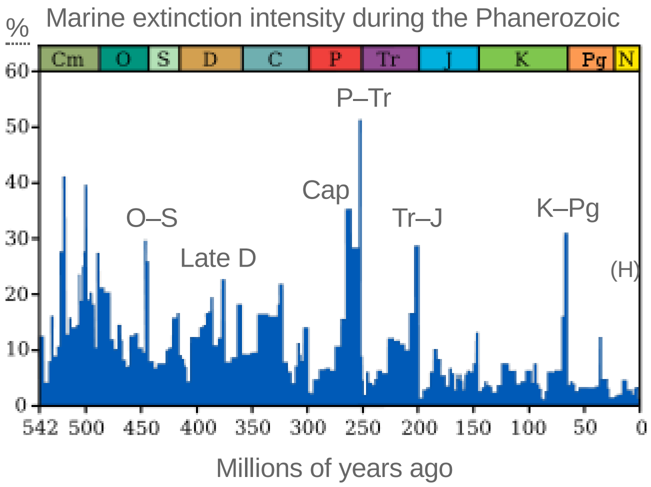
Permian–Triassic extinction event



Plot of extinction intensity (percentage of marine genera that are present in each interval of time but do not exist in the following interval) vs time in the past.[1] Geological periods are annotated (by abbreviation and colour) above. The Permian–Triassic extinction event is the most significant event for marine genera, with just over 50% (according to this source) perishing. *(source and image info)*

The **Permian–Triassic extinction event**, also known as the **P–Tr extinction**,[2] the **P–T extinction**,[3] the **End-Permian Extinction**,[4] and colloquially as the **Great Dying**,[5] formed the boundary between the Permian and Triassic geologic periods, as well as between the Paleozoic and Mesozoic eras, approximately 252 million years ago. It is the Earth's most severe known extinction event, with up to 96% of all marine species[6][7] and 70% of terrestrial vertebrate species becoming extinct.[8] It was the largest known mass extinction of insects. Some 57% of all biological families and 83% of all genera became extinct.

There is evidence for one to three distinct pulses, or phases, of extinction.[8][9][10][11] Potential causes for those pulses include one or more large meteor impact events, massive volcanic eruptions (such as the Siberian Traps[12]), and climate change brought on by large releases of underwater methane or methane-producing microbes.[13]

The speed of the recovery from the extinction is disputed. Some scientists estimate that it took 10 million years (until the Middle Triassic), due both to the severity of the extinction and because grim conditons returned periodically for another 5 million years.[14] However, studies in Bear Lake County, near Paris, Idaho, showed a relatively quick rebound in a localized Early Triassic marine ecosystem, taking around 2 million years to recover,[15] suggesting that the impact of the extinction may have been felt less severely in some areas than others.

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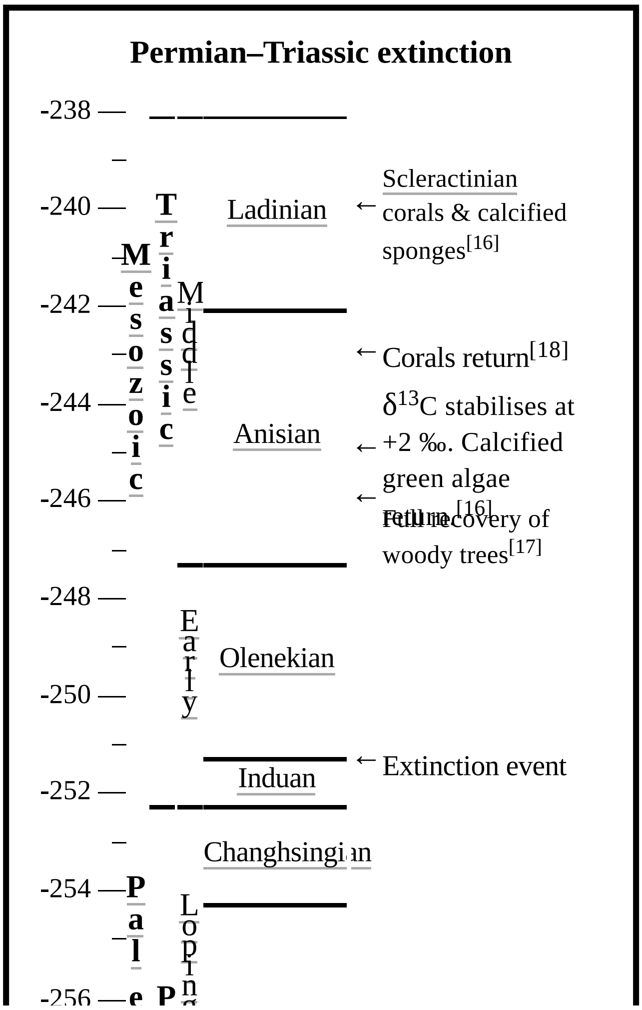
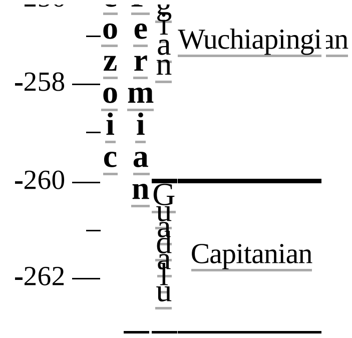
Dating

Until 2000, it was thought that rock sequences spanning the Permian–Triassic boundary were too few and contained too many gaps for scientists to reliably determine its details.[19] However, it is now possible to date the extinction with millennial precision. U–Pb zircon dates from five volcanic ash beds from the Global Stratotype Section and Point for the Permian–Triassic boundary at Meishan, China, establish a high-resolution age model for the extinction – allowing exploration of the links between global environmental perturbation, carbon cycle disruption, mass extinction, and recovery at millennial timescales. The extinction occurred between 251.941 ± 0.037 and 251.880 ± 0.031 Ma ago, a duration of 60 ± 48 ka.[20] A large (approximately 0.9%), abrupt global decrease in the ratio of the stable isotope ^{13}C to that of ^{12}C, coincides with this extinction,[17][21][22][23][24] and is sometimes used to identify the Permian–Triassic boundary in rocks that are unsuitable for radiometric dating.[25] Further evidence for environmental change around the P–Tr boundary suggests an 8 °C (14 °F) rise in temperature,[17] and



an increase in CO_2 levels by 2000 ppm (for comparison, the concentration immediately before the industrial revolution was 280 ppm,[17] and the amount today is about 410 ppm[26]). There is also evidence of increased ultraviolet radiation reaching the earth, causing the mutation of plant spores.[17]



An approximate timescale of events around the P–Tr boundary.
Axis scale: millions of years ago.

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PreЄ Є O S D C P T J K Pg N

It has been suggested that the Permian–Triassic boundary is associated with a sharp increase in the abundance of marine and terrestrial fungi, caused by the sharp increase in the amount of dead plants and animals fed upon by the fungi.[27] For a while this "fungal spike" was used by some paleontologists to identify the Permian–Triassic boundary in rocks that are unsuitable for radiometric dating or lack suitable index fossils, but even the proposers of the fungal spike hypothesis pointed out that "fungal spikes" may have been a repeating phenomenon created by the post-extinction ecosystem in the earliest Triassic.[27] The very idea of a fungal spike has been criticized on several grounds, including: *Reduviasporonites*, the most common supposed fungal spore, may be a fossilized alga;[17][28] the spike did not appear worldwide;[29][30] and in many places it did not fall on the Permian–Triassic boundary.[31] The reduviasporonites may even represent a transition to a lake-dominated Triassic world rather than an earliest Triassic zone of death and decay in some terrestrial fossil beds.[32] Newer chemical evidence agrees better with a fungal origin for *Reduviasporonites*, diluting these critiques.[33]

Uncertainty exists regarding the duration of the overall extinction and about the timing and duration of various groups' extinctions within the greater process. Some evidence suggests that there were multiple extinction pulses[8] or that the extinction was spread out over a few million years, with a sharp peak in the last million years of the Permian.[31][34] Statistical analyses of some highly fossiliferous strata in Meishan, Zhejiang Province in southeastern China, suggest that the main extinction was clustered around one peak.[9] Recent research shows that different groups became extinct at different times; for example, while difficult to date absolutely, ostracod and brachiopod extinctions were separated by 670,000 to 1.17 million years.[35] In a well-preserved sequence in east Greenland, the decline of animals is concentrated in a period 10,000 to 60,000 years long, with plants taking an additional several hundred thousand years to show the full impact of the event.[36]

An older theory, still supported in some recent papers,[8][37] is that there were two major extinction pulses 9.4 million years apart, separated by a period of extinctions well above the background level, and that the final extinction killed off only about 80% of marine species alive at that time while the other losses occurred during the first pulse or the interval between pulses. According to this theory one of these extinction pulses occurred at the end of the Guadalupian epoch of the Permian.[8][38] For example, all but one of the surviving dinocephalian genera died out at the end of the Guadalupian,[37] as did the Verbeekinidae, a family of large-size fusuline foraminifera.[39] The impact of the end-Guadalupian extinction on marine organisms appears to have varied between locations and between taxonomic groups — brachiopods and corals had severe losses.[40][41]

Extinction patterns

Marine organisms

Marine invertebrates suffered the greatest losses during the P–Tr extinction. Evidence of this was found in samples from south China sections at the P–Tr boundary. Here, 286 out of 329 marine invertebrate genera disappear within the final two sedimentary zones containing conodonts from the Permian.[9] The decrease in diversity was probably caused by a sharp increase in extinctions, rather than a decrease in speciation.[43]

The extinction primarily affected organisms with calcium carbonate skeletons, especially those reliant on stable CO_2 levels to produce their skeletons.[44] These organisms were susceptible to the effects of the ocean acidification that resulted from increased atmospheric CO_2.

Among benthic organisms the extinction event multiplied background extinction rates, and therefore caused maximum species loss to taxa that had a high background extinction rate (by implication, taxa with a high turnover).[45][46] The extinction rate of marine organisms was catastrophic.[9][47][48][49]

Surviving marine invertebrate groups included articulate brachiopods (those with a hinge),[50] which had undergone a slow decline in numbers since the P–Tr extinction; the Ceratitida order of ammonites;[51] and crinoids ("sea lilies"),[51] which very nearly became extinct but later became abundant and diverse.

The groups with the highest survival rates generally had active control of circulation, elaborate gas exchange mechanisms, and light calcification; more heavily calcified organisms with simpler breathing apparatuses suffered the greatest loss of species diversity.[16][52] In the case of the brachiopods, at least, surviving taxa were generally small, rare members of a formerly diverse community.[53]

Marine extinctions	Genera extinct	Notes
Arthropoda		
Eurypterids	**100%**	May have become extinct shortly before the P–Tr boundary
Ostracods	59%	
Trilobites	**100%**	In decline since the Devonian; only 2 genera living before the extinction
Brachiopoda		
Brachiopods	96%	Orthids and productids died out
Bryozoa		
Bryozoans	79%	Fenestrates, trepostomes, and cryptostomes died out
Chordata		
Acanthodians	**100%**	In decline since the Devonian, with only one living family
Cnidaria		
Anthozoans	96%	Tabulate and rugose corals died out
Echinodermata		
Blastoids	**100%**	May have become extinct shortly before the P–Tr boundary
Crinoids	98%	Inadunates and camerates died out
Mollusca		
Ammonites	97%	Goniatites died out
Bivalves	59%	
Gastropods	98%	
Retaria		
Foraminiferans	97%	Fusulinids died out, but were almost extinct before the catastrophe
Radiolarians	99%[42]	

The ammonoids, which had been in a long-term decline for the 30 million years since the Roadian (middle Permian), suffered a selective extinction pulse 10 million years before the main event, at the end of the Capitanian stage. In this preliminary extinction, which greatly reduced disparity, or the range of different ecological guilds, environmental factors were apparently responsible. Diversity and disparity fell further until the P–Tr boundary; the extinction here (P–Tr) was non-selective, consistent with a catastrophic initiator. During the Triassic, diversity rose rapidly, but disparity remained low.[54]

The range of morphospace occupied by the ammonoids, that is, their range of possible forms, shapes or structures, became more restricted as the Permian progressed. A few million years into the Triassic, the original range of ammonoid structures was once again reoccupied, but the parameters were now shared differently among clades.[55]

Terrestrial invertebrates

The Permian had great diversity in insect and other invertebrate species, including the largest insects ever to have existed. The end-Permian is the largest known mass extinction of insects;[56] according to some sources, it is the *only* insect mass extinction.[57][58] Eight or nine insect orders became extinct and ten more were greatly reduced in diversity. Palaeodictyopteroids (insects with piercing and sucking mouthparts) began to decline during the mid-Permian; these extinctions have been linked to a change in flora. The greatest decline occurred in the Late Permian and was probably not directly caused by weather-related floral transitions.[47]

Most fossil insect groups found after the Permian–Triassic boundary differ significantly from those before: Of Paleozoic insect groups, only the Glosselytrodea, Miomoptera, and Protorthoptera have been discovered in deposits from after the extinction. The caloneurodeans, monurans, paleodictyopteroids, protelytropterans, and protodonates became extinct by the end of the Permian. In well-documented Late Triassic deposits, fossils overwhelmingly consist of modern fossil insect groups.[57]

Terrestrial plants

Plant ecosystem response

The geological record of terrestrial plants is sparse and based mostly on pollen and spore studies. Plants are relatively immune to mass extinction, with the impact of all the major mass extinctions "insignificant" at a family level.[17] Even the reduction observed in species diversity (of 50%) may be mostly due to taphonomic processes.[17] However, a massive rearrangement of ecosystems does occur, with plant abundances and distributions changing profoundly and all the forests virtually disappearing;[17][59] the Palaeozoic flora scarcely survived this extinction.[60]

At the P–Tr boundary, the dominant floral groups changed, with many groups of land plants entering abrupt decline, such as *Cordaites* (gymnosperms) and *Glossopteris* (seed ferns).[61] Dominant gymnosperm genera were replaced post-boundary by lycophytes—extant lycophytes are recolonizers of disturbed areas.[62]

Palynological or pollen studies from East Greenland of sedimentary rock strata laid down during the extinction period indicate dense gymnosperm woodlands before the event. At the same time that marine invertebrate macrofauna declined, these large woodlands died out and were followed by a rise in diversity of smaller herbaceous plants including Lycopodiophyta, both Selaginellales and Isoetales. Later, other groups of gymnosperms again become dominant but again suffered major die offs. These cyclical flora shifts occurred a few times over the course of the extinction period and afterwards. These fluctuations of the dominant flora between woody and herbaceous taxa indicate chronic environmental stress resulting in a loss of most large woodland plant species. The successions and extinctions of plant communities do not coincide with the shift in $\delta^{13}C$ values, but occurred many years after.[30] The recovery of gymnosperm forests took 4–5 million years.[17]

Coal gap

No coal deposits are known from the Early Triassic, and those in the Middle Triassic are thin and low-grade.[18] This "coal gap" has been explained in many ways. It has been suggested that new, more aggressive fungi, insects and vertebrates evolved, and killed vast numbers of trees. These decomposers themselves suffered heavy losses of species during the extinction, and are not considered a likely cause of the coal gap.[18] It could simply be that all coal-forming plants were rendered extinct by the P–Tr extinction, and that it took 10 million years for a new suite of plants to adapt to the moist, acid conditions of peat bogs.[18] Abiotic factors (factors not caused by organisms), such as decreased rainfall or increased input of clastic sediments, may also be to blame.[17]

On the other hand, the lack of coal may simply reflect the scarcity of all known sediments from the Early Triassic. Coal-producing ecosystems, rather than disappearing, may have moved to areas where we have no sedimentary record for the Early Triassic.[17] For example, in eastern Australia a cold climate had been the norm for a long period, with a peat mire ecosystem adapted to these conditions. Approximately 95% of these peat-producing plants went *locally* extinct at the P–Tr boundary;[63] Coal deposits in Australia and Antarctica disappear significantly *before* the P–Tr boundary.[17]

Terrestrial vertebrates

There is enough evidence to indicate that over two thirds of terrestrial labyrinthodont amphibians, sauropsid ("reptile") and therapsid ("proto-mammal") families became extinct. Large herbivores suffered the heaviest losses.

All Permian anapsid reptiles died out except the procolophonids (although testudines have *morphologically*-anapsid skulls, they are now thought to have separately evolved from diapsid ancestors). Pelycosaurs died out before the end of the Permian. Too few Permian diapsid fossils have been found to support any conclusion about the effect of the Permian extinction on diapsids (the "reptile" group from which lizards, snakes, crocodilians, and dinosaurs (including birds) evolved).[64][65]

The groups that survived suffered extremely heavy losses of species, and some terrestrial vertebrate groups very nearly became extinct at the end of the Permian. Some of the surviving groups did not persist for long past this period, but others that barely survived went on to produce diverse and long-lasting lineages. However, it took 30 million years for the terrestrial vertebrate fauna to fully recover both numerically and ecologically.[66]

Possible explanations

An analysis of marine fossils from the Permian's final Changhsingian stage found that marine organisms with low tolerance for hypercapnia (high concentration of carbon dioxide) had high extinction rates, and the most tolerant organisms had very slight losses.

The most vulnerable marine organisms were those that produced calcareous hard parts (from calcium carbonate) and had low metabolic rates and weak respiratory systems, notably calcareous sponges, rugose and tabulate corals, calcite-depositing brachiopods, bryozoans, and echinoderms; about 81% of such genera became extinct. Close relatives without calcareous hard parts suffered only minor losses, such as sea anemones, from which modern corals evolved. Animals with high metabolic rates, well-developed respiratory systems, and non-calcareous hard parts had negligible losses except for conodonts, in which 33% of genera died out.[67]

This pattern is consistent with what is known about the effects of hypoxia, a shortage but not total absence of oxygen. However, hypoxia cannot have been the only killing mechanism for marine organisms. Nearly all of the continental shelf waters would have had to become severely hypoxic to account for the magnitude of the extinction, but such a catastrophe would make it difficult to explain the very selective pattern of the extinction. Mathematical models of the Late Permian and Early Triassic atmospheres show a significant but protracted decline in atmospheric oxygen levels, with no acceleration near the P–Tr boundary. Minimum atmospheric oxygen levels in the Early Triassic are never less than present-day levels and so the decline in oxygen levels does not match the temporal pattern of the extinction.[67]

Marine organisms are more sensitive to changes in CO_2 (carbon dioxide) levels than terrestrial organisms are for a variety of reasons. CO_2 is 28 times more soluble in water than is oxygen. Marine animals normally function with lower concentrations of CO_2 in their bodies than land animals, as the removal of CO_2 in air-breathing animals is impeded by the need for the gas to pass through the respiratory system's membranes (lungs' alveolus, tracheae, and the like), even when CO_2 diffuses more easily than oxygen. In marine organisms, relatively modest but sustained increases in CO_2 concentrations hamper the synthesis of proteins, reduce fertilization rates, and produce deformities in calcareous hard parts.[67] In addition, an increase in CO_2 concentration is inevitably linked to ocean acidification, consistent with the preferential extinction of heavily calcified taxa and other signals in the rock record that suggest a more acidic ocean.[68] The decrease in ocean pH is calculated to be up to 0.7 units.[69]

It is difficult to analyze extinction and survival rates of land organisms in detail because few terrestrial fossil beds span the Permian–Triassic boundary. Triassic insects are very different from those of the Permian, but a gap in the insect fossil record spans approximately 15 million years from the late Permian to early Triassic. The best-known record of vertebrate changes across the Permian–Triassic boundary occurs in the Karoo Supergroup of South Africa, but statistical analyses have so far not produced clear conclusions.[67] However, analysis of the fossil river deposits of the floodplains indicate a shift from meandering to braided river patterns, indicating an abrupt drying of the climate.[70] The climate change may have taken as little as 100,000 years, prompting the extinction of the unique *Glossopteris* flora and its herbivores, followed by the carnivorous guild.[71] End-Permian extinctions did not occur at an instantaneous time horizon; particularly, floral extinction was delayed in time.[72]

Biotic recovery

Earlier analyses indicated that life on Earth recovered quickly after the Permian extinctions, but this was mostly in the form of disaster taxa, opportunist organisms such as the hardy *Lystrosaurus*. Research published in 2006 indicates that the specialized animals that formed complex ecosystems, with high biodiversity, complex food webs and a variety of niches, took much longer to recover. It is thought that this long recovery was due to the successive waves of extinction, which inhibited recovery, and prolonged environmental stress to organisms, which continued into the Early Triassic. Research indicates that recovery did not begin until the start of the mid-Triassic, 4 to 6 million years after the extinction;[73] and some writers estimate that the recovery was not complete until 30 Ma after the P–Tr extinction, i.e. in the late Triassic.[8]

A study published in the journal *Science*[74] found that during the Great Extinction, ocean surface temperatures reached 40 °C (104 °F) in some places. This explains why recovery took so long: it was too hot for life to survive.[75] Anoxic waters may have also delayed the recovery.[76]

A braided river, the Waimakariri River on the South Island of New Zealand

During the early Triassic (4 to 6 million years after the P–Tr extinction), the plant biomass was insufficient to form coal deposits, which implies a limited food mass for herbivores.[18] River patterns in the Karoo changed from meandering to braided, indicating that vegetation there was very sparse for a long time.[77]

Each major segment of the early Triassic ecosystem—plant and animal, marine and terrestrial—was dominated by a small number of genera, which appeared virtually worldwide, for example: the herbivorous therapsid *Lystrosaurus* (which accounted for about 90% of early Triassic land vertebrates) and the bivalves *Claraia*, *Eumorphotis*, *Unionites* and *Promylina*. A healthy ecosystem has a much larger number of genera, each living in a few preferred types of habitat.[61][78]

Disaster taxa took advantage of the devastated ecosystems and enjoyed a temporary population boom and increase in their territory. Microconchids are the dominant component of otherwise impoverished Early Triassic encrusting assemblages. For example: *Lingula* (a brachiopod); stromatolites, which had been confined to marginal environments since the Ordovician; *Pleuromeia* (a small, weedy plant); *Dicroidium* (a seed fern).[78][79][80]

Changes in marine ecosystems

Sessile filter feeders like this Carboniferous crinoid, the mushroom crinoid (*Agaricocrinus americanus*), were significantly less abundant after the P–Tr extinction.

Prior to the extinction, about two thirds of marine animals were sessile and attached to the sea floor. During the Mesozoic, only about half of the marine animals were sessile while the rest were free-living. Analysis of marine fossils from the period indicated a decrease in the abundance of sessile epifaunal suspension feeders such as brachiopods and sea lilies and an increase in more complex mobile species such as snails, sea urchins and crabs.[81]

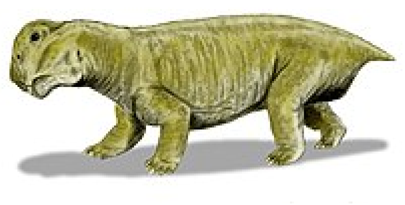
Before the Permian mass extinction event, both complex and simple marine ecosystems were equally common. After the recovery from the mass extinction, the complex communities outnumbered the simple communities by nearly three to one,[81] and the increase in predation pressure led to the Mesozoic Marine Revolution.

Bivalves were fairly rare before the P–Tr extinction but became numerous and diverse in the Triassic, and one group, the rudist clams, became the Mesozoic's main reef-builders. Some researchers think much of the change happened in the 5 million years between the two major extinction pulses.[82]

Crinoids ("sea lilies") suffered a selective extinction, resulting in a decrease in the variety of their forms.[83] Their ensuing adaptive radiation was brisk, and resulted in forms possessing flexible arms becoming widespread; motility, predominantly a response to predation pressure, also became far more prevalent.[84]

Land vertebrates

Lystrosaurus, a pig-sized herbivorous dicynodont therapsid, constituted as much as 90% of some earliest Triassic land vertebrate fauna. Smaller carnivorous cynodont therapsids also survived, including the ancestors of mammals. In the Karoo region of southern Africa, the therocephalians *Tetracynodon*, *Moschorhinus* and *Ictidosuchoides* survived, but do not appear to have been abundant in the Triassic.[85]



Lystrosaurus was by far the most abundant early Triassic land vertebrate.

Archosaurs (which included the ancestors of dinosaurs and crocodilians) were initially rarer than therapsids, but they began to displace therapsids in the mid-Triassic. In the mid to late Triassic, the dinosaurs evolved from one group of archosaurs, and went on to dominate terrestrial ecosystems during the Jurassic and Cretaceous.[86] This "Triassic Takeover" may have contributed to the evolution of mammals by forcing the surviving therapsids and their mammaliform successors to live as small, mainly nocturnal insectivores; nocturnal life probably forced at least the mammaliforms to develop fur and higher metabolic rates,[87] while losing part of the differential color-sensitive retinal receptors reptilians and birds preserved.

Some temnospondyl amphibians made a relatively quick recovery, in spite of nearly becoming extinct. *Mastodonsaurus* and trematosaurians were the main aquatic and semiaquatic predators during most of the Triassic, some preying on tetrapods and others on fish.[88]

Land vertebrates took an unusually long time to recover from the P–Tr extinction; Palaeontologist Michael Benton estimated the recovery was not complete until 30 million years after the extinction, i.e. not until the Late Triassic, in which dinosaurs, pterosaurs, crocodiles, archosaurs, amphibians, and mammaliforms were abundant and diverse.[6]

Theories about cause

Pinpointing the exact causes of the Permian–Triassic extinction event is difficult, mostly because it occurred over 250 million years ago, and since then much of the evidence that would have pointed to the cause has been destroyed or is concealed deep within the Earth under many layers of rock. The sea floor is also completely recycled every 200 million years by the ongoing process of plate tectonics and seafloor spreading, leaving no useful indications beneath the ocean.

Yet, scientists have gathered significant evidence for causes, and several mechanisms have been proposed. The proposals include both catastrophic and gradual processes (similar to those theorized for the Cretaceous–Paleogene extinction event).

- The *catastrophic* group includes one or more large bolide impact events, increased volcanism, and sudden release of methane from the sea floor, either due to dissociation of methane hydrate deposits or metabolism of organic carbon deposits by methanogenic microbes.
- The *gradual* group includes sea level change, increasing anoxia, and increasing aridity.

Any hypothesis about the cause must explain the selectivity of the event, which affected organisms with calcium carbonate skeletons most severely; the long period (4 to 6 million years) before recovery started, and the minimal extent of biological mineralization (despite inorganic carbonates being deposited) once the recovery began.[44]

Impact event


Artist's impression of a major impact event: A collision between Earth and an asteroid a few kilometres in diameter would release as much energy as several million nuclear weapons detonating.

Evidence that an impact event may have caused the Cretaceous–Paleogene extinction event (Cretaceous–Tertiary) has led to speculation that similar impacts may have been the cause of other extinction events, including the P–Tr extinction, and thus to a search for evidence of impacts at the times of other extinctions, such as large impact craters of the appropriate age.

Reported evidence for an impact event from the P–Tr boundary level includes rare grains of shocked quartz in Australia and Antarctica;[89][90] fullerenes trapping extraterrestrial noble gases;[91] meteorite fragments in Antarctica;[92] and grains rich in iron, nickel, and silicon, which may have been created by an impact.[93] However, the accuracy of most of these claims has been challenged.[94][95][96][97] For example, quartz from Graphite Peak in Antarctica, once considered "shocked", has been re-examined by optical and transmission electron microscopy. The observed features were concluded to be due not to shock, but rather to plastic deformation, consistent with formation in a tectonic environment such as volcanism.[98]

An impact crater on the sea floor would be evidence of a possible cause of the P–Tr extinction, but such a crater would by now have disappeared. As 70% of the Earth's surface is currently sea, an asteroid or comet fragment is now perhaps more than twice as likely to hit ocean as it is to hit land. However, Earth's oldest ocean-floor crust is only 200 million years old as it is continually being destroyed and renewed by spreading and subduction. Furthermore, craters produced by very large impacts may be masked by extensive flood basalting from below after the crust is punctured or weakened.[99] Yet, subduction should not be entirely accepted as an explanation for the lack of evidence: as with the K-T event, an ejecta blanket stratum rich in siderophilic elements (such as iridium) would be expected in formations from the time.

A large impact might have triggered other mechanisms of extinction described below,[100] such as the Siberian Traps eruptions at either an impact site[101] or the antipode of an impact site.[100][102] The abruptness of an impact also explains why more species did not rapidly evolve to survive, as would be expected if the Permian–Triassic event had been slower and less global than a meteorite impact.

Possible impact sites

Several possible impact craters have been proposed as the site of an impact causing the P–Tr extinction, including the 250 km (160 mi) Bedout structure off the northwest coast of Australia[90] and the hypothesized 480 km (300 mi) Wilkes Land crater of East Antarctica.[103][104] An impact has not been proved in either case, and the idea has been widely criticized. The Wilkes Land sub-ice geophysical feature is of very uncertain age, possibly later than the Permian–Triassic extinction.

The 40 km (25 mi) Araguainha crater in Brazil has been most recently dated to 254.7 ± 2.5 million years ago, overlapping with estimates for the Permo-Triassic boundary.[105] Much of the local rock was oil shale. The estimated energy released by the Araguainha impact is insufficient to have directly caused the global mass extinction, but the colossal local earth tremors would have released huge amounts of oil and gas from the shattered rock. The resulting sudden global warming might have precipitated the Permian–Triassic extinction event.[106]

A 2017 paper[107] by Rampino, Rocca and Presser (after a 1992 abstract by Rampino) noted the discovery of a circular gravity anomaly near the Falkland Islands which might correspond to an impact crater with a diameter of 250 km (160 mi),[107] as supported by seismic and magnetic evidence. Estimates for the age of the structure range up to 250 million years old. This would be substantially larger than the well-known 180 km (110 mi) Chicxulub impact crater associated with a later extinction. However, Dave McCarthy and colleagues from the British Geological Survey illustrated that the gravity anomaly is not circular and also that the seismic data presented by Rocca, Rampino and Baez Presser did not cross the proposed crater or provide any evidence for an impact crater.[108]

Volcanism

The final stages of the Permian had two flood basalt events. A smaller one, the Emeishan Traps in China, occurred at the same time as the end-Guadalupian extinction pulse, in an area close to the equator at the time.[109][110] The flood basalt eruptions that produced the Siberian Traps constituted one of the largest known volcanic events on Earth and covered over 2,000,000 square kilometres (770,000 sq mi) with lava.[111][112][113] The date of the Siberian Traps eruptions and the extinction event are in good agreement.[20][114]

The Emeishan and Siberian Traps eruptions may have caused dust clouds and acid aerosols, which would have blocked out sunlight and thus disrupted photosynthesis both on land and in the photic zone of the ocean, causing food chains to collapse. The eruptions may also have caused acid rain when the aerosols washed out of the atmosphere. That may have killed land plants and molluscs and planktonic organisms which had calcium carbonate shells. The eruptions would also have emitted carbon dioxide, causing global warming. When all of the dust clouds and aerosols washed out of the atmosphere, the excess carbon dioxide would have remained and the warming would have proceeded without any mitigating effects.[100]

The Siberian Traps had unusual features that made them even more dangerous. Pure flood basalts produce fluid, low-viscosity lava and do not hurl debris into the atmosphere. It appears, however, that 20% of the output of the Siberian Traps eruptions was pyroclastic (consisted of ash and other debris thrown high into the atmosphere), increasing the short-term cooling effect.[115] The basalt lava erupted or intruded into carbonate rocks and into sediments that were in the process of forming large coal beds, both of which would have emitted large amounts of carbon dioxide, leading to stronger global warming after the dust and aerosols settled.[100]

In January 2011, a team, led by Stephen Grasby of the Geological Survey of Canada—Calgary, reported evidence that volcanism caused massive coal beds to ignite, possibly releasing more than 3 trillion tons of carbon. The team found ash deposits in deep rock layers near what is now the Buchanan Lake Formation. According to their article, "coal ash dispersed by the explosive Siberian Trap eruption would be expected to have an associated release of toxic elements in impacted water bodies where fly ash slurries developed.... Mafic megascale eruptions are long-lived events that would allow significant build-up of global ash clouds."[116][117] In a statement, Grasby said, "In addition to these volcanoes causing fires through coal, the ash it spewed was highly toxic and was released in the land and water, potentially contributing to the worst extinction event in earth history."[118] In 2013, a team led by Q.Y. Yang reported the total amounts of important volatiles emitted from the Siberian Traps are 8.5×10^7 Tg CO_2, 4.4×10^6 Tg CO, 7.0×10^6 Tg H_2S and 6.8×10^7 Tg SO_2, the data support a popular notion that the end-Permian mass extinction on the Earth was caused by the emission of enormous amounts of volatiles from the Siberian Traps into the atmosphere.[119]

In 2015, evidence and a timeline indicated the extinction was caused by events in the large igneous province of the Siberian Traps.[120][121][122][123][124]

Methane hydrate gasification

Scientists have found worldwide evidence of a swift decrease of about 1% in the $^{13}C/^{12}C$ isotope ratio in carbonate rocks from the end-Permian.[49][125] This is the first, largest, and most rapid of a series of negative and positive excursions (decreases and increases in $^{13}C/^{12}C$ ratio) that continues until the isotope ratio abruptly stabilised in the middle Triassic, followed soon afterwards by the recovery of calcifying life forms (organisms that use calcium carbonate to build hard parts such as shells).[16]

A variety of factors may have contributed to this drop in the $^{13}C/^{12}C$ ratio, but most turn out to be insufficient to account fully for the observed amount:[126]

- Gases from volcanic eruptions have a $^{13}C/^{12}C$ ratio about 0.5 to 0.8% below standard ($\delta^{13}C$ about −0.5 to −0.8%), but an assessment made in 1995 concluded that the amount required to produce a reduction of about 1.0% worldwide requires eruptions greater by orders of magnitude than any for which evidence has been found.[127] (However, this analysis addressed only CO_2 produced by the magma itself, not from interactions with carbon bearing sediments, as later proposed.)
- A reduction in organic activity would extract ^{12}C more slowly from the environment and leave more of it to be incorporated into sediments, thus reducing the $^{13}C/^{12}C$ ratio. Biochemical processes preferentially use the lighter isotopes since chemical reactions are ultimately driven by electromagnetic forces between atoms and lighter isotopes respond more quickly to these forces, but a study of a smaller drop of 0.3 to 0.4% in $^{13}C/^{12}C$ ($\delta^{13}C$ −3 to −4 ‰) at the Paleocene-Eocene Thermal Maximum (PETM) concluded that even transferring all the organic carbon (in organisms, soils, and dissolved in the ocean) into sediments would be insufficient: even such a large burial of material rich in ^{12}C would not have produced the 'smaller' drop in the $^{13}C/^{12}C$ ratio of the rocks around the PETM.[127]
- Buried sedimentary organic matter has a $^{13}C/^{12}C$ ratio 2.0 to 2.5% below normal ($\delta^{13}C$ −2.0 to −2.5%). Theoretically, if the sea level fell sharply, shallow marine sediments would be exposed to oxidation. But 6500–8400 gigatons (1 gigaton = 10^9 metric tons) of organic carbon would have to be oxidized and returned to the ocean-atmosphere system within less than a few hundred thousand years to reduce the $^{13}C/^{12}C$ ratio by 1.0%, which is not

thought to be a realistic possibility.[47] Moreover, sea levels were rising rather than falling at the time of the extinction.[128]

- Rather than a sudden decline in sea level, intermittent periods of ocean-bottom hyperoxia and anoxia (high-oxygen and low- or zero-oxygen conditions) may have caused the $^{13}C/^{12}C$ ratio fluctuations in the Early Triassic;[16] and global anoxia may have been responsible for the end-Permian blip. The continents of the end-Permian and early Triassic were more clustered in the tropics than they are now, and large tropical rivers would have dumped sediment into smaller, partially enclosed ocean basins at low latitudes. Such conditions favor oxic and anoxic episodes; oxic/anoxic conditions would result in a rapid release/burial, respectively, of large amounts of organic carbon, which has a low $^{13}C/^{12}C$ ratio because biochemical processes use the lighter isotopes more.[129] That or another organic-based reason may have been responsible for both that and a late Proterozoic/Cambrian pattern of fluctuating $^{13}C/^{12}C$ ratios.[16]

Other hypotheses include mass oceanic poisoning releasing vast amounts of CO_2[130] and a long-term reorganisation of the global carbon cycle.[126]

Prior to consideration of the inclusion of roasting carbonate sediments by volcanism, the only proposed mechanism sufficient to cause a global 1% reduction in the $^{13}C/^{12}C$ ratio was the release of methane from methane clathrates.[47] Carbon-cycle models confirm that it would have had enough effect to produce the observed reduction.[126][130] Methane clathrates, also known as methane hydrates, consist of methane molecules trapped in cages of water molecules. The methane, produced by methanogens (microscopic single-celled organisms), has a $^{13}C/^{12}C$ ratio about 6.0% below normal ($\delta^{13}C$ −6.0%). At the right combination of pressure and temperature, it gets trapped in clathrates fairly close to the surface of permafrost and in much larger quantities at continental margins (continental shelves and the deeper seabed close to them). Oceanic methane hydrates are usually found buried in sediments where the seawater is at least 300 m (980 ft) deep. They can be found up to about 2,000 m (6,600 ft) below the sea floor, but usually only about 1,100 m (3,600 ft) below the sea floor.[131]

The area covered by lava from the Siberian Traps eruptions is about twice as large as was originally thought, and most of the additional area was shallow sea at the time. The seabed probably contained methane hydrate deposits, and the lava caused the deposits to dissociate, releasing vast quantities of methane.[132] A vast release of methane might cause significant global warming since methane is a very powerful greenhouse gas. Strong evidence suggests the global temperatures increased by about 6 °C (10.8 °F) near the equator and therefore by more at higher latitudes: a sharp decrease in oxygen isotope ratios ($^{18}O/^{16}O$);[133] the extinction of *Glossopteris* flora (*Glossopteris* and plants that grew in the same areas), which needed a cold climate, with its replacement by floras typical of lower paleolatitudes.[134]

However, the pattern of isotope shifts expected to result from a massive release of methane does not match the patterns seen throughout the early Triassic. Not only would such a cause require the release of five times as much methane as postulated for the PETM,[16] but would it also have to be reburied at an unrealistically high rate to account for the rapid increases in the $^{13}C/^{12}C$ ratio (episodes of high positive $\delta^{13}C$) throughout the early Triassic before it was released again several times.[16]

Anoxia

Evidence for widespread ocean anoxia (severe deficiency of oxygen) and euxinia (presence of hydrogen sulfide) is found from the Late Permian to the Early Triassic. Throughout most of the Tethys and Panthalassic Oceans, evidence for anoxia, including fine laminations in sediments, small pyrite framboids, high uranium/thorium ratios, and biomarkers for green sulfur bacteria, appear at the extinction event.[135] However, in some sites, including Meishan, China, and eastern Greenland, evidence for anoxia precedes the extinction.[136][137] Biomarkers for green sulfur bacteria, such as isorenieratane, the diagenetic product of isorenieratene, are widely used as indicators of photic zone euxinia because green sulfur bacteria require both sunlight and hydrogen sulfide to survive. Their abundance in sediments from the P-T boundary indicates hydrogen sulfide was present even in shallow waters.

This spread of toxic, oxygen-depleted water would have devastated marine life, causing widespread die-offs. Models of ocean chemistry suggest that anoxia and euxinia were closely associated with hypercapnia (high levels of carbon dioxide).[138] This suggests that poisoning from hydrogen sulfide, anoxia, and hypercapnia acted together as a killing mechanism. Hypercapnia best explains the selectivity of the extinction, but anoxia and euxinia probably contributed to the high mortality of the event. The persistence of anoxia through the Early Triassic may explain the slow recovery of marine life after the extinction. Models also show that anoxic events can cause catastrophic hydrogen sulfide emissions into the atmosphere (see below).[139]

The sequence of events leading to anoxic oceans may have been triggered by carbon dioxide emissions from the eruption of the Siberian Traps.[139] In that scenario, warming from the enhanced greenhouse effect would reduce the solubility of oxygen in seawater, causing the concentration of oxygen to decline. Increased weathering of the continents due to warming and the acceleration of the water cycle would increase the riverine flux of phosphate to the ocean. The phosphate would have supported greater primary productivity in the surface oceans. The increase in organic matter production would have caused more organic matter to sink into the deep ocean, where its respiration would further decrease oxygen concentrations. Once anoxia became established, it would have been sustained by a positive feedback loop because deep water anoxia tends to increase the recycling efficiency of phosphate, leading to even higher productivity.

Hydrogen sulfide emissions

A severe anoxic event at the end of the Permian would have allowed sulfate-reducing bacteria to thrive, causing the production of large amounts of hydrogen sulfide in the anoxic ocean. Upwelling of this water may have released massive hydrogen sulfide emissions into the atmosphere and would poison terrestrial plants and animals and severely weaken the ozone layer, exposing much of the life that remained to fatal levels of UV radiation.[139] Indeed, biomarker evidence for anaerobic photosynthesis by Chlorobiaceae (green sulfur bacteria) from the Late-Permian into the Early Triassic indicates that hydrogen sulfide did upwell into shallow waters because these bacteria are restricted to the photic zone and use sulfide as an electron donor.

The hypothesis has the advantage of explaining the mass extinction of plants, which would have added to the methane levels and should otherwise have thrived in an atmosphere with a high level of carbon dioxide. Fossil spores from the end-Permian further support the theory: many show deformities that could have been caused by ultraviolet radiation, which would have been more intense after hydrogen sulfide emissions weakened the ozone layer.

Supercontinent Pangaea

In the mid-Permian (during the Kungurian age of the Permian's Cisuralian epoch), Earth's major continental plates joined, forming a supercontinent called Pangaea, which was surrounded by the superocean, Panthalassa.

Map of Pangaea showing where today's continents were at the Permian–Triassic boundary

Oceanic circulation and atmospheric weather patterns during the mid-Permian produced seasonal monsoons near the coasts and an arid climate in the vast continental interior.[140]

As the supercontinent formed, the ecologically diverse and productive coastal areas shrank. The shallow aquatic environments were eliminated and exposed formerly protected organisms of the rich continental shelves to increased environmental volatility.

Pangaea's formation depleted marine life at near catastrophic rates. However, Pangaea's effect on land extinctions is thought to have been smaller. In fact, the advance of the therapsids and increase in their diversity is attributed to the late Permian, when Pangaea's global effect was thought to have peaked.

While Pangaea's formation certainly initiated a long period of marine extinction, its impact on the "Great Dying" and the end of the Permian is uncertain.

Encounter with spiral arm

John Gribbin argues that the Solar System last passed through a spiral arm of the Milky Way around 250 million years ago and that the resultant dusty gas clouds may have caused a dimming of the Sun which combined with the effect of Pangaea to produce an ice age.[141]

Microbes

A hypothesis published in 2014 posits that a genus of anaerobic methanogenic archaea known as *Methanosarcina* was responsible for the event.[142] Three lines of evidence suggest that these microbes acquired a new metabolic pathway via gene transfer at about that time, enabling them to efficiently metabolize acetate into methane. That would have led to their exponential reproduction, allowing them to rapidly consume vast deposits of organic carbon that had accumulated in the marine sediment. The result would have been a sharp buildup of methane and carbon dioxide in the Earth's oceans and atmosphere, in a manner that may be consistent with the $^{13}C/^{12}C$ isotopic record. Massive volcanism facilitated this process by releasing large amounts of nickel, a scarce metal which is a cofactor for enzymes involved in producing methane.[142] On the other hand, in the canonical Meishan sections, the nickel concentration increases somewhat after the $\delta^{13}C$ concentrations have begun to fall.[143]

Combination of causes

Possible causes supported by strong evidence appear to describe a sequence of catastrophes, each worse than the last: the Siberian Traps eruptions were bad enough alone, but because they occurred near coal beds and the continental shelf, they also triggered very large releases of carbon dioxide and methane.[67]

The resultant global warming may have caused perhaps the most severe anoxic event in the oceans' history: according to this theory, the oceans became so anoxic, anaerobic sulfur-reducing organisms dominated the chemistry of the oceans and caused massive emissions of toxic hydrogen sulfide.[67]

However, there may be some weak links in this chain of events: the changes in the $^{13}C/^{12}C$ ratio expected to result from a massive release of methane do not match the patterns seen throughout the early Triassic;[16] and the types of oceanic thermohaline circulation that may have existed at the end of the Permian are not likely to have supported deep-sea anoxia.[144]

See also

- Extinction events
- List of possible impact structures on Earth
- Siberian Traps
- Silurian hypothesis
- Wilkes Land crater

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External links

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