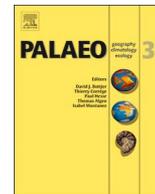




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Mixed continental-marine biotas following the Permian-Triassic mass extinction in South and North China

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ABSTRACT

Correlation between marine and continental Permian-Triassic (P-Tr) strata is crucial for full understanding of the nature of this global extinction event, but it has proved difficult to achieve. Here, we show that two sections in South China and North China record similar mixed continental-marine biota in the post-extinction stratigraphic interval, including conchostracans, plants, insects, marine bivalves and lingulid brachiopods. In addition, the continental P-Tr mass extinction was represented by a sharp decrease in the diversity and abundance of the *Gigantopteris* flora in South China, but eliminated the Palaeozoic-type conifer flora and herbivorous pareiasaurs in North China. These mixed continental-marine biota provide the biological evidence for stratigraphic correlation between marine and continental P-Tr transitional beds in South China and North China, especially the co-occurrence of the *Pteria-Towapteria-Eumorphotis* bivalve assemblage and the *Euestheria gutta*-bearing conchostracan fauna or *Euestheria gutta-Magniestheria mangaliensis-Palaeolimnadiopsis vilujensis* conchostracan assemblage. We propose that these specific marine bivalve and continental conchostracan assemblages could be considered as markers of P-Tr transitional beds in marine-continental siliciclastic settings.

1. Introduction

The largest biotic extinction event of the entire Phanerozoic occurred at the Permian-Triassic (P-Tr) boundary and affected both marine and continental life (Erwin, 2006; Benton, 2015). Numerous killing agents for this mass extinction event have been proposed, either singly or in concert, such as global warming, anoxia, ocean acidification, wild fire, rapid sea level changes, enhanced continental weathering and others (e.g. Wignall and Hallam, 1992; Wignall and Twitchett, 1996; Isozaki, 1997; Benton and Twitchett, 2003; Shen et al., 2006, 2011; Payne et al., 2007; Algeo and Twitchett, 2010; Algeo et al., 2011; Clapham and Payne, 2011; Hinojosa et al., 2012; Joachimski et al., 2012; Sun et al., 2012; Sedlacek et al., 2014; Tian et al., 2014; Clarkson et al., 2015; Ikeda et al., 2015; Song et al., 2015; Rey et al., 2016), but no consensus has been reached. Detailed estimates of species loss, timing, pattern and duration of the marine P-Tr biotic event are relatively well established (e.g. Jin et al., 2000; Shen et al., 2011; Song et al., 2013; Burgess et al., 2014), while the nonmarine record has been harder to analyse in such close detail. However, the terrestrial P-Tr mass extinction (PTME) is confirmed by a significant turnover and loss of life on land, such as tetrapods, insects and plants, based on global

palaeontological data from Russia, western Europe, northwestern China, South China, South Africa, Australia and the Antarctic (e.g. Retallack et al., 1996, 2011; Looy et al., 1999, 2001; Smith and Ward, 2001; Rees, 2002; Benton et al., 2004; Grauvogel-Stamm and Ash, 2005; Ward et al., 2005; Shcherbakov, 2008; Hermann et al., 2011; Benton and Newell, 2014; Schneebeil-Hermann et al., 2015; Yu et al., 2015; Cascales-Miñana et al., 2016). To date, there is no general agreement on whether the mass extinctions of marine and nonmarine life were synchronous during the P-Tr biotic crisis, due to lack of the marks for correlation between marine and continental deposition (Twitchett et al., 2001; Cao et al., 2008; Kozur and Weems, 2011; Shen et al., 2011; Metcalfe et al., 2015; Zhang et al., 2016; Chu et al., 2016). During the PTME interval and its aftermath, both marine and continental ecosystems were characterized by a burst of monotonous, opportunistic, and cosmopolitan disaster taxa, such as the marine bivalves *Claraia*, *Eumorphotis*, *Unionites* and *Promyalina*, the brachiopod *Lingula*, and stromatolites, and the terrestrial tetrapods *Lystrosaurus* and *Tupilakosaurus*, and the plant *Pleuromeia* (Schubert and Bottjer, 1992; Rodland and Bottjer, 2001; Peng et al., 2007; Huang and Tong, 2014; Benton and Newell, 2014; Benton, 2015). These disaster taxa flourished for only a brief spell immediately after the crisis, but their worldwide

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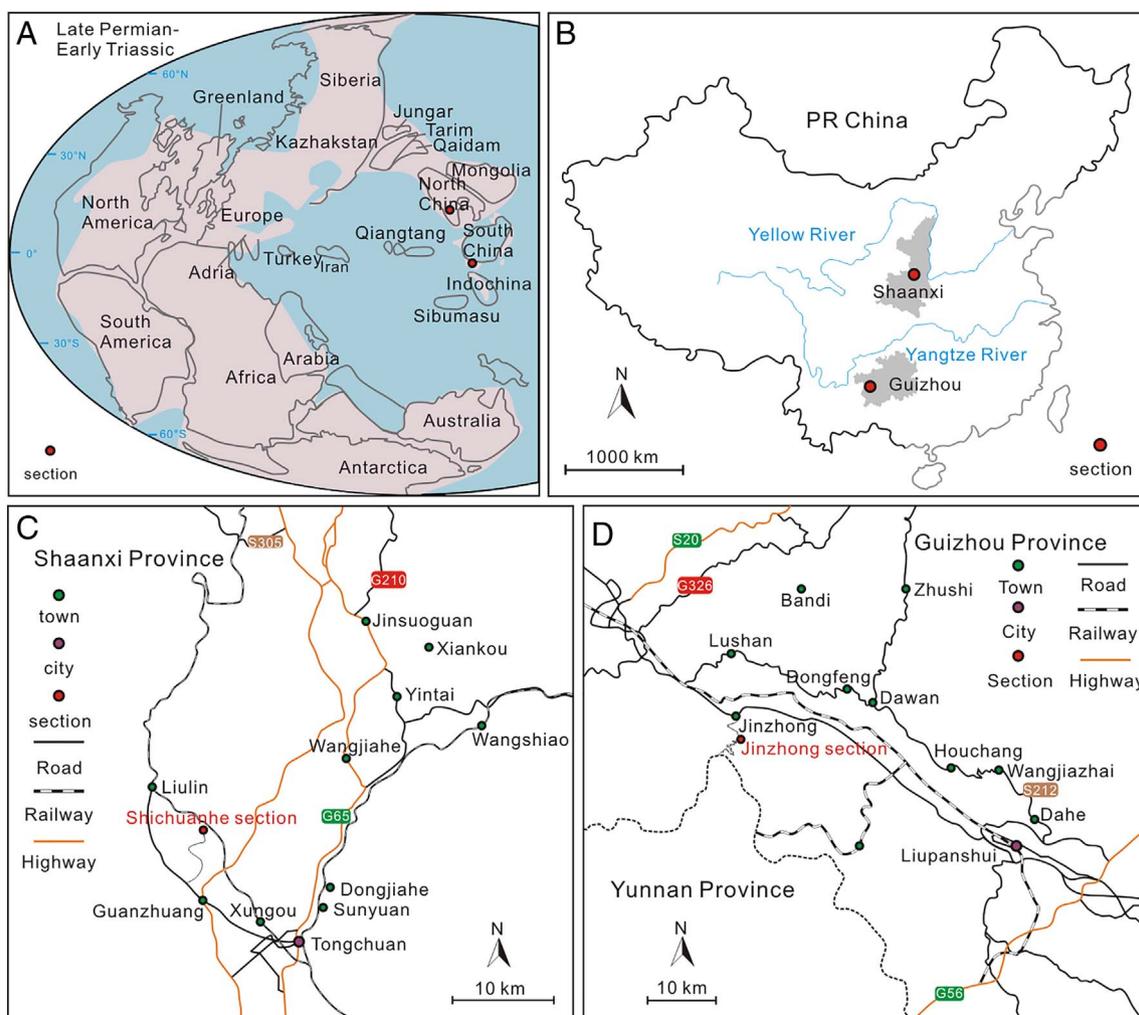


Fig. 1. Investigated localities. A. Palaeogeographic map of Late Permian to Early Triassic (after Muttoni et al., 2009). The studied sections (marked by red dots) are located in South China and North China. B. Sketch map of China, showing the locations of Guizhou Province and Shaanxi Province (grey shading). C. Detailed location of the Shichuanhe section. D. Detailed location of the Jinzhong section. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

distribution provides important palaeontological evidence for biostratigraphic correlation among the facies that lack conodonts, ammonites and other widely acknowledged age-diagnostic fossils.

To date, P-Tr marine biostratigraphy, chemostratigraphy and chronostratigraphy have become widely established for global correlation, and the Global Stratotype Section and Point (GSSP) of the P-Tr boundary is defined at the Meishan section in South China, which is accepted as the first appearance datum of the conodont *Hindeous parvus* (Yin et al., 2001). Conversely, it has proved difficult to test the age of continental redbed successions, and in the case of the Karoo in South Africa, the position of the P-Tr boundary is disputed (Smith and Ward, 2001; Ward et al., 2005; Botha and Smith, 2006; Gastaldo et al., 2015; Neveling et al., 2016), and in Russia the P-Tr boundary is also debated (Taylor et al., 2009). Hitherto, a fossil vertebrate-based biostratigraphic scheme was the main correlative tool for continental P-Tr sections (Smith and Ward, 2001; Benton et al., 2004; Lucas, 2006, 2010; Viglietti et al., 2016), but these vertebrate biozones are not easy to obtain and cannot be directly correlated with marine sequences. Geomagnetic polarity and carbon isotopes were used to mark the position of the P-Tr boundary or PTME in continental sections, but this has proved difficult because of a lack of a composite magnetostratigraphic record and the non-global nature of carbon isotope excursions (MacLeod et al., 2000; Gallet et al., 2000; Ward et al., 2005; Steiner, 2006; Szurlies, 2007, 2013; Cao et al., 2008; Shen et al., 2011; Gastaldo et al., 2014, 2015; Metcalfe et al., 2015; Zhang et al., 2016). In this

regard, high-precision dating might be a good way to correlate between marine and continental strata (Shen et al., 2011; Metcalfe et al., 2015), but datable volcanic ash beds are only preserved in relatively few sections and recorded in multi-phases in stable basins with successive deposition during the P-Tr transition. So, it is difficult to explore the correlation between marine and continental strata due to absence of shared fossil assemblages.

Recently, marine-continental transitional siliciclastic settings were considered to be a potential link for correlation between marine and continental sections (Peng et al., 2005; Peng and Shi, 2009; Chu et al., 2016; Zhang et al., 2016). Here, we report two P-Tr boundary sections from South China and North China that contain an exceptional mixed continental-marine biota. Our study shows that rocks in both South China and North China record a similar mixed continental-marine biota in the post-extinction stratigraphic interval, including conchostracans, plants, insects, marine bivalves and lingulid brachiopods, which allows us, for the first time, to assess the correlation between the marine and continental P-Tr transitional beds among the sections in South China and North China.

2. Geological and stratigraphic settings

South China was located within the Palaeo-Tethys Ocean at equatorial palaeolatitudes (Fig. 1). An almost continuous outcrop records a gradual change from continental to marine facies in the adjoining area

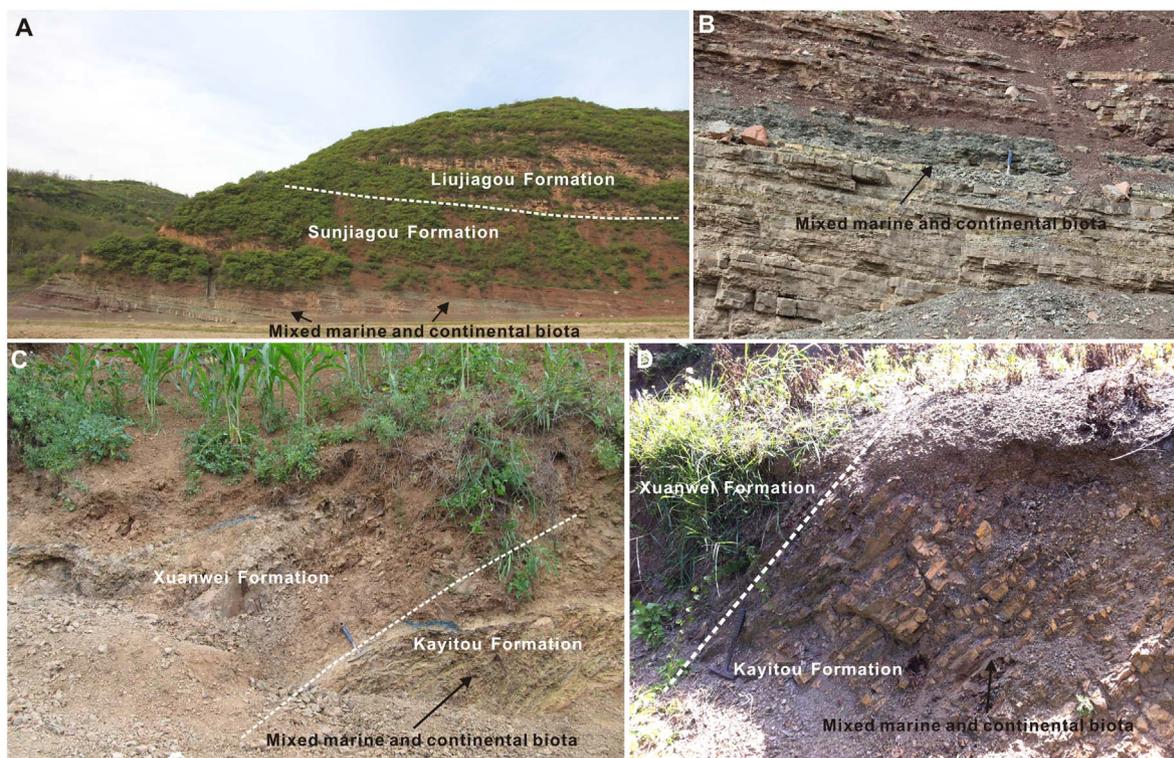


Fig. 2. Outcrops of the studied sections. A. Lithological boundary between the Sunjiagou and Liujiagou formations in the Shichuanhe section; B. Marine interbeds with mixed marine-continental biota in the upper part of the Sunjiagou Formation in the Shichuanhe section; C. Lithological boundary between the Xuanwei and Kayitou formations in the Jinzhong section, and horizon of the marine-continental biota preserved in the lower part of the Kayitou Formation; D. Outcrop of the lithological boundary between the Xuanwei and Kayitou formations near the Jinzhong section, also recording the marine-continental biota.

between western Guizhou and eastern Yunnan (WGEY). The continental P-Tr succession in WGEY consists of three main formations, the Xuanwei, Kayitou and Dongchuan formations, in ascending order. Of these, the key characteristic of the Xuanwei Formation is the presence of a rich *Gigantopteris* flora and common coal beds or seams (Yu et al., 2015). The P-Tr transitional Kayitou Formation is similar to the underlying Xuanwei Formation, but shows no coal beds or seams. The Dongchuan Formation is characterized by a thick succession (over 800 m thick) of purple-red siliciclastic sandstones, siltstones and mudstones, with very rare fossils.

North China was located at low palaeolatitudes, around 20° N, during the P-Tr transitional period (Fig. 1, Muttoni et al., 2009). The P-Tr redbed succession is composed of the Sunjiagou and Liujiagou formations. The Sunjiagou Formation consists of fine-grained sandstones, reddish siltstones and mudstones, containing Palaeozoic-type plants, pareiasaurs and rich bioturbation. Previous study showed that the upper part of the Sunjiagou Formation records the mass extinction of plants and vertebrates, and corresponds to the P-Tr transitional interval (Benton, 2016; Chu et al., 2017). In addition, the Sunjiagou Formation contains marine bivalves and brachiopods in the Baoji and Tongchuan areas, which might indicate the occurrence of a transgression (Yang et al., 1979; Yin and Lin, 1979). The overlying Liujiagou Formation comprises reddish and brown-reddish fine-grained sandstones with interbedded siltstones and conglomerates. Common microbially-induced sedimentary structures (MISS) occur in the lower-middle part of the Liujiagou Formation (Chu et al., 2015, 2017; Tu et al., 2016), and the typical Early Triassic plant fossil *Pleuromeia* occurs in the upper part of the Liujiagou Formation (Wang, 1996).

3. Materials

We measured two stratigraphic sections in detail and collected over 500 fossil specimens, including bivalves, brachiopods, conchostracans,

plants and insects, from the Kayitou Formation of the Jinzhong section in South China (26°43'47.63"N, 104°26'7.42"E) and the Sunjiagou Formation of the Shichuanhe section in North China (35°01'44.6"N, 108°52'42.3"E). Well-preserved *Gigantopteris*-flora plant fossils with large leaves and entire margin were collected from the underlying Xuanwei Formation at the Jinzhong section in the present and our previous study (Chu et al., 2016). These original collections, combined with re-evaluation of previously published data are the materials of the present study.

Fossils were carefully sought bed by bed throughout the stratigraphic sequences and they were marked with the bed number and thickness level during fieldwork. Plant and bivalve fossils were photographed using a Canon EOS 7D digital camera, while the conchostracan specimens were examined and photographed using a LEICA-DM-750P microscope equipped with an automatic camera stack-image system. Ultramicroscopic study of the conchostracan specimens was carried out under a Hitachi SU8010 scanning electron microscope (SEM). All fossil material in this study is stored in the palaeontological collection of the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (BGE, Wuhan). The catalogue numbers of the studied specimens include the profile name of the section and specimen number, followed by the storage location (BGE). The Jinzhong and Shichuanhe sections are abbreviated as JZ and SCH.

4. Mixed continental-marine biota

4.1. Mixed continental-marine biota in Jinzhong section of South China

The Jinzhong section, located 15 km south of Jinzhong Town, Guizhou Province (Fig. 1), comprises a continuously exposed outcrop of the upper part of the Xuanwei Formation, the Kayitou Formation and the lower part of the Dongchuan Formation. Coal beds and a typical *Gigantopteris* flora are observed in the Xuanwei Formation. The P-Tr

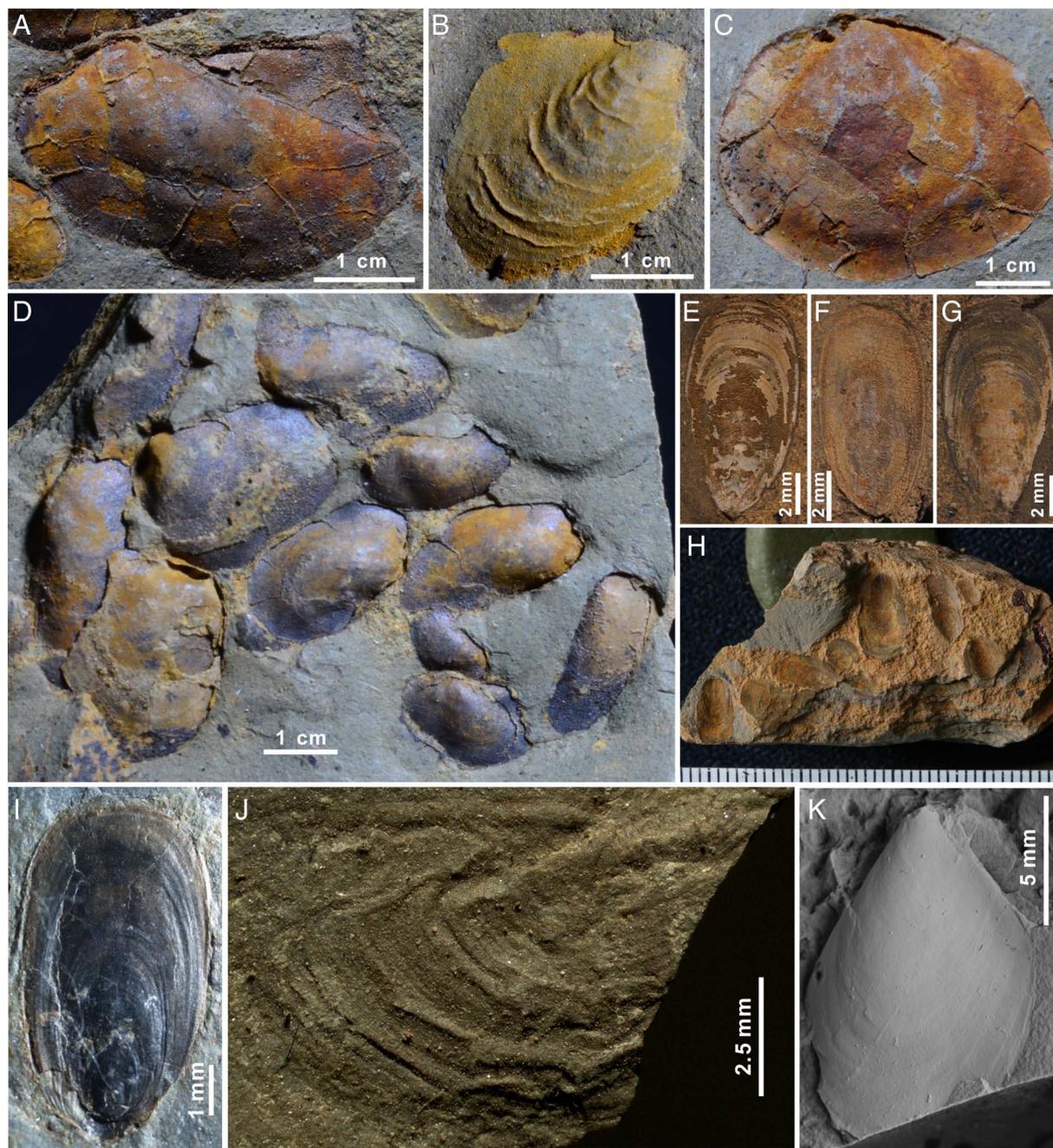


Fig. 3. Bivalves and lingulids of the mixed marine-continental biota. A. *Pteria ussurica variabilis* Chen, JZ-09-010; B. *Promyalina schamarae* Bittner, JZ-09-015; C. *Neoschizodus laevigatus* Zieten, JZ-10-025; D. Several bivalves preserved on the same bedding surface; E–H. Lingulid brachiopod specimens, JZ-10-008, JZ-10-010, JZ-10-013, JZ-09-021; I. Lingulid brachiopod, SCH-08-021; J. *Pteria ussurica variabilis* Chen, SCH-08-006; K. *Promyalina putiatinensis* Kiparisova, SCH-08-011.

transitional beds are represented by the 65-m-thick Kayitou Formation (Fig. 2), which corresponds to a shallow coastal lagoon evolving towards coastal transitional deposition, and which has yielded a mixed continental-marine biota including bivalves, brachiopods (lingulids), plants, conchostracans and insects.

4.1.1. Bivalves and lingulid brachiopods

Most of these small to medium-sized bivalves were well preserved and collected from specific horizons in the lower part of the Kayitou Formation, while they were sporadically observed in the middle and upper parts of the Kayitou Formation. These bivalves are assigned to *Pteria ussurica variabilis*, *Neoschizodus orbicularis*, *Neoschizodus laevigatus*, *Promyalina schamarae*, *Eumorphotis venetiana* and *Permophorus bregeri*, and over 70% of the specimens belong to *Pteria ussurica*

variabilis, *Neoschizodus orbicularis* and *Promyalina schamarae*, which is named as the *Pteria-Neoschizodus-Promyalina* assemblage (Fig. 3).

Abundant lingulid brachiopods occurred at different levels of the Kayitou Formation in the Jinzhong section and they are preserved as complete internal and external moulds of disassociated valves (Fig. 3). Here, we use the general term “lingulids” rather than a particular genus name because the critical evidence of muscle-scar traces and other internal features within the valves for generic identification is absent. Lingulids have been widely reported from Lower Triassic strata, and they are regarded as disaster taxa that flourished in shallow marine deposits in the aftermath of the PTME (Rodland and Bottjer, 2001).

4.1.2. Conchostracans

Conchostracans are abundant and well preserved on many bedding

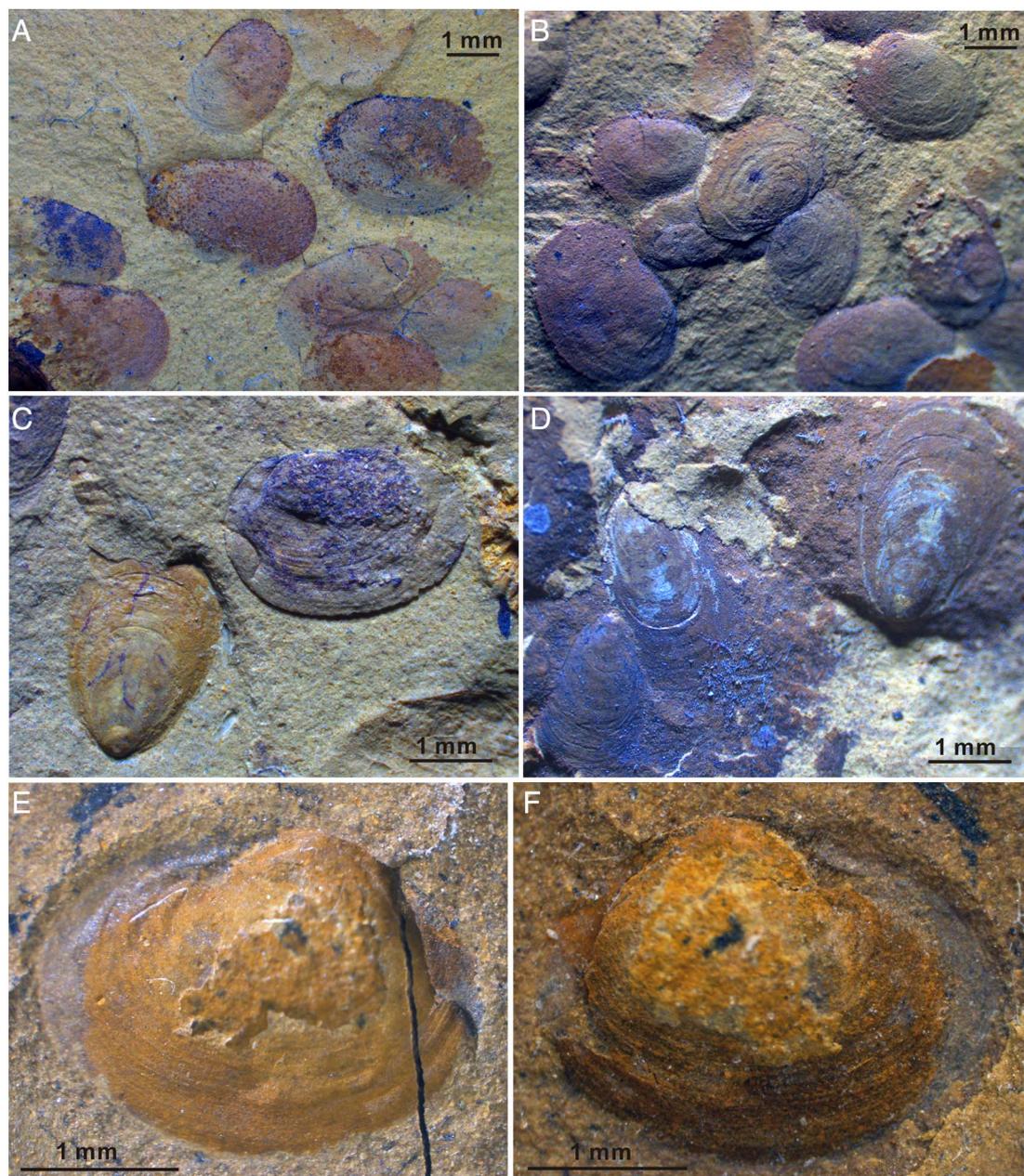


Fig. 4. Conchostracans collected from the Kayitou Formation of the Jinzhong section. A, B. Several conchostracan specimens preserved together, JZ-09-030-1, JZ-09-030-2; C, D. conchostracans and ligulids preserved on the same bedding surface, JZ-010-20, JZ-010-24; E, F. *Euestheria gutta* Lutkevitch, with a strong convex relief at the umbo, JZ-010-01, JZ-010-03.

surfaces in the Kayitou Formation of the Jinzhong section (Fig. 4). They are the most common fossils in this mixed biota, and some specimens are preserved on the same bedding surface with bivalves or lingulids (Fig. 4). The preservation of altered chitinous material could be observed by the evidence of colour and texture variations (Fig. 4), while other specimens are preserved as detailed impressions. The classification of fossil conchostracans is restricted to the morphology of the carapaces, especially specific valve characteristics such as carapace margins, growth bands, growth lines, larval valve and umbo. Here, we describe and identify conchostracan fossils by using a normalized carapace terminology that was improved by Scholze and Schneider (2015) based on a set of quantitative and semi-quantitative measurements. In addition, some well-preserved specimens were employed for ultra-microscopic studies to observe the microsculptures on their larval valves and growth bands.

Most of the conchostracans from the Kayitou Formation were assigned to the genus *Euestheria*, and dominated by the particular species

Euestheria gutta. The carapaces of *Euestheria gutta* are small to medium-sized, 2.0–3.0 mm in length and oval to round in shape, with a straight and short dorsal margin, position of umbo anterior and inframarginal, umbo does not extend above the dorsal margin, larval valve small to large, growth lines up to 30, anterior and posterior margins very sharply curved, and undeformed and weakly deformed specimens showing a strong convex relief with its maximal convexity at the umbo (Fig. 5). A pitted ornamentation could be observed on larval valves and growth bands in specimens in which the shell substance or derivatives of the primary shell substance are preserved (Fig. 5N). The other *Euestheria* specimens are also small- to medium-sized, oval to round in shape, and with a short dorsal margin, but the umbo extends above the dorsal margin, and these might belong to *Euestheria nordvikensis* or another species. Considering the large number of *Euestheria gutta* specimens, these conchostracans were named the *Euestheria gutta*-bearing fauna.

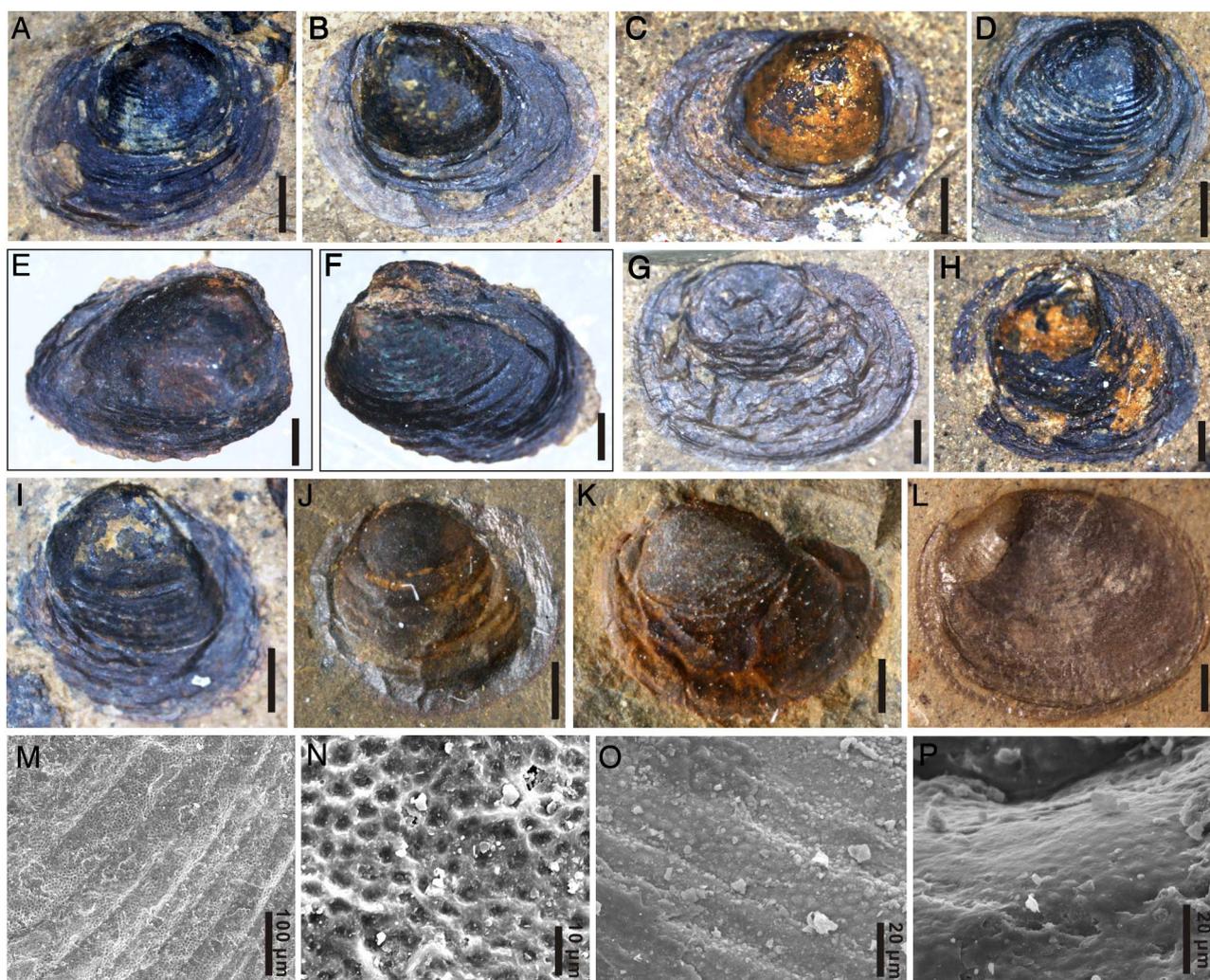


Fig. 5. *Euestheria gutta* Lutkevitch specimens with various deformation characteristics, collected from the Kayitou Formation at the continental sections in WGEY (Chu et al., 2016). A–L, different appearances of the fossils, depending on ontogenetic age and preservation conditions, the scale bars represent 1 mm. M–P, SEM shots of the carapace ornament, showing growth lines (M, O), and surface pitted ornament (N).

4.1.3. Plant fossils

Abundant plant fossils were collected in the Kayitou Formation of the Jinzhong section, including *Annalepis*, *Peltaspermum* and *Gigantopteris* (Fig. 6). Numerous plant fossils assigned to *Annalepis* were collected from different horizons of the Kayitou Formation in the Jinzhong section. Traditionally, *Annalepis* has been considered as an important marker for late Early Triassic and Middle Triassic successions (Retallack, 1975, 1997; Wang and Wang, 1990; Grauvogel-Stamm and Lugardon, 2001; Liu et al., 2004). The presence of *Annalepis* in the WGEY sections represents the first occurrence of a typical Triassic element in the base or lower part of the Kayitou Formation, associated with the earliest Triassic ammonoid *Ophiceras* and marine bivalves, and therefore is regarded as earliest Triassic in age in WGEY (Yu et al., 2010). In addition, Yu et al. (2015) suggested that *Annalepis* might have originated in WGEY during the recovery of land plants following the PTME, and then might have migrated to other regions. Additionally, abundant fragments belonging to genus *Peltaspermum* were collected from the lower to middle part of the Kayitou Formation in the Jinzhong section. The genus *Peltaspermum* was present in the Early Permian in Northwest China and has also been recorded in the Late Permian Sunjiagou and Sunan formations and in Early to Middle Triassic rocks in North China (Wang and Wang, 1990; Huang, 1996; Huang and Ding, 1998). Accordingly, the presence of the genus *Peltaspermum* in the Kayitou Formation indicates that this genus survived the PTME (Yu

et al., 2015). *Gigantopteris* flora remains were observed and collected from the Kayitou Formation, but only a few fragmentary specimens, and no complete large leaves or entire margins preserved (Fig. 6). These relict taxa of the *Gigantopteris* flora might have resulted from long-distance transport or reworking, or they might indicate that rare elements of the *Gigantopteris* flora survived the PTME.

4.2. Mixed continental-marine biota in Shichuanhe section of North China

The Shichuanhe section, located 10 km east of Tongchuan new district, Shaanxi Province (Fig. 1), comprises a continuously exposed outcrop of the Sunjiagou, Liujiagou, and Heshanggou formations. In the present study, the mixed continental-marine biota was preserved in the greyish-green calcareous mudstones and siltstones of the upper part of the Sunjiagou Formation in the Shichuanhe section (Fig. 2), including bivalves, lingulid brachiopods, conchostracans and insects.

4.2.1. Bivalves and lingulid brachiopods

Only two marine bivalve specimens were collected from the continental-marine beds, and were assigned to *Pteria ussurica variabilis* and *Promyalina putiatinensis* (Fig. 3). Conversely, abundant lingulid brachiopods were collected at this site, and well preserved as complete internal and external moulds of disassociated valves. The colour with oily lustre suggests the preservation of altered chitinous material

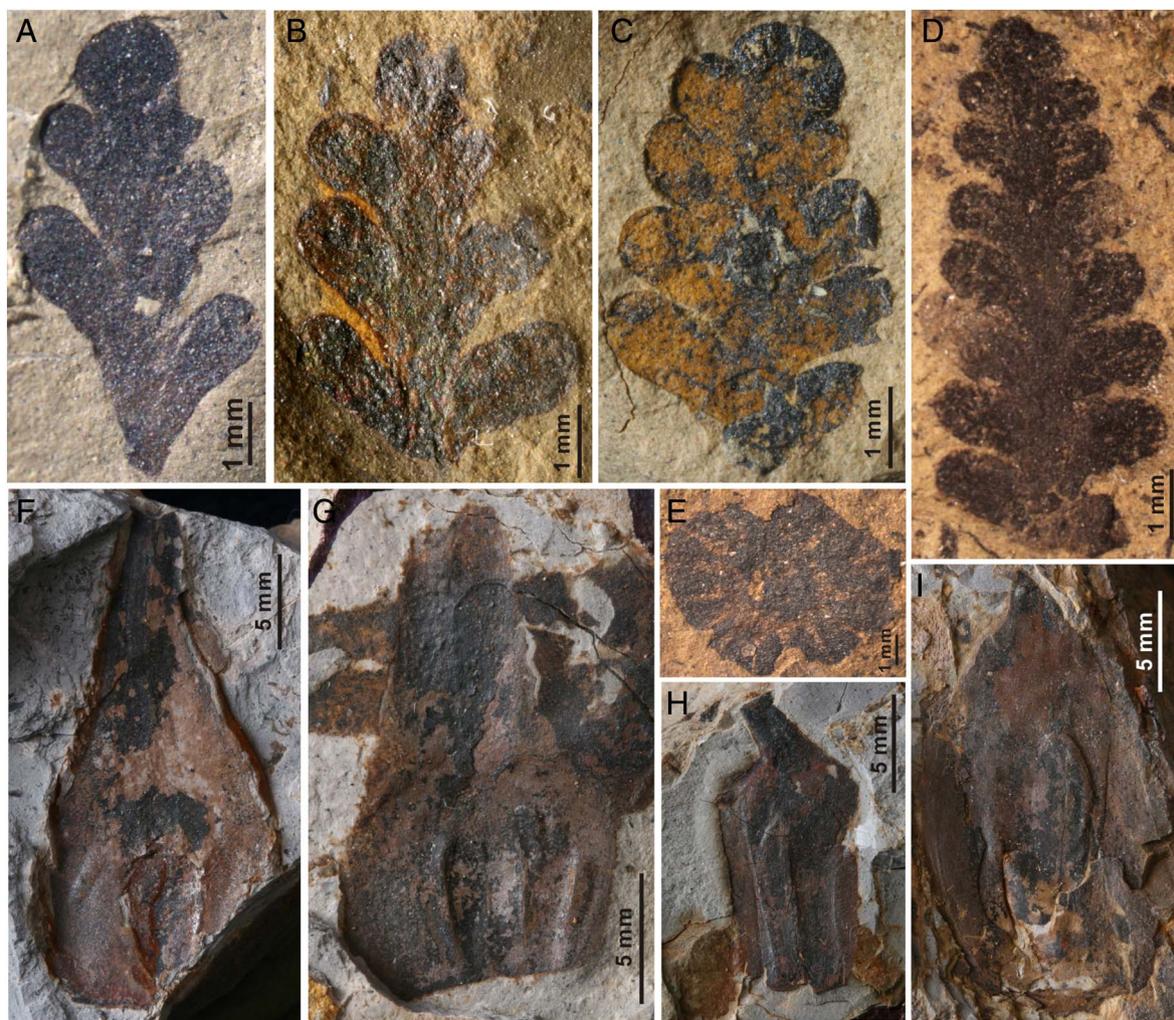


Fig. 6. The plant fossils *Peltaspermum* and *Annalepis* from the Kayitou Formation. A–E. *Peltaspermum* cf. *martinsii* (Harris) Poort et Kerp, collected from the Kayitou Formation of the Jinzhong section, JZ-09-020, JZ-09-022, JZ-10-014, JZ-11-010, JZ-12-013; F–I. *Annalepis* specimens, collected from the base of the Feixianguan Formation and Kayitou Formation in WGEY, JZ-10-020, JJB-159-7, JJB-159-8, JZ-11-22.

(Fig. 3). In addition, some specimens of lingulids were preserved on the same bedding surface with the conchostracans and the plant fragments.

4.2.2. Conchostracans

Conchostracans are the most abundant fossils in the mixed continental-marine biota of the Sunjiagou Formation in the Shichuanhe section (Figs. 7–9), with a higher diversity than the conchostracan fauna from the Kayitou Formation in the Jinzhong section. We collected over 100 specimens from the 15-m thick continental-marine beds, and these conchostracans are obviously different in size. Over 80% of the conchostracans are small- to medium-sized, 2.0–3.5 mm in length, while the others are large- to very large-sized, 4.5–8.0 mm in length. The small- to medium-sized conchostracans belong to the genus *Euestheria* and *Magniestheria*, and most of them are assigned to the stout morphotype of *Magniestheria mangaliensis* (Fig. 7), and the ornamentation is preserved as microsculpture patches or not preserved on larval valves and growth bands (Fig. 8).

A few large-sized conchostracans were preserved as detailed impressions, associated with the small-sized specimens on the mudstone and siltstone bedding surfaces (Fig. 9), and were assigned to *Palaeolimnadiopsis vilujensis* and *Magniestheria mangaliensis*. The *Palaeolimnadiopsis vilujensis* collected from the Shichuanhe section has a large and oval carapace and very large larval valve, with long and straight dorsal margin and concave recurvature of the posterior margin below the dorsal margin, and about ten growth lines. Generally, the genus

Palaeolimnadiopsis is characterized by recurvature of the growth lines at the posterior margin below the dorsal margin, and two separated fine lines for the growth lines. However, the double-lines form could only be observed on the well-preserved growth lines of a *Palaeolimnadiopsis vilujensis* specimen (Fig. 9D), which is probably explained by the incomplete preservation on the siltstone bedding surfaces. The *Magniestheria mangaliensis* specimens from the Shichuanhe section are large-sized and elongated oval in shape, with straight and short to long dorsal margins and small to large larval valves, anterior and posterior margins sharply curved, and about 20–35 growth lines (Fig. 9).

5. Discussion

5.1. The continental PTME in South and North China

Evidence from the fossil record suggests that both the fauna and flora in continental ecosystems suffered a sharp extinction during the P-Tr transition (Benton, 2015). A common understanding of tetrapod evolution through the P-Tr crises is that the complex latest Permian ecosystems dominated by herbivorous pareiasaurs, dicynodonts and carnivorous gorgonopsians were replaced by new clades of archosaurs and synapsids (e.g. Smith and Ward, 2001; Benton et al., 2004; Benton and Newell, 2014). Meanwhile, previous analyses of palaeobotanical and palynological data have shown extensive evidence for worldwide catastrophic die-off of the different plant groups in different geographic

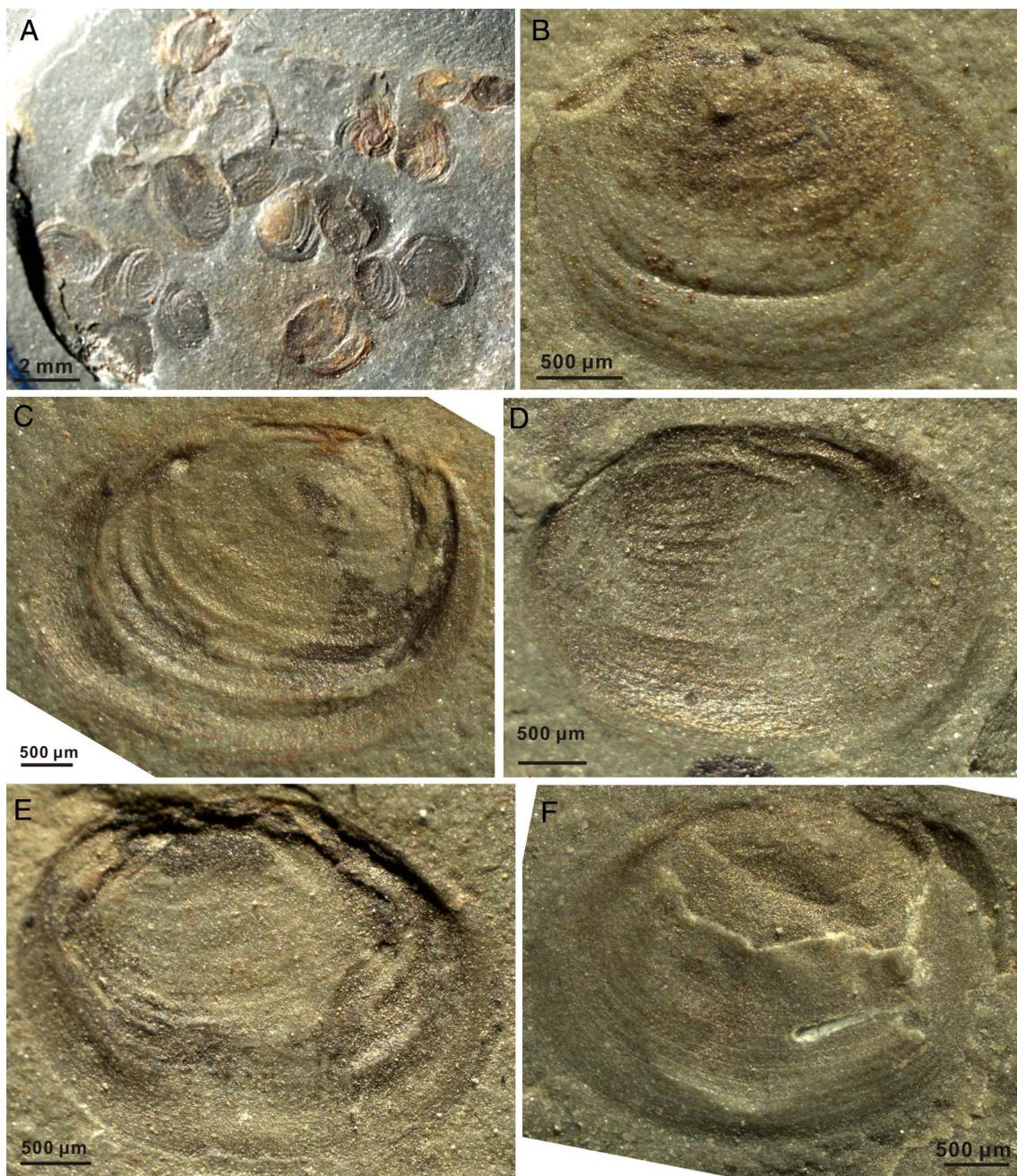


Fig. 7. Small to medium-sized conchostracans from the upper part of the Sunjiagou Formation of the Shichuanhe section. A. Conchostracan assemblage; B. *Euestheria gutta* Lutkevitch, showing the convex relief at the umbo, SCH-08-003; C–F. The stout morphotype of *Magniestheria mangaliensis* Jones, SCH-08-005, SCH-08-013, SCH-08-023, SCH-08-025.

and climatic zones during the P-Tr crisis, which reset plant evolutionary history and contributed to the Early Triassic “coal gap” (e.g. Retallack, 1995; Retallack et al., 1996; Looy et al., 1999; Rees, 2002; Hermann et al., 2011; Yu et al., 2015; Cascales-Miñana et al., 2016).

For the plant fossil collections in the various P-Tr boundary sections of WGEY, we find that the diversity and abundance of the rainforest-type *Gigantopteris* flora experienced a sharp decrease at the base of the Kayitou Formation with a loss of 94% (110/117) at species level and 50% (22/44) at generic level (see supplementary materials), and associated with the disappearance of the coal. Up to 49% (54/111) of these taxa became extinct within a ~2-m interval above the remarkable ash bed that is nearly consistent in age with bed 25 of the Meishan section (Shen et al., 2011). The floral data in South China suggest that a rapid mass extinction of the rainforest-type vegetation occurred and represented the collapse of the end-Permian tropical continental

ecosystem (Fig. 10). Similarly, the Changhsingian gymnosperm-dominated floras in North China, assigned to the *Ullmannia-Yunia* assemblage (Wang and Wang, 1986), also experienced a catastrophic extinction during the P-Tr transition (Fig. 10). A total of 27 genera and 32 species of Late Permian plants from the Sunjiagou Formation became extinct, and approximately 54% (14/26) of plant genera were lost, associated with a loss of 88% (28/32) at species level (see supplementary materials). The subsequent earliest Triassic floras throughout Eurasia and the southern continents were dominated uniformly by the lycopod *Pleuromeia*, this being regarded as a classic “disaster taxon”.

Based on global-scale tetrapod generic data, there was an 89% generic loss of tetrapods near the P-Tr boundary (Benton and Newell, 2014). Among extinct taxa, pareiasaurs flourished worldwide from Wordian to Changhsingian, but died out during the PTME (Benton, 2016 and references therein). In North China, the pareiasaurs

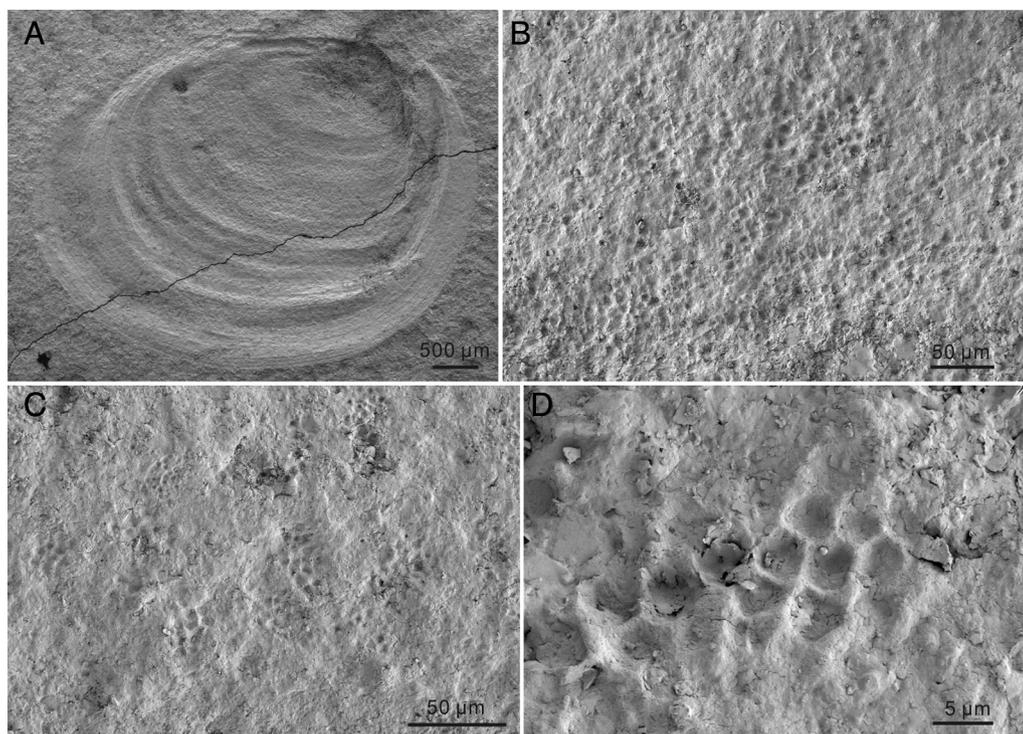


Fig. 8. Ornamentation of the Conchostraca. A. *Magniostheria mangaliensis* Jones, the same specimen as Fig. 7C; B, C. SEM images showing microsculpture patches in the growth bands; D. Close-up of the ornamentation in Fig. 8C, showing the reticular microsculptures, some 5 μm in length.

disappeared in the upper part of the Sunjiagou Formation (Benton, 2016), which represented the mass extinction of tetrapods (Fig. 10). Meanwhile, an absence of metazoans and decreased bioturbation intensity were also observed in the upper part of the Sunjiagou Formation and Liujiagou Formation in North China, coinciding with the mass extinction of invertebrates (Chu et al., 2015, 2017). In addition, microbially-induced sedimentary structures flourished in Early Triassic strata, which might be related to the mass extinction of metazoans and the decrease in bioturbation intensity (Chu et al., 2015, 2017; Tu et al., 2016).

The continental mass extinction was also demonstrated by abiotic factors, including evidence from organic carbon isotopes and lithology. A negative shift of $^{13}\text{C}_{\text{org}}$ was recorded in the Kayitou Formation in various continental sections of South China (Zhang et al., 2016), and associated with the mass extinction of the *Gigantopteris* flora. The distinct change in lithology of sedimentary facies had been observed both in South China and North China during the P-Tr transitional interval (Chu et al., 2016; Zhang et al., 2016), which indicates a change of sedimentary system. The most probable causes of this sedimentary system turnover, associated with enhanced soil erosion and continental weathering, are the widespread die-off of plants and the decrease of vegetation coverage during the P-Tr biotic crisis (e.g. Retallack et al., 1996; Looy et al., 1999, 2001; Ward et al., 2000; Newell et al., 1999; Benton and Newell, 2014; Benton, 2015).

5.2. Records of transgression following the end-Permian mass extinction

In the Meishan section, the base of Bed 27 marks the onset of a rapid marine transgression in the aftermath of the end-Permian mass extinction (Zhang et al., 1996; Yin et al., 2014). For WGEY, the Late Permian Xuanwei Formation is characterized by the common occurrence of coal beds and *Gigantopteris* flora, which corresponds to freshwater lake-swamp or river flat environments (Yu et al., 2010; Bercovici et al., 2015; Zhang et al., 2016). Subsequently, a marine bivalve and brachiopod fauna was recovered in the overlying Kayitou Formation or Feixianguan Formation of the marine-continental transitional siliciclastic settings in South China, which indicates a distinct marine transgression immediately after the extinction of the peat-forming

Gigantopteris flora (Fig. 10).

Generally, the Sunjiagou Formation in North China is regarded as comprising fluvial, lakeshore and shallow lake deposits with frequent paleosols. However, the appearance of marine bivalves and lingulids in the upper part of the Sunjiagou Formation suggests the occurrence of a short time of rapid and sharp transgression (Fig. 10), and which results in the occurrence of the mixed continental-marine biota. In addition, a late Permian conifer flora is preserved in the lower part of the Sunjiagou Formation, but became extinct in the upper part of the Sunjiagou Formation, associated with the disappearance of Palaeozoic-style pariasaurs and a decrease in the intensity of bioturbation (Chu et al., 2017), which indicates that the upper part of the Sunjiagou Formation records the P-Tr biotic crisis in North China. Therefore, the transgression event that is recorded in the upper part of the Sunjiagou Formation also occurred in the aftermath of the mass extinction.

5.3. Implications for marine-continental biostratigraphic correlation during the P-Tr transition

In the present study, we reported a similar mixed continental-marine biota from the upper part of Sunjiagou Formation in North China and the Kayitou Formation in South China (Fig. 10), which provides the biological evidence for correlation between the marine and continental P-Tr deposits. The mixed continental-marine biota contains marine bivalves and brachiopods, and continental conchostracans, insects and plants. The bivalves are assigned to the *Pteria-Neoschizodus-Promyalina* assemblage, which is widely distributed in the conodont-free P-Tr transitional interval of marine shallow-water siliciclastic settings (Yin, 1985; Shen et al., 1995; Fang, 2004; Komatsu et al., 2008; Chen et al., 2009; Huang and Tong, 2014; Chu et al., 2016). This bivalve assemblage is coupled with the numerous lingulid brachiopods that began to occur in the aftermath of the PTME (Sheng et al., 1984; Zhang et al., 2016; Chu et al., 2016). Currently, the *Pteria-Neoschizodus-Promyalina* bivalve assemblage has been regarded as a very useful marker for the P-Tr transitional beds, even the P-Tr boundary, in marine shallow-water siliciclastic deposits (e.g. Chen et al., 2009).

The conchostracans were preserved associated with the aforementioned marine bivalves and brachiopods in the studied sections. In the

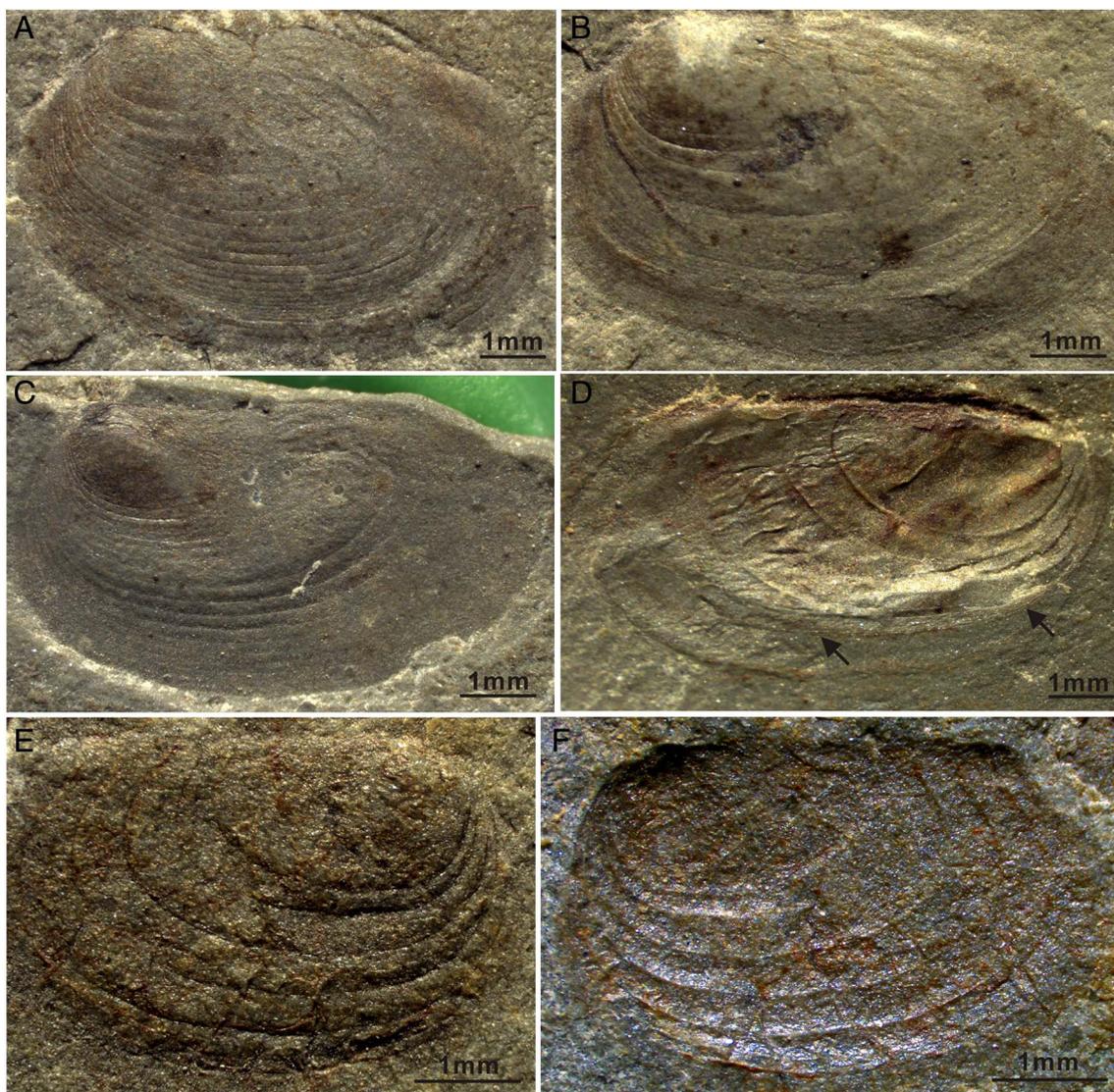


Fig. 9. Large-sized conchostracans from the upper part of Sunjiagou Formation of the Shichuanhe section. A–C. *Magniesteria mangaliensis* Jones, cast of the left valve preserved in fine-grained siltstones, SCH-08-016, SCH-08-017, SCH-08-018; D. *Palaeolimnadiopsis vilujensis* Varentsov, preserved as a combination of a cast of the right valve and an imprint of the left valve, with the double-lines form growth line (marked by arrows), SCH-08-030; E, F. *Palaeolimnadiopsis vilujensis* Varentsov, cast of the right valve and its imprint, SCH-08-032.

Kayitou Formation of the Jinzhong section, the conchostracana fauna is characterized by the occurrence of abundant *Euestheria gutta* specimens. Our previous studies showed that the *Euestheria gutta*-bearing conchostracana fauna was widespread in the P-Tr transitional Kayitou Formation of the continental sections in WGEY (Chu et al., 2013, 2016). It was also reported in Early Triassic deposits from different areas, including the Calvörde Formation and Bernburg Formation of the Germanic Basin (Kozur and Seidel, 1983; Scholze et al., 2016), the Rybinskian horizon on the Russian platform (Lutkevich, 1937), and the Vokhma Formation in the Moscow Syncline (Scholze et al., 2015). Similarly, *Euestheria gutta* also occurs widely in the upper part of the Sunjiagou Formation in the Shichuanhe section, coupled with other species including *Palaeolimnadiopsis vilujensis* and *Magniesteria mangaliensis* that were also found in the Lower Triassic of the Moscow syncline and the Germanic Basin (Liu and He, 2000; Scholze et al., 2015, 2016). In addition, the post-extinction *Peltaspermum-Annalepis* floral assemblage represents the Permian-Triassic transitional flora in South China (Yu et al., 2015; Chu et al., 2016).

Fossil data have shown that a similar mixed continental-marine biota occurred in the stratigraphic interval above the horizon of the PTME in both the Jinzhong and Shichuanhe sections. Both the *Pteria-*

Neoschizodus-Promyalina bivalve assemblage and the *Euestheria gutta*-bearing or *Euestheria gutta-Magniesteria mangaliensis-Palaeolimnadiopsis vilujensis* conchostracana assemblage were found in this specific mixed continental-marine biota in the South China and North China sections, which provides fossil markers to explore biostratigraphic correlation between the marine and continental P-Tr transitional beds. Considering the co-occurrence of the specific bivalve, conchostracana and plant fossil assemblages, the upper part of the Sunjiagou Formation in North China and most of the Kayitou Formation in South China are P-Tr transitional in age.

6. Conclusions

The PTME led to a sharp decrease in the diversity and abundance of the *Gigantopteris* flora in South China, while it eliminated the Palaeozoic-type conifer flora and herbivorous pareiasaurs in North China. Following the beginning of the PTME, a rapid and sharp transgression event occurred and is recorded at the base of the Kayitou Formation in the Jinzhong section and in the upper part of the Sunjiagou Formation of the Shichuanhe section. This transgression resulted in the mixed continental-marine biota, including marine bivalves

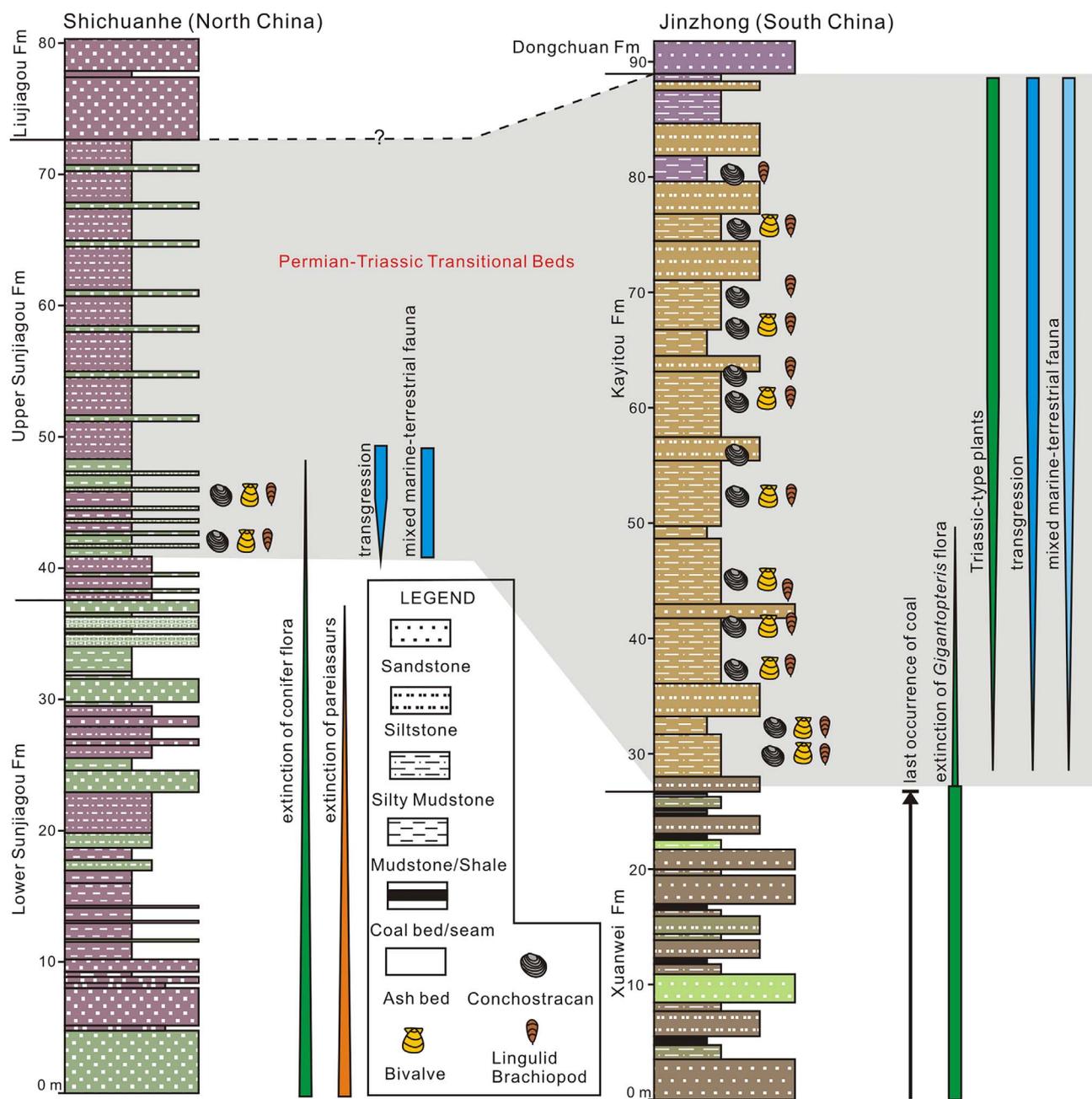


Fig. 10. The distribution of the mixed continental-marine biota in the studied sections and the correlation of the Permian-Triassic transitional beds and mass extinction. The continental mass extinction in South China is revised from Zhang et al. (2016). Grey area showing the Permian-Triassic transitional beds in this study.

and lingulid brachiopods, as well as continental conchostracans, plants and insects. Our study shows that both the Jinzhong and Shichuanhe sections contained a similar mixed continental-marine biota in the aftermath of the biotic crisis, especially the co-occurrence of the *Pteria-Towapteria-Eumorphotis* bivalve assemblage and the *Euestheria gutta-bearing* conchostracan fauna or *Euestheria gutta-Magniestheria mangaliensis-Palaeolimnadiopsis vilujensis* conchostracan assemblage, which provide evidence for correlation between marine and continental P-Tr deposits, and corresponds to the P-Tr transitional beds. We propose that these specific marine bivalve and continental conchostracan assemblages could be considered as markers of the PTME and P-Tr transitional beds in marine-continental siliciclastic settings.

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