

Brachiopod diversity patterns from Carboniferous to Triassic in South China

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It has long been recognized that the trend of marine diversity from the Carboniferous to the Triassic includes an approximately 100-myr-long stable biodiversity stage ranging from the Late Carboniferous to the late Middle Permian, the most severe end-Permian mass extinction in the Phanerozoic (pre-Lopingian crisis and end-Changhsingian mass extinction together), a bleak stage in the Early Triassic and a rapid recovery stage in the Middle Triassic. However, little attention has been paid to smaller diversity fluctuations among relatively stable stages in the Carboniferous and Permian. Here, we establish a database of the brachiopod fossil records from the Carboniferous to Triassic in South China, including 104 families, 373 genera, 2081 species recorded by 7948 occurrences with relatively detailed biostratigraphic controls. Analyses based on the raw taxonomic richness at familial, generic and specific levels, proportional and total extinction/origination/turnover rates, and rarefaction analyses for 21 different intervals from the Carboniferous to Triassic reveal that the brachiopod diversity trends can be generally divided into two distinctly different stages. Brachiopods were highly diversified during the Carboniferous and Permian Periods, whereas they were dramatically reduced in diversity after the end-Changhsingian mass extinction. Brachiopods were abundant during the Early Carboniferous Tournaisian and Viséan, and were characterized by many genera extending from the Late Devonian. This was followed by a significant simple diversity decline in the Serpukhovian Stage. The Early Permian (either in Sakmarian or Artinskian) diversity decline previously perceived by coral and fusulinid workers is indicated by the raw generic and familial richness, and taxonomic richness per million years. However, it is not expressed by the rarefied brachiopod trajectory, which is probably affected by sampling effect or taxonomic selectivity. Brachiopods apparently declined from Capitanian to Early Wuchiapingian. Thus, the brachiopod diversity trajectory from Pennsylvanian Bashkirian to Late Guadalupian Capitanian generally characterises a long stable stage. Brachiopods are extremely abundant in the Late Wuchiapingian and Changhsingian in view of raw taxonomic richness, but a rarefied trajectory reveals a flat step following the pre-Lopingian (end-Guadalupian) crisis until the end-Changhsingian mass extinction. Therefore, the previously widely perceived Lopingian radiation after the pre-Lopingian crisis appears to be at least partly over-stated. Brachiopods experienced a long bleak stage in the Early Triassic, followed by a rapid recovery in the Anisian, and reached their acme in the Norian, but never recovered to such a flourishing degree during the Carboniferous and Permian Periods. Brachiopods were eliminated in South China by the end-Triassic withdrawal of the sea from this region. Copyright © 2006 John Wiley & Sons, Ltd.

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1. INTRODUCTION

Many questions in biotic macroevolution require accurate measures of diversities, extinctions and originations. During the last three decades, taxonomic quantitative analysis compiled from published literature has revealed that prolonged time intervals with relatively low extinction rates (radiation and stasis) are punctuated by much shorter

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intervals of changes and reorganization (extinction and recovery) (Sepkoski 1978, 1981, 1984; Raup and Sepkoski 1982). Sepkoski (1981, 1984) and Bambach *et al.* (2004) divided the life history of the Phanerozoic into three successive Evolutionary Faunas (EFs), which have distinctive compositions and progressively increasing diversity. Boucot (1983) subdivided the marine Phanerozoic record into 12 different ecologic evolutionary units (EEUs). This was subsequently revised into nine EEU's by Sheehan (1996). No matter which division of the evolutionary stages of the Phanerozoic is accepted, the interval from Carboniferous to Triassic has been unanimously regarded as the most distinctive stage, preceded by the Late Devonian Frasnian-Famennian mass extinction, interrupted by the end-Permian mass extinctions and closed by the Late Triassic mass extinctions. Recently, patterns and causes of these mass extinctions have been intensively studied (e.g. Weems 1992; McGhee 1996; Jin *et al.* 2000a; Rong and Shen 2002). However, relatively little attention has been paid to the diversity pattern of prolonged intervals with less biotic turnover between mass extinctions.

The Carboniferous, Permian and Triassic Periods experienced more than 159.6 million years (Gradstein *et al.* 2004) and were a time of high diversity of various organisms during the Palaeozoic, suddenly terminated by the end-Changhsingian mass extinction and followed by recovery and reorganization of the Mesozoic organisms. This time interval (from Carboniferous to Triassic) has long been recognized as consisting of a longer than 100-million-year stage of stasis from Carboniferous to Permian followed by the Earth's most severe end-Permian mass extinction (Sepkoski 1981; Raup and Sepkoski 1982) and then the Triassic recovery. However, this recognition is largely based on some previous diversity patterns on a global scale and at relatively high taxonomic level and very broad intervals (e.g. Sepkoski 1978, 1981). Relatively little work has been done on the diversity patterns from the Carboniferous to Triassic based on detailed fossil record databases. In this paper we specifically investigate the temporal variation in diversity patterns from the Carboniferous to Triassic based on brachiopod occurrences with relatively detailed biostratigraphic controls in South China. Utilizing the composite brachiopod database, we also determined the effects of sample size for different intervals. Particularly, we focus on whether a long evolutionary stage of stasis is present or not in terms of brachiopods and if not, what are the characteristics of the diversity pattern from the Carboniferous to Permian. The Permian brachiopod diversity pattern has been previously presented, mainly for the purpose of unravelling the end-Permian mass extinction pattern (pre-Lopingian crisis and end-Changhsingian extinction) by taking into account palaeobiogeography (Shen and Shi 1996, 2002; Shi *et al.* 1999; Shi and Shen 2000; Rong and Shen 2002) and recently reviewed by Chen *et al.* (2005a,b) again, and therefore will not be repeated in this paper. The Middle and Late Triassic brachiopod records in South China are very limited due to the wide regression after the Middle Triassic (Sun and Shen 2004; Chen *et al.* 2005b), therefore only a general and semi-quantitative analysis is provided in this paper.

2. DATA

The data employed in this paper is restricted to Brachiopoda recorded from the Carboniferous and Triassic of South China. Palaeogeographically, South China was centred on the Yangtze block and surrounded by a few other tectonic units (Figure 1). These include the Cathaysian block in the east, the Lanping-Simao block and the Changning-Menglian belt in the southwest, the Songpan-Ganzi belt in the northwest and the Qinling fold belt in the north. These tectonic terranes/belts were all either attached to or very close to the Yangtze block (see a regional construction map provided by Yin *et al.* 2004, Figure 2) during the Carboniferous and Permian, and therefore are included in the database. On the other hand, the Baoshan, Tengchong, Qiangtang and Lhasa blocks, despite the fact that they belong to the same palaeobiogeographical province after the Late Permian, are not included in our databases because they have very strong Gondwanan affinities (Shen *et al.* 2000; Shen and Shi 2000, 2004) during the Carboniferous and Early Permian.

The basic database for the present study was compiled specially for the 973 Major Basic Research Projects of the Ministry of Science and Technology of China. Sources of data include published systematics and unpublished/in press faunal lists, biostratigraphical, geographical, palaeogeographical, lithological and tectonic investigations for

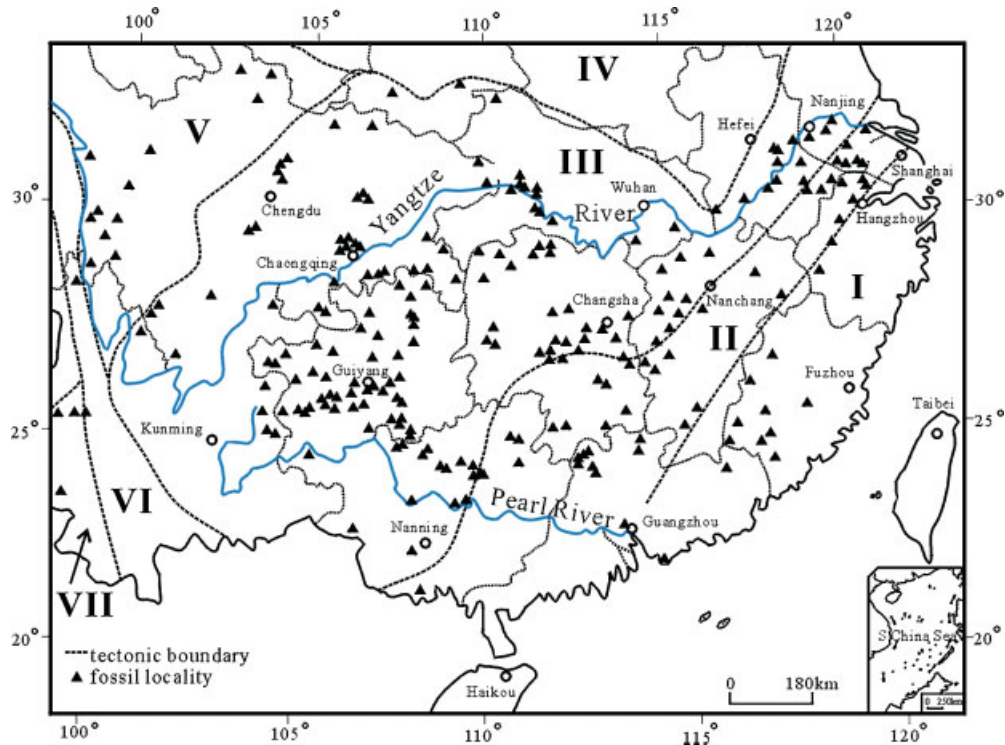


Figure 1. Map of South China showing the tectonic units and the distribution of the Carboniferous–Triassic brachiopod fossil localities for this study. I–Cathaysian block, II–Jiangnan basin, III–Yangtze block, IV–Qingling fold belt, V–Songpan–Ganzi fold belt, VI–Lanping–Simao block, VII–Changning–Menglian fold belt.

each collection. The format of the current brachiopod database mainly follows the palaeobiology network information page at the website <http://flatpebble.nceas.ucsb.edu/public/tips/tips.html#collection> by Arnie Miller and John Alroy. The database includes 34 different fields and documents individual fossil collections, provides a list of orders, superfamilies, families, genera and species (both recorded and revised), 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 occurrences in the database. The detailed primary data fields were designed to facilitate palaeobiogeographical (Shen *et al.* 2000; Shen and Shi 2000, 2004; Shi and Shen 2000) and macroevolutionary analyses.

In compiling the database, we have examined all available published Carboniferous, Permian and Triassic brachiopod literature of the region, and updated the taxonomy and age determinations of the published records in light of the latest developments of brachiopod taxonomy and biostratigraphy (Carter *et al.* 1994; Williams *et al.* 1997, 2000a,b, 2002). Nevertheless, some probable errors could be yet present in our compilation. These include possible incorrect/different systematic or stratigraphic assignments, and difficulties in stratigraphic correlation for some old records. More than 10 000 records have been entered in the database. However, the fossil records with very poor biostratigraphic controls (e.g. Carboniferous, Permian etc. without any further detailed biostratigraphic information) are excluded from the database for the final analysis. Thus, a total of 104 families, 373 genera and 2081 species derived from 7948 records in 233 localities (Figure 1) are used in the revised and updated database.

Five time intervals for the Carboniferous, nine intervals for the Permian and seven intervals for the Triassic are utilized in accordance with the Carboniferous, Permian and Triassic chronostratigraphic scale (integrated by

chronostratigraphy	stage	age	duration	basal fossil zone of stages		interval				
				conodonts	fusulinids					
Mesozoic	Triassic	Late Triassic	Rhaetian	199.6	4.0		21			
			Norian	203.6	12.9	<i>Epigondolella bidentata</i>	20			
			Carnian	216.5	11.5	<i>Epigondolella cf. primitia</i>				
		Middle Triassic	Ladinian	228.0	9.0		18			
			Anisian	237.0	8.0	<i>Neogondolella excelsa</i>				
			Olenekian	245.0	4.7	<i>Neogondolella regale</i>	17			
		Early Triassic	Induan	249.7	1.3	<i>Neospathodus waageni</i>	16			
			Changhsingian	251.0	1.3	<i>Hindeodus parvus</i>	15			
		Late Palaeozoic	Permian	Lopingian	Changhsingian	253.8	2.8	<i>Clarkina wangi</i>	<i>Palaeofusulina minima</i>	14
					Wuchiapingian	260.4	6.6		<i>Nanlingella simplex/</i> <i>Codonofusulina kwanghsiana</i>	13
					Capitanian	265.8	5.4	<i>Clarkina postbitteri postbitteri</i>	11	
				Wordian	268.0	2.2	<i>Jingondolella posterrata</i>	<i>Lepidolina (Yabeina) gubleri</i>		
				Roadian	270.6	2.6	<i>Jingondolella nankingensis</i>	<i>Neoschwagerina margaritae</i>	10	
				Guaadalupian	Kungurian	275.6	5.0	<i>Neostreptognathodus exculptus</i>	<i>Misellina claudiae</i>	9
					Artinskian	284.4	8.8	<i>Sweetognathus whitei</i>	<i>Chalaroschwagerina</i>	8
Sakmarian	294.6				10.2		7			
Asselian	299.0			4.4	<i>Streptognathodus postfusus</i>	<i>Sphaeroschwagerina</i>				
Pensylvanian	Gzhelian			303.9	4.9	<i>Streptognathodus zethus</i>	<i>Triticites schwageriniformis mosquensis</i>	5		
	Kasimovian			306.5	2.9	<i>Idiognathodus sagittalis</i>	<i>Protriticites/obsoletus</i>			
	Moscovian			311.7	5.2		<i>Eofusulinella</i>	4		
	Bashkirian			318.1	6.4	<i>Declinognathodus noduliferus</i>	<i>Millerella marblensis/</i> <i>Eostaffella postmosquensis</i>			
	Mississippian			Serpukhovian	326.4	8.3		3		
Viséan				345.3	18.9	<i>Adetognathus unicornis</i>	<i>Eostaffella</i>			
Tournaisian		359.2	13.9	<i>Gnathodus texanus</i>	2					
			<i>Siphonodella sulcata</i>	1						

Figure 2. Carboniferous-Triassic chronostratigraphy, isotopic ages, key conodont and fusulinid zones and duration of intervals employed in this paper. Carboniferous chronostratigraphy and fossil zones after Jin *et al.* (2000b); Permian chronostratigraphy after Jin *et al.* (1997, 2000c); isotopic ages follow the latest international chronostratigraphic chart of IUGS (Gradstein *et al.* 2004); fusulinid zones from Shi and Yang (2004). Stage heights scaled to duration.

Gradstein *et al.* 2004) (Figure 2). The Late Devonian brachiopods are also investigated in order to remove the origination bias for the subsequent (mainly Early Carboniferous) intervals. Ideally, the finer the time intervals are; the better to recognize the diversity pattern. However, this depends on the overall biostratigraphical quality of the original literature and the size of the database. A higher resolution time interval will give a more precise time control on the diversity profile, but accordingly, will reduce the database size which is not good for bio-diversity standardization analysis. Therefore, a few time intervals do not strictly follow the precise stage boundaries of the chronostratigraphical scale considering both the sufficiency of the data and the biostratigraphic resolution. Some groupings are necessary because either the ages of some of the brachiopod faunas span stage boundaries or the stage boundaries have not been clearly defined yet. For the Pennsylvanian (Late Carboniferous), Bashkirian is grouped with Moscovian, because these two stages are biostratigraphically difficult to be discriminated for many previously documented collections in South China in terms of brachiopods, without accompanying fusulinid and conodont data. So are Kasimovian and Gzhelian, and Roadian and Wordian of the Guadalupian (Middle Permian). On the other hand, the Wuchiapingian can be easily subdivided into two intervals because of the intensive studies on the Lopingian in South China during recent decades (e.g. Jin *et al.* 1998). This is because there is a widespread unconformity between the Lopingian and Maokouan (Late Guadalupian) in South China, which is called the Dongwu Movement by Chinese workers. The Early Wuchiapingian has so far been confirmed only in the Laibin area, Guangxi Province, the Chenxian area in Hunan Province and the Dukou area in Sichuan Province in South China. The widespread coal-bearing Lungtan Formation in South China is largely Late Wuchiapingian (Jin *et al.* 1998). This subdivision is also helpful for recognizing the previously perceived (e.g. Jin 1993; Jin *et al.* 1994; Stanley and Yang 1994) pre-Lopingian or end-Guadalupian crisis. Recently, Chen *et al.* (2005c) described a few brachiopods from the Lungtan Formation at the Daijiagou section in Sichuan province, which was claimed to be of Early Wuchiapingian age, but not evidenced by any ammonoid, conodont and even brachiopod data. By contrast, the boundary between the Maokou Formation and the Lungtan Formation at that section is clearly marked by a distinct unconformity (workable limonite unit), which is widespread in South China.

Using a variety of metrics to verify whether they yield concordant results it is necessary to examine the variations in diversity patterns through time (Van Valen 1984; Sepkoski 1986; Sepkoski and Raup 1986; Gilinsky and Bambach 1987; Foote 1994, 2002). We employed four series of quantitative measures: raw taxonomic richness at familial, generic and specific levels, standing diversity and proportional and extinction/origination/turnover rates. In addition, the durations of different time intervals vary greatly; therefore, the total extinction/origination/turnover rates are calculated by the ratio of taxa becoming extinct or originating in a time interval over the duration (million years) of the interval.

As has been documented intensively in the literature, sample intensity plagues the compilation of diversity because it is dependent upon the variations of rock availability and palaeontological interests (Miller 2000; Alroy *et al.* 2001; Foote 2001, 2002; Jackson and Johnson 2001; Bush *et al.* 2004). During the establishment of our database, we found that sample intensities are apparently different for different intervals. So we use rarefaction analysis to test the possible bias caused by sample intensity for the diversity pattern. Rarefaction analysis is basically an interpolation technique (Sanders 1968), making it possible to estimate how many species/genera/families would have been found had the sample been smaller than it actually was. That is, numbers of occurrences, species, genera and families in each interval were counted, and each sample was rarefied so that the brachiopods with different number of species/genera/families in the different intervals could be compared by reducing all samples to the same at a common sample size. Most of the literature on brachiopods in South China lacks abundance data. Therefore, we use data on the occurrences within genera for rarefaction analysis following the methodology of Miller and Foote (1996). The shift of taxonomic rank does not change the method mathematically or conceptually (see Raup 1975 for more detail). 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%) is preferred to show the robustness of the observed values. To calculate the standard deviations at any point on the curves, the computer program compiled by S. M. Holland released on the website <http://www.uga.edu/strata/software/index.html> was used.

3. BRACHIOPOD DIVERSITY PATTERNS FROM CARBONIFEROUS TO TRIASSIC

Figure 3 exhibits the brachiopod diversity patterns from the Carboniferous to Triassic based on species/genus/family numbers. The simple (number of taxa) and standing diversities (total genera minus genera confined to the interval) at familial, generic and specific levels all display a similar trajectory from the Carboniferous to Triassic (Figure 3A and 3C). The brachiopod diversity from the Carboniferous to Triassic can be divided into two major

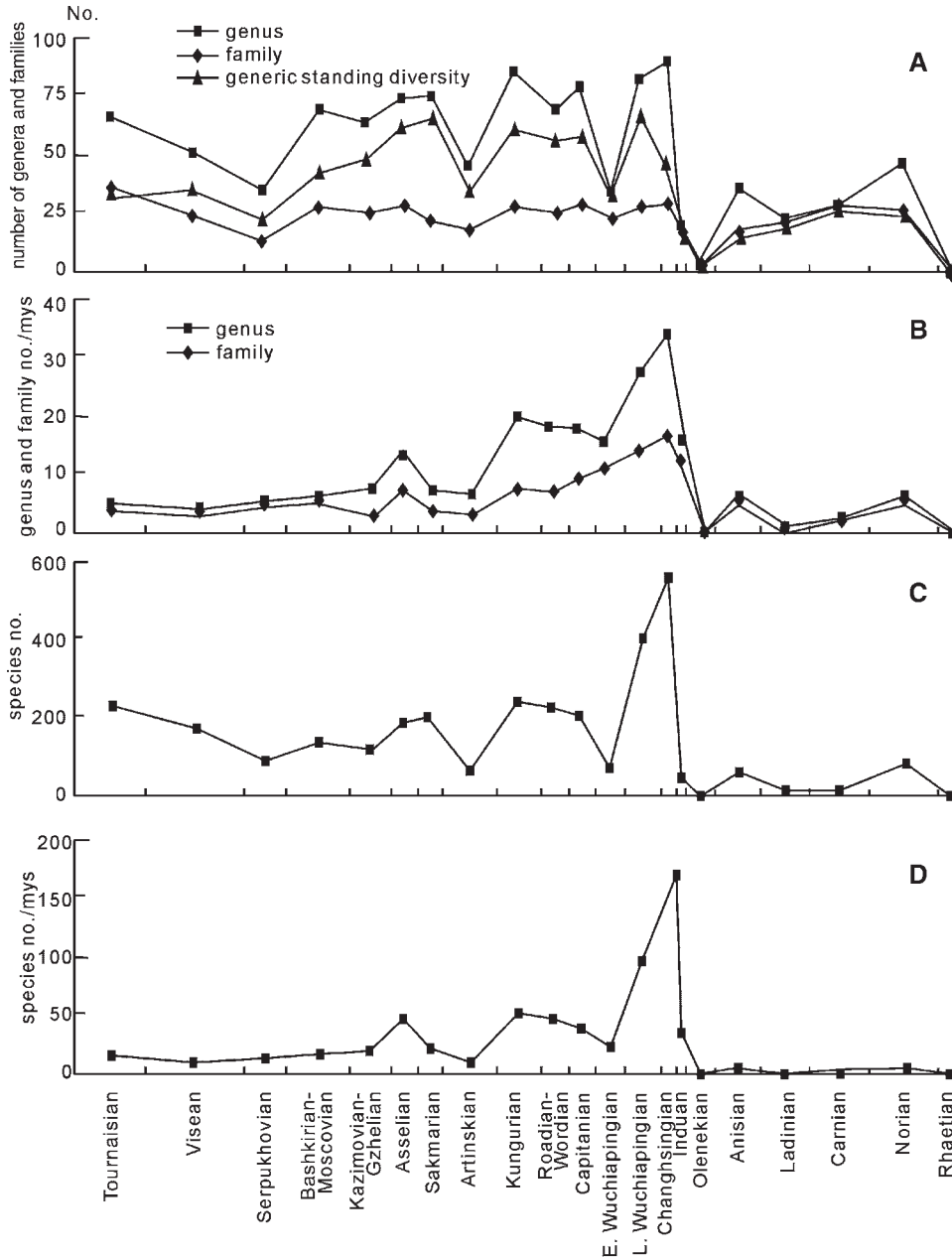


Figure 3. Brachiopod diversity patterns from Carboniferous-Triassic. (A) family, genus numbers and generic standing diversity; (B) family and genus numbers per million years; (C) species number; (D) species number per million years. Standing diversity = Total genera minus genera confined to the interval. Stage width scaled to duration.

distinctive stages separated by the end-Changhsingian mass extinction. One is the flourishing stage from the Carboniferous to Permian and the other is the depleted stage in the Triassic. Brachiopods were no longer present after the Triassic in South China, concomitant with the withdrawal of the sea. During the stage from Carboniferous to Permian, brachiopods fluctuated between 25 and 40 in family number, but never recovered to this level after the end-Changhsingian mass extinction in South China. The Carboniferous-Permian stage is punctuated by three relatively minor diversity falls, respectively in the Serpukhovian, Artinskian and Early Wuchiapingian (Figure 3A and 3C). However, the Serpukhovian fall is not expressed in terms of the taxa (family, genera and species) divided by duration (taxa/myrs) (Figure 3B and 3D). Family, genus and species numbers per million years reveal that brachiopods are nearly stable from the Tournaisian to the Kasimovian-Gzhelian interval, followed by the Asselian spike. The Artinskian and the Early Wuchiapingian falls are also reflected by the taxonomic number per million years; both constrain another distinct flourishing stage of brachiopods from the Kungurian to Capitanian. Brachiopod diversity is markedly peaked based on species/genus/family numbers in the Lopingian (Late Wuchiapingian and Changhsingian) in South China that is followed by the end-Changhsingian mass extinction. Eight families and 14 genera (including the inarticulates *Lingula* and *Orbiculoidea*) survived into the earliest Triassic (mostly until Early Induan only), then brachiopods experienced a long bleak stage of about 6-million years with little origination, followed by the Middle Triassic Anisian rapid recovery (Figure 3) in South China (Rong and Shen 2002; Sun and Shen 2004; Chen *et al.* 2005b).

We also calculated the (standing) extinction rates, (standing) origination rates, (standing) turnover rates and total extinction rates for all intervals using the formula designed by Harper (1996) (Figure 4). Figure 4 shows that extinction/turnover rates and total extinction rates all peaked in the Changhsingian and Norian except for the extinction rate 1 (total genera becoming extinct divided by total genera) and turnover rate 1 (equals the proportion of taxa occurring in the time interval that either become extinct or originate in the time interval but are not confined to it), and all origination rates declined in the Changhsingian (Figure 4A and 4C). Therefore, the end-Changhsingian and Late Triassic mass extinctions are markedly expressed. The profiles of extinction rates before the end-Changhsingian mass extinction indicate that the diversity trajectory from Carboniferous to Permian was interrupted by two relatively smaller events. One is in the Serpukhovian and the other in the Capitanian (Figure 4A). The Serpukhovian diversity depletion event is also supported by very low origination rates and relatively high extinction rates (Figure 4A and 4B). The extinction rates after the Serpukhovian show no substantial change until the Roadian-Wordian. Origination profiles show that the Serpukhovian origination valley is followed by a plateau of high origination in the Bashkirian-Moscovian and the Kasimovian-Gzhelian intervals (Figure 4B). Then the extinction/origination rates remain little changed until the Capitanian (Figure 4A and 4B). The Early Wuchiapingian diversity depletion is gently reflected by the slightly higher extinction and total extinction rates in the Capitanian (Figure 4A and 4D), but not well expressed by the origination rates in the Capitanian (Figure 4B).

The high extinction/turnover rates after the end-Changhsingian mass extinction are clearly due to some Permian-type survival genera which became extinct during the earliest Induan (Figure 4), but the main extinction phase is apparently in the Changhsingian as exhibited by the much lower total extinction rate in the Induan than that in the Changhsingian (Figure 4D). The lowest extinction/origination/turnover rates 2 and standing rates [excluding the genera restricted to the interval, see Harper (1996) for the formula and explanation] indicate the late Induan and Olenekian intervals are the bleak stage for brachiopods after the end-Changhsingian mass extinction. The very high extinction/origination/turnover rates 1 [including the genera restricted to the interval, see Harper (1996) for the formula and explanation] in the Olenekian are over-enhanced in proportion by a few genera restricted to the interval over a small number of total genera of the interval. Brachiopods recovered in the Anisian as indicated by the high origination rates and low extinction rates in the Anisian (Figure 4A and 4B) in South China. This recovery is followed by another distinct drop in the Ladinian with low origination and high extinction rates, which are probably due to the regression in South China (see more discussion below). Brachiopods disappeared after the Triassic in South China.

In order to estimate the biases from sample intensities, we also carried out the rarefaction analyses for all intervals with reasonably sufficient occurrences (Figure 5). Most of the Triassic intervals do not have sufficient fossil records; therefore rarefaction analyses were carried out only for the Induan, Anisian and Norian intervals.

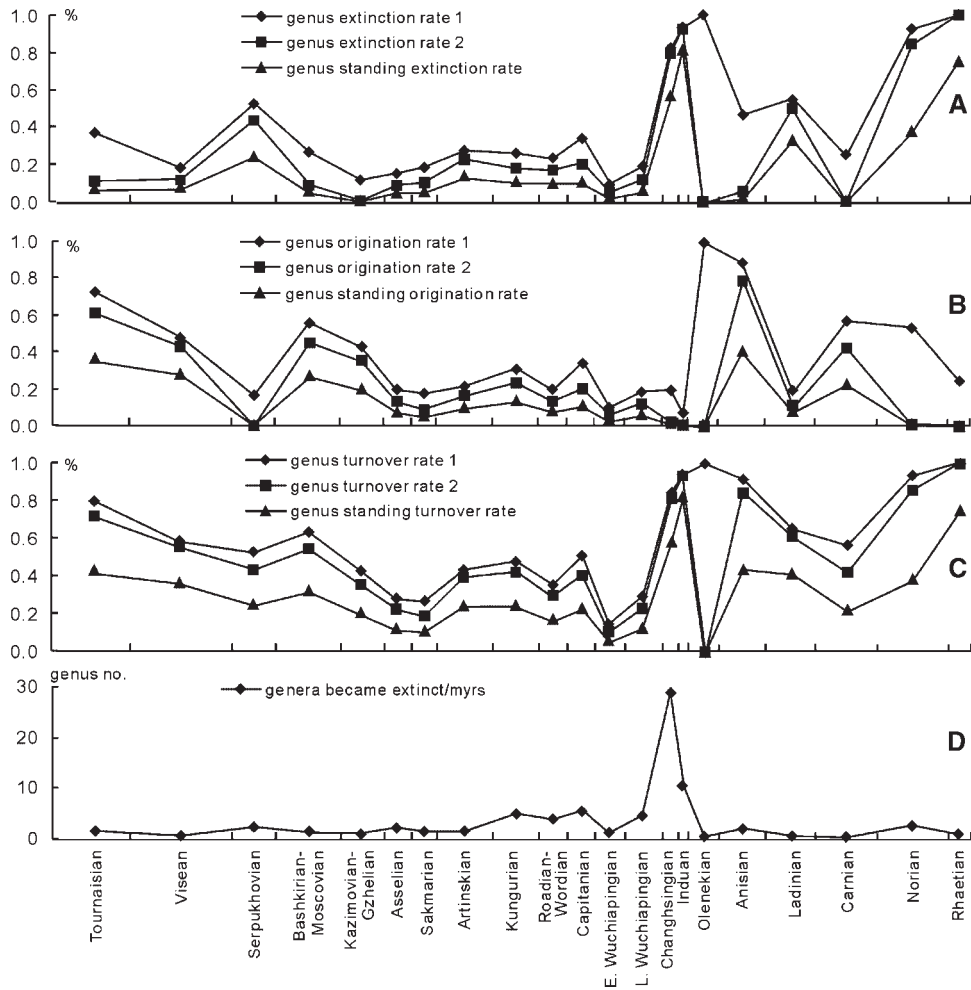


Figure 4. Brachiopod extinction (A), origination (B), turnover rates (C) and (D) number of genera that became extinct/myrs from Carboniferous to Triassic. (Calculation formula see Harper 1996; Shen *et al.* 2004. Stage width scaled to duration.)

The diversity trajectory, on the basis of rarefaction estimates of generic richness at a sample size of 100 generic occurrences, indicates a general plateau from the Bashkirian to Changhsingian, bracketed by the diversity depletions in the Serpukhovian and Early Triassic (Figures 5 and 6). Therefore, the end-Changhsingian mass extinction and the Serpukhovian diversity declines are probably robust. The Sakmarian-Artinskian diversity decline revealed by the taxonomic richness is not confirmed by the diversity trajectory (Figure 6). As shown in Figure 6, brachiopods gradually declined from the Tournaisian to Serpukhovian, then rapidly climbed until the Bashkirian-Moscovian, slightly declined in the Asselian and recovered to a plateau from the Sakmarian to Kungurian, followed by another low point in the Roadian-Wordian. Brachiopods were still flourishing in the Capitanian, and then declined from the Capitanian to Early Wuchiapingian. Brachiopods in the Lopingian (Late Permian) recovered slightly, but this was followed by their sharp decline at the end-Changhsingian, then a partial recovery in the Middle Triassic Anisian (Figure 6). The diversity patterns revealed by the raw taxonomic richness and the rarefied trajectory are not completely consistent for the Asselian, Artinskian and Roadian-Wordian. This uncertainty is either due to relatively low sampling intensities or pitfalls in the rarefaction technique.

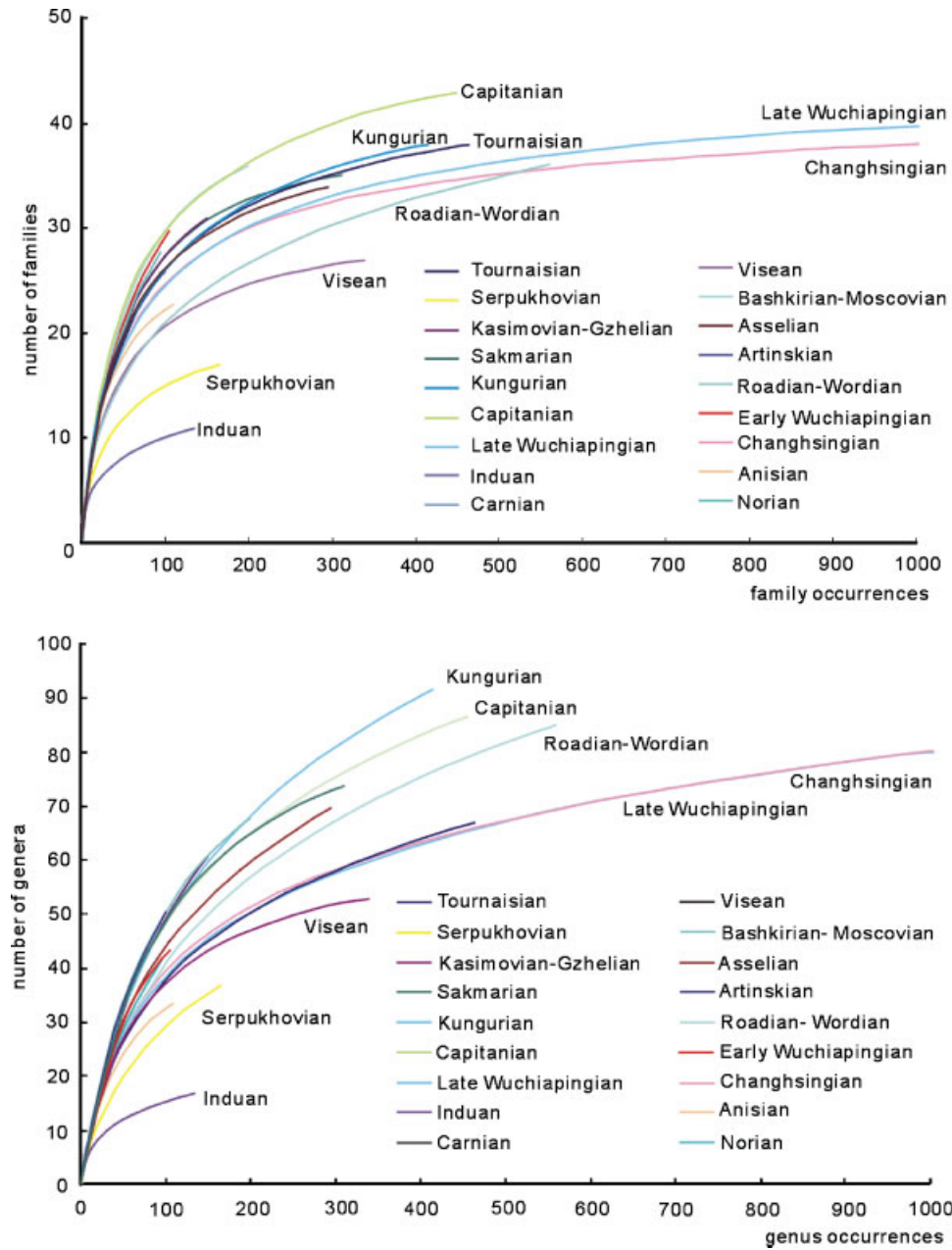


Figure 5. Occurrence/genus (below) and occurrence/family (above) rarefaction curves of intervals from Carboniferous to Triassic in South China.

4. FAUNAL CHARACTERISTICS AND CHANGES OF BRACHIOPOD COMPOSITION FROM THE CARBONIFEROUS TO TRIASSIC

In order to reveal the compositional changes at generic level for each brachiopod order from the Carboniferous to Triassic, the generic numbers and dominated elements of all orders are analysed (Figure 8). Inarticulates only

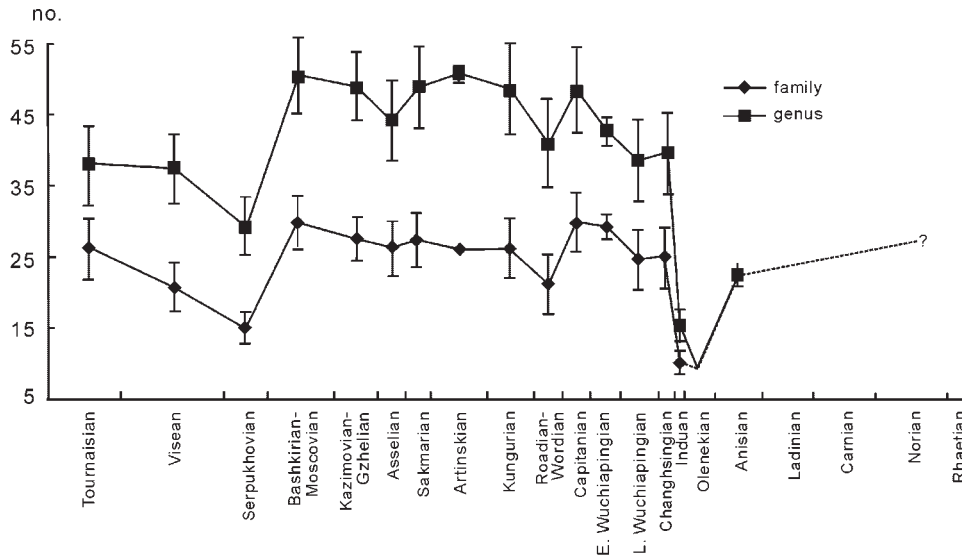


Figure 6. Familial and generic diversity trajectories from Carboniferous to Early Triassic based on rarefaction estimates at a sample size of 100 generic occurrences, error bars depict 95% confidence intervals around the estimates. (The computer program compiled by S. M. Holland on the website <http://www.uga.edu/strata/software/index.html> was used. Stage width scaled to duration.)

occupy a very small portion of brachiopods, therefore are treated as one taxonomic unit for analysis. They are recorded from nearly all intervals with very little change in diversity, but commonly with very high abundance. The generic and specific numbers of different articulate orders from the Carboniferous to Triassic are respectively 162 genera and 867 species (Productida), 45 genera and 298 species (Spiriferida), 46 genera and 199 species (Rhynchonellida), 30 genera and 186 species (Athyridida), 31 genera and 165 species (Terebratulida), 17 genera and 142 species (Orthotetida), 9 genera and 107 species (Orthida) and 28 genera and 93 species (Spiriferinida) (Figure 7). Articulate brachiopods from the Carboniferous to Triassic are distinctly divided into two EFs or EEUs by the end-Changhsingian mass extinction (Sepkoski 1981; Boucot 1983; Shen and Shi 1996, 2002; Shi and Shen 2000). At the end-Changhsingian, the brachiopod order Orthotetida totally became extinct below the Permian-Triassic boundary. Productida, the largest group in the Late Palaeozoic, mostly disappeared at end-Changhsingian. Only a few small thin-shelled taxa (e.g. *Neochonetes*, *Cathaysia*, *Spinomarginifera*) struggled into the earliest Induan. Orthida and Spiriferida are two common groups in the Late Palaeozoic, only three genera (*Acosarina*, *Crurithyris*, *Paracrurithyris*) extended into Early Induan. Therefore, four orders out of eight articulate brachiopod orders were eliminated by the end-Changhsingian mass extinction (Shen and Shi 1996, 2002; Shi and Shen 2000; Rong and Shen 2002; Chen *et al.* 2005a, 2005b). Only Athyridida, Rhynchonellida, Spiriferinida, Terebratulida and inarticulates continued to be present after the end-Changhsingian mass extinction. They are all characterized by relatively small size, biconvex shell, weak ornamentation and pediculate (attached to substrate by pedicle) shells.

Brachiopods from the Carboniferous to Permian remained relatively stable in view of the composition of different orders. Three diversity declines can be more or less recognized for most orders although the magnitudes of the three declines are much weaker than the end-Changhsingian mass extinction. They are in the Serpukhovian, Artinskian and Early Wuchiapingian (Figure 7).

Productida is the most dominant brachiopod group in all intervals from Carboniferous to Permian. It flourished in the stages from Asselian to Sakmarian, from Kungurian to Capitanian and from late Wuchiapingian to Changhsingian, slightly declined in the Serpukhovian and remarkably declined in the Artinskian and Early Wuchiapingian in terms of generic number. Spiriferida generally display a pattern of decline from the Carboniferous to Permian. It was most abundant in the Tournaisian, significantly declined in the Viséan and Serpukhovian, partly recovered in the Bashkirian-Moscovian and then experienced a general decline trend until the

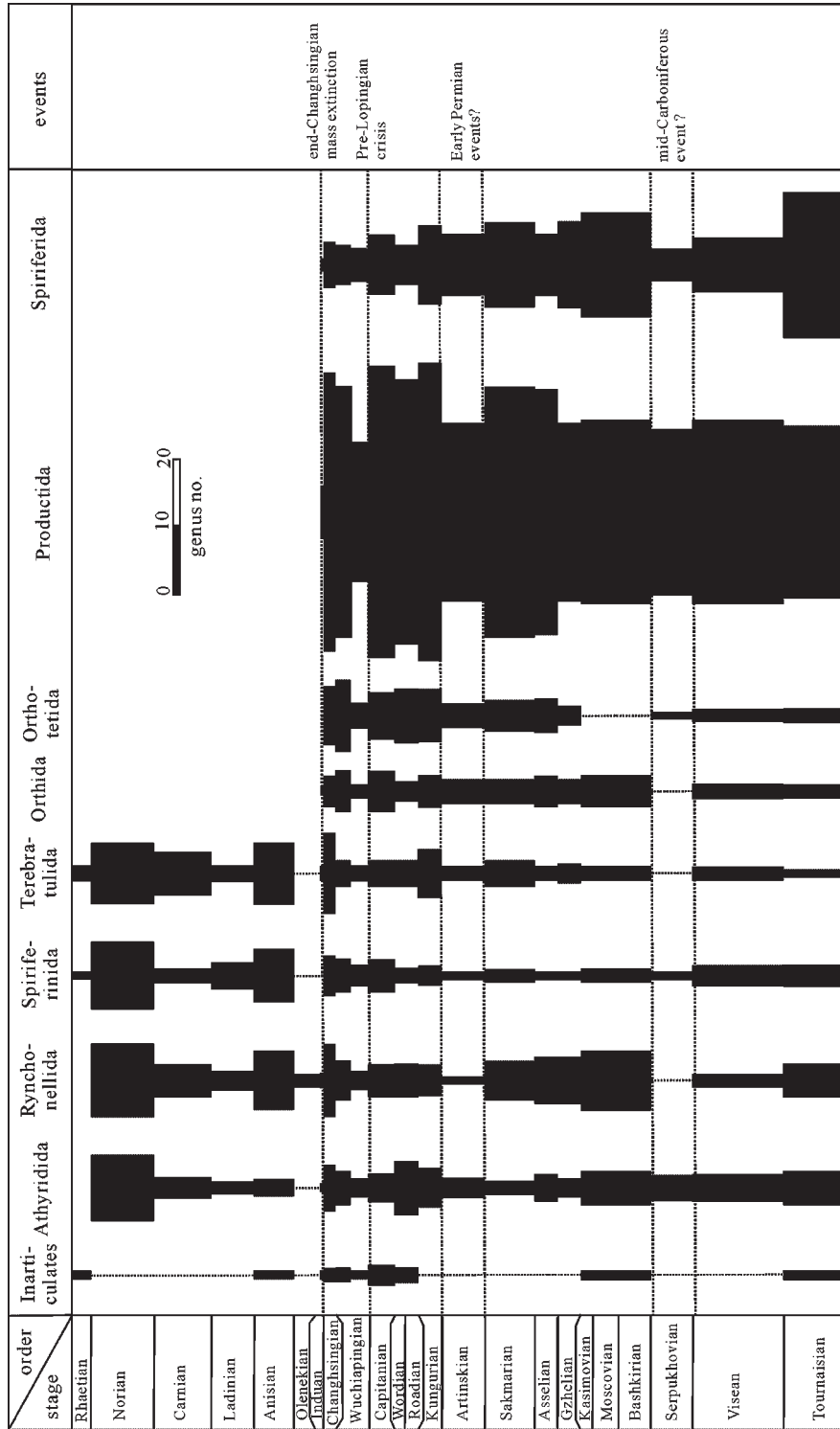


Figure 7. Generic numbers of inarticulate brachiopods and different orders of articulate brachiopods in different intervals from Carboniferous to Triassic in South China.

end-Changhsingian (Figure 7). Orthotetida, Orthida, Rhynchonellida, Spiriferinida and Terebratulida all suffered significant losses in generic number in the Serpukhovian, but immediately recovered or radiated out in the Bashkirian-Moscovian. As for the Artinskian interval, the generic decline is only expressed in Rhynchonellida, Spiriferinida and Terebratulida. All the orders reduced in generic number in the Early Wuchiapingian.

In addition to inarticulates, brachiopods in the Early Triassic after the end-Changhsingian mass extinction are rare in South China. Four rhynchonellid species (*Piarorhynchia gujiaoensis*, Feng in Feng and Jiang 1978; *Paranorellina changxingensis* Liao, 1984; *Laevorhynchia tenuis* Shen and He, 1994; *Meishanorhynchia meishanensis* Chen and Shi in Chen *et al.* 2002) are recorded (Chen *et al.* 2005b). These four species (at least the latter three) are highly likely synonyms in terms of their similar stratigraphic occurrences and structures. Therefore, they are tentatively treated as one species and one genus (*Laevorhynchia* Shen and He 1994) in our database. In addition to the rhynchonellid, two spiriferids (*Paracrurithyris*, *Crurithyris*) were recorded from the late Griesbachian or Early Dienerian (Yang *et al.* 1987) and a spiriferinid (*Spiriferina* sp.) from the Dienerian was mentioned by Xu and Grant (1994), but has no description. Terebratulida, Spiriferinida, Rhynchonellida and Athyridida recovered in the Middle Triassic, declined in the Ladinian and Carnian, flourished again in the Norian and disappeared in the Late Triassic in South China (Figure 7).

5. CONCLUDING REMARKS

5.1. Carboniferous-Triassic diversity pattern

As analysed above, the brachiopod diversity profile from the Carboniferous to Triassic can be divided into two distinct EEUs, which are separated by the end-Changhsingian mass extinction. Four out of eight articulate brachiopod orders were eliminated by the end-Changhsingian mass extinction. Brachiopods experienced a long bleak stage in the Early Triassic and recovered in the Middle Triassic, but never reached the Late Palaeozoic diversification. The brachiopod diversity trend from the Carboniferous to Permian generally indicates a plateau from the Pennsylvanian Bashkirian to the Middle Permian Capitanian bracketed by the Serpukhovian diversity decline and the pre-Lopingian crisis (Figure 6).

5.2. Mid-Carboniferous event is probably a long minor event

The mid-Carboniferous event seems to be well exhibited by the declines of both raw taxonomic richness and the rarefied curves in the Early Carboniferous. It has been documented in some previous studies (Saunders and Ramsbottom 1986; Raymond *et al.* 1990; Nemirovskaya and Nigmadganov 1994; Kossovaya 1996), but the magnitude and duration ascribed to this event vary greatly between different authors and different fossil groups. This event is in the European Namurian Stage and largely corresponds to the Mississippian-Pennsylvanian boundary of North America and is in the upper part of the Russian-Serpukhovian Stage. Ziegler and Lane (1987) and Weems (1992) ranked it as a mass extinction comparable to the 'Big Five'. Sepkoski's (1986) data suggest it was a major event. Saunders and Ramsbottom (1986) also called it a major extinction based on the disappearance of many major ammonoid lineages. Conodonts underwent a crisis and reached a low diversity point at the mid-Carboniferous boundary (Ziegler and Lane 1987; Nemirovskaya and Nigmadganov 1994). The coral decline can be traced for all morphotypes from simple corals without dissepiments to colonial corals in the North Island of Novaya Zemlya (Kossovaya 1996). Palaeoreef analysis indicates that the mid-Carboniferous event is a first-order reef crisis and caused the loss of about 97% of reefs (Flügel and Kiessling 2002). However, some other detailed investigations suggest that no distinct intra-Carboniferous event can be discerned (e.g. Ausich *et al.* 1994).

Our brachiopod diversity pattern in South China displays a continuing decline in diversity from Tournaisian to Serpukhovian (Figures 3, 4, 6 and 7), which probably suggests that the so-called 'mid-Carboniferous extinction' is a gradual event and was experienced over a long time. A distinct lowest simple diversity point in the Serpukhovian is recognized based on the brachiopod data of South China (Figures 3, 4, 6 and 7). However, detailed statistical data

in South China indicate that brachiopods have no substantial changes at familial and supra-familial levels between the Early and Late Carboniferous. Three families (Rafinesquinidae, Lochengidae, Araksalosiidae) became extinct in the Serpukhovian, but only four genera (*Leptagonia*, *Lochengia*, *Galeatathyris*, *Chonetipustula*) are included in these three families in South China. Gigantoproductidae is probably the family (now treated as a subfamily in the new treatise of Williams *et al.* (2000a) to be significantly affected (Raymond *et al.* 1989, 1990). Some most common genera of Gigantoproductinae in the Viséan and Serpukhovian in South China, such as *Datangia*, *Gigantoproductus*, *Kansuella* and *Kueichowella*, became extinct after the Serpukhovian. Brachiopods in the Tournaisian and Viséan are characterized by many genera extended from the Late Devonian (e.g. *Marginatia*, *Yanguania*, *Balakhonia*, *Camarotoechia*, *Ptychomaletoechia*). These genera became extinct after the Serpukhovian. Spiriferida seems to have suffered a significant loss in the Viséan and continued to decline in the Serpukhovian (Figure 7). Therefore, the brachiopod compositional changes between the Early and Late Carboniferous seem to be recognizable only at generic and specific levels in South China and the effect may be qualified as community-type level changes within an established ecological structure (for more detailed definition see Droser *et al.* 2000) rather than a mass extinction.

5.3. Early Permian (Late Sakmarian to Late Artinskian) events are not well reflected in South China based on brachiopod data

The Early Permian was another time with biotic changes that have been discussed by different authors (Beauchamp *et al.* 1987; Leven 1993; Beauchamp and Theriault 1994; Kossovaya 1994; Leven *et al.* 1996; Kossovaya *et al.* 2001). The reef ecosystem was probably the most severely-affected group by the Early Permian (either in Sakmarian or Artinskian) events, with a decline of 97% in reefal carbonate production rate (Flügel and Kiessling 2002). Great changes in rugose corals from fasciculate and massive colonial Rugosa to small primitive ahermatypic diaphragmatophoral corals have also been recorded from the Late Sakmarian to Late Artinskian in western, northern and eastern marginal basins of Pangea (Kossovaya *et al.* 2001). Fusulinids suffered significant changes across the Sakmarian–Artinskian boundary. Characteristic Asselian and Sakmarian elements such as *Sphaeroschwagerina*, *Pseudoschwagerina*, *Paraschwagerina*, *Rugosofusulina*, *Zellia* and *Quasifusulina* became extinct or considerably reduced in abundance (Leven *et al.* 1996; Shi and Yang 2004). Conodonts also experienced distinctive changes, as indicated by the disappearance of the Carboniferous genera such as *Streptognathodus* and *Adetognathus*, and appearance of some new forms such as *Neostreptognathus* and *Sweetognathus* (Clark 1972; Ritter 1986, 1987; Barskov and Reymers 1992; Mei *et al.* 2002).

However, the Early Permian events are not well exhibited based on the brachiopod data in South China in terms of extinction/origination/turnover rates (Figure 4) and rarefaction analyses (Figure 6), but are weakly reflected in terms of simple diversity (Figure 3). Brachiopods in South China experienced a minor low diversity stage from the Sakmarian to Artinskian (Figure 3), but have less change in view of brachiopod composition even than that between the Mississippian and Pennsylvanian. Three families, Pseudodielasmataidae, Psilocamaridae and Spiriferellidae [The record by Li *et al.* (1986) for this family is questionable], disappeared in the Sakmarian in South China, but these three families are mostly represented by cold-water type brachiopods and all continued to be present in other regions in the world (Shen and Shi 2000, 2004). No family became extinct in the Artinskian in South China. Productida is probably the most affected group in brachiopods as indicated by the disappearance of some genera extended from the Carboniferous such as *Alexenia*, *Chaoiella*, *Costachonetes*, *Echinoconchus*, *Juresania*, *Mistproductus*, *Plicatifera* and *Proanidanthus*, and the appearance of some newcomers such as *Dictyoclostoidea*, *Liosotella*, *Strigospina* and *Tyloplecta*. Rhynchonellida seems significantly reduced in the Artinskian in generic number (Figure 7). However, only *Nantanella* and *Pugnax* became extinct, all other genera continued to be present in the Kungurian. Therefore, the results indicate that the Early Permian event is taxonomically selective in extinction and/or is probably affected by sampling effect, because all previous studies that document the event are based on simple diversities (taxonomic numbers) and have not been verified by other approaches (e.g. rarefaction analysis employed in this paper).

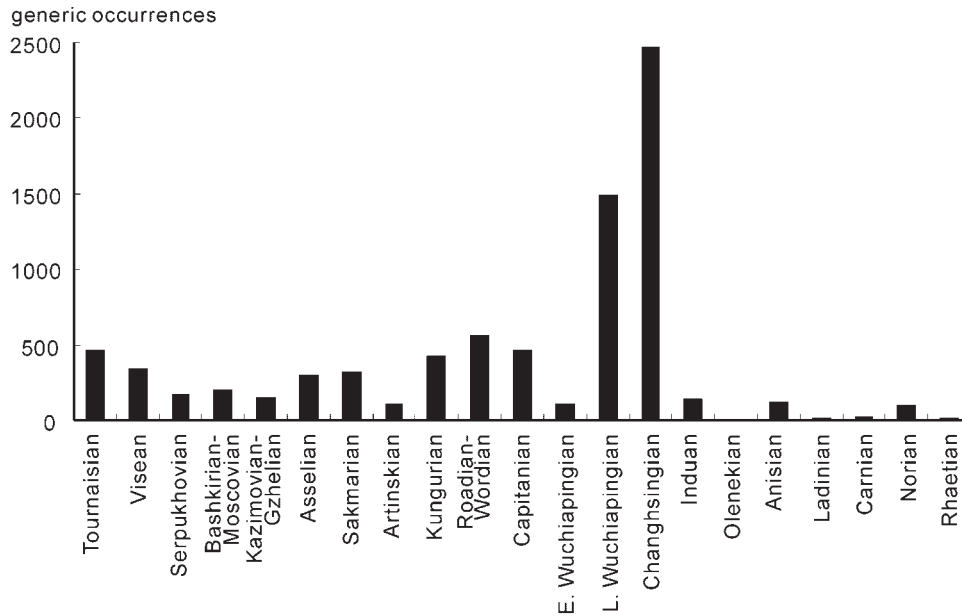


Figure 8. Histogram showing brachiopod generic occurrences of different intervals from Carboniferous to Triassic.

5.4. *Lopingian radiation is largely over-stated?*

The end-Permian mass extinction is the most severe first-order (*sensu* Droser *et al.* 2000) mass extinction and is the most intensively-studied extinction event (Sepkoski 1978, 1981, 1984; Raup and Sepkoski 1982). Recent statistical data show that the previously-perceived end-Permian mass extinction (Sepkoski 1978, 1981, 1984; Raup and Sepkoski 1982) actually consists of two phases (Jin 1993; Jin *et al.* 1994; Stanley and Yang 1994; Shen and Shi 1996, 2002; Shi *et al.* 1999; Shi and Shen 2000; Wang and Sugiyama 2000). One is the pre-Lopingian (end-Guadalupian) crisis and the other is the end-Changhsingian mass extinction that bracketed a 'radiation' stage from Late Wuchiapingian to Late Changhsingian. This 'radiation' is remarkably expressed in terms of the simple/standing diversities at familial, generic and specific levels, and genus and species number per million years (Shen and Shi 1996, 2002; Shi and Shen, 2000; Figure 3). It is of particular interest that the rarefied generic diversity profile indicates that brachiopods gradually declined from the Capitanian to Early Wuchiapingian, followed by a flat step in the Wuchiapingian and Changhsingian. Therefore, the so-called Lopingian major radiation is at least partly over-estimated and needs to be re-estimated in more detail. One of the possible reasons is that the high species and genera numbers are due to the most intensive studies on the Lopingian faunas in South China. As indicated in Figure 8, the Changhsingian and Late Wuchiapingian have much higher generic occurrences than all other intervals in South China. Thus, the end-Permian mass extinction (pre-Lopingian and end-Changhsingian mass extinctions together) was probably a two-step-down extinction (Figure 6).

5.5. *Brachiopod recovery and disappearance in the Triassic of South China*

Middle and Late Triassic brachiopod records are relatively limited because of limited marine deposits in South China (Sun and Shen 2004; Chen *et al.* 2005b). Sampling intensities of most Middle and Late Triassic intervals cannot be estimated by rarefaction because of insufficient occurrences. Only the Induan, Anisian and Norian have sufficient data for rarefaction analysis (Figure 5). As exhibited in Figures 3, 5 and 7, brachiopods experienced a long bleak stage after the end-Changhsingian mass extinction that is about 6 million years in terms of the latest timescale

(Gradstein *et al.* 2004). Only two brachiopod genera were recorded from the Olenekian Stage of the Early Triassic. Athyridida, Rhynchonellida, Spiriferinida and Terebratulida rapidly recovered from the Early Triassic bleak stage in terms of the data from South China. Fifty-seven brachiopod species of 30 genera were recorded from the Anisian in South China. The generic and species numbers reached a peak (40 genera and 70 species) in the Norian, which was followed by a distinct, sharp drop in the Rhaetian, concomitant with the seawater withdrawal from South China. Brachiopods in the Triassic never recovered to the levels in the Late Palaeozoic diversification. Brachiopods in the Ladinian and Carnian were substantially reduced, but we do not know whether this reduction is derived from less marine deposits in South China or a reflection of a significant diversity depletion event in the Ladinian or Carnian. The widely perceived Late Triassic (Late Norian–Rhaetian) mass extinction cannot be assessed appropriately on the basis of brachiopod data in South China because no Jurassic marine deposits are available.

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