Palaeogeography, Palaeoclimatology, Palaeoecology 487 (2017) 118–135

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Community replacement, ecological shift and early warning signals prior to the end-Permian mass extinction: A case study from a nearshore clastic-shelf section in South China

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ARTICLE INFO

Keywords:
Permian–Triassic boundary
Benthonic ecosystem
Regime shift
Disaster group
Zhongzhai section

ABSTRACT

A quantitative investigation of the ecological changes of shallow-marine benthos was undertaken at the Permian–Triassic boundary section at Zhongzhai, South China. The studied fossil material primarily included brachiopods and bivalves owing to their abundance throughout the section, but other subordinate taxonomic groups including ostracods and microgastropods were also integrated for discussion.

Overall, a succession of three benthonic paleocommunities was recognized representing three connected ecological evolutionary stages across the Permian–Triassic transition. Both Stage 1 and Stage 2 paleocommunities predated the end-Permian boundary mass extinction, and were characterized by relatively high diversity of brachiopods and bivalves, with no or very rare other taxa. Approaching the end-Permian mass extinction and the PTB itself, the paleocommunity abruptly changed and was replaced by the Stage 2 paleocommunity that was characterized by a relatively low Shannon's diversity (H) coupled with a high Simpson's dominance index (D) and, most notably, a changeover from *Neochonetes* to *Tethyochonetes* (both are brachiopod genera) as the most significant ecological dominants. This Simpson's dominance index (D) shift correlates well with food shortage (i.e. much reduced terrestrial influx and acritarch abundance), and is therefore interpreted to signify, possibly, intensified interspecific competitions with *Tethyochonetes* seemingly outcompeting *Neochonetes* presumably due to its preadapted smaller body size. The post-extinction (Stage 3) paleocommunity is distinguished by a highly characteristic low-diversity and high-abundance fauna comprised mainly of lingulid brachiopods, *Claraia* bivalves, microgastropods and ostracods, suggesting a unique and highly stressful ecological regime. In this paleocommunity, *Claraia* might have acted like a "disaster taxon" and, as such, its ecological functional role in the paleocommunity was activated and elevated because of exceptional ecological conditions (e.g., anoxia, hyperthermal and/or severe food shortage).

From the studied section, a number of ecological traits including species abundance distribution, Shannon's diversity (H), community dominance and body-size structure were identified as demonstrating significant changes accompanying community replacement prior to the end-Permian mass extinction. The fact that these changes preceded the mass extinction may suggest that these traits could represent some early warning signals for an impending ecological regime shift. This extended interpretation clearly has significant implications for modern ecological studies to predict future impending ecological regime shifts.

1. Introduction

The end-Permian mass extinction (EPME) is the biggest of its kind in Earth's Phanerozoic history, marked by the loss of over 90% of marine species and > 70% of terrestrial species (Sepkoski, 1981; Erwin, 1994; Jin et al., 2000; Xiong and Wang, 2011; Shen et al., 2011; Stanley, 2016). This was an epic event in the history of life. Scientific investigation into this catastrophic event has become one of the core

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http://dx.doi.org/10.1016/j.palaeo.2017.07.042
Received 12 April 2017; Received in revised form 20 July 2017; Accepted 24 July 2017
Available online 24 August 2017

research topics in modern paleobiology. Not only did the crisis completely wipe out many taxonomic groups at a global scale, it also severely affected both the terrestrial and marine ecosystems (Sepkoski, 1981; Xiong and Wang, 2011). For the marine realm, for example, the ecosystem experienced a profound shift from the Paleozoic-type communities (brachiopod-dominated faunas) to Mesozoic and Cenozoic-type communities (molluscan-dominated faunas) (Sepkoski, 1981; Fraiser and Bottjer, 2007; Chen and Benton, 2012). The severity of the paleoecological changes associated with the EPME is difficult to quantify but can be appropriately appreciated in comparison with other Phanerozoic mass extinctions. According to Droser et al. (1997), the magnitude of paleoecological changes associated with major global mass extinctions may be classified into four levels: first, appearance/disappearance of an entire ecosystem; second, structural changes within an ecosystem; third, community-type level changes within an established ecological structure; fourth, community-level changes. In this context, the paleoecological changes associated with the EPME may be equated to the second level in Droser et al.'s model, namely the marine ecosystem was completely reconstructed after the EPME, rather than recovered from it (Dineen et al., 2014). Although as a scientific scenario this has been widely accepted, primarily based on analyses of pooled regional to global datasets (Hallam and Wignall, 1997; Fraiser and Bottjer, 2005, 2007), detailed quantitative studies demonstrating this profound paleoecological shift across the Permian–Triassic boundary have been limited, albeit with several notable recent exceptions (e.g., Chen et al., 2010, 2015; Dineen et al., 2014; Petsios and Bottjer, 2016). Among published, quantitative ecological studies concerning the Permian–Triassic transition, most are based on carbonate or mixed carbonate-siliciclastic sections. To date, similar quantitative studies based on Permian–Triassic shallow-water clastic-shelf settings are rare. To this end, the present study has been designed to reduce this knowledge gap by undertaking a section-based quantitative study of how the marine benthonic communities changed across the EPME in a nearshore clastic environment (Zhongzhai section, South China), using several taxonomic groups including brachiopods, bivalves, gastropods and ostracods. Our aim was to first compare the composition and structures of the benthonic paleocommunities before and after the EPME, and then discuss the factors and mechanisms considered possibly responsible for these changes with special reference to the transition from the pre-EPME brachiopod-dominated paleocommunity to the bivalve-dominated paleocommunity in the aftermath of the EPME.

2. Location and geological setting

The studied materials were collected from the upper Longtan Formation (Changhsingian) and lower Feixianguan Formation (Griesbachian) of the Zhongzhai PTB section (26.15°N and 105.29°E), which is located approximately 1 km northeast of Zhongzhai Town, Liuzhi County, southwestern Guizhou Province, South China (Fig. 1A). Both formations are mainly characterized by mudstone, silty mudstone, calcareous mudstone, siltstone and sandstone (Fig. 2, for detailed description of lithostratigraphy see Zhang et al., 2013), and both have yielded diverse and well-preserved fossils, including brachiopods (Peng, 2006; Peng and Shi, 2008; Zhang et al., 2013, 2014a, 2015), bivalves (Yao et al., 1980; Gao et al., 2009; Yang, 2015), conodonts (Metcalfe and Nicoll, 2007; Zhang et al., 2014b), microgastropods (He et al., 2008) and phytoplankton (Lei et al., 2012).

Paleogeographically, the Zhongzhai section was located in the western margin of the South China platform. During the Permian–Triassic transition, this area was situated in a shallow-water clastic-shelf environment (Feng et al., 1997; Shen et al., 2011; Zhang et al., 2014b) (Fig. 1B). At this section, the Permian–Triassic boundary has been placed at the bottom of Bed 30 based on multiple lines of evidence, including the conodont *Hindeodus parvus* Zone (Metcalfe and Nicoll, 2007; Zhang et al., 2014b), radiometric ages and organic carbon isotope (Shen et al., 2011), as well as bivalve- and ammonoid-based biostratigraphy (Gao et al., 2009; Zhang et al., 2014b).

3. Materials and methods

3.1. Taxonomic data, sampling control and temporal resolutions

The Zhongzhai section is generally very fossiliferous and has yielded a diverse range of fossils representing an array of lifestyles. Among these taxa, brachiopods are the most abundant and the most thoroughly studied group, with 22 genera and 62 species already described (Peng, 2006; Peng and Shi, 2008; Zhang et al., 2013, 2014a, 2015) (Fig. 2A). The next common and relatively well studied group are bivalves, comprised of 29 genera and 71 species (Gao et al., 2009; Yang, 2015) (Fig. 2B). Owing to their sheer abundance, robust biostratigraphy and taxonomy, these two taxonomic groups constitute the primary source of data for this paper. Other fossil groups, such as foraminifers, ostracods, microgastropods and ammonoids, are only sporadically present throughout the section (Fig. 3) and, where relevant and appropriate, they were also used as supplementary data and incorporated into the analysis and discussions. As for the palynomorphs, they are locally (within certain beds) extremely abundant and represented by *Punctatosporites* and *Laevigatosporites*. Additionally, acritachs have also been found in a few horizons throughout the section (e.g., uppermost Permian interval), and are dominated by *Micrhystridium breve* (59%) and *Baltisphaeridium* sp. (36%) (Lei, 2013). As will be noted later, palynomorphs are referred to in this paper as a proxy for terrestrial nutrient flux while acritachs are used to approximate the level of marine primary productivity. Combined together, the temporal fluctuation of these two indicators is deployed here to indicate the varying level of food supply through the Zhongzhai section, as has been used elsewhere (e.g., McCarthy et al., 2004; Pross et al., 2006).

Locally (i.e., within certain stratigraphic beds of this section), brachiopods or bivalves are so abundant that they form thin shell beds (see Fig. 11). In the vast majority of cases, these fossils have attained exceptional preservation quality as demonstrated by, for example, the presence of very fine micro-ornament and delicate spines on brachiopod shell surfaces (see Zhang et al., 2013), suggesting that they have been preserved mostly in situ with little post-mortem transportation. Thus, it is no surprise that these fossils have attracted the attention of many paleontologists in recent years, who not only have very carefully collected these fossils but also have systematically described them in a series of taxonomic studies (see references mentioned above). No doubt, the high quality of fossil preservation, together with detailed taxonomic studies already published, provides an excellent basis for the present study aimed at documenting the ecological shift of the paleocommunities of the Zhongzhai section.

As for the brachiopods, a total of 7627 specimens have been collected over the past 8 years from the upper part of the Longtan Formation (Beds 1 – 4, 6, 7, 10, 12, 14, 16, 27 and 28) and the lower part of the Feixianguan Formation (Beds 30, 32 – 46) and were included in this study (see supplementary material for detailed bed-by-bed distributions of brachiopod species and abundances). Due to their excellent preservation, most of the specimens (> 90%) are well-preserved individuals, presenting an ideal condition for taxonomy and paleoecological analysis (Zhang et al., 2013, 2014a, 2015).

For the purpose of this study, the number of brachiopod species and the number of specimens of each species were counted in each brachiopod-bearing horizon (bed) (Beds 1 – 4, 6, 7, 10, 12, 14, 16, 27, 28, 30, 32 – 46) precisely following the method described by He et al. (2015). The faunal compositions at genus-level were analyzed for Beds 4, 6, 12, 14 and 27, owning to their adequate sampling as demonstrated by rarefaction analysis (see Fig. 2 in Zhang et al., 2016). In comparison, Beds 1 – 3, 16, 28, 30, 32 – 46 have only yielded sparse brachiopods material and consequently were excluded from quantitative analysis, although they are included in the 'Results' and overall 'Discussion' sections.