

Aysheaia prolata from the Utah Wheeler Formation (Drumian, Cambrian) is a frontal appendage of the radiodontan *Stanleycaris*

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Aysheaia prolata, was described as the only lobopodian from the Drumian (Cambrian) Wheeler Formation in Utah, USA, and the sole representative of this genus besides the type species *Aysheaia pedunculata*, from the Cambrian (Stage 5) Stephen Formation, British Columbia. A redescription of *Aysheaia prolata* reveals previously overlooked morphological features, including segmental boundaries between putative lobopods, and curved terminal spines on the putative anterior end. These observations undermine lobopodian affinities of *Aysheaia prolata*, and instead we interpret this specimen as an isolated radiodontan frontal appendage. The presence of 11 podomeres, five of which possess elongate and anteriorly recurved ventral blades with auxiliary spines, together with shorter robust dorsal spines, identify the specimen as *Stanleycaris*. This represents the first report of *Stanleycaris* outside of the Cambrian Stage 5 thin Stephen Formation in British Columbia, expanding its palaeobiogeographic and stratigraphic range. *Aysheaia* is left as a monotypic genus endemic to the Burgess Shale. The Spence Shale luolishaniid *Acinocrinus stichus* is currently the only lobopodian known from the Cambrian of Utah.

Key words: Euarthropoda, Radiodonta, Hurdiidae, Cambrian, United States.

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Introduction

Radiodontans, a diverse group of large nektonic predators, are among the most recognizable faunal components in Lower Palaeozoic Burgess Shale-type biotas (e.g., Daley et al. 2009, 2013a, b; Daley and Edgecombe 2014; Van Roy et al. 2015; Cong et al. 2016; Zeng et al. 2017). Despite their fundamentally soft-bodied construction, there is a comprehensive record of radiodontan diversity owing to the preferential preservation of their sclerotized frontal appendages (e.g., Caron et al. 2010; Daley and Budd 2010; Daley and Peel 2010; Wang et al. 2013; Lerosey-Aubril et al. 2014; Vinther et al. 2014). Recent work has expanded the palaeobiogeographic and stratigraphic occurrence of radiodontan taxa previously known only from the Cambrian (Stage 5) Burgess Shale in British Columbia, including new reports from the Cambrian (Series 3) of Utah (Pates et al. in press). Here we demonstrate that *Aysheaia prolata* Robison, 1985, widely regarded for over

30 years as the only lobopodian from the Wheeler Formation (Drumian), is actually a radiodontan frontal appendage, and discuss implications for the known diversity of middle Cambrian radiodontans and lobopodians from Utah, USA.

Institutional abbreviations.—KUMIP, University of Kansas Natural History Museum, Lawrence, Kansas, USA; ROM, Royal Ontario Museum, Toronto, Canada; USNM, Smithsonian Institution National Museum of Natural History, Washington D.C., USA.

Other abbreviations.—Pn, podomere n; sag., sagittal; trans., transverse.

Material and methods

The only known specimen (KUMIP 153923) is housed at the University of Kansas Natural History Museum. A Canon

EOS 500D DSLR camera, with Canon EF-S 60 117 mm Macro Lens, controlled for remote shooting with EOSUtility 2 was used for photography. Photographs were taken wet, dry, under cross-polarized and non-polarized light. Lengths and angles were measured from photographs using ImageJ 2. Photoshop CS6 was used to convert photographs to black and white and manipulate colour channels.

Systematic palaeontology

Phylum Euarthropoda Lankester, 1904

Order Radiodonta Collins, 1996

Family Hurdiidae Vinther, Stein, Longrich, and Harper, 2014

Genus *Stanleycaris* Caron, Gaines, Mángano, Streng, and Daley, 2010

Type species: Stanleycaris hirpex Caron, Gaines, Mángano, Streng, and Daley, 2010; Stephen Formation (Cambrian Series 3, Stage 5), near Stanley Glacier (Kootenay National Park), British Columbia, Canada.

Remarks.—*Stanleycaris* was originally described from the thin Stephen Formation near Stanley Glacier (Cambrian Stage 5), British Columbia. 37 specimens of the type species, *S. hirpex*, have been described: disarticulated assemblages including frontal appendages, oral cones, and carapace material; no post cephalic remains have yet been found.

Stratigraphic and geographic range.—Thin Stephen Formation (Cambrian Series 3, Stage 5), British Columbia, Canada (Caron et al. 2010); Wheeler Formation (Cambrian Series 3, Drumian), Utah, USA (this study).

Aysheaia prolata Robison, 1985 nomen dubium
= *Stanleycaris* sp.

Figs. 1A, 2, 3A.

- 1985 *Aysheaia prolata* sp. nov.; Robison 1985: 226–235, text-fig. 3.
1989 *Aysheaia? prolata* Robison, 1985; Dzik and Krumbiegel 1989: 175.
1995 *Aysheaia? prolata* Robison, 1985; Hou and Bergström 1995: 13.
1998 *Aysheaia prolata* Robison, 1985; Ramsköld and Chen 1998: 108, 134, 138–139, 143–144.
2001 *Aysheaia? prolata* Robison, 1985; Bergström and Hou 2001: 238, 245.
2004 *Aysheaia? prolata* Robison, 1985; Hou et al. 2004: 238.
2009 *Aysheaia? prolata* Robison, 1985; Whittle et al. 2009: 562.
2011 *Aysheaia? prolata* Robison, 1985; Ou et al. 2011: 587.
2011 *Aysheaia? prolata* Robison, 1985; Gámez Vintaned et al. 2011: 211.
2015 *Aysheaia? prolata* Robison, 1985; Robison et al. 2015: 27, fig. 56.
2016 *Aysheaia prolata* Robison, 1985; Foster and Gaines 2016: 299, 303, 330, fig. 9H.

Material.—KUMIP 153923, isolated frontal appendage, preserved flattened in light grey shale collected from locality 114 of Robison and Richards (1981: 3), Utah, USA, ap-

proximately 100 m below the top of the Wheeler Formation (Cambrian Series 3, Drumian; Robison 1985).

Description.—The appendage measures 26.5 mm in length (sag.), and displays 11 podomeres, indicated by the preservation of serially repeated segmental boundaries. P1 differs from the other podomeres in having a subrectangular outline (length [sag.] ca. 7.0 mm; width [trans.] ca. 4.6 mm). P2 to P11 are shorter (sag.) and wider (trans.). A layer of sediment between P1 and P2 suggests that P1 has shifted forwards to cover the posterior border of P2 (Fig. 2), making the precise dimensions of P2 unclear. P3 to P8 are similar lengths (sag. ca. 2 mm). P3 to P6 maintain a stable width (trans. ca. 3.5 mm), whereas P7 to P11 taper distally (P7 ca. 3.2 mm; P11 ca. 2.2 mm). P9 to P11 are flexed laterally towards the rock surface, slightly overlapping one another. It is not possible to measure the dimensions of these podomeres owing to their orientation. The armature consists of well-developed spinose ventral blades with auxiliary spines, and short dorsal spines. P1 lacks ornamentation altogether. P2 to P6 possess ventral blades (“lobopods 1–5” in Robison 1985: fig. 3.2), which emerge approximately perpendicular to the limb axis. The most complete of the blades (on P4, Fig. 3A₂), has a length (sag.) of approximately 8 mm and possesses two distally-pointing auxiliary spines. The tip curves sharply towards the distal end of the appendage, giving the blade a crescent-shape. A ventral blade on P7 is approximately a third of the length (sag.) of the others, with no visible auxiliary spines. Dorsal spines are observed on P4, P6, and P7. The most complete dorsal spine is on P6; it has a subtriangular outline with a robust base (“lobopod 1” in Robison 1985: fig. 3.2), projects at an angle of 71° from the main limb axis, and shows no evidence for more than a single-point. P4 and P7 show poorly preserved dorsal spine bases (“anterior appendage” in Robison 1985: fig. 3.2). Armature is absent from P8 to P10. P11 preserves two recurved terminal spines (Fig. 3A₁; “papillae?” in Robison 1985: fig. 3.2).

Remarks.—The recognition of podomere boundaries, together with the occurrence of ventral, dorsal, and terminal spines, support the reinterpretation of KUMIP 153923 as an isolated radiodontan appendage. Robison’s (1985) original lobopodian interpretation was largely based on the similar outline of this specimen to *Aysheaia pedunculata* preserved in lateral view (Fig. 4; Whittington 1978). Although *A. pedunculata* frequently displays compaction wrinkles that may resemble segmental boundaries (e.g., Fig. 3D; Ma et al. 2014: fig. 5B), these are generally restricted to the lobopodous limbs. The features identified as podomere boundaries in KUMIP 153923 occur along the main axis of the fossil, rather than on the putative limbs. Furthermore, the podomere boundaries cross the whole width of the specimen, and are more widely spaced than annulations on the trunk of *A. pedunculata* (Fig. 4). The putative lobopods and oral papillae of *A. prolata* described by Robison (1985) are best regarded as ventral blades and terminal spines respectively. The ventral blades are curved and bear auxiliary spines pointing to

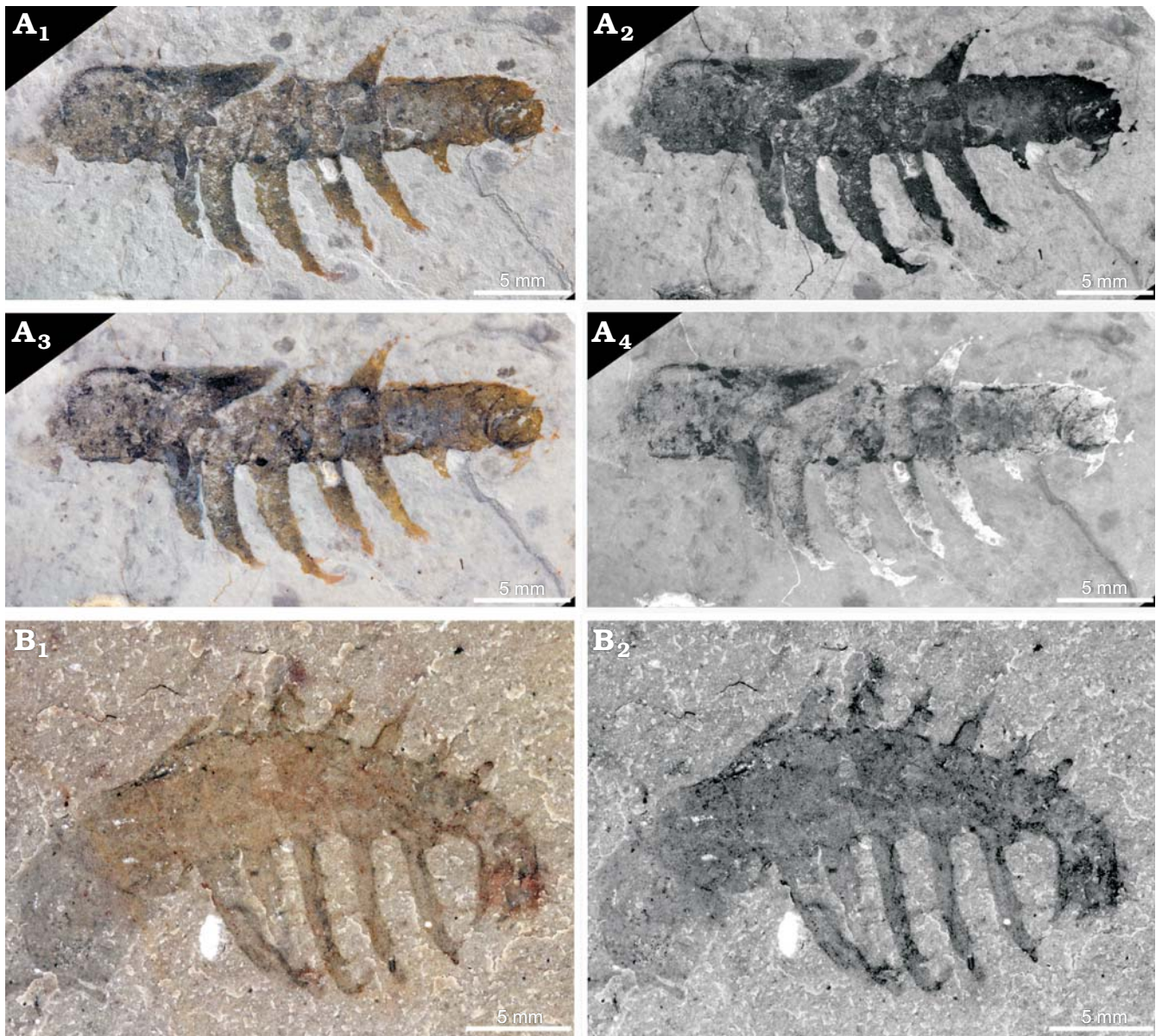


Fig. 1. **A.** Radiodontan euarthropod *Stanleycaris* sp., KUMIP 153923 from the Wheeler Formation (Cambrian Series 3, Drumian), Utah, USA; non-polarized light (A₁), cross-polarized light, red and yellow channels reduced (A₂), cross polarized light (A₃), cross-polarized light, red and yellow channels enhanced (A₄). **B.** *Stanleycaris hirpex* Caron, Gaines, Mángano, Streng, and Daley, 2010, ROM 59944 (holotype) from the Stephen Formation (Cambrian Series 3, Stage 5), British Columbia, Canada; cross-polarized light (B₁), black and white (B₂).

the anterior end, as also observed in in *Stanleycaris hirpex* (compare Fig. 3A₂ and 3C). The ventral blades lack compaction wrinkles often preserved on limbs of *A. pedunculata* (Figs. 3D, 4; Ma et al. 2014: fig. 5B). The terminal spines at the anterior end of the specimen are short, recurved, and have a sharp termination. This morphology is similar to that of the spines in *S. hirpex*, and quite unlike the straight and less robust oral papillae of *A. pedunculata* (compare Fig. 3A₁ and 3B). It should be noted that Robison (1985) studied the specimen before the extent of radiodontan frontal appendage morphological diversity was known (e.g., Daley and Budd 2010; Caron et al. 2010), and so lacked the appropriate context for correctly interpreting KUMIP 153923.

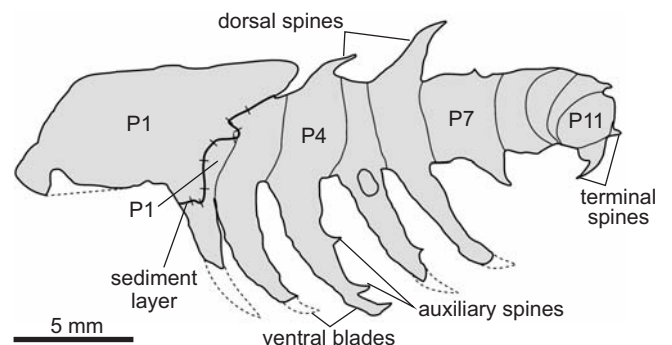


Fig. 2. Explanatory drawing of radiodontan euarthropod *Stanleycaris* sp., KUMIP 153923 from the Wheeler Formation (Cambrian Series 3, Drumian), Utah, USA. Hachure direction indicates lower sediment level. Dotted lines indicate expected path of incomplete ventral blades.



Fig. 3. Comparison between terminal spines and ventral blades of *Stanleycaris* and oral papillae and lobopodous limbs of *Aysheiaia*. **A.** *Stanleycaris* sp., KUMIP 153923 from the Wheeler Formation (Cambrian Series 3, Drumian), Utah, USA; anterior end showing recurved terminal spines (A₁), ventral blade (A₂). **B.** *Aysheiaia pedunculata* Walcott, 1911, USNM 189199 from the Stephen Formation (Cambrian Series 3, Stage 5), British Columbia, Canada; anterior end showing anterior appendages and oral papillae. **C.** **D.** *Stanleycaris hirpex* Caron, Gaines, Mángano, Streng, and Daley, 2010 from the Stephen Formation (Cambrian Series 3, Stage 5), British Columbia, Canada. **C.** ROM 59975 (paratype), ventral blade. **D.** USNM 83942, trunk section and lobopods. Abbreviation: Pn, podomere n.

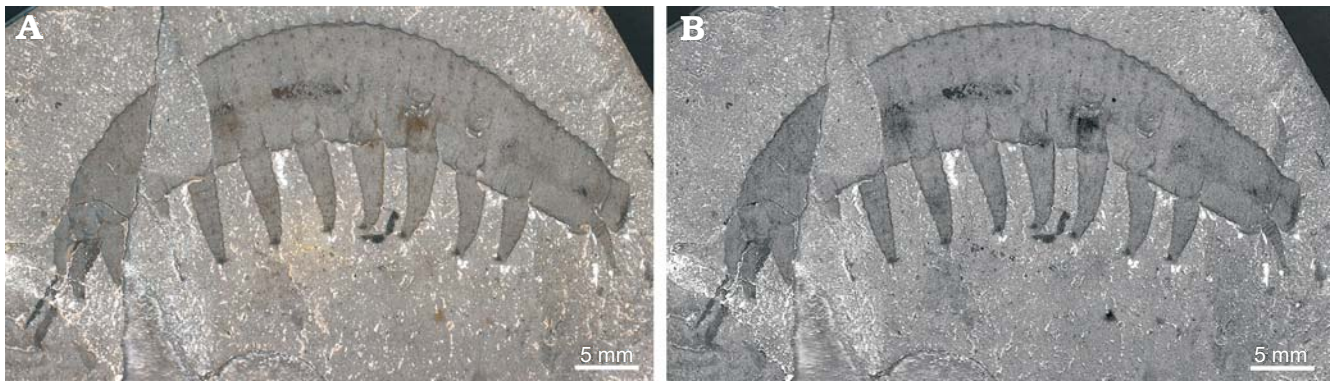


Fig. 4. Lobopodian *Aysheia pedunculata* Walcott, 1911, USNM 365608 from the Stephen Formation (Cambrian Series 3, Stage 5), British Columbia, Canada; in cross-polarized light (A), cross-polarized light, red and yellow channels reduced (B).

Within the known diversity of radiodontan frontal appendages, the presence of five elongated ventral blades with auxiliary spines on P2 to P6, and differentiated distal podomeres, support a more specific classification as a hurdiid (e.g., Daley and Budd 2010; Daley et al. 2013a). Within hurdiids, KUMIP 153923 most closely resembles *Stanleycaris hirpex* (Figs. 1B, 5): both have 11 podomeres, including an elongated P1; long, curved ventral blades

with auxiliary spines on P2–P6; and a distally tapering P7–P11. The only significant difference is that the dorsal spine preserved on P6 of KUMIP 153923 appears to be single-pointed, whereas dorsal spines of *Stanleycaris* from Stanley Glacier are double-pointed (Figs. 1B, 5; Caron et al. 2010). The lack of a double-point may be the result of incomplete preservation in KUMIP 153923, as the size of the dorsal spine relative to podomere width (trans.), robustness, and angle relative to the dorsal surface of the podomere all conform to the morphology of dorsal spines in *Stanleycaris* from Stanley Glacier (Figs. 1B, 5). Additionally KUMIP 153923 fits within the size-range described for Stanley Glacier specimens (12.5–30.3 mm length [sag.]).

KUMIP 153923 differs from *Hurdia* frontal appendages in the possession of 11 podomeres and more than one terminal spine; *Hurdia* usually displays nine podomeres (rarely 10 or 11) and only one terminal spine (Daley et al. 2013a). KUMIP 153923 differs from *Peytoia* frontal appendages in the presence of a small ventral spine on P7; *Peytoia* displays no small ventral spines (Daley et al. 2013a). Furthermore, KUMIP 153923 has a large dorsal spine which projects at a 71° angle to the surface of P6, contrasting with the smaller, more inclined, dorsal spines of both *Hurdia* and *Peytoia* appendages (Daley et al. 2013a).

Aysheia prolata should be considered a nomen dubium due to the lack of distinguishing characters. As the incomplete preservation of KUMIP 153923 precludes a more detailed comparison with the type material of *Stanleycaris hirpex* (Figs. 1B, 5; Caron et al. 2010), we regard KUMIP 153923 as *Stanleycaris* sp. (see Table 1 for comparison between the two species). Additional material from the Wheeler Formation is necessary to determine if the presence of single-pointed dorsal spines in *Stanleycaris* sp. is a legitimate morphological feature or a preservational artefact.

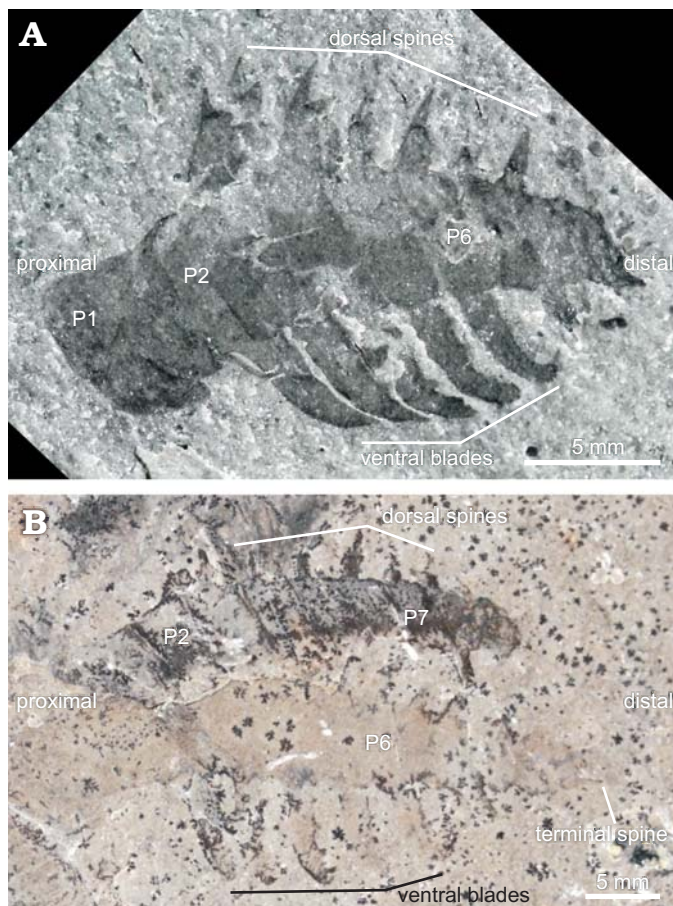


Fig. 5. Radiodontan euarthropod *Stanleycaris hirpex* Caron, Gaines, Mángano, Strenig, and Daley, 2010 from the Stephen Formation (Cambrian Series 3, Stage 5), British Columbia, Canada. A. ROM 59975 (paratype). B. ROM 59976 (paratype). Abbreviation: Pn, podomere n.

Concluding remarks

The recognition of KUMIP 153923 as a radiodontan frontal appendage directly impacts the known diversity of these extinct organisms for the lower Palaeozoic of Laurentia.

Table 1. Comparison between *Stanleycaris* sp. and *Stanleycaris hirpex*.

	<i>Stanleycaris</i> sp.	<i>Stanleycaris hirpex</i>
Occurrence	Wheeler Formation Cambrian Series 3, Drumian	Stephen Formation Cambrian Series 3, Stage 5
Number of specimens	1	37
Number of podomeres	11	11
Length	26.5 mm	12.5–30.3 mm
Number of large ventral blades	5, on P2–P6	5, on P2–P6
Morphology of large ventral blades	elongate, curved, with auxiliary spines	elongate, curved, with auxiliary spines
Number of short ventral blades	1, on P7	1, on P7
Number of dorsal spines	evidence for dorsal spines on P4, P6, P7, but dorsal surface poorly preserved	9, on P2–P10
Morphology of dorsal spines	robust, single pointed (?)	robust, double pointed
Angle of projection of dorsal spines	71°, for dorsal spine on P6	45–90°
Morphology of terminal spines	recurved, pointed	recurved, pointed
Reference	this study	Caron et al. 2010

Table 2. Diversity of Cambrian radiodontans from Canada and Utah. A, appendage; C, carapace element; O, oral cone; P, post cephalic remains.

	Burgess Shale (Stage 5)	Stanley Glacier (Stage 5)	Spence Shale (Stage 5)	Wheeler Formation (Drumian)	Marjum Formation (Drumian)	Weeks Formation (Guzhangian)
<i>Anomalocaris canadensis</i>	A, C, O, P	A				
<i>Anomalocaris</i> sp.			P	P		A
<i>Hurdia victoria</i>	A, C, O, P	A, C	A, C, O			
<i>Hurdia triangulata</i>	A, C, O, P					
<i>Hurdia</i> indet. sp.				C		
<i>Caryosyntrips serratus</i>	A, C					
<i>Peytoia nathorsti</i>	A, O, P			A, O	O, P	
<i>Amplectobelua stephenensis</i>	A					
<i>Stanleycaris hirpex</i>		A, C, O				
<i>Stanleycaris</i> sp.				A		
References	Daley et al. 2009, 2013a, b; Daley and Budd 2010; Daley and Edgecombe 2014	Caron et al. 2010	Briggs et al. 2008; Pates et al. in press	Briggs et al. 2008; Pates et al. in press; this study	Pates et al. in press	Lerosey-Aubril et al. 2014

Stanleycaris can now be added to the list of radiodontan taxa have been reported from the Cambrian (Series 3) of Utah and Canada (Table 2). *Peytoia nathorsti* and *Hurdia victoria* (Briggs et al. 2008; Pates et al. in press) are known in both regions from frontal appendages, mouthparts, and carapace material. *Anomalocaris* has also been described from post cephalic remains in both the Spence Shale and Wheeler Formation (Briggs et al. 2008), and isolated frontal appendages in the younger (Guzhangian) Weeks Formation (Lerosey-Aubril et al. 2014). The Wheeler Formation specimen is the youngest stratigraphic occurrence of *Stanleycaris*, expanding its temporal range from the *Bathyriscus*–*Elrathina* Zone to the *Ptychagnostus atavus* Zone.

Aysheaia prolata is here shown to be an invalid lobopodian taxon, reducing the known diversity of these organisms for the Cambrian of Laurentia. For over three decades, *A. prolata* was regarded as the first lobopodian to be discovered from the numerous Cambrian (Series 3) Konservat-Lagerstätten exposed in Utah (Robison 1985) and was widely referenced as such in subsequent studies (e.g., Dzik and Krumbiegel 1989; Hou and Bergström 1995;

Ramsköld and Chen, 1998; Bergström and Hou 2001; Hou et al. 2004; Whittle et al. 2009; Ou et al. 2011; Gámez Vintaned et al. 2011; Robison et al. 2015; Foster and Gaines 2016). Our reappraisal of KUMIP 153923 leaves the luolishaniid *Acinocricus stichus* (Conway Morris and Robison 1988) from the Spence Shale as the only Cambrian lobopodian currently known from the USA (Ramsköld and Chen 1998; García-Bellido et al. 2013; Yang et al. 2015).

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