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Biostratigraphic correlation and mass extinction during the Permian-Triassic transition in terrestrial-marine siliciclastic settings of South China

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ABSTRACT

The Permian-Triassic boundary marks the greatest mass extinction during the Phanerozoic, which was coupled with major global environmental changes, and is known especially from well-preserved marine fossil records and continuous carbonate deposits. However, the placement of the Permian-Triassic boundary in terrestrial sections and accurate correlation with the marine strata are difficult due to the absence of the key marine index fossils in terrestrial-marine siliciclastic settings. Here, we present detailed fossil data from four terrestrial sections, two paralic sections and one shallow marine section in South China. Our data show that the rapid mass disappearance of the *Gigantopteris* flora in various sections represents the end-Permian mass extinction and the base of the Permian-Triassic transitional beds in terrestrial-marine siliciclastic settings of South China. In particular, we find a mixed marine and terrestrial biota from the coastal transitional sections of the Permian-Triassic transitional Kayitou Formation, which provides a unique intermediate link for biostratigraphic correlation between terrestrial and marine sequences. Accordingly, the *Euestheria gutta*-bearing conchostracan fauna and the *Pteria ussurica variabilis-Towapteria scythica-Eumorphotis venetiana* bivalve assemblage are proposed as markers of the Permian-Triassic transitional beds in terrestrial-marine siliciclastic settings of South China.

1. Introduction

The Permian-Triassic (P-Tr) mass extinction event, the greatest such event in the Phanerozoic, eliminated >90% of marine species and up to 70% of terrestrial vertebrate species, entirely restructuring ecosystems (Erwin, 1993; Benton and Twitchett, 2003; Song et al., 2013; Benton, 2015). Further, major changes in plant communities have also been documented (Retallack, 1995; Looy et al., 1999, 2001; Hermann et al., 2011; Schneebeli-Hermann et al., 2015; Yu et al., 2015; Zhang et al., 2016). A large number of studies have proposed environmental stressors as potentially responsible for the unusual and extreme conditions during the P-Tr crisis and its aftermath, such as global warming, anoxia, ocean acidification, wildfire, enhanced terrestrial weathering, rapid sea level changes and others (Wignall and Twitchett, 1996; Isozaki, 1997; Benton and Twitchett, 2003; S.Z. Shen et al., 2006, 2011a; Wu et al., 2006; Payne et al., 2007; Algeo and Twitchett, 2010; Algeo et al., 2011; Clapham and Payne, 2011; Shen et al., 2011b; Hinojosa et al., 2012; Joachimski et al., 2012; Sun et al., 2012; Benton and Newell, 2014; Sedlacek et al., 2014; Tian et al., 2014; Yin et al., 2014; Clarkson et al., 2015; Ikeda et al., 2015; Song et al., 2015; Rey et al., 2016). Biotic changes associated with the extinction have been documented in detail, including the Lilliput effect (Urbanek, 1993; Twitchett, 2007) in most marine organisms (Hayami, 1997; Fraiser and Bottjer, 2004; Chen et al., 2005; Payne, 2005; Twitchett et al., 2005, Twitchett, 2007; He et al., 2007a, 2010, 2015; Luo et al., 2008; McGowan et al., 2009; Mutter and Neuman, 2009; Song et al., 2011; Forel et al., 2015; Romano et al., 2016) as well as in some terrestrial/freshwater organisms (Tverdokhlebov et al., 2002; Huttenlocker, 2014; Chu et al., 2015a; Romano et al., 2016), cyanobacterial and microbialite blooms (Kershaw et al., 2002, 2012; Wang et al., 2005; Cao et al., 2009; Xie et al., 2010; Mata and Bottjer, 2012; Wu et al., 2014; Chu et al., 2015b), and bursts of low-diversity, opportunistic, and cosmopolitan taxa (Schubert and Bottjer, 1992; Shen et al., 1995; Rodland and Bottjer, 2001; Peng et al., 2007; Huang and Tong, 2014). Recent reviews indicate that tetrapods on land suffered a massive loss during the P-Tr crisis, as severe as that for life in the oceans, but the extinction seems to have been less profound for plants and insects (Benton and Newell, 2014). Some works also suggested that the destruction of terrestrial ecosystems happened simultaneously with the decline in marine diversity

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during the P-Tr transition (Twitchett et al., 2001; Shen et al., 2011a; Metcalfe et al., 2015; Zhang et al., 2016). However, less is known about the specific changes in terrestrial ecosystems during the P-Tr transition. In fact, stratigraphic investigation of the terrestrial P-Tr boundary (PTB) succession lags behind that of marine environments because of more variable sedimentary facies and lower preservation of fossils (Peng and Shi, 2009; Benton and Newell, 2014).

Most work on the biostratigraphy of the terrestrial P-Tr transition has focused on vertebrates, palaeobotany and palynology, with key sections located in China, Russia, Central Europe, South Africa, Australia and Antarctica (Benton, 1985; Retallack, 1995, 2013; Retallack et al., 1996, 2003, 2011; Ward et al., 2000, 2005; Benton et al., 2004; Grauvogel-Stamm and Ash, 2005; Peng and Shi, 2009; Retallack, 2013; Benton and Newell, 2014; Benton, 2015; Chu et al., 2015b; Yu et al., 2015; Zhang et al., 2016; Pereira et al., 2016). However, the placement of the PTB in terrestrial sections and accurate correlation with marine strata are difficult because typical marine index fossils, such as conodonts and ammonoids, are absent in terrestrial facies. So far, the methods of magnetostratigraphy, sequence stratigraphy, cyclostratigraphy, geochemistry and isotopic dating have been employed in the terrestrial PTB and Lower Triassic studies (Aigner and Bachmann, 1992; Szurlies et al., 2003, 2012; Bachmann and Kozur, 2004; Cao et al., 2008; Taylor et al., 2009; Shen et al., 2011a; Cui et al., 2015; Gastaldo et al., 2015; Metcalfe et al., 2015; Zhang et al., 2016). In addition, an eventostratigraphic correlation of the PTB successions has been adopted in terrestrial deposits using the mass extinction or environmental event index itself as a marker (Peng et al., 2001; Cao et al., 2008; Peng and Shi, 2009; Chu et al., 2015a; Zhang et al., 2016), but such an approach is far from ideal and the reliability of such a correlation must be proved. High-precision age-dating associated with multidisciplinary data, especially biostratigraphy, would be the most effective method for the correlation of the PTB from the marine to terrestrial facies (Shen et al., 2011a; Gastaldo et al., 2015; Metcalfe et al., 2015).

Among all the terrestrial P-Tr transitional strata around the world, the joint area of western Guizhou and northeastern Yunnan in southwest China has been subject to much recent attention, being regarded as an ideal place to investigate the correlation between terrestrial and marine P-Tr sequences because it contains good outcrops of shallow marine, marginal or coastal marine, and terrestrial PTB sections, all in close geographic proximity (Wang and Yin, 2001; Peng et al., 2005; Yu et al., 2007, 2015; Peng and Shi, 2009; Shen et al., 2011a; Bercovici et al., 2015; Cui et al., 2015; Zhang et al., 2016). Thus far, the Kayitou Formation has been regarded as comprising P-Tr transitional beds (PTTB), which record a typical P-Tr mixed biota and the process of terrestrial mass extinction, though the placement of the PTB within this succession is still controversial (Yu et al., 2007, 2015; Shen et al., 2011a; Zhang et al., 2016).

Here, we document new fossil data from four terrestrial sections, the Guanbachong section in northeastern Yunan, and the Chahe, Jiucaichong and Xiaohebian sections in western Guizhou; two coastal transitional sections, the Jinzhong section in western Guizhou, and the Jinjibang section in southern Sichuan; and one shallow marine section, the Wadu section in western Guizhou (Fig. 1). The PTB of these sections have been extensively studied to retrieve fossil data in order to establish a correlation among the various facies. A mixed marine and terrestrial biota from the Kayitou Formation of the paralic Jinzhong and Jinjibang sections has been recognized, which provides a unique link from the marine to terrestrial facies. Moreover, seven P-Tr sections have been studied in order to understand the biofacies of transitional shallow marine to terrestrial settings.

2. Materials and methods

We measured seven stratigraphic sections and collected over 1550 fossils, including bivalves, brachiopods, conchostracans and plants from the Xuanwei, Kayitou, Dongchuan and Feixianguan formations of the studied sections. Fossils were carefully hunted bed by bed throughout the stratigraphic sequences and all were recorded with their bed number and thickness level. All identified fossils were numbered and photographed. Detailed lithological logs of the seven sections are provided to mark the positions of the fossils recovered and support the correlation. 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 Quanta-200 SEM. All of the 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, Wuhan (BGEG). The catalogue numbers of the studied specimens include the profile name of the section and specimen number, followed by the storage location. The Guanbachong, Chahe, Xiaohebian, Jiucaichong, Jinzhong, Jinjibang and Wadu sections are abbreviated as GBC, CH, XHB, JCC, JZ, JJB and WD, respectively.

3. General lithostratigraphy

The Sichuan-Yunnan old landmass is recognized in southwestern China during the P-Tr interval (Fig. 1). Eastwards from this old landmass, an almost continuous series of P-Tr sections records a gradual change from terrestrial to marine facies via the terrestrial-marine siliciclastic facies in the adjoining area between western Guizhou and eastern Yunnan (WGEY). The terrestrial P-Tr succession in WGNY consists of three main formations: the Xuanwei, Kayitou and Dongchuan formations, in ascending order (Fig. 2). Of these, the Xuanwei Formation consists mainly of siliciclastic sandstone deposits with intercalations of organic-rich mudstones and coal beds or seams that lie unconformably on the Emeishan basalts and are of latest Permian Wuchiapingian and Changhsingian age (He et al., 2007b). The key characteristic of the Xuanwei Formation in South China is the presence of a rich *Gigantopteris* flora and coal beds or seams (Yu et al., 2007). The Kayitou Formation is similar to the underlying Xuanwei Formation, mainly comprising a 10- to 70-m-thick succession of mudstone, shale and silty sandstone. The difference between the Kayitou and Xuanwei formations is that the Kayitou Formation contains no coal beds or seams. The rocks of the Kayitou Formation, in ascending order, are yellowish green sandstone, siltstone, claystone and shale in the lower part, brownish-yellow siltstone, claystone and shale in the middle part, and purple-red siltstone increasing in proportion upwards in the upper part. The Dongchuan Formation is characterized by a thick succession (over 800 m thick) of purple-red siliciclastic sandstones, siltstones and mudstones, but contains some thin beds of marine muddy limestone at the top. In the eastern part of the area the lower lithostratigrahical unit is also the Xuanwei Formation, while the Kayitou and Dongchuan formations are laterally replaced by the Feixianguan Formation, comprising marine siliciclastic sandstones, mudstones and limestones.

4. Biostratigraphy of the studied sections

4.1. Guanbachong section

The Guanbachong section, located in Leju Country, Zhaotong City, Yunnan Province (Fig. 1), records a succession comprising terrestrial Late Permian to Early Triassic siliciclastic deposits of the Xuanwei, Kayitou and Dongchuan formations. For biostratigraphic investigation, well-preserved Late Permian or Palaeozoic-type plants with large leaves and entire margins were collected in the Xuanwei Formation and the lower part of the Kayitou Formation (Fig. 3), such as *Gigantopteris*, *Gigantonoclea*, *Lobatannularia*, *Annularia*, *Compsopteris*, *Paracalamites*, *Fascipteris*, and *Pecopteris*. Both the data of our palaeobotanical collection and the report by Shen et al. (2011a) indicate a dramatic reduction in the diversity and abundance of the *Gigantopteris* flora in the lower

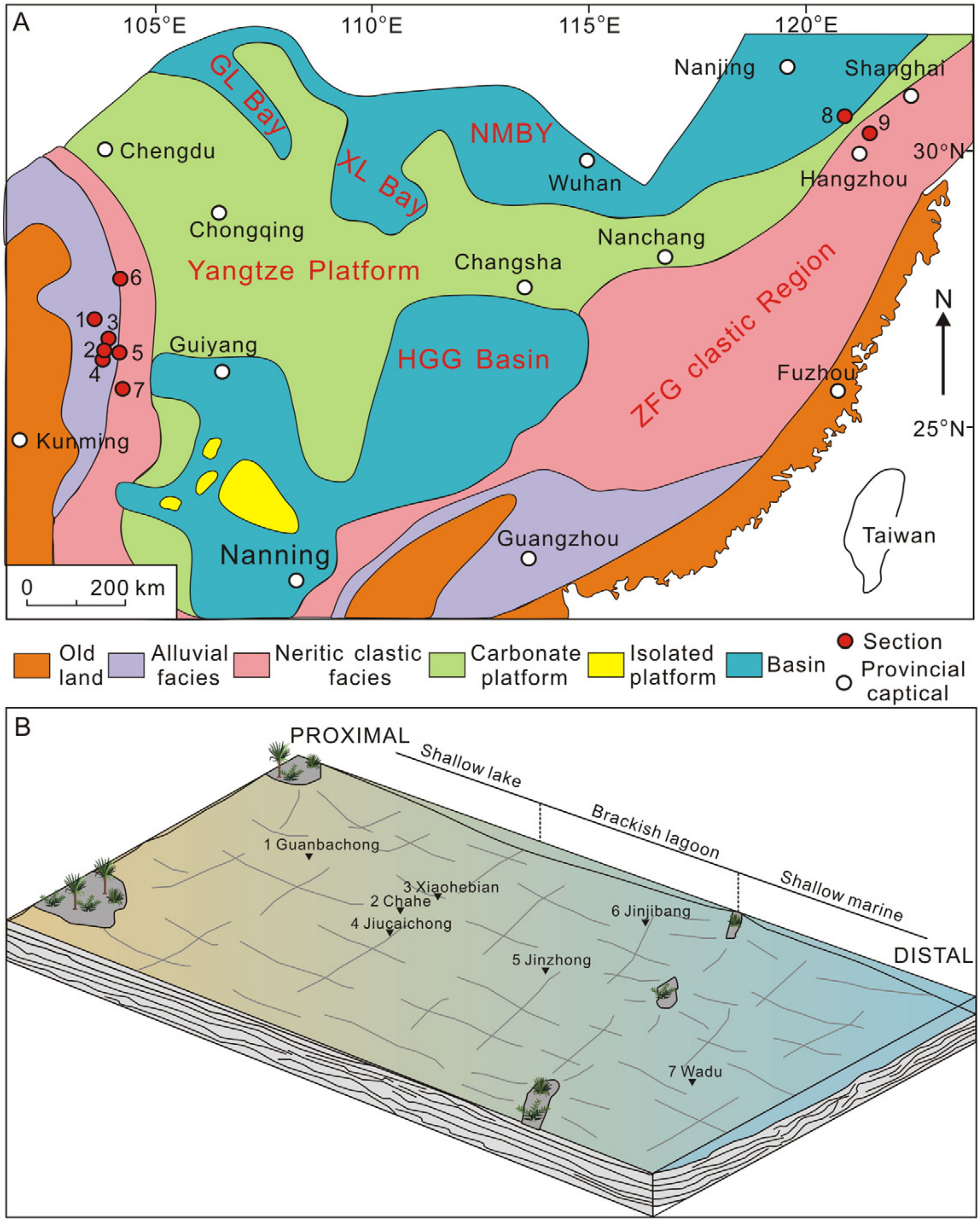


Fig. 1. Investigated localities and simplified lithofacies of South China during the Permian-Triassic transition. A. Palaeogeographic map of South China during the Permian-Triassic transition (after Yin et al., 2014). The studied sections (marking by red dots) were located in different facies. B. The reconstruction of the depositional environment during the Permian-Triassic transition (modified from Bercovici et al., 2015), and position of the seven studied sections is indicated relative to the proximal/distal transect. Abbreviations: GL, Guangyuan-Liangping; XL, Xiakou-Lichuan; NMBY, north marginal basin of Yangtze Platform; HGG, Hunan-Guizhou-Guangxi; ZFG, Gejiang-Fujian-Guangdong. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

part of the Kayitou Formation of the Guanbachong section (Fig. 3). In addition, a negative organic carbon isotope anomaly occurs in the Kayitou Formation, only slightly younger than the disappearance of the *Gigantopteris* flora (Zhang et al., 2016). The loss of the *Gigantopteris* flora and the organic carbon isotope negative shift represent the P-Tr mass extinction of plants as well as the collapse of the tropical rainforest ecosystem.

The PTB succession in the Kayitou Formation consists mainly of brownish-yellow siltstone, mudstone and purple-red siltstones, containing relatively few small conchostracans and plants. About 30 conchostracan specimens with small elliptical carapaces <3.5 mm were collected in the upper part of the Kayitou Formation, approximately 2 m below the top, and they are attributed to the genus *Euestheria* (Fig. 4). The carapace of *Euestheria* is characterized by a very small, strongly convex umbo and dense, narrow growth bands; in particular, well-preserved specimens show an indistinct, regular and very small reticular (<10 μm) microsculpture (Figs. 4–15). In addition, plant fossils assigned to the genus *Peltaspermum* were found in association with

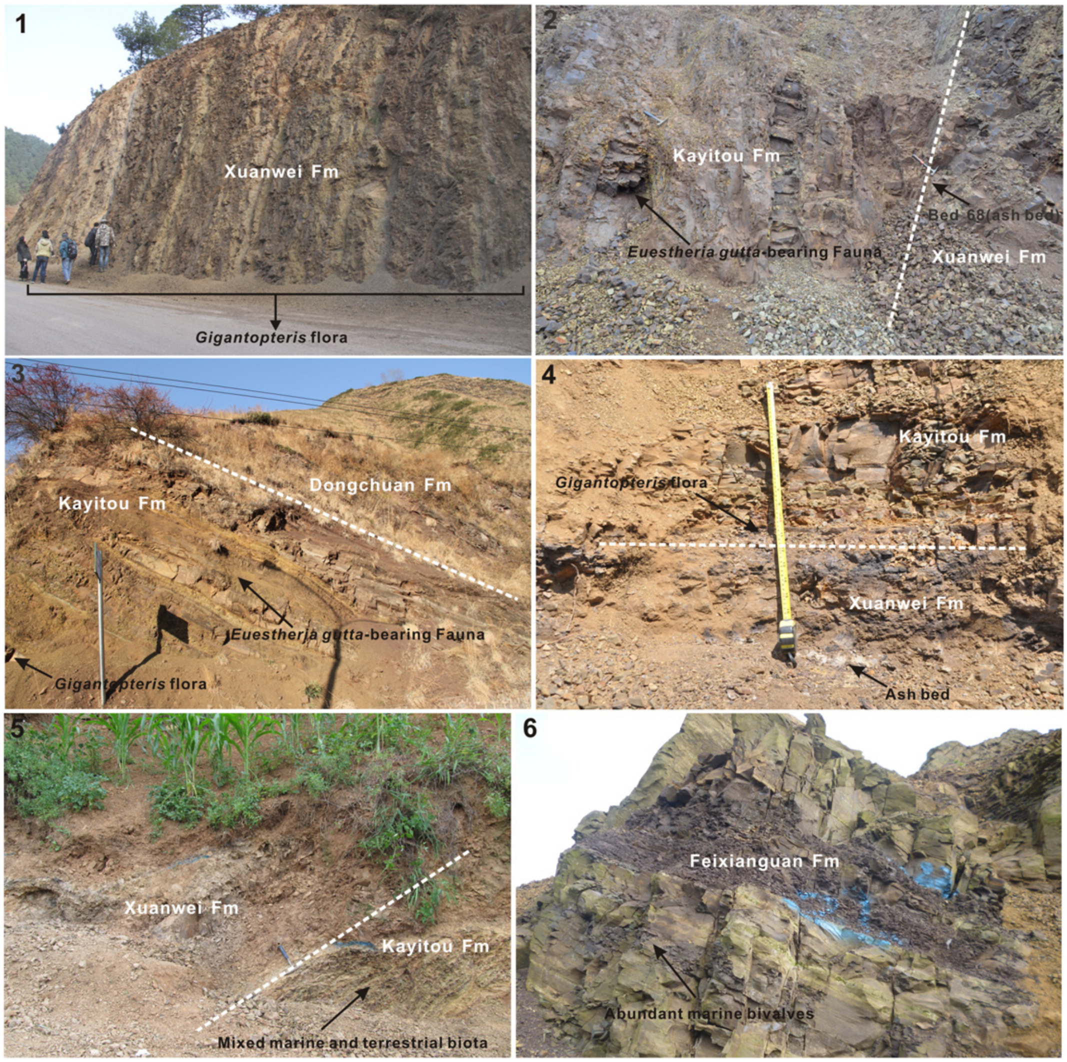


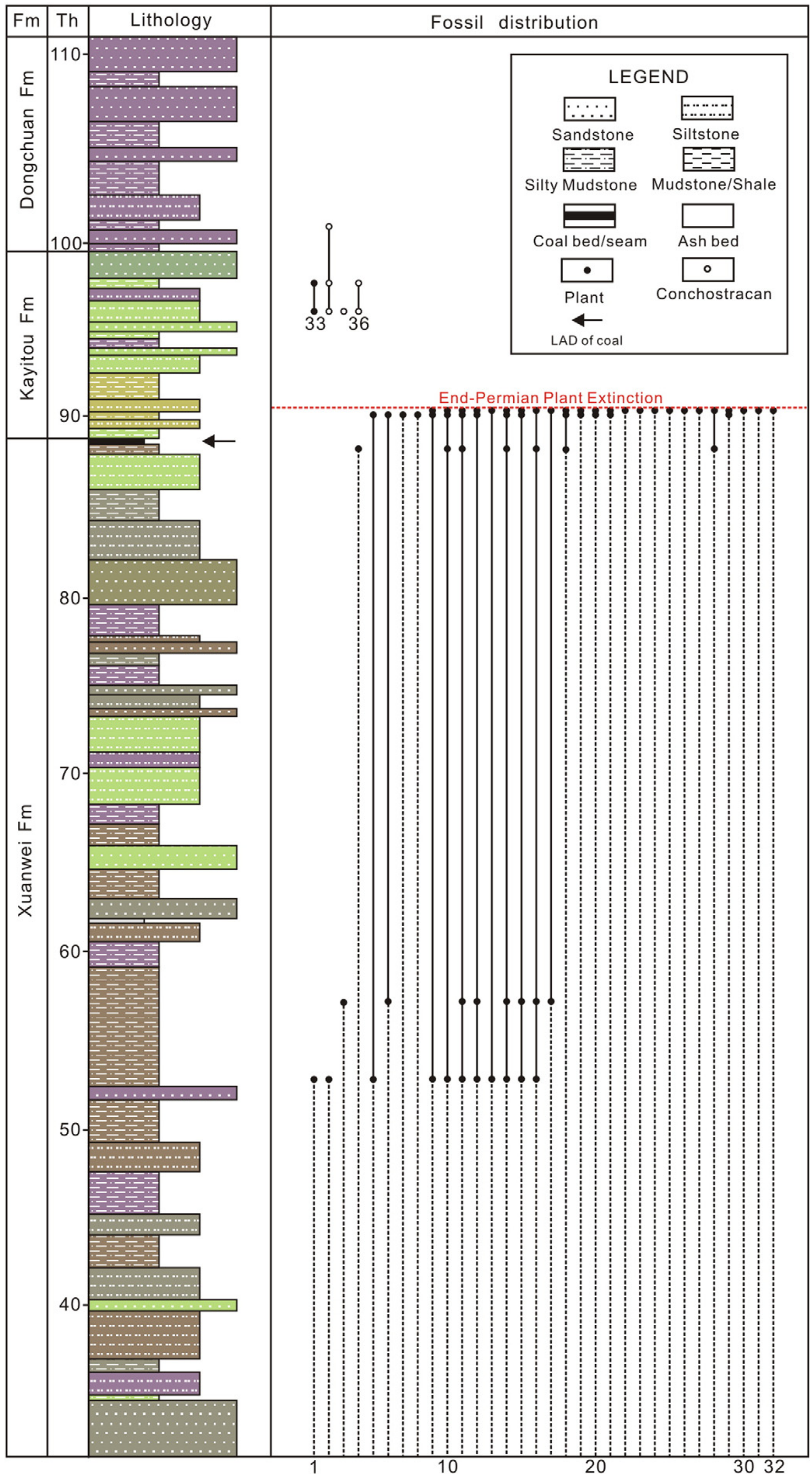
Fig. 2. Permian-Triassic sections in terrestrial-marine siliciclastic settings of South China. 1. The Xuanwei Formation with abundant *Gigantopteris* flora at Chahe section; 2. The lithological boundary between the Xuanwei and Kayitou formations; the base of Kayitou Formation is marked by a thin coal seam and an ash bed which is dated as 252.30 ± 0.07 Ma (Shen et al., 2011a); 3. The lithological boundary between the Kayitou and Dongchuan formations in the Guanbachong section; 4, 5. Lithological boundaries between the Xuanwei and Kayitou formations in the Jiucaichong and Jinzhong sections; 6. The Feixianguan Formation with abundant bivalves in the Wadu section.

the conchostracans (Fig. 3). The genus *Peltaspermum* was present in the Early Permian in Northwest China and has also been recorded in the Sunjiagou and Sunan formations of the Late Permian and in Early and 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 P-Tr mass extinction (Yu et al., 2015). The immediately overlying deposits are largely barren of fossils, and only a few conchostracans and plant fragments were discovered.

4.2. Chahe section

The Chahe section, located near Chahe Town, Weining County, Guizhou Province (Fig. 1) is a classical terrestrial P-Tr section. It has received much recent attention and has been subjected to many high-resolution stratigraphic methods, including biostratigraphy, eventostratigraphy, chronostratigraphy and chemostratigraphy, because of its continuous exposure and well-preserved fossils (Peng et al., 2005; Yu et al., 2007, 2015; Peng and Shi, 2009; Shen et al., 2011a; Cui et al., 2015; Bercovici et al., 2015; Zhang et al., 2016). The *Gigantopteris* flora consists of >30 genera and 81 species in the Xuanwei Formation in the Chahe section, dominated by hygrophilous and thermophilous plant groups such as pecopterids, gigantopterids, Lycopsiales, and Equisetales (Fig. 5; Yu, 2008; Yu et al., 2008, 2015). In addition, further palaeobotanical study indicates a dramatic reduction in the diversity and abundance of the *Gigantopteris* flora in the topmost Bed 68 (Fig. 6), a <3-cm-thick coal seam mixed with an ash bed, which is nearly consistent in age with Bed 25 in the Meishan section (252.30 ± 0.07 Ma, major mass extinction event horizon; Shen et al., 2011a). During our study of the Kayitou Formation in the Chahe section, we found 14 genera and 20 species of plant fossils belonging to the *Gigantopteris* flora, including a certain number of large leaves with entire margins in Bed 69 and the base of Bed 70, such as *Gigantopteris*, *Gigantonoclea*, *Pecopteris*, *Fascipteris*, *Compsopteris*, and *Lobatannularia*, which represent the last occurrence (LO) of the *Gigantopteris* flora at this site (Fig. 7).

Fig. 3. Lithostratigraphy and fossil distribution in the Guanbachong section. Solid lines indicate known stratigraphic ranges; dotted lines indicate uncertain ranges up from below or upwards (Plant fossil data are from Zhang et al., 2016). Abbreviations: Fm, formation; Th, thickness. The list of the fossils is provided in the electronic Supplementary material.


Fm
Th
Lithology
Fossil distribution
LEGEND
Sandstone
Siltstone
Silty Mudstone
Mudstone/Shale
Coal bed/seam
Ash bed
Plant
Conchostracan
LAD of coal
Dongchuan Fm
Kayitou Fm
Xuanwei Fm
End-Permian Plant Extinction
110
100
90
80
70
60
50
40
33
36
1
10
20
30
32

In the overlying section, plant fossils surviving from the Late Permian disappear above Bed 71, while plants of the genus *Peltaspermum* occur in association with conchostracans in the middle-upper part of Bed 71, which is a conchostracan-rich horizon similar to that in the Guanbachong section (Fig. 6). A total of 45 conchostracan specimens were collected in an approximately 8-m-thick interval between Bed 71 and Bed 78, including the genera *Euestheria* and *Palaeolimnadia*, similar to the assemblage from the Guanbachong section; *Palaeolimnadia* also have small-sized rounded carapaces but with low convexity and a smooth unsculptured surface (Chu et al., 2013). In the red-purple Dongchuan Formation, except in the basal part, neither conchostracans nor any other fossils have been observed, but a few plant fragments.

4.3. Xiaohebian section

The Xiaohebian section is situated near Xiaohebian Village of Halahe Town, Guizhou Province (Fig. 1). It consists of a well-developed upper Permian coal-bearing exposure of the Xuanwei Formation, the overlying PTB succession of the brownish-yellow Kayitou Formation, and the red-purple Dongchuan Formation. In our study, an abundant *Gigantopteris* flora was recovered from the Xuanwei Formation below the last ash bed (Bed 8), consisting of *Gigantopteris*, *Gigantonoclea*, *Fascipteris*, *Pecopteris*, etc. (Fig. 8). A dramatic reduction in diversity and abundance of the *Gigantopteris* flora occurs at the top of Bed 8, although a few plant fragments belonging to the this flora are occasionally observed in the overlying strata (Fig. 8). Considering the similarity of the *Gigantopteris* flora with that in the Chahe section, the isotopic age of the youngest ash bed (Bed 8), above a 3-cm-thick coal seam, may be nearly consistent with Bed 68 of the Chahe section as well as Bed 25 of the Meishan section (Shen et al., 2011a), also representing the mass extinction horizon.

Plant fossils of the *Gigantopteris* flora disappear above Bed 9, while *Peltaspermum* and abundant conchostracans were collected in the interval between Bed 10 and the top of the Kayitou Formation (Fig. 8). >85 conchostracan specimens were collected from Beds 10 to 15, including *Euestheria gutta*, *Palaeolimnadia xuanweiensis* and *Euestheria* sp.; 65 specimens were identified as belonging to the genus *Euestheria* (Fig. 4).

4.4. Jiucaichong section

The Jiucaichong section is situated near Jiucaichong Village of Heishitou Town, Guizhou Province (Fig. 1), and exposes a continuous outcrop of the upper part of the Xuanwei Formation, the Kayitou Formation and the lower part of the Dongchuan Formation. Similarly, several well-preserved plants of the *Gigantopteris* flora were collected in the Xuanwei Formation under the last appearance datum (LAD) of coal (Bed 23, Fig. 9). Above the LAD of coal, nine large-leaved plant species belonging to the *Gigantopteris* flora were found at the base of the Kayitou Formation, representing the LO of the *Gigantopteris* flora. In the overlying strata, only fragmentary *Gigantopteris* flora plant fossils in association with *Peltaspermum* were collected.

The dramatic mass extinction of the *Gigantopteris* flora is recorded at the base of the Kayitou Formation (Fig. 9). The strongly contrasting conchostracan fauna appears in the lower part of this formation; over 100 specimens were collected, and *Euestheria gutta* dominates (Fig. 4). Neither the plant nor conchostracan fossils were found in the overlying strata.

4.5. Jinzhong section

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. The successions within the Xuanwei Formation were deposited chiefly in the alluvial-plain to fluvial and lacustrine facies. The *Gigantopteris* flora is commonly observed below the LAD of coal (Bed 7) in the Xuanwei Formation (Fig. 10). Above Bed 7, the diversity of the *Gigantopteris* flora decreases sharply, and only a few plant fragments were collected at the base of the Kayitou Formation in our study (Fig. 10).

The P-Tr transition is represented by the 65-m-thick Kayitou Formation, which corresponds to a shallow coastal lagoon evolving towards coastal transitional deposition, and has yielded a mixed terrestrial-marine biota including plants, conchostracans, bivalves, brachiopods (lingulids), gastropods and insects (Fig. 11). From the base of Bed 9 to the top of the Kayitou Formation, we found the plant fossils *Annalepis* and *Peltaspermum* in abundance (Fig. 10). *Annalepis* is a Triassic lycopsid related to *Isoetes*, with similar growth habits to *Pleuromeia* (Grauvogel-Stamm and Duringer, 1983; Grauvogel-Stamm and Lugardon, 2001; Yu et al., 2010; Naugolnykh, 2013), and is regarded as an important marker fossil for identifying deposits of late Early and Middle Triassic age (Grauvogel-Stamm, 1999; Grauvogel-Stamm and Ash, 2005). Previous work in an adjacent area (Yu et al., 2010, 2015; Bercovici et al., 2015) suggested that the *Annalepis*-*Peltaspermum* assemblage represents the beginning of a new terrestrial flora after the disappearance of the Permian flora following the P-Tr mass extinction, as it contrasts significantly with the *Gigantopteris* flora recovered from the underlying Xuanwei Formation.

In addition, conchostracans are common at this locality and are very abundant on some bedding surfaces of the brownish-yellow mudstones in the Kayitou Formation. Over 200 collected conchostracan specimens are preserved as detailed impressions, commonly with a complete and lightly mineralized chitin carapace; these were identified as belonging to two genera, *Euestheria* and *Palaeolimnadia*, similar to the conchostracans collected from the aforementioned four sections (Fig. 4). Of these, *Euestheria gutta* was most abundant in all of the various levels collected.

Like the characteristically mixed terrestrial-marine biotic communities of the Kayitou Formation in this same facies, the marine fauna, including bivalves and brachiopods (lingulids), also occupies an important position. Several distinct marine bivalve species were recovered from the lower part of the Kayitou Formation (beds 9–13) and were identified as *Pteria ussurica variabilis*, *Neoschizodus orbicularis*, *Promyalina schamarae*, *Neoschizodus laevigatus*, *Eumorphotis venetiana* and *Permophorus bregeri* (Fig. 11). These bivalves are well preserved as both internal and external moulds in weathered shale layers, and several specimens were collected in association with the lingulids. Most of the bivalve specimens are small to medium sized, ranging from 6 to 12 mm in height and 4–15 mm in length, commonly slightly longer than height. This bivalve assemblage represents an Early Triassic fauna. Lingulid brachiopods are very abundant at this site, and most are preserved as complete small-sized internal and external moulds of disassociated valves ranging from 4 to 8 mm in height and 3–5 mm in length (Fig. 11), assigned to the genus *Sinolingularia*, by the evidence of the shape of the shell and the value of the width/length ratio (Peng and Shi, 2008). This lingulid fauna is characterized by low taxonomic diversity, but high abundance of individuals, and some lingulid specimens are preserved associated with the conchostracans and plant fossils (Fig. 11). Early Triassic lingulids were adapted to a wide range of environmental conditions, including variable salinity, dissolved oxygen, and pH, from high-latitude to low-latitude and from the coastal to the relatively deep sea environments, and have been reported world-wide, having survived the catastrophic event as a result of being environmentally opportunistic (Rodland and Bottjer, 2001; Peng et al., 2007). Rare monospecific and similarly mm-sized and trochospiral gastropods were collected in association with the bivalves, and these might belong to a recorded Early Triassic microgastropod form (Fraiser and Bottjer, 2004).

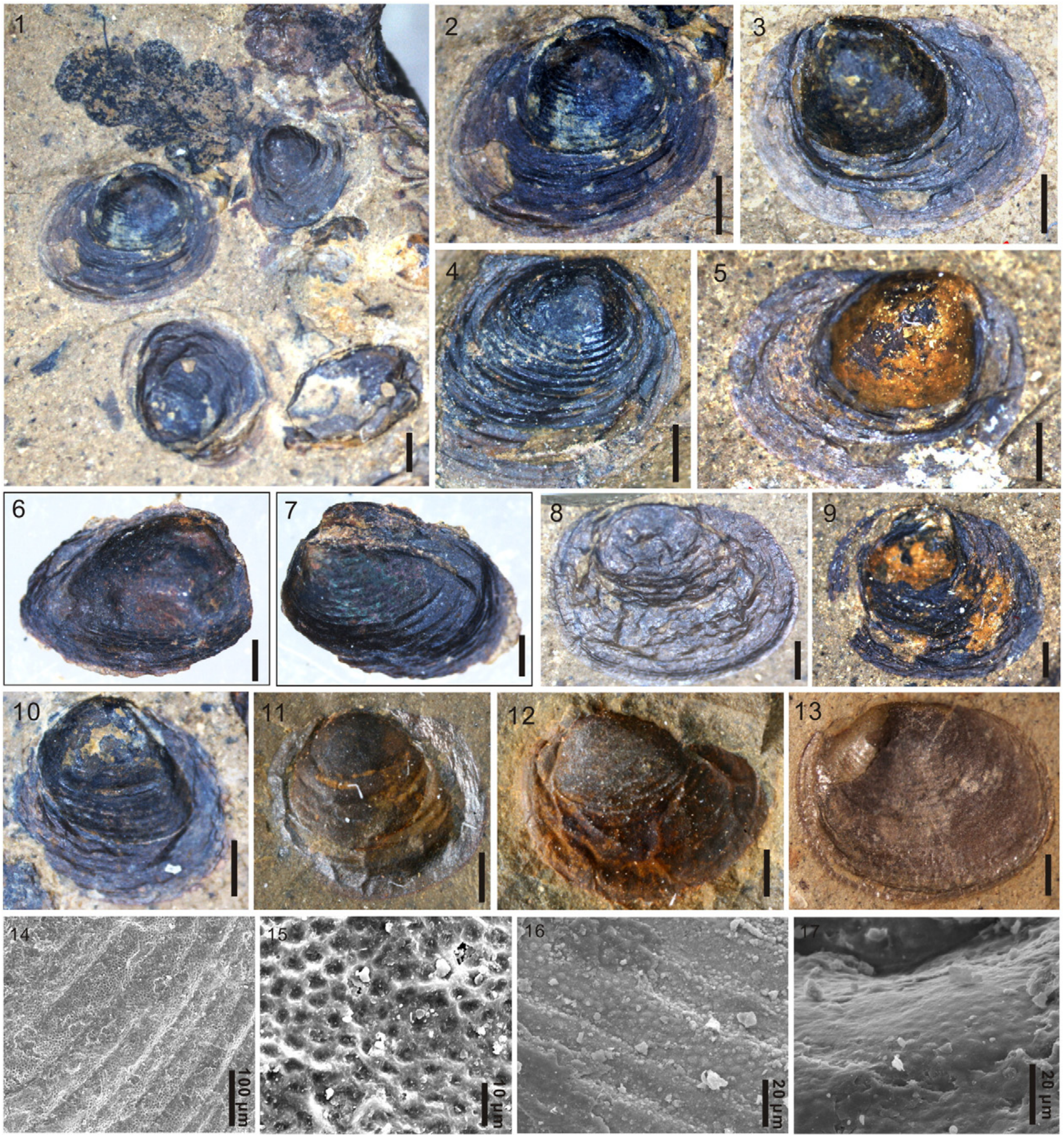


Fig. 4. *Euestheria gutta* Lutkevitch specimens with various deformation characteristics. 1–5, 8–10. *Euestheria gutta* specimens collected from the middle part of the Kayitou Formation of the Jiucaichong section, JCC-26-1, JCC-26-1-1, JCC-26-7, JCC-26-13, JCC-26-22, JCC-27-4, JCC-27-10, JCC-27-17; 6, 7. *Euestheria gutta* specimens collected from the upper part of the Kayitou Formation of the Xiaohebian section, XHB-10-12a, XHB-10-12b; 11, 12. *Euestheria gutta* specimens collected from the lower part of the Kayitou Formation of the Chahe section, CH-71-7, CH-71-9; 13. *Euestheria gutta* specimens collected from the lower part of the Kayitou Formation of the Jinzhong section, JZ-9-11; 14–17. SEM images showing growth bands and reticular microsculptures. The scale bars in 1–13 represent 1 mm.

4.6. Jinjibang section

The Jinjibang section is located near Jinji village, approximately 5 km southwest of Zhenzhou town, Junlian County, Sichuan Province (Fig. 1), and exposes a continuous outcrop of the upper part of the Xuanwei Formation and the lower part of the Feixianguan Formation. Latest Permian deposition is represented by the Xuanwei Formation, which is composed of siliciclastic sandstones, mudstones, claystones, coal beds or seams associated with a diverse *Gigantopteris* flora, marine bivalves and brachiopods (lingulids). In previous studies, the coal-bearing Xuanwei Formation was locally divided into two parts in this area: in ascending order, the Junlian and Jinjibang formations. The overlying lower part of the Feixianguan Formation is composed of yellowish-green siltstone, claystone and shale, which contain marine bivalves, brachiopods, conchostracans and plants. The PTB succession is the lower part of the Feixianguan Formation, which corresponds to a shallow coastal lagoon evolving towards a coastal transitional deposition.

The latest Permian megaflora recovered from the Xuanwei Formation consists of 45 genera and 83 species, and these are dominated by pteridosperms, Equisetales, lycophytes and Filicales, such as *Gigantopteris*, *Gigantonoclea*, *Compsopteris*, *Lobatannularia*, *Paracalamites*, *Lepidodendron*, *Lepidostrobophyllum*, *Pecopteris*, and

Fig. 5. Typical *Gigantopteris* flora from the Xuanwei Formation of the Chahe section. 1. *Lobatannularia cathaysiana* Yao, CH-18-29; 2. *Cladophlebis permica* Lee et Wang, CH-18-12a; 3. *Stigmaria ficoides* (Sternb.) Brongnairt, CH-46-1; 4. *Fascipteris densata* Gu et Zhi, CH-18-42; 5. *Pecopteris orientalis* (Schenk) Potonie, CH-18-59; 6. *Compsopteris* sp., CH-58-5; 7. *Guizhoua gregalis* Zhao, CH-58-17b; 8. *Pecopteris marginata* Gu et Zhi, CH-58-14a; 9. *Compsopteris contracta* Gu et Zhi, CH-58-6; 10. *Gigantonoclea hallei* (Asama) Gu et Zhi, CH-29-1; 11. *Rajahia guizhouensis* Zhang, CH-67-13. The scale bars represent 1 cm.

Fascipteris, which represent a tropical rainforest community (Fig. 12; Li et al., 1982; Zhu et al., 1984). Similar to other sections, the diversity of the end-Permian rainforest-type vegetation is drastically reduced at the top of the Xuanwei Formation, associated with the disappearance of coal seams (Fig. 12). The PTB succession is represented by the yellowish-green siltstone, claystone and shale deposits of the lower part of the Feixianguan Formation, <10 m thick, yielding a mixed terrestrial-marine biota including plants, conchostracans, bivalves, brachiopods (lingulids), and gastropods. The abundant and monogeneric *Annalepis* flora replaces the *Gigantopteris* flora in this interval, associated with low-diversity marine bivalves including *Pteria ussurica variabilis* and *Neoschizodus orbicularis* (Fig. 12). In addition, a few conchostracans

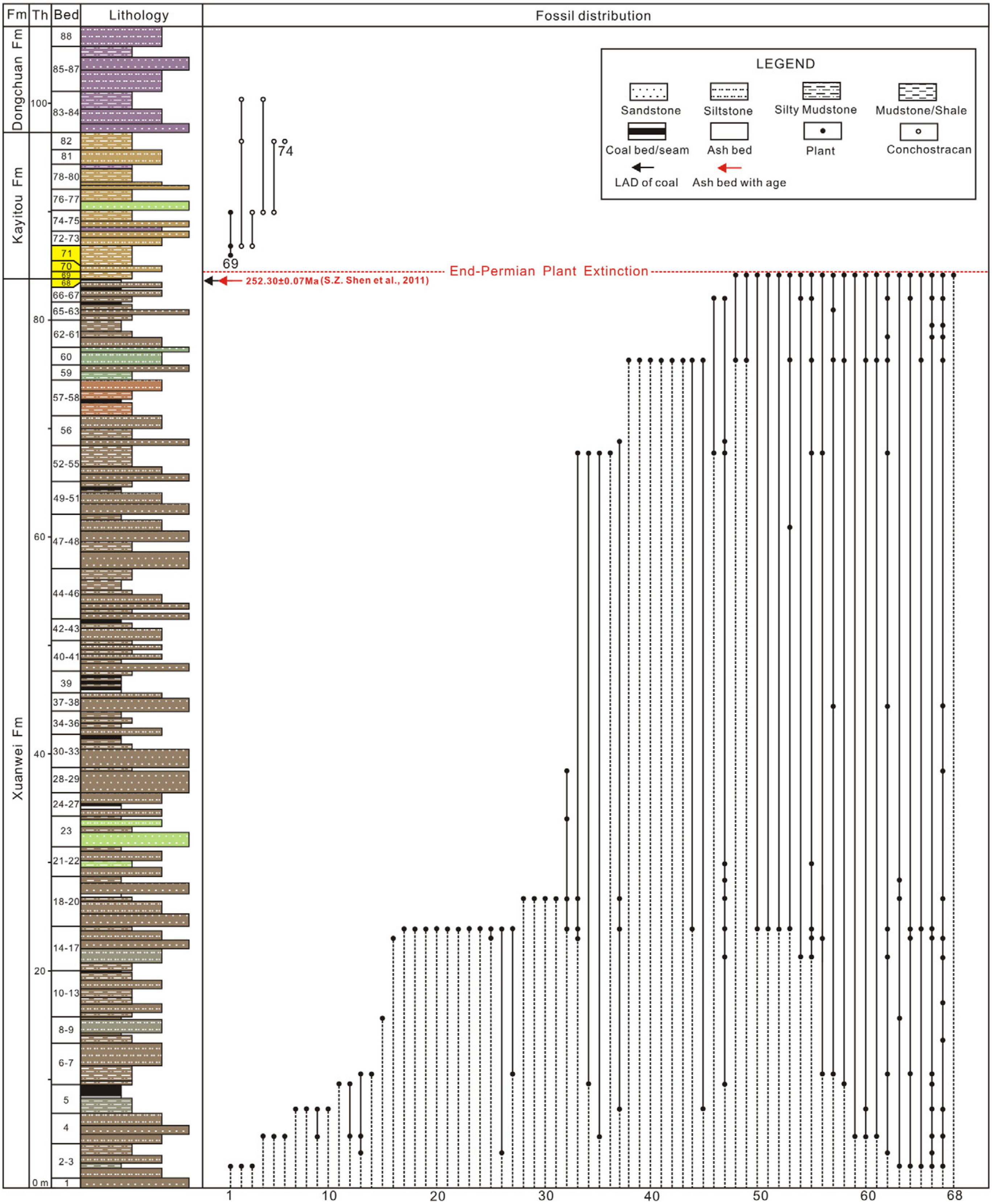


Fig. 6. Lithostratigraphy and fossil distribution in the Chahe section. The age data based on Shen et al. (2011a). Solid lines indicate known stratigraphic ranges; dotted lines indicate uncertain ranges up from below or upwards. Abbreviations: Fm, formation; Th, thickness. The list of the fossils is provided in the electronic Supplementary material.

Fig. 7. Typical *Gigantopteris* flora from the lower part of the Kayitou Formation of the Chahe and Jiucaichong sections. 1. *Gigantopteris dictyophylloides* Gu et Zhi, CH-69-13; 2. *Rajahia guizhouensis* Zhang, CH-69-2; 3. *Stigmaria ficoides* (Sternb.) Brongnairt, CH-69-36; 4. *Gigantopteris* sp., JCC-24-2; 5, 6. *Gigantonoclea plumosa* Mo, JCC-24-13; 7, 8. *Rajahia guizhouensis* Zhang, CH-69-7, JCC-24-6. The scale bars in 1–3, 7, 8 represent 1 cm.

were collected 2 m above the LO of the *Gigantopteris* flora and were identified as *Euestheria*, dominated by the species *Euestheria gutta* (Fig. 11).

4.7. Wadu section

The Wadu section, located south of Wadu village, Panxian County, Guizhou Province (Fig. 1), records the well-developed Xuanwei and Feixianguan formations. The Xuanwei Formation is composed of sandstones, siltstones, claystones and coal seams, and approximately 160 m of outcrop was measured. In ascending order, the Feixianguan Formation consists mainly of yellowish green siltstone, claystone and shale in the bottom 10 m, brownish-yellow sandstone, siltstone and shale in the >30 m of the middle part, and >500 m of purple-red sandstone in the upper part. The yellowish green deposits at the bottom of the Feixianguan Formation at this site laterally correlate with strata of the Kayitou Formation and represent the PTB succession.

Among the fossils recovered from the Xuanwei Formation, an abundant *Gigantopteris* flora with large leaves and entire margins was collected below the LAD of coal (Bed 17), including *Gigantopteris*,

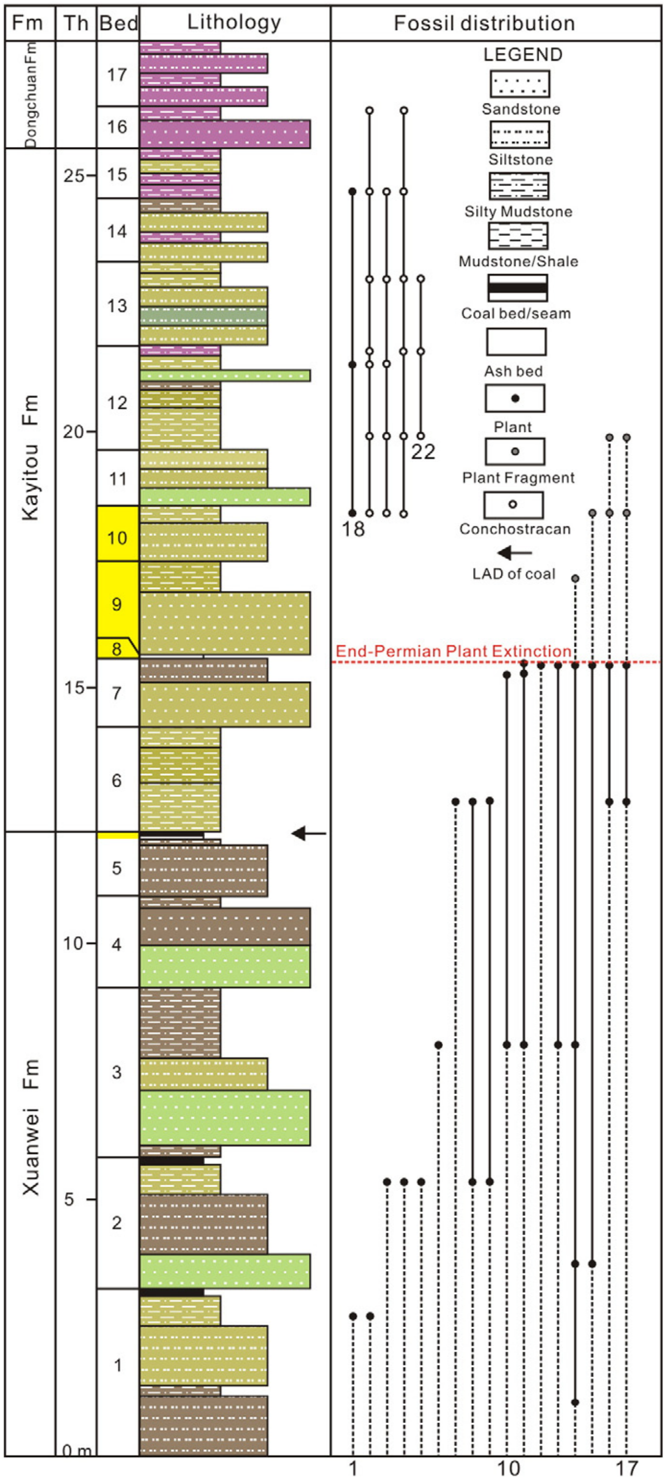


Fig. 8. Lithostratigraphy and fossil distribution of the Xiaohebian section. Solid lines indicate known stratigraphic ranges; dotted lines indicate uncertain ranges up from below or upwards. Abbreviations: Fm, formation; Th, thickness. The list of the fossils is provided in the electronic Supplementary material.

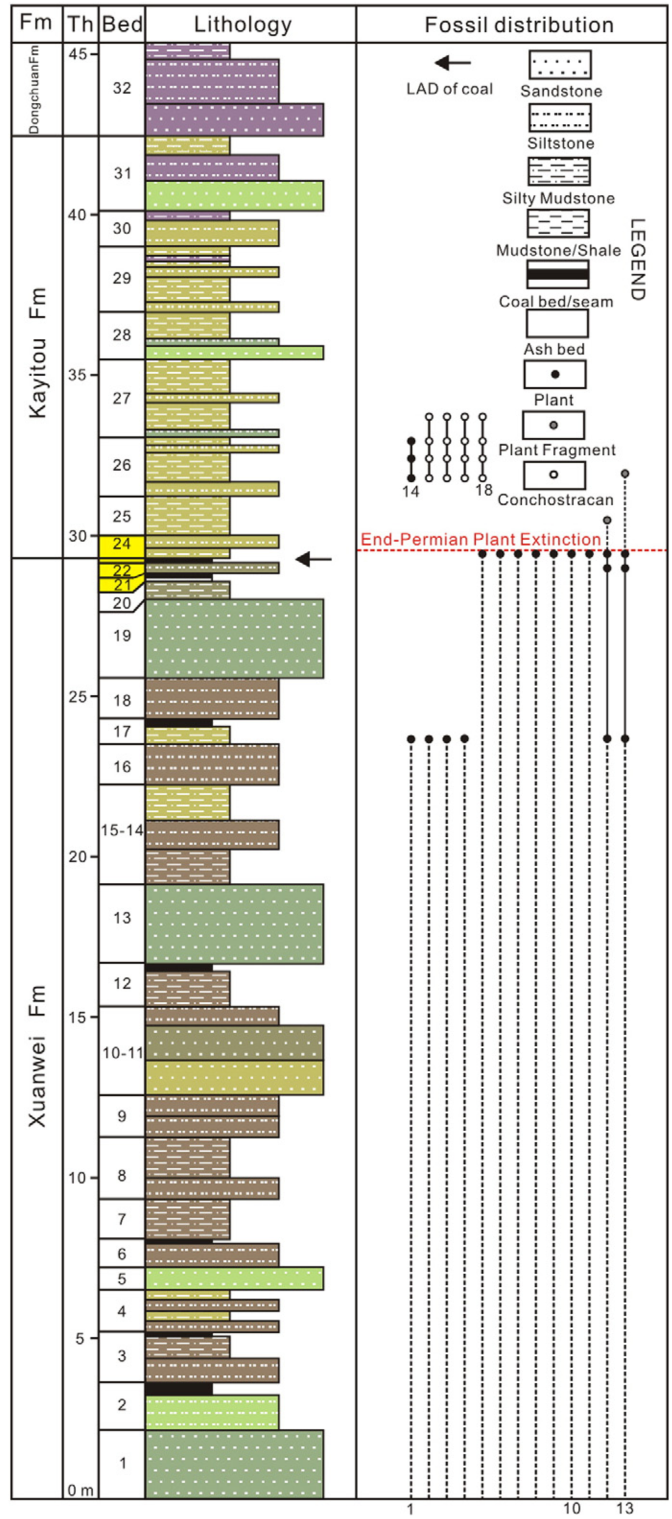
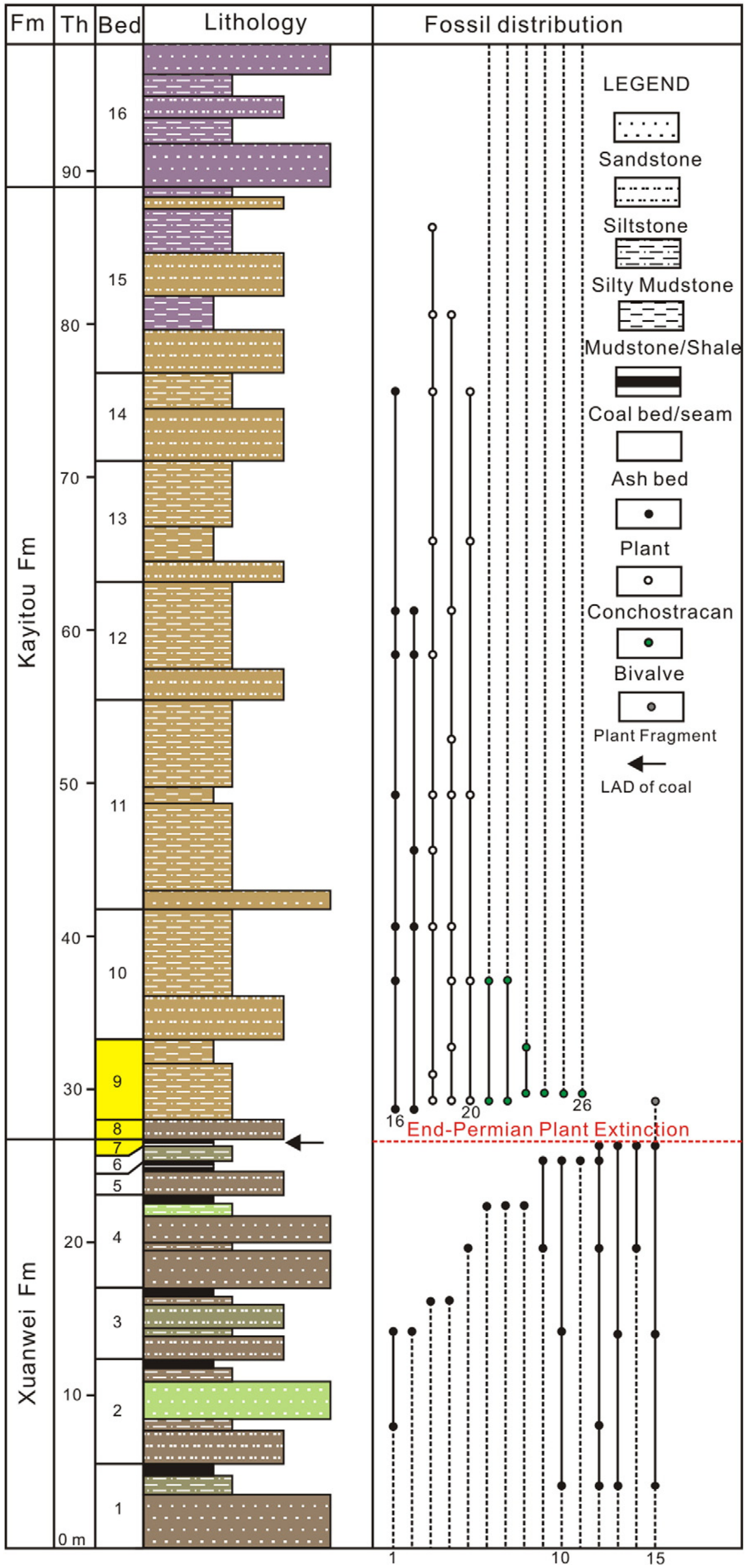


Fig. 9. Lithostratigraphy and fossil distribution of the Jiucaichong section. Solid lines indicate known stratigraphic ranges; dotted lines indicate uncertain ranges up from below or upwards. Abbreviations: Fm, formation; Th, thickness. The list of the fossils is provided in the electronic Supplementary material.

Gigantonoclea, *Lobatannularia*, *Stigmaria*, *Annularia*, *Paracalamites*, *Fascipteris*, and *Pecopteris* (Fig. 13). Only a few fragmentary plant remains were collected from Bed 18 (15-cm-thick claystones), and the *Gigantopteris* flora disappears above this level (Fig. 13). The marine bivalve fauna begins to appear at the base of Bed 19, coupled with lingulid brachiopods, including *Pteria ussurica variabilis*, *Promyalina schamarae*, *P. putiatinensis*, *P. spathi*, *Neoschizodus orbicularis*, *Astartella* sp., *Unionites fassaensis*, *Claraia bioni*, *Eumorphotis venetiana*, *Permophorus bregeri*, *Neoschizodus laevigatus*, *Towapteria scythica*, *Leptochondria virgalensis*, and *Bakevellia goldfussi* (Fig. 14). Obviously, the mean size of these bivalves is larger than the value measured from the last two sections



Fm
Th
Bed
Lithology
Fossil distribution
Kayitou Fm
Xuanwei Fm
90
80
70
60
50
40
30
20
10
0 m
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
LEGEND
Sandstone
Siltstone
Silty Mudstone
Mudstone/Shale
Coal bed/seam
Ash bed
Plant
Conchostracan
Bivalve
Plant Fragment
LAD of coal
16
20
26
End-Permian Plant Extinction
1
10
15

because of the appearance of larger forms. In particular, the lingulid brachiopods with articulated valves are vertically positioned in the sandstone of Bed 19, which may indicate that the fossils were preserved in situ. In addition, bivalves and lingulid brachiopods are common in the upper deposits.

5. Biostratigraphic correlation and the end-Permian mass extinction

5.1. Biostratigraphic correlation among different siliciclastic settings in South China

In the four continental sections described here, the fossil records reveal the same pattern of ecosystem evolution during the Permian-Triassic transitional interval, namely that the diversity of the *Gigantopteris* flora is drastically reduced in the lower part of the Kayitou Formation, representing the terrestrial end-Permian mass extinction in South China. The plants of the *Gigantopteris* flora, with large leaves and entire margins, appear at intervals of 2.2 m, 1 m, 2 m and 0.7 m above the occurrence of the last coal bed or seam in the Kayitou Formation, in the Guanbachong, Chahe, Xiaohebian and Jiucaichong sections respectively, and this variability of thickness to the last coal bed or seam across space might reflect the changes in the local depositional environment. The fragmentary remains of the *Gigantopteris* flora commonly appear in overlying beds associated with abundant and low-diversity peltaspermalean foliage in the Kayitou Formation (Fig. 15). The *Euestheria gutta*-bearing conchostracan fauna appears in the Kayitou Formation at 1.8 m, 2 m and 5 m above the occurrence of the last coal bed or seam, associated with peltaspermalean foliage and *Gigantopteris* flora remains. These characteristics of fossil distribution appear to be common in the terrestrial Permian-Triassic transitional Kayitou Formation in South China.

The mixed marine-terrestrial biota from the Kayitou Formation of the Jinzhong and Jinjibang sections contains a range of fossil groups, including plants, conchostracans, bivalves, brachiopods (lingulids), gastropods and insects. The distribution of the mixed assemblage is represented by the following characteristics: the diversity of the *Gigantopteris* flora decreases significantly at the base of the Kayitou Formation or the top of the Xuanwei Formation, corresponding to the horizon of the terrestrial end-Permian mass extinction in South China; the *Euestheria gutta*-bearing conchostracan fauna is recovered from the Kayitou Formation at the Jinzhong and Jinjibang sections and is related to the same assemblage from the terrestrial sections; the Triassic-type plant *Annalepis* associated with the peltaspermalean flora first appears at the base of the Kayitou Formation; the marine bivalve assemblage associated with the *Euestheria gutta*-bearing conchostracan fauna is recovered from the Kayitou Formation and is dominated by *Pteria ussurica variabilis*, *Neoschizodus orbicularis*, *Promyalina schamarae*, *Neoschizodus laevigatus*, *Eumorphotis venetiana* and *Permophorus bregeri*, assigned to the *Pteria ussurica variabilis-Eumorphotis venetiana-Promyalina schamarae* assemblage. The mixed terrestrial-marine biota records both the process of the mass extinction and the biostratigraphic evidence of the correlation of the Permian-Triassic transitional interval between marine and terrestrial successions.

In the latest Permian Xuanwei Formation, the Wudu section comprises terrestrial-marine sediments, which contain abundant plant fossils of the *Gigantopteris* flora, and also records the mass extinction of plants at the top of the Xuanwei Formation associated with the LAD of the coal bed. Typical Permian-Triassic transitional marine siliciclastic deposits contain abundant bivalves, brachiopods (lingulids), and ostracods, all recovered from the Wudu section in our study. At the base of the Feixianguan Formation, the marine bivalve fauna is represented by the *Pteria ussurica variabilis-Towapteria scythica-Eumorphotis venetiana* assemblage. This bivalve fauna is widespread in shallow-water facies PTB sections in South China (Sheng et al., 1984, 1987; Shen et al., 1995; Chen et al., 2009; Huang and Tong, 2014).

Therefore, we have provided evidence that the same fossil assemblage and variation trends appear in both the Kayitou Formation in the terrestrial and coastal sections, and in the lower part of the Feixianguan Formation in the shallow marine section. We infer that these intervals were deposited simultaneously and should be considered transitional from the latest Permian to earliest Triassic based on the P-Tr mixed character of the various fossils from these PTTB (Fig. 16).

5.2. The end-Permian mass extinction in the studied area

It is important to focus on plants during mass extinction intervals in terrestrial successions because plants are some of the most important elements and the primary producers in the terrestrial ecosystem, and plant abundance and diversity are key indices of ecosystem functioning in both geological and modern times. The terrestrial mass extinction during the P-Tr transitional interval is commonly associated with a significant decrease in the diversity of plant fossils (Retallack, 1995; Looy et al., 1999, 2001; Shen et al., 2011a; Benton and Newell, 2014; Yu et al., 2015). Furthermore, the current study has revealed that the PTB crisis had a much more profound effect on vegetation than the other mass extinctions that not only impacted individual organisms but also whole families, and so it can really be regarded as being a global mass extinction event that widely affected both the marine and terrestrial ecosystems (Cascales-Miñana and Cleal, 2014; Cascales-Miñana et al., 2015). Previous studies have suggested that the main terrestrial P-Tr crisis occurred at the base of the Kayitou Formation in the area of western Guizhou and eastern Yunnan, and this is based on biostratigraphic, isotopic and geochronological data (Yu et al., 2007, 2015; Peng and Shi, 2009; Shen et al., 2011a). Recently, a credible multidisciplinary study suggested that the Kayitou Formation records the process of the terrestrial Permian-Triassic mass extinction (Zhang et al., 2016). In our studied sections, the rainforest-type *Gigantopteris* flora is commonly observed and mostly well-preserved, with large leaves and entire margins in the coal-bearing Xuanwei Formation (Fig. 16). Our detailed investigation of the plant fossils indicates a dramatic reduction in the diversity and abundance of this flora at the base of the Kayitou Formation, a few metres above the LAD of coal beds, in the Guanbachong, Chahe, Xiaohebian, and Jiucaichong sections (Fig. 16). In the Jinzhong and Jinjibang sections, the *Gigantopteris* flora disappears at the top of the Xuanwei Formation or the base of the Feixianguan Formation, which corresponds to the level of the extinction event in the four terrestrial sections (Fig. 16). The absence of coal and plant fossils in the immediately overlying deposits, associated with the negative shift of $^{13}C_{org}$ in the Guanbachong and Chahe sections, indicates the terrestrial end-Permian mass extinction and the collapse of the tropical rainforest ecosystem (Shen et al., 2011a; Zhang et al., 2016).

From the plant fossil records in the series of PTB sections in WGEY, we find that the diversity and abundance of the rainforest-type *Gigantopteris* flora experiences a sharp decrease at the base of the PTTB and shows a similar pattern among the studied sections that record the terrestrial end-Permian biotic crisis (Fig. 16). Considering the high-precision isotopic age from the Chahe section and the correlation among the continuous sequences, the time horizon of the biotic crisis in the studied area is simultaneous with the end-Permian mass extinction or the first stage of the Permian-Triassic mass extinction (Song et al., 2013) in marine facies.

Fig. 10. Lithostratigraphy and fossil distribution of the Jinzhong section. Solid lines indicate known stratigraphic ranges; dotted lines indicate uncertain ranges up from below or upwards. Abbreviations: Fm, formation; Th, thickness. The list of the fossils is provided in the electronic Supplementary material.

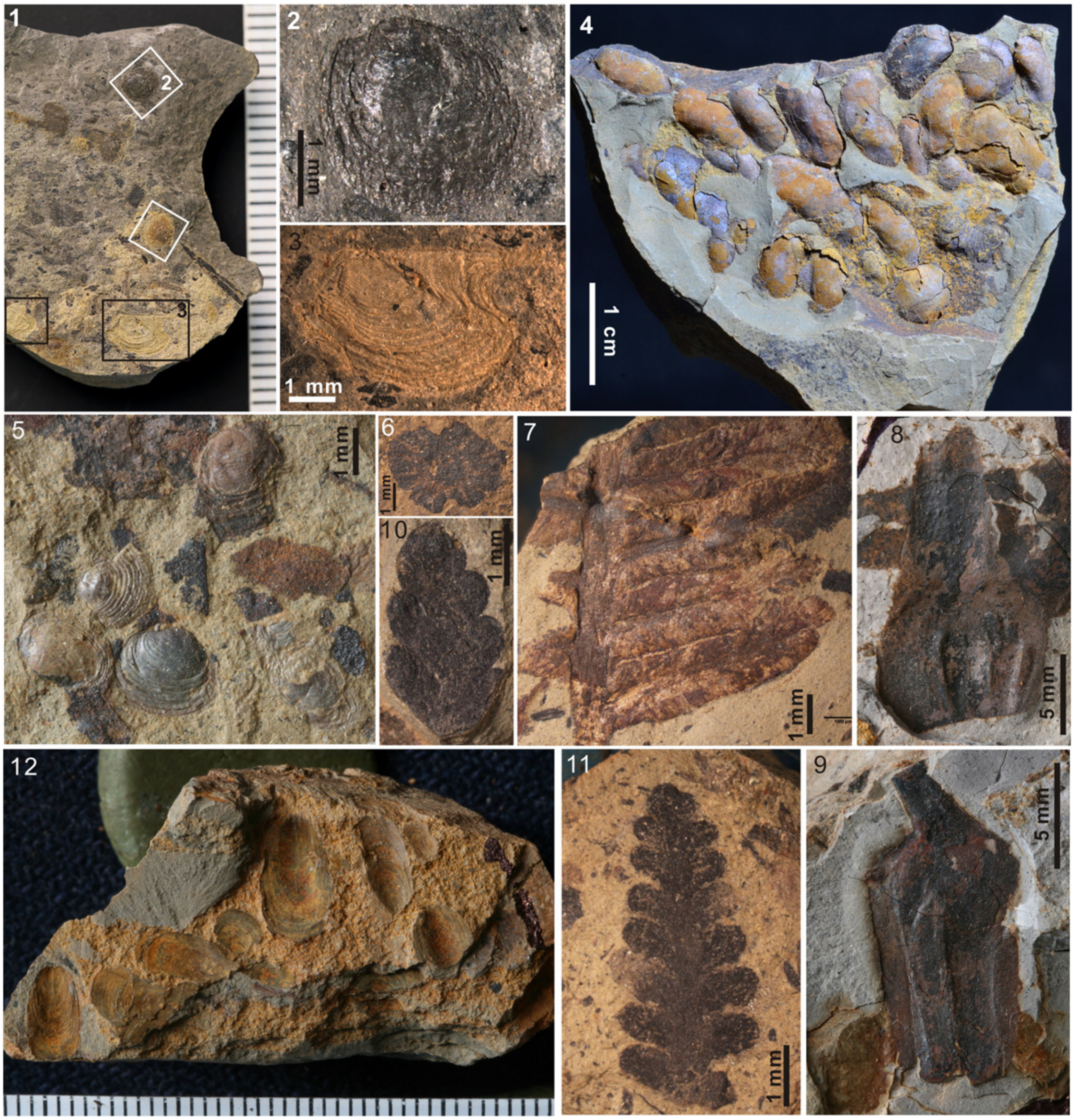


Fig. 11. Mixed marine and terrestrial biota from the coastal transitional Jinzhong and Jinjibang sections. 1. Conchostracans and marine bivalves preserved on the same bedding surface, collected from the base of the Feixianguan Formation in the Jinjibang section, JJB-158,002; 2. *Euestheria gutta* Lutkevitch, close-up views of indicated portions of 1, JJB-158-1; 3. *Pteria ussurica variabilis* Chen, close-up views of indicated portions of 1, JJB-158-3; 4. Marine bivalves collected from the Kayitou Formation in the Jinzhong section, JZ-9-13; 5. Conchostracans collected from the Kayitou Formation of the Jinzhong section, JZ-9-22; 6. *Peltaspermum* sp., collected from the Kayitou Formation of the Jinzhong section, JZ-10-2; 7. *Pecopteris* sp., collected from the Kayitou Formation of the Jinzhong section, JZ-9-14; 8. *Annalepis brevicystis* Meng, collected from the base of the Feixianguan Formation of the Jinjibang section, JJB-159-7; 9. *Annalepis zeilleri* Fliche, collected from the base of the Feixianguan Formation of the Jinjibang section, JJB-159-8; 10, 11. *Peltaspermum* cf. *martinsii* (Harris) Poort et Kerp, collected from the Kayitou Formation of the Jinzhong section, JZ-10-14, JZ-11-10; 12. lingulid brachiopod specimens, assigned to *Sinolingularia*, collected from the Kayitou Formation of the Jinzhong section, JZ-9-21.

Most of the Permian-type plant taxa were wiped out in the PTB crisis, with only a few relicts persisting into the PTTB. These relict taxa of the *Gigantopteris* flora, however, are usually represented by only a few fragmentary specimens from the lower part of the Kayitou Formation (Fig. 15), suggesting long-distance transport or reworking. In the aftermath of the main biotic crisis, the *Gigantopteris* flora is replaced by a low-diversity opportunistic flora dominated by the genera *Annalepis* and *Peltaspermum*, which demonstrates stressed environmental conditions on land. Meanwhile, conchostracans appear in abundance a few metres above the main extinction horizon in the Kayitou Formation of the four terrestrial sections and the two coastal Jinzhong and Jinjibang sections, but disappear immediately at the horizon of the lower part of the overlying Dongchuan Formation. The disappearance of conchostracans was probably caused by dramatically shrinking niches as the regional facies turned from a shallow lake or brackish lagoon into braided rivers within an alluvial plain, between the Kayitou and Dongchuan formations in western Guizhou and eastern Yunnan (Bercovici et al., 2015).

This sedimentary switch from low-energy meandering streams to high-energy braided streams has been noted before in the terrestrial red bed successions of Russia (Newell et al., 1999), South Africa (Ward et al., 2000), and Spain (Arche and López-Gómez, 2005) at or close to the PTB. The switch had been explained by changes in regional tectonics or increased rainfall, but the most likely explanation is that stripping of

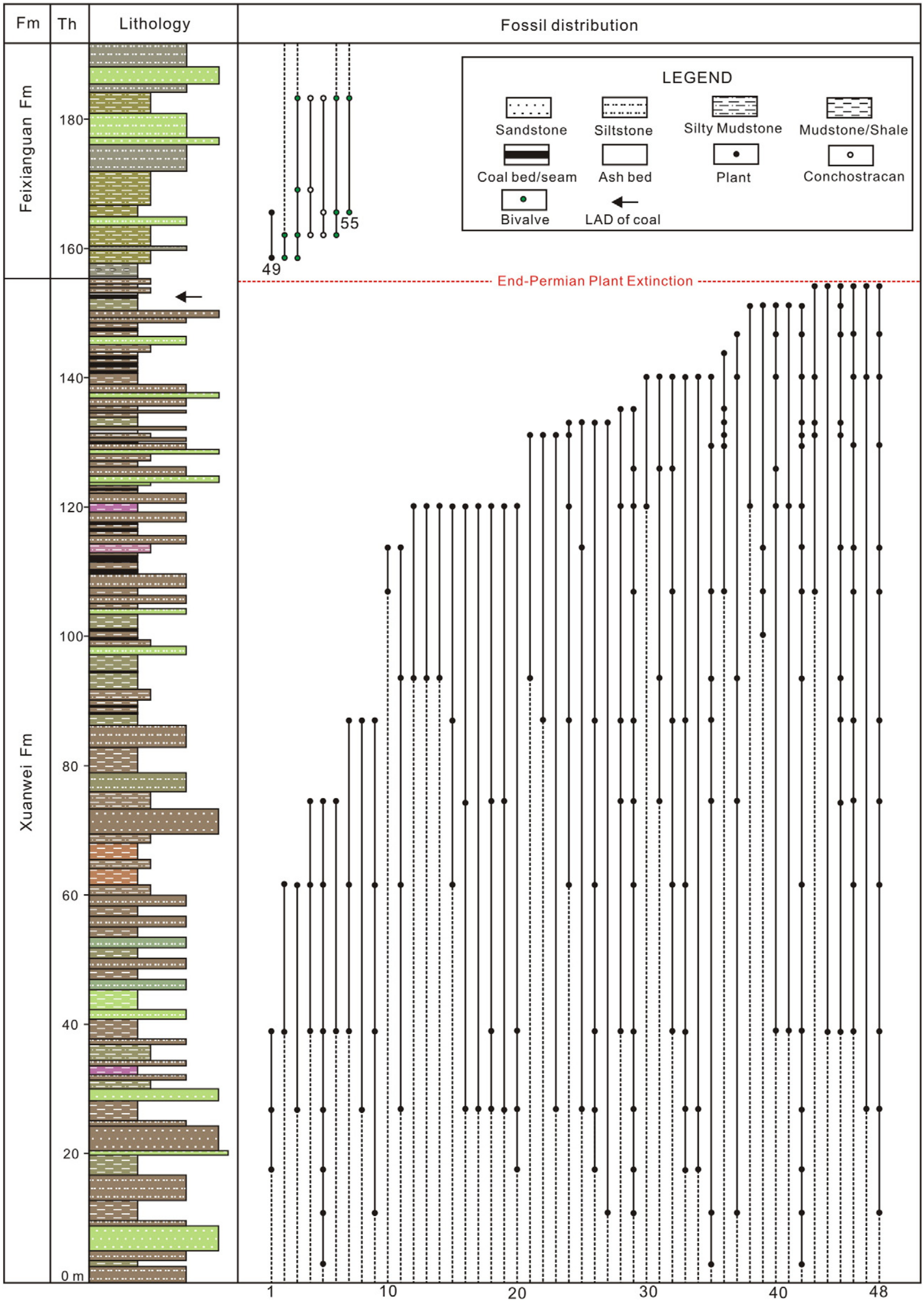


Fig. 12. Lithostratigraphy and fossil distribution of the Jinjibang section. Solid lines indicate known stratigraphic ranges; dotted lines indicate uncertain ranges up from below or upwards. Abbreviations: Fm, formation; Th, thickness. The list of the fossils is provided in the electronic Supplementary material.

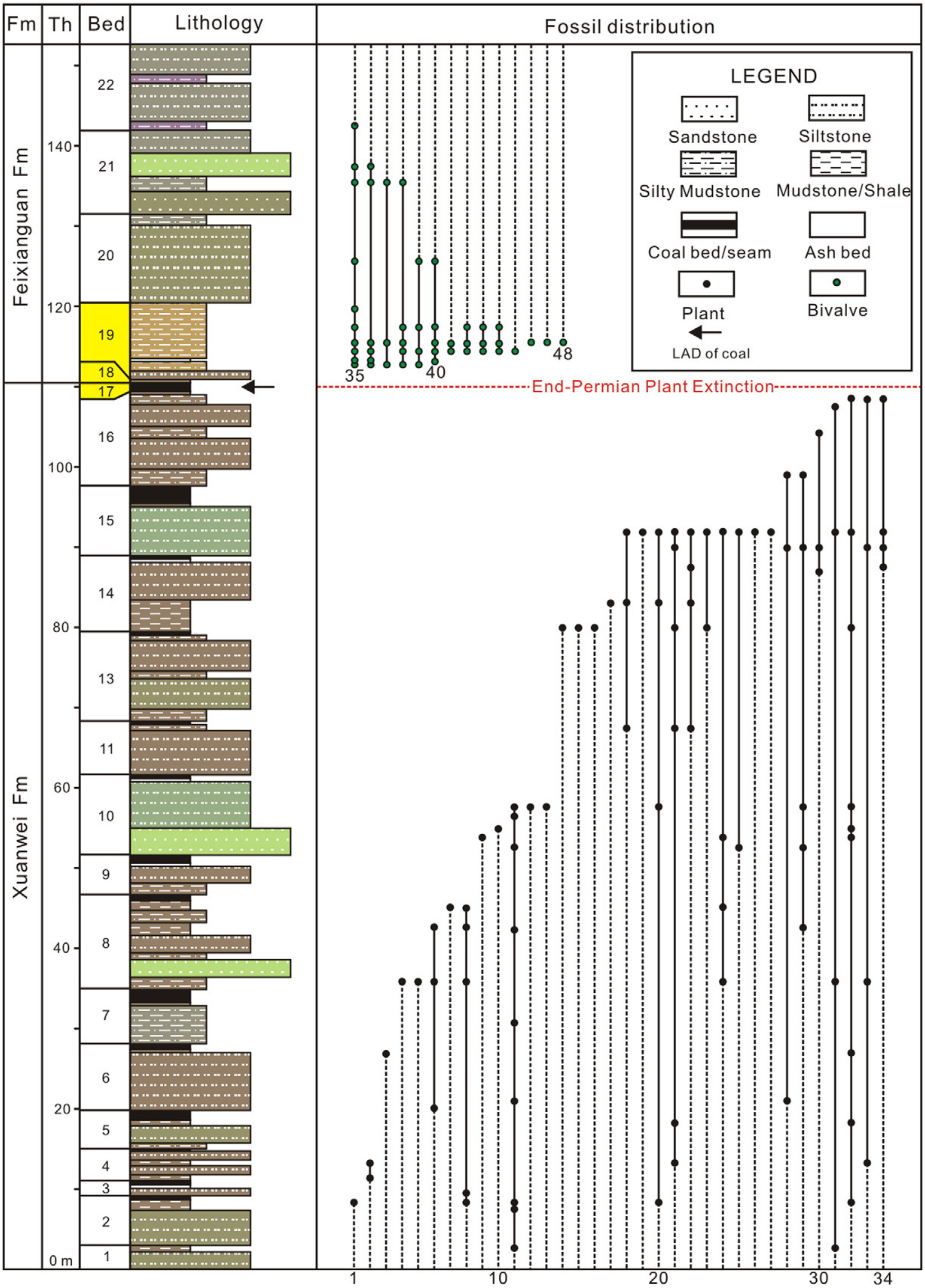


Fig. 13. Lithostratigraphy and fossil distribution of the Wadu section. Solid lines indicate known stratigraphic ranges; dotted lines indicate uncertain ranges up from below or upwards. Abbreviations: Fm, formation; Th, thickness. The list of the fossils is provided in the electronic Supplementary material.

forests from the land, presumably by acid rain and global warming, released soils and led to massive erosion of uplands onto alluvial plains. The timing of the sedimentary regime switch is interesting (Fig. 16), whether it was precisely at the level of the end-Permian plant extinction (EPPE) or estimated-PTB (e-PTB), and these South China sections provide better age control than was possible elsewhere.

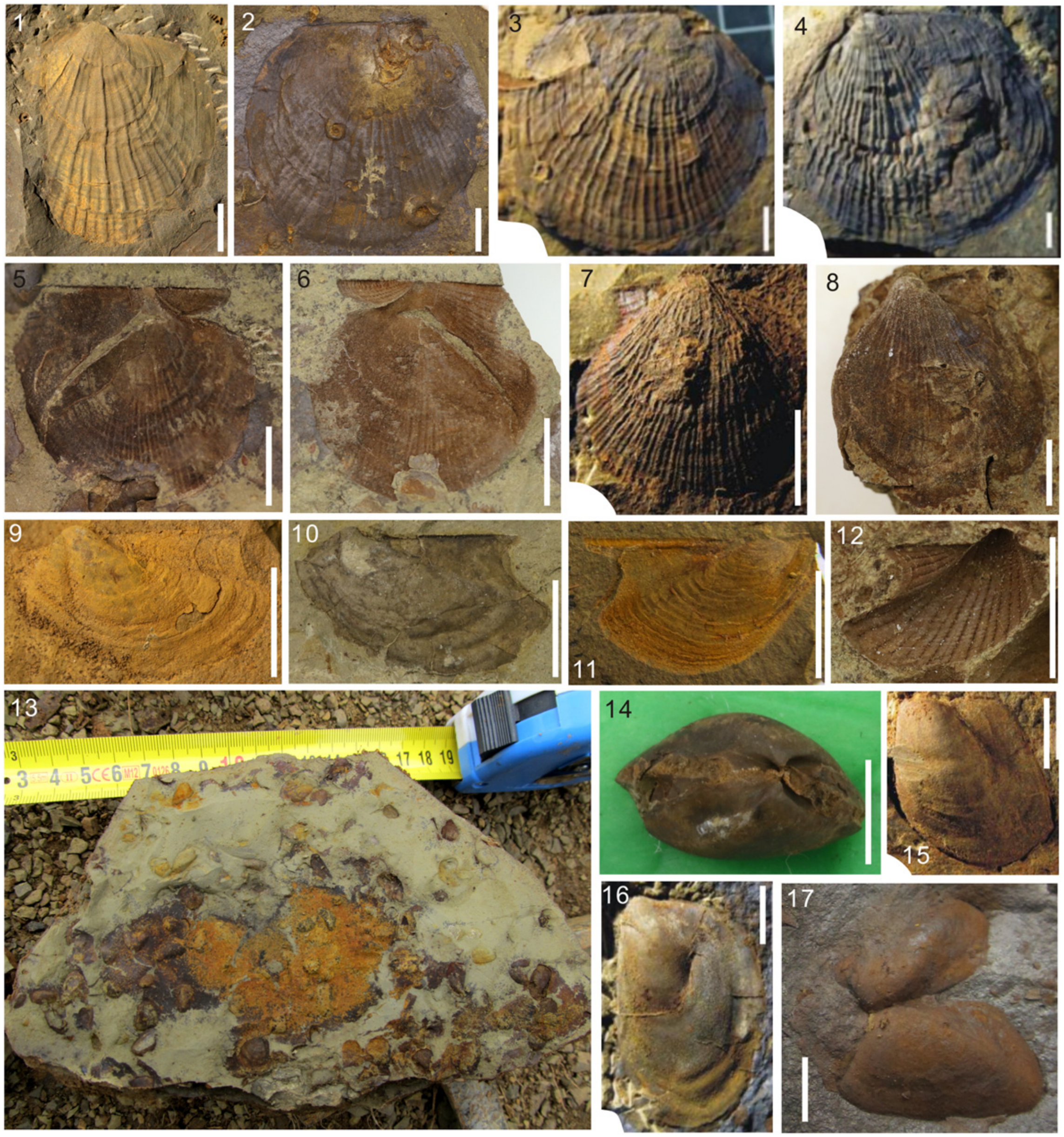


Fig. 14. Triassic-form bivalve fossils from the lower part of the Feixianguan Formation of the Wadu section. 1–4. *Claraia bioni* Nakazawa, WD-801190, WD-904059, WD-905002, WD-905006; 5–8. *Eumorphotis venetiana* Hauer, WD-902130a, WD-902130b, WD-801189, WD-801188; 9–11. *Pteria ussurica variabilis* Chen, WD-902120, WD-902124, WD-902126; 12. *Towapteria scythica* Wirth, WD-801210; 13. *Pteria ussurica variabilis-Eumorphotis venetiana-Promyalina schamarae* assamblage, WD-190001; 14. *Neoschizodus laevigatus* Ziethen, WD-903108; 15. *Promyalina schamarae* Bittner, WD-903095; 16. *Promyalina putiatinensis* Kiparisova, WD-904061; 17. *Permophorus bregeri* Girty, WD-903090a/WD903090b. The scale bars represent 5 mm.

6. The importance of bivalve and conchostracan faunas for the correlation of the terrestrial-marine siliciclastic PTB

Bivalves are very common in the marine record, especially in shallow-water siliciclastic settings. More or less complete latest Permian to earliest Triassic successions with abundant bivalve fossils enhance our understanding of the evolution of bivalves and benthic ecosystems during this period in various areas, such as South China, the Southern Alps, Pakistan and western North America (Broglio-Loriga et al., 1986; Schubert and Bottjer, 1995; Fraiser and Bottjer, 2007; Wasmer et al., 2012; Huang and Tong, 2014). Bivalve assemblage zones are generally valuable for Triassic biostratigraphy and regional or global stratigraphic correlation (Gao et al., 2009; McRoberts, 2010; Huang and Tong, 2014). For PTB sections that lack conodonts and ammonoids, biostratigraphic subdivisions and correlations are often based on bivalve assemblages. From the end of the Late Palaeozoic to the Late Mesozoic, conchostracans have the highest biostratigraphic significance of all terrestrial fossils, and in some intervals (Kozur and Weems, 2010, 2011; Scholze et al., 2015), they play the same role as ammonoids and conodonts in pelagic marine beds. They are distributed across a wide range of ecological dimensions and geographic regions, as well as in a variety of facies, such as freshwater deposits, brackish deposits, deltaic marginal marine beds, and some bedding planes or brackish intervals of very shallow marine deposits, which offer the greatest potential for correlation with marine facies (Kozur and Weems, 2010). Here, we discuss the biostratigraphic significance of the specific bivalve and

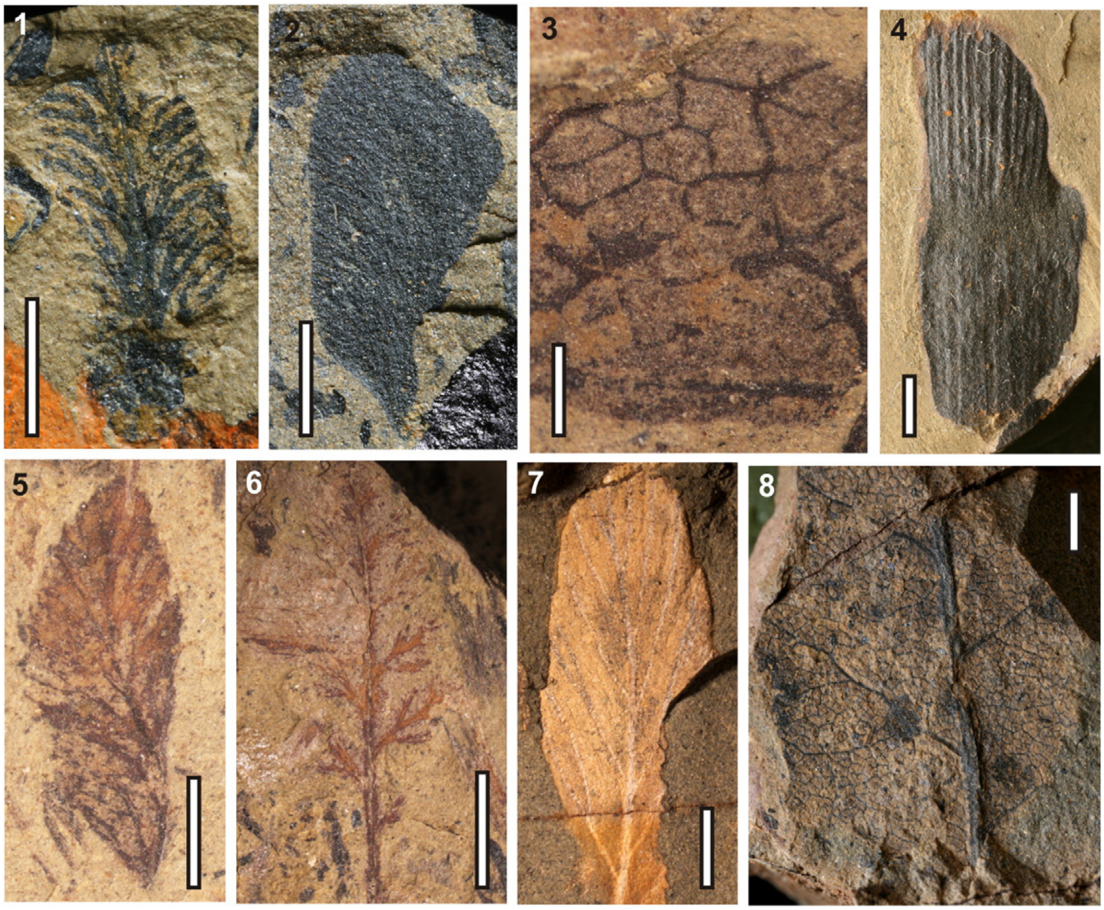


Fig. 15. *Gigantopteris* flora fragmented specimens from the lower part of the Kayitou Formation of the terrestrial sections. The scale bars represent 2 mm.

conchostracan faunas that are widespread in the P-Tr transition interval from our studied area and propose that they are of great use for the definition and correlation of the PTB in South China, and even globally.

6.1. The Pteria-Towapteria-Eumorphotis bivalve fauna

We collected abundant bivalve fossils from the Jinzhong, Jinjibang and Wadu sections, including *Pteria ussurica variabilis*, *Promyalina schamarae*, *P. putiatinensis*, *P. spathi*, *Neoschizodus orbicularis*, *Astartella* sp., *Unionites fassaensis*, *Claraia bioni*, *Eumorphotis venetiana*, *Permophorus bregeri*, *Neoschizodus laevigatus*, *Towapteria scythica*, *Leptochondria virgalensis*, and *Bakevellia goldfussi* (Figs. 11, 14). The *Pteria-Towapteria-Eumorphotis* bivalve fauna is widespread in shallow-water facies of conodont-free PTB sections in South China. The bivalve fauna of the transitional beds of the basal Triassic is represented by the *Pteria ussurica variabilis-Towapteria scythica-Eumorphotis venetiana* assemblage in South China (Yin, 1985; Shen et al., 1995; Chen et al., 2009; Huang and Tong, 2014). Other studies also recognized it as corresponding to the mixed fauna in Bed 26 at the Meishan section (Sheng et al., 1984, 1987; Zhang et al., 2016), which is clearly of latest Permian age. In addition, this assemblage is also regarded as the Permian-Triassic transitional bivalve fauna that flourished in the extinction interval, typified by opportunistic survivor taxa (Fang, 2004). In any case, the *Pteria ussurica variabilis-Towapteria scythica-Eumorphotis venetiana* bivalve assemblage can be considered as the marker of the P-Tr transitional interval in conodont-barren PTB sections and the end-Permian mass extinction horizon in shallow, siliciclastic facies PTB sections.

6.2. The Euestheria gutta-bearing conchostracan fauna

Chu et al. (2013) reported the occurrence of the *Euestheria gutta*-bearing conchostracan fauna from the Kayitou Formation in three terrestrial sections of South China. Meanwhile, four other species of Chu et al. (2013) were assigned to the genus *Euestheria,* and six species were assigned to the genus *Palaeolimnadia*. Considering deformation issues and intraspecific variation, diversity at the species level might have been overestimated in this previous study. In any case, *Euestheria gutta* dominated in this conchostracan fauna in association with a few *Palaeolimnadia xuanweiensis* specimens. Here, we collected abundant and well-preserved conchostracan fossils from the Guanbachong, Chahe, Xiaohebian, Jiucaichong, Jinzhong and Jinjibang sections (Fig. 4). *Euestheria gutta* was the dominant conchostracan fossil in each section. Previous studies have shown that *Euestheria gutta* was widespread in Early Triassic deposits from different areas, including the Calvörde Formation and Bernburg Formation of the Germanic Basin (Kozur and Seidel, 1983), the Rybinskian horizon on the Russian platform (Lutkevitch, 1937), and the Vokhma Formation in the Moscow Syncline (Scholze et al., 2015). The *Euestheria gutta*-bearing conchostracan fauna has been assigned an Early Triassic stratigraphic range in Central Russia and Germany, though the real lowest stratigraphic extent of this species seems to be less certainly known, due to the poorly-preserved specimens that were found in the uppermost Zechstein

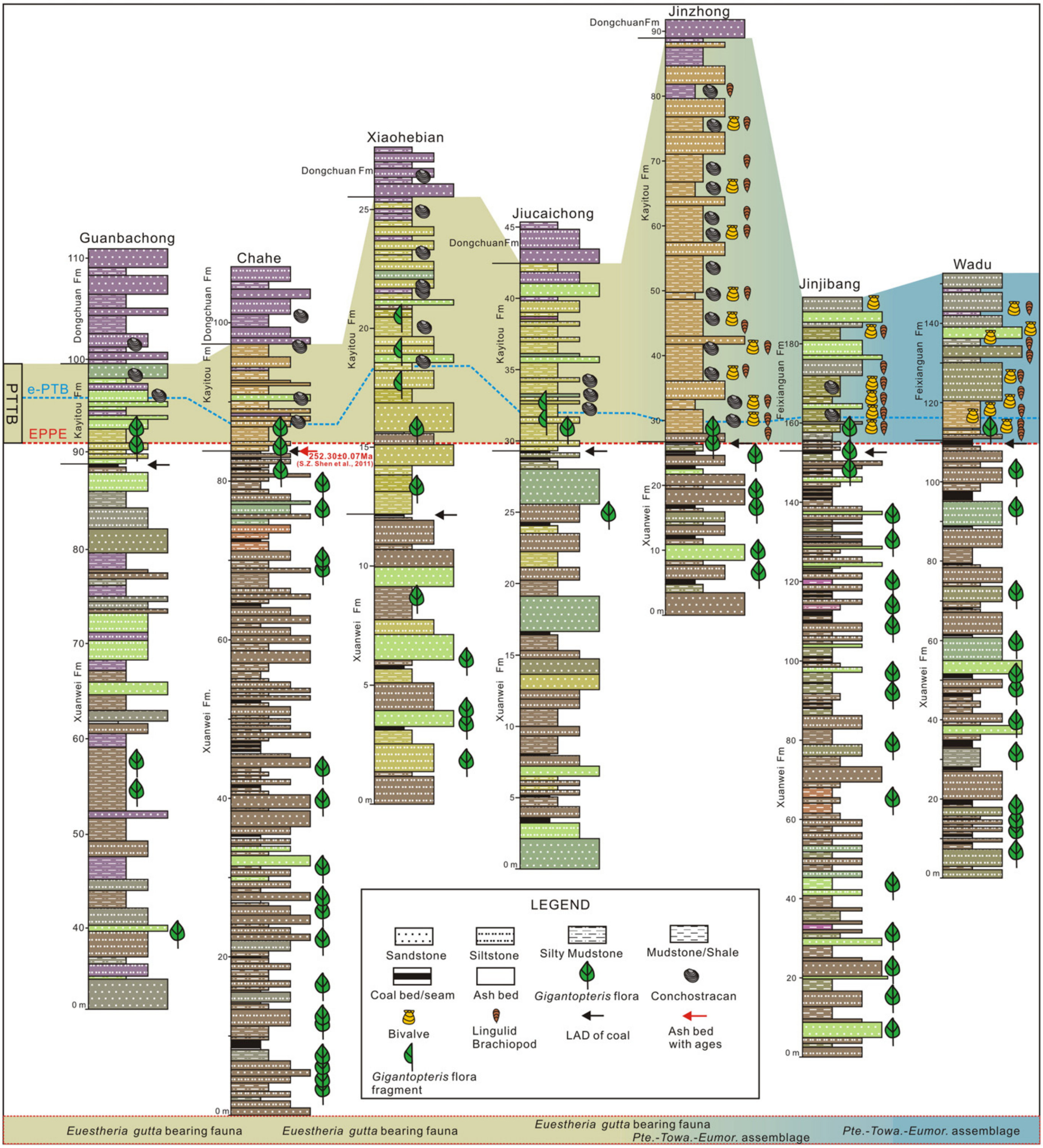


Fig. 16. The distribution of the *Gigantopteris* flora, conchostracans, bivalves, lingulid brachiopods, and LAD of the coal and ash bed, with ages showing the correlation among the studied sections in the Permian-Triassic transitional beds and the end-Permian mass extinction of the *Gigantopteris* flora. PTTB, Permian-Triassic transitional beds; e-PTB, estimated Permian-Triassic boundary; EPPE, end-Permian plant mass extinction; *Pte.-Towa.-Eumor.* assemblage, *Pteria-Towapteria-Eumorphotis* assemblage.

Group (Fulda Formation; Late Permian) of the Germanic Basin (Kozur and Weems, 2010).

6.3. The definition of the PTB in siliciclastic settings of South China

The end-Permian mass extinction horizon at the base or lower part of the Kayitou Formation in this area corresponds to a significant decrease in the diversity of plant fossils, which is nearly consistent in age with Bed 25 in the Meishan section from isotopic dating and biostratigraphic data in South China. In the present study, we observed almost the same pattern of biological evolution in the various sections, i.e. the *Gigantopteris* flora became extinct in the similar interval that contained a specific ash bed (Shen et al., 2011a), the subsequent occurrence of the low-diversity opportunistic flora, the conchostracan fauna and mixed terrestrial-marine biota in the Kayitou Formation. Accordingly, we propose that the collapse of end-Permian tropical marine and non-marine ecosystems is synchronous, at least, in this studied area. The synchronous collapse of end-Permian tropical ecosystems in this area is an effective marker for the correlation between non-marine and marine facies (Zhang et al., 2016). In addition, the occurrence of Triassic-type uniform conchostracan and bivalve faunas in the Kayitou Formation or the base of the Feixinguan Formation in the studied sections is the key basis for the biostratigraphic correlation, which indicates that the Kayitou Formation is latest Permian to earliest Triassic in age, and the PTB can be placed at a horizon within the Kayitou Formation (Fig. 16).

In fact, comprehensive biostratigraphic and geochemical data have been documented from various terrestrial sections in South China, suggesting that the Kayitou Formation is the witness of the terrestrial end-Permian mass extinction, mostly or entirely of latest Changhsingian age, especially from the evidence of the last appearance of plant remains and charcoal fossils (Zhang et al., 2016). In addition, a marine transgression beginning at the top of the Xuanwei Formation or the base of the Kayitou Formation was recognized based on a number of terrestrial and transitional sections in South China, and it was also well documented to be latest Changhsingian in age in the marine carbonate sections (this study; Yin et al., 2014; Zhang et al., 2016), which demonstrates that the base of the Kayitou Formation corresponds to the latest Changhsingian rather that the earliest Triassic. However, clear criteria are still lacking for the definition of the PTB in terrestrial sections stemming from uncertainty in identifying and using index fossils.

We suggest that the occurrence of the *Euestheria gutta*-bearing conchostracan fauna marks the PTB in terrestrial sections in South China, and that the mixed biota of the *Pteria ussurica variabilis-Towapteria scythica-Eumorphotis venetiana* bivalve assemblage coupled with the *Euestheria gutta*-bearing conchostracan fauna marks the PTTB in coastal transitional sections. The *Pteria ussurica variabilis-Towapteria scythica-Eumorphotis venetiana* bivalve assemblage can be considered as a marker of the PTTB in shallow water conodont-barren PTB sections. All of the above fossil assemblages appear at different levels in the Kayitou Formation or the lower part of the Feixianguan Formation in the different sections; for example, the *Euestheria gutta*-bearing conchostracan fauna appears in the upper part of the Kayitou Formation in the Guanbachong section, while it appears in the lower middle part of Kayitou Formation in the Chahe section, indicating time-transgressive formation boundaries (Fig. 16).

7. Conclusions

The collapse of terrestrial ecosystems probably happened simultaneously with the decline in marine diversity during the P-Tr mass extinction, from the latest Changhsingian to earliest Triassic, which corresponds to Beds 25 to 28 in the Meishan sections. The loss of the *Gigantopteris* flora and the organic carbon isotope negative shift represent the beginning of the mass extinction and the collapse of the tropical rainforest ecosystem in the lower part of the Kayitou Formation (this study; Shen et al., 2011a; Zhang et al., 2016). All previous publications agree with our detailed biostratigraphic studies in finding that the Kayitou Formation was the witness of the terrestrial Permian-Triassic mass extinction in South China, and that it documents the transition from the latest Permian to the earliest Triassic (Shen et al., 2011a; Yu et al., 2015; Zhang et al., 2016). In this study, we describe detailed biological records from seven studied PTB sections, including four terrestrial sections, three coastal transitional sections and one shallow marine section, and demonstrate biostratigraphic correlations in the PTTB among contrasting siliciclastic settings in South China. In particular, we conclude that the mixed marine and terrestrial biota from the coastal transitional PTB sections constitutes an intermediate link for biostratigraphic correlation between terrestrial and marine deposits. Finally, we propose that the occurrence of the *Euestheria gutta*-bearing conchostracan fauna and the *Pteria ussurica variabilis-Towapteria scythica-Eumorphotis venetiana* bivalve assemblage can be treated as markers of the PTTB in terrestrial-marine siliciclastic settings of South China, and perhaps more widely.

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Appendix A. Supplementary data

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