



Two episodes of foraminiferal extinction near the Permian–Triassic boundary at the Meishan section, South China

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Stratigraphic distributions of foraminifer species from the Permian–Triassic (P/Tr) transition of the Meishan section, South China demonstrate two episodes of biotic mass extinction near the P/Tr boundary. The first episode is calibrated to the top of Bed 24 and is indicated by a loss of 49 out of 64 Changhsingian species (77%). The second phase is expressed by the disappearance of 32 out of 34 species (94%) recorded in Beds 25–27 and corresponds to the base of Bed 28. Only *Nodosinelloides aequi ampla* survived into the early Griesbachian and another species, *Glomospira regularis*, rebounded in the late Griesbachian. The Lagenida and Textulariida lost 71% and 50% of species, respectively, in the first episode of the P/Tr extinction. In the Lagenida, only one taxon temporarily survived over the second crisis but became extinct soon after in Bed 29, while one newcomer occurred in the late Griesbachian. In the Textulariida, one Lazarus species rebounded in the late Griesbachian when two new forms rose. Both the Fusulinida and Miliolida suffered a great loss in the first extinction event, losing about 85% and 89% of the species, respectively. Their temporary survivors were wiped out in the second episode of the P/Tr crisis. The large, architecturally complex taxa suffered the first crisis much more severely than the small, simple tests. Selective extinction and rebound among the forms bearing various test walls probably indicate the different physiological reactions of various foraminifer groups to the defaunation events such as biocalcification crisis, hypercapnia, elevated CO₂ content and global warming that prevailed in the aftermath of the P/Tr mass extinction.

KEY WORDS: China, extinction pattern, foraminifera, Meishan section, Permian, Triassic.

INTRODUCTION

The end-Permian mass extinction is the most catastrophic event among all the Phanerozoic mass extinctions (Erwin 1993). This event has been extensively reported, but its extinction pattern and cause remain in dispute (Raup 1979; Sepkoski 1981; Erwin 1993; Yang *et al.* 1993; Stanley & Yang 1994; Hallam & Wignall 1997; Bowring *et al.* 1998; Jin *et al.* 2000; Ward *et al.* 2005; Xie *et al.* 2005; Yin *et al.* 2007). Whether the extinction pattern is abrupt or episodic has long been debated. Yang *et al.* (1993) proposed that the extinction was episodic and consisted of three phases. The first episode, reflected by the collapse of the last Permian reef ecosystem in South China, is calibrated to the base of Bed 24e at the Meishan section where the Global Stratotype Section and Point of the Permian–Triassic (P/Tr) boundary is defined at the base of Bed 27c (Yin *et al.* 2001). The sharp disappearance of the Permian benthic forms marks the second episode at the base of Bed 25. The third phase is indicated by the extinction of

most Permian relicts at the base of Bed 28. In contrast, Rampino & Adler (1998) and Jin *et al.* (2000) considered that the end-Permian mass extinction was a single abrupt event based on the statistical analysis of the fossil records from the Tesero section, north Italy and the Meishan section, South China, respectively. However, recent biomarker analysis of microbial contents across the P/Tr boundary at the Meishan section suggests a pattern of two episodes of mass extinction over the P/Tr transition (Xie *et al.* 2005). Yin *et al.* (2007) further summarised three episodes of the P/Tr mass extinction: a prelude extinction, main extinction and post-extinction event. The episodic extinction scenario is also reinforced by the newly obtained paleontological data from the P/Tr sections in both north Italy and South China (Farabegoli *et al.* 2007; Feng *et al.* 2007). Accordingly, additional fossil records across the era boundary are desirable to test biotic extinction patterns near the P/Tr boundary. Here, we document the change-over of foraminifers across the P/Tr boundary at the

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Meishan section, South China (Figure 1) to test the P/Tr mass extinction from foraminiferal evidence.

The foraminifers are one of the most important fossil groups that provide a better understanding of biotic extinction pattern in the P/Tr catastrophe simply because they are small-sized and very common throughout the P/Tr transition and thus can be studied quantitatively (Yang *et al.* 1987, 1993; Tong & Kuang 1990; Rampino & Adler 1998; Jin *et al.* 2000; Groves *et al.* 2005), although the sampling resolution can strongly affect the statistical extinction patterns.

At Meishan, Zhao *et al.* (1981) first reported 65 species and subspecies in 27 foraminifer genera from the Changhsingian Stage and P/Tr boundary beds. These taxonomic data are the main source used in the influential study of the P/Tr mass extinction of foraminifer undertaken by Jin *et al.* (2000). Nevertheless, although Zhao *et al.* (1981) listed foraminifer taxa bed-by-bed when they described stratigraphic features throughout the Changhsingian to lowermost Triassic they failed to provide detailed sampling horizons. Furthermore, the classification employed in Zhao *et al.* (1981) followed the early taxonomy of Loeblich & Tappan (1964), which has been extensively revised recently (Loeblich & Tappan 1984, 1988; Groves *et al.* 2004, 2005; Groves & Altiner 2005), and this may have changed the extinction-survival patterns of foraminifera over this critical period.

We have resampled the Meishan section through the Changhsingian to the Lower Triassic at a very high resolution especially across the P/Tr transition. Foraminifers from the P/Tr transitional beds are very abundant. Song *et al.* (2006, 2007) have described systematically most of the key taxa from the collections. The foraminifers found from Meishan are one of the most diverse Changhsingian assemblages reported so far in South China, containing all of the genera and about 90% of the species described elsewhere in South China (Rui *et al.* 1988). Thus, the foraminifer collections from Meishan provide a proper understanding of the change-over of this group across the P/Tr boundary. Meldahl's

(1990) method is also employed herein to eliminate the Signor–Lipps effect (Signor & Lipps 1982; Raup 1986; Raup *et al.* 1989) when foraminifer extinction-survival patterns are assessed.

SAMPLING AND METHODOLOGY

Foraminifers analysed here were collected from the Meishan section F, about 100 m west of the Meishan section D, the Global Stratotype Section and Point of the P/Tr boundary (Yin *et al.* 2001). The P/Tr succession cropping out at the Meishan section F is almost the same as that recorded at the section D (Tong *et al.* 1996). The section has been continuously sampled from the P/Tr boundary downward to Bed 22 and upward to Bed 40. Beds 13–21 were thin-sectioned in a 25 cm interval, and Beds 22–24d in a 2–5 cm (average 3 cm) interval; the thin-sections were cut vertical to the bedding surface. Twenty-four thin-sections were made from the samples of Bed 24e (10 cm in thickness), eight from Bed 25 (4 cm), 12 from Bed 26 (6 cm), eight from Bed 28 (6 cm), 10 from Bed 29 (18 cm), and 32 from Bed 27 (16 cm); these beds were thin-sectioned in directions both parallel to and vertical to the bedding surface. The claystone beds, Beds 25, 26 and 28, were also thin-sectioned, but very few foraminiferal tests were recovered from these beds. The foraminifers of Bed 25 used in the quantitative analysis are taken from Rui *et al.* (1988). Additional samples from Beds 24e–29 were also obtained from Meishan sections A and C, 300 m and 100 m west of the section F, respectively. In total, 7273 foraminifer specimens are recognised from 304 thin-sections collected from the middle Changhsingian (Bed 13) to upper Griesbachian (Bed 40). If the tests cannot be precisely identified to the species level but their generic classification is certain, they are also employed to the quantitative analysis undertaken here.

Although foraminifers from Meishan have been extensively studied (Zhao *et al.* 1981; Rui *et al.* 1988; Song *et al.* 2006, 2007), the incompleteness of fossil

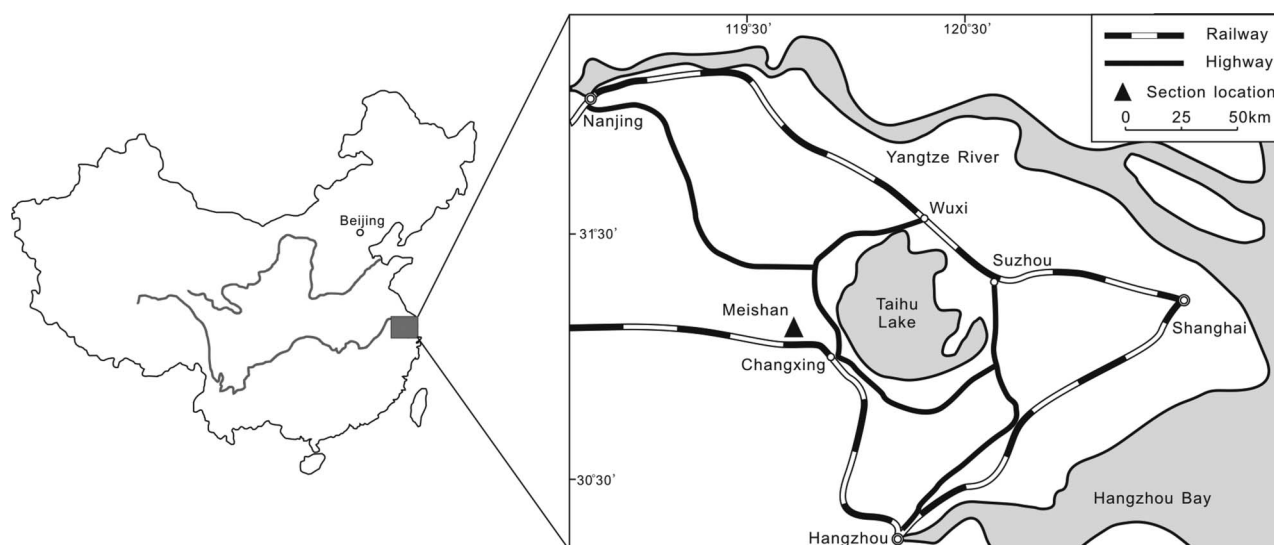


Figure 1 Location map of the Meishan section, Zhejiang Province, South China.

records may still bias the statistical extinction pattern to some extent. Signor & Lipps (1982) found that the inconsistency of the stratigraphic distribution of fossil records has considerably affected various extinction patterns. This phenomenon was later termed the Signor–Lipps effect (Raup 1986; Raup *et al.* 1989). To minimise this effect, Meldahl (1990) developed a ‘stratigraphic abundance *vs* last occurrence’ plot to predict the extinction patterns based on the stratigraphic distribution of fossil records. This method has been successfully applied to test the foraminifer extinction pattern over the P/Tr transition (Rampino & Adler 1998; Jin *et al.* 2000; Groves *et al.* 2005). Here, Meldahl’s method is also employed to test the foraminifer extinction–survival relationship across the P/Tr boundary on the basis of the newly obtained data from the Changhsingian–Griesbachian at Meishan. To calibrate the precise extinction horizons, last occurrence data of foraminifers from the boundary bed are collected in each 10-cm interval to calculate taxonomic stratigraphic abundance and frequency distribution.

RESULTS AND DISCUSSION

Extinction pattern of foraminifera

Of the 83 species in 44 foraminifer genera obtained from Meishan, 64 species of 36 genera occur in the middle–upper Changhsing Formation, 33 species of 21 genera in Beds 25–27, and only one species, *Nodosinelloides aequi ampla*, in Bed 29. No foraminifers are observed in Beds 30–40 (Figure 2). In addition, three species including two new taxa rebounded in Bed 60 and higher strata (Song *et al.* 2007). Stratigraphic distribution of foraminifera also exhibits a gradual decline from Bed 22 to Bed 24 and a stepwise disappearance pattern near the P/Tr boundary (Figure 2). There are 16 species out of 64 species, about 25%, that disappear gradually from the base of Bed 22 to the top of Bed 24 (Table 1). The first distinctive disappearance surface of foraminifera occurs at the top of Bed 24e, which sees a loss of 33 species (a drop of 52%: Table 1). After this event the foraminifer diversity rebounded in Bed 27, where 33 species including 19 new taxa are observed. However, they declined down to one species, losing 94% across the boundary between Beds 27 and 28 (Table 1) and this marks the second major disappearance surface (Figure 2).

Taxonomic plots of the Signor–Lipps effect through the Changhsingian to Griesbachian show a more or less ‘hollow curve’ (Figure 3a), as the expected distribution for a sudden extinction elsewhere (Meldahl 1990). However, the plots do not match the curve, typical of an abrupt extinction, derived from the Tesero section (Rampino & Adler 1998). This may be due to either different sedimentary facies or various sampling resolutions.

The plots of stratigraphic abundance *vs* the last occurrences of taxa from the P/Tr boundary beds (i.e. Beds 24–30) show a marked double extinction pattern (Figure 3b). The first one occurs at about 20 cm below the P/Tr boundary, corresponding to the topmost Bed 24e, while the second is at the base of Bed 28 (Figure 3c). It should be noted that 33 out of 49 foraminifer species

(67%) have their last occurrences between the interval –20 and –30 cm (the negative number indicating sampling depth below the P/Tr boundary at the base of Bed 27c). Of these, 14 species are abundant in this interval with each species having >15% individuals of the total foraminiferal tests that occur in the interval (Figure 3b). This last appearance interval corresponds to the strata of 0–10 cm below the base of Bed 25. This contrasts with observation under the microscope as very rare foraminifers are seen in the thin-sections from the topmost Bed 24e. However, the sampling resolution of 10 cm interval does not permit the recognition of the exact extinction horizon within the uppermost 10 cm of Bed 24e.

Another last occurrence peak of foraminifer species occurs in the 10 cm interval above the P/Tr boundary. This interval extends from Bed 27c–d (8 cm in thickness) to Bed 28, a 4 cm-thick white claystone. However, no foraminifers are recovered from Bed 28. Thus, the actual disappearance interval is in the uppermost 8 cm of Bed 27, corresponding to Bed 27c–d. Foraminifer species declined from 32 down to 6, dropping 81% across the event interval. Nine abundant species having >15% individuals of the total foraminiferal tests in the uppermost 10 cm strata (Figure 3b).

Between these two last occurrence peaks, only a few unidentified foraminifer fragments are observed under the microscope from Beds 25–26. Rui *et al.* (1988) reported eight genera *Bradyina*, *Globivalvulina*, *Geinitzina*, *Hemigordius*, *Glomospira*, *Nodosaria*, *Tetrataxis* and *Textularia* from Bed 25, but each taxon is represented by very few specimens. Above the second last occurrence peak (base of Bed 28), *Nodosinelloides aequi ampla* is the only survivor persisting into Bed 29 and higher strata at Meishan.

As a result, fossil records of foraminifers at Meishan clearly show two distinct episodes of extinction around the P/Tr boundary, corresponding to the uppermost part of Bed 24e and the top of Bed 27. A total 49 out of 64 Changhsingian species (77%) disappeared within the topmost 10 cm of Bed 24e or slightly below this interval. There are 34 foraminifer species occurring in the aftermath of the first crisis (Beds 26–27), but 32 species (94%) became extinct at the base of Bed 28, showing the same pattern as the brachiopod faunas over the P/Tr transition at Meishan (Chen *et al.* 2005, 2006).

Similarly, the foraminifer abundance has undergone a two-step decline through the P/Tr transition (Figure 4). Foraminiferal tests are abundant in thin-sections in Bed 24 and strata below, with an average abundance of 32.5 specimens visible within a 22 × 22 mm thin-section (all subsequent measurements refer to this size of thin-section). As outlined above, foraminifers are very rare in Beds 25–26, and their diversity increases rapidly in Bed 27 (33 species). However, foraminifer abundance is extremely low, with an average abundance of only 4.1 specimens per thin-section. Above Bed 27, foraminifers become rarer, averaging, <1 specimen per thin-section in Bed 29 and overlying strata. As a consequence, foraminifer abundance declined from 32.5 down to 4.1 per thin-section, a drop of 87.3% across the boundary between Beds 24 and 25. A >76% drop characterises the

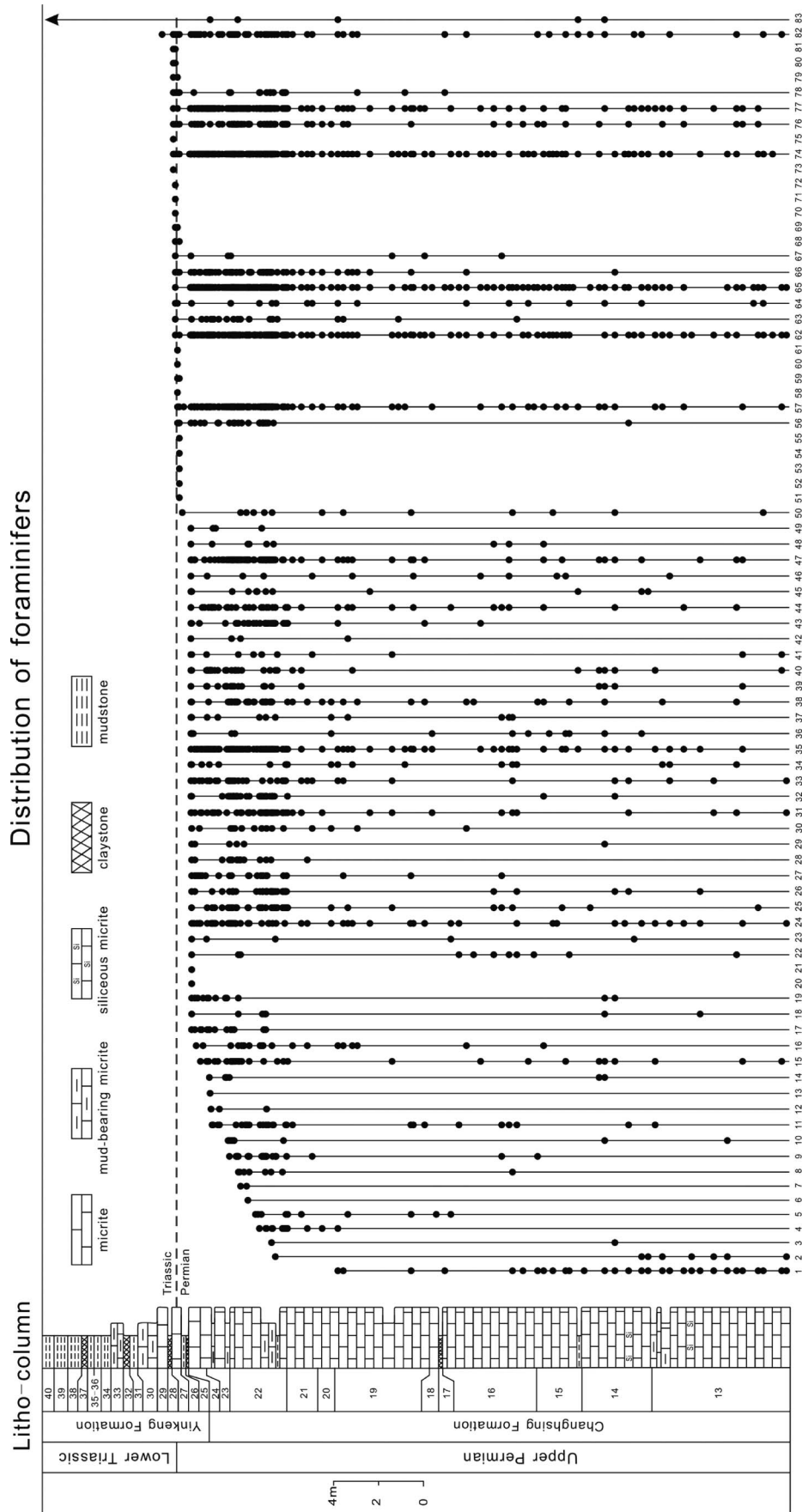
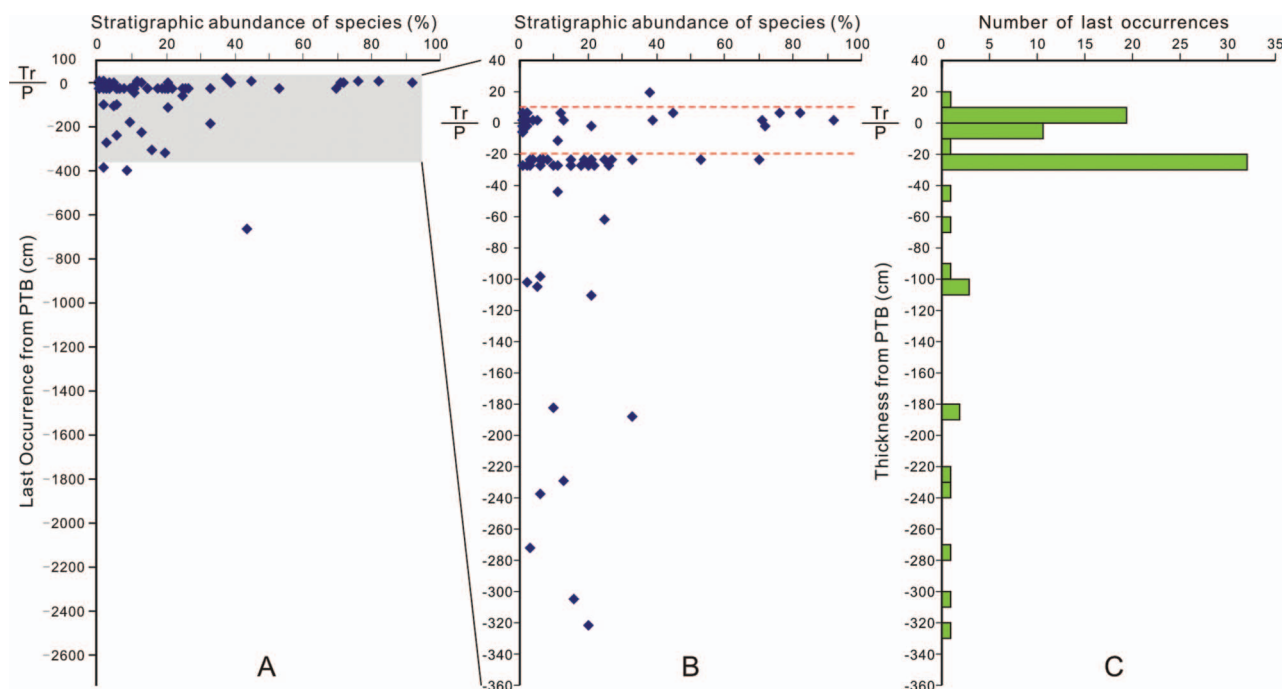


Figure 2 Distribution of foraminifers from upper Changhsingian to lower Induan at the Meishan Section, South China. 1, *Protonodosaria* spp.; 2, *Millerella* sp.; 3, *Tetrataxis angusta*; 4, *Rectostipulina* spp.; 5, '*Pseudoglandulina inflataeformis*'; 6, *Cryptomorphina limonitica*; 7, *Palaeofusulina* sp.; 8, *Biorbis* spp.; 9, *Postendothyra guangxiensis*; 11, *Dagmarita chanakchiensis*; 12, *?Tourmayella* spp.; 13, *Partisania* sp.; 14, *Hemigordius guangdongensis*; 15, *Hemigordius rotundus*; 16, *Pachyphloia robusta*; 17, *Ammovertella inversus*; 18, *Colaniella nana*; 19, *Hemigordius parvus*; 20, *Hemigordius* sp. B; 21, *Hemigordius* sp. C; 22, *Multidiscus padangensis*; 23, *Neoendothyra permica*; 24, *Neotuberitina maljavukini*; 25, *Nodosinelloides camerata*; 26, *Nodosinelloides ronda*; 27, *Nodosinelloides sagitta*; 28, *Pachyphloia ovata*; 29, *Palaeotextularia* spp.; 30, *Rectostipulina pentamerata*; 31, *Aeolisaccus dumingtoni*; 32, *Colaniella* spp.; 33, *Cryptoseptida fragilis*; 34, *Dagmarita altitis*; 35, *Dagmarita* spp.; 36, *Geinitzina spandelei*; 37, *Geinitzina uralica*; 38, *Geinitzina* spp.; 39, *Hemigordius zaniettiae*; 40, *Hemigordius bronnimanni*; 41, *Hemigordius regularis*; 42, *Neoendothyra parva*; 43, *Nodosinelloides acraeformis*; 44, *Paraglobivaivulina* sp.; 45, *Pseudammmodiscus parvus*; 46, '*Pseudoglandulina conica*'; 47, *Reichelina* spp.; 48, *Sengoerina argandii*; 49, *Vervilleina bradyi*; 50, *Glomospira* spp.; 51, *Cryptoseptida* sp.; 52, *Fronidina* sp. A; 53, '*Nodosaria*' *skyphica*; 54, '*Nodosaria*' sp.; 55, *Robuloides* sp.; 56, *Cryptoseptida anatoliensis*; 57, *Hemigordius* sp. A; 58, *Neoendothyra* sp.; 59, indeterminate genus and species A; 60, indeterminate genus D species B; 61, indeterminate genus D species D; 62, *Fronidina permica*; 63, *Ichthyofronidina palmata*; 64, *Nodosinelloides netschajewi*; 65, *Nodosinelloides* sp.; 66, *Rectostipulina quadrata*; 67, *Tuberitina* sp.; 68, indeterminate genus and species C; 69, indeterminate genus and species E; 70, indeterminate genus and species F; 71, indeterminate genus and species F; 72, indeterminate genus and species F; 73, *Ammodiscus* sp.; 74, *Diplophaerina inaequalis*; 75, *Fronidina* sp. B; 76, *Geinitzina araxensis*; 77, *Globivaivulina bulloides*; 78, *Robuloides lens*; 79, indeterminate genus and species B; 80, indeterminate genus D species C; 81, indeterminate genus D species E; 82, *Nodosinelloides aequiampila*; 83, *Glomospira regularis*.

Table 1 Number and percentage of last occurrences of foraminifer species in the Permian–Triassic boundary beds at Meishan.

Bed no.	Upper Permian							Lower Triassic							
	Changhsing Formation							Yinkeng Formation							
	22	23	24a	24b	24c	24d	24e	25	26	27a	27b	27c	27d	28	29
Number	7	6	0	0	1	1	33	0	1	5	6	11	9	0	1
Percentage	8.5	7.3	0	0	1.2	1.2	40.2	0	1.2	6.1	7.3	13.4	11.0	0	1.2

**Figure 3** Plots of the stratigraphic abundance *vs* last occurrence below the P/Tr boundary at the Meishan Section. The negative number on the y-axis indicates the depth below the P/Tr boundary. (a) Data derived from a sample interval of 2 m, showing a single extinction pattern. (b) Data derived from a sample interval of 10 cm, showing a double extinction pattern. (c) Frequency distributions of last occurrences in a sample interval of 10 cm, showing a double extinction pattern.

second abundance decline across Beds 27 and 28. Interestingly, these two distinct declines in abundance coincide with two microbial proliferations recognised by biomarker analysis (Xie *et al.* 2005) and negative shifts of carbon isotope composition (Xie *et al.* 2007) from the same section. This coincidence is probably because foraminifers are the direct consumers of microbes, and disappearance of consumers gave the microbes an opportunity to bloom.

Foraminifer evolution across the P/Tr boundary

ORDER LAGENIDA

The Lagenida of calcareous tests originated in the Moscovian (Late Carboniferous) (Tappan & Loeblich 1988) and proliferated significantly after the end-Guadalupian mass extinction, while the other foraminifer groups suffered a considerable loss (Kaiho *et al.* 2005). The Lopingian lagenids were abundant in the inner to central neritic environments throughout the Paleotethyan region and the northern high-latitude regions (Groves *et al.* 2005).

At Meishan, lagenids dominate the foraminifer assemblage in the uppermost Changhsingian and are more abundant and diverse than fusulinids (Figures 3, 4). In our collections 15 genera from the Changhsingian Formation belong to the Lagenida, such as *Nodosinelloides*, *Geinitzina*, *Pachyphloia*, *Protonodosaria*, *Ichthyofrondina*, *Frondina*, *Colaniella*, *Cryptoseptida*, *'Pseudoglandulina'*, *Rectostipulina* and *Robuloides*. Lagenids declined from 31 species down to 22 species, dropping 71%, across the first extinction event horizon. In particular, all species of genera such as *Pachyphloia*, *Protonodosaria* and *Colaniella*, which have large and have complex tests, characteristic of the Changhsingian assemblages, were wiped out in the first episode of the P/Tr mass extinction. Although the Lagenida suffered a dramatic loss of the Permian forms, which marks the first extinction event, the diversity of this foraminifer group remains considerably high in the aftermath (Bed 27). This is due to a high origination rate in the aftermath of the first crisis, with 16 new species in Bed 27. In addition, nine species survived the first extinction event. Accordingly, the first extinction event facilitated a dramatic revolution in faunal compositions within the

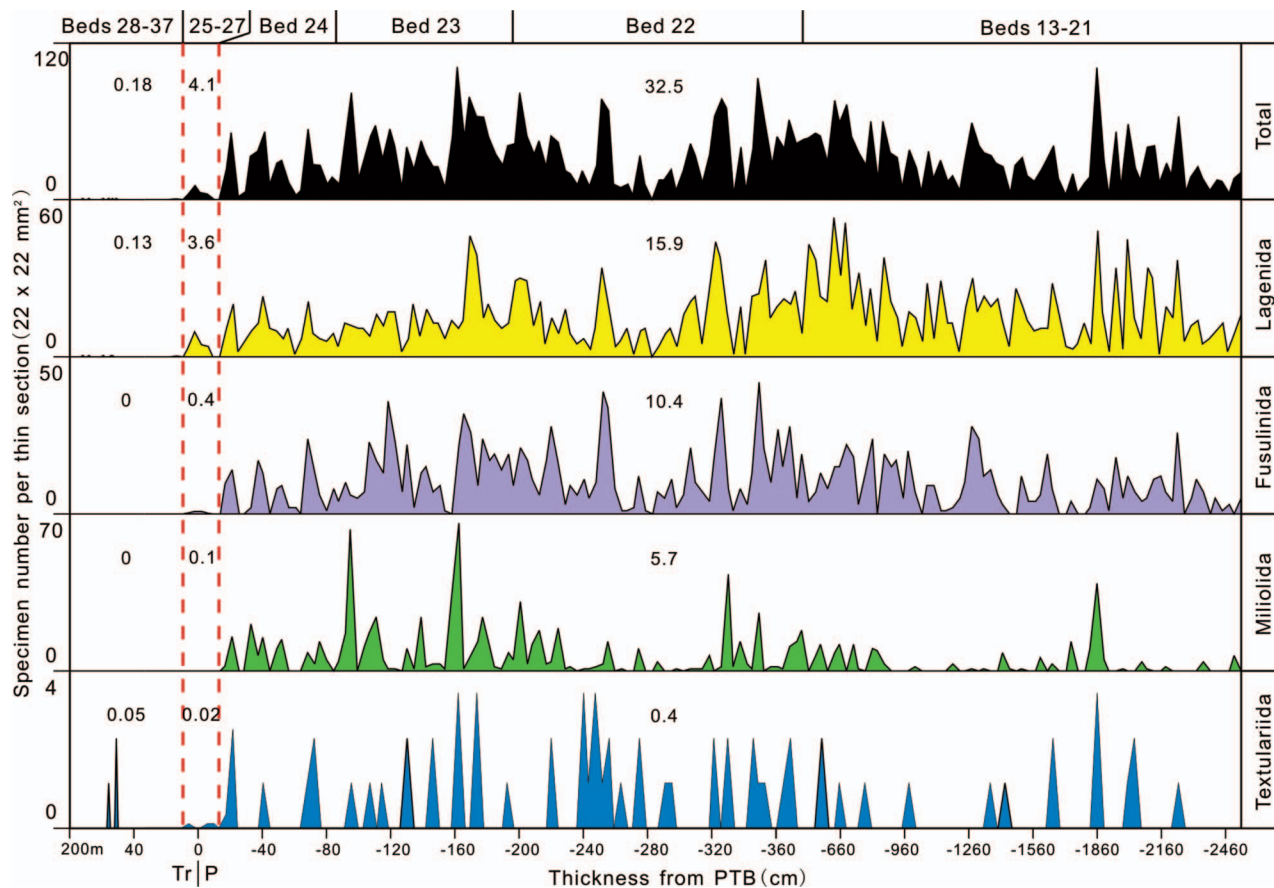


Figure 4 Abundance distributions of various foraminifer groups from the upper Changhsingian to Induan at the Meishan section. Note that the depth scales are changed at 40 cm and -360 cm. The vertical dashed lines indicate the two episodes of extinction. The numbers above each graph represent the average abundance in the corresponding interval.

Lagenida. Over the first P/Tr extinction event, the typical Permian forms having relatively complex tests were replaced by small, simple forms that comprised both survivors and newcomers (Song *et al.* 2007). The morphologically simplified forms, characteristic of high-stressed, post-extinction assemblages (Groves *et al.* 2007), dominate the Bed 27 foraminifer faunas at Meishan. Although the lagenids are relatively common, the post-extinction foraminifer community (Bed 27) overall has a very low abundance, with only 3.6 specimens per thin-section, as representatives of other foraminifer groups are extremely rare (Figure 4). The dominant elements, notably *Nodosinelloides*, *Geinitzina* and *Robuloides*, are typical of the Late Permian foraminifer genera.

At Meishan *Nodosinelloides aequi ampla* is the only survivor from the second P/Tr mass extinction at the base of Bed 28, and only two specimens of that species are observed in Bed 29. No lagenids are found in the upper part of the Meishan section except for *Ligulina* sp., which is occasionally present in the upper Yinkeng Formation and Helongshan Formation (Song *et al.* 2007). Thus, foraminifers are very rare in the middle-late Griesbachian at Meishan, in sharp contrast to the Neo-Tethys region, where three Permian relicts (*Geinitzina* sp., *Syzrania* sp. and '*Nodosaria*' *elabugae*) survived into the early Induan in Turkey (Altiner *et al.* 2005), and

three forms (*Geinitzina* spp., *Nodosinelloides* spp. and *?Pachyphloia schwageri*) have also been reported from the early Induan in Italy (Groves *et al.* 2007).

ORDER FUSULINIDA

In the low-latitude tropical regions such as South China, fusulinids dominated benthic assemblages in the Carboniferous–Permian oceans. Like lagenids, fusulinids have calcareous tests. The fusulinacean fusulinids such as large fusulinids (Superfamily Fusulinacea) underwent a severe decline in both abundance and diversity at the end-Guadalupian mass extinction (Leven & Korchagin 2001) and did not recover in the Lopingian (Stanley & Yang 1994; Tong & Shi 2000; Tong 2004). By contrast, the non-fusulinacean fusulinids proliferated rapidly and dominated the Lopingian foraminifer assemblages. This group later developed some relatively complex test architectures. The Fusulinida was the second largest group in the Late Permian foraminifer assemblages in terms of abundance and diversity, subordinate only to the Lagenida. A total of 20 species of 17 fusulinid genera are identified from the Changxing Formation. However, $\sim 85\%$ of fusulinid species were wiped out in the first extinction event. Of these, all fusulinacean genera such as *Palaeofusulina* and *Reichelina* became extinct.

Diplosphaerina inaequalis dominates the surviving fusulinid assemblage, which was characterised by a rather low abundance, with only 0.4 specimens per thin-section. All of the surviving fusulinids eventually became extinct during the second episode of the P/Tr mass extinction. Thus, no fusulinids survived into the middle-late Griesbachian (Early Triassic) in South China, although some forms occur in the P/Tr boundary bed (Bed 27). It should be noted that one fusulinid form, *Globivalvulina* aff. *cyprica*, is reportedly present in the early Induan in Turkey (Altiner *et al.* 2005).

ORDER MILIOLIDA

The foraminifers of the Order Miliolida have calcareous porcellanous tests and usually have a high degree of endurance against environmental stress. They include many evolutionary generalists and ecological opportunists (Hallam & Wignall 1997; Groves & Altiner 2005). Here, miliolids comprise only two genera, *Hemigordius* and *Multidiscus*. Of these, *Hemigordius* includes nine species contrasting sharply with *Multidiscus*, which is monospecific. The former is abundant in the Changhsingian at Meishan (Figures 3, 4). However, eight species of *Hemigordius* (88.9%) vanished in the first extinction event and only one species survived into the P/Tr boundary bed (Bed 27). The surviving hemigordiopsids have a very low abundance, with an average of 0.1 specimens per thin-section. All miliolids were wiped out in the second extinction event.

ORDER TEXTULARIIDA

Unlike the major Late Permian groups, the foraminifers of the Textulariida construct agglutinated tests. The agglutinated Textulariida has not only the longest geological record but also the broadest range of habitats among living foraminifers. However, this group was not diverse in the Paleozoic oceans. About one-third of the Permian agglutinated genera did not survive the end-Permian mass extinction (Tappan & Loeblich 1988). The textulariides, including *Ammonovertella inversus*, *Pseudoammodiscus parvus* and *Glomospira* spp., are present in the upper Changxing Formation at Meishan, but they are obviously less abundant and diverse than the calcareous foraminifers of the Lagenida, Fusulinida and Miliolida in the same assemblage (Figures 4, 5). *Glomospira* spp. was the only survivor from the first extinction event, and it became extinct in the second event. Curiously, the agglutinated textulariides rebounded in the middle-late Induan when the Lazarus taxon *Glomospira regularis*, together with a new textulariide form, dominated the post-extinction fauna at Meishan (Song *et al.* 2007 figure 9).

SUMMARY

Both Lagenida and Textulariida have relatively lower extinction rates, 71% and 50% respectively, at species level, in the first extinction event. However, almost all taxa were wiped out in the second P/Tr extinction, except for one lagenid species which survived the

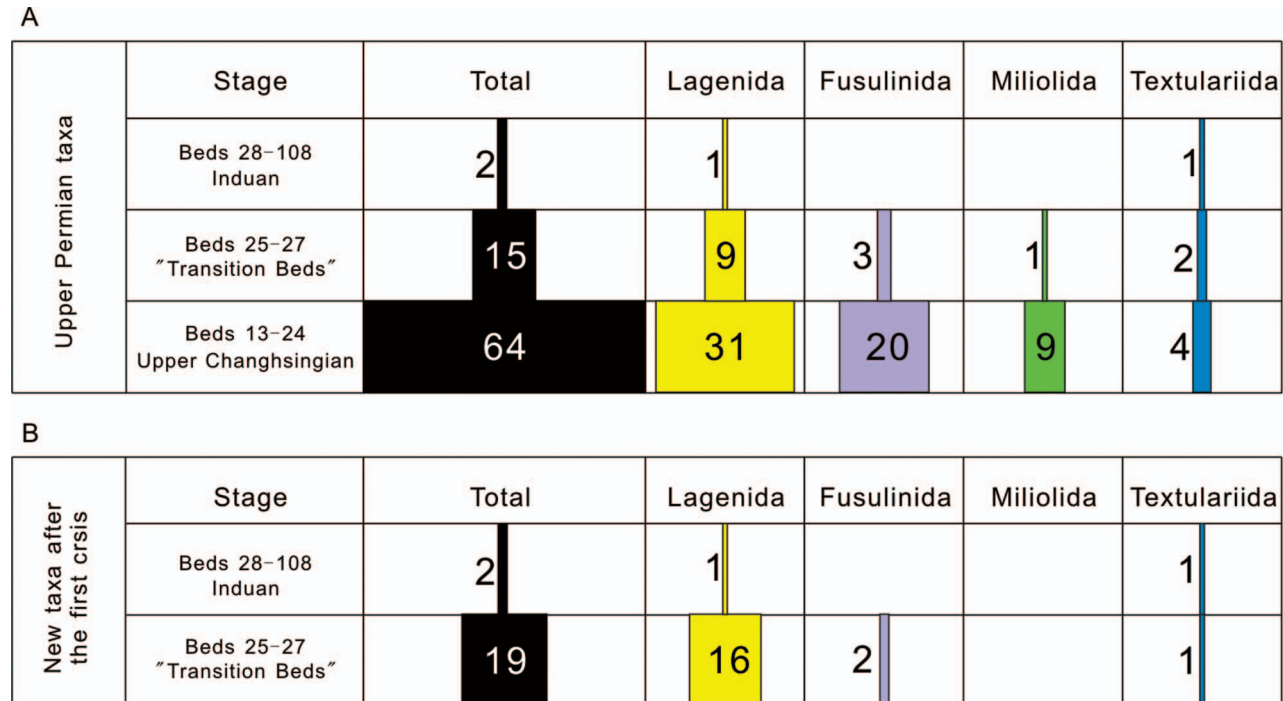


Figure 5 Number of foraminifer species recorded at the Meishan section from the Changhsingian to Induan. Note that the numbers include the Permian taxa and relicts (A) as well as the newcomers (B) after the first episode of the P/Tr extinction. At the Meishan section, the Upper Changhsingian includes Beds 13-24, the 'Transition Beds' (Yin 1985) includes Beds 25-27 and the Induan includes Beds 28-108.

event. In addition, the Lazarus species *Glomospira regularis* rebounded in the middle–late Induan. In contrast, both the Fusulinida and Miliolida suffered losses of 85% and 89% at species level, respectively, in the first P/Tr extinction. Their temporary survivors also became extinct in the second crisis. No new taxa of these two orders occurred in the late Induan, although the disaster forms such as *Earlandia* sp. of the Fusulinida and both *Rectocornuspira kalhori* and *Cornuspira mahajeri* of the Miliolida have been found in the Lower Triassic elsewhere in the Paleo-Tethyan region [Dajiang area of Guizhou and the Liangfengya area of Chongqing, South China (J. Tong unpubl. data); P/Tr boundary sites in southern Turkey (Groves *et al.* 2005; Angiolini *et al.* 2007); Gerennavár in Hungary (Hips & Haas 2006); Tesero and Bulla in Italy (Groves *et al.* 2007)].

Physiologically, the large foraminifers such as *Pachyphloia* of the Lagenida and *Multidiscus* of the Miliolida, and architecturally complex forms such as *Colaniella* and *Pachyphloia* of the Lagenida were killed off in the first episode of the P/Tr extinction. In contrast, the small simple taxa such as the indeterminate genera A, B, C, and E having primitive or no septa (Song *et al.* 2007) and the species of *Diplospherina* and *Tuberitina* survived the first crisis, and they make up a low-abundance and moderate-diversity surviving assemblage. Thus, various foraminifer groups selectively became extinct. In particular, the small, simple foraminifers more easily survived the P/Tr ecological crisis than did the large, complex forms. However, most of the survivors and newcomers became extinct soon after at the beginning of the Triassic. In general, the Meishan collections also show that the calcareous foraminifers dominated the Late Permian assemblages, while the agglutinated taxa dominated the Early Triassic communities together with a depauperate fauna of calcareous forms (Brasier 1988; Groves *et al.* 2005, 2007; Groves & Altiner 2005; Márquez 2005). This phenomenon is interpreted as the physiological reactions of foraminifera to several defaunation events such as biocalcification crisis, hypercapnia, elevated CO₂ content and global warming that prevailed in the aftermath of the P/Tr mass extinction (Knoll *et al.* 2007). These devastation events usually resulted in high mortality in marine ecosystems where organisms are characterised by low basal metabolic rate, limited or no circulatory system, little elaboration of respiratory surfaces and precipitation of CaCO₃ skeletons under conditions of minimal physiological buffering (Knoll *et al.* 2007). Thus, those foraminifers with a calcium carbonate skeleton have been mortally affected and suffered from a severe biocalcification crisis and related events, as exhibited by corals and calcitic brachiopods (Chen *et al.* 2007; Fraiser & Bottjer 2007). In contrast, the agglutinated foraminifers did not suffer from such defaunation events (Groves & Altiner 2005; Knoll *et al.* 2007).

CONCLUSIONS

(1) Foraminifers have undergone two distinct extinctions over the P/Tr transition with the first episode

calibrated to the uppermost Bed 24e and the second to the base of Bed 28. Foraminifers suffered a loss of 77% Changhsingian species in the first crisis. A decline of 94% foraminifer species characterises the second phase of the P/Tr extinction.

(2) Foraminifer extinction is selective among various major groups during the P/Tr crisis. Both the Lagenida and Textulariida had a relatively low extinction rate at species level in the first extinction event, losing 71% and 50% of species, respectively. Only one lagenid species survived over the second extinction episode but became extinct soon after. One Lazarus taxon of the Textulariida rebounded in the middle–late Induan. Both the Fusulinida and Miliolida underwent severe extinction in the first crisis, with 85% and 89% of species, respectively, disappearing. The temporary survivors and newcomers characterise the foraminifer assemblage in the aftermath of the first crisis, and most became extinct in the second extinction event.

(3) Most of the large forms having architecturally complex tests were wiped out in the first P/Tr extinction. The survivors are usually small and have simple tests. They form a low-abundance and low-diversity community in the aftermath of the first crisis. Selectivity of extinction and rebounds among the various test forms probably indicates their various physiological reactions to the defaunation events such as biocalcification crisis, hypercapnia, elevated CO₂ content and global warming that prevailed in the Early Triassic oceans.

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