



Preservation of soft tissues in an Ordovician linguloid brachiopod from China

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The findings of preserved soft body parts including pedicle in the linguloid brachiopods are extremely rare in the fossil record of which the early Cambrian Chengjiang (southern China) and Burgess Shale (British Columbia) faunas are the most important. However, these characteristic Cambrian soft-bodied faunas largely disappeared from the fossil record well before the end of the Cambrian. Here we describe the first record of the pedicle in a linguloid brachiopod from the post-Cambrian strata, preserved with remarkable fidelity. Contrary to the Chengjiang and Burgess Shale-type faunas which are commonly preserved as essentially two-dimensional aluminosilicate or degraded organic carbon films or pyritized compressed fossils, the specimens now recovered from the Ordovician of China show a three-dimensional, pyritized pedicle with preserved external morphology, in detail. The presence of streamlined shell shape and burrowing shell sculpture in our specimens supports an assumption for infaunal mode of life of the genus. Since all linguloid brachiopods of the early Cambrian are interpreted as epifaunal or semi-infaunal, it seems that the here described Ordovician linguloid is the oldest representative of fully infaunal brachiopods. Apparently, the long vermiform and flexible linguloid pedicle has appeared as a functionally optimized construction.

Introduction

Among brachiopods with organo-phosphatic shells grouped in the subphylum Linguliformea one of the lineage, Linguloidea, has the longest fossil record as the oldest representatives were first revealed in the early Cambrian (Holmer and Popov 2000). They achieved the greatest diversification in the Cambrian and Ordovician, but today are represented by only two genera: *Lingula* Bruguière, 1797 and *Glottidia* Dall, 1870. The former has been widely quoted as an example of “living fossil” due to its simple and conservative shell shape, very similar to the Ordovician ancestors (Shimizu and Miura 1971; Hammond and Poiner 1984; but see Baliński 1997, 2001; Emig 2003). The exceptionally preserved fossil material from China described in this report, is referred to this lineage.

The findings of preserved pedicles in the linguloid brachiopods are extremely rare in the fossil record. The first findings were reported more than a century ago in *Lingula? lesueuri* Rouault, 1850 by Davidson (1881) from the Devonian of Devonshire (England) and in *Lingula equalis* by Walcott (1888)

from the Ordovician of New York (USA). Those findings are, however, quite incomplete and not very informative (Jin et al. 1993; Pettersson Stolk et al. 2010). Recently, discovery at the beginning of 20th century of numerous Cambrian fossils with preserved soft parts (Konservat-Lagerstätte) in the famous Burgess Shale (British Columbia) and later on in the Chengjiang Formation of Yunnan Province (China) unearthed also many findings of linguloid brachiopods with preserved pedicle (Jin et al. 1993; Zhang et al. 2003, 2004, 2006, 2007; Hou et al. 2004; Pettersson Stolk et al. 2010). However, these characteristic Cambrian soft-bodied faunas largely disappeared from the fossil record well before the end of the Cambrian (Van Roy et al. 2010). Recent discovery of soft-bodied assemblages in the Tremadocian (Lower Ordovician) Fezouata Formation in Morocco (Van Roy et al. 2010) and the Hirnantian (Upper Ordovician) Soom Shale of South Africa (Bassett et al. 2009) indicates that the Burgess Shale-type faunas on one hand, and specific preservational conditions on the other, persisted sporadically after the Cambrian (see examples for other brachiopods and invertebrates in, e.g., Südkamp 1997; Samuelsson et al. 2001; Sutton et al. 2005; Young et al. 2007; Bassett et al. 2009; Van Roy et al. 2010; Wang et al. 2012). This is also exemplified by the here reported discovery from the Floian sediments of China. However, contrary to the preservational characteristic of the Chengjiang and Burgess Shale-type faunas which are commonly preserved as two-dimensional aluminosilicate or degraded organic carbon films or pyritized compressed fossils (Gabbott et al. 2004; Butterfield et al. 2007), the specimens now recovered represent almost three-dimensional mineralized body fossils (Fig. 4E, F). Thus, this finding of the fossilized soft body preserved with remarkable fidelity in the Ordovician of China is of considerable palaeobiological and taphonomic significance.

Institutional abbreviations.—PKUM, Geological Museum of Peking University, Beijing, China; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Geological setting and preservational characteristics

The specimens of *Leontiella* sp. described here come from the strata representing the upper part of the Fenxiang Formation which is exposed near the village of Tianjialing in the Yichang area (known as Three Gorge area) of Hubei Province, southern China (Fig. 1). At this section the formation attains about 10 m

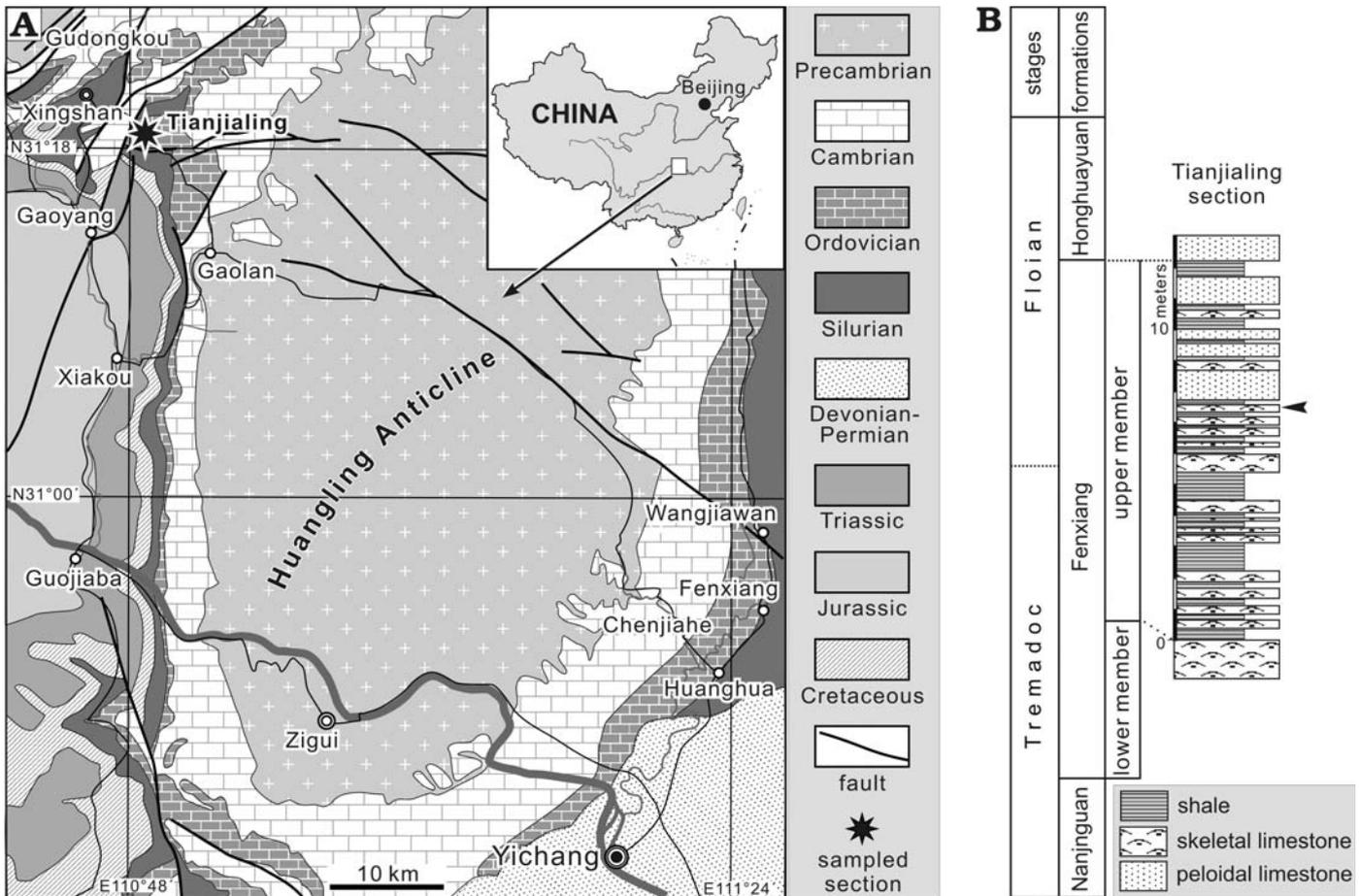


Fig. 1. Geographic and stratigraphic location of the Ordovician linguloid fauna. **A.** Geological sketch map of Yichang area, Hubei Province, China, showing locality of the Tianjialing section. **B.** Position of the bed from which the present material was collected (arrow head) in the Fenxiang Formation rock column at the Tianjialing section (after Baliński et al. 2012, modified).

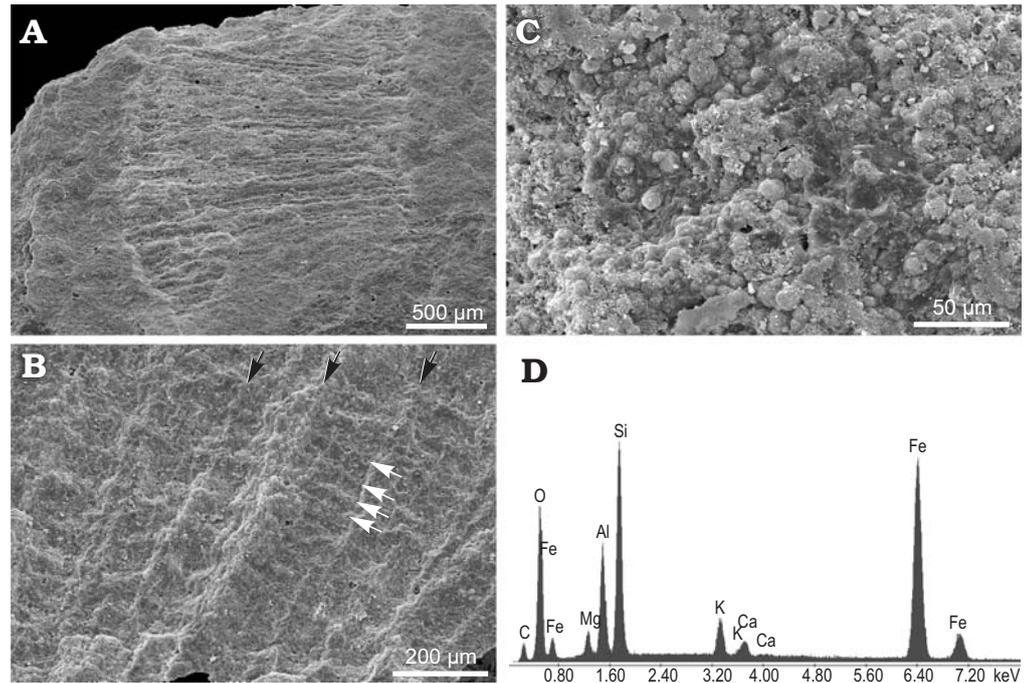
in thickness and consists mainly of dark grey to grey skeletal and peloidal limestones and greenish grey shales (Zhan and Jin 2007) which could be correlated with the Floian stage of the Ordovician period. The linguloid brachiopods with preserved soft parts found in the Fenxiang Formation are exceptionally rare: only six specimens were revealed from a single, few cm thick bed of greenish grey shale.

The shale with linguloid *Leontiella* sp. contains also trepostome and rhabdomesonate bryozoans, trilobites, benthic graptolites (*Acanthograptus* and *Koremograptus*; under preparation), orthid brachiopods, and conodonts. Especially important for the site is the recent discovery of the probably oldest reliable, pyritized colony of hydroids (Baliński et al. in press a) and pyritized horizontal burrows which probably represent the oldest record of life activity of marine nematodes (Baliński et al. in press b). Also noteworthy is discovery of remnants of the first fossil antipatharian corals (Baliński et al. 2012).

The fossilised pedicles are bright reddish-yellow in colour and thus are in striking contrast to the surrounding rock (Fig. 4A, C–E). The present appearance of the preserved soft tissue is a result of the oxidation of pyrite during the process of weathering paired with its pseudomorphosis with addition of clay minerals. Similar effects of weathering on preservational characteristics of

fossilised soft tissue have been recorded in the Cambrian, Ordovician, and Devonian fossils (e.g., Briggs et al. 1996; Gabbott et al. 2004; Zhang et al. 2007; Van Roy et al. 2010). The process of rapid and efficient pyritization of the soft tissue buried in sediment have taken place in the reducing microenvironment in which organic matter is broken down by the sulfate-reducing anaerobic bacteria to hydrogen sulfide. The latter reacts with dissolved iron from the surroundings to form pyrite or iron monosulfide which subsequently is transformed into pyrite (Briggs et al. 1991, 1996; Berner 1984; Schieber 2002; Rickard and Luther 2007). It should be noted that although pyrite is quite common in fine-grained marine sediments, the fossil record of pyritization of the soft tissue is extremely rare and can occur only in exceptional circumstance of sediment chemistry (Canfield and Raiswell 1991; Briggs et al. 1996; Farrell et al. 2009; Selden and Nudds 2012). According to Farrell et al. (2009) and Botting et al. (2011) only two Paleozoic faunas with abundant soft-tissue pyritization are known: Beecher's Trilobite Bed (Ordovician of New York State; Farrell et al. 2009) and Hunsrück Slate (Devonian of Germany; Bartels et al. 1998). However, occurrence of soft-tissue pyritization may be more widespread than has been recognized, but this oversight is caused by rapid weathering deterioration of pyritic specimens (Botting et al. 2011: 879).

Fig. 2. Fossilized pedicle of linguloid *Leontiella* sp. (ZPAL Bp 70/5) from the Early Ordovician Fenxiang Formation of Hubei Province, China. **A.** SEM micrograph of pedicle showing condensed transverse annulations. **B.** SEM micrograph of pedicle showing transverse annulations (black arrows) and longitudinal ridges (white arrows). **C.** SEM enlargement of the pyritized pedicle showing pseudomorphed framboids of pyrite. **D.** X-ray energy-dispersion spectrum (EDS) revealing relative composition of pseudomorphed framboids. Note the Fe peak, the total absence of S, and presence of Si, Al, Mg, and K connected with disseminated clay minerals; specimen coated with carbon.



The SEM studies revealed that the soft tissue of linguloid *Leontiella* sp. was preserved in the result of authigenic pyritization. The preserved pedicle consists of the tightly packed spherical framboids ranging from 6–12 µm in diameter (Fig. 2C). This implies that the original mineral was pyrite (FeS₂). However, elementary spot analyses confirms that Fe is abundant in the framboids whereas sulfur is totally absent (Fig. 2D). In addition to Fe the spectrum shows elevated quantity of Si, O, Al and less significant peaks for K and Mg, which indicate the presence of clay minerals.

Taxonomic remarks

The shell material from the studied outcrop are invariably disarticulated and crushed, frequently to very small pieces indicating that a transport of brachiopod shells for a notable distance was involved. The material consists of 5 fragments of ventral and 7 dorsal valves, and numerous small undetermined fragments. General outline of the shell, which can be deduced from the growth lines, appears elongate oval to somewhat spatulate. The most characteristic feature of the ventral valve is a subtriangular pseudointerarea divided by quite wide pedicle groove (Fig. 3A, C). A single internal mould of the fragmentary preserved dorsal valve shows a presence of low but long median ridge extending at least two-thirds of the valve length anteriorly (Fig. 3B). The exterior of valves is covered by weak concentric growth lines and fine but sharp radial rows of papillae or, more common, ridges (10–18 in 1 mm) with sawtooth-shaped crest (Fig. 3D). Although no complete adult valve is available it can be assumed that the total length of the shell may reach about 30–35 mm (see specimen in Fig. 4A). Our specimens are closely comparable with *Leontiella gloriosa* Yadrenkina, 1982 described from the Llanvirn of Siberia (Yadrenkina 1982: 73–74, pls. 9: 1–8; 10: 1–6, 13; 11: 1, 2) having very similar ventral pseudointerarea, dorsal internal structure, and similar ex-

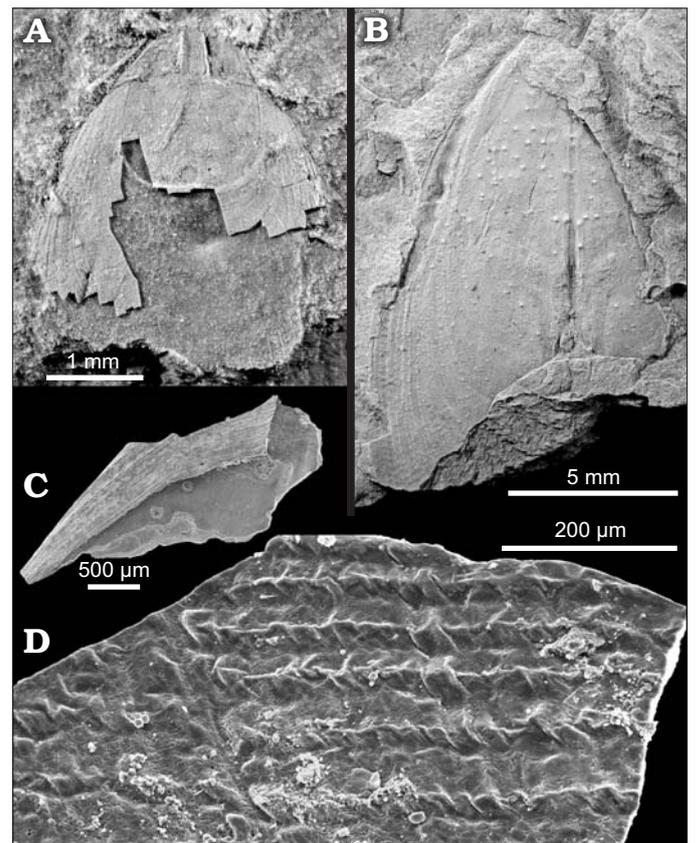


Fig. 3. Linguloid *Leontiella* sp. from the Early Ordovician Fenxiang Formation of Hubei Province, China. **A.** Incomplete ventral interior showing pseudointerarea and pedicle groove (ZPAL Bp 70/1). **B.** Incomplete dorsal internal mould showing median ridge (ZPAL Bp 70/2). **C.** Fragment of ventral valve showing left pseudointerarea and partly preserved pedicle groove (ZPAL Bp 70/3). **D.** External surface ornament (ZPAL Bp 70/4). C, D, SEM micrographs.

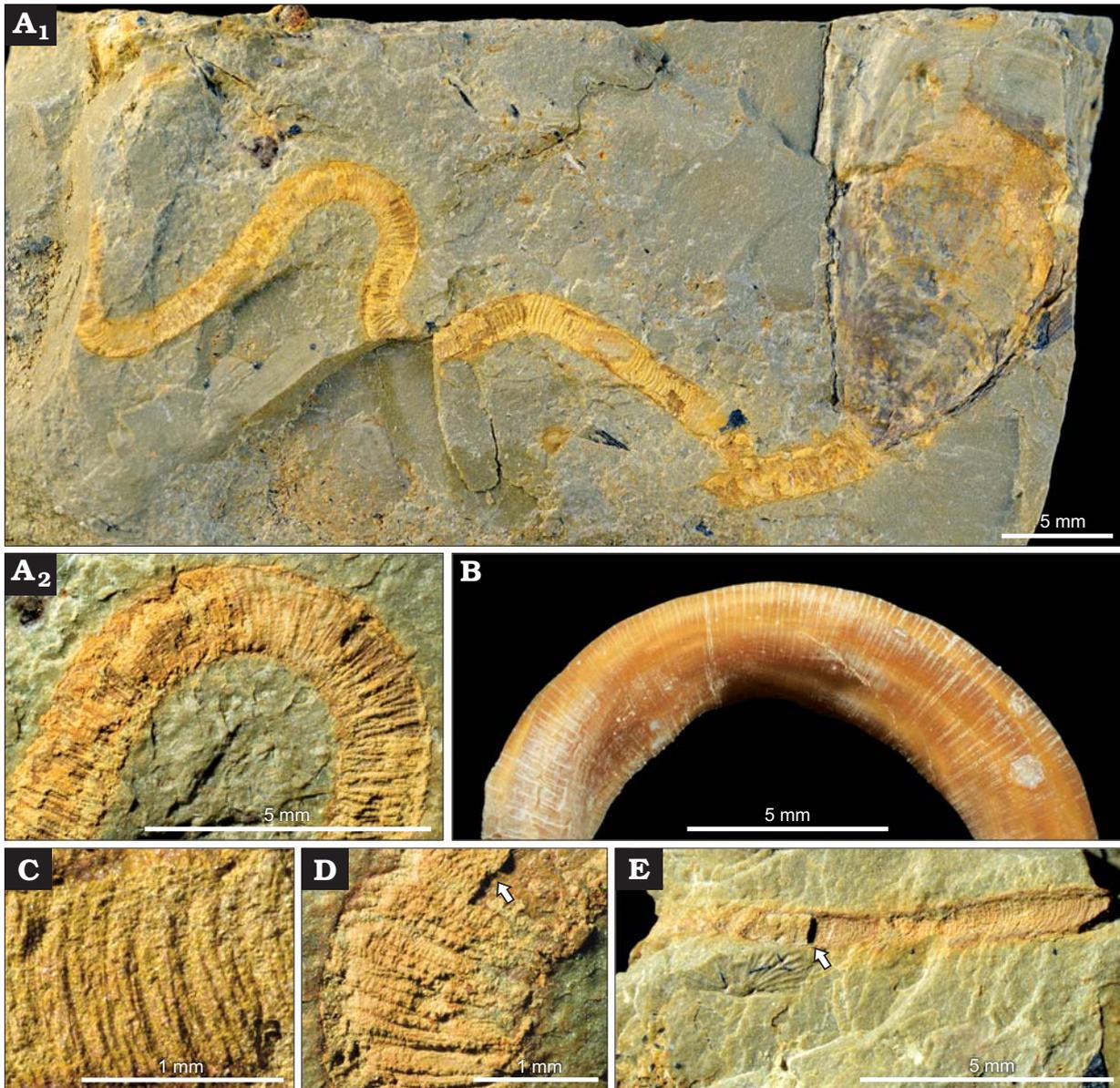


Fig. 4. Pedicle of the Early Ordovician and Recent linguloid brachiopods. **A**. The most complete specimen of *Leontiella* sp. from the lower Ordovician Fenxiang Formation of Hubei Province, China (PKUM02-0614a); general view showing partially preserved shell (in upper right of the photograph) and pyritized vermiform pedicle (A_1) and more detailed view (A_2). **B**. External morphology of the pedicle of extant *Lingula anatina* Lamarck, 1801, locality unknown (ZPAL Bp 70/6) (compare with A_2). **C**, **D**. Two enlargements of pedicle from Fenxiang Formation, Hubei Province, China; PKUM02-0614b (**C**) and PKUM02-0615 (**D**). Note the surface fine transverse annuli and wider transverse wrinkles, as well as short longitudinal ridges well preserved in **D**. A slight damage in the upper part of **D** (arrowed) shows some thickness of the preserved pedicle. **E**. Fragment of pedicle with well preserved external morphology from Fenxiang Formation, Hubei Province, China (PKUM02-0616); a damage shows three-dimensional aspect of the preserved pedicle.

ternal ornamentation which, however, in the Chinese species more frequently consists of sharp ridges. Unfortunately, the incomplete and very fragmentary material from Tianjialing makes specific assignment impossible.

Description

In the material presently recovered the most complete specimen is preserved on a small slab of greenish-grey shale measuring about 49 by 34 mm (Fig. 4A). The specimen shows posterior part of the shell together with the pedicle which emerges between valves'

beaks. Both the pedicle and the shell extend on the same bedding plane. There is no evidence of other preserved soft parts. The total length of the shell is not possible to measure with confidence because it is not preserved in its full length but may be estimated at about 30–35 mm. The preserved pedicle is 48.4 mm long, but including its presumable distal end which is visible at the margin of a slab, the pedicle total length can be estimated at about 62 mm. It appears that the pedicle is approximately two times longer than the shell. The presumable distal end of the pedicle is provided with a terminal short bulb. The pedicle is gently, to rather tightly S-shaped, and also folded over once at about 5 mm from the proxi-

mal end. The thickness of the pedicle is greatest in the proximity to the shell where it attains 2.4 mm embracing the umbonal region of the ventral valve; its remaining part maintains almost an even thickness which ranges from 1.8 to 1.6 mm distally and thus corresponding to 8–10% of the total width of the shell.

The surface of the pedicle is preserved in exceptional detail and shows very clear transverse, parallel annulations which constitutes of very fine rings of frequency 30–40 in 1 mm (disposed at intervals 25–33 μm) (Figs. 2A, B, 4A₂, C, D). On the annulation a second order of slightly wider transverse wrinkling is often superimposed (Fig. 4C). Each of the wrinkles encompass about 2–7 fine annulations. The annulation is equally conspicuous on the whole length of the pedicle, most probably excluding the terminal bulb. Besides the transverse annulation and wrinkling the surface of the fossil pedicle bears longitudinal ridges (Figs. 2B, 4A₂, D). These ridges are short being usually disrupted by the annulation. There are about 10–12 ridges in mm.

Besides the most complete specimen described above, there are also five other specimens (including two counterparts) showing fragments of pedicle. They are preserved without a shell but in all probability belong to the same species. The specimens preserve 9, 22, and 29 mm long fragments of pedicle, respectively. Dimensions and details of their surface morphology generally are very similar to those in the specimen described above.

Discussion

Both extant linguloid genera are infaunal burrowers and this mode of life has been assumed for the majority of the fossil representatives of the group. However, the earliest history of the linguloids shows, that in the early Cambrian some of them were epibenthic with the pedicle attached to a hard substrate whereas other were semi-infaunal with only the distal end of pedicle buried in the soft sediment (Zhang et al. 2008). *Xianshanella haikouensis* Zhang and Han, 2004 and problematic *Longtancunella chengjiangensis* Hou, Bergström, Wang, Feng, and Chen, 1999 from the Chengjiang are examples of the epibenthic and fixosessile early brachiopods (Holmer and Caron 2006; Zhang et al. 2006; Zhang et al. 2011; see also Wang et al. 2012 for an example of attached epibenthic acrotretide linguliform). On the other hand "*Lingulella*" *chengjiangensis*, *Lingulellotretra malongensis*, *Acanthotretella spinosa*, and presumably *Lingulella waptaensis* and *Diandongia pista* represent most probably the semi-infaunal mode of life (Zhang et al. 2006; Hu et al. 2010; Pettersson Stolk et al. 2010). Thus, up to now no truly infaunal burrower among the early Cambrian linguloids has been revealed.

In comparison with the Cambrian linguloid brachiopods which were characterised by rather sub-circular to oval shell outline which is not very suitable for burrowing, *Leontiella* sp. from the Ordovician of China possessed a more elongate, "streamlined" shell. The described specimens possess also a characteristic sculptural pattern in form of radially arranged sharp, sawtooth-shaped ridges (Fig. 3D) similar to those in, e.g., Middle–Late Ordovician lingulomatid *Lingulasma* Ulrich, 1889 (Cooper 1956). Savazzi (1986, 1991) suggests that several genera of the family Obolidae (*Leontiella* belongs to this family) were infaunal and had special-

ized burrowing sculptures of the shell exterior as divaricate terraces, triangular spines, and tubercles. *Lingulasma*, possessing similar burrowing sculptures as *Leontiella* sp., was found in the Middle Ordovician of the USA in the life position within vertical burrows (Cooper 1956; Pickerill 1973). Thus, the spatulate and streamlined shell shape and the presence of radial sawtooth-shaped ridges in *Leontiella* sp. supports assumption for infaunal mode of life of the genus. This assumption is supported also by comparison of the pedicle anatomy of *Leontiella* sp. with the extant representatives of the group. For example, the density of the fine pedicle annulation measured in the studied specimen of extant *Lingula anatina* is almost identical with the annulation in Ordovician specimen and attains about 40 annuli in 1 mm (30–40 in 1 mm in *Leontiella* sp.; Fig. 4B). Although the extent of the visceral area of both valves is poorly defined and development of muscle system suitable for burrowing in the Ordovician form is difficult to assess, it seems that its strong pedicle might have been well adapted to burrowing. It should be noted, however, that similarity in a general appearance of pedicle seems not conclusive for burrowing because, as noted above, long muscular pedicle is known also in the Cambrian epibenthic linguliforms. Thus, although the pedicle morphology of *Leontiella* sp. is not an unambiguous argument for burrowing, it does not contradict an infaunal life style either.

It seems probable that transition from epifaunal fixosessile to fully infaunal mode of life in the linguloid brachiopods developed after the early Cambrian but before early Ordovician. The Upper Cambrian obolid *Rebrovia* Popov and Kazanovych, 1989 (see Holmer and Popov 2000: 52, fig. 20: 2) which possesses ornament in the form of fine undulating rugae (may be regarded as burrowing sculpture) may appear as an early candidate for acquiring infaunal life style. As noted above some of the early Cambrian forms were most likely semi-infaunal (Zhang et al. 2008; Pettersson Stolk et al. 2010) and thus reveal the beginning of this process. According to Savazzi (1986, 1991), however, the characteristics of burrowing sculptures in Obolidae (and Lingulasmataidae) indicate that, contrary to Lingulidae, they burrowed by entering the sediment pedicle-first and thus suggesting an independent acquisition of infaunal life habit by these families.

It appears that the long vermiform and flexible linguloid pedicle appeared quite functionally successful and persisted for about 500 Ma without major morphological modification.

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