

Review

The great Ordovician radiation of marine life: Examples from South China

Renbin Zhan ^{a,*}, Jisuo Jin ^b, Yuandong Zhang ^a, Wenwei Yuan ^a

^a State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

^b Department of Earth Sciences, University of Western Ontario, London Ont., Canada N6A 5B7

Received 14 March 2007; received in revised form 23 July 2007; accepted 27 July 2007

Abstract

The Ordovician radiation is the earliest and most important biodiversification event in the evolution of the Paleozoic Evolutionary Fauna (PEF), when the basic framework of PEF was established. The radiation underwent a gradual, protracted process spanning more than 40 million years and was marked by several diversity maxima of the PEF. Case studies conducted on the Upper Yangtze Platform (South China Palaeoplate) showed that the Ordovician radiation was characterized by drastic increases in α - and β -diversity in various groups of organisms. During the radiation, brachiopods, trilobites, and graptolites of the PEF became more diverse to dominate over the Cambrian Evolutionary Fauna (CEF) in all marine environments. At either global or regional scales, however, the Ordovician radiation was highly heterogeneous in time and space, and the rate and pattern of radiation exhibited by different major fossil groups were also variable.

© 2007 National Natural Science Foundation of China and Chinese Academy of Sciences. Published by Elsevier Limited and Science in China Press. All rights reserved.

Keywords: Ordovician radiation; Paleozoic Evolutionary Fauna; α -diversity; β -diversity; Upper Yangtze Platform

1. Introduction

Since Sepkoski [1–4] proposed the biodiversity curve of Phanerozoic marine fauna and recognized three evolutionary faunas (Fig. 1), increasingly greater efforts have been directed to the study of diversity change in Ordovician marine faunas. The Ordovician became a main focus of palaeobiological investigation for several reasons: (1) during this period, the Cambrian Evolutionary Fauna (CEF) was gradually replaced by the Paleozoic Evolutionary Fauna (PEF), and the PEF underwent its first radiation after its origination in Late Cambrian time; (2) globally, the Ordovician epicontinental seas became much more widespread [5], resulting in a diverse suite of lithofacies,

biofacies, and ecotypes (e.g., the ecological regime and tiering), and the number of taxa of various marine organisms increased rapidly; (3) the fundamental knowledge of the Ordovician (taxonomy, biostratigraphy, palaeoecology, and palaeobiogeography), accumulated for more than a century has made it possible for carrying out large-scale analyses of the rates and patterns of evolution of various marine organisms.

The globally coordinated IGCP Project 410 (Great Ordovician Biodiversification, 1997–2002) has been a great stimulus for the investigation of Ordovician biodiversity fluctuations. During the great Ordovician biodiversification, the basic framework of the PEF and its dominant position in the Paleozoic marine ecosystems were established and persisted for more than 200 million years (Ma) until the end-Permian mass extinction. It was also during this time that the CEF (represented by the Ibexian-type

* Corresponding author.

E-mail address: rbzhan@nigpas.ac.cn (R. Zhan).

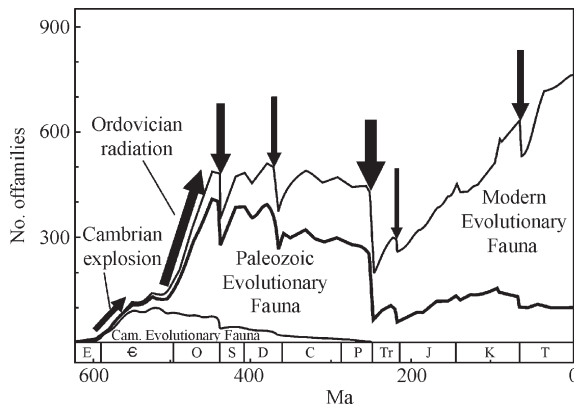


Fig. 1. Familial biodiversity curves of Phanerozoic marine faunas showing the three evolutionary faunas and five mass extinctions (the width of the dark, downward arrows indicates the approximate severity of each extinction) (modified from Sepkoski [1–4]). E, Ediacara; C, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; T, Tertiary.

trilobites and phosphatic-shelled brachiopods) declined drastically, whereas the PEF (dominated by calcareous-shelled brachiopods, crinoids, stromatoporoids, rugose corals, bryozoans, nautiloids) increased sharply. Bivalves and gastropods, both major components of the Modern Evolutionary Fauna (MEF), originated during the Cambrian but went through their first major radiation also during the Ordovician [6]. Among more than 500 publications (including the monumental summary volume of IGCP Project 410, see [7]) dealing with the Ordovician biodiversification, the scopes of study are highly diverse—some dealing with regional or global trend (e.g. [8,9]), some with diversity change and palaeoecological synthesis (e.g. [10–12]), and some with regional case studies (e.g. [13]). Jablonski et al. [14] detected a major ecological evolutionary pattern for three evolutionary faunas that showed an onshore–offshore expansion, which subsequently was supported by data from many regions [10,15–20]. Adrain et al. [21] noted a major transition between two trilobite faunas, the Ibexian Fauna and the Whiterockian Fauna. On the basis of global fossil data of trilobites, brachiopods, bryozoans, bivalves, etc., Webby [8] suggested that there were three diversity maxima during the great Ordovician biodiversification, in the latest Arenig (earliest Darriwilian), mid-late Caradoc (late Sandbian), and mid Ashgill (late Katian) respectively.

In the extensive previous studies, there are several common problems that need to be solved. (1) Up-to-date taxonomic database is the foundation for any analyses of biodiversity. Many global or regional patterns or trends of biodiversity have been based, at least partly, on outdated taxonomy. (2) Many studies emphasize broad trend of faunal evolution, without detailed, convincing, regional case studies. There is also a general scarcity of integrated biodiversity study involving the major Ordovician fossil groups. (3) There have been numerous analyses of taxonomic diversity (i.e., α -diversity), but only limited investigations of community diversification (β -diversity), and far few studies of palaeobiogeographical diversification (γ -diversity). (4)

Most previous studies tend to focus on large-scale, low-resolution trends of biodiversity change, limited by available field data and species- or genus-level taxonomic database. These analyses reveal only broad macroevolutionary trends at the stage or even series intervals, resulting in obliteration of detailed processes of faunal evolution or even false trends that deviate from detailed case studies. (5) The environmental and palaeobiological controlling factors of the Ordovician biodiversification require more in-depth investigation, as most studies are confined to analyses of the patterns and processes of biodiversity change during the Ordovician.

As one of the key working groups of IGCP Project 410, the Chinese geologists and palaeontologists have conducted extensive and intensive studies dealing with the great Ordovician biodiversification event, with a focus on the South China palaeoplate. South China serves as an ideal place for this research project for several reasons. (1) Here, the Ordovician stratigraphical succession is continuous and widespread, with numerous well-exposed sections. (2) There is a wide range of palaeogeographical divisions, from the shallow-water Yangtze Platform, to the deeper-water Jiangnan Slope, and to the deep-water Zhujiang Basin (Fig. 2). In addition, there are highly heterogeneous and diverse lithofacies and biofacies across the Yangtze Platform. (3) In a single stratigraphical section, various major fossil groups of different palaeoecological niches (e.g., vagile trilobites, sessile brachiopods, planktonic graptolites, and nekctic nautiloids) often occur in the same strata or closely intercalated strata, providing reliable biostratigraphical correlations across different lithofacies in different areas or regions. (4) The palaeontological and biostratigraphical work in South China has had a long history of more than a century, leading to the accumulation of a wealth of geological and palaeontological data. Most of the work, however, has been published in Chinese, which was probably the chief reason why South China and other regions of China were treated as *terrae incognitae* in some previous global palaeogeographical reconstructions [22,23]. Taking these advantages, and supported by the Ministry of Science and Technology of China, National Natural Science Foundation of China, and the Chinese Academy of Sciences, the Chinese Ordovician workers carried out a series of team-oriented, multidisciplinary research projects in the field and in the laboratories, with a concentrated effort to investigate the Ordovician biodiversification event. Based on detailed taxonomy and high-resolution biostratigraphy, these studies have led to some significant discoveries of the timing, scale, pattern, process, diachroneity, heterogeneity, and other characteristics of Ordovician biodiversification [24].

2. Major characteristics of the Ordovician biodiversification

The great Ordovician biodiversification is marked by a rapid increase in the diversity of middle- to lower-rank taxa of many marine invertebrate groups, in the scale and com-

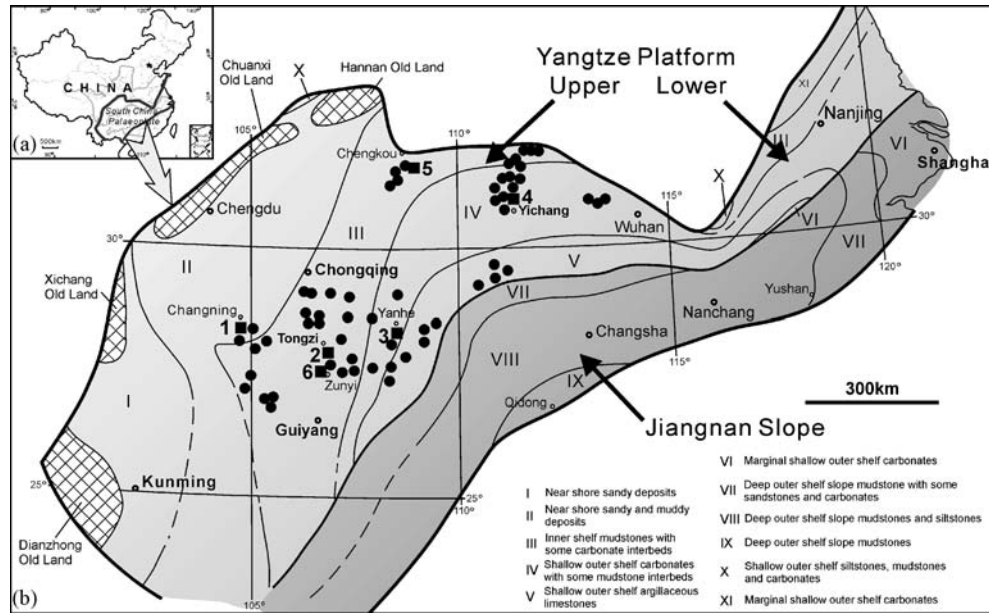


Fig. 2. Palaeogeographical map and the different sedimentological belts during the Early and Mid Ordovician of South China (based on the map from [25]). (a) Map of China with the South China Palaeoplate highlighted by two thick lines. (b) Enlarged view of the Yangtze Platform (light grey) and the Jiangnan Slope (dark grey) of the South China Palaeoplate. Solid circles show the position of investigated Ordovician sections, and the solid squares show the positions that have been measured in great detail, and with the fossils collected: 1, Shuanghe, Changning County, southeastern Sichuan Province; 2, Honghuayuan, Tongzi County, northern Guizhou Province; 3, Shatuo, Yanhe County, northeastern Guizhou; 4, Chenjiahe, Yichang City, western Hubei Province; 5, Houping, Chengkou County, Chongqing District; 6, Shizipu, Gaoqiao of Zunyi City, northern Guizhou.

plexity of ecospace, and in the multiplication of biogeographical provinces. This diversification event lasted for more than 40 million years formed the framework of the PEF, and represented by three diversity maxima. During the Ordovician, the CEF was replaced gradually but decidedly by the PEF. Compared to the well-known Cambrian explosion, however, the Ordovician biodiversification is distinct in a number of features.

- (1) Taxonomic level of radiation: The Cambrian explosion is characterized by the abrupt appearance of most phyla and classes of animals, including some distinct high-rank taxa [26,27]. In contrast, the Ordovician biodiversification is marked by the abrupt increase in middle- and low-rank taxa (orders, families, genera, species), with bryozoans being the only new comers at the phylum level (with the earliest known occurrence in the lower Tremadocian Fenghsiang Formation of South China; see [28]). In the metaphorical tree of life, it can be said that the trunk and major branches formed during the Cambrian explosion, whereas the large canopy took shape in the Ordovician biodiversification.
- (2) Scale of radiation: Apart from the failed bauplan experimentation of the Ediacara biota in the Ediacaran Period (latest Precambrian), the extant animal bauplans at the phylum level appear to have formed from scratch during the Cambrian explosion. Simultaneous biomineralization to form exoskeletons among many phyla was one of the giant steps in life history. At that time, however, most phyla were represented by single class, order, family, or even genus [29], and the overall diversity of marine life was low. During the Ordovician, the increase in the number of taxa, from primary producers to top carnivores, was three times higher than that in the Cambrian [8]. The cumulative number of taxa at the end of the Ordovician radiation was seven times higher than that at the end of the Cambrian [9].
- (3) Effects of the radiation: The CEF originated during the Cambrian explosion, peaked in diversity in Late Cambrian, declined during the Ordovician, markedly reduced by the end of the Ordovician, and then diminished gradually through the rest of the Paleozoic to a negligible component of the evolutionary faunas by Permian time. The PEF produced by the Ordovician radiation maintained a high diversity plateau spanning 280 million years, punctuated by many minor diversity fluctuations, leading to a dramatic increase in the complexity of life on Earth.
- (4) Constituents and ecological structures of the evolutionary faunas. The CEF was dominated by arthropods (particularly trilobites), phosphatic brachiopods, archaeocyathids, and echinoderms. The ecological niches of these organisms were simple, either vagile or sessile, ranging from deposit feeders, scavengers, to suspension filter feeders, mostly with a slow rate of metabolism. Calcimicrobes and archaeocyathids initiated true skeletal reef building for the first time in life history, although the diversity of

the archaeocyathid reefs was notably low compared to the coral-stromatoporoid reefs that began in the Mid Ordovician. From the Early Ordovician, many order-level taxa appeared in the phylum Brachiopoda, with their evolutionary vitality manifest in their morphological innovations, such as various new types of calcareous shells with punctae, pseudopunctae, complex cardinal processes and internal skeletal supports for muscle and lophophore attachment (e.g., dalmanelloid orthides, strophomenides, and pentmerides). Brachiopods rapidly evolved to become the dominant group in the PEF. Hemichordates (graptolites), echinoderms, trilobites, bryozoans, and molluscs (nautiloids and bivalves), corals, and stromatoporoids were also major components of the PEF. Different combinations of these groups in time and space formed various subsets of the PEF. Anatomical and morphological innovations were associated with exploration and adaptation to a wider range of ecological settings and niches, and to more complex competition and increasing predation pressure. Planktonic–nektonic invertebrates, such as graptolites, achieved a dominant status in the pelagic realm for the first time. By Mid Ordovician time, a rapid change occurred in the shallow marine reef ecosystem from sponge-dominated to bryozoan-dominated, and finally replaced by the coral-stromatoporoid reefs that expanded subsequently into the grandest reef ecosystems in life history [30,31]. Palaeoecological diversification was also reflected in the increased tiering in benthic communities. In general, the marine ecosystem became much more complex in time and space during the Ordovician biodiversification.

The differences between the Cambrian explosion and the Ordovician biodiversification, as outline above, are clearly exhibited on the South China palaeoplate. During the Cambrian, much of South China, especially the Yangtze Platform, was a shallow-water, stable carbonate craton, with arthropods, and particularly trilobites, being the predominant and most abundant fossil group. In Ordovician time, various litho- and biofacies commonly persisted laterally for tens of kilometres. Brachiopod-dominated benthic shelly biofacies were diverse and widespread. Such biofacies were often mixed or intercalated with pelagic graptolite facies. These, together with many other groups of marine invertebrates, constituted a thriving Ordovician ecosystem.

3. Faunal diversity and turnover during the Ordovician biodiversification

Since the late 1990s, we have conducted extensive field investigations on the Upper Yangtze Platform, including more than 30 continuous and well-exposed Ordovician sections in Hubei, Hunan, Sichuan, Guizhou, and Yunnan. Among these, six classic sections were measured bed-by-bed, with detailed fossil collections (Fig. 2). More than

40,000 macrofossil specimens were collected (approximately 80% being brachiopods), accompanied by systematic collections of microfossils and key lithological samples, as well as sedimentological data. Such field data formed a solid basis for detailed taxonomic, biostratigraphical, and palaeoecological studies in the laboratory. With further benefit from broad international research collaboration, we have by now recognized some interesting patterns of the Ordovician radiation using South China as a window.

3.1. Taxonomic diversity

Taxonomic diversity (α -diversity) is the most commonly used proxy of the Ordovician radiation worldwide. Many case studies from South China indicate that the biodiversity change during the Early–Mid Ordovician was not an abrupt, clear-cut event, but a gradual, protracted process. In the case of brachiopods (see Fig. 7 in [32]), their diversity increase started from the early Tremadocian, accelerated in the early Floian, and attained their first acme of α -diversity in the *Didymograptellus eobifidus* Biozone (late Floian, late Early Ordovician). This predates the first diversity maximum of the global biodiversity curve and the integrated global biodiversity curve by about four graptolite biozones (6–8 million years), as the first global diversity maximum occurred in the lower *Undulograptus austrodentatus* Biozone (earliest Darriwilian).

The increase in taxonomic diversity is reflected not only in the rapid proliferation of existing taxa, but also in the rapid diversification of newly evolved taxa. Among the brachiopods of South China, the orthides, which made their first appearance during the Late Cambrian, played a major role in the radiation towards the first diversity maximum, with a drastic increase from three genera (two superfamilies, two families) in the lower Tremadocian to 22 genera (five superfamilies, ten families) in the upper Floian. The dalmanelloids and plectambonetoids, newly evolved during the early Floian, also contributed to the first diversity acme. Strophomenoids first appeared in South China during the early Dapingian (*Expansograptus hirundo* Biozone), and became key components in the second and third diversity acmes. Atrypides and rhynchonellides made their first appearance in South China during the Sandbian, notably later than in some other palaeoplates or terranes, whereas spiriferides first appeared during the mid-Ashgill (late Katian), much earlier than in other regions. These three orders of brachiopods did not diversify in South China until Silurian time.

3.2. Palaeoecological diversity

Palaeoecological diversity is also known as community diversity or β -diversity. During the Tremadocian, the brachiopod *Tritoechia* Fauna developed in the shallow-

water, level-bottom, carbonate depositional environment of South China. The fauna was characterized by a low species diversity but locally high abundance. By early Floian time, The *Sinorthis* Fauna appeared in the fine-grained siliciclastic depositional settings of the middle part of the Upper Yangtze Platform (Tongzi area) and rapidly proliferated and spread to other areas of the platform, evolving into various brachiopod communities or associations [33], such as the *Desmorthis* Community in the Changning area of Sichuan, the *Paralenorthis* Community and *Sinorthis* Community in the Tongzi area of northern Guizhou and the Yanhe area of northeastern Guizhou. The *Euorthisina* Community first appeared somewhat later than the *Sinorthis* Community in the middle part of the Upper Yangtze Platform and subsequently, with the multiplication of brachiopod faunas and increasing competition pressure in relatively shallow-water platform environments (BA3), migrated successfully to relatively deep-water platform settings (BA4) during the Mid Ordovician [18]. The radiation of the *Sinorthis* Fauna attained a β -diversity acme during the late Floian, occurred mainly in the middle part of the Yangtze Platform (BA3), and was characterized by a high degree of differentiation of brachiopod communities in time and space [34].

The brachiopod β -diversity maxima in the Ordovician of South China were represented by highly endemic brachiopod faunas. In addition to the *Sinorthis* Fauna, such radiation events include the *Saucrorthis* Fauna (Darriwilian) and the *Altaethyrella* Fauna (late Katian). The *Sinorthis* Fauna originated in South China and was most abundant here, with wide regional distribution, broad palaeoecological range, long geological duration, and most variable community differentiation. Outside South China, *Sinorthis* occurs only sporadically in Tarim (China) and Montagne Noir (France) and it is unknown whether it is associated with other brachiopods typical of the *Sinorthis* Fauna in these regions. The *Saucrorthis* Fauna is largely confined to the Upper Yangtze Platform [35], with a minor occurrence in Burma (Sibumasu terrane), where its diversity and abundance are far lower than on the Upper Yangtze Platform [36]. The *Altaethyrella* Fauna has been reported from southern Kazakhstan, the western margin of the North China palaeoplate, and the Zhejiang-Jiangxi border area in the southeastern part of the South China palaeoplate. The *Altaethyrella* Fauna appeared in South China slightly later (in the *Dicellograptus complexus* Biozone) than in the other two regions, but had a much higher level of species diversity and richness.

The high level of faunal endemism and provincialism does not seem to have been linked to any major global environmental perturbations. As a distinct feature of the β -diversity radiation, it probably reflects the rapid, temporally diachronous, and palaeogeographically heterogeneous evolution of brachiopod faunas in separate palaeoplates or terranes during the great Ordovician biodiversification event.

3.3. Faunal turnover

On the basis of the high-resolution biostratigraphy in South China, it is now possible to analyse brachiopod faunal turnovers at the scale of graptolitic biozones. In our study, a binary dataset, using graptolite biozones as cases and brachiopod genera as variables, was subjected to a multivariate analyses (principal component and cluster analyses) to detect major faunal dissimilarities between stratigraphically adjacent faunas (faunal turnovers) in the Ordovician of South China (Fig. 3). The cluster analysis indicated that the *Sinorthis* Fauna is the most distinct brachiopod fauna, showing a maximum difference in its generic composition from any other Ordovician brachiopod faunas in South China. This implies two major brachiopod faunal turnover events, one being the transition from the Tremadocian *Tritoechia* Fauna to the Floian *Sinorthis* Fauna, the other being the transition from the *Sinorthis* Fauna to the Darriwilian *Saucrorthis* Fauna. The former turnover was a transition from a relatively low-diversity, cosmopolitan fauna to a high-diversity, orthide-dominated, endemic fauna, leading to the first diversity peak in South China; the latter turnover was a change between similarly endemic brachiopod faunas (i.e. from the *Sinorthis* to the *Saucrorthis* Fauna), resulting in the second peak of Ordovician brachiopod radiation [35]. The *Saucrorthis* Fauna was less diverse than the *Sinorthis* Fauna (see Appendix A for details) and was characterized by a rapid increase in the plectambonitoids and strophomenoids. During the second faunal turnover, the strophomenidides replaced the pentameridides as a dominant brachiopod group for the first time in the course of brachiopod faunal evolution in South China. The transition from the *Saucrorthis* Fauna to the *Foliomena* Fauna occurred during a major rise in sea level (early Sandbian) and the development of relatively deep-water *Foliomena* Fauna. Later, the *Foliomena* Fauna expanded into shallower, mid-shelf settings [37]. The *Altaethyrella* Fauna appeared in a relatively shallow-water shelf environment in South China during the late Katian, but was confined to a small area in the border region of Zhejiang and Jiangxi provinces, East China. The *Hirnantia* Fauna was cosmopolitan, developed during the Hirnantian glaciation during the latest Ordovician. It is usually regarded as a highly distinct brachiopod fauna, but it seems to have a certain degree of affinity to the *Foliomena* and the *Altaethyrella* faunas because several brachiopod genera extended from the latter two faunas to the *Hirnantia* Fauna.

The Ordovician trilobite radiation was manifested by the turnover between the Cambrian Ibexian Fauna and the Ordovician Whiterockian Fauna [21,38]. The Ibexian Fauna declined from the beginning of Ordovician time and became extinct during the end Ordovician mass extinction. In South China, the Ibexian Fauna can be further differentiated into Ibexian-I and Ibexian-II faunas, and the Ibexian-II Fauna experienced a brief, minor radiation during the Early Ordovician. The Ibexian and the Whiterocki-

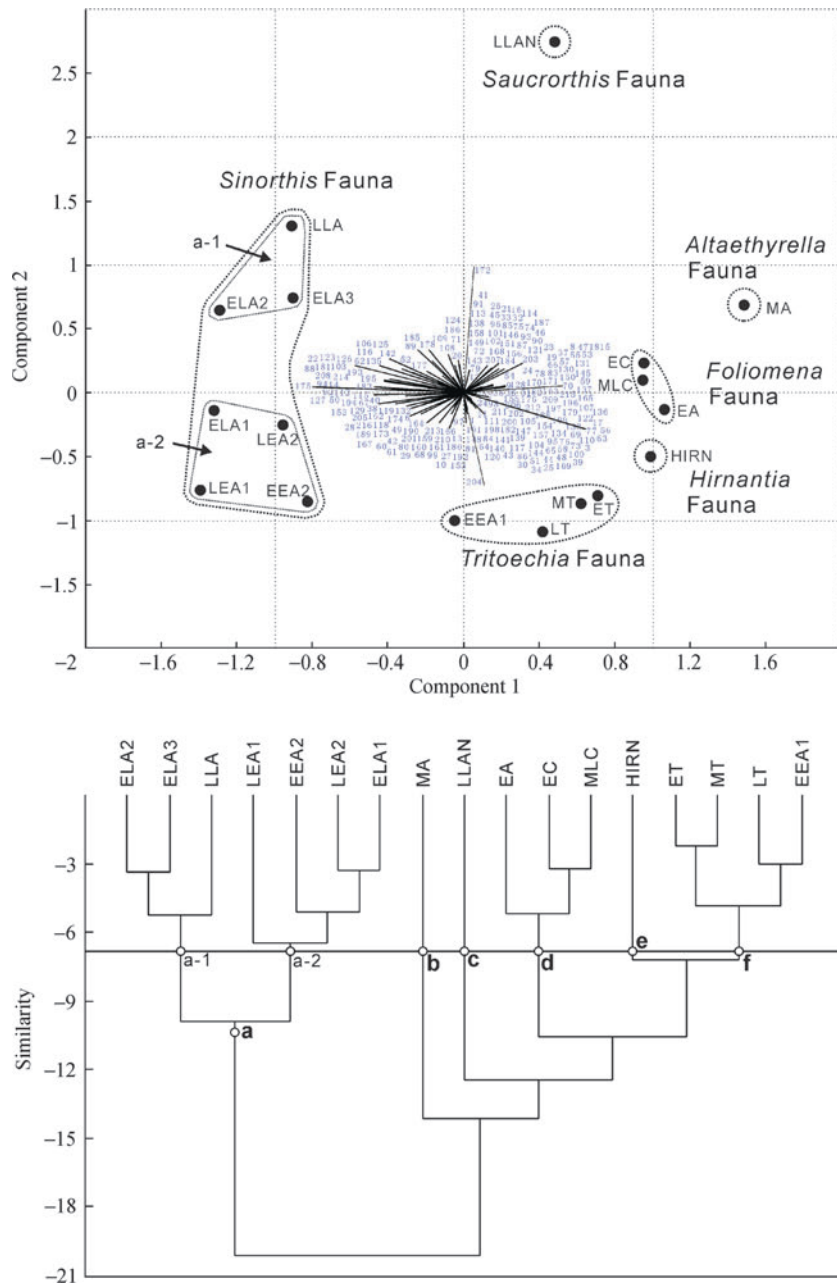


Fig. 3. Principal component analysis (a) and cluster analysis (b) of Ordovician brachiopods of South China using time intervals as cases (based on graptolitic biozones) and brachiopod genera in each interval as variables. Six brachiopod faunas are recognized in the Ordovician: the *Tritoechia* Fauna, the *Sinorthis* Fauna, the *Saucrorthis* Fauna, the *Folioimena* Fauna, the *Altaethyrella* Fauna, and the *Hirnantia* Fauna. The *Sinorthis* Fauna could also be further differentiated into the *Sinorthis* Subfauna (a-2) and the *Euorthisina* Subfauna (a-1). The major faunal turnovers were represented by the appearance and disappearance of the *Sinorthis* Fauna. See Appendix A for details of faunal composition and the number code of brachiopod genera.

an faunas lived contemporaneously in South China for a long time, and the Ibexian Fauna died out during the first episode of the end Ordovician mass extinction [39–41].

4. Heterogeneity of the Ordovician radiation

The Ordovician radiation was influenced by the combination of intrinsic factors (variable rates and patterns of evolution in different marine organisms) and extrinsic factors (plate tectonics, palaeogeography, palaeoclimate, pal-

aeoceanography). Variations in local or regional characteristics of these intrinsic and extrinsic factors would lead to variable rates and patterns of radiation among different groups of organisms and different regions.

4.1. Heterogeneity of a single fossil group among different palaeogeographical regions

In South China, brachiopod α -diversity achieved its first peak in early Floian (*D. eobifidus* Biozone), and β -diversity

in early Dapingian (*E. hirundo* Biozone). In the Precordillera region of Argentina, brachiopod α -diversity reached its first peak during the late Floian, slightly later than in South China but predating the global trend [13]; the first β -diversity acme was similarly delayed compared to that in South China (Benedetto, personal communication, 2006). In Bohemia, the transition between Cambrian-type and Ordovician-type brachiopod faunas and communities was achieved in Darriwilian time [42], influenced by immigrants from South China and other regions (such as the *Nocturnellia* Community and the *Euorthisina* Community). In North America, brachiopod α -diversity attained its first peak in the Darriwilian. The delayed radiation was partly due to the delayed major marine transgression and flooding of the Laurentian interior by epicontinental seas, which began in Sandbian time and reached a maximum extent by late Katian. The Cambrian-Early Ordovician trilobite fauna was not replaced by the Mid-Late Ordovician trilobite fauna until latest Darriwilian time in Laurentia [10,21,43].

4.2. Heterogeneity among different ecotypic fossil groups in a single palaeogeographical region

In South China, the benthic sessile brachiopods reached their first α -diversity and β -diversity acmes earlier than the vagile, deposit-scavenging trilobites or the planktonic-nektic graptolites. The α -diversity change of trilobites attained the first acme only by mid-late Sandbian time. Despite its general abundance in the Ordovician rocks of South China, the graptolites did not undergo any drastic diversity fluctuations or abrupt, major radiations at the generic level on the Yangtze Platform. During the early Floian, when brachiopod α -diversity change reached a maximum, graptolites experienced a minor radiation, with the number of genera increased to nine from the three in late Tremadocian. Subsequently, graptolite diversity remained stable, with only minor fluctuations until late Katian time when the Wufeng graptolitic shale was deposited. It has been shown that, in South China, graptolite radiation occurred mainly in the Jiangnan Slope region [44,45]. The anisograptids, dichograptids and diplograptids, for example, originated in the deep-water settings of the Jiangnan Slope, then migrated to, and diversified in, the shallow-water environment of the Yangtze Platform as well as the open-ocean, pelagic realm, and eventually became cosmopolitan [46]. The epibenthic to infaunal bivalves constituted a major part of the Modern Evolutionary Fauna. In the Ordovician of South China, bivalves were usually subordinate to minor components of benthic shelly communities. Bivalve-dominated communities have been found locally in some beds, usually in near-shore, shallow-water settings with silty to sandy substrates. The only bivalve α -diversity peak detected in the Ordovician of South China (Yangtze Platform) occurred in the Dapingian [6].

4.3. Heterogeneity among the subgroups of a single fossil group in a single palaeogeographical region

During approximately 40 million years of the Ordovician biodiversification, various groups of brachiopods showed different rates and patterns of radiation. In the first α -diversity acme, the main contributors were orthoids, with syntrophiidine pentamerides and lingulates also showing increases in diversity. Dalmanelloids, plectambonitoids, and strophomenoids first appeared on the Yangtze Platform during the first radiation but were only very minor elements. The subsequent diversification of these three groups developed into the main portion of the second α -diversity acme in South China during Darriwilian time. The third brachiopod α -diversity acme in South China (late Katian) was due to the adaptive radiation of orthoids, plectambonitoids, and strophomenoids. Other brachiopod groups, such as rhynchonellides, atrypides, and spiriferides, made their first appearances at relatively late stages of the Ordovician biodiversification—the former two in Sandbian, and the last in late Katian time. With their morphological innovations (e.g., strong shell costae, prominent fold and sulcus, and spiralia) and increased potential for adaptive radiation, these groups formed the basis for the diversification of brachiopod faunas during the ensuing Silurian Period.

4.4. Heterogeneity of a single fossil group in various palaeoecological settings of a single palaeogeographical region

Jablonski et al. [14] recognized a broad pattern of onshore-offshore migration of the three evolutionary faunas, with newly evolved faunas pushing older faunas to increasingly offshore settings. This hypothesis is supported by some case studies but unsupported by other cases in South China, as many dominant taxa of the brachiopod faunas did not originate in shallow water, but commonly in deeper, BA3–BA6 settings [34,47]. A few brachiopod genera, such as *Desmorthis* or some undescribed strophomenoids, did appear first in near-shore, shallow-water, siliclastic-rich rocks during the early Floian, and subsequently expanded palaeogeographically and diversified taxonomically towards the middle part of the Yangtze Platform. On the other hand, there are many genera that have been shown to be of deep-water origin. For example, in the Sandu area of southeastern Guizhou, which was located on the upper part of the Jiangnan Slope during the Early and Mid Ordovician, *Nereidella*, *Paralenorthis*, *Protoskenidioides*, *Nocturnellia* and some others made their earliest known appearance in the lower *Tetragraptus approximatus* Biozone (earliest Floian). These genera migrated onto increasingly shallower waters of the Yangtze Platform in increasingly younger graptolite biozones [47].

In the six measured Lower-Middle Ordovician sections shown in Fig. 2, each occupied a different palaeoecological setting on the Upper Yangtze Platform. Because of the

variable substrate conditions (e.g. water depth, water turbulence level, sediment type, and sedimentation rate), the rate and pattern of brachiopod radiation differed considerably from one to the other across correlative stratigraphical intervals. The brachiopod α -diversity change reached its first acme early in the relatively deep-water (BA3) settings of the Tongzi, Yanhe, and Chengkou areas (*D. eobifidus* Biozone, Meitan and Yingpan formations, Lower Floian), later in Yichang (lower *C. deflexus* Biozone, Dawan Formation, upper Floian), and still later in the shallow-water environment of the Changning area (*E. hirundo* Biozone, upper Dapingian). This implies that the timing and rate of brachiopod radiation were not uniform in different palaeoecological settings across the Yangtze Platform.

5. Conclusions

The great Ordovician biodiversification spanned nearly the entire Ordovician Period, lasting approximately 40 million years, and marked by at least three α -diversity peaks. The diversification event was not associated with any abrupt and drastic global environmental change, but was characterized by long, gradual, and multi-phased radiations. The radiations were manifested not only in terms of increase in the number of taxa (α -diversity) but also in autecological and synecological differentiations (β -diversity) in time and space. The succession and proliferation of various types of benthic shelly faunas in different palaeoenvironmental and geological settings are important features of the α - and β -diversity increase. Many case studies in South China improved our understanding of the rate, pattern, and other detailed macroevolutionary processes of the Ordovician biodiversification. Our study clearly shows that the community succession and faunal evolution during this event did not follow a unitary model. Various types of heterogeneity, as discussed above, can be considered an important feature of the biodiversification event. Such heterogeneity was most likely the result of the interactions between palaeobiological (intrinsic) and palaeoenvironmental (extrinsic) factors. The Ordovician Period featured a sustained major greenhouse episode, grand-scale sea-level rise and marine transgression that created widespread, epicontinental, tropical seas, prevailing carbonate platforms, limited emergent landmasses, active orogenic activities with volcanic and magnetic events, and so on, which have been considered as the extrinsic factors for the Ordovician biodiversification. Local or regional variations in these factors would have led to differences in the timing, rate, and pattern of biotic radiations.

The Ordovician biodiversification is a particularly significant event in life history, when the Paleozoic Evolutionary Fauna evolved and subsequently sustained a high level of diversity for 280 million years. Because of its rich rock and fossil record, South China holds key data for many aspects of the biodiversification event.

Our immediate future research needs to focus on the controlling mechanisms of the diversification. Other important, potentially ground-breaking research areas include investigations on the ancestors and origins of the Ordovician faunas, the origin and long-term development of these faunas in terms of their α - and β -diversities, and the development of endemism and provincialism during the Ordovician.

Acknowledgements

This work was supported by the Chinese Academy of Sciences (KZCX3-SW-149), the Ministry of Science and Technology of China (2006CB806400), and the National Natural Science Foundation of China (40540420130, 40532009). This paper is a contribution to IGCP Project 503: Ordovician Palaeogeography and Palaeoclimate. Rong Jiayu and Zhou Zhiyi kindly offered helpful comments on an early version of this paper.

Appendix A

A.1. Faunal list and abbreviations used in multivariate analyses in Fig. 3

- ET:** Early Tremadoc (*Rhabdinopora flabelliforme* Zone): *Lingulella*; *Nanorthis*, *Apheorthis*, *Finkelburgia*; *Syntrophinella*, *Imbricatia*, *Punctolira*, *Tetralobula*.
- MT:** Mid Tremadoc (*Psigraptus* Zone): *Lingulella*; *Conotreta*; paterinid indet. 1; *Archaeorthis*, *Nanorthis*, *Fasciculina*; *Tritoechia*; *Syntrophina*, *Syntrophinella*, *Tetralobula*.
- LT:** Late Tremadoc (*Adelograptus-Clonograptus* Zone): *Lingulella*, *Obolus?*; *Conotreta?*; *Archaeorthis*, *Nanorthis*, *Xinanorthis*, *Apheorthis*, *Fasciculina*, *Oligorthis*, *Pseudomimella*; *Tritoechia*; *Imbricatia*, *Syntrophina*, *Yangtzeella*, *Punctolira*, *Tetralobula*.
- EEA1:** Early early Arenig (*Tetragraptus approximatus* Zone, early Floian): *Ectenoglossa*, *Lingulella*, *Obolus?*, *Schmidtites*, *Westonia*; *Acanthocrania?*; *Archaeorthis*, *Xinanorthis*, *Euorthisina*, *Diparelasma*, *Desmorthis*, *Pseudomimella*, *Nocturnellia*, *Tarfaya*; *Tritoechia*; *Fenxiangella*, *Syntrophina*, *Yangtzeella*, *Pseudoporambonites*, *Tetralobula*.
- EEA2:** Early early Arenig (*Acrograptus filiformis* Zone, early Floian): *Ectenoglossa*, *Obolus*, *Palaeoglossa*, *Schmidtites?*, obolid indet. 1; *Acanthocrania?*; *Orthis*, *Paralenorthis*, *Sinorthis*, *Taphrorthis*, *Trondorthis*, orthid indet. 1, *Archaeorthis*, *Xinanorthis*, *Euorthisina*, *Diparelasma*, *Desmorthis*, *Pseudomimella*, *Nothorthis*, *Nocturnellia*, *Tarfaya*, *Nereidella*, *Virgoria*; *Anchigonites*, *Tritoechia*; *Leptella*, plectambonitid indet. 1; *Fenxiangella*, *Stichtrophia*, *Syntrophina*, *Yangtzeella*, syntrophiid indet. 1, *Pseudoporambonites*, *Doloresella*, *Imbricatia*, *Punctolira*.

- LEA1:** Late early Arenig (*Didymograptellus eobifidus* Zone, late Floian): *Apatobolus*, *Ectenoglossa*, *Elliptoglossa*, *Ferrobolus*, *Lingulella*, *Obolus?*, *Palaeoglossa*, *Schmidites?*, *Westonia*, lingulid indet. 1, *Pseudolingula*, *Orbiculoidea*; *Conodiscus*, *Conotreta?*; *Acanthocrania?*, *Philhedra*; *Orthis*, *Orthambonites*, *Paralenorthis*, *Sinorthis*, *Taphrorthis*, *Trondorthis*, orthid indet. 1, *Archaeorthis*, *Xinanorthis*, *Euorthisina*, *Diparelasma*, *Corineorthis*, *Desmorthis*, *Pseudomimella*, *Nothorthis*, *Protoskenidioides*, *Skenidioides*, *Drabovinella*, *Nocturnellia*, *Tarfaya*, *Nereidella*, *Paurorthis?*, *Virgoria*; *Anchigonites*, *Atelelasmoidea*, *Progonambonites?*, estlandid indet. 1, *Martelia*, *Tritoechia*; sowerbyellid indet. 1, *Leptella*, *Schedophyla*; *Idiostrophia*, *Trigonotrophia*, *Fengxiangella*, *Stichotrophia*, *Syntrophinella*, *Yangtzeella*, syntrophiid, *Pseudoporambonites*, *Syntrophopsis*, *Doloresella*, *Punctolira*.
- LEA2:** Late early Arenig (*Corymbograptus deflexus* Zone, late Floian): *Elliptoglossa*, *Obolus*, *Palaeoglossa*; *Conotreta?*; *Paralenorthis*, *Sinorthis*, *Taphrorthis*, *Trondorthis*, *Euorthisina*, *Diparelasma*, *Desmorthis*, *Pseudomimella*, *Nothorthis*, *Skenidioides*, *Nocturnellia*, *Tarfaya*, *Nereidella*, *Paurorthis?*; *Anchigonites*, *Atelelasmoidea*, estlandid indet. 1, *Martelia*, *Tritoechia*; *Leptella*, *Schedophyla*; *Fengxiangella*, *Stichotrophia*, *Syntrophinella*, *Yangtzeella*, syntrophiid indet. 1, *Pseudoporambonites*, *Syntrophopsis*, *Punctolira*.
- ELA1:** Early late Arenig (*Azygograptus suecicus* Zone, latest Floian to earliest Dapingian): *Ectenoglossa*, *Elliptoglossa*, *Lingulella*, *Obolus?*, *Palaeoglossa*, *Schmidites*, obolid indet. 1, *Orbiculoidea*; *Conotreta?*; *Paralenorthis*, *Sinorthis*, *Taphrorthis*, *Trondorthis*, orthid indet. 1, orthid indet. 2, *Lepidorthis*, *Xinanorthis*, *Metorthis*, *Euorthisina*, *Diparelasma*, *Desmorthis*, *Pseudomimella*, *Nothorthis*, *Protoskenidioides*, *Skenidioides*, *Nocturnellia*, *Dalmanella*, *Tarfaya*, *Nereidella*, *Paurorthis?*; *Anchigonites*, *Atelelasmoidea*, estlandid, *Martelia*, *Tritoechia*; *Leptestia?*, sowerbyellid indet. 2, *Leptella*, *Schedophyla*; *Trigonotrophia*, *Diaphelasma?*, *Fengxiangella*, *Stichotrophia*, *Yangtzeella*, syntrophiid, *Pseudoporambonites*, *Syntrophopsis*.
- ELA2:** Early late Arenig (*Expansograptus hirundo* Zone, early Dapingian): *Ectenoglossa*, *Elliptoglossa*, *Leontiella*, *Lingulella*, *Obolus?*, *Palaeoglossa*, obolid indet. 1; *Conotreta?*; *Orthis*, *Paralenorthis*, *Sinorthis*, *Sivorthis*, *Taphrorthis*, *Trondorthis*, orthid indet. 1, orthid indet. 2, orthid indet. 3, *Glyptorthis*, *Lepidorthis*, *Dolerorthis*, *Metorthis*, platystrophid indet. 1, *Euorthisina*, *Diparelasma*, *Desmorthis*, *Pseudomimella*, *Nothorthis*, *Skenidioides*, *Nocturnellia*, *Horderleyella*, *Tarfaya*, *Nereidella*, *Paurorthis?*, *Virgoria*; *Atelelasmoidea*, *Martelia*, *Tritoechia*, *Leptestia?*, sowerbyellid indet. 2, *Leptella*, *Schedophyla*, strophomenid indet. 1, strophomenid indet. 2; *Camerella*, *Diaphelasma?*, *Fengxiangella*, *Stichotrophia*, *Yangtzeella*, syntrophiid indet. 1, *Syntrophopsis*.
- ELA3:** Early late Arenig (*Exigraptus clavus* Zone, late Dapingian): *Elliptoglossa*, *Obolus?*, *Orbiculoidea*; *Conotreta?*; *Paralenorthis*, *Sinorthis*, *Sivorthis*, *Glyptorthis*, *Lepidorthis*, *Monorthis*, *Metorthis*, *Euorthisina*, *Diparelasma*, *Desmorthis*, *Pseudomimella*, *Nothorthis*, *Skenidioides*, *Eodiorthelasma*, *Nocturnellia*, *Nereidella*, *Paurorthis?*, *Virgoria*; *Atelelasmoidea*, *Martelia*, *Tritoechia*; *Leptestia?*, sowerbyellid indet. 2, *Leptella*, strophomenid indet. 1, *Glyptomena*, *rafinesquinid* indet. 1; *Camerella* indet. 1, *Fengxiangella*, *Stichotrophia*, *Yangtzeella*, syntrophiid indet. 1, *Porambonites*, *Syntrophopsis*.
- LLA:** Late Arenig (*Undulograptus austrodentatus* Zone, earliest Darriwilian): *Obolus*, *Orbiculoidea*; *Orthis*, *Paralenorthis*, *Sinorthis*, *Sivorthis*, *Sulcatorthis*, *Taphrorthis?*, orthid indet. 1, orthid indet. 2, *Glyptorthis*, *Lepidorthis*, *Parisorthis*, *Hesperonomia*, *Monorthis*, *Nicoloidea*, *Metorthis*, *Multicostella*, *Nicolella*, *Saucrorthis*, *Euorthisina*, *Diparelasma*, *Phragmorthis*, *Desmorthis*, *Pseudomimella*, *Nothorthis*, *Skenidioides*, *Eodiorthelasma*, *Nocturnellia*, *Tarfaya*, *Nereidella*, *Paurorthis?*, *Virgoria*; *Atelelasmoidea*, *Martelia*, *Tritoechia*; *Calyptolepta*, *Leptastichidia*, *Leptella*, *Glyptomena*, *Pentagomena*; *Fengxiangella*, *Stichotrophia*, *Yangtzeella*, *Syntrophopsis*.
- LLAN:** Llanvirn (*Undulograptus intersitus* Zone-Gymnograptus *linnarsoni* Zone, Darriwilian): *Lingula*, *Lingulella*; *Orthambonites*, *Paralenorthis*, orthid indet. 1, *Glyptorthis*, *Lepidorthis*, *Parisorthis*, *Monorthis*, *Dolerorthis*, *Nicolella*, *Saucrorthis*, *Plectorthis*, *Phragmorthis*, *Nothorthis*, *Skenidioides*, *Drabovia?*, *Drabovinella*, *Onniella?*, dalmanellid indet. 1, dalmanellid indet. 2, *Horderleyella*, *Tarfaya*, *Paurorthis*, tyronellid indet. 1; clitambonitid indet. 1, *Raunites*, *Peritritoechia*, *Tritoechia*; *Triplesia*; *Calyptolepta*, *Leptellina*, *Leptastichidia*, *Leangella?*, *Eoplectodonta*, *Aporthophyla*, *Chonetoidea?*, *Christiania*, *Glyptomena*, *Platymena*, *Heteromena*, *Kjaerina*, *Leptaena*, *Macrocoelia*, *Pentagomena*, *Bellimurina*, *Longvillia*, *Strophomena*, strophomenid indet. 1, strophomenid indet. 2; *Camerella*, *Yangtzeella*, *Porambonites*.
- EC:** Early Caradoc (early Sandbian): *Acrotreta?*; *Sulcatorthis*, *Taphrorthis?*, *Glyptorthis*, *Dolerorthis*, *Nicoloidea*, *Dedzetina*; *Skenidioides*; *Diambonioidea*, *Anoptambonites?*, *Durranelia*, *Kassinella?*, *Bilobia*, *Leangella*, *Leptellina*, *Anisopleurella*, *Eoplectodonta*, *Multiridgia*, *Chonetoidea?*, *Christiania*, *Foliomena*.
- MLC:** Mid-late Caradoc (late Sandbian to early Katian): *Petrocrania*; maturellid; *Glyptorthis*, dalmanelloid, *Epitomyonia*; *Skenidioides*, *Leangella*, *Anisopleurella*, *Eoplectodonta*, *Chonetoidea*, *Christiania*, *Nubi-alba*, *Foliomena*; *Cyclospira*.

- EA:** Early Ashgill (late Katian): lingulid, *Paterula*; *Orbiculoidea*, *Acrothele*?; *Philhedra*; *Trimerella*, *Costitrimerella*, *Eodinobolus*, *Fengzuella*, *Gyrosele-*
nella, *Palaeotrimerella*, *Paradinobolus*, *Sinotrimer-*
rella; *Glyptorthis*?, *Dedzetina*; plectambonitoid,
Durranelia, *Kassinella*, *Leptestiina*, *Eoplectodonta*,
Kozlowskites, *Chonetoidea*, *Christiania*, *Foliomena*;
Cyclospira.
- MA:** Mid Ashgill (late Katian): *Ectenoglossa*, *Plecto-*
glossa; *Acanthocrania*; *Pseudopholidops*?; *Peritri-*
merella; orthine, *Glyptorthis*, *Zhejiangorthis*,
Ptychopleurella?, *Plaesiomya*?, *Retrorsirostra*?,
Plectorthis, *Dalmanella*, *Dedzetina*, *Onniella*, dal-
manelloid, *Epitomyonia*, *Wangyuella*; *Skenidioides*;
Triplesia, *Oxoplecia*, *Fardenia*; *Bimuria*?, *Anop-*
tambonites, *Kassinella*, *Leptellina*, *Reversella*, *Sow-*
erbyella, *Rugosowerbyella*, *Metambonites*,
Synambonites, xenambonitid, *Strophomena*,
Fenomena, *Holtedahlina*, *Katastrophomena*, *Lepta-*
ena, *Tashanomena*, teratelasmine, *Christiania*,
Foliomena, *Eopholidostrophia*; *Parastrophinella*,
Eosotrophina, parastrophinid, *Brevilammulella*,
Deloprosopus; *Altaethyrella*; *Antizygospira*, *Eospir-*
igerina, *Ovalospira*, atrypid, *Cyclospira*; *Eospirifer*.
- HIRN:** Hirnantian: lingulid 2, *Lingulella*?; *Orbiculoidea*,
Trematis; *Acanthocrania*, *Philhedra*; *Pseudopholid-*
ops; *Dalmanella*, *Mirrorthis*, *Onniella*, *Trucizetina*,
Toxorthis, *Draborthis*, *Drabovinella*, *Hirnantia*,
Kinnella, *Dysprosorthis*; *Triplesia*, *Cliftonia*, *Ony-*
choplecia, *Fardenia*; *Aegiromena*, *Leptaena*, *Paro-*
malomena, *Eostropheodonta*; *Sphenotreta*,
Dorytreta, *Plectothyrella*; *Hindella*, *Whitfieldella*;
Eospirifer.

A.2. Number code for the genera used in Fig. 3

1. *Acanthocrania*; 2. *Acrothele*?; 3. *Acrotreta*?; 4. *Aegi-*
romena; 5. *Altaethyrella*; 6. *Anchigonites*; 7. *Anisopleurella*;
8. *Anoptambonites*; 9. *Antizygospira*; 10. *Apatobolus*; 11.
Apheoorthis; 12. *Aporthophyla*; 13. *Archaeorthis*; 14. *Atel-*
elasmoidea; 15. atrypid; 16. *Bellimurina*; 17. *Bilobia*; 18.
Bimuria?; 19. *Brevilammulella*; 20. *Calyptolepta*; 21. *Came-*
rella; 22. camerellid indet. 1; 23. *Chonetoidea*; 24. *Christi-*
ania; 25. *Cliftonia*; 26. clitambonitid indet. 1; 27.
Conodiscus; 28. *Conotreta*; 29. *Corineorthis*; 30. *Costitrime-*
rella; 31. *Cyclospira*; 32. dalmanelid indet. 1; 33. dalmane-
lid indet. 2; 34. *Dalmanella*; 35. dalmanelloid; 36.
Dedzetina; 37. *Deloprosopus*; 38. *Desmorthis*; 39. *Diambo-*
noidea; 40. *Diparelasma*; 41. *Dolerorthis*; 42. *Doloresella*;
43. *Dorytreta*; 44. *Draborthis*; 45. *Drabovia*?; 46. *Drabovi-*
nella; 47. *Durranelia*; 48. *Dysprosorthis*; 49. *Ectenoglossa*;
50. *Elliptoglossa*; 51. *Eodinobolus*; 52. *Eodiorthelasma*; 53.
Eopholidostrophia; 54. *Eoplectodonta*; 55. *Eosotrophina*;
56. *Eospirifer*; 57. *Eospirigerina*; 58. *Eostropheodonta*; 59.
Epitomyonia; 60. estlandid indet. 1; 61. estlandid; 62. *Euor-*
thisina; 63. *Fardenia*; 64. *Fasciculina*; 65. *Fengzuella*; 66.

Fenomena; 67. *Fenxiangella*; 68. *Ferrobolus*; 69. *Finkelbur-*
gia; 70. *Foliomena*; 71. *Glyptomena*; 72. *Glyptorthis*; 73.
Gyroselenella; 74. *Hesperonomia*; 75. *Heteromena*; 76.
Hindella; 77. *Hirnantia*; 78. *Holtedahlina*; 79. *Horderleyella*;
80. *Idiostrophia*; 81. *Imbricatia*; 82. *Kassinella*; 83. *Kata-*
strophomena; 84. *Kinnella*; 85. *Kjaerina*; 86. *Kozlowskites*;
87. *Leangella*; 88. *Leontiella*; 89. *Lepidorthis*; 90. *Leptaena*;
91. *Leptastichidia*; 92. *Leptella*; 93. *Leptellina*; 94. *Leptes-*
tia?; 95. *Leptestiina*; 96. *Lingula*; 97. *Lingulella*; 98. lingulid
2; 99. lingulid indet. 1; 100. lingulid; 101. *Longvillia*; 102.
Macrocoelia; 103. *Martellia*; 104. maturellid; 105. *Metamb-*
onites; 106. *Metorthis*; 107. *Mirrorthis*; 108. *Monorthis*; 109.
Multicostella; 110. *Multiridgia*; 111. *Nanorthis*; 112. *Nereid-*
ella; 113. *Nicolella*; 114. *Nicoloidea*; 115. *Nocturnellia*; 116.
Nothorthis; 117. *Nubialba*; 118. obolid indet. 1; 119. *Obolus*;
120. *Oligorthis*; 121. *Onniella*; 122. *Onychoplecia*; 123.
Orbiculoidea; 124. *Orthambonites*; 125. orthid indet. 1;
126. orthid indet. 2; 127. orthid indet. 3; 128. orthine;
129. *Orthis*; 130. *Ovalospira*; 131. *Oxoplecia*; 132. *Palaeo-*
glossa; 133. *Palaeotrimerella*; 134. *Paradinobolus*; 135. *Par-*
alenorthis; 136. *Parastrophinella*; 137. parastrophinid; 138.
Parisorthis; 139. *Paromalomena*; 140. paterinid indet. 1;
141. *Paterula*; 142. *Paurorthis*; 143. *Pentagomena*; 145.
Peritrimera; 146. *Peritritoechia*; 147. *Petrocrania*; 148.
Philhedra; 149. *Phragmorthis*; 150. *Plaesiomya*?; 151.
Platymena; 152. platystrophid indet. 1; 153. plectambonitid
indet. 1; 154. plectambonitoid; 155. *Plectoglossa*; 156. *Plec-*
torthis; 157. *Plectothyrella*; 158. *Porambonites*; 159. *Progo-*
nambonites?; 160. *Protoskenidioides*; 161. *Pseudolingula*;
162. *Pseudomimella*; 163. *Pseudopholidops*; 164. *Pseudop-*
orambonites; 165. *Ptychopleurella*?; 166. *Punctolira*; 167.
rafinesquinid indet. 1; 168. *Raunites*; 169. *Retrorsirostra*?;
170. *Reversella*; 171. *Rugosowerbyella*; 172. *Saucrorthis*;
173. *Schedophyla*; 174. *Schmidtites*; 175. *Sinorthis*; 176. *Sin-*
otrimerella; 177. *Sivorthis*; 178. *Skenidioides*; 179. *Sowerby-*
ella; 180. sowerbyellid indet. 1; 181. sowerbyellid indet. 2;
182. *Sphenotreta*; 183. *Stichtotrophia*; 184. *Strophomena*;
185. strophomenid indet. 1; 186. strophomenid indet. 2;
187. *Sulcatorthis*; 188. *Synambonites*; 189. syntrophiid
indet. 1; 190. syntrophiid; 191. *Syntrophina*; 192. *Syntrophi-*
nella; 193. *Syntrophopsis*; 194. *Taphrorthis*; 195. *Tarfaya*;
196. *Tashanomena*; 197. teratelasmine; 198. *Tetralobula*;
199. *Toxorthis*; 200. *Trematis*; 201. *Trigonotrophia*; 202.
Trimerella; 203. *Triplesia*; 204. *Tritoechia*; 205. *Trondorthis*;
206. *Trucizetina*; 207. tyronellid indet. 1; 208. *Virgoria*; 209.
Wangyuella; 210. *Westonia*; 211. *Whitfieldella*; 212. xenam-
bonitid; 213. *Xinanorthis*; 214. *Yangtzeella*; 215. *Zhejian-*
gorthis; 216. *Diaphelasma*.

References

- [1] Sepkoski Jr JJ. A kinetic model of Phanerozoic taxonomic diversity I: analysis of marine orders. *Paleobiology* 1978;4(3):223–51.
- [2] Sepkoski Jr JJ. A kinetic model of Phanerozoic taxonomic diversity II: early Phanerozoic families and multiple equilibria. *Paleobiology* 1979;5:222–52.
- [3] Sepkoski Jr JJ. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 1981;7(1):36–53.

- [4] Sepkoski Jr JJ. A kinetic model of Phanerozoic taxonomic diversity III: post-Paleozoic families and mass extinctions. *Paleobiology* 1984;10:246–67.
- [5] Barnes CR, Fortey RA, Williams SH. The pattern of global bio-events during the Ordovician period. In: *Global events and event stratigraphy in the phanerozoic*. Berlin: Springer; 1996. p. 139–72.
- [6] Fang ZJ. Ordovician bivalve radiation in the southern China with a discussion on the causes of radiation. In: *Biotic origination and radiation (in Chinese)*. Beijing: Science Press; 2006. p. 215–58, 861–63.
- [7] Webby BD, Paris F, Droser ML, et al., editors. *The great ordovician biodiversification event*. New York: Columbia University Press; 2004. p. 484.
- [8] Webby BD. In search of triggering mechanisms for the great Ordovician biodiversification event. *Palaeontology Down Under* 2000. Geological Society of Australia Abstracts, 2000;61:129–30.
- [9] Sepkoski Jr JJ. The Ordovician radiations: diversification and extinction shown by global genus-level taxonomic data. In: *Ordovician Odyssey: short Papers for the Seventh International Symposium on the Ordovician System*. California: Pacific Section SEPM, 1995. p. 393–96.
- [10] Sepkoski Jr JJ, Sheehan PM. Diversification, faunal change, and community replacement during the Ordovician radiations. In: *Biotic interactions in recent and fossil benthic communities*. New York: Plenum Press; 1983. p. 673–718.
- [11] Droser ML, Sheehan PM. Paleocological significance of the Ordovician radiation and end Ordovician extinction: evidence from the Great Basin. In: *Ordovician of the Great basin*. California: Pacific Section SEPM; 1995. p. 64–106.
- [12] Droser ML, Sheehan PM, Fortey RA, et al. The nature of diversification and paleoecology of the Ordovician radiation with evidence from the Great Basin. In: *Ordovician Odyssey, Short Papers for the Seventh International Symposium on the Ordovician System*. California: Pacific Section SEPM; 1995. p. 405–8.
- [13] Waisfeld BG, Sanchez TM, Carrera MG. Biodiversification patterns in the early Ordovician of Argentina. *Palaios* 1999;14:198–214.
- [14] Jablonski D, Sepkoski Jr JJ, Bottjer DJ, et al. Onshore-offshore patterns in the evolution of Phanerozoic shelf communities. *Science* 1983;222:1123–5.
- [15] Sepkoski Jr JJ, Miller AI. Evolutionary faunas and the distribution of Paleozoic benthic communities in space and time. In: *Phanerozoic diversity patterns: profiles in macroevolution*. Princeton: Princeton University Press; 1985. p. 191–253.
- [16] Cocks LRM. Lower Palaeozoic brachiopod communities. In: *Brachiopods, Proceedings of the Third International Brachiopod Congress*. Rotterdam: A.A. Balkema; 1996. p. 69–71.
- [17] Harper DAT, Rong JY and Zhan RB. Late Ordovician development of deep-water brachiopod faunas. In: *Quo vadis Ordovician? Short Papers of the 8th International Symposium on the Ordovician System*. Acta Universitatis Carolinae Geologia; 1999;43(1–2):351–53.
- [18] Rong JY, Zhan RB, Harper DAT. Late Ordovician (Caradoc-Ashgill) brachiopod faunas with *Foliomena* based on data from China. *Palaios* 1999;14:412–31.
- [19] Harper DAT, Gallagher E. Diversity, disparity and distributional patterns amongst the orthide brachiopod groups. *J Czech Geol Soc* 2001;46(3–4):87–93.
- [20] Bassett MG, Popov LE and Holmer LE. Brachiopods: Cambrian-Tremadoc precursors to Ordovician radiation events. In: *Palaeobiogeography and Biodiversity Change: the Ordovician and Mesozoic-Cenozoic Radiation*. Geological Society London Special Publications; 2002;194:13–23.
- [21] Adrain JM, Fortey RA, Westrop SR. Post-Cambrian trilobite diversity and evolutionary faunas. *Science* 1998;280(19):1922–5.
- [22] Jaanusson V. Ordovician articulate brachiopods. In: *Atlas of Palaeobiogeography*. Amsterdam: Elsevier Scientific Publishing Company; 1973. p. 19–26.
- [23] Williams A. Distribution of brachiopod assemblages in relation to Ordovician palaeogeography. *Special Papers in Palaeontology* 1973;12:241–69.
- [24] Rong JY, Fang ZJ, Zhou ZH, et al., editors. *Originations, radiations and biodiversity changes—evidence from the Chinese fossil record (in Chinese)*. Beijing: Science Press; 2006. p. 1–962.
- [25] Zhang YB, Zhou ZY, Zhang JM. Sedimentary differentiation during the latest Early Ordovician-earliest Darriwilian in the Yangtze Block. *J Stratigraphy (in Chinese)* 2002;26(4):302–14.
- [26] Gould SJ. *Wonderful life: the Burgess shale and the nature of history*. New York: Norton; 1989. p. 1–347.
- [27] Chen JY. *The dawn of animal life (in Chinese)*. Nanjing: Jiangsu Science and Technology Publishing House; 2004. p. 1–366.
- [28] Hu ZX, Spjeldnaes N. Early Ordovician bryozoans from China. *Bulletin de la Societe des Sciences Naturelles de l'Ouest de la France Mémoire Hors* 1991;1:179–85.
- [29] Valentine JW. Why no new phyla after the Cambrian? *Genome and ecospace hypotheses revisited*. *Palaios* 1995;10:190–4.
- [30] Copper P. Structure and development of early Paleozoic reefs. In: *Proceedings of the Second International Coral Reef Symposium 1*. Brisbane; 1974. p. 365–384.
- [31] Copper P. Silurian and Devonian reefs: 80 million years of greenhouse between two ice ages. *SEPM Special Publication* 2002;72:181–238.
- [32] Zhan RB, Rong JY, Cheng JH, et al. Early-middle Ordovician brachiopod diversification in South China. *Science China (Series D)* 2005;48(5):662–75.
- [33] Zhan RB, Jin JS, Rong JY. Community differentiation and diversification in Early-Mid Ordovician brachiopods of southwest China. *Geol J* 2006;41(3):217–88.
- [34] Zhan RB, Rong JY. Early to mid Ordovician brachiopod radiation of South China. In: *Biotic origination and radiation (in Chinese)*. Beijing: Science Press; 2006. p. 250–83, p. 865–66.
- [35] Zhan RB, Jin JS, Li GP. The *Saucrorthis* Fauna (Brachiopoda) and its implications for the Ordovician radiation in South China. *Acta Palaeontologica Sinica* 2007;46(Suppl.):515–22.
- [36] Cocks LRM, Zhan RB. Caradoc brachiopods from the Shan States, Burma (Myanmar). *Bull Natural History Museum London (Geology)* 1998;54(2):109–30.
- [37] Zhan RB, Jin JS. New data on the *Foliomena* fauna (Brachiopoda) from the Upper Ordovician of South China. *Journal of Paleontology* 2005;79(4):669–85.
- [38] Adrain JM, Edgecombe GD, Fortey RA, et al. Trilobites. In: *The great Ordovician biodiversification event*. New York: Columbia University Press; 2004. p. 231–54.
- [39] Zhou ZY. Notes on the Ordovician trilobite radiation in the South China block. In: *Ordovician from the Andes*. INSUGEO Serie Correlación Geológica 2003;17:355–61.
- [40] Zhou ZY, Yuan WW, Zhou ZQ. Ordovician trilobite radiation in the South China block. In: *Biotic origination and radiation (in Chinese)*. Beijing: Science Press; 2006. p. 197–213, p. 857–59.
- [41] Zhou ZY, Zhen YY, Zhou ZQ, et al. A new approach to the division of Ordovician geographic units of China. *Acta Paleontologica Sinica (in English)* 2007;46(Suppl.):558–63.
- [42] Mergl M. Inarticulated brachiopod communities in Tremadoc-Arenig of Prague Basin: a review. In: *Quo vadis Ordovician? Short Papers of the 8th International Symposium on the Ordovician System*. Acta Universitatis Carolinae Geologia; 1999;43(1–2):337–40.
- [43] Droser ML, Sheehan PM. Palaeoecology of the Ordovician radiation: resolution of large-scale patterns with individual clade histories, palaeogeography and environments. *Geobios Mémoire Spécial* 1997;20:221–9.
- [44] Zhang YD, Chen X. Evolutionary radiation of the Early-Middle Ordovician graptolites in South China. In: *Biotic origination and radiation (in Chinese)*. Beijing: Science Press; 2006. p. 285–316, p. 867–69.
- [45] Zhang YD, Chen X, Goldman D. Diversification patterns of Early and Mid Ordovician graptolites in South China. *Geol J* 2007;42:315–37.
- [46] Zhang YD, Chen X. Palaeobiogeographic distribution of *Pseudisograptus* and early biserials in South China and its implication for the

- origination of major graptolite faunas in the Ordovician. *Acta Palaeontologica Sinica* 2007;46(Suppl.):530–6.
- [47] Zhan RB, Jin JS. Onshore migration of a deep-water brachiopod fauna from the Lower Ordovician Tonggao Formation, Jiangnan Slope, southeastern Guizhou Province, South China. In: *The Dynamic Reef and Shelly Communities of the Paleozoic: A Tribute to the Research Career of Paul Copper*. Canadian Journal of Earth Sciences, 2007, p. 44.