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Global brachiopod palaeobiogeographical evolution from Changhsingian (Late Permian) to Rhaetian (Late Triassic)

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Previous studies suggest that the end-Permian mass extinction caused a dramatic drop of marine biodiversity near the Permian–Triassic boundary. However, it is unclear how profoundly this severe extinction might have changed the global provincialism, and how global provincialism responded to the protracted process of this extinction and subsequent recovery through the Triassic. In this paper, we carried out quantitative time-series analyses of global brachiopod palaeobiogeography over a timespan of nine consecutive stages/substages from the latest Permian Changhsingian to the latest Triassic Rhaetian based on a global brachiopod database of 483 genera and 2459 species from 1425 localities. Our results suggest that the extinction resulted in a global 'biogeographical eclipse' in the ensuing Early Triassic Griesbachian and Dienerian times in that neither biogeographic realm nor province could be recognized. It was characterized by an extreme low-diversity, mostly dwarfed and nearly globally distributed brachiopod fauna, coupled with persistently high sea surface temperature and a flattened global latitudinal thermal gradient. Global provincialization emerged again during the Olenekian at province level and reached its peak stage during the Carnian when three realms and six provinces were clearly recognized. Global provincialism became weakened again in the latest Triassic Rhaetian, marked by three general realms, but no province distinguished. Our analyses suggest that both palaeolatitude-related thermal gradient and the presence of Pangea (a profound geographic barrier) were most effective in explaining the spatial patterns. In addition, oceanic currents along the northwestern coast of Pangea also played an important (albeit regional) role in linking southern North and Central America brachiopod faunas with those of the Boreal Realm. This study also revealed that the brachiopod biodiversity center moved northwards over the studied interval, accompanied and hence accountable for by the northward drift of a large number of tectonic blocks in the Palaeotethys and Neotethys during the Triassic.

1. Introduction

Recognized as the mother of mass extinctions in earth history, the end-Permian mass extinction is said to have wiped out >90% marine species and permanently altered the trajectory of macroevolution of the marine evolutionary fauna (Sepkoski, 1984; Erwin, 1994). Brachiopods were among the most affected marine invertebrate groups by this event and consequently lost their long-held dominance role in the Palaeozoic marine ecosystems to mollusks in the ensuing Mesozoic and Cenozoic eras (Sepkoski, 1984; Payne et al., 2014). Many papers have been published on the regional and global diversity patterns of brachiopods across the Palaeozoic–Mesozoic transition and during the subsequent survival, recovery and radiation (Shen and Shi, 1996, 2002; Rong and Shen, 2002; Chen et al., 2005, 2006, 2015; Shen et al., 2006a, 2006b; Powers and Bottjer, 2009; Ruban, 2010, 2012). From these researches, it has been well documented that four major brachiopod orders (Productida, Spiriferida, Orthida, Orthotetida) became extinct near the Permian–Triassic boundary; while four other orders (Terebratulida, Rhynchonellida, Athyridida, Spiriferinida) as well as some Linguliformea survived the extinction (Shen and Shi, 1996; Chen et al., 2005; Shen et al., 2006a, 2006b). Following this mass extinction, not only brachiopod species diversity remained low (Rong and Shen, 2002; Shen et al., 2006a, 2006b), their average body size was also significantly reduced (Peng et al., 2007; He et al., 2014a).

The Permian Period is well known for its pronounced global marine provincialism in general, as well as for its dynamic changes through the Permian. Among the key factors that contributed to this high level of global provincialism, both geographic barriers and a strong latitude-related thermal gradient are known to have played a crucial role (Waterhouse and Bonham-Carter, 1975; Shi and Grunt, 2000). In general, three Permian marine biogeographical realms (Boreal, Palaeoequatorial/Tethyan and Gondwanan realms) are recognized and these three realms in turn have been subdivided into provinces

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(Waterhouse and Bonham-Carter, 1975; Shi et al., 1995; Shen and Shi, 2000, 2004; Shen et al., 2000a, 2009, 2013b; Shi and Grunt, 2000; Shi and Shen, 2000; Angiolini, 2001; Angiolini et al., 2013; Wang et al., 2014) leading to a general perception of a high γ diversity for the Permian global marine ecosystem.

By comparison with the Permian, data and knowledge on Triassic global marine biogeography are still very scanty, notwithstanding some excellent earlier papers published (Valentine and Moores, 1973; Stevens, 1980; Ager and Sun, 1988; Dagys, 1993; Ehiro, 1997). To the best of our knowledge, detailed Triassic stage-by-stage brachiopod biogeography is lacking. In particular, relatively less research has been undertaken to examine the secular variation of global brachiopod biogeography across the Permian–Triassic transition. To this end, for example, we do not know if (and how) the high level γ diversity observed for the Permian might have been impacted upon by the end-Permian extinction, and how the global brachiopod provincialism evolved in the Triassic. Though Shen et al. (2000a) carried out a study of Changhsingian global brachiopod biogeography, they did not comment on patterns and features of brachiopod provincialism beyond the Permian. Also, the primary data used in their study now requires updating as numerous significant new taxonomic data have been published since 2000 (e.g., the monographic work by Shen et al., 2000b, 2001, 2003; Shen and Shi, 2007; He et al., 2014b; Angiolini and Carabelli, 2010; Angiolini et al., 2015; Gaetani and Mantovani, 2015). As for the Triassic, the most significant recent analyses of brachiopod biogeography were works by Chen et al. (2005) and Chen et al. (2015), but they were most concerned on the aspects of Early and Middle Triassic brachiopod faunas especially aspects in relation to their survival strategies and recovery processes. Additionally, much of the discussion in these two papers was focused on regional datasets and qualitative comparisons. Different to any previous work, the present paper is designed to undertake a systematic, stage-by-stage quantitative analysis of the global brachiopod biogeography from the latest Permian Changhsingian to the latest Triassic Rhaetian, thus covering not only the end-Permian mass extinction interval, but also its ensuing episodes of survival, recovery and radiation. As such, this study should provide some useful insights into the dynamic processes between brachiopod mass extinction, survival and recovery, and their global provincialism.

2. Data and methods

All quantitative analyses in this paper were based on our latest global brachiopod database established using the software Filemaker Pro following the methodology described by Shen et al. (2009, 2013b). Within our database, more than 30 fields including the brachiopod names originally recorded and their updated taxonomic assignments, detailed biostratigraphic constraints, geographical information of locality, lithofacies, tectonic affinity etc., were digitized from published literatures for each collection [Supporting Online Materials 1 (SOM 1)]. Palaeolatitude and palaeolongitude were calculated using the software PointTrack Version 7.0 (designed and provided by Christopher R. Scotese).

In establishing the database (SOM 1), all the brachiopod species and higher taxonomic assignments were carefully screened and, when and if necessary, revised and updated in light of the latest developments in brachiopod taxonomy based on our knowledge and the revised Treatise (Williams et al., 2000, 2002, 2006, 2007). Age determinations of brachiopod faunas from literature have been updated based on the latest international timescale for the Permian (Shen et al., 2013a) and Triassic, as well as taking into account new biostratigraphical and geochronologic data (Ovtcharova et al., 2006; Balini et al., 2010; Lucas, 2010; Ogg, 2012; Lehrmann et al., 2015). The brachiopod faunas from 14 localities (<1% of total localities) were excluded from the present analysis because there is no stage-level age determination available in the literature. The biostratigraphical definitions for the nine consecutive stages/substages from uppermost Permian to Upper Triassic [Changhsingian, Griesbachian (early Induan), Dienerian (late Induan), Olenekian, Anisian, Ladinian, Carnian, Norian, Rhaetian] are primarily based on the widely used fossil groups of ammonoids and conodonts, which also formed the basis for the global correlation of the relevant lithostratigraphical units in different regions (Ovtcharova et al., 2006; Balini et al., 2010; Lucas, 2010; Ogg, 2012; Lehrmann et al., 2015), as shown in Table 1.

In total, 105 families, 483 genera and 2459 species of brachiopods from 9935 occurrences in 1425 localities from around the world have been included in this study (Fig. 1; SOM 1). Those localities were then assigned to different stations or operational geographical units (OGUs) to identify the different kinds of spatial units for palaeobiogeographical analysis mainly based on tectonic borders or major geographic regions following the principles suggested by Crovello (1981), Shi (1993) and a number of subsequent studies (e.g., Shi and Archbold, 1995; Shen et al., 2009, 2013b). Following this procedure, 181 stations were initially recognized; they were comprised of 23 stations in the Changhsingian, 11 in the Griesbachian, 4 in the Dienerian, 14 in the Olenekian, 25 in the Anisian, 18 in the Ladinian, 33 in the Carnian, 32 in the Norian and 21 in the Rhaetian (Fig. 1, Appendix A). We subdivided the Induan Stage into two substages because some Permian brachiopod genera persisted into the earliest Triassic Griesbachian, but mostly disappeared in the Dienerian. Stations with limited genera (<5 genera) were excluded from our quantitative analyses, but were considered in our discussions concerning the global palaeobiogeographical patterns. Following this ‘data cleaning’ procedure, 110 stations were maintained in our final database for quantitative analysis (SOM 1).

Initially, nine data matrices of genus occurrence were created from the 110 different stations using binary/abundance coefficients, and each matrix corresponds to one of the nine stages/substages. These matrices were then transformed to data matrices made of presence/absence (1/0) data of genera. The binary data was used following the recommendation by Shi (1993).

The next step was to calculate the compositional similarity between stations based on the binary/abundance dataset. We employed the Jaccard (Jaccard, 1901) and Ochiai coefficients (Ochiai, 1957) as the principal similarity coefficients for cluster analysis in this paper because these two coefficients have been recommended as the relatively more reliable coefficients and have been widely used (Shi, 1993; Shang and Jin, 1997). In addition, considering the diverse range of compositional similarity coefficients available in the literature (e.g., Raup and Crick, 1979; Hubalek, 1982; Shi, 1993; Shen and Shi, 2004; Shen et al., 2009, 2013b) and the potential impact of sampling bias on similarity coefficients, we also used other six coefficients including Dice (Dice, 1945), Simpson Index, Yule's Q and Yule's Y (Yule and Hendall, 1950), abundance coefficient Cosine (Ochiai, 1957) and the Probabilistic Index (SI) of Raup and Cricks (1979) to test the results produced by the binary coefficients [Figs. 2, 3 and Figs. S1–S8 of SOM 2]. Employing abundance coefficients (e.g., Cosine and SI) is also important because these coefficients identify not only the taxa shared, but also extract more community level information from species occurrence data. When we interpret the data finally, we will see whether the results derived from those coefficients are consistent or not. If the results generally agree with one another mostly, then we believe that the results are robust.

All the similarity matrices derived from the Jaccard and Ochiai similarity coefficients were then subjected to the hierarchical cluster analysis method (CA) in order to reveal and depict the ‘biogeographical distances’ among the stations in a hierarchical manner. This was done by using PAST v. 2.12 software (Hammer et al., 2001). It is normal that somewhat different topologies of dendrograms may be produced when using different similarity coefficients. PAST was also employed to perform the Non-metric Multidimensional Scaling (NMDS) and the Minimum Spanning Tree (MST) as mechanisms to test the robustness of the results derived from the cluster analysis. Result of MST was superimposed on the NMDS ordination plots. NMDS is a multivariate statistical method that reduces the multivariate space into two or