Paleobiogeographical extinction patterns of Permian brachiopods in the Asian–western Pacific region

Shen Shu-zhong and G. R. Shi

Abstract.—Spatial and temporal variations in biological diversity are critical in understanding the role of biogeographical regulation (if any) on mass extinctions. An analysis based on a latest database of the stratigraphic ranges of 89 Permian brachiopod families, 422 genera, and 2059 species within the Boreal, Paleoequatorial, and Gondwanan Realms in the Asian–western Pacific region suggests two discrete mass extinctions, each possibly with different causes. Using species/family rarefaction analysis, we constructed diversity curves for late Artinskian–Kungurian, Roadian–Wordian, Capitanian, and Wuchiapingian intervals for filtering out uneven sampling intensities. The end-Changhsingian (latest Permian) extinction eliminated 87–90% of genera and 94–96% of species of Brachiopoda. The timing of the end-Changhsingian extinction of brachiopods in the carbonate settings of South China and southern Tibet indicates that brachiopods suffered a rapid extinction within a short interval just below the Permian/Triassic boundary.

In comparison, the end-Guadalupian/late Guadalupian extinction is less profound and varies temporally in different realms. Brachiopods in the western Pacific sector of the Boreal Realm nearly disappeared by the end-Guadalupian but experienced a relatively long-term *press* extinction spanning the entire Guadalupian in the Gondwanan Realm. The end-Guadalupian brachiopod diversity fall is not well reflected at the timescale used here in the Paleoequatorial Realm because the life-depleted early Wuchiapingian was overlapped by a rapid radiation phase in the late Wuchiapingian. The Guadalupian fall appears to be related to the dramatic reduction of habitat area for the brachiopods, which itself is associated with the withdrawal of seawater from continental Pangea and the closure of the Sino-Mongolian seaway by the end-Guadalupian.

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Introduction

The supercontinent Pangea, formed in the Permian, stretched almost from pole to pole in a meridional orientation. On the eastern shelves of Pangea and around the microcontinents scattered in the eastern Paleotethys (e.g., South China, Indochina, Sibumasu; see Fig. 1), Permian marine benthic organisms were abundant and exhibited a highly dynamic history of provincialism. Among them, brachiopods were particularly ubiquitous but highly varied in geographical distribution. The Permian brachiopods of the Asian–western Pacific region have been the subject of several detailed paleobiogeographical studies (Nakamura et al. 1985; Shi et al. 1995; Shen and Shi 2000; Shi and Shen 2000). However, only recently has the relationship between Permian brachiopod biogeography and the mass extinctions in this region attracted attention. Geographic selectivities have been inves-

tigated for the Cretaceous–Tertiary mass extinction (e.g., Raup and Jablonski 1993) and the end-Ordovician mass extinctions (e.g., Sheehan and Coorough 1990), and a plea has been raised for similar studies on the Permian–Triassic mass extinction (Valentine and Moores 1973; Erwin 1993). However, it is not known whether the end-Permian mass extinction varied paleobiogeographically in terms of timing, magnitude, and taxonomic selectivity, nor whether provincialism had any role in regulating diversity and extinction patterns through the Permian.

In this paper, we investigate aspects related to the first issue by examining the Permian brachiopod faunas of the Asian–western Pacific region. Specifically we address two questions: (1) Are brachiopod mass extinction patterns comparable among different Permian biogeographical realms in terms of timing, magnitude, and taxonomic groups affected?
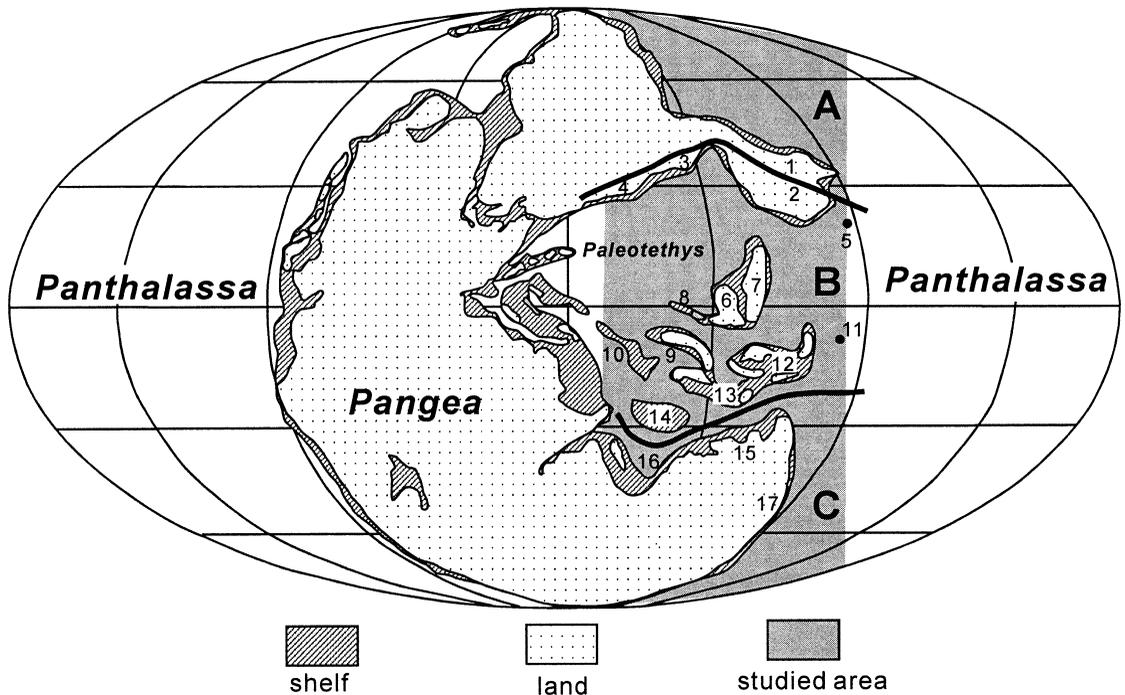
FIGURE 1. Schematic reconstruction of Permian paleogeography and paleobiogeography showing the study region and three major biotic realms. A, Boreal Realm. B, Paleoequatorial Realm. C, Gondwanan Realm. 1 = Mongolia and Russian Far East; 2 = Inner Mongolia and northeast China; 3 = Tarim Basin; 4 = Transcaucasia; 5 = Southern Kitakami and Hida Gaien, Japan; 6 = South China; 7 = Southeast China; 8 = Western Yunnan; 9 = Qiangtang block; 10 = Iran block; 11 = Inner Zone, Japan; 12 = Indochina block; 13 = Sibumasu Arc; 14 = Lhasa block; 15 = Western Australia; 16 = Himalayan terrane; 17 = Eastern Australia and New Zealand. Base map after Ziegler et al. 1997.

(2) If the brachiopod mass extinctions did exhibit paleobiogeographical variations, then what were the likely causes of these variations?

In an earlier report (Shi and Shen 2000), we analyzed paleobiogeographical patterns of Permian brachiopod extinctions in this region. The earlier study was based on a series of databases compiled by Shi and colleagues. Their main conclusions were (1) that Permian brachiopod faunas in the Asian–western Pacific region suffered two major mass extinctions, respectively at the end-Guadalupian/late Guadalupian and Changhsingian, and (2) that these two extinctions are only broadly comparable among different Permian biogeographical realms. With respect to the latter, we also noted that (1) the end-Guadalupian/late Guadalupian extinction is most pronounced in the Gondwanan and Boreal Realms and less well expressed in the Paleoequatorial Realm, and that (2) the end-Changhsingian extinction

appears to have been much more severe than the end-Guadalupian extinction and of shorter duration. However, given its preliminary nature, this initial study suffered from several pitfalls. First, the brachiopod data for the late Kungurian–Roadian interval was not investigated because a detailed international timescale of the Permian System was not available when the databases were compiled. Second, although we made every effort to ensure that the database was both taxonomically and biostratigraphically sound, variations in sampling intensity and their potential effect on diversity and extinction patterns were not considered. Finally, our initial study was focused on diversity and extinction patterns only, and was not intended to consider causal mechanisms. These aspects are dealt with in the present study, which is based on a revised and expanded database and uses the recently proposed threefold Permian chronostratigraphical timescale (Jin et al. 1997).

Data and Methods

This study is restricted to Brachiopoda recorded from the Permian of the Asian–western Pacific region. This region is ideal as a proxy for Permian global shallow-marine provincialism because the three widely recognized Permian biogeographical realms, i.e., Boreal, Paleoequatorial (term of Grunt and Shi 1997), and Gondwanan Realms, are all distinctly represented in this region (Fig. 1). The biogeographical characteristics of these realms and their spatial and temporal ranges/boundaries have been discussed in a number of studies (Waterhouse and Bonham-Carter 1975; Nakamura et al. 1985; Grunt and Shi 1997; Shi and Grunt 2000) and will not be repeated here.

The basic database for the present study was taken from that of Shi and Shen (1999), which was collated and summarized from a succession of Permian stage-by-stage data sets compiled for the Asian–western Pacific region by Shi and colleagues since 1992 (see Shi and Shen 1999 for references and details of these published databases). However, such databases must be updated regularly. We have therefore updated and expanded the initial database by adding the late Kungurian–Roadian interval and including new Permian brachiopod faunas published since 1992. Thus, the new database includes all the time segments of the Permian necessary for extinction analysis. The chief sources of additional faunal data have been the works of Briggs (1998), Shi and Shen (1998), Shen and Jin (1999), and Shen et al. (2000, 2001, in press).

In compiling the database, we have examined all available published Permian brachiopod literature of the region and updated the taxonomy and age determinations of the published records in light of the latest developments of Permian brachiopod taxonomy and biostratigraphy. A total of 89 families, 422 genera, and 2059 species in the three realms are recorded in the revised and updated database. Seven Permian time intervals are utilized in accordance with the recently proposed threefold Permian chronostratigraphic scale (Fig. 2). Brachiopods in the early Griesbachian of the earliest Triassic are also investigated. The seven Permian intervals do not

Chronostratigraphy (Jin et al. 1997)			Geochronology		
			Time	Duration	Interval
Tri.		Griesbachian	251Ma		8
Permian	**Lopingian**	Changhsingian	253Ma	2myr	7
		Wuchiapingian	259Ma	6myr	6
	Guadalupian	Capitanian	265Ma	6myr	5
		Wordian		5myr	4
		Roadian	270Ma		
	Cisuralian	Kungurian		9.5myr	3
		Artinskian L. Artinskian	279.5Ma		
		E. Artinskian		9.5myr	2
		Sakmarian L. Sakmarian	289Ma		
		E. Sakmarian		9myr	1
		Asselian	298Ma		

FIGURE 2. The newly proposed threefold Permian timescale (Jin et al. 1997) and the intervals used in this paper. The absolute ages of the Permian/Triassic boundary, Changhsingian/Wuchiapingian boundary, and the base of Capitanian are from Bowring et al. 1998. The other ages are interpolated based on the timescale of Young and Laurie (1996).

strictly follow the precise stage boundaries of the chronostratigraphical scale. Some grouping is necessary because the ages of some of the brachiopod faunas span stage boundaries. To allow rarefaction analysis for intervals in the Guadalupian (middle Permian), we grouped Roadian with Wordian to achieve comparable time durations for the Roadian–Wordian, Capitanian, and Wuchiapingian intervals (see below).

To examine the variations in brachiopod diversity and extinction patterns through time, we used three quantitative measures: raw taxonomic richness and proportional and total extinction rates. The proportional extinction rate refers to the proportion of extinct taxa recorded in a time interval divided by the total number of taxa recorded in that interval, whereas the total extinction rate is calculated by the ratio of taxa becoming extinct in a time

interval over the duration (million years) of the interval. These two extinction metrics are selected for this study from many other alternative measures (Foote 1994) and have also been used in our earlier analysis (Shi and Shen 2000).

During the establishment of our database, we found that the sample intensities are clearly different in different realms and intervals. Various methodologies are available to assess the sampling problems. Considering the nature of our present brachiopod database, species/family rarefaction analyses were carried out to evaluate the actual effects of sampling intensities in the different realms or time intervals, following the methodology of Raup (1975). Rarefaction analysis is basically an interpolation technique (Sanders 1968), making it possible to estimate how many species would have been found had the sample been smaller than it actually is. Ideally, to evaluate the sampling intensities, rarefaction analysis is commonly carried out at the level of numbers of individual organisms or biomass, but the fossil record of species and individuals is much too spotty for this to be possible, and the numbers of individual brachiopods were often not recorded in most early publications. In this paper, therefore, we use data on the occurrences of species within families rather than specimens within species for rarefaction analysis. The shift of taxonomic rank does not change the method mathematically or conceptually (Raup 1975). That is, numbers of species, genera, and families in each interval of each realm were counted, and each sample was rarefied so that the brachiopod assemblages with different number of species/genera/families in the same interval in different realms, or different intervals with the same/similar durations in the same realm, could be compared by reducing all samples to the size of the smallest assemblage. Species/genus or genus/family rarefaction analysis is not used herein because rarefaction analysis between closer taxonomic ranks may reduce or obscure the differences among diversity curves with high confidence limits. Rarefaction analysis applied in a single phylum (Brachiopoda in this paper) clearly meets the basic requirements as discussed by Tipper (1979).
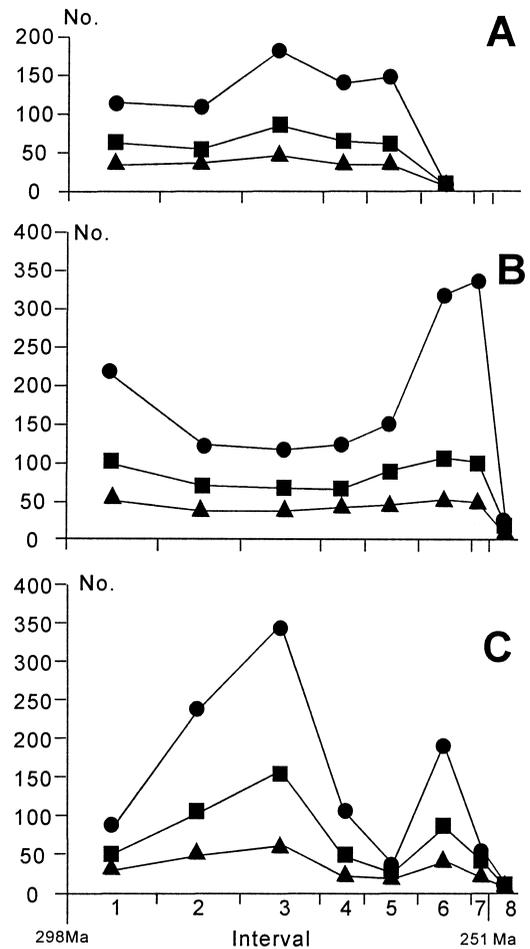

FIGURE 3. Simple diversities at familial (▲), generic (■), and specific (●) levels in the three realms. Interval numbers are same as in Figure 2. Interval widths are scaled to duration. A, Boreal Realm. B, Paleoequatorial Realm. C, Gondwanan Realm.

Two bars—one above the observed value and one below it—are used to estimate the uncertainties of the rarefaction curves. A confidence limit (95%) shows the robustness of the observed values. To calculate the standard deviations at any point on the curves, we used the computer program compiled by S. M. Holland released on the website http://www.uga.edu/strata/software/index.html.

Results and Discussion

Biogeographical Patterns of Diversity and Extinctions

The diversity and extinction patterns in the three realms are summarized in Figures 3 and 4. Figure 3A shows that the simple diversity

of Permian brachiopods in the Boreal Realm peaked during the late Artinskian–Kungurian, then declined considerably toward the end of the Capitanian (end-Guadalupian). Late Permian marine faunas in the Russian Far East are dominated by abundant ammonoids with very few brachiopods. Only four Tethyan-type genera and four species (*Haydenella* sp., *Paracrurithyris pigmaea* [Liao], *Crurithyris flabelliformis* Liao, *Araxathyris minor* Grunt) were recorded, with no description or illustrations (Zakharov and Oleinikov 1994; Zakharov et al. 1995). These warm-water species are considered to have migrated from the more southerly Cathysian region during the closure of the Sino-Mongolian seaway and therefore are assigned to the Paleoequatorial Realm. The diversity curves dropped sharply during the Late Permian. Both the proportional and total extinction profiles depict troughs for the late Sakmarian–early Artinskian, then steady climbs toward the Capitanian (Fig. 4A).

The simple diversities in the Paleoequatorial Realm (Fig. 3B) show no late Guadalupian declines. The number of families, genera, and species increase from the late Artinskian–Kungurian to the Changhsingian and then drop abruptly at the end of Changhsingian. Only 22 small and thin-shelled Permian-type brachiopod species of 12 genera persisted into the earliest Triassic (Griesbachian). Although the proportional extinction rates are slightly higher at specific level (54%) in the Capitanian than those in the preceding Roadian–Wordian (50%) and succeeding Wuchiapingian (49%) intervals, they were clearly dwarfed by the peak extinction rates of the end-Changhsingian (96%). Proportional extinction rates based on the generic data and the total extinction rates show an acceleration from the late Artinskian–Kungurian to the Changhsingian (Fig. 4B). However, the subdued extinction signal at the end-Guadalupian in the Paleoequatorial region may be an artifact related to use of a coarse timescale (see discussion below). It is interesting to note that some Early and middle Permian brachiopod genera of antitropical (term of Grunt and Shi 1997) distribution (e.g., *Attenuatella*, *Waagenites*, *Strophalosiina*, *Comuqia*) appeared in the Paleoequatorial Realm for the first time in the latest middle Permian (late Capitanian) and persisted into the Late Permian.

The simple diversities at familial, generic, and specific levels in the Gondwanan Realm all peaked in the late Artinskian–Kungurian, then dropped significantly toward the end of Capitanian, indicating a long-term *press* extinction (term of Erwin 1996), which is followed by a modest recovery in the Wuchiapingian and a significant drop again after the Wuchiapingian (Fig. 3C). Only three species (*Pustula* sp., *Linoproductus lineatus* Waagen, and *Retimarginifera* sp.) are recorded in the earliest Triassic (Griesbachian) in the Gondwanan Realm (Nakazawa et al. 1975; Shimizu 1981). Both the proportional extinction rate and the total extinction rate clearly demonstrate a two-phase extinction pattern at both the generic and specific levels (Fig. 4C) for the Gondwanan Realm.

Testing by Rarefaction Analysis

It is worth noting that rarefaction analysis between species and families is sensitive to interval durations because of the likely effect of interval length on taxonomic richness of samples (Raup 1975; Tipper 1979). Among the seven Permian intervals that we investigated in this study, the Roadian–Wordian, Capitanian, and Wuchiapingian intervals are similar in duration (5–6 Myr), as are the Asselian–early Sakmarian, late Sakmarian–early Artinskian, and late Sakmarian–Kungurian intervals (9–9.5 Myr). But the latter three intervals are not related to the middle and end-Permian mass extinctions, and were therefore not tested by rarefaction analysis in this study. Thus, we analyzed only the upper three intervals (Roadian–Wordian, Capitanian, and Wuchiapingian) by rarefaction analysis, in an attempt to assess the veracity of the diversity change and extinction patterns recognized above by using diversity and extinction measures and to compare these patterns between the Gondwanan and Paleoequatorial Realms (Fig. 5A, B) (the Boreal Realm in northeast Asia was not included because it lacks Late Permian, Boreal-type brachiopod faunal data). All three realms were also compared for specific time intervals (Fig. 5C–F).
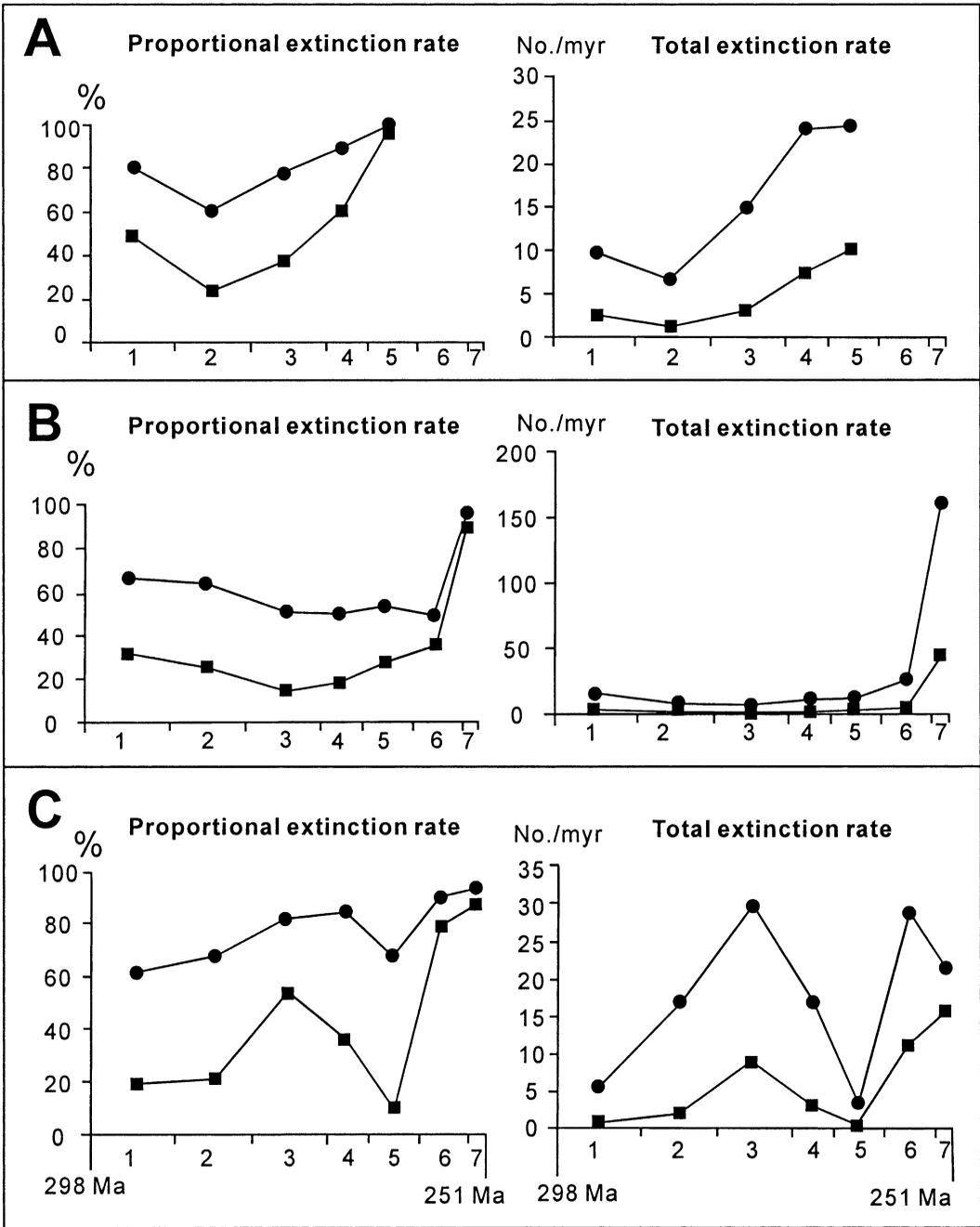
As exhibited in Figure 5A, the diversity tra-

FIGURE 4. Proportional extinction and total extinction rates at generic (■) and specific (●) levels in the seven intervals of the Permian for the three realms. Interval widths are scaled to duration. Proportional extinction rate equals the number of taxa that become extinct in the interval divided by the total number of the taxa in the interval; total extinction rate equals the number of taxa that become extinct in the interval divided by the duration of the interval in millions of years. A, Boreal Realm. B, Paleoequatorial Realm. C, Gondwanan Realm.

jectories for time intervals 3–6 of the Gondwanan Realm clearly indicate the lowest diversity in the Roadian–Wordian interval, followed by the Capitanian and Wuchiapingian intervals. The Capitanian rarefaction curve significantly differs in length from those of the Roadian–Wordian and Wuchiapingian intervals, implying that the Capitanian is poorly
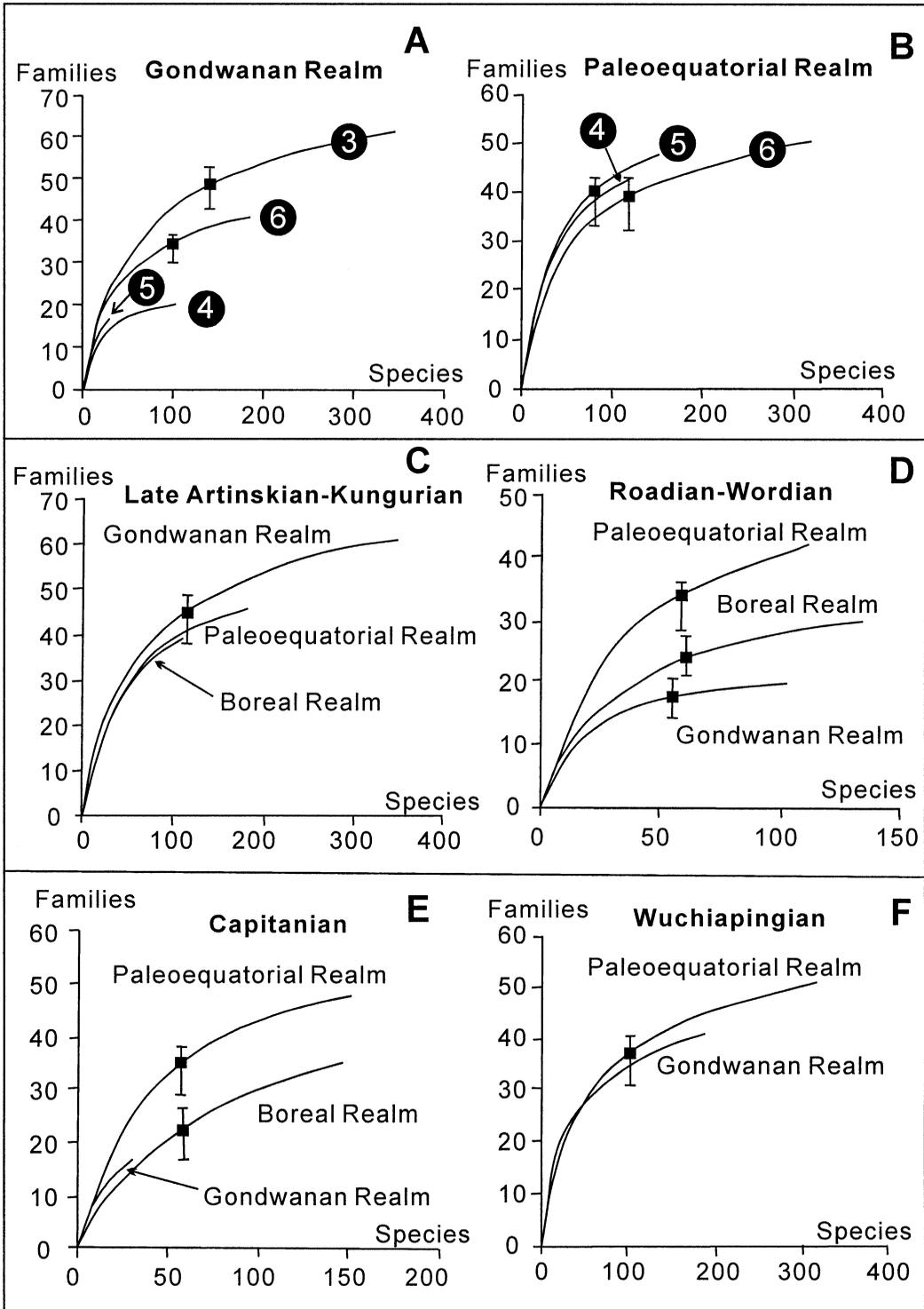
FIGURE 5. Species/family rarefaction curves for different intervals or realms (numbers on the curves of A and B are the interval numbers as shown in Fig. 2). Vertical bars depict the deviation with 95% confidence limits based on the program compiled by S. M. Holland.

sampled, and therefore its trend is difficult to predict. This curve also may indicate that the middle Permian extinction began earlier in the Gondwanan Realm, an implication that is reflected also in the raw diversity (see Fig. 3C).

The rarefaction curves for the Paleoequatorial Realm show that family diversities in the three time intervals are not significantly different, as evidenced by the overlapping of the standard deviations with 95% confidence limit (Fig. 5B), suggesting that the differences in simple diversity among the Roadian–Wordian, Capitanian, and Wuchiapingian (see Fig. 3B) are most likely due to sampling intensities. Rarefaction curves comparing the three realms during the different intervals (Fig. 5C–F) demonstrate that the three realms had comparable family diversities during both the late Artinskian–Kungurian and the Wuchiapingian intervals (Fig. 5C,F). However, the rarefaction curves of the Roadian–Wordian (Fig. 5D) and the Capitanian (Fig. 5E) intervals show clearly that the family diversities of the Paleoequatorial Realm are higher than those of the Boreal and Gondwanan Realms. Therefore, the important conclusion to be drawn from Figure 5 is that the Guadalupian decline of familial diversities in the Boreal and Gondwanan Realms is statistically robust and most likely true.

The End-Guadalupian/Late Guadalupian Extinction

The scenario that some major mass extinctions are associated with, and may be a direct consequence of, large-scale or global marine regressions (e.g., Simberloff 1972; Jablonski 1985; Hallam 1989) appears particularly applicable to the middle Permian, when major land masses assembled together to form Pangea and, as a consequence, a major worldwide regression was initiated (Holser and Margaritz 1987). This global regression subsequently led to the withdrawal of seawater from a large part of the Pangean shelves and epicontinental seas. One of the earliest attempts to reveal the relationship between the distribution of epicontinental sea areas and diversities was carried out by Schopf (1974), who plotted diversities against epicontinental sea areas using then available paleogeographical recon-

struction maps. Schopf (1974) was able to demonstrate that a sharp decrease in the percentage of the continents covered by shallow marine seas, from 40% in the Early Permian to about 15% at near the P/T boundary, then followed by a rapid recovery to 34% in the Early Triassic, was closely matched by variations in diversity. Since Schopf's study, many versions of Permian global reconstruction maps have been published with varied accuracy, but invariably they all suggest that the total global continental shelf area was reduced significantly after the end-Guadalupian (see, for example, the reconstruction maps in Ziegler et al. 1997) (Fig. 6). This reduction, we believe, may have been the direct cause of the end-Guadalupian/late Guadalupian mass extinction, particularly with respect to the Boreal and Gondwanan Realms where this middle Permian mass extinction manifested itself best (see below).

Boreal Realm.—The brachiopod faunas in the Early and middle Permian in the Boreal Realm were widely distributed on the Russian Platform, the Urals, the Sino-Mongolian seaway between the North China Platform and the Siberian Platform, the Russian Far East, and northeast Japan. However, the end-Guadalupian regression eliminated most of the shelf areas (Fig. 6), and this could have been the direct cause of the almost total extinction of Brachiopoda in the Late Permian in the Boreal Realm. Although it might be argued that some of the Boreal taxa could have migrated into other realms or deep seas during or following the regression, an extensive search in the available stratigraphic records indicates that 37% genera and 78% species known from the Capitanian in the Boreal Realm never occurred anywhere in the later intervals of all realms in the Asian–western Pacific region. Elsewhere in the Boreal Realm (e.g., East Greenland) Late Permian brachiopods may have persisted in some local areas although information on such faunas is still very scanty. Throughout the Late Permian and Early Triassic a narrow seaway probably extended down to the northeast coast of Greenland from the Arctic Ocean, in which some marine deposits accumulated with a low-diversity brachiopod fauna (Dunbar 1955). Another
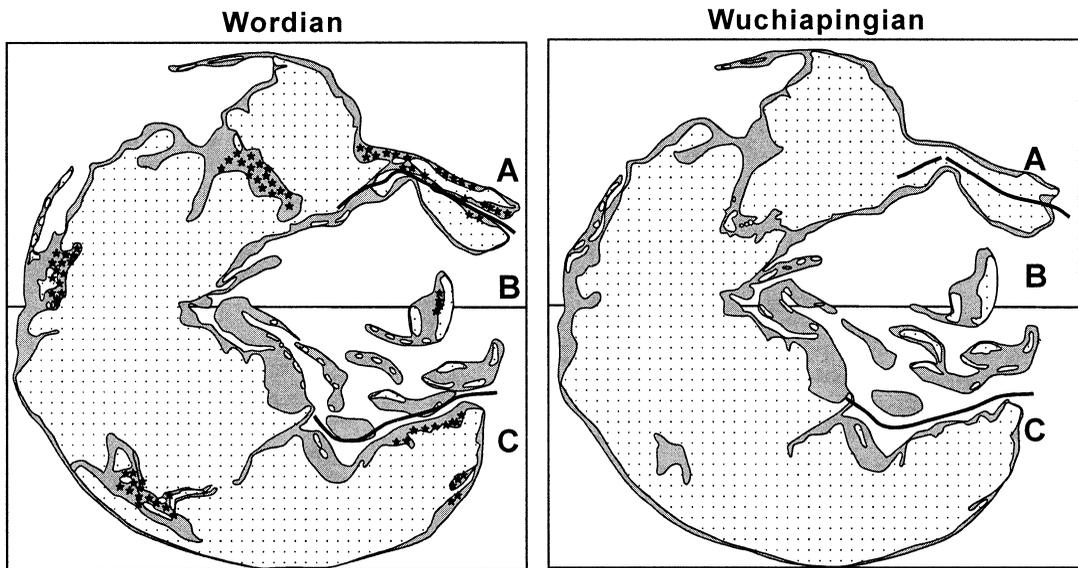
FIGURE 6. Changes in habitat area from the Wordian (middle Guadalupian) to Wuchiapingian (early Lopingian). Reconstruction map after Ziegler et al. 1997. Brachiopod habitat area is indicated by oblique dotted lines. Area with stars indicate habitat areas for brachiopods present during the Guadalupian but lost in Wuchiapingian. A, Boreal Realm. B, Paleoequatorial Realm. C, Gondwanan Realm.

possible area of Late Permian shallow-marine sediments with brachiopods is represented by the Kapp Starostin Formation in western Spitsbergen, but the upper age limit of this formation is still controversial (Stemmerik 1988; Gruszczynski et al. 1989; Malkowski et al. 1989; Nakamura et al. 1992). However, even if we accept the Spitsbergen and Greenland faunas as Late Permian, as argued by Stemmerik (1988), these faunas contain a total of 43 species from 26 genera (Dunbar 1955; Nakamura et al. 1992), which would constitute only 29.5% species and 42.6% genera for Capitanian faunas of the Boreal Realm in the Asian–western Pacific sector. The actual percentages for both species and genera would be much lower if calculated relative to the whole Boreal Realm.

Gondwanan Realm.—Sea level dropped during the middle Permian and through the Late Permian over much of Gondwana (Fig. 6), as suggested by the formation of extensive coal measures in Australia and India (Veevers et al. 1994; Mishra 1996), South Africa (Visser 1995), and South America (Harrington 1962). The timing of this eustatic event agrees well with the Guadalupian brachiopod extinction in the Gondwanan Realm. For instance, in Western

Australia, Early Permian and early middle Permian strata bearing abundant marine faunas are replaced by late middle and Late Permian sandstone-dominated strata in many basins (see Archbold 1999: Fig. 3). In the Sydney Basin of eastern Australia, the youngest marine Permian faunal horizon is Midian (= Capitanian) in age (Briggs 1998), lying immediately below the Late Permian Illawarra Coal Measures. However, there are limited areas in the Gondwanan Realm where marine deposition occurred during the Late Permian. One case is the Himalayan region including southern Tibet, Nepal, and northern India. Here, Late Permian deposits used to be considered absent, but they have been confirmed by recent studies based on faunas from the upper part of the Kuling Group in northern India (Garzanti et al. 1996), the Thini Chu Group in central Nepal (Garzanti et al. 1994), and the Selong Group in southern Tibet (Shen et al. 2000). It is interesting to note that in this peri-Gondwanan region Guadalupian brachiopod faunas are actually very limited. This may be due to a prolonged period of low sea-level stand and erosion, as suggested by Garzanti et al. (1996). However, a significant transgression beginning in the early Wuchiapingian

brought about extensive marine deposition across the region, and with it, a flourishing brachiopod fauna.

Paleoequatorial Realm.—Differing from the two realms mentioned above, the Paleoequatorial Realm experienced only a short, but distinct, regression at the end-Guadalupian, as marked by a regional unconformity between the Guadalupian and the Lopingian Series in central Iran, South China, and Japan. In South China, this event has long been recognized and known as the Dongwu Movement, which resulted in the Longtan Coal Measures overlying directly and unconformably on the middle Permian Maokou and/or Lengwu Limestones (Formations). Only in the central part of the Jiangnan Basin in southwest China were there localized areas (e.g., the Laibin area in Guangxi of southwest China) where marine deposition continued 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 oncolites and skolithos trace fossils, indicating a nearshore high-energy environment (Jin et al. 1998). However, as constrained by conodonts across the Guadalupian and boundary at the Laibin section (Mei et al. 1998), this shallowing event was relatively short lived, lasting no more than 2 million years (see Jin et al. 1998: Fig. 3). This rapid event resulted not only in a significant reduction of epicontinental seas on South China (see Wang and Jin 2000: Fig. 3F,G) and consequently a crisis for the middle Permian marine benthos (Jin et al. 1994), but also in profound changes in the paleogeographical settings of South China. Despite this rapid eustatic event, the end-Guadalupian extinction in the whole Paleoequatorial Realm of the Asian–western Pacific region is not well expressed relative to the Boreal or Gondwanan Realm. In fact, as shown in Figures 3–5 and also discussed above, the extinction is rather weak in comparison with the extinctions at that time in the other two realms. But this subdued extinction signal from the Paleoequatorial region may be an artifact because the timescale is coarse relative to the rapidity of the actual geological event, as can be explained using the example of South China. Shen and Shi (1996) docu-
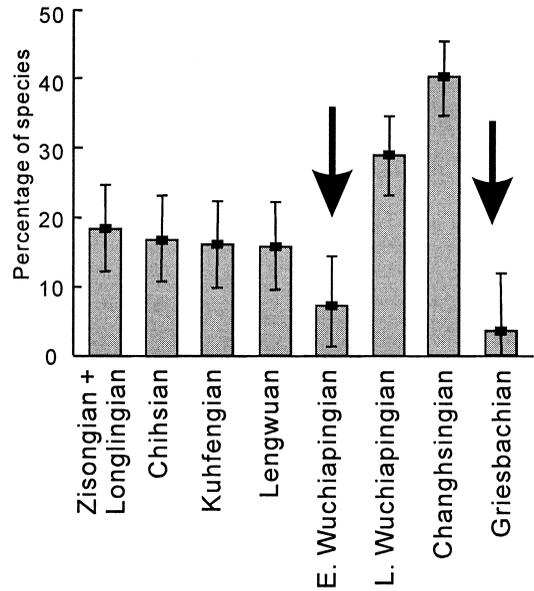

FIGURE 7. Diversity pattern of Permian–Triassic brachiopods in South China. Original data from Shen and Shi (1996). Vertical error bars depict the deviation with 95% confidence limits based on the program of Raup 1991.

mented an 87% proportional extinction rate of brachiopods near the Maokouan/Lopingian boundary in South China. Their study was based on various measured stratigraphic sections with relatively higher biostratigraphic resolution. They were therefore able to analyze the brachiopod extinction rates using biozones/substages rather than stages or superstages as in the present study. Thus they recognized that the end-Maokouan extinction was in fact concentrated in the late Maokouan (or Lengwuan); its appearance as a boundary extinction had been enhanced by the paucity of life in the subsequent early Wuchiapingian. The following late Wuchiapingian is marked by a radiation of numerous new taxa (Fig. 7). In the current study, however, the whole of the Maokouan Stage is treated as one time interval, as is the Wuchiapingian Stage. This treatment, which is inevitable with the much broader regional scale of the present study, has combined two substages, hence lumping diversities and condensing the pattern of diversity variation that would otherwise be more varied on a finer time resolution. In other words, it remains reasonable to suggest an end-Guadalupian extinction of some magni-

tude for the Paleoequatorial Realm, but the manifestation of this event is not well recognized in this study because the extinction was rapid and quickly replaced by a rapid phase of origination in late Wuchiapingian. Nevertheless, the end-Guadalupian/late Guadalupian extinction is probably taxonomically selective. Fusulinids and corals apparently suffered heavy losses (Stanley and Yang 1994; Wang and Sugiyama 2000), whereas gastropods were less affected (Erwin 1996). However, studies on these taxa did not mention the life-depleted early Wuchiapingian, so it is hard to make comparisons with the brachiopods in this study.

The End-Changhsingian Extinction

The brachiopod disappearance pattern during the end-Changhsingian in the shallow-water carbonate sequences (e.g., Changhsing Formation) of South China appears to support a scenario of rapid extinction process as advocated by Rampino and Adler (1998) and Jin et al. (2000). For example, the abruptness of the mass extinction is well exhibited at the Beifengjing section in Chongqing City of South China (Fig. 8). Here, the Permian/Triassic boundary is well defined by the first appearance of the Triassic index conodont *Hindeodus parvus* (Yin 1985; Yang et al. 1987). The total thickness of the Changhsingian strata is 91.5 m. Shen and He (1991) identified 155 brachiopod species in the Changhsing Formation. Of these, 126 species disappeared within an interval of 0.91 m below the Permian/Triassic boundary, only 29 species disappeared well below (56.47 m) the Permian/Triassic boundary, and 2 species persisted across the Permian/Triassic boundary (Shen and He 1991) (Fig. 8). Evidence indicating paleoenvironmental deterioration within the top 0.91 m of the Changhsingian includes the occurrence of framboidal pyrites, a lithologic shift from thick-bedded biosparite into middle/thin-bedded argillaceous limestone, a decrease in the density of bioclasts and the diameter of burrows (Wignall and Hallam 1996), and a changeover from brachiopod communities with numerous pro-reef forms to those with stress-tolerant forms (Shen and He 1991). There is also evidence for contemporaneous volcanism, as shown by the occurrence of sev-
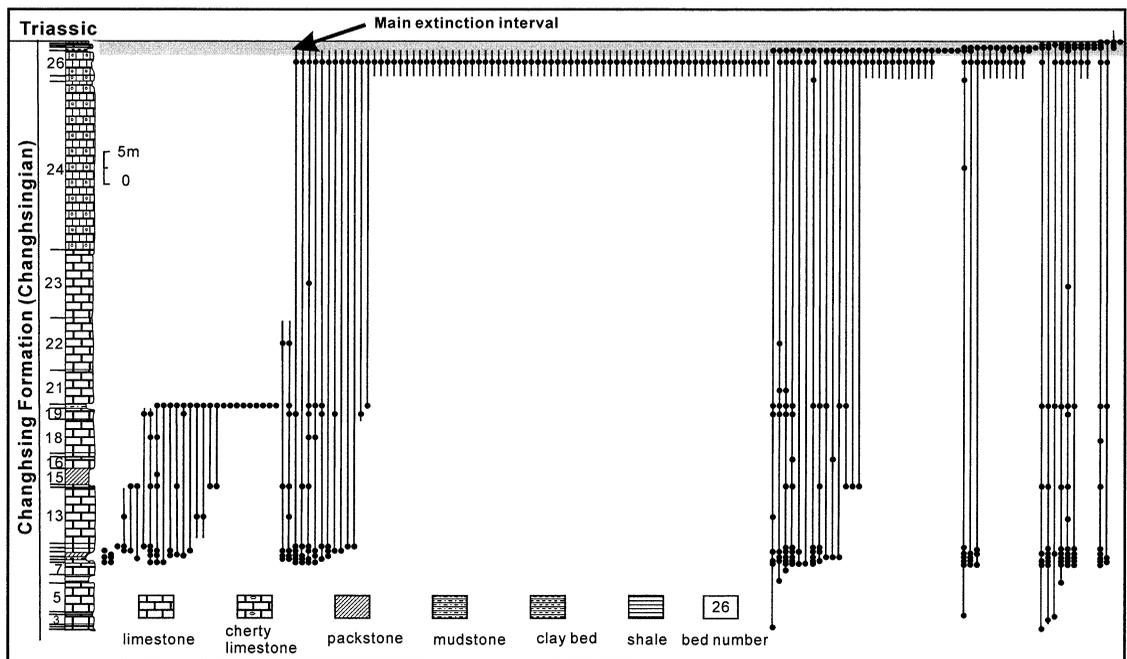

FIGURE 8. Stratigraphic ranges of brachiopod species (by vertical lines with dots indicating the occurrences of brachiopods) at the Beifengjing section near Chongqing City of Sichuan Province, South China. Fossil ranges scaled to thickness of the Changhsing Formation. Data after Shen and He 1991.

eral clay layers of illite/smectites with microspherules (Yang et al. 1987). It is thus clear that the end-Changhsingian mass extinction was concentrated within the very end of the Changhsingian now represented by 0.91 m in the stratigraphic record at this section. Although the sedimentation rate within the Changhsing Formation at this section is not exactly known, a rapid extinction clearly occurred at the very end of the Changhsingian. In fact, because of the Signor-Lipps effect (Signor and Lipps 1982; Rampino and Adler 1998) and the artifact of incomplete preservation (Marshall 1995), the extinction may have been even more rapid than it appears.

The rapid extinction event in the Paleoequatorial Realm is also well expressed in the Gondwanan Realm. The Selong Xishan section in southern Tibet (Fig. 9) may serve as a good example to compare relatively high-latitude extinction patterns with that of the Paleoequatorial Realm. At this section, 49 Wuchiapingian to Changhsingian brachiopod species have been recorded (Shen and Jin 1999; Shen et al. 2000). Brachiopods, corals, and bryozoans became extinct within a short interval beneath the Permian/Triassic boundary (Fig. 9). The end-Changhsingian transgression begins at the base of the *Waagenites* Bed (Shen and Jin 1999) of the Kangshare Formation. Below the *Waagenites* Bed, a caliche bed is present (Jin et al. 1996), indicating a regression event, which in turn is underlain by the topmost part of the Selong Group consisting of nearshore bioclastic limestone with bioclasts dominated by brachiopod, coral, and crinoid fragments. The Changhsingian strata at this section are only 0.17 m thick (Wang et al. 1989; Shen and Jin 1999) or, at most, no more than 2.25 m thick (Shen et al. 2000). The lithology of the Changhsingian strata is predominantly well-sorted bioclastic grainstone containing 35–80% bioclastics (Jin et al. 1996). The reduced thickness and extremely high content of bioclastics indicate that the Changhsingian strata at this section were deposited during a period of sediment starvation (Shen and Jin 1999). According to Jin et al. (1996), the uppermost Permian *Waagenites* Bed represents carbonate deposits formed in shallow, medium-energy shoals. The overlying Early Triassic *Otoceras* Bed consists
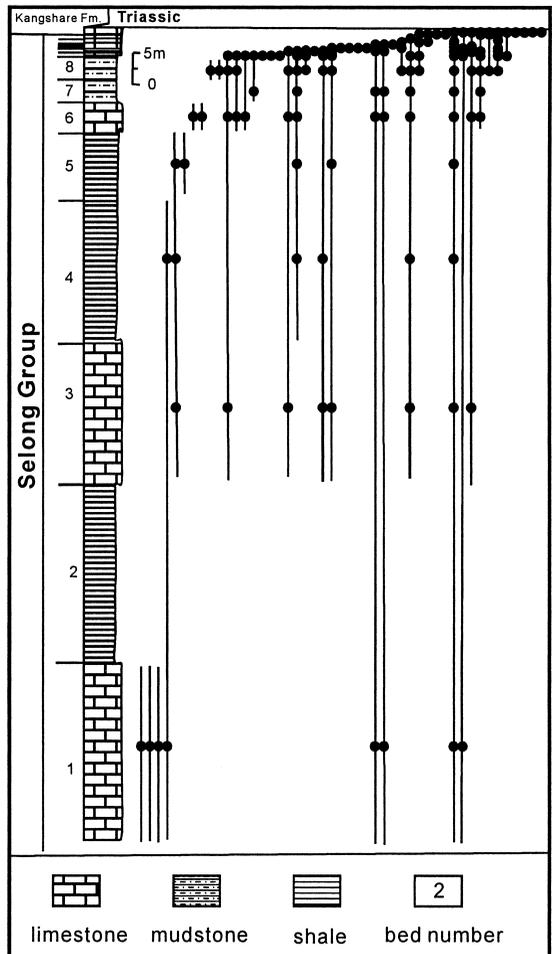

FIGURE 9. Stratigraphic ranges of brachiopod species at the Selong Xishan section in southern Tibet. Data after Shen et al. 2000 and Shen and Jin 1999.

of stylo-compacted corroded packstone with crinoid fragments and bioturbation structure. A dramatic drop in $\delta^{13}C$ value from +3.2 in the Caliche Bed to −2.89 per mil (‰) in the *Waagenites* Bed is evident (Wang et al. 1997). This isotopic excursion is very similar to signals known from many other P/T boundary sections (e.g., the Meishan section [Cao et al. 2001]), and it suggests that the depletion of $\delta^{13}C$ value may not reflect a single triggering event but a complex web of causality (Erwin 1993).

Conclusions

Our analysis indicates that Permian brachiopods in the Asian–western Pacific region suffered two discrete, closely spaced extinc-

tions, at the end-Guadalupian/late Guadalupian and at the end-Changhsingian, but possibly with different causes. The end-Guadalupian/late Guadalupian extinction can be related to a reduction of the habitable shelf areas leading to decreased population sizes.

The end-Changhsingian extinction happened rapidly in both the Paleoequatorial and the Gondwanan Realms. Shallow-water carbonate settings of South China and southern Tibet show evidence of a rapid and severe main extinction within a short interval just below the Permian/Triassic boundary. This extinction appears to be proceeded by a rapid regression event, as evidenced by the presence of highly diverse plant fossils at the Penglaitan section (Jin et al. 2001) and the Caliche Bed at the Selong Xishan section in the very late Changhsingian (Jin et al. 1996), which is followed by a rapid transgression event resulting in the occurrence of framboidal pyrites, a lithologic shift from thick-bedded biosparite into middle/thin-bedded argillaceous limestone, and a faunal shift from diverse pro-reef forms to monotonous stress-tolerant forms.

Acknowledgments

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