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Guadalupian (Middle Permian) paleobiogeography of the Neotethys Ocean

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ABSTRACT

A matrix of presence/absence data of Guadalupian (Middle Permian) brachiopod genera from Sicily, Tunisia, Oman, Turkey, north Iran, central Afghanistan, Karakoram, Salt Range, and south Thailand has been analyzed by multivariate methods (cluster analysis, principal coordinate analysis, minimum spanning trees) and Parsimony Analysis of Endemicity. The application of these different and independent paleobiogeographical methods has led to the individuation of three bioprovinces: the Cathaysian (Sicily and Tunisia), Cimmerian (Oman, Turkey, north Iran, Salt Range, south Thailand) and Transhimalayan (Karakoram and central Afghanistan) provinces. These provinces have been placed on a paleogeographical reconstruction based on paleomagnetic data, which we used to decipher the principal factors that governed brachiopod distribution in the Neotethys Ocean during the Guadalupian. As a conclusion, the pattern of biotic provinces at this time resulted from the complex interplay between latitudinal thermal gradient, oceanic paleocurrents, and the continental drift of the Cimmerian terranes across zonal climate belts.

1. Introduction

The Guadalupian (Middle Permian, 272–260 Ma; IUGS 2012) was a period of climate change and tectonic plate reconfiguration. Climate changed from glacial conditions at the dawn of the Permian to global warming in the Guadalupian. Data from stable isotope composition of soil-formed minerals, plants and brachiopods (Montañez et al., 2007) indicate that $p\mathrm{CO}_2$ had increased up to 8PAL (PAL = pre-anthropogenic $p\mathrm{CO}_2$ level: 280 ppm) by the end of the Sakmarian (Early Permian), and global average temperature rose by 9.6 °C, with greater increase over continental areas than over the oceans (Peyser and Poulsen, 2008); at the same time, continental precipitation also decreased by 40%. Deglaciation and increased $p\mathrm{CO}_2$ levels may have caused tropical latitude drought, intensification of monsoonal circulation, and an increase in surface temperatures over Pangea (e.g. Parrish, 1993; Tabor and Montañez, 2004; Peyser and Poulsen, 2008), producing a sharp climate shift from the Early to the Middle Permian.

In these changing climate conditions, major plate tectonic reconfigurations took place, namely the northward drift of the Cimmerian terranes across the Tethys Ocean – first described by Sengör (1979) – that some authors think was coeval to, and tectonically linked with, the transformation of Pangea from an Irvingian B to a Wegenerian A-type configuration (Muttoni et al., 2009a and references therein; see also below). The Cimmerian terranes migrated from southern Gondwanan paleolatitudes in the Early Permian to subequatorial paleolatitudes by the Middle–Late Permian as the result of the opening of the Neotethys Ocean. According to the available – albeit scanty – paleomagnetic data, this opening was asymmetrical, with higher seafloor spreading rates for the central Cimmerian terranes (central Afghanistan, Karakoram) than for the western blocks (Iran) (Muttoni et al., 2009a,b).

During this seemingly rapid Early to Middle Permian tectono-climatic transition, bioprovincial patterns are expected to evolve equally rapidly, making fossil brachiopods as useful proxies to test for paleogeography.

However, since Wegener's times, more emphasis has been given to fossils as tools to constrain plate tectonics than to marine paleocurrent patterns and climate models. By placing Early Permian biota from Gondwana and Laurasia on a Pangea paleogeography constrained by selected paleomagnetic data, we have recently shown the importance of ice cap distribution and marine paleocurrents in shaping bioprovincial patterns across the Tethys around the Carboniferous–Permian boundary (Angiolini et al., 2007).

Here we show, using the same approach of Angiolini et al. (2007), how the distribution of brachiopod provinces responded to the changing climate and paleogeography boundary conditions across the southern and northern margins of the opening Neotethys Ocean during the Middle Permian, and attempt to infer the principal factors (e.g., zonal paleocurrents and thermal gradients, continental drift and proximity, etc.) that governed this response. In doing so, we will place Neotethyan paleobiogeographical patterns obtained by two different methods – statistical multivariate analysis and Parsimony Analysis of Endemicity – on a paleogeographical reconstruction based on selected paleomagnetic data from the literature. Our approach differs from that followed in previous Middle Permian global paleobiogeographical

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reconstruction insofar as (i) it is based on congruent taxonomic data that we retrieved from faunas of certain provenance and age either collected by us in the field or pertaining to accurately coded museum collections, (ii) it comprises new taxonomic data that we acquired from key and focused regions of the Neotethys (i.e. Tunisia, Sosio, Turkey, Iran), (iii) it is based on two independent methodologies, one of which – the Parsimony Analysis of Endemicity – has been very rarely applied to Permian brachiopod faunas, and, finally, (iv) it places the obtained faunal stations on a paleogeographical map based on a robust (and traceable) set of paleomagnetic data.

2. Material and methods

The faunal lists of brachiopods from nine key regions of the Neotethys realm – Sicily, Tunisia, Turkey, Oman, north Iran, central Afghanistan, Karakoram, Salt Range, and south Thailand – considered as Operative Geographical Unities (OGUs; Crovello, 1981), were compiled from personal collections, museum collections and the published literature (Table 1, Fig. 1). These faunas were systematically revised by two of us (LA and GC) in order to obtain a consistent taxonomy, thus minimizing bias due to systematic subjectivity, following the guidelines and criteria of Cecca (2002). All these faunas are Roadian–Wordian (early–middle Middle Permian) in age based on the associated conodont and fusulinid faunas (see references in Table 1). The selected OGUs have been placed on a Middle Permian paleogeographical map (Fig. 2) based on paleomagnetic data from the literature (Table 2; see discussion below) and paleolatitudes have been calculated (Table 3).

To test the quality of the sampling and avoid misinterpretation resulting from incomplete documentation, we have calculated the Permian Ratio and the Sampling Efficiency Index (Stehli, 1970; Stehli and Grant, 1971; Shi and Archbold, 1996), for all the OGUs (Table 3). These indices are based on the number of families found, the number of cosmopolitan families found, and the number of cosmopolitan families expected for the time interval considered (a total of 16 cosmopolitan families are expected in the Roadian–Wordian according to Shen et al., 2009); they provide a measure of both biodiversity (Permian Ratio) and sampling completeness (Sampling Efficiency Index). In this study, the Sampling Efficiency Index is above 40% for all OGUs, indicating that sampling is sufficiently complete (Stehli and Grant, 1971) and unlikely to affect the grouping resulting from multivariate analysis.

A data matrix consisting of the presence/absence (1/0) data of 140 genera from the nine OGUs has been compiled using personal data and revised published systematic descriptions (Supplementary file). This presence/absence matrix was culled prior to numerical analysis in order to remove biogeographically uninformative taxa, i.e., genera occurring in only one OGU or in all OGUs. Consequently, the original data matrix was reduced to a matrix of 78 genera. The binary data matrix was then analyzed by Q-mode analysis using multivariate statistical techniques – Cluster Analysis (CA), Principal Coordinates Analysis (PCO) and Minimum Spanning Tree (MST) – with the PAST Program (Hammer et al., 2001). CA dendrograms produce groups of OGUs that may be equated to biotic provinces (e.g. Shi, 1995); PCO shows the variation of faunal stations along certain major axes that are supposed to represent environmental factors.

Table 1
Repository and references for the brachiopod faunas used in this paper for the paleobiogeographical analysis.

Sicily (Sosio Valley)	Gemmellaro (1899)
Tunisia (Djebel Tebaga de Medenine)	Termier et al. (1977), Verna et al. (2010)
Turkey (Antalya)	Verna et al. (2011)
Oman (Haushi-Huqf)	Angiolini and Bucher (1999), Angiolini (2001a), Angiolini et al. (2003, 2004)
N Iran (Alborz Mountains)	Fantini Sestini (1965), Gaetani et al. (2009), Crippa and Angiolini (2012)
C Afghanistan	Termier et al. (1974)
Karakorum (Hunza-Chapursan)	Angiolini (1995, 1996, 2001a,b)
Salt Range	Waagen (1882–1885)
S Thailand	Waterhouse and Piyasin (1970), Yanagida (1971), Grant (1976), Archbold (1999)

The data were also processed in R-mode to find associations of brachiopod genera, which could characterize groups of faunal stations and thus paleobiogeographical provinces. The CA of the reduced data matrix was carried out by flexible UPGMA (unweighted pair-group arithmetic averaging) based both on the Simpson Index (Simpson, 1960) and on the Jaccard Coefficient (Jaccard, 1901), which have been widely used for statistical paleogeographical analysis (for a detailed review of the similarity indices see Shi, 1993). PCO analysis was performed using the Jaccard Coefficient (Shi, 1993, 1995).

Parsimony analysis (PA) was performed on the presence/absence matrix by using Parsimony Analysis of Endemicity (PAE) techniques, in order to obtain area cladograms of OGUs that can be interpreted in terms of relative recency of biotic contact between sample areas (Rosen and Smith, 1988). For PAE and cladogram analysis, PAUP 4 (Swofford, 2001) and Mesquite (Maddison and Maddison, 2011) softwares were used. In analogy with PA, a hypothetical ancestral (outgroup) OGU was added to the matrix, where all of the genera are missing, for rooting the cladograms. PA generates cladograms, nesting hierarchically OGUs according to the taxa that are shared between them. A Consistency Index (CI, ranging from 0 to 1) provides a measure of confidence in tree topology. Hierarchical subgrouping of OGUs reflects progressively narrowing synendemic taxa (Rosen, 1992); OGUs of terminal clades share taxa that are not found in any other area of the data set. Exhaustive (maximum parsimony) search outgroup-rooted PAE was performed with PAUP's ACCTRAN option, either using unordered characters or Dollo (Dollo.up) type characters.

3. Middle Permian paleogeography

The selected faunal stations and the inferred bioprovinces have been placed on a Middle Permian paleogeographical reconstruction of Pangea (Fig. 2) obtained following criteria and methods outlined in Muttoni et al. (2009a). We first compiled Early Permian and Late Permian–Early Triassic paleomagnetic poles (hereafter paleopoles) from Adria (the circum-Adriatic promontory of Africa) and Africa (Morocco, Sudan) as representatives of Gondwana, as well as from Europe as representative of Laurasia (Table 2). Adria is considered tectonically coherent with Northwest Africa (within paleomagnetic error resolution of typically a few degrees) since the Permian, and provided several good-quality Permian–Triassic paleopoles that can be used to approximate the apparent polar wander path (APWP) of Africa, as discussed in Muttoni et al. (2003, 2004, 2009a, and references therein). Early Permian and Late Permian–Early Triassic overall mean paleopoles for Adria-Northwest Africa (Gondwana) and Europe (Laurasia) were calculated using standard Fisher statistics, and used to interpolate the location of Middle Permian (~270 Ma) paleopoles for the same continents [Table 2, paleopoles (c) and (f)]. Internal Gondwana continents (South America, Northeast Africa, South Africa, Greater India, Antarctica, and Australia) were then rotated into Middle Permian Adria–Northwest Africa coordinates using Euler poles of Lottes and Rowley (1990), whereas North America attached to Greenland was rotated into Europe-Siberia using Euler poles of Bullard et al. (1965). Finally, key Cimmerian terranes (Iran, Karakoram, central Afghanistan, Qiangtang) were placed in this reconstruction using paleomagnetic data summarized in Muttoni et al. (2009a,b and references therein), whereas additional Asia-China terranes (Junggar, Qaidam, Tarim, Mongolia, North China, South China, and Indochina) were placed following criteria and references outlined in Muttoni et al. (2009a).