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Early Triassic trace fossils from the Three Gorges area of South China: Implications for the recovery of benthic ecosystems following the Permian–Triassic extinction

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ABSTRACT

The Lower Triassic Daye and Jialingjiang formations of the Three Gorges area (South China) record the recovery interval of benthic tracemaking invertebrates following the P–Tr mass extinction. A total of 17 ichnospecies in 14 ichnogenera are documented from Smithian and Spathian strata. Our trace fossil data, in combination with previously published studies, show that ichnodiversity in the Middle Yangtze region increased markedly in the early Spathian. Trace fossils in the Smithian are dominated by simple, small, horizontal burrows, including *Didymaulichnus* and *Planolites*, whereas Spathian trace fossils are diverse and abundant with moderate–high bioturbation levels and complex burrow networks, such as *Thalassinoides*. Both burrow sizes and penetration depths increased gradually from the early Spathian to the middle–late Spathian, implying a gradual recovery pattern for benthic ecosystems. Early Triassic ichnofossils are characterised by aspects of opportunistic behaviour (e.g., low-to-moderate ichnodiversity, low-to-moderate bioturbation, small burrow widths, and shallow tiering), suggesting stressed environmental conditions. The recovery tempo and pattern of ichnocoenoses in South China is likely structured by temporal and spatial changes of the refuge zone in the Early Triassic.

1. Introduction

The largest mass extinction in geological history happened near the Permian–Triassic (P–Tr) boundary and killed over 90% of marine species (Erwin, 1993; Song et al., 2013). Biotic recovery following this event has attracted much attention in recent years and remains the topic of much debate. It has long been considered that the P–Tr mass extinction was followed by a period of delayed biotic recovery that lasted until the Middle Triassic (Stanley, 1990). The Early Triassic is an interval characterised by continued low biodiversity (Erwin, 1993), blooms of opportunistic and disaster taxa (Bottjer et al., 2008), reduction in the size of both metazoans (Twitchett, 2007) and protozoans (Song et al., 2011a), and the absence of metazoan reefs (Flügel, 2002) and of calcareous algae (Flügel, 1985). Carbon and sulphur isotopic data illustrate a series of large fluctuations throughout the Early Triassic (Payne et al., 2004; Tong et al., 2007; Song et al., 2014a), reflecting stressed marine environments. Recent geochemical data show that the stressed environments of the Early Triassic are characterised by a long-term hot climate (Sun et al., 2012; Romano et al., 2013) as well as severe oceanic anoxia (Wignall et al., 2010; Song et al., 2012; Grasby et al., 2013). However, recent palaeontological data show that a fitful recovery of many marine organisms began in the Smithian and Spathian, including nektons, such as ammonoids and conodonts (Brayard et al., 2009; Stanley, 2009), benthic foraminifers and calcareous algae (Song et al., 2011b), and even metazoan reefs (Brayard et al., 2011). As a result, the mechanisms that caused biotic recovery in the Early Triassic are still a subject of debate.

Trace fossils are good indicators of palaeoenvironmental conditions and the behaviours of benthic invertebrates. They have been used to reveal the tempo and pattern of ecologic recovery following the P–Tr mass extinction (e.g., Twitchett and Wignall, 1996; Wignall et al., 1998; Twitchett, 1999, 2006; Pruss and Bottjer, 2004; Twitchett and Barras, 2004; Zonneveld, 2004; Beatty et al., 2005, 2008; Fraiser and Bottjer, 2009; Zonneveld et al., 2010a, 2010b; Chen et al., 2011, 2012; Hofmann et al., 2011; Baucon et al., 2014). These ichnofossil data, derived from global localities, show that benthic invertebrate trace-makers at boreal palaeolatitudes, e.g., Spitsbergen (Wignall et al., 1998) and western Canada (Zonneveld, 2004; Beatty et al., 2005, 2008; Zonneveld et al., 2010a, 2010b), recovered before those at low and middle palaeolatitudes, e.g., the western United States (Pruss and Bottjer, 2004; Twitchett and Barras, 2004; Fraiser and Bottjer, 2009), northern Italy (Twitchett and Wignall, 1996; Twitchett, 1999; Twitchett and Barras, 2004), the Lower Yangtze region of South China (Chen et al., 2011), and Western

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Australia (Chen et al., 2012). However, recent studies showed that a diverse and complex ichnofauna began to occur in the late Griesbachian in Italy (Hofmann et al., 2011). Thus, the environmental factors that structure the temporal and spatial patterns of Early Triassic ichnofossil assemblages are still unclear and additional quantitative analyses are required (Fraiser and Bottjer, 2009).

In this study, abundant and diverse trace fossils from the Lower Triassic successions in the Three Gorges area were described and analysed. Five proxies, including ichnodiversity, forms and complexity, bioturbation index, burrow sizes, and tiering levels, were used to evaluate the tempo and pattern of benthic ecosystem recovery in the aftermath of the P–Tr mass extinction in the Middle Yangtze region of South China. Additionally, the latest geochemical data combined with a hypothesised recovery model (Song et al., 2014b) were used to explain the temporal and spatial patterns of Early Triassic ichnofossil assemblages.

2. Studied sections and stratigraphic setting

The South and North Xiakou sections are situated 3 km west of Jianyangping, Xiakou Town, Xingshan County of Hubei Province and approximately 80 km away from Yichang City (Fig. 1). These two sections are located along both banks of the Xiangxi River, a branch of the Yangtze River. The present study made use of a previously established site along the south bank (starting at 110°48′13″ E, 31°06′52″ N, referred to as South Xiakou section) as well as a newly surveyed section on the north bank of the Xiangxi River (starting at 110°48′17″ E, 31°06′53″ N, referred to as North Xiakou section). The trace fossil assemblages of both sites have been systematically studied in this study.

Lower Triassic successions widely crop out across the entire Yangtze Platform (Tong and Yin, 2002). The studied area belonged to the middle part of the upper Yangtze platform located at the eastern Tethys during the Early Triassic (Feng et al., 1997). The P–Tr boundary and Lower Triassic rocks at the Three Gorges area are well exposed (Fig. 2A). Lower Triassic sequences deposited in the Three Gorges region of South China constitute the Daye and Jialingjiang formations (Figs. 3, 4), which lie conformably above the Upper Permian Dalong Formation and are in turn overlain by the Middle Triassic Badong Formation (Wang and Xia, 2004; Zhao et al., 2005, 2010, 2013).

The Daye Formation in this area is subdivided into four members. Member I is composed of laminated black shale interbedded with grey muddy limestone and is dominated by horizontal lamination (Fig. 2A). It is approximately 51.3 m thick at the South Xiakou section and 46.6 m thick at the North Xiakou section. This member yields an abundance of thin-shelled fossils, including the bivalves *Claraia* spp., *Eumorphotis* spp., and *Posidonia* spp., as well as the ammonoids *Ophiceras*, *Lytophiceras*, *Prionolobus*, and *Gyronites* (Li et al., 2009). Trace fossils are absent. Thus, the black shale- and muddy limestone-dominated sequences preserving epifaunal bivalves and ammonoids indicate an offshore setting.

Member II consists mainly of light-grey medium to thickly bedded micritic limestone and vermicular limestone. The Early Triassic vermicular limestone has been proposed to be produced by chemical or microbial coacervation, or the diagenetic differentiation under low-energy environmental conditions (see Zhao et al., 2008). It is approximately 50.9 m thick at the South Xiakou section and 43.4 m thick at the North Xiakou section. This member yields the bivalve *Posidonia* spp. and the ammonoid *Flemingites* (Li et al., 2009). Trace fossils are very rare. Only

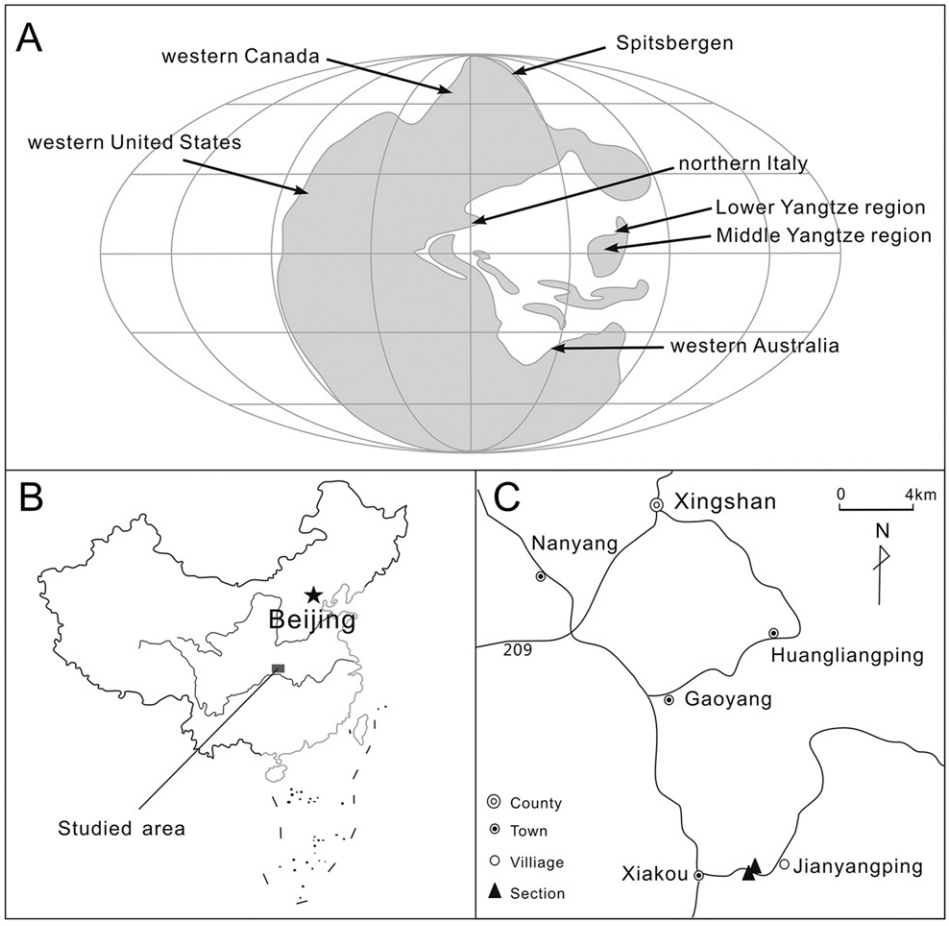

Fig. 1. A, Palaeogeographic map of the Early Triassic with approximate locations of the Lower Triassic successions containing ichnofossil assemblages. B, Inset map of the People's Republic of China. C, Locality of the studied sections.
Modified after Scotese (2001).