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Radiolarian evolution during the latest Permian in South China

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Abstract

Investigations on the Upper Changhsingian radiolarian fauna in South China allow us to trace, in detail, extinction processes and to research relations between the Permian and Triassic radiolarian faunas. Evolution of the radiolarian fauna is divided into three stages: radiation, extinction and survival intervals. In the radiation interval (10.28–2.68 m below the PTB), the radiolarian fauna consists of 137 species belonging to 50 genera and includes 8 representative Triassic genera. Two crises are recognized in the extinction interval (2.68–0.77 m below the PTB). The first crisis is characterized by extinction at species level and the second crisis, by disappearance of many genera. In the survival interval (0.77 m below the PTB to lower Lower Triassic), the radiolarian fauna includes only Paleozoic-type taxa and its diversity and abundance are unusually low. The first crisis corresponds to the extinction located at the top of Bed 24d in Meishan Section D and the second crisis, to the extinction located at the top of Bed 24e of Meishan Section D.

Keywords: Radiolaria; mass extinction; evolution; Upper Changhsingian; South China

1. Introduction

The end-Permian mass extinction is the largest event among the “Big Five” during the Phanerozoic history in terms of the severity of taxonomic diversity losses (Sepkoski, 1981; Erwin, 1994). Significant progress has been made in recent years regarding the biotic extinction pattern of this event and about the survival and recovery after the mass extinction. For Radiolaria, extensive literature is available on the taxonomy and biostratigraphy of Permian and Triassic radiolarians from Europe (Kozur and Mostler, 1994; Kozur et al., 1996), North American (Blome and Reed, 1992, 1995), Japan (Sashida, 1983; Caridroit and De Wever, 1986; Sashida, 1991; Sugiyama, 1992; Nagai and Mizutani, 1993; Sugiyama, 1997; Kuwahara, 1999; Kuwahara and Yao, 2001; Xia et al., 2004), northeastern Russia (Bragin, 1991; Vishnevskaya, 1997), China (Wang et al., 1994; Wu et al., 1994; Feng et al., 1996; Yao and Kuwahara, 1997; Feng et al., 1998; Yao and Kuwamura, 1999, 2000; Feng et al., 2000; Feng et al., 2001; Feng and Gu, 2002; Kuwahara et al., 2003), Thailand (Sashida and Igo, 1992; Caridroit, 1993; Sashida et al., 1998, 2000a,b), Philippines (Cheng, 1989), and New Zealand (Kamata et al., 2003, 2005). Some paleontologists have attempted to analyze and elucidate the evolution of radiolarian faunas across the Permian–Triassic transition and found that

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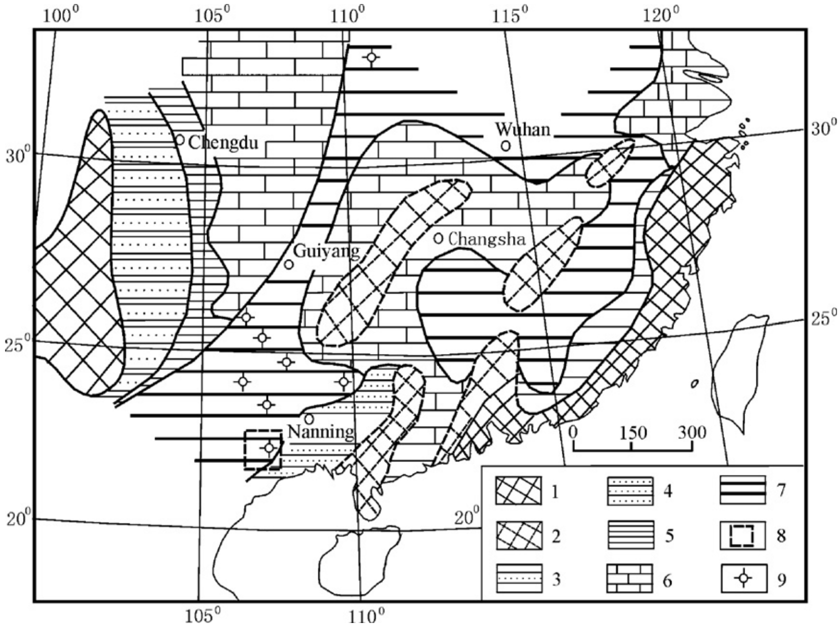


Fig. 1. Changhsingian paleogeography of South China. 1, ancient land; 2, rise under sea surface; 3, continental facies strata; 4, detrital deposits in shallow marine; 5, littoral detrital deposits; 6, carbonate formed in shallow marine setting; 7, deep-water siliceous-muddy strata; 8, studied area; 9, locality of radiolarians.

about 80% of radiolarian taxa became extinct by the end-Permian and that some Paleozoic taxa have been observed to survive into the Mesozoic (Kozur and Mostler, 1982; Sashida, 1983; Baumgartner, 1984; Yeh, 1987; Vishnevskaya, 1997; Sugiyama, 1997; Yao and Kuwahara, 1997; Kozur, 1998; Sashida et al., 1998; Feng et al., 2001). At present, however, we still know little about the detailed process of the radiolarian extinction and progenitor taxa of the Triassic radiolarian faunas.

In recent years, we have been engaged in stratigraphic studies of deep-sea sediments and radiolarian faunas in south and southwest China (Fig. 1). This study aims to investigate extinction of Permian radiolarian faunas bed by bed and to research the evolutionary relationship between the Changhsingian and Triassic radiolarian faunas. As a consequence, we have found some Mesozoic-type progenitors and evolutionary processes of the Upper Changhsingian Radiolaria. In this paper we report these results, and also discuss the evolutionary pattern of the fauna.

2. Geological setting and stratigraphy

Marine Permian–Triassic sequences are regarded as continuous in many sections in South China (Yang et al., 1987). The uppermost Permian Changhsingian varies in lithology in response to various effects of regional basement movement, and can be subdivided into two types, namely deep-water and shallow-water types (Fig. 1). The deep-water type Changhsingian, the Dalong Formation and its equivalent strata, was deposited in slope to basin environments of intraplatform troughs. Exposures of the Dalong Formation containing well-preserved radiolarian faunas have been reported from Guangxi, Guizhou, and Sichuan provinces, southwest China (Feng et al., 2000; Feng and Gu, 2002). The radiolarian fauna from the Dalong Formation in Liuqiao area, southern Guangxi (Fig. 1), has been studied bed by bed and this radiolarian faunal succession has offered important information on the evolution of the Upper Changhsingian radiolarian fauna.

The Dalong Formation in the Liuqiao area is divided into three units (Fig. 2). Unit 1, conformally overlies the Upper Permian limestone with siliceous concretion, and consists of bedded cherts, shales and mudstones. Unit 2 comprises mudstones, chert and silty mudstones with calciturbidite interbeds. Unit 3 is divided into 12 beds. The lower part of the unit (Bed 2–Bed 5) is mainly composed of bedded siliceous rocks, muddy siliceous rocks, and mudstones, yielding abundant radiolarians, foraminiferas, ostracods, and a few ammonites and brachiopods. Bed 6 is claystones with thin bedded siliceous rock interbeds bearing a few radiolarians. The claystones contain some minerals formed in high temperature, such

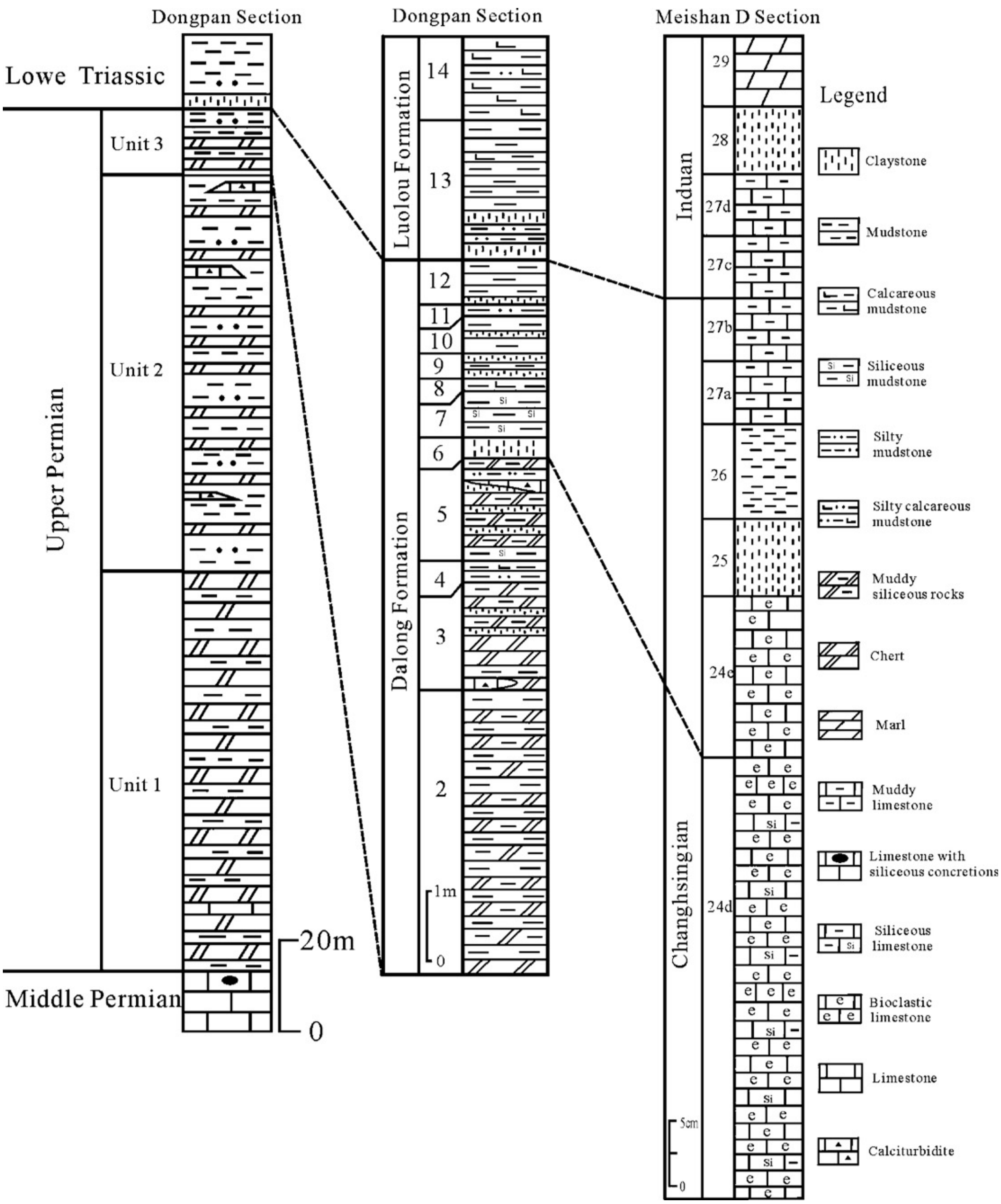


Fig. 2. Upper Permian sequence in the Liuqiao area, southern Guangxi.

as hexagonal bipyramidal quartz, apatite and zircon, which originated from volcanic tuff. Bed 7 is characterized by siliceous mudstones containing abundant radiolarians, brachiopods, and a few ammonites. The brachiopod fauna is characterized by small, thin-shelled individuals, with low diversity, and includes antitropical genus — *Costatumulus*, which indicates a deep-sea environment (He et al., 2005). The upper part (Bed 8–Bed 12) consists of mudstones and silty mudstones with thin intercalations of claystones. The top of Bed 12 contains Changhsingian ammonoids *Huananoceras* cf. *perornatum* Chao et Liang, *Laibinoceras* cf. *compressum* Yang, *Qianjiangoceras* sp. and Upper Permian bivalves *Euchondria jingxianensis* Gu et Liu, *Nuculopsis* cf. *yangtzeensis* (Frech), *Claraia liuqiaoensis* n. sp. Bed 13, a basal part of the Luolou Formation, is dominated by mudstones and silty mudstones with thin claystones. A few Triassic ammonoids *Ophiceras* sp., *Ophiceras tingi* Tien, bivalve *Claraia dieneri* Nakazawa are obtained from the base of Bed 13. According to the distribution of the bivalves and ammonoids, the Permian–Triassic Boundary in this section should be located between Bed 12 and Bed 13 (Fig. 2).

In the Dongpan Section, the radiolarian fauna from the lower part of the unit 3 is characterized by abundant *Neoalbaillella optima*, *Albaillella triangularis* and *Albaillella yaoi*, and it corresponds to the *A. yaoi* zone (Xia et al., 2004). According to investigations on conodonts and radiolarians in the Ubara Section, Southwest Japan the *A. yaoi* zone could be correlated with the *Clarkina changxingensis–C. postsubcarinata–C. postwangi–C. deflecta* assemblage zone of the Meishan Section (Xia et al., 2004). The top of this assemblage zone locates at the top of 24d in the Meishan Section (Mei et al., 1998). Therefore, the top limit of Bed 5 in the Dongpan Section should be correlated with the upper limit of Bed 24d in the Meishan Section D (Fig. 2).

3. Methods and material

Seventy-two samples were collected from Unit 3 of the Dongpan Section. The hydrofluoric acid (HF) technique (Pessagno and Newport, 1972) was utilized to extract radiolarian tests. The samples were placed in dilute hydrofluoric acid (about 3%) for eight hours, and then the waste liquid was removed. The waste liquid and muddy residue were collected separately. After

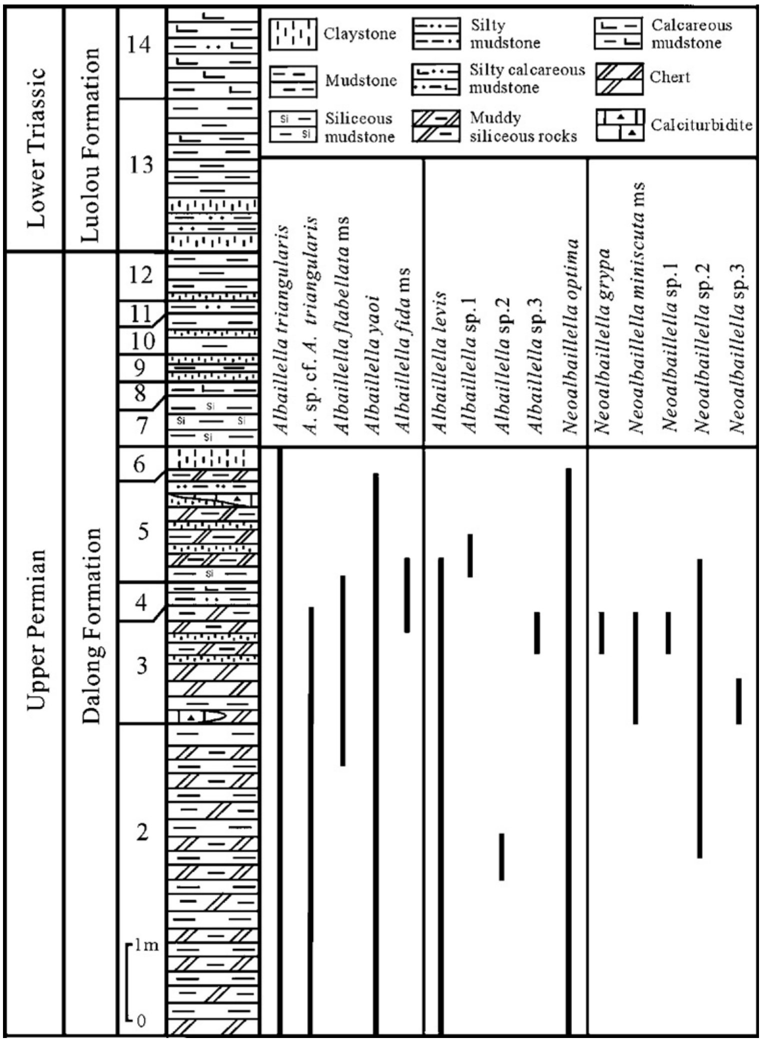


Fig. 3. Distribution of Order Albaillellaria from the Upper Changhsingian of Dongpan section in the Liuqiao area.

repetition of this process for two weeks, the residues were sieved (0.054 mm) and dried. Radiolarians were picked up from the dry resides with a fine brush under a stereoscopic microscope and preliminarily determined. The best-preserved specimens were later mounted on stubs and photographed with a scanning electronic microscope (SEM) for more precise determination. For this study, about 9000 radiolarian specimens were

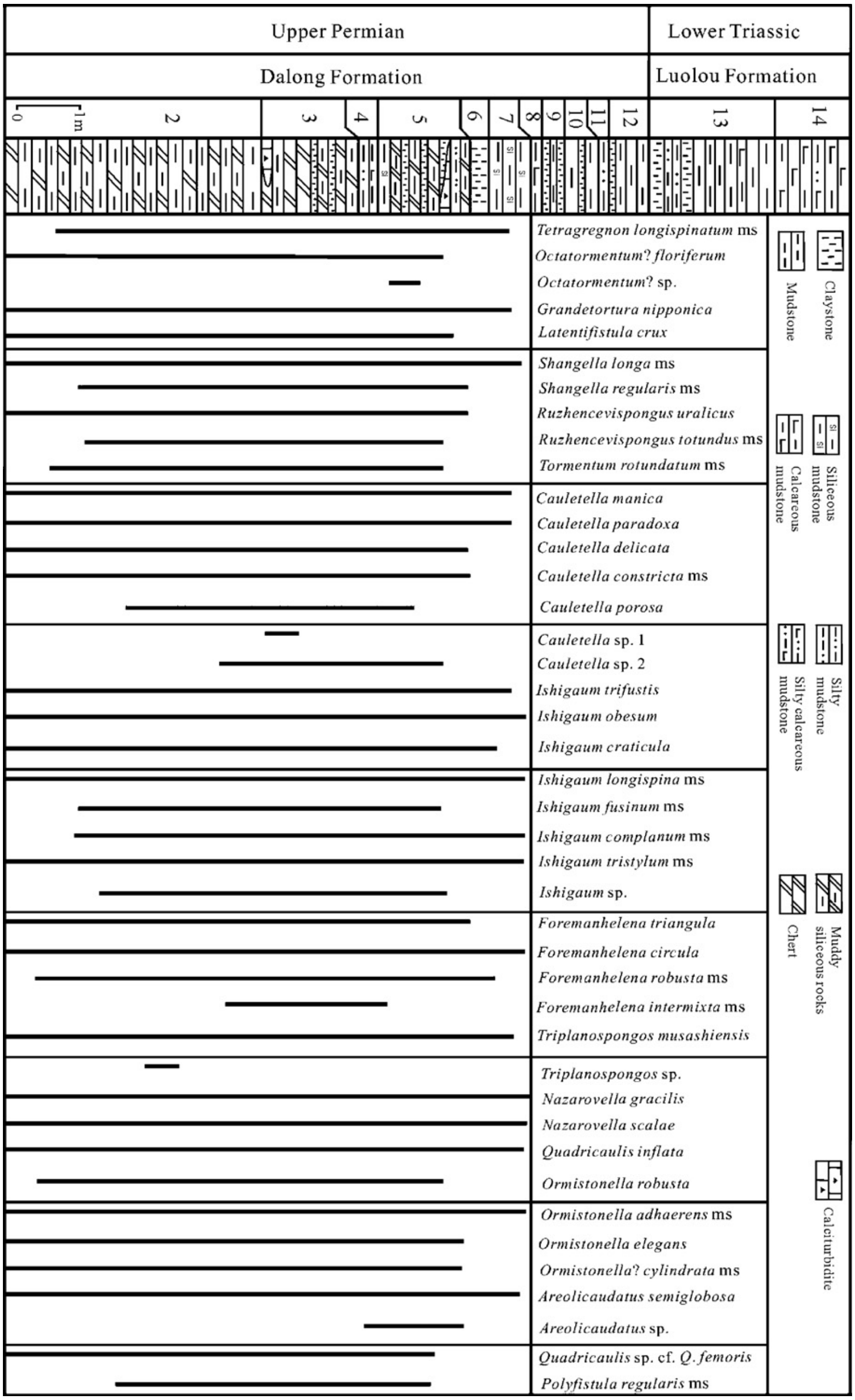


Fig. 4. Distribution of Order Latentifistularia from the Upper Changhsingian of Dongpan section in the Liuqiao area.

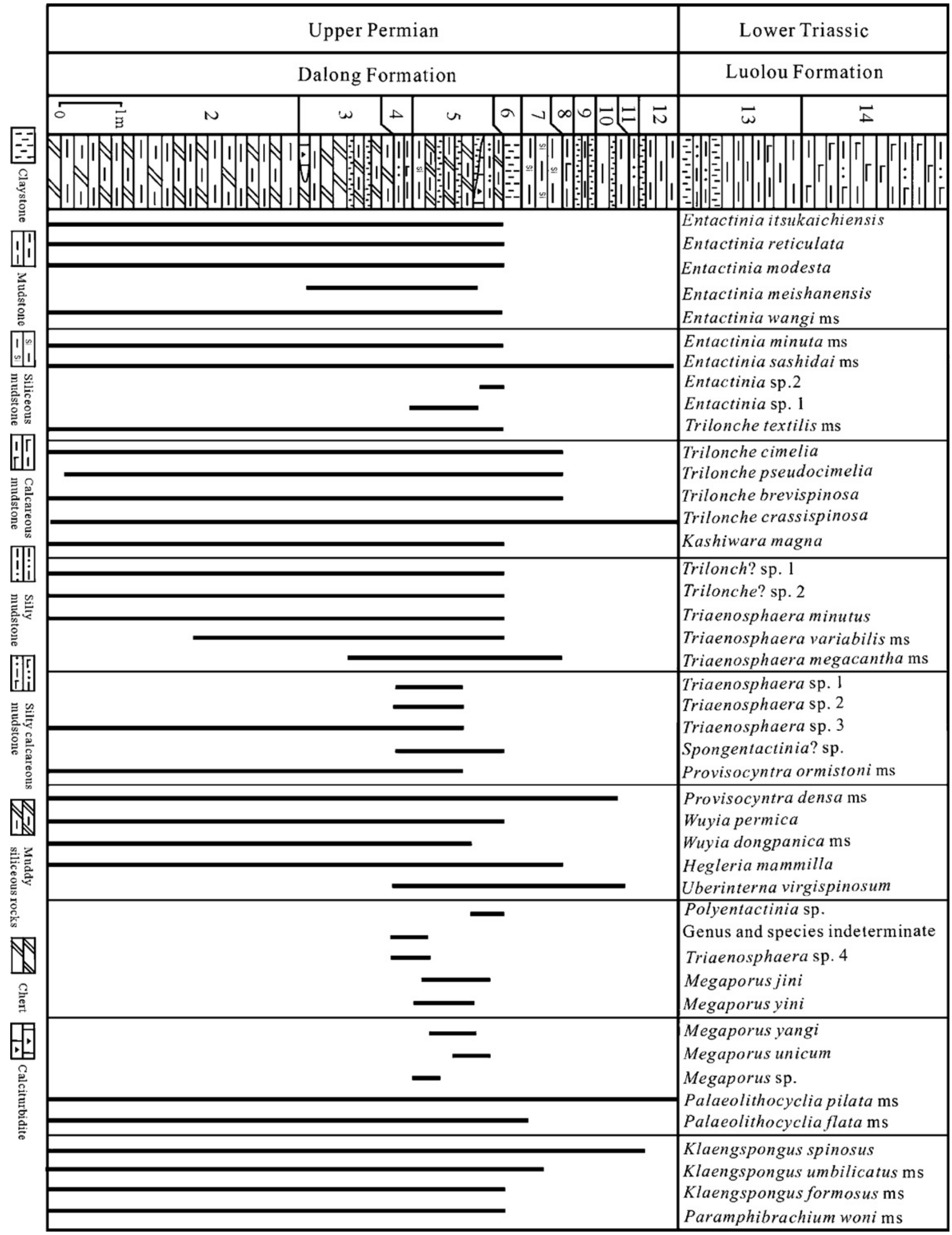


Fig. 5. Distribution of Order Entactinaria from the Upper Changhsingian of Dongpan section in the Liuqiao area.

obtained and over 2000 specimens photographed with a SEM. 137 species, belonging to Albaillellaria, Entactinaria, Spumellaria and Latentifistularia were identified and described (Feng et al., 2004, 2006a,b, in press-a,b; Jin et al., in press). Their distributions in these samples are presented in Figs. 3–6.

4. Analyses and results

4.1. Late Changhsingian radiolarian radiation

The evolutionary pattern of the Paleozoic radiolarian assemblages can be divided into a number of distinct periods, or ‘megacycles’. The Changhsingian is the last bloom of the Paleozoic radiolarians and this prosperous phase is characterized by an acme in diversity and abundance of the orders Latentifistularia and Entactinaria, and by the occurrence of the Mesozoic-type taxa.

Our detailed investigation of the Dongpan Section, South China shows that the Upper Changhsingian Radiolaria, including four known orders—Entactinaria, Spumellaria, Latentifistularia and Albaillellaria, enjoyed a high diversity. 137 species belonging to 50 genera are identified. The Order Albaillellaria had the lowest diversity, including 2 genera, *Albaillella* and *Neoalbaillella*, and 15 species and indeterminate species (Fig. 3). 7 of the 15 species were discovered only in the Upper Changhsingian of South and Southwest China, Thailand, and Japan (Yao and Kuwahara, 1997; Feng et al., 1998; Sashida et al., 2000a,b).

The Upper Changhsingian is the most prosperous stage for the Order Latentifistularia in terms of their diversity. 16 genera including 42 species are identified in the Dongpan Section (Fig. 4). About two-thirds of the 42 species were found only in the Upper Changhsingian,

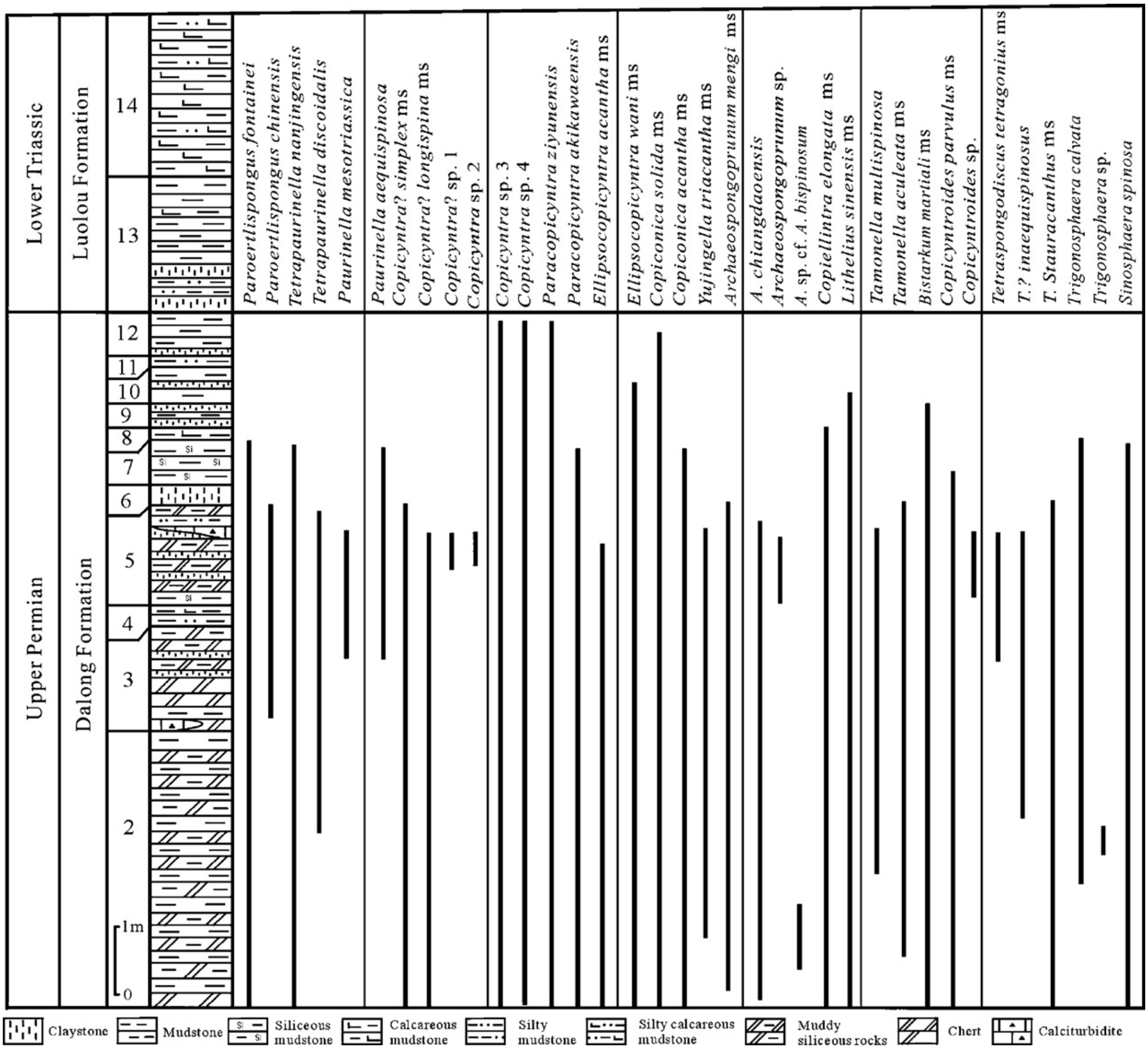
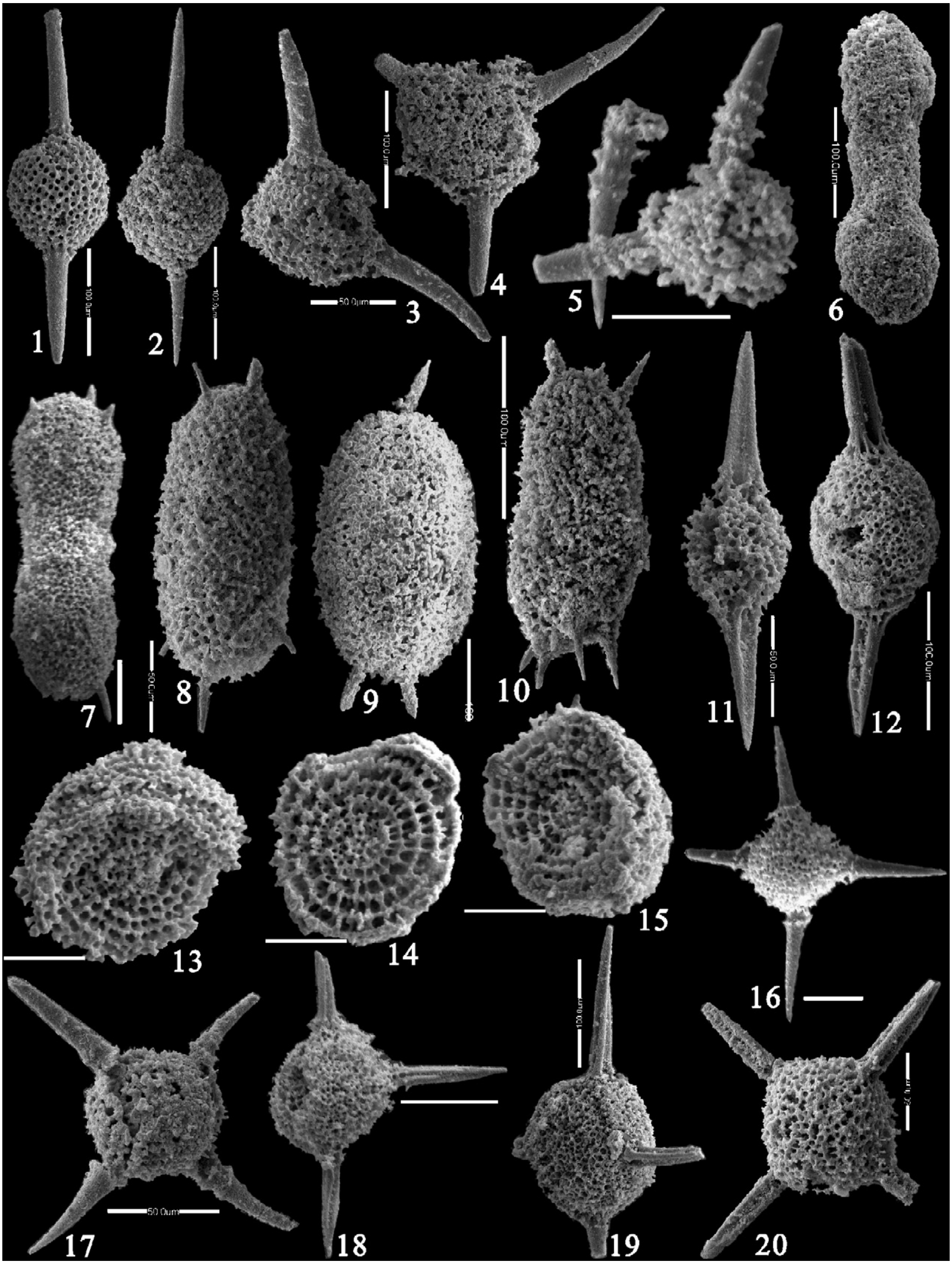


Fig. 6. Distribution of Order Spumellaria from the Upper Changhsingian of Dongpan section in the Liuqiao area.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but most of the 16 genera have been reported from older strata. Some species are highly specialization in their morphology, such as *Tormentum rotundatum*, *Cauletella paradoxa*, *Foremanhelena circula*, *Ormistonella adhaerens*, and *Ormistonella*? *cylindrata*. Therefore, the bloom of the Order Latentifistularia in the Upper Changhsingian is characterized by a highly diversified fauna at species level.

In the Order Entactinaria, 44 species belonging to 15 genera are identified. This order is similar to the Order Latentifistularia in composition (Fig. 5): about two-thirds of those species are restricted to the Upper Changhsingian, but only 20% of the genera are known from the Dalong Formation and corresponding strata. Some genera, such as *Entactinia*, *Entactinosphaera* and *Triaenosphaera*, exhibit high diversity at species level, including 6 to 9 species, which is rare amongst Paleozoic faunas. New genera highly resemble some Mesozoic genera in outline, but their inner structures may put them into the Order Entactinaria. For example, *Megaporus* is very similar to some genera of subfamily Pantanelliinae Pessagno in morphology (Feng et al., in press-a), and *Klaengspongus* Sashida is similar to *Orbiculiforma* Pessagno in morphology (Feng et al., 2000; Sashida et al., 2000b; Feng and Gu, 2002).

The Order Spumellaria is different from the three orders above-mentioned in composition. 36 species belonging to 17 genera of the order are identified in the Dongpan Section (Fig. 6). Two-thirds of the genera and about 90% of species are new or were discovered from the Mesozoic strata. Typical Mesozoic genera include *Paroertlispongus* Kozur and Mostler, *Tetrapaurinella* Kozur and Mostler, *Paurinella* Kozur and Mostler, *Archaeospongoprunum* Pessagno, *Tamonella* Dumitrica, Kozur and Mostler, *Bistarkum* Yeh, and *Tetraspongodiscus* Kozur and Mostler, and *Lithelius* Haeckel (Fig. 7). Some new genera and species have exotic-looking skeletons. For example, *Copiconica* is coniform in outline and *Bistarkum martiali* is characterized by a zonary spongy test with or without a middle constriction.

In summary, the Upper Changhsingian is the last prosperous phase of the Paleozoic radiolarian assemblages. The high diversity at species level and the occurrence of typical Mesozoic taxa are characteristic features of this radiation interval. Some new genera and species have highly specialized morphologies.

4.2. Late Changhsingian radiolarian extinction

After the Upper Changhsingian radiation interval, the radiolarian fauna experienced a rapid extinction in the latest Changxingian. The extinction was a stepwise process and included two episodes of biotic crisis (Figs. 8 and 9).

First crisis took place at the top of Bed 5 where 53% species and 22% genera of the diversified radiolarian fauna became extinct. Only one species of the Order Albaillellaria extends to the upper part of Bed 6. Half of all the species died out amongst the Order Spumellaria and Latentifistula. About 64% of species vanished in the Order Entactinaria. Extinct species of the Orders Spumellaria and Entactinaria are characterized by having long outer spines. Disappearance at genus level is obviously less than that at species level. The Orders Spumellaria, Entactinaria and Latentifistularia lost 1, 3 and 5 genera, respectively. Therefore, the first extinction is characterized by a main extinction at species level. Most of the surviving genera contain only one species after the first crisis.

In the Dongpan Section, the radiolarian crisis is accompanied by sharp extinctions of foraminifers and ostracods at genus and species levels.

A second crisis is shown near the boundary between Beds 7 and 8 in the Dongpan Section. In the second extinction, 25% of species and 35% of genera disappear. For the Order Latentifistularia, about two-thirds of the genera and nearly one half of the species vanish in the crisis. The Order Entactinaria sees 7 species and 3 genera dying out and in the Order Spumellaria 8 species and 3 genera disappear. It is a characteristic feature of the second extinction that disappearance at genus level is greater than that at species level.

After the second crisis, the radiolarian fauna still had an elevated extinction rate in Beds 8, 9 and 10. This phenomenon can also be found amongst foraminifer and ostracod faunas. Most of the radiolarian genera found in Beds 11 and 12 had been reported from the Triassic (Kozur et al., 1996; Sashida et al., 1998; Feng et al., 2001; Kamata et al., 2003, 2005), which indicates that Beds 11 and 12 belong to the survival interval of the radiolarian fauna.

4.3. Late Changhsingian radiolarian survival

According to previously published data and our unpublished data, the Order Albaillellaria possibly vanished

Fig. 7. The Mesozoic-type progenitors from the Upper Changhsingian in southern Guangxi, China (scale bar is 50 μm in Figs. 3, 7–9, 11, 13–17; 100 μm in Figs. 1, 2, 4–6, 10–12, 18–20). 1–2, *Paroertlispongus chinensis* (Feng); 3–5, *Paurinella mesotriassica* Kozur and Mostler; 6–7, *Bistarkum* martiali Feng; 8–10, *Tamonella multispinosa* Dumitrica, Kozur and Mostler; 11–12, *Archaeospongoprunum chiangdaoensis* (Sashida); 13–15, *Lithelius sinensis* Feng; 16–17, *Tetrapaurinella discoidalis* Kozur and Mostler; 18–20, *Tetraspongodiscus*? *inaequispinosus* (Kozur and Mostler).

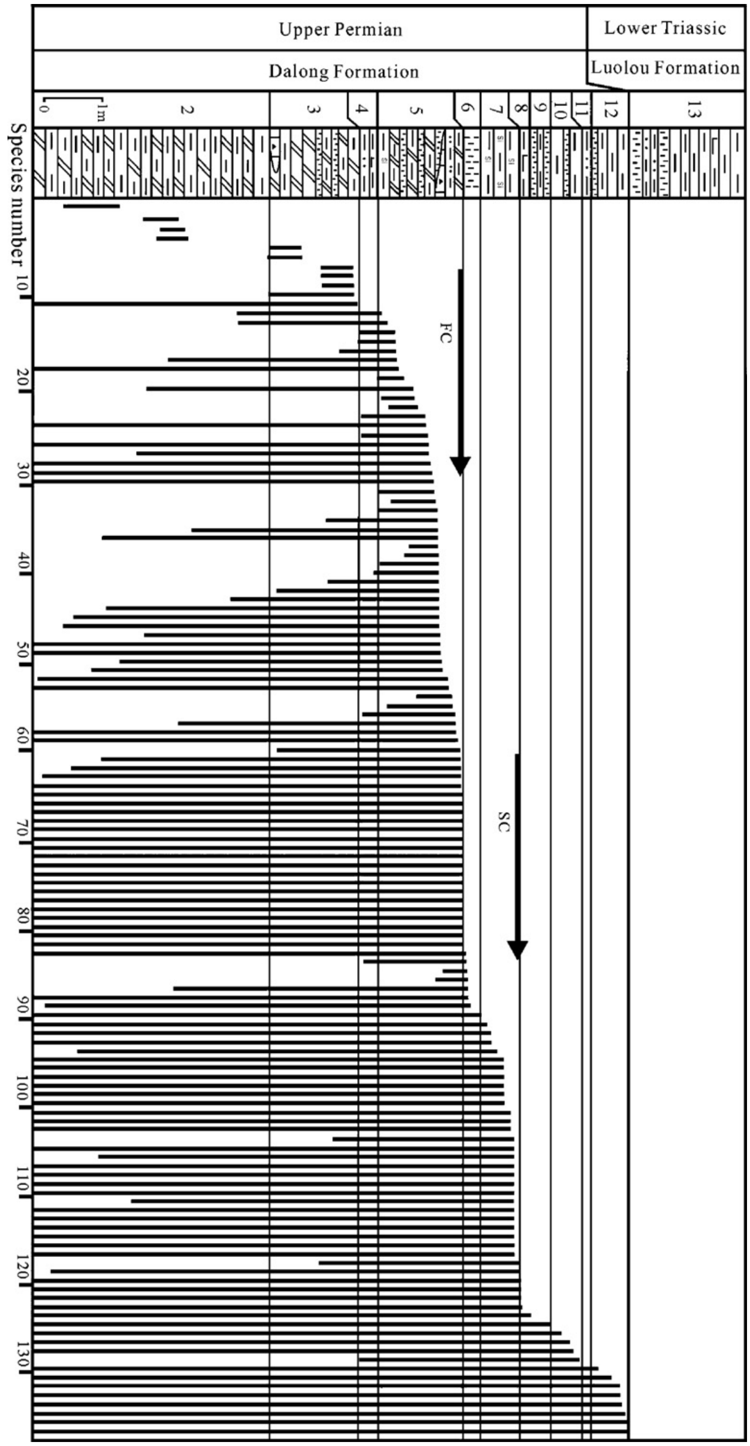

Fig. 8. Stratigraphic ranges of the radiolarian species from the Upper Changhsingian of Dongpan section in the Liuqiao area (FC: first crisis; SC: second crisis).

at the end-Permian and a very small number of the Permian genera of other three orders extended to the Triassic (Figs. 10 and 11). Most of these genera, such as *Ishigaum*, *Hegleria*, *Uberinterna*, *Polyentactinia*, *Copicyntra*, have been never discovered in the lower Lower Triassic, but were reported only from the upper Lower Triassic (Kozur et al., 1996; Sashida et al., 1998; Feng et al., 2001; Kamata et al., 2003, 2005), which are considered as a Larazus taxa

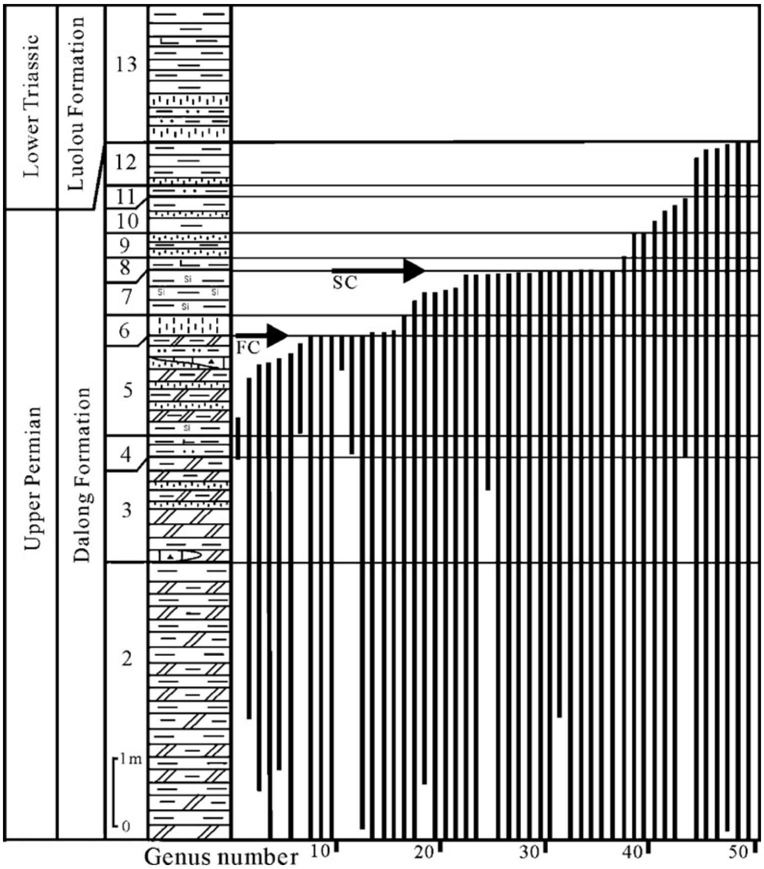

Fig. 9. Stratigraphic ranges of the radiolarian genera from the Upper Changhsingian of Dongpan section in the Liuqiao area (FC: first crisis; SC: second crisis).

(Kauffman and Erwin, 1995). Two genera, *Trilonche* and *Entactinia*, survived to the Jurassic (Kozur and Mostler, 1982; Yeh, 1987; Vishnevskaya, 1997; Feng et al., 2001). Therefore, some radiolarian paleontologists thought that there are no directive relations between the Mesozoic and Permian Spumellaria in evolution and that the former possibly comes from the simple spherical radiolarians, rather than the Permian complex radiolarians (Jones, 1991).

As stated above, however, eight typical Middle Triassic spumellarian genera, *Paroertlispongus* Kozur and Mostler, *Tetrapaurinella* Kozur and Mostler, *Paurinella* Kozur and Mostler, *Lithelius* Haeckel, *Archaeospongoprunum* Pessagno, *Tamonella* Dumitrica, Kozur and Mostler, *Bistarkum* Yeh, and *Tetraspongodiscus* Kozur and Mostler, are discovered from the Upper Changhsingian in southern Guangxi. The eight genera belong to seven families and a subfamily of the Order Spumellaria, including Oertlispongidae Kozur and Mostler, Pyramispongiidae Kozur and Mostler, Litheliidae Haeckel, Archaeospongoprunidae Pessagno, Tamonellinae Kozur and Mostler, Angulobrachiidae Baumgartner, and Relindellidae Kozur and Mostler. These families and subfamily are the most important and characteristic spumellarian families in the Middle Triassic fauna. Therefore, these genera play a very important role in the radiation of the Middle to Late Triassic Spumellaria. The characteristic features of the eight genera are as follows: (1) smaller test, (2) most genera have columniform external spines or very short three-bladed spines.

According to the results mentioned above, the evolution of the Upper Changhsingian radiolarian fauna from southern Guangxi can be divided into radiation, extinction and survival intervals. In the Dongpan Section, the radiation interval is located between 10.28–2.68 m below the PTB, the extinction interval, 2.68–0.77 m below the PTB, and the survival Interval extends from 0.77 m below the PTB to the lowermost Triassic.

5. Discussion and conclusions

5.1. Dynamics of morphological diversification and evolution

On the eve of the Upper Changxingian radiolarian mass extinction there was a bloom in morphological

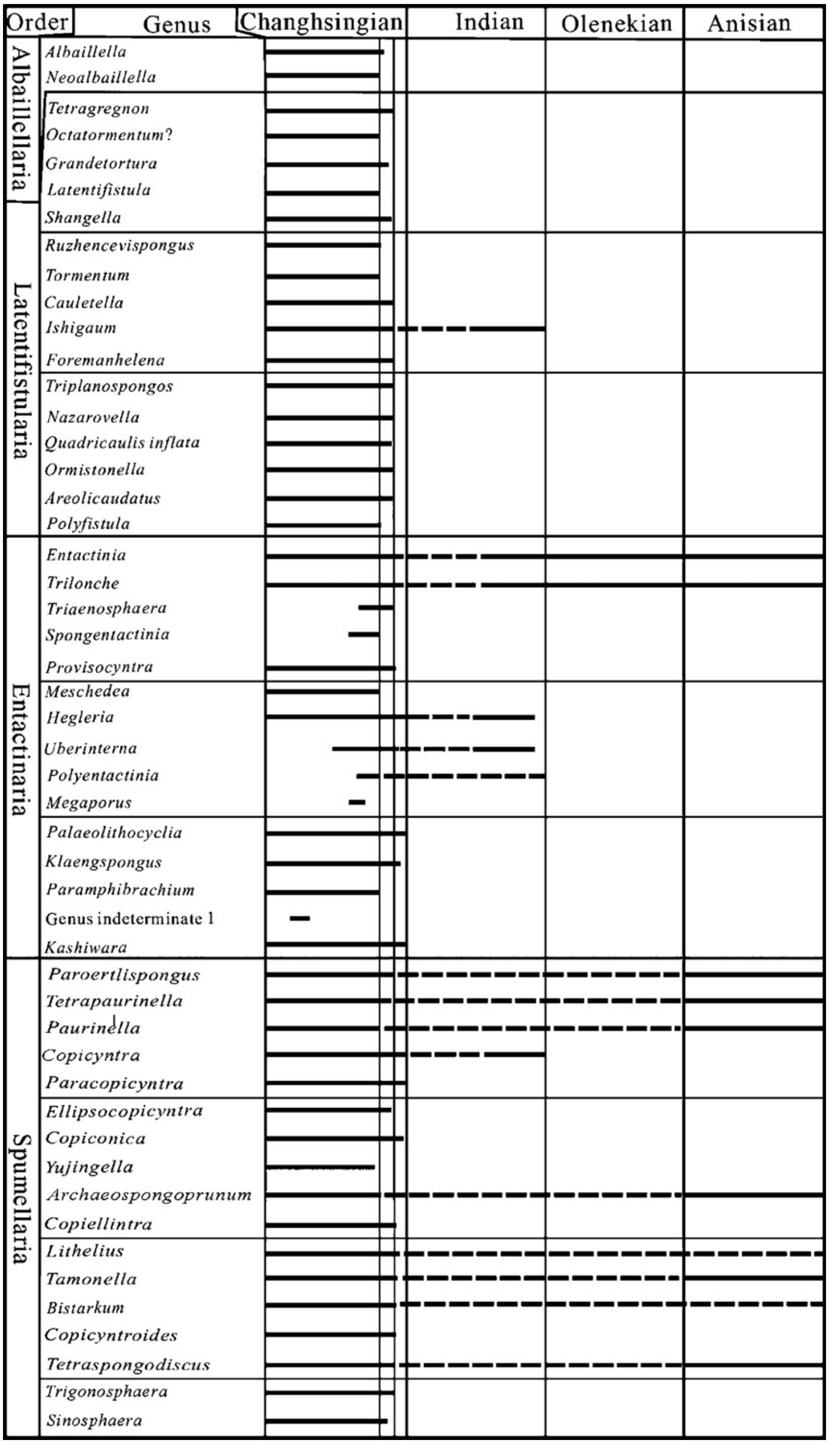

Fig. 10. Stratigraphic ranges of the radiolarian genera from the Upper Changhsingian of the Dongpan section during Changhsingian–Anisian (their Triassic distributions are after Kozur et al., 1996; Sashida et al., 1998; Feng et al., 2001; Kamata et al., 2003, 2005).

diversity corresponding to a rapid evolutionary stage. Many highly specialized tests formed besides normally shaped tests. Many new species and genera appeared, including many Paleozoic-type taxa and some Mesozoic-type progenitors. A great degree of morphological variation prior to mass extinction has also been reported

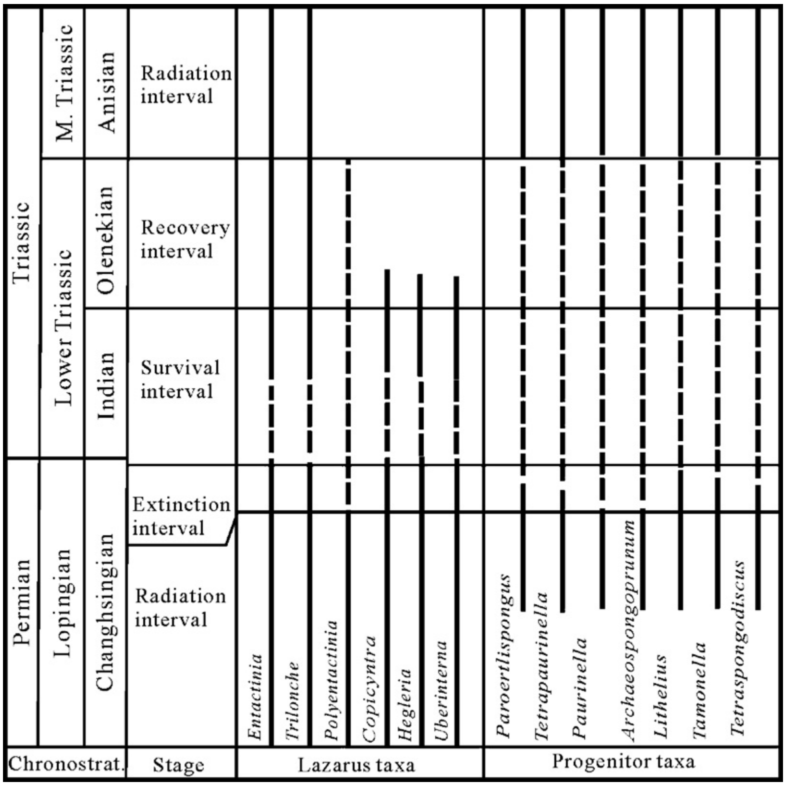

Fig. 11. Evolutionary stages of the Lazarus and progenitor taxa from the Upper Changhsingian of the Dongpan section.

from the Permian–Triassic interval in other fossil groups (Korchagin, 1995; Scubert and Bottjer, 1995). Exotic-looking skeletons and the maximum morphological diversity may have been caused by environment stress, such as an anoxia event, tectonic activity, extensive volcanism or other geological events (Vishnevskaya, 1997). The maximum taxonomic diversity is explained as an attempt to accommodate changing environments (Leleshus, 1994). The more accommodating forms survived in order to give rise to new trends and provide evolutionary progress (Vishnevskaya, 1997). With rapid speciogenesis many short-lived species and some species adapting a catastrophic environment came into being. The latter includes the Mesozoic-type progenitors and the Paleozoic-type survivors and they facilitate some new evolutionary branches of the Triassic Radiolaria.

5.2. Process of the main extinction

For the Upper Changhsingian radiolarian fauna from southern Guangxi, the extinction interval started from the first crisis located at the top of Bed 5 and ended near the boundary between Beds 10 and 11. The extinction progress was short, stepwise and consists of two episodes of biotic crisis. The first crisis brought two prominent results: (1) the radiolarian population density abruptly decreased. The evidence is not only that the content of each species was obviously reduced from Beds 5 to 7, but also that the lithology of the strata suddenly change from bedded chert in Bed 5 to siliceous mudstone in Bed 7, which indicates a rapid reduction of productivity of siliceous organism, especially radiolarians. (2) The major community was destroyed. Before the crisis, about 70% genera of this fauna had more than 2 species and some genera contained 7–9 species. After the crisis, 22% of genera in this fauna disappeared and 51% of genera had only one species. The foraminifer and ostracods diversities show synchronous sharp reductions at genus and species levels. In the second crisis, disappearances of some species induced extinction of some related genera because many genera only contained one species. In Beds 11, 12 and the base of the Lower Triassic, few radiolarians were observed. These radiolarians are characterized by smaller, simple forms lacking any external spines and they belong to the Paleozoic-type survivors. The Mesozoic-type progenitors have never been discovered in these strata. This stage is considered as the survival interval. In the interval, the radiolarian diversity is unusually low and there is no bloom of disaster taxa. These features in the survival interval are also reported in other radiolarian faunas from the Permian–Triassic boundary interval (Feng et al., 1998, 2000; Feng and Gu, 2002).

On the whole, the process of the main extinction can be divided into two stages. In the first stage, the scale of the community rapidly declined and the radiolarian population density rapidly diminished. In the second stage, many higher taxonomic levels, such as genus and family, disappeared, causing deep-sea ecosystem collapse.

5.3. Correlation with other sections

Yang et al. (1993, Table 1-1) stated a 3-phases mass extinction at the PTB in South China. The three delineations are, in ascending order: 1. line of important biotic extinction (i.e. between Beds 24d and 24e at Meishan); 2. base of the Transitional Bed (i.e. between Beds 24 and 25); and 3. top of the Transitional Bed (i.e. between Beds 27 and 28). Wignall and Hallam (1993) reported that there were three biotic crises during the Permian–Triassic transition stage in the Meishan Section: between Beds 24d and 24e, Beds 24 and 25, Beds 27 and 28. Yin and Zhang (1996), however, thought that the three biotic crises near the Permian–Triassic Boundary in the Meishan Section took place between Beds 24d and 24e, Beds 26 and 27 and the top of 28, respectively. All these three opinions agree that the first extinction event coincides with the line between Beds 24d and 24e at Meishan.

The first radiolarian crisis in the Dongpan Section can well be corresponded to the biotic crisis located at the top of 24d because the top of Bed 5 in the Dongpan Section can be biostratigraphically correlated with the top of 24d in the Meishan Section. The second crisis located at the top of Bed 7 maybe correlate to that located at the top of 24e on the basis of isotopic stratigraphy correlation and event sequences. In the Ubara and Gujo-hachiman sections, southwest Japan, two typical pelagic sections, there is also an obvious radiolarian extinction at the top of the *A. yaoi* zone (Xia et al., 2004). This extinction can be correlated with the first radiolarian crisis in the Dongpan Section.

In conclusion, during the Upper Changhsingian two biotic crises can be well correlated among some Permian–Triassic boundary sections containing different sedimentary facies.

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