



Global paleobiogeography of brachiopods during the Mississippian—Response to the global tectonic reconfiguration, ocean circulation, and climate changes



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ABSTRACT

Changes in Mississippian global paleogeography derived from the reconfiguration of the continents, a reversal in ocean currents and global cooling. Although the tectonic and climatic changes are well-documented, their effects on the distribution of brachiopod fauna are poorly documented. Here we present systematic quantitative analyses on global paleobiogeography based on a global brachiopod database from the Mississippian (i.e., Tournaisian, Visean, and Serpukhovian). The dataset consists of 2123 species of 344 brachiopod genera from 1156 localities. Our results reveal that global provincialism was not evident during the Tournaisian and Visean Stages. Two realms, i.e., the Gondwanan and Paleoequatorial Realms, are recognized during the Tournaisian. The Paleoequatorial Realm dominates during the Visean Stage, whereas the Gondwanan Realm is not documented due to the absence of data points. In contrast to the early and middle Mississippian stages, faunal provincialism is greatly enhanced in the Serpukhovian Stage with Paleotethyan and North American realms easily distinguished. This indicates that the Rheic Ocean was closed before the Serpukhovian due to the collision between Gondwana and Laurussia, that disrupted faunal interchange between the Paleotethys and North America. In addition, the paleolatitude-related thermal gradient was enhanced and the Boreal Realm was distinguished from the Paleotethyan Realm during the onset of the Late Palaeozoic Ice Age (LPIA) in the Serpukhovian. The paleolatitude diversity gradient pattern further shows a distinct shift of diversity center from the southern tropic zone in the Tournaisian and Visean to the northern tropic zone in the Serpukhovian.

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1. Introduction

The Mississippian was one of the most critical transitions during the earth history. First of all, two major continents, Gondwana in the south and Laurussia in the north, approached each other. This resulted in the closure of the Rheic Ocean, which had been an extremely important seaway for biotic interchange between Gondwana and Laurussia during the Late Palaeozoic (Mckerrow et al., 2000; Scotese, 2001; Franke, 2006; Nance, 2010; Meert, 2012). It is natural to suppose that this kind of major geographic changes will dramatically alter the global oceanic currents and faunal distributions. However, previous studies on this topic were mostly from a tectonic perspective (e.g., Bozkurt et al., 2008; Sintubin et al., 2008; Nance, 2010; Nance et al., 2010; Romer and Hahne, 2010; Jastrzębski et al., 2013; Klootwijk, 2013), and relatively little has been done from a perspective of faunal distribution. Second, the Mississippian also witnessed notable climate changes between greenhouse and icehouse climates (Veevers, 2004; Shi and Waterhouse, 2010), that led to substantial global sea-level changes (Stanley and Powell, 2003; Bambach et al., 2004; Powell, 2007;

Isaacson et al., 2008). Third, the Mississippian is sandwiched between the Hangenberg event at the Devonian–Carboniferous boundary and the Mid–Carboniferous event (Caplan and Bustin, 1999; Kaiser et al., 2006; Shen et al., 2006; Wang et al., 2006; McGhee et al., 2012).

Throughout geological history marine faunas have responded to external forcing such as changes in climate and tectonism though evolutionary change. Examples include bryozoans (Ross and Ross, 1985, 1990), foraminifers (Kalvoda, 2002), and corals (Wang et al., 2003; Aretz, 2010, 2011). It has also been noted that the gradually increasing provinciality during the Mississippian was closely related to the global tectonic reconfiguration (Ross and Ross, 1985, 1990; Korn, 1997). A recent study on the Mississippian pelagic ammonoid associations using quantitative methods has demonstrated that provinciality became pronounced in the latest Visean and Serpukhovian due to a major reconfiguration of shelf area (Korn et al., 2012).

However, so far no study has been systematically done based on brachiopods. Brachiopods are one of the dominant benthic fossil groups during the Carboniferous and Permian with a very short swimming larvae stage, inhabiting on oceanic shelf from the tidal zone down to ocean floor. Brachiopods are strongly affected by their environment, including sediment composition, water depth, temperature and water salinity (Zezina, 1997, 2008). Brachiopods are mostly sensitive to the

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latitude-related thermal gradient, but relatively less sensitive to longitude change unless natural barriers like oceans and mountains separate them. Therefore, brachiopods have important implications for paleogeographical reconstruction. Quantitative methods on paleobiogeography based on the Permian brachiopods (Shi, 1993; Shi and Archbold, 1995, 1996; Shen and Shi, 2000, 2004; Shen et al., 2009, 2013; Angiolini, 2013) demonstrated that this fossil group is one of the most useful in order to reconstruct global paleogeography and faunal distributions.

Our present work aims to carry out a quantitative study of the Mississippian brachiopods. We first focus on the spatial and temporal paleobiogeographical patterns within the three consecutive Mississippian stages (i.e., Tournaisian, Visean, and Serpukhovian), based on a recently-established global brachiopod database. We further analyze and discuss the major factors controlling the distribution of brachiopods including climate and paleogeography.

2. Data and methods

Global brachiopod occurrences in three consecutive stages of the Mississippian (i.e., Tournaisian, Visean and Serpukhovian) all over the world (Table 1) are compiled using the software Filemaker Pro. The dataset consists of 4778 occurrences involving 2123 species of 344 brachiopod genera from 1156 localities (Fig. 1). The items entered into the brachiopod database include the systematic, biostratigraphic, modern coordinates, and paleo-latitude data that were calculated using Track Point 7.0 designed by Christopher Scotese, as well as the lithological, and tectonic data from published literatures for each collection.

All the brachiopod species and higher taxonomic assignments were revised and updated in light of recent developments in brachiopod taxonomy. We take recorded taxa that have been systematically attributed to certain genera and species. Records with uncertain taxonomic assignments are excluded, such as *overtoniini* gen. et sp. indet., *orthotetid?* indet., *productacean* indet., *Spiriferidina* gen. et sp. indet., *dielasmaticid*, *choristitid*, and *choristitid*. Some species with questionable occurrences are revised, such as *Spiriferella* sp. recorded in the Visean in Sichuan, South China. Species with qualified names such as aff., cf. etc. are treated as the species without the qualifiers. Age determinations of different brachiopod faunas from literature have been updated as well based on the global stratigraphic and chronostratigraphic timescale (Davydov et al., 2012), whereas the records without stage-level age determination are excluded. We note that the durations of the three age stages of the Mississippian are quite different (i.e. the Visean is twice as long as either the Tournaisian or the Serpukhovian). While somewhat of an issue, we note that further sub-division is difficult because many of the fauna do not have biostratigraphic control below the stage level.

All localities with brachiopods are assigned to different paleogeographical analysis units or operational geographic units (OGUs) following the principles suggested by Crovello (1981). Decisions related to the choice of OGUs include size and shape of OGUs, each of the OGUs has to be uniform to be delimited, and it is critical that the area of an OGU must be geographically and tectonically contiguous. However, it is inevitable that sampling intensity or data quality may affect the analysis results. To reduce the unevenness in different regions, we divided intensively studied regions (e.g., South China, North China, Western Europe etc.) into smaller units. In addition, stations with limited genera (less than 5; e.g., some stations in South America) are not included. Thus, a total of 58 OGUs (see Table 1) are used in our analyses.

Initial genus occurrence and binary (presence/absence, “1/0”) data matrices for the three stages from 58 different paleogeographical analysis units are derived from the Mississippian brachiopod database using fossil occurrences (see Supplementary data). Four similarity coefficients, i.e., Jaccard, Dice, SI and Yule's Y, are used in this paper. The Jaccard (Jaccard, 1901) and Dice (Dice, 1945) coefficients have

been preferentially recommended and extensively used in many biogeographical studies. They are preferable when the shared taxa between two regions are demonstrated (Shi, 1993; Shen and Shi, 2000). Because of the Yule's Y coefficient's emphasis on the taxon that is included in the total sample but absent in the observed small regional samples (Yule and Hendall, 1950), it is adopted in this paper with the purpose of measuring the similarity or dissimilarity when the data contain a relatively high proportion of endemic taxa, as suggested by Huang et al. (2012). To test the possible shortcomings derived from the binary coefficients, the probabilistic index (SI) developed by Raup and Crick (1979) was also used. The SI index uses a randomization (“Monte Carlo”) procedure to compare taxon in common in the observed paleogeographic regions. It considers statistical significance in determining similarities; therefore, the biogeographical data are weighted on the basis of frequency of occurrence by this method so that widespread genera do not have a disproportionate effect on measurement of similarity (Schmachtenberg, 2008; Shen et al., 2013). When we interpret the data we will see whether the results derived from those different approaches and coefficients are consistent or not. If the results generally agree with one another based on different coefficients, then we think that the results are robust.

Hierarchical Cluster Analysis (CA) is employed to calculate brachiopod fauna's distance based on Jaccard, Dice, SI, and Yule's Y similarity coefficients using PAST v. 2.12 software (Hammer et al., 2001). The Non-metric Multidimensional Scaling (NMDS) which superimposed the Minimum spanning tree (MST) was performed by PAST with the purposes of cross-verifying the results derived from the cluster analysis. NMDS is a multivariate statistical method that reduces the taxonomical space into two or three dimensions based on fauna similarities and therefore builds the linkage between the distance in plots of faunal stations (equal to OGUs in this paper) and fauna distance (Shi, 1993). Similar plots based on Jaccard, Dice, SI, and Yule's Y similarity coefficients are showed respectively, and only results based on the Jaccard coefficient are given in Fig. 6 for controlling the article in suitable length. MST usually is attached to NMDS and provides perspicuous mind about the fauna distance by finding the smallest distance between plots (Pettie and Ramachandran, 2002). Sheppard diagram and “stress value” are simultaneously calculated to quantitatively weigh the level of “goodness of fit” between the original input data matrix and the ultrametric matrix of the resultant NMDS scatter plots (Kruskal and Wish, 1978; Babcock, 1994; Shen and Shi, 2000, 2004).

3. Results and interpretations

3.1. Tournaisian

The Tournaisian brachiopod faunas recorded from 34 stations worldwide are generally grouped into two distinct supergroups (Supergroups A and B) based on all coefficients (Fig. 2). Supergroup A consists of two stations only (the San Juan Basin and Sierra de Almeida, Argentina), both of which were situated in the southwestern margin of Gondwana. All other stations are grouped into Supergroup B. Further division at group level is poorly delineated. However, three groups (Groups B₁, B₂, and B₃) can be roughly separated based on their binary coefficients. Group B₁ is defined by two North American stations, i.e., Appalachian Basin and San Andres Mts., New Mexico. The Missouri River Basin is occasionally clustered with Group B₁ based on the SI index. Group B₂ is a geographically dispersed large complex group, embracing the OGUs in North America, Europe, China, Cimmeria, Australia, and Siberia. Clusters within Group B₂ are very weak although a few vague clusters of several geographically close stations are grouped, such as stations from South China or eastern Australia. Group B₃ is represented by Algeria Sahara and the Murzuq Basin, both of which were situated in northern Africa. This group, however, occasionally merged with Group B₂ based on the SI and Yule's Y coefficients.

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