# The Brachiopod World

Abstracts for IBC 7

Edited by:

HUANG Bing and SHEN Shuzhong

Nanjing, China. 2015

7th International Brachiopod Congress

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The 7th International Brachiopod Congress: The Brachiopod World

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23–25 May, 2015, Nanjing China

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China University of Geosciences (Wuhan)

The 7th International Brachiopod Congress

23-25 May, 2015, Nanjing China

Itinerary and Programme

Friday 22 May

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Saturday 23 May

Opening ceremony (Chair: ZHAN Renbin)

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Welcoming Remarks
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Prof. YANG Qun (Director of Nanjing Institute of Geology and Palaeontology);
Dr. LIU Yu (National Natural Science Foundation of China)

Academic Sessions

Plenary sessions

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9:15-9:45 am	**RONG Jiayu**: Phanerozoic brachiopod genera of China: A brief introduction
9:45-10:15 am	**Uwe BRAND**: Trace and isotope chemistry of brachiopods: proxies of geologic events
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10:35-11:05 am	**ZHANG Zhifei**: Exceptionally preserved brachiopods from fossil-Lagerstätten in southwestern China: perspectives on the Cambrian explosion of metazoans

Session 1: Systematics, phylogeny and morphological patterns of brachiopods

Chairs: Jisuo JIN and Lars HOLMER

11:05-11:25 am	**Glenn A. BROCK**, Marissa J. BETTS, Lars E. HOLMER et al.: Lower Cambrian brachiopod assemblages from east Gondwana – biostratigraphic review and correlation **(keynote)**
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Chairs: Lucia ANGIOLINI and Uwe BRAND

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10:25-10:40 am   **Horng-Sheng MII**, Tsai-Wen LIN, Shih-Wei WANG et al.: Carbon and oxygen isotope records of Devonian brachiopods from the southern China and their palaeoenvironmental implications

10:40-10:55 am   **SUN Yuanlin**, SHEN Bing, HUANG Kangjun et al.: Response of brachiopod fauna to environmental change related to the Upper Kellwaser Event --a case study on a carbonate platform section in central Guangxi, China

10:55-11:10 am   **Claudio GARBELLI**, Lucia ANGIOLINI, Uwe BRAND et al.: Neotethys seawater chemistry and temperature at the dawn of the latest Permian events

11:10-11:25 am   **Hideko TAKAYANAGI**, Ryuji ASAMI, Tsuguo OTAKE et al.: Within- and inter-shell variations in carbon and oxygen isotope composition of modern brachiopods

11:25-11:45 am   **Alberto PÉREZ-HUERTA**, Ethan L. GROSSMAN, Gregory A. HENKES et al.: Electron backscatter diffraction (EBSD) as a tool for evaluating fossil brachiopod shell preservation: Implications for carbonate clumped isotope paleothermometry **(key note)**

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9:35-9:50 am	**ZHANG Zhiliang** and ZHANG Zhifei: The epithelial cell moulds on the shells of the earliest acrotretoids from the Cambrian Series 2 (Shuijingtuo Formation) in the Three Gorges area, China
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Chairs: Guang SHI and Robin COCKS

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11:35-11:50 am	**SHEN Shuzhong**, ZHANG Yichun, LI Wenzhong et al.: Permian brachiopods from the Gyanyima exotic block in southwestern Tibet, China and their palaeogeographical and palaeoenvironmanetal implications
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BUONO, Giuseppe: Mena Daniela Schemm-Gregory: remembering a colleague and a friend.

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GASPARD, Danièle: Hierarchical structure of calcite layers in the shell of the brachiopod *Aerothyris kerguelenensis*.

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A silicified brachiopod fauna from the Cisuralian-Guadalupian Gundara Formation of Darvaz, Pamir, Tajikistan

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Here we describe a silicified brachiopod fauna composed by more than five hundred specimens, collected in the upper Cisuralian-lower Guadalupian (with the Cisuralian corresponding to the Lower Permian and the Guadalupian to the Middle Permian) Gundara Formation of Darvaz, N Pamir, Tajikistan (Fig. 1). The fauna has been collected from a stratigraphic section of marly bioclastic limestones located above the stratotype section for the Bolorian stage (Leven, 1979), which is the last stage of the Cisuralian in the Tethyan Scale. Notwithstanding heavy sampling only very few conodonts have been recovered, but foraminifers are abundant in warm water shallow water grainstone, floatstone, rudstone and microbialites allowing to constrain the age of the Safet Dara Formation - below the Gundara Formation - to the uppermost Cisuralian. Previous dating of the Gundara Formation suggests a Bolorian-Kubergandian age (Leven et al. (1983, 1992) which, depending on correlation (Angiolini et al., 2015), may suggest that the formation spans the Cisuralian-Guadalupian boundary.

Even if rich in term of number of specimens and remarkable for its preservation, the brachiopod fauna comprises only seven genera and nine species of the orders Productida, Rhynchonellida, Athyridida, Spiriferida, Spiriferinida, and Terebratulida. Besides *Posicomta gundarensis*, *Orbicoelia* sp. ind., *Spiriferellina* sp. ind., *Paraspiriferina* sp. ind., *Fredericksolasma lata*, *Fredericksolasma rhomboidale,* and *Fredericksolasma* sp. ind., a new species of *Hemileurus* and a new genus close to *Richthofenia*, are described. The latter (Fig. 2) is characterized by distinctive internal characters suggesting a rather unusual articulation system and musculature. The ventral valve interior comprises blisters filling the lower part of the cone and a body chamber with a myocoelidium, which is composed of three septa and seems to develop only at the adult stage, raising up from the floor of the body chamber in a moderately anterior position. The body chamber is divided into two cavities by a longitudinal ridge extending from the base of the myocoelidium anteriorly to the wall of the chamber opposite the hinge; the body cavity reaches its maximum depth in the space comprised between the myocoelidium and the hinge. These characters make this taxon very distinctive from allied Richthofeniidae.

The described brachiopods comprise both shelly-attached and pedicle-attached taxa forming life to neighbourhood assemblages. The reconstructed palaeoenvironment is that of cluster to segment reefs possibly associated to turbid water bioconstructions growing at tropical northern latitudes along the active Palaeotethys margin.
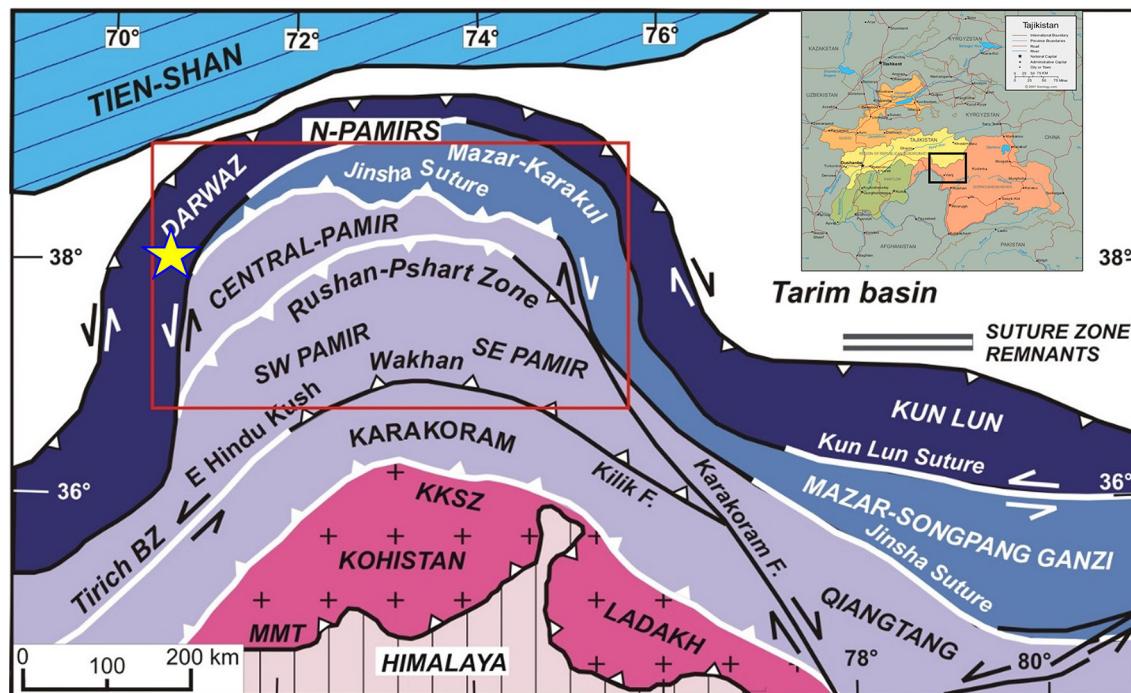
Fig. 1. Present tectonic setting of the Pamirs showing the position of Darvaz in N Pamir (star).
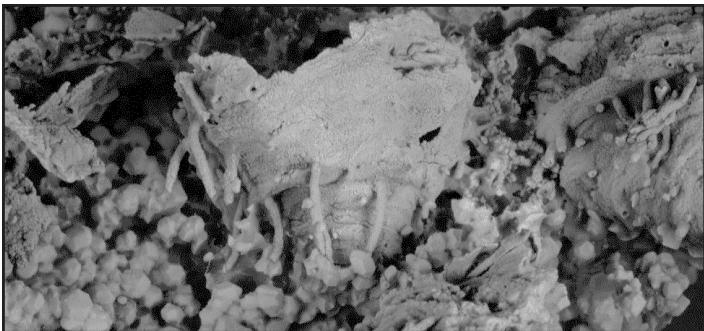
Fig.2. Richthofeniidae in life position from the Gundara Formation, Darvaz, Pamir.

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What can a shell tell you? The many stories told by *Gigantoproductus*, a multiproxy-archive brachiopod genus

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Large, thick-shelled species of *Gigantoproducus* are abundant in tropical shallow marine bioclastic limestones of Visean-Serpukhovian age in England (Pattison, 1981) (Fig. 1). They are also widespread in successions deposited in the same time interval in the Palaeotethys Ocean and along its shores, from the Moscow Basin to northern Gondwana and Cathaysia. These brachiopods lived semi-infaunally, partially buried in coarse, mobile sediment, stabilized by their extended ears, postero-ventral shell thickening, and long trails protruding high above the sediment surface and facing waves and tidal currents.

Their distinctive shape and size made them well known since the time of Sowerby in 1822, who described Productus giganteus, chosen - about one hundred years later - by Sarytcheva as type-species for her genus Gigantella, which however was pre-occupied and thus it was finally renamed Gigantoproductus by Prentice in 1950.

Several species of *Gigantoproductus* were the main protagonists of a morpho-functional analysis by Ferguson (1978), who, based on field analysis and flume experiments, showed that their different growth patterns were the results of population density and/or colonization of high energy coarse sediments vs. quiet soft muds.

After this detailed palaeoecological study, the interest in *Gigantoproductus* waned, to be resumed very recently in different directions. Qiao & Shen (2015) reconstructed the distribution of the genus from its origination in the Moscow Basin to its migration in the tropical and subtropical Palaeotethys regions and showed its potentials as palaeoclimatic and palaeobiogeographic tool in the Visean-Serpukhovian.
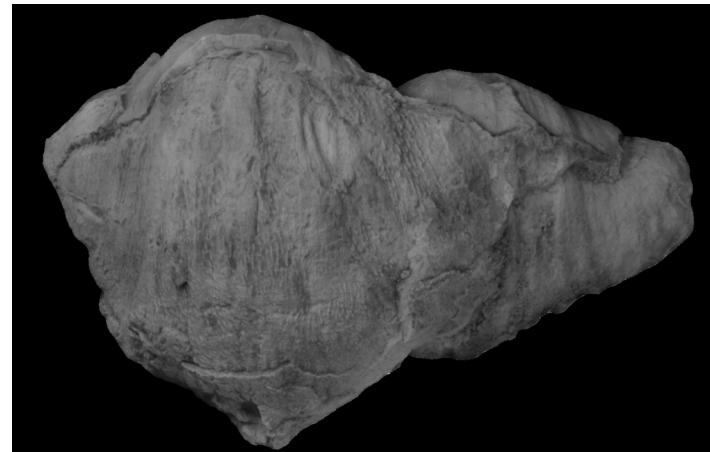
Fig.1. *Gigantoproductus inflatus* (Sarytcheva, 1928), from the Visean Eyam Limestone, Derbyshire, UK.

On the other hand, Angiolini et al. (2012) used the large sized thick shell of species of *Gigantoproductus* for detailed analyses of shell growth, structure and geochemical composition. In fact, this taxon has already been used as an archive of isotopic proxies in general geochemical analyses by Popp (1986). In particular, Angiolini et al. (2012) showed that, notwithstanding the complex diagenetic evolution undergone by the shell, its pristine parts, crossed by conspicuous growth lines indicating reduction or cessation of growth during winter, recorded high seasonal variations

of the upper Visean equatorial seas.

The surprises recorded by *Gigantoproductus* are not finished as, very recently, specimens from the Visean of Derbyshire, UK have been discovered to contain bitumen in the residual porosity of their shell cavity, so their study may also offer insights into hydrocarbon fluid flow pathways.

Finally, gigantism of the species of *Gigantoproductus* has been addressed and several explanations have been proposed ranging from adaptation to warm climates, high nutrient input, oxygen pulse into the atmosphere (Qiao & Shen, 2015). However, biotic relations as primary causes of the gigantism have not be considered so far.

This poster is meant to revise and describe some of the case studies involving species of *Gigantoproductus*, to underscore the potential of brachiopods as very good multi-proxy archives.

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The aberrant Middle Devonian ambocoeliid *Cyrtinoides* Yudina and Rzhonsnitskaya, 1985 from China

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The family Ambocoeliidae constitutes a group of about 36 genera of commonly small- and smooth-shelled Silurian to Triassic spiriferides. Within the family the Eifelian–Givetian genus *Cyrtinoides* Yudina and Rzhonsnitskaya, 1985 can be distinguished from all members of the group by a number of aberrant internal features. The unusual nature of the *Cyrtinoides* shell interior is marked by the presence of spondylium with tichorhinum in the ventral valve. As a matter of fact, *Cyrtinoides* is the only known genus with a tichorhinum not only within Ambocoeliidae, but in the whole order Spiriferida. It is worth to note that the tichorhinum was originally described as a structure characteristic for Cyrtinidae, the family of punctate spirolophous brachiopods representing the order Spiriferinida. There is, however, a difference in the structure of the tichorhinum of *Cyrtinoides* and that of Cyrtinidae. The latter have tichorhinum with median partition completely developed in the majority of species whereas in *Cyrtinoides* the hollow of the tichorhinum is not divided.

Here we re-describe the interior and systematic position of the species originally described as *Echinocoelia guangsiensis* Sun, 1992 (= *Cyrtinoides guangsiensis* herein) from the late Eifelian–earliest Givetian Mingtang Formation of Liujing section in Guangxi Province (Sun 1992; Xian 1998). The silicification of the brachiopod material from Liujing enabled the study of the internal shell characters as well as growth variability.

There is a controversy concerning the presence of crural plates in *Cyrtinoides*. Yudina and Rzhonsnitskaya (1985) revealed the presence of crural plates in the original description of the type species *Cyrtinoides ajica* coming from the Givetian of the western slope of the Southern Urals, whereas Johnson and Blodgett (1993, p. 952), with the aid of the material from New York and Nevada (*Cyrtinoides eliei* and *C. septata*), reinterpreted the structure as recumbent crural bases. Goldman and Mitchell (1990) noted the absence of the crural plates in the latest Eifelian *Mucroclipeus*, a junior synonym of the genus *Cyrtinoides* according to Johnson and Blodgett (1993). On the other hand Sun (1992) noted the presence of crural plates in *Echinocoelia guangsiensis* (= *Cyrtinoides guangsiensis*) from the late Eifelian Mingtang Formation of Liujing section in Guangxi Province. Indeed, the present re-examination of the type material of *C. guangsiensis* clearly shows that the crural bases in this Chinese form hang quite high above the valve floor and are supported by thin plates variable in their extent. These plates are fused to the valve floor and therefore should be regarded as short crural plates. It appears that the support of the crura is variously developed in different species of *Cyrtinoides*. What is more, this difference shows some palaeogeographic aspect as the species from the easternmost Laurussia and South China (*C. guangsiensis* and, reportedly, *C. ajica*) possess crural plates whereas species occurring more to the west, i.e. form North America (*C. eliei* and *C. septata*) have apparently recumbent crural bases.

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Morphometric study of asymmetric rhynchonellids from the Coniacian (Upper Cretaceous) of northern Spain

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The Upper Cretaceous asymmetric rhynchonellid brachiopods constitute an easily recognizable and frequently cited group, but their classification and functional interpretation is to date very controversial. The main purpose of this paper is to analyze the morphometric variability of asymmetric rhynchonellids (*Cyclothyris* aff. *difformis*) from three Coniacian sections located in the Province of Burgos (Northern Spain) (Fig.1A), inferring the possible relationships between their systematics and functional morphology. For this work, 270 specimens with asymmetric commissure were collected in the field, of which 67 were chosen for this study because of their better preservation. To study their asymmetry, geometric morphometric analyses (Bookstein, 1991; Hammer and Harper, 2006) were applied. For this purpose four "landmarks" on the commissure line were established, from which measurements were taken to analyse the "step length" between the two lobes of the shell.

The morphometric analyses revealed the existence of a high variability in the development of the asymmetric commissure in *Cyclothyris* aff. *difformis*. This feature does not seem to be dependent of age or geographic occurrence, and does not seem to differ from the asymmetric pattern present in other rhynchonellids with similar asymmetric commissures. Consequently, this feature apparently has no systematic value, as already suggested by some authors, but it is more likely related to variations within the studied populations, and probably of constructional origin.

This analysis showed a significant correlation between the size (or growth) of the shell and the development of the step of the commissure, measured as the distance between the landmarks 2 and 3. Thus, the shells were symmetrical until they reached a certain size, which is determined by the basic shape of the shell. Most interesting was the discovery that the internal structure is not influenced by the external asymmetry of the shell, most probably because when asymmetrical growth starts, the crura have attained their final form. Thus, the asymmetry can be interpreted as a constructional alternative to the plication in the symmetrical forms, which is typical of the genus *Cyclothyris*.

In the first species of the genus where asymmetry appears (the Cenomanian *C. difformis*), both symmetrical and asymmetrical shapes have been recorded together (Owen, 1962; Motchurova-Dekova, 1995) in littoral environments according to the last author. Asymmetry reappears in the genus in the Coniacian,
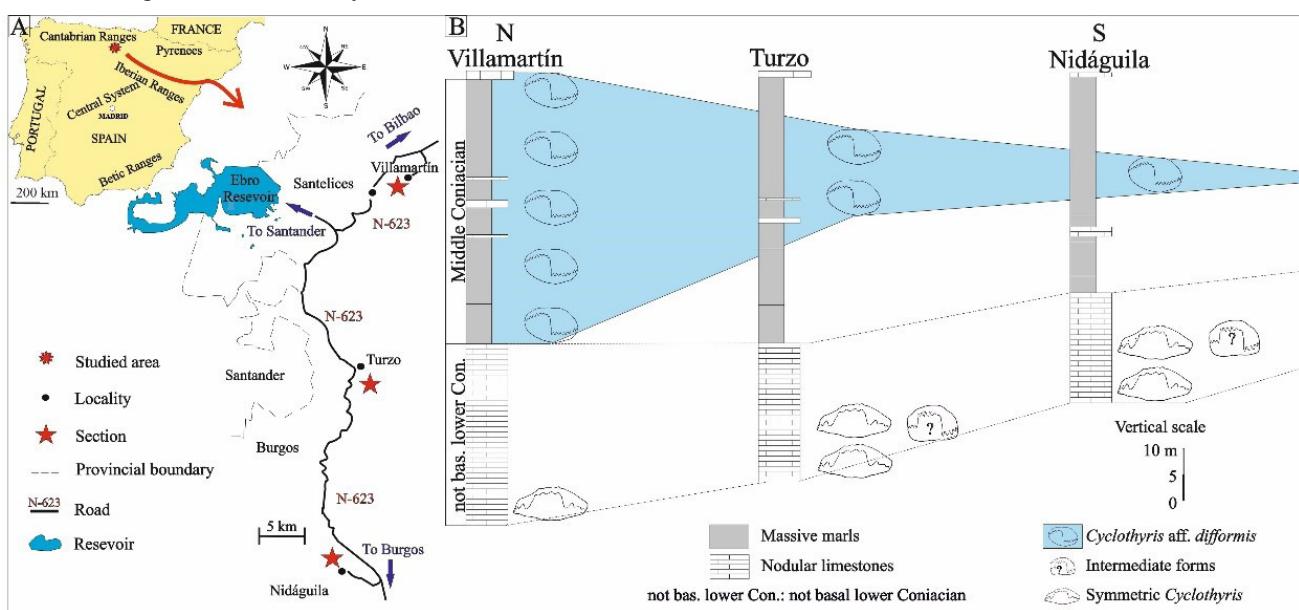
Fig.1. A) Geographical and geological setting of the material collected for this study. B) Commissure morphology of *Cyclothyris* aff. *difformis* collected in the lower and middle Coniacian of the studied sections. Note that at the carbonate lower levels symmetrical shapes appear, but in the uppermost beds they appear together with specimens with intermediate commissures. At the marly upper levels only asymmetric brachiopods (*Cyclothyris* aff. *difformis*) are found.

but here symmetrical and asymmetrical shapes are never found together. All the *Cyclothyris* collected in the levels where *C.* aff. *difformis* occurs are asymmetric. Despite this difference, the variability observed in the asymmetric frontal commissure is similar to that found in the Cenomanian *C. difformis* or in other species of *Cyclothyris* with asymmetric commissure, the twisting process being well defined and seemingly channeled through development to the extent that the Coniacian species are called *C. difformis* or *C.* aff. *difformis* in most previous works, because there is no obvious morphological difference with the Cenomanian asymmetric form.

However, an interesting observation carried out in the field is that the development of the Coniacian asymmetry seems to be related to the abundance of fine detrital sediments. The asymmetrical shapes appear in the studied sections when the sedimentation changes from predominantly calcareous to mainly marly with finely grained detritics. Something similar has been reported from other Coniacian basins by Muñoz (1985, 1994) and Gaspard (1991). These records suggest that asymmetry is positively selected by a changing environment. This idea is supported by the fact that in the uppermost beds with symmetric *Cyclothyris*, some specimens with intermediate characters in the commissure appear (Fig. 1B). The advantages an asymmetrical commissure might have in such environments, however, is difficult to interpret and should be subject of further research.

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Recent Brachiopoda from the Mozambique-Madagascar area, western Indian Ocean

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While the diversity and abundance of brachiopods have been significantly reduced since the Mesozoic, such that today they are considered a minor phylum comprising only about 110 genera, they are widely distributed globally, living in all oceans at depths ranging from the intertidal to more than 5000 m. However, brachiopods are still relatively poorly known from the Indian Ocean. Here we report on recent brachiopods collected during three French deep-sea cruises MAINBAZA, MIRIKY and ATIMO VATAE to the Mozambique-Madagascar region during the years 2009-2010. Twenty-five species belonging to the genera *Discradisca* Stenzel, *Novocrania* Lee & Brunton, *Basiliola* Dall, *Cryptopora* Jeffreys, *Gryphus* Megerle von Mühlfeld, *Dallithyris* Muir-Wood, *Stenosarina* Cooper, *Xenobrochus* Cooper, *Terebratulina* d'Orbigny, *Chlidonophora* Dall, *Eucalathis* Fischer & Oehlert, *Macandrevia* King, *Frenulina* Dall, *Jolonica* Dall, *Argyrotheca* Dall, *Phaneropora* Zezina, *Nipponithyris* Yabe & Hatai, *Megerlia* King and a kraussinid gen. nov. have been identified from dredged samples. One new genus and four new species have been recognised in the studied collections. The genus *Macandrevia* and the species *Frenulina sanguinolenta* (Gmelin) are recorded for the first time from the Indian Ocean. In a new biogeographical classification (Spalding *et al.* 2007) Southern Madagascar and Western and Northern Madagascar constitute two ecoregions, i.e. areas of relatively homogeneous species composition, distinct from adjacent areas. Our study also reveals that regional differences occur within the three study areas of Madagascar. The brachiopods collected in North-West Madagascar during the cruise MIRIKY are represented by 10 species belonging to nine genera. Those collected in the Mozambique Channel during the cruise MAINBAZA are represented by 12 species belonging to 11 genera. The brachiopods collected in South Madagascar during the cruise ATIMO VATAE display the greatest diversity, with 17 species belonging to 15 genera. Only one species, *Jolonica suffusa* (Cooper) has been identified in all three regions, whereas there are 12 species found only in one of those three regions. The North-West Madagascar region and Mozambique Channel have four species in common, also North-West Madagascar has four species in common with the South Madagascar region. A greater affinity is observed between the areas of Mozambique Channel and South Madagascar where six species are in common.

Although a marked endemism can be found among other groups, especially in South Madagascar, a similar high endemism is not observed in the southern Madagascar brachiopods where only two new forms were found exclusively in this region. Five species among those recognized have a very wide distribution; *Xenobrochus africanus* (Cooper), *Frenulina sanguinolenta*, *Phaneropora galatheae* Zezina, and *Nipponithyris afra* Cooper are also known from the West Pacific (Laurin 1997; Bitner 2009, 2010), and *Megerlia truncata* (Linnaeus) was reported

from the Persian Gulf (Jackson 1921) and is very common in the Mediterranean Sea and Eastern Atlantic (Logan 1979, 2007). The absence of thecideide brachiopods in the study collection from Madagascar that are known from the Red Sea (Logan & Bitner 2013) and the Madagascar region (Cooper 1981; Zezina 1987; Baker & Logan 2011; Simon & Hoffmann 2013), may result from the fact that they are generally shallow-water forms usually associated with coral reefs, and thus are absent in our deeper water offshore samples.

The composition of the brachiopod fauna from this part of the Indian Ocean, apart from the Madagascar region, was briefly discussed by Cooper (1981) who summarized earlier studies of brachiopods (e.g. Jackson 1952; Cooper 1973a), including those collected by the RV *Vema* from Agulhas Bank, South Africa where three kraussinid species were identified (Cooper 1973b). More recently Hiller (1986, 1991, 1994) described South African brachiopods and discussed their regional affinities, pointing out that their geographical distribution is controlled by two oceanographic systems, the Agulhas Current on the east and the Benguela Upwelling System on the west. He noted that this fauna is dominated by kraussinids and this is also the case in the collection from Madagascar. A comparison of the overall Madagascar brachiopod biota with those of other parts of the Indian Ocean shows the strongest similarity to those from southern Africa, with 11 out of 25 species occurring in both areas.

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Badenian (Middle Miocene) brachiopod assemblage from Yasen, northwestern Bulgaria (Central Paratethys): composition and biogeographic significance

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The Central Paratethys was an epicontinental sea that com-

prised the area from the present-day Austria and southern Poland to Romania and northern Bulgaria. Brachiopods, even not diverse, are common fossils in the Middle Miocene deposits of the Central Paratethys. Although described from many Paratethyan localities, Miocene brachiopods of Bulgaria are still poorly known. Those described here come from the locality of Yasen, situated in northwestern Bulgaria, in the most southern part of the Central Paratethys. The brachiopod-bearing deposits cropping out at Yasen are represented by extremely fossiliferous clayey detrital limestone of Early Badenian age. This newly discovered brachiopod assemblage contains nine species belonging to nine genera, i.e. *Discradisca* sp., *Cryptopora lovisati* (Dreger), *Novocrania anomala* (Müller), *Megathiris detruncata* (Gmelin), *Argyrotheca cuneata* (Risso), *Joania cordata* (Risso), *Megerlia truncata* (Linnaeus), *Platidia anomioides* (Scacchi & Philippi), and *Minutella* sp. nov. The species *N. anomala*, *A. cuneata*, *J. cordata*, *M. truncata*, and *P. anomioides* have been already reported from the Miocene of Bulgaria (Kojumdgieva 1960; Bitner 1993), while the genera *Discradisca*, *Cryptopora* and *Megathiris* are noted for the first time. Like most other Paratethyan assemblages the Yassen assemblage is dominated by the megathyridids, i.e. *Megathiris*, *Argyrotheca*, and *Joania*, however, the presence of the thecideide *Minutella* makes the Bulgarian assemblage unique among brachiopod assemblages of the Central Paratethys.

The genus *Minutella* was erected, based on Recent material, for those *Thecidellina* species which possess a pseudodeltidium, long believed to be a variable character within the genus (Hoffmann & Lüter 2010). Today *Minutella* is known from the Indo-West Pacific Province and the West Atlantic, being not found in the Mediterranean Sea and East Atlantic. Thus, its occurrence in the Miocene of the Paratethys explains well the disjunct recent distribution of this genus as a Tethyan legacy. A very similar disjunct geographic distribution is observed among Recent representatives of the genus *Discradisca* (Bitner & Cahuzac 2013) what also suggests a relict of an ancient Tethyan fauna.

The dominance of megathyridids and the presence of thecideides, brachiopods characteristic for cryptic habitats, indicate a shallow-water, warm environment what supports the previous interpretations (Nikolov 1995), based on sediment character and associated molluscan fauna.

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Trace and isotope chemistry of brachiopods: proxies of geologic events

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With the discovery of biotic events and crises throughout Earth's geologic time, the search was on to find the causes for these, at times, catastrophic events (e.g., Sepkoski, 1981; Erwin, 1994). The advent of isotope geochemistry with the apparent robustness of isotopes (C, O and Sr) and the establishment of isotope thermometers (Epstein et al., 1953) we were one step closer to unraveling the mysteries of the underlying causes. Distinct negative carbon isotope (nCIE) and radiogenic strontium isotope excursion (rSIE) trends have been identified with the greatest of these events; the end Permian mass extinction (e.g., Holser et al., 1989; Cao et al., 2002; Brand et al., 2012a (Fig. 1), Chen and Bottjer, 2014). The primary nature of the isotope composition and thus trends was never in question until recently, when incontrovertible evidence using a multitude of screening tools was advanced demonstrating the folly of this assumption. The intensive screening of archival material using visual, optical, microstructural, trace chemistry distribution and stable isotope trends has raised serious questions about the veracity of the proxy material and thus their results (e.g., Brand and Veizer, 1980; Knauth and Kennedy, 2009; Brand et al., 2012b). Post-depositional diagenetic and hydrothermal alteration may profoundly change the primary contents and compositions of the carbonate and phosphate archives, and with it the resolved paleoenvironmental and paleoclimatic parameters surrounding geologic events. Lately, a renaissance has invigorated the field with the presentation of rare Earth elements (REEs; Azmy et al., 2011) and clumped isotopes ($\Delta 47$; Ghosh et al., 2006; Came et al., 2014) and water composition independent thermometers as tracers/proxies of environmental parameters such as redox and seawater temperature. Despite some issues concerning the absolute veracity of these newest of concepts, our knowledge is steadily increasing about the complex issues of timing, duration, intensity (Fig. 2) and source(s) about the greatest mass extinction and other events in Earth history (e.g., Shen et al., 2012; Burgess et al., 2014).

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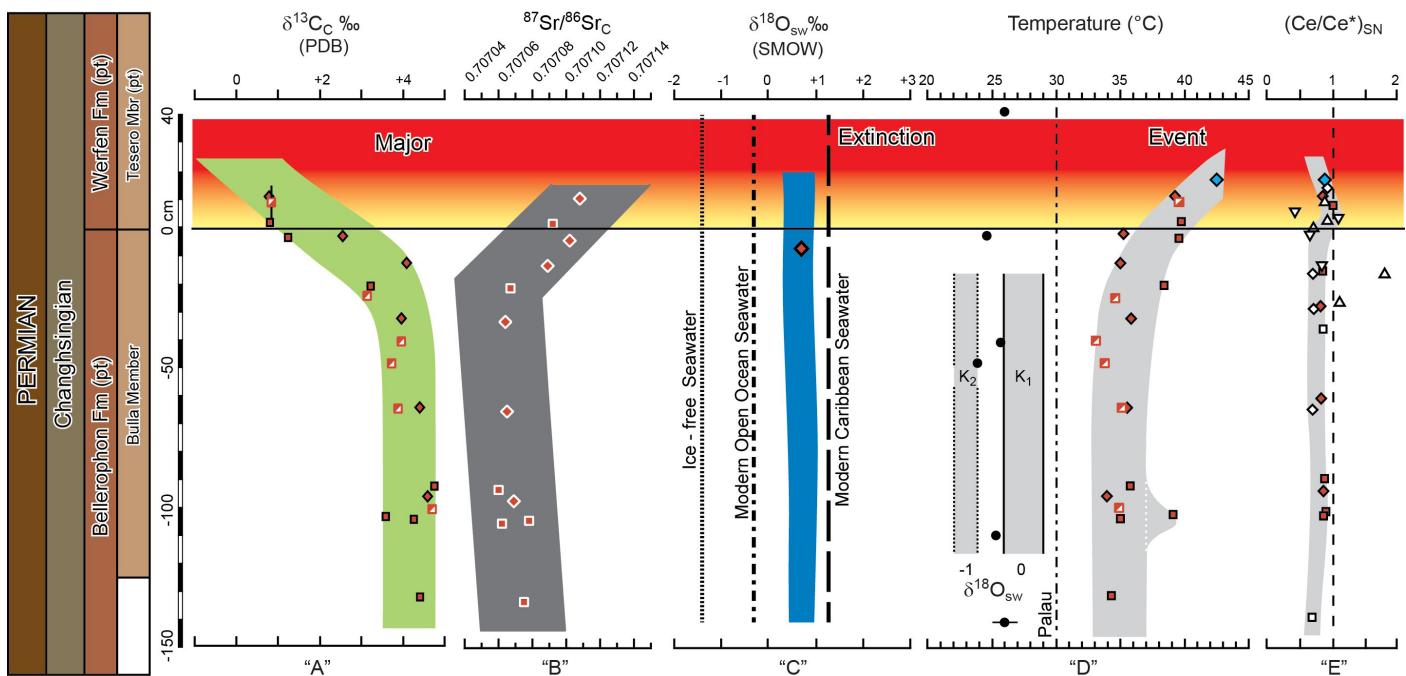
Fig.1. Updated geochemical trends and seawater temperature and composition during the end Permian of northern Italy (cf. Brand et al., 2012a).
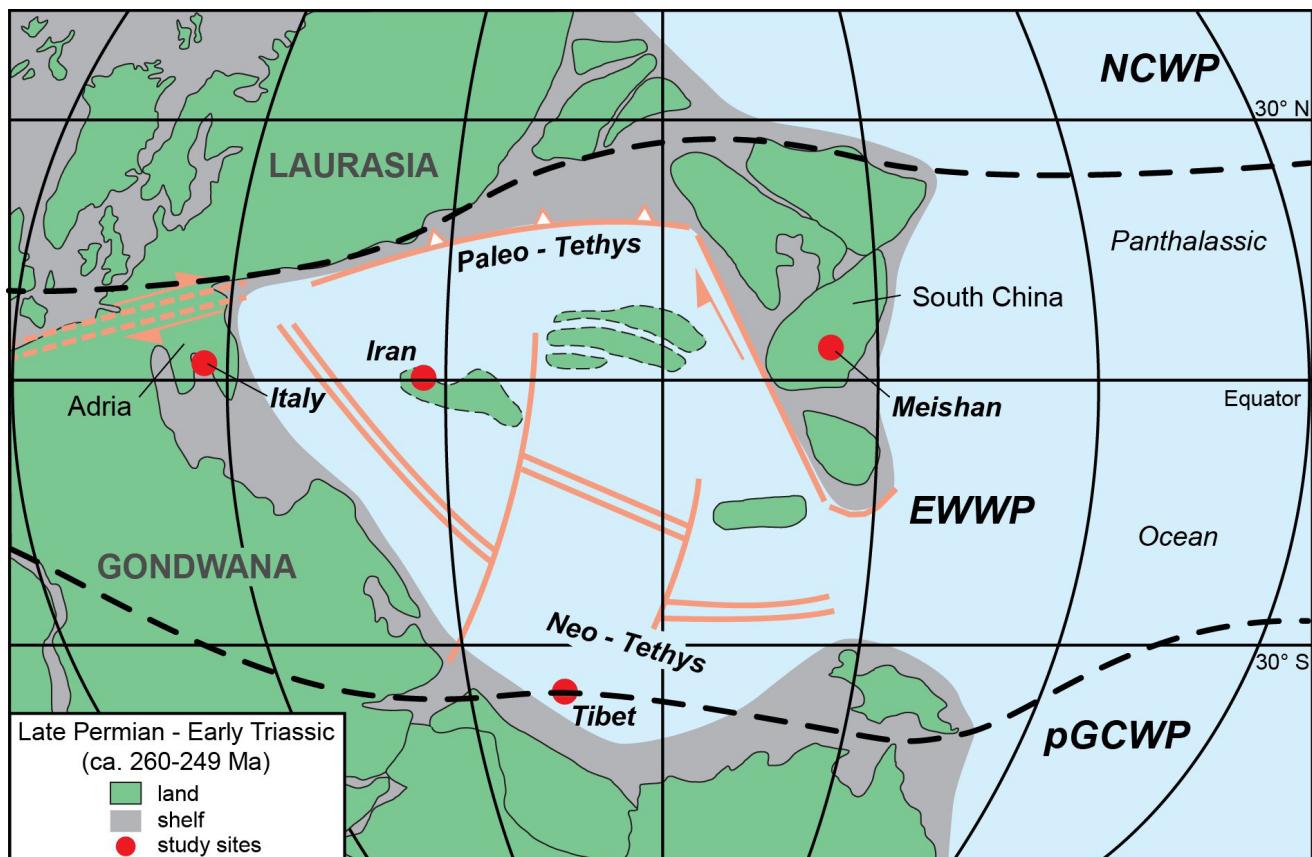
Fig.2. Paleogeography of Laurasia and Gondwana with close-up of the Tethys Sea during the end Permian and showing conodont provinces (Equatorial Warm Water Province – EWWP; North Cool Water Province – NCWP; peri-Gondwana Cool Water Province – pGCWP; modified after Ziegler et al. 1997).

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Lower Cambrian brachiopod assemblages from east Gondwana – biostratigraphic review and correlation

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The continents of Antarctica and Australia have a long and intimate geological history. They were joined together in a complex plate tectonic dance for more than 3 billion years, initially as juxtaposed cratonic elements forming the Mawson Continent (Rodgers 1996). This later became an integral part of the assembly of the supercontinent Rodinia, around 1 billion years ago (Cawood 2005), and emerged unscathed through the opening of the proto Pacific ocean as part of the *Terra Australis* Orogen around 800 Ma (Cawood, 2005) until final separation during the last 45 Ma (Muller 2001). During the critical period of expansive biotic radiation in the Early Cambrian, Antarctica and southern Australia were sutured together near the equator forming East Gondwana. The rocks deposited during this interval (incorporating parts of the Transantarctic Mountains in Antarctica and the Stansbury, Officer and Arrowie Basins in South Australia) provide ample evidence of a shared geological, palaeontological and palaeogeographic heritage (Flöttmann et al. 1993; Brock et al. 2000; Jago et al. 2006). Brachiopods from strategic units in South Australia and Antarctica will be reviewed and placed in a broad biostratigraphic context.

South Australia. The best exposures of lower Cambrian rocks in Australia are found in the Arrowie and Stansbury basins in South Australia where richly diverse and abundant stem and crown group brachiopod faunas are well represented, especially in the carbonate dominated facies of the Hawker Group in the Arrowie Basin (Jago et al. 2006; Topper et al. 2009; Skovsted et al. 2009; Holmer et al. 2011). Detailed systematic fieldwork in the Arrowie Basin over the last decade has culminated in the establishment of three new shelly fossil assemblage zones based largely on eccentrothecimorph and camenellan tommotiids and organophosphatic brachiopods (Betts et al. in review).

Shelly Assemblage Zone 1 [SAZ 1] includes the oldest known brachiopod from the lower Cambrian succession in South Australia, the paterinate *Askepasma saproconcha* Topper, Holmer, Skovsted, Brock, Balthasar, Larsson, Petterson Stolk, and Harper. SAZ 1 is defined by the overlapping ranges of *A. saproconcha* and the eccentrothecimorph tommotiid *Kulparina rostrata* along with

the camenellan tommotiids *Dailyatia ajax* and *D. macroptera*. SAZ 1 occurs in pre-trilobitic strata (Terreneuvian, late Stage 2) in the lower-middle part of the Wilkawillina Ajax and Wirrapowie Limestones. Undescribed, though rare, calciate brachiopods are also known from the upper Wirrapowie Limestone in the Chase Range, Arrowie Basin and probably fall within SAZ 1.

Shelly Assemblage Zone 2 [SAZ 2] is restricted to the Winnitinny Creek Member of the Wilkawillina Limestone and temporal equivalents in the Wirrapowie and Ajax Limestones. SAZ 2 is characterised by much higher diversity and abundance of shelly fossils and broadly correlates with the *Abadiella/ Parabadiella huoi* trilobite biozone = Series 2, Stage 3. SAZ 2 is defined by the co-occurrence of the stem group brachiopod *Micrina etheridgei*, the paterinate *Askepasma toddense*, the tubiform stem lophophorate *Eccentrotheca helenia* and the camenellid tommotiids *Dailyatia ajax* and *Dailyatia macroptera* which range through both SAZ 1 and 2. The lower boundary of SAZ 2 is defined by the FAD of *A. toddense* and/or *M. etheridgei*, while the upper boundary is defined by the last appearances of the tommotiid taxa: *D. ajax*, *D. macroptera*, *Dailyatia* n. sp. 1, *Dailyatia* n. sp. 2 and *E. helenia*. Taxa previously referred to as *Eoobolus* aff. *priscus* and *E. viridus* appear to be ecophenotypes of the same taxon (see Holmer & Ushatinskaya 2001; Jago et al. 2006) and the taxon is conspecific with *Sukharilingula luchininae* Ushatinskaya, 2012 from the lower Cambrian (Botoman) of the NW Siberian Platform. This taxon first makes its first appearance in SAZ 2 (broadly late Atdabanian), but ranges into the succeeding SAZ 3 assemblage Zone. This assemblage zone also contains FADs of *Minlatonia tuckeri*, *Eodicellomus elkaniiformis*, *Karathele yorkensis* and *Kyrshabaktella davidi* in the uppermost part of the Zone. All these taxa range through and are more abundant in the succeeding SAZ 3

Shelly Assemblage Zone 3 [SAZ 3] occurs above the regionally significant hiatus, the Flinders Unconformity and is defined by the extinction of all *Dailyatia* species found in SAZs 1 and 2 and the first appearance of *Dailyatia odyssei* and the problematic SSF *Stoibostrombus crenulatus* and *Cambroclavus absonus*. *S. luchininae*, *K. yorkensis*, *K. davidi*, *M. tuckeri*, *E. elkaniiformis* are all present in large numbers. The FAD of *Eohadrotreta* sp. cf. *E. zhenbaensis* Li & Holmer, 2004, the oldest known acrotretoid in Australia occurs in the upper part of SAZ 3. In addition, the first record of a chileate brachiopod, *Chile*? sp. from the Parara Limestone in Horse Gully, Yorke Peninsula (Holmer et al. 2011) and the first mickwitziid brachiopod, *Mickwitzia* sp., from East Gondwana (Skovsted et al. 2009) is also from SAZ 3. Undescribed and new silicified calciate taxa are also known from the Mernmerna Formations in the Chambers Gorge area. In the Arrowie Basin, SAZ 3 includes the Second Plain Creek Member of the uppermost Wilkawilina Limestone and the overlying/ onlapping Mernmerna Formation and Andamooka Limestone on the Stuart Shelf and Parara Limestone (in part) in the Stansbury Basin and correlates with the *Pararaia tatei* and *P. buneryooensis* trilobite Zones. Paterson and Brock (2007) described a trilobite fauna from the *P. bunyerooensis* zone that included species of *Wutingaspis* and *Yunannocephalus* suggesting corelation with the *Yunnanocephalus* subzone (upper *Eoredlichia-Wutingaspsis* Zone) of the Chiungchussuan (=Qiongzhusian) Stage of China.

Brachiopods are very rare in the Cambrian Series 2, Stage 4 Emu Bay Shale Lagerstätten on Kangaroo Island, but one taxon very similar to *Diandongia* from the Chinese Chengjiang Lagerstätten is present (GAB pers observation). The latest Botoman to early Toyonian succession of red beds across the Arrowie (Yarrawurta Shale and Billy Creek Formation) and Stansbury (Minlaton Formation) Basins has thus far yielded no identifiable brachiopods.

Shelly Assemblage Zone 4 [SAZ 4] The youngest brachiopods in the lower Cambrian succession belong to the SAZ 4 and include the acrotretoid *Vandalotreta djagoran* which also occurs in the Ramsay and Coobowie Limestones on Yorke Peninsula (Stansbury Basin) and the Wirrealpa and Aroona Creek Limestones of the Arrowie Basin. This assemblage zone is defined by the first acrotretid *Vandalotreta djagoran* plus *Karathele napuru*, *Kyrshabaktella certa,* and *Eoobolus* sp. The calciate obolellid taxon *Trematobolus wirrealpensis* is also a common element throughout the Wirrelapa Limestone in the central Flinders Ranges. These taxa characterise late Toyonian and Amgan (early Middle Cambrian) strata in Australia, Antarctica and elsewhere.

Antarctica.The Holyoake Range succession sampled during fieldwork by GAB, LEH and CBS in 2011 produced fossils derived from a shallow water carbonate platform of the upper Shackleton Limestone which includes burrowed and oolitic limestones and skeletal wackestone that grade upwards into light coloured, massive isolated peri-reefal archaeocyath-dominated bioherms. The bioherms and interbiohermal strata are capped by a thin, laterally extensive phosphatic crust that is sharply overlain by up to 8.5 m of interbedded shales and nodular limestones (with agnostid trilobites) representing carbonate ramp transition of the Holyoake Formation. This is conformably overlain by siltstones (with trilobites and helcionellids in basal part) which grade upward into coarse sandstones and conglomerates of the Starshot Formation.

Preliminary results derived from acetic acid dissolution of samples from the Shackleton Limestone in the Holyoake has produced a moderately diverse assemblage of shelly fossils dominated by linguliformean brachiopods including *Eohadrotreta* sp., *S. luchininae*, *K. yorkensis* and *E. elkaniiformis*. Other key taxa include *Cambroclavus absonus* and *Dailyatia odyessi*. Fragmentary remains of the spinose bradoriid arthropod *Spinospitella coronatum* are reported for the first time from Antarctica. This newly discovered assemblage from the Shackelton Limestone can be correlated closely and with some precision with lower SAZ 3 in South Australia. It is also remarkably similar to faunas described from exotic clasts on King George Island, West Antarctica (Wrona 2003, 2004; Holmer et al. 1996).

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Silicification bias in brachiopods: implications for paleoecological studies

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Fossil brachiopods are frequently used to understand the depositional environment and paleoecology of the rocks in which they occur. Silicified fossils are easy to extract and prepare and are often used for these types of analyses, as well as being ideal for systematic studies. When brachiopod shells are replaced with silica (as opposed to silica precipitating in a dissolution mold), a taphonomic bias is inevitably introduced. Understanding this bias is integral to accurate analyses of paleoecology and has broader implications for our interpretation of the fossil record.

This talk will discuss silicification bias at brachiopod localities of three ages from three localities: the Permian of Texas (USA), the Devonian of New York (USA), and the Carboniferous of the western United States. It will discuss the role of taxonomic and lithologic biases in the selective silicification of fossils from these localities and the commonalities and differences in taphonomic bias between these localities. Recent experimental research on silicification provides further justification for the factors that make brachiopods well-suited to silicification and elucidates the nature of the bias.

Permian rocks in the Delaware Basin have one of the most complete Permian records and contain abundant silicified fossils, including the well-known Permian brachiopod reef complexes. The brachiopod systematics were covered exhaustively in the publications of Cooper and Grant in the 1970s. Although considered one of the best examples of silicified brachiopods, the fidelity of replacement at the ultrastructural level is low. Devonian rocks of New York have heterolithic bedding with carbonate and siliciclastic units and also mixed carbonate/siliciclastic rocks. Silicification is common in the carbonate matrix, but rare in the siliciclastic matrix. The Carboniferous of the western United States has many examples of silicification. The Early Carboniferous is primarily carbonate and shifts to mixed carbonate-siliciclastics with the transition from a greenhouse climate to an icehouse climate at the mid-Carboniferous boundary. Bias in these rocks has been attributed to both lithological and taxonomic factors. All three examples occur in basins with coeval ash deposits providing and ample source of silica.

Brachiopods and collections: the Philatelic record

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In the last decades paleontology has having an always higher number of philatelic issues, so that even books (Ernst and Rudolph 2002; Ernst and Klug 2011) and web-sites (see references) have been dedicated to this target. Unfortunately this increasing interest has interested only marginally invertebrate paleontology, and even less brachiopods. However a detailed survey on brachiopod and brachiopod related stamps and other philatelic / postal issues has allowed to find few interesting ones and to build a small data-

base, whose selection has been shown in tab.1 and fig.1.

A part for collectors, I suggest that those kind of issues have at least two important reasons of interest for researchers and the scientific community. First of all they represent an alternative way to do scientific divulgation attracting interest for our discipline. Then, even more stimulating, there is the challenge to correct errors and/or update the info provided on the stamps.

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Web sites: a) http://www.paleophilatelie.eu/ - b) http://www.stampedout.nl/

Mena Daniela Schemm-Gregory: remembering a colleague and a friend

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This year at the 7[th]IBC unfortunately we will miss one of most promising joung "brachiopodologist", Mena Daniela Schemm-Gregory. And I guess I will be not the only one who will miss her cheerfulness and smile, without forget her funny anecdotes (often about colleagues) neither of course her competence about "our loved little friends brachiopods", as she used to call them. I have already written something on my personal memories about Mena (Buono 2013) and possibly I will do it again in asnother place; here instead I try to keep the focus on her scientific life and production.

Mena's scientific career start at Seckenberg institute of Frankfurt where she began to work on one of the largest brachiopod collections in the word under the supervision of her mentor and our colleague Ulrich Jansen. Already in this period she showed her capacities with a huge PhD thesis and some relevant articles. After a short period of struggling looking for new position, she finally get a post-PhD position in Coimbra (Portugal). Here apart of some burocratic problems (sometime quite frustrating, as example a salary decreasing as consequence of the economical crisis which affected Portugal in the last years), she

Pertinence	Country	year	kind of philatelic/postal issue	Brachiopod related subject	Classification: correction or updating	Ref. in Fig 1
Brachiopods	BAT	1990	stamps	Lingulella	*Notiobolus tenuis* Popov	F
Brachiopods	DDR	1990	minisheet border	not specif. brachiopod	*Platystrophia sp.*	B
Brachiopods	DDR	1990	minisheet border	not specif. brachiopod	*Platystrophia sp.*	B
"Brachiopodologist"	Czech Rep.	1994	minisheet	Joachim Barrande		A
Brachiopods	Czech Rep.	1994	minisheet	not indicated	*Sieberella sieberi*	A
Brachiopods	Czech Rep.	1994	MS (bottom left tab)	not indicated	*Pompeckium kuthami*	A
Brachiopods	Ethiopia	1977	stamp	*Terebratula abyssinica*	*Somalirhynchia africana*	G
Brachiopods	Ethiopia	1977	stamp	*Terebratula subalata*	*Somalirhynchia africana*	G
Brachiopods	Mauritania	1972	stamp	not indicated	Spiriferida ind. (? *Euryspirifer sp.)*	D
Brachiopods	Mauritania	1974	stamp (overprinted)	not indicated	Spiriferida ind. (? *Euryspirifer sp.*)	E
Brachiopods	Saint Kitts	1994	stamp	not indicated	brachiopoda undet. (?)	
Brachiopods	Saint Kitts	1994	stamp (overprinted)	not indicated	brachiopoda undet. (?)	
Brachiopods	Slovenia	1995	stamp, FDC, postmark	*Karavankina schellwieni*	*Karavankina schellwieni* Ramovš 1966	C
Brachiopods	Somalia	1997	stamp	not specif. brachiopod	not specif. brachiopod	H
"Brachiopodologist"	Poland	1990	stamp	Roman Kozlowsky		K
"Brachiopodologist"	Bolivia	2002	stamps	Alcide d'Orbigny		
"Brachiopodologist"	France	2002	Meter frankings	Alcide d'Orbigny		
Brachiopods	Germany	1976	Meter frankings	*Spirifer alatus*	*Pterospirifer alatus* (von Schlotheim 1813)	
Brachiopods	Germany	1987	Meter frankings	*Spirifer alatus*	*Pterospirifer alatus* (von Schlotheim 1813)	J
Brachiopods	France	2008	Meter frankings	Spiriferida ind.	Spiriferida ind.	

Tab.1 and associated Fig.1 (next page) Brachiopods and "brachiopodologists" in philately. Legend: BAT: British Anctartic territories;DDR: "*Deutsche* Demokratische *Republik*" (German Democratic Republic); FDC: "First Day Cover"; MS: "mini-sheet").

A

B

C

D

E

F

G

H

I

J

K

found the ideal environment to work, also thanks to the good feeling with her supervisor Maria Helena Henriques.

The first aspect coming out reading Mena's works is probably the completeness and the accuracy of taxonomical and systematic description (as example see Schemm-Gregory 2009, 2010). I also remember that when I express her my admiration for such completeness she told me just: "of course!". And of course it should be so, even if in reality this does not happen always instead, especially at such excellent level. Part of this completeness is represented by the excellent figuration of the specimens, thanks also to excellent camera lucida derived sketches and to the mg-coating of photographed specimens. And this was also often implemented by 3D reconstruction of brachiopod internal structures, which probably she has introduced for the first time for brachiopod tax-

onomy. Noticeably those 3d reconstructions are based on manual (and not CT scan derived) serial sections and who tried to do it knows that it is really a hard and time consuming work.

Even if Mena probably reached the top her competence in taxonomy, she was also interested in all possible aspects interesting the study of brachiopods, as for example paleoecology, taphonomy, paleogeography. In addition we also planned and started together some projects regarding brachiopods evolution, geometric morphometry, geochemistry; topics on which we already produced something (e.g. Buono and Schemm-Gregory 2013), and possibly some more relevant articles will came out in future.

Her capacity has allowed her to get many academic rewards, and as consequence also several collaborations with many research group leaders as W. Kiessling, H. Feldman, C. Klug and

A - Mid-congress field trip at the 5th IBC (Copenhagen 2005) [Photo by Ulrich Jansen]

B - Field trip at Eype (Dorset, UK - 16/10/2010) [Photo by Giuseppe Buono]

C - Field trip in Morocco (March 2013) [Photo by Ladislav Slavik]

D - Post congress field trip at the 6th IBC (Melbourne 2010) [Photo by Liisa Lang]
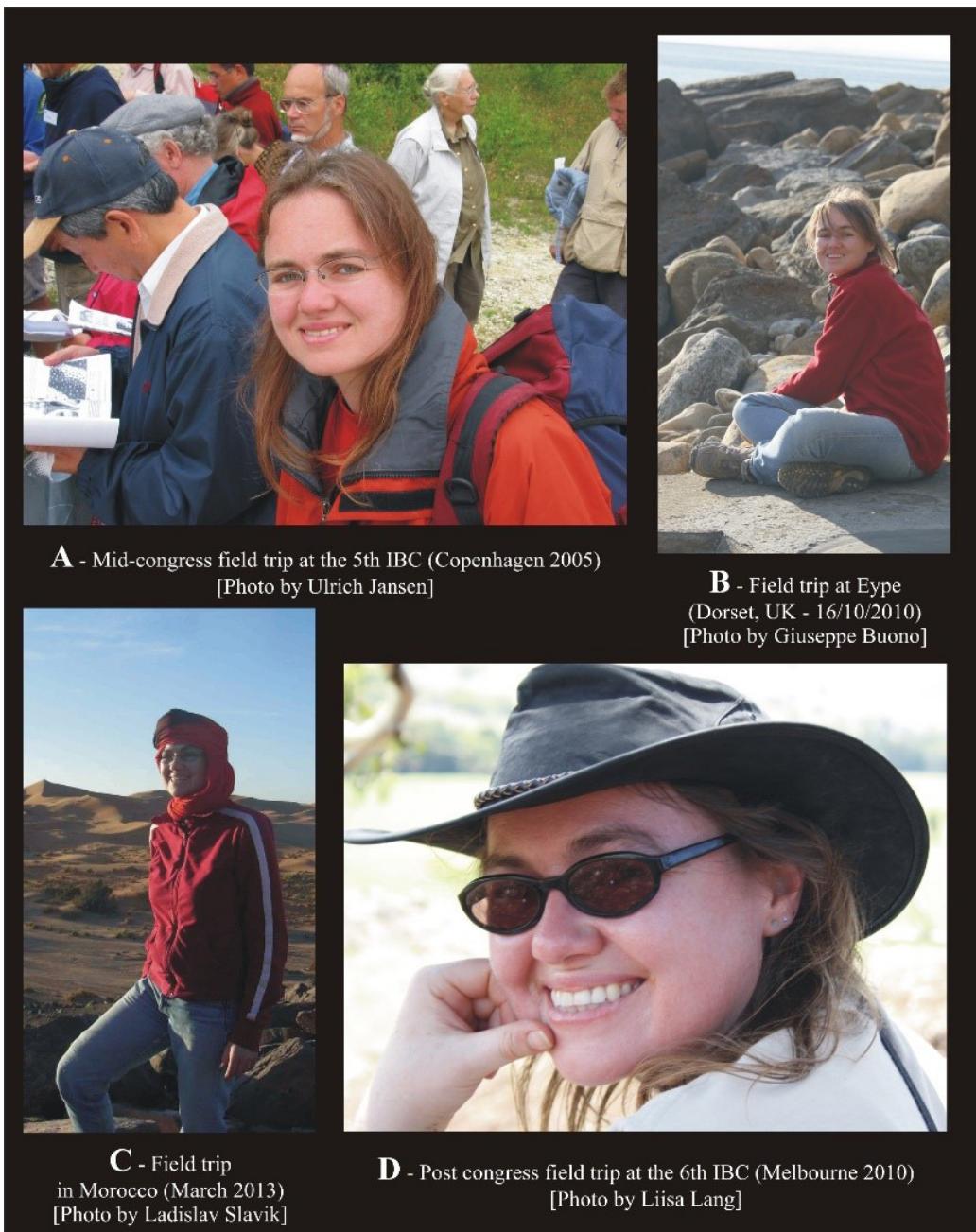
Plate 1 – Mena Daniela Schemm-Gregory during several field trips.

M. Sutton; without forget of course the collaboration with few of our more eminent colleagues "brachiopodologists" (Harper et al. 2010). And this of course has allowed her to investigate many fossil associations different in time and space, even if the core of her research remained Devonian and Jurassic brachiopods.

At the end I want just express my admiration for Mena's work and my deep sadness because we cannot see her in our congresses anymore. Also I remember with great pleasure that a new brachiopod species has been already dedicated to her, the recent terebratulid *Rectocalathis schemmgregoryi* (Seidel and Lüter 2014).

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Brachiopod geochemistry and the Early-middle Paleozoic of Estonia

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With this study we take steps toward filling the gap in the knowledge of stable isotopes evolution in fossils for the Early-Middle Paleozoic of Baltic countries, through $\delta^{13}C_{shell}$ and $\delta^{18}O_{shell}$ analyses (calcitic brachiopods, trilobites, corals), coupled with correspondent samples of rock matrix ($\delta^{13}C_{rock}$), from Ordovician and Silurian of Estonia. Due to low resolution, most of the second-order stable carbon isotopic excursions, except for the Ireviken Event, are not well reflected in the new $\delta^{13}C_{rock}$ and $\delta^{13}C_{brach.}$ data. More interesting are the results from $\delta^{18}O_{brach.}$ values. Most of the Ordovician values are generally higher than those reported in literature from other brachiopod data (especially from Laurentia and Southern China blocks). Silurian values (lower Sheinwoodian, upper Ludfordian, Pridoli) are similar to those reported for Gotland. Taking into account that $\delta^{18}O$ is susceptible to various other environmental changes, interpreting those values in terms of paleotemperatures may suggest the following: Katian high values support a cooling suggested by the Katian $\delta^{13}C_{rock}$ isotope excursions (in agreement with data from $\delta^{13}C_{rock-ESTONIA}$; see Ainsaar et al. 2010); Ordovician values point out a thermal latitudinal gradient when compared with those from Laurentia, which is in agreement with paleogeography and brachiopod paleobioprovinces (cfr. Hareper et al. 2013); during Silurian the isotopic values tend to be similar to those from Laurentia, which is also compatible with northward drifting of Baltica paleocontinent. Additionally, direct comparisons from specimens from same beds show that $\delta^{13}C_{brach}$ is almost always heavier than $\delta^{13}C_{rock}$ (so as supported by literature). Tests with trilobites and corals show that $\delta^{13}C$ and $\delta^{18}O$ values are in a similar range to those obtained from brachiopods.

Fossil phosphatic shelled (lingulate) brachiopods, instead, show a variation in the apatite chemistry along shell lamination and their direct use for isotopic analyses should be handled with care (Lang et al. 2015). Infrared (ATR FT-IR) and energy dispersive spectroscopic (EDS) mapping of the cross sections of Furongian lingulate brachiopod *Ungula ingrica* shells show that the apatite in porous baculate laminae differs from the apatite in compact laminae mainly by its higher carbonate anion and fluorine contents. Less pronounced differences appear also in the relative contents of various cations (Ca, Na, Mg).

Additional crystallographic investigation with electron backscatter diffraction (EBSD) and electron probe microanalysis (EPMA) on the cross sections of calcitic brachiopods is currently in progress to investigate further their preservation, and to assess the influence of crystallography on Mg^{2+} concentration and distribution in brachiopods calcite bio-minerals (with implications for Mg/Ca thermometry and for "vital effect") (see a.e. Pérez-Huerta et al. 2011).

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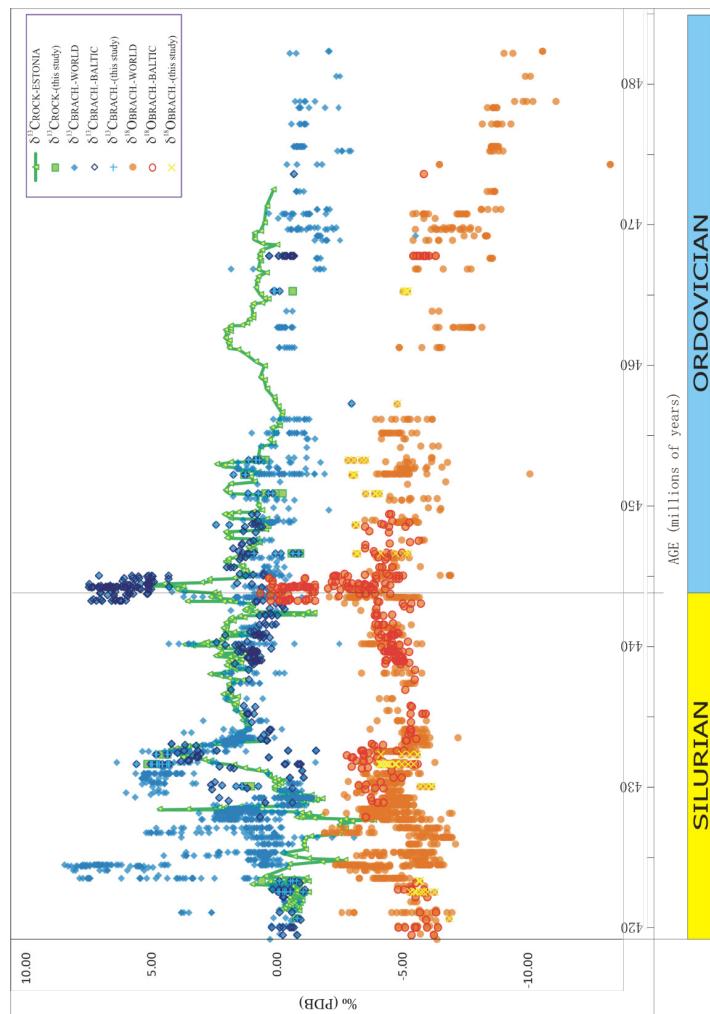
Fig 1.   Brachiopod stable isotopes geochemistry: $\delta^{13}C_{brach\ and}$ $\delta^{18}O_{brach}$ from this study and literature and $\delta^{13}C_{rock-ESTONIA.}$

Estonirhynchia estonica and Uncinuloidea (Brachiopoda): a multidisciplinar investigation

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We examined more than 700 specimens of *Estonirhynchia estonica* coming from 24 localities from Silurian (from Adavere to Paadla stage, Llandovery *p.p.* to Ludlow *p.p.*) of Estonia, plus other uncinuloids (mostly also from Silurian Baltoscandian paleobasin). The study favored the identification of several morphotypes (distinguishable on the base of outline shape, ribs number width and length, umbo and foramen morphology) proofing a high phenotypic plasticity in *E.estonica*. The same is deducible from literature for its strict relatives *Plagiorhyncha* and *Spherirhynchia*, also found in the Silurian of the Baltoscandian paleobasin but in different temporal and facies setting.

A distinctive taphonomic aspect of *Estonirhynchia* from Paramaja outcrop (Estonia, early Sheinwoodian) is a widespread evident to strong plastic deformation mostly localized in the anterior area (*cf.* Zuschin *et al.* 2003). Additionally, dependent on age and locality, we also recorded breakage, dislocation, shell dissolution and/or replacement, shell perforations associated to pyrite crystal growth. Encrusting epifauna (bryozoans and serpulids) is rare and mostly localized in the anterior area, suggesting commensal relationship. Deformation pattern and distribution of epifauna, together with other anatomical features (in particular the commonly atrophied peduncle), suggests that: a) most of specimens was subject to an early diagenetic plastic deformation in life position in course of sediment compaction; b) *E.estonica* changed its life style during ontogenesis from benthic to semi-infaunal, as already suggested for its relative *Spherirhynchia*.

E.estonica flourishing during early Sheinwoodian stable isotopic (C and O) positive excursion (Ireviken event) recorded in Paramaja outcrop, during a sea level transgressive phase, proof as this specie was able to thrive in "difficult" ecological environment. Considering Silurian Baltoscandian basin sea level evolution and features of uncinuloids there found, we suggest that this group gradually moved to the shallow-water environments, i.e. from relatively deep sea *Plagiorhyncha* (flatter and smooth) to the shallower *Estonirhynchia* (spherical, more ribbed, partially smooth), and then to *Spherirhynchia* (spheroidal, fully ribbed, geniculation and spines) adapted to high-energy environments.

High *phenotypic plasticity* in *Plagiorhyncha-Estonirhynchia-Spherirhynchia* lineage (so as blooming during transgressive sea level and stable isotopic positive excursion of *Estonirhynchia*) resembles that one of *Apringia-Soaresirhynchia-Stolmorhynchia* (Early Jurassic) within Basiliolidae (Permian-recent). For Basiliolidae it has been proposed that the capacity to use thalassobathyal platform as *refugia* during ecological unfavorable conditions (Vörös 2005) and *phenotypic plasticity* (Buono and Schemm-Gregory 2013) may have been determinant factors which favored their evolution until today. We suggest that presumably same mechanisms have been a key for the long lineage evolution of Uncinuloidea too.

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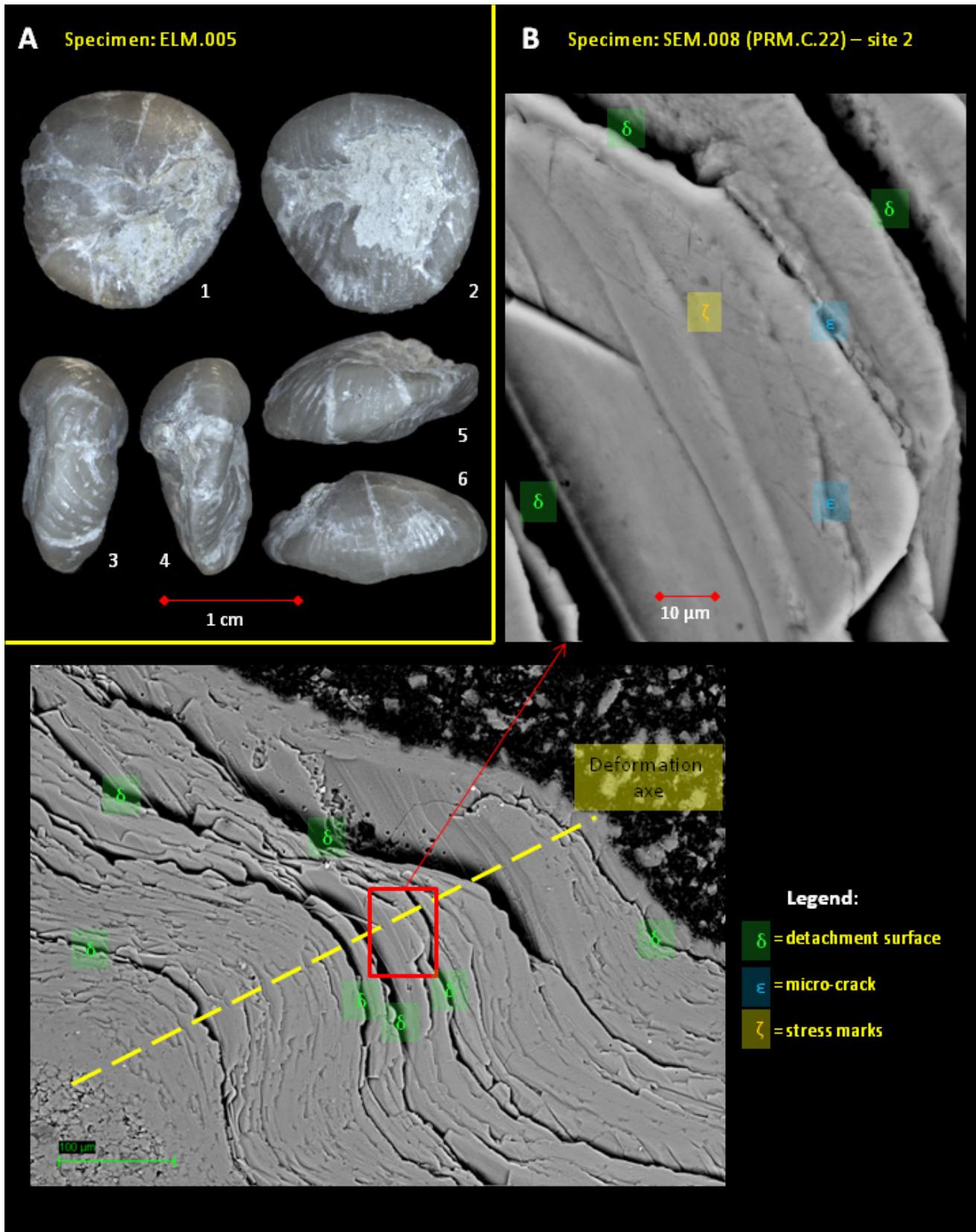
Plate 1. - *Estonirhynchia estonica* from Paramaja, Estonia (Paramaja Fm., early Sheinwoodian). A) highly deformed specimen (deformation >50% in length and proceeding from anterior area), 1: posterior view, 2: anterior/frontal view, 3: left lateral view, 4: right lateral view, 5: brachial/dorsal view, 6: pediclar/ventral view; B) ultrastructural features associated to the deformation in a shell section at the SEM.

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ally concordant to the host bedding layer or inclined in a low angle with the sediment surface. In three slabs of 15cm×8cm, 15cm×12cm and 10cm×13cm respectively, there are 149 shell moulds or casts with compete outline as a whole. Nevertheless, the shell concentration on the different deposition layers is estimated to vary in density. In some cases, the *Palaeobolus* individuals are likely stacked together with one individual overlapping on others. Nevertheless, they exhibited a general similarity in shell size, ranging from 12-18 mm in length according to an incomplete statistics of 149 individuals.

Shell concentration of *Palaeobolus* (Lingulata, Brachiopoda) from the Cambrian (Stage 4) Hongjingshao Formation of eastern Yunnan

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Shell concentrations, referred as relatively dense accumulations of fossil animal remains, are widely known from different sedimentary sequences of mudstone, limestone, and sandstone from Early Paleozoic to Cenozoic across Asia, America, Africa, and Europe. They are of key importance for our understanding of the relationship between paleoenvironments and the fossil communities. In the shell concentrations, fossil components are mostly composed of brachiopods, gastropods, echinoderms, bivalves and trilobites. Nevertheless, brachiopod-dominated shell concentrations are largely known since the Middle Cambrian in the world.

Here, we document for the first time the monotaxic shell concentration of lingulate brachiopods in details from the upper quartz sandstone-siltstone sequence of Early Cambrian (Stage 4) Hongjingshao Formation. The Hongjingshao Formation represented a post-Chiungzhussian (Chengjiang fauna) regression event that is clearly evidenced by a thick-bedded sequence of quartz sandstone interbedded with siltstone. The deposition sequence was widely developed and exposed in the Kunming-Wuding area. Therefrom, few fossils were so far revealed. In the Malong-Qujing area, the Hongjingshao Formation, however, consists of a sequence of sandstone intercalated with purple thin-bedded shale or silty mudstone that contains an abundant variety of abundant shelly fossils dominated by multi-taxonomic trilobites and rich lingulids, named as Malong fauna (Luo et al., 2008). The lingulate brachiopod was originally referred to *Lingulepis yunnanensis* Rong, 1974. Nevertheless, a further study made by Zhang et al. (2011, 2014) suggested the brachiopod taxon was better assigned to the genus *Palaeobolus*. The taxonomic assignment was endorsed by the densely spaced concentric growth lines and subtriangular outline of shell valves.

Preliminary analysis suggests individual lingulids are usu-

Recovery pattern of brachiopods after the Permian-Triassic crisis in South China

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The Permian-Triassic (P-Tr) mass extinction is the largest biotic crisis that occurred in the Phanerozoic (Sepkoski, 1981; Hallam and Wignall, 1997) and caused the extinction of more than 90% of the marine species (Raup, 1979; Erwin, 1993; Jin et al., 2000). Brachiopods were one of the most abundant invertebrates in the Permian oceans, but they suffered a severe extinction during the P-Tr crisis (Carlson, 1991; Erwin, 1993). In South China, the Changhsingian brachiopods are extraordinarily abundant and diverse, comprising 447 species in 143 genera. However, approximately 99% of brachiopod species were eliminated during the Permian-Triassic (P-Tr) mass extinction event. In this study, a total of 56 species in 32 genera were identified from the Early and Middle Triassic strata at the Zhongzhai, Chaohu, Zunyi, Susong, and Qingyan sections. These brachiopod data, in combination with the published literature, suggest that Brachiopods in the aftermath of the P-Tr mass extinction were highly rare, but only one disaster taxon, *Lingula*, occasionally occurred in the Griesbachian and Smithian at a high abundance. Species-
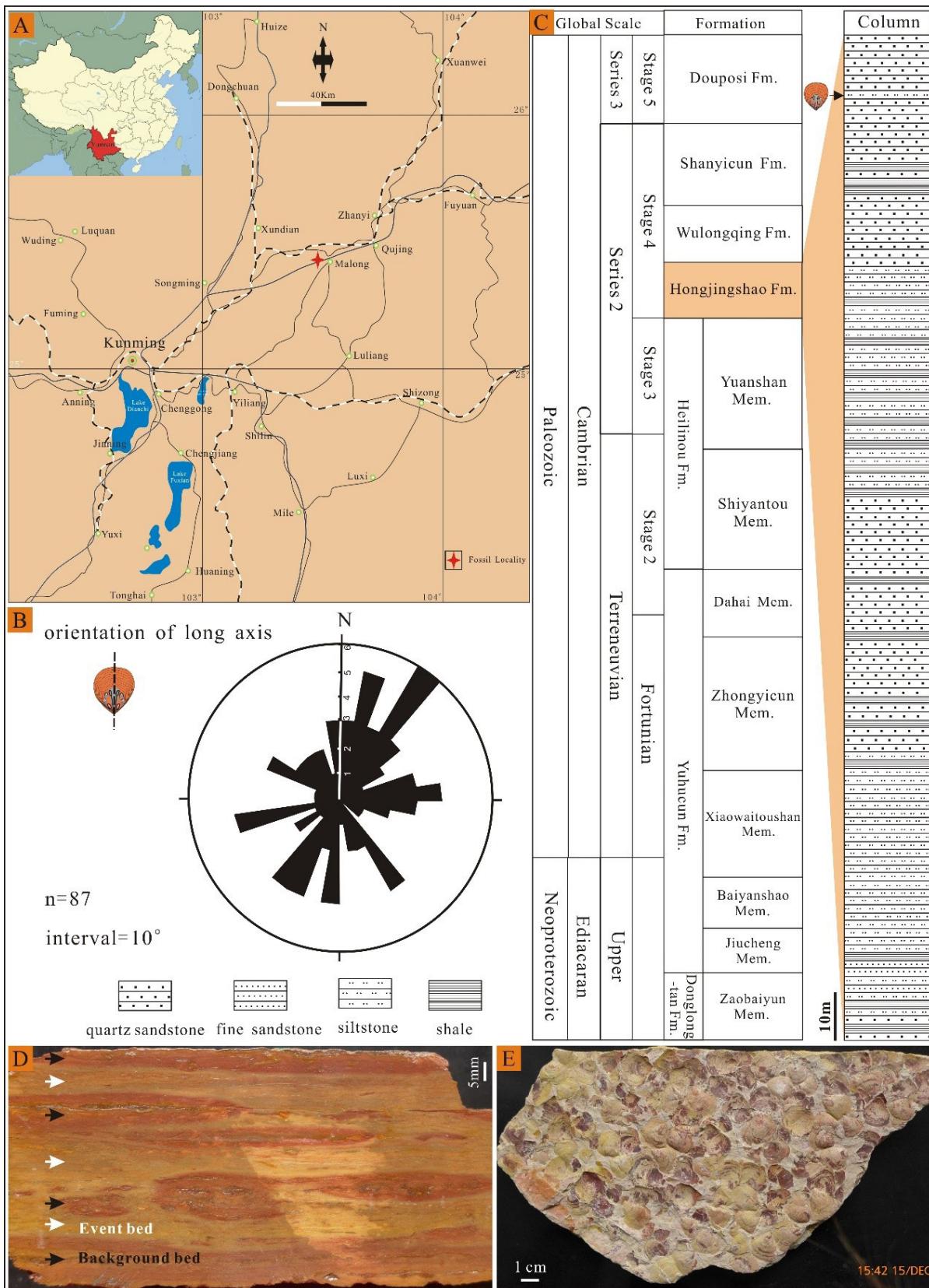
Fig. 1. A. Geographical map of Luoshuidong section in Malong, Yunnan Province showing the fossil locality of *Palaeobolus* (Lingulata, Brachiopoda); B. Rose diagram showing no obvious preferred orientation of shell valves; C. Stratigraphic column of the Lower Cambrian in the Luoshuidong section and the occurrence of *Palaeobolus* (Lingulata, Brachiopoda); D. Cross-cut section showing couples of event beds (EB) and background beds (BGB); E. Shell concentration of *Palaeobolus* from the Early Cambrian Hongjingshao Formation (Stage 4) at Luoshuidong section.

diversity of articulated brachiopods in the early Griesbachian, late Griesbachian, Dienerian, and Smithian are 34, 2, 2, and 1, respectively. Although a number of Mesozoic-type species occurred in the Griesbachian, Dienerian and Smithian, a marked diversification of brachiopods occurred in the Spathian and early Anisian and was characterised by 9 and 17 Mesozoic-type species, respectively. The two-phase diversification of brachiopods coincides with the two explanations of the refuge zone, suggesting that the improvement of marine environmental conditions (e.g., lethally hot temperature and anoxic seawater) played a key role in brachiopod recovery after the P-Tr mass extinction.

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The distribution of the Lower Devonian brachiopod genus *Paraspirifer* Wedekind, 1926 and its palaeo-biogeographic implications

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Lower Devonian strata are widely distributed in northeastern Inner Mongolia. The abundant benthic fossil faunas have been collected from the Lower Devonian beds in East Ujimqin Banner, Inner Mongolia; they include for example, brachiopods (Su 1976), bryozoans, tabulate corals, and trilobites. 176 specimens of "*Paraspirifer*" were collected from the Lower Devonian Bayuntehua and Aobaotinghundi formations. The specimens of this genus are characterized by large size, high fold and shallow sulcus, the frequent presence of bifurcating lateral plications and short dental plates. The most specimens of "*Paraspirifer*" found in East Ujimqin Banner are preserved as molds.

The specimens of *Paraspirifer* are widely distributed in the upper Emsian (upper Lower Devonian) and lowermost Eifelian (lowermost Middle Devonian) of Central Germany and preserved mostly by articulated shells, but also by molds (Solle 1971). This genus has been reported also from the Lower Devonian of northeastern China (Great Khingan district), Beishan of Gansu, Junggar Basin (Zhang *et al.* 1983) and Central Kazakhstan. The distribution of *Paraspirifer* is useful to explain the affinities between these regions and plays an important role in palaeobiogeographic analysis. A detailed morphological comparison of taxa from the different regions is still in preparation.

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Permian-Triassic evolutionary dynamics of the Brachiopoda: paleobiogeography, extinction-survival-recovery, latitudinal diversity gradients, body size variation, and longevity changes

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A critical review on global brachiopods from the Late Permian to Middle Triassic reveals that the Permian-Triassic (P-Tr) brachiopod provincial changeover exhibits a tendency towards simplification from the latest Changhsingian to Induan, and then diversification from the Olenekian to Anisian. Brachiopods diversified in Anisian and retained a very high provinciality. Their radiation, however, cannot be readily related to the lineages that initially recovered during Olenekian. Brachiopods experienced extremely high extinction rates and the greatest loss of biodiversity during the first phase of the P-Tr mass extinction (PTME). Frequent speciation was probably an important survival strategy for the survivors populating the devastated environments of Early Triassic. Two significant biodiversity increases, coupled with high origination rates, coincided with the initial recovery of the clade during Smithian and full recovery during Anisian. Nevertheless, final recovery or radiation of the clade did not occur until the Pelsonian of the middle-late Anisian, about 8-9 myr after the PTME. Four of the nine Changhsingian orders, the Orthotetida, Orthida, Productida and Spiriferida, eventually became extinct in the PTME and its aftermath, although they had a few Dead Clade Walking (DCW) forms persisting into the Griesbachian. Moreover, four lifestyles of the six lifestyles common in Changhsingian were lost in the PTME: body cementation, body spines anchoring on substratum, clasping spines on other shells/or objects, and pedicle attaching on objects. Of the five orders that diversified during Anisian, the Rhynchonellida particularly proliferated around the world. Pedicle attaching on substratum is the commonest life mode among the recovery faunas. Ecologic selectivity of the P-Tr brachiopods suggests that rapidly elevated seawater temperature, rather than anoxia and ocean acidification, may be accountable for the morality of the clade in the P-Tr biocrisis.

The Changhsingian, Induan and Anisian faunas in the northern hemisphere show pronounced latitudinal diversity gradients, exhibiting a decline in biodiversity from tropics toward high latitudes. Latitudinal controls on brachiopod extinction and origination rates are also conspicuous in the Changhsingian faunas in the northern hemisphere, indicating that elevated seawater temperature may have facilitated speciation. Increasing extinction rates from high latitudes toward the tropics also indicate that elevated temperature may have impacted niches in high to moderate latitudes more seriously than in the tropics. The high origination rate in tropics may have facilitated faunal radiation in Anisian. Like other benthos, brachiopods have also suffered the Lilliput effect in the P-Tr biocrisis, which not only resulted in a dramatic reduction in body size, but also narrowed size variation range. Several extinct orders, i.e., the Productida and Spiriferida, severely suffered the Lilliput effect, whereas the mean body size of recovery groups, such as the Lingulida, Athyridida, Rhynchonellida and Spiriferinida, were less affected by the crisis. The post-extinction increase in body sizes, coupled with a broadening size variation range, coincided with initial to final recovery process through the Smithian to Anisian. Longevity of brachiopod genera was relatively short prior to the PTME, but increased significantly during Early Triassic, and returned to a reasonably low level after final recovery in Anisian. The Early Triassic genera usually lived an average of 24-34 myr longer than both pre-extinction and the recovery genera. This is probably because the post-extinction faunas are dominated by long-range, opportunistic taxa, and also implies that slower evolutionary rates, hence a longer mean longevity, was an important life strategy for the genera that survived the PTME. The recovery brachiopods show slightly shorter longevity than the pre-extinction faunas.

Carboniferous postglacial brachiopod faunas in the southwestern Gondwana margin

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The glaciomarine sediments related to the Late Paleozoic Ice Age (LPIA), have an excellent stratigraphic record in Argentina, particular those associated to the Late Carboniferous glacial episode identified along the southwestern South American basins (López Gamundí, 1997). The deglaciation processes connected to this event produced an important sea level rise and consequently an extended postglacial transgression from Bolivia (Tarija basin) to Argentina (Precordillera and Patagonia).The aim of this contribution is mainly a biostratigraphy update of the carboniferous brachiopod faunas that occur in the earliest postglacial interval (late Serpukhovian-Bashkirian) in Precordillera and its regional correlation with those equivalent in the nearby basins (Fig. 1A).

Two faunal assemblages with significant taxonomic, taphonomic and paleoecological differences, appear associated to the earliest postglacial transgression in the Carboniferous diamictite-bearing sequences of the Calingasta-Uspallata basin in Precordillera (Fig. 1B): the *Levipustula* fauna, widely studied because its biostratigraphic, paleocologic and paleobiogeographic implications (Cisterna and Sterren, 2010), and a less known assemblage from the El Paso Formation. The *Levipustula* fauna is composed by bryozoans, bivalves and brachiopods, with less abundant gastropods and crinoids. Brachiopods that integrate this fauna are dominated by spiriferids (*Costuloplica leoncitensis*, *Kitakamithyris booralensis*, *Kitakamithyris immensa*, *Kitakamithyris* sp., *Torynifer tigrensis*, *Spiriferellina octoplicata*, *Septosyringothryis keideli*), accompanied by the ubiquitous productid *Levipustula levis* and the terebratulid *Beecheria* sp. This fauna has been particularly studied from the postglacial shales of the Hoyada Verde Formation in the core of Barreal Hill, where it occurs either as shell beds of 1-5 cm thick or as nests. Brachiopod communities herein recognized would have been developed in an open shelf with moderate bottom currents; paleocological variations identified appear to be controlled by substrate types and
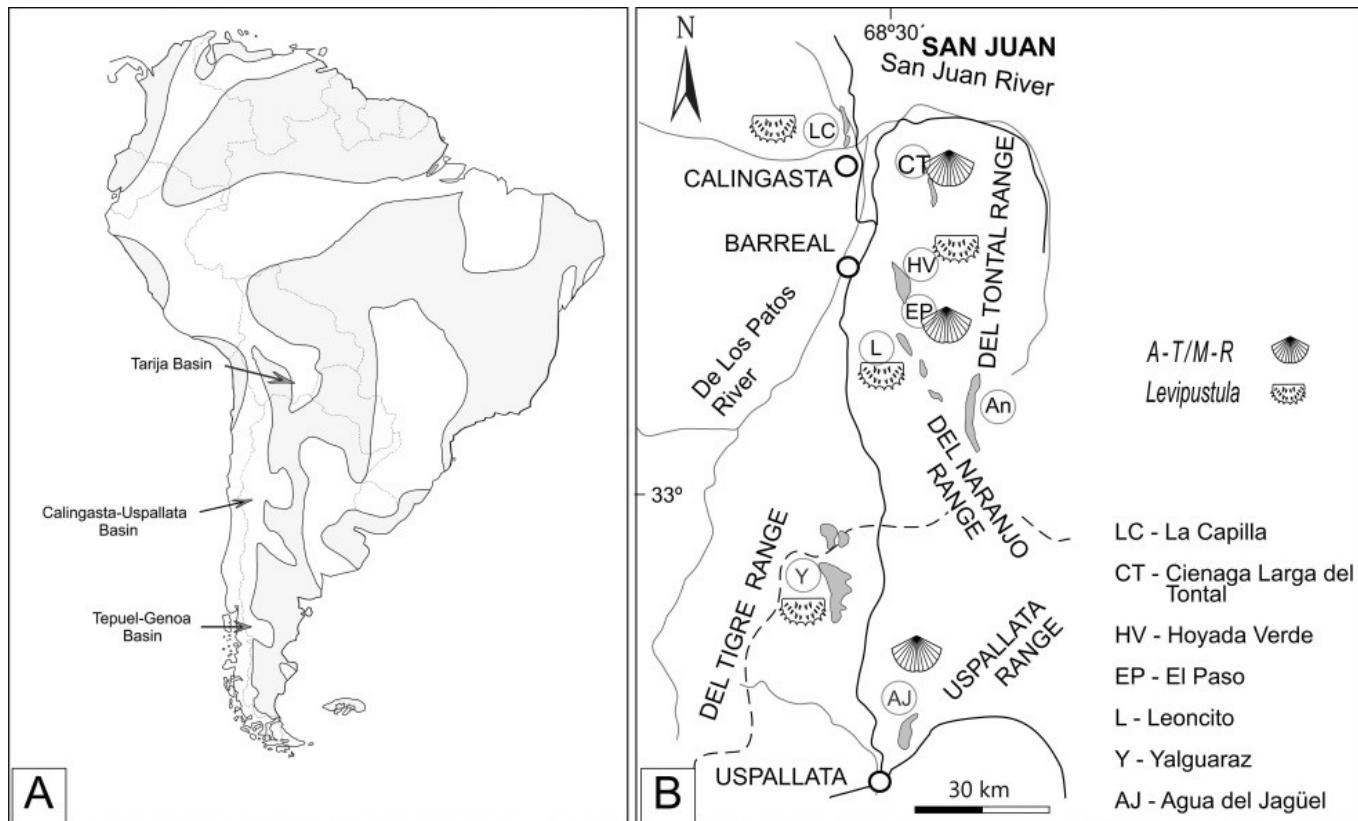
Fig. 1. Location Map

food supply fluctuations during the postglacial transgression. The fauna described from the glaciomarine succession of the El Paso Formation occurs a few kilometers from the Hoyada Verde Formation outcrops, in the southernmost part of the Barreal Hill. The fossil assemblage appears very scattered in thick mudstone packages with calcareous concretions to the upper part of this unit. The brachiopod faunas recognized, that integrate an assemblage composed of bivalves, gastropods, conularids, nautiloids and corals, are dominated by productids (*Aseptella* aff. *patriciae*, *Tuberculatella peregrina*, Productellidae indet., Linoproductidae indet.), accompanied by chonetids (*Micraphelia indianae*, Chonetoidea indet.), orthids (*Rhipidomella* sp.), inarticulates (lingulids and *Orbiculoidea* sp.), terebratulids (*Beecheria patagonica*) and athyrids indet. Analyzed under of the sequence stratigraphy viewpoint, these invertebrate faunas would be housed in the glacial submarine retreat (transgressive) facies association (López Gamundí, 1997) and it consists of open marine, fine-grained sediments with or without ice-rafted debris in mudstones and claystones. This study suggests that the El Paso Formation can be considered equivalent to the Hoyada Verde Formation (López Gamundí and Martínez, 2003). However, compositional and paleoecological features of their faunal assemblages are different. The brachiopod association *Aseptella-Tuberculatella*/*Rhipidomella-Micraphelia* from the El Paso Formation exhibits a particular biostratigraphic correlation value: *Aseptella-Tuberculatella* has been also identified in the Calingasta-Uspallata basin from the glacial interval of the Ciénaga Larga del Tontal Formation, and *Rhipidomella-Micraphelia* has been recognized in the earliest postglacial transgression of the Agua del Jagüel Formation. The

age of *Aseptella-Tuberculatella/Rhipidomella-Micraphelia*, has been recently defined as late Serpukhovian-Bashkirian by the palynological data associated, i.e. *Raistrickia densa-Convolutispora muriornata* (DM) Palynozone (Cisterna et al., 2013; Vergel et al., in press).

In the Tarija Basin from Sub Andean Bolivian area, the brachiopod *Levipustula levis* Maxwell was described from the postglacial sequences of Taiguatí Formation (Rocha-Campos et al., 1977); the Bolivian species has been considered comparable with western Argentinian specimens and the Australian type material of *Levipustula levis* (Taboada and Shi, 2011).

In Patagonia the two faunal assemblages related to the carboniferous glacial episode integrate the *Lanipustula* biozone (late Serpukhovian-Bashkirian? Pagani and Taboada, 2010) and the *Tuberculatella* biozone assigned to Kasimovian-early Asselian interval (Taboada, 2008), mainly recognized in the glaciomarine intervals with diamictite and mudstones of the Pampa de Tepuel Formation (Tepuel-Genoa Basin). Considering the database available (Pagani and Taboada, 2010), the *Lanipustula* fauna would be particularly dominated by bivalves and bryozoans, accompanied by gastropods, echinoderms, ostracods and cnidarians with scarce cephalopods and trilobites. Brachiopods are mainly represented by the key species *Lanipustula patagoniensis* and *Lanipustula kletsi,* although a diversified spiriferid fauna has been also cited. The brachiopod assemblage of the *Tuberculatella* biozone, mainly composed by bivalves, brachiopods, gastropods and cephalopods, is characterized by *Tuberculatella? laevicaudata*, *Amosia sueroi* and *Verchojania archboldi*. The species *Aseptella patriciae* and *Beecheria patagonica* have been also included in this biozone

(Simanauskas and Sabattini, 1997) but their stratigraphic location is not clear.

In conclusion, two postglacial faunas associated to the diamictite bearing sequences of the late Serpukhovian-Bashkirian interval are recognized: the widely extended *Levipustula* fauna identified in the Argentine Precordillera and Bolivia, and the *Aseptella-Tuberculatella/Rhipidomella-Micraphelia* association from Precordillera. Strong faunal contrasts between western Argentina and Patagonia have been proposed because of the paleogeographical position of Patagonia, considered to be a terrane accreted to Gondwana in the Late Paleozoic (Ramos, 2008). However, the *Lanipustula* fauna dominated by bryozoans and bivalves with diversified spiriferid brachiopods appears to be comparable with the *Levipustula* fauna from western Argentina. Also, the brachiopod assemblage from *Tuberculatella* biozone would exhibit some common elements (*Tuberculatella, Aseptella, Beecheria*) with the *Aseptella-Tuberculatella/Rhipidomella-Micraphelia* association, hence it could have also an interbasinal correlation value. The significant compositional differences observed between this assemblage and the relatively equivalent *Levipustula* fauna, should be explained by paleoecological controls. The present review offers an appropriated scenario to future statistics paleoecological analyzes, with the purpose of to understand the evolution of the Carboniferous postglacial faunas in Gondwana.

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Application of shell spiral deviation methodology to fossil brachiopods: Implications for obtaining specimen ontogenetic ages

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Knowledge of specimen ontogenetic ages of fossil brachiopods has great utility in paleoecological and paleoclimatic studies, but there is currently no efficient means of obtaining this information. Previous studies have shown that shell spiral deviations correspond to ontogenetic ages and seasonal growth in modern brachiopods, but this approach has not been tested on fossil specimens. In this study, we analyze the application of this methodology using four species of fossil brachiopods, including *Laqueus rubellus, Terebratula terebratula, Platystrophia ponderosa*, and *Pseudoatrypa* sp., each of which possesses different shell outline and surface ornamentation patterns. The computer programs Vextrator and R were used for digitizing and morphometric analyses, respectively. Our results indicate that smooth biconvex shells produce spiral deviation graphs with a biological meaning that represents accurate specimen-based ontogenetic ages, but without providing by itself information on seasonal growth, and factors controlling shell growth. Finally, the R-based spiral devia-

tion methodology for ontogenetic age determination, which was originally developed for brachiopods, has a potential application to any modern and fossil marine invertebrates secreting shells by accretion.

Ordovician to Devonian brachiopod distributions and palaeogeography

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Following their initial radiation during the Cambrian, brachiopods continued to diversify throughout the Ordovician, Silurian and Devonian; however, most of that later radiation was within the articulate groups, chiefly the Subphylum Rhynchonelliformea. Brachiopods were initially confined to shallow waters, but expanded their habitats downslope to the edge of the continental shelf and beyond, enabling differentiation into numerous marine brachiopod-dominated benthic communities. After the original analysis for the Early Silurian by Ziegler et al. (1968), those com-

munities have been documented by many authors during the past half century, particularly those of the Late Ordovician, Silurian and Devonian.

At the start of the Ordovician, wide oceans separated the largest continents, so that provincialisation between brachiopods, which had started during the Late Cambrian, is striking. The chief groups, which are named from the trilobites which lived in association with the brachiopods (Fortey and Cocks 2003), characterised the continents of Laurentia, Baltica, and Gondwana. For example, the orthoid *Lycophoria*, which occurs in rock-forming abundance in the early Ordovician of Baltica, is not only endemic to that continent, but is the only genus within the family Lycophoriidae, whose relationships to other orthoids is obscure. However, as the Ordovician progressed, the oceans narrowed between those continents, so that by the Late Ordovician only the remnants of the distinct Laurentian brachiopod communities had survived in the Cincinnatti region of America, whilst descendants of separate genera which had originally lived apart in the Avalonian sector of Gondwana and also Baltica occupied most of the Laurentian continent.

The global climates changed much during the Ordovician to Devonian, sometimes rapidly, such as during the onset of the Late Ordovician Hirnantian glacial event, but more often at a more measured pace. During the cooler periods the overall global temperatures were much less equitable, so that there was a much greater temperature range between the tropical Equator and the
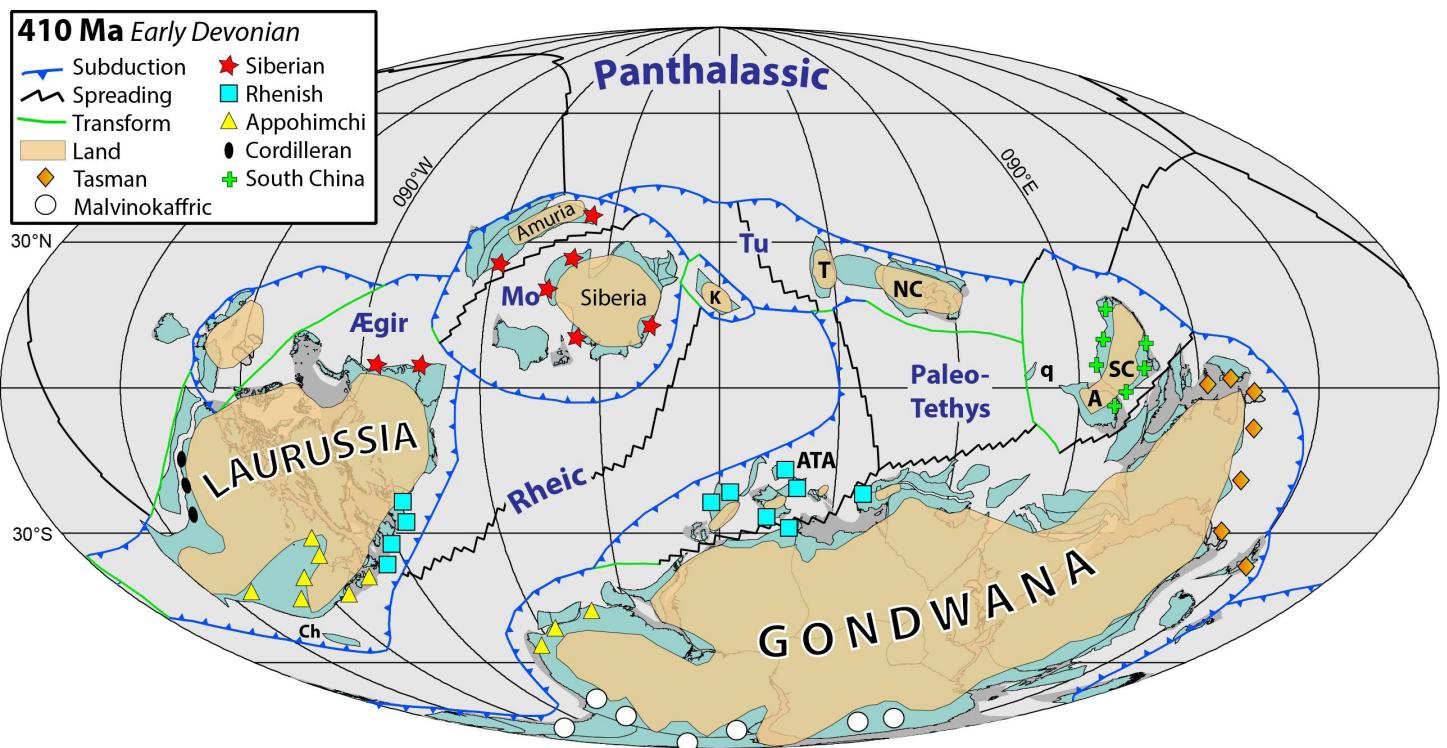
Fig. 1. The Early Devonian (Emsian) world, showing the major land areas and the outlines of the tectonic blocks which have survived, although not the Devonian shore lines. Also shown are the major subduction zones and spreading centres (after Domeier & Torsvik 2014), and the major sites of the brachiopod provinces with their symbols in the box (data partly from Boucot et al. 1969). A, Annamia (Indochina); ATA, Armorican terrane Assemblage; Ch, Chilenia; K, Kolyma-Omolon; Mo, Moldanubian Ocean; q, South Qiantang; NC, North China; SC, South China, T, Tarim; Tu, Turkestan Ocean. New diagram (to be published in our forthcoming Cambridge University Press book).

two much cooler poles. The brachiopod communities reflected those changes; for example, during the Silurian and Early Devonian the successive lower-diversity Malvinokaffric communities were entirely confined to the higher southern latitudes. In contrast, the lack of land in most of the vast Panthalassic Ocean, which covered much of the northern hemisphere for the whole of the period, precluded the colonisation of comparable high-latitude communities near the North Pole.

The Hirnantian glaciation lasted for less than a million years, a period which was characterised by various brachiopod associations grouped under the name *Hirnantia* Fauna. However, the *Hirnantia* Fauna is not itself a cooler-water fauna, although some of its less diverse associations lived at cool higher latitudes, but consists of pioneer species within genera such as *Hirnantia, Eostropheodonta* and *Hindella* which quickly adapted to the deeper water which had become oxygenated due to the glaciation.

After the Hirnantian glacial episode the global temperature both slowly rose and also became more uniform, so that by the end of the Llandovery the faunas were in general rather cosmopolitan. However, an exception to that is the later Silurian *Tuvaella* Fauna, which was restricted to Siberia and peri-Siberia, which was the only substantial continent north of the Equator in those times and at some distance from the other land masses.

Presumably again because of an increased latitudinal temperature gradient, during the Early Devonian, several provinces again became distinguishable. In addition to the Malvinokaffric Province in the higher southern latitudes, Fig. 1 shows the Emsian provinces, revised from a variety of data much of which was first published by Boucot et al. (1969).

However, after the Emsian, Devonian climates were not only generally warm but there was also much less latitudinal differentiation than the Phanerozoic average. There were no proven Devonian icecaps until the Late Devonian (Famennian), and they are only known from glaciogenic rocks in South America. Thus the brachiopod provincialisation was less extreme during the latter two-thirds of Devonian time than it had been in the Ordovician and Silurian. In particular, the high-latitude Malvinokaffric Province became obliterated by its more temperate neighbours. In addition, the distances between many of the major continents gradually became shorter than the Phanerozoic average.

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Evidences of taphonomic reelaboration in jurassic

brachiopods from the Iberian Range (NE Spain)

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Taphonomic reelaboration consists in the exhumation and displacement of previously buried elements. The recognition of reelaborated elements is utterly important for both the biostratigraphic and sequential analysis since they are always older than the bed containing them and their occurrence is indicative of environments with high hydrodynamic energy and low sedimentation rates (Fernández-López 1991; Fernández-López & Meléndez 1995).

Brachiopod (Terebratulida and Rhynchonellida) remains showing clear evidences of reelaboration are found in the ferruginous oolitic limestones recorded at the Callovian-Oxfordian (Middle-Upper Jurassic) boundary in the Iberian Range, Northeastern Spain. These facies have been interpreted as condensed, irregular and episodic deposits formed in a very shallow to temporarily emerged platform (Aurell et al. 1995, Ramajo & Aurell 2008).

The criteria for the recognition of reelaborated brachiopods are mainly those defined for ammonites by Fernández-López (1984) such as:

• Textural (petrographic), chemical or mineralogical differences between the inner mould and the enclosing sedimentary rock, which indicates that sedimentary infilling and burial represent two different deposition events;

• Fracture or abrasion surfaces affecting the inner mould, which requires previous lithification;

• Ferruginous crusts coating inner moulds, which requires previous corrasion of the shell in addition to lithification.

Some reelaborated brachiopod moulds display a characteristic abrasion surface consisting in a furrow tracing the shape of the commissure, named commissural furrow. Several developmental stages of commissural furrows have been recognized, showing a progressive increment in the width of the furrow and the roundness of its edges, which is consistent with the fragmentation pattern observed in some recent brachiopods with three layered shells (Emig 1991).

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New taxonomically important observations on the microestructure of the cardinalia of Jurassic Norellidae (Rhynchonellida)

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The Superfamily Norelloidea AGER is characterized by bearing crura of the arcual group, and its division in families is established according to crural types. The classification at the subfamily level among Norellidae AGER (arcuiform crura) is based on the development of dorsal septum and septalium besides other criteria (Manceñido et al. 2002): in Norellinae AGER, Laevirhynchiinae DAGYS and Monticlarellinae CHILDS both septalium and dorsal septum are absent or much reduced while in Paranorellininae XU, Holcorhynchellinae DAGYS, Praemonticlarellinae MANCEÑIDO & OWEN and Diholkorhynchiinae XU & LIU, although variable, both structures are present.

Williams & Brunton (1997) define the septalium as a "trough-like structure of dorsal valve between crural bases, consisting of crural plates fused medially and usually supported by a median septum". Nevertheless, new insights in the microstructure of the cardinalia in *Praemonticlarella distercica* GARCÍA JORAL (type-species of the type-genus of Praemonticlarellinae), reveal a similar but microstructurally different structure. It is formed by callosities enclosing the cardinal plates, growing concentrically from them, and fusing with a median ridge in the dorsal valve floor. These structures could not be named crural plates nor septum, the latter is rather a pseudoseptum in the sense of Westbroek (1967). The same structure has been observed in *"Rhynchonella" solitaria* OPPEL, another Jurassic species with arcuiform crura (Colás 2014). Moreover, the Oxfordian (Late Jurassic) representatives of the genus *Monticlarella* QUENSTEDT (type-genus of Monticlarellinae) recorded in the Iberian Range (NE Spain) show callosities enclosing the cardinal plates and lining the dorsal umbonal cavity, not fusing medially to the pseudoseptum, microstructurally identical to that described above. Due to the differences in microstructure between the cardinal structure in *P. distercica* and *"Rh." solitaria* and the true septalium, they should

be considered as non-homologous structures, but they could be analogous for the reinforcement of cardinalia, as the so-called "septalium" displayed by some terebratellids (Delance & Laurin 1973). On the other hand, the cardinal callosities in *P. distercica* and *"Rh." solitaria* and those in *Monticlarella* could be considered homologous based on their microstructural similarity and phylogenetic relationship, despite other morphological differences.

According to these observations, a deep review on the microstructure of the cardinal structures of norellids seems necessary for its comprehensive systematic arrangement. Representatives of the group bearing true septalium (consisting in crural plates and septum) should be grouped separately from representatives with cardinal reinforcement consisting in enclosing callosities and pseudoseptum, as it is done among the Palaeozoic Ancistrorhynchoidea COOPER (García-Alcalde 2009).

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Oligocene and Miocene brachiopods of the Maltese Islands: taxonomy, diversity, distribution

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Miocene brachiopod fauna of the Central Paratethys is relatively well-known by now, as modern revisions and new studies were published during the last few decades. At the same time, the Mediterranean Sea represents a much larger area, and knowledge of its brachiopod fauna is uneven. Brachiopod studies are known mainly from Italy and Spain, but most of these papers deal with Pliocene and Pleistocene assemblages. Miocene brachiopods are less known, especially from the southern part of the Mediterranean. Paleogene and Neogene brachiopods have been sparsely studied from the Oligo-Miocene succession of the Maltese islands. Although a few works have been produced on the subject in the middle 19th century, and a new genus and species described in the middle-late 20th century, brachiopods generally were only mentioned in context with other geological and palaeontological issues being discussed. Davidson (1864) published a short paper from Malta, and surprisingly this is not only the first but also the last significant systematic work on Maltese fossil brachiopods. Another two papers worth mentioning are Pedley (1976) on palaeoecological study of brachiopods and bryozoans of the *Terebratula-Aphelesia* Bed and Cooper (1983) who described genus *Maltaia*. In all the other papers only faunal lists were published, therefore a modern systematic study on the Maltese Oligocene-Miocene brachiopod fauna is highly topical.

Maltese brachiopods are studied in detail in the present work and extensive new materials from three different sources are investigated. The most diverse brachiopod material (1311 specimens) including both micro- and macromorphic species is a private property of one of the contributing author (MG). These specimens were collected through visual picking and extraction of fossils in the field at 30 different localities. Numerous micromorphic brachiopods and additionally some macromorphic ones (altogether 1363 specimens) derived from the field work connected to bryozoan studies of another contributing authors (PM). The brachiopod material was selected from 22 washed bulk samples of five sections. The third brachiopod material collected by third contributing author (AWJ) forms part of an extensive material investigated during the preparation and publication of a monograph on Maltese holoplanktonic Mollusca (Janssen 2012). This brachiopod material was derived primarily from the dissolution of limestones and associated phosphorites through the use of formic acid and acetic acid (37 samples from 18 localities; 117 specimens). Some historical brachiopod faunas from Malta were also studied by the corresponding author (AD) in the Natural History Museum in London, in the framework of a Synthesys project (268 specimens).

Additionally to the nine species of brachiopods already recorded in previously published works (*Aphelesia bipartita*, *Terebratula terebratula*, *Maltaia maltensis*, *Gryphus minor*, *Terebratulina retusa*, *Megathiris detruncata*, *Joania cordata*, *Megerlia truncata*, *Lacazella adamsi*), a further ten species are being added: *Novocrania anomala*, *Aphelesia margineplicata*, *Cryptopora lovisati*, *Terebratula maugerii*, *Gryphus sphenoideus*, *Argyrotheca bitnerae*, *A. cuneata*, *Platidia anomioides*, *Dallina septigera*, *Megerlia eusticta*. A few specimens of a possibly new *Aphelesia* species were also recorded.

Stratigraphical distribution of the identified species within the Maltese Oligo-Miocene strata is also investigated in detail. Used abbreviations of the lithostratigraphic units from older to younger are the following: LCLF – Lower Coralline Limestone Formation (?Rupelian); LGLM – Lower Globigerina Limestone Member (Chattian); LPC C1 – Lower Phosphorite Conglomerate, base of MGLM (Chattian); MGLM – Middle Globigerina Limestone Member (Burdigalian); UPC C2 – Upper Phosphorite Conglomerate (Langhian); UGLM – Upper Globigerina Limestone Member (Langhian); BCF – Blue Clay Formation (Serravallian/ Tortonian); GSF – Greensand Formation (Tortonian); UCLF – Upper Coralline Limestone Formation, base: grey marls, yellow marly micrites, yellow micrites, coralgal bioherms (Tortonian).

Novocrania anomala is known from C1 and C2 Phosphorite Conglomerates and from UGLM just above C2. Among the different *Aphelesia* species *A. bipartita* is the most common (LGLM, GSF and especially frequent in different facies of the base of UCLF). *A. margineplicata* and the new *Aphelesia* species are less common but occur both in GSF and at base of the UCLF. *Cryptopora* has never been recorded from Malta; however, on the basis of our new materials it was present in several horizons from Chattian to Tortonian (LGLM, MGLM, UGLM, BCF, UCLF). *Terebratula* is one of the most widespread brachiopod in Maltese sediments. *T. terebratula* seems to be present from the Rupelian to the Tortonian (LCLF/LGLM boundary, C1, C2, UGLM, BCF, GSF, UCLF base; being most common in Langhian and Tortonian, especially in GSF and UCLF). *T. maugerii* was recorded only from the Tortonian GSF. *Maltaia maltensis* occurs only in different facies of the UCLF base (grey marls, yellow marly micrites and especially in coralgal bioherms). *Gryphus* is represented by two species in Malta, but *G. minor* shows much wider stratigraphic range (LCLF, LGLM, MGLM, C1, UGLM, C2, GSF, base of UCLF), while *G. sphenoideus* occurs only in the lower horizons (LCLF, LGLM, C1, C2 and UGLM). The otherwise very widespread *Terebratulina retusa* has limited records in Malta, being known only from one locality of C2, and two localities of UCLF base. Among megathiridid brachiopods, *Megathiris detruncata* is the most common species (LCLF, UGLM, BCF, GSF, and especially UCLF base). *Joania cordata* is also relatively frequent (BCF top, GSF, UCLF base), *Argyrotheca cuneata* was found in the same levels, however, with smaller specimen numbers (BCF top, GSF and UCLF base), while *A. bitnerae* is present only in limited numbers at UCLF base (3 specimens / 2 localities). *Platidia anomioides* is represented only by 3 juvenile specimens in washed residues (BCF top and UCLF base). *Dallina septigera* has even more limited record (1 uncertain juvenile specimen from MGLM). *Megerlia truncata* shows a wide stratigraphic range (C1,

C2, UGLM, BCF, GSF, UCLF base), while *M. eusticta* was found only at a GSF locality. *Lacazella adamsi* is known only from the Globigerina Limestone (LGLM, MGLM).

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Paleobiogeographical reconstruction by location of Tropic of Capricorn and Cancer

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The recognition of paleobiogeographic provinces or even realms is different for different organisms or different geologic time intervals. The astronomical climatic zone could help to differentiate Realms, while the biotic similarities are useful to recognize provinces and subprovinces. Compared to the methods of recognizing tropic and temperate zones, the differentiation of bipolar faunas is more reliable. There are quite a few methods for us to reconstruct ancient continent, such as paleogeomagnetism, paleoclimate, paleotemperature, paleobiogeography, etc.. This paper suggests a new method, called positioning the ancient tropic Capricorn, which belongs to the category of paleobiogeography. Such method animates those paleoplates with different biotas, and was tried by many geologists and particularly paleontologists (e.g., Boucot and Gray 1979; Cocks and Torsvik 2007; Dean 1976; Eldredge and Ormiston 1979; Havlicek 1974,1980; Hints and Eriksson 2007; Olson 1979; Paris and al. 2007; Paul 1976; Pojeta 1979; Rich 1979; Ross 1979; Sheehan 1979; Telford 1979; Zinsmeister 1979).

Positioning the ancient Tropic Capricorn. The position where tropic and temperate biotas co-occur is the location of ancient tropic Capricorn running across. Ideally, we have to find such locations as many as possible, and connect them together to get the position of ancient tropic Capricorn. Both Middle-Late Ordovician and Early Carboniferous have such examples.

Once the positions of southern and northern ancient tropic Capricorn are settled, and then we can calculate their distance and furthermore the dipping angle of Earth's axis. Consequently, the exact position of North Pole and South Pole of a particular geological period could be fixed. And these positions of other geological time intervals could also deduced according to their relative loca-

tions taking into account of the relevant tectonic movements.

Attached are the paleobiogeographic distribution maps of Cambrian, Ordovician, Silurian, Devonian, Carboniferous and Permian, and the reconstruction maps of ancient continents of these periods.

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The ancestral brachiopod larval eye – a glimpse of bilaterian eye evolution

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Brachiopod larvae, during their short pelagic stage, respond to light by means of their cerebral eyes. Early on they are positively phototactic, but prior to settlement they switch to photonegative behavior preferring dim-light to light-free substrates to attach to before they enter stage of metamorphosis. Their eyes consist of two light- sensitive photoreceptor cells (PRCs), one of which forms a lens, the other provides an array of pigment granules to prevent scattered light from unwanted directions to interfere with the photoreceptors. In contrast to (almost) all other protostomes, which use rhabdomeric photoreceptors, the photosensitive pig-

ment (opsin) in brachiopod larvae is embedded in the enlarged outer membrane of the PRC's cilia. This applies not only to larvae of the laqueoid Terebratalia transversa, as shown by Passamaneck et al. (2011), but also to larvae of megathyridoid, kraussinoid, and thecideoid brachiopods, thus covering all brachiopod superfamilies eye-bearing developmental stages have been described from.

We were able to reconstruct 3D models of larval eyes of five different species on the basis of TEM data showing that they all share a common morphological pattern: both PRCs have an enlarged cilium carrying the ciliary opsin and a proximal axon connecting the receptor cell to the neuropil of the larval nervous system. Deploying a taylor-made antibody against Terebratalia transversa ciliary opsin (Tt c-opsin) based on transcriptomic information, we detected this light sensitive protein in the ciliary membranes with confocal microscopy using fluorescent dyes and transmission electron microscopy using gold labelling techniques.

Our results suggest that the larva of the last common ancestor of Thecidoidea, Megathiridoidea, Kraussinoidea, and Terebratelloidea was supposedly equipped with at least two pairs of cerebral eyes each of which containing a c-opsin as the photoreceptive protein in the ciliary membranes of its PRCs. According to the common theory of PRC evolution in Bilateria, the split between rhabdomeric and ciliary PRCs may be the product of a gene duplication and successive cell differentiation along the bilaterian stem lineage. Whereas protostomes and non- chordate deuterostomes were thought to exclusively rhabdomeric PRCs for vision, ciliary PRCs were supposed to fulfil non-visional purposes (e.g. circadian rhythmicity) in these groups. Phylogenetically, brachiopods clearly belong to (lophotrochozoan) protostomes, but in deploying c-opsins in their visional organs they resemble vertebrates, for instance, light-sensitive proteins of the c-opsin class are located in the rods and cones of their eye retina. The discovery of c-opsins used for visional purposes in (protostome) brachiopod larvae as shown here contradicts the theory of a dual split of rhabdomeric and ciliary PRCs in bilaterian eyes and calls for a detailed investigation of other "exceptions to the rule" scattered throughout protostomian animals in order to elucidate eye evolution in Bilateria.

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Brachiopods biomineralization patterns during the Late Permian

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The Permian has been an interval of major global changes in the Earth's geodynamics, climate, seawater and atmosphere geochemistry, and thus it represents an interesting case study to understand the response of organisms to environmental changes, a topic which is of increasing interest to the scientific community. In fact, in the Permian the biotic response was dramatic, culminating at the end of the period (PTB) with the greatest mass extinction of the Phanerozoic.

During the Late Permian brachiopods were the rulers of the benthic communities, and mostly comprised two classes of calcifying brachiopods: the Strophomenata and the Rhynchonellata, which show important differences in the structural and chemical composition of the shell. These differences are likely related to the biomineralization process responsible for the formation of their shell, namely a collective process where arrays of mantle cells secrete the biocomposite in the Strophomenata, versus a discrete, single cell driven process in the Rhynchonellata. This profound diversity offers the chance to test if there is a differential response of the two classes during the Late Permian events, also in term of biomineralization.

Our study reveals that Strophomenata apparently thrived better at the beginning of the end Permian events, but soon they got extinct. On the contrary, Rhynchonellata were able to adapt, diversify and survive the end Permian mass extinction. Taking into account the type of shell fabric, a general trend toward production of calcitic shells with higher organic content is recorded up to the PTB in most brachiopod groups. This may have been likely the result of changes in the physical and chemical composition of seawater that produced an increase in the energetic cost for carbonate precipitation in low buffered organisms such as brachiopods.

Our research has important implications for the understanding of modern organism pattern and behavior related to change in climate and in seawater and atmosphere geochemistry. It further shows that the detailed study of brachiopods using a multidisciplinary paleontological approach is essential to understand modern counterpart and their response to the climate changes.

Neotethys seawater chemistry and temperature at the dawn of the latest Permian events

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The end of the Permian was a time of biotic crisis and massive upheaval in the biosphere, atmosphere and hydrosphere (e.g. Erwin, 2006; Shen et al., 2011; Brand et al., 2012a). Over the last decades, many causes have been suggested for that catastrophe, such as global warming and anoxia. After careful diagenetic screening using a multitude of tests (Brand et al., 2012a), we reconstructed carbonate/seawater curves from the archival data stored in pristine brachiopod shells from the Changhsingian Gyanyima Formation of Tibet, which was deposited on an open ocean seamount at subtropical latitudes in the southern Neotethys. The reconstructed strontium isotope curve for the late Changhsingian is relatively invariant at about 0.707000 until the upper part of the formation; subsequently the values become more radiogenic and climax at a high of about 0.707213 (cf. Brand et al., 2012b). The presence of brachiopods and corals in the Gyanyima Formation right up to the end Permian event suggests normal open-ocean conditions, which is confirmed by Ce/Ce* anomaly values ranging from 0.310 to 0.577 for the brachiopods and from 0.237 to 0.655 for the whole rock. These Ce* values are typical of normal open-ocean oxic seawater observed in their modern counterparts (Azmy et al., 2011). Carbon isotopes of brachiopod shells from Tibet are invariant for most of the Late Permian, without the typical negative carbon isotope excursion (e.g., Brand et al., 2012b; Schobben et al., 2014). Estimates of seawater temperature at shallow depth fluctuate from 23 to 29°C below the boundary, but rise suddenly to values exceeding 35°C just before the onset of the extinction interval at Tibet. This dramatic increase in seawater temperature has been observed in many end-Permian successions from tropical to mid latitude and from restricted to open ocean localities (Joachimski et al., 2012; Chen et al., 2013, Schobben et al., 2014). Our brachiopod archive and its geochemical proxies support the paradigm that global warming is a key factor to understanding the end Permian event culminating with the greatest biotic crisis of the terrestrial and marine faunas and floras of the late Paleozoic world (Erwin, 2006).

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Size changes in brachiopods at the Early Toarcian (Jurassic) mass extinction event

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The Mass Extinction Event of the Early Toarcian is probably the most important in the post-Paleozoic history of brachiopods. As a consequence of this event two orders, Spiriferinida and Athyridida disappeared. The Order Rhynchonellida suffered a significant renewal and only the Order Terebratulida seems to be less influenced by it. The loss of diversity is seen globally during the Late Spinatum Chronozone of the Pliensbachian and the Tenuicostatum Chronozone of the Toarcian, which is considered the "Extinction Interval". However, in the Iberian Peninsula

there are a number of stratigraphical sections in which the diversity of the brachiopods is relatively high until just the extinction boundary, thus enabling to conduct a detailed study of the assemblages (cf. García Joral et al., 2011; Comas-Rengifo et al., 2013, 2015). The aim of this work is to study the changes in size of the brachiopods in the assemblages from the extinction interval in different localities of the basins surrounding the Iberian Massif to the East, the North and the West, in which the environmental conditions change from well oxygenated and shallow to oxygen depleted and deeper (Gómez and Goy, 2005, Quesada *et al*., 2005, Duarte, 2007). Among the several ways in which body size in brachiopods may be approached, the length of the shell is commonly assumed to be directly related to other variables such as the occupied volume or the mass of living tissue (Peck et al., 1997). Estimation of changes in body size using shell length has been used in several previous works to be linked with environmental stress situations.

The length of 907 specimens belonging to four orders of rhynchonelliform brachiopods has been measured. They were collected at 7 representative localities of the Iberian, Basque-Cantabrian, Asturian and Lusitanian basins. The order best represented in these sections is Rhynchonellida, with several species in most of the localities. Spiriferinida and Terebratulida species are scarce particularly in the northern basins (Asturias and the Basque-Cantabrian), while the Athyridida, represented by the Koninckellidae Family, has been only recorded in the Lusitanian basin.

At Order level a significant reduction in size is observed in all groups from the Iberian basin towards the external areas of the Lusitanian basins. In the Asturian and Basque-Cantabrian basins only rhynchonellids could be compared, due to the scarce representation of other groups, where a reduced size is also observed when compared to the assemblages from the Iberian Basin. When this reduction of size is analyzed at a lower taxonomic level, this decrease in overall size is found to be in all cases a consequence of differences in the relative abundances of the bigger species compared to smaller species from one basin to another. Thus, the brachiopods of the north and west are not smaller specimens of the same species as in the East, but are simply small sized species that display their standard size. These differences in size have been related with the generally accepted environmental changes in food supply or oxygen levels between the basins.

Size increase within species, however, is observed in the specimens of the dominant species when the assemblages from the older to the more recent levels are compared. This change is observed both in the big spiriferinids of the East and in the small rhynchonellids of the West, and seems to be related to the rise of sea water temperatures inferred in all the basins at the Tenuicostatum Chronozone (Gómez and Goy, 2011).

Thus, two crossing gradients of size have been detected in the studied assemblages: the first involving a decrease in size due to the transition from well oxygenated and shallower environments to oxygen depleted and deeper environments; the second involving an increase in size linked to the sea water warming during the Tenuicostatum Chronozone. The first phenomenon involves the taxonomic composition of the assemblages; whereas the second concerns the size of the individuals within the same species.

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Hierarchical structure of calcite layers in the shell of the brachiopod *Aerothyris kerguelenensis*

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Among the three subphyla recognized in the phylum Brachiopoda (Williams, 1996), our attention focuses on the subphylum rhynchonelliformea. The shells of these rhynchonelliform brachiopods are observed, particularly on living taxa with the purpose of understanding how the shell is built and biologically controlled while we realize that they are composed of biominerals. The shells of this latter generally comprise two layers (three in some cases): the outer primary layer composed of acicular calcite and the inner secondary layer composed of fibres, essentially low Mg-calcite. Mg mapping allow highlighting where peaks of Mg are observed in the thickness of the shell. One of the fauna studied: *Aerothyris kerguelenensis* (Davidson) shells come from the Kerguelen Islands (Marion Dufresnes = MD cruises and Poker II cruise) in the south of the Indian Ocean. The observations using the Scanning electron microscopy (SEM) have allowed highlighting the structure of the shell (Williams, 1968; Gaspard, 1990) and the intimate association of the inorganic phase (calcite) with the organic phase (insoluble and soluble organic matrices (Cusack et al., 1997; Gaspard et al. 2005, 2008). The calcite fibres are particularly interesting to reveal the hierarchical architecture existing when the shell construction takes place. Each fibrous element corresponds to one crystal with the c-axis perpendicular to the fibre length. But the apparent morphological unit represents the final stage. A fibre is marked by growth-lines, and between two of these is found elementary units: the granules (Gaspard, 1991). These granules have different sizes considering different species. The granules are well identified under SEM, with different orientation from a fibre to their neighbours and the Atomic force microscopy (AFM) allows an approach at a nanoscale. A possible composite structure of the granules is under investigation.

Organization of the coelom in *Lingula anatina*: 3D and ultrastructural studies

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Organization of coelomic system is traditionally used in phylogenetic analysis to establish the relationships between major taxa. Brachiopods and their closest relatives – phoronids and bryozoans (or ectoprocts) – were traditionally integrated into the single group called Lophophorata. During last two decades, existence of the lophophorates is being discussed and bryozoans are allocated as a separated clade, which is not relative to group Brachiozoa that now includes phoronids and brachiopods. On the other hand, Lophophorata is usually united with Deuterostomia due to data on embryonic development and coelomic organization: both Deuterostomia and Lophophorata have tripartite coelom. However, new data of molecular phylogeny testify that there is a relationship of brachiopods as a part of Brachiozoa and a currently protostomes, for last one the tripartite coelom is not a

typical characteristic. Investigation of the coelomic organization in brachiopods let us understand the evolution of Lophophorata and also sheds light on fundamental questions about appearance of the last common bilaterian ancestor. The organization of the coelom in *Lingula anatina* was investigated by methods of histology, semi-thin sectioning, scanning electron microscopy, and 3D-reconstructions.

The coelom of *L. anatina* consists of three main compartments – preoral coelom, lophophoral coelom, and trunk coelom (Fig. 1A). The preoral coelom is a narrow cavity, which extends at the base of the brachial fold (=epistome) along each brachium of the lophophore and above the mouth. It has its own epithelial lining, which is formed by ciliated cells. These cells are connected via desmosomes and tight junctions and underlined by basal lamina. Muscle cells are located under the coelomic epithelium in some parts of the preoral coelom, where numerous muscles, which are responsible for brachial fold's mobility, take pass. The lophophoral coelom is divided into paired coelomic sacs: large and small sinuses (=canals) of the lophophore. The large canal of the lophophore is located along each brachium at its base. The small canal of the lophophore extends above the large canal and gives rise to coelomic channels into each tentacle. The lophophoral coelom exhibits great variety of types of the lining. The lining of both canals in the point of their connection with each other as well as with the trunk coelom is formed by podocyte-like cells. Those are large cells with big nucleus and numerous long basal projections (Fig. 1B, C). These basal projections are connected via desmosomes and form typical to this kind of cells profile (Fig. 1B). The major part of small and large canals is paved by epithelial and muscle cells, which are alternated (Fig. 1D). Muscle cells are located as separated bundles and connect basal lamina via hemidesmosomes. Between muscle cells there are numerous adhesive. Usually epithelial cells are located over the muscle cells. If there are no muscle cells, long projections of epithelial cells have a connection with a basal lamina. Adherens junctions, tight junctions, and septate junctions are found between epithelial cells. If there are no epithelial cells, muscle cells have a connection with body cavity (Fig. 1D). In those sites, epithelium cells and muscle cells are united by desmosomes. In the small canal of the lophophoral coelom, cells, which form the wall of the tentacular blood capillaries, present as flagellated myoepithelial cells. Their basal surfaces form long thin microvilli, which are jutting out into the lumen of the blood vessel. Myofilaments, which form circular muscle of the tentacle capillary, extend in the basal part of cell. The coelomic lining of the lateral sides of each tentacle is formed by flagellated epithelial cells. The trunk coelom has practically the same organization of the lining (Fig. 1C).

The coelomic lining of *L. anatina* demonstrates huge variety of structure. We can find the most simple type of organization with only epithelial-muscle cells as well as the most complex type with alternated epithelial and muscle cells, and there are also specialized lining forming by podocyte-like cells. Such a big variety of structure of the colomic lining is firstly described for echinoderms podia (Rieger, Lombardi, 1987), and recently is shown in phoronids (Temereva, 2015). It is important to make a point that there are huge quantities of cellular junctions, which are used in coelomic lining structure. Those connections can afford

Fig. 1. The organization of the coelom in *Lingula anatina*. A – Cross semi-thin section of the esophagus (es) with all of the coelomic compartments. B – Projections of podocyte-like cells; TEM. The typical structure of podocyte-like cells is well visible. C – Dissepiment between the trunk coelom and the large canal of the lophophore; TEM. Podocyte-like lining of the large canal and epithelial lining of the trunk coelom are shown. D – Lining of the large canal of the lophophoral coelom. Different cellular junctions are shown.

a co-function of epithelial and muscle cell forming cytologically complex tissue.

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Description of the preoral coelom in adult brachiopods and its phylogenetic significance

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Brachiopoda is a relict group of marine invertebrate animals with a rich paleontological history. Over 30000 species of Brachiopods are known in fossils while only about 300 species are described in a present-day fauna (Zezina, 1979). There is lack of information in Brachiopod's morphology and anatomy as most of the data describing living Brachiopods was collected more than a hundred years ago without the use of modern techniques. Brachiopods are traditionally united with phoronids and bryozoans into the Lophophorata. The lophophorates have a tentacle organ called lophophore, a polyfunctional apparatus with a highly variable structure (Kuzmina, Malakhov, 2011). Taxonomic position of Lophophorata is being now a subject of intense discussion. Lophophorata were claimed as the closest relatives of the Deuterostomia due to the similarities of the coelom organization in the lophophorates and deuterostomes. This division of the phoronid coelom into three compartments that appears similarly to the tripartite coelomic cavities of ambulacral deuterostomes was the basis of this homology inference of the unity of the lophophorata and deuterostomia, which form a clade called archicoelomata. Coelomic system of Brachiopoda was described as bipartite, including two parts - the lophophore coelom and trunk coelom (Lüter, 1996, 2011). Literature data mention the existence of some cavities in the base of epistome in brachiopod lophophore, but the nature and structure of these cavities had not been studied (Pross, 1981). In the present report, the organization of the coelomic system of the lophophore in the inarticulate brachiopod *Lingula anatina* is studied by methods of histology, semi-thin sectioning, scanning electron microscopy, and 3D-reconstructions (Fig. 1, 2).

According to present data, in *L. anatina* brachial fold contains a system of cavities. These cavities have large volume at the base of the brachial fold, and along its ventral side form numerous small chambers (Fig. 1A, B). Three-dimensional reconstruction evidences that cavities, which are located at the base of brachial fold, form single cavity that extends along each brachium and above the mouth and is isolated from canals of the lophophore coelom (Fig. 2A, B). TEM investigation reveals that the cavity has its own lining, which consists of non-muscular monociliated epithelial cells connected via desmosomes and tight junctions. The isolation and presence of own lining allow regard the epistomal cavities of *L. anatina* as a true coelom. Presence of the isolated coelom in the epistome of *L. anatina* demonstrates that Brachiopoda might have both bipartite and tripartite coelom.

An analysis of the coelomic system organization reveals that tripartite coelom is a plesiomorphy for all lophophorates. The tripartite coelom is also typical for all deuterostomes. Because the tripartite coelom is found in two main lineages of bilateria – protostomia and deuterostomia, we can suggest that this type of the coelom might be inherited from the last common bilaterian ancestor. This suggestion is consistent with published gene expression studies, in which *Hox* genes are never expressed in the two first segments of the body, whereas *Otx* genes are expressed in the most anterior segments of some bilaterians. Interesting, phoronids, brachiopods, and some deuterostomes exhibit the metameric organization of the trunk coelom. Such combination of trimery and metamery might be also regarded as plesiomorphy of all bilaterians.
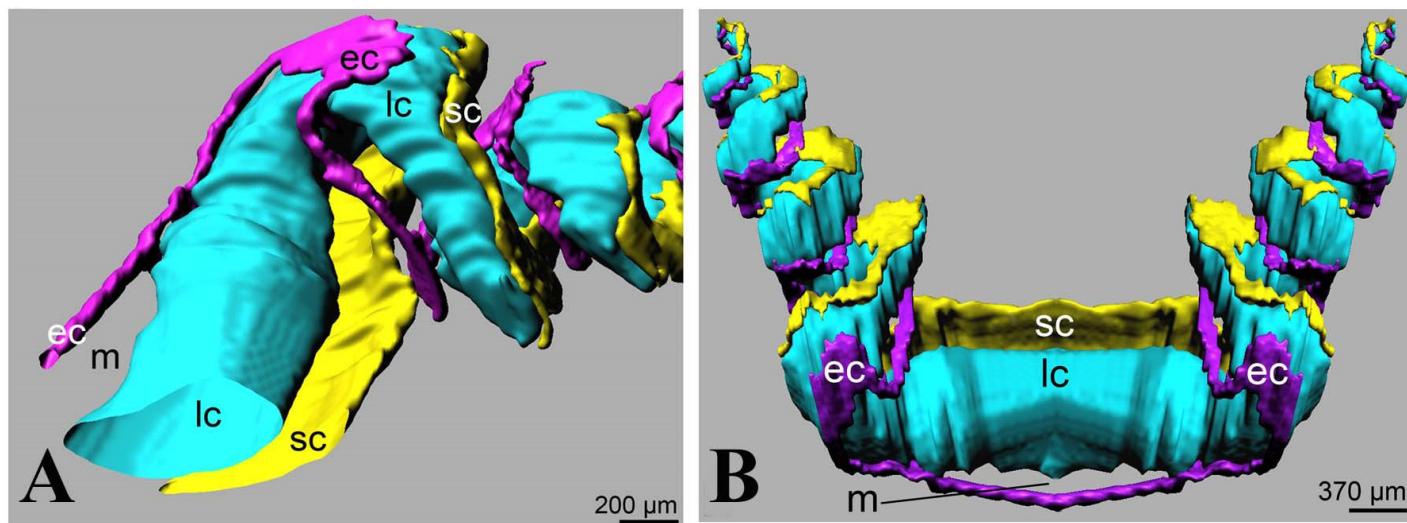
Fig. 1. Preoral coelom of *Lingula anatina*. (A) Cross section of a brachium of the lophophore; seni-thin section. (B) Cross section of the lophophore; scanning electron microscopy. Abbreviations: ec – preoral coelom; ep – epistome; lc – large canal of lophophoral coelom; sc – small canal of lophophoral coelom; t –tentacles.
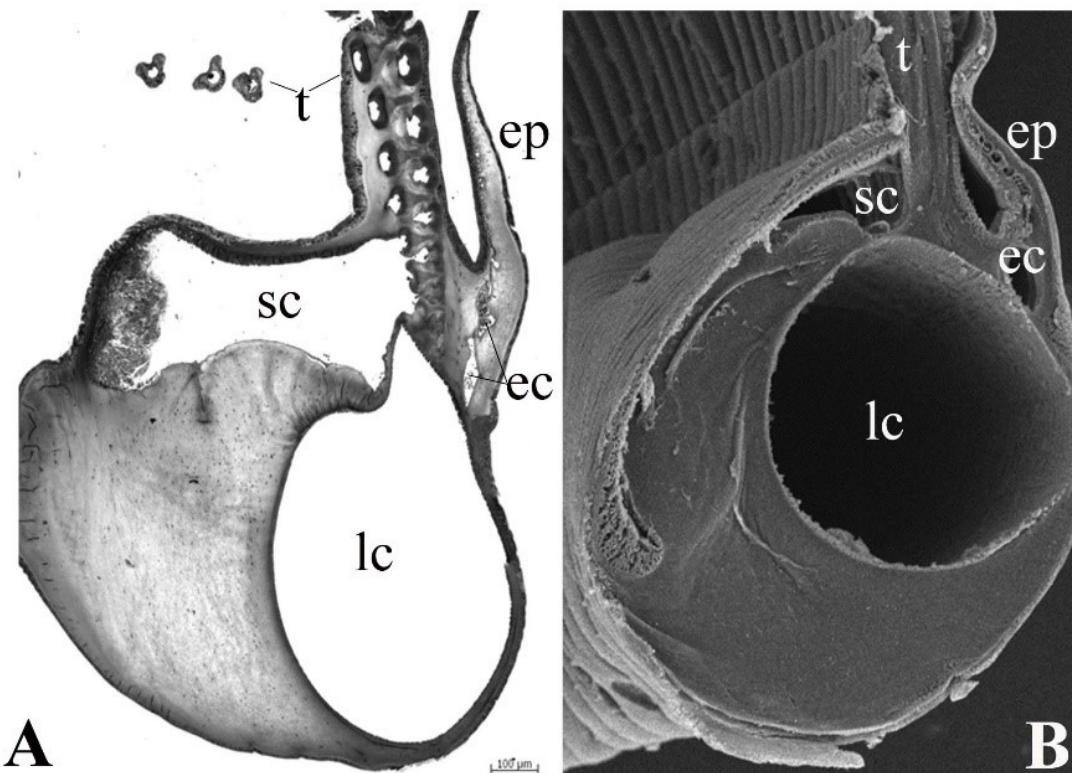
Fig. 2. Three-dimensional reconstructions of the coeloms of the lophophore in *Lingulaanatina*. (A) Side view of the right half of lophophore. (B) Dorsal view of the whole lophophore. Abbreviations: Ec – epistomic (preoral) coelom; lc – large canal of lophophore coelom; m – mouth; sc – small canal of lophophore coelom.

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Genetic variations and species boundaries among the Pacific populations of *Lingula*

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For the biological importance as a living fossil and the readily accessible intertidal habitat, *Lingula* is among the most studied living brachiopods, and yet, some of their species boundaries remain uncertain. Emig (1982) postulated that Recent *Lingula* comprises a total of seven species, with several species in the Indo-West Pacific having been synonymized with *L. anatina*, an interpretation supported by their possession of planktotrophic larvae with a long pelagic existence. Endo et al. (2001), however, showed that the northwestern Pacific populations of *L. anatina* are structured and separated with each other by considerable genetic distances. A deep intraspecific divergence was also suggested by Nishizawa et al. (2010), who found that the karyotype of *L. anatina* from Amami, southern Japan (2n = 20) is different from that reported by Yatsu (1902) for *L. unguis* (= *L. anatina*) from Misaki, central Japan (2n = 16). Here, in order to further address this problem, we carried out molecular phylogenetic analyses of lingulid brachiopods using a much more complete coverage of taxa and localities, including *L. anatina* from Japan, South Korea, China, Indonesia, Papua New Guinea, Fiji, New Caledonia, and Australia, *L. adamsi* from Japan and South Korea, *L. reevei* from Hawaii, and *Glottidia* from Florida and Panama. The results with mitochondrial *cox1* and nuclear 28S rDNA sequences indicated that (1) *Lingula* and *Glottidia* form a monophyletic group, respectively, (2) the populations of *Lingula anatina* are divided into two major clades with a depth of divergence comparable to that between *L. adamsi* and *L. reevei*, and (3) the two clades of *L. anatina* are further divided into genetically divergent clades, possibly

embracing six sibling species. The results suggest that *Lingula* experienced a complex history of speciation and that the slow rate of morphological evolution in *Lingula* cannot be explained by the lack of speciation events involving genetic isolations.

Once more on the problem of the name-bearing type of the Middle Devonian brachiopod *Athyris concentrica* (Buch, 1834)

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There exists a controversy between Alvarez *et al.* (1996), Grunt, Weyer (2002) and Alvarez, Brunton (2005) concerning the type of *Athyris concentrica* (Buch, 1834), the type species of the genus *Athyris* M'Coy, 1844 standing in the centre of the family Athyrididae and higher categories up to the level of the order Athyridida

A 'critical' comment was published by Alvarez, Brunton (2005) about the publication of Grunt, Weyer (2002), where the lectotype for *Athyris concentrica* (Buch, 1834) had been selected instead of the unnecessary neotype selected by Alvarez *et al.* (1996).

According the International Code of Zoological Nomenclature (1999; Art. 75.8) the neotype of *Athyris concentrica* must be set aside (unless, following an application, the Commission rules that the neotype is to be retained as the name-bearing type)'). We did not respond the publication of Alvarez, Brunton (2005) expecting their appeal to the International Commission on Zoological Nomenclature for the admission of the neotype of *Athyris concentrica*. As we know, up to now there was no appealing to the Commission by Alvarez and his co-authors, neither any decision of the ICZN. That is why the question perhaps might be still somewhat open for outsiders and needs further discussion.

It is well known that L. von Buch had (in full accordance to the taxonomic level of his times) united nearly all Middle Devonian athyridids from the Eifel region within his one new species which became more and more restricted after first local revisions up to the recent studies, because of separation of several additional new taxa. But, the concept of *Athyris concentrica* remained fixed along all these investigations. Of course, at first this was done without the philosophy of the type specimen, not yet invented officially in the 19th century.

The complete revision of the original L. von Buch collection of *Athyris concentrica* was not executed up to the end of the 20th century. So, Grunt and Weyer started with this special research work in March of 1995 in the Berlin Museum of Natural History. It was ascertained along this investigation that this collection entirely exists in the Berlin Museum being represented by 33 specimens itemized in 1836 by F.A. Quenstedt in the handwrit-

ten so-called "Quenstedt Catalogue", which was compiled by him very soon after Buch's publication of 1834 (for a review(see Grunt & Weyer 2002; Fig. 1). In April of 1995 one of us (Grunt) visited W. Struve in Frankfurt-am-Main in order to show him and to discuss that part of the Buch collection he had not seen before, surely being syntypes of *Athyris concentrica* according to the "Quenstedt Catalogue", not 'identified' by Weyer, as declared by Alvarez and Brunton (2005; p. 86). The opinion of Struve was, that '….not a single specimen even superficially agreed with the original description of *"T. concentrica"* and they are more close to the (sub)species of the *Athyris gutta* group' (Alvarez *et al.* 1996; p. 69). For us this seems strange, because the pictorial, but, of course, subjective reconstruction of *Athyris concentrica* by Struve, based only on the original description of Buch (1834; p. 102) does not show striking differences against the syntypes of Buch's original collection. The information, presented by Grunt was completely ignored by Alvarez and his co-authors probably because their manuscript being in the last stage of preparation at that time (see Alvarez *et al.* 1996; p. 69).

The single SMF 54800 specimen known as "Kowalsky specimen" collected from the Eifelian Ahrdorf Formation, southern foot of Auberg hill (locality Ge 27 of Heintz Kowalski collection, 1984–1987, temporary excavations immediately north of Gerolstein) was proposed as neotype (see Alvarez *et al.* 1996; p. 80, Pl.1, fig. 1). As far as the internal structures of the species could not be investigated from that unique specimen, the interiors of *Athyris concentrica* were illustrated by a specimen from quite another locality of perhaps nearly the same age from the Eifel district; but these only longitudinal sections are useless and do not show even the necessary diagnostic generic features (see Alvarez *et al.* 1996; Text-fig. 12). External photos of this specimen – SFM 50013 – which could demonstrate an identity or similarity with the "neotype", are not available. A second illustration (see Alvarez *et al.* 1996; Text-fig. 11] comes from another, much younger (Frasnian) "subspecies" *Athyris concentrica murchisoni* (Brice 1988) from Ferques, Boulonnais, northern France, being for us definitely a separate *Athyris murchisoni* species (and in the meantime now also for Prof. Denise Brice, personal communication, 2010). That means that Alvarez *et al.* (1996) in reality followed the classical concept of Murchison (1840), who had given the first, of course not conspecific illustration of *Athyris concentrica*.

So, Alvarez *et al.* (1996; p. 80) according their own declaration '…redescibed *Athyris concentrica* based on new observations of internal and external morphology'. The series of Buch's syntypes now existing in the Berlin Museum of Natural History was entirely excluded from this description. This was done contrary the ICZN (1999; Art. 75.3). Alvarez *et al.* (1996) published a neotype for *Athyris concentrica* in spite of being informed in time about the presence of the complete Buch original collection in the Berlin Museum of Natural History. The only reason for such a decision was the simple, in our view obviously incorrect declaration that among still existing syntypes of Buch's collection, preserved in the Museum of Natural History (Berlin) there is no longer the specimen corresponding precisely or even superficially to the original description (Alvarez *et. al.* 1996).

This erroneous believe was also based on the loan of only

some selected specimens of the Buch collection to Struve (Senckenberg Museum, Frankfurt am Main) and to Brunton (British Museum of Natural History, London). Brunton had the first loan in September 1979; this included six specimens from the Buch *concentrica*-collection (three of them were illustrated in Brunton [1980, text-fig. 1, 2, 3] as well as the original of *Athyris monticulata* (Schlotheim, 1820) (No. MB.B.282., inventory of modern time = old no. 120 of Beyrich Catalogue). The second loan to Brunton was in February 1987. This collection was borrowed by Alvarez, who visited Berlin Museum in 1987 and '….. studied in detail, with the help of H. Jaeger and C. Brime, those collections and borrowed about 200 sp. of athyridids for further study in London with Howard Brunton and in Frankfurt with W. Struve' (see Alvarez and Brunton 2005). We regret to say, that all the 197 specimens selected by Alvarez did not include one single specimen of the original syntype Buch *concentrica*-collection, but were collected much later (this was clearly indicated by H. Jaeger – then responsible custodian for Brachiopoda – on the official loan list). The numbers of athyridids from the Berlin Museum (B.503.3; B.499.10; B.499.19; B.499.24; B.499.10; B.504.5; 503.16; B.510.1; B.499.16; B.513.4) pointed in the publication of Alvarez and Brunton (2005) also did never belong to the old collection of Buch (if compared with the complete list of specimens definitely belonging to this collection according to the Quenstedt Catalogue).

Considering the incomplete published data of Alvarez et al. (1996), Grunt and Weyer had to continue the study of the original *Atyris concentrica*-collection. Judging from the Quenstedt Catalogue) the Berlin Museum now hosts the complete original collection of Leopold von Buch containing 33 specimens. The contents of this collection are shown in Tables 1–3 (Grunt and Weyer, 2002).

Four shells from the group [11-1 of Quenstedt Catalogue] were originally identified as *Terebratula concentrica* from Gerolstein. Now, there is only one specimen (MB.B.922.) which certainly belongs to the group [11-1]. Exactly this shell was proposed for the choice as lectotype of *Athyris concentrica* (see: Grunt and Weyer, 2002, Pl. I, fig. 1), since its parameters fit to the original description.

As it was correctly pointed by Alvarez and Brunton (2005), in the '*concentrica*' situation there was never any holotype or lectotype (or previous neotype) to be rediscovered as none was ever selected. But the hand-written Quenstedt Catalogue presents the complete series of Buch's syntypes preserved in the old collections of Berlin Museum. According to the ICZN (1999; Art.74D, 75.3, 75.3.4, 75.7) the neotype of *A. concentrica*, selected by Alvarez *et al.* (1996) is no longer valid and must be set aside.

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Lower Emsian (Lower Devonian) brachiopod fauna from Nandan, Guangxi, South China

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Mode section is located along the highway from Nandan to Tian'e County near Mode village, Nandan County, Guangxi Province of China, where the Lower Devonian Yilan Formation is well exposed along the highway and contains abundant brachiopod fossils. The formation is about 70 m thick, and lithologically, can be divided into three units on this section. The lower unit is composed of purple to brownish yellow mudstone (ca. 14 m thick), the middle unit is dominated with marl and nodular limestone (c. 21 m thick) and the upper unit is characterized with dark grey mudstone with some lenses of marl and calcareous concretions (c. 35 m thick).

The lower and middle units of the Yilan Formation contain abundant middle to large sized brachiopods. Spiriferids and strophomenides are especially abundant in the lower unit, including six genera (*Rostrospirifer, Howellella, Howittia, Xenostrophia, Megastrophia,* and *Dicoelostrophia*). The biodiversity of the brachiopod fauna of the Yilan Formation reaches the highest in the middle unit. Besides those appeared in lower
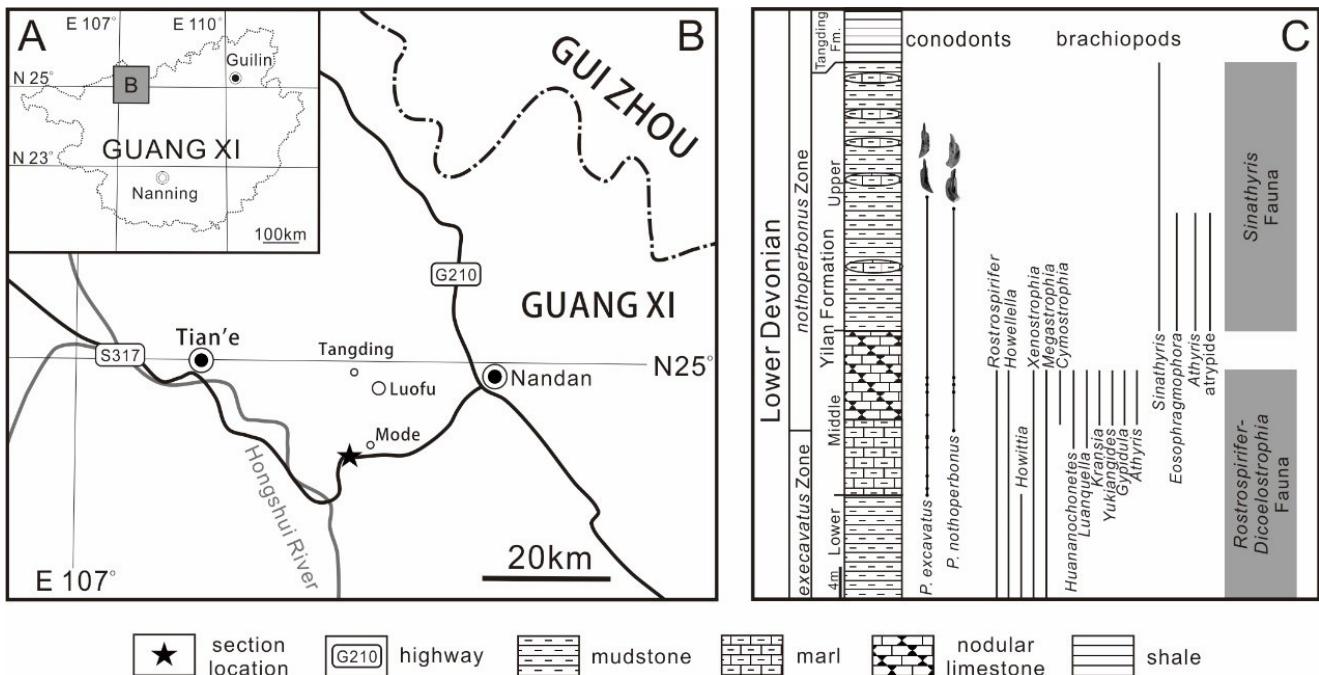
FIG. 1. Geographical location and stratigraphy of Mode section. A, regional map of Guangxi Province. B, detailed map of study area near the village of Mode, Nandan County. C, stratigraphical column at the Mode section with brachiopod and conodont ranges.

unit except *Howittia,* many other forms can also be found in the middle unit, including one strophomenid (*Cymostrophia*), two chonetids (*Huananochonetes* and *Luanquella*), one pentamerid (*Gypidula*), two rhynchonellids (*Kransia* and *Yukiangides*)*,* and one athyrid (*Athyris*), reflecting a continuous development of the brachiopod fauna from the lower unit to the middle unit lived in an open and neritic environment. All the brachiopods from the lower and middle units are characteristic for the "*Rostrospirifer–Dicoelostrophia*" fauna that is widely distributed in the Lower Devonian neritic marine sediments of South China.

Compared to the lower and middle units, the upper unit of the Yilan Formation yields a rather monotonous brachiopod fauna which is dominated by the small sized, double spirala-bearing athyride *Sinathyris crassa*, accompanied with the very rare orthide *Eosophragmophora sinensis*, atrypides and athyride *Athyris pauca*. The abundant pyrite in the sediment and interiors of the brachiopod shells, as well as the abundant coexisited thin-shelled tentaculitids strongly suggested that the brachiopod fauna in the upper unit of the Yilan Formation was lived in a quiet, relatively deep marine setting with probable intermittent dysoxic conditions. Thus the difference of the brachiopod faunas between the lower-middle and upper parts of the Yilan formation is resulted from the envirnmental change from a neritic platform to basinal facies in the studied area. The conodont analysis suggested that the transformation of the enivironment was taken place in the conodont *Polygnathus northoperbonus* Zone (Lower Emsian).

Case studies in evolution and palaeobiogeography of Devonian brachiopods

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Detailed systematic treatment of a number of Devonian brachiopod faunas from the Old World Province allowed tracing three evolutionary lineages. The genus *Bifida* (Athyridida) is represented in the Lower Devonian solely by species with concavo-convex shells, whereas in the Middle Devonian the shell morphology is plano-convex to biconvex. The Middle to Late Devonian representatives of the genus *Skenidioides* (Protorthida) from the Holy Cross Mountains form a sequence of three groups, distinguished by biometric characters. Morphological characters of stratigraphically earlier juveniles are those of stratigraphically younger adults; *Bifida* and *Skenidioides* sequences can thus be interpreted as paedomorphic. The Eifelian to Frasnian representatives of the genus *Schizophoria* (Orthida) can be separated solely on the basis of subtle biometric internal characters (Halamski 2012). This may be an example of stasis.

The analysis of the systematic composition of an early Frasnian fauna (27 species) from the Holy Cross Mountains (Halamski *in* Baliński *et al.* in prep.) in comparison with Middle Devonian assemblages from the same area allowed interpreting 7 species (26%) as having evolved in place, 8 (30%) as immigrants, whereas 12 species (44%) represent uncertain cases. This underscores the difficulty of tracing individual lineages even in a relatively favourable geological context.

A comparison of Middle Devonian brachiopod faunas from the northern and southern shores of the Rheic Ocean showed their remarkable similarity (ca. 80% of species found in the Moroccan Anti-Atlas are known either from the Eifel or from the Holy Cross Mountains; Halamski & Baliński 2013). This

unexpected similarity is a strong argument in favour of the hypothesis of a narrow Rheic Ocean (against that on a wide Rheic Ocean based mainly on palaeomagnetic data).

It should be stressed that reconstruction of evolutionary lineages or serious palaeobiogeographic analysis is impossible unless a modern systematic treatment of all involved taxa (preferably by a single author) is available. This is to emphasize that primary 'old-style' taxonomic research is inevitable.

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A large-scale paedomorphic evolutionary lineage among terebratulides (Permian to Recent)

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The systematic description of a silicified assemblage of Ladinian brachiopods from Mt. Svilaja in Croatia, including an atypical new terebratulide genus characterised by a dorsal median septum with a septal cavity, allowed linking Permian *Disphenia* Grant, 1988 and Jurassic *Zellania* Moore, 1855 into an evolutionary sequence, represented also by Recent *Gwynia* King, 1859 and *Simpliciforma* Bitner & Zezina, 2013. Members of this lineage (to be described as a new suborder of the Terebratulida; Halamski *et al.* in press) are characterised by secondary loss of the loop, a paedomorphic simplification when compared to ancestral terebratulides, themselves having originated also through progenesis (Jin & Chatterton 1996). The evolutionary trend within the lin-

eage is also that of gradual simplification and of loss of several internal structures, the most derived *Simpliciforma* having particularly simple interiors (Bitner *et al.* 2013). This trend is correlated with ecological change (passage from reefal environments to deeper water).

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The Ordovician rhynchonelliform brachiopod fauna: Occupation of morphospace during the Great Ordovician Biodiversification Event

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The 'Great Ordovician Biodiversification Event' (GOBE) was the most rapid and sustained increase of marine biodiversity in the Phanerozoic. During a geologically short time interval of some 40 myr, diversity escalated at family, genus and species levels within the context of fundamental climatic and environmental change. Not only a sharp increase in taxonomic diversity is obvious, but also very significant changes within the palaeoecological context of the biotas (Droser and Sheehan 1997), as the 'Paleozoic Evolutionary Fauna' progressively replaced the 'Cambrian Evolutionary Fauna' with suspension-feeding organisms, dominated by the Brachiopoda (Harper, 2006, 2010). The GOBE has been linked to a variety of possible drivers, intrinsic and extrinsic, regional and global, many of which were interconnected, and segue into each other. These data provide tests of a whole variety of biological and environmental hypotheses, framed to explain the event (Miller, 2012). During this expansion brachiopods fully participated in large increases in alpha, beta and gamma diversity (Harper 2010). The morphology of rhynchonelliform brachiopods is, however, constrained by operations associated with the opening and closing of the valves, the function and support of the lophophore and the relationship of the shells to the substrate. During the Ordovician a relatively simple, archetypal 'orthide' body plan was modified by a number of key adaptations: the development of biplanar to concavoconvex shells, introducing a recumbent mode of life in the strophomenides, cyrtomatodont rather than deltidiodont dentition, developed across the atrypides, athyridides, rhynchonellides and spiriferides and a variety of more elaborate lophophore support structures most apparent in the atr-

ypides, athyridides and spiriferides (Harper *et al.* 2004). With the exception of the terebratulides, with their supportive loops, and the bizarre coral and oyster-like strophomenides of the Permian most morphological innovations had already appeared during the GOBE, their hosts occupying a wide range of marine environments and provinces (Harper *et al.* 2013). Nevertheless despite these critical architectural and functional constraints, the main Ordovician orders continued to innovate, evolving a huge variety of shell morphologies, promoting taxonomic variety (some 300 genera at the peak of the event) and a spectrum of life styles, defining narrower niches in more packed communities and occupying much of the predictable morphospace.

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The brachiopod fauna of the Portrane Limestone (Upper Ordovician), County Dublin, Ireland

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The silicified fauna from the well-known Upper Ordovician limestones on the north Dublin coast at Portrane, Ireland, was for many years the classic yardstick for taxonomic studies of Ashgill (upper Katian) brachiopods, through the careful researches of the late Professor A.D. (Tony) Wright. The Portrane fauna helped form the basis for the shelly assemblage that characterised the

Cautleyan Stage of the Ashgill Regional Series which was defined by Ingham and (Wright 1972). Nevertheless, only two bulletins from his PhD thesis (1963) on the brachiopod fauna were ever published, covering the nonarticulated (1963) and orthide (1964) brachiopods, respectively. Through access to Wright's collections in The Natural History Museum and his thesis, we have developed a full census of the fauna, which now comprises some 75 brachiopod taxa, which is dominated by nonarticulated genera and orthides. Together with lists of the corals, trilobites, bryozoan and other phyla which have also been described from the Portrane fauna, we are planning to publish a summary of the whole biota, together with systematic descriptions of the remainder of the brachiopods, particularly the strophomenides. Size-frequency graphs for the common taxa and a virtual lack of articulated specimens apart from the more robust atrypides and rhynchonellides, indicate the assemblage was transported. Many genera are long-ranging, persisting in some cases from the Sandbian through into the Silurian, but at the species level the fauna is consistent with a mid Katian (late Cautleyan) age for the Portrane Limestone. Apart from a new chilidiopsoid, there are currently no endemics at the generic level, reflecting the widespread distribution of the majority of brachiopods during the mid and late Katian, although the fauna is key in helping to define a mid-latitude, Anglo-Welsh and Baltic province (Harper *et al.* 2013).

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Late Permian marine ecosystem collapse began in deeper waters: evidence from brachiopod diversity and body size changes

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Analysis of Permian-Triassic brachiopod diversity and body-size changes from different water depths spanning the continental shelf to basinal facies in South China provides insights into the process of environmental deterioration. Comparison of the temporal changes of brachiopod diversity between deep-water and shallow-water facies demonstrates that deep-water brachiopods disappeared earlier than shallow-water brachiopods (Figure 1). This indicates that high environmental stress commenced first in deep water settings and later extended to shallow waters. This environmental stress is attributed to major volcanic eruptions, which first led to formation of a stratified ocean and a chemocline in the outer shelf and deeper-water environments, causing the disappearance of deep marine benthos including brachiopods. The chemocline then rapidly migrated upward and extended to shallow waters, causing widespread mass extinction of shallow marine benthos. We predict that the spatial and temporal patterns of earlier onset of disappearance/extinction and ecological crisis in deeper water ecosystems will be recorded during other episodes of rapid global warming.

Changhsingian (latest Permian) deep-water brachiopod fauna from South China

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Forty Five brachiopod species (including 15 undetermined species) in 23 genera of seven orders (Productida, Spiriferida, Athyridida, Orthida, Orthotetida, Rhynchonellida, and Lingulida) have been discovered from the Talung Formation (Changhsingian, latest Permian) of the marine deep-water facies of South China. Two genera were proposed: *Chaohochonetes* He and Shi, 2014 (Fig. 1) and *Parapygmochonetes* He and Shi, 2014 (Fig. 2); along with the proposed 9 species: *Tethyochonetes rectangularis*, *Tethyochonetes*? *sinuate* He and Shi, 2014, *Chaohochonetes triangusinuata* He and Shi, 2014, *Neochonetes* (*Zhongyingia*?) *liaoi* He and Shi, 2014, *Neochonetes* (*Huangichonetes*?) *wufengensis* He and Shi, 2014, *Paryphella majiashanensis* He and Shi, 2014, *Paryphella minuta* He and Shi, 2014, *Parapygmochonetes parvulus* He and Shi, 2014 and *Meekella sparsiplicata* He and Shi, 2014.
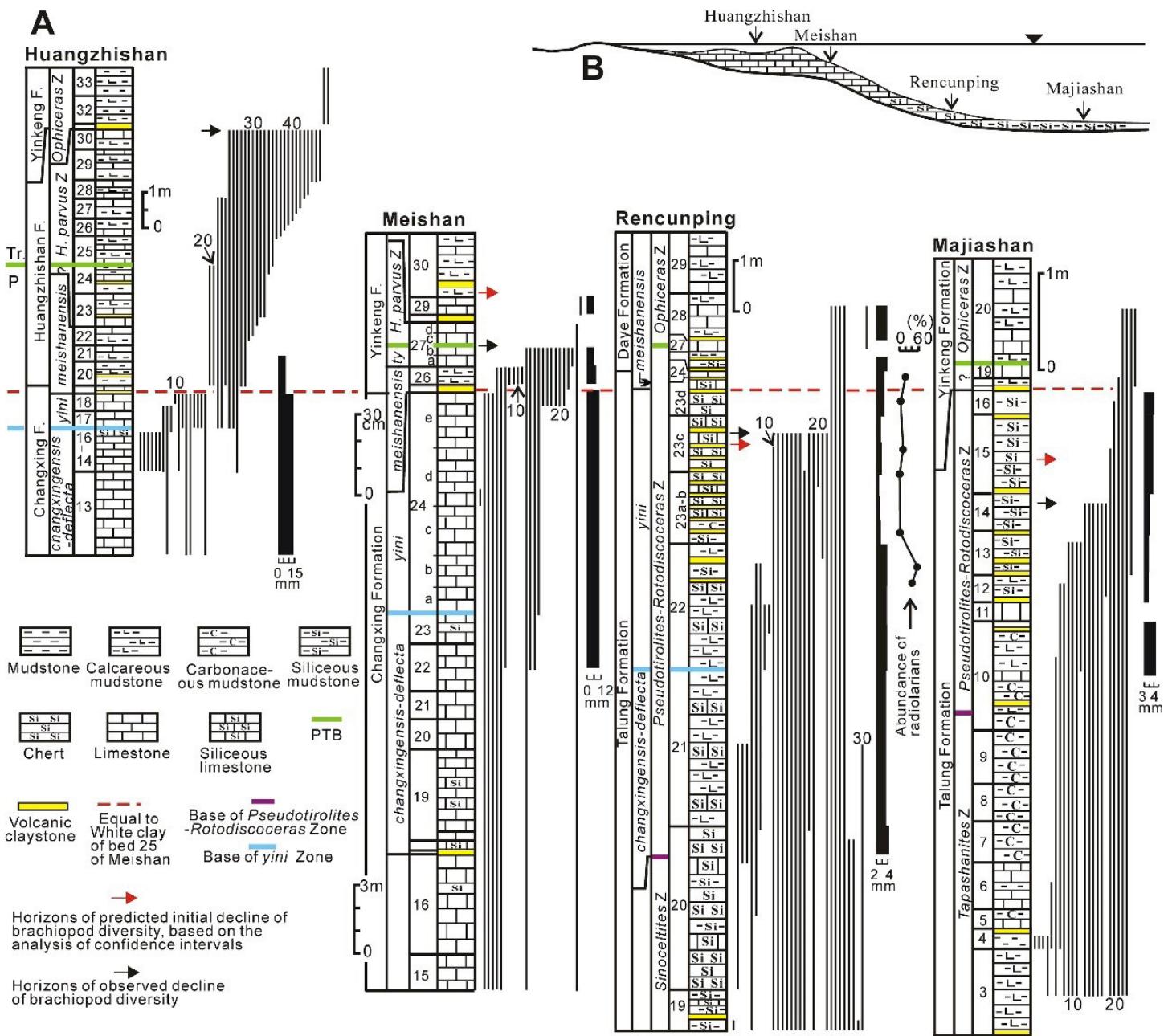
Figure 1 (**A**) Stratigraphic ranges of brachiopod species (indicated by vertical lines) from the PTB from shallow-water carbonate facies (Huangzhishan and Meishan sections) and deep-water siliceous facies (Majiashan and Rencunping sections). The numbers attached to vertical lines refer to species name (e.g., at Huangzhishan, 1, …, 49 respectively corresponding to HU1, …, HU49 in Table SI1). Thick black bars refer to the size of brachiopods in mm at Huangzhishan, Meishan, Rencunping and Majiashan sections of South China or to the size of radiolarians in μm at the Akkamori of Japan. Size data from the Huangzhishan refer to the mean size across all specimens in *Spinomarginifera* sp. (calculated from Chen *et al.*, 2009). Size data from the Rencunping and Majiashan refer to the mean size across all specimens in *Paracrurithyris pigmaea* (Table 1). Size data from the Meishan are mean size across all measured species (details see Table SI2 in the Supporting Information). Conodont zones of the Huangzhishan revised after Chen *et al.* (2008); conodont zones of the Meishan after Yin *et al.* (2001) and Yuan *et al.* (2014); data of the Majiashan revised after He *et al.* (2010). F.=Formation, Ch.= Changxing, P=Permian, Tr.=Triassic, *yini=C. yini* Zone, *meishan.=meishanensis=C. meishanensis* Zone, *parvus=Hindeodus parvus* Zone, *Ophiceras=Ophiceras* Zone, *changxingensis-deflecta= Clarkina changxingensis-C. deflecta* Zone, *zh-ch=C. zhejiangensis-Hindeodus changxingensis* Zone, *Pseudo.=Pseudotirolites*, Z.=Zone, *hauschkei=C. hauschkei* Zone, *taylorae-parvus=C. taylorae* Zone-*H. parvus* Zone, *tay.=taylorae*, SE= Siliceous Spongy extinction, RE=Radiolarian extinction. (**B**) Sketch diagram showing the paleogeographical settings of the studied sections; Majiashan and Rencunping sections were located on outer shelf, Huangzhishan section was located on the carbonate platform, Meishan section was located at the ramp facies along the carbonate platform (Yang *et al.*, 1991).
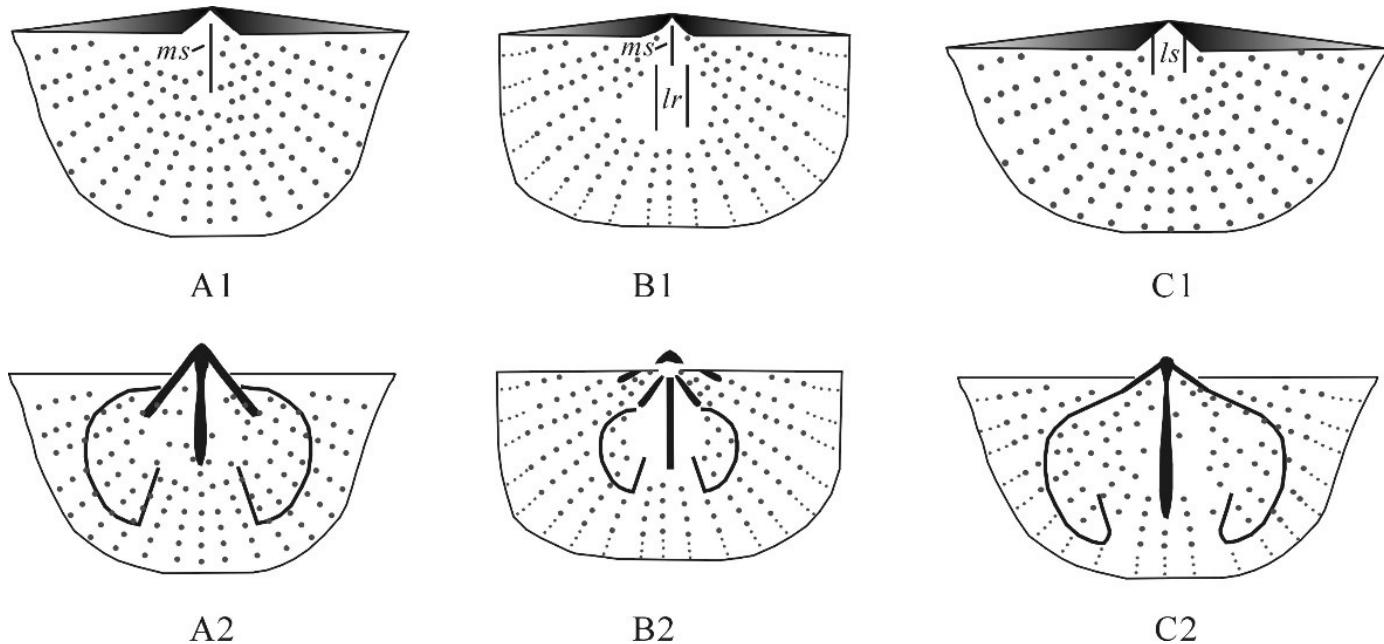
Fig.1. Comparison of interiors of *Tethyochonetes* Chen et al., 2000, *Neochonetes* Muir-Wood, 1962 and *Chaohochonetes* He & Shi 2014. A1- Ventral interior of *Tethyochonetes*, showing a median septum (*ms*) and the radially-arranged papillae. A2- Dorsal interior of *Tethyochonetes*, showing a stout median septum and two lateral septa. B1- Ventral interior of *Neochonetes*, showing a median septum (*ms*), two lateral ridges (*lr*), and the radially-arranged papillae which increased in number and decrease in size towards margin; B2- Dorsal interior of *Neochonetes*, showing a stout median septum and two lateral septa. C1- Ventral interior of *Chaohochonetes*, showing two short lateral septa (*ls*) and the radially-arranged papillae; C2- Dorsal interior of *Chaohochonetes*, showing a stout median septum, two lateral ridges connecting with a pair of brachial scars, and the radially-arranged papillae which increased in number and decrease in size towards margin. *ms*- median septum; *ls*- lateral septa.

Genus	Shape of umbo	Hinge-spines	Cardinal angle	Costellae	Concentric lines	Ventral median septum	Papillae of ventral interior	Papillae of dorsal interior	Sketch	
									Outline	Ventral interior
Para-pygmochonetes He & Shi gen.nov.	Hillock	Inclined towards midline with an angle of 40-50 to hingeline	90°	Bifurcated in flanks, irregular in width	Dis-continuous and irregularly arranged	Long and extending to a half of shell length	nearly radially arranged	nearly radially arranged, and occasionally connected with each other to form radial ridges		
Pygmochonetes Jin & Hu, 1978	Hillock	Projecting postero-laterally with an angle of about 60	65°	Bifurcated in flanks, straight and evin in width	Absent	Same to the above genus	Same to the above genus	Same to the above genus		

Fig.2. Comparision between *Parapygmochonetes* He & Shi 2014 and *Pygmochonetes* Jin & Hu, 1978. Data of *Pygmochonetes* based on Jin & Hu (1978).

Additionally, this paper also summarized the taxonomic composition, significant morphological features and palaeoecological implications of this deep-water brachiopod fauna and compared this fauna with the Permian-Triassic boundary (PTB) mixed brachiopod fauna of South China. The results revealed that the Changhsingian (latest Permian) deep-water brachiopod fauna of South China shares some common features with the PTB mixed brachiopod fauna, especially in terms of taxonomic composition and certain apparent morphological adaptations. This commonality is interpreted to indicate a time and a broad marine environment of widespread low oxygen supply and/or reduced trophic resources during the end-Permian life crisis in South China.

Covariations between seawater temperature and benthic biodiversity immediately after the glacial maxima of the Late Palaeozoic ice age, Western Australia

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Growing evidence shows that articulate brachiopod shells are one of ideal materials to indicate seawater temperature through measuring their oxygen isotopes during the Palaeozoic. Here, we present analytical results of brachiopod and bivalve shells across the glacial-nonglacial transition from the southern Carnarvon Basin of Western Australia during the ebb of glacial maxima and its aftermath (late Sakmarian, Early Permian), one of extreme climatic regimes of Earth during the Phanerozoic history. The glacial-nonglacial transition in the southern Carnarvon Basin, Western Australia, part of the interior seas of northern Gondwana during the Permian, is represented by the tillites of the Carrandibby Formation followed by the muddy carbonates of the Callythara Formation, which are typically exposed at the Callythara Spring section of the southern Carnarvon Basin. The latter unit is very fossiliferous and represents the only carbonate unit among the marine Permian successions in Western Australia, indicating deposition in a relatively warm seawater condition immediately after the glacial maxima. The Sakmarian successions in the study section show a distinct climatic change from the cold to cool-warm regimes. The glacial succession yields few brachiopods and moderately abundant bivalves, which usually occur in the form of shell beds. In contrast, the Callythara Formation yields abundant brachiopods, crinoids, corals, and foraminifera. All fossil shells are isolated from surrounding muddy rocks due to weathering and dray climatic conditions and thus allow quantitative sampling. Total three and 30 samples, each ~6000 cm^3 and ~3 kg, were collected from the glacial (uppermost Carrandibby Formation) and nonglacial (Callythara Formation) successions. Each sample yields 2-3 analyses from one bivalve or brachiopod shell for measuring their oxygen isotopes. The least diagenetically altered sample was selected by comparing modern brachiopod (main component is low-Mg calcite) with the Sakmarian articulate brachiopod/bivalve shells using several approaches including the Scanning Electron Microscopy, cathodoluminescence, trace element, and Raman spectroscopy. Then, the unaltered shells (mainly in the medium layer) were drilled using micro-driller to measure their oxygen isotopes (^{18}O) using Finnigan MAT 253 mass-spectrometer. The preliminary result shows that temperature derived from bivalve shells preserved in the glacial deposits is much lower than those measured from the brachiopod shells of the Callythara Formation, indicating clearly a glacial-nonglacial climatic variation. Moreover, brachiopod diversity of each analyzed sample is also measured by a means of various proxies such as the Shannon index (H), Dominance (D) and Evenness (E) based on counting generic and specific richness. The fluctuations of brachiopod diversities (Shannon Index) match well the seawater temperature variations, indicating that an elevated seawater temperature facilitated benthic diversification immediately after the glacial maxima during the Late Palaeozoic ice age in northern Gondwana.

Recovery brachiopod associations from late Rhuddanian in South China and its ecological significance

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Following the end-Ordovician mass extinction, the latest Ordovician and early Silurian was marked by a widespread transgression. The earliest Silurian brachiopod fauna has been described from a number of regions (see Cocks and Rong, 2008 for review). However, with rare exceptions (e.g. Rong *et al.*, 2013), the precise age of most assemblages is not sure. Recently, we reported a *Dicoelosia* (Brachiopoda) population occurred in benthic shelly assemblages of the lower Niuchang Formation from South China (Huang *et al.*, 2013). Constrained by graptolite data, the shelly fauna containing the population was assigned to the recovery interval after the end Ordovician mass extinction (upper Rhuddanian, Llandovery). Here, we will simply analyze the taxonomic composition of the brachiopod fauna, and conduct a paleoecological analysis for it including differentiating brachiopod-dominated associations and their living environments. The material was collected from the lower Niuchang formation at Xinglongchang section, 1 km southeast of Xinglong Village, southeast of Meitan County Town, northern Guizhou, South China. The strata are characterized by near shore, shallow water,

brownish-yellow silty mudstone or grey mudstone that is fossiliferous of several fossil groups, such as brachiopods, trilobites, and a few bryozoans and graptolites.

A preliminary study on the brachiopods (from 9 collections: AGI521–522, 524–527 and 530–532, see Fig. 1) indicates the presence of 6 major groups of brachiopods, including orthids, strophomenids, rhynchonellids, atrypids, athyridids, and spiriferids, represented by 14 genera, amongst which *Eostropheodonta*, *Katastrophomena*, *Levenea*, *Dicoelosia*, *Meifodia?* and *Eospirifer* are the most abundant, and *Aegiria*, *Merciella*, *Fardenia*, *Chrustenopora?*, *Epitomyonia*, *Zygospiraella*, *Eospirigerina* and *Whitfieldella* the minorities. Orthids and strophomenids are predominant in both abundance and generic diversity. We made a CA (cluster analysis) for all those collections. Three associations were clearly recognized (Fig. 1): 1) AGI521–522, *Dicoelosia–Zygospiraella* association; 2) AGI524–527 together with AGI530, *Levenea–Eostropheodonta* association; 3) AGI531–532, *Meifodia?–Eospirifer* association.

Dicoelosia population was assigned to BA3 environment with several lines of evidences (Huang *et al*., 2013). After careful analysis on the Dicoelosia–Zygospiraella association, the bathymetry of the collections AGI521–522 was assigned to "lower BA3" rather than simple "BA3". The brachiopods younger than the *Dicoelosia–Zygospiraella* association, i.e. the

Levenea–Eostropheodonta association, were thought to live in a shallower environment owing to their sharply decreasing generic diversity (from 10 to 5). Meanwhile, those deeper water indicators, such as *Epitomyonia* and *Dicoelosia*, disappeared from the collection AGI 524, which also suggests the water became shallower.

Meifodia?–Eospirifer association is the most interesting brachiopod assemblages of all collections, and several similar assemblages of similar age are found in other areas, all of which will be systematically studied in another paper. Its diversity further decreases compared with the association 2. Only 3 brachiopod genera are found, and the association is dominated by *Meifodia?* and *Eospirifer*. Compared with its underlying *Levenea–Eostropheodonta* association, it has much higher abundance and lower diversity, indicating a shallow environment corresponding to BA2.

Is this contradicted to the global transgression? The regional environment should be emphasized to answer this question. The locality of the Xinglongchang section in Meitan County yielding those fossils is paleogeologically located in the northern marginal belt of the Qianzhong (Central Guizhou) Old Land, southern Upper Yangtze Region. Although the beginning of Silurian was marked by a significant and rapid rise of sea level worldwide, in northern Guizhou, the Qianzhong Uplift was still progressing during the Rhuddanian (e.g. Rong *et al*.,
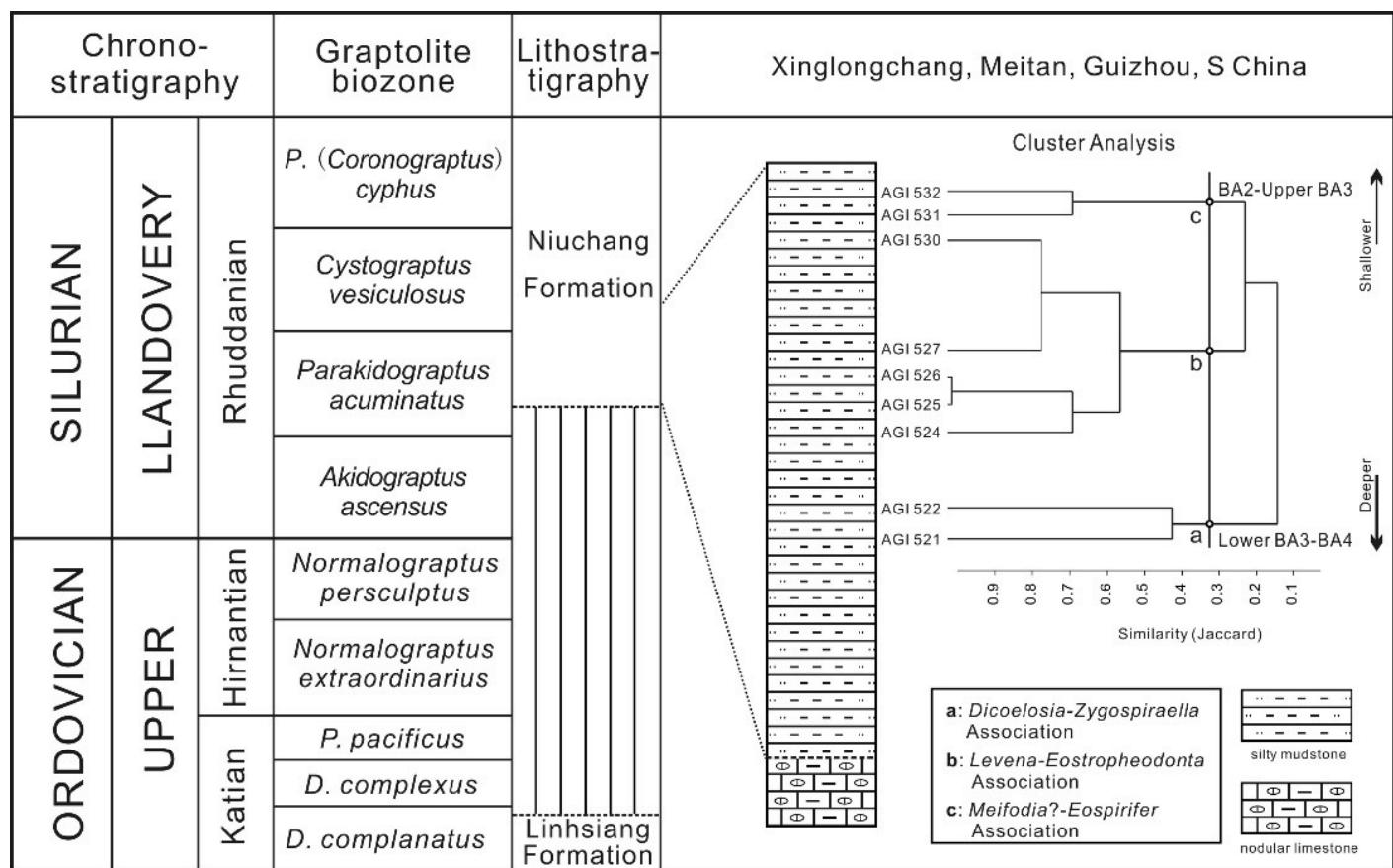
Fig. 1. Nine collections made in the lower Niuchang Formation of Meitan County, Guizhou Province, South China. The result of Cluster Analysis for the fossil bed was superimposed.

2011). The global sea level drop together with the Qianzhong Uplift at the end Ordovician excised the youngest Ordovician rocks in northern Guizhou, South China. Consequently, the near shore shelly fauna inhabited this area in the southern marginal area of the Upper Yangtze Epicontinental Sea first during the Rhuddanian transgression. The Xinglongchang section is very close to the paleoshoreline, indicating a relatively shallow water environment.

The "seesaw battle" between the global transgression and the Qianzhong Uplift helped sustain a stable regional environment, probably the Qianzhong Uplift get the upper hand during the recovery interval of the end Ordovician mass extinction, which made the shallower trend found in this section. Such situation provided a shallow water habitat to favor the recovery of brachiopods in South China.

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Brachiopod fossil richness controlled by the intensity of chemical weathering

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The Lower Carboniferous Jiusi Formation in South China is composed of limestone-shale alternations, which consist of interlayers of limestone and shale beds. Monospecific brachiopod fossil (*Pugilis hunanensis*) is discovered from most shale beds with various abundance. The fossil richness shows an increasing trend upward in the studied section, although there is no detectable difference in lithology. Increase in fossil richness may reflect higher reproduction and/or survivorship of brachiopods under more favorable environments or enhanced preservation rate of brachiopod fossils. These two competing arguments correspond to the two scenarios of the formation of limestone-shale alternations. The rhythmic limestone-shale alternations might be generated by the cyclic fluctuations of terrestrial input, which might be driven by orbital forces (Milankovitch cycles), or by the differential diagenesis of relatively homogeneous sediments, resulting in the accumulation of siliciclastic contents as predominant carbonate dissolution in shale beds.

To test whether increase in the brachiopod richness is environmental or diagenetic control, we measured Mg isotopic compositions of the siliciclastic component in the limestone-shale alternations of the Jiusi Formation. Our results show that Mg isotopic compositions of the siliciclastic components of the shale beds ($\delta^{26}Mg_{shale}$) and the limestone beds ($\delta^{26}Mg_{lst}$) display different stratigraphic trends. $\delta^{26}Mg_{shale}$ remains relatively stable (0.4‰ to 0.8‰), while $\delta^{26}Mg_{lst}$ shows an overall increasing trend from -0.4‰ to 1.6‰. This observation argues against the diagenetic origin of the limestone-shale alternations, because siliciclastic components in the shale and limestone beds have different isotopic compositions and decoupled stratigraphic trends. Therefore, increase in the richness is not resulted from diagenetic accumulation of brachiopod fossils. The stratigraphic variation in $\delta^{26}Mg$ implies that deposition of limestone-shale alternations is driven by the cyclic fluctuation of terrestrial input, which is mainly controlled by chemical weathering in continentals. Higher $\delta^{26}Mg$ of the siliciclastic components implies chemical weathering with higher intensity, because light Mg is preferentially dissolved in fresh water, leaving heavy Mg in weathering residues.

In the lower part of the studied section (cycles 1-11), $\delta^{26}Mg_{shale}$ is higher than $\delta^{26}Mg_{lst}$, suggesting that chemical weathering is more intensive during the interval of shale deposition. In the upper part of the section (cycles 12-20), there is a sharp increase in $\delta^{26}Mg_{lst}$ from 0.2‰ to 1.6‰, while $\delta^{26}Mg_{shale}$ remain unchanged. This implies that enhanced chemical weathering during carbonate deposition. Sudden increase in the intensive of chemical weathering is coincident with increase in the richness of brachiopod fossils. Thus, brachiopod fossil richness might be coupled with

the intensity of chemical weathering. As a benthic sessile organism, the size of brachiopod community is determined by the availability of organic particles. We suggest that enhanced chemical weathering in continents delivers more nutrients into oceans, which in turn stimulate higher organic matter production in surface oceans, accordingly provide more food for brachiopods.

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Thomas Davidson was the most important brachiopod worker of the 19th century. Even though he did not erect so many taxa as some others, he was the first person to classify the group in depth, and influenced international workers such as James Hall and Joachim Barrande. His collections span the geological history of the Brachiopoda and he described material from many countries, and ranging from the Cambrian to today. Although he had no formal geological or zoological training, he studied art in Paris and also attended geological lectures at the university there. The Natural History Museum in London was bequeathed his collections and also the associated notebooks which are the bound leaves with individual sketches of all the illustrated specimens, many highlit with ink wash and which are thus art objects in themselves. The notebooks formed the basis of the series of monographs which are still heavily used today, and for which Davidson himself carved the images on the lithographic stones used for the many plates. Highlights of his collection include the beautiful Silurian, Devonian and Carboniferous spiriferids and other brachiopods whose spiralia were previously unknown, which were patiently prepared by the Reverend Norman Glass using acetic acid drip by drip over many months. It was from the Silurian Wenlock Limestone that Davidson first collected brachiopods himself, and he also persuaded a local squire there to employ labourers to undertake excavations of the the Wenlock Shale as well as laundresses who spent weeks hand washing and sifting the shales, from which we have thousands of specimens.

Other highlights of the brachiopod collections held at the NHM include Ordovician and Silurian collections made Mrs Thomas Gray and her family from Girvan, Scotland, and (perhaps more importantly) Alwyn Williams, who was perhaps the greatest brachiopod worker of the twentieth century, and Helen Muir-Wood and Howard Brunton whose collections came from the Carboniferous. Also in our holdings is material collected by Charles Darwin during his famous Beagle voyage, and other Recent material collected by HMS Challenger during her historic cruise to survey the ocean floors.

Proteome analysis of shell matrix proteins in the brachiopod *Laqueus rubellus*

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The calcitic brachiopod shells contain proteins that play pivotal roles in shell formation and are important in understanding the evolution of biomineralization. Here, we performed a large-scale exploration of shell matrix proteins in the brachiopod *Laqueus rubellus* using proteomics combined with transcriptomics. As a result, a total of 75 shell proteins were identified. The results revealed some known proteins such as ICP-1, which is the brachiopod shell matrix protein sequenced partially in previous studies, and MSP130, which is a skeletal protein identified from sea urchins and oysters. Our data also showed many novel shell proteins containing unique structures. One such shell matrix protein was identified with a domain architecture that includes a NAD(P) binding domain, an ABC-type transport system, a transmembrane region, and an aspartic acid rich region, a multidomain protein which has not been found in other biominerals. We also identified pectin lyase-like, trypsin inhibitor, and saposin B functional domains in the shell matrix proteins of *L. rubellus*. The repertoire of brachiopod shell matrix proteins also contains two basic amino acid-rich proteins and proteins that have a variety of repeat sequences. Our study suggests an independent origin and unique mechanisms for brachiopod shell formation.

Pridolian to Eifelian brachiopod faunas, biofacies

and events of the Rhenish Massif (Germany)

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Pridolian (latest Silurian) to Eifelian (early Middle Devonian) strata in the Rhenish Massif (Rheinisches Schiefergebirge, Germany) contain a succession of rhynchonelliformean brachiopod faunas reflecting palaeoenvironmental changes in a tropical epeiric sea, driven by regional and global forces during a time span of approximately 30 million years (Jansen, subm.). These faunas, sets of assemblages named after characteristic spiriferide species, are separated by events discernible by facies change and faunal turnover; the events are related to palaeoenvironmental changes caused by the interplay of eustatic sea-level fluctuations (Johnson *et al.* 1985; T-R cycles mentioned below) and varying rates of crustal subsidence and sedimentation. The present study in connection with the still ongoing monographic revision of the Rhenish faunas is an attempt to elucidate these interrelationships.

Distribution and composition of the Rhenish brachiopod faunas are also dependent on spatio-temporal variations of the shallow-marine, largely siliciclastic rhenotypic ("Rhenish") facies, which is subdivided into three newly defined larger subfacies (Jansen, subm.), each characterised by a specific faunal composition and more or less terrigenous influence: (1) eurhenotypic, (2) pararhenotypic and (3) allorhenotypic facies. These facies reflect (1) shallow marine, arenaceous palaeoenvironments with turbid water, (2) marginal marine, deltaic, coastal-lagoonal or intertidal palaeoenvironments with strongly changeable conditions and (3) more calcareous, open shelf palaeoenvironments with clear water. The rhenotypic facies as a whole is typically developed in neritic strata of Pridolian to Frasnian age in Europe and North Africa.

The first rhenotypic brachiopod assemblages of the Rhenish area belong to the earliest Gedinnian (late Pridolian) *Quadrifarius dumontianus* Fauna. Ecological effects of the transgressive Klonk Event (Jeppsson 1998) may have caused its extinction near the Silurian-Devonian boundary.

With the Hüinghausen Event in the early Gedinnian (early Lochkovian), shallow marine conditions suitable for the eurhenotypic *Howellella mercurii* Fauna arose. This fauna went extinct still within Gedinnian (Lochkovian) time, with the onset of the "Rhenish Gap", a strong regressive interval during the late Gedinnian to early Siegenian with a duration of 6-8 m. a., only partly reflected by the global sea-level curve and presumably caused mainly by strong siliciclastic input from the Old Red Continent; continental, lagoonal, deltaic or intertidal conditions expanded in wide parts of the Ardenno-Rhenish region. Still within this phase, a weak marine influence near the beginning of the Rhenish Siegenian (approximately Lochkovian-Pragian boundary level or early Pragian), probably caused by increasing subsidence and decreasing sedimentary supply or already linked to an early Pragian transgressive pulse within T-R Cycle I a, is described as the Hermeskeil Event (Mittmeyer 2008). It led to the local establishment of conditions of the pararhenotypic facies characterised by representatives of *Crassirensselaeria*.

Environmental conditions of the normal marine, eurhenotypic facies widely spread with the Gensberg Event at the beginning of the middle Siegenian, documenting a transgression of supra-regional importance. It introduced the highly diverse middle to late Siegenian *Acrospirifer primaevus* Fauna. It is still a working hypothesis that this development could correspond to the transgressive Zinzilban Event documented in Uzbekistan (Yolkin *et al.* 1994) or a (corresponding?) transgressive pulse of the middle Pragian. In contrast, the faunal turnover at the beginning of the late Siegenian Kürrenberg Event (Mittmeyer 2008) was mainly governed by increased supply of siliciclastics and higher sedimentation rates probably in combination with a eustatic sea-level fall during the late T-R Cycle I a. Organisms with clear water preference diminished so that faunas with reduced diversity and turbidicolous species (e. g., *Hysterolites hystericus*) became dominant.

The late Siegenian Saxler Event (Mittmeyer 2008) marks the beginning of a transgression which may coincide with the onset of T-R Cycle I b of the global sea-level curve (Johnson *et al.* 1985) and the "Basal Zlíchov Event" *sensu* García-Alcalde (1997). It resulted in the onset of brachiopod-dominated eurhenotypic facies. The transgressive phase continued into the early Emsian and led to the facies change from the pararhenotypic and eurhenotypic Taunusquarzit Group to the largely hercynotypic Hunsrück Slate Group in the southern Rhenish Massif. The early Emsian *Arduspirifer antecedens* Fauna shows a gradual evolution of the rhenotypic brachiopods within the Ardenno-Rhenish Shelf region, exemplified by the genera *Euryspirifer* and *Arduspirifer*. A peak of marine influence is reached with the transgressive Stadtfeld Event (Mittmeyer 2008) in the late early Emsian. Regressive tendencies in the latest early Emsian, mainly caused by very high sedimentation rates accommodated by concomitant strong subsidence, led to local extinctions and pararhenotypic to continental-fluvial facies.

After the system of rapid subsidence and high sedimentation rates had ceased, the rising sea-level in connection with the earliest late Emsian Berlé Event (Mittmeyer 2008) provided a more continuous connection to the sea and allowed the immigration of many taxa. The eurhenotypic facies with the late Emsian *Euryspirifer paradoxus* Fauna developed. It is possible that the Berlé Event was linked to the global Daleje Event (e. g., Walliser 1996), which was merely a transgressive phase (Ferrová *et al.* 2012). The overall transgressive trend during the late Emsian was accompanied by a modest, stepwise faunal change. One of the most conspicuous features is the radiation of the genus *Paraspirifer*. The beginning of T-R Cycle I c may correspond with a transgressive pulse within the Kondel (latest Emsian) time. While the eurhenotypic Kondel fauna died out in the central and eastern Rhenish Massif near the Emsian-Eifelian boundary, resulting from the onset of deep water, hercynotypic conditions, allorhenotypic late Kondel faunas lived on in the Eifel and Sauerland regions and survived into the Eifelian. With the transgression, the genus *Intermedites* appeared near the lower boundary of this stage; it was probably an immigrant from the South China region (Schemm-Gregory 2010). The *Paraspirifer cultrijugatus* Fauna went extinct with the Kirberg Event (Struve 1990) within the *Polygnathus costatus costatus* Biochron at the end of the Lauch time, following with some delay

after the Basal Choteč Event.

To conclude, the Pridolian to early Eifelian sedimentary successions of the Rhenish Massif exemplify the dependence of the faunal development on the interplay of eustatic sea-level changes in combination with varying subsidence and sedimentation rates in the Ardenno-Rhenish Shelf area. The effects of possible climate changes are still unclear. Extinction, habitat-tracking, emigration and immigration of brachiopod species in connection with major events governed the composition of faunas. The evolutionary change partly took place in small, isolated populations within or outside the Ardenno-Rhenish region; it is not necessarily documented in the fossil record. With the onset of more suitable conditions after the events, faunas immigrated from outside or spread over the shelf from isolated habitats, and benthic assemblages could re-establish. Relatively modest or minor evolutionary change took place between the events and within the Ardenno-Rhenish Shelf.

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Paleoecological and paleogeographical gradient of Late Ordovician dalmanelloid brachiopods in Laurentia

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Dalmanelloid brachiopods first appeared in the Early Ordovician (e.g. *Paurorthis* from the East Baltic and *Nereidella* from South China, Floian), most likely in the cool/cold water marine environment of Gondwana or peri-Gondwana terranes (Harper, 2000). Their first diversification in Laurentia, however, did not occur until the Late Ordovician (Sandbian–Katian), and their first radiation was especially well recorded in the continental-margin basins of southeastern Laurentia (including the Appalachian foreland basin in the Katian), and the Cincinnati Arch region. Dalmanelloid taxa are notoriously difficult to differentiate at the generic and specific levels due to their relatively small shell, fine costae and costellae, and highly variable internal structures. Despite their cool water origin, dalmanelloid diversification in Laurentia took place almost exclusively in tropical marine environment. During the Late Ordovician, Laurentia straddled the equator (Cocks and Torsvik, 2011; Jin et al. 2012), and an unusually high sea level and marine transgression created vast epicontinental seas that inundated much of the continental interior. Due to its large size and lack of notable drifting during the Late Ordovician, Laurentia facilitated the formation of distinct paleoecological gradients from equatorial to subtropical latitudes and from inland epicontinental seas to continental-margin basins. As in many other groups of brachiopods, dalmanelloid evolution clearly responded to these paleoenvironmental gradients, which was reflected in their shell modifications in different paleogeographical and paleoecological settings.

From the early Katian to Hirnantian, there was a clear and persistent paleolatitudinal differentiation of dalmanelloids in Laurentia. In the high tropics south of the equator, *Cincinnetina*, *Onniella*, and *Heterorthina* were the dominant taxa, often forming relatively low-diversity benthic shelly communities preserved as localized shell pavement. These occurrences were replaced by draboviid enteletoids (sister superfamily of the Dalmanelloidea) during the Hirnantian, such as *Hirnantia* and *Kinnella* in the Gaspé Peninsula and Anticosti Island along the southeastern margin of Laurentia (Jin and Zhan, 2008). In the mid-tropics, *Paucicrura* became the most common dalmanelloid genus, both south and north of the equator. Along the paleoequatorial belt, *Diceromyonia* was the single most common dalmanelloid genus, well preserved in Richmondian (upper Katian) carbonate rocks of the northwestern Hudson Bay basin, southern Manitoba and Wyoming (Williston Basin), as well as in the Utah-Nevada and Texas-New Mexico border areas along the southwestern cratonic margin of Laurentia.

Among the various dalmanelloid lineages in different paleotropical latitudes, a number of morphological changes from high-tropical to paleoequatorial taxa mark a paleoecological or paleogeographical gradient.

1. Increased shell thickness from high tropics to the equator.

Many early Katian dalmanelloid species from high tropical paleo-latitudes (e.g. Cincinnati Arch area) commonly have a paper-thin shell and an especially thin dorsal valve, resulting in a common taphonomic feature of crushing and caving-in of the valves. This is exemplified by the well-known *Heterorthina marcfarlani* from the Lexington Limestone (Chatfieldian), *H. emacerata* and *Cincinnetina multicosta* from the Kope Formation (Edenian) of Ohio and Kentucky. In comparison, various species of *Paucicrura* from mid-tropical paleolatitudes exhibits a thicker shell that rarely show crushed preservation, even when they are preserved in relatively soft micritic mudstone or shale. This can be observed in *Paucicrura rogata* from the Derorah Shale (Chatfieldian) of Minnesota and in the carbonate mudstone and wackestone of the Advance Formation of northern Canadian Rocky Mountains. Dalmanelloid shell thickening is most obvious in *Diceromyonia storeya*, which occurs predominantly in paleoequatorially located inland epicontinental seas, such as the Hudson Bay and Williston basins during the late Katian. Here, thickening of the shell wall is associated also with extravagant development other shell characteristics, such as the enlargement of muscle attachment structures.

2. Enlargement of muscles and their skeletal attachment structures. In southern Laurentia, where Late Ordovician dalmanelloids are most common, *Heterorthina* was a typical dalmanelloid genus in the high tropical paleolatitudes. As in the type species, *H. praeculta* Bancroft, 1928 from the Cheneyan (basal Katian) of Shropshire, UK, the early–mid Katian forms of *Heterorthina* in the Cincinnati Arch area, such as *H. macfarlani* Neuman, 1967 and *H. emacerata* (Hall, 1860), typically have a small ventral muscle field (average 35% shell length), and notably small dorsal adductor muscle scars (average 30% shell length). Towards mid-tropical paleolatitudes, *Heterorthina* disappears and *Paucicrura* becomes more common, with the addition of *Cincinnetina* which extends from Cincinnati Arch area to the Illinois Basin, the upper Mississippi valley, and the Michigan Basin (Jin, 2012). These mid-paleotropical dalmanelloids are marked by somewhat larger muscle scars, especially larger dorsal adductor muscle scars. In *Cincinnetina multisecta* and *C. meeki*, for example, the dorsal muscle field reaches near the mid-length of the valve. Within the family Dalmanellidae, a striking enlargement of the ventral diductor muscle scars was particularly notable in the paleoequatorial *Diceromyonia*, as well as a gradational change from a bilobate to trilobate cardinal process, as seen in the *Cincinnetina–Paucicrura–Diceromyonia* lineages, from subtropical to equatorial localities. It remains poorly understood at present as to why dalmanellid shells evolved larger and more complex muscle attachment structures, which was presumably related to a more voluminous musculature, towards the paleoequator.

3. Increased shell perforations. As is shown in *Diceromyonia* that are predominant in paleoequatorial basins of Laurentia, this modification in shell microstructures is manifest in two ways: first, the size and density of large punctae are notably greater and, second, the single-columned aditicules are better developed and more densely spaced, when compared to dalmanelloid shells that were confined mostly to subtropical–temperate settings. In *Diceromyonia storeya* from the Williston and Hudson Bay basins, for example, the course punctae and aditicules are so prominently developed so as to make its shells perforated like a sieve.

The increased in size and density of shell punctae may have been an adaptive response to living in equatorial epicontinental seas, where the lack of severe storms (hurricanes or cyclones) and a constantly high annual water temperature may have resulted in poorly oxygenated bottom conditions at relatively shallow water depth (Jin et al. 2012). It has been demonstrated that the mantle tissue (caesa) extended into the punctae can aid oxygen intake and gas exchange in living terebratulides (Thayer, 1986; Pérez-Huerta et al., 2009). It is thus most likely that the Late Ordovician dalmanelloids developed distinctly dense but large punctae to cope with the oxygen-poor substrate conditions in equatorial to low-tropical epicontinental seas of Laurentia (estimated at 10–70 m depth). This interpretation seems further supported by the change in dalmanelloid shell microstructures within a single basin during climatic change. In the Anticosti basin, for example, *Paucicrura* in the upper Vaureal Formation lived during the Richmondian (late Katian) greenhouse episode and correspondingly developed highly perforated shells with large punctae, whereas in the overlaying Ellis Bay Formation that corresponded to the Hirnantian icehouse climate, *Paucicrura* was replaced by *Onniella* (of the same Family Dalmanellidae), which had such fine punctae as to give the shell a solid appearance. It is possible that the cooler and perhaps better circulated sea during the Hirnantian became well oxygenated, without significant selection pressure for a highly perforated shell to improve respiration.

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Palaeoenvironment and palaeoclimate from geochemistry of low-Mg calcite brachiopod shells

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Low-Mg-calcite (LMC) shells of articulate brachiopods have

been successfully used for more than 50 years (e.g. Compston, 1960) to reconstruct palaeoenvironments and climate of the past by analyzing and interpreting their isotopic (C, O, Sr, and other) and elemental compositions. LMC is relatively resistant to diagenesis and the brachiopod shells can therefore carry the original geochemical seawater signal over hundreds of millions of years. To evaluate preservation state, the samples can be screened by optical (binocular microscopy, cathodoluminescence microscopy, scanning electron microscopy) and chemical (trace element abundances, isotopic ratios) techniques (Ullmann and Korte, 2015).

Textural modification is easily recognizable by optical inspection. Chemical changes usually follow characteristic trends with enrichment in manganese and depletion in strontium during progressing alteration (Brand and Veizer, 1980). Mn enrichment is traceable qualitatively by cathodoluminescence microscopy or quantitatively by ICP-OES analyses. For the latter, fixed upper limits are frequently used to exclude diagenetically altered samples from palaeoenvironmental reconstructions. Manganese as well as strontium limits cannot be universally applied, but must be evaluated from case to case. This is necessary because Mn and Sr concentrations in seawater vary temporarily and spatially, and Sr incorporation in biogenic calcite is controlled by environmental factors (Korte and Hesselbo, 2011; Ullmann and Korte, 2015).

More than 15 years after the 'second generation' of brachiopod carbon, oxygen and strontium isotope records for the Palaeozoic and Mesozoic (Veizer et al., 1999), new datasets have become available showing in greater detail results from different palaeolatitudes, regions, and water depths (e.g., Voigt et al., 2003; Korte et al., 2008; Ullmann et al., 2014; Jelby et al., 2014). By using these recently generated data, in comparison to literature results of other researchers, a better evaluation in terms of regional versus global climate and environmental change is possible for different time spans, and new carbon cycle perturbations and seawater temperature changes have been discovered. These seawater temperature changes often correlate with biotic events in several periods of the Phanerozoic, and this is the case for long- and short-term events. The first oxygen isotope data from microbrachiopods of the Danish chalk are available for the time span across the Cretaceous-Palaeogen transition. These data suggest a slight, short-term cooling in the event bed (Fishclay) of the K/T boundary. The new results also show temperature fluctuations at that time, when the cold water reef at Faxe was formed in the Danian, the latter characterised by distinct changes of coral types.

More isotopic and elemental work on brachiopod calcite, including heavier isotopes such as those of chromium, is currently in progress, and will further contribute to discovery of climate and environmental changes of the past for different periods in the Phanerozoic.

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The accessory hearts of the rhynchonellid brachiopod *Hemithyris psittacea*

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Some recent brachiopods have several small accessory hearts in addition to the main large heart. However, the critical factors that determine the location of the accessory hearts and their fine structure remained unclear. We studied the ultrastructure of the accessory hearts and the anatomical variability in their position in the rhynchonellid brachiopod *Hemithyris psittacea* (Gmelin, 1790). The blood system anatomy was studied in detail by manual dissection of eight specimens. The fine structure of the accessory hearts was studied using the transmission electron microscopy. All of the specimens that we observed had accessory hearts, which varied in their number

and location. None of the brachiopods, among the eight specimens examined, showed the same pattern of accessory heart arrangement. At the same time, the general regularity is that the accessory hearts are near the nephridial funnels and near the proximal parts of the gonad vessel net. Only two of our specimens showed accessory hearts on the ventrolateral vessels in the proximal part of the ileoparietal mesenteria (not around the nephridium). The accessory heart wall is composed of outer coelomic epithelium, extracellular matrix, and inner amoebocytes. The coelomic epithelium consists of epithelio-muscle cells with the basal muscle processes, which give rise to the secondary thin non-muscular processes, interdigitating with each other and forming irregular ultrafiltration slits. The inner amoebocytes do not form a continuous layer and lack desmosomes; thus, they cannot be considered as a true epithelium. Brachiopod accessory hearts apparently fulfill two functions. The well-developed muscular net in the accessory heart wall performs the propulsion of blood to branched gonad vessels. The epithelio-muscle cells in the accessory heart wall are the podocyte-like cells; therefore, the accessory heart wall can be interpreted as the ultrafiltration site. The association of accessory hearts with nephridia suggests their involvement in excretion.

Structure of the blood system in rhynchonellid brachiopods

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Brachiopods are a relict group of marine invertebrates that first appeared in the early Cambrian. Some organ systems of recent brachiopods especially their blood systems are still poorly known. We have studied the anatomy and ultrastructure of the blood system rhynchonellid brachiopod *Hemithyris psittacea* (Gmelin, 1790).

Our anatomical studies showed that the main heart is located on the dorsal side of the stomach behind the attachment of the gastroparietal mesentery to the stomach. The main heart subdivides the dorsal vessel into the anterior and the posterior ones. The anterior dorsal vessel runs forward from the main heart along the stomach and the esophagus. At the level of the stomach, it gives rise two pairs of the vessels running to the digestive diverticula. At the level of the esophagus, the anterior dorsal vessel gives rise to the branches running to the sinuses of the periesophageal coelom. At the circumoral region, the anterior dorsal vessel splits into two lophophoral vessels running along the lophophoral brachia. Each lophophoral vessel goes within the brachium along the small coelomic canal and gives rise to blind blood vessels penetrating the tentacles. Posteriorly to the main heart, the posterior dorsal vessel divides into two dorsal vessels. Each of them in their turn bifurcates, so that a pair of dorsolateral and a pair of ventrolateral vessels form. The dorsolateral vessels run along the lateral stomach sides, pass on the left and the right gastroparietal mesenteries, go along the funnels of the anterior nephridia, and form a network of gonad vessels in the dorsal mantle. The ventrolateral vessels run along the left and the right ileoparietal mesenteries, supply the posterior nephridia with blood, and give rise to a network of ventral gonad vessels in the ventral mantle. The mantle vessels end blindly on the periphery of the gonad. We found the vesicle-like accessory hearts on the lateral vessels behind the nephridial funnels, close to the gonad vessels. Except the well structured blood vessels mentioned above, there are two blood sinuses. The circumintestinal blood sinus envelopes the guts from the mouth to blind hind end. The periesophageal sinus is blood filled spaces within the numerous septa crossing the periesopageal coelom. Two mentioned sinuses communicate at the level of esophagus.

We studied the fine structure of the wall of the ventrolateral, dorsal, lophophoral, tentacle and gonad blood vessels, the main heart and the accessory hearts using the transmission electron microscopy. In all cases the wall consists of the outer coelomic epithelium, the extracellular matrix (ECM) and inner amoebocytes forming the endothelial lining. The ECM consists of basal lamina contouring the basal parts of coelomic cells and fibro-reticular layer. The amoebocytes are not connected by desmosomes and lacks of the basal lamina. Thus, the inner amoebocyte lining cannot be considered as a true epithelium. The mantle gonad vessel is very specific because its wall functions as the genital lamella that produces gonia. The coelomic epithelium of the dorsal, lophophoral, tentacle vessels, the main and accessory hearts comprises of the podocyte-like cells with numerous interdigitating pedicels.

The structure of the main heart wall was studied using the transmission electron microscopy, cytochemestry and confocal laser scanning microscopy. The main heart is just an evagination of the dorsal blood vessel. It is sac-like organ communicating with the dorsal vessel through the narrow tube-like stalk. The wall of the main heart consists of the outer coelomic epithelium, ECM and inner amoebocytes. The outer coelomic epithelium of the main heart wall consists of two types of cells. The first type is epithelia-muscle podocyte-like cells with long thick muscle processes forming strong muscle network in the heart wall and thin interdigitading pedicels. Cells of the first type are strongly stained for phalloidin but have weak reaction against α-tubulin. The second type is muscle-free peritoneal cells containing numerous inclusions and abundant rough endoplasmic reticulum. They exhibit strong α-tubulin-like immunoreactivity and are not stained for phalloidin. Except the obvious propulsatory function, the main heart wall may play an important role in ultrafiltration. In a diastolic condition, the coelomic epithelium stretches; the ECM

becomes thin, and the basal lamina straightens. The basal lamina between the pedicels of podocytes faces the coelomic space. The gaps between amoebocytes widen because they are not fastened together by desmosomes. So, the liquid may go from blood to periviceral coelom trough ECM of the main heart wall.

Thus we proposed the sites of ultrafiltration in the periviceral coelom. The wall of the periesophageal sinus is supposed to be the second site of ultrafiltration, because the coelomic lining of the periesophageal coelom comprises of podocyte-like cells. In this case, the liquid goes from blood to periesophageal coelom which is interconnected with coelom of small lophophore canals. It should be emphasized that the walls of lophophoral and tentacle vessels also contain of podocyte-like cells. So, two isolated compartments of coelom (periviceral and periesophageal+small lophophoral canal coelom) have two sites of ultrafiltration.

Antitropicality and convergent evolution: a case study of Permian neospiriferine brachiopods

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Antitropicality is a distinct biogeographical pattern characterised by the natural occurrences of the same species or members of the same clade in the middle or middle to high latitudinal habitats of both hemispheres without the appearance in the intervening tropical environments (Hubbs, 1952). Numerous cases of the antitropical distribution of ancient life have been reported from the Permian Period. For most examples, particularly in marine invertebrates, the antitropical disjunctions have been mainly explained with either dispersal or vicariance models (Shi and Grunt, 2000). However, the genuine mechanism underlying the Permian antitropicality is still being unravelled. This study investigated the antitropicality of some Permian neospiriferine brachiopods through detailed morphological examination, comparison of palaeobiogeographical distribution, and phylogenetic analysis.

According to our taxonomic revision, several brachiopod species, previously treated as *Kaninospirifer* Kulikov and Stepanov *in* Stepanov *et al.*, 1975, are reassigned to other genera, especially to *Fasciculatia* Waterhouse, 2004 in the northern hemisphere and to *Quadrospira* Archbold, 1997 in the southern hemisphere of the Permian Earth. Both *Kaninospirifer* and *Fasciculatia*

appear to have been distributed in northern Pangea and in northeastern Asia during the Permian, but were seemingly unable to migrate to the southern hemisphere where *Imperiospira* Archbold and Thomas, 1993 and *Quadrospira* exclusively existed. In spite of the distributional separation between the genera under the Permian palaeobiogeographical regime, some neospiriferine brachiopods that were limited to mid-latitudinal regions of each hemisphere share considerable morphological characters, such as large shell, subdued fasciculation, and reduction of ventral adminicula. However, the phylogenetic reconstruction of the neospiriferine brachiopods does not support a close relationship among the examined genera, thus suggesting that these similar morphological features must have been independently acquired. Consequently, we consider that these morphological similarities were caused by the resemblance in environmental conditions between the mid-latitudinal areas of both hemispheres during the Permian, implying a convergent evolution.

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Virtual palaeontology: x-ray microtomography of Palaeozoic brachiopod fossils embedded in various rocks

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In recent years, the adoption of computed tomographic techniques, especially X-ray microtomography (XMT), to the study of diverse fossils has become increasingly popular. With the high accessibility lf the hardware, the development of sophisticated computer software that support various image processing has

enabled palaeontologists not only to visualise dissections of the X-ray scanned fossil material and but also to reconstruct high-resolution three-dimensional (3-D) models of fossil (external and internal) morphology, heralding a new era for virtual palaeontology (Cunningham *et al.* 2014; Sutton *et al.* 2014). However, the resolution of XMT images critically depends on the contrast between the fossil material and its surrounding rock. We here apply XMT to eleven Palaeozoic brachiopod specimens embedded in a range of rocks in order to 1) visualise practical XMT images which display fossil shell interiors in various associations of brachiopod shell and the hosting matrix and, ultimately, to 2) investigate the extent of effects of composition and texture of various fossil shells and their hosting sediment rock matrices on the quality of XMT outcomes.

Although most of our XMT results for the selected brachiopods provide recognisable information about the internal morphologies of brachiopod shell, particularly in the cardinal area, the results display a spectrum of visibility by the type of the brachiopod shells and the its infilling matrices. Brachiopod samples with their original calcitic carbonate shell, embedded in and surrounded by highly siliceous sediment matrices, generally display a high resolution of XMT images characterised by sharply defined shell internal structures, whereas a calcareous shell associated with calcareous grainstone provides poor images of the shell internal structures, clearly suggesting the limitation of the currently available XMT technique. Consequently, it seems that sufficient contrast in mineral composition and texture between the brachiopod shell and its infilling sediment matrix is required to warrant the reproduction of high-quality XMT results.

Our results also demonstrate that diagenesis is significant in determining the XMT quality. Both silicification and recrystallisation, caused by diagenetic alternation, of the brachiopod shell and/or the infilling sediment matrix generally tend to diminish the quality of the XMT results, although the degree of diagenetic effect is clearly dependent on the degree of the diagenetic alteration and also on the difference in diagenetic processes between the shell and the infilling matrix. Another factor of minor significance concerns the presence of bioclastic inclusions scattered in the hosting sediment that potentially could be confused with genuine shell internal structures.

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Early Cambrian stem-group brachiopods from China

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The early Cambrian is a crucial period for the brachiopod diversification. Not only did major crown groups made their first appearance during this interval (Zhang and Holmer, 2013), but also there existed some stem groups. There are several stem-group brachiopod fossils recovered from Lower Cambrian rocks in South China, including some cap-like calcareous microfossils (e.g., *Tianzhushanella* and *Lathamella*), some tommotiids of organo-phosphatic sclerites (e.g., *Micrina*, *Tannuolina* and *Lapworthella*), *Heliomedusa* (organo-phosphatic shell) and *Yuganotheca* (agglutinated valves), etc. But there is only one stem group brachiopod, i.e., *Apistoconcha*, recovered from the Lower Cambrian Xinji Formation of North China Platform (Li *et al.*, 2014). These fossil records could provide important material for studying the origin and early evolution of brachiopods.

Heliomedusa and *Yuganotheca* are two exceptionally preserved fossils from the Chengjiang Lagerstätte. Although *Heliomedusa* had been referred to the craniopsids (Jin and Wang, 1992) or discinids (Chen *et al.*, 2007), the unique lophophore organization of *Heliomedusa*, consisting of a pair of lophophoral arms that freely arch posteriorly, differs from any previously known fossil or living crown-group brachiopods. The distinctive microstructure and ornamentation of *Heliomedusa* shell indicate its affinity to the stem-group brachiopod *Mickwitzia* (Zhang *et al.*, 2009). *Yuganotheca* represents a bizarre stem-group brachiopod. It is characterized by having an agglutinated quadripartite tubular body plan and a pair of brachiopod-like valves with a horse-shoe-shape lophophore inside (Zhang *et al.*, 2014). Its lower part was a long coelomic pedicle providing anchorage. It may represent a key intermediate form between phoronids and brachiopods.

The Tannuolinidae (tommotiids), including *Micrina* and *Tannuolina*, is a group of early Cambrian enigmatic animals with phosphatic bimembrate (mitral and sellate) sclerites. Based on the morphology and microstructure of the sclerites, Holmer *et al.* (2002) first suggested that tannuolinids might represent stem group brachiopods like *Halkieria* (the sellate and mitral sclerites respectively as the anterior and posterior shells). But the discovery of the articulated *Eccentrotheca* scleritome from South Australia (Skovsted *et al.*, 2008) indicates that most of tommotiids may be tubular sessile animals with organo-phosphatic multi-sclerites, although *Micrina* may represent an evolved tommotiid as a sessile bivalved stem-group brachiopod with a pedicle emerging between the mitral sclerite and the duplicature of the sellate sclerite (Holmer *et al.*, 2008). The position of tommotiids in the stem group of brachiopods is supported by similarities in mineralogy, shell structures and larval shell morphology between the tommotiids and the earliest brachiopods (linguliforms). In China, *Micrina* was only recovered from the lower Cambrian in eastern Yunnan. *Tannuolina* and *Lapworthella* were both recovered from the lower Cambrian in South China and Tarim Platform.

Many cap-like calcareous small shelly fossils from the pre-

trilobitic Cambrian (Terreneuvian) of South China were initially described as brachiopods since they morphologically like brachiopod valves, but none of them deems to have a confirmative affinity with brachiopods (Laurie, 2000). Altogether 18 genera of SSFs from South China were tentatively described as brachiopods. However, all of these fossils are generally represented by a single valve and are usually preserved by secondary phosphatization. They do not exhibit any interior structures of typical brachiopods. After further taxonomic scrutiny, only two genera, *i.e.*, *Tianzhushanella* and *Lathamella*, may be possibly referred to the stem group brachiopods. The other 16 genera should be excluded from the Brachiopoda, including: *Acidotocarena*, *Artimyctella*, *Dolichomocelypha*, *Ernogia*, *Hanshuiella*, *Heosomocelypha*, *Ocruranus*, *Parapunctella*, *Plicatolingula*, *Protobolus*, *Psamathopalass*, *Punctella*, *Ramenta*, *Scambocris*, *Xianfengella*, *Yuanjiapingella*. Although some of them may be stem-group members of molluscs (*e.g. Ocruranus* and *Xianfengella*), most of them are too poorly understood to be confidently assigned to any phylum. *Tianzhushanella* is often taken as a senior synonym of *Lathamella* since both genera are cap-like and bear a pair of recessed cavities in the umbonal region. New SEM examination of the holotype of *T. ovata* shows 7 rows of nodes on the surface of the internal mould, opposing the synonymy of the genera. Unlike the bivalved *Apistoconcha* and *Aroonia* from the lower Cambrian of South Australia, both *Tianzhushanella* and *Lathamella* from South China have been only recovered with one type of valve, without "ventral" and "dorsal" differentiation. It remains unclear whether they were univalved, or bivalved with two nearly equal valves.

The early Cambrian calcareous bivalved *Apistoconcha* is characterized by its two valves having posterior teeth and internal umbonal cavities. In China, it was only recovered from the Xinji Formation (Tsanglangpuan stage, Botomian-equivalent) in southeast Shaanxi Province (Li *et al.*, 2014). The shell of *Apistoconcha* possesses an 'antero-posterior' plane of bilateral symmetry, and its two valves apparently articulated in life, although the tooth-like structures and pits show little resemblance to the teeth and sockets, respectively, of bivalved shells of rhynchonelliform brachiopods or pelecypods. *Apistoconcha* cannot be assigned to the crown groups of either brachiopods or molluscs, even though functional morphological analysis indicates that *Apistoconcha* may be a stem-group brachiopod.

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Predatory drillholes from the Lower Permian brachiopods, Carnarvon Basin, Western Australia: marine predatory interactions immediately after glaciation of the Late Paleozoic ice age

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The topic of palaeo-predation has received a great deal of attention, principally in relation to economically viable shellfish. Most of the work has centred around the predatory gastropods of two families, the Naticidae and Muricidae. The naticids are

primarily infaunal hunters that prey on the majority of benthic infaunal shelled molluscs, whereas the muricids utilize a more diverse range of epifaunal prey. Growing evidence shows that predation is commonly present in the Late Palaeozoic marine shelly communities. In particular, the predatory activities on brachiopod shells are the best known, although the predation pressure is considerably low on articulate brachiopods in modern marine because of the very low tissue density and high inorganic content of the internal tissues. Here, we document relatively abundant borings on brachiopod shells from the Lower Permian Callythara Formation, the only carbonate stratigraphic unit of the marine Permian successions in Western Australia. This unit overlies immediately the glacial succession of the Carrandibby Formation, representing the Late Palaeozoic ice age in northern Gondwana. The Callythara Formation yield abundant benthic fossils such as brachiopods, corals, crinoids, bryozoans, and foraminifera. All drillholes are recorded on brachiopod shells. Total 30 shells among ~1000 brachiopod shells are bored and they belong to four genera of the Productida and two genera of the Spiriferida. In particular, the majority of drilled shells are *Elivina hoskingae*, on which drillholes are only present on ventral valves. Drillholes occur in both ventral and dorsal valves in the productids. All drillholes are nearly circular with smooth walls, suggesting muricid boreholes. The drilling frequency is ~3%, slightly higher than the average drilling frequency (2%) of the Permian faunas.

Putting 3D models to the test: quantifying loop variability in *Laqueus erythraeus* and *Terebratalia transversa*

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The loop, a calcareous structure that supports the lophophore, has been an important character in organizing terebratulide classification and deciphering evolutionary relationships. Not surprisingly, this structure has been the focus of many descriptive studies, predominantly centered on morphology, ontogeny, and ultrastructure. Nonetheless, a quantitative framework for studying loop morphology and variability is lacking, and much needed. The objective of this study is to provide such a foundation for the analysis of long loop morphology. The main motivation driving this research is to understand how crura, short loops, and long loops relate to one another, ontogenetically or phylogenetically, with respect to transformations in morphology over time.

Recently, 3D scanning has become an accessible tool for imaging small, complicated, and fragile internal shell structures.
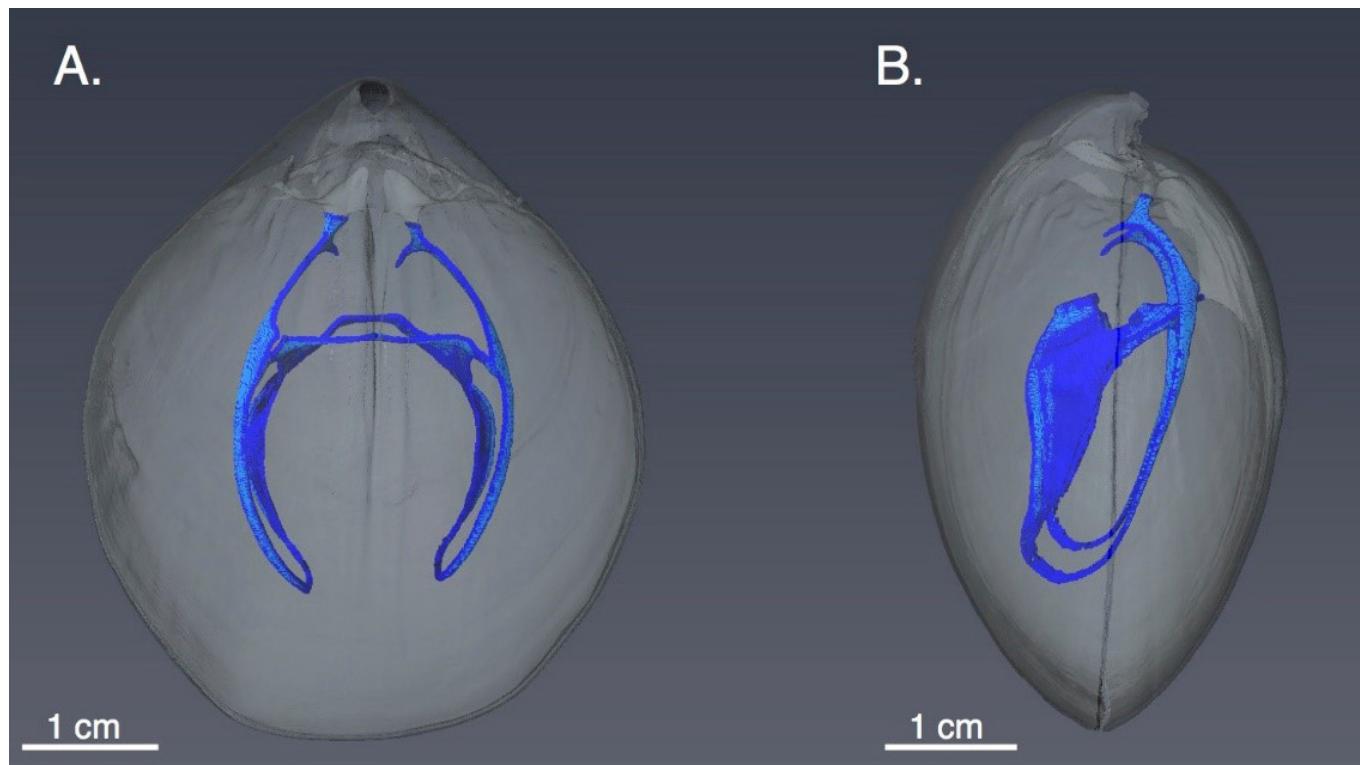
Fig. 1. Dorsal (A.) and lateral (B.) view of the long loop of *Laqueus erythraeus.*

Imaging techniques, such as X-ray Computed Tomography (CT), offer non-destructive, high-resolution 3D reconstructions. To study loop variability, 3D imaging is necessary since 2D landmark analysis does not fully capture the complexity of this structure. Four extant adult specimens of *Laqueus erythraeus* from the Invertebrate Zoology and Geology collection at the California Academy of Sciences (CAS) were selected based on the completeness of the loop and shell shape. These specimens were collected near Santa Catalina Island, California at a depth of 62 to 79 m. Additionally, three *Terebratalia transversa* specimens from Friday Harbor, Washington were chosen for imaging. The specimens were CT scanned in the Center for Molecular and Genomic Imaging (CMGI) at the University of California, Davis at a resolution of 50 μm. Isosurface models were then created using the software Amira (*e.g.* Fig. 1). Once shell reconstructions are formed, 3D landmark morphometric analysis will be performed to quantify intraspecific and interspecific loop variability. Landmark schemes for *L. erythraeus* and *T. transvera* were established based on putative homologous points, covering the loop and cardinal area. Semilandmarks along the crura, descending and ascending branches, and transverse bands were also determined to capture loop curvature. Once 3D Cartesian coordinates are collected, size variation in landmark configurations will be eliminated using a superimposition method such as the Generalized Procrustes Analysis (GPA). To quantify loop variation, a multivariate analysis of variance (MANOVA) will be performed as well as a principal component analysis (PCA), both on Procrustes-fitted coordinates. The results from this study will help understand the intricate ontogenetic history as well as the evolution and phylogenetic changes of long loops, particularly facilitating comparisons among individuals at different growth stages, and in different populations and species.

The brachiopod genome of *Lingula anatina* and the evolution of lophotrochozoans and biomineralization

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An abundance of the Silurian Period, *Lingula* fossils with morphology very similar to that of extant species inspired Darwin with the idea of "living fossils". Although they superficially resemble bivalve molluscs, lingulid brachiopods show unique features, including radial cleavage and dorsoventrally oriented shells. In particular, their shells are composed of calcium phosphate and collagen fibers, characters shared only by evolutionarily distant vertebrates, one of the biggest mysteries of metazoan evolution. To gain insights into brachiopod evolution, we decoded the 425-megabase genome of *Lingula anatina*. Comprehensive phylogenomic analyses place *Lingula* close to molluscs, but distant from annelids. Among lophotrochozoans, *Lingula* shows the slowest evolutionary rate of genes associated with basic metabolism. Its gene number increased to ~34,000 by extensive expansion of gene families, especially those associated with shell formation. In addition, we found that *Lingula* shared shell formation-related genes and mechanisms similar to molluscs, such as chitin synthase and bone morphogenetic protein (BMP) signaling. Although *Lingula* and vertebrates share similar hard tissue components, our genomic, transcriptomic, and proteomic analyses showed that *Lingula* lacks genes involved in bone formation, indicating a classical example of convergent evolution. Furthermore, we showed that *Lingula* has experienced domain combinations to produce shell matrix collagens with epidermal growth factor (EGF) domains and carries lineage specific shell matrix proteins, such as alanine-rich fibers. We propose that gene family expansion, domain shuffling, and co-option of genes appear to be the genomic background of *Lingula*'s unique biomineralization.

Small-sized brachiopods from the late Frasnian (Devonian) of the Jiangjiaqiao section, Hunan, China

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Abundant and diverse brachiopod fossils are found in the uppermost Frasnian of the Jiangjiaqiao section, Shaoyang County, Hunan Province, South China. Interestingly, abundant small-sized brachiopod fossils, including both juveniles and adults, are collected for the first time. The fossil-bearing horizon is just below the F/F boundary. We intend to study the external and
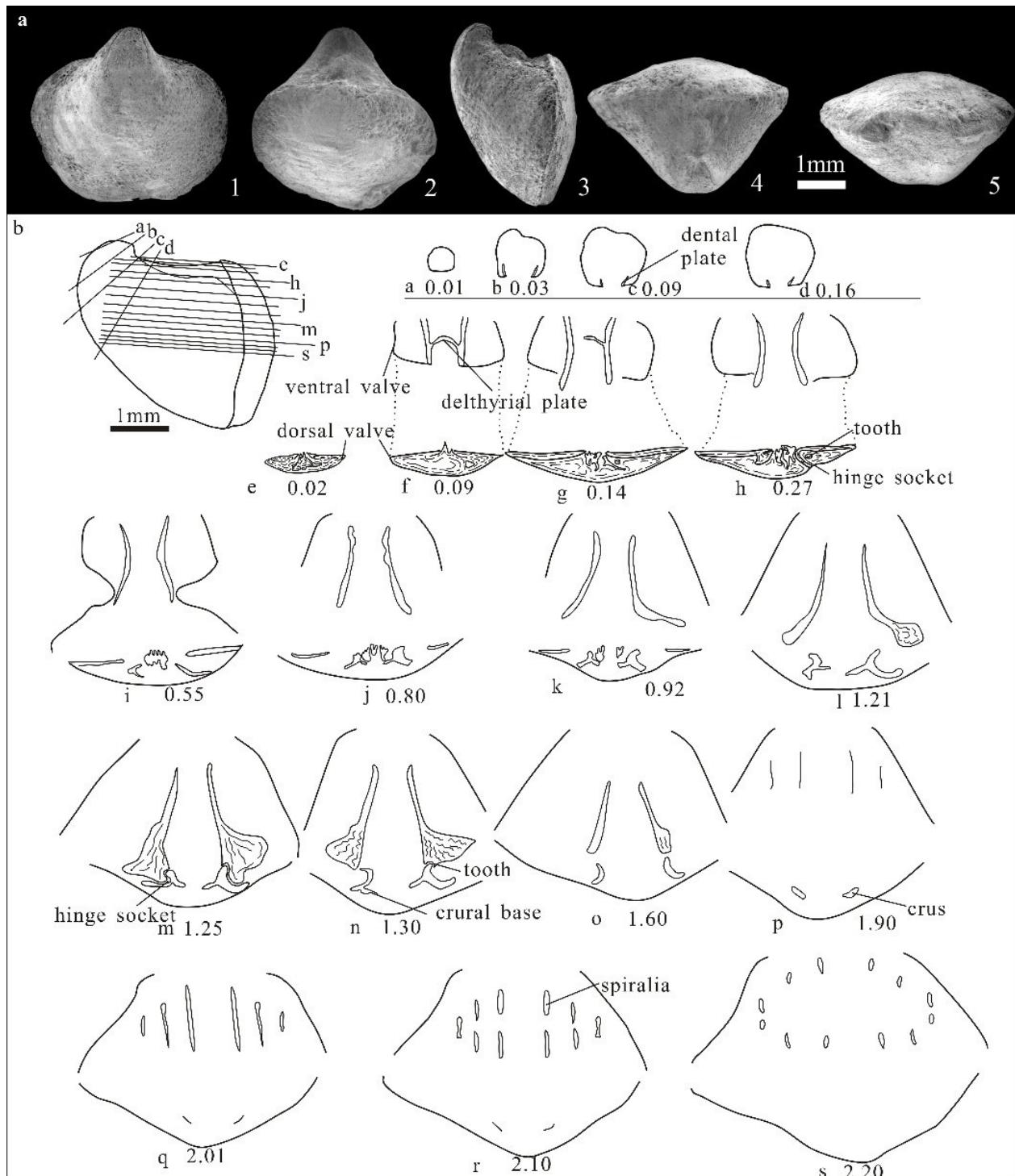
Fig.1. **a** 1-5, *Zhonghuacoelia* sp., ventral, dorsal, lateral, posterior, and anterior views, sample C1-0. **b**, transverse serial sections of *Zhonghuacoelia* sp.
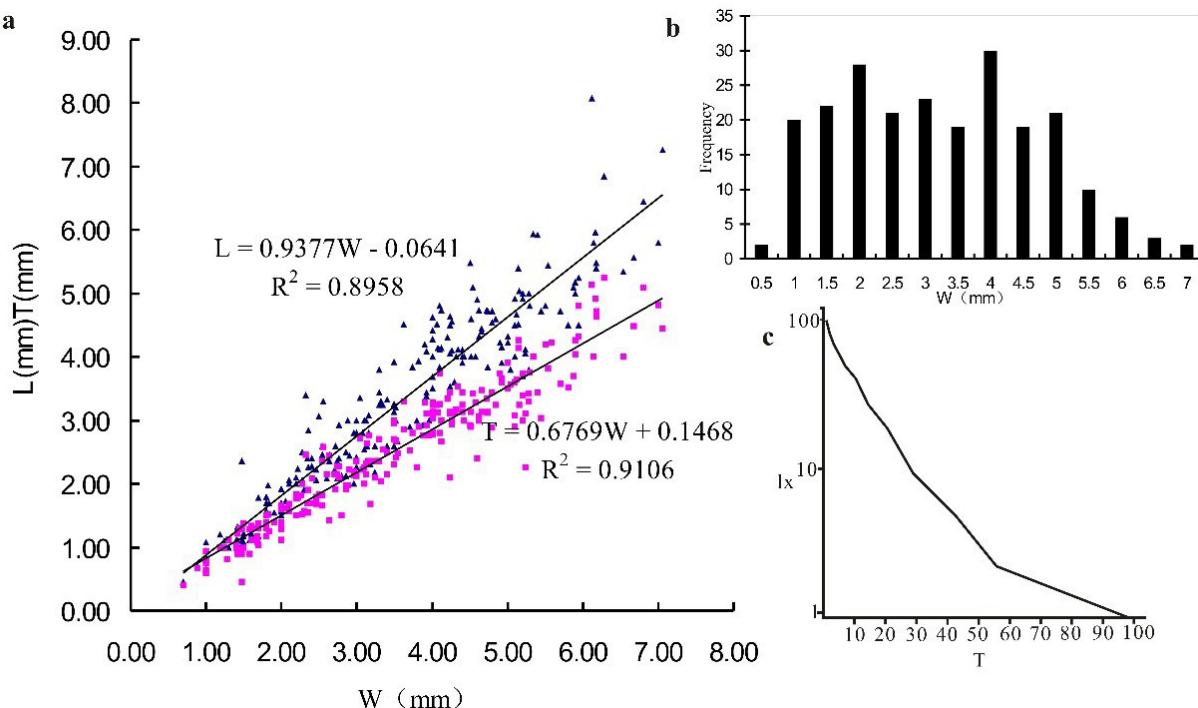
Fig.2. **a**, width/length and width/thickness scatter diagram of *Zhonghuacoelia* sp. **b**, frequency distribution of shell width of *Zhonghuacoelia* sp. **c**, survivership curve of *Zhonghuacoelia* sp.

internal morphology of these small-sized brachiopods for a better taxonomy and understanding of their species composition in this critical interval before the F/F mass extinction event. So far, at least 8 species are revealed, and the population survival curves of these taxa have been analyzed. Here only one taxon is presented.

Stratigraphy of the studied section: Jiangiiaqiao Section is located in the shaly facies. Total Frasnian thickness is about 500-600 m, made up of grayish black thin-bedded siliceous shale interbedded with cherts, yielding abundant bivalves *Buchiola* sp. in the lower part of 70-90 m in thickness and grayish yellow and grayish blue thin-bedded marl and marly limestone in the middle and upper parts of 400-500 m in thickness, yielding abundant *Buchiola* sp. and the ammonoid *Manticoceras* sp., a few corals, brachiopods, and ostracods. Brachiopod fossils are especially abundant across the supposed F/F boundary. The uppermost Frasnian interval that bears the small-sized brachiopods is composed of alternating gray oncolitic limestone and shelly limestone yielding abundant brachiopods, a few ammonoids, gastropods, ostracods, and crinoids (Ma, 1998). The atrypid brachiopods are *Iowatrypa pseudobodini* (Ma et al., 2005), *Iowatrypa? qidongensis*, and *Spinatrypa* sp.; other brachiopods include *Productella* sp., *Gypidula* sp., *Hypothyridina hunanensis*, *Cyrtospirifer* sp., *Athyris supervittata*. Bed C1 can be assigned to the *Polygnathus linguiformis* Zone (Ma, 1998).

Systematics of *Zhonghuacoelia* sp.
Spiriferida Waagen, 1883
Spiriferidina Waagen, 1883
Ambocoelioidea George, 1931
Ambocoeliidae George, 1931
Zhonghuacoelia Chen, 1978

Zhonghuacoelia sp.

MATERIALS: 238 complete shells including some juveniles, a few slabs with some disarticulated or complete shells.

DESCRIPTION: Small-sized (ca. 5–7 mm wide), subcircular–subpentagonal in outline, width subequal to length or slightly greater (Figure 1), maximum width at or a little posterior to mid-length. Hinge line short, approximately 2/3–3/4 of greatest width, cardinal angles rounded, anterior commissure nearly straight. Ventribiconvex with high apsacline (to catacline) ventral interarea. Dorsal area linear, sulcus and fold obsolete. Ventral interior with a rudimentary delthyrial plate (apical plate), short dental plates that are slightly convergent dorsally; teeth blunt. Dorsal interior with short and discrete crural plates; spiralia directed (postero-)laterally.

COMPARISION: We assign the Hunan specimens to the genus *Zhonghuacoelia* Chen, 1978 based on the following characteristics: small-size, similar shape and outline, and a pair of short dental plates. *Zhonghuacoelia* sp. is similar to *Z. bispina* Chen, but *Zhonghuacoelia* sp. has a high catacline to apsacline ventral interarea (versus a low apsacline interarea in *Z. bispina*) and very distinct fold and sulcus (obsolete in *Z. bispina*).

Size-frequency histograms: in *Zhonghuacoelia* sp., the minimum and maximum individual shell lengths are ca. 0.5 mm and 7 mm (Fig. 2a), respectively. Based on data obtained from 238 complete shells, the size frequency histogram has been built (Fig. 2b), which shows a slightly right-skewed, weak bimodal distribution. Such distribution suggests that the juvenile stage possesses a higher birth and mortality rate than the old stage.

Population structure: The "bulk sampling" method of Cate and Evans (1992) was used during the population analysis. A bulk sample of marl about 2 kg was collected from the C1 layer of the

Jiangjiaqiao section. The sample was then soaked in water firstly, and was subsequently rinsed and sieved with a 30 mesh sieve. All the brachiopod individuals are chosen and sorted under a magnifier or a stereoscope. According to Hallam (1972), the fossil population is formed by a long-period accumulation of natural mortalities and could be considered as a normal population, which can keep the record of population changes for ages.

Relative age determination is based on the formula of Levinton and Bambach (1970). The survivorship curve of *Zhonghuacoelia* sp. could be established from the conversion of its size frequency histograms (Fig. 2c). It exhibits high mortality rate during the juvenile stage, falling between B type and C type curve of Deevey (1947). Nevertheless, such survivorship curve displays differentiated age structures at the gerontic stage of the population.

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Peeping through a bivalved shield – non-destructive X-ray micro-computed tomography (µCT) elucidates brachiopod internal anatomy

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Comparative morphology of brachiopod exo- and endoskeletons is a traditional method to infer brachiopod relationships of both fossil and extant species. In contrast to destructive methods like serial sectioning or chemical treatment and successive scanning electron microscopy of brachiopod shells, non-destructive high-resolution micro-computed tomography (µCT) digitizes characters of the external and internal shell anatomy at the micron

level simultaneously. The non-destructive scanning results in 2-dimensional X ray images naturally aligned to image stacks and allows virtual sectioning of whole brachiopods, showing not only the morphology of the shell and the brachidium, but also the structure and position of tissue-bound skeletal elements (e.g. spicules) of extant species.

Our investigation of representatives of 20 genera (19 extant and one fossil) yielded new taxonomically and phylogenetically informative characters (synapomorphies) which would have been lost in the ordinary way of sample preparation, such as a row of interconnected spicules in the dorsal mantle of Eucalathinae or a massive plate formed by spicules in the lophophore base of *Gryphus vitreus and Liothyrella neozelanica*. Fossil brachiopod shells if at all preserved are often filled with matrix to the effect that separating the valves is impossible without destroying the specimen. In order to reveal the internal shell anatomy, we scanned different *Gemmarcula* specimens from Cenomanian green sand in Western Germany and identified two species, *G. menardi* and *G. canaliculata*, the latter being sometimes synonymized with the former by previous authors. Our µCT data show that the two species can clearly be told apart on the basis of external and internal (brachidial) shell characters. This study demonstrates the potential of µCT for taxonomic decisions without previous labor-intensive preparation, which furthermore may fail to elucidate all morphological information embedded in the specimen.

Non-invasive, high resolution X-ray micro-tomography has additional advantages over classical treatment of at least extant species. Museum specimens (especially type material) are often banned from prevalent destructive preparation methods, however µCT can be used to reveal their external and hidden internal morphological details. Secondly, all morphological and even molecular methods (e.g. SEM, TEM and DNA sequencing, respectively) can be applied to the scanned specimen after collection of the 3D data. A desirable integrative taxonomy approach needs both, morphology and molecular sequence information. For either investigation method ideal preservation protocols are often incompatible, and µCT may fill this gap especially when only few or single specimens are available for investigation. Thirdly, interactive digital specimens provide consistent and comparable perspectives and allow 3-dimensional analyses, including segmentation of certain sets of characters (e.g. dorsal valve, ventral valve, brachidium, spicules etc.). Virtual deconstruction of the animal for example in common 3D PDF-files using the free Acrobat Reader is easily done.

Finally, the digital data can also be applied for 3D printing to reproduce and rescale replica of biological specimens. We deployed our µCT data to build enlarged models of brachiopods featuring most of the relevant skeletal characters which have a high explanatory power for educational purposes.

New observations on *Spinatrypina* brachiopods from the Frasnian (Upper Devonian) Refrath Formation of the Bergisch Gladbach area, Germany
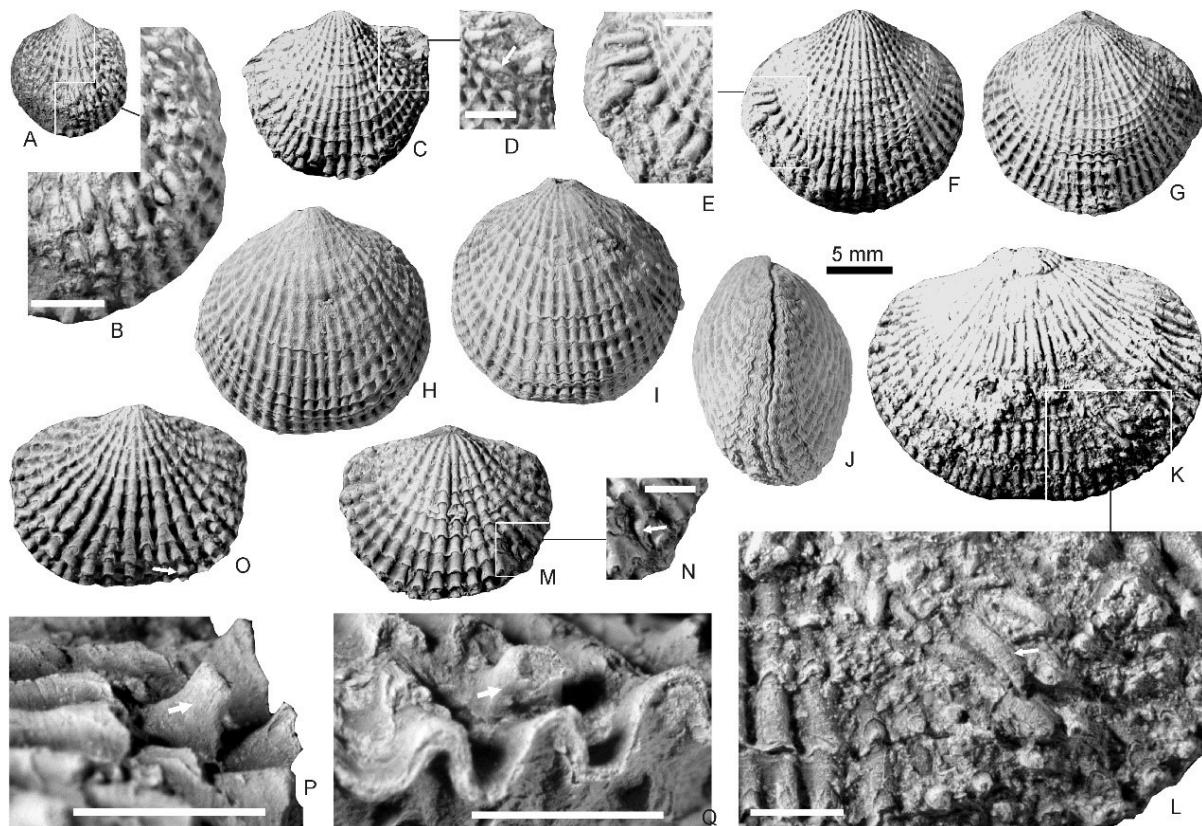
Fig. 1 *Spinatrypina* from the Refrath Formation: nature of spines. White arrows point to spines; the 5 mm black bar is for images of complete specimens; all other white bars are 2 mm for enlarged parts. A-J. *Spinatrypina comitata* Copper, 1967: A-B, ventral view and enlarged lateral-anterior part showing many spines (most of them broken); C-D, ventral view and enlarged part showing spines; E-G, enlarged left flank (note spines), ventral, and dorsal views; H-J, ventral, dorsal, and lateral views of the sectioned specimen in Fig. 2. K-L. *Spinatrypina* (*Exatrypa*) *explanata* (Schlotheim, 1820): ventral view and enlarged part showing spines. M-Q. *Spinatrypina* (*Exatrypa*) *tubaecostata* (Paeckelmann, 1820): M-N, dorsal view and enlarged part showing a spine; O-Q, ventral view (O) showing a spine base (white arrow) and its lateral (P) and anterior (Q) views.
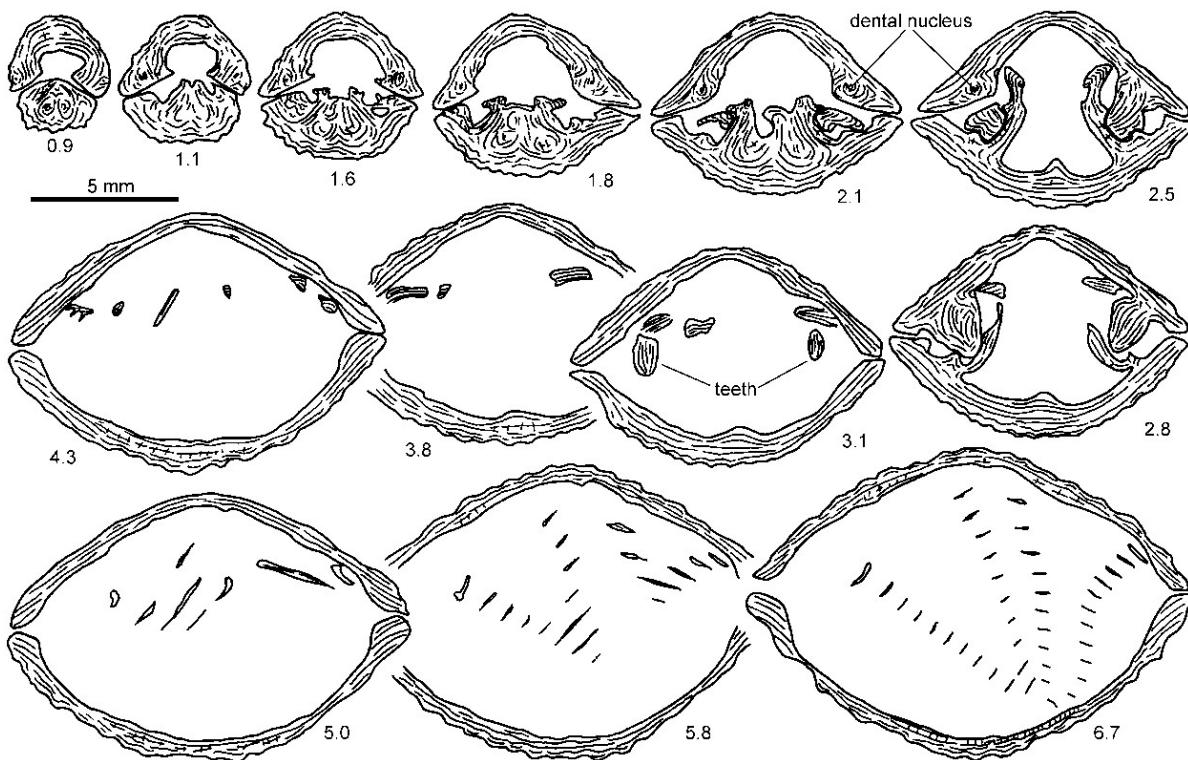
Fig. 2 Transverse serial sections of *Spinatrypina comitata* (see images H-J), numbers refer to distance in mm from ventral apex.

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The Bergisches Land is in Germany a famous Frasnian outcrop area with abundant well-preserved brachiopod faunas in neritic, shallow-water limestones and calcareous shales. The atrypid fauna of the Refrath Formation of this region was described by Copper (1967a), and recently by Ma et al. (2008, with an emphasis on internal structures of *Desquamatia* and related forms). However, some questions still need to be resolved, especially morphological details in *Spinatrypina*, e.g., the internal structures of *Spinatrypina comitata*. In addition, traces of spines have been observed in a number of specimens, which gives us an opportunity to investigate the nature of spines in *Spinatrypina*. Here we present results of related aspects. For details of locality and stratigraphy see Becker and Ebbighausen in Ma et al. (2008).

Spinatrypina brachiopods of the Ebbighausen Collection from the Refrath Formation of the type area include three species: *S.* (*Exatrypa*) *explanata* (Schlotheim, 1820), *S.* (*Exatrypa*) *tubaecostata* (Paeckelmann, 1820), and *Spinatrypina* (*Spinatrypina*) *comitata* Copper, 1967.

Spines: The presence or absence of spines is one of the features to distinguish *Spinatrypa* and *Spinatrypina* (Copper, 2002). Copper (1967a,b) pointed out that *Spinatrypina* is non-spinose or only embryonically spinescent, but it seems that no specimens are illustrated with such spines. Although spines are generally not preserved in *Spinatrypina*, there are indeed some specimens in the Refrath material that possess short spines (probably corresponding to Copper's "embryonically spinescent"). In *Spinatrypina comitata*, spines may be over 2.5 mm long (Fig. 1E); in *S.* (*Exatrypa*) *explanata*, they are about 2 mm long (Fig. 1L); in *S.* (*Exatrypa*) *tubaecostata*, they are also about 2 mm long (Fig. 1N).

Spines are rarely preserved because of their weak connection with the shell. They originate from lamellar extensions. When a lamella begins to arise above the shell surface, the portion in the lateral grooves begins to wrap up to form a hollow spine on the rib (Fig. 1Q). The coarseness of spines is directly proportional to the rib strength. Spines are mostly found on ventral valves (Fig. 1A, C, F, K, O); preservation of spines on dorsal valves is very rare (Fig. 1M). This fact suggests that these spinatrypinids lived with the ventral valve partly or entirely lying on the substrate, so that some shells still possess probably original substrate material, protecting spines from falling off the shell.

Even in *Spinatrypa*, spines are also not commonly preserved. Those that do exist are much coarser than in *Spinatrypina*. In transitional forms in terms of rib strength, the distinction of *Spinatrypa* from *Spinatrypina* should be manifested in other aspects. In *Spinatrypa*, deltidial plates are commonly lost or obscured by beak incurvature; ribs are undulose and coarse to very coarse. On the other side, *Spinatrypina* has a protruding beak, commonly well-developed and distinct deltidial plates, and tubular-imbricate ribs.

Internal structures of *Spinatrypina comitata*: It seems that this is the first report of internal structures of the species based on transverse serial sections (Fig. 2) since its establishment in 1967. No median septum or ridge is found in the ventral valve. The tooth is relatively strong, with a dental nucleus or small dental cavity. A median ridge appears in front of the cardinal platform in the dorsal valve, bisecting the posterior half of the muscle field. Crural bases are ball-like, rising anteriorly to feathered crura; disjunct jugal processes are tipped by jugal plates. The spiralia have about 11 whorls.

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Terebratulide brachiopods from the Middle and Late Jurassic of New Zealand

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Terebratulide brachiopods are found throughout the New Zealand Mesozoic, and by the Jurassic are second only to rhynchonellides in abundance and diversity. Only two species have been described from the Late Jurassic, *Kutchithyris hendersoni* Marwick 1953 and *Holcothyris* (?) *kaiwaraensis* Campbell 1965. In this study, about fifteen to twenty species are recognised.

Nearly all the material comes from the Murihiku Terrane on the west coast of the North Island south of Auckland, and most from a small number of shellbeds with diverse faunas. Two key localities for Middle Jurassic (Bajocian-Bathonian) brachiopods are Opuatia Cliff at Port Waikato, and a quarry in the Marokopa Valley. Two species of fairly large terebratulide are tentatively assigned to the genus *Loboidothyris*. Two further species which may also belong to *Loboidothyris* are found in the Awakino Valley

	1	2	3v	3d	4	5	6	7	8	9	10	11	12
radial folds on the outer surface	+										+		
posterolateral muscle platforms	+	+	+	+	+	+	+	+	+	+	+	+	
Umbonal cavity	+	+	+	+	+								
Median septum										+	+		
Central platform			1	1	2	2	2	2	2				
Thickened valve bottom	+	+											+
three short thick septae												+	
Mantle canals system	1	1	5;6	2;5	2	2; 3	2;4	2;3;4	2;3	2	2;3		1;5

Table 1. Characterizing features of 12 valve morphotypes (next page). Morphotypes are in horizontal lines, characteristic features are in vertical columns; the only complete specimen (*Egyngolella lenae* Malakhovskaya, 2014) is referred to the morphotype 3. Designations: (v) ventral valve; (d) dorsal valve; central platform: (1) suspended; (2) boundec on all sides; types of the mantle canals system: (1) simple baculate canals composed of singular trunks of vascula lateralia and vascula media (this type characterizes obolellids); (2) complicated baculate canals: several main trunks may be developed, the trunks may diverge and branch laterally (such system is known for craniids and trimerellids); (3) bifurcating vascula lateralia with posterior branches running on the posterolateral valve margins outside muscle impressions (this type is known for trimerellids and lingulids); (4) complicated vascula lateralia located between anterior and posterior adductors on the posterior slope (this arrangement is typical for billingsellids and ancient orthids); (5) imprints of small and short canals on the posterolateral valve margins similar to vascula genitalia of ancient articulates, billingsellids and orthids; (6) pinnate mantle canals.

to the south. Two species of *Zeilleria* and one of *Aulacothyris* are also recognised. A new species of *Kutchithyris*, less strongly folded than *hendersoni,* is also present.

Captain Kings Shellbed is a metre-thick (Oxfordian) shellbed that can be traced from Kawhia to the Awakino Valley. It has a rich and diverse fauna in which terebratulides are prominent. *Kutchithyris hendersoni* is the most abundant. A species with distinctive wavy concentrics probably represents a new genus. The fauna also includes the same two species of *Zeilleria* as in the Temaikan, a more strongly sulcate *Aulacothyris*, and a species of the costellate terebratulide *Terebratulina*.

Brachiopods are much less common in the later part of the Jurassic (Kimmeridgian and Tithonian). A further species of *Kutchithyris*, a second species of *Terebratulina* and one of *Zeilleria* are present. A rare form is the small subcircular *Disculina. Holcothyris* (?) *kaiwaraensis* is known only from the Late Jurassic Pahau Terrane of North Canterbury.

Affinities of the fauna are poorly known, due to the lack of nearby faunas for correlation. *Aulacothyris Terebratulina* and *Zeilleria* are cosmopolitan. *Kutchithyris* is Tethyan. *Loboidothyris* is more widely distributed but generally Tethyan. *Disculina* is described from Southern England and France, but has since been recognised in the Caucasus and Japan.

New Lower Cambrian calcareous-shelled brachiopods from the South Prihubsugul region of northwestern Mongolia

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Rich assemblage of calcareous-shelled brachiopods was found for the first time in the upper part of Egiin Gol Formation, Atdabanian Stage, Lower Cambrian of Northwestern Mongolia. Black, fine-grained, thin- and medium-laminated limestones of the upper part of Egiin Gol Formation contain accumulations of separate, variously directed, not rolled, and thin-walled carbonate valves. The collection contains one complete and about 150 separate valves, which are mostly inner molds. The specimens are 2-15 mm, convex, with posteromarginal umbos. Most of them are rounded and have external surface covered with fine growth lines, sometimes in combination with radial folds. The inner structures that may serve for hard valve articulation are absent. The characteristic feature of the assemblage are the posterolateral muscle platforms shaped as paired projections on the posterior slope that served for the muscle attachment. The posterolateral muscle platforms differ in size and orientation relative to the commissural plane. Narrow umbonal cavity may be developed. Visceral area of the valve is usually occupied with median septum or central platform. The central platforms differ in shape, size and relief. The bottom of the visceral area of the valve may be considerably flattened. One specimen has three short thick septae in the visceral area. The morphological variability of the assemblage is formed by the listed above features. The studied specimens may be divided into 12 morphotypes.

Most of the inner molds bear muscle impressions and imprints of the mantle canals. Six types of the mantle canals system may be distinguished, whose combination supplements the morphotype characteristic.

I assume that morphotypes 1-12 may characterize new taxon of a high rank (Table 1).

Carbon and oxygen isotope records of Devonian brachiopods from the southern China and their palaeoenvironmental implications

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We have analyzed fossil brachiopod samples collected from South China and Xinjiang to study the tropical environment in Devonian. All samples were thin sectioned and examined under the petrographic and cathodoluminescence microscopes for evaluation of shell preservation.

A total of 180 isotopic analyses were performed. The most well preserved (NL; non-luminescent) mean carbon isotope values of middle Emsian, late Emsian, Eifelian, Givetian, early Frasnian, late Frasnian, and late Famennian were respectively 0.8 ± 1.0‰ (N= 13), 1.1 ± 0.2‰ (N = 10), -0.3 (N = 1), 0.5 ± 1.7‰ (N = 12), 0.0 ± 0.8‰ (N = 11), -0.0 ±0.7‰ (N = 3), and 0.9 ± 0.6‰ (N = 4) and mean oxygen isotope values were respectively -6.1± 0.9‰, -7.9 ± 1.6‰, -7.1, -6.1 ± 1.2‰, -6.6 ± 0.9‰, -6.6 ± 1.2‰, and -6.3 ± 1.1‰. Within the uncertainty of the stratigraphical correlation, mean carbon isotope values of South China are comparable to those of contemporary North America and Europe indicating possible high atmospheric CO_2 concentration globally during Devonian.

Mean oxygen isotope values of south China are comparable to those of contemporary North America and Europe from early Frasnian to late Famennian, whereas are 3‰ to 4‰ lower than those of North America and Europe between middle Emsian and Givetian. Lower mean oxygen isotope values in South China may indicate South China seawater was15°C to 20°C warmer than those of North America and Europe or South China samples were still more or less influenced by diagenesis.

Assuming the oxygen isotope value was -1‰ for late Devonian seawater, the calculated oxygen isotope temperatures were between 42°C and 44°C between early Frasnian and late Famennian. High atmospheric CO_2 concentration thus warm temperatures is expected according to carbon isotope values. However, further study is necessary to identify if these oxygen isotope records reflect a warm Devonian seawater or signal of diagenesis.

New knowledge of productinide brachiopods from the Tangbagou Formation (Tournaisian, Lower Carboniferous) of Dushan, South Guizhou

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Dushan area of south Guizhou is the type locality of the Chinese Aikuanian (also spelling as Yanguanian, equivalent to Tournaisian) stage that initially included two formations (Gelaohe and Tangbagou) and now only the Tangbagou Formation is attributed to the stage. During the Late Devonian and Early Carboniferous Dushan area was located on the southern margin of the Qiannan Oldland and the Tangbagou Formation is, mainly consisting of shallow water carbonates intercalated with calcareous silty shale, formed in a nearshore neritic setting. Previously, ten genera and sixteen species of brachiopods had been described from the Tangbagou Formation of this area and the brachiopod fauna had long been considered as endemic. Among these brachiopods, however, only two genera (*Yanguania* and *Praewaagenoconcha*) belong to the productinide group. Recently we collected abundant brachiopods from the lower-middle part of the formation at the Qilinzhai Section. Among them, besides the already reported *Yanguania* and *Praewaagenoconcha* before, six other productinide generic forms, at least, can be recognized. They are *Spinocarinifera*, *Hunanoproductus*, *Tomiproductus*, *Ozora*, *Productella*?, and an undetermined form that is similar to *Yanguania* in some external features but being of a strongly-concaved dorsal valve and large ears. *Spinocarinifera* is a world-wide distributed Tournaisian genus and previously no reliable fossil record was found in south China besides the questionable material found in the deep water facies from Muhua of Guizhou Province. *Hunanoproductus* is an endemic taxon of South China and previously only known from the neritic Tournaisian deposits in central Huanan and western Hubei provinces. *Tomiproductus* is a typical Lower Tournaisian representative of north hemisphere and it was reported to present in central Hunan. The finding of these two taxa in the Tangbagou Formation suggested that the neritic brachiopod fauna in southern Guizhou had a close relationship with that in central Hunan. *Ozora* was only recorded in the lower Visean deposits of central North America before. The Chinese material is, if our identification is correct, the oldest representative of the genus. The specimens questionably attributed to *Productella* are also very similar to *Quasiavonia* in external shape and ornamentation but lack spines in the dorsal valve. The finding of these productinide brachiopods from the Tangbagou Formation demonstrates that the productinide brachiopods is one of the taxonomic diversified group in the neritic Tournaisian brachiopod fauna of South China and the brachiopod fauna of South China of that time

had close biogeographic relationship with that from other parts of the world.

New discoveries of the Late Devonian brachiopod genus *Dzieduszyckia* Siemiradzki, 1909 in south China

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Dzieduszyckia is one of the largest Paleozoic rhynchonelloids, characterized by bisulcate, strongly costate shell. It is normally discovered as monospecific fauna, and has a wide range of geographic distributions. This genus has been considered by some researchers as one of the typical representatives of fossil brachiopods that habit in a cold-seep related environment (Ager et al., 1976; Campell & Bottjer, 1995). In South China, *Dzieduszyckia* has been reported from the Upper Devonian (Famennian) Daihua Formation in Dushan, Puding, and Changshun counties of southern Guizhou Province (Xian & Jiang, 1978; Hou et al., 1985). Here we report new discoveries of *Dzieduszyckia* in south China. In the Duli and Changtang sections, southern Guizhou Province, *Dzieduszyckia* is found from the banded limestone of the Upper

Devonian Wuzhishan Formation (equvolent to the Daihua Formation in Guizhou Province), which was considered as deposition in deep water environments. The conodont biostratigraphy indicates that *Dzieduszyckia* at Duli section is probably within the conodont *rhomboidea* Zone. In the Dazhai section, *Dzieduszyckia* is collected from the Upper Devonian Rongxian Formation deposited in a shallow water carbonate platform environment. Furthermore, three layers of *Dzieduszyckia* are found in a 15 m thick sequence of the Upper Devonian Rongxian Formation in the Dalong section, Tiandeng County, Guangxi Province, which was situated in an isolated carbonate bank during Late Devonian. *Dzieduszyckia* in the Dalong section is constrained within the Upper *triangularis* to Lower *crepida* conodont zones. Preliminary analyses of the carbon and oxygen isotopes of the shell fabrics and rock matrix do not indicate any cold-seep signals, suggesting that *Dzieduszyckia* may not be strictly restricted within cold-seep fields. This conclusion is consistent with the occurrences of *Dzieduszyckia* in diverse depositional environments.

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Zonal species complexes of Devonian and Lower Carboniferous rhynchonellids from Transcaucasia

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More than half a century the Devonian and the Carboniferous brachiopods from Transcaucasia are the objects of an attention of the stratigraphers (Gretchischnikova et al., 1983; Rzhonsnitskaya, Mamedov, 2000; Gretchischnikova, Levitsky, 2011). Sea sediments beginning from the Upper Emsian till the Visean presented in Transcaucasia. A Devonian – Carboniferous boundary is well tracking. These deposits are interesting in terms of the boundary Frasnian – Famennian and Famennian – Tournaisian faunal changes, when there were mass extinctions. Brachiopods are numerous in the Devonian deposits of Transcaucasia, including rhynchonellids. A first detailed description of the rhynchonellid species complexes by G.T. Mirieva (2010) is done. However the

some species presence is open to argument, and some complexes are not completed. An aim of this study is a revision of the Lower Devonian – Lower Carboniferous Transcaucasian brachiopods from order Rhynchonellida. It necessary to characterize brachiopod zones by using rhynchonellid species complexes. Brachiopod zones are accepted by these papers (Gretchischnikova et al., 1983, Gretchischnikova, Levitsky, 2011) with some additions and corrections (I.A. Gretchischnikova, personal communications).

Megastrophia uralensis – Zdimir pseudobaschkiricus Zone (Emsian - Eifel) is characterized by following species: *Septalaria subtetragona*, *Schnurella transversa*, *Glosshypothyridina procuboides*, *Beckmannia pentagona*, *Isopoma brachyptycta*, *Kransia* sp. Zonal species *Uncinulus keltibericus*, indicated by M.A. Rzhonsnitskaya and A.B. Mamedov (2000), is not found. A most important species for this zone is *Septalaria subtetragona*. Representatives of the superfamily Uncinuloidea dominated. Rhynchonellids in the deposits of the *Arduspirifer intermedius* Zone (Emsian – Lower Eifel) are absent. *Alatiformia araxica – Dagnachonetes caucasicus* Zone (Middle Eifel) is characterized by following species: *Oligoptycherhynchus daleidensis*, *Uncinulus subwilsoni*, *Beckmannia angularis*, *Kransia parallelepipeda*, *Beckmannia pentagona*, *Solidipontirostrum* sp., *Nymphorhynchia* sp. A most important species for a stratigraphy is *Oligoptycherhynchus daleidensis*. It will be used as a zonal. Representatives of the superfamily Rhynchotrematoidea are appeared in the sediments of this zone. They were very rare in the Middle Devonian of Transcaucasia. Dominant superfamily did not change. *Mucrospirifer diluvianoides – Radiomena irregularis* Zone (Upper Eifel) is most rich in rhynchonellids. They are *Kransia parallelepipeda*, *Kransia praecedens*, *Primipilaria primipilaris*, *Beckmannia pentagona*, *Pseudocamarophoria undulataeformis*, *Pugnax praevius*, *Isopoma brachyptycta*, *Camerophorina pachyderma*, *Schnurella transversa*, *Glosshypothyridina procuboides*, *Kransia subcordiformis*, *Uncinulus korovini*, *Beckmannia minor*, *Corvinopugnax* sp., *Mirantesia* sp. In this case rhynchonellids from superfamily Uncinuloidea are dominated again. The deposids of *Stringocephalus burtini* Zone (Lower Givetian) are poor by rhynchonellids. They are *Kransia parallelepipeda* and *Glosshypothyridina procuboides*. *Indospirifer pseudowilliamsi* Zone (Upper Givetian) is characterized by following species: *Uncinulus korovini*, *Kransia parallelepipeda*, *Kransia subcordiformis*, *Beckmannia minor*, *Isopoma brachyptycta*, *Schnurella transversa*, *Pugnax praevius*, *Beckmannia pentagona*, *Glosshypothyridina procuboides*, *Ripidiorhynchus* sp. In these sediments there is a first species of a genus *Ripidiorhynchus*, which more occurs in the Upper Devonian. A significant change of the rhynchonellid fauna at the Eifel – Givetian boundary did not observed. Most common genera, found in the Lower and Middle Devonian, are *Beckmannia* and *Kransia*. *Beckmannia pentagona* observed with a break from the Emsian till Upper Givetian, and *Kransia parallelepipeda* – through all of the Eifel and Givetian. In first part of the Frasnian rhynchonellid species content was depleted.

Adolphia zickzack Zone (Lower Frasnian) is characterized by following species: *Ripidiorhynchus gnishikensis*, *Cyphoterorhynchus arpaensis*, *Paropamisorhynchus kotalensis*, *Porthmorhynchus ferquensis*, *Coeloterorhynchus tabasensis*, *Pugnax acuminatus*, *Kransia* sp., Uncinulidae gen. et sp. nov., Septalariidae gen. et sp. indet. Last three species are very interesting. They are a continuation of the Lower – Middle Devonian fauna, which are extinct in the Givetian (Uncinulidae, *Kransia*) and the Frasnian (Septalariidae). *Cyrtospirifer subarchiaci-Cyphoterorhynchus arpaensis* Zone (Upper Frasnian) is characterized by following species: *Ripidiorhynchus gnishikensis*, *Cyphoterorhynchus arpaensis*, *Paropamisorhynchus kotalensis*, *Porthmorhynchus ferquensis*. Most numerous from the rhynchonellids was *Cyphoterorhynchus arpaensis*. The remains of the Givetian fauna are completely disappeared. A first the Famennian zone – *Cyrtospirifer asiaticus-Mesoplica meisteri* is a different increase of a rhynchonellid diversity. In these deposits are found: *Paropamisorhynchus kotalensis*, *Stenaulacorhynchus* sp., *Sartenaerus letiensis*, *Sharovaella mirabilis*, *Greira transcaucasica*, *Sartenaerus charakensis*, *Sinotectirostrum* sp., *Sinotectirostrum zobeida*, *Gesoriacorostrum cf. boloniensis*, *Ptychomaletoechia* sp. For the first time in these sediments there were punctate rhynchonellids, represented by two genera and two species. A species amount of Trigonirhynchiidae sharply increased. Beginning the Frasnian they have become the dominant rhynchonellids of the Upper Devonian. A next zone, related to the lowermost Upper Famennian is *Cyrtospirifer pamiricus–Enchondrospirifer ghorensis* Zone. It is characterized by species: *Sartenaerus charakensis*, *Paropamisorhynchus kotalensis*, *Sharovaella mirabilis*, *Zaigunrostrum* sp. nov., *Sartenaerus letiensis*, *Araratella dichotomians*, *Navalicria* sp., *Stenaulacorhynchus* sp., *Sinotectirostrum* sp., Platyterorhynchinae gen et sp. indet. In deposits of the *Paurogastroderhynchus nalivkini* Zone (Upper Famennian) are found rhynchonellids: *Paurogastroderhynchus nalivkini*, *Araratella dichotomians*, *Sartenaerus charakensis*, *Sartenaerus letiensis*, *Sharovaella mirabilis*, *Zaigunrostrum* sp. nov., *Gesoriacorostrum cf. boloniensis*, *Paropamisorhynchus kotalensis*, *Sinotectirostrum* sp. The species *Paropamisorhynchus kotalensis* is only crossed from the Frasnian to Famennian, but in the later zones it is not found. *Sartenaerus letiensis* dominated in the all Famennian zones, excluding a last zone. *Sphenospira julii–Spinocarinifera nigra* Zone is characterized by species: *Araratella dichotomians*, *Tchanakhtchirostrus araraticum*, *Sharovaella mirabilis*, *Zaigunrostrum* sp. nov., *Ptychomaletoechia panderi*, *Sinotectirostrum delicatacostata*, *Leptocaryorhynchus* sp. The Upper Devonian marked by the new increase of the rhynchonellid diversity. The dominant group was family Trigonirhynchiidae. In Famennian, in superfamilies Rhynchotrematoidea and Camarotoechioidea, appeared rhynchonellids with punctate shells. Their first representatives are known from *Cyrtospirifer asiaticus-Mesoplica meisteri* Zone. Transcaucasian territory is a center of an origin of punctate rhynchonellids both superfamilies. Only two species, *Ptychomaletoechia panderi* and *Tchanakhtchirostrum araraticum*, crossed from the Famennian to the Lower Carboniferous.

A first the Lower Tournaisian zone is *Unispirifer praeulbanensis – Rhytiophora curtirostris*. It is characterized by species of superfamily Rhynchotrematoidea: *Ptychomaletoechia panderi*, *Tchanakhtchirostrum araraticum* and *Hemiplethorhynchus* sp. 1. In sediments of *Unispirifer tornacensis – Rhipidomella michelini* Zone (Upper Tournaisian) rhynchonellids are not found.

Two species from *Spirifer baiani – Marginatia burlingtonensis* Zone (Upper Tournaisian) are known: *Hemiplethorhynchus* sp. 2, Wellerellinae gen et sp. indet. Probably, representatives of superfamily Welleroidea appeared in the Upper Tournaisian rhynchonellid fauna.

Thus, the faunal complexes of the Devonian and the Lower Carboniferous rhynchonellids from Transcaucasia are characterized. Almost complete change of rhynchonellid fauna at the Givetian – Frasnian boundary are noted. Beginning the Upper Devonian the dominant rhynchonellid groups have been changing. Superfamily Uncinuloidea as the dominant are replaced by rhynchonellids from family Trigonirhynchiidae. These species as *Beckmannia minor*, *Kransia subcordiformis*, *Uncinulus korovini*, *Isopoma brachyptycta*, *Schnurella transversa*, *Kransia parallelepipeda*, characterized for the Upper Givetian, are completely extinct. In the Lower Frasnian there was new faunal content. The biodiversity of rhynchonellids at the Frasnian – Famennian boundary is down by half. The Lower Famennian is a time of an origin of unique punctate rhynchonellids. A little biodiversity reduction was in a last part of the Famennian. A strong reduction of biodiversity in the Lower Carboniferous are noted. If superfamilies Uncinuloidea and Rhynchotrematoidea were the dominants, the superfamilies Camarotoechioidea and Pugnacoidea always were the secondary representatives of rhynchonellid fauna. The reported study was supported by the RFBR, research project No. 13-05-00459.

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Katian (Late Ordovician) lingulate brachiopods from eastern Australia – an appraisal of their palaeoecology and palaeobiogeographical affinities

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The diverse Late Ordovician lingulate brachiopod faunas from central New South Wales have now been fully described (Percival *et al.* in review) and a contemporaneous fauna including many of the same species has also been recognized and documented from north Queensland (Zhen *et al.* in review). The brachiopods from the Macquarie Volcanic Province at Cliefden Caves and Bowan Park in central New South Wales fall into two main ecological associations, one populating shallow water (shelfal) carbonate-dominated environments surrounding volcanic islands, and the other inhabiting deep water settings on the shelf edge to upper slope, where the brachiopods are preserved in allochthonous limestones as well as the fine-grained clastic sediments into which these limestone blocks were redeposited. Elements of the latter fauna are found in allochthonous limestones in the Broken River Province in north Queensland.

The shallow water lingulates that inhabited Benthic Assemblages 1-3 are represented by the lingulides *Pseudolingula*? and *Plectoglossa* and discinide *Acrosaccus*. Evidence of the typical burrowing habitat of the two lingulides is found in the Fossil Hill Limestone. *Acrosaccus* is more common in the deeper water limestone faunas inhabiting BA4-5, along with a diverse suite of acrotretides including *Conotreta*, *Hisingerella*, *Spondylotreta*, *Scaphelasma*, *Rhysotreta*?, *Ephippelasma*, and *Undiferina*, together with the lingulide *Atansoria* and siphonotretide *Nushbiella*. Graptolitic and spiculitic siltstones, assigned to BA5, preserve *Anomaloglossa*, *Hisingerella*, *Paterula* and *Elliptoglossa* (all previously described by Percival 1978), associated with a new species of *Apatobolus*. All of these deep water species are interpreted as being tethered to an organic substrate (most likely sponges or spicule accumulations), although it is possible that some may have drifted attached to algae at more shallow depths in the water column. Examples of the fauna are depicted in Figure 1.

Biogeographic affinities of Late Ordovician lingulates from New South Wales align most strongly with those from Kazakhstan terranes, areas along the perimeter of Laurentia, and to a lesser extent with South China (Popov *et al.* 2013). The Kazakhstan connection is particularly evident from the presence of *Atansoria*, *Apatobolus* and *Nushbiella*. Baltic and Laurentian affinities are indicated from several acrotretide taxa (Fig. 2).

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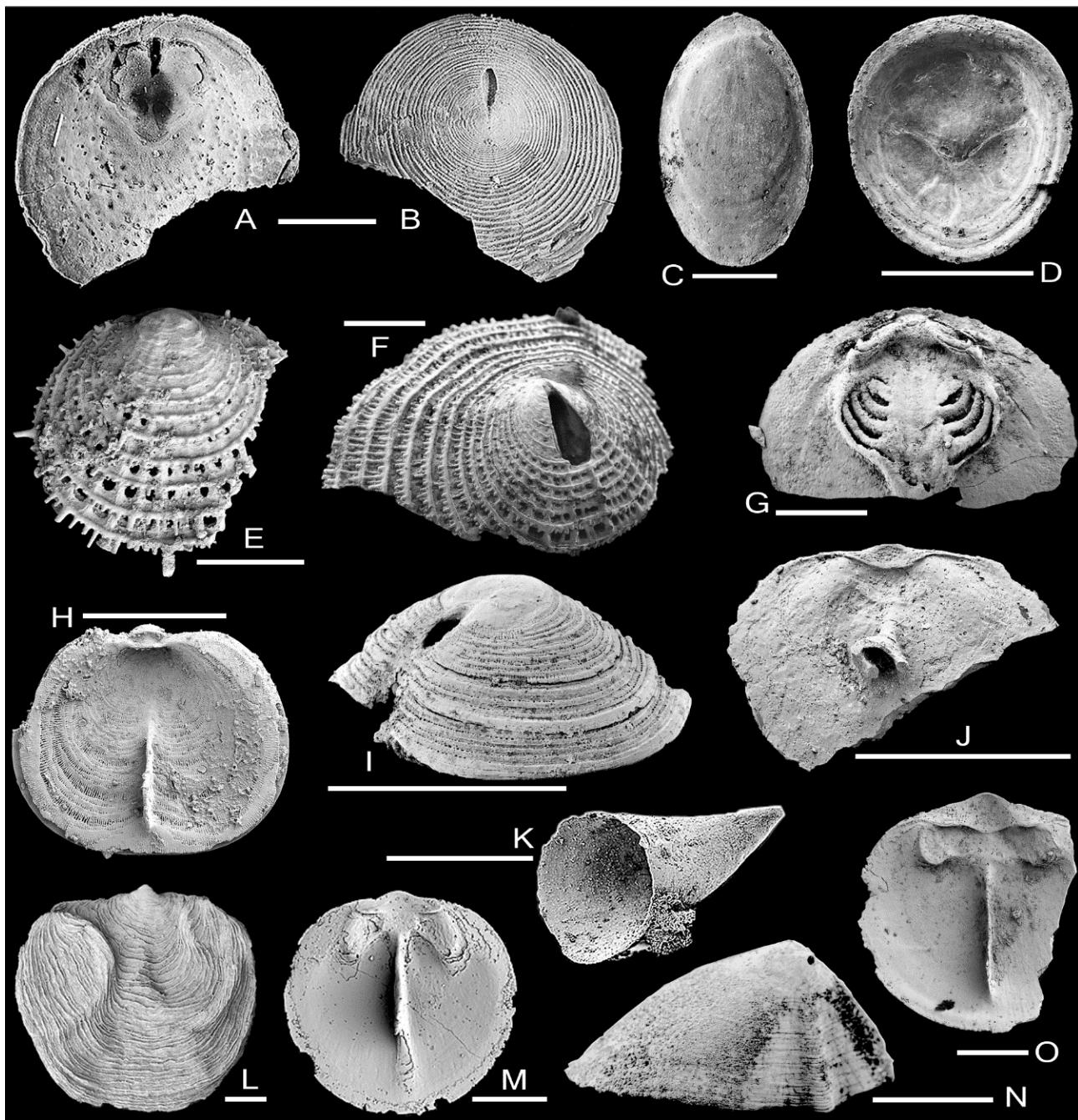
Fig. 1. Representative Late Ordovician linguliformean brachiopods from central New South Wales. A, B. *Acrosaccus* sp. nov., interior and exterior views of ventral valve, from lower Malongulli Formation at Cliefden Caves. C. *Elliptoglossa adela* Percival, 1978, interior view of dorsal? valve, from Downderry Limestone Member of Balingoole Limestone at Bowan Park. D. *Paterula malongulliensis* Percival, 1978, interior view of dorsal valve, from lower Malongulli Formation at Cliefden Caves. E, F. *Nushbiella* sp. nov., exterior view of dorsal valve, and oblique exterior view of ventral valve, both from Downderry Limestone Member of Balingoole Limestone at Bowan Park. G. *Atansoria* sp. nov., interior view of dorsal valve from lower Malongulli Formation at Cliefden Caves. H, I. *Scaphelasma scutula* Popov et al., 1994, interior view of dorsal valve from Downderry Limestone Member of Balingoole Limestone at Bowan Park, and oblique exterior view of ventral valve, from lower Malongulli Formation at Cliefden Caves. J. *Ephippelasma* cf. *minutum* Cooper, 1956, interior of dorsal valve, from allochthonous limestone in Barnby Hills Shale. K. *Biernatia* sp., oblique postero-dorsal view of ventral valve, from allochthonous limestone in Barnby Hills Shale. L. *Undiferina* cf. *rugosa* Cooper, 1956, exterior view of dorsal valve, from Malongulli Formation. M. *Conotreta mica* Goryansky, 1969, interior view of dorsal valve, from Downderry Limestone Member of Balingoole Limestone at Bowan Park. N, O. *Hisingerella hetera* Percival, 1978, posterolateral view of ventral valve exterior, and interior view of dorsal valve, both from Malongulli Formation at Cliefden Caves. Scale bars in all cases represent 1 mm.

	Kazakhstan						South China	Laurentia		Baltica	
	Chingiz Terrane	Chu-Ili Terrane	Chu-Ili Terrane	Atasu-Zhamshi	Ishim-Selety	Boshchekul	Hunan	Nevada	Alabama	Sweden	Estonia
	Bestamak Fm	Uzanbulak Fm	Karakan Fm	Kurchilik Fm	Mayatas Fm	Bestyube Fm		Antelope Valley	Pratt Ferry Fm	Uhaku Stage	Harju Stage
Apatobolus	▲										
Atansoria					▲						
Elliptoglossa	▲	▲	▲	▲				▲	▲	▲	
Paterula	▲	▲	▲		▲			▲	▲	▲	▲
Rowellella	▲	▲	▲		▲			▲	▲	▲	
Acrosaccus	▲				▲				▲	▲	
Nushbiella	▲	▲				▲		■	▲	▲	
Conotreta	▲				▲	▲		■	▲	■	
Hisingerella										▲	
Spondylotreta										▲	⬓
Scaphelasma	▲		▲	▲	▲	▲	▲	▲		▲	■
Ephippelasma	▲	▲			▲	▲	▲		●	●	
Biernatia	▲	▲				▲	▲	▲			
Eoconulus	▲		▲			▲	▲	▲			▲
Undiferina							▲	▲	●		

Fig.2. Global distribution of linguliformean genera from the Late Ordovician of New South Wales; triangles indicate presence at genus-level; circles indicate cf. species comparisons; squares are species-level similarities.

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Wulingian (middle Cambrian) linguliformean brachiopods from Hunan Province, South China

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Compared to those from the Early Cambrian Chengjiang Fauna of Yunnan Province and an Early Cambrian fauna from Shaanxi Province (Li and Holmer 2004), middle (Cambrian series 3) and late Cambrian (Furongian) lingulate brachiopods of China are quite poorly known, with only three descriptive papers published in the past 25 years (Mei, 1993; Engelbretsen and Peng, 2007; Zhan et al., 2010). The present contribution and an accompanying taxonomic paper (Percival et al. submitted) completes description of the Wulingian (series 3) lingulates from the Paibi section through the Huaqiao Formation in Huayuan county of northwest Hunan Province, commenced by Engelbretsen and Peng (2007), making this one of the most thoroughly documented Cambrian brachiopod faunas from the region.

Engelbretsen and Peng (2007) concentrated on describing acrotretids from the Paibi section, including the following: *Anabolotreta tegula* Rowell & Henderson, 1978, *Anabolotreta? glabra* Streng & Holmer, 2006, *Araktina?* sp., *Dactylotreta* n. sp., *Linnarssonia ophirensis* (Walcott, 1902), *Neotreta* sp. cf. *N. tumida* Sobolev, 1976, *Pegmatreta clavigera* Engelbretsen, 1996, *Quadrisonia* sp. and *Treptotreta jucunda* Henderson & MacKinnon, 1981. Additionally they described an undetermined obolidid, another lingulate tentatively referred to *Dysoristus?* sp., and the paterinide *Micromitra* sp. cf. *M. modesta* (Lochman, 1940). We now recognize the following lingulates from this fauna (Fig. 1): *Eoobolus?* n. sp, cf. *Canalilatus* n. sp., *Experilingula?* n. sp., cf. *Kyrshabaktella* sp. nov., and an indeterminate zhanatellid. Uncertainty surrounds these identifications, as several of the taxa represent new genera as well as new species. The undetermined obolidid of Engelbretsen and Peng (2007) can be referred to *Experilingula?* n. sp., while their *Dysoristus?* sp. is now assigned to cf. *Canalilatus* n. sp. with the benefit of better material.

Age of the fauna documented ranges from the lowermost part of the *Ptychagnostus atavus* Zone to the *Linguagnostus reconditus* Zone, slightly below the *Glyptagnostus stolidotus* Zone, thus spanning the Drumian and Guzhangian stages. Not surprisingly, the lingulate component of this fauna from Hunan Province has very little in common with that described by Mei (1993) from Hebei Province, North China, not only due to biogeographical differences but also because the Hebei Province material is considerably younger.

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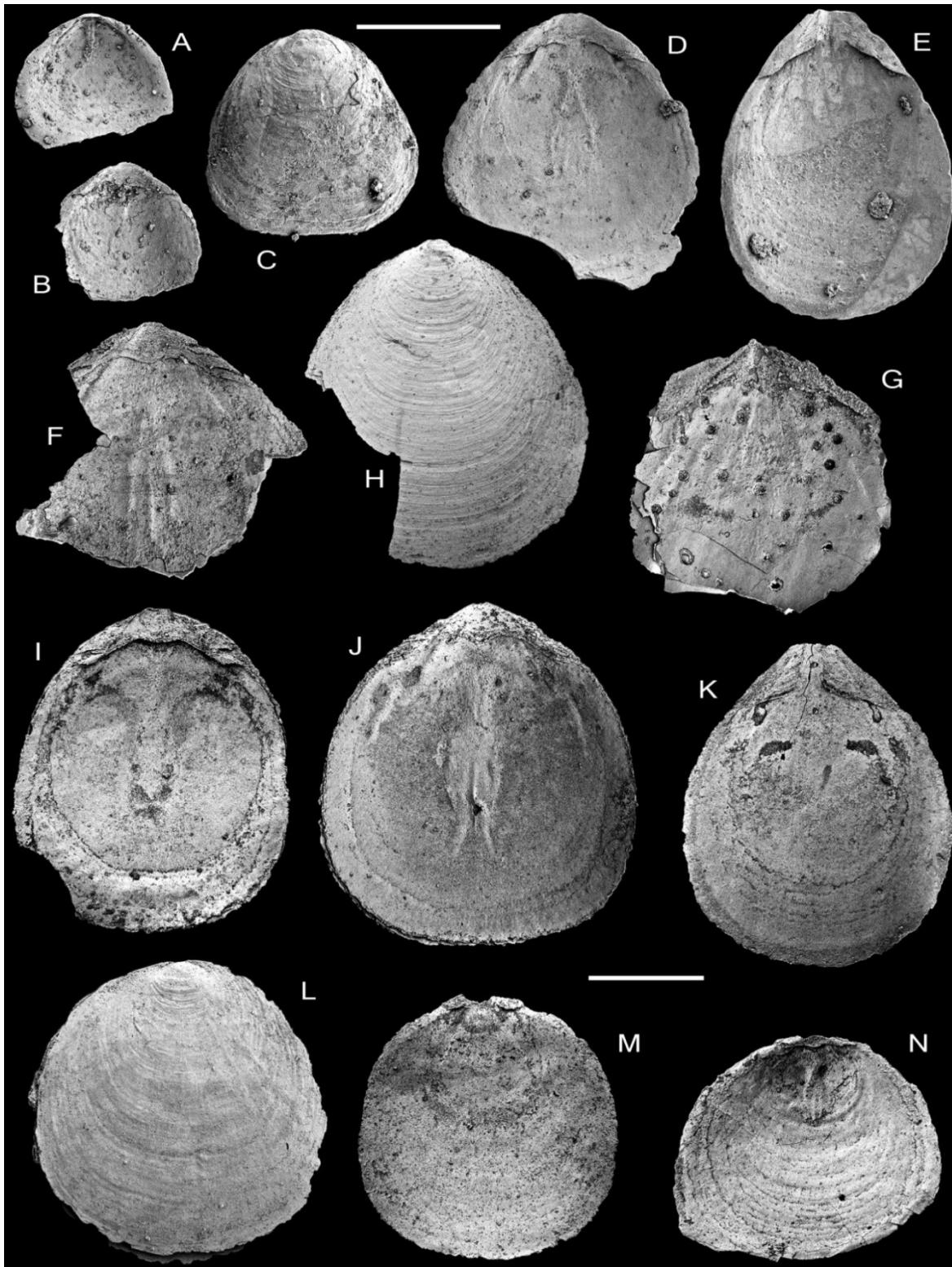
Fig.1. Middle Cambrian lingulate brachiopods from the Paibi section, Hunan Province, South China. A, C. cf. *Canalilatus* n. sp., A, dorsal valve interior; C, dorsal valve exterior, both from 105m. B, D, E. *Eoobolus*? n. sp, B, dorsal valve interior from 37m; D, dorsal valve interior; E, ventral valve interior, both from 7.6m. F, G. indeterminate zhanatellid, F, dorsal valve interior, and G, ventral valve interior, both from 122.6-136.7m. H-K, *Experilingula*? n. sp., H, ventral valve exterior; I, gerontic dorsal valve interior from 326m; J, dorsal valve interior; K, ventral valve interior, all from 318m. L-N. cf. *Kyrshabaktella* sp. nov. L, dorsal valve exterior from 346.7m; M, ventral valve interior; N, dorsal valve interior, both from 344.6m. Both scale bars represent 1 mm; that between C and D refers to specimens A-E; scale bar above M refers to specimens F-N. Sample levels in metres are heights above base of Huaqiao Formation in the section.

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Electron backscatter diffraction (EBSD) as a tool for evaluating fossil brachiopod shell preservation: Implications for carbonate clumped isotope paleothermometry

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Electron backscatter diffraction (EBSD) is an *in situ* microscopy technique that provides high-resolution crystallographic information at nano- to micro-scales and it is widely used to characterize biomineral structures, including brachiopod shells (e.g., Schmahl et al., 2004; Cusack et al., 2008). Its expediency has been also demonstrated in detecting diagenesis in fossils used in paleoclimate reconstructions (e.g., Dalbeck et al., 2011; Pérez-Huerta et al., 2012). Likewise, using the highest resolution of EBSD, crystal lattice modifications can be identified and associated to closed-system recrystallization during diagenesis.

Here, we present the use of EBSD to detect open and closed-system recrystallization in fossil brachiopod shells used in carbonate clumped isotope thermometry. Accurate temperature estimates rely on fossil preservation; thus imaging and chemical techniques are routinely used for sample screening. While conventional textural, chemical, and isotopic techniques are effective at detecting open-system recrystallization, they are not always helpful at detecting the closed-system recrystallization or isotopic reordering that can influence clumped isotope compositions.

For example, Paleozoic brachiopod shells that appear to exhibit good preservation can have unreasonably high clumped isotope temperatures ($D_{47} > 100°C$), reflecting burial rather than environmental temperatures. EBSD reveals the presence of poorly ordered lattices and/or loss of original crystal orientation consistent with recrystallization. In contrast, specimens exhibiting preservation of original crystallographic orientations in shells typically preserve lower temperature values. Thus, EBSD data can provide evidence for fossil preservation, distinguishing between original crystal structure, closed-system recrystallization, and open-system recrystallization.

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A preliminary report on the Lower Carboniferous brachiopod fauna from the Qiangtang area (northwestern Tibet) and its palaeobiogeographical significance

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The Qinghai-Tibet Plateau comprises a complex assembly of Gondwana-derived continental blocks divided by major fault or suture zones. The sutures may represent palaeo-oceans or back arc basins with different age constrains. There has been controversial for a long time about the boundary between Gondwana and South China involved the evolution of the Palaeotethys and rifting
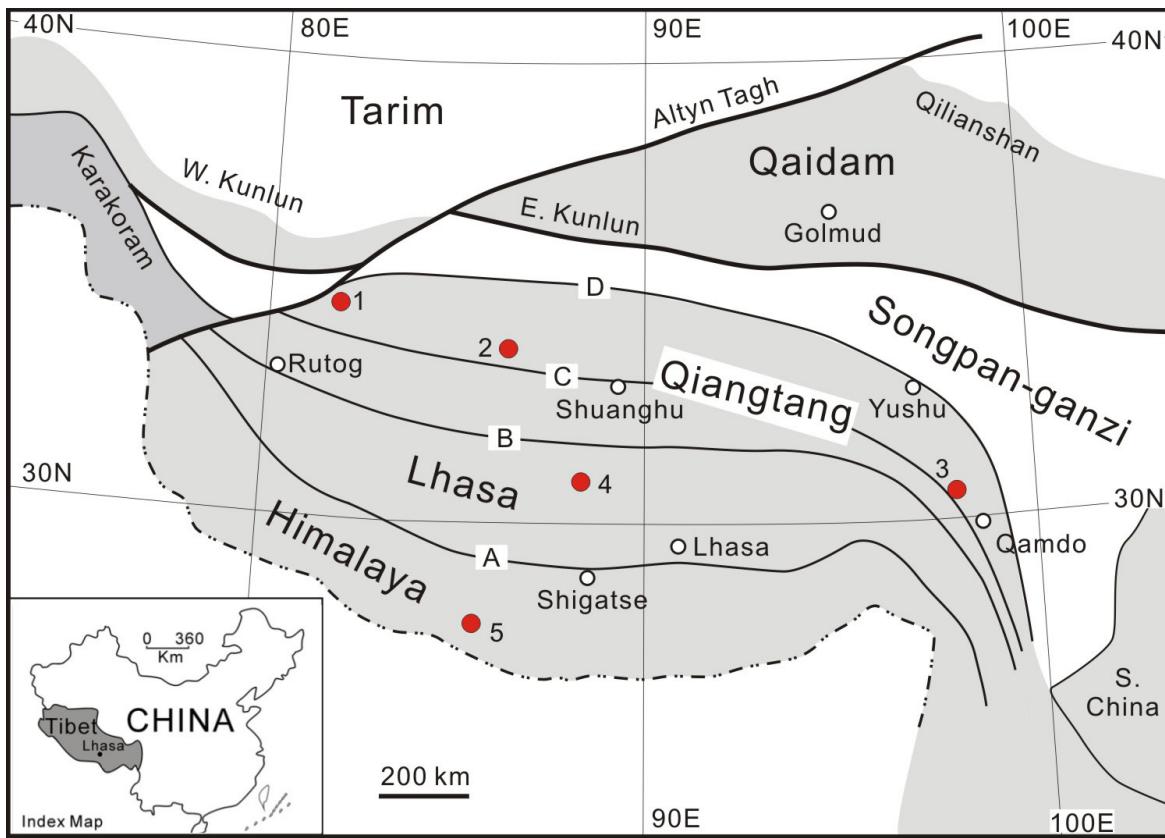
Fig. 1. Schematic tectonic map of the Qinghai–Tibet Plateau, showing the main tectonic units and localities of the Lower Carboniferous brachiopod faunas discussed above (tectonic map modified from Xiao et al. 2005). Sutures: A, Yarlung-zangbo Suture; B, Bangong–Nujiang Suture; C, Longmu Co–Shuanghu Suture; D, Jinshajiang Suture. Fossil localities: 1, Shuangdiandaban (this study); 2–5, some Lower Carboniferous brachiopod faunas recorded in neighboring regions: 2, Riwanchaka; 3, Leiwuqi; 4, Yongzhu; 5, Nyalam.

and separation of the continental terranes from eastern Gondwana in the Late Paleozoic. The Longmu Co–Shuanghu suture that separated the North and South Qiangtang terrane was generally regarded as the Palaeotethys suture in Devonian–Permian times (Li et al., 2007; Metcalf, 2013), though the suture was also located north (Jinshajiang suture), or south (Bangong–Nujiang Suture or Yarlung-zangbo Suture) in light of the sedimentary rocks and provinciality of fauna and flora with different age constrains. Nevertheless, the rock successions and faunas within some time intervals, Devonian and Carboniferous in particular, in Qiangtang terrane are far from understood.

Here we reported a Lower Carboniferous brachiopod fauna collected by Professor Sun Dong-li from the Shuangdiandaban section during the integrated scientific expedition of the Karakoram and Kunlun Mountains between 1987–1990. The section locates about 1.5 km northeast of Shuangdiandaban, north Rutog County of Tibet (Fig. 1). It was mainly composed of limestone-dominated sequences that bearing abundant brachiopods, corals and foraminifers which range from the Lower Devonian to the Lower Carboniferous (Sun and Chen, 1998). The Lower Carboniferous brachiopods were collected from three levels in the Yueyahu Formation, and one level in the Shuangxiandaban Formation.

This fauna is generally indicative of the Tournaisian to early–middle Visean, because of occurrences of *Ectochoristites*, *Syringothyris*, *Tylothyris*, *Rhytiophora*, *Marginatia*, *Dictyoclostus*, *Ovatia*, *Linoproductus* together with some other cosmopolitan taxa. Comparable elements can be found from the Riwanchaka in north of Gêrzê or Leiwuqi near Qamdo where bearing some similar elements of Cathaysian province, as well as from Yongzhu (Xainza) and Nyalam where yielding cold water faunas (Yang et al., 1983) (as referred in Fig. 1, fossil localities 2–5). As a preliminary conclusion, the brachiopod fauna from the northwestern Qiangtang terrane during the Tournaisian to early–middle Visean intervals has general links to those both from the Gondwanan realm and the warm-water Cathaysian realm, though no endemic taxa of Gondwana or Cathaysia were found there. Nevertheless, comparisons with similar faunas in a broader region and discussions on the paleobiogeography are needed in following work.

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A review of extant species in the craniid brachiopod genus *Novocrania*

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The taxonomic status of all extant species of *Novocrania* is reviewed, based (as far as possible) on examining and comparing specimens. Of the fourteen species currently in the literature five are definite species, two may be separate species or synonymous, six species are considered to be synonymous and one species is based on a specimen that is not a craniid. Mediterranean – North Atlantic species *N. anomala* and *N. turbinata* are confirmed as two separate species, based on the morphology of the ventral valve. *N. japonica* (Japan, Korea, Indonesia) and *N. reevei* (Australia) are synonyms of *N. turbinata*. The ventral valve morphology of *N. turbinata* suggests this species may belong in the genus *Ancistrocrania* rather than *Novocrania*. 'Sunken' muscle scars in extant and fossil craniids may be misnamed and may, in fact, represent where organic muscle scar tissue was present but has not been preserved.

Phanerozoic brachiopod genera of China: A brief introduction

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With contributions from Jin Yugan, Shen Shuzhong, Zhan Renbin, Sun Dongli, Hou Honghfei, Chen Xiuqin, Li Guoxiang, Qiao Li, Huang Bing, Zhang Zhifei, Zhang Yan, Fu Lipu, Shi Xiaoying, Su Yangzheng, Xian Siyuan, Xu Hankui, Xu Guirong, and Elizabeth Weldon.

It is 132 years since the first fossil brachiopod genus *Leptodus* was established based on a Chinese species by Kayser in 1883. Up-to-now, there are 754 genera named on the basis of type species from China and assigned to the phylum Brachiopoda (Fig. 1). These Chinese genera were erected in a heterogeneous spectrum of publications, such as palaeontological atlases, journals, proceedings, monographs and others; many were published only

in Chinese without an English abstract, many appeared in various Chinese journals which were printed by a local press, not widely distributed and poorly represented in international libraries; and many of the original specimens were inadequately presented, despite having a short English summary. Thus, due to all of these obstacles it has proved difficult for *non*-Chinese researchers to access information on these key genera. It is hoped that a comprehensive book on the fossil brachiopod genera of China may facilitate evaluation of the genera by researchers who are interested in fossil brachiopods and can easily refer to the Chinese data.

A new book, "Phanerozoic brachiopod genera of China" is nearly complete and will be published by Science Press, Beijing. All brachiopod genera, erected on type species from China are included. Those genera, although well known in the Chinese literature (e.g., the Devonian *Cyrtospirifer, Rostrospirifer* and *Tenticospirifer*), established by Chinese scholars (e.g., the Ordovician *Paromalomena*, the Triassic *Tulungospirifer*, and Jurassic *Obsoletirhynchia*), named in honor of Chinese scholars (e.g., the Lower Permian *Liufaia*), and critically revised on Chinese material (e.g., *Planovatirostrum*), are not covered in this publication because their type species are from outside of China.

The book begins with an introduction which includes a historical review, general features, taxonomic treatment, temporal distribution, palaeobiogeography, notes on macro-evolution, and the edited format. Cambrian explosive radiation, Ordovician biodiversifivation, and Middle Triassic radiation, associated with end-Ordovician, Frasnian-Fammenian and end-Permian mass extinctions are discussed mainly in terms of brachiopod data of China. In addition to the introduction, there are nine chapters in the book which are arranged in line with the geological periods including Cambrian, Ordovician, Silurian, Devonian, Carboniferous, Permian, Triassic, Jurassic and Cretaceous. These chapters are written by the following authors with the number of genera involved in brackets:

1. Introduction	Rong Jiayu *et al.*
2. Cambrian (32)	Li Guoxiang, Zhang Zhifei and Rong Jiayu
3. Ordovician (113)	Rong Jiayu, Zhan Renbin, Huang Bing and Fu Lipu
4. Silurian (51)	Rong Jiayu, Huang Bing, Zhan Renbin and Fu Lipu
5. Devonian (179)	Hou Hongfei, Chen Xiuqin, Rong Jiayu, Zhang Yan, Xu Hankui, Su Yangzheng and Xian Siyuan
6. Carboniferous (58)	Shen Shuzhong, Qiao Li, Zhang Yan and Jin Yugan
7. Permian (208)	Shen Shuzhong, Jin Yugan, Zhang Yan and Elizabeth Weldon
8. Triassic (88)	Sun Dongli, Xu Guirong, and Qiao Li
9. Jurassic (12)	Sun Dongli, Shi Xiaoying, Zhang Yan and Qiao Li
10. Cretaceous (13)	Sun Dongli, Zhang Yan and Qiao Li

Each chapter covers a summarized review of geographical distributions, stratigraphic correlation, brachiopod faunal succession, palaeobiogeography and systematic palaeontology. The latter constituting a major part of this book encompasses type

Fig.1. Cumulative abundance of 1) all genera originally assigned to brachiopods based on type species of China (black line), 2) genera revised as valid and *nomen dubium* in this book (red line) and 3) genera described in the revised brachiopod *Treatise* (blue line) (Curry and Brunton, 2007). The longitudinal axes are composed of left (black for 1 and 2) and right (blue for 3) ones. The horizontal axis is divided into stages of Palaeozoic and Mesozoic and systems are divided by vertical lines.

species, etymology, diagnosis, comparison (or remarks and discussion), species assigned and rejected, and stratigraphic range and geographical distribution.

There is a substantial amount of new information including revised diagnoses and corrected temporal and spatial distributions. The holotype and/or paratypes of the type species are restudied and/or re-illustrated. In total about 125 plates along with a large number of text-figures are presented. A few neotypes are designated and some type material is illustrated for the first time. Through collective revisions provided in this book, relevant Chinese genera are revised according to the following seven groups: 1) valid (about 62%); 2) junior subjective synonyms (about 20%); 3) *homonyms* including *homonymum senius* and *homonymum junius*; 4) objective synonyms (=*synonymum homotypica*); 5) doubtful names (*nomen dubia*) (about 10%) which have taxonomic problems mainly due to the poorly preserved specimens they are based on, inadequate original descriptions, and/or poor knowledge about their internal structures; 6) invalid names (*nomen nuda*) (about 5%) including those that fail to satisfy the provisions stipulated in Article 11 of the ICZN (1999) published before 1931 (unaccompanied by a designation, definition, description and illustrations of the type species and specimens) and names published after 1930 (lacking an accompanying statement of characters that differentiate the taxon, without a definite bibliographical reference and others); and 7) rejected from the

brachiopods, including one each from Silurian and Devonian and 16 genera which from the Lower Cambrian Small Shelly Faunas. In addition, there occur 62 Chinese genera including some *nomen nuda* which were published before 2007, but not covered in the new edition of the brachiopod Treatise. All genera mentioned above are numbered in each chapter.

Moreover, with the exception of the above genera, there are 38 genus names which are treated as *nomen nulla*, and eight taxonomic names which were originally placed in subsections below subgenus level, these can be regarded neither as genera, nor subgenera, only as *nomen vetita*, although the respective authors proposed these names with a designation of a so-called genotype. These names are not itemized in this book.

A series of brachiopod assemblages through the Ordovician to Cretaceous of China was initially documented by Wang *et al*. (1981) for the purpose of biostratigraphic subdivision and correlation. Later, more assemblages were recognized in the various epochs which are mostly reviewed in relevant chapters providing a prodigious amount of information on the occurrences of Brachiopoda in China. Meanwhile, the stratigraphic correlation and brachiopod classification have undergone great changes, a synthetic and radical revision of the Chinese brachiopod genera which were established on Chinese type species is provided in each chapter in terms of newly and widely accepted standardized stratigraphic units (stages, series and systems) of the International

Stratigraphic Committee (ISC) along with a correlation of local lithostratigraphic units. In the range charts, all genera are arranged in the order of the major taxonomic groups applied in the new edition of the brachiopod Treatise, and within each major group, each genus is arranged in order of their first appearance.

This book has been completed during two periods, totally 14 years (1989-1994 and 2008-2015) by nearly 20 contributors. During that time all of us enjoyed the work and the support of various agencies. In addition to the authors mentioned above, the comprehensive nature of this book critically emphasizes the importance of team work dependent on collaboration with colleagues. There are many persons meriting special mention at this juncture, for their contributions to the project, including the loan type specimens and/or providing us with photos of type specimens and references, such as Chen Yuanren, Ding Peizhen, Duan Chenghua, Fang Runsen, Gu Feng, Han Nairen, He Weihong, He Xilin, Jin Xiaochi, Li Li, Li Luozhao, Li Wenguo, Liang Wenping, Liao Zhuoting, Liu Diyong, Ma Xueping, Shan Huizhen, Sun Yuanlin, Tan Zhengxiu, Tong Zhengxiang, Wan Zhengquan, Wang Chengwen, Yang Deli, Yao Shoumin, Ye Songling, Zeng Qingluan, Zeng Yong, Zhan Lipei, Zhang Zixin, Zhao Ruxuan and others. Clearly this work could not be accomplished without the efforts of all these colleagues.

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Permian brachiopods from the Gyanyima exotic block in southwestern Tibet, China and their palaeogeographical implications

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The Indus-Tsangpo Suture marks the zone of collision between the Indian and Eurasia plates and has been widely regarded as a remnant of the Neotethys or Mesotethys Ocean. One of the most spectacular features in this suture zone is that it contains decimeter to kilometer-scale exotic limestone blocks. These blocks have shown some lithological and palaeontological similarities, but their general palaeogeographical and palaeobiogeographical affinities are still controversial. Thus, detailed investigations of the palaeontological contents of these isolated limestone blocks become critical to understand the evolution of the Palaeotethys.

In this paper, we reported diverse brachiopods from the Gyanyima Formation at the Gyanyima (Jiangyema) section in southeastern Zhada county, Tibet, China. A total of 28 species belonging to 19 genera have been identified. A detailed study of brachiopods and other associated faunas suggests the age of the fauna is mostly Changhsingian (Shen et al., 2010; Wang and Ueno, 2009). The brachiopod fauna from Gyanyima is totally comparable with those from the Chitichun limestone block reported by Diener (1897) and the Chhidru Formation in the Salt Range, Pakistan (Waagen, 1882-1885), and generally exhibits transitional/mixed characters between the Cathaysian and Gondwanan faunas, in contrast to those from the Selong Group at Selong, Tulong and Qubu sections in southern Tibet, which are exclusively composed of typical cold-water Gondwanan and cosmopolitan taxa. Based on lithofacies and faunas from the limestone block, these limestone blocks are most likely to represent some carbonate deposits on seamount or small carbonate buildups in the Neotethys.

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Onshore–offshore–basin species diversity and body size patterns in Changhsingian (Late Permian) brachiopods

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Body size is a fundamental and defining character of an organism, and its variation in space and time is generally considered to be a function of its biology and interactions with its living environment. A great deal of body size related ecological and evolutionary research have been undertaken, mostly in relation to extant animals. Among the many body size-related hypotheses proposed and tested, the *size–depth* relationship is probably the least studied. In this study, we compiled a global body size dataset of Changhsingian (Late Permian, ca. 254 Ma-252 Ma) brachiopod species from low-latitude areas (30˚S–30˚N) and analyzed their species diversity and body size distribution patterns in relation to the onshore–offshore–basin bathymetric gradient. The dataset contained 1768 brachiopod specimens in 435 species referred to 159 genera and 9 orders, from 135 occurrences (localities) of 18 different palaeogeograpgic regions. With the whole of the Changhsingian stage treated as a single time slice, we divided the onshore–offshore–basin bathymetric gradient into three broad depth-related environments: nearshore, offshore and basin environments, and compared how the species diversity and body size varied along this large-scale bathymetric gradient.

Here, we report an array of complex patterns. First, we found a clear overall inverse correlation between species diversity and water depth along the onshore–offshore–basin gradient, with most species concentrating in the nearshore environment. Second, when the median sizes of all low-latitude brachiopod species from the three environments were compared, we found that there was no significant size difference between the nearshore and offshore environments, suggesting that neither the wave base nor the hydrostatic pressure exerts a critical influence on the body size of brachiopods. On the other hand, the median sizes of brachiopods from both the nearshore environment and, to a lesser extent, the offshore environment were found to be significantly larger than that of basinal brachiopods. This trend of significant size reduction in basinal brachiopods mirrors the relative low species diversity in the basin environment, and neither can be easily explained by the tendency of decreasing food availability towards deeper sea environments. Rather, both trends are consistent with the hypothesis of an expanding Oxygen Minimum Zone (OMZ) in the bathyal (slope to deepsea) environments, where hypoxic to anoxic conditions are considered to have severely restricted the diversification of benthos and favored the relative proliferation of small-sized brachiopods. Finally, a significant difference was also found between eurybathic and stenobathic species in their body size response to the onshore–offshore–basin gradient, in that eurybathic species (species found in all three environments) did not tend to change their body size significantly according to depth, whereas stenobathic forms (species restricted to a single environment) exhibit a decline in body size towards the basinal environment. This pattern is interpreted to suggest that bathymetrically more tolerant species are less sensitive to depth control with respect to their body size change dynamics, in contrast to stenobathic species which tend to grow larger in shallower water depths.

Keywords: Onshore–offshore–basin gradient, Changhsingian brachiopods, body size change and control, Oxygen minimum zone, end-Permian mass extinction

Die hard under high energy flow conditions: a case of shell functionality in the spiriferinide brachiopod *Pachycyrtella*

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The adaptation and radiation of benthic animals is reflected in the variety of morpho-functions within their environment. In particular, immobile benthic animals need a reliable life posture to avoid the risk of rollover or burial. Once postural stability has been reached, they can exploit other biological capabilities such as feeding and respiration.

The Permian spiriferinide brachiopod *Pachycyrtella omanensis* is characterised by a large, thick shell with a massive protruding umbo. The animal adapted to a shallow marine sandy bottom with the aid of a partially buried thick protruding umbo (Angiolini 2001; Angiolini et al. 2003). In addition to the physical stability of this posture, its "spirifer" shape could have functioned to generate passive flows for feeding inside the shell (Shiino 2010).

To clarify the synergistic function of the physical and bio-physiological performance of the shell form of *Pachycyrtella omanensis*, water flow experiments were performed using a flow

tank and shell models, which were made of polycarbonate plates utilizing a vacuum-forming method. The posterior part of the ventral valve was formed by plaster to mimic the massive protruding umbo of *Pachycyrtella omanensis*. Two types of experiments were conducted: 1) examination of the threshold velocity at which the shell model was removed from the coarse sandy bottom and 2) visualisation of flows around the shell model using dye fluids.

In the first test, the ideal life posture, with the lateral commissures oriented vertically to the sea bottom, withstood ambient flows up to 0.5 m/s; however, both dorsal and ventral valve down postures were apparently more stable, as they were capable of withstanding higher ambient flow velocities (Shiino and Angiolini 2014). On the other hand, the experimental results of flow visualisation showed that the ideal posture could generate constant spiral flows inside the model regardless of the shell orientation, with the ventral or dorsal valve facing upstream. The filtration of food particles could have benefitted from the vortices because of its alignment with the spiral lophophore in *Pachycyrtella omanensis* (Shiino 2010; Shiino et al. 2009; Shiino & Kuwazuru 2010, 2011; Shiino and Angiolini 2014). These results imply that the real life posture is not necessarily the most physically stable but represents a compromise that optimizes both physical and biological functions. Moreover, flow experiments using models with different valve opening angles showed that the spiral flows were stable with a more widely opened valve under low velocity ambient flow and with a narrowly opened valve under high velocity flow. Hence, the morpho-function of *Pachycyrtella* has the potential to adjust the intensity and movement of the passive feeding flow by changing the valve opening angle (Shiino and Angiolini 2014).

If *Pachycyrtella* could adjust its internal spiral flow with respect to the ambient flow, how did the animal detect changes in the surrounding condition and feed back to adjust the valve opening angle? One likely possibility is that stimulation of the tactile receptors of the setae could have controlled the muscle system to adjust the opening angle of the valve. In fact, fluid pressure around the gape between the ventral and dorsal valve margins is crucial to the generation of inflow and outflow (e.g., Shiino et al. 2009), and thus, setae along the valve margins could function to perceive ambient flow conditions. Mature individuals of *Pachycyrtella* have wide and radially arranged diductor muscles, possibly functioning to regulate the precise angle of valve opening.

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How does flow recruit epizoans onto brachiopod shells?

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Fossil evidence of epizoans on skeletal animals confirms the presence of direct interactions regarding interspecific relationships, which have the potential to be driving forces of co-evolution. In brachiopods, it has been suggested that their shells have provided immobile attachment sites for epizoans, such as cornulitids, bryozoans and corals, commensally. However, great attention should be paid because there is no guarantee that the disposition of epizoans causes a symbiotic characteristic but merely a taphonomic feedback after the death of the host shell organism. Planktonic larvae, as observed for most epizoans, are inferior to those with active swimming ability, as they can be cast adrift on water flows (e.g., Abelson and Denny 1997). For immobile larvae, a feasible place to attach onto the host would depend heavily on the hydrodynamic properties of the host shape. As a preliminary step toward understanding adaptation and evolution in terms of the fossil symbiotic associations, we exemplified mechanisms of larval recruitment to accomplish spiriferide-epizoan relationships.

In the passive route, a floating larva moves along the same streamline route when its density is low or moderate, and it subsequently collides with an attachment site where the interval of streamlines narrows (Fig. 1: direct interception). If the density of the larva is sufficiently greater than that of the medium, inertial force allows the movement of the larva to deviate from the streamline route, resulting in attachment onto a host site (Fig. 1: inertial impaction). From the hydrodynamic viewpoint, direct interception occurs at a host site with lower pressurization, thus a higher flow velocity along the surface, whereas inertial impaction is likely at other sites with higher pressurization.

A computational fluid dynamics simulation was performed to identify areas that are potentially prone to larval settlement. The pressure distribution on the shell surfaces of *Paraspirifer* and
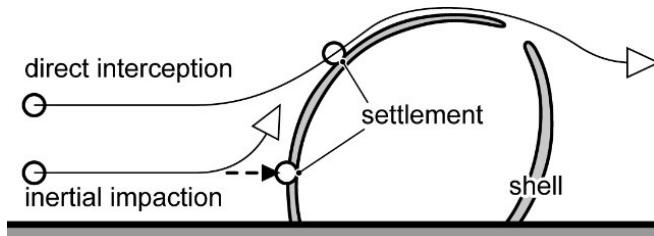
Fig. 1. Schematic illustration of larval settlement. White arrows show the schematic streamline.
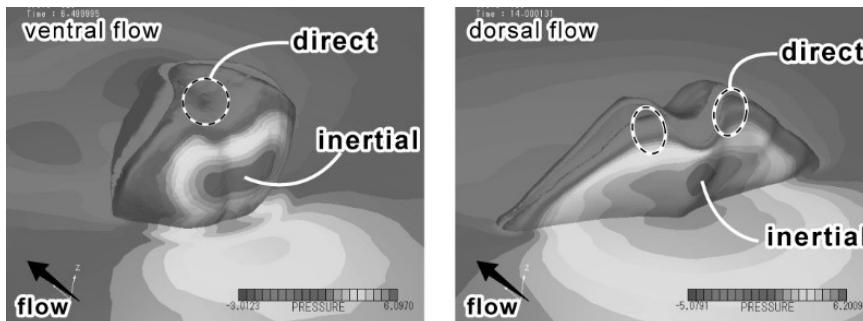

Fig. 2. Pressure distributions on *Paraspirifer* (left) and *Cyrtospirifer* (right).

Fig. 3. Cornulitids on *Eospirifer* sp.

Cyrtospirifer showed that forward stagnation points received the highest pressure, while lower pressure occurred along the shell margin of the lateral gape, regardless of flow direction with ventral or dorsal valve facing upstream. Both sites seem to be well available for epizoans (e.g., Schumann 1967; Zapalski 2005; Manceñido and Gourvennec 2008), possibly due to such ways of direct interception and inertial impaction. The lowest pressure was around the innermost lateral gapes when the dorsal valve was facing upstream and around the anterior part of the sulcus with the ventral valve facing upstream, where many brachiopods with sulcus and folds, including spiriferides, appear to provide attachment sites for epizoans (e.g., Li and Sproat 2010).

It is worth considering the biological reaction of epizoans. For example, a specimen of Silurian *Eospirifer* carries cornulitids on the right and left innermost lateral gapes of the dorsal valve, which seem to be attached by direct interception. Following settlement, the cornulitids developed in the antero-median direction of the spiriferide shell, possibly constituting evidence for cornulitid autecology (Fig. 3).

Epizoan settlements on dead shells are well preserved in the spiriferide *Paraspirifer* from Ohio, USA (Sparks et al. 1980). The shell margin of *Paraspirifer* occasionally shows xenomorphic patterns of epizoans, suggesting a commensal association. However, it is very difficult to determine whether the epizoans

demonstrated a commensal or taphonomic relationship when they attached on the shell surface without a margin. A unique specimen of *Paraspirifer* with bifurcated tabulate coral *Aulopora* has a pair of broken brachidia with a geopetal structure on the left dorsal side. Returning to the taphonomic process, the animal had positioned itself with the left dorsal side down before its burial, and another exposed surface was harvested by *Aulopora*. Using flow experiments and simulations, the first individual of *Aulopora* was transported and settled onto the shell via inertial impaction after the host *Paraspirifer* was dead and turned over on the sea floor (Fig. 4).

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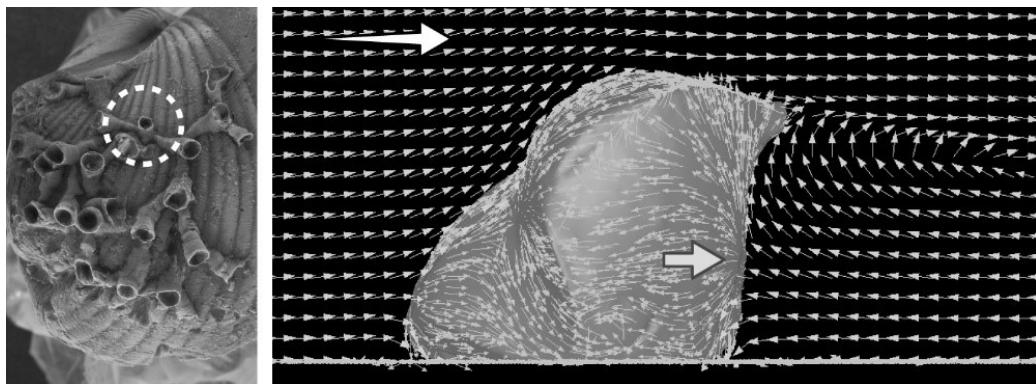
Fig. 4. *Auropora* on right dorsal side of *Paraspirifer*. First individual (whute circle) would be settled through the inertial impact (white arrow).

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A revisited Silurian- Lower Devonian brachiopod biostratigraphy of North Patagonian Massif, Ventania system and Southern Paraná Basin. A regional correlation

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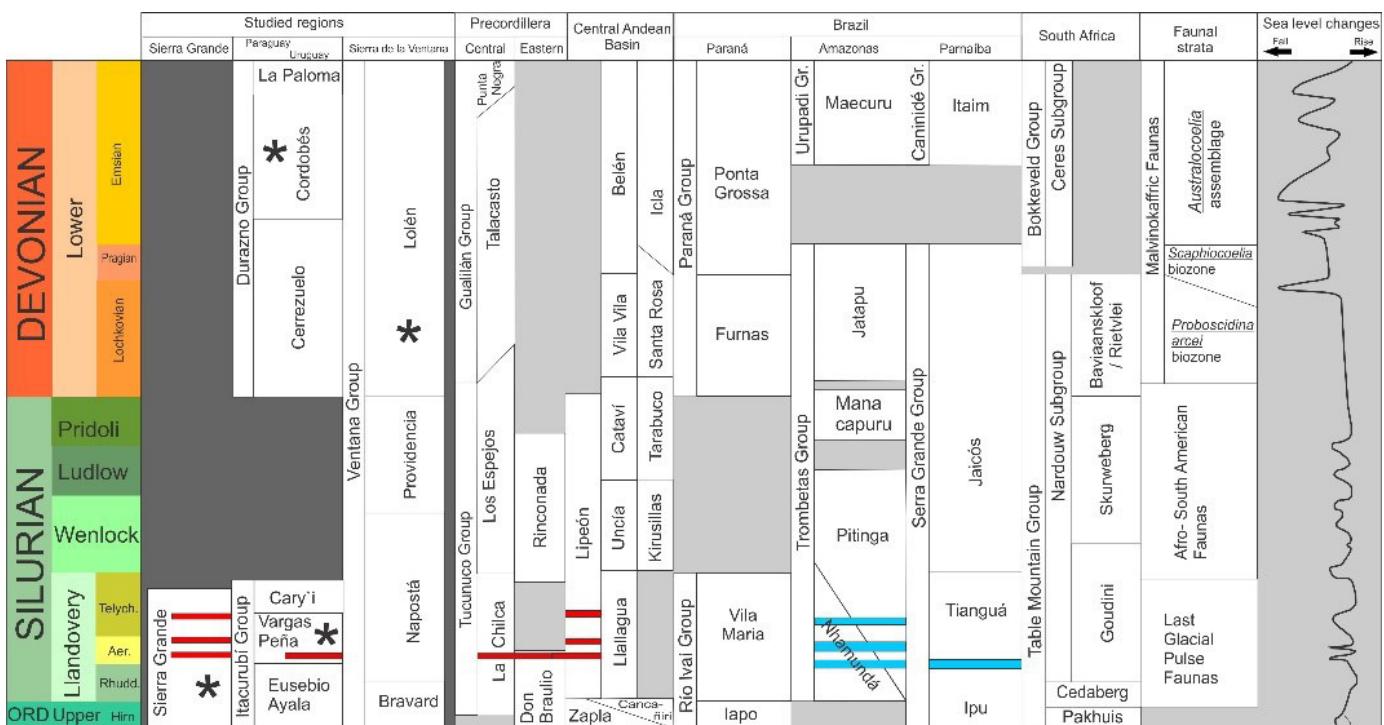
The first collections of Silurian-Devonian brachiopods from South America were realized by Charles Darwin (1833) in the Malvinas Islands, during his voyage on the H.M.S. Beagle around the world and they were lately described by Morris and Sharpe (1846). After that Clarke's monograph (1913) provided an approach on systematics and paleobiogeography of this fauna. Contemporary works were mainly focused in the Proto-Andean margin but the Silurian-Devonian faunas from the Atlantic outcrops (Fig. 1) especially those of North Patagonian Massif (Müller, 1965), Ventania (Andreis, 1964), Eastern Paraguay (Harrington, 1950; Wolfart, 1961) and Uruguay (Méndez-Alzola, 1938), remained poorly studied.

The Silurian brachiopods reviewed come from Sierra Grande Formation (Northern Patagonia) and Vargas Peña Formation (Eastern Paraguay, Parana Basin). This two sections bearing iron levels, ranging from iron coating to oolitic ironstones. From the Sierra Grande Formation two oolitic iron levels are recognised; below the first iron level it is found the fauna described as *Heterorthella freitana-Clarkeia antisiensis* (Müller, 1965); below the second iron level, the suggested presence of *Conularia quichua-Bainella* sp hinted a Lower Devonian age. However, recent studies (Siccardi et al. 2014), allowed recognized the Llandoverian brachiopods *Eostropheondonta chilcaensis* (BENEDETTO, 1995), *Heterorthella*? sp, *Dalmanella*? sp, *Hindella*? sp. and Ressellerids (*Resserella*?, *Vysbiella*?). In addition, a trilobite assemblage dominated by *Eoleonaspis* sp, supports the Llandoverian age (Rustán et al. 2013). The Vargas Peña Formation is included in the siliciclastic sequence of the Itacurubí Group (Hirnantian-Lower Silurian) and its brachiopod faunas known from are composed by *Anabaia paraguayensis* (HARRINGTON, 1950), accompanied of scarce inarticulates (Obolidae? indet.); the age assigned to this assemblage is Aeronian to late Telychian (Tortello et al. 2012 and references therein). Even though, in the Paraguayan outcrops oolitic ironstones have not been found, they are mentioned in subsurface drills.

Fig.1. Outcrop location. **(A)** Eastern Paraguay. **(B)** Uruguay (Durazno Department). **(C)** Sierra de la Ventana. **(D)** Sierra Grande.

The Lower Devonian brachiopod faunas that integrate this study have been collected from outcrops of the Lolén Formation (Sierra de la Ventana) and the Cordobés Formation (Uruguay, Durazno Department). In the base of the Lolén unit, the uppermost in the Ventana Group (Silurian?-Middle Devonian), an assemblage composed by *Cryptonella sp*, *Schellwienella sp*, *Leptocoelia* sp and *Derbyia* sp was originally mentioned by Andreis (1964) Following contributions (Isaacson, 1975, 1991), have also mentioned the presence of *Proboscidina arcei* ISAACSON, 1977. The fauna of the Lolen Formation is characterized by the low diversity and the strong deformation. However, the new collection from the recent field works has allowed to confirm the presence of the taxon previously described, as well as to identify the brachiopods Mutationelidae? indet, *Orbiculoidea*? sp, and *Pleurothyrella?*sp., accompanied by the bivalves *Nuculites* sp. The age suggested for this brachiopod assemblage is Lochkovian-Pragian (Suarez-Soruco, 2000). Devonian brachiopods from Uruguay registered in the Cordobés Formation (Durazno Group) are more diversified and associated to the Cordobés Formation, a dominantly shaly sequence. An Emsian faunal assemblage, dominated by the brachiopods *Australocoelia palmata* (MORRIS AND SHARPE, 1846) and *Orbiculoidea bainii*? SHARPE, 1856, accompanied by the less abundant *Derbyina? sp.*, *Pleurochonetes falklandicus* (MORRIS AND SHARPE, 1846), *Iridistrophia? sp.* and *Gigadiscina collis* (CLARKE,1913) has been herein recognized. The mixed dominance could be explained due to the overlap of the *Orbiculoidea* and *Australocoelia* communities.

Fig.2. Regional correlations. Red lines represent oolitic ironstones, light blue lines glacial horizons. The brachiopods assemblages mentioned are pointed in the columns as asterisk.

According to the available data the Silurian correlations with others South American basins could be based on key faunal assemblages and sedimentary events: oolitic ironstones in the Proto-Andean margin and the glacial event in the Northeastern Brazil. The presences of oolitic ironstones between the faunas considered would provide an additional correlation tool. The oolitic ironstones are well-known from the Proto-Andean margin and having a biostratigraphical control. The oldest ages defined are Late Rhuddanian and the youngest, Late Telychian. When considering the hypothesis of the ironstones deposition and the glaciation events (Caputo, 1998), they could be traced as a response of interglacial early transgressive stages, during the last pulse of the Early Palaeozoic Glacial event. In the Sierra Grande Formation the *Eostropheondonta* and Ressellerids association dominate the brachiopod assemblage having an Ordovician mark, plus the absence of Ordovician key genera indicate a (Lower?) Rhuddanian age. Wenlockian faunas have not been registered in the studied sections. The correlations proposed are schematised in Fig.2.

Within the Lower Devonian interval, three key species could be recognised: *Proboscidina arcei*, *Scaphiocoelia boliviensis* WHITFIELD, 1890 and *Australocoelia palmata*. The first one, apart from being founded in Sierra de la Ventana, it is abundant during Lochkovian-Pragian times in several Bolivian localities and South Africa (Uppermost Nardouw Subgroup, Baviaanskloof Formation. Meanwhile *Scaphiocoelia* is traditionally proposed as a Pragian key genus, but it restricted to Bolivia and South Africa and records from others basins (Brazil and Precordillera) are confusing. During the Emsian stage, *Australocoelia palmata* became a common (and dominant) component of most of the shallow water brachiopod assemblages.

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The tommotiid *Dailyatia* from the Lower Cambrian of South Australia – Complications to the brachiopod stem

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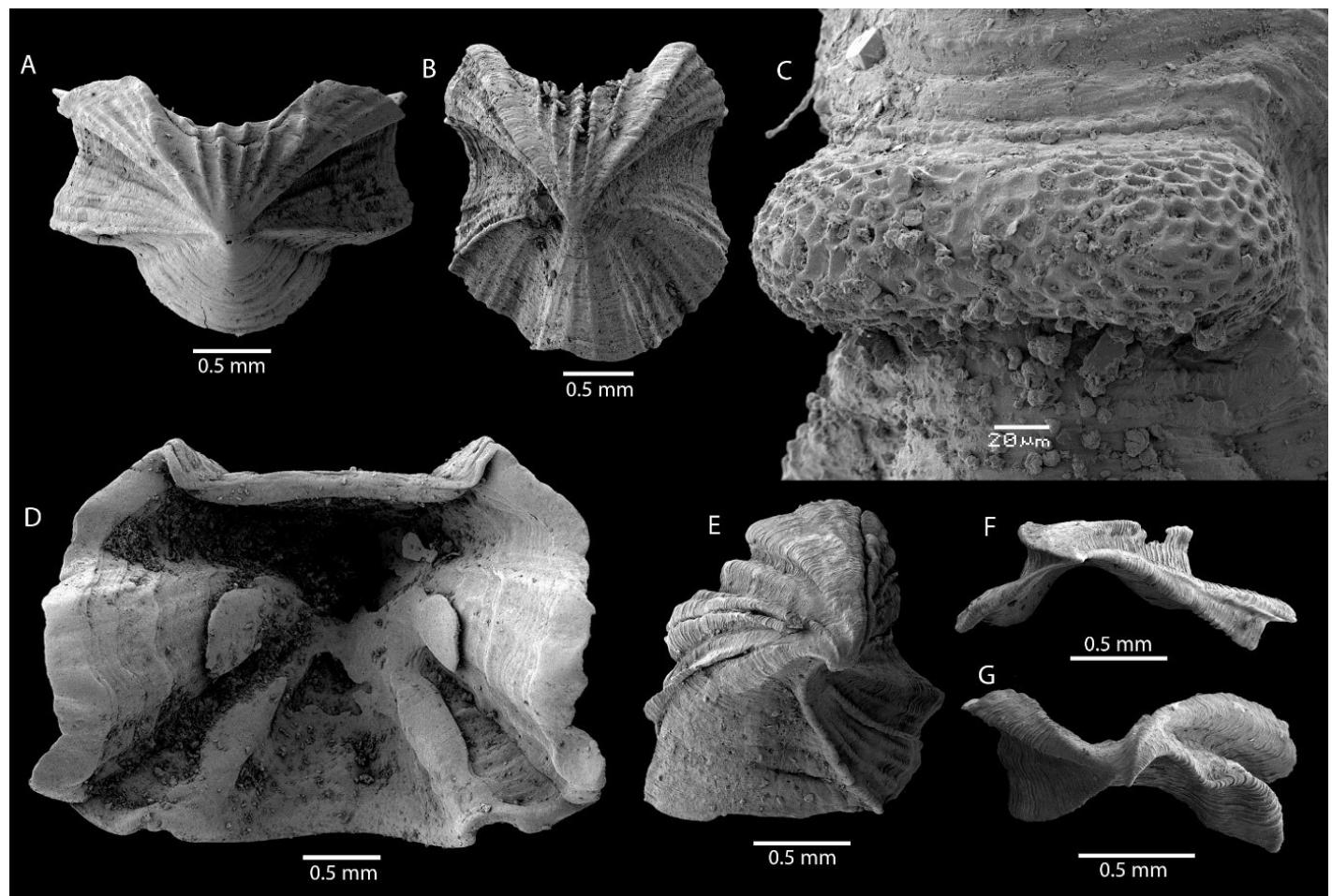

Fig. 1. *Dailyatia* sclerites from the Arrowie Basin of South Australia. A, A1 sclerite in apical view. B, A2 sclerite in apical view. C, detail of A1 sclerite apex with preserved "larval" structures. D, internal view of A1 sclerite showing two pairs of internal platforms and scar-like features. E, B sclerite in apical view. F, C1 sclerite in apical view. G, C2 sclerite in apical view.

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Tommotiids, organophosphatic cap-shaped sclerites from the Lower Cambrian, have been considered the basal stem group of the phylum Brachiopoda, based on similarities in morphology and shell ultrastructure with the earliest bivalved brachiopods (Cryptotretids). The tommotiid genus *Dailyatia* from the Lower Cambrian of South Australia is one of the most diverse tommotiid genera known. Although restricted to Australia and Antarctica, assemblages of *Dailyatia* sclerites may include up to four different species. *Dailyatia* also has one of the most complicated scleritomes of all tommotiids with as many as six different identifiable sclerite morphs in each species. However, due to detailed investigation of large collections of *Dailyatia* sclerites over more than a decade it is now possible to elucidate species level taxonomy, the relative proportions of sclerite types in the scleritome, and the shell microstructure. The sclerites show a wide range of internal and external features that may relate to sensory organs and muscular attachment. Taken together, this information provides evidence for a new reconstruction of the *Dailyatia* scleritome.

Our interpretation is that *Dailyatia* was a vagrant worm-like bilaterian with a complex, imbricating array of sclerites over the dorsal body surface. The scleritome is composed of bilaterally symmetrical A sclerites and pairs of asymmetrical B sclerites forming a central sclerite row. This sclerite row is flanked on both sides by one or two rows of imbricating laterally compressed C sclerites. This construction and the commonly preserved internal scars and platforms, which may be interpreted to represent muscular attachment, provided considerable flexibility to the scleritome. We envisage *Dailyatia* as having a worm- or sluglike body; a vagrant member of the benthos.

The new model diverges significantly from the tubular scleritome demonstrated conclusively in the eccentrothecimorph tommotiids, *Eccentrotheca* and *Paterimitra*. The new data presented here strengthens the interpretation that tommotiids can be divided into two different clades or lineages – the eccentrothecimorphs (sessile with tubular scleritomes) and the camenellans (vagrant, worm-like with dorsal scleritomes; including *Dailyatia*). The fundamental differences in body plan between these two groups suggest that tommotiids are polyphyletic. Eccentrothecimorph tommotiids show greatest similarities to brachiopods and are likely to form the proximal stem group of the Brachiopoda, whilst the position of camenellans is currently unresolved within the stem of the Lophotrochozoa.

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The shell substance microstructure was studied in various groups of Early Cretaceous from the rhynchonellids central and eastern parts of Mediterranean paleozoogeographic region, which includes Crimea, North Caucasus, and Dagestan. The collection included taxa from the superfamilies Rhynchonelloidea, Pugnaceoidea, and Norelloidea. The shell microstructure of Rhynchonelloidea was studied in the families Praecyclothyrididae (genera *Praecyclothyris, Belbekella, Sulcirhynchia, Lamellaerhynchia* (Smirnova, 2012, 2014) and *Cyclothyrididae (genera Cyclothyris, Burrirhynchia, Lobatschevina*, and *Kudrjavzevina* (Smirnova, 2012). All Praecyclothyrididae (23 species) have the shell, consisting of three layers: microcrystalline outer layer, prismatic middle layer, and fibrous inner layer. The shell of Cyclothyrididae (8 species) consists of two layers: the outer microcrystalline, and inner fibrous. The number of substance the shell layers can be used for the diagnosing rhynchonelloid families. The following characters of shell microstructure are characteristic of the superfamily Rhynchonelloidea: relatively small fibers with their trapeziform or rhomboidal cross-sections with rounded angles; small angles between bunches of fibers. Pugnacioidea are represented in the Lower Cretaceous by the family Basiliolidae, the genera Lacunosella and Orbirhynchia (3 species). Their fibers are twice as large as those of Rhynchonelloidea, with their cross-sections mostly rectangular, square or more rarely rhomboidal with sharp angles; the bunches of fibers oriented perpendicular direction. The shell microstructure of Norelloidea was studied in Suiaella (Smirnova, Zhegallo, in press.). It shows significant similarity to that of the Lower Cretaceous Basiliolidae but its fibers are less strogless within one bunch. The Lower Cretaceous Pugnacioidea and Norelloidae have highly similar microstructure and form one group. Both families occur in the west part of Mediterranean Basin. The other group includes Rhynchonelloidea, which occurs widely in Mediterranean. The size of fibers and the shape of their cross-sections can be used for diagnosing superfamilies of the Lower Cretaceous rhynchonellids.

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Microstructural peculiarity of the shell of Early Cretaceous rhynchonellids; importance for taxonomy

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Lower-Middle Permian brachiopods from two localities of Central-South Mexico; faunas of a closing ocean

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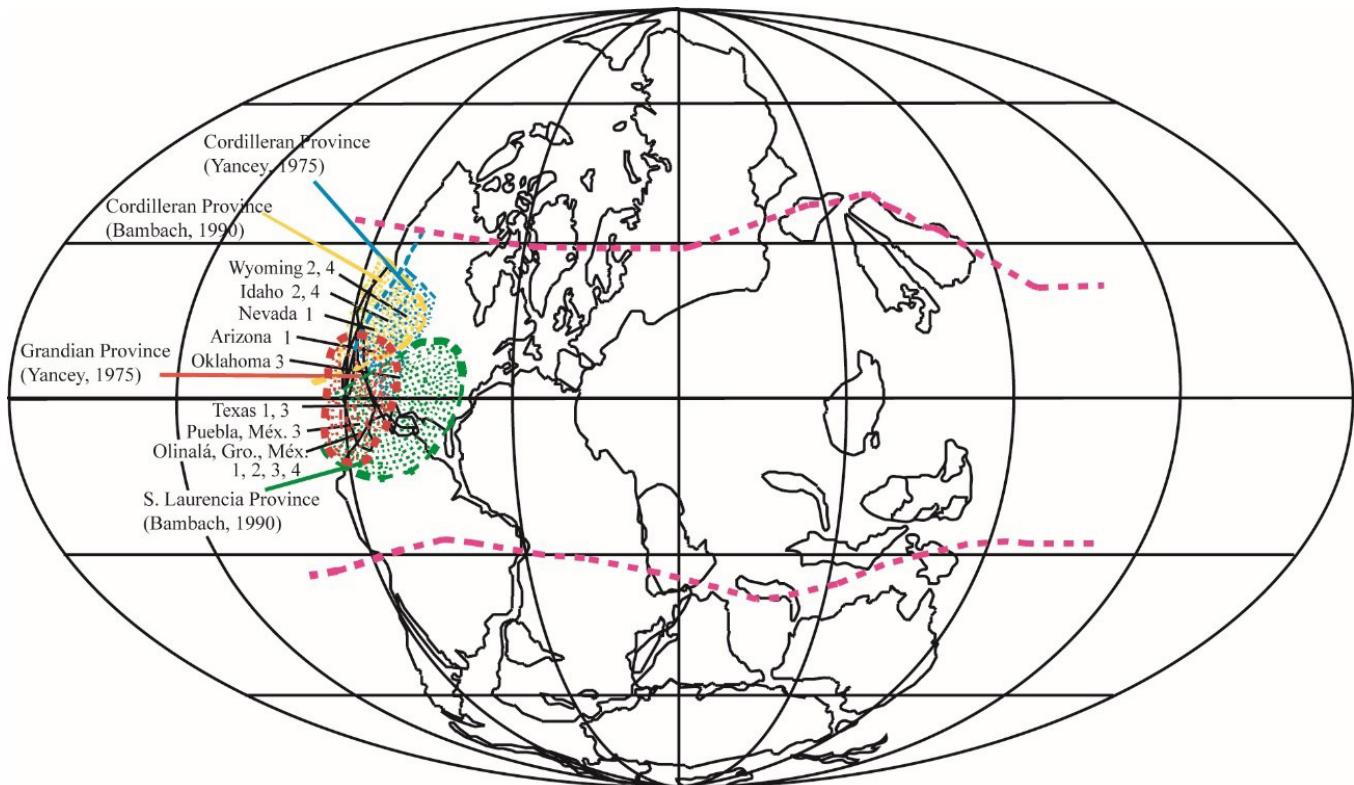
Fig.1. (Modified from Guerrero-Sánchez and Quiroz-Barroso, 2013)

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Several outcrops of Lower-Middle Permian age are aligned in south-central territory of Mexico. They consist of marine sedimentary deposits associated with island arcs that were developed in the western margins of Gondwana-Laurussia during their approach and pre-integration in the supercontinent Pangea. In this context, faunas found in these Permian localities, including brachiopods, indicate the modification of biogeographical provinces of shallow water when the major continents were approaching to each other. In this work, the species of brachiopods that have been found in localities of the states of Hidalgo and Guerrero are listed, and the changes in their biogeographic relationships are discussed.

The brachiopods *Krotovia* sp., *Dasysaria* sp., *Derbyoides* cf. *D. dunbari*, *Neospirifer* cf. *N. amphigyus*, *Neospirifer* sp., *Spiriferellina tricosa* and ?*Holosia* sp. have been refered for Tuzancoa Formation, which crops up in the south of the village of Otlamalacatla, in the state of Hidalgo, central México, (Sour-Tovar et al., 2005). These brachiopods are found together with trilobites (op. cit.), five species of gastropods and 20 of bivalves (Quiroz-Barroso et al., 2012), as well as isolated plates of crinoids. The fossiliferous rocks represent turbiditic and calcareous debris flows deposited within a volcanic sequence linked to a subma-

rine magmatic arc, geological structure product of the collision of the two great continents (Rosales-Lagarde et al., 2005; Centeno-García et al., 2005). The identified species are characteristic of the Kungurian (Late Cisuralian,) and have a strong affinity with tropical and subtropical faunas of the Grandian Province (Yancey, 1975) that occupied the area of New Mexico-Texas-Coahuila during the Early Permian (Sour-Tovar et al., 2005; Rosales-Lagarde et al., 2005; Quiroz-Barroso et al, 2012).

Around the town of Olinalá, in the state of Guerrero, southern Mexico, outcrops of the Olinalá Formation represent a mixed sedimentary succession of carbonates and terrigenous deposited in a platform in tropical latitudes (Juárez-Arriaga, 2006; Sour-Tovar et al., 2009). Conulariids, gastropods, bivalves, nautiloids, ammonites, plates of crinoids, other invertebrates, and plant remains are abundant in the terrigenous facies. Among the invertebrates that has been recognized are the brachiopods *Orbiculoidea ovalis*, *Thamnosia depressa*, *Spiriferellina cristata*, *Cancrinella rugosa*, *Leiorhynchoidea schucherti*, *Krotovia* sp., *Wellerella* sp., *Hustedia* sp., *Composita* sp., and *Costiferina* sp. (González-Arreola et al., 1994). There are also two species of the families Pugnacidae and Elythidae, representing two new genera, and one species that is tentatively assigned to the genus *Carteridina* (Sour-Tovar et al., 2009). The diversity of invertebrates studied so far, confirms the Middle Permian (Guadalupian) age of the Olinalá Formation and suggests a possible Roadian age for the level where fossils were found.

The genera and species of invertebrates from both localities have affinities with Lower-Middle Permian faunas of North America and particularly with faunas of the Cordilleran and Grandian Provinces, part of the Paleoecuatorial Realm (Shen

et al., 2009). A paleo-geographic map of the Earth, during the Early-Middle Permian, is displayed in Figure 1 (Modified from Guerrero-Sánchez and Quiroz-Barroso, 2013); in that map, the paleo-provinces proposed by Bambach (1990) and Yancey (1990) are shown and it is possible to locate the site where Olinalá Formation was deposited. If the systematic determination of *Carteridina* is confirmed, its presence in the Permian of Guerrero State, could be considered as a case of relict endemism. This same phenomenon is observed with the bivalve *Posidoniella*, also present in the Olinalá Formation, and like *Carteridina* previously only been referred to the Carboniferous. The explanation for this pattern may be the gradual closure of the ocean that occupied the Cordilleran and Grandian provinces and where the Permian localities of southern Mexico represents the last relic of that ocean in the Western margin of Gondwana- Laurussia.

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Redefining the Middle–Late Ordovician brachiopod *Plectorthis* from North America

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During the early Late Ordovician, eastern North America was being flooded due to a eustatic rise in sea level (Haq and Schutter 2008) and the downward flexure of the eastern margin caused by the Taconic orogeny (Coakley and Gurnis 1995). The resulting marine transgression flooded the continental margin and much of the continental interior, creating vast tropical epicontinental seas for colonization by shelly benthos. To study the faunal evolutionary response to the changing environment, a solid taxonomic foundation is needed for any paleoecological or paleobiogeographical analysis. Most of these studies rely on taxonomic data at the generic and specific levels, but recent and ongoing studies are revealing that taxonomy of several brachiopod genera can be further refined to more accurately reflect their evolution, ecology, and biogeography. This re-examination of the *Plectorthis* brachiopod genus will contribute to this effort.

Plectorthis Hall and Clarke, 1892 is known from rocks ranging from the Darriwilian to Katian, as part of a semi-cosmopolitan brachiopod fauna during the early Late Ordovician. The genus was most diverse during the early Katian, but disappeared completely by the end of the stage. Species of *Plectorthis* have been documented from North America, Scotland, Northern Ireland, Kazakhstan, Australia, China, and Russia. In North America, *Plectorthis* was part of the shelly benthos that initially colonized the carbonate platforms of Late Ordovician eastern North America. It was confined mostly to pericratonic settings and mostly absent from the inland epicontinental seas in equatorial and low tropical paleolatitudes. The genus is particularly common in the Cincinnati Arch region, but also occurs elsewhere in eastern North America.

Although widely reported, the type species, *Plectorthis plicatella* (Hall, 1847), has not been described in detail since the work of Foerste (1910). This has led to a variety of forms being placed in the genus with differing characteristics. The type species has simple costae, although other species with various branching multicostellae or fasciccostellae have been attributed to the genus. The outline of *Plectorthis* are generally subelliptical, but varies considerably intraspecifically in width and is of little use in taxon-

omy. Schuchert and Cooper (1932) described a typical *Plectorthis* as having a heart-shaped ventral muscle field with slender, sub-cresentic diductor scars, but some species assigned to this genus have a subtriangular diductor field with divergent, almost linear adductor scars. The presence of double rows of aditicules along rib crests have been previously documented in *Plectorthis punctata* (see Cooper 1956, pl. 84, fig. E35), but the taxonomic utility of this feature in the genus is yet unknown due to the poor preservation of many specimens.

The genus can be broadly subdivided into three clades. The first two clades resemble each other in outline and profile, and are defined based on ribbing patterns. The first clade is typified by the type species *P. plicatella* which has relatively simple costae that multiply once near the umbo, with secondary ribs sometimes developed near the anterior margin of larger specimens. A distinct pattern of double-column aditicules is present in some species of this group. The second clade is marked by the more complex ribbing pattern in *Plectorthis fissicosta*. Species of this clade have more complex fascicostellate and multicostellate ornamentation.

The third clade consists of a group of species that have a ventral muscle field different from that of the typical *Plectorthis*, as can be clearly seen in *Plectorthis ponderosa* (see Cooper 1956, pl. 83, fig. C32). These species should be reassigned to a different genus, as the ventral muscle field is generally considered to be relatively stable at the genus level in brachiopods. In addition, while these species possess ribs that superficially resemble the simple ribbing of the first clade typified by *P. plicatella*, the ribs occasionally branch at apparently random positions along the length of the shell. Species of this clade are less strongly ventribiconvex than the other two clades and seem to possess a more bulbous cardinal process than the simple ridge of other species. The musculature and cardinal process of this clade show a greater degree of similarity to some common forms of the Plaesiomyidae (e.g. *Plaesiomys*) than to the typical *Plectorthis*.

The objective of this study is to evaluate whether these clades can be used to further divide the *Plectorthis* genus into groups that better reflect the evolution of the genus and thus enable more accurate paleoecological and paleobiogeographical analysis of the Late Ordovician brachiopod fauna of both North America and globally. Measurements of specimens and figured specimens will supplement qualitative descriptions of the species already available in references. In addition, specimens are documented for the first time from the area near Lake Simcoe in Ontario, Canada.

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Palaeoecology and palaeobiogeographical significance of Silurian (Wenlock-Ludlow) brachiopods from Quidong, New South Wales, Australia

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Silurian rocks have long been recognised at Quidong, on the Delegate River east of the Snowy Mountains in far southeastern New South Wales, but the fauna is poorly known. The only fossils documented from the area are trilobites e.g. *Onycopyge liversidgei*, and rare graptolites. This preliminary report on the brachiopods from Quidong is based on an intensive study which is intended to provide detailed systematic descriptions of the entire rhynchonelliformean fauna.

The area lies on a southerly extension of the Canberra-Yass Shelf within the eastern Lachlan Orogen. During the Silurian, the Lachlan Orogen was divided into a series of elongate extensional basins separated by upraised blocks. The sequence was folded and faulted during the subsequent Tabberabberan and Kanimblan orogenies.

The Silurian succession unconformably overlies Ordovician deepwater sedimentary rocks of the Adaminaby Group, and commences with the unfossiliferous Tombong Formation, succeeded by the Merriangaah Siltstone containing graptolites of the late Llandovery *spiralis* Zone. Another unconformity separates these strata from the Quidong Limestone which is rich in corals, stromatoporoid sponges and algae, and yields conodonts that suggest a Wenlock age. Only a few brachiopods, including ribbed pentamerids (*Rhipidium* or *Kirkidium*), *Leptaena* and rare *Atrypoidea*, occur in the limestone. The transition to the overlying Delegate
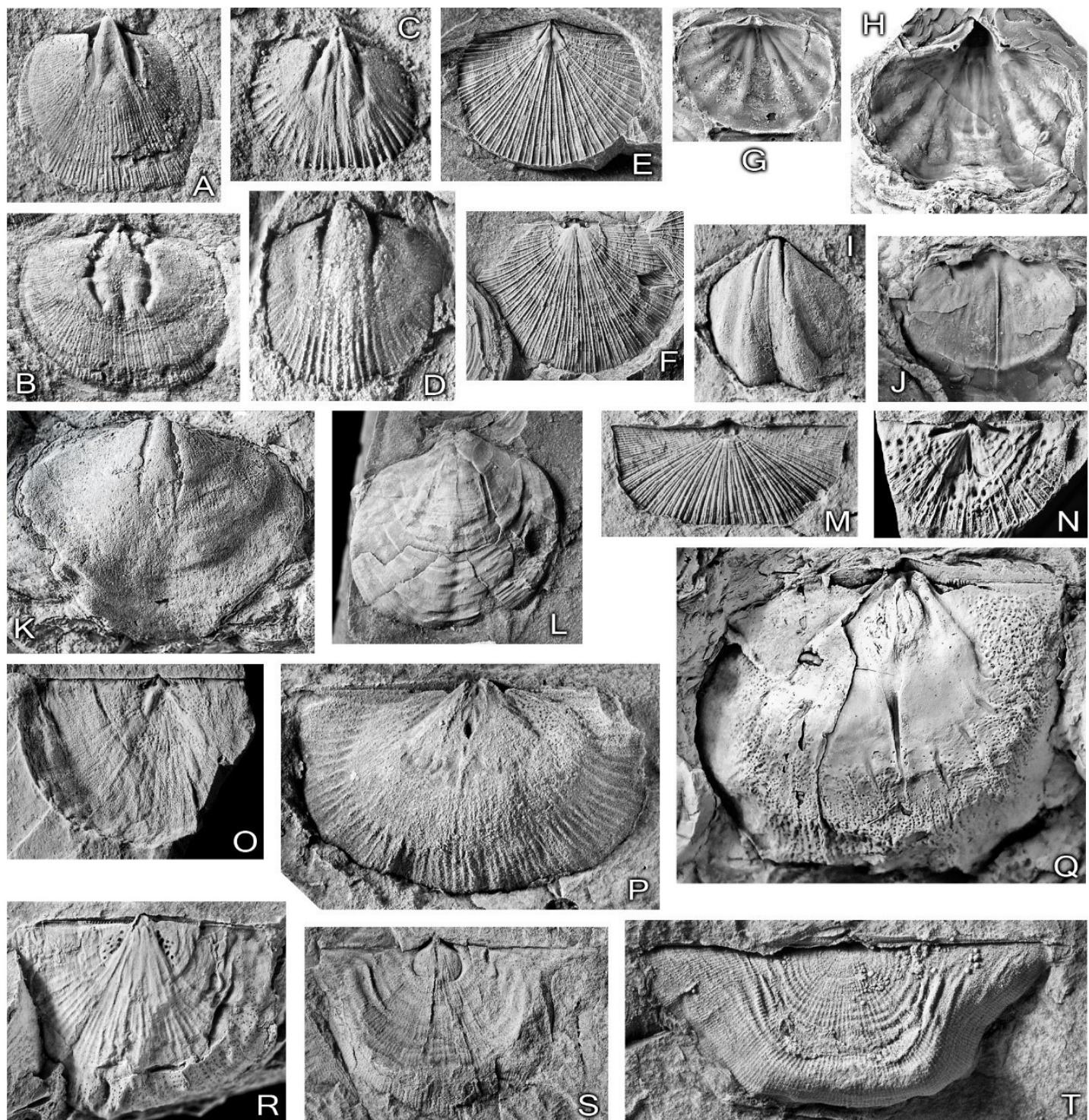
Fig. 1. A, B. *Isorthis* (*Arcualla*) sp., internal moulds of ventral and dorsal valves, X2. C, D. *Salopina mediocostata*, internal moulds of dorsal and ventral valves, X4. E, F. *Morinorhychus* sp., internal moulds of ventral and dorsal valves, X2. G, H. *Retziella* sp., latex casts from internal moulds of dorsal and ventral valves, X2. I, *Hedeina* sp., internal mould of ventral valve, X3. J, *Nucleospira* sp., latex cast from internal mould of dorsal valve, X2. K, *Ascanigypa* sp., internal mould of dorsal valve, X2. L, trimerelloid?, partly exfoliated ventral valve showing visceral field, X2. M, N. *Epelidoaegiria minuta*, exterior and interior moulds of dorsal valves, X4. O, P. *Mesopholidostrophia* cf. *bendeninensis*?, internal moulds of dorsal and ventral valves. Q, *Eopholidostrophia* (*Megapholidostrophia*) sp. nov., internal mould of ventral valve, X2. R, *Mesoleptostrophia* cf. *oepiki*, internal mould of ventral valve, X3. S, T. *Leptaena* sp., internal mould of ventral valve, and external mould of dorsal valve, X2. All specimens from Delegate River Mudstone, Quidong, southern New South Wales.

River Mudstone is gradational, passing from massive to bedded limestone into pyritic bioturbated mudstones dominated by small plectambonitacean brachiopods (*Epelidoaegiria*).

The majority of the brachiopods from Quidong are found in the Delegate River Mudstone. The fauna (representative examples of which are shown in Figure 1) is dominated by strophomenates, particularly *Mesoleptostrophia*, *Mesopholidostrophia*, *Leptaena* and *Epelidoaegiria* as well as *Eopholidostrophia (Megapholidostrophia)*. Also commonly present are *Isorthis* (*Arcualla*), *Salopina*, *Morinorhynchus*, *Nucleospira*, *Retziella* and *Howellella*, and less frequent *Ascanigypa*, *Atrypoidea* and *Atrypa*. Several of the species recognized are known also from the Homerian (late Wenlock) to earliest Gorstian (early Ludlow) strata of the Canberra and Yass districts to the north (Strusz 2010). Associated fossils include less common trilobites (an encrinurid and a scutelluid), bivalves and gastropods.

The depositional environment of the Delegate River Mudstone is one of slow quiet sedimentation, below storm base, probably in a sheltered embayment. There is a gradual increase in layers of fine to coarse siltstones and occasional sandy layers above the *Epelidoaegiria*-dominated mudstones, with a richer fauna in which the most common taxa are the larger strophomenates. This suggests a shallowing-upwards sequence, which progressively changed to communities characterised by *Leptaena*, leptostrophiids and eopholidostrophiids, then by the small spiriferide *Howellella*, and finally to a fauna including mainly *Ascanigypa* and *Atrypa*. These upper layers also show much greater variability in facies both vertically and horizontally; they include cross-bedded fine sandstones, lack pyrite, and towards the preserved top of the Silurian succession there is a recurrence of bedded limestone with stromatoporoids, all indicating a subtidal environment close to or above storm base.

The presence of new species of *Eopholidostrophia (Megapholidostrophia)* and *Retziella* raise interesting questions of palaeobiogeography and phylogeny. The former was recently described from the lower Llandovery of South China (Rong et al. 2013), which in the Silurian lay north of the equator west of Western Australia. *Retziella* is part of a distinctive Wenlock-Late Silurian fauna confined to the Silurian equatorial zone extending westward from Australia to the vicinity of North China and Tadzhikistan (Rong et al. 1995). A normal westward equatorial current pattern easily explains the distribution of *Retziella*, but the occurrence of *E. (Megapholidostrophia)* in the eastern Australian Wenlock (and early Llandovery of South China) is contrary to normal circulation, as most *Eopholidostrophia* are from the Lower Llandovery of Baltica, which then lay south of the equator. Is the Australian occurrence of the subgenus a result of parallel evolution from a pholidostrophiid ancestor, or was there slow distribution by way of inter-island gyres along the equator, counter to the general westward current direction?

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Response of brachiopod fauna to environmental change related to the Upper Kellwaser Event —a case study on a carbonate platform section in central Guangxi, China

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To explore the response of benthos to environmental changes related to the Upper Kellwaser Event near the Frasian-Famennian boundary, an integrated study of the conodont and brachiopod biostratigraphy, and carbon isotope chemostratigraphy is carried out in an isolated carbonate platform near Sian Village, Wuxuan County of central Guangxi Province, South China. The Upper Kellwaser Event (UKE) in this section is represented by a 1.2-m-thick dark gray thin-bedded micritic limestone (bed 3), which is bracketed between the conodont *linguiformis* Zone and Lower *triangularis* Zone. The UKE bed conformably overlies the white gray massive limestone of the Rongxian Formation, which contains abundant ctenoid shell-like structures (beds 1 and 2, measured down to about 6 m thick), suggesting the influence of fresh-water leaching at low sea level. No conodont is discovered from the ctenoid shell-like limestone below the UKE bed. A gradual change in conodont biofacies from the benthic *Icriodus-Polygnathus* assemblage to the pelagic *Palmatolepis* assemblage demonstrates a transgression since UKE. Only two brachiopod genera (*Cyrtospirifer* and *Hypothyridina*) are discovered from limestone below the UKE
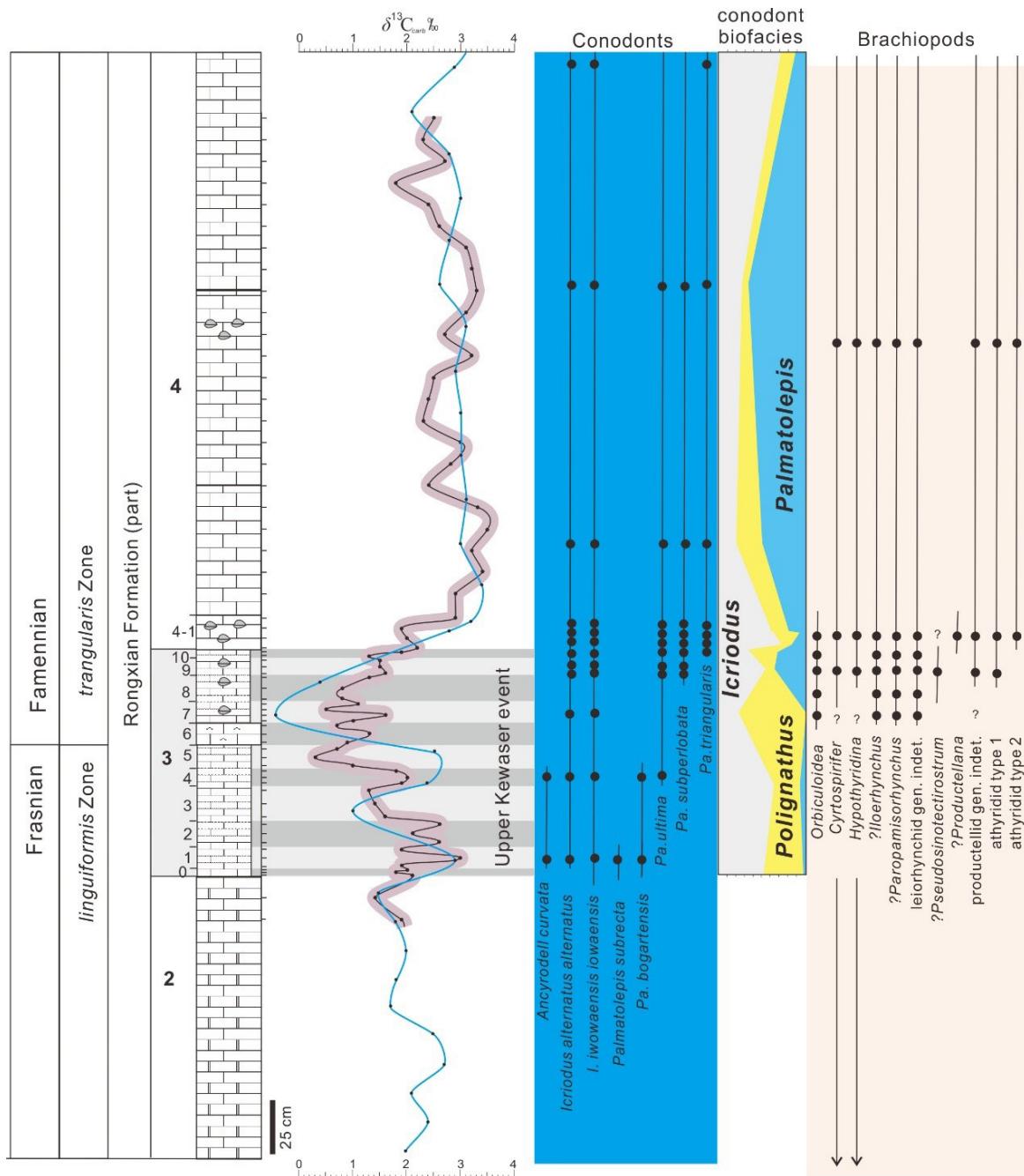
Fig. 1 Carbon isotpe excursion and distribution of conodonts and brachiopods across the Frasian-Famennian boundary at the Si'an Section, Wuxian, Guangxi, China

bed. These two brachiopods as well as other benthos disappear in the lower UKE bed (layers 0-6 of bed 3). Brachiopods reoccur in the upper part of the UKE bed (layers 7-10 of bed 3) and range up into the massive limestone of bed 4 (rich in certain levels as shelly limestone). At least, 11 brachiopod generic forms can be recognized, including *Cyrtospirifer* and *Hypothyridina* that occur below the UKE bed, *Orbiculoidea,* two productidines, four rhynchonellids and two athyridides. The brachiopod fauna is dominated by the rhynchonellids in abundance. Carbonate carbon isotope (δ^{13}C) exhibits a 1.5~2‰ negative excursion in the lower UKE bed, followed by a 2~3‰ positive excursion in the upper UKE bed. This δ^{13}C profile is different from that of the basinal

setting, which is characterized by a 2~2.5‰ positive shift within the UKE bed. Disappearance of brachiopods in the lower UKE bed is coincident with the negative δ^{13}C excursion, while reappearance of brachiopods in the upper UKE bed is associated with the positive excursion in δ^{13}C. This observation indicates that the brachiopod evolution and environmental perturbation are tightly coupled during UKE. Disappearance of brachiopod in the lower UKE bed (layer 1-6 of bed 3) may be attributed to the transgressive upwelling bringing ^{13}C-depleted anoxic bottom water into the carbonate platform, smothering brachiopod or other benthos. The recovery and diversification of brachiopod fauna since late UKE (from layer 7 of bed 3 to bed 4) may reflect the subsequent oceanic

oxidation that ameliorates benthic niches in carbonate platform. Finally, because there is no extinction in brachiopod fauna during UKE in the studied section, either Frasian-Famennian extinction of brachiopods took place before the UKE or brachiopods were not suffered during the Frasian-Famennian mass extinction.

Within- and inter-shell variations in carbon and oxygen isotope composition of modern brachiopods

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Carbon isotope ($\delta^{13}C$) and oxygen isotope ($\delta^{18}O$) composition of Rhynchonelliformea brachiopods (hereafter, "brachiopod") have been used as powerful tools for reconstructing $\delta^{13}C$ values of dissolved inorganic carbon (DIC) ($\delta^{13}C_{DIC}$) and seawater $\delta^{18}O$ ($\delta^{18}O_{SW}$)/temperature values throughout the Phanerozoic, especially in the Paleozoic. The common use of the isotopic composition of brachiopod shells can be ascribed to abundant occurrences of fossil brachiopods throughout the Phanerozoic, relatively low susceptibility of brachiopod shells to diagenetic alteration due to their mineralogy (low-magnesium calcite) and dense microstructure, and the assumed precipitation of shells in isotopic equilibrium with ambient seawater. Recent investigations of the $\delta^{13}C$ and $\delta^{18}O$ values of modern brachiopod shells, however, have shown that the shells were not necessarily precipitated in isotopic equilibrium with ambient seawater. Such partial or entire disequilibria during shell secretion limit the use of brachiopod-shell $\delta^{13}C$ and $\delta^{18}O$ values as paleoenvironmental proxies. Therefore, the appropriate selection of brachiopod taxa and shell portions whose $\delta^{13}C$ and $\delta^{18}O$ values identical or close to those of calcite precipitated in isotopic equilibrium with ambient seawater (equilibrium calcite) is required to for more precise paleoenvironmental reconstructions. However, limited studies have been conducted on within- and inter-shell variations in the $\delta^{13}C$ and $\delta^{18}O$ values based on high-resolution sampling. In this presentation, we report within- and inter-shell variations in the $\delta^{13}C$ and $\delta^{18}O$ values of samples from the outer and inner surfaces of the secondary shell layer of the subtropical water brachiopod *Basiliola lucida* collected around Okinawa-jima and of the cool-temperate water brachiopod *Terebratulina crossei* collected from Otsuchi Bay, northeastern Honshu, Japan. Our results clearly indicate that $\delta^{13}C$ values of brachiopod shells can be used as a reliable proxy of annual average $\delta^{13}C_{DIC}$ values with high accuracy and precision if appropriate shell portions are selected. On the other hand, great care should be taken to use $\delta^{18}O$ values as seawater temperature/$\delta^{18}O_{SW}$ proxies.

Immunocytochemical and ultrastructural peculiarities of the innervation of tentacles and the lophophore among brachiopods

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Organization of the nervous system is traditionally used for phylogenetic and comparative analyses that are very important to establish relationships between different taxa. The phylum Brachiopoda is a monophyletic group, which is characterized by unique body plan. All brachiopods have the lophophore: a specialized part of the mesosome, which bears tentacles and provides several important functions. Among brachiopods, there are six main types of the lophophore organization, however peculiarities of the lophophore function are very similar among brachiopods. The lophophore is also known in phoronids, whose body plan is considerably different from that of brachiopods. In spite of this difference, phoronids and brachiopods are regarded as the closest relatives, which form a united clade called Brachiozoa. At the same time, modern molecular data revealed that Brachiozoa does not exist. In order to resolve this contradiction, we have studied the innervation of the lophophore and tentacles in brachiopods of two different groups with two different types of the lophophore morphology and compared this data with innervation of the phoronid lophophore.

The lophophores of inarticulate brachiopod *Lingula anatina* Lamarck, 1801 and articulate brachiopod *Hemithyris psittacea* (Gmelin, 1790) are studied by method of immunocytochemistry, laser confocal microscopy, and transmission electron microscopy.

In two different brachiopods, the general morphology of the nervous system of the lophophore is similar. The lophohpore contains three brachial nerves, which extend along each brachium of the lophophore: the main, accessory, and lower brachial nerves. All these nerves exhibit serotonin-like, FMRFamide-like, and α-tubulin-like immunoreactivity. All brachial nerves are located intraepidermally and have stratified structure. Thus, the uppermost layer is composed by epidermal cells, which form long thin basal projection attached to the basal lamina. The second layer

is formed by perikarya of different types. These perikarya differ from each other in location, density of cytoplasm, density of karyoplasm, and characteristics of vesicles, which are the dominant organelles in the cytoplasm. Some perikarya, which are apparently sensory, contact the surface of the epidermis and bear a cilium. The third layer is formed by nerve projections. These neurites differ in diameter, orientation, and types of synaptic vesicles. Most of these neurites are 0.4 to 1 μm in diameter, are located near the basal membrane, and pass along the brachia of the lophophore. Some of neurites have the same diameter but pass in a cross direction and form an outer layer. In *L. anatina*, among the smaller neurites, there are one to three larger neurites, with diameters from 4 to 8 μm. The cytoplasm of these giant neurites is filled with numerous thick microtubules and small mitochondria. In both studied brachiopod species there are cross nerves, which extent in the connective tissue and connect the main and accessory brachial nerves. The cross nerves are not made visible by immunostaining. All of these cross nerves are organized in the same way. They consist of numerous neurites of different diameter. The large-diameter neurites are usually located on the periphery, whereas the small-diameter neurites occupy the central portion of the nerve. The larger neurites usually contain very electron-dense inclusions. Each cross nerve is surrounded by a thick layer of basal lamina. Each nerve is also composed of an envelope cell. The envelope cell is located on the periphery of the nerve and has long thin projections that surround the neurites. Cross nerves are often associated with outer envelope cells.

The outer tentacles are innervated by neurite bundles that extend from the lower and accessory brachial nerves. The lower brachial nerve gives rise to the abfrontal and latero-abfrontal neurites, which form a thick net along the abfrontal side of each outer tentacle. These neurites exhibit serotonin-like immunoreactivity and can also be recognized by staining against α-tubulin. The abfrontal neurite bundles exhibit weak FMRF-amide-like immunoreactivity. The accessory brachial nerve gives rise to the latero-frontal and mediofrontal neurite bundles of outer tentacles. The latero-frontal neurite bundles exhibit strong α-tubulin-like immunoreactivity. On the tip of each tentacle, the latero-frontal neurite bundles contact each other and form a loop. According to TEM data, the organization of the latero-frontal neurite bundles is complex and includes numerous neurites of different types and perikarya. The perikarya usually form a basal layer. The cytoplasm of the perikarya is filled with numerous electron-lucent synaptic vesicles. Above the perikarya, large neurites form a second layer. Each neurite bundle contains several hundred neurites. The large neurites, whose diameters may reach 1 μm, have electron-lucent cytoplasm that is filled with thick microtubules. Some of the large neurites contact the basal lamina, and their cytoplasm contains many synaptic vesicles with electron-lucent content. Small neurites form a third layer and are usually located above the large neurites. The frontal neurite bundles exhibit FMRFamide-like immunoreactivity and can also be recognized by staining against α-tubulin. According to TEM data, the frontal neurite bundles are represented by several compact aggregations of neurites. The inner tentacles are innervated by the accessory brachial nerve. The abfrontal side of each inner tentacle is innervated by the medioabfrontal neurite bundle, which exhibits serotonin-like,

FMRFamide-like, and α-tubulin-like immunoreactivity. These neurite bundles originate from the FMRFamide-like immunoreactive perikarya, which are grouped along the line between the two rows of tentacles. Two thick neurite bundles extend along the latero-abfrontal sides of the tentacles. They are organized in the same way as the latero-frontal neurite bundles in the outer tentacles and consist of many large neurites. The frontal side of the inner tentacles is innervated by seven to eight small neurite bundles, which exhibit serotonin-like and α-tubulin-like immunoreactivity. In both brachiopod species, tentacles of both rows contain subperitoneal neurites. They pass along the abfrontal and lateral sides of the tentacles and are located between the basal lamina and coelothelial cells. These neurites have a large diameter (about 1 μm), electron-lucent cytoplasm, and many thick microtubules. The subperitoneal neurites are abundant in tentacles of *Hemithyris psittacea*. In this species, subperitoneal neurites exhibit strong α-tubulin-like immunoreactivity. The subperitoneal neurites arise from cells, which are located at the base of each tentacle. The bodies of these cells can also be recognized with staining against α-tubulin.

According to our data, nerve elements of the brachiopod lophophore have a stratified organization, and the nerve elements form rows: the inner row consists of neurites, the middle row is formed by perikarya and the somata of glial cells, and the outer row is formed by epidermal cells. The same stratified structure of all nerve elements is described in dorsal ganglion, tentacular nerve ring, and trunk nerve plexus of phoronids. The ultrastructure of the main nerves is very similar in phoronids and brachiopods. The main brachial nerve of brachiopods and dorsal ganglion of phoronids contain several types of perikarya, which differ in sets of organelles, types of synaptic vesicles, and cytoplasm and karyoplasm density. The giant nerve fibers have never been described in brachiopods before and are reported here for the first time. The presence of giant nerve fibers is a characteristic element of the nervous system in phoronids and some other invertebrates. These fibers are usually used for fast conduction of the nerve impulses providing escape responses. In *L. anatina*, the giant fibers extend along each brachium and, apparently, contribute to fast conduction of the nerve impulses along lengthy brachia. According to our data, the epidermis of the thickest zones is innervated by special latero-frontal (in outer tentacles) and latero-abfrontal (in inner tentacles) neurite bundles. These are huge aggregations of neurites with large diameters. In the outer tentacles, these aggregations of neurites have a complex organization and include perikarya and a layer of small-diameter neurites. Interestingly, the large-diameter neurites do not exhibit neither serotonin-like or FMRFamide-like immunoreactivity but do react strongly to anti α–tubulin. The innervation of the latero-frontal zones of the outer tentacles seems very similar to the innervation of the latero-abfrontal zones of the inner tentacles, and the nervous system of the inner tentacles appears to mirror the nervous system of the outer tentacles. This similarity correlates with the density of cilia along the tentacles: along both rows, the areas along tentacles with the most cilia are innervated in the same way. Using one of the homology criteria about the special quality of the structure, we can infer that the latero-abfrontal zones of the inner tentacles and latero-frontal zones of the outer tentacles are homologous. Thus,

the frontal zone is very wide in inner tentacles but narrow in outer tentacles.

Data on innervation of the lophophore in brachiopods support the monophyly of the lophophorates

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Evolutionary relationships among member of the Lophophorata remain unclear. Traditionally, the Lophophorata included three phyla: Brachiopoda, Bryozoa or Ectoprocta, and Phoronida. All species in these phyla have a lophophore, which is a tentacle-bearing part of the mesosome. The lophophore is one of the main morphological characters used to suggest the unity of lophophorates. If the Lophophorata are truly monophyletic, we further suggest that the lophophore should have been inherited by all lophophorates from a common ancestor. If this were the case, the presence of common features of lophophore innervation in all lophophorates would help establish the homology of the lophophore and would also support the traditional view that the lophophorates represent a monophyletic group.

Using methods of immunocytochemistry and laser confocal microscopy, we have studied the innervation of the lophophore of inarticulate brachiopod *Lingula anatina* Lamarck, 1801.

The lophohpore of *L. anatina* contains three brachial nerves, which extend along each brachium of the lophophore: the main, accessory, and lower brachial nerves (Figure 1). The main brachial nerve gives rise to the cross neurite bundles, which connect the main and accessory brachial nerves. The accessory brachial nerve gives rise to the frontal, latero-frontal, and latero-abfrontal neurite bundles in tentacles of inner and outer rows. The lower brachial nerve gives rise to the abfrontal neurite bundles of the outer tentacles. The tentacles are innervated by accessory and lower brachial nerves. The accessory nerve gives rise to bundles of thin neurites, which pass between inner tentacles. At the tentacle base, these bundles form thick sites, where neurites subdivide into several groups (Figure 1). The first group consists of the frontal neurites of the inner tentacles. In each inner tentacle, frontal neurites arise from two bundles:

left and right (Figure 1). The second group consists of the frontal neurites of the outer tentacles. This group of thick bundles passes from the inner to the outer side of the lophophore and then passes along the deep frontal groove of the outer tentacle. The third group of neurites gives rise to the lateral neurite bundles (Figure 1). They pass between the two rows of tentacles. Here, each lateral neurite bundle has a T-like shape and forms two branches: one branch passes to the latero-frontal side of the outer tentacle, and the other passes to the latero-abfrontal side of the inner tentacle. The latero-frontal bundles of adjacent outer tentacles connect between tentacles and form short nerves, which are located between the two rows of tentacles along the longitudinal axis of the lophophore (Figure 1). In the middle of each short nerve, a group of FMRF-amide-reactive perikarya is located. Each group of perikarya gives rise to the medioabfrontal neurite bundle of the inner tentacles.
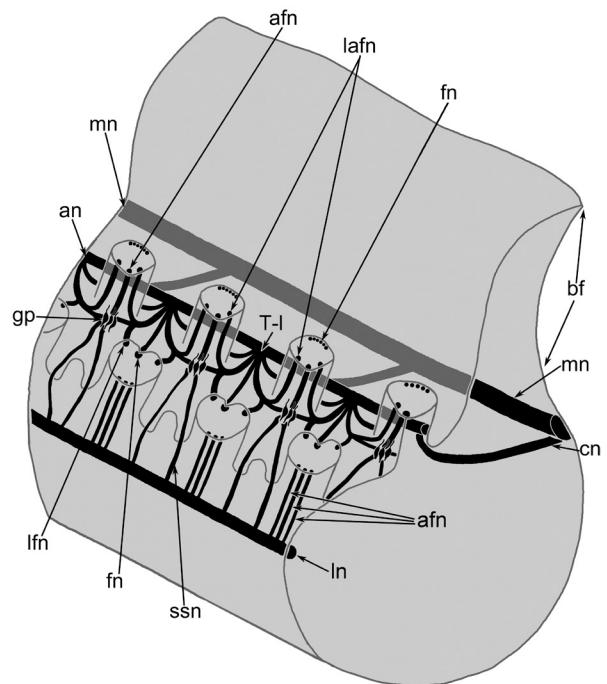
Fig. 1. The scheme of the innervation of the brachium in *Lingula anatina*. Nerve elements are shown in black. Nerve elements, which are screened by other structures, are shown in dark grey. Abbreviations: an – accessory brachial nerve, afn – abfrontal neurite bundle in tentacles, bf – brachial fold, cn – cross nerve, fn – frontal neurite bundle in tentacles, gp – group of FMRFamide-immunoreactive perikarya, lafn – latero-abfrontal neurite bundle in tentacles, lfn – latero-frontal neurite bundle in tentacles, ln – lower nerve, mn – main brachial nerve, ssn – neurite bundles, which extend between outer tentacles.

The lophophore of all lophophorates contains identical nerve elements. Their location with respect to other organs suggests that the main brachial nerve of *L. anatina*, the dorsal ganglion of phoronids, and the cerebral ganglion of bryozoans are likely homologous. The accessory brachial nerve of *L. anatina* can be regarded as a homolog of the minor nerve ring of
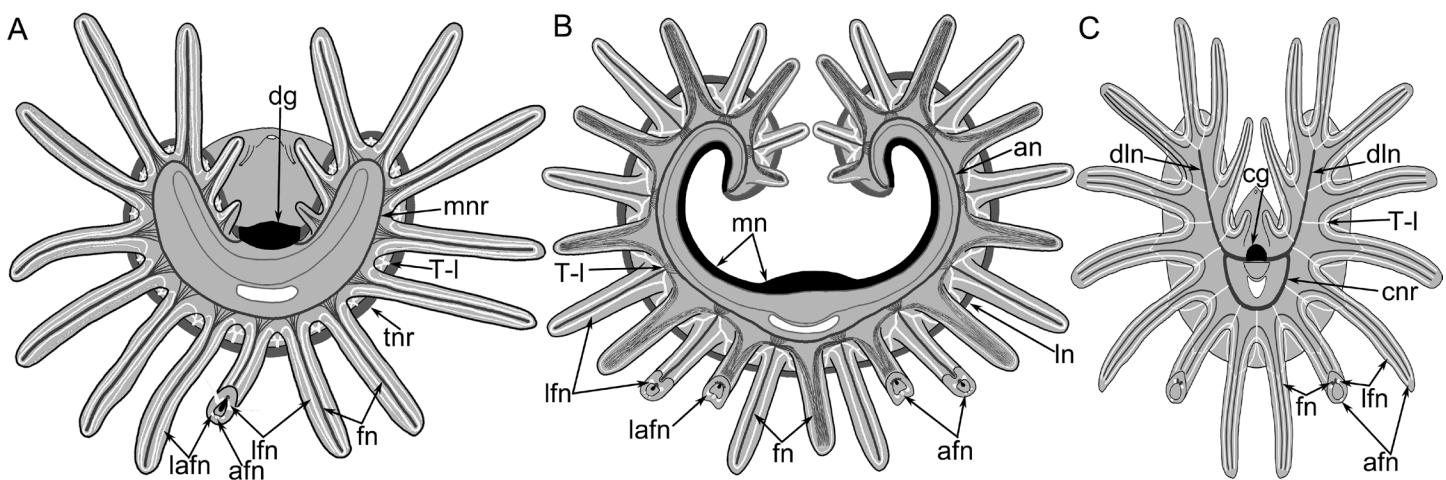
Figure 2. Schemes of lophophore innervation in the lophophorates. The lophophore is viewed from the top; the number of tentacles is reduced; the shape of the lophophore is simplified. (A) Phoronids. (B) Brachiopods. (C) Bryozoans. Abbreviations: afn – abfrontal neurite bundle in tentacle; cg – cerebral ganglion, cnr – circumoral nerve ring, dg – dorsal ganglion, dln – dorso-lateral nerves, fn – frontal neurite bundle in tentacles; lafn – latero-abfrontal neurite bundles in tentacle; lfn – latero-frontal neurite bundle in tentacle; mn – main brachial nerve, mnr – minor nerve ring, T-l – T-like branches of intertentacular neurite bundles, tnr – tentacular nerve ring.

phoronids and the circum-oral nerve ring of bryozoans. In *L. anatina* and phoronids, the lophophore has an outer nerve. This nerve extends along the abfrontal side of the tentacles at their bases (Figure 2A, B). In *L. anatina*, this nerve is represented by the lower brachial nerve. In phoronids, the outer lophophoral nerve corresponds to the tentacular nerve ring. Bryozoans lack an outer lophophoral nerve (Figure 2C). The absence of the outer nerve in bryozoans might also be attributed to a reduction due to the small body size. The innervation of tentacles exhibits the following features in all lophophorates: the presence of intertentacular neurite bundles, peculiarities of the innervation of the frontal side of the tentacles, and the presence of the sub-peritoneal neurites. These similarities correlate in part with the similar mechanism of filter feeding, which is common in the lophophorates and may in part reflect homology between tentacles of the lophophorates. We conclude that innervation of the lophophore and tentacles has a similar ground plan in the lophophorates. Our results support the homology of the lophophore and the monophyly of the Lophophorata.

Water above and mud below: life strategies of brachiopods from the middle Cambrian Burgess Shale

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In terms of species diversity and relative abundance, one of the most successful benthic organisms throughout the Palaeozoic marine realm are the brachiopods. Amidst the radiation of animal life in the Cambrian seas, these bivalved, lophophorates were one of the first animal phyla to emerge and rapidly diversify, their cosmopolitan distribution making the group a significant component of Cambrian ecosystems. Like many phyla however, the rarity of preserved soft-tissues has hindered discussions regarding their early evolution and also impeded ecological studies. Our understanding of the evolution and ecology of animals during this crucial Cambrian interval is largely driven by the examination of exquisitely preserved, soft-bodied organisms entombed in Cambrian Konservat Lagerstätten. Much of our knowledge regarding the early ecology and adaptive morphologies of the Brachiopoda has been provided by superb finds from the lower Cambrian Chengjiang Lagerstätte biota of Yunnan, China (Zhang

and Holmer, 2013). The lack of comparative data however, leaves a plethora of questions regarding the biodiversity, distribution, ecological interactions and temporal trajectory of brachiopod communities through the Cambrian.

Arguably one of the most famous Cambrian Lagerstätte deposits is the iconic Burgess Shale of western Canada (Caron and Jackson, 2008). Brachiopods, represent one of the most common sessile suspension feeders in the Burgess community, however the group has seen little attention since the original descriptions in the early 20th century (Walcott, 1912) despite the Burgess Shale Lagerstätte representing one of the few deposits where direct interaction of brachiopods with other organisms is preserved. The key to unveiling these early ecological relationships hinges on the documentation of exquisitely preserved brachiopods from Cambrian Lagerstätten, yet it is precisely in these deposits where brachiopods tend to be neglected.
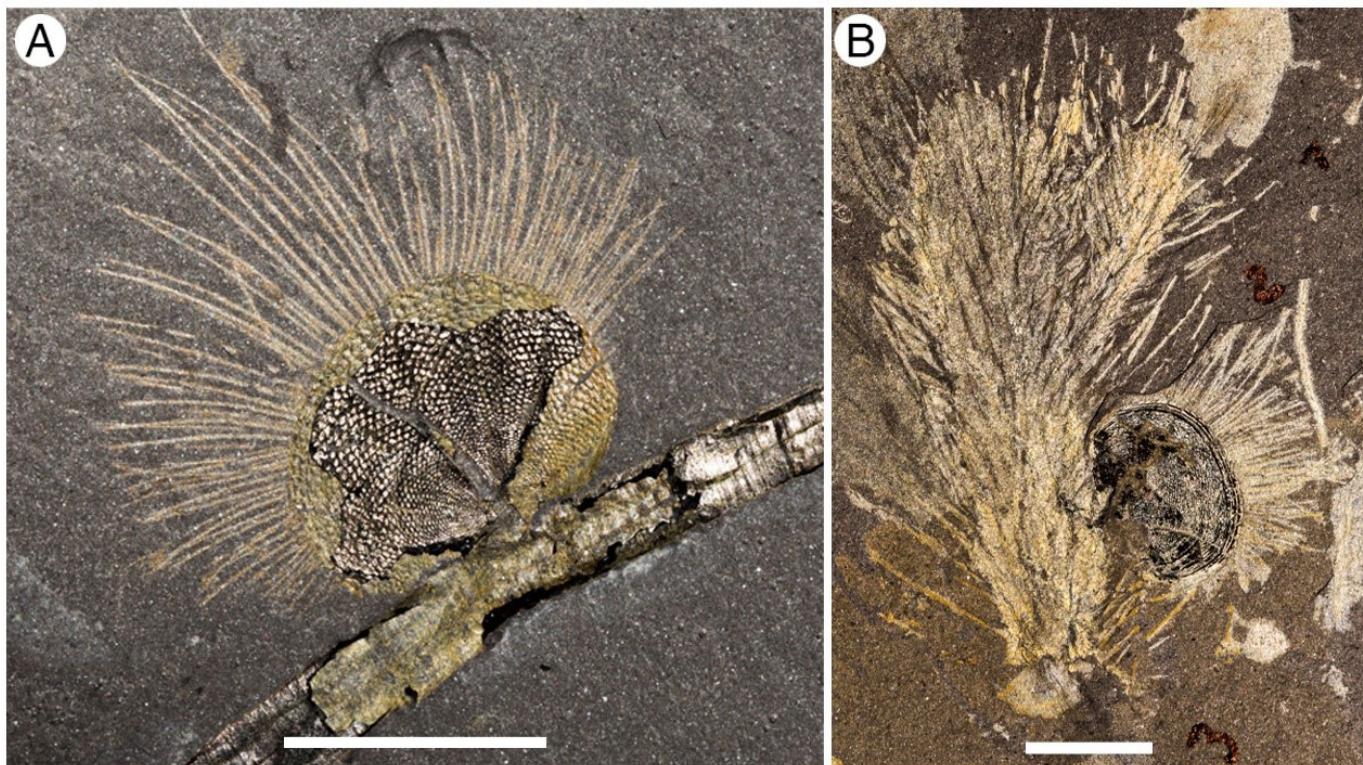
Here we provide the first detailed study on the ecology of the Burgess Shale brachiopod assemblage by analysing the composition of the community, the attachment and tiering strategies of individual species, interaction with other organisms and placing this in context of the Burgess Shale community (Fig. 1). The prominence of attached specimens stresses the importance of the availability of hard substrates for attachment, provided in this case predominately by sponges and skeletal debris. Brachiopod individuals showed a strong preference to the sponge *Pirania muricata* as a substrate choice, even in bed assemblages where *P. muricata* individuals are rare, indicating that brachiopod larvae potentially had some control over their area of settlement. The dependence on *P. muricata* for attachment appears to have been a shortcoming for some brachiopod species and in the younger Raymond Quarry community where *P. muricata* is absent only two species successfully adapted to settlement on alternative substrates.

Brachiopods in the Burgess Shale although not contributing greatly in the overall maximum tiering height of the community, are evenly distributed and demonstrate a clear subdivision and partitioning of vertical space within the brachiopod community. Individual species do not show a particular tiering preference regardless of the maximum height of the substrate indicating that brachiopods were not attempting to reach higher tiering levels, despite the presence of suitable attachment points higher in the water column. The abundance of brachiopods in low tiering levels in the Burgess Shale community implies that nutrient levels immediately above the sediment-water interface was adequate to support the coexistence of seven brachiopod species and variations in tiering height are directly related to the partitioning of available space for attachment and unimpeded growth of the organism, rather than nutrient partitioning. Comparison to the brachiopod community of the Chengjiang Biota confirm that brachiopods had already evolved a plethora of complex attachment strategies and modes of life by Cambrian Series 3, Stage 5 providing significant clues into to ecological significance of brachiopods in Cambrian ecosystems.

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Fig.1. *Micromitra burgessensis* from the middle Cambrian Burgess Shale attached to *Tubulella* (**A**) and *Pirania muricata* (**B**). Scale bars 5 mm.

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Productid brachiopods from the Carboniferous of Ixtaltepec Formation, Oaxaca, Southern Mexico

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In the Santiago Ixtaltepec area, in Oaxaca State, Southern México, twenty-four species of productid brachiopods have been found. The species belonging to the superfamilies Productoidea (*Semicostella* sp., *Antiquatonia* sp., ?*Keokukia* sp., *Dictyoclostus* sp., *Inflatia inflata*, *Inflatia* sp., *Reticulatia* cf. *huecoensis*, *Buxtonia websteri*, *Buxtonia* sp. and *Flexaria* sp.), Echinoconchoidea (*Echinoconchus zapoteco*, *Echinaria knighti*, *Karavankina*

Fig. 1. Shows the stratigraphic sequence in the region of Santiago Ixtaltepec and the stratigraphic distribution of each of the 24 species of productids that have been found in the Ixtaltepec Formation.

cf. *fasciata*, *Echinoconchella elegans*), Linoproductoidea (*Linoproductus* cf. *prattenianus*, *Linoproductus platyumbonus*, *Linoproductus* sp., *Marginovatia minor*, *Marginovatia aureocollis*, *Marginovatia* cf. *pumila*, *Cancrinella nunduva*, *Ovatia muralis* and *Nuanducosia sulcata*) and Aulostegoidea (?*Sinuatella* sp.). The fauna in general, including other taxa of invertebrates, has affinities with several Carboniferous associations described for the central-eastern United States territory, however the discovery of two new genera, *Nuanducosia (Torres-Martínez and Sour-Tovar, 2012),* and a genus of Productidae, and new eigth species of productids, *Echinoconchus zapoteco, Cancrinella nunduva, Nuanducosia sulcata (Torres-Martínez and Sour-Tovar, 2012),* one species of Productidae*, Dictyoclostus* sp., *Inflatia* sp., *Buxtonia* sp. and *Flexaria* sp., which are described the first time, allows establishes the presence of a moderate percentage of endemism in Oaxacan rocks. The specimens were collected in seven stratigraphic levels of Ixtaltepec Formation; the presence of *Semicostella* sp., *Inflatia inflata*, *Marginovatia minor* and *Ovatia muralis* in basal strata, units 1-3 of the formation, indicate a Chesterian (Mississippian) age. *Reticulatia* cf. *huecoensis*, *Buxtonia websteri*, *Echinaria knighti*, *Karavankina* cf. *fasciata*, *Linoproductus* cf. *prattenianus*, *L. platyumbonus*, *Marginovatia aureocollis* and *M.* cf. *pumila* were found in Units since 5 to 8 and their finding confirm the Pennsylvanian (Morrowan-Desmoinesian) age for upper strata of Ixtaltepec Formation.

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How did bivalve take over brachiopod's governorship over the Permian-Triassic transition? An old question with new insights

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One of the most pronounced biotic turnover marking life evolution over the Permian-Triassic (P-Tr) transition is the phyletic switch from brachiopods (mainly rhynchonelliforms) to bivalves in marine communities. Growing evidence shows that the P-Tr mass extinction may have precipitated the governorship changeover in marine ecosystems between these two clades. Previously, most authors attempted to answer the "brachiopod-bivalve switch (BBS) question" by comparing these two clades in terms of functional ecology and physiologic advantage and disadvantage to adapt the stressed environments. More recently, Fraiser and Bottjer (2007) quantitatively assessed the bivalve ecologic takeover and concluded that, as an ecological dominant, bivalve replaced brachiopod at the P-Tr boundary. Based on detailed community ecologic analysis from South China, Chen et al. (2010) further bracketed the BBS to the 60 ka after the P-Tr mass extinction (PTME). These authors also detected the BBS started from shallow to deep habitats. The updated global paleobiology database enables us to evaluate the climatic and environmental selectivities of the BBS over the P-Tr transition at global context. Here, we present quantitatively analytical results of latitudinal diversity gradients and environmental selectivity of global brachiopods and bivalves from the Changhsingian to Anisian.

Prior to the P-Tr extinction, both brachiopods and bivalves appear distinct latitudinal gradients of biodiversities in specific, generic and familial levels in northern hemisphere. In southern hemisphere the highest diversities of both clades occurred in moderate zone. Brachiopods are more diverse than bivalves, usually 2-3 times as the latter clade, in almost all latitude zones except for the north high latitudes in which bivalves are slightly more diverse than brachiopods. After the PTME, bivalve diversity appears a distinct latitudinal gradient in both north and south hemispheres, while brachiopod's latitudinal gradients of diversities only occurred in northern hemisphere in generic and familial levels. However, the post-extinction brachiopods and bivalves behaved differently in each latitudinal zone. Brachiopods suffered major depletions of diversity in all latitude zones. In particular, this clade underwent a loss of 80-90% in specific and generic levels in several important habitats such as northern tropic and moderate zones, in which brachiopods proliferated prior to the PTME. Brachiopods' depauperation contrasts markedly with their competitors: bivalves, which increased significantly in diversity in most zones except for the north tropical, north high latitudes, and south moderate latitudes in which bivalves experienced a minor loss in all levels of taxa. However, brachiopod/bivalve ratios changed to 1/2 to 1/14 in all climatic zones, indicating bivalves took over brachiopods' governorship in all climatic zones.

In Olenekian brachiopods continued to decrease in biodiversity in all climate zones. In contrast, bivalves underwent a minor to moderate increase in various latitude zones. During ecosystem recovery in Anisian (Chen and Benton, 2012), most bivalves migrated to north tropic zone in which this clade increased about 120% in specific richness. Brachiopods diversified in all latitude zones and particularly proliferated in tropic zones in which brachiopod species increased from 18 in Olenekian to 155, surging 760%. Brachiopod/bivalve ratios also increased to 1:2 to ~1:1 in north tropic to moderate zones. In contrast, the same ratios became 4:1 to 5:2 in other zones, showing that faunal composition pattern turned back to the Changhsingian.

Environmental settings ranging from nearshore, carbonate platform/ramp, reefs, clastic shallow sea, offshore, to shelf basin are selected to evaluate the SSB over the P-Tr transition. Most brachiopods inhabited carbonate platform/ramp and clastic shallow sea in Changhsingian, when bivalves mostly lived in clastic shallow sea and nearshore settings. Brachiopods are much more diverse than bivalves in all niches. In particular, brachiopods are nearly right times than bivalves in specific level in carbonate plat-

form/ramp. After the PTME, brachiopods suffered major loses in all types of niches, while bivalves experienced a pronounced increase and a minor decrease in specific diversity in offshore and carbonate platform/ramp settings, respectively, although this clade also suffered a moderate loss in diversity in other niches. However, bivalves became much more diverse than brachiopods in all types of environments except for reefs in which both clade became extinct. Brachiopods continued to decrease in diversity in all environments during the Olenekian. Bivalves increased significantly in biodiversity in both carbonate platform/ramp and clastic shallow sea settings in that time. Bivalves are much more diverse than brachiopods in all niches during the same time interval. During the Anisian bivalves continued to diversify in both carbonate platform/ramp and clastic shallow sea settings, particularly increasing >100% in species diversity in the latter niche. In comparison, brachiopods increased significantly in biodiversity in all niches. In particular, brachiopods increased from 25 species in Olenekian to 161 species in Anisian, surging >500%. Bivalves are more diverse than brachiopods in most niches during the Anisian except for in offshore where brachiopods are much diverse than bivalves.

In a word, bivalve's invasion to the brachiopod-dominated communities in the tropic and moderate latitudes in both hemispheres, and nearshore, carbonate platform/ramp, and clastic shallow sea settings during the P-Tr mass extinction. Bivalve's bloom incorporating with the contemporaneous losses of brachiopods continued through the entire Early Triassic. Brachiopods diversified in all environmental settings and all climatic zones, while bivalves mostly proliferated in both carbonate platform/ramp and clastic shallow sea settings in northern tropic zone during the Anisian. Although bivalves are still numerically more than brachiopods in most environmental settings and climate zones during the Anisian, brachiopods took over the governorship in southern moderate and high latitudes as well as, at least, offshore setting in the same time.

New observations on the most mineralized brachiopod *Diandongia* from the Chengjiang Lagerstätte (Cambrian, Stage 3) of eastern Yunnan, China

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Diandongia Rong, 1974 is the most thick-shelled and strongly

mineralized of all the brachiopods that have been recorded from the base to the topmost of the Yu'anshan Formation. The well-preserved and abundant material of *Diandongia* from Chengjiang includes preserved pedicles and mantle canals. Detailed internal and external shell morphologies of the type species *Diandongia pista* Rong 1974 is described for the first time based on BSEM and SEM observations. A neotype is selected among the specimens of *D. pista* from the type locality in eastern Yunnan. The shell shape, pseudointerareas and pustulose ornamentation of *Diandongia* are most similar to that of the Botsfordiidae. In particular, many species of *Botsfordia* are provided with a *Diandongia*-like rhombic pattern of pustules in the juvenile apical region only. The dorsal visceral field forms a narrow, elevated, three-lobed platform, which is similar to that of *Edreja* Koneva, from the Cambrian (Stage 5) of Kazakhstan; however, the notion that *Diandongia* is a junior synonym of *Edreja* can be rejected, as the species from Kazakhstan clearly lacks pustulose ornamentation. Moreover, *Diandongia* differs from the Botsfordiidae in the apparent lack of apical tubercles in the ventral and dorsal valves. The most unusual aspect of *Diandongia* is that the terminal branches of the mantle canals are directed peripherally only. This type of vascular pattern was previously known only from craniiform and rhynchonelliform brachiopods, indicating that that the earliest brachiopods that appeared during the Cambrian explosion interval have a previously unsuspected wide range of unusual morphological features.

A global review on *Neochonetes* and *Tethyochonetes* (Brachiopoda) in late Palaeozoic and early Mesozoic: Palaeobiogeographical distributions, sedimentary facies and size changes

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Analysis of world-wide data of the two resemblant genera *Neochonetes* and *Tethyochonetes* (Brachiopoda) from the Carboniferous to the Early Triassic provides insights into the palaeoenvironments and the biotic response to palaeoenvironmental changes. That the larger or smaller body size of *Neochonetes* does not correspond to a certain lithfacies (such as clastic-rock facies

or carbonate-rock facies) from the Carboniferous to the Permian indicates that the body size changes of *Neochonetes* were not controlled by the substrate. The body size of *Neochonetes* decreased in the Middle Permian and increased in the Wuchiapingian (early Late Permian), which is inferred to respectively link to the temperature rising in the Middle Permian and the transgression in the early Late Permian. Comparison of the occurrence frequency of *Neochonetes* and *Tethyochonetes* in three different facies (shallow-water clastic-rock facies and carbonate-rock facies and deep-water siliceous-rock facies) demonstrates that both genera occurred more commonly in the shallow-water facies, and in the deep-water facies *Tethyochonetes* dominates and has a larger average size, which means that *Tethyochonetes* could perform better in deep-water environments than *Neochonetes*. More interestingly, *Tethyochonetes* occurred more frequently in the Early Triassic than *Neochonetes* did, suggesting *Tethyochonetes* coping with the end-Permian crisis stress better and surviving more during the Early Triassic.

A new sample processing protocol: an important update for procuring reliable ree signatures

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Cleaning of brachiopod shells is a fundamental step that should be conducted with great care and attention to detail prior to processing their rare earth element (REE) contents. Without cleaning, the concentrations would represent the REE compositions not only of the shells calcitic structure but also of lattice bound oxides, detritus, particulates and organic remnants. Developing a sensitive and precise analytical protocol is of utmost importance required for isolating contaminants on biogenic and abiogenic carbonates in order to acquire a robust REE signal that enhances our confidence in oceanographic applications. To achieve this goal, 26 shell fragments separated from recently dead *Liothyrella neozelanica* shells, recovered from the deep water's of the southwest Pacific, north of New Zealand, were extensively washed and rinsed with distilled water. Five parts did not receive any further cleaning; protocol – 1 (P-1). A set of four parts was physically cleaned using a sharp stainless-steel blade (P-2). Another set of four parts was immersed in 2.5 % hydrogen peroxide (H_2O_2) for three continuous days (P-3). A further set of four parts was physically cleaned then dropped into 10% hydrochloric acid (HCl) until the fragments were deemed clean (P-4). The last nine parts were processed using all cleaning protocols: water washed, physically cleaned, H_2O_2 immersed, and then HCl leached (P-5).

Attached detritus and nano-particulates adsorbed on the calcitic structure of brachiopod shells besides the organic tissue, proteinaceous periostracum (Carpenter and Lohmann, 1995) may lead to elevated ΣREE, anomalous Ce anomaly (Fig. 1A) and elevated Mn, Fe (Fig. 2A) and U concentrations as documented by the P-1 set. Physical cleaning removes mainly the adsorptive nano-particulates and the periostracum. This protocol leads to depleted ΣREE and lower Mn, Fe, and U concentrations but with a slight Ce anomaly: set P-2. Hydrogen peroxide eliminates primarily the organic tissue; however it requires physical cleaning to remove the periostracum or the nano-particulates, which leads to partial depletion in the Ce anomaly: set P-3. Physical cleaning followed by chemical cleaning removes adsorptive particulates, organic remnants, periostracum and the primary layer. This protocol is reflected in the drastic reductions of the ΣREE, Mn, Fe, U concentrations and 'normal' Ce anomalies in the P-4 and P-5 sets (Figs. 1A, 2A).

Protocol P-4 was applied to Ordovician, Silurian, Pennsylvanian and Permian brachiopods and their enclosing lime matrix collected from Canada, USA and China to test for the reliability of REEs in fossil and Deep-Time carbonates. The immersion in H_2O_2 was omitted since no organic tissue was documented in any fossil samples. The fossil shells display ΣREEs, Mn, Fe, U concentrations and Ce anomalies comparable to their modern counterparts, while the lime matrixes are slightly to extensively enriched (Figs. 1B& 2B). This unequivocally documents the veracity of the processing protocols and if we expect, want reliable REEs, the need for its rigorous application to fossil material such as brachiopods, conodonts, corals, molluscs, foraminiferas and whole rock.

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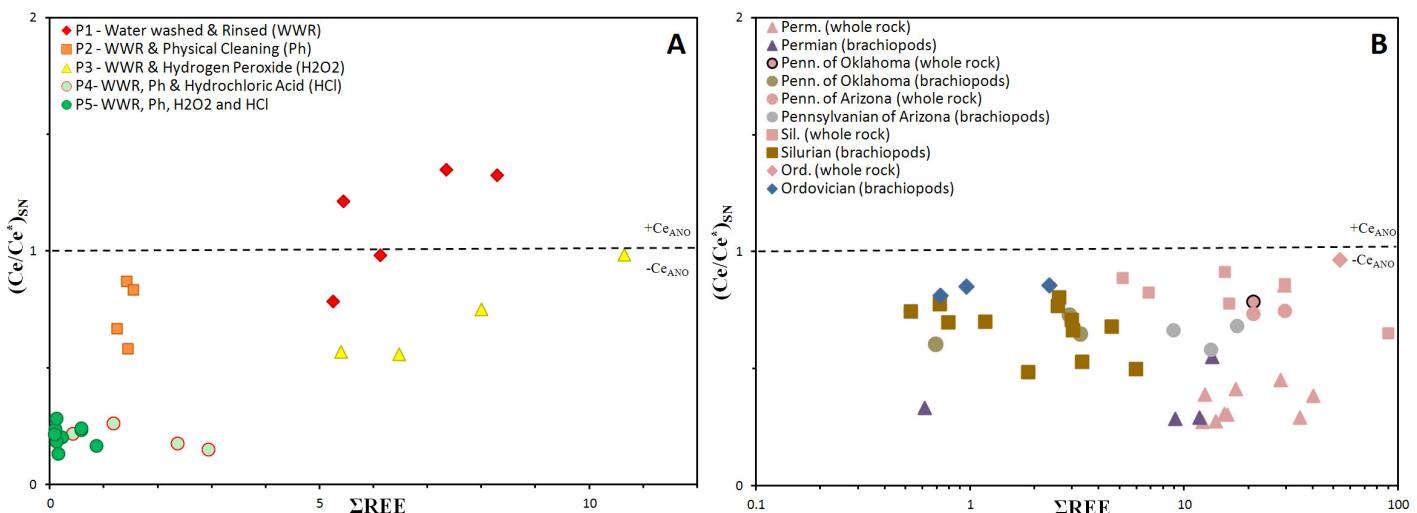
Fig. 1: Ce anomaly $(Ce/Ce^*)_{SN}$ - ΣREE evaluation of the different cleaning protocols conducted with a modern brachiopod shell (A) and on Ordovician, Silurian, Pennsylvanian and Permian brachiopods and their whole rock.
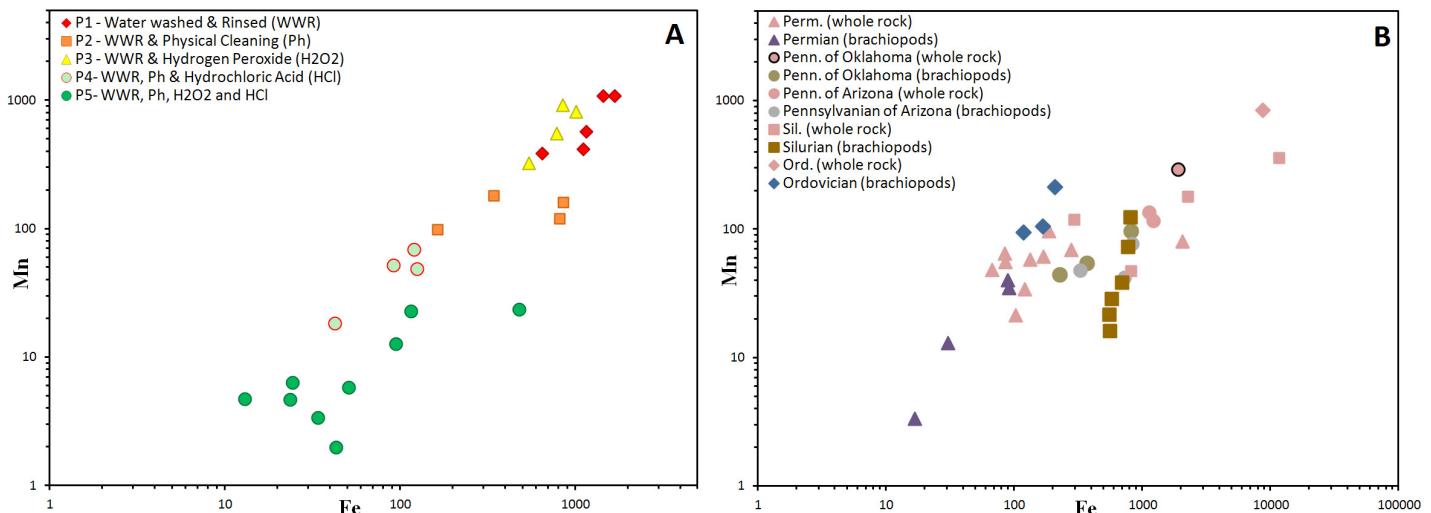

Fig. 2: Distribution of Mn and Fe contents with the different cleaning protocols of the modern brachiopod shell (A) and in their Paleozoic counterparts and enclosing whole rock (B).

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Rare earth elements of modern shelf and deep-water articulated brachiopods: evaluation of seawater masses

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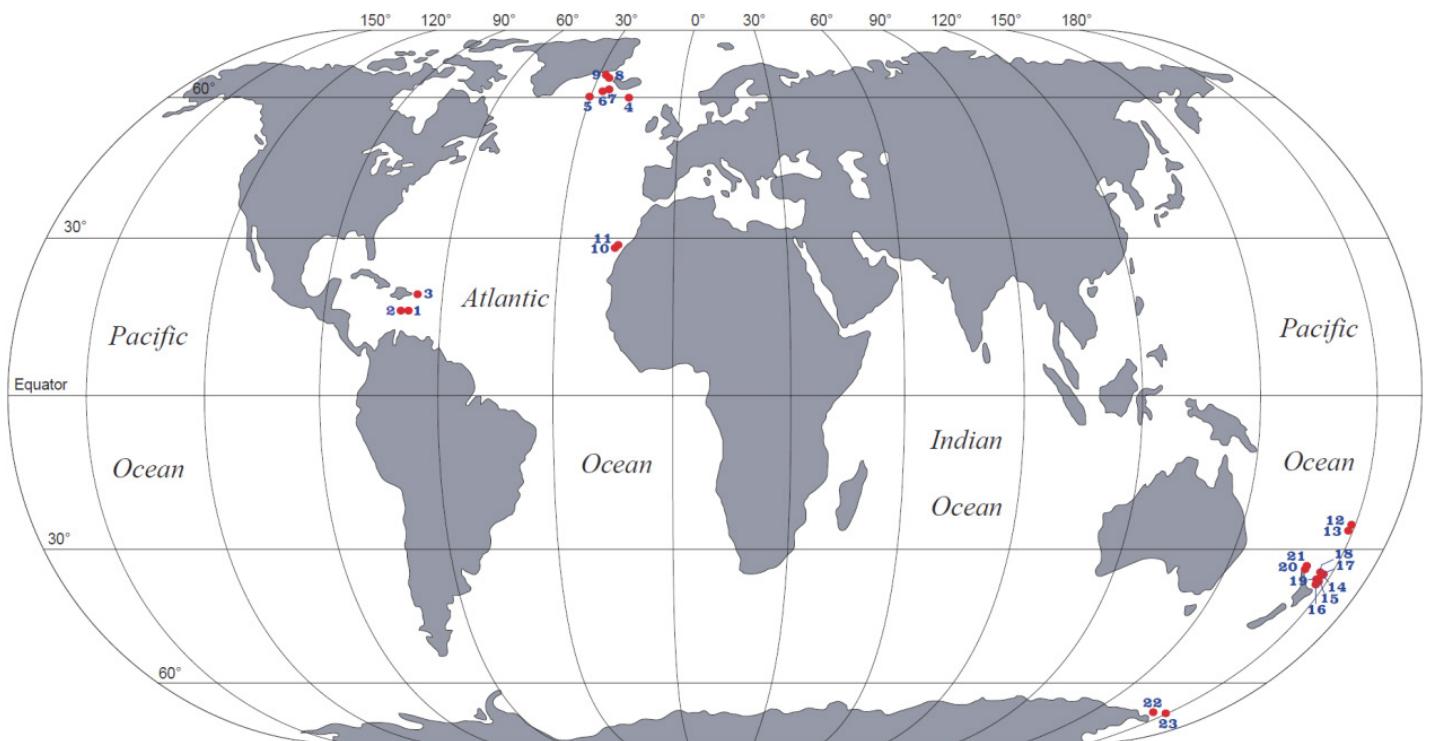
Fig. 1: Geographic distribution of the shelf and deep-water collection stations of the investigated brachiopod archives.

Table 1: Location, setting and depth of the shelf and deep-water stations and brachiopod taxonomy.

	Station	Depth (m)	Bathymetry	Order	Taxon
CARIBBEAN SEA					
VENEZUELA					
Venezuela Basin	1	3986	Deep Sea	*Terebratulida*	*Chlidonophora incerta*
	2	3998			
US VIRGIN ISLANDS					
Vigin Islands Basin	3	3940	"	"	"
NORTH ATLANTIC OCEAN					
ICELAND					
Iceland Basin	4	2567.7-2568.5	"	"	*Waldheimia cranium*
	5	2504.7-2531.8	"	"	"
Irminger Basin	6	698.1-678.5	Continental shelf	"	"
	7	724.4-704.9			
Denmark Strait	8	742.5-603.1	"	"	"
	9	696.9-706.4			
CANARY ISLANDS					
Continental slope of northwest Africa	10	1265	Deep Sea	"	*Dallina septigera*
	11				*Hispanirhynchia cornea*
SOUTHWEST PACIFIC OCEAN					
TONGA					
Lau Arc (Tonga-1)	12	589	Lau Arc	"	*Basiliola beecheri*
Colville Arc (Tonga-2)	13	660	Colville Arc	*Terebratulida*	*Dallina sp.*
NEW ZEALAND					
	14	1244	Thomson seamount	"	*Stenosarina crosnieri*
Kermadec Arc (New Zealand-1)	15	1460	Clark Seamount, south cone	"	*Dallina triangulari, Stenosarina crosnieri*
	16	1583	Clark Seamount south flank	"	*Dallina triangularis*
	17	1740	Brothers Seamount West	"	*Goniobrochus ewingi*
Havre Trough (New Zealand-2)	18	1172-1115	Seamount west of Volcano L	"	*Liothyrella neozelanica*
	19	1520	Seamount west of Rumble II West	"	*Goniobrochus ewingi*
Northland Plateau (New Zealand-3)	20	1293	Seamount #441 "Ballance Seamount"	*Rynchonellida* *Terebratulida*	*Basiliola pompholyx* *Stenosarina sp.*
	21	1583	Unnamed volcanic peak	"	*Abyssothyris wyvillei*
SOUTHERN OCEAN					
ANTARCTICA					
Balleny Spreading Corridor	22	547	Northeastern knoll of Admiralty seamount	"	*Magellania fragilis*
	23	1130	Seamount close to Scott Island	"	*Liothyrella sp.*

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Modern Rhynchonellids and Terebratulids, obtained from water depths below the neritic zone (>500m) at 23 stations in the Caribbean Sea, North Atlantic, South Pacific and Southern Oceans, were investigated for their rare earth element (REE) contents (Fig. 1, Table 1). The ΣREE of shelf (500-1000 m) or deep-water (>1000 m) brachiopod populations do not vary significantly between oceans/seas irrespective of water mass origins or influences by major currents.
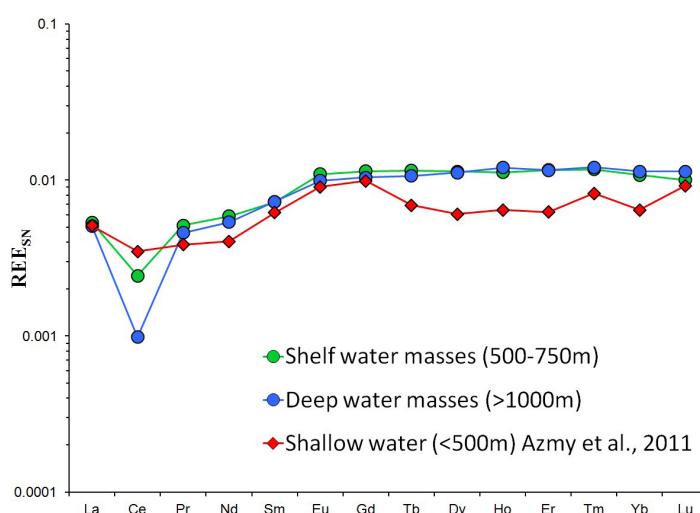
Fig. 2. Mean REE_{SN} patterns of the shelf and deep-water masses revealed by articulated brachiopods, and the REE_{SN} pattern of shallow water articulated brachiopods (<500m) of Azmy et al. (2011).

Four brachiopod populations from the shelfs of the Irminger Basin and Denmark Strait (North Atlantic) and from the Lau and Colville Arcs (South Pacific) display a mean REE_{SN} pattern of gradual enrichment with increasing atomic number punctuated by negative Ce excursions (Fig. 2). In contrast to the four above, the population from the Ross Sea (Southern Ocean) is relatively depleted in ΣREE reflecting local sea ice formation and conse-

quent down-flow of saline water. Although similar in pattern to the four shelf populations, the REE_{SN} trend of the five deep-water brachiopod populations from the Venezuela Basin (Caribbean Sea), Iceland Basin (North Atlantic) and from the Kermadec Arc, Havre Trough and Northland Plateau (South Pacific) is more pronounced as well as its Ce excursion is more prominent (Fig. 2). Furthermore two populations from the Irminger Basin and Canary Islands are influenced by local environmental parameters such as deep convection and the remineralization of bottom sediments enhanced by turbidity current flows, respectively. Overall, the REE patterns of the shelf and deep-water brachiopod populations are similar to that of open ocean seawater, but remarkably different to that of shallow water counterparts.

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A Katian (Late Ordovician) minute *Foliomena* fauna from the Sibumasu paleoplate

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Foliomena Havlíček, 1952 is a relatively small, thin and smooth shelled strophomenid brachiopod genus of mainly Late Ordovician age. The *Foliomena* fauna (Harper, 1979) represents a group of small or even minute brachiopods of various diversity in the Upper Ordovician of many paleoplates or terranes (see Cocks and Rong, 1988; Rong *et al*., 1999, Zhan and Jin, 2005, and references therein). It is the first successful invasion of brachiopods into the deep and deeper water benthic regime with the carrying forward of the Great Ordovician Biodiversification Event (GOBE) (Zhan *et al*., 2010). It was thought to be confined to Late Ordovician (Rong and Zhan, 1995; Harper *et al*., 1999) with its youngest occurrence from the Králův Dvůr Formation (Rawtheyan, upper Katian) of Sardinia, Italy (Villas *et al*., 2002). Recently, a reliable latest Middle Ordovician occurrence of the *Foliomena* fauna was reported by Liang *et al*. (2014) from the basal Miaopo Formation of Yichang area, western Hubei, central China where abundant graptolites belonging to the *Hustedograptus teretiusculus* Biozone (uppermost Darriwilian, Middle Ordovician) (Zhan and Jin, 2007; Chen *et al*., 2011) were found together with the brachiopods at the same locality and horizon.

The *Foliomena* fauna has been known from the Sibumasu paleoplate for a long time (e.g. Cocks and Rong, 1988; Fortey, 1997; Fortey and Cocks, 1998), but it has never been systematically described although it was mentioned from time to time at various localities in Myanmar, Thailand and western Yunnan, SW China (Rong *et al*., 1999; Zhou Zhiyi, personal comm., 2015). It was known to be poorly diversified with a few brachiopod genera or even just *Foliomena* itself (Rong and Zhan, 1996). In this paper, we systematically describe, for the first time, a very diversified but extremely small shelled *Foliomena* fauna (about 3 mm long and wide or even smaller) from the middle to upper parts of the Pupiao Formation (lower to middle Katian) of Baoshan, western Yunnan, SW China, which is the northern extension (present day orientation) of the Sibumasu paleoplate (Metcalfe, 1988, 1992). Systematically, it contains at least 20 brachiopod species and genera such as *Anisopleurella*, clitambonitid n. gen., *Ectenoglossa*, *Foliomena*, *Glyptorthis*, *Horderleyella*, *Hulterstadia*, *Kassinella* (*Kassinella*), *Laticrura*, *Nicoloidea*, *Nubialba*, *Paurorthis*, *Plectoglossa*, *Protoskenidioides*, *Protozyga*, *Sericoidea*, strophomenid n. gen., *Tropidothyris*, *Tyronella*, and xenambonitid gen. et sp. indet., amongst which *Foliomena* itself is the most abundant constituent. It is apparently of Ordovician brachiopod faunal affinity because Orthida and Strophomenida are two major groups of this fauna. *Sericoidea* was thought to be mutual exclusive with *Foliomena* in the deep water benthic regimes (Candela, 2011), and it is now known to co-occur with *Foliomena* in two paleoplates, Tarim (Zhan *et al*., 2014) and Sibumasu (this paper), both of which are characterized by very minute brachiopod shells. *Nubialba* is not common in the *Foliomena* fauna either. It was first reported to be a minority of the *Foliomena* fauna from the Pyle Mountain Argillite (middle Katian) of northeastern Maine, eastern United States (Neuman, 1994), and also known to occur in the Pagoda Formation (middle Sandbian to middle Katian) of several provinces in South China. Its occurrence in the Pupiao Formation (middle Katian) is its first record in the Sibumasu paleoplate. Moreover, some further discussions on the paleoecological and paleogeographical implications of the Pupiao *Foliomena* fauna are also made with the help of numerical analyses.

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Leiorhynchid brachiopods across the Middle-Upper Devonian boundary in South China

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Rhynchonellide brachiopods are an important group across the Middle-Upper Devonian boundary, of which leiorhynchids are predominant in the ambocoeliid-leiorhynchid Assemblage Zone at the boundary in South China. In this biozone, *Ypsilorhynchus* Sartenaer, 1970, *Leiorhynchus* Hall, 1860 and *Yocrarhynchus* Sartenaer, 1995 are three characteristic genera. However, lack of detailed morphological description and stratigraphic data in the very numerous so-called *Leiorhynchus* of South China has posed various difficulties to make clear their classification and stratigraphic distribution.

Four genera and five species of the Leiorhynchidae are described from three Givetian-Frasnian sections (Dabakou Section in Hunan, Longmenshan Section in Sichuan and Panxi Section in Yunnan). They are *Leiorhynchus kwangsiensis* Grabau, *Ypsilorhynchus globosus* (Wang *et al.*), "*Yp.*" *subellipticus* (Fang), *Yocrarhynchus orientalis* (Chen), *Calvinaria sinensis* (Fang), of which the former three genera of the Leiorhynchinae have been further investigated regarding their differences in external morphology and internal structure based on specimens in this study from South China (Fig. 1).

Ypsilorhynchus can be distinguished by numerous well-developed costae, which start from near the beak and cover the whole shell; dental plates converge and join ventrally, supported by the ventral septum to form an inverted Y-shaped spondylium; umbonal cavities are distinct. Costae of *Leiorhynchus* appear at mid-length of the shell, which are weak, especially on the flanks; dental plates are sub-parallel or convergent ventrally to merge into the valve floor directly; umbonal cavities are distinct; *Yocrarhynchus* is comparatively small; costae are few and coarse, which originate from the posterior; dental plates are strongly convergent ventrally and can meet the valve floor; umbonal cavities are narrow.

"*Yp.*" *subellipticus* (Fig. 1D) is similar to *Ypsilorhynchus* in external morphology, especially in the nature of costation, but possesses subparalell dental plates instead of the inverted Y-shaped spondylium as in true *Ypsilorhynchus*, therefore a question mark is added. *Nudirostra sinensis* Fang is also characterized by a pair of subparalell dental plates (Fig. 1e), however, its transversity outline suggests that it should be assigned to the genus *Calvinaria* as diagnosed by Savage *et al.* (2002, p.1028).

It is clear through our study that *Leiorhynchus* is present in the lower Frasnian in South China, but reports of their presence in the Middle Devonian of that region need further investigation; several so-called "*Leiorhynchus*" species previously described from South China should be assigned to other genera, e.g. *Ypsilorhynchus globosus* (Wang *et al.*), "*Yp.*" *subellipticus* (Fang), "*Yp.*" d*eprati* (Mansuy), *Calvinaria sinensis* (Fang), *Yocrarhynchus xiheensis* (Tan), etc.

In addition to *Leiorhynchus kwangsiensis* Grabau, another lower Frasnian species from South China, *L. obesus* Grabau, is very likely a true *Leiorhynchus*, whereas a large number of other so-called species of *Leiorhynchus* of South China should be excluded from the genus, e.g. *L. ex gr. quadricostatus* Vanuxem sensu Zhang, 1987, *L. submesacostale* Chen, *L. rotundus* Zhang, *L. biplicatus* Nalivkin (from Yunana and Guizhou provinces), *L. dayaoensis* Xian, *L. paucicostatus* Xian, *L. bisulcatus* Xian, *L. politus* Lyashenko sensu Tan *et al.*, in addition to those exclusions by Chen (1984) and Sartenaer (1996).

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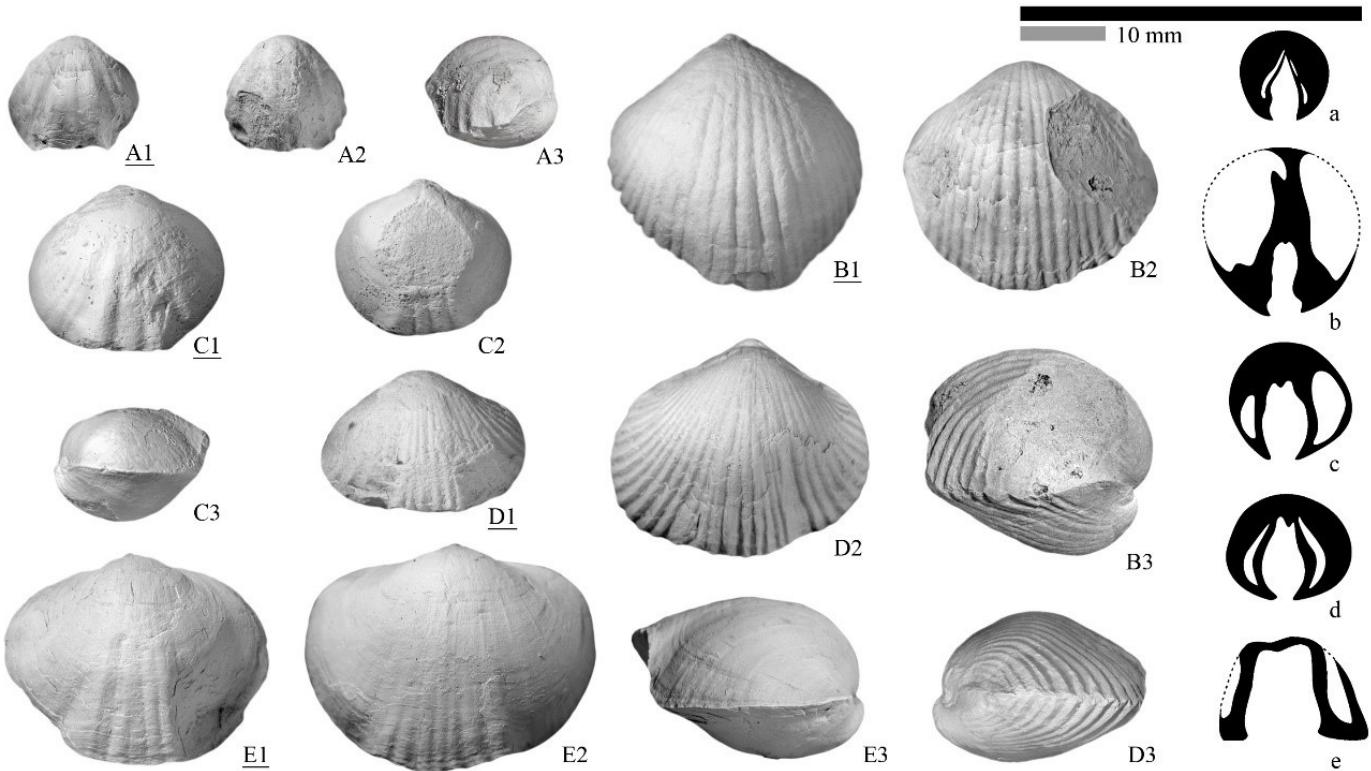
Fig. 1 External and internal structures of the five leiorhynchid species described in the present paper. A, a: *Yocrarhynchus orientalis* (Chen), from Longmenshan, Middle Frasnian; B, b: *Ypsilorhynchus globosus* (Wang *et al.*), from Panxi, Upper Givetian; C, c: *Leiorhynchus kwangsiensis* Grabau, from Dabakou, Lower-Middle Frasnian; D, d: "*Yp.*" *subellipticus* (Fang), from Panxi, Upper Givetian; E, e: *Calvinaria sinensis* (Fang), from Panxi, Middle Frasnian. a-e: ventral transverse sections shwoing the dental plate of A1-E1 respectively; Gray scale is for images of shells, black is for transverse sections.

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Study of Changhsingian (Late Permian) brachiopod fauna of shallow-water clastic-shelf facies in South China: see Zhongzhai section as an example

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Zhongzhai section, as its unique location (Figure 1, 26.15°N, 105.29°E) in the shallow-water clastic-shelf facies, which provides a well-preserved brachiopod fauna differing from the other faunas in the shallow-water carbonate platform and deep-water siliciclastic facies of South China and serves as a correlation between marine and non-marine Permian–Triassic boundary (PTB) section in western Guizhou and eastern Yunnan provinces by its stratigraphy work (Metcalfe & Nicoll 2007, Shen et al. 2011, Zhang et al. 2014b).

Fifty-six brachiopod species [including ten new species: *Tethyochonetes sheni*, *T. cheni*, *T. minor*, *Neochonetes* (*Huangichonetes*) *archboldi*, *N.* (*Sommeriella*) *waterhousei*, *N.* (*S.*) *rectangularis*, *N.* (*Zhongyingia*) *transversa*, *N. semicircularis*, *Paryphella acutula*, *Orbiculoidea liaoi*; ten undetermined species and three comparative species] have been systematically described for the exceptionally well-preserved and diverse Zhongzhai brachiopod fauna of late Changhsingian age (Zhang et al. 2013, 2014a, 2015). This is the first systematic palaeontological study of a diverse Changhsingian brachiopod fauna representing the shallow-water clastic-shelf facies anywhere in South China.

Fig.1. Location of Zhongzhai section

In addition, several morphologic terms (e.g., hinge spines, tubes) have been renewed and some endemic South China *Orbiculoidea* species have been first described in English.

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Exceptionally preserved brachiopods from fossil-Lagerstätten in southwestern China: perspectives on the Cambrian explosion of metazoans

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In the last decades, fossil discoveries from around the world, particularly from the Chengjiang and Guanshan Konservat-Lagerstättens in South China, have greatly added to our understanding of the magnitude, tempo and ecological complexity of the explosive radiation of metazoans during the Cambrian.

The Brachiopoda is one of the most important lophotrochozoan phyla that dominated the benthic communities throughout all the Palaeozoic era, and it has an extensive fossil record, exhibiting morphological diversity and geological continuity. In South China, the earliest crown brachiopods can be traced back to the base of the Chiungchussian (Qiongzhusian), where they are found mostly as small fragmentary pieces of phosphatic shells in the black bioclastic siltstone of the uppermost Shiyantou Formation. Even small pieces of phosphatic shells can be readily identi-

fied as lingulate brachiopods thanks to their characteristic with regularly pustulose or pitted ornamentation. In a few cases, the lingulate brachiopods can be found as partial or incomplete internal mold of shell valves. In the early publications, these lingulate brachiopods were referred to *Botsfordia* sp. Re-investigation and re-examination of tens of specimens, derived from the black siltstone of the uppermost Shiyantou Formation at the Meishucun section in Jinning, permits us to re-assign them to *Diandongia pista* Rong 1974 of the Family Botsfordiidae. *Diandongia* is one of the most abundant and mineralized brachiopods from the overlying muddy and siltstone deposits of Yu'anshan Formation, typified by its ornamentation of regularly distributed pustules or pits on the external surface of immature shell valves.

The onset of a more highly diversified brachiopod fauna took place in muddy deposits of the Maotianshan Shale Member (Chengjiang muddy deposits) belonging to *Eoredlichia-Wudingaspis* Zone. Aside from *Diandongia pista*, *Eoglossa chengjiangensis*, *Lingulellotreta ergalievi*, *Xianshanella haikouensis*, *Longtancunella chengjiangensis*, *Kutorgina chengjiangensis*, *Heliomedusa orienta*, *Yuganotheca elegans* and an unidentified species of *Alisina* make their first appearance in the Middle Chiungchussian Maotianshan Shale. Of these, *Lingulellotreta ergalievi* and *Heliomedusa orienta* are two of the most numerically abundant and characteristic forms, and thus thought as representatives of the Chengjiang Maotianshan shale brachiopod assemblages. The Late Chiungchussian brachiopods are found in the upper siltstone of the Yu'anshan Formation at Kuangshan section in Malong County of eastern Yunnan. With the exception of *Diandongia pista*, Late Chiungchussian brachiopods are typified by the occurrence of the acrotretid *Kuangshanotreta malungensis* Zhang, Holmer and Hu, in a slab of fossil which is accompanied by the trilobite *Malungia laevigata* whose occurrences suggest the uppermost part of *Eoredlichia* Zone (Chiungchussian Stage) or the lowermost Botomian. Recently, a new fossil assemblage of late Chiungchussian Stage has been found in the muddy siltstone intercalated within thick-bedded quartz sandstone of lower Hongjingshao Formation exposed around the Guanshan reservoir in Xiazhuang Village of Chenggong county of Kunming, eastern Yunnan. It is in the lower Hongjingshao siltstone that yields a high-density concentration of monotaxic shell of brachiopods, prominently allied with *Kutorgina*. In some cases, the strongly crushed and closely stacked specimens of shell valves have soft bodied preservation of stout pedicles. However, the detailed systematic description of the brachiopod species has not yet been completed. The monotaxic aggregation of shell valves with high density suggests the first expansion, in species abundance and ecological dominance, of calcareous-shelled brachiopods from the brachiopod Subphylum Rhynchonelliformea.

Higher up, the components of Chiungchussian brachiopod fauna are sharply diminished and then disappear in East Yunnan. Most likely this can be linked to a regressive event and the shallow-water environment is evident by the thick-bedded quartz sandstone of lower Hongjingshao Formation in Kunming-Wuding area, and by the coarse-grained siltstone interbedded with sandstone in Malong-Yiliang area. However, the siltstone that are intercalated within the thick sandstone in the middle-upper Hongjingshao Formation around Hongjingshao village in Malong

county contains high-density accumulation of *Palaeobolus* shells, which are found in clusters on bedding planes. The rich stacked well-sorted shells of *Palaeobolus* have usually been referred to *Lingulepis yunnanensis* Rong, 1974 in earlier publications, dealing with Cambrian fauna in eastern Yunnan. The Early Tsanglangpuan brachiopod assemblage is characterized by a large number of *Palaeobolus* that are strikingly different from assemblages in the Chiungchussian fauna, and *Diandongia pista* is replaced by a new genus and species of botsfordiid brachiopod, *Hongjingshaothele rectangulatus* gen et sp. Nov. in the restricted shallow water environment. *H. rectangulatus* is characterized by a rectangular shell with strongly developed muscles on the raised muscular platform. Late Tsanglangpuan brachiopods are well preserved in the silty mudstone of Wulongqing Formation, containing the soft-bodied Guanshan fauna (Hu et al., 2013). The brachiopods of Guanshan fauna were largely collected from the Gaoloufang section in the Chenggong county of Kunming. Until now, the fauna includes ten brachiopod species, assigned to eight genera, including *Acanthotretella decaius* Hu et al., 2010, *Eoobolus malongensis* (Rong) 1974, *Heliomedusa minuta* Luo et Hu 2008, *Palaeobolus liantuoensis* Zeng 1987, *Kutorgina sinensis* Rong 1979, two indeterminate brachiopod *Diandongia* sp. and *Nisusia sp.* All the brachiopods await to be described in detail. It is interesting to note that *Nisusia* sp. represents the FAD of the Superfamily Nisusioidea, and *Diandongia* sp. and *Eoobolus malongensis* are one of the numerically predominant brachiopod taxa in the Guanshan fauna. Of these, *A. decaius*, *E. malongensis*, *P. liantuoensis* and *Diandongia* sp. have thin and elongate pedicles preserved; *H. minuta* and *Diandongia* sp have exceptionally preserved setae fringing around the marginal edge of shells. Moreover, the exceptionally preserved specimens of *A. decaius* shows a spiral lophophore. In addition, the high concentration of acrotretid brachiopods, herein referred for the first time to cf. *Eohadrotreta zhenbaensis*, was recovered from the mudstone of Wulongqing Formation at Shijiangjun and Sapushan sections in Wuding county ca. 60 km northwest of Kunming.

In summary, the brachiopods from the Chengjiang fauna show a rather high diversity with ten families, first occurring in the Chiungchussian (Stage 3) of China. By contrast, each family is represented uniquely by a monotaxic species. The low-diversity and high-disparity of Chiungchussian brachiopods coincides well with the explosive radiation of metazoans in general among phyla. Studies of Chengjiang brachiopods demonstrate that the Cambrian Stage 3 brachiopods developed a remarkable varied organization of tissues and organs shortly after the onset of Cambrian explosion. All the Cambrian brachiopods have an epibenthic lifestyle either cemented by a ventral valve or attached by variable pedicles to establish complex ecological community encompassing primary tierers and variable secondary tierers. Upwards, the Chiungchussian assemblage was succeeded by 11 species and eight families of brachiopods, dominated by components from Eoobolidae, Obolidae and Acrotretidae, showing an accelerated radiation at the species level, in contrast, slower addition at the family level.

An agglutinated early Cambrian actinotroch-like phoronid from the Chengjiang Lagerstätten and its implications

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The Lophotrochozoa (which is sometimes equated with Spiralia), most likely represents a clade of non-ecdysozoan protostomes that mainly comprises two groups - the Trochozoa and the Lophophorata (Dunn et al., 2008; Giribet, 2008). The lophophorate phyla (comprising the Bryozoa, Entoprocta, Phoronida and the Brachiopoda) are united by the presence of a fan of ciliated tentacles surrounding the mouth. Although considerable advance have recently been made in unveiling the Cambrian morphology and diversity of brachiopods as well as other lophophorate animals (recently including bryozoans and entoprocts) (Landing et al., 2010; Zhang et al., 2013), the most conspicuous phylogenetic gap in the fossil record is for the Phoronida. *Iotuba* Chen & Zhou, 1997 (an early synonym of *Eophoronis* Chen 2004) was proposed as a phoronid candidate, but it has more recently been considered as a species of sipunculids (Huang, 2006).

Here we describe abundant well preserved material of *Archisaccophyllia kunmingensis* (Hou et al., 2005), from the Cambrian (Series 2) Chengjiang deposits, reinterpreted here as a stem-group phoronid with actinotroch-like larval characters. The phoronid affinity is supported by the sessile body plan and interior soft anatomy. The body consists of an upper agglutinated calyx and a lower stout stalk with a distal holdfast. The soft anatomy includes a U-shaped gut with a mouth surrounded by a fan of flexible tentacles. *Archisaccophyllia kunmingensis* differs from extant phoronid actinotroch larvae in being much larger with a sessile lifestyles, as well as in having the calyx covered by agglutinated quartz grains that is reminiscent of the agglutination that is known both in extant adult phoronids as well as from the enigmatic lophophorate *Yuanotheca* (Zhang et al., 2014)*,* recently described from the Chengjiang fauna. The occurrence of an actinotroch-like phoronid from the Chengjiang biota traces the ancestry of yet another lophotrochozoan phylum back to the Cambrian radiation, and has important implications for the earliest evolution of lophotrochozoans, and shows that an agglutinated lophotrochozoan body plan may have evolved earlier or commoner than previously suspected.

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The epithelial cell moulds on the shells of the earliest acrotretoids from the Cambrian Series 2 (Shuijingtuo Formation) in the Three Gorges area, China

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Polygonal networks of epithelial cell moulds have been reported in a series of fossil specimens of bradoriids, ostracods, conodonts, tommotiids, mollusks, black corals and plants. However, the well-recognized polygonal moulds in brachiopods are hitherto known largely from the acrotretids that are known to have a cosmopolitian distribution from Lower Cambrian to Silurian. Herein we present for the first time an exquisitely preserved epithelial cell moulds and shell microstructure in the oldest-known Acrotretid brachiopod *Eohatrotreta zhenbaensis* derived from the Shuijingtuo Formation (Series 2) of Aijiahe section in Yichang, Hubei Province of China. The ventral epithelial cell moulds (17 μm on average) usually are convex or concave polygonal in outline, with variation of tetragon, pentagon and hexagon. The epithelial imprints are densely concentrated on
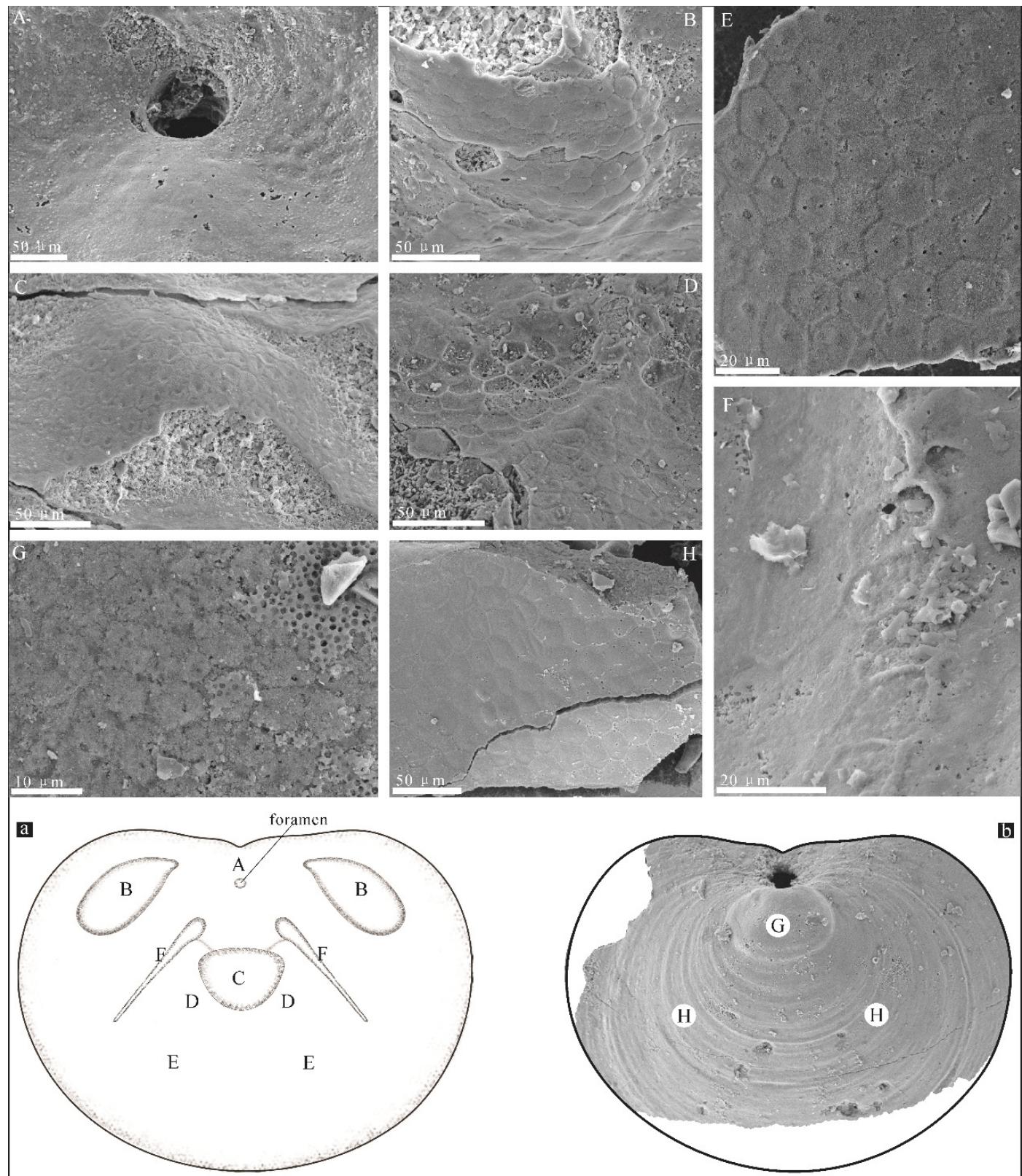
Fig.1. Disposition of the epithelia cell moulds on the ventral shell surface of *Eohadrotreta zhenbaensis*. A. ventral apical internal, AJH SJT S05 E021; B. cardinal muscle scar, AJH SJT S05 E043; C. apical process, AJH SJT S05 F035; D. the surrounding of apical process, AJH SJT S05 E047; E. valve floor, AJH SJT S05 E075; F. vascula lateralia, AJH SJT S05 E116; G. larval shell, AJH SJT S05 E033; H. post-larval shell, AJH SJT S05 E093; a and b. schematic reconstructure of ventral valve interior and exterior: A-apical internal, B-cardinal muscle scar, C-apical process, D-surrounding of apical process, E-valve floor, F-vascula lateralia, G-larval shell, H-post-larval shell.

the regions across the apical process, cardinal muscle scars, vascula lateralia, valve floor and ventral apical interior. In the dorsal valve, the cell moulds are mainly revealed along the regions of the median buttress, cardinal muscle scars, vascula lateralia, median septum and valve floor, which have a general resemblance in outline, but wider range of dimension to those from ventral valves. In addition, the epithelial imprints on the larval shells are also well revealed on 9 specimens. The polygonal networks preserved in the secondary layers of shells can be clearly distinguished in morphology from the pitted structures widely known from the primary layer of the larval shell in all the different types of acrotretids.

Investigation of these new materials demonstrates that the distribution of different shapes of epithelial cell moulds in different regions of ventral and dorsal valves may be characteristic of different taxa, and may also potentially provide available information on the evolutionary changes of the shell textures of brachiopods during the Early Cambrian. Nevertheless, comparative study of such epithelial mircostructures of acrotretids and other brachiopod taxa remains to be done, despite having consequence for our understanding the phylogenetic relationships of in-group brachiopods.

Key words: epithelia cell moulds, acrotretid brachiopods, early Cambrian, Shuijingtuo Formation, polygonal network.

Comparative study of Late Devonian (Famennian) brachiopod assemblage successions, depositional environments, and geo-events in northwestern Junggar, Xinjiang and central Hunan, China

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Late Devonian (Famennian) strata, which bear abundant post-F/F extinction faunas (corals and brachiopods), are well developed in northwestern Junggar, Xinjiang, where the Bulongguoer section has been regarded as the most important reference section for the recognition of the Famennian stratigraphic and faunal sequence and subdivisions. Six brachiopod assemblages from the Hongguleleng and Heishantou formations of this section and adjacent areas are recognized, in ascending order: *Caenanoplia*? aff. *logani* subassemblage in the lower part of the Saerba Member (refer to Ma et al., 2013 and in press for detailed stratigraphic divisions of the Hongguleleng Formation and the lower part of the Heishantou Formation), *Cyrtospirifer-Palaeospirifer* subassemblage in the middle and upper parts of the Saerba Member; *Athyris-Megalopterorhychus* assemblage in the lower part of the Duguer Member; *Ambocoelia*? cf. *unionensis* assemblage in the Wulan Member (only locally in the Bulongguoer section); *Austrospirifer*? sp. assemblage in the Chasi Member; and *Syringothyris-Spirifer* assemblage in the Namu Member of the Heishantou Formation. Compared with the *Yunnanella* (=*Yunnanellina* Grabau, 1931)-*Sinospirifer* and *Nayunnella* (=*Yunnanella* Grabau, 1931)-*Hunanospirifer* assemblages in the Xikuangshan section of central Hunan, the contemporaneous assemblages in the Saerba and Duguer members of western Junggar (*Caenanoplia*? aff. *logani*, *Cyrtospirifer-Palaeospirifer* and *Athyris-Megalopterorhychus*) are distinctly different in composition, implying that the two areas were located in different biogeographical regions, which, however, have a similar and decreasing bio-diversity trend.

The *Caenanoplia*? aff. *logani* subassemblage is represented by chonetids in high abundance and low diversity (Figs. 1.1-1.4). The *Cyrtospirifer-Palaeospirifer* subassemblage is dominated by well persevered cyrtospiriferids with high diversity, including *Cyrtospirifer* (Figs. 1.7-1.11) and "*Uchtospirifer*" (Figs. 1.12-1.14), the latter of which has short hinge line, obtuse cardinal extremities and narrowly high ventral interarea; the ulbospiriferid *Palaeospirifer* (Figs. 1.5-1.6) firstly occurred in this subassemblage. The *Athyris-Megalopterorhychus* assemblage exhibits the highest diversity and abundance, and athyrides and rhynchonellides are two major types (Figs. 1.15-1.22); moreover, peculiar *Planovatirostrum* also occurs in this assemblage. The *Ambocoelia*? cf. *unionensis* assemblage (Figs. 1.23-1.26) is characterized by species that have small shells about 5 mm in width and smooth to weak ornamentations. The *Austrospirifer*? sp. assemblage consists of brachiopods preserved as molds in moderate abundance. The *Syringothyris-Spirifer* assemblage is dominated by spiriferides and spiriferinides (Zong and Ma, 2012).

Two transgression-regression cycles may be recognized in the Bulongguoer section. The first cycle includes the whole Hongguleleng Formation (from the Saerba Member through the Chasi Member), with the largest sea level rise recorded in the lower part of the Wulan Member. The second cycle consists of the Heishantou Formation. The sea level change of the Bulongguoer section can be compared to the platform facies of South China during the early-middle and latest Famennian. In the late Famennian, the sea level rose gradually till the climax at the supposed *Annulata* level in northwestern Junggar, as revealed in the Bulongguoer section; whereas in South China the sea level became shallower, which reflects the regional differences between Junggar and South China.

The succession of brachiopod assemblages in northwestern Junggar, probably associated with the sea level changes, could approximately be correlated with the Famennian events recognized from other regions. The replacement of the *Athyris-*
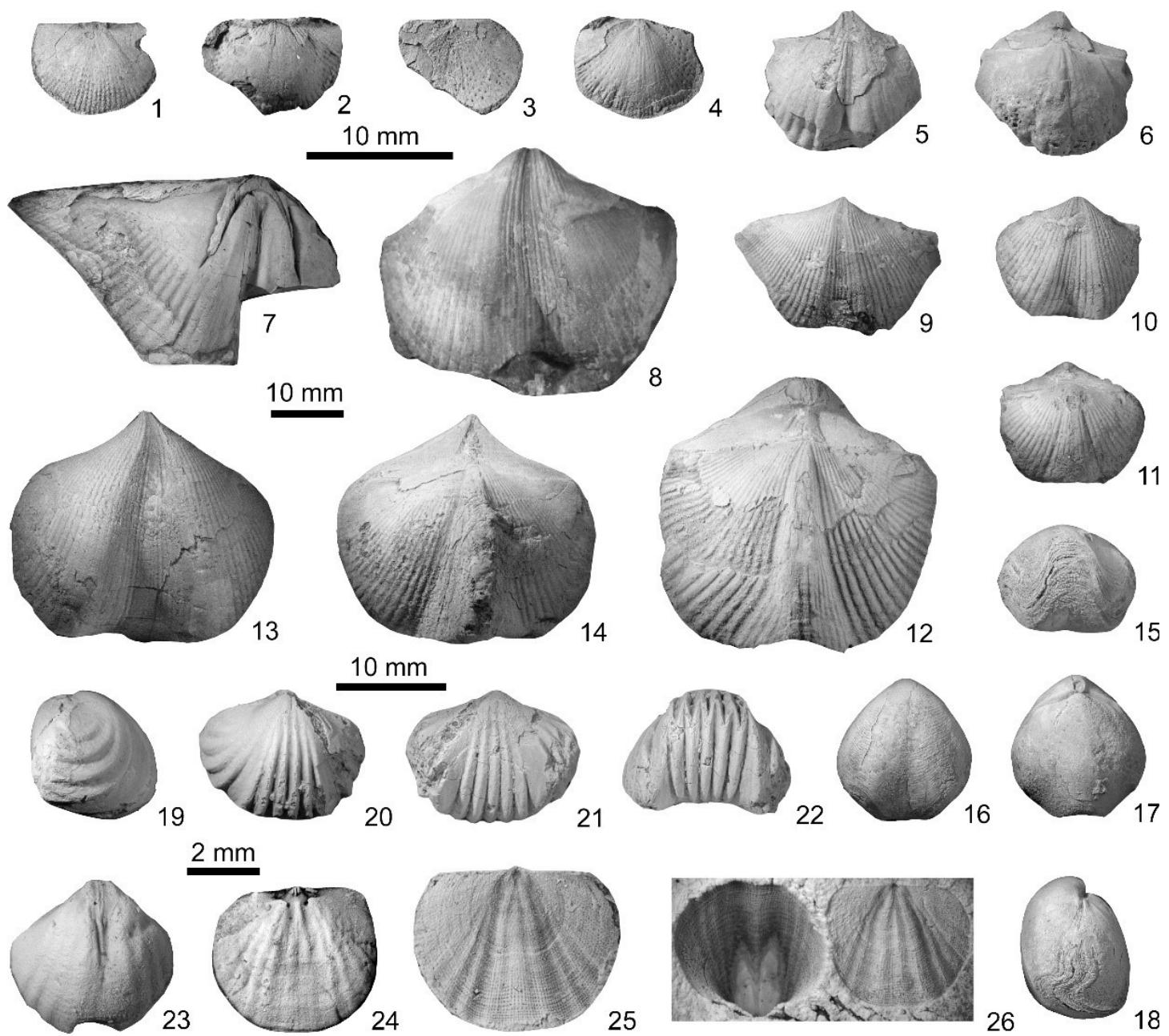
Figure 1. Representatives of various subassemblage and assemblage in the Bulongguoer section and adjacent areas. The upper black 10 mm scale bar is for images 1–4; the middle black 10 mm scale bar is for images 5–18; the lower black 10 mm scale bar is for images 19–22; the black 2 mm scale bar is for images 23–26. 1–4. *Caenanoplia*? aff. *logani* (Norwood & Pratten, 1855): 1. dorsal valve in interior view showing the cardinal process pit; 2. ventral view; 3. the internal mold of dorsal valve showing the accessory septa; 4. ventral valve in interior view showing medium septa. 5–6. *Palaeospirifer honggulelengensis* (F M Zhang, 1983): ventral and dorsal views. 7. *Cyrtospirifer sulcifer* (Hall & Clarke, 1894): ventral view. 8. *Cyrtospirifer* sp.: ventral view. 9. *Crytospirifer* cf. *inermis* (Hall, 1843): ventral view. 10–11. *Cyrtospirifer quadratus* (Nalivkin, 1937): ventral and dorsal views. 12. "*Uchtospirifer*" cf. "*Cyrtiospirifer*" *archiaci* (Murchison, 1840): ventral view. 13–14. "*Uchtospirifer*" cf. "*Cyrtospirifer*" *kurban* (Nalivkin, 1937): ventral and dorsal views. 15–18. *Athyris sulcifera* Nalivkin, 1937: anterior, ventral, dorsal and lateral views. 19–22. *Megalopterorhychus boulongourensis* Chen & Yang, 2011: lateral, dorsal, ventral and anterior views. 23–26. *Ambocoelia*? cf. *unionensis* Weller, 1914: 23. interior ventral view; 24. interior dorsal view; 25. the external mold of dorsal valve; 26. the external molds of the ventral (left) and dorsal (right) valves.

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Megalopterorhychus assemblage by the *Ambocoelia*? cf. *unionensis* assemblage, may correspond to the Oujiachong event recognized in South China; and the replacement of the *Austrospirifer*? sp. assemblage in the Chasi Member by the overlying the *Syringothyris-Spirifer* assemblage, is probably correlated with the Hangenberg event.

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