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Extinction pattern of reef ecosystems in latest Permian

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Studies of two Permian-Triassic boundary (PTB) sections on top of a Changhsingian reef in Ziyun, Guizhou Province, southwestern China indicate that the end-Permian mass extinction of reef ecosystems occurred in two steps. The first step is the extinction of all stenotropic organisms such as calcisponges and fusulinids in the latest Permian (in the *Clarkina yini* conodont zone). The biota after the first extinction is simple, comprising eurytropic organisms including microgastropods, ostracods, and some small burrowing organisms, or only algal mats. At the beginning of the Early Triassic (i.e. the beginning of the *Hindeodus parvus* zone), the environments became anoxic, and the microgastropod dominated biota or algal mats disappeared, which constituted the second episode of the mass extinction. The biota after the second extinction comprises small spherical microproblematica, some kinds of specialized organisms tolerant of anoxic or oxygen-poor conditions. As the environments became oxygenated, the specialized biota was replaced by a microgastropod-dominated simple biota. When the environmental conditions improved further, the simple biota was replaced by a diverse biota with normal-sized ammonoids, bivalves, and gastropods, representing restoration of normal oceanic conditions. Comparison with PTB sections in Dolomites, Italy and Meishan, Zhejiang Province shows that non-reef ecosystems had a similar first episode of mass extinction in the latest Permian. In the case that oceanic anoxia happened, non-reef ecosystems had a second extinction episode similar to that of reef ecosystems.

end-Permian, reef, mass extinction, Guizhou, Permian-Triassic boundary

The largest mass extinction in the Phanerozoic occurred in the latest Permian[1]. It killed more than 90% of marine species[2,3], 70% of terrestrial vertebrate genera[4], most terrestrial plants[5,6], and all reef ecosystems[7,8].

Studies of extinction pattern began with non-reef marine ecosystems and terrestrial biota. Early studies were conducted at such resolution as stratigraphic unit stage[9]. Biotic composition of latest Permian Changhsingian was compared to that of lowest Triassic Griesbachian to look for evolutionary messages. The progress in conodont biostratigraphy in the 1990s brought about higher resolution in studies of P-T boundary strata. In the GSSP section of the PTB in Meishan, Zhejiang Province, the 0.5 m interval from the top of Changhsingian to the bottom of Griesbachian was divided into four conodont zones[10]: *Clarkina yini*, *C. meishanensis*, *Hindeodus typicalis*, and *H. parvus* zones. This provides a high-resolution biostratigraphic framework for more detailed study of P-T boundary strata, as well as pattern of the mass extinction.

With the high-resolution conodont timing framework, Jin et al.[11] systematically surveyed the species and genera in Meishan and the nearby PTB sections, and found that the mass extinction comprised one sudden event at 251.4 Ma and the gradual decline in generic and specific numbers in the following one Ma. Studies on biomarkers[12] concluded that the mass extinction included more than one episode. Wang et al.[13] found that

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one bed had higher content of biomarker related to some planktons and some special organisms. Discovery of microbial deposits in the reef-related PTB sections in Chongqing, Hubei, Guizhou, and Guangxi provinces[14－18] indicates that the post-extinction oceanic conditions are unusual.

Contrary to conspicuous progresses in study of extinction pattern of non-reef ecosystems, progress in study of extinction pattern of reef ecosystems was slow. One might ask whether the extinction of reef ecosystems in latest Permian happened in one step or several steps? Did the extinction of reef ecosystems happen before, or after, or at the same time as non-reef ecosystems? In this paper, two PTB sections on top of a typical Upper Permian Changhsingian reef in Ziyun, Guizhou Province (Figure 1), at Gendan and Tanluzhai, were examined in detail, with focus on biotic evolution.

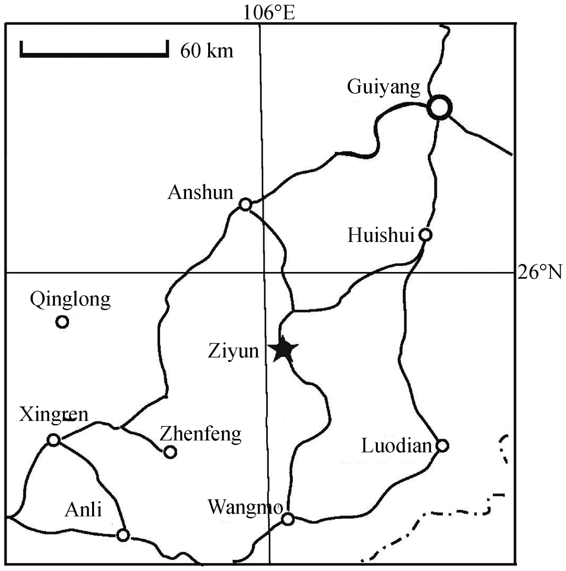

Figure 1 Location of the PTB sections in Ziyun.

1 Extinction pattern of the reef ecosystem at Gendan, Ziyun in latest Permian

1.1 Petrology of the section

The Gendan section, 2 km south of Ziyun town, is divided lithologically into five beds (Figure 2(a)). The basal Bed 1 is a reef limestone, containing a diverse biota composed of calcareous sponges, bryozoans, echinoderms, fusulinids, brachiopods, bivalves, gastropods, foraminifers and algae (Figure 3(a)). Mud cracks are present in top of this bed[19].

Bed 2 is 2.4 m thick yellow, laminated dolomitic mudstone, with algal laminar structure and various mud cracks (Figure 3(b)). No other fossils are present.

Bed 3 is 0.2 m thick black, dolomitic mudstone, with flat laminar structure. Examination under ESM found tiny (<5 μm), scattered pyrite framboids. The top 2 mm of this bed consists of irregular pyrite aggregation. Pyrite crystals are generally cubic in form. The content of pyrite declines downward from the bed top. This bed contains abundant small (<15 μm) spherical microproblematica (Figure 3(c)), ostracods, and some thin-shelled larger bivalves (up to 1 cm or more). Some spherical microproblematica are elongate in form, and different in size, generally below 0.25 mm in diameter. They were generally filled by microspar. The ostracods are generally complete, and increase in abundance upward (Figure 3(d)).

Bed 4 is 3 mm thick bioclastic packstone (Figure 3(e)). The grains are microgastropods. They are commonly conic in form, generally 1 mm in size, with relatively thick walls. This bed does not contain pyrite, and is light in color.

Bed 5 is 0.4 m thick grainstone. The grains are normal-sized (1－2 cm) ammonoid and bivalves shells. The rock is generally reddish or brownish in color.

1.2 Biostratigraphy

The conodont *Clarkina parasubcarinata* (Mei et al., 1998) (Figure 4(a)) is present at 1 m below the top of Bed 1. The holotype of this conodont (Figure 4(b)) was first reported from Beds 24d to 24e of Meishan section[20], and was regarded as an important component of the *Clarkina yini* conodont zone. Mei et al. (1998) described *Clarkina changxingensis yini* (=*Clarkina yini*) from the top of the Bed 21 they named (numbered Mc-41, Mc-43). Yin et al. reported *C. yini* from Beds 24d to 24e of Meishan section (GSSP). So, Mei et al.'s Bed 21 is biostratigraphically equal to Yin et al.'s Beds 24d to 24e. The specimens described by Mei et al. from two beds were figured: those from Bed 14 and those from top of Bed 21. The specimens from the latter were used as holotype of this species, while those from Bed 14 cannot be assigned to this species. Both *Clarkina parasubcarinata* and *Clarkina yini* occurred in the top of Mei et al.'s Bed 21. Occurrence of *Clarkina parasubcarinata* in Bed 1 of Gendan indicates that our Bed 1 is correlative to Beds 24d to 24e of Meishan section. Conodont *Hindeodus parvus* (Figure 4(c)) occurs in Bed 3 of Gendan. It is a worldwide distributed species and its first appearance has been defined as the beginning of the

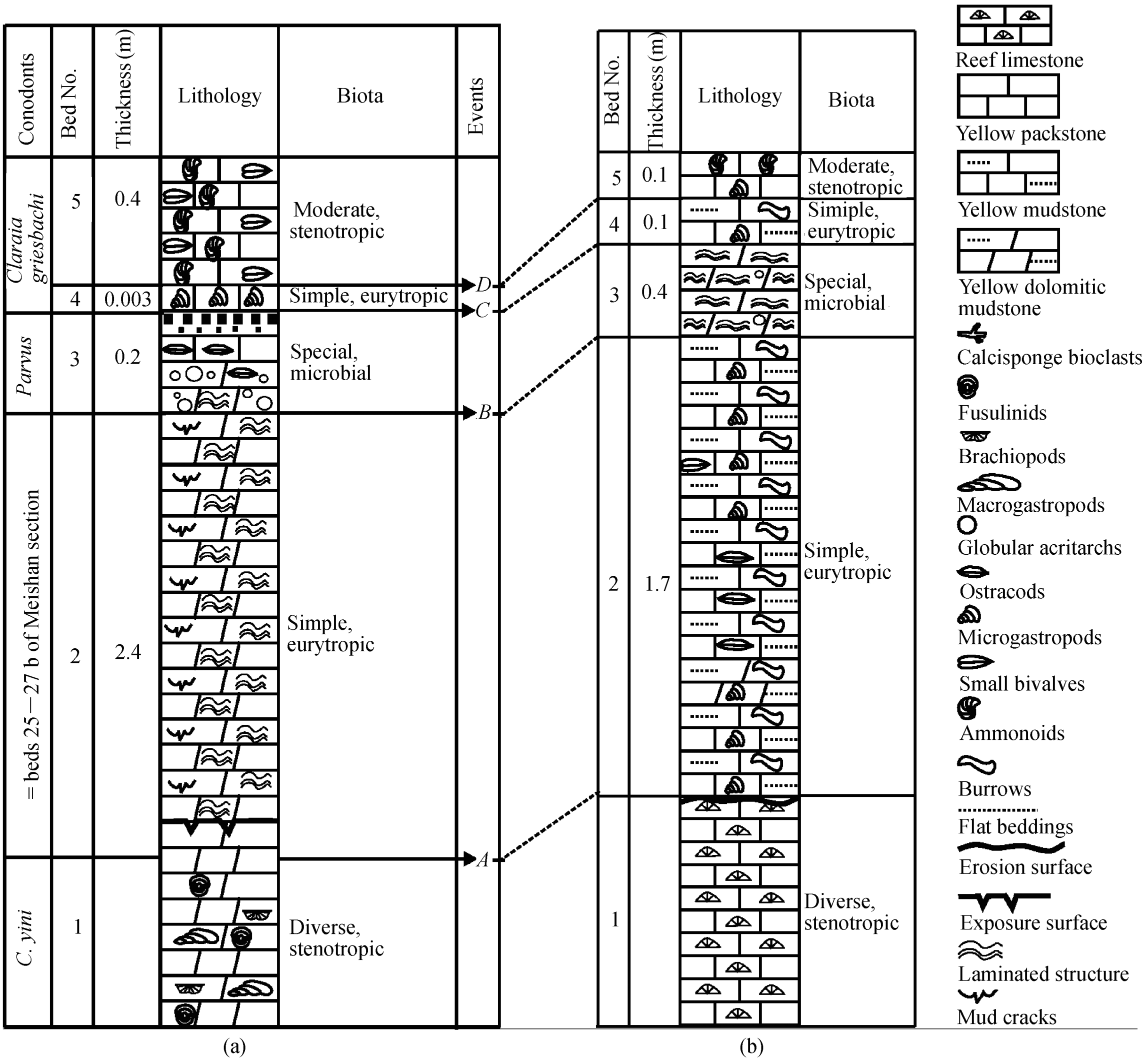

Figure 2 Lithology and biotic evolution in PTB sections at Gendan (a) and Tanluzhai (b) in Ziyun, Guizhou Province, China. Event *A* is extinction of stenotropic organisms (the first episode of mass extinction). Event *B* is extinction of most eurytropic organisms (the second extinction episode). Event *C* is the replacement of specialized biota by simple biota. Event *D* is the replacement of simple biota by diverse marine biota.

Triassic System. Thus, the Permian-Triassic boundary in Gendan section lies between Beds 2 and 3. Bed 3 of Gendan is correlative to Beds 27c to 27d of Meishan section. Consequently, Bed 2 of Gendan is correlative to Beds 25 to 27b of Meishan.

1.3 Sedimentary environmental changes

Bed 1 of Gendan represents reef environments. Bed 2 has algal laminar structure and mud cracks, indicating tidal-flat environments. The flat laminar structure in Bed 3 indicates all absence of bioturbation, burrowing organisms, as well as wave action. Tiny (<8 μm) pyrite framboids have been regarded as indicator of anoxic conditions[21]. Presence of abundant scattered tiny pyrite framboids in Bed 3 indicates oceanic anoxia. Bed 4 is light in color and contains no pyrite, representing oxygenated conditions. Bed 5 is brownish to reddish in color, reflecting oxygenated environments.

1.4 Biotic evolution

The biota of Bed 1 is diverse. The presence of calcisponges and fusulinids indicates that it was a pre-extinction biota. Bed 2 contains a simple algal mat community. The disappearance of calcisponges and fusulinids from Bed 2 indicates that the mass extinction occurred between Beds 1 and 2. The simple biota of Bed 2 disappeared before deposition of Bed 3, which constitutes the second episode of the mass extinction. The biota in Bed 3 is very simple, composed of small spherical microproblematica, some ostracods, and sparse thin-shelled bivalves. The spherical microproblematica may be some kind of bacteria adapted to anoxic condition. The thin-

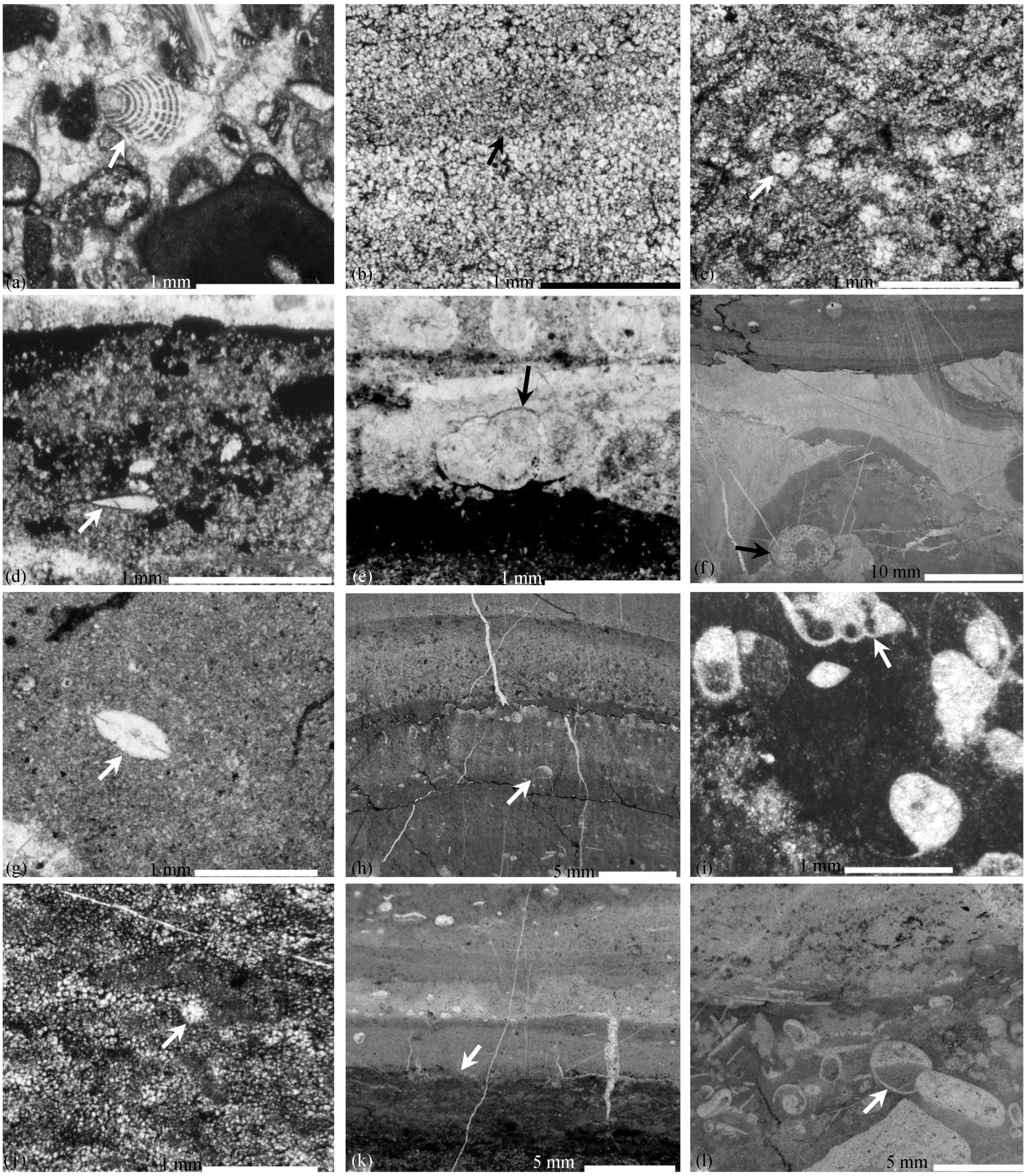

Figure 3 Microphotographs of thin sections from Gendan ((a)—(e)) and Tanluzhai sections ((f)—(l)) showing biotic evolution from diverse ((a), bottom of (f)), to simple ((b), (g), (h), (i)), to specialized ((c), (d), (j), (k)), back to simple (upper of (k)), and finally moderately diverse (l). (a) Bed 1, arrow to *Colaniella*; (b) Bed 2, showing algal laminar structure; (c) Bed 3, showing small spherical microproblematica; (d) top of Bed 3, showing ostracods; (e) pyrite of top of Bed 3 and microgastropods of Bed 4; (f) Bed 1, showing erosional surface and calcisponges in reef rock; (g) Bed 2, showing ostracods; (h) Bed 2, tidal flat deposits with microgastropods; (i) Bed 2, enlargement of microgastropods; (j) Bed 3, showing small spherical microproblematica; (k) Bed 3 (lower) and Bed 4 (upper), tidal-flat facies lime mudstone, with microgastropods; (l) Bed 5, showing ammonoids.

shelled bivalves may be floating in life. Some researchers found that, in latest Permian and earliest Triassic, some ostracods were adapted to dysoxic condition[22]. Thus, ostracods in Bed 3 were adapted to dysoxic or anoxic condition. The biota of Bed 4 is simple and is dominated by microgastropods. There is no report that microgastropods can live in anoxic condition. So, the biota of Bed 4 lived in oxygenated environments. The

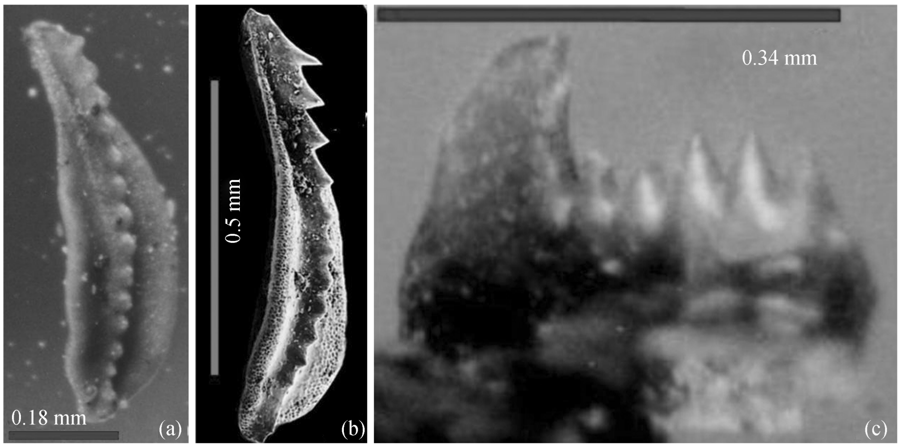

Figure 4 Key conodonts from PTB section at Gendan, Ziyun, Guizhou Province. (a): *Clarkina parasubcarinata*, from 1 m below top of Bed 1 of Gendan. (b): holotype of *Clarkina parasubcarinata* (Mei et al., 1998), from Beds 24d and 24e of Meishan section. (c): *Hindeodus parvus*, from Bed 3 of Gendan.

biota of Bed 5 comprises normal-sized marine organisms, indicating further restoration of marine ecosystems under normal oceanic conditions.

2 Extinction pattern of the reef ecosystem at Tanluzhai in the latest Permian

The Tanluzhai section, 2 km east of Ziyun town, is divided into five beds lithologically (Figure 2(b)). The basal Bed 1 is a gray massive reef limestone, composed of bafflestone or framestone (Figure 3(f)). The framestone of the top of this bed has multi-generation calcite cements. This bed contain a diverse biota composed of reef-building calcareous sponges, hydrozoans, bryozoans, echinoderms, brachiopods, foraminifers, fusulinids, bivalves, gastropods, algae, *Archaeolithoporella*, *Tubiphytes*, and microproblematica. The calcisponges are diverse, including at least 8 species of inozoans and 2 species of sclerosponges (*Bauneia*, *Reticulocoelia*)[23]. The top surface of this bed is an erosional surface, indicating subaerial exposure of deposits.

Bed 2 is 1.7 m thick brownish, partially dolomitized lime mudstone, containing a simple biota of microgastropods, ostracods (Figure 3(g)—(i)), and abundant biotic burrows. The fabric and structure of deposits and burrow type indicates that the sedimentary environments of this bed might be tidal flat.

Bed 3 is 0.4 m thick black, dolomitic lime mudstone, with developed flat laminated structure (Figure 3(j)), reflecting absence of both bioturbation and wave action. Examination under ESM found tiny pyrite framboids, which is composed of cubic or octahedral tiny crystals and indicates anoxic condition[21]. This bed contains only small spherical microproblematica and some ostracods. The microproblematica are similar to those in Bed 3 of Gendan section in shape and size.

Bed 4 is 0.1 m thick brownish lime mudstone, and contains microgastropods and small biotic burrows. No pyrite has been found from this bed, which indicates that the sedimentary environment was oxygenated. This bed is similar to Bed 2 in lithology and biotic (Figure 3(k)).

Bed 5 is brownish to reddish packstone and grainstone, containing a moderately diverse biota of abundant normal-sized ammonoids and gastropods (Figure 3(l)).

Tanluzhai section is less than 3 km away from Gendan section. Both of these two sections have a dark-colored, anoxic bed of similar thickness. Thus, these two sections are correlative. The Permian-Triassic boundary in Tanluzhai section lies between Beds 2 and 3. Beds 1—5 of Tanluzhai section are correlative to Beds 1—5 of Gendan section.

Bed 1 of Gendan contains a diverse biota. The presence of reef-building calcisponges in this biota indicates that it is a pre-extinction biota. The disappearance of calcisponges and other stenotropic organisms from Bed 2 indicates that the first episode of mass extinction happened before the deposition of Bed 2. The biota of Bed 2 was simple, composed of microgastropods, ostracods and small biotic burrows. This simple biota disappeared before the deposition of Bed 3, constituting the second extinction episode in this section. The biota in Bed 3 was simpler, composed of small spherical microproblematica. The microproblematica are interpreted as being adapted to anoxic condition. The sedimentary environment of Bed 4 became oxygenated, and the biota restored to that of Bed 2, which was composed of microgastropods, ostracods, and small biotic burrows. The biota of Bed 5 was composed of normal marine organisms, indicating restoration of normal oceanic conditions.

3 Discussion

3.1 Extinction pattern of reef ecosystems in Ziyun in latest Permian

Examination of two PTB sections in Ziyun shows that the mass extinction of reef ecosystems in the latest Permian happened in two steps. In the first step, all stenotropic organisms including reef-building calcisponges and fusulinids became extinct. The following biota was simple, composed of microgastropods, ostracods, and many small unknown biotic burrows, or of tidal-flat algal mats. The extinction of this simple biota caused by development of oceanic anoxia was the second episode of the mass extinction. The following biota was adapted to anoxic condition, composed of small spherical microproblematica, ostracods, and some floating bivalves. In both Gendan and Tanluzhai sections, there is no obvious change in lithology from Bed 2 to Bed 3. However, the rock color changed: the color of Bed 2 is light, while that of Bed 3 is dark. The development of oceanic anoxia as indicated by dark rock color and presence of pyrite framboids was responsible for the extinction of the microgastropod biota.

Algal mats represent restricted environments, and generally unstable tidal-flat environments. Even unstable in temperatures and salinity, tidal-flat environments are generally oxygenated. Anoxic condition is deathful to most organisms. Only some specialized organisms can be adapted to anoxic environments. In the PTB section studied by Wignall and Hallam[24], the organisms living in dysoxic oceans were *Lingula* and *Claraia*. With the development of anoxic condition, the extinction of algal mats and microgastropods are expectable. During the P-T transition, oceanic anoxia developed in many places[25−29], making up a significant oceanic crisis. So, the extinction caused by the anoxic event is regarded as a minor episode of the mass extinction.

As the environments became oxygenated, the biota restored to the level before the anoxic event. When the oceanic conditions became normal, a diverse biota containing normal-sized ammonoids and gastropods appeared.

The two sections show that: (1) The mass extinction of reef ecosystems in the latest Permian consists of more than one episode; (2) The restoration of marine ecosystems in the earliest Triassic consists of more than one step, too; (3) The first and biggest episode of extinction of reef ecosystems happened in the latest Permian, being some distance below the P-T boundary; (4) The happening of the second episode of the mass extinction was caused by oceanic anoxia; (5) It was not a long time before the restoration of marine conditions to normal and of biota to diverse.

3.2 Significance of the PTB sections in Ziyun

In China, the study of reefs began from the 1960s. The study of Changhsingian reefs cannot avoid discussing the P-T boundary. However, since these studies did not aim at P-T boundary, their studies on P-T boundary did not have a resolution as high as those orienting to P-T boundary. .

On the other hand, the study of P-T boundary is constrained by the level in study of the conodonts from the PTB sections. In the later 1990s, studies on the conodonts from the GSSP of PTB, Meishan section, and from the candidates Shangsi section in Sichuan, Selong section in Tibet made substantial progresse[20,30−33], resulting in the establishment of the standard conodont zones for the P-T boundary strata[8,34]. The high-resolution biostratigraphic framework makes it possible to carry out high-resolution multiple disciplinary studies on P-T boundary strata.

The known occurrence of Changhsingian reefs was mostly in China. Other places with Changhsingian reefs include Skyros Island[35]. In China, the earliest studied Changhsingian reef is in Lichuan, Hubei Province[36]. However, the P-T boundary in this reef section has not been thoroughly studied. This reef did not last into latest Permian[19]: it was covered by late Changhsingian lagoonal deposits. The later discovered Changhsingian reef at Laolongdong, near Chongqing City, however, was more thoroughly studied by more researchers[37,38]. An early study by Reinhardt[37] on this reef involved the sedimentology of the PTB interval and revealed evidence for tidal-flat environments. In his section, however, the Changhsingian reef was covered by latest Changhsingian lagoonal deposits. Another shortcoming is that his study did not include conodont biostratigraphy. Fan and Wu made a systematic study on a Changhsingain reef section 500 m from Reinhardt's[39]. However, the Changhsingian reef in this section did not grow to the end of the Permian Period. It was covered by 26.3 m of platform facies packstone and wackestone. In more resent years, many researchers made studies on the P-T boundary interval[40 – 43]. In the PTB sections at Laolongdong and Baizhuyuan studied by Kershaw et al.[14,15], the interval between Changhsingian reef and P-T boundary is crinoidal limestone: the Changhsingian reef did not grow to the happening of the mass extinction. The big progress made by them is the discovery of (?)microbialites[14,15], a mysterious dendroid structure within the rock. Up to now, its features and origin remains open. The Changhsingian reef in Skyros Island did not grow to latest Permian, too. It was capped by an interval of shale[35].

3.3 Comparison with extinction of non-reef ecosystems

In China, the most studied non-reef PTB section is in Meishan, Zhejiang Province. Jin et al.[11] found that the mass extinction in Meishan section consists of one main episode at 251.4 Ma[44] (in Beds 25 and 26) and the gradual decline of the survived taxa in the following one Ma. In other words, the extinction in Meishan contains one main episode. Xie et al.[12] found that the content of the biomarker related to cynobacteria has two peak valves in Beds 25 to 26 and Beds 28 to 29, respectively. The flourishing of cyanobacteria might be related to the unusual environment following the main episode of the mass extinction. Xie et al.'s study indicates that there may be two extinction episodes in Meishan: one at below Bed 25 (within Bed 24e) and the other at below Bed 28 (within Bed 27) respectively.

Yang et al.[45] studied 14 non-reef PTB sections in South China, and found that an "extinction line" is present in dozens of centimeters to several meters below the P-T boundary. Most stenotropic benthic organisms became extinction at this line. Within the interval from the extinction line to the P-T boundary, the biota was monotonous, and was dominated by small brachiopods. It is obvious that this extinction line represents the first and main episode of extinction of non-reef ecosystems. Unfortunately, Yang et al.'s studies do not have conodont framework.

In Meishan section[46], fusulinids were present till middle Bed 24e. So, in our opinion, the first episode, and the main episode of extinction in Meishan happened at the middle of Bed 24e, that is, within the conodont *Clarkina yini* zone. The sparse brachiopods and ammonoids in Bed 26[46] should be survivors. It is unknown if there was the second episode in Meishan.

The extinction of reef ecosystems in Ziyun consists of two episodes. The first main episode happened within *C. yini* zone, and is characterized by disappearance of all stenotropic organisms. The pattern and timing of this episode are similar to those of Meishan. Some researchers proposed that the extinction of reef ecosystems predated that of non-reef ecosystems[47]. This study, however, does not support this viewpoint. The second extinction episode in Ziyun happened at the base of *Hindeodus parvus* zone, and was related to oceanic anoxic event. Probably because anoxic event in Meishan happened in different patterns and different time, the second extinction episode of Ziyun does not have counterpart in Meishan.

A typical PTB section is at Tesero of Dolomites, Italy. According to Noé[48] and Wignall et al.[24], in this section, the pre-extinction biota is platform facies, diverse, containing 36 species. Most of them (72% species), especially fusulinids, disappeared at 2.2 m below the P-T boundary, which constitutes the first episode of the extinction. The survived biota was low-diversity, composed of sparse foraminifers and algae. The second extinction episode happened at the base of *Hindeodus parvus* zone, where most taxa became extinct. Only some ostracods survived the second crisis. The mass extinction in Ziyun is similar to that in Tesero section in that both had two episodes, and in the timing of the second episode, and the types of the organisms that became extinct. The second extinction episode in Tesero also happened at the base of *H. parvus* zone, and seemed to be caused by oceanic anoxia.

The Changhsingian deposits in Ursula Creek, British Columbia are deep-water facies[49]. The first extinction episode in this section happened at 1.6 m below the P-T boundary, characterized by the disappearance of all stenotropic radiolarians. Benthic siliceous sponges became extinct at 0.8 m below the P-T boundary, which constitutes the second extinction episode. Oceanic anoxia began at 0.8 m below the P-T boundary, too. In the PTB section at Jameson Land, eastern Greenland[50], the extinction of stenotropic organisms happened several meters below the P-T boundary, with eurytropic small organisms such as microgastropods survived. These cases show that in the latest Permian, the mass extinction of reef ecosystems happened in a way similar to that of non-reef ecosystems encountering oceanic anoxia. The non-reef ecosystems that did not encounter oceanic anoxia, however, seemed not to have an obvious second extinction episode.

4 Conclusions

Based on the examination of two reef related P-T boundary sections in Ziyun, Guizhou Province, southwestern China and comparison with extinction ways of several non-reef PTB sections in other places, the following conclusions can be drawn.

The mass extinction of reef ecosystems in the latest Permian consists of two episodes. The first and the main episode is the extinction of all stenotropic organisms such as reef-building calcisponges and fusulinids in *Clarkina yini* zone. The following biota was simple, low-diversity, and was composed of microgastropods, some small burrowing organisms, and some ostracods, or only algal mats. The extinction of this simple biota at the base of *Hindeodus parvus* zone, probably caused by oceanic anoxia, made up the second extinction episode. The following biota was very simple, adapted to anoxic environment, and was composed of some unknown small spherical microproblematica, some ostracods, and some thin-shelled bivalves that were probably neustons. As the environment became oxygenated, the specialized biota was replaced by a simple biota dominated by microgastropods, which marked the beginning of the improvement of oceanic conditions. After that, with the further improvement of physical-chemical conditions of oceans, the simple biota was replaced by a more or less diverse biota composed of normal-sized ammonoids, bivalves, and gastropods, reflecting restoration of normal marine ecosystems.

Non-reef ecosystems that did not experience oceanic anoxia had the first extinction similar to that of reef ecosystems in terms of timing of extinction and type of organisms that became extinct: both happened in *Clarkina yini* zone; both were extinction of stenotropic organisms. Reef ecosystems had a second extinction episode related to oceanic anoxia. Non-reef ecosystems that encountered oceanic anoxia had the second extinction episode, too. However, to those non-reef ecosystems that did not encounter oceanic anoxia, the second extinction episode was not obvious, or not present.

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