UPPSALA
UNIVERSITET

<http://uu.diva-portal.org>

This is an author produced version of a paper published in *Acta Zoologica* (published by Blackwell Publishing on behalf of The Royal Swedish Academy). This paper has been peer-reviewed but does not include the final publisher proof-corrections or journal pagination.

Citation for the published paper:

Sandra Pettersson Stolk, Lars Erik Holmer and Jean-Bernard Caron
"First record of the brachiopod *Lingulella waptaensis* with pedicle from the
Middle Cambrian Burgess Shale"

Acta Zoologica, 2010, Vol. 91, Issue 2, pp. 150-162

URL: <http://dx.doi.org/10.1111/j.1463-6395.2009.00394.x>

The definitive version is available at <http://wileyonlinelibrary.com>.

Access to the definitive version may require subscription.

First record of the brachiopod Lingulella waptaensis with pedicle from the Middle Cambrian Burgess Shale

Sandra Pettersson Stolk¹, Lars Erik Holmer¹ and Jean-Bernard Caron²

¹Uppsala University, Department of Earth Sciences / Palaeobiology, Villav. 16, SE-75236 Uppsala, Sweden; ²Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6.

Abstract

Pettersson Stolk S., Holmer L.E, and Caron, J-B. 200#: First record of the brachiopod Lingulella waptaensis with pedicle from the Middle Cambrian Burgess Shale.- *Acta Zoologica* (Stockholm) ##: ###-###

The organophosphatic shells of linguloid brachiopods are a common component of normal Cambrian-Ordovician shelly assemblages. Preservation of linguloid soft-part anatomy, however, is extremely rare, and restricted to a few species in Lower Cambrian *Konservat Lagerstätten*. Such remarkable occurrences provide unique insights into the biology and ecology of early linguloids not available from the study of shells alone. Based on its shells, Lingulella waptaensis Walcott, was originally described in 1924 from the Middle Cambrian Burgess Shale but despite the wide-spread occurrence of soft-part preservation associated with fossils from the same levels, no preserved soft parts have so far been reported. L. waptaensis is restudied herein based on 396 specimens collected by

Royal Ontario Museum field parties from the Greater Phyllopod Bed (Walcott Quarry Shale Member, British Columbia). The new specimens, including three with exceptional preservation of the pedicle, were collected *in-situ* in discrete obrution beds. Census counts show that L. waptaensis is rare but recurrent in the Greater Phyllopod Bed, suggesting that this species might have been generalist. The wrinkled pedicle protruded posteriorly between the valves, was composed of a central coelomic space, and was slender and flexible enough to be tightly folded, suggesting a thin chitinous cuticle and underlying muscular layers. The nearly circular shell and the long, slender, and highly flexible pedicle suggest that L. waptaensis lived epifaunally, probably attached to the substrate. Vertical cross-sections of the shells show that L. waptaensis possessed a virgose secondary layer, which has previously only been known from Devonian to Recent members of the Family Lingulidae.

Sandra Pettersson Stolk. 2008. Department of Earth Sciences /

Palaeobiology, Villav. 16, SE-75236 Uppsala, Sweden.

E-mail: Sandra.Pettersson@geo.uu.se

Keywords

Brachiopoda, Lingulella, pedicle, Middle Cambrian, Burgess Shale.

Introduction

The shells of organophosphatic linguloid brachiopods, routinely referred to the poorly understood genus Lingulella Salter, are common in Cambrian-Ordovician deposits

(Sutton *et al.* 2000), where only the shell morphology can be used for reconstructing elements of the soft anatomy and mode of life. Two major Cambrian *Konservat Lagerstätten* have yielded abundant linguloid brachiopods; the Middle Cambrian Burgess Shale and the Lower Cambrian Yuanshan Formation Maotianshan Shale (Chengjiang) biota (Briggs *et al.* 1994; Chen and Zhou 1997; Hou *et al.* 2004; Shu *et al.* 2003). In the Yuanshan Formation, two linguloid species ('Lingulella' chengjiangensis, Lingulellotreta malongensis) as well as more problematic linguliforms, (e.g. Longtancunella chengjiangensis, Xianshanella haikouensis), were described with preserved soft parts such as lophophores and pedicles (e.g., Zhang *et al.* 2004, 2005, 2006, 2007a; Hou *et al.* 2004). Jin *et al.* (1993, Fig. 3:6) illustrated one specimen of Lingulella sp. with a preserved proximal part of a pedicle from the Burgess Shale, but this specimen belongs to the unrelated stem-group brachiopod *Acanthotretella* (Holmer and Caron, 2006). The only morphological study of L. waptaensis available to date (Walcott, 1924) was based on shells alone. Unfortunately, in addition to the lack of anatomical characters, Walcott's study (1924) was based on only a few specimens with unclear stratigraphic provenance, information on shell microstructure was lacking and the morphological descriptions of the shell itself remained preliminary. Here we redescribe this taxon based on abundant new material that was collected *in-situ* and includes specimens with preserved pedicles. In addition to exceptionally preserved soft parts the new material offers novel data on the shell microstructure and contributes towards understanding the mode of life of this poorly known brachiopod.

Materials and methods

This study is based on 396 specimens (representing both part and counterpart when available), many of them complete articulated shells with both valves preserved. The specimens come from *in-situ* collections made by Royal Ontario Museum teams between 1993 and 2000 from fine-grained siliciclastic mudstone beds in the Greater Phyllopod Bed (GPB, Walcott Quarry Member on Fossil Ridge, British Columbia). The 325 specimens of L. waptaensis previously identified during a census of 15,875 slabs by JBC from the GPB community (Caron and Jackson 2006) in 28 bed assemblages (BA) were re-examined by SP to confirm their taxonomic identifications (Fig. 1). 321 out of the previously-identified 325 L. waptaensis specimens occurred in 26 BAs, each of which contained at least 300 specimens of various other taxa. Relative abundances of L. waptaensis in the GPB provided in this paper were calculated only for these 26 BAs (Caron and Jackson 2006). Additional specimens were studied by SP in previously unstudied collections from the GPB. These specimens, including the three specimens with soft parts described in this paper, are not included in the relative abundance counts presented in Fig. 1.

Pictures were taken with polarization filters on both the camera and the light source in order to increase contrast and reduce the amount of light reflected from some shiny areas of the specimens.

Scanning electron microscope (SEM) photographs of both coated and uncoated specimen (surfaces and cross-sections) and, where necessary, of rubber moulded specimens, were taken using a Zeiss Supra 35 VP microscope and a FEI-Electroscan ESEM 2020 microscope. Images were processed in Adobe Photoshop 6.0 using LucisArt software to correct variations of exposure within the same image. Measurements were

taken from live digital images using ECLIPSE NET 1.2 and Nis-Elements D 2.3 from a Nikon DS-5M digital camera mounted on a Nikon SMZ-1500 stereoscopic microscope at the Royal Ontario Museum.

Three vertical cross-sections of ventral valves of L. waptaensis specimens were prepared in order to study the shell microstructure. Element analysis (EDS) was performed on polished, cleaned and etched (using 5 percent HCl) cross-sections. In this study, shells are measured according to Sutton *et al.* (2000). The different parameters measured are provided in Figs. 2, 3, 4, and Table 1.

The specimens here designated as syntypes of L. waptaensis were collected by Charles D. Walcott from locality 35k and illustrated in Walcott (1924). Locality 35k corresponds to the Phyllopod Bed (Whittington 1971), an informal stratigraphic unit representing the upper two meters of the GPB. The exact horizons from which the specimens have been recovered are unknown.

Relative abundance and taphonomy

L. waptaensis is the most abundant brachiopod species in the GPB (see Fig.1). The relative abundance of individuals per BA (max 3.7 percent), and within the GPB as a whole (less than 1 percent) indicate that L. waptaensis is rare in the GPB community. This species however, is recurrent (present in 20 out of 26 BAs) suggesting that it could be adapted to a wide range of environmental conditions (eurytopic) (see Caron and Jackson 2008).

The only three specimens with preserved pedicles all come from a single level (BA-130) which also contains the majority of exceptionally preserved specimens of

Acanthotretella spinosa, the only other brachiopod with preserved pedicle from the Burgess Shale (Holmer and Caron 2006). Quantitative taphonomic and palaeoecological analyses of the different BAs in the GPB (Caron and Jackson 2006, 2008) show that BA-130 is characterized by the presence of well preserved soft-bodied organisms from a wide range of taxa. Many of these organisms were probably buried alive (e.g. brachiopod with pedicle) whereas other animals had died and started to decay prior to burial and thus represent time-averaged assemblages (e.g. brachiopod without pedicle) (Caron and Jackson 2006).

The specimens of L. waptaensis occur individually and sometimes in clusters with parallel bed orientation (Fig. 5A). When occurring in clusters there is no evidence of sorting or preferred orientation and the lack of isolated valves (shells are either articulated or, if disarticulated, with both valves in close proximity) suggests little or no transportation after death. Most shells are dorsoventrally compressed parallel to the bedding plane. Some fossils so strongly flattened that it is very difficult to distinguish between dorsal and ventral valves. In some rare cases, the shells appear to be preserved laterally. The shells are often cracked which suggests that they were originally mineralized (Fig. 5B, C, D, E, F).

The pedicle is preserved as a dark, possibly carbonaceous and partially aluminosilicified flattened compression like other compression fossils from the Burgess Shale (Butterfield *et al.* 2007). Judging by its orientation and loops, the pedicle extends parallel to the bedding plane and was highly flexible. No other clear evidence of soft tissue preservation has been observed, except perhaps putative symmetrical muscle markings on the shell (Fig. 5C).

Systematic palaeontology

Class Lingulata Gorjansky and Popov, 1985

Order Lingulida Waagen, 1885

Superfamily Linguloidea Menke, 1828

Family Obolidae King, 1846

Genus Lingulella Salter, 1866

Type species. By subsequent designation of Dall, 1870, p.159; Lingula davisii M'Coy, 1851b.

Diagnosis. (see Sutton *et al.* 1999, 2000).

Remarks. Based on their revision of the type species Lingulella davisii (M'Coy, 1851), Sutton *et al.* (2000) compared the genus Lingulella and a selection of related taxa (e.g. Obolus Eichwald, 1829, Ungula Pander, 1830, Palaeobolus Matthew, 1899, Palaeoglossa Cockerell, 1911, Lingula Bruguière, 1797) in an attempt to clarify the generic relationships among them. The type species L. davisii (M'Coy, 1851) is the only well studied member of the genus Lingulella after its redefinition by Sutton *et al.* (2000). The same authors compared L. davisii with the few well known species of Lingulella in close stratigraphic and palaeogeographic proximity as Lingulella bella (Walcott, 1888) and Lingulella antiquissima (Jeremeyew, 1856), although the latter has been shown to represent a new genus (Popov *et al.* 2002). L. antiquissima (Jeremeyew, 1856) was

synonymized with the British species Lingulella nicholsoni Callaway, 1877 by Popov and Holmer (1994) and considered two distinct species by Sutton *et al.* (1999). The Lower Cambrian lingulid 'Lingulella' chengjiangensis was first described and assigned to the genus Lingulella by Jin *et al.* (1993); however, since little is known about its internal morphology and shell features the generic assignment is uncertain (see also Zhang *et al.* 2008); moreover, the detailed anatomy of the pedicle of 'L.' chengjiangensis differs from that of Lingulella waptaensis described below.

Lingulella waptaensis Walcott, 1924

Figs. 5, 6, 7, 8, 9, 10.

Synonymy. Lingulella waptaensis - Walcott (1924), p. 496, pl. 122. Figs. 5, 6, 7, 8.

Lingulella waptaensis; Whittington (1985), p. 51, Fig. 4.13. Lingulella waptaensis;

Briggs *et al.* (1994), p. 100-101. Figs. 50, 51.

Type material. Because there is no designated holotype, Walcott's specimens are considered as syntypes (1924; USNM-numbers 69822-69824) (Fig. 5A, F).

Revised diagnosis. Elongate sub-oval in outline, weakly biconvex. Ornamentation on both valves consists of growth lines only. Interiors of both valves ornamented with irregularly distributed pits, visceral areas weakly impressed. Pseudointerareas of both valves with flexure lines; ventral pseudointerarea concave, divided into two subtriangular propareas by a pedicle groove; ventral interior with a poorly resolved central cluster of

muscle scars; dorsal interior with central and anterior lateral muscle scars, and median ridge markings; *vascula lateralia* divergent proximally and distally; *vascula media* diverging anteriorly. Pedicle slender and wrinkled, with a coelomic cavity, and protruding between the valves.

Remarks. Briggs *et al.* (1994) and Whittington (1985) presented brief descriptions accompanied with some general illustrations of L. waptaensis, which represent the only previous information published subsequent to the equally brief original description. Walcott (1924) considered L. waptaensis as the Pacific Province representative of Lingulella ferruginea Salter (1867) (in Murchison 1867) of the Atlantic Province Middle and Upper Cambrian formations of eastern North America and northwestern Europe. However, this species has not been restudied since Walcott (1912) and is too poorly known to compare it with L. waptaensis and determine if they are closely related, as Walcott suggested.

Description

Pedicle. Altogether, three specimens of L. waptaensis with pedicle impressions have been found. The total length of the pedicle is impossible to measure because it does not seem to be preserved in its full length (Fig. 5B, C, D, E) and the proximal part is too thin to be prepared (Fig. 5D). The pedicle protrudes posteriorly between the valves. The surface is wrinkled with strong annulations about 40-60 µm apart (Fig. 6A). In one of the specimens it is tightly folded into S-shapes and apparently rotated across itself (Fig. 6B),

suggesting a very flexible and easily deformable thin chitinous cuticle and muscular layers. No terminal bulb has been observed. The possible central coelom of the pedicle appears as a dark lineation which extends along the length of the pedicle and maintains its relative width throughout (50-120 μm) (Fig. 6C). The pedicle has a maximum length of 16.48 mm, corresponding to about two times the total valve length, and an average diameter of 0.312 mm which represents about 4 percent of the valve's total width. The pedicle maintains an even thickness as it emerges between the two valves through the ventral pedicle groove (Fig. 6D, E).

External shell morphology. The shell of L. waptaensis is elongate sub-oval and weakly biconvex. The ornamentation on the external surface of both valves consists of concentric growth lines that may vary in thickness along the length of the shell (Fig. 7A, B). The pseudointerareas of the ventral and the dorsal valve are both striated transversely and have well-defined flexure lines (Fig. 7C, D, E). The ventral pseudointerarea is concave and divided into two subtriangular propareas by a pedicle groove that is about 0.22 mm wide (Fig. 7C, D), extends along the posterolateral margin for 21 percent of the total valve length, and represents 61 percent of the total width of the valve. The dorsal pseudointerarea extends along the posterolateral margin for 13 percent of the total valve length, and represents 53 percent of the total valve width. The total size of the ventral valve ranges from 1.52 to 9.44 mm in length and from 1.26 to 9.08 mm in width, and from 1.44 to 8.58 in length and 1.26 to 9.08 in width for the dorsal valves.

Internal shell morphology. The interior surface of both valves is ornamented with irregularly shaped and distributed pits, varying in size from 0.15 mm to 0.28 mm in diameter. The ventral visceral area is poorly defined, occupies approximately 32 percent of the valve's length and includes a central cluster of muscle scars that is here interpreted as a composite of central, outside lateral, and middle lateral muscle scars (Fig. 8A, B, C). The dorsal interior shows umbonal (Fig. 7E), central, and anterior lateral muscle scars, a median ridge (Fig. 8D, E), and the impressions of the *vascula lateralia* (Fig. 8F) and *vascula media* (Fig. 8D, E). The pair of divided umbonal muscles appears as 'knob-like' scars (Fig. 7E) situated anterior to the pseudointerarea, 13 percent of the total valve width apart; the suboval central muscle scars are located submedially and in the center, 14 percent of the valve width apart. They are weakly divergent anteriorly, extending from 45 to 51 percent of the valve length. The pair of suboval scars of anterior lateral muscle is situated anteromedially, slightly diverging posteriorly and extending from 56 to 64 percent of the valve length; the lateral margins are 14 percent of the valve width apart. One specimen bears two symmetrically placed lighter stains on the anteriomedial portion of the darkened shell surface, possibly interpreted as muscle impressions (Fig. 5C). The *vascula lateralia* diverges initially and converges again anteriorly, at its widest it encloses 62 percent of the valve's width. The *vascula media* is well defined and diverges anteriorly. Especially on partially exfoliated specimens the impressions of fine radial canals occur on the inner side of the anterior and lateral margins of both valves. We interpret these as the terminal branches of vascular canals (Fig. 8E).

Shell structure. The shell of L. waptaensis is thin, ranging between just 5-51 μm in total thickness. Despite this, the shells show no signs of high flexibility like for example the co-occurring *Acanthotretella spinosa* (see Holmer and Caron 2006), but exhibit brittle deformation and are fractured when compressed on bedding planes (Fig. 5B, C, D, E, F). The shell of L. waptaensis most commonly shows signs of kaolinization and throughout the shell there are bands and areas of kaolinite (Fig. 9A, B).

Shell surface and primary layer. The outer shell surface carries irregular and variably arranged deformational folds that are up to 3 μm across (Fig. 7F). At a much lower magnification, the shell surface bears an ornamentation consisting of regular growth lines that are arranged into irregularly distributed and outwardly convex drapes that are defined by nick points up to 400 μm apart (Fig. 7B).

In cross-section no well-defined primary shell is identifiable. However, the outermost surface of the shell features a micro ornamentation with a 'fibrous-like' pattern with anatomizing, fine, slightly elevated rows, less than 1 μm wide, arranged orthogonal to the growth lines and the shell edge (Fig. 7G, H). It is composed of a series of thin platy layers, each around 100 nm thick and composed of cryptocrystalline apatite (Fig. 10A, B, C). This layer may partly represent a very thin recrystallized primary shell.

Secondary layer. The secondary layer is composed of thin, laterally not persistent stratiform successions of laminae that are each up to about 5-20 μm thick. Unlike most other Palaeozoic linguliforms there is neither evidence for any kind of baculate structure (in the sense of Holmer 1989, and Cusack *et al.* 1999), nor is there any well-defined evidence for compact laminae (in the sense of Cusack *et al.* 1999). The secondary layer is mainly characterized by a virgose structure (in the sense of Cusack and Williams 1996,

and Williams *et al.* 2000) which is mostly composed of various densely dispersed aggregates of spherulitic apatite taking the form of aggregates of various shapes including rings, mosaics and short rods. The individual aggregates are most commonly around 1-5 μm across with the smallest observed granular component somewhat less than 300 nm across (Fig. 9C). Successive virgose laminae are separated by stacks of thin platy layers, each around 100 nm thick and composed of cryptocrystalline apatite (Fig. 10D, E, F, G, H). A transverse cross-section of one specimen shows tube-like structures orthogonal to the shell lamination that can be traced through the laminae and that would probably correspond to the chitinous-wall canals described by Williams and Cusack (1999) (Fig. 9D, E).

Comparative discussion

Shell morphology

The combination of the sub-oval outline of L. waptaensis, with a smooth shell surface that only bears growth lines, and the internal davisate pits on the inside of both valves are typical features of the genus Lingulella (Sutton *et al.* 1999, 2000).

Although many of the internal morphological characters are not well known, the shell of L. waptaensis is most similar to the type species, L. davisii, in having pseudointerareas with transverse striations and well defined flexure lines in both valves and an anteriorly convergent *vascula lateralia* enclosing approximately the same area of the dorsal valve. However, the general shape of the shell differs slightly in that the lateral margins are more parallel in L. davisii as compared with L. waptaensis, which gives L.

waptaensis a more rounded outline. Internally, the pseudointerareas of L. waptaensis and L. davisii are similar in size relative to the valve. The pedicle groove of L. waptaensis is about half of the width of the pedicle groove of L. davisii.

Shell structure

Conway Morris (1990) first demonstrated that the linguliform brachiopods of the Burgess Shale can retain their phosphatic composition, and this is confirmed by this study. Moreover, this study indicates that the shell structure of L. waptaensis is well preserved enough to be interpreted in the light of what is known of Recent lingulids. The general good preservation of original phosphatic structures is also indicated by a brief preliminary study of the associated acrotretoid brachiopod Acrothyra gregaria, where the typical columnar shell structure (in the sense of Holmer 1989 and Williams and Holmer 1992) is well-preserved (Fig. 9F).

In Recent linguliforms (Lingula, Discina and Glottidia), the basic components of the mineralized shell are organically coated apatite granules, up to 10 nm across (Williams *et al.* 1992, 1994; Cusack *et al.* 1999); however, such minute details have been most likely obscured by recrystallization in L. waptaensis. All Recent linguliforms (e.g. Williams *et al.* 1992) and most studied fossil examples (e.g. Holmer 1989), have a well-defined outermost primary layer; however, this is not clearly observable in L. waptaensis, but it may be partly represented in the outer thin platy layer.

The most surprising aspect of the shell structure of L. waptaensis is the completely non-baculate and virgose nature of the secondary layer. Clear evidence for this type of shell structure has previously not been described from the Early Palaeozoic

(see also Cusack and Williams 2007), and the virgose-shelled stocks have been proposed as a potential monophyletic group that evolved from the more primitive baculate-shelled linguliforms in the Carboniferous (Williams *et al.* 2000; Williams 2007, Fig. 1898). A similar shell structure can be inferred from the work of Sutton *et al.* (2000, Fig. 10) for the type species Lingulella davisii. Although it cannot yet be completely ruled out that the apparent virgose structure described here represents a completely recrystallized baculate structure, the well preserved shell structure of the associated Acrothyra indicates that preservation of the original structure is relatively good.

The thin platy aphanitic layers in the outermost layer, as well as similar layers separating the virgose laminae of L. waptaensis, are most similar to laminar structures in the Carboniferous L. squamiformis, interpreted by Cusack and Williams (1996) as phosphatized organic membranes. This view is supported here. However, L. squamiformis lacks the outer platy aphanitic layers as well as the micro-ornamentation with fine elevated rows. This ornamentation is most similar to the pattern of anastomosing fibres of possible collagenous composition described from Recent Lingula by Curry and Williams (1983, p. 116, Fig. 7c), and it may represent a phosphatized fibrous layer at the base of the degraded periostracum and/or a thin primary layer. The larger surface patterns with drapes and nick points correspond entirely to those produced by stresses at the mantle edge caused by the movement of the setae, as suggested by Williams and Holmer (1992). The fine kaolinitic plates variously disposed within the virgose laminae of L. waptaensis are here interpreted as the kaolinization of the spaces originally filled by glycosaminoglycans (GAGs), as was proposed for similar structures in L. squamiformis by Cusack and Williams (1996) and Williams and Cusack (1996).

Pedicle

The pedicle of L. waptaensis is similar to that of the acrotheloid Diandongia pista, in that it protrudes posteriorly from a triangular pedicle groove (Zhang *et al.* 2003; 2008). The other known pedunculate Lower Cambrian Chinese brachiopods, including the linguloid ‘Lingulella’ chengjiangensis (Jin *et al.* 1993), and the problematic linguliforms Longtancunella chengjiangensis, Xianshanella haikouensis have pedicles protruding from the two valves (Jin *et al.* 1993; Zhang *et al.* 2006; 2007; 2008). In the Lower Cambrian lingulellotretid Lingulellotreta malongensis from the Chengjiang Fauna, the pedicle instead emerges through a ventral apical circular foramen at the end of an external pedicle tube that is continuous with an internal pedicle tube (Holmer *et al.* 1997; Holmer and Popov 2000). A similar type of pedicle is also found in the potential stem group brachiopod Acanthotretella spinosa from the Burgess Shale, but in this form the pedicle emerges from the apical foramen through a narrow external tube (Holmer and Caron 2006). In L. malongensis, X. haikouensis, and ‘Lingulella’ chengjiangensis the proximal portion of the pedicle encloses the apex of the ventral valve (Jin *et al.* 1993; Zhang *et al.* 2006).

The pedicles of L. waptaensis, A. spinosa, X. haikouensis, ‘Lingulella’ chengjiangensis and L. malongensis, show indications of a coelomic cavity and exterior circular annulations (Holmer and Caron 2006; Zhang *et al.* 2006; Jin *et al.* 1993). A central coelomic space has also been found in D. pista with no evidence of surface annulation (Zhang *et al.* 2003, 2007). A short smooth pedicle also appears to be present in the poorly known Middle Ordovician ‘Lingula’ aequalis (Walcott 1888, Jin *et al.*

1993). The pedicle of the problematic L. chengjiangensis lacks evidence of a coelomic cavity and its exterior is wrinkled (Zhang *et al.* 2003, 2007).

The pedicles of all Lower Cambrian pedunculate linguliforms are either folded into a gently S-shape (e.g. L. malongensis, 'Lingulella' chengjiangensis) or relatively straight (e.g. L. chengjiangensis, X. haikouensis). The pedicle of L. waptaensis is rather slender and tightly folded into S-shapes as described for A. spinosa (Holmer and Caron 2006). Lingulids like 'Lingulella' chengjiangensis, L. malongensis, L. chengjiangensis, and the problematic X. haikouensis have a much thicker pedicle (up to 19 percent of the valve width) when compared to 'L.' aequalis and A. spinosa (6-8 percent of the valve width), while D. pista and L. waptaensis both show a thin pedicle in proportion to the size of the valve (4 percent of the valve width).

According to Zhang *et al.* (2008), the wide morphological variety of lingulid pedicles from Cambrian deposits can be divided into two main groups based on their size, length and the nature of the substrate they were attached to. The first group includes elongate and slim pedicles with the distal end embedded into soft sediment, while the second group refers to thick and medium-length pedicles with the distal part attached to hard substrate. Lingulids like 'Lingulella' chengjiangensis, L. malongensis, the Middle Ordovician 'Lingula' aequalis, the potential stem group brachiopod A. spinosa, and presumably L. waptaensis would belong to the first category with their small shells possibly suspended above turbulence at the sediment-water boundary. The pedicle of the acrotheloid D. pista was also slim and long but it is difficult to imagine that its well-mineralized shell was suspended above the sea floor. More likely, it was semi-infaunal with its pedicle buried in the sediment and its ventral valve resting above it (Zhang *et al.*

2003, 2008). The second group only comprises the pedicles of L. chengjiangensis and X. haikouensis, whose relatively short and thick pedicles were adapted to an epibenthic mode of life.

Based on the available material it is not possible to reconstruct the exact mode of life for L. waptaensis, but it is unlikely that this species lived infaunally as suggested by the more rounded shape of the shell and the long and slender pedicle (Zhang *et al.* 2004a). L. waptaensis would have been more likely to rest on the sediment and, as proposed by Holmer and Caron (2006) for A. spinosa, the pedicle may have anchored the organism, thus allowing it to float above the sediment surface to prevent excessive mud intake. However, the lack of preserved terminal bulbs makes it impossible to identify which type of substrate the pedicle would have been attached to. A strong association between lingulate brachiopods and sponges has been previously reported based on qualitative estimates (e.g., Popov *et al.* 1994, from the Upper Ordovician of Estonia; Holmer *et al.* 2005, from the Lower Ordovician of USA), but there is no direct evidence that L. waptaensis was attached to sponges. Quantitative analyses of species association using abundance data, however, suggest that L. waptaensis tends to co-occur in bed assemblages with sponges and other suspension filter feeding organisms through the Greater Phyllopod Bed (Group 1 in Caron and Jackson 2008). The co-occurrence of the possibly benthic cyanobacterium Morania (Caron and Jackson 2006) with L. waptaensis on the same slabs indicates the existence of suitable substrates in the primary benthic community.

Acknowledgements

J-B Caron acknowledges the support of a Natural Sciences and Engineering Research Council of Canada postdoctoral fellowship. This is Royal Ontario Museum Burgess Shale Research Project Number 11. We thank Parks Canada for granting access to Royal Ontario Museum field crews (led by Desmond Collins) to collect specimens from the Burgess Shale. Grants from the Swedish Research Council (VR) supported Pettersson Stolk's and Holmer's work. We thank Sara Scharf and Uwe Balthasar for editorial corrections and comments.

References

- Briggs, D. E. G., Erwin, D. H. and Collier, F. J. 1994. *The Fossils of the Burgess Shale*.- Smithsonian Institution Press, Washington. pp. 238.
- Bruguère, J. G. 1797. Vers, coquilles, mollusques et polypiers. *Tableau encyclopédique et méthodique des trois règnes de la nature*, vol. 2. Agasse, Paris, pl. 190-286.
- Butterfield, N. J., Balthasar, U. and Wilson, L. A. 2007. Fossil diagenesis in the Burgess Shale.- *Palaeontology* **50**: 537-543.
- Callaway, C. 1877. On a new area of Upper Cambrian rocks in South Shropshire, with a description of a new fauna.- *Quarterly Journal of the Geological Society* **33**: 652-672.
- Caron, J-B. and Jackson, D. A. 2006. Taphonomy of the Greater Phyllopod Bed community, Burgess Shale.- *Palaios* **21**: 451-465.
- Caron, J-B. and Jackson, D. A. 2008. Paleocology of the Greater Phyllopod Bed community, Burgess Shale.- *Palaeogeography, Palaeoclimatology, Palaeoecology* **258**: 222-256.
- Chen J. Y. and Zhou, G. Q. 1997. Biology of the Chengjiang fauna.- *Bulletin of the National Museum of Natural Science* **10**: 11-106.
- Cockerell, T. D. A. 1911. The name *Glossina*.- *Nautilus* **25**: 96.
- Conway Morris, S., 1990. Burgess Shale. In Briggs, D.E.G. (Ed.): *Palaeobiology a synthesis*, 270-274. Blackwell Science.

- Curry, G.B. and Williams, A. 1983. Epithelial moulds on the shells of the early Palaeozoic brachiopod *Lingulella*.- *Lethaia* **16**: 11-118.
- Cusack, M. and Williams, A. 1996. Chemico-structural degradation of Carboniferous lingulid shells.- *Philosophical Transactions of the Royal Society of London, Series B* **351**: 33-49.
- Cusack, M., Williams, A. and Buckman, J. O 1999. Chemico-structural evolution of the shell of linguloid brachiopods.- *Palaeontology* **42**: 799-840.
- Cusack, M. and Williams, A. 2007. Biochemistry and diversity of brachiopod shells. In Kaesler, R. L. (Ed.): *Treatise on Invertebrate Paleontology. Part H. Brachiopoda*, pp. 2373-2395. The Geological Society of America and Kansas University Press, Lawrence, KS.
- Dall, W. H. 1870. A revision of the Terebratulidae and Lingulidae, with remarks on and descriptions of some Recent forms.- *American Journal of Conchology* **6**: 88-168, pl. 6-8.
- von Eichwald, C. E. 1829. Zoologia specialis, quam expositis animalibus tum vivis, tum fossilibus potassium Rossiae in universum, et Poloniae in specie, in usum lectionum publicarum in Universitate Caesarea Vilmensi habendarum, vol. 1. Josephi Zawadzki. Vilnae. 314 p., pl. 5.
- Gorjansky, V. Y. and Popov, L. Ye. 1985. Morfologiya, sistematicheskoye polozheniye I proiskhozhdeniye bezzamkovykh brachiopod s karbonatnoy rakovinoi (The morphology, systematic position, and origin of inarticulate brachiopods with carbonate shells).- *Paleontologicheskii Zhurnal* 1985: 3-13.
- Holmer, L. E. 1989. Middle Ordovician phosphatic inarticulate brachiopods from Västergötland and Dalarna, Sweden.- *Fossils and Strata* **26**: 1-172.
- Holmer, L. E., Popov, L. E., Koneva, S. P. and Rong, J. Y. 1997. Early Cambrian *Lingulellotreta* (Lingulata, Brachiopoda) from South Kazakhstan (Malyi Karatau Range) and South China (eastern Yunnan).- *Journal of Paleontology* **71**: 577-584.
- Holmer, L. E. and Popov, L. E. 2000. Class Lingulata. In Williams *et al.* (Ed.): *Treatise on Invertebrate Paleontology. Part H. Brachiopoda*, pp. 30-146. The Geological Society of America and Kansas University Press, Lawrence, KS.
- Holmer, L. E., Popov, L. E., Streng, M. and Miller, J. F. 2005. Lower Ordovician (Tremadocian) lingulate brachiopods from the House and Fillmore Formations, Ibex Area, Western Utah, USA.- *Journal of Paleontology* **79**: 884-906.

- Holmer, L. E. and Caron, J.-B. 2006. A spinose stem group brachiopod with pedicle from the Middle Cambrian Burgess Shale.- *Acta Zoologica* **87**: 273-290.
- Hou, X. G., Aldridge, R. J., Bergström, J., Siveter, D. J., Siveter, D. J. and Feng, X. H. 2004. *The Cambrian fossils of Chengjiang, China: the flowering of early animal life*. Blackwell Publishing, Oxford.
- Jeremejew, P. 1856. Geognostische Beobachtungen an den Ufern des Wolchow.- *Russisch-Kaiserliche Mineralogische Gesellschaft zu St. Petersburg, Verhandlungen* **10**: 63-84.
- Jin, Y. G., Hou, X. G. and Wang, H. Y. 1993. Lower Cambrian pediculate lingulids from Yunnan, China. *Journal of Paleontology* **67**: 788-798.
- King, W. 1846. Remarks on certain genera belonging to the class Palliobranchiata.- *Annals and Magazine of Natural History* **18**:26-42.
- Matthew, G. F. 1899. Preliminary notice of the Etcheminian fauna of Cape Breton.- *Bulletin of the New Brunswick Natural History Society* **4**: 198-208, pl. 4.
- M'Coy, F. 1851a. On some new Silurian Mollusca.- *Annals and Magazine of Natural History*, 2nd Series, **7**: 45-63.
- M'Coy, F. 1851b. On some new Cambro-Silurian Mollusca.- *Annals and Magazine of Natural History*, 2nd Series, **8**: 387-409.
- Menke, C. T. 1828. *Synopsis methodica molluscorum generum omnium et specierum earum quae in Museo Menkeano adservantur*. G. Uslar. Pyramonti. 91 p.
- Murchison R. I. 1867. *Siluria. A history of the oldest rocks in the British Isles and other countries. with sketches of the origin and distribution of native gold, the general succession of geological formations, and changes of the Earth's surface*. Third edition [as Fourth Edition, Including "The Silurian System"]. John Murray, London.
- Pander, C. H. 1830. Beiträge zur Geognosie des Russischen Reiches. St. Petersburg, xx + 165 p.
- Popov, L. E., Nolvak, J. and Holmer, L. E. 1994. Late Ordovician brachiopods from Estonia. *Palaeontology* **37**: 627-650.
- Popov, L. E. and Holmer, L. E. 1994. Cambrian-Ordovician lingulate brachiopods from Scandinavia, Kazakhstan, and South Ural Mountains. *Fossils and Strata* **35**: 156 pp.

- Popov, L. E., Holmer, L. E. and Miller, J. F. 2002. Lingulate brachiopods from the Cambrian-Ordovician boundary beds of Utah.- *Journal of Paleontology* **76**: 211-228.
- Salter, J. W. 1866. On the fossils of North Wales. In Ramsay A. C. (Ed.): *The geology of North Wales*, pp. 239-381, pl. 1-26. Memoirs of the Geological Survey of Great Britain and of the Museum of Practical Geology **3**.
- Shu, D. G., Conway Morris, S., Han, J., Zhang, Z. F., Yasui, K., Janvier, P., Chen, L., Zhang, X. L., Liu, J. N., Li, Y. and Liu, H. Q. 2003. Head and backbone of the Early Cambrian vertebrate *Haikouichthys*.- *Nature* **421**: 526-529.
- Sutton, M. D., Bassett, M. G. and Cherns, L. 1999. Lingulate brachiopods from the Lower Ordovician of the Anglo-Welsh Basin. *Monograph of the Palaeontographical Society, London* **1**: 1-60, pl. 1-8 (Publ. No. 610, part of Vol. 153).
- Sutton, M. D., Bassett, M. G. and Cherns, L. 2000. The type species of *Lingulella* (Cambrian Brachiopoda).- *Journal of Paleontology* **73**: 426-438.
- Waagen, W. H. 1885. Salt Range fossils, vol. I, Part 4. *Productus* Limestone fossils, Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologia Indica* (series 13) **5**: 729-770, pl. 82-86.
- Walcott C. D. 1888. A fossil *Lingula* preserving the cast of the peduncle.- Proceedings of the United States National Museum **11**: 480.
- Walcott, C. D. 1912. Cambrian Brachiopoda.- *United States Geological Survey Monograph* **51**: 1235 pp.
- Walcott, C. D. 1924. Cambrian and Ozarkian Brachiopoda. Cambrian geology and paleontology IV.- *Smithsonian Miscellaneous Collections* **67**: 477-554.
- Whittington, H. B. 1971. The Burgess Shale: history of research and preservation of fossils. In *Proceedings of the North American Paleontological Convention*, pp. 1170-1201. Field Museum of Natural History, Chicago.
- Whittington, H. B. 1985. *The Burgess Shale*. Yale University Press, New Haven.
- Williams, A. and Holmer, L. E. 1992. Ornamentation and shell structure of acrotretoid brachiopods.- *Palaeontology* **35**: 657-692.
- Williams, A., Mackay, S., and Cusack, M. 1992. Structure of the organo-phosphatic shell of the brachiopod *Discina*.- *Philosophical Transactions of the Royal Society, London, Series B* **337**: 83-104.

- Williams, A., Cusack, M., and Mackay, S. 1994. Collagenous chitinophosphatic shell of the brachiopod *Lingula*.- *Philosophical Transactions of the Royal Society, London, Series B* **346**: 223-266.
- Williams, A. and Cusack, M. 1996. Lingulid shell mediation in clay formation.- *Lethaia* **29**: 349-360.
- Williams, A. and Cusack, M. 1999. Evolution of a rhythmic lamination in the organophosphatic shells of brachiopods.- *Journal of Structural Biology* **126**: 227-240.
- Williams, A., Cohen, B.L., Cusack, M., and Long, S. 2000. Provenance of Atlantic lingulid brachiopods.- *Palaeontology* **43**: 999-1018.
- Williams, A. 2007. Evolution of the integument (mantel epithelium). In Williams *et al.* (Ed.): *Treatise on Invertebrate Paleontology, Part H. Brachiopoda*, pp. 2838-2842. The Geological Society of America and Kansas University Press, Lawrence, KS.
- Zhang, Z. F., Han, J., Zhang, X. L., Liu, J. and Shu, D. G. 2003. Pediculate brachiopod *Diandongia pista* from the Lower Cambrian of South China.- *Acta geologica sinica* **77**: 288-293.
- Zhang, Z. F., Shu, D., Han, J. and Liu, J. N. 2004. New data on the lophophore anatomy of Early Cambrian linguloids from the Chengjiang Lagerstätte, Southwest China.- *Carnets de Géologie* Letter 2004/04(CG2004-L04)-online.
- Zhang, Z. F., Han, J., Zhang, X. L., Liu, J. N. and Shu, D. G. 2004a. Soft tissue preservation in the Lower Cambrian linguloid brachiopod from South China.- *Acta Palaeontologica Polonica* **49**: 259-266.
- Zhang, Z., Shu, D., Han, J. and Liu, J. 2005. Morpho-anatomical differences of the Early Cambrian Chengjiang and Recent lingulids and their implications.- *Acta Zoologica* **86**: 277-288.
- Zhang, Z. F., Shu, D., Han, J. and Liu, J. N. 2006. New data on the rare Chengjiang (Lower Cambrian, South China) linguloid brachiopod *Xianshanella haikouensis*.- *Journal of Paleontology* **80**: 203-211.
- Zhang, Z. F., Shu, D., Han, J. and Liu, J. N. 2007. A gregarious lingulid brachiopod *Longtancunella chengjiangensis* from the Lower Cambrian, South China.- *Lethaia* **40**: 11-18.
- Zhang, Z. F., Han, J., Zhang, X. L., Liu, J., Guo, J. and Shu, D. G. 2007a. Note on the gut preserved in the Lower Cambrian *Lingulellotreta* (Lingulata, Brachiopoda) from southern China.- *Acta Zoologica* **88**: 65-70.
- Zhang, Z. F., Robson, S. P., Emig, C. and Shu, D. 2008. Early Cambrian radiation of brachiopods: A perspective from South China.- *Gondwana Research* **14**, (in press), doi: 10.1016/j.gr.2007.08.001.

Fig. 1 - Left, relative abundance of Lingulella waptaensis in bed assemblages (BA) with at least 300 specimens from the Middle Cambrian Greater Phyllopod Bed (Burgess Shale). Right, relative abundance of all brachiopods in the same stratigraphic interval. (modified from Caron and Jackson 2006).

Fig. 2 - Parameters measured for the dorsal and ventral valves of Lingulella waptaensis.

Wpi, pseudointerarea width; Lpi, pseudointerarea length; Wpg, pedicle groove width; L_{C1}, distance between posterior termination of central muscle scar and valve anterior; L_{C2}, distance between anterior termination of central muscle scar and valve anterior; L_{AL1}, distance between posterior termination of anterior lateral muscle scar and valve anterior; L_{AL2}, distance between anterior termination of anterior lateral muscle scar and valve anterior; L, valve maximum length; W_{VL}, *vascula lateralia* maximum width; L_{VA,C,OL,ML}, distance between anterior termination of cluster of central, outside lateral, and middle lateral muscle scars, together with the visceral area, and valve posterior; W, valve maximum width.

Fig. 3 - Plots of width/length for dorsal and ventral valves of *Lingulella waptaensis* based on 58 dorsal valves and 108 ventral valves from the Greater Phyllopod Bed (Burgess Shale).

Fig. 4 - Reconstruction of interior characters of the dorsal and ventral valves of Lingulella waptaensis. PG, pedicle groove; PIA, pseudointerarea; F, flexure line; U, divided umbonal muscle scar; VA, visceral area; C, central muscle scar; ML, middle lateral muscle scar; AL, anterior lateral muscle scar; M, median ridge; VL, *vascula lateralia*; VM, *vascula media*.

Table 1 Summary statistics for ventral and dorsal valves of Lingulella waptaensis from the Greater Phyllopod Bed (Burgess Shale).

Fig.5 - Digital camera photographs of Lingulella waptaensis from the Greater Phyllopod Bed (Burgess Shale); overall view. **A, F**. Syntypes. **B, C, D, E**. Specimens with preserved pedicle. **A**. USNM 69824, slab showing a group of dorsal and ventral valves parallel to the bedding plane. **B**. ROM 943484, specimen showing pedicle with its distal part missing. **C**. ROM 943315, specimen showing pedicle and two symmetrically placed lighter stains on the anterio medial portion of the darkened shell surface interpreted as putative muscle markings. **D**. ROM 943315, specimen showing part of pedicle preserved. **E**. ROM 940518, specimen showing part of pedicle preserved. **F**. USNM 69822, dorsal and ventral valves turned sideways from each other. Scales bars are 1 mm.

Fig. 6 - Lingulella waptaensis from the Greater Phyllopod Bed (Burgess Shale). **A**, **E**, are SEM photographs; **B**, **C**, **D**, are digital camera photographs. **A**, **B**, **C**. ROM 943315, detail of the pedicle with **annulations** in **A**; folding in **B**; coelomic cavity in **C**; all indicated by arrows. **D**. ROM 940518, detail of the pedicle insertion between the two valves. **E**. ROM 943484, detail of the anterior part of the pedicle. Scale bars are 30 μm in **A**; 1 mm in **B**, **D**, **E**; 500 μm in **C**.

Fig. 7 - SEM photographs of Lingulella waptaensis from the Greater Phyllopod Bed (Burgess Shale). **A.** ROM 971652, detail of the external surface of the shell showing concentric growth lines. **B.** ROM 970489, detail of the external surface of the shell showing drapes and nickpoints indicated by arrows. **C, D.** PMUCa16, detail of ventral pseudointerarea showing transverse striation and flexure lines, box in **C** indicates position of **D**. **E.** Same specimen as B, **G, H** after being etched, interior surface of the shell showing dorsal pseudointerarea with transverse striation and flexure lines, arrows point to umbonal muscle scars. **F.** PMUCa16, detail of folds on the external surface of the shell. **G, H.** ROM 970489, detail of the external surface of the shell showing micro ornamentation with 'fibrous-like' pattern indicated by arrows in **H**, box in **G** indicates position of **H**. Scale bars are 500 μm in A; 100 μm in B, **C, D, E**; 2 μm in **F, H**; 30 μm in **G**.

Fig. 8 - Lingulella waptaensis from the Greater Phyllopod Bed (Burgess Shale). **A, B, C**, are digital camera photographs. **D, E, F**, are scanning electron microscope photographs of an etched specimen. **A**. ROM 57786, specimen showing visceral area and muscle impressions; va = visceral area, c = central, ol = outside lateral, ml = middle lateral. **B**. ROM 980228, specimen showing visceral area and muscle impressions; va = visceral area, c = central, ol = outside lateral, ml = middle lateral. **C**. ROM 943484, specimen showing putative muscle striated impressions. **D, E**. ROM 970489, details of two slightly overlapping dorsal valve interior areas showing muscle impressions; **D**, vm = *vascula media*, c = central muscles, al = anterior lateral muscles; **E**, vc = vascular canals, mr = median ridge. **F**. ROM 970489, dorsal valve interior showing impressions of *vascula lateralia* (vl). Scale bars are 1 mm in **A, B, C**; 200 μ m in **D, E, F**.

Fig. 9 – A, B, C, D, E. SEM photographs of Lingulella waptaensis from the Greater Phyllopod Bed (Burgess Shale). **A, B.** ROM 89342, transverse cross-section through the pseudointerarea of a ventral valve showing areas of kaolinization and bands of kaolinite indicated by arrows in B, box in A indicates position in B. **C.** ROM 89342, transverse cross-section of an etched ventral valve showing the virgose structure of the shell. **D, E.** ROM 89342, transverse cross-section of an etched ventral valve showing putative tubes indicated by arrows. **F.** ROM 84600, SEM image of Acrothyra gregaria from the Greater Phyllopod Bed (Burgess Shale) showing detail of the columnar structure of the shell. Scale bars are 2 μm in A, E, F; 1 μm in B, C, D.

Fig. 10 - SEM photographs of Lingulella waptaensis from the Greater Phyllopod Bed (Burgess Shale). **A, B, C.** PMUCa16, detail of the shell showing the thin primary layer and the virgose structure of the secondary layer, box indicates position of B and C. **D, E, F.** ROM 89434, detail of the shell showing the virgose structure and lamination of the secondary layer. **G.** ROM 89432, transverse cross-section of a ventral valve showing the stratiform succession of laminae. **H.** PMUCa16, transverse cross-section of the shell showing the phosphatic composition. Scale bars are 10 μm in A, G, H; 1 μm in B, C, D, E, F.

Fig 1

<i>Lingulella waptaensis</i>		
BA*	# ind.*	Rel. abund.*
120	10	1.94%
0	19	1.34%
-110	2	0.34%
-120	8	0.24%
-130	2	0.06%
-150	46	1.57%
-170	5	0.34%
-210	6	0.13%
-235	5	0.22%
-245	172	3.73%
-250	9	0.36%
-265	1	0.05%
-310	7	0.77%
-320	5	0.32%
-370	2	0.34%
-380	2	0.44%
-430	4	0.93%
-445	2	0.13%
-465	11	1.60%
-480	3	0.79%

*Modified from Caron and Jackson, 2006

Fig 2

Dorsal

Ventral

Fig 3

Fig 4

Fig 5

Fig 6

Fig. 7

Fig. 8

Fig. 9

Fig. 10