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 Paleotethys, whereas the other four provinces occurred mainly on the continental shelves of Pangea: the Western Tethyan Province along the western coast of the Paleotethys, 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.

Keywords: brachiopoda; palaeobiogeography; Permian; provincialism; quantitative analysis

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
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 and the base of the ammonoid Iranites Zone or the conodont Clarkina subcarinata Zone marks its upper boundary. The Djhulfian (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 of 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 Djhulfian (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 = Gansu and Qinghai, North China; 5 = Turkestan, 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 = Tonle; 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 Schuchertiidae, Orthotetidae, Chonetidae, Marginiferidae, Echinaconchidae, Buxtoniidae, Dictyoclostidae, Linoproductidae, Stenoscistidae, Rhychoconchidae, Athyrididae, Spiriferidae, Brachythyrionidae, Spiriferinidae, Elythiidae 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.

<table>
<thead>
<tr>
<th>No.</th>
<th>Stations</th>
<th>Mean latitude, longitude</th>
<th>Palaeolatitude (Ref.)</th>
<th>Tectonic units (Ref.)</th>
<th>Stratigraphic units</th>
<th>Total genera</th>
<th>Sampling efficiency (%)</th>
<th>Permian ratio</th>
<th>Principal reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>South China</td>
<td>29°20'N, 108°30'E</td>
<td>29°S (Zhao and Coe, 1999)</td>
<td>Yangtze Block</td>
<td>Longtan/Wuchiaping Fm.</td>
<td>61</td>
<td>100</td>
<td>4.43</td>
<td>Zhao (1979), Liao (1980, 1987), Yang (1984), Li et al. (1989), Wang et al. (1992), Hu (1989), Shi et al. (unpublished data)</td>
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<td>2</td>
<td>Southeast China</td>
<td>28°30'N, 116°17'E</td>
<td>12°S (Yin et al., 1999)</td>
<td>Cathaysia Terrane (Yin et al., 1999)</td>
<td>Longtan/Loping Fm.</td>
<td>53</td>
<td>71.4</td>
<td>3.71</td>
<td>Wang et al. (1982), Hu (1989), Yin et al. (1999)</td>
</tr>
<tr>
<td>3</td>
<td>Western Yunnan</td>
<td>23°02'N, 101°05'E</td>
<td>1° (Yin et al., 1999)</td>
<td>Loping/Sensuo Block</td>
<td>Yangb涓 Fm.</td>
<td>9</td>
<td>26.6</td>
<td>0.86</td>
<td>Wang et al. (1982), Hu (1989), Yin et al. (1999)</td>
</tr>
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<td>4</td>
<td>Germa and Qinghai, North China</td>
<td>35°05'N, 99°64'E</td>
<td>8°N (Yin et al., 1999)</td>
<td>Qidem Block</td>
<td>Kaizhen Group</td>
<td>39</td>
<td>85.7</td>
<td>2.57</td>
<td>Wang et al. (1982), Hu (1989), Yin et al. (1999)</td>
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<td>5</td>
<td>Taosi, eastern Tibet</td>
<td>31°20'N, 97°50'E</td>
<td>3.3°N (Huang et al., 1992)</td>
<td>Northern Guangdong Block</td>
<td>Taosi Fm.</td>
<td>13</td>
<td>57.1</td>
<td>0.71</td>
<td>Wang et al. (1982), Hu (1989), Yin et al. (1999)</td>
</tr>
<tr>
<td>6</td>
<td>Inner Zone, Southwest Japan</td>
<td>34°00'N, 132°25'E</td>
<td>3.5°N (Hatton and Hirooka, 1979)</td>
<td>Indo-China Block</td>
<td>Aving/Gua Ming Fm.</td>
<td>8</td>
<td>26.6</td>
<td>0.57</td>
<td>Tan (1979), Tan and Sun (1981)</td>
</tr>
<tr>
<td>7</td>
<td>Bootah Ris, Northeast Malaysia</td>
<td>4°55'N, 102°10'E</td>
<td>1°S (Bunopas, 1981)</td>
<td>Indo-China Block</td>
<td>Unnamed Fm.</td>
<td>8</td>
<td>42.9</td>
<td>0.57</td>
<td>Tan (1979), Tan and Sun (1981)</td>
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<tr>
<td>8</td>
<td>Central Vietnam</td>
<td>16°77'N, 107°14'E</td>
<td>14°S (Ziegler et al., 1997)</td>
<td>Indo-China Block</td>
<td>Unnamed Fm.</td>
<td>8</td>
<td>42.9</td>
<td>0.57</td>
<td>Tan (1979), Tan and Sun (1981)</td>
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<td>9</td>
<td>Central Thailand</td>
<td>17°15'N, 100°75'E</td>
<td>18°S (Ziegler et al., 1997)</td>
<td>Indo-China Block</td>
<td>Unnamed Fm.</td>
<td>17</td>
<td>71.4</td>
<td>1.43</td>
<td>Tan (1979), Tan and Sun (1981)</td>
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<td>10</td>
<td>Western Australia</td>
<td>19°10'S, 125°28'E</td>
<td>40°S (Ziegler et al., 1997)</td>
<td>Cuming and Bonaparte Gulf Ranges</td>
<td>Unnamed Fm.</td>
<td>19</td>
<td>26.6</td>
<td>1.57</td>
<td>Archbold (1993)</td>
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<td>11</td>
<td>Takaiku Mts., New Zealand</td>
<td>40°99'S, 17°19'E</td>
<td>55°S (Ziegler et al., 1997)</td>
<td>Cuming and Bonaparte Gulf Ranges</td>
<td>Hardiman Fm., unnamed limestone</td>
<td>14</td>
<td>57.1</td>
<td>1.29</td>
<td>Archbold (1993)</td>
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<td>12</td>
<td>Kanjorum Range, Pakistan</td>
<td>38°00'N, 78°75'E</td>
<td>53°N (Ziegler et al., 1997)</td>
<td>Kichter Block</td>
<td>Shyok Group</td>
<td>35</td>
<td>71.4</td>
<td>2.57</td>
<td>Archbold (1993)</td>
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<td>14</td>
<td>Julfa, southern Armenia</td>
<td>35°80'N, 45°49'E</td>
<td>45° (Krivtsov, 1984)</td>
<td>Julfa Terrane (Saidi et al., 1997)</td>
<td>Dhulic Fm.</td>
<td>35</td>
<td>71.4</td>
<td>2.57</td>
<td>Archbold (1993), Khadka et al. (1993)</td>
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<td>16</td>
<td>Salt Range, Pakistan</td>
<td>32° 47' N, 71° 59' E</td>
<td>Indian Morainic</td>
<td>34° 09' (Ziegler et al., 1997)</td>
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<td>48° 06' N, 20° 43' E</td>
<td>Indian Morainic</td>
<td>15° 34' (Ziegler et al., 1997)</td>
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<td>18</td>
<td>Slovenia</td>
<td>46° 53' N, 14° 30' E</td>
<td>Indian Morainic</td>
<td>17° 57' (Ziegler et al., 1997)</td>
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<td>19</td>
<td>West Serbia</td>
<td>44° N ± 2°</td>
<td>Indian Morainic</td>
<td>15° N (Ziegler et al., 1997)</td>
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<td>20</td>
<td>Southeastern Parir</td>
<td>37° 44' N, 74° 07' E</td>
<td>Indian Morainic</td>
<td>16° S (Ziegler et al., 1997)</td>
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<td>21</td>
<td>Slovenia</td>
<td>20° 59' N, 95° 50' E</td>
<td>Indian Morainic</td>
<td>44° 57' (Klootwijk, 1984)</td>
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<td>22</td>
<td>Timor</td>
<td>9° 74' S, 124° 07' E</td>
<td>Indian Morainic</td>
<td>39° 8' (Wannik and Hartwiek, 1990)</td>
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<td>23</td>
<td>Klangungun Region, Northern Tibet</td>
<td>28° 27' N, 86° 97' E</td>
<td>Indian Morainic</td>
<td>44° 58' (Klootwijk, 1984)</td>
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<td>24</td>
<td>Chichun Southwestern Tibet</td>
<td>30° 19' N, 10° 26' E</td>
<td>Indian Morainic</td>
<td>44° 8' (Klootwijk, 1984)</td>
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<td>25</td>
<td>Zanda, southwestern Tibet</td>
<td>31° 46' N, 79° 86' E</td>
<td>Indian Morainic</td>
<td>44° 57' (Klootwijk, 1984)</td>
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<td>26</td>
<td>Nei-pian, Central Himalaya, India</td>
<td>30° 39' N, 74° 26' E</td>
<td>Indian Morainic</td>
<td>44° 9' (Klootwijk, 1984)</td>
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<td>27</td>
<td>Tibet</td>
<td>31° 00' N, 17° 10' E</td>
<td>Indian Morainic</td>
<td>44° 10' (Klootwijk, 1984)</td>
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<td>East Greenland</td>
<td>74° 15' N, 20° 90' W</td>
<td>Indian Morainic</td>
<td>44° 9' (Ziegler et al., 1997)</td>
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<td>30</td>
<td>Svalbard</td>
<td>78° 55' N, 23° 91' E</td>
<td>Indian Morainic</td>
<td>44° 9' (Ziegler et al., 1997)</td>
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</table>
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), 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 matrices for multivariate statistical analyses.

The secondary data matrices 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 Pearson 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 order to preserve 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.

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The secondary data matrices 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 Pearson 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 order to preserve 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.
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 matrices 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 Derbiya, 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,
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 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) demonstrate 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 example, 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 Richtofena and many specialised lyttoniids, including Leptodus, Oldhamina, permianellids etc., all of warm-water origin. In particular, the province is characterised by the Oldhamina-Orthotherina-Squamularia association. Other common genera include Tethyochonetes, Spinomarginifera, Meekella, Leptodus, Haydenella, Araxathyris, Cathaysia and Enteteles, 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-
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 Edrioesteges.

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 Palaeoetethys. 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, Acosaurus and Notothyris. However, typical or common elements...
of the Cathaysian Province such as *Oldhamina*, *Orthothenia*, *Cathaysia*, *Haydenella* and *Squamularia* are lacking in this province, while *Lmoproductus* and *Reticularia* are usually not present in the faunas of the Cathaysian Province during the Wuchiapingian. *Tschermschewia* 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 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*, *Reticulimarginifera*, *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*, *Plenokinella*, *Spinomarinina*, *Terraecia* and *Tonsipris*. The recognition of this group (Group D) by CA readily confirms to the continued presence of Austrazeian 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 hemisphere record of *Yakovlevia* (= *Muirwoodia*) from Chile (Minato and Tazawa, 1977) has been discredited (Shi, 1995). In addition, some genera of antitropical distribution, such as *Wageneroconcha* 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 Djhulfian 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 Djhulfian 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 Austroazeian Province, primarily controlled by a cool to cold-
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 Lamnimargus (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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