the Hovea-3 core (Thomas et al. 2004) opens the possibility that the biomarkers derive from photosynthetic seafloor microbial mats rather than organisms living within a euxinic water column. The former possibility is consistent with recently reported uranium isotope evidence for an expansion of ocean anoxia coincident with the mass extinction event (Brennecke et al. 2011).

Biomarker data also point toward an increase in the proportional contribution of microbial biomass to organic deposits through the boundary interval. At Meishan, increases in the abundances of 2-methylhopanes relative to other hopanes, and of hopanes relative to steranes (Xie et al. 2005), have been interpreted to reflect increased cyanobacterial contribution to primary production and overall changes to microbial community composition (Cao et al. 2009). However, recent

genetic and phylogenetic work shows that other bacterial groups also produce 2-methylhopanoids, limiting the utility of this molecule as a cyanobacterial biomarker (Welander et al. 2010).

Organic geochemical data from marine sections have also been interpreted to reflect the collapse of terrestrial ecosystems. Dibenzofurans and other polycyclic aromatic hydrocarbons occur in elevated abundance in Upper Permian strata from China, Italy, and Greenland (Fenton et al. 2007, Sephton et al. 2005, Wang & Visscher 2007), possibly reflecting increased contributions of soil organic carbon and even catastrophic collapse of the terrestrial flora (e.g., Sephton et al. 2005). However, Grice et al. (2007) observed a negative excursion in the $\delta^{13}\text{C}$ of these molecules across the P-Tr boundary within the Hovea-3 core. Permian $\delta^{13}\text{C}$ values are consistent with a terrestrial source, whereas Triassic values are more consistent with a marine source, likely algae. Cao et al. (2009) argued that long-term organic records indicate lithological and diagenetic controls on the abundances of these molecules, rather than indicating denudation of the land surface. Consequently, the extent to which the organic geochemical record reflects terrestrial ecosystem collapse remains uncertain.

SUMMARY OF PATTERN

Any successful explanation for the end-Permian mass extinction must account for the following observations. First, the extinction was the most severe biotic crisis of the Phanerozoic, affecting both marine and terrestrial ecosystems. Second, the main extinction pulse occurred over a timescale shorter, and likely much shorter, than a few hundred thousand years. Third, marine animals with limited physiological capacity to buffer themselves against changes in ambient $p\text{CO}_2$, temperature, pH, and oxygen concentration were preferentially victimized. Fourth, sedimentary fabrics, pyrite framboid abundances, and organic biomarkers suggest widespread ocean anoxia and euxinia that reached shallow-marine habitats at least episodically, beginning during Changhsingian time but peaking in intensity around the main extinction pulse. Fifth, the $\delta^{13}\text{C}$ composition of carbonate rocks and organic carbon began to decrease shortly before the main extinction pulse and dropped most abruptly, coincident with the mass extinction. Sixth, environmental disruption and its biological consequences continued through much of the Early Triassic.

GEOLOGICAL TRIGGERS

During the past decade, debate over the causes of the end-Permian mass extinction has focused on three geological triggers. These are (a) bolide impact; (b) overturn or upwelling of deep water in a stratified, anoxic ocean; and (c) flood basalt volcanism.

Bolide Impact

A major bolide impact is consistent with the rapidity and magnitude of the mass extinction, but it does not easily explain the selectivity against physiological traits rather than dietary traits, the evidence for persistent ocean anoxia, or the long-term perturbations recorded by carbon and sulfur isotopes.

Beyond these issues, the geological and geochemical evidence for bolide impact has been strongly challenged. Reports of fullerene molecules trapping helium and argon with extraterrestrial isotopic compositions (Becker et al. 2001) have not been reproduced in independent analyses of the same samples (Farley & Mukhopadhyay 2001) or from additional P-Tr boundary localities (Farley et al. 2005, Koeberl et al. 2004). A subsurface feature off the coast of Australia interpreted by Becker et al. (2004) as an end-Permian impact crater has been similarly challenged on the basis of poorly constrained age (Renne et al. 2004) and the absence of tsunami-type deposits at the P-Tr

boundary in nearby sedimentary basins (Wignall et al. 2004). The unusually pristine condition of meteorite fragments at the P-Tr boundary in terrestrial deposits from Australia (Basu et al. 2003) has raised questions regarding the likelihood that such grains could be preserved unaltered (French & Koeberl 2010). Subsequent attempts to identify additional meteorite grains from the original samples have so far failed (reported in French & Koeberl 2010). Overall, this paucity of evidence for impact stands in stark contrast to the plenitude of evidence that has emerged at the Cretaceous-Paleogene boundary (Schulte et al. 2010) and suggests that bolide impact is unlikely to have caused the end-Permian mass extinction.

Ocean Anoxia and Euxinia

Intrusion of oxygen-depleted waters into shallow-marine habitats at the end of the Permian can account for extinction rate and magnitude, assuming end-Permian ocean anoxia was more pervasive or prolonged than other ocean anoxic events. It can also explain the deposition of laminated sediments, small framboids, and biomarkers for green sulfur bacteria, as well as short- and long-term perturbation of the carbon and sulfur isotope records.

However, anoxia and euxinia alone are insufficient to account for several aspects of end-Permian global change. In isolation, anoxia and euxinia would be unlikely to cause the observed pattern of physiological selectivity (Knoll et al. 2007) and the lack of selectivity across environments (Chen et al. 2011). Furthermore, persistent shallow-marine anoxia could be sustained only in areas of upwelling because wind mixing tends to keep the surface ocean in near equilibrium with atmospheric composition (Meyer et al. 2008). Shallow-marine anoxia or euxinia could not have been both temporally persistent and geographically widespread unless atmospheric oxygen levels were far lower than the values indicated by model reconstructions (e.g., Berner 2006). Similarly, global ocean biogeochemical models suggest that deep-marine anoxia is maintained by high nutrient levels in seawater and that scenarios involving simple overturn of a stratified ocean with CO₂- and H₂S-charged deep waters are physically unrealistic (e.g., Meyer et al. 2008). Finally, the mechanism by which ocean anoxia and euxinia could cause simultaneous terrestrial and marine extinctions (Twitchett et al. 2001) remains poorly understood. Hydrogen sulfide release from the ocean to the atmosphere was proposed as a link between the two (Kump et al. 2005), but more recent 3D models (Harfoot et al. 2008) suggest that the required magnitude of sulfur release is higher than that proposed by Kump et al. (2005) and that the rate of release of H₂S from the oceans is less than required owing to biological utilization of reduced sulfur in the surface ocean (Meyer et al. 2008). Low sulfur concentrations in P-Tr seawater (Luo et al. 2010) would further reduce the likelihood that H₂S release factored in terrestrial extinctions.

Although end-Permian scenarios triggered by overturn of a stratified, anoxic and euxinic ocean continue to be advocated (Şengör & Atayman 2009), the currently more common view is that ocean anoxia and euxinia were sustained via high productivity in a nutrient-rich ocean (e.g., Meyer et al. 2008). These biogeochemical conditions may have contributed to the severity of marine extinctions but were neither the ultimate trigger of the catastrophe nor the only proximal cause of population collapse (e.g., Erwin 2006, Knoll et al. 2007, Meyer & Kump 2008, Wignall 2001).

Flood Basalt Volcanism

Recent advances in understanding the volcanism of the Siberian Traps suggest that emplacement of this large igneous province (> 5 million km³ of basalt intruded into the Tunguska Basin of central Russia) can account for nearly all features associated with the end-Permian mass extinction.

First, eruption of the Traps can explain the timing of the extinction event. Radiometric evidence that emplacement of the Siberian Traps was broadly coeval with marine extinctions has existed

for two decades (Renne et al. 1995), but increasingly precise dating of both the basalts and the mass extinction has greatly strengthened the case for synchronicity (Kamo et al. 2003, Mundil et al. 2004, Reichow et al. 2009, Shen et al. 2011).

Second, the unparalleled magnitude of the extinction event can be accounted for by Traps eruptions. The Siberian Traps (including extensive basalts in the subsurface of the West Siberia Basin) constitute one of the largest, if not the largest, continental flood basalt provinces that erupted during Phanerozoic time (Reichow et al. 2002, Wignall 2001). Beyond the simple volume of the Siberian Traps, increasing recognition of the extent of interaction between the basalts and sedimentary rocks in the Tunguska Basin has strengthened the case that the basalt eruptions could have released a sufficient quantity of volatiles to disturb climate as well as atmospheric and ocean chemistry and thereby cause mass extinction. Campbell et al. (1992) recognized that extensive interaction between basalts and anhydrite in the sedimentary cover of the Tunguska Basin could have led to massive release of sulfur volatiles into the upper stratosphere. They hypothesized that resulting global cooling, ice sheet growth, and sea-level fall could account for the mass extinction. However, there is no evidence for glaciation at this time. Svensen et al. (2004) hypothesized that degassing of carbon from organic deposits could also have resulted in massive CO₂ release. Svensen et al. (2009) illustrated the numerous gas explosion structures near the margins of the Siberian Traps and interpreted them to reflect catastrophic gas release events owing to overpressure in the subsurface when magma volatilized sedimentary country rock. They calculated that Traps eruptions could have released more than 30,000 GT (1 GT = 10¹⁵ g) of carbon into the atmosphere, more than five times as much as past and estimated future anthropogenic carbon emissions (Caldeira & Wickett 2003). Comparative analysis suggests not only that the Siberian Traps were the largest continental flood basalt province, but also that they interacted more extensively with volatile-rich country rock than did any other province (Black et al. 2012, Ganino & Arndt 2009).

Third, the release of vast amounts of CO₂ can account for the preferential extinction of heavily calcified marine animals with limited physiological buffering capacity (Knoll et al. 2007), as well as account for the limited selectivity on biogeographic parameters such as geographic range (Clapham & Payne 2011, Payne & Finnegan 2007) or environmental preference (Chen et al. 2011). Although changes in ocean redox state are better recorded than changes in *p*CO₂, pH, and temperature, we reason that ocean pH, *p*CO₂, and carbonate saturation state were the more important drivers of extinction. As discussed above, hypoxia and anoxia are difficult to maintain over long timescales in the mixed layer (upper 100–200 m) owing to wind mixing with the large atmospheric oxygen reservoir. In contrast, release of acid volatiles (e.g., CO₂ and SO₂) would cause reductions in ocean pH and carbonate saturation state even in the surface ocean and may preferentially affect the surface ocean if emitted quickly enough (Caldeira & Wickett 2003). In the absence of a large reservoir of fine-grained, unlithified deep-sea carbonate sediment, whole-ocean acidification could likely last for tens of thousands of years (Archer et al. 1997), and few refugia would exist—survival would depend primarily on long-term physiological tolerance of altered conditions.

Fourth, Siberian Traps volcanism can explain the increased prevalence of marine hypoxia and anoxia associated with the P-Tr boundary interval. Biogeochemical modeling shows that extensive and prolonged marine anoxia requires increased nutrient supply and is maintained by the excess flux of organic carbon relative to oxygen supplied by physical mixing, rather than resulting simply from global warming or a reduction in the rate of physical mixing (Meyer et al. 2008). On geological timescales, phosphate supplied by the chemical weathering of silicate rocks is likely the nutrient that limits productivity in marine systems. An increase in chemical weathering rates on land is predicted on the basis of the Siberian Traps volatile flux and can therefore account for the increased prevalence of ocean anoxia at this time, as well as increased sediment fluxes to marine depositional

systems (Algeo & Twitchett 2010). Beyond explaining marine extinctions, climate change induced by Siberian Traps volatile emissions and possible destruction of the ozone layer by organohalogen release (Svensen et al. 2009, Visscher et al. 2004) may explain the coincident collapses of terrestrial and marine ecosystems.

We hypothesize that ongoing Siberian Traps volcanism during Early Triassic time (Kamo et al. 2003, Reichow et al. 2009) explains the persistence of $\delta^{13}\text{C}$ excursions (**Figure 1**) and repeated episodes of shallow-marine anoxia (Wignall & Twitchett 2002) and associated evidence of delayed biotic recovery (e.g., Fraiser & Bottjer 2005, Hallam 1991), although the record is not yet sufficiently resolved to quantify rates and magnitudes of magmatic and volatile release within individual substages or biostratigraphic zones. Sustained anoxia can also explain the positive excursion in the $\delta^{34}\text{S}$ of Early Triassic evaporites through the preferential burial of sulfur as pyrite under euxinic conditions.

LESSONS FOR THE TWENTY-FIRST CENTURY

As human impacts push environmental conditions to extremes not experienced in the recent past, the geological record is increasingly essential as an archive of past experiments in global change. Carbon release events from the more recent geological past, such as the Paleocene-Eocene Thermal Maximum and other hyperthermal events, allow for more detailed documentation of Earth system changes on short timescales. However, the rates of carbon release associated with these events may have been smaller than those that Earth is currently experiencing (Cui et al. 2011) and so may lead us to underestimate the potential biotic response. The end-Permian rock record cannot currently provide the temporal and spatial resolutions to make specific predictions about expected changes in the coming decades or centuries, but increasing evidence that the end-Permian mass extinction was precipitated by rapid release of CO_2 into Earth's atmosphere is a valuable reminder that the best—and most sobering—analogs for our near future may lie deeper in Earth's past.

SUMMARY POINTS

1. The end-Permian mass extinction event eliminated 79% of marine invertebrate genera and had similarly severe effects on the terrestrial biota.
2. The main pulse of extinction was a single, geologically rapid event that occurred over less, and likely much less, than 200,000 years.
3. In the oceans, heavily calcified animals with limited physiological capacity to buffer internal fluid composition against a changing external environment were preferentially victimized.
4. Ocean anoxia was widespread, if episodic, during Changhsingian time. The prevalence of anoxia increased near the time of the main extinction pulse, and widespread anoxia continued, perhaps intermittently, during Early Triassic time. Anoxic and sulfide-bearing waters commonly extended into shallow-marine habitats. Although selectivity patterns appear better explained by the effects of changes in ocean pH, $p\text{CO}_2$, and carbonate saturation level, widespread hypoxia would have increased the sensitivity of many organisms to changes in these other environmental parameters.

5. The scenario that best explains these observations invokes the eruption of the Siberian Traps large igneous province as the primary trigger of extinction. Release of volcanic CO₂ as well as volatilized sedimentary organic carbon and evaporite minerals led to global warming, ocean acidification, and perhaps destruction of atmospheric ozone, while enhanced weathering and nutrient runoff exacerbated preexisting ocean anoxia. These Earth system changes caused global population declines and resulted in mass extinction.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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