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Early Cambrian "soft-shelled" brachiopods as possible stem-group phoronids

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Brachiopods and phoronids are widely recognised as closely related lophophorate phyla, but the lack of morphological intermediates linking the bivalved bodyplan of brachiopods with tubular phoronids has frustrated precise phylogenetic placement. Here we describe *Lingulosacculus nuda* gen. et sp. nov., a new "soft-shelled" brachiopod from the Early Cambrian Mural Formation of western Alberta which provides a plausible candidate for a phoronid stem-group within (paraphyletic) Brachiopoda. In addition to its non-biomineralised shell, *L. nuda* had a ventral valve with an exceptionally long, pocket-like extension (pseudointerarea) that would have allowed the transformation of criss-crossing brachiopod-type musculature to the longitudinal arrangement typical of phoronids. "Soft-shelled" linguliform brachiopods have previously been reported from both the Chengjiang and Burgess Shale Lagerstätten which, together with *L. nuda*, probably represent two independent losses of shell mineralisation in brachiopods.

Key words: Lophophorata, Lophotrochozoa, Brachiopoda, Phoronida, exceptional preservation, problematica.

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Introduction

The Cambrian "explosion" is famous for its sudden appearance of novel body plans, some of which are readily assignable to extant clades, but many others that defy even phylum-level categorisation. These problematic forms typically exhibit character combinations unknown among extant organisms, and are now widely recognised as occupying the stems that link extant crown-group phyla (Budd and Jensen 2000). By associating symplesiomophic characters common to groups of phyla with some (but not all) of the synapomorphic characters of a particular phylum, fossil stem-groups provide a unique view into deep metazoan phylogeny. Stem-group relationships have been proposed for a diverse range of Early Cambrian "problematica" including sponges (Botting and Butterfield 2005), echinoderms (Shu et al. 2004), arthropods (Budd 2008), and brachiopods (Williams and Holmer 2002; Balthasar 2004; Skovsted and Holmer 2003).

Relationships within the superphylum Lophotrochozoa (Halanych 2004) have yet to be resolved, either palaeontologically (Butterfield 2006) or molecularly (see below), though a number of associations are fairly clear. Brachiopods and phoronids, for example, are united by the possession of a lophophore, distinct metacoelomic metanephridia, embryology (Peterson and Eernisse 2001; Freeman 2003), and by recent molecular analyses (e.g., Dunn et al. 2008; but see Yokobori et al. 2008). At the same time, there are obvious pronounced differences between these two phyla, on the one hand a bivalved biomineralised construction with a complex muscle system occupying much of the body cavity and on the other a vermiform body plan that is lined by a system of subepithelial longitudinal muscles and a chitinous tube that is often decorated with grains of sand (Emig 1982; Herrmann 1997).

There is no compelling fossil record of phoronids (Valentine 2004; Carlson 2007), presumably due to their lack of mineralised hard parts, although Skovsted et al. (2008) have proposed that the tommotiid *Eccentrotheca* represents a stem-group phoronid, largely based on its sessile and tube-dwelling mode of life and presumed affinities with the probable stem-group brachiopod *Micrina* (Williams and Holmer 2002; Holmer et al. 2008). Unlike the chitinous tubes of phoronids, however, the tube of *Eccentrotheca* is formed from several rings of actively biomineralised phosphatic sclerites, suggesting its tube-dwelling habit may have evolved convergently.

The particular interrelationship of brachiopods and phoronids has yet to be resolved. Although a sister-group relationship is generally invoked, the only molecular study to specifically address the phoronid-brachiopod relationship with combined SSU and LSU identified the phoronids as a brachiopod ingroup (Cohen and Weydmann 2005), making the brachiopods paraphyletic. Such a relationship suggests a quite different view of the phoronid stem-group. Here we describe a new problematic fossil from the early Cambrian of western Canada that can be identified as an unambiguous

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crown group brachiopod, but exhibiting a suite of unique characters with intriguing morphological links to the phoronids.

Institutional abbreviation.—GSC, Geological Survey of Canada, Ottawa.

Other abbreviations.—GAG, glucosaminoglycans; LSU, large ribosomal subunit; SSU, small ribosomal subunit.

Geological setting

The fossils come from the Early Cambrian (upper "*Nevadella*" Zone) Mural Formation in Jasper National Park, Alberta (Fritz and Mountjoy 1975; Balthasar 2004) and are associated with the large stem-group brachiopod *Mickwitzia*, linguliform and obolellid brachiopods, trilobites, hyoliths and an assortment of non-mineralising Burgess Shale-type macrofossils (NJB and UB, unpublished data). The predominately mudstone sequence includes localised lenses of bioclastic debris and occasional trace fossils, suggestive of a mid-shelf, often dysaerobic environment subject to occasional storm activity.

Materials

There are just two specimens of *Lingulosacculus nuda* gen. et sp. nov. (one with an associated counterpart), and both are preserved primarily as dark, two dimensional aluminium-silicate films, comparable to co-occurring Burgess Shale-type fossils and to non-biomineralising fossils in the Burgess Shale itself (Butterfield et al. 2007).

Systematic palaeontology

Phylum Bachiopoda Duméril, 1806

Subphylum Linguliformea Williams, Carlson, Brunton, Holmer, and Popov, 1996

Class Lingulata Gorjansky and Popov, 1985

Family Lingulellotretidae Koneva and Popov, 1983

Subfamily Lingulosacculinae nov.

Diagnosis.—Lingulellotretidae with non-mineralised shells; all other characters as for family.

Included genera.—*Lingulosacculus* gen. nov.

Remarks.—The published images (Zhang et al. 2007: fig. 4; Zhang et al. 2008: fig. 4J) of the soft-shelled lingulid that is referred to as "*Wangyuia chengjiangensis*" in Zhang et al. (2007) are sufficient to justify its inclusion in the Lingulosacculinae, including lack of mineralisation. However, this brachiopod has not yet been legitimately published.

Genus *Lingulosacculus* nov.

Etymology: *Lingulosacculus* from lingulid and Latin *sacculus* (pouch).

Type species: *Lingulosacculus nuda* gen. et sp. nov. Early Cambrian, Waucoban series, Dyeran stage, Mural Formation, Mumm Peak section (53°11'97'' N; 119°08'84'' W).

Diagnosis.—Dorsal interior with anterior projection terminating in a baculate vascula media; ventral valve is more than twice as long as the dorsal valve and has a prominent pocket-shaped pseudointerarea that projects beyond the hinge-line; visceral area extending far beyond hinge line.

Lingulosacculus nuda sp. nov.

Figs.1, 2.

Etymology: Latin *nuda*, naked, alluding to the lack of mineralisation.

Type material: Holotype, GSC-34953 (part and counterpart).

Type locality: Mumm Peak section (53°11'97'' N, 119°08'84'' W), Jasper National Park, Alberta, Canada.

Type horizon: Early Cambrian, Waucoban series, Dyeran stage, "*Nevadella*" Zone, Mural Formation

Material.—Holotype plus one other specimen (GSC-34952), both from the same layer.

Diagnosis.—Dorsal valve elongate oval, maximum width somewhat anterior of midline; ventral valve elongate drop-shaped with maximum thickness in the anterior part at about 75% of its length; small opening angle of the ventral pseudointerarea (around 25°).

Measurements.—The maximum width is 13 mm (GSC-34953) and 12 mm (GSC-34952), the maximum length of the most complete specimen is 32 mm (GSC-34953 counterpart), and the oval anterior part is 14 mm (GSC-34952) and 15 mm (GSC-34953) long.

Description.—*Lingulosacculus nuda* has an anteriorly rounded conical shape which in GSC-34952 (Fig. 1A) consists of two distinct elements: a larger conical valve and a smaller, superimposed oval valve that matches the anterior part of the conical valve. GSC-34953 (Fig. 1B) shows the reverse aspect of the larger conical valve, with the smaller oval valve only visible where it protrudes at the anterior margin.

The oval valve in GSC-34952 (Fig. 1A) is medially subdivided by a parallel-sided furrow that widens into a funnel-shape in the posterior third of the valve. Dark stains run in diffuse bands parallel to the outer margin of the median furrow and slightly diverge at the anterior end. Another set of diffuse dark stains runs approximately parallel to the outer margin of the valve (Fig. 1A). Under low-angle light, two curved ridges can be observed in front of the anterior end of the median furrow, originating from opposite sides of the median furrow (Fig. 2). The left ridge extends slightly beyond the valve margin.

The larger conical valve is best preserved in GSC-34953 (Fig. 1B) and has an anterior oval portion that is darker than the tapering posterior extension. The posterior part of this oval part exhibits a distinct triangular- to funnel-shaped area, while its posterior margin exhibits two straight edges that run obliquely inwards (white arrows in Fig. $1B_1$). The tapering

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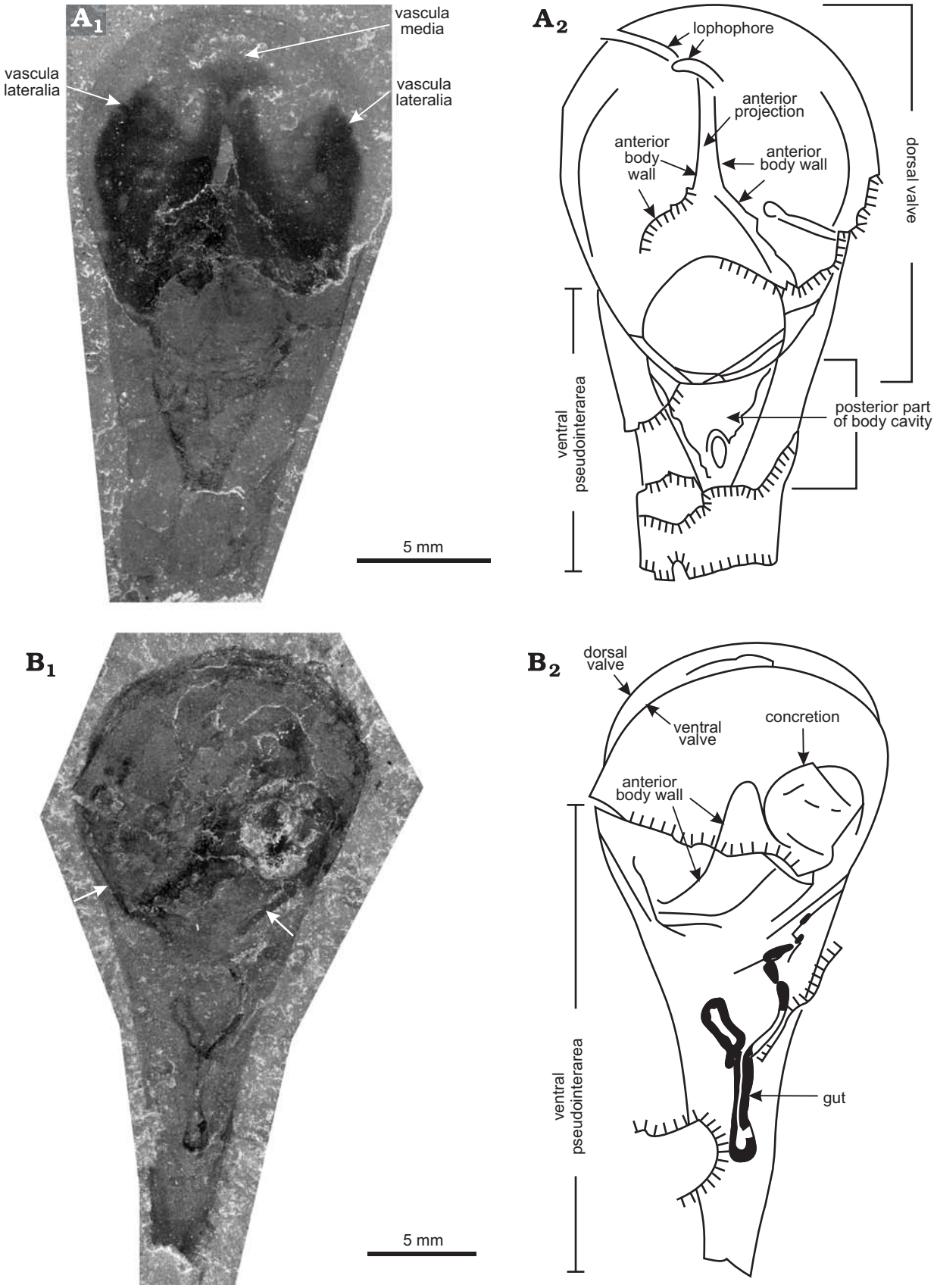


Fig. 1. Light micrographs (A_1, B_1) and camera lucida drawings (A_2, B_2) of lingullotretid brachiopod *Lingulosacculus nuda* gen. et sp. nov. **A**. GSC-34952, with the smaller oval-shaped dorsal valve superimposed on the larger coniform ventral valve. **B**. GSC-34953 (holotype), with the smaller dorsal valve largely obscured by the superimposed ventral valve; white arrows in B_1 indicate the margins of the propareas on the ventral pseudointerarea.

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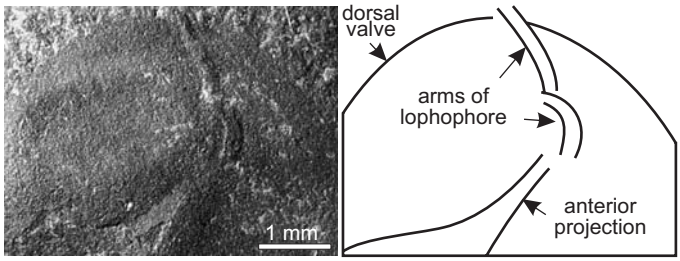


Fig. 2. Anterior portion of lingullotretid brachiopod *Lingulosacculus nuda* gen. et sp. nov. (GSC-34952) in low-angle light, showing lophophore arms.

posterior extension originates at about the maximum width of the valve and then tapers backwards to form an elongate cone. It includes a distinct dark line that originates in the anterior oval part of the valve and extends through the first two thirds of the posterior extension before twice looping back on itself (Fig. 1B).

In GSC-34952 (Fig. 1A), only the tapering posterior part of the larger valve is visible as the anterior part is overlain by the oval valve. The outline of the posterior extension is visible as a clear line that demarcates the fossil from the brighter rock matrix. Inside the posterior extension a darker triangular area forms the continuation of the funnel-shaped area in posterior part of the oval valve.

Remarks.—The morphology of *Lingulosacculus nuda* is closely comparable with that of exceptionally preserved linguliform brachiopods from the Chengjjiang biota of South China (Zhang et al. 2007), most notably in the triangular body cavity at the posterior part of the shorter oval valve and the oval portion of the elongate valve. The median furrow of the short oval valve can be readily identified as the anterior projection regularly encountered on the dorsal valves of many linguliform brachiopod groups, while the short curved ridges are in the correct position and of the right size to represent the partially preserved arms of a lophophore. Together with the diverging dark stain at its anterior end (interpretable as a brachiopod vascula media; Fig. 1A) and the dark staining along the lateral margin (vascula lateralia; Fig. 1A), these features make a clear case for identifying *L. nuda* as a linguliform brachiopod (Fig. 3).

The conical posterior extension of *L. nuda*'s ventral valve is directly comparable to the ventral pseudointerarea of fossil Lingulellotretidae, a family of organophosphatic brachiopods known from four Early Cambrian to Early Ordovician genera (Jin et al. 1993; Holmer et al. 1997; Holmer and Popov 2000). In this light, the straight oblique edges along the anterior margin of the posterior extension in *L. nuda* (white arrows in Fig. $1B_1$) can be identified as the margins of the propareas of the ventral pseudointerarea. In the Lingulellotretidae the ventral pseudointerarea forms a closed posterior outgrowth that extends well beyond the hinge-line and is known to accommodate a significant portion of the body cavity, including the posterior loop of the gut (Zhang et al. 2007). This same arrangement occurs in *L. nuda*, with the looped dark line tracking the same course as the exceptionally preserved guts of Chengjiang lingulellotretids, including the median position of its posterior loop and the sharp right turn as it exits the posterior extension of the ventral valve (cf., Zhang et al. 2007: fig. 2C); the anterior end of the gut in GSC-34953 (Fig. 1B), however, has been broken and is now curled back and folded over itself. *Lingulosacculus nuda* is also presumed to have had a long fleshy pedicle, comparable to that of Chengjiang lingulellotretids (see Jin et al. 1993; Zhang et al. 2007), but neither of the specimens preserves the posterior-most tip of the ventral valve.

The conspicuous two-dimensionality of *L. nuda* stands in sharp contrast to co-occurring, three-dimensionally preserved lingulid and mickwitziid brachiopods, but is directly comparable to co-occurring *Vetulicola* and *Anomalocaris* claws, both of which are widely accepted as lacking any primary biomineralisation. Unless it was originally mineralised by aragonite—which is not three-dimensionally preserved in co-occurring hyolithids—there is little doubt that *L. nuda* was soft-shelled.

Discussion

Affinities of soft-shelled brachiopods.—In addition to *Lingulosacculus nuda*, two other Cambrian brachiopods have been interpreted as lacking primary mineralisation: *Acanthotretella spinosa* from the Middle Cambrian Burgess Shale (Holmer and Caron 2006) and a poorly known lingulid from Chengjiang that has been referred to as "*Wangyuia*" *chengjiangensis* (Zhang et al. 2007), a name that is, however, already occupied by a Silurian orthid (Zhang 1989). Of these three soft-shelled species, it is clear that *L. nuda* and the Chengjiang lingulid are the most closely related. Both, for

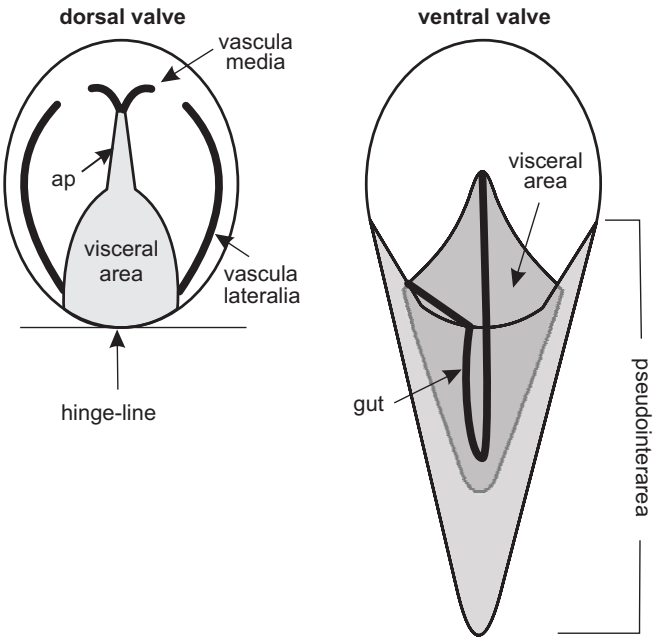


Fig. 3. Schematic reconstruction of lingullotretid brachiopod *Lingulosacculus nuda* gen. et sp. nov. Abbreviation: ap, anterior projection.

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example, have a closed ventral pseudointerarea that extends dramatically beyond the hinge-line, providing space for more than half the length of the body cavity. A detailed description of the soft-shelled Chengjiang lingulid has yet to be published, but it appears to differ from *L. nuda* primarily in its shell shape anterior of the hinge-line, which in the Chengjiang species is wider than long and broadly trapezoidal in outline (Zhang et al. 2007: fig. 4; Zhang et al. 2008: fig. 4J). Jin et al. (2004) have also interpreted a granular texture on the ventral interior surface of the pseudointerarea in the soft-shelled Chengjiang lingulid as evidence of an agglutinated skeleton, but this is more likely to represent secondary pyritisation, a common taphonomic pathway among Chengjiang fossils (e.g., Gabbott et al. 2004).

With its long pocket-shaped ventral pseudointerarea and long fleshy pedicle, there is little doubt that the yet undescribed Chinese form, along with similarly non-mineralised *Lingulosacculus*, is correctly assigned to the Lingulellotretidae, a Cambrian–Ordovician family of linguliform brachiopods characterised by a closed pouch-like ventral pseudointerarea (Holmer et al. 1997; Holmer and Popov 2000). Even so, the lack of shell mineralisation in *Lingulosacculus* and the soft-shelled Chengjiang lingulid sets them apart from the rest of the family, which leads us to propose a new soft-shelled subfamily of lingulellotretids, the Lingulosacculinae

The third soft-shelled genus, *Acanthotretella*, differs conspicuously from the Lingulosacculinae in that its shell is pierced by long setae/spines, and its thin thread-like pedicle passes through the shell via a small external tube. Indeed, Holmer and Caron (2006) have presented a compelling case for identifying *Acanthotretella* as a stem-group siphonotretid, an unrelated order of organophosphatic linguliform brachiopods.

Their occurrence in the upper *Nevadella* Trilobite Zone puts *L. nuda* and the co-occurring mineralised *Eoobolus* (Balthasar 2007) among the oldest recorded lingulates and it might be tempting to view the soft-shelled condition as primitive for linguliforms or brachiopods in general (e.g., Zhang et al. 2008; Ushatinskaya 2008). Such a scenario, however, appears unlikely in the context of recent work on tommotiids (Williams and Holmer 2002; Skovsted et al. 2008; Holmer et al. 2008). It now looks increasingly likely that the phosphatic sclerites of tommotiids represent the basal stem group of brachiopods which is connected to the proximal stem and basal crown group through various problematic taxa possessing organophosphatic shells pierced by setae (Holmer et al. 2002; Skovsted and Holmer 2003; Balthasar 2004; Holmer et al. 2006; but see Li and Xiao 2004; Carlson 2007). An important consequence of the tommotiid-brachiopod hypothesis is that brachiopod shells were derived from the organophosphatic sclerites of tommotiids which identifies both strongly reduced mineralisation and calcitic compositions as secondarily derived characters. This secondary loss of mineralisation in some Cambrian brachiopods together with the documentation of novel microstructures and mixed carbonate-phosphate mineralogy in others (e.g., Balthasar 2007, 2008; Holmer et al. 2009), points to an unusual degree of evolutionary variability in early brachiopod biomineralisation. It is presumably the underlying organic framework that represents the common, phylogenetically unifying component of their shells, and upon which the emerging diversity of Cambrian brachiopod shells was built. It thus appears that the conservative pattern of brachiopod shell evolution only manifested itself after a Cambrian phase of experimentation when shell mineralisation did not evolve parsimoniously.

***Lingulosacculus nuda* and phoronids**.—Brachiopods and phoronids have traditionally been regarded as separate but closely related phyla with a basal position among the deuterostomes (Lüter and Bartholomaeus 1997; Nielsen 2001, 2002). Although molecular work has now convincingly transferred them to the new protostome superphylum Lophotrochozoa (Halanych et al. 1995; Halanych 2004), the inter-relationship of these two lophophorate clades has yet to be resolved. Molecular results are inconsistent, with almost any constellation within the Lophotrochozoa appearing feasible. For example, a recent comprehensive molecular analysis identifies the brachiopods and phoronids as sister groups (Dunn et al. 2008), in agreement with earlier analysis combining SSU and morphological data (Giribet et al. 2000; Peterson and Eernisse 2001), while analyses of housekeeping genes (Helmkampf et al. 2008) and mitochondrial genome data (Yokobori et al. 2008) suggest that they are not closely related, albeit within Lophotrochozoa. Even so, it is important to appreciate that little of this molecular work has been directed specifically at the relationship of brachiopods and phoronids with taxon sampling typically limited to one or two species. The only exception has been a SSU and combined SSU + LSU analysis which included a diverse range of brachiopods and two phoronids (Cohen and Weydmann 2005). In this case, phoronids were recovered as a brachiopod ingroup.

On both morphological (Rowell 1982; Zrzavý et al 1998; Peterson and Eernisse 2001; Nielsen 2002) and embryological (Freeman 2003) grounds brachiopods and phoronids have conventionally been viewed as monophyletic clades derived from a common lophophorate ancestor (Carlson 1995; Williams et al. 1996). It is possible, however, that this apparent sister-group relationship is simply the by-product of a missing fossil record (Valentine 2004; Carlson 2007). Between the first documented appearance of brachiopods (in the Tommotian; Pelman 1977; Ushatinskaya and Malakhovskaya 2006) and the first documented appearance of phoronids (in the Recent), lies more than enough time to accommodate alternative scenarios, not least the possibility that phoronids are a highly derived group of brachiopods (Cohen and Weydmann 2005). The test lies with the intermediate body plans of the phoronid stem group which is exclusive to the fossil record (Budd and Jensen 2000).

Brachiopods are subdivided into three distinct subphyla that exhibit substantial differences in their development and body plan (Williams et al. 1996; 1997) including the disposition of the gut, shell composition, nature of the pedicle, posi-

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tion of the gonads, and muscle system. Interestingly, when compared with these brachiopod subphyla, phoronids share various characters with the Linguliformea, while none of the other subphyla have unique morphological features in common with phoronids. Shared phoronid and linguliform characters include the presence of glycosaminoglycans (GAGs) and chitin, dermal muscles, a U-shaped gut, lateral mesenteria bearing gonads (Herrmann 1997; Williams et al. 1997), and a bulbous posterior ending of the coelomic cavity used for anchoring in the burrow or tube (Mackay and Hewitt 1978; Herrmann 1997).

Compared with brachiopods, phoronids have a simplified body plan that lacks both mineralised valves and the complex muscle system necessary to manipulate them (Emig 1982; Herrmann 1997). If phoronids did originate from within the Brachiopoda, the basal stem-group would presumably appear as a somewhat unusual brachiopod showing evidence of reduced shells, reduced mineralisation, and the initiation of a chitinous tube. With its shell showing strongly reduced mineralisation and its long posterior pocket containing some 50% of the body cavity, *Lingulosacculus* presents an intriguing combination of phoronid-like characters superimposed on a brachiopod body plan. In particular the posterior pocket is intriguing as its position behind the hinge line would have precluded the insertion of shell-operating muscles. This part of *L. nuda*, which comprises around 50% of its length, would have possessed longitudinal dermal muscles, and a protective cuticle composed of a single, presumably chitinous structure, all of which is strikingly similar to phoronids. In the course of evolution towards the phoronid crown group, further shell reduction would have resulted in the successive shortening of the ventral valve, the eventual loss of the dorsal valve, and the associated loss of the shell operating musculature. In this scenario of shell reduction the posterior pouch would have formed an ideal preadaptation to accommodate the body cavity and thus maintain effective protection against predation.

Acrotretids and the problematic *Anomalocalyx* (Brock 1999) also develop a cone-shaped ventral valve superficially similar to that of lingulellotretids, but in both these cases the conical elongation is directed dorso-ventrally. Assuming that the main body axes of phoronids are homologous to those of brachiopods, the phoronid body plan cannot be derived from such dorso-ventrally extended brachiopods.

While the formation of a posterior pouch also applies to other lingulellotretids, the accompanying loss of mineralisation in the Lingulosacculinae places this group in a more derived, potentially basal phoronid, position. Assuming that linguliform shell secretion during the Cambrian was broadly similar to that of extant lingulids, the lack of apatite would have left the Lingulosacculinae with a chitinous and polysaccharide-rich cuticle (Cusack et al. 1997) that is more reminiscent in composition to the chitinous tubes of phoronids than any mineralised shell. In this view, the phoronid tube would have derived from the ventral pseudointerarea of lingulellotretids, while its organic composition was modified from the organic constituents of the primitive linguliform shell. In the light of a probable sessile filter-feeding stem group with organophosphatic skeletal composition, most of the characters linguliforms share with phoronids are likely to be plesiomorphic which is most apparent for the presence of GAGs which are known from various other phyla including molluscs and chordates (Rees et al. 2002; Volpi and Maccari 2005). Dermal muscles are probably retained from a deep vagrant ancestor, while the U-shaped gut is likely to represent an adaptation to sessile life.

Conclusions

At least two groups of soft-shelled brachiopods can be recognised in the Cambrian: the single species of *Acanthotretella spinosa* (Holmer and Caron, 2006) and the Lingulosacculinae which include *Lingulosacculus nuda* and a not yet named soft-shelled lingulid from Chengjiang (Zhang et al. 2007, 2008). Their respective affinities to siphonotretids and Lingulellotretidae suggest an independent loss of mineralisation, adding to the emerging view that brachiopod shell composition was less tightly controlled in the Cambrian than through the rest of the Phanerozoic.

With their radically extended pseudointerarea and secondary loss of shell mineralisation, the Lingulosacculinae were uniquely pre-adapted for the transformation to a phoronid body plan, including the initiation of a tube-like body chamber and the opportunity for developing a longitudinally oriented muscle system. As such, they present a plausible, possibly even compelling candidate for a deep phoronid stem-group rooted within the linguliform Brachiopoda. The transition to more crown-ward phoronids would have involved the transfer of the entire body cavity to a position behind the hinge-line, followed by loss of the dorsal valve.

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