End-Permian mass extinctions: A review

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ABSTRACT

Two mass extinctions brought the Paleozoic to a close: one at the end of the Guadalupian, or middle Permian (ca. 260 Ma), and a more severe, second event at the close of the Changhsingian Stage (ca. 251.6 Ma). Here we review work over the past decade that defines the probable causes of the mass extinction, and evaluate several extinction hypotheses. The marine extinctions were selective; epifaunal suspension feeders were more affected than other clades, although significant variations occurred even among the filter feeders. In southern China, the Changhsingian marine extinction was nearly catastrophic, occurring in <0.5 m.y. On land, vertebrates, plants, and insects all underwent major extinctions. The event coincides with (1) a drop of $\delta^{13}C$ in carbonates, from $\sim +2‰$ to $-2‰$ in both marine and terrestrial sections; (2) the eruption of the massive Siberian continental flood basalts; and (3) evidence of shallow-water marine anoxia, and perhaps deep-water anoxia. Although the cause of the extinction remains unclear, a series of constraints on speculation have been established in the past few years. Leading contenders for the cause are the climatic effects, including acid rain and global warming, possibly induced by the eruption of the Siberian flood basalts; and marine anoxia. An extraterrestrial impact is consistent with the geochronological and paleontological data from southern China and elsewhere, and some possible evidence for impact has recently been advanced.

INTRODUCTION

The role of mass extinctions and subsequent biotic recoveries in determining the course of the history of life has become widely appreciated in the past two decades. At least five major mass extinctions occurred during the past 540 m.y., and while many paleontologists accept an extraterrestrial impact as the primary cause of the end-Cretaceous mass extinction, other causes are much less well understood. A full understanding of mass extinctions requires an integration of the details of the fossil record, changes in the chemistry of oceans and atmo-

spheres, the tempo of extinction, and the distinction between triggers and mechanisms. The end-Permian mass extinctions are the most profound in the past 540 m.y., and although our understanding of these extinctions has advanced considerably in the past decade, we remain far from understanding either the trigger or mechanisms of extinction.

Many once widely accepted views of the end-Permian extinction have now been repudiated. For example, new data have led to rejection of older views of a single prolonged extinction (Teichert, 1990), perhaps peaking in the latest Permian (Erwin, 1993). Careful analysis has demonstrated the presence of two

discrete pulses of extinction, the first near the Capitanian-Wuchiapingian boundary, and the second at the close of the Changhsingian Stage (Fig. 1) (Stanley and Yang, 1994; Jin et al., 1994). The development of a reliable conodont biostratigraphy, coupled with chemostratigraphy and a reliable temporal framework from geochronology, has produced a detailed picture of events during the Permian-Triassic (P-Tr) transition (Fig. 2). Less is known of the earlier extinction phase, in part because development of a reliable global chronostratigraphy is pending.

The information developed over the past decade constrains the possible explanations of this event, and using this information we evaluate a number of proposed causes of the latest Permian or Changhsingian mass extinction. The classic argument that the extinction is a result of the formation of the supercontinent of Pangea has long been untenable (Erwin, 1993). Other hypotheses have been rejected by the rapidity of the extinction, now shown to be <0.5 m.y. at marine sections in southern China (Bowring et al., 1998; Jin et al., 2000a). Simi-

larly, other explanations invoked a global lowstand in sea level, based in part on the apparent paucity of marine boundary sections across the P-Tr boundary (Erwin, 1993). Although regression may have been involved in the relatively poorly known end-Guadalupian event, sequence stratigraphic analysis has shown that a transgression began in late Changhsingian time and extended across the boundary into the Early Triassic (Wignall and Hallam, 1997).

In this chapter we review the stratigraphic framework and then turn to the pattern of extinction through the Late Permian and the geological context. This review focuses largely on developments since earlier reviews (Erwin, 1993, 1994; Wignall and Hallam, 1997). We close with a brief discussion of the aftermath of the extinction, the biotic recovery in the Early Triassic.

BIOSTRATIGRAPHIC FRAMEWORK

The Late Permian has been the subject of more detailed biostratigraphic analysis than the Early Triassic, yet widespread marine regression and biotic provincialism have made the Late Permian the most problematic part of the P-Tr boundary sequence. Earlier reliance upon ammonoid, brachiopod, and fusulinid foraminiferal biozones has now largely been replaced by higher resolution conodont biostratigraphy through the P-Tr boundary (e.g., Sweet et al., 1992; Mei et al., 1998). Although some difficulties still persist over precise conodont identifications, conodont biostratigraphy has produced important advances in global correlations of marine sections, including fewer latitudinal, facies, and biogeographic problems, although direct Tethyan-Boreal-Gondwanan correlations remain difficult. Attempts to correlate Permian successions of conodont zones in warm water and cold water are particularly encouraging. For example, the Salt Range sequence of the Permian was reestablished as a link between the Tethyan and Gondwanan realms. Work by the Permian Subcommission of the International Union of Geological Sciences has produced a widely accepted biostratigraphic framework for the Permian (Fig. 1) in which conodont zones define stage boundaries (Jin et al., 1997). Detailed discussions of global and regional biostratigraphic correlation (Sweet et al., 1992; Dickins et al., 1997; Jin et al., 1998; Lucas and Yin, 1998; Yin et al., 2000) have been supplemented by detailed chemostratigraphy and magnetostratigraphy for many critical sections. The sharp shift in carbon isotopes at the P-Tr boundary provides additional support for biostratigraphic correlations.

Correlations between the marine and terrestrial realm, however, have proven far more difficult. The first appearance of the *Lystrosaurus* vertebrate assemblage has long been taken as the P-Tr boundary, particularly in the relatively abundant faunas of southern Africa (Rubidge, 1995; Ward et al., 2000). The overlap between *Lystrosaurus* and the underlying *Dicynodon* zone in South Africa has increased the problems in precisely identifying the position of the P-Tr boundary (Smith,

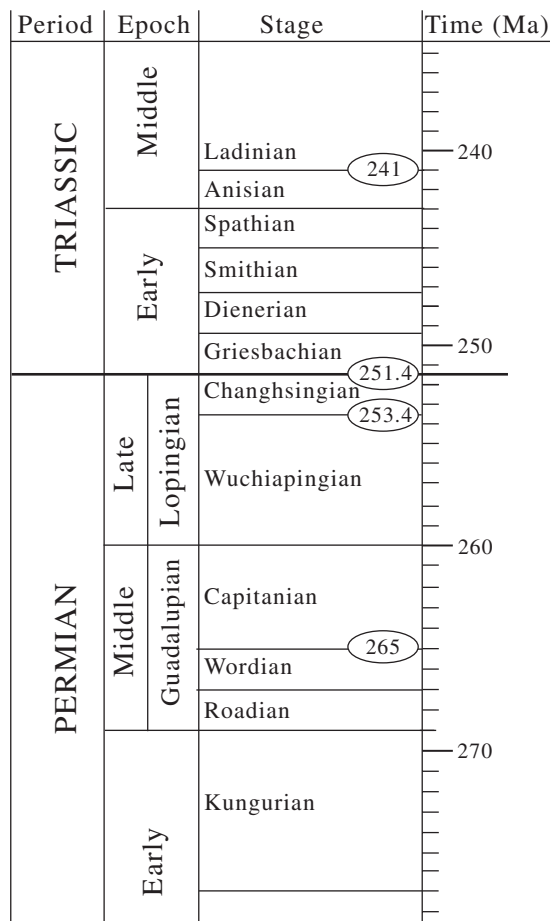| Period	Epoch		Stage	Time (Ma)
TRIASSIC	Middle		Ladinian	241 — 240
			Anisian	
	Early		Spathian	
			Smithian	
			Dienerian	
			Griesbachian	— 250
PERMIAN	Late	Lopingian	Changhsingian	251.4
				253.4
			Wuchiapingian	
	Middle	Guadalupian	Capitanian	— 260
			Wordian	265
			Roadian	
	Early		Kungurian	— 270

Figure 1. Stratigraphic framework for Permian and Early and Middle Triassic, including geochronologic date control. Established geochronology is in circles; interpolated time scale is to right. Permian dates are from Bowring et al. (1998) and Ladinian date is from Brack et al. (1996).
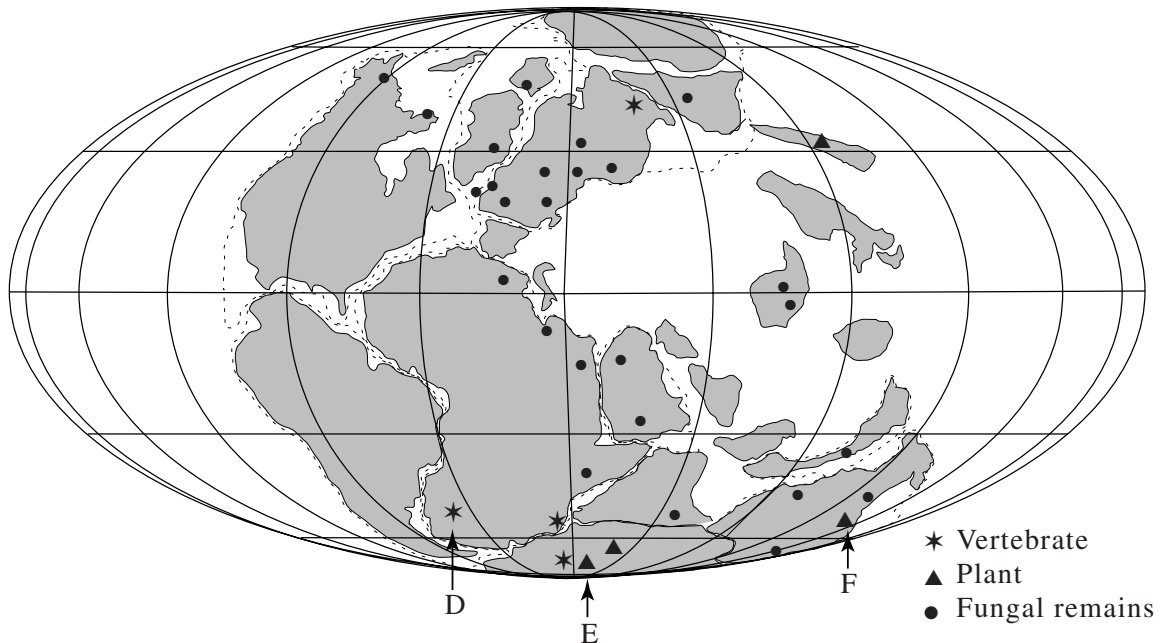
Marine sites
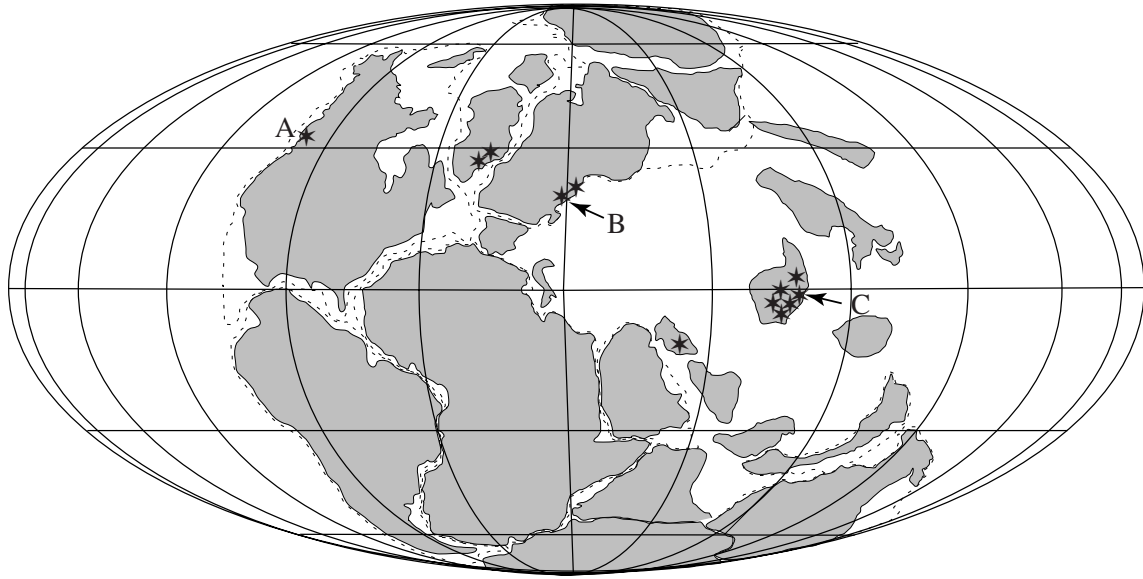
Terrestrial sites

Figure 2. Marine sites: Distribution of important marine Permian-Triassic (P-Tr) boundary sites on Late Permian continental reconstruction. Note paucity of sites outside southern China, where more than 50 putative P-Tr boundary sites have been described. Marine sites: A—terranes in British Columbia, Canada; B—Garternkofel core in western Austria; C—southern China. Terrestrial sites: Distribution of terrestrial P-Tr boundary information on Late Permian continental reconstruction, showing distribution of vertebrate, plant, and fungal remains. D—Karoo deposits of South Africa; E—plant and vertebrate material from Antarctica; F—plant deposits from eastern Australia. Data were compiled from variety of sources cited in text.

1995; MacLeod et al., 2000; Ward et al., 2000). However, the wide distribution of many tetrapod genera across Pangea has aided interregional correlations, and the co-occurrence of amphibians with ammonoids in some sections has strengthened correlation between marine and terrestrial sections (Lozovsky, 1998). Chemostratigraphy (e.g., MacLeod et al., 2000), magnetostratigraphy (Jin et al., 2000b), pollen (Visscher et al., 1996), and a fungal spike at the boundary have all served as the basis of intraregional correlation, as has the disappearance of coal (e.g., Retallack et al., 1996; Faure et al., 1995). The strongest evidence for a close correlation between marine and terrestrial events comes from sections in East Greenland where terrestrial palynomorphs are found with marine fossils across the Permian-Triassic boundary (Twitchett et al., 2001). An abrupt shift in $\delta^{13}C_{carbonate}$ and changes in fossil abundance and diversity occur about 24 m below the first appearance of the diagnostic earliest Triassic conodont *Hindeodus parvus*. This establishes that the marine and terrestrial disturbances are roughly synchronous. Despite these advances, placement of the boundary in some areas remains difficult (e.g., Australia; Foster et al., 1998).

EXTINCTION PATTERNS AND SELECTIVITY

Patterns of extinction and survival have been analyzed on global, regional, and local scales for the marine realm and on global and regional scales for plants and terrestrial vertebrates.

Marine

The end-Permian mass extinction marks the demise of distinctive Paleozoic communities dominated by epifaunal, suspension-feeding clades, including articulate brachiopods, crinoids, blastoids, tabulate and rugose corals, and stenolaemate bryozoans (summarized in Erwin, 1993; Wignall and Hallam, 1997). Clades that dominate modern shallow-marine ecosystems, including bivalve and gastropod molluscs, arthropods, and nautiloid cephalopods, underwent far less extinction. Some relatively minor Permian groups, including blastoids and the last few trilobites, disappeared completely, while others, notably the echinoids, survived with only a few species. Even within these broad clades, however, considerable variation in extinction selectivity has been identified, and clues to the causes of this severe biotic crisis may be within such selective patterns.

Sepkoski's (1992) compendium of marine families and genera remains the best global view of patterns of extinction and survival, despite continuing questions about the reliability of some of the stratigraphic data. The compendium provides a benchmark for more detailed investigations of individual clades. Overall, Sepkoski's data show a 54% extinction of marine families, with generic disappearances of 58% at the Capitanian, and 67% for the Changhsingian (Stanley and Yang, 1994). From the 1979 estimates of 52% loss of families and 17% of orders, Raup (1979) applied the rarefaction curves from modern echinoids to estimate the species extinction as 96% for the entire Late Permian interval; rarefaction based on 65% loss of genera yielded an estimated species loss of 88%. These results were criticized by Stanley and Yang (1994), in part because the extinctions were clearly taxonomically selective, rather than random, as assumed by a rarefaction approach. Their revised estimate of global marine extinction, based on observed generic extinctions, is 76%–84%, although Stanley and Yang conceded that this is an underestimate. (Stanley and Yang subtracted the effects of background extinction from their estimates, but also underestimated the duration of the Lopingian.) Calculated species extinctions in southern China (Yang et al., 1993), the only region where data are available at this level, are much closer to Raup's original result than to Stanley and Yang's revised estimate.

Different patterns of extinction are also well documented among reef communities. Although many well-developed middle Permian reefs disappeared at the close of the Capitanian as their marine basins were eliminated (e.g., west Texas, Zechstein), other diverse reefs persisted through the Late Permian in southern China (Fan et al., 1990; Reinhardt, 1988), including probably the youngest Paleozoic coral reef (Shen et al., 1998), in Greece (Flügel and Reinhardt, 1989; see also Flügel, 1994, for discussion), and as calcisponge-dominated reefs in Tunisia (Toomey, 1991). Thus, reefs were not completely eliminated by the first phase of the Permian extinctions, as previously thought.

The highly selective patterns of extinction received a new explanation from Knoll et al.'s (1996) analysis of differences in metabolic capability. Using Sepkoski's (1992) generic data set, Knoll et al. recorded 65% extinction during the Capitanian, and 81% extinction during the Changhsingian among groups characterized by a heavy, calcified skeleton, gas-permeable surfaces rather than gills, weak internal circulation, and low metabolic rates. This group includes tabulate and rugose corals, stenolaemate bryozoans, brachiopods, and blastoid and crinoid echinoderms. In contrast, clades with active gills, active circulatory systems, and relatively high metabolic rates exhibit 49% and 38% extinction percentages during these two intervals. This group includes most molluscs, arthropods, conodonts, and other vertebrates. Knoll et al. (1996) proposed that this pattern of extinction selectivity matches that expected for extinctions induced by hypercapnia, or high concentrations of carbon dioxide (see following discussion).

The first pulse of extinction occurred at the end of the Capitanian, and what some had viewed as a statistical artifact of a poor fossil record now appears to be a discrete episode (Stanley and Yang, 1994; Jin et al., 1994; Shen and Shi, 2000, for brachiopods; Wang and Sugiyama, 2000, for corals), although the duration of this episode and whether it is simultaneous across the globe remain unexamined. Stanley and Yang (1994) used three statistical tests to determine whether the apparent Capitanian extinction phase could have been produced by preservational bias; the results do not support a preservational artifact. Blastoid echinoderms became extinct at this point, and most

tabulate and rugose corals became extinct; only a few survived into the Wuchiapingian before disappearing during the Changhsingian (Wang and Sugiyama, 2000). Crinoids and fusulinid foraminifera nearly disappeared

This first crisis was coincident with a major global sea-level fall in the late Guadalupian that drained the shallow epicontinental seas of the Gondwana, North America, and Boreal realms. The endemic faunas in these epicontinental seas were extinguished as their habitats were eliminated, but the magnitude of the extinction may be exaggerated by limited records of Lopingian faunas. In the Tethys, benthic groups that flourished on carbonate platforms, such as the corals, fusulinids, and bryozoans, underwent a significant decline, but the survivors did not produce any new families during the Lopingian. Turnover occurred among ammonoids and conodonts, although diversity remained essentially the same during the Lopingian. The number of brachiopod families did not decrease significantly, although all the dominant elements of the Guadalupian brachiopod faunas disappeared. Nonfusulinid foraminifera, bivalves, and gastropods did not show distinctive changes at the family and generic levels (Jin et al., 1994).

Ammonoids have been particularly well studied because of their biostratigraphic utility. A global generic analysis of Permian ammonoids shows only a 44% (14 of 32 genera) extinction at the close of the Capitanian, within the range of other stage level boundaries, and far less than the 87% at the close of the Wuchiapingian. Of 33 genera, 32 (97%) disappeared at the end-Changhsingian (Zhou et al., 1996). This difference seems to suggest that the end-Capitanian was not as large as the end-Permian event, at least among ammonoids. However, the reliability of these data is uncertain. For example, Guadalupian ammonoid genera seemingly disappeared slightly later than most benthic faunas. In southern Hunan Province, China, the Guadalupian genera *Paraceltites*, *Roadoceras*, *Strigogoniatites*, *Cibolites*, *Altudocera*, *Doulingoceras*, and *Neogeoceras* extend to the very basal part of the Wuchiapingian, the *Clarkina postbitteri* zone, and Zhou et al. (1996) assigned them to the Wuchiapingian. However, they arguably disappeared as part of the end-Guadalupian event, significantly increasing the apparent rate of ammonoid extinction. In contrast, Yang and Wang (2000) referred the ammonoids from the very basal part of the Wuchiapingian to the Guadalupian fauna. Consequently they found the extinction rates of family, genera, and species to be 69%, 91%, and 100%, respectively, in southern China. Most genera that originated in the Wordian and Capitanian did not persist into the Lopingian; almost all genera that disappeared during the Wuchiapingian and Changhsingian also originated during these two stages Zhou et al. (1996).

The P-Tr boundary section at Meishan, Zhejiang Province, southern China, has been intensively studied, and is the global boundary stratotype; detailed investigations have revealed the faunal content of each bed. In addition, the carbon isotopes have been well studied, and many of the volcanic ash beds in the sequence have been precisely dated (Bowring et al., 1998; see

following). These data allowed Jin et al. (2000a) to evaluate the pattern of extinction within a well-defined chronostratigraphic and geochemical framework. By employing two statistical analyses of the extinction data, Jin et al. were able to test proposals for as many as three pulses of extinction at this locality (e.g., Yang et al., 1993; Yin and Tong, 1998).

The claim of multiple extinction horizons includes a first horizon corresponding to the disappearance of shallow-marine forms. The second proposed extinction pulse occurs in the middle of the boundary beds and is marked by the disappearance of Permian conodonts and the appearance of the first Triassic elements, as well as widespread marine anoxia. The third proposed extinction horizon corresponds to the disappearance of Permian relicts, including the final Permian brachiopods, and the initial diversification of Triassic faunal elements (Yang et al., 1993; Yin and Tong, 1998). Yin and Tong correlated the shift in $\delta^{13}C$ to the second extinction level, and suggested that a minute iridium anomaly, denoting the onset of the extinction, precedes the lower extinction horizon. These extinction levels correspond to inferred sequence boundaries, which, in combination with the carbon isotopic shifts, allow both regional and global correlation to other sections.

The development of statistical techniques based upon actual occurrence data has greatly aided interpretation of apparent extinction patterns (e.g., Meldahl, 1990; Marshall, 1994; Marshall and Ward, 1996). Due to preservational effects (the Signor-Lipps [1982] effect), the final occurrence of a taxon will precede the actual extinction. By analyzing fossil occurrences leading up to the apparent extinction horizon, the difference between the last known occurrence and the probable level of extinction may be estimated. This estimate places statistical constraints on discussions of extinction pattern.

Jin et al. (2000a) assembled data on the Meishan fauna, using the volcanic ash beds to construct a composite section of 64 horizons between the five local sections. In 162 genera, 333 species were recorded among foraminifera, fusulinids, radiolarians, rugosan corals, bryozoans, brachiopods, bivalves, cephalopods, gastropods, ostracods, trilobites, conodonts, fish, calcareous algae, and others. Of the 333 species, 161 disappeared below the P-Tr boundary beds (the extinction rate is <33% for each of these horizons). Confidence intervals were calculated for the 93 genera (265 species) with multiple occurrences. When the analysis was performed based on rock thickness, the 95% confidence intervals extend well above the boundary, reflecting the well-established depositional hiatus at the boundary beds. Using the dated ash beds, depositional rates were calculated and rock thickness converted to time. The confidence interval analysis was rerun; the 50% confidence intervals for all 93 genera are consistent with a sudden extinction at 251.4 Ma. The most reasonable interpretation of the data is a sudden extinction at 251.4 Ma followed by the gradual disappearance of a small number of surviving genera over the following million years. To test for higher or lower extinction horizons, the analysis was rerun with the 38 genera that cross the boundary, and

for the genera having confidence intervals that did not reach the P-Tr boundary. No support was found for a stepwise extinction. Stepwise, gradual, and catastrophic extinctions are expected to produce different patterns of decline (Meldahl, 1990). Jin et al. (2000a) plotted the age of last occurrence versus stratigraphic abundance for all 162 genera, and the results support a sudden extinction at 251.4 Ma followed by a gradual decline in surviving species.

Correlation to the dates from Meishan has allowed other groups to infer accumulation rates and assess the duration of the extinction. For the East Greenland section, Twitchett et al. (2001) estimated an extinction duration of between 10 and 60 k.y. Analysis of apparent Milankovitch cycles in the Gartnerkofel-1 core from western Austria suggest the extinction occurred in <60 k.y., with the carbon shift in <30 k.y. (Rampino et al., 2000).

Terrestrial

The Karoo basin of South Africa remains the key area for understanding terrestrial vertebrate extinction patterns through the P-Tr interval. Excellent fossiliferous sections crop out throughout the basin, and sediment accumulation rates were evidently high. Although precise correlation to marine rocks remains uncertain, a generally accepted correlation places the Oudeberg Member of the Balfour Formation and the *Cistecephalus* biozone as uppermost Guadalupian, with the *Dicynodon* biozone encompassing the entire Lopingian (Tatarian) (Rubidge, 1995). The P-Tr boundary occurs within a zone of overlap between *Dicynodon* and *Lystrosaurus* (Hotton, 1967; Smith, 1995; King and Jenkins, 1997), as supported by recent δ^{13}C chemostratigraphy (MacLeod et al., 2000). King (1991) recorded 85 reptilian genera (including therapsids) from the *Cistecephalus* zone, 16 from the *Dicynodon* zone and 23 from the *Lystrosaurus* zone of the earliest Triassic (including new forms). Unfortunately, identification of many of these genera is problematic, even with well-preserved and well-prepared material. Rubidge's (1995) detailed biostratigraphic analysis documents the extinction of 9 of 26 reptilian genera (including 8 genera of therapsids) between the *Cistecephalus* and *Dicynodon* zones. Of the 44 genera in the *Dicynodon* zone, 7 have been recovered from the overlying *Lystrosaurus* zone (at least one additional genus, a cynodont, must also have survived because the lineage persists into the Triassic; C. Sidor, 2001, personal commun.). The redescription of the amphibian *'Lydekkerina' puterilli* Broom from the *Lystrosaurus* zone of South Africa, previously thought to be a lydekkerinid or juvenile rhinesuchid, as a paedomorphic rhinesuchid (Shiskin and Rubidge, 2000) means that the most common amphibians of the Early Triassic are all small or medium sized, which Shiskin and Rubidge argued is consistent with increased aridity relative to the Permian.

Correlative with the overlap zone between *Dicynodon* and *Lystrosaurus*, Ward et al. (2000) reported a rapid change in sedimentary style from meandering to braided river systems

(see Smith, 1995), similar to the pattern reported from the P-Tr boundary in the Ural Mountains of Russia (Newell et al., 1999). This change in sedimentary style suggests a rapid die-off of terrestrial vegetation, a more arid climate, and rapid increases in sedimentation rate (Newell et al., 1999; Ward et al., 2000). Earlier work in the Karoo (e.g., Smith, 1995) suggested that the change in sedimentary style was diachronous across the basin, induced by uplift of the Cape Fold Belt, producing a more arid climate and a shift in vegetation. Thus, the conclusions of Ward et al. (2000) are highly dependant upon both their new correlations and the age of initiation of uplift relative to the extinction.

Similar evidence for a warmer and drier climate has been described in China, Australia, and Antarctica. Wang (1993, 2000) documented multiple charcoal horizons, desertification, and a decline in plant remains through the extensive Upper Permian red beds of the North China block, with a decimation of the flora at the P-Tr boundary. In both the Sydney basin, Australia (Retallack, 1999), and sections in Antarctica (Retallack and Krull, 1999), latest Permian swamps of the *Glossopteris* flora record a seasonal, humid, cold temperate climate. Although there is no difference in inferred paleolatitude, Early Triassic paleosols indicate a warmer climate with higher sedimentation rates (Retallack, 1999). The change in sedimentary style and inferred shift in climate correlate to the carbon isotopic shift at the P-Tr boundary, plant extinctions, and an increase in fungal remains. The record from Australia suggests that the change from the *Glossopteris*-dominated Permian floras to the *Dicroidium*-dominated earliest Triassic floras was abrupt (Retallack, 1995), and Retallack (1999) interpreted this as evidence of a post-apocalyptic greenhouse.

The global nature of the environmental disturbance is indicated by the widespread preservation of apparent fungal remains at the P-Tr boundary. Visscher et al. (1996) reported abundant fungal remains from the terrestrial component of palynomorph assemblages in marine rocks from the western Alps and from southern Israel, and summarized evidence of a similar horizon from the Canadian Arctic through paleo-Tethys to southern China, India, Malaysia, and Australia. This fungal spike is reminiscent of the increased abundance of fern spores immediately after the Cretaceous-Tertiary (K-T) boundary, but actually begins before the marine P-Tr extinction. The geochronologic results from the Meishan section (Bowring et al., 1998), in conjunction with the record of fungal spores from this section (Ouyang and Utting, 1990), establish that the increase in fungal remains began gradually below the P-Tr boundary and the associated isotopic shift, and decreased abruptly above the boundary. This pattern confirms the suggestion of Visscher et al. (1996) that the duration of the fungal anomaly was more than 1 m.y. Visscher et al. (1996) argued that this pattern represents an extensive die-back of terrestrial vegetation and ecosystem collapse. Megafloral evidence is consistent with an extinction of Permian conifers at the family level in Europe, and a temporary increase in bryophyte abundance in the earliest

Triassic. Further evidence of the magnitude of the terrestrial crisis comes from the complete lack of coal deposition during the Early Triassic (Faure et al., 1995; McLoughlin et al., 1997; Retallack et al., 1996; Veevers et al., 1994).

GEOLOGICAL CONTEXT

Here we consider the general geological setting of the end-Permian mass extinction, including stable isotopes, magneto-stratigraphy, geochronology, and the climate record. To avoid repetition, elements common to several extinction hypotheses are discussed here, including changes in sea level and the general issue of marine anoxia. Aspects specific to single extinction hypotheses are discussed in the following section.

Stable isotopes

The Late Permian to Early Triassic interval encompassed some of the most dramatic shifts in carbon isotopes since the late Neoproterozoic and Cambrian. An early synthesis for six Tethyan sections (Baud et al., 1989) described a gradual decline from ~ +4‰ during the Guadalupian and a sharp fall to −1‰ near the Dzulfian-Dorashamian boundary (now approximately equal to the Wuchiapingian-Changhsingian boundary), a recovery to +4‰ in the basal Dorashamian, and a gradual decline to ~ −2‰ at the P-Tr boundary. The Early Triassic data are fairly stable at ~ +0.5‰ to +1‰. In addition to the short-term shifts associated with the extinction, the overall pattern involves an abrupt drop of ~3‰ from the Late Permian into the Early Triassic, indicating a major, long-term shift in the carbon cycle. In other words, there was no Early Triassic recovery to Permian values following the extinction.

Subsequent work has considerably elaborated this picture. At the Wuchiaping-Changhsing transition, two sections in southern China reveal a shift from ~ +4.5‰–5.0‰ during the Wuchiapingian to +2.0‰–3.0‰ during deposition of the Changhsing Formation (Shao et al., 2000). Shao et al. reported a single very negative point at 0‰ just above the Wuchiapingian-Changhsingian boundary at Matan in Guangxi Province, but additional data are required to confirm this result.

A negative shift in carbon isotopes is a consistent marker of the P-Tr interval in marine carbon (Holser and Magaritz, 1987; Holser et al., 1989; Baud et al., 1989), marine organic carbon (Magaritz et al., 1992; Wang et al., 1994; Isozaki, 1997; Krull et al., 2000), and terrestrial organic carbon (Morante, 1996; Retallack and Krull, 1999), tooth apatite (Thackery et al., 1990), and pedogenic carbon (MacLeod et al., 2000; Krull and Retallack, 2000), although the correlation between marine and terrestrial sections is often based on the assumption of a single global shift that must be at the P-Tr boundary. (See de Wit et al. (in press) for a criticism of this claim). The apparent abruptness of the shift may vary between sections, in part because of differences in sediment accumulation rates. The global extent of the isotopic shift is confirmed by analyses of shallow-water carbonates from seamounts in Panthallasa (Musashi et al., 2001).

The abrupt shift in carbonate carbon isotopes coincident with the peak extinction at the Meishan section (Bowring et al., 1998; Jin et al., 2000a) and seen globally in marine sections has been interpreted not as a whole-ocean shift (e.g., involving both surface and deep waters; Erwin, 1993), but as a composite of a transient, shallow-water shift associated with a decline in productivity superimposed on a long-term shift of ~2‰. The abrupt negative spike in <500 k.y. (Bowring et al., 1998) and associated changes in organic carbon (e.g., Wang et al., 1994) are too rapid to be explained by a whole-ocean shift. The most reasonable explanation is a reduction in productivity with a drop in surface-water $\delta^{13}C$ coupled with a shift in the carbon cycle. The rapid loss of terrestrial vegetation may have been at least partly responsible for the transient negative shift in carbon isotopes at the P-Tr boundary (e.g., Visscher et al., 1996; Newell et al., 1999; Ward et al., 2000).

Several complexities affect the analysis of the carbon isotopic record from marine carbonates. Scholle (1995) described processes that may alter carbon isotopic signals, and cautioned that the common assumption that the signal reflects a single, global event may be unwarranted. In many cases independent biostratigraphic data have been used to identify the boundary, although there are many other cases, particularly in sections in Australia and Antarctica, where the chemostratigraphy has been used in isolation. Krull et al. (2000) reported $\delta^{13}C_{org}$ data from the Little Ben Sandstone in New Zealand, and documented a shift of ~7‰, from −25‰ to −32‰, with a briefer transient to −38‰ where they place the P-Tr boundary; however, there is no biostratigraphic support for this assignment. Krull et al. (2000) proposed the release of methane hydrates as the only reasonable source of such depleted carbon, perhaps from a submarine slide or warming of permafrost. In support of this contention, they charted the latitudinal variations in the isotopic shift, from −7‰ to −10‰ in higher latitudes, and from −4‰ to −2‰ in equatorial latitudes (their point for southern China was based on incorrect data; results in Jin et al. [2000a place the southern China shift with comparable latitudinal data). However, Krull et al. (2000) included analyses from Gruszy-zynski et al. (1989), which Mii et al. (1997) showed to be diagenetic artifacts, a problem that may affect some other high-latitude points reported from this group. Removal of these data eliminates all of the Northern Hemisphere high-latitude points, except those reported from west Spitsbergen by Wignall et al. (1998). Thus, confirmation of the latitudinal gradient suggested by Krull et al. (2000) requires additional paleomagnetically defined high-latitude data and additional checks for diagenetic complications, as described by Mii et al. (1997) and Scholle (1995).

Krull and Retallack (2000) presented further support for release of methane during this interval in $\delta^{13}C_{org}$ analyses of paleosols from sections through the P-Tr boundary in Antarctica. Unusual variation in $\delta^{13}C_{org}$ in depth profiles of Early

Triassic paleosols compared with Permian and modern soils, and values as low as $-42‰$ imply significant isotopic fractionation. They argued that the most plausible explanation is derivation of most of the organic material from methanogenesis. Specifically, this requires that atmospheric methane must have been sufficiently abundant when the soils were formed to support large populations of methanotrophs, and there must have been preferential preservation of the methanotrophic carbon relative to soil carbon to preserve the isotopic signal. In light of the short atmospheric residence time of methane (>10 yr), their data seem to require a continuing methane input into the atmosphere in the earliest Triassic.

The shift in organic carbon described by Krull et al. (2000) is plausibly related to release of methane, but more subtle shifts in isotopic values may reflect other shifts in sources, and thus complicate interpretation of the results. Foster et al. (1998) showed that the organic carbon record in Australia could be affected by the input of organic matter with a different isotopic values, specifically terrestrial material in the case they studied. Krull and Retallack (2000) argued, however, that the mechanism proposed by Foster et al. (whom they did not cite) will not influence bulk $\delta^{13}C_{org}$ unless much of the organic matter is derived from a depleted source.

A rapid shift in sulfur isotopes of sulfides has also been documented through the uppermost Permian. At the Sasayama section in Japan, the $\delta^{34}S$ values from pyrite range from $-35‰$ to $-25‰$ through the middle Permian (Kajiwara et al., 1994), but shift rapidly to $\sim -15‰ \pm 5‰$ beginning near the base of what Kajiwara called the middle-Upper Permian boundary, although whether this corresponds to the Capitanian-Wuchiapingian or younger is unclear. From the P-Tr into the earliest Triassic, values remain at $-15‰$ except for a brief negative excursion to as much as $-40‰$ at the assumed P-Tr boundary. Sulfates, in contrast, evidently remained at $\sim -10‰$. Kajiwara et al. (1994) argued that this is persuasive evidence for an anoxic interval at the P-Tr boundary. Thus, as with the carbon record, Kajiwara et al. found a long-term shift in sulfur isotopes from the Permian to the Triassic, and a transient spike at the P-Tr boundary, although unlike the carbon isotopes, the sulfur spike is in the opposite sense of the general shift from the Permian to Triassic. Broecker and Peacock (1999) suggested that the carbon and sulfur isotopes indicate a major change in the burial of organic matter between the Permian and Triassic, associated with a disruption in terrestrial ecosystems and the introduction of less efficient processing of organic matter in marine ecosystems. Kaiho et al. (2001) report highly resolved $\delta^{34}S$ sulfate date from the upper portion of Bed 24 at the Meishan section, with a sharp drop from about 20‰ to about 4‰ at the boundary with Bed 25. They argue that this reflects a global negative shift in sulfur isotopes, from injection of a large volume of isotopically light sulfur. They attribute this to an impact event, with oxidation of reduced sulfur. This model is further discussed under impact hypotheses.

The strontium isotopic composition of seawater also changed dramatically through the Late Permian. Martin and Macdougall (1995) showed a minimum in $^{87}Sr/^{86}Sr$ in the Capitanian (0.7070). The Late Permian rise in the strontium ratio was fairly rapid, and Martin and Macdougall (1995) invoked increased continental weathering due to a change in the riverine flux and a global shift in the $^{87}Sr/^{86}Sr$ ratio, perhaps associated with global warming. The recent analysis by Kaiho et al. (2001) of the Meishan section includes a sharp drop in strontium isotopes from 0.715 to 0.708 in the uppermost part of Bed 24, followed by an increase to as high as 0.733 in Bed 27. This suggests a shift from continental to mantle sources, and then a return to a continental source. While the long-term shift documented by Martin and Macdougall (1995) may plausibly reflect a change in weathering regimes (and corresponds to the McLoughlin et al. 1997 qualitative analysis of increasing red beds), it may reflect mantle-derived ejecta. Kaiho et al. (2001) favor an impact origin for this strontium.

Magneotostratigraphy

Magnetic reversals are a key tool for correlation, but have been difficult to apply to the P-Tr boundary because of the frequent reversals, and resetting of the magnetic signal in many key sections. The long Permian-Carboniferous reversed polarity superchron ended during the Capitanian Stage of the middle Permian, and is succeeded by the Illawarra mixed polarity superchron (Menning, 1995). These two events provide important benchmarks in the correlation of Late Permian rocks across biogeographic boundaries (Jin et al., 2000b). Menning and Jin (1998) suggested that as many as 13 reversals may have occurred during the Late Permian and thus the paleomagnetic record is best used in conjunction with biostratigraphic and chemostratigraphic data. Where such data exist, however, the magnetostratigraphy may help to define the continuity of the sections.

The composite record for the P-Tr boundary (Ogg and Steiner, 1991) indicates a normal interval during at least the late Changhsingian, with short reversal during the very latest Changhsingian, followed by normal polarity through most of the overlying Griesbachian stage of the Early Triassic (Steiner et al., 1989; Menning, 1995). Results matching this pattern, and thus confirming continuity of sections to the level of magnetostratigraphic resolution, have come from southern China (summarized in Jin et al., 2000b), the southern Alps (Scholger et al., 2000), and elsewhere, although some correlation problems continue to plague the details (e.g., Orchard and Krystyn, 1998).

Geochronology

Precise geochronology is essential for understanding the causes of extinction, especially where triggering events such as the eruption of the Siberian Traps or a bolide impact have been proposed. In particular, precise geochronology allows for the

testing of global synchroneity of an extinction event as well as determining the tempo of extinction and recovery and/or rapid shifts in isotopic signals across a boundary. The type section at Meishan is rich in volcanic ash beds and thus has been the site of numerous attempts to define the age and duration of the end-Permian extinction (Claoue-Long et al., 1991; Renne et al., 1995; Bowring et al., 1998; Mundil et al., 2001) using both Ar-Ar and U-Pb geochronology. In addition, both U-Pb (Kamo et al., 1996, 2000; Fedorenko et al., 2000; Campbell et al., 1992) and Ar-Ar geochronology (Renne et al., 1995; Basu et al., 1995) have been applied in order to determine the age of the Siberian Traps and evaluate their temporal coincidence with the P-Tr boundary. Despite the large amount of geochronological data, there is still some disagreement regarding the age and duration of the P-Tr boundary. In part, the debate over the age of the boundary reflects difficulties in comparing U-Pb and Ar-Ar geochronology.

U-Pb zircon geochronology takes advantage of two independent decay schemes (^{235}U-^{207}Pb and ^{238}U-^{206}Pb), allowing for evaluation of closed-system behavior; inheritance of older zircon components and diffusive Pb loss are the two most common causes of open-system behavior. It has become apparent that there is significant bias between Ar-Ar and U-Pb dates, U-Pb dates being ~1% older; this discrepancy has been attributed in part with to uncertainty in the ^{40}K decay constant (Renne et al., 1995, 1998; Min et al., 2000, 2001). Unfortunately, simple corrections are complicated by the fact that the values of the fluence monitor in many Ar laboratories (usually the Fish Canyon Tuff) have changed over the past decade. A recent U-Pb geochronological study of the Fish Canyon Tuff (Schmitz and Bowring, 2001) highlights this problem. Zircon from the Fish Canyon Tuff yield a crystallization age of 28.5 ± 0.035 Ma, a minimum of 400–500 k.y. older than the generally accepted Ar-Ar date of sanidine from the same sample. This >1% discrepancy is thought to be the result of a combination of uncertainty in the decay constants for K and the possibility of magmatic residence time for the zircons. Thus considerable care must be taken when comparing dates from the to decay systems. This systematic bias is much larger than calculated uncertainties associated with dates of individual volcanic layers. Geochronological studies of the extinction must now be taken to new levels, with multiple ages for volcanic rocks in stratigraphic succession a high priority. Thus, considerable care must be taken when comparing dates from the two decay systems.

The first published U-Pb geochronology from Meishan was the SHRIMP ion-probe study of Claoue-Long et al. (1991), who dated an ash bed (bed 25) just below the paleontologically defined P-Tr boundary and concluded that its age was 251.1 ± 3.4 Ma. Campbell et al. (1992) published a SHRIMP date of 248 ± 4 Ma for zircons from the Noril'sk-1 intrusion, a sill that intrudes the lower third of the Siberian Traps, and concluded that within error, the flood basalts and the Permo-Triassic boundary were synchronous. Renne et al. (1995) compared high-precision Ar-Ar geochronology of sanidine and

plagioclase feldspars from bed 25 at Meishan with Ar-Ar results from the Noril'sk-1 intrusion and concluded that they were synchronous, ca. 250 Ma. Bowring et al. (1998) presented U-Pb geochronology from a series of ash beds at Meishan and two other localities in southern China that they interpreted to indicate that the extinction occurred in <500 k.y., ca. 251.7-251.4 Ma. Mundil et al. (2001) questioned the results of Bowring et al. (1998), and suggested an age for the boundary that is closer to 253 or 254 Ma. While much effort has been expended to define the age and duration of the boundary, it is clear that more work will be needed. Geochronological data from marine sections other than those in southern China and terrestrial sections such as the Karoo basin in South Africa are essentially nonexistent. One notable exception where both Ar-Ar and U-Pb dating methods have been applied are rocks from the Delaware basin of northwest Texas and southeastern New Mexico, where Renne et al. (1998) reported a ^{40}Ar/^{39}Ar date of 251.0 ± 0.2 Ma on langbeinite (a potassium-rich evaporite mineral) from the Salado Formation (Wuchiapingian). If we apply an approximate bias of 1%, the date would be ca. 254 Ma, consistent with the results of Bowring et al. (1998). In addition, Renne et al. (1996) reported both conventional and SHRIMP U-Pb dates of 248–250 Ma from volcanic ashes in the stratigraphically younger Quartermaster Formation in Texas. The Quartermaster Formation has been viewed as latest Permian on the basis of biostratigraphy. Clearly more data are needed to evaluate global synchroneity and duration of the end-Capitanian and end-Changhsingian extinction.

Sea level

For decades the apparent widespread absence of marine P-Tr boundary sections from much of the world led to the acceptance of the occurrence of a widespread marine regression beginning in the Capitanian and extending until the earliest Triassic (Newell, 1967; Dickins, 1983; Holser and Magaritz, 1987; Ross and Ross, 1987; Erwin, 1993). This perspective was largely based on North American and Russian sections. Over the past decade, detailed studies of many P-Tr boundary sections, improved conodont biostratigraphy for reliable placement of the boundary, and application of sequence stratigraphic approaches has overturned this view, although distinguishing between global and regional sea-level signals remains difficult in some regions. For example, new sequence stratigraphic (Mertmann, 2000) and conodont data indicate that the Chhidru Formation in the Salt Range sections of Pakistan must be early Changhsingian in age, rather than Wuchiapingian (cf. Wignall and Hallam, 1993; Hallam and Wignall, 1999). This revision places the onset of the transgression in the mid-Changhsingian. Sections in Italy also show transgression beginning in the Changhsingian and continuing into the Triassic (Wignall and Hallam, 1992), and similar results were reported from Spitsbergen (Hallam and Wignall, 1999).

Sections from throughout China indicate a significant

lowstand near the Guadalupian-Wuchiapingian boundary, followed by generally rising sea level through the Lopingian (Chen et al., 1998). Yang et al. (1993; see also Wignall and Hallam, 1993; Chen et al., 1998) demonstrated that the major transgression, previously described as beginning in the basal Griesbachian, actually began during the latest Changhsingian, but prior to the extinction. Slightly different views were provided by Zhang et al. (1996), who identified three third-order sequence boundaries, at the lower and upper Changhsingian boundaries and the basal Griesbachian, and by Tong et al. (1999) who identified two distinct transgressive systems tracts during the Changhsingian, but a slight regression during the latest Changhsingian. Whether these differences reflect local variations or differences in interpretation is unclear, but the general global picture that results is the onset of transgression in lower to mid-Changhsingian time, and extending through the P-Tr boundary into the Early Triassic.

Climate record

The movement of Pangea northward through the Permian helped end the Permian-Carboniferous glaciation by the close of the Early Permian, and marked a transition to much warmer climates that persisted through the Mesozoic (Parrish, 1995). The continued northward movement of Pangea led to a gradual warming and drying of many continental regions. McLoughlin et al. (1997) compiled sedimentologic indicators of this climate change, including the spread of red beds, but emphasized that more rapid climatic changes near the P-Tr boundary were superimposed on this long-term trend. These changes had substantial effects on both marine and terrestrial biota (e.g., Archibold and Shi, 1996, western Pacific brachiopods; Wang, 1993, 2000, plants from northern China; McLoughlin et al., 1997, Antarctic plants). The sedimentological record in South Africa, Australia, and Antarctica, and the plant record in northern China raise the possibility of a very rapid global warming during the earliest Triassic, possibly associated with the extinction.

Marine anoxia

Many arguments for both shallow- and deep-water anoxia have been advanced (Wignall and Hallam, 1992, 1993, 1997; Kajiwara et al., 1994; Isozaki, 1995, 1997; Kakuwa, 1996), and the existence of at least some degree of marine anoxia is now widely accepted, although interpretations of the causes and the relationship to the P-Tr mass extinction have varied widely.

In the deep sea, radiolarian siliceous mudstones and claystones through the P-Tr boundary interval in Japan have provided some of the most detailed records of deep-sea anoxia, including a prolonged sharp shift in sulfur isotopes. Although the boundary is difficult to unambiguously locate in these sections, Kajiwara et al. (1994) interpreted the sedimentological evidence as anoxia associated with a stagnant, stratified ocean.

Isozaki (1995, 1997) proposed a global, deep-sea anoxic episode based on the occurrence of black chert and carbonaceous claystone with framboidal pyrite; biostratigraphically useful radiolarians and conodonts bracket the anoxic interval (see Kakuwa, 1996). He interpreted a gray siliceous claystone from the ?Early Triassic of the Cache Creek terrane in British Columbia, Canada, as evidence of the global extent of this anoxic episode.

Arguments in favor of shallow-water anoxia, possibly associated with the marine transgression, were developed by Paul Wignall and Tony Hallam and colleagues. Their initial studies of the earliest Triassic of the western United States, northern Italy (Wignall and Hallam, 1992), and Pakistan and China (Wignall and Hallam, 1993) invoked laminated sediments, apparently dysaerobic groups such as lingulid brachiopods and pectins such as *Claraia*, pyrite, and geochemical signatures. They argued that the Changhsingian extinction coincides with the appearance of anaerobic and dysaerobic facies. This theme was further developed in later papers (Wignall et al., 1995), including detailed analyses of high-latitude sections in Spitsbergen (Wignall and Twitchett, 1996; Wignall et al., 1998) and a comparison between high-latitude and low-latitude sections (Wignall and Twitchett, 1996). Trace fossils and additional geochemical proxies, including pyrite and sulfur/carbon ratios, were applied to bolster the evidence for anoxia. One of the difficulties in confirming this hypothesis is that many of the indicators of anoxia, including laminated sediments and the disappearance of active bioturbation, could simply reflect the extinction rather than anoxia, and some of the pyrite is clearly diagenetic and may reveal little about oxygen levels in the water column. The evidence appears to favor shallow-water anoxia coincident with the extinction in many sections, and extending into earliest Triassic sediments.

EVALUATION OF EXTINCTION HYPOTHESES

Extraterrestrial impact

The growing evidence of a rapid, even catastrophic, extinction at the P-Tr boundary continues to stimulate those favoring an extraterrestrial impact as the cause of the extinction. To date no generally accepted evidence of such an impact has been published, although Bowring et al. (1998) and Jin et al. (2000a) noted that the geochronology, stable isotopes, and marine paleontological data are largely consistent with an impact scenario. However, early analyses of boundary clays at Meishan (Zhejiang Province) and the Wachapo Mountains (Guizhou Province), China, revealed <0.5 ppb of iridium. Trace element geochemistry supported a volcanic origin for the clays (Asaro et al., 1982), which has been born out by many subsequent studies, although studies by some Chinese geologists (summarized in Xu et al., 1985, 1989) continued to support a possible extraterrestrial source of iridium. Xu Daoyi's group proposed a stony achondritic meteorite as the impactor to account for the low iridium abundances (Xu et al., 1989). Repeated

attempts to replicate these reports of iridium have not met with success (Clark et al., 1986; Orth, 1989; Orth et al., 1990; Zhou and Kyte, 1988). The Gartnerkofel-1 core in western Austria contains two minor peaks in iridium abundance, the lower of which corresponds with the $\delta^{13}C$ minima at the top of the Tesero Oolite, but above the P-Tr boundary; the second anomaly occurs ~40 cm above the Tesero Oolite and is associated with pyrite, and a trace element chemistry is inconsistent with a chondritic meteorite (Orth et al., 1990).

Shocked quartz provides another indication of impact. In their study of two Antarctic and one Australian P-Tr boundary sections, Retallack et al. (1998) published evidence of what they interpreted as shocked quartz. The grains are rare, much smaller than those at K-T boundary sites, and do not clearly contain characteristic planar deformation features. Iridium anomalies are reported in the picogram range (rather than as ppt or ppb), and occur below the apparent boundary. Retallack et al. accept that this is not convincing evidence for an impact. (The stratigraphic placement of the P-Tr boundary in the Antarctic localities was also questioned by Isbell and Askin, 1999).

Perhaps the most suggestive evidence of an extraterrestrial component associated with the P-Tr boundary is the presence of helium and argon trapped in fullerenes (C_{60} and C_{70}) from sections in Japan and southern China (Becker et al., 2001; a section from Hungary was also sampled, but with no significant recovery). Fullerenes were also reported from a P-Tr boundary section in central Japan, although they were linked to production in terrestrial wildfires and preservation in anoxic marine sediments (Chijiwa et al., 1999). Becker et al. (2001) have documented a variety of fullerenes containing trapped helium and argon, similar to reports from the K-T boundary. The ^3He abundances are similar to the Murchison and Sudbury meteorites, and the $^3He/^{36}Ar$ ratios support an origin in the planetary nebula. Moreover, Becker et al. (2001) suggest that only a star or a collapsing gas cloud could produce the observed partial pressures of helium in the fullerenes: all of these lines of evidence, they suggest, support an extraterrestrial source for the fullerenes, and thus an impact at the P-Tr boundary. They propose that an object of 9 ± 3 km would have been sufficient to produced the observed ^3He. The Becker et al analysis has been criticized by Farley and Mukhopadhyay (2001) and Isozaki (2001). Farley and Mukhopadhyay (2001) searched for ^3He in samples we provided from Bed 25 at the Meishan boundary section and from the Shangshi boundary section. In neither sample could they identify a ^3He signal consistent with the results of Becker et al. (2001). Becker and Poreda (2001) responded to Farley and Mukhopadhyay (2001) with more details of their approach and a criticism of Farley and Mukhopadhyay's techniques. They also claim evidence of spatial variation in $\delta^{34}C$ through the section, and suggest a similar variability in fullerenes may explain the failure of Farley and Mukhopadhyay to replicate the results of Becker et al. (2001). Despite this, reproduction of experimental results was absolutely critical to validation of the impact at the Cretaceous-Tertiary boundary.

The absence of confirmation of the Becker et al. results is troubling. Isozaki (2001) noted that the placement of the boundary at the Sasayama section is difficult and notes that the samples analyzed by Becker et al. (2001) came from a point about 0.8 m below the actual boundary. Although stimulating, this hypothesis clearly requires further verification.

Additional suggestive evidence of impact at the Meishan locality comes from Ni-rich-Fe-Si-Ni particles at the top of Bed 24, evidently produced by condensation from a post-impact vapor cloud (Kaiho et al., 2001). Volcanic eruptions tend to be Ni-poor, with temperatures too low to form Fe-Si-Ni grains (Kaiho et al., 2001). Whether the Siberian flood basalts, where eruption rates are believed to have been an order of magnitude higher than most continental flood basalts, were also Ni-poor is unclear. The shifts in sulfur and strontium isotopes have been interpreted as impact related (Kaiho et al., 2001). Kaiho et al. estimate the maximum diameter of the crater at 600 to 1200 km (and thus the asteroid diameter at 30 to 60 km) based on the volume of vaporized reduced sulfur. They acknowledge that the object may have been much smaller if sulfur was derived from impact-induced volcanism. Finding an impact structure convincingly dated to the P-Tr boundary would also support an impact scenario. Mory et al. (2000a) suggested that a possible impact structure near Woodleigh in the Carnavon basin of Western Australia might be associated with the P-Tr extinction. Their evidence includes an apparent multiring structure with an outermost diameter of 120 km, shock-induced planar deformed quartz, and other impact features; however, there are no precise age data. Mory et al. (2000a) claimed that the structure was filled with Lower Jurassic lacustrine deposits, and that shale clasts contain palynomorphs from the Sakmarian (Early Permian). Rb-Sr geochronology of biotite reported by Mory et al. (2000a) yield 835 Ma dates corresponding to widespread basement ages. Apatite fission-track ages suggest a regional thermal peak in the range 280–250 Ma, but it is unclear whether this relates to the Woodleigh impact structure (Mory et al., 2000a). Although emphasizing the need for further study, Reimold and Koeberl (2000) questioned the reliability of the data, particularly the shock deformation structures, and suggested that the structure may be only 40 km wide. In response, Mory et al. (2000b) provided additional evidence for shocked quartz and the structure of the impact feature, but also noted unpublished data suggesting a possible Late Devonian to Early Carboniferous age for the impact. Although additional study of the structure seems warranted, at present there is no evidence to link it to the end-Permian mass extinction.

The association between the Siberian flood basalts and the P-Tr extinction has raised the issue of whether impacts can trigger continental flood basalt eruptions, and even superplume initiation (e.g., Rampino and Strothers, 1988; Alt et al., 1988). As discussed in the following, there is considerable doubt that the Siberian volcanism is plume related. Gilkson (1999) estimated that a 300-km-diameter impactor with 10%–50% mantle melting could produce 0.22×10^6 km^3 of basaltic magma,

about an order of magnitude less than the Deccan flood basalts at the K-T boundary, and far less than the Siberian flood basalts. Melosh (2000) reached similar conclusions, and noted that there is no evidence of impact-induced volcanism from the Earth or any other planetary body. These studies suggest that impact was an unlikely trigger for the Siberian volcanism.

Abbas et al. (2000) suggested that the double extinction during the Late Permian was caused by the collision of Earth with weakly interacting massive particles (WIMPS), a class of postulated dark matter. They argued that accumulation of WIMPS in the core would produce massive heating, initiating a superplume that would rise toward the crust, causing eruption of flood basalt. Abbas et al. (2000) postulated that accompanying changes in tectonics and oceanic circulation would trigger anoxia, and possibly release of gas hydrates; they suggested that eruption of the superplume would take 5 m.y., but the source of this estimate is obscure. In the Abbas et al. (2000) model the initial extinction is due to increased carcinogenesis and anoxia consequent to the extinctions. Among other difficulties, there is no evidence that carcinogenicity is an effective cause of extinction.

Oceanic overturn and CO_2 poisoning

Widespread Late Permian seafloor carbonate marine cements and microbial precipitates led Grotzinger and Knoll (1995) to note a strong similarity to carbonates from the Proterozoic. They suggested that an increased upwelling of calcium-rich, anoxic deep waters produced waters with increased alkalinities and promoted the formation of these unusual deposits. Knoll et al. (1996) combined this insight with additional geochemical data in a model where overturn of anoxic deep waters liberated large volumes of carbon dioxide, leading to the preferential extinction of susceptible clades via carbon dioxide poisoning, or hypercapnia. In their original model, a preextinction, stagnant ocean sequestered carbon by burial of organic material from photosynthesis in surface waters, reducing atmospheric carbon dioxide; glaciation induced overturn of a stagnant ocean, introducing large volumes of carbon dioxide into the atmosphere.

This hypothesis, however, lumps large clades that exhibit distinct patterns of extinction and survival. For example, the life habits, environmental preferences, and resulting extinction patterns of prosobranch gastropods vary substantially (Erwin, 1990). The euomphalids are essentially sessile as adults and are ecologically closer to brachiopods than other gastropods: it is not surprising that they became extinct. While this example strengthens the claims of Knoll et al. (1996), whether they have carried out the analysis at the appropriate taxonomic level remain unclear. In addition, Knoll et al. (1996) appeared to conflate different physiological patterns, although whether this invalidates the results is unclear. The absence of any evidence for Late Permian glaciation is another difficulty with the Knoll et al. (1996) hypothesis, as is the considerable uncertainty over

whether stagnant deep oceans can persist as long as proposed by Knoll et al. (1996). A global climate simulation by Hotinski et al. (2001) with a Permian paleography was designed to test this model. Hotinski et al. (2001) concluded that although low oxygen levels could build up in the deep sea, they would be insufficient to produced the high levels of preoverturn carbon dioxide required by the Knoll et al. (1996) model without very high levels of phosphate concentration. Hallam and Wignall (1997) also noted that the Early Triassic evidence for global warming and increased anoxia of the oceans, rather than oxygenation, are both exactly opposite to the trends suggested by Knoll et al. (1996), and Isozaki (1997) emphasized that the persistence of apparent deep-sea anoxia at two deep-sea sections in Japan and Canada is inconsistent with an oceanic overturn at the P-Tr boundary. The Japanese section, and less certainly the Canadian section, suggests persistence of the anoxia well into the Early Triassic. Whereas such evidence tends to reject the mechanism proposed by Knoll et al. (1996), the pattern of extinction selectivity is independent of the mechanism they proposed to explain it.

Suggestive evidence for unusual oceanographic conditions at the P-Tr boundary comes from a peculiar carbonate deposit in eastern Sichuan Province, southern China. At several localities an ~1-m-thick anomalous carbonate caps the shallow-water crinoidal limestones that form part of a reef complex at the top of the Changhsing Formation. The crust is overlain by Lower Triassic shales and micrites (Kershaw et al., 1999). The genesis of this carbonate has been disputed, and karst, calcrete, and a microbial origin have all been proposed. Kershaw et al. (1999) discounted the calcrete and karst interpretations, and suggested that the carbonate crust is either microbial, with recrystallization having largely destroyed diagnostic microbial features, or an inorganic carbonate precipitate. Two of their four likely solutions involve CO_2-rich waters.

Marine anoxia and transgression

An alternative anoxia model was advanced by Wignall, Hallam, and colleagues (Wignall and Hallam, 1992, 1993; Wignall et al., 1995, 1998; Wignall and Hallam, 1997; Hallam, 1994; Wignall and Twitchett, 1996).: they proposed that a latest Permian-earliest Triassic transgression brought a dysaerobic to anoxic layer onshore, the extinction coinciding with the appearance of the dysaerobic waters at that locality. Wignall and Hallam (1993) noted that this implies that the extinction should be diachronous, with the extent of the anoxia, rather than its duration as the effective extinction agent through the reduction of oxygenated shallow-marine habitats. Possible diachroneity of the extinction has been suggested by conodont biostratigraphy of a variety of sections (Wignall et al., 1995). Wignall et al. noted that the earliest appearance of dysaerobic facies is in the *Hindeous latidentatus* conodont zone of the Changhsingian in basinal sections in Kashmir and possibly southern China. In contrast, in the shallow-water section in the Italian Alps anoxia

and extinction occur at the base of the overlying *Hindeotus parvus* conodont zone. In the Salt Range of Pakistan anoxia did not arrive in until the *Clarkina carinata* zone of the Early Triassic. These conclusions depend on sedimentologic criteria for identifying anoxia, and the reliability of the biostratigraphic correlation. Wignall and Hallam (1993) suggested that the Siberian Traps may have been the cause of the extinction, via production of extensive warm saline bottom waters. Wignall and Twitchett (1996), however, suggested that the link between the extinction, anoxia, and the Siberian Traps was through a decline in oceanic circulation due to reduction or elimination of the latitudinal temperature gradient. Contributory factors may have been the decrease in oxygen solubility in water as temperature rose.

Isozaki's (1997) superanoxia model links the onset of the stagnant ocean to the Capitanian extinction episode, and links the Changhsingian event to the climax of the superanoxia in the deep sea through unspecified changes in ocean dynamics. This prolonged stratified ocean thus lasts into the lower Anisian, or ~20 m.y., with a superanoxic ocean lasting from within the Changhsingian to the Dienerian, and then waning through the Smithian and Spathian. An alternative interpretation of the Japanese record by Kakuwa (1996) interprets the Griesbachian carbonaceous mudstone as representing dysaerobic but not anoxic conditions, the accompanying pyrite being diagenetic. He also indicated that the decline in radiolarian abundance (an index of marine productivity) occurred during the Changhsingian, but before the production of the black chert. In contrast to Isozaki (1997), Kakuwa (1996) interpreted the Griesbachian carbonaceous mudstone as evidence of phytoplankton blooms and consequent spread of anoxia in epicontinental seas that influenced the deep sea. This hypothesis should be testable via organic geochemistry and biomarker studies. For example, organic biomarker evidence from the relatively shallow water Phosphoria Formation (mid-Late Permian) of Montana is consistent with anoxia along a chemocline separating normal marine surface waters from saline, evidently anoxic bottom waters; anoxia and salinity appear to have increased during the Late Permian (Dahl et al., 1993). Similar studies have yet to be carried out in deep-water P-Tr sections.

While some degree of deep- and shallow-water anoxia may have occurred during this interval, Isozaki's data suggest that the deep-water anoxia began before the marine mass extinction. Neither of these models seem capable of explaining the shift in carbon isotopes, nor can the plausibly produce the terrestrial extinctions. Thus, if anoxia played any role in the extinction it appears to have been a subsidiary one, and we must look elsewhere for the primary cause of the extinction.

Methane release

A possible role for methane release, possibly triggered by marine regression, was first suggested by Erwin (1993) on the basis of simple models of the carbon isotopic shifts. Growing evidence for marine transgression rather than regression raised substantial questions about this model, as did the suggestion that the shift in carbon isotopes involved both a long-term shift and a transient shift associated with a productivity decline at the extinction horizon, rather than a whole-ocean shift. Variants of the methane hypothesis have been invoked (e.g., Morante, 1996).

Krull and Retallack (2000; and see Krull et al., 2000) suggested involvement of methane release based on the very light organic carbon record from New Zealand and other regions, and $\delta^{13}C_{org}$ profiles in soils from the Early Triassic of Antarctica. Krull et al. (2000) also described a latitudinal gradient in $\delta^{13}C_{org}$, with high values in higher latitudes. Such isotopically depleted values reported are difficult to explain without a methanotrophic source. Krull et al. (2000) claimed that there is not a single highly depleted signal, as suggested by most previous authors, but several, which would require persistent input of methane over a long interval (>10 k.y.). Krull and Retallack (2000) suggested that a drop in sea level initially destabilized clathrates while the Siberian Traps further exacerbated greenhouse warming. In their model, this in turn destabilized polar clathrates, continuing the positive feedback and climatic destabilization. This model requires an isotopic shift coincident with the lowstand in sea level, but numerous studies suggest that the lowstand occurred well before the onset of extinction. The existence of a large volume of polar clathrates seems unlikely in view of the global warming since the mid-Permian. At present, while methane release remains a plausible explanation of the carbon shift, the only apparent mechanism of releasing sufficient marine clathrates is a substantial warming of the oceans, presumably by the Siberian Traps (Bowring et al., 1998).

Siberian flood basalt volcanism

The Siberian flood basalts are one of the two largest continental flood basalt (CFB) provinces. With an estimated volume of $2–3 \times 10^6$ km^3, the complex includes both intrusive and extrusive rocks and ranges from 100 to 3000 m thick, covering an area almost two-thirds the size of the continental United States. In the Noril'sk area 45 flows in 11 sequences with a total thickness of 3700 m have been identified (Renne and Basu, 1991).

Campbell et al. (1992) first drew attention to the coincidence in the ages of Siberian flood basalt eruption and the age of the P-Tr extinction (with relatively large errors). They used zircons to date the Noril'sk intrusion to 248 ± 4 Ma; this date overlapped the date for bed 25 at Meishan obtained by Claoue-Long et al. (1991) of 251.1 ± 3.4 Ma. Campbell et al. (1992) proposed an extinction model involving injection of large amounts of sulfur dioxide aerosols into the upper atmosphere with attendant global cooling and growth of polar ice caps with attendant drops in sea level. On the basis of available paleomagnetic data, Campbell et al. (1992) also speculated that the eruption of the basalts occurred in ~600 k.y. Renne et al. (1995)

published high-precision Ar-Ar data from both the Noril'sk gabbro and ash beds from Meishan and showed that they were the same age, within uncertainties, ca. 250 $\pm$ 0.2 Ma.

Kamo et al. (1996) obtained high-precision, single-grain, U-Pb geochronological data on both zircon and badellyite from the ore-bearing Noril'sk-1 intrusion that yielded an age of 251.2 $\pm$ 0.3 Ma. In addition, Kamo et al. (2000) and Fedorenko et al. (2000) reported and discussed, respectively, U-Pb geochronological results from the Maymecha-Kotuy area that confirm the suggestion that the entire sequence erupted in <1 m.y. From near the base of the sequence in the Maymecha-Kotuy area, perovskite from a melanephelinite gave a date of 252.1 $\pm$ 0.4 Ma and two lavas near the top yielded U-Pb zircon dates of 251.1 $\pm$ 0.5 Ma. Basu et al. (1995) reported a ^{40}Ar/^{39}Ar date of 253.3 $\pm$ 2.6 Ma from a lava stratigraphically below the one dated as 252.1 $\pm$ 0.4 Ma. The age and duration of the Siberian Traps overlap the extinction based on the U-Pb dates obtained at Meishan (Bowring et al., 1998), with the oldest dates ca. 252.1 Ma and the youngest ca. 251.1 Ma. In contrast, if the age of the extinction is as old as 253–254 Ma, as proposed by Mundil and Ludwig (1998), the majority of the volcanism is distinctly younger. This discrepancy is a matter that must be resolved with better data on the age of the boundary both in China and in other localities. It is clear that we need to know the age and duration of both the Siberian Traps and the P-Tr boundary to better than 200 k.y. to test for contemporaneity. However, the evident coincidence between the formation of the Siberian flood basalts and the mass extinction should be considered in any model for the extinction. Although paleomagnetic results from the Noril'sk area suggest that the eruption occurred during a normal magnetic polarity interval, inferred to be the earliest Triassic (Lind et al., 1994), the reversal history during the P-Tr boundary is sufficiently complex (M. Steiner, 2000, personal commun.), that paleomagnetic inferences about age of eruption are uncertain.

The close temporal association between the dates for the P-Tr boundary in southern China and the flood basalt in Siberia has spurred many hypotheses about possible links between these events (Rampino and Strothers, 1988; Campbell et al., 1992; Renne et al., 1995; Visscher et al., 1996; Kozur, 1998). The coincidence between the age of the Deccan flood basalts in India and the K-T boundary and the more recent demonstration of apparent coincidence in the formation of the central Atlantic magmatic province and the end-Triassic mass extinction (Marzoli et al., 1999; Palfy et al., 2000) have strengthened suggestions of a general link between mass extinctions and CFB eruptions—a faint echo of the enthusiasm for impacts. Wignall (2001) reexamined the postulated correlation between flood basalts and mass extinctions. Improved dating suggests the correlation only exists for three large and one smaller biotic crisis, and that even in these cases the eruptions appear to postdate the main phase of the extinctions. Further, Wignall questioned many of the postulated causal links between the eruptions and mass extinctions, suggesting the most plausible connection was

a runaway greenhouse effect, perhaps involving a release of gas hydrates.

Several possibilities have been advanced to link a massive eruption of flood basalt to the mass extinctions in both marine and terrestrial ecosystems. Campbell et al. (1992) proposed the release of sulfate aerosols, perhaps augmented by release of sulfates from evaporates encountered during ascent of the magma as a source of acidic aerosols. Renne et al. (1995) suggested the release of sulfate aerosols, perhaps augmented by release of sulfates from evaporates encountered during ascent of the magma, as a source of acidic aerosols. In the Renne et al. (1995) model, global cooling was triggered by stratospheric sulfate aerosols as well as ice-sheet formation, particularly in the region lifted by the Siberian plume; the glaciation would in turn have produced marine regression. The marine extinctions result from both global cooling and regression. In this model the brief cooling episode would be followed by global warming resulting from build up of volcanic carbon dioxide.

A more involved model (Veevers et al., 1994) begins with formation of a mantle plume coincident with the end of the Kiaman paleomagnetic superchron and production of a large volume of carbon dioxide during eruption of the flood basalts. The resulting global greenhouse triggers most extinctions, lowers organic productivity, and leads to oxidation of surface organic carbon to shift the carbon isotopes. The anoxia is explained as a result of reduced ocean circulation due to global warming. A greenhouse climate would directly lower marine oxygen levels simply because of the drop in oxygen solubility as water temperature increases. The remainder of the hypothesis is independent of the cause of the Siberian Traps, and this model is not inconsistent with available data, although the postulated changes in oceanic circulation due to global warming are dependant on the (unknown) causes of Permian oceanic circulation. Another issue that requires further attention is the potential role of volcanic sulfates and carbon dioxide. Visscher et al. (1996) suggested that the fungal spike reflects destruction of terrestrial ecosystems by acid rain produced by the release of sulfur and chlorine from the Siberian volcanism. This model appears to be consistent with the terrestrial data, although whether it is consistent with the marine extinction patterns remains unknown.

Several of these models make specific assumptions about the source of the Siberian Traps. Golonka and Bocharova (2000) support the view, originally suggested by Morgan (1981), linking the Siberian flood basalts to the Jan Mayen hotspot near Iceland via a Middle Triassic track through the Yenisei-Khtanga trough south of the Taimyr Peninsula. Nevertheless, a number of questions have been raised about a plume origin for the Siberian volcanism (earlier work summarized in Erwin, 1993). Although Renne et al. (1995) proposed 1–3 km uplift in a core region of 500 km, Czamanske et al. (1998) argued that subsidence, rather than uplift, occurred during the formation of the flood basalt and was conclusive evidence against a plume origin. Czamanske et al. argued instead for

partial melting associated with lithospheric shear and extension, although alternative models of the interaction between the plume and the upper mantle (e.g., Arndt, 2000) remain possibilities. Courtillot et al. (1999) argued for a close correlation between continental flood basalts and continental breakup and noted that the Siberian flood basalts and the probably Guadalupian-age Emeishan flood basalt in China are the only major episodes not associated with continental breakup. They suggested that the Siberian flood basalts represent a failed rifting event and offered as evidence the enormous deep sedimentary basin in western Siberia, which they suggest opened in the latest Permian to Early Triassic. Further support of the Courtillot et al. (1999) model comes from comparative analysis of elemental compositions of CFBs, which has demonstrated distinct differences between most CFBs and Siberia, CAMP, and a South African CFB (Puffer, 2001). The latter are very similar to volcanic arcs, suggesting they reflect reactivation of arc or backarc sources, consistent with the Courtillot et al. views of the Siberian flood basalt. Tanton and Hager (2000) developed a somewhat different model for Siberian magmatism that is consistent with the geological observations that rule out uplift associated with the magmatism (Fedorenko et al., 1996; Czamanske et al., 1998). They propose a model in which precursor melt intrudes and heats the lithospheric mantle, lowers its viscosity, and increases its density as melt turns to eclogite. This results in foundering and removal of lithospheric mantle. Consequently, a large volume of mantle melt would be produced in a very short time interval without a large amount of surface uplift. The widely assumed link between the flood basalt and a mantle plume does not appear to be supported.

The evidence for a rapid interval of global warming during the earliest Triassic has been linked to carbon dioxide released from the eruptions; however, with little hope of determining the volume of carbon dioxide released, this may remain merely an appealing, but untestable, suggestion. The effects of increased atmospheric carbon dioxide would be pervasive, whatever the source. In addition to global warming, the increase would change surface-ocean pH and carbonate chemistry (Wolf-Gladrow et al., 1999), and experimental evidence has shown that it reduces calcification rates in corals, coralline algae, and calcifying phytoplankton (Riebesell et al., 2000). The apparent temporal overlap between the eruption of the Siberian basalt and the mass extinction remains intriguing, and some part of these explanations may be correct. However, establishing a close causal link between the eruption and the patterns of differential marine and terrestrial extinction remains a task for future research. In addition, a detailed chronology of the Siberian flood basalts to compare with that of the extinction is critical for a full evaluation of this hypothesis.

EXTINCTION MECHANISMS AND SYNTHESIS

The available geological, geochemical, and paleontological data establish a set of constraints on mechanisms for the Changhsingian extinction (Bowring et al., 1998, 1999). These observations must be accommodated within any acceptable model for the extinction. (1) There is widespread evidence for shallow anoxia and some evidence for deep-water anoxia; the deep-water anoxia corresponds in part to a positive shift in carbon isotopes during the Lopingian that could reflect the burial of a massive volume of organic carbon. (2) The $\delta^{13}C$ excursion occurs in both marine and terrestrial sections, and in the marine sections in China corresponds within precision with the primary extinction horizon, although finer scale analyses are warranted. (3) The age of the extinction in southern China and the eruption of the major phase of the Siberian flood basalts are coincident within experimental error. (4) The marine extinction occurred in <500 k.y. and during a rise in sea level, not a regression. (5) There is no evidence for latest Permian glaciation. (6) Evidence suggestive of rapid global warming has been accumulating from Russia, Australia, and possibly South Africa. (7) The increase in fungal spores, indicating a disturbance in terrestrial ecosystems, begins before the marine extinction in many sections, including southern China, and has a duration exceeding 1 m.y. (8) Possible, although not yet conclusive, evidence of impact has recently been advanced in the form of fullerenes containing trapped helium and argon gases with ratios indicating an extraterrestrial origin. (9) The early onset of the fungal spike and the deep-sea anoxia suggest the possibility that disruption began on land and in the deep sea before shallow-marine ecosystems were affected.

Although recent research has dramatically reduced the range of viable possibilities, the cause, or causes, of the end-Permian mass extinction remain unclear. The principal disagreements between the various hypotheses described herein involve whether the growing evidence for rapid earliest Triassic greenhouse is correct, and if so, its origin and relationship to the extinction; whether the shift in carbon isotopes preceded or was isochronous with the mass extinction; and whether the magnitude of the transient spike in light carbon at the P-Tr boundary can be explained solely by a drop in productivity, or requires the input of additional light carbon, from methane hydrates, terrestrial organic, or an extraterrestrial (cometary) source.

Among the many remaining unanswered issues are whether there is a causal link between the Capitanian and Changhsingian extinction pulses; and if the terrestrial and marine extinction pulses during the Changhsingian were isochronous. The presence of a sharp carbon isotopic shift in South African and other terrestrial sections is compelling, but not yet conclusive evidence for isochroneity. Carbon isotopic evidence is similarly taken to demonstrate the isochroneity between the well-studied marine extinctions in southern China and those elsewhere, particularly around Pangea. Other issues are whether, at a fine scale, the carbon isotopic shift precedes or lags the peak of marine extinction, and what are the latitudinal and onshore-offshore (i.e. shallow to deep) gradients in carbon isotopes across the P-Tr boundary. Can we test different hypotheses for

the causes of surface and deep-water anoxia? The pattern of transgression and the link to the appearance of anoxic sediments remains unclear. Some Chinese workers see the major transgression beginning in latest Changhsingian time, yet this would require a lag between the onset of transgression and the appearance of shallow-water anoxic facies beyond that suggested by Wignall and Hallam (1993; see also Wignall et al., 1995, Wignall and Twitchett, 1996).

Most explanations for mass extinctions involve a single triggering event, although often with a variety of subsequent proximal causes of extinction. Although this approach is intuitively satisfying, and such hypotheses are easier to test, there is no a priori reason why mass extinction could not result from a more complex web of causality (Erwin, 1993; see also MacLeod et al., 2000). The evident rapidity of this extinction adds credence to the search for a single causal force. The report by Becker et al. (2001) may be the first valid extraterrestrial signal associated with the P-Tr boundary, although it will require considerable additional confirmation. The evidence discussed here is largely consistent with an extraterrestrial impact, but does not require one, and may be consistent with other extinction scenarios. The strong correlation between the timing of eruption of the Siberian flood basalts and the extinction continues to strengthen suggestions of a link between these events, although the causal connection remains unclear and is possibly difficult to test. Against this correlation, however, is the evidence from China and elsewhere that the increase in fungal spores and apparent disruption of terrestrial ecosystems began before the marine extinction, and possibly before the onset of the Siberian eruptions.

POSTEXTINCTION BIOTIC RECOVERY

From the perspective of the history of life, one of the most intriguing aspects of the end-Permian mass extinction remains the delay in the onset of recovery in most groups during the earliest Triassic (Erwin, 1998). With the exception of ammonoids, which diversified quickly during the earliest Triassic, other marine groups exhibit a survival interval of low-diversity, cosmopolitan assemblage of generalists until near the close of the Early Triassic, perhaps 5 m.y. after the P-Tr boundary. These assemblages often contain the brachiopod *Lingula* and the bivalve *Claraia* in large numbers. The common association of these two genera with anoxic conditions led Hallam (1991, 1994) to invoke persistent anoxia as a cause of the delayed recovery. In the western United States, for example, low-diversity, low-complexity assemblages are common, often with particular species in very high abundance (Schubert and Bottjer, 1995; Woods and Bottjer, 2000). Many of these taxa exhibit nearly cosmopolitan distribution and low provinciality during the Early Triassic. By the Spathian, the final substage of the Early Triassic, new taxa began to appear, and marine communities achieved a more normal aspect by the Anisian (Middle Triassic), although stromatolites are still found in the Spathian

(Schubert and Bottjer, 1995; whether these are truly biogenic stromatolites or inorganic precipitates requires further study.) Wignall et al. (1998) noted that reasonably diverse faunas, by Early Triassic standards, are found in Spitsbergen and suggest that recovery may have begun earlier in high latitudes. This area is clearly one where considerable additional research is required; there is far too little information on the biogeographic architecture of recovery. Although reefs constructed with a metazoan framework appear to be largely missing from the Early Triassic (Flügel, 1994), calcimicrobial mounds and biostromes have been recorded from the Griesbachian and Smithian-Spathian in the Nanpanjiang basin of Guizhou, China (Lehrmann, 1999).

Many lineages are known from Middle to Upper Permian rocks, and again from latest Lower Triassic to Middle Triassic deposits, but are missing from the latest Permian and Lower Triassic. Such Lazarus taxa (Jablonski, 1986), first described for gastropods (Batten, 1973), reveal the ecological and preservational complexities of this recovery and that it affected a variety of taxa (Erwin, 1993). In contrast to earlier reports, claims of extensive Lazarus lineages among reef organisms appear to be have been due to inadequate systematic treatment (Flügel, 1994). Among gastropods, ~30% of Permian genera became Lazarus taxa (Erwin, 1996). The significance of this effect should not be overestimated, because preservational bias clearly accounts for some missing taxa; e.g., the many lineages only known from silicified specimens are unlikely to be recovered from Early Triassic rocks, because no appropriate silicified assemblages are known from the Early Triassic (Erwin, 1996). The missing lineages reappear from the Smithian into the Middle Triassic, essentially coincident with the diversification of new taxa in a variety of marine clades. The lineages must have persisted during the missing interregnum, but whether population sizes were too small to ensure recovery or species migrated to as-yet undiscovered refugia remains a controversy (although the utility of oceanic islands as refugia has been overestimated; Erwin, 1993). Wignall and Benton (1999) criticized Erwin's analysis and attempted to discriminate between these alternatives, albeit with inadequate methods. They counted the total number of shallow-marine formations, and concluded that because Changhsingian and Griesbachian units were approximately equal in number, deficiencies in the fossil record were unlikely to be significant. Their analysis is essentially meaningless because they failed to quantify the presence of formations with silicified faunas.

The recovery of terrestrial communities was evidently similarly delayed. Following the demise of the conifer-dominated floras at the P-Tr boundary, lycopsids dominated the Early Triassic. The weedy lycopsid *Isoetes* was widespread, and a single earliest Triassic species gave rise to 4 additional genera and 11 species in the Early Triassic (Retallack, 1997). Lycopsids also dominated European floras during the Early Triassic (Looy et al., 1999). Coals are unknown from the Early Triassic (McLoughlin et al., 1997; Retallack and Krull, 1999; Veevers et al.,

1994). There is evidence for an earliest Triassic greenhouse climate from Australia (Retallack, 1999), Antarctica (Retallack and Krull, 1999; although McLoughlin et al., 1997, suggested that in the Lambert graben, red beds do not appear until ~100 m above the P-Tr boundary, in ?Anisian deposits), and Russia (Newell et al., 1999). A study of the Karoo in South Africa (Ward et al., 2000) documented a change in sedimentary style to braided streams at the P-Tr boundary, plausibly interpreted as the result of rapid loss of vegetation. Although further study is required, macrofloral, pollen, soil, sedimentologic, and carbon isotopic records all suggest an interval of low-diversity plant assemblages in a warm and arid environment through the Early Triassic. Pollen evidence suggests that conifers returned to dominance near the end of the Early Triassic in Europe, where there was a rapid transition to new floral assemblages, perhaps in 0.5 m.y. (Looy et al., 1999). A similar pattern has been described from Australia, where floras did not return to Permian levels of biodiversity until the Middle Triassic (Retallack, 1995; Retallack and Krull, 1999).

The two leading explanations for the delayed onset of recovery are: (1) continuing environmental perturbation, or dampening, from the P-Tr boundary through the Smithian (Hallam, 1991; Woods and Bottjer, 2000); or (2) a delay simply reflecting the ecological disturbance associated with the magnitude of the extinction (Erwin, 1996, 1998). If the former is correct, we should, in principle, be able to identify environmental factors inhibiting biotic recovery, and the recovery of marine and terrestrial ecosystems might occur at the same point in time. Hallam (1991) suggested that the prolonged delay in recovery during the Early Triassic reflected a persistent anoxic marine layer associated with the Early Triassic transgression, although some of the evidence in that paper, including the cerium enrichment patterns, is of questionable utility (Erwin, 1993). There is evidence for anoxia through the Early Triassic, although largely in the earliest and latest parts of the stage. Wignall and Hallam (1993) documented apparent dysaerobic shallow-water marine facies through much of the Griesbachian in the Salt Range of Pakistan and southern China, and Twitchell and Wignall (1996) found a similar pattern based on trace fossils in Early Triassic sections in northern Italy. Further evidence of the unusual nature of the Early Triassic is in reports of inorganic carbonate cements in outer slope deposits of the Smithian Union Wash Formation in California (Woods et al., 1999). However, similar deposits are not found throughout the Early Triassic, suggesting that the occurrence of such conditions was at best episodic. Tosk and Andersson (1988) described a diverse foraminiferal assemblage from dysaerobic to anaerobic environments in the Thaynes Formation of Idaho (Spathian).

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