Comparative Earth History and Late Permian Mass Extinction

A. H. Knoll, R. K. Bambach, D. E. Canfield, J. P. Grotzinger

The repeated association during the late Neoproterozoic Era of large carbon-isotopic excursions, continental glaciation, and stratigraphically anomalous carbonate precipitation provides a framework for interpreting the reprise of these conditions on the Late Permian Earth. A paleoceanographic model that was developed to explain these stratigraphically linked phenomena suggests that the overturn of anoxic deep oceans during the Late Permian introduced high concentrations of carbon dioxide into surficial environments. The predicted physiological and climatic consequences for marine and terrestrial organisms are in good accord with the observed timing and selectivity of Late Permian mass extinction.

Life in the oceans nearly disappeared 250 million years ago (Ma). Of the more than 500 families of marine animals represented by fossils in Upper Permian rocks, fully half do not persist into basal Triassic or younger successions (*1*). At the genera and species levels, extinction estimates run as high as 84% (*2*) and 93 to 95% (*3*), respectively. Many hypotheses have been proposed to explain end-Permian mass extinction, but most of these do not account for observed taxonomic, physiological, ecological, and biogeographic patterns of extinction or do not provide geological and geochemical tests of proposed mechanisms (*4*). Here, we present a hypothesis for the Permian mass extinction that does both. We propose that the Late Permian biological crisis was precipitated by the rapid overturn of deep anoxic oceans, which introduced toxic concentrations of CO_2 and, perhaps, H_2S into surficial environments.

Lessons from the Neoproterozoic Record

Many aspects of Late Permian geology and geochemistry are unusual in the sedimentary record of the past 500 million years (My) (*4*). At an earlier time, however, many of these features occurred repeatedly over a 250-My interval comprising the late Neoproterozoic Era (~800 to 543 Ma). For this reason, we take the late Neoproterozoic geological record as our point of departure for exploring Late Permian events.

The late Neoproterozoic was a time of continental aggregation, with narrow seaways separating land masses and a pan-Thalassic ocean of hemispheric proportions (*5*). Carbon cycling in late Neoproterozoic oceans was unusual, as shown by the C-isotopic record. At least four times, $\delta^{13}C$ values of shelf and platform carbonates rose to ≥8 per mil; coeval organic matter shows comparable ^{13}C enrichment (*6*). Each positive excursion was followed by a relatively rapid drop of at least 10 per mil to $\delta^{13}C$ values of ≤ -2 per mil in carbonates. Further, continental ice sheets formed and decayed during the four intervals bracketed by the positive and negative extremes (*6*). In each case, these climatic and biogeochemical events were accompanied by the formation of stratigraphically anomalous carbonates, commonly with unusual textures that include macroscopic precipitates on the shallow ocean floor (*7*).

This repeated association of isotopic excursions, ice ages, and anomalous carbonates can be explained in terms of a relatively simple paleoceanographic model. In a world characterized by continental aggregation and no continental ice sheets, it is unlikely that ocean circulation patterns—in particular, low-latitude deep-water formation—could supply enough oxygen to the deep sea to maintain oxic environments throughout the world's oceans (*8–10*). Consequently, anoxia would develop in narrow ocean basins and the deep hemispheric ocean.

Under these conditions, continuing photosynthesis would act as a biological pump, drawing CO_2 from the atmosphere and exporting it to sediments or the anoxic deep ocean as organic matter (Fig. 1A). The organic matter would be either buried or remineralized by sulfate reduction, leading to a buildup of H_2S, HCO_3^-, and CO_2 in deep waters. Enhanced organic carbon burial would reduce atmospheric CO_2 and shift the $\delta^{13}C$ of surface seawater to more positive values; in contemporaneous deep waters, dissolved inorganic carbon would become comparatively enriched in ^{12}C. Decreasing atmospheric greenhouse capacity would facilitate the growth of continental glaciers, but after high-latitude cooling reached a critical threshold, vigorous, thermo-haline bottom circulation would be induced, causing oceanic overturn and the rapid return of HCO_3^- and CO_2–charged waters to the surface (Fig. 1B) (*11*). Carbon dioxide would be released to the at-

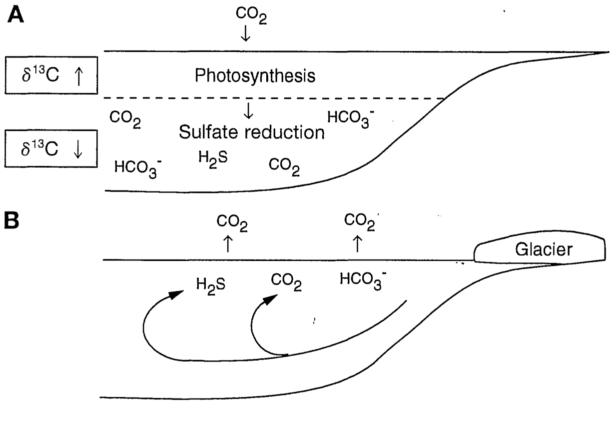

Fig. 1. Illustration of paleoceanographic model developed to explain late Neoproterozoic and Late Permian geological and geochemical observations. (**A**) When continents are aggregated and no continental ice sheets exist, sluggish circulation leads to deep-ocean anoxia. Continuing photosynthesis draws CO_2 from the surface ocean and atmosphere and exports it to sediments and the deep ocean as organic matter. In deep anoxic waters, remineralization of organic matter by sulfate reduction leads to increased concentrations of CO_2, HCO_3^-, and H_2S. Enhanced organic C burial causes atmospheric CO_2 to decline and $\delta^{13}C$ of ΣCO_2 to increase in the shallow ocean; remineralization of organic matter causes $\delta^{13}C$ of ΣCO_2 to decrease in the deep ocean. (**B**) Reduced atmospheric greenhouse capacity facilitates the growth of continental ice sheets and sea ice, leading to rapid mixing of the ocean and the return of isotopically light CO_2 and HCO_3^- to the surface.

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mosphere, causing a transient increase in atmospheric temperatures, which in turn would melt the ice caps; CO_2 degassing would also drive the precipitation of the isotopically light bicarbonate as $CaCO_3$ in highly oversaturated surface waters (*7*, *12*).

This scenario provides an attractive way of linking disparate but stratigraphically linked phenomena and potentially answers the long-standing question of why Neoproterozoic successions should feature tillites and warm-water carbonates in close stratigraphic juxtaposition. Its validity, however, rests on the quantity of CO_2 that can be stored and released from anoxic deep waters. As a test, we considered a simple biogeochemical model of the CO_2 evolution of a parcel of ocean water that becomes anoxic (Fig. 2). The model is static, that is, it has no provision for dynamic ocean processes; however, it reproduces with reasonable accuracy the observed chemistry of modern anoxic basins (*13*). At the outset, organic matter entering the water parcel is oxidized by aerobic respiration. As O_2 concentration declines, ΣCO_2 increases (Fig. 2A). After oxygen is exhausted, sulfate reduction ensues, producing a further increase in ΣCO_2 as H_2S accumulates. The partial pressure of CO_2 gas ($P\text{CO}_2$) increases markedly during this evolution because of the increasing acidity of deep waters (Fig. 2B). For a reasonable maximum H_2S buildup of 500 μM (assumed on the basis of likely limits on organic carbon and phosphate fluxes), $P\text{CO}_2$ can reach ~10,000 μatm (beneath a surface ocean with a $P\text{CO}_2$ of 300 μatm, the modern value). The effect of returning such deep water to the surface rapidly is shown in Fig. 2C. An admixture of just 25% anoxic deep water results in a transient order-of-magnitude increase in surficial $P\text{CO}_2$; a 50:50 mix of anoxic deep and surface waters raises surficial $P\text{CO}_2$ to nearly 6000 μatm. As equilibrium is reestablished, atmospheric $P\text{CO}_2$ settles at ~1900 μatm.

Carbon isotopes permit a direct test of this model. The minima of negative C-isotopic excursions provide a conservative estimate of $\delta^{13}C$ for deep-water ΣCO_2 before overturn. Because isotopically light deep-water ΣCO_2 is generated by the oxidation of organic matter, we can estimate how much organic matter must be remineralized to make this value 8 to 10 per mil lighter than that of coeval surface waters. All reasonable estimates of $\delta^{13}C$ values for surface ΣCO_2, deep ΣCO_2, and organic carbon require the generation of ~500 μM H_2S in late Neoproterozoic deep water (Fig. 2, A and B) (*14*). Sulfate reduction on this scale would be associated with deep-ocean phosphate concentrations higher than those seen today; however, these concentrations would be predicted if the oceans circulated at about one-third the present rate (*9*). Indeed, the increased reservoir of reactive phosphate in anoxic deep waters would be sufficiently large to offset the effect of sluggish circulation on surface ocean primary productivity and to sustain extensive photosynthesis despite a decrease in vertical mixing (*9*, *15*). Deep anoxic ocean waters can thus build up CO_2 concentrations sufficient to drive the climatic changes observed in the Neoproterozoic record, and apparently did so.

Late Permian Iteration

The repeated history of Neoproterozoic climatic and biogeochemical change provides a framework for ordering Late Permian geological observations. Like the late Proterozoic, the Late Permian was a time of aggregated continents, with narrow and partially isolated marine basins separating land masses and, once the great Gondwana ice sheets waned, ice-free poles (*16*). Subtidal carbonate buildups along Late Permian platform margins include abundant ocean-floor precipitates. Such encrustations are otherwise rare in Phanerozoic sedimentary successions; however, they can be linked to the texturally unusual carbonates found in late Neoproterozoic successions, as well as to precipitate structures common in Archean and Paleoproterozoic carbonates deposited before increasing surface $P\text{O}_2$ made the oxygenation of deep oceans possible (*7*, *17*).

Deep-water anoxia has long been proposed for the latest Permian oceans (*12*, *15*), but documentation has been difficult because subduction has destroyed most pelagic sediments older than the Jurassic. In Japan, however, the latest Permian pelagic successions are preserved in accreted terrains. Their abundance of highly carbonaceous pyritic chert and claystone prompted Isozaki (*18*) to coin the term "superanoxia" for Late Permian deep oceans. In the Japanese successions, $\delta^{34}S$ values for pyrite show a shift from −35 ± 5 per mil in Middle Permian strata to −15 ± 5 per mil in uppermost Permian and basal Triassic rocks, with a transient return to isotopically light sulfide at or near the Permian-Triassic (P-T) boundary (*19*). Viewed in isolation, the pyrite data might be interpreted as recording a latest Permian increase in the proportional burial of sulfide versus sulfate; however, sulfate $\delta^{34}S$ decreases slightly from +15 to +12 per mil through the same interval (*20*). Thus, either most biogenic H_2S did not undergo the oxidation and bacterial disproportionation that would cause the observed isotopic difference between sulfates and pyrite to exceed the fractionation of ~25 to 30 per mil physiologically associated with sulfate reduction (*21*), or deep waters received substantial mantle-derived sulfide from mid-ocean ridges. In either case, Late Permian and earliest Triassic deep waters must have been isolated from the oxygen-rich surface ocean, with rapid and transient turnover near the boundary (*19*).

The Late Permian interval that is marked by continental aggregation, anomalous carbonate precipitates, and distinctive S-isotopic signatures is also distinguished by a reprise of unusual secular variation in the C-isotopic composition of carbonates ($\delta^{13}C_{carb}$) (*20*, *22–24*). During the Wordian and Capitanian stages (Fig. 3) (*25*), $\delta^{13}C_{carb}$ values rose to a Phanerozoic maximum of 8 per mil. This peak was followed by a decline in surficial $\delta^{13}C$, culminating in a rapid drop to values of <0 per mil at the P-T boundary. Thus, C-isotopic variation in the Late Permian was comparable in magnitude to that seen repeatedly during the late Neoproterozoic. The Late Permian record may also contain evidence for more than one negative isotopic excursion. Almost all geochemical investigation of this interval has concentrated on boundary

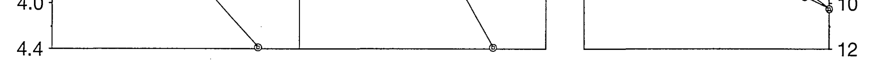

Fig. 2. Model of water chemistry evolution in a parcel of deep anoxic seawater (*13*). (**A** and **B**) Relations among O_2 depletion, H_2S buildup, ΣCO_2 (= $[CO_2]$ + $[H_2CO_3]$ + $[HCO_3^-]$ + $[CO_3^{2-}]$), and $P\text{CO}_2$. (**C**) Mixing line for shallow ocean water (with a chemistry similar to that of the present-day surface ocean) and deep anoxic water containing 500 μM H_2S. Two scenarios are presented: either no H_2S is oxidized during mixing, or H_2S is oxidized to sulfate in amounts controlled by the oxygen provided during mixing.

events per se, but data from four continents suggest that one or more negative C-isotopic excursions (to values of –2 to –3 per mil) occurred well before the boundary event (22, 24, 26). At present, low sampling densities and limited investigation of diagenesis require that this aspect of Late Permian isotopic change be regarded as prediction rather than fact.

Given the Neoproterozoic relation among C-isotopic signatures, climate, and carbonate precipitation, this secular pattern in Late Permian C-isotopes and carbonate deposition might imply that there was short-lived glaciation at that time. Indeed, a brief episode of high-latitude glaciation and sea ice formation occurred in northern Siberia during the interval bracketed by the C-isotopic maximum and minimum (27). Thus, the paleoceanographic model proposed to explain aspects of Neoproterozoic history can be applied to the Late Permian record.

Physiological Consequences of Acute and Prolonged Hypercapnia

What effect would rapid oceanic turnover and release of CO_2 have on Late Permian biology? In animals, elevated CO_2 can disrupt the acid-base balance of internal fluids, leading to narcotizing acidosis; aquatic animals are routinely anesthetized with CO_2 (28–30). Increasing acidity also causes hemoglobin and other respiratory pigments to change conformation, decreasing their affinity for oxygen (the Bohr effect); at high partial pressures, CO_2 binds directly with respiratory pigments, further decreasing their ability to carry oxygen. Elevated internal CO_2 concentrations also contribute to physiological mechanisms that trigger metabolic slowing or arrest (31). Organisms that produce $CaCO_3$ skeletons are particularly sensitive to hypercapnia, because carbonate biomineralization requires precise control of the acid-base balance (32).

Paleobiological prediction is possible because animals vary in their ability to compensate for imposed increases in internal PCO_2. In general, land animals have much higher blood PCO_2 than do aquatic animals and can compensate for hypercapnia by increasing ventilation (28). In aquatic animals, blood PCO_2 is never very different from inspired PCO_2 (29); compensation by increased ventilation is rare and may be limited to animals with high rates of energy metabolism (30, 33). Thus, for aquatic animals, an increase in ambient CO_2 of even a few torr (1 torr = 1316 μatm) causes hypercapnic acidosis by passive CO_2 loading (29). Compensation by increased internal HCO_3^- is rarely complete (28) and may be ineffective when externally induced hypercapnia is acute and protracted.

In our model (Fig. 2C), a transient shallow-ocean PCO_2 of 5 torr (6580 μatm) results from a 55:45 mix of deep anoxic waters (500 μM H_2S) and normal shallow ocean water. For deep water with 300 μM H_2S (about the lowest concentration that is consistent with C-isotopic data), a deep/shallow mixing ratio of 75:25 is required. (Lower mixing ratios require a $\delta^{13}C$ of deep-water ΣCO_2 much lower than values observed in excursion minima, which necessitates correspondingly higher deep-water PCO_2.) In the limiting case in which all ocean waters below the surficial wind-mixed layer were anoxic, rapid overturn would produce a transient surficial PCO_2 of 10,000 μatm (7.6 torr). Thus, Late Permian oceanic overturn would have induced physiological effects that, if they persisted over an interval greater than the life-span of individual organisms, could lead directly or indirectly to widespread mortality (34).

Within the marine realm, animals with active circulation and gills compensate for elevated CO_2 better than do animals with passive gas exchange, and thus they should be more likely to survive acute and prolonged hypercapnia. Also, animals that normally experience high internal PCO_2 (because of high rates of exercise metabolism or confinement to poorly ventilated burrows) tolerate hypercapnia better than do animals that are unaccustomed to elevated CO_2. As noted above, organisms that form carbonate skeletons should be comparatively at risk because of their sensitivity to internal acid-base balance. On land, the direct physiological effects of CO_2 may be limited, but animals and plants would be strongly affected by rapid, greenhouse-induced warming, particularly at high latitudes.

The Timing and Pattern of Late Permian Mass Extinction

In concert, our model and comparative physiology predict that Late Permian mass extinction (i) occurred in pulses associated with oceanic overturn, and (ii) differentially affected organisms that were most sensitive to hypercapnia and rapid climatic warming.

Timing. As noted above, the available geological and geochemical data support the hypothesis that anoxic deep oceans turned over rapidly at the P-T boundary (35). Some data, including the multiple-excursion interpretation of the C-isotopic record, further suggest at least one earlier turnover event near the Capitanian-Wujiapingian boundary. This hypothesis requires further testing, but it is consistent with aspects of the paleontological record that suggest two or more extinction pulses.

Sepkoski's (36) compilation of family-level data for marine animals shows approximately equal numbers of extinctions for the earlier (Wordian and Capitanian) and later (Wujiapingian and Changxingian) stages of the Late Permian. Although recent revisions of stratigraphic ranges [on the basis of improved intercontinental correlation (37) and exceptionally well-preserved faunas from China (38)] indicate that some taxa previously thought to have disappeared at the end of the Capitanian persisted into the Wujiapingian or Changxingian, the number of families with last appearances in the Capitanian is still about equal to those exiting in the Changxingian (38).

Consistent with this family-level pattern, Sepkoski's (39) compilation of stratigraphic ranges for fossil genera shows that 58% of all marine animal genera recorded in Capitanian strata do not occur in younger rocks and that 67% of the remaining genera disappeared

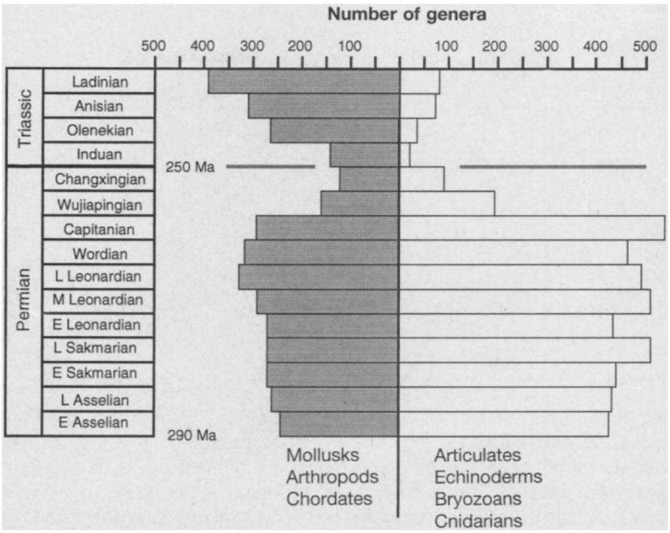

Fig. 3. Generic diversity throughout the Permian and Early to Middle Triassic periods, showing the timing and physiological selectivity of Late Permian extinctions as well as their consequences for the subsequent biological makeup of marine ecosystems. Data are from the generic database of Sepkoski (39). L, M, and E refer to late, middle, and early, respectively.

during or at the end of the Wujiapingian and Changxingian stages (*40*). Because origination rates were low during the Late Permian, this finding means that the consistently high proportionality of generic last appearances through the last three stages of the Late Permian was accomplished by successively smaller numbers of extinctions (Fig. 3 and Table 1). In the well-preserved Late Permian succession of South China, last appearances of marine families (*38*), genera (*41*), and species (*4*) all show high concentrations at the Capitanian-Wujiapingian as well as P-T boundaries.

The idea that significant extinction preceded the P-T boundary is not new (*40*, *42*); however, the Signor-Lipps effect—the apparent smearing of catastrophic extinctions backward in time as a function of incomplete sampling (*43*)—may provide an alternative to this interpretation. If the observed paleontological pattern is primarily a Signor-Lipps artifact, it is unusual both because the effect increases as one recedes from the actual boundary event and because common and widespread taxa are removed along with the rare forms whose ranges are predicted to be truncated by poor sampling.

In an attempt to ascertain whether mass extinction could result from regional rather than global disturbance, Raup (*44*) estimated that the eradication of all life in fully half the area of the Earth would engender only a 15% decrease in generic diversity. Thus, a failure of the record by 50% in the latest Permian (Wujiapingian and Changxingian) intervals would not produce a diversity drop nearly as great as the magnitude actually recorded. More to the point, Stanley and Yang (*40*) devised three independent statistical procedures to test whether Capitanian or Wujiapingian last appearances principally reflect an extinction pulse or Signor-Lipps artifact; all tests supported the hypothesis of a true extinction event.

Although Signor-Lipps artifacts undoubtedly contribute to the observed stratigraphic pattern of extinctions, the foregoing arguments all support the hypothesis of genuinely elevated extinction beginning near the end of the Capitanian and culminating at the end of the Permian Period. Our model provides a mechanism for pulsed Late Permian mass extinction and predicts that future studies will confirm the pattern of multiple C-isotopic excursions outlined above.

Selectivity. As shown in Fig. 3 and Table 1, the physiological selectivity of Late Permian extinctions conforms well to the pattern expected for acute and prolonged hypercapnia. Corals, articulate brachiopods, bryozoans, and echinoderms—groups characterized by heavily calcified skeletons, elaborated gas-permeable surfaces, weak circulation of internal fluids, and low metabolic rates—lost 65% of their genera in the Capitanian, 67% of surviving and new genera in the Wujiapingian, and 81% of their few remaining genera in the Changxingian. In contrast, genera of mollusks, arthropods, and chordates—groups with gills, active circulatory systems, and, in many cases, relatively high rates of energy metabolism—declined by 49% in the Capitanian and just 38% in each of the Wujiapingian and Changxingian stages. This physiological pattern is predicted by our model, but it is opposite to that required by hypotheses that call for oxygen depletion in shelf waters or nutrient collapse. Both of these hypotheses predict that metabolically active animals should be unusually vulnerable to extinction, when in fact they survived differentially well (*45*).

Patterns of differential extinction for genera within larger groups provide further support for the hypothesis of hypercapnia-mediated extinction. For example, extinction probabilities within the articulate brachiopod order that includes the most highly elaborated lophophores [Terebratulida (*46*)] are lower than those for other Articulata (Table 1). Similarly, stenolaemate bryozoans lost 88% of their genera during the Late Permian, whereas the still uncommon gymnolaemates, with their more highly elaborated lophophores (*47*), lost only one of four genera. Infaunal bivalves, which would have encountered somewhat elevated CO_2 concentrations in their burrows, survived better than did epifau-

Table 1. Extinction of genera within major groups of skeletonized marine animals and foraminifera for the last four stages of the Permian. Data are from the generic database of Sepkoski (*39*). *N*, number of genera recorded within a stage; *E*, number of last appearances; and *P*, percent extinction.

Taxonomic group	Wordian			Capitanian			Wujiapingian			Changxingian		
	N	*E*	*P*	*N*	*E*	*P*	*N*	*E*	*P*	*N*	*E*	*P*
Animals with no gills, weak internal circulation, and low metabolic rates												
Tabulates	9	1	11	14	8	57	6	6	100	–	–	–
Rugose corals	39	6	15	45	19	42	27	17	63	10	10	100
Stenolaemate bryozoans	95	3	3	108	66	61	42	25	60	18	5	28
Terebratulid brachiopods	25	1	4	32	16	50	19	14	74	5	3	60
Other articulates	234	46	20	229	135	59	110	75	68	56	54	96
Blastoid echinoderms	10	0	0	15	15	100	–	–	–	–	–	–
Crinoid echinoderms	32	3	9	87	87	100*	–	–	–	–	–	–
Total	444	60	14	530	346	65	204	137	67	89	72	81
Animals with gills, active internal circulation, and relatively high metabolic rates												
Prosobranch gastropods	109	38	35	79	33	42	46	16	35	30	4	13
Infaunal bivalves	22	2	9	24	5	21	20	8	40	13	2	15
Epifaunal bivalves	86	13	15	89	48	54	48	16	33	36	16	44
Nautiloid cephalopods	17	6	35	14	5	36	10	3	30	7	2	29
Ammonoid cephalopods	46	26	57	38	28	74	18	11	61	15	13	87
Arthropods†	19	5	26	21	13	61	9	4	44	6	2	33
Conodonts	8	2	25	8	2	25	6	1	17	6	2	33
Other vertebrates	13	4	31	14	9	64	7	3	43	6	3	34
Total	320	95	30	288	142	49	166	63	38	120	45	38
Foraminifera (benthic protists)												
Fusulinids‡	56	12	21	54	18	33	42	7	7	40	40	100
Textulariids	34	0	0	34	2	6	32	0	0	32	6	19

*Although no crinoids are known from the latest Permian rocks, at least one genus survived to initiate a Mesozoic radiation of the group. †Trilobites (which suffered total extinction) and malacostracans (which suffered few extinctions). ‡Ross (*65*) showed a greater concentration of fusulinid extinctions at the end of the Capitanian, but still reported total extinction of the group at the P-T boundary.

nal bivalves, with 21% versus 54% generic loss in the Capitanian and 15% versus 44% extinction in the Changxingian (Table 1).

Our model may also help to explain an unusual pattern of extinction within the cephalopods. Nautiloid cephalopods had a fairly high rate of turnover throughout the Permian, but their extinction rates in the latest Permian were no higher than those for earlier intervals (Table 1). In contrast, ammonoid cephalopods, which had turnover comparable to nautiloids through the Early and Middle Permian, had an extinction rate twice that of nautiloids in the Late Permian (Table 1). Living *Nautilus* provides a reasonable model for most ancient nautiloids (*48*): it is a motile predator with four gills and almost no Bohr effect (*49*). Although ammonoids have often been interpreted in similar terms, *Nautilus* may provide a poor physiological model for these fossils (*48, 50*). Coleoid cephalopods, the extant sister group of ammonoids (*48, 51*), have only two gills and exhibit a modest to strong Bohr effect (*49*). Functional and paleoenvironmental arguments also suggest that many ammonoids were microphagous drifters or benthos that were unlikely to sustain high metabolic rates (*52*). If these observations are correct, the differential extinction of ammonoid versus nautiloid cephalopods also conforms to the hypercapnia model.

Effects related to the possible interference of hypercapnia with calcification are also evident. The calcareous fusulinid foraminifera died out completely during the Late Permian, whereas textulariid forams, which have agglutinated skeletons, suffered only modest diversity loss (Table 1). Conodonts and corals differ both in skeletal mineralogy and physiology; the phosphatic conodonts, now known to have been produced by metabolically active vertebrates, suffered relatively few losses during the Late Permian, whereas the sedentary and heavily calcified rugose and tabulate corals disappeared completely (Table 1). Alternative hypotheses fail to provide an explanation for extinction bias with respect to skeleton composition.

Inadequate sampling and poor stratigraphic control have hindered attempts to evaluate global patterns of tetrapod extinction near the P-T boundary (*4*). Research in the Karoo Basin, South Africa, shows that, at least regionally, tetrapod diversity declined during the earlier part of the Late Permian and then dropped sharply at the P-T boundary, coincident with sedimentological evidence for increased aridity (*53*). Given the ability of terrestrial animals to tolerate hypercapnic stress, tetrapod extinctions might best be explained by rapid climatic change associated with elevated CO_2 concentrations in the atmosphere; nonetheless, the only group of large tetrapods to increase rather than decrease in diversity across the P-T boundary was the mammal-like reptile group Cynodontia (*54*). The Cynodontia were the only Late Permian tetrapods to have the full suite of skeletal characters (bony secondary palate, differentiated thoracic and lumbar regions, nasal turbinal complex) that enable rapid ventilation and high aerobic capacity in their descendants, the mammals (*55*).

Also on land, cool- to cold-temperate vegetation in both high northern and southern paleolatitudes was replaced rapidly near the end of the Permian by warm-temperate plants drawn from ancestral low-latitude populations (*16, 56*). An unusual feature of the palynological record is the high abundance of fungal remains beginning just below the P-T boundary; this record independently implies that widespread environmental stress engendered mass mortality and the decay of vegetation (*57*).

Conclusions and Predictions

The preceding sections address numerous features of Late Permian geology, geochemistry, and paleontology in need of explanation. Although each observation, considered in isolation, can potentially be explained in half a dozen ways, our model provides a single mechanism to account for all. In stressing a physiological role for CO_2 in Late Permian mass extinction, we do not reject potential roles for associated phenomena. Both on land and in the sea, the indirect effects of rapid, transient climatic change must have exacerbated extinction, and it is possible that the observed physiological selectivity resulted from the combined effects of physiological and climatic stress. CO_2-rich bottom waters were also charged with H_2S, which provided a further poison for marine animals and algae. Even the large-scale return of nutrients to the surface ocean (*15*) would have contributed to the demise of sensitive animals such as corals (*58*). Unusually low Late Permian sea level (*59*) would also have exacerbated extinctions by limiting shallow marine biotas to the margins of deep basins, where the toxic effects of overturn would be maximized (*60*).

Variants of the model are possible and can be tested by careful stratigraphic, geochronometric, and geochemical investigation. For example, oceanic turnover need not be driven by glaciation. Bolide impact could engender catastrophic turnover (*19*), although independent evidence for Late Permian impact is weak (*4*). P-T boundary turnover might alternatively be engendered by changes in oceanic circulation driven by plate tectonic alteration of continental positions and basin geometries; the massive flood basalts documented in Siberia (*61*) might thus be viewed as a volcanic expression of tectonic realignment. In any event, massive volcanism would have delivered additional CO_2 and acidity to the oceans and atmosphere.

Given the stratigraphic resolution available in interbasinal correlation, the biostratigraphic data cannot currently supply a definitive test for this or any other Late Permian extinction hypothesis. Nonetheless, our model predicts that high-resolution stratigraphy within basins will show extinctions to be rapid and pulsed, with clustered last appearances associated with C-isotopic excursions and other evidence for the turnover of anoxic deep oceans (*62*). The mechanism proposed here may also be applicable to other Paleozoic crises, notably Late Ordovician mass extinction, which has similarly been associated stratigraphically with marked C-isotopic shifts and short-lived continental glaciation (*63*).

When continents are clustered and climates are equable, the deep ocean can sow the seeds of biological disaster. Rapid overturn of CO_2-charged anoxic deep waters can lead to a transient increase in surface $P\mathrm{CO}_2$ sufficient to cause widespread physiological shock, climatic shock, or both, resulting in mass mortality and extinction. More generally, this model exemplifies an emerging view of Earth history in which the present provides only one of several keys to the past. Other such keys will be derived from models that explore how the biosphere worked under conditions of geography and oceanic circulation very different from those of today (*7, 17, 64*).

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$$\delta^{13}C = \left[\frac{(^{13}C/^{12}C)_{\mathrm{sample}}}{(^{13}C/^{12}C)_{\mathrm{standard}}} - 1\right] \times 10^3$$

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    $$\delta^{13}C_{SO}[(\Sigma CO_2)_{SO}] + \delta^{13}C_{OM}(x) = \delta^{13}C_{DO}[(\Sigma CO_2)_{SO} + x]$$

    where SO, DO, and OM denote shallow ocean, deep ocean, and organic matter, respectively. If $(\Sigma CO_2)_{SO}$ is set at its modern value of 2100 μM, and if $\delta^{13}C_{SO} = +6$ per mil, $\delta^{13}C_{DO} = -4$ per mil, and $\delta^{13}C_{OM} = \delta^{13}C_{SO} - 28$ per mil (conservative estimates for the late Neoproterozoic), then $x =$ 1170 μM. An O_2 concentration of 300 μM can oxidize (or liberate) 23 μM ΣCO_2; the remaining 940 μM ΣCO_2 must be generated by means of bacterial sulfate reduction, requiring 470 μM H_2S (see Fig. 2).
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