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Capitanian (Late Guadalupian, Permian) global brachiopod palaeobiogeography and latitudinal diversity pattern

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Abstract

A global database containing 3365 occurrences, 821 species and 251 genera of the Capitanian (Late Guadalupian, Permian) brachiopod faunas from 24 stations has been analyzed by cluster analysis using the Jaccard and Otsuka coefficients and the probabilistic index of similarity, nonmetric multidimensional scaling and minimum spanning tree. Two supergroups, three groups and six subgroups are revealed and interpreted as representing, respectively, two biotic realms (the Palaeoequatorial and Gondwanan Realms), two regions and six provinces. An additional realm (the Boreal Realm), based on the fauna from Spitsbergen, also appears recognizable although it also shows considerable similarities with southwestern North America and the northern margin of Gondwana as revealed by the statistical analysis. The Palaeoequatorial Realm can be further subdivided into the North America Region and the Asian Tethyan Region. The six biotic provinces are the Cathaysian Province in the Palaeotethys and Mesotethys, the Greenland-Svalbard Province in the Arctic region, the Austrazean Province in eastern Australia and New Zealand, the Grandian Province in western North America and the two transitional zones (the Himalayan Province in the southern temperate zone and the Sino–Mongolian–Japanese Province in the northern temperate zone). Polynomial regression analysis and rarefaction analysis indicate that the generic diversities of brachiopod faunas during the Capitanian peaked in the Palaeoequatorial Cathaysian Province and the two transitional zones (Himalayan Province and Sino–Mongolian–Japanese Province), but fell dramatically in the polar regions. The generic diversity of the Palaeoequatorial Grandian Province is apparently lower than in the two transitional zones of temperate palaeolatitudes, suggesting that the generic diversity of Capitanian brachiopod faunas does not exhibit a strict negative correlation with palaeolatitudes. This in turn would suggest that biogeographical determinants (such as geographical barriers, inhabitable area and ocean currents) other than latitude-related temperature control may also have played an important role in the dispersal of some brachiopods and the characterization of some local provinces and high diversities. The Capitanian global brachiopod palaeobiogeography is generally comparable with those in the Wuchiapingian and Changhsingian, but with some notable differences. These include: (1) that the Grandian Province of the Capitanian in western North America vanished after the end-Guadalupian regression, (2) that the western Tethyan Province of the Lopingian could not be

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distinguished in the Capitanian, and (3) that the Austrazean Province was larger in area than either in the Wuchiapingian or in the Changhsingian.

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1. Introduction

The Capitanian Stage (Late Guadalupian, Permian) has gained global importance as a key interval (Fig. 1) to study the patterns and possible mechanisms of the end-Guadalupian mass extinction (Jin et al., 1994; Stanley and Yang, 1994; Shen and Shi, 1996; Wang and Sugiyama, 2000). A recent study of the brachiopod palaeobiogeographical extinction patterns indicates that the end-Guadalupian mass extinction is well displayed in the Gondwanan Realm in the south and the Boreal Realm in the north, but less pronounced in the intervening Palaeoequatorial Realm (Shen and Shi, 2002). Ap-

parently associated with this mass extinction is a global regression event, which resulted in the withdrawal of sea water from all major landmasses of Pangea (Ross and Ross, 1987). However, the exact cause-and-effect relationship between the regression and the end-Guadalupian mass extinction remains a subject of debate. The lack of a definitive understanding about this relationship may be attributed to many factors, one of which is the lack of studies on the global provincialism of the Capitanian at a more regional or provincial scale and the possible relationships of this provincialism with the end-Guadalupian sea level drop and the mass extinction.

Series	Global standard (Jin et al., 1997)	Leven, 1996	conodonts	fusulinids	Ma	
Lopingian	Changhsingian	Dorashamian	<i>Clarkina meishanensis</i>	<i>Palaeofusulina sinensis</i>	251.4 ±0.4	end-Permian mass extinction
			<i>Clarkina wangi</i>	<i>Palaeofusulina minima</i> <i>Gallowayinella meitianensis</i>	252.3 ±0.2	
	Wuchiapingian	Dzhulfian	<i>Clarkina orientalis</i> <i>Clarkina guanyuanensis</i> <i>Clarkina leveni</i> <i>Clarkina postbitteri postbitteri</i>	<i>Nanlingella simplex</i> <i>Codonofusiella kwangsiana</i>	253.4 ±0.2	
Guadalupian	Capitanian	Midian	<i>Clarkina postbitteri hongshuiensis</i> <i>Jinogondolella granti</i> <i>Jinogondolella postserrata</i>	<i>Lepidolina Yabeina</i>	265.3 ±0.2	end-Guadalupian extinction
	Wordian	Murgabian	<i>Jinogondolella aserrata</i>	<i>Neoschwagerina margaritae</i> <i>Neoschwagerina craticulifera</i>		
	Roadian		<i>Jinogondolella nankingensis</i>	<i>Cancellina</i>		

Fig. 1. Chronostratigraphic subdivisions and selected fossil zones for the Guadalupian and Lopingian (integrated from Jin et al., 1997; Leven, 1996, isotopic ages are from Bowring et al., 1998).

This study is a continuation of our effort to systematically and quantitatively document, stage by stage, the Permian marine palaeobiogeography of the world, following a sequence of recent studies by Shi and colleagues on the brachiopod palaeobiogeography of some selected Permian stages of the Asian–Western Pacific region (Shi and Archbold, 1993, 1995a, 1995b, 1996). In our two previous papers on a global scale patterns (Shen and Shi, 2000; Shen et al., 2000), we studied the global brachiopod palaeobiogeography of, respectively, the Wuchiapingian and Changhsingian stages of the Lopingian Series (Late Permian), and revealed a dynamic pattern of shallow marine provincialism as manifested by the brachiopod faunas and also diversity trends related to palaeogeographical and palaeobiogeographical variables. In this paper, we aim to analyze the global palaeobiogeographical patterns of Capitanian brachiopod faunas using a range of multivariate statistical methods, and attempts to elucidate the diversity trends of the brachiopod faunas in relation to contemporaneous marine provincialism.

2. Data and methodology

The brachiopod database used in this paper is housed in the State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology) for palaeobiogeographical and diversity analyses. Sources of data have included published systematics and unpublished/in press faunal lists, biostratigraphical, geographical, palaeogeographical, lithological, and tectonic investigations for each collection. The format of the current brachiopod database mainly followed the palaeobiology network information page at the website <http://www.flatpebble.nceas.ucsb.edu/public/tips/tips.html#collection> by Arnie Miller and John Alroy. The database includes more than 30 different fields and documents individual fossil collections, provides a list of orders, superfamilies, families, genera and species, and where available, abundance data. It also includes biostratigraphical and lithostratigraphical data resolvable to fossil zone/member levels, and detailed geographic and palaeogeographical data. As such, any taxon may have multiple recorded occur-

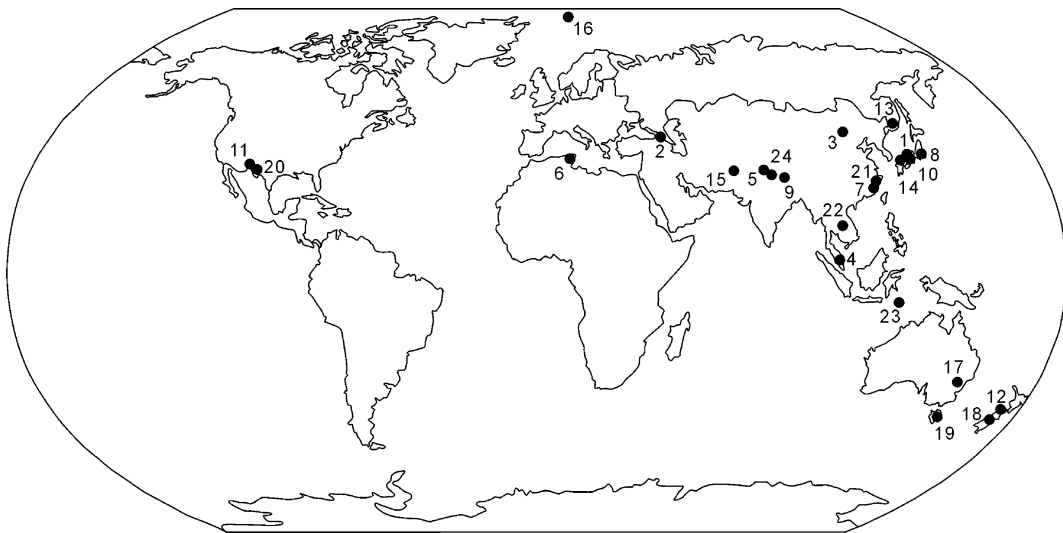


Fig. 2. Areas and/or localities containing the Capitanian brachiopod faunas for palaeobiogeographical analysis in this paper. 1 = Akiyoshi, Japan; 2 = Transcaucasia; 3 = Central Inner Mongolia; 4 = Central Malaysia; 5 = Chitichun, southern Tibet; 6 = Djeffara Basin, Tunisia; 7 = Fujian, Southeast China; 8 = Kitakami, Northeast Japan; 9 = Lhaze, southern Tibet; 10 = Maizuru, central Japan; 11 = Coahuila, Mexico; 12 = Nelson, New Zealand; 13 = Primorye, Russian Far East; 14 = Sakawa Basin, Japan; 15 = Salt Range, Pakistan; 16 = Spitsbergen; 17 = Sydney Basin, eastern Australia; 18 = Takatimu Mountains, New Zealand; 19 = Tasmania, Australia; 20 = West Texas, USA; 21 = Tonglu, Southeast China; 22 = West Cambodia; 23 = West Timor; 24 = Zhongba, southern Tibet.

Table 1
Capitanian brachiopod faunas of the world—basic data and statistics

Stations	Mean latitude, longitude	Palaeolatitude (Ref.)	Tectonic units	Stratigraphic units	Total genera	Sampling efficiency (%)	Permian ratio	Principal references
1 Akiyoshi, Central Japan	34°15N, 131°15E	10° N ± (Ziegler et al., 1997)	inner zone	Tsunemori formation, Akiyoshi limestone	12	11	0.89	Yanagida (1996)
2 Transcaucasia	38°98N, 45°49E	4°S ± (Klootwijk, 1984)	Julfa Terrane	Khachik formation	25	67	1.0	Ruzhentsev and Sarytcheva (1965); Kotljar and Zakharov (1989) Duan and Li (1985)
3 Central Inner Mongolia	42°33N, 110°50E	10°N (Pruner, 1987)	southern subzone, inner Mongolian trough	Yihewusu formation	26	56	2.0	
4 C. Peninsula Malaysia	3°10N, 102°40E	15°S ± (Ziegler et al., 1997)	Indochina block	Bera formation	15	22	0.78	Sone et al. (2001)
5 Chitichun, Southern Tibet	30°70N, 80°26E	40°S ± (Ziegler et al., 1997)	exotic block	Chitichun limestone	22	67	1.44	Diener (1897)
6 Djeffara basin, Tunisia	34°00N, 10°00E	4°N (Ziegler et al., 1997)	Djeffara basin	Djebel Tebaga upper Permian formation	18	33	1.0	Termier et al. (1977)
7 Fujian, Southeast China	25°10N, 117°00E	5.9°N (Ma and Zhang, 1986)	Cathaysian block	Tongziyan Fm.	38	67	2.0	Zhu (1990)
8 Kitakami, Japan	38°33N, 141°31E	5°N (McElhinny et al., 1981)	Kitakami Belt	Kanokura Fm	17	67	1.0	Minato et al. (1979)
9 Lhaze, Southern Tibet	29°10N, 87°96E	40° ± S (Ziegler et al., 1997)	Lhasa block	Quxia limestone	16	56	0.89	Shen et al. (2003)
10 Maizuru, central Japan	35°30N, 135°30E	3.8°N (Sasajima, 1981)	Maizuru zone	upper formation of Maizuru group	21	89	1.0	Shimizu (1961)
11 Coahuila, Mexico	26°40N, 103°00W	7°N (Ziegler et al., 1997)	North America platform	unnamed	16	33	1.0	King et al. (1944)

12	Nelson, New Zealand	41°18N, 173°16E	44.5°S (Ziegler et al., 1997)	Torlesse Terrane	Lee river group	3	11	0.22	Waterhouse (1964, 1970, 1982)
13	Primorye, Russian Far East	43°10N, 133°07E	33.9°N ± (McElhinny et al., 1981)	Mongolian arc	Barabashi formation	47	67	2.0	Licharew and Kotljar (1978)
14	Sakawa, Japan	33°15N, 133°15E	10°S ± (Ziegler et al., 1997)	Kurosegawa belt	Yamaba limestone	15	44	0.78	Yanagida (1973)
15	Salt Range, Pakistan	32°47N, 71°39E	34.05°S (Ziegler et al., 1997)	Tethyan Himalayan zone	lower part of the Wargal Fm	45	100	2.67	Waagen (1882–1885); Waterhouse and Gupta (1983)
16	Spitsbergen	78°55N, 23°91E	45°N ± (Ziegler et al., 1997)	Nordfjorden High	Voringen Member, Kapp Starostin Formation	18	44	1.11	Nakamura et al. (1992)
17	Sydney Basin, Australia	33°S ±, 151°E ±	70°S (Embleton, 1984)	Sydney Basin	Peawaddy formation, flat top formation	7	22	0.33	Briggs (1998)
18	Takatimu Mt., New Zealand	46°69S, 171°19E	55°S ± (Ziegler et al., 1997)	Brook Street Terrane	Takitimu group	18	67	0.89	Waterhouse (1964, 1970, 1982)
19	Tasmania, Australia	42°88S, 147°22E	80°S (Embleton, 1984)	Tasmania	Member E, Malbina Formation	12	22	0.56	Clarke (1987)
20	Texas, USA	30°15N, 103°15W	7°N (Ziegler et al., 1997)	North American platform	Capitan formation, Bell Canyon formation	79	100	3.67	Cooper and Grant (1974, 1975, 1976a, 1976b)
21	Tonglu, Southeast China	29°80', 119°62E	5.9°N (Ma and Zhang, 1986)	Cathaysian block	Lengwu Fm	66	100	3.11	Liang (1990)
22	West Cambodia	13°58N, 103°29E	15°S (Ziegler et al., 1997)	Indochina block	Member A, Sisophon limestone	31	89	1.89	Ishii et al. (1969)
23	West Timor	9°74S, 124°07E	39°S (Wensink and Hartosukohardjo, 1990)	Aileu-Mau Ex. block	unnamed	40	100	1.78	Broili (1916), Hamlet (1928), Archbold and Bird (1989)
24	Zhongba, Southern Tibet	29°79N, 84°00E	40° ± S (Ziegler et al., 1997)	Lhasa block	Lasaila limestone	23	56	1.11	Jin and Sun (1981)

References for palaeolatitude and tectonic units are indicated.

rences in the database. The detailed primary data fields were designed to facilitate a wide array of co-current and future palaeobiogeographical, macroevolutionary and palaeoecological analyses.

The Capitanian brachiopod database used for the present study contains 3365 taxonomic occurrences of 821 species and 251 genera (Appendix 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.

The latest time scale of the Permian System (Jin et al., 1997) is adopted for the chronostratigraphical definition of the Capitanian (Fig. 1). The upper boundary of the Capitanian is constrained by the first appearance of the conodont *Clarkina postbitteri postbitteri* (Jin et al., 2001; Henderson et al., 2002). This boundary is easily recognized in most areas in the world by a distinct unconformity between the Lopingian and the Guadalupian Series derived from a global regression. Only in a few areas of the world (e.g., the Laibin area in Guangxi of southwest China) did marine deposition continue across the Guadalupian/Lopingian boundary. Even in these areas, the end-Guadalupian regression is evident and clearly marked by the deposition of crinoid grainstones with *Skolithos* trace fossils, indicating a nearshore high energy environment (Jin et al., 1998). The lower boundary of the Capitanian is placed at the base of the conodont *Jinogondolella postserrata* Zone (Fig. 1). However, this boundary is difficult to recognize in the field without detailed conodont biostratigraphy. Therefore, as an alternative measure we employed the definition of the Midian Stage by Leven (1996) containing the fusulinid *Yabeina*–*Lepidolina* genozone (Fig. 1) to substitute for the Capitanian Stage although discussion on the precise correlation between the two stages is still ongoing. The lower boundary of the Midian Stage is placed at the first occurrence level of advanced fusulinid species of *Yabeina* and *Lepidolina*, which also mark the mass abundance of aberrant forms such as *Kahlerina*, *Dunbarula*, *Lantschichites*, *Chusenella*, *Polydioxodina* and *Metadoliolina* along with highly evolved *Neoschwagerina* (Leven, 1996).

In addition to the possible complications mentioned above, the age of some brachiopod faunas may straddle across the Wordian/Capitanian or Capitanian/Wuchiapingian boundaries either because of a lack of a decisive conodont- or fusulinid-based age marker associated with brachiopod faunas or these brachiopod faunas are naturally diachronous in age. For instance, the base of the Capitanian is defined by the first occurrence of the conodont *Jinogondolella postserrata* (Wardlaw, 2000; Mei et al., 2002), which is within the lower part of the Altuda Formation in West Texas, USA. However, the brachiopods from this formation are included in our database regardless of their horizons because such biostratigraphical information is not available in the original literature. The same is also true for the faunas from the Chitichun Limestone (Diener, 1897) and the West Timor collections (Broili, 1916; Hamlet, 1928). According to the associated ammonoids and fusulinids, the Chitichun and West Timor brachiopod collections may partly include some Wuchiapingian elements as indicated by the co-existence of the ammonoids *Cyclolobus*, *Xenaspis*, *Timorites* and the fusulinids *Newschwagerina* and *Pseudodoliolina*. However, it is impossible to chronostratigraphically divide the faunas without further detailed biostratigraphical work. The age of the brachiopods from the Kapp Starostin Formation in Spitsbergen is also a subject of considerable debate (Nakamura et al., 1987; Stemmerik, 1988; Gruszczynski et al., 1989). The brachiopods from the upper part of this formation were included into the Wuchiapingian database (Shen and Shi, 2000), whereas those from the middle part of the Kapp Starostin Formation are included in this study, even though the age of those brachiopods still remains controversial (see discussion by Shen and Shi, 2000, p. 312).

Occurrences of Capitanian brachiopods are relatively limited in distribution because of a lack of outcrops, possibly due to the end-Guadalupian worldwide regression. In total, 251 brachiopod genera from 24 different stations or operational geographical units (OGUs) (Crovello, 1981) are included in this study (Fig. 2, Table 1). Stations are as extensive as possible so as to embrace all correlative fossil communities from various substrates and water depths, provided that geological evidence clearly indicates 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 (see [Shi and Archbold, 1995a](#) for details on the methodology). A taxonomic presence/absence matrix of genera at each of the 24 stations is assembled (Appendix A).

Three statistical indices (sampling efficiency, Permian ratio and simple generic diversity, see [Table 1](#)) are employed to indicate the nature of faunas from each OGU ([Table 1](#)). Sample efficiency ([Stehli, 1970](#); [Stehli and Grant, 1971](#)) is defined as:

$$\frac{\text{cosmopolitan families found}}{\text{cosmopolitan families expected}}$$

This index is aimed to provide a measure of the sampling quality of a faunal station; the greater the index value, the more complete or efficient a faunal station has been sampled. A similar index, called Permian Ratio ([Stehli, 1970](#); [Shi and Archbold, 1996](#)), is defined as:

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

The cosmopolitan dominants used in calculating the Permian ratio index as a proxy of sampling efficiency have been amended in this study based on the notion that brachiopod cosmopolitan dominants changed from time to time as a common feature of evolution. Therefore, for the Capitanian, the nine most common families that would be expected to occur in any shallow marine environment throughout the world (if the sampling were sufficient) are Productellidae Schuchert, Dielasmataidae Schuchert, Athyrididae Davidson, Rugosochonetidae Muir-Wood, Wellerellidae Licharew, Crenispiriferidae Cooper and Grant, Aulostegidae Muir-Wood and Cooper, Neoretziidae Dagys, and Martinidae Waagen ([Table 2](#)). The index “simple generic diversity” refers to the number of genera present in each fauna.

As shown in [Table 1](#), the brachiopod faunas from the Salt Range, Pakistan (Station 15), Tonglu, Zhejiang, South China (Station 21) and West Timor (Station 23) are ‘perfectly’ sampled (Sample efficien-

Table 2

Cosmopolitan families during the Capitanian and their generic occurrences

Families	Generic occurrences
Productellidae schuchert	284
Dielasmataidae schuchert	202
Athyrididae Davidson	187
Rugosochonetidae Muir-Wood	160
Wellerellidae Licharew	133
Crenispiriferidae cooper and grant	126
Aulostegidae Muir-Wood and Cooper	111
Neoretziidae Dagys	110
Martinidae Waagen	100

cies = 100%). In contrast, the faunas from Akiyoshi, central Japan (Station 1), Nelson, New Zealand (Station 12), Central Peninsular Malaysia (Station 4), Sydney Basin (Station 17) and Tasmania, Australia (Station 19) are relatively poorly sampled (sample efficiencies < 30%). Nevertheless, all of these stations are included in the quantitative analyses for the sake of preserving all the stations in one complete statistical sample. However, we have taken every caution in our interpretations (see below) of the results from these quantitative analyses when involving faunal stations with low or very low sample efficiencies, in a similar approach used by [Shen and Shi \(2000\)](#).

As with our previous studies, the initial presence/absence data matrix of 251 genera from 24 stations was analyzed by three common multivariate statistical techniques [cluster analysis (CA), non-metric multidimensional scaling (NMDS) and minimum spanning tree (MST)] on the IBM compatible PC using PATN ([Belbin, 1992](#)) and STATISTICA for Windows (1995 version). Various binary coefficients have been employed for calculating the biotic similarities/dissimilarities between OGUs and degree of associations between taxa. As reviewed by [Shi \(1993\)](#), [Shang and Jin \(1997\)](#) and many other previous work (e.g., [Shen and Shi, 2000](#); [Belasky et al., 2002](#)), the Jaccard ([Jaccard, 1901](#)) and Otsuka ([Ochiai, 1957](#)) coefficients have been shown to be the most consistent and robust binary similarity measures against sampling biases. Therefore, we have used these two coefficients to calculate the dissimilarities ([Table 3](#)) between the stations and derive secondary matrices for multivariate statistical analyses.

Table 3
Faunal dissimilarities between 24 stations based on the Jaccard coefficient (upper half of the matrix) and the Otsuka coefficient (lower half of the matrix)

Stations	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1 Akiyoshi, Japan	0	0.97	0.89	0.92	0.91	0.88	0.98	0.85	0.96	1	0.96	1	0.89	0.96	0.98	0.97	1	0.97	1	0.96	0.92	0.95	0.94	0.94
2 Transcaucasia	0.94	0	0.84	0.92	0.89	0.89	0.83	0.81	0.95	0.9	0.95	1	0.86	0.68	0.8	0.98	1	0.95	1	0.91	0.8	0.74	0.8	0.88
3 Central Inner Mongolia	0.78	0.73	0	0.98	0.76	0.8	0.9	0.82	0.83	0.85	0.92	1	0.69	0.85	0.81	0.88	1	0.93	1	0.91	0.84	0.7	0.71	0.84
4 C. Peninsular Malaysia	0.85	0.84	0.95	0	0.89	0.96	0.89	0.9	0.88	0.87	1	1	0.9	0.92	0.95	0.93	1	0.97	1	0.97	0.86	0.84	0.9	0.94
5 Chitichun, Southern Tibet	0.83	0.8	0.62	0.79	0	0.82	0.88	0.81	0.71	0.88	0.95	1	0.75	0.88	0.76	0.87	1	0.87	1	0.93	0.85	0.74	0.62	0.63
6 Djeffara Basin, Tunisia	0.78	0.79	0.65	0.93	0.69	0	0.9	0.82	0.85	0.97	0.93	1	0.88	0.83	0.95	0.97	1	0.97	1	0.92	0.89	0.81	0.85	0.91
7 Fujian, Southeast China	0.95	0.71	0.81	0.78	0.77	0.79	0	0.9	0.9	0.91	0.94	1	0.89	0.86	0.87	0.94	1	0.98	1	0.94	0.7	0.76	0.89	0.95
8 Kitakami, Japan	0.73	0.67	0.68	0.81	0.67	0.7	0.81	0	0.9	0.91	0.93	1	0.83	0.85	0.9	0.84	1	0.91	1	0.9	0.88	0.83	0.77	0.83
9 Lhaze, Southern Tibet	0.93	0.9	0.7	0.79	0.54	0.73	0.79	0.82	0	0.87	0.93	1	0.88	0.92	0.88	0.9	1	0.9	0.96	0.96	0.89	0.78	0.8	0.77
10 Maizuru, Japan	1	0.82	0.74	0.76	0.78	0.94	0.82	0.84	0.77	0	0.94	0.95	0.85	0.93	0.83	0.88	1	0.94	1	0.95	0.85	0.8	0.82	0.98
11 COahuila, Mexico	0.92	0.89	0.85	1	0.89	0.86	0.87	0.87	0.86	0.88	0	1	0.93	1	0.93	0.93	1	1	1	0.92	0.92	0.95	0.94	0.94
12 Nelson, New Zealand	1	1	1	1	1	1	1	1	1	0.87	1	0	1	1	1	1	0.86	0.83	0.93	1	1	1	1	1
13 Primorye, Russian Far East	0.76	0.75	0.51	0.77	0.58	0.74	0.79	0.67	0.74	0.72	0.85	1	0	0.85	0.8	0.89	1	0.95	1	0.89	0.77	0.77	0.73	0.86
14 Sakawa Basin, SE Japan	0.92	0.48	0.72	0.85	0.77	0.7	0.72	0.73	0.85	0.87	1	1	0.67	0	0.89	0.97	1	0.93	1	0.94	0.85	0.79	0.87	0.94
15 Salt Range, Pakistan	0.96	0.65	0.67	0.88	0.6	0.89	0.77	0.8	0.74	0.68	0.85	1	0.67	0.75	0	0.84	0.98	0.94	0.98	0.92	0.81	0.8	0.74	0.82
16 Spitsbergen	0.93	0.95	0.77	0.87	0.76	0.94	0.89	0.72	0.82	0.79	0.87	1	0.77	0.93	0.69	0	1	0.94	1	0.92	0.96	0.91	0.84	0.89
17 Sydney Basin, Australia	1	1	1	1	1	1	1	1	1	1	1	0.74	1	1	0.94	1	0	0.9	0.87	1	1	1	1	1
18 Takitimu Mt., New Zealand	0.93	0.91	0.86	0.94	0.76	0.94	0.96	0.83	0.82	0.89	1	0.59	0.9	0.86	0.86	0.89	0.79	0	0.8	0.97	0.96	0.91	0.88	0.92
19 Tasmania, Australia	1	1	1	1	1	1	1	1	0.93	1	1	0.83	1	1	0.96	1	0.74	0.66	0	1	1	1	1	1
20 West Texas, USA	0.87	0.8	0.81	0.91	0.84	0.8	0.87	0.76	0.89	0.88	0.79	1	0.8	0.84	0.84	0.82	1	0.92	1	0	0.9	0.9	0.88	0.96
21 Tonglu, Southeast China	0.79	0.63	0.69	0.67	0.7	0.75	0.52	0.74	0.75	0.7	0.8	1	0.62	0.64	0.68	0.91	1	0.91	1	0.82	0	0.72	0.81	0.91
22 West Cambodia	0.89	0.59	0.54	0.7	0.59	0.66	0.61	0.69	0.62	0.67	0.9	1	0.61	0.62	0.65	0.82	1	0.82	1	0.79	0.52	0	0.67	0.89
23 West Timor	0.86	0.65	0.54	0.79	0.43	0.71	0.79	0.59	0.63	0.68	0.87	1	0.58	0.73	0.59	0.7	1	0.78	1	0.77	0.67	0.5	0	0.76
24 Zhongba	0.88	0.79	0.72	0.89	0.46	0.84	0.9	0.71	0.62	0.95	0.89	1	0.73	0.88	0.67	0.8	1	0.85	1	0.91	0.82	0.81	0.6	0

Table 4

Values of the SI (lower half of the matrix) and genera in common (upper half of the matrix) between the stations with Capitanian brachiopods

Stations	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1 Akiyoshi, Japan	12	1	4	2	3	3	1	4	1	1	1	0	6	1	1	1	0	1	0	4	6	2	3	2
2 Transcaucasia	0.17	25	7	3	5	4	9	7	2	4	2	0	9	9	12	1	0	2	0	9	15	11	11	5
3 Central Inner Mongolia	0.87	0.86	26	1	9	7	6	6	6	7	3	0	17	5	11	4	0	3	0	9	13	13	14	6
4 C. Peninsular Malaysia	0.71	0.54	0.08	15	4	2	5	3	4	4	0	0	6	3	3	3	1	1	0	3	10	6	6	3
5 Chitichun, Southern Tibet	0.79	0.67	0.99	0.85	22	6	7	6	9	4	2	0	14	4	12	4	0	5	0	7	12	12	17	12
6 Djeffara Basin, Tunisia	0.86	0.66	0.98	0.49	0.97	18	5	5	5	1	3	0	7	5	3	3	1	1	0	7	8	7	8	4
7 Fujian, Southeast China	0.05	0.85	0.29	0.67	0.67	0.51	38	5	5	5	3	0	9	6	10	3	0	1	0	7	24	13	8	3
8 Kitakami, Japan	0.97	0.98	0.95	0.81	0.97	0.96	0.58	17	3	5	2	0	9	4	5	4	0	3	0	9	9	7	10	5
9 Lhaze, Southern Tibet	0.34	0.26	0.96	0.94	1	0.97	0.64	0.76	16	4	2	0	7	3	7	4	1	3	1	4	8	8	10	8
10 Maizuru, Japan	0.25	0.54	0.94	0.88	0.61	0.1	0.33	0.92	0.83	21	3	1	10	2	9	6	0	2	0	6	11	8	10	1
11 Coahuila, Mexico	0.37	0.26	0.49	0.06	0.31	0.71	0.2	0.48	0.51	0.62	16	0	4	1	4	2	1	0	0	7	6	2	3	2
12 Nelson, New Zealand	0.37	0.26	0.25	0.34	0.28	0.32	0.18	0.33	0.33	0.76	0.34	3	0	0	0	0	1	3	1	0	0	0	0	0
13 Primorye, Russian Far East	0.87	0.63	1	0.69	1	0.68	0.09	0.96	0.8	0.92	0.23	0.14	47	8	15	5	0	3	0	13	22	16	18	8
14 Sakawa Basin, SE Japan	0.39	1	0.9	0.85	0.84	0.98	0.83	0.92	0.8	0.4	0.26	0.35	0.95	15	6	2	2	2	0	5	10	7	7	3
15 Salt Range, Pakistan	0.03	0.96	0.89	0.16	0.99	0.07	0.26	0.42	0.85	0.86	0.25	0.15	0.6	0.75	45	9	1	4	1	10	18	14	17	10
16 Spitsbergen	0.31	0.05	0.63	0.74	0.75	0.64	0.14	0.87	0.89	0.97	0.43	0.31	0.32	0.5	0.95	18	1	2	0	6	3	4	8	4
17 Sydney Basin, Australia	0.25	0.11	0.09	0.6	0.12	0.54	0.05	0.16	0.56	0.14	0.59	0.91	0.02	0.87	0.15	0.56	7	2	2	0	0	0	1	1
18 Takitimu Mt. New Zealand	0.32	0.19	0.37	0.22	0.9	0.15	0.01	0.66	0.72	0.29	0.04	1	0.06	0.48	0.16	0.4	0.83	18	5	3	3	4	6	3
19 Tasmania, Australia	0.15	0.03	0.02	0.09	0.04	0.06	0.01	0.08	0.34	0.05	0.08	0.85	0	0.1	0.03	0.07	0.93	0.99	12	0	0	0	0	0
20 West Texas, USA	0.1	0.05	0.04	0.01	0.03	0.13	0	0.53	0.02	0.02	0.26	0.05	0	0.06	0	0.05	0	0	0	79	13	11	13	4
21 Tonglu, Southeast China	0.62	0.97	0.75	0.96	0.84	0.49	1	0.76	0.65	0.77	0.27	0.07	0.77	0.96	0.34	0.01	0.01	0.01	0	0	66	21	17	7
22 West Cambodia	0.31	0.99	1	0.94	1	0.93	0.98	0.96	0.99	0.96	0.14	0.22	1	0.98	0.96	0.48	0.07	0.47	0.02	0.03	1	31	18	5
23 West Timor	0.37	0.97	1	0.82	1	0.94	0.15	1	1	0.97	0.18	0.17	0.98	0.93	0.97	0.93	0.21	0.66	0.01	0	0.48	1	40	12
24 Zhongba	0.49	0.66	0.83	0.61	1	0.71	0.04	0.89	1	0.05	0.29	0.28	0.58	0.61	0.89	0.71	0.42	0.49	0.05	0	0.08	0.45	0.99	23

The values in bold along the diagonal of the matrix represent number of brachiopod genera at each station.

In addition to the binary coefficients, the probabilistic index (SI) developed by Raup and Crick (1979) was also used in this paper to test the possible defects derived from the binary coefficients. The probabilistic index takes into account statistical significance in determining similarities; therefore, the biogeographical data are weighted on the basis of frequency of occurrence by this method so that widespread genera do not have a disproportionate effect on measurement of similarity (Raup and Crick, 1979). The probabilistic index between any two stations was calculated using the program especially developed by N. McLeod (RCSII.1/PC). The similarity data derived from the binary coefficients (Table 3) and the probabilistic index (Table 4) were then imported into PATN and STATISTICA for Q-mode cluster analysis (CA), non-metric multidimensional scaling (NMS) and minimum spanning tree (MST).

In addition to the CA, NMDS and MST analyses designed to evaluate the global distribution patterns of the Capitanian brachiopod faunas, we have also employed polynomial regression to evaluate palaeogeographical diversity trends with respect to palaeolatitudes. In comparing the diversities from different palaeogeographical regions, we found that the sampling intensities are clearly different in different realms/regions/provinces, therefore demanding an adjustment of the diversity trends against possible sampling biases. To this end, we have also carried out genus occurrence/genus rarefaction analyses to evaluate the actual effects of sampling intensities in the different provinces based on the palaeobiogeographical results by CA, NMDS and MST. Thus, diversities in different provinces can be compared to one another in the same sampling intensities (for more discussion see Shen and Shi, 2002).

3. Results

Fig. 3 gives the dendrograms derived from unweighted pair-group arithmetic averaging (UPGMA) cluster analysis (CA) using the Jaccard and Otsuka coefficients and SI. These three dendrograms form the basis of our interpretation of group patterns of stations. Cophenetic correlation values are respectively 0.8123 for the CA based on Otsuka coefficient and 0.8393 for the CA based on the Jaccard coefficient,

both indicating strong robustness of the dendrograms compared to their respective original similarity matrices. Stress values used in the NMDS analysis for the two coefficients and SI are very low, also suggesting high coherence (or little distortion) (Fig. 4). Three lines (I–III) were chosen in the dendrograms to delineate clusters of stations, which may represent different ranks of biochores (biogeographic units such as realm, region, province, etc.). All three dendrograms reveal two distinct core supergroups (labeled A and B in Fig. 3) at the chosen division line I without any discrepancies. These two supergroups can also be readily distinguished by NMDS and MST based on Otsuka, Jaccard coefficients and SI (Fig. 4).

Among the two supergroups, Supergroup A is large, geographically dispersed, and can be further divided into two groups (Groups A₁, A₂) at the chosen line II in the dendrograms by CA (Fig. 4) and in the scatter plots by NMDS and MST (Fig. 5), despite some minor discrepancies among the three dendrograms. In the dendrograms based on the Otsuka coefficient and SI, Group A₁ consists of two stations only, both located in southwestern North America (Coahuila, Mexico and West Texas, USA). However, Spitsbergen and Akiyoshi are grouped with West Texas, USA and Mexico in the dendrogram based on the Jaccard coefficient. This statistically derived relationship among Akiyoshi, Spitsbergen and western North America is interesting considering their wide geographical separation today and the implication of this for palaeobiogeographical reconstruction will be discussed below.

Group A₂ consists of 18 stations based on the Otsuka coefficient and SI and 16 stations based on the Jaccard coefficient (Fig. 3). In spite of some minor discrepancies in group memberships among the three dendrograms, the group, in all cases, appears to contain three readily recognizable subgroups (Subgroup A₂₋₁, A₂₋₂, and A₂₋₃) at the chosen line III. Subgroup A₂₋₁ consists of four stations based on the Jaccard coefficient, all of which are today located in or close to South China. In the Otsuka- and SI-based dendrograms, however, this subgroup additionally also encompasses Transcaucasia, Sakawa of Japan and West Cambodia. Therefore, the membership of the Subgroup A₂₋₁ cannot be defined precisely based on the graphic output of the CA alone and will be

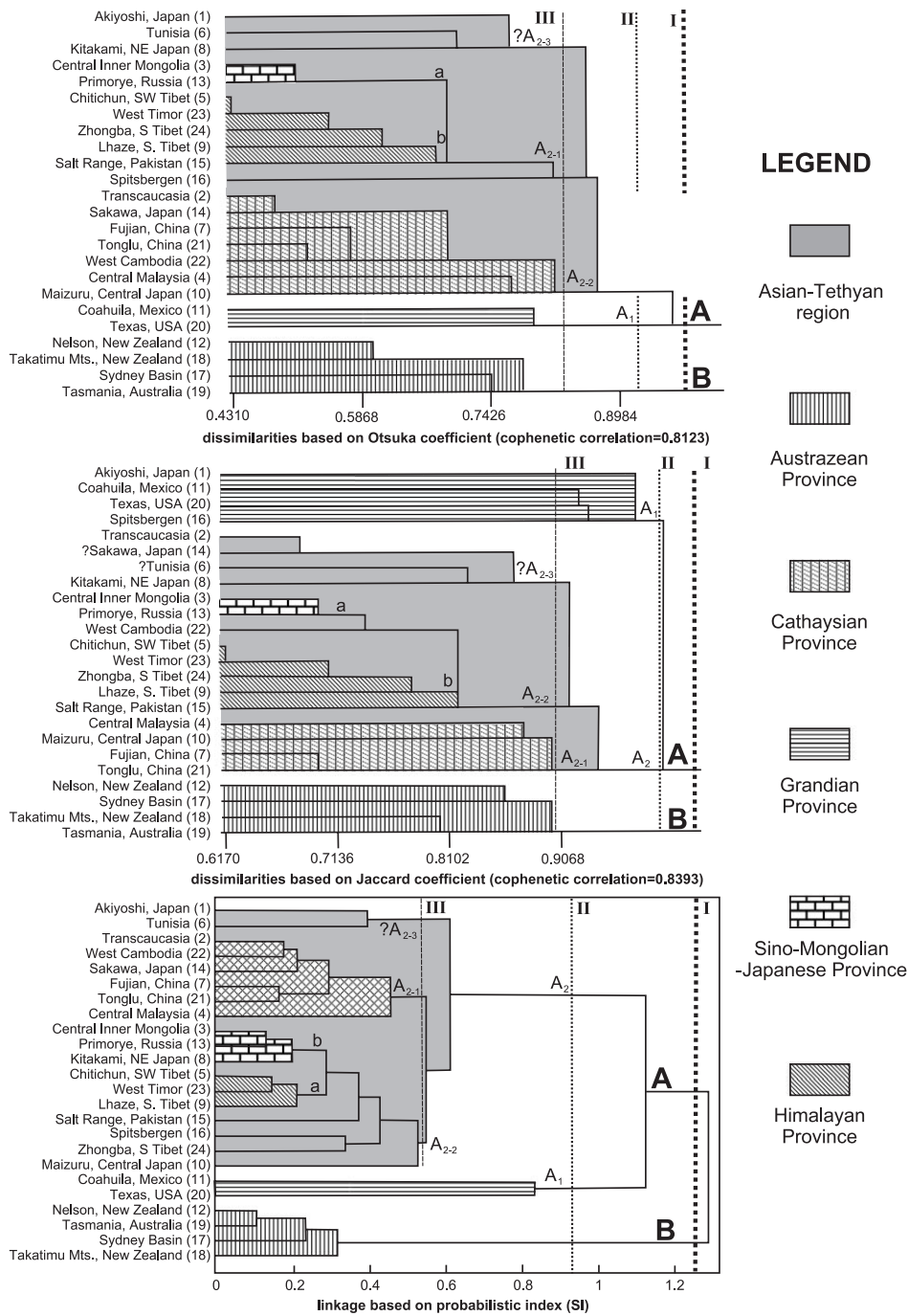


Fig. 3. Dendrograms of Capitanian brachiopod stations derived from UPGMA based on Otsuka, Jaccard coefficients and Probabilistic Index (SI). A, B—two supergroups; A₁, A₂—two groups in supergroup A; A₂₋₁, A₂₋₂, A₂₋₃—three subgroups in group A₂; a, b—two associations in subgroup A₂₋₂.

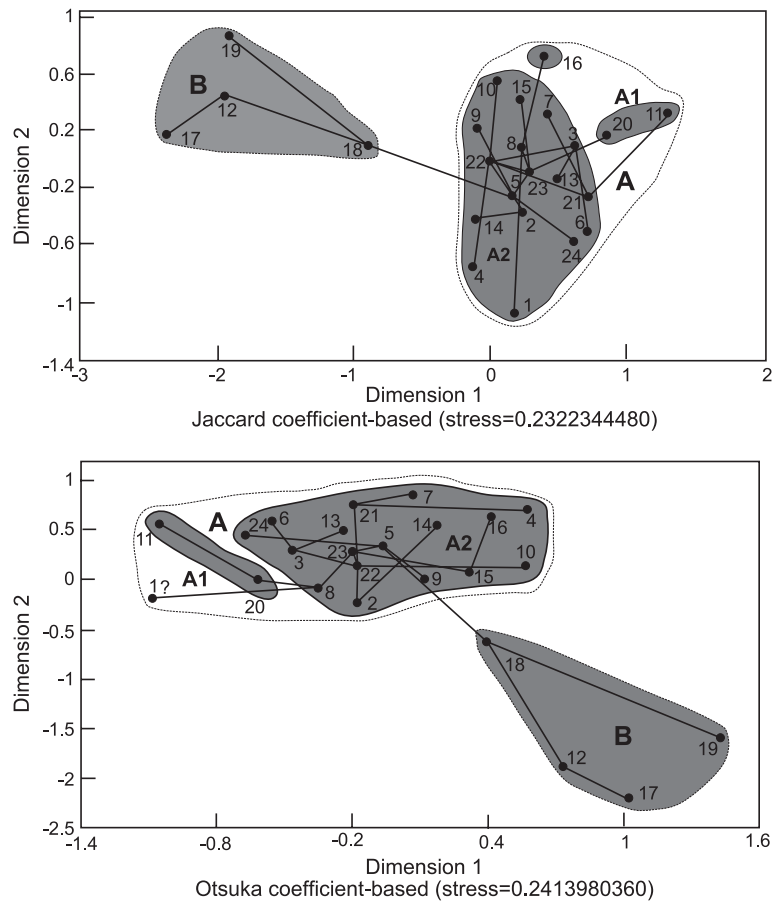


Fig. 4. An ordination plot of faunal stations on the first two principal dimensions of NMDS based on Otsuka, Jaccard coefficients superimposed with MST. Letters A, B, A₁ and A₂ correspond to those in Fig. 3. Sequential numbers (1–24) indicate faunal stations in Fig. 2 and Table 1.

further considered below in conjunction with the result from NMDS (Fig. 4).

Subgroup A₂₋₂ includes 8–9 stations and appears to embrace two subordinate associations (labeled as a, b in Fig. 3) in view of the Otsuka and Jaccard coefficients. Association *a* contains only two stations (Central Inner Mongolia in North China and South Primorye in Russian Far East) based on the Otsuka coefficient and three stations (Central Inner Mongolia, South Primorye and West Cambodia) based on the Jaccard coefficient, while Association *b* comprises five stations (Chitichun, Zhongba, Lhaze in southern Tibet, Salt Range in Pakistan and West Timor). In the dendrogram based on SI, however, these two associations are not readily recognizable although two other

core entities, one incorporating South Primorye, South Kitakami and Central Inner Mongolia, and the other with Chitichun, West Timor and Lhaze, remain distinctive, while the remainder of the stations in the subgroup (Zhongba, Salt Range, Maizuru and Spitsbergen) are only loosely linked to the two core entities (Fig. 3).

Graphically, the three dendrograms also reveal another vague subgroup (Subgroup A₂₋₃) with varying constituent members depending on the similarity coefficient used (Fig. 3). Stations in this subgroup are widely dispersed on modern geographical map. Thus, given the lack of integrity in its membership and wide geographical spread of stations, this subgroup is most likely an artifact of outlying stations

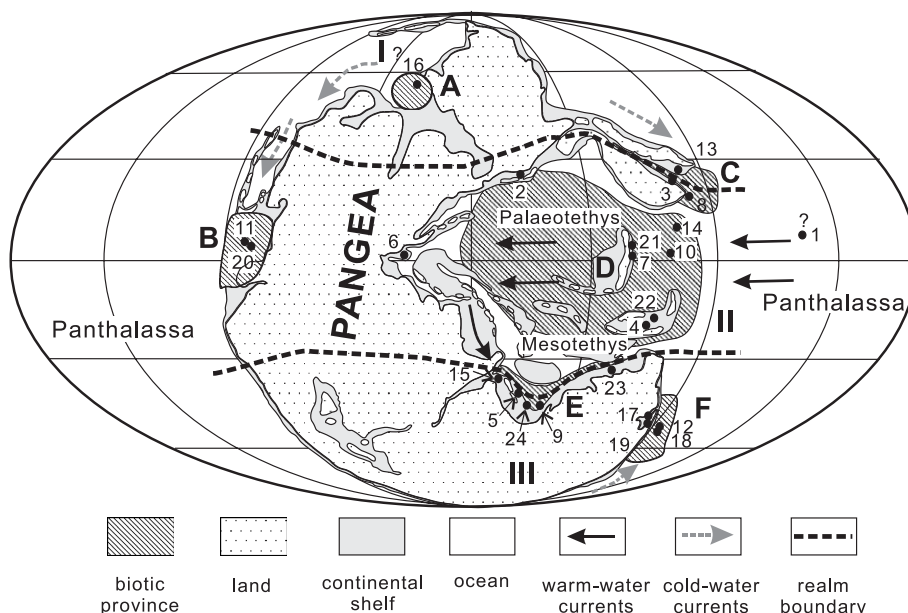


Fig. 5. Schematic reconstruction map of Capitanian global palaeogeography and palaeobiogeography (with base map modified from Ziegler et al., 1997). I—Boreal Realm; II—Palaeoequatorial Realm; III—Gondwanan Realm; A—Greenland-Svalbard Province; B—Gratian Province; C—Sino-Mongolian-Japanese Province; D—Cathaysian Province; E—Himalayan Province; F—Australasian Province.

loosely grouped together because of defects of the statistical methods employed. On account of this, Subgroup A₂₋₃ will not be discussed further below as a group entity, although the group and hence provincial affinities of its member stations are considered in conjunction with the other groups and stations.

The supergroups and groups are also well distinguished by NMDS (Fig. 4). However, not all subgroups within Group A₂ identified by CA are substantiated by NMDS. This reflects the instability of some stations in their status of group memberships and most likely is a result of insufficient data.

4. Interpretation

In this paper, we equate the supergroups, groups and subgroups described above to realms, regions and provinces respectively, following the recommendation by Grunt and Shi (1997) for Permian biogeographic units (biochores). Alternatively, Westermann (2000a,b) recommended a slightly

different hierarchy of biogeographical units in which a subrealm is used as a biogeographic unit between realm and province in place of region used in this paper.

4.1. Palaeoequatorial realm (Supergroup A)

This realm is represented by Supergroup A in the three dendrograms (Fig. 3). The Palaeoequatorial Realm includes regions situated in low palaeolatitudes during the Permian and can be distinguished from the northern Boreal Realm and the southern Gondwanan Realm by its abundant warm-water faunas, reef buildups, and high diversity. Brachiopods are dominated by many warm-water elements such as lytoniids and richthofeniids. In view of the statistical analyses and graphic outputs described in the preceding section, this realm appears to include two regions.

4.1.1. North American region (Group A1)

This region is represented by Group A₁ in Figs. 3 and 4 based on the Otsuka coefficient and SI. In the Jaccard-based dendrogram, the Akiyoshi terrane

and Spitsbergen are also grouped with West Texas, USA and Mexico in North America (Group A). Akiyoshi is composed of oceanic carbonates ranging from the Early Carboniferous to the Middle Permian and as such has been widely interpreted to represent a reef complex built on basaltic and pyroclastic rocks in an palaeoequatorial latitude located somewhere in Panthalassa between North America and the Palaeotethys (Kanmera and Nishi, 1983; Sano and Kanmera, 1988, 1996; Yanagida et al., 1971) and was displaced to its current position in Japan since the Permian (Hada et al., 2001, 2002). This tectonic history may suggest why the brachiopod fauna of Akiyoshi exhibits similarities with both the Palaeotethys in the west and western North America in the east. This dual similarity relationship may in part have also been contributed by the inadequate sampling of the Capitanian fauna of Akiyoshi (sampling efficiency=0.11).

In the dendrograms shown in Fig. 3, Spitsbergen is grouped with West Texas, USA and Coahuila, Mexico in Group A₁ based on the Jaccard coefficient but linked with some other stations in Group A₂ of northern peri-Gondwanan margin based on the Otsuka coefficient and SI. Spitsbergen is therefore highly unstable in its group membership. This may be due to either its relative low sampling efficiency and/or the fact that it shares many genera with western North America (e.g., *Kochiproductus*, *Cleiothyridina*, *Dyoros*, *Yakovlevia*, etc.) as well as some bipolar or antitropical genera with the peri-Gondwanan region of the Gondwanan Realm (such as *Waagenoconcha*, *Spiriferella*, *Neospirifer*, etc.). In view of this cross-linkage of Spitsbergen with all the key supergroups and groups recognized above and its mixed nature of faunal composition (endemic elements, bipolar/bi-temperate taxa and taxa shared with western North America), we are inclined to separate Spitsbergen from Supergroup A and treat it as an independent entity possibly representing the Boreal Realm (see below).

Grandian Province (Group A₁): The North American Region appears to be represented by a single province during the Capitanian Stage. Herein we adopt the term Grandian Province defined by Yancey (1975). Tropical and subtropical biotas of the Grandian Province occupied the Texas–New

Mexico–Coahuila area during the Early and Middle Permian (Yancey, 1975). The Grandian Province can be distinguished from other provinces by the presence of very large fusulinids, compound corals, sponges, algae, ornate brachiopods and ornate molluscs. In terms of the Capitanian brachiopods, the Grandian Province is characterized by many endemic genera (e.g., *Anteridocus*, *Aphaurosia*, *Arionthia*, *Bryorhynchus*, *Craspedona*, *Daltarina*, *Holosia*, *Lirellaria*, *Polymorpharia*, *Ptilotorhynchus*, *Xenosaria*), warm-water genera (e.g., *Ombonia*, *Geyerella*, *Meekella*, *Orthothenina*, *Tropidelasma*) and highly specialized lyttoniids (e.g., *Collemataria*, *Leptodus*, *Oldhamina*, *Pseudoleptodus*, *Rigbyella*) and richthofeniids (e.g., *Cyclacantharia*, *Prorichthofenia*). It is noteworthy that the Grandian Province also contains some Boreal or bipolar genera (e.g., *Kochiproductus*, *Spiriferella*, *Cleiothyridina*, *Anemaloria*, *Dyoros*, *Elivina*, *Yakovlevia*), indicating substantial palaeobiogeographical connections with the Boreal region. This link in the Permian brachiopod faunas has been noted before (Ustritsky, 1961; Shi, 1995; Shi and Grunt, 2000) and may be explained by the southward invasion of temperate to cold Arctic sea waters and faunas to low palaeolatitude areas of western North America (Fig. 5, see also Shen and Shi, 2000).

4.1.2. Asian Tethyan region (Group A₂)

This region is represented by Group A₂ in the dendrograms based on Otsuka, Jaccard coefficients and SI. Group A₂ is large and geographically dispersed in view of its membership (Figs. 3 and 5), but most of the members were located in the Palaeotethys and the surrounding areas in the reconstruction maps (e.g., Scotese and Langford, 1995; Scotese and McKerrow, 1990; Ziegler et al., 1997). Further subdivision of the group cannot be recognized by NMSD and MST (Fig. 4). This region is characterized by containing a large number of warm-water brachiopod genera. Other fossils include large verbeekiniid fusulinids (Ross, 1967; Yancey, 1975), compound waagenophyllid corals (Stevens, 1985; Belasky, 1994) and serrated gondolellid conodonts (Mei and Henderson, 2001). Cold-water brachiopod genera such as *Yakovlevia*, *Kochiproductus*, *Spiriferella*, *Anemaloria* and *Waagenoconcha* are totally

absent or only present in the northern and southern transitional zones between this region and polar regions (i.e., the Boreal Realm). All endemic genera listed in the North American Region above are not present in this region, while many common members of Superfamily Permianelloidea (e.g., *Permianella*, *Dicystoconcha*), *Peltichia*, *Orthothenina*, *Perigeyerella* are particularly abundant in this region. One province and two transitional zones (provinces) can be recognized in this region based on the three dendrograms (Fig. 3).

Cathaysian Province (Subgroup A₂₋₁): Group A₂₋₁ is an assembly of stations from southeast China (Tonglu and Fujian), Central Malaysia and probably also Maizuru of central Japan (Kobayashi, 2003) based on the Jaccard and Otsuka coefficients and may also include West Cambodia, Sakawa (Kurosegawa Belt) of Japan and Transcaucasia if based on the Otsuka coefficient and SI (Fig. 3). Despite some discrepancies in the three dendrograms, these stations have all been interpreted as islands in the Palaeotethys (e.g., Yin et al., 1999) with the exception of Transcaucasia, which was located in the western margin of the Palaeotethys during the Permian (e.g., Scotese and McKerrow, 1990; Ziegler et al., 1997). This province is characterized by numerous warm-water brachiopod genera such as *Peltichia*, *Cathaysia*, *Enteletes*, *Monticulifera*, *Permianella*, *Spinomarginifera*, *Tyloplecta*, *Vediproductus*, *Urushtenoidea*, etc. Cold-water or bipolar brachiopods such as *Kochiproductus*, *Yakovlevia*, *Spiriferella* are totally absent in this province.

The Cathaysian Province was first defined by Fang (1985) and has since been extended to also include parts of Japan, Indochina, some Cimmerian blocks in the Capitanian and Late Permian (Lopingian) (Fig. 5). This province has been well recognized by the earlier studies carried out on the Western Pacific region (Shi and Archbold, 1995a, 1995b, 1996) and Late Permian global brachiopod palaeobiogeography (Shen and Shi, 2000; Shen et al., 2000).

Transcaucasia is grouped with the stations of the Cathaysian Province based on SI, but only done so as an outlying station based on the Otsuka and Jaccard coefficients. Nevertheless, the strong palaeobiogeographical relationship of this station with the

Cathaysian Province is clearly indicated by many brachiopod genera common to both Transcaucasia and South China (e.g., *Edriosteges*, *Leptodus*, *Meekeella*, *Orthothenina*, *Richthofenia*, *Spinomarginifera*, *Terebratuloida*).

Transitional zones (Himalayan Province and Sino–Mongolian–Japanese Province, Subgroup A₂₋₂): As shown in the three dendrograms (Fig. 3), the Subgroup A₂₋₂ contains eight stations which were all (except Spitsbergen which is discussed separately, see below) situated in either northern or southern Palaeotethys/Meostethys. These eight stations can be readily subdivided into two associations: one consisting of Central Inner Mongolia in North China and South Primorye in Russian Far East, both located in the northern margin of the Palaeotethys; the other comprising Chitichun, Lhaze, Zhongba (southern Tibet), Salt Range (Pakistan) and West Timor all situated in northern peri-Gondwanan region (Fig. 5). This inter-hemispheric disjunction pattern of Subgroup A₂₋₂, as revealed by both CA and NMDS, is a very interesting feature and underlines a significant Permian global palaeobiogeographical disjunction that has received much recent attention. Shi et al. (1995) and Shi and Grunt (2000) have recently categorized and discussed the characteristics of the so-called Permian palaeobiogeographical transitional zones between the three major realms (Gondwanan, Boreal and Palaeoequatorial). In particular, they have noted the presence of two such distinct transitional zones in Asia: one to be found in East Asia (NE China, Japan and Russian Far East) between the Boreal Realm and the Palaeoequatorial Realm, and the other to be found in South and SE Asia between the Palaeoequatorial and Gondwanan Realms. Therefore, Subgroup A₂₋₂ seems to encompass both of these transitional zones. Thus, the association of Central Inner Mongolia and South Primorye can be equated to the Northern Transitional Zone of Shi et al. (1995) or the ‘Sino–Mongolian–Japanese Province’ (Tazawa, 1998; Shi and Tazawa, 2001; Shen and Shi, 2000), and the association of Chitichun, Lhaze, Zhongba, Salt Range (Pakistan) and West Timor may be assigned to the “Southern Transitional Zone” of Shi et al. (1995) or the Himalayan Province as defined by Singh (1987) and Shen and Shi (2000).

The Sino–Mongolian–Japanese Province is distinguished by the admixture of marine invertebrate

genera indicative of both Cathaysian (e.g., *Enteletes*, *Haydenella*, *Leptodus*, *Meekella*, *Richthofenia*, *Spinomarginifera*) and Boreal/bipolar (e.g., *Anemolaria*, *Bathymyonia*, *Megousia*, *Spiriferella*, *Timaniella*, *Waagenoconcha*, *Yakovlevia*) affinities.

Arguably, this province may also include the South Kitakami Belt in northeast Japan. Tazawa (2000, 2001, 2002) has repeatedly emphasized the palaeobiogeographical linkage between the South Kitakami Belt with the Sino–Mongolian–Japanese Transitional Zone. However, according to Otsuki (1992), Ehiro and Kanisawa (1999), Ehiro (2001) and Hada et al. (2002), the South Kitakami Belt originated in the northern margin of Gondwanaland and in the Permian was located in the vicinity of South China. In view of the Capitanian brachiopods, the south Kitakami Belt contains both Boreal-type or bipolar brachiopods such as *Yakovlevia*, *Waagenoconcha*, *Megousia*, *Spiriferella*, as well as many warm-water Cathaysian-type elements such as *Leptodus*, *Spinomarginifera*, *Richthofenia*, *Geyerella* and *Tyloplecta*.

Another controversial station is the Sakawa Basin in Shikoku, Japan belonging to the Kurosegawa Belt. This station, together with the South Kitakami Belt, has been considered to be in the southern hemisphere during the Permian by Ehiro (2001) and Hada et al. (2001). However, linkages also exist between some brachiopod faunas of the Kurosegawa Belt and those of the Sino–Inner Mongolian–Japanese Province, suggesting a close palaeobiogeographical affinity between them, as previously suggested by Tazawa (2002).

The Himalayan Province is not significantly different from the same province of the Wuchiapingian age in terms of spatial distribution and palaeogeographical setting (Shen and Shi, 2000; Shen et al., 2000), suggesting that the province was well developed across the Guadalupian–Lopingian boundary. However, the Himalayan Province differs substantially from the earlier palaeobiogeographical entities in the same general palaeogeographical region during the late Early Permian and early Middle Permian when the region was characterized by the Sibumasu Province (Shi and Archbold, 1998).

Brachiopod faunas in the Capitanian Himalayan Province are characterized by intermingling both Gondwanan/bipolar/bi-temperate elements (e.g., *Asperlinus*, *Cleiothyridina*, *Costiferina*, *Elivina*, *Fletcherithyris*, *Himathyris*, *Hunzina*, *Spiriferella*, *Spi-*

rigerella, *Stereochia*, *Waagenoconcha*) and Cathaysian/palaeoequatorial elements (e.g., *Enteletes*, *Vediproductus*, *Richthofenia*, *Leptodus*, *Haydenella*, *Tschernyschewia*, *Tyloplecta*, *Urushtenoidea*).

4.2. Greenland-Svalbard Province (Boreal Realm)

Insufficient number of Arctic stations in the current brachiopod database precludes the unequivocal recognition of the generally accepted Boreal Realm by CA, NMDS and MST. The only station from this region included in the database was Spitsbergen. In our statistical analyses, the station was grouped with either North American stations or peri-Gondwanan stations by CA. Palaeogeographically and tectonically, it is extremely unlikely that Spitsbergen was in the southern hemisphere during the Permian (Fig. 5). This suggests that the apparent group relationship of Spitsbergen with western North America and peri-Gondwana is more than likely an artifact of statistical influence generated by a relative high proportion (compared to the total number of genera sampled from Spitsbergen) of genera shared with western North America and a high proportion of bipolar/bi-temperate genera shared with peri-Gondwana. Therefore, while recognizing the significant links between Spitsbergen and western North America and Peri-Gondwana as demonstrated by common genera, we herein treat Spitsbergen as representing an independent province of the Boreal Realm for which we adopt the name Greenland-Svalbard Province as proposed and defined by Grunt and Shi (1997). Capitanian brachiopods in the Greenland-Svalbard Province is characterized by the typical Boreal-type or bipolar genera such as *Anemolaria*, *Cleiothyridina*, *Dyoros*, *Horridonia*, *Kochiproductus*, *Lissochonetes*, *Paeckelmanna*, *Pinegathyris*, *Spiriferella*, *Waagenoconcha*, *Yakovlevia*. Warm-water brachiopods such as lyttoniids and richthofenids which are common in the Palaeoequatorial Realm are totally absent in this province.

4.3. Gondwanan Realm (Group B)

This realm is well distinguished in the three dendrograms by CA (Fig. 3) and the scatter plots by NMDS (Fig. 4) and located in the high latitudes of Southern Hemisphere. Only one province, the Aus-

trazean Province, is recognizable within this realm during the Capitanian.

Austrazean Province (Group B): Permian marine faunas with Gondwanan affinities were widespread on the supercontinent during the Early Permian and early middle Permian. However, seawater withdrew from most areas of Gondwana as a result of the major regression during the Late Guadalupian. During the Capitanian, brachiopod faunas of Gondwanan Realm were restricted to eastern Australia and New Zealand, indicating the continuous presence of the Austrazean Province (Archbold, 1983) which originated in the Early Permian. At this time and throughout the Permian (Asselian is an exception, see Shi and Archbold, 1993), the Austrazean Province was yet characterized by a highly endemic fauna. The endemic brachiopod genera include *Capillonia*, *Fletcherithyris*, *Filiconcha*, *Glendonina*, *Lamnaespina*, *Lethamia*, *Lipanteris*, *Magniplicatina*, *Maorielasma*, *Marinurnula*, *Notospirifer*, *Plekonella* and *Terrakea*. In addition, a significant percentage of bipolar and bi-temperate taxa were also present (e.g., *Echinalosia*, *Eliva*, *Costatumulus*, *Cleiothyridina* and *Tomiopsis*). Typical palaeoequatorial elements are completely absent in this province. The Austrazean Province also differs from the Greenland-Svalbard Province by the absence of typical Boreal elements such as *Yakovlevia* and *Kochiproductus*.

5. Discussion

5.1. Latitudinal diversity pattern

Following Shi and Shen (2000), we have carried out a quantitative analysis between generic richness and palaeolatitudes as an attempt to test the widely held perception (e.g., Fischer, 1960; Belasky, 1994) that species diversity is primarily controlled by latitude-related thermal gradients. In carrying out this test, we compiled a data matrix of species/genera diversities of the Capitanian brachiopods from the operational geographical units (OGUs) against the average palaeolatitude settings of the OGUs. We obtained the palaeolatitude measurements from the published literature of palaeomagnetism (Table 1) and, where such data were not available, extrapolated them from the stage-by-stage reconstruction maps of

Ziegler et al. (1997). Polynomial regression analysis was then applied to the data in order to reveal the statistical relationship between the generic diversity and palaeolatitude. As shown in (Fig. 6), the simple generic diversities of brachiopods during the Capitanian peaked in the two transitional zones (Himalayan Province and Sino–Mongolian–Japanese Province, respectively) and fell dramatically in the poles. Therefore, the general large-scale biotic pattern of high diversity does not exhibit strict correlation with low latitude in terms of the Capitanian data (Fig. 6). This diversity pattern is slightly different from that based on rugose corals. According to Belasky (1994), rugose corals exhibit the highest diversity in the tropical regions and progressively decrease toward poles. Therefore, they are generally controlled by latitude-related thermal gradients. It may be interpreted that the difference in brachiopod and coral diversity patterns is due to their different sensitivities to water temperature. As we all know, brachiopods apparently have less sensitivity to temperature and wider geographic distribution than rugose corals. However, rugose corals are much more sensitive to water temperature, and largely distributed in the tropical and subtropical regions.

Of course, generic diversities of certain palaeolatitude regions and provinces were influenced by sampling intensities. This effect, if present, can be revealed by rarefaction analysis. Rarefaction analysis is basically an interpolation technique (Sanders, 1968), making it possible to estimate how many taxa would have been found had the sample been smaller

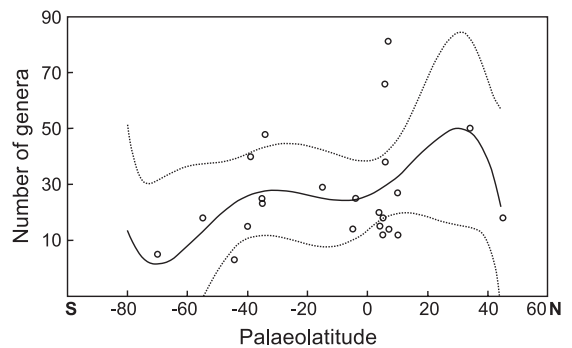


Fig. 6. Relationship of Capitanian brachiopod generic diversities with the palaeolatitude gradient. Solid line depicts number of genera against palaeolatitude; dotted lines depict 95% confidence bands of the diversity pattern curve.

than it actually was. We have therefore carried out a generic occurrences/genera rarefaction analysis for the global Capitanian brachiopod faunas to allow a comparison of diversity trends of different provinces in a framework of standardized or equalized sampling efficiency (Raup, 1975, 1991; Miller and Foote, 1996). In simple terms, the occurrences of genera in each sample (herein refer to province) were counted, and each sample was rarefied so that the samples with different number of generic occurrences could be compared by reducing all samples to the same of the smallest sample. To avoid possible biases, all the outlying OGU's with palaeobiogeographical uncertainties indicated by CA and MNDS in the previous palaeobiogeographical analyses (e.g. Akiyoshi, Sakawa in Japan and Tunisia) were excluded. Thus, the Cathaysian Province only included five stations (Fujian, Tonglu, West Cambodia, Central Malaysia, Maizuru of central Japan), the Himalayan Province five stations (Chitichun, Salt Range, Zhongba, Lhaze, West Timor), the Sino–Mongolian–Japanese Province three stations (central Inner Mongolia, Russian Far East and Kitakami in northeast Japan), the Grandian Province two stations (West Texas, USA and Coahuila, Mexico), the Greenland-Svalbard Province one station only (Spitsbergen), and the Austrazean Province three stations (Sydney Basin, Tasmania, and Nelson and Takatimu Mountains of New Zealand). As shown in Fig. 7, the generic diversity trajectories for the six provinces indicate that the diversities were lowest in the Austrazean and Greenland-Svalbard Provinces, which were both located in the polar regions during the Permian. By contrast, the diversity of the Cathaysian Province in the palaeoequatorial region appeared to be the highest, and the diversities of the two transitional zones were nearly as high as that of the Cathaysian Province (Fig. 7). The generic diversity of the Grandian Province, however, is clearly lower than those of the two transitional zones even though it was located in a lower palaeolatitude setting than the former two zones.

As shown by the palaeobiogeographical and diversity patterns (Figs. 5–7), the spatial arrangement of provinces and generic diversity of the Capitanian brachiopods were generally related to variations of palaeolatitudes, but this relationship is not as clearly inverse as one would expect, as the transitional zones of middle palaeolatitudes tend to have higher diversi-

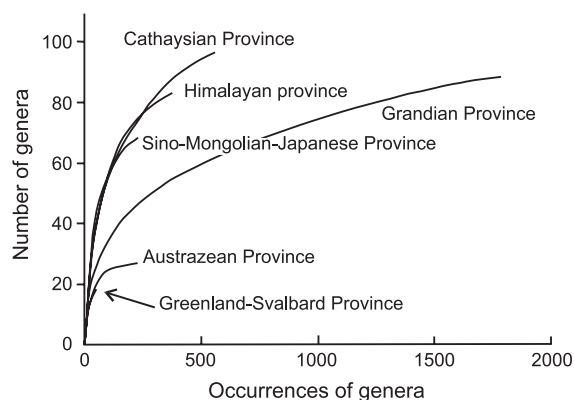


Fig. 7. Comparative rarefaction curves for the six provinces based on analysis of the worldwide database of genus occurrences. The rarefaction curves for the tropical Cathaysian Province, and the temperate Himalayan and Sino–Mongolian–Japanese Provinces are similar and indicate higher diversities than other provinces as indicated by the highest curves in the figure. The two bipolar provinces, Austrazean and Greenland-Svalbard Provinces, are lowest in generic diversity as indicated by the lowest curves in the figure. The Grandian Province is between the bipolar provinces and the tropical and subtropical provinces in diversity.

ties than some lower palaeolatitudes. This deviation from the generally accepted model that lower latitudes harbor higher diversities demands additional factors other than latitudes alone in explaining global trends of diversity patterns. One possible mechanism is that the temperate zones are mesothermal, and therefore would draw taxa of greater adaptabilities from not only the palaeoequatorial Cathaysian Province but also the temperate/polar provinces (Shen and Shi, 2000; Shi and Shen, 2000). Another possible mechanism in favor of an area effect in latitudinal diversity is simply that continental areas were greater in the two transitional zones along the continental margin of Pangea, and therefore provided more inhabitable areas for brachiopods (Fig. 5).

On the other hand, the Grandian Province in western North America was clearly affected by cool-water currents from the Boreal region as indicated by the invasion of some Boreal- and bipolar-type brachiopods such as *Yakovlevia*, *Kochiproductus*, *Spiriferella*, *Waagenoconcha*, *Anemolaria*, *Dyoros*, *Megousia*, etc. (Fig. 5). In addition, the continental shelves in western North America were gradually exposed during the end-Guadalupian regression. This may have also contributed to the low diversity of the

Grandian Province compared with the two transitional zones of temperate palaeolatitudes.

5.2. *Comparison with the Wuchiapingian and Changhsingian brachiopod palaeobiogeography and the Capitanian palaeobiogeography based on other fossil groups*

The quantitative analyses based on brachiopod faunas from Capitanian to Changhsingian (Shen and Shi, 2000; Shen et al., 2000) indicate that the Cathaysian, Austrazean, Greenland-Svalbard Provinces and the two transitional zones (Himalayan and Sino–Mongolian–Japanese Provinces) were recognizable during the whole interval. The western Tethyan Province is recognized in the Wuchiapingian and Changhsingian (Shen and Shi, 2000; Shen et al., 2000) but cannot be distinguished from the Cathaysian Province in terms of the Capitanian brachiopods, and is therefore incorporated into the Cathaysian Province (e.g., Transcaucasia). The Austrazean Province during the Capitanian was clearly larger in area than during Wuchiapingian and Changhsingian due to the presence of the Capitanian brachiopod faunas in the Sydney Basin and Tasmania in eastern Australia. The Grandian Province in western North America was no longer present during the Lopingian due to the global regression at the end of Guadalupian (Shen and Shi, 2000).

Permian palaeobiogeography at a global or regional scale based on fusulinids, corals and conodonts has been presented by different workers (e.g., Ross, 1967; Stevens, 1985; Belasky, 1994; Mei and Henderson, 2001). Although these different groups evolved and dispersed independently, previous studies suggest that the broad distributional patterns for these various fossil groups were generally comparable at realm and region levels during the Carboniferous and Permian Periods.

According to Ross (1967), the distribution of fusulinids is closely related to marine shelves adjacent to the continents. The Tethyan Realm, identified by the verbeekiniid association, extended from Tunisia, Sicily, and Yugoslavia eastward through Central Asia and branched into southeast Asia and Indonesia and north through China, Japan and Primorye and into British Columbia, Washington, Oregon and California, and largely comparable with the Palaeoequatorial

Realm and two transitional zones (Himalayan Province and Sino–Mongolian–Japanese Province) in this paper based on brachiopods. However, further division of the biogeographic units was not dealt with by Ross (1967).

Similarly, the Tethyan Province, identified based on the presence of the family Waagenophyllidae (Stevens, 1985), is largely comparable to the Asian–Tethyan region in this paper. The waagenophyllid corals are widely represented in the Tethyan region, from Tunisia, Sicily, Yugoslavia and Austria on the west, extending eastward through central Asia to Vietnam, Sumatra, Timor, China, Japan and the Russian Far East (Stevens, 1985). The faunal composition and Permian palaeogeography suggest that the Texas faunas occupied a minor sea between the Tethys and Panthalassan Ocean and contain a variety of Tethyan faunal elements. Therefore it can be assigned to the Palaeoequatorial Realm together with the Tethyan region above. However, most Early Permian Texas fusulinids seem to have non-Tethyan affinities and non-Tethyan massive corals are also common in the Early Permian in Texas. This was used to recognize the Grandian Province by Yancey (1975) and Stevens (1985).

Three provinces of Permian conodonts, referred to as the North Cool Water Province (NCWP), the Equatorial Warm Water Province (EWWP), and the peri-Gondwana Cool Water Province (GCWP) have been recognized (Mei and Henderson, 2001). The NCWP and GCWP are both dominated by cold-water genera such as *Merrillina* and *Mesogondolella* and the absence of *Sweetognathus* in the Guadalupian. The NCWP and the GCWP are largely comparable with the Boreal and Gondwanan Realms based on brachiopods. On the other hand, the EWWP is characterized by the abundance of *Sweetognathus* and the serrated *Jinogondolella* in the Guadalupian, and the *Clarkina* and *Iranognathus* in the Lopingian which are all warm-water elements. The EWWP is comparable with the Palaeoequatorial Realm based on brachiopods. It is interesting that mixed faunas are also recognized in the transitional regions between the EWWP and GCWP including West Timor, Pamirs and the Salt Range, Pakistan during the Guadalupian and Lopingian based on conodonts (Mei and Henderson, 2001). This transitional zone is apparently the Himalayan Province discussed in this paper although

a provincial name was not given by Mei and Henderson (2001).

5.3. Biogeographical determinants

As already indicated, palaeolatitude seems to have played a critical role in controlling the global distribution of generic diversity as well as the spatial distribution of provinces during the Capitanian. That is, all of the provinces recognized more or less followed the zonation pattern of palaeolatitudes (Fig. 5). As indicated by the analysis from NMDS (Fig. 4), Dimension 1 seems to be largely related to the palaeolatitude, although the scatter plots are different based on different coefficients. In the scatter plots based on the Jaccard coefficient, the stations of the Gondwanan Realm are located in the left side, whereas all other stations are in the right side (Fig. 5). In the scatter plots based on the Otsuka coefficient, the stations of the Gondwanan Realm are located in the right side. Geographically, the relationship between the brachiopod palaeobiogeography and palaeolatitude can be well displayed by the symmetrical distribution of the biogeographical provinces in the eastern Panthalassa–Palaeotethyan region (Fig. 5). The palaeoequatorial Cathaysian Province was in the middle, whereas the Greenland-Svalbard Province was in the Arctic region and the Austrazean Province in the Gondwanan Realm. In the temperate zones between the Boreal Realm and the Palaeoequatorial Cathaysian Province and between the Gondwanan Realm and the Cathaysian Province two transitional zones typified by the mixed brachiopod faunas were developed (Fig. 5).

The circulation of ocean currents was probably another important factor to affect the brachiopod palaeobiogeography at least in some local areas/provinces. This argument is particularly relevant to the Grandian Province. This province contains many endemic taxa mixed with some Boreal/bipolar elements although warm-water elements remain dominant. The presence of these Boreal/bipolar taxa in the otherwise low-palaeolatitude Grandian Province can possibly be explained by the presence of an ocean current similar to the modern “California current” that flowed from the Arctic along the coast of north-western Pangea to low palaeolatitude areas of south-western USA (Texas and Mexico) and brought with it

cold-water Boreal taxa to intermingle with endemic warm-water faunas (Shi, 1995).

6. Conclusions

Six marine biotic provinces can be recognized during the Capitanian based on the brachiopod faunas. This Capitanian palaeobiogeographical pattern is largely comparable with those of the Wuchiapingian and Changhsingian (Shen and Shi, 2000; Shen et al., 2000), but differs in (1) the absence of the Grandian Province in western North America in the Lopingian because of the end-Guadalupian global regression and (2) the incorporation of the Western Tethyan Province into the Cathaysian Provinces during the Capitanian. The Austrazean Province was much larger in area than during the Lopingian due to the presence of the brachiopod fauna in the Sydney Basin of eastern Australia and Tasmania. The differences among provinces were primarily controlled by variations in palaeolatitude-or palaeolatitude-related thermal gradient. The expected “bell-shaped” model of low latitude with high diversity is not observed in terms of the Capitanian brachiopod diversity patterns. The diversities of the two transitional zones were probably enhanced by the intermingling of both the Cathaysian and bipolar/bi-temperate taxa and the location of Tethyan shelves in these localities. In addition, the movement of ocean currents along continental margins also played an important role in the dispersal of brachiopods and characterization of some provinces.

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