

The protracted Permo-Triassic crisis and multi-episode extinction around the Permian–Triassic boundary

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Abstract

The Permo-Triassic crisis was a major turning point in geological history. Following the end-Guadalupian extinction phase, the Palaeozoic biota underwent a steady decline through the Lopingian (Late Permian), resulting in their decimation at the level that is adopted as the Permian–Triassic boundary (PTB). This trend coincided with the greatest Phanerozoic regression. The extinction at the end of the Guadalupian and that marking the end of the Permian are therefore related. The subsequent recovery of the biota occupied the whole of the Early Triassic. Several phases of perturbations in $\delta^{13}\text{C}_{\text{carb}}$ occurred through a similar period, from the late Wuchiapingian to the end of the Early Triassic. Therefore, the Permian–Triassic crisis was protracted, and spanned Late Permian and Early Triassic time. The extinction associated with the PTB occurred in two episodes, the main act with a prelude and the epilogue. The prelude commenced prior to beds 25 and 26 at Meishan and coincided with the end-Permian regression. The main act itself happened in beds 25 and 26 at Meishan. The epilogue occurred in the late Griesbachian and coincided with the second volcanogenic layer (bed 28) at Meishan. The temporal distribution of these episodes constrains the interpretation of mechanisms responsible for the greatest Phanerozoic mass extinction, particularly the significance of a postulated bolide impact that to our view may have occurred about 50,000 Myr after the prelude. The prolonged and multi-phase nature of the Permo-Triassic crisis favours the mechanisms of the Earth's intrinsic evolution rather than extraterrestrial catastrophe. The most significant regression in the Phanerozoic, the palaeomagnetic disturbance of the Permo-Triassic Mixed Superchron, widespread extensive volcanism, and other events, may all be related, through deep-seated processes that occurred during the integration of Pangea. These combined processes could be responsible for the profound changes in marine, terrestrial and atmospheric environments that resulted in the end-Permian mass extinction. Bolide impact is possible but is neither an adequate nor a necessary explanation for these changes.

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The pattern and mechanism of the mass extinction across the Permian–Triassic Boundary (PTB), the most severe biotic crisis in the Phanerozoic, is the subject of intense research and discussion. Some workers advocate an

abrupt (Rampino et al., 2000) and single-phase (Jin et al., 2000b) pattern, and the probability of an extraterrestrial impact as the mechanism that induced catastrophic environmental changes (Becker et al., 2001; Kaiho et al., 2001; Basu et al., 2003; Becker et al., 2004). Others regard the extinction as more gradual and multi-phase, and seek different causal mechanisms (De Wit et al., 2002; Benton,

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2003). The results of research on biostratigraphy and interregional correlation in South China (Yang et al., 1987, 1993; Yin et al., 2000) favour the latter view and indicate a prolonged and multi-phase pattern of biotic and environmental change in the Late Permian–Early Triassic that may help constrain explanations of the causes and the mechanism of this most severe Phanerozoic crisis.

1. The protracted Late Permian–Early Triassic crisis

1.1. The biotic crisis

1.1.1. Two-phase (end-Guadalupian and PTB) mass extinctions

Two phases of late-Permian mass extinction, at the end of the Guadalupian and at the PTB (Fig. 1), have

been reported by Jin et al. (1994) and Stanley and Yang (1994), but opinions differ as to whether these events were related or independent. Proponents of the latter case hold that the end-Guadalupian extinction was largely due to regression, that the biosphere did not show a tendency to deteriorate after that extinction, and that a sudden catastrophe at the PTB was unrelated to sea-level change (Fang, 2004). If, however, the extinctions are related, a decline in diversity and shell structure should persist from the end of the Guadalupian to the PTB, and be related to environmental causes, such as sea-level changes. Fusulinids, tetracorals and brachiopods are the most abundant Late Palaeozoic shallow marine invertebrates, and all suffered end-Guadalupian and PTB extinctions. The following discussion is devoted mainly to new data from South China and does not repeat the

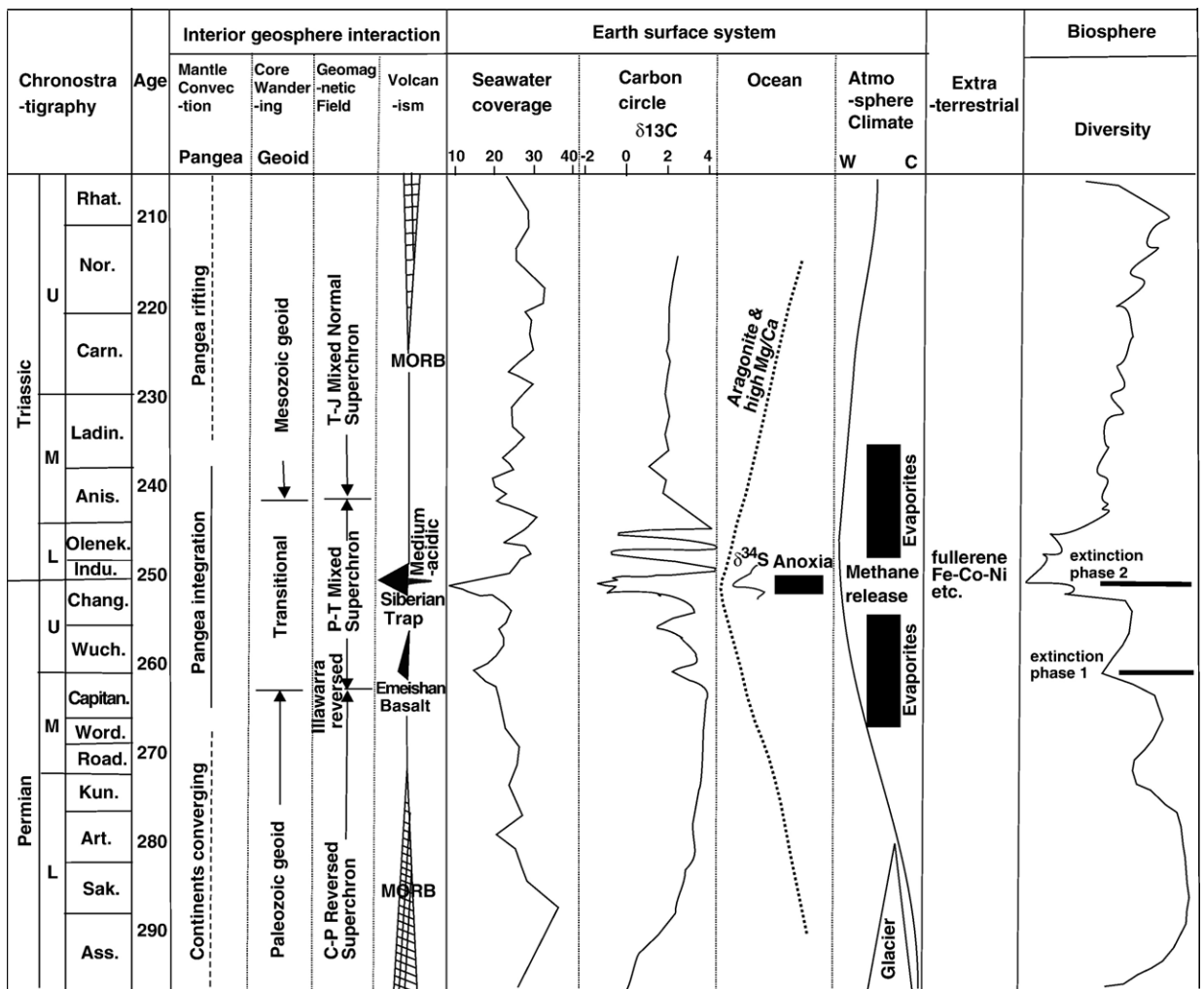


Fig. 1. Causal relationships between geosphere disturbances and mass extinction during the Late Permian and Early Triassic. Seawater coverage modified from Holser and Magaritz (1987), $\delta^{34}S$ from Kaiho et al. (2001), Ma/Ca curve from Horita et al. (2002), $\delta^{13}C_{carb}$, climate and biodiversity curves are synthesized (see text and Fig. 2).

synthesis by Erwin (1993); the conclusions are also broadly applicable to Tethyan and palaeo-tropical areas.

Fusulinids (calcareous microgranular shell) reached their acme in size, structure and diversity in the Guadalupian with, for example, the Verbeekiniidae, Neoschwageriniidae and the structurally complicated genera of the Schwageriniidae. Forms up to 1 cm in size are not uncommon in the Guadalupian, and advanced wall structures, such as septulum, parachoma and cuniculi, had been developed by that time. All these advanced or specialized forms disappeared at the end-Guadalupian extinction, with only a few taxa with anomalous shell, e.g. *Reichelina*, ranging into the Lopingian. Only eight genera survived into the late Changhsingian; these are either relatively primitive, with walls subject to silicification (*Ozawainella*, *Staffella*, *Nankinella*, *Sphaerulina*), or have specialized test structures (*Codonofusiella*, *Reichelina*). Calcareous microgranular non-fusulinid foraminifers, the Endothyriina, flourished for a short time during the Late Permian, notably during the Changhsingian, when Colaniellacea replaced the dominant fusulinids. There are two phases of foraminifer extinctions: the end-Guadalupian fusulinid extinction and the PTB extinction of calcareous microgranular forms (all fusulinids, most of Endothyriina) (Stanley and Yang, 1994). Foraminifer faunas underwent a great change at the PTB, characterised by the replacement of the Late Palaeozoic calcareous microgranular foraminifers by hyaline, perforate, calcareous forms in the Mesozoic and Cenozoic (Tong and Shi, 2000). These extinction phases are regarded as related to two regressions, after which foraminifers were forced to migrate into new habitats. The Palaeozoic forms were mainly stenotopic, normal neritic. During the earliest Triassic eurytopic *Earlandia* bloomed (Groves and Altiner, 2005). In Early Triassic, the percentage of eurytopic forms (from littoral to deep water) greatly increased—the agglutinated Textulariina and small Nodosareacea, followed by porcelaneous Miliolina and planktic ancestors in Late Triassic, thus initiated the ecologically diversified Mesozoic and Cenozoic foraminifer biota (Tong, 2004).

During the Guadalupian corals also reached an acme in structural complication, characterised by colonial, often massive forms with marginarium, axial structure, and minor or even tertiary septa. Tetracorals and tabulates both suffered end-Guadalupian (generic extinction rate 77.8%) and PTB (extinction rate 100%) extinctions (Wang and Sugiyama, 2000). After the end-Guadalupian extinction these structurally complicated forms became extinct. Lopingian tetracorals mainly comprised branched colonial forms

with simplified structure (Waagenophyllidae), or solitary genera without dissepiments (Lophophyllidiidae, Polycoelidae). In South China only seven genera (*Waagenophyllum*, *Liangshanophyllum*, *Ipciphyllum*, *Huayunophyllum*, *Tachylasma*, *Lophophyllidium*, *Pterophyllum*) survived into the Changhsingian, and these all disappeared before the PTB extinction. Tabulates declined from an Early Permian maximum to only two genera (*Michelinia*, *Sinopora*) in the Lopingian, and became extinct at the PTB (Li and Gong, 1993).

After the late Guadalupian extinction brachiopod faunas were of low diversity during the early Wuchiapingian. In other parts of Pangea (Gondwanan margin, Boreal), the end-Guadalupian regression continued into the latest Permian, and this low diversity persisted up to the PTB. However, in the Tethys, and especially in South China, a transgression initiated in the late Wuchiapingian resulted in an influx of Guadalupian survivors and eurytopic invaders from high-latitudes (Shen and Shi, 1996). The majority of Lopingian brachiopods belong to the Strophomenida, particularly the Chonetacea and Productacea, and include specialized forms such as lobate and oyster-shaped attaching lytoniaceans (*Oldhamina*, *Leptodus*) and coralliform *Richthofenia*. The disappearance of reef-dwelling brachiopods by late Changhsingian time was followed by a widespread miniaturization ('Lilliput effect') of the brachiopod fauna, with forms typically <1 cm in size in the uppermost, commonly pyrite-bearing, few metres to decimetres of the Changxing Formation, and extending up into the Griesbachian (He, 2005). Most genera, especially those of the Strophomenida, became extinct at the PTB, and the more primitive inarticulate lingulids proliferated in the early Griesbachian, both in South China and around the world (Xu and Grant, 1992). During the late Changhsingian, pectinacean bivalves and ammonoids largely replaced brachiopods in the biota, as in the Dongpan section (Fig. 5).

Gastropods also underwent two phases of extinction, at the end of the Guadalupian (Capitanian) and at the PTB (Batten, 1973; Pan, 2004). In the first phase diversity decreased by 60%, from 123 genera in the Wordian to 60 in the Capitanian (Erwin and Pan, 1996). In South China this phase was not very remarkable but that at the PTB was catastrophic, with 20 families and 63 genera present in the Changhsingian but only five families and 13 genera surviving into the Induan. The tendency of decline persisted throughout the Late Permian, especially among normal marine forms, notably the Pleurotomariina, a diverse component of Early and Middle Permian gastropod faunas. Following more

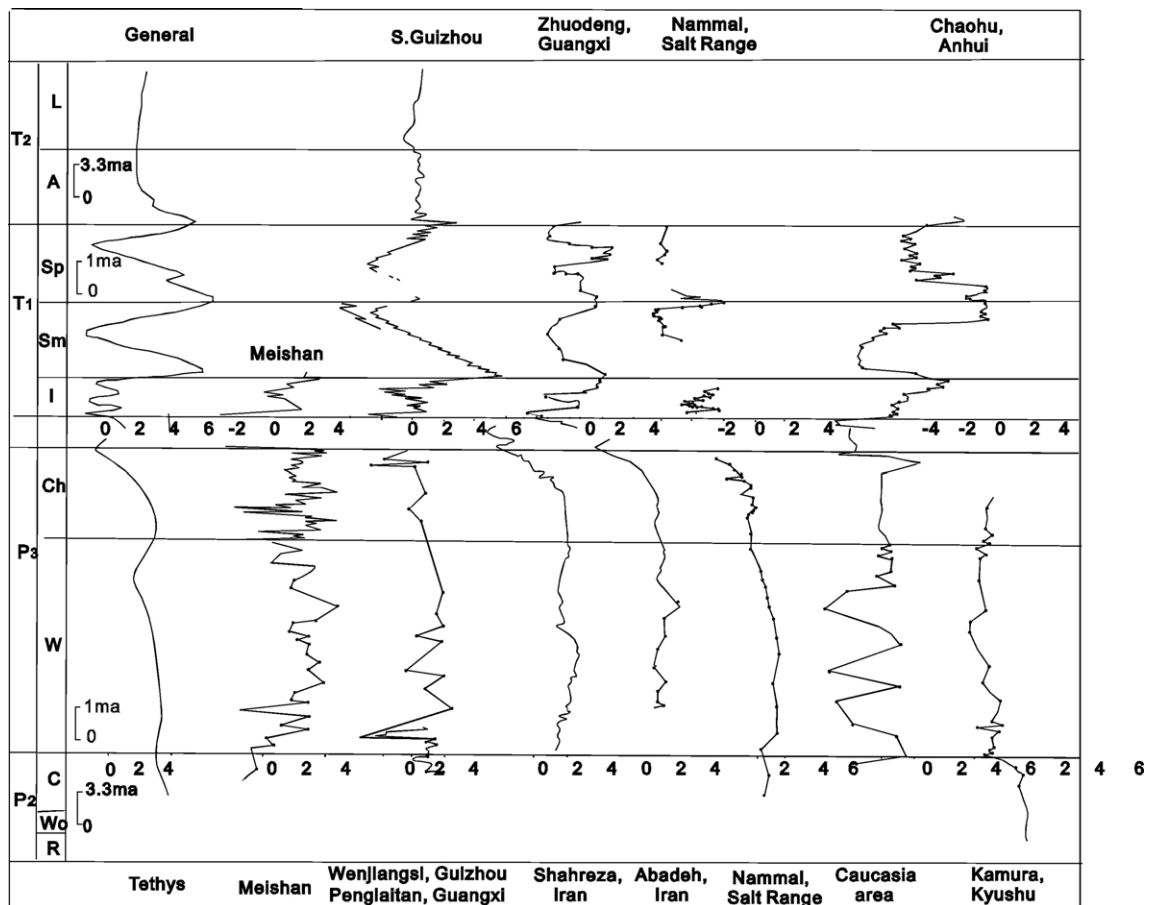


Fig. 2. Correlation of Late Permian–Early Triassic carbon isotope ($\delta^{13}\text{C}_{\text{carb}}$) curves (note that the ordinate scale is amplified 3.3 times between P_3 and T_1). The subdivision and duration (scale 1 Ma) of Late Permian–Early Triassic stages are adopted from Gradstein et al. (2004), with the Middle Permian and Middle Triassic much reduced in scale (scale 3.3 Ma). The original figures have been redrawn with their ordinate adjusted to the time scale and their abscissa adjusted to the same scale of $\delta^{13}\text{C}_{\text{carb}}$ ‰, so the redrawn curves may look quite different from the original ones. In the original figures dots, broken lines or curves were used; we aim to show the general pattern of the $\delta^{13}\text{C}_{\text{carb}}$ fluctuation and the redrawn figures do not show every detail of the originals. Sources: TRIASSIC: General: Corsetti et al. (2005); Meishan: Zuo et al. (2006); S. Guizhou: Payne et al. (2004); Zhuodeng: Zhang et al. (2005); Chaohu: Tong et al. (2005). PERMIAN: Tethys: Baud et al. (1989); Meishan: Jin et al. (2003) for Wuchiapingian; Li (1998) for Changhsingian; Wenjiangsi: Shao et al. (2000) for Upper Permian; Penglaitan: Wang et al. (2004) for Capitanian/Wuchiapingian; Shahreza: Korte et al. (2004b); Abadeh: Korte et al. (2004a); Caucasia area: Zakharov et al. (2005); Nammal: Baud et al. (1996); Kamura: Isozaki et al. (2007-this issue).

severe extinction of endemic genera, the proportion of eurytopic genera increased from 69% in the Capitanian to 83% in the Wuchiapingian. In South China, Salt Range, Kashmir, Alps and Japan, the monotonous assemblage of relatively primitive Bellerophonina flourished in the latest Permian and survived into earliest Triassic (Yang et al., 1987). The Early Triassic was characterised by low diversity and microgastropod biofacies (Pan, 2004; Fraiser et al., 2005). These features indicate eurytopic adaptation to stressed environments from latest Permian to Early Triassic. Several caenastropod groups and the opisthobranchs have their first occurrence in the Olenekian, indicating a major gastropod turnover (Nützel, 2005).

In addition to a decline and/or specialization in structure and ecology, the diversity of most marine invertebrates in South China declined after the end-Guadalupian extinction (Table 1). However the record is complicated and not all taxa show the same tendency. Bivalves generally show a marked worldwide reduction in diversity after the end-Guadalupian extinction (Yin, 1993), but in South China diversification appears to have occurred during the Lopingian (Fang, 2004), partly because its clastic facies favours bivalve habitats and preservation. Brachiopod diversity increased from a low level in the early Wuchiapingian. The extraordinary abundance of Changhsingian non-fusulinid foraminifera and ammonoids reflects the ecological

replacement of fusulinids by endothyrids and of brachiopods by molluscs.

Replacement of the Palaeophytic by the Mesophytic flora was a long stepwise process, commenced during Late Permian. In the northern hemisphere, it may have progressed diachronously from north and west to south and east, following a trend in increasing aridity (Qu, 2005); in China, the gymnosperms, reflected by an abundance of striate pollen, appeared during the late Bashkirian (Late Carboniferous) in northern Xinjian, during the late Early Permian in Tarim, and during the late Late Permian in North and South China (Shen, 1995), and the last elements of the *Gigantopteris* flora survived until the earliest Triassic in Yunnan and Guizhou (Yin et al., in press). However this replacement may also have shifted regionally, from drier highland to wetter lowland settings (Di Michele and Aronson, 1992). In North China the total land plant species number passed from 146 in the lower Upper Permian to 54 in the later Upper Permian, 16 in the Induan and 58 in the Olenekian (Wang, 1989). The Early Triassic was a time for plant survival characterised by the proliferation of the lycopsid *Pleuromeia*, and the recovery lasted until the end of the Middle Triassic (Grauvogel-Stamm and Ash, 2005).

The end-Guadalupian extinction has generally been related to an end-Guadalupian regression (Erwin, 1993; Shi and Shen, 2000; Tong, 2004; Pan, 2004). The causes of the PTB extinction are controversial, but we consider that the prelude to that event was directly related to the end-Permian regression (see Section 3.1). The two regressions are not, as previously thought, independent

Table 1
Diversities of Permian–Triassic marine invertebrate genera in South China

Taxa	AA	KR	RC	W	C	I	O	A	Referece
Fusulinids	60	45	75	15	8	0	0	0	Tong and Shi (2000)
Non-fusulinid foraminifers	34	42	44	37	44	13	22	39	Tong and Shi (2000)
Tetracorals	94	83	97	19	9	0	0	0	Li and Gong (1993)
Brachiopods	49	78	82/61	82/29	83	12	3	41	Shen and Shi (1996)
Ammonoids			37	28	43	24	77	51	Yang and Wang (2000)

Legends: Regional stage names of the original authors have been changed into international stage names. AA: Asselian–Artinskian; KR: Kungurian+Lower Roadian; RC: Upper Roadian–Capitanian; W: Wuchiapingian; C: Changhsingian; I: Induan; O: Olenekian; A: Anisian; Gen: genera; numbers **/** are numbers of taxa in lower stage/upper stage respectively; corals include tetracorals and tabulates; the end-Guadalupian extinction is at the Capitanian/Wuchiapingian (RC/W) boundary.

and separated by a 9 million year interval, but are related phases in a general sea-level fall that probably resulted from the integration of Pangea. Along the northern Gondwanan margin, where Lopingian strata were formerly unknown, occurrences of the *Cyclolobus* fauna in the Himalayas and western Australia show that deposits of that age are in fact widespread. The presence of late Wuchiapingian or even early Changhsingian strata in the Salt Range, Pakistan, is demonstrated by studies of conodonts and palaeomagnetism, and the presence of *Cyclolobus* (Wardlaw and Mei, 1998; Jin et al., 2000a). In the Boreal region, the Ravnefield Formation of eastern Greenland and the Trolld Fiord Formation of the Sverdrup Basin, Arctic Canada, both previously regarded as Guadalupian, have been reassessed as late Guadalupian to early Lopingian, based on conodont and ammonoid evidence (Henderson and Mei, 2000). These findings reduce the gap between the two regressions, because the non-deposition interval is now restricted between early Lopingian (Boreal) or middle Changhsingian (Gondwana) to latest Changhsingian (new transgression). It is therefore now possible to envisage a continuous but diachronous regression that began at the end of the Guadalupian and finished in the latest Changhsingian. Only in Tethyan regions were these regressions separated by the early–mid Changhsingian transgression, which may be related to rifting in Mesotethys.

In summary, much of the Palaeozoic neritic invertebrate fauna declined significantly in terms of both shell structure and diversity after the end-Guadalupian extinction. During the Late Permian, both marine and terrestrial Palaeozoic biota experienced a long-term decline that culminated in their decimation at the PTB. This decline coincided with continuous regression, in areas outside Tethys, from the end of the Guadalupian until the latest Permian, and with a progressive increase in aridity from north and west to south and east. The Late Permian extinction occurred in two phases and lasted for about 9 Myr (Gradstein et al., 2004) (Fig. 1).

1.1.2. Biotic recovery in the Early Triassic

It is widely accepted (Erwin, 1993) that the recovery of the biota after the PTB extinction was protracted and occupied the entire Early Triassic. The recovery was, however, staggered, occurring in bivalves in the early Induan, in ammonoids in the early Olenekian, and in brachiopods in the late Olenekian, but not until the Anisian in the case of foraminifers and hexacorals (Table 1).

Ichnologic records show a pattern of greatly reduced water depth as well as a reduced amount of bioturbation throughout the Early Triassic (Pruss and Bottjer, 2004). This agrees with the depauperate Early Triassic

biodiversity, because reductions in biodiversity generally reduce bioturbation, particularly the depth of bioturbation (Solan et al., 2004). There were phases of enhanced bioturbation, suggesting that periods of relatively normal conditions, too short to allow substantial recovery, were separated by periods of environmental stress that generally kept bioturbation reduced throughout the Early Triassic (Pruss and Bottjer, 2004).

The protracted biotic crisis is also recorded in widespread post-crisis occurrences of microbialites, or carbonates that formed through interaction between the environment and a benthic microbial community, particularly cyanobacteria. They include stromatolites, thrombolites, dendrolites, travertine and cryptic microbial carbonates (autochthonous micrites) (Riding, 1991). The benthic microbial community has formed the basis of all marine ecosystems since the late Archean. However, it was dominant only in the Precambrian and during abnormal Phanerozoic episodes when skeletal microbial communities disappeared; in the Phanerozoic it was, under normal marine conditions, constrained by microbial communities that formed skeletal carbonates and even reefs. The changes in the biota at the PTB coincided with the onset of a major change in carbonate system. This is recorded in the shallow sea deposits of the tropical–subtropical domain by a shift from a skeletal carbonate factory to a microbial carbonate factory. The latter began in the latest Permian, when the prolific Upper Palaeozoic skeletal carbonate factory was abruptly replaced by a non-skeletal carbonate factory, characterised by calcimicrobialites, and extended throughout the Early Triassic, thus created a worldwide ‘reef gap’. Baud et al. (2005a) reported that massive mounds of thrombolites, stromatolites and oncoids developed in four phases: latest Permian to earliest Triassic (*meishanensis* zone–*parvus* zone; latest Changhsingian to earliest Induan), mid to late Induan (late Griesbachian to Dienerian), early Olenekian (Smithian) and latest Olenekian (late Spathian). The coincidence of these microbial phases with $\delta^{13}\text{C}$ negative excursions (see Section 1.2, below) suggests a causal relationship between the two; that this may not be fortuitous is suggested by a similar coincidence between lipid biomarker peaks and $\delta^{13}\text{C}$ values (Xie et al., 2007–this issue). Environmental changes, such as oxidation/reduction pulses, may have controlled both the microbial and the $\delta^{13}\text{C}$ excursions; alternatively, the primary productivity of microbes, which comprise the bulk of the biomass, may have fully controlled the $\delta^{13}\text{C}$ values. The latter would, if feasible, be an important factor in interpretations of the worldwide end-Permian $\delta^{13}\text{C}$ excursion.

Radiolarians flourished between Sakmarian and late Changhsingian times, forming widespread radiolarian cherts (the Permian Chert Event: Beauchamp and Baud, 2002). Radiolarian chert deposition was interrupted at the top of the Dalong Formation, a lateral equivalent of the Changxing Formation, and did not recommence until late Early Triassic times, after the four million year long ‘Early Triassic Chert Gap’ (Isozaki, 1997; Yao and Kuwahara, 2000).

Coal deposits did not form during the Early Triassic, indicating that the terrestrial flora was in a stressed condition at that time (Retallack et al., 1996). Reefs, radiolarian chert and coal represent, under normal oxygenated conditions, the high productivity deposits of shallow water, deep-water and terrestrial ecosystems, respectively. The gaps in the occurrences of these three rock types imply that an anomalous high-stress environment persisted throughout the Early Triassic. The post-Permian recovery process occupied about 6 Myr, but the full scenario of decline, extinction and recovery occupied the whole of Late Permian and Early Triassic time, about 15 Myr (Gradstein et al., 2004), forming the longest biotic crisis in geological history.

1.2. Carbon isotope perturbation

Carbon isotope profiles of some Tethyan Permian sections were recorded by Baud et al. (1989), and summarized in their figure 18 which is reproduced here in modified form (Fig. 2).

The authors of Permian–Triassic carbon isotope studies published after 1989 used different parameters for the ordinate and abscissa of their carbon isotope curves, giving rise to problems of correlation. For the ordinate, either the duration or equidistant length for each stage would facilitate correlation, but many authors used thickness, which may vary greatly in different areas. For the abscissa, the use of different scales for each 1‰ of $\delta^{13}\text{C}_{\text{carb}}$ results in curves that are either very abrupt or very gentle. To achieve a unified scale for correlation, published figures have been redrawn using unified and normalized coordinates. The abscissa is divided equally for every 2‰ for all sections. The ordinate is divided by the age ranges of stages (Gradstein et al., 2004); within each stage marking of the points is based on averaged sedimentation rate. Some of the resulting curves appear quite different from the originals, but the use of standard coordinates facilitates correlation (Fig. 2).

The carbon isotope profile shows a depletion of 2 to 4‰ (except in the Caucasian curve) at or near the Capitanian–Wuchiapingian transition; this appears to coincide with either the end-Guadalupian regression (a

sequence boundary) or with the transgression above that boundary (Penglaitan, Guangxi; Wang et al., 2004); this small discrepancy may reflect inadequate biostratigraphic control. Recent biostratigraphic work (Shang et al., 2004) has shown that an excursion recorded by Baud et al. (1989, 1996) in Nammal Gorge, and attributed by them to a ‘Murgabian–Midian’ level, should be correlated with the Capitanian–Wuchiapingian boundary. Above this excursion, curves from the Wuchiapingian and lower Changhsingian remain at high values (around 2 to 5‰) in most sections, but show varying degrees of fluctuation. Palaeotethyan sections (Meishan, Penglaitan, Caucasia) show strong variations and Mesotethyan and Peri-Gondwanan sections (Nammal Gorge, Shahreza, Abadeh) have relatively smooth curves (Fig. 2). Whether the character of the former is original or due to diagenesis or sampling requires further investigation. Late Wuchiapingian and early Changhsingian curves are mostly relatively smooth, but an unusual excursion recorded in the Meishan section (Li, 1998) requires further investigation. After this relatively stable period, all late Changhsingian curves show an increasingly rapid decrease in values, becoming negative just below the PTB (Corsetti et al., 2005). This ubiquitous feature is important because it marks the beginning of a profound global change prior to the PTB.

Curves from Early Triassic sections show numerous large fluctuations and contrast with smooth curves from the Middle Triassic (Corsetti et al., 2005). Very similar records have been obtained from Early Triassic sections in southern Guizhou (Payne et al., 2004), western Guangxi (Zhang et al., 2005), the lower Yangtze and Meishan (Zuo et al., 2006), the Salt Range (Baud et al., 1996), Iran (Horacek et al., 2005) and the Alps (Horacek et al., 2000). Above the strong negative excursion, from 0 to –5‰, at the PTB, most curves from the Induan fluctuate between –1 and +3‰, though there is a negative excursion to –2 or –3‰ in the mid Induan (late Griesbachian–early Dienerian). The first positive Early Triassic peak occurs at the Induan–Olenekian boundary. In Iran and Italy the first positive peak appears to occur higher, in the lower Olenekian (lower Smithian), but this is uncertain as the absence of the index conodont *Neospathodus waageni* limits the biostratigraphic control. A second positive peak occurs at the Smithian–Spathian boundary, and a third slightly above the Spathian–Anisian boundary. Thus there were three negative phases during the Early Triassic: early Induan (excursions at the PTB and late Griesbachian–early Dienerian), mid-Smithian and mid-Spathian; these appear to be intercontinental in scope. Variations in $\delta^{13}\text{C}_{\text{carb}}$ during Late Permian–Early Triassic times were larger than those that preceded or followed that interval;

the Early Triassic range of fluctuation (up to 8 to 10‰), in particular, is much larger. Carbon isotope variations reflect changes in the atmospheric and oceanic carbon cycles, and thus changes of environment on the Earth’s surface. The wide fluctuations from the Late Permian–Early Triassic interval indicate that this was a period of environmental stress. The different pattern and range of fluctuation in $\delta^{13}\text{C}_{\text{carb}}$ in Late Permian and Early Triassic times implies that environmental changes at those times resulted from different processes.

2. The multi-episode PTB mass extinction

Previous suggestion of a multi-episode PTB mass extinction (Yang et al., 1991, 1993, Tab. 1-1; Yin et al., 1996; Wignall and Hallam, 1996) was challenged by viewpoints of a sudden extinction. This latter viewpoint was at first published, based on range statistics of 362 fossils in South China, by our team-workers (Xu and Tong, 1991) together with the three-episode viewpoint in the same book (Yang et al., 1991). Rampino et al. (2000) estimated that the PTB extinction probably occurred during 10^4 yr. Based on statistics of 333 fossil species recorded at Meishan, Jin et al. (2000a) disagreed with the first episode, in bed 24e, and regarded the last episode, in bed 28, as an event tail, thus leaving only the main or middle episode, but with the start of this at the base of bed 25, rather than bed 26. They concluded that, statistically, most genera disappeared within a short interval at the base of bed 25, implying a sudden, single extinction episode. We accept the inclusion of beds 25 and 26 in the main extinction episode. Moreover, there is a growing evidence of an earlier biotic crisis (prelude of the main extinction) from sections throughout the Tethys region. We therefore maintain the multi-episode PTB extinction and present reasons in the following part of this contribution.

2.1. Multi-episode biomarker excursions

Research on both environment-related and biogenic biomarkers at Meishan provides strong evidence of multiple events at the PTB. The 2-methylhopane (2-MHP) index (a ratio of the abundance of cyanobacterial biomarkers to more general bacterial biomarkers) shows two minima, in beds 24e–25 and 27–28, (Xie et al., 2005; Fig. 3). Xie et al. (this volume) reported that environment-related biomarker ratios, including Pr/Ph (minima), $\gamma/\text{C}_{31}\text{HP}$, and Ts/Tm¹, vary in association with anoxic

¹ Pr/Ph: pristane to phytane ratios, $\gamma/\text{C}_{31}\text{HP}$: gammacerane to C_{31} homohopane ratios and Ts/Tm: C_{27} 18 α (H)-22,29,30-trinorneo-hopane to C_{27} 17 α (H)-22,29,30-trinorhopane ratios.

conditions that coincide with maximum $\delta^{13}\text{C}$ values. In particular, beds 25 and 28 have biomarker ratios consistent with anoxic conditions and elevated *n*-alkane $\delta^{13}\text{C}$ values. Fluctuations of about 9‰ in *n*-C₁₉ $\delta^{13}\text{C}$ values suggest that changes in environmental conditions and/or organic matter source inputs were episodic during the PTB extinction. Aryl isoprenoids and isorenieratane are biomarkers diagnostic of anoxygenic photosynthesis by Chlorobiaceae, and thus reflect photic-zone euxinic conditions; the former show multi-phase maxima at the PTB in beds 24, 25, 26 and 29, and the latter in beds 24, 25 and 27 (Grice et al., 2005a, Fig. 3). Many biomarkers show anomalies in beds 24, 25 and 28, but the cyanobacterial and chlorobiacean anomalies do not correspond to each other, and the 2-MHP and Pr/Ph indices may be marked by minima instead of maxima. Because the phytoplankton constitute the basis of the marine ecosystem and are sensitive to changes in environmental stress; wide fluctuations in their biogenic and environment-related biomarkers strongly suggest a multi-episode environmental deterioration and biotic crisis.

2.2. The prelude of the main extinction

The prelude in the end-Permian mass extinction has been detected in bed 24e at Meishan (Fig. 3) and its equivalents throughout the Tethys (Yin et al., submitted for publication). This stage is characterised by the extinction of a range of fauna, including corals, most fusulinids and ammonoids, deep-water radiolarians and many Permian brachiopods. Its start, 0.3 to 14 m below the PTB (Fig. 6), and 0.07 to 5.0 m below the acknowledged mass extinction at the event beds (beds 25 and 26) and their equivalents, coincides with the end-Permian sequence boundary (SB; Zhang et al., 1997) caused by a worldwide marine regression. In addition to the sea-level fall (SB) and biotic decline, there are molecular and isotopic changes that reflect environmental stress and microbial community development. Minima in the 2-MHP index detected in beds 24e–25 and 27–28 (Xie et al., 2005) reflect the response of cyanobacteria to events that caused the extinction. $\delta^{13}\text{C}_{\text{carb}}$ values decrease slowly from bed 23, and decline suddenly through a range of 2.3‰ in bed 24e. Biomarkers indicating anoxygenic photosynthesis by Chlorobiaceae also show multi-stage maxima at the PTB, including one in bed 24 (Grice et al., 2005a).

The miniaturization ('Lilliput effect') of marine invertebrates, signifying the existence of environmental stress and deterioration of habitats, is a significant feature of the prelude of the main extinction, or may

even precede that prelude. Measurements of the size of 391 individuals of the conodont *Neogondolella*, a taxon that survived the PTB crisis, show that bed 24e is also marked by the onset of a sharp reduction in average size (from 0.63–0.69 to 0.54 mm) as well as deviation to juvenile or dwarfed size (Fig. 4). Brachiopods also became dwarfed in the latest Permian. At Meishan and Zhongliangshan, 50 to 90% of the brachiopods in the highest Changhsingian limestone and the overlying clay beds are smaller than 1 cm, while in the underlying Changhsingian limestones 50% are larger than 1 cm. Similar dwarfed brachiopod faunas occur in the PTB strata in many other sections in South China (He, 2005). Gastropods, such as bellerophonitids, and inarticulate brachiopods (lingulids) also show a 'Lilliput effect' during the latest Permian–earliest Triassic interval (Xu and Grant, 1992; Pan, 2004).

Ecological change at the PTB was induced by a major change in the carbonate system and shows a prelude prior to the main extinction at the event beds. A marked reduction in the numbers of bioclasts in latest Permian rocks also marks the prelude of the main extinction. In the Balvány-North section in the Bükk Mts., Hungary (Haas et al., 2004, 2007-this issue), this first phase occurred in the topmost limestone layers below the boundary shale bed (BSB, bed 7). A reduction in bioclast content, from 40% to <20%, that occurred 3.5 m below the BSB, was accompanied by a decline in $\delta^{13}\text{C}_{\text{carb}}$, from 2‰ to near 0‰. The 1 m-thick BSB is of *praeparvus* age and correlates with the event beds (25 and 26) at Meishan. The second biotic decline coincides with the sharp $\delta^{13}\text{C}$ negative excursion in the upper part of the BSB.

In the Aligoudarz section, Central Zagros (Wang et al., 2005), the $\delta^{13}\text{C}_{\text{carb}}$ curve is comparable to that from Meishan, with a major negative excursion (regarded by them as the PTB) in the middle of the calcimicrobial cap rock (stromatolites) and an earlier negative shift in the dolostone which represents the onset of shallowing of the latest Permian limestone succession (Dalan Formation). The major excursion therefore corresponds to the event beds (25 and 26) at Meishan, while the earlier shift corresponds to the negative shift in bed 24e at Meishan.

Two extinction episodes occurred in deep-water environments below the PTB. In the Dongpan section, Guangxi, South China (Fig. 5), the prelude of the main extinction corresponds with the base of bed 6, a silty, calcareous mudstone, with an unusual yellow colour. The late Changhsingian beds 2 to 5 are dominated by radiolarites in which all four radiolarian orders (Albaillellaria, Latentifistularia, Entactinaria, Spumellaria) are represented. This interval is regarded as bathyal because abundant Albaillellaria and thin-shelled psychrophilic

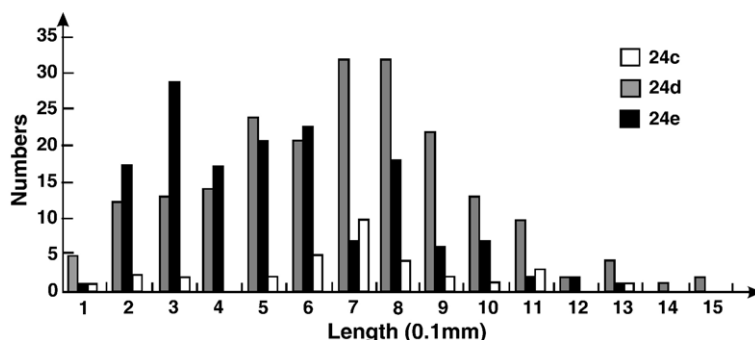


Fig. 4. Histogram showing the 'Lilliput effect' in conodonts in the prelude of the PTB extinction (bed 24e at Meishan). The statistics are based on measurements of the length of 391 complete *Neogondolella* specimens, all individuals taken at random, from beds 24c (white), d (grey), and e (black). The abscissa denotes the length of the measured specimens from 0.1 to 1.5 mm. The ordinate denotes the number of measured specimens in each length category. In contrast to the normal distribution (0.7 to 0.8 mm) in beds 24c and 24d, the distribution curve from bed 24e shows remarkable deviation toward small size (0.3 mm), representing a dominance by dwarfed or juvenile forms.

is not necessarily synchronous everywhere, because it reflects the onset of environmental deterioration and biotic decline which may be diachronous. Even at Meishan, brachiopod miniaturization and the reduction of $\delta^{13}\text{C}$ values began below bed 24e, in beds 23 and 24. Nevertheless, there should be independent indications of the prelude because deep-water radiolarians and shallow water microbials, the basic elements in the ecosystems at Donpan and Meishan respectively, experienced extinction or profound change. Shallow water microbial taxa were not recorded at Meishan and therefore were not included in previous statistics (e.g. Jin et al., 2000a,b). According to the rate of sedimentation calculated by Jin et al. (2000b), the prelude predates a postulated bolide impact (bed 25) by ca. 50,000 yr and therefore provides an important constraint on the pattern and mechanism of the end-Permian mass extinction.

2.3. The main extinction episode

The main episode in the extinction is represented by the 'event beds' (25 and 26) at Meishan, and their equivalents, and has been extensively reported and discussed. It is reflected in the most significant biotic extinctions (Yang et al., 1987, 1993; Jin et al., 2000a, b), $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{13}\text{C}_{\text{org}}$ negative excursions (Baud et al., 1989; Cao et al., 2002), superanoxia (Wignall et al., 1996; Grice et al., 2005a), the *Reduviasporonites* (algae or fungi) spike (Visscher et al., 1996), methane release (Bernier, 2002), microsphaerules (Yin et al., 1992), fullerenes with 'extraterrestrial' ^3He ratios (Becker et al., 2001), Fe–Ni–Si particles of 'meteoritic' origin (Basu et al., 2003), gigantic sulphur release (Kaiho et al., 2001), and a possible bolide impact (Becker et al., 2004). Amongst these, advances in the

study of molecular biomarkers around the PTB extinction are noteworthy. A sudden increase in C_{33} *n*-alkylcyclohexane has been proposed as a biomarker for the PTB (Grice et al., 2005b). Xie et al. (2007-this issue) show that the Changhsingian at Meishan is characterised by less variable and smaller ($\sim 0.5\%$) carbon isotope offsets between C_{19} and C_{21} *n*-alkanes ($\Delta^{13}\text{C}_{19-21}$), generally high Pr/Ph ratios, low $\gamma/\text{C}_{31}\text{HP}$ indices, and low Ts/Tm ratios. In contrast, the Induan is characterised by more variable and larger ($\sim 2\%$) carbon isotope offsets between C_{19} and C_{21} *n*-alkanes ($\Delta^{13}\text{C}_{19-21}$), generally low Pr/Ph ratios, high $\gamma/\text{C}_{31}\text{HP}$ indices, and high but variable Ts/Tm ratios. These features suggest that major changes in input from organisms, or in sedimentary conditions, occurred during and after the PTB mass extinction.

The main PTB extinction is coincident with an abrupt shift from a skeletal carbonate factory to a calcimicrobial carbonate factory in the latest Permian. At the Bulla section in southern Alps (Farabegoli and Perri, 1998) and the Curuck Dagh section in SW Turkey (Baud et al., 2005b), this shift occurs in two steps: the first step was an abrupt change from late Changhsingian skeletal wackestone–packstone to oolitic packstone–grainstone (= beds 7–12 of lower Tesero Member, Farabegoli and Perri, 1998), and the second from ooids to a calcimicrobial cap rock. In southern Alps as in South China, the calcimicrobial rock yields *Hindeodus parvus* (bed 12b of lower Tesero Member) and is thus earliest Triassic. The underlying ooids between Changhsingian limestone and the *parvus* zone thus corresponds to the event beds of Meishan. The main extinction occurred around the base of oolitic member just as around the base of bed 25 in Meishan.

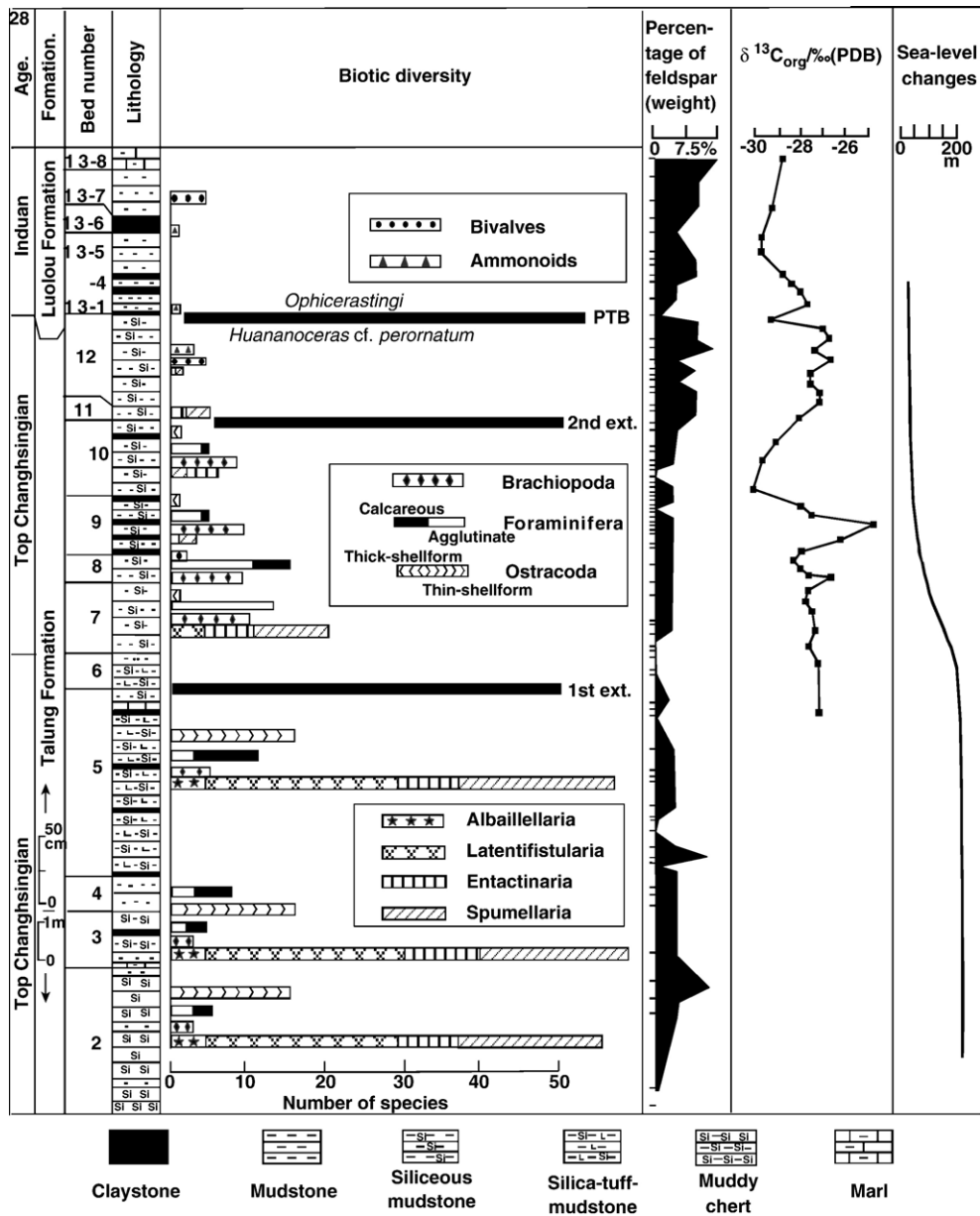


Fig. 5. PTB strata in the Dongpan section, showing fossil distribution and two episodes of extinction. Captions of different organic taxa are shown in the three rectangular frames under 'Biotic diversity'. The numbers of species of each taxon are expressed by the length of the bar (compare the scale at the bottom of that column). The two episodes of extinction and the PTB are in coarse black bars. Horizontal bars in the 'Percentage of feldspar' column represent sampling horizons.

2.4. The epilogue episode

Recent studies have confirmed the existence of a second episode in the PTB extinction, between beds 27 and 28 (Early Triassic) at Meishan (Yang et al., 1991, 1993; Yin et al., 1996). Fang (2004) claimed that the extinction occurred in two episodes; the main episode represented by beds 25 and 26 and a second by the base

of bed 28. He indicated that extinction of ammonoids of the *Hypophiceras* faunule, Permian relict bivalves, and relicts of the *Gigantopteris* flora, occurred in the second episode—the base of bed 28. Wu (2005) proposed two episodes of conodont extinction at the base of bed 27 (*Clarkina*-dominated fauna replaced by *Hindeodus*-dominated fauna) and the base of bed 28 (disappearance of most *Hindeodus* components of bed 27) respectively.

Statistics of brachiopods (Chen, 2005) indicate three survival phases, at the bases of beds 25, 27 and 28 (Table 2); the second highest proportional extinction rate of species (80.5%), at the base of the *isarcica* zone, corresponds with our epilogue episode and included the extinction of most miniaturized brachiopod relicts. It is clear, therefore, that the epilogue episode, at the base of bed 28 or its equivalents, affected many groups and should be regarded as an independent event. In general this episode eliminated the Permian relicts that survived the main episode, thus is the epilogue of the PTB extinction.

We conclude that the PTB extinction comprised two episodes and was caused mainly by endogenic changes on the Earth and the interactive co-evolution of the biota. We refer to it as the PTB extinction, rather than the end-Permian extinction, because it extended into the earliest Triassic. The possibility of an extraterrestrial impact at the event beds (Becker et al., 2004) as the mechanism which inducing catastrophic environmental changes is not excluded, but the evidence is considered equivocal. If such an event occurred, its effects should not be over-estimated in the context of a prolonged crisis and a prelude extinction that preceded it.

3. Effects of Pangean integration on the Permo-Triassic environmental and biotic revolution

The pattern of mass extinction is related to its causes. The protracted and multi-episode pattern of the PTB extinction necessitates long-term factors generated by the intrinsic evolution of the Earth and its biota rather than extraterrestrial causes. Fig. 1, inspired by Erwin (1993) but more expanded, shows the synchronous changes in the interior geosphere, the Earth's surface system and the biosphere. It seems unlikely that such synchronicity is a mere coincidence; certain interactions among the Earth's spheres should have existed to generate these synchronous changes. The formation of Pangea, which reached its acme during the Late Permian and Early Triassic, was a turning point in geological history. Links between the PTB extinction and Pangea integration, including causal relations with regression, methane release and anoxia have been discussed by Erwin (1993), Sweet et al. (1992), and many others. Additional evidence of such links, based on recent research, is presented below.

3.1. The greatest Phanerozoic regression

The relationship between the end-Guadalupian regression, resulting from the integration of Pangea, and mass extinction has been noted by Jin et al. (1994)

and Stanley and Yang (1994). This regression was worldwide, but its effects are particularly marked in the Boreal region, where shelf areas were almost exposed, while sedimentation continued in basins. Lack of biostratigraphically significant fossils impedes correlation in this region. In the Tethyan region this regression was also widespread, but was followed by a Wuchiapingian–Changhsingian transgression. A widespread regression occurred in the late Changhsingian and, with the earlier regression in the Boreal region, comprised one of the most significant regressive episodes in the Phanerozoic (Erwin, 1993); this was followed by a rapid transgression at the PTB.

The end-Permian regression and PTB transgression at Meishan, South China, is reflected in its sequence stratigraphy (Yin et al., 1996; Zhang et al., 1997). A sequence boundary (SB) of Type 2² is placed at the base of bed 24e, the lithology of which indicates sudden shallowing, and in which environment-related biomarkers show stress buildup; additionally, conodonts and brachiopods exhibit dwarfism and there is an anomalous decline of cyanobacteria. The shelf margin system tract (SMST) at Meishan is very thin (0.3 m) because the section is condensed. It yields a mixed, but impoverished, fauna including dwarfed brachiopods, relict pseudotirrolitids and fusulinids, Permian conodonts and molluscs of Triassic aspect, such as otoceratid ammonoids and *Claraia*-like bivalves. This fauna becomes extinct at the bed 26–27 boundary. A transgressive surface (TS) occurs at the base of limestone bed 27, which overlies clayrocks of beds 25 and 26; the cosmopolitan conodont *H. parvus* appears 8 cm above the TS.

This SB is widespread in South China. The end-Permian SMST is usually 0.3 to 3.7 m thick, is separated from the underlying Changxing or Dalong Formation by a Type 2 SB, and is distinguished by a significant increase in clastics and a decrease in the calcareous and siliceous components (Wang et al., 2003). Mass extinction has also been found to occur at this SB (Yang et al., 1993). In the Liangfengya section, 1100 km west to the GSSP, the SMST is 0.52 m thick; fusulinids, corals and pseudotirrolitid ammonoids disappear, and non-fusulinid foraminifera and brachiopods decrease in abundance at the SB at the base of bed 41 (Yin et al., submitted for publication).

Fang (2004) argued against the late Changhsingian regression. Using the transverse section in Meishan area of Wu et al. (1986), he claimed that the transgression began since middle–late Changhsingian and reached an

² Type 1 SB: sequence boundary with disconformity, followed by lowstand system tract; Type 2 SB: sequence boundary with paraconformity, followed by shelf margin system tract.

acme at the base of event bed 25. In fact, in the transverse section Wu et al. (1986) only indicated the middle–late Changhsingian transgression, but later Wu (1993) stressed that it was followed by late Changhsingian regression and end-Changhsingian transgression. At the Meishan section, the deepest lithofacies (turbidites) is located at beds 11–12 of lower–middle Changxing Fm (Zhang et al., 1997), and the deepest biofacies (radiolarians) is also located at beds 11–12 (He et al., 2005). The upper part of Upper Changxing Fm is gradually shallowing toward the SB at bed 24e, and there is no continuous transgression up to event beds at Meishan as claimed by Fang (2004). Besides, Fang's (2004) correlation with the other parts of the world is inconsistent with the following facts.

In many sections of shallow water deposits throughout the world the SB, the ebb point of end-Permian sea-level fall, does not correspond with the marine PTB but is slightly below that level which lies above the TS, as at Meishan (Fig. 6). The SB may be of different duration at different sites, but there should be at least partial synchronicity. In the Tethys region, it is either continuous, with slight hiatus (paraconformity), or a disconformity. In the Guryul ravine, Kashmir, the inferred SB should be drawn between limestone member D of the Zewan Formation and shale member E1 of the Kuhnamuh Formation. The former contains Permian-type brachiopods, gastropods, bivalves and foraminifers, whereas the latter has a mixed Permian–Triassic fauna characterised by dwarfed brachiopods (Nakazawa et al., 1975). At the Narmia section, Salt Range, Pakistan (Pakistani–Japanese Research Group, 1985), the SB is a disconformity between a 0.3 and 5.0 m white sandstone (ss in Fig. 6) atop the limestone Unit 4 of the Chhidru Formation, with *Cyclolobus*, and the overlying dolostone of the lower Kathwai Member of the Mianwali Formation. The PTB, at the FAD of *H. parvus*, lies 1.6 m above the SB, at the base of the middle Kathwai Member. In the lower Kathwai Member there is a reduction in the numbers of small, dwarfed (?) brachiopods of Permian type, and of foraminifera and

bellerophontids, though a few survived just into the *parvus* zone. In the Selong section, south Tibet, the SB is a disconformity between the Caliche Bed of the Selong Formation and the overlying *Waagenites* Bed of the Kangshare Formation. Abundant tabulate and rugose corals occur in the Coral Bed directly below the Caliche Bed. The *Waagenites* Bed contains Permian conodonts and small brachiopods (Jin et al., 1996). In the Hambast C section, Abadeh, central Iran, the SB is a paraconformity or disconformity (Iranian–Japanese Research Group, 1981; Golshani et al., 1986) between limestone Unit 7 of the Hambast Formation and the basal shale (0.6 m) of the overlying Elikah Formation; the *hauschkei* zone, the uppermost zone recorded from the Hambast Formation, is absent in the easternmost section at Abadeh (Korte et al., 2004a). This SB in Abadeh marks the final disappearance of Permian pseudotirolitids (*Paratirolites*, *Iranites*). The succession, consisting of a basal shale in which initial biotic decline is evident, microbialitic bed 1, and bed 2 with the FAD of *H. parvus*, resembles that of beds 25 to 27 at Meishan and is a transgressive sequence. In the Ali Bashi section, NW Iran, the SB is between the limestone *Paratirolites* beds of the Ali Bashi Formation and the overlying bed 21 or *Marnes rouges* (Altiner et al., 1980), a 1.0 m-thick unit of shale and marl. The first occurrence of *H. parvus* is in the upper part of bed 22, a 2.8 m-thick limestone (Teichert et al., 1973). Pseudotirolitids have not been found in or above the *M. rouges*. In the Dorasham II-3 section, Transcaucasia, the SB occurs between limestone and marl (beds 1–4), with *Pleuronodoceras* and *Paratirolites*, and red argillite and marl (beds 5 to 13a), with latest Permian conodonts and bellerophontids that become extinct 1.6 m higher, at the PTB (Zakharov, 1992). In the Bulla section, in the Western Dolomites, southern Alps, Italy, the disconformity at the base of Bulla Member of the Bellerophon Formation (Farabegoli and Perri, 1998) should represent the SB. At Tesero section, the overlying lower Tesero Member of the Mazzin Formation yields a 'mixed fauna' with relict brachiopods—the *Ombonia*–?*Crurithyrus* Assemblage

Table 2
The three survival phases of brachiopods at the PTB (modified from Chen, 2005)

Episodes	Conodont zone	Corresp. Meishan bed no.	Number of taxa			Proportional extinction rate (%)			Origination rate (%)		
			Sp	Gen	Fam	Sp	Gen	Fam	Sp	Gen	Fam
3	<i>isarcica</i>	28–	15	8	7	80.5	63.2	55.5	40	0	0
2	<i>parvus</i>	27 (c,d)	41	19	11	57.7	52.5	56.0	19.5	0	0
1	<i>meishanensis</i>	25–26	78	40	25	91.2	72.8	50.0	52.5	0	0
Pre-ext		–24	420	143	50						

Pre-ext: pre-extinction; Corresp: corresponding; Sp: species; Gen: genera; Fam: families.

Period	Stage	Fossil beds	Sequence stratigr.	Meishan, SE. China	Guryul Ravine, Kashmir	Naimia, Salt Range, Pakistan	Selong, S. Tibet	Hambast C, C. Iran	AliBashi, NW. Iran	Dorasham, Transcaucasia	Bulla, Italy	Otto Fiord, Canada
Triassic	Induan	<i>Hindeodus parvus</i>		Bed 27c (ls) Hp	Kuhnamub E ₂ Bed 56–59 (sh) Hp	M Kathwai (ls) Hp	<i>Otoceras</i> Bed 10 (ls) Hp	Elikah Bed 2 (ls) Hp	U Bed 22a (ls) Hp ²	<i>Claraia</i> Beds 13b–22 (sh+m) Hp	Maggin Bu 12b (ls) Hp	U boreale Bed (csi) Hp
Permian	Latest Changhsingian	<i>Hindeodus typicalis</i> interval	TST	Bed 27ab (ls) Ht TS	E ₂ Bed 55 (sh) Ht		Bed 9 (ls)	Bed 1 (ls) TS	L Bed 22a (ls) TS		Bu 12a (ls) TS	L boreale Bed (si) TS
		<i>Hindeodus praeparvus</i> - <i>Clarkina meishanensis</i>	TS	Event Beds 25, 26 (c) Pc Pbd	E ₂ Beds 52–54 (sh) Pbd	L Kathwai (ls+ss) Pbd	<i>Waagenites</i> Bed 8 (ls) Pbd	Bed 0 (sh)	Bed 21 (sh)	Bed 5–13a (c+m) Pc	L Tesero (oolite+sh) Pbd	Concavum Bed (sh+si) Pc
		<i>Clarkina yini</i> - <i>C. Zhangi</i>	SMST	Bed 24e (ls) Pc Pbd 2	Kuhnamuh E ₁ (sh) Pbd 2	2	2	2	2	2	2	2
	Changhsingian or earlier		SB	Beds 4–24d (ls) Pt Pc Fu	Zewan D (ls) Pb	(ss) Chhidru 4 (ls) <i>Cyclobus</i>	(caliche) Selong (ls) Pb Corals	Hambast 7 (ls) Pt	Ali Bashi (ls) Pt	<i>Pleuronodoceras</i> Zone (m+ls) Pt Pc	Bulla Mb, Bellerophon (ls) Pb Fu	Degerbols (chert+ls)
Distance from SB to PTB (m)				0.30	5.0	1.6	0.07	0.3±	1.0	1.6	0.8	14
Distance between 2-events from SB to TS (m)				0.38	6.0	1.6	0.17	0.9±	2.5	1.6	1.2	30

Fig. 6. Correlation of sequence stratigraphy in the PTB interval. For reference to the sections in this figure please refer to the discussions in Section 3.1. *Fu* — Fusulinids; *Hp* — *Hindeodus parvus*; *Ht* — only *Hindeodus typicalis*; *Pb* — Permian brachiopods (un-dwarfed): *Comelicania*; *Pbd* — Permian brachiopods (usually dwarfed or derived, as at Guryul Ravine): *Crurithyrus*, *Waagenites*, *Spinomarginifera*, *Araxothyrus*, *Neowellerella*, *Wellerella*; *Pc* — Permian conodonts: *Clarkina changhsingensis*, *C. deflecta*, *C. subcarinata*, *C. meishanensis*, *Hindeodus latidentatus*; *Pt* — Pseudotiroplitids: *Pseudotiroplites*, *Pleuronodoceras*, *Rotodiscoceras*; LST — lowstand systems tract; SB — sequence boundary: 1 — SB Type 1; 2 — SB Type 2; TS — transgressive surface; SMST — shelf margin system tract; c — claybed; ls — limestone; m — micrite or marl; sh — shale; si — siltstone; ss — sandstone; L — lower; M — middle; U — upper.

(Broglia-Loriga et al., 1988). The FAD of *parvus* at Bulla lies within lower Tesero Member, 1.3 m above the Tesero/Bellerophon boundary.

Correlation of these well-known sections shows that throughout Tethys there is a latest Permian sequence boundary (SB) marked by para- or disconformity and an abrupt lithologic shift that results in a change in formation names. A thin (0.3 to 5.0 m) shelf margin system tract (SMST) above the SB is topped by a transgressive surface (TS); the PTB, at the FAD of *H. parvus*, is generally several centimetres to a few metres above the TS. The SB represents the first end-Permian extinction event, with extinctions of corals, most fusulinids, most pseudotiroplitid ammonoids, and the majority of un-dwarfed Permian brachiopods. In South China (including Meishan), and in the Guryul ravine and Tesero sections, the overlying SMST contains a ‘mixed fauna’ of small (dwarfed) or reworked Permian brachiopods, molluscs, including otoceratids and some bivalves, of Triassic aspect, and relict fusulinids and pseudotiroplitid ammonoids; Permian conodonts extend

to this level. The TS represents the main extinction episode where the mixed fauna of the SMST became extinct; at Meishan this corresponds with the event beds. In many sections, only the Permian *Hindeodus typicalis* persisted after the transgression, to be followed, slightly higher, by the first Triassic marker, *H. parvus*.

In the Boreal region the regression occurred much earlier. The succession in the Otto Fiord section, Arctic Canada (Veevers and Tewari, 1995), comprises, in ascending order:

- the HST of the previous sequence — early Wuchiapingian (early Late Permian) chert or limestone
- Type 1 SB represented by a conspicuous disconformity
- LST — latest Changhsingian shale and siltstone with Permian conodonts and the ammonoid *Otoceras concavum*, overlain by claystone representing the TS (Henderson and Baud, 1997 called this TS a maximum flooding surface)
- TST — earliest Triassic siltstone — *Otoceras boreale* bed; the FAD of *H. parvus* occurs 10 m above the TS.

This sequence correlates well with those in the Tethys (Fig. 6), except that the pre-SB strata are older, and the SB is of Type 1 and followed by a much thicker LST. Similar situations occur in Greenland (*Hypophiceras* Bed/Földvik Creek Formation, Teichert et al., 1976) and Siberia (*Otoceras* Bed/Imtchan Formation, Dagsy et al., 1979). In the Boreal region this disconformity coincides with the final occurrences of many Permian taxa and a biotic change so remarkable that, prior to 1993, this level was regarded as the PTB (Yin et al., 2001). However, the disappearance of Permian taxa at this level occurred in the early Lopingian, (see Section 1.1), and is not, therefore, comparable with the first extinction episode in the Tethys region.

Yin and Tong (1995, 2000) stated that most SBs are stratigraphically lower than the related chronostratigraphic boundaries; the intervening succession usually comprises the SMST or LST of the next sequence. This is because the chronostratigraphic boundary is usually placed at the appearance of new biota, typically in association with a new transgression (i.e. immediately above the TS). Conversely, a SB is produced during the fall of sea level from a highstand systems tract (HST) and is, therefore, at the base of an SMST or LST; the older biota flourished during a HST, but declined during the next SMST or LST, because of a reduction of ecologic niches and habitats, and finally became extinct below the next TS, which introduced new biota. Theoretically, therefore, there should be two extinction events during the biotic turnover. The first, comprising a reduction in the numbers of the older biota, corresponding with the SB, and a later one, with the extinction of the older biota, corresponding with the TS (Fig. 7). This is exactly the situation in the case of the end-Permian extinction.

3.2. Link between Late Permian volcanism and mass extinction

Temporal links between the Emeishan Basalt and Siberian Traps, and the end-Guadalupian and end-Permian mass extinctions (Fig. 1), have been reported (Renne et al., 1995; Zhou et al., 2002), and the possible causal relationships discussed (Wignall, 2001; Racki, 2003). Volcanics around the PTB time were widespread along the western Panthalassa margin, in Primorye (Vrzhosek, 1997), South China (Yin et al., 1992) and Gondwanaland (Veevers and Tewari, 1995), which are mostly acidic to intermediate, sometimes bimodal, and may therefore be linked with convergent plate tectonics or rifting, rather than with the Siberian Traps. Little is known about the original extent of these volcanics

because most should have been subducted at what is now the Pacific margin. Several beds with volcanoclastics occur around the PTB; the first volcanogenic claybed in South China is a few metres below that level, covered more than 1 million km² in South China alone, and may also exist elsewhere in the Tethys region (Yin et al., 1992). Both the continental basaltic Siberian Traps and the acidic to intermediate volcanism were contemporary with the PTB mass extinction. The peak of acidic to intermediate volcanism, which usually produces huge volumes of gas, corresponded with the main episode of mass extinction (beds 25 and 26); eruptions occurred in areas with thick limestone deposits and could, therefore, have resulted in the production of considerable amounts of CH₄ and CO₂ (Racki, 2003). Therefore, in addition to that of the Siberian Traps, the effect of this volcanism should not be overlooked when considering the contribution of volcanism to the PTB mass extinction. Both the continental basalt eruptions (mantle plume?) and continent margin acidic to intermediate (island arc?) volcanics may have been connected with the integration and rifting of Pangea. This is another aspect of Pangea's influence on Permo-Triassic mass extinction.

The Permo-Triassic Mixed Superchron (PTMS), from the late Wordian (or Early Capitanian) Illawara Reversal to the early Anisian, represented a long period with frequent alternation between normal and reversal polarity (Menning, 1995), and coincides with the period of biotic crisis in the Late Permian and Early Triassic. The possibility of causal links between palaeomagnetic disturbance and biotic crisis (Hays, 1971) should not be overlooked and, if valid, may reinforce the relationship between the history of Pangea and mass extinction. The formation of Pangea and Panthalassa reflected changes

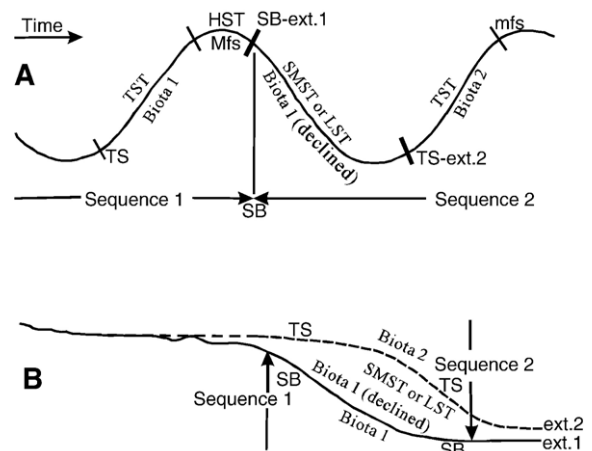


Fig. 7. Two extinctions in relation to the SB and the succeeding TS.

in geoid, mantle convection, and even a shift of the core, which would have induced changes in the frequency of geomagnetic reversal (Vogt, 1975). Causal links between remote causes (Pangea assembly and linked sea-level change, volcanism and palaeomagnetic disturbance) and direct causes (methane release, anoxia and related stratification of seawater) have been comprehensively discussed (Erwin, 1993). Other changes induced by the integration of Pangea, such as the eastward progress of arid conditions and the absence of coal-forming conditions in the Early Triassic, need to be investigated. A scenario for these causal links is presented in Fig. 1.

4. Conclusions

1. The Permo-Triassic mass extinction consists of two phases, the end-Guadalupian and the PTB. Its recovery lasted the entire Early Triassic. $\delta^{13}\text{C}_{\text{carb}}$ perturbations occurred from the late Wuchiapingian to the end of the Early Triassic and were also multi-phase. The protracted Late Permian–Early Triassic crisis, lasting 15 Myr, was a period of great change.
2. The PTB mass extinction took place in two episodes, the main episode and the epilogue. The prelude of the main episode commenced prior to the event beds (beds 25 and 26) at Meishan and coincided with the ebb of the end-Permian regression. The main episode is the publicly recognized main extinction (beds 25–26). The second episode occurred in the late Greisbachian and coincided with the second volcanogenic layer (bed 28) at Meishan. The temporal distribution of these episodes constrains interpretation of the causes of this greatest Phanerozoic mass extinction and in particular, the role of a postulated bolide impact that occurred about 50,000 Myr after the start of the first episode.
3. The prolonged and multi-phase pattern of the Permo-Triassic crisis favours mechanisms connected with the Earth's intrinsic evolution which can evoke long-term effects. The integration of Pangea may have been linked with the greatest Phanerozoic regression, the PTMS palaeomagnetic disturbance, widespread extensive volcanism, and the transformation of the geoid through geosphere interactions at depth. These processes may, in combination, have induced the profound changes in marine, terrestrial and atmospheric environments that are manifested in the Permian–Triassic mass extinction. A bolide impact is possible, but is neither adequate nor necessary to explain these changes; if one occurred it only triggered a latent crisis that had been developing for some time, and which would have climaxed sooner or later, regardless of an impact event.

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