Brachiopod faunas after the end Ordovician mass extinction from South China: Testing ecological change through a major taxonomic crisis

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Abstract

Classification of extinction events and their severity is generally based on taxonomic counts. The ecological impacts of such events have been categorized and prioritized but rarely tested with empirical data. The ecology of the end Ordovician extinction and subsequent biotic recovery is tracked through abundant and diverse brachiopod faunas in South China. The spatial and temporal ranges of some 6,500 identified specimens, from 10 collections derived from six localities were investigated by network and cluster analyses, nonmetric multidimensional scaling and a species abundance model. Depth zonations and structure of brachiopod assemblages along an onshore-offshore gradient in the late Katian were similar to those in the latest Ordovician–earliest Silurian (post–extinction fauna). Within this ecological framework, deeper-water faunas are partly replaced by new taxa; siliciclastic substrates continued to be dominated by the more ‘Ordovician’ orthides and strophomenides, shallow-water carbonate environments hosted atrypides, athyridides and pentamerides, with the more typical Ordovician brachiopod fauna continuing to dominate until the late Rhuddanian. The end Ordovician extinctions tested the resilience of the brachiopod fauna without damage to its overall ecological structure; that commenced later at the end of the Rhuddanian.

Keywords: earliest Silurian; survival; recovery; depth zonations; palaeoecology.

1. Introduction

The end Ordovician mass extinction was ignited by a brief but intense glacial interval that generated two pulses of taxonomic loss (Berry and Boucot, 1973; Sheehan, 1973; Brenchley et al., 1994; Sheehan, 2001; Brenchley et al., 2003; Harper et al., 2014). The end Ordovician events, led to a catastrophic biodiversity crisis, in taxonomic terms, which was ranked as the second largest (Sepkoski, 1996; Bambach et al., 2004) or the third largest (Alroy, 2010) within the big five extinctions of the Phanerozoic. However, in terms of ecological severity, the mass extinction was of minimal impact and is ecologically ranked as the least severe of the big five (Droser et al., 2000; McGhee et al., 2004). In a recent study, the ecological severity of the end Ordovician event was considered even less significant than that of the Serpukhovian (McGhee et al., 2012), and is ranked only sixth within the eleven largest Phanerozoic crises since the beginning of the Ordovician Period (McGhee et al., 2013). According to the ‘four-level’ ranking system of ecological impacts of extinction crises presented by Droser et al. (2000), only the third and fourth-level palaeoecological changes were triggered during the end Ordovician mass extinction, which means only community or community-type changes occurred during the event.

Brachiopods were the most common component of the marine benthos during the Ordovician–Silurian transition. The change in brachiopod communities from pre-extinction (Late Ordovician) to rediversification (early Silurian) was considered an important criterion among the five Bambachian megaguilds, commonly used to evaluate the ecological severity of the mass extinction (McGhee et al., 2013).

However, the ecological characteristics of brachiopod faunas immediately after the biotic event (e.g. survival to recovery time interval) has not been examined in detail possibly due to a sparsity of relevant data.

South China offers a key opportunity to examine the ecological changes through the event in detail. The *Cathaysiorthis* fauna is a shelly fauna dominated by brachiopods from the uppermost Ordovician to lowermost Silurian of SE China, succeeding the cool-water *Hirnantia* Fauna. The fauna is abundant and has a relatively high diversity; these data were reported with the detailed systematic descriptions of the fauna (Rong et al., 2013). In this study, the abundance data for the brachiopod fauna will be analyzed by cluster analysis (CA), nonmetric multidimensional scaling (NMDS) and network analysis (NA) to recognize the associations and detect any ecological gradients. A relatively new method in palaeoecology, the species abundance model, is adopted to further evaluate the ecological circumstances of the survival brachiopod fauna after the end Ordovician mass extinction.

Other, older brachiopod faunas, *Altaethyrella* fauna and *Foliomena* fauna, characterizing the late Katian within the same area are compared in terms of diversity, population structure, benthic assemblage zones and relative abundance together with their major components to help further elucidate the ecological ‘turnover’ through the end Ordovician extinction event in South China. The widths of ecological range are similar between before and immediately after the crisis that may suggest the limited ecological effect of the event. The decoupling between clear diversity loss and limited ecological severity are considered indicative of the resilience of the ecosystem captured by the Paleozoic Evolutionary Fauna. The benthic environment, possibly saturated before the end Ordovician mass extinction, was distinguished by more niches during the event, and new communities with lower diversities were distributed across each benthic regime.

2. Data and Methods

2.1 Data

The *Cathaysiorthis* Fauna occurs following the second episode of the latest Ordovician mass extinction. Detailed reports on the biostratigraphy, faunal composition and systematic description for *Cathaysiorthis* Fauna were recently published (Rong et al., 2013), and preliminary work on its community ecology based on limited data (20 species from 4 localities) was published (Rong and Zhan, 2006). In this study, an updated dataset of the fauna is investigated, in which almost 7000 brachiopod specimens assigned to 44 species, collected from 17 collections of 9 localities (Rong et al., 2013, table 1) have been incorporated.

For statistical confidence and justification of the methods used (see below), collections with specimen numbers fewer than 100 are excluded, with the exception of AFL130 since it was a representative of a particular association used in a previous study. Furthermore, since the brachiopod compositions of AFL296-299 are very similar, but apparently different from AFL303, these four collections are thus combined and treated as a single sample in the analysis. There are 6364 specimens in

10 collections from six localities (Fig. 1) involved in the analysis.

2.2 Methods

In order to quantify the ecological severity of the end Ordovician mass extinction in the studied area, several numerical methods have been adopted. The ten collections were assigned to four benthic assemblages by Rong et al. (2013) mainly according to different water depth representatives and previous studies (Rong and Zhan, 2006; Rong and Huang, 2007). Here, four main methods are applied.

Recently, a relatively new method, Network analysis (NA) has been used in biogeographic studies (e.g. Sidor et al., 2013, Vilhena and Antonelli, 2015). Compared with the widely-accepted methods currently used in palaeontology (such as cluster analysis [CA] and Principal Components Analysis [PCA]), NA can provide a network diagram, displaying even more information about the structure of the dataset. The method was recently successfully applied to palaeoecological studies (Huang et al., 2016). Here, the method will be adopted to show how a collection link to others via the taxa they shared, by which the overview of the brachiopod fauna will be visualized. More importantly, the distribution of the individual brachiopods across benthic assemblages can be illustrated by the method.

Traditionally, cluster analysis (CA) is used to classify fossil associations or assemblages generally with binary data, which contains very limited information. This methodology is partly due to inadequate sampling or unevenness of sample sizes. However, the sampling sufficiency of the *Cathaysiorthis* Fauna has been tested (Rong et al., 2013; Huang et al., 2014), which means the abundance data can be used for analysis. For unevenness or bias due to sample size, the Morisita similarity measure is adopted since it is virtually independent of sample size, except for those with very small numbers. Morisita (1959) did extensive simulation experiments to demonstrate this, and these results were confirmed by Wolda (1981), who recommended Morisita's index as the best overall measure of similarity for ecological use. Implementing Morisita’s index within CA with abundance data, will aid more precise recognition of brachiopod associations within the fauna.

Compared to CA, Nonmetric multidimensional scaling (NMDS) can provide a stress value (a goodness of fit, Takane et al., 1977) and Shepard plot (a scatter plot of ordination distances against dissimilarities; see Shepard, 1980), which can statistically evaluate the reliability of the results. The outcome of NMDS analyses can be superimposed on a Minimum Spanning Tree (MST), where the relationship between collections are clearer than in cluster analysis. Using NMDS, we are able to detect the bathymetrical gradient along major component axes.

The spectrum of relative abundances of the species is a key to understanding the ecological traits of the community. The species-abundance model is one of the crucial methods for interrogating community structures in modern communities; ecologists can describe species abundance distributions (Tokeshi, 1993). If a community (or a collection) consists of species with similar resource requirements (indicating similar niche space), the process of niche apportionment for all species can be divided by some key rules (Tokeshi, 1990). Importantly, these rules vary in different species-abundance models, which can generate different ecological interpretations. The species-abundance model is widely used in modern biology. It has recently been introduced to palaeoecological studies and its validity was tested with the Akaike Information Criterion (AIC) (Huang and Zhan, 2014). In this study, the method is used for supporting the bathymetric differences among collections, indicating the varying life strategies within the different benthic assemblages.

3. Ecological range of the *Cathaysiorthis* Fauna

3.1 Overview of the fauna

The network diagram shown in Fig. 2, displays almost all the major ecological characteristics of the fauna. The taxonomic information for each collection, together with links between collections via the taxa they share is illustrated. For example, there are 49 species in total, with only 10 species confined to one collections, which is represented by the smallest node with only one branch. Additionally, the diversity of each collection can also be observed by the size and grey scale (or colour) of the collection nodes through the “out degree”, which is represented by the number of branches of each node. It is clear that AFL161 is the collection with highest diversity since it has the largest node, whereas AFL2 displays the lowest diversity, containing only four species (four branches connected to the node).

The diagram further indicates a bathymetric gradient for the brachiopod assemblages across the different samples; the typical deeper-water taxa, such as *Leangella* (*Leangella*) *scissa*, *Skenidioides woodlandensis* and *Epitomyonia* *subquadrata* connect with their localities (AFL303, AFL296-299 and AFL140 etc.) and are distributed in the top right of the diagram, whereas the shallow-water taxa *Cathaysiorthis yushanensis, Leptaena rugosa* are in the top left.

3.2 Synecological analysis and bathymetric gradient

Benthic Assemblages (BA) refer to the different benthic communities, subcommunities or associations developed on the seafloor from nearshore shallow-water to offshore deeper-water benthic regimes (Boucot, 1975). To investigate the bathymetric gradient with BA assignments shown in the network diagram in more detail, CA and NMDS were performed by PAST (Hammer et al., 2001). Six brachiopod-dominated associations are recognized based mainly on faunal composition (Fig. 3): 1) *Levenea llandoveriana* association (AFL2, AFL30); 2) *Levenea-Brevilamnulella* association (AFL67); 3) *Katastrophomena-Leptaena-Levenea* association (AFL68, 161); 4) *Glyptorthis–Levenea* association (AFL130, AFL140); 5) *Whitfieldella angustifrons* association (AFL159); 6) *Leangella-Aegiromena* association (AFL296-299, AFL303). Both typical shallow and deep-water components were selected and their proportions in each collection were calculated to describe relative bathymetry in detail (Table 1).

Levenea llandoveriana association (AFL2, AFL30) is represented by two samples with 791 specimens from AFL2 and AFL30: 5-7 species occur in each of the collections, indicating that they contain the lowest diversity among all the collections studied. The eponymous *Levenea llandoveriana* accounts for 89.5% of the total and

Leptaena rugosa (5.4%) is the second most common. Rong and Huang (2007) discovered and collected the fossils from locality AFL2, recording the lowest diversity amongst all the samples studied. This was assigned to a nearshore, shallow-water environment (inner BA2), shallower than that of AFL30 (outer BA2).

Levenea-Brevilamnulella association (AFL67) is represented by only one collection at AFL67, and includes 16 brachiopod species with 334 shells (152 specimens of *Levenea llandoveriana*), indicating a diversity significantly higher than that at AFL30. The collection was assigned to an association together with AFL68 and AFL161 (Rong and Zhan, 2006), and is now separated mainly due to the presence of *Brevilamnulella kjerulfi* which accounts for 19.5% of total specimens in AFL67 but only 2.4% in the association represented by AFL68 and AFL161. Based on previous studies, its species diversity and relative abundance of the sample, an assignment of this association to inner BA3 can be inferred.

Katastrophomena-Leptaena-Levenea association (AFL68, 161) contains 4196 specimens (63.2% of the total of the fauna), and is represented by two samples of AFL68 and AFL161, in which 22 and 31 species occur respectively, signaling both the highest diversity and highest abundance among the associations recognized. Faunal compositions at AFL68 and AFL161 were described in detail by Rong and Zhan (2006), where 1202 specimens assigned to 13 species were involved. According to updated data, the abundance and diversity are much higher than those previously reported, but the dominant species of the two collections are unchanged. The association was assigned to BA3. Based on the new data, the water depth of this association is most likely outer BA3. Compared to AFL68, AFL161 is considered deeper in light of its higher diversity and the occurrence of more deep-water indicator (e.g. *Skenidioides* and *Epitomyonia*).

For *Glyptorthis–Levenea* association (AFL130, AFL140), collection AFL140 is relatively newly-discovered, and occurs immediately below a bed corresponding to AFL130 (Rong et al., 2013). The composition of AFL140 is similar to that of AFL130: *Glyptorthis wenchangensis* accounts for 33.9% of the total (25.7% in AFL130), *Levenea llandoveriana* 28.1% (25.7% in AFL130) respectively. Compared with the shallower-water samples at AF68 and 161, AFL130 accounts for a much higher proportion of the typical deep-water genus *Epitomyonia* (18.9%, Table 1), and is assigned to deeper-water BA4. Since the proportion of *Epitomyonia* is significantly lower in AFL140 (2.5%), the collection is considered shallower than AFL130.

For *Whitfieldella angustifrons* association (AFL159), AFL159 occurs immediately below AFL161, however, the composition of the collection is significantly different from the latter. The eponymous *Whitfieldella angustifrons* accounts for 38.1% of the total specimens. This association is unique since *Whitfieldella angustifrons* only occurs in AFL159, which has been recognized separately by the CA. AFL159 was considered as inner BA3 (Rong et al., 2013) mainly because of the relative abundance of the dominant species, as well as the absence of deeper-water indicators. Compared with the samples at AFL67, there are more gastropods and solitary rugose corals in AFL159, which may suggest the association is shallower than AFL67.

Leangella-Aegiromena association (AFL296-299, AFL303) is represented by several samples of AFL296-299 and AFL303, in which 18-24 species occurs. The *Leangella–Dalmanitina* (*Songxites*) assemblage from AFL303 reported as from deeper-water, off-shore environments (BA5) was correlated with the uppermost Hirnantian (Rong et al., 2008a). New data for AFL303 highlight the five most common genera, *Anisopleurella* (16.0%), *Leangella* (15.5%), *Aegiromena* (*Aegiromenella*) (14.4%), *Yuhangella* (11.3%), and *Epitomyonia* (10.3%), associated with the trilobite *Dalmanitina* (*Songxites*). The brachiopod components from AFL296–299 are similar to those of AFL303, and can be assigned to deeper-water facies (BA5) too. Because both diversity and abundance in a single bed of AFL303 is higher than those of AFL296–299, we infer that the AFL296–299 might be a little shallower than AFL303.

The bathymetry of the *Cathaysiorthis* fauna was assessed primarily on ecological, bathymetric indicators using brachiopods and trilobites, together with evidence from sedimentology (Rong et al., 2013). In this study, six associations were recognized and relative bathymetry is inferred in more detail mainly by deeper or shallow-water indicators (Table 1). The diversity curve is superimposed on the benthic assemblage assignment chart to reveal more information (Fig. 4). The diversity together with abundance data are correlated with BA in a nonlinear fashion, and support previous studies of brachiopods that lived in normal environments (Boucot, 1975), this implies normal living condition for the *Cathaysiorthis* fauna. The six associations recognized, based on ten collections in this study, indicate the heterogeneity of *Cathaysiorthis* fauna, together with a bathymetric gradient for the collections shown above. These also display a variety of benthic conditions after the end Ordovician mass extinction in South China.

3.3 **Niche differentiation**

Since all brachiopods feed with a lophophore, the feeding strategies for the organisms from different water depths should be broadly similar. The range of abundance is moderated by the partition of niches occupied by brachiopods. Using R project (version 3.0.3) within R-studio, calculations using five abundance models and their AIC values are programed and performed for each collection except AFL2 (the diversity is too low to be analyzed) and AFL159 (*Whitfieldella angustifrons* is predominant in the collection and is not found in any other collections). Huang and Zhan (2014) introduced the method into palaeoecology, and tested the abundance models with 4 collections from *Cathaysiorthis* fauna. Here, the results from 8 collections support previous study (Fig. 5, Table 2), the AIC values indicate that Zipf model is best fit for AFL30, Mandelbrot for AFL67, 68 and 140, and the pre-emption model for AFL161, 130, 296-299 and 303.

From shallow to deep water, the best fit abundance model changes from Zipf, Mandelbrot to pre-emption with the exception of AFL161 (Huang and Zhan, 2014). All the Zipf, Mandelbrot and pre-emption models emphasize that the existence of a species is dependent on the environment and its pre-occupied species, but the different function of each model may reflect different ecological traits. The results indicate there are at least three different niche settings in the *Cathaysiorthis* fauna, mainly controlled by the physical environment.

4. Discussion

4.1 The brachiopod fauna before the end Ordovician mass extinction

The *Cathaysiorthis* fauna displays a broad variety of eco-types. However, to place these in context the bathymetric range of brachiopod faunas before the end Ordovician mass extinction in the study area are first compared in brief. Before the end Ordovician mass extinction, the bio- and litho-facies as well as palaeogeography were strongly differentiated across the study area during the late Katian. Stratified limestones together with reef-building biotas developed on the Zhe-Gan Platform; thick and massive carbonate mud mounds occurred along the margin of the platform, and fine grained clastic rocks with a deep-water benthic fauna inhabited the Zhexi Slope (Rong and Chen, 1987; Zhan and Fu, 1994). Together within such palaeogeographical framework, the rocks display a spectrum of environments from nearshore shallow water (BA1) to offshore deep water (BA5) (Rong et al., 2010).

The brachiopod-dominated communities and subcommunities together with their synecology have already been investigated in detail (Zhan and Rong, 1995; Zhan et al., 2002), including the *Ectenoglossa minor* Community of Tashan, at Yushan, Jiangxi Province, indicating a BA1 benthic regime, the *Eospirifer praecursor* Community (BA2) and the *Antizygospira*-*Sowerbyella* Community (BA2) at Zhuzhai, at Yushan, the *Altaethyrella zhejiangensis* Community and the *Ovalospria dichotoma*

Community (BA3) at Shiyanshan in Yushan, the *Kassinella-Epitomyonia* Community (BA4) at Mulinlong and Wujialong in Jiangshan, Zhejiang Province, and the *Foliomena* Community (BA5) at Fengzu and Shangwu in Jiangshan. Based on data updated from Zhan and Cocks (1998), NA was performed and an overview of relationships between these brachiopod communities is shown in the network diagram (Fig. 6).

A general trend is clear in the southwest part of this area (upper part of the network diagram); Tashan and Zhuzhai were located in the shallowest water depth during the late Katian, and the sea gradually deepened towards Shangwu (lower right), Zhe-Gan Sea lay to the southeast.

The *Cathaysiorthis* Fauna occupied a wide range of benthic regimes from BA2 to the transition zones of BA3, BA4 and to BA5, describing a similar bathymetric pattern to the fauna of the upper Katian. The occurrence and success of all these brachiopod communities were associated with the development of heterogeneous nearshore to offshore deep-water benthic regimes, that provided a variety of ecological settings for the fauna. Apparently benthic organisms survived the end Ordovician mass extinction in South China and recovered very quickly, immediately after the extinction. This result apparently suggests that the end Ordovician mass extinction did not interrupt the dominance of brachiopods as common and key constituents of the benthic assemblages in Ordovician and Silurian seas. Ecological disturbance was minimal.

4.2 Was South China a Refuge?

Recently, Finnegan et al. (2016) suggested that the end Ordovician mass extinction was strikingly selective with respect to bathymetric distribution. Brachiopod genera that ranged into shallower waters (BA 1–2) experienced much lower extinction rates than those restricted to deeper waters (BA 3–6) during the first phase of the event, which suggests that the deeper-water brachiopods were rare from the Hirnantian to Rhuddanian.

The bathymetric range elucidated above contains typical brachiopods from BA4-5. Does this suggest that South China was an ecological refuge for deep-water benthos? Evidence of migration, however, into a refuge has not been documented in brachiopod data for the end Ordovician extinction, and migration may not have been a key mechanism for escaping extinction (Rong et al., 2006).

There are also some deeper-water brachiopod faunas reported elsewhere following the end Ordovician mass extinction (Fig. 7), such as the early Rhuddanian brachiopod assemblage described by Baarli and Harper (1986) from the Oslo Region, Norway, and a deeper-water brachiopod fauna with small shells illustrated by Jin and Chatterton (1997) from the Ordovician–Silurian boundary strata in the Mackenzie Mountains, Canada. The lower-middle Rhuddanian brachiopods from Juuru (G_{1-2}: Varbola and Tamsalu on the shelf and Õhne in the basin) of Estonia have been revised recently by Rubel (2011). In total, they contain 25 genera, among which the typical deep-water taxa *Epitomyonia* and *Dicoelosia* are reported. These data indicate that the brachiopod assemblages following the biotic event contained not only near-shore, inner-shelf taxa, but also outer-shelf assemblages, and may have experienced rapid ecological differentiation immediately after the end Ordovician extinction event; the deep seas were quickly recolonized following the loss of the *Foliomena* fauna (Rong et al., 1999).

The high diversity of the *Cathaysiorthis* Fauna, South China is also not unique. More than 20 species from the basal strata (A1-A4) of the Llandovery area were recorded by Williams (1951). In particular, the early Llandovery brachiopods from Ffridd Mathrafal, near Meifod described by Temple (1970) have a very higher diversity (over 40 species). Recently, evidence from South China suggests that the Edgewood fauna appeared in the latest Hirnantian and extended into Rhuddanian, slightly younger than previously believed (Wang et al., 2016). The brachiopod fauna across Ordovician-Silurian boundary from Oklahoma, Illinois and Missouri, USA include 23 species assigned to 20 genera (Amsden, 1974). A surprisingly rapid biotic recovery after the end Ordovician bio-event represented by the radiation of diverse shelly faunas with broad bathymetric ranges, prompts the question as to whether brachiopods were driven into unhealthy bathymetric niches and remained there after the event? To address the question, the population structure for dominant species from both before and after the end Ordovician mass extinction will be tested below.

4.3 Population dynamics before and after the end Ordovician mass extinction

Although the *Cathaysiorthis* fauna exhibits both high diversity and abundance together with ecological traits suggesting a normal marine environment, study of population dynamics is a useful proxy for environmental conditions since the population is the smallest unit in any ecological study, most sensitive to the environment (Dodd and Stanton, 1990; Brenchley and Harper, 1998). To display the ecological effect of the end Ordovician mass extinction in detail, size frequency charts were constructed for brachiopod populations selected from both *Altaethyrella* fauna and *Cathaysiorthis* fauna. Some populations from the *Cathaysiorthis* fauna were previously assigned to normal marine environments using population analysis during an identification of the Lilliput effect across the Ordovician–Silurian boundary (Huang et al., 2010). Populations of six species in three pairs were selected according to their dominance in assemblages (*Levenea llandoveriana* and *Altaethyrella zhejiangensis*), taxa with similar ecological traits (*Eospirigerina putilla* and *Antizygospira liquanensis*) and similar species (*Eospirifer* (*Eospirifer*) *eosinensis* and *Eospirifer* (*Protospirifer*) *praecursor*). The population structure is demonstrated in the size frequency plots and curve fitting (Fig. 8). Irrespective of whether species had similar ecological traits or were assigned to the same genus, their respective populations apparently inhabited normal marine environments indicated by the curve that approximates to a normal distributions and is slightly right skewed.

4.4 Ecological effect on higher rank taxa

The end Ordovician mass extinction had, apparently, a limited ecological effect on brachiopods. However, a drastic turnover from the Ordovician to the Silurian brachiopod faunas did occur later, after the early Rhuddanian (Rong et al., 2013), because of the persistence of many Ordovician relicts immediately following the end Ordovician extinction (Baarli and Harper, 1986; Harper and Rong, 1995; Rong and Harper, 1999; Harper and Rong, 2001; Rong and Zhan, 2004; Rong et al., 2006, 2008a). This faunal turnover is signaled by a gradual decline in the strophomenides and orthides (characterized by a cardinal area, deltidiodont teeth, and simple brachial apparatus) and a proliferation of the pentamerides, atrypides and athyridides (with a palintrope, cyrtomatodont teeth, and relatively complex brachial apparatus) through long-ranging ecological adaptation together competition with changing environments and to a lesser extent other brachiopod taxa (Rong et al., 2008b). This major change is one of the most significant events in the history of Palaeozoic brachiopod evolution. As the turnover was a long-ranging process and occurred across Ordovician-Silurian boundary, what was the role of the end Ordovician mass extinction in the process?

The ecological effect of the biotic event on higher rank taxa with diversity information has been evaluated (McGhee et al., 2013). However, due to the difficulty of accessing abundance data, which contains more ecological information, these have not been involved in previous studies. Taking the study area as an example, the abundance data from both the upper Katian and brachiopods at the Ordovician-Silurian boundary is firstly compared together with diversity information, to detect the ecological effect of the event in this study (Fig. 9). The data for latest Hirnantian-earliest Silurian brachiopods are derived from the *Cathaysiorthis* fauna (Rong et al., 2013) and data for the upper Katian brachiopods are updated from Zhan and Cocks (1998).

From the simple pie charts, the diversity of both brachiopod groups is similar except that strophomenides significantly dropped their quotient. The difference is clearly displayed on the abundance pie chart. The abundance distribution for the *Cathaysiorthis* fauna is coherent with its diversity rank whereas there is a decoupling of abundance and diversity for upper Katian brachiopod assemblages. The highly abundant rhynchonellides, pentamerides and atrypides which demonstrate a low diversity, were significantly less dominant following the end Ordovician mass extinction in the area, possibly indicating that this newly evolved group had limited adaptive abilities compared with those typical Ordovician components. Actually, the typical Silurian group has a well-defined and invariant life strategy, such as those in the *Borealis* and *Virgiana* community, which flourished in the early Silurian that are very similar to their progenitors in the *Deloprosopus* community. The newly evolved progenitors commonly thrived as only one or two species representing the higher taxonomic (ordinal level) they occupied in the community before the end Ordovician mass extinction. Taking the vast majority of the upper Katian brachiopods as an example, rhynchonellides *Altaethyrella zhejiangensis* (33.9% of the total, representing the only species of Rhynchonellida in the fauna), pentamerides *Deloprosopus jiangshanensis* (16.2% of the total, representing the only species of Pentamerida in the fauna), and atrypides *Antizygospira liquanensis* (8.6% of the total), all went extinct during the first episode of the biotic crisis. In the study area, the ecological effect of the biotic event apparently focused on the newly-evolved progenitors. These progenitors decreased in both population size (lower abundance) and body size across the end Ordovician mass extinction (see Huang et al., 2010) while some Ordovician relics increased in both individual and population size, such as *Levenea llandoveriana*, thriving as opportunists during the earliest Silurian.

The extinction of the majority of the fauna signposts the disappearance of the typical community they represented. But with the lack of evidence for more severe ecological impact than community replacement, McGhee et al. (2012, 2013) attributed the ecological severity of the end Ordovician mass extinction to a level two ecological loss, defined by Droser et al. (1997). Although the community replacement was drastic, the benthic regimes did not shrink their reach or widths. The decoupling between clear diversity loss and limited ecological severity may thus suggest a resilience already acquired by the Paleozoic evolution fauna. The benthic environment which was crowded before the end Ordovician mass extinction released more niches during the event, and new communities with lower diversity were distributed across each benthic regime. For the brachiopods in the study area, marked changes in the composition of the Late Ordovician and earliest Silurian brachiopod faunas include, firstly removal of the late Katian deeper-water *Foliomena* fauna and the shallow-water *Altaethyrella* fauna (Rong et al., 1999; Zhan and Cocks, 1998), along with the appearance of the *Hirnantia* fauna in other regions (Rong and Harper, 1988); secondly the demise of the *Hirnantia* fauna as a whole in the late Hirnantian (Rong, 1979, 1984; Rong and Harper, 1988) which is not recorded in the immediate study area, and thirdly the diachronous replacement by the *Cathaysiorthis* fauna in both shallower and deeper water during the late Hirnantian – earliest Rhuddanian (Zeng and Hu, 1997; Rong and Zhan, 2006; Rong and Huang, 2007; Huang, 2008; Rong et al., 2008b).

Since typical Silurian brachiopods such as atrypides, athyridides and pentamerides commonly lived in shallow-water carbonate regimes, deep-water, silciclastic regimes continued to be occupied by Ordovician types (strophomenides and orthides) both before and after the end Ordovician mass extinction (see also Harper and Rong, 2001). Rapid recovery of the deep-water benthos after the extinction indicates that strophomenides and orthides (containing deep-water taxa) recovered faster than the typical Silurian brachiopods (thriving until the late Rhuddanian). For those brachiopods above (represent specimens are shown in Fig. 10), the deep-water *Foliomena* fauna, was partially replaced by deep-water *Leangella-Aegiromena* association in the *Cathaysiorthis* fauna, both are dominated by strophomenides. The quick recovery also suggests limited the ecological severity of the end Ordovician mass extinction. A rapid palaeogeographical proliferation of brachiopods after the early Rhuddanian also support existence of a robust ecological structure of brachiopod faunas immediately after the extinction (Huang et al., 2012). The end Ordovician only delayed the ongoing process of the replacement of the Ordovician brachiopod fauna by Silurian brachiopods.

5. Conclusions

A substantial dataset of early Silurian brachiopods from South China suggests very minimal ecological disruption occurred in the aftermath of the end Ordovician extinction events. Recovery was rapid. A similar depth zonation and pattern of brachiopod assemblages along an onshore offshore gradient to that in the late Katian is established for the latest Ordovician–early Silurian (post-extinction fauna) using a range of multivariate techniques. Within this ecological structure, the deeper-water faunas are partially replaced by new players, the siliciclastic substrates continued to be dominated by more ‘Ordovician’ elements such as the orthides and strophomenides and shallow-water carbonate environments hosted atrypides, athyridides and pentamerides. These data suggest too that the more typical Ordovician brachiopod fauna continued to dominate until the late Rhuddanian when more Silurian type assemblages invaded the oceans. Significantly the end Ordovician extinctions tested the resilience of the brachiopod fauna without damage to its overall ecological structure.

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Figure captions:

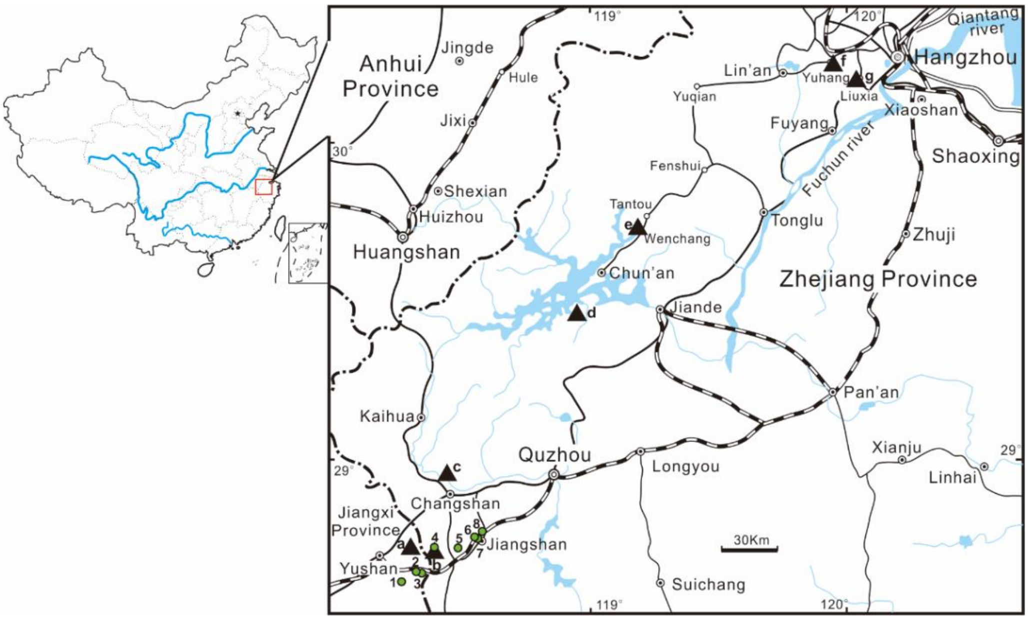

Fig. 1. Location map of the Upper Katian and Ordovician–Silurian boundary strata sections in the Zhejiang–Jiangxi border region, Southeast China. Triangles represent

lower Rhuddanian (a–f) and upper Hirnantian (g) localities, circles represent upper Katian (1-8) localities (used in discussion section). Ordovician–Silurian boundary strata are: a, Shangwu (AFL67, 68), Yushan, Jiangxi Province; b, Jianshan at Daqiao, Jiangshan (AFL30); c, Tongjia, Changshan (AFL2); d, Dakenwu (AFL159, 161) of Lishang, Chun’an; e, Wenchang (AFL130, 140) at Tantou, Chun’an; f, Laojiaoshan (AFL310) at Liuxia, Yuhang; g, Tangshan (AFL303–296), Yuhang (b-g from Zhejiang Province). Upper Katian localities are: 1, Zhuzhai, Yushan; 2, Tashan, Yushan; 3, Shiyanshan, Yushan; 4, Dianbian, Jiangshan; 5, Mulinlong, Jiangshan; 6, Wujialong, Jiangshan; 7, Pengli, Jiangshan; 8, Shangwu, Jiangshan (1-3 from Jiangxi Province, 4-8 from Zhejiang Province). Revised from Huang et al., 2010.

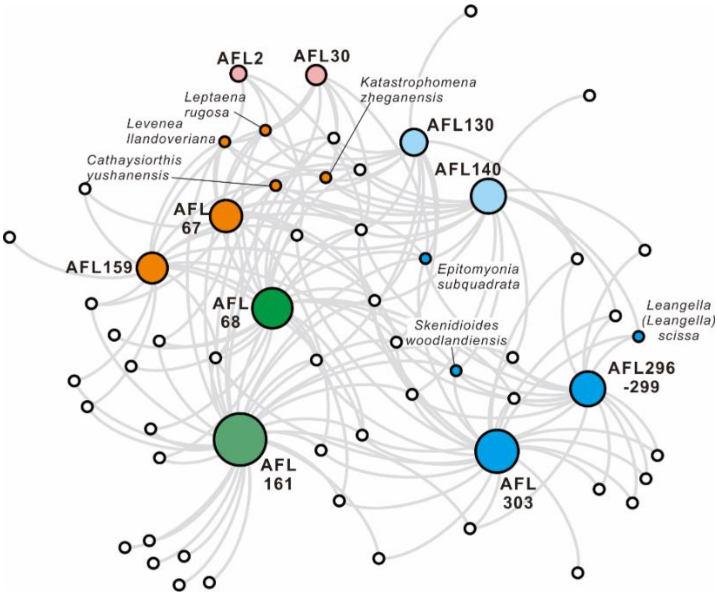

Fig. 2. The network diagram generated by NA shows an overview of the *Cathaysiorthis* fauna.

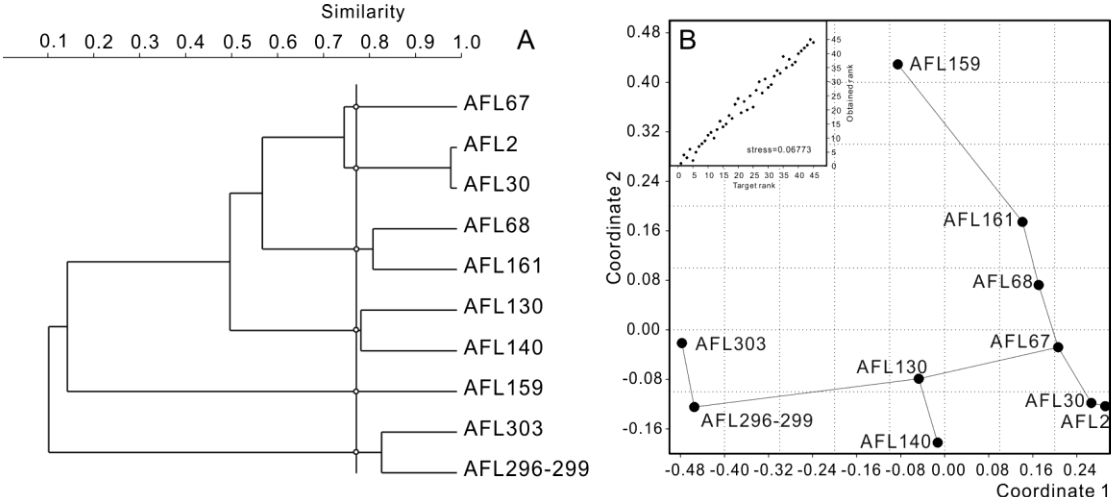

Fig. 3. The results of cluster analysis (CA) (A) and NMDS (B) for the 10 collections of the *Cathaysiorthis* fauna. Six brachiopod associations were consistently recognized.

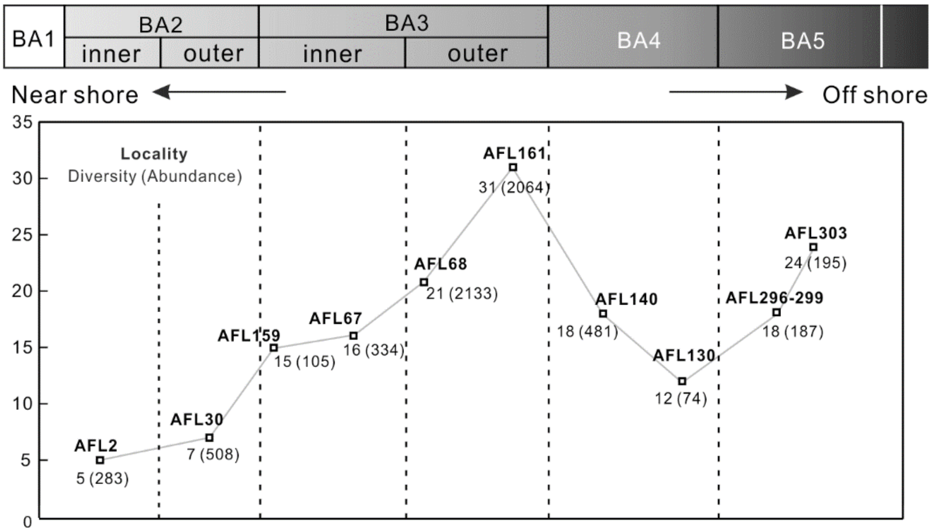

Fig. 4. Assignments of Benthic Assemblage Zones to various brachiopod collections through the Ordovician–Silurian boundary strata in the study area. The diversity and number of specimens (in brackets) are superimposed on the chart. Revised from Rong et al. (2013).

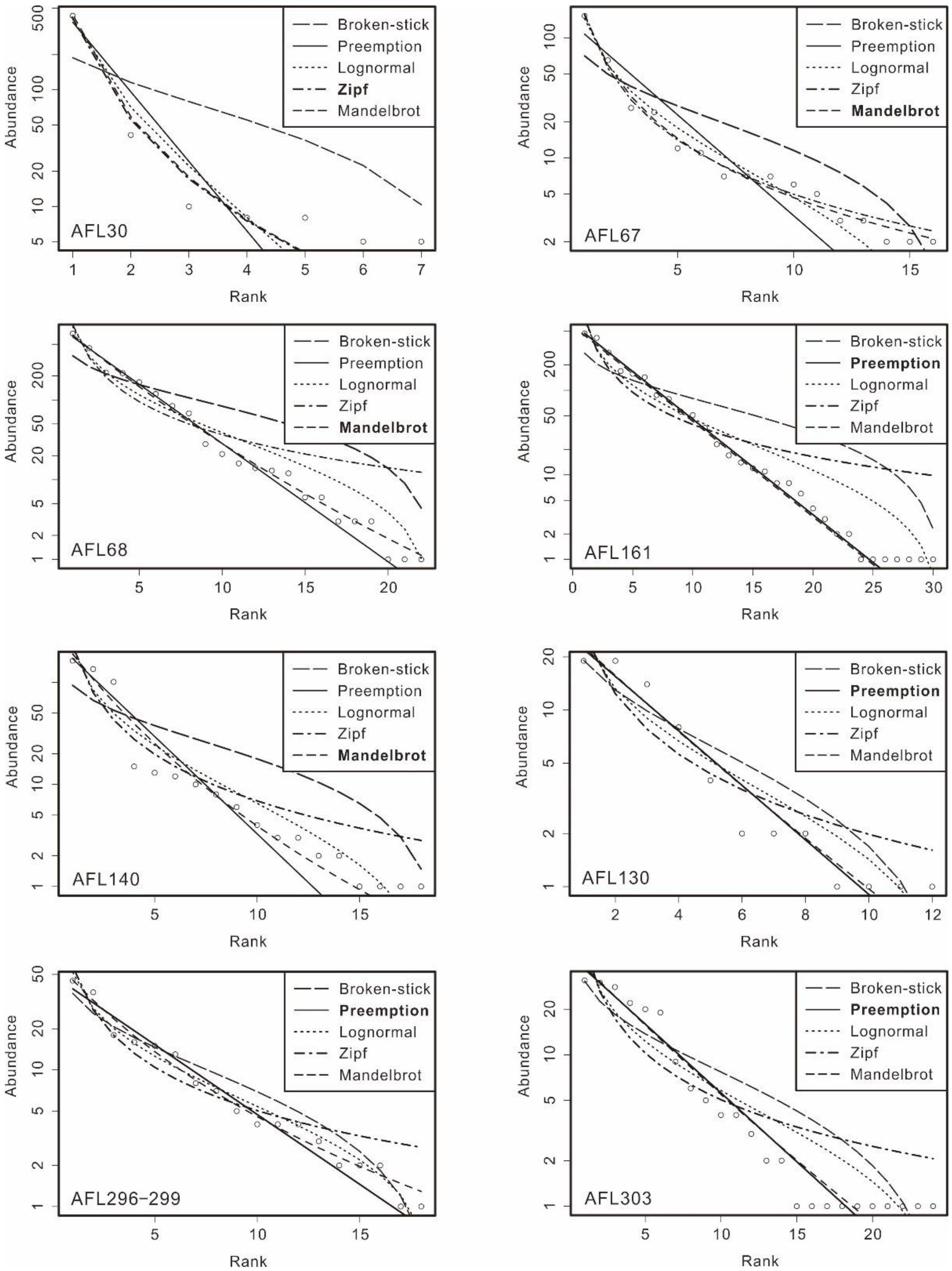

Fig. 5. Curve fitting for the 5 abundance models for the 8 collections of the *Cathaysiorthis* fauna, curves in bold represent the best fit model for the collection. Subfigures for AFL30, 68, 161, 303 are from Huang and Zhan, 2014.

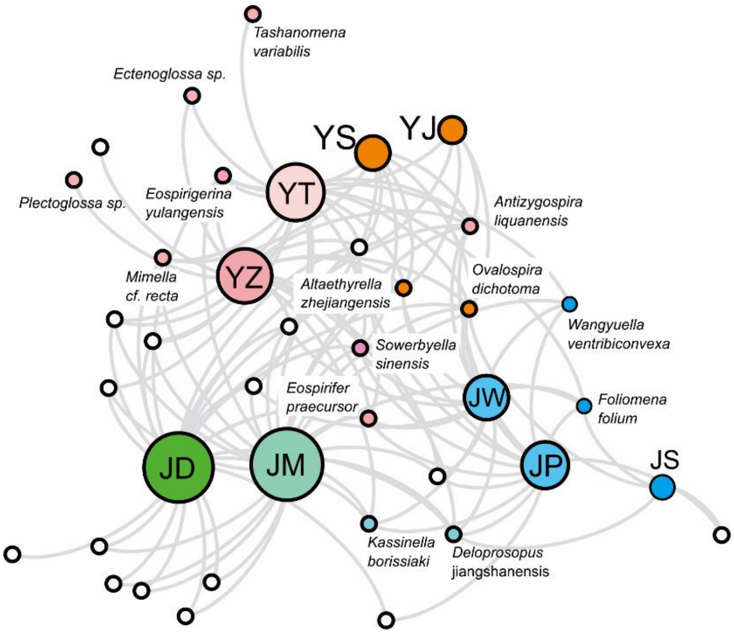

Fig. 6. The network diagram generated by NA shows an overview of the brachiopods from the upper Katian in the study area. Abbreviation for localities: YZ: Zhuzhai, Yushan; YT: Tashan, Yushan; YS: Shiyanshan, Yushan; YJ: Jitoushan, Yushan; JD: Dianbian, Jiangshan; JM: Mulinlong, Jiangshan; JW: Wujialong, Jiangshan; JP: Pengli, Jiangshan; JS: Shangwu, Jiangshan. Data updated from Zhan and Cocks, 1998.

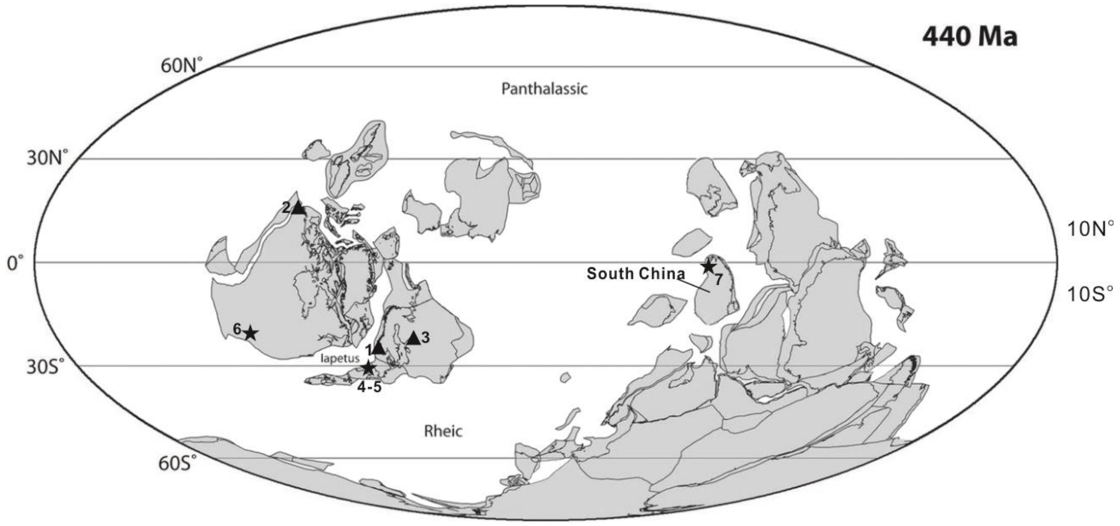

Fig. 7. Selected early Llandovery brachiopod localities plotted on the 440 Ma global

palaeogeographic reconstruction based on Rong and Cocks (2014), showing deeper-water (triangles) and highly diversified brachiopod faunas (stars): 1, Oslo Region, Norway; 2, Mackenzie Mountains, Canada; 3, Estonia; 4, Llandovery, Wales; 5, Meifod, Wales; 6, Oklahoma, Illinois and Missouri, USA; 7, Southeast China.

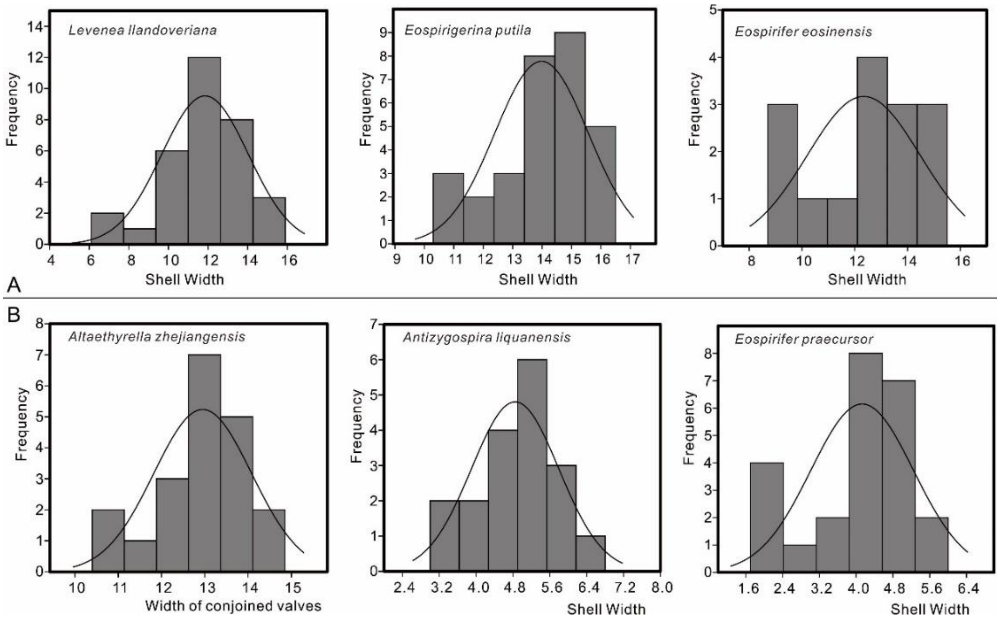

Fig. 8. Size frequency analyses for brachiopods from Ordovician-Silurian boundary sections (A) and upper Katian (B) of study area. The size frequency distribution of each genus fits closely the normal distribution.

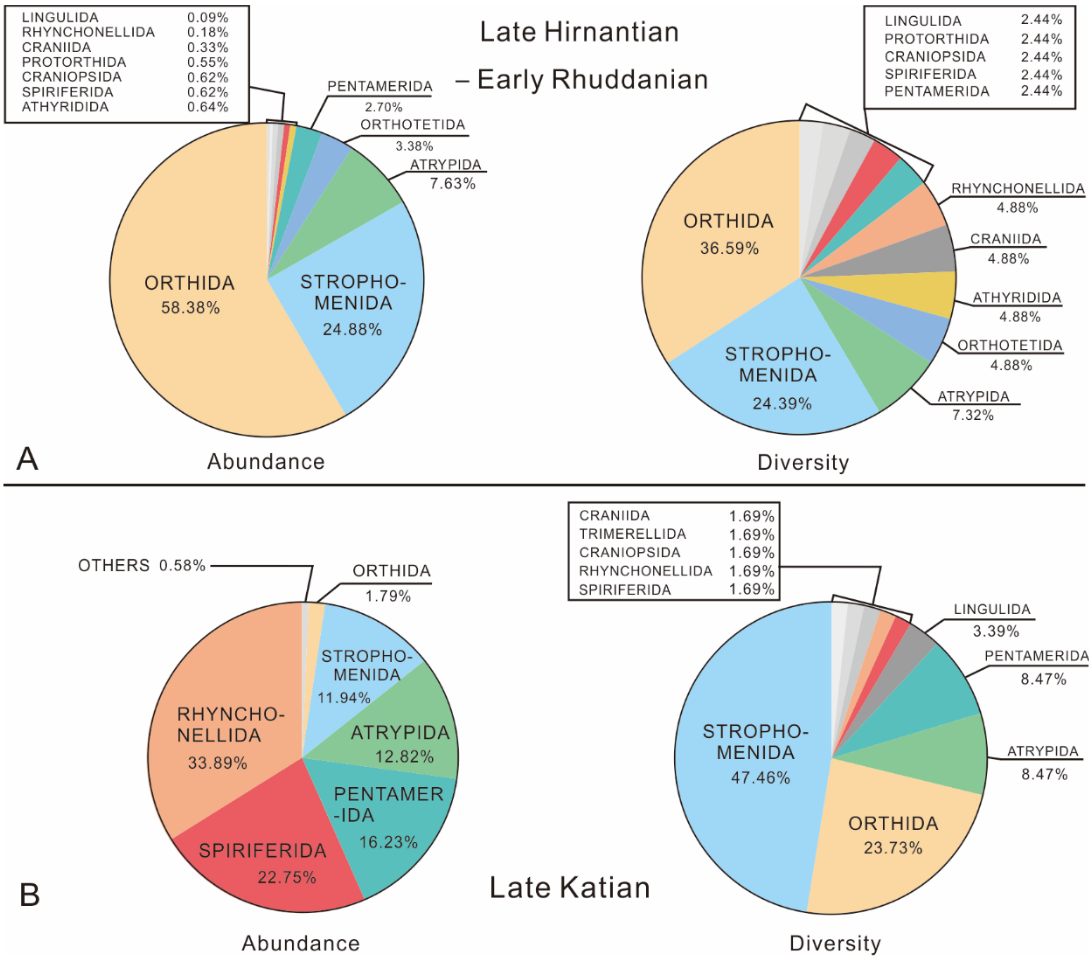

Fig. 9. Diagram showing the generic (diversity) and specimen (abundance) percentages of various major groups of late Hirnantian and early Rhuddanian brachiopods (the *Cathaysiorthis* fauna), and late Katian brachiopods in the Jiangnan Region, Southeast China. A and right part of B are revised from Rong et al., 2013.

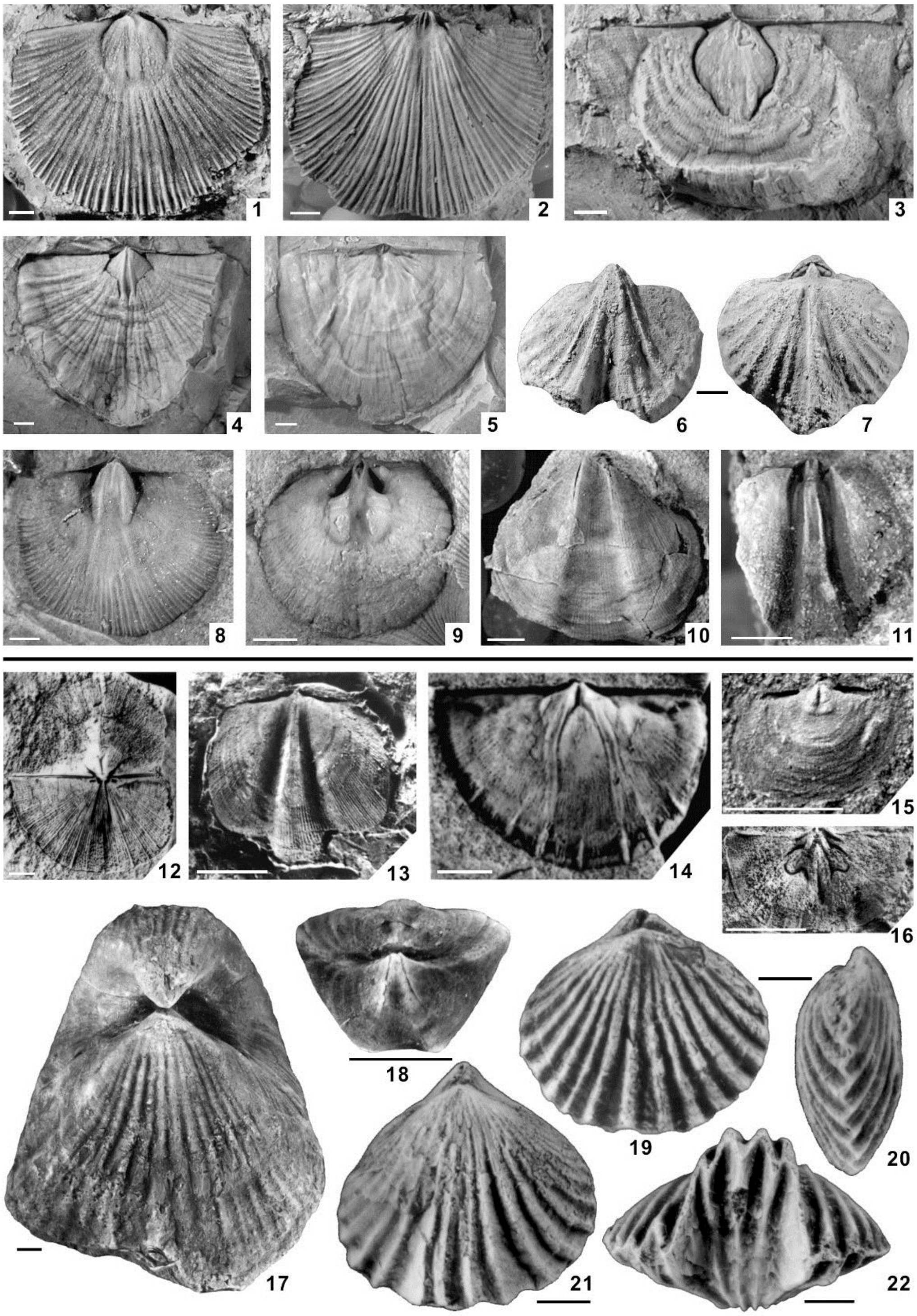

Fig. 10. Selected representative or comparable components of brachiopod faunas from lowest Silurian (1-11) and upper Katian (12-22). 1, 2. *Cathaysiorthis yushanensis* (Zeng and Hu, 1997); 1, ventral internal mould (NIGP148361); 2, dorsal internal mould (NIGP 148369); both from AFL68. 3. *Leptaena rugosa* Dalman, 1828, ventral

internal mould (NIGP152557, AFL68). 4, 5. *Katastrophomena zheganensis* Rong et al., 2013; 4, ventral internal mould (NIGP151731); 5, dorsal internal mould (NIGP151737); both from AFL68. 6,7. *Eospirigerina putilla* (Hall and Clarke, 1894); ventral and dorsal views of an internal mould of conjoined valves (NIGP 152759, From AFL161). 8, 9. *Levenea llandoveriana* (Williams, 1951); 8, ventral internal mould (NIGP152640); 9, dorsal internal mould (NIGP142255); both from AFL30. 10, 11. *Eospirifer* (*Eospirifer*) *eosinensis* Rong et al., 2013; 10, ventral internal mould (NIGP 139428, AFL68); 11, dorsal internal mould (NIGP139429, AFL67). 12, *Sowerbyella sinensis* Wang, 1964, conjoined internal moulds (NIGP128061); Xiazhen Formation, Daqiao, Jiangshan County. 13, 18. *Eospirifer* (*Protospirifer*) *praecursor* Rong et al., 1994; 13, dorsal internal mould (NIGP118704), Changwu Formation, Pengli, Jiangshan County; 18, posterior view of conjoined valves showing dental plates (NIGP124756), Xiazhen Formation, Zhuzhai, Yushan County. 14. *Kassinella shiyangensis* Zhan and Cocks, 1998, ventral internal mould (NIGP128057); Xiazhen Formation, Shiyang, Jiangshan County. 15. *Foliomena folium* (Barrande, 1879), ventral internal mould (NIGP128080); Changwu Formation, Shangwu, Jiangshan County. 16. *Tashanomena variabilis* Zhan and Rong, 1994, dorsal internal mould (NIGP121553); Xiazhen Formation, Tashan, Yushan County. 17. *Deloprosopus jiangshanensis* (Liang in Liu et al., 1983), dorsal view of conjoined valves (NIGP128087); Xiazhen Formation, Zhuzhai, Yushan County. 19, 20. *Ovalospira dichotoma* Fu, 1982, dorsal and lateral view of conjoined valves (NIGP128099); Xiazhen Formation, Xiazhen, Yushan County. 21, 22. *Altaethyrella zhejiangensis*

(Wang, 1964); 21, dorsal view of conjoined valves (NIGP128092); 22, anterior view of conjoined valves (NIGP128091); Xiazhen Formation, Xiazhen, Yushan County. Scale bars represent 2 mm for all.

Table Captions:

	Shallow-water taxa			Deep-water taxa		
	Katastrophomena zheganensis	*Leptaena rugosa*	*Levenea llandoveriana*	*Leangella (Leangella) scissa*	*Skenidioides woodlandiensis*	*Epitomyonia subquadrata*
AFL303	0.00%	0.00%	0.00%	15.38%	1.54%	10.26%
AFL296-299	0.00%	0.00%	0.00%	19.79%	2.14%	24.06%
AFL130	2.70%	1.35%	25.68%	0.00%	0.00%	18.92%
AFL140	0.83%	0.62%	28.07%	1.66%	0.62%	2.49%
AFL161	22.77%	6.93%	20.25%	0.00%	1.11%	0.53%
AFL68	10.36%	21.00%	31.93%	0.00%	0.14%	1.31%
AFL67	7.78%	3.59%	45.51%	0.00%	0.00%	2.10%
AFL30	0.98%	8.07%	84.84%	0.00%	0.00%	0.98%
AFL2	0.00%	0.71%	97.88%	0.00%	0.00%	0.00%

Table 1. Proportion of the selected species from the 10 collections that support the assignment of a benthic assemblage.

				AIC Values				
	Abundance	Diversity	Benthic Assemblage	broken-stick	pre-emption	Zipf	Mandelbrot	log-Normal
AFL30	508	7	BA2	542.76	151.64	**55.64**	57.64	101.04
AFL67	334	16	BA3	198.87	125.83	82.58	**73.21**	74.31
AFL68	2133	22	BA3	1049.83	163.13	506.59	**157.80**	284.11
AFL161	2063	30	BA3	1094.45	**165.39**	675.77	169.38	402.53
AFL140	481	18	BA4	379.02	141.98	208.57	**132.85**	180.12
AFL130	74	12	BA4	47.90	**43.45**	55.26	47.38	51.02
AFL296-299	187	18	BA5	78.36	**73.73**	84.76	74.96	75.30
AFL303	195	24	BA5	117.40	**89.81**	135.61	93.50	115.07

Table 2. Abundance, diversity, and AIC values of five abundance models for eight collections of *Cathaysiorthis* fauna. AICs in bold represent the corresponding model

is the best fit for the collections.