

New soft-bodied panarthropods from diverse Spence Shale (Cambrian; Miaolingian; Wuliuan) depositional environments

Julien Kimmig,^{1,2,3*} Stephen Pates,⁴ Rhiannon J. LaVine,^{5,6} L.J. Krumenacker,^{7,8} Anna F. Whitaker,⁹ Luke C. Strotz,^{10,11} Paul G. Jamison,¹² Val G. Gunther,¹³ Glade Gunther,¹⁴ Matt Witte,¹⁵ Allison C. Daley,¹⁶ and Bruce S. Lieberman^{5,6}

¹Paläontologie und Evolutionsforschung, Abteilung Geowissenschaften, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe 76133, Germany <julien.kimmig@smnk.de>

²Department of Geosciences, The Pennsylvania State University, University Park, Pennsylvania 16802, USA <jkimmig@psu.edu>

³The Harold Hamm School of Geology and Geological Engineering, University of North Dakota, Grand Forks, North Dakota 58202, USA

⁴Department of Zoology, University of Cambridge, Cambridge, CB2 3EQ, United Kingdom <sp587@cam.ac.uk>

⁵Biodiversity Institute, University of Kansas, Lawrence, Kansas 66045, USA <rlavine@ku.edu>

⁶Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045, USA <blieber@ku.edu>

⁷Department of Geosciences, Idaho State University, Pocatello, Idaho 83209, USA <krumlaur@isu.edu>

⁸Department of Physical Sciences, College of Eastern Idaho, Idaho Falls, Idaho 83404, USA <lj.krumenacker@cei.edu>

⁹Department of Chemical and Physical Sciences, University of Toronto Mississauga, 3359 Mississauga Road, Mississauga, Ontario L5L 1C6, Canada <a.whitaker@mail.utoronto.ca>

¹⁰State Key Laboratory of Continental Dynamics, Shaanxi Key Laboratory of Early Life and Environments and Department of Geology, Northwest University, Xi'an, 710069, China <lukestrotz@nwu.edu.cn>

¹¹Department of Palaeontology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria

¹²Department of Geosciences, Utah State University, Logan, Utah 84322, USA <paul.jamison@usu.edu>

¹³71 North 200 West, Brigham City, Utah 84302, USA <val@geo-tools.com>

¹⁴Brigham City, Utah 84302, USA <glade@geo-tools.com>

¹⁵PaleoWest LLC (Los Angeles Office), 55 E Huntington Drive, Suite 238, Arcadia, California 91006, USA <mwitte@paleowest.com>

¹⁶Institut des Sciences de la Terre (ISTE), Université de Lausanne, Lausanne, Vaud, Switzerland <allison.daley@unil.ch>

Abstract.—The Cambrian (Miaolingian; Wuliuan) Spence Shale Lagerstätte of northern Utah and southern Idaho is one of the most diverse Burgess Shale-type deposits of Laurentia. It yields a diverse fauna consisting of abundant biomineralized and locally abundant soft-bodied fossils, along a range of environments from shallow-water carbonates to deep-shelf dark shales. Panarthropods are the dominant component throughout the deposit, both in time and space, but whereas the trilobites and agnostoids are abundant, most of the soft-bodied taxa are only known from very few specimens. Additionally, the knowledge of soft-bodied panarthropods is currently largely limited to locations in the Wellsville Mountains of northeastern Utah. This contribution describes 21 new soft-bodied panarthropods from six locations, including the first occurrences of soft-bodied panarthropods in the High-Creek, Smithfield Creek, Spence Gulch, and Two-Mile Canyon localities. Additionally, we report the presence of bradoriids—i.e., *Branchiocaris pretiosa* Resser, 1929, *Perspicularis? dilatatus* Robison and Richards, 1981, *Naraoia? sp. indet.*, *Thelxiope cf. T. palaeothalassia* Simonetta and Delle Cave, 1975, and *Tuzoia guntheri* Robison and Richards, 1981—for the first time from the Spence Shale Lagerstätte; the first reported occurrence outside of the Burgess Shale for *Thelxiope cf. T. palaeothalassia*; and the first Wuliuan occurrence of *Tuzoia guntheri*. We also report on a new hurdiid carapace element and additional specimens of *Buccaspinea cooperi? Pates et al.*, 2021, *Dioxycares argenta* Walcott, 1886, *Hurdia sp. indet.*, and *Tuzoia retifera* Walcott, 1912. This new material improves our understanding of the panarthropod fauna of the Spence Shale Lagerstätte and substantially increases our understanding of the distribution of the described taxa in time and space.

Introduction

The Great Basin of the western United States preserves numerous Cambrian (Stage 3 to Guzhangian) Burgess Shale-type (BST) deposits (Robison et al., 2015; Foster and Gaines,

2016; Lieberman et al., 2017; Kimmig, 2021). The best known examples are the Pioche Formation of Nevada (Lieberman, 2003; Kimmig et al., 2019a), the Spence Shale Lagerstätte (Spence Shale from here on) of Utah and Idaho (Kimmig et al., 2019b; Whitaker and Kimmig, 2020), the Drum Mountains and House Range Wheeler Formation Lagerstätten (Robison et al., 2015; Lerosey-Aubril et al., 2020a), the Marjum Formation (Robison et al., 2015; Leibach

*Corresponding author.

et al., 2021; Pates et al., 2021a), and the Weeks Formation (Lerosey-Aubril et al., 2018).

The Cambrian (Miaolingian, Wuliuan) Spence Shale of northeastern Utah and southeastern Idaho occupies a distinctive position among the Lagerstätten of the Great Basin, because it preserves a range of environments from shallow-water carbonates to deep-shelf shales. Although this by itself is not unique, the fact that biomineralized and soft-bodied organisms are found in all of these environments, and the biota differs between localities (Kimmig et al., 2019b; Whitaker et al., 2022) makes the Spence Shale a deposit of utmost importance to understanding Cambrian communities and biodiversity. Whereas the depositional environment varies within the Spence Shale, all known exposures are dominated by panarthropods (Kimmig et al., 2019b; Whitaker and Kimmig, 2020). This is not surprising, because panarthropods usually dominate Cambrian Lagerstätten (Robison et al., 2015; Paterson et al., 2016; Hou et al., 2017; Nanglu et al., 2020; Yang et al., 2021).

Here we describe 21 new specimens of exceptionally preserved panarthropods from six localities of the Spence Shale, including a new hurdiid carapace element; the first specimens of *Naraoia?* Walcott, 1912, *Thelxiope* cf. *T. palaeothalassia* Simonetta and Delle Cave, 1975, *Perspicaris? dilatus* Robison and Richards, 1981, *Branchiocaris pretiosa* Resser, 1929, and *Tuzoia guntheri* Robison and Richards, 1981; the first bradoriids; as well as new specimens of *Dioxycares argenta* Walcott, 1886 from the deposit. In addition, *Naraoia?* sp. indet. represents the first occurrence of a soft-bodied taxon from the Two-Mile Canyon locality; *Dioxycares argenta* and the bradoriids are the first soft-bodied panarthropods from the Spence Shale type-locality of Spence Gulch; *Branchiocaris pretiosa* is the first soft-bodied panarthropod from the Smithfield Creek locality; and the bradoriid from High Creek represents the first soft-bodied panarthropod from this location. These specimens not only extend the geographic and stratigraphic range of these taxa, but also add to the already diverse panarthropod fauna of the Spence Shale, suggesting that there might be more species to be found in currently understudied Spence Shale localities.

Geological setting

There are several Lagerstätte intervals that preserve soft tissues within the Spence Shale Member of the Langston Formation. The deposit is regionally extensive, with outcrops in southeastern Idaho and northeastern Utah (Fig. 1). The Spence Shale Member ranges in age from *Mexicella mexicana* to *Glossopleura walcotti* biozones (Cambrian, Miaolingian, Wuliuan, 507.5–506 Myr) (Liddell et al., 1997; Kimmig et al., 2019b), with all soft-bodied fossils to date coming from the *Glossopleura walcotti* Biozone. It was deposited on a slope on the passive western margin of Laurentia, and outcrops record an overall increase in depth from Utah to Idaho. The Spence Shale Member ranges from ~9 m at Blacksmith Fork to ~120 m at Oneida Narrows, conformably overlies the Naomi Peak Limestone Member of the Langston Formation and, in turn, conformably overlain by the High Creek Limestone member of the Langston Formation.

The specimens described herein come from six localities: Antimony Canyon and Miners Hollow in the Wellsville Mountains, north of Brigham City, Utah; High Creek and Smithfield

Creek, in the Bear River Range, north of Logan, Utah; the type locality of the Spence Shale, Spence Gulch, in the Bear River Range, near Montpelier, Idaho; and Two-Mile Canyon, the westernmost Spence Shale locality, near Malad City, Idaho (Fig. 1). They are preserved in carbonate-rich siliciclastic mudstones in all localities except Two-Mile Canyon, where the *Naraoia?* sp. indet. specimen is preserved in siliciclastic shale.

Materials and methods

The specimens collected since 2016 were collected under U.S. Department of Agriculture Forest Service permits to JK and LJK. All specimens collected prior to 2016 were collected by avocational paleontologists and donated to the relevant repositories by those individuals. All specimens were collected with hand tools.

The specimens were photographed using a Nikon D5500 digital single-lens reflex camera with a Nikon 40 mm DX Micro-Nikkor Lens at the MCZ, a Canon EOS 60D digital single-lens reflex camera with a 60 mm EF-S macro lens at the YPM, a Canon EOS 7D equipped with a Canon macro lens at the IMNH, and a Canon EOS 5D Mark II digital single-lens reflex camera equipped with a Canon 50 mm macrolens at the KUMIP. Pictures of IMNH and KUMIP specimens were taken with specimens submerged in alcohol. Pictures of MCZ and YPM specimens were taken with cross-polarized lights. Close-ups of KUMIP 314201 were taken with a Nikon SMZ-1500 stereoscope with a DS-Ri1 camera and Nikon NIS Elements v. 2 and 3 software. The contrast, color, and brightness of images were adjusted using Adobe Photoshop ver. 24. Fossil images were kept in grayscale for improved contrast and visibility of structures. Line drawings were created in Adobe Illustrator ver. 27.4.1.

Ratios of endite length:podomere height for radiodont appendages were made using ImageJ (Schneider et al., 2012) from specimens of *Hurdia* and *Buccaspinea* spp. published in the literature (full list of sources and figure numbers in Table 2). Only the proximalmost two endites and associated podomeres were measured for each specimen. These ratios were visualized as a jitter plot using the ggplot2 package (Wickham, 2016) in R (R Core Team, 2022).

Classification and terminology herein followed Kimmig and Pratt (2015), Lerosey-Aubril and Pates (2018), Lerosey-Aubril et al. (2020a, b), Pates et al. (2021a), Wu et al. (2021a, b), and Zhu et al. (2021).

Repositories and institutional abbreviations.—BPM, Back to the Past Museum, Quintana Roo, Mexico; IMNH, Idaho Museum of Natural History, Pocatello, Idaho, USA; KUMIP, Division of Invertebrate Paleontology, Biodiversity Institute, University of Kansas, Lawrence, USA; MCZ IP, Invertebrate Paleontology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; ROM and ROMIP, Royal Ontario Museum, Toronto, Ontario, Canada; USNM, National Museum of Natural History [United States National Museum], Washington, DC, USA; UU, Department of Geology & Geophysics of the University of Utah, Salt Lake City, USA; YPM, Yale Peabody Museum, Yale University, New Haven, Connecticut, USA.

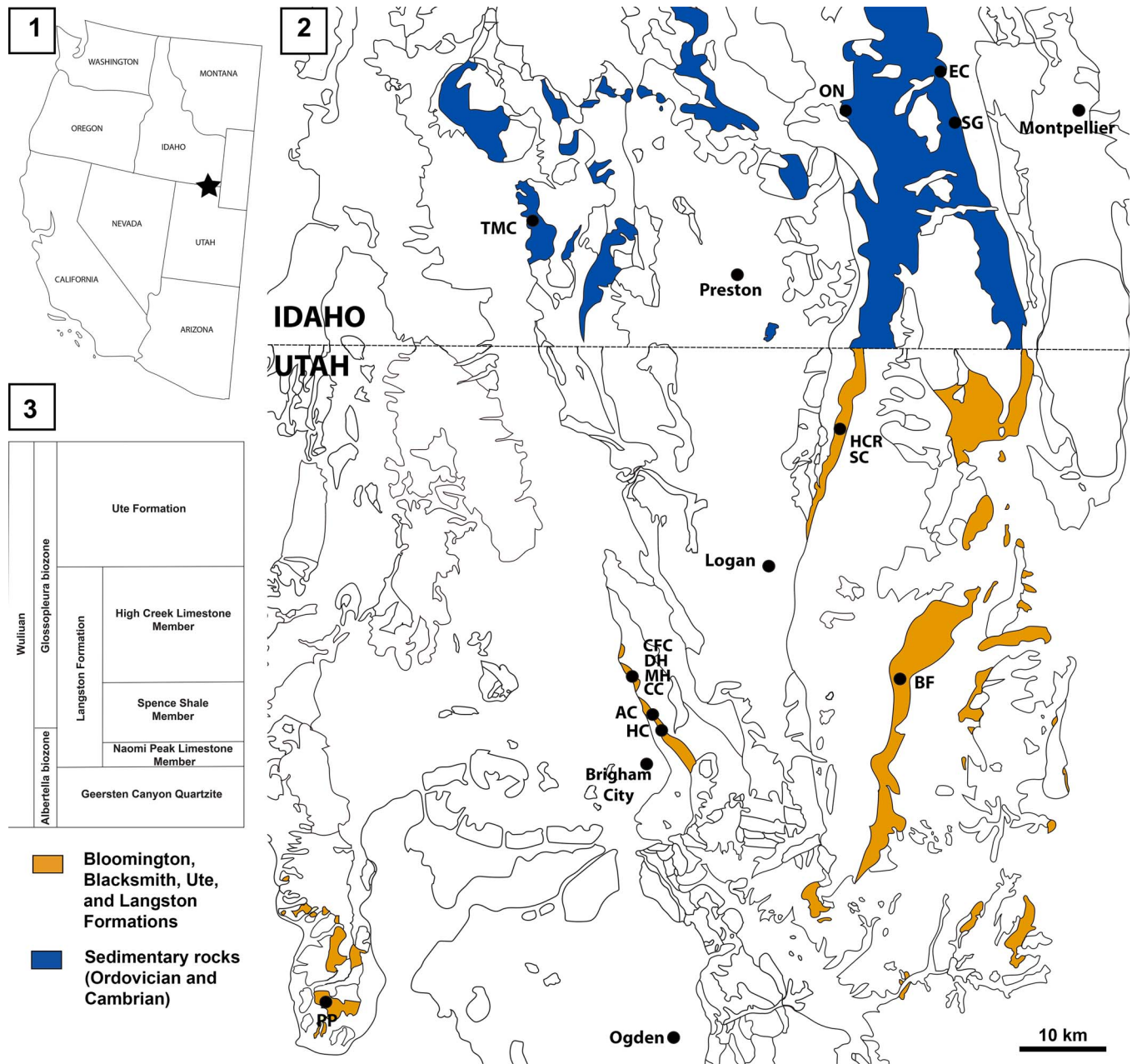


Figure 1. Locations of the Spence Shale Lagerstätte: (1) map of the western USA showing the location of the Spence Shale; (2) geological map (based on the USGS state maps for Google Earth Pro) of northern Utah and southern Idaho showing the principal localities within the Spence Shale; (3) simplified stratigraphy of the Langston Formation. AC, Antimony Canyon; BF, Blacksmith Fork; CC, Cataract Canyon; CFC, Calls Fort Canyon; DH, Donation Canyon; EC, Emigration Canyon; HC, Hansen Canyon; HCR, High Creek; MH, Miners Hollow; ON, Oneida Narrows; PP, Promontory Point; SC, Smithfield Creek; SG, Spence Gulch; TMC, Two Mile Canyon.

Systematic paleontology

Superphylum Panarthropoda Nielsen, 1995
 Order Radiodonta Collins, 1996
 Family Hurdiidae Lerosey-Aubril and Pates, 2018

Included genera.—*Aegirocassis* Van Roy, Daley, and Briggs, 2015; *Buccaspinea* Pates et al., 2021a; *Cambroraster* Moysiuk and Caron, 2019; *Cordaticaris* Sun, Zeng, and Zhao, 2020; *Hurdia* Walcott, 1912; *Pahvantia* Robison and Richards, 1981; *Peytoia* Walcott, 1911; *Stanleycaris* Pates et al., 2018b; *Titanokorys* Caron

and Moysiuk, 2021; and *Ursulinacaris* Pates et al., 2019. Questionably *Schinderhannes* Kühl, Briggs, and Rust, 2009.

Hurdiidae gen. indet. sp. indet.
 Figures 2, 3

Occurrence of new material.—KUMIP 495355 and 495356 originate from the Lower Cycle 6 of the Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, Miners Hollow locality (GPS: 41.602, -112.033), Wellsville Mountains, Box Elder County, Utah.

Table 1. Radiodont specimen fragments reported from the Spence Shale, Langston Formation (Cambrian: Wuliuan), Utah, USA. Specimens described in this contribution in bold font.

Taxon/Spm no.	Fragment(s)	Locality	Figures
<i>Buccaspinea?</i> cooperi? Pates et al., 2021a			
KUMIP 314040	Frontal appendage	Miners Hollow	Pates et al., 2018a, fig. 2.3, 2.4
KUMIP 495356	Frontal appendage	Miners Hollow	Fig. 2.3, 2.4
KUMIP 579779	Frontal appendage	Wellsville Mountains	Fig. 2.1, 2.2
ROM 59634	Frontal appendage	Miners Hollow	Daley et al., 2013, fig. 24C
<i>Hurdia victoria</i> Walcott, 1912			
KUMIP 314039	Central carapace element	Miners Hollow	Pates et al., 2018a, fig. 4.2
KUMIP 314050	Central carapace element	Miners Hollow	Pates et al., 2018a, fig. 4.1, 4.4
KUMIP 314056	Central carapace element	Miners Hollow	Pates et al., 2018a, fig. 4.3, 4.5
<i>Hurdia</i> sp.			
KUMIP 312405	Pair of frontal appendages and oral cone	Miners Hollow	Pates et al., 2018a, fig. 3
KUMIP 314042	Frontal appendage	Miners Hollow	Pates et al., 2018a, fig. 2.5
KUMIP 314057	Flap	Miners Hollow	Pates et al., 2018a, fig. 4.6, 4.7
KUMIP 314145	Frontal appendage	Miners Hollow	Pates et al., 2018a, fig. 2.1
KUMIP 314175	Oral cone	Miners Hollow	Pates et al., 2018a, fig. 2.6
KUMIP 314178	Frontal appendage	Miners Hollow	Pates et al., 2018a, fig. 2.2
KUMIP 314265	Oral cone	Miners Hollow	Pates et al., 2018a, fig. 2.7
<i>Hurdia?</i>			
KUMIP 491056	Frontal appendage	Miners Hollow	Kimmig et al., 2019b, fig. 4h; Fig. 3.1, 3.2
KUMIP 495355	Pair of frontal appendages	Miners Hollow	Fig. 3.3, 3.4, 3.5
ROM 59633	Pair of frontal appendages and oral cone	Miners Hollow	Daley et al., 2013, fig. 24A
ROM 59650	Frontal appendage	Miners Hollow	Daley et al., 2013, fig. 24B
ROM 59651	Frontal appendage	Miners Hollow	Daley et al., 2013, fig. 24D
<i>Hurdiidae?</i> gen. indet. sp. indet.			
KUMIP 314127	Oral cone	Miners Hollow	Not figured
KUMIP 490912	Partial frontal appendage	Miners Hollow	Fig. 4
KUMIP 491057	Possible central carapace element	Antimony Canyon	Fig. 5
<i>'Anomalocaris'</i> sp.			
KUMIP 314037	Nearly complete specimen	Miners Hollow	Briggs et al., 2008, fig. 1

Table 2. Specimens, references, figure numbers, and generic assignments for ratios of endite length to podomere height visualized as jitter plot in Figure 4. Only proximal two endites were measured for each specimen. * = same specimen measured multiple times because it was figured in multiple studies. Specimen numbers reproduced as written in original publications.

Specimen	Reference	Figure no.	Ratio	Genus
Spence Shale				
KUMIP 579779	This study	2.1	3.1:1	<i>Buccaspinea?</i>
KUMIP 579779	This study	2.1	2.8:1	<i>Buccaspinea?</i>
KUMIP 495355	This study	3.4	3.1:1	<i>Hurdia?</i>
KUMIP 495355	This study	3.4	2.8:1	<i>Hurdia?</i>
KUMIP 314178	Pates et al., 2018a	2.2	1.1:1	<i>Hurdia</i>
KUMIP 314178	Pates et al., 2018a	2.2	1.1:1	<i>Hurdia</i>
KUMIP 314145	Pates et al., 2018a	2.1	1.7:1	<i>Hurdia</i>
KUMIP 314145	Pates et al., 2018a	2.1	2.0:1	<i>Hurdia</i>
KUMIP 312405	Pates et al., 2018a	3	1.2:1	<i>Hurdia</i>
KUMIP 312405	Pates et al., 2018a	3	1.2:1	<i>Hurdia</i>
KUMIP314040	Pates et al., 2018a	2.3	2.8:1	<i>Buccaspinea?</i>
KUMIP314040	Pates et al., 2018a	2.3	2.9:1	<i>Buccaspinea?</i>
Burgess Shale				
ROM 60026	Daley et al., 2013	12A	1.6:1	<i>Hurdia</i>
ROM 60026	Daley et al., 2013	12A	2.2:1	<i>Hurdia</i>
ROM 60048*	Daley et al., 2013	12C	1.7:1	<i>Hurdia</i>
ROM 60048*	Daley et al., 2013	12C	1.7:1	<i>Hurdia</i>
ROM 60020	Daley et al., 2013	12E	1.5:1	<i>Hurdia</i>
ROM 60020	Daley et al., 2013	12E	1.8:1	<i>Hurdia</i>
USNM 240928	Daley et al., 2013	12G	2.1:1	<i>Hurdia</i>
USNM 240928	Daley et al., 2013	12G	1.9:1	<i>Hurdia</i>
ROMIP 60048*	Moysiuk and Caron, 2019	3e	1.7:1	<i>Hurdia</i>
ROMIP 60048*	Moysiuk and Caron, 2019	3e	1.6:1	<i>Hurdia</i>
ROM 59259	Lerosey-Aubril et al., 2020a	3C	1.8:1	<i>Hurdia</i>
ROM 59259	Lerosey-Aubril et al., 2020a	3C	1.7:1	<i>Hurdia</i>
Wheeler Formation House Range				
UU 18056.34	Lerosey-Aubril et al., 2020a	3A	5.2:1	<i>Buccaspinea?</i>
UU 18056.34	Lerosey-Aubril et al., 2020a	3A	3.9:1	<i>Buccaspinea?</i>
Marjum Formation				
BPM 1108	Pates et al., 2021a	4	4.9:1	<i>Buccaspinea</i>
BPM 1108	Pates et al., 2021a	4	6.4:1	<i>Buccaspinea</i>

KUMIP 491056 originates from Cycle 6, ~47.2 m from the base of the Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, Miners Hollow locality (GPS: 41.602, -112.033), Wellsville Mountains, Box Elder County, Utah. KUMIP 579779 originates from an unknown locality of the Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, Wellsville Mountains, Box Elder County, Utah.

Description of new material.—KUMIP 579779 (Fig. 2.1, 2.2) is an isolated frontal appendage that measures ~13 mm along the dorsal margin. Eight well-defined podomeres with tall rectangular outlines (Fig. 2.2, pd2–pd9) are preserved. The appendage is bent, with the five podomeres of the distal region orientated near-parallel to the endites borne by the podomeres of the intermediate region. Evidence for an additional ninth podomere is provided by the endites. Four endites, approximately three times as long as the height of the podomere to which they attach, are preserved (Fig. 2.2, en1–en4). The distal three clearly attach to a podomere, but the podomere that should bear en1 is missing. Endites are curved, with their tips approximately perpendicular to the bases, and bear robust triangular auxiliary spines 2–3 mm in length (Fig. 2.2, aux). A short (submillimeter), straight terminal spine is present (Fig. 2.2, ts).

KUMIP 495356 (Fig. 2.3, 2.4) is a more poorly preserved partial frontal appendage. At least four, possibly five, endites are present (Fig. 2.4, en1–en5?) proximal to poorly preserved organic material that might represent distal podomeres orientated ventrally as in KUMIP 579779 (Fig. 2.4, pd?). Endites are incomplete at their tips, but display a prominent curve, and bear robust triangular auxiliary spines ~1 mm in length (Fig. 2.4, aux).

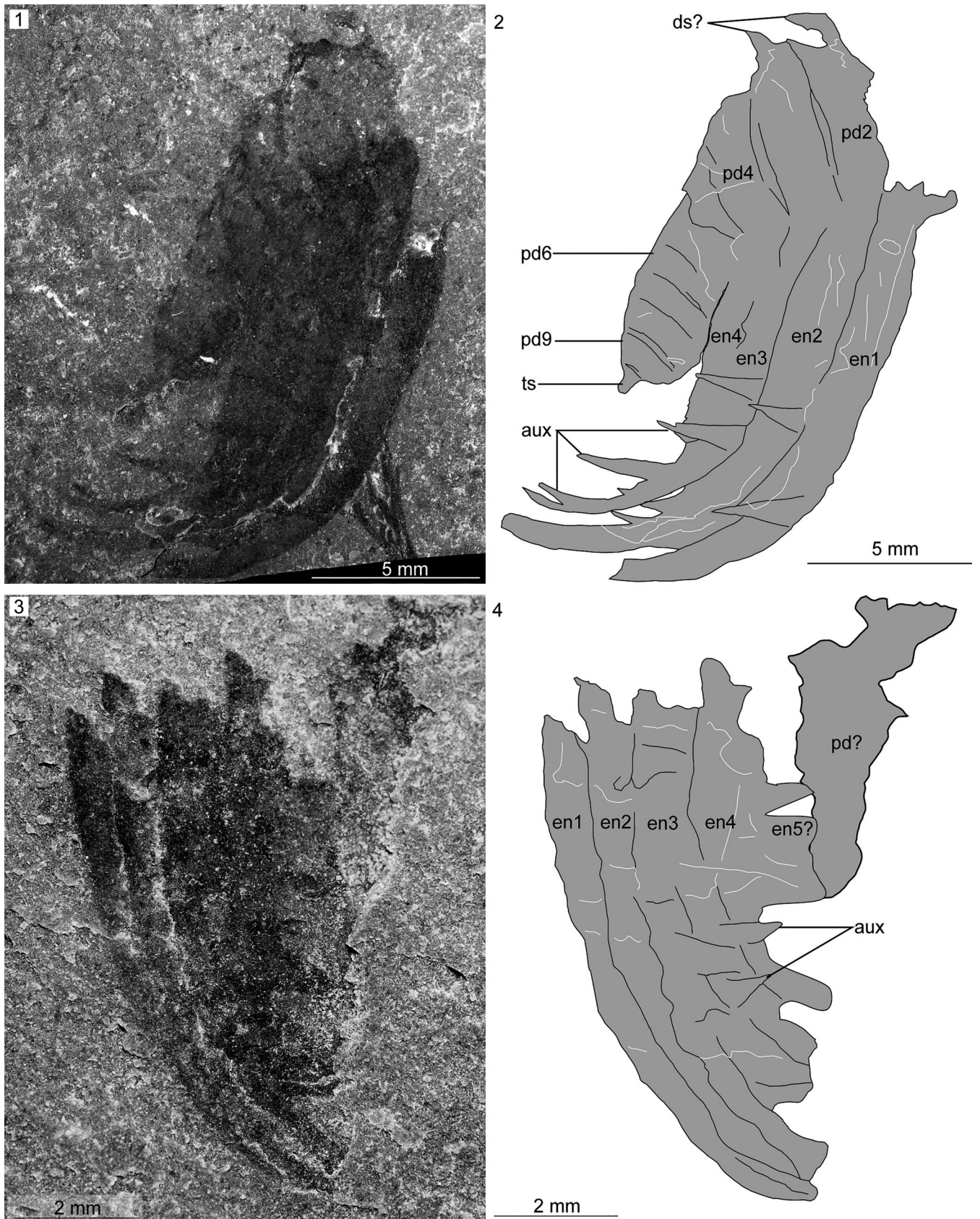


Figure 2. Isolated frontal appendages of *Buccaspinea?* from the Spence Shale Member, Langston Formation (Cambrian: Wuliuan), Utah, USA: (1, 2) KUMIP 579779 (Wellsville Mountains), collected by the Gunther family, and explanatory drawing; (3, 4) KUMIP 495356 (Miners Hollow), collected by Paul Jamison, and explanatory drawing. aux, auxiliary spines; ds, dorsal spines; en#, endite; pd#, podomere; ts, terminal spine.

KUMIP 491056 (Fig. 3.1, 3.2) is an isolated frontal appendage preserved laterally compressed that comprises at least 10, likely 11, podomeres and measures ~11 mm along the dorsal margin. Podomeres have tall rectangular outlines and decrease in size distally. Six plate-like endites, borne by intermediate-region podomeres (pd3–pd8), can be observed. The proximal three endites (Fig. 3.2, en3–en5) measure ~6 mm along the long axis, approximately twice the length of the height of the podomere to which they attach. These endites display a slight curve, orientated convex forward. The distal three endites in the intermediate region (Fig. 3.2, en6–en8) are incomplete, but run parallel to the proximal part of en3–en6. Two reduced endites are observed on the distal podomeres (Fig. 3.2, de). No dorsal spines or terminal spines were observed.

KUMIP 495355 (Fig. 3.3–3.5) is an incomplete isolated frontal appendage preserved laterally compressed (Fig. 3.3, app1), in close association (~10 mm) with additional organic material, potentially a second poorly-preserved partial appendage in oblique ventral view (Fig. 3.3, app2). The well-preserved appendage (Fig. 3.3, app1) measures ~9 mm along the dorsal margin, and comprises at least six, possibly up to eight, tall rectangular podomeres (Fig. 3.5, pd). Five endites approximately three times as long as the height of the podomere to which they attach are preserved (Fig. 3.5, en2–en6). The proximal four endites (Fig. 3.5, en2–en5) measure ~8 mm along the long axis, the distalmost endite (Fig. 3.5, en6) measures ~6 mm. A possible broken endite is associated with pd1 (Fig. 3.5, en1?). Complete endites are straight and bear small (submillimeter) auxiliary spines, with a larger ~1 mm auxiliary spine orientated distally at their tips. The dorsal surface and distal part of the appendages are incomplete, precluding the observation of dorsal or terminal spines. The associated organic material tentatively interpreted as a partial poorly preserved appendage (Fig. 3.3, app2) measures ~7 mm along its dorsal margin. A number of linear divisions observed are interpreted as podomere boundaries. A ventral protrusion extends from the most proximal of these, interpreted as an incomplete endite (Fig. 3.3, en), but at least five further divisions can be observed (Fig. 3.3, arrows). The proximal and distal portions of this appendage are not preserved, and it is associated with additional unidentified organic remains.

New material.—KUMIP 491056, 495355, 495356, and 579779, frontal appendages preserved as lateral compressions.

Remarks.—These appendages can be confidently assigned to the family Hurdiidae within Radiodonta, because they are composed of podomeres bearing unpaired plate-like endites with endites along a single margin only. Although both appendages are incomplete, the separation of the distal articulated region of the appendage into two distinct regions—the intermediate one with plate-like endites and distal one with either reduced or no endites—provides further support for this assignment. Within Hurdiidae, these appendages bear most similarities to genera *Buccaspinea* and *Hurdia*. Distinguishing between these genera based only on frontal appendages is not straightforward. Both genera possess elongate endites that can bear robust and elongate auxiliary spines. Endites in *Buccaspinea* are far longer than the height of the podomere to

which they attach (up to six times; Pates et al., 2021a; Fig. 4), and auxiliary spines are very robust in this genus. Endite length to podomere height ratios in *Hurdia* are generally between 1:1 and 2:1 (Fig. 4), and auxiliary spines can be elongate and hooked (e.g., Moysiuk and Caron, 2019), but are generally less robust than in *Buccaspinea*. Reduced endites in the distal region have been observed in both *Buccaspinea* and *Hurdia* (e.g., Pates et al., 2019, 2021a) but are not known in all *Hurdia* appendages (e.g., Daley et al., 2013). The extent of curvature and relative width of endites observed in hurdiid fossilized appendages can depend on orientation of preservation relative to bedding (Pates et al., 2018a) and/or relative mesial and distal curvature (Moysiuk and Caron, 2019).

Considering all of these details together, KUMIP 579779 and 495356 are considered more likely to be *Buccaspinea* and KUMIP 491056 and 495355 more likely *Hurdia*, although these assignments are only tentative, as outlined below.

Evidence in support of identifying the two appendages as possible *Buccaspinea* (Fig. 2) comes from the relative length of their endites to podomeres, and the robust nature of the auxiliary spines. The relative length of endites to podomeres in KUMIP 579779 (~3:1) exceeds those of figured *Hurdia* specimens from the Burgess Shale and Spence Shale (Fig. 4) and is comparable to that of KUMIP 314040 (Pates et al., 2018, fig. 2.3) that was recently tentatively reassigned to *Buccaspinea* (Pates et al., 2021a). The lack of clear podomeres in KUMIP 495356 precludes measurement of this ratio for this specimen. Both specimens display robust auxiliary spines that overlap the endite immediately distal to the one to which they are attached, just as in the holotype (Pates et al., 2021a) and other Spence Shale specimens tentatively reassigned to the genus: ROM 59634 (Daley et al., 2013, fig. 24C), KUMIP 314040 (Pates et al., 2018a, fig. 2.3, 2.4), and UU 18056.34 (Lerosey-Aubril et al., 2020a). *Hurdia* appendages typically display less-elongate auxiliary spines that only partly overlap the endite anterior to the one to which they are attached (e.g., Daley et al., 2013, fig. 12, fig. 24A, B, D), although this could in part be due to the distal tips of endites not being completely prepared out the matrix (compare Moysiuk and Caron, 2019, fig. 3e to Daley et al., 2013, fig. 12 C). *Hurdia* auxiliary spines also tend to be less robust than those of *Buccaspinea*. However, these two appendages (KUMIP 579779 and 495356; Fig. 2) cannot be confidently assigned to *Buccaspinea* because they could be considered *Hurdia* appendages with particularly elongate endites and robust auxiliary spines, because these features do vary within the genus. Furthermore, the lack of reduced endites in the distal region (four are observed in the type specimen of *Buccaspinea*; Pates et al., 2021a) also precludes confident assignment to the genus. Reduced distal endites are known from a single Spence Shale *Hurdia* specimen, ROM 59651 (Daley et al., 2013, fig. 24D), and numerous Burgess Shale specimens (e.g., Daley et al., 2013, fig. 12), although other published examples lack evidence for distal endites.

Evidence in support of identifying KUMIP 491056 and 495355 as *Hurdia*, rather than *Buccaspinea*, comes from the robustness of the auxiliary spines, as well as comparison to other specimens previously assigned to *Hurdia*. Endites of KUMIP 495355 (Fig. 3.4) are more elongate relative to podomere height than published Burgess Shale and Spence Shale

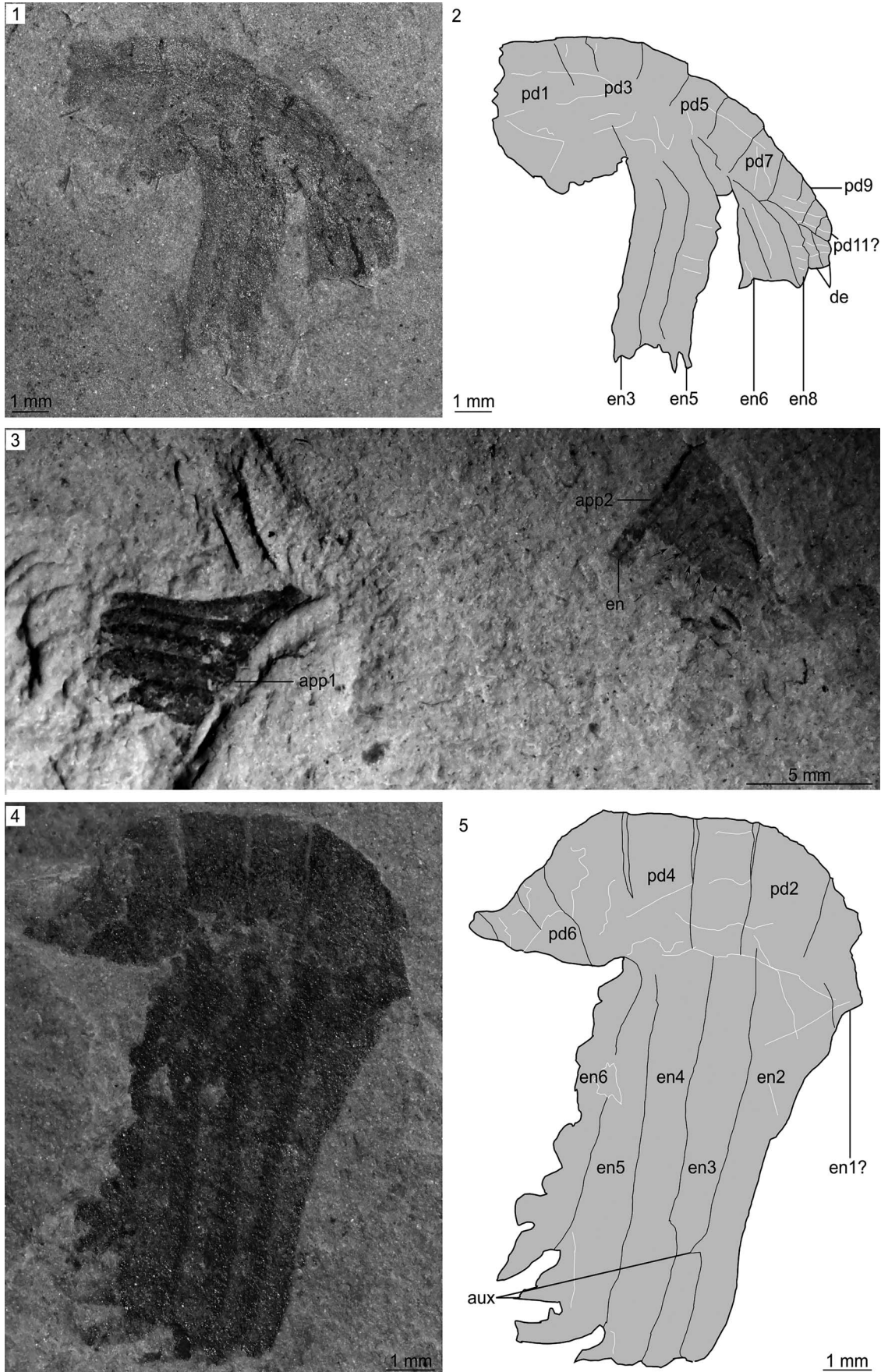


Figure 3. Isolated frontal appendages of *Hurdia?* collected by Paul Jamison from the Miners Hollow locality, Spence Shale, Langston Formation (Cambrian: Wuliuan), Utah, USA: (1, 2) KUMIP 491056 and explanatory drawing; (3) Overview of slab KUMIP 495355 (counterpart); (4, 5) close-up of well-preserved *Hurdia?* sp. indet. appendage on slab KUMIP 495355 (part) and explanatory drawing. app#, appendage; aux, auxiliary spine; de, reduced distal endite; en#, endite; pd#, podomere.

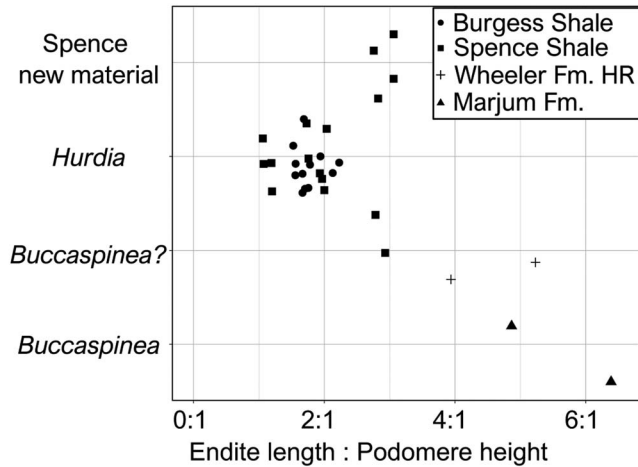


Figure 4. Jitter plot showing ratio of endite length to podomere height for published *Buccaspinea* and *Hurdia* appendages, alongside appendages recently tentatively reassigned to *Buccaspinea?* by Pates et al. (2021a), and those described in this contribution. Proximal two endites and associated podomeres measured for each specimen. Numeric values for ratios and sources for published images are provided in Table 2.

specimens (Fig. 4), comparable to what was measured for KUMIP 579779 (Fig. 2). Those of KUMIP 491056 are incomplete, precluding measurement of a ratio, however what is preserved is $< 2:1$, the usual range for *Hurdia* appendages. Both specimens lack prominent auxiliary spines, although this could be due to these spines being overlain by the endites, due to the orientation of preservation. These two specimens appear to display different extents of curvature. The convex forward curvature of endites observed for KUMIP 491056 is also known from KUMIP 314145, a previously described *Hurdia* appendage from the Spence Shale (Pates et al., 2018a, fig. 2.1). KUMIP 495355 endites can be determined to be mostly straight and lack a prominent mesial or distal curvature, because the spines at the tips of the endites farthest from the ventral margin of the podomeres can be observed (on endites 5, 6, and

possibly 4), and the visible podomere boundaries provides evidence of lateral (rather than frontal) compression. If endites had a prominent mesial curve, then the tips of the endites would not be visible (as they are not in KUMIP 491056). In addition, breaks or deformities from compression would be visible, or the curvature would be visible in the specimen. The straight endites of KUMIP 495355 (Fig. 3.3, app1) are best compared to KUMIP 314042 and 312405 (Pates et al., 2018a, figs. 2.5, 3). In addition to relatively straight endites, both of these previously described specimens display a distalmost plate-like endite that is shorter than the others—a feature also observed in KUMIP 495355 (Fig. 3.3, app1) and other Spence Shale *Hurdia* appendages (Daley et al., 2013, fig. 24A, B, D; Pates et al., 2018a, fig. 2.1, 2.2). The oral cone adjacent to the pair of appendages in KUMIP 312405 bears internal tooth rows, confirming the identity of these appendages as *Hurdia* (Daley and Bergström, 2012; Pates et al., 2018a, fig. 3). Thus, despite the relatively elongate nature of the endites in this specimen, assignment to *Hurdia* is preferred, albeit only very tentatively.

The affinities of the possible second appendage on slab KUMIP 495355 (Fig. 3.3, app2) are less clear. If the single endite in this possible appendage is interpreted as the distalmost of the plate-like endites of a hurdiid appendage, a total of six podomeres lacking endites would be present distal to the series of podomeres bearing plate-like endites. Notably, KUMIP 314178 (Pates et al., 2018a, fig. 2.2) also displays a similar array of five very tall rectangular podomeres distal to the podomeres bearing plate-like endites, which are similar to those of KUMIP 495355 (Fig. 3.3, app1), as noted above. Thus KUMIP 495355 (Fig. 3.3, app2) is tentatively identified as the pair of KUMIP 495355 (Fig. 3.3, app1).

Family indet.

Gen. et sp. indet.

Figure 5

Occurrence.—KUMIP 490912 originates from the Lower Cycle 6, ~45.7 m from the base of the Wuliuan Spence Shale Member

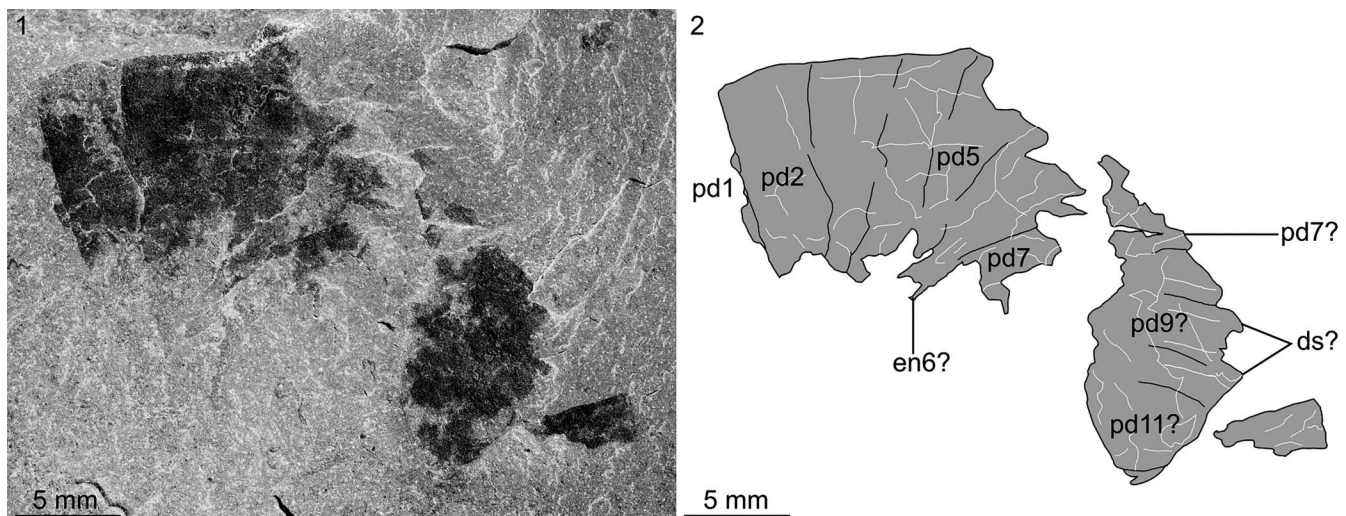


Figure 5. Partial radiodont frontal appendage tentatively assigned to Hurdiidae (KUMIP 490912) collected by Paul Jamison from Miners Hollow locality, Spence Shale, Langston Formation (Cambrian: Wuliuan), Utah, USA: (1, 2) specimen in lateral view and explanatory drawing. ds, dorsal spine; en#, endite; pd#, podomere.

(*Glossopleura walcotti* Biozone) of the Langston Formation, Miners Hollow locality (GPS: 41.602, -112.033), Wellsville Mountains, Box Elder County, Utah.

Description.—KUMIP 490912 (Fig. 5) is a partial isolated appendage that measures ~40 mm along the dorsal margin. Evidence of at least 11 podomeres can be tentatively identified. Only a small amount of material remains of pd1, which is separated from pd2 by a curved boundary (Fig. 5, pd1, pd2). Podomeres display a tall rectangular outline in both intermediate and distal regions of the appendage (proximal region most likely not preserved). The middle part of the appendage is not preserved, and the distal region is curved ventrally, approximately perpendicular to the intermediate region. The ventral margin is not well preserved, and only the base of a single endite can be tentatively identified (Fig. 5, en6?). The dorsal margin is well preserved proximally but not distally. No dorsal spines are present on pd2–pd4, and the dorsal margin is not preserved between pd5–pd8. Small protrusions from the dorsal surface can be seen on pd9 and pd10, which might be dorsal spines (Fig. 5, ds?), however these features cannot be confidently distinguished from the incomplete dorsal margin and indents resulting from boundaries between podomeres.

Material.—KUMIP 490912, a partial frontal appendage preserved as a lateral compression.

Remarks.—This specimen can be identified as a partial arthropodized appendage, because it is sclerotized and composed of articulating segments (Ma et al., 2014). The curvature, podomere shape, and podomere number are all compatible with a radiodont affinity. Because the appendage is incomplete, and only the base of endites in the proximal region are preserved, assignment to the family level is difficult, with possible arguments favoring an ampletobeluid or hurdiid affinity. The comparatively low number of podomeres (11, assuming that there are no additional proximal podomeres missing) and the distal region approximately perpendicular to the proximal region are both characters observed in hurdiid radiodonts. This includes both *Buccaspinea* and *Hurdia*, the hurdiid radiodonts known from other material from Miners Hollow in the Spence Shale (described above), although the ampletobeluid *Lyrarapax* (only currently known from the Stage 3 Chengjiang in China) also bears only 11 podomeres in its distal articulated region (Cong et al., 2014, 2016; Liu et al., 2018). The putative dorsal spines lack the size and recurved nature common for distal podomeres of ampletobeluid and anomalocaridid radiodonts (e.g., *Ampletobelua stephenensis* Daley and Budd, 2010, *Anomalocaris canadensis* Whiteaves, 1892; see Daley and Budd, 2010; Daley and Edgecombe, 2014), however this could be accounted for by their poor preservation. The strong curvature or the appendage distally is also observed in both ampletobeluid and hurdiid appendages. Features that would allow more confidence in assigning the isolated appendage specimen to Hurdiidae (e.g., plate-like spines, presence of auxiliary spines on one margin of endites only) or Ampletobeluidae (e.g., hypertrophied proximal endite,

spiniform endites with few or no auxiliary spines) are not preserved, and so this specimen is left in open nomenclature and not identified to the family level.

Notably all radiodont appendages that are known from the Spence Shale have been assigned to Hurdiidae. A single body specimen from which frontal appendages are unknown was assigned to *Anomalocaris* Whiteaves, 1892 (Briggs et al., 2008, fig. 1), however following the vast number of new radiodont taxa described since then, the exact taxonomic placement of this specimen within Radiodonta is unclear. Given that ampletobeluids and anomalocaridids are known from both older and younger deposits in the Great Basin (e.g., Lerosey-Aubril et al., 2014, 2020a; Pates et al., 2021b), it might be expected that representatives of these families will be discovered in the future, and are lacking due to their rarity in Laurentian deposits of Wuliuan age and younger, rather than truly absent.

Order Radiodonta? Collins, 1996

Figure 6

Occurrence.—KUMIP 491057 originates from the Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, Antimony Canyon locality (GPS: 41.563, -112.018), Wellsville Mountains, Box Elder County, Utah.

Description.—KUMIP 491057 is a euarthropod carapace with a vase-shaped outline (Fig. 6). It measures ~23 mm along its long axis, and ~9 mm at the widest point perpendicular to the long axis (in dorsal view). The posterior part of the nuchal region and anterior part of the carapace are not preserved. The nuchal region is ~3 mm wide. The carapace element then broadens to its widest point at approximately one-third of the distance from the nuchal region to the anteriormost preserved point. The carapace then narrows anteriorly, with the outline changing from concave to convex at approximately two-thirds of the distance from the nuchal region to the anteriormost preserved point (Fig. 6, arrows). Relief is highest in the main region (Fig. 6, mr), with slender lateral extensions (Fig. 6, le) delineated by faint lines parallel to the long axis. On the left side of the element, these lines are associated with near-parallel compression wrinkles.

Material.—KUMIP 491057, a possible central carapace element preserved compressed dorsoventrally.

Remarks.—The specimen is likely a radiodont, and the vase-shaped outline and apparent relief allows this specimen to be tentatively identified as a hurdiid central carapace element. This specimen displays features comparable to a number of different hurdiid radiodonts, however the differences indicate that if a hurdiid affinity is confirmed, it most likely represents a new genus and species or belongs to a hurdiid for which the carapace is currently unknown, e.g., *Buccaspinea*.

The identification of a nuchal region (known in hurdiids, e.g., *Cordaticaris* and *Pahvantia*; Lerosey-Aubril and Pates, 2018; Sun et al., 2020) allows the anteroposterior axis of the

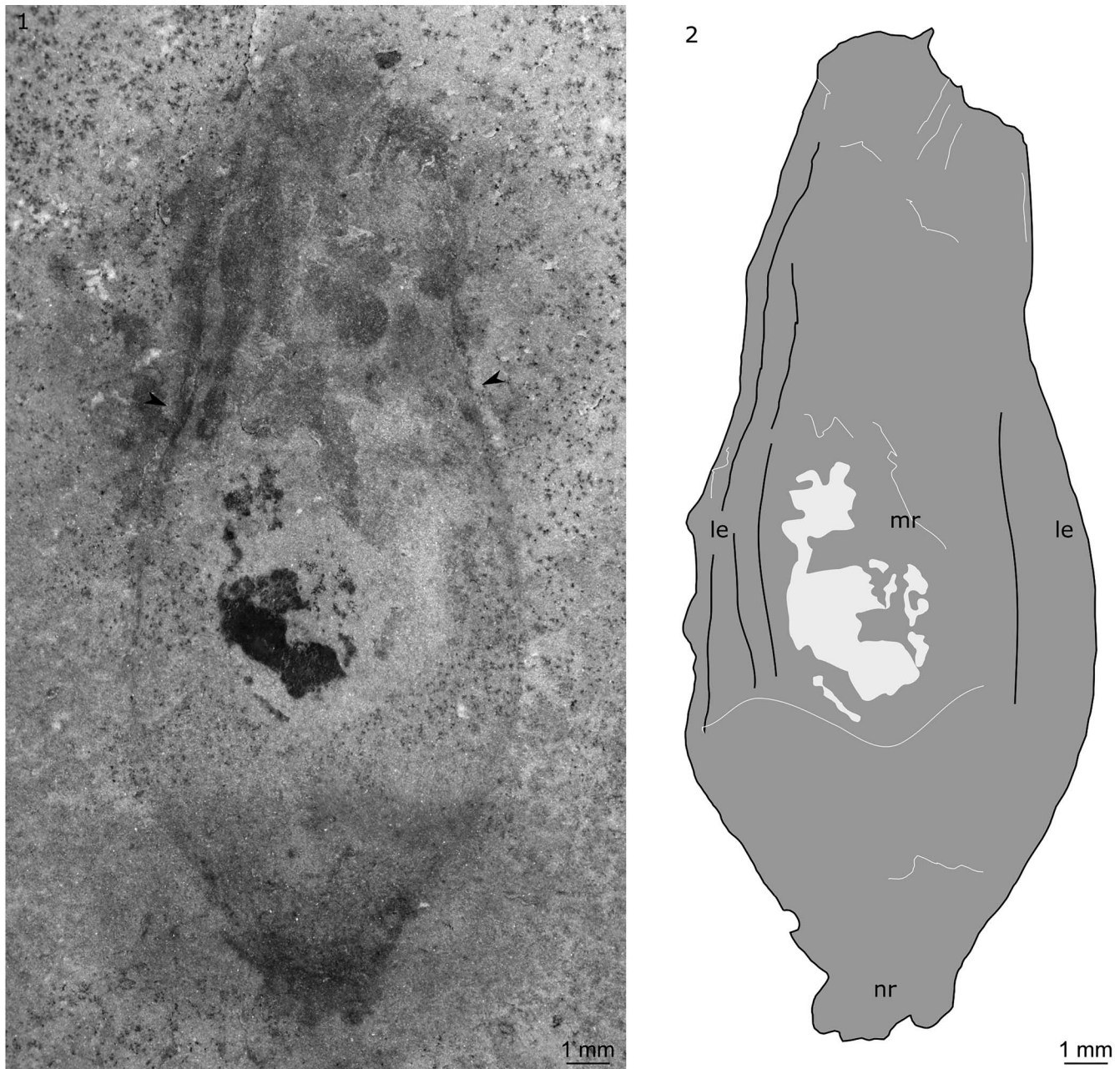


Figure 6. Radiodonta? (KUMIP 491057) collected by the Gunther family from the Antimony Canyon locality, Spence Shale, Langston Formation (Cambrian; Wuliuan), Utah, USA: (1, 2) possible central carapace element of a hurdiid radiodont in dorsal view and explanatory drawing. le, lateral extension; mr, main region; nr, nuchal region. Arrows indicate change in slope of outer margin from concave to convex.

carapace to be identified. The widest part of the carapace is closest to the posterior, as in all hurdiid central carapace elements. The slender outline of KUMIP 491057 is similar to that known in *Aegirocassis*, *Hurdia victoria* Walcott, 1912, and *Pahvantia*, and contrasts with the broad central elements of *Cambroraster*, *Cordaticaris*, and *H. triangulata* Walcott, 1912. However, the specific shape of the outline differs. A nuchal region (identified in KUMIP 491057, present in *Pahvantia*) is unknown in *Aegirocassis* and *H. victoria*. However, although the presence of lateral extensions separated from the main region by faint lines is also known in *Pahvantia* (Lerosey-Aubril and Pates, 2018), KUMIP 491057 lacks the prominent ocular

notches and associated spines described for *Pahvantia* (Lerosey-Aubril and Pates, 2018; Lerosey-Aubril et al., 2020a; Pates et al., 2021a). A change in outline from convex to concave is also known in *Cordaticaris* and *Hurdia* (Daley et al., 2013; Sun et al., 2020). However, in these two genera, this change in slope occurs very close to the distal tip of the carapace, not one-third of the distance from the tip as in KUMIP 491057.

Although the morphological features above support a hurdiid affinity for this euarthropod carapace element, a positive assignment to Hurdiidae, or indeed Radiodonta, requires the recognition of associated radiodont elements, e.g., frontal appendages, oral cones, or other body parts. Caution is warranted

because previous euarthropod carapaces that have been assigned to Hurdiidae based on the morphology of carapace elements alone (e.g., Zeng et al., 2018) have subsequently been re-assigned following the recognition of tergites (Cong et al., 2018)—a feature that precludes a radiodont affinity.

Phylum Euarthropoda Lankester, 1904
 Subphylum Chelicerata? Heymons, 1901
 Order Mollisoniida Lerosey-Aubril et al., 2020
 Family Mollisoniidae Lerosey-Aubril et al., 2020
 Genus *Thelxiope* Simonetta and Delle Cave, 1975

Type species.—*Thelxiope palaeothalassia* Simonetta and Delle Cave, 1975.

Other species.—*Thelxiope holmani* Lerosey-Aubril et al., 2020b; *Thelxiope spinosa* Conway Morris and Robison, 1988; *Thelxiope* sp. nov. A (Van Roy et al., 2010; Lerosey-Aubril et al., 2020b).

Diagnosis.—Mollisoniids with well-developed sagittal spines on cephalic shield (one), thorax (one per tergite), and pygidium (three); length of each thoracic spine at least 1.5 times length (sag.) of corresponding tergite. (Lerosey-Aubril et al., 2020b)

Occurrence.—Laurentia, middle Cambrian, Miaolingian, Wuliuan and Drumian; possibly Tremadocian strata of the Fezouata Shale in the Ternata Plain, southeastern Morocco.

Thelxiope cf. *T. palaeothalassia* Simonetta and Delle Cave, 1975
 Figure 7

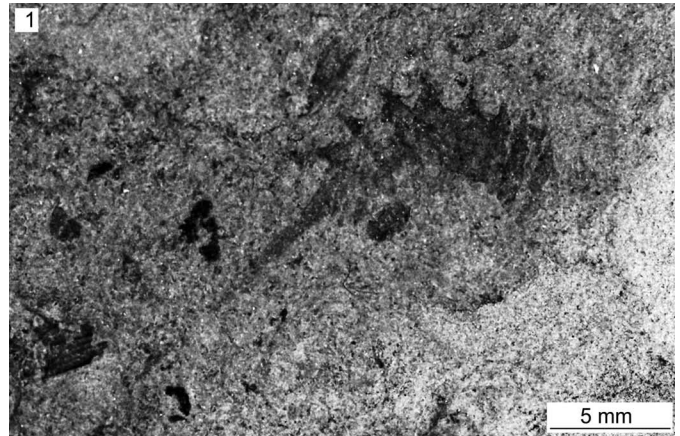
cf. 1975 *Thelxiope palaeothalassia* Simonetta and Delle Cave, p. 28, pl. 3, fig. 1, pl. 12, figs. 3–5.
 cf. 2020b *Thelxiope palaeothalassia*; Lerosey-Aubril et al., p. 6, figs. 2, 3.

Diagnosis.—Species of *Thelxiope* characterized by relatively short cephalic, thoracic, and pygidial sagittal spines, except for posteriormost pygidial spine hypertrophied and exceeding main body length. (Lerosey-Aubril et al., 2020b)

Occurrence.—KUMIP 314201 originates from approximately two-thirds from the top of the Spence Shale, Wuliuan Spence Shale Member (*Glossopleura walcottii* Biozone) of the Langston Formation, Miners Hollow locality (GPS: 41.602, -112.033), Wellsville Mountains, Box Elder County, Utah.

Description.—Most of cephalic shield missing; only posteriormost part preserved. Posterior margin straight with short cephalic sagittal spine extending dorsally (Fig. 7.1).

Thorax 10 mm long and up to 7 mm wide, composed of seven tergites (Fig. 7, T1–T7), each ~7 mm wide and 3 mm long. Anterior part of each tergite partially concealed by tergite in front of it and spineless. Posterior part preserving short, thick-based, dorsally projecting sagittal spine.



2

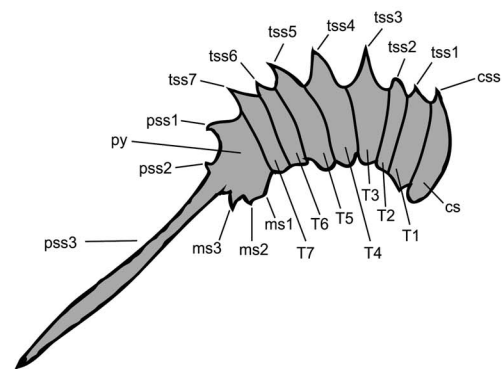


Figure 7. *Thelxiope* cf. *T. palaeothalassia* Simonetta and Delle Cave, 1975 (KUMIP 314201), collected by Phil Reese from the Miners Hollow locality, Spence Shale Member, Langston Formation (Cambrian: Wuliuan), Utah, USA: (1, 2) general view and explanatory drawing. cs, cephalic shield; css, cephalic sagittal spine; ms#, marginal spine; pss#, pygidial sagittal spine; py, pygidium; T#, thoracic tergite; tss#, thoracic sagittal spine.

Center part of pygidium not preserved. Pygidium 2 mm long and 3 mm wide, not including posterior spine, appearing to be composed of three nonarticulated tergites similar in morphology to those of thorax based on presence of three pygidial sagittal spines. Two anterior pygidial sagittal spines extending dorsally, slenderer and shorter than thoracic ones, whereas third spine hypertrophied, straight, and projecting posteriorly. Posterior spine approximately same length (12 mm) as thorax and pygidium combined (12 mm), appearing to be mostly complete; particularly thick proximally, but gently narrowing distally until reaching approximate half of its proximal diameter at distal tip.

Material.—KUMIP 314201, an almost complete specimen in lateral view.

Remarks.—*Thelxiope* cf. *T. palaeothalassia* from the Spence Shale has a thoracic tergite arrangement, and thoracic sagittal spines, resembling the holotype from the Burgess Shale, although the specimen is not as well preserved as the Burgess Shale specimens, and is missing most of the cephalon. The hypertrophied, straight, and posteriorly projecting third pygidial spine is also only known from *Thelxiope palaeothalassia*. This is the first and currently only occurrence of *Thelxiope*

palaeothalassia outside of the Burgess Shale, although it still suggests that *Thelxiope palaeothalassia* was restricted to the Wuliuan of Laurentia.

Order Hymenocarina Clarke, 1900
Family Perspicaridae Briggs, 1978
Genus *Perspicaris* Briggs, 1977

Type species.—*Canadaspis dictynna* Simonetta and Delle Cave, 1975, by original designation.

Other species.—*Perspicaris recondita* Briggs, 1977; *Perspicaris? dilatus* Robison and Richards, 1981; *Perspicaris? ellipsopelta* Robison and Richards, 1981.

Diagnosis.—Carapace with hinge line, valves suboval, tapering anteriorly, rostral plate absent. Pendunculate eyes large, borne on elongate projection of cephalon. Abdominal somites lacking appendages, telson not posteriorly produced, caudal furca spinose. (Briggs, 1977)

Occurrence.—Laurentia, middle Cambrian, Miaolingian, Wuliuan, and Drumian.

Perspicaris? dilatus Robison and Richards, 1981
Figure 8.1, 8.2

1981 *Perspicaris? dilatus* Robison and Richards, p. 4, pl. 1, fig. 4, pl. 2, figs. 5–7.

2003 ?*Perspicaris dilatus*; Lieberman, p. 677, fig. 1.2.

2015 *Perspicaris? dilatus*; Kimmig and Pratt, p. 55, figs. 6.1–6.9, 7.1–7.6, 9.4, 9.6, 11.3, 11.4, 11.6.

2020a *Perspicaris? dilatus*; Lerosey-Aubril et al., p. 22, fig. 12.

Holotype.—Right valve (KUMIP 135128) from the Wheeler Formation, House Range, Utah, USA (Robison and Richards, 1981, pl. 1, fig. 4).

Diagnosis.—*Perspicaris?* with valve subovate in outline, posterior process larger than anterior process. (Kimmig and Pratt, 2015)

Occurrence.—YPM IP 530101 originates from the Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, southern side of Antimony Canyon locality, approximately half-way up slope between stream and ridge (GPS: 41.561, -112.006), Wellsville Mountains, Box Elder County, Utah.

Description.—Valve subovate in outline; posterior portion moderately wider than anterior, with maximum width approximately two-thirds along length of hinge line from anterior margin. Maximum length 41 mm, maximum width

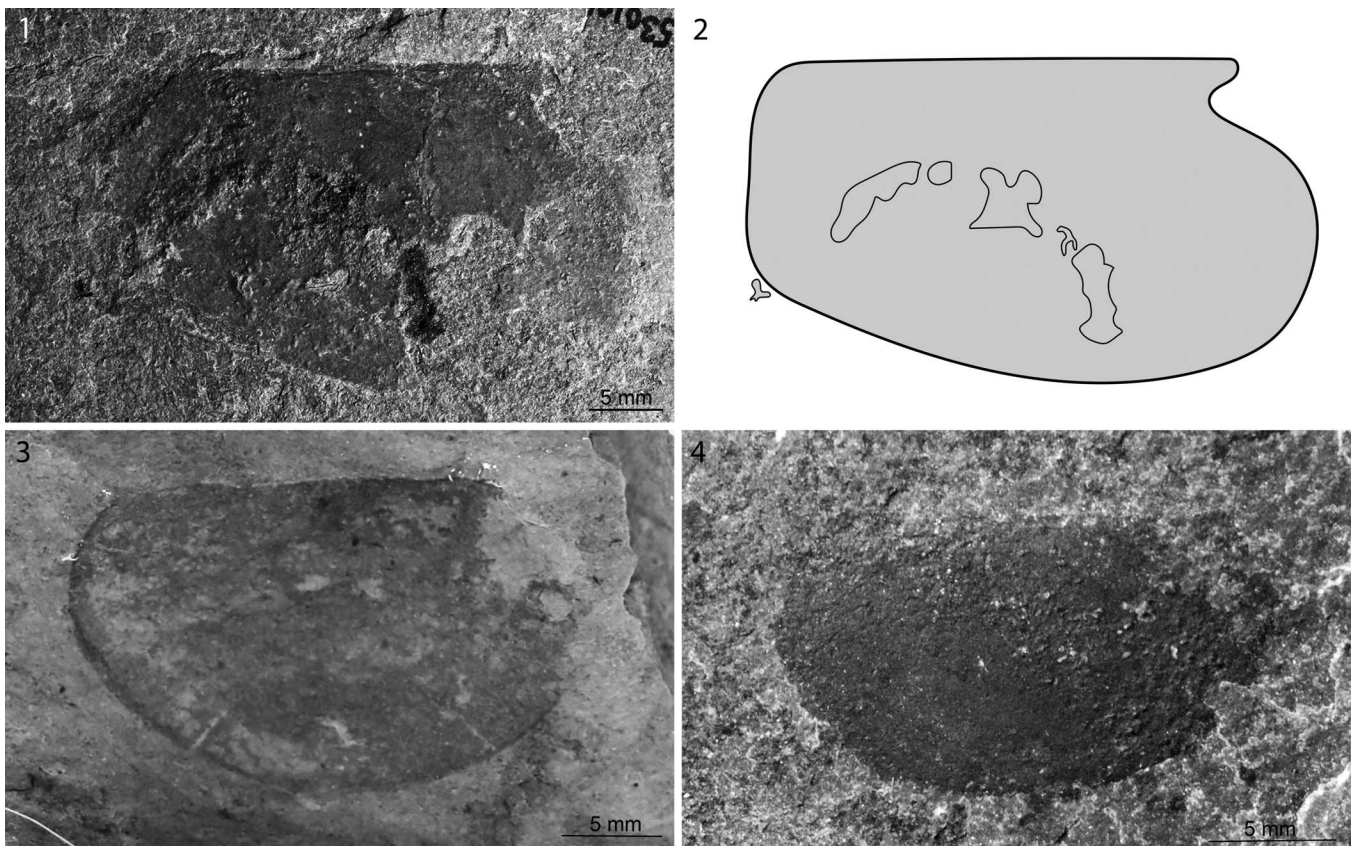


Figure 8. Bivalved panarthropods from the Spence Shale Member, Langston Formation (Cambrian: Wuliuan), Utah, USA: (1, 2) *Perspicaris? dilatus* Robison and Richards, 1981 (YPM IP 530101), Antimony Canyon, collected by Lloyd Gunther, and explanatory drawing; (3) *Branchiocaris petriosa* Resser, 1929 (KUMIP 314058), Smithfield Creek locality, collected by Reboul; (4) *Branchiocaris petriosa* (MCZ IP 164071, part), Antimony Canyon, collected by Lloyd Gunther.

24 mm. Posterior process larger than anterior process and exhibiting angle of $\sim 100^\circ$. Hinge line straight.

Material.—YPM IP 530101, one valve in lateral view.

Remarks.—Although valves and complete carapaces of *Perspiscaris? dilatus* are relatively common, YPM IP 530101 is the only known specimen to contain soft tissues (black film) possibly representing the animal being protected by said valves. Unfortunately, the preservation does not allow for a conclusive assessment, because no segments or other morphological information are preserved. The specimen is conspecific with *Perspiscaris? dilatus* based on the outline of the valve (Fig. 8.2) with the maximum width being near the posterior end, and the relatively large posterior process. The shape also fits within the variation of the *Perspiscaris? dilatus* valves from the Rockslide Formation (Kimmig and Pratt, 2015). The valve overlies a *Marpolia* sp. specimen (Fig. 8.1).

Family uncertain

Genus *Branchiocaris* Briggs, 1976

Type species.—*Protocaris pretiosa* Resser, 1929, by original designation.

Diagnosis.—As for species.

Occurrence.—Laurentia and China, middle Cambrian, Miaolingian, Wuliuan, and Drumian; possibly China, Series 2, Stages 3 and 4.

Branchiocaris pretiosa Resser, 1929
Figure 8.3, 8.4

1929 *Protocaris pretiosa* Resser, p. 6, pl. 4, figs. 1, 2.

1944 *Protocaris pretiosa*; Shimer and Shrock, p. 655, pl. 277, figs. 3, 4.

1969 *Protocaris pretiosa*; Rolfe, p. 331, fig. 154.6.

1976 *Branchiocaris pretiosa*; Briggs, p. 6, fig. 2.4–2.7, pl. 1, figs. 5, 6; pls. 2–5; pl. 6, fig. 1.

1984 *Branchiocaris pretiosa*; Briggs and Robison, p. 6, figs. 5–9.

2017 *Branchiocaris pretiosa*; Aria and Caron, p. 90, fig. 2a, e, i, j, l, n, extended data figs. 6, 7.

2020 *Branchiocaris pretiosa*; Saleh et al., p. 2, fig. 1b.

Holotype.—Nearly complete specimen (USNM 80843) from the Burgess Shale, Stephen Formation, between Wapta Mountain and Mount Field, British Columbia, Canada (Resser, 1929, pl. 4, figs. 1, 2).

Diagnosis.—Carapace valves subovate, dorsal margin produced anteriorly and posteriorly into short pointed process, border with unevenly spaced, elongate, shallow pits normal to margin. Cephalic region bearing pair of uniramous antennae, anterior to pair of large segmented appendages. Trunk with up to 47 divisions; appendages lamellate, with segmented proximal element, attached to full length of trunk anterior to telson; telson processes short, pointed, blade-like. (Briggs, 1976)

Occurrence.—KUMIP 314058 originates from the Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, Smithfield Creek locality (GPS: 41.874, -111.754), north of Logan, Wasatch Range, Cache County, Utah. MCZ IP 164071 and 164074 originate from the Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation Antimony Canyon locality (GPS: 41.561, -112.006), Wellsville Mountains, Box Elder County, Utah.

Description.—Valve semicircular in outline; maximum length 25 mm, maximum width 14 mm. Anterior process slightly smaller than posterior process, both relatively small. Anterior muscle scar indistinct (Fig. 8.3, 8.4), located close to anterior margin.

Material.—Partial valve in lateral view (KUMIP 314058) and one complete valve in part and counterpart (MCZ IP 164071, 164074).

Remarks.—Two valves are placed in *Branchiocaris pretiosa* because of their semicircular outline and the size and positioning of the anterior and posterior processes similar to previously described specimens of *Branchiocaris pretiosa*, which occurs in strata of approximately the same age (Briggs, 1976; Briggs and Robison, 1984). These are the first specimens of *Branchiocaris pretiosa* from the Spence Shale. Although the specimens do not preserve soft tissues, the valve of *Branchiocaris pretiosa* is fairly unique in its outline among carapaces of Cambrian arthropods and differs from *Perspiscaris? dilatus* and *Dioxyaris argenta* in the smaller processes, the anterior process that is slightly smaller than the posterior process, and the semicircular rather than subovate to subelliptical outline of the valve.

Family Tuzoidea Raymond, 1935

Genus *Tuzoia* Walcott, 1912

Type species.—*Tuzoia retifera* Walcott, 1912, by original designation.

Other species.—*Tuzoia burgessensis* Resser, 1929; *Tuzoia canadensis* Resser, 1929; *Tuzoia polleni* Resser, 1929; *Tuzoia manchuriensis* Resser and Endo in Endo and Resser, 1937; *Tuzoia sinensis* Pan, 1957; *Tuzoia australis* Glaessner, 1979; *Tuzoia guntheri* Robison and Richards, 1981; *Tuzoia bispinosa* Yuan and Zhao, 1999; *Tuzoia tyloides* Luo and Hu in Luo et al., 2006; *Tuzoia jianheensis* Chen and Zhao in Chen et al., 2017; and *Tuzoia lazizhaiensis* Wen et al., 2019a. Questionably *Tuzoia? parva* Walcott, 1912; and *Tuzoia? peterseni* Robison and Richards, 1981.

Diagnosis.—Tuzooid with ocular segment extending beyond carapace margin, bearing pair of elongated peduncular lobes. Carapace bearing spinose lateral ridge. Midposterior spine present in most species. Additional small marginal spines present in some species, mostly on ventroposterior margin of carapace. Endopod heptopodomerous with elongated basipod; distalmost podomere claw-shaped, second distalmost podomere

always bearing series of spines. At least first two pairs of legs bearing spines on each podomere. Body terminating in two pairs of caudal rami, one on top of other, each pair fused into singular truncate paddle. (Izquierdo-López and Caron, 2022)

Occurrence.—Laurentia, China and South Australia, lower and middle Cambrian, Series 2 and Miaolingian, Stage 3 to Drumian.

Tuzoia retifera Walcott, 1912
Figure 9.1

- 1912 *Tuzoia retifera* Walcott, p. 187, pl. 33, fig. 2.
1929 *Tuzoia retifera*; Resser, p. 7, pl. 1, fig. 2.
1975 *Tuzoia retifera*; Simonetta and Delle Cave, p. 8, pl. 47, fig. 2.
1981 *Tuzoia retifera*; Robison and Richards, p. 14, pl. 8, fig. 3.
2007 *Tuzoia retifera*; Vannier et al., p. 459, figs. 3–5, 25.1, 26, 27.2, 31.
2022 *Tuzoia retifera*; Izquierdo-López and Caron, p. 3, figs. 3, 5.

Holotype.—Right valve (USNM 57720) from the Burgess Shale, Stephen Formation, between Wapta Mountain and

Mount Field, British Columbia, Canada (Walcott, 1912, pl. 33, fig. 2).

Diagnosis.—*Tuzoia* with ovoid amplete to slightly postplete/preplete outline (mean L:H 1.45, N=47, specimens in lateral aspect clearly showing ventral margin). Carapace length 20–120 mm; mean length ~77 mm (N=47, SD=16.5). Dorsal margin straight to slightly convex. Anterior cardinal processes broad-based, very short, not pointed, directed slightly downward. Well-developed anterior notch. Posterior cardinal processes Blunt, very small. Midposterior spine and posteroventral spine present, but very short. Midposterior spine often longer than posteroventral spine. One additional marginal spine between midposterior spine and posteroventral spine present or not. Posterior cardinal angle ~110°. No dorsal spines. Low-relief lateral ridge running almost parallel to dorsal margin (H:A ~2.0) underlined by very narrow frill with very small crenulation. Reticulate pattern dense, uniform, very small along anterior, posterior, and dorsal margins. Juvenile morphology similar to that of adults. (Vannier et al., 2007)

Occurrence.—KUMIP 561726 originates from the Cycle 3 ‘Kootenia Quarry’ of the Wuliuan Spence Shale Member

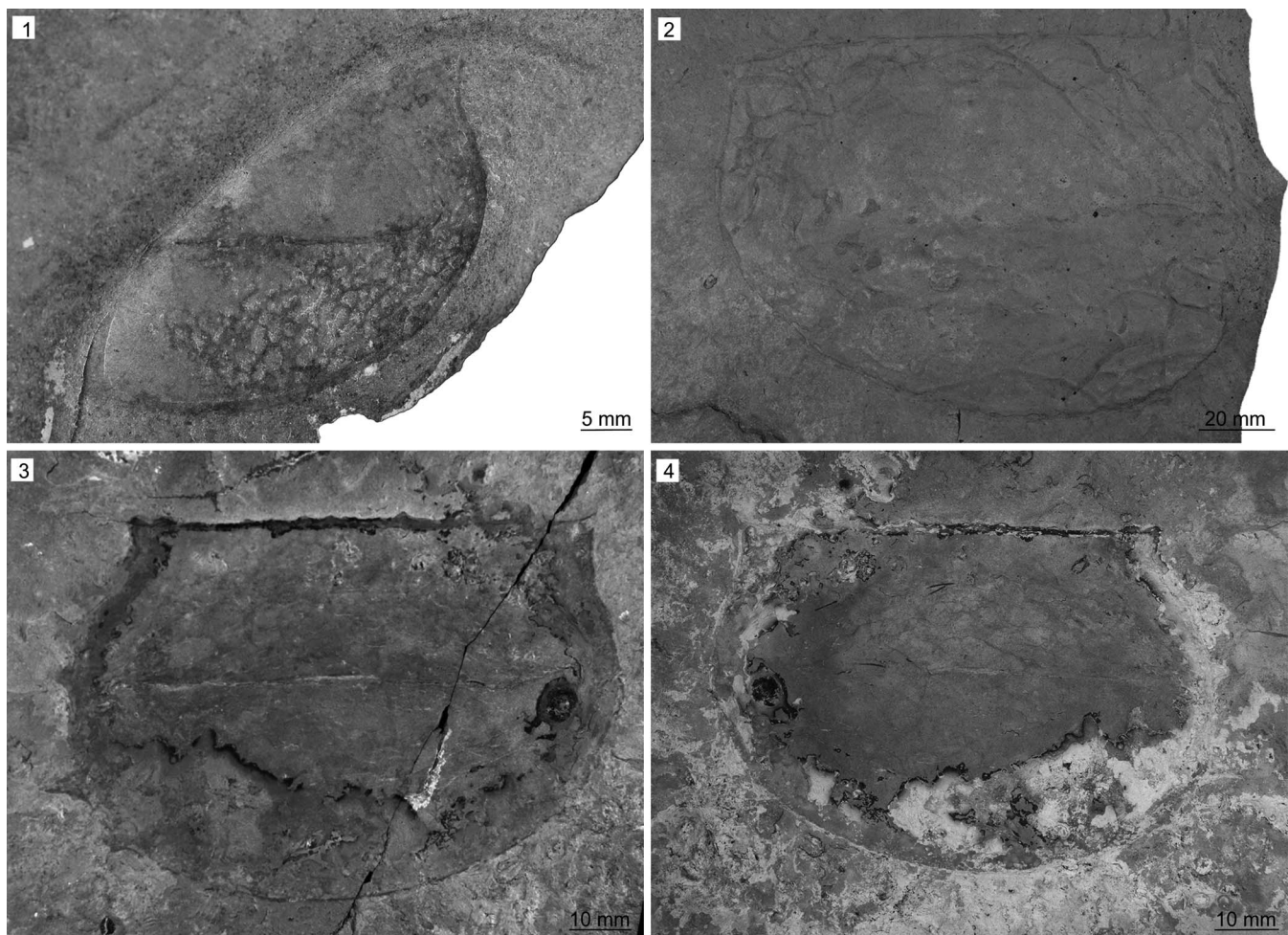


Figure 9. *Tuzoia* spp. from the Miners Hollow locality, Spence Shale Member, Langston Formation (Cambrian: Wuliuan), Utah, USA: (1) *Tuzoia retifera* Walcott, 1912 (KUMIP 561726), collected by Paul Jamison; (2) *Tuzoia guntheri* Robison and Richards, 1981 (KUMIP 314036), valve in lateral view with burrows beneath, collected by Phil Reese; (3, 4) *Tuzoia guntheri* (KUMIP 561725, part and counterpart), collected by Paul Jamison.

(*Glossopleura walcotti* Biozone) of the Langston Formation, Miners Hollow locality (GPS: 41.602, -112.033), Wellsville Mountains, Box Elder County, Utah.

Description of new material.—KUMIP 561726 represents a partial single valve in lateral view. Only approximately half of the anterior part of the specimen is exposed and the posterior part is covered. The exposed part of the specimen is 48 mm long and ~41 mm in height at its widest point. The anterior cardinal process is exposed and projects 2 mm from the anterior margin at an angle of ~105°. The exterior surface is covered by somewhat irregular reticulate pattern of fine carbonaceous lines surrounding slightly convex interiors. The specimen preserves compaction wrinkles in the center of the valve, suggesting this area was vaulted in life.

New material.—KUMIP 561726, partial right valve in lateral view.

Other material.—KUMIP 153918, partial left valve (part and counterpart).

Remarks.—*Tuzoia retifera* was previously known from a single specimen (KUMIP 153918) in the Spence Shale. This new specimen might represent a mostly complete valve, but preparation attempts were unsuccessful and, as such, the above description is based on the exposed part of the specimen. The specimen is assigned to *Tuzoia retifera* based on the exposed outline of the valve, the angle of the anterior cardinal process, and the somewhat irregular reticulate pattern of fine grooves surrounding slightly convex interiors covering the exterior surface of the valve. The pattern on the exterior surface of the valve is reminiscent of the pattern exhibited by *Tuzoia guntheri* (see Kimmig and Pratt, 2015).

Tuzoia guntheri Robison and Richards, 1981
Figure 9.2–9.4

- 1981 *Tuzoia guntheri* Robison and Richards, p. 13, pl. 7, figs. 1, 2, pl. 8, figs. 4, 5, pl. 9, fig. 2.
1991 *Tuzoia guntheri*; Robison, p. 84, fig. 7.1.
2003 *Tuzoia guntheri*; Lieberman, p. 679, fig. 1.3.
2007 *Tuzoia guntheri*; Vannier et al., p. 462, figs. 16, 25.4, 26, 31.
2015 *Tuzoia guntheri*; Kimmig and Pratt, p. 57, fig. 9.2, 9.3.
2015 *Tuzoia guntheri*; Robison et al., p. 62, fig. 173.
2019b *Tuzoia* sp.; Kimmig et al., p. 614, fig. 4e.

Holotype.—Left valve (KUMIP 153917) from the Marjum Formation, House Range, Utah, USA (Robison and Richards, 1981, pl. 7, fig. 2).

Diagnosis.—*Tuzoia* with ovoid, slightly postplete outline (L:H 1.35 in holotype). Length (exclusive of spine) can exceed 80 mm. Dorsal margin straight to slightly convex. Anterior cardinal processes pointing straight forward, overhanging notch. Posterior cardinal processes shorter than anterior cardinal processes, directed upward and backward. At least two dorsal spines (one large and subvertical), both inserted

along anterior third of dorsal margin. Posteroventral spine long, slender. Midposterior spine short. Two additional marginal spines present: one, very small, dorsal of midposterior spine; the other, longer, ventral of posteroventral spine. Lateral ridge with low relief, running obliquely (H:A ~3.0 at valve midlength in holotype). Reticulate pattern over entire lateral surface. (Vannier et al., 2007)

Occurrence.—KUMIP 561725 originates from the Cycle 3 ‘Kootenia Quarry’ of the Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, Miners Hollow locality (GPS: 41.602, -112.033), Wellsville Mountains, Box Elder County, Utah. KUMIP 314036 originates from the Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, Miners Hollow locality (GPS: 41.602, -112.033), Wellsville Mountains, Box Elder County, Utah.

Description of new material.—KUMIP 561725 (Fig. 9.3, 9.4) is 120 mm long and 77 mm wide and preserved as part and counterpart. The valve has four spines on the posterior margin; the most dorsal 5 mm long, the midposterior spine 5 mm long, the posteroventral spine 10 mm long, and the ventral spine 2 mm long; and two dorsal spines (Fig. 9.3), the more anterior of which is 4 mm long, and the more posterior one 2 mm long. The preserved part of the anterior cardinal projects 2 mm from the anterior margin at an angle of ~110°. The posterior cardinal process projects 2 mm from the posterior margin at an angle of ~110°. Dorsal margin straight.

KUMIP 314036 (Fig. 9.4) is 165 mm long and 115 mm wide. None of the spines are preserved, but the outline of the valve corresponds to the outline of *Tuzoia guntheri*. The anterior cardinal process projects 2 mm from the anterior margin at an angle of ~110°.

Material.—Two valves in lateral view (KUMIP 314036, 561725).

Remarks.—*Tuzoia guntheri* has been previously reported from the Cambrian (Wulian to Drumian) of the Great Basin and the Drumian Rockslide Formation of northern Canada (Robison and Richards, 1981; Liebermann, 2003; Vannier et al., 2007; Kimmig and Pratt, 2015), but this is its first record in the Spence Shale.

KUMIP 314036 preserves groove-shaped, simple burrows between 1 and 3 mm wide and several centimeters long (Fig. 9.2). Bifurcation is observed in a few instances, but likely due to intersection rather than true branching. They resemble the structures described from below panarthropod valves in other BST deposits (Zhang et al., 2007; Mángano, 2011; Mángano et al., 2012; Kimmig and Pratt, 2016) and are closest in shape and size to those described on valves of *Perspicaris? dilatatus* from the Drumian Ravens Throat River Lagerstätte of northern Canada (Kimmig and Pratt, 2016).

Order and Family uncertain
Genus *Dioxyaris* Gürich, 1929

Type species.—*Lerpeditia argenta* Walcott, 1886.

Diagnosis.—As for species.

Occurrence.—Laurentia, middle Cambrian, Miaolingian, Wuliuan.

Dioxycaris argenta Walcott, 1886
Figure 10

- 1886 *Lerpeditia argenta* Walcott, p. 146, pl. 8, fig. 5.
1929 *Dioxycaris argenta*; Gürich, p. 36, text-fig. 1.3.
1953 *Dioxycaris argenta*; Roger, p. 311, pl. 1, fig. 4a.
1956 *Dioxycaris argenta*; Brooks and Caster, p. 11, fig. 1.6.
1969 *Dioxycaris argenta*; Rolfe, p. 325, fig. 150.4.
1976 *Dioxycaris argenta*; Briggs, p. 13, pl. 6, figs. 3, 4.
1981 *Dioxycaris argenta*; Robison and Richards, p. 7, pl. 3, figs. 4–6.
2019b *Dioxycaris argenta*; Kimmig et al., p. 614, fig. 4j.
2022 *Dioxycaris argenta*; Whitaker et al., p. 6, fig. 2C.

Holotype.—Probably right valve (USNM 15401) from the lower member of the Ophir Shale, Cottonwood Canyon, Utah, USA (Walcott, 1886, pl. 8, fig. 5).

Diagnosis.—Carapace bivalved with hinge line. Valves subelliptical with slight posteroventral expansion; anterodorsal

process of moderate size, posterodorsal process large; lateral surfaces and free margins lacking spines. (Robison and Richards, 1981)

Occurrence.—KUMIP 314048 and MCZ IP 164072, 164073 originate from the Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, Antimony Canyon locality (GPS: 41.561, -112.006), Wellsville Mountains, Box Elder County, Utah. KUMIP 491904 originates from the Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, Miners Hollow locality (GPS: 41.602, -112.033), Wellsville Mountains, Box Elder County, Utah. KUMIP 558518 originates from +6 m from the base of the exposed Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, Spence Gulch locality (GPS: 42.306, -111.515), Bear River Range, Bear Lake County, Idaho.

Description of new material.—Valve subelliptical in outline; posterior portion moderately wider than anterior, with maximum width at approximately two-thirds along length of hinge line from anterior margin. Maximum length 25 mm, maximum width 11 mm; smallest 15 mm length, 10 mm width. Posterior process slightly larger than anterior process, exhibiting angle of $\sim 110^\circ$. Anterior angle hinge line straight.

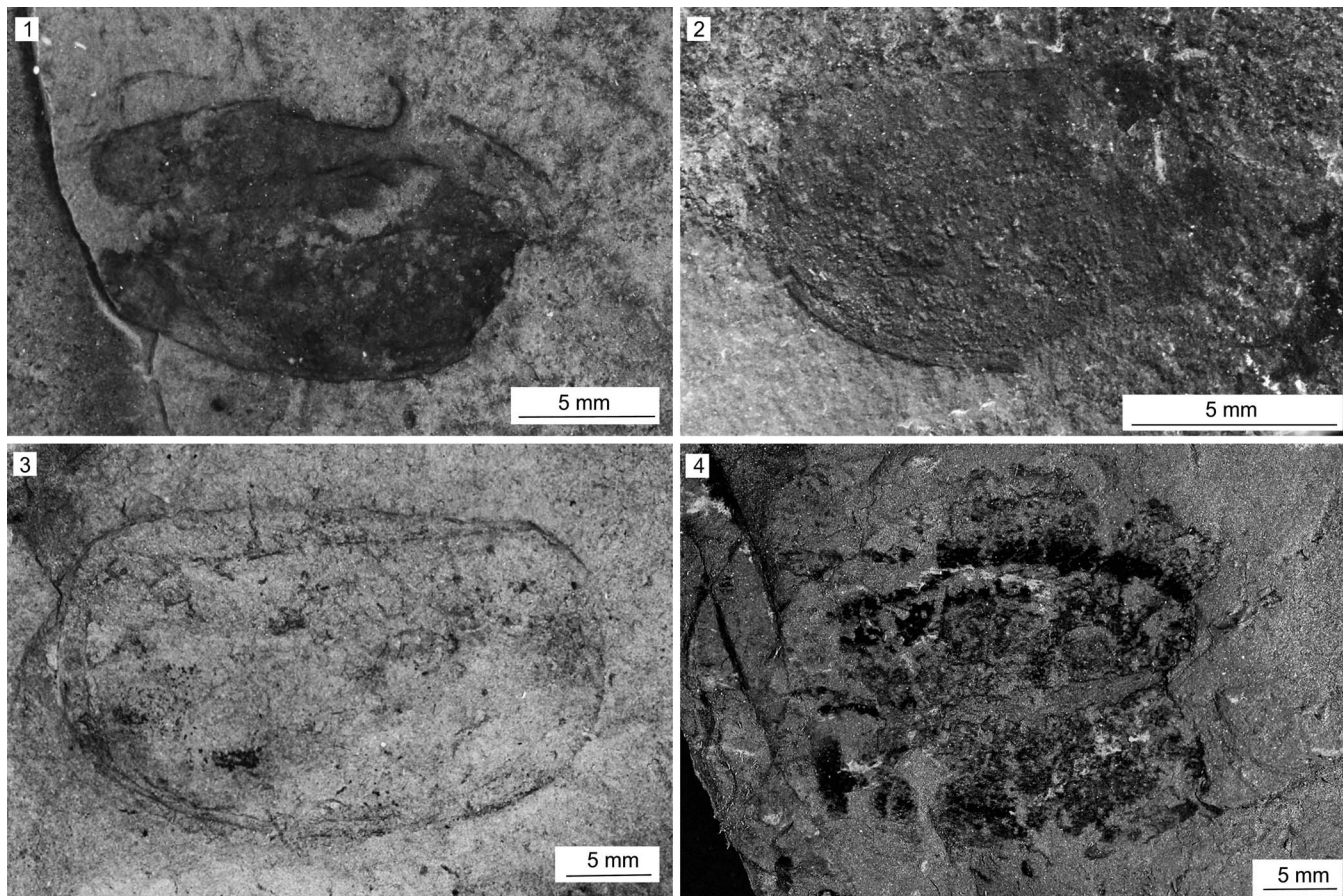


Figure 10. *Dioxycaris argenta* Walcott, 1886 from the Spence Shale Member, Langston Formation (Cambrian: Wuliuan), Idaho and Utah, USA: (1) KUMIP 314048, Antimony Canyon, collected by the Gunther family; (2) MCZ IP 164073 (part), Antimony Canyon, collected by Lloyd Gunther; (3) KUMIP 491904, Miners Hollow, collected by the Gunther family; (4) KUMIP 558518 (part), Spence Gulch, collected by Julien Kimmig.

Circular muscle scar inconspicuous in larger valves; located on one smaller specimen (Fig. 10.3) close to anterior margin and three times its diameter from hinge line.

New material.—Two complete carapaces in dorsal view and two isolated valves in lateral view (KUMIP 314048, 491904, 558518, MCZ IP 164072, 164073).

Other material.—Three isolated valves in lateral view (KUMIP 135145–135147).

Remarks.—*Dioxycares argenta* is the most common bivalved panarthropod in the Spence Shale, however the valves and carapaces seemingly have a tendency to decompose more rapidly than those of other bivalved panarthropods. Although this might have to do with varying taphonomic conditions in different Spence Shale outcrops (Whitaker et al., 2022), it also suggests that the valves might have been thinner than those of other bivalved panarthropods. With the specimens described herein, there are now at least nine specimens known from the Spence Shale, five of them from Antimony Canyon. This value likely underestimates the relative abundance of this taxon, because many fragmentary specimens from the Spence Shale doubtless represent fragments of *D. argenta*.

Order Bradoriida Raymond, 1935

Family uncertain

Genus *Walcottella* Ulrich and Bassler, 1931

Type species.—*Walcottella apicalis* Ulrich and Bassler, 1931 from the middle Cambrian of the Grand Canyon, Arizona, USA.

Walcottella? sp. indet.

Figure 11.1–11.4

Occurrence.—KUMIP 579390 originates from +5 m from the base of the exposed Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, Spence Gulch locality (GPS: 42.306, -111.515), Bear River Range, Bear Lake County, Idaho. KUMIP 579391 originates from +1 m from the base of the exposed Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, Spence Gulch locality (GPS: 42.306, -111.515), Bear River Range, Bear Lake County, Idaho. YPM 530096 originates from the Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, Antimony Canyon locality (GPS: 41.563, -112.018), Wellsville Mountains, Box Elder County, Utah.

Description.—The valve is elongate-ovate in outline and a possible antero-central node is present in KUMIP 579391 and YPM 530096 (Fig. 11). Faint ornamentation appears to be present on KUMIP 579390, a valve ~7 mm in length and 5 mm in width. Possible anterodorsal node or nodes are present. A narrow marginal ridge extends continuously from the posterior end of hinge to at least the intersection of the possible node(s). KUMIP 579391 is 8 mm in length and 5 mm in width.

YPM IP 530096: Carapace postplete; valve ~11 mm length, 8 mm width, ovate in outline. Hinge line well-developed, midanterior surface showing marked indentation, possibly indicative of single anterior lobe. Faint furrow demarcating a moderately wide margin.

Material.—Three isolated valves (YPM 530096, and part and counterpart of KUMIP 579390, 579391).

Remarks.—All three specimens are flattened and show signs of weathering. KUMIP 579390 and 579391 are partially obscured by matrix and overlapping nondescript skeletal elements. The valve outline is more symmetrical than that of *Anabarochilina* cf. *A. australis* Hinz-Schallreuter, 1993, described from the Cambrian Marjum and Weeks formations of Utah, and *Liangshanella burgessensis* Sieveter and Williams, 1997 from the Burgess Shale of Canada (Sieveter and Williams, 1997). However, the outline and the position of the possible antero-central node is similar to that of *Walcottella apicalis* Ulrich and Bassler, 1931 from the Cambrian (Wuliuan) Bright Angel Shale of Arizona. For these reasons, we tentatively assign these specimens to *Walcottella*. It is worth noting that the Bright Angel Shale specimens are preserved in three dimension and these specimens are flattened.

Bradoriida gen. indet. sp. indet.

Figure 11.5, 11.6

Occurrence.—KUMIP 585568 originates 1 m from the top of the Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, High Creek locality (GPS: 41.896, -111.711), north of Logan, Wasatch Range, Cache County, Utah.

Description.—Valve almost semicircular in outline, 10 mm long, 8 mm wide. Hinge probably short. Anterior process short; posterior process unknown. Narrow marginal ridge.

Material.—Isolated valve with part and counterpart (KUMIP 585568).

Remarks.—The valve and the trilobite were likely digested and are part of a coprolite or regurgitate that appears to have lost its soft parts. Coprolites are common in the Spence Shale (Kimmig and Strotz, 2017) and bradoriid shells have been identified in coprolites from other deposits (Kimmig and Pratt, 2018).

Subphylum Artiopoda Hou and Bergström, 1997

Superclass Trilobitomorpha Størmer, 1944

Order Nektaspida Raymond, 1920

Family Naraoidae Walcott, 1912

Genus *Naraoia?* Walcott, 1912

Type species.—*Naraoia compacta* Walcott, 1912, by original designation.

Other species.—*Naraoia spinifer* Walcott, 1931; *N. spinosa* Zhang and Hou, 1985; *N. bertensis* Caron et al., 2004; *N.*

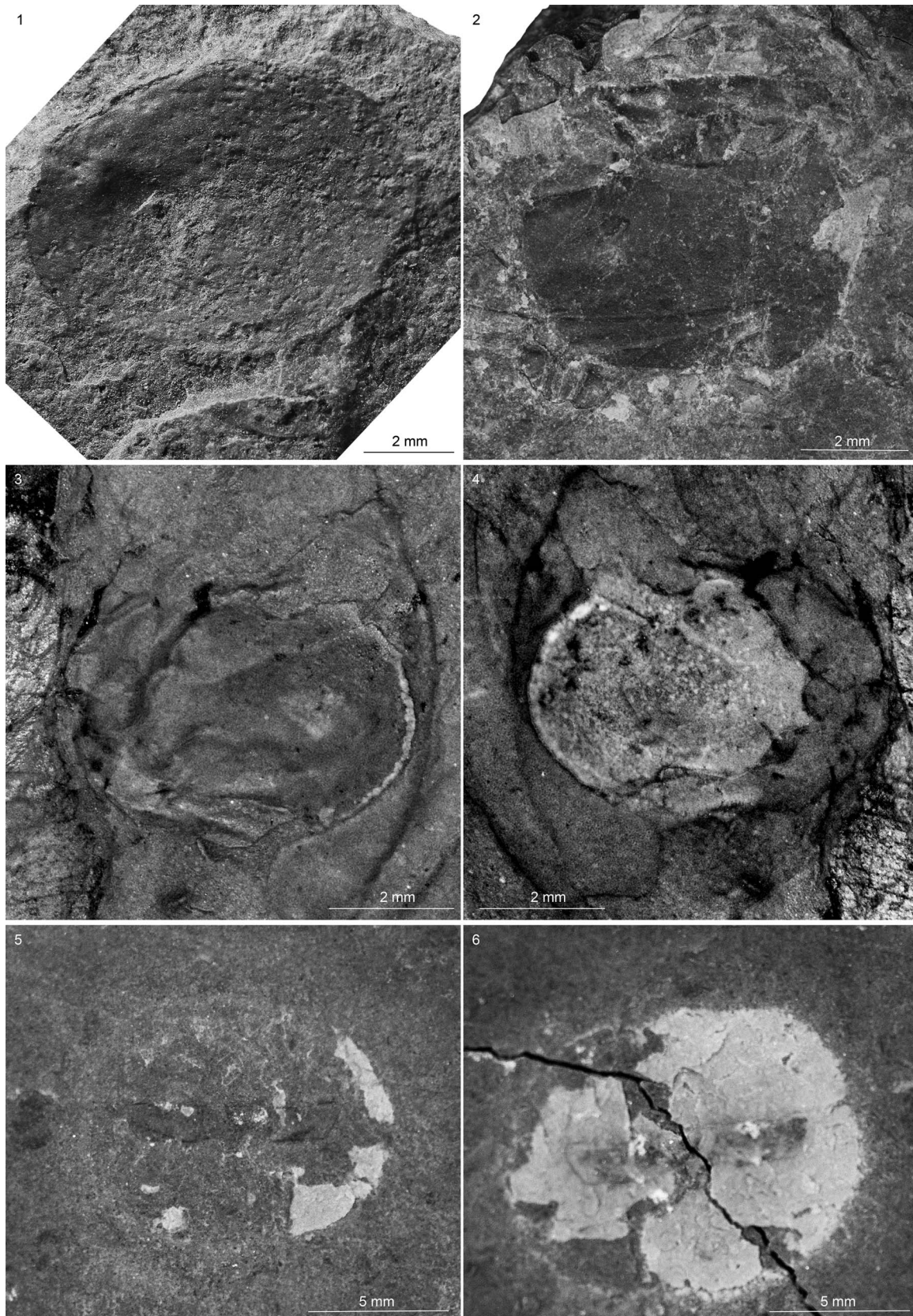


Figure 11. Bradoriids from the Spence Shale Member, Langston Formation (Cambrian: Wuliuan), Idaho and Utah, USA: (1) *Walcottella?* sp. indet. (YPM 530096), Antimony Canyon, collected by Lloyd Gunther; (2) *Walcottella?* sp. indet. (KUMIP 579390), Spence Gulch, collected by Rhiannon LaVine; (3, 4) *Walcottella?* sp. indet. (KUMIP 579391, part and counterpart), Spence Gulch, collected by Rhiannon LaVine; (5, 6) Bradoriida gen. indet. sp. indet. (KUMIP 585568, part and counterpart), High Creek, valve in lateral view, likely part of a coprolite, collected by Julien Kimmig.

taijiangensis Peng, Zhao, and Sun, 2012; *N. magna* Mayers et al., 2019; *N. arcana* Mayers et al., 2019.

Diagnosis.—Naraoiid nektaspids with trunk length/total length ratio < 0.65; cephalic and trunk margins smooth or spinose. (Mayers et al., 2019)

Occurrence.—Laurentia, China, and South Australia, lower and middle Cambrian, Series 2 and Miaolingian, Stage 3 to Drumian.

Naraoia? sp. indet.

Figure 12

Occurrence.—Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, Two Mile Canyon locality (GPS: 42.166, -112.209), near Malad, Oneida County, Idaho.

Description.—Dorsoventrally compressed, 9.8 mm long (reconstructed pre-disarticulation), preserving cephalon and trunk (partly separated, with greatest degree of separation on

right side of specimen). Cephalic shield ovoid in outline, 4.9 mm long, 3.9 mm at widest point 0.5 mm from posterior end. Left portion of cephalon broken off, separated from main body of cephalon (Fig. 12). Genal angles rounded, spineless. Narrow marginal rim preserved on sides of cephalon. One cephalic appendage pair preserved at posterior end of cephalon, partly overlapped by cephalic shield and oriented posteriorly. Partial left antennule appears to be preserved.

Trunk elongated, suboval in outline, 4.9 mm length, 3.8 mm at widest point 1.6 mm from anterior end. Median keel apparent and appears to run entire length of pygidium, 0.4 mm at widest point. Faint marginal rim, 0.2 mm wide, bordering pygidium.

Three appendage pairs apparent on each side of specimen with same morphology as preserved cephalic appendages; right side appears to preserve exopods in addition to endopods. These angled posteriorly, with those on left side more completely preserved. Longest limb, occurring most posteriorly on left side, 1.7 mm length, 0.2 mm at its widest point.

Material.—One specimen in dorsal view (IMNH 555/1725).

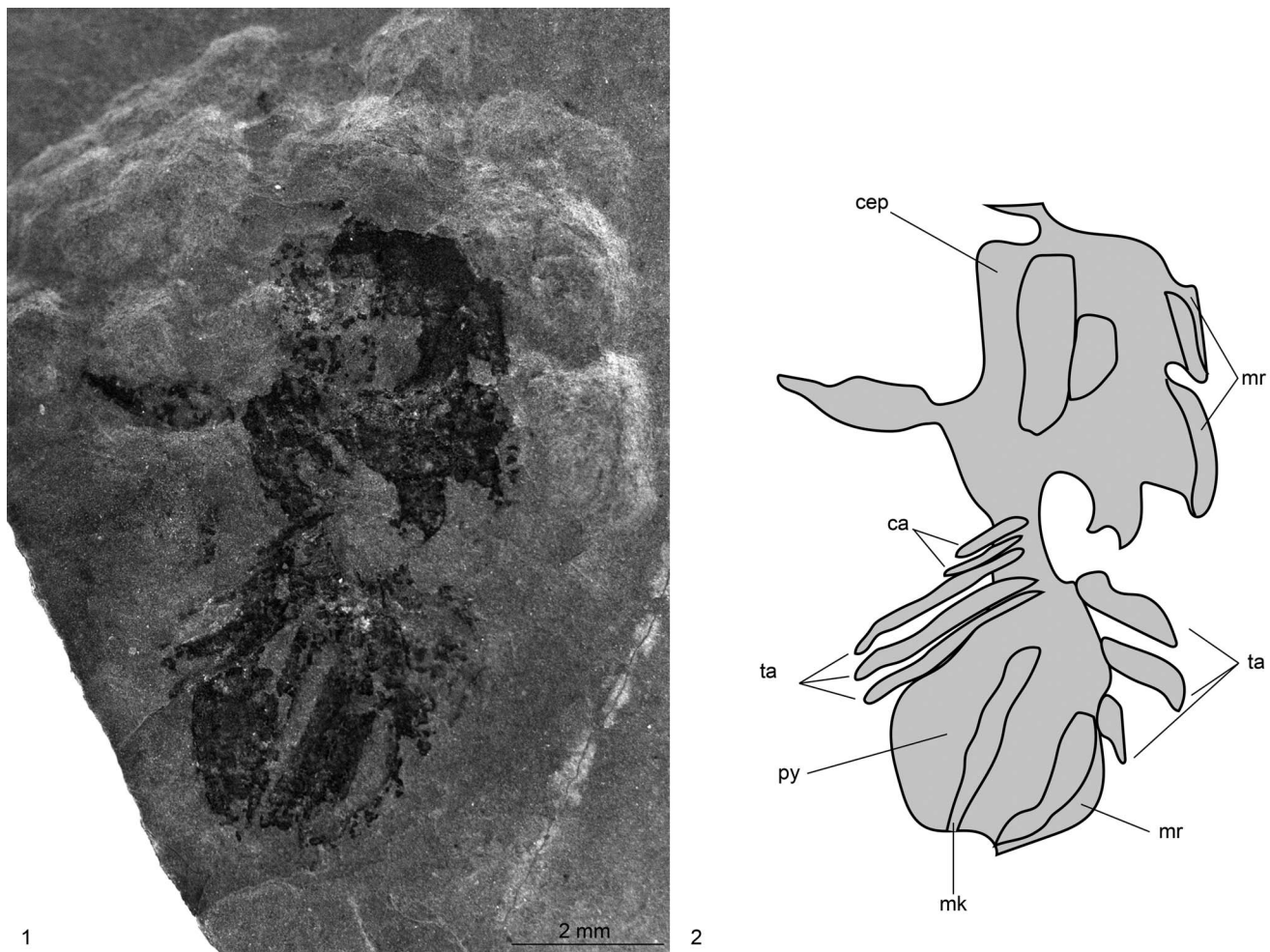


Figure 12. *Naraoia?* sp. indet. (IMNH 555/1725), collected by L.J. Krumenacker from the Two-Mile Canyon locality, Spence Shale Member, Langston Formation (Cambrian: Wuliuan), Idaho, USA: (1, 2) specimen in dorsal view and explanatory drawing. ca, cephalic appendages; cep, cephalon; mk, median keel; mr, marginal rim; py, pygidium; ta, thoracic appendages.

IDENTIFIED SPECIMENS IN MUSEUM COLLECTIONS

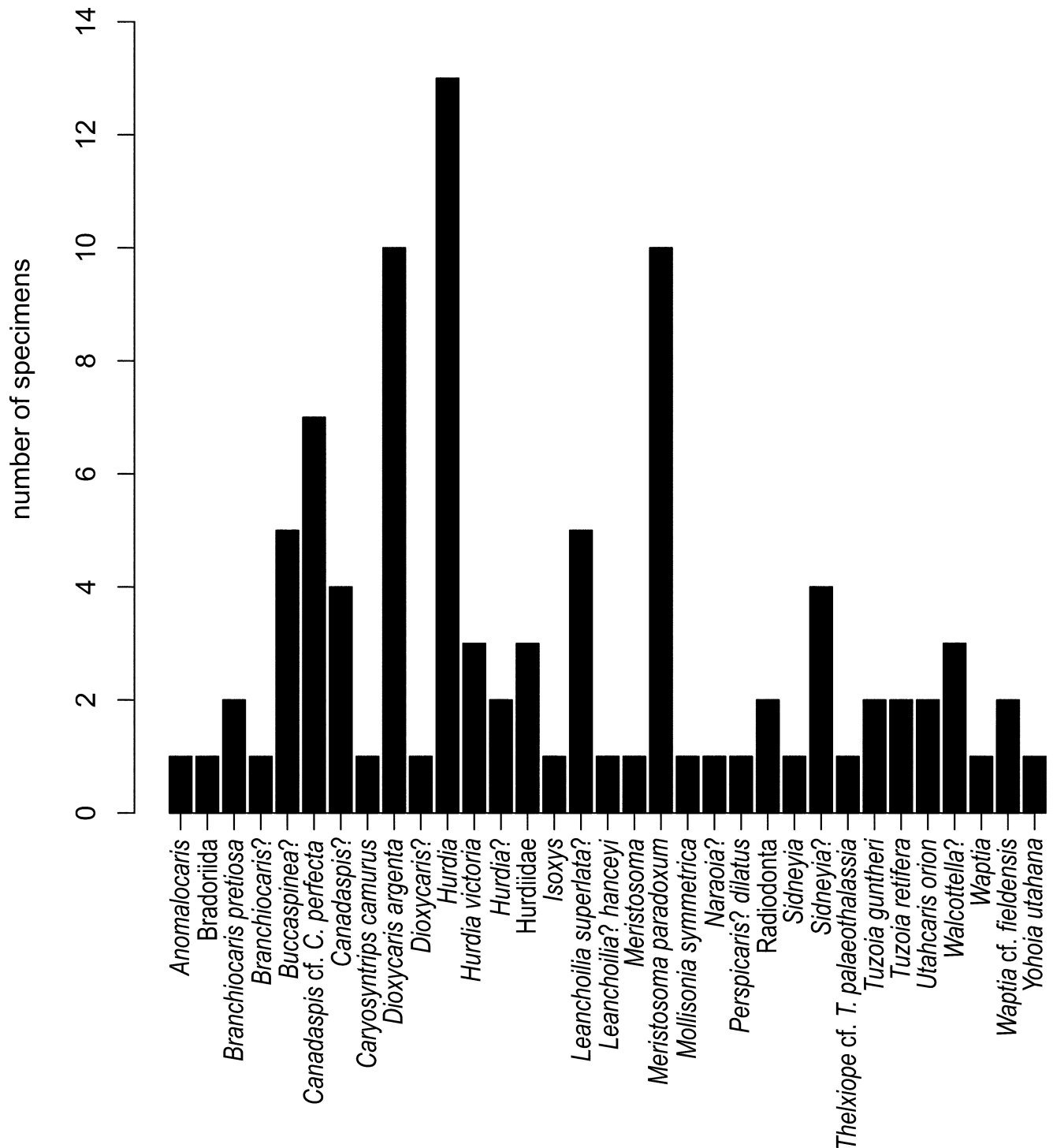


Figure 13. Identified soft-bodied arthropods in the IMNH, KUMIP, MCZ, ROM, USNM, and YPM Spence Shale collections by specimen counts.

Remarks.—Preservation of this specimen is poor, and it appears to be a molt because the left part of the cephalon is partially broken off. The specimen preserves sufficient anatomical detail—including the subequally divided dorsal section, the single transverse articulation between the cephalon and the

trunk, and the narrow marginal rim of the cephalon—that it can be attributed to *Naraoia?* sp. indet. The specimen is considered to likely belong to *Naraoia* also based on the dorsal carapace being divided into two subequal parts that are separated by a single transverse articulation.

Discussion

Panarthropods are by far the most diverse group of animals in the Spence Shale and the new material adds 10 species, bringing the total diversity to 67 species. This makes the Spence Shale the second most diverse panarthropod fauna of the Cambrian of Laurentia, only surpassed by the Burgess Shale of Canada. Unsurprisingly, the most abundant and diverse panarthropods in the Spence Shale are radiodonts and bivalved panarthropods, but the distribution of these two groups differs. So far, radiodonts are restricted to the shales of the Wellsville Mountains, whereas bivalved panarthropods are also found at the High Creek and Spence Gulch localities, in shallower water carbonates (Maxey, 1958; Liddell et al., 1997; Kimmig et al., 2019b; unpublished data, Kimmig, 2021). This difference in distribution could have several explanations: (1) it might be that hurdiid radiodonts preferred deeper-water environments, an explanation indeed offered for their rarity in early Cambrian deposits (Wu et al., 2022); (2) there could be taphonomic factors that allowed radiodonts to be preserved in the Wellsville Mountains strata that were not present at other localities (Whitaker et al., 2022); or (3) this could be due to collection biases, because the Wellsville Mountains localities have been extensively excavated, whereas the other localities have not been sampled to the same extent (Whitaker and Kimmig, 2020). This difference in distribution also applies in general to the abundance of panarthropod and other species in the Spence Shale, because the Wellsville Mountain localities, especially Antimony Canyon and Miners Hollow, are the only known localities for many of the species described (Conway Morris et al., 2015; Legg and Pates, 2017; Kimmig et al., 2019b; Whitaker and Kimmig, 2020).

The soft-bodied panarthropod fauna was previously thought to be limited to the Spence Shale in the Wellsville Mountains and the material presented herein demonstrates that this is definitely not the case. It is now apparent that soft-bodied panarthropods can be preserved in all of the environments present in the Spence Shale, from the shallower-water carbonates of High Creek and Spence Gulch, to the more distal deposits of Two Mile Canyon.

Conclusions

The Spence Shale preserves a unique panarthropod fauna in the Miaolingian of Laurentia, because radiodonts are the most abundant soft-bodied panarthropods, comprising approximately one-third of the identified specimens (Fig. 13). Most of these specimens are hurdiids. Additionally, the Spence Shale not only preserves arthropod species that are found in the Wuliuan-age Burgess Shale of Canada, i.e., *Branchiocaris pretiosa*, *Dioxycaris argenta*, *Thelxiope* cf. *T. palaeothalassia*, and *Tuzoia retifera*, but also species that are otherwise confined to the Drumian deposits of Laurentia, i.e., *Buccaspinea cooperi* Pates et al., 2021a and *Tuzoia guntheri*.

The new panarthropod specimens described herein also provide additional information on the distribution of soft-bodied taxa in the Spence Shale and suggest that other exposures beyond those currently sampled might also preserve soft-bodied

fossils. For instance, most of the collecting in the Spence Shale has been done in the Wellsville Mountains (Whitaker and Kimmig, 2020), and thus, the majority of soft-bodied fossils are known from this region (Kimmig et al., 2019b; Whitaker and Kimmig, 2020). It might be that much of the diversity of the Spence Shale remains to be discovered, and species currently known from one or a few specimens—e.g., *Armillimax* Kimmig and Selden, 2021, *Shaihuludia* Kimmig et al., 2023, *Siphusauctum* O'Brien and Caron, 2012 (see Kimmig et al., 2017), *Utahscolex* Whitaker et al., 2020, and *Totiglobus* Bell and Sprinkle, 1978 (see Wen et al., 2019b)—might be more abundant than previously thought.

Acknowledgments

We would like to thank J. Cundiff (MCZ), C. Green (MCZ), S. Losso (Harvard University), and S. Butts (YPM) for taking and providing pictures of Spence panarthropods in their collections. N. López Carranza (KUMIP) is thanked for accessioning material. We thank J. Ortega-Hernández (MCZ) for use of photography equipment. J. Cundiff (MCZ) provided curatorial support for the loan of radiodont specimens. We also thank the U.S. Department of Agriculture Forest Service for permits, and N. López Carranza and L. Schlenker (KUMIP) for assistance obtaining these, J. Young for access to his land, and J. Skabelund for access to his lease. L. Gunther and P. Reese are thanked for collecting and donating specimens. JK was supported by a Paleontological Society Arthur James Boucot Research Grant, a Western Interior Paleontological Society Karl Hirsch Memorial Grant, and an Association of Earth Science Clubs of Greater Kansas City Research Grant. AW was supported by an Association of Earth Science Clubs of Greater Kansas City Research Grant, a University of Kansas Biodiversity Institute Panorama Grant, a Geological Society of America Graduate Student Research Grant, and a Paleontological Society Kenneth E. and Annie Caster Student Research Award. SP was supported by a Herchel Smith Postdoctoral Fellowship. We thank D. Fu and an anonymous reviewer, associate editor T. Hegna, editor O. Vinn, and managing editor J. Kastigar for their comments and help that significantly improved the manuscript.

Declaration of competing interests

The authors declare that no competing interests exist.

Data availability statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.fn2z34v0h>.

References

- Aria, C., and Caron, J.-B., 2017, Burgess Shale fossils illustrate the origin of the mandibulate body plan: *Nature*, v. 545, p. 89–92, <https://doi.org/10.1038/nature22080>.
- Bell, B.M., and Sprinkle, J., 1978, *Totiglobus*, an unusual new edrioasteroid from the middle Cambrian of Nevada: *Journal of Paleontology*, v. 52, p. 243–266.

- Briggs, D.E.G., 1976, *The arthropod Branchiocaris n. gen., middle Cambrian, Burgess Shale, British Columbia*: Geological Survey of Canada, Bulletin 264, 29 p.
- Briggs, D.E.G., 1977, Bivalved arthropods from the Cambrian Burgess Shale of British Columbia: *Palaeontology*, v. 20, p. 595–621.
- Briggs, D.E.G., 1978, The morphology, mode of life, and affinities of *Canadaspis perfecta* (Crustacea: Phyllocarida), middle Cambrian, Burgess Shale, British Columbia: *Philosophical Transactions of the Royal Society of London B*, v. 281, p. 439–487.
- Briggs, D.E.G., and Robison, R.A., 1984, Exceptionally preserved nontrilobite arthropods and *Anomalocaris* from the middle Cambrian of Utah: University of Kansas Paleontological Contributions, v. 111, 23 p.
- Briggs, D.E.G., Lieberman, B.S., Hendricks, J.R., Halgedahl, S.L., and Jarrard, R.D., 2008, Middle Cambrian arthropods from Utah: *Journal of Paleontology*, v. 82, p. 238–254, <https://doi.org/10.1666/06-086.1>.
- Brooks, H.K., and Caster, K.E., 1956, *Pseudoarctolepis sharpi*, n. gen., n. sp. (Phyllocarida), from the Wheeler Shale (middle Cambrian) of Utah: *Journal of Paleontology*, v. 31, p. 9–14.
- Caron, J.-B., and Moysiuk, J., 2021, A giant nektobenthic radiodont from the Burgess Shale and the significance of hurdiid carapace diversity: *Royal Society Open Science*, v. 8, n. 210664, <https://doi.org/10.1098/rsos.210664>.
- Caron, J.-B., Rudkin, D.M., and Milliken, S., 2004, A new Late Silurian (Pridolian) naraoid (Euarthropoda: Nektaspida) from the Bertie Formation of southern Ontario, Canada: Delayed fallout from the Cambrian explosion: *Journal of Paleontology*, v. 78, p. 1138–1145, [https://doi.org/10.1666/0022-3360\(2004\)078<1138:ANLSPN>2.0.CO;2](https://doi.org/10.1666/0022-3360(2004)078<1138:ANLSPN>2.0.CO;2).
- Chen, W.Y., Zhao, Y.L., Yang, X.L., and Wen, R.Q., 2017, *Tuzoia* Walcott, 1912 from the Cambrian ‘Tsingshutung Formation’ of Guizhou, China: *Acta Palaeontologica Sinica*, v. 56, p. 301–311.
- Clarke, J.M., 1900, Phyllopoda, Phyllocarida, in Zittel, K.A. von, ed., *Textbook of Palaeontology* (English edition): New York, Macmillan, p. 653–659.
- Collins, D., 1996, The ‘evolution’ of *Anomalocaris* and its classification in the arthropod class Dinocarida (nov.) and order Radiodonta (nov.): *Journal of Paleontology*, v. 70, p. 280–293.
- Cong, P., Ma, X., Hou, X., Edgecombe, G.D., and Strausfeld, N.J., 2014, Brain structure resolves the segmental affinity of anomalocaridid appendages: *Nature*, v. 513, p. 538–542, <https://doi.org/10.1038/nature13486>.
- Cong, P., Daley, A.C., Edgecombe, G.D., Hou, X., and Chen, A., 2016, Morphology of the radiodontan *Lyrarapax* from the early Cambrian Chengjiang biota: *Journal of Paleontology*, v. 90, p. 663–671, <https://doi.org/10.1017/jpa.2016.67>.
- Cong, P.Y., Edgecombe, G.D., Daley, A.C., Guo, J., Pates, S., and Hou, X.G., 2018, New radiodonts with gnathobase-like structures from the Cambrian Chengjiang biota and implications for the systematics of Radiodonta: *Special Papers in Palaeontology*, v. 4, p. 605–621, <https://doi.org/10.1002/spp2.1219>.
- Conway Morris, S., and Robison, R.A., 1988, More soft-bodied animals and algae from the middle Cambrian of Utah and British Columbia: *University of Kansas Paleontological Contributions*, v. 122, 48 p.
- Conway Morris, S., Selden, P.A., Gunther, G., Jamison, P.G., and Robison, R.A., 2015, New records of Burgess Shale-type taxa from the middle Cambrian of Utah: *Journal of Paleontology*, v. 89, p. 411–423, <https://doi.org/10.1017/jpa.2015.26>.
- Daley, A.C., and Bergström, J., 2012, The oral cone of *Anomalocaris* is not a classic ‘Peytoia’: *Naturwissenschaften*, v. 99, p. 501–504, <https://doi.org/10.1007/s00114-01200910-8>.
- Daley, A.C., and Budd, G.E., 2010, New anomalocaridid appendages from the Burgess Shale, Canada: *Palaeontology*, v. 53, p. 721–738, <https://doi.org/10.1111/j.1475-4983.2010.00955.x>.
- Daley, A.C., and Edgecombe, G.D., 2014, Morphology of *Anomalocaris canadensis* from the Burgess Shale: *Journal of Paleontology*, v. 88, p. 68–91, <https://doi.org/10.1666/13-067>.
- Daley, A.C., Budd, G.E., and Caron, J.-B., 2013, Morphology and systematics of the anomalocaridid arthropod *Hurdia* from the middle Cambrian of British Columbia and Utah: *Journal of Systematic Palaeontology*, v. 11, p. 743–787, <https://doi.org/10.1080/14772019.2012.732723>.
- Endo, R., and Resser, C.E., 1937, The Sinian and Cambrian formations and fossils of southern Manchoukuo: *Bulletin of the Manchurian Science Museum*, v. 1, p. 1–406.
- Foster, J.R., and Gaines, R.R., 2016, Taphonomy and paleoecology of the ‘middle’ Cambrian (Series 3) formations in Utah’s West Desert: Recent finds and new data, in Comer, J.B., Inkenbrandt, P.C., Krahulec, K.A., and Pinnell, M.L., eds., *Resources and Geology of Utah’s West Desert*: Utah Geological Association, Publications, v. 45, p. 291–336.
- Glaessner, M.F., 1979, Lower Cambrian Crustacea and annelid worms from Kangaroo Island, South Australia: *Alcheringa*, v. 3, p. 21–31.
- Gürich, G., 1929, *Silesiacaris* von Leipe und die Phyllocariden überhaupt: *Mitteilungen aus dem Mineralogisch-geologischen Staatsinstitut*, v. 11, p. 21–90.
- Heymons, R., 1901, Die Entwicklungsgeschichte der Scolopender: *Zoologica*, v. 33, p. 1–244.
- Hinz-Schallreuter, I., 1993, Cambrian ostracodes mainly from Baltoscandia and Morocco: *Archiv für Geschiebekunde*, v. 1, p. 385–448.
- Hou, X., and Bergström, J., 1997, Arthropods of the lower Cambrian Chengjiang fauna, southwest China: *Fossils and Strata*, v. 45, 116 p.
- Hou, X.-G., Siveter, D.J., Siveter, D.J., Aldridge, R.J., Cong, P.-Y., Gabbott, S.E., Ma, X.-Y., Purnell, M.A., and Williams, M., 2017, *The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life* (second edition): New York, Wiley, 316 p., <https://doi.org/10.1002/9781118896372>.
- Izquierdo-López, A., and Caron, J.-B., 2022, The problematic Cambrian arthropod *Tuzoia* and the origin of mandibulates revisited: *Royal Society Open Science*, v. 9, n. 220933, <https://doi.org/10.1098/rsos.220933>.
- Kimmig, J., 2021, Burgess Shale Fauna, in Elias, S., and Alderton, D., eds., *Encyclopedia of Geology* (second edition): Oxford, UK, Elsevier, p. 576–582.
- Kimmig, J., and Pratt, B.R., 2015, Soft-bodied biota from the middle Cambrian (Drumian) Rockslide Formation, Mackenzie Mountains, northwestern Canada: *Journal of Paleontology*, v. 89, p. 51–71, <https://doi.org/10.1017/jpa.2014.5>.
- Kimmig, J., and Pratt, B.R., 2016, Taphonomy of the middle Cambrian (Drumian) Ravens Throat River Lagerstätte, Rockslide Formation, Mackenzie Mountains, Northwest Territories, Canada: *Lethaia*, v. 49, p. 150–169, <https://doi.org/10.1111/let.12135>.
- Kimmig, J., and Pratt, B.R., 2018, Coprolites in the Ravens Throat River Lagerstätte of northwestern Canada: Implications for the middle Cambrian food web: *Palaios*, v. 33, p. 125–140, <https://doi.org/10.2110/palo.2017.038>.
- Kimmig, J., and Selden, P.A., 2021, A new shell-bearing organism from the Cambrian Spence Shale of Utah: *Palaeoworld*, v. 30, p. 220–228, <https://doi.org/10.1016/j.palwor.2020.05.003>.
- Kimmig, J., and Strotz, L.C., 2017, Coprolites in mid-Cambrian (Series 2–3) Burgess Shale-type deposits of Nevada and Utah and their ecological implications: *Bulletin of Geosciences*, v. 92, p. 297–309, <https://doi.org/10.3140/bull.geosci.1667>.
- Kimmig, J., Strotz, L.C., and Lieberman, B.S., 2017, The stalked filter feeder *Siphosuctum lloydguntheri* n. sp. from the middle Cambrian (Series 3, Stage 5) Spence Shale of Utah: Its biological affinities and taphonomy: *Journal of Paleontology*, v. 91, p. 902–910, <https://doi.org/10.1017/jpa.2017.57>.
- Kimmig, J., Meyer, R.C., and Lieberman, B.S., 2019a, *Herpetogaster* from the early Cambrian of Nevada (Series 2, Stage 4) and its implications for the evolution of deuterostomes: *Geological Magazine*, v. 156, p. 172–178, <https://doi.org/10.1017/S0016756818000389>.
- Kimmig, J., Strotz, L.C., Kimmig, S.R., Egenhoff, S.O., and Lieberman, B.S., 2019b, The Spence Shale Lagerstätte: An important window into Cambrian biodiversity: *Journal of the Geological Society*, v. 176, p. 609–619, <https://doi.org/10.1144/jgs2018-195>.
- Kimmig, J., LaVine, R.J., Schiffbauer, J.D., Egenhoff, S.O., Shelton, K.L., and Leibach, W.W., 2023, Annelids from the Cambrian (Wuliuan Stage, Miaolingian) Spence Shale Lagerstätte of northern Utah, USA: *Historical Biology*, <https://doi.org/10.1080/08912963.2023.2196685>.
- Kühl, G., Briggs, D.E.G., and Rust, J., 2009, A great-appendage arthropod with a radial mouth from the Lower Devonian Hunsrück Slate, Germany: *Science*, v. 323, p. 771–773, <https://doi.org/10.1126/science.1166586>.
- Lankester, E.R., 1904, The structure and classification of Arthropoda: *Quarterly Journal of Microscopical Science*, v. 47, p. 523–582.
- Legg, D.A., and Pates, S., 2017, A restudy of *Utahcaris orion* (Euarthropoda) from the Spence Shale (middle Cambrian, Utah, USA): *Geological Magazine*, v. 154, p. 181–186, <https://doi.org/10.1017/S0016756816000789>.
- Leibach, W.W., Lerosey-Aubril, R., Whitaker, A.F., Schiffbauer, J.D., and Kimmig, J., 2021, First palaeoscolecid from the Cambrian (Drumian, Miaolingian) Marjum Formation of western Utah, USA: *Acta Palaeontologica Polonica*, v. 66, p. 663–678, <https://doi.org/10.4202/app.00875.2021>.
- Lerosey-Aubril, R., and Pates, S., 2018, New suspension-feeding radiodont suggests evolution of microplanktivory in Cambrian micronekton: *Nature Communications*, v. 9, n. 3774, <https://doi.org/10.1038/s41467-018-06229-7>.
- Lerosey-Aubril, R., Hegna, T.A., Babcock, L.E., Bonino, E., and Kier, C., 2014, Arthropod appendages from the Weeks Formation Konservat-Lagerstätte: New occurrences of anomalocaridids in the Cambrian of Utah, USA: *Bulletin of Geosciences*, v. 89, p. 269–282, <https://doi.org/10.3140/bull.geosci.1442>.
- Lerosey-Aubril, R., Gaines, R.R., Hegna, T.A., Ortega-Hernández, J., Van Roy, P., Kier, C., and Bonino, E., 2018, The Weeks Formation Konservat-Lagerstätte and the evolutionary transition of Cambrian marine life: *Journal of the Geological Society*, v. 175, p. 705–715, <https://doi.org/10.1144/jgs2018-042>.
- Lerosey-Aubril, R., Kimmig, J., Pates, S., Skabelund, J., Weug, A., and Ortega-Hernández, J., 2020a, New exceptionally preserved panarthropods from the Drumian Wheeler Konservat-Lagerstätte of the House Range of Utah: *Papers in Palaeontology*, v. 6, p. 501–531, <https://doi.org/10.1002/spp2.1307>.

- Lerosey-Aubril, R., Skabelund, J., and Ortega-Hernández, J. 2020b, Revision of the mollisoniid chelicerate(?) *Thelxiope*, with a new species from the middle Cambrian Wheeler Formation of Utah: PeerJ, v. 8, n. e8879, <https://doi.org/10.7717/peerj.8879>.
- Liddell, W.D., Wright, S.H., and Brett, C.E., 1997, Sequence stratigraphy and paleoecology of the middle Cambrian Spence Shale in northern Utah and southern Idaho: Brigham Young University Geology Studies, v. 42, p. 59–78.
- Lieberman, B.S., 2003, A new soft-bodied fauna: The Pioche Formation of Nevada: Journal of Paleontology, v. 77, p. 674–690, [https://doi.org/10.1666/0022-3360\(2003\)077<0674:ANSFTP>2.0.CO;2](https://doi.org/10.1666/0022-3360(2003)077<0674:ANSFTP>2.0.CO;2).
- Lieberman, B.S., Kurkewicz, R., Shinogle, H., Kimmig, J., and MacGabhann, B.A., 2017, Disc-shaped fossils resembling porpitiids (Cnidaria: Hydrozoa) from the early Cambrian (Series 2: Stage 4) of western U.S.A.: PeerJ, v. 5, n. e3312, <https://doi.org/10.7717/peerj.3312>.
- Liu, J., Lerosey-Aubril, R., Steiner, M., Dunlop, J.A., Shu, D., and Paterson, J.R., 2018, Origin of raptorial feeding in juvenile euarthropods revealed by a Cambrian radiodont: National Science Review, v. 5, p. 863–869, <https://doi.org/10.1093/nsr/nwy057>.
- Luo, H.L., Fu, X.P., Hu, S.X., Li, Y., Chen, L.Z., You, T., and Liu, Q., 2006, New bivalved arthropods from the early Cambrian Guanshan fauna in the Kunming and Wuding area: Acta Palaeontologica Sinica, v. 45, p. 460–472.
- Ma, X., Edgecombe, G.D., Legg, D.A., and Hou, X., 2014, The morphology and phylogenetic position of the Cambrian lobopodian *Diania cactiformis*: Journal of Systematic Palaeontology, v. 12, p. 445–457, <https://doi.org/10.1080/14772019.2013.770418>.
- Mángano, M.G., 2011, Trace-fossil assemblages in a Burgess Shale-type deposit from the Stephen Formation at Stanley Glacier, Canadian Rocky Mountains: Unraveling ecologic and evolutionary controls: Palaeontographica Canadiana, v. 31, p. 89–118.
- Mángano, M.G., Bromley, R.G., Harper, D.A.T., Nielsen, A.T., Smith, M.P., and Vinther, J., 2012, Nonbiomineralized carapaces in Cambrian seafloor landscapes (Sirius Passet, Greenland): Opening a new window into early Phanerozoic benthic ecology: Geology, v. 40, p. 519–522, <https://doi.org/10.1130/G32853.1>.
- Maxey, G.B., 1958, Lower and middle Cambrian stratigraphy in northern Utah and southeastern Idaho: Geological Society of America Bulletin, v. 69, p. 647–688.
- Mayers, B., Aria, C., and Caron, J.-B., 2019, Three new naraoid species from the Burgess Shale, with a morphometric and phylogenetic reinvestigation of Naraoidae: Palaeontology, v. 62, p. 19–50, <https://doi.org/10.1111/pala.12383>.
- Moyssiuk, J., and Caron, J.-B., 2019, A new hurdiid radiodont from the Burgess Shale evinces the exploitation of Cambrian infaunal food sources: Proceedings of the Royal Society B, Biological Sciences, v. 286, n. 20191079, <https://doi.org/10.1098/rspb.2019.1079>.
- Nanglu, K., Caron, J.B., and Gaines, R.R., 2020, The Burgess Shale paleocommunity with new insights from Marble Canyon, British Columbia: Paleobiology, v. 46, no. 1, p. 58–81, <https://doi.org/10.1017/pab.2019.42>.
- Nielsen, C., 1995, Animal Evolution: Interrelationships of the Living Phyla: Oxford, UK, Oxford University Press, 402 p.
- O'Brien, L.J., and Caron, J.-B., 2012, A new stalked filter-feeder from the middle Cambrian Burgess Shale, British Columbia, Canada: PLoS ONE, v. 7, n. e29233, <https://doi.org/10.1371/journal.pone.0029233>.
- Pan, J., 1957, On the discovery of Homopoda from South China: Acta Palaeontologica Sinica, v. 5, p. 523–526.
- Paterson, J.R., García-Bellido, D.C., Jago, J.B., Gehling, J.G., Lee, M.S.Y., and Edgecombe, G.D., 2016, The Emu Bay Shale Konservat-Lagerstätte: A view of Cambrian life from East Gondwana: Journal of the Geological Society, London, v. 173, p. 1–11, <https://doi.org/10.1144/jgs2015-083>.
- Pates, S., Daley, A.C., and Lieberman, B.S., 2018a, Hurdiid radiodontans from the middle Cambrian (Series 3) of Utah: Journal of Paleontology, v. 92, p. 99–113, <https://doi.org/10.1017/jpa.2017.11>.
- Pates, S., Daley, A.C., and Ortega-Hernández, J., 2018b, Reply to comment on 'Aysheaia prolata from the Utah Wheeler Formation (Drumian, Cambrian) is a frontal appendage of the radiodontan *Stanleycaris*' with the formal description of *Stanleycaris*: Acta Palaeontologica Polonica, v. 63, p. 105–110, <https://doi.org/10.4202/app.00443.2017>.
- Pates, S., Daley, A.C., and Butterfield, N.J., 2019, First report of paired ventral endites in a hurdiid radiodont: Zoological Letters, v. 5, n. e18, <https://doi.org/10.1186/s40851-019-0132-4>.
- Pates, S., Lerosey-Aubril, R., Daley, A.C., Kier, C., Bonino, E., and Ortega-Hernández, J., 2021a, The diverse radiodont fauna from the Marjum Formation of Utah, USA (Cambrian: Drumian): PeerJ, v. 9, n. e10509, <https://doi.org/10.7717/peerj.10509>.
- Pates, S., Daley, A.C., Edgecombe, G.D., Cong, P. and Lieberman, B.S., 2021b, Systematics, preservation and biogeography of radiodonts from the southern Great Basin, USA, during the upper Dyeran (Cambrian Series 2, Stage 4): Papers in Palaeontology, v. 7, p. 235–262, <https://doi.org/10.1002/spp2.1277>.
- Peng, J., Zhao, Y., and Sun, H., 2012, Discovery and significance of *Naraoia* from the Qiangdongian (lower Cambrian) Balang formation, eastern Guizhou, South China: Bulletin of Geosciences, v. 87, p. 143–150, <https://doi.org/10.3140/bull.geosci.1231>.
- R Core Team, 2022, R: A language and environment for statistical computing: Vienna, R Foundation for Statistical Computing, <https://www.r-project.org/>.
- Raymond, P.E., 1920, The appendages, anatomy, and relationships of trilobites: Memoirs of the Connecticut Academy of Arts and Sciences, v. 7, p. 1–169.
- Raymond, P.E., 1935, *Leancoilia* and other mid-Cambrian Arthropoda: Bulletin of the Museum of Comparative Zoology, Harvard University, v. 76, p. 205–230.
- Resser, C.E., 1929, New lower and middle Cambrian Crustacea: Proceedings of the United States National Museum, v. 76, p. 1–18.
- Robison, R.A., 1991, Middle Cambrian biotic diversity: Examples from four Utah Lagerstätten, in Simonetta, A., and Conway Morris, S., eds., The Early Evolution of Metazoa and the Significance of Problematic Taxa: Cambridge, UK, Cambridge University Press, p. 77–98.
- Robison, R.A., and Richards, B.C., 1981, Larger bivalve arthropods from the middle Cambrian of Utah: The University of Kansas Paleontological Contributions, v. 106, 28 p.
- Robison, R.A., Babcock, L.E., and Gunther, V.G., 2015, Exceptional Cambrian fossils from Utah: A window into the age of trilobites: Utah Geological Survey, Miscellaneous Publications, v. 15, p. 1–97.
- Roger, J., 1953, Sous-classe des Malacostraca, 3, in Piveteau, J., ed., Traité de Paléontologie: Paris, Masson, p. 309–378.
- Rolfé, W.D.I., 1969, Phyllocarida, in Moore, R.C., ed., Treatise on Invertebrate Paleontology, Part R, Arthropoda 4, Volume 1: Boulder, Colorado, Geological Society of America (and University of Kansas Press), p. R296–R331.
- Saleh, F., Antcliffe, J.B., Lefebvre, B., Pittet, B., Laibl, L., Peris, F.P., Lustrì, L., Gueriau, P., and Daley, A.C., 2020, Taphonomic bias in exceptionally preserved biotas: Earth and Planetary Science Letters, v. 529, n. 115873, <https://doi.org/10.1016/j.epsl.2019.115873>.
- Schneider, C.A., Rasband, W.S., and Eliceiri, K.W., 2012, NIH Image to ImageJ: 25 years of image analysis: Nature Methods, v. 9, p. 671–675, <https://doi.org/10.1038/nmeth.2089>.
- Shimer, H.W., and Shrock, R.R., 1944, Index fossils of North America: New York, John Wiley and Sons, 837 p.
- Sieveter, D.J., and Williams, M., 1997, Cambrian bradoriid and phosphatocopid arthropods of North America: Special Papers in Palaeontology, v. 57, 69 p.
- Simonetta, A.M., and Delle Cave, L., 1975, The Cambrian non-trilobite arthropods from the Burgess Shale of British Columbia: A study of their comparative morphology, taxonomy and evolutionary significance: Palaeontographica Italiana, v. 69, no. ser. 39, p. 1–37.
- Størmer, L., 1944, On the relationships and phylogeny of fossil and Recent Arachnomorpha: Skrifter Utgitt av Det Norske Videnskaps-Academi I Oslo, I, Matematisk-Naturvidenskapelig Klasse, v. 5, p. 1–158.
- Sun, Z., Zeng, H., and Zhao, F., 2020, A new middle Cambrian radiodont from North China: Implications for morphological disparity and spatial distribution of hurdiids: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 558, n. 109947, <https://doi.org/10.1016/j.palaeo.2020.109947>.
- Ulrich, E.O., and Bassler, R.S., 1931, Cambrian bivalved Crustacea of the order Conchostraca: Proceedings of the United States National Museum, v. 78, p. 1–130.
- Van Roy, P., Orr, P.J., Botting, J.P., Muir, L.A., Vinther, J., Lefebvre, B., El Hariri, K., and Briggs, D.E.G., 2010, Ordovician faunas of Burgess Shale type: Nature, v. 465, p. 215–218, <https://doi.org/10.1038/nature09038>.
- Van Roy, P., Daley, A.C., and Briggs, D.E.G., 2015, Anomalocaridid trunk limb homology revealed by a giant filter-feeder with paired flaps: Nature, v. 522, p. 77–80, <https://doi.org/10.1038/nature14256>.
- Vannier, J., Caron, J.-B., Yuan, J.-L., Briggs, D.E.G., Collins, D., Zhao, Y.-L., and Zhu, M.Y., 2007, *Tuzoia*: Morphology and lifestyle of a large bivalved arthropod of the Cambrian seas: Journal of Paleontology, v. 81, p. 445–471, <https://doi.org/10.1666/pleo05070.1>.
- Walcott, C.D., 1886, Second contribution to the studies on the Cambrian fauna of North America: Bulletin of the United States Geological Survey, v. 30, p. 1–369.
- Walcott, C.D., 1911, Cambrian geology and paleontology II: Middle Cambrian holothurians and medusa: Smithsonian Miscellaneous Collections, v. 57, p. 41–68.
- Walcott, C.D., 1912, Cambrian geology and paleontology II: Middle Cambrian Branchiopoda, Malacostraca, Trilobita, and Merostomata: Smithsonian Miscellaneous Collections, v. 57, p. 145–228.
- Walcott, C.D., 1931, Addenda to descriptions of Burgess Shale fossils: Smithsonian Miscellaneous Collections, v. 85, p. 1–46.
- Wen, R., Babcock, L.E., Peng, J., Liu, S., and Liang, B., 2019a, The bivalved arthropod *Tuzoia* from the Balang Formation (Cambrian Stage 4) of Guizhou, China, and new observations on comparative species: Papers in Palaeontology, v. 5, p. 719–742, <https://doi.org/10.1002/spp2.1262>.

- Wen, R., Babcock, L.E., Peng, J., and Robison, R.A., 2019b, New edrioasteroid (Echinodermata) from the Spence Shale (Cambrian), Idaho, USA: Further evidence of attachment in the early evolutionary history of edrioasteroids: *Bulletin of Geosciences*, v. 94, p. 115–124, <https://doi.org/10.3140/bull.geosci.1730>.
- Whitaker, A.F., and Kimmig, J., 2020, Anthropologically introduced biases in natural history collections, with a case study on the invertebrate paleontology collections from the middle Cambrian Spence Shale Lagerstätte: *Palaeontologia Electronica*, v. 23, n. a58, <https://doi.org/10.26879/1106>.
- Whitaker, A.F., Jamison, P.G., Schiffbauer, J.D., and Kimmig, J., 2020, Re-description of the Spence Shale palaeoscolecid in light of new morphological features with comments on palaeoscolecid taxonomy and taphonomy: *Paläontologische Zeitschrift*, v. 94, p. 661–674, <https://doi.org/10.1007/s12542-020-00516-9>.
- Whitaker, A.F., Schiffbauer, J.D., Briggs, D.E.G., Leibach, W.W., and Kimmig, J., 2022, Preservation and diagenesis of soft-bodied fossils and the occurrence of phosphate-associated rare earth elements in the Cambrian (Wuliuan) Spence Shale Lagerstätte: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 592, n. 110909, <https://doi.org/10.1016/j.palaeo.2022.110909>.
- Whiteaves, J.F., 1892, Description of a new genus and species of phyllocarid Crustacea from the middle Cambrian of Mount Stephen, B.C.: *Canadian Record of Science*, v. 5, p. 205–208.
- Wickham, H., 2016, *ggplot2: Elegant Graphics for Data Analysis*: New York, Springer-Verlag, <https://ggplot2.tidyverse.org>.
- Wu, Y., Fu, D., Ma, J., Lin, W., Sun, A., and Zhang, X., 2021a, *Houcaris* gen. nov. from the early Cambrian (Stage 3) Chengjiang Lagerstätte expanded the palaeogeographical distribution of tamisiocaridids (Panarthropoda: Radiodonta): *Paläontologische Zeitschrift*, v. 95, p. 209–221, <https://doi.org/10.1007/s12542-020-00545-4>.
- Wu, Y., Ma, J., Lin, W., Sun, A., Zhang, X., and Fu, D., 2021b, New anomalocaridids (Panarthropoda, Radiodonta) from the lower Cambrian Chengjiang Lagerstätte, Biostratigraphic and paleobiogeographic implications: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 569, n. 110333, <https://doi.org/10.1016/j.palaeo.2021.110333>.
- Wu, Y., Pates, S., Ma, J., Lin, W., Wu, Y., Zahng, X., and Fu, D., 2022, Addressing the Chengjiang conundrum: A palaeoecological view on the rarity of hurdiid radiodonts in this most diverse early Cambrian Lagerstätte: *Geosciences Frontiers*, v. 13, n. 101430, <https://doi.org/10.1016/j.gsf.2022.101430>.
- Yang, X., Kimmig, J., Zhai, D., Liu, Y., Kimmig, S.R., and Peng, S., 2021, A juvenile-rich palaeocommunity of the lower Cambrian Chengjiang biota sheds light on palaeo-boom or palaeo-bust environments: *Nature Ecology & Evolution*, v. 5, p. 1082–1090, <https://doi.org/10.1038/s41559-021-01490-4>.
- Yuan, J.-L., and Zhao, Y.-L., 1999, *Tuzoia* (bivalved arthropods) from the lower–middle Cambrian Kaili Formation of Taijiang, Guizhou: *Palaeontologica Sinica*, v. 38, supplement, p. 88–93.
- Zeng, H., Zhao, F., Yin, Z., and Zhu, M., 2018, Morphology of diverse radiodontan head sclerites from the early Cambrian Chengjiang Lagerstätte, south-west China: *Journal of Systematic Palaeontology*, v. 16, p. 1–37, <https://doi.org/10.1080/14772019.2016.1263685>.
- Zhang, W.T., and Hou, X.G., 1985, Preliminary notes on the occurrence of the unusual trilobite *Naraoia* in Asia: *Acta Paleontologica Sinica*, v. 24, p. 591–595.
- Zhang, X., Bergström, J., Bromley, R.G., and Hou, X., 2007, Diminutive trace fossils in the Chengjiang Lagerstätte: *Terra Nova*, v. 19, p. 407–412, <https://doi.org/10.1111/j.1365-3121.2007.00765.x>.
- Zhu, X., Lerosey-Aubril, R., and Ortega-Hernández, J., 2021, Furongian (Jiangshanian) occurrences of radiodonts in Poland and South China and the fossil record of the Hurdiidae: *PeerJ*, v. 9, n. e11800, <https://doi.org/10.7717/peerj.11800>.

Accepted: 27 March 2023