Early–Middle Ordovician brachiopod diversification in the middle Yangtze region of South China

<table>
<thead>
<tr>
<th>Journal:</th>
<th>Canadian Journal of Earth Sciences</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manuscript ID</td>
<td>cjes-2019-0141.R3</td>
</tr>
<tr>
<td>Manuscript Type:</td>
<td>Article</td>
</tr>
<tr>
<td>Date Submitted by the Author:</td>
<td>18-Jan-2020</td>
</tr>
<tr>
<td>Complete List of Authors:</td>
<td>Song, Zhenyu; Yangtze University, Geosciences School Xiao, Yunpeng; Yangtze University, Geosciences School Xiao, Chuantao; Yangtze University, Geosciences School</td>
</tr>
<tr>
<td>Keyword:</td>
<td>Brachiopods, richness trends, The Great Ordovician Biodiversification Event, global comparison of diversity curves, controlling factors of richness</td>
</tr>
<tr>
<td>Is the invited manuscript for consideration in a Special Issue?</td>
<td>Not applicable (regular submission)</td>
</tr>
</tbody>
</table>
Early–Middle Ordovician brachiopod diversification in the middle Yangtze region of South China

Zhenyu Song, Yunpeng Xiao, Chuantao Xiao*

Geosciences School of Yangtze University, Wuhan, Hubei 430100, China

*Corresponding author: Chuantao Xiao, E-mail: ctxiao@yangtzeu.edu.cn, Tel: +8618986663388

Abstract

The evolution of the Early–Middle Ordovician brachiopod diversity in the middle Yangtze region of South China has been analyzed. The brachiopods in this region originated in the early Tremadocian and radiated from the late Floian to the late Dapingian. The composition of rhynchonelliformean brachiopods underwent major changes in the late Floian, and endemic genera migrated from the upper Yangtze region to replace the cosmopolitan genera. A global comparison of the brachiopod diversity curves of South China, Laurentia and Baltica reveals that (1) the processes and scales of brachiopod radiation in different paleocontinents were distinct; (2) unlike the global evolution of graptolites and chitinozoans, the correlation between brachiopod diversification and regional habitat change was more obvious, and the impact of habitat heterogeneity was reflected not only between plates but also in the interior of the plates, such as the closely connected middle and upper Yangtze regions of South China; and (3) geographical isolation was a key factor in the differential radiation on different paleocontinents.
1. Introduction

The Great Ordovician Biodiversification Event (GOBE) represented a dramatic increase in global metazoan diversity (Sepkoski and Sheehan, 1983), one of the major events in marine organism evolution, and this event facilitated the vast ecosystem change that paved the way for the Paleozoic Evolutionary Fauna (Sepkoski, 1981). In recent years, the GOBE has received considerable attention. Stigall et al. (2019) suggested using “Ordovician Radiation” when referring to the broader diversification that occurred throughout the Ordovician and restricting the term “GOBE” to indicate the rapid diversification and ecosystem change centered on the Darriwilian Age. The GOBE took place during a short period spanning just 15 Myr (Rasmussen et al., 2019). The causes and controlling factors of this event are the focus and primary challenge of current GOBE research. A series of theoretical results on environmental factors have been proposed, such as cooling climate (Trotter et al., 2008; Rasmussen et al., 2016), increased oxygenation (Edwards et al., 2017), increased rock volume (Rasmussen et al., 2019), increased nutrient supply (Stigall et al., 2019), plate tectonic movements (Zaffos et al., 2017), and extraterrestrial material impact (Schmitz et al., 2008, 2019), which reflect the complexity of the occurrence of the GOBE. During the GOBE, brachiopods replaced trilobites as the dominant species in the early Paleozoic fauna (Zhan et al., 2005). Brachiopod fossils make up one of the most complete fossil records preserved during the GOBE (Harper and Servais, 2013). Therefore, the changes in habitat reflected by their evolution can provide a basis for GOBE research.

A number of scholars have conducted meticulous research on the evolution of Early–Middle
Ordovician brachiopod diversity in various regions, including Baltica, Laurentia and the upper Yangtze region of South China (Zhan, 2003; Zhan et al., 2005; Rasmussen et al., 2007; Hansen and Holmer, 2010; Trubovitz and Stigall, 2016, 2018; Stigall, 2018). Research on Early–Middle Ordovician brachiopods in the middle Yangtze region has been performed previously (Xu and Liu, 1984; Wang S, 1984; Zeng et al., 1987, 1991; Zhu et al., 1990). Some scholars have also discussed the evolution of brachiopod diversity in certain sections or formations, such as the Huanghuachang section in Yichang (Zhan and Harper, 2006; Zhan and Chen, 2006; Zhan et al., 2007, 2010), but there are still some sections rich in brachiopod fossils that have not been reported, and there is no specific paper that discusses the evolution of Early–Middle Ordovician brachiopod diversity throughout the whole region.

To study the form and scale of the evolutionary radiation of Early–Middle Ordovician brachiopods in the middle Yangtze region, three stratigraphically complete, fossil-rich sections with good exposure (Zeng et al., 1987; Zhu et al., 1995) were selected. The diversity and evolution of brachiopods in the study area were analyzed using range-through richness. The results of the analyses were compared with other regions to analyze the characteristics and controlling factors of the evolution of brachiopod diversity in the Early–Middle Ordovician.

2. Geological background

South China was located on the western edge of Gondwana during the Ordovician (Fortey and Cocks, 2003) and had completely rifted away from Gondwana by the middle Devonian (Zhang et al., 2013). The main tectonic units of South China include the Yangtze and Cathaysia blocks (Zhou et al., 2017). The middle Yangtze region is located in the central part of the Yangtze block and is separated from the lower and upper Yangtze regions to the east and west by the Tanlu and Qiyueshan faults, respectively (Mei et al., 2008). This region includes most of Hubei Province and northwestern Hunan Province in terms of the
present administrative division (Fig. 1). The area is topographically complex and diverse, with hills, uplands, plains and, especially, mountains. Structurally, the area can be divided into the Jianghan Plain and the western Hunan and Hubei areas, with a total region of approximately 155,000 km$^2$. The region is divided into eastern and western parts by the Huangling uplift, and both parts are subjected to the combined action of the Qinling-Dabie orogenic belt and the Jiangnan uplift. The strong differential fault depression in the Paleozoic–Mesozoic periods caused the structure of the region to become more complicated than that of the upper Yangtze region (Guo et al., 2006). The evolution of the basin in the middle Yangtze region occurred during two periods in the Ordovician: the Caledonian craton developed during the Early–Middle Ordovician, and the foreland basin developed during the Late Ordovician (Zhou, 2015). With the continuous expansion of the South China Sea from the late Ediacaran to the Middle Ordovician, the area extensively subsided and accumulated shallow-water carbonate deposits with a thickness of 2000–4000 m, and then, during the Late Ordovician, it developed deep-water deposits (Xiao et al., 1996, 2006; Xu et al., 2004; Gao et al., 2008).

3. Materials and methods

Based on previous studies (Zeng et al., 1987; Zhu et al., 1995; Xiao et al., 2018) and recent field sampling analyses, the current study selected well-exposed, fossil-rich Ordovician strata in the Huanghuachang section in Yichang, the Liujiachang section in Songzi and the Huaqiao section in Changyang to conduct fieldwork. The Lower Ordovician strata from the bottom up include the Nanjinguan Formation, the Fenxiang Formation and the Honghuayuan Formation, and the Middle Ordovician strata include the Dawan Formation and Guniutan Formation. The Early–Middle Ordovician conodont species in this region present the same characteristics as conodonts from the same period in the Yangtze-Southwest China region, and the main species are basically comparable to those of the North Atlantic conodont realm (Zeng et al., 1987). Furthermore, these conodont zones are more continuous than the graptolite zones in the
region. Therefore, the Lower and Middle Ordovician strata in the region are divided into the Tremadocian, Floian, Dapingian, and Darriwilian with ten conodont zones. The stratigraphic, lithological and fossil data from the Liujiachang section in Songzi are mainly from Zhu et al. (1995). The specimens mentioned in the monograph are stored in the Geosciences School of Yangtze University. The data from the Huanghuachang section in Yichang and the Huaqiao section in Changyang are from Wang et al. (1987). The brachiopod specimens mentioned in the monograph are stored in the Wuhan Center of China Geological Survey. To ensure the accuracy of the data, we carefully compared the details of the brachiopod charts with their descriptions, and the taxonomic information for the brachiopods was revised according to Rong et al. (2017). We also went into the field to verify the three sections, and thus, the data used in this paper are reliable. The biostratigraphic measurement methods applied to the three sections were the same, and fossil collection of multiple phyla was carried out. Fossils in the shelly facies strata were collected at an interval of 20–50 cm, while fossils from the graptolite facies strata were collected at an interval of 2–10 cm, and continuous collection was carried out near the formation boundaries (Wang et al., 1987; Zhu et al., 1995), thereby obtaining the stratigraphic distribution of brachiopods. The data from the three sections were integrated and binned by time slices (Webby et al., 2004), with the conodont zones of the middle Yangtze region and the stage slices partitioning for the Ordovician introduced by Bergström et al. (2009) as additional stratigraphical controls. This process allowed the chronological distribution of brachiopod species from the Tremadocian to the Darriwilian to be obtained. We applied range-through richness to calculate the total diversity ($N_{tot}$), estimated mean standing diversity ($N_{emsd}$), number of originations ($N_o$) and number of extinctions ($N_e$) at the species level and genus level after Cooper (2004) to analyze the evolution of brachiopod diversity.
4. Results

4.1. Stratigraphic distribution of brachiopods

4.1.1. Huanghuachang section in Yichang

The Huanghuachang section is the Global Stratotype Section and Point (GSSP) for the Lower–Middle Ordovician boundary (Wang X et al., 2005). The section is located on the eastern flank of the Huangling anticline and was located on the north–central part of the Yangtze carbonate platform during the Ordovician Period. The Lower–Middle Ordovician strata in the section are approximately 247.9 m thick. The overall lithology is dominated by limestone; there are also several layers of dolomite in the lower part, and the contents of biolithite and mudstone gradually increase in the upper part (Fig. 2).

The earliest brachiopods in the section were found in the lower section of the Nanjinguan Formation. A total of seven species assigned to six genera were identified; these brachiopods are typically fragmented and are dominated by *Tritoechia abnormis*. The Fenxiang Formation limestone features some interbedding with mudstone. There were few macrofossils in the lower section, with only a few fragments of brachiopods such as *Tritoechia* and *Disepta*. In the upper section, 13 brachiopod species assigned to four genera were identified, including *Tritoechia*, *Nanorthis*, *Eopunctata* and *Punctolira*. In particular, *Tritoechia* reached peak abundance in this section, and the bioclastic limestone in these strata is mostly composed of this genus. With the exception of *Eopunctata*, the other genera are important members of the Canadian Stage brachiopod assemblage in North America (Zeng et al., 1987). The lithology of the Honghuayuan Formation is relatively simple and is primarily composed of cephalopod–sponge limestone. The representative brachiopod genera in the Honghuayuan Formation are extended from the Fenxiang Formation.

The Dawan Formation represents a very important developmental stage in the Ordovician on the
Yangtze Platform. Fossils of various species are highly abundant in this area, and members of both the Atlantic and Pacific provinces appeared simultaneously (Zeng et al., 1987). The brachiopods are particularly abundant in the lower section. The most important feature is, however, the near absence of all genera in the strata underlying the Ordovician strata, with the exception of a small number of *Tritoechia*; these genera were replaced by 11 new genera, including *Leptella*, *Nereidella*, *Yangtzeella*, *Sinorthis*, *Mimella*, *Euorthisina*, *Pseudoporambonites*, etc. The middle section is dominated by cephalopods, with only three brachiopod genera, *Yangtzeella*, *Nereidella*, and *Sinorthis*. In the upper section, 30 brachiopod species assigned to 16 genera were identified and all share continuity with, but exhibit obvious differences from, those in the lower two sections. *Tritoechia*, *Nereidella*, *Yangtzeella*, *Mimella*, *Euorthisina*, *Sinorthis* and *Martellia* extend from the lower section, while *Nereidella*, *Euorthisina*, *Martellia* and *Yangtzeella* continue to be abundant. In addition to the above genera, *Eremotoechia*, *Protoskenidiodes*, *Skenidioides*, *Lepidorthis*, *Atelelasmoidea*, *Diorthelasma*, *Sulcatorthis*, *Nicoledoidea* and *Orcicoloides* are present as well. Notably, brachiopods are highly abundant in the upper section of the Dawan Formation, but only *Nereidella* and *Yangtzeella* are present in the Guniutan Formation micritic limestone, all other genera having disappeared (Fig. 2).

### 4.1.2. Huaqiao section in Changyang

The Huaqiao section is located 15 km south of Changyang County. The Lower–Middle Ordovician strata in the section are 246.8 m thick. Brachiopods are rare, with 15 identified species assigned to 13 genera (Fig. 3). The earliest brachiopods identified in the section are *Stichotrophia* fragments in the lower section of the Nanjinguan Formation. The lithology and thickness of the Fenxiang Formation are similar to those of the Huanghuachang section. Only *Tetralobula fenxiangensis* is present in the lower section. The composition of brachiopods in the upper section is essentially the same as that of the Huanghuachang section, with
Tritoechia, Nanorthis and Eopunctata being the main genera that extend upwards to the clastic limestone of the Honghuayuan Formation. The Dawan Formation also contains new brachiopod fauna, including Leptella, Nereidella, Yangtzeella, Sinorthis, Mimella, Euorthisina, and Pseudoporambonites (Fig. 3).

4.1.3. Liujiachang section in Songzi

The Ordovician stratigraphic sequence of the Liujiachang section is the same as that in the Three Gorges region; only the Upper Ordovician Wufeng Formation is missing. The lithology of the Lower–Middle Ordovician strata is dominated by thick (428 m) carbonate deposits with intercalated shale or calcareous shale.

The Nanjinguan Formation in the Liujiachang section is characterized by the presence of shale in the lower section and abundant stromatolites in the middle section (Xiao et al., 2016, 2018). Brachiopods are mainly present in the shale of the lower section and include Nanorthis, Martellia, Siphonotreta, and Lingula. Among them, the Lingulida, as represented by Lingula, appears only in this section and extends to the lower section of the Dawan Formation. In other sections, Nanorthis and Martellia are present through to the upper section of the Fenxiang Formation and the lower section of the Dawan Formation, respectively. The middle–upper stromatolite and dolomite sections lack brachiopods, while the top of the formation is characterized by a large number of Tritoechia. The brachiopods in the Fenxiang Formation include Tritoechia, Sinorthis, Syntrophinella, Lingula and Martellia, which extend upwards from the underlying strata. The Honghuayuan Formation is characterized by the return of Nanorthis and the emergence of Paurothis. The main lithology of the Dawan Formation is argillaceous limestone. A total of 19 brachiopod species assigned to 10 genera, including Sinorthis, Paurothis, Pseudoporambonites, Lepidorthis, Yangtzeella and Martellia, were identified (Fig. 4).
4.2. Evolution of brachiopod diversity

A total of 67 brachiopod species were identified in the above three sections. The *Hirsutodontus simplex–Monocostodus sevierensis* Zone from the late Cambrian to the Early Ordovician corresponds to the dolomite facies, suggesting that the hot, dry and high-salinity environment was not suitable for the survival of brachiopods at that time. Therefore, no brachiopods were found in this zone. The brachiopods in the middle Yangtze region originated in the *Cordylodus angulatus–Sanxiagnathus sanxiaensis* Zone in the Tremadocian. In this zone, a total of nine species were identified. Among them, three species assigned to linguliformean brachiopods were observed: *Siphonotreta* and *Iphidella* are present in all three sections, while *Lingula* appears only in the Liujiachang section. Rhynchonelliformean brachiopods appeared in abundance in the early Tremadocian and include *Tritoechia, Martellia, Nanorthis, Stichotrophia* and *Punctolira*.

The radiation of brachiopods in the middle Yangtze region occurred during the late Floian to late Dapingian. During the late Floian, $N_{tot}$ and $N_{emsd}$ increased rapidly, and $N_o$ was much higher than $N_e$. Notably, this was an adjustment period and represented a major turning point in the composition of the brachiopod fauna, that is, the endemic genera replaced the cosmopolitan genera. With the exception of a small number of *Lingula, Tritoechia, Orthis* and *Nanorthis, Eopunctata* and *Punctolira* disappeared in the region, replaced by *Yangtzeella, Sinorthis, Martellia, Lepidorthis, Leptella* and *Schedophyla*. Among them, *Leptella* was the earliest Strophomenida in this region.

Both the generic and specific $N_{emsd}$ peaked in the Dapingian. *Diorthelasma, Nicoloidea, Sulcatorthis, Atelelasmoidea* and *Eremotoechia* all developed in the late Dapingian. Protorthida, represented by *Protoskenidiodes* and *Skenidiodes*, first appeared in the region. Until this time, all five orders of rhynchonelliformean brachiopods were present in this region in the Early–Middle Ordovician. In the
Darriwilian, the \( N_e \) was much higher than \( N_o \), the diversity of brachiopods began to decrease continuously, and only one species of *Yangtzeella* remained by the late Darriwilian.

Based on the distribution of brachiopods, the decrease in both the generic and specific \( N_{tot} \) in the early Dapingian was mainly caused by the disappearance of *Lingula*, *Yichangorthis*, *Schedophyla* and *Eosericoidea*, and a decrease in the species-level diversity of *Martellia*, *Mimella* and *Yangtzeella*. However, the key genera of the greater brachiopod faunal assemblage did not change much (Fig. 5), and the \( N_{emsd} \) continued to show an upward trend (Fig. 6). There are few brachiopods in the lower Dapingian strata of the Huanghuachang section in Yichang, but cephalopods are abnormally abundant (Zeng et al., 1987). Therefore, it is speculated that the environment in this period was suitable for cephalopods but not conducive to the survival of brachiopods, and the decrease in \( N_{tot} \) was possibly caused by environmental fluctuations. This hypothesis will be pursued in further studies. However, the brachiopod radiation can certainly be considered one long, continuous event through the late Floian–early Darriwilian interval in the middle Yangtze region.

The Early–Middle Ordovician brachiopods in the middle Yangtze region included two subphyla: Linguliformea and Rhynchonelliformea. The linguliformean brachiopods mainly existed in the early Tremadocian, and *Lingula* persisted into the late Floian; only one species, *Orbiculoides huanghuaensis*, was present in the Middle Ordovician. The composition of the rhynchonelliformean orders Clitambonitidina, Orthida and Pentamerida underwent major changes in the late Floian, namely, endemic genera replaced cosmopolitan ones. Strophomenida and Protorthida began to appear in this region in the late Floian and late Dapingian, respectively.
5. Discussion

5.1. Comparison of the evolution of brachiopod diversity in different regions

In recent years, many scholars have summarized the diversity and evolution of brachiopods in the Early–Middle Ordovician in major regions around the world and drawn biodiversification curves for brachiopods in each region.

The brachiopods in the middle and upper Yangtze regions of South China had a certain degree of diversity in the Tremadocian and early Floian. The brachiopods in the middle Yangtze region began to radiate steadily in the middle Floian, reached a diversity peak in the Dapingian, and then gradually declined until the late Darriwilian, when all brachiopods disappeared in this region. The generic diversity of brachiopods in the upper Yangtze region increased steadily in the Tremadocian, and the radiation process accelerated in the early Floian, reaching a diversity peak in the late Floian and continuing until the early Sandbian (Zhan et al., 2005; Stigall et al., 2019). Compared to the middle Yangtze region, the upper Yangtze region featured an earlier start of the brachiopod radiation process, a much higher generic $N_{\text{tot}}$, and a longer duration of the diversification peak.

The northeastern Spitsbergen region and south-central Oklahoma were located in the northeastern margin and western margin of the Laurentia Plate, respectively, in the Early–Middle Ordovician, but the brachiopod evolutionary processes in these two regions were quite different (Hansen and Holmer, 2010; Trubovitz and Stigall, 2018). The brachiopod diversity in the northeastern Spitsbergen region was low before the middle Floian, suddenly rose to a peak in the late Floian and continued until the middle Darriwilian. The radiation process and diversity of brachiopods in south-central Oklahoma were similar to those in the east Baltic region of the Baltica Plate: the diversity increased in a stepwise manner in the late...
Dapingian, experienced plateaus in the early Darriwilian and peaked in the middle Darriwilian (Rasmussen et al., 2007; Trubovitz and Stigall, 2016; Hints et al., 2018). The Baltic peak diversity seems more dramatic in the *holodentata* Zone as the sections are condensed, and the Darriwilian diversity decline was exacerbated by edge effects (Rasmussen et al., 2007; Trubovitz and Stigall, 2016); these processes are the reasons for the difference between the Laurentia and Baltica curves.

The above comparison demonstrates that the evolution of the Early–Middle Ordovician brachiopod diversity in different regions was not synchronous, except for south-central Oklahoma and the east Baltic region, where the trends were basically similar. In addition, the diachroneity – that is, the brachiopods in South China radiated earlier than those in other regions, discovered by Zhan and Harper (2006), Rasmussen et al. (2007) and Stigall et al. (2019) based on data from the upper Yangtze region – is reconfirmed. The brachiopod radiation in the middle Yangtze region began in the middle Floian, which is also earlier than that on other paleoplates.

### 5.2. Controlling factors for the evolution of brachiopod diversity

Trubovitz and Stigall (2016) compared the brachiopod evolutionary processes of south-central Oklahoma and the eastern Baltic region and concluded that their synchronicity was the result of global factors. However, through the comparison in the previous section, it was found that, unlike the global evolution of graptolites and chitinozoans (Zhang et al., 2007; Liang and Tang, 2016), the radiation processes and scales of Early–Middle Ordovician brachiopods in most regions were quite distinct.

Some scholars believe that global sea level changes may have been an important factor affecting Ordovician biodiversity (Winston and Zhang, 1995; Finney and Berry, 1997; Zhang et al., 2008). There were two global transgressions in the Early–Middle Ordovician: the first transgression occurred during the
Tremadocian, and another, large-scale, long-lasting transgression occurred from the Floian to the Darriwilian (Ross and Ross, 1992; Haq and Schutter, 2008; Rasmussen et al., 2019). However, the degree of brachiopod diversity before the middle Floian was generally low, indicating that the global transgression in the Tremadocian apparently failed to promote an increase in brachiopod diversity. Some scholars speculate that the climatic conditions in the Early–Middle Ordovician were responsible for the GOBE (Trotter et al., 2008; Giles, 2012). The results of paleogeography reconstructions show that during the Middle Ordovician, the Laurentia was located near the equator, South China was located at a middle–low latitude, and Baltica was located at a middle latitude (Scotese and Mckerrow, 1990). The south-central Oklahoma region of Laurentia and the east Baltic region of Baltica had similar brachiopod diversity curves, but South China, with a latitude intermediate between these two regions, had distinct curves. The above findings indicate that global factors can control the overall trend of Ordovician biodiversity but fail to explain more regional trends.

The radiation process of the Early–Middle Ordovician brachiopods in the middle Yangtze region has a certain degree of correspondence with sea level changes: the peaks of $N_{\text{tot}}$ in the late Floian and late Dapingian correspond to flooding periods in the region, and the diversity decline in the Darriwilian seems to be related to the sea level regression that began at the end of the Dapingian (Liu, 2006). This phenomenon also occurred in the Spitsbergen region, where evolutionary diversity lagged slightly behind sea level changes (Hansen and Holmer, 2010). The above phenomenon indicates that benthic brachiopods were sensitive to changes in water depth, and regional sea level change was indeed one of the causes of brachiopod radiation. However, the sea level curves do not correspond exactly to the brachiopod diversity curves. This could be caused by interference from artificial factors (such as sampling biases) or other regional environmental factors (such as climate conditions, seawater oxygen content, or nutrient supply).
Starting in the late Floian, endemic genera, such as *Yangtzeella, Sinorthis, Martellia, Lepidorthis, Leptella, and Schedophyla*, appeared in the middle Yangtze region of South China and gradually became dominant (Zeng et al., 1987). The species accumulation rate and evolution in the Baltica and Laurentia regions were similar, but there were significant differences among the endemic genera that were produced and dominated through the radiation interval (Rasmussen et al., 2007; Stigall, 2018). Following the Cambrian, the supercontinent Rodinia broke apart into many daughter continents, some of which formed Gondwana, while Laurentia and Baltica were in relatively isolated positions. South China was located on the western edge of Gondwana during the Ordovician (Fortey and Cocks, 2003). These three plates were clearly geographically isolated from each other. Therefore, as Valentine and Moores (1970) first proposed, geographical isolation is indeed a key factor in promoting speciation.

5.3. Causes of the differential evolution of brachiopod diversity in South China

The radiation of brachiopods began earlier in South China than in other regions. Rasmussen et al. (2007) proposed that this was due to the favorable environment caused by a low-temperature ocean current near the coastline of Gondwana. However, there were differences in the evolution of brachiopod diversity in the closely connected middle and upper Yangtze regions; the radiation process of brachiopods in the upper Yangtze region started earlier, and the generic \( N_{\text{tot}} \) was much higher than that in the middle Yangtze region.

Sedimentary facies analysis demonstrates that the first peak in brachiopod diversity in the middle Yangtze region corresponded to the open platform facies, and almost no brachiopods were present in the restricted platform facies or evaporite facies. The late Tremadocian to the middle Darriwilian was the main interval of brachiopod diversification in this region, and it also corresponded to the open platform deposition interval (Xiao et al., 1993, 2018). The upper Yangtze region featured an open platform facies during the early Floian and a shelf facies until the middle Darriwilian (Hu et al., 2018). The water depth in the upper
Yangtze region was also greater than that in the middle Yangtze region. In addition, the results of a paleogeography reconstruction have shown that during the Early–Middle Ordovician, the upper Yangtze region was located to the southwest of the middle Yangtze region, putting it deeper into the Tethys (Nie et al., 2015). According to the Early Ordovician global ocean current distribution (Wang C. and Wang X., 2011), after entering the Tethys, the West Wind Drift flowed north along the western coast of Gondwana and then quickly turned westward to form ocean circulation. The upper Yangtze region, which was located at a higher latitude and closer to the ancient continental margin subduction zone, was more exposed to low-temperature ocean currents carrying food resources (Rasmussen et al., 2007). The above evidence indicates that different seawater depths, along with the effects of ocean currents, were the causes of the differential evolution of brachiopods in South China.

The two regions have similar endemic genera (Zhan et al., 2005), but *Sinorthis, Martellia, Leptella* and *Schedophyla* appeared one graptolite zone later in the middle Yangtze region than in the upper Yangtze region, and *Yangtzeella* appeared three graptolite zones later. Therefore, it is speculated that these endemic genera originated in the upper Yangtze region and migrated to the middle Yangtze region as the water depth in the middle Yangtze region increased.

The above analysis suggests that the differences in the evolution of the Early–Middle Ordovician brachiopods in different regions were the result of a combination of many factors. Brachiopod diversity can increase rapidly in environments with adequate food resources and relatively high sea levels. The geographical isolation caused by continental break-up and plate drift was a key factor in the development of new species. The prosperity of the endemic genera in different regions during the GOBE and the subsequent migration of these genera greatly increased the complexity of the Ordovician global brachiopod fauna.
6. Conclusions

The brachiopods in the middle Yangtze region originated from the *Cordylodus angulatus*–*Sanxiagnathus sanxiaensis* Zone and radiated through the late Floian to the late Dapingian interval. The composition of rhynchonelliformean brachiopods underwent major changes in the late Floian: the endemic genera migrating from the upper Yangtze region replaced the cosmopolitan genera.

Comparison of the brachiopod diversity curves in multiple regions in South China, Laurentia and Baltica reveals that, unlike the global evolution of graptolites and chitinozoans, the processes and scales of Early–Middle Ordovician brachiopod radiation in different regions were noticeably different and that brachiopod radiation occurred earlier in South China than in other regions.

Compared with global environment changes, brachiopod diversification is more dependent on regional habitat conditions, such as seawater depth, ocean currents and environmental setting. The environmental heterogeneity caused by geographical isolation was the key factor in the differential radiation that occurred in different regions.

Acknowledgments

This work was supported by the National Natural Science Fund of China (grant number 41572322) and Hubei Innovation Group Fund (grant number 2015CFA024). We thank reviewers for the constructive reviews that greatly improved the manuscript.

References

Bergström, S.M., Chen, X., Gutiérrez-Marco, J.C., and Dronov, A. 2009. The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to δ13C


**Figure captions**

**Fig. 1.** Map of South China and the locations of the three Early–Middle Ordovician sections in the middle Yangtze region (modified from Zhang et al., 2002).
Fig. 2. Distribution of brachiopods in the Lower–Middle Ordovician of the Huanghuachang section, Yichang. I: *Eoplacognathus foliaceus* Zone; II: *Oepikodus evae* Zone; III: *Cordyloodus angulatus–Sanxiagnathus sanxiaensis* Zone; IV: *Hirsutodontus simplex–Monocostodus sevierensis* Zone.

Fig. 3. Distribution of brachiopods in the Lower–Middle Ordovician of the Huaqiao section, Changyang.

Fig. 4. Distribution of brachiopods in the Lower–Middle Ordovician of the Liujiachang section, Songzi. I: *Eoplacognathus foliaceus* Zone; II: *Oepikodus evae* Zone; III: *Cordyloodus angulatus–Sanxiagnathus sanxiaensis* Zone; IV: *Hirsutodontus simplex–Monocostodus sevierensis* Zone.

Fig. 5. Distribution of Early–Middle Ordovician brachiopods in the middle Yangtze region. Ts: time slices; Ss: stage slices; Prot: Protorthida; Stro: Strophomenida.

Fig. 6. Diversification curves of Early–Middle Ordovician brachiopods in the middle Yangtze region. Ts: time slices; Ss.: stage slices; \( N_{\text{tot}} \): total diversity; \( N_{\text{emsd}} \): estimated mean standing diversity; \( N_{o} \): number of originations; \( N_{e} \): number of extinctions.
Fig. 1. Map of South China and the locations of the three Early–Middle Ordovician sections in the middle Yangtze region (modified from Zhang et al., 2002).
Fig. 2. Distribution of brachiopods in the Lower–Middle Ordovician of the Huanghuachang section, Yichang. I: Eoplacognathus foliaceus Zone; II: Oepikodus evae Zone; III: Cordylodus angulatus–Sanxiagnathus sanxiaensis Zone; IV: Hirsutodontus simplex–Monocostodus sevierensis Zone.
Fig. 3. Distribution of brachiopods in the Lower–Middle Ordovician of the Huaqiao section, Changyang
Fig. 4. Distribution of brachiopods in the Lower–Middle Ordovician of the Liujiachang section, Songzi. I: Eoplacognathus foliaceus Zone; II: Oepikodus evae Zone; III: Cordylodus angulatus–Sanxiagnathus sanxiaensis Zone; IV: Hirsutodontus simplex–Monocostodus sevierensis Zone.

<table>
<thead>
<tr>
<th>Tremadocian</th>
<th>Floian</th>
<th>Dapingian</th>
<th>Darriwilian</th>
</tr>
</thead>
<tbody>
<tr>
<td>G. quadruplicatum–P. deltiger pristinus</td>
<td>P. deltiger</td>
<td>T. bicostatus</td>
<td>B. navis–P. parrallae</td>
</tr>
<tr>
<td>Nanjing Fm.</td>
<td>Eoxiang Fm.</td>
<td>Houshanyuan Fm.</td>
<td>Davan Formation</td>
</tr>
<tr>
<td>Lower</td>
<td>Middle</td>
<td>Upper</td>
<td>Lower</td>
</tr>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
</tbody>
</table>

- Lingula sp.1
- Martello sp.1
- Nanaorthus sp.1
- Syntrophinella sp.1
- Nanaorthus typica
- Panarthothis sp.2
- Martello ichangensis
- Pseudoporatambites ichangensis
- Yangtzeella poloi
- Nanaorthus sp.1
- Syntrophinella sp.2
- Nanaorthus multicosatum
- Nanaorthus sp.3
- Pseudoporatambites ichangensis
- Yangtzeella sp.3
- Lepidarthrotis typicus
- Lepidarthrotis sp.
Fig. 5. Distribution of Early–Middle Ordovician brachiopods in the middle Yangtze region. Ts: time slices; Ss: stage slices; Prot: Protorthida; Stro: Strophomenida.
Fig. 6. Diversification curves of Early–Middle Ordovician brachiopods in the middle Yangtze region. Ts: time slices; Ss.: stage slices; Ntot: total diversity; Nemsd: estimated mean standing diversity; No: number of originations; Ne: number of extinctions.

184x154mm (300 x 300 DPI)