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A new shell-bearing organism from the Cambrian Spence Shale of Utah

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Abstract

A new shell-bearing organism with preserved soft tissue, *Armilimax pauljamisoni* n. gen. n. sp., is reported from the middle Cambrian (Miaolingian: Wuliuan) Miners Hollow locality of the Spence Shale of northern Utah. The described organism is known from a single articulated specimen and preserves a prominent shell, a slug-like body, as well as a U-shaped digestive tract. Its overall appearance is similar to halkieriids, but it does not preserve sclerites. The possible affinities of the new taxon and potential reasons for the presence of a U-shaped gut are discussed. *Armilimax pauljamisoni* is the first shell-bearing animal of its kind from the Great Basin and extends the diversity of body plans in the Spence Shale Fossil-Lagerstätte.

Keywords: Burgess Shale-type preservation; Lophotrochozoa; *Halkieria*; Sipuncula; Great Basin; Lagerstätte

1. Introduction

The Great Basin of the western USA preserves some of the most important Cambrian-aged Burgess Shale-type deposits in the world, preserving assemblages from Series 2 to the upper Miaolingian. Five of the most diverse and productive Cambrian Fossil-Lagerstätten occur in Utah: the Spence Shale in northeastern Utah, and the two Wheeler Lagerstätten (House Range and Drum Mountains), the Marjum Lagerstätte and the Weeks Lagerstätte of western Utah (Robison and Babcock, 2011; Robison et al., 2015; Foster and Gaines, 2016; Lerosey-Aubril et al., 2018, in press; Kimmig et al., 2019; Kimmig, in press). The Spence Shale is the oldest (Miaolingian: Wuliuan) of the Cambrian Lagerstätten in Utah and preserves a diverse soft-bodied and biomineralized fauna, including several problematic species: e.g., *Banffia episoma* Conway Morris and Selden in Conway Morris et al., 2015a; *Eldonia ludwigi* Walcott, 1911; *Siphusauctum lloydguntheri* Kimmig, Strotz and Lieberman, 2017 (Conway Morris et al., 2015a, 2015b; Robison et al., 2015; Kimmig et al., 2017, 2019).

Vermiform taxa are present in the Spence Shale, including *Utahscolex ratcliffei* Robison, 1969; *Ottoia prolifica* Walcott, 1911; *Selkirkia spencei* Resser, 1939; and *S.* cf. *columbia* Walcott, 1911 (Robison et al., 2015; Kimmig et al., 2019; Whitaker et al., in press), all of which represent priapulids, but are not common. More prevailing are unidentified vermiform remains which often cannot be attributed to any phylum (e.g., Broce and Schiffbauer, 2017). Shell-bearing organisms present in the Spence Shale include several brachiopod genera, hyoliths, as well as the mollusks *Latouchella arguta* Resser, 1939 and *Skeemella radians* Babcock and Robison, 1988 (Kimmig et al., 2019). Halkieriids, Cambrian vermiform fossils covered by sclerites and bearing at least one shell (Conway Morris and Peel, 1995; Conway Morris and Caron, 2007; Zhao et al., 2017), have not been described from the Spence Shale, nor any of the other Utah Lagerstätten, but are known from the slightly younger Burgess Shale (Conway Morris and Caron, 2007).

Here, we document and describe *Armilimax pauljamisoni* n. gen. n. sp., a new shell-bearing, slug-like organism of unknown affinity from the Spence Shale and discuss possible taxonomic affinities of the animal.

2. Geological setting

The middle Cambrian (Miaolingian: Wuliuan) Spence Shale Member of the Langston Formation of northeastern

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Utah and southeastern Idaho, ranges in age from the *Albertella* to *Glossopleura* Biozones (Liddell et al., 1997; Robison and Babcock, 2011; Kimmig et al., 2019). The Spence Shale was deposited on the passive western margin of Laurentia. Trace fossils and geochemical analyses indicate that dynamic redox conditions occurred during deposition (Garson et al., 2012; Kloss et al., 2015; Kimmig and Strotz, 2017; Hammersburg et al., 2018).

The Spence Shale is a dark grey to brown calcareous shale with interlayered lime mudstone units, about 50 to 65 m thick in the study area of the Wellsville Mountains, north of Brigham City, Utah (Liddell et al., 1997; Kimmig et al., 2019). It overlies the Naomi Peak Limestone Member and is itself overlain by the High Creek Limestone Member (Maxey, 1958; Liddell et al., 1997; Kimmig et al., 2019). The Langston Formation lies above the Precambrian/Cambrian Geertsen Canyon Quartzite of the Brigham Group, a pale grey to white quartzite with scattered pebbles that, at the top, contains persistent *Skolithos* traces and a few trilobite tracks (Crittenden et al., 1971). No body fossils have been recovered from the Geertsen Canyon Quartzite.

The specimen described here was found at the Miners Hollow locality, which is situated on the west flank of the Wellsville Mountains north of Brigham City, UT (Section 14, T10N, R02W; 41.6023°N, 112.0334°W; Fig. 1A, B). The specimen was recovered from the third parasequence (or carbonate cycle), approximately 33–36 m above the base of the Spence Shale (Fig. 1C) as measured by Julien Kimmig and described by Liddell et al. (1997).

3. Preservation

An energy dispersive X-ray spectroscopy (EDS) analysis of part and counterpart (Figs. S1–S3) identified carbon throughout, but no consistent film, likely due to the diagenetic alteration of the rock, as well as surface weathering. Spectral maps indicated the following variations in percentage by weight for different detectable elements throughout the specimen (9 data points): O, 40.5–43.9%; Si, 19.1–27.4%; Al, 10.3–13.2%; C, 0.0–8.6%; Fe, 0.8–6.9%; K, 3.6–5.8%; N, 2.4–13.9%; Ca, 1.4–3.6%; Mg, 1.0–1.9%; S, 0.0–0.9%; Ti, 0.0–1.8%; P, 0.0–0.6%. The fossil has an enhanced signature of C, Ca, and Mg in the shell, indicating an original calcium carbonate composition. Carbon is found throughout the specimen, showing the preservation of at least part of the specimen as carbon film.

There is indication of phosphatization of the shell (up to ~0.2 Wt%, Figs. S1, S3), and some minor phosphatization in the specimen (up to ~0.6 Wt%, Fig. S3), but it was not a major part of the fossilization process. Overall, the preservation of the specimen appears to be comparable to other fossils from the Spence Shale. The preservation is similar to vermiform fossils described in recent studies of fossils from the same locality (Broce and Schiffbauer, 2017; Whitaker et al., in press). In addition, diagenetic processes altered the original calcium carbonate of the shell and parts of the other body to dolomite, as has been reported from palaeoscolecids from the Spence Shale (Whitaker et al., in press).

The preservation of *Armilimax pauljamisoni* suggests that the animal was likely decomposing on the ocean floor for a short period of time, likely less than a week, based on decay experiments performed with modern priapulids (Sansom, 2016), before being buried. This is suggested by the partial decomposition of the gut. Laboratory-based decay experimentation of the modern priapulid *Priapulus caudatus* Lamarck, 1816 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). The part of the specimen opposite to the shell was covered by sediment when it was split, and is only preserved on the part, after preparation.

4. Material and methods

The specimen was collected by Paul G. Jamison of Logan, Utah. It was photographed under ethanol with cross-polarized light using a Canon 5D MkII camera equipped with 100 mm macro lens using DSLR Assistant (www.kaasoft.com). The focus stacks were merged and the contrast, colour, and brightness adjusted using Affinity Photo (www.serif.com). Close-ups of the shell were taken under ethanol with a Leica DMS 300 Digital Microscope, unless otherwise specified; the contrast, colour, and brightness of images were adjusted using Adobe Photoshop (www.adobe.com).

Elemental mapping utilizing EDS was conducted at the University of Kansas Microscopy and Analytical Imaging Laboratory using an Oxford Instruments 80 mm^2 x-Max silicon drift detector (SDD), mounted on a FEI Versa 3D Dual Beam. Analyses used a horizontal field width of 2.39 mm, a low accelerating voltage of 10 kV, a spot size of 4.5 μm, and a 1000 μm opening (no aperture). The EDS maps were collected at a pixel resolution of 512 × 512 with a total of 18 passes.

The specimen described in this paper is housed in the Division of Invertebrate Paleontology, Biodiversity Institute, University of Kansas (KUMIP 490943).

5. Systematic palaeontology

Phylum, Class, Order, Family Uncertain

Genus *Armilimax* n. gen.

Etymology: From the Latin '*armis*' and '*limax*', meaning 'armour' and 'slug' respectively, in reference to the slug-like shape and the presence of a shell.
Type and only known species: *Armilimax pauljamisoni* n. sp.
Diagnosis: Same as species.
Remarks: *Armilimax* n. gen. is not assigned to a phylum at this point. A detailed discussion on its affinities is provided below.

Armilimax pauljamisoni n. sp.
(Figs. 2–5)

Etymology: After the collector of the specimen, Paul Jamison.
Holotype: KUMIP 490943, part and counterpart.

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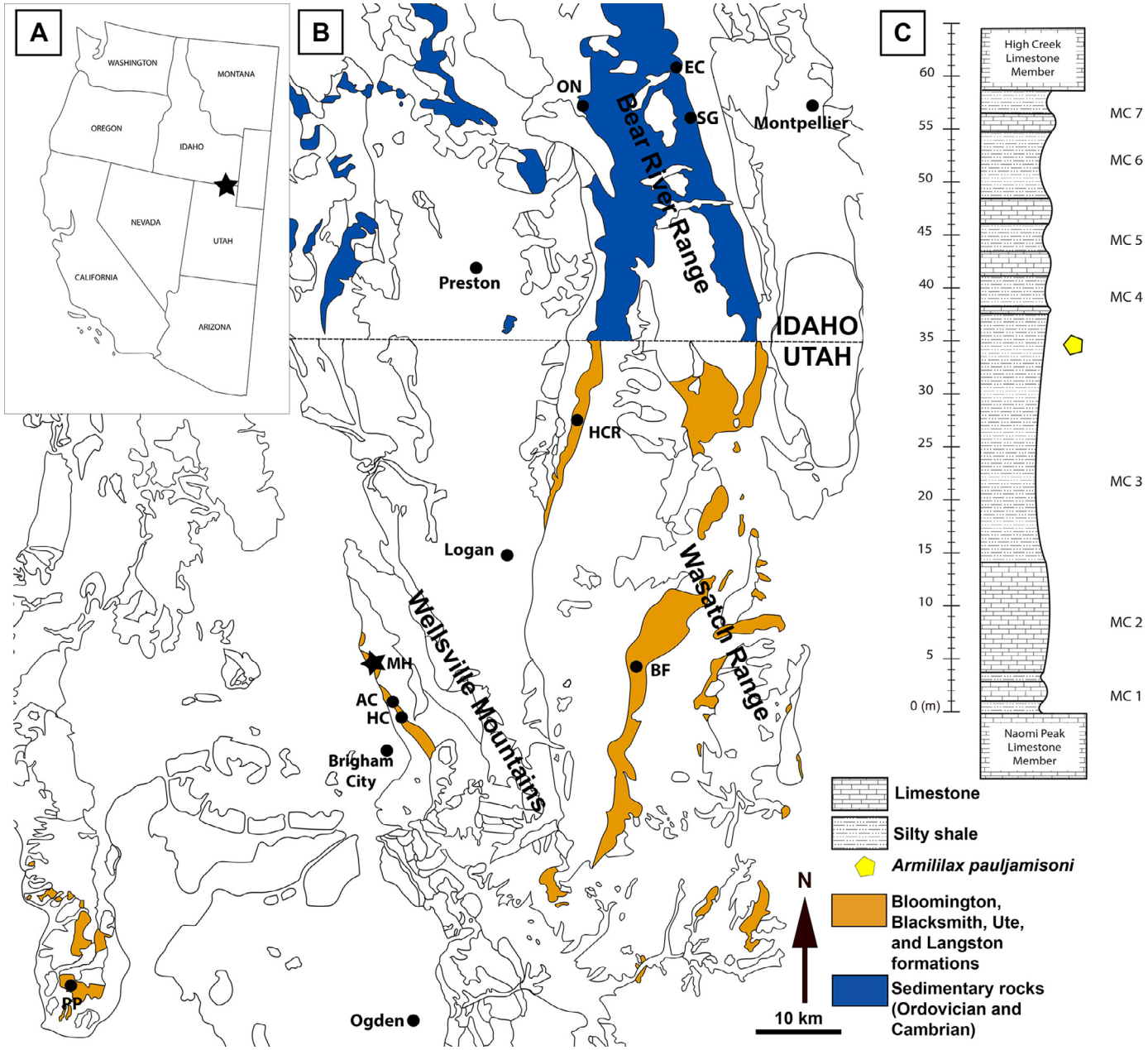

Fig. 1. (A) Map of the western USA showing the location of the Spence Shale. (B) Geological map (based on the USGS state maps for Google Earth Pro) of northern Utah and southern Idaho showing the location of Miners Hollow (star), and other major Spence Shale localities in northern Utah and southern Idaho (modified from Kimmig et al., 2019); AC, Antimony Canyon; BF, Blacksmith Fork; EC, Emigration Canyon; HC, Hansen Canyon; HCR, High Creek; MH, Miners Hollow; ON, Oneida Narrows; PP, Promontory Point; SG, Spence Gulch. (C) Stratigraphic column and approximate horizon from which the specimen was collected, courtesy of Anna Whitaker; MC, Miners Hollow cycle.

Type locality: Miners Hollow, Wellsville Mountains, Box Elder County, Utah; Section 14, T10N, R02W; 41.6023˚N, 112.0334˚W.

Type horizon: Langston Formation, Spence Shale Member, cycle 3; Cambrian (Miaolingian: Wuliuan), *Glossopleura* trilobite zone.

Diagnosis: Elongated, unsegmented, slug-like organism bearing conical subquadrate carbonate shell at one end with umbo and concentric growth lines, U-shaped or coiled digestive tract bearing fine annuli.

Description: Elongated, unsegmented slug-like body in dorsal view. 30.1 mm long, 4.9–5.6 mm wide (Fig. 2). Symmetrical, conical, subquadrate shell, with rounded edges 2.4 mm wide, 2.9 mm long, preserved at one end, with umbo (Figs. 2, 4). The shell shows concentric growth rings (Fig. 4). It is partially surrounded by soft tissue and there is soft tissue preserved in the broken parts of the shell (Fig. 4A, B). A suboval, poorly preserved structure is preserved at the other end (Fig. 3). This structure is 2.4 mm wide, 2.9 mm long, with no relief, 4.3 mm from the non-shell bearing end of the specimen. Isolated

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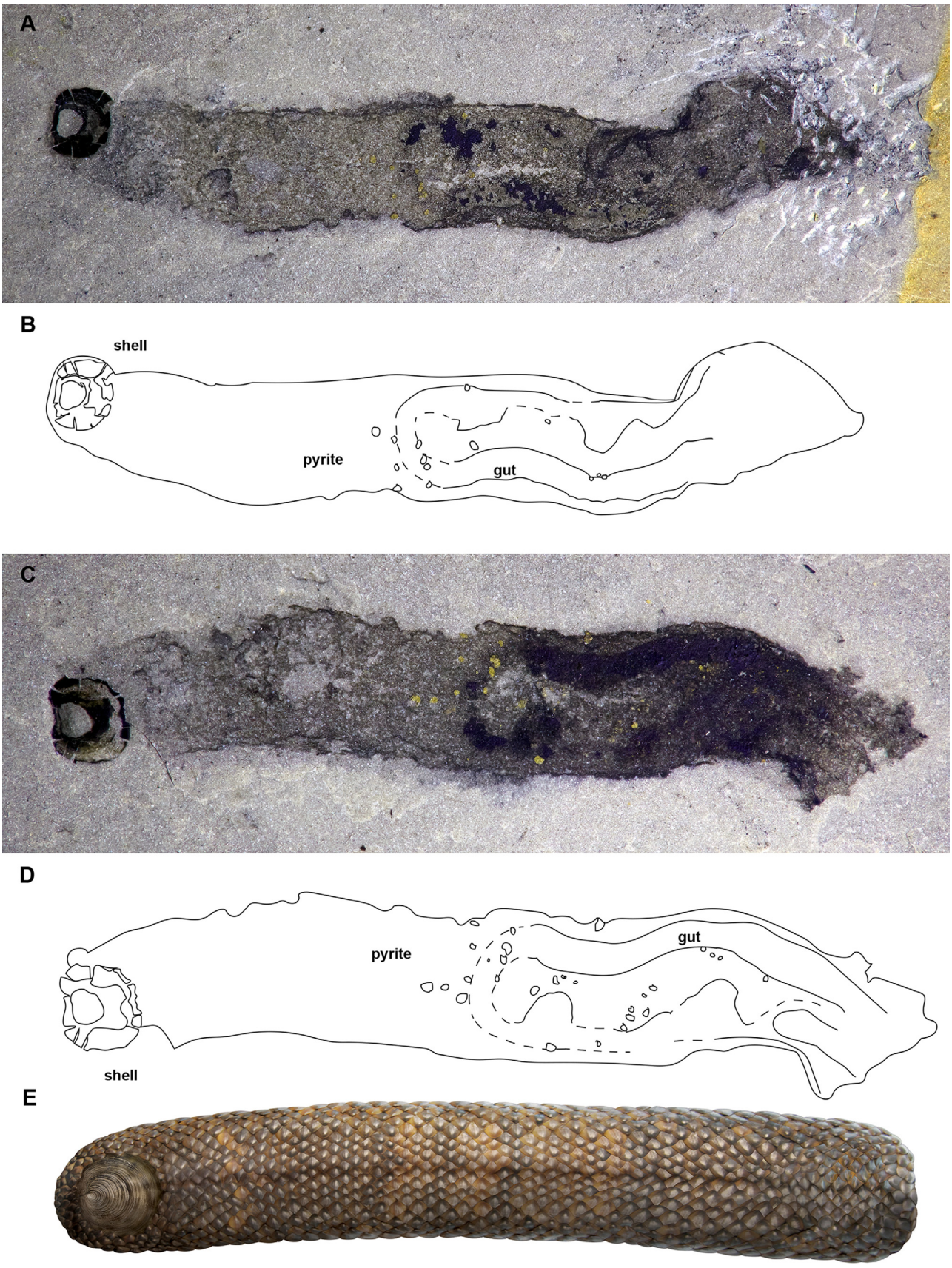

Fig. 2. Holotype of *Armilimax pauljamisoni* n. gen. n. sp. (KUMIP 490943) from the Spence Shale, middle Cambrian, Miners Hollow, Utah, in dorsal view. (A) Part after preparation. (B) Interpretative drawing of the part showing the gut, pyrite replacement, and the shell. (C) Counterpart. (D) Interpretative drawing of the counterpart showing the gut, pyrite replacement, and the shell. (E) Possible reconstruction of the animal (created by Laura Mohr). Scale bars are 5 mm.

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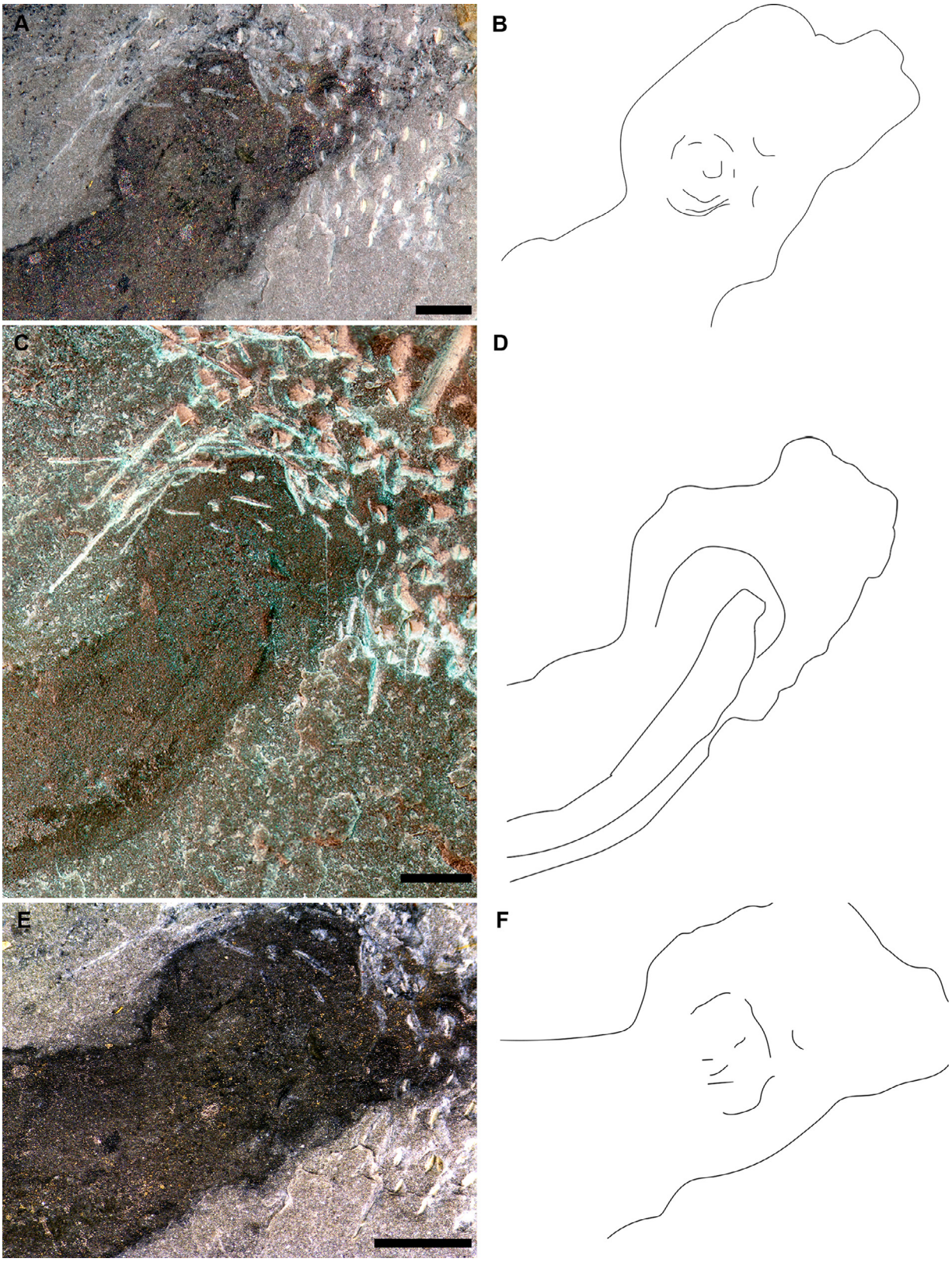

Fig. 3. Close-ups of the non-shell bearing end of the part of the holotype of *Armilimax pauljamisoni* n. gen. n. sp. (KUMIP 490943) from the Spence Shale, middle Cambrian, Miners Hollow, Utah, in dorsal view, showing differences in appearance based on light and microscope. (A) Close-up taken with Leica M205C stereomicroscope, under diluted alcohol, with low angle light. (B) Interpretative drawing of (A), showing dark lines forming an unidentified suboval shape. (C) Close-up taken with Olympus SZX16 microscope under diluted alcohol, with low angle light. (D) Interpretative drawing of (C), showing gut and an unidentified suboval shape. (E) Close-up taken with Leica DMS 300 microscope under diluted alcohol, with low angle light. (F) Interpretative drawing of (E), showing gut and an unidentified suboval shape. Scale bars are 2 mm.

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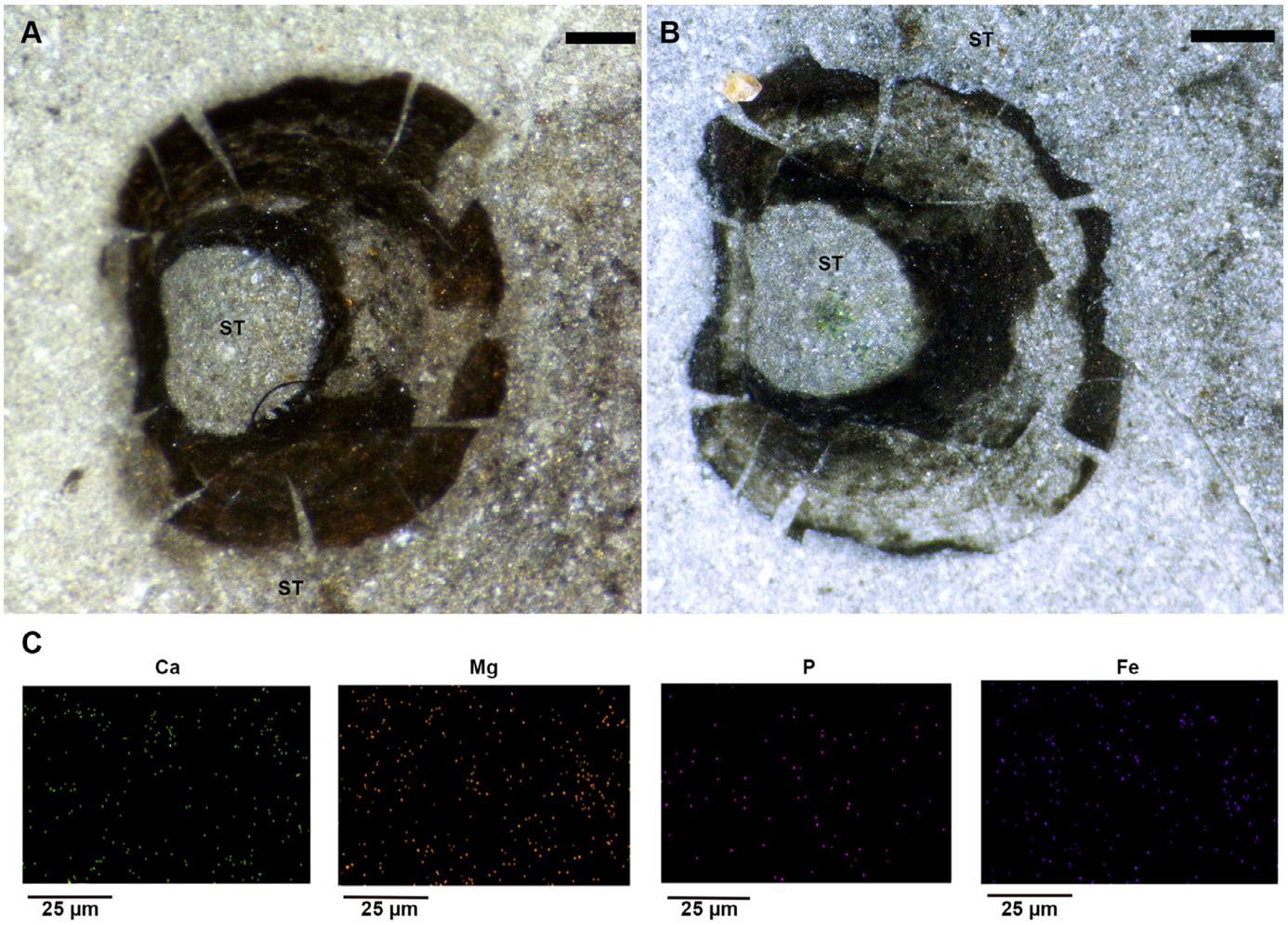

Fig. 4. Holotype of *Armilimax pauljamisoni* n. gen. n. sp. (KUMIP 490943) from the Spence Shale, middle Cambrian, Miners Hollow, Utah, in dorsal view. (A) Close-up of the shell in the part. (B) Close-up of the shell in the counterpart. (C) Elemental maps showing the major elements composing the of the shell on the counterpart. ST indicates soft tissue. Scale bars are 0.5 mm in (A, B).

semicircular pyrite structures are preserved but vary in size and do not form a consistent pattern (Figs. 2, 5B), suggesting they are of diagenetic origin.

The darker structure at the non-shell bearing end of the specimen is interpreted as the digestive tract (Figs. 2, 5A). The preserved structure is U-shaped and bears fine annuli (Fig. 5A).

Remarks: The interpretation of posterior versus anterior is difficult due in part to the location of the shell and the shape of the digestive tract. Both the halkieriid *Orthrozanclus* Conway Morris and Caron, 2007 and the suggested halkieriid relative *Calvapilosa* Vinther, Parry, Briggs and Van Roy, 2017 preserve one shell and, in both taxa, it is located at the anterior end (Conway Morris and Caron, 2007; Vinther et al., 2017; Zhao et al., 2017). Additionally, the umbonal region is at the anterior tip in *Orthrozanclus*, as it is in *A. pauljamisoni* in this interpretation. In *Calvapilosa* the apex (or mucro) is also more to the anterior (Vinther et al., 2017). But, if the gut is actually U-shaped, it would indicate that the shell is at the posterior end of the animal, similar to a snail. We further discuss the gut shape below and presently leave the interpretation of posterior and anterior open.

On the opposite end of the shell (Fig. 3), the preservation is poor but a semicircular structure can be seen based on lighting. It does not show any relief and might represent part of the gut or possibly the feeding apparatus. If this is, indeed, the feeding apparatus of the animal, it would suggest that this is the anterior end. There are two additional structures which show some three-dimensionality on the right of the semicircular structure (Fig. 3A, B), which are visible in low-angle light. It is unclear if these structures represent parts of the animal or not. There is no evidence that *A. pauljamisoni* did have three types of sclerites, as present in halkieriids.

Stratigraphic and geographic range: Type locality and horizon only.

6. Discussion

6.1. Gut

There are several possibilities why the gut of *Armilimax pauljamisoni* is or appears U-shaped: (1) The gut is actually U-shaped as it is in other mollusks, including gastropods and

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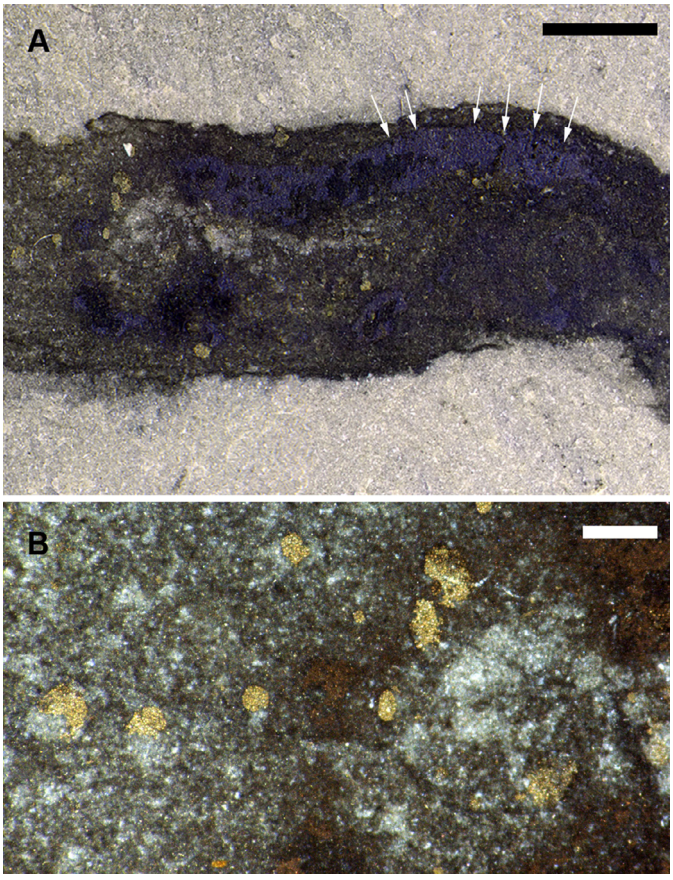

Fig. 5. Holotype of *Armilimax pauljamisoni* n. gen. n. sp. (KUMIP 490943) from the Spence Shale, middle Cambrian, Miners Hollow, Utah, in dorsal view. (A) Close-up of the digestive tract, taken with cross-polarized lights, showing fine annulations (indicated by arrows) and some pyrite in the counterpart. (B) Close-up of some pyrite replacement. Scale bars are 2 mm in (A) and 0.5 mm in (B).

cephalopods (Budd and Jackson, 2016). This would be reasonable to assume, as the specimen likely did not decompose for an extended period of time. An argument against the gut being U-shaped is that these kinds of digestive tracts are often associated with sessile animals, e.g., brachiopods and stalked filter feeders (O'Brien and Caron, 2012), in the Cambrian. (2) The preserved gut represents only part of the digestive tract and the coiled section is preserved. This is observed in some mollusks, including chitons and monoplacophorans (Greenfield, 1972; Haszprunar and Schaefer, 1996). The argument in favor of this is that the shell is at the anterior end, as it is suggested for halkieriids with one shell (Conway Morris and Caron, 2007; Zhao et al., 2017). (3) The gut was originally straight and reached from the anterior to the posterior end, but the decomposition of the specimen is advanced, and the gut became loose and curled up *post mortem*. The detachment and movement of the digestive tract in worms has been shown in taphonomic experiments (e.g., Monge-Nájera and Hou, 2002) and might have happened in our specimen. (4) The U-shaped structure is not the gut but actually, represents the visceral mass surrounding the intestines. This would indicate that the gut was straight and likely connected to the shell, which would be at the anterior end. This interpretation would suggest that the internal anatomy of *Armilimax* would be similar to the halkieriid *Orthrozanclus elongate* Zhao and Smith in Zhao et al., 2017. An argument against this is, the gut structures in fossils from the Spence Shale are usually preserved as the darkest structures in the fossil based on the taphonomic pathways in the deposit (Briggs et al., 2008; Conway Morris et al., 2015a, 2015b; Kimmig et al., 2017; Whitaker et al., in press) and it is unlikely that this would not be the case in *Armilimax*.

To clarify the shape of the gut and if it is really U-shaped, partially coiled up, or straight, more specimens will be needed in the future. As we are dealing with a single specimen, it is difficult to assess the interpretation of the U-shaped or coiled gut, but the presence of it suggests that curved or coiled guts might have been common in non-sessile animals in the Cambrian.

6.2. Biological affinities

There are few Cambrian organisms known that bear a shell and have a slug-like body. The closest animals that have both these features are halkieriids, Cambrian vermiform fossils covered by sclerites and bearing at least one shell (Conway Morris and Peel, 1995; Conway Morris and Caron, 2007; Zhao et al., 2017). Complete specimens are known from several Cambrian deposits, including the Sirius Passet Lagerstätte (Conway Morris and Peel, 1990, 1995), the Burgess Shale (Conway Morris and Caron, 2007), and the Chengjiang Lagerstätten (Zhao et al., 2017). While *Armilimax pauljamisoni* shares the presence of a shell and the elongated body with these animals, there is no indication that *A. pauljamisoni* had a scleritome consisting of three distinct sclerite types, which all other described halkieriids share. In addition, *A. pauljamisoni* has a coiled/U-shaped gut, while *Halkieria* Poulsen, 1967 and *Orthrozanclus* Conway Morris and Caron, 2007 both have straight digestive tracts (Conway Morris and Peel, 1995; Conway Morris and Caron, 2007; Zhao et al., 2017).

Other animals that *Armilimax pauljamisoni* shares similarities with are peanut worms (Sipuncula). These enigmatic animals have been placed in the annelids but differ from most annelids in that they have an unsegmented body and do not bear chaetae (e.g., Kristof and Maiorova, 2016). Modern sipunculans have a U-shaped gut, and some modern sipunculans secret a horny or calcified cuticular plate: the anal shield (Gibbs and Cutler, 1987; Kristof and Maiorova, 2016). Unfortunately, these animals have a sparse fossil record (Huang et al., 2004; Muir and Botting, 2007), but at least two Cambrian species have been reported from the Chengjiang biota (Huang et al., 2004). Similar to *A. pauljamisoni*, *Archaeogolfingia caudata* Huang, Chen, Vannier and Salinas, 2004 and *Cambrosipunculus tentaculatus* Huang, Chen, Vannier and Salinas, 2004, have a U-shaped gut and an elongated unsegmented body. However, the gut in both species extends from the mouth at the anterior end of the body to the posterior end, curves and terminates about halfway through the body. In contrast, the gut in *A. pauljamisoni* curves about halfway through the body. Additionally, neither *A. caudata* nor *C. tentaculatus* bear shells.

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Other Cambrian animals preserving U-shaped or twisted guts and a calcified shell are hyoliths (Devaere et al., 2014; Sun et al., 2016; Moysiuk et al., 2017), but they do not have an elongated soft-bodied trunk and the shells are conical. While they have been considered to be closely related to sipunculans at one point (e.g., Sun et al., 2016), they are now considered stem-group lophophorates (Moysiuk et al., 2017).

Recently, specimens of the gastropod *Pelagiella exigua* Resser and Howell, 1938 with chaetae have been described from the lower Cambrian (Stage 4) Kinzers Formation of Pennsylvania (Thomas et al., in press). But they do not preserve a slug-like body, the shell is coiled, and *Armilimax pauljamisoni* does not preserve chaetae. Due to this it is unlikely that *A. pauljamisoni* represents a Cambrian gastropod. *Armilimax pauljamisoni* shell also differs in shape from *Latouchella arguta* Resser, 1939 and *Scenella radians* Babcock and Robison, 1988, the only known mollusk shells from the Spence Shale.

It is unlikely the animal is a brachiopod, as the shell does not correspond to any brachiopod shells found in the Spence Shale and the amount of soft tissue is uncharacteristically large compared to the size of the shell. It is also unlikely that the specimen represents a digested or regurgitated shell in a burrow, as the preserved gut suggest that what is preserved is an animal. Additionally, the burrows found in the Spence Shale usually preserve elongated pellets (Kimmig and Strotz, 2017).

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.palwor.2020.05.003.

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