

The Permo–Triassic extinction

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The end-Permian mass extinction brought the Palaeozoic great experiment in marine life to a close during an interval of intense climatic, tectonic and geochemical change. Improved knowledge of latest Permian faunas, coupled with recent advances in isotopic studies and biostratigraphy, have greatly enhanced our understanding of the events of 250 million years ago and have begun to provide answers to many questions about the causes of extinction.

KILLING over 90% of the species in the oceans^{1,2} and about 70% of vertebrate families on land^{3,5} is remarkably difficult. The end-Permian mass extinction was the closest metazoans have come to being exterminated during the past 600 million years. The effects of this extinction are with us still, for it changed the structure and composition of marine communities far more than any event since the Cambrian radiation. The end-Permian extinction brought the world of the Palaeozoic to a close, permitting the expansion of new marine community types which continue to dominate modern oceans. This event plays a critical role in debates over the nature of mass extinctions and their role in structuring the evolution of life.

By 1840, Phillips⁶ recognized that the history of macroscopic life on Earth could be divided into three great eras, which he named the Palaeozoic, Mesozoic and Cenozoic; he also recognized two dramatic drops in diversity, each associated with the appearance of new types of organisms. Yet until well into this century, palaeontologists paid little attention to these events. Since publication of the impact hypothesis⁷, interest has focused on the Cretaceous/Tertiary (K/T) mass extinctions and other events with a possible extraterrestrial cause. In part this stems from the widespread, if erroneous, view that the record across the Permo–Triassic (P/Tr) boundary is too poor for detailed study, a presumption based on apparent evidence for a widespread marine regression and depositional hiatus at the boundary.

The pattern of disappearances across the Permo–Triassic boundary is complex, with some clades disappearing well below the boundary, others quite diverse right up to the boundary, and still others seemingly oblivious to the extinction^{2,8}. Analysing such patterns is complicated by distortions including the regression, backward smearing of true last occurrences⁹, and many Lazarus taxa. Lazarus taxa¹⁰ disappear from the record during the Late Permian, but did not become extinct, for they reappear in Middle Triassic rocks. First recognized in gastropods¹¹, the phenomenon is widespread among bivalves, brachiopods and

other taxa, demonstrating both the extent of sampling problems and the importance of undiscovered refugia in preserving many lineages.

Detailed palaeontological, geochemical and sedimentological studies of sections in Italy, Pakistan and south China are revealing a rich and complex pattern of events. New correlations based on conodonts permit more precise and more accurate intercontinental correlations and comparison of extinction patterns among regions. These new data have, in turn, led to the re-examination of older hypotheses about the causes of the extinction and the proposal of additional scenarios.

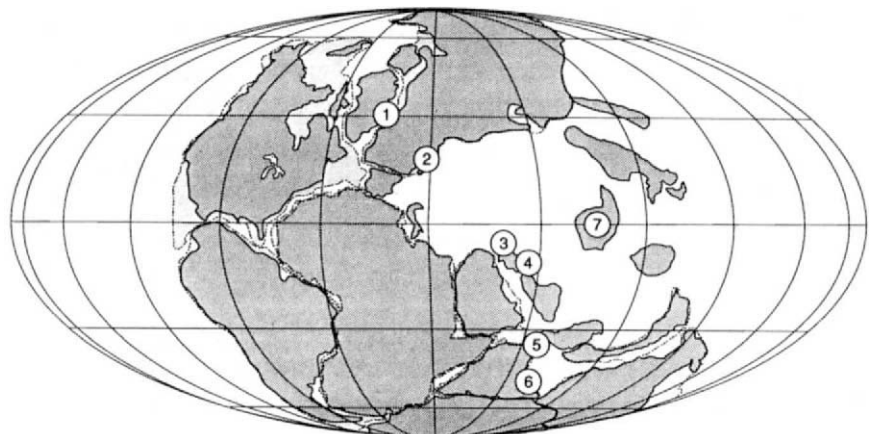
The cause of the end-Permian mass extinction appears to involve a tangled web rather than a single mechanism. Three phases can be identified. The first began with the onset of the marine regression which dried out many marine basins, reduced habitat area and increased climatic variability. The regression accelerated during the second phase, triggering the release of gas hydrates and the erosion and oxidation of marine carbon. In conjunction with the eruption of the Siberian flood basalts, these carbon sources exacerbated climatic instability; an increase in atmospheric carbon dioxide may have produced oceanic anoxia and global warming. The final phase of the extinction involved the destruction of near-shore terrestrial habitats during the rapid earliest Triassic marine transgression.

Marine extinctions

The marine fossil record provides the most complete and detailed record of the extinction. Examining the temporal, biogeographical and ecological pattern of extinction allows evaluation of proposed extinction scenarios, all of which ultimately requires high-resolution biostratigraphic correlation between the sections spanning the Permo–Triassic boundary.

Boundary sections. The Permo–Triassic boundary was traditionally recognized by the first occurrence of the ammonoid *Otoceras woodwardi* and the more easily identifiable bivalve *Claraia*. Correlating between the primary boundary sections

FIG. 1 Continental positions in the Late Permian, showing the location of important Permo–Triassic boundary sections. The number and continuity of individual sections in the southern Alps, Iran and south China belies earlier claims for a worldwide period of non-deposition spanning the Permo–Triassic boundary. (1) Greenland; (2) Southern Alps; (3) Iran–Armenia border (Kuh-e-Ali Bashi section); (4) Central Iran; (5) Salt Range, Pakistan; (6) Guryl Ravine, Kashmir; (7) numerous sections in South China.



(Fig. 1) has been difficult, but correlations based on conodonts have resolved these problems, although they have dramatically altered the relationships among boundary sections (reviewed in refs 2, 8, 12 and 13, but see ref. 14) (Fig. 2). These results suggest *O. woodwardi* first appeared during latest Permian boreal, cold-water faunas¹³. In contrast, *Otoceras* is absent from contemporary warm-water faunas of the Tethyan realm, including the magnificent Changxingian faunas of South China. Moreover, these correlations offer the prospect of the first global, high-resolution analysis of extinction and survival patterns.

Contrary to earlier claims¹⁵, recent studies of the Permian Bellerophon Formation and the overlying Werfen Formation in the Alps indicate that this classic sequence preserves a detailed palaeontological¹⁶ and geochemical¹⁷ record of the extinction interval. The boundary lies within the Tesero Horizon at the base of the Werfen Formation, which contains a fauna transitional between the Permian and Triassic, similar to mixed faunas from South China¹⁸. A gradual shift in carbon isotopes ($\delta^{13}\text{C}$) from +3‰ to -1‰ is associated with the extinction horizon¹⁷. A curious spike in spores of the fungus *Tympanicysta*¹⁹ may indicate widespread collapse and decay of terrestrial ecosystems.

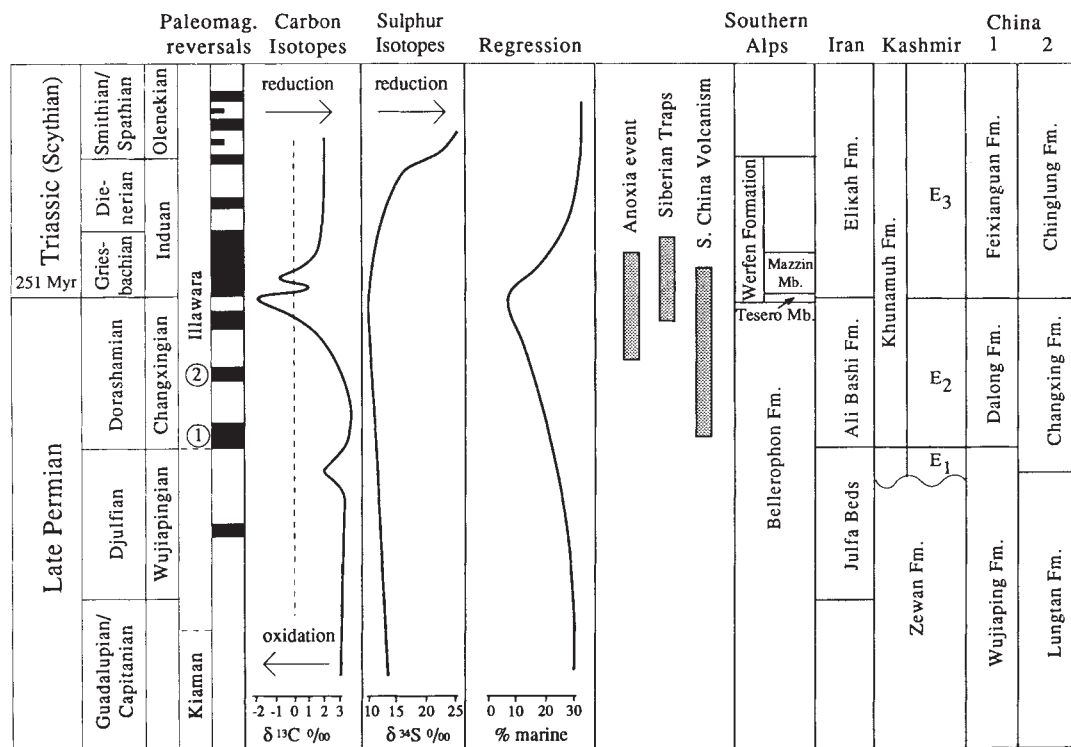
The widespread Permo-Triassic boundary deposits in South China²⁰⁻²⁴ contain a diverse fauna. In the latest Permian Changxing Formation, 435 of 476 invertebrate species, or 91%, disappear (ref. 24, cited in ref. 25), including 98% of ammonoids species, 85% of bivalve species and 75% of the shallow-water fusulinid foraminifera. However, taxonomic inconsistencies and lack of Lower Triassic sediments may overstate the magnitude of the extinction. Furthermore, in contrast to the gradual shift in $\delta^{13}\text{C}$ in the Alps, sections of South China record a relatively abrupt shift²⁶, suggesting that the Chinese sections are condensed relative to those in the Alps. This may account for claims of a catastrophic extinction in the Chinese sections²⁷. The youngest known Palaeozoic reefs are found in the Changxing Formation,

in Sichuan and Hubei Provinces²⁸. Thus a diverse Permian reef fauna disappears before the boundary as evaporites develop, but their presence belies claims of prolonged environmental deterioration before the P/Tr boundary, at least in South China.

Clay layers, apparently of volcanic origin, occur throughout the latest Permian Changxing formation and a particularly thick clay marks the basal Triassic. A tuffaceous texture, bipyramidal quartz, volcanic shards and geochemistry all indicate an explosive silica-rich volcanic source for the ash²⁹⁻³¹, probably associated with a subduction zone. This ash covers >10⁶ km² (ref. 30), representing eruption of 1,000-4,000 km³ of material³¹. This volcanism has been linked to the extinction^{20,24,29,30}, but is no larger than many other pyroclastic eruptions, with no discernable biological effects³². Reports of iridium enrichment within boundary clays^{25,33,34} cannot be replicated^{30,35,36}, arguing against the kind of impact associated with the Cretaceous-Tertiary mass extinction. The lack of an impact signature also raises questions about the nature of the cause of the apparently periodic mass extinctions stretching from the late Permian into the Miocene³⁷. Immediately overlying the boundary clay are a series of characteristic transitional beds containing three distinctive mixed faunas of both Permian and Triassic fossils²³; remixing after deposition has been ruled out as a cause of this assemblage³⁸.

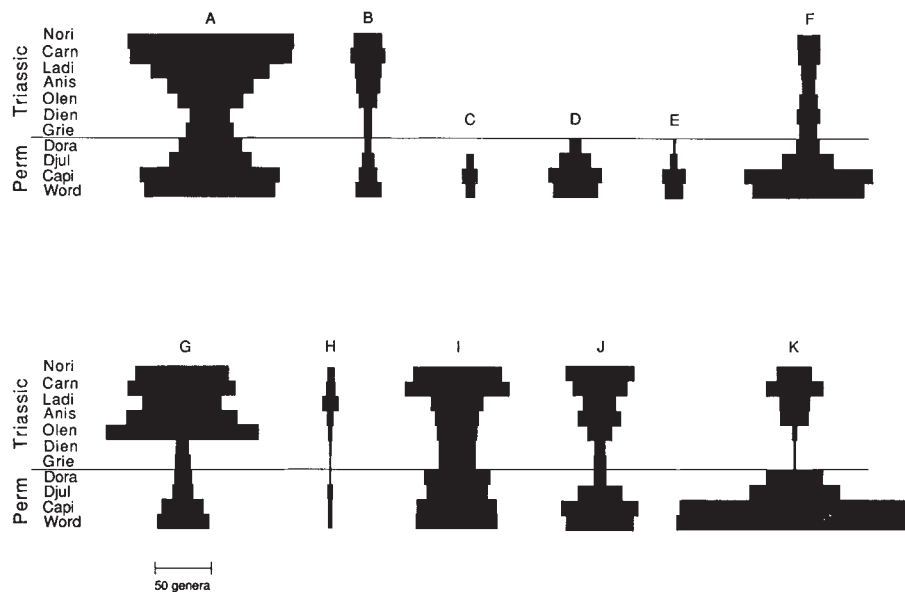
Extinction patterns. Global diversity of durably skeletonized marine families declined from 536 to 267 (49%) between the Capitanian and the end of the Permian; about 72% of corresponding genera disappeared^{37,39-41}. In comparison, only 57% of genera disappeared during the end-Ordovician mass extinction, the second largest of the Phanerozoic³⁷. Rarefaction analysis suggests that global species extinction was >90% (ref. 1), although the magnitude and pattern varied considerably among different clades (Figs 3 and 4). This included a 79% extinction among families from Sepkoski's Palaeozoic evolutionary fauna (predominantly epifaunal, suspension feeders, including Palaeo-

FIG. 2 Permo-Triassic geological events and correlation between major boundary sections. Standard geological stages are shown to left, with two alternative names given for latest Permian. Zircons from the boundary clay at Meishan, China provide a date for the Permo-Triassic boundary of 251.2 ± 3.4 Myr ago⁷². The end of the Kiaman Reversed Superchron and the onset of the mixed polarity interval at the base of the Illawara Superchron is not well delineated. It has been placed near the base of the Changxingian stage^{73,74}, but other work suggests it may have occurred as early as the latest Capitanian (M. Menning, personal communication). Black is normal magnetic polarity, white is reversed polarity (1, *Neogondolella orientalis* zone; 2) base of the *N. changxingensis* zone. Shifts in carbon isotopes¹⁷ and sulphur isotopes⁵⁰ are schematic. Strontium isotopes show a similar pattern to the carbon isotopes, declining to the lowest value of the Phanerozoic near the boundary, indicating an influx of light strontium from juvenile basalts, generally on mid-ocean ridges. Other significant events include the eruption of the massive Siberian flood basalts, a lengthy (1-3 Myr)



anoxia event in deep-water marine rocks in Japan (Y. Isozaki, personal communication), a widespread pyroclastic volcanism in south China. Correlation between boundary sections in the southern Alps; Kuh-e-Ali Bashi, northeastern Iran; Guryl Ravine, Kashmir; and Shangsi (1) and Meishan (2) in southern China are based on conodont analyses¹².

FIG. 3 Generic diversity patterns among marine invertebrates from the mid-Permian through to the Triassic. All stages are of equal width, although they range in duration from 1–2 Myr for the Djulfian, Dorashamian and Griesbachian to ~13 Myr for the Norian. There is great variability in extinction–survival–recovery pattern. Nautiloids (B), sponges (I), non-fusulinid foraminifera, conodonts and some gastropods (none shown) were almost oblivious to the extinction; although some species disappeared, the level of extinction was far less than among other taxa. A second group appears to decline together with the marine regression. These include the tabulate and rugose corals (C, D), the trilobites (E), the bryozoa (F), the articulate brachiopods (J, K) and the crinoids and blastoids, although the poor fossil record of the last two during the Permian makes this pattern suspect. This pattern is partly an artefact of the declining quality of the fossil record, however, because many of these taxa, including fusulinid foraminifera, articulate brachiopods, ammonoids (G) and several gastropod groups exhibit high diversity in latest Permian rocks, particularly in South China, but decline rapidly near the boundary. Abbreviations: Word, Wordian; Capi, Capitanian; Djul, Djulfian; Dora, Dorashamian (=Changxingian); Grie, Griesbachian; Olen, Olenkian; Anis, Anisian; Ladi, Ladinian; Carn, Carnian; Nori, Norian. A, Bivalvia; B, Nautiloidea; C, Tabulata; D, Rugosa; E, Trilobita; F, Bryozoa; G, Ammonoidea; H, Echinoidae; I, Porifera; J, Rhyncbone-liida+Terebratulida (brachiopods);



zoic corals, articulate brachiopods, stenolaemate bryozoans and stalked echinoderms). In contrast, the modern evolutionary fauna (gastropods, bivalves, echinoids) declined by only 27% (ref. 41).

The reliability of the patterns shown in Fig. 3 is unclear. For example, the decline of the foraminiferid suborder Fusulinina was thought to have begun by mid-Permian times. Yet fusulinids are diverse in the Changxing Formation before disappearing rapidly near the boundary. Non-fusulinid forams, which lived in deeper water, experienced only slight extinction, although architecturally more complex taxa seem to suffer more than less complex forms across all suborders⁴². Does this mean the apparently gradual extinction simply reflected the loss of shallow marine sediments outside of South China? Perhaps, but South China was an isolated tectonic block during the latest Permian (Fig. 1). It may have served as a refugium for groups already declining on Pangea. Palaeontologists do not yet have the high-resolution data on global extinction and survival patterns that will resolve these questions. There is, however, little support for claims that the mass extinction occurred over eight million years⁸, but it is unclear whether the extinction lasted two million years, 1 million years or even less.

Several generalities seem secure however. Clades of sessile, epifaunal, filter-feeders generally suffered, but such clades often share other risk factors, including near-shore distribution, or restricted environmental distribution⁴³. The apparent increased extinction among marine invertebrates with planktotrophic larval development^{44,45} may simply reflect the increased extinction in near-shore environments and in the tropics, both areas where planktotrophs dominate.

The terrestrial record

Most palaeontologists have emphasized the extensive marine extinctions and hence most descriptions have emphasized marine processes. Data from terrestrial vertebrates and insects reveal widespread extinctions during the Late Permian, although the data are not sufficiently detailed to resolve the duration or timing of the extinctions.

K, all other articulate brachiopods; mostly spiriferids in the Triassic. These data have not been corrected for the latest conodont correlations and suffer from the deficiencies of such broad scale-compedia. Nonetheless, they provide the best available overview of extinction and survival patterns. The new conodont correlations¹² will permit higher-resolution analysis of the immediate boundary interval. Data provided by J. J. Sepkoski Jr.

Although plagued by taxonomic and sampling problems, 21 of 27 families of reptiles and six of nine amphibian families disappeared during the latest Permian, for an overall 75% drop in diversity³. The well studied vertebrate faunas from the Karoo Basin in South Africa reveal two extinction peaks, one roughly correlative with the end of the Capitanian, the other in the upper Permian, but below the Permo-Triassic boundary⁴. This may reflect nothing more than sampling bias and the difficulties correlating within the Karoo Basin and between marine and terrestrial sections, but does suggest a complex extinction event.

Among insects, 27 orders have been recorded from the Permian, of which eight disappear during the Late Permian, four suffer considerable declines in diversity but recover, and three straggle into the Triassic with such reduced diversity that they became extinct during the period⁴⁶. The end-Permian mass extinction induced the most profound changes in insect diversity patterns in the history of the class.

The plant record is far more equivocal. The distinctive plant floras of the Carboniferous are replaced by the Mesophytic flora throughout the Permian with the onset of global warming following the Permo-Carboniferous glaciation, but plant fossils show little direct evidence of mass extinction^{47,48}. Pollen undergoes a marked change at the Permo-Triassic boundary. In addition to the spike in fungal spores noted earlier, gymnosperm pollen virtually disappears and a new, arid-resistant pollen type appears^{2,19,49}. Some of the changes may actually reflect changes in terrestrial communities that accompany the rapid earliest Triassic marine transgression².

Changes in the physical environment

The supercontinent of Pangea formed by the Early Permian, but the end-Permian regression led to exposure of the continent⁵⁰, widespread evaporite deposition⁵⁰, global warming and increased climatic instability⁵¹. Other events include eruption of the Siberian flood basalts (1.5 million km²; the largest flood basalt of the Phanerozoic) in less than 1 million years⁵², evidence of global warming and marked shifts in carbon, oxygen, sulphur and strontium isotopes^{17,49,53} (Fig. 2).

The shifts in carbon isotopes have been linked to the extinction through erosion and oxidation of organic carbon previously sequestered on the continental shelves⁷, or oxidation of deep-sea sapropel-like deposits following overturn of a previously stratified, anoxic ocean^{54, 56}. Each hypothesis postulates oxidation reducing atmospheric oxygen and increasing atmospheric carbon dioxide, perhaps leading to anoxia and global warming, although there are no data on the extent of likely anoxia or warming. Alternatively, the signal may represent the spread of anoxic bottom waters across the shelves during the earliest Triassic transgression^{14, 57, 58}. The geochemical data present difficulties for each of these hypotheses^{2, 59}. In particular, they ignore the impact of methane gas hydrates ($\delta^{13}\text{C} \approx -65\%$) released during the regression². Regressions release hydrates locked in the outer continental shelf^{60, 61}, and may modulate ice ages via negative feedback⁶¹. No negative feedback occurs during non glacio-eustatic regressions and larger volumes of methane may be released.

Extinction mechanisms

Supernovas, declining numbers of marine provinces and salinity changes are among the proposed causes; these are discussed elsewhere^{2, 10, 50, 62, 63}. Recent models emphasize volcanism, extraterrestrial impact and global anoxia, but evaluating these is difficult because they often fail to make specific, unique predictions about extinction patterns. Without such predictions, most scenarios are just-so stories: comforting perhaps, but of little use. Given the lack of consistent patterns of extinction or survival which point to a specific cause, geological evidence is crucial in evaluating these scenarios.

The widespread pyroclastic volcanism in South China and the eruption of the Siberian flood basalts have been invoked as causes of the extinction through global cooling^{20, 24, 29, 30, 50}, although the pyroclastic volcanism is too small to have been effective³². Whereas the Siberian traps apparently began erupting near the boundary, most of the flood basalt was emplaced during the earliest Triassic. Moreover, modelling results suggest that the climatic effects of SO₂ are self-limiting: at large volumes the molecules condense into larger particles⁶⁴. Thus it is unclear if this eruption could have caused sufficient cooling to cause the extinction. The claimed iridium enrichment at the boundary in South China^{25, 33, 34} is not supported^{17, 35, 36, 59}. It has been suggested that a period of bipolar glaciation triggered the extinction⁶⁵, but without tying it to a specific cause. However, this glaciation was mid-Permian, representing the final pulse of the Permo-Carboniferous glaciation (J. C. Crowell, personal communication).

Ignoring the lack of evidence, is the pattern of extinction consistent with global cooling, either from volcanism, impact or glaciation? Not really. Although filter-feeders suffer severely, carbon isotopes provide no evidence for elimination of primary productivity, unlike the K/T boundary⁵⁹. This also fails to explain the differential extinction of fusulinid over non-fusulinid foraminifera. The apparently heightened extinction among shallow-water taxa is more consistent with global warming or habitat destruction than with global cooling.

Perhaps the various anoxia hypotheses provide the answer^{14, 54, 58}. Suggestive evidence has been developed for the spread of anoxic waters associ-

ated with the rapid earliest Triassic transgression^{14, 57, 58}. The geochemical data advanced to support the hypothesis⁵⁷ actually provides little support²; indeed, the shift in $\delta^{13}\text{C}$ permits only a moderate shift in atmospheric oxygen levels, limiting the extent of marine anoxia². The sedimentological data are more promising, but remain subject to alternative interpretations. Additionally, global anoxia is a diversity-independent mode of extinction, thus survival should be enhanced by broad oxygen tolerance and large population size, yet many of the surviving taxa had small population sizes. Additionally, although molluscs contain many groups that are well adapted to dysaerobic environments and had higher-than-average survival, a closer look reveals no association between survival and oxygen tolerance.

Although there is much about this event palaeontologists do

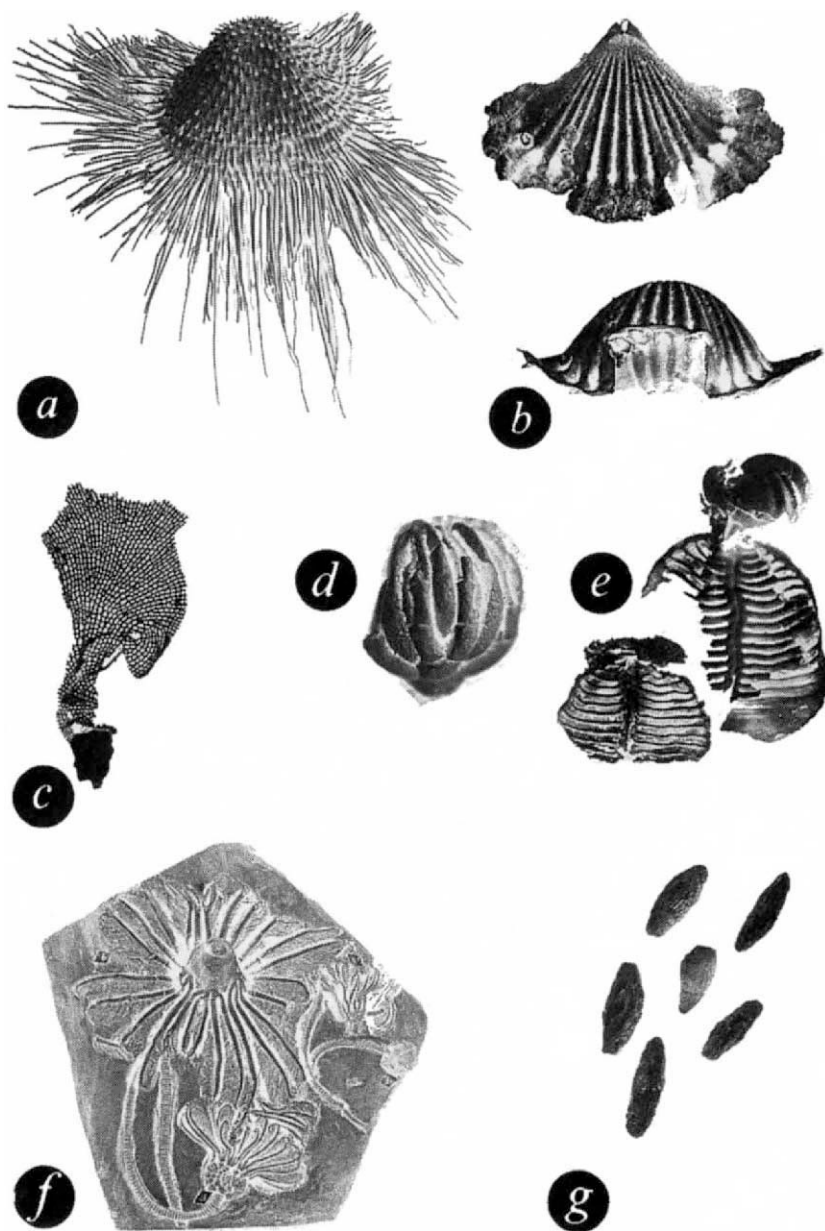


FIG. 4 Representative late Palaeozoic marine invertebrates. Brachiopods a, *Waagenochoncha albichi*; $\times 1.0$, Khisor Range, Pakistan. Late Permian. b, *Stenosicisma venustum*; $\times 1.0$, Texas. Lower Permian. c, The bryozoan *Fensetrella* sp.; $\times 0.9$. d, An unusual crinoid, *Timorocrinus multicostatus*, $\times 1.0$, Timor. ?mid-Permian. e, An unusual articulate brachiopod, *Leptotus nobilis*, $\times 0.5$, Khisor Range, Pakistan. f, The Mississippian crinoid *Platyrcrinus aggaszi*; $\times 0.4$. g, A typical Permian fusulinid foraminifera, *Fusulina* sp.; $\times 1$. Photos a, b, e by R. E. Grant. Photos c, d, f, g by D.H.E. and E. Valiulis.

BOX 1 Life and times of *Miocidaris*

ALTHOUGH echinoids are ubiquitous and familiar members of modern marine communities, only six echinoid genera are known from the Permian and the group might easily have disappeared like blastoids, or other unusual Palaeozoic echinoderm groups. Only a single genus, *Miocidaris* (Fig. 5), is known to have survived the extinction (although cladistic analysis suggests that a related, as-yet undiscovered form survived as well and gave rise to the euechinoids⁶⁶). Its persistence ensured the survival of the class, but fortuitously turned echinoid evolution in a new direction. *Miocidaris* has only two columns of interambulacral plates between each of the five files of ambulacral plates (which cover the tube feet), in contrast to the highly variable number (1–8) of interambulacral plates of other Palaeozoic echinoids. The survival of *Miocidaris* fixed this relationship for all later echinoids.

Was the survival of *Miocidaris* truly fortuitous? Or did this morphological innovation aid the survival of the genus? Would echinoids with two columns of interambulacral plates dominate modern oceans even if the end-Permian extinction had not occurred? These questions are at the centre of one of the great questions in the history of life. To what extent are the long-term patterns in the history of life driven by long-term patterns of adaptation versus the seemingly random patterns of survival during occasional mass extinction events?^{43,67,68} Both equilibrium and non-equilibrium diversity models suggest that the Modern evolutionary fauna would have displaced the Palaeozoic evolutionary fauna even without help from the Permian mass extinction^{37,40,69}. In this view the lower rates of extinction in the clades comprising the Modern fauna ensured their success. Palaeoecological analysis suggests that elements of the Modern fauna began to displace the Palaeozoic fauna by the Late Ordovician^{70,71}. My analysis of Palaeozoic gastropods (a major component of the modern fauna) indicates the pattern is more complex^{43,68}. Palaeozoic and post-Palaeozoic gastropods are very different, and there is no indication that the post-Palaeozoic groups were expanding before the extinction. For gastropods and echinoids at least, the end-Permian mass extinction was a very critical event in their history.

not understand, our difficulties may stem from our search for a single cause. Few complex events stem from a single cause; more common is a complex web of causality, a web that can be difficult to untangle. My own view is that the cause of the end-Permian extinction lies in such a tangled web. The most plausible explanation would appear to be a three-phase model combining elements of several mechanisms described previously. The extinction began with the loss of habitat area as the regression dried out many marine basins, converting the two-dimensional coastlines of the mid-Permian to more linear coastlines. The increased exposure of Pangea as the regression progressed exacerbated climatic instability. This instability, coupled with the effects of continuing volcanic eruptions and an increase in atmospheric carbon dioxide (with some degree of global warming), led to increasing environmental degradation and ecological collapse. Certainly many of the marine groups that disappeared were

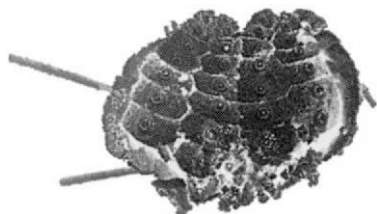


FIG. 5 *Miocidaris* sp. $\times 1.0$ Texas. A representative of the only clade of echinoids (2 species) to survive the end-Permian mass extinction. Note the arrangement of 2 rows of ambulacral plates separated by 2 rows of interambulacral plates. This pattern is found only in this lineage in the Permian. The survival of this clade insured that all subsequent echinoids share this pattern of construction rather than the variable number of rows of interambulacral plates found in other Permian echinoids.

those most tightly integrated into the dominant community types. Some degree of oceanic anoxia may have developed also but, as described earlier, it does not appear that either global warming or anoxia were sufficient to cause such a massive extinction. The final phase of the extinction occurred in the earliest Triassic. The rapid transgression destroyed near-shore terrestrial habitats, causing the shifts in spores and pollen and perhaps much of the decline in insects and tetrapods.

Prospects

Recent geochemical, biostratigraphic and palaeontological studies have considerably sharpened our understanding of the biodiversity crisis that brought the Permian to a close, and the broad spectrum of environmental perturbations that accompanied it. The development of new correlations brings the promise of high-resolution data on the rate and timing of extinction and survival. Comparative analysis of the palaeoecological, geographical and environmental characteristics of these taxa should in turn provide important clues to survival during the greatest biodiversity crisis in the history of life. □

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ARTICLES

Regulation of progression through the G1 phase of the cell cycle by the *rum1*⁺ gene

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The *rum1*⁺ gene is identified as a new regulator of G1 progression in fission yeast. It influences three aspects of G1 regulation: determination of the length of G1, dependence of S phase upon completion of mitosis, and restraint of mitosis until G1 is finished. We propose that it has a central role in regulating the G1 phase of the cell cycle.

THE major controls of the eukaryotic cell cycle are concerned with regulating the onset of S-phase and mitosis, and with ensuring that these two events are coupled together in the correct order. In the fission yeast *Schizosaccharomyces pombe*, two requirements are important for determining the onset of S phase. The first is the need for a cell to attain a minimum critical cell mass^{1–3}. Small cells in G1 cannot undergo S phase until they have attained this mass, and the time taken to reach this mass determines the length of G1. The second is the need for a cell to complete mitosis, demonstrated by the fact that cells blocked in G2 cannot undergo S phase^{3,4}. In both budding and fission yeast these two requirements are thought to operate through Start, the point in G1 where the cell becomes committed to the cell cycle^{1,5–7}. The molecular basis for Start is not fully understood, but in fission yeast involves the p34^{cdc2} protein kinase encoded by *cdc2*⁺ and transcription factors encoded by *cdc10*⁺ and *res1*⁺/*sct1*⁺ (refs 7–10). Here we describe the characterization of the gene *rum1*⁺, which is important in G1 regulating Start. When *rum1*⁺ is overexpressed it breaks the dependence of Start upon completion of mitosis, initially leading to a transient G1 delay, followed by repeated rounds of DNA replication. When *rum1*⁺ is deleted, the pre-Start G1 interval is eliminated and the critical cell mass required for Start is reduced. This indicates that *rum1*⁺ is a major element determining the length of G1. *rum1*⁺ is also important for defining the cell in the pre-Start G1 interval: when *rum1*⁺ is deleted in a mutant that normally arrests before Start, cells proceed to undergo mitosis and cell division. These results indicate that the *rum1*⁺ gene product

is central for regulating G1 progression and the onset of S phase in fission yeast.

Overreplication

Certain mutant alleles of *cdc2*⁺ induce an extra round of DNA replication in G2 cells, breaking the normal dependence upon mitosis and generating cells with enlarged nuclei¹¹. This work led to the proposal that entry into S phase and mitosis is determined by the state of p34^{cdc2}. In order to identify new genes inducing overreplication, we used an *S. pombe* cDNA library (gift from B. Edgar and C. Norbury) under the control of the repressible *nmI*⁺ promoter¹². Expression from this promoter begins at 12 h and becomes maximal at 14–16 h after transfer of cells to minimal medium lacking thiamine. The library was used to screen for clones that induced cells to generate enlarged nuclei. Among such clones we expected to find some that induced cells to undergo several rounds of DNA replication in the absence of mitosis. The most dramatic phenotype encountered of this type was associated with a 1.5-kilobase (kb) complementary DNA derived from a gene we called *rum1*⁺ (for replication uncoupled from mitosis). When *rum1*⁺ cDNA was overexpressed, it induced massive overreplication, producing highly enlarged nuclei (Fig. 1a, left). DNA content per cell estimated using flow cytometry was very much increased. An example of 16C cells is shown in Fig. 1a (right), but cells with still greater amounts of DNA were observed after prolonged exposure to elevated expression of *rum1*⁺.

The increase in DNA content was a result of complete rounds of DNA replication. During a time course of *rum1*⁺ overexpression, discrete subpopulations of 4C and 8C cells were observed (Fig. 1b), which would not be expected if there were only partial rounds of DNA replication. Also, if *rum1*⁺ was derepressed for

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