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Carbon isotopic evidence for terminal-Permian methane outbursts and their role in extinctions of animals, plants, coral reefs, and peat swamps

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Dedicated to the memory of William T. Holser, colleague and friend.

ABSTRACT

A gap in the fossil record of coals and coral reefs during the Early Triassic follows the greatest of mass extinctions at the Permian-Triassic boundary. Catastrophic methane outbursts during terminal Permian global mass extinction are indicated by organic carbon isotopic ($\delta^{13}C_{org}$) values of less than –37‰, and preferential sequestration of ^{13}C-depleted carbon at high latitudes and on land, relative to low latitudes and deep ocean. Methane outbursts massive enough to account for observed carbon isotopic anomalies require unusually efficient release from thermal alteration of coal measures or from methane-bearing permafrost or marine methane-hydrate reservoirs due to bolide impact, volcanic eruption, submarine landslides, or global warming. The terminal Permian carbon isotopic anomaly has been regarded as a consequence of mass extinction, but atmospheric injections of methane and its oxidation to carbon dioxide could have been a cause of extinction for animals, plants, coral reefs and peat swamps, killing by hypoxia, hypercapnia, acidosis, and pulmonary edema. Extinction by hydrocarbon pollution of the atmosphere is compatible with many details of the marine and terrestrial fossil records, and with observed marine and nonmarine facies changes. Multiple methane releases explain not only erratic early Triassic carbon isotopic values, but also protracted (~6 m.y.) global suppression of coral reefs and peat swamps.

Keywords: Permian, Triassic, boundary, methane, mass extinction, coal, reef

INTRODUCTION

Mass extinctions of the past, like a good murder mystery, can be instructive for the living. The Permian-Triassic boundary, for example, not only was the greatest biodiversity crisis of the past 500 m.y. (Erwin, 1993), but it also was followed by the longest temporal gap in the fossil record of coals since their Late Devonian appearance (Retallack, et al., 1996) and of coral reefs since their Ordovician appearance (Weidlich et al., 2003). No coals or coral reefs are known for the entire Early Triassic (Fig. 1), which has a currently dated duration of ~6 m.y. (Mundil et al., 2004; Gradstein et al., 2005). The causes of this global ecological crisis are potentially relevant to modern anthropogenic extinctions, wetland pollution (Whiting and Chanton, 2001), and

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coral reef predation and bleaching (Pandolfi, 1992; Marshall and McCulloch, 2002).

A diagnostic clue to the life-crisis at the Permian-Triassic boundary is a marked carbon isotopic anomaly (negative $\delta^{13}C$ spike) in both carbonate and organic matter (Magaritz et al., 1992; Morante, 1996), which has been instrumental for recognition of this mass extinction at many localities worldwide (Fig. 2). When comprehensively sampled and well preserved, the isotopic anomaly has a characteristic shape of rapid but steady decline to a very low value, then rebound followed by one or more low spikes, before settling on Early Triassic values often a little lower than during the Late Permian (Figs. 3–5). Other abrupt or erratic carbon isotopic excursions at the Permian-Triassic boundary may reflect local disconformities and inadequately dense sampling, but one or more negative spikes and later persistent lower values are common to most carbon isotopic records across the Permian-Triassic boundary. Here we consider the magnitude, shape, and paleogeographic distribution of numerous Permian-Triassic carbon isotopic spikes as evidence for the nature of the carbon-cycle crisis some 251 m.y. ago.

The negative carbon isotopic anomaly at the Permian-Triassic boundary has been variously attributed to curtailed biological productivity in the ocean (Kump, 1991; Wang et al., 1994), curtailed biological productivity on land (Broecker and Peacock, 1999), change from woody to herbaceous vegetation (Gorter et al., 1995; Foster et al., 1998), erosion of coals exposed during low sea level (Holser and Magaritz, 1987; Magaritz et al., 1992), overturn of a stratified ocean carbonated with dissolved CO_2 (Hoffman et al., 1991; Kajiwara et al., 1994; Knoll et al., 1996), introduction of extraterrestrial carbon from comet or asteroid

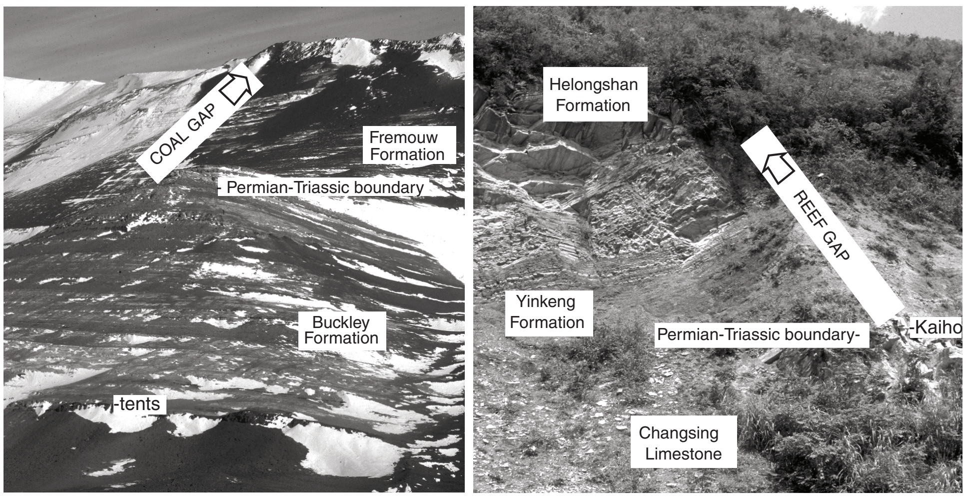

Figure 1. Permian-Triassic boundary sections showing strata (A) within the global coal gap in nonmarine strata of Graphite Peak, Antarctica and (B) within the global reef gap in marine strata of Meishan, China. For scale: at Graphite Peak, small triangular tents; at Meishan, Kunio Kaiho collecting samples.

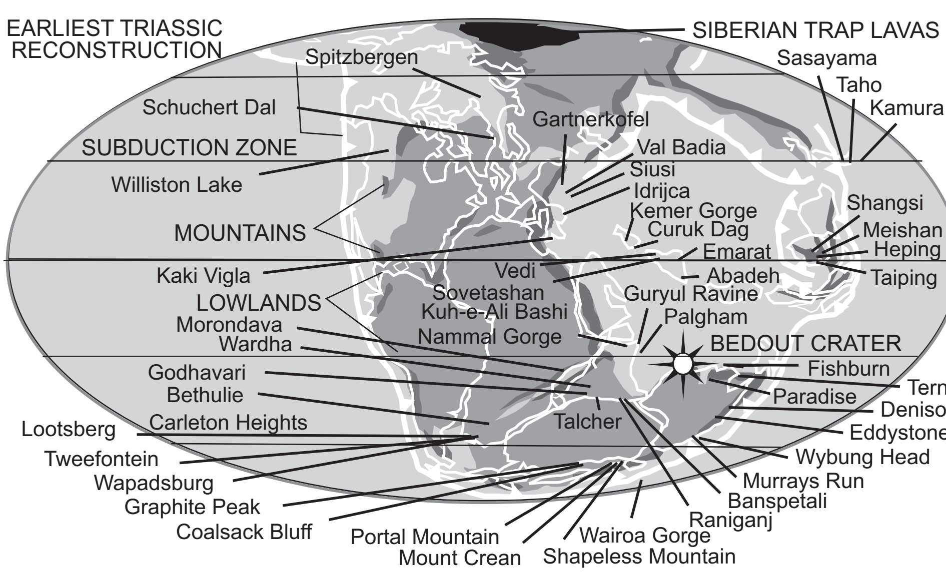

Figure 2. World paleogeographic map at the Permian-Triassic boundary (251 Ma, from Scotese 1994) showing sites analyzed for carbon isotopic anomalies.

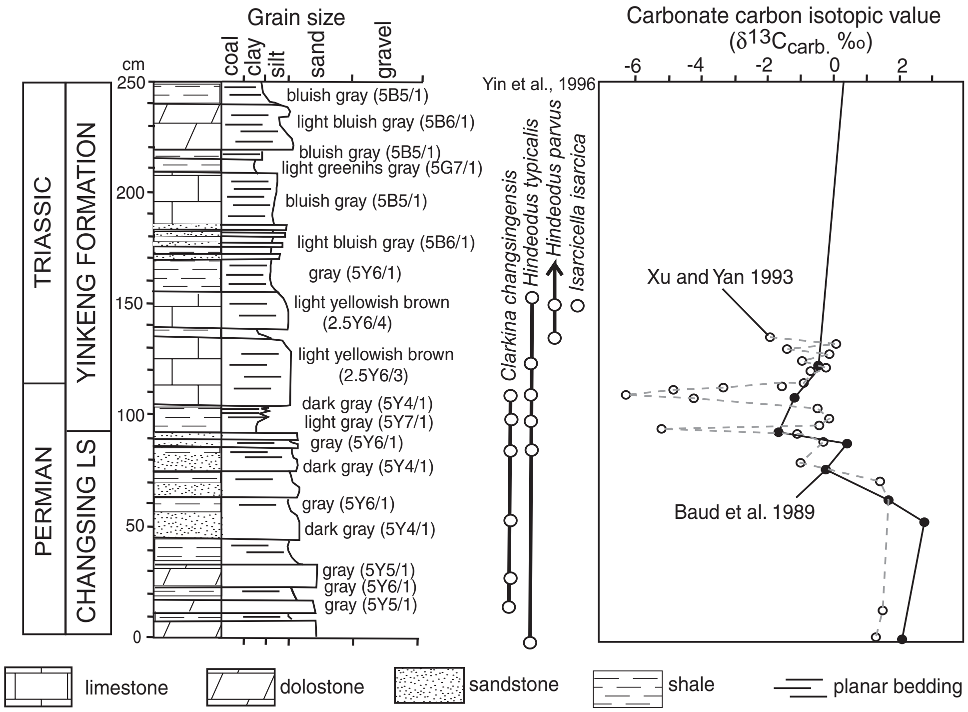

Figure 3. Stratigraphic section at the global Permian-Triassic stratotype in Meishan quarry D, China, measured by Retallack, with conodont ranges from Yin et al. (1996) and carbonate carbon isotopic data after Xu and Yan (1993) and Baud et al. (1989). Additional isotopic data of d'Hondt et al. (2000) show a shift comparable to that in the data of Baud et al. (1989), which were preferred for our compilation (Table 1).

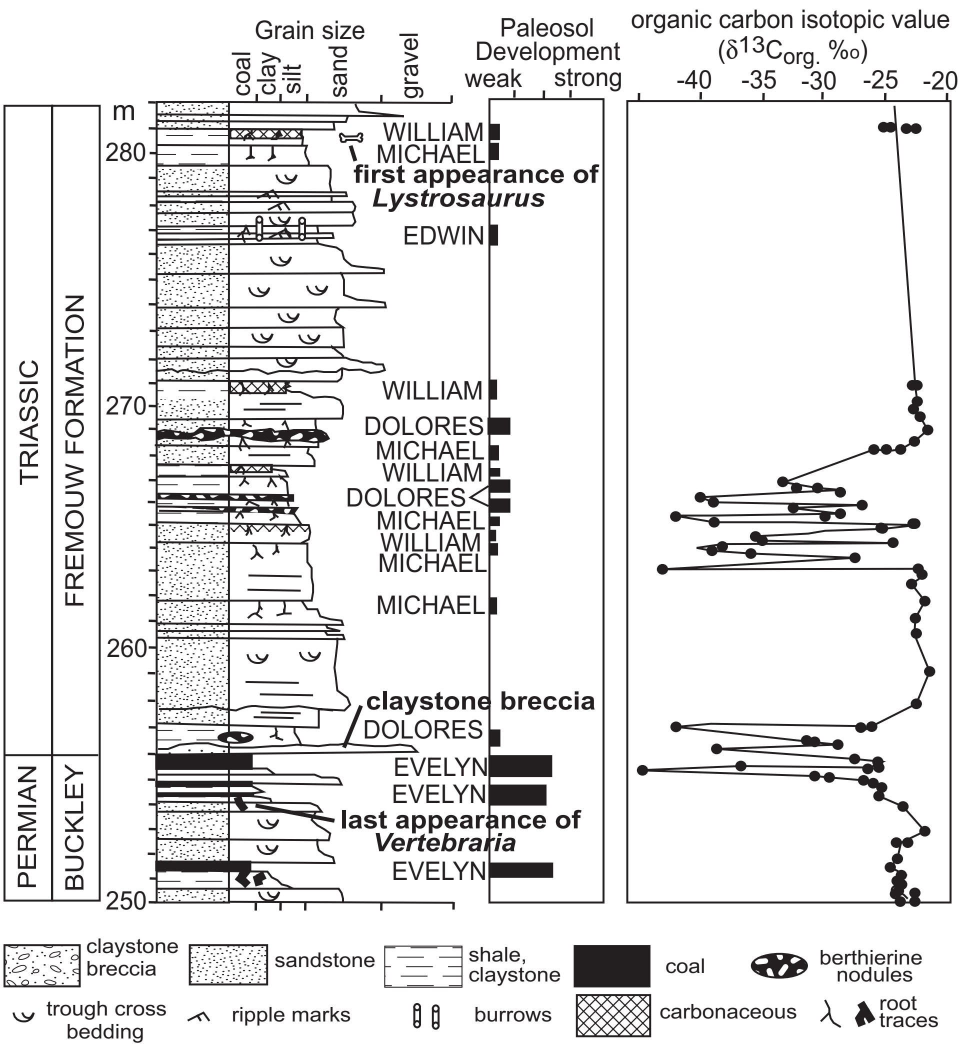

Figure 4. Stratigraphic section of the Permian-Triassic boundary at Graphite Peak, with stratigraphic and fossil range data from Retallack and Krull (1999) and carbonaceous carbon isotopic data from Krull and Retallack (2000) and Retallack et al. (2005).

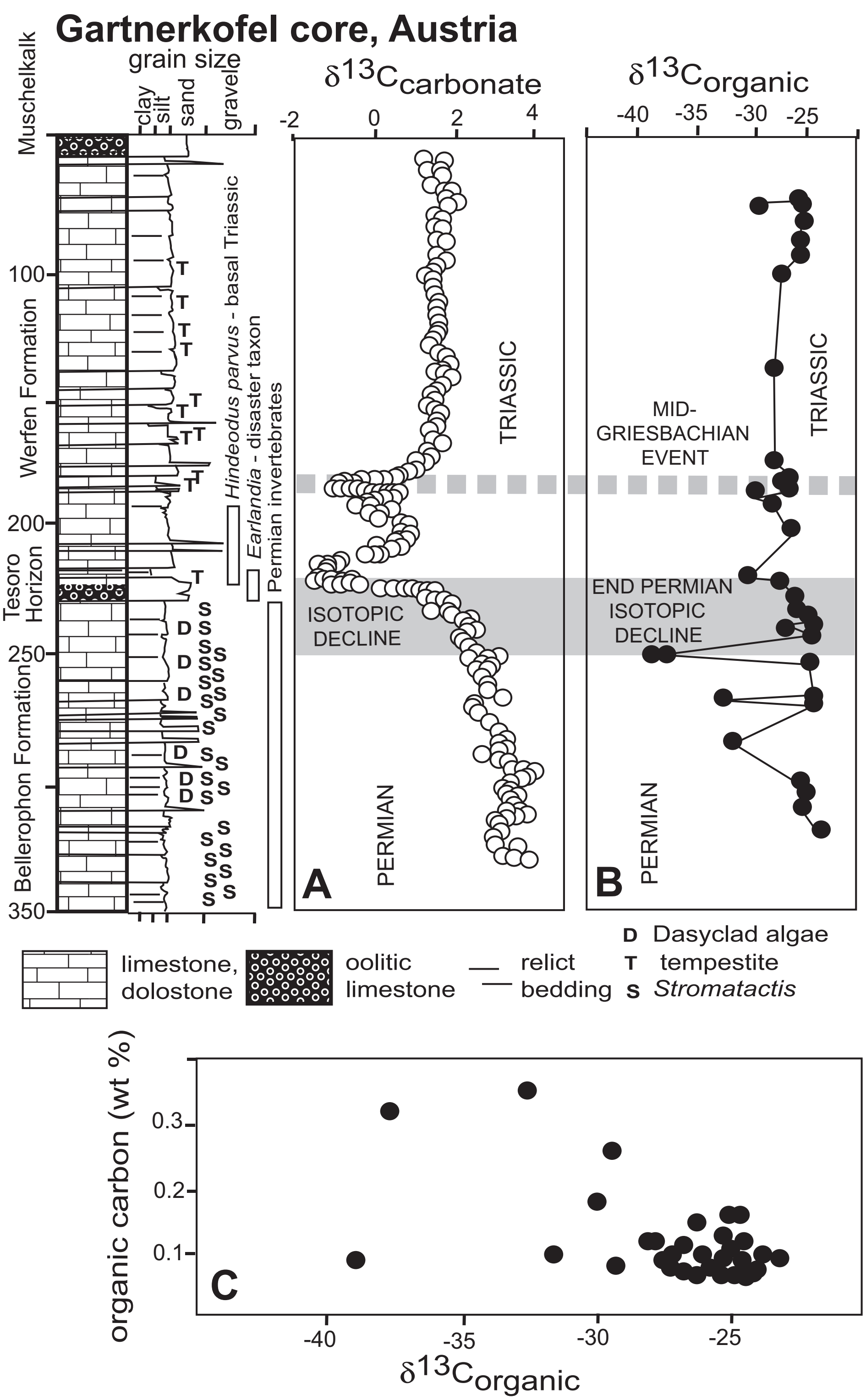

Figure 5. A pronounced negative excursion in carbon isotopic value ($\delta^{13}C$) of carbonate at the Permian-Triassic boundary in the Gartnerkofel-1 core, Austria (A), corresponds to very low isotopic values for organic carbon (B) but no correlation between total organic carbon content and carbon isotopic value of carbon in these samples (C). Samples with low values are mostly high in organic carbon content and so are inferred to be reliable analyses (data from Holser et al. 1991; Magaritz et al. 1992).

impact (Rampino and Haggerty, 1996), degassing associated with flood basalt eruption (Landis et al., 1996; Conaghan et al., 1994; Isozaki, 1997), methane clathrate dissociation (Morante, 1996; Vermeij and Dorritie, 1996; de Wit et al., 2002), and thermogenic methane outbursts from volcanic intrusion of coal measures (suggested here, as in Paleocene case described by Svensen et al., 2004). All of these hypotheses were viable when the isotopic excursion was only thought to be some –3‰ δ^{13}C and was unknown in nonmarine sections across the Permian-Triassic boundary. Now that numerous isotopic spikes of much larger magnitude have been discovered from a global network of carbon isotopic profiles in both marine and nonmarine facies (Table 1), the most likely explanation for the carbon isotopic shift is atmospheric pollution from massive outbursts of coalbed or clathrate methane. Such methane release and atmospheric pollution events have already been hypothesized from the postglacial (12 ka: Thorpe et al., 1998; Kennett, 2003), Ypresian (55 Ma, Paleocene-Eocene boundary: Sinha et al., 1995; Bains et al., 1999), Danian (65 Ma, Cretaceous-Tertiary boundary: Max et al. 1999), Aptian (117 Ma, Early Cretaceous: Jahren et al. 2001), Toarcian (175 Ma, Early Jurassic: Hesselbo et al. 2000), and Hettangian (200 Ma, earliest Jurassic: Hesselbo et al., 2002).

Productivity and vegetation-change hypotheses all imply that the carbon isotopic excursion was a consequence of mass extinction, but the methane outburst scenario, like the ocean overturn, bolide, and volcanic hypotheses, allows a causative role for CH_4 and CO_2 as kill mechanisms. Neither gas is benign at high concentrations. Methane reacts with atmospheric NO_x to create formaldehyde, and forms explosive mixtures with air when between 5.5 vol% and 14 vol% (Patnaik, 1992). Methane asphyxiates humans at concentrations high enough to displace oxygen (87%–90%) and anesthetizes at concentrations in excess of 1000 ppmV (Clough, 1998). Methane oxidizes to CO_2 in the atmosphere within 7–24 yr (Khalil et al., 2000), and CO_2 is also an asphyxiant, fatal to humans in excess of 15 vol% and inducing headache and breathing difficulty in excess of 2% (Kulkarni and Mehendale, 1998). Acidosis and pulmonary edema from high CO_2 levels can both be fatal (Fiddian-Green, 1995; Engoren, 2004; Retallack 2004c). Key questions for assessing the role of methane in extinction of organisms and ecosystems are timing and dose, which we address before discussing mechanisms of release and kill.

DATA COMPILATION AND METHODS

We have compiled data on the transient δ^{13}C excursion and long-term offset across the Permian-Triassic boundary at all studied localities, together with estimates of paleolatitude and paleoelevation of those sites (Table 1). Localities in Nammal Gorge (Pakistan), Schuchert Dal (Greenland), and near Meishan (China) have been analyzed for δ^{13}C several times with different results, but published protocols encourage us to use the most recent studies (Baud et al., 1996; Bowring et al., 1998; D'Hondt et al., 2000; Twitchett et al., 2001). Our estimates of paleolatitude from paleogeographic maps (Scotese, 1994) are limited by propagation of errors in plate restoration transects (±600 km) and uncertainties in position of small terranes (±2000 km). The highest paleoelevation (+300 m) was for the sequence at Graphite Peak, Antarctica, which was deposited in a fluvial basin well inland of an Andean-style volcanic mountain range (Retallack and Krull, 1999). Negative paleoelevations were used for depth below sea level, which for many sequences of limestone with marine algae was within the photic zone. The lowest paleoelevation (–3000 m) was for the cherty deep-marine sequence at Sasayama, Japan, assumed to have been deposited below calcium carbonate compensation depth for its paleolatitude (Ishiga et al., 1993). Uncertainties in depth below sea level reflect the coarseness of facies and biotic depth zonation as well as marine transgression across the Permian-Triassic boundary (Table 1).

New isotopic analyses of Early Triassic fossil plants also are presented here (Table 2) in order to assess natural variability of plant sources for early Triassic organic carbon. These were obtained by one of us (ESK) following protocols outlined by Bestland and Krull (1999) in the Department of Geological Sciences, Indiana University.

ISOTOPIC EVIDENCE FOR COMPLETENESS OF BOUNDARY SEQUENCES

The Permian-Triassic carbon isotopic sequence most comprehensively sampled and analyzed is still, after a decade of subsequent studies, the Gartnerkofel core of the Carnic Alps of Austria (Fig. 5). This sequence has Permian marine faunas to a depth of 230 m, the first appearance of the conodont *Hindeodus parvus* at 225 m, and a crisis fauna of *Earlandia* foraminifera and microgastropods from 224 to 190 m (Holser et al., 1991). The first appearance of *Hindeodus parvus* at the stratotype section of Meishan in China marks the Permian-Triassic boundary (Jin et al., 2000). Late Permian carbonate δ^{13}C values remain fairly constant at about +3.0‰ until 251 m, which is 26 m below the boundary defined by the newly evolved conodont *H. parvus*, and estimated using cyclostratigraphy to be 260 k.y. before the boundary (Rampino et al., 2000). Carbonate isotopic values then begin a regular decline like that of a mixing curve to the lowest values of –1.3‰ δ^{13}C at 220 m. The beginning of this decline in carbonate corresponds to anomalously low organic carbon isotopic values in the same core (at 251 m in Fig. 5B). After this point, carbon and carbonate isotopic values track each other more closely. Following the Permian-Triassic boundary, carbonate isotopic values rebound to a maximum of +0.7‰ δ^{13}C at 206 m, estimated to be some 190 k.y. after the boundary (Rampino et al., 2000). Carbonate isotopic values then fall to –1.1‰ δ^{13}C at 186 m some 390 k.y. after the boundary, then rebound to an earliest Triassic plateau of about +1.3‰ δ^{13}C at 162 m, some 630 k.y. after the boundary. The two declines in isotopic values have been attributed to soil formation from two separate horizons (Heydari et al., 2001), but there is no independent evidence of soil formation in the core or nearby outcrop other than pervasive dolomitization, which can

TABLE 1. CARBON ISOTOPIC OFFSET AND EXCURSION ACROSS THE PERMIAN-TRIASSIC BOUNDARY

LOCALITY	Reference	$\delta^{13}C$ offset	$\delta^{13}C$ excursion	Paleolatitude	Paleoelevation (m)
Carbonate					
Abadeh, Iran	Heydari et al., 2000	–1.3	–5.1	–15 ± 10	–50 ± 40
Çürük Dağ, Turkey	Baud et al., 1989	–2.9	–3.3	+5 ± 6	–6 ± 10
Emarat, Iran	Baud et al., 1989	–3.2	–4.9	–7 ± 10	–10 ± 15
Gartnerkofel-1, Austria	Magaritz et al., 1992	–1.7	–4.6	+26 ± 6	–120 ± 100
Guryul Ravine, India	Baud et al., 1996	–3.5	–5.6	–29 ± 6	–40 ± 30
Heping, China	Krull et al., 2004	–0.9	–3.4	+1 ± 6	–10 ± 15
Idrijca, Slovenia	Baud et al., 1989	–3.6	–2.6	+13 ± 6	–10 ± 15
Kaki Vigla, Greece	Baud et al., 1989	–1.3	–2.5	+6 ± 6	–500 ± 400
Kamura, Japan	Musashi et al., 2001	–0.5	–2.3	30 ± 6	–6 ± 12
Kemer Gorge, Turkey	Baud et al., 1989	–2.8	–3.7	+6 ± 6	–10 ± 10
Kuh-e Ali Bashi, Iran	Baud et al., 1989	–2.2	–3.3	–3 ± 10	–20 ± 15
Lootsberg, South Africa	de Wit et al., 2002	–1.2	–3.3	–54 ± 6	+200 ± 150
Meishan-D, China	d'Hondt et al., 2000	–3	–4.6	+2 ± 6	–40 ± 30
Nammal Gorge, Pakistan	Baud et al., 1996	–3.6	–4.4	–26 ± 6	–10 ± 20
Palgham, India	Baud et al., 1996	–4.2	–5.8	–28 ± 6	–40 ± 30
Schuchert Dal, Greenland	Twitchett et al., 2001	–5	–8	+38 ± 6	–100 ± 90
Shangsi, China	Baud et al., 1989	–3.5	–5	+3 ± 10	–100 ± 100
Siusi, Italy	Newton et al., 2004	–3.1	–6.9	+24 ± 6	–120 ± 100
Sovetashan, Armenia	Baud et al., 1989	–1.6	–3.5	–2 ± 10	–6 ± 12
Taho, Japan	Musashi et al., 2001	–0.7	–2.1	0 ± 6	–6 ± 12
Taiping, China	Krull et al., 2004	–2.1	–3.4	10 ± 15	10 ± 15
Vedi, Armenia	Baud et al., 1989	–2.2	–2	+2 ± 10	–8 ± 12
Nonmarine carbonate					
Bethulie, South Africa	MacLeod et al., 2000	–2	–13.1	–53 ± 6	+200 ± 150
Tweefontein, South Africa	Ward et al., 2004	–3.9	–9.6	–56 ± 6	+200 ± 150
Wapadsberg, South Africa	Ward et al., 2004	–5.8	–8.4	–56 ± 6	+200 ± 150
Marine organic					
Abadeh, Iran	Heydari et al., 2000	–0.9	–3.2	–15 ± 10	–50 ± 40
Fishburn-1, Australia	Morante, 1996	–6.6	–8	–40 ± 6	–100 ± 80
Gartnerkofel-1, Austria	Magaritz et al., 1992	–1.8	–5.8	+31 ± 6	–120 ± 100
Heping, China	Krull et al., 2004	–2.7	–5.3	+1 ± 6	–10 ± 15
Kamura, Japan	Musashi et al., 2001	–1.0	–2.2	30 ± 6	–6 ± 12
Paradise 1–6, Australia	Morante, 1996	–7.7	–9.4	–37 ± 6	–50 ± 50
Sasayama, Japan	Ishiga et al., 1995	–0.9	–6.5	+31 ± 6	–3000 ± 1000
Schuchert Dal, Greenland	Twitchett et al., 2001	–6	–9	+38 ± 6	–100 ± 90
Festningen, Spitzbergen	Wignall et al., 1998	–5.3	–5.6	+46 ± 6	–100 ± 90
Taiping, China	Krull et al., 2004	–1.7	–4.4	0 ± 6	–10 ± 15
Taho, Japan	Musashi et al., 2001	–0.3	–2.5	29 ± 6	–6 ± 12
Tern-3, Australia	Morante, 1996	–3.1	–10.6	–35 ± 6	–60 ± 80
Wairoa Gorge, New Zealand	Krull et al, 2000	–5.2	–15	–70 ± 10	–400 ± 300
Williston Lake, Canada	Wang et al., 1994	–1.8	–4.1	+35 ± 30	–2000 ± 1000
Nonmarine organic					
Banspetali, India	Sarkar et al., 2003	–1.9	–9.7	–42 ± 10	+40 ± 40
Carleton Heights, S. Africa	Ward et al., 2004	–0.9	–3.3	–54 ± 6	+200 ± 150
Coalsack Bluff, Antarctica	Retallack et al., 2004	–0.8	–4.4	–69 ± 6	+40 ± 50
Denison, Australia	Morante, 1996	–3.4	–5.5	–48 ± 6	+200 ± 90
Eddystone, Australia	Morante, 1996	–2	–3.2	–52 ± 6	+150 ± 90
Godhavari Coalfield, India	de Wit et al., 2002	–3.0	–11.2	–44 ± 6	+40 ± 40
Lootsberg, South Africa	Ward et al., 2004	–0.8	–2.2	–55 ± 6	+200 ± 150
Morondava, Madagascar	de Wit et al., 2002	?	–7.9	–42 ± 6	+20 ± 20
Graphite Peak, Antarctica	Krull and Retallack, 2000	–4	–22.2	–70 ± 6	+300 ± 100
Mount Crean, Antarctica	Retallack et al., 2004	–1.0	–3.3	–65 ± 6	+40 ± 50
Murrays Run, Australia	Morante, 1996	–1.7	–2.9	–58 ± 6	+40 ± 50
Portal Mountain, Antarctica	Retallack et al., 2004	–1.0	–3.1	–66 ± 6	+40 ± 50
Raniganj Coalfield, India	de Wit et al., 2002	–4.2	–13.8	–42 ± 10	+40 ± 40
Shapeless Mt, Antarctica	Retallack et al., 2004	–3.2	–3.4	–64 ± 6	–40 ± 50
Talcher Coalfield, India	de Wit et al., 2002	–3.1	–8.8	–45 ± 6	–50 ± 40
Wardha Coalfield, India	de Wit et al., 2002	–2.1	–3.7	–41 ± 6	+40 ± 40
Wybung Head, Australia	Retallack and Jahren, unpub.	–1.3	–2.4	–59 ± 6	+40 ± 50

TABLE 2. CARBON ISOTOPIC COMPOSITION OF FOSSIL PLANT LEAVES FROM THE SYDNEY BASIN, AUSTRALIA

Taxon	Locality	Triassic age	Specimen	C wt%	$\delta^{13}C_{org}$
Tomiostrobus australis	Terrigal	Late Early	P12194C	10.5	–27.5
Tomiostrobus australis	Terrigal	Late Early	P5594C	6.9	–26.8
Cylostrobus sydneyensis	Turimetta Head	Late Early	P4031C	9.8	–22.5
Isoetes beestonii	South Bulli Mine	Earliest	P12200a	8.4	–26.8
Lepidopteris callipteroides	South Bulli Mine	Earliest	P12200a	5.4	–27.9

be explained in other ways (Boeckelman and Magaritz, 1991). In any case, known depression of carbonate isotopic values by soil formation on carbonates is less profound and does not show such strongly curved depth-functions (Allan and Matthews, 1977). Soil formation also fails to explain decoupled carbon isotopic variation in coexisting organic matter (Fig. 5). Instead, the smooth variation of isotopic values in these marine rocks suggest oceanic mixing curves and recovery from at least two massive injections of isotopically light carbon.

Not all carbon isotopic records through the Permian-Triassic boundary show the high sampling density or stratigraphic completeness of the Gartnerkofel Core. For example, several sequences (Abadeh carbonate, Bethulie carbonate, Çürük Dağ, Paradise 1–6, Sovetashan, and Talcher Coalfield of Table 1) go from values within the range of the Late Permian analyses to the lowest of boundary isotopic values from one sample to the next. Such records probably reflect incompleteness of sampling or of stratigraphic record (Heydari et al. 2001). Conversely, there are other sequences, such as Meishan, China (Fig. 3), Graphite Peak, Antarctica (Fig. 4), and Murrays Run bore, southeastern Australia (Morante and Herbert, 1994; Morante, 1996), where disconformities have long been a local stratigraphic issue (Yin et al., 1996; Retallack and Krull, 1999; Retallack, 1999a), but which appear comparable in completeness to the Gartnerkofel core in resolving decline from latest Permian to earliest Triassic isotopic values.

ISOTOPIC EVIDENCE FOR EARLY TRIASSIC ATMOSPHERIC METHANE

A surprising discovery of recent years is that the carbon isotopic anomaly of the Permian-Triassic boundary is not merely a phenomenon of marine carbonates. The carbon isotopic excursion and offset are similar for both marine carbonate and organic carbon in the Gartnerkofel core (Fig. 5B) and elsewhere (Heydari et al., 2000; Twitchett et al., 2001; Musashi et al., 2001; Krull et al., 2004). Isotopic excursions also are seen in paleosol organic matter (Krull and Retallack, 2000), paleosol carbonate, and tusks of therapsid reptiles (MacLeod et al., 2000). The ubiquity and magnitude of this signal are clues that it reflects more than just marine productivity, different plant physiological pathways, or diagenetic artifacts.

Magnitude of Carbon Isotopic Spike

The magnitude of the carbon isotopic anomaly is an important new clue. Some organic carbon isotopic values are so low (–39‰ to –29‰ $\delta^{13}C$) that they were not at first thought credible by Magaritz et al. (1992), but very low isotopic values of organic carbon are now known from 12 Permian-Triassic boundary sections (Ghosh et al., 1998; Krull et al., 2000; Krull and Retallack, 2000; de Wit et al., 2002; Sarkar et al., 2003; Newton et al., 2004; Ward et al., 2005). The very low Gartnerkofel values are from samples at least as high in total organic carbon as other samples analyzed (Fig. 3C), so it is unlikely that these low values are due to contamination in carbon-lean samples.

Carbon isotope values less than –37‰ in organic matter are known from biologically produced methane, which is typically –60‰ and can have values as low as –110‰ (Whiticar, 2000), and from coalbed thermogenic methane which is –35 to –55‰ (Clayton, 1998). The average isotopic excursion for organic carbon in both marine and nonmarine rocks at the Permian-Triassic boundary is –6.4 ± 4.4‰ (n = 30; Table 1). The average nonmarine excursion in organic carbon of –6.0 ± 5.1‰ (n = 16) is not significantly different from the marine organic carbon excursion of –7.0 ± 3.5‰ (n = 14). Such a global average isotopic excursion requires rapid release to the atmosphere of at least 622 ± 589 Gt (= 10^{15}g) of carbon in methane (using the mass balance equation of Jahren et al., 2001, assuming methane at –60‰ $\delta^{13}C$, and pCO_2 from Retallack, 2001, 2002, recalculated by method of Wynn, 2003). Earliest Triassic methane release and oxidation of 299 ± 285 ppmV CH_4 added to Late Permian CO_2 inventories of 1385 ± 631 ppmV (Retallack, 2001; Wynn, 2003) would have created a transient atmosphere with 1684 ± 916 ppmV CO_2, a value with the same order of magnitude as estimates from the stomatal index of earliest Triassic seed ferns (Retallack, 2001, 2002; Wynn, 2003). This large amount of released methane is much less than proposed for the Permian-Triassic boundary by Ryskin (2003), and no more than 6% of the current inventory of methane hydrates in the world as estimated by Kvenvolden (2000). However, Milkov (2004) estimates global inventories of methane hydrates at only 500–2500 Gt. If Permian reservoirs were similar in size, they would not have yielded methane in amounts sufficient to explain the observed carbon isotope excursion. A more voluminous source is thermogenic methane release by igneous intrusion of carbonaceous sediments (Svensen et al., 2004), because this mechanism can generate 1000 Gt methane from 300–1800 tonnes of coal (Clayton, 1998). High levels of methanogenic CH_4 would not have been sustained in the atmosphere for more than a few tens of years because of oceanic mixing, biotic recycling, and burial with organic matter (Berner, 2002). Claystone breccias, paleosol development, and braided stream paleochannels of the earliest Triassic all indicate an accelerated rate of erosion, sedimentation, and carbon burial following this greatest of all life crises (Retallack et al., 1998, 2003; Retallack 1999a; Retallack and Krull, 1999; Ward et al., 2000).

Our estimates of *minimum* emission volume (n) are based on equilibration of land plant organic carbon isotopic composition with atmospheric carbon isotopic composition, according to the relationship

$$(GtC_{atmosphere}Permian + n\ GtC)\cdot(\delta^{13}C_{atmosphere}Triassic) =$$

$$GtC_{atmosphere}Permian \cdot(\delta^{13}C_{atmosphere}Permian) + n\ GtC\cdot(\delta^{13}C_{emission})$$

This formulation of Jahren et al. (2001) equilibrating organic matter with the atmosphere is comparable to an earlier formulation of Dickens et al. (1995) equilibrating carbonate carbon with oceanic bicarbonate, which is suspect for Permian-Triassic applications because of likely diagenetic alteration of isotopic values of marine carbonate. We are not convinced by the argument of Heydari et al. (2001) that covariance of oxygen and carbon isotopic composition in latest Permian and earliest Triassic carbonates necessarily indicates diagenetic alteration, because plant physiological processes can create such covariance in terrestrial organic matter (Farquhar et al.1993), which contaminates most marine environments. More troubling is the finding of Mii et al. (1997) that Permian-Triassic brachiopod and bivalve shells are variably recrystallized and their carbon isotopic composition altered from original values. Yet another problem is assumed equilibration of the entire ocean with such transient events as massive outbursts of methane from clathrates (Dickens et al., 1995) or intruded carbonaceous sediments (Svensen et al., 2004). Rapid dispersal and oxidation of methane to carbon dioxide, then assimilation by terrestrial vegetation and marine phytoplankton, may keep much methanogenic carbon from equilibration with deep oceanic bicarbonate. For these reasons, our estimates are based entirely on nonmarine organic carbon isotopic values. Nevertheless, dynamic modeling including land and sea data by de Wit et al. (2002) and Berner (2002) gives comparable magnitudes and time scales of Permian-Triassic atmospheric hydrocarbon pollution following massive methane outbursts.

These calculations allow reassessment of past explanations for the Permian-Triassic carbon cycle perturbation involving (1) non-methanogenic organic carbon such as biomass oxidation (Wang et al., 1994; Twitchett et al., 2001), vegetation change (Foster et al., 1998), coal erosion (Magaritz et al., 1992), and oceanic overturn (Knoll et al.,1996); (2) meteoritic carbon from extraterrestrial impacts (Rampino and Haggerty, 1996); or (3) Earth's mantle carbon from general degassing (Isozaki, 1997) or eruptive degassing of the Siberian traps (Conaghan et al., 1994). None of these mechanisms can explain the magnitude of the carbon isotopic excursions by themselves, as outlined below.

Non-methanogenic biomass and fossil fuels have carbon isotopic composition ranging from –35‰ to –15‰. Early Triassic plant values show less range (Table 2). Even if all the oxidized organic matter from biomass, vegetation change, or oceanic overturn had the unrealistically low carbon isotopic value of –35‰, some 4017 GtC would be needed to lower global isotopic organic carbon composition by –6.4‰ (calculations again by formula above). This large mass of carbon is five times the current biomass and more than twice the current soil carbon reserves (including peats) of Earth (Siegenthaler and Sarmiento, 1993), unlikely for the Late Permian (Hotinski et al., 2001; Beerling and Woodward, 2001).

Meteorites have carbon isotopic values of – 47‰ to +1100‰ (Grady et al., 1986; Pillinger, 1987), and comets and interplanetary dust particles have carbon isotopic values down to –120‰ (Jessberger, 1999; Messenger, 2000). Carbonaceous chondrite fragments from the Permian-Triassic boundary in Antarctica are much less carbonaceous and more mineral rich than comets or interplanetary dust particles (Basu et al., 2003). Assuming all the carbon of a carbonaceous chondrite had an isotopic value of –47‰, carbon content as high as 7 wt% (Vdyovkin and Moore 1971), and bulk density as low as 2.2 $g.cm^{-3}$ (Wasson, 1974), the observed –6.4‰ isotopic shift would require a 25-km-diameter asteroid or comet to deliver 1262 GtC at the Permian-Triassic boundary. Evidence from size of shocked quartz, magnitude of iridium anomalies, amounts of extraterrestrial-helium-bearing fullerenes, and size of Bedout Crater all indicate a Permian-Triassic impactor no bigger than the Cretaceous-Tertiary impactor of ~10 km (Retallack et al., 1998; Becker et al., 2001, 2004). A 10–60 km bolide has been proposed on the basis of sulfur isotopic anomalies at one site (Kaiho et al., 2001), but this result has been challenged as more likely due to changes in marine bacterial sulfate reduction (Koeberl et al., 2002).

The Permian-Triassic isotopic anomaly is also too large to be explained by carbon from mantle degassing by way of hydrothermal vents or volcanic eruptions. Addition of volcanic gas with carbon isotopic value of –7‰ to –5‰ (Dickens et al. 1995) into an atmosphere already with carbon isotopic composition of –6.4‰ to –9.6‰ (Arens et al., 2000) would not increase $\delta^{13}C$ of organic matter from its usual value of about –27‰ (Erwin, 1993).

Catastrophic methane outbursts near the Permian-Triassic boundary also explain multiple negative isotopic excursions in many sections (Magaritz et al., 1992; Morante, 1996; Ghosh et al., 1998; Krull et al., 2000; Krull and Retallack, 2000; Heydari et al., 2000; de Wit et al., 2002). Continued Triassic releases of methane may have contributed to unusually protracted recovery from the mass extinction extending some 6 m.y. through most of the Early Triassic (Retallack et al., 1996, 2005; Twitchett et al., 2001; time scale of Gradstein et al., 2005). Additional injections of methane also could have contributed to the generally lower carbon isotopic values of early Triassic organic matter and carbonate (long-term offset of Fig. 6B, 6D), but the size of this difference from late Permian values (~ –2‰ $\delta^{13}C$) is not uniquely methanogenic and could be as much due to productivity, oceanic, volcanic, or paleoclimatic effects (Kump, 1991; Broecker and Peacock, 1999). Modeling indicates that methane outbursts at the Permian-Triassic boundary probably did not continue to destabilize all near-surface methane reservoirs as temperatures rose (de Wit et al., 2002). Instead, methane was released in distinct and transient pulses.

Paleogeographic Variation of Isotopic Anomalies

Organic carbon isotopic data show greater overall variation and paleogeographic spread than carbonate carbon isotopic data, although much deep-water organic matter was presumably formed at shallower depths than where it was preserved. Both long-term carbon isotopic offset and the transient excursion across the Permian-Triassic boundary are less at low latitudes than at high ones (Fig. 6A, B). In addition, the largest long-term offsets and transient excursions were on land, and the smallest in the sea (Fig. 6C, D).

Why would high-latitude land plants have been such effective sinks for isotopically light carbon compared with low-latitude plants and phytoplankton? This problem is exacerbated by lack of evidence for peat-forming ecosystems as a carbon sink during the earliest Triassic at any paleolatitude, probably as a consequence of the extinctions in wetland ecosystems (Retallack et al., 1996). Also distinctive of the earliest Triassic is global warming indicated by migration of thermophilic plants and paleosols into high latitudes of both the Northern and Southern Hemispheres (Retallack, 1999a; Retallack and Krull, 1999; Looy, 2000). There were pioneering plant communities of herbaceous quillworts, and woody seed ferns and conifers at high latitudes (Retallack, 1997, 2002; Retallack and Krull, 1999; Twitchett et al., 2001). Tropical earliest Triassic vegetation was similar, with perhaps a greater abundance of herbaceous isoetaleans (Looy, 2000; Wang and Chen, 2001). From these perspectives the latitudinal difference in isotopic composition could be attributed to differences in plant decay, productivity, woodiness, or physiology. Polar versus tropical differences in decay, productivity, water stress, or herbaceous versus woody plants cannot account for the magnitude of the isotopic differences or their absolute values, because these effects do not alter plant carbon isotopic composition by more than 5‰ (Bestland and Krull, 1999; Beerling and Woodward, 2001). Another possibility is that tropical plants had C_4 or CAM photosynthetic pathways and were thus isotopically heavier than high-latitude plants. This does not account for the extremely light absolute values either (de Wit et al., 2002), and in any case is not supported by our C_3 isotopic values of $\delta^{13}C_{org}$ for earliest Triassic fossil *Isoetes*, a genus that today includes aquatic CAM species (Table 2). The C_4 and CAM pathways are adaptations for conservation of CO_2 in the atmosphere or underwater when CO_2 is limiting (Beerling and Woodward, 2001), but neither the Late Permian nor Early Triassic had such low levels (<500 ppmV) of CO_2 (Retallack, 2001, 2002).

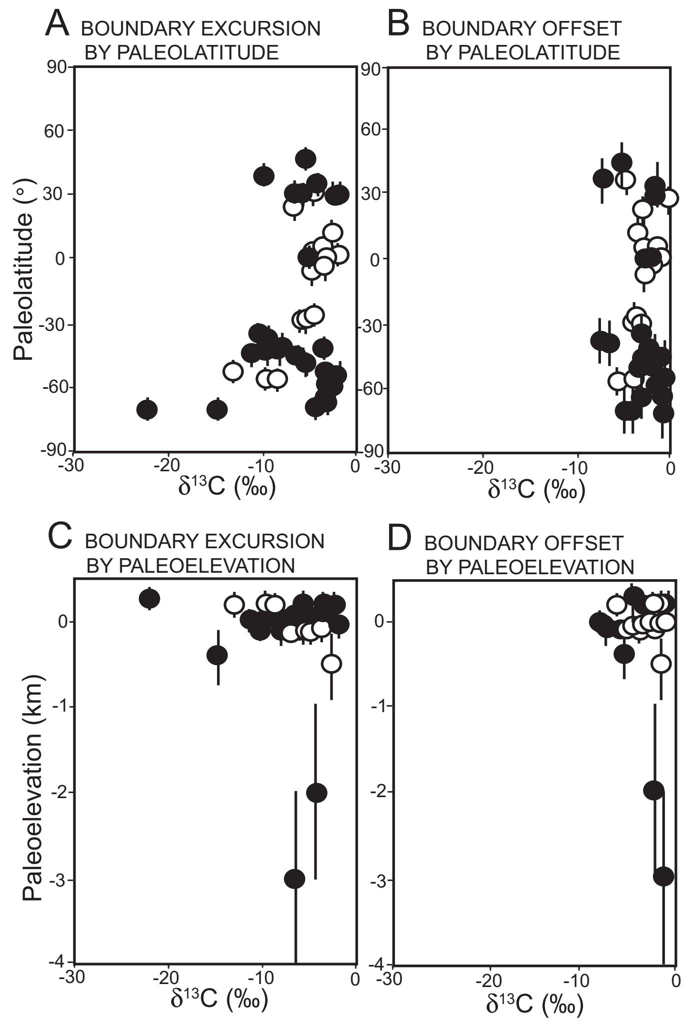

Figure 6. Preferential sequestration of anomalously light carbon at high latitudes and near surface environments is indicated by paleolatitudinal (+ to north, – to south) and paleoelevational (+ on land, – below sea level) distribution of the magnitude of carbon isotopic ($\delta^{13}C$) boundary excursion (A, C) and long-term offset (B, D) of organic matter (solid symbols) and carbonate (open symbols) across the Permian-Triassic boundary (data from Table 1). Carbonate carbon results may be compromised by diagenetic alteration (Mii et al. 1997; Heydari et al. 2001), but comparable patterns are shown by organic carbon results.

Perhaps high latitudes were a source as well as a sink for isotopically light carbon. High-latitude lakes, peat, permafrost, marine continental shelves, and coal measures are currently the largest near-surface methane reservoirs (Clayton, 1998; Kvenvolden, 2000). There was high-latitude permafrost and peat during the modest Late Permian greenhouse, but not during the Early Triassic postapocalyptic greenhouse (Retallack et al., 1996; Retallack, 1999a, 1999b; Retallack and Krull, 1999). Once released, CH_4 is oxidized to CO_2 after ~7 yr in the tropical atmosphere and 24 yr in temperate atmospheres (Khalil et al., 2000), The CO_2 then loses its $\delta^{13}C$ signature as it mixes with CO_2 from other sources (Whiticar, 2000). Time scales for global atmospheric mixing of isotopically distinct CH_4 and CO_2 are probably less than a century, because Greenland and Antarctic ice cores show rapid postglacial rise of CO_2 and CH_4 coincident within a century (Chapellaz et al., 2000). Global mixing times are probably more than two years because the ^{14}C pulse from nuclear weapons testing peaked in Germany in August 1963 after the test ban treaty, but ^{14}C peaked in January 1965 in South Africa and South America, remote from test sites (Levin et al., 1992). Since that time, the main source of ^{14}C has been from nuclear power plants in the Northern Hemisphere, and cruises in 1986 and 1988 showed that ^{14}C in atmospheric CO_2 and CH_4 declined markedly from northern to southern latitudes (Levin et al., 1992). Differences in carbon isotopic composition of plants proximal and distal to burning coal also indicate that uptake of local carbon dioxide can be more rapid than atmospheric mixing (Gleason and Kryser, 1984). Similarly, the paleolatitudinal and paleoelevational variation of carbon isotopic values of earliest Triassic disaster-recovery communities (Fig. 6), indicates that biotic uptake of methane-derived CO_2 was more rapid than global mixing of this isotopically distinct gas.

The paleogeographic distribution of carbon isotopic anomalies also allows reconsideration of past hypotheses for the isotopic excursion. The more profound excursion on land than in the sea cannot be explained by losses of only marine biomass and productivity (Wang et al., 1994). In scenarios in which isotopically light CO_2 bubbled up out of the deep ocean, in a way comparable to the fatal degassing of Lake Nyos in Cameroon (Knoll et al., 1996; Ryskin, 2003), one would expect that the largest excursions would be closer to marine sources, yet the largest isotopic excursions in South Africa, Australia, and Antarctica were well inland and isolated from the ocean by an Andean-style volcanic and fold-mountain range (Fig. 2). The ocean-overturn hypothesis also requires a positive carbon isotopic excursion in deep water and a negative carbon isotopic excursion in shallow water (Hoffman et al., 1991), yet both deep and shallow marine carbon isotopic excursions are negative. The greater polar than equatorial pattern of the carbon isotopic anomalies is also a difficulty for hypotheses that the carbon isotopic anomalies came from eruptive degassing of the Siberian Traps (Isozaki, 1997), a single bolide impact (Becker et al., 2004), or any other single point source.

MECHANISMS FOR MASSIVE METHANE OUTBURST

The massive amounts of methane indicated by the magnitude of the carbon isotopic anomaly at the Permian-Triassic boundary require an efficient release mechanism, which could overwhelm natural methane sinks. Annual sinks of methane now are ~5 Gt (Khalil et al., 2000). Extraterrestrial impact, large volcanic eruptions, submarine landslides, or a combination of these could have exceeded a comparable threshold, releasing methane from hydrates in permafrost and high latitude continental shelves or from thermal alteration of coal measures. These mechanisms are not mutually exclusive, because flood basalt eruption and submarine slides could have been consequences of bolide impact (Boslough et al., 1996; Max et al., 1999). There is evidence of varying quality for each of these methane-clathrate release mechanisms at the Permian-Triassic boundary, as outlined below.

Volcanic Eruption and Intrusion

Substantial amounts of methane could have come from melting of Angaran permafrost by lavas of the Siberian Traps (Vermeij and Dorritie, 1996), which erupted beginning at the Permian-Triassic boundary (Renne et al., 1995; Reichow et al., 2002). Some of these flows are pillowed, vesiculated, and brecciated (Daragan-Sushchov, 1989; Wooden et al., 1993), but latest Permian paleosols overrun by the Siberian Traps have not yet been studied for evidence of permafrost and lava-ice interaction. There is paleosol evidence of permafrost in *Glossopteris*-dominated Middle and Late Permian peatlands at comparable high paleolatitudes of the Gondwana supercontinent, antipodal to the Siberian Traps (Conaghan et al., 1994; Krull, 1999; Retallack, 1999b; Retallack and Krull, 1999).

Intrusions into organic sediments could also have played a role comparable to that proposed for terminal Paleocene global warming (Svensen et al., 2004). The Siberian Traps are prime suspects because of their earliest Triassic age (Renne et al., 1995; Reichow et al., 2002), and extensive thermal metamorphism of coal measures in the Tunguska Basin by feeder dikes to the lavas (Bogdanova, 1991; Mazor et al., 1979). In addition, the Pourakino Trondjemite and Hekeia Gabbro intrusions into Permian marine rocks of the Longwood Range of the South Island of New Zealand have been radiometrically dated at the Permian-Triassic boundary ($^{40}Ar/^{39}Ar$ plateau ages 251.2 ± 0.4 and 249.0 ± 0.4 respectively; Mortimer et al., 1999).

Also plausible is release of marine methane hydrates destabilized by global greenhouse from release of CO_2 and water vapor from Siberian Traps (Krull et al., 2000; Kidder and Worsely, 2004). Modeling by Berner (2002) indicates that the Siberian traps did not release sufficient greenhouse gases to destabilize marine clathrates, but that independently added CO_2 from flood basalts exacerbated atmospheric greenhouse. Such models need to be revised, because yields of CO_2 from lavas may have been higher than previously thought: as much as 2100 ppm from FTIR studies of glasses (Wallace, 2003) and as much as 8500 metric tons/day from volcano monitoring (Gerlach et al., 2002). Alkaline volcanics, such as the Siberian Trap precursor Miamecha-Kotui carbonatites, are much more prolific sources of CO_2 and could be related to flood basalt eruptive cycles (Morgan et al., 2004).

Bolide Impact

The Bedout High in the offshore, subsurface Canning Basin of Western Australia is the most promising of candidate Permian-

Triassic-boundary craters, although this interpretation remains controversial (Glikson, 2004; Renne et al., 2004; Wignall et al., 2004). Impact breccia from its central uplift has an $^{40}Ar/^{39}Ar$ plateau age of 250.1 ± 4.5 Ma (Harrison for Becker et al., 2004; but see analytical reservations of Mundil et al., 2004). This new age determination supports an earlier K-Ar age of 253 ± 5 Ma (Gorter 1996). Remote sensing by gravity and seismic data suggest that Bedout Crater was ~100 km in diameter (Becker et al., 2004). Most breccia clasts from its central peak are Late Permian volcanics, but there are also clasts of fossiliferous limestone in the breccia (Becker et al., 2004). Late Permian shallow marine sediments are a plausible source of methane clathrates. Late Permian permafrost paleosols have been found along the southeast coast of Australia (Retallack, 1999b), but a long way south of Bedout Crater at 32° south paleolatitude (Fig. 2), where permafrost was unlikely in the modest greenhouse of the Late Permian (Retallack, 2002).

Other plausible craters are inadequately documented or not quite the right age. A possible small (35 km diameter) impact crater has been reported near latest Permian cold temperate to frigid peatlands, in New South Wales, Australia (Tonkin, 1998). Lorne Crater includes fossil pollen of the *Protohaploxypinus samoilovichi* zone and fossil plants of the *Dicroidium zuberi* zone high in its conglomeratic fill (Pratt and Herbert, 1973; Holmes and Ash, 1979; Retallack, 1995; Tonkin, 1998), indicating an age at the base of the sequence close to the Permian-Triassic boundary. The Noril'sk iron ores of Siberia have been proposed as remains of a large (20 km diameter) metallic asteroid, whose enormous (>200 km diameter) crater was obliterated by subsequent eruption of the Siberian Traps (Dietz and McHone, 1992; Jones et al., 2002). Araguainha Crater of Brazil is well documented and dated, but small (40 km), and its age ($^{40}Ar/^{39}Ar$ plateaus of 245.5 ± 3.5 Ma and 243.3 ± 3.0 Ma) is some 5 m.y. after the Permian-Triassic boundary (Hammerschmidt and Engelhardt, 1995). The Woodleigh Crater of Western Australia may be either 40 or 120 km in diameter (Reimold et al., 2000), and though poorly dated is most likely the Early Jurassic age of its lacustrine fill (Mory et al., 2000).

Impact of an asteroid a few kilometers in diameter at the Permian-Triassic boundary also is indicated by iridium anomalies in the range 80–130 ppt ($ng.g^{-1}$), shocked quartz grains, Fe-Si-Ni-microspherules, fullerenes with extraterrestrial noble gases, and chondritic meteorite fragments (Zhou and Chai, 1991; Retallack et al., 1998; Chijiwa et al., 1999; Becker et al., 2001, 2004; Kaiho et al., 2001; Basu et al., 2003; Poreda and Becker, 2003; Shukla et al., 2003). Some of these supposed shocked quartz grains have subsequently turned out to be metamorphic quartz grains (Langenhorst et al., 2005). An unusual positive europium anomaly in rare earth elements of the Permian-Triassic boundary near Spiti, India, has been attributed to an eucritic bolide impact (Bhandari et al., 1992), but a thick sequence of sandstone with comparable europium anomalies near Banspetali, India, has been interpreted as due to erosion of Archaean gneisses (Sarkar et al., 2003).

Submarine Landslide

Methane also could have come from large submarine slides, as in the Permian-Triassic boundary sequences at Kaki Vigla, Greece (Baud et al., 1989), and Wairoa Gorge, New Zealand (Krull et al., 2000). The Little Ben Sandstone of New Zealand is an enormous marine mass emplacement deposit mappable throughout the South Island, and it contains a profound methane-related isotopic excursion (Krull et al., 2000). Submarine landslide unroofing of continental shelf clathrates can release massive amounts of methane (Thorpe et al., 1998; Kennett, 2003).

DEATH BY METHANE

Many theories of Permian-Triassic boundary events treat the carbon isotopic excursion as a consequence of death and destruction of biomass (Twitchett et al., 2001), but could methane and its oxidation product, CO_2, have been a cause of the extinctions? Two observations support this idea.

First, both marine and terrestrial extinctions were close to the low point of the carbon isotopic excursion in sequences of suitable stratigraphic resolution. Onset of the isotopic excursion before final extinction near the isotopic minimum is well established in the marine sections near Meishan, China (Fig. 3), in the Gartnerkofel core, Austria (Fig. 5), and Bonaparte Basin of Western Australia (Morante 1996), in coal measures of Graphite Peak, Antarctica (Fig. 4), Murrays Run bore, southeastern Australia (Morante and Herbert, 1994), and in the vertebrate-bearing beds of Bethulie, South Africa (MacLeod et al., 2000). A marine sequence at Schuchert Dal in Greenland was claimed to show marine extinction before the isotopic excursion (Twitchett et al., 2001), but sample spacing and temporal resolution of data presented fail to make this case, as is common with mass extinctions (Marshall 1995). The last marine body and trace fossils at Schuchert Dal are only one sample below the sample showing the beginning of the carbon isotopic excursion. Final extinction of Permian pollen and spores at Schuchert Dal is at a second and higher carbon isotopic minimum and fungal spike (Looy et al., 2001). In no case do the extinctions or isotopic minimum coincide exactly with the Permian-Triassic boundary which is defined at the first appearance of the newly evolved Triassic conodont *Hindeodus parvus* at Meishan, China (Fig. 3; Erwin, 1993; Jin et al., 2000). Initiation of isotopic decline, isotopic minima, and extinctions, were all close to modeled times for methane outburst and dispersal (Berner, 2002).

Second, the magnitude of the carbon isotopic excursion when converted to likely amount of methane released into the atmosphere correlates very well with contemporaneous percentage of generic extinction (Fig. 7). Extinction percentages were taken from Sepkoski (1996). Our calculations of methane release (Table 3) use only nonmarine organic carbon and follow an algorithm using the mass of carbon in the atmosphere (Jahren et al., 2001), rather than the mass of carbon in the ocean (Dickens et al., 1995), because of problems of mixing of such transient

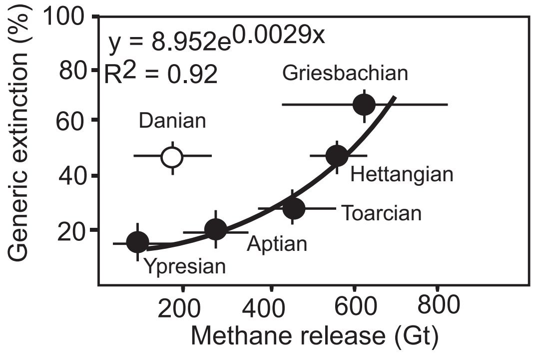

Figure 7. The amount of isotopically light CH_4 released from late Paleocene (Ypresian, 55 Ma), Early Cretaceous (Aptian, 117 Ma), Early Jurassic (Toarcian, 175 Ma), Triassic-Jurassic (Hettangian, 200 Ma), and Permian-Triassic boundary (251 Ma) methane-hydrate dissociation events (Sinha et al. 1995; Hesselbo et al. 2000, 2002; Jahren et al. 2001) correlates well with percentage of generic extinction at those times (Sepkoski 1996). The Cretaceous-Tertiary boundary (65 Ma) isotopic excursion (open circle; after Arens and Jahren 2000, 2002; Beerling et al. 2001) lies off the curve and has overwhelming evidence of asteroid impact. Calculations are for the transient isotopic excursion based on equilibration of land plant and atmospheric carbon, and do not include suspect marine isotopic data or effects of oceanic mixing.

releases (Berner, 2002) and of diagenesis of marine records (Mii et al., 1997; Heydari et al., 2001). Methane isotopic composition is assumed to be –60‰, and estimates of initial atmospheric CO_2 are from stomatal index of fossil plants (Retallack, 2001, 2002; Wynn, 2003). We have not found any comparably significant relationship between extinction magnitude and impact crater diameter, iridium anomalies, shocked quartz abundance, flood basalt volumes, strontium isotopic variation, or sea-level change (see also Wignall, 2001).

Methane could have killed by reacting with atmospheric NO_x to form formaldehyde, by igniting in concentrations greater than 5% by volume, or by anesthetizing and asphyxiating with prolonged exposure in excess of 0.1% by volume (Patnaik, 1992; Clough, 1998). Even release of 622 Gt C in methane would not maintain concentrations greater than 0.1% for more than a few hundred kilometers from individual point sources. Because of methane oxidation to CO_2 in only 7–24 yr (Khalil et al., 2000), the most widespread lethal effects of methane would be similar to those of an unusually severe CO_2 greenhouse. This would include respiratory difficulties and acidosis (Knoll et al., 1996; Retallack et al., 2003), as well as possible effects of acid rain (Retallack 1996, 2004b).

Oceanic Hypercapnia, Hypoxia, Warming, and Reef Gap

In the ocean, excess CO_2 (hypercapnia) and low O_2 (hypoxia) have been suggested to explain preferential extinction of marine invertebrates with heavily calcified skeletons, poor respiratory and circulatory systems, and low basal metabolic rate, such as corals, bryozoans, and brachiopods (Knoll et al. 1996). Hypercapnia also has been invoked to explain unusual abiotic calcite seafloor cements, which occur at the Permian-Triassic boundary, as well as at other stratigraphic levels of negative carbon isotopic excursions within the Early Triassic (Woods et al., 1999). Unlike the model developed from these observations by Knoll et al. (1996), in which CO_2 bubbled out of formerly stratified deep-ocean water, our scenario envisages limited CO_2 from marine oxidation of local rapid release of clathrate or coalbed methane, with the principal global CO_2 enrichment of the ocean being diffusion back from the atmosphere of oxidized CH_4.

Some degree of anoxia (O_2 deficit) also may explain unbioturbated, gray marine shales and cherts of earliest Triassic age (Ishiga et al., 1993; Wignall et al., 1998). It has been tempting to compare Permian-Triassic anoxia to oceanic anoxic events, marked by very pyritic (>3% pyrite) and carbonaceous (>10% TOC) shales, due to high biological productivity and oceanic stagnation (Wignall, 1994; Kuhnt et al., 2002). The biggest problem with the stagnation-anoxia model for the Permian-Triassic extinctions has always been the low pyrite and organic carbon

TABLE 3. ESTIMATED METHANE HYDRATE RELEASE FOR TRANSIENT ORGANIC CARBON ISOTOPIC EXCURSIONS

Age	Ma	Initial CO_2 ppmV	Initial $\delta^{13}C_{org}$	$\Delta^{13}C_{org}$ excursion	Methane release (Gt)	Methane release (ppmV)	Genera extinct (%)
Ypresian	55	333 ± 31	–23.5	–3.6 ± 0.7	75 ± 16	36 ± 7	13 ± 2
Danian	65	748 ± 364	–23.5	–3.4 ± 0.4	159 ± 21	77 ± 10	46 ± 3
Aptian	117	871 ± 706	–22.2	–4.9 ± 1.5	268 ± 92	130 ± 45	17 ± 5
Toarcian	175	871 ± 28	–25.5	–7.0 ± 1.0	459 ± 82	222 ± 40	26 ± 6
Hettangian	200	1935 ± 466	–25.5	–4.2 ± 1.3	570 ± 202	275 ± 98	46 ± 5
Griesbachian	250	1385 ± 631	–24.0	–6.4 ± 5.0	622 ± 589	299 ± 285	66 ± 4

Note: Methane release has been estimated in both GtC (= 10^{15} g) and ppmV. Initial CO_2 is from unsmoothed data of Retallack (2001) recalculated using method of Wynn (2003); isotopic excursions from Sinha et al. (1995), Hesselbo et al. (2000, 2002), Jahren et al. (2001) and herein; extinction values from Sepkoski (1996); methane release calculated by method of Jahren et al. (2001).

content of marine shales of earliest Triassic age (Retallack, 2004a; Wignall and Newton, 2004). Although Isozaki (1997) claimed that shales of the earliest Triassic are carbonaceous, he presented no analytical data. Hundreds of published total organic carbon and inorganic sulfur analyses of marine shales of earliest Triassic age do not exceed 3 wt%, whereas shales of Late Permian and Middle Triassic age in the same sequences are much more carbonaceous (Suzuki et al., 1993; Kajiwara et al., 1994; Wang et al., 1994; Wolbach et al., 1994; Morante, 1996; Wignall et al., 1998; Krull et al., 2000, 2004). By our methane poisoning scenario, anoxia arises not from respiration in a highly productive surface ocean, but from oxidation of methane in depopulated seas, which would result in only local and minor accumulation of organic matter and pyritization.

Postapocalyptic earliest Triassic greenhouse warming is indicated by evidence from fossil soils (Retallack, 1999a), plants (Retallack, 2002), and vertebrates (Retallack et al., 2003). Oceanic warming is a prime culprit in coral bleaching today (Marshall and McCulloch, 2002) and may also enable outbreaks of coral predation (Pandolfi, 1992). A combination of warm tropical sea temperatures and hypercapnia may explain the lack of fossil coral reefs anywhere in the world during the Early Triassic, the longest gap in the geological record of reefs (Weidlich et al., 2003). Trepostome and fenestellid bryozoans and rugose and tabulate corals are prominent among casualties of the mass extinction, and hexacorals did not appear until after the Early Triassic (Erwin, 1993). These simple organisms had limited ventilatory capacity, and oxygen deficiency would have been exacerbated once their oxygenating symbiotic zooxanthellae were expelled during thermal bleaching. Abundant earliest Triassic cyanobacterial stromatolites (Schubert and Bottjer 1992) and algal wrinkle structures (Pruss et al., 2004) recall greenhouse conditions of the Late Cambrian.

Soil Warming, Acidification, Hypoxia, Erosion, and Coal Gap

On land, there are multiple lines of evidence for a postapocalyptic greenhouse supplementary to the already modest Late Permian greenhouse (Retallack 1999a, 2002). A contribution of methane is needed to explain extreme fluctuations in carbon isotopic depth variation within earliest Triassic paleosols (Krull and Retallack, 2000). Abrupt onset of earliest Triassic warmth at high latitudes is indicated by unusually strong chemical weathering compared with physical weathering of Antarctic and Australian paleosols, which include such deeply weathered soils as Ultisols (Retallack, 1999a; Retallack and Krull, 1999). In addition, fossil leaves of *Lepidopteris* immediately above the Permian-Triassic boundary in Australia and India have exceptionally low stomatal index, which, by comparison with comparable modern leaves of *Ginkgo*, indicates atmospheric CO_2 levels of 7876 ± 5693 ppmV or 28 ± 20 PAL (1 PAL is present atmospheric level: Retallack, 2001, 2002, Wynn, 2003). Early Triassic fossil plants are notably herbaceous, succulent, heterophyllous, sclerophyllous, and thickly cutinized, characteristics that can be considered adaptations to hot or dry conditions (Retallack, 1997; Looy, 2000) but also are adaptations to high levels of atmospheric CO_2 (Retallack, 2001, 2002).

Evidence for acid rain at the Permian-Triassic boundary is mixed. Australian terrestrial sequences have strongly leached, kaolinitic Permian-Triassic boundary breccias, but coeval boundary breccias in Antarctica are little leached (Retallack et al., 1998). Nevertheless, paleosol sequences examined chemically in Australia, Antarctica, and South Africa show evidence of increased precipitation and chemical weathering across the Permian-Triassic boundary (Retallack, 1999a; Retallack and Krull, 1999; Retallack, et al., 2003). Strontium-isotopic composition of carbonates provide a global proxy of acidic leaching of continents, but the predicted rise of $^{87}Sr/^{86}Sr$ due to acid rain is difficult to distinguish from a longer-term mid-Permian to mid-Triassic steep rise in $^{87}Sr/^{86}Sr$ values (Martin and MacDougall, 1995). High-resolution $^{87}Sr/^{86}Sr$ analyses across the boundary in the stratotype section at Meishan, China, do show a rise compatible with acidification between the boundary beds and the first appearance of the earliest Triassic conodont *Hindeodus parvus* (Kaiho et al., 2001). Thus there is evidence for increased rainfall, and for chemical weathering due to higher atmospheric CO_2 levels, but not yet clear indications of strong acid rain, such as nitric and sulfuric acid rain created by impact at the Cretaceous-Tertiary boundary (Retallack, 1996, 2004b).

Soil hypoxia in wetlands is indicated by earliest Triassic paleosols directly above coal measures (Retallack, 1999a; Retallack and Krull, 1999). Large berthierine nodules indicating unusually low soil oxidation are found in earliest Triassic Dolores paleosols of Antarctica (Sheldon and Retallack, 2002). Signs of hypoxia are not evident from red, highly oxidized earliest Triassic paleosols, interpreted as originally well drained (Retallack, et al., 2003). Elevated levels of carbon dioxide and methane that are not serious problems for plants of well-drained soils could have harmed plants of wetland soils already marginally aerated. Mass balance modeling suggests a drop in atmospheric O_2 to as low as 12% by volume as methane oxidized to carbon dioxide during the earliest Triassic (Berner, 2002). Such low oxygen levels in the air would be further lowered a short distance down into biologically active, swampy soils, thus restricting root respiration to very shallow levels within soils (Jenik, 1978). When waterlogged soils become completely stagnant, swampland trees die and peats are inundated by lakes and lagoons.

A variety of sedimentary features attest to extensive plant dieback in marginally aerated lowland sedimentary environments. Sedimentary response to terminal Permian plant extinctions may be compared to the response to forest clear-cutting today (Retallack, 2005). Unlike underlying alluvial sequences of latest Permian age, those of earliest Triassic age are dominated by weakly developed paleosols (Retallack and Krull, 1999; Retallack et al., 2003) and extensive claystone breccias from local soil erosion (Retallack et al., 1998; Retallack, 2005). Of similar origin is a 9-m-thick mudflow deposit at the Permian-Triassic boundary in the Raniganj Basin, India (Sarkar et al., 2003). Following wetland plant dieback, mudflows and gully erosion of floodplain soils would have propagated into upland regions and induced the observed replacement of latest Permian meandering streams by earliest Triassic braided streams (Retallack and Krull, 1999; Ward et al., 2000).

Extinction by hypoxia is also an explanation for the Early Triassic coal gap. This was a time when peat formed nowhere in the world for 6 m.y. (following time estimates of Gradstein et al., 2005), and the only long-term hiatus in peat formation documented since the Devonian evolution of swamps (Retallack et al., 1996). The idea of methane-induced soil hypoxia explains not only preferential extinction of wetland plants, but also the protracted duration of the coal gap, prolonged by additional methane outbursts throughout the Early Triassic (Fig. 4; 5; Krull and Retallack, 2000). *Vertebraria*'s aquatically adapted glossopterid roots extend down as much as 80 cm into latest Permian peaty paleosols (Fig. 8B), but it was extinguished at the Permian-Triassic boundary throughout the Gondwana supercontinent (Retallack and Krull, 1999). Similarly, peat-forming

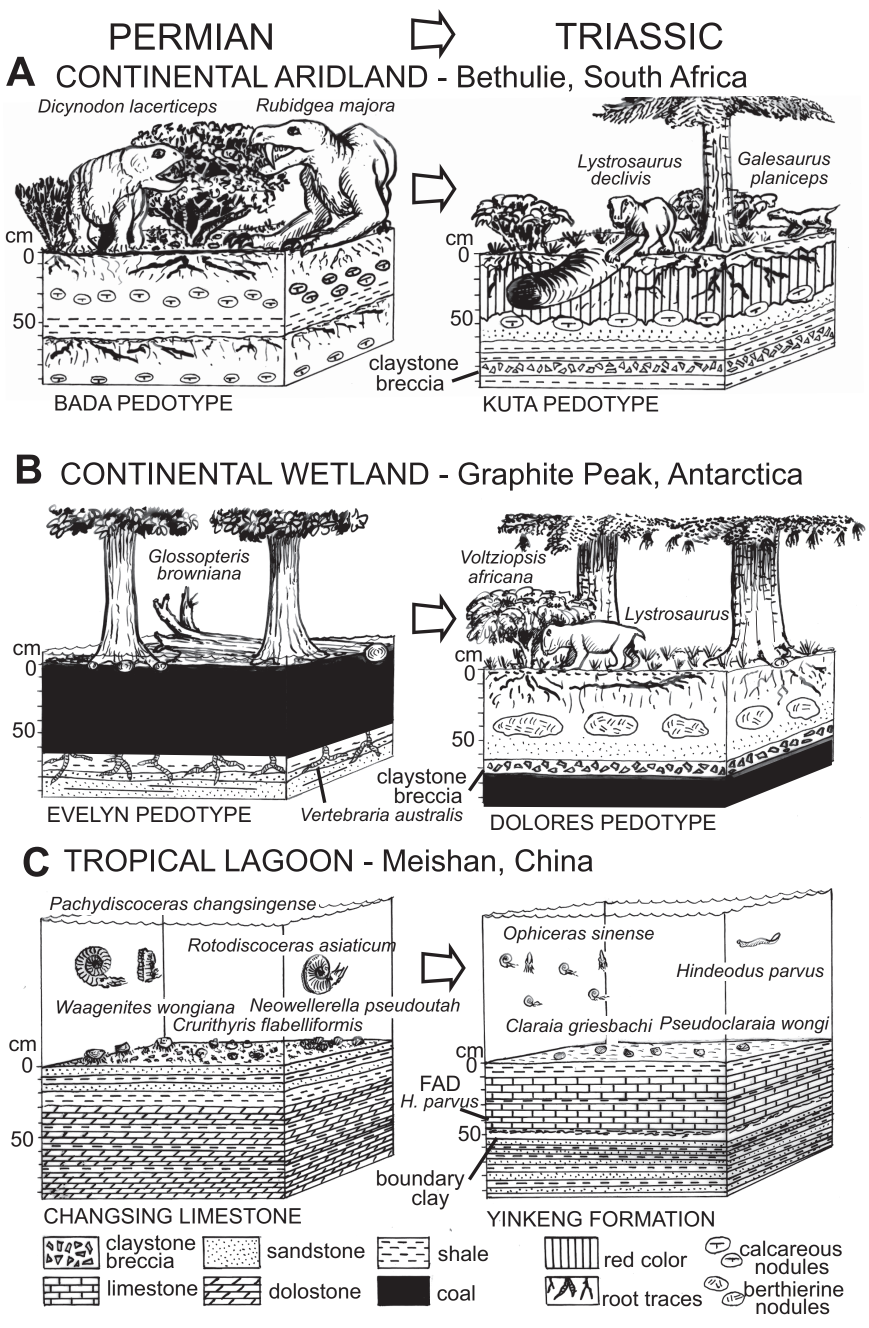

Figure 8. Reconstructed paleoenvironments before and after the Permian-Triassic boundary at (A) Bethulie, South Africa (Retallack et al., 2003); (B) Graphite Peak, Antarctica (Retallack and Krull, 1999); and (C) Meishan, China (Yin et al., 1996).

ecosystems of ruflorian cordaites in Siberia (Meyen, 1982), and of lycopsids in China (Wang and Chen, 2001) were destroyed utterly at the end of the Permian. Other regions without Late Permian coal, such as Europe and North America, do not show such profound levels of extinction (Rees, 2002). This is partly a taphonomic artifact, because coal measures preserve most fossil plants, but even within Permian-Triassic coal-measure-terminating sequences, non-peat-forming plants such as conifers and seed ferns survived preferentially (Meyen, 1982; Retallack, 1995; Wang and Chen, 2001). Terminal-Permian lowland woody plant dieback and decay also is indicated by unusually abundant fungal spores, preferential extinction of gymnosperms relative to pteridophytes, and shifting composition of palynodebris (Visscher et al., 1996; Looy, 2000). One problem with this interpretation is that many hyphae previously interpreted as fungal may instead have been zygnematalean algae (Krassilov and Afonin, 1999; Foster, 2001), but some fungal spikes are still evident from fungal spores (Retallack, 1995). When peat-forming ecosystems reappeared during the Middle Triassic (ca. 245 Ma), they were dominated by conifers and cycad-like plants, which were upland plants during the Permian (DiMichele et al., 2001) and unrelated to plants thought to have formed Late Permian coals (Retallack et al., 1996).

Vertebrate Hypoxia, Acidosis, and Pulmonary Edema

Among large animals on land, high methane and carbon dioxide and low oxygen would impair mitochondrial oxidative phosphorylation (Fiddian-Green 1995). Consequent changes in blood pH would be most telling in the lungs, and death by pulmonary edema formerly restricted to high altitudes would have occurred at lower altitudes. Early Triassic oxygen levels of 12 vol% of the atmosphere, estimated by modeling (Berner, 2002), would have made oxygenation near sea level comparable to that in mountains more than 4000 m high (Retallack et al., 2003), where mountaineers are vulnerable to nausea, headache, hypertension, and pulmonary edema, a group of maladies commonly called mountain sickness (Hultgren, 1997). Although the Permian-Triassic hydrocarbon pollution crisis envisaged here would have been normobaric hypoxia with acidosis, and mountain sickness today is hypobaric hypoxia with alkalosis, both elicit similar physiological responses in experiments with rats (Russell and Crook, 1968; Schoene, 1990). These responses include exaggerated (Cheney-Stokes) breathing, pulmonary vasoconstriction, and high red blood cell count (Hultgren, 1997). Fossilizable adaptations to hypoxia of altitude among large mammals include large barrel chests relative to body size and low-birth-weight babies (Beall, 1982; Bouverot, 1985; Schoene, 1990). Earliest Triassic survival of small, barrel-chested *Lystrosaurus* (Fig. 8A, 8B) offers support to this concept of extinction by hypoxia. Evolution of a muscular diaphragm giving greater aerobic scope of survivors may also explain the thickened thoracic but reduced lumbar ribs of Triassic compared with Permian therapsid reptiles, especially *Galesaurus* and *Thrinaxodon* (Fig. 8A, 8B; Brink, 1956). Another ventilatory advantage of many modern mammals over reptiles is a short snout and long secondary palate, creating a less obstructed airway in *Lystrosaurus* and all subsequent dicynodonts compared with their Permian ancestors (Cruickshank, 1968; King, 1991). Mammals and birds also can acclimate to low oxygen, unlike frogs, which are more closely related to Permian amphibians and reptiles. Acclimatization may also have aided survival of therapsids such as *Lystrosaurus* (Engoren, 2004; Retallack, 2004c). Finally, there is evidence from fossil skeletons in burrows that *Lystrosaurus*, like other Permian therapsids, was a burrower (Smith, 1987; Groenewald, 1991). Burrows are poorly aerated spaces, and burrowing animals adapt to hypercapnia and hypoxia. Large, non-burrowing reptiles were not under such selection pressures and did not survive the Permian-Triassic boundary (Smith and Ward, 2001; Benton et al., 2004). The Permian-Triassic acquisition of near-mammalian nares, palate, and rib-cage was "a defining moment for amniote physiology and evolution" (Graham et al., 1997).

RAGNAROK HYPOTHESIS

We call our hypothesis of terminal-Permian death by methane the Ragnarok hypothesis. In ancient Norse mythology, Ragnarok is the twilight of the gods, a mythic end of the world as we know it, and harbinger of a new age of harmony. "First will come a triple winter .... and the sun impart no gladness…. The earth…. will tremble, the sea leave its basin, the heavens tear asunder, and men perish in great numbers…. The gods and their enemies having fallen in battle, Surtur, having killed Freya, darts fire and flames over the world" (Bullfinch, 1993). The Ragnarok myth captures our concept of impact or volcanic winter with massive methane outbursts and CO_2+CH_4 greenhouse as a cause for the Permian-Triassic mass extinction.

Our Ragnarok hypothesis of terminal-Permian death by methane outbursts is a testable hypothesis that explains more effectively than competing hypotheses (Table 4) a variety of observations on the carbon isotopic excursion across the Permian-Triassic boundary at a global network of localities (Fig. 2, Table 1). It is a disturbing vision of biotic vulnerability to impact, volcanic, or other destabilization of coalbed and clathrate methane. Parallels with historic atmospheric pollution with hydrocarbons and consequent global warming, coral bleaching, and wetland stagnation are especially intriguing.

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TABLE 4. EVALUATION OF ALTERNATIVE HYPOTHESES FOR SEVERAL OBSERVATIONS OF THE CARBON ISOTOPIC EXCURSION AT THE PERMIAN-TRIASSIC BOUNDARY

Hypotheses	$\Delta^{13}C$ excursion as much as –8‰	Greater $\delta^{13}C$ excursion at high than low latitude	Greater $\delta^{13}C$ excursion on land than in sea	Negative $\delta^{13}C$ excursion in deep sea	$\delta^{13}C$ excursion on land and in sea
Methane outburst	Yes	Yes	Yes	Yes	Yes
Comet/asteroid impact	Maybe (1)	Maybe (2)	Yes	Yes	Yes
Volcanic degassing	No	Maybe (3)	Yes	Yes	Yes
Erosion of coal	No	Yes	Yes	Yes	Yes
Change from trees to herbs	No	No	Yes	Yes	Yes
Curtailed productivity on land	No	No	Yes	Yes	Yes
Curtailed productivity in sea	No	No	No	Yes	Yes
Overturn of seltzer ocean	No	No	No	No	Yes

Note: The "maybe" entries are dependent on (1) chemically rare chondritic bolide, >25 km diameter; (2) bipolar impacts; and (3) bipolar eruptions.

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