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Annelids from the Cambrian (Wuliuan Stage, Miaolingian) Spence Shale Lagerstätte of northern Utah, USA

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ABSTRACT

The Spence Shale Member of the Langston Formation in northern Utah and southern Idaho preserves generally non-biomineralized fossil assemblages referred to as the Spence Shale Lagerstätte. The biota of this Lagerstätte is dominated by panarthropods, both biomineralized and soft-bodied examples, but also preserves diverse infaunal organisms, including species of scalidophorans, echinoderms, lobopodians, stalked filter feeders, and various problematic taxa. To date, however, only a single annelid fossil, originally assigned to *Canadia* sp., has been described from the Spence Shale. This lone specimen and another recently collected specimen were analysed in this study using scanning electron microscopy and energy dispersive X-ray spectrometry. The previous occurrence was reassigned to *Burgessochaeta* cf. *B. setigera*. The new fossil, however, has been identified as a novel polychaete taxon, *Shaihuludia shurikeni* gen. et sp. nov., characterised by the presence of fused, bladed chaetae and a wide body. The occurrence of *Burgessochaeta* is the first outside the Burgess Shale and its vicinity, whereas *Shaihuludia shurikeni* gen. et sp. nov. adds to the diversity of annelids in the middle Cambrian and highlights the diversity of the Spence Shale Lagerstätte.

ARTICLE HISTORY

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KEYWORDS

Exceptional preservation;
worms; Burgess Shale-type
preservation; Great Basin;
Laurentia

Introduction

The Cambrian (Wuliuan Stage, Miaolingian; ca. 507.5–506 Ma) Spence Shale Lagerstätte (Spence Shale hereafter) of northeastern Utah and southeastern Idaho preserves one of the most diverse Burgess Shale-type biotas in Laurentia (Kimmig et al. 2019a; Whitaker and Kimmig 2020; Kimmig 2021). Its fauna comprises over 90 species, of which about one-third are soft-bodied (Robison et al. 2015; Kimmig et al. 2019a; Whitaker and Kimmig 2020; Whitaker et al. 2022). The soft-bodied remains are dominated by arthropods, but also include algae, cyanobacteria, deuterostomes (hemichordates; Vetulicolia), scalidophorans, and sponges. Vermiform fossils are relatively common in the Spence Shale and can be found in all outcrops, except those that record the deepest water environments (Kimmig et al. 2019a; Whitaker and Kimmig 2020; Whitaker et al. 2022). Among the identifiable worm fossils, scalidophorans are the most diverse and are represented by the palaeoscolecoid *Utahscolex ratcliffei*, as well as the well-known priapulid *Otoia prolifica*, and two species of *Selkirkia*, *S. spencei* and *S. cf. S. columbia* (Kimmig et al. 2019a; Whitaker et al. 2020; Foster et al. 2022). Other vermiform fossils include the lobopodian *Acinocricus stichus* (Conway Morris and Robison 1988; Caron J–B and Aria 2020) and the possible halkieriid *Armillimax pauljamisoni* (Kimmig and Selden 2021). Annelids, however, have proven to be extraordinarily rare. To date, only one specimen, originally assigned to *Canadia* sp. (Robison 1969), has been described.

Annelids are an extremely diverse phylum (~21,000 described species) and have conquered a variety of terrestrial, freshwater, and marine environments (Read 2019). However, their whole-body fossil record is sparse. Their soft-bodied nature typically results in rapid decay (e.g. Briggs and Kear 1993), restricting most of their

fossil occurrences to Lagerstätten-type deposits (Parry et al. 2015a, b, 2019). The oldest accepted whole-body annelids appear in the early Cambrian (Series 2; Stage 3) of China and Greenland (Conway Morris and Peel 2008; Han et al. 2019; Parry et al. 2019) and are present from this point forward in the Lagerstätten of the Cambrian (Liu et al. 2015b). They reach a peak known-diversity within the Period by the middle Cambrian, with six species from the Burgess Shale alone (Conway Morris 1979; Nanglu and Caron 2018; Parry et al. 2019). Most annelid taxa known from the Cambrian belong to the annelid stem group (Parry et al. 2016; Han et al. 2019). These organisms typically show homonymous segmentation with a single pair of head appendages and in some cases with a median antenna (Nanglu and Caron 2018; Parry et al. 2019). Crown group taxa include only the early Cambrian palaeoannelid *Dannychaeta tucolus* (Chen et al. 2020), as well as slightly older putative sipunculans (Huang et al. 2004). The latter are recovered nested within annelids in all recent analyses of annelid phylogeny using molecular sequences (Struck et al. 2007; Weigert and Bleidorn 2016). Outside of the Burgess Shale, middle Cambrian annelids are rare within Laurentian deposits. Here, we document and describe *Shaihuludia shurikeni* gen. et sp. nov., a new stem annelid from the Spence Shale, and re-assess the taxonomic placement of the Spence Shale specimen UU 1021, formerly *Canadia* sp. Additionally, we discuss the variable preservation of both specimens and other vermiform fauna of the Spence Shale.

Geological context

The Spence Shale is the middle member of the Langston Formation, conformably overlying the Naomi Peak Limestone Member and

overlain by the High Creek Limestone Member (Kimmig et al. 2019a). It is regionally extensive and crops out in northeastern Utah and southeastern Idaho at multiple exposures in the Wellsville Mountains, the Bear River Range, the Wasatch Range, and the Malad Range (Figure 1). The Spence Shale includes the upper *Mexicella mexicana* and lower *Glossopleura walcotti* trilobite biozones and has been interpreted to represent deposition in the middle to outer detrital belt of a (presently) westward-oriented carbonate platform (Robison 1991; Liddell et al. 1997; Kimmig et al. 2019a).

The specimens described herein come from two localities:

KUMIP 585569 was collected ~1 metre from the top of the Spence Shale at the High Creek locality, north of Logan, UT, in the Bear River Range (Figure 1). In the High Creek area, the upper 5 metres of the Spence Shale expose carbonate facies belts as well as

transitional siliciclastic-carbonate facies (siliciclastic mud-rich, carbonate mudstones) of a Cambrian carbonate ramp system. However, the proximal facies of this ramp, which likely consisted of packstones to grainstones (see Burchette and Wright 1992), is absent in these outcrops. The facies change up-section. Strata at the bottom of the succession are rich in marls and siliciclastic mud-rich carbonate mudstones and contain some laminae of intercalated packstones; towards the top, however, packstone becomes the dominant to exclusive lithology. The grain types also change upward: bioclasts, some brachiopod shells and muscovite flakes float in the matrix in the lower part of the succession, and peloids and echinoderms, as well as shell debris from brachiopods, compose the grain assemblage in the upper portion of the unit. All facies show significant burrowing, mostly indistinct, millimetre- to sub-millimetre in diameter, and are hard to recognise. However, the

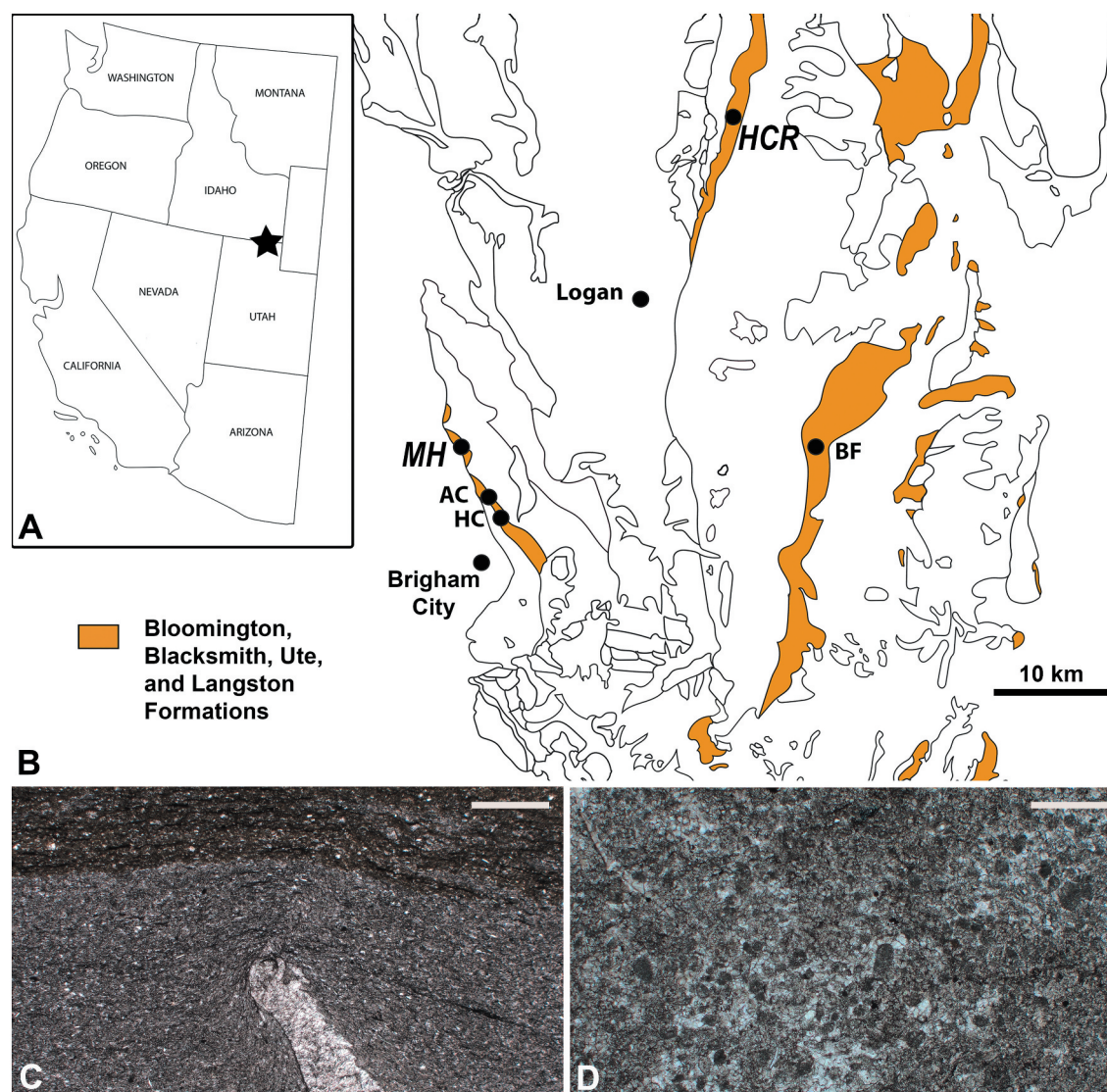


Figure 1. Geographic and geologic setting of the Spence Shale. (A) Map of the western United States showing the location of the Spence Shale (asterisk) (B) Geological map (based on the USGS state maps for Google Earth Pro) of northern Utah showing the main localities of the Spence Shale, including the two that yielded the annelids in italics. AC, Antimony Canyon; BF, Blacksmith Fork; HC, Hansen Canyon; HCR, High Creek; MH, Miners Hollow. (C) Thin section image showing the boundary between a carbonate mudstone (base) and an overlying siliciclastic mudstone (top) typical of the Spence Shale at the Miners Hollow locality. In the image, the carbonate mudstone is grey in colour while the overlying siliciclastic mudstone is dark brown. A several millimetre-long recrystallised shell, likely of a brachiopod, is present in the carbonate mudstone and is oriented vertically thereby leading to the observed distortion of the bedding. (D) Thin section image of typical peloid packstone from the Spence Shale of the High Creek area. This sample from the upper part of the unit shows characteristic peloids (slightly darker than the rest of the image, circular to oval) in a matrix and groundmass of mostly carbonate mud (greyish areas) and some carbonate cement (whitish areas). Both the grains as well as the matrix and cements are partly recrystallised. Note that the peloids are of significantly different sizes; it is therefore likely that they originated from different types (?) or sizes of organisms. Some recrystallised shell fragments are present, too (left upper corner). Scale bars: (C, D) 1 mm.

upper packstones have burrows that are several millimetres in diameter and are partly filled with carbonate mud and grains or with carbonate cement. The succession is interpreted as having been deposited in a ramp-like setting with minor relief, based on the absence of synsedimentary deformation features such as slumps. The succession, as a whole, reflects a decrease in water depth going from wackestones with intercalated packstone laminae, interpreted as middle ramp deposits at the base to peloidal packstones with biogenes and bioclasts at the top, likely representing upper ramp sediments. The progressive decrease in carbonate mud throughout the succession reflects an increase in depositional energy up-section. Based on the preserved fossil remains, there seems to be an increase in fossil abundance up-section, too, indicating an increase in biodiversity towards shallower water environments. KUMIP 585569 was recovered from an interval of siliciclastic mud-rich carbonate mudstones.

Specimen UU 1021 was collected from the float of carbonate cycle 3 of the Miners Hollow locality (Robison 1969), north of Brigham City, UT, in the Wellsville Mountains (Figure 1). The Spence Shale at Miners Hollow consists of an alternation of fine-grained siliciclastic and carbonate lithologies and belongs to the Langston Formation (Liddell et al. 1997). The lithologies exposed vary between mud-rich siliciclastic and mud-rich carbonates and represent the mid-to-deep shelf of a carbonate ramp system (see Burchette and Wright 1992), similar to the High Creek locality. Following our own and Liddell et al. (1997) stratigraphic sections, the successions consist of mostly carbonate mudstones with varying abundances of siliciclastic mud, and some intercalated carbonate beds (Figure 1). Nevertheless, the succession contains large amounts of carbonate in its basal part with some distinct siliciclastic mudstone units, a central section composed predominantly of siliciclastic mudstones, and an upper section characterised by intercalated carbonates and siliciclastic mudstones. All samples show well-developed, fine- and coarse-grained laminae, the latter often only millimetric in thickness. The sediment is always bioturbated to some degree and thoroughly burrowed in places. The basal few metres consist of carbonate-rich siliciclastic mudstones that show very well-preserved shells oriented parallel to bedding and no intercalation of coarse-grained laminae. On top of that, coarse-grained laminae become common and are present in every thin section consisting of both bioclasts of sub-millimetre size and shell fragments. This succession is overlain by mud-to-packstones with storm beds that are several millimetres thick, consisting mostly of fragments of carbonate shells and echinoderms. The succession is interpreted to record an overall shallowing of the depositional environment from a deep shelf characterised by siliciclastic mudstones to limestones both rich in carbonate mud and, in places, grains. Deposition seems to have occurred in cycles likely governed by sea-level fluctuations (Liddell et al. 1997). The environment was well oxygenised as inferred from the intact shells throughout the succession, and frequent burrowing. Deposition of the sediments must have been above the storm-wave base for much of the succession; only in the basal metres is it unclear if storm waves reached the ocean floor. UU 1021 was preserved in an interval of siliciclastic mudstones.

Material and methods

Studied material

KUMIP 585569 was collected as part of a broader study of the Spence Shale fauna by Rhiannon J. LaVine and Julien Kimmig in 2021 at the High Creek locality of the Spence Shale in northern Utah (Figure 1). This locality is less well known than the localities in the Wellsville Mountains that have produced most of the soft-bodied fossils of the Spence Shale biota (Kimmig et al. 2019a;

Whitaker and Kimmig 2020). UU 1020 was collected by Lloyd Gunther from the talus slope of the Spence Shale Member at the well-known Miners Hollow locality, and probably came from the lower 50 feet of the exposure (Robison 1969). The specimens were photographed under non-polarised light using a GIGAmacro Magnify2 robotic imaging system. High-resolution composite images of the whole specimens were created by stitching together z-stacked photographs of their parts using GIGAmacro Flow. Affinity Photo was used for basic photo manipulation (colour, contrast, and brightness) of those composite images.

Thin sections

Samples of thin sections were taken at c. 1 m intervals along the Spence Shale exposures at High Creek and Miners Hollow. Ultrathin (<20 µm) polished thin sections of the shale, and about 40 µm-thick limestone thin sections were prepared by TPS Enterprises LLC. Thin sections were analysed and photographed using a Zeiss Axioscope 5 microscope with an Axiocam 202 mono camera.

Scanning electron microscopy and energy dispersive X-ray spectroscopy analyses

The specimens were examined using scanning electron microscopy (SEM) with integrated energy dispersive X-ray spectrometry (EDS). SEM-EDS analyses were conducted using a Zeiss Sigma 500 VP variable pressure SEM with dual, co-planar Bruker XFlash EDS detectors (30 mm²), located at the X-ray Microanalysis Laboratory at the University of Missouri. Using the Fibics Incorporated ATLAS interface, large-area secondary and backscattered electron mosaics were compiled for both specimens, one of which (KUMIP) included both part and counterpart imaging. Secondary electron images (topography) were collected using a low-vacuum-specific VPGSE4 detector (variable pressure secondary electron imaging, VPSE), and backscattered images (composition) using a high-definition 5-segment backscatter detector (high-definition backscatter electron imaging, HDBSE). All imaging analyses were conducted with the following operating conditions: 15 mm ± 1 mm working distance (minor differences due to variation in sample thickness or surface topography), 20 keV beam accelerating voltage, 40 nA beam current, 25 Pa chamber pressure (low vacuum), 60 µm aperture for imaging, and 120 µm aperture for EDS analysis to improve X-ray count rate. EDS analyses were conducted with both detectors active (in tandem), aiding in the avoidance of topographic shadowing artefacts and improving X-ray count rate (>150 kilocounts per second, combined, on average).

Institutional abbreviations

KUMIP: Division of Invertebrate Palaeontology, Biodiversity Institute, University of Kansas, Lawrence, KS, USA; UU: Department of Geology & Geophysics of the University of Utah, Salt Lake City, UT, USA.

Nomenclatural acts. This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:2C4E7ECF-2088-4810-B307-36B7FAA0B090

Systematic palaeontology

Phylum Annelida Lamarck (1809) Stem group Annelida **Genus *Shaihuludia* nov.**

LSID.

urn:lsid:zoobank.org: act:A09C9E95-83F0-49EA-B3DA-02D5920EDA64

Type species

Shaihuludia shurikeni *sp. nov.* (Figures 2–4)

LSID.

urn:lsid:zoobank.org: act:3159C205-C013-4B9F-AA42-A7D493980EB5

Holotype

KUMIP 585569, part and counterpart of dorso-ventrally preserved almost complete specimen. (Figures 2, 3)

Diagnosis of genus and species by monotypy

Soft-bodied annelid with flattened fans of fused blade-like chaetae covering the dorsum along the midline.

Derivation of name

Shai-Hulud: the indigenous name for the sandworms on the planet Arrakis in the Dune novels written by Frank Herbert; *shuriken*: the

Japanese word for throwing star, for the overall shape of the blade-like chaetae.

Description

The preserved specimen is about 33 mm long, 15 mm at its widest point. It is mostly complete, but due to preservation, it is unclear whether the anterior and posterior parts of the specimen have been completely preserved. The specimen preserves four complete flattened circular fans of blade-like chaetae, and two partial ones. The fans vary in size from 9 mm to 10 mm in diameter. Several of the sclerites have longitudinal striations (Figure 3(C)). The fans overlay each other partially, appear to have covered the entire dorsum and are centred along the midline of the specimen, and are bilaterally symmetrical in dorsal view, best seen in the posterior most fan (Figure 3(B)). The individual blades are the thinnest at the pointed base and then widen until about two-thirds up the blade, where they reach their widest point (2 to 3 mm), they then thin out to a terminal point again. Each fan consists of about 6 to 8

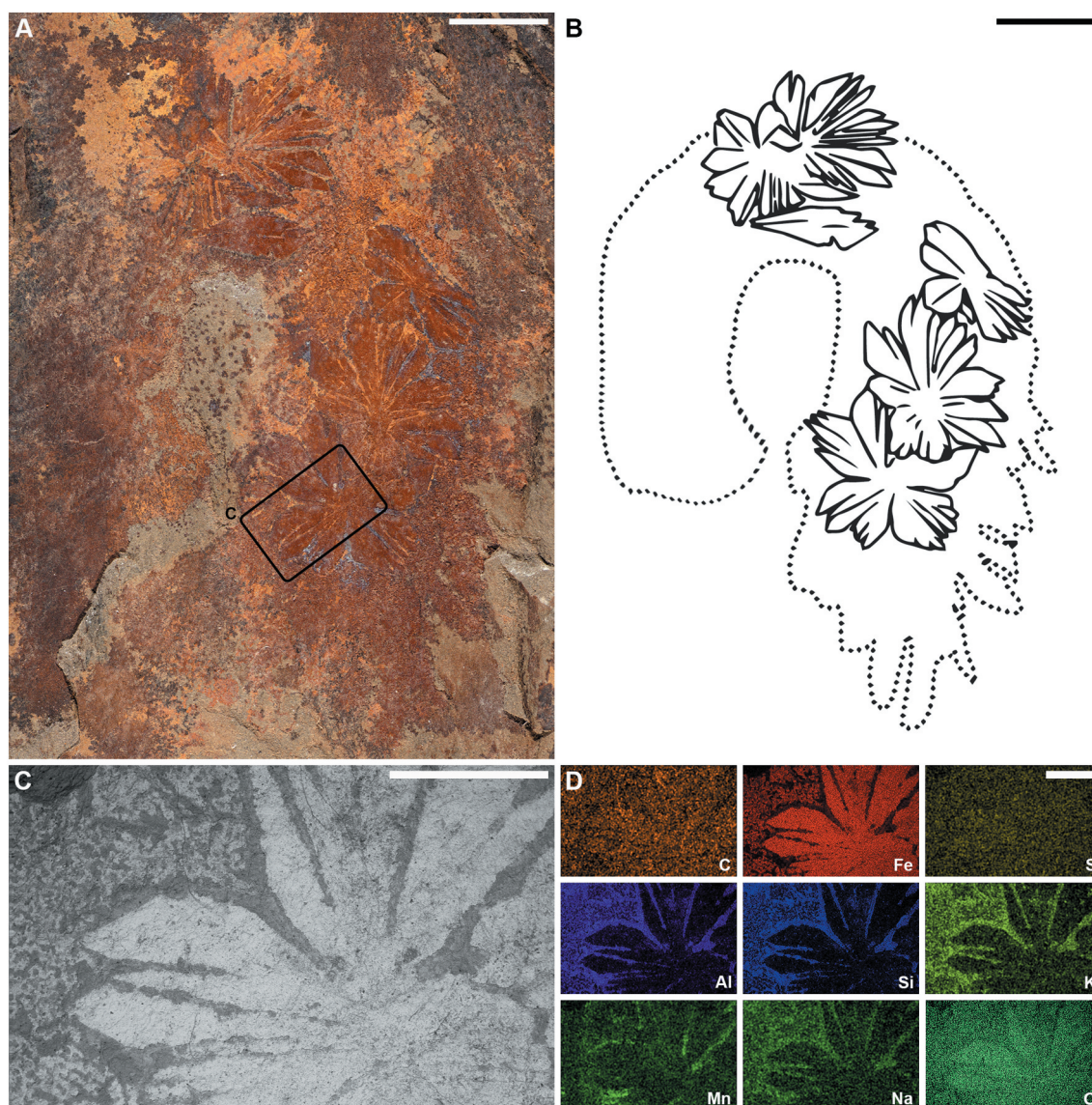


Figure 2. *Shaihuludia shurikeni* gen. et sp. nov. from the High Creek locality, Spence Shale Member of the Langston Formation (Wuliuan; Miaolingian). (A) Holotype part KUMIP 585569 complete specimen immersed in dilute ethanol under non-polarised light. (B) Interpretive drawing of A with uncertain soft tissue extent denoted with a dotted line. (C) Enlargement of boxed inset in A, showing preserved chaetae and soft-tissue. (D) SEM-EDS elemental maps of the area in A the chaetae and soft-tissue show enhanced levels of Fe, O, and some C, while the host matrix shows enhanced levels of Al, K, Mn, Na, and Si. Scale bars: (A, B) 5 mm, (C, D) 2 mm.

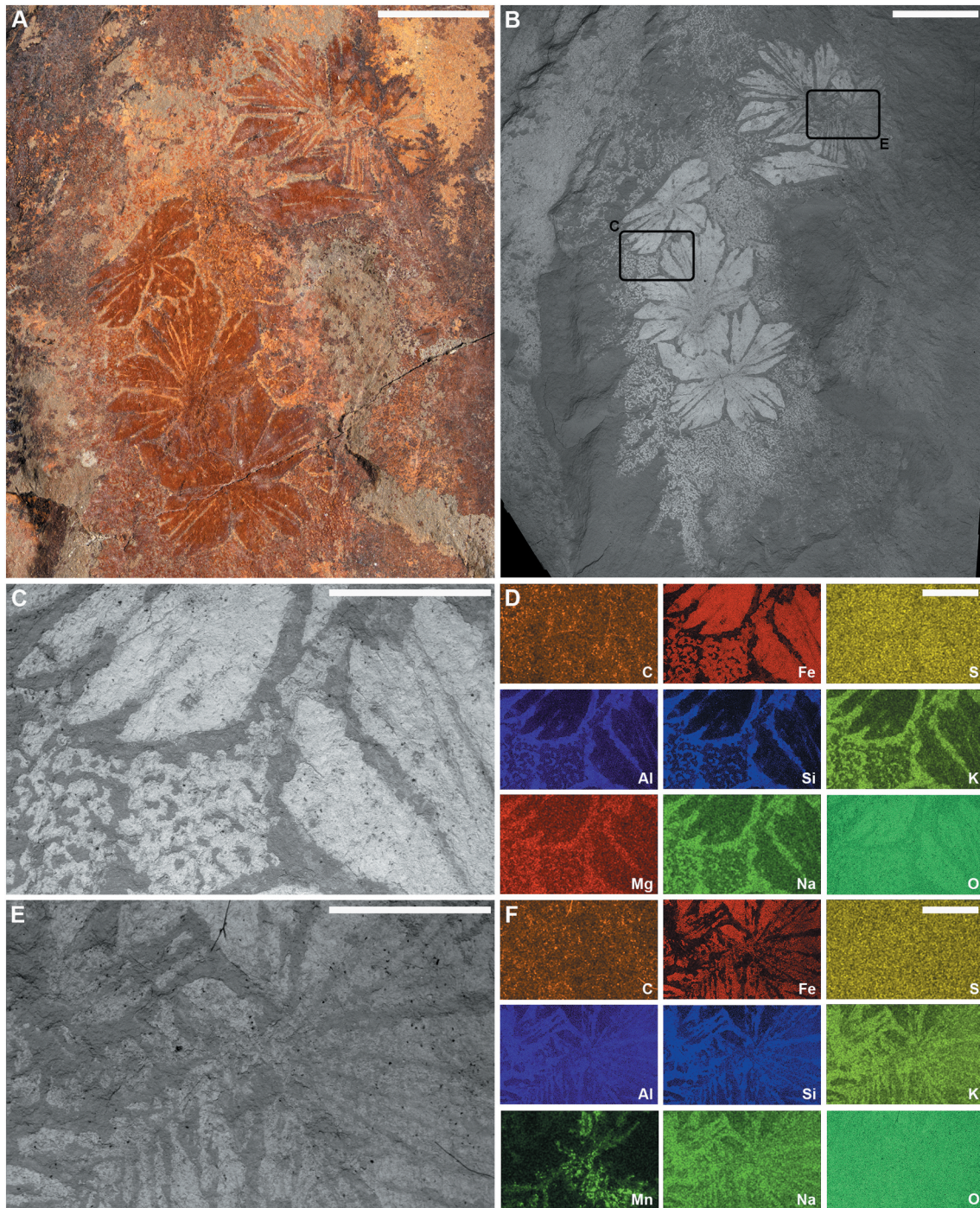


Figure 3. *Shaihuludia shurikeni* gen. et sp. nov. from the High Creek locality, Spence Shale Member of the Langston Formation (Wuliuan; Miaolingian). (A) Holotype counterpart KUMIP 585569 complete specimen immersed in dilute ethanol under non-polarised light. (B) SEM-micrograph of the counterpart of KUMIP 585569 (C) Enlargement of boxed inset in B, showing preserved chaetae with longitudinal striations and soft-tissue. (D) SEM-EDS elemental maps of the area in B the chaetae and soft-tissue show enhanced levels of Fe and O, while the host matrix shows enhanced levels of Al, K, Mg, Na, and Si. (E) Enlargement of boxed inset in B, showing the longitudinal striations of the chaetae. (F) SEM-EDS elemental maps of the area in D the chaetae and soft-tissue show enhanced levels of Fe and O, while the host matrix shows enhanced levels of Al, K, Mn, Na, and Si. Scale bars: (A, B) 5 mm, (C, D, E, F) 2 mm.

individual blades. The soft parts of the specimen are completely replaced by iron oxides and no anatomical details are identifiable. The body of the animal extends about 4 mm from under the chaetae on both sides and about 11 mm at the preserved terminal end.

Occurrence

KUMIP 585569 was collected ~1 m from the top of the Spence Shale Member at High Creek, Langston Formation, Cambrian, Miaolingian, Wuliuan, *Glossopleura walcotti* Biozone, ~ 25 km north of Logan, Cache County, Utah, USA, Sec. 3 T13N, R02E; 41.8964, -111.7118.



Figure 4. Reconstruction of *Shaihuludia shurikeni* gen. et sp. nov. from the Spence Shale of Utah. Artistic reconstruction of an adult specimen by R. LaVine.

Remarks

Flattened dorsal chaetae are known from the middle Cambrian polychaete *Canadia spinosa* (Conway Morris 1979; Butterfield 1990; Eibye-Jacobsen 2004) and the cosmopolitan early to middle Cambrian, possibly Ordovician, genus *Wiwaxia* (Butterfield 1990; Conway Morris 1985; Eibye-Jacobsen 2004; Kimmig et al. 2019b). Similarities between these chaetae in both taxa as well as in extant Chrysopetalidae led to several hypotheses surrounding their relevance to annelid origins (see review in Eibye-Jacobsen 2004), but these taxa are now referred to the annelid and mollusc stem groups, respectively. Both taxa differ in several respects from *Shaihuludia shurikeni*. Notably, the paleae (scale like chaetae) in *Canadia* are situated on a notopodial ridge normal to the body axis, with differentiation along the notopodial row (i.e. the presence of the shorter, thinner, more capillary like chaetae on both the adaxial and abaxial margins of the chaetal row, the ‘imperfect chaetae’ sensu Conway Morris 1979). In *S. shurikeni* there is no such clear differentiation, and the sclerites appear to arise from a common point of origin, indicating that they are not situated on a notopodial row but are instead in a fascicle/bundle. In *Wiwaxia* the sclerites also occur in transverse rows (Conway Morris 1979; Eibye Jacobsen 2004) and arise from common points of origin in fascicles/bundles (Zhang et al. 2015). The sclerites in *S. shurikeni* do not have a stalk in the root-blade transition zone, a feature typical of *Wiwaxia* (Butterfield 1990; Zhang et al. 2015).

The dorsal preservation of the specimen does not show any evidence of ventral chaetae on parapodia, as is the case in *Canadia*, though the absence of their preservation does not necessarily mean that they were absent in vivo. However, it cannot be completely discounted that *S. shurikeni* was a *Wiwaxia*-like animal with a single pair of dorsal chaetal rows without evidence for ventral chaetae/parapodia/notopodial chaetal rows. However, it is less likely than it being an annelid, as it is missing the stalk and *Wiwaxia*, which has been interpreted as a polychaete in the past (e.g. Butterfield 1990), is a kind of dome-like animal with numerous flat and erected sclerites.

The specimens are not of cnidarian origin, as they lack the evidence of deformation/pliability, as well as the consistency in number and arrangements of divisions that would be expected in medusae. An eldoniid origin, or Ediacaran-like discoidal fossil affinity is also unlikely, as no ridges, or circular structures are preserved; typical features of such fossils (Liu et al. 2015a; Burzynski et al. 2017; Lieberman et al. 2017; McMahan et al. 2017; Sappenfield et al. 2017; Young and Hagadorn 2020;

Whitaker et al. 2022). Additionally, several of the sclerites have longitudinal striations (Figure 3(C)).

A non-metazoan origin of the specimens, for example, whorled algae or similar, is also unlikely, but could remain a viable possibility if better preserved specimens are discovered. At present, however, a comparison to the structure and preservation of fossil cyanobacteria and macroalgae (e.g. Javaux 2007; LoDuca et al. 2017; Demoulin et al. 2019) has not yielded any potential forms that would be comparable to the sclerites of *S. shurikeni*.

It is also unlikely that the specimens represent abiotic mineral crystals or their subsequent replacements (Cloud 1973). Rosettes of various minerals can develop parallel to bedding in shales (Nuelle and Shelton 1986; Zorz 2022), such as sulphates (barite, coelestine, gypsum), carbonates (aragonite, calcite), phosphates (vivianite, wavellite), and sulphides (marcasite, pyrite). However, none of the chemical compositions of these minerals are consistent with the Fe-Mn-O chemistry determined for the specimens (Figure 2(D)). Furthermore, the features observed in the specimens display lower symmetry and a lack of well-developed euhedral crystal faces, unlike what should be observed if they were crystals or pseudomorphic replacements of them. *Shaihuludia shurikeni* also differs in shape from colonies of the Mn- and Fe-oxidising bacterium *Metallogenium personatum* to which the Precambrian *Eoastrion simplex* has been linked (Barghoorn and Tyler 1965; Hofmann 1971; Lieberman et al. 2017).

If the studied specimens instead represent casts formed by the complex dissolution and infilling of precursor abiotic minerals, they should not have preserved the finer structural details observed in these specimens (Figures 2, 3). For these reasons, we interpret the specimens to be biological in origin.

Genus *Burgessochaeta* Conway Morris (1979)

Type species

Burgessochaeta setigera Walcott (1911) from the Cambrian (Wuliuan Stage), Burgess Shale, British Columbia, Canada.

Diagnosis

Slender body. Pairs of elongated tentacles are probably arising from prostomium. Trunk with up to at least 24 segments. The trunk surface is smooth, with few details. Equant parapodial rami, paired palps and simple chaetae with bifid tips. Segment 1 ramus is slightly smaller than on the following segments. Biramous parapodia on all segments, all rami similar with uniform development along the entire body. Parapodial rami conical, without branchiae or cirri. Palps are clearly differentiated from the body segments, are not in close association with parapodia. Neuro- and notochoetae with bidentate to furcate tips. Inter-ramal spacing moderate. Straight gut with anal opening on pygidium. (following Eibye-Jacobsen 2004; Parry et al. 2015b)

Burgessochaeta cf. *B. setigera* (Walcott 1911) (Figure 5)

1969 *Canadia* sp. Robison: 1170, pl. 138, fig. 3.

1979 Polychaete gen. et sp. undetermined Conway Morris: 261, figs. 130–131.

1991 Polychaete gen. et sp. undetermined Robison: 85, fig. 6.4.

Description

The specimen is 29 mm long, has a flattened inter-parapodial trunk width of about 2 mm, and a maximum width of 6 mm including the

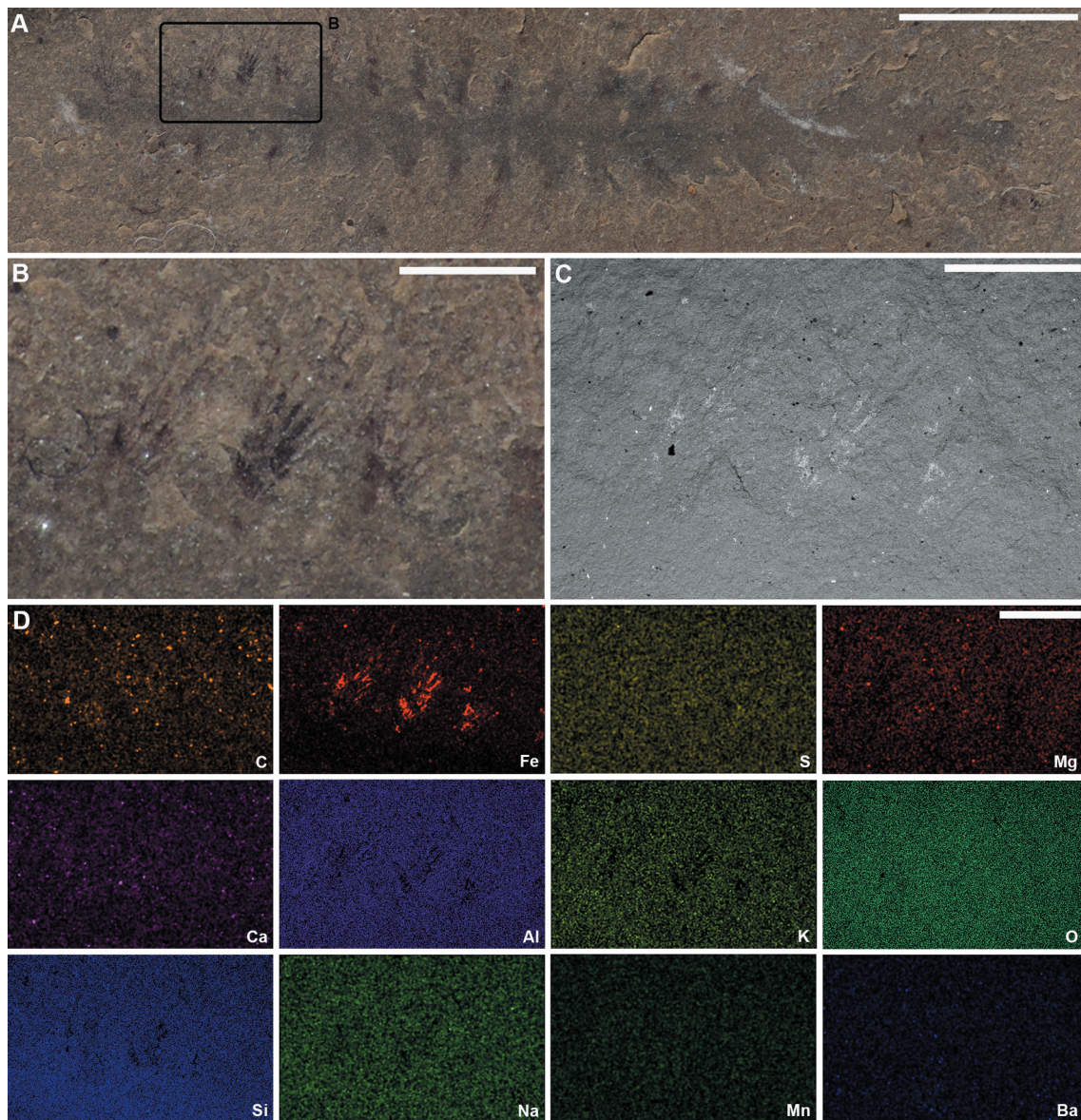


Figure 5. *Burgessochaeta* cf. *B. setigera* (Walcott 1911) from the Miners Hollow locality, Spence Shale Member of the Langston Formation (Wuliuan; Miaolingian). (A) UU 1021 complete specimen immersed in dilute ethanol under non-polarised light. (B) Enlargement of boxed inset in A, showing preserved chaetae and soft-tissue. (C) SEM micrograph of B showing preserved chaetae and soft-tissue. (D) SEM-EDS elemental maps of the area in B the chaetae and soft-tissue show enhanced levels of Fe and S, while the host matrix shows slightly enhanced levels of Al, K, Mg, Mn, Na, and Si. Scale bars: (A) 5 mm, (B, C, D) 2 mm.

parapodia. At least 21 segments can be recognised, each about 2 mm long, based on the presence of lateral pairs of relatively large parapodia. Each parapodium has a distal bundle of up to six chaetae. The chaetae are black, needle-shaped, non-jointed, and range up to 2 mm in length. Details of the prostomium are not preserved. (modified from Robison 1969)

Material

UU 1021, almost complete specimen (Figure 5).

Occurrence

UU 1021 was collected from the talus slope of the Spence Shale Member at Miners Hollow, and probably came from the lower 50 feet (~15 m) of the member (Robison 1969), Langston Formation, Cambrian, Miaolingian, Wuliuan, *Glossopleura walcotti* Biozone,

near Calls Fort, Wellsville Mountains, Box Elder County, Utah, USA, SE 1/4 Sec. 14, T10N., R02W; 41.6023, -112.0334.

Remarks

This specimen was originally assigned to *Canadia* sp. by Robison (1969) based on the 'large chaetose parapodia and general body outline', but while he refrained from assigning a species based on the preservation quality of the specimen, he mentioned that 'the needle-like chaetae of the Spence specimen' resemble those of *B. setigera*. Our investigation of the specimen, including light microscopy, SEM, and SEM-EDS analyses, support the assignment of UU 1021 to *Burgessochaeta* cf. *B. setigera* based on the shape, placement and number of the chaetae and the overall body shape, but as the anterior part of the specimen is missing, the species assignment remains tentative. When compared to *B. setigera* specimens from the Burgess Shale (e.g. Conway Morris 1979; Eibye-

Jacobsen 2004), the Spence specimens' chaetae and inter-parapodial trunk are average in size, and do not support the *Canadia* sp. assignment (Robison 1969). Additionally, the specimen is missing any dorsal scales/sclerites. The specimen was mislabelled as KUMIP 204389 in Robison (1991).

Discussion

Preservation

Spence Shale soft-bodied fossils have a preservation mode comparable to preservation types from other BST deposits, showing early taphonomic precipitation of phosphate and pyrite, maturation of carbonaceous remains to kerogen, later metamorphic alteration of phosphate to monazite, and other effects of modern weathering (e.g. oxidation of pyrite) (Whitaker et al. 2022). In the case of the herein-described annelids, however, both specimens lack a distinctive carbon signature in SEM-EDS analyses (Figure 2 (D), 3(C), 5(D)). Additionally, no discernible carbonaceous film via backscattered or secondary electron imaging can be observed (Figure 5 (C)). Using EDS, Whitaker et al. (2020) detected an elevated carbon signal associated with a Spence Shale palaeoscolecid worm fossil but here too observed no discernible carbonaceous film via backscattered or secondary electron imaging. The absence of detectable carbonaceous films or local enrichments of carbon in these new annelid fossils suggest that the elevated carbon signal in the EDS analyses arose from interstitial carbonaceous materials between sediment grains, as has previously been suggested for fossils from the Marjum Formation (Broce and Schiffbauer 2017). We suggest that the absence of a distinct carbonaceous film within these fossils may be a result of late-stage burial (after some decay), as it is not representative of soft-tissue preservation in the Spence Shale in general (Whitaker et al. 2022). Further support to this hypothesis is provided by a distinct C signature within a variety of taxa from the Spence Shale (Whitaker et al. 2022). However, organic carbon removal could have continued through diagenesis as well.

The holotype of *Shaihuludia shurikeni* (KUMIP 585569) is poorly preserved, with no visible preservation of the gut and no discernible soft-tissue features (Figures 2(A), 3(A)), as stated, and is interpreted to have died within the uppermost oxic-to-suboxic layers of sediment, allowing for efficient microbial decay of the organic carbon by oxygenic microbes or sulphate-reducing bacteria that consumed tissues and aided the precipitation of pyrite. If it had been exposed upon death, scavengers would have likely removed any potential for preservation of soft tissues. It is unlikely that the specimen was transported far or disturbed much between its death and prior to burial, given the well-preserved aligned chaetae. Both the soft tissue and the chaetae are preserved as iron oxide- and/or oxyhydroxide-weathering products of pyrite, also evidenced by the rusty red-orange colouration of the fossil. In contrast, the host matrix shows enhanced levels of Al, K, Mg, Mn, Na, and Si.

The *Burgessochaeta* cf. *B. setigera* specimen (UU 1021) is better preserved than the holotype of *Shaihuludia shurikeni*, as the soft tissue is clearly identifiable, and a partial gut tract is visible (Figure 5 (A)). Decay experiments of the extant priapulid *Priapululus caudatus* showed that labile, non-cuticular features, such as the gut, begin decaying immediately following death, and are lost in under a week of decay (Sansom 2016). But *Priapululus* in contrast to *Burgessochaeta* has a very thin cuticle and a large internal cavity filled with a fluid. *Burgessochaeta*, however, has bunches of decay-resistant chaetae and a compartmentalised body. Suggesting that *Burgessochaeta*, if buried and not disturbed by bioturbators, would have retained its original appearance for a relatively long time.

However, the missing anterior part of the specimen and only partially preserved gut tract suggest that enhanced early decay was likely, unless they were retained on the unknown counterpart. Like the holotype of *Shaihuludia shurikeni*, the soft-tissue and the chaetae are preserved as iron oxide- and/or oxyhydroxide-weathering products of pyrite, which is also fairly common in other deposits, e.g. the Chengjiang Lagerstätte (Han et al. 2019). While the fossil appears to have a carbonaceous film preserved (Figure 5(A)), it may be too thin and electron-transparent for BSE imaging if indeed present, but might result in the slight optical contrast observed (Supplement Figure 4). In contrast, the host matrix shows enhanced levels of Al, K, Mg, Mn, Na, and Si.

The Spence Shale worm fauna

The Spence Shale preserves the most diverse worm fauna in the Great Basin (Lieberman 2003; Robison et al. 2015; Leibach et al. 2021) and the richest in specimen count outside of the Weeks Formation (Lerosey-Aubril et al. 2018; Leibach et al. 2021). It is also one of the most species- and specimen-rich worm faunas in Laurentia, with the exception of the Burgess Shale (Nanglu et al. 2020), and within the Cambrian in general (e.g. García-Bellido et al. 2013; Nanglu et al. 2020; Yang et al. 2021a).

The first vermiform organisms described from the Spence Shale were six worm tubes, belonging to the priapulid worm *Selkirkia* (Resser 1939) which secreted a conical tube (Wang et al. 2021; Yang et al. 2021b). These were also the first soft-bodied organisms mentioned from the Great Basin and were the only known vermiform organisms from the Spence Shale until Robison (1969) described two 'annelids' from it. The first specimen was UU 1021, which he assigned to *Canadia* sp. and was later referred to polychaete gen. et sp. undetermined by Conway Morris (1979). The other specimen Robison described is the holotype of the palaeoscolecid *Utahscolex ratcliffi* (Whitaker et al. 2020), leaving UU 1021 as the only known polychaete from the Spence Shale. Conway Morris and Robison (1986) later also identified the priapulid *Ottoia prolifica* from the Spence Shale. In addition to the described specimens, there are dozens of unidentified 'worms' from the Spence Shale in the KUMIP collections (Broce and Schiffbauer 2017; Whitaker and Kimmig 2020). These worms likely represent scaldiphorans, though some may be decomposed annelids or other clades, similar to the interpretations for other deposits (e.g. Kimmig and Pratt 2015).

Our reinvestigation of UU 1021 demonstrates that it represents the first specimen of *Burgessochaeta* outside of the Burgess Shale vicinity and confirms Robison's (1969) suspicion that it might be *B. setigera*. Additionally, the find of *Shaihuludia shurikeni* indicates that the annelid fauna of the Spence Shale was likely more diverse than previously thought, and the underrepresentation of annelid specimens is likely due to the lack of systematic excavation of the Spence Shale (Whitaker and Kimmig 2020). This is supported by the lack of specimens from the High Creek locality in museum collections. Because of the overall appearance of *Shaihuludia shurikeni*, it might have been that similar specimens were mistaken for stellate groups of minerals by collectors in the past (Cloud 1973; Retallack 2015) and left behind in the field.

The scaldiphorans, especially *Selkirkia*, and unidentified 'worms' have been found in all Spence Shale localities apart from the deeper water shales of Oneida Narrows and Two-Mile Canyon (Kimmig et al. 2019a; Whitaker and Kimmig 2020; Foster et al. 2022), suggesting that they conquered several environments along the shelf, as the outcrops have been interpreted as ranging from shallow water carbonates to deeper shelf deposits (Kimmig et al. 2019a). This diversity of depositional environments, as well as the

abundance of specimens in the outcrops, and the quality of preservation of many of the worm fossils also support that most specimens were buried *in situ* or close to their original life-space.

While not an annelid or scalidophoran, the possible halkieriid *Armillimax pauljamisoni* (Kimmig and Selden 2021), which has a slug-like body partially covered by a prominent shell, is also part of the vermiform fauna and likely co-existed with the scalidophorans and *Burgessochaeta*, as all can be found in the lower part (cycle 3 of Liddell et al. 1997) of Miners Hollow.

Additionally, *Margaretia dorus*, which has been interpreted as the tubes of the enteropneust *Oesia disjuncta* (Nanglu et al. 2016), is fairly common in the Spence Shale localities of the Wellsville Mountains (Kimmig et al. 2019a; Whitaker and Kimmig 2020; Foster et al. 2022) and suggests that these vermiform hemichordates also inhabited the middle shelf areas of the Spence Shale biota.

Conclusions

The new annelids add to a diverse and thriving worm fauna of the Spence Shale and show that there is likely still a lot to be discovered from this important window into Cambrian biodiversity. However, recognising these annelids might be difficult, as the described specimens show post-mortem decomposition and diagenetic alteration, which can make their taxonomic identification challenging, especially in the field. This might be part of the reason behind the scarcity of annelid remains in the Spence Shale, but it also mirrors the biotic compositions observed from most Cambrian Lagerstätten of the Great Basin, with the exception of the abundant single annelid taxon in the Weeks Formation (Lerosey-Aubril et al. 2018). In addition to their taxonomic diversity, the annelids further show that the Spence Shale had a diverse benthic fauna and was likely one of the most diverse ecosystems in the Cambrian.

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