

# Wuchiapingian (early Lopingian, Permian) global brachiopod palaeobiogeography: a quantitative approach

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## Abstract

A global presence/absence database of 212 Wuchiapingian (early Lopingian, Permian) brachiopod genera from 30 stations is analysed by cluster analysis, nonmetric multidimensional scaling and minimum spanning tree to document the global palaeobiogeographical patterns. Five core groups are revealed by the quantitative analysis and interpreted as representing five marine biotic provinces. They are the Cathaysian (tropical), Western Tethyan (tropical), Himalayan (warm temperate), Austrazean (cold temperate) and Greenland–Svalbard Provinces (cold temperate). The Cathaysian Province is composed of many isolated or semi-isolated islands situated in the Palaeotethys, whereas the other four provinces occurred mainly on the continental shelves of Pangea: the Western Tethyan Province along the western coast of the Palaeotethys, the Himalayan Province on the northern margin of Gondwanaland, the Austrazean Province along the southeastern margin of Gondwanaland, and the Greenland–Svalbard Province on the northern margin of Pangea. In addition, nonmetric multidimensional scaling helped to identify key biogeographic determinants: latitude-related thermal gradient appears to have accounted for most of the variance in the data; geographic distance and ocean circulation may have also played a major, but subordinate, role in the delineation and/or enhancement of some of the provinces. Comparison with Early and Middle Permian global marine provincialism indicates that marine biotic provinces had significantly reduced during the Lopingian (Late Permian) in the lead up to the end-Permian mass extinction. © 2000 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

In many aspects, the Lopingian (Late Permian) marks a major turning stage in geological history. For instance, it has been increasingly recognised that the Middle (Guadalupian) and Late Permian (Lopingian) intervals were decimated by two major mass extinctions, respectively at or towards the

ends of Guadalupian and Lopingian (Jin et al., 1994; Stanley and Yang, 1994; Shen and Shi, 1996, 2000), which collectively marks the traditional ‘Late Permian’ [= Upper Guadalupian and Lopingian of Jin et al. (1997)] mass extinction as the mother of all mass extinctions (Erwin, 1994). The Lopingian and the Permian–Triassic transition also signifies the zenith of Pangea, during which most continents were assembled together in the form of a supercontinent stretching nearly from pole to pole (e.g. Scotese and McKerrow, 1990; Ziegler et al., 1998) and, as such, provided a

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continuous barrier to zonal atmospheric and oceanic circulations. Probably induced by the assembly and ultimate formation of Pangea, seawater withdrew from most areas of the continental Pangea by the end-Guadalupian, resulting in very patchy distribution of Lopingian marine strata and fossils on Pangea and extremely limited records of continuous marine Permian–Triassic sequences around the world.

One of the possible effects brought about by the global environmental changes associated with the formation of Pangea might be its impact on global marine provincialism, which in turn may have inflicted changes upon the evolutionary dynamics of marine biota through the Guadalupian and Lopingian and the Permian–Triassic transition. To elucidate these intricate relationships among biotic and environmental factors and to understand in particular how the world and regional marine provincialism waxed and waned through the Permian, herein we continue on our series of studies on Permian intercontinental and global brachiopod biogeography with a specific focus on the Wuchiapingian Stage [results of our studies on other Permian time slices in a regional/global scale have already been published, see Shi and Archbold (1993, 1995a,b, 1996) and Shen et al. (2000a)].

The Wuchiapingian marks the first stage of the Lopingian and succeeded the major mass extinction at the end of the Guadalupian. Positioned as such in the Permian timeline, this stage would therefore straddle a critical interval in the evolution of biota during the Permian. On the one hand, this stage punctuates the seemingly long, protracted late Permian mass extinction process (Isozaki, 1997); on the other hand, it delineates two temporarily closely spaced but clearly separable, therefore probably unrelated, extinction events (Shi et al., 1999). To date, no studies have been conducted on the role and significance of the Wuchiapingian in the transition of the Guadalupian to the Lopingian. In this paper we therefore attempt to make a starting point towards a better understanding of this stage by studying its global marine biogeography based on the brachiopod faunas and using a range of multivariate methods.

## 2. Data and methodology

A presence/absence database of genera from 30 stations with Wuchiapingian brachiopod faunas has been assembled (Fig. 1). Except for the authors' personal unpublished/in press data, information on other brachiopod faunas has been taken from different sources, as shown in Table 1. In compiling the database, we have examined all available published Permian brachiopod literature and updated the taxonomy and age determinations of the published records in light of the latest developments in Permian brachiopod taxonomy and biostratigraphy. A station is a geological entity, such as an intracratonic basin, a marginal basin, or an epicontinental basin or seaway. Stations are as extensive as possible so as to embrace all correlative fossil communities from various substrates and water depths, provided that geological evidence is clear that only one basin is involved. Therefore, a station may represent a fauna from a single locality or a composite record of several assemblages from the same geological entity. This sampling strategy is designed to minimise the possible effect of local ecology on biogeographical analysis (Shi and Archbold, 1993). We consider that the fossil records of species are too imperfect to use for large-scale palaeobiogeographical analysis and that they are also more sensitive to local environments. Family-level taxa, on the other hand, are too broad to reveal detailed palaeobiogeographical structure. Therefore, the generic data were employed for our quantitative analysis.

The latest time scale of the Permian System (Jin et al., 1997) is adopted for the chronostratigraphical definition of the Wuchiapingian. The lower boundary of the Wuchiapingian is placed at the base of the conodont *Clarkina postbitteri* Zone, and the base of the ammonoid *Iranites* Zone or the conodont *Clarkina subcarinata* Zone marks its upper boundary. The Djulfian (Dzhulfian) has been commonly used for more or less the same time interval by many authors and is also considered to be chronostratigraphically equivalent to the Wuchiapingian in this paper.

In total, 212 brachiopod genera from 30 stations worldwide are included in this study. We employed three statistical indices to illustrate the basic nature

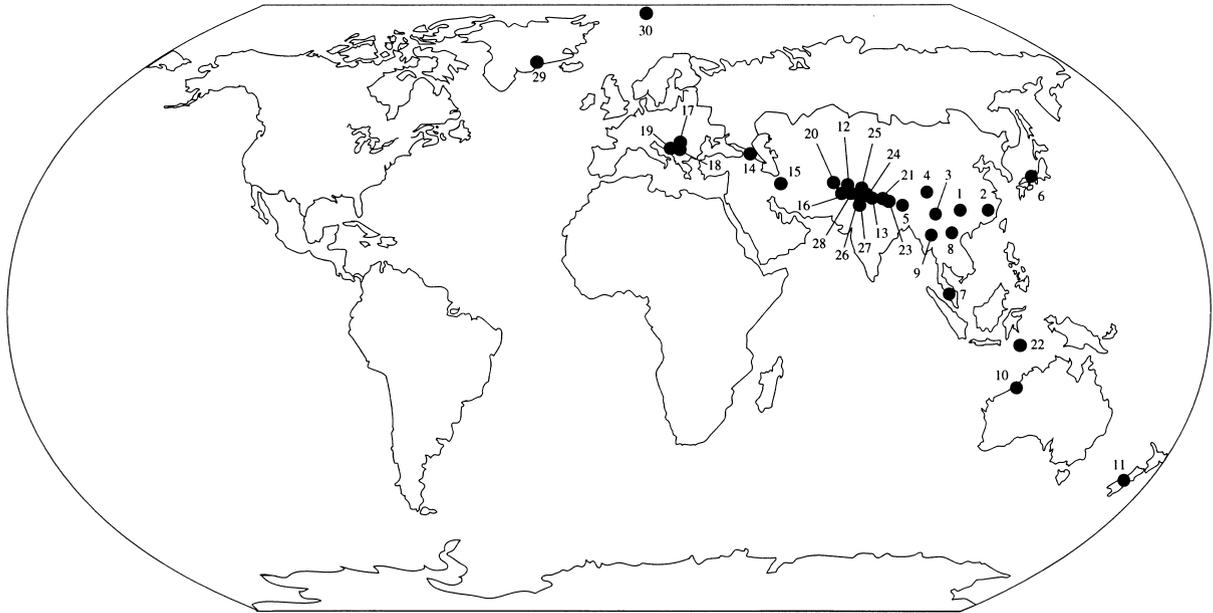


Fig. 1. Area and/or localities selected for this paper. 1=South China; 2=Southeast China; 3=Western Yunnan, southwest China; 4=Germu and Qinghai, North China; 5=Tuoba, eastern Tibet (Xizang), China; 6=Southwest Japan; 7=Sungai Relai, Malaysia; 8=Central Vietnam; 9=Central Thailand; 10=Western and northwestern Australia; 11=New Zealand; 12=Karakorum Range, Pakistan; 13=Northwest Nepal; 14=southern Armenia; 15=Iran; 16=Salt Range, Pakistan; 17=Hungary; 18=Slovenia; 19=West Serbia; 20=Southeastern Pamir; 21=Selong, southern Tibet, China; 22=Timor; 23=Qomolangma region, southern Tibet, China; 24=Chitichun, southwestern Tibet, China; 25=Zanda, southwestern Tibet, China; 26=Niti area, central Himalayas, India; 27=Spiti, north India; 28=Kashmir; 29=East Greenland; 30=Svalbard (Spitsbergen).

of these faunas: total genera, sampling efficiency and Permian ratio (see Table 1). The total genera refers to the number of genera recorded in each station.

Sampling efficiency (Stehli and Grant, 1971) is an index designed to check on the adequateness of sampling of each station based on the finding of actual cosmopolitan families at each station, standardised by the number of cosmopolitan families expected for each station. The brachiopod cosmopolitan families suggested by Stehli and Grant (1971) included Schuchertellidae, Orthotetidae, Chonetidae, Marginiferidae, Echinoconchidae, Buxtonidae, Dictyoclostidae, Linoproductidae, Stenoscleritidae, Rhynchoporidae, Athyrididae, Spiriferidae, Brachythyrididae, Spiriferinidae, Elythidae and Dielasmatidae. Stehli and Grant (1971) claimed that these cosmopolitan families should occur in probably all Permian brachiopod-bearing fossil localities. Therefore, the proportion of cosmopolitan families in a fauna should give a

measure of sampling efficiency for that fauna. However, Waterhouse (1982) argued that this kind of evaluation method may lead to errors because the above-mentioned families are not all truly ubiquitous. Subsequently, Waterhouse (1982) reduced the cosmopolitan families to only seven, namely Streptorhynchidae, Chonetidae, Linoproductidae, Syringothyrididae, Spiriferidae, Reticulariidae and Dielasmatidae. This list was further amended to the Streptorhynchidae, Rugosochonetidae, Linoproductidae, Marginiferidae, Athyrididae, Spiriferidae and Dielasmatidae by Shi and Archbold (1995a). We consider that cosmopolitan dominants in different regions may change from time to time in response to evolution and adaptation. Therefore, it is necessary to revise further the list of the brachiopod cosmopolitan dominants with respect to the Wuchiapingian. Thus, in this study we only counted as cosmopolitan families those that have more than half occurrences (15 out of 30 stations in this paper) and are found in all the three general realms

Table 1  
Wuchiapingian brachiopod faunas in the world — basic data and statistics. References for palaeolatitude and tectonic units of non-common terms are indicated

No.	Stations	Mean latitude, longitude	Palaeolatitude (Ref.)	Tectonic units (Ref.)	Stratigraphic units	Total genera	Sampling efficiency (%)	Permian ratio	Principal references
1	South China	29°26'N, 108°80'E	5.9°S (Zhao and Coe, 1989)	Yangtze Block	Longtan/Wuchiaping Fm.	61	100	4.43	Zhan (1979); Liao (1980, 1987); Yang (1984); Li et al. (1989)
2	Southeast China	28°39'N, 116°17'E	12°S ± (Yin et al., 1999)	Cathaysian Terrane (Yin et al., 1999)	Longtan/Loping Fm.	53	71.4	3.71	Wang et al. (1982); Hu (1989)
3	Western Yunnan	23°02'N, 101°03'E	12°S ± (Yin et al., 1999)	Lanping-Simaob Block	Yangbazhai Fm.	9	28.6	0.86	Shi et al. (unpublished data)
4	Germu and Qinghai, North China	35°65'N, 99°64'E	8°N ± (Yin et al., 1999)	Qaidam Basin	Kaixilin Group	39	85.7	2.57	Qinghai Stratigraphic Group (1980)
5	Tuoba, eastern Tibet	31°20'N, 97°50'E	3.36°N (Huang et al., 1992)	Northern Qiangtang Block	Tuoba Fm.	13	57.1	0.71	Wen (1979); Jin and Sun (1981)
6	Inner Zone, Southwest Japan	34°00'N, 132.25E	3.5°N (Hattori and Hirooka, 1979)	Inner Zone	Karita Fm.	9	14.3	1	Imamura (1953); Yanagida (1993)
7	Sungai Relai, Northeast Malaysia	4°55'N, 102°10'E	19.0°S (Bunopas, 1981)	Indo-China Block	Aring/Gua Musang Fm.	8	28.6	0.57	Yanagida and Aw (1979)
8	Central Vietnam	16°77'N, 107°14'E	14°S ± (Ziegler et al., 1997)	Indo-China Block	Unnamed Fm.	8	42.9	0.57	Tien Chi-Thuan (1962)
9	Central Thailand	17°15'N, 100°75'E	14°S ± (Ziegler et al., 1997)	Indo-China Block	Unnamed Fm.	17	71.4	1.43	Yanagida (1988)
10	Western Australia	19°10'S, 125°28'E	40°S ± (Ziegler et al., 1997)	Canning and Bonaparte Gulf Basins	Hardman Fm.; unnamed limestone	19	28.6	1.57	Archbold (1988, 1993)
11	Takitimu Mt., New Zealand	46°69'S, 171°19'E	55°S ± (Ziegler et al., 1997)	Brook Street Terrane (Landis et al., 1999)	Takitimu Group	14	57.1	1.29	Waterhouse (1964, 1970, 1982)
12	Karakorum Range, Pakistan	38°00'N, 78°75'E	34°S ± (Ziegler et al., 1997)	Karakorum Block (Gaetani et al., 1996)	Shyok Group	35	71.4	2.57	Waterhouse and Gupta (1983)
13	Nepal	24°46'N, 83°00'E	44.5°S (Klootwijk, 1984)	Himalayan Terrane	Senja Fm.	58	100	3.57	Waterhouse (1966, 1978)
14	Julfa, southern Armenia	38°98'N, 45°49'E	4°S ± (Klootwijk, 1984)	Julfa Terrane (Saïdi et al., 1997)	Djulfia Fm.	35	71.4	2.29	Ruzhentsev and Sarycheva (1965); Kotljars et al. (1983)

15	Alborz Mts. North Iran	34°27'N, 51°87'E	4°S (Matsumoto et al., 1995)	Alborz Mts. (Saidi et al., 1997)	Djhulfa/Nesen Fm.	29	57.1	2.29	Sestini and Glaus (1966); Iranian-Japanese Working Group (1981)
16	Salt Range, Pakistan	32°47'N, 71°39'E	34°05'S (Ziegler et al., 1997)	Indian Massif	Wargal and Chhidru Fm.	80	100	4.86	Waagen (1883, 1884, 1885); Reed (1944)
17	Hungary	48°06'N, 20°43'E	15°N ± (Ziegler et al., 1997)	Dinarides Belt (Vai, 1998)	Nagyvisnyo Limestone Fm.	12	57.1	1	Schreier (1963); Pestic et al. (1986)
18	Slovenia	46° ± N, 14°30'E	15°N ± (Ziegler et al., 1997)	Dinarides Belt (Vai, 1998)	Zazar Development	7	28.6	0.71	Pestic et al. (1986)
19	West Serbia	44°N ± 20'E ±	15°N ± (Ziegler et al., 1997)	Dinarides Belt (Vai, 1998)	Jadar Development	13	42.9	1.14	Pestic et al. (1986)
20	Southeastern Pamir	37°64'N, 74°07'E	16°S ± (Ziegler et al., 1997)	Afghan-south Pamirian folded area	Djhulfa Fm.	23	42.9	2.29	Grunt and Dmitriev (1973)
21	Selong, southern Tibet	28°39'N, 85°50'E	44.5°S (Klootwijk, 1984)	Himalayan Terrane	Selong Group	29	85.7	1.86	Zhang and Jin (1976); Shi and Shen (1997); Shen et al. (2000b)
22	Timor	9°74'S, 124°07'E	39°S (Weusink and Hartosukohardjo, 1990)	Aileu-Mau Ex. Block	Unnamed	24	100	1.86	Broili (1916); Hamlet (1928)
23	Qomolangma Region, Southern Tibet	28°27'N, 86°97'E	44.5°S ± (Klootwijk, 1984)	Himalayan Terrane	Qubuega Fm.	23	71.4	1.29	Shen et al. (unpublished data)
24	Chitichun Southwestern Tibet	30°70'N, 80°26'E	?	?Exotic Terrane	Chitichun Limestone	22	71.4	1.71	Diener (1897a)
25	Zanda, southwestern Tibet	31°46'N, 79°86'E	44.5°S ± (Klootwijk, 1984)	Himalayan Terrane	U. Mangzong-long Fm.	14	28.6	1.29	Yang and Nie (1990)
26	Niti pass, Central Himalayas, India	30°93'N, 74°26'E	44.5°S ± (Klootwijk, 1984)	Himalayan Terrane	Productus Shale	13	57.1	0.57	Diener (1897b)
27	Spiti, India	32°00'N, 178°10'E	44.5°S ± (Klootwijk, 1984)	Himalayan Terrane	Kuling Group	7	28.6	0.71	Diener (1899); Angiolini cited in Garzanti et al. (1996)
28	Kashmir	34°00'N, 75°00'E	42°8'S (Ziegler et al., 1997)	Himalayan Terrane	Zewan Fm.	25	100	1.57	Nakazawa et al. (1975); Shimizu (1981)
29	East Greenland	74°15'N, 20°50'W	37°N ± (Ziegler et al., 1997)	Eskimonia High	Martiniakalk	16	85.7	1.43	Dunbar (1955)
30	Svalbard (Spitsbergen)	78°55'N, 23°91'E	45°N ± ° (Ziegler et al., 1997)	Nordfjorden High	U. Kapp Starostin Fm.	19	71.4	1.29	Nakamura et al. (1992)

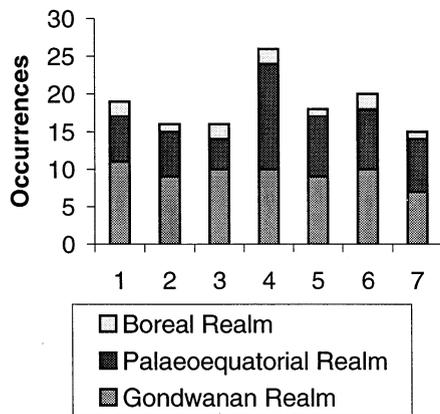


Fig. 2. Cosmopolitan families during Wuchiapingian and their occurrences in three realms. 1 = Athyrididae McCoy; 2 = Dictyoclostidae Stehli; 3 = Linoproductidae Stehli; 4 = Marginiferidae Stehli; 5 = Martiniidae Waagen; 6 = Rugosochonetidae Muir-Wood; 7 = Stenoscismatidae Oehlert. Occurrences refer to station number in each realm with the cosmopolitan families.

(Gondwanan, Palaeoequatorial and Boreal Realms). As a result, the Wuchiapingian cosmopolitan brachiopod families include Athyrididae, Dictyoclostidae, Linoproductidae, Marginiferidae, Martiniidae, Rugosochonetidae and Stenoscismatidae. The proportions of each cosmopolitan family in each of the three realms are shown in Fig. 2.

The Permian Ratio (Stehli, 1970) was originally defined as:

$$\frac{\text{Families present} - \text{cosmopolitan families found}}{\text{Cosmopolitan families found}}$$

However, this formula is biased in favour of poorly sampled stations by giving them higher values. Therefore, it has been revised by replacing the denominator with 'cosmopolitan families expected' (Shi and Archbold, 1996).

Among the 30 stations with Wuchiapingian brachiopod faunas, the Inner Zone of Japan has the lowest sampling efficiency (14%), and the other six stations have sampling efficiencies below 0.3, which indicates that these seven stations were relatively poorly sampled. Nevertheless, all stations are included in the quantitative analyses for the

sake of preserving all the stations in one complete statistical sample. Exclusion of such poorly sampled stations from the statistical sample, as done in several other studies (e.g. Shi and Archbold, 1993, 1996), would only enhance the patterns underlying the data if they are indeed present and robust in the original dataset. However, caution must be taken when interpretation is to be derived from these quantitative analyses involving faunal stations with low or very low sampling efficiency values.

The initial presence/absence data matrix of 212 genera from 30 stations was analysed by three common multivariate statistical techniques [cluster analysis (CA), nonmetric multidimensional scaling (NMDS) and minimum spanning tree (MST)] on an IBM compatible PC using PATN (Belbin, 1992) and STATISTICA (1995 version). Various binary coefficients have been employed in literature for calculating the biotic similarities between stations and degree of associations between taxa. As evaluated by Cheetham and Hazel (1969), Shi (1993), Shang and Jin (1997) and many other previous works, Jaccard and Cosine/Ochiai (Otsuka) coefficients have been shown to be the most consistent and least liable to sampling biases or inefficiencies. Accordingly, we have used these two coefficients to calculate the dissimilarities between the stations and derive secondary matrixes for multivariate statistical analyses.

The secondary data matrixes of faunal dissimilarities among the 30 stations were then analysed by CA, NMDS and MST. The unweighted pair-group arithmetic averaging (UPGMA) CA was first used to classify the different stations into discrete core groups. The degree of robustness of the core groups recognised by CA was tested in two different ways. Firstly, the cophenetic correlation coefficient values (a confidence indication of the analysis) of the CA were calculated by the PATN program. The cophenetic correlation values ranging from zero to one and calculated by the Pearsons product moment correlation coefficient provide an effective measure to verify how much distortion may have been imposed by a particular clustering approach between the input dissimilarity matrix and the resultant ultrametric matrix derived from a dendrogram (Belbin, 1992; Shi, 1993). In

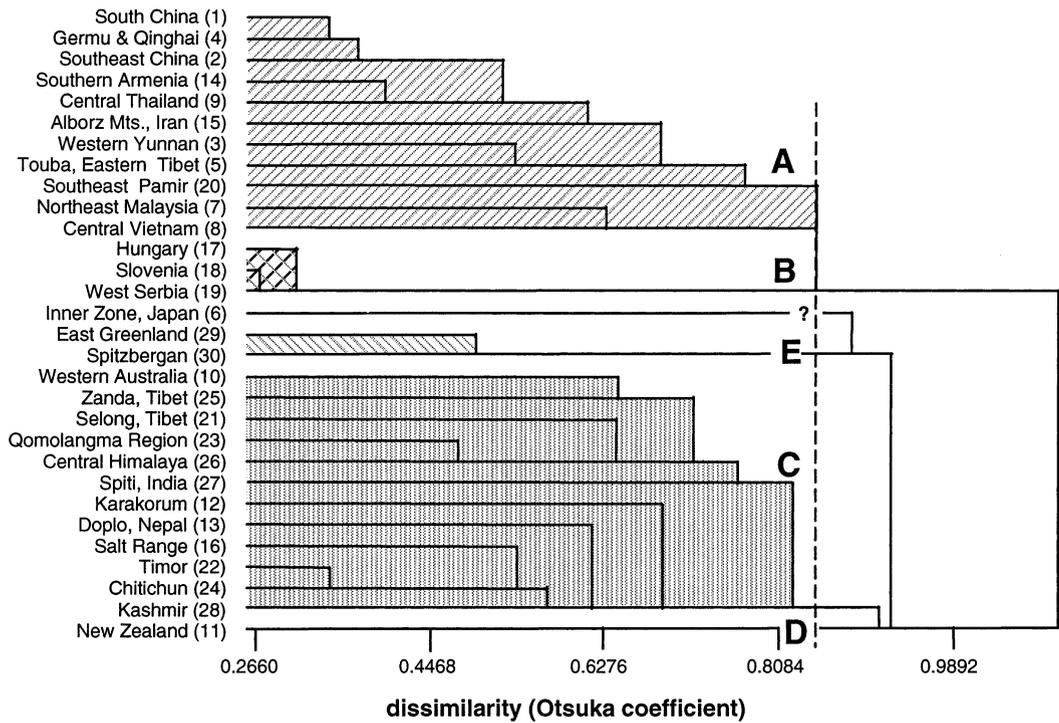
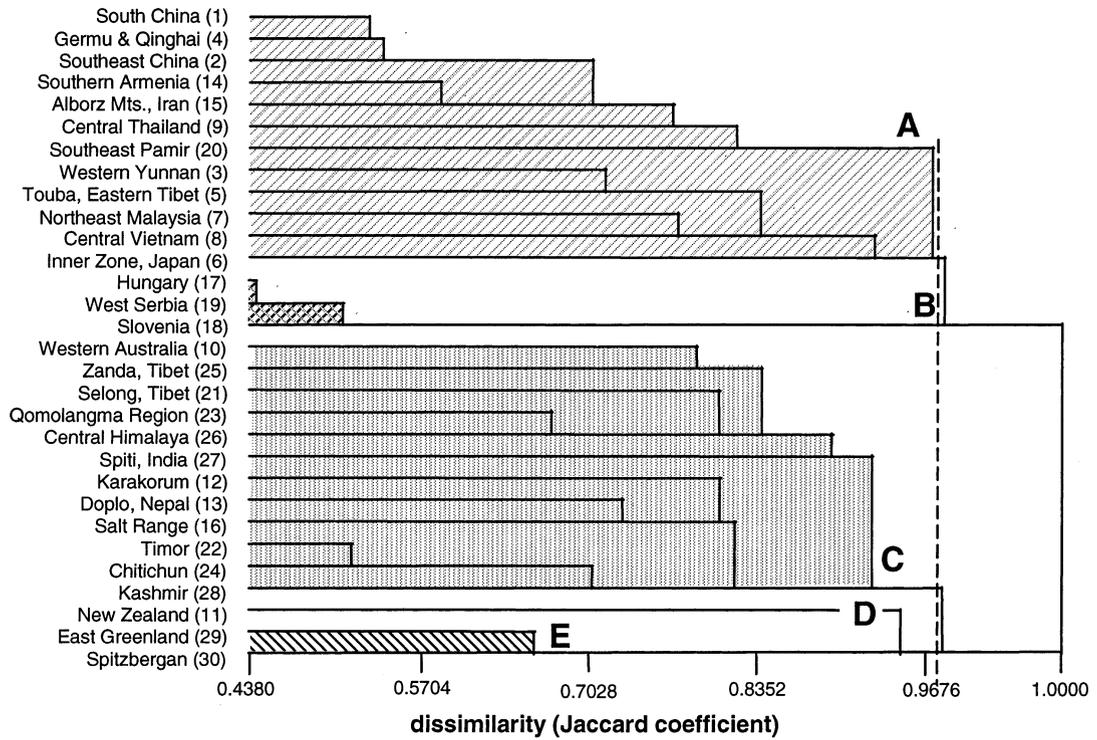
this paper, the cophenetic correlation values for the Jaccard coefficient-based CA and the Otsuka-based CA are valued at 0.7798 and 0.7257 respectively, indicating strong robustness and minimal distortions for both cluster analyses. A second testing strategy of the CA results was provided by NMDS. This is an ordination technique aimed at reducing the multiple dimensions of variance in the original data to two or three dimensions while trying to maintain the basic spatial structure of the data (Shi, 1993). NMDS was performed using STATISTICA after the two secondary dissimilarity matrixes were standardised using the Euclidean distance measure. In simple terms, the goal of NMDS is to reduce a complex dataset with multiple variables (i.e. taxa in this paper) to a simple two- or three-dimensional space (or coordinate system) in which the samples (i.e. the faunal stations of our study) are rearranged in such a way that the variance of the data is maximised along these first two or three dimensions and the loss of relevant information is kept minimal. Graphically, NMDS allows the data structure to be visually inspectable and, in most cases, interpretable with relative ease. Therefore, if the original data set does possess any grouping structure, these potential groups would appear in NMDS scatter plots and they would correspond to those recognised by CA. Further detailed discussions on the use of NMDS in palaeobiogeographical analysis and a description of the various types of scaling technique are beyond the scope of this paper but can be found in Shi (1993) and Shi and Archbold (1993, 1996). An indication of the reliability of NMDS is called stress. Very much like the cophenetic values of CA, each NMDS analysis was accompanied by the calculation of a 'stress' value ranging from zero to one. The stress value indicates the level of 'goodness of fit' between the original input data matrix (the dissimilarity matrix) and the ultrametric matrix of the resultant NMDS scatter plot; thus, the lower the stress value, the less distortion the NMDS has introduced to the original input, and hence the more robust the NMDS scatter plot.

To test further the congruency between the core groups of CA and the groups recognised from NMDS, we superimposed an MST to each NMDS

plot. An MST is a set of line segments formed by connecting stations together in order that (1) it will give the minimum overall line length, (2) all stations in the tree must have at least one connection and (3) there are no circuits or loops in the same tree (Gower and Ross, 1969; Belbin, 1992). To some extent, the MST approach provides a useful measure of biogeographical relationships between different stations within the same group as well as the relationships between the groups. However, the MST approach may also generate ambiguous biogeographical signals rather than a unique solution. This is particularly so when the groups detected by CA are not robust enough (e.g. a group that includes stations which may straddle several groups by virtue of its constituent genera). When this occurs to an MST, a group is connected to another group by more than one line, as in the case between Groups A and B and between Groups A and C in this paper (see Section 3). However, the 'extra' connections between the groups may not necessarily indicate a weakness or defect for the MST approach. To the contrary, the 'extra' connections may signify the existence of 'impurity' associated with these groups caused by either inconsistent data and/or data embodied with faunal stations of either 'transitional' nature (i.e. stations with a significant number of wide-ranging genera) or variable sampling efficiencies. In these cases, any geological interpretations of the groups must be taken with caution.

### 3. Results

Fig. 3 gives the dendrograms derived from the UPGMA CA based on both the Jaccard and Otsuka coefficients. Both dendrograms reveal five generally consistent core groups (labelled A–E) at the chosen division line. Among the five core groups, Groups A–C appear to be fairly robust entities, as indicated by the same set of constituent stations for each group between the two dendrograms. Recognition of Groups D and E is less evident because they do not appear to show consistent relationships with other groups when compared between the two dendrograms. Nevertheless, these two groups do tend to form fairly indepen-



dent entities by the division lines. In general, among all the faunal stations only the Inner Zone of Japan could not be clearly assigned to any group, despite the Jaccard coefficient-based CA showing that it has a broad alliance to Group A. The uncertainty over the group membership of the Inner Zone of Japan is most likely due to its extremely low sampling efficiency of 0.14 (see Table 1, and also discussion in Section 2). This station, as it is presently known, only contains some wide-ranging (but not all are cosmopolitan) genera such as *Derbyia*, *Hustedia*, *Leptodus*, *Spiriferellina*, etc., therefore preventing it from being demarcated from any particular group.

As shown by the dendrograms of Fig. 3 and data in Table 1, Group A consists of 12 stations, all of low palaeolatitudes in the palaeoequatorial region. The geographical extent of this group is also of note: with the exception of the Alborz Mts and the Julfa region of southern Armenia and northwestern Iran, both of the Iranian block, all other stations come from East and Southeast Asia, which during the Permian were all located in the eastern Palaeotethys. The association of the Alborz Mts and Julfa region with this group is interesting because these two stations, in their modern geographic positions, are closer to stations of Group B (Hungary, Serbia and Slovenia) located in the western Palaeotethys. Yet, our statistical analysis shows that their Wuchiapingian faunas have stronger links to eastern Palaeotethyan faunas than to those of the Western Tethyan stations. The implication of the varied faunal links of the Iranian block with eastern and western Palaeotethys will be discussed further later in this paper.

Group C is also diverse in terms of its memberships, but most of its constituent member stations come from the Southern Tibet–Himalayan region, with additions of Western Australia and Timor. In the dendrogram derived from the Jaccard coefficient-based CA, New Zealand was grouped with East Greenland and Svalbard (Spitsbergen). However, New Zealand is shown distinct from the

other two stations according to the Otsuka coefficient-based CA. Clearly, this cross-linkage of New Zealand with both Group C and E reflects its dual relationships with these two groups and can be explained by the nature of its faunal composition. Palaeogeographically and tectonically, New Zealand was unlikely to be in close proximity with East Greenland or Svalbard during the Permian, but their high mutual faunal similarity could be a reflection of bipolar or antitropical distributions of Brachiopoda during the Permian (Shi and Grunt, 2000). An analysis of our Wuchiapingian brachiopod database indicates that New Zealand shares some antitropically distributed genera with East Greenland and Svalbard, including *Neospirifer*, *Waagenoconcha* and probably *Horridonia*.

All the major groups identified by CA are largely substantiated by NMDS (Fig. 4). Five groups (also labelled A–E) are easily divisible using three dimensions based on either the Jaccard or Otsuka coefficients. The stress values are 0.079 101 for Jaccard coefficient-based NMDS and 0.044 314 9 for Otsuka coefficient-based NMDS, indicating fairly strong robustness for both analyses.

In Fig. 4, Groups A and B of low palaeolatitude faunas are located on the lower left sides of the figures, whereas Groups D and E of high palaeolatitudes are placed near the upper right corners of the figures, and Group C is in between. This direction of spatial arrangement of the groups probably implies that a palaeolatitude-related thermal gradient from warm to cool environments may be underlain by Dimension 1. On the other hand, the reflection of palaeolatitude by Dimension 2 is not evident through the spatial arrangement of the groups along this axis, but this dimension appears most likely to be related to geographical separation. This is because Groups A and B are both placed in similar spatial positions with respect to Dimension 1, yet they are distanced from each other along Dimension 2. Similarly,

Fig. 3. Dendrograms of Wuchiapingian brachiopod stations derived from UPGMA based on Jaccard coefficient with cophenetic coefficient value at 0.7798 and Otsuka coefficients with cophenetic coefficient value at 0.7257. In this figure, five core groups labelled as A–E are clearly delineated at the chosen division (dashed) lines.

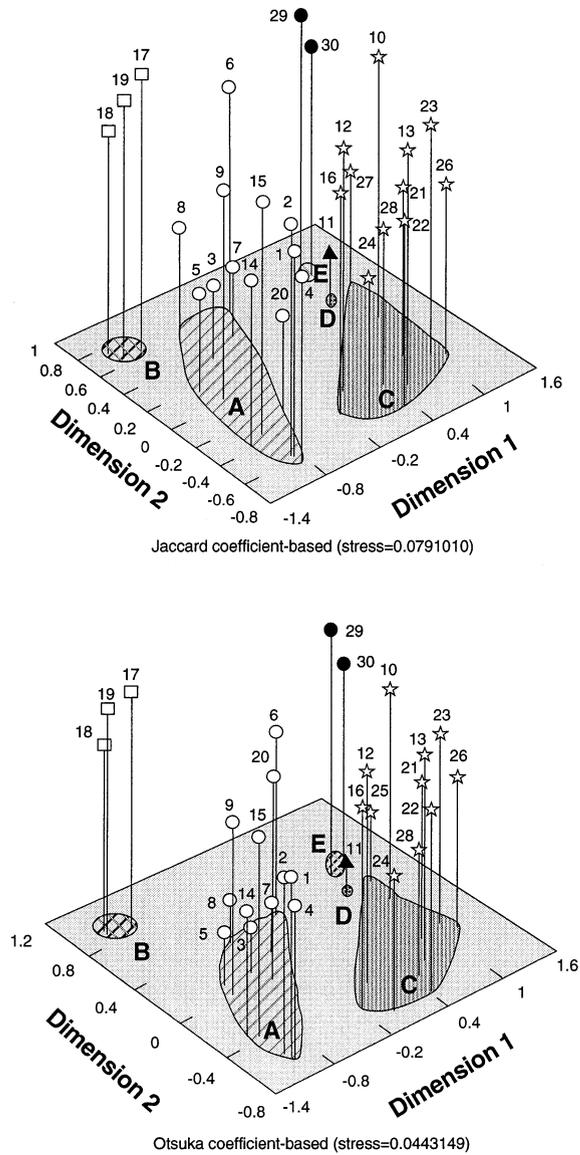


Fig. 4. An ordination plot of faunal stations on the first three principal dimensions of NMDS. Letters A, B, C, D, E correspond to those in Fig. 3. Sequential numbers (1–30) indicate faunal stations in Fig. 1 and Table 1.

Groups C and E are positioned very similarly with respect to Dimension 1 and well separated along Dimension 2. Therefore, the most plausible interpretation for the inter-group separation along Dimension 2 would be the effect of palaeogeographic distance. This conclusion becomes even

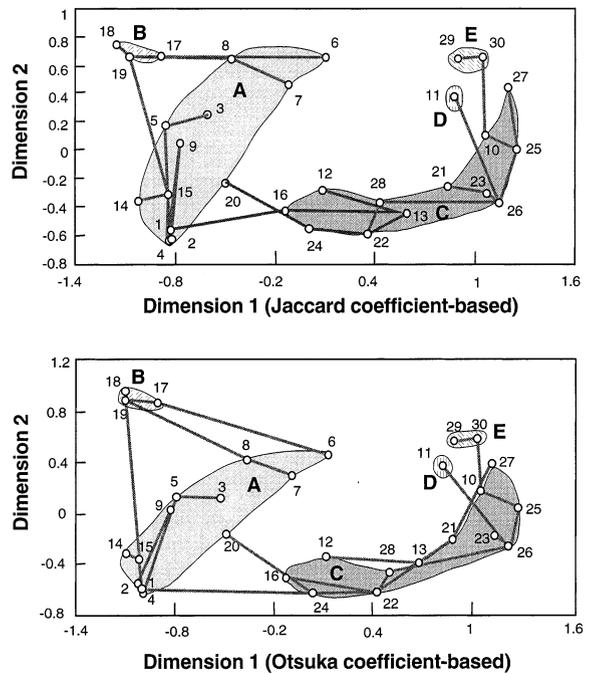


Fig. 5. An ordination plot of faunal stations on the first two principal dimensions of NMDS based on Jaccard (upper) and Otsuka (lower) coefficient, superimposed with an MST. Letters A, B, C, D, E correspond to those in Figs. 3 and 4. Sequential numbers (1–30) indicate faunal stations in Fig. 1 and Table 1.

more apparent if the groups, interpreted below as representing biotic provinces, are plotted in a Wuchiapingian global reconstruction map (see Section 4). Variation of positioning of the faunal stations along Dimension 3 is complicated, with no clear pattern. Therefore, the palaeoenvironmental significance of this axis is difficult to interpret. Nevertheless, this dimension could help to discriminate some groups that are close to each other with respect to Dimensions 1 and 2. For instance, Group D is shown very close to Group E along the first two dimensions in both NMDS scatter plots (Fig. 4), but they are readily distinguishable from each other by Dimension 3.

The patterns by the MST analysis based on Jaccard and Otsuka coefficients (Fig. 5) demonstrates broad agreement with the results of both CA and NMDS. However, there are multiple linkages between Groups A and B and between Groups A and C. On the other hand, linkages of Groups D and E are both unique to Group C,

suggesting that Group C probably represents a fauna of 'transitional nature' with affinities to both Groups D and E. This observation is also consistent with the spatial arrangement of these three groups along Dimension 3 in Fig. 4, where the vertical bars of Group C are consistently in between those of Groups D and E. The existence of multiple linkages between Groups A and B and between Groups A and C suggests that these groups, as defined by CA, are not particularly robust, and their boundaries are blurred by the presence of one or more 'outlying' stations in each of the groups. These 'outlying' stations are those that contain a significant number of genera shared only by these stations and virtually absent from all other stations of the same group or the paired groups. For instance, Group A is linked to Group C through two pairs of stations: South China (Station 1) with Salt Range (Station 16), and Southeast Pamir (Station 20) to Chitichun (southern Tibet) (Station 24) (see Jaccard coefficient-based MST in Fig. 3).

#### 4. Palaeobiogeographical interpretations

The five core groups revealed by CA and largely verified by NMDS and MST are interpreted as representing five palaeobiogeographical provinces. The provinces are plotted on the Lopingian (Late Permian) reconstruction map (Fig. 6).

##### 4.1. Cathaysian Province (Group A)

This province is represented by faunas mainly from some small blocks, including Yangtze block, Cathaysian terrane, Qaidam basin, Shan-Thai terrane, Qiangtang terrane, Indochina block, Iranian block and possibly the Inner Zone of Japan. All these tectonic units were located in the Palaeotethys, and near the palaeoequator; therefore, it is highly likely that this province was associated with shallow, warm-water masses, as also suggested by the abundant occurrences of parent-reef brachiopods (Grant, 1971) such as *Richthofenia* and many specialised lytoniids, including *Leptodus*, *Oldhamina*, permianellids etc., all of warm-water origin. In particular, the prov-

ince is characterised by the *Oldhamina*–*Orthothesina*–*Squamularia* association. Other common genera include *Tethyochonetes*, *Spinomarginifera*, *Meekella*, *Leptodus*, *Haydenella*, *Araxathyris*, *Cathaysia* and *Enteletes*, etc.

The Cathaysian Province was first defined for Permian faunas from South China by Fang (1985), and has since been extended to include parts of Japan and Indochina by Shi and Waterhouse (1990). This province has been well recognised by the earlier studies carried out by Shi and Archbold (1993, 1995a, 1996) in the Asian–western Pacific region for the Early (Cisuralian) and Middle Permian (Guadalupian), although with different palaeogeographical extents. In the late Cisuralian and particularly Guadalupian, two distinct transitional biogeographical units, Sino-Mongolian Province in the north between North China and Siberia and the Cimmerian Region in the south between Gondwanaland in the south and Cathaysialand to the north, were developed (Shi and Archbold, 1995a,b; Shi et al., 1995). The Sino-Mongolian transitional province is not recognised in the present study for the Wuchiapingian because the seaway between Siberia and North China had closed by the end of Guadalupian, resulting in the emergence of a mixed flora of both Cathaysian and Angaran affinities in the Lopingian [see Shi et al. (1995)].

In the present study, Western Yunnan, Southeast Pamir and the Alborz Mts of Iran are grouped with South China and Indochina in the expanded Cathaysian Province during the Wuchiapingian. However, these stations belonged to a separate biogeographical entity, the Cimmerian Region (Grunt and Shi, 1997), during the late Cisuralian and Guadalupian, characterised by intermingling both Gondwanan and Cathaysian elements. The Cimmerian biogeographical region stretched from the Middle East through Afghanistan and the Himalayas southeastwards to the Shan-Thai terrane and Timor, and is typified by an admixture of genera representing both the Cathaysian and Gondwanan affinities (Shi and Archbold, 1995a). This biogeographical region appeared to have reached its zenith during the early Guadalupian and diminished by the end of Guadalupian when the region was entirely incorpo-

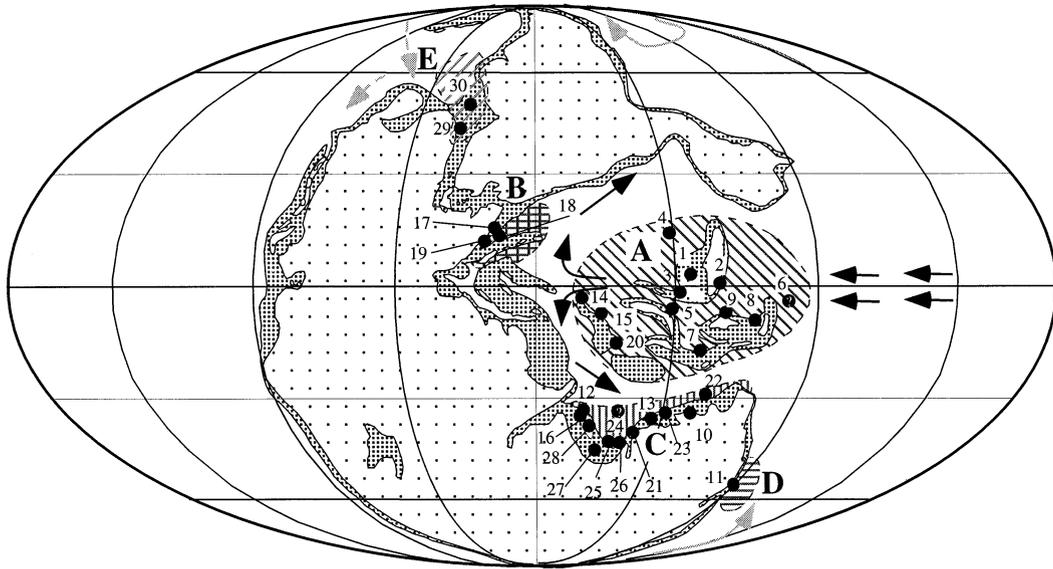


Fig. 6. Schematic reconstruction map of Wuchiapingian global palaeogeography and palaeobiogeography [with base map modified from Ziegler et al. (1997)]. The solid black arrows indicate inferred warm-water currents and the dashed arrows cool or cold-water currents.

rated into the greater Cathaysian Province (Shi and Archbold, 1998). The mechanism underlying the relatively rapid shift in provinciality for the Cimmerian continental blocks and terranes has been attributed to the interplay between terrane rifting and climatic amelioration through the Permian (Shi et al., 1995; Shi and Archbold, 1998). The Wuchiapingian faunas of these three stations are characterised by typical Cathaysian brachiopod elements such as *Oldhamina*, *Enteletes*, *Richthofenia*, *Peltichia* and *Haydenella* (Grunt and Dmitriev, 1973; Waterhouse, 1983; Shi et al., unpublished data from Western Yunnan), as well as fusulinids (e.g. Leven, 1997).

Also included in the Cathaysian Province are brachiopod faunas of the Julfa region of southern Armenia and the Alborz Mts., both of the Iranian block. This has probably resulted from the fact that these two stations share with the Cathaysian Province many genera, including, notably *Tyloplecta*, *Oldhamina*, *Peltichia*, *Haydenella* and *Edriostege*s.

The Inner Zone of Japan is tentatively classified with the Cathaysian Province in this study, but we note that its palaeobiogeographical assignment

remains unclear until its sampling efficiency is improved. The brachiopod fauna from this station is mainly composed of wide-ranging genera including *Hustedia*, *Derbyia* and *Neochonetes*. However, the presence of *Oldhamina* and *Leptodus* indicates a strong affinity with the Cathaysian Province, as do the fusulinids (Kobayashi, 1999).

#### 4.2. Western Tethyan Province (Group B)

The name Western Tethyan Province is adopted from Nakamura et al. (1985) and Shi (1996). This province includes Hungary (Station 17), Slovenia (Station 18) and West Serbia (Station 19), which are all situated in the Mediterranean region of South Europe. According to the reconstruction map of Ziegler et al. (1997), the palaeo-positions of the above three stations were in the western coast of the Palaeotethys. The brachiopod faunas from these stations are similar to those of the Cathaysian Province discussed above, with many genera in common, such as *Spinomarginifera*, *Tyloplecta*, *Leptodus*, and several widely distributed elements, including *Derbyia*, *Acosarina* and *Notothyris*. However, typical or common elements

of the Cathaysian Province such as *Oldhamina*, *Orthothena*, *Cathaysia*, *Haydenella* and *Squamularia* are lacking in this province, while *Linoproductus* and *Reticularia* are usually not present in the faunas of the Cathaysian Province during the Wuchiapingian. *Tschernyschewia* is one of the commonest genera in this province, but is very rare in the Cathaysian Province.

#### 4.3. Himalayan Province (Group C)

This province was originally named by Singh (1987) for late Early Permian to Late Permian brachiopod faunas of the greater Himalayan region. In the Wuchiapingian, this province appears to have stretched from the Salt Range of Pakistan in the west, through the Himalayan region including northern India, Nepal and southern Tibet, to probably Western Australia in the southeast. Thus defined for the Wuchiapingian, this province occupied the southern shelves of the Mesotethys [term of Metcalfe (1998)] (Fig. 7). West and northwestwards, this province likely overlapped with the Western Tethyan Province

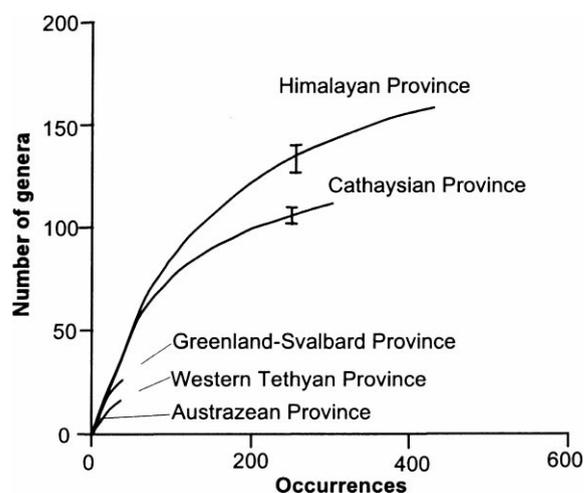


Fig. 7. Occurrences/genera rarefaction curves for different provinces to show the generic diversities regardless of sample sizes. Vertical error bars depict the deviation with 95% confidence limits based on the methodology of Raup (1991). The Western Tethyan Province, Greenland-Svalbard Province and the Austrazean Province are all under-sampled because their rarefaction curves are short and entirely/largely overlapped by the curves of the Cathaysian and the Himalayan Provinces.

through the southwestern part of the Mesotethys, facilitated by the southerly flow of the warm-water ocean currents deflected from the equatorial currents (Fig. 6). However, this suggestion cannot be substantiated at present owing to the lack of brachiopod data of Wuchiapingian age from the Middle East region.

Brachiopod faunas of the Himalayan Province are complex. In the southern part (e.g. Western Australia, southern Tibet, Spiti), Wuchiapingian brachiopods are composed of typical Gondwanan/antitropical genera such as *Taeniothaerus*, *Fusispirifer*, *Neospirifer*, *Retimarginifera*, *Costiferina* and *Spiriferella*. In contrast, faunas from more northerly stations (e.g. Salt Range, Karakorum and Kashmir, Timor, and probably Chitichun as well) are intermingled with some Cathaysian genera such as *Enteletes*, *Spinomarginifera* and *Leptodus*. This, apparently palaeolatitude-related variation in faunal composition within the Himalayan Province, suggests that faunal migration across the Mesotethys occurred during the Wuchiapingian. The mixed nature in faunal composition within at least the northern portion of the Himalayan Province is reminiscent of the characteristics of the mid-Permian (Artinskian–Capitanian) transitional faunas of the Cimmerian Region, but the mechanisms of their faunal intermingling are apparently very different. As already mentioned, the origin of the transitional Cimmerian biogeographical region is most likely related to the rifting, followed by rapid northward drifting of the Cimmerian microcontinents, at times (especially in the middle Cisuralian) accompanied and enhanced by climatic amelioration (Shi, 2000). On the other hand, we consider the presence of Cathaysian elements in the northern Himalayan Province during the Wuchiapingian as a consequence of southerly invasion of Cathaysian faunas, initiated by climatic amelioration across Gondwanaland in response to its continued northward drifting through the Permian.

#### 4.4. Austrazean Province (Group D)

This province is composed of a single station from the Takitimu Mt of New Zealand (Station 11). The Wuchiapingian fauna from this station is

characterised by *Marinurnula*, *Notospirifer*, *Plekonella*, *Spinomartinia*, *Terrakea* and *Tomioopsis*. The recognition of this group (Group D) by CA readily confirms to the continued presence of Austrazean Province (Archbold, 1983) along the southeastern coast of Gondwanaland during the Lopingian (Fig. 6). Our interpretation of the New Zealand Wuchiapingian brachiopod fauna is based on fossil identification and overall faunal composition rather than stratigraphic position within a sequence. Since the original descriptive work of the New Zealand faunas (e.g. Waterhouse, 1982), mapping has established that they were collected from allochthonous blocks or out-of-sequence units within the Dun Mountain–Maitai Terrane and the Brook Street Terrane in New Zealand (Landis et al., 1999).

#### 4.5. Greenland–Svalbard Province (Group E)

Greenland and Svalbard Islands (Spitsbergen) constitute a distinct Boreal-type province in the north Arctic region during the Lopingian. The term Greenland–Svalbard Province proposed by Grunt and Shi (1997), initially for the Cisuralian and Guadalupian brachiopod faunas, is maintained herein to accommodate the Wuchiapingian brachiopod faunas of Group E. This province is characterised by the typical Boreal-type *Kochiproductus*–*Yakovlevia*–*Paeckelmanella* association. *Kochiproductus* and *Yakovlevia* have never been recorded from the Palaeoequatorial or Gondwanan Realms. The only southern hemispheric record of ‘*Yakovlevia*’ (= *Muirwoodia*) from Chile (Minato and Tazawa, 1977) has been discredited (Shi, 1995). In addition, some genera of antitropical distribution, such as *Waagenoconcha* and *Spiriferella*, and several cosmopolitan genera, including *Streptorhynchus*, *Derbyia* and *Cleiothyridina*, are also present in this province. Genera of typical warm water aspect are totally absent in this province.

Included in this province are brachiopods from the upper part of the Kapp Starostin Formation of Svalbard (Spitsbergen). Since the age of these brachiopods remains controversial, a brief discussion is appropriate here. Nakamura et al. (1987, 1992) suggested an age range from Ufimian (=

Roadian) to the Djulfian for the Kapp Starostin Formation. However, Stemmerik (1988) argued that the overwhelmingly ecological control on the distribution of brachiopod taxa makes such a broad age assignment highly suspect, thus he regarded the Kapp Starostin Formation in very general terms as Kazanian–early Tatarian (Late Permian). This age assignment was further revised and narrowed to be within Djulfian to Dorashamian (=Changhsingian) by means of carbon isotope stratigraphical studies of the Kapp Starostin Formation (Gruszczynski et al., 1989; Malkowski et al., 1989). Our study shows that the brachiopod faunas of the upper part of the Kapp Starostin Formation and the Folvik Creek Group in East Greenland are strongly close to each other, which may also suggest an overall correlation between the two units, as has already pointed out by Stemmerik (1988). The close links in the brachiopod faunas of East Greenland and Spitsbergen may also imply that throughout the Late Permian a narrow seaway extended from the Boreal Ocean southwards between the Russian and North American Platforms.

## 5. Discussion

### 5.1. Biogeographical determinants

The distribution of brachiopod faunas and province seems to have been primarily controlled by the variation of palaeolatitude (Fig. 6). This interpretation has been borne out from NMDS analysis, as already discussed. However, geographical barrier and ocean circulation may also have played a significant role in the brachiopod distribution. The Western Tethyan Province was clearly affected by the inferred ocean currents from east through the Cathaysian Province, hence resulting in relatively strong similarities of brachiopod faunas between them. The Himalayan Province was primarily separated from all other provinces by both a latitude-related thermal gradient and also an east–west Mesotethys seaway. New Zealand constitutes an independent Austrazean Province, primarily controlled by a cool to cold-

water regime derived from the cold currents from the South Pole (Fig. 6).

### 5.2. Diversity variation of faunal provinces

As a measure to compare the degree of sampling intensity and generic diversity patterns between the five recognised provinces, we employed rarefaction analysis much in the same manner as Raup (1975, 1991). It is clear from Fig. 7 that the Western Tethyan Province, Greenland–Svalbard Province and the Austrazean Province are all under-sampled because their rarefaction curves are short and far below expected truncation or platform level. One possibility for this phenomenon is that these provinces each contain only a few stations (two for the Greenland–Svalbard Province, one for the Austrazean Province, and three for the Western Tethyan Province); therefore, their real diversity levels may have been underestimated. In these circumstances, comparison of diversity patterns between these provinces and between these and the other two provinces (the Cathaysian and Himalayan Provinces) would be inappropriate.

On the other hand, the rarefaction curves of the Himalayan and Cathaysian Provinces do indicate that they are both sufficiently sampled for mutual comparison of generic diversity patterns. Both provinces contain the same number of stations, 12 in each province, yet the Himalayan Province tends to demonstrate a considerably higher generic diversity. This was somehow unexpected considering that the Himalayan Province is thought to be located in the southern temperate zone and the Cathaysian Province in the palaeoequatorial belt during the Wuchiapingian (Fig. 6). This diversity trend between temperate and tropical provinces is also at odds with the widely accepted notion that biotic diversity correlates inversely with latitude settings (Fisher, 1960). However, reversed diversity trend with respect to latitude gradient has also been noted previously. For instance, in a study of the Late Artinskian–Early Kungurian brachiopod faunas of the Asian–western Pacific region, Shi and Archbold (1995b) also discovered that two temperate provinces, the Cimmerian Province in the south and the Sino-Mongolian Province in the north, also exhibited

considerably higher generic diversity than that of the palaeotropical Cathaysian Province. In a more extensive study, Shi and Shen (2000) applied polynomial regression analysis to the relationship of brachiopod generic diversity of six Permian intervals with palaeolatitudes. They found that in no case was there a restricted inverse correlation between generic diversity and palaeolatitude gradient. In most cases, a polymodal pattern was observed, rather than the simple ‘bell-shaped’ classic, low latitude, high diversity ‘model’.

Understanding of the above-noted reversed diversity trend is limited at present. There may have been a number of factors contributing to the occurrence of this phenomenon, including sampling bias, analytical procedures and genuine biological and biogeographical controls. One plausible mechanism for deriving a higher generic diversity at temperate zones is the fact that temperate settings are mesothermal and, as such, would draw taxa of greater adaptabilities from adjacent tropical and temperate/polar provinces to intermingle with each other and with their own endemic taxa. This process at the end would result in the formation of a ‘mixed’ fauna consisting of endemic taxa, wide-ranging taxa and taxa characteristic of, but not endemic to, adjacent provinces. The Himalayan Province in the present study seems to fit well into this scenario. It contains, particularly in its northern portion, immigrants from the Cathaysian Province and also taxa that are common in the Austrazean Province further to the southeast. In addition, the province also embraces several unique genera, such as *Biplatyconcha*, *Himathyris* and *Lammimargus* (Waterhouse, 1978).

### 5.3. Asymmetrical distribution of provinces with respect to palaeolatitudes

It is clear from Fig. 6 that the distribution of the recognised marine provinces on the shelves of eastern Pangea and within the Tethys (both Palaeotethys and Mesotethys), though generally parallel to latitude-related zonation, is asymmetrical with respect to the palaeoequator. This is so because there is no counterpart of the Himalayan Province to the north of the Cathaysian Province. Failure to recognise this province in the eastern

part of the Northern Hemisphere is due to the absence of brachiopod data of Wuchiapingian age. At present, it is not known whether this is a result of loss of habitats for brachiopods or insufficient sampling in this area for Wuchiapingian brachiopods. The former is likely because the Sino-Mongolian seaway, which during the Guadalupian hosted a transitional fauna of mixed Cathaysian and Boreal elements, had vanished by the end of the Guadalupian due to the collision and terminal uplifting between the North China and Mongolian blocks (Zorin, 1999). It is interesting to note that, in the Lopingian, the flora of the border region between North China and Mongolia developed a distinctively mixed Cathaysian/Angaran flora (Wang, 1985; Li and Wu, 1995). Although no marine faunas of Wuchiapingian age are found along the border region, the mixed nature of the Late Permian flora is comparable to the faunal admixture of the Himalayan Province in the Southern Hemisphere. Shi et al. (1995) have suggested that zones of biotic intermingling, like those of the Himalayan Province and the mixed Angaran/Cathaysian flora, imply mesothermal or temperate climatic regime.

#### 5.4. Change of marine provinciality of the Iranian block through the Middle and Late Permian

Our study shows that during the Wuchiapingian the Iranian block was assembled together with other Cimmerian continents and eastern Palaeotethyan terranes in the same biogeographical unit, the Cathaysian Province (see Fig. 6). This biogeographical unification with the Cathaysian Province probably commenced in the Late Guadalupian (Capitanian), as evidenced by the distributional pattern of *Cryptospirifer* Huang. This genus is one of the key index fossils for the Wordian of South China (Sheng and Jin, 1994). However, its occurrences in Iran and central Turkey (Nakamura and Golshani, 1981) are slightly younger, in the Capitanian. This age difference may imply a possible westerly migration route for the genus during the middle and late Middle Permian.

The late Lopingian (Changhsingian) brachiopod faunas of the Iranian block, on the other hand, exhibits stronger faunal affinity with the

Western Tethyan Province than to the Cathaysian Province (Shen et al., 2000a). Therefore, there was a shift in marine provinciality for the Iranian block from the Wuchiapingian to the Changhsingian: changing from the Cathaysian Province to the Western Tethyan Province. This change of marine provinciality could be explained by the block's position within the Palaeotethys and rifting through the Lopingian. Unlike all other microcontinents of the Cimmerian continental strip (Sengor, 1979), the Iranian block was probably located on the western end of this continental strip and more northerly located than other Cimmerian components to the south and southeast. Therefore, naturally, when the Cimmerian continental strip drifted to the north as a whole through the Permian, as has been proposed by many workers (e.g. Nakamura et al., 1985), the Iranian block would have warmed up earlier and more rapidly than the rest of the Cimmerian continental strip, resulting in a distinctive path of biogeographical transition, from Gondwana-affiliated fauna through a transitional stage to a typical warm-water fauna. Probably by the Changhsingian, the Iranian block had reached the vicinity of the western Palaeotethys, allowing the incorporation of its fauna with other Western Palaeotethyan blocks to form a unified Western Tethyan Province.

## 6. Conclusions

Multivariate quantitative analysis reveals that five marine biotic provinces appear to have existed during the Wuchiapingian (early Late Permian) in terms of the distributions of brachiopod faunas, of which the Cathaysian Province is composed of isolated or semi-isolated islands distributed in the Palaeotethys. The other four provinces occurred on the continental shelves of Pangea. This palaeobiogeographical pattern is notably different from that of the Guadalupian (Middle Permian) time. The well-recognised southern transitional Cimmerian Province during the Guadalupian has been incorporated into the Cathaysian Province as a result of the interplay of terrane rifting and climatic amelioration. The Himalayan Province proximal to the northern Gondwanaland became the successor of the Cimmerian Province during

the Wuchiapingian. The Guadalupian northern transitional Sino-Mongolian Province vanished during the Wuchiapingian in the wake of the collision between the North China and Mongolian blocks and, as a consequence, was replaced by a distinct Angaran/Cathaysian mixed flora zone during the Lopingian.

The Wuchiapingian palaeobiogeography shown by brachiopod faunas appears to be mainly controlled by a latitude-related thermal gradient, while geographic distance and ocean circulation may also be important biogeographical barriers to brachiopod exchange during the Wuchiapingian.

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### References

- Archbold, N.W., 1983. Permian marine invertebrate provinces of the Gondwana Realm. *Alcheringa* 7, 59–73.
- Archbold, N.W., 1988. Permian Brachiopoda and Bivalvia from Sahul Shoals No. 1, Ashmore block, northwestern Australia. *Proc. R. Soc. Victoria* 100, 33–38.
- Archbold, N.W., 1993. A zonation of the Permian brachiopod faunas of western Australia. In: Findlay, R.H., Unrug, R., Banks, M.R., Veevers, J.J. (Eds.), *Gondwana Eight—Assembly Evolution and Dispersal*. A.A. Balkema, Rotterdam, pp. 313–321.
- Belbin, L., 1992. PATN, Pattern analysis package. Division of Wildlife and Ecology, CSIRO, Canberra, program and technical reference, 235pp.
- Broili, F., 1916. Die Permischen brachiopoden von Timor. *Palaeontol. Timor* 7 (12), 1–104.
- Bunopas, S., 1981. Paleogeographic history of western Thailand and adjacent parts of southeast Asia: a plate tectonic interpretation. In: *Geological Survey Paper 5*. Department of Mineral Resources, Bangkok. 180 pp.
- Cheetham, A.H., Hazel, J.E., 1969. Binary (presence-absence) similarity coefficients. *J. Paleontol.* 43 (5), 1130–1136.
- Diener, C., 1897a. Himalayan fossils. The Permocarboniferous fauna of Chitichun No. 1. *Mem. Geol. Surv. Ind. Palaeontol. Ind. Ser. 15* 1 (3), 1–105.
- Diener, C., 1897b. Himalayan fossils. The Permian fossils of the *Productus* Shales of Kumaon and Gurhwal. *Mem. Geol. Surv. India Palaeontol. Ind. Ser. 15* 1 (4), 1–54.
- Diener, C., 1899. Himalayan fossils. Anthracolithic fossils of Kashmir and Spiti. *Mem. Geol. Surv. Ind. Palaeontol. Ind. Ser. 15* 1 (2), 1–95.
- Dunbar, C.O., 1955. Permian brachiopod faunas of central East Greenland. *Medd. Groenl.* 110 (3), 1–169.
- Erwin, D.H., 1994. The Permo-Triassic extinction. *Nature* 367, 231–236.
- Fang, Z.J., 1985. A preliminary investigation into the faunal province. *Acta Palaeontol. Sin.* 24 (3), 344–348.
- Fisher, A.G., 1960. Latitudinal variations in organic diversity. *Evolution* 14, 64–81.
- Gaetani, M., Le Fort, P., Tanoli, S., Angiolini, L., Nicora, A., Sciunnach, D., Khan, A., 1996. Reconnaissance geology in Upper Chitral, Baroghil and Karambar district (northern Karakorum, Pakistan). *Geol. Rundsch.* 85, 683–704.
- Garzanti, E., Angiolini, L., Sciunnach, D., 1996. The Permian Kuling Group (Spiti, Lahaul and Zaskar, NW Himalaya): sedimentary evolution during rift/drift transition and initial opening of Neo-Tethys. *Riv. Ital. Paleontol. Stratigr.* 102 (2), 175–200.
- Gower, J.C., Ross, G.J.S., 1969. Minimum spanning trees and single linkage cluster analysis. *Appl. Stat.* 1, 54–64.
- Grant, R.E., 1971. Brachiopods in the Permian reef environment of West Texas. In: *1st North American Paleontological Convention, Part J*, 1444–1481.
- Grunt, T.A., Dmitriev, V.Yu., 1973. Permskie brachiopody Pamira (Permian Brachiopoda of the Pamir). *Akad. Nauk SSSR Paleontol. Inst. Trudy* 136, 8–209.
- Grunt, T.A., Shi, G.R., 1997. A hierarchical framework of Permian global marine biogeography. *Proceedings of the 30th International Geological Congress. Palaeontol. Hist. Geol.* 12, 2–17.
- Gruszczynski, M., Halas, S., Hoffman, A., Malkowski, K., 1989. A brachiopod calcite record of the oceanic carbon and oxygen isotope shifts at the Permian/Triassic transition. *Nature* 337, 64–68.
- Hamlet, B., 1928. Permische brachiopoden, Lamellibranchiaten und gastropoden von Timor. *Jaarb. Mijnwezen* 562, 1–109.
- Hattori, I., Hirooka, K., 1979. Paleomagnetic results from Permian Greenstones in central Japan and their geologic significance. *Tectonophysics* 57, 211–235.
- Hu, S.Z., 1989. Discovery of brachiopods from coal-bearing member of Lungtan Formation and its significance. A new understanding of Lungtan Formation coal-forming environment. *Acta Palaeontol. Sin.* 28 (4), 474–479.
- Huang, K.N., Opdyke, N.D., Peng, X.J., Li, J.G., 1992. Paleomagnetic results from the Upper Permian of the eastern Qiangtang Terrane of Tibet and their tectonic implications. *Earth Planet. Sci. Lett.* 111, 1–10.
- Imamura, S., 1953. New occurrence of *Lyttonia* from the Environs of Hiroshima, Japan. *Hiroshima Univ. J. Sci. Ser. C* 1 (3), 11–16.
- Iranian-Japanese Working Group, 1981. The Permian and Lower Triassic Systems in Abadeh Region, Central Iran. *Mem. Fac. Sci. Kyoto Univ. Ser. Geol. Mineral.* 47 (2), 66–133.

- Isozaki, Y., 1997. Timing of Permian–Triassic anoxia. *Science* 277, 1748–1749.
- Jin, Y.G., Sun, D.L., 1981. Paleozoic brachiopods from Xizang. In: Nanjing Institute of Geology and Palaeontology, (Eds.), *Palaeontology of Xizang part III*. Science Press, Beijing, pp. 127–176.
- Jin, Y.G., Zhang, J., Shang, Q.H., 1994. Two phases of the end-Permian mass extinction. In: *Canadian Society of Petroleum Geologists Memoir* 17., 813–822.
- Jin, Y.G., Wardlaw, B.R., Glenister, B.F., Kotlyar, G.V., 1997. Permian chronostratigraphic subdivisions. *Episodes* 20, 10–15.
- Klootwijk, C.T., 1984. A review of Indian Phanerozoic palaeomagnetism: implications for the Indian–Asia collision. *Tectonophysics* 105, 331–353.
- Kobayashi, F., 1999. Tethyan uppermost Permian (Dzhulfian and Dorashamian) foraminiferal faunas and their paleogeographic and tectonic implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 150, 279–307.
- Kotlyar, G.V., Zakharov, Yu.D., Koczyrkevich, B.V., Kropacheva, G.S., Rostovcev, K.O., Chedija, I.O., Vuks, G.P., Guseva, E.A., 1983. *Pozdnepermiskii Etap Evoliutsii Organicheskogo Mira Dzhulfinskii i Dorashamskii Iarusy SSSR (Evolution of the Latest Permian Biota–Dzhulfian and Dorashamian Regional Stages in the USSR)*. Nauka, Leningrad. 200 pp
- Landis, C.A., Campbell, H.J., Aslund, T., Cawood, P.A., Douglas, A., Kimbrough, D.L., Pillai, D.D.L., Raine, J.I., 1999. Permian–Jurassic strata at Productus Creek, Southland, New Zealand: implications for terrane dynamics of the eastern Gondwanaland margin. *N.Z. J. Geol. Geophys.* 42 (2), 255–278.
- Leven, E.J., 1997. Permian stratigraphy and Fusulinida of Afghanistan with their palaeogeographic and paleotectonic implications. In: *The Geological Society of America Special paper* 316. 134 pp.
- Li, X.X., Wu, X.Y., 1995. Late Paleozoic phytogeographic provinces in China and its adjacent regions. In: Wnuk, C., Pfefferkorn, H.W. (Eds.), *Palaeozoic Phytogeography*, *Rev. Palaeobot. Palynol.* 90, 1–2, 41–62.
- Li, Z.S., Zhan, L.P., Zhu, X.F., Zhang, J.H., Huang, H.Q., Xu, D.Y., Yan, Z., Li, H.M., 1989. Study on the Permian–Triassic biostratigraphy and event stratigraphy of northern Sichuan and southern Shaanxi. In: *PRC Ministry of Geology and Mineral Resources, Geological Memoir, Ser. 2 vol. 9*. Geological Publishing House, Beijing. 435 pp
- Liao, Z.T., 1980. Upper Permian brachiopods from western Guizhou. In: Nanjing Institute of Geology and Palaeontology, (Eds.), *Stratigraphy and Paleontology of the Upper Permian Coal-Bearing Formation in Western Guizhou and Eastern Yunnan*. Science Press, Beijing, pp. 241–277.
- Liao, Z.T., 1987. Paleocological characters and stratigraphic significance of silicified brachiopods of the Upper Permian from Heshan, Laibin, Guangxi. In: Nanjing Institute of Geology and Palaeontology, (Eds.), *Stratigraphy and Palaeontology of Systemic Boundaries in China, Permian–Triassic Boundary*. Nanjing University Press, Nanjing, pp. 81–125.
- Malkowski, K., Gruszczynski, M., Hoffman, A., Halas, S., 1989. Oceanic stable isotope composition and a scenario for the Permo-Triassic crisis. *Hist. Biol.* 2, 289–309.
- Matsumoto, R., Zheng, Z., Kakuwa, Y., Hamdi, B., Kimura, H., 1995. Preliminary results of paleomagnetic study on the Cambrian to the Triassic rocks of the Alborz, Northeast Iran. *J. Fac. Sci. Univ. Tokyo, Sect. 2 Geol. Mineral. Geogr. Geophys.* 22 (4), 233–249.
- Metcalfe, I., 1998. Palaeozoic and Mesozoic geological evolution of the SE Asian region: multidisciplinary constraints and implications for biogeography. In: Hall, R., Holloway, J.D. (Eds.), *Biogeography and Geological Evolution of SE Asia*. Backbuys, Leiden, pp. 25–41.
- Minato, M., Tazawa, J., 1977. Fossils of the Huentelauquen Formation at the locality F. Coquimbo Province, Chile. In: Ishikawa, T., Aguirre, L. (Eds.), *Comparative Studies on the Geology of the Circum-Pacific Orogenic Belt in Japan and Chile, 1st report*. Japan Society for the Promotion of Science, Tokyo, pp. 95–112.
- Nakamura, K., Golshani, F., 1981. Notes on the Permian brachiopod genus *Cryptospirifer*. *J. Fac. Sci. Hokkaido Univ. Ser. 4* 20, 67–77.
- Nakamura, K., Shimizu, D., Liao, Z.T., 1985. Permian palaeobiogeography of brachiopods based on the faunal provinces. In: Nakazawa, K., Dickins, J.M. (Eds.), *The Tethys, her Paleogeography and Paleobiogeography from Paleozoic to Mesozoic*. Tokai University Press, Tokyo, pp. 185–198.
- Nakamura, K., Kimura, G., Winsnes, T.S., 1987. Brachiopod zonation and age of the Permian Kapp Starostin Formation (central Spitsbergen). *Polar Res.* 5, 207–219.
- Nakamura, K., Tazawa, J., Kumon, F., 1992. Permian brachiopods of the Kapp Starostin Formation, west Spitsbergen. In: Nakamura, K. (Ed.), *Investigations on the Upper Carboniferous–Upper Permian Siccation of West Spitsbergen 1989–1991*. Hokkaido University, Saporu, pp. 77–95.
- Nakazawa, K., Kapoor, H.M., Ishii, K., Bando, Y., Okimura, Y., Tokuoka, T., 1975. The Upper Permian and the Lower Triassic in Kashmir, India. *Kyoto Univ. Fac. Sci. (Geol. Mineral.) Mem.* 42 (1), 1–106.
- Pesic, L., Ramovs, A., Sremac, J., Pantic-Prodanovic, S., Filipovic, I., Kovacs, S., Pelikan, P., 1986. Upper Permian deposits of the Jadar region and their position within the Western Paleotethys. In: Cassinis, G. (Ed.), *Permian and Permian–Triassic boundary in the South-Alpine segment of the Western Tethys, and additional regional reports*, *Societa Geologica Italiana Memorie* 34., 211–219.
- Qinghai Stratigraphic Group, 1980. *Regional Stratigraphic Table of Northwestern China, Qinghai Volume*. Geological Publishing House, Beijing. 276 pp
- Raup, D.M., 1975. Taxonomic diversity estimation using rarefaction. *Palaeobiology* 1, 333–342.
- Raup, D.M., 1991. The future of analytical paleobiology. In: Gilinsky, N.L., Signor, P.W. (Eds.), *Analytical Paleobiology: Short Courses in Paleontology no. 4*. Paleontological Society, Knoxville, pp. 207–216.

- Reed, F.R.C., 1944. Brachiopoda and Mollusca from the *Productus* Limestones of the Salt Range. Geol. Survey Ind. Mem. Palaeontol. Ind. 23 (2), 1–678.
- Ruzhentsev, V.E., Sarytcheva, T.G. (Eds.), *Razvitie i Smena Morskikh Organizmov na Rubezhe Paleozoiia i Mezozoiia* (The development and change of marine organisms at the Palaeozoic–Mesozoic boundary). Akad. Nauk SSSR Paleontol. Inst. Trudy 108 1965., 209–232.
- Saidi, A., Brunet, M.F., Ricou, L.E., 1997. Continental accretion of the Iran Block to Eurasia as seen from Late Palaeozoic to Early Cretaceous subsidence curves. *Geodinam. Acta* 10 (5), 189–208.
- Schreter, Z., 1963. A Buekkhegyseg Felso–Permi Brachiopodai (Die Brachiopoden aus dem oberen Perm des Buekkgebirges in Nordungarn). *Geol. Hung. Ser. Palaeontol.* 28, 79–179.
- Scotese, C.R., McKerrow, W.S., 1990. Revised world maps and introduction. In: McKerrow, W.S., Scotese, C.R. (Eds.), *Palaeozoic Palaeogeography and Biogeography*. Geological Society Memoir 12., 1–21.
- Sengor, A.M.C., 1979. Mid-Mesozoic closure of Permo-Triassic Tethys and its implications. *Nature* 279, 590–593.
- Sestini, F.N., Glaus, M., 1966. Brachiopods from the Upper Permian Nesen Formation (North Iran). *Riv. Ital. Paleontol. Stratigr.* 72 (4), 887–931.
- Shang, Q.H., Jin, Y.G., 1997. Quantitative evaluation on paleozoogeographic evidences of Permian brachiopods. *Acta Palaeontol. Sin.* 36 (1), 93–121.
- Shen, S.Z., Shi, G.R., 1996. Diversity and extinction patterns of Permian brachiopoda of South China. *Hist. Biol.* 12, 93–110.
- Shen, S.Z., Archbold, N.W., Shi, G.R., 2000a. Changhsingian (Late Permian) brachiopod palaeobiogeography. *Hist. Biol.* in press
- Shen, S.Z., Archbold, N.W., Shi, G.R., Chen, Z.Q., 2000b. Permian brachiopods from the Selong Xishan section, Xizang (Tibet), China, part 1: stratigraphy, Strophomenida, Productida and Rhynchonellida. *Geobios.* in press
- Sheng, J.Z., Jin, Y.G., 1994. Correlation of Permian deposits in China. In: Jin, Y.G., Utting, J., Wardlaw, B.R. (Eds.), *Paleontology and Stratigraphy, Palaeoworld 4. Permian Stratigraphy, Environments and Resources vol. 1*. Nanjing University Press, Nanjing, pp. 14–113.
- Shi, G.R., 1993. Multivariate data analysis in palaeoecology and palaeobiogeography — a review. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 105, 199–234.
- Shi, G.R., 1995. The Late Palaeozoic brachiopod genus *Yakovlevia* Fredericks, 1925 and the *Yakovlevia transversa* Zone, northern Yukon Territory, Canada. *Proc. R. Soc. Victoria* 107 (1), 51–71.
- Shi, G.R., 1996. A model of quantitative estimate of marine biogeographic provinciality. *Acta Geol. Sin.* 70 (4), 351–360.
- Shi, G.R., 2000. Terrane rafting enhanced by contemporaneous climatic amelioration as a mechanism of biogeographical vacariance: Permian marine biogeography of the Shan–Thai terrane in SE Asia. *Hist. Biol.* in press
- Shi, G.R., Archbold, N.W., 1993. Distribution of the Asselian to Tastubian (Early Permian) brachiopod faunas in the circum-Pacific region. In: Association of Australasian Palaeontologists Memoir 15., 343–351..
- Shi, G.R., Archbold, N.W., 1995a. Palaeobiogeography of Kazanian–Midian (Late Permian) western Pacific brachiopod faunas. *J. SE Asian Earth Sci.* 12, 1–2, 129–141.
- Shi, G.R., Archbold, N.W., 1995b. A quantitative analysis on the distribution of Baigendzinian–Early Kungurian (Early Permian) brachiopod faunas in the western Pacific region. *J. SE Asian Earth Sci.* 12 (3), 189–205.
- Shi, G.R., Archbold, N.W., 1996. A quantitative palaeobiogeographical analysis on the distribution of Sterlitamakian–Aktastinian (Early Permian) western Pacific brachiopod faunas. *Hist. Biol.* 11, 101–123.
- Shi, G.R., Archbold, N.W., 1998. Permian marine biogeography of SE Asia. In: Hall, R., Holloway, J.D. (Eds.), *Biogeography and Geological Evolution of SE Asia*. Backbuys, Leiden, pp. 57–72.
- Shi, G.R., Grunt, T.A., 2000. Permian Gondwana-Boreal anti-tropicality with special reference to brachiopod faunas. *Palaeogeog., Palaeoclimatol., Palaeoecol.* 155, 239–263.
- Shi, G.R., Shen, S.Z., 1997. A Late Permian brachiopod fauna from Selong, Southern Xizang (Tibet), China. *Proc. R. Soc. Victoria* 109 (1), 37–56.
- Shi, G.R., Shen, S.Z., 2000. Asian–western Pacific Permian Brachiopoda in space and time: biogeography and extinction patterns. In: Yin, H.F., Dickins, J.M., Shi, G.R., Tong, J.N. (Eds.), *Permian-Triassic evolution of Tethys and Circum-Pacific and Marginal Gondwanan*. Elsevier, Amsterdam, pp. 327–352.
- Shi, G.R., Waterhouse, J.B., 1990. Sakmarian (Early Permian) brachiopod biogeography and constrains on the timing of terrane rifting drift and amalgamation in SE Asia with reference to the nature of Permian Tethys. *Proceedings of the Pacific Rim Congress 90 vol. 2*. Australasian Institute of Mining and Metallurgy, Melbourne.
- Shi, G.R., Archbold, N.W., Zhan, L.P., 1995. Distribution and characteristic of mixed (transitional) mid-Permian (Late Artinskian–Ufimian) marine faunas in Asia and their palaeogeographical implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 114, 241–271.
- Shi, G.R., Shen, S.Z., Tong, J.N., 1999. Two discrete possibly unconnected Permian marine mass extinctions. In: Yin, H.F., Tong, J.N. (Eds.), *Proceedings of the International Conference on Pangea and the Palaeozoic–Mesozoic Transition*. China University of Geosciences Press, Wuhan, pp. 148–151.
- Shimizu, D., 1981. Upper Permian brachiopod fossils from Guryul Ravine and its spur three kilometers of Barus. *Palaeontol. Ind. N. Ser.* 46, 67–85.
- Singh, T., 1987. Permian biogeography of the India subcontinent with special reference to the marine faunas. In: *Gondwana Six: Stratigraphy, Sedimentology and Palaeontology*. Geophysical Monograph, American Geophysical Union 41., 239–249..
- Stanley, S.M., Yang, X.N., 1994. A double mass extinction at the end of the Paleozoic Era. *Science* 266, 1340–1344.

- Stehli, F.G., 1970. A test of the Earth's magnetic field during Permian time. *J. Geophys. Res.* 75 (17), 3325–3342.
- Stehli, F.G., Grant, R.E., 1971. Permian brachiopods from Axel Heiberg Island, Canada, and an index of sample efficiency. *J. Paleontol.* 45 (3), 502–521.
- Stemmerik, L., 1988. Discussion: Brachiopod zonation and age of the Permian Kapp Starostin Formation (central Spitsbergen). *Polar Res.* 6, 179–180.
- Tien Chi-Thuan, T.T., 1962. Les brachiopodes permien de Cam-lô (Province de Quang-Tri). *Ann. Fac. Sci. Univ. Saigon* 1962, 485–498.
- Vai, G.B., 1998. Field trip through the southern Alps: an introduction with geologic settings, palaeogeography and Palaeozoic stratigraphy. *Giorn. Geol. Ser. 3* (60), 1–38.
- Waagen, W., 1883. Salt Range fossils. I. Productus-Limestone fossils. *Geol. Sur. Ind. Mem. Palaeontol. Ind. Ser. 13* 4 (2), 391–546.
- Waagen, W., 1884. Salt Range fossils. I. Productus-Limestone fossils. *Geol. Sur. Ind. Mem. Palaeontol. Ind. Ser. 13* 4 (4), 611–728.
- Waagen, W., 1885. Salt Range fossils. I. Productus-Limestone fossils. *Geol. Sur. Ind. Mem. Palaeontol. Ind. Ser. 13* 4 (5), 729–770.
- Wang, G.P., Liu, Q.Z., Jin, Y.G., Hu, S.Z., Liang, W.P., Liao, Z.T., 1982. Brachiopoda. In: Nanjing Institute of Geology and Mineral Resources (Eds.), Late Paleozoic. Paleontological Atlas of Southeast China vol. 2. Geological Publishing House, Beijing, pp. 186–256.
- Wang, Z.Q., 1985. Palaeovegetation and plate tectonics: palaeophytogeography of North China during Permian and Triassic times. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 49, 25–45.
- Waterhouse, J.B., 1964. Permian brachiopods of New Zealand. *Geol. Surv. N. Z. Palaeontol. Bull.* 35, 1–287.
- Waterhouse, J.B., 1966. Lower Carboniferous and Upper Permian brachiopods from Nepal. *Geol. Bundesanst. Jahrb.* 12, 5–99.
- Waterhouse, J.B., 1970. The world significance of New Zealand Permian stages. *R. Soc. N. Z. (Geol.) Trans. (Earth Sci.)* 7 (7), 97–109.
- Waterhouse, J.B., 1978. Permian Brachiopoda and Mollusca from north-west Nepal. *Palaeontogr. Abt. A* 160, 1–6, 1–175.
- Waterhouse, J.B., 1982. New Zealand Permian brachiopod systematics, zonation and paleoecology. In: New Zealand Geological Survey Paleontological Bulletin 48. 158 pp.
- Waterhouse, J.B., 1983. A Late Permian *lyttoniidi* fauna from northwest Thailand. *Pap. Dept. Geol. Univ. Queensl.* 10 (3), 111–153.
- Waterhouse, J.B., Gupta, V.J., 1983. An Early Dzhulfian (Permian) brachiopod faunule from Upper Shyok Valley, Karakorum Range, and the implications for dating of allied faunas from Iran and Pakistan. *Contrib. Himalayan Geol.* 2, 188–233.
- Wen, S.X., 1979. New stratigraphic materials from northern Xizang. *J. Stratigr.* 3 (2), 150–155.
- Wensink, H., Hartosukohardjo, J., 1990. The paleomagnetism of Late Permian–Early Triassic and Late Triassic deposits on Timor: an Australian origin? *Geophys. J. Int.* 101, 315–328.
- Yanagida, J. (Ed.), 1988. Biostratigraphic study of Paleozoic and Mesozoic groups in central and northern Thailand, an interim report. Kyushu University, Kyushu, 47pp.
- Yanagida, J., 1993. Reexamination of the brachiopod fauna from the Permian Karita Formation, southwest Japan. *Mem. Fac. Sci. Kyushu Univ. Ser. D (Earth Planet. Sci.)* 28 (1), 1–21.
- Yanagida, J., Aw, P.C., 1979. Upper Carboniferous, Upper Permian and Triassic brachiopods from Kelantan, Malaysia. *Geol. Palaeontol. Southeast Asia* 20, 119–141.
- Yang, D.L., 1984. Brachiopoda. In: Feng, S.N., Xu, S.Y., Lin, J.X., Yang, D.L. (Eds.), Biostratigraphy of the Yangtze Gorge Area, 3–Late Paleozoic Era. Geological Publishing House, Beijing, pp. 203–239.
- Yang, Z.Y., Nie, Z.T., 1990. Paleontology of Ngari Tibet (Xizang). The China University of Geosciences Press, Wuhan. 380 pp.
- Yin, H.F., Wu, S.B., Du, Y.S., Yan, J.X., Peng, Y.Q., 1999. South China as a part of archipelagic Tethys during Pangea time. In: Yin, H.F., Tong, J.N. (Eds.), Proceedings of the International Conference on Pangea and the Palaeozoic–Mesozoic Transition. China University of Geosciences Press, Wuhan, pp. 69–73.
- Zhan, L.P., 1979. Brachiopoda. In: Hou, H.F., Zhan, L.P., Chen, B.W. (Eds.), The Coal-Bearing Strata and Fossils of the Late Permian from Guangdong. Geological Publishing House, Beijing, pp. 61–100.
- Zhang, S.X., Jin, Y.G., 1976. Late Paleozoic brachiopods from the Mount Jolmo Lungma region. In: Xizang Scientific expedition team of Chinese Academy of Sciences, (Eds.), A Report of Scientific Expedition in the Mount Jolmo Lungma Region (1966–1968) 2. Science Press, Beijing, pp. 159–271.
- Zhao, X.X., Coe, R.S., 1989. Tectonic implications of Permian–Triassic paleomagnetic results from north and South China. *Geophys. Monogr.* 50, 267–283.
- Ziegler, A.M., Hulver, M.L., Roeley, D.B., 1997. Permian world topography and climate. In: Martini, I.P. (Ed.), Late Glacial and Postglacial Environmental Changes — Quaternary, Carboniferous–Permian and Proterozoic. Oxford University Press, New York, pp. 111–146.
- Ziegler, A.M., Gibbs, M.T., Hulver, M.L., 1998. A mini-atlas of oceanic water masses in the Permian period. In: Shi, G.R., Archbold, N.W., Grover, M. (Eds.), The Permian System: Stratigraphy, Palaeogeography and Resources, *Proc. R. Soc. Victoria* 110, 1–2, 323–344.
- Zorin, Yu.A., 1999. Geodynamics of the western part of the Mongolia–Okhotsk collisional belt, Trans-Baikal region (Russia) and Mongolia. *Tectonophysics* 306 (1), 33–56.