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Ostracods after the end-Permian extinction in South China: insights into non-microbial survival

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ABSTRACT: The taxonomy of ostracods from one deep-water, one shallow shelf and three paralic sections spanning the end-Permian extinction in South China (Guizhou and Yunnan) is summarized and discussed. We report on the occurrence of nine species, including mass occurrences of *Hollinella panxiensis* Wang, on the surface of these clastic Permian-Triassic transitional beds. The preservation of the material allows for the description of the central muscle scar field of *Langdaia suboblunga* Wang, which is the first observation of this character for the genus. These firstly described assemblages differ from those from post-extinction microbial deposits in being dominated by Palaeocopida. They illustrate survival without recovery after the end-Permian crisis, as none of the reported taxa participated in the subsequent Triassic diversification. We relate this phenomenon to clastic input and show that the patchy survival of benthic faunas following the crisis is an interplay between environments and adaptive potential. The persistence of Palaeocopida as a function of their depth distribution is discussed with the illustration of short-term survival of Hollinellidae in shallow areas, as opposed to the survival of Kirkbyidae in deep-marine waters until, at least, the Late Triassic.

Keywords. Permian-Triassic transitional beds, Palaeocopida, Survival, Terrestrial input

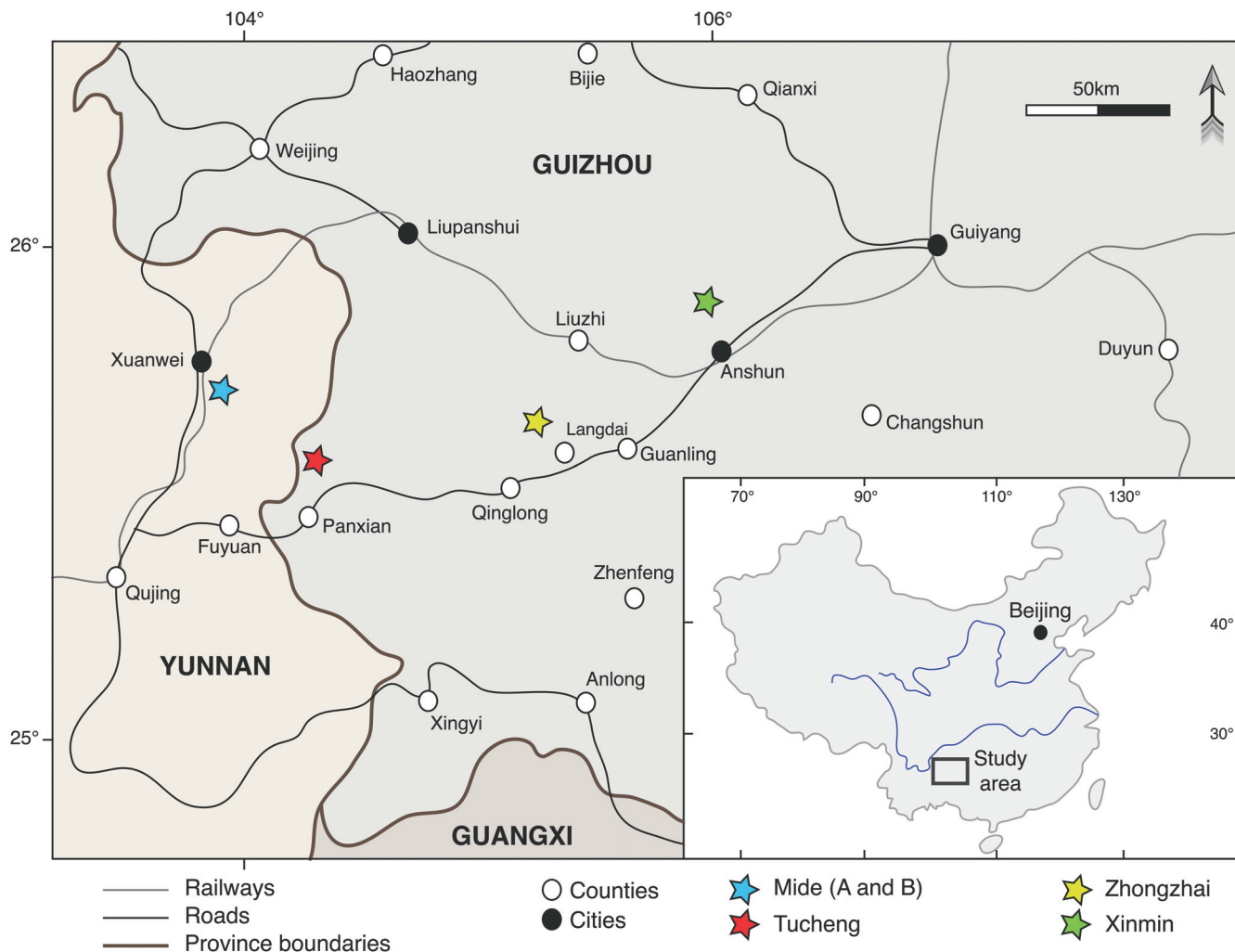
INTRODUCTION

The end-Permian Extinction (EPE; between 251.941 ± 0.037 Ma and 251.880 ± 0.031 Ma, Burgess *et al.* 2014) was the most severe loss of marine and terrestrial organisms in the last 542 My (e.g., Sepkoski 1984; Erwin 1993; Stanley 2016; Alroy *et al.* 2008). This period witnessed major rapid biotic and environmental changes, as shown for instance by the widespread development of microbial carbonates on the shallow marine shelves essentially within 30° of the equator around the Paleo-Tethys and eastern Panthalassa oceans (e.g., Kershaw *et al.* 2007, 2012). The emission of the Siberian continental flood basalts is currently considered as the main trigger for the crisis. Its environmental and ecological stresses were reinforced by the associated release of aerosols and/or CO₂ and their feedbacks on oceanic and terrestrial systems (e.g., Lucas 2009; Wignall 2001, 2007; Krull and Retallack 2000; Clapham and Payne 2011; Payne and Clapham 2012; Bond and Wignall 2014; Burgess and Bowring 2015; Renne *et al.* 1995; Cao *et al.* 2009; Preto *et al.* 2010).

Ostracods are millimeter-length aquatic crustaceans that today dwell in oceans, seas, estuaries, lagoons, lakes, rivers, ponds and springs. They have been only marine during the Early Paleozoic (e.g., Salas *et al.* 2007; Ghobadi Pour *et al.* 2011), colonized the water column during the Silurian (e.g., Siveter *et al.* 1991; Perrier *et al.* 2011) and ultimately invaded non-marine water bodies during the Carboniferous (e.g., Bennett 2008; Iglukowska 2014; Williams *et al.* 2006; Bennett *et al.* 2012).

Numerous studies have scrutinized Permian and Triassic marine ostracod assemblages worldwide (e.g., Wang 1978; Yi 1992; Hao 1994; Mette 2008, 2010; Forel 2012, 2015; Chen and Shi 1982; Shi and Chen 1987; Forel and Crasquin 2011a, b; Crasquin-Soleau *et al.* 2006; Yuan *et al.* 2007, 2009; Crasquin *et al.* 2010; Forel *et al.* 2009, 2013a, b, 2015) and described important losses through the EPE (see Crasquin and Forel 2015 for a summary). Their continuous record through the crisis provides unique insight into the marine environments and timing of the post-extinction survival and recovery. A short-lived survival interval has been reported in association with post-extinction microbial mats around the Paleo-Tethys that were exploited by abundant Bairdiidae ostracods for O₂ and food resources (Forel 2012, 2015; Forel *et al.* 2009, 2013a, b, 2015; see Hautmann *et al.* 2015, Martindale *et al.* 2019 and below for discussion). Bairdiidae are traditionally considered as restricted to stable and normal marine water bodies (e.g., Melnyk and Maddocks, 1988) but the post-EPE assemblages associated with microbialites challenge this paradigm in illustrating unexpected adaptive faculties including modifications of growth rates and body sizes (Forel 2018; Forel *et al.* 2013b, 2015).

The EPE interval was also of paramount importance for the macroevolution of ostracods as it marked the replacement of the Paleozoic fauna by the Meso-Cenozoic one (e.g., McKenzie 1982; Crasquin and Forel 2015; Crasquin-Soleau *et al.* 2007). The Paleozoic ostracod fauna was dominated by Palaeocopida, which were widespread from shallow to deep marine waters (e.g., Jones 1989; Becker and Wang 1992; Casier and Lethiers

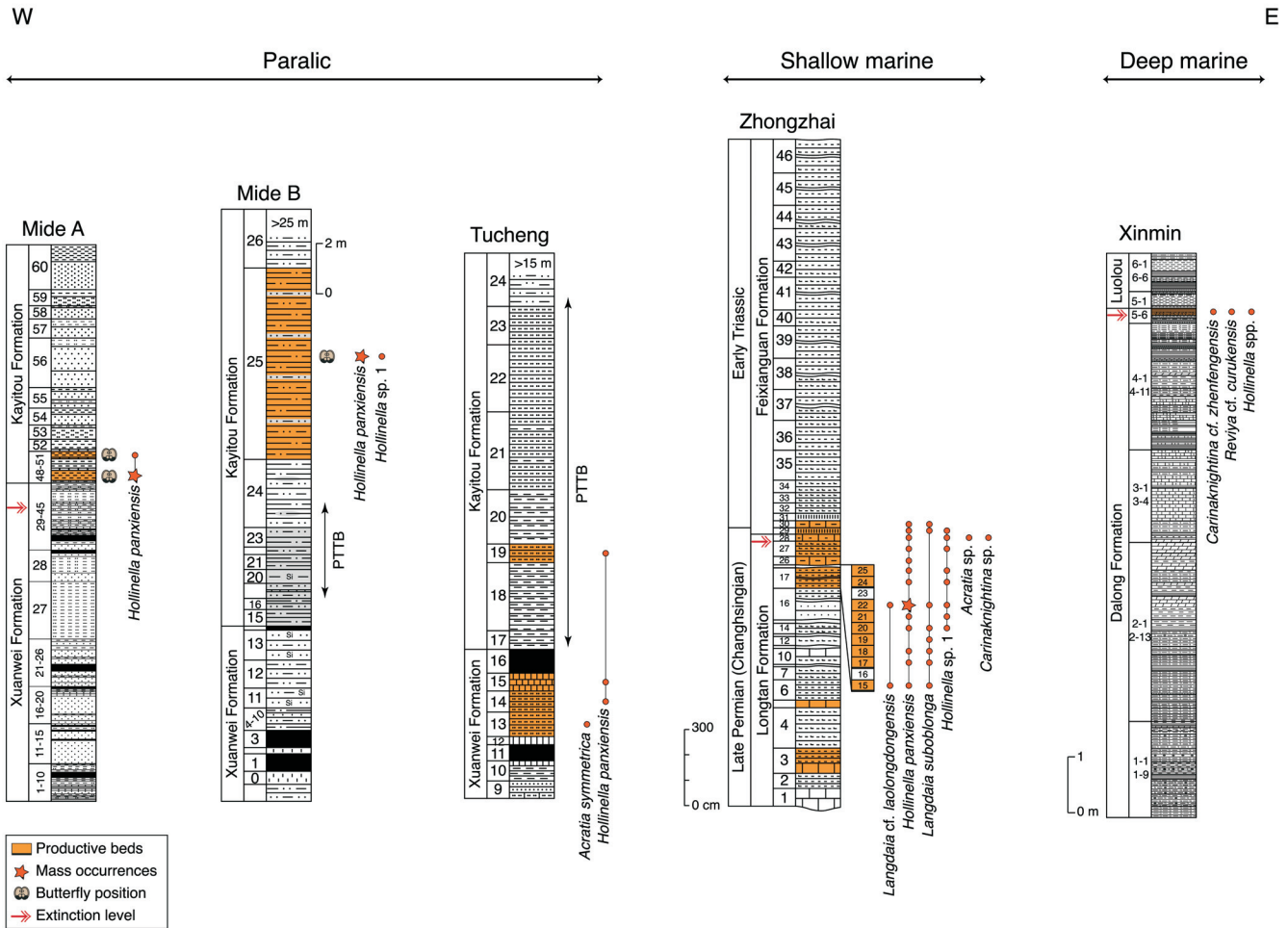


TEXT-FIGURE 1

Geographical map of the studied area showing the locations of the five studied sections in Yunnan Province (Mide A and B) and Guizhou Province (Tucheng, Zhongzhai and Xinmin sections).

1998; Olempska and Chauffe 1999; Chitnarin et al. 2012). They were traditionally thought to have gone extinct at the EPE (e.g., Moore 1961) but since the 80's, a growing body of literature documented their survival into the Early Triassic (Crasquin and Forel, 2015 and references therein). In the current state of our knowledge, Palaeocopida residually range up to the Anisian, Middle Triassic, in neritic, deep-subtidal waters of Tibet (Forel and Crasquin 2011a; Forel et al. 2011) and up to the Carnian, Late Triassic, in deeper waters of Turkey (Kirkbyidae; Forel et al. 2019). The existence of living Palaeocopida has been evoked, Kirkbyoidea being considered by some as the forerunners of the Cretaceous to Recent Punciidae (e.g., Schallreuter 1968; Swanson 1991). This question is still debated: some consider that there might be no living Palaeocopida and that Punciidae should rather be attributed to Cytherellidae (e.g., Becker 1997a; Martin and Davis 2001; Whatley et al. 1993; Martens et al. 1998) while others recently revived the order Punciocopida Schallreuter, 1968 (Danielopol and Swanson 2019).

The recent report of abundant Palaeocopida (*Hollinella*) through the EPE in Vietnam (Crasquin et al. 2018) is of major significance to further characterize the temporal, geographical and ecological patterns of their Triassic residual occurrences. Here we perform the first large-scale investigation of ostracod assemblages from five sections of the western Yangtze platform in South China distributed along an environmental transect from west to east, from paralic conditions (Mide A and B and Tucheng sections), shallow marine clastic (Zhongzhai section) to deep marine clastic (Xinmin section). This study aims at the first integrative analysis of the diversity and environmental distribution of ostracods in clastic sections through the end-Permian extinction. We report on the occurrence of nine species, one Podocopida (*Acratia*) and six Palaeocopida (*Carinaknightina*, *Hollinella*, *Langdaia*, *Reviya*), preserved on the surface of disaggregated rocks from the Permian-Triassic transitional beds of the studied sections. The preservation of *Langdaia suboblonga* Wang, 1978 in Zhongzhai section allows for the first observation of the cen-



TEXT-FIGURE 2
Correlated lithological columns of the Mide A and B, Tucheng, Zhongzhai and Xinmin sections.

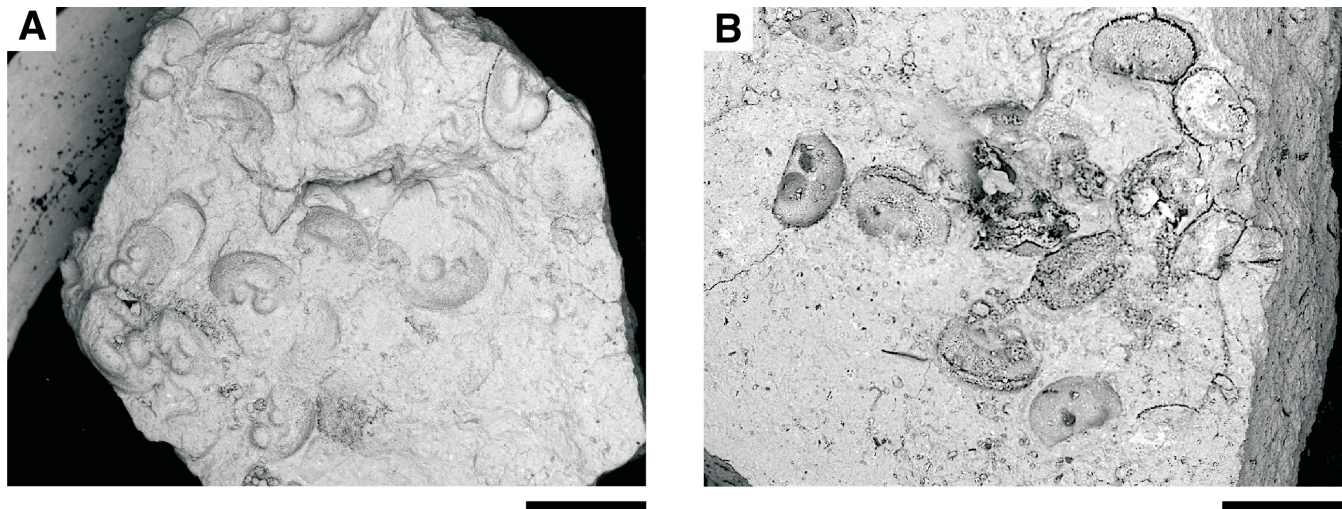
tral muscle scar field for this species and genus. Noteworthy, ostracods from Zhongzhai section have been previously discussed and some taxa identified (Zhang et al. 2017): they are revised and debated in the present contribution. Including taxa revised from Zhang et al. (2017), nine species are reported through the EPE over the studied area. In nearshore conditions, these assemblages span the Permian-Triassic transitional beds and illustrate the dead-end survival of ostracod taxa that are adapted to very shallow waters under the influence of clastic influx in the absence of microbial developments. The analysis of the survival pattern of Palaeocopida following the EPE allow us to relate their bathymetrical and environmental distribution to the duration of their survival in the Triassic. We here show that Hollinellidae survived for a short interval in shallow water clastic zones, from which other Palaeocopida such as Kirkbyidae are excluded. Conversely, Kirkbyidae survived through the Triassic in deeper purely marine conditions such as recorded in Xinmin and other areas in China (Meishan section, Forel and Crasquin 2011b), Turkey (Forel 2015; Crasquin-Soleau et al. 2004a, b), Hungary (Forel et al. 2013a) and up to the Carnian in Turkey (Forel et al. 2019).

GEOLOGICAL SETTING AND STUDIED SAMPLES

For the present analysis, samples from five clastic sections exposed in Yunnan and Guizhou provinces, South China, have been examined (text-fig. 1): Mide A and B (Yunnan), Tucheng (Guizhou), Zhongzhai (Guizhou) and Xinmin (Guizhou). These five sections are located along an environmental transect from west to east: from paralic (alternating marine and terrestrial) in Mide and Tucheng, shallow marine clastic in Zhongzhai, to deep water, basinal conditions in Xinmin. Mide B was sampled by MBF in 2012 while the other sections were sampled by JXY from 2001 to 2009. Ostracods have often been reported from these clastic localities (e.g., Yu et al. 2010; Zhang et al. 2017) but the present work is the first complete taxonomic description and discussion of these peculiar assemblages.

Mide sections

Two different Mide sections have been described in the literature: Mide A and Mide B (Yu 2008). Mide B section is located in eastern Yunnan Province, about 13 km southeast of Xuanwei city and about 256 km southwest of Guiyang city (text-fig. 1). During the Permian-Triassic transition, Mide B was located close to the northern edge of the Nanpanjiang basin in the south-



TEXT-FIGURE 3
Examples of ostracods present on the disaggregated surfaces of bed 28 of the Longtan Formation in Zhongzhai (A) and bed 49 of Mide A section (B). Scale bars – 1 mm.

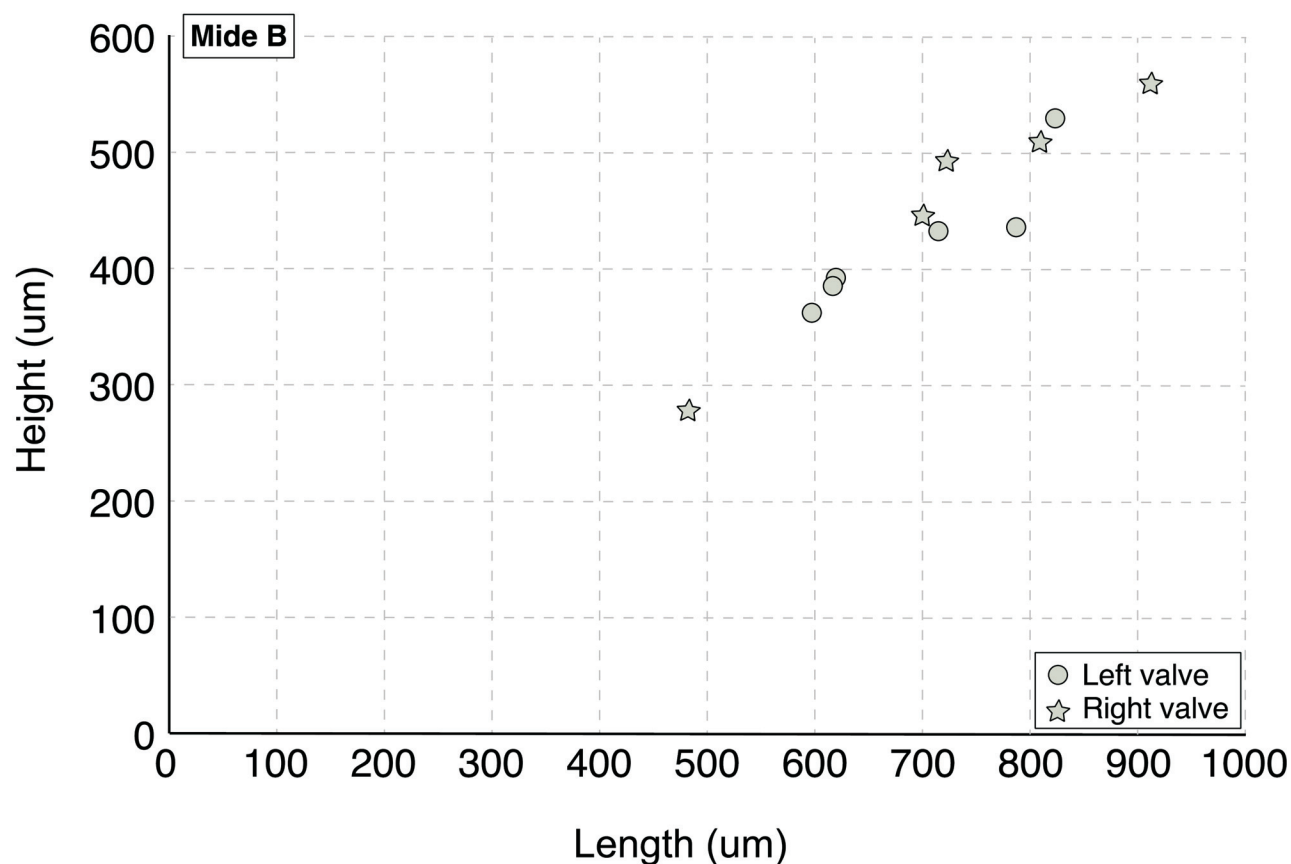
ern Yangtze platform (e.g., Lehrmann et al. 2005). Paleoenvironmental investigations document an evolution from alluvial and lacustrine setting to coastal marine and lastly braided rivers on semi-arid alluvial plains over the Mide B section (Bercovici et al. 2015). Only a brief description of the lithological succession is provided here and the reader is referred to Bercovici et al. (2015) and references therein for further details and discussion. In ascending order, this section is composed of the Xuanwei, Kayitou and Dongchuan formations (text-fig. 2; Dongchuan Formation was not sampled for the present investigation and is not illustrated). The Xuanwei Formation is 4 m thick and unconformably overlies the Upper Permian Emeishan basalts. It is subdivided into 14 beds (labelled 1 to 14) mostly consisting of terrigenous siliciclastic deposits with intercalated organic-rich mudstones and coal seams. It yields abundant *Gigantopteris* belonging to the Cathaysian flora, acritarchs and diverse fungal spores at its top (Yu et al. 2010; Bercovici et al. 2015). Lateral age equivalents of the Xuanwei Formation are marine limestone of the Changxing Formation exposed in the Meishan section, Zhejiang Province (Yin et al. 2001). The Kayitou Formation is 36 m in thickness and conformably overlies the Xuanwei Formation. It is subdivided into 17 beds (labelled 15 to 31) of massive and silty sandstone, grading from tan-green to yellow at its base to purple at its top. Plants are only found at the very base, with the appearance of some new floral elements of the *Annalepis*–*Peltaspermum* assemblage. Ostracod species *Langdaia suboblona* Wang, 1978 and *Hollinella tingi* (Patte, 1935) have been reported but not illustrated from beds 21 to 26 (e.g., Yu et al. 2010), their record is discussed in this study. The facies gradually change to the red-purple terrigenous siliciclastic deposits of the overlying Dongchuan Formation. Lateral age equivalents are marine limestone of the Yinkeng Formation of the Meishan section (Yin et al. 2001). An anomalously high abundance of fungal spores occurs within a restricted stratigraphic interval at the very top of the Xuanwei Formation, corresponding to latest Permian deposits (Peng and Shi 2009; Bercovici et al. 2015). The occurrence of the ammonoid *Ophiceras* sp. in bed 25 (Tian

et al. 2008; Yu et al. 2010) points to a Griesbachian, Early Triassic, age (Brühwiler et al. 2008). The bivalve assemblage reported from bed 25 by Yu et al. (2010) also represents a Lower Triassic range (Rong and Fang 2004; Posenato et al. 2005; Bercovici et al. 2015). The turnover of both marine faunas and terrestrial plants with the appearance of the first Triassic element is coeval, located several meters below the carbon isotope excursion (Zhang et al. 2016; Cui et al. 2017) and PTB, consistent with findings outside of China (Fielding et al. 2019; Mays et al. 2019).

The Mide A section is no longer accessible but was sampled by JXY in 2001 and 2002. Mide A was located in Lile Village, 3 km east of Xuanwei city in Yunnan Province (text-fig. 1). It exposed the Xuanwei Formation (beds 1 to 45) conformably overlain by the Kayitou Formation (beds 46 to 60; text-fig. 2). The upper portion of the Kayitou Formation was not complete due to coverage and faulting. Lateral age equivalent of beds 35 to 37 are boundary claystones of the Meishan section (Wang and Yin 2001; Yin et al. 2001). Geochemical analyses indicate that beds 31 to 35 record the event interval in Mide A section (Zhao 2003; Yu 2008).

Tucheng section

The Tucheng section is located in Panxian County, western Guizhou Province, about 10 km north of Panxian city (text-fig. 1). This section provides a good outcrop of the upper Permian beds dominated by plant remains and lower Triassic beds that are characterized by plants, bivalves and ostracods (Yu 2008). The succession in Tucheng is also composed of the Xuanwei Formation (beds 1–16) conformably overlain by the Kayitou Formation (beds 17–23; text-fig. 2). *Annalepis* is common in the Middle Triassic of Europe and South China, but at Mide and Tucheng it is encountered in the lowermost part of the Kayitou Formation, which has consequently been assigned to the lowermost Triassic (Yu et al. 2010). In Tucheng, persisting fragments of the *Gigantopteris* flora were also encountered within the *Annalepis*–*Peltaspermum* macrofloral assemblage (Yu et al.



TEXT-FIGURE 4

Height/Length scatter plot of *Hollinella panxiensis* Wang 1978, all specimens from the Early Triassic, bed 25, Kayitou Formation, Mide B section.

2010) and interpreted as short-term survivorship of relicts of the Late Permian taxa (Bercovici et al. 2015).

Zhongzhai section

The Zhongzhai section is located in Liuzhi County, southwestern Guizhou Province, about 1 km northeast of Zhongzhai city (text-fig. 1). This section recorded a shallow clastic-shelf environment during the Permian-Triassic transition (e.g., Feng et al. 1997; Zhang Y. et al. 2014). The Zhongzhai section exposes the upper part of the Longtan Formation and the lower part of the Feixianguan Formation, with a conformable contact (Gao et al. 2009). The upper Longtan Formation consists of yellowish green silty mudstones and horizontally bedded argillaceous siltstones with limestone intercalations. The basal Feixianguan Formation is made of purple mudstone, siltstone, and sandstone (text-fig. 2). This section is very fossiliferous and has yielded well-preserved brachiopods (e.g., Peng and Shi 2008; Zhang et al. 2013), bivalves, conodonts (e.g., Zhang Y. et al. 2014), gastropods (He et al. 2008) as well as phytoplankton (Lei et al. 2012). Recently, ostracods have been reported throughout the section with three identified and illustrated species from bed 28 (*Acratia* sp., *Kindlella* sp., *Amphissites* sp.; Zhang et al. 2017). These identifications as well as their implications are revised and discussed in this contribution. In Zhongzhai, the extinction level is located between beds 27 and 28 (e.g., Zhang et al. 2017) and the Permian/Triassic boundary is positioned at the bottom of bed 30 (e.g., Metcalfe and Nicoll 2007; Zhang Y. et al. 2014).

Xinmin section

The deep-water Xinmin section is located about 30 km north of Anshun city in Anshun County, Guizhou Province (text-fig. 1). The Xinmin section exposes about 7.2 m of the upper Permian Dalong Formation (beds 1-4), which consists of black marls with frequent interbeds of thin black shale, calcareous-mudstone and numerous volcanic tuff beds (text-fig. 2). It yielded abundant conodonts, foraminifers, radiolarians, ammonoids, brachiopods and plants (e.g., Shen et al. 2013b). The overlying Luolou Formation (beds 5-9) is mainly made of volcanic tuff and yellow mudstone with few fossils. The continuous sedimentation from the thin-bedded siliceous mudstone of the Dalong Formation to mudstone of the Luolou Formation has been considered as indicative of a deep-water basinal facies (Zhang N. et al. 2014). The level of the EPE is unstable in the literature discussing the Xinmin section: at the base of bed 6 in Shen et al. (2013a), within bed 5 in Shen et al. (2013b) or at the base of bed 5 in Shen et al. (2014). The position of the Permian/Triassic boundary in Xinmin has also been disputed in recent years, successively placed at the top of bed 5-6 (Feng et al. 2011), within bed 5-3-3 (Xu et al. 2012) or within the 15 cm overlying the contact between beds 5 and 6 (Shen et al. 2013a). The recent conodont biostratigraphy documented the first occurrence of *Hindeodus parvus*, and thus the position of the Permian/Triassic boundary at the base of bed 5-3-3 (Zhang N. et al. 2014). The ostracods reported here occur on the surface of siliceous mudstone from bed 5-3 collected by JXY in 2009. How-

ever, it is not clear whether this sample comes from below or above the Permian/Triassic boundary position that was later established by Zhang N. et al. (2014). For this reason, we refer this sample as issued from the Permian-Triassic transition beds *lato sensu*. If we consider the most recent position of the EPE in Xinmin given in Shen et al. (2014), the studied sample might be located above the extinction level.

MATERIAL AND METHODS

For the present ostracod analysis, a set of samples has been collected from the Kayitou Formation in Mide A and B, the Xuanwei and Kayitou formations in Tucheng, Longtan and Feixianguan formations in Zhongzhai and the Luolou Formation in Xinmin (text-fig. 2). The samples were not chemically processed because of their clastic nature and we rather performed a visual investigation of the surfaces of cracked sediments. The preservation and density of ostracods on these disaggregated surfaces are variable as shown in text-fig. 3. The specimens are preserved on the surface of cracked sediments and each new crack reveals a new stock of material: thus, it was not possible to estimate the abundance as a function of the surface of rock investigated and only the relative abundance is discussed here. The specimens are preserved as internal casts, external casts, as well as original carapaces/valves. Open carapaces with attached valves, here referred to as the butterfly position (see also Williams et al. 2005, 2011), are frequent in Mide B (Pl. 1, Fig. H) and Mide A but are absent from the other studied localities. In Mide, ostracods occur in beds 49 and 51 of the Kayitou Formation outcropping at section A, and bed 25 at section B. In Tucheng, ostracods have been recovered from beds 13 to 15 of the Xuanwei Formation and bed 19 of the Kayitou Formation. The present investigation of Zhongzhai deposits documents the occurrence of ostracods in beds 15A, 15B, 17, 20-22, 24-28 of the Longtan Formation, as well as in beds 29 and 30 of the Feixianguan Formation. In Xinmin, ostracods occur in bed 5-3 (text-fig. 2).

In the present contribution, we follow the general classification of Moore (1961) and Horne et al. (2002). All species are illustrated to allow future comparison and understanding of these assemblages and their implications (Plates 1, 2). All specimens are deposited in the Micropaleontology collections of the Muséum national d'Histoire naturelle, Paris, France (MNHN), under the inventory numbers MNHN.F.F62990-MNHN.F.F62999, MNHN.F.F63170- MNHN.F.F63180.

Abbreviations used in the text are as follow: L₁-L₄, lobes; S₁-S₄: sulcus.

TAXONOMY AND DESCRIPTION OF TAXA

Class OSTRACODA Latreille 1806

Subclass PODOCOPA Müller 1894

Superfamily BAIRDIOIDEA Sars 1887

Family BAIRDIIDAE Sars 1887

Genus *Acratia* Delo 1930

Type species: *Acratia typica* Delo 1930, by original designation.

Acratia symmetrica Hao 1992b

Plate 1, figures A-C

Acratia symmetrica HAO 1992b, p. 41, 44, pl. 1, figs 18–20. – HAO 1994, fig. 1/5. – HAO 1996, pl. 2, fig. 7.

Material: eight external casts (Tucheng section).

Discussion: *Acratia symmetrica* Hao, 1992b was described from a dark brown clay of the Lower Triassic Feixianguan Formation outcropping in the Zhenfeng area about 100 km east of Tucheng section, in western Guizhou (text-fig. 1; Hao 1992b). According to Hao (1994, 1996), the distribution of *A. symmetrica* during the Early Triassic extends northward to Zunyi area, in Guizhou Province. The present record of *A. symmetrica* from the Xuanwei Formation exposed in Tucheng is the first Upper Permian occurrence of this species: *A. symmetrica* is therefore recognized for the first time through the EPE. It is worth noting that none of the two *Acratia* illustrated by Zhang et al. (2017) from bed 28 in Zhongzhai section immediately overlying the extinction level belongs to *A. symmetrica*.

Occurrence: Feixianguan Formation, Zhenfeng, Guizhou Province, South China, Griesbachian, Early Triassic (Hao 1992b, 1994, 1996); bed 13, Xuanwei Formation, Tucheng section, Guizhou Province, South China, Changhsingian, Late Permian (this work; text-fig. 2).

Order PALAEOCOPIIDA Henningsmoen 1953

Suborder BEYRICHICOPINA Scott 1961

Superfamily HOLLINOIDEA Swartz 1936

Family HOLLINELLIDAE Bless and Jordan 1971

Genus *Hollinella* Coryell 1928

Type species: *Hollinella dentata* Coryell 1928 by original designation.

Remarks: *Hollinella tingi* (Patte 1935) has long been reported from the Permian-Triassic transitional beds exposed in South China (e.g., Zheng 1976; Wang, 1978; Wei 1981; Wei et al. 1983; Yu et al. 2010). However, Crasquin-Soleau et al. (2004b) and more recently Crasquin et al. (2018) demonstrated that these assignments are incorrect and that *H. tingi* is restricted to the Early Permian. Without considering conformis species, open nomenclature species and those of questionable generic attribution, nine species occur at the Permian-Triassic transition worldwide:

H. capacilacuna Wang 1978 from the Wuchiapingian-Changhsingian interval in South China (Wang 1978; Wei et al. 1983);

H. echinata Hao 1993 from the Changhsingian of Guizhou Province, South China (Hao 1993);

H. fengqinglaii Crasquin in Forel et al. 2013a from the Changhsingian of Hungary (Forel et al. 2013a);

H. lungcamensis Crasquin in Crasquin et al. 2018 from the Late Changhsingian-Griesbachian interval exposed in northern Vietnam (Crasquin et al. 2018);

H. magninoda Wang 1978 from the Wuchiapingian-Changhsingian interval in South China (Wang 1978; Wei et al. 1983). *H. unispinata* Hao, 1992b from the Griesbachian of Guizhou, South China (Hao 1992b) is a junior synonym of *H. magninoda* according to Crasquin et al. (2018);

H. martensiformis Crasquin in Crasquin et al. 2010 from the Changhsingian of Meishan section, Zhejiang Province, South China (Crasquin et al. 2010);

H. panxiensis Wang 1978 from the Wuchiapingian-Griesbachian interval of Guizhou, Yunnan, Zhejiang, Hubei provinces, South China (Zheng 1976; Wang 1978; Hao 1992a, b, 1993, 1994, 1996; Shi and Chen 1987; Wei et al. 1983; Liu et al. 2010) according to Crasquin et al. (2018) and this work;

H. plana Jiang in Wei et al. 1983 from the Griesbachian of Yunnan Province, South China (Wei et al. 1983);

H. qurenensis Guan in Guan et al. 1978 from the Changhsingian, Longtan Formation of Guangxi Province, South China (Guan et al. 1978);

H. tuberculata Belousova 1965 from the Upper Permian of Azerbaijan (Belousova 1965) and Dzhulfian-Dorashamian of Northwest Iran (Mette 2010).

Hollinella is the only genus found in all sections studied here, at some levels as mass occurrences. It was however not mentioned as part of the ostracod assemblages in Zhonghai by Zhang et al. (2017).

***Hollinella panxiensis* Wang 1978**

Plate 1, figures D-I

Hollinella tingi (PATTE 1935) – ZHENG 1976, p. 77, 80, pl. 1, figs 1–4. – WANG 1978, p. 17, pl. 1, figs 5–7. – WEI et al. 1983, p. 34, pl. 7, fig. 18. – SHI and CHEN 1987, p. 30, pl. 16, figs 2–5. – HAO 1992a, p. 238, pl. 1, fig. 1. – HAO 1993, pl. 1, figs 1, 2. – HAO 1994, fig. 1/6. – HAO 1996, pl. 1, fig. 1. – LIU et al. 2010, fig. 2/1. – pars HAO 1992b, p. 39, pl. 1, fig. 6.

Hollinella panxiensis WANG, 1978, p. 16, 17, pl. 1, figs 1–4. – WEI et al. 1983, p. 33, pl. 7, fig. 16.

Material: more than 30 specimens (Mide A section); more than 50 specimens (Mide B section); more than 10 specimens (Tucheng section); more than 60 specimens (Zhongzhai section).

Discussion: The abundance of *H. panxiensis* Wang 1978 is variable in the Permian-Triassic transitional beds over the studied area. In Tucheng, it is low in abundance. In Mide A, it is abundant in bed 49 and relatively scarcer in bed 51. In Mide B, it is abundant in bed 25 where it frequently occurs in butterfly position (Pl. 1, Fig. H). In Zhongzhai, the abundance of *H. panxiensis* is low from bed 15A to bed 27, with the maximum of abundance in bed 22; it becomes more abundant up to bed 30 (text-fig. 2). Noteworthy, Zhang et al. (2017) do not mention the occurrence of this species or genus although specimens attributable at least to *Hollinella* are visible on their Figs. 2G, H that illustrate the cracked sediments of bed 28.

We take the opportunity to clarify the synonymy of *H. tingi* (Patte 1935) *sensu* Shi and Chen, 1987 from the Changhsingian of Meishan section in Zhejiang Province, South China (Shi and Chen 1987). Of the three specimens identified as *H. tingi* by Shi and Chen (1987), two (plate 16, figs 2, 4 in Shi and Chen 1987) were re-attributed to *H. martensiformis* Crasquin in Crasquin et al. (2010), which was described from the Changhsingian of the same section (Crasquin et al. 2010). Simultaneously, all specimens attributed to *H. tingi* (Patte 1935) by Shi and Chen (1987) were attributed with doubt to *H. tuberculata* Belousova 1965 by Mette (2010), who highlighted the important difference in size between the specimens of Meishan and *H. tuberculata*. All the specimens illustrated by Shi and Chen (1987) were ultimately placed in *H. panxiensis* by Crasquin et al. (2018), without discussing the previous attributions to *H. martensiformis* and *H. tuberculata*. The diagnostic features of *H. martensiformis* are its sharp cardinal angles, frill consisting of a row of small tubercles and lobes poorly marked. Although the specimens shown by Shi and Chen (1987) are rather poorly preserved, the lobes are more pronounced than in the type-material of *H. martensiformis*, the ventral lobe is clearly inflated, cardinal angles are more rounded and the frill of small tubercles is significantly lacking. For these reasons, we subscribe to the recent re-attribution of these specimens to *H. panxiensis*.

Occurrence: Feixianguan Formation, Bijie, Guizhou Province, South China, Griesbachian, Early Triassic (Zheng 1976); Panxian, western Guizhou Province, South China, Late Changhsingian, Late Permian (Wang 1978); Langdai, Panxian, western Guizhou Province, South China, Griesbachian, Early Triassic (Wang 1978); Guizhou and Sichuan provinces, South China, Changhsingian-Griesbachian, Late Permian-Early Triassic (Wei et al. 1983); Meishan section, Zhejiang Province, South China, Early-Middle Changhsingian, Late Permian (Shi and Chen 1987); Zhenfeng, Qinglong, Zunyi, Guizhou Province, South China, Changhsingian, Late Permian (Hao 1992a, 1993, 1994, 1996); Zhenfeng, Qinglong, Guizhou Province, South China, Griesbachian, Early Triassic (Hao 1992b, 1993, 1994, 1996); Chongyang section, Hubei Province, South China, Changhsingian, Late Permian (Liu et al. 2010); bed 25, Kayitou Formation, Mide B section, Yunnan Province, South China, Griesbachian, Early Triassic (this work); beds 49 and 51, Kayitou Formation, Mide A section, Yunnan Province, South China, Permian-Triassic transition (this work); beds 15A, 15B, 17, 18, 20-22, 24-30, Longtan and Feixianguan formations, Zhongzhai section, Liupanshui city, Guizhou Province, South China, Changhsingian-Griesbachian, Late Permian-Early Triassic (this work); beds 14, 15, 19, Xuanwei and Kayitou formations, Tucheng section, Panxian County, Guizhou Province, South China, Permian-Triassic transition (this work).

***Hollinella* sp. 1**

Plate 1, figures J-L

Material: more than twenty external casts.

Discussion: *Hollinella* sp. 1 is characterized by reticulation and spines all over its lateral surface. *Hollinella* sp. 1 is close to *H. lungcamensis* Crasquin in Crasquin et al. (2018) from the Permian-Triassic transition of northern Vietnam (Crasquin et al. 2018) from which it differs by a distinct ventral lobe and the lack of L₄. However, all the specimens recovered from Zhongzhai and Mide B are poorly preserved, fragmented external casts: this preservation state precludes the observation of the complete extension of the frill, which is of high taxonomic significance. *Hollinella* sp. 1 is new to science but it is kept in open nomenclature until complete specimens are discovered to fully describe its diagnostic features.

Occurrence: Beds 20-22, 24, 25, 27-29, Longtan and Feixianguan formations, Zhongzhai section, Liupanshui City, Guizhou Province, South China, Changhsingian, Late Permian (this work); bed 25, Kayitou Formation, Mide B section, Yunnan Province, South China, Griesbachian, Early Triassic (this work).

***Hollinella* spp.**

Material: Xinmin section: numerous broken external casts.

Discussion: Numerous fragments of *Hollinella* occur in bed 5-3 of the Xinmin section. Nevertheless, their poor preservation state and incompleteness do not allow any attempt of precise specific attribution: they are therefore referred to as *Hollinella* spp.

Occurrence: Bed 5-3, Luolou Formation, Xinmin section, Guizhou Province, South China, Permian-Triassic transition (this work).

Superfamily KIRKBYOIDEA Ulrich and Bassler 1906
Family KIRKBYIDAE Ulrich and Bassler 1906
Genus *Reviya* Sohn 1961
Type species: *Amphissites? obesus* Croneis and Gale 1939 subsequently designated by Sohn (1961).

Reviya* cf. *curukensis Crasquin-Soleau et al. 2004b
Plate 1, figures M-O

Material: more than 30 external casts (Xinmin section).

Discussion: *Reviya* cf. *curukensis* is close to *R. curukensis* Crasquin-Soleau in Crasquin-Soleau et al., 2004b from the Griesbachian, Early Triassic of western Taurus in Turkey (Forel 2015; Crasquin-Soleau et al. 2004a, b). Since its description, *R. curukensis* has been reported from Griesbachian layers of the Gerennavár Formation exposed in the Bükk Mountains in Hungary (Forel et al. 2013a) and from the Yinkeng Formation outcropping in Meishan section, Zhejiang Province, China (Forel and Crasquin 2011b). The nature of the material from Xinmin precludes undoubtedly establishing the conspecificity of *R. cf. curukensis* with *R. curukensis* but the elongate carapace and lateral compression along anterior margin, which are diagnostic characters of *R. curukensis*, are visible in *R. cf. curukensis*. The kirkbyan pit is also located relatively ventrally but seems slightly more expressed than in *R. curukensis*.

Occurrence: Bed 5-3, Luolou Formation, Xinmin section, Guizhou Province, South China, Permian-Triassic transition (this work).

Family KNIGHTINIDAE Sohn 1970
Genus ***Carinaknightina*** Sohn 1970
Type species: *Carinaknightina carinata* Sohn 1970 by original designation.

Carinaknightina* cf. *zhenfengensis Hao 1992b
Plate 2, figures A, B

Material: more than 15 external casts (Xinmin section).

Discussion: *Carinaknightina zhenfengensis* Hao 1992b was described from the Feixianguan Formation (written Feih sienkuan) of Zhenfeng and Zunyi areas in Guizhou Province (Hao 1992b). The external casts reported here from the Xinmin section are morphologically close to *C. zhenfengensis* but in the absence of extracted material exposing the entire lateral surface and margins, the specimens from Xinmin can only be compared to *C. zhenfengensis*.

We take the opportunity to clarify the taxonomic attributions of *Amphissites* sp. and *Kindlella* sp. reported from bed 28 in the Zhongzhai section (respectively Fig. 2Db and Fig. 2Dc in Zhang et al. 2017). Amphissitidae Knight 1928 are, among other characters, diagnosed by the presence of one or more nodes on the lateral surface (see Sohn 1961 and Becker 1997b for summary and discussion). Of the genera belonging to the Amphissitidae, *Amphissites* Girty 1910 is characterized by vertical carinae on each side of a sub-central node (Sohn 1961; Becker 1997b). The specimen identified as *Amphissites* sp. from bed 28 in the Zhongzhai section lacks the pronounced ornamental characters of both these genus and family: the specimen

PLATE 1

Ostracods from the clastic Permian-Triassic transitional beds in South China, Guizhou and Yunnan provinces. Scale bars – 100 µm.

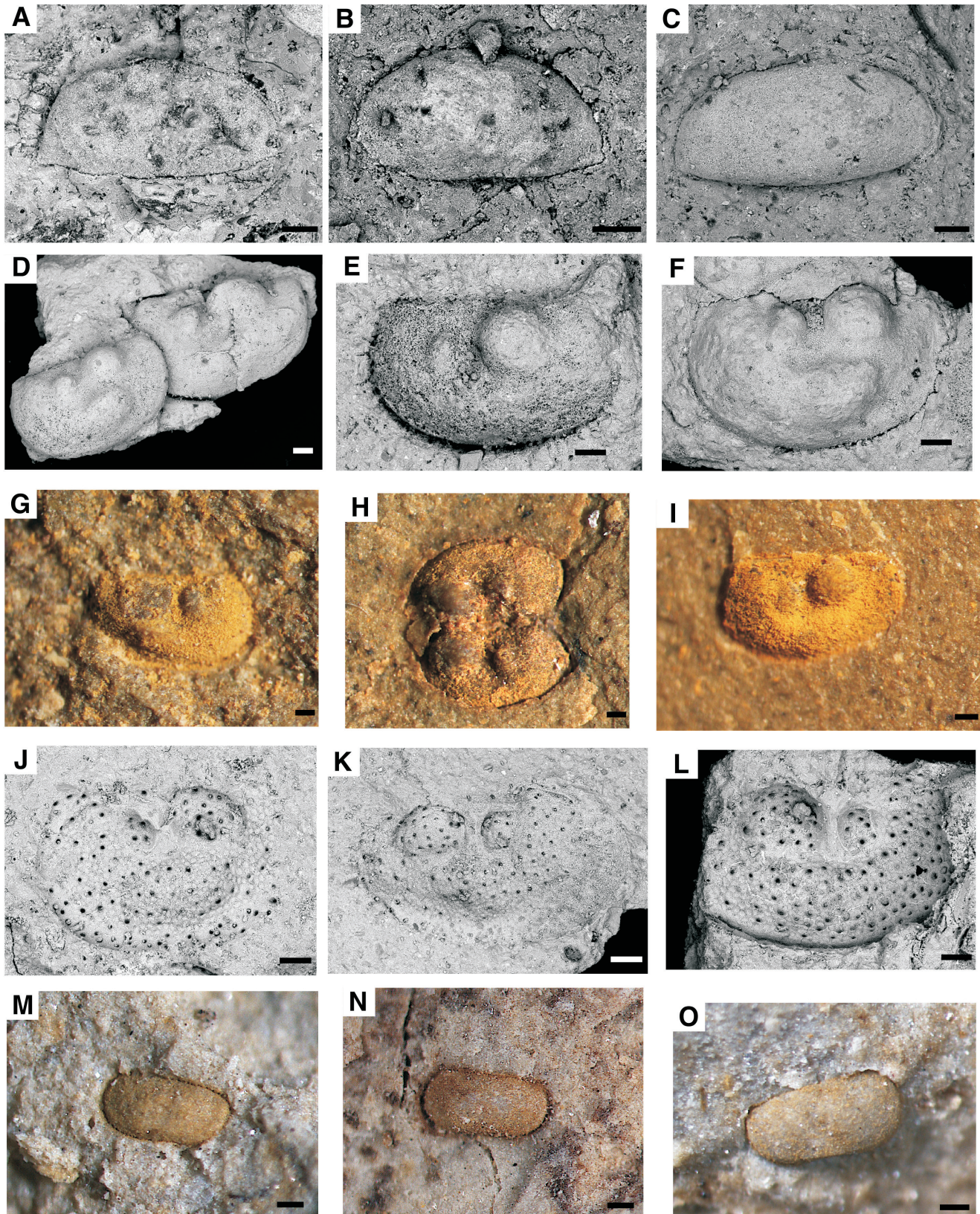
A-C *Acratia symmetrica* Hao 1992b, Late Permian, bed 13, Xuanwei Formation, Tucheng section. A – lateral view of a right valve, coll. MNHN.F.F62990, B – lateral view of a left valve, coll. MNHN.F.F62991, C – lateral view of a right valve, coll. MNHN.F.F62992.

D-I *Hollinella panxiensis* Wang 1978, Early Triassic, bed 25, Kayitou Formation, Mide B section, except specimens D and F from Late Permian, bed 22, Longtan Formation, Zhongzhai section. D – lateral view of two left valves, coll. MNHN.F.F62993, E – Lateral view of a left valve, coll. MNHN.F.F62994, F – lateral view of a left valve, coll. MNHN.F.F62995, G – lateral view of a right valve, coll. MNHN.F.F62996, H – lateral view of valves in butterfly position, coll.

MNHN.F.F62997, I – lateral view of a left valve, coll. MNHN.F.F62998.

J-L *Hollinella* sp. 1, Late Permian, bed 22, Longtan Formation, Zhongzhai section. J – external cast of a right valve, coll. MNHN.F.F62999, K – external cast of a left valve, coll. MNHN.F.F63170, L – external cast of a left valve, coll. MNHN.F.F63171.

M-O *Reviya* cf. *curukensis* Crasquin-Soleau in Crasquin-Soleau et al. 2004b, Permian-Triassic transition, bed 5-3, Luolou Formation, Xinmin section. M – lateral view of a left valve, coll. MNHN.F.F63172, N – lateral view of a left valve, coll. MNHN.F.F63173, O – lateral view of a right valve, coll. MNHN.F.F63174.



shown in Fig. 2Db in Zhang et al. (2017) belongs neither to *Amphissites* nor to Amphissitidae. Similarly, Kellettinidae Sohn, 1954 are characterized by two lateral nodes, among other diagnostic characters (Sohn 1954; Becker 1997c). *Kindlella* Sohn, 1954 is a bilobate ostracod with lobes extending below mid-height (Sohn 1954). However, the specimen identified as *Kindlella* sp. from Zhongzhai in Zhang et al. (2017) lacks lobation and thus does not belong to *Kindlella* nor to Kellettinidae. Therefore, *Amphissites* and *Kindlella* do not occur in bed 28 of the Zhongzhai section. *Amphissites* sp. and *Kindlella* sp. might rather be conspecific and should be attributed to *Carinaknightina* but only the close observation of properly oriented specimens will allow further discussing this hypothesis.

Occurrence: Bed 5-3, Luolou Formation, Xinmin section, Guizhou Province, South China, Permian-Triassic transition (this work).

Suborder KLOEDENELLOCOPINA Scott, 1961 emend. Lethiers 1981
Superfamily KLOEDENELLOIDEA Ulrich and Bassler 1908
Family KNOXITIDAE Egorov 1950 nom. correct Zanina 1971 [= Geisiniidae Sohn in Moore 1961]

Genus *Langdaia* Wang 1978

Type species: *Langdaia suboblonga* Wang 1978 by original designation and by monotypy.

Remarks: *Langdaia* Wang 1978 was described from the Feixianguan (written Feihshienkuan) and Chiaitou (written Chayashao) formations of Early Triassic age outcropping in western Guizhou and northeastern Yunnan provinces, South China (Wang 1978). Since then, four species have been added to this genus, without considering conformis species and species of questionable generic attribution:

- L. hornei* Crasquin-Soleau in Crasquin-Soleau et al. 1999 from the Wordian, Middle Permian, of Oman (Crasquin-Soleau et al. 1999);
- L. laolongdongensis* Crasquin-Soleau and Kershaw 2005 from the earliest Griesbachian, Early Triassic, of Sichuan Province, South China (Crasquin-Soleau and Kershaw 2005);
- L. meesooki* Chitnarin in Chitnarin et al. 2012 from the Capitanian, Middle Permian, of central Thailand (Chitnarin et al. 2012);
- L. bullabalvanyensis* Crasquin in Forel et al. 2013 from the Griesbachian, Early Triassic, of Bükk Mountains in Hungary (Forel et al. 2013a).

Crasquin-Soleau and Grădinaru (1996) reported on the possible occurrence of *Langdaia* in the Anisian, Middle Triassic, of North Dobrogea in Romania (cf. *L. suboblonga* Wang 1978). However, this species was not illustrated and its attribution is not confirmable so that we do not consider this Middle Triassic occurrence. In the present state of our knowledge, *Langdaia* is hence typical of the Permian and Triassic time interval, from the Wordian, Middle Permian, to the Griesbachian, Early Triassic. Its residual occurrence up to the Anisian, Middle Triassic, is for the moment not confirmed until the discovery of new material from North Dobrogea.

In the present analysis, *Langdaia* is only observed in the Zhongzhai section. However, *Langdaia* was not mentioned as part of the ostracod assemblages in this locality by Zhang et al. (2017).

Langdaia suboblonga Wang 1978

Plate 2, figures C-E

Langdaia suboblonga WANG 1978, p. 289, pl. 2, figs 8–11. – WEI 1981, p. 501, 502, pl. 1, figs 4–7. – WEI et al. 1983, p. 42, 43, pl. 10, fig. 3. – HAO 1992b, p. 41, pl. 1, figs 13–16. – HAO 1994, fig. 1/4. – HAO 1996, pl. 1, fig. 15. – CRASQUIN-SOLEAU and KERSHAW 2005, pl. 2, figs 1–6.
non *Langdaia suboblonga* – CRASQUIN et al. 2008, p. 238, pl. 1, fig. 3 = *Langdaia bullabalvanyensis* CRASQUIN in FOREL et al. 2013a.

Material: more than 25 external casts (Zhongzhai section).

Discussion: During the course of the present analysis, several corroded *Langdaia* specimens have been discovered on the surface of cracked muddy limestone of the Longtan and Feixianguan formations outcropping in the Zhongzhai section. The surface of four partially exfoliated specimens display exceptionally preserved adductor muscle scars (Pl. 2, Fig. C, D) that allow the first description of the adductor muscles field for the genus *Langdaia*. The original diagnosis of *Langdaia* does not include information on the muscle scar pattern and is as follows: “Carapace small; suboblong to subelliptical in lateral view. Dorsal margin straight, antero-dorsal angle more obtuse than postero-dorsal one; ventral margin straight. Anterior end more rounded and broader than posterior one. Right valve larger, overlapping the left, except in hinge margin where the left valve is slightly above the right. Surface marked by a median sulcus or pit (S_2), which is usually indistinct when outer lamella is preserved. Median node (L_2) absent. Dimorphism prominent, tecomorphs lenticulate in dorsal view, greatest thickness near posterior to middle; heteromorphs cuneiform in dorsal view, greatest thickness in posterior portion of carapace” (Wang 1978). In the species described more recently, no element of muscle scar patterns was visible. The specimens from the Zhongzhai section have a large adductor muscle spot, subcircular to ovoid in shape, elongate antero-posteriorly, located in front of mid-length and above mid-height, at the base of the median sulcus (Pl. 2, Fig. D). It consists of a loose cluster of about 25 randomly arranged individual polygonal scars. Mandibular and frontal spots are not observed.

Langdaia suboblonga was reported from the Griesbachian of the Bulla section in northern Italy (Crasquin et al. 2008) but this material has later been re-attributed to *L. bullabalvanyensis* Crasquin in Forel et al. 2013 from Hungary (Forel et al. 2013a). *Langdaia suboblonga* is therefore limited to South China and it is here for the first time reported from Late Permian levels. Yu et al. (2010) documented the occurrence of *L. suboblonga* from Mide A but they did not provide any illustration of the specimens to confirm this observation. The present investigation of Mide sections did not provide any specimen that is sufficiently well preserved to be attributed at least to the genus *Langdaia*. For these reasons, the report of *L. suboblonga* in Mide is here not confirmed and not taken into consideration.

Occurrence: Guizhou and Yunnan provinces, South China, Griesbachian, Early Triassic (Wang 1978); Sichuan Province, South China, Griesbachian, Early Triassic (Wei 1981; Wei et al. 1983); Guizhou Province, South China, Griesbachian (Hao 1992b, 1994, 1996); Feixianguan Formation, Laolongdong section, Huaying Mountains, eastern Sichuan Province, South China, Griesbachian, Early Triassic (Crasquin-Soleau and Kershaw 2005); beds 15A, 15B, 17-20, 22, 29, 30, Longtan and Feixianguan formations, Zhongzhai section, southwestern

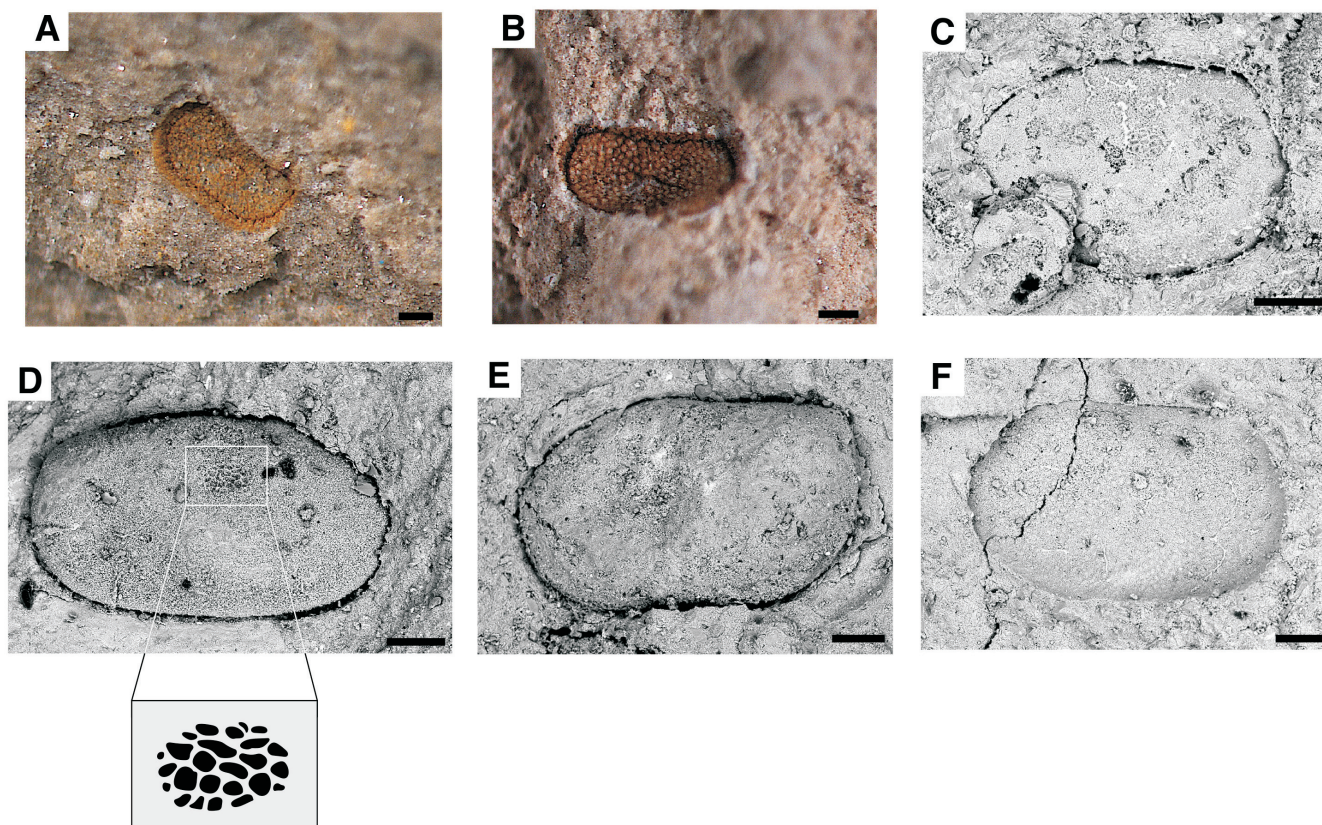


PLATE 2

Ostracods from the clastic Permian-Triassic transitional beds in South China, Guizhou and Yunnan Provinces. Scale bars – 100 μm .

- A,B *Carinaknightina* cf. *zhenfengensis* Hao 1992b, Permian-Triassic transition, bed 5-3, Luolou Formation, Xinmin section. external casts of right valves (A, coll. MNHN.F.F63175; B, coll. MNHN.F.F63176).
- C-E *Langdaia suboblonga* Wang 1978, Late Permian, bed 22, Longtan Formation, Zhongzhai section. C – lateral view of a right valve, coll. MNHN.F.F63177, D – lateral view of a right valve, coll. MNHN.F.F63178, enlargement shows the details of the preserved adductor muscle scars, E – lateral view of a left valve, coll. MNHN.F.F63179.
- F *Langdaia* cf. *laolongdongensis* Crasquin-Soleau and Kershaw 2005, Late Permian, Longtan Formation, Zhongzhai section, external cast of a ?left valve, coll. MNHN.F.F63180.

Guizhou Province, South China, Changhsingian–Griesbachian, Late Permian–Early Triassic (this work).

Langdaia cf. *laolongdongensis* Crasquin-Soleau and Kershaw 2005

Plate 2, figure F

Material: four external casts (Zhongzhai section).

Discussion: *Langdaia laolongdongensis* Crasquin-Soleau and Kershaw 2005 has been described from microbial deposits of the Feixianguan Formation in southeastern Sichuan Province, South China (Crasquin-Soleau and Kershaw 2005). Since then, this species has also been documented from the Griesbachian Werfen Formation exposed in Bulla section in northern Italy (Crasquin et al. 2008) and is therefore restricted to the Griesbachian, Early Triassic. *L.* cf. *laolongdongensis* observed in the Zhongzhai section has a subquadrangular outline and a punctate or slightly reticulate surface, which are both diagnostic of *L. laolongdongensis*. In the lack of complete specimens and because *L. laolongdongensis* shows a well-developed S₂ in some specimens that is not observed here, the present species is only referred to *L. laolongdongensis*.

Occurrence: Beds 15A, 22, Longtan Formation, Zhongzhai section, southwestern Guizhou Province, South China, Changhsingian, Late Permian (this work).

DISCUSSION

Standardizing the Zhongzhai records

Prior to the present study, ostracods from the Zhongzhai section have only been reported by Zhang et al. (2017). However, as shown in the systematic paleontology part of this contribution, several aspects of this report are problematic and the records need to be standardized before any attempt of analysis and discussion.

Zhang et al. (2017) first state that ostracods are “present with reasonably sufficient abundance” in Zhongzhai, being sporadically found in beds 12, 26 and 27 and much more abundant from bed 28 upward. It is not clear what is a reasonably sufficient abundance and if this abundance was estimated based on thin sections, extracted material and/or surfaces inspection. No distribution chart is provided and the only illustrated, and thus potentially debatable, taxa are issued from bed 28 and have been here re-attributed to *Acratia* sp. and *Carinaknightina* sp. (see Results chapter). The methodology used in Zhang et al. (2017) for ostracod analysis in Zhongzhai is not described but it is likely that these taxa were extracted by hot acetolysis processing (Lethiers and Crasquin-Soleau 1988; Crasquin-Soleau et al. 2005) of the muddy limestone of bed 28. This difference in the methodologies used between the present work (visual inspection of sediments cracks) and Zhang et al. (2017) might explain why these taxa have not been observed during the present investigation of Zhongzhai deposits.

A second important point that calls for homogenization are the mass occurrences and the problematic record of *Hollinella*. Mass occurrences are mentioned in Zhang et al. (2017) from bed 27 upwards. It is furthermore stated that “Taxonomically, they are mainly represented by three genera: *Acratia*, *Amphissites*, *Kindella*” (= *Acratia* and *Carinaknightina* according to this contribution) and that “where they occur they are consistently low in species diversity, but appear in massive

numbers and are crowdedly compacted [...] as illustrated in Figs 2E–H” (pp. 8 and 9 in Zhang et al. 2017). However, the Figs 2E–H referred to in Zhang et al. (2017) show numerous *Hollinella* specimens on the surface of the sediments, which nevertheless failed to be listed as part of the assemblage. Because of this lack of mention of *Hollinella* and taxonomic issues discussed higher, the abundance chart provided in Fig. 3 of Zhang et al. (2017) can hardly be used as it is impossible to correlate it with any taxonomic information that would be pivotal to decipher which taxa build-up the reported mass occurrences in Zhongzhai. Because of the lack of distribution chart in Zhang et al. (2017) and in the absence of additional evidence, we consider that *Acratia* sp. and *Carinaknightina* sp. in Zhongzhai are restricted to bed 28. The distribution chart of ostracod species documented in Zhongzhai is shown in text-fig. 2, which summarizes the taxa updated from Zhang et al. (2017) and those newly identified here.

Diversity and composition

We report on ostracod assemblages preserved on the surface of disaggregated clastic sediments from five sections spanning the EPE in Yunnan and Guizhou provinces, South China (text-figs. 1, 2). As detailed earlier, it is impossible to quantify the abundance of ostracods at the scrutinized localities, but differences are still noticeable. All studied sections are characterized by low diversity assemblages, often in relatively high abundances. The observed diversity increases eastward over the studied area, which corresponds to an increase in depth and marine influence (text-fig. 2). This pattern might be partially exaggerated as most of the sections also yielded scarce indeterminable taxa that may slightly increase the diversity westward.

The westernmost paralic sections, Mide A and B, record the lowest diversity of this study with one identifiable species in Mide A (*H. panxiensis*) and two in Mide B (*H. panxiensis* and *H.* sp. 1). Other ostracod taxa are present, although rare, in both sections but their poor preservation did not allow any attempt of identification. No ostracod was found from the Xuanwei Formation in Mide A and B so that they are restricted to the Kayitou Formation in this study. In Mide A, the relative maximum of abundance occurs in bed 49. In Mide B, only bed 25 was productive and yielded a high abundance of *H. panxiensis*.

Two species are identified in the easternmost paralic Tucheng section: *A. symmetrica* is restricted to the Xuanwei Formation (bed 13) while *H. panxiensis* occurs in both Xuanwei (beds 14, 15) and Kayitou formations (bed 19). None of the species is abundant in Tucheng. The two species are not occurring in the same levels of the Xuanwei Formation so that each productive bed yielded monospecific assemblages. Only *H. panxiensis* crosses the Permian/Triassic boundary in Tucheng.

The maximum of diversity observed in the present analysis occurs in Zhongzhai where four species are newly identified here: *H. panxiensis*, *H.* sp. 1, *L.* cf. *laolongdongensis* and *L. suboblonga*. At least two additional species have been illustrated in Zhang et al. (2017) from bed 28, the taxonomic attribution of which has been discussed and modified in this contribution (*Carinaknightina* sp. and *Acratia* sp.). In the present work, beds 16 and 23 in Zhongzhai are devoid of ostracods and the species diversity ranges from one (beds 19 and 26 of the Longtan Formation) to four (beds 22 and 28 of the Longtan Formation). In terms of abundance, *H. panxiensis* is by far dominant with a peak in bed 22, a medium abundance in beds 24, 29,

30 and lower abundances in beds 15A, 15B, 17, 18, 20, 21, 25-28. *L. suboblonga* is secondary in most samples where it occurs, with a maximum in bed 22. *H. sp. 1* (beds 20-22, 24, 25, 27-29) and *L. cf. laolongdongensis* (beds 15A, 22) are accessory components of the assemblages where they occur. High abundances are reported for the upper part of Zhongzhai section in Zhang et al. (2017) but they are disconnected from taxonomy and cannot be satisfactorily discussed as detailed before. For this reason, the ostracod record for bed 30 upwards in Zhongzhai provided in Zhang et al. (2017) is not considered here. In Zhongzhai, only *H. panxiensis*, *H. sp. 1* and *L. suboblonga* cross the PTB. Conversely, *L. cf. laolongdongensis*, *C. sp.* and *A. sp.* are restricted to the Late Permian levels. Until now, no species is known as restricted to the Triassic layers in Zhongzhai section.

The bed 5-3 of the easternmost Xinmin section provided at least three species (*C. cf. zhenfengensis*, *H. spp.*, *R. cf. curukensis*) but this diversity level is clearly underestimated as shown by the *Hollinella* spp. group. However, this material and more precisely the representatives of Kirkbyidae (*C. cf. zhenfengensis* and *R. cf. curukensis*) are of key significance in unravelling the survival patterns of ostracods during the Triassic as discussed below.

Nine species are recorded through the EPE over the studied area, without considering indeterminable taxa. Of them, *A. symmetrica*, *H. panxiensis* and *L. laolongdongensis* are already known from this interval in South China (see occurrences lists in the results part). *H. panxiensis*, *H. sp. 1* and *L. suboblonga* cross the Permian/Triassic boundary over the studied area. *H. panxiensis* crosses the Permian/Triassic boundary in Tucheng and Zhongzhai while it is restricted to Triassic beds in Mide sections. *A. symmetrica* is here restricted to the Permian levels exposed in Tucheng but it occurs in Triassic beds of Zhenfeng in western Guizhou (Hao 1992b, 1994, 1996). *A. sp.*, *C. sp.* and *L. cf. laolongdongensis* are restricted to Permian layers of Zhongzhai.

Autochthonous or allochthonous thanatoconosis?

The Permian-Triassic transitional beds in Mide A, B and in Zhongzhai are characterized by levels of mass occurrences of *Hollinella*, primarily *H. panxiensis* (text-fig. 2). Mass occurrences of low diversity ostracod assemblages in Zhongzhai have already been noted by Zhang et al. (2017), but they were disconnected from taxonomic information. The possibility of them being related to transportation processes is of utmost importance as regards to their implications and requires to be addressed. The proportion of complete carapaces versus isolated valves and the demographic structure of populations can be used to determine the autochthonous or allochthonous nature of ostracod assemblages (e.g., Boomer et al. 2003). Mass occurrences of ostracods are indeed not rare in the fossil record and in modern environments where for example they occur in shallow muddy bays in French Polynesia or along the Andaman Sea on the southwest coast of Thailand (MBF, personal observations and works in progress). In these cases, most specimens are relatively well preserved detached valves that might have been transported by currents from more offshore zones.

At all studied sections, the specimens are preserved on the surface of cracked sediments: most of them are still partly covered with sediments and it is complex to determine if the exposed portion corresponds to a disarticulated valve or rather to a com-

plete carapace. This feature hardens the measurements of enough specimens to fully characterize the demographic structure of the assemblages. An attempt can nevertheless be performed for bed 25 in Mide B where 11 specimens of *H. panxiensis* with the entire margins exposed have been measured: their H/L scatter plot is shown in text-fig. 4. The successive ontogenetic stages are hardly distinguishable but the size range of these specimens indicates that this assemblage is composed of adults as well as several juvenile instars. Following Boomer et al. (2003) and because the assemblage in bed 25 at Mide B is *in situ* with no preferred alignment or orientation of the specimens, it might correspond to a thanatoconosis. The assemblage is furthermore composed of a mixture of adults and juveniles, which might represent only the larger instars, as their smaller length is 486 μm (text-fig. 4). Mide B section slightly differs from other localities under analysis by the frequent preservation of *H. panxiensis* in butterfly position (Pl. 1, Fig. H). This type of preservation occurs in all productive beds of Mide A section (beds 49 and 51) and Mide B section (bed 25 where it is quite frequent). This witnesses relatively fast and quiet burial conditions in soft sediments without transport and suggests that the fossil assemblages in both Mide sections preserve the original communities (Williams et al. 2005). Altogether, these elements point to a relatively low energy thanatoconosis with little post-mortem disturbance, which is considered as a relatively good indicator of environmental conditions. The preservation in butterfly position of Cambrian bradoriid arthropods has also been related to the relative weakness of adductor muscles that ensured the closing of their valves (Williams et al. 2011). Such abundant record in Mide B, and to a lesser extent in Mide A, could be related to the interplay of the low hydrodynamic context of deposition and the weakness of the adductor muscles of *H. panxiensis*, which stay unknown to date.

In Zhongzhai, the presence of very fine micro-ornament and delicate spines on brachiopod shells led Zhang et al. (2013, 2017) to consider that the fossil assemblages have not been subjected to significant post-mortem changes and that they represent the original living communities, in line with the present conclusions.

Microbial versus non-microbial: the multiple faces of ostracods' survival

A point on ostracod lifestyles

The lifestyles of ostracods have been used as evidence to discuss the evolution of organisms' lifestyles through the EPE at Zhongzhai section (Zhang et al. 2017). In this discussion, *Acratia*, *Amphissites* and *Kindella* (here re-attributed to *Acratia* and *Carinaknightina*) are presented as indices of the Stage 3 post-extinction benthonic paleocommunity developed from beds 32 to 46, which is dominated by bivalves, lingulid brachiopods, microgastropods and ostracods (Zhang et al. 2017). Of the three ostracods identified, only *Amphissites* is classified, without reference nor discussion, to the "epifaunal I: slow-moving suspension feeders" functional trait category, a classification that needs to be reviewed.

We hypothesize that the classification of suspension feeder for *Amphissites* (= *Carinaknightina*) relies on the paradigm that Palaeocopida were filter-feeders based on morphological analysis comparing Palaeocopida and Platycopida, while Podocopida are traditionally considered as deposit-feeders (e.g., Adamczak 1969; Whatley 1991; Lethiers and Whatley 1994, 1995). How-

ever, this antithetic view of Palaeocopida and Podocopida is now out of date and its implications are problematic. The discovery of a fulcral point (a small cavity on the inner surface of the valves produced by the action of the coxa of the mandible) and mandibular scars in Palaeozoic Palaeocopida (Beyrichioidea) implies that these ostracods were actually actively deposit-feeding rather than filter-feeding (Olempska 2008). Palaeocopida as a whole can therefore no longer be classified as filter-feeders. Controversy also arises from the side of Podocopida, with the description of filtering structures in the extant podocopid *Vitjasiella* (Schornikov 1976) and a plumose mandible bristle in Rockalliidae (Cytheroidea, Podocopida), which is also related to filter-feeding (Neale 1988). Extant Platycopida themselves are not widely accepted as filter-feeders, some considering them as deposit-feeders (Swanson et al. 2005). This view is generally not admitted and Brändao and Horne (2009) and Horne et al. (2011) consider that platycopids are filter-feeders adapted to food of particular dimension, which is typical of the plankton available in oligotrophic conditions. For these reasons, it is no longer possible to use the traditional Manichean views of ostracods' lifestyles without new data possibly including exceptional preservations of soft parts as well as a full re-evaluation of how to use these concepts in the fossil record.

Zhang et al. (2017) document a major shift in the community structure following the EPE from motile suspension feeders and infaunal motile deposit feeders to slow-moving suspension feeding ostracods. Beds 1 to 26 record the *Neochonetes*-dominated paleocommunity that is largely dominated by brachiopods, with ostracods being “sparser, restricted to the bed 12”, without taxonomic information. According to the data and observations gathered in the present analysis, four species occur for this interval (text-fig. 2): *H. panxiensis*, *H. sp. 1*, *L. suboblonga* and *L. cf. laolongdongensis*. It is quite hard to understand the basement of the classification of slow-moving suspension feeding ostracods in this context. Bed 27 corresponds to the stage 2 *Tethyochonetes*-dominated paleocommunity dominated by brachiopods with the increasing abundance of bivalves, ostracods occur in low numbers, without taxonomic indications (Zhang et al. 2017). According to the present work, two ostracod species occur in bed 27: *H. panxiensis* and *H. sp. 1*. The stage 3 paleocommunity spans from bed 28 to bed 46, with ostracods reported as “extremely abundant” and “at very low species richness”, corresponding to *Acratia*, *Amphissites* and *Kindlella* according to Zhang et al. (2017). Following the present revisions, five species occur during this interval: *H. panxiensis*, *H. sp. 1*, *L. suboblonga*, *Carinaknightina sp.* and *Acratia sp.* The present investigation of Zhongzhai section furthermore indicates that mass occurrences are chiefly composed of *Hollinella* specimens.

Consequently, the only taxonomic differences between the pre- and post-extinction ostracod assemblages in Zhongzhai are the occurrences of *Carinaknightina sp.* and *Acratia sp.*, and the disappearance of *L. cf. laolongdongensis* in post-extinction communities. If applying the traditional views exposed higher of filter versus deposit-feeders, the pre-extinction ostracod communities are integrally composed of filter-feeders (*H. panxiensis*, *H. sp. 1*, *L. cf. laolongdongensis*, *L. suboblonga*) and lack deposit-feeders. Conversely, the post-extinction ostracod assemblages are composed of both deposit (*Acratia sp.*) and filter-feeders (*H. panxiensis*, *H. sp. 1*, *L. suboblonga*, *Carinaknightina sp.*). The change of ostracod communities re-

ported by Zhang et al. (2017) is not supported by the data, even when applying the old-style views of fossil ostracod feeding modes. Paleocommunities change in Zhongzhai are reported as largely dominated by the brachiopod shift from *Neochonetes* to *Tethyochonetes*, which may relate to food availability, competition for resources and environmental factors (Zhang et al., 2017). Here ostracods provide good arguments regarding environmental parameters as discussed below.

A new understanding of ostracod diversity through the EPE: survivors rather survival

Until the present large-scale analysis of clastic shelf deposits, the survival of marine ostracods in the direct aftermath of the EPE was only known from microbial formations (e.g., Forel et al. 2013b). This “microbial survival” is taxonomically limited to Bairdiidae that have been hypothesized to exploit the microbial mats as food resources, grazing on microbes, and as local O₂ sources in an O₂-impoverished context (e.g., Forel et al. 2013b). This peculiar pattern led the groundwork for a re-evaluation of the adaptive potential of Bairdiidae. Bairdiidae are known from marine environments from the Ordovician to present days (e.g., Moore 1961; Maddocks 1969; Brandão 2008) and are traditionally considered as restricted to normal stable marine waters (e.g., Melnyk and Maddocks 1988). However, the taxa that abundantly survived directly after the EPE in association with microbial deposits displayed an unexpected large array of physiological and population adaptations (e.g., Forel 2015; Forel et al. 2013b, 2015). These features are undeniably indicative of relatively stressful environments but they preclude long-term anoxic waters. Here we take the opportunity to mention the works of Hautmann et al. (2015) and Martindale et al. (2019) that consider that the hypothesis of the microbial refuge proposed by Forel et al. (2013b) could not be valuable for all groups. We are in line with this conclusion of Hautmann et al. (2015) and Martindale et al. (2019) as the microbial refuge mechanism was integrally derived from ostracod data. An explanation to this specificity of Bairdiidae following the EPE is that owing to their small sizes, their O₂ requirements might have been significantly lower than any other metazoan group. Extant Bairdiidae furthermore have important adaptabilities to cope with low O₂ levels for several hours (Forel, personal observations and work in progress), which would have allowed them to adapt to stressful environments following the EPE based on uniformitarianism. It is worth noting that another type of survival of Bairdiidae in the absence of microbial deposits following the crisis in northwest Iran is currently under description and analysis (Gliwa et al. 2018, 2020).

The present records through clastic Permian-Triassic transitional beds in South China radically differ from the previous microbial record and provide a new glimpse on the diversity of the survival mechanisms of ostracods. The only occurrence of Bairdiidae in the present analysis is *A. symmetrica* from the Late Permian of Tucheng section (bed 13, Xuanwei Formation; text-fig. 2). It is an accessory component of the scrutinized assemblage, is restricted to the Late Permian Xuanwei Formation in Tucheng and the preservation of the specimens does not preclude that they were transported from more distal areas. Conversely, Palaeocopida are relatively rare in the post-extinction survival patches associated with microbial deposits documented to date, where they only occur as accessory components when present (e.g., Turkey, Forel 2015; Crasquin-Soleau et al. 2004a, b).

Palaeocopida have long been considered as emblematic victims of the EPE (e.g., Moore 1961) and currently, their latest unquestionable occurrence is of Late Triassic, Carnian age (Forel et al. 2019). In more details, *Triassicindivisia*, of unknown superfamilial and familial attributions, occurs in the Anisian, Middle Triassic, of the subtidal zone in southern Tibet (Forel and Crasquin 2011a; Forel et al. 2011). Conversely, Kirkbyoidea range up to the Carnian, Late Triassic, in deep waters of southern Turkey (Forel et al. 2019). The last known occurrence of *Hollinella* and Hollinellidae is of Late Griesbachian age at Meishan section, Zhejiang Province, China (Forel and Crasquin 2011b). Contrary to the present record of mass occurrences of *Hollinella*, these latest Palaeocopida all correspond to residual low abundance records. The abundance of *H. panxiensis* in the present analysis rather reflects a new figure of the temporary and local survival of ostracod species related to peculiar environmental conditions to which they were adapted. This unusual pattern of post-extinction proliferation of *Hollinella* is only known from the studied area in South China and from northern Vietnam (Crasquin et al. 2018) and might illustrate similar environmental conditions following the EPE. This pattern corresponds to survival, as the Hollinellidae do not take part to the post-extinction recovery. It is interesting to note that this pattern is not only recorded by ostracods as the short-term survivorship of relicts of the Late Permian *Gigantopteris* flora has also been encountered within the *Annalepis–Peltaspermum* macrofloral assemblage at the Tucheng section (Yu et al. 2010; Bercovici et al. 2015).

The present assemblages might illustrate the “palaeocopid association” recognized by Wang (1988) in the Late Paleozoic of South China with a predominance of Palaeocopida (and Cavellinidae). The ostracods of the “palaeocopid association” occupied shallow-water near-shore inner shelf environments, as opposed to the smooth podocopid association *sensu* Wang 1988. This association is dominated by bairdiids, accompanied by Kirkbyoidea, and might have inhabited outer shelf regions, relatively more offshore than the palaeocopid association (Wang 1988).

On the other hand, Kirkbyoidea are absent from all paralic sections studied here. They occur in the shallow marine Zhongzhai section as shown by Zhang et al. (2017; *Carinaknightina* sp. following the re-attribution detailed above) but it is difficult to estimate their abundance as they have not been recognized in the present analysis. Kirkbyoidea are more abundant in deeper waters of the Xinmin section, represented by two genera and two species (*C. cf. zhenfengensis* and *R. cf. curukensis*). Although relatively abundant in these localities, Kirkbyidae are more frequent in association with post-EPE microbialites in Turkey (Forel 2015; Crasquin-Soleau et al. 2004a, b) and Hungary (Forel et al. 2013a) respectively from inner ramp/shelf and distal ramp/shelf (Martindale et al. 2019). They are also found in the Griesbachian of Meishan (Forel and Crasquin 2011b) and disappear from the fossil record until their last known occurrence during the Carnian, Late Triassic, in the deep-waters from Turkey (Forel et al. 2019).

The geographical distribution of *H. panxiensis* during the Changhsingian prior to the EPE is large and extends eastward to the marine Meishan section in Zhejiang Province (Crasquin et al. 2010). However, this species is restricted to the eastern part of this area where it proliferates in clastic shallow to very shallow conditions after the EPE, being absent from purely marine

zones, including those characterized by the growth of post-extinction microbial mats. Noteworthy, the only record of *H. panxiensis* in association with post-extinction microbial deposits is from the Hubei Province (Liu et al. 2010) but no information is given on its abundance to further discuss this record. This pattern might be indicative of environmental requirements radically distinct from those of Bairdiidae surviving in post-extinction microbial patches.

The proliferation of *Hollinella* in clastic areas while absent from more marine deposits at the same interval is in line with the common view that they were representative of shallow to very-shallow water marine faunas (e.g., Melnyk and Maddocks 1988). Their environmental restriction might however indicate that they radically differ from Bairdiidae in terms of adaptative abilities and that they were rather able to cope with high detrital influx, which seem impossible to Bairdiidae.

CONCLUSION

The present analysis scrutinized the ostracods from five clastic sections spanning the end-Permian extinction in South China (Guizhou and Yunnan provinces), corresponding to paralic to deep-water conditions. We report on the occurrence of nine species, some of which were known from these or coeval sections in South China, and discuss their taxonomy. The excellent preservation of some specimens of *Langdaia suboblunga* allow us to describe for the first time the central muscle scar field of this palaeocopid genus. We document the exceptional survival of Palaeocopida, mainly Hollinellidae, which is here related to the influence of important clastic inputs. These assemblages allow us to discuss and illustrate the plurality and the complexity of the survival of benthic microfaunas after the end-Permian extinction, under the strong influence of environmental conditions.

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