The Permian mass extinction and Triassic faunal explosion, what happened?

The boundary between the Permian and Triassic, 251 million years ago, is marked by the most severe mass extinction known. At this time around 95% of marine species and 70% of land vertebrates were wiped out (Bowring *et al*, 1999). Levels of diversity took longer to recover after this extinction than any other, possibly up to 6 million years (Goodwin *et al*, 2001). Rock strata and fossil records appear to show a gradual decline in diversity throughout the Permian with a sharp drop at the end of the period, indicating a catastrophic event or combination of events (Goodwin, *et al* 2001) (Figure 1).

There appears to be a significant negative shift in carbon isotopes across the Permian-Triassic boundary (Figure 2), indicating possibly a decrease in productivity (Korte *et a*l, 2004), although there are many explanations for this. A layer of abiotic seafloor cement found in parts of Iran, Armenia, Turkey and China has an isotopic composition of $\delta^{13}C$, which is 4‰ to 5‰ PDB lower than typical Permian values (Heydari & Hassanzade, 2003).

Figure 1. Extinction rates and number of families over geological periods.
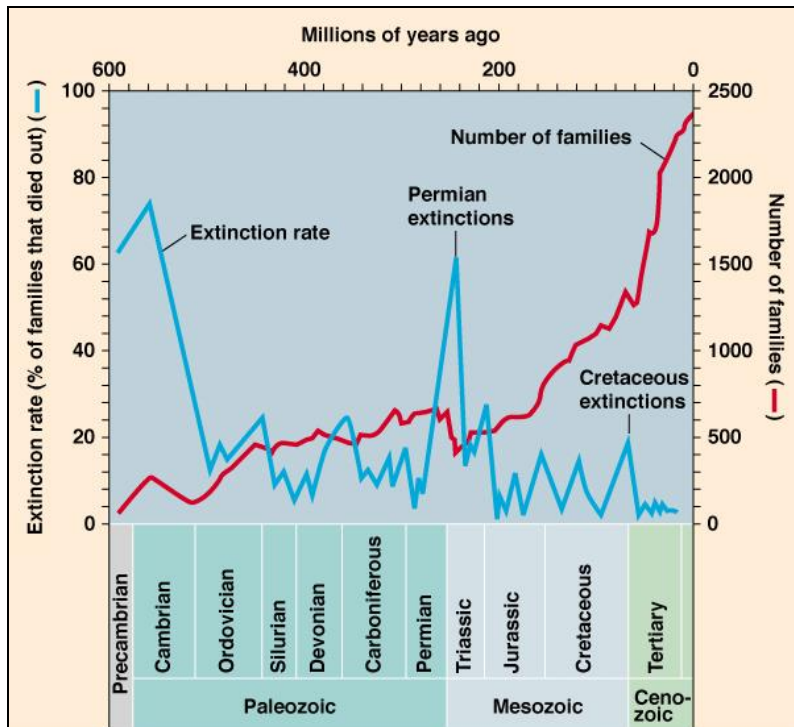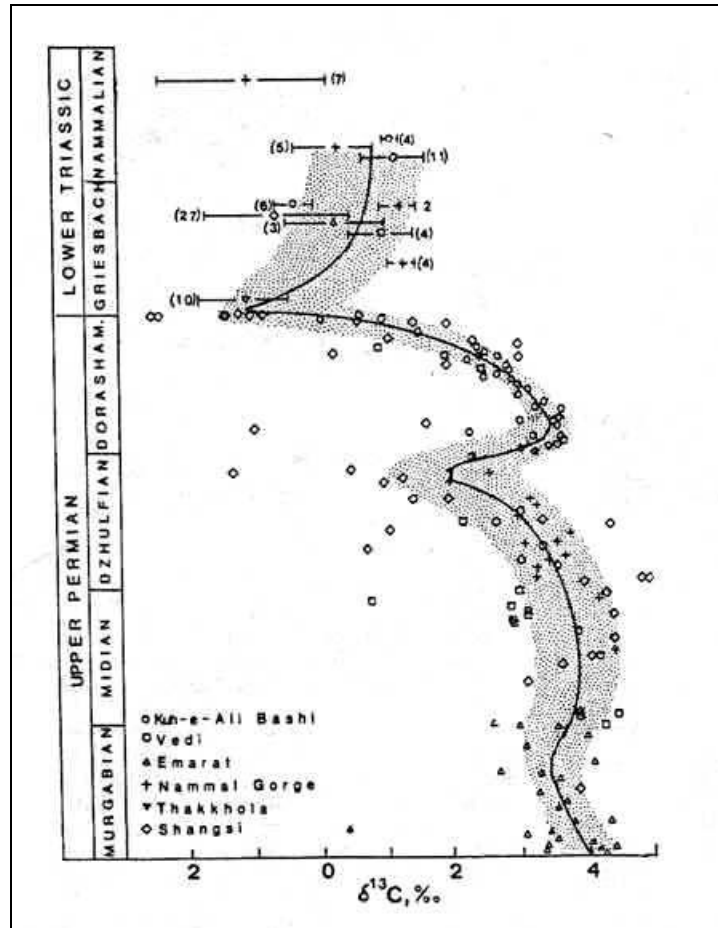© Addison Wesley Longman, Inc.

Figure 2. Synthesis of δ¹³C curves for six sections from western to eastern Tethys for the late Permian and early Triassic. From Baud, Magaritz and Holser (1989), drawn by W.T.Holser.

Fluctuations in carbon isotopes continued into the Triassic making it complicated to identify a single trigger (Knoll *et al,* 2007). Other evidence comes in the form of major shifts in sulphur and strontium isotopes (Erwin, 2003). Many theories about the type of event responsible have been put forward, some of which although once widely accepted have now been repudiated with the unearthing of new evidence.

During the Permian, the supercontinent Pangaea was formed as the continents that had fragmented from the earlier supercontinent Rodinia drifted back together and collided. The vast ocean surrounding Pangaea is known as Panthalassa and the smaller sea to the east of the continent was the Tethys. It is generally believed that the interior of Pangaea was dry with only some areas receiving any rainfall (Chang *et al*, 1998). Land vertebrates

at the time were dominated by carnivorous pelycosaurs and mammal-like dyconodont therapsids. Large amphibians thrived at the beginning of the Permian, but were gradually replaced in many ecological niches by amniotes (Goodwin, *et al* 2001). Marine fauna at the time included brachiopods, ammonoids, sharks, bony fish, gastropods, fusilinid foraminiferans and some types of coral (HVPM, 1996). Pollen records indicate that floras were dominated by glossopterids, but also included conifers, ferns, cordaitaleans, ginkgoaleans, gnetaleans and cycadaleans (Vajda & McLoughlin, 2005).

Marine organisms suffered higher extinction rates than terrestrial life forms. Rugose and tabulate corals, trilobites and blastoids did not survive past the Permian-Triassic boundary (Monroe & Wincander, 2005). Planktonic species including fusulinid foraminiferans and two orders of radiolarians became extinct (De Wever, *et al* 2003). Bryozoa declined steadily throughout the Permian, with only 28 genera from 128 surviving into the Triassic. Similarly, brachiopods which suffered a gradual decline during the Permian were reduced from 60 genera to 10. One genus of crinoid survived into the Triassic (Goodwin *et al*, 2001). Bivalve and gastropod molluscs were less affected, as were aquatic arthropods, nautiloid cephalopods and echinoids (Erwin et al 2001).

On land, dicynodont therapsids were greatly reduced in diversity and became extinct during the Triassic (Behrensmeyer, 1992). Pelycosaurs were extinct by the end of the Permian. Of the anapsids, only procolophonoids survived the Permian-Triassic extinction, but died out during the Triassic (Laurin, 1998). The insect fauna was also transformed at the end of the Permian. Many lineages were wiped out, so that only a small fraction of them now appear in the modern insect fauna (Labandeira & Eble). Floras were transformed as a result of the end-Permian biotic crisis. There is a period in which woody gymnosperms show a sudden decline, indicated by an interval lacking in coal accumulation known as the "coal gap" (Vajda & McLoughlin, 2005). Cordaites died out, but other gymnosperms reappeared in the Triassic and greatly diversified (Goodwin *et al,* 2001).

The beginning of the Triassic is marked by a fungal spike (Looy *et al*, 2001), probably a result of large amounts of decaying organic matter. The selectivity of the extinction has served as a clue to the reasons behind it. For example, it has been observed that epifaunal suspension-feeders were worst affected and that these faunas are characterized by heavily calcified skeletons, low metabolism and gas permeable surface area rather than gills (Heydari & Hassanzade, 2003). After the period of mass extinction, some of the marine faunas that survived, such as brachiopods, gastropods, bi-valves and ammonoids, exhibited dwarfism, known as the "Lilliput effect" (Isozaki *et al*, 2006, Price-Lloyd & Twitchett, 2002) and pre-extinction sizes did not recur until the mid-Triassic. This may have been due to ocean anoxia or food shortages (Twitchett, 2006). Many taxa that disappeared from the fossil record, such as gastropods, sponges and bi-valves, re-appeared millions of years later. This is known as the Lazarus effect. The phenomenon may be due to a period of poor fossil preservation or because affected taxa become extremely rare and possibly move to refugia where environmental conditions are less harsh (Wignall & Benton, 1999).

The fossil record provides some clues about the Permian-Triassic extinction patterns, particularly in the case of marine organisms, but sediments containing fossils do not always provide a continuous record, due to marine regression reducing sediment deposition rates (Goodwin et al 2001). Evidence is also available in the form of stable carbon or oxygen isotope ratios, which can provide an indication of changes in climate and biomass. Sources of these isotopes include marine carbonate strata and tooth apatite, the ratios of which are believed to reflect atmospheric ratios at that time (Thackeray *et al*, 1990). Important sites for the collection of data related to the Permian extinctions include the Karoo in South Africa (Wignall, 2001), the Meishan section in China (Dao-Yi & Zheng, 1993) (Figure 3), East Greenland (Looy *et al,* 2001) and the Southern Alps (Kozur, 1998).

There is no dispute over the fact that there was a change in climate towards the end of the Permian and that this change occurred on a global scale. Most evidence points to a rapid extinction period in geological terms, U-Pb dating suggesting approximately 500,000

Figure 3. Profile through the global stratotype section at Meishan, China. Note the excursion to isotopically 'light' carbon at the extinction horizon. Numbers at left refer to bed numbers. Bed thicknesses based on field observations by ADS.
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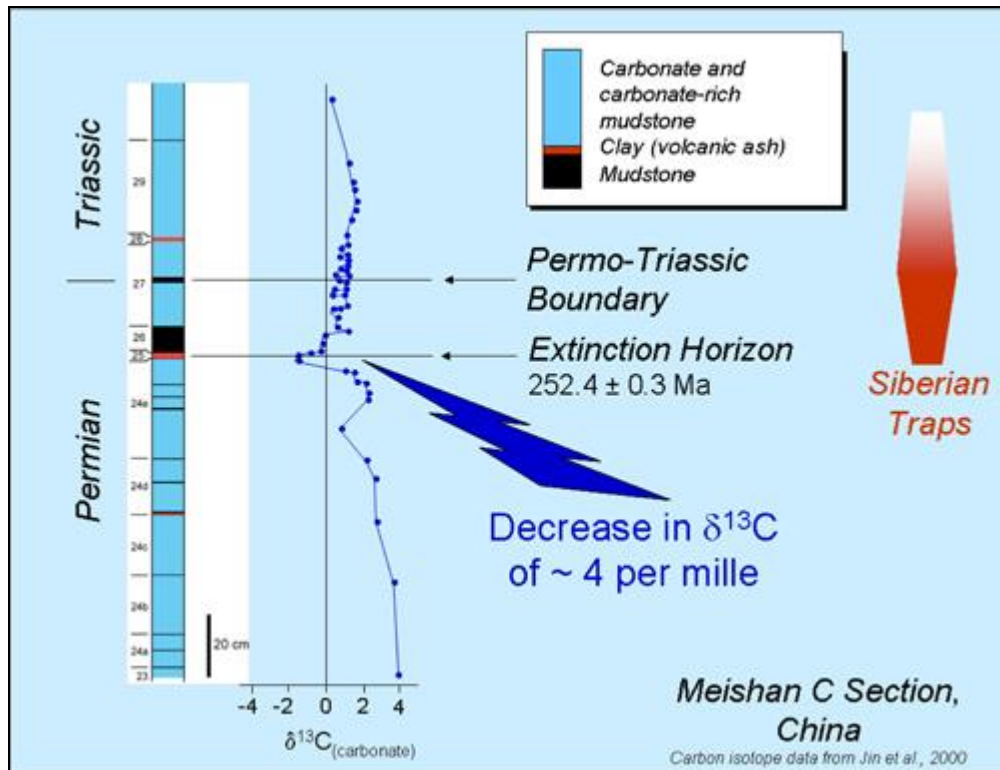
years (Knoll *et al*, 2007), but many studies have concluded that there were two separate extinctions, a minor one followed by a more severe one at the Permian-Triassic boundary. However, analyses of different data and discrepancies between results of studies have lead to diverse hypotheses for the reasons behind the mass extinction.

A popular theory based on volcanically triggered environmental change focuses on the Siberian Traps, a large igneous province originally measuring between 1 million and 4 million cubic kilometres. The flood basalt flows probably resulted from a mantle plume with eruptions estimated by radiometric dating to have lasted around 1 million years beginning around the same time as the Permian-Triassic boundary (Wignall, 2001). Whether this volcanic activity was the cause of the mass extinction or simply a coincidental occurrence is the topic of much debate. Studies of more recent large volcanic eruptions show that they discharge vast amounts of SO_2 and CO_2 into the atmosphere

along with soot, fine ash and sulphate particles. These gradually spread to cover the entire planet. The high levels of aerosols in the stratosphere block light reaching the surface of the Earth and cause low latitude temperatures to drop, leading to reduced photosynthesis (Oppenheimer, 2002). Cooling may be more extreme if the level of sulphuric gases is high, as these combine with water vapour in the stratosphere, absorbing solar radiation and preventing it from reaching the troposphere (Camp, 2006).

The high proportion of tuffs in the Siberian Traps indicates a high level of volcanic dust and aerosols, which is consistent with the theory of global cooling. It has been estimated that these would probably have stayed in the atmosphere for a short period from several months (Kozur, 1998) up to five years (Wignall, 2001) after a large eruption. According to Kozur (1998) this would be a sufficiently prolonged period to trigger mass extinctions in the tropical-subtropical oceanic shelf areas, where the water would drop below the critical temperature for warm-water organisms, but the affect on high-latitude faunas would be far less severe. He believes that there may have been two such large eruptions, one just before the Permian-Triassic boundary and another just after with 100,000-200,000 years separating them, corresponding with the main extinction horizons. The suggestion that volcanism led to major glaciation in the late Permian has been put forward by some researchers. Even if this was the case, Kozur rejects it as being a contributing factor towards the end-Permian crisis, as other glacial periods did not result in mass extinctions, but simply altered or restricted the geographical range of organisms.

Wignall (2001) does not believe that the period of cooling would even have been sufficient to cause a level of cooling required to disturb warm-water taxa. While global warming due to increased levels of carbon dioxide due to volcanic activity is usually countered by aerosols and sulphuric water vapour blocking solar radiation (Camp, 2006), carbon dioxide remains in the atmosphere for a much longer period of time (Goodwin et al, 2001). This in theory would cause a greenhouse effect, leading to an increase in global temperatures, possibly exacerbated by subsequent dissociation of methane hydrates (Wignall, 2001). Evidence for this comes from floras such as the cold adapted glossopteridales, which started to decline at the beginning of the Triassic to be replaced

by warm temperate floras. There is no record of cold-temperature or polar floras at this time (Hallam & Wignall, 1999).

This warming is an effect postulated by Hallam and Wignall (1997), but while Kozur (1998) does not deny that this happened, his evidence suggests it occurred after the Permian-Triassic boundary and that the major impact on ecosystems at the end-Permian was due to the volcanic winter. This is supported by Knoll et al (2007), who consider the possibility that the event at the Permian-Triassic boundary initially only reduced photosynthesis and faunal extinctions followed as a result of starvation.

Another consequence of prolonged volcanic activity is widespread acid rain, which is likely to have been responsible for the destruction of woody gymnosperms. One plant order that continued to flourish throughout the Permian-Triassic crisis was Lycopodiales. These plants are suited to very acidic soils, supporting the theory that high levels of acidity were present (Kozur, 1998). Much evidence suggests that a prolonged period of anoxia occurred in at least some areas of ocean, a feasible result of increased temperature or high atmospheric concentrations of carbon dioxide (Knoll *et al*, 2007), which may be related to volcanic activity. High CO_2 levels may even have led to hypercapnia in both marine and land organisms (Knoll *et al*, 2007). However, there are claims that the quantity of CO_2 produced by the Siberian Traps alone would not have been sufficient to cause such a level of devastation and that another factor, possibly the release of methane was responsible (Benton & Twitchett, 2003).

If massive volcanic activity was in fact the trigger for the Permian-Triassic crisis, the question remains which of the many possible resulting effects of volcanism was actually the main factor contributing to the extinction. It is estimated that the Siberian Traps emitted 2-3 million cubic kilometres of material over a period of 1 million years, correlating with a period of elevated CO_2. It is hypothesized that with the extinction of terrestrial floras and faunas, the continental carbon deposition rate decreased, thus sustaining elevated atmospheric CO_2 (Fraiser & Bottjer, 2006). This would have resulted in global warming, although to what degree is not agreed upon. Other consequences of

high atmospheric CO_2 include release of frozen methane, hypoxia and hypercapnia in both terrestrial and marine life (Erwin, 1993). Fraiser and Bottjer (2006) propose that high CO_2 may be the explanation for the "Lilliput effect" observed in some marine invertebrate groups. This would possibly be due to the increase in energy costs of secreting a carbonate skeleton with elevated pCO_2 in seawater that is undersaturated with calcium carbonate (Knoll et al, 2007).

It has been pointed out by proponents of other theories that gigantic volcanic eruptions, such as Toba 75,000 years ago and one in North America in the Ordovician, while causing a temporary reduction in global temperatures have not been associated with significant long-term climate change or mass extinctions (Wignall, 2001). However, the high proportion of pyroclastic flows within the Siberian Traps indicate that these eruptions were particularly violent and this may be the deciding factor for the level of long-term climatic change that follows them (Wignall, 2001). Although most volcanism theories focus on the Siberian Traps, another source of volcanic activity that possibly contributed to the mass extinction has been identified in Chaotian, South China (Isozaki et al, 2002). The tuff beds corresponding with the main extinction horizon suggest that felsic rather than flood basalt volcanism was responsible for the severe loss of biodiversity.

Indications of low oxygen levels have been discovered in oceanic sediments in most Permian-Triassic boundary sections, leading to a theory that the mass extinctions were caused by anoxia (Hallam & Wignall, 1997). Erwin (1993) claims that anoxia was more likely to have occurred after the Permian-Triassic boundary, however estimations that the event may have lasted several million years (Wignall, 2001) suggest that it may be responsible for the long delay in recovery if not for the extinctions themselves. Evidence for anoxia is found in numerous locations including the Changxing Limestone in Meishan and black shales in areas such as the Mazzin Member in the Southern Alps (Erwin, 2003). Black shales, which are rich in unoxidised carbon, an indicator that they are produced in anoxic environments, are frequently put forward as evidence of anoxia contributing to the mass extinction. However, some scientists assert that they postdate the

end-Permian (Knoll *et al*, 2007). Others claim that there is abundant oxygen-restricted deposition coinciding exactly with the main extinction horizon (Hallam & Wignall, 1999), which strengthens the argument that anoxia was responsible for the large part of the extinctions.

It seems likely that given the amount of evidence pointing to oceanic anoxia and the undisputed level of destruction within marine ecosystems in the end-Permian, that this was a contributing factor to extinction or at the very least, a major impediment to recovery. However, what is still not clear is the degree of anoxia and where it occurred. Some studies have shown that in some areas evidence of anoxia occurs at the same level as highly oxygenated sediments in other locations (Kozur, 1998), leading to the belief that anoxia was a localised phenomenon. In fact, given that certain taxa survived the biotic crisis, there is little doubt that global anoxia could not have occurred, however opinion is divided on whether anoxia followed a latitudinal or a stratified pattern.

Reworked pyrite grains, an indicator of anoxia, have been discovered in Spitsbergen on the lower shoreface and laminated, pyretic micrite has been found in Italian sections, passing gradationally upwards into peritidal facies. These suggest that the most severe anoxia occurred in shallow waters (Hallam & Wignall, 1999). A theory that an upwelling of deep water anoxia moved into shallower waters is based on the presence of microbial reef mounds, which during periods of biotic crisis are able to thrive in marine level-bottom environments due to relaxation of normal ecological constraints. Evidence of reefs that lack any indication of metazoan construction has been found at locations in Western USA, China, Armenia and Greenland (Pruss & Bottjer, 2004). Some studies conclude that the development of anoxic conditions in very shallow water was responsible for the lethality of the event (Hallam & Wignall, 1999) and that a level of ventilation was maintained in deep ocean areas (Winguth & Maier-Reimer, 2004).

Some theories about the cause of anoxia are based on eustatic rise associated with the Permian-Triassic boundary. Ocean circulation modelling carried out by Hotinski *et al* (2001) shows that the end-Permian anoxia was consistent with reduced thermohaline

circulation. This is linked to a difference in solubility of oxygen at warmed high-latitude regions and is facilitated by increased temperatures and a possible high phosphate concentration. Another hypothesis is that carbon that was previously deposited by land plants was subsequently transferred from the continental surface to the ocean, which is implied by analyses of carbon and sulphur isotopes (Winguth & Maier-Reimer, 2004).

Anoxia in paleosols is suggested by the success of isoetalean lycopsids, which had shallow, hollow rootlets, well-adapted to poor aerated soils. Evidence for soil anoxia comes from paleosols that show strong chemical rather than physical weathering and the presence of oxygen intolerant minerals such as berthierine and siderite (Retallack *et al*, 2007).

The theory proposed by Alvarez et al (1980) that the asteroid collision resulting in the Chicxulub crater in Yucatan, Mexico was responsible for the Cretaceous-Tertiary mass extinction has been widely accepted. It is therefore unsurprising that some theories concerning the end-Permian extinctions focus on an extra-terrestrial impact. Some of the effects of an asteroid or meteorite collision would be similar to that of large-scale volcanic activity. Dust and soot would enter the atmosphere, blocking out sunlight for up to a year. More significantly, aerosols comprising SO_2 and water vapour could remain for up to 12 years (Pope *et al*, 1998).

Critical evidence for the Cretaceous-Tertiary impact is a thin stratum of clay at the Chicxulub site which has a concentration of iridium far higher than anywhere else on the Earth's surface. Results from Chinese geologists showed an iridium spike at the Permian-Triassic boundary section at Meishan, but this has not been replicated by subsequent investigations (Erwin, 2003). Iridium peaks were also recorded in the Southern Alps, but were later explained by errors in the apparatus (Kozur, 1998). Other vital evidence required to prove an impact includes a resulting impact structure and debris such as shocked quartz. The identification of an impact structure formed at the relevant period would be extremely difficult, due to successive remodelling of the Earth's crust (Erwin, 2003), but potential contenders have been identified. One of them was proposed by

Becker *et al* (2004) is a crater similar in size to Chicxulub, represented by the Bedout High, on the continental margin of Northwestern Australia. Seismic imaging, melt rocks and impact breccias containing near pure silica glass and shocked minerals are consistent with the existence of a buried impact crater, which according to radiometric dating was formed 250 million years ago. However, Glikson (2004) refutes these claims, stating that the particles are in fact consistent with those found in pyroclastic flows.

Other evidence of impact debris includes a discovery of Ni-rich layers containing Fe-Si-Ni grains at the Meishan Permian-Triassic boundary (Kaiho *et al*, 2002). It is argued that Ni is a proxy for an extraterrestrial impact and that a volcanic event would not have produced a sufficiently high temperature to form Fe-Si-Ni grains. Investigations of sediments at some Permian-Triassic boundary sites in Japan and China uncovered fullerenes containing trapped helium and argon in ratios that suggest an extraterrestrial origin (Becker *et al*, 2001). Attempts to replicate these findings have been unsuccessful. It has been argued that the samples came from a layer substantially below the Permian-Triassic boundary section and that there was no proof that the helium and argon molecules were trapped inside the fullerenes (Farley *et al*, 2005).

Much evidence, such as carbon isotopic shifts, is consistent with an impact event, but it could just as easily be linked to other causes. Moreover, the data specifically related to an extraterrestrial impact is controversial. Analyses of the fossil record and ash layers frequently point to one prolonged or two separate events, which is not consistent with the impact theory. Vajda and McLoughlin (2005) cite a study conducted on *Reduviasporonites* in Greenland, which suggests that the fungal spike extends for a period of 54,000 years, and therefore unlikely to be reliant on a single devastating event.

Pangaea drifted northwards during the Permian and Triassic, bringing a large part into the tropical-subtropical belt, leading to arid conditions with large daily fluctuations in temperature. The northern part of Pangaea moved into the Boreal realm, resulting in the cooling of the climate. This movement may have triggered the gradual decline of warm-water faunas such as fusulinid foraminiferans during the late Permian (Kozur, 1998).

There is a possibility that the formation and drift of Pangaea contributed to loss of productivity on land and reduced thermohaline circulation in the ocean. However, it is more likely that this would have a factor in gradual decline before the Permian-Triassic boundary.

Early Triassic organic matter with unusually light carbon isotopic composition has been discovered in Arctic paleosols and New Zealand marine sequences. One interpretation is that it indicates a major release of methane (Retallack *et al*, 2007). Subsequent analyses of other sediments strengthen this theory, although the magnitude of carbon isotopic excursion varies from section to section, suggesting localized methane sources. Suggested mechanisms responsible for triggering a methane outburst include volcanism, a comet impact, marine faulting or landslides on the ocean floor. Methane from volcanic activity alone, while potentially being a contributory factor, would not have led to the high levels estimated (Retallack *et al*, 2007).

Heydari & Hassanzade (2003) believe that the $\delta^{13}C$ isotopes found in a layer of sedimentation can be explained by accumulation-dissociation cycles of gas hydrates. Gas hydrates are composed of water molecules forming a rigid cage around a molecule of natural gas, usually methane. They typically occur in areas with subzero temperatures or at low pressure, for example polar regions or in deep sea sediments, as they are only stable in these conditions. There are several possible mechanisms for triggering a dissociation event including sea level changes and mantle heating beneath the ocean bed. The dissociation events would have been short and destructive, releasing large quantities of methane into the ocean, accounting for the low oxygen levels suggested by many studies. Leakage of methane into the atmosphere would have led to a super-hot climate responsible for the terrestrial extinctions. A high level of atmospheric methane would be consistent with conclusions of numerous studies that there was considerable global warming at the beginning of the Triassic.

Figure 4. Global sea level changes over time. © Global Climate Change (www.global-climate-change.org.uk)
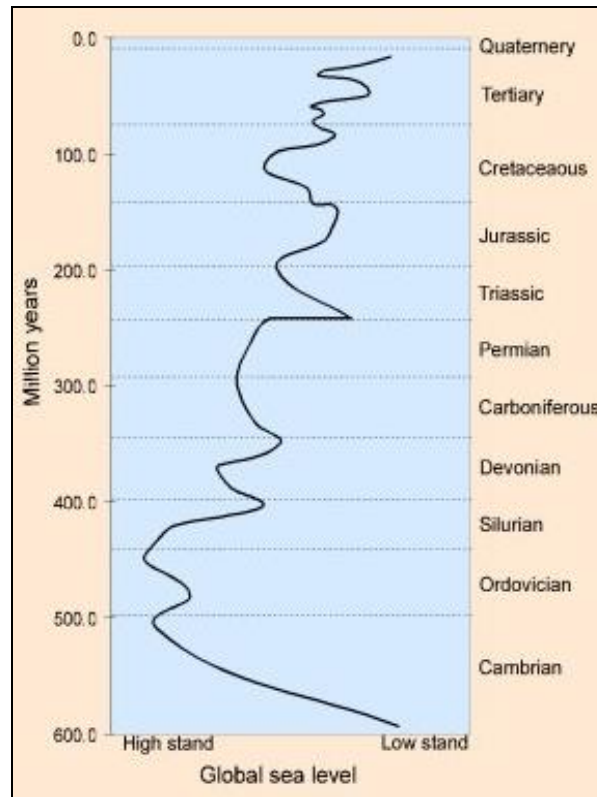
Most mass extinctions over time have been associated with fluctuating sea levels, but there is no clear pattern to link them with any particular point in the regression-transgression cycle (Hallam & Wignall, 1999). Accelerated regression is thought to have occurred during the Dzulfian followed by rapid transgression at the start of the Triassic (Erwin, 1990) (Figure 4). There is speculation that submarine volcanism could be the cause of sea-level rise, and the release of CO_2 into the water is consistent with ocean anoxia theories, but it would be almost impossible to prove this as any oceanic crust produced would since has been lost (Hallam & Wignall, 1999). Knoll *et al* (2007) hypothesize hydrogen sulphide poisoning as a kill mechanism, which could have resulted from increased sulphide levels due to anaerobic respiration of certain types of bacteria in anoxic marine waters.

Studies of patterns of recovery are less common than investigations into the processes and causes of the extinction, but useful data has been gathered in Western USA, China

and the Alps (Erwin, 1999). These show a long period of very low diversity throughout the early Triassic with biotic recovery starting in the mid-Triassic, defined by criteria including an increase in biodiversity, reappearance of Lazarus taxa, re-establishment of reef systems and return to normal size of organisms exhibit the "Lilliput effect" (Chen et al, 2006). A study of *Meishanorhynchia*, a Mesozoic brachiopod, at Meishan suggests that an improvement in oceanic conditions occurred within 1-2 million years after the end-Permian extinction. Sedimentation and geochemical analysis show increased oxygenation on the marine shelf in that area. (Chen et al, 2006). In other parts of Pangaea, recovery may have taken longer with extinctions continuing for 5-8 million years into the Triassic (Erwin, 1990).

Some of the few large land animals to survive the Permian-Triassic extinction include *Lystrosaurus*, a cynodont synapsid, (Hallam & Wignall, 1997) and the proterosuchids, which may have the predecessor of the archosaurs (Benton, 2000). It has been postulated that L*ystrosaurus* was able to better acclimatize to higher temperatures than other large vertebrates and was well adapted to low oxygen levels in the burrows in which it lived (Retallack *et al*, 2007). Small therocephalians, cynodonts and procolophonoids have also been discovered in the Karoo, and similar faunas at other locations (Benton, 2000). Archosaurs appeared during the early Triassic and filled the ecological niches left by the Permian carnivores. They radiated into several groups. One lineage led to the crocodilians, and another eventually to pterosaurs, dinosaurs and birds. Although most evidence indicates that it took a long time for biodiversity to return to levels akin to those before the extinction took place, the late Triassic faunal richness suggests that a period of explosive evolution must have occurred (Anderson *et al*, 1996). However, diversification suffered a further set back with another less severe mass extinction at the end of Triassic.

More precise dating of the Permian-Triassic boundary and the Siberian Traps, showing that the two events coincide has led to this theory for the mass extinction becoming the most popular. Added to this, evidence for an extraterrestrial impact is becoming increasingly contentious as new studies are unable to replicate previous findings. However, there is still no consensus on what the main kill mechanism was. It is difficult

to determine what the consequences of volcanism of such a scale would have been or which of the effects would have been most devastating. There are many discrepancies between interpretations of evidence such as sedimentation and isotope shifts, leading to contradictory conclusions from different studies. Assumptions that sedimentation is continuous can lead to poor interpretation of data. There may be differing rates of sedimentation or even gaps of undeterminable time periods (Erwin, 1993). Ocean crust formations are difficult to pinpoint since they have changed considerably within the last 251 million years due to plate tectonics.

Investigations into the causes of the end-Permian mass extinction continue to unearth new evidence. In fact, a precise date for the Permian-Triassic boundary has only been agreed upon within the last ten years, when U-Pb zircon dating was carried out on volcanic ash bands in the Meishan section. Before this, dates popularly quoted for the event were generally too recent (Benton & Twitchett, 2003) and led to misinterpretation of evidence. As dating and analytical techniques improve and with an increasing accumulation of data, it might one day be possible to solve the mystery of the end-Permian mass extinction and possibly learn some valuable lessons about potential future environmental catastrophes.

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