



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.

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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 $p\text{CO}_2$ had increased up to 8PAL (PAL = pre-anthropogenic $p\text{CO}_2$ 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 $p\text{CO}_2$ 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.

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).

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)

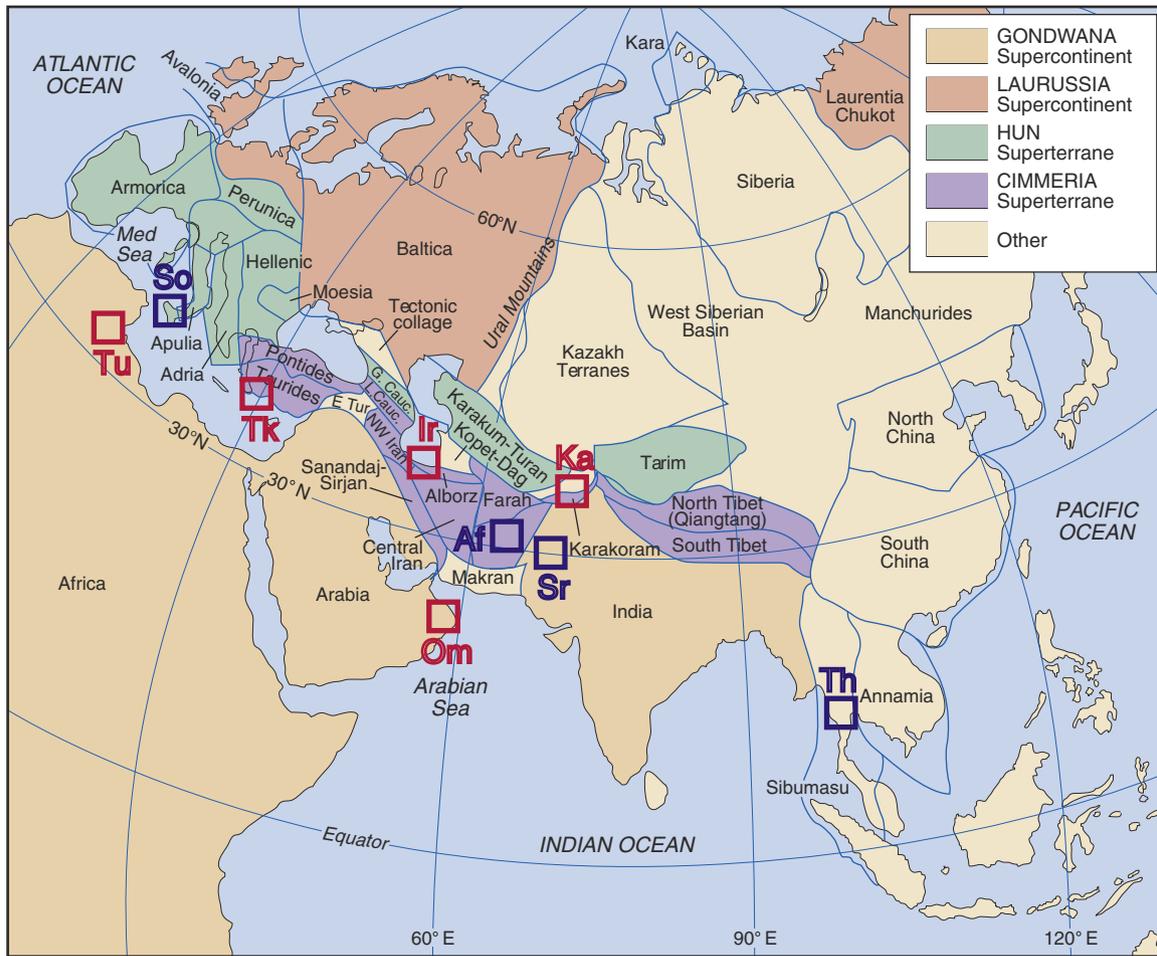


Fig. 1. Location of the selected faunal stations on a map showing the present-day distribution of main Cimmerian terranes (in purple) amid Gondwanan and Eurasian plates (adapted from Torsvik and Cocks, 2004; Ruban et al., 2007; Muttoni et al., 2009a). Those Cimmerian terranes discussed in this study are Iran (consisting of NW Iran, Alborz, central Iran, and Sanandaj-Sirjan), Afghanistan (Helmand and Farah), Karakoram in northern Pakistan, and Qiangtang in North Tibet. Note that Karakoram in northern Pakistan is Cimmerian and distinct from the Hunic Karakum-Turan Terrane. Tu = Tunisia; So = Sosio, Sicily.

The obtained reconstruction (Fig. 2) is virtually identical to the Middle Permian reconstruction of Muttoni et al. (2009a); the main difference is the Late Permian–Early Triassic overall mean paleopole of Adria (Gondwana) that is 3.4° away (great circle distance) from the coeval mean paleopole of Muttoni et al. (2009a) as a consequence of a different selection of entry paleopoles from the Dolomites (Table 2). This minor difference introduced an even smaller difference of 1.8° in the interpolated Middle Permian Gondwana paleopole of this study relative to the paleopole of Muttoni et al. (2009a). As a final word of caution, we stress that the Middle Permian paleopoles used in our reconstruction could potentially be affected by inclination shallowing, which can lead to an underestimation of paleolatitudes, essentially because the Late Permian–Early Triassic paleopoles used for interpolation are from sediments (Table 2) that can be associated with shallow bias magnetic directions (Tauxe and Kent, 1984). While we could not undertake a systematic investigation of inclination shallowing in our database, we notice that adopting an average flattening factor $f=0.8$, which we obtained by applying the statistical method of Tauxe and Kent (2004) to paleomagnetic directions from the Early Triassic Werfen Formation at Bulla, Dolomites (Scholger et al., 2000), would result in interpolated Middle Permian paleopoles differing from the coeval paleopoles of Muttoni et al. (2009a) by 1.4° (Gondwana) and 2.8° (Laurasia). This notion, in conjunction with the observation that all paleopoles of our compilation are from the same (northern) hemisphere, implies that the entire Pangea

supercontinent could have been located about $\sim 1.5\text{--}3^\circ$ to the north relative to our best-guess reconstruction of Fig. 2 (and of Muttoni et al., 2009a).

Our Middle Permian reconstruction captures Pangea undergoing transformation from a B-type configuration (Irving, 1977) to a classic Wegenerian A geometry by way of an intra-Pangea dextral shear system between Gondwana and Laurasia as described in Muttoni et al. (2009a,b and references therein) and more recently in Aubele et al. (2012) (we refer to Irving (2005), and to Domeier et al. (2012) versus Aubele et al. (2012) for an updated discussion with references on the debated issue of Pangea during the Permian). Within this transforming Pangea, the Cimmerian terranes migrated at different rates from southern hemisphere Gondwanan paleolatitudes in the Early Permian to northern hemisphere Laurasian paleolatitudes over the course of the Permian–Triassic (Fig. 2). In particular, terranes in the middle part of Cimmeria (Karakoram, central Afghanistan, and Qiangtang) appear to have moved initially fast, attaining sub-equatorial paleolatitudes by the Middle Permian, while Iran (and possibly also Sibumasu) does not seem to have moved much in the Middle Permian relative to its large displacement in the Late Permian–Early Triassic (see Muttoni et al., 2009a for details). This is in contrast to classic reconstructions from the literature where Cimmeria is depicted as a string of terranes opening at drift rates more or less linearly graded along the line of the moving string (e.g., Sengör, 1979; Stampfli and Borel, 2002).

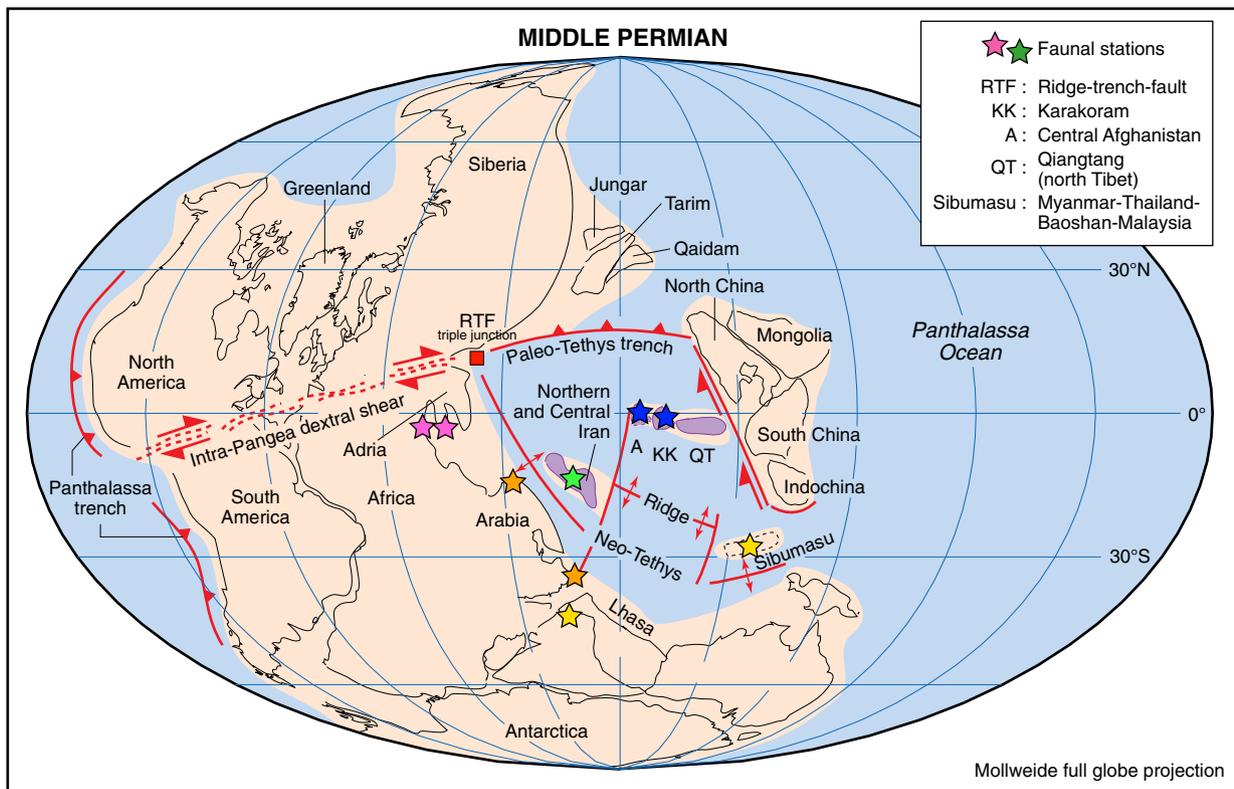


Fig. 2. The selected faunal stations from Sicily, Tunisia, Turkey, Oman, north Iran, central Afghanistan, Karakoram, Salt Range, and south Thailand (stars; colors as in Figs. 3 and 4), used to define three distinct bioprovinces (Cathaysian, Cimmerian, and Transhimalayan), have been placed on a paleomagnetic-based paleogeographical reconstruction of Pangea (based on paleomagnetic data in Table 2) and the main Cimmerian terranes during the Middle Permian. Key Cimmerian terranes of uncertain position due to substantial lack of paleomagnetic data are represented by dashed lines (i.e., A—central Afghanistan; Sibumasu); central Afghanistan is assumed to have moved in conjunction with Karakoram as suggested by stratigraphic and biotic data (e.g., Gaetani, 1997). The square to the northeast of Adria indicates the hypothetical location of a ridge–trench–fault (RTF) triple junction adjoining the Gondwana, Laurasia, and Paleo-Tethys plates. The Paleo-Tethys and Panthalassa trenches are indicated by solid triangles, the Neo-Tethys ridge by small diverging arrows, while half arrows indicate transcurrent plate motion. A = central Afghanistan, KK = Karakoram, QT = Qiangtang (north Tibet), Sibumasu = Myanmar–Thailand–Baoshan–Malaysia. See text and also Muttoni et al. (2009a,b) for further details.

4. Results

4.1. Multivariate analysis

The CA of the binary matrix produced two different dendrograms, one based on the Jaccard Coefficient and the other on the Simpson Coefficient (Fig. 3). In both cases the cophenetic correlation is high, indicating that both dendrograms maintain faithfully the original distances, and that the one based on Jaccard is the clustering solution which more accurately reflects the data. The grouping pattern is comparable in the two dendrograms and comprises three major groups defined by a division line corresponding to a Jaccard Coefficient of 0.3 and a Simpson Coefficient of 0.5, and labeled A, B and C in Fig. 3.

- (I) Group A consists of four faunal stations located along the Gondwanan margin (Oman, Turkey, Salt Range) or close to it (north Iran), as well as south Thailand as part of Sibumasu, whose paleolatitude is however poorly constrained (see above).
- (II) Group B comprises Afghanistan and Karakoram, which are Cimmerian terranes located at equatorial paleolatitudes in the Middle Permian.
- (III) Group C comprises Sicily (Sosio Valley) and Tunisia located at a similar paleolatitudes in the western Tethys close to Pangea.

The main discrepancy in the two dendrograms concerns the position of north Iran in Group A, whereby it forms a single outgroup of the Turkey–Oman and Salt Range–south Thailand clusters in the Jaccard Coefficient based-dendrogram, whereas it is linked to Turkey and Oman according to the Simpson Coefficient. These two different patterns will be explained in the Discussion section below.

The three groups identified by CA are also recognizable in the scatter plot of PCO with MST (Fig. 4) obtained using the Jaccard Coefficient. All the OGUs located at subequatorial paleolatitudes fall in the lower part of the scatter plot, whereas those at paleolatitudes higher than 12° south fall in the upper part, suggesting that coordinate 2 may broadly represent paleolatitude. The spatial distribution along coordinate 1 suggests instead a trend related to continental proximity, with Sicily and Tunisia located in the western Tethyan Gulf very close to Pangea, Karakoram and central Afghanistan in the middle of the Tethys far from continental masses, and, finally, group A stations (Oman, Turkey, Salt Range, north Iran) in intermediate positions along – or close to – the Gondwanan margin.

Interestingly, MST shows that Iran is more linked to Oman and Turkey than to the Salt Range and south Thailand, as revealed also by the CA dendrogram obtained using the Simpson Coefficient.

The CA based on correlation coefficient using R-mode analysis allowed to define the generic associations characteristic of each main group identified by the Q-mode analysis. Group A is characterized by the association of the genera *Nongtaia*, *Haydenella*, *Bilotina*, *Celebetes*, *Kotlaia*, and *Perigeyerella*; Group B by *Sommeriella*, *Callytharella*, *Gruntoconcha*, *Karawankina*, *Compressoproductus*, and *Peltichia*; Group C by *Sicularia*, *Sicelia*, *Scacchinella*, and *Gemmellaroia* (Fig. 5).

4.2. PAE

Exhaustive maximum parsimony search of PAE area cladograms using unordered characters produced a single most parsimonious tree (length = 154, Consistency Index (CI) = 0.513, Retention Index (RI) = 0.50); exhaustive Dollo (Dollo.up) search also produced a

Table 2

Paleomagnetic reference poles from West Gondwana and Laurasia.

Age	Long.	Lat.	A95 dp/dm	References
<i>Adria and Africa (Gondwana) in NW African coordinates</i>				
Early Permian (~284–276 Ma)				
Southern Alps volcanics, N Italy	236	50	5/9	Muttoni et al. (2003)
Lugano (Ganna) Porphyries, Ticino	243	43	10	Heiniger (1979)
Auccia volcanics, Lombardy	245	38	8	Heiniger (1979)
Arona volcanics, Lombardy	248	35	14	Heiniger (1979)
Bolzano Porphyries, Alto Adige	236@	45.5	4	Zijderveld et al. (1970)
Bolzano Porphyries, Alto Adige	228	47	2/5	Becke and Mauritsch (1984)
L. Collio & Auccia volcanics, Lombardy	252.5	38.5	20	Zijderveld and De Jong (1969)
Taztot Trachyandesites, Morocco	237	39	5	Daly and Pozzi (1976)
Chougrane & Mechra volcs., Morocco	238	36	20	Westphal et al. (1979)
Jebel Nehoud ring complex, Sudan	248^	46.5^	6	Bachtadse et al. (2002)
(a) Early Permian mean pole	241.6	42.0	4.4	(N = 10, K = 120.5) this study +
Late Permian–Early Triassic (~260–245 Ma)				
Werfen Formation, Dolomites	232.5	42	3/7	Channell and Doglioni (1994)
Werfen Formation, Bulla, Dolomites	228	46	2/4	Scholger et al. (2000)
Werfen Formation, Siusi, Dolomites	229	47.5	2/3	Scholger et al. (2000)
Verrucano Lomb. Metass. and red beds	241	46	4/7	Kipfler and Heller (1988), 12 sites combined
Val Gardena Ss., Dolomites	237	42	9/18	Manzoni (1970)
(b) L. Permian–E. Triassic mean pole	233.6	44.8	4.4	(N = 5, K = 309) this study §
(c) Middle Permian (~270 Ma)	~237.5	~43.5	–	interpolated between (a) and (b); see also \$
<i>Europe (Laurasia) in European coordinates</i>				
Early Permian				
Exeter Lavas, U.K.	163	48	10	Cornwell (1967)
Exeter Lavas, U.K.	149	50	4	Zijderveld (1967)
Thuringer Volc., Germany	170	37	7	Mauritsch and Rother (1983)
Oslo Graben Lavas, Norway	157	47	1	Van Everdingen (1960)
Arendal Diabase, Norway	160	43	7	Halvorsen (1972)
Saar-Nahe Volcanics, Germany	167	41	16	Berthold et al. (1975)
Nahe Volcanics, Germany	167	46	13	Nijenhuis (1961)
Black Forest Volc., Germany	174	48	6	Konrad and Nairn (1972)
Ny-Hellesund diabbases, Norway	161	39	3	Halvorsen (1970)
Mt. Billingen Sill, Sweden	174	31	2	Mulder (1971)
Mt. Hunneberg Sill, Sweden	166	38	5	Mulder (1971)
Skaane Dolerite Dikes, Sweden	174	37	7	Mulder (1971)
Black Forest Volc., Germany	173	42	0.5/1	Edel and Schneider (1995)
Bohemia Quartz Porphyry., Germany	161	36.5	3/7	Thomas et al. (1997)
Bohemia Quartz Porphyry., Germany	166	42	6	Soffel and Harzer (1991)
North Sudetic Volc., Poland	174	42	4/8	Nawrocki (1997)
Intrasudetic Volc., Poland	172	43	1.5/3	Nawrocki (1997)
Ringerike Lavas, Norway	157	45	9/15	Douglass (1988)
(d) Early Permian mean pole	166.2	42.2	3.1	(N = 18, K = 126; Muttoni et al., 2003, 2009a,b)
Late Permian–Early Triassic (~260–245 Ma)				
North Sudetic Sed. Zechstein	168	51	5.5	Nawrocki (1997)
Intraudetic Sed. Zechstein	160	51	3	Nawrocki (1997)
Lower Buntsandstein	166	51	3	Szurlies et al. (2003)
Buntsandstein Holy Cross	155	49	2	Nawrocki et al. (2003)
Saint-Pierre pelites	163	50	5	Diego-Orozco and Henry (1993)
Massif du Maures pelites	161	51	4	Merabet and Daly (1986)
St Affrique sediments	167	50	12	Cogné et al. (1993)
Lunner dykes 243 ± 5 Ar/Ar	164	53	6	Torsvik et al. (1998)
(e) L. Permian–E. Triassic mean pole	162.9	50.8	2	(N = 8, K = 764; Muttoni et al., 2009a,b)
(f) Middle Permian (~270 Ma)	~164.5	~46.4	–	Interpolated between (d) and (e); see also #

Long = longitude of paleomagnetic pole in °E; Lat. = latitude of paleomagnetic pole in °N; A95 = estimated radius of circle of 95% confidence about the paleomagnetic pole in °; dp/dm = estimated axes of ellipse of 95% confidence about the paleomagnetic pole in °; K = Fisher precision parameter; N = number of paleomagnetic pole entries.

Notes:

@ Erroneously reported as 239° E in Muttoni et al. (2003).

^ Rotated to NW Africa using rotation parameters of Lottes and Rowley (1990).

+ Based on same paleopole entries as in Muttoni et al. (2009a,b) but corrected for note @.

§ Updated with respect to the Late Permian–Early Triassic paleopole of Muttoni et al. (1996, 2009a,b; Long. = 237.6° E, Lat. = 46.8° N, A95 = 3.1, N = 8), from which it differs by 3.4° (great circle distance).

\$ This interpolated paleopole differs from the Middle Permian interpolated paleopole of Muttoni et al. (2009a,b; Long. = 239.9° E, Lat. = 44.1° N) by 1.8° (great circle distance).

Same as in Muttoni et al. (2009a,b).

single most parsimonious tree (length = 203, CI = 0.389, RI = 0.713) (Fig. 6). The most parsimonious tree obtained by maximum parsimony and unordered characters shows three nested groupings of OGU, closely corresponding to the three groups A–C identified by CA using the Jaccard Coefficient, with a minor difference, i.e. Oman appears to have a closer relationship with the Salt Range–south Thailand subgroup than with Turkey. By contrast, the Dollo character single most

parsimonious tree, which has a relatively low CI, has a more pectinate topology. Whereas this tree corroborates the subgroups which are congruently evidenced by CA and maximum parsimony (central Afghanistan–Karakoram; Salt Range–south Thailand), it suggests a relative recency of faunal contact between regions along a more linear gradient, in which Oman occupies an intermediate position. Interestingly, Tunisia and Sicily, either as a single area clade or as part of

Table 3
Paleolatitudes and biodiversity (genera richness, Permian Ratio, Sampling efficiency) of the faunal stations considered in the analysis. Typical errors on paleolatitudes are on the order of $\pm 5^\circ$.

	Tunisia	Sosio	Turkey	Oman	N Iran	C Afghanistan	Karakorum	Salt Range	S Thailand
Paleolatitude	$\sim 1^\circ\text{S}$	$\sim 1^\circ\text{S}$	$\sim 15^\circ\text{S}$	20–30°S	12°S	$\sim 0^\circ$	$\sim 0^\circ$	37°S	25–30°S
Genera	20	24	29	47	33	37	37	36	75
<i>Permian ratio</i>									
PR (Stehli, 1970)	PR 1.43	PR 2.0	PR 1.22	PR 1.0	PR 0.42	PR 0.77	PR 0.71	PR 1.0	PR 1.40
PR (em. Shi and Archbold, 1996)	PR 0.62	PR 0.87	PR 0.69	PR 0.94	PR 0.31	PR 0.62	PR 0.62	PR 0.87	PR 1.31
<i>Sampling efficiency</i>									
(Stehli and Grant, 1971)	SE 43%	SE 43%	SE 56%	SE 94%	SE 75%	SE 81%	SE 87%	SE 87%	SE 94%

$$\text{PR(Stehli, 1970)} = \frac{(\text{fam found} - \text{cosm fam found})}{\text{cosm fam found}}$$

$$\text{PR(Shi and Archbold, 1996)} = \frac{(\text{fam found} - \text{cosm fam found})}{\text{cosm fam expected}}$$

$$\text{SE(Stehli and Grant, 1971)} = \frac{\text{cosm fam found}}{\text{cosm fam expected}}$$

cosm fam = cosmopolitan families.

progressively less inclusive area subclades, occupy a consistently basal position in both area cladograms. PAE is known to interpret comparatively less diverse biota (see Table 3), typically reflecting small sample sizes in the more outlying areas, as primitive, although this pattern may represent the effect of ecological gradients (Rosen and Smith, 1988), such as continental proximity (see Discussion).

5. Discussion

The selected faunal stations belong to different provinces of the Asian-Tethyan region (Shi et al., 1995) in the Paleoequatorial realm (sensu Shen et al., 2009). If we follow strictly the concept that CA dendrograms generate groups of OGU that may be equated to biotic

provinces (Shi, 1995), we may identify three provinces, each corresponding to a specific cluster. These three groupings of OGU are fully corroborated by maximum parsimony PAE analysis (Fig. 6).

In our case (Fig. 6), Group A would represent the Cimmerian Province (Archbold, 1983), Group B the Transhimalayan Province (Angiolini, 2001a), and Group C the Cathaysian Province (Fang, 1985; Shen et al., 2009).

5.1. Group A: Cimmerian Province

The Cimmerian Province was introduced by Archbold (1983) to include faunas from the blocks separating from Gondwana in the Permian and this concept was followed among others by Shen et al.

Cluster analysis

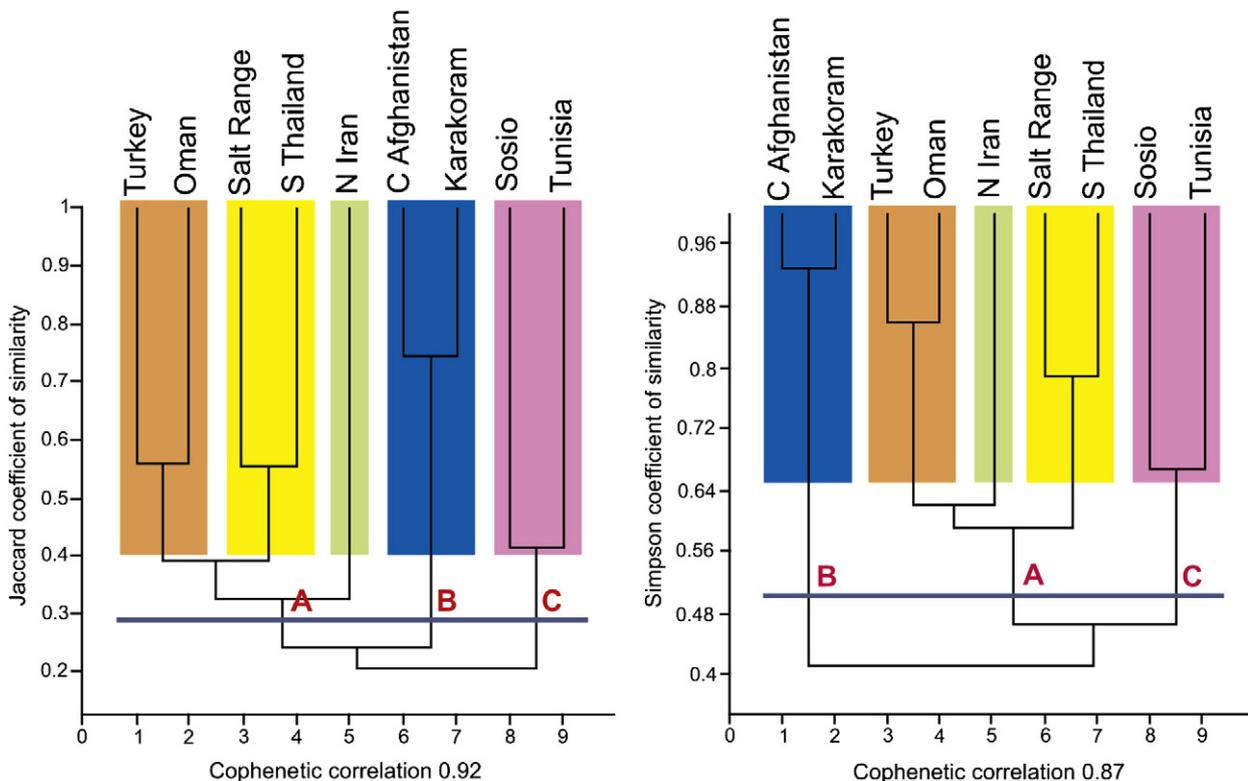


Fig. 3. Dendrograms of the selected OGU derived from Q-mode CA applied to a binary matrix using Jaccard Coefficient (left) and Simpson index (right). The cophenetic correlation value of the Jaccard dendrogram is 0.92, whereas that of the Simpson dendrogram is 0.87.

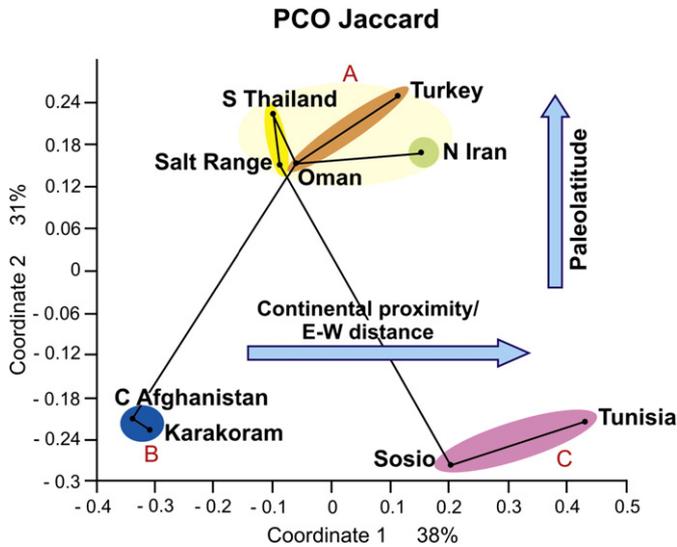


Fig. 4. Two-dimensional ordination plot of the selected OGU on the first two axes of principal coordinates analysis. Letters A, B, C correspond to those in Fig. 3.

(2009). Our analysis of revised brachiopod faunas from these regions provides further insights in its geographic circumscription and characteristic biotic association.

If we compare our results with the paleobiogeography proposed by Shen et al. (2009, Fig. 9) for the Roadian–Wordian, we obtain a very similar pattern for what concerns the Cimmerian Province in terms of its geographic distribution. The Cimmerian generic association identified by the R-mode analysis by Shen et al. (2009) is also

very similar to that obtained by us (Fig. 5). However, in our interpretation, the Cimmerian Province mainly comprises faunal stations that were part of the Gondwanan margin at Middle Permian times, as testified to by paleomagnetic data (Fig. 2 and Muttoni et al., 2009a,b). The Cimmerian Province does not include terranes that rifted from Gondwana in the Early Permian, except for north Iran, which in fact detached from the Gondwanan margin in the Sakmarian, but was still rather close to it in the Middle Permian (Gaetani et al., 2009; Muttoni et al., 2009a,b) (Fig. 7).

A previous analysis (Angiolini et al., 2005) has shown that the brachiopod faunule from the allochthonous unit of Chios Island (Greece) has a strong link with the Perigondwanan faunal stations; so we also include the allochthonous unit of Chios in the Cimmerian Province.

As stated above, no reliable paleomagnetic data are available for the Guadalupian of south Thailand (Sibumasu) (Richter and Fuller, 1996); its position within the southeastern Tethys is traditionally based on the assumption that “there are no post-early Permian faunas with Gondwanaland affinities on Sibumasu” (Metcalf, 1988, p. 103). Metcalfe (2011) synthesized the paleogeographical evolution of Sibumasu using as constraints its faunas of Gondwanan affinity in the Asselian–Sakmarian evolving to endemic and, finally, to Cathaysian affinity in the Late Permian, and suggested that collision of Sibumasu with the Sukhothai Island Arc terranes and Cathaysia land occurred as early as Late Permian–Early Triassic.

In contrast, our analysis, as well as that of Shen et al. (2009), shows that the paleobiogeographical affinity of Sibumasu in the Middle Permian is still with the OGU located along the Gondwana margin. According to the data and interpretation of Shen et al. (2009), the same holds true also for central Lhasa and the Baoshan Block, which can thus be considered as part of the Cimmerian Province.

The Cimmerian Province seems thus to be a well-defined biogeographic unit both in our geographically focused analysis and in the

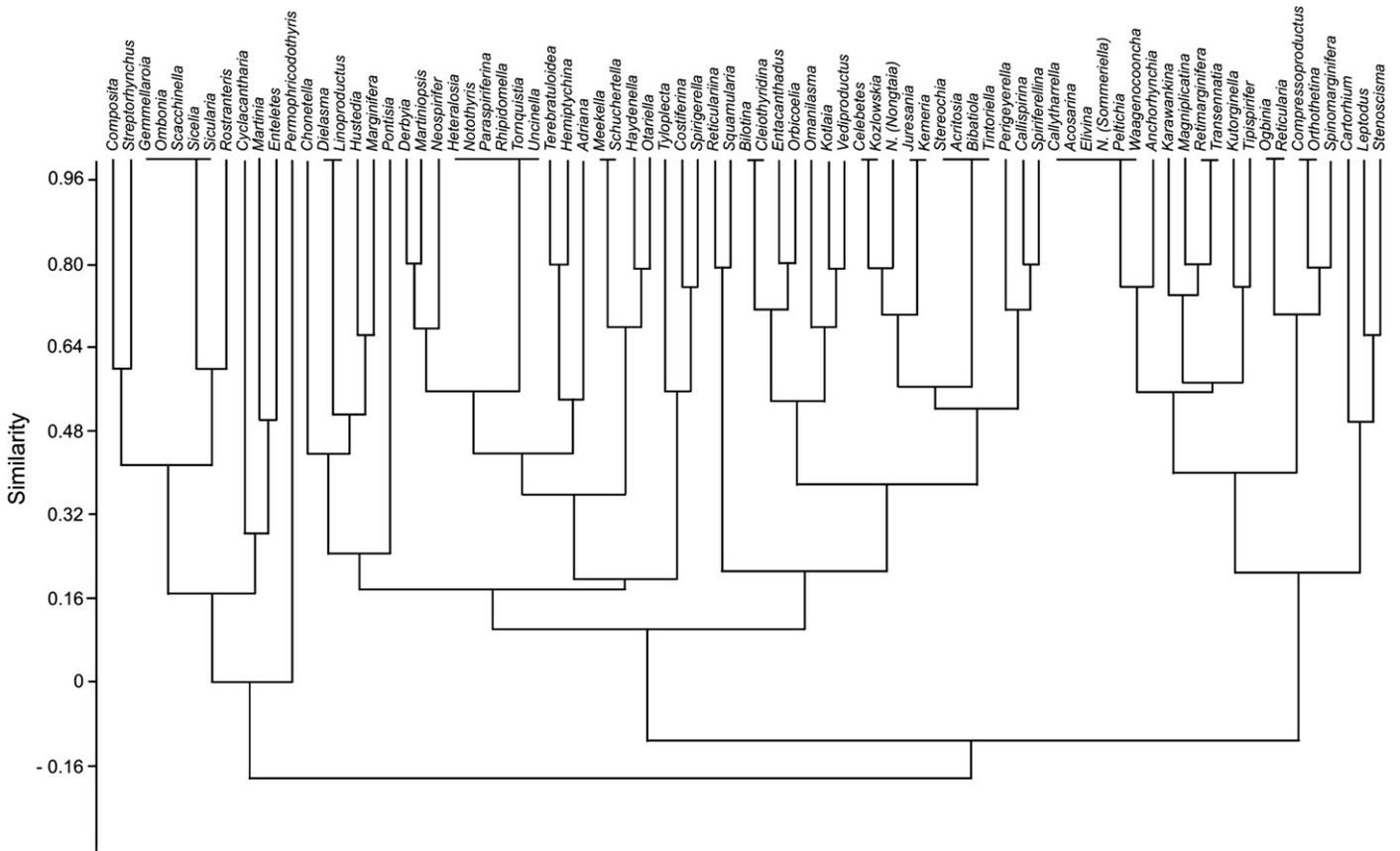


Fig. 5. Dendrogram of the brachiopod genera derived from CA applied to the binary matrix in R-mode analysis, which reveals the most recurrent brachiopod genera associations.

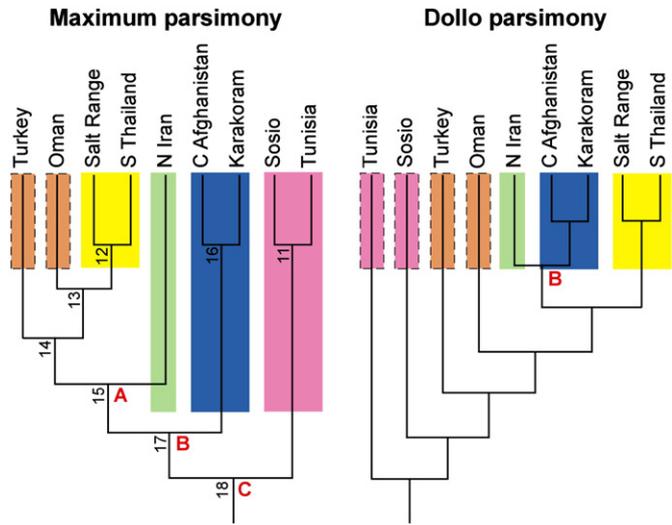


Fig. 6. The two most parsimonious sample locality cladograms obtained through PAE using maximum parsimony and unordered (CI=0.513) or Dollo type (CI=0.389) characters. Numbers refer to the number of shared genera at each node. Colored rectangles and letters (A, B, C) as in Fig. 3; broken lines identify CA groupings that are differently resolved by PAE.

more global one of Shen et al. (2009), at least for the Roadian–Wordian. According to Shi and Archbold (1995) and Shen and Shi (2004), the Cimmerian Province starts to lose identity and becomes incorporated in the Cathaysian Province from the Capitanian onward.

5.2. Group B: Transhimalayan Province

Our analysis shows that Karakoram constitutes, together with central Afghanistan, a well-defined province different from both the Cimmerian and the Cathaysian provinces, which we refer to as the Transhimalayan Province (Angiolini, 2001a), a biogeographic unit consisting of the faunas of those Cimmerian blocks that drifted rapidly northward to reach paleoequatorial latitudes at Roadian–Wordian times. Recently collected data suggest that also southeast Pamir belongs to the same province (Angiolini, unpublished). In the global paleobiogeography of Shen et al. (2009, Fig. 9), Karakoram and SE Pamir are part of the Cimmerian Province at this time, even if in some dendrograms/plots (Shen et al., 2009, Figs. 2, 3 and 6a) they also show loose relations with the South China faunal stations.

Our analysis, based on revised brachiopod faunas from the Cimmerian blocks and Perigondwana, shows that Karakoram and central Afghanistan have a very distinct biota, with very limited faunal exchange with the Cimmerian Province. Furthermore, their Middle Permian brachiopod fauna lacks most of the genera (except for *Spinomarginifera*) regarded by Shen et al. (2009, p. 177) as typical of the Cathaysian Province (although it shares with South China a number of other genera: *Acosarina*, *Transennatia*, *Paramesolobus*, *Compressoproductus*, *Ogbinia*). For these reasons, we think they belong to a separate biogeographic unit.

We agree with Shen et al. (2009) that the faunal stations from central Afghanistan, Karakoram, and southeast Pamir were affected by paleoequatorial currents in the Paleotethys Ocean (Kutzbach et al., 1990; Kiessling et al., 1999), explaining their loose faunal link with the Cathaysian OGU, but both their northward drift and their isolation between the Neotethys and Paleotethys Oceans

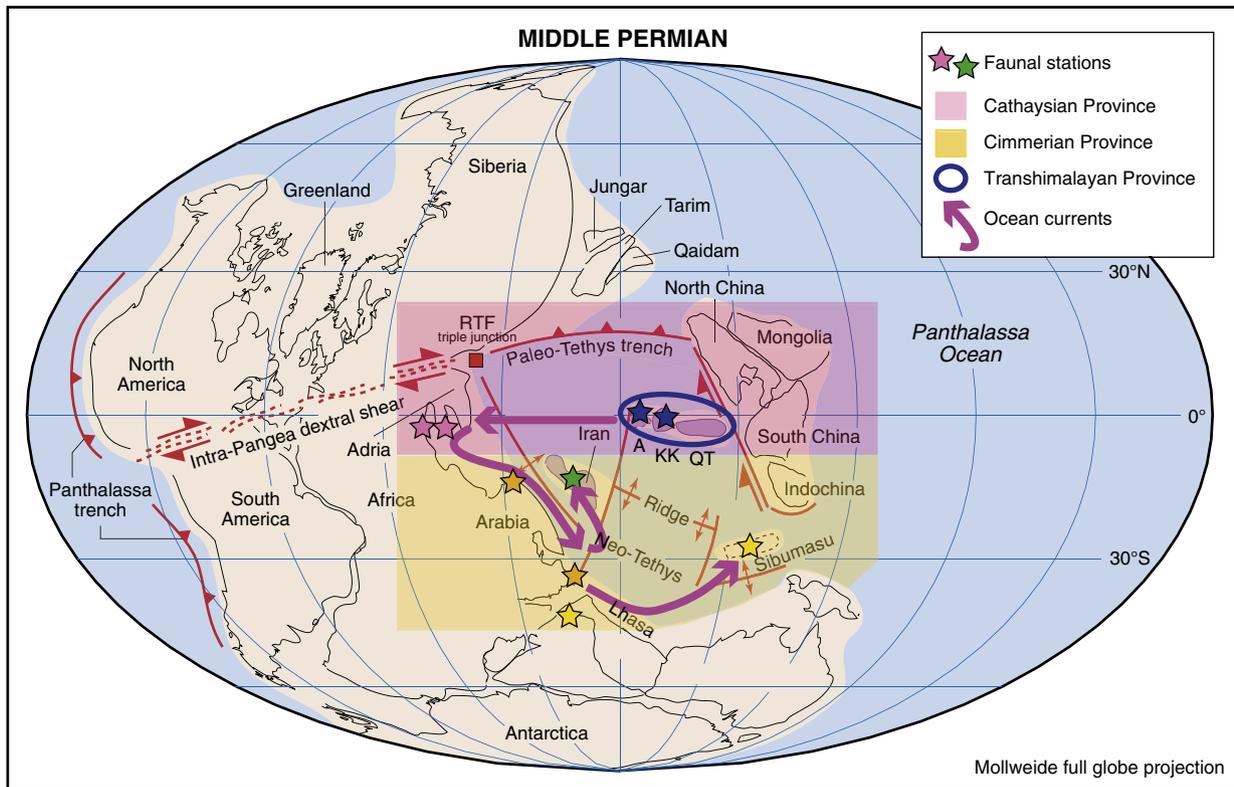


Fig. 7. The selected faunal stations of this study (stars; colors as in Figs. 2–4) placed on the Middle Permian paleogeographical reconstruction of Pangea and Cimmeria of Fig. 2 (from Muttoni et al., 2009a) are used to draw hypothetical ocean currents across the Tethys (purple arrows) as discussed in the text. A = central Afghanistan, KK = Karakoram, QT = Qiangtang (north Tibet), Sibumasu = Myanmar–Thailand–Baoshan–Malaysia (other symbols as in Fig. 2). The Cathaysian Province has been mainly drawn following the interpretation of Shen et al. (2009).

(Fig. 7) played a role in the evolution of faunal endemism, as discussed below.

5.3. Group C: Cathaysian Province

The Cathaysian Province of Shen et al. (2009) includes OGUs mostly related to South China. Sicily and Tunisia are also included in this province (Shen et al., 2009, Fig. 9) albeit based on rather limited similarities with South China possibly accounted for by faunal interchanges assisted by westward paleoequatorial currents in the Tethys Ocean. Indeed, while Sicily and Tunisia do seem to be more or less related to South China in most dendrograms and ordination plots presented by Shen et al. (2009), they generally form a separate cluster that in some instance may include Perigondwanan faunal stations (i.e. Oman and Baoshan in Shen et al., 2009, Figs. 4–5; or Karakoram and Crimean Mountains in their Figs. 2 and 3).

It is thus plausible that the brachiopod faunas of Tunisia and Sosio could form a distinct biogeographic unit in the Middle Permian, characterized by links with the Perigondwanan margin stretching southeastward, the southern Eurasian margin (Crimea) stretching northeastward, and even with Karakoram–Afghanistan and South China through the paleoequatorial current (Fig. 7). In any case, until a congruent taxonomy is established including the core stations of the Cathaysian Province and some Eurasian localities, we prefer not to introduce another biogeographic unit, and follow Shen et al. (2009) in considering the faunal stations of Tunisia and Sosio as part of the Cathaysian Province.

5.4. What are the factors that governed the biotic distribution of brachiopods across the Neotethys during the Middle Permian?

Although restricted only to a limited region across the southern and northern shores of the opening Neotethys Ocean, our analysis shows that faunal provinces respond to a complex interplay of different paleogeographical factors. These include:

- (i) distribution of continents and oceans, (ii) paleolatitudes and related zonal thermal gradients, (iii) proximity to – or isolation from – continental masses, (iv) E–W distance, (v) oceanic circulation patterns, (vi) continental drift across climate belts, and (vii) paleoecology.

Latitudinal variation seems to be expressed by coordinate 2 of the ordination plot (Fig. 4) and by the results of PAE (Fig. 6). However, it is interesting to note that whereas Karakoram, central Afghanistan, Sicily and Tunisia are located near the paleoequator, the OGUs of Group A stretch from ~12° S to ~37° S, thus comprising a broader latitudinal thermal gradient. Contrary to Shen et al. (2009), who found in their global paleobiogeographical analysis a distinct latitudinal-related diversity pattern, with diversity increasing from pole to the equator, we did not observe any specific latitudinal trend, and actually, the faunal stations with higher generic diversity are those at paleolatitudes between 20° and 37° S. This may be due to the fact that the selected OGUs were distributed along a latitude span mostly straddling the tropical gyre of the southern hemisphere or by the fact that the Gondwana margin was largely E–W oriented with northern Australia extending at relatively low-intermediate latitudes (45° S) from where no obvious pools of cool-water taxa could migrate to the area from higher latitude.

Another important reason of the observed increase in biodiversity in OGUs from intermediate latitudes could be preservation and sampling bias of silicified faunas, which are thus not only very well preserved, but which allow to extract many more specimens through preparation techniques and thus to find rare taxa.

Continental proximity is a factor that seems to explain the distribution of the faunal stations along coordinate 1 of the ordination plot (Fig. 4) and the basal position of OGUs in the cladograms

(Tunisia, Sicily). Continents play a major role in controlling biotic distribution providing nutrient runoff as well as a greater habitat and spatial diversification for benthic biota, favoring larval settling. Perez Huerta and Sheldon (2006) have neatly shown that nutrients play an important role in controlling brachiopod distribution. Particularly important is the lophophore filtering efficiency which differs among brachiopod orders, so that for instance athyrids and spiriferids are better adapted to high nutrients conditions, whereas productids are adapted to settings depleted in food resources.

Continental proximity can explain the distribution of the three groups along axis 1 – with the more continental localities, Tunisia and Sosio, on the right side of the axis, and the oceanic localities, Karakoram and central Afghanistan, to the left of it; however, the OGUs within Group A do not plot consistently along the same continental proximity gradient. The distribution along coordinate 1 of the ordination plot can also be controlled by the E–W distance of the faunal stations, as in all groups the westerly samples plot toward the right end of the axis.

The paleoequatorial current, which upon reaching the western Tethyan Gulf is predicted from paleogeography to be deflected southeastward along the Gondwanan margin (similar to what happens today in the western Pacific Ocean), is regarded as responsible for larval dispersal in the Perigondwanan OGUs as far southeast as South Thailand, as well as for the observed weak degree of faunal interchange between stations at the paleoequator (Karakoram, central Afghanistan, Sicily and Tunisia) (Fig. 7). It seems likely that a tropical current gyre linking Turkey, Oman, and N Iran could have been responsible for the faunal similarities among these OGUs observed in the Simpson CA dendrogram, in the PAE cladograms, and through MST in the ordination plot (Fig. 7).

Continental drift is the principal factor causing the individualization of the Transhimalayan Province, which is characterized by a mixed brachiopod fauna of endemic, Cathaysian, and Gondwanan genera, the latter evolved in the Early Permian when Karakoram and central Afghanistan were still attached to the Gondwanan margin.

We speculate that the rapid northward drift of central Afghanistan and Karakoram, due to the asymmetrical opening of the Neotethys Ocean from the Early to the Middle Permian (Fig. 7) (Muttoni et al., 2009a), caused (i) the interruption of the faunal exchange with Perigondwana, (ii) the evolution of endemic genera, and (iii) their intermingling with Cathaysian taxa brought in by the paleoequatorial current. Continental drift may also explain the relationships observed in the cluster plot based on the Jaccard Coefficient (Fig. 3), where North Iran is separated from the two clusters Turkey–Oman and Salt Range–Thailand possibly due to its incipient northward drift caused by the opening of the Neotethys Ocean.

Finally we have to consider that, even if we have examined brachiopod faunas collected from different paleoenvironmental settings of the selected OGUs, paleoecology could be an additional factor that could interfere at a more detailed scale with the main factors discussed above. More specifically, a gradient operating on the low latitude samples could account for reef vs. non-reef faunal associations. Both Sosio and Tunisia have reef or peri-reef brachiopod faunas, whereas Afghanistan and Karakoram comprise mostly open ramp assemblages. These differences could explain in part why we did not observe a link between these two groups notwithstanding the fact that they are bathed by the paleoequatorial current.

6. Conclusions

We conducted paleobiogeographical analyses on Middle Permian brachiopod associations from the Tethys Ocean, and placed the derived bioprovinces on a paleogeographical reconstruction based on selected paleomagnetic data in order to decipher the factors controlling the observed biotic patterns. In particular, we have shown that:

- (i) Central Afghanistan and Karakoram (Group B), and possibly also SE Pamir (as indicated by our unpublished data), belong to a biogeographic unit termed the Transhimalayan Province, and were located in the middle of the Tethys Ocean (between the Neotethys and the Paleotethys), paleobiogeographically isolated from the surrounding Pangea landmasses; even if they were bathed by a paleoequatorial current that could have dispersed larvae towards the western Tethyan Gulf and the Gondwanan margin, they had very limited faunal exchange with N Iran and the Gondwanan margin, as well as with Socio-Tunisia, and, according to Shen et al. (2009), also with South China.
- (ii) Tunisia and Sicily (Group C) were located in the westernmost part of the Tethyan Gulf and were dominated by reef or peri-reef brachiopod faunas. The distribution of these faunas was thus controlled paleobiogeographically by the proximity of the supercontinent Pangea and paleoecologically by the life style of the constituent reefal communities. The brachiopod fauna of Tunisia and Sicily forms a distinct group that is markedly different from the Cimmerian and Transhimalayan provinces while possibly bearing a weak affinity with the Cathaysian Province.
- (iii) N Iran belongs to the Cimmerian Province and was in connection with the Perigondwanan regions of Turkey and Oman (Group A), being only slightly detached from the Gondwanan margin due to the incipient opening of the Neotethys Ocean; these faunal similarities can be explained by a current gyre bathing both the N Iran terrane and the still nearby Gondwanan margin from which it was drifting away.
- (iv) South Thailand and the Salt Range (Group A) show affinities to the northern Gondwanan margin and they are therefore attributed to the Cimmerian Province (see below).
- (v) The Cimmerian Province appears to be a well defined biogeographic unit, with a characteristic faunal association that extends along the Gondwanan margin from Greece to the Salt Range and Lhasa, and comprises also the drifting Cimmerian blocks still located close to the rifted margin, such as N Iran, Baoshan, and Sibumasu.

According to the analyses above we conclude, that the most important factors controlling brachiopod paleobiogeography in the Middle Permian were paleolatitude, ocean paleocurrents, and the continental drift of the Cimmerian terranes across zonal climate belts.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.gr.2012.08.012>.

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