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Complete biotic and sedimentary records of the Permian-Triassic transition from Meishan section, South China: ecologically assessing mass extinction and its aftermath

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The Meishan section, South China is the Global Stratotype Section and Point (GSSP) for the Permian-Triassic boundary (PTB), and also is well known for the best record demonstrating the Permian-Triassic mass extinction (PTME) all over the world. This section has also been studied using multidisciplinary approaches to reveal the possible causes for the greatest Phanerzoic biocrisis of life on Earth; many important scenarios interpreting the great dying have been proposed on the basis of data from Meishan. Nevertheless, debates on biotic extinction patterns and possible killers still continue. This paper reviews all fossil and sedimentary records from the Permo-Triassic (P-Tr) transition, based on previously published data and our newly obtained data from Meishan, and assesses ecologically the PTME and its aftermath to determine the biotic response to climatic and environmental extremes associated with the biocrisis. Eight updated conodont zones: *C. yini*, *C. meishanensis*, *H. changxingensis*, *C. taylorae*, *H. parvus*, *I. staeschei*, *I. isarcica*, and *C. planate* Zones are proposed for the PTB beds at Meishan.
Major turnover in fossil fragment contents and ichnodiversity occurs across the boundary between Bed 24e-5 and Bed 24e-6, suggesting an extinction horizon in thin section. The irregular surface in the middle of Bed 27 is re-interpreted as a firmground of *Glossifungites* ichnofacies rather than the previously proposed submarine dissolution surface or hardground surface. Both fossil fragment contents and ichnodiversity underwent dramatic declines in Beds 25–26a, coinciding with metazoan mass extinction. Fossil fragment content, ichnodiversity and all ichnofabric proxies (including burrow size, tiering level, bioturbation level) indicate that the P-Tr ecologic crisis comprises two discrete stages, coinciding with the first and second phases of the PTME in Meishan. Ecologic crisis lagged behind biodiversity decline during the PTME. Pyrite framboid size variations suggest that depositional redox condition was anoxic to euxinic in the latest Changhsingian, became euxinic in Beds 25–26a, turned dysoxic in Bed 27, then varied from euxinic to anoxic through most of the Griesbachian. The ~9 °C increase in seawater surface temperature from Bed 24e to Bed 27 at Meishan seems to result in dramatic declines in biodiversity and fossil fragment contents in Beds 25–26a, but had little effect on all ecologic proxies. Both metazoans and infauna seem not to be affected by the pre-extinction anoxic-euxinic condition. The anoxic event associated with the PTME
may have occurred in a much shorter period than previously thought and is only recorded in Beds 25–26a at Meishan. Fossil fragment contents, ichnofaunas, ichnofabrics and pyrite framboid size all show that no signs of oceanic acidification and anoxia existed in Bed 27. The early Griesbachian anoxia may have resulted in rarity of ichnofauna and metazoans in the lower Yinkeng Formation, in which the ichnofauna is characterized by small, simple horizontal burrows of *Planolites*, and metazoan faunas are characterized by low diversity, high abundance, opportunist-dominated communities. The rapid increase of ~9 °C in sea-surface temperature and a short anoxia or acidification coincided with the first-pulse biocrisis, while a prolonged and widespread anoxia probably due to a long period of high seawater temperate condition may be crucial in mortality of most organisms in the second-pulse PTME. Marine ecosystems started to recover, coupled with environmental amelioration, in the late Griesbachian.

*Keywords: mass extinction, Permian-Triassic, fossil fragment, trace fossils, redox condition, Meishan section*
1. Introduction

2. Biochronostratigraphy: an update
   2.1. Biostratigraphy and correlations
   2.2. Geochronology
   2.3. Duration of key conodont zones across the P-Tr boundary

3. Microstratigraphy, fossil fragment contents and paleoenvironmental analysis of the
   P-Tr transition
   3.1. Bed 23
   3.2. Bed 24
   3.3. Bed 25
   3.4. Bed 26
   3.5. Bed 27
   3.6. Bed 28
   3.7. Beds 29-59

4. Biotic changeover through the P-Tr transition
   4.1. Biodiversity variations over the P-Tr transition
4.2. Fossil fragment content variations through the P-Tr transition

4.3. Community structural changes of shelly faunas

5. Trace fossils and bioturbation

5.1. P-Tr ichnotaxa and their stratigraphic distributions at Meishan

5.1.1. Stratigraphic distributions of ichnoassemblages

5.1.2. Ichnofabric changes within Bed 27

5.2. Extent of bioturbation

5.3. Changeover of trace-fossil diversity over the P-Tr transition

5.4. Burrow size variations through the P-Tr transition

5.5. Trace fossil form and complexity

5.6. Infaunal tiering

6. Size variations of pyrite framboinds and redox conditions over the P-Tr transition

7. Assessing ecologically PTME and its aftermath

7.1. Testing extinction patterns

7.2. Ecologic crisis lagging behind biodiversity drop at the PTME

7.3. Dramatic increase in seawater temperature and its consequences

7.4. Anoxic events and biotic response
7.4.1. Anoxic events

7.4.2. Biotic response

7.5. Testing extinction mechanisms

7.6. Post-extinction amelioration of marine ecosystems in late Griesbachian

8. Conclusions
1. **Introduction**

As the greatest biocrisis of life on Earth (Sepkoski, 1981), the Permian-Triassic mass extinction (PTME) changed Earth’s ecosystems fundamentally (Benton and Twitchett, 2003; Erwin, 2006). After they had recovered, the marine ecosystems after the PTME gave rise to the forerunners of modern-day ecosystems, both the Triassic and modern ecosystems being comparable to each other in composition of functioning groups and trophic structure (Chen and Benton, 2012). However, the causes of this enigmatic biocrisis have long been disputed despite intense study, and the same is true of the profoundly delayed recovery following the PTME (Erwin, 2001). Thus, studies of these issues have enjoyed a surge in scientific interest in the past 30 years that shows no sign of abating (Chen et al., 2014a).

Although this era-boundary crisis has been widely recognized in Permian–Triassic boundary (PTB) sections around the world, many important hypotheses have been proposed based on paleontological and experimental data sampled from the Meishan section of Changhsing County, Zhejiang Province, east China (Fig. 1A; Renne et al., 1995; Bowring et al., 1998; Jin et al., 2000; Yin et al., 2001, 2012; Kaiho et
al., 2001, 2006a, b; Mundil et al., 2001, 2004; Grice et al., 2005; Xie et al., 2005, 2007; Riccardi et al., 2007; Wang and Visscher, 2007; Cao et al., 2009; Chen et al., 2009, 2010a; Song et al., 2009, 2013a, b; Shen et al., 2011b; Huang et al., 2011; Wu et al., 2013; Wang et al., 2014; Burgess et al., 2014; Fig. 1A). This section is the Global Stratotype Section and Point (GSSP) for the PTB (Yin et al., 2001; Fig. 1C) and also well known for the best record of both biotic and geochemical signals demonstrating the PTME all over the world. Here, the exposures of the PTB beds are spectacular, extending about 2 km laterally along the Meishan hill (Fig. 1E). The PTME has been well demonstrated by Jin et al. (2000), whose study based on paleontological data from Meishan reveals that this extinction event was abrupt and dramatic, with most Permian organisms being wiped out within a very short interval, which was precisely calibrated to the base of Bed 25, a white clay bed, in Meishan (Fig. 1B, D), while the PTB is placed at the middle of Bed 27, about 16-20 cm above the base of Bed 25 in the same section (Yin et al., 2001; Fig. 1C). As such, the biocrisis clearly pre-dated the PTB (Fig. 1D). The P-Tr ecologic crisis is also marked by a pronounced negative carbon isotopic excursion (Xu and Yan, 1993; Jin et al., 2000; Kaiho et al., 2001; Cao et al., 2002; Xie et al., 2005, 2007; Fig. 2) and is also associated with an end-Permian sulfur event (Kaiho et al., 2006; Riccardi et al., 2006).
After Jin et al.‘s (2000) influential study, which was largely based on fossil data obtained in 1980s (i.e., Zhao et al., 1981; Sheng et al., 1984; Liao, 1984; Sheng et al., 1987; Shi and Wang, 1987), abundant brachiopod and foraminifer faunas have been detected from Beds 25–27, immediately above the PTME horizon in Meishan (Chen et al., 2005a, 2006b; Song et al., 2007, 2009). Quantitative analysis of the updated foraminifer data from Meishan revealed a two-stage extinction pattern near the P-Tr boundary (Song et al., 2009), which agrees well with two distinct peaks of cyanobacteria, detected by biomarker analysis from the same section, suggesting two extinction events corresponding to Beds 25 and 28 (Xie et al., 2005). The two-stage extinction pattern is also strengthened by extremely abundant benthic fossils obtained from a shallow platform facies of the PTB section at Huangzhishan, about 40 km from Meishan (Chen et al., 2009). However, Shen et al. (2011b) clarified an abrupt biotic decline in a short interval equivalent to Beds 25-28 of Meishan based on quantitative analysis of fossil records from Meishan and other PTB sections in South China. In contrast, Song et al. (2013a) demonstrated nicely a two-stage extinction pattern for the P-Tr crisis based on quantitative analysis of paleontological data derived from Meishan and a further six PTB sections in South China. Thus, debate on whether the PTME was either a single crisis or
episodic extinctions still continues (Shen et al., 2011b; Song et al., 2013a; Wang et al., 2014). Regardless of whether the extinction was single or a two-phase pattern, an increasing number of faunas have been found in Beds 25-28 of Meishan and its counterparts across all of South China, although this interval may just last 60 kyr (Burgess et al., 2014).

In addition, a further extinction event resulting in depletion of Permian reefs in South China was calibrated to the base of Bed 24e at Meishan (Yang et al., 1993). Yin et al. (2007) re-documented biotic and geochemical signal changes across this horizon, which is reinforced by several lines of evidence, including reduction in conodont sizes (Luo et al., 2006), possible extinction of radiolarians in deep habitats and a negative shift in organic carbon isotope values (Cao et al., 2009). To sum up, biotic variations based on sound paleontology over the P-Tr transition have been far less studied in comparison with the intense geochemical studies of this catastrophe in most PTB sections. Current, updated fossil records from extensive PTB sections are crucial to reveal the true biotic responses to these environmental crises.

As briefly summarized above, there have been great advances in research on the PTME at Meishan in recent years. Multiple scenarios interpreting the causes of the P-Tr
biocrisis have been proposed based on experimental data sampled from this section. Nevertheless, any reasonable models interpreting the P-Tr crisis need to be tested by analysis of precise biotic extinction patterns and physiological reactions of victims and survivors (Knoll et al., 2007). As a result, we herein document the updated, complete fossil and sedimentary records, including microfacies, microfossils, body and trace fossils, and pyrite frambooids, throughout the P-Tr transition and attempt to test biotic responses to various environmental and climatic catastrophes from the GSSP Meishan.

2. Biochronostratigraphy: an update

2.1. Biostratigraphy and correlations

After Yin et al.’s (2001) placement of the PTB at the base of Bed 27c, marked by the first appearance datum (FAD) of the conodont *Hindeodus parvus*, Jiang et al. (2007) established gondolellid and hindeodid conodont zones across the PTB in Meishan. The former include the *Clarkina yini, C. meishanensis* and *C. taylorae* Zones, while the latter comprise the *Hindeodus latidentatus, H. praeparvus, H. changxingensis, H. parvus,*
Isarcicella staeschei, and I. isarcica Zones (Jiang et al., 2007, fig. 2). Later, Zhang et al. (2009) integrated them as one conodont zonation series: C. yini Zone (Bed 24), C. meishanensis Zone (Bed 25), H. changxingensis Zone (Beds 26-27b), H. parvus Zone (Bed 27c), I. staechei Zone (Beds 27d-28), I. isarcica Zone (Beds 29-51), and C. tulongensis-C. planata Zone (Beds 52-72, top of the Yinkeng Formation).

Given that C. taylorae is confined to Bed 27a-28 in Meishan (Jiang et al., 2007; Zhang et al., 2009) and has also been widely reported from PTB beds around the world (Orchard et al., 1994; Orchard and Krystn, 1998; Nicoll et al., 2002; Algeo et al., 2012; Zhao et al., 2013b), the C. taylorae Zone is regarded as a discrete zone beneath the H. parvus Zone and retained for Bed 27a-b (Fig. 2). In addition, we have also re-examined stratigraphic distributions of some key conodont species based on previously published data and newly extracted specimens from Meishan. An updated conodont zonation is proposed for the P-Tr succession of the GSSP Meishan (Fig. 2). The new conodont zones, with their stratigraphic ranges in brackets, include C. changxingensis Zone (Beds 22-23), C. yini Zone (Bed 24), C. meishanensis Zone (Bed 25), H. changxingensis Zone (Bed 26), C. taylorae Zone (Bed 27a-b), H. parvus Zone (Bed 27c-d), I. staechei Zone (Beds 28-29a), I. isarcica Zone (Bed 29b), C. planata Zone (Beds 30-54), and Neoclarkina
discreta Zone (Bed 35 and above) (Fig. 2).

It is noteworthy that Yuan et al. (2014) confined the *C. changxingensis* Zone to mid-Bed 10 to mid-Bed 22, *C. yini* Zone to mid-Bed 22 to Bed 24d, and *C. meishanensis* Zone to Bed 24e to Bed 25. The fist occurrence of the nominal species of these conodont zones seems to be lower than they occurred in our samples. In particular, *C. meishanensis* occurs in the so-called ‘white boundary clay’ bed and above strata in most PTB sections in South China (Zhang et al., 2007; Jiang et al., 2007, 2011, Zhao et al., 2013b) and is rarely present in the Permian bioclastic limestone. The *C. meishanensis* Zone is also associated with a pronounced negative shifting excursion of carbon isotopes in most of the PTB sections in South China. Accordingly, the bases of these Changhsingian conodont zones remain tentative and need to be confirmed when additional conodont samples are processed in future.

Other important findings from the PTB beds include restriction of *Isarcicella peculiaris* to Bed 28 and the first occurrences of *Hindeodus eurypyge* and *Isarcicella lobata* at the bases of Bed 27a and Bed 28, respectively (Jiang et al. 2007; fig. 2). These species also have the potential to serve as key elements marking the PTB beds (Jiang et al., 2007, 2011, 2014). Of these, *I. lobata*, confined to Beds 28-29 in Meishan, was proposed
as a distinct zone between the *H. parvus* and *I. staeschei* Zones in the southern Alps (Perri and Farabegoli, 2003, 2012; Fig. 2). This species therefore occurred slightly earlier in the southern Alps than in the GSSP Meishan. In the new conodont zonation, the *I. isarcica* Zone is retained for Bed 29b, and thus has a much narrower stratigraphic range than before. The *C. planata* Zone is newly proposed for Beds 30-54 and the *Neoclarkina discreta* Zone for Bed 55 and higher strata in Meishan (Fig. 2) based on re-examination of their stratigraphic distributions (Zhang et al., 2007, 2009).

The updated conodont zonation enables the PTB beds of Meishan to be correlated precisely with their counterparts recorded elsewhere in the Tethys region, such as North Italy, Iran, Germanic basin, and Spiti of Himalaya region (Fig. 2). The *H. parvus*, *I. staeschei* and *I. isarcica* Zones have also been recognized in both Spiti and North Italy (Fig. 2). Both *H. parvus* and *I. isarcica* Zones occur in the Abdadeh region, Iran (Korte et al., 2004). Korte et al. (2004) also argued that there might be a hiatus between Beds 24e and 25 because both the *C. iranica* and *C. hauschkei* Zones, between the *C. yini-C. zhangi* and *C. meishanensis-H. praeparvus* Zones, are absent in Meishan. *C. hauschkei* does occur in Meishan, but shares the same stratigraphic range with both *C. yini* and *C. zhangi* in Bed 24 (Jiang et al., 2007, 2011). More importantly, no sedimentary gap has been
found in this interval in the GSSP Meishan (see below). The last occurrence of both C. 
yini and C. zhangi has been calibrated to the top of Bed 24e (Yin et al., 2001; Zhang et al.,
2007; Jiang et al., 2007). The depositional succession between the C. meishanensis and C.
yini Zones shows no sign of a hiatus. Thus, both C. hauschkei and C. iranica either can be
recognized from the upper part of the N. yini Zone in the future, or do not occur due to
different biofacies controls (Korte et al., 2004).

Recognition and correlations of PTB beds in conodont-barren sections have long
remained problematic. Chen et al. (2009) established the bivalves Claraia huzhouensis-C.
cf. bioni and Eumorphotis venetiana-Towapteria scythica-Pteria ussurica variabilis
Assemblages from the PTB beds of both the Meishan and adjacent Huangzhishan
sections. The former is coeval with the C. meishanensis and H. changxingensis Zones of
the GSSP Meishan (Chen et al., 2009). The small, weakly costated Claraia-like species
“Peribositra” baoqingensis from Bed 26 of Meishan (Zhao et al., 1981) has been
re-assigned to Claraia (Chen, 2004). These primitive Claraia species from Meishan are
diagnostic of the C. huzhouensis-C. cf. bioni Assemblage and locate the PTME in the
shallow-water, conodont-barren PTB sections in South China (Chen et al., 2009). The
latter bivalve assemblage is contemporaneous with the H. parvus Zone in the
Huangzhishan section, pointing to an age of earliest Triassic (Chen et al., 2009). Both Claraia wangi and C. griesbachi are also abundant in Beds 29b-54 in Meishan, and thus form the C. wangi-C. griesbachi Assemblage (Chen et al., 2010a), which is coeval with the I. isarcica and C. planata Zones (Fig. 2). The ammonoids Rotodiscoceras, Hypophiceras, Ophiceras, and Lytophiceras characterize the assemblages from Beds 22-24, Beds 25-26, Beds 27-50, and Beds 51-55, respectively in Meishan (Fig. 2; Zhao et al., 1984; Sheng et al., 1984; Yin et al., 2001; Chen et al., 2010a). Brachiopods are also reasonably abundant in Beds 25-26, Bed 27 and Beds 51-55 of Meishan (Chen et al., 2002, 2006b, 2007). They are assignable to the Tethyochonetes liaoi Assemblage (Beds 25-26), Paryphella triquetra Assemblage (Bed 27), and Meishanorhynchia meishanensis Assemblage (Beds 51-55) (Chen et al., 2010a). Song et al. (2007, 2009) also reported diverse foraminifers from the Changhsing and lowest Yinkeng Formations in Meishan, but did not establish biozones. A palynological Lundbladispora-Taeniaesporites-Equisetosporites Assemblage was established from Beds 33-53 of the Yinkeng Formation (Zhang et al., 2007), which, therefore, correlates collectively with the conodont C. planata Zone (Fig. 2).
In Meishan, volcanic ash beds are well exposed and conspicuous in the uppermost Permian to Lower Triassic successions. In particular, Beds 25 and 28 near the PTB have been dated by multiple research groups using various techniques (Table 1). The most updated radiometric ages for Beds 25 and 28 are 251.941 ± 0.037 Ma and 251.880 ± 0.031 Ma, respectively (Burgess et al., 2014), which constrain the duration between those two phases of the PTME (Song et al., 2013a) or the duration of the PTME (Shen et al., 2011b; Wang et al., 2014) as 60 ka (Burgess et al., 2014). Burgess et al. (2014) have also given updated estimates for sediment accumulation rates through the P-Tr transition, which show that sedimentation rates of the Changhsing Formation decline towards the end of the Permian, reach the lowest value during the time of extinction (Beds 25-28), and then increase gently in the early Griesbachian (Beds 28-37) and steeply in the early-middle Griesbachian (Beds 37-48) in Meishan (Burgess et al., 2014). In addition, these authors estimated that the abrupt decline in δ^{13}C_{carb} in Bed 24e took place at 251.950 ± 0.042 Mya, while the FAD of *H. parvus* at the GSSP Meishan is at 251.902 ± 0.024 Mya (Burgess et al., 2014).
2.3. Duration of key conodont zones across the P-Tr boundary

At Meishan, intense high-precision dating of volcanic ash beds (Table 1) and high resolution conodont zones (Fig. 2) allow reasonable estimates of the duration of each conodont zone. The widespread *H. parvus* Zone is estimated to have lasted 16 ka (Table 2), while the *C. meishanensis* Zone, the PTME marker, lasted 8 ka, which is much shorter than previously thought. The last conodont zone prior to the PTME, the *C. yini* Zone, may have lasted 28 ka (Table 2).

3. Microstratigraphy, fossil fragment contents and paleoenvironmental analysis of the P-Tr transition

At Meishan, the P-Tr succession comprises the Changhsing and Yinkeng Formations below and above. The former unit is a 41-m-thick carbonate succession consisting of medium- to thin-bedded limestone, while the Yinkeng Formation is about 15 m thick and dominated by mudstone and muddy limestone in the lower part and
characterized by thin-bedded limestone in the upper part (Fig. 3). These two formations have been frequently described (Zhao et al., 1981; Sheng et al., 1984, 1987; Yang et al., 1987; Yin et al., 1996, 2001; Zhang et al., 2005). Cao and Zheng (2007) re-described the Changhsing Formation (Beds 1-24) and recognized 247 natural, single layers, each 2 to 37 cm in thickness. Chen et al. (2007) gave an updated description for the Yinkeng Formation (Beds 25-59), in which 183 natural layers are recognizable. In addition, Cao and Shang (1998) conducted the first cm-scale stratigraphy, also termed microstratigraphy, of the P-Tr boundary beds in Meishan. Since then, microstratigraphy of the Beds 24-29 of the Meishan section has been intensely studied (Cao and Zheng, 2009; Zhao and Tong, 2010; Zheng et al., 2013).

The top two beds of the Changhsing Formation, Beds 23-24, record important sedimentary and paleontological information just prior to the PTME, while most parts of the Yinkeng Formation record the severe biotic extinction and its consequences. Thus, microstratigraphy of the uppermost Changhsing Formation to Yinkeng Formation succession (Beds 23-59) is summarized here in view of the previously published data and our new observations in petrologic thin sections. These thin sections were sampled almost continuously in Beds 24e to 29 and in a 20-cm-interval in Beds 22 to 24d of the
Changhsing Formation. The sampling interval is 0.5 m throughout Bed 30 to Bed 59 of the Yinkeng Formation in the GSSP Meishan.

Point counting is a relatively quick method that quantifies the occurrence of skeletal fragments of major fossil groups in different horizons under the microscope (Flugel, 1984; Payne et al., 2006). However, care must be taken when using the point-counting method because large shell fragments of some clades may bias counting results (Jacobsen et al., 2011). As an alternative, Jacobsen et al. (2011) proposed the equal area approach to quantify the occurrence of skeletal fragments in thin section. In order to eliminate biases of counting areas, it is suggested that at least eight equal area fields of view ought to be counted per thin section sample (Jacobsen et al., 2011). Similar to the equal area approach, fragment percentage data of various clades from each thin section are estimated based on the observation of 300 to 350 views under a magnification of ×50 in one sample, collected for microfacies analysis of the PTB beds. Then, percentages of various skeletal components, micrite, cavities and undertermined particles (i.e., pyrites and other minerals) from samples throughout Bed 22 to Bed 60 of Meishan were combined to yield the mean abundance of each composition in each sample throughout the study succession (Table 3).
Bed 23 of the upper Changhsing Formation comprises dark gray thin-to medium-bedded bioclastic limestone interbedded with thin-bedded muddy limestone and siliceous mudstone layers. Small-scale wavy cross bedding is commonly present in the bioclastic limestone, while horizontal stratification occurs in the muddy limestone and siliceous mudstone (Fig. 4G, H). Grain bedding structures are also occasionally present in the bioclastic limestone unit. The bioclastic limestone usually has a packstone to grainstone texture. The former texture is very common, while a grainstone texture is also occasionally present (Fig. 5C). This unit is usually strongly bioturbated in comparison with the weakly bioturbated thin siliceous layers that are usually horizontally stratified (Fig. 3). The autochthonous and allochthonous fossil assemblage is highly diverse and dominated by foraminifers, crinoids, and brachiopods with minor constituents of ostracods, echinoids, bryozoans, sponge spicules, calcareous sponges, gastropods, radiolarians, and macroalgae (Fig. 6). The matrix comprises micrite (about 20-23%, Fig. 6). Cavities, pyrites and other undetermined particles are also commonly present (Table 3). The alternating occurrence of horizontal stratification and small-scale cross bedding
and/or grain-grading bedding structures indicates that Bed 23 was deposited on a carbonate ramp between fair-weather wavebase and storm wavebase (Fig. 3; Zhang et al., 2005).

3.2. Bed 24

Bed 24, the topmost unit of the Changhsing Formation, consists mainly of thin- to medium-bedded bioclastic packstone rich in large ammonoids and other macrofossils (Fig. 4E). This bed has attracted intense attentions in terms of fossil record and sedimentary characterization because of its stratigraphic position just beneath the biotic extinction horizon (base of Bed 25; Jin et al., 2000). Bed 24, 71-90 cm in thickness, is usually labelled as Bed 24a-e (Yin et al., 1996) and consists of 14 layers, with the thinnest being 2 cm thick (Cao and Zheng, 2007). The conodonts from Bed 24 belong to the Clarkina yini Zone (Mei et al., 1998), which is distinct from the underlying C. changxingensis Zone (Beds 22-23). Bed 24a-c has similar petrographic features to Bed 23 (Figs. 5D, 6). The dark organic-rich muddy limestone or siliceous mudstone, usually about 2 cm in thickness, has
well-developed horizontal stratifications and possesses packstone to micritic textures with tiny, highly fragmented fossil skeletons of brachiopods and ostracods. These horizontally stratified layers are usually weakly bioturbated. In contrast, the bioclastic limestone unit, usually > 5cm thick, possesses small-scale wavy cross bedding and bioclastic packstone to grainstone texture. These layers are also highly bioturbated (Zheng et al., 2013). All skeletal components of Bed 23 also persist into Bed 24 (Fig. 6). Accordingly, Bed 24a-c was likely deposited in the same environment as Bed 23. Although Bed 24d has similar petrographic texture to Bed 24a-c (Fig. 6), the presence of abundant fecal pellets and peloids characterizes the grain assemblage of Bed 24d. Fossil fragment contents in rocks from both Bed 24d and Bed 24a-c are also comparable with one another (Fig. 6). In addition, burrows are commonly present near the boundary between bioclastic limestone unit and organic-rich muddy limestone or siliceous mudstone layer. Bed 24d yields abundant trace fossils (see Section 5). Pronounced cross-bedding and vertical burrows characterize the upper part of Bed 24d (Fig. 4J). The top of Bed 24d is, however, weakly bioturbated and characterized by smooth cone-shaped surfaces, which was termed a hard-ground structure representing interrupted or highly condensed deposits (Cao and Zheng, 2009). Cao and Zheng (2009)
regarded this irregular contact as a sequence boundary indicating a changeover interface from lowermost level to rapid rise. The same contact, however, has been interpreted as an erosional surface, serving as a sequence base of a 3rd-order depositional sequence following a major fall in sea level (Zhang et al., 1997; Yin et al., 2014). This interpretation is reinforced by the presence of a diverse shallow-water facies trace fossil assemblage including vertical burrows of *Balanoglossites* (Fig. 4J; see also Section 5). Cao and Zheng (2007) have also noted that abundant burrows of *Planolites* and *Skolithos* and mud-crack structures are present near the boundary between Beds 24d and 24e. Accordingly, Bed 24d, overall, is inferred to have been deposited in the upper part of the subtidal zone of a carbonate ramp (Fig. 3; Zhang et al., 1997).

The topmost 10 cm thick limestone of Bed 24 is labelled Bed 24e, which consists of eight natural layers (Cao and Zheng, 2009) and these were sampled at six horizons here (Bed 24e-1 to Bed 24e-6). Trace fossils occur near the irregular contact between Beds 24d and 24e-1 (see Section 5). Bed 24e, except for the topmost 3 cm (24e-5, 24e-6), is a dark gray bioclastic packstone containing abundant fossil fragments of foraminifers, brachiopods, and crinoids. Other fossil groups such as bryozoans, gastropods, macroalgae, ostracods, calcareous sponges, and sponge spicules are also seen
in thin sections, which have no major difference from the underlying Bed 24d (Fig. 6).

The uneven top surface is always capped by several muddy laminae. Cylindrical, vertical burrows, ranging from 0.1 to 0.5 cm in diameter and from 3.0 to 1.0 cm in length occur in the upper bedding surface. Bed 24e saw a slight increase in lime mud in the matrix and pyrite within the bed (see below). Bed 24e therefore was probably deposited in the fair-weather wave action zone (Fig. 3) and was interpreted as a lowstand platform margin wedge of a 3rd sequence (Zhang et al., 1997; Yin et al., 2014).

The topmost 2-3-cm-interval, labelled as Bed 24e-5 and 24e-6, is characterized by relatively low contents of P and Ca and high Ni content (Kaiho et al., 2001, 2006b).

Bed 24e-5, about 1.0-1.1 cm in thickness, comprises bioclastic packstone and contains abundant fossil fragments of foraminifers, crinoids, brachiopods, and ostracods. Fragments of calcareous sponges, sponge spicules, gastropods, bryozoans and macroalgae are also occasionally present, and these are comparable in major fossil components with Beds 24e-1 to 24e-4 (Fig. 6). Moreover, abundant, reasonably large horizontal burrows (*Planolites*) are densely packed on the surface of Bed 24e-6 (also see Section 5).

The contact between Beds 24e-5 and 24e-6 is a laminated wavy lime layer (Fig. 6).
Bed 24e-6 is a 10- to 19-mm-thick bioclastic packstone and dominated by silica bars, which were interpreted as sponge spicules (Kaiho et al., 2006). The elongate bars are actually longitudinal outlines and the circular grains are cross sections of spicules (Fig. 7A-C). This identification is reinforced by the abundant isolated silicified sponge spicule specimens extracted from Bed 24e-6 (Fig. 7E). Contrasting to the predominance of sponge spicules, fragmentary contents of foraminifers, crinoids, echinoids and brachiopods decline dramatically. The skeletal grain assemblage experienced a dramatic reduction in both abundance and diversity across the contact between Beds 24e-5 and 24e-6 (Fig. 7E), to which the PTME was calibrated (Kaiho et al., 2006a).

3.3. Bed 25

This bed is the so-called “Boundary clay bed” or “White clay bed” (Zhao et al., 1981; Sheng et al., 1984; Yang et al., 1987). Its thickness ranges from 2 cm to 6 cm depending on the weathering intensity, the higher the intensity the thicker the bed. The bed grades upward into Bed 26 as a consequence of a gradual increase in organic and calcareous content and decrease in volcanic ash layers. The total thickness of these two
The basal part of Bed 25 comprises a 0.1- to 0.2-mm-thick layer of greyish black mudstone rich in Fe grains, termed Bed 25-1, which usually becomes a reddish ferruginous layer capping the dark Bed 24e-6 and is conspicuous at outcrops in all Meishan quarries owing to weathering. Previously, this Fe-rich layer was termed the “pyrite lamina” layer (Wignall and Hallam, 1993; Shen et al., 2007) or Pyrite layer (Cao and Zheng, 2009), based on the abundant pyrite-like grains visible at outcrops. Elemental analysis shows that these Fe grains are either Fe-Ni grains (Kaiho et al., 2001, 2006b) or goethites (Liang et al., 2002). Pyrite framboids are also commonly present in this layer (Shen et al., 2007). In addition, Zheng et al. (2013) detected abundant irregular volcanic glasses from this layer.

The reddish ferruginous surface of Bed 25-1, together with the absence of both the *N. iranica* and *N. hauschkei* conodont zones, was considered as evidence indicating an exposure surface and representing a hiatus (Korte et al., 2004). However, the presence of marine fossils such as foraminifers and brachiopods (Rui et al., 1988; Yin et al., 2001) in Bed 25 and abundant sponge spicules and other fossil fragments in Bed 24e-6 (Fig. 6) indicates the absence of a paleo-exposure surface or an aerial hiatus. The absence of these
two conodont zones may relate to biofacies controls and cannot bracket a hiatus, as discussed in Section 2.1.

The overlying thin layer (Bed 25-2), 0.3-1 mm thick, is dark yellowish orange, and encompasses mainly gypsum and Fe (Table 4). The remaining part of Bed 25 (Layer 25-3, 2-4 cm thick; Kaiho et al., 2006b) is a light gray illite-montmorillonite-kaolinite claystone (white clay) (Table 4). Gypsum and pyrite are very common in thin section. No fossil fragments are seen in thin section (Fig. 5A). Marine fossils of conodonts, foraminifers, ostracods and tiny brachiopods have been found from this bed, but are always sparse (Rui et al., 1988; Jiang et al., 2007). Benthic carbonate skeletal fossils diminished dramatically in this bed. Calcareous shells are often pyritized and attached with crystals and frambooidal pyrites on the surface (Rui et al., 1988). Conodonts from Bed 25 are included in the *C. meishanensis* Zone (Fig. 2). Microspherules and β-type quartz crystals are much more abundant in this bed than in other ash clay beds, and could be products of acid volcanic eruptions (He et al., 1987). However, comparable microsphaerules are also abundant in the background soils in Meishan and other PTB sections in South China, suggesting that they may be the modern industrial products rather than geological objects (Zhang et al., 2014). Both Hf-isotope and elemental
analysis of magmatic zircons suggests these ash clays near the PTB in South China may have been sourced from volcanism taking place along the convergent continent margins during the formation of the Pangea supercontinent (Gao et al., 2013).

3.4. Bed 26

Bed 26, the so-called “black clay bed” (Yang et al., 1987), comprises black shale, 4-6 cm in thickness. Nine pronounced yellow clay layers are interbedded in the black shale. Horizontal laminae and pyrite are common. The clay layer is composed mainly of montmorillonite–illite, which is similar to that of Bed 25 (Table 4). Fossil fragments are very rare in most parts of this bed (Fig. 5B) except for the top 2-cm-interval where fossil fragments are fairly abundant in calcareous nodules (Fig. 8), including foraminifers, ostracods, echinoids, bryozoans, and brachiopods (Table 3; Figs. 6, 8). Microspherules or/and α-quartz (in the form of β quartz pseudomorphs; He, 1981) are rich in the lower part, but they may be the products of modern industry (Zhang et al., 2014). Various burrowing systems are common in the upper part of Bed 26, from which Cao and Zheng (2009, fig. 5b) identified Chondrites, Planolites and Zoophycos. The identification of the
last ichnogenus, however, is problematic based on insufficient information illustrated by these authors. The upper part of the bed, Bed 26b, therefore is highly bioturbated (Fig. 3; Cao and Zheng, 2009).

Skeletal fossils are rare but considerably diverse, including ammonoids, brachiopods, bivalves, ostracods, and conodonts. Co-occurrence of the Triassic-type faunas (i.e., *Otoceras, Claraia* and many conodont species) and Permian-type elements (i.e., ammonoids *Pseudogastroceras* and *Xinodiscus*, and many brachiopods and foraminifera) is particularly interesting. Brachiopods are small in size and thin-shelled, and include species of *Orbicoiella, Prelissoryhnchia, Cathaysia, Paryphella*, *Tethyochonetes*, and *Spinomarginifera* (Chen et al., 2006b; Chen and McNamara, 2006).

The presence of the relatively diverse fossil assemblage in the upper part of Bed 26 indicates the earliest re-colonization of epifauna on the barren soft substratum immediately after volcanic eruption. Most of these shelly fossils are complete and well preserved regardless of the delicacy of the skeleton. The change from Bed 26 to Bed 27 is gradual and no boundary surface can be recognized. Crystal and frambooidal pyrite are concentrated in a discontinuous dark lamina with rich organics (Shen et al., 2007). The slow sedimentation rate, and quiet and anoxic environment (Shen et al., 2007) suggest
that Bed 26 probably represents a semi-closed, low-energy subtidal zone (Fig. 3). The
succession of Beds 24e, 25 and 26, overall, shows that continuing fall of sea level through
Bed 24e turned to a rise in the upper part of Bed 26, with the lowest point of sea level
corresponding probably to the base of Bed 25 (Yin et al., 2014).

3.5. Bed 27

Bed 27 comprises biotic packstone to wackestone with occasionally micrite
texture and contains fairly abundant fossil skeletons and pyrite crystals throughout the
bed (see Section 6). Relatively complete shells of ostracodes, foraminifers and
thin-shelled brachiopods are reasonably abundant. This bed contains three major irregular
contact surfaces, termed hardground surfaces (Cao and Shang, 1998) and firmground
surfaces (Cao and Zheng, 2009), at various levels (Fig. 9). Of these, the first irregular
surface is rather pronounced, about 5 cm above the base of Bed 27 and near the boundary
between Beds 27a and 27b. The second occurs near the contact between Bed 27c and 27d,
while the third is not prominent and occurs within Bed 27d (Fig. 9). These ‘firmground’
surfaces divide Bed 27 into three depositional cycles, with each beginning with dark
muddy limestone and grading upwards into pale bioclastic limestone. Rich organic and
muddy laminae parallel to the bedding plane decrease upward from the base within each
cycle. The upper unit of each cycle was disturbed by repeated burrowings, which form
part of the firmground (see Section 5). Microscopic examination reveals that the dark,
early-lithified rock contains a minor percent of clay, rich organic shreds and bioclasts (Fig.
9; Table 4).

Microfossils in Bed 27 are much more abundant and diverse than previously
thought (Fig. 6). Of these, foraminifera are most abundant among all clades. Echinoids
are also remarkably abundant, although they cannot be identified beyond a certain
taxonomic level (Figs. 10-12). Bed 27a contains fossil skeletons of foraminifers,
ostracods, echinoids, and brachiopods (Fig. 10), which is similar in component
composition to Bed 26 (Fig. 6). Bed 27b comprises marls and clays in the lower part, in
which fossil fragments are very rare (Fig. 9). The remainder of Bed 27b yields a fossil
fragment abundance (FFA) composed mainly of foraminifers and brachiopods (Fig. 6).

Both Beds 27c and 27d contain much more abundant and diverse FFA than Bed 27b (Figs.
10-12), both of which are dominated by foraminifers, ostracods and brachiopods with
minor constituents of echinoids (Fig. 6).
It should be noted that Bed 27 is usually subdivided into four layers (Yin et al., 2001). Cao and Zheng (2009), however, divided this bed into six layers (units) including a stromatolite layer (Bed 27-5) and mudstone (Bed 27-6) in the upper part of Bed 27. Later, Zheng et al. (2013) denied the existence of the stromatolite layer and divided Bed 27 into five layers; no stromatolitic structures are seen in our thin sections either. Except for the topmost 0.5 cm thick layer of carbonaceous mudstone, another four layers are similar to those recognized by Yin et al. (2001). In addition, Cao and Zheng (2009) and Zheng et al. (2013) interpreted the irregular surface separating Beds 27a and 27b (Fig. 9) as firmground surface as a result of a rapid transgression. Here, we agree with the firmground interpretation of these irregular surfaces within Bed 27 (Cao and Zheng, 2009; Zheng et al., 2013) because of the presence of abundant burrows typical of the Glossifungites ichnofacies (Seilacher, 1967) and distinct lithological interfaces, typically dark muddy micrite overlain by light gray, coarser-grained bioclastic packstone-wackestone, within Bed 27 (Fig. 9; see also Section 5). Firmgrounds of the Glossifungites ichnofacies, also termed omission surfaces (Knaust, 1998), have been extensively used in sequence stratigraphy to identify and characterize discontinuity surfaces (Pemberton and Frey, 1985; MacEachern et al., 1992, 2007; Buatois and
Within Bed 27, the unlined burrows penetrating into muddy limestone are passively filled with coarser grains from the overlying stratum. This means that the burrows remained open after the trace maker had left, thereby permitting bioclast grains from subsequent depositional events to fill the open, stable burrows. Although the majority of documented *Glossifungites* ichnofacies are from shallow-marine settings (Knaust, 1998; Buatois and Mángano, 2011), this ichnofacies is also present in relatively deep marine contexts, such as incision of submarine canyons during relative sea-level falls (e.g. Dasgupta and Buatois, 2012) or autogenic erosional episodes by turbidity currents and bottom currents (Savrda et al., 2001; Gérard and Bromley, 2008; Hubbard and Shultz, 2008). As such, the *Glossifungites* ichnofacies from Bed 27 may represent an omission surface, but cannot indicate a precise depositional environment for Bed 27. Integration of lithofacies, paleoecologic and ichnofacies indicates that Bed 27 may have been deposited on a carbonate ramp near the storm wave action zone (Fig. 3), as suggested by Zhang et al. (1997; 2005).

### 3.6. Bed 28
Bed 28 comprises yellow claystone having similar composition to Bed 25 (Table 4), dominated by montmorillonite mixed with illite. Apart from conodonts (Jiang et al., 2007), no other fossils have been recovered from this bed.

3.7. Beds 29-59

Bed 29 encompasses wackestone with rare foraminifer tests (Fig. 13). Pyrite is commonly seen in thin section and pyrite content increases up-section. A minor omission surface, equivalent to the erosional surface of Zhang et al. (2007) is developed in the middle part of Bed 29 (Zhang et al., 2007). Fossil fragments are very rare and their contents decrease upwards within the bed (Fig. 6; Table 3). Bed 30 is a marlstone, which has a micritic texture and lacks any fossil fragments (Table 3). Both beds contain laminated stratification and lack any cross bedding, indicating a low-energy environment. Beds 29-30 therefore may have been deposited in the upper part of the offshore setting that is below fair-weather wavebase (Chen et al., 2007).

Beds 31-51 are typified by alternating black shale, greenish gray mudstone, and gray marlstone in the lower part, and interbeds of gray calcareous mudstone and pale
muddy limestone in its upper part. They are subdivided into 39 cm-scale cycles (Chen et al., 2007; Fig. 3). In general, the lower unit of the cycle is characterized by black shale or greenish mudstone rich in bivalve and ammonoid fossils (Fig. 4F, I), while the upper unit is dominated by calcareous mudstone and marlstone. The mudstone-dominated cycles are transitional to the marl-dominated cycles up-section, indicating a long-term up-shallowing cycle (Chen et al., 2002, 2007; Tian et al., 2014). In addition to the lithologic variation, Beds 31-34 are characterized by the calcareous mudstone and shale where laminated stratifications are commonly preserved (Fig. 4C), while the upper part of the formation (Beds 35-51) is typified by an increasing number of laminated marl beds (Fig. 3). Fossil fragments occur occasionally in Beds 45, 50 and 51, characterized by foraminifer and ostracod skeletons (Table 3; Fig. 6). Horizontal burrows of Planolites are present in Beds 36-51, which also yield a few shell beds of bivalves (i.e., Claraia griesbachi) and ammonoids (Ophiceras spp.) (Chen et al., 2007). This unit was interpreted as the result of sedimentation relatively deep offshore (Fig. 3; Zhang et al., 2005; Chen et al., 2007).

Beds 52-53 comprise alternations of shale and marlstone, yielding reasonably abundant burrows of Chondrites and Planolites. Increasing fossil fragment content is
seen in both Beds 52 and 53, in which foraminifer, ostracod and echinoid shell fragments are remarkable (Fig. 13), although they are definitely minority components in thin section (Fig. 6; Table 3). Moreover, horizontal stratification is commonly present in both shale and marlstone. These two beds were interpreted as the result of sedimentation in the relatively deep offshore below storm wavebase (Chen et al., 2007).

Towards the top of the Yinkeng Formation, the succession (Beds 54-59) is dominated by marl-dominated cycles. A thin- to medium-bedded marl is hummocky cross-stratified (HCS; Fig. 4A, B, D) and often displays multidirectional tool marks on its base, and horizons of loading and soft sediment deformation are very common (Chen et al., 2002). Fossil fragments are reasonably abundant in Beds 54-59 (Fig. 13), although they are still in the minority in thin section (Fig. 6; Table 3). Foraminifers, ostracod and echinoids characterize their FFA (Fig. 6; Table 3). Trace fossils are also commonly present in these beds, including *Planolites* isp. 2, *Treptichnus* sp., and *Thalassinoides* isp. 3. Moreover, the sedimentary structure HCS was interpreted as having been generated by offshore storm currents. Beds 54-59 therefore may have been deposited offshore, near storm wavebase (Chen et al., 2007).
4. Biotic changeover through the P-Tr transition

4.1. Biodiversity variations over the P-Tr transition

Comprehensive paleontological studies of the Meishan section were undertaken in the 1980s (Zhao et al., 1981; Sheng et al., 1984; Yang et al., 1987; Shi and Chen, 1987). The fossil record employed by Jin et al. (2000) to document the PTME pattern, which shows an abrupt extinction calibrated to the base of Bed 25, was sourced mainly from these studies. Since then, more diverse faunas and floras have been documented from Meishan, including foraminifers (Song et al., 2007, 2009), radiolarians (He et al., 2005), brachiopods (Chen et al., 2002, 2005a, 2006b; Li and Shen, 2008; Chen and Liao, 2009), conodonts (Nicoll et al., 2002; Tong and Yang, 2004; Luo et al., 2006, 2008; Jiang et al., 2007, 2008; Zhang et al., 2007, 2009; Yuan et al., 2014), ostracods (Crasquin et al., 2010; Forel and Crasquin, 2011), palynomorphs (Zhang et al., 2007), and arctitarchs (Li et al., 2004). Additional macrofossils were collected throughout the upper Changhsing Formation to the Yinkeng Formation. Several shelly fossil communities from Beds 24, 26, 27, 32, 40, and 53-55 were quantitatively analysed (Chen et al., 2010a).
Shen et al. (2011b) and Wang et al. (2014) demonstrated a steep decline zone of species richness corresponding to the interval between Beds 25 and 28 in Meishan by a means of quantitative analysis on fossil records from more than ten PTB sections (including Meishan) from South China. In contrast, Song et al. (2013a) calculated species richness of each layer marked in microstratigraphic analysis (Beds 24-29) based on the updated fossil record mentioned above. Species richness of single layers experienced a stepwise but minor decline within Bed 24. Two distinct declines in species richness were well demonstrated and calibrated to Beds 25 and 28. The same pattern is also indicated in seven PTB sections in South China (Song et al., 2013a). Above Bed 28, species richness remains very low in the remaining part of the Yinkeng Formation.

Here, additional fossil specimens, primarily brachiopods, ammonoids and bivalves, have been collected from Beds 24e, 26, 27 to document biotic turnover across the PTB. Moreover, microfossils were observed in the petrologic thin sections used for microfacies analysis (see Section 3). Of these, foraminifers are the most abundant skeletal fragments among all clades. Most of these foraminifer tests, however, were illustrated by Song et al. (2007, 2009), so the newly obtained fossil record does not affect the biotic extinction pattern revealed by Song et al. (2013a).
4.2. Fossil fragment content variations through the P-Tr transition

The abundance and diversity of skeletal grains within the late Changhsingian samples (Beds 22-24) is remarkably high. Skeletal grains from all sampled levels except for the top 1-2 cm (Bed 24e-6) of Bed 24e comprise 68-74% of the total rock volume in the uppermost Changhsing Formation (Fig. 14). Fossil fragment assemblages are strikingly similar to one another in all sampled layers within the interval between Bed 22 and 24e-5, and each of these is dominated by foraminifers, crinoids and brachiopods.

Other major constituents include ostracods, bryozoans, sponge spicules, and macroalgae (Fig. 14). Skeletal grains of gastropods, calcareous sponges and radiolarians are relatively rare and absent in some horizons (Fig. 14).

It is noteworthy that FFAs do not appear to differ at all across the contact between Beds 24d and 24e, although an omission surface, also a 3rd sequence boundary (Zhang et al., 1997), separates these two layers (Zhang et al., 1997). In contrast, FFAs experienced a dramatic reduction in diversity across a lime laminae layer between Beds 24e-5 and 24e-6 (Figs. 6, 14). Above this lamina layer (Fig. 7D), skeletal grains of Bed
24e-6 comprise about 60% of all rock in thin section in comparison with nearly 70% in Beds 22-24e-5 (Fig. 14). The overwhelming majority of the FFA in Bed 24e-6 is sponge spicules (35%) with minor constituents of foraminifers (8%), brachiopods (7%), crinoids (6%), and echinoids (4%) (Table 3; Fig. 6). Furthermore, fusulinids disappeared forever at this lamina (Kaiho et al., 2006b). The FFA experiences a loss of five major orders (i.e., ostracods, bryozoans, calcareous sponges, gastropods, and macroalgae) across the boundary between Beds 24e-5 and 24e-6 (Figs. 6, 14). More importantly, this horizon coincides with a pronounced negative carbon isotope excursion and a sulfur isotopic excursion anomaly (Kaiho et al., 2006a, b), and thus marks the actual biotic extinction horizon (Kaiho et al., 2006b).

Fossil fragment contents form a high plateau in both abundance and diversity, comprising nearly 70% of total rock and including almost all skeletal clades recognized from the Changshing Formation. They underwent a dramatic depletion in both abundance and diversity in Beds 25-26a, which are nearly barren of skeletal grains (Fig. 14). This severe depletion therefore is calibrated to the base of Bed 25, coinciding with the PTME (Jin et al., 2000; Shen et al., 2011b) or the first phase of the PTME (Song et al., 2013a). After the PTME, skeletal grains started to rebound in Bed 26b, the top 2-cm interval of...
the bed and 8-10 cm above the base of Bed 25. Fossil fragments in Bed 26b, however, comprise only 32% of all rock in comparison with nearly 70% before the PTME (Figs. 6, 14). The FFA in Bed 26b comprises mainly foraminifers, ostracods, brachiopods, bryozoans, and echinoids (Fig. 7). Both foraminifers and echinoids are the most abundant among all clades (Fig. 6). Of particular interest is the presence of both echinoids and bryozoans, with bryozoans represented by fenestellid fragments. These two clades have generally been believed to have gone extinct at the PTME (Sepkoski, 1981, 2002), but instead they occur in the aftermath of the PTME at Meishan. Their body fossils were also found in association with the _H. parvus_ Zone in the neighbouring Huangzhishan section of western Zhejiang Province (Chen et al., 2009).

Fossil fragment abundance remains almost same as in Bed 26b, comprising nearly 31-38% through the entire Bed 27, except for Bed 27b, in which skeletal grains are only 10% of all rock. Thus, fossil fragments rebounded and reached nearly half their pre-extinction level with a major depletion occurring in mid-Bed 27 (Fig. 14). If considering the FFA of the entire Bed 27, which contains elements of brachiopods, bryozoans, foraminifers, and ostracods (Table 3), then recovery of FFA diversity in Bed 27 is marked by the re-appearance of 45.5% of all pre-extinction orders.
FFA experienced a major loss in Bed 29, down to less than 10% (Fig. 14). Fossil fragments are absent in Beds 28-44. After rebounding in Bed 45, the skeletal grain assemblage underwent a stepwise abundance recovery in Beds 50-51 and remained at a relatively stable level, occupying nearly 16% of all rock in Beds 52-60. FFA diversity, however, remains at a rather low level, with the re-appearance of only three orders: foraminifera, ostracods and echinoids (Fig. 14).

4.3. Community structural changes of shelly faunas

The P-Tr shelly communities are characterized by a mixture of large-sized ammonoids and small brachiopods in the uppermost Changhsing Formation and by numerous shell beds in the Yinkeng Formation (Fig. 15). Chen et al. (2010a) recognized six macrofossil communities from the uppermost Permian to lowest Triassic in Meishan, including the *Rotodiscoceras* sp.–*Paracrithyris pigmaea* (*R–P*) Community (Bed 24), *Tethyochonetes liaoi* (*T*) Community (Bed 26), *Paryphella triquetra–Tethyochonetes liaoi* (*P–T*) Community (Bed 27), *Claraia griesbachi–Ophiceras* sp. (*C–O*) Community (Bed 32), *Claraia wangi* (*C*) Community (Beds 40), and
Meishanorhynchia–Lytophiceras (M–L) Community (Beds 53-55).

Several diversity indices (Shannon and Simpson indices and Dominance) are usually employed to measure community structures. It should be noted that the Shannon measures are the only standard diversity indices that generate meaningful independent alpha and beta components when the community weights are unequal or sampling is uneven (Jost, 2007). Dominance index (D) measures ‘evenness’ of the community from 0 to 1, 0 being the most even distribution amongst taxa. Simpson index = 1–Dominance index, and values range from 0 (one taxon dominates the community completely) to 1 (all taxa are equally present) (Hammer et al., 2001). Note that these diversity indices are useful in estimating diversity but are not themselves measures of diversity. Their numerical equivalent indicates changes of true diversity (Jost, 2007; Kosnik and Wagner, 2006). Conversion of both Shannon and Dominance indices to true diversities developed by Jost (2006, 2007) is performed to indicate true diversity changes over the P-Tr transition. In addition, the bias-corrected Simpson evenness index (Olszewski, 2004) is also applied to estimate the evenness within and among communities examined here.

Detailed community structural indices are listed on Table 5.

The late Changhsingian R–P community has Shannon index (H) of 2.029, which
is slightly smaller than the same index of 2.796 for the Changhsingian brachiopod Cathaysia–Martinia (C–M) community reported from the Shaiwa Group of southern Guizhou Province, southwest China (Chen et al., 2006a), but is slightly larger than the same index of 1.879 for the Wuchiapingian brachiopod Edriosteges poyangensis–Spinomarginifera lopingensis (E–S) Community reported from the basal Lungtan Formation of the Daijiagou section, Chongqing city, southwest China (Chen et al., 2005b). Dominance of the R–P community, D = 0.1519, also lies between the same indices of the above Changhsingian and Wuchiapingian brachiopod communities, with D = 0.07375 and 0.178, respectively (Chen et al., 2010b, table 4). It is also true for evenness of community (E) that the R–P community has E of 0.8453, which lies between 0.9262 and 0.822, the values of E for the C–M and E–S communities, respectively (Chen et al., 2010b). Accordingly, the R–P community is typical of Late Permian shelly communities.

In contrast, H values of all post-extinction communities, 1.47, 1.565, 0.7559, 0, and 1.288 for the T, P–T, C–O, C, and M–L communities, respectively (Table 5) are much smaller than the same values of the Changhsingian and Wuchiapingian communities, H = 2.796 and 1.879, respectively. These post-extinction communities therefore are much less diverse than the pre-extinction communities of the Late Permian, indicating the severe
impact of the PTME on marine communities.

Changes in both standard diversity Shannon index [Exp (H)] and dominance index (D’) between neighboring pairs of communities show that major losses in diversity coincide with the turnovers of the R–P/T and P–T/ C–O communities, losing 43.6% and 55.5% respectively. Similarly, standard diversity dominance (D’) increases by 34% and 54%, respectively (Table 6). Thus, community structural collapse indicated by a decrease in diversity, coupled with increase in dominance, coincides with two extinctions bracketed at the bases of Beds 25 and 28 at Meishan (Song et al., 2013a). In addition, Exp (H) value increases by 262.6% from the C to M–L communities, and also increases by 70%, coupled with a decrease of 15.2% in D’ values, from the C–O to M–L communities, suggesting an improvement in shelly community structures in Beds 53-55 at Meishan.

Structural improvement of the M-L community is also reinforced by comparison between the M–L community and the Anisian Madonia sp.–Rhaetina angustaeformis (M–R) Community, which marks the recovery of benthic communities in the Anisian (Chen et al., 2010b). The Anisian community has H and D values of 2.051 and 0.1501 respectively (Chen et al., 2010b, table 4), but the same values for the M-L community are H = 1.288 and D = 0.4379, respectively. Consequently, the M–L community embraces
much more improved diversity indices than other Griesbachian communities in Meishan, but instead has a much lower diversity and higher dominance index than both pre-extinction and recovery communities.

5. Trace fossils and bioturbation

At Meishan, Bottjer et al. (1988) made the first attempt to ecologically test the PTME based on trace-fossil assemblages. These authors, however, could not collect sufficient trace fossils because of restricted exposure at that time, but they noted that ichnotaxa from the PTB beds are dominated by *Planolites* and *Chondrites*, which indicate generally a poorly oxygenated environment (Bottjer et al., 1988). Later, Cao and Shang (1998) reported a few ichnotaxa such as *Thalassinoides*, *Planolites* and *Skolithos* from the PTB beds of Meishan, but *Skolithos* was later rejected by these authors (Cao and Zheng, 2009; Zheng et al., 2013). Zhang and Tong (2010) also examined trace fossils recorded in drilling cores through the P-Tr transition in Meishan. Although these authors clarified that trace fossil evidence suggests two ecologic crises, coinciding with Beds 24e-27 and Beds 34-39, respectively (Zhang and Tong, 2010), the documented
ichnofossils are too few to support such a conclusion (see Section 7). As a result, several lines of evidence show that trace fossils are reasonably abundant in the PTB beds in Meishan. They however remain poorly understood owing to inadequate trace fossil specimens.

Here, we document our observations at all PTB sites newly exposed during the construction of the geological park in the GSSP Meishan in the 2000s, which uncovered extensive fresh exposures along all the quarries (Fig. 1E). Abundant trace fossils were collected from Beds 8-9 and 23-24 of the Changhsing Formation and Beds 26-27 and 35-57 of the Yinkeng Formation. The ichnofabric indices (ii, sensu Droser and Bottjer, 1986) and bedding plane bioturbation index (BPBI, Miller and Smail, 1997) throughout the upper Changhsing Formation and entire Yinkeng Formation are also examined.

5.1. P-Tr ichnotaxa and their stratigraphic distributions in Meishan

5.1.1. Stratigraphic distribution of ichnoassemblages

A total of 17 ichnospecies in 13 ichnogenera and a problematic ichnotaxon have
been found in the P-Tr transition at Meishan (Figs. 16-18). Major characteristics, stratigraphic distributions and interpretation of each ichnotaxon are tabulated here (Table 7). Trace fossils are distributed mainly in Beds 8-9 and Beds 23-24 of the Changhsing Formation, and in Beds 27, 35-53, 55-57 of the Yinkeng Formation. Of these, the lower Changhsing Formation (Beds 8-9) ichnoassemblage is dominated by relatively large burrows of *Thalassinoides* isp. 1 (Fig. 16A, D) and resting traces of *Lockeia* isp. (Fig. 16F). *Paleophycus* isp. (Fig. 16B) is also commonly present in Beds 8-9.

The trace-fossil assemblage from Beds 23-24e is characterized by tree-like traces of *Dendrorhaphe* isp. (Fig. 17F) and abundant burrows of problematic status. The latter is represented by simple, straight, unbranched burrows (Fig. 17B-C), each originating at a small, close end and extending distally to form a horn-shaped burrow with an open distal end (Fig. 17B-C). Burrow diameters vary from 20-27 mm. Some burrows penetrate the bedding at acute angles, and others are horizontally distributed on bedding planes.

The burrow has a distinct circular wall, about 2-5 mm thick. These burrows are preserved in dark organic muddy limestone and filled with light-colored, coarse-grained sediments. These morphologies suggest that this problematic form differs from all known ichnotaxa.

Another feature of the Bed 24 ichnoassemblage is the presence of abundant
ichnofossils near the contact between Beds 24d and 24e, including several distinct burrowing ichnotaxa: *Balanoglossites triadicus*, *Taenidium* isp., *Thalassinoides* isp. 1, and *Planolites* isp. 1. Of these, *Balanoglossites* is represented by vertical tubes (Fig. 16C) that penetrate to a depth of 5-10 cm perpendicular to bedding. This ichnogenus occurs usually at omission surfaces that served as sequence boundaries (i.e., Knaust, 1998). These traces are preserved in limestone of the upper part of Bed 24d (Fig. 3). *Taenidium* burrows (Fig. 16E, 17E) are also very common in Bed 24d-e, and they are usually cylindrical, straight, unbranched, and backfilled. This ichnoassemblage as a whole represents the *Balanoglossites* ichnofacies associated with the omission surface, as described by Knaust (1998, 2004). In addition, horizontal burrows of *Planolites* isp. are densely packed on top of Bed 24e (Fig. 17A, E), which is just beneath the base of Bed 25, in which the PTME horizon is placed (Jin et al., 2000).

Abundant burrows were also found in association with an omission surface within Bed 27. These burrows and the possible firmground surface have long remained disputed, although several recent studies have addressed an ichnoassemblage of this bed (Cao and Shang, 1998; Cao and Zheng, 2009; Zheng et al., 2013). Burrow systems preserved in Bed 27 therefore are re-studied here (see below).
Beds 28-34 are barren of trace fossils. The remaining part of the lower Yinkeng Formation (Beds 35-51) yields rare trace fossils, which are dominated by simple, horizontal burrows of *Planolites* isp. 2 (Fig. 18A-B). Increasing numbers of ichnotaxa occur in the upper Yinkeng Formation and are characterized by the presence of the tree-like burrow system of *Chondrites* isp. (Bed 52; Fig. 18C) and relatively complicated burrows of *Thalassinoides* isp. 3 (Fig. 18D-E) and *Treptichnus* isp. (Fig. 18G-H).

### 5.1.2. Ichnofabric changes within Bed 27

Within Bed 27, intensive burrowing on an omission surface, characteristic of the *Glossifungites* ichnofacies, caused a pronounced relief on the firmground surface up to 3 cm high near the boundary between Beds 27a and 27b (Figs. 19-20). The firmground of *Glossifungites* ichnofacies is partly covered by a faintly laminar black muddy limestone that seems resistant to weathering. Highly irregular relief at the surface of the firmground indicates that the solid rock was affected deep subsolution (Savrda, 1992). Trace fossils increase upward to the contact between Beds 27c and 27d, which is overlain by finely laminated muddy limestone (Bed 27d) again.
To reconstruct complete burrowing systems within Bed 27, one complete sample of the bed (from base to top) was cut and separated into three blocks (Fig. 19). The transverse view from three polished slabs shows the colonizing zonation (CZ) from base to top of the bed by various ichnocoenoses within a 16-cm-thick unit (Fig. 20).

CZ I: This is a historical zone, a unit that is beyond the reach of even the deepest burrows (Fig. 20). CZ I includes the first 2-3 cm of the lower part of Bed 27, which comprises gray, calcareous mudstone to muddy limestone and is almost barren of trace fossils. Minor bioturbation is also limited. Body fossils are scarce, except some small, thin-bedded brachiopods and foraminifers. Pyrite frambooids and crystals are relatively rich and occur in both sediments and fossil shells (see Section 6).

CZ II: This is a transitional zone (Fig. 20), which is extremely heterogeneous from the activity of deeper burrows (Savrda, 1992). Sediments in this zone were semi-lithified to form a firmground substratum. Firmground sediments are dark-colored, and are disrupted by passively filled burrows of an ichnoassemblage characteristic of the *Glossifungites* ichnofacies. Representative ichnogenera include *Arenicolites*, *Gastrochaenolites*, *Psilonichnus*, and *Thalassinoides*. Of these, *Arenicolites* comprises vertical burrows that penetrate into the dark gray sediments. *Gastrochaenolites* comprises
tear-shaped borings, now filled with light gray, coarse-grained sediments in a
dark-colored firmground lime muddy substrate. This ichnogenus is commonly present in
the Trypanites ichnofacies as well (Wilson and Palmer, 1998; Benner and Ekdale, 2004).
The vertical cylindrical burrows of Psilonichnus are inclined, with bedding in the distal
end (Buatois and Mángano, 2011). Thalassinoides is typified by its Y-shaped ramification.
All these burrows have unlined walls and are filled with light gray-colored,
coarse-grained sediments of the overlying layer, indicating that these burrows were
passively filled.

CZ III: This is a very thin, highly condensed omission surface (Fig. 20), which is
characterized by some coarse-grained, reworked sediments that were generated by
frequent activity of wave currents. This omission surface is distinguished from the
underlying firmground ichnocoenosis of Glossifungites ichnofacies and overlying
softground ichnocoenosis of Cruziana ichnofacies (see below).

CZ IV: This is a mixed unit (Fig. 20), which is saturated with water and totally
homogenized by bioturbation. This unit, about 5 cm thick, yields ichnocoenoses
represented by minute burrows of Diplocraterion isp. and tear-shaped borings, which
resemble the vertical features of Chondrites and small Planolites. Owing to the soft
nature of substrate and intensive bioturbation, burrow boundaries and morphologies have become blurred, making it difficult to identify them confidently to ichnogenus level. This ichnoassemblage, together with the soft substrate, is characteristic of the softground ichnocoenosis of *Cruziana* ichnofacies (Seilacher, 1977).

CZ V: This thin unit is devoid of bioturbation and comprises finely laminated muddy layers (Fig. 20), which yield small pyrite frambooids (see Section 6), indicating the establishment of a quiet, low energy and probably reduced environment.

5.2. Extent of bioturbation

Ichnofabric indices (Droser and Bottjer, 1986) of the Upper Changhsing Formation (Beds 22–24) are usually rather low (ii1-2) with several peaks reaching 3 (ii3) except for the horizons near the boundary between Beds 24d and 24e (Fig. 3) that records an ichnofabric index of 4 (ii4), but bioturbated strata are about 80% of the entire measured units of the Changhsing Formation. Ichnofabric indices decrease to 2 (ii 2) again at the upper part of Bed 24e, then increase to 3 (ii3) at the top of the bed. No ichnofabrics are observed in Beds 25-26a. The ii value surges to 3 (ii3) in Beds 26b-27,
with 40% strata bioturbated. Beds 28-34 are void of ichnofabrics again. The ii value of Beds 35-57 remains rather low (ii1) except for several peaks reaching 2 (ii2) in Beds 42, 46, 52-53, and 56-57 (Fig. 3). Only 15% of the examined units are bioturbated. Accordingly, ichnofabric indices of the upper Changhsing Formation vary from 2 to 4 (ii2–4). Averagely 80% strata of the upper Changhsing Formation are significantly bioturbated. Ichnofabric indices from Bed 27 remain relatively high (ii4), although only 40% strata are bioturbated. The remaining part of the lower Yinkeng Formation records a rather low ii value (ii1) and no strata are significantly bioturbated. Ichnofabric indices in the middle and upper parts of the Yinkeng Formation vary from 1 to 2 (ii1-2). On average, 15% of strata are significantly bioturbated.

In the upper Changhsing Formation, the two bedding planes in Bed 23 containing *Dendrorhaphe* isp. (Fig. 17F) and the problematic trace (Fig. 17D), show coverage of 90% and thus indicate a BPBI of 5 (Fig. 3). The same BPBI value (ii 5) is also estimated from two horizons of Beds 24d, containing *Taenidium* burrows. Bedding planes from other horizons in the upper Changhsing Formation generally have bioturbation coverage varying from 10% to 60%, indicating BPBI of 1-5. For the top bedding plane of Bed 24e, just below the mass extinction horizon, containing *Planolites* (Fig. 17A, E) the
coverage was up to 90%, indicating a BPBI of 5. Beds 25-26a have the lowest BPBI, with almost no bioturbation recorded. Several bedding planes from Beds 26b-27 show changes in coverage from 20% to 40%, indicating a BPBI of 2-4. Bedding plane coverage in Beds 28-34 is generally rather low because bioturbation is broadly absent. Beds 35-51, overall, have bioturbation coverage <10%, but some bedding planes containing Planolites show coverage up to 20%, indicating a BPBI of 2. Another bedding plane containing Chondrites has coverage up to 90%, indicating a BPBI of 5. In the upper Yinkeng Formation, one bedding plane containing Thalassinoides shows coverage up to 20%, indicating a BPBI of 2.

5.3. Changeover of trace-fossil diversity over the P-Tr transition

Ichnodiversity, represented by ichnogeneric richness, decreased remarkably over the P-Tr transition. Eight ichnogenera are commonly encountered in the uppermost Changhsing Formation: Balanoglossites, Dendrorhaphe, Lockeia, Paleophycus, Planolites, Problematica, Taenidium, and Thalassinoides (Fig. 21A). Only Planolites is present at the top of Bed 24e, dropping to 87.5% in the upper part of Bed 24e. All
ichnotaxa disappear at the top of Bed 24e, coinciding with the PTME. As a consequence, Beds 25-26a are barren of ichnotaxa. The ichnofauna rebounded in Bed 26b and diversified in Bed 27, including seven ichnogenera: Arenicolites, Diplocraterion, Gastrochaenolites, Psilonichnus, Thalassinoides, Chondrites, and Planolites. Of particular interest is the presence of four vertically burrowing ichnogenera (Arenicolites, Diplocraterion, Gastrochaenolites, Psilonichnus) and one relatively complicated burrowing ichnogenus (Thalassinoides), implying that ichnodiversity almost reached the pre-extinction level in Bed 27 (Fig. 21A). All ichnotaxa disappeared soon after (in Bed 28). As a consequence, Beds 28-34, ranging through conodont zones I. isarcica and I. planata Zones, lack any ichnotaxa and remained poorly bioturbed (Fig. 3). The post-extinction rebound of ichnotaxa is marked by the presence of Planolites in Bed 35. Since then, ichnodiversity remained at a rather low level and did not increase until the middle-late Griesbachian, which saw the rise of Chondrites in Bed 52. Although Chondrites disappeared in the middle-late Griesbachian, the trace-fossil assemblage slightly diversified and included Planolites, Treptichnus and Thalassinoides. As a result, P-Tr ichnotaxa underwent two pronounced reductions in diversity coinciding with the two episodes of PTME calibrated to the bases of Beds 25 and 28.
Ichnofaunas fell to their lowest diversity in the early Griesbachian, and experienced a slow increase in diversity throughout the middle-late Griesbachian (Fig. 21A). However, post-extinction trace-fossil diversity never returned to the pre-extinction level.

5.4. Burrow size variations through the P-Tr transition

Nine bedding planes were examined to determine the size distribution of burrow diameters of *Arenicolites*, *Dendrorhaphe*, *Diplocraterion*, *Paleophycus*, *Planolites*, *Problematica*, *Taenidium*, *Thalassinoides*, and *Treptichnus* (Fig. 22). Burrow size change over the P-Tr transition is apparent, especially in *Planolites*, as well as other traces such as *Balanoglossites*, *Chondrites*, *Dendrorhaphe*, *Taenidium*, *Thalassinoides*, *Treptichnus*, and *Problematica* (Fig. 22). *Planolites* is distributed in ten horizons throughout the uppermost Changhsingian to middle-upper Griesbachian, and thus is a good proxy for size variation of trace fossils over the P-Tr transition. Mean diameters of the Changhsing Formation *Planolites* burrows are 7 mm, 8.5 mm, and 5.5 mm, respectively from three horizons, with maximum burrow diameter up to 9.2 mm (Fig. 22A). Burrow sizes decrease remarkably across the boundary between Beds 24 and 25, the PTME horizon.
(Fig. 1B), with mean burrow diameters of 1.7 mm and the greatest burrow diameter only 2.2 mm in Bed 27 (Fig. 22A). Burrow sizes of *Planolites* remain very small throughout the early-middle Griesbachian and become larger by the late Griesbachian (Beds 54-57). These late Griesbachian traces are still much smaller than their counterparts recorded in the pre-extinction strata (Fig. 22A). Comparable size change over the P-Tr transition is also demonstrated by both the greatest size and mean size of *Thalassinoides* from the same interval (Fig. 22B).

Several other ichnotaxa in the uppermost Permian have mean and maximum diameters, such as *Balanoglossites* (4.6 mm, 6.4 mm), *Dendrorhape* (12 mm, 17 mm), *Problematica* (22 mm, 28 mm), and *Taenidium* (7.8-8.8 mm, 9.2 mm), that are obviously larger than that of those ichnotaxa confined to the lowest Triassic, i.e., *Chondrites* (2.8 mm, 5.6 mm) and *Treptichnus* (6.3 mm, 6.3 mm) (Fig. 22C-D). When the measurements of all 273 burrows measured from the P-Tr strata of Meishan are combined, both mean and maximum diameters exhibit remarkable reduction across the boundary between Beds 24 and 25 and remain very low values until Bed 27. The same values further decline from Bed 27 to Beds 28-34, and then undergo a stepwise increase through Beds 35-57 (Fig. 21B).
Trace-fossil size variations over the P-Tr transition are consistent with figures from northern Italy (Twitchett, 1999; Twitchett and Barras, 2004) and South China (Chen et al., 2011). It should be noted that the Early Triassic Planolites traces are much smaller than their Changhsingian counterparts at Meishan (Fig. 22A), unlike the same traces elsewhere (Pruss and Bottjer, 2004). Planolites is supposed to be the least susceptible to mass extinction because this simple trace can be produced by a variety of organisms (Pruss and Bottjer, 2004). Accordingly, the Changhsingian Planolites and their Early Triassic counterparts may have been made by different organisms.

5.5. Trace fossil form and complexity

The Changhsing Formation trace fossils are morphologically diversified, and include simple, horizontal burrows (Planolites), vertical or oblique burrows (Balanoglossites and Problematica), resting traces (Lockeia), and complex forms (Dendrorhape, Taenidium, and Thalassinoides). They, however, disappear across the PTME horizon (base of Bed 25). Both Planolites and Thalassinoides rebound in Bed 27, but decrease markedly in size in comparison with their Changhsingian counterparts.
Thalassinoides is also less complex than the same trace recorded in the Changhsingian.

Complex forms, and resting and vertical traces of the Changhsingian (Balanoglossites, Lockeia, Taenidium, Dendrorhapa, and Problematica) vanish in Bed 27. Instead, the relatively complex burrow systems of the Glossifungites ichnofacies, i.e., Arenicolites, Gastrochaenolites, Psilonichnus, and Thalassinoides, characterize the ichnoassemblage in the lower part of Bed 27. Vertical burrows of Diplocraterion, together with Chondrites and Planolites also occur in the upper part of Bed 27. Accordingly, ichnotaxa recovered from the pre-extinction level are similar to those in Bed 27 in terms of complexity, although these burrows are much smaller than their counterparts elsewhere.

Early Griesbachian traces are dominated by small, simple, horizontal burrows of Planolites, as reported elsewhere (Twitchett and Barras, 2004; Pruss and Bottjer, 2004; Fraiser and Bottjer, 2009; Chen et al., 2011, 2012). In the middle-late Griesbachian trace fossils become slightly more complex and are marked by the presence of Chondrites, Thalassinoides and Treptichnus, although these burrows are still very small. Nevertheless, these middle-late Griesbachian burrows are branched and form slightly complex networks, and thus are more complex than the Planolites-dominated ichnoassemblage in the early Griesbachian.
As a result, trace-fossil complexity, reflecting behavioral complexity of the trace-makers, decreased dramatically during the PTME. Then, the trace-fossil assemblage shows an increase in complexity, varying from simple, horizontal traces (i.e., *Planolites*) in the early Griesbachian to relatively complex traces (*Chondrites*, *Thalassinoides* and *Treptichnus*) in the middle-upper Griesbachian. In particular, the reappearance of *Thalassinoides* and *Treptichnus* probably implies increasing behavioral complexity that typically indicates the beginning of biotic recovery elsewhere (Twitchett and Barras, 2004).

5.6. Infaunal tiering

Levels of tiering above and below the sediment were greatly reduced after the PTME (Ausich and Bottjer, 1982, 2002). At Meishan, the change in infaunal tiering over the P-Tr transition is reflected by the penetration depth of burrows (Fig. 21C), which was measured in the field. Vertical burrows of the Changhsing Formation may extend a maximum depth of 10 cm into the sediment, indicating a rather deep tiering level (ii5). In contrast, burrows of *Planolites* and *Thalassinoides* recorded in Bed 27 may penetrate to <
2 cm into the sediment. In particular, *Thalassinoides* commonly shows the second tiering
level (ii2) (Bottjer and Droser, 1994). Early Griesbachian *Planolites* has burrows
extending to a maximum depth of only 0.5 cm (Fig. 21C) indicating the lowest tiering
level (ii1) (Bottjer and Droser, 1994). Thus, tiering fell to its minimum level in the early
Griesbachian. An increase in tiering level during the middle Griesbachian is marked by
the presence of *Chondrites*, an anoxic burrow system penetrating to a depth up to 1-2 cm
and indicating the second tiering level (ii2) (Bottjer and Droser, 1994). The same tiering
level is also reflected in upper Griesbachian *Thalassinoides* and *Treptichnus* burrows,
which may extend to a maximum depth of 1-2 cm (Fig. 21C). Accordingly, the tiering
level decreases significantly across the PTME horizon in Meishan, and then increases
throughout the Griesbachian (Fig. 21C).

6. *Size variations of pyrite frambooids and redox conditions over the P-Tr transition*

Pyrite is commonly present in the latest Changhsingian to Griesbachian rocks at
Meishan (Wignall and Hallam, 1993), which is also confirmed by our observations of
thin sections through the P-Tr transition at Meishan. Several pyrite-enriched beds have
been treated as indications of anoxic conditions at Meishan (Wignall and Hallam, 1993).

In particular, pyrite framboids, which are spherical aggregates of pyrite microcrystals, are rather abundant in these pyrite-enriched beds near the PTB at Meishan (Jiang et al., 2006; Shen et al., 2007). Pyrite framboids in ancient and modern sediments are interpreted as the result of redox conditions (e.g., Bond and Wignall, 2010), and these authors show that small framboids, usually 3-5 µm in diameter, indicate euxinic conditions (H₂S-bearing, O₂-free bottom waters). Accordingly, pyrite framboids have been considered as one of the most important pieces of evidence indicating redox conditions over the P-Tr transition worldwide (Wignall et al., 1998, 2005; Jiang et al., 2006; Shen et al., 2007; Gorjan et al., 2007; Bond and Wignall, 2010; Algeo et al., 2011b).

At Meishan, Jiang et al. (2006) reported that pyrite framboids are commonly present in all beds through the PTB (Beds 24-29), based on etched residues from bulk samples. Shen et al. (2007) also observed framboids in situ on polished blocks and etched residues. Both studies detected that framboids are abundant in Bed 25. Contrasting to Jiang et al.’s (2006) observation, Shen et al. (2007) found no pyrite framboids in Bed 27. However, unequal sampling in various beds near the PTB, for instance, 40 g each from Beds 25 and 26, but only 5 g each from Beds 24, 27, 28 and 29 may have biased their
observation (Shen et al., 2007). Bed 27 comprises various lithologies from its base to top, which may have been deposited in different environments (Figs. 19-20). Thus, pyrite framboids may be absent in these bioturbated layers (i.e., CZs II, III-IV in Bed 24; Fig. 20), but instead may occur in finely laminated layers without bioburbation (i.e., CZs I and V; Fig. 20).

We have also observed pyrite framboids in continuous thin sections throughout Beds 24-30. We used a FEI Quanta 400 Scanning Electron Microscope (SEM) equipped with a GENESERS 2000 energy dispersive spectrometer (EDS) at the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Wuhan, China. SEM images and EDS spectra were produced by the Zeiss VPSEM coupled with an energy dispersive X-ray spectrometer. We confirmed Jiang et al.’s (2006) observation that both pyrite framboids and crystals occur in Bed 27 on brachiopod shells and in foraminiferal tests and sediments (Fig. 23). In addition, we measured framboid sizes in samples from Beds 29-60 using the SEM. Pyrite framboids are abundant in samples from 17 horizons over the P-Tr transition (Fig. 24). The majority of framboid diameters in most measured beds are smaller than, or around 5 µm, except for Beds 28 and 44, in which most framboids have diameters of 7-8µm. Moreover, framboid
diameters are concentrated in a narrow size range (<10µm) in Beds 27, 28, 43, and 58. In contrast, they have a greater size range in Beds 24b, 24e, 25-26, 29-30, 39, 42, 49, 51-52 and 56, with maximum diameter up to 20µm in Bed 51.

Bond and Wignall (2010, table 1) proposed several characters, including framboid diameter and pyrite morphology, to determine redox conditions during deposition. In general, when framboids are small (mean diameters: 3-5 µm), abundant, with a narrow size range, and form the dominant pyrite fraction, they could have been deposited in euxinic condition (with a persistently sulfidic lower water column). If framboids are small (mean diameters: 4-6 µm), abundant, with a few, larger forms, and dominate the pyrite fraction, then they could have been deposited in anoxic condition (without oxygen in bottom waters for long periods). When framboids have mean diameters of 6-10 µm and are moderately common, with a few, larger framboids together with some crystalline pyrite, they could have been deposited in lower dysoxic condition (with weakly oxygenated bottom waters). In upper dysoxic condition (with partial oxygen restriction in bottom waters) framboids are commonly to rarely present, with a broad range of sizes, only a small proportion of framboids < 5µm, and the majority of pyrite as crystals. In oxic condition (without oxygen restriction), no framboids are present,
and pyrite crystals occur rarely.

If these five criteria given by Bond and Wignall (2010) are followed, we can determine redox conditions over the P-Tr transition in Meishan. Bed 24 contains abundant framboids, usually around 5 µm in diameter with some larger framboids, and their size range is relatively broad, pointing to anoxic conditions. Framboids in Beds 25-26 are usually 3-5 µm in diameter, a narrow size range, and no pyrite crystals are present, suggesting euxinic conditions (Fig. 25). Framboids from Bed 27 have a relatively large diameter and a broad size range (Fig. 24), and are also associated with some large pyrite crystals, pointing to a lower to upper dysoxic condition (Fig. 25). Pyrite framboids are moderately common in Bed 28 and have mean diameters of 8-9 µm, but no larger framboids and crystalline pyrite occur. Thus, Bed 28 is inferred to be deposited in a transitional zone between anoxic and lower dysoxic conditions based on the criteria determining redox conditions proposed by Bond and Wignall (2010). Redox conditions became euxinic soon after in Bed 29, in which framboids are very small (3-5 µm) and have a narrow size range, without pyrite crystals. It should be noted that no pyrite framboids were found in Beds 30-35, although a pronounced negative excursion of carbon isotopes (Xie et al., 2007) and environmental stress indicated by biomarker
signals (Yin et al., 2012) occur in these beds. Framboids from Beds 39 and 42 indicate euxinic-anoxic transitional conditions in terms of diameter, size range and association with pyrite crystals. Framboids from Bed 43 are 4-6 µm in diameter, but have some larger forms and are also associated with some pronounced pyrite crystals, and thus indicate a lower to upper dysoxic condition. Then, redox conditions indicated by pyrite framboids changed to anoxic to euxinic transitional conditions. Surprisingly, framboids from Bed 58 suggest euxinic condition, which coincides with the last negative excursion of carbon isotopes in the middle-late Griesbachian detected by Burgess et al. (2014).

7. Assessing ecologically PTME and its aftermath

7.1. Testing ecologically extinction patterns

The updated fossil record from Meishan shows two pronounced declines of species richness at the bases of Beds 25 and 28 (Song et al., 2013a; Fig. 26). Similarly, fossil fragment contents recorded in thin sections also show two distinct drops in both abundance and diversity corresponding to the top of Bed 24e and base of Bed 28 (Figs. 6,
Further, ichnodiversity also declined within Beds 24 and 27. In Bed 24, trace fossils are rather abundant and comprise four distinct ichnogenera: *Balanoglossites*, *Planolites*, *Taenidium* and *Thalassinoides* in horizons near the boundary between Beds 24d and 24e, but only *Planolites* persisted into Bed 24e-6, in which relatively large burrows are densely packed, indicating a considerably high bioturbation level. All ichnotaxa disappeared in Beds 25-26a. Similarly, ichnotaxa decline from five ichnogenera (*Arenicolites*, *Gastrochaenolites*, *Planolites*, *Psilonichnus*, and *Thalassinoides*) in CZ II (Bed 27b) to three ichnogenera (*Diplocraterion*, *Chondrites* and *Planolites*) in CZ IV (Bed 27c), and then further declined and disappeared at the top of Bed 27d. Other proxies of trace fossils and bioturbation also show two pronounced declines corresponding to the bases of Beds 25 and 28. Clearly, the PTME ecologic crisis comprised two phases, coinciding with metazoan extinctions calibrated to the bases of Beds 25 and 28 (Song et al., 2013a).

In addition, both fossil fragment contents and ichnodiversity show that a pronounced decline in diversity and abundance started at the stratal interval 10 to 19 mm below the top of Bed 24e. The boundary between Beds 24e-5 and 24e-6 is the most distinct eliminated horizon of skeletal fragment of major fossil groups, coinciding with
end-Permian sulfur anomaly (Kaiho et al., 2006a) and the start of the negative
end-Permian carbon isotopic excursion (Kaiho et al., 2009), and thus may indicate the
PTME. Abundant sponge spicules above this event horizon indicate that they lasted in
seawater for a while, although complete sponge fossils disappeared at the PTME event. It
is therefore unlikely that the disappearance of calcareous fossils at the top of bed 24e-6
was a result of an increase in the input of terrestrial material associated with the facies
shift, as indicated by the lithologic shift from the limestone of Bed 24 to the claystone of
Bed 25 and black shale of Bed 26. Instead, the extinction of calcareous biota and the
associated environmental perturbation was most likely caused the lithologic change from
limestone to mudstone. As a result, the sharp decline in biotic abundance and diversity
10-19 mm below the top of Bed 24e may signal the first episode of the PTME previously
inferred from statistical paleontological data (Song et al., 2013a).

7.2. Ecologic collapse lagging behind biodiversity crisis during the PTME

At Meishan, the Permian biota experienced a dramatic drop in diversity at the
base of Bed 25, with 172 species (94%) being wiped out in Beds 25-26 and no
pronounced reduction of species richness in Bed 28 (Jin et al., 2000). The updated fossil
record obtained from Meishan shows that species richness was reduced by at least 79%
across the boundary between Beds 24e and 25, compared to 65% loss in species richness
across the boundary between Beds 27d and 28 (Song et al., 2013a). This means that
marine animals suffered a more severe depletion in species richness in the first phase of
the PTME than in the second phase of the same event (Fig. 26). The biodiversity decline
pattern from Meishan is confirmed by the same pattern at a further seven PTB sections in
South China (Song et al., 2013a). It should also be noted that generic richness declined by
a similar magnitude, 85% and 82%, in the first and second phases of the PTME,
respectively in Meishan, but both generic and species richness underwent a stepwise
decline from the uppermost Changhsingian to lowest Griesbachian (Fig. 26).

Consequently, biotic diversity suffered a larger loss in the first episode than in the second
episode of the PTME in terms of the number of lost taxa. This pattern is reinforced by
fossil fragment content variations across the PTME horizons. Fossil components usually
occupy nearly 70% in all rock in strata below Bed 25, but only about 30% in Bed 27, and
FFA lost nearly 60% in thin section (Fig. 14). Over the same period, 11 Permian orders
declined to five orders in Bed 27, losing 54.5% in ordinal richness.
Both the standard diversity Shannon index \([\text{Exp} (H)]\) and dominance index \((D')\) assess whether the shelly community possesses a healthy structure. \(\text{Exp} (H)\) values declined by 43.6% from the \(R-P\) to \(T\) communities, and 55.5% from the \(P-T\) to \(C-O\) communities, coinciding with the first and second phases of the PTME, respectively. This means that the shelly communities suffered a greater loss in community diversity in the second phase of the PTME than in the first phase. Similarly, standard diversity dominance \((D')\) increases by 34% and 54% during the two pronounced drops in diversity, respectively (Table 6). This means that the shelly communities became more uneven after the second phase of the PTME than after the first phase. Thus, shelly communities underwent relatively more serious ecologic crisis in the second phase than in the first phase of the PTME. This observation is also reinforced by ichnofaunal variations and ichnofabric changes over the P-Tr transition in Meishan.

The presence of seven ichnogenera in Bed 27 suggests that ichnogeneric richness nearly recovered to the pre-extinction level, although there was a taxonomic loss in Beds 25-26a. In contrast, a more dramatic ichnofaunal loss occurred in the second phase of the PTME, corresponding to Bed 28. As a consequence, Beds 28-34 are barren of ichnotaxa. Thus, ichnofaunas suffered a more severe decline in the second phase of the
PTME. This pattern is also strengthened by burrow size variations and tiering level changes, both of which remained relatively high in the Changhsingian, and experienced a stepwise decline through Beds 23-27, then fell to their lowest values in the early Griesbachian (Beds 28-34). Ichnofabric variation also shows that Bed 27 still remains highly bioturbated and yields rather complex burrow systems of the *Glossifungites* ichnofacies and *Cruziana* ichnofacies, which are commonly present in the pre-extinction period, thus showing the largest turnover at the base of Bed 28 rather than at the base of Bed 25. In contrast, ichnotaxa became very rare after the second phase of the PTME, although 2-3 ichnotaxa rebounded in the middle-late Griesbachian. Consequently, the greatest losses of ichnotaxa correspond to the top of Bed 27, simultaneous with the second phase of metazoan extinction in Meishan (Song et al., 2013a). This ichnodiversity drop coincides with a remarkable decrease in tiering level (Fig. 21) and burrowing intensity (Fig. 3). Ichnofabric indices recorded in the upper Changhsing Formation are rather high (ii4-5) (Fig. 3). Complex traces of both the *Glossifungites* and *Cruziana* ichnofacies recorded in Bed 27 (Figs. 19-20) also indicate a fairly high ichnofabric index (ii3-4). Consequently, there was not a sharp decrease, but a gradual decrease, in burrowing intensity (ii4-5 down to ii3-4) over the first phase of the PTME. This is in
sharp contrast to the pronounced drop in biodiversity of metazoans in this phase of the PTME (Fig. 26), suggesting a gradual worsening in environmental conditions. In contrast, almost all of the complex traces of the *Glossifungites* and *Cruziana* ichnofacies disappeared in the second phase of the PTME. The early Griesbachian *Planolites* is confined to discrete horizons (ii1-2) separated by metres of unbioturbated sediment, and indicates a rather low ichnofabric index (ii1) (Fig. 3). A low ichnofabric index indicates an absence or rarity of burrowing infauna, which in turn implies a stressed environment immediately after the PTME (Chen et al., 2011). Accordingly, the great loss of burrowing infauna and associated environmental stress occur at the horizon between Beds 27 and 28. These facts imply that ecologic collapse of marine ecosystems post-dated the metazoan biodiversity crisis at Meishan.

Contrasting to the two-stage extinction pattern (Song et al., 2013a), Shen et al. (2011b) and Wang et al. (2014) argued that the severest biodiversity declines fell in a short period equivalent to Beds 25-28 of Meishan, and there was one prolonged extinction rather than two discrete episodes. Indeed, Beds 25-28 represent a very short duration of about 60 ky (Burgess et al., 2014). However, all lines of evidence, including fossil fragment contents, and ichnofabric and community structural changes, show that
the P-Tr ecologic crisis clearly comprises two pronounced steps, at the bases of Beds 25 and 28 (Figs. 14, 21, 26). Nevertheless, whether the mass extinction occurred as one prolonged event or two pulses, all studies agree that Beds 25-28 of Meishan and their equivalents represent a critical period when the greatest biotic turnover of life on Earth took place in Meishan. During this critical turnover period, the ecologic crisis clearly lagged behind the diversity decline. As a result, the Meishan fossil record shows that the mass extinction started with a dramatic depletion of biodiversity and ended with a severe ecologic crisis.

7.3. Dramatic increase in seawater surface temperature and its consequence

Recent oxygen isotopic studies of conodont bioapatites reveal that sea surface temperature rose ~9 °C from Bed 24e to Bed 27a in Meishan (Joachimski et al., 2012; Sun et al., 2012; Fig. 26). However, the precise relationship between temperature increase and biotic extinction remains unclear owing to the lack of oxygen isotopic values from Bed 25, the base of which coincides with the PTME (Shen et al., 2011b) or the first phase of the PTME (Song et al., 2013a). The same is also true for the relationship
between the temperature rise and the dramatic negative carbonate carbon isotopic excursion (Fig. 26). The solution is to undertake more detailed study of conodont oxygen isotopes of the PTB beds from less condensed sections than Meishan to evaluate whether temperature change leads or lags the extinction (Burgess et al., 2014). Hinojosa et al. (2012) found a negative shift in $\delta^{44/40}$Ca of conodont bioapatite in the Great Bank of Guizhou, South China during the same interval as temperature increase in Meishan. This $\delta^{44/40}$Ca excursion is also coupled with a major shift in $\delta^{13}$C$_{carb}$ composition from an average of approximately $+3.5\%_{\text{oo}}$ in the latest Permian to approximately $-1\%_{\text{oo}}$ in the earliest Triassic (Payne et al., 2004). The anomaly of $\delta^{44/40}$Ca therefore was interpreted as a consequence, in part, of acidification of the ocean. Thus, oceanic acidification in platform areas of the Great Bank of Guizhou may have resulted from elevated seawater temperature (Burgess et al., 2014). However, this ocean acidification seems not to have spread to the Meishan area because rather abundant and diverse complex traces of both Glossifungites and Cruziana ichnofacies occur in Bed 27 (Figs. 19-20), although calcareous skeletons decreased significantly in Beds 25-28 (Fig. 14).

Previously, the irregular surface occurring in the middle of Bed 27 at Meishan was interpreted as a submarine dissolution surface, explained by a regional ocean
acidification in South China (Payne et al., 2007, but see Wignall et al., 2009). This pronounced irregular surface, however, was re-interpreted as a distinct firmground surface, on which abundant complex traces of *Glossifungites* ichnofacies occur (see Section 3.5). Firmgrounds of *Glossifungites* ichnofacies are usually characteristic of initial transgression, and such horizons are usually employed to define sequence boundaries (Buatois and Mángano, 2011). Thus, no sign of acidification is recorded in Bed 27 in Meishan.

Another potential consequence of elevated temperature is intensified chemical weathering (Sheldon, 2006) and consequent increased physical erosion of soils on land (Sephton et al., 2005; Xie et al., 2007), or a combination of these processes. These processes are also indicated by the increased chemical index of alteration (CIA) profile immediately after the first phase of the PTME (Bed 25; Fig. 26). It should be noted that the CIA value was calculated as \( \frac{Al_2O_3}{(Al_2O_3+K_2O+Na_2O)} \) (Zhao et al., 2013a), a modification of the original CIA equation (Nesbitt and Young, 1982). Increased chemical weathering during the PTME and its aftermath is also mirrored by the Eu/Eu* profile of conodont bioapatites (Zhao et al., 2013a). The latter rare-earth elemental (REE) proxy is a useful tracer of sediment provenance because fractionation between Eu\(^{+2}\) and Eu\(^{+3}\) does
not occur under Earth-surface conditions (Elderfield and Greaves, 1982). Eu$^{+2}$ tends to become segregated into feldspar during magmatic differentiation, resulting in Eu/Eu* values >1.0 in the crystal fraction and <1.0 in the residual fluid (Zhao et al., 2013a). Eu/Eu* ratios >1.0 are characteristic of magmas from lower crustal or mantle sources where substantial feldspar crystallization has taken place (Condie, 2001). Although the REE “fingerprint” of the ash-rich clastics is reflected by both CIA and Eu/Eu* profiles that match one another throughout P-Tr transition in Meishan (Fig. 26) and these ash beds near the PTB likely sourced from regional convergent continent marginal volcanisms (Gao et al., 2013, 2014), the shift toward Eu/Eu* values of 1.0–1.5 in Bed 24e, immediately preceding the PTME, may be evidence of a transient influx of volcanic material with a lower crustal or mantle source. Zhao et al. (2013a) argued that these mantle-sourced ash fingerprints indicated by Eu/Eu* values could be the product of the Siberian trap eruption (Reichow et al., 2009). Thus, this volcanic eruption could have caused the severe biocrisis and rapid increase in sea-surface temperature occurring ~20-80 kyr later following the estimate of maximum and minimum sedimentation rates given by Burgess et al. (2014).

Burgess et al. (2014) also estimated the rate of temperature rise in Beds 25-28 as
an ~1 °C increase per 6,000 y, which is comparable with the rate and magnitude of the increase at the Paleocene–Eocene Thermal Maximum (Zeebe et al., 2009) and Pleistocene/Holocene postglacial warming (~2 °C/5 ka) (Lea et al., 2000). However, this estimate of the rate of temperature rise needs to be cautious because no temperature data is available from Bed 25 and the temperature rise spans Beds 24e-27 (Sun et al., 2012). To sum up, although the killing mechanism of the ~9 °C increase of seawater surface temperature on organisms remains unclear, this rapid temperature increase coincides with biotic turnover and ecologic collapse during the PTME at Meishan. Nevertheless, the elevated temperature seems to have had little effect on ichnofaunas and ichnofabrics, as indicated by abundant ichnofaunas living in the firmground of the Glossifungites ichnofacies (Bed 27), but instead resulted in dramatic losses of fossil skeletons in sediments (Fig. 14).

In addition, Sun et al. (2012) reported the acme of high seawater temperatures occurred in the late Griesbachian, corresponding to the upper I. isarcica Zone and lower C. planata Zone (Sun et al., 2012, fig. 2), which range from Beds 48-54. These two zones are amended herein (Fig. 2) and are equivalent to the upper part of C. planata Zone in the revised conodont zation (Fig. 2). This acme of high temperature postdates the second
negative shift excursion of carbon isotops of Xie et al. (2007) and includes the second
negative shifting excursion of carbon isotopes of Burgess et al. (2014). Surprisingly, this
interval saw an increase in biodiversity (Chen et al., 2002, 2007), ichnological
amoraliation and bioturbation (Fig. 3). Accordingly, the acme of high temperature has
little effect on faunas.

7.4. Anoxic events and biotic response

7.4.1. Anoxic events

At Meishan, Wignall and Hallam (1993) recognized an anoxic
event associated with the PTME, but considered that the greatest acme of anoxia, coupled
with a maximum flooding event, occurs in the lower Yinkeng Formation. Wignall and
Twitchett (2002) believed that the oxygen-deficient waters spread into exceedingly
shallow settings near the PTB in the Tethys regions (i.e., South China). More recently,
multiple geochemical signals indicate the existence of anoxic to euxinic conditions
before, during and after the PTME at Meishan.

An exceptional increase in sea surface temperature is also believed to be
synchronous with the flooding of shelf areas with anoxic and euxinic waters during the
P-Tr transition (Sun et al., 2012). Both extremely high values of total organic content (TOC) (Yin et al., 2012) and reduced sizes of pyrite framboids (Fig. 26) indicate euxinic to anoxic condition in Beds 25-26, coinciding with the PTME. However, pyrite framboids from Bed 27 are generally larger than 5 µm in diameter with abundant crystals and thus indicate the upper part of dysoxic conditions (Fig. 25). Moreover, high bioturbation levels are also observed in upper part of Bed 26 and multiple layers of Bed 27. Thus, a euxinic to anoxic condition was probably limited only to Beds 25-26a, which is less than 20 ka based on duration estimate of conodont zones from these beds (Table 2), a much shorter period than previously thought. The anoxic condition of the water column is also reflected by the abrupt increase of Ce/Ce* values of conodont bioapatite from ~0.7–0.8 in Beds 23-24 to 0.9–1.1 in Beds 25-27b (Zhao et al., 2013a; Fig. 26). Values of 0.7–1.0 are sustained through Beds 27c to 30, above which Ce/Ce* decreases to 0.5–0.7. It should be noted that Ce/Ce* ratios derived from Bed 27a-d are not totally in accordance with size analysis of pyrite framboids, which shows that Bed 27a-d may represent redox conditions ranging from anoxia to upper level of dysoxia (Fig. 25). Although Ce/Ce* values from Meishan may have been biased by the fingerprint of clay input, Ce/Ce* values of 0.9–1.1 indicate an anoxic depositional system (Zhao et al., 2013a; Shen et al.,
This inference is consistent with the results of earlier studies documenting anoxia around the PTME in South China PTB sections (Grice et al., 2005; Algeo et al., 2007; Shen et al., 2007; Cao et al., 2009; Bond and Wignall, 2010; Luo et al., 2010) and globally (Algeo et al., 2010, 2011b; Brennecka et al., 2011). Euxinic condition may have occurred prior to the PTME in Meishan, i.e., Beds 22-24, demonstrated by the anomaly of sulfur isotopes (Shen et al., 2011a) and various biomarker signals in Beds 22-24 (Grice et al., 2005; Cao et al., 2009; Luo et al., 2010, 2011). Algeo et al. (2011a) also interpreted the anoxic and euxinic conditions as a result of an expansion of the oxygen minimum zone (OMZ) in the water column over the P-Tr transition. These authors considered that the OMZ may have expanded prior to the PTME in Meishan.

A post-extinction reduced condition is also indicated by a pronounced negative excursion of carbon isotopes in Beds 34-36 (Xie et al., 2007; Luo et al., 2010; Fig. 26), coupled with an increase in TOC and terrestrial input indicated by various biomarker signals (Yin et al., 2012), and elevated contents of CO₂ (Fraiser and Bottjer, 2007). The CIA profile slightly increases in Beds 34-36, indicating elevated chemical weathering on land, which is consistent with the increased TOC and terrestrial input (Yin et al., 2012).
addition, conodont bioapatite from Beds 33–39 generally yields lower Ce/Ce* ratios (0.4–0.7) that may indicate an oxic to suboxic depositional environment. Conodont bioapatite Ce, however, was probably derived mainly from detrital clay minerals and taken up during diagenesis, as indicated by other REE proxies (Zhao et al., 2013). If so, the observed Ce/Ce* ratios only reflect the REE composition of the source clays (Zhao et al., 2013a).

Alternatively, size variations of pyrite framboids indicate that Beds 27-29 record a dramatic redox change from upper dysoxic to euxinic conditions (Fig. 25). A euxinic to anoxic condition prevailed throughout Bed 29 to Bed 42 (Fig. 25). The combination of mean size of framboids and presence of both larger framboids and crystal pyrites indicates Bed 43 may be deposited in a lower to upper dysoxic condition. If a redox interpretation is warranted, then this pattern suggests that the anoxic episode following the PTME in Meishan lasted a relatively long duration, probably ~50 kyr. Moreover, mean sizes and morphologies of framboids from Beds 44-58 also generally reflect an anoxic to euxinic condition, which, however, is not supported by various ichnological proxies.
7.4.2. Biotic response

The pre-extinction anoxic to euxinic conditions are generally supported by the presence of abundant small pyrite framboids, 3-5 µm in diameter, in Beds 23-24 (Figs. 23-24). However, biodiversity of metazoans remains very stable, with 64-78 species in 34-44 genera in each layer through Beds 24a to 24e (Fig. 26). Bed 24 contains 82 species in 47 genera, and there are similar numbers in Bed 23 (Jin et al., 2000). Thus, no major losses in species and generic richness are recognizable in Beds 23-24. Fossil fragment contents are almost the same in each layer through Beds 22-24, except for the top 1-2 cm of Bed 24e, in which there is a pronounced loss in fossil components across the boundary between Beds 24e-5 and 24e-6 (Figs. 6, 14). Fossil fragment contents fell by >16% in thin section from Beds 24e-5 to 24e-6. The FFA of Bed 24e-5 comprises 10 major fossil groups that are commonly present in all Permian limestones, but five clades, ostracods, bryozoans, calcareous sponges, gastropods, and macroalgae, disappeared, losing 50%, across this boundary (Figs. 6, 14). The FFA of Bed 24e-6 is dominated by sponge spicules (35%) and thus has a high dominance and low diversity and evenness, in contrast to the low dominance, high diversity/evenness FFA in Bed 24e-5 (Fig. 6). Furthermore, the last
occurrence of Permian fusulinids was also bracketed to the base of Bed 24e-6 (Kaiho et al., 2006b).

Ichnodiversity also declined significantly across the boundary between Beds 24e-5 and 24e-6 (Fig. 21A). These relatively complex or vertical burrows such as *Balanoglossites* and *Thalassinoides*, which usually occur in oxygenated settings, disappeared at the base of Bed 24e-6. Instead, only simple, horizontal burrows of *Planolites* occur in Bed 24e-6. Ichnofabrics, however, do not exhibit a major change across the same boundary (Fig. 3), with abundant *Planolites* burrows being densely packed on the surface of Bed 24e-6. However, most geochemical studies do not have such a high sampling intensity, and thus neglected this boundary.

Both metazoan biodiversity and fossil fragment contents experienced dramatic declines in Beds 25-26a. Other ecologic measures, such as community structures, ichnodiversity, burrow size, tiering level, and ichnofabric variation, also indicate an ecologic crisis in Beds 25-26a, coinciding with the anoxia indicated by both pyrite framboid sizes and various geochemical signals (Fig. 26). However, the metazoan fauna from Bed 27 is rather abundant and diverse, including 66 species in 34 genera (Song et al., 2013a). Both community structural indices and fossil fragment contents indicate that
metazoans had recovered well in Bed 27. The presence of abundant complex burrows in Bed 27 indicates the infaunal proliferation in the firmground of *Glossifungites* ichnofacies (Fig. 20). The occasional occurrence of pyrite frambooids in Bed 27 may indicate a very short period of anoxic condition, but Bed 27, as a whole, represents a dysoxic to oxic condition in which benthos and infaunas proliferated. By contrast, all data, including the low ichnodiversity (only *Planolites*), small burrow size, low trace complexity, low ichnofabric from Beds 29-51 indices and low tiering level as well as low-diversity metazoans (Chen et al., 2007, 2010a), support the view that anoxic conditions may have prevailed throughout the early Griesbachian in Meishan (Wignall and Hallam, 1993; Xie et al., 2007; Yin et al., 2012). Of these, Beds 29-34 are barren of trace fossils and bioturbation. This is supported by trace fossil size, which is also regarded as a proxy for paleoenvironmental conditions (Twitchett, 1999; Pruss and Bottjer, 2004). In general, small-sized traces are usually found in poorly oxygenated sediments (Savrda and Bottjer, 1987) or brackish environments (Pemberton et al., 1982; Buatois et al., 2005) or habitats with low nutrient supply (Jumars and Wheatcroft, 1989). Thus small traces are characteristic of stressed environments (Twitchett, 1999; Pruss and Bottjer, 2004). The dramatic size reduction of trace fossils
after the PTME indicates environmental stresses associated with the PTME, and the small sizes of Early Triassic traces suggest prolonged environmental stress following the event (Bottjer et al., 2008).

7.5. Testing extinction mechanisms

Multiple scenarios have been proposed to interpret the killing mechanisms of the PTME, including widespread anoxia, hypercapnia, massive volcanic eruption, global warming, ocean acidification, and increased sediment flux (Erwin, 2006; Knoll et al., 2007; Clapham and Payne, 2011; Algeo and Twitchett, 2010; Algeo et al., 2011a; Joachimski et al., 2012; Sun et al., 2012; Burgess et al., 2014; Song et al., 2014). However, the true causes of this biocrisis still remain unclear due to the incomplete record of evidence supporting any of these alternatives. Recently, Song et al. (2013a) suggested that different extinction mechanisms may have driven each of these two pulses given their differences in biodiversity and ecologic losses. These authors considered that anoxia may be related to the first-pulse losses of biota, but played a crucial role in the second-pulse biocrisis (Song et al., 2013a). Elevated sea-surface temperature not only resulted in the spread of anoxia but also killed
directly shallow-water taxa, while the anoxia killed the deep-water organisms (Song et al., 2014). However, extinction and survival selectivity of various fossil groups is more complicated than previously thought (i.e., Song et al., 2013a, 2014). This is because various elements of the same clade may have different lifestyles. For instance, the P-Tr brachiopods have six types of lifestyles based on attachment modes on the substratum: burrowing, body cementation, pedicle attaching on substratum, body spines anchoring on substratum, pedicle attaching on objects, and clasping spines on other shells/or objects (Chen et al., 2006a, 2011b). These brachiopods having the last two types of attachment modes behaviour like nektons. Moreover, some shallow-water elements were also able to survive in deep niches during the latest Permian (Chen et al., 2006a). It is also true for the P-Tr bivalves that embrace several lifestyles (Huang et al., 2014). Accordingly, our high resolution comprehensive analyses of biodiversity, community structural, fossil fragment, ichnological, and redox condition changes associated with these two discrete events allow an evaluation of the proposed kill mechanisms for these two ecologic crises.

Most of the Permian brachiopods became extinct in the first extinction. The survivors are dominated by chonetids or chonetid-like productids or small, thin-shelled spiriferids/rhynchonellids that usually have attachment modes of clasping spines on other
shells/or objects or pedicle-attaching on other shells or objects (Chen et al., 2005a, 2011b). These survivors attached their bodies on some float objects (i.e., other shells and algae) suspending above the seafloor (Chen et al., 2005a, 2011b), and thus provided brachiopods higher adaptability surviving the deleterious environments, i.e., increased acidity of precipitation (Wignall, 2007), large-scale marine acidification (Clapham and Payne, 2011) and widespread anoxia (Wignall and Twitchett, 2002; Payne and Clapham, 2012) during the first biocrisis. Inarticulated brachiopods i.e., lingulids also survived this event, although having a burrowing lifestyle. This is because lingulids are able to survive in poorly oxygenated waters due to having respiratory pigment acting the function to transport oxygen or to store oxygen within the body tissues under anoxic conditions or during cessation of respiration (Williams et al., 1997).

Similarly, Huang et al. (2014) argued that the anoxia or acidification may have impacted seriously on bivalve’s extinction and survival selectivity during the first extinction based on ecologic analysis of the P-Tr bivalves. As a result, both brachiopod’s and bivalve’s evidence indicates that anoxia impacted clearly by in the first-pulse biocrisis (Chen et al., 2011b; Huang et al., 2014). The acidification associated with this extinction cannot be excluded (Clapham and Payne, 2011; Hinojosa et al., 2012).
anoxia or acidification, however, lasted a very short duration, ~30 ka, as discussed above.

Furthermore, a rapid increase of about ~9°C of sea-surface temperature (within a period of ~30 ka) across Beds 24e-27a (Sun et al., 2012) must have facilitated respiratory frequency and accelerated oxygen consumption of most brachiopods and become lethal to brachiopods, and thus causes morality, regardless their shallower or deeper habitats (Chen et al., 2014b in this volume). The rapidly elevated seawater temperature also coincides with the first dramatic losses of body fossil biodiversity and fossil fragments as well as moderate losses of ichnodiversity and community diversity, and a moderate decrease in bioturbation, tiering levels of infaunas and burrow sizes.

However, marine ecosystems seem not to have collapsed completely during the first-pulse crisis (Chen and Benton, 2012), some organisms survived the short environmental and climatic devastation. Thus, both biodiversity and ichnodiversity, and all of ichnological and community structural measures rebounded rapidly in Bed 27a-d (Fig. 26).

Like the first extinction, the second-pulse biocrisis is also associated with a clay bed (Bed 28), in which pyrite frambooids indicate a lower dysoxic to anoxic condition (Fig. 25). However, the redox condition became euxinic soon after and is indicated by
framboids obtained from the base of Bed 29. Thus, a dramatic change from upper dysoxic to oxic condition in Bed 27 to euxinic condition in basal Bed 29 indicates an anoxia/euxinia coincided with the 2nd biocrisis, which is followed by a long period of euxinic to anoxic conditions, which was probably driven by a relatively long (>62 ka) acme of high temperature (up to 35-37°C) in earliest Griesbachian. Accordingly, both epifaunal and infaunal ecosystems collapsed after suffering such a long period of lethally hot seawater temperature and widespread anoxia in earliest Triassic oceans (Fig. 26). This is reinforced by the replacement of free-lying brachiopod-dominated communities in Bed 27 with nekton-dominated communities in Beds 31-37 (Chen et al., 2010a) and Beds 28-34 barren of bioturbation and ichnofossils (Figs. 3, 26). As stated above, these surviving brachiopods yielded from Beds 26-27 should have enhanced resistant ability to anoxic or acidified water mass near seafloor because they survived from the first-pulse crisis. The morality of the free-lying brachiopods in the second-pulse crisis is probably due to the loss of other shells or float algae, on which the brachiopods attach using either pedicle or clasping spines. Accordingly, the killing mechanisms for these two extinction events near the PTB seem not to be fundamentally different from one another, although no sign of acidification has
been reported in the second phase of the PTME. However, a short anoxia or acidification probably caused by a rapid increase in seawater temperature may have played an important role in the first-pulse biocrisis, while the long-lasting and widespread anoxia induced by a long period of high temperature condition may have killed most organisms in the second-pulse crisis.

7.6. Post-extinction amelioration of marine ecosystems in late Griesbachian

Post-extinction benthic communities did not appear to return to normal until the early Middle Triassic (Chen and Benton, 2012). The deleterious environment that prevailed in early Triassic oceans may be largely responsible for this long-delayed recovery (Bottjer et al., 2008). In particular, Early Triassic carbon isotopic records show several negative excursions that indicate sharp global warming (Payne et al., 2004), and these coincide with diversity drops. Furthermore, intrinsic relationships between organisms and ecosystem structures may also have slowed down biotic recovery following the PTME (Chen and Benton, 2012). Recent studies show that the biotic recovery process may be mirrored by stepwise establishment of trophic structures of marine ecosystems throughout Olenekian-Anisian interval (Chen and Benton, 2012).
However, biotic recovery may occur earlier in oxygenated environments (Twitchett et al., 2004; Beatty et al., 2008; Zonneveld et al., 2010). As a result, Early Triassic marine environments were not always deleterious globally. Chen et al. (2007) also detected that marine environments had greatly ameliorated during the late Griesbachian in Meishan. The sea-floor recuperation, including shallowing water depth, increasing oxygenation and oceanic productivity, coincides with an increase in benthic biodiversity, signalling that ecologic and environmental restoration might have initiated in the late Griesbachian (Chen et al., 2002, 2007).

The example of elevated recovery of the benthic community in late Griesbachian at Meishan is also strengthened by community structural changes and ichnofabric variation through the PTB to late Griesbachian. The Exp (H) value increases by 262.6% from the C to M–L communities, and also increases 70%, coupled with a decrease of 15.2% in D’ values, from the C–O to M–L communities, suggesting an improvement in shelly community structures in the upper Yinkeng Formation at Meishan (Chen et al., 2002, 2007).

Trace fossils and ichnofabrics documented here also show that the late Griesbachian trace-fossil assemblage is marked by significant increases in ichnodiversity,
burrow size, trace complexity, tiering level, and bioturbation level, in comparison with early Griesbachian ichnoassemblages, although they did not achieve Changhsingian levels (Fig. 21). Thus, the Meishan trace fossils, together with increasing diversity in the shelly community, sedimentary structures (HCS), up-shallowing sedimentary cycle and geochemical proxies (Chen et al., 2007), suggest that biotic recovery recorded in the upper Yinkeng Formation may be categorized as recovery stage 2 (sensu Twitchett, 2006), and also mark the return of parts of the meso-consumer functioning group within the ecosystem trophic structure, which usually occurs in the Spathian around the world (Chen and Benton, 2012).

8. Conclusions

Updated conodont biostratigraphy allows the establishment of eight conodont zones from the latest Changhsingian to early Griesbachian at Meishan, the C. yini, C. meishanensis, H. changxingensis, C. taylorae, H. parvus, I. staeschei, I. isarcica, and C. planate zones. Microstratigraphic analysis shows that a major turnover in fossil fragment contents and ichnodiversity occurs across the boundary between Beds 24e-5 and 24e-6,
suggesting the actual mass extinction horizon in thin section. Bed 27 contains a
firmground of *Glossifungites* ichnofacies rather than the previously proposed submarine
dissolution surface or hardground surface. Fossil fragment contents show a dramatic
decline in both fossil component percentage and assemblage diversity in Beds 25-26a,
coinciding with metazoan mass extinction. Fossil fragment content, ichnodiversity and
all ichnofabric proxies (including burrow size, tiering level, and bioturbation level)
throughout the uppermost Changhsing to Yinkeng formations indicate that the P-Tr/ecologic crisis comprises two discrete stages, coinciding with the first and second phases
of the PTME, in support of a proposed two-stage extinction pattern of metazoans over the
P-Tr transition. The PTME was of short duration, lasting about 60 kyr. A biodiversity
crisis indicates the start of the extinction interval, but its end is marked by the ecologic
collapse of ecosystems. Thus, the ecologic crisis lagged behind the biodiversity decline
during the PTME. Pyrite framboid size variations suggest that the depositional redox
condition was anoxic to euxinic in the latest Changhsingian, became euxinic in Beds
25-26a, turned to be dyoxic in Bed 27, then varied from euxinic to anoxic through most of
the Griesbachian. Although metazoan biodiversity and fossil fragment contents show
dramatic declines, coinciding with a ~9 °C increase in seawater surface temperature, from
Bed 24e to Bed 27 in Meishan, all ecologic proxies show much smaller effects from the elevated seawater temperature. Bed 27 contains abundant infauna and shows no signs of ocean acidification. Pre-extinction anoxic-euxinic conditions had little effect on both metazoans and infauna. The anoxic event associated with the PTME may have lasted for much less time than previously thought, and is limited to Beds 25-26a at Meishan. Fossil fragment contents, ichnofaunas, ichnofabrics and pyrite frambooid size all show that anoxic conditions did not exist in Bed 27. Early Griesbachian anoxia is possible, and may have caused the rarity of ichnofaunas and metazoans in the lower Yinkeng Formation. The ichnofauna is characterized by small, simple horizontal burrows of Planolites, while metazoan faunas are characterized by low diversity, high abundance, opportunist-dominated communities. The killing mechanisms for these two extinction events near the PTB similar to one another. A rapid increase of ~9 °C in seawater temperature and its inducing short anoxia or acidification may have played an important role in the first-pulse biocrisis, while the long-time and widespread anoxia probably caused by long-time high temperature condition may have resulted in morality of most organisms in the second-pulse crisis. Initial recovery of marine ecosystems coupled with environmental amelioration occurred in the late Griesbachian, marking the return of parts
of the meso-consumer functioning group.

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**Figure captions**

**Fig. 1.** The GSSP for the Permian-Triassic boundary at Meishan, Changxing county, northwestern Zhejiang Province, east China. A, location of the Meishan section. B, close-up of the white volcanic ash bed (Bed 25) in Meishan. C, geopark of the GSSP Meishan showing GSSP position at the Meishan section. D, the P-Tr boundary beds showing biostratigraphic boundary through the mid-Bed 27 and the mass extinction horizon at the base of Bed 25. E, outcrop of the P-Tr boundary beds and Yinkeng Formation along strike on the Meishan hill from the geopark section.
Fig. 2. Biostratigraphy of the P-Tr transition at the Meishan section with the updated conodont zones and correlations with ammonoid, bivalve, brachiopod and microfloral assemblages from Meishan as well as conodont zones from North Italy, Iran and Germany, and India. Note that the updated conodont zonation is revised from those documented by Jiang et al. (2007) and Zhang et al. (2009) and our new observations. White arrows indicate that conodont zones extend to horizons below Bed 22 of Meishan and its equivalents.

Fig. 3. P-Tr succession exposed in the GSSP Meishan showing lithology, facies types, depositional environments, stratigraphic distributions of trace fossils, and bioturbation levels. Ichnofabric indices (ii: Droser and Bottjer, 1986) are assessed as 1 to 6, indicating bioturbation from lowest to highest levels. Bedding plane bioturbation index (bpbi) is evaluated based on bedding plane coverage of burrows (Miller and Smail, 1997). Facies symbols: om = offshore mudstone facies, bs = basinal black shale facies, ow = offshore wackestone facies, os = offshore siltstone facies; ew = epeiric sea wackestone facies, HCS = hummocky cross stratification, hb = horizontal bedding. Depositional environment (DE): ns = nearshore, fw = fair-weather wave base, sw = subtidal zone to fair-weather wave base, swb = storm wavebase.
Fig. 4. Lithology and fossils from the exposure of the P-Tr transition in Meishan. A-B, D, field photograph, polished surface and microphotograph showing hummocky cross-stratified (HCS) muddy limestone (Bed 54), upper Yinkeng Formation; pen is 15 cm long; scale bars are 2 cm. C, pale mudstone and calcareous mudstone (Bed 41) showing horizontal stratification, lower Yinkeng Formation; pen is 15 cm long. E, F, I, ammonoid fossils across the P-Tr boundary with large ammonoid shell (E) in Bed 24e of the Changhsing Formation contrasting to small shells (F, I) recorded in the middle and upper Yinkeng Formation; coins are 1.5 cm in diameter; scale bar is 1 cm. G, dark thin-bedded limestone interbedded with bioclastic limestone bands, Bed 24e; pen is 10 cm long. H, irregular contact between Beds 24d and 24e; cross-bedding is pronounced in the uppermost Bed 24d; scale bar is 1 cm. J, vertical burrow of Balanoglossites in the upper part of Bed 24d; scale bar is 1.5 cm.

Fig. 5. Microfacies and fossil fragment assemblages from Beds 23-26, upper Changhsing Formation. A, microphotograph of claystone, Bed 25. B, microphotograph showing horizontal laminae (black arrow) of black shale, Bed 26. C, bioclastic packstone of Bed 23a showing brachiopod (b), crinoid (c), and ostracod (o) fragments. D, bioclastic packstone of Bed 24c showing abundant foraminifer (f), brachiopod (b), crinoid (c),
ostracod (o) and other fragments.

**Fig. 6.** Pie diagrams showing percentage of major components in all rocks sampled from Beds 22-60 in Meishan. Detailed fossil fragment contents (%) of each sample are tabulated in Table 3. Component symbols: 1 = foraminifers, 2 = ostracods, 3 = crinoids, 4 = echinoids, 5 = brachiopods, 6 = bryozoans, 7 = sponge spicules, 8 = calcareous sponges, 9 = gastropods, 10 = radiolarians, 11 = macroalgae, 12 = micrites, 13 = cavities, 14 = other particles (fecal pellets, peloids, pyrites and undetermined particles).

**Fig.7.** Microfacies across the boundary between Beds 24e-5 and 24e-6. A, transverse view of one sponge spicule. B-C, cross-section view of sponge spicules. D, microphotograph showing the laminated horizon separating bioclastic layer (Bed 24e-5) from the overlying sponge spicule-rich layer (Bed 24e-6). E, SEM image of one isolated specimen of a sponge spicule. B-C, scale bars are both 50µm; E, Scale bar is 40 µm.

**Fig. 8.** Microfacies and fossil fragment assemblages from Bed 26b, 8-10 cm above the base of Bed 25. A, microphotograph showing foraminifer (f), bryozoan (bry), echinoid (e), and brachiopod (bra) fragments. B, microphotograph showing ostracod (o), echinoid (e), and brachiopod (bra) fragments. C, microphotograph showing brachiopod (bra) and echinoid (e) fragments. D, microphotograph showing bryozoan (bry) and brachiopod (bra)
fragments. E, microphotograph showing foraminifer (f) and echinoid (e) fragments. F, microphotograph showing brachiopod (bra) and foraminifer (f) fragments. G, microphotograph showing foraminifer (f) and echinoid (e) fragments. H, microphotograph showing bryozoan (bry) and foraminifer (f) fragments. I, microphotograph showing foraminifer (f) and echinoid (e) fragments. J, microphotograph showing foraminifer (f) and echinoid (e) fragments. K, microphotograph showing bryozoan (bry) and echinoid (e) fragments. L, microphotograph showing foraminifer (f) and echinoid (e) fragments. All scale bars are all 100 µm.

Fig. 9. Polished surface of Bed 27 and its microfacies features. A, polished surface showing the entire bed is subdivided into four parts (labelled a, b, c, d) by two sets of pronounced irregular surfaces, in which burrows (red arrows) are commonly present. B, microphotograph of the basal part of Bed 27a, 11-13 cm above the base of Bed 25, showing foraminifer (f) and brachiopod (bra) fragments. C, microphotograph of the upper part of Bed 27a, 13-15 cm above the base of Bed 25, showing foraminifers (f) and other fossil fragments. D, microphotograph of the lower part of Bed 27b, 15-17 cm above the base of Bed 25, showing claystone-dominated texture. E, microphotograph of the upper part of Bed 27b, 18-20 cm above the base of Bed 25, showing echinoid (e) and
other fossil fragments. F, microphotograph of the upper part of Bed 27c, 21-23 cm above the base of Bed 25, showing abundant foraminifer (f), echinoid (e) and brachiopod (bra) fragments. G, microphotograph of Bed 27d, 23-28 cm above the base of Bed 25, showing abundant ostracod (o), foraminifer (f), echinoid (e), and other fragments. H, microphotograph of the upper part of Bed 26b, 8-10 cm above the base of Bed 25, showing abundant foraminifer (f) and other fossil fragments.

Fig. 10. Bioclastic packstone to wackestone showing various fossil fragments from Bed 27a, 13-15 cm above the base of Bed 25. A, foraminifer (f). B, brachiopod (bra) and other fragments. C, foraminifer (f), echinoid (e) and other undetermined fragments. D, foraminifer (f). E, foraminifer (f). F, foraminifer (f), brachiopod (bra) and other undetermined fragments. G, I-K, foraminifer tests. H, echinoid (e) fragment. Scale bars are all 50 µm.

Fig. 11. Bioclastic packstone and various fossil fragments from Bed 27c, 21-23 cm above the base of Bed 25. A, foraminifer (f) and brachiopod (bra) fragments. B, foraminifer *Frodina permica* test. C, echinoid (e) and brachiopod (bra) fragments; D, bryozoan (bry), foraminifer (f) and other undetermined fragments. E, foraminifer (f) *Nodosinelloides netschajewi* test and echinoid (e) fragments. F, foraminifer test of *Hemigordius* sp. G,
brachiopod (bra) fragment. H, bryozoan (bry) fragment. I, foraminifer (f) *Hemigordius* sp.

test. J, foraminiferal (f) fragment. K, echinoid (e) and foraminifer (f) fragments. L-M, echinoid fragments. Scale bars are all 50 µm.

**Fig. 12.** Bioclastic packstone to wackestone showing various fossil fragments from Bed 27d, 23-28 cm above the base of Bed 25. A, foraminifer test of *Nodosinelloides* sp. B, brachiopod (b), foraminifer (f), and echinoid (e) fragments. C-D, foraminifer tests of *Nodosinelloides* sp. and *Nodosaria* sp., respectively. E, brachiopod (bra), foraminifer (f), and other fragments. F, echinoid fragment. G, sponge spicule. H, foraminiferal fragment of *Tuberitina maljavkini*. I, echinoid fragment. J, brachiopod (bra) and sponge spicule (ss); K, foraminifer test of *Nodosinelloides* sp. L, foraminifer *Nodosinelloides* aequiampla and brachiopod (bra) fragments. M, foraminifer (f) fragment. N, ostracod (o), foraminifer (f), and echinoid (e) fragments. O, brachiopod (bra) and echinoid (e) fragments; P, brachiopod (bra) and echinod (e) fragments. B, scale bar is 100 µm; F-G, scale bars are 20µm; other scale bars are all 50 µm.

**Fig. 13.** Microfacies and fossil fragment assemblage from strata of Bed 29 and above. A, bioclastic wackestone with ostracod (o) and brachiopod (bra) fragments, Bed 29. B, bioclastic wackestone with brachiopod (bra) and ostracod (o) fragments, Bed 29. C,

Fig. 14. Fossil fragment distributions over the P-Tr transition (Beds 22-60) in Meishan. Vertical axis represents percentage of various fossil fragments in all rock.

Fig. 15. Shell beds from the Yinkeng Formation in Meishan. A, Claraia concentrations (white arrows) from Bed 40; scale bar is 1 cm; B, shell concretions of Claraia griesbachi c) and Ophiceras sp. (o) of the O-P community from Bed 32; coin is 1.5 cm in diameter; C, shell concretions of Claraia griesbachi from Bed 35; coin is 1.5 cm in diameter; D, shell concretions of Claraia wangi of the C community from Bed 40; coin is 1.5 cm in diameter; E, shell concretions of Claraia griesbachi from Bed 36; coin is 1.5 cm in diameter; F, shell concretions of Meishanorhynchia (m), Lytophiceras (ly) and ophiceratid (o) of the M-L community from Bed 55; Scale bar is 4 mm.

Fig. 16. Trace fossils from the Changhsing Formation of the Meishan section. A, D,
*Thalassinoides* sp. 1 on base of Bed 8; coin is 1.5 cm; B, *Paleophycus* isp. from Bed 9; scale bar is 1 cm; C, *Balanoglossites triadicus* from Bed 24d; coin is 1.5 cm in diameter; E, *Taenidium* isp. from upper surface of Bed 24d; coin is 1.5 cm in diameter; F, *Lockeia* isp. on the upper surface of Bed 9; coin is 1.5 cm in diameter.

**Fig. 17.** Trace fossils from the Changhsing Formation (Beds23-24) continued. A, E, horizontal burrows of *Planolites* isp. 1 from upper surface of Bed 24e-6; USB is 2 cm long; B-C, problematica from upper surface of Bed 23; Coins are 1.5 cm in diameter; D, *Taenidium* isp. from upper surface of Bed 24e; Coin is 1.5 cm in diameter; F, *Dendrorhaphe* isp. from upper surface of Bed 23; Coin is 1.5 cm in diameter.

**Fig. 18.** Trace fossils from the Yinkeng Formation. A-B, F, *Planolites* from upper surfaces of Bed 36, 41, and 56, respectively; coins are 1.5 cm, 2 cm and 1.5 cm in diameter, respectively; C, *Chondrites* isp. on upper surface of Bed 52; Coin is 1.5 cm in diameter; D-E, *Thalassionoides* isp. 3 from upper surfaces of Bed 53 and 56, respectively; coins are 1.5 in diameter; G-H, sketch reconstruction and trace of *Treptichnus* isp. on upper surface of Bed 57; coin is 1.5 cm in diameter.

**Fig. 19.** Polished slabs and sketches showing the successions of trace-fossil assemblages in Bed 27. A–C, vertical cross section of Bed 27 showing the ichnofabric change from a

**Fig. 20.** Polished surface and its portrait of Bed 27 showing burrow systems in firmground of the *Glossifungites* ichnofacies and vertical colonization by ichnofaunas on different substrates. A, polished slab across the entire Bed 27 (from base to top). B, sketch reconstruction showing ichnofabrics manifested in Fig. 25A. C, cartoon reconstruction showing the generalized colonization zonation of ichnofaunas. For abbreviations of ichnotaxon names see caption of Fig. 19.

**Fig. 21.** Trace fossil evolution at Meishan. A, ichnodiversity change throughout the uppermost Changhsingian to Griesbachian in Meishan. B, burrow size variations (in mean diameter and maximum diameter) over the P-Tr transition. C, tiering level change through the P-Tr transition.

**Fig. 22.** Burrow sizes of selected ichnogenera through the P-Tr transition. A, burrow size variation of *Planolites* through the P-Tr transition. B, burrow size variation of
Thalassinoides through the P-Tr transition. C, burrow sizes of both Dendrorhaphe and problematic trace from the upper Changhsing Formation. D, burrow sizes of Balanoglossites, Taenidium, Chondrites, and Treptichnus from the P-Tr transition in Meishan.

Fig. 23. Pyrite framboids and crystals preserved on fossil skeletons and in sediments of Bed 27. A-C, pyrite crystals (white arrows) on brachiopod shells of Paryphella. D-E, pyrite crystals (white arrows) preserved in sediments and foraminiferal test; scale bars are 40 µm; F-G, pyrite crystals (white arrows) preserved in foraminiferal tests; scale bars are all 40 µm. H, L, SEM images showing pyrite framboids preserved on brachiopod shells of Bed 27; I-K, pyrite framboids preserved in sediments of Bed 27; M-N, EDS results showing mineral composition of framboids of Fig. 23L and Fig. 23J, respectively.

Fig. 24. Sizes of pyrite framboids from 17 horizons through the P-Tr transition in Meishan. MD = mean diameter, SD = standard derivation, N = Number of framboid grains.

Fig. 25. Redox conditions indicated by pyrite framboid sizes through the P-Tr transition at Meishan. Two SEM images show morphologies of pyrite framboids from Bed 24 (left) and Bed 39 (right). PTB = Permo-Triassic boundary; PTME = Permo-Triassic mass
extinction.

**Fig. 26.** Composite figure showing exceptionally increased seawater surface temperature, carbon isotopic excursion, Chemical index of alternation (CIA) and Eu/Eu* profiles, through the P-Tr transition at Meishan. Total organic content (TOC) and Ce/Ce* profiles, framboid size variation, specific and generic richness variations, and community structural changes indicated by true diversity index (Exp (H)) and dominance (D) through the P-Tr transition in Meishan. Note: seawater temperature data after Joachimski et al. (2012) and Sun et al. (2012); CIA value is calculated using published data by Zhang et al. (2005); Carbon isotopic excursion after Burgess et al. (2014); Eu/Eu* and Ce/Ce* values after Zhao et al. (2013a). TOC profile after Yin et al. (2012). Framboid size data from this study. Detailed bioturbation data see Fig. 3; II = Ichnofabric indices; BPBI = Bedding plane bioturbation index. Datum source of burrow diameters sees Fig. 24. More details of fossil fragment contents see Fig. 14. Species and genus richness data after Song et al. (2013a). Community structure data from Chen et al. (2010a).

**Table captions**
Table 1. Radiometric ages obtained from the P-Tr succession at the GSSP Meishan (in $^{2456}\text{Ma}$).

Table 2. Key conodont zones with their durations across the PTB in Meishan.

Table 3. Percentage of major components in all rocks sampled from Beds 22-60 in Meishan.

Table 4. X-ray diffraction (XRD) data of the PTB beds at Meishan (sourced from Liang, $^{2461}2002$).

Table 5. Structural indices of the latest Permian to earliest Triassic shelly communities from Meishan (Chen et al., $^{2464}2010a$).

Table 6. Major indices showing community structural changes over the P-Tr transition in Meishan.

Table 7. Characteristics of major trace fossils from the uppermost Permian to lowest Triassic in Meishan.
Complete biotic and sedimentary records of the Permian-Triassic transition from Meishan section, South China: ecologically assessing mass extinction and its aftermath

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ABSTRACT

The Meishan section, South China is the Global Stratotype Section and Point (GSSP) for the Permian-Triassic boundary (PTB), and also is well known for the best record demonstrating the Permian-Triassic mass extinction (PTME) all over the world. This section has also been studied using multidisciplinary approaches to reveal the possible causes for the greatest Phanerozoic biocrisis of life on Earth; many important scenarios interpreting the great dying have been proposed on the basis of data from Meishan. Nevertheless, hot debates on biotic extinction patterns and possible killers still continue. This paper reviews all fossil and sedimentary records from the Permo-Triassic (P-Tr) transition, based on previously published data and our newly obtained data from Meishan, and assesses ecologically the PTME and its aftermath to determine the biotic response to climatic and environmental extremes associated with the biocrisis. Eight updated conodont zones: C. yini, C. meishanensis, H. Changhsingensis changxingensis, C. taylorae, H. parvus, I. staeschei, I. isarcica, and C. planate Zones are proposed for the
PTB beds at Meishan. Major turnover in fossil fragment contents and ichnodiversity occurs across the boundary between Bed 24e-5 and Bed 24e-6, suggesting an extinction horizon in thin section. The irregular surface in the middle of Bed 27 is re-interpreted as a firmground of *Glossifungites* ichnofacies rather than the previously proposed submarine solution surface or hardground surface. Both fossil fragment contents and ichnodiversity underwent dramatic declines in Beds 25–26a, coinciding with metazoan mass extinction. Fossil fragment content, ichnodiversity and all ichnofabric proxies (including burrow size, tiering level, bioturbation level) indicate that the P-Tr ecologic crisis comprises two discrete stages, coinciding with the first and second phases of the PTME in Meishan. Ecologic crisis lagged behind biodiversity decline during the PTME. Pyrite framboïd size variations suggest that depositional redox condition was anoxic to euxinic in the latest Changhsingian, became euxinic in Beds 25–26a, turned dysoxic in Bed 27, then varied from euxinic to anoxic through most of the Griesbachian. The ~10°C increase in seawater surface temperature from Bed 24e to Bed 27 at Meishan seems to result in dramatic declines in biodiversity and fossil fragment contents in Beds 25–26a, but had little effect on all ecologic proxies. Both metazoans and infauna seem not to be affected by the pre-extinction anoxic-euxinic condition. The anoxic event associated with
the PTME may have occurred in a much shorter period than previously thought and is only recorded in Beds 25–26a at Meishan. Fossil fragment contents, ichnofaunas, ichnofabrics and pyrite frambooid size all show that no signs of oceanic acidification and anoxia existed in Bed 27. The early Griesbachian anoxia may have resulted in rarity of ichnofauna and metazoans in the lower Yinkeng Formation, in which the ichnofauna is characterized by small, simple horizontal burrows of *Planolites*, and metazoan faunas are characterized by low diversity, high abundance, opportunist-dominated communities.

The rapid increase of ~9 °C in sea-surface temperature and a short anoxia or acidification coincided with the first-pulse biocrisis, while a prolonged and widespread anoxia probably due to a long period of high seawater temperate condition may be crucial in morality of most organisms in the second-pulse PTME. Marine ecosystems started to recover, coupled with environmental amelioration, in the late Griesbachian.

*Keywords:* mass extinction, Permian-Triassic, fossil fragment, trace fossils, redox condition, Meishan section
## Contents

1. Introduction

2. Biochronostratigraphy: an update
   2.1. Biostratigraphy and correlations
   2.2. Geochronology
   2.3. Duration of key conodont zones across the P-Tr boundary

3. Microstratigraphy, fossil fragment contents and paleoenvironmental analysis of the P-Tr transition
   3.1. Bed 23
   3.2. Bed 24
   3.3. Bed 25
   3.4. Bed 26
   3.5. Bed 27
   3.6. Bed 28
   3.7. Beds 29-59

4. Biotic changeover through the P-Tr transition
   4.1. Biodiversity variations over the P-Tr transition
4.2. Fossil fragment content variations through the P-Tr transition

4.3. Community structural changes of shelly faunas

5. Trace fossils and bioturbation

5.1. P-Tr ichnotaxa and their stratigraphic distributions at Meishan

5.1.1. Stratigraphic distributions of ichnoassemblages

5.1.2. Ichnofabric changes within Bed 27

5.2. Extent of bioturbation

5.3. Changeover of trace-fossil diversity over the P-Tr transition

5.4. Burrow size variations through the P-Tr transition

5.5. Trace fossil form and complexity

5.6. Infaunal tiering

6. Size variations of pyrite frambooids and redox conditions over the P-Tr transition

7. Assessing ecologically PTME and its aftermath

7.1. Testing extinction patterns

7.2. Ecologic crisis lagging behind biodiversity drop at the PTME

7.3. Dramatic increase in seawater temperature and its consequences

7.4. Anoxic events and biotic response
7.4.1. Anoxic events

7.4.2. Biotic response

7.5. Testing extinction mechanisms and biotic response

7.6. Post-extinction amelioration of marine ecosystems in late Griesbachian

8. Conclusions
1. Introduction

As the greatest biocrisis of life on Earth (Sepkoski, 1981), the Permian-Triassic mass extinction (PTME) changed Earth’s ecosystems fundamentally (Benton and Twitchett, 2003; Erwin, 2006). After they had recovered, the marine ecosystems after the PTME gave rise to the forerunners of modern-day ecosystems, both the Triassic and modern ecosystems being comparable to each other in composition of functioning groups and trophic structure (Chen and Benton, 2012). However, the causes of this enigmatic biocrisis have long been disputed despite intense study, and the same is true of the profoundly delayed recovery following the PTME (Erwin, 2001). Thus, studies of these issues have enjoyed a surge in scientific interest in the past 30 years that shows no sign of abating (Chen et al., 2014).

Although this era-boundary crisis has been widely recognized in Permian–Triassic boundary (PTB) sections around the world, many important hypotheses have been proposed based on paleontological and experimental data sampled from the Meishan section of Changhsing County, Zhejiang Province, east China (Fig. 1A; Renne et al., 1995; Bowring et al., 1998; Jin et al., 2000; Yin et al., 2001, 2012; Kaiho et
This section is the Global Stratotype Section and Point (GSSP) for the PTB (Yin et al., 2001; Fig. 1C) and also well known for the best record of both biotic and geochemical signals demonstrating the PTME all over the world. Here, the exposures of the PTB beds are spectacular, extending about 2 km laterally along the Meishan hill (Fig. 1E). The PTME has been well demonstrated by Jin et al. (2000), whose study based on paleontological data from Meishan reveals that this extinction event was abrupt and dramatic, with most Permian organisms being wiped out within a very short interval, which was precisely calibrated to the base of Bed 25, a white clay bed, in Meishan (Fig. 1B, D), while the PTB is placed at the middle of Bed 27, about 16-20 cm above the base of Bed 25 in the same section (Yin et al., 2001; Fig. 1C). As such, the biocrisis clearly pre-dated the PTB (Fig. 1D). The P-Tr ecologic crisis is also marked by a pronounced negative carbon isotopic excursion (Xu and Yan, 1993; Jin et al., 2000; Kaiho et al., 2001; Cao et al., 2002; Xie et al., 2005, 2007; Fig. 2) and is also associated with an end-Permian sulfur event (Kaiho et al., 2006; Riccardi et al., 2006).
After Jin et al.’s (2000) influential study, which was largely based on fossil data obtained in 1980s (i.e., Zhao et al., 1981; Sheng et al., 1984; Liao, 1984; Sheng et al., 1987; Shi and Wang, 1987), abundant brachiopod and foraminifer faunas have been detected from Beds 25–27, immediately above the PTME horizon in Meishan (Chen et al., 2005a, 2006b; Song et al., 2007, 2009). Quantitative analysis of the updated foraminifer data from Meishan revealed a two-stage extinction pattern near the P-Tr boundary (Song et al., 2009), which agrees well with two distinct peaks of cyanobacteria, detected by biomarker analysis from the same section, suggesting two extinction events corresponding to Beds 25 and 28 (Xie et al., 2005). The two-stage extinction pattern is also strengthened by extremely abundant benthic fossils obtained from a shallow platform facies of the PTB section at Huangzhishan, about 40 km from Meishan (Chen et al., 2009). However, Shen et al. (2011b) clarified an abrupt biotic decline in a short interval equivalent to Beds 25-28 of Meishan based on quantitative analysis of fossil records from Meishan and other PTB sections in South China. In contrast, Song et al. (2013a) demonstrated nicely a two-stage extinction pattern for the P-Tr crisis based on quantitative analysis of paleontological data derived from Meishan and a further six PTB sections in South China. Thus, debate on whether the PTME was either a single crisis or
episodic extinctions still continues (Shen et al., 2011b; Song et al., 2013; Wang et al., 2014). Regardless of whether the extinction was single or a two-phase pattern, an increasing number of faunas have been found in Beds 25-28 of Meishan and its counterparts across all of South China, although this interval may just last 60 kyr (Burgess et al., 2014).

In addition, a further extinction event resulting in depletion of Permian reefs in South China was calibrated to the base of Bed 24e at Meishan (Yang et al., 1993). Yin et al. (2007) re-documented biotic and geochemical signal changes across this horizon, which is reinforced by several lines of evidence, including reduction in conodont sizes (Luo et al., 2006), possible extinction of radiolarians in deep habitats and a negative shift in organic carbon isotope values (Cao et al., 2009). To sum up, biotic variations based on sound paleontology over the P-Tr transition have been far less studied in comparison with the intense geochemical studies of this catastrophe in most PTB sections. Current, updated fossil records from extensive PTB sections are crucial to reveal the true biotic responses to these environmental crises.

As briefly summarized above, there have been great advances in research on the PTME at Meishan in recent years. Multiple scenarios interpreting the causes of the P-Tr
biocrisis have been proposed based on experimental data sampled from this section.

Nevertheless, any reasonable models interpreting the P-Tr crisis need to be tested by analysis of precise biotic extinction patterns and physiological reactions of victims and survivors (Knoll et al., 2007). As a result, we herein document the updated, complete fossil and sedimentary records, including microfacies, microfossils, body and trace fossils, and pyrite frambooids, throughout the P-Tr transition and attempt to test biotic responses to various environmental and climatic catastrophes from the GSSP Meishan.

2. Biochronostratigraphy: an update

2.1. Biostratigraphy and correlations

After Yin et al.’s (2001) placement of the PTB at the base of Bed 27c, marked by the first appearance datum (FAD) of the conodont *Hindeodus parvus*, Jiang et al. (2007) established gondolellid and hindeodid conodont zones across the PTB in Meishan. The former include the *Clarkina yini, C. meishanensis* and *C. taylorae* Zones, while the latter comprise the *Hindeodus latidentatus, H. praeparvus, H. Changhsingensis, Changxingensis*.
Given that *C. taylorae* is confined to Bed 27a-28 in Meishan (Jiang et al., 2007; Zhang et al., 2009) and has also been widely reported from PTB beds around the world (Orchard et al., 1994; Orchard and Krystn, 1998; Nicoll et al., 2002; Algeo et al., 2012; Zhao et al., 2013b), the *C. taylorae* Zone is regarded as a discrete zone beneath the *H. parvus* Zone and retained for Bed 27a-b (Fig. 2). In addition, we have also re-examined stratigraphic distributions of some key conodont species based on previously published data and newly extracted specimens from Meishan. An updated conodont zonation is proposed for the P-Tr succession of the GSSP Meishan (Fig. 2). The new conodont zones, with their stratigraphic ranges in brackets, include *C. Changhsingensis-changxingensis* Zone (Beds 22-23), *C. yini* Zone (Bed 24), *C. meishanensis* Zone (Bed 25), *H. Changhsingensis-changxingensis* Zone (Bed 26), *C. taylorae* Zone (Bed 27a-b), *H. parvus* Zone (Bed 27c), *I. staechei* Zone (Beds 27d-28), *I. isarcica* Zone (Beds 29-51), and *C. tulongensis-C. planata* Zone (Beds 52-72, top of the Yinkeng Formation).
parvus Zone (Bed 27c-d), *I. staechei* Zone (Beds 28-29a), *I. isarcica* Zone (Bed 29b), *C. planata* Zone (Beds 30-54), and *Neoclarkina discreta* Zone (Bed 35 and above) (Fig. 2).

It is noteworthy that Yuan et al. (2014) confined the *C. changxingensis* Zone to mid-Bed 10 to mid-Bed 22, *C. yini* Zone to mid-Bed 22 to Bed 24d, and *C. meishanensis* Zone to Bed 24e to Bed 25. The first occurrence of the nominal species of these conodont zones seems to be lower than they occurred in our samples. In particular, *C. meishanensis* occurs in the so-called ‘white boundary clay’ bed and above strata in most PTB sections in South China (Zhang et al., 2007; Jiang et al., 2007, 2011, Zhao et al., 2013) and is rarely present in the Permian bioclastic limestone. The *C. meishanensis* Zone is also associated with a pronounced negative shifting excursion of carbon isotopes in most of the PTB sections in South China. Accordingly, the bases of these Changhsingian conodont zones remain tentative and need to be confirmed when additional conodont samples are processed in future.

Other important findings from the PTB beds include restriction of *Isarcicella peculiaris* to Bed 28 and the first occurrences of *Hindeodus eurypyge* and *Isarcicella lobata* at the bases of Bed 27a and Bed 28, respectively (Jiang et al. 2007; fig. 2). These species also have the potential to serve as key elements marking the PTB beds (Jiang et al.,
Of these, *I. lobata*, confined to Beds 28-29 in Meishan, was proposed as a distinct zone between the *H. parvus* and *I. staeschei* Zones in the southern Alps (Perri and Farabegoli, 2003, 2012; Fig. 2). This species therefore occurred slightly earlier in the southern Alps than in the GSSP Meishan. In the new conodont zonation, the *I. isarcica* Zone is retained for Bed 29b, and thus has a much narrower stratigraphic range than before. The *C. planata* Zone is newly proposed for Beds 30-54 and the *Neoclarkina discreta* Zone for Bed 55 and higher strata in Meishan (Fig. 2) based on re-examination of their stratigraphic distributions (Zhang et al., 2007, 2009).

The updated conodont zonation enables the PTB beds of Meishan to be correlated precisely with their counterparts recorded elsewhere in the Tethys region, such as North Italy, Iran, Germanic basin, and Spiti of Himalaya region (Fig. 2). The *H. parvus, I. staeschei* and *I. isarcica* Zones have also been recognized in both Spiti and North Italy (Fig. 2). Both *H. parvus* and *I. isarcica* Zones occur in the Abdadeh region, Iran (Korte et al., 2004). Korte et al. (2004) also argued that there might be a hiatus between Beds 24e and 25 because both the *C. iranica* and *C. hauschkei* Zones, between the *C. yini-C. zhangi* and *C. meishanensis-H. praeparvus* Zones, are absent in Meishan. *C. hauschkei* does occur in Meishan, but shares the same stratigraphic range with both *NC. yini* and *NC.*
zhangi in Bed 24 (Jiang et al., 2007, 2011). More importantly, no sedimentary gap has been found in this interval in the GSSP Meishan (see below). The last occurrence of both C. yini and C. zhangi has been calibrated to the top of Bed 24e (Yin et al., 2001; Zhang et al., 2007; Jiang et al., 2007). The depositional succession between the C. meishanensis and C. yini Zones shows no sign of a hiatus. Thus, both AC. hauschkei and AC. iranica either can be recognized from the upper part of the N. yini Zone in the future, or do not occur due to different biofacies controls (Korte et al., 2004).

Recognition and correlations of PTB beds in conodont-barren sections have long remained problematic. Chen et al. (2009) established the bivalves Claraia huzhouensis-C. cf. bioni and Eumorphotis venetiana-Towapteria scythica-Pteria ussurica variabililis Assemblages from the PTB beds of both the Meishan and adjacent Huangzhishan sections. The former is coeval with the C. meishanensis and H. Changxingensis changxingensis Zones of the GSSP Meishan (Chen et al., 2009). The small, weakly costated Claraia-like species “Peribositra” baoqingensis from Bed 26 of Meishan (Zhao et al., 1981) has been re-assigned to Claraia (Chen, 2004). These primitive Claraia species from Meishan are diagnostic of the C. huzhouensis-C. cf. bioni Assemblage and locate the PTME in the shallow-water, conodont-barren PTB sections in South China.
(Chen et al., 2009). The latter bivalve assemblage is contemporaneous with the \textit{H. parvus} Zone in the Huangzhishan section, pointing to an age of earliest Triassic (Chen et al., 2009). Both \textit{Claraia wangi} and \textit{C. griesbachi} are also very-abundant in Beds 29b-54 in Meishan, and thus form the \textit{C. wangi-C. griesbachi} Assemblage (Chen et al., 2010a), which is coeval with the \textit{I. isarcica} and \textit{C. planata} Zones (Fig. 2). The ammonoids \textit{Rotodiscoceras}, \textit{Hypophiceras}, \textit{Ophiceras}, and \textit{Lytophiceras} characterize the assemblages from Beds 22-24, Beds 25-26, Beds 27-50, and Beds 51-55, respectively in Meishan (Fig. 2; Zhao et al., 1984; Sheng et al., 1984; Yin et al., 2001; Chen et al., 2010a). Brachiopods are also reasonably abundant in Beds 25-26, Bed 27 and Beds 51-55 of Meishan (Chen et al., 2002, 2006b, 2007). They are assignable to the \textit{Tethyochonetes liaoi} Assemblage (Beds 25-26), \textit{Paryphella triqueta} Assemblage (Bed 27), and \textit{Meishanorhynchia meishanensis} Assemblage (Beds 51-55) (Chen et al., 2010a). Song et al. (2007, 2009) also reported diverse foraminifers from the Changhsing and lowest Yinkeng Formations in Meishan, but did not establish biozones. A palynological \textit{Lundbladispora-Taeniaspore-Equisetosporites} Assemblage was established from Beds 33-53 of the Yinkeng Formation (Zhang et al., 2007), which, therefore, correlates collectively with the conodont \textit{C. planata} Zone (Fig. 2).
2.2. Geochronology

In Meishan, volcanic ash beds are well exposed and conspicuous in the uppermost Permian to Lower Triassic successions. In particular, Beds 25 and 28 near the PTB have been dated by multiple research groups using various techniques (Table 1). The most updated radiometric ages for Beds 25 and 28 are 251.941 ± 0.037 Ma and 251.880 ± 0.031 Ma, respectively (Burgess et al., 2014), which constrain the duration between those two phases of the PTME (Song et al., 2013a) or the duration of the PTME (Shen et al., 2011b; Wang et al., 2014) as 60 ka (Burgess et al., 2014). Burgess et al. (2014) have also given updated estimates for sediment accumulation rates through the P-Tr transition, which show that sedimentation rates of the Changhsing Formation decline towards the end of the Permian, reach the lowest value during the time of extinction (Beds 25-28), and then increase gently in the early Griesbachian (Beds 28-37) and steeply in the early-middle Griesbachian (Beds 37-48) in Meishan (Burgess et al., 2014). In addition, these authors estimated that the abrupt decline in δ¹³C_carb in Bed 24e took place at 251.950 ± 0.042 Mya, while the FAD of *H. parvus* at the GSSP Meishan is at 251.902 ±
2.3. Duration of key conodont zones across the P-Tr boundary

At Meishan, intense high-precision dating of volcanic ash beds (Table 1) and high resolution conodont zones (Fig. 2) allow reasonable estimates of the duration of each conodont zone. The widespread *H. parvus* Zone is estimated to have lasted 16 ka (Table 2), while the *C. meishanensis* Zone, the PTME marker, lasted 8 ka, which is much shorter than previously thought. The last conodont zone prior to the PTME, the *C. yini* Zone, may have lasted 28 ka (Table 2).

3. Microstratigraphy, fossil fragment contents and paleoenvironmental analysis of the P-Tr transition

At Meishan, the P-Tr succession comprises the Changhsing and Yinkeng Formations below and above. The former unit is a 41-m-thick carbonate succession consisting of medium- to thin-bedded limestone, while the Yinkeng Formation is about
15 m thick and dominated by mudstone and muddy limestone in the lower part and characterized by thin-bedded limestone in the upper part (Fig. 3). These two formations have been frequently described (Zhao et al., 1981; Sheng et al., 1984, 1987; Yang et al., 1987; Yin et al., 1996, 2001; Zhang et al., 2005). Cao and Zheng (2007) re-described the Changhsing Formation (Beds 1-24) and recognized 247 natural, single layers, each 2 to 37 cm in thickness. Chen et al. (2007) gave an updated description for the Yinkeng Formation (Beds 25-59), in which 183 natural layers are recognizable. In addition, Cao and Shang (1998) conducted the first cm-scale stratigraphy, also termed microstratigraphy, of the P-Tr boundary beds in Meishan. Since then, Microstratigraphy microstratigraphy of the PTB beds (Beds 24-29) of the Meishan section has also been intensely studied (Cao and Shang, 1998; Cao and Zheng, 2009; Zhao and Tong, 2010; Zheng et al., 2013).

The top two beds of the Changhsing Formation, Beds 23-24, record important sedimentary and paleontological information just prior to the PTME, while most parts of the Yinkeng Formation record the severe biotic extinction and its consequences. Thus, microstratigraphy of the uppermost Changhsing Formation to Yinkeng Formation succession (Beds 23-59) is summarized here in view of the previously published data and
our new observations in petrologic thin sections. These thin sections were sampled almost continuously in Beds 24e to 29 and in a 20-cm-interval in Beds 22 to 24d of the Changhsing Formation. Their sampling interval is 0.5 m throughout Bed 30 to Bed 59 of the Yinkeng Formation in the GSSP Meishan.

In addition, point counting is a relatively quick method that quantifies the occurrence of skeletal fragments of major fossil groups in different horizons under the microscope (Flugel, 1984; Payne et al., 2006). However, care must be taken when using the point-counting method because large shell fragments of some clades may bias counting results (Jacobsen et al., 2011). As an alternative, Jacobsen et al. (2011) proposed the equal area approach to quantify the occurrence of skeletal fragments in thin section. In order to eliminate biases of counting areas, it is suggested that at least eight equal area fields of view ought to be counted per thin section sample (Jacobsen et al., 2011). Similar to the equal area approach, fragment percentage data of various clades from each thin section are estimated based on the observation of 300 to 350 views under a magnification of × 50 in one sample, collected for microfacies analysis of the PTB beds. Then, percentages of various skeletal components, micrite, cavities and undetermined particles (i.e., pyrites and other minerals) from samples throughout Bed 22 to Bed 60 of Meishan
were combined to yield the mean abundance of each composition in each sample throughout the study succession (Table 3).

3.1. Bed 23

Bed 23 of the upper Changhsing Formation comprises dark gray thin-to-medium-bedded bioclastic limestone interbedded with thin-bedded muddy limestone and siliceous mudstone layers. Small-scale wavy cross bedding is commonly present in the bioclastic limestone, while horizontal stratification occurs in the muddy limestone and siliceous mudstone (Fig. 4G, H). Grain grading bedding structures are also occasionally present in the bioclastic limestone unit. The bioclastic limestone usually has a packstone to grainstone texture. The former texture is very common, while a grainstone texture is also occasionally present (Fig. 5C). This unit is usually strongly bioturbated in comparison with the weakly bioturbated thin siliceous layers that are usually horizontally stratified (Fig. 3). The autochthonous and allochthonous fossil assemblage is highly diverse and dominated by foraminifers, crinoids, and brachiopods with minor constituents of ostracods, echinoids, bryozoans, sponge spicules, calcareous sponges,
gastropods, radiolarians, and macroalgae (Fig. 6). The matrix comprises micrite (about 20-23%, Fig. 6). Cavities, pyrites and other undetermined particles are also commonly present (Table 3). The alternating occurrence of horizontal stratification and small-scale cross bedding and/or grain-grading bedding structures indicates that Bed 23 was deposited on a carbonate ramp between fair-weather wavebase and storm wavebase (Fig. 3; Zhang et al., 2005).

3.2. Bed 24

Bed 24, the topmost unit of the Changhsing Formation, consists mainly of thin- to medium-bedded bioclastic packstone rich in large ammonoids and other macrofossils (Fig. 4E). This bed has attracted intense attentions in terms of fossil record and sedimentary characterization because of its stratigraphic position just beneath the biotic extinction horizon (base of Bed 25; Jin et al., 2000). Bed 24, 71-90 cm in thickness, is usually labelled as Bed 24a-e (Yin et al., 1996) and consists of 14 layers, with the thinnest being 2 cm thick (Cao and Zheng, 2007). The conodonts from Bed 24 belong to the Clarkina yini Zone (Mei et al., 1998), which is distinct from the underlying Clarkina.
Bed 24a-c has similar petrographic features to Bed 23 (Figs. 5D, 6). The dark organic-rich muddy limestone or siliceous mudstone, usually less than 1-2 cm in thickness, has well-developed horizontal stratifications and possesses packstone to micritic textures with tiny, highly fragmented fossil skeletons of brachiopods and ostracods. These horizontally stratified layers are usually weakly bioturbated. In contrast, the bioclastic limestone unit, usually > 5 cm thick, possesses small-scale wavy cross bedding and bioclastic packstone to grainstone texture. These layers are also highly bioturbated (Zheng et al., 2013). All skeletal components of Bed 23 also persist into Bed 24 (Fig. 6). Accordingly, Bed 24a-c was likely deposited in the same environment as Bed 23.

Although Bed 24d has similar petrographic texture to Bed 24a-c (Fig. 6), the presence of abundant fecal pellets and peloids characterizes the grain assemblage of Bed 24d. Fossil fragment contents in rocks from both Bed 24d and Bed 24a-c are also comparable with one another (Fig. 6). In addition, burrows are commonly present near the boundary between bioclastic limestone unit and organic-rich muddy limestone or siliceous mudstone layer. Bed 24d yields abundant trace fossils (see Section 5).
Pronounced cross-bedding and vertical burrows characterize the upper part of Bed 24d (Fig. 4J). The top of Bed 24d is, however, weakly bioturbated and characterized by smooth cone-shaped surfaces, which was termed a hard-ground structure representing interrupted or highly condensed deposits (Cao and Zheng, 2009). Cao and Zheng (2009) regarded this irregular contact as a sequence boundary indicating a changeover interface from lowermost level to rapid rise. The same contact, however, has been interpreted as an erosional surface, serving as a sequence base of a 3rd-order depositional sequence following a major fall in sea level (Zhang et al., 1997; Yin et al., 2014). This interpretation is reinforced by the presence of a diverse shallow-water facies trace fossil assemblage including vertical burrows of *Balanogossites* (Fig. 4J; see also Section 5).

Cao and Zheng (2007) have also noted that abundant burrows of *Planolites* and *Skolithos* and mud-crack structures are present near the boundary between Beds 24d and 24e. Accordingly, Bed 24d, overall, is inferred to have been deposited in the upper part of the subtidal zone of a carbonate ramp (Fig. 3; Zhang et al., 1997).

The topmost 10 cm thick limestone of Bed 24 is labelled Bed 24e, which consists of eight natural layers (Cao and Zheng, 2009) and these were sampled at six horizons here (Bed 24e-1 to Bed 24e-6). Trace fossils occur near the irregular contact.
between Beds 24d and 24e-1 (see Section 5). Bed 24e, except for the topmost 3 cm (24e-5, 24e-6), is a dark gray bioclastic packstone containing abundant fossil fragments of foraminifers, brachiopods, and crinoids. Other fossil groups such as bryozoans, gastropods, macroalgae, ostracods, calcareous sponges, and sponge spicules are also seen in thin sections, which have no major difference from the underlying Bed 24d (Fig. 6).

The uneven top surface is always capped by several muddy laminae. Cylindrical, straight, vertical burrows, ranging from 0.1 to 0.5 cm in diameter and from 3.0 to 1.0 cm in length occur in the lateral margin of the upper natural bedding surface. Bed 24e saw a slight increase in lime mud in the matrix and pyrite within the bed (see below). Bed 24e therefore was probably deposited in the fair-weather wave action zone (Fig. 3) and was interpreted as a lowstand platform margin wedge of a 3rd sequence (Zhang et al., 1997; Yin et al., 2014).

The topmost 2-3-cm-interval, labelled as Bed 24e-5 and 24e-6, is characterized by relatively low contents of P and Ca and high Ni content (Kaiho et al., 2001, 2006b).

Bed 24e-5, about 1.0-1.1 cm in thickness, comprises bioclastic packstone and contains very abundant fossil fragments of foraminifers, crinoids, brachiopods, and ostracods. Fragments of calcareous sponges, sponge spicules, gastropods, bryozoans and
Macroalgae are also occasionally present, and these are comparable in major fossil components with Beds 24e-1 to 24e-4 (Fig. 6). Moreover, abundant, reasonably large horizontal burrows (*Planolites*) are densely packed on the surface of Bed 24e-6 (also see Section 5).

The contact between Beds 24e-5 and 24e-6 is a laminated wavy lime layer (Fig. 7D). Bed 24e-6 is a 10- to 19-mm-thick bioclastic packstone and dominated by silica bars, which were interpreted as sponge spicules (Kaiho et al., 2006). The elongate bars are actually longitudinal outlines and the circular grains are cross sections of spicules (Fig. 7A-C). This identification is reinforced by the abundant isolated silicified sponge spicule specimens extracted from Bed 24e-6 (Fig. 7E). Contrasting to the predominance of sponge spicules, fragmentary contents of foraminifers, crinoids, echinoids and brachiopods decline dramatically. The skeletal grain assemblage experienced a dramatic reduction in both abundance and diversity across the contact between Beds 24e-5 and 24e-6 (Fig. 7E), to which the PTME was calibrated (Kaiho et al., 2006a).

3.3. Bed 25
This bed is the so-called “Boundary clay bed” or “White clay bed” (Zhao et al., 1981; Sheng et al., 1984; Yang et al., 1987). Its thickness ranges from 2 cm to 6 cm depending on the weathering intensity, the higher the intensity the thicker the bed. The bed grades upward into Bed 26 as a consequence of a gradual increase in organic and calcareous content and decrease in volcanic ash layers. The total thickness of these two beds is around 10 cm.

The basal part of Bed 25 comprises a 0.1- to 0.2-mm-thick layer of grayish black mudstone rich in Fe grains, termed Bed 25-1, which usually becomes a reddish ferruginous layer capping the dark Bed 24e-6 and is conspicuous at outcrops in all Meishan quarries owing to weathering. Previously, this Fe-rich layer was termed the “pyrite lamina” layer (Wignall and Hallam, 1993; Shen et al., 2007) or Pyrite layer (Cao and Zheng, 2009), based on the abundant pyrite-like grains visible at outcrops. Elemental analysis shows that these Fe grains are either Fe-Ni grains (Kaiho et al., 2001, 2006b) or goethites (Liang et al., 2002). Pyrite framboids are also commonly present in this layer (Shen et al., 2007). In addition, Zheng et al. (2013) detected abundant irregular volcanic glasses from this layer.

The reddish ferruginous surface of Bed 25-1, together with the absence of both
the N. iranica and N. hauschkei conodont zones, was considered as evidence indicating an
exposure surface and representing a hiatus (Korte et al., 2004). However, the presence of
marine fossils such as foraminifers and brachiopods (Rui et al., 1988; Yin et al., 2001) in
Bed 25 and abundant sponge spicules and other fossil fragments in Bed 24e-6 (Fig. 6)
indicates the absence of a paleo-exposure surface or an aerial hiatus. The absence of these
two conodont zones may relate to biofacies controls and cannot bracket a hiatus, as
discussed in Section 2.1.

The overlying thin layer (Bed 25-2), 0.3-1 mm thick, is dark yellowish orange,
and encompasses mainly gypsum and Fe (Table 4). The remaining part of Bed 25 (Layer
25-3, 2-4 cm thick; Kaiho et al., 2006b) is a light gray illite–montmorillonite–kaolinite
claystone (white clay) (Table 4). Gypsum and pyrite are very common in thin section. No
fossil fragments are seen in thin section (Fig. 5A). Marine fossils of conodonts,
foraminifers, ostracods and tiny brachiopods have been found from this bed, but are
always sparse (Rui et al., 1988; Jiang et al., 2007). Benthic carbonate skeletal fossils
diminished dramatically in this bed. Calcareous shells are often pyritized and attached
with crystals and frambooidal pyrites on the surface (Rui et al., 1988). Conodonts from
Bed 25 are included in the C. meishanensis Zone (Fig. 2). Microspherules and β-type
quartz crystals are much more abundant in this bed than in other ash clay beds, and could be products of acid volcanic eruptions (He et al., 1987). However, comparable microsphaerules are also very-abundant in the background soils in Meishan and other PTB sections in South China, suggesting that they may be the modern industrial products rather than geological objects (Zhang et al., 2014). Both Hf-isotope and elemental analysis of magmatic zircons suggests these ash clays near the PTB in South China may have been sourced from volcanism taking place along the convergent continent margins during the formation of the Pangea supercontinent (Gao et al., 2013).

3.4. Bed 26

Bed 26, the so-called “black clay bed” (Yang et al., 1987), comprises black shale, 4-6 cm in thickness. Nine pronounced yellow clay layers are interbedded in the black shale. Horizontal laminae and pyrite are common. The clay layer is composed mainly of montmorillonite–illite, which is similar to that of Bed 25 (Table 4). Fossil fragments are very rare in most parts of this bed (Fig. 5B) except for the top 2-cm-interval where fossil fragments are fairly abundant in calcareous nodules (Fig. 8), including foraminifers,
ostracods, echinoids, bryozoans, and brachiopods (Table 3; Figs. 6, 8). Microspherules or/and α-quartz (in the form of β quartz pseudomorphs; He, 1981) are rich in the lower part, but they may be the products of modern industry (Zhang et al., 2014). Various burrowing systems are common in the upper part of Bed 26, from which Cao and Zheng (2009, fig. 5b) identified Chondrites, Planolites and Zoophycos. The identification of the last ichnogenus, however, is problematic based on insufficient information illustrated by these authors. The upper part of the bed, Bed 26b, therefore is highly bioturbated (Fig. 3; Cao and Zheng, 2009).

Skeletal fossils are rare but considerably diverse, including ammonoids, brachiopods, bivalves, ostracods, and conodonts. Co-occurrence of the Triassic-type faunas (i.e., Otoceras, Claraia and many conodont species) and Permian-type elements (i.e., ammonoids Pseudogastroceras and Xinodiscus, and many brachiopods and foraminifera) is particularly interesting. Brachiopods are small in size and thin-shelled, and include species of Orbicoiella, Prelissoryhchnia, Cathaysia, Paryphella, Tethyochonetes, and Spinomarginifera (Chen et al., 2006b; Chen and McNamara, 2006). The presence of the relatively diverse fossil assemblage in the upper part of Bed 26 indicates the earliest re-colonization of epifauna on the barren soft substratum.
immediately after volcanic eruption. Most of these shelly fossils are complete and well
preserved regardless of the delicacy of the skeleton. The change from Bed 26 to Bed 27 is
gradual and no boundary surface can be recognized. Crystal and frambooidal pyrite are
concentrated in a discontinuous dark lamina with rich organics (Shen et al., 2007). The
slow sedimentation rate, and quiet and anoxic environment (Shen et al., 2007) suggest
that Bed 26 probably represents a semi-closed, low-energy subtidal zone (Fig. 3). The
succession of Beds 24e, 25 and 26, overall, shows that continuing fall of sea level through
Bed 24e turned to a rise in the upper part of Bed 26, with the lowest point of sea level
corresponding probably to the base of Bed 25 (Yin et al., 2014).

3.5. Bed 27

Bed 27 comprises biotic packstone to wackestone with occasionally micrite
texture and contains fairly abundant fossil skeletons and pyrite crystals throughout the
bed (see Section 6). Relatively complete shells of ostracodes, foraminifers and
thin-shelled brachiopods are reasonably abundant. This bed contains three major irregular
contact surfaces, termed hardground surfaces (Cao and Shang, 1998) and firmground
surfaces (Cao and Zheng, 2009), at various levels (Fig. 9). Of these, the first irregular
surface is rather pronounced, about 5 cm above the base of Bed 27 and near the boundary
between Beds 27a and 27b. The second occurs near the contact between Bed 27c and 27d,
while the third is not prominent and occurs within Bed 27d (Fig. 9). These ‘firmground’
surfaces divide Bed 27 into three depositional cycles, with each beginning with dark
muddy limestone and grading upwards into pale bioclastic limestone. Rich organic and
muddy laminae parallel to the bedding plane decrease upward from the base within each
cycle. The upper unit of each cycle was disturbed by repeated burrowings, which form
part of the firmground (see Section 5). Microscopic examination reveals that the dark,
early-lithified rock contains a minor percent of clay, rich organic shreds and bioclasts (Fig.
9; Table 4).

Microfossils in Bed 27 are much more abundant and diverse than previously
thought (Fig. 6). Of these, foraminifera are most abundant among all clades. Echinoids
are also remarkably abundant, although they cannot be identified beyond a certain
taxonomic level (Figs. 10-12). Bed 27a contains fossil skeletons of foraminifers,
ostracods, echinoids, and brachiopods (Fig. 10), which is similar in component
composition to Bed 26 (Fig. 6). Bed 27b comprises marls and clays in the lower part, in
which fossil fragments are very rare (Fig. 9). The remainder of Bed 27b yields a fossil
fragment abundance (FFA) composed mainly of foraminifers and brachiopods (Fig. 6).

Both Beds 27c and 27d contain much more abundant and diverse FFA than Bed 27b (Figs.
10-12), both of which are dominated by foraminifers, ostracods and brachiopods with
minor constituents of echinoids (Fig. 6).

It should be noted that Bed 27 is usually subdivided into four layers (Yin et al.,
2001). Cao and Zheng (2009), however, divided this bed into six layers (units) including a
stromatolite layer (Bed 27-5) and mudstone (Bed 27-6) in the upper part of Bed 27. Later,
Zheng et al. (2013) denied the existence of the stromatolite layer and divided Bed 27 into
five layers; no stromatolitic structures are seen in our thin sections either. Except for the
topmost 0.5 cm thick layer of carbonaceous mudstone, another four layers are similar to
those recognized by Yin et al. (2001). In addition, Cao and Zheng (2009) and Zheng et al.
(2013) interpreted the irregular surface separating Beds 27a and 27b (Fig. 9) as
firmground surface as a result of a rapid transgression. Here, we agree with the
firmground interpretation of these irregular surfaces within Bed 27 (Cao and Zheng, 2009;
Zheng et al., 2013) because of the presence of abundant burrows typical of the
Glossifungites ichnofacies (Seilacher, 1967) and distinct lithological interfaces, typically
dark muddy micrite overlain by light gray, coarser-grained bioclastic packstone-wackestone, within Bed 27 (Fig. 9; see also Section 5). Firmgrounds of the *Glossifungites* ichnofacies, also termed omission surfaces (Knaust, 1998), have been extensively used in sequence stratigraphy to identify and characterize discontinuity surfaces (Pemberton and Frey, 1985; MacEachern et al., 1992, 2007; Buatois and Mángano, 2011). Within Bed 27, the unlined burrows penetrating into muddy limestone are passively filled with coarser grains from the overlying stratum. This means that the burrows remained open after the trace maker had left, thereby permitting bioclast grains from subsequent depositional events to fill the open, stable burrows. Although the majority of documented *Glossifungites* ichnofacies are from shallow-marine settings (Knaust, 1998; Buatois and Mángano, 2011), this ichnofacies is also present in relatively deep marine contexts, such as incision of submarine canyons during relative sea-level falls (e.g. Dasgupta and Buatois, 2012) or autogenic erosional episodes by turbidity currents and bottom currents (Savrda et al., 2001; Gérard and Bromley, 2008; Hubbard and Shultz, 2008). As such, the *Glossifungites* ichnofacies from Bed 27 may represent an omission surface, but cannot indicate a precise depositional environment for Bed 27. Integration of lithofacies, paleoecologic and ichnofacies indicates that Bed 27 may have
been deposited on a carbonate ramp near the storm wave action zone (Fig. 3), as suggested by Zhang et al. (1997; 2005).

3.6. Bed 28

Bed 28 comprises yellow claystone having similar composition to Bed 25 (Table 4), dominated by montmorillonite mixed with illite. Apart from conodonts (Jiang et al., 2007), no other fossils have been recovered from this bed.

3.7. Beds 29-59

Bed 29 encompasses wackestone with rare foraminifer tests (Fig. 13). Pyrite is commonly seen in thin section and pyrite content increases up-section. A minor omission surface, equivalent to the erosional surface of Zhang et al. (2007) is developed in the middle part of Bed 29 (Zhang et al., 2007). Fossil fragments are very rare and their contents decrease upwards within the bed (Fig. 6; Table 3). Bed 30 is a marlstone, which has a wackestone to micritic texture and lacks any fossil fragments (Table 3). Both beds...
contain laminated stratification and lack any cross bedding, indicating a low-energy environment. Beds 29-30 therefore may have been deposited in the upper part of the offshore setting that is below fair-weather wavebase (Chen et al., 2007).

Beds 31-51 are typified by alternating black shale, greenish gray mudstone, and gray marlstone in the lower part, and interbeds of gray calcareous mudstone and pale muddy limestone in its upper part. They are subdivided into 39 cm-scale cycles (Chen et al., 2007; Fig. 3). In general, the lower unit of the cycle is characterized by black shale or greenish mudstone rich in bivalve and ammonoid fossils (Fig. 4F, I), while the upper unit is dominated by calcareous mudstone and marlstone. The mudstone-dominated cycles are transitional to the marl-dominated cycles up-section, indicating a long-term up-shallowing cycle (Chen et al., 2002, 2007; Tian et al., 2014). In addition to the lithologic variation, Beds 31-34 are characterized by the calcareous mudstone and shale where laminated stratifications are commonly preserved (Fig. 4C), while the upper part of the formation (Beds 35-51) is typified by an increasing number of laminated marl beds (Fig. 3). Fossil fragments occur occasionally in Beds 45, 50 and 51, characterized by foraminifer and ostracod skeletons (Table 3; Fig. 6). Horizontal burrows of Planolites are present in Beds 36-51, which also yield a few shell beds of bivalves (i.e., Claraia
griesbachi) and ammonoids (Ophiceras spp.) (Chen et al., 2007). This unit was interpreted as the result of sedimentation relatively deep offshore (Fig. 3; Zhang et al., 2005; Chen et al., 2007).

Beds 52-53 comprise alternations of shale and marlstone, yielding reasonably abundant burrows of Chondrites and Planolites. Increasing fossil fragment content is seen in both Beds 52 and 53, in which foraminifer, ostracod and echinoid shell fragments are remarkable (Fig. 13), although they are definitely minority components in thin section (Fig. 6; Table 3). Moreover, horizontal stratification is commonly present in both shale and marlstone. These two beds were interpreted as the result of sedimentation in the relatively deep offshore below storm wavebase (Chen et al., 2007).

Towards the top of the Yinkeng Formation, the succession (Beds 54-59) is dominated by marl-dominated cycles. A thin-to medium-bedded marl is hummocky cross-stratified (HCS; Fig. 4A, B, D) and often displays multidirectional tool marks on its base, and horizons of loading and soft sediment deformation are very common (Chen et al., 2002). Fossil fragments are reasonably abundant in Beds 54-59 (Fig. 13), although they are still in the minority in thin section (Fig. 6; Table 3). Foraminifers, ostracod and echinoids characterize their FFA (Fig. 6; Table 3). Trace fossils are also commonly
present in these beds, including *Planolites* isp., *Treptichnus* sp., and *Thalassinoides* isp. Moreover, the sedimentary structure HCS was interpreted as having been generated by offshore storm currents. Beds 54-59 therefore may have been deposited offshore, near storm wavebase (Chen et al., 2007).

**4. Biotic changeover through the P-Tr transition**

**4.1. Biodiversity variations over the P-Tr transition**

Comprehensive paleontological studies of the Meishan section were undertaken in the 1980s (Zhao et al., 1981; Sheng et al., 1984; Yang et al., 1987; Shi and Chen, 1987). The fossil record employed by Jin et al. (2000) to document the PTME pattern, which shows an abrupt extinction calibrated to the base of Bed 25, was sourced mainly from these studies. Since then, more diverse faunas and floras have been documented from Meishan, including foraminifers (Song et al., 2007, 2009), radiolarians (He et al., 2005), brachiopods (Chen et al., 2002, 2005a, 2006b; Li and Shen, 2008; Chen and Liao, 2009), conodonts (Nicoll et al., 2002; Tong and Yang, 2004; Luo et al., 2006, 2008; Jiang et al., 2009).
2007, 2008; Zhang et al., 2007, 2009; Yuan et al., 2014), ostracods (Crasquin et al., 2010; Forel and Crasquin, 2011), palynolomorphs (Zhang et al., 2007), and arcritarchs (Li et al., 2004). Additional macrofossils were collected throughout the upper Changhsing Formation to the Yinkeng Formation. Several shelly fossil communities from Beds 24, 26, 27, 32, 40, and 53-55 were quantitatively analysed (Chen et al., 2010a).

Shen et al. (2011b) and Wang et al. (2014) demonstrated a steep decline zone of species richness corresponding to the interval between Beds 25 and 28 in Meishan by a means of quantitative analysis on fossil records from more than ten PTB sections (including Meishan) from South China. In contrast, Song et al. (2013a) calculated species richness of each layer marked in microstratigraphic analysis (Beds 24-29) based on the updated fossil record mentioned above. Species richness of single layers experienced a stepwise but minor decline within Bed 24. Two distinct declines in species richness were well demonstrated and calibrated to Beds 25 and 28. The same pattern is also indicated in seven PTB sections in South China (Song et al., 2013a). Above Bed 28, species richness remains very low in the remaining part of the Yinkeng Formation.

Here, additional fossil specimens, primarily brachiopods, ammonoids and bivalves, have been collected from Beds 24e, 26, 27 to document biotic turnover across
the PTB. Moreover, microfossils were observed in the petrologic thin sections used for microfacies analysis (see Section 3). Of these, foraminifers are the most abundant skeletal fragments among all clades. Most of these foraminifer tests, however, were illustrated by Song et al. (2007, 2009), so the newly obtained fossil record does not affect the biotic extinction pattern revealed by Song et al. (2013a).

4.2. Fossil fragment content variations through the P-Tr transition

The abundance and diversity of skeletal grains within the late Changhsingian samples (Beds 22-24) is remarkably high. Skeletal grains from all sampled levels except for the top 1-2 cm (Bed 24e-6) of Bed 24e comprise 68-74% of the total rock volume in the uppermost Changhsing Formation (Fig. 14). Fossil fragment assemblages are strikingly similar to one another in all sampled layers within the interval between Bed 22 and 24e-5, and each of these is dominated by foraminifers, crinoids and brachiopods. Other major constituents include ostracods, bryozoans, sponge spicules, and macroalgae (Fig. 14). Skeletal grains of gastropods, calcareous sponges and radiolarians are relatively rare and absent in some horizons (Fig. 14).
It is noteworthy that FFAs do not appear to differ at all across the contact between Beds 24d and 24e, although an omission surface, also a 3rd sequence boundary (Zhang et al., 1997), separates these two layers (Zhang et al., 1997). In contrast, FFAs experienced a dramatic reduction in diversity across a lime laminae layer between Beds 24e-5 and 24e-6 (Figs. 6, 14). Above this lamina layer (Fig. 7D), skeletal grains of Bed 24e-6 comprise about 60% of all rock in thin section in comparison with nearly 70% in Beds 22-24e-5 (Fig. 14). The overwhelming majority of the FFA in Bed 24e-6 is sponge spicules (35%) with minor constituents of foraminifers (8%), brachiopods (7%), crinoids (6%), and echinoids (4%) (Table 3; Fig. 6). Furthermore, fusulinids disappeared forever at this lamina (Kaiho et al., 2006b). The FFA experiences a loss of five major orders (i.e., ostracods, bryozoans, calcareous sponges, gastropods, and macroalgae) across the boundary between Beds 24e-5 and 24e-6 (Figs. 6, 14). More importantly, this horizon coincides with a pronounced negative carbon isotope excursion and a sulfur isotopic excursion anomaly (Kaiho et al., 2006a, b), and thus marks the actual biotic extinction horizon (Kaiho et al., 2006b).

Fossil fragment contents form a high plateau in both abundance and diversity, comprising nearly 70% of total rock and including almost all skeletal clades recognized
from the Changshing Formation. They underwent a dramatic depletion in both abundance and diversity in Beds 25-26a, which are nearly barren of skeletal grains (Fig. 14). This severe depletion therefore is calibrated to the base of Bed 25, coinciding with the PTME (Jin et al., 2000; Shen et al., 2011b) or the first phase of the PTME (Song et al., 2013a). After the PTME, skeletal grains started to rebound in Bed 26b, the top 2-cm interval of the bed and 8-10 cm above the base of Bed 25. Fossil fragments in Bed 26b, however, comprise only 32% of all rock in comparison with nearly 70% before the PTME (Figs. 6, 14). The FFA in Bed 26b comprises mainly foraminifers, ostracods, brachiopods, bryozoans, and echinoids (Fig. 7). Both foraminifers and echinoids are the most abundant among all clades (Fig. 6). Of particular interest is the presence of both echinoids and bryozoans, with bryozoans represented by fenestellid fragments. These two clades have generally been believed to have gone extinct at the PTME (Sepkoski, 1981, 2002), but instead they occur in the aftermath of the PTME at Meishan. Their body fossils were also found in association with the H. parvus Zone in the neighbouring Huangzhishan section of western Zhejiang Province (Chen et al., 2009).

Fossil fragment abundance remains almost same as in Bed 26b, comprising nearly 31-38% through the entire Bed 27, except for Bed 27b, in which skeletal grains are
only 10% of all rock. Thus, fossil fragments rebounded and reached nearly half their pre-extinction level with a major depletion occurring in mid-Bed 27 (Fig. 14). If considering the FFA of the entire Bed 27, which contains elements of brachiopods, bryozoans, foraminifers, and ostracods (Table 3), then recovery of FFA diversity in Bed 27 is marked by the re-appearance of 45.5% of all pre-extinction orders (Table 3).

FFA experienced a major loss in Bed 29, down to less than 10% (Fig. 14). Fossil fragments are absent in Beds 28-44. After rebounding in Bed 45, the skeletal grain assemblage underwent a stepwise abundance recovery in Beds 50-51 and remained at a relatively stable level, occupying nearly 16% of all rock in Beds 52-60. FFA diversity, however, remains at a rather low level, with the re-appearance of only three orders: foraminifera, ostracods and echinoids (Fig. 14).

4.3. Community structural changes of shelly faunas

The P-Tr shelly communities are characterized by a mixture of large-sized ammonoids and small brachiopods in the uppermost Changhsing Formation and by...
numerous shell beds in the Yinkeng Formation (Fig. 15). Chen et al. (2010a) recognized six macrofossil communities from the uppermost Permian to lowest Triassic in Meishan, including the *Rotodiscoceras* sp.–*Paracrithyris pigmaea* (*R–P*) Community (Bed 24), *Tethyochonetes liaoi* (*T*) Community (Bed 26), *Paryphella triquetra–Tethyochonetes liaoi* (*P–T*) Community (Bed 27), *Claraia griesbachi–Ophiceras* sp. (*C–O*) Community (Bed 32), *Claraia wangi* (*C*) Community (Beds 40), and *Meishanorhynchia–Lytophiceras* (*M–L*) Community (Beds 53-55).

Several diversity indices (Shannon and Simpson indices and Dominance) are usually employed to measure community structures. It should be noted that the Shannon measures are the only standard diversity indices that generate meaningful independent alpha and beta components when the community weights are unequal or sampling is uneven (Jost, 2007). Dominance index (D) measures ‘evenness’ of the community from 0 to 1, 0 being the most even distribution amongst taxa. Simpson index = 1–Dominance index, and values range from 0 (one taxon dominates the community completely) to 1 (all taxa are equally present) (Hammer et al., 2001). Note that these diversity indices are useful in estimating diversity but are not themselves measures of diversity. Their numerical equivalent indicates changes of true diversity (Jost, 2007; Kosnik and Wagner,
Conversion of both Shannon and Dominance indices to true diversities developed by Jost (2006, 2007) is performed to indicate true diversity changes over the P-Tr transition. In addition, the bias-corrected Simpson evenness index (Olszewski, 2004) is also applied to estimate the evenness within and among communities examined here.

Detailed community structural indices are listed on Table 5.

The late Changhsingian R–P community has Shannon index (H) of 2.029, which is slightly smaller than the same index of 2.796 for the Changhsingian brachiopod *Cathaysia–Martinia (C–M)* community reported from the Shaiwa Group of southern Guizhou Province, southwest China (Chen et al., 2006a), but is slightly larger than the same index of 1.879 for the Wuchiapingian brachiopod *Edriosteges poyangensis–Spinomarginfera lopingensis (E–S)* Community reported from the basal Lungtan Formation of the Daijiagou section, Chongqing city, southwest China (Chen et al., 2005b). Dominance of the R–P community, D = 0.1519, also lies between the same indices of the above Changhsingian and Wuchiapingian brachiopod communities, with D = 0.07375 and 0.178, respectively (Chen et al., 2010b, table 4). It is also true for evenness of community (E) that the R–P community has E of 0.8453, which lies between 0.9262 and 0.822, the values of E for the C–M and E–S communities, respectively (Chen et al., 2006a).
Accordingly, the R–P community is typical of Late Permian shelly communities. In contrast, H values of all post-extinction communities, 1.47, 1.565, 0.7559, 0, and 1.288 for the T, P–T, C–O, C, and M–L communities, respectively (Table 5) are much smaller than the same values of the Changhsingian and Wuchiapingian communities, H = 2.796 and 1.879, respectively. These post-extinction communities therefore are much less diverse than the pre-extinction communities of the Late Permian, indicating the severe impact of the PTME on marine communities.

Changes in both standard diversity Shannon index [Exp (H)] and dominance index (D’) between neighboring pairs of communities show that major losses in diversity coincide with the turnovers of the R–P/T and P–T/ C–O communities, losing 43.6% and 55.5% respectively. Similarly, standard diversity dominance (D’) increases by 34% and 54%, respectively (Table 6). Thus, community structural collapse indicated by a decrease in diversity, coupled with increase in dominance, coincides with two extinctions bracketed at the bases of Beds 25 and 28 at Meishan (Song et al., 2013a). In addition, Exp (H) value increases by 262.6% from the C to M–L communities, and also increases by 70%, coupled with a decrease of 15.2% in D’ values, from the C–O to M–L communities, suggesting an improvement in shelly community structures in Beds 53-55 at Meishan.
Structural improvement of the M-L community is also reinforced by comparison between the M–L community and the Anisian Madonia sp.–Rhaetina angustaeformis (M–R) Community, which marks the recovery of benthic communities in the Anisian (Chen et al., 2010b). The Anisian community has H and D values of 2.051 and 0.1501 respectively (Chen et al., 2010b, table 4), but the same values for the M-L community are H = 1.288 and D = 0.4379, respectively. Consequently, the M–L community embraces much more improved diversity indices than other Griesbachian communities in Meishan, but instead has a much lower diversity and higher dominance index than both pre-extinction and recovery communities.

5. Trace fossils and bioturbation

At Meishan, Bottjer et al. (1988) made the first attempt to ecologically test the PTME based on trace-fossil assemblages. These authors, however, could not collect sufficient trace fossils because of restricted exposure at that time, but they noted that ichnotaxa from the PTB beds are dominated by Planolites and Chondrites, which indicate generally a poorly oxygenated environment (Bottjer et al., 1988). Later, Cao and Shang
(1998) reported a few ichnotaxa such as *Thalassinoides*, *Planolites* and *Skolithos* from the PTB beds of Meishan, but *Skolithos* was later rejected by these authors (Cao and Zheng, 2009; Zheng et al., 2013). Zhang and Tong (2010) also examined trace fossils recorded in drilling cores through the P-Tr transition in Meishan. Although these authors clarified that trace fossil evidence suggests two ecologic crises, coinciding with Beds 24e-27 and Beds 34-39, respectively (Zhang and Tong, 2010), the documented ichnofossils are too few to support such a conclusion (see Section 7). As a result, several lines of evidence show that trace fossils are reasonably abundant in the PTB beds in Meishan. They however remain poorly understood owing to inadequate trace fossil specimens.

Here, we document our observations at all PTB sites newly exposed during the construction of the geological park in the GSSP Meishan in the 2000s, which uncovered extensive fresh exposures along all the quarries (Fig. 1E). Abundant trace fossils were collected from Beds 8-9 and 23-24 of the Changhsing Formation and Beds 26-27 and 35-57 of the Yinkeng Formation. The ichnofabric indices (ii, *sensu* Droser and Bottjer, 1986) and bedding plane bioturbation index (BPBI, Miller and Smail, 1997) throughout the upper Changhsing Formation and entire Yinkeng Formation are also examined.
5.1. P-Tr ichnotaxa and their stratigraphic distributions in Meishan

5.1.1. Stratigraphic distribution of ichnoassemblages

A total of 17 ichnospecies in 13 ichnogenera and a problematic ichnotaxon have been found in the P-Tr transition at Meishan (Figs. 16-18). Major characteristics, stratigraphic distributions and interpretation of each ichnotaxon are tabulated here (Table 7). Trace fossils are distributed mainly in Beds 8-9 and Beds 23-24 of the Changhsing Formation, and in Beds 27, 35-53, 55-57 of the Yinkeng Formation. Of these, the lower Changhsing Formation (Beds 8-9) ichnoassemblage is dominated by relatively large burrows of *Thalassinoides* isp. 1 (Fig. 16A, D) and resting traces of *Lockeia* isp. (Fig. 16F). *Paleophycus* isp. (Fig. 16B) is also commonly present in Beds 8-9.

The trace-fossil assemblage from Beds 23-24e is characterized by tree-like traces of *Dendrorhaphe* isp. (Fig. 17F) and abundant burrows of problematic status. The latter is represented by simple, straight, unbranched burrows (Fig. 17B-C), each originating at a small, close end and extending distally to form a horn-shaped burrow with an open...
distal end (Fig. 17B-C). Burrow diameters vary from 20-27 mm. Some burrows penetrate the bedding at acute angles, and others are horizontally distributed on bedding planes. The burrow has a distinct circular wall, about 2-5 mm thick. These burrows are preserved in dark organic muddy limestone and filled with light-colored, coarse-grained sediments. These morphologies suggest that this problematic form differs from all known ichnotaxa.

Another feature of the Bed 24 ichnoassemblage is the presence of abundant ichnofossils near the contact between Beds 24d and 24e, including several distinct burrowing ichnotaxa: *Balanoglossites triadicus*, *Taenidium* isp., *Thalassinoides* isp. 1, and *Planolites* isp. 1. Of these, *Balanoglossites* is represented by vertical tubes (Fig. 16C) that penetrate to a depth of 5-10 cm perpendicular to bedding. This ichnogenus occurs usually at omission surfaces that served as sequence boundaries (i.e., Knaust, 1998). These traces are preserved in limestone of the upper part of Bed 24d (Fig. 3). *Taenidium* burrows (Fig. 16E, 17E) are also very common in Bed 24d-e, and they are usually cylindrical, straight, unbranched, and backfilled. This ichnoassemblage as a whole represents the *Balanoglossites* ichnofacies associated with the omission surface, as described by Knaust (1998, 2004). In addition, horizontal burrows of *Planolites* isp. are densely packed on top of Bed 24e (Fig. 17A, E), which is just beneath the base of Bed 25,
in which the PTME horizon is placed (Jin et al., 2000).

Abundant burrows were also found in association with an omission surface within Bed 27. These burrows and the possible firmground surface have long remained disputed, although several recent studies have addressed an ichnoassemblage of this bed (Cao and Shang, 1998; Cao and Zheng, 2009; Zheng et al., 2013). Burrow systems preserved in Bed 27 therefore are re-studied here (see below).

Beds 28-34 are barren of trace fossils. The remaining part of the lower Yinkeng Formation (Beds 35-51) yields rare trace fossils, which are dominated by simple, horizontal burrows of *Planolites* isp. 2 (*Fig. 18A-B*). Increasing numbers of ichnotaxa occur in the upper Yinkeng Formation and are characterized by the presence of the tree-like burrow system of *Chondrites* isp. (Bed 52; *Fig. 18C*) and relatively complicated burrows of *Thalassinoides* isp. 3 (*Fig. 18D-E*) and *Treptichnus* isp. (*Fig. 18G-H*).

5.1.2. Ichnofabric changes within Bed 27

Within Bed 27, intensive burrowing on an omission surface, characteristic of the *Glossifungites* ichnofacies, caused a pronounced relief on the firmground surface up to 3
cm high near the boundary between Beds 27a and 27b (Figs. 19-20). The firmground of

Glossifungites ichnofacies is partly covered by a faintly laminar black muddy limestone

that seems resistant to weathering. Highly irregular relief at the surface of the firmground

indicates that the solid rock was affected deep subsolution (Savrda, 1992). Trace fossils

increase upward to the contact between Beds 27c and 27d, which is overlain by finely

laminated muddy limestone (Bed 27d) again.

To reconstruct complete burrowing systems within Bed 27, one complete sample

of the bed (from base to top) was cut and separated into three blocks (Fig. 19). The

transverse view from three polished slabs shows the colonizing zonation (CZ) from base

to top of the bed by various ichnocoenoses within a 16-cm-thick unit (Fig. 20).

CZ I: This is a historical zone, a unit that is beyond the reach of even the deepest

burrows (Fig. 20). CZ I includes the first 2-3 cm of the lower part of Bed 27, which

comprises gray, calcareous mudstone to muddy limestone and is almost barren of trace

fossils. Minor bioturbation is also limited. Body fossils are scarce, except some small,

thin-bedded brachiopods and foraminifers. Pyrite framoids and crystals are relatively

rich and occur in both sediments and fossil shells (see Section 6).

CZ II: This is a transitional zone (Fig. 20), which is extremely heterogeneous
from the activity of deeper burrows (Savrda, 1992). Sediments in this zone were semi-lithified to form a firmground substratum. Firmground sediments are dark-colored, and are disrupted by passively filled burrows of an ichnoassemblage characteristic of the *Glossifungites* ichnofacies. Representative ichnogenera include *Arenicolites*, *Gastrochaenolites*, *Psilonichnus*, and *Thalassinoides*. Of these, *Arenicolites* comprises vertical burrows that penetrate into the dark gray sediments. *Gastrochaenolites* comprises tear-shaped borings, now filled with light gray, coarse-grained sediments in a dark-colored firmground lime muddy substrate. This ichnogenus is commonly present in the *Trypanites* ichnofacies as well (Wilson and Palmer, 1998; Benner and Ekdale, 2004). The vertical cylindrical burrows of *Psilonichnus* are inclined, with bedding in the distal end (Buatois and Mángano, 2011). *Thalassinoides* is typified by its Y-shaped ramification. All these burrows have unlined walls and are filled with light gray-colored, coarse-grained sediments of the overlying layer, indicating that these burrows were passively filled.

**CZ III:** This is a very thin, highly condensed omission surface (Fig. 20), which is characterized by some coarse-grained, reworked sediments that were generated by frequent activity of wave currents. This omission surface is distinguished from the
underlying firmground ichnocoenosis of *Glossifungites* ichnofacies and overlying softground ichnocoenosis of *Cruziana* ichnofacies (see below).

CZ IV: This is a mixed unit (Fig. 20), which is saturated with water and totally homogenized by bioturbation. This unit, about 5 cm thick, yields ichnocoenoses represented by minute burrows of *Diplocraterion* isp. and tear-shaped borings, which resemble the vertical features of *Chondrites* and small *Planolites*. Owing to the soft nature of substrate and intensive bioturbation, burrow boundaries and morphologies have become blurred, making it difficult to identify them confidently to ichnogenus level. This ichnoassemblage, together with the soft substrate, is characteristic of the softground ichnocoenosis of *Cruziana* ichnofacies (Seilacher, 1977).

CZ V: This thin unit is devoid of bioturbation and comprises finely laminated muddy layers (Fig. 20), which yield small pyrite frambooids (see Section 6), indicating the establishment of a quiet, low energy and probably reduced environment.

### 5.2. Extent of bioturbation

Ichnofabric indices (Droser and Bottjer, 1986) of the Upper Changhsing
Formation (Beds 22–24) are usually rather low (ii1-2) with several peaks reaching 3 (ii3) except for the horizons near the boundary between Beds 24d and 24e (Fig. 3) that records an ichnofabric index of 4 (ii4), but bioturbated strata are about 80% of the entire measured units of the Changhsing Formation. Ichnofabric indices decrease to 2 (ii 2) again at the upper part of Bed 24e, then increase to 3 (ii3) at the top of the bed. No ichnofabrics are observed in Beds 25-26a. The ii value surges to 3 (ii3) in Beds 26b-27, with 40% strata bioturbated. Beds 28-34 are void of ichnofabrics again. The ii value of Beds 35-57 remains rather low (ii1) except for several peaks reaching 2 (ii2) in Beds 42, 46, 52-53, and 56-57 (Fig. 3). Only 15% of the examined units are bioturbated. Accordingly, ichnofabric indices of the upper Changhsing Formation vary from 2 to 4 (ii2–4). Averagely 80% strata of the upper Changhsing Formation are significantly bioturbated. Ichnofabric indices from Bed 27 remain relatively high (ii4), although only 40% strata are bioturbated. The remaining part of the lower Yinkeng Formation records a rather low ii value (ii1) and no strata are significantly bioturbated. Ichnofabric indices in the middle and upper parts of the Yinkeng Formation vary from 1 to 2 (ii1-2). On average, 15% of strata are significantly bioturbated.

In the upper Changhsing Formation, the two bedding planes in Bed 23
containing *Dendrorhaphe* isp. (Fig. 17F) and the problematic trace (Fig. 17D), show coverage of 90% and thus indicate a BPBI of 5 (Fig. 3). The same BPBI value (ii 5) is also estimated from two horizons of Beds 24d, containing *Taenidium* burrows. Bedding planes from other horizons in the upper Changhsing Formation generally have bioturbation coverage varying from 10% to 60%, indicating BPBI of 1-5. For the top bedding plane of Bed 24e, just below the mass extinction horizon, containing *Planolites* (Fig. 17A, E) the coverage was up to 90%, indicating a BPBI of 5. Beds 25-26a have the lowest BPBI, with almost no bioturbation recorded. Several bedding planes from Beds 26b-27 show changes in coverage from 20% to 40%, indicating a BPBI of 2-4. Bedding plane coverage in Beds 28-34 is generally rather low because bioturbation is broadly absent. Beds 35-51, overall, have bioturbation coverage <10%, but some bedding planes containing *Planolites* show coverage up to 20%, indicating a BPBI of 2. Another bedding plane containing *Chondrites* has coverage up to 90%, indicating a BPBI of 5. In the upper Yinkeng Formation, one bedding plane containing *Thalassinoides* shows coverage up to 20%, indicating a BPBI of 2.

5.3. Changeover of trace-fossil diversity over the P-Tr transition
Ichnodiversity, represented by ichnogenic richness, decreased remarkably over the P-Tr transition. Eight ichnogenera are commonly encountered in the uppermost Changhsing Formation: *Balanoglossites, Dendrorhaphe, Lockeia, Paleophycus, Planolites, Problematica, Taenidium, and Thalassinoides* (Fig. 21A). Only *Planolites* is present at the top of Bed 24e, dropping to 87.5% in the upper part of Bed 24e. All ichnotaxa disappear at the top of Bed 24e, coinciding with the PTME. As a consequence, Beds 25-26a are barren of ichnotaxa. The ichnofauna rebounded in Bed 26b and diversified in Bed 27, including seven ichnogenera: *Arenicolites, Diplocraterion, Gastrochaenolites, Psilonichnus, Thalassinoides, Chondrites, and Planolites*. Of particular interest is the presence of four vertically burrowing ichnogenera (*Arenicolites, Diplocraterion, Gastrochaenolites, Psilonichnus*) and one relatively complicated burrowing ichnogenus (*Thalassinoides*), implying that ichnodiversity almost reached the pre-extinction level in Bed 27 (Fig. 21A). All ichnotaxa disappeared soon after (in Bed 28). As a consequence, Beds 28-34, ranging through conodont zones *I. isarcica* and *I. planata* Zones, lack any ichnotaxa and remained poorly bioturbed (Fig. 3). The post-extinction rebound of ichnotaxa is marked by the presence of *Planolites* in Bed 35.
Since then, ichnodiversity remained at a rather low level and did not increase until the middle-late Griesbachian, which saw the rise of *Chondrites* in Bed 52. Although *Chondrites* disappeared in the middle-late Griesbachian, the trace-fossil assemblage slightly diversified and included *Planolites, Treptichnus* and *Thalassinoides*.

As a result, P-Tr ichnotaxa underwent two pronounced reductions in diversity coinciding with the two episodes of PTME calibrated to the bases of Beds 25 and 28.

Ichnofaunas fell to their lowest diversity in the early Griesbachian, and experienced a slow increase in diversity throughout the middle-late Griesbachian (Fig. 21A). However, post-extinction trace-fossil diversity never returned to the pre-extinction level.

### 5.4. Burrow size variations through the P-Tr transition

Nine bedding planes were examined to determine the size distribution of burrow diameters of *Arenicolites, Dendrorhaphe, Diplocraterion, Paleophycus, Planolites, Problematica, Taenidium, Thalassinoides*, and *Treptichnus* (Fig. 22). Burrow size change over the P-Tr transition is apparent, especially in *Planolites*, as well as other traces such as *Balanoglossites, Chondrites, Dendrorhaphe, Taenidium, Thalassinoides, Treptichnus*. 
Planolites is distributed in ten horizons throughout the uppermost Changhsingian to middle-upper Griesbachian, and thus is a good proxy for size variation of trace fossils over the P-Tr transition. Mean diameters of the Changhsing Formation Planolites burrows are 7 mm, 8.5 mm, and 5.5 mm, respectively from three horizons, with maximum burrow diameter up to 9.2 mm (Fig. 22A). Burrow sizes decrease remarkably across the boundary between Beds 24 and 25, the PTME horizon (Fig. 1B), with mean burrow diameters of 1.7 mm and the greatest burrow diameter only 2.2 mm in Bed 27 (Fig. 22A). Burrow sizes of Planolites remain very small throughout the early-middle Griesbachian and become larger by the late Griesbachian (Beds 54-57). These late Griesbachian traces are still much smaller than their counterparts recorded in the pre-extinction strata (Fig. 22A). Comparable size change over the P-Tr transition is also demonstrated by both the greatest size and mean size of Thalassinoides from the same interval (Fig. 22B).

Several other ichnotaxa in the uppermost Permian have mean and maximum diameters, such as Balanoglossites (4.6 mm, 6.4 mm), Dendrorhapes (12 mm, 17 mm), problematica (22 mm, 28 mm), and Taenidium (7.8-8.8 mm, 9.2 mm), that are obviously larger than that of those ichnotaxa confined to the lowest Triassic, i.e., Chondrites (2.8
mm, 5.6 mm) and Treptichnus (6.3 mm, 6.3 mm) (Fig. 22C-D). When the measurements of all 273 burrows measured from the P-Tr strata of Meishan are combined, both mean and maximum diameters exhibit remarkable reduction across the boundary between Beds 24 and 25 and remain very low values until Bed 27. The same values further decline from Bed 27 to Beds 28-34, and then undergo a stepwise increase through Beds 35-57 (Fig. 21B).

Trace-fossil size variations over the P-Tr transition are consistent with figures from northern Italy (Twitchett, 1999; Twitchett and Barras, 2004) and South China (Chen et al., 2011). It should be noted that the Early Triassic Planolites traces are much smaller than their Changhsingian counterparts at Meishan (Fig. 22A), unlike the same traces elsewhere (Pruss and Bottjer, 2004). Planolites is supposed to be the least susceptible to mass extinction because this simple trace can be produced by a variety of organisms (Pruss and Bottjer, 2004). Accordingly, the Changhsingian Planolites and their Early Triassic counterparts may have been made by different organisms.

5.5. Trace fossil form and complexity
The Changhsing Formation trace fossils are morphologically diversified, and include simple, horizontal burrows (*Planolites*), vertical or oblique burrows (*Balanoglossites* and *Problematica*), resting traces (*Lockeia*), and complex forms (*Dendrorhaphes*, *Taenidium*, and *Thalassinoideae*). They, however, disappear across the PTME horizon (base of Bed 25). Both *Planolites* and *Thalassinoideae* rebound in Bed 27, but decrease markedly in size in comparison with their Changhsingian counterparts. *Thalassinoideae* is also less complex than the same trace recorded in the Changhsingian. Complex forms, and resting and vertical traces of the Changhsingian (*Balanoglossites*, *Lockeia*, *Taenidium*, *Dendrorhaphes*, and *Problematica*) vanish in Bed 27. Instead, the relatively complex burrow systems of the Glossifungites ichnofacies, i.e., *Arenicolites*, *Gastrochaenolites*, *Psilonichnus*, and *Thalassinoideae*, characterize the ichnoassemblage in the lower part of Bed 27. Vertical burrows of *Diplocraterion*, together with *Chondrites* and *Planolites* also occur in the upper part of Bed 27. Accordingly, ichnotaxa recovered from the pre-extinction level are similar to those in Bed 27 in terms of complexity, although these burrows are much smaller than their counterparts elsewhere. Early Griesbachian traces are dominated by small, simple, horizontal burrows of *Planolites*, as reported elsewhere (Twitchett and Barras, 2004; Pruss and Bottjer, 2004;
Fraiser and Bottjer, 2009; Chen et al., 2011, 2012). In the middle-late Griesbachian trace fossils become slightly more complex and are marked by the presence of *Chondrites*, *Thalassinoides* and *Treptichnus*, although these burrows are still very small. Nevertheless, these middle-late Griesbachian burrows are branched and form slightly complex networks, and thus are more complex than the *Planolites*-dominated ichnoassemblage in the early Griesbachian.

As a result, trace-fossil complexity, reflecting behavioral complexity of the trace-makers, decreased dramatically during the PTME. Then, the trace-fossil assemblage shows an increase in complexity, varying from simple, horizontal traces (i.e., *Planolites*) in the early Griesbachian to relatively complex traces (*Chondrites*, *Thalassinoides* and *Treptichnus*) in the middle-upper Griesbachian. In particular, the reappearance of *Thalassinoides* and *Treptichnus* probably implies increasing behavioral complexity that typically indicates the beginning of biotic recovery elsewhere (Twitchett and Barras, 2004).

5.6. Infaunal tiering

63
Levels of tiering above and below the sediment were greatly reduced after the PTME (Ausich and Bottjer, 1982, 2002). At Meishan, the change in infaunal tiering over the P-Tr transition is reflected by the penetration depth of burrows (Fig. 21C), which was measured in the field. Vertical burrows of the Changhsing Formation may extend a maximum depth of 10 cm into the sediment, indicating a rather deep tiering level (ii5). In contrast, burrows of Planolites and Thalassinoides recorded in Bed 27 may penetrate to <2 cm into the sediment. In particular, Thalassinoides commonly shows the second tiering level (ii2) (Bottjer and Droser, 1994). Early Griesbachian Planolites has burrows extending to a maximum depth of only 0.5 cm (Fig. 21C) indicating the lowest tiering level (ii1) (Bottjer and Droser, 1994). Thus, tiering fell to its minimum level in the early Griesbachian. An increase in tiering level during the middle Griesbachian is marked by the presence of Chondrites, an anoxic burrow system penetrating to a depth up to 1-2 cm and indicating the second tiering level (ii2) (Bottjer and Droser, 1994). The same tiering level is also reflected in upper Griesbachian Thalassinoides and Treptichnus burrows, which may extend to a maximum depth of 1-2 cm (Fig. 21C). Accordingly, the tiering level decreases significantly across the PTME horizon in Meishan, and then increases throughout the Griesbachian (Fig. 21C).
Pyrite is rather commonly present in the latest Changhsingian to Griesbachian rocks at Meishan (Wignall and Hallam, 1993), which is also confirmed by our observations of thin sections through the P-Tr transition at Meishan. Several pyrite-enriched beds have been treated as indications of anoxic conditions at Meishan (Wignall and Hallam, 1993). In particular, pyrite framboids, which are spherical aggregates of pyrite microcrystals, are rather abundant in these pyrite-enriched beds near the PTB at Meishan (Jiang et al., 2006; Shen et al., 2007). Pyrite framboids in ancient and modern sediments are interpreted as the result of redox conditions (e.g., Bond and Wignall, 2010), and these authors show that small framboids, usually 3-5 µm in diameter, indicate euxinic conditions (H₂S-bearing, O₂-free bottom waters). Accordingly, pyrite framboids have been considered as one of the most important pieces of evidence indicating redox conditions over the P-Tr transition worldwide (Wignall et al., 1998, 2005; Jiang et al., 2006; Shen et al., 2007; Gorjan et al., 2007; Bond and Wignall, 2010; Algeo et al., 2011b).
At Meishan, Jiang et al. (2006) reported that pyrite framboids are very commonly present in all beds through the PTB (Beds 24-29), based on etched residues from bulk samples. Shen et al. (2007) also observed framboids in situ on polished blocks and etched residues. Both studies detected that framboids are very abundant in Bed 25. Contrasting to Jiang et al.’s (2006) observation, Shen et al. (2007) found no pyrite framboids in Bed 27. However, unequal sampling in various beds near the PTB, for instance, 40 g each from Beds 25 and 26, but only 5 g each from Beds 24, 27, 28 and 29 may have biased their observation (Shen et al., 2007). Bed 27 comprises various lithologies from its base to top, which may have been deposited in different environments (Figs. 19-20). Thus, pyrite framboids may be rare absent in these bioturbated layers (i.e., CZs II, III-IV in Bed 24; Fig. 20), but instead may occur in finely laminated layers without bioburbation (i.e., CZs I and IV; Fig. 20).

We have also observed pyrite framboids in continuous thin sections throughout Beds 24-30. We used a FEI Quanta 400 Scanning Electron Microscope (SEM) equipped with a GENESERS 2000 energy dispersive spectrometer (EDS) at the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Wuhan, China. SEM images and EDS spectra were produced by the Zeiss VPSEM.
coupled with an energy dispersive X-ray spectrometer. We confirmed Jiang et al.’s (2006) observation that both pyrite framboids and crystals occur in Bed 27 on brachiopod shells and in foraminiferal tests and sediments (Fig. 23). In addition, we measured framboid sizes in samples from Beds 29-60 using the SEM. Pyrite framboids are very-abundant in samples from 17 horizons over the P-Tr transition (Fig. 24). The majority of framboid diameters in most measured beds are smaller than, or around 5 µm, except for Beds 28 and 44, in which most framboids have diameters of 7-8 µm. Moreover, framboid diameters are concentrated in a narrow size range (< 10 µm) in Beds 27, 28, 43, and 58. In contrast, they have a greater size range in Beds 24b, 24e, 25-26, 29-30, 39, 42, 49, 51-52 and 56, with maximum diameter up to 20 µm in Bed 51.

Bond and Wignall (2010, table 1) proposed several characters, including framboid diameter and pyrite morphology, to determine redox conditions during deposition. In general, when framboids are small (mean diameters: 3-5 µm), abundant, with a narrow size range, and form the dominant pyrite fraction, they could have been deposited in euxinic condition (with a persistently sulfidic lower water column). If framboids are small (mean diameters: 4-6 µm), abundant, with a few, larger forms, and dominate the pyrite fraction, then they could have been deposited in anoxic condition.
(without oxygen in bottom waters for long periods). When framboids have mean diameters of 6-10 µm and are moderately common, with a few, larger framboids together with some crystalline pyrite, they could have been deposited in lower dysoxic condition (with weakly oxygenated bottom waters). In upper dysoxic condition (with partial oxygen restriction in bottom waters) framboids are commonly to rarely present, with a broad range of sizes, only a small proportion of framboids < 5µm, and the majority of pyrite as crystals. In oxic condition (without oxygen restriction), no framboids are present, and pyrite crystals occur rarely.

If these five criteria given by Bond and Wignall (2010) are followed, we can determine redox conditions over the P-Tr transition in Meishan. Bed 24 contains abundant framboids, usually around 5 µm in diameter with some larger framboids, and their size range is relatively broad, pointing to anoxic conditions. Framboids in Beds 25-26 are usually 3-5 µm in diameter, a narrow size range, and no pyrite crystals are present, suggesting euxinic conditions (Fig. 25). Framboids from Bed 27 have a relatively large diameter and a broad size range (Fig. 24), and are also associated with some large pyrite crystals, pointing to a lower to upper dysoxic condition (Fig. 25). Pyrite framboids are moderately common in Bed 28 and have mean diameters of 8-9 µm, but no larger
framboids and crystalline pyrite occur. Thus, Bed 28 is inferred to be deposited in a transitional zone between anoxic and lower dysoxic conditions based on the criteria determining redox conditions proposed by Bond and Wignall (2010). Redox conditions became euxinic soon after in Bed 29, in which framboids are very small (3-5 µm) and have a narrow size range, without pyrite crystals. It should be noted that no pyrite framboids were found in Beds 30-35, although a pronounced negative excursion of carbon isotopes (Xie et al., 2007) and environmental stress indicated by biomarker signals (Yin et al., 2012) occur in these beds. Framboids from Beds 39 and 42 indicate euxinic-anoxic transitional conditions in terms of diameter, size range and association with pyrite crystals. Framboids from Bed 43 are 64-40-6 µm in diameter, but have some larger forms and are also associated with some pronounced pyrite crystals, and thus indicate a lower to upper dysoxic condition. Then, redox conditions indicated by pyrite framboids changed to anoxic to euxinic transitional conditions. Surprisingly, framboids from Bed 58 suggest euxinic condition, which coincides with the last negative excursion of carbon isotopes in the middle-late Griesbachian detected by Burgess et al. (2014).

7. Assessing ecologically PTME and its aftermath
7.1. Testing ecologically extinction patterns

The updated fossil record from Meishan shows two pronounced declines of species richness at the bases of Beds 25 and 28 (Song et al., 2013a; Fig. 26). Similarly, fossil fragment contents recorded in thin sections also show two distinct drops in both abundance and diversity corresponding to the top of Bed 24e and base of Bed 28 (Figs. 6, 14). Further, ichnodiversity also declined within Beds 24 and 27. In Bed 24, trace fossils are rather abundant and comprise four distinct ichnogenera: *Balanoglossites*, *Planolites*, *Taenidium* and *Thalassinoides* in horizons near the boundary between Beds 24d and 24e, but only *Planolites* persisted into Bed 24e-6, in which relatively large burrows are densely packed, indicating a considerably high bioturbation level. All ichnotaxa disappeared in Beds 25-26a. Similarly, ichnotaxa decline from five ichnogenera (*Arenicolites*, *Gastrochaenolites*, *Planolites*, *Psilonichnus*, and *Thalassinoides*) in CZ II (Bed 27b) to three ichnogenera (*Diplocraterion*, *Chondrites* and *Planolites*) in CZ IV (Bed 27c), and then further declined and disappeared at the top of Bed 27d. Other proxies of trace fossils and bioturbation also show two pronounced declines corresponding to the
bases of Beds 25 and 28. Clearly, the PTME ecologic crisis comprised two phases, coinciding with metazoan extinctions calibrated to the bases of Beds 25 and 28 (Song et al., 2013a).

In addition, both fossil fragment contents and ichnodiversity show that a pronounced decline in diversity and abundance started at the stratal interval 10 to 19 mm below the top of Bed 24e. The boundary between Beds 24e-5 and 24e-6 is the most distinct eliminated horizon of skeletal fragment of major fossil groups, coinciding with end-Permian sulfur anomaly (Kaiho et al., 2006a) and the start of the negative end-Permian carbon isotopic excursion (Kaiho et al., 2009), and thus may indicate the PTME. Abundant sponge spicules above this event horizon indicate that they lasted in seawater for a while, although complete sponge fossils disappeared at the PTME event. It is therefore unlikely that the disappearance of calcareous fossils at the top of bed 24e-6 was a result of an increase in the input of terrestrial material associated with the facies shift, as indicated by the lithologic shift from the limestone of Bed 24 to the claystone of Bed 25 and black shale of Bed 26. Instead, the extinction of calcareous biota and the associated environmental perturbation was most likely caused the lithologic change from limestone to mudstone. As a result, the sharp decline in biotic abundance and diversity
10-19 mm below the top of Bed 24e may signal the first episode of the PTME previously inferred from statistical paleontological data (Song et al., 2013a).

7.2. Ecologic collapse lagging behind biodiversity crisis during the PTME

At Meishan, the Permian biota experienced a dramatic drop in diversity at the base of Bed 25, with 172 species (94%) being wiped out in Beds 25-26 and no pronounced reduction of species richness in Bed 28 (Jin et al., 2000). The updated fossil record obtained from Meishan shows that species richness was reduced by at least 79% across the boundary between Beds 24e and 25, compared to 65% loss in species richness across the boundary between Beds 27d and 28 (Song et al., 2013a). This means that marine animals suffered a more severe depletion in species richness in the first phase of the PTME than in the second phase of the same event (Fig. 26). The biodiversity decline pattern from Meishan is confirmed by the same pattern at a further seven PTB sections in South China (Song et al., 2013a). It should also be noted that generic richness declined by a similar magnitude, 85% and 82%, in the first and second phases of the PTME, respectively in Meishan, but both generic and species richness underwent a stepwise
decline from the uppermost Changhsingian to lowest Griesbachian (Fig. 26).

Consequently, biotic diversity suffered a larger loss in the first episode than in the second episode of the PTME in terms of the number of lost taxa. This pattern is reinforced by fossil fragment content variations across the PTME horizons. Fossil components usually occupy nearly 70% in all rock in strata below Bed 25, but only about 30% in Bed 27, and FFA lost nearly 60% in thin section (Fig. 14). Over the same period, 11 Permian orders declined to five orders in Bed 27, losing 54.5% in ordinal richness.

Both the standard diversity Shannon index \( [\text{Exp} (H)] \) and dominance index \( (D') \) assess whether the shelly community possesses a healthy structure. \( \text{Exp} (H) \) values declined by 43.6% from the \( R–P \) to \( T \) communities, and 55.5% from the \( P–T \) to \( C–O \) communities, coinciding with the first and second phases of the PTME, respectively. This means that the shelly communities suffered a greater loss in community diversity in the second phase of the PTME than in the first phase. Similarly, standard diversity dominance \( (D') \) increases by 34% and 54% during the two pronounced drops in diversity, respectively (Table 6). This means that the shelly communities became more uneven after the second phase of the PTME than after the first phase. Thus, shelly communities underwent relatively more serious ecologic crisis in the second phase than in the first
phase of the PTME. This observation is also reinforced by ichnofaunal variations and ichnofabric changes over the P-Tr transition in Meishan.

The presence of seven ichnogenera in Bed 27 suggests that ichnogeneric richness nearly recovered to the pre-extinction level, although there was a taxonomic loss in Beds 25-26a. In contrast, a more dramatic ichnofaunal loss occurred in the second phase of the PTME, corresponding to Bed 28. As a consequence, Beds 28-34 are barren of ichnotaxa. Thus, ichnofaunas suffered a more severe decline in the second phase of the PTME. This pattern is also strengthened by burrow size variations and tiering level changes, both of which remained relatively high in the Changhsingian, and experienced a stepwise decline through Beds 23-27, then fell to their lowest values in the early Griesbachian (Beds 28-34). Ichnofabric variation also shows that Bed 27 still remains highly bioturbated and yields rather complex burrow systems of the Glossifungites ichnofacies and Cruziana ichnofacies, which are commonly present in the pre-extinction period, thus showing the largest turnover at the base of Bed 28 rather than at the base of Bed 25. In contrast, ichnotaxa became very rare after the second phase of the PTME, although 2-3 ichnotaxa rebounded in the middle-late Griesbachian. Consequently, the greatest losses of ichnotaxa correspond to the top of Bed 27, simultaneous with the
second phase of metazoan extinction in Meishan (Song et al., 2013a). This ichnodiversity drop coincides with a remarkable decrease in tiering level (Fig. 21) and burrowing intensity (Fig. 3). Ichnofabric indices recorded in the upper Changhsing Formation are rather high (ii4-5) (Fig. 3). Complex traces of both the Glossifungites and Cruziana ichnofacies recorded in Bed 27 (Figs. 19-20) also indicate a fairly high ichnofabric index (ii3-4). Consequently, there was not a sharp decrease, but a gradual decrease, in burrowing intensity (ii4-5 down to ii3-4) over the first phase of the PTME. This is in sharp contrast to the pronounced drop in biodiversity of metazoans in this phase of the PTME (Fig. 26), suggesting a gradual worsening in environmental conditions.

In contrast, almost all of the complex traces of the Glossifungites and Cruziana ichnofacies disappeared in the second phase of the PTME. The early Griesbachian Planolites is confined to discrete horizons (ii1-2) separated by metres of unbioturbated sediment, and indicates a rather low ichnofabric index (ii1) (Fig. 3). A low ichnofabric index indicates an absence or rarity of burrowing infauna, which in turn implies a stressed environment immediately after the PTME (Chen et al., 2011). Accordingly, the great loss of burrowing infauna and associated environmental stress occur at the horizon between Beds 27 and 28. These facts imply that ecologic collapse of marine ecosystems
Contrasting to the two-stage extinction pattern (Song et al., 2013a), Shen et al. (2011b) and Wang et al. (2014) argued that the severest biodiversity declines fell in a short period equivalent to Beds 25-28 of Meishan, and there was one prolonged extinction rather than two discrete episodes. Indeed, Beds 25-28 represent a very short duration of about 60 ky (Burgess et al., 2014). However, all lines of evidence, including fossil fragment contents, and ichnofabric and community structural changes, show that the P-Tr ecologic crisis clearly comprises two pronounced steps, at the bases of Beds 25 and 28 (Figs. 14, 21, 26). Nevertheless, whether the mass extinction occurred as one prolonged event or two pulses, all studies agree that Beds 25-28 of Meishan and their equivalents represent a critical period when the greatest biotic turnover of life on Earth took place in Meishan. During this critical turnover period, the ecologic crisis clearly lagged behind the diversity decline. As a result, the Meishan fossil record shows that the mass extinction started with a dramatic depletion of biodiversity and ended with a severe ecologic crisis.

7.3. Dramatic increase in seawater surface temperature and its consequence
Recent oxygen isotopic studies of conodont bioapatites reveal that sea surface temperature rose ~9°C from Bed 24e to Bed 27a in Meishan (Joachimski et al., 2012; Sun et al., 2012; Fig. 26). However, the precise relationship between temperature increase and biotic extinction remains unclear owing to the lack of oxygen isotopic values from Bed 25, the base of which coincides with the PTME (Shen et al., 2011b) or the first phase of the PTME (Song et al., 2013a). The same is also true for the relationship between the temperature rise and the dramatic negative carbonate carbon isotopic excursion (Fig. 26). The solution is to undertake more detailed study of conodont oxygen isotopes of the PTB beds from less condensed sections than Meishan to evaluate whether temperature change leads or lags the extinction (Burgess et al., 2014).

Hinojosa et al. (2012) found a negative shift in $\delta^{44/40}$Ca of conodont bioapatite in the Great Bank of Guizhou, South China during the same interval as temperature increase in Meishan. This $\delta^{44/40}$Ca excursion is also coupled with a major shift in $\delta^{13}$C$_{carb}$ composition from an average of approximately +3.5‰ in the latest Permian to approximately −1‰ in the earliest Triassic (Payne et al., 2004). The anomaly of $\delta^{44/40}$Ca therefore was interpreted as a consequence, in part, of acidification of the ocean. Thus,
oceanic acidification in platform areas of the Great Bank of Guizhou may have resulted from elevated seawater temperature (Burgess et al., 2014). However, this ocean acidification seems not to have spread to the Meishan area because rather abundant and diverse complex traces of both *Glossifungites* and *Cruziana* ichnofacies occur in Bed 27 (Figs. 19-20), although calcareous skeletons decreased significantly in Beds 25-28 (Fig. 14).

Previously, the irregular surface occurring in the middle of Bed 27 at Meishan was interpreted as a submarine dissolution surface, explained by a regional ocean acidification in South China (Payne et al., 2007, but see Wignall et al., 2009). This pronounced irregular surface, however, was re-interpreted as a distinct firmground surface, on which abundant complex traces of *Glossifungites* ichnofacies occur (see Section 3.5). Firmgrounds of *Glossifungites* ichnofacies are usually characteristic of initial transgression, and such horizons are usually employed to define sequence boundaries (Buatois and Mángano, 2011). Thus, no sign of acidification is recorded in Bed 27 at Meishan.

Another potential consequence of elevated temperature is intensified chemical weathering (Sheldon, 2006) and consequent increased physical erosion of soils on land.
(Sephton et al., 2005; Xie et al., 2007), or a combination of these processes. These processes are also indicated by the increased chemical index of alteration (CIA) profile immediately after the first phase of the PTME (Bed 25; Fig. 26). It should be noted that the CIA value was calculated as Al$_2$O$_3$/(Al$_2$O$_3$+K$_2$O+Na$_2$O) (Zhao et al., 2013a), a modification of the original CIA equation (Nesbitt and Young, 1982). Increased chemical weathering during the PTME and its aftermath is also mirrored by the Eu/Eu* profile of conodont bioapatites (Zhao et al., 2013a). The latter rare-earth elemental (REE) proxy is a useful tracer of sediment provenance because fractionation between Eu$^{+2}$ and Eu$^{+3}$ does not occur under Earth-surface conditions (Elderfield and Greaves, 1982). Eu$^{+2}$ tends to become segregated into feldspar during magmatic differentiation, resulting in Eu/Eu* values $>1.0$ in the crystal fraction and $<1.0$ in the residual fluid (Zhao et al., 2013a). Eu/Eu* ratios $>1.0$ are characteristic of magmas from lower crustal or mantle sources where substantial feldspar crystallization has taken place (Condie, 2001). Although the REE “fingerprint” of the ash-rich clastics is reflected by both CIA and Eu/Eu* profiles that match one another throughout P-Tr transition in Meishan (Fig. 26), these ash beds near the PTB likely sourced from regional convergent continent marginal volcanisms (Gao et al., 2013, 2014), the shift toward Eu/Eu* values of 1.0–1.5 in Bed 24e,
immediately preceding the PTME, may be evidence of a transient influx of volcanic material with a lower crustal or mantle source. Zhao et al. (2013a) argued that these mantle-sourced ash fingerprints indicated by Eu/Eu* values could be the product of the Siberian trap eruption (Reichow et al., 2009). Thus, this volcanic eruption could have caused the severe biocrisis and rapid increase in sea-surface temperature occurring ~20-kyr and 80 kyr later, respectively, following the estimate of maximum and minimum sedimentation rates given by Burgess et al. (2014).

In addition, Burgess et al. (2014) also estimated the rate of temperature rise in Beds 25-28 as an ~1 °C increase per 6,000 y, which is comparable with the rate and magnitude of the increase at the Paleocene–Eocene Thermal Maximum (Zeebe et al., 2009) and Pleistocene/Holocene postglacial warming (~2 °C/5 ka) (Lea et al., 2000). However, this estimation of the rate of temperature rise needs to be cautious because no temperature data is available from Bed 25 and the temperature rise spans Beds 24e-27 (Sun et al., 2012). Accordingly, although the killing mechanism of the ~40 °C increase of seawater surface temperature on organisms remains unclear, this rapid temperature increase coincides with biotic turnover and ecologic collapse during the PTME at Meishan. Nevertheless, the elevated temperature seems to have had little effect
on ichnofaunas and ichnofabrics, as indicated by abundant ichnofaunas living in the firmground of the Glossifungites ichnofacies (Bed 27), but instead resulted in dramatic losses of fossil skeletons in sediments (Fig. 14).

In addition, Sun et al. (2012) reported the acme of high seawater temperatures occurred in the late Griesbachian, corresponding to the upper *I. isarcica* Zone and lower *C. planata* Zone (Sun et al., 2012, fig. 2), which range from Beds 48-54. These two zones are amended herein (Fig. 2) and are equivalent to the upper part of *C. planata* Zone in the revised conodont zation (Fig. 2). This acme of high temperature postdates the second negative shift excursion of carbon isotops of Xie et al. (2007) and includes the second negative shifting excursion of carbon isotopes of Burgess et al. (2014). Surprisingly, this interval saw an increase in biodiversity (Chen et al., 2002, 2007), ichnological amoraliation and bioturbation (Fig. 3). Accordingly, the acme of high temperature has little effect on faunas.

7.4. Anoxic events and biotic response

7.4.1. Anoxic events
At Meishan, Wignall and Hallam (1993) recognized an anoxic event associated with the PTME, but considered that the greatest acme of anoxia, coupled with a maximum flooding event, occurs in the lower Yinkeng Formation. Wignall and Twitchett (2002) believed that the oxygen-deficient waters spread into exceedingly shallow settings near the PTB in the Tethys regions (i.e., South China). More recently, multiple geochemical signals indicate the existence of anoxic to euxinic conditions before, during and after the PTME at Meishan.

An exceptional increase in sea surface temperature is also believed to be synchronous with the flooding of shelf areas with anoxic and euxinic waters during the P-Tr transition (Sun et al., 2012). Both extremely high values of total organic content (TOC) (Yin et al., 2012) and reduced sizes of pyrite frambooids (Fig. 26) indicate euxinic to anoxic condition in Beds 25-26, coinciding with the PTME. However, pyrite frambooids from Bed 27 are generally larger than 5 µm in diameter with abundant crystals and thus indicate the upper part of dysoxic conditions (Fig. 25). Moreover, high bioturbation levels are also observed in upper part of Bed 26 and multiple layers of Bed 27. Thus, a euxinic to anoxic condition was probably limited only to Beds 25-26a, which is less than 20 ka based on duration estimate of conodont zones from these beds (Table 2).
a much shorter period than previously thought. The anoxic condition of the water column is also reflected by the abrupt increase of Ce/Ce* values of conodont bioapatite from ~0.7–0.8 in Beds 23-24 to 0.9–1.1 in Beds 25-27b (Zhao et al., 2013a; Fig. 26). Values of 0.7–1.0 are sustained through Beds 27c to 30, above which Ce/Ce* decreases to 0.5–0.7. It should be noted that Ce/Ce* ratios derived from Bed 27a-d are not totally in accordance with size analysis of pyrite framboids, which shows that Bed 27a-d may represent redox conditions ranging from anoxia to upper level of dysoxia (Fig. 25). Although Ce/Ce* values from Meishan may have been biased by the fingerprint of clay input, Ce/Ce* values of 0.9–1.1 indicate an anoxic depositional system (Zhao et al., 2013a; Shen et al., 2012). This inference is consistent with the results of earlier studies documenting anoxia around the PTME in South China PTB sections (Grice et al., 2005; Algeo et al., 2007; Shen et al., 2007; Cao et al., 2009; Bond and Wignall, 2010; Luo et al., 2010) and globally (Algeo et al., 2010, 2011b; Brennecka et al., 2011).

Euxinic condition may have occurred prior to the PTME in Meishan, i.e., Beds 22-24, demonstrated by the anomaly of sulfur isotopes (Shen et al., 2011a) and various biomarker signals in Beds 22-24 (Grice et al., 2005; Cao et al., 2009; Luo et al., 2010, 2011). Algeo et al. (2011a) also interpreted the anoxic and euxinic conditions as a result...
of an expansion of the oxygen minimum zone (OMZ) in the water column over the P-Tr transition. These authors considered that the OMZ may have expanded prior to the PTME in Meishan.

A post-extinction reduced condition is also indicated by a pronounced negative excursion of carbon isotopes in Beds 34-36 (Xie et al., 2007; Luo et al., 2010; Fig. 26), coupled with an increase in TOC and terrestrial input indicated by various biomarker signals (Yin et al., 2012), and elevated contents of CO$_2$ (Fraiser and Bottjer, 2007). The CIA profile slightly increases in Beds 34-36, indicating elevated chemical weathering on land, which is consistent with the increased TOC and terrestrial input (Yin et al., 2012).

However, in addition, conodont bioapatite from Beds 33–39 generally yields lower Ce/Ce* ratios (0.4–0.7) that may indicate an oxic to suboxic depositional environment. Conodont bioapatite Ce, however, was probably derived mainly from detrital clay minerals and taken up during diagenesis, as indicated by other REE proxies (Zhao et al., 2013). If so, the observed Ce/Ce* ratios only reflect the REE composition of the source clays (Zhao et al., 2013a).

Alternatively, size variations of pyrite framboids indicate that Beds 27-29 record a dramatic redox change from upper dysoxic to euxinic conditions (Fig. 25).
anoxic condition prevailed throughout Bed 29 to Bed 42 (Fig. 25). The combination of mean size of framboids and presence of both larger framboids and crystal pyrites indicates Bed 43 may be deposited in a lower to upper dysoxic condition. If a redox interpretation is warranted, then this pattern suggests that the anoxic episode following the PTME in Meishan had lasted a relatively short duration, probably no more than ~50 kyr. Moreover, mean sizes and morphologies of framboids from Beds 44-58 also generally reflect an anoxic to euxinic condition, which, however, is not supported by various ichnological proxies.

7.4.2. Biotic response

The pre-extinction anoxic to euxinic conditions are generally supported by the presence of abundant small pyrite framboids, 3-5 µm in diameter, in Beds 23-24 (Figs. 23-24). However, biodiversity of metazoans remains very stable, with 64-78 species in 34-44 genera in each layer through Beds 24a to 24e (Fig. 26). Bed 24 contains 82 species in 47 genera, and there are similar numbers in Bed 23 (Jin et al., 2000). Thus, no major losses in species and generic richness are recognizable in Beds 23-24. Fossil fragment
contents are almost the same in each layer through Beds 22-24, except for the top 1-2 cm of Bed 24e, in which there is a pronounced loss in fossil components across the boundary between Beds 24e-5 and 24e-6 (Figs. 6, 14). Fossil fragment contents fell by >16% in thin section from Beds 24e-5 to 24e-6. The FFA of Bed 24e-5 comprises 10 major fossil groups orders that are commonly present in all Permian limestones, but five orders clades, ostracods, bryozoans, calcareous sponges, gastropods, and macroalgae, disappeared, losing 50%, across this boundary (Figs. 6, 14). The FFA of Bed 24e-6 is dominated by sponge spicules (35%) and thus has a high dominance and low diversity and evenness, in contrast to the low dominance, high diversity/evenness FFA in Bed 24e-5 (Fig. 6). Furthermore, the last occurrence of Permian fusulinids was also bracketed to the base of Bed 24e-6 (Kaiho et al., 2006b).

Ichnodiversity also declined significantly across the boundary between Beds 24e-5 and 24e-6 (Fig. 21A). These relatively complex or vertical burrows such as _Balanoglossites_ and _Thalassinoides_, which usually occur in oxygenated settings, disappeared at the base of Bed 24e-6. Instead, only simple, horizontal burrows of _Planolites_ occur in Bed 24e-6. Ichnofabrics, however, do not exhibit a major change across the same boundary (Fig. 3), with abundant _Planolites_ burrows being densely
packed on the surface of Bed 24e-6. However, most geochemical studies do not have such a high sampling intensity, and thus neglected this boundary.

Both metazoan biodiversity and fossil fragment contents experienced dramatic declines in Beds 25-26a. Other ecologic measures, such as community structures, ichnodiversity, burrow size, tiering level, and ichnofabric variation, also indicate an ecologic crisis in Beds 25-26a, coinciding with the anoxia indicated by both pyrite framboid sizes and various geochemical signals (Fig. 26). However, the metazoan fauna from Bed 27 is rather abundant and diverse, including 66 species in 34 genera (Song et al., 2013a). Both community structural indices and fossil fragment contents indicate that metazoans had recovered well in Bed 27. The presence of abundant complex burrows in Bed 27 indicates that the infaunal was little affected by the anoxic event and proliferated proliferation in the firmground of Glossifungites ichnofacies (Fig. 20). The occasional occurrence of pyrite framboids in Bed 27 may indicate a very short period of anoxic condition, but Bed 27, as a whole, represents a dysoxic to oxic condition in which benthos and infaunas proliferated.

By contrast, all data, including the low ichnodiversity (only Planolites), small burrow size, low trace complexity, low ichnofabric from Beds 29-51 indices and low
tiering level as well as low-diversity metazoans (Chen et al., 2007, 2010a), support the view that anoxic conditions may have prevailed throughout the early Griesbachian in Meishan (Wignall and Hallam, 1993; Xie et al., 2007; Yin et al., 2012). Of these, Beds 29-34 are barren of trace fossils and bioturbation. This is supported by trace fossil size, which is also regarded as a proxy for paleoenvironmental conditions (Twitchett, 1999; Pruss and Bottjer, 2004). In general, small-sized traces are usually found in poorly oxygenated sediments (Savrda and Bottjer, 1987) or brackish environments (Pemberton et al., 1982; Buatois et al., 2005) or habitats with low nutrient supply (Jumars and Wheatcroft, 1989). Thus small traces are characteristic of stressed environments (Twitchett, 1999; Pruss and Bottjer, 2004). The dramatic size reduction of trace fossils after the PTME indicates environmental stresses associated with the PTME, and the small sizes of Early Triassic traces suggest prolonged environmental stress following the event (Bottjer et al., 2008).

7.5. Testing extinction mechanisms

Multiple scenarios have been proposed to interpret the killing mechanisms of the PTME, including widespread anoxia, hypercapnia, massive volcanic eruption, global
warming, ocean acidification, and increased sediment flux (Erwin, 2006; Knoll et al., 2007; Clapham and Payne, 2011; Algeo and Twitchett, 2010; Algeo et al., 2011a; Joachimski et al., 2012; Sun et al., 2012; Burgess et al., 2014; Song et al., 2014). However, the true causes of this biocrisis still remain unclear due to the incomplete record of evidence supporting any of these alternatives.

Recently, Song et al. (2013a) suggested that different extinction mechanisms may have driven each of these two pulses given their differences in biodiversity and ecologic losses. These authors considered that anoxia may be related to the first-pulse losses of biota, but played a crucial role in the second-pulse biocrisis (Song et al., 2013a).

Elevated sea-surface temperature not only resulted in the spread of anoxia but also killed directly shallow-water taxa, while the anoxia killed the deep-water organisms (Song et al., 2014). However, extinction and survival selectivity of various fossil groups is more complicated than previously thought (i.e., Song et al., 2013a, 2014). This is because various elements of the same clade may have different lifestyles. For instance, the P-Tr brachiopods have six types of lifestyles based on attachment modes on the substratum: burrowing, body cementation, pedicle attaching on substratum, body spines anchoring on substratum, pedicle attaching on objects, and clasping spines on other shells/or objects.
These brachiopods having the last two types of attachment modes behaviour like nektons. Moreover, some shallow-water elements were also able to survive in deep niches during the latest Permian (Chen et al., 2006a). It is also true for the P-Tr bivalves that embrace several lifestyles (Huang et al., 2014). Accordingly, our high resolution comprehensive analyses of biodiversity, community structural, fossil fragment, ichnological, and redox condition changes associated with these two discrete events allow an evaluation of the proposed kill mechanisms for these two ecologic crises.

Most of the Permian brachiopods became extinct in the first extinction. The survivors are dominated by chonetids or chonetid-like productids or small, thin-shelled spiriferids/rhynchonellids that usually have attachment modes of clasping spines on other shells/or objects or pedicle-attaching on other shells or objects (Chen et al., 2005a, 2011b). These survivors attached their bodies on some float objects (i.e., other shells and algae) suspending above the seafloor (Chen et al., 2005a, 2011b), and thus provided brachiopods higher adaptability surviving the deleterious environments, i.e., increased acidity of precipitation (Wignall, 2007), large-scale marine acidification (Clapham and Payne, 2011) and widespread anoxia (Wignall and Twitchett, 2002; Payne and Clapham, 2012) during the first biocrisis. Inarticulated brachiopods i.e., lingulids also survived this
event, although having a burrowing lifestyle. This is because linguilds are able to survive in poorly oxygenated waters due to having respiratory pigment acting the function to transport oxygen or to store oxygen within the body tissues under anoxic conditions or during cessation of respiration (Williams et al., 1997).

Similarly, Huang et al. (2014) argued that the anoxia or acidification may have impacted seriously on bivalve’s extinction and survival selectivity during the first extinction based on ecologic analysis of the P-Tr bivalves. As a result, both brachiopod’s and bivalve’s evidence indicates that anoxia impacted clearly by in the first-pulse biocrisis (Chen et al., 2011b; Huang et al., 2014). The acidification associated with this extinction cannot be excluded (Clapham and Payne, 2011; Hinojosa et al., 2012). The anoxia or acidification, however, lasted a very short duration, ~30 ka, as discussed above.

Furthermore, a rapid increase of about ~9°C of sea-surface temperature (within a period of ~30 ka) across Beds 24e-27a (Sun et al., 2012) must have facilitated respiratory frequency and accelerated oxygen consumption of most brachiopods and become lethal to brachiopods, and thus causes morality, regardless their shallower or deeper habitats (Chen et al., 2014b in this volume). The rapidly elevated seawater temperature also coincides with the first dramatic losses of body fossil biodiversity and fossil fragments as
well as moderate losses of ichnodiversity and community diversity, and a moderate decrease in bioturbation, tiering levels of infaunas and burrow sizes. However, marine ecosystems seem not to have collapsed completely during the first-pulse crisis (Chen and Benton, 2012), some organisms survived the short environmental and climatic devastation. Thus, both biodiversity and ichnodiversity, and all of ichnological and community structural measures rebounded rapidly in Bed 27a-d (Fig. 26).

Like the first extinction, the second-pulse biocrisis is also associated with a clay bed (Bed 28), in which pyrite frambooids indicate a lower dysoxic to anoxic condition (Fig. 25). However, the redox condition became euxinic soon after and is indicated by frambooids obtained from the base of Bed 29. Thus, a dramatic change from upper dysoxic to oxic condition in Bed 27 to euxinic condition in basal Bed 29 indicates an anoxia/euxinia coincided with the 2nd biocrisis, which is followed by a long period of euxinic to anoxic conditions, which was probably driven by a relatively long (>62 ka) acme of high temperature (up to 35-37°C) in earliest Griesbachian. Accordingly, both epifaunal and infaunal ecosystems collapsed after suffering such a long period of lethally hot seawater temperature and widespread anoxia in earliest Triassic oceans (Fig. 26).
This is reinforced by the replacement of free-lying brachiopod-dominated communities in Bed 27 with nekton-dominated communities in Beds 31-37 (Chen et al., 2010a) and Beds 28-34 barren of bioturbation and ichnofossils (Figs. 3, 26). As stated above, these surviving brachiopods yielded from Beds 26-27 should have enhanced resistant ability to anoxic or acidified water mass near seafloor because they survived from the first-pulse crisis. The morality of the free-lying brachiopods in the second-pulse crisis is probably due to the loss of other shells or float algae, on which the brachiopods attach using either pedicle or clasping spines.

 Accordingly, the killing mechanisms for these two extinction events near the PTB seem not to be fundamentally different from one another, although no sign of acidification has been reported in the second phase of the PTME. However, a short anoxia or acidification probably caused by a rapid increase in seawater temperature may have played an important role in the first-pulse biocrisis, while the long-lasting and widespread anoxia induced by a long period of high temperature condition may have killed most organisms in the second-pulse crisis.
Post-extinction benthic communities did not appear to return to normal until the early Middle Triassic (Chen and Benton, 2012). The deleterious environment that prevailed in early Triassic oceans may be largely responsible for this long-delayed recovery (Bottjer et al., 2008). In particular, Early Triassic carbon isotopic records show several negative excursions that indicate sharp global warming (Payne et al., 2004), and these coincide with diversity drops. Furthermore, intrinsic relationships between organisms and ecosystem structures may also have slowed down biotic recovery following the PTME (Chen and Benton, 2012). Recent studies show that the biotic recovery process may be mirrored by stepwise establishment of trophic structures of marine ecosystems throughout Olenekian-Anisian interval (Chen and Benton, 2012).

However, biotic recovery may occur earlier in oxygenated environments (Twitchett et al., 2004; Beatty et al., 2008; Zonneveld et al., 2010). As a result, Early Triassic marine environments were not always deleterious globally. Chen et al. (2007) also detected that marine environments had greatly ameliorated during the late Griesbachian in Meishan. The sea-floor recuperation, including shallowing water depth, increasing oxygenation and oceanic productivity, coincides with an increase in benthic biodiversity, signalling
that ecologic and environmental restoration might have initiated in the late Griesbachian

(Chen et al., 2002, 2007).

The example of elevated recovery of the benthic community in late

Griesbachian at Meishan is also strengthened by community structural changes and

ichnofabric variation through the PTB to late Griesbachian. The Exp (H) value increases

by 262.6% from the C to M–L communities, and also increases 70%, coupled with a

decrease of 15.2% in D’ values, from the C–O to M–L communities, suggesting an

improvement in shelly community structures in the upper Yinkeng Formation at Meishan

(Chen et al., 2002, 2007).

Trace fossils and ichnofabrics documented here also show that the late

Griesbachian trace-fossil assemblage is marked by significant increases in ichnodiversity,

burrow size, trace complexity, tiering level, and bioturbation level, in comparison with

early Griesbachian ichnocoassemblages, although they did not achieve Changhsingian

levels (Fig. 21). Thus, the Meishan trace fossils, together with increasing diversity in the

shelly community, sedimentary structures (HCS), up-shallowing sedimentary cycle and

geochemical proxies (Chen et al., 2007), suggest that biotic recovery recorded in the

upper Yinkeng Formation may be categorized as recovery stage 2 (sensu Twitchett, 2006),
and also mark the return of parts of the meso-consumer functioning group within the ecosystem trophic structure, which usually occurs in the Spathian around the world (Chen and Benton, 2012).

8. Conclusions

Updated conodont biostratigraphy allows the establishment of eight conodont zones from the latest Changhsingian to early Griesbachian at Meishan, the C. yini, C. meishanensis, H. changhsingensis, C. taylorae, H. parvus, I. staeschei, I. isarcica, and C. planate zones. Microstratigraphic analysis shows that a major turnover in fossil fragment contents and ichnodiversity occurs across the boundary between Beds 24e-5 and 24e-6, suggesting the actual mass extinction horizon in thin section. Bed 27 contains a firmground of Glossifungites ichnofacies rather than the previously proposed submarine solution surface or hardground surface. Fossil fragment contents show a dramatic decline in both fossil component percentage and assemblage diversity in Beds 25-26a, coinciding with metazoan mass extinction. Fossil fragment content, ichnodiversity and all ichnofabric proxies (including burrow size, tiering level, and
bioturbation level) throughout the uppermost Changhsing to Yinkeng formations indicate that the P-Tr ecologic crisis comprises two discrete stages, coinciding with the first and second phases of the PTME, in support of a proposed two-stage extinction pattern of metazoans over the P-Tr transition. The PTME was of short duration, lasting about 60 kyr. A biodiversity crisis indicates the start of the extinction interval, but its end is marked by the ecologic collapse of ecosystems. Thus, the ecologic crisis lagged behind the biodiversity decline during the PTME. Pyrite framboid size variations suggest that the depositional redox condition was anoxic to euryxic in the latest Changhsingian, became euryxic in Beds 25-26a, turned to be dyoxic in Bed 27, then varied from euryxic to anoxic through most of the Griesbachian. Although metazoan biodiversity and fossil fragment contents show dramatic declines, coinciding with a $\sim$10$^9$ °C increase in seawater surface temperature, from Bed 24e to Bed 27 in Meishan, all ecologic proxies show much smaller effects from the elevated seawater temperature. Bed 27 contains abundant infauna and shows no signs of ocean acidification. Pre-extinction anoxic-euryxic conditions had little effect on both metazoans and infauna. The anoxic event associated with the PTME may have lasted for much less time than previously thought, and is limited to Beds 25-26a at Meishan. Fossil fragment contents, ichnofaunas, ichnofabrics and pyrite framboid size all

97
show that anoxic conditions did not exist in Bed 27. Early Griesbachian anoxia is possible, and may have caused the rarity of ichnofaunas and metazoans in the lower Yinkeng Formation. The ichnofauna is characterized by small, simple horizontal burrows of Planolites, while metazoan faunas are characterized by low diversity, high abundance, opportunistic-dominated communities. The killing mechanisms for these two extinction events near the PTB similar to one another. A rapid increase of ~9 °C in seawater temperature and its inducing short anoxia or acidification may have played an important role in the first-pulse biocrisis, while the long-time and widespread anoxia probably caused by long-time high temperature condition may have resulted in mortality of most organisms in the second-pulse crisis. Initial recovery of marine ecosystems coupled with environmental amelioration occurred in the late Griesbachian, marking the return of parts of the meso-consumer functioning group.

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Figure captions

Fig. 1. The GSSP for the Permian-Triassic boundary at Meishan, Changxing county, northwestern Zhejiang Province, east China. A, location of the Meishan section. B, close-up of the white volcanic ash bed (Bed 25) in Meishan. C, geopark of the GSSP Meishan showing GSSP position at the Meishan section D. D, the P-Tr boundary beds showing biostratigraphic boundary through the mid-Bed 27 and the mass extinction horizon at the base of Bed 25. E, outcrop of the P-Tr boundary beds and Yinkeng Formation along strike on the Meishan hill from the geopark section.

Fig. 2. Biostratigraphy of the P-Tr transition at the Meishan section with the updated conodont zones and correlations with ammonoid, bivalve, brachiopod and microfloral assemblages from Meishan as well as conodont zones from North Italy, Iran and
Germany, and India. Note that the updated conodont zonation is revised from those documented by Jiang et al. (2007) and Zhang et al. (2009) and our new observations.

White arrows indicate that conodont zones extend to horizons below Bed 22 of Meishan and its equivalents.

**Fig. 3.** P-Tr succession exposed in the GSSP Meishan showing lithology, facies types, depositional environments, stratigraphic distributions of trace fossils, and bioturbation levels. Ichnofabric indices (ii: Droser and Bottjer, 1986) are assessed as 1 to 6, indicating bioturbation from lowest to highest levels. Bedding plane bioturbation index (bpbi) is evaluated based on bedding plane coverage of burrows (Miller and Smail, 1997). Facies symbols: om = offshore mudstone facies, bs = basinal black shale facies, ow = offshore wackestone facies, os = offshore siltstone facies, ew = epeiric sea wackestone facies, HCS = hummocky cross stratification, hb = horizontal bedding. Depositional environment (DE): ns = nearshore, fw = fair-weather wave base, sw = subtidal zone to fair-weather wave base, swb = storm wavebase.

**Fig. 4.** Lithology and fossils from the exposure of the P-Tr transition in Meishan. A-B, D, field photograph, polished surface and microphotograph showing hummocky cross-stratified (HCS) muddy limestone (Bed 54), upper Yinkeng Formation; pen is 15
cm long; scale bars are 2 cm. C, pale mudstone and calcareous mudstone (Bed 41) showing horizontal stratification, lower Yinkeng Formation; pen is 15 cm long. E, F, I, ammonoid fossils across the P-Tr boundary with large ammonoid shell (E) in Bed 24e of the Changhsing Formation contrasting to small shells (F, I) recorded in the middle and upper Yinkeng Formation; coins are 1.5 cm in diameter; scale bar is 1 cm. G, dark thin-bedded limestone interbedded with bioclastic limestone bands, Bed 24e; pen is 10 cm long. H, irregular contact between Beds 24d and 24e; cross-bedding is pronounced in the uppermost Bed 24d; scale bar is 1 cm. J, vertical burrow of Balanoglossites in the upper part of Bed 24d; scale bar is 1.5 cm.

Fig. 5. Microfacies and fossil fragment assemblages from Beds 23-24, upper Changhsing Formation. A, microphotograph of claystone, Bed 25. B, microphotograph showing horizontal laminae (black arrow) of black shale, Bed 26. C, bioclastic packstone of Bed 23a showing brachiopod (b), crinoids (c), and ostracods (o) fragments. D, bioclastic bioclastic packstone of Bed 24c showing abundant foraminifer (f), brachiopod (b), crinoids (c), ostracods (o) and other fragments.

Fig. 6. Pie diagrams showing percentage of major components in all rocks sampled from Beds 22-60 in Meishan. Detailed fossil fragment contents (%) of each sample are
tabulated in Table 3. Component symbols: 1 = foraminifers, 2 = ostracods, 3 = crinoids, 4 = echinoids, 5 = brachiopods, 6 = bryozoans, 7 = sponge spicules, 8 = calcareous sponges, 9 = gastropods, 10 = radiolarians, 11 = macroalgae, 12 = micrites, 13 = cavities, 14 = other particles (fecal pellets, peloids, pyrites and undetermined particles).

Fig. 7. Microfacies across the boundary between Beds 24e-5 and 24e-6. A, transverse view of one sponge spicule. B-C, cross-section view of sponge spicules. D, microphotograph showing the laminated horizon separating bioclastic layer (Bed 24e-5) from the overlying sponge spicule-rich layer (Bed 24e-6). E, SEM image of one isolated specimen of a sponge spicule. B-C, scale bars are both 50µm; E, Scale bar is 40 µm.

Fig. 8. Microfacies and fossil fragment assemblages from Bed 26b, 8-10 cm above the base of Bed 25. A, microphotograph showing foraminifer (f), bryozoan (bry), echinoid (e), and brachiopod (bra) fragments. B, microphotograph showing ostracod (o), echinoid (e), and brachiopod (bra) fragments. C, microphotograph showing brachiopod (bra) and echinoid (e) fragments. D, microphotograph showing bryozoan (bry) and brachiopod (bra) fragments. E, microphotograph showing foraminifer (f) and echinoid (e) fragments. F, microphotograph showing brachiopod (bra) and...
foraminifer (f) fragments. G, microphotograph showing foraminifer (f) and echinoid (e) fragments. H, microphotograph showing bryozoan (bry) and foraminifer (f) fragments. I, microphotograph showing foraminifer (f) and echinoid (e) fragments. J, microphotograph showing foraminifer (f) fragments. K, microphotograph showing bryozoan (bry) and echinoid (e) fragments. L, microphotograph showing foraminifer (f) and echinoid (e) fragments. All scale bars are all 100 µm.

**Fig. 9.** Polished surface of Bed 27 and its microfacies features. A, polished surface showing the entire bed is subdivided into four parts (labelled a, b, c, d) by two sets of pronounced irregular surfaces, in which burrows (red arrows) are commonly present. B, microphotograph of the basal part of Bed 27a, 11-13 cm above the base of Bed 25, showing foraminifer (f) and brachiopod (bra) fragments. C, microphotograph of the upper part of Bed 27a, 13-15 cm above the base of Bed 25, showing foraminifers (f) and other fossil fragments. D, microphotograph of the lower part of Bed 27b, 15-17 cm above the base of Bed 25, showing claystone-dominated texture. E, microphotograph of the upper part of Bed 27b, 18-20 cm above the base of Bed 25, showing echinoid (e) and other fossil fragments. F, microphotograph of the upper part of Bed 27c, 21-23 cm above the base of Bed 25, showing abundant foraminifer (f), echinoid (e) and brachiopod (bra) fragments.
fragments. G, microphotograph of Bed 27d, 23-28 cm above the base of Bed 25, showing abundant ostracods (o), foraminifers (f), echinoid (e), and other fragments. H, microphotograph of the upper part of Bed 26b, 8-10 cm above the base of Bed 25, showing abundant foraminifer (f) and other fossil fragments.

**Fig. 10.** Bioclastic packstone to wackestone showing various fossil fragments from Bed 27a, 13-15 cm above the base of Bed 25. A, foraminifer (f). B, brachiopod (bra) and other fragments. C, foraminifer (f), echinoid (e) and other undetermined fragments. D, foraminifer (f). E, foraminifer (f). F, foraminifer (f), brachiopod (bra) and other undetermined fragments. G, I-K, foraminifer tests. H, echinoid (e) fragment. Scale bars are all 50 µm.

**Fig. 11.** Bioclastic packstone and various fossil fragments from Bed 27c, 21-23 cm above the base of Bed 25. A, foraminifer (f) and brachiopod (bra) fragments. B, foraminifer *Frodina permica* test. C, echinoid (e) and brachiopod (bra) fragments; D, bryozoan (bry) , foraminifer (f) and other undetermined fragments. E, foraminifer (f) *Nodosinelloides netschajewi* test and echinoid (e) fragments. F, foraminifer test of *Hemigordius* sp. G, brachiopod (bra) fragment. H, bryozoan (bry) fragment. I, foraminifer (f) *Hemigordius* sp. test. J, foraminiferal (f) fragment. K, echinoid (e) and foraminifer (f) fragments. L-M,
echinoid fragments. Scale bars are all 50 µm.

**Fig. 12.** Bioclastic packstone to wackestone showing various fossil fragments from Bed 2371d, 23-28 cm above the base of Bed 25. A, foraminifer test of *Nodosinelloides* sp. B, brachiopod (b), foraminifer (f), and echinoid (e) fragments. C-D, foraminifer tests of *Nodosinelloides* sp. and *Nodosaria* sp., respectively. E, brachiopod (bra), foraminifer (f), and other fragments. F, echinoid fragment. G, sponge spicule. H, foraminiferal fragment of *Tuberitina maljavkini*. I, echinoid fragment. J, brachiopod (bra) and sponge spicule (ss); K, foraminifer test of *Nodosinelloides* sp. L, foraminifer *Nodosinelloides* aequiampla and brachiopod (bra) fragments. M, foraminifer (f) fragment. N, ostracod (o), foraminifer (f), and echinoid (e) fragments. O, brachiopod (bra) and echinoid (e) fragments; P, brachiopod (bra) and echinod (e) fragments. B, scale bar is 100 µm; F-G, scale bars are 20µm; other scale bars are all 50 µm.

**Fig. 13.** Microfacies and fossil fragment assemblage from strata of Bed 29 and above. A, bioclastic wackestone with ostracod (o) and brachiopod (bra) fragments, Bed 29. B, bioclastic wackestone with brachiopod (bra) and ostracod (o) fragments, Bed 29. C, echinoid fragment, Bed 53. D, ostracods test, Bed 52. F, ostracod test, Bed 53. I, K, M, ostracods tests, Bed 54. N, ostracods test, Bed 55. P-R, ostracod tests, Beds 56, 57 and 58,
respectively. E, foraminifer fragment, Bed 29. J, L, foraminifer fragments, Beds 52 and
53, respectively. G, foraminifer *Nodosaria* sp., Bed 56. H, foraminifer *Nodosaria rostrata* Trifonova, Bed 56. O, micrite containing pyrite particles (black) and tiny tubes (t), Bed 44. Scale bars are all 50 µm.

**Fig. 14.** Fossil fragment distributions over the P-Tr transition (Beds 22-60) in Meishan. Vertical axis represents percentage of various fossil fragments in all rock.

**Fig. 15.** Shell beds from the Yinkeng Formation in Meishan. A, *Claraia* concentrations (white arrows) from Bed 40; scale bar is 1 cm; B, shell concretions of *Claraia griesbachi* (c) and *Ophiceras* sp. (o) of the O-P community from Bed 32; coin is 1.5 cm in diameter; C, shell concretions of *Claraia griesbachi* from Bed 35; coin is 1.5 cm in diameter; D, shell concretions of *Claraia wangi* of the C community from Bed 40; coin is 1.5 cm in diameter; E, shell concretions of *Claraia griesbachi* from Bed 36; coin is 1.5 cm in diameter; F, shell concretions of *Meishanorhynchia* (m), *Lytophiceras* (ly) and ophiceratid (o) of the M-L community from Bed 55; Scale bar is 4 mm.

**Fig. 16.** Trace fossils from the Changhsing Formation of the Meishan section. A, *Thalassinoides* sp. 1 on base of Bed 8; coin is 1.5 cm; B, *Paleophycus* isp. from Bed 9; scale bar is 1 cm; C, *Balanoglossites triadicus* from Bed 24d; coin is 1.5 cm in diameter;
**Fig. 17.** Trace fossils from the Changhsing Formation (Beds 23-24) continued. A, E, horizontal burrows of *Planolites* isp. 1 from upper surface of Bed 24e-6; USB is 2 cm long; B-C, problematica from upper surface of Bed 23; Coins are 1.5 cm in diameter; D, *Taenidium* isp. from upper surface of Bed 24e; Coin is 1.5 cm in diameter; F, *Dendrorhaphe* isp. from upper surface of Bed 23; Coin is 1.5 cm in diameter.

**Fig. 18.** Trace fossils from the Yinkeng Formation. A-B, F, *Planolites* from upper surfaces of Bed 36, 41, and 56, respectively; coins are 1.5 cm, 2 cm and 1.5 cm in diameter, respectively; C, *Chondrites* isp. on upper surface of Bed 52; Coin is 1.5 cm in diameter; D-E, *Thalassinoides* isp. 3 from upper surfaces of Bed 53 and 56, respectively; coins are 1.5 in diameter; G-H, sketch reconstruction and trace of *Treptichnus* isp. on upper surface of Bed 57; coin is 1.5 cm in diameter.

**Fig. 19.** Polished slabs and sketches showing the successions of trace-fossil assemblages in Bed 27. A–C, vertical cross section of Bed 27 showing the ichnofabric change from a firmground ichnocoenoses of *Glossifungites* ichnofacies in the lower to a softground ichnocoenose in the upper. Note these three sample blocks (A-C) were cut from one
complete sample of Bed 27. D–F, portraits of blocks A–C, respectively. Ar. = *Arenicolites*

Fig. 20. Polished surface and its portrait of Bed 27 showing burrow systems in firmground of the *Glossifungites* ichnofacies and vertical colonization by ichnofaunas on different substrates. A, polished slab across the entire Bed 27 (from base to top). B, sketch reconstruction showing ichnofabrics manifested in Fig. 25A. C, cartoon reconstruction showing the generalized colonization zonation of ichnofaunas. For abbreviations of ichnotaxon names see caption of Fig. 19.

Fig. 21. Trace fossil evolution at Meishan. A, ichnodiversity change throughout the uppermost Changhsingian to Griesbachian in Meishan. B, burrow size variations (in mean diameter and maximum diameter) over the P-Tr transition. C, tiering level change through the P-Tr transition.

Fig. 22. Burrow sizes of selected ichnogenera through the P-Tr transition. A, burrow size variation of *Planolites* through the P-Tr transition. B, burrow size variation of *Thalassinoides* through the P-Tr transition. C, burrow sizes of both *Dendrorhaphe* and problematic trace from the upper Changhsing Formation. D, burrow sizes of
Balanoglossites, Taenidium, Chondrites, and Treptichnus from the P-Tr transition in Meishan.

**Fig. 23.** Pyrite framboids and crystals preserved on fossil skeletons and in sediments of Bed 27. A-C, pyrite crystals (white arrows) on brachiopod shells of *Paryphella*. D-E, pyrite crystals (white arrows) preserved in sediments and foraminiferal test; scale bars are 40 µm; F-G, pyrite crystals (white arrows) preserved in foraminiferal tests; scale bars are all 40 µm. H, L, SEM images showing pyrite framboids preserved on brachiopod shells of Bed 27; I-K, pyrite framboids preserved in sediments of Bed 27; M-N, EDS results showing mineral composition of framboids of Fig. 23L and Fig. 23J, respectively.

**Fig. 24.** Sizes of pyrite framboids from 17 horizons through the P-Tr transition in Meishan. MD = mean diameter, SD = standard derivation, N = Number of framboid grains.

**Fig. 25.** Redox conditions indicated by pyrite framboid sizes through the P-Tr transition at Meishan. Two SEM images show morphologies of pyrite framboids from Bed 24 (left) and Bed 39 (right). PTB = Permo-Triassic boundary; PTME = Permo-Triassic mass extinction.

**Fig. 26.** Composite figure showing exceptionally increased seawater surface temperature,
carbon isotopic excursion, Chemical index of alternation (CIA) and Eu/Eu* profiles,

through the P-Tr transition at Meishan. Total organic content (TOC) and Ce/Ce* profiles,

framboid size variation, specific and generic richness variations, and community

structural changes indicated by true diversity index (Exp (H)) and dominance (D) through

the P-Tr transition in Meishan. Note: seawater temperature data after Joachimski et al.

(2012) and Sun et al. (2012); CIA value is calculated using published data by Zhang et al.

(2005); Carbon isotopic excursion after Burgess et al. (2014); Eu/Eu* and Ce/Ce* values

after Zhao et al. (2013a). TOC profile after Yin et al. (2012). Framboid size data from this

study. Detailed bioturbation data see Fig. 3; II = Ichnofabric indices; BPBI = Bedding

plane bioturbation index. Datum source of burrow diameters sees Fig. 24. More details of

fossil fragment contents see Fig. 14. Species and genus richness data after Song et al.


Table captions

Table 1. Radiometric ages obtained from the P-Tr succession at the GSSP Meishan (in

Ma).
Table 2. Key conodont zones with their durations across the PTB in Meishan.

Table 3. Percentage of major components in all rocks sampled from Beds 22-60 in Meishan.

Table 4. X-ray diffraction (XRD) data of the PTB beds at Meishan (sourced from Liang, 2002).

Table 5. Structural indices of the latest Permian to earliest Triassic shelly communities from Meishan (Chen et al., 2010a).

Table 6. Major indices showing community structural changes over the P-Tr transition in Meishan

Table 7. Characteristics of major trace fossils from the uppermost Permian to lowest Triassic in Meishan
Figure 1

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## Conodont zonation

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<th>System Stage</th>
<th>North Italy</th>
<th>Iran and Germany</th>
<th>Spiti</th>
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*from the Huangzhishan section (Chen et al., 2009)
Figure 3
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Table 1. Radiometric ages obtained from the P-Tr succession in GSSP Meishan (in Ma)

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* 40Ar/39Ar age; others are 206Pb / 238U ages. Note: Beds 33 and 34 of Bowring et al. (1998), Shen et al. (2011) and Burgess et al. (2014) are equivalent to Beds 37 and 48 of this study, respectively.
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Table 3. Percentage of major components of rocks sampled from Beds 22-60 in Meishan

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*Elev. = Elevation, referring to accumulative distance (in cm) of sampling horizon to the base of Bed 25; minus value indicates sampling horizon below Bed 25.
Component codes: Foram. = foraminifers, Ostra. = ostracods, Crin. = crinoids, Echin. = echinoids, Brach. = brachiopods, Bryo. = bryozoans, Spon. = sponge spicules, Cal. sp. = calcareous sponges, Gastr. = gastropods, Radio. = radiolarians, Algae = macroalgae, Particles = other particles (fecal pellets, peloids, pyrites and undetermined particles).
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<tr>
<td>Bed 27c-d</td>
<td>MD 27cd</td>
<td>80</td>
<td>calcite 33%, ankerite 38%, silica 23%, illite 4%, kaolinite 2%</td>
<td>grey</td>
<td>marlstone</td>
</tr>
<tr>
<td>Bed 27a-b</td>
<td>MD 27ab</td>
<td>80</td>
<td>calcite 30%, ankerite 38%, silica 26%, illite 4%, kaolinite 2%</td>
<td>grey</td>
<td>marlstone</td>
</tr>
<tr>
<td>Bed 26</td>
<td>MD 26</td>
<td>60</td>
<td>gypsum 21%, calcite 8%, silica 36%, illite 18%, kaolinite 17%</td>
<td>black</td>
<td>shale</td>
</tr>
<tr>
<td>Beds 25-2, 25-3</td>
<td>MD 25</td>
<td>40</td>
<td>gypsum 34%, chloride 9%, montm 28%, illite 10%, kaolinite 19%</td>
<td>white</td>
<td>claystone</td>
</tr>
<tr>
<td>Bed 25-1</td>
<td>MD 25mr</td>
<td>0.3</td>
<td>gypsum 63%, goethite 25%, chloride 12%</td>
<td>red</td>
<td></td>
</tr>
<tr>
<td>Bed 24e-3</td>
<td>MD 25 my</td>
<td>0.3</td>
<td>gypsum 76%, chloride 6%, silica 18%</td>
<td>yellow</td>
<td></td>
</tr>
<tr>
<td>Bed 24e-3</td>
<td>MD 25mb</td>
<td>0.3</td>
<td>gypsum 35%, calcite 11%, chloride 4%, silica 50%</td>
<td>brown</td>
<td></td>
</tr>
<tr>
<td>Beds 24e-2, 24e-1</td>
<td>MD 24e</td>
<td>200</td>
<td>calcite 97%, illite 0.5%, kaolinite 0.5%, silica 2%</td>
<td>black</td>
<td>packstone</td>
</tr>
<tr>
<td>Bed 24d</td>
<td>MD 24d</td>
<td>230</td>
<td>calcite 98%, silica 2%</td>
<td>black</td>
<td>packstone</td>
</tr>
</tbody>
</table>

BT. = Bed thickness
Table 5. Structural indices of the latest Permian to earliest Triassic shelly communities from Meishan (Chen et al., 2010a).

<table>
<thead>
<tr>
<th>CC</th>
<th>Beds</th>
<th>Age</th>
<th>SR</th>
<th>N</th>
<th>H</th>
<th>Exp(H)</th>
<th>D</th>
<th>D'</th>
<th>Δ</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>R–P</td>
<td>24</td>
<td>Changhsingian</td>
<td>9</td>
<td>42</td>
<td>2.029</td>
<td>7.60648</td>
<td>0.1519</td>
<td>1.1791</td>
<td>0.15561</td>
<td>0.8453</td>
</tr>
<tr>
<td>T</td>
<td>26</td>
<td>Changhsingian</td>
<td>8</td>
<td>36</td>
<td>1.47</td>
<td>4.34942</td>
<td>0.3673</td>
<td>1.5805</td>
<td>0.37779</td>
<td>0.5439</td>
</tr>
<tr>
<td>P–T</td>
<td>27</td>
<td>Griesbachian</td>
<td>7</td>
<td>67</td>
<td>1.565</td>
<td>4.78267</td>
<td>0.2658</td>
<td>1.3620</td>
<td>0.26983</td>
<td>0.6836</td>
</tr>
<tr>
<td>C–O</td>
<td>32</td>
<td>Griesbachian</td>
<td>3</td>
<td>125</td>
<td>0.7559</td>
<td>2.12953</td>
<td>0.5233</td>
<td>2.0978</td>
<td>0.52752</td>
<td>0.7098</td>
</tr>
<tr>
<td>C</td>
<td>40</td>
<td>Griesbachian</td>
<td>1</td>
<td>129</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>?</td>
<td>1.00781</td>
<td>1</td>
</tr>
<tr>
<td>M–L</td>
<td>53-55</td>
<td>Griesbachian</td>
<td>8</td>
<td>143</td>
<td>1.288</td>
<td>3.62553</td>
<td>0.4379</td>
<td>1.7790</td>
<td>0.44098</td>
<td>0.4531</td>
</tr>
</tbody>
</table>

CC: Community codes; SR: species richness; N: individual number; H: Shannon entropy; Exp (H): standard diversity Shannon index; D: Dominance entropy; D’: standard diversity dominance index [1/(1-D)]; Δ: bias-corrected Simpson’s evenness [N×D/(N-1)]; E: evenness index (e^H/S).
Table 6. Major indices showing community structural changes over the P-Tr transition in Meishan

<table>
<thead>
<tr>
<th>Community boundary</th>
<th>Diversity [Exp (H)] changes</th>
<th>D’ changes</th>
</tr>
</thead>
<tbody>
<tr>
<td>R–P/T</td>
<td>-43.6%</td>
<td>+34.0%</td>
</tr>
<tr>
<td>T/P–T</td>
<td>+10%</td>
<td>-14.1%</td>
</tr>
<tr>
<td>P–T/C–O</td>
<td>-55.5%</td>
<td>+54%</td>
</tr>
<tr>
<td>C–O/C</td>
<td>-53%</td>
<td>?</td>
</tr>
<tr>
<td>C/M–L</td>
<td>+262.6%</td>
<td>?</td>
</tr>
<tr>
<td>C–O/M–L</td>
<td>+70%</td>
<td>-15.2%</td>
</tr>
</tbody>
</table>

Exp (H): standard diversity Shannon index; D’: standard diversity dominance index [1/(1-D)]; - indicates decrease, while + represents increase
Table 7. Characteristics of major trace fossils from the uppermost Permian to lowest Triassic in Meishan

<table>
<thead>
<tr>
<th>Ichnotaxa</th>
<th>Beds</th>
<th>Illustration</th>
<th>Description</th>
<th>Interpretation</th>
</tr>
</thead>
</table>
| Arenicolites isp.     | 27   | Figs. 24-25  | U-shaped burrows with unbranched, parallel limbs, 0.5 to 3.0 mm in diameter,  
                                | Domicinia with trace-makers of polychaete worms, amphipod and crustaceans (Knaust, 2004; Chen et al., 2011, 2012). |
| Balanoglossites triadicus | 24d  | Fig. 20C     | Vertical tubes, 14-18 mm wide and 10 cm long, perpendicular to bedding plane,  
                                | Produced by polychaete-like or enteropneust worms (Hantzsche, 1975). |
| Chondrites isp. 1     | 52   | Fig. 25C     | Plantlike dendritic system composed of fine, branching, cylindrical ramifying burrows, parallel to bedding plane in compact groups, and filled with yellow, coarsely grained sediments distinct from surrounding dark, fine-grained sediments.  
                                | Fodinichnia, feeding structures of sediment-eating animals (Bromley and Ekdale, 1984; Chen et al., 2011). |
| Chondrites isp. 2     | 27   | Fig. 24      | Small branching, cylindrical burrows forming plantlike dendritic systems, penetrating into sediments, and filled with light, coarsely grained sediments and distinguished from surrounding dark, fine-grained sediments.  
                                | Same as above |
| Dendrorhapha isp.     | 23   | Fig. 21G     | Tree-like trace system comprises a rather straight main axis, along which side branches are mostly perpendicular to the main axis and given off on both sides. Minor branches also give birth to further secondary branches in same way.  
                                | Occurring in deep-water or oxygen-deficient niches; feeding structures of sediment-eating animals (Seilacher, 1977). |
| Diplocraterion isp.   | 27   | Fig. 24      | U-shaped burrows with unbranched, parallel limbs, perpendicular to bedding plane, and having spreite; filled with light-grey, coarse sediments that are distinguished from surrounding dark, fine-grained sediments.  
                                | Produced by polychaete worms, amphipod and crustaceans (Knaust, 2004) |
| Gastrochaenolites isp.| 27   | Figs. 24-25  | Irregular, tear-shaped borings filled by light grey sediments in a dark-colored firmground lime mudstone substrate, penetrating down to the firmground layer at a maximum depth of 4 cm.  
                                | Produced by various organisms i.e., bivalves, annelids and sipunculans (Benner and Ekdale, 2004). |
| Lockeia isp.          | 8-9  | Figs. 20F, 21B | Small, almond-shaped oblong structure, 8-18 mm long and 7-12 mm wide, tapering to sharp points at both ends; preserved in either concave impressions on the tops or convex relief on the soles.  
                                | Resting impressions of bivalves (Bromley, 1996; Ekdale and Bromley, 2001). |
| Paleophycus isp.      | 8-9  | Fig. 20B     | Branching, slightly curved, cylindrical burrows, 2–7 mm in diameter, with wall typically lined and preserved as positive reliefs on top of bed.  
<pre><code>                            | Repichnion or domicinium, produced by predaceous or suspension-feeding animals (Gouramis et al., 2003). |
</code></pre>
<table>
<thead>
<tr>
<th>Trace</th>
<th>Figs.</th>
<th>Description</th>
<th>Reference/Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Psilonichnus</em> isp.</td>
<td>27</td>
<td>Vertical cylindrical burrows that are inclined with bedding in its distal end.</td>
<td>Trace of ocypodid ghost crabs (Buatois and Mángano, 2011).</td>
</tr>
<tr>
<td><em>Psilonichnus</em> isp.</td>
<td>24e</td>
<td>Simple, unbranched, unornamented, vermiform burrows that are straight and horizontally distributed on bedding tops, with some intersecting the sediment irregularly. Burrows, 3-9 mm in diameters, are occasionally densely packed.</td>
<td>Deposit-feeding activities of polychaetes or worm-like creatures, or feeding burrow of deposit-feeders (Bromley, 1996).</td>
</tr>
<tr>
<td><em>Planolites</em> isp. 1</td>
<td>24e</td>
<td>Simple, unbranched, vermiform burrows that are straight and horizontally distributed on bedding surfaces.</td>
<td>Same as above</td>
</tr>
<tr>
<td><em>Problematic trace</em></td>
<td>23</td>
<td>Simple, straight, unbranched burrows, 20-27 mm in diameter, with 2-5 mm thick tube wall. Single burrow originates at a small, rounded end and extends distally to form a horn-shaped burrow with an open distal end.</td>
<td>Sharing the same trace-makers with <em>Planolites</em>.</td>
</tr>
<tr>
<td><em>Taenidium</em> isp.</td>
<td>24d-e</td>
<td>Cylindrical, straight, unbranching burrows with backfilling structures; Some tubes are horizontal on tops of beds, and others are slightly oblique to bedding planes. Tube diameters are 6-9.5 mm.</td>
<td>Feeding behaviours of worm-like animals (Keighley and Pickerill, 1994).</td>
</tr>
<tr>
<td><em>Thalassinoides</em> isp. 1</td>
<td>23-24</td>
<td>Large Y-shaped, branching, smooth, rounded burrows, 10-14 mm in diameter (Fig. 22), penetrating a depth of &lt; 1 cm into sediment and forming incomplete intricate networks.</td>
<td>Behaviour of cerianthid sea anemones, worms and decapod crustaceans (Myrow, 1995; Bromley, 1996; Ekdale and Bromley, 2003).</td>
</tr>
<tr>
<td><em>Thalassinoides</em> isp. 2</td>
<td>27</td>
<td>Small Y-shaped, branching burrows, 1-2 mm in diameter, penetrating a depth of &lt; 1 cm into sediment, filled with light coarsely grained sediments distinct from surrounding dark, fine-grained sediments.</td>
<td>Same as above</td>
</tr>
<tr>
<td><em>Thalassinoides</em> isp. 3</td>
<td>53-56</td>
<td>Medium-sized Y-shaped, branching burrows, 3-4.5 mm in diameter, mostly horizontal on tops of beds and filled with dark, organic sediments.</td>
<td>Same as above</td>
</tr>
<tr>
<td><em>Treptichnus</em> isp.</td>
<td>56-57</td>
<td>Meandering burrow system with one main burrow, 6 mm in width, terminates its growth after bifurcating to give a minor branch on its outer side. The minor branch ceases its growth soon after giving birth to further secondary branch.</td>
<td>Deposit-feeding of worm-like organism in a zigzag or other segmented pattern with older segments abandoned after use (Rindsberg and Kopaska-Merkel, 2005; Seilacher, 2007).</td>
</tr>
</tbody>
</table>

*Illustr.* = *Illustration*