



## THE MACRO- AND MICROFOSSIL RECORD OF THE CAMBRIAN PRIAPULID *OTTOIA*

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**Abstract:** The stem-group priapulid *Ottoia* Walcott, 1911, is the most abundant worm in the mid-Cambrian Burgess Shale, but has not been unambiguously demonstrated elsewhere. High-resolution electron and optical microscopy of macroscopic Burgess Shale specimens reveals the detailed anatomy of its robust hooks, spines and pharyngeal teeth, establishing the presence of two species: *Ottoia prolifica* Walcott, 1911, and *Ottoia tricuspida* sp. nov. Direct comparison of these sclerotized elements with a suite of shale-hosted mid-to-late Cambrian microfossils extends the range of ottoiid priapulids throughout the middle to upper Cambrian strata of the Western Canada Sedimentary Basin.

Ottoiid priapulids represented an important component of Cambrian ecosystems: they occur in a range of lithologies and thrived in shallow water as well as in the deep-water setting of the Burgess Shale. A wider survey of Burgess Shale macrofossils reveals specific characters that diagnose priapulid sclerites more generally, establishing the affinity of a wide range of Small Carbonaceous Fossils and demonstrating the prominent role of priapulids in Cambrian seas.

**Key words:** Burgess Shale, Small Carbonaceous Fossils, priapulid diversity, *Selkirkia*.

STEM-group priapulid worms were a conspicuous component of level-bottom Cambrian faunas (Conway Morris 1977; Conway Morris and Robison 1986; Budd and Jensen 2000; Han *et al.* 2004; Caron and Jackson 2008; Zhao *et al.* 2014), even though their modern macroscopic counterparts are in general restricted to marginal, typically anaerobic settings (van der Land 1970; Oeschger and Vetter 1992). The most familiar and prolific Cambrian priapulid is perhaps *Ottoia*, best known from the Burgess Shale Lagerstätte (Cambrian Series 3, Stage 5; British Columbia) (Lieberman 2003; Caron and Jackson 2008; Vannier 2012). Like other Cambrian priapulids, *Ottoia* is an annulated worm whose eversible introvert and pharynx are adorned with a complex armature of toughened cuticular ‘sclerites’ (introvert scalids and pharyngeal teeth; Conway Morris 1977). Modern priapulids exhibit a comparable array of spinose and denticulate elements, which serve various roles in sensing, feeding and locomotion (Calloway 1975; Vannier *et al.* 2010; Sørensen *et al.* 2012). Sclerite morphology underlies much genus-level taxonomy in modern priapulids (Higgins *et al.* 1993; Storch *et al.* 1995) and can be expected to do so in fossils as well. *Ottoia* has been subjected to detailed anatomical description (Walcott 1911; Banta and Rice 1976; Conway Morris 1977), and its anterior morphology weighs heavily

in analyses of its ecological and evolutionary significance (Wills 1998; Bruton 2001; Vannier 2012; Wills *et al.* 2012). Previous descriptions nevertheless fail to capture the exquisitely detailed morphology and microstructure preserved in the Burgess Shale fossils.

Despite the diverse range of sclerite morphologies and arrangements in Cambrian priapulids, 15 of the 17 fossil genera are monospecific (Table S1, see online Supporting Information); in contrast, all but one modern genus contains multiple species. *Ottoia* itself initially included three species (Walcott 1911), but subsequent revisions have reduced this number to one: fossils originally assigned to *O. minor* Walcott, 1911, are now recognized as members of a different genus, *Ancalagon* (Conway Morris 1977); *O. tenuis* Walcott, 1911, long recognized as an enteropneust (Conway Morris 1979), is now assigned to *Spartobranchus* (Caron *et al.* 2013a).

Because *Ottoia* is the most abundant and familiar priapulid in the Burgess Shale, indeterminate priapulids are often uncritically referred to this genus, even in the absence of clear diagnostic features. For example, specimens from the Pioche Shale, Nevada, have been assigned to *Ottoia* based on their annulated cylindrical body with radial symmetry and the presumed presence of a proboscis (Lieberman 2003), even though these characters are

consistent with almost any position in the Cycloneuralian total group (Budd and Jensen 2000; Harvey *et al.* 2010). Similarly, reports of *Ottoia* from the Marjum Formation and Spence Shale, Utah (Conway Morris and Robison 1986), the Conasauga Formation of Georgia, USA (Schwimmer and Montante 2007), the Chancellor Basin, Canada (Johnston *et al.* 2009), and the Kaili Formation, China (Zhao *et al.* 2005), remain insecure in the absence of more definitive preserved character sets, or remain difficult to assess pending full detailed descriptions. As such, and despite intense sampling effort (Dornbos and Chen 2008; Zhao *et al.* 2014), there are no confirmed records of *Ottoia* macrofossils outside the Burgess Shale.

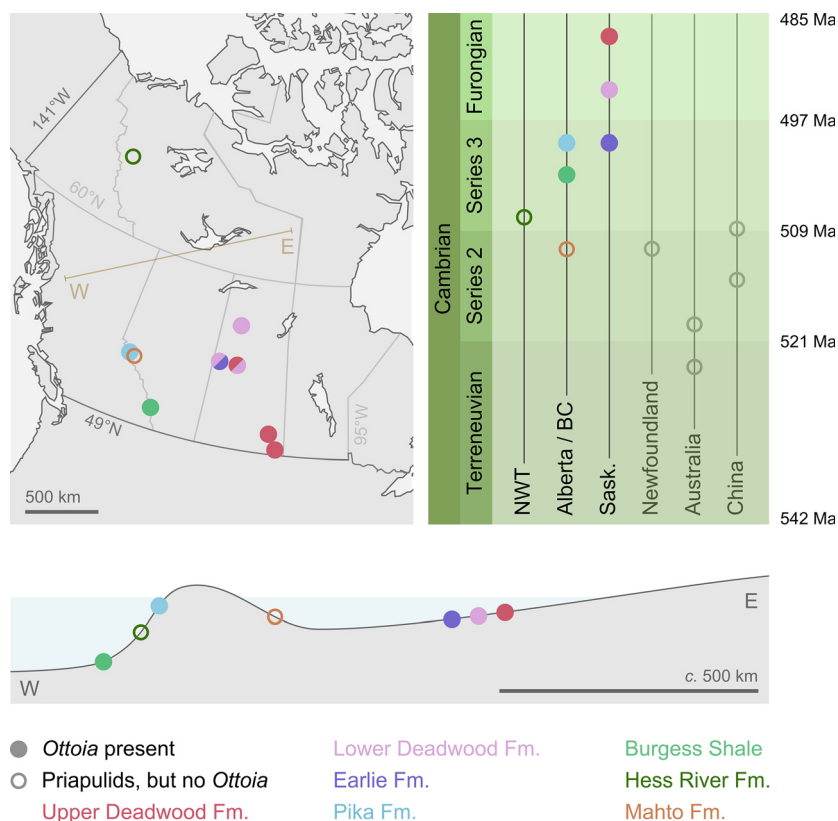
The narrow distribution and diversity of *Ottoia* macrofossils might simply reflect the rarity of Burgess Shale-type deposits. Priapulid-like sclerites, however, are commonly recovered as Small Carbonaceous Fossils (SCFs) (Butterfield and Harvey 2012; Harvey *et al.* 2012a), representing an alternative record that does not require such exceptional preservational circumstances. This complementary record of non-biomineralizing organisms has a widespread distribution in Cambrian mudrocks (Butterfield and Harvey 2012), thereby providing an opportunity to extend the geographic, stratigraphic and taxonomic resolution of Cambrian priapulids.

Here we resolve new details of the constitution of *Ottoia* sclerites. In addition to resolving two distinct species from the Burgess Shale itself, we demonstrate the presence of ottoiid sclerites in a wide range of facies in middle to late Cambrian mudstones from the Western Canada Sedimentary Basin.

## MATERIAL AND METHODS

We examined *Ottoia* macrofossils from the Burgess Shale (Cambrian Series 3, Stage 5; Fossil Ridge, British Columbia), a series of moderately metamorphosed mudstones deposited below storm wave base at the outboard edge (shelf/slope break) of the Western Canada Sedimentary Basin (Piper 1972) (Fig. 1). Two separate horizons were examined: the Upper Walcott Quarry (UWQ), sampling the Phyllopod Bed and layers immediately above (Walcott Collection, Smithsonian Institution, c. 40 specimens), and the Lower Walcott Quarry (LWQ), 120–130 cm below the Phyllopod Bed (Royal Ontario Museum collections, c. 70 specimens). Examination of other Burgess Shale priapulids allowed an assessment of sclerite diversity at the genus level.

SCFs were extracted from two substantially more near-shore units within the Western Canada Sedimentary



Basin. Mudcracked shales from the Pika Formation (late Guzhangian, latest Series 3) of westernmost Jasper National Park, Alberta, represent a periodically emergent setting on the outer margin of the ‘middle carbonate facies belt’ (Aitken 1966; Westrop 1989; Butterfield and Harvey 2012). By contrast, mudstones from the Deadwood Formation (Series 3 and Furongian) in the subsurface of Saskatchewan were deposited in the ‘inner detrital belt’ some 800 km landwards of the shelf break (Fig. 1), but show no direct evidence of subaerial exposure.

Palaeontologically, all three of these units preserve priapulid-like scalids, as well as *Wiwaxia* sclerites (Butterfield 1990; Butterfield and Harvey 2012), but are distinguished by their associated arthropod biotas: whereas the Burgess Shale is dominated by deeper and more open water forms, such as agnostid trilobites (Melzak and Westrop 1994), the Pika assemblage contains no agnostids (Melzak and Westrop 1994), and the Deadwood of south Saskatchewan has yet to yield trilobite faunas of any type; the dominant arthropods instead appear to be phylogenetically derived crustaceans (Harvey *et al.* 2012b).

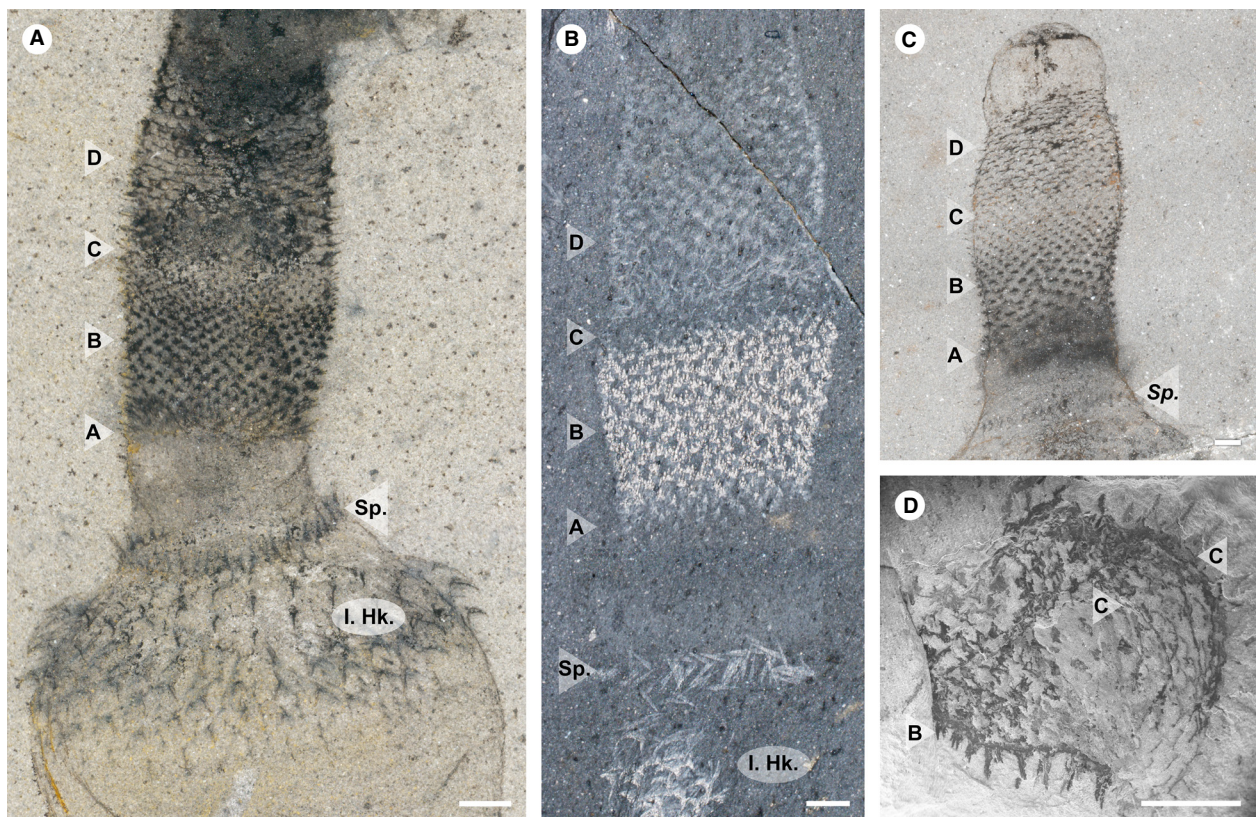
Burgess Shale fossils were examined using the complementary techniques of optodigital microscopy, environmental pressure backscatter electron microscopy, and secondary electron imaging (Orr *et al.* 2002; Kearns and Orr 2009), which together allow the observation of subtle compositional differences at a range of scales – and thus the recovery of high-resolution anatomical detail and internal structure. HF acid-isolated SCFs (see Butterfield and Harvey 2012 for processing techniques) were imaged using transmitted light microscopy.

To account for taphonomically induced variation in sclerite form, our sclerite analysis was based on *c.* 40 articulated specimens from each of the Walcott Quarry horizons and over 200 specimens from each SCF population.

## OTTOIA IN THE BURGESS SHALE

### Terminology

In order to describe the form of *Ottoia* sclerites, it is useful to have a systematic terminology. The armature of



**FIG. 2.** Distribution of sclerite morphologies in *Ottoia*. A, *O. prolifica* (NMNH 172983), lateral view showing introvert hooks (*I. Hk.*), coronal spines (*Sp.*) and tooth morphologies A–D. B, *O. prolifica* (NMNH 198759), lateral view of isolated proboscis; introvert hooks (*I. Hk.*) are partially disarticulated; bright-field photography highlights highly reflective nature of thick carbon film in Type B teeth. C, *O. prolifica* (NMNH 57622, paratype), complete specimen in lateral view. D, *O. tricuspida* sp. nov. (ROM 63058), SEM showing distal view of proboscis, everted to boundary between Type B and Type C teeth. All scale bars represent 1 mm.



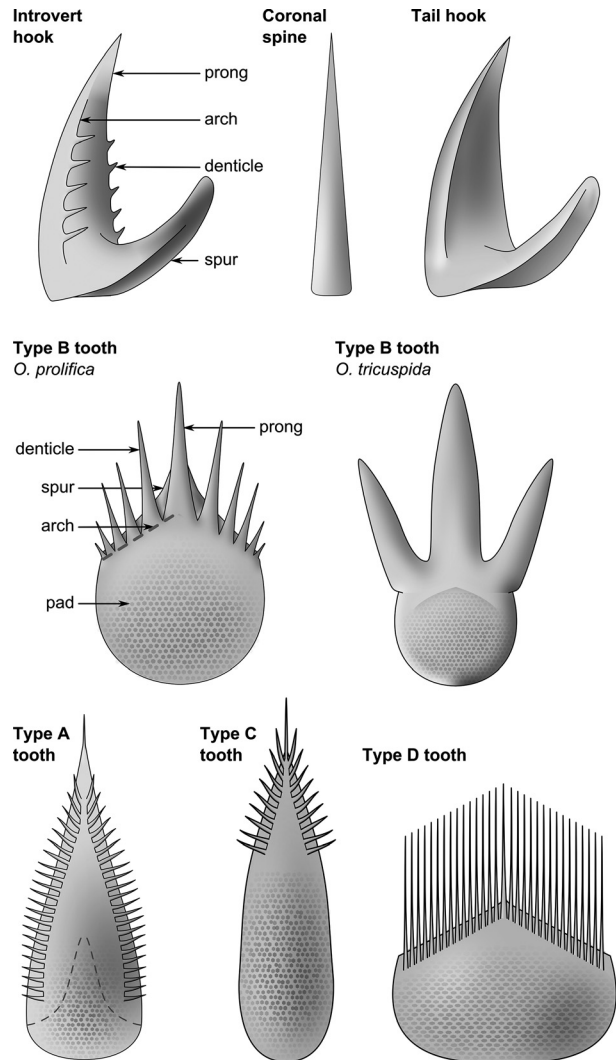
priapulid worms comprises sclerotized elements ('sclerites', elsewhere termed 'papillae' (Walcott 1911) or 'spinules' (Banta and Rice 1976; Conway Morris 1977)) that are divided into two major groups: the introvert 'scalids', an array of posterior-pointing hooks on the introvert and trunk, and the pharyngeal 'teeth', which adorn the eversible pharynx and point forwards when the pharynx is everted (van der Land 1970; Conway Morris 1977). In *Ottoia*, the introvert armature (Fig. 2; Banta and Rice 1976; Conway Morris 1977) comprises rows of quincunxially arranged 'introvert hooks' ('proboscis hooks' in Conway Morris 1977) interspersed with small narrow spines. The aspect, length and curvature of the hooks varies along a row, and they are reported to bear six lateral denticles (see Fig. 3). The base of the eversible introvert bears a single ring of long setiform 'coronal spines' (*sensu* Maas *et al.* 2007; termed 'proboscis spines' in Conway Morris 1977). Conway Morris (1977) recognized four distinct tooth morphologies on the pharynx: one to two circles of 'Type A' teeth, conical spines fringed with accessory denticles; *c.* 20 rows of 'Type B' teeth, arranged in a quincunxial pattern – each tooth comprising a wide base and broad spines, and resembling a bear's footprint; *c.* five rows of elongate 'Type C' teeth, edentate cones arranged in a quincunx formation; and a field of 'Type D' teeth, similar to Type B teeth but flatter and broader. A separate series of hooked sclerites with an excavate concave surface, 'tail hooks', occur at the tail end of the organism (Banta and Rice 1976; Conway Morris 1977).

We introduce new terms to describe the morphology of individual scalids and teeth (Fig. 3). The tip of an element is termed the 'prong', and often forms the apex of an 'arch' that may be arrayed with 'denticles'. Beneath the arch lies a broad and often ornamented 'pad'. An oblique 'spur' is conspicuous in many of the fossil elements – and a comparable structure is developed to a greater or lesser degree in modern priapulid sclerites, most prominently as the 'manubrium' of the pharyngeal teeth of *Tubiluchus* (van der Land 1970).

### Preservation

Various taphonomic effects complicate the interpretation of the fossils. Carbonaceous components are subject to an extreme degree of flattening and therefore exhibit a range of two-dimensional outlines depending upon their original sedimentary orientation. Moreover, variation in the original degree of sclerotization leads to variation in preservation potential between different sclerite types and within individual sclerites.

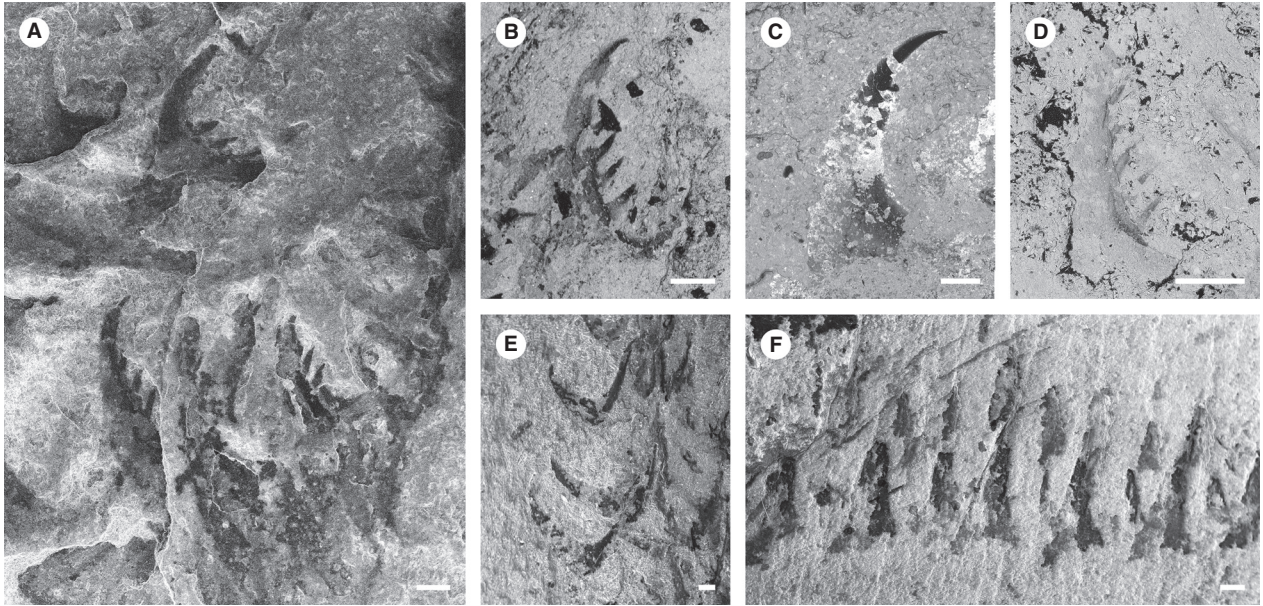
The original constitution of sclerotized elements is reflected in the Burgess Shale by the nature of preservation. Sclerites typically preserve as carbonaceous compres-



**FIG. 3.** Schematic diagrams of *Ottoia* sclerite morphologies, as reconstructed in the present study. Sclerites comprise a broad, flat basal pad and a thickened, usually triangular arch. Denticles arise from the lateral margins of the arch; distal extension of the arch gives rise to a prong. An oblique spur arises from the basal region.

sions paired with aluminosilicate films (Orr *et al.* 1998; Butterfield *et al.* 2007), with the relative prominence of carbonaceous and aluminosilicate components reflecting the degree of original sclerotization. The most robust elements, such as the spines of *Hallucigenia* or the mouthparts of *Wiwaxia/Odontogriphus*, are primarily represented by carbon films that contain trace amounts of phosphorous (Smith 2012; Caron *et al.* 2013b). Aluminosilicate films become more prominent in sclerites with a less robust but still heavily sclerotized constitution, such as the dorsal armature of *Wiwaxia* (Butterfield *et al.* 2007). The carbonaceous component is least apparent in thin or weakly sclerotized components such as arthropod cuticle (Orr *et al.* 1998). This preservational continuum is





**FIG. 4.** Introvert hooks (A–E) and coronal spines (F) in *O. tricuspidata* sp. nov., Lower Walcott Quarry. A, ROM 63060, grouping of spines showing variability of aspect. B, ROM 63057, with marginal denticles. C, ROM 63059, no marginal denticles, well-preserved carbon film at tip shows no microstructure. D–E, ROM 63058, with (D) and without (E) marginal denticles. F, ROM 63058, coronal spines. All scale bars represent 100  $\mu\text{m}$ .

of course overprinted by other factors including grain size, carbonate content and the extent of weathering.

The introvert hooks, coronal spines and tail hooks are the least sclerotized components of the *Ottoia* armature; aluminosilicates routinely silhouette these sclerites, but the corresponding carbon film tends to be very thin (Fig. 4) or absent. Type A, Type C and Type D teeth, as well as the pads of Type B teeth, are somewhat more robust, such that their aluminosilicate component is less prominent and the carbonaceous component is more readily observed (Fig. 5). The denticles of Type B teeth are the most robust components of the *Ottoia* scleritome; they consistently preserve as a thick, phosphorous-associated carbon film (Fig. 5A–H; Smith *et al.* 2015).

A secondary taphonomic signal is provided by pyrite, which is typically associated with voids (Anderson *et al.* 2011). The prong and denticles of Type B teeth have a narrow (c. 5  $\mu\text{m}$ ) central cavity that is filled with pyrite framboids (Fig. 5G–H). Additional elongate pyrite crystals run parallel to the edges and, by analogy with comparable features within the sclerites of *Wiwaxia* (Smith 2014), presumably reflect an internal microstructure. The frequent silhouetting of introvert hooks and spines by pyrite crystals indicates that these sclerites had an extensive central cavity (Smith *et al.* 2015).

**Description.** *Ottoia* specimens from the Upper Walcott Quarry (UWQ) and Lower Walcott Quarry (LWQ)

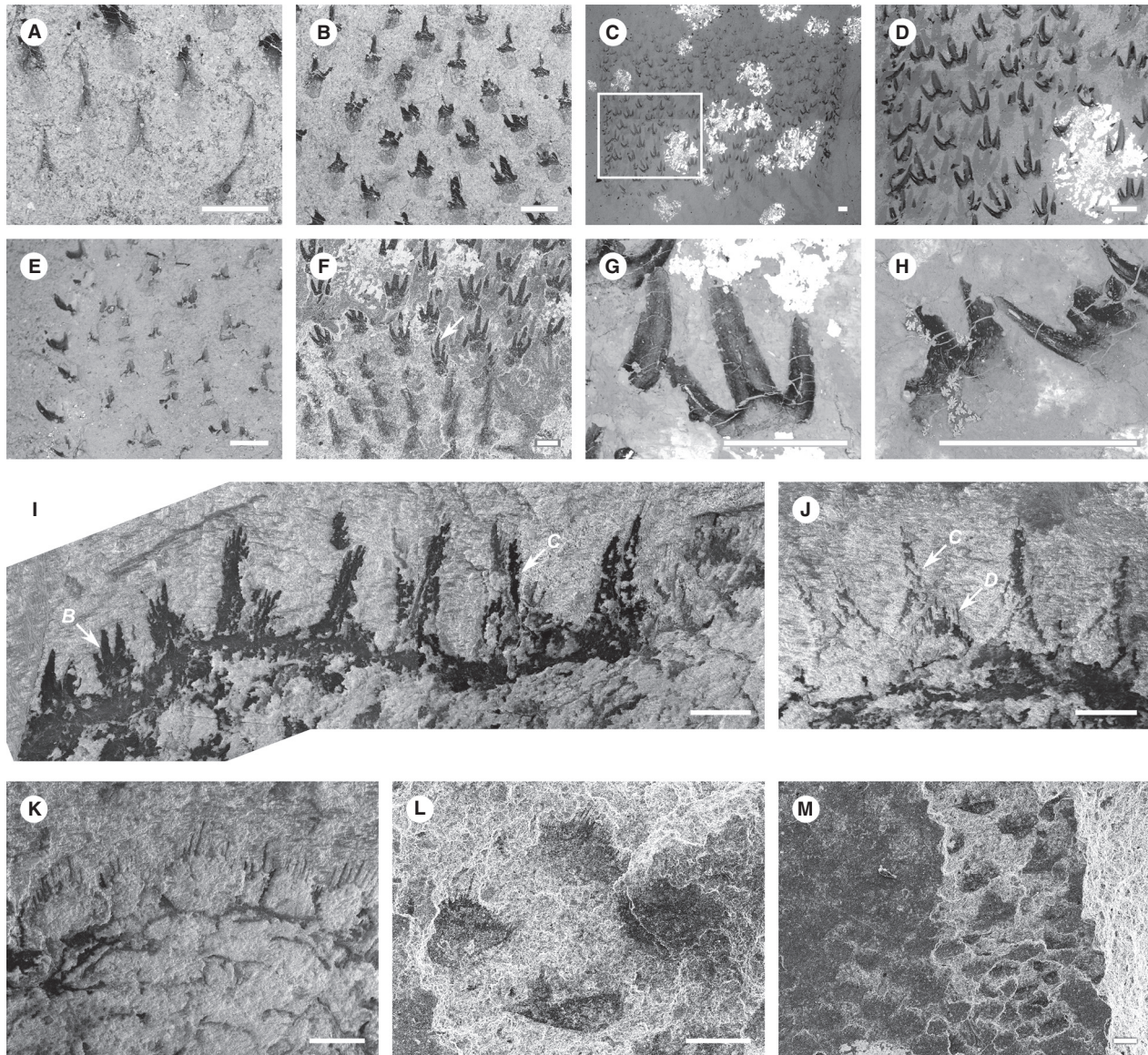
exhibit the same overall range of size and form (proboscis width at maturity: 4–5 mm). In both horizons, the introvert hooks comprise a triangular prong with an extended anterior-directed base (Fig. 4E). A long and slender robustly rimmed triangular arch extends from the base for 50–70% of the length of the spine. On some specimens (Fig. 4A, B, D), a series of up to six evenly spaced anterior-projecting conical denticles extends from each side of this arch, which is slightly offset from the concave edge of the prong (Figs 3, 4A–E, 6A–C).

The coronal spines are simple and unornamented; the absence of a discernable basal aperture or arch may reflect their delicate constitution, but the absence of denticles seems to be original (Fig. 4F).

Type A teeth (Fig. 5A, F) comprise a single triangular prong and an equilateral spur, with a thin and rounded basal pad. In the UWQ, the arch of each Type A tooth additionally bears slender, finely spaced denticles (Fig. 6D–F); the apparent absence of such denticles in the LWQ material (Fig. 5A) may reflect non-preservation of these gracile structures. In the UWQ, Type A teeth occupy a single proximal ring of the armature field; in the LWQ, two rings of Type A teeth occur at the base of the proboscis, followed by a third ring intermediate in form between Type A and Type B teeth.

Type B teeth (Fig. 5A–H) consistently comprise a rounded, lightly carbonized ‘pad’, a central prong, and robust denticles extruding from a prominent arch. The prong and denticles curve gently antieriad, and decrease





**FIG. 5.** Teeth of *Ottoia tricuspida* sp. nov., Lower Walcott Quarry. A–B, ROM 63060; A, Type A teeth at base of proboscis armature; B, Type B teeth, showing rounded base. C–D, ROM 63061; C, entire proboscis width, showing recalcitrant nature of Type B teeth; D, enlargement of boxed area showing tricuspid nature of teeth. E, ROM 63062, Type B teeth on proboscis margin preserved in lateral view, showing curvature. F, ROM 63061, base of pharyngeal armature, showing intermediates (arrowed) between Type A and Type B teeth; tooth bases show faint polygonal texture. G, ROM 63061, tooth prongs contain pyrite crystals; note raised margin of base. H, ROM 63060, narrow pyrite needles accentuate fibrous construction of teeth. I–J, ROM 63058, margin of proboscis preserved in cross-sectional aspect; I, teeth gradational from Type B (left of image) to types C/D (extreme right of image); J, teeth transitional from Type C to Type D. K–M, Type D teeth; K, ROM 63058; L–M, ROM 63061. A–E, G, H, backscattered electron; F, I–M, variable pressure secondary electron. All scale bars represent 200  $\mu$ m.

symmetrically in size away from the midline. The concave surface of the prong and denticles bears a medial rib that emanates from the broad and robust arch at the front edge of the pad; the pad itself bears a faint polygonal patterning. Perpendicular to the denticles, directed anteriad when the introvert is everted, is a stout spur. Type B teeth are conspicuously different in *Ottoia* from the two Burgess Shale

horizons: in UWQ specimens, the tooth bears between four and eight denticles (Fig. 6G–H), whereas the same structure in LWQ specimens has only two denticles (Fig. 5D, F–G).

Type C *Ottoia* teeth exhibit a common morphology in both horizons; they are four to five times longer than wide, with an elongate base and a central prong flanked by a number of fine denticles (Figs 5I–J, 6I–L). A



morphological continuum exists between Type C teeth and teeth of Type B and Type D (Figs 5I, 6J). Proximally, Type C teeth resemble Type B teeth; the arch is triangular but more elongate, and its denticles are smaller and more numerous. Distally, the teeth bear a more uniform and pectinate margin and become progressively more equilateral in form, albeit with an extended tip.

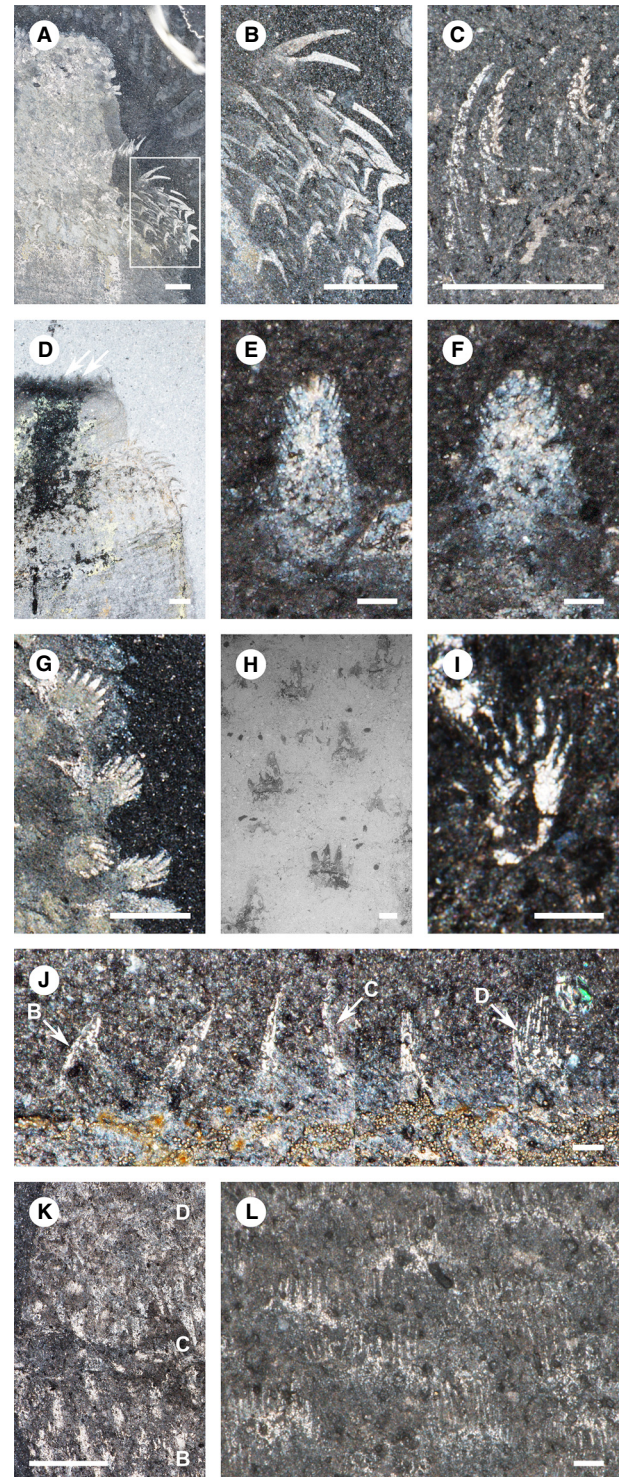
There is a smooth transition from this morphology (Fig. 5J) into typical Type D teeth (Fig. 5K–M), which are short and broad in outline, with a broad and slightly rounded arch that bears dozens of slender denticles in a pectinate arrangement.

The tail hooks of *Ottoia* (Fig. 7) are strongly curved and excavate; the margins of their excavate surface are thickened and appear more prominent, apparently denoting an edentate arch that extends to the tip of the hook. They are substantially larger than corresponding introvert hooks. A broad, flat spur extends in the direction of curvature.

#### Morphological variation

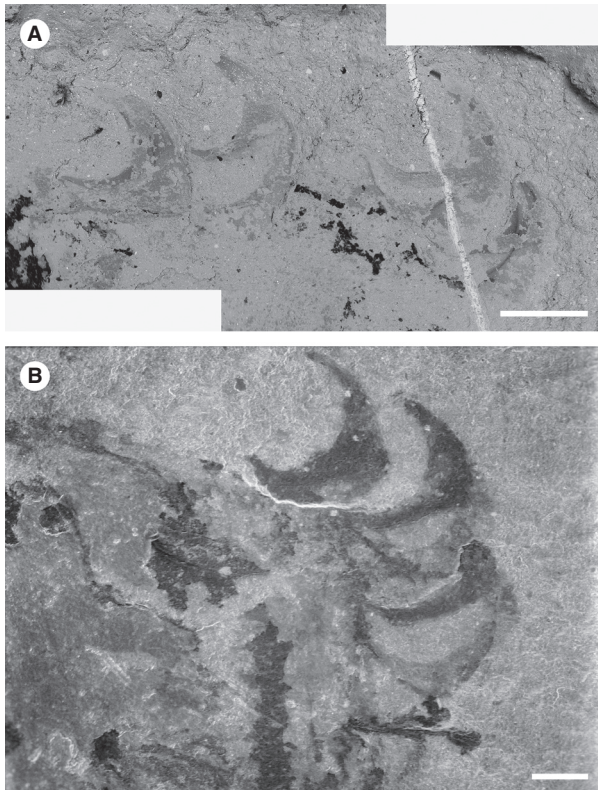
The UWQ and LWQ strata host two distinct morphotypes of *Ottoia*, distinguished by the pronounced differences of their Type A and Type B teeth. These morphotypes could conceivably represent two sexually dimorphic phases, but this is difficult to reconcile with their stratigraphic distribution: each horizon consists almost exclusively of a single morphotype. Furthermore, we observed no relationship between tooth morphology and body size, which discounts ontogenetic effects, and the possibility of phenotypic plasticity is undermined by the limited variation within each morphological category. In modern priapulids, this degree of differentiation is considered taxonomically significant at the species level (e.g. in *Priapulius australis* vs. *P. caudatus*, Storch

et al. 1995). As such, we consider the two Burgess Shale morphotypes to represent separate species of *Ottoia*: the type, *O. prolifica*, from the UWQ, and *O. tricuspida* sp. nov. from the LWQ (see Systematic Palaeontology below).



**FIG. 6.** Scalds and teeth in *O. prolifica*, Upper Walcott Quarry. A–B, NMNH 198818; smaller spines are interspersed between the hooks, which bear no evident denticles. C, NMNH 188609, up to six denticles occur near concave margin. D–F, NMNH 198591, arrows on D denote position of E (enlarged Type A tooth) and F (tooth intermediate in morphology between Type A and Type B). G, NMNH 198818, Type B teeth. H, NMNH 188594, Type B teeth (SEM). I, NMNH 198578, tooth intermediate between Type B and Type C. J, NMNH 172984, teeth displaying progression of morphology from Type B to Type D (labelled). K, NMNH 198578, everted proboscis showing progression from Type B to Type D teeth (labelled). L, NMNH 198578, Type D teeth. High-resolution images captured using Olympus DSX100 optodigital microscope under bright-field illumination with focal stacking. Scale bars represent 1000  $\mu\text{m}$  except E–F (10  $\mu\text{m}$ ); H–J, L (100  $\mu\text{m}$ ).



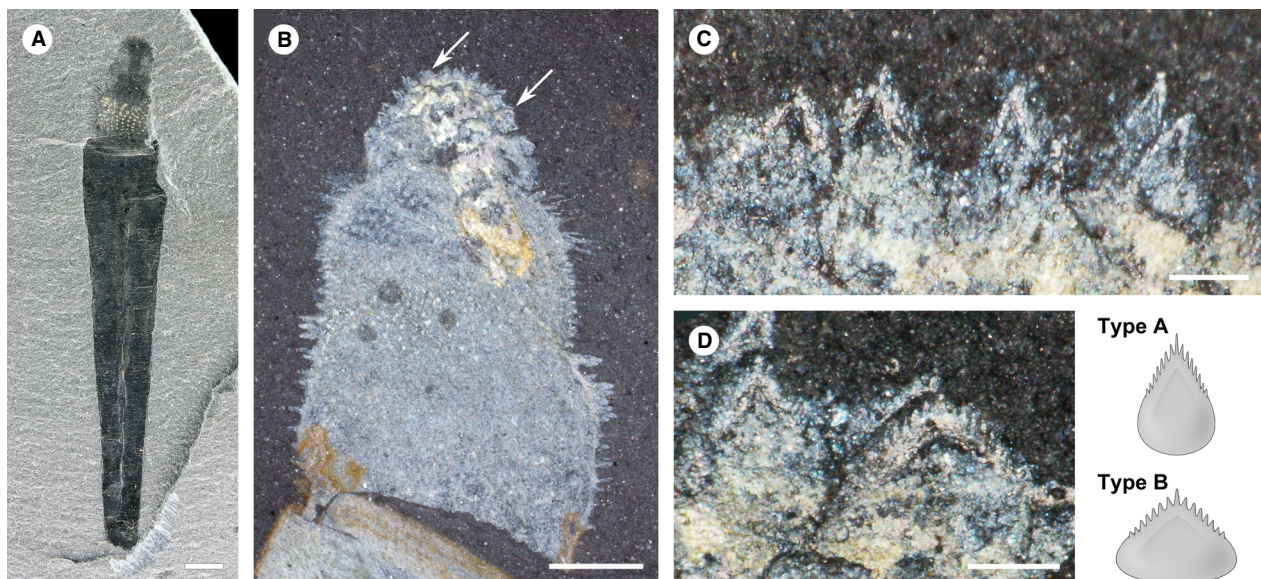


**FIG. 7.** Tail hooks. A, *O. tricuspidata* sp. nov. (ROM 63058, Lower Walcott Quarry), showing excavate habit. B, *O. prolifica* (NMNH 172983, Upper Walcott Quarry), cluster of four hooks. Both scale bars represent 500 µm.

To test whether *Ottoia* sclerites are recognizably distinct from those of other Cambrian priapulids, we examined the sclerites of co-occurring *Fieldia*, *Louisella*, *Ancalagon*, *Lecythioscopa*, *Scolecifurca* and *Selkirkia*. Of these, only *Selkirkia* exhibits distinctively elaborated teeth comparable to those of *Ottoia*, including two types of proboscis teeth: Type A, described as equidimensional with around seven spinules (Conway Morris 1977), and Type B, described as broader, with around ten spinules (Conway Morris 1977).

*Selkirkia* teeth (Fig. 8) can be distinguished from those of *Ottoia* by their relatively diminutive prong, which is similar in size to neighbouring denticles, the regular spacing and size of its denticles, and the equilateral, angular form of the arch. The height of each denticle is equal to the width of the arch, and each denticle is half as wide as it is tall. *Selkirkia* teeth are further characterized by the prominence of their triangular arch relative to their diminutive pad. Whereas the teeth of *Ottoia* are typically elongate (Types A–C) or broad (Type D), those of *Selkirkia* are more equilateral, with the height:width ratio of the arch approximately 2:1 in Type A teeth (Fig. 8C) and 1:2 in Type B teeth (Fig. 8D).

Taken together, these features serve to distinguish the teeth of *Ottoia* from *Selkirkia*. As complex dentition is not evident in other Burgess Shale priapulids and has not been reported in other Cambrian priapulids, we conclude that ottoiid (and selkirkiid) priapulids can be reliably recognized on the basis of their differentiated tooth morphologies.



**FIG. 8.** *Selkirkia* pharyngeal teeth. A, ROM 63131, complete specimen showing pyritization of introvert hooks. B–D, NMNH 83941a, distalmost teeth (arrowed in B, enlarged in C and D) have a broad triangular aspect with a serrated margin; C, Type A teeth; D, Type B teeth. Scale bars represent 2 mm (A–B), 0.2 mm (C–D).

## SMALL CARBONACEOUS FOSSILS

The detailed new anatomical data from Burgess Shale specimens of *Ottoia* and *Selkirkia* provide a test of the priapulid affinity of various disarticulated SCFs and open the possibility of linking particular SCFs with corresponding macrofossil genera or species. Comparisons across the two taphonomic modes must however account for the different preservational filters involved and thus require detailed morphological assessment. Here we identify general criteria for distinguishing priapulid sclerites in the SCF record, which we test via reference to exceptionally abundant and well-preserved assemblages from western Canada, before critically assessing the wider distribution of priapulid SCFs based on previously published specimens.

*General identification of priapulid SCFs.* Several recurrent features exhibited throughout the disparate sclerite morphologies of *Ottoia* and *Selkirkia* (Fig. 3) point to some general rules for the identification of disarticulated priapulid sclerites in the SCF record. Every sclerite in *Ottoia* and *Selkirkia* is bilaterally symmetrical (although this is often obscured by the angle of flattening; see Figs 4B, 6B) with a central prong, a thinner (typically polygonally patterned) basal pad, a robust triangular arch, a basal opening, and a perpendicular or oblique spur. As in modern priapulids (van der Land 1970), these features are typically (but not universally) accompanied by subsidiary spines or denticles arising from the arch, with denticles decreasing in size monotonically away from the central prong; the spinose projections are typically recumbent with respect to the pad of basal cuticle.

*Identification of ottoiid and selkirkiid SCFs.* The scalids and teeth of *Ottoia* and *Selkirkia* differ notably from those of other Burgess Shale priapulids by the presence of a denticulate arch and (in general) a more strongly sclerotized construction. Although no single feature is unique to the sclerites of *Ottoia*, the denticulate nature of introvert hooks and the distinctive morphology of each tooth (types A–D) provide grounds for recognizing sclerites more precisely. Indeed, the rich SCF assemblages from the Deadwood and Pika formations (Fig. 9) include exact morphological counterparts for most or all of the sclerite morphotypes expressed in *Ottoia*, sometimes within a single sample horizon.

Comparatively straight-sided, thin-walled SCFs with an expanded base (Fig. 9E) may represent coronal spines, although a secure comparison is undermined by the simple anatomy and the generally poor preservation of these sclerites in the Burgess Shale. Probable tail hooks are represented among the SCFs by comparably robust, sickle-shaped forms with broad proximal flanks and a conspicuous elongate arch (Fig. 9A–B).

Candidate introvert hooks express a prominent, gently curved prong and a pronounced spur (Figs 9C–D, N–O, 10D). As in *Ottoia*, the SCF scalids exhibit a robust triangular arch that may be unornamented or bear short conical denticles (Fig. 9C–D, N); individual scalids exhibit a smooth cuticular surface and an approximately even cuticle thickness.

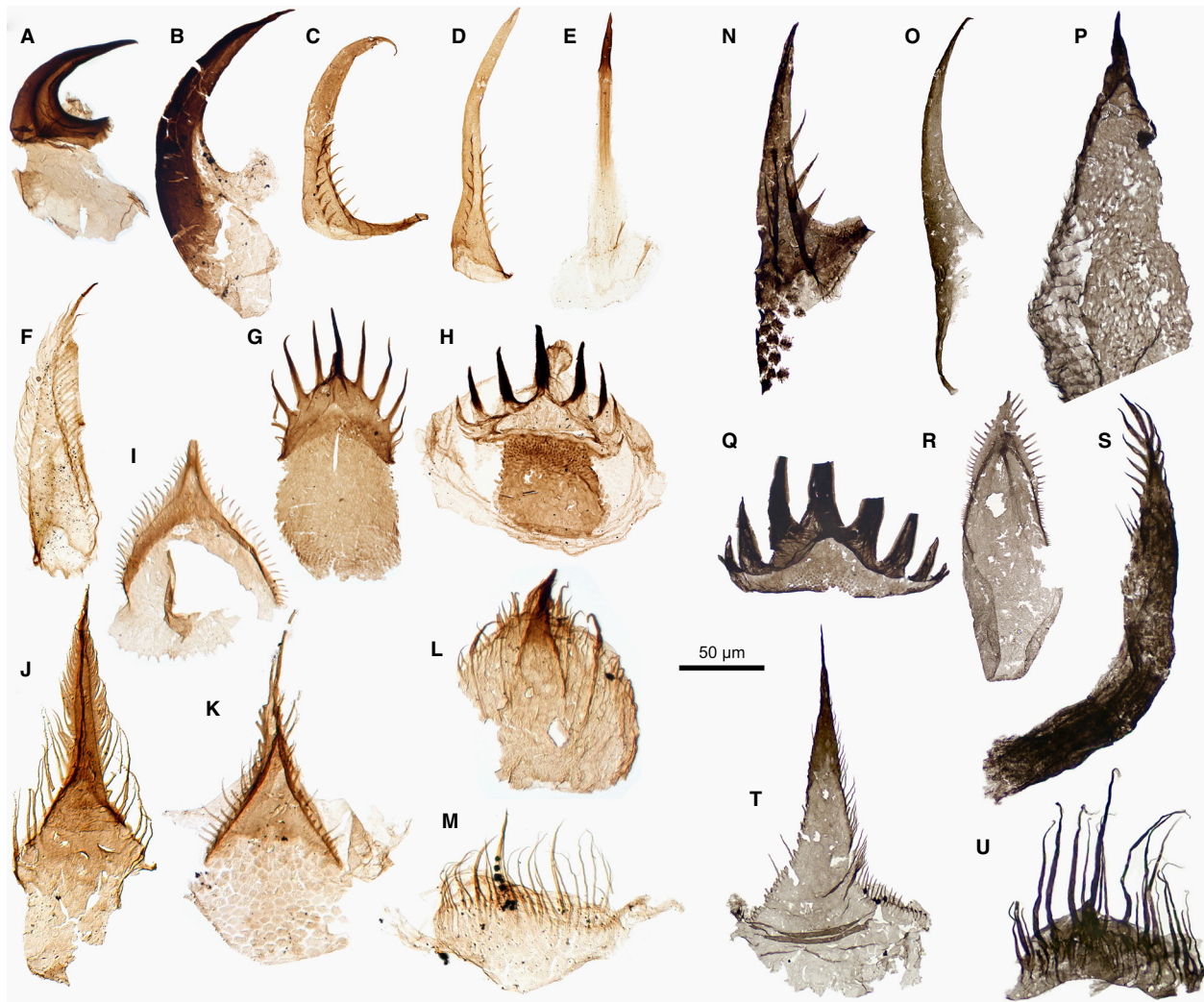
The more distinctive morphologies of the pharyngeal teeth in *Ottoia* allow a more confident identification of counterparts among the SCF assemblages. SCFs comparable to Type A teeth exhibit an elongate triangular outline and a slender, finely denticulate arch that occupies most of the length of the sclerite (Fig. 9F). Type B teeth ('bear paws') are particularly distinctive among the SCFs, characterized by their series of four to eight robust anterior-facing denticles and triangular basal opening, their pronounced anterior prong overlying a stout spur, and their rounded posterior pad with a polygonal microstructure (Figs 9G–H, 10A–C). Occasional specimens preserve remnants of the surrounding cuticle, which is notably thinner and unornamented (Fig. 9H).

Other tooth-like SCFs (Fig. 9I–M, R–U) bear much finer denticles and are more readily compared to the more distal pharyngeal teeth in *Ottoia* (cf. Figs 5, 6). These grade in morphology between triangular forms with an elongate, sharply pointed central prong and contiguous denticles (Type C; Fig. 9I–L, R–T) to progressively broader, shorter forms with delicate fringing denticles and a highly reduced prong (Type D; Fig. 9M, U). Well-preserved specimens exhibit a thin-walled pad with a well-defined margin and either laevigate or polygonally ornamented cuticle (e.g. Fig. 9G–K).

The ottoiid affinity of tooth-like SCFs is readily established based on their precise morphological correspondence with the teeth of types A, B, C and D displayed in *Ottoia* macrofossils. Specifically, the presence of four to eight denticles (plus the central prong) in the Type B-like Deadwood and Pika teeth signifies a relationship with *O. prolifica* rather than *O. tricuspidata* sp. nov. SCFs that resemble introvert hooks and spines can be assigned to the priapulids based on their denticulate arch, where present, but their identification as ottoiid scalids rests primarily on their co-occurrence with other *Ottoia* sclerites. The SCF assemblages also contain priapulid-like sclerites that do not correspond with *Ottoia* sclerites, possibly reflecting the presence of multiple worm taxa. Indeed, SCFs of the Pika Formation include *Selkirkia*-like sclerites recognizable by their triangular aspect, prominent arch, inconspicuous prong, and regularly spaced denticles with a height:width ratio of 2:1 (Figs 10E–H, 11).

*Wider occurrence of priapulid SCFs.* The taxonomic resolution attainable for isolated SCFs is of course dependent





**FIG. 9.** Small Carbonaceous Fossils from the Deadwood and Pika formations assigned to *Ottoia prolifica*. A–M, GSC 138082–138094, teeth from a single sample of the Deadwood Formation (Riley Lake drillcore at 1300 m), interpreted as tail hooks (A–B), introvert hooks (C–D), a coronal spine (E), a Type A tooth (F), a Type B tooth (G), a Type B tooth with surrounding cuticle (H), morphologies intermediate between tooth types B, C and D (I–L), and a Type D tooth (M). N–U, GSC 138095–138102, teeth from the Pika Formation, interpreted as an introvert hook (N), an introvert hook without submarginal denticles (O), a Type A-like tooth (P), a Type B tooth (Q), a tooth possibly intermediate between Type B and Type C (R), a Type C tooth (S), an intermediate between Type C and Type D morphologies (T), and a Type D tooth (U). Scale bar represents 50  $\mu\text{m}$ .

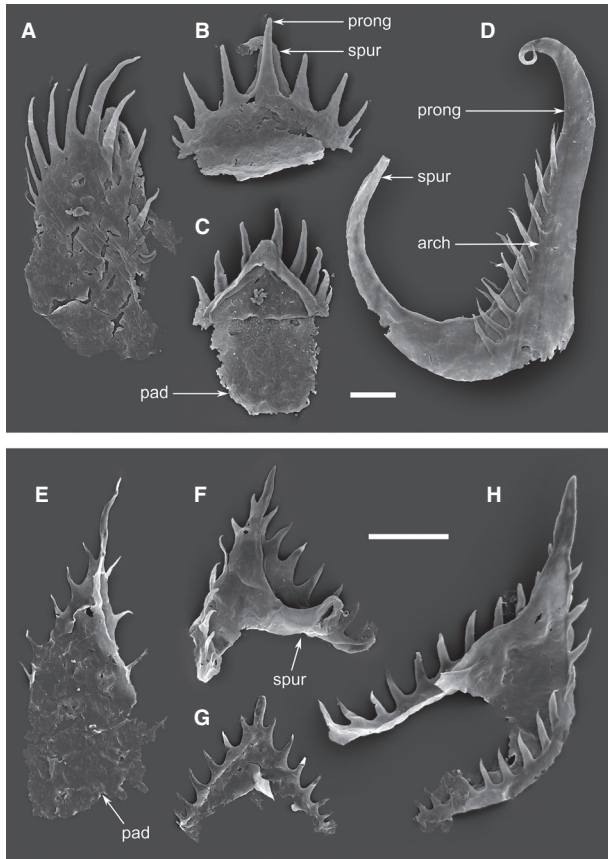
on the level of preserved diagnostic characters. Although many simple spine-like SCFs can only be classified into artificial form taxa, a significant subset can now be recognized as priapulid sclerites based on details of their construction – most importantly, the presence of a denticulate arch.

On the broadest scale, a priapulid affinity has been proposed for certain members of *Ceratophyton* (Butterfield and Harvey 2012), an acritarch form genus currently represented by five ‘species’ of spine-shaped microfossils (Moczyłowska 2008). Insofar as *C. dumufuntum* and *C. spinuconum* exhibit a triangular aperture, robust

arch, central prong, thin basal region, reinforced spine margins and marginal denticles (Gravestock *et al.* 2001), they are directly comparable to the teeth of ottoiid and selkirkid priapulids and cannot be comfortably accommodated in the concept of *Ceratophyton*. By contrast, the double cones of *C. duplicum* and the circular basal opening of *C. circufuntum* have no clear analogue in priapulids; as such, these ‘species’, along with *C. vernicosum* (the type species, and a synonym of *C. groetlingboensis* (Moczyłowska 2008)), remain taxonomically unresolved.

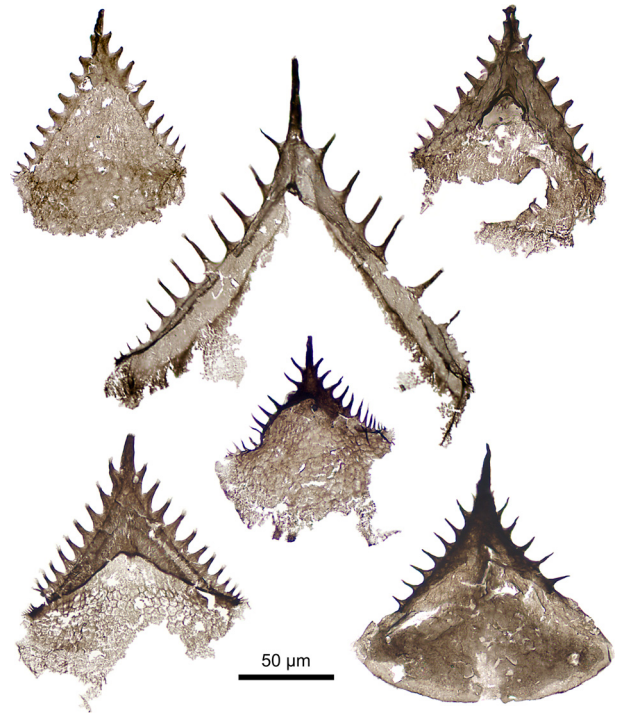
Further priapulid sclerite candidates are preserved in the shallow water mudrocks of the Mahto Formation,





**FIG. 10.** SEM images of fossil priapulid teeth. A–D, GSC 138170–138173, teeth from the Deadwood Formation assigned to *Ottoia prolifica*; A–C, Type B teeth, outer (A–B) and inner (C) surfaces, triangular spur visible in proximal view; D, introvert hook with two rows of denticles, elongate spur and extended prong (distal curling is presumably an artefact of preservation). E–H, GSC 138174–138177, teeth from the Pika Formation assigned to *Selkirkia*; E, Type A; F–H, Type B. Both scale bars represent 50 µm.

western Alberta (Cambrian Series 2, Stages 3–4). Subtriangular elements with approximate bilateral symmetry have been interpreted as elements of a molluscan-type feeding apparatus (Butterfield 2008, fig. 6.18), but our new observations from *Ottoia* challenge this hypothesis. With a regularly denticulate robust triangular arch and a pronounced central prong, the elements compare favourably with Type C *Ottoia* teeth and are more convincingly interpreted as priapulid sclerites. The same applies to co-occurring elements with a prominent hollow prong and a denticulate subterminal triangular structure resembling the arch of priapulid sclerites (Butterfield 2008, fig. 6.1–12, 19). ‘Radula-like’ elements from the contemporaneous Mount Cap Formation (Harvey and Butterfield 2011 fig. 7b) also exhibit a central prong and regular denticles, though in this case the lateral



**FIG. 11.** *Selkirkia* teeth; Small Carbonaceous Fossils from the Pika Formation (GSC 138103–138108). Scale bar represents 50 µm.

aspect of the specimens prevents conclusive taxonomic identification.

A single SCF specimen from the Kaili biota, China (Harvey *et al.* 2012a, fig. 5A), consists of three articulated tooth-like sclerites that each exhibit an equilateral arch with short, regularly spaced denticles, in conjunction with a diminutive, denticle-like prong – reminiscent of the teeth of *Selkirkia*, a genus that occurs in the Kaili macrofossil biota (Zhao *et al.* 2005). However, *Selkirkia* macrofossils do not preserve the distinctive setal bundles present in the Kaili SCFs.

Candidate *Ottoia* teeth are represented by sclerites from the Hess River Formation (early Series 3 of the Northwest Territories, Canada), which exhibit a morphology intermediate between Type B and Type C *Ottoia* teeth (Butterfield and Harvey 2012, fig. 2e). The absence of teeth corresponding to any of the more common tooth morphologies casts doubt on whether these teeth truly belong to an ottoiid, notwithstanding the possibility of taphonomic filtering (by analogy with Purnell and Donoghue 2005). Sclerites from the Earlie or lower Deadwood Formation (late Series 3 of Saskatchewan, Canada), however, are readily recognized as the Type B teeth of *Ottoia prolifica* based on the shape of their pad and arch, and the size and distribution of their denticles (Butterfield and Harvey 2012, fig. 2g).

## DISCUSSION

### *Taxonomical implications*

Our new observations emphasize the systematic importance of priapulid sclerite morphology. Fine details of pharyngeal teeth are key to the identification of a second species of *Ottoia*; as such, the high proportion of seemingly monospecific macrofossil genera in Burgess Shale-type assemblages (Table S1, see online Supporting Information) may reflect the vulnerability of species-level morphological variety to taphonomic filtering. Failure to recognize species-level diversity in the palaeontological record likely underlies the low number of species in Cambrian priapulid genera relative to their extant counterparts; unrecognized fossil species may well await discovery in existing fossil collections.

Even so, the detailed interrogation of the pharyngeal armature necessary for the recognition of species-level variation requires exquisite preservation; as such, the degradation of carbon films in other Cambrian Lagerstätten (e.g. Zhu *et al.* 2005; Conway Morris and Peel 2010; Steiner *et al.* 2012) provides a fundamental limit on the taxonomic resolution available from these sites. This emphasizes the unique role of the Burgess Shale in understanding the diversity of Cambrian priapulids.

*Ecological implications.* SCFs profoundly expand our view of soft-bodied organisms, complementing the narrow window of exceptional preservation and providing a geographically and temporally inclusive window on non-mineralizing life. Despite the obvious trade-offs, these microscopic and disarticulated components provide a broader perspective on Cambrian communities that would be impossible to resolve based on Lagerstätten alone. As such, SCFs allow the record of ottoiids and other priapulids to be tracked beyond the rarefied settings of exceptional Burgess Shale-type preservation.

The ubiquity of priapulid SCFs contrasts with the patchy occurrence of priapulid macrofossils in Cambrian Lagerstätten. Priapulid macrofossils are only known from the Burgess Shale, Chengjiang, and a handful of North American localities (Table S1); they are absent in diverse and well-sampled faunas such as the Emu Bay Shale (Australia) and Sirius Passet (Greenland). This absence is likely to reflect local-scale ecological factors rather than temporal or geographical trends: within the Burgess Shale, for example, there are hundreds of priapulid specimens in the Walcott Quarry, but just three at the nearby Marble Canyon locality, and none at all at Stanley Glacier (Caron *et al.* 2014).

The sampling of time-averaged SCFs assemblages from multiple stratigraphic horizons goes some way to mitigating

these local ecological biases and, in principle, allows a fundamentally more complete record of priapulid distribution. This phenomenon is particularly apparent in *Ottoia*, whose macrofossils are only known from the deep-water environments of the Burgess Shale ('Thick Stephen' Formation, Fossil Ridge). In contrast to the specialized and restricted niche that this implies, the presence of *Ottoia* SCFs from the shallow marine, periodically emergent settings of the epicratonic Pika Formation and the non-trilobitic inboard seas of the Earlie and Deadwood formations establishes *Ottoia* as an ecologically versatile organism that prospered in a range of water depths and sedimentological settings (Fig. 1) – a clear contrast to the deeper water, dysaerobic settings typically occupied by extant macroscopic priapulid worms (van der Land 1970).

*Stratigraphical and palaeobiological implications.* SCFs provide an important perspective on the stratigraphical and geographical distribution of Cambrian priapulids; the apparently global occurrence of priapulid SCFs is indicated by the occurrence of *Ceratophyton dumufuntum* and *C. spinuconum* SCFs in pericratonic mudstones from the Stansbury Basin, southern Australia (Gravestock *et al.* 2001), and distinctive priapulid sclerites from platformal deposits in Kaili, China (Harvey *et al.* 2012a). Our intensive sampling within the Western Canada Sedimentary Basin (Fig. 1) allows the distribution of priapulids to be tracked on a finer scale, from late Series 2 to the late Furongian and across a disparate range of palaeoenvironments.

Based on our current dataset, *Ottoia* appears to exhibit a conspicuously restricted temporal and spatial distribution: its sclerites have so far only been encountered in strata of Burgess Shale age and younger (mid-Series 3 onwards), and are not demonstrably present outside of Alberta and Saskatchewan. Indeed, the distinctive Type B teeth of *O. tricuspidata* sp. nov. are known only from the Burgess Shale. This pattern is at least consistent with a late (Series 3, post-Chengjiang) origin and limited geographic distribution, but may expand with further sampling.

The seemingly narrow geographical range of *Ottoia* stands in contrast to the significant faunal connectivity between the Burgess Shale and the distant Chengjiang biota (Conway Morris 1989; Han *et al.* 2008). A wide range of genera and species have been documented in both localities, including *Nectocaris pteryx*, *Hallucigenia sparsa*, the priapulid *Selkirkia*, and various euarthropods (*Alalcomenaeus*, *Anomalocaris*, *Canadaspis*, *Isoxys*, *Leancoilia*, *Liangshanella*, *Misszhouia*, *Naraoia*, *Primicaris*, *Waptia*), sponges (*Choia*, *Leptomitrus*) and problematica (*Banffia*, *Dinomischus*, *Eldonia*, *Wiwaxia*) (Briggs *et al.* 1994; Hou *et al.* 2003; Steiner *et al.* 2012; Smith

2013; Caron *et al.* 2014; Zhao *et al.* 2015). On the other hand, certain groups display little overlap between the two localities. Palaeoscolecsids and lobopodians are diverse in Chengjiang but are represented by just one or two species in the Burgess Shale, and there is little overlap in the trilobite fauna of the two localities (Briggs *et al.* 1994; Hou *et al.* 2003; Liu and Dunlop 2014).

These faunal differences may be explained by incomplete sampling, provincial geographical ranges, environmental differences or – given that the two sites are separated by some 10 million years – extinction and origination. To determine which of these factors accounts for the absence of *Ottoia* from China, more sampling is necessary. The only intermediate SCF data currently available are from the Kaili biota, which is geographically close to Chengjiang and marginally older than the Burgess Shale. This assemblage contains priapulid SCFs, but no *Ottoia* sclerites. As with each other priapulid assemblage that lacks *Ottoia*, this adds weak but cumulative evidence to the tentative hypothesis that *Ottoia* was truly restricted to the Western Canada Sedimentary Basin.

The new morphological details resolved from the Burgess Shale combine to provide a distinctive search image for the recognition of *Ottoia* at both a macroscopic and microscopic level, setting the stage for future SCF discoveries to establish the full breadth of this ecologically tolerant and locally prolific Cambrian worm.

*Institutional abbreviations.* NMNH, Smithsonian Institution National Museum of Natural History, Washington, DC; ROM, Royal Ontario Museum, Toronto, Ontario; GSC, Geological Survey of Canada.

## SYSTEMATIC PALAEONTOLOGY

This published work and the nomenclatural acts it contains have been registered in Zoobank: <http://zoobank.org/References/E7C3A0BF-B3E6-4751-A71B-60AC701751E0>

Stem group of Phylum PRIAPULIDA Delage and Hérouard,  
1897

Family OTTOIIDAE Walcott, 1911

Genus OTTOIA Walcott, 1911

*Emended diagnosis.* Cylindrical and extensible body bilaterally symmetrical, but with pronounced anterior external radial symmetry. Divisible into pharynx, introvert and annulated trunk. Anterior trunk cylindrical; posterior trunk expanded and bulbous. Proboscis invaginable into trunk, armed from posterior to anterior in everted

proboscis, anterior end extensible. Proboscis teeth with regularly denticulate robust triangular arch, polygonally ornamented basal pad, and pronounced central prong, falling into four morphological categories. Posteriormost teeth in everted pharynx (Type A) originally weakly carbonized with prominent triangular prong and elongate arch with or without denticles, succeeded by teeth (Type B) with small number of prominent hollow denticles extruding from robust arch, rounded pad of teeth bearing polygonal ornament. Type B teeth grading anteriorly into elongate teeth (Type C) with finely denticulate arch extending towards tip of prong. Type C teeth grading distally into short and insubstantial teeth (Type D) with broad, rounded arch that bears many long, fine, cirrus-like denticles. Trunk has about a hundred annulations, posterior end armed with dorsal and lateral hooks, posterior eversible as unannulated bursa. Trunk flexible, but with curvature restricted to a single direction, lending fossils U-shaped appearance. Mouth at end of proboscis, leading to pharynx, gizzard (?), and thence to straight or irregularly looped intestine with folded internal walls. Anus at posterior end of the trunk or bursa if everted. Undivided spacious body cavity. Musculature consists of body-wall muscles, four sets of anterior retractor muscles, and one or two sets of posterior retractor muscles. Mesenteries and gut suspensor muscles support internal organs.

Note that this is an emendation of the diagnosis presented by Conway Morris (1977); readers should refer to that study for further information on morphological details that are not discussed here.

*Ottoia prolifica* Walcott, 1911

Figures 2A–C, 6, 7B, 9, 10A–D

*Emended diagnosis.* A species of *Ottoia* with a single proximal ring of Type A teeth, and with Type B teeth bearing a central prong flanked by four to eight denticles that decrease in size laterally.

*Stratigraphical distribution.* Macrofossils only recorded in strata above the Phyllopod Bed at the base of the Walcott Quarry (Cambrian Stage 5). A subset of SCFs from the Guzhangian and Paibian Deadwood and Pika formations (Figs 9, 10A–D) are assigned to *Ottoia* based on the recovery of associations of sclerites that morphologically correspond to each sclerite type observed in Burgess Shale macrofossils. Assignment to *O. prolifica* is supported by the detailed anatomy of Type B teeth, pending new information from corresponding soft anatomy. This criterion also identifies sclerites from the Earle Formation (late Series 3) as Type B teeth of *O. prolifica*, whereas the more tentative identification of *O. cf. prolifica* from the early Series 3 Hess River would be confirmed by the recovery of other *Ottoia* tooth morphologies.



*Ottoia tricuspidata* sp. nov.

Figures 2D, 4, 5, 7A, 12

LSID. urn:lsid:zoobank.org:act:F4367645-2D7D-48F3-97EA-B1B2B611DABA

*Derivation of name.* With reference to the three cusps of the diagnostic Type B teeth.

*Type specimen.* ROM 63057 (Fig. 12).

*Paratypes.* ROM 63058–63064.

*Diagnosis.* A species of *Ottoia* in which two rings of Type A teeth occur at the base of the proboscis armature, with Type B teeth bearing a central prong that is flanked by a pair of long, slender, hollow denticles.



**FIG. 12.** Holotype of *O. tricuspidata* sp. nov., ROM 63057. A, complete specimen. B, enlargement of proboscis. Scale bars represent 10 mm (A); 2 mm (B).

*Stratigraphical distribution.* Present in the horizon 120–130 cm below the base of the Phyllopod Bed, with a single possible occurrence in the Upper Walcott Quarry (NMNH 196328); not known from the SCF record.

*Remarks.* As the distinction between the two *Ottoia* species rests on microscopic detail of the proboscis, it is likely that material previously referred to *O. prolifica* belongs instead to *O. tricuspidata* sp. nov. Even though stratigraphy serves as strong predictor of taxonomic affinity, microscopic examination is necessary to confirm or refute the assignment of existing material to *O. prolifica*.

## Family SELKIRKIIDAE Conway Morris, 1977

## Genus SELKIRKIA Walcott, 1911

*Emended diagnosis.* Tubicolous priapulid. Body divisible into anterior armed proboscis and trunk. Introvert armed with hollow edentate triangular spines of various sizes. Proboscis partially invertible, armed with teeth that exhibit a pronounced, approximately equilateral triangular arch bearing central prong and regularly spaced triangular denticles of modest proportion; terminal area of proboscis anterior to spinules smooth and conical. Trunk located within tube, armed with anterior rows of papillae. Gut straight with terminal openings, externally unregionated, mouth surrounded by proboscis spinules. Undivided body cavity. Finely annulated tube, open at both ends, with oval cross section.

Note that this is an emendation of the diagnosis presented by Conway Morris (1977); readers should refer to this study for further information on morphological details that are not discussed here.

*Selkirkia* sp.

Figures 10E–H, 11

*New material.* Scalids from the Pika Formation (Figs 10E–H, 11) are assigned to *Selkirkia* based on their shape and the dimensions and distribution of their denticles. Attribution at a species level is not attempted pending description of tooth morphology in species of *Selkirkia* besides *S. columbia*.

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*Author contributions.* MS conceived the study. Preparation, study and imagery of material was undertaken by MS (Burgess Shale), TH (Deadwood Formation) and NB (Pika Formation). MS, TH and NB wrote the manuscript.

## DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad digital repository: <http://dx.doi.org/10.5061/dryad.km109>.

*Editor.* Artem Kouchinsky

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Diversity of fossil priapulids. Occurrence and validity of fossil priapulid taxa.

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