

Dynamic patterns of latest Proterozoic-Palaeozoic-early Mesozoic marine biodiversity in South China

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Analyses of global biodiversity curves have been important for the interpretation of co-evolution between organisms and environments through geological time. Global curves can be better understood if all the data collected from a multitude of palaeocontinents are analysed and explained separately. South China is a major block possessing more advantages for regional research than any of the other blocks in China. There exists a well-developed succession of marine strata from the Ediacaran through to the Triassic with a relatively high resolution of bio- and chrono-stratigraphy and an extensive marine fossil record. Stratigraphic occurrences of 5685 genera and 1386 families within 32 phyla or subphyla plus groups with uncertain affinities from this interval have been compiled by a large team of palaeontologists. With the exception of the Ediacaran, 50 time intervals with an average duration of 6.8 Ma are investigated. Diversity curves constructed at the levels of genus, family and order indicate that marine biodiversity peaked six times within the intervals: (1) Early Cambrian explosive radiation, (2) Early-Mid Ordovician radiation mainly of the Paleozoic Evolutionary Fauna, (3) Early Silurian radiation, (4) late Early-Mid Devonian radiation, (5) Mid-Late Permian radiation and (6) Mid Triassic radiation chiefly of the Modern Evolutionary Fauna. Drops in biodiversity are controlled by various factors: (1) global catastrophes, which produced rapid losses of biodiversity during short time intervals; (2) global environmental perturbations with long term effects, as in the Carboniferous; (3) regional tectonics and palaeogeographical constraints, resulting in a lack of marine sedimentary rocks in many areas with biodiversity declining, as in the Wenlock; (4) unique sedimentary facies in large areas resulting in biodiversity losses, as in the Late Cambrian and (5) artifactual constraints associated with a lack of fossil record or low research intensity for some intervals, as in the period of about 30 Ma following the Early Cambrian explosive radiation. Copyright © 2007 John Wiley & Sons, Ltd.

Received 3 March 2006; revised version received 15 November 2006; accepted 20 December 2006

KEY WORDS marine biodiversity; latest Proterozoic; Palaeozoic; early Mesozoic; South China

1. INTRODUCTION

Because a global-scale outlook is required for a better understanding of evolutionary history, Phanerozoic trends in global biodiversity through geological time have been investigated intensively by many palaeobiologists (e.g. Valentine 1969; Raup 1972; Sepkoski 1979, 1981, 1993; Benton 1995; Miller and Foote 1996; Alroy *et al.* 2001). However, in attempting to understand what causes the major transitions recognized globally, there remains much to be learned through regional studies. Given that global patterns are derived from local or regional occurrences, there may have been a direct link between global and regional diversification during any interval, but it does not necessarily follow that parallel trajectories will be exhibited at regional and global scales (Miller 2000, 2004). Furthermore, while a growing number of investigations have focused on the history of biodiversity at regional or

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palaeocontinental scales, there have been few attempts to synthesize these trajectories through extended intervals of geological time, such as a sequence of several periods or an entire era. To understand the relationship between biotic evolution and physical environmental changes, the investigation of regional diversity trajectories may be particularly important, because at this scale, definitive comparisons between biological and physical variables become possible. With these considerations in mind, the purpose of this paper is to present, for the first time, a comprehensive marine biodiversity trajectory for South China that spans more than half of the Phanerozoic.

This investigation is focused on an analysis of marine biodiversity in the South China Block (Figure 1) from the latest Proterozoic (Ediacaran) through the Palaeozoic (Cambrian to Permian), to the early Mesozoic (Triassic), an interval of about 430 Ma. Pre-Ediacaran and post-Triassic intervals are not included, since marine fossils were scarce prior to the Ediacaran and marine environments were largely absent from South China after the Triassic. There are several reasons why South China is particularly well suited for this investigation. First, there is a thick sedimentary sequence in South China through this interval that begins with Ediacaran rocks, followed by a continuous Palaeozoic to early Mesozoic successions of marine origin. Second, there is a long history of palaeontological and stratigraphical research on these rocks in South China, with a much higher intensity of study, collection and synthesis than other regions in China. Third, high resolution and reliability of international correlation of the sequence has yielded standard sections for some systems, series and stages, such as the Global Stratotype Section and Point (GSSP) of the Permian–Triassic boundary (Yin *et al.* 2001). Finally, the palaeogeographical position of South China through this interval is becoming increasingly well understood, which will ultimately be of importance in the interpretation of the diversity trajectory presented here.

The marine biotas investigated herein include representatives of many ecological groups, including benthic taxa (brachiopods, bryozoans, bivalves, crinoids, corals, dacyocornarids, fusulinid foraminifers, gastropods, ostracodes, stromatoporoids and trilobites), planktonic organisms (acritarchs, chitinozoans and graptolites) and pelagic groups (nautiloids, ammonoids, conodonts, fishes and trilobites). Many of these are common fossil groups in marine sedimentary sequences. A few questionable or extremely rare groups are not included here because of the lack of specialists who work on these taxa, thereby inhibiting the development of reliable data. The data used here, which depict the first and last known appearances of taxa at the genus, family and ordinal levels, are derived from many published sources dating back as far as the early part of the 20th century. Some unpublished contributions have also been included, and some taxa, mainly at the genus level, have been revised during this research. A full list of fossil groups and the workers who contributed those data is provided in the Appendix.

Historical constraints on scientific development have impeded the earlier synthesis of a database permitting the depiction of an ancient biodiversity trajectory for South China. However, with the establishment of a large project (2000–2005) entitled ‘Biological Origination, Radiation, Extinction and Recovery in Major Geological Time Intervals’ funded by the Ministry of Science and Technology of China, it became possible to develop and investigate this major field (Rong *et al.* 2006b).

2. QUALITY OF THE FOSSIL RECORD

During our investigation, the quality of the fossil record for South China has been considered in various ways. Many factors, including the development of marine sediments and surface outcrop area of rocks, influence the quality and even our understanding of the true picture of life history in any region. In the South China Block, for example, there is a large area where Ordovician and Llandoveryan marine sedimentary rocks are widely distributed, so a meaningful picture of marine biodiversity can emerge. Conversely, however, South China was not flooded in the great majority of areas for the rest of the Silurian through the early-mid Early Devonian, and this is associated with an apparent marked reduction of biodiversity during this interval.

In addition, variations in the intensity of sampling (Sheehan 1977), which are not independent of variations in the availability of sedimentary rocks and fossils (Raup 1977) are further considered to be important. In some cases, apparent biodiversity trends for South China are related to changes in the number of counties from which fossil occurrence data have been derived (Figure 2). Because the number of counties containing fossils for a given interval

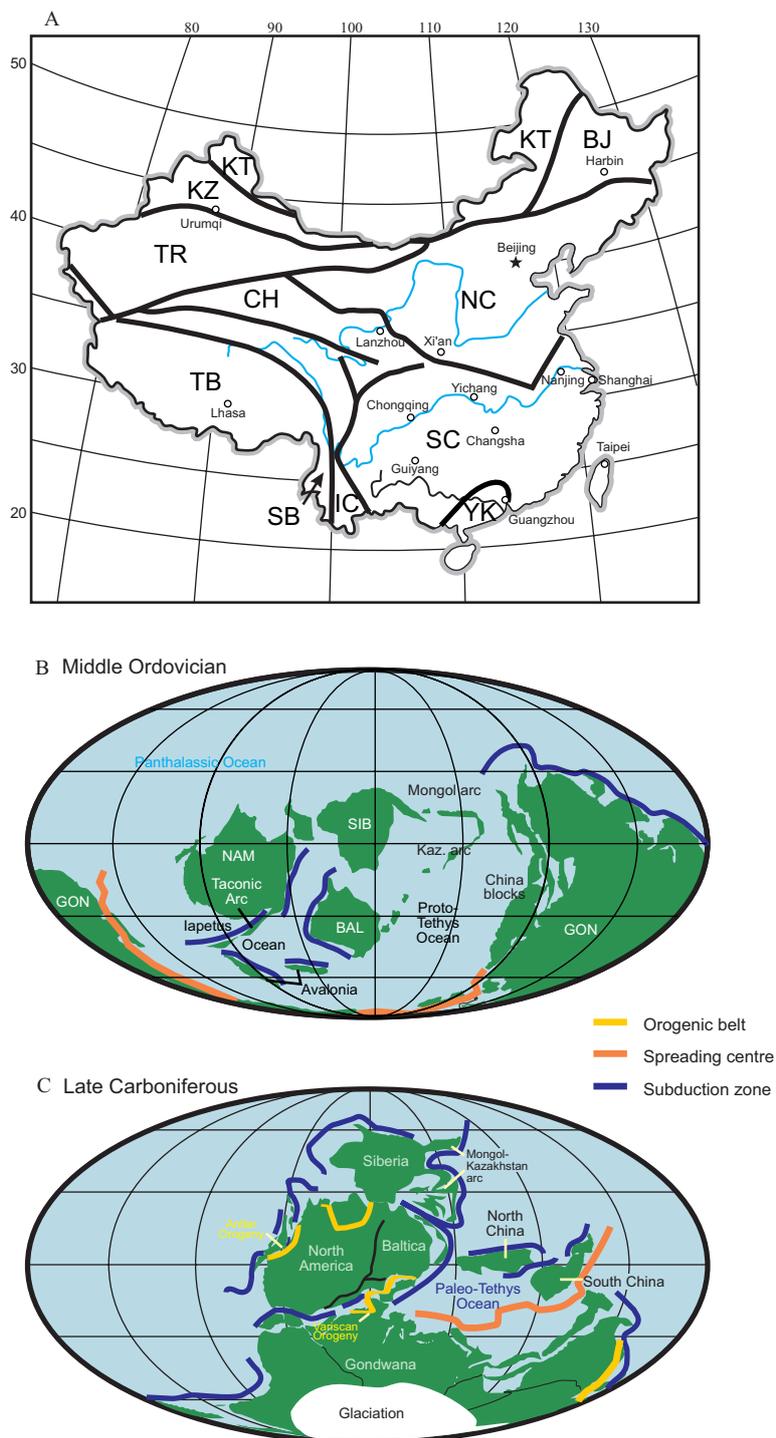


Figure 1. The position of the South China Palaeoplate. A: Chinese geological map showing the main palaeoplates (revised from Rong *et al.* 2003; mainly for the early Palaeozoic); B and C: Palaeogeographic reconstruction maps for the Mid Ordovician and the Late Carboniferous (from Gradstein *et al.* 2004). BJ = Bureya-Jiamusi; CH = Chaidamu; IC = Indochina; KT = Khingan-Tuva; KZ = Kazakhstan; NC = North China; SB = Sibumasu; SC = South China; TB = Tibet (Xizang); TR = Tarim; YK = Yunkai.

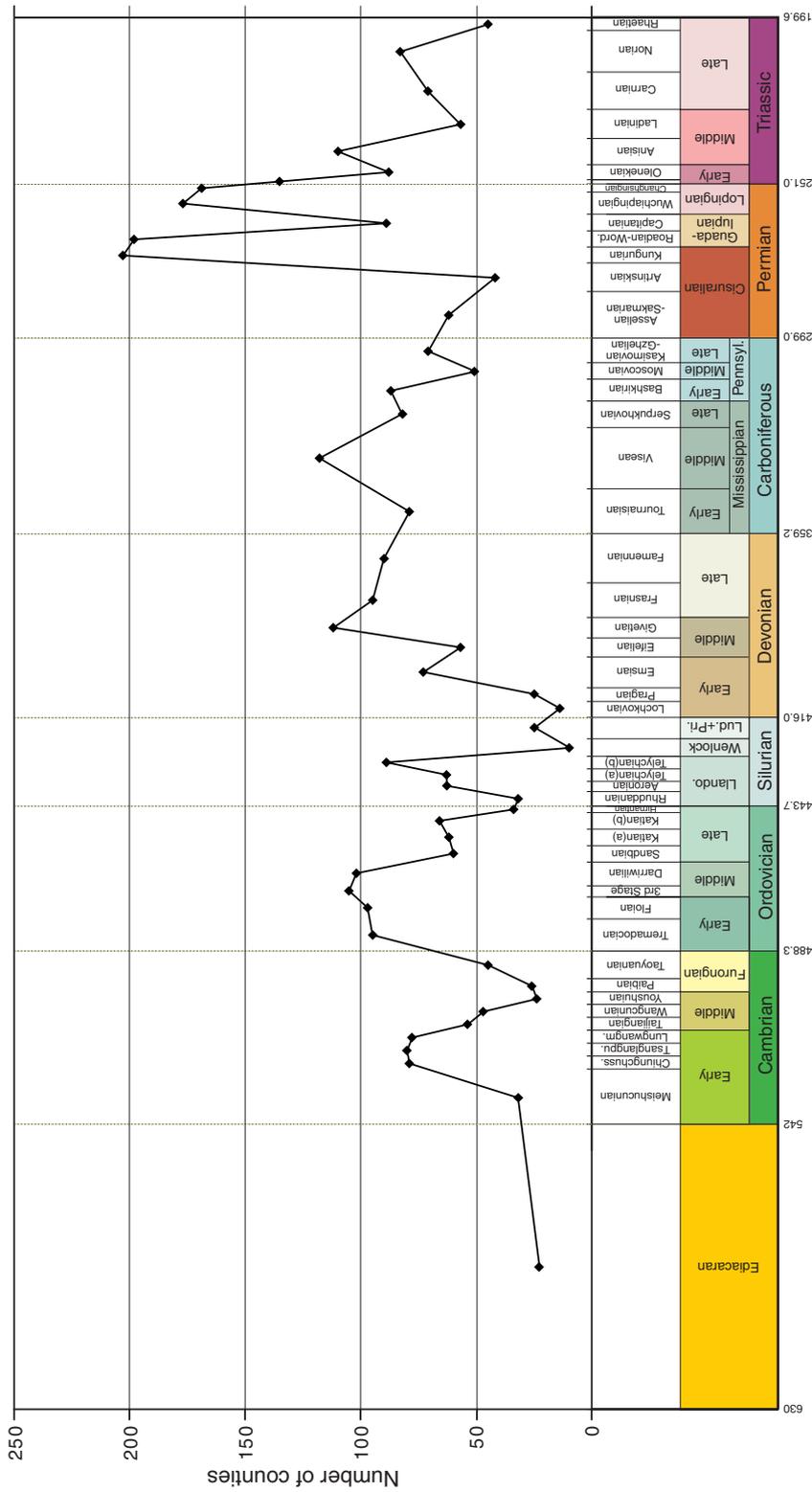


Figure 2. Distribution of fossil records (number of counties) from the Ediacaran to the Triassic in South China. County is an administrative subdivision of a city in China. The time slices are from Gradstein *et al.* (2004).

can be taken as a proxy for the extent of the fossil record for that interval, a correlation between an apparent biodiversity trend and a trend in the number of counties might suggest that the biodiversity trend is an artefact of the record. On the other hand, if the apparent biodiversity trend differs from the trend in the number of counties, then there is greater reason to be confident that the biodiversity trend is biologically meaningful.

The quality of the fossil record also depends on the nature of preservation. For example, silicified gastropod specimens from the Lower-Middle Permian and Middle Triassic have been studied intensively, but there occur only rare silicified specimens from the Lower Triassic, creating many Lazarus taxa through the Permian–Triassic transition (Pan and Erwin 1994; Erwin 1996). From these points of view, the fossil record should be viewed and treated with caution.

The present authors consider that most of the fossil record is a true record of past biodiversity. Palaeontology has unique access to historical data, and our understanding of ancient diversification is critically dependent on the analysis of a reliable fossil record (Conway Morris 1999), even though the fossil record is far from perfect, and there are preservational issues that have not been entirely resolved. Of course, the robustness of the biodiversity curves we present herein for South China are by no means final, and we will not be reluctant in refining them in the future. This effort should be viewed as a first step, but a good beginning is half the battle won.

3. DATA AND METHODS

Fossil data were collected and collated for South China from most stages representing the 430 Ma time interval. Since finer subdivisions are available in many cases, several stages were split into two parts, such as the lower and upper Katian (6th Stage: more than 10 Ma) of the Upper Ordovician Series, and the lower and upper Telychian Stage (nearly 10 Ma) of the Llandovery Series of the Silurian. In other cases, however, a few neighbouring stages are grouped into a single unit, such as the Kasimovian and Gzhelian stages (2.6 and 4.9 Ma) of the Carboniferous, and the Asselian and Sakmarian stages (4.4 and 10.2 Ma) of the Permian, because their boundaries cannot be finely defined in South China. Two of the Silurian series, the Ludlow and Přídolí (4.2 and 2.7 Ma), have been combined in a single unit for the same reason.

The absolute age and duration of each unit follows the recently published timescale of Gradstein *et al.* (2004). With the exception of the Ediacaran System (88 Ma), there occur 50 stratigraphic units with an average duration of 6.8 Ma that are treated herein. The resulting plots are of simple biodiversity at taxonomic levels range from genus, family to order (Figure 3). Singletons (i.e. taxa restricted to a single time unit) are also included. A set of normalized marine biodiversity curves (Figure 4) based on the method of Cooper (2004) is also presented here for South China for the first time. In addition, we have followed Sepkoski's definition (1981) of the three Phanerozoic evolutionary faunas, and present here a genus diversity curve with genera sorted by membership in each of the faunas (Figure 5).

In all, our database depicts the stratigraphical occurrences of 5685 genera, 1386 families and 244 orders within 32 phyla or subphyla (see Appendix). There are some additional occurrences that we did not include here because they are of uncertain taxonomic affinity. The total numbers at the three taxonomic levels reflect the compilation efforts of our team. Most of the data are from sources published as far back as early in the 20th century, with the rare inclusion of unpublished material investigated by some contributors involved in this study. There have been some taxonomic revisions in association with data compilation, where possible.

4. PEAKS OF BIODIVERSITY

Six peaks in the biodiversity trajectories of genera, families and orders from the Ediacaran to Triassic in South China are recognized in Figures 3 and 4. They include (1) the Early Cambrian (reflecting the Cambrian Explosion), (2) the Mid Ordovician (the Ordovician Radiation mainly for the Paleozoic Evolutionary Fauna (PEF; Figure 5)), (3) the Early Silurian, that is the Aeronian—Telychian (mid-late Llandovery) radiation after the end-Ordovician mass extinction, (4) the late Early to Mid Devonian, that is, the Emsian—Eifelian—Givetian diversification, (5) the Mid to Late Permian and (6) the Mid Triassic, chiefly for the Modern Evolutionary Fauna (MEF). All of these intervals are related to adaptive radiations at various scales, as we will discuss below, with features unique to each event, but all reflecting times when environmental conditions were suitable for the proliferation of marine biotas in

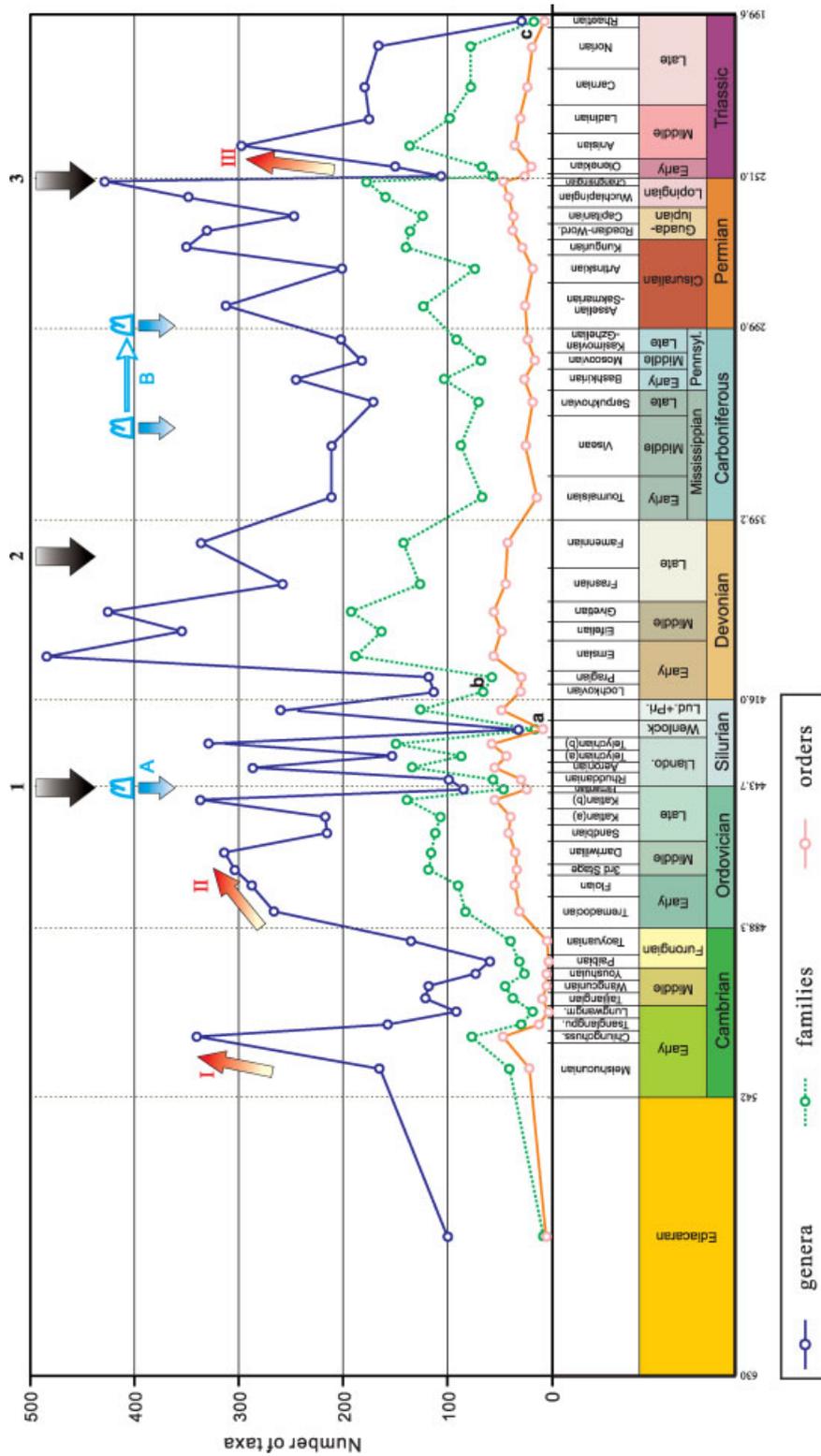


Figure 3. Marine biodiversity curves at genus, family and order levels from the latest Proterozoic to the Triassic in South China. Red arrows indicate three major radiations: (I) the Early Cambrian explosive radiation, (II) Ordovician sustained radiation and (III) Mid-Triassic radiation. Black arrows indicate three mass extinctions of the Palaeozoic: (1) end-Ordovician, (2) Frasnian-Famennian and (3) end-Permian mass extinctions. Blue arrows indicate two glaciations that occurred in the end Ordovician (A), and Carboniferous to earliest Permian (B). These curves were based on the sum of all taxa (including singletons) reported in South China unit by unit, mostly stage by stage with a single unit of two series (e.g. Ludlow–Prídolí), rarely a combination of two stages (e.g. Asselian–Sakmarian as a unit) and a few subdivisions of stages (e.g. the Katian Stage in the Ordovician and Telychian Stage in the Silurian). Significant biodiversity declines are indicated by ‘a’, ‘b’ and ‘c’. See text.

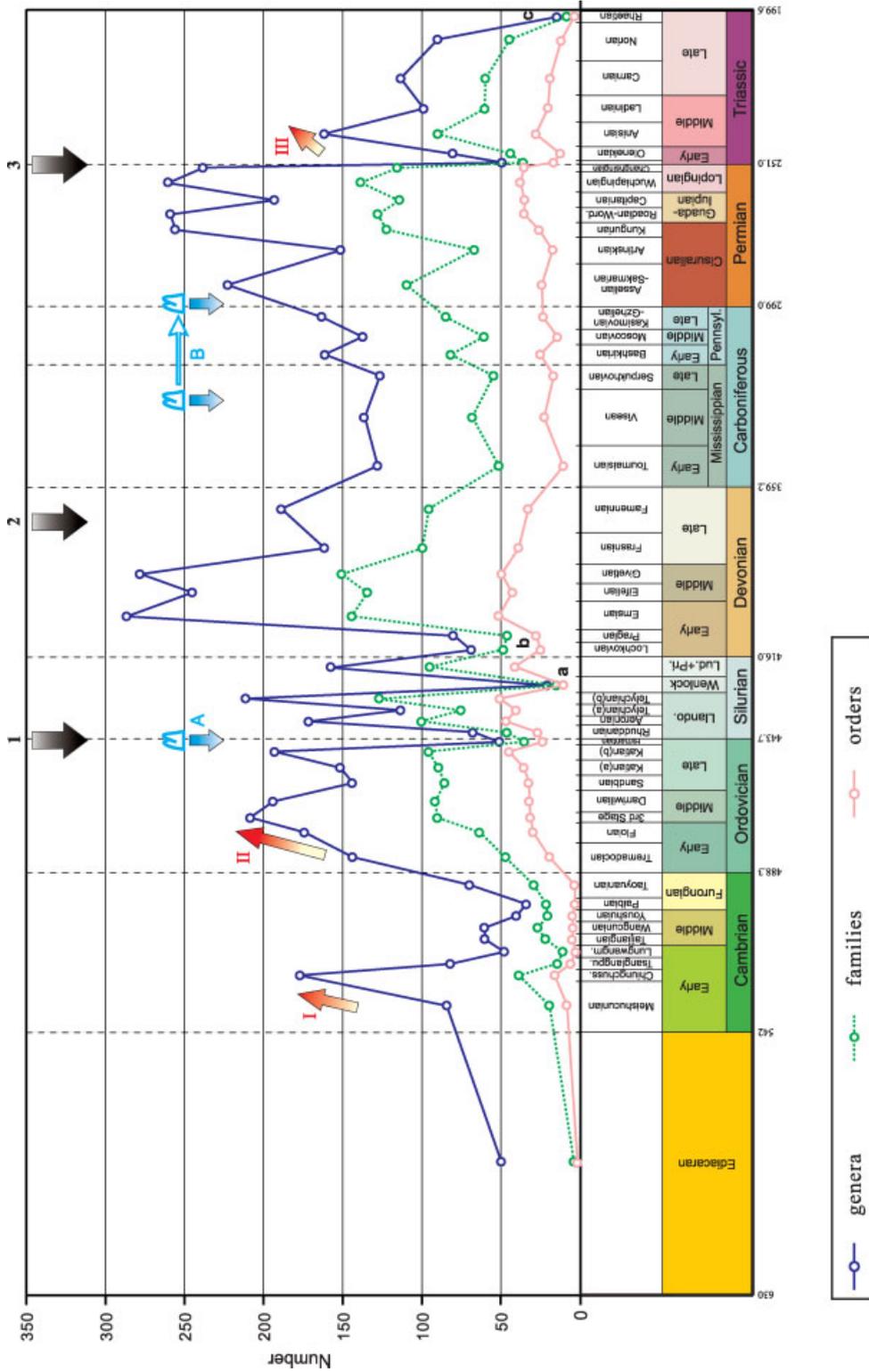


Figure 4. Normalized marine biodiversity curves at genus, family and order levels from the latest Proterozoic to the Triassic in South China. We follow the formula of Cooper (2004) and use the program StratDraw 2.0 designed by Fan Junxuan and Chen Feng to count the normalized diversities. The normalized diversity is the sum of genera that range from the interval below to the interval above, plus half the number of genera that range beyond the time interval but originate or become extinct within it, plus half of those that are confined to the time interval itself (singletons) (Cooper 2004). See Figure 3 for explanation of symbols, numbers and letters.

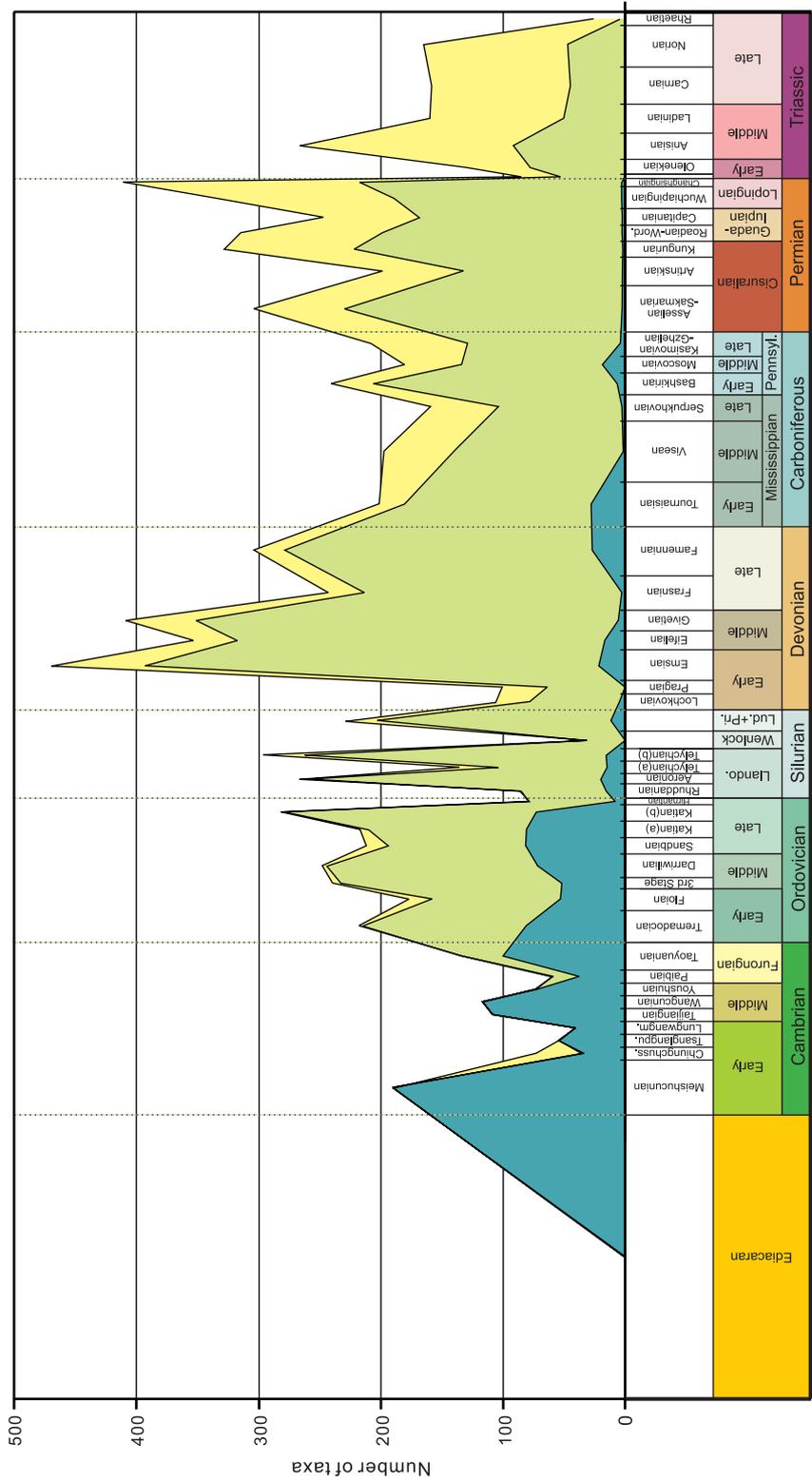


Figure 5. Diagram showing the three evolutionary faunas of marine animals at generic level from the latest Proterozoic to the Triassic in South China. We follow the division by Sepkoski (1981) and others. CEF (in blue), Cambrian Evolutionary Fauna; PEF (in green), Paleozoic Evolutionary Fauna; MEF (in yellow), Modern Evolutionary Fauna. Note that some animals (e.g. Porifera and Phoronida) and many soft-bodied fossils in the Chengjiang Fauna are not included due to their unknown assignments among the three Evolutionary Faunas.

South China. Among them, the radiations in the Early Cambrian, Mid Ordovician, and Mid Triassic are most significant with respect to transitions in the evolution and ecology of marine organisms.

Although the diversification patterns in South China throughout the study interval exhibit notable similarities to the global trend through the same interval (e.g. Sepkoski 1997, figure 1), there are also some departures from the global trend. Interestingly, the early Palaeozoic diversification of the MEF appears to have been far more subdued in South China than it was in the world taken as a whole. Whereas the MEF comprised some 10% or more of global marine diversity during much of the Ordovician and Silurian, the MEF is barely discernable in South China until the Devonian (Figure 5). It seems to the authors that this phenomenon may have been controlled at least by two factors: 1) rare development of the MEF in South China in the early Palaeozoic, and 2) much less research on components of the MEF than those of the PEF.

4.1. Early Cambrian

Available evidence from skeletal metazoan fossils (Bengtson and Conway Morris 1992), Konservat Lagerstätte (Conway Morris 1993; Chen 2004) and trace fossils (Crimes 1992; Jensen *et al.* 2005) indicates that the Early Cambrian witnessed a striking increase in the biodiversity of metazoan fossils (Sepkoski 1992; Zhuravlev 2001). Although the origin and early diversification of some extant metazoan clades can be traced back to the late Neoproterozoic (Budd 2003; Chen *et al.* 2000), the Early Cambrian record reveals a geologically abrupt bioevent, the Cambrian Explosion, at different taxonomic levels (Cloud 1948; Knoll and Carroll 1999; Bengtson 2003; Budd and Jensen 2000, 2003). With well-developed Lower Cambrian sedimentary successions and abundant fossils, South China is one of the most important regions for studying Early Cambrian metazoan diversity and the Cambrian Explosion. Our new data compilation enables us to analyse the diversity of the Lower Cambrian metazoan fossils in South China for a quantitative understanding of the radiation patterns.

Only a limited number of metazoan fossil genera are known in the Ediacaran in South China, such as *Cloudina* and *Gaojiashania* from the Gaojiashan Biota (Hua *et al.* 2000; Hua *et al.* this volume), and a secondary phosphatized cnidarian fossil from the Weng'an Biota (Xiao *et al.* 2000). Sponge fossils have occasionally been reported from Ediacaran rocks (Li *et al.* 1998). The affinities of most of the tubular fossils from the Gaojiashan Biota are debatable, but some have been tentatively assigned to the bilaterians (Hua *et al.* 2005). In addition, there are abundant phosphatized embryo fossils of uncertain affinities from the Weng'an Biota (Xiao *et al.* 1998; Chen *et al.* 2000; Chen 2004; JY Chen *et al.* 2006; Hagadorn *et al.* 2006). Collectively, the earliest metazoan record in South China is known from the lower Ediacaran Doushantuo Formation (Zhou *et al.* this volume), which represents an interval well in advance of the Cambrian Explosion.

Compared with the limited diversity of metazoan fossils in the Ediacaran, the Early Cambrian is marked by an extraordinary turnover. Among the 34 extant animal phyla, about 19 are found in the Early Cambrian Chiungchussian Stage in South China, including Chordata (Shu *et al.* 1999; Chen 2004). In addition, many extinct clades exhibit their first appearance in the Early Cambrian. This explosive radiation occurs mainly in the Meishucunian and Chiungchussian stages (see Figures 3 and 4). The small shelly fossil (SSF) record of the Meishucunian Stage includes the extant phyla Porifera, Cnidaria, Annelida (?), Mollusca, Chaetognatha as well as many extinct taxa, such as Vetulicolia (Shu *et al.* 2001), Hyolitha, stem-group brachiopods, tomotiids, coeloscleritophorans, cambroclaves and coleoloids (Qian 1999). About 155 SSF genera have been described from the Meishucunian rocks, dominated by helcionellids, orthothecimorph hyoliths and other problematic fossils. Most of these skeletal fossils have enigmatic biological affinities, and scarcely extend upwards into the Chiungchussian. The Meishucunian assemblages are fairly consistent with the concept of the Tommotian Fauna (Sepkoski 1992). The abrupt occurrence of abundant SSFs in the Meishucunian could therefore be taken as the first phase of the Cambrian Explosion (Qian 1999).

Upwards into the Chiungchussian Stage, metazoan diversity increased continuously, reaching its Cambrian climax at several taxonomic levels with the appearances of approximately 19 extant metazoan phyla (more than 10 phyla with their first appearances), more than 77 families and about 300 genera. Considering that the Chiungchussian Stage may represent an interval of only a few million years (Babcock *et al.* 2001), the rate of

metazoan diversification is remarkably rapid, partly because of the soft-bodied preservation of the Chengjiang Biota, and can be viewed as the major phase of the Cambrian Explosion. The genus diversity peak in the Chiungchussian is fully half of that observed for the Cambrian peak in Sepkoski's (1997) global compilation, indicating that South China contains an unusually rich biota for this interval. The Chiungchussian faunas are mainly characterized by the occurrence and dominance of pan-arthropods including true arthropods and their soft-bodied relatives, the tardigrades and onychophorans (all share a number of unique apomorphic features). These faunas also exhibit a decline in SSF diversity, being partly related to a significant reduction in phosphogenesis, since most of the SSFs are preserved through secondary phosphatization (Porter 2004). The dominance of the pan-arthropods (Hou *et al.* 2004) and the occurrence of crown-group brachiopods (Li and Holmer 2004) indicate that the Chiungchussian faunas represent an initial phase of the Cambrian Evolutionary Fauna (*sensu stricto*; Figure 5; Sepkoski 1981, 1992).

Exceptionally preserved fossils of the Chengjiang Biota partly contribute to the peak value in generic diversity: among 162 metazoan genera in the Chengjiang Biota, more than 90 have been discovered only from this biota. The diversity of metazoan fossils shows a continuous decline through the Tsanglangpuian (about 30 families and 150 genera) and Lungwangmiaoran (about 19 families and 70 genera). The skeletal assemblage consists mainly of trilobites, archaeocyaths, hyoliths, and brachiopods. The sedimentary sequences are composed of coarse-grained siliciclastic rocks that are unfavourable for soft-bodied preservation and impede obtaining SSFs by acid maceration. This feature is more or less consistent with the global extinction event observed at the end of the Early Cambrian (Sepkoski 1992; Zhuravlev and Wood 1996), although the aforementioned preservational issues raise the possibility that the decline is a preservational artefact, at least in part. If accepted at face value, however, the declining diversity may be due primarily to a eustatic regression in South China through the two stages.

The generic diversity pattern through the Early Cambrian in South China (Figure 6A) is fairly similar to the global pattern presented by Zhuravlev (2001; Figure 6B), although there is no unanimous agreement on global correlation of the Lower Cambrian rocks. The secondary peak of generic diversity in the mid Meishucunian Stage of South China is close to the early Tommotian peak in the global pattern. The diversity decline through late Meishucunian and early Chiungchussian may be compared with the decline through the late Tommotian and early Atdabanian. Most striking is a major increase of diversity in the Chiungchussian that may correspond to that in early Botomian, when generic diversity for South China was nearly half of that observed globally. The diversity decline through the Tsanglangpuian and Lungwangmiaoran is more or less consistent with the global pattern through the late Botomian and Toyonian, reflecting a diversity loss at the end Early Cambrian. However, the percentage of genus loss appears to have been somewhat greater in South China than in the world as a whole.

4.2. Early-Middle Ordovician

During this remarkable and sustained increase interval in the evolution of marine biodiversity, a major radiation event mainly of the PEF occurs in South China that likely corresponds with the same event worldwide (Miller and Foote 1996; Droser and Sheehan 1997; Miller 2000, 2004; Webby *et al.* 2004; Harper 2006). Miller and Mao (1998) reported the Ordovician radiation record in South China based on Chinese publications before 1990. In light of the present data, this radiation is unlike the Cambrian explosion, but there was a huge increase in diversity at the family, genus (Figures 3 and 4) and species levels. This radiation was characterized by significant new morphological innovation and related eco-space expansion (Bambach 1985). As also suggested by Miller and Mao (1998), the Ordovician diversification of bivalve and gastropod molluscs, major contributors to the MEF, appears limited in South China, in comparison with other parts of the world.

Although it was not as profound as the Cambrian Explosion with respect to the origination of fundamentally new, phylum-level body plans, the Ordovician radiation marks the first major diversification of the PEF, which would dominate marine benthos for the rest of the Palaeozoic Era and, in some environments and regions, beyond the Palaeozoic (Miller 2004). The composition of the PEF in South China mainly includes brachiopods (Zhan and Harper 2006; Zhan and Rong 2006; Zhan *et al.* 2006), graptolites (X Chen *et al.* 2006; Zhang and Chen 2006; Zhang *et al.* this volume), trilobites (Zhou *et al.* 2006, this volume), bryozoans and echinoderms, which were associated with acritarchs (Li and Yan 2006a,b). There were some bivalves (Fang 2006a,b) and gastropods of the MEF in

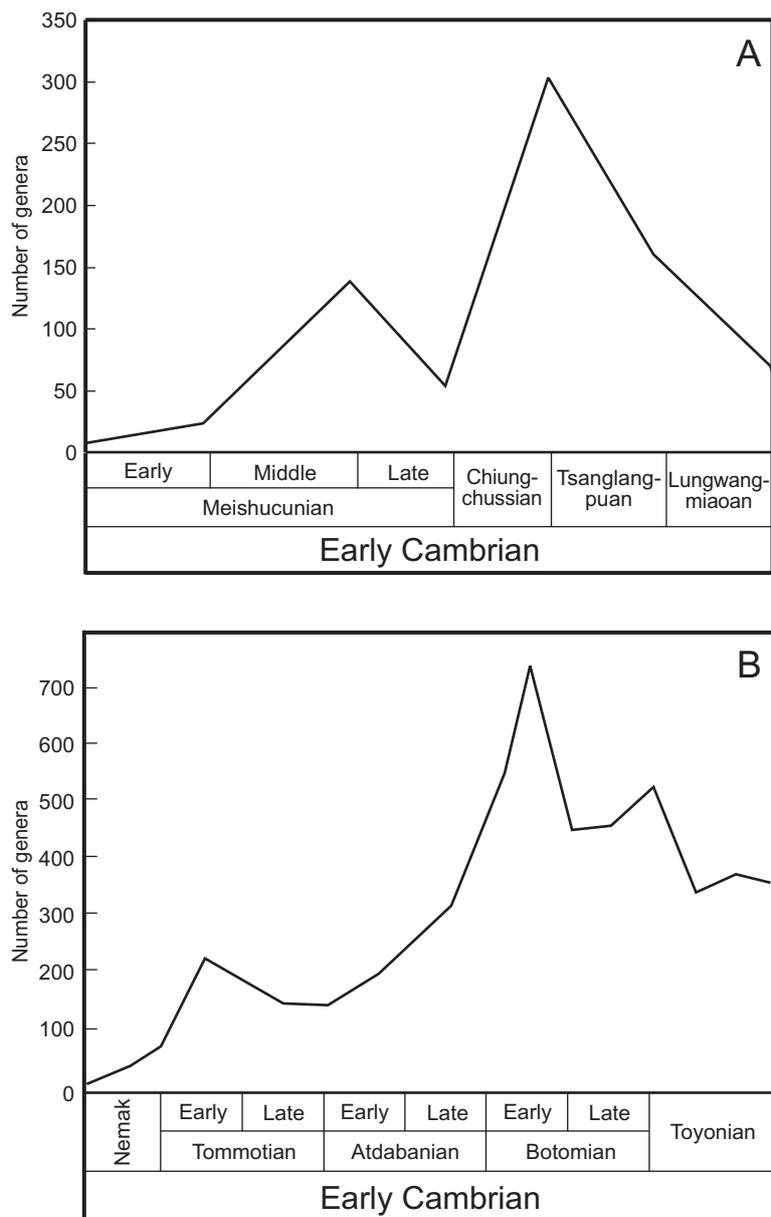


Figure 6. Patterns of metazoan generic diversity through the Early Cambrian: (A) Diversity curve for South China and (B) Diversity curve for the whole world (redrawn and compiled from Zhuravlev 2001, figure 8.1 A). Note that the correlation of the Lower Cambrian rocks in South China and Siberia is difficult and debatable.

near-shore, shallower water settings. A great increase in the number of genera, families and orders occurred in the Early Ordovician, from 59 genera, 32 families and 4 orders in the early Furongian (Late Cambrian) to 266 genera, 83 families and 32 orders in the Tremadocian. Although most phyla arose in the Early Cambrian, the earliest known fossils of bryozoans were discovered in Upper Tremadocian strata in South China (Hu and Spjeldnaes 1991) and the earliest known ostracodes in South China were also found in the Tremadocian.

Globally, the total number of brachiopod genera at its peak in the Ordovician was six times that of the Cambrian, and 117 genera newly established in the Tremadocian occupy one-third of the total number (Harper *et al.* 2004). However, because of the constraints of palaeogeography and sedimentary facies (mainly shallow-water limestone), the diversity of Tremadocian brachiopods in South China is lower than that of the late Early and Middle Ordovician, although much higher than the Late Cambrian with its poor record. After that, many major groups of marine organisms in South China started to radiate at different scales and steps. For example, the radiation of brachiopods began in shallow-water environments, that is lower Benthic Assemblage (BA)2-BA3, fine-grained clastic substrates in the late Early Ordovician (Zhan *et al.* 2006) with the subsequent occupation of deeper-water environments, characterized by the *Foliomena* fauna in an interval from early Caradocian to mid Ashgill, Late Ordovician (Rong *et al.* 1999). Trilobites radiated at the end of the early Mid Ordovician associated with the transition from the Ixerid Fauna to the Whiterock Fauna (Adrain *et al.* 1998), and afterwards dispersed to calcareous and calcareous muddy substrates of deeper water with an important establishment of the cyclopygid facies, an indicator of radiation in the Darriwilian, late Mid and Late Ordovician (Zhou *et al.* 2006, this volume). In addition, the radiation patterns of graptolites in different regions (platform versus slope) vary as well. Diplograptids, originated from a deep-water regime in the Jiangnan Region, and played a leading role in the radiation, attaining a diversity peak in the Darriwilian, late Mid Ordovician (X Chen *et al.* 2006; Zhang and Chen 2006; Zhang *et al.* this volume). New investigation indicates that the Ordovician radiation was a gradual but complex process, which was substantially variable within and between each major fossil group of the PEF, such as brachiopods, trilobites and graptolites. As for bivalve molluscs, which were major contributors to Sepkoski's (1981) MEF, they became established during the Early-Mid Ordovician in South China (Fang 2006), with the development of taxa and morphotypes that dominated marine ecosystems later, but, as noted earlier, bivalves did not contribute as extensively to Ordovician biotas of South China as they did to biotas in some other parts of the world (Novack-Gottshall and Miller 2003).

4.3. Early Silurian (mid-late Llandovery)

The Early Silurian fossil record in South China comprises two biodiversity peaks that attained their highest generic and familial levels respectively, in the mid-late Aeronian and mid-late Telychian, when shallow-water communities (mainly BA2–3) dominated the marine ecosystem (Rong *et al.* 2003). In addition, reef deposits were well developed in the shallow-water regime mainly in northeastern Guizhou during the mid-late Aeronian and in the Sichuan–Shaanxi border area during the mid-late Telychian (Li *et al.* 2002). A number of different taxa are common in mudstones (e.g. brachiopods, trilobites, bivalves and gastropods) or limestone (e.g. rugose corals, tabulates, stromatoporoids, nautiloids, brachiopods and conodonts).

The two Silurian diversity peaks are separated by a regional extinction in the early Telychian, when all the fossil groups exhibit a minor decrease in diversity (Figures 3 and 4), characterized by common, shallower-water brachiopods associated with bivalves and gastropods. This may have been controlled mostly by a regional regression triggered by a westward movement of the Cathaysian Oldland in east China that led to an accumulation of thick siliciclastic deposits (Chen and Rong 1996; Holland and Bassett 2002; Rong *et al.* 2003). In contrast to the early Telychian diversity trough, the faunas of the two Silurian peaks contain diverse and abundant brachiopods, associated with corals, trilobites, nautiloids and other taxa. There is a strong provincial character to these shelly faunas, particularly among pentamerid brachiopods (Rong *et al.* 2005) and corals (JQ Chen *et al.* 2006) in the Aeronian. The 'Xiushan Fauna', occurring in the middle-upper Telychian mudstones in the upper and lower Yangtze Region is represented by the *Salopinella–Sichuanoceras–Stomatograptus sinensis–Coronocephalus* fauna occupying a shallow-water regime (BA2–3). Trilobites in the middle-upper Telychian show many well-established genera (Wu 1990), some of which are regarded as endemic forms. Only in the Sichuan and Shaanxi border area does there occur reef deposition, in which abundant and diversified corals, tabulates, bryozoans and stromatoporoids are well developed in packstone or wackestone (Li *et al.* 2002), whereas remaining areas are dominated by siliciclastic deposits without reef constituents (Chen and Rong 1996).

4.4. Late Early to Middle Devonian (Emsian to Givetian)

After the early-mid Early Devonian there occurred a regional transgressive event reflected by a notable increase in marine biodiversity in the Emsian, representing the highest levels recognized during the study interval, with levels nearly as high as in the Givetian (Figures 3 and 4). A diverse array of clades in various communities inhabited mainly shallow-water regimes in Guangxi, Guizhou, Yunnan and Sichuan provinces. In the late Emsian, there was a significant muddy facies in which deeper-water communities predominated, yielding ammonoids, brachiopods (BA4–5), dacryoconarids and other taxa; they were well developed in some deep-water depressions of South China. Reefs were also well developed, with diverse rugose corals, tabulates and stromatoporoids on some platforms. This dramatic increase can also be observed in global-scale compilations (Sepkoski 1997, figure 1), which also exhibit peak Palaeozoic diversity at that time. However, the unusually high diversity relative to other Palaeozoic peaks may also relate to the fact that the Emsian was longer in duration than some of the other stages with peaks, including the 3rd Stage (unnamed) of the Ordovician, the Telychian Stage of the Silurian and the Wuchiapingian Stage of the Permian. While this alone does not demonstrate that the unusually high peak for the Emsian was an artefact, we should expect some inflation associated with the likelihood that more fossils would be recovered from this interval, given its greater length. On the other hand, it is worth pointing out that the number of counties containing Emsian fossils (Figure 2) was less than that for the other aforementioned three intervals, which would argue against the view that the Emsian peak was simply a consequence of increased sampling.

4.5. Late Early to Late Permian

Permian marine biodiversity of South China exhibited a lot of volatility, basically increasing significantly after the Artinskian, but with a couple of descending values reflecting moderate environmental perturbations (Shen *et al.* 2006a; Wang *et al.* 2006). Diversity at the genus and family levels in the Asselian–Sakmarian and Kungurian, Early Permian shows the first and second peaks of the Permian (Figure 3), with a very low trough in the Artinskian (Figure 4). The initial small decrease in the Artinskian may be partly an artefact of a somewhat inflated value in the preceding interval, caused by the combination of the Asselian and Sakmarian stages into a very lengthy interval (4.4 and 10.2 Ma = 14.6 Ma). This combination was required because no clear boundary between these two stages can be defined in many areas in South China. On the other hand, the dramatic diversification in the Kungurian, is likely not an artefact, although there is a dramatic increase in the number of counties containing fossils for this interval (Figure 2).

The Wuchiapingian and Changhsingian stages show a sharp rise in marine biodiversity, apparently paralleling the Late Permian increase observed globally (Sepkoski 1997) and attaining the third highest peak during the study interval in South China (Figure 3). Normalized diversity for the Changhsingian is somewhat lower than that for the Wuchiapingian (Figure 4), being different from the pattern in Figure 3, and consistent with the conclusion provided by Shen *et al.* (2006a,b) who used rarefaction to overcome the effects of varying sampling intensity. Marine biodiversity at the generic level in the Changhsingian Stage of the highest Permian is markedly higher than that in the immediately preceding Wuchiapingian Stage, whereas the normalized diversity at the generic level in the Changhsingian is lower than that in the Wuchiapingian. This may be controlled partly by factors related to the quality of the fossil record, such as the large number of silicified specimens in the Changhsingian, compared to other stages (Pan and Erwin 1994; Erwin 1996; Erwin and Pan 1996), and enhanced sampling efforts and increased research intensity of the Changhsingian faunas, given the great interest in the end-Permian mass extinction.

5. MAJOR DECLINES IN BIODIVERSITY

A variety of factors caused reductions in the marine biodiversity of South China during particular intervals. They are summarized as follows.

5.1. Mass extinctions

During global environmental catastrophes, there were rapid crashes in biodiversity within short timeframes (generally less than 2 Ma) during several intervals, indicating the occurrence of mass extinctions. The data available from this study strongly confirm the influence of three well-known mass extinctions of the Palaeozoic (the end Ordovician, Frasnian-Famennian (F-F) and end Permian) in South China (Rong and Fang 2004).

A sharp decline in biodiversity in the late Ashgill (Hirnantian) is attributed to the end-Ordovician mass extinction (Figures 3 and 4). Taxonomic loss was heavy at lower taxonomic levels (mainly family, genus and species). About 60% and 45% of genera became extinct in the first and second phases, respectively (Rong *et al.* 2004, Rong *et al.* 2006a). The first phase was much more severe than the second for graptolites, brachiopods and trilobites (Chen *et al.* 2004, 2005; Rong and Zhan 2004; Zhou *et al.* 2004), whereas 37.5% and 60% of rugose corals disappeared in the first and second phases, respectively (He and Chen 2004). Rapid rates of environmental perturbations have been seen as being the most important in triggering the two phases, related to formation and decay of the Gondwanan glaciation with major changes in climate, oceanic overturn and sea-level fluctuations accompanied by an anoxic event (e.g. Brenchley 1984; Sheehan 1988, 2001; Brenchley *et al.* 1995; Harper and Rong 1995). A higher extinction percentage for the rugose corals in the second phase may have been due to the anoxic event in South China (Rong *et al.* 2004).

It may seem strange that a diversity increase occurs across the F-F boundary in Figures 3 and 4, but the data for important shallow-water groups in South China show a significant taxonomic loss during the F-F event (Rong and Fang 2004; Figure 7). The contrast between the pattern observed in Figures 3 and 4 versus that observed in Figure 7 suggests the F-F event chiefly affected shallow-water regimes (e.g. McGhee 1996; Racki 1998; Racki and House 2002; Liao 2004). The increase observed in Figures 3 and 4 seems to relate partly to the greater duration of the Famennian, relative to the Frasnian (15.3 versus 10.8 Ma). If the greater length of the Famennian duration really matters, we would expect it to contain more singletons than the Frasnian. The Famennian consistently possesses 169 singleton genera, whereas the Frasnian has only 67 singletons. Furthermore, origination in the Famennian was enough to match the elevated extinction for that interval, which is why there is no diversity drop in the Famennian (Bambach *et al.* 2004; Bambach 2006). Sea-level fluctuations and global climatic changes have been regarded as two major causes for the event (Walliser 1995; McGhee 1996; Racki 1998; Copper 2001; Liao 2002, 2004), but details are still unclear. No major volcanism or impact around the F-F boundary has been definitely recorded in South China.

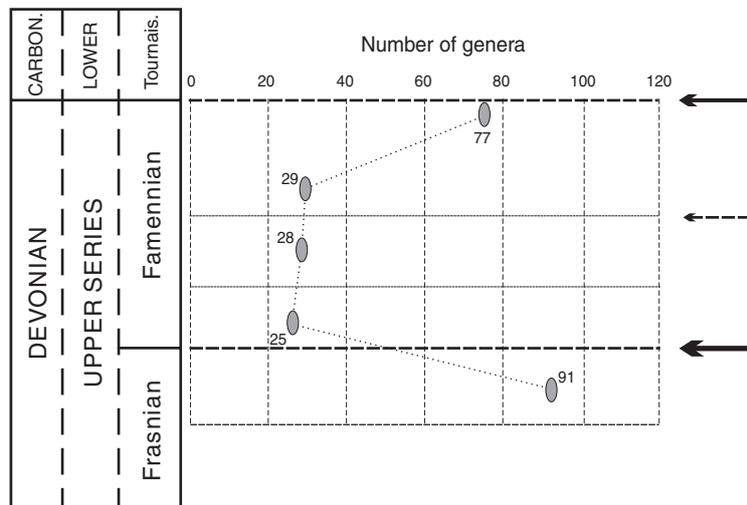


Figure 7. Diversity pattern of common fossil groups including brachiopods, rugose corals, tabulates, stromatoporoids, dactyloconarids and ammonoids in the shallow-water regime from late Frasnian to late Famennian in South China (redrawn from Rong and Fang 2004, fig. 5.1.12 B). Arrows (from the bottom up) represent the Frasnian-Famennian mass extinction, a minor extinction event with the Famennian and a major extinction event at the Devonian-Carboniferous boundary.

The heaviest diversity loss across the Permian and Triassic boundary supports the general view that the end-Permian mass extinction of marine metazoans is the severest in life's history (Jin *et al.* 1994, 2000; Yin 1994; Erwin 1994; Yin and Zhang 1996; Wang and Sugiyama 2000; Rong and Shen 2002; Fang 2004a, 2004b). About 75% of orders and 80% of families became extinct. At the genus level, about 80% of brachiopods and gastropods and some 53% of bivalves went extinct (Jin *et al.* 2000; Rong and Shen 2002; Rong and Fang 2004). As many as 94% of all the marine species of metazoans, including all trilobites and rugose corals, vanished in a very short interval at the Permian–Triassic boundary in South China (see Jin *et al.* 2000: Beds 25 and 26). Many of the taxa with range endings in the Changhsingian (including the singletons) had range terminations spread unevenly through the interval. This extinction terminated the dominance of the PEF in marine ecosystems (Figure 5). After the mass extinction, all the ecosystems were extremely impoverished, with the disappearance of coal marsh environments, stratified siliceous rocks and metazoan reefs in the Early Triassic in South China (Yin and Tong 1997; Fang 2004a, 2004b).

All three mass extinctions described earlier vary in many aspects. They are far from being identical with respect to biological selectivity, rate, likely causes and long-term effects (Rong *et al.* 2004; Bambach 2006). Different responses are observed among taxa during each extinction, reflecting different strategies in response to deteriorating conditions likely tied to functional morphology, life mode and adaptive capability (Rong *et al.* 2004).

5.2. General biodiversity declines

Because of longer-term environmental perturbations (from latest Devonian, through the Carboniferous to the earliest Permian), there is a continuous decline to a low level of biodiversity from the Devonian into the Carboniferous with a subsequent recovery in the Mid-Late Permian. The decline was associated with the Hangenberg event at the Devonian–Carboniferous boundary (Walliser 1995; Wang and Shen 2004; Figure 4) when the early Carboniferous-type corals that were established in late Famennian became largely extinct.

During the Tournaisian–Viséan interval, the biodiversity curve exhibits the lowest level of the Late Palaeozoic. Continued low values of biodiversity in the Serpukhovian, Bashkirian and Moscovian in South China may have been related to the glaciation in Gondwana (Smith and Read 2000; Stanley and Powell 2003), and global regression (Heckel 1986; Veevers and Powell 1987; Cornette *et al.* 2002) led to the extinction of large solitary rugose corals (Wang *et al.* 2006). In the Bashkirian, there occurred, however, an interesting, temporary increase in the number of genera, families, and orders (Figures 3 and 4) with a new diversification of many organisms, such as rugose corals, and the increase was related to the appearance of relatively clean and shallow-water environments in South China. This may be attributed to a regional transgression. There was a small, subsequent decline in the Moscovian, followed by a slight increase in the Kasimovian–Gzhelian. The latter, however, may be related to the combination of two stages that, separately, would have exhibited lower diversity. After a more pronounced increase in the Asselian–Sakmarian, diversity fell to its lowest level of the Permian, but it was nevertheless higher than at any time in the Carboniferous. This decline, prominently in the Artinskian, may be related to several factors, such as deglaciation, the development of siliciclastic facies (e.g. the Liangshan Formation) and collecting bias.

Biodiversity decline at the end-Maokouan (Capitanian, Guadalupian) is also striking (Figures 3 and 4). It may have been caused by a global regression and volcanic eruptions that produced the Emei basalt (Wang and Sugiyama 2000; Shen and Shi 2004). Various major fossil groups responded differently to the end-Maokouan (Guadalupian) event (Jin *et al.* 1994; Stanley and Yang 1994). Some groups, such as rugose corals (Wang and Sugiyama 2000) and foraminifers (Tong 2004), were seriously affected, whereas the others, such as bivalves, appear to have benefited greatly from this transition (Fang 2004a, 2004b).

5.3. Local biodiversity declines

Owing to the effect of regional tectonics and palaeogeography in South China, there were particularly pronounced regional biases during the Wenlockian of the Silurian, the Lochkovian–Pragian of the Devonian, and the Rhaetian of the Triassic. During these time intervals, the greater part of the South China Block was subaerially exposed, and it

should therefore come as no surprise that marine biodiversity curves during all three of these intervals show significant declines (points labelled 'a', 'b' and 'c' in Figures 3 and 4). Importantly, the biotas of these intervals were mainly preserved in narrowly distributed marine sedimentary rocks yielding only near-shore biotas (BA 1–2) of low diversity. These striking decreases in biodiversity are notably different from many regions in the world, suggesting a distinctive regional feature for South China.

5.4. Biodiversity biases

In addition to the causes of diversity decline described above, unique and widely distributed sedimentary facies during some intervals may also be responsible for some declines. The Upper Cambrian Loushanguan Dolomite of shallower-water origin, for example, is very common on the Yangtze Platform, and contains low diversity trilobite associations with low intensity of study. In addition, the Caradocian (Sandbian and early Katian of the Ordovician) Pagoda Limestone of deep-water origin was widely distributed on the Yangtze Platform, and yields rare and small brachiopods (chiefly the *Foliomena* fauna; Rong *et al.* 1999), gastropods and ostracodes, the latter two having a low diversity and a low research intensity as well, although there is a diversity peak for trilobites and nautiloids with a stronger intensity of study. Overall, however, diversity in the Sandbian and early Katian (Late Ordovician) of South China was fairly low. As pointed out by Miller and Mao (1998), the range of palaeoenvironments in South China was rather different from those in Laurentia at the same time, and this has had an effect on the nature of the biotas in the two places, and in South China versus the world as a whole.

It should be pointed out that there is a low level of biodiversity in the entire Mid to Late Cambrian (about 33 Ma) following the Early Cambrian Explosion in South China (Figures 3 and 4). The reasons for this phenomenon are still unknown. However, it may relate to the quality of the fossil record, including rare fossil occurrences, insufficient material and low intensity of research. In these respects, we note that the low levels of biodiversity in this interval coincide closely with low levels of areal coverage of fossil occurrences (Figure 2).

6. ORIGINATION AND EXTINCTION RATES

Curves of origination and extinction rates at the generic level are shown in Figure 8. It is important to note that both the origination and extinction rates exhibit a long-term decline from the Early Cambrian to Permian although they fluctuated throughout this long period. These declines parallel those recognized globally in marine and terrestrial settings by previous authors (e.g. Raup and Sepkoski 1982; Sepkoski 1998; Eble 1999), although the explanation for these declines is still debated. In addition, there are several finer-scale features that are recognized as described below:

6.1. Origination rate

At the generic level, the origination rate attained its first peak, that is the highest peak in Early Cambrian that corresponds to the 'Cambrian Explosion' (Chen 2004), and its lowest point in the latest Triassic almost certainly related to the lack of marine sediments (Yin 2003). The origination rate during the Emsian is also fairly high, but the extinction rate is also strikingly low during this interval, which probably explains the radiation in South China in the Devonian. The dramatic increase in the rate of origination relates at least partly to the dramatic increase in the likely number of records for the Emsian, as suggested in Figure 2.

However, it is most interesting to note that origination rates in the Mid Ordovician do not show an elevated tendency to match that of the Ordovician radiation event recognized in South China. It is possible that there simply was not a significant amount of generic origination in South China during the second half of the Ordovician. The same may be true for the Eifelian and Givetian. These units possess relatively higher diversity, but the origination rates are again quite low. The Famennian possesses a relatively higher origination rate. Rates in both the Carboniferous and Permian are relatively stable and fairly low. After the end-Permian mass extinction the origination rates became intensively elevated and attained the highest point in the early Mid Triassic since the Mid Ordovician, reflecting the first major radiation of the MEF in South China (Figure 8).

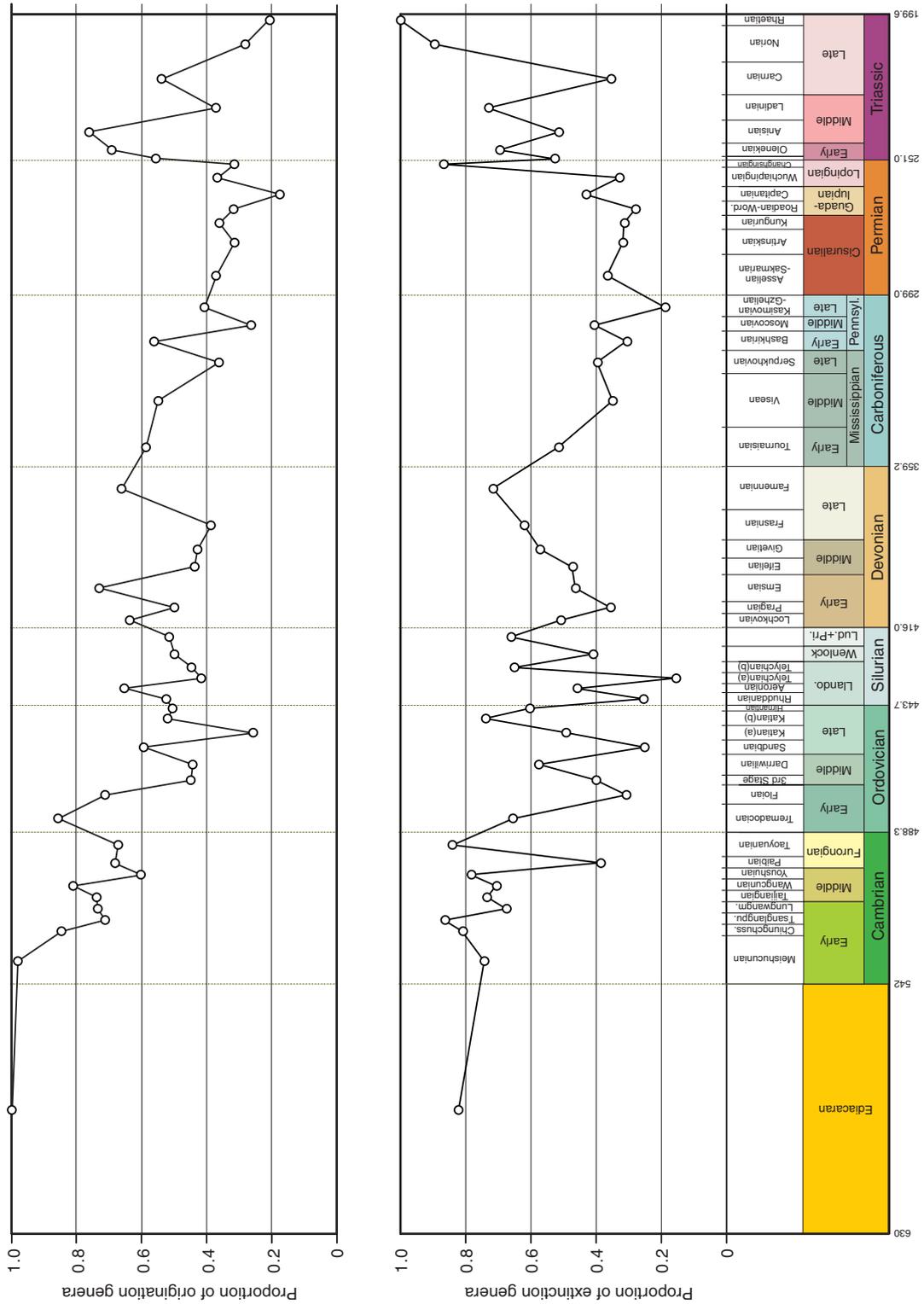


Figure 8. Proportions of originations (both new established and first appearing taxa) and extinctions (both extinct and disappearing taxa) at genus level from the latest Proterozoic to the Triassic in South China. The counting result is made through the program StratDraw 2.0 designed by Fan Junxuan and Chen Feng. For details see Figure 3.

6.2. Extinction rate

The highest rate of extinction occurred at the end Permian, coinciding with the severest mass extinction, as noted earlier in this paper. With this exception, the extinction rate shows a tendency similar to origination, from very high in the Cambrian, then gradually decreasing to the low values in both the early Telychian and late Pennsylvanian (Figure 8).

The rate in the Famennian is high enough to be distinguished from neighbouring stages, but may have been partially caused by the higher origination rate and the longer duration of the stage. The rate peak from late Telychian to Přídolí is an artefact of the lack of fossil records in many parts of South China. There occurs a broad, low level of extinction rates from the Viséan through the Kasimovian–Gzhelian that may partially represent the effect of ice sheet expansion in Gondwana, as there is also limited origination during this interval, indicating a general lack of turnover.

It should be noted that the three mass extinctions in South China show different patterns in extinction and origination rates (Figure 8). (1) The end-Ordovician extinction is accompanied by low origination and significantly higher extinction rates. Subsequently, the extinction rate continuously declines with a prominently increased origination rate, indicating a transition from survival-recovery to radiation in the Early-Mid Llandovery; (2) The Frasnian shows both lower extinction and origination rates, but the Famennian exhibits higher rates for both and (3) The highest Permian stage shows a very high extinction rate (the largest value) with a moderate origination rate.

7. CONCLUSIONS

Dynamic changes of marine biodiversity from the Ediacaran to the Triassic are analysed based on simple and normalized diversities in South China for the first time. From the point of view of diversity change, it demonstrates significant manifestations of macroevolution, including radiations and extinctions. Emerging in the early 1980s, a consensus (Sepkoski *et al.* 1981) indicated that global marine invertebrate diversity at multiple taxonomic levels rose through the Cambrian and Ordovician periods to a plateau that, with brief extinction-related interruptions, was maintained from the mid-Palaeozoic to the mid-Mesozoic. However, the new data from South China show both similarities and differences from the global trajectories. With the exception of the similarities (such as three mass extinctions and three major radiations), the main differences include: (1) a prominent decline in the Mid-Late Cambrian; (2) strong fluctuations in the Early Silurian and Permian; (3) a high diversity in the late Early Devonian; (4) long periods with low and broad troughs in the Carboniferous and (5) a strong decline in the late Mid Triassic. They were caused by local and regional factors, suggesting that there are characteristic and distinctive features of marine biodiversity changes in South China through time.

The reasons for the rises and falls in biodiversity in South China are complex, in that they likely reflect the interplay of global and regional factors. A remaining challenge is to distinguish between these factors, particularly at times when diversity changed significantly. Given that the Palaeozoic Era was a time of dynamic biological and geological transitions, it is also important to determine the extent to which biodiversity transitions were contingent on physical forcing factors versus biotic interactions, and to understand what may well be the complex feedback loops between physical and biological mechanisms. For example, Peterson (2005) recently presented a compelling case based on a combination of molecular clock and fossil data, that, during the Ordovician radiation, taxa with life cycles that include a feeding, planktotrophic larval stage evolved independently from ancestors with nonfeeding lecithotrophic larvae at least four and possibly more times and this, in turn, coincides well with the diversification of epifaunal suspension feeders, which were major elements of the PEF (Sepkoski 1981). This suggests a possible, major role of escalation in the biotic transitions of the Ordovician radiation because planktotrophy would have constituted an effective way of avoiding suspension feeders, which lived near the sediment-water interface.

To help us unravel these kinds of relationships throughout the geological history of South China, we are undertaking a project to produce a new database of taxonomic occurrences for South China that includes information on the lithological, geographic and stratigraphic attributes of each occurrence. This should permit a far

more definitive assessment in the future of the importance of regional environmental factors to the trajectory of biodiversity throughout the study interval. The database will also permit a direct assessment of the extent to which variations in sample size affect the raw diversity signal (Miller and Foote 1996; Alroy *et al.* 2001; Shen *et al.* 2006b), something that is not possible currently.

Since this is the first step in our efforts to document the diversity pattern for South China through geological time, there are several questions to be resolved in the future. In particular, we need to explore further: (1) the relationship of the diversity pattern of South China to the global pattern and to that of other major blocks; (2) the extent to which the pattern for South China was controlled by sedimentary area and volume; (3) the relationship of the diversity pattern to variations in collecting intensity (Alroy *et al.* 2001; Miller and Foote 1996); (4) the effect of alternative origination and extinction metrics, as well as other numerical methods, on the patterns we observe and (5) the relationship of overall diversity trends to variations observed between deeper- and shallower-water regimes, or pelagic and benthic groups.

ACKNOWLEDGEMENTS

This research was funded by the projects of the National Basic Research Program of China (2006CB806400, G2000077700), the Chinese Academy of Sciences (KZCX3-SW-149) and the National Natural Science Foundation of China (40532009, 40572006). A. I. Miller acknowledges the support of the National Aeronautics and Space Administration (USA), Program in Exobiology. We are very grateful to all the members of our project (Appendix) who established the palaeontological database cited here. This paper could not have been completed without their contributions. We would like to thank Mr Ma Zhen-gang for his help in the arrangement of the database. We would like to thank the helpful reviews of Richard Bambach and Dave Harper. This is a contribution to the Geobiodiversity Database led by Fan Junxuan. We thank Xu Juntao, Fang Zongjie, Wang Xiangdong, Zhan Renbin, Yuan Xunlai, Shen Shuzhong, Chen Jinhua, Chen Xiuqin, Chen Zhe, Deng Zhanqiu, Dong Deyuan, Hu Jie, Hu Zhaoxun, Huang Diying, Li Jun, Li Wenzhong, Liao Weihua, Lin Caihua, Mu Daocheng, Pan Huazhang, Peng Shanchi, Qi Yuping, Sun Weiguo, Tang Peng, Wang Chengyuan, Wang Shangqi, Wang Xiaojuan, Xia Fengsheng, Yan Kui, Yuan Jinliang, Yuan Wenwei, Zhang Hua, Zhang Yuandong, Zhang Yunbai, Zhao Fangchen, Zhou Zhiyi, Zhu Maoyan and Zhu Xuejian from State key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences; Chen Jianqiang and He Xinyi from China University of Geosciences; Hou Xianguang from Yunnan University; Ma Xueping and Sun Yuanlin from Peking University; Shang Qinghua and Wang Wei from Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; Shi Yukun and Yang Xiangning from Nanjing University and Tong Jinnan and Yang Fengqing from China University of Geosciences for their valuable contributions to this work.

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8. APPENDIX: LIST OF CONTRIBUTORS PROVIDING THE BASIC DATA SETS

Age	Fossil group	Provider of the data set
Precambrian	Various kinds of fossils	Yuan Xunlai Chen Zhe Hu Jie
Early Cambrian During Cambrian explosion	All kinds of fossils	Li Guoxiang Zhu Maoyan Hou Xianguang Huang Diying Zhao Fangchen Sun Weiguo
Cambrian	Trilobites	Peng Shanchi Zhu Xuejian
Cambrian–Devonian	Nautiloids	Zhang Yunbai
Triassic Cambrian–Devonian Triassic	Conodonts	Wang Chengyuan
Ordovician–Devonian	Graptolites	Zhang Yuandong Fan Junxuan
Ordovician–Silurian	Trilobites	Zhou Zhiyi Yuan Wenwei
Ordovician–Silurian Ordovician–Triassic	Brachiopods Acritarchs	Zhan Renbin Li Jun Yan Kui
Ordovician–Silurian	Rugose corals	Chen Jianqiang He Xinyi
Ordovician–Triassic Ordovician, Carboniferous–Permian Silurian–Devonian Devonian	Gastropods Bivalves Bivalves Brachiopods	Pan Huanzhang Fang Zongjie Xu Juntao Chen Xiuqin Ma Xueping
Devonian Carboniferous–Permian Carboniferous–Permian	Rugose corals Trilobites Fusulinids	Liao Weihua Yuan Jinliang Yang Xiangning Shi Yukun
Carboniferous–Permian Carboniferous–Triassic	Conodonts Brachiopods	Qi Yuping Shen Shuzhong Sun Yuanlin Zhang Hua Li Wenzhong
Carboniferous–Permian	Rugose corals and tabulates	Wang Xiangdong Wang Xiaojuan
Triassic Palaeozoic Palaeozoic	Bivalves Tabulates Bryozoans	Chen Jinhua Deng Zhanqiu Hu Zhaoxun Xia Fengsheng
Palaeozoic Palaeozoic–Triassic Palaeozoic–Triassic Devonian Late Palaeozoic Late Palaeozoic–Triassic Silurian–Devonian Carboniferous–Triassic Triassic	Stromatoporoids Crinoids Ostracodes Dacryoconarids Ammonoids Foraminifers Pisces Pisces Reptilia	Dong Deyuan Lin Caihua Wang Shangqi Mu Daocheng Yang Fengqing Tong Jinnan Wang Wei Shang Qinghua Shang Qinghua