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First report of linguloid brachiopods with soft parts from the lower Cambrian (Series 2, Stage 4) of the Three Gorges area, South China

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ABSTRACT

Chengjiang-type fossil brachiopods with preservation of non-mineralized tissues are reported for the first time from the lower Cambrian Shipai Formation of the Three Gorges area, western Hubei Province, China. Recent excavation in the Wangjiaping and Aijiahe sections resulted in the new discovery of some linguloid brachiopods, showing strong similarity in preservation with those occurring in the well-known Chengjiang fauna (Yu'an-shan Formation of eastern Yunnan, China). The brachiopods can be referred to *Palaeobolus liantuoensis*, *Lingulellotreta malongensis* and *Eoobolus*. sp. The new material of *Palaeobolus* exhibits a flattened impression of proximal pedicle, which also represents the first report of pedicle known from this cosmopolitan linguloid. The occurrence of *Lingulellotreta* in the Shipai Formation (*Redlichia meitanensis* and *Palaeolenus lantenoisi* zones) represents an important geological extension of this genus to upper Tsanglangpuan Stage (Series 2, Stage 4) in the Yangtze Platform, and signifying that FAD of *Lingulellotreta* in the regional lower Cambrian of the Yangtze Platform seems not synchronous.

Keywords: Cambrian, Brachiopods, Linguloidea, Soft-bodied fossils, The Three Gorges area

1. Introduction

Exceptionally preserved Cambrian fossils, such as those from Burgess Shale-Type Fossil-Lagerstätte (Forchielli et al., 2013), have aroused considerable scientific attention because of their unique contributions to our knowledge of early animals, such as their organization of body plans and soft-tissue character states (Briggs et al., 1994; Hou et al., 2004; Zhang et al., 2004, 2007a, 2009). The articulated nature of skeletal elements (Conway Morris and Peel, 1995; Vannier et al., 2007) has provided clues to the behaviors of extinct organisms (Vannier and Chen, 2005; Zhang et al., 2011c), that are usually unobtainable from shelly and skeletonized fossils alone (Conway Morris and Caron, 2007; Zhang et al., 2010, 2013, 2014a). In the last

decades, systematic investigations of the Cambrian sediments around the world led to findings of tens of Konservat Lagerstätten that yielded a rich abundance of fossils with exceptional preservation (Conway Morris, 1992; Hou et al., 2004; Zhao et al., 2005; Zhang et al., 2008a). In particular, these deposits have an abundance of exceptionally preserved ecdysozoans, such as arthropods and pan-arthropods (Fu and Zhang, 2011; Ma et al., 2012). Until now, not so many taxa of soft-bodied fossil lophotrochozoans are known from Cambrian Konservat-Lagerstätten (e.g. Peel and Ineson, 2011; Zhang and Holmer, 2013), but include the mollusk-like scleritome-bearing *Wiwaxia* (Smith, 2012; Smith, 2013), *Orthrozanclus* (Conway Morris and Caron, 2007) and *Halkieria* (Conway Morris and Peel, 1995; Vinther and Nielsen, 2005), as well as the entirely soft-bodied *Odontogriphus* (Caron et al., 2006) from the classic Burgess Shale Konservat-Lagerstätten. Recent fossil discoveries of lower Cambrian sipunculans (Huang et al., 2004), polychaetes (Vinther et al., 2011), chaetognaths (Chen and Huang, 2002) and entoprocts (Zhang et al., 2013) have considerably reduced the number of lophotrochozoan animal phyla missing from the Cambrian explosion, albeit there is still a conspicuous phylogenetic gap in the Cambrian explosion for Platyzoa (Edgecombe et al., 2011).

Brachiopods, firmly nested within Lophotrochozoa (Dunn et al., 2008; Paps et al., 2009), are among the most important components of marine communities during the Paleozoic, dominating the benthos of both the Cambrian Evolutionary Fauna and Paleozoic Evolutionary Fauna (Sepkoski, 1984). They provide some of the earliest Phanerozoic evidence for fully skeletonized metazoans. Their skeletal remains are preserved as early as the upper Fortunian (Tommotian equivalent) Stage of the Terreneuvian Series (=lowermost Cambrian) well below the first trilobite body fossils (Skovsted et al., 2014). Nevertheless, most fossil brachiopods are known exclusively from their shells; soft parts are preserved only in a few deposits with exceptional preservation (Zhang and Holmer, 2013), most notably the Cambrian Stage 3 Chengjiang Konservat-Lagerstätten (Zhang et al., 2007b, 2009, 2014a; Wang et al., 2012;). Such remarkable occurrences offer extraordinary insight into the evolutionary paleobiology, autoecology and community ecology of early brachiopods that are unobtainable from the study of fossil shells alone (Holmer and Caron, 2006; Zhang et al., 2008b, 2010, 2011c). Recently, exceptionally preserved fossil brachiopods with soft parts, including pedicles, are increasing in number, and extending in temporal and paleogeographic ranges (Balinski and Sun, 2013; Balthasar and Butterfield, 2009; Bassett et al., 2009; Sutton et al., 2005; Zhang et al., 2010) (Fig. 1).

Here, we describe three genera of lingulid brachiopods from the muddy siltstone of the Cambrian Series 2, unnamed Stage 4 Shipai Formation (Zhang and Hua, 2005), showing comparable preservation with those from Chengjiang fauna and Guanshan fauna recovered in eastern Yunnan province of China (Zhang et al., 2008b, 2010).

This is the first report of Cambrian brachiopods with preserved pedicle outside of eastern Yunnan in China, and represents the first record on the occurrence of *Lingulellotreta malongensis* Rong 1974 in the Three Gorges area of South China, thus extending the palaeogeographic range of Family Lingulellotretidae to the centre of the Yangtze platform.

2. Geological setting, Locality and Stratigraphy

The present-day Yangtze platform is located between the Qinling orogenic belt to the North and the *Cathaysia* suture to the Southeast (Fig. 2). The Yangtze platform rifted from the Cathaysia block around 800 Ma (Li et al., 2008), and developed in a continental margin of the Yangtze block, with Neoproterozoic to Cambrian strata widely distributed in South China (Zhang et al., 2008a; Zhu et al., 2007). These sedimentary rocks were deposited in a basin related to the rifting of the Yangtze and *Cathaysia* Blocks coincident with the breakup of the *Rodinia* supercontinent (Li et al., 2008).

The Yangtze gorges area (Fig. 2.2), geographically located in the north margin of the upper Yangtze platform, is another important and famous auxiliary stratotype section proposed for the Precambrian-Cambrian boundary in China (Wang et al., 2008). In this region, the terminal Neoproterozoic-Cambrian sedimentary successions are well developed and widely distributed in outcrops around the southeastern limbs of Huangling Anticline (Ishikawa et al., 2014). The Series 3—Furongian Cambrian is dominated by thick dolostones, ordinarily thought to be unsuitable for exceptional preservation of fossils. By contrast, the depositional succession through the Ediacaran-Cambrian boundary yielded abundant shale-hosted fossils that aroused broad interests of evolutionary biologists and paleontologist (Guo et al., 2014). The Neoproterozoic deposits consist of a thick sequence (ca. 300m) of thick-bedded or thin-bedded carbonate rocks, assigned to the Ediacaran Dengying Formation, disconformably overlain by the traditional “Lower Cambrian” of Terreneuvian-Series 2. The traditional “Lower Cambrian” is divided into five lithostratigraphic units, in ascending order, the Yanjiahe, Shuijingtuo, Shipai, Tianheban and Shilongdong formations. On account of the fossiliferous nature of these rocks, the Ediacaran-Cambrian strata in the Three Gorges area has classically been the focus of studies of bio-, sequence and chemostratigraphy (Ishikawa et al., 2014; Wang, 1987; Wang et al., 2008; Zhu et al., 2007) through the Ediacaran-Cambrian boundary (Fig. 2.2-3). In some recent publications (Jiang et al., 2012; Wang et al., 2008), the Yanjiahe and Shuijingtuo Formations are collectively termed as the Niutitang Formation, though the former is limestone-dominated exclusively with rich pre-trilobite Small Shelly Fossils and the latter is black shale-dominated containing abundant trilobites. The overlying ca. 180 m-thick Shipai Formation consists of thin-laminated siltstone in its

lowest part, and argillaceous siltstone and silty mudstone in the middle and calcareous shale and siltstone with limestone laminations in the upper part (Fig. 2.4). The linguloid fossils dealt with in this paper were collected from the mid-upper mudstone and muddy siltstone of Shipai Formation (Fig. 2.4).

3. Fossil occurrences and regional correlations

The absolute age of the Lower Cambrian from this region is not yet available, but the fossils provide straightforward evidence for correlating the lower Cambrian Formations of the Three Gorges area.

The Yanjiahe Formation mainly crops out on the south and western limbs of Huangling anticline (Fig. 2.3), and is well developed in the Three Gorges and Changyang areas (Fig. 2.3). The Yanjiahe Formation near Aijiahe Village about 25 km southwest of Yichang City consists of 40 m of grayish-black carbonate yielding abundant Small Shelly Fossils (SSFs) (Guo et al., 2014). The SSF assemblages can be differentiated into 3 recognizable assemblage zones, in ascending order, the *Anabarites trisulcatus*–*Protohertzina anabarica* assemblage zone (Bed 2), the *Purella antiqua* assemblage zone (Bed 3), and the *Aldanella yanjiaheensis* assemblage zone (Bed 5). Based on the biozones of SSFs listed above, the Yanjiahe Formation was suggested to be correlated with early to middle Meishucunian in age (Fortunian Stage, equivalent to the Nemakit-Daldynian and early Tommotian in Siberia). In addition, the occurrence of *Aldanella yanjiaheensis* (possibly a junior synonym of *A. attleborensis*) in the uppermost Yanjiahe Formation indicates the uppermost bed corresponds to Cambrian unnamed Stage 2; see detailed discussion made by Guo et al., (2014).

The Yanjiahe Formation is overlain with disconformity by the Shuijingtuo Formation, which consists of grayish black to black shales and carbonaceous shales intercalated with grayish black thin-bedded or lenticular limestones. The base of the Shuijingtuo Formation is typified by occurrence of common black carbonate concretions approaching 2 m in diameter. The Shuijingtuo Formation is usually thought to be correlated with the *Parabadiella* Zone in eastern Yunnan (equivalent to *Abadiella huoi* Zone in Australia) mostly because of the first occurrence of eodiscoid trilobites *Tsunyiidiscus acutus* and *Sinodiscus changyangensis*, 5-8 m above the base of this Formation (Dai and Zhang, 2011; Lin et al., 2004). Nevertheless, the brachiopods assemblage recently recovered from the upper Shuijingtuo (our unpublished material) provides a line of evidence of brachiopods, suggestive of mid Canglangpuian age (equivalent to the Botomian of Siberia) (Zhang et al., 2011d).

The Shipai Formation, which hosts the brachiopods with preservation of soft parts is a siltstone, muddy siltstone and calcareous siltstone-dominated succession. Typical Burgess Shale Type preservation of non-mineralized fossils, such as *Vetulicola* and palaeoscolecoidan worms, has been documented from the muddy deposits (Zhang and

Hua, 2005). The stratigraphy and localities of the soft-bodied fossil occurrence in the Shipai Formation were discussed in Zhang and Hua (2005) and Zhang et al., (2008a). The absolute age of the Shipai Formation is presently unknown, but regional and intercontinental correlation indicates that it is likely to equate with an age of Cambrian Stage 4. It is characterized by the first occurrence of true *Redlichia* trilobite in the sequence (Figs.2.4, 3.1). Two trilobite biozones were recognized and differentiated in the sequence, in ascending order, *Redlichia meitanensis* and *Palaeolenus lantenoisi* zones (Figs. 2.4, 3.1-6). The Shipai Formation is thus considered to correspond to the lower Wulongqing Formation of Tsanglangpuan Stage in eastern Yunnan (Wang, 1987). Apart from trilobites, the silty mudstones of the Shipai Formation also yield rare bradoriids and some lingulate brachiopods (see below). Accordingly, the Shipai Formation may be of Tsanglangpuan age (Epoch 2, Age 4), certainly younger than the Cambrian Stage 3 Chengjiang fauna (Hou et al., 2004), but much older than the Cambrian Stage 5 Kaili fauna of Guizhou (Zhao et al., 2005) in the Yangtze platform (Fig. 2.2), and the Burgess Shale fauna of Canada (Briggs et al., 1994). Contemporary deposits containing soft-bodied fossils are reminiscent of the Emu Bay Shale Konservat-Lagerstätten in Australia (Paterson et al., 2012), Balang fauna of Guizhou Province (Peng et al., 2005) and Guanshan Fauna of Eastern Yunnan province in China (Hu et al., 2013) (Fig. 2.2). All these faunas can be assumed to correspond to the Tsanglangpuan Stage when the occurrence of the trilobite *Redilichia* is taken into account (Zhang and Hua, 2005; Zhang et al., 2008a).

4. Discovery of exceptionally preserved fossil linguloid brachiopods from the Shipai Formation

The fossils were recovered and exposed by crack-out from the argillaceous siltstone and silty mudstone in the middle part of the Shipai Formation, approximately 60-80 m above the base of the Shipai Formation in the Aijiahe and Wangjiaping sections (Fig. 2.3). So far, eight specimens of *Lingulellotreta* and two specimens of *Eoobolus*. sp have been collected from the hillside bank of the Yangtze River close to the Shipai Village, approximately 15 km northwest of Yichang City, Hubei Province (Fig. 2.3). In addition, there are three slabs with 3-7 individuals of *Palaeobolus liantuoensis* present (Holmer et al., 2001; Li and Holmer, 2004). Of these, one was collected from the roadside section of Wangjiaping Village at the north bank of the Yangtze River, and the other two with pedicle were obtained from the section close to Aijiahe Village of Sandouping county, about 25 km northwest of Yichang city of western Hubei Province (Fig. 2.3).

All the individuals of *P. liantuoensis* were distinctly flattened and compressed with concentric growth lines closely spaced in reddish-brown color (Fig.4). As seen in the specimen of Fig. 4.1 and 4.2, the shell valves are completely compressed and flattened

with pronounced outline in color contrast to the surrounding muddy matrix. The specimens appear to be preserved as composite mould with dorsal and ventral valves conjoined together. Due to the truncation on the marginal edge of a valve (Fig.4.1), the two valves of the specimen are distinctly recognizable. In another slab, hosting 4 individuals that appear to be smaller than the specimen of *Palaeobolus* described above. Nevertheless, the coeval occurrence and closely spaced shell growth lines link the four small individuals to *Palaeobolus* (Li and Holmer, 2004; Zeng, 1987). However, the posteromedian symmetrical disposition of muscular scars has a remarkable similarity to the muscular pattern in bostfordioid brachiopods (Holmer et al., 1996). The exact taxonomic placement of these individuals in Class Lingulata (Brachiopoda) remains uncertain and additional specimens are required to confirm the classification in the future.

Eight specimens of *Lingulellotreta* were collected from argillaceous mudstones in the middle part of Shipai Formation (Fig. 5). All the specimens are preserved as reddish-brown composite mould with two shell valves conjoined together. The lingulid specimen reported herein (Fig. 5.1-7) have striking similarities in the morphology, size and pseudointerarea to the lingulid brachiopods recovered from the slightly younger Yu'an-shan Formation of the Chengjiang fauna (Jin et al., 1993; Zhang et al., 2007a; Zhang et al., 2004) (Fig. 5.8-9).

Two specimens of *Eoobolus*.sp were recovered from the same level as *Lingulellotreta* in the Shipai Formation (Fig. 6.1-2). *Eoobolus* differs markedly from *Lingulellotreta* in possessing a short ventral pseudointerarea, as well as in terms of the lack of an elongate oval foramen but instead having a deep pedicle groove in the ventral pseudointerarea (Fig.7.2-3). The shell surface is provided with some vague and closely spaced concentric growth line. The morphology, size and pseudointerarea of the specimen illustrated herein (Fig. 6.1-2) has striking resemblance to the lingulid brachiopods recovered from the Guanshan fauna (Hu et al., 2013; Zhang et al., 2007a; Zhang et al., 2014b) (Fig. 6.3). In the earlier publications (Hu et al., 2013; Luo et al., 2008), the lingulid brachiopods from the Guanshan fauna were taken to refer to the Genera of *Lingulellotreta*, but actually akin to *Eoobolus* (Zhang et al., 2014b). The detailed revision and taxonomic discussion of lingulids from Guanshan is beyond the scope of this paper and thus remains to be resolved (in preparation).

5. Systematic paleontology

All figured and illustrated specimens are deposited in the Early Life Institute and Department of Geology, Northwest University, Xi'an, China (Prefix: ELI).

Subphylum Linguliformea Williams et al., 1996

Class Lingulata Gorjansky and Popov, 1985

Order Lingulida Waagen, 1885

Family Obolidae King, 1846

Subfamily Obolinae King, 1846

Genus *Palaeobolus* Matthew, 1899

Type species: *Palaeobolus bretonensis* Matthew, 1899; Middle Cambrian (Amgian), Cape Breton, Canada (Nova Scotia).

Diagnosis: See Holmer and Popov 2000. p. 50.

Remarks: *Palaeobolus* is characterized by having a subtriangular shell bearing strongly developed concentric ornamentation. *Palaeobolus* is so far known from the lower Cambrian of Canada, Kazakhstan and South China. Detailed description of the genus from Canada and Kazakhstan has been provided in Holmer et al. (2001). Nonetheless, a few specimens are known from siliciclastic deposits around the world. When compared to those specimens etched from argillaceous carbonate (Li and Holmer, 2004), the specimens illustrated herein (Fig.4) appear to be larger. The shell shape and ornamentation of closely spaced concentric growth-lines on the shell surface permit us to refer the fossils to *Palaeobolus liantuoensis* Zeng, 1987. If interpreted correctly, this therefore represents the first report of *Palaeobolus* with soft-part preservation from muddy deposits.

Palaeobolus liantuoensis Zeng, 1987

1987 *Palaeobolus liantuoensis* Zeng p. 209; pls 8, 9-13.

2001 *Palaeobolus liantuoensis* Holmer et al., p. 44; Pls. 9,1-13.

2004 *Palaeobolus liantuoensis* Li and Holmer, p.195, figs. 3, 4, 5.

Stratigraphy and locality: Shipai Formation (*Redlichia meitanensis*—*Palaeolenus lantenoisi* trilobite Zone), Cambrian Series 2, Stage 4. Specimens were derived from a road cut section near Aijiahe village (N: 30° 44'55.2 " , E: 111° 03' 58.5 ") about 25 km southwest of Yichang City, western Hubei Province (Fig. 2.3).

Material: two compressed specimens, with one complete shell comprising two conjoined two valves; other fragmented valves from mechanically split the silty mudstone slabs (Fig. 4).

Description: The shell valves are biconvex and equivalved, circular in outline. They are relatively large, with a maximum width at mid-valve, about 12.8 mm from the posterior margin. The maximum shell length is approximately 13.6 mm. The pseudointerarea is not preserved, most likely due to the strong compression and flattening during preservation. It is apparent that there are some impressions delineated by reddish-grown tints of haematite, probably representing some remains of soft tissues. Just beyond the posteromedian margin of the shell, the annulated pedicle is preserved. The number of annulations is estimated to be 8-10 in the preserved 2.3 mm long proximal pedicle (Fig. 4.3). The pedicle is thin and around 1.1 mm in width,

corresponding to approximately 8.6 % of shell width. There is no evidence of a coelomic canal in the preserved pedicle.

Comparison and Discussion: The circular shape and flattened preservation of the shell is reminiscent of the two enigmatic brachiopod *Xianshanella* and *Longtancunella* from the lower Cambrian Chengjiang fauna. However, the new specimens can be distinctly distinguished from these genera in possessing strong and well-developed incremental shell growth lines that are vague or vestigial in the Chengjiang brachiopods *Xianshanella* and *Longtancunella*. In addition, the pedicles in *Xianshanella* and *Longtancunella* are always better preserved and more robust as compared with the shell valves, to the extent that the shell valves sometimes were more readily torn off than the pedicle detached from the attachment substrate (Zhang et al., 2006, 2007c). Distinctly different from the pedicle in *Xianshanella* and *Longtancunella* (Zhang et al., 2006, 2007c), the pedicle illustrated here for *Palaeobolus liantuoensis* (Fig. 3.3) seems much thinner and weaker. Furthermore, *Longtancunella* is also typically found in gregarious occurrences of different individuals together.

Superfamily Linguloidea Menke, 1828

Family Lingulellotretidae, Koneva & Popov, 1983

Lingulellotreta Koneva, 1983 (In Gorjansky & Koneva, 1983) { These are not in the reference list, but perhaps that is OK? But perhaps then we can remove the "in Gorjansky & Koneva?"

Type and only species: *Lingulepis malongensis* Rong, 1974 (= *Lingulellotreta ergalievi* Koneva, 1983 (In Gorjansky & Koneva, 1983)

Diagnosis: See Holmer et al., 1997.

Remarks: The genus *Lingulellotreta* was originally erected based on the type and only known species of *Lingulellotreta ergalievi* Koneva, 1983 from Kazakhstan. Holmer et al. (1997) restudied the material from Kazakhstan and made detailed morphological comparison to specimens described as "*Lingulepis*" *malongensis* by Jin et al. (1993) from mudstone of Chengjiang Lagerstätte in eastern Yunnan. Holmer et al. (1997) argued that the materials of "*Lingulepis*" *malongensis* from the Chengjiang fauna should be referred to the genus of *Lingulellotreta* and regarded *L. malongensis* as a senior synonym of *Lingulellotreta ergalievi* Koneva, 1983. However, the type specimen of "*Lingulepis*" *malongensis* is derived from the Wulongqing Member (recently elevated as Wulongqing Formation) of Tsanglangpu Formation at Siqitian Section of Malong county, eastern Yunnan Province. Unfortunately, the holotype is lost and formerly housed in the Nanjing Institute of Geology and Palaeontology (NIGP 22154).

Lingulellotreta malongensis Rong 1974

1974 *Lingulepis malongensis*, Rong 1974: p.114, Pl. 44: 27, 32.

- 1993 *Lingulepis malongensis*, Jin et al., p.794, figs. 6-8.
1997 *Lingulellotreta malongensis*, Holmer et al., figs. 4.1-4.14.
2000 *Lingulellotreta malongensis*, Holmer and Popov, Vol. 2, p.72, Fig 34, 1a-d.
2004 *Lingulellotreta malongensis*, Zhang et al., figs.1-4.
2004 *Lingulellotreta malongensis* Hou et al., p.182-183.
2004 *Lingulellotreta malongensis*, Li and Holmer, 126:193-211.
2005 *Lingulellotreta malongensis*, Zhang et al., 86:277-288.
2007 *Lingulellotreta malongensis* Zhang et al., 88:65-70.
2008 *Lingulellotreta malongensis*, Zhang et al., 14:241-254.

Holotype: Wulongqing Formation (Series 2, Stage 4, *Palaeolenu*—*Megapalaeolenus* trilobite Zone, Malong county, eastern Yunnan province. Holotype is lost and formerly housed in the Nanjing Institute of Geology and Palaeontology (NIGP 22154).

Material: eight specimens derived from the Shipai Formation at Wangjiaping section.

Diagnosis: As for genus, by monotype.

Description: The shell valves of *Lingulellotreta* are small with the ventral valve ranging from 3.4-5.6 mm long; average length ~4.6 mm in length (Figs 5.1-5.3). The pseudointerarea of the pedicle valve is elongated and extends anteriorly to 45% of valve length (Fig. 5.4-5). The pedicle foramen is elongate oval and placed at the posterodorsal tip of ventral pseudointerarea. It is formed and enclosed during postlarval growth stage. As seen in Fig. 5.1-5.7, the pedicle groove was usually preserved in fossils as mud-infilled ridge or groove, approximately 0.8 mm in length.

Remarks: The shells are tear-shaped, with elongate, triangular pseudointerarea (Fig. 5.1-7). The triangular and crescent-shaped pseudointerarea of adult specimens develops as an enclosed homeopseudodeltidium and an internal pedicle tube that opens via an elongate oval pedicle foramen at the tip (Fig. 5.4-7). An oval foramen and internal pedicle tube are characteristic of *Lingulellotreta* (Holmer et al., 1997) and the material described here has strong similarities to specimens of *Lingulellotreta* recovered from the mudstones of Yu'an-shan Formation (Chengjiang fauna) of eastern Yunnan (Fig. 5.8 and 5.9), as well as those acid-etched from the carbonate of the Shuijingtuo Formation of South Shaanxi province (Li and Holmer, 2004).

Recent revaluation (Zhang et al., 2014) of a large number of specimens of "*Lingulellotreta*" *malongensis* (formerly *Lingulepis malongensis* Jin et al., 1993) derived from the Lower Cambrian Yu'an-shan Formation (Chengjiang Biota) and the slightly younger Wulongqing Formation (Guanshan Biota) reveals that the Chengjiang and the Guanshan specimens should be referred to two different taxa, with the former to *Lingulellotreta* Koneva, 1983, and the latter to *Eoobolus* Matthew, 1902. As discussed above, the genus *Lingulellotreta* was originally erected based on *Lingulellotreta ergalievi* Koneva, 1983 from Kazakhstan. As discussed by Holmer et al.

(1997), the Chengjiang specimens of *Lingulellotreta* have striking similarities to those from Kazakhstan.

Family Eoobolidae Holmer, Popov & Wrona, 1996

Genus *Eoobolus* Matthew, 1902

Type Species: *Obolus (Eoobolus) triparilis* Matthew, 1902; Middle Cambrian Amgian, Bourinot Group), Cape Breton, Canada.

Diagnosis: See Holmer et al. (1996, p. 41)

Eoobolus sp.

Figure.6

Material: Only two specimens were collected, preserved as composite moulds with dorsal and ventral valves conjoined together.

Description: Shell ventrobiconvex, tear-shaped or triangular in outline. Ventral pseudointerarea well-developed and orthocline, with apical angle around 80° ; Pedicle groove deep and roughly 0.8mm long, infilled and preserved as a parallel-sided ridge (Fig.6.1-2), extending posteriorly across and dividing the pseudointerarea into two portions comprising proparea. Flexure lines not well preserved. The shell is about 5.14mm long and 4.1mm wide with the maximum wide anterior to midlength (Fig 6.1). The pedicle groove in the ventral pseudointerarea is slightly wide and preserved as a parallel-sided ridge with pronounced relief, estimated approximately 0.8 mm in width (Fig 6.2). The shell surface is provided with some vague and closely spaced concentric growth line.

Remarks: The shape and outline of the shell strongly resemble *Eoobolus* from the lower Cambrian mudstone of Wulongqing Formation (Guanshan fauna) in eastern Yunnan (Hu et al., 2013). A specimen of the shell of *Eoobolus* from the Guanshan fauna is illustrated here for comparison (Fig. 6.3). As seen in Fig. 6.1, the shell has subtriangular shell outline and well-defined and developed pedicle groove. When compared to acid-etched specimens from contemporary carbonates, the specimens have no recognizable distinctive pustulose ornamentation on the postlarval shell surface. However, the biases in shell ornaments could be attributed to coarser preservation of brachiopod shells in siliciclastic deposits.

The lingulid brachiopods of *Eoobolus* have a cosmopolitan distribution, largely known from the Botomian Stage (Series 2, Stage 4) and up to Stage 5 of Series 3 in many regions of the world, such as southern China (Hu et al., 2013; Zhang et al., 2014b), Siberia (Ushatinskaya and Korovnikov, 2014), Canada (Balthasar, 2009), Greenland (Skovsted and Holmer, 2005), Antarctica (Holmer et al., 1996). They are characterized by finely pitted larval and pustulose postlarval shells, and placed in a separate family

Eoobolidae coined by Holmer, Popov and Wrona 1996, in view of the diagnostic shell ornamentation characters. Nevertheless, Balthasar (2009) questioned the validity of the diagnostic features of *Eoobolus*, and reclassified the genera *Eoobolus* into the family Zhanatellidae Koneva, 1986. However, most specimens known belonging to *Eoobolus* exhibit no apical emarginature in ventral valve that forms the basis for diagnosis of Family Zhanatellidae. The early-middle Cambrian lingulid brachiopods, widely occurring in Siberian platform and frequently assigned to the genera *Lingulella* in earlier time (Pelman, 1977), have been revised and re-described most recently by Ushatinskaya and Korovnikov (2014). As a result, the oldest lingulids known from the Siberian platform can be referred to *Eoobolus*, with the earliest occurrence of the species *E. pelmani* Ushatinskaya et Korovnikov, 2014 in the Judomia Zone of Atdabanian Stage, and other species of *Eoobolus* since Botomian upwards (Ushatinskaya and Korovnikov, 2014).

6. Discussion

Recently, records of soft-part preservation in brachiopods have increased markedly. Nevertheless, most of the known soft parts are restricted to fossilized pedicles notably from the exceptional Cambrian Chengjiang Lagerstätte (Hou et al., 2004; Hu et al., 2010; Zhang and Holmer, 2013). The exceptionally preserved pedicles provide unique insights into the palaeoecology of early brachiopods and their commensal relationships with other organisms (Zhang et al., 2010), which are not usually available from the study of shells alone (Zhang et al., 2006, 2007b, c, 2008b, 2011a, b; Wang et al., 2012). According to the current studies and discoveries from the Chengjiang fauna (Zhang et al., 2008b, 2010), early Cambrian calcareous-shelled brachiopods from among Kutorginida (Zhang et al., 2007b), Obolellida (Zhang et al., 2011b) and Chileida (Zhang et al., 2011a), have thick, stout and massive pedicles with their distal ends normally attached to fragmentary bioclasts of other organisms (Zhang and Holmer, 2013). By contrast, organophosphatic-shelled brachiopods are commonly provided with thin and elongate pedicles with their bulb-like distal ends buried into soft sediments thus providing anchorage; some specimens are known to wrap the pedicle around other erect sessile benthos, such as sponges (Zhang and Holmer, 2013). The latter cases have been broadly known from Lingulida (Jin et al., 1993), Acrotretida (Wang et al., 2012), Siphonotretida (Holmer and Caron, 2006; Zhang et al., 2010; Hu et al., 2010) and lingulids-like stem group (Zhang et al., 2014a).

Palaeobolus is a cosmopolitan linguloid brachiopod from the Cambrian Stage 4 (Botomian) to Stage 5 (Amgaian), and hitherto known only from Canada, Kazakhstan and China (Holmer and Popov, 2000). In China, *Palaeobolus* was first introduced by Zeng, 1987, who described *P. liantuoensis* Zeng, 1987 based on material derived from the Lower Cambrian Shuijingtuo Formation in the Yangtze gorges area of South China.

Since then, no further investigation of this brachiopod genus has been published. This is the first report of pedicle remains from *Palaeobolus*.

In eastern Yunnan, the Family Lingulellotretidae is represented exclusively by *Lingulellotreta ergalievi* (formerly *Lingulepis malongensis*) with a lowermost occurrence in the middle-upper Yu'an-shan Formation (*Eoredlichia* trilobite Zone) and disappears in the subsequent stratigraphic successions including the silty mudstone that host the Guanshan biota (Hu et al., 2013; Zhang et al., 2014b). By contrast, *Eoobolus* (Zhang et al., 2014b), like the coeval acrotretoid brachiopods, have a lowermost occurrence at the base of the Wulongqing Formation (*Palaeolenus* trilobite Zone) where it can be accumulated into lower-diversity and high-abundance of shell concentrations at the middle *Palaeolenus* trilobite Zone.

Nonetheless, the discovery of *Lingulellotreta* in the Shipai Formation (*Redlichia meitanensis* and *Palaeolenus lantenoisi* zones) represents an important stratigraphical extension of the range of this genus to the upper Series 2, Stage 4 (equivalent to upper Botomian Stage in Siberia) of the Yangtze Platform. This suggests that the occurrence of *Lingulellotreta* in the lower Cambrian of South China seems likely diachronous. In the Three Gorges area, the two lingulid taxa have a FAD in the uppermost bioclastic limestone of the Shuijingtuo Formation (our unpublished material) and range into the overlying siltstone and muddy siltstone of the Shipai Formation (*Redlichia* trilobite Zone), which is normally correlated with the late Botomian in Siberia. In Kazakhstan, *Lingulellotreta ergalievi* Koneva, 1983 also appears for the first time as well in the late Botomian (*Redlichia chinensis* Zone) (Holmer et al., 1997).

In summary, lingulids and acrotretids became abundant for the first time in the late Tsanglangpuan Stage in China, and the high-abundance occurrence of lingulid and acrotretid brachiopod faunas in themselves are evidence of a late Tsanglangpuan or Botomian-equivalent age (Epoch 2, Age 4); there is limited evidence for presence of concentrations of lingulid and acrotretid assemblages in the Chiungchussian (equivalent to Age 3) Stage of China. The same pattern of lingulid occurrence also exists in Siberia (Ushatinskaya, 2008; Ushatinskaya and Korovnikov, 2014), Australia (Ushatinskaya and Holmer, 2001), and Antarctica (Holmer et al., 1996).

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648

649 **Fig.1.** Showing the stratigraphical range of the Shipai fauna containing the
650 brachiopods with pedicle described in this paper, and the early Paleozoic occurrence of
651 soft-part preservation of brachiopods in geological records with references, in
652 ascending order, respectively to Zhang et al., 2008; Zhang and Hua, 2005; Hu et al.,
653 2010; Balthasar and Butterfield, 2009; Holmer and Caron, 2006; Balinski and Sun,
654 2013; Bassett et al., 2009 and Sutton et al., 2005.

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656

658 **Fig.2.** Simplified geological map, Palaeogeography, fossil localities, and stratigraphy.
659 1. distribution of principal continental blocks, arc terranes and sutures of China. 2. the
660 early Cambrian paleogeographic map of the Yangtze platform, modified from Zhang
661 X.L. et al., 2008; showing the fossil localities of exceptional Cambrian faunas, such as
662 the Chengjiang (1), Guanshan (2), Balang (3), Shipai (4) and Kaili (5) faunas from the
663 Yangtze platform; the inset box indicating the location of the Three Gorges area. 3.
664 Geological map of the Yangtze Gorges region showing of the localities of the
665 Wangjiaping section close to Shipai old town and the Aijiahe section. 4. stratigraphic
666 column with Trilobite (T) and Small Shelly Fossils (S) biozones of the Aijiahe Section
667 where most fossils illustrated in this paper were recovered (the specific level marked
668 by the black arrow).

Fig.3. Some specimens of trilobites accompanying the linguloid brachiopods from the Shipai Formation (Series 2) at Aijiahe section in the Three Gorges area of South China. 1. an indeterminate *Redlichia*, ELI SPT017. 2-5. Indeterminate trilobite probably akin to *Palaeolenus*, No. ELI SPT003, ELI SPT007, ELI SPT011A and ELI SPT009B; 6. A indeterminate juvenile trilobite, NO. ELI SPT016.

679

680 **Fig.4.** exceptionally preserved linguloid brachiopods tentatively referred to
681 *Palaeobolus liantuensis* from the Shipai Formation (Series 2) at Aijiahe section in the
682 Three Gorges area of South China. 1. A flattened specimen with dorsal and ventral
683 valves strongly compressed; note the proximal pedicle, ELI SP P001A. 2. Counterpart
684 of 1, ELI SP P001B, showing the well-defined and closely spaced growth lines.
685 Close-up view of 1, enlarged view of the impression of proximal pedicle. 4. A small
686 adult individual, ELI SP P003A. 5. Enlarged view of the counterpart of 4, showing the
687 paired symmetrical disposition of muscular scars. 6. Another small individual in the
688 same slab with 4, ELI SP P003(2).

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Fig.5. The linguloid brachiopod *Lingulellotreta* from the lower Cambrian Shipai Formation at the Wangjiaping section close to Shipai old town of Yichang City, Hubei province of southern China. 1-7. *Lingulellotreta* collected from the Cambrian Shipai Formation (Series 2) of the Three Gorges area. 1-3. General view of the composit mould of shell valves. 1. ELI SPB L001. 2. ELI SPB L002A. 3. ELI SPB L002B. 4-5. close-up and posterior view of the elongate oval foramen and enclosed homopseudodeltidium in the well-developed crescent pseudointerarea of *Lingulellotreta* in 1 and 2. 6-7. General and detailed views of ELI SPB L004. 8-9. two specimen of *Lingulellotreta* from the Maotianshan Shale Member of Yu'an Shan Formation (Chengjiang fauna) of eastern Yunnan. 8. ELI BL Lp002, 9. ELI BL 0079.

Fig.6. The linguloid brachiopod referred to *Eoobolus* from the Shipai Formation (Series 2) at Aijiahe section in the Three Gorges area and Yunnan Province of South China. 1-2. General and detailed view of the specimen of ELI SPB E001, showing the mud-infilled pedicle groove. 3. A specimen from lower Cambrian Wulongqing Formation (Series 2, Stage 4) in eastern Yunnan used to compare to 1 and 2.

Fig.7. Sketch drawings of the specimens of linguloid brachiopods from the Shipai Formation (Cambrian, Series 2) in the Three Gorges area, western Hubei Province, southern China. 1. Sketch of Fig. 4.1. 2. Sketch of Fig. 5.1. 3. Sketch of Fig. 6.1.