

New Cambrian vermiform organisms from Burgess Shale-type deposits of the western United States

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We report new occurrences of scalidophorans, enteropneusts, and other soft-bodied taxa in several middle Cambrian (Miaolingian) formations of the western United States. Among these are the first occurrence of the tubicolous priapulid worm *Selkirkia* Walcott, 1911 from the Ophir Formation of Utah and possibly from the Bright Angel Formation of Arizona (both *Glossopleura* Assemblage Biozone, Wuluan). We document additional *Selkirkia willoughbyi* Conway Morris & Robison, 1986, *S. columbia* Conway Morris, 1977, and possible *S. spencei* Resser, 1939, from the Drum Mountains Wheeler fauna (Wheeler Formation of Utah; *Bolaspiddella* Zone, Drumian). *Selkirkia spencei* occurs in the Spence Shale Member of the Langston Formation of Idaho (Wuluan), from which we also describe more specimens. The enteropneust tube *Margaretia* Walcott, 1931 is quite common at some levels of the Wheeler Formation in the Drum Mountains of Utah, and new *Margaretia* specimens are also illustrated from the Wheeler Formation in the House Range and the Spence Shale in the Wellsville Mountains. The Wheeler Formation in the Drum Mountains also contains a *Spartobranchus*-like enteropneust, other possible enteropneusts, and additional undetermined worm-like organisms gen. et sp. indet. Several other taxonomically enigmatic organisms, burrows, or coprolites also occur in the Wheeler faunas of the Drum Mountains and House Range. These occurrences hint at greater diversity of scalidophorans and enteropneusts in the Wheeler ecosystems than has been previously documented, and extend the geographic distribution of the scalidophorans to the Ophir and possibly the Bright Angel formations in western Laurentia. • Key words: Lagerstätten, *Selkirkia*, *Margaretia*, Scalidophora, Miaolingian, Ophir, Wheeler, Spence, Bright Angel.

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Soft-bodied vermiciform organisms are a key element of Cambrian Konservat-Lagerstätten that exhibit Burgess Shale-type preservation (see review in Hagadorn 2002). Some groups, such as scalidophoran worms, can be quite abundant in deposits like the Burgess Shale, Chengjiang, Xiaoshiba, Haiyan, Fandian, and Drum Mountains and House Range biotas, among many others (e.g., Huang *et al.* 2004, Han *et al.* 2007, Caron & Jackson 2008, Tian *et al.* 2014, Zhao *et al.* 2014, Smith *et al.* 2015, Leroosey-Aubrill *et al.* 2018, Du *et al.* 2020, Nanglu *et al.* 2020, Wang *et al.* 2021, Yang *et al.* 2021a, Shi *et al.* 2022). The genus *Ottoia* can be extremely abundant in the Wuluan Burgess Shale of British Columbia, with slabs from the Walcott Quarry bearing as many as 70 specimens Conway Morris (1977) and a concentration of more than a hundred specimens per square meter at “The Monarch” locality (Tremaine 2003). In addition, palaeoscolecids occur in great abundance on

slabs with less common lobopodians in the Chengjiang Biota (Vannier & Martin 2017), and the long, annulated tube-dwelling scalidophoran *Paraselkirkia* Luo & Hu, 1999 (Yang *et al.* 2021b) can be relatively abundant in the Maotianshan Shale in China, representing up to 16% of specimens (Dornbos & Chen 2008).

Tubicolous (tube-living) scalidophoran worms are typically less abundant but are widespread. For example, *Selkirkia* Walcott, 1911 has been documented in many Konservat-Lagerstätten across western North America: the Cambrian Stage 4 Ruin Wash (Pioche Formation; Lieberman, personal communication 2022); the Wuluan Burgess Shale (Walcott 1911, Conway Morris 1977, Smith *et al.* 2015) and Spence Shale (Resser 1939, Conway Morris & Robison 1986); and the Drumian Wheeler (House Range and Drum Mts.) and Marjum formations (Conway Morris & Robison 1986, Robison *et al.* 2015,

Foster & Gaines 2016); and the Guzhangian Pika (Smith *et al.* 2015) and Weeks formations (Lerosey-Aubril *et al.* 2018, Lerosey-Aubril personal communication 2022). Selkirkids are also known from the Chengjiang, Xiaoshiba, and Kaili biotas in Asia and from the Sirius Passet Biota in Greenland (Wang *et al.* 2021). Some vermiform taxa, such as lobopodians and scalidophorans, can be more diverse or abundant in the Chengjiang Biota than in the Burgess Shale (Ma *et al.* 2010, Ou *et al.* 2011).

Enteropneusts are another soft bodied tube-building group whose fossils are rare, but widely distributed in such deposits. Of note is *Margaretia* Walcott, 1931, a Cambrian fossil originally hypothesized to be a chlorophyte alga (e.g., Conway Morris & Robison 1988). Discovery of the enteropneust hemichordate *Oesia* Walcott, 1911a within *Margaretia* structures indicated that the latter was likely the hollow, fenestrated living tube of a tubicolous *Oesia* worm (Nanglu *et al.* 2016). Other enteropneusts, like *Spartobranchus* Caron, Conway Morris & Cameron, 2013, are more restricted in their distribution, being known only from the Burgess Shale and House Range Wheeler fauna (Caron *et al.* 2013; Lerosey-Aubril, personal communication 2022). Lobopodians are another group that is rare, but widely distributed in Cambrian Burgess Shale-type deposits (Liu & Dunlop 2014, Caron & Aria 2017).

Cambrian strata of Utah are notable among these deposits, because they contain a variety of undescribed, reinterpreted, or well-known vermiform organisms, some of which can be abundant on bedding planes (Conway Morris & Robison 1986, 1988). For example, in the Drum Mountains Wheeler fauna (Lerosey-Aubril & Skabelund 2018), tubular fossils are dominated by *Selkirkia*, the enteropneust hemichordate *Margaretia*, and to a lesser extent, by morphologically enigmatic forms. At least three other morphologies of vermiform specimens of unknown affinities are relatively abundant in the Wheeler Formation (Conway Morris & Robison 1986, 1988). Less abundant in the Cambrian of Utah are scalidophorans, including *Selkirkia* and other forms such as *Ottoia*? Walcott, 1911a and palaeoscolecids (Robison 1969, Conway Morris & Robison 1986, Robison *et al.* 2015, Lerosey-Aubril *et al.* 2018, Whitaker *et al.* 2020, Leibach *et al.* 2021). The lobopodian *Aysheaia* Walcott, 1911a was previously thought to occur in the Wheeler strata in the House Range (Robison 1985), but the sole available specimen has been controversially re-interpreted as a radiodont frontal appendage (Pates *et al.* 2017, 2018; Gámez Vintaned & Zhuravlev 2018); otherwise, the group occurs in the Spence Shale (Gunther & Gunther 1981, Conway Morris & Robison 1988, Caron & Aria 2020) and the Marjum Formation (Lerosey-Aubril & Ortega-Hernández 2022).

Here we report new occurrences of vermiform fossils from this region. These include the first known occurrence

of *Selkirkia* from the Ophir Formation of Utah, additional specimens of *Selkirkia spencii* Resser, 1939 from the Spence Shale of Utah, and possible *S. spencii* from the Wheeler Formation of the Drum Mountains, Utah. We also report the first probable *Selkirkia* from the Bright Angel Formation of Arizona. Additional specimens of *Margaretia* are illustrated from the Wheeler Formation of the Drum Mountains and Spence Shale of Utah, along with possible *Spartobranchus*? and indeterminate enteropneusts(?) from the Drum Mountains Wheeler. We also report a number of indeterminate worm-like organisms gen. et sp. indet. from the Wheeler Formation of the Drum Mountains and House Range, some of which may be poorly preserved scalidophorans or enteropneusts.

Materials and methods

Specimens were collected from eight localities in the Wheeler, Ophir, Langston (Spence Shale Member), and Bright Angel formations between 2009 and 2022, and were encountered while splitting shale for trilobites for biostratigraphic data and during subsequent visits specifically targeting vermiform taxa. The collection consists of 58+ total specimens, and all are reposed at the Utah Field House of Natural History, Denver Museum of Nature & Science, or the Museums of Western Colorado. Specimens were studied with a Nikon SMZ-2B microscope. All measurements were made with digital calipers and rounded to nearest 0.1 mm. Photos were taken with a Canon 5D Mark IV camera with a Laowa 100 mm F2.8 CA-Dreamer Macro2X lens or with a Canon EOS R5 camera with a Canon RF 100 mm F2.8 L Macro IS USM lens. Photo modification in Photoshop consisted only of cropping and brightness/contrast adjustments to exposure.

Abbreviations. – DMNH – Denver Museum of Nature & Science, Denver, Colorado; FHPR – Utah Field House of Natural History State Park Museum, Vernal, Utah; KUMIP – University of Kansas, Biodiversity Institute, Division of Invertebrate Paleontology, Lawrence, Kansas; MWC – Museums of Western Colorado, Dinosaur Journey Museum, Fruita, Colorado; USNM – National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Geologic setting and localities

Specimens collected for this study were recovered from sites mostly in the Drum Mountains (1 site) and House Range (3 sites) of western central Utah (Wheeler Formation), the Oquirrh and Wasatch (Wellsville Mountains) ranges (2 sites) of northern Utah (Ophir and Langston formations, respectively), the Bear River Range of Idaho (Langston Formation), and the Grand Wash Cliffs

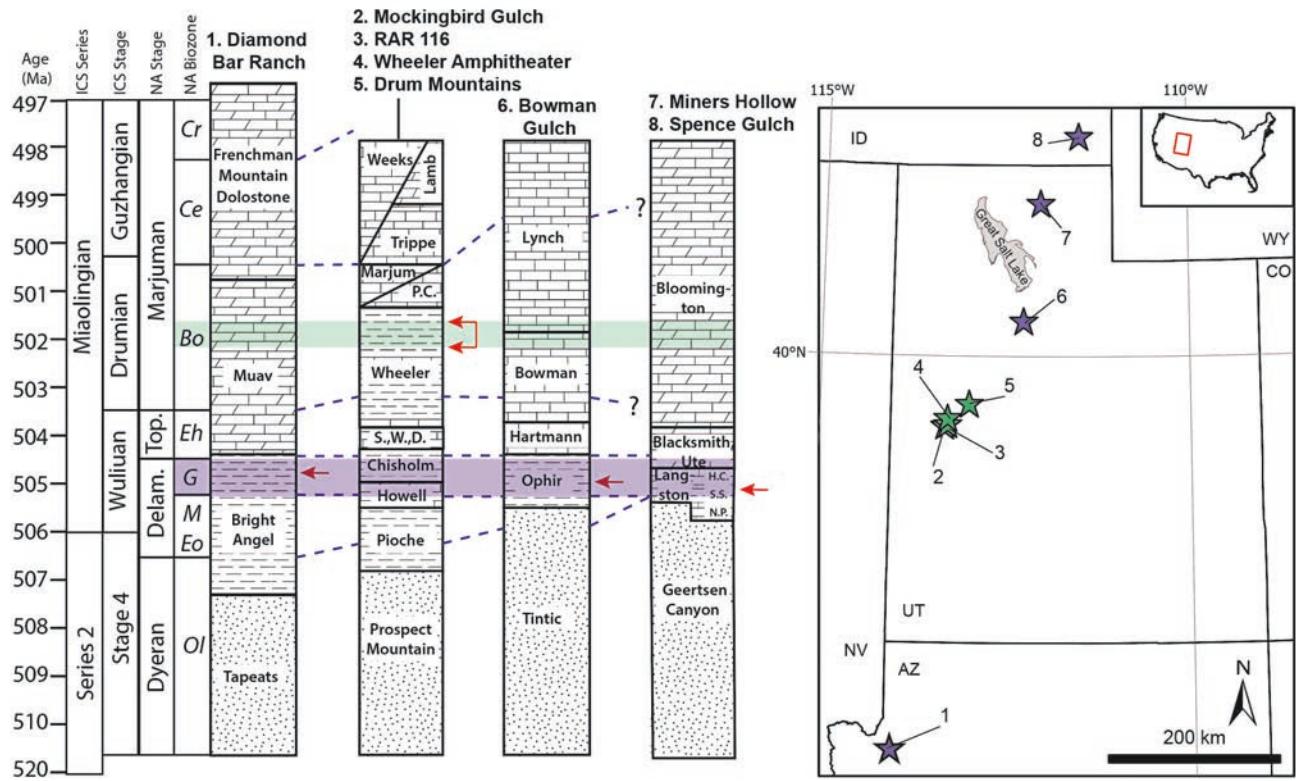


Figure 1. Contextual framework for fossils studied here, with red arrows indicating stratigraphic positions of occurrences at numbered localities, noted for geographic position on map at right. Purple bar indicates approximate position of *Glossopleura* (G) Zone, and light green bar indicates approximate range of Wheeler Formation sites within the *Bolaspidella* (Bo) Zone. Dashed blue lines show approximate trilobite biozone boundaries across the sections. Localities on map (stars) color coded by biostratigraphic zone interval as on sections (darker for visibility). Abbreviations: North American stages – Delam. = Delamaran, Top. = Topazan; North American trilobite biozones – Ol = *Olenellus*, Eo-M = *Eokochaspis*–*Mexicella*, Eh = *Ehmaniella*, Ce = *Cedaria*, Cr = *Crepicephalus*; Formations – HC = High Creek Limestone, NP = Naomi Peak Limestone, SS = Spence Shale, SWD = Swasey Limestone-Whirlwind Formation-Dome Limestone, PC = Pierson Cove Formation; States – AZ = Arizona, CO = Colorado, ID = Idaho, NV = Nevada, UT = Utah, WY = Wyoming. Based on data in Maxey (1958), Liddell *et al.* (1997), Hintze & Davis (2003), Kirby (2012), Karlstrom *et al.* (2020), and Sundberg *et al.* (2020).

on the western edge of the Colorado Plateau (Diamond Bar; Bright Angel Formation) in Arizona (Fig. 1). All the fossils are middle Cambrian (Miaolingian) in age (Fig. 1) and more specifically Wulian age for the ones coming from the Bright Angel, Ophir, and Spence Shale (*Glossopleura* Assemblage Biozone, Morgan 2021 or *Ptychagnostus praecurrens* agnostoid Zone, Peng *et al.* 2020), and Drumian for those collected in the Wheeler Formation (*Bolaspidella* trilobite Zone or *Ptychagnostus atavus* agnostoid Zone) (Robison & Babcock 2011).

The four formations have a long history of study, and readers are referred to previous literature for depositional, age, and stratigraphic context for these units. For example, the Wheeler Formation has been studied since the time of Walcott, with numerous geological and paleontological assessments over the decades (e.g., Walcott 1908; Robison 1964a, b; Gunther & Gunther 1981; Conway Morris & Robison 1986, 1988; Hintze & Davis 2003; Gaines & Droser 2003; Gaines *et al.* 2005; Robison *et al.* 2015; Gaines & Vorhies 2016; Lerosey-Aubril *et al.* 2020). The

Spence Shale has also attracted its share of attention both geologically and paleontologically (e.g., Walcott 1908, Resser 1939, Liddell *et al.* 1997, Robison *et al.* 2015, Kimmig *et al.* 2019). The geology of the Bright Angel Formation is well-studied (Noble 1914, 1922; McKee & Resser 1945; Wanless 1973; Hardy 1986; Middleton & Elliott 2003; Rose 2003, 2006, 2011; Karlstrom *et al.* 2020), and although its paleontological record is extensive, it is less well studied. Trace fossils are abundant in the Bright Angel Formation (Martin 1985; Baldwin *et al.* 2004; Miller *et al.* 2021), and both metazoan body fossils and spores can also be abundant in the formation (McKee & Resser 1945, Middleton & Elliott 2003, Taylor & Strother 2008, Foster 2011, Lassiter *et al.* 2021). The Ophir Formation in the Oquirrh Mountains is not as well studied; Rigby (1959) and Kirby (2012) characterized the geology and Walcott (1916), Resser (1935), and Palmer (1954) provided insights on the units' trilobites.

Localities are summarized below, alphabetically by the names by which they appear in the text (see Appendix

for geographic locality information; more precise locality data are available from the FHPR, DMNH, MWC, or KUMIP):

Bowman Gulch (Ophir Formation, Wuluan, Glossopleura Assemblage Biozone). – This site occurs ~33 m above the base of the 120 m thick Ophir Formation (Fig. 1), at outcrops near the town of Ophir on the western side of the Oquirrh Mountains in Tooele County, Utah. At this site the Ophir Formation overlies the Tintic Quartzite and underlies the Hartmann Limestone (Kirby 2012). The lithology of the productive layer sampled here is a light greenish gray silty shale to fine-grained sandstone. Specimens occur with dolichometopid trilobites (*Glossopleura producta* Hall & Whitfield, 1877; see Palmer 1954), brachiopods, and hyoliths.

Diamond Bar Ranch (Bright Angel Formation, Wuluan, Glossopleura Assemblage Biozone). – This site is ~2 m above the top of the Meriwitica Member of the Bright Angel Formation (Fig. 1), east of the historic Diamond Bar Ranch in Mohave County, Arizona, near the Grand Wash Cliffs. This locality level is the same as the lower 2 m of the Chisholm Shale of Hardy's (1986) stratigraphic section. The site's lithology is a greenish to reddish brown fissile shale. Specimens here occur with ptychopariid and dolichometopid trilobites (*Anoria* [= *Glossopleura?*] *bessus* Walcott, 1916, *Glossopleura* sp.) and brachiopods. This section was described by McKee & Resser (1945), Hardy (1986), and Rose (2003).

Drum Mountains (Wheeler Formation, Drumian, upper Bolaspidella Zone). – The Drum Mountains locality in the upper Wheeler Formation (Fig. 1) is the same as locality 712 of Conway Morris & Robison (1986), and probably equivalent to the localities mentioned in Rigby & Church (1990), Rigby *et al.* ("locality 2"; 2010), and Briggs *et al.* (2008, p. 250; the locality yielding *Canadaspis* Briggs, 1978). Here the Wheeler Formation lies above the Swasey Limestone and below the Pierson Cove Formation. The site is in the lower level of the upper Wheeler, within ~20 m of the top of the unit. Specimens occur in hard, light gray, calcareous shale along with agnostids, trilobites such as *Elrathia* Walcott, 1924 (including one with an injury, Bicknell *et al.* 2022) and *Asaphiscus* Meek, 1873, and bivalved arthropod remains. Because the biotas of the Wheeler Formation differ between localities (Leroosey-Aubril & Skabelund 2018), we refer to fossils from Wheeler

Formation sites as being part of the Drum Mountains Wheeler or House Range Wheeler faunas (see below).

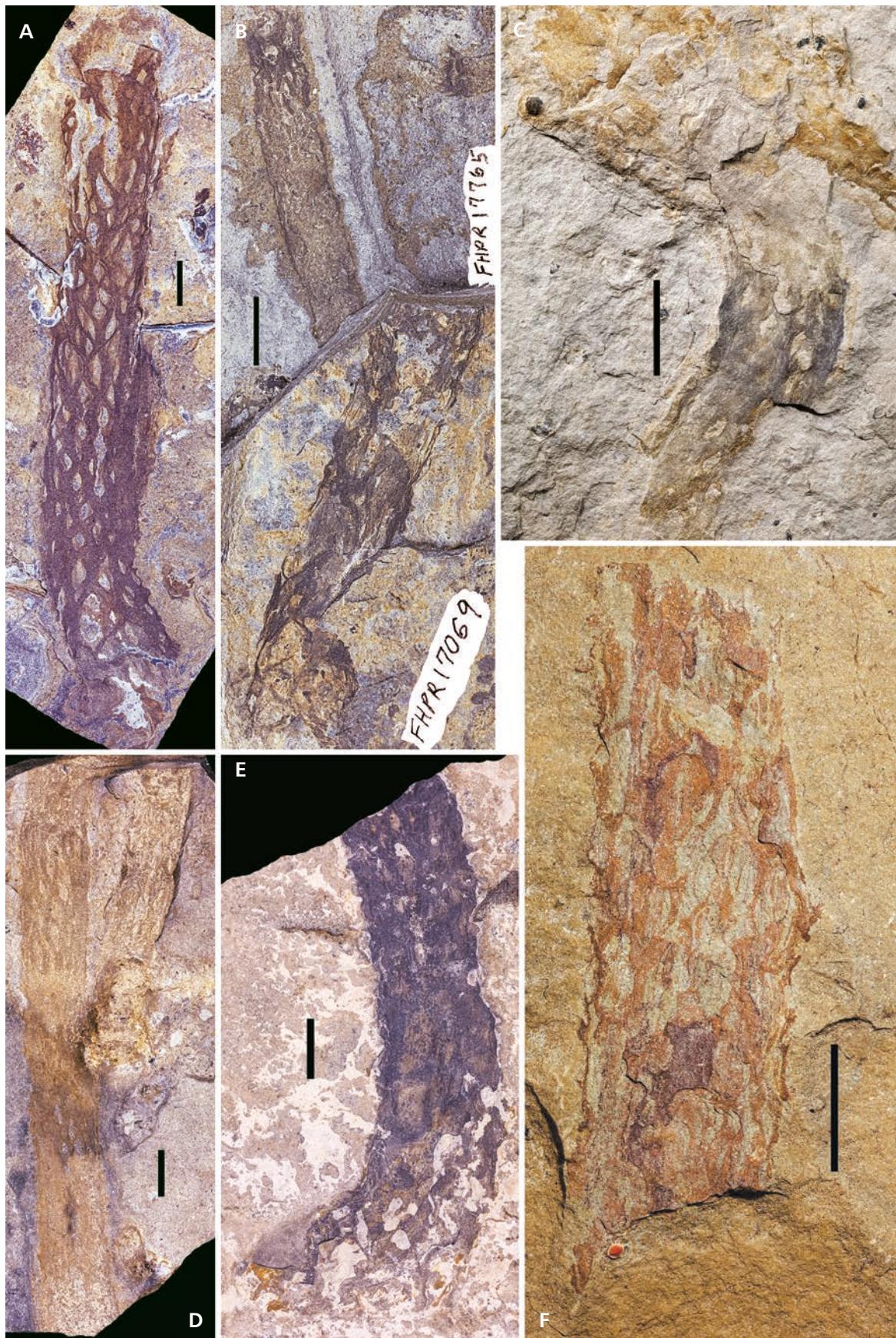
Miners Hollow (Spence Shale Member, Langston Formation, Wuluan, Glossopleura Assemblage Biozone). – The sample level at Miners Hollow (Fig. 1) is from a shale ~35–38 m (upper Cycle 3 or Cycle 4) above the base of the 54 m thick Spence Shale section (Liddell *et al.* 1997, Garson *et al.* 2011) north of Brigham City in Box Elder County, Utah. The Spence overlies the Naomi Peak Member and is overlain by the High Creek Limestone Member of the Langston Formation. The Langston Formation overlies the Geertsen Canyon Quartzite and underlies the Ute Formation. Specimens occur in indurated light to dark gray calcareous shale with other soft-bodied material (e.g., *Eldonia* Walcott, 1911b) and trilobites such as *Amecephalus* Walcott, 1924.

Mockingbird Gulch (Wheeler Formation, Drumian, Bolaspidella Zone). – This site is in the upper Wheeler Formation along the east side of the House Range ("House Range Wheeler"; Fig. 1), just off the road running north from Marjum Pass up to Wheeler Amphitheater, in Millard County, Utah. The Wheeler Formation in the House Range lies above the Swasey Limestone and below the Marjum Formation. This site is also within ~20 m of the top of the Wheeler. Specimens occur in light gray shale that is sometimes diagenetically stained to a light pink. Other biota from this locality include trilobites, agnostids, and other unmineralized material such as *Morania* and probable algae.

Antelope Mountains ("Red Wheeler locality"; Wheeler Formation, Drumian, Bolaspidella Zone). – This site is in the upper Wheeler Formation in the House Range ("House Range Wheeler"; Fig. 1), Millard County, Utah, and corresponds to locality 116 of Conway Morris & Robison (1988). The site is in the upper 20 m of the formation. Calcareous shale at the site is light gray to orange-red, and material here occurs with agnostids, *Elrathia*, and chancelloriids. Indeterminate worms occur at this site (Conway Morris & Robison 1988).

Spence Gulch (Spence Shale Member, Langston Formation, Wuluan, Glossopleura Assemblage Biozone). – Spence Gulch is located in the basal part of the Langston Formation (Fig. 1), which is ~150 m thick here. The section here consists of a dip slope of Geertsen Canyon

Figure 2. New specimens of *Margaretia dorus* Walcott, 1931 from the Wheeler Formation (A–E) and Langston Formation (Spence Shale) (F). A – FHPR 11648. B – FHPR 17764 (left) and FHPR 17069 (right). C – FHPR 16709. D – FHPR 11672. E – FHPR 13137. F – FHPR 16746. Specimens in A, B, D, and E from Drum Mountains (Wheeler), in C from Wheeler Amphitheater (Wheeler), and in F from Miners Hollow (Spence). All scale bars = 1 cm.



Quartzite to the east (*i.e.*, Prospect Mountain Quartzite of Maxey 1958), overlain by a ~6 m covered interval accounting for the Naomi Peak Member of the Langston Formation and the basal beds of the Spence Shale. The combined thickness of these two members is ~26 m (Maxey 1958). Specimens for this study were collected from the lower 2–4 m of the ~20 m exposure of Spence Shale, which equates to a level ~8–10 m above the top of the Prospect Mountain Quartzite (Maxey 1958). This site is the traditional creek cut-bank locality in the eastern Bear River Range in Bear Lake County, Idaho, that was designated as the type locality for the Spence Shale and which was first collected around the turn of the 20th century (Walcott 1906). The overlying Ute Formation is exposed farther north toward Mill Creek from the cut-bank exposure. Material occurs in a soft, dark gray, slightly calcareous shale in the lower levels of the cut-bank, along with abundant trilobites, agnostids, hyoliths, and brachiopods.

Wheeler Amphitheater (Wheeler Formation, Drumian, Bolaspidella Zone). – This site is in the center of the Wheeler Amphitheater in the House Range (“House Range Wheeler”; Fig. 1) and is the same as the Robert Harris Quarry of Rigby (1978) and the locality 115 of Robison & Richards (1981) and Conway Morris & Robison (1986). This locality is thought to be the type locality of the Wheeler Formation as defined by Walcott (Robison & Babcock 2011). It is ~7 m below the Wheeler-Marjum contact (Gaines, personal communication 2021). Specimens occur in hard light gray calcareous shale, and the associate biota includes trilobites, agnostids, sponges, chancelloriids, and other taxa.

Systematic Paleontology

Phylum Hemichordata Bateson, 1885
Class Enteropneusta Gegenbaur, 1870

Genus *Margaretia* Walcott, 1931

Margaretia dorus Walcott, 1931

Figure 2

Material. – FHPR 16709 (Wheeler Amphitheater), FHPR 11645, FHPR 11648–11649, FHPR 11654, FHPR 11672, FHPR 13088, FHPR 13137, FHPR 16644, FHPR 17068–17071, FHPR 17628–17629, FHPR 17764 (all Drum Mountains), FHPR 16746 (Miners Hollow), all fenestrated living tubes.

Description. – The best-preserved of the 14 Drum Mountains specimens is FHPR 11648 (Fig. 2A), which

is 120 mm long and ~15–20 mm wide, with undulating edges. Numerous well preserved, mostly diamond-shaped pores of various sizes are visible along its length. Specimen FHPR 13137 (Fig. 2E) is ~100 mm long and 20 mm wide and is not as well preserved; FHPR 17069 and FHPR 17764 comprise two specimens in different layers of the same slab (Fig. 2B), one 75 mm by 14 mm and the other 54 mm by 9 mm. Specimen FHPR 17628 is 76 mm long by 17 mm wide, and consists of a fibrous tube with numerous pores similar to other specimens. Specimen FHPR 11672 is a possibly branched specimen 123 mm long and 15 mm wide (Fig. 2D), with moderately well preserved pore structures.

Specimen FHPR 16709 from Wheeler Amphitheater is 60 mm long and ~14 mm wide, with a near 90° bend about mid-length (Fig. 2C).

Specimen FHPR 16746 from Miners Hollow is 113 mm long and 20 mm wide (Fig. 2F) and is missing a central portion of its length due to weathering of an oval piece of shale from the slab’s center. Pores are irregularly distributed through these latter two specimens but their form is standard for this genus; typical fibrous elements make up most of the fossils.

Discussion. – Because these fossils show no indication of the enteropneust *Oesia*, found to be living inside tubes previously assigned to *Margaretia* in the Burgess Shale (Nanglu *et al.* 2016), we identify them as the tube structures *Margaretia* rather than the worm taxon itself. These specimens represent a previously reported taxon from each area, but they add to the known abundance at each. In the Wheeler Formation, *Margaretia dorus* Walcott, 1931 is particularly common in the Antelope Mountains (locality 116), the Wheeler Amphitheater (*e.g.*, the type locality), and further north in the Drum Mountains. However, it has not yet been reported from the southern sites of the House Range (*e.g.*, Mockingbird Gulch, Marjum Pass), possibly due to them representing deeper parts of the House Range Embayment (Lerosey-Aubril personal communication 2022).

Occurrence. – Drum Mountains and Wheeler Amphitheater, Wheeler Formation, Miaolingian (Drumian); Miners Hollow, Spence Shale Member of Langston Formation, middle Cambrian, Miaolingian (Wuluan).

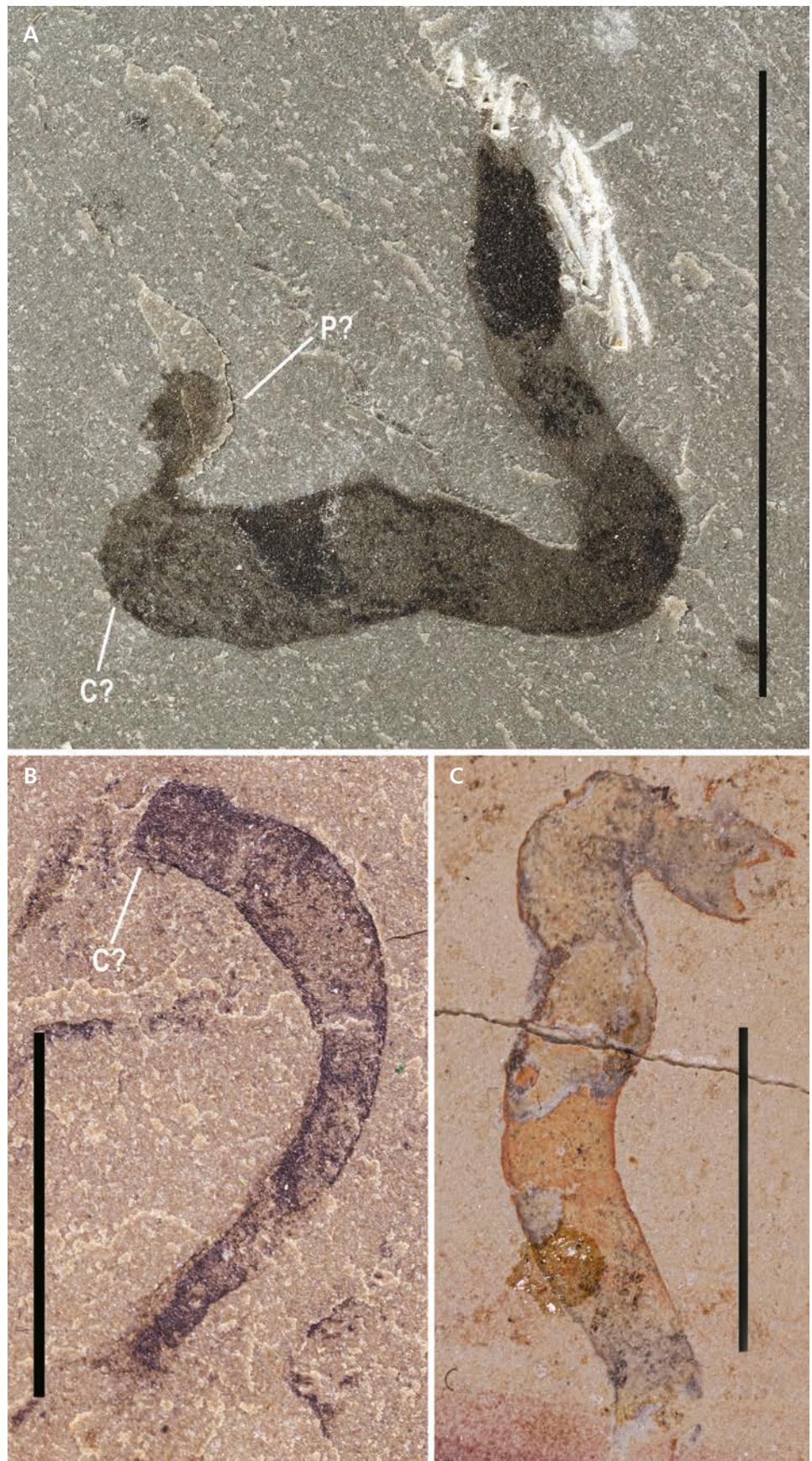
Genus *Spartobranchus* Caron, Conway Morris & Cameron, 2013

Spartobranchus? sp.

Figure 3

Material. – FHPR 11436, FHPR 16664 (partial bodies), FHPR 11437 (partial tube?).

Figure 3. New possible enteropneust (*Spartobranchus*? Caron, Conway Morris & Cameron, 2013) specimens from the Wheeler Formation, all from the Drum Mountains. A – FHPR 16664, showing anterior expansion of body diameter and possible collar and proboscis. B – FHPR 11436, showing possible collar and similar anterior expansion of body. C – FHPR 11437, possible tube. Abbreviations: C? = possible collar; P? = possible proboscis. All scale bars = 1 cm.



Description. – FHPR 16664 is 23.4 mm long and 2.7 mm wide at its widest point (Fig. 3A). From the apparent posterior end, it widens gradually until it reaches the anterior(?) 2.1 mm, where it is greatly constricted, resulting in a very bulbous anterior end. Specimen FHPR 16664 appears to consist of the proboscis, collar, and anterior trunk (Nanglu *et al.* 2015) of a possible enteropneust worm, although none of the internal structures of these regions of the worm is discernable (Caron *et al.* 2013).

Specimen FHPR 11436 is preserved in a C-shaped bend, tapering toward the posterior(?) and with blunt rounding at the anterior(?) ends (Fig 3B). It is 16.8 mm long along its arc and is a maximum of 3.3 mm in width. Specimen FHPR 11436 appears to consist of the collar and anterior trunk region of a possible poorly preserved enteropneust worm.

Specimen FHPR 11437 is curved and bent in a J-shape at the anterior(?) end (Fig. 3C). This same end appears to have a V-shaped central indentation and to represent the opening to a hollow structure, possibly a tube. Other details cannot be distinguished, and the specimen is cut off by the edge of the shale piece. It is 30.1 mm long and 3.7 mm wide.

Discussion. – FHPR 16664 and FHPR 11436 are tentatively interpreted as incomplete bodies of *Spartobranchus*, based on compatibilities in overall shape (e.g., bulbous proboscis-like anterior end in FHPR 16664, gradually anteriorly expanding body in both specimens) and size with this taxon, and the fact that it is known to occur in the Wheeler Formation (Caron *et al.* 2013), although previously in the House Range (Gaines personal communication 2022). Another parallel with that taxon is preservational differences in the shade of the body between the anterior and posterior ends (Caron *et al.* 2013). If confirmed by the discovery of better preserved specimens displaying details of the internal anatomy, the presence of this taxon in the Drum Mountains would indicate that it was a common component of both Wheeler biotas, like *Margaretia/Oesia*.

Although little detail is preserved in FHPR 11437, it is similar in overall form and preservation to tubular structures associated with *Spartobranchus* bodies (Caron *et al.* 2013), although this identification is even more tentative than with the body fossils FHPR 11436 and FHPR 16664.

Occurrence. – Drum Mountains, Wheeler Formation, middle Cambrian, Miaolingian (Drumian).

Enteropneusta? gen. et sp. indet.

Figures 4–6

Material. – FHPR 11477 (Drum Mountains), curled individual preserved in its living tube or burrow; FHPR

18283 (Drum Mountains), curled individual; MWC 6919 (Mockingbird Gulch), nearly complete body.

Description. – FHPR 11477 is preserved as a part and counterpart, with one end cut off by the edge of the piece (Fig. 4). The specimen includes a 57.1 mm long, 5.8 mm wide dark gray structure interpreted as a possible living

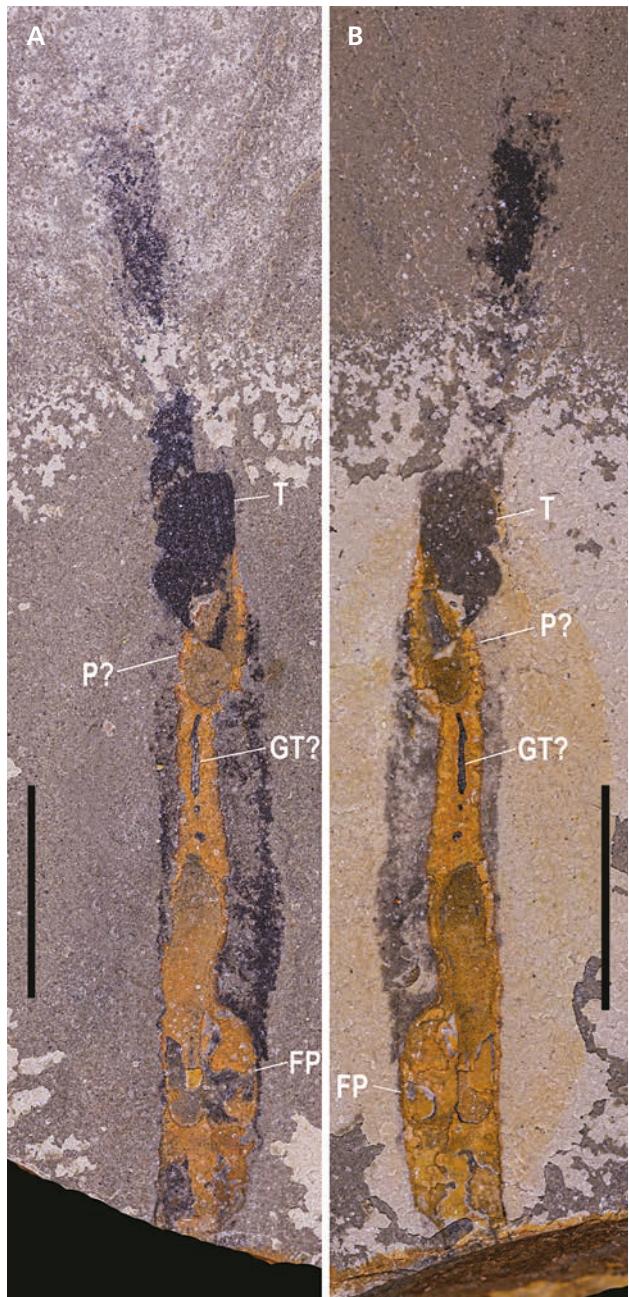


Figure 4. Possible enteropneust specimen FHPR 11477 from the Wheeler Formation of the Drum Mountains. Worm body preserved in orange, possible living tube in dark gray. A – part. B – counterpart. Scale bars = 1 cm. Abbreviations: FP = folded portion of posterior body; GT? = possible gut trace; P? = possible proboscis; T = living tube.

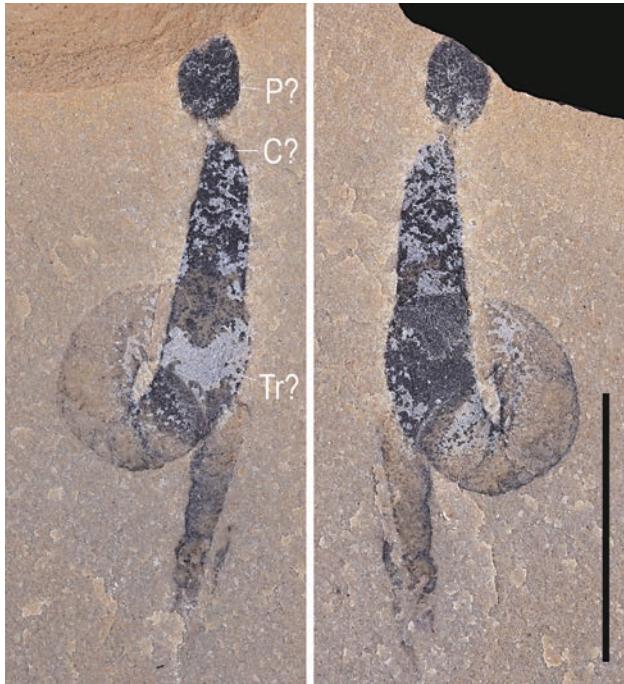


Figure 5. Part and counterpart of possible enteropneust specimen FHP 18283 from the Wheeler Formation of the Drum Mountains. Scale bars = 1 cm. Abbreviations: C? = possible collar; P? = possible proboscis; Tr? = possible trunk.

tube or mucus-lined burrow. The margins of this tube are blurred slightly anteriorly due to preservation. The posterior(?) half of this tube/burrow houses an orange, ferruginous mineral (possibly limonite) structure, which we regard as the curled body of a worm. It reaches 42.3 mm in (outstretched) length and 3.4 mm in maximum width, and exhibits a distinct teardrop shaped anterior end, here interpreted as the proboscis that strongly tapers anteriorly. This proboscis is separated by an abrupt narrowing from the rest of the body, which gently widens posteriorly and folds over in a J- or hook-like shape. Internally, a dark central line in the region immediately posterior to the proboscis may represent a short portion of the gut (Fig. 4).

Specimen FHP 18283 is an individual 3.9 mm maximum body width and 22.6 mm long as preserved (longer due to curling) (Fig. 5). The body is curled into what appears to be a complete 360° loop. The anterior(?) end has a distinctly bulbous structure (proboscis?), and the posterior(?) end tapers and becomes lighter in color.

In MWC 6919 the posterior(?) end of the body appears to be rounded and the anterior(?) end slightly spade-shaped, with a slight constriction of the body outline just posterior to the anterior end (Fig. 6). The body is 24.9 mm long and 5.9 mm wide (L:W 4.2), and bounded by smooth, entire margins – there is no clear indication of lateral lobes. Transverse, curved to chevron-shaped carbonaceous bands associated with a similarly preserved

central longitudinal band may represent remains of the digestive system or other internal organs.

Discussion. – FHP 11477 appears to represent a worm inside its living tube or mucus-lined burrow (e.g., Nanglu & Caron 2021). The anterior end of the worm lacks hooks or spines typical of priapulids (at least in its state of



Figure 6. Possible enteropneust specimen MWC 6919 from the Wheeler Formation, Mockingbird Gulch (House Range). Scale bar = 1 cm.

preservation), but instead displays an elongate teardrop shape that is reminiscent of the shape of the proboscis of some modern enteropneusts (e.g., *Ptychodera* Eschscholtz, 1825). This elongate shape contrasts with the short, rounded shape of the proboscis in *Oesia* (Nanglu *et al.* 2016) and *Spartobranchus* (Caron *et al.* 2013), suggesting that this specimen likely represents a distinct enteropneust taxon. However, the lack of a distinct collar region prevents a more confident assignment to the Enteropneusta.

Specimen FHPR 18283 has an anterior end that also lacks hooks or spines typical of priapulids and instead displays a rounded shape that is similar to some enteropneusts (including FHPR 16664, Fig. 3A, and specimens illustrated by Nanglu *et al.* 2015), though it is rather different from FHPR 11477 or MWC 6919. The posteriorly tapering body with different posterior preservation may also be characteristic of some enteropneusts.

Specimen MWC 6919 is similar to enteropneusts in having in spade-shaped to bulbous apparent anterior end (proboscis?) devoid of spines or hooks. The internal structure appears to differ from that of the “undetermined worms” of Conway Morris & Robison’s (1988: pp. 43, 44), also from the House Range, in having paired structures projecting laterally from an axial structure of some kind.

Occurrence. – Drum Mountains, upper Wheeler Formation, Miaolingian (Drumian); Mockingbird Gulch, upper Wheeler Formation, Miaolingian (Drumian).

Unranked Scalidophora Lemburg, 1995

Phylum Uncertain

Family Selkiriidae Conway Morris, 1977

Genus *Selkirkia* Walcott, 1911

Selkirkia willoughbyi Conway Morris & Robison, 1986

Figure 7A, B

Material. – FHPR 16654, FHPR 11652, both tubes.

Description. – FHPR 16654 is a small tube with smooth external surface, length ~5.1 mm with a maximum width of 1.8 mm (Fig. 7A); FHPR 11652 is 22 mm long and 5.0 mm wide (Fig. 7B). The ratios of anterior width/posterior width for both is ~2.2.

Discussion. – The two specimens are assigned to *S. willoughbyi* Conway Morris & Robison, 1986, based on the anterior width/posterior width ratio, which is in the range of this species and above that of *S. columbia* Conway Morris, 1977 and *S. spencei* (Conway Morris & Robison 1986). Both specimens match the distinctive narrower

posterior width of *S. willoughbyi*, reflecting preservation of a more compressed living oval cross-section. Specimen FHPR 11652 is relatively large, but FHPR 16654 is approximately one-third the average length of Conway Morris and Robison’s (1986) paratypes of *Selkirkia willoughbyi* from the same Wheeler site in the Drum Mountains. Importantly, while common in the Drum Mountains, this species is as-yet unknown in the Wheeler strata of the House Range; there, it has been found in the slightly younger Marjum Formation (holotype; Conway Morris & Robison 1986).

Occurrence. – Drum Mountains, Wheeler Formation, Miaolingian (Drumian).

Selkirkia spencei Resser, 1939

Figure 7C–H

Material. – FHPR 11230, FHPR 11233, and FHPR 11235 (Spence; all tubes occurring on slabs with trilobites); FHPR 11290A and 11290B (Ophir; both tubes); FHPR 11651 (Drum Mountains, tube).

Description. – Spence specimens FHPR 11230 and 11233 are long, only slightly tapering tubes with smooth external surface, and lengths of 37.6 mm (as preserved) and 47.6 mm, respectively, with maximum widths of 5.2 and 6.7 mm (Fig. 7D and 5E). The ratio of anterior width/posterior width for these specimens is ~1.16–1.52. Specimen FHPR 11235 (Fig. 7F) is 35.1 mm long and has an anterior and posterior width of 6.7 and 4.8 mm (yielding a ratio of 1.39, similar to the other Spence specimens).

Both Ophir specimens on FHPR 11290 (Fig. 7G and 7H), which also contains cranidia and pygidia of the dolichometopid trilobite *Glossopleura producta*, are only slightly tapering anterior to posterior with ratios of 1.5 and 1.71. At 29.0 and 30.6 mm, the specimens are slightly shorter than those from Spence Gulch but are otherwise similar.

Specimen FHPR 11651 is 34 mm long and 7.0 mm in anterior width. The specimen’s anterior width:posterior width ratio (AW:PW) is 1.3, as preserved, but some of the posterior length and taper appears to be missing. The sides are relatively straight and nearly parallel.

Discussion. – These specimens match Resser’s (1939) original material of *S. spencei* in the long tubes with only slight tapering from anterior to posterior so that the edges appear nearly parallel. This is confirmed by their low anterior width/posterior width ratios that rarely exceed 1.5, a value well below that of *S. willoughbyi* and *S. columbia* (~2.1 and ~1.7–1.9, respectively; Conway Morris & Robison 1986).

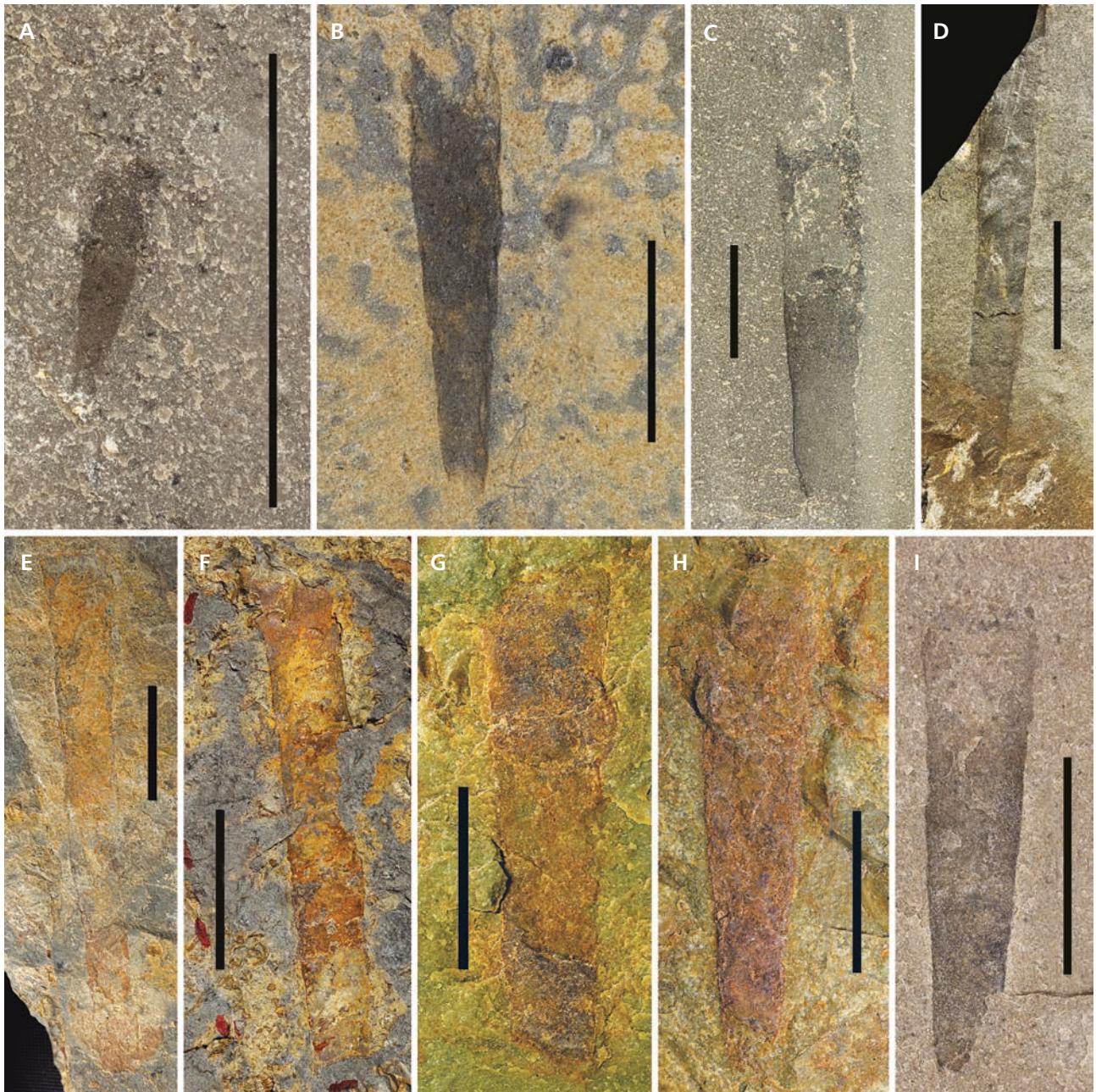


Figure 7. New specimens of *Selkirkia* Walcott, 1911 from the Wheeler Formation, Drum Mountains, (A–C, I), Langston Formation (Spence Shale), Spence Gulch (D–F), and Ophir Formation, Bowman Gulch (G–H). • A, B – *Selkirkia wiloughbyi* Conway Morris & Robison, 1986; A – FHPR 16654, B – FHPR 11652. • C–H – *Selkirkia spencei* Resser, 1939; C – FHPR 11651, D – FHPR 11230, E – FHPR 11233, F – FHPR 11235, G – FHPR 11290A, H – FHPR 11290B. • I – *Selkirkia columbia* Conway Morris, 1977, FHPR 18287. All scale bars = 1 cm.

Specimens FHPR 11290A and 11290B represent the first occurrence of *Selkirkia* reported from the Ophir Formation. *Selkirkia spencei* are not abundant but neither are they rare at Spence Gulch. Their first appearance in the coeval and geographically proximal Ophir Formation, therefore, is not entirely surprising. Other related taxa are not as period.

Specimen FHPR 11651 is too incomplete to calculate an accurate AW:PW ratio, but its overall only slightly

tapering form is similar to *S. spencei*; this would be the first occurrence of this species in the Wheeler Formation.

Occurrence. – Spence Gulch, Spence Shale Member of Langston Formation, Miaolingian (Wuliuan); Bowman Gulch, Ophir Formation, Miaolingian (Wuliuan); Drum Mountains, Wheeler Formation, Miaolingian (Drumian).

***Selkirkia columbia* Conway Morris, 1977**

Figure 7I

Material. – FHPR 18287, tube.

Description. – FHPR 18287 is a medium-sized tube with smooth external surface, length 20.7 mm with a maximum width of 4.8 mm and a posterior width of 2.8 mm (Fig. 7I). The ratio of anterior width/posterior width is ~1.7.

Discussion. – The tube form and AW:PW ratio of FHPR 18287 are similar to those of *Selkirkia columbia* (Conway Morris & Robison 1986) and are distinct from *S. willoughbyi* and *S. spencei*.

Occurrence. – Drum Mountains, Wheeler Formation, Miaolingian (Drumian).

***Selkirkia* sp.**

Figure 8

Specimen. – DMNH EPI.42918, tube.

Description. – Bright Angel specimen DMNH EPI.42918 is 12.1 mm long as preserved, 5.4 mm in anterior width, and 4.1 mm in posterior width (Fig. 8); it is in a shale with abundant detrital mica.

Discussion. – This specimen appears to be the anterior end of a *Selkirkia* tube, possibly *S. spencei* based on the size and apparently very slight taper. There are no

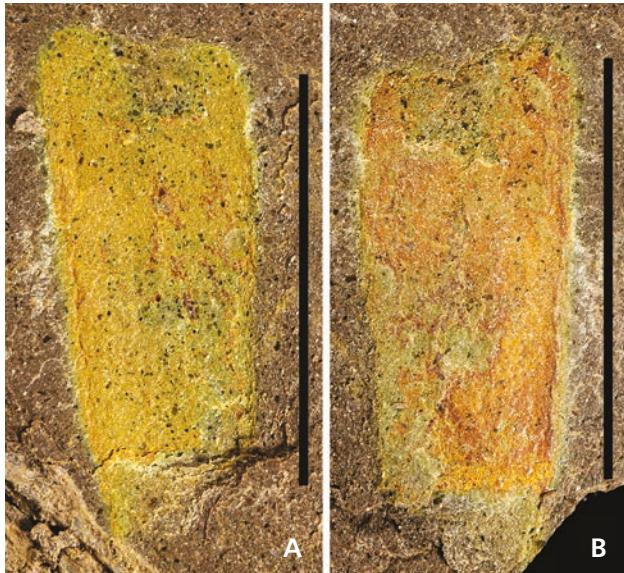


Figure 8. *Selkirkia* sp. from the Bright Angel Formation at the Diamond Bar Ranch section. A, B – part and counterpart of DMNH EPI.42918. Scale bars = 1 cm.

indications of spicules suggestive of a sponge, nor of chancelloriid sclerites, and annuli suggestive of *Cambrohytium* Conway Morris & Robison, 1988 are also lacking. This is the first report of *Selkirkia* in the Bright Angel Formation.

Occurrence. – Diamond Bar Ranch, Bright Angel Formation, Miaolingian (Wuluan).

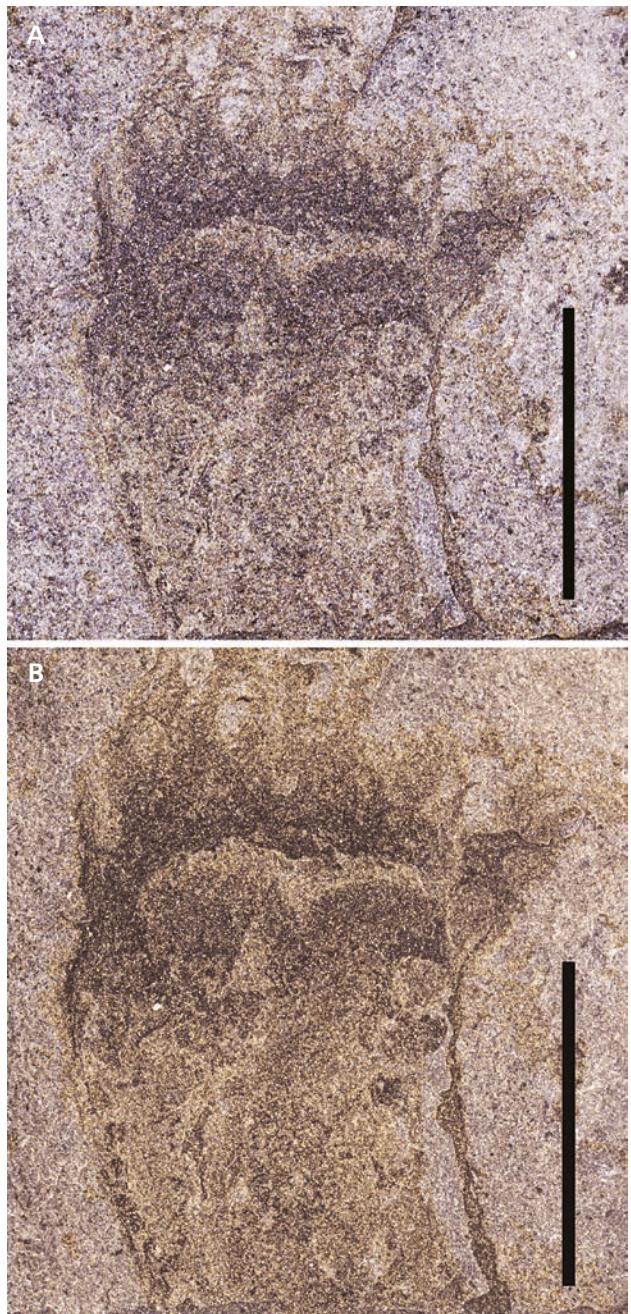


Figure 9. Indeterminate tube gen. et sp. indet., FHPR 17765, from the Wheeler Formation in the Drum Mountains. A – regular lighting. B – under polarized light. Scale bars = 5 mm.

Phylum incertae sedis

Indeterminate tube gen. et sp. indet.

Figure 9

Material. – FHPR 17765, partial tube.

Occurrence. – Drum Mountains, Wheeler Formation, Miaolingian (Drumian).

Description. – FHPR 17765 occurs on the edge of a slab with two *Margaretia* specimens (FHPR 17069, FHPR 17764) and consists of a partial tube 9 mm by 6.9 mm (Fig. 9). The preserved end appears to have filaments, but no pores are discernable. This end also has some coloration appearing to indicate that the tube may have been hollow.

Discussion. – Although it is incomplete and only moderately well preserved, FHPR 17765 may represent a torn tube of some type, possibly of *Margaretia*.

Occurrence. – Drum Mountains, Wheeler Formation, Miaolingian (Drumian).

Worm-like organism gen. et sp. indet.

Figure 10

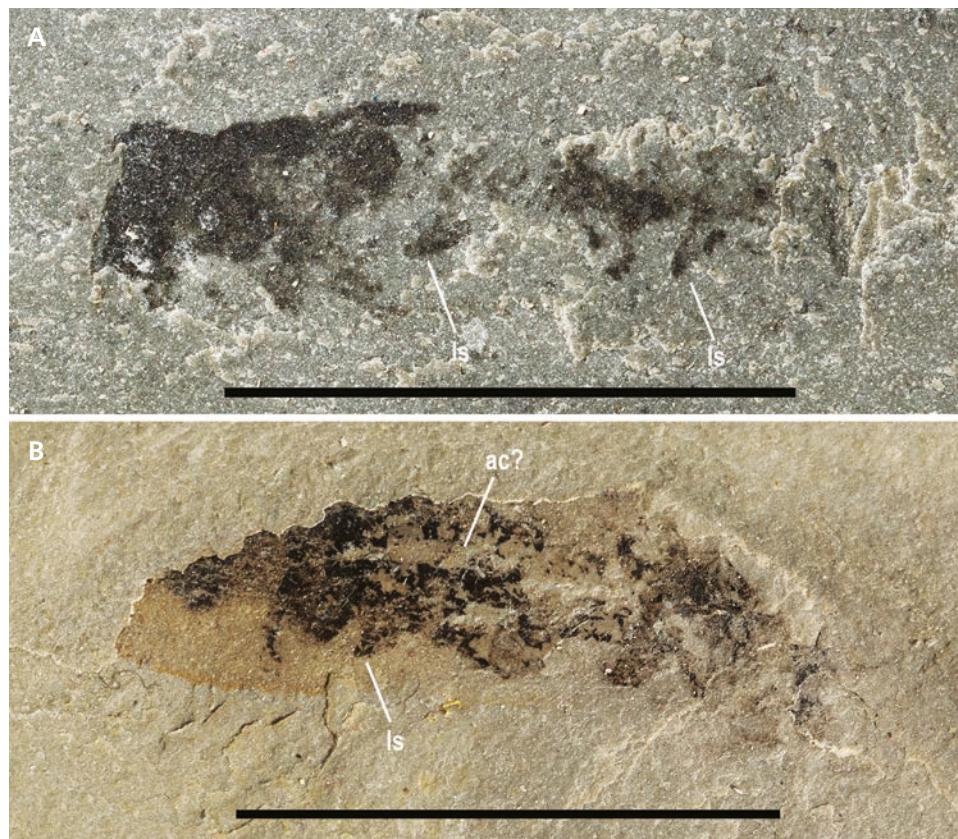
Figure 10. Indeterminate worm-like organisms gen. et sp. indet. from the Wheeler Formation. A – FHPR 16646, from the Drum Mountains. B – FHPR 16663, from Mockingbird Gulch (House Range). Abbreviations: ac? = possible alimentary canal trace; ls = lobate structures. Both scale bars = 1 cm.

Material. – FHPR 16663 (Mockingbird Gulch), FHPR 16646 (Drum Mountains).

Description. – FHPR 16646 has a low length to width ratio of 2.9 (13.0 mm long and 4.4 mm wide), although it is possible that this specimen is preserved in lateral view rather than a dorsal or ventral view (Fig. 10A). Specimen FHPR 16646 may also be preserved incomplete in its length, thus, this is a maximum length to width ratio (L:W). The body appears to be short, smooth, and featureless. Most prominent, however, are three to six lateral (or ventral?) lobate structures that are better defined and more acuminate than those on FHPR 16663.

Specimen FHPR 16663 also has a low length to width ratio of 3.3 (15.3 mm long and 4.6 mm wide) and has a bluntly rounded anterior(?) end and a tapering posterior(?) end (Fig. 10B), although it is partially covered dorsally(?). It is preserved as a dark presumably carbonaceous material that shows hints of segmentation or annulation, a central alimentary canal, and possible lateral or ventral lobate structures.

Discussion. – Although the best preserved of the lobate structures in both specimens bear some resemblance to lobopodian appendages (lobopods) in overall shape,



neither annulation on the specimen nor terminal claws on the apparent appendages can be identified, and preservation is in general too poor to identify the specimens with certainty. The specimens are similar in shape, proportions, and in having suggestions of lobopods or parapods, to some undetermined worms illustrated by Conway Morris & Robison (1988: fig. 31.1a, b). Alternatively, these may represent decayed polychaetes or arthropods in lateral view.

Occurrence. – Mockingbird Gulch (House Range) and Drum Mountains, upper Wheeler Formation, Miaolingian (Drumian).

Worm-like structures *incertae sedis*

Figure 11

Material. – FHPR 11438, FHPR 11439, FHPR 11441, FHPR 11443, FHPR 11444, FHPR 11476, FHPR 16652, FHPR 16659, FHPR 16660, FHPR 16662, FHPR 18284, FHPR 18286 (all Drum Mountains); FHPR 11424 (Mockingbird Gulch); FHPR 11418–FHPR 11420 (Antelope Mountains locality 116).

Description. – These specimens are long, with blunt “anterior” and tapering “posterior” tips in the best-preserved specimens. Most of the lengths of the middle sections of the bodies are of consistent width. Specimens are typically smooth and featureless with no hint of segmentation or lobate structures, although in many specimens this absence of features may be due to poor preservation.

Among specimens from the Drum Mountains, FHPR 16652 is the best preserved and most complete of the specimens at 44.9 mm long and 3.6 mm wide (L:W = 12.5), although neither end appears to preserve the body’s full outline (Fig. 11A and B). Despite the sharp preservation, no internal details are preserved.

Specimen FHPR 11444 is 57.7 mm long, with 13.3 mm of one end folded back near the rest of the body in a loop shape (Fig. 11C). This “hooked” end of the body may be the anterior end, but preservation is not good enough to be sure, and details along the length of the body are not apparent. The width of the body is ~5.5 mm (L:W = 10.49).

Specimen FHPR 11438 is 33.6 mm long and 3.6 mm wide and is preserved straight and uncurved (Fig. 11D). What appears to be the anterior end is slightly tapered, with a bulbous tip. The main body has numerous round, infilling(?) patches of matrix in shapes reminiscent of palaeoscolecid plates, although they are not arranged with circumaxial regularity as those should be.

Specimen FHPR 16662 is shorter and appears to preserve less of its length at 31.3 mm long and 4.3 mm

wide (untapered “posteriorly” where it is incomplete), but it does preserve what appears to be a bluntly rounded anterior end (Fig. 11E).

Specimen FHPR 18286 is 31.6 mm long and up to 4.2 mm wide (Fig. 11F). No internal structures or variation is apparent in this specimen, although there is some strong variation in width of the specimen, particularly near the center of its preserved length. Specimen FHPR 18284 is 62.3 mm long and up to 6.9 mm wide (Fig. 11G). One end is incomplete and the intact end is blunt; changes in shade suggest varied preservation, or perhaps folding, along its length. One section of dark material near the center of the specimen is of varied width along its length and appears to be within the rest of the specimen.

Specimen FHPR 11439 is 39.2 mm long by 3.9 mm wide; it has well defined, straight lateral edges and one apparently complete, blunt end but no internal features. Specimen FHPR 11443 is 38.5 mm long and 4.5 mm wide; it appears to be incomplete and featureless. Specimen FHPR 11476 is 54.2 mm long and a fairly consistent ~6 mm wide (L:W = 9.03); preservation is too poor to discern features along the body.

From Mockingbird Gulch, FHPR 11424 is 50.8 mm long and 3.4 mm wide. It is incomplete at both ends, and no structures can be discerned along its length, although a possible gut trace may be indicated by a slight central linear depression (Fig. 11H).

Three poorly preserved specimens from Antelope Mountains include FHPR 11418, which is 90.7 mm long and 3.5 mm wide. It is preserved as a red film with some hints of a mid-line canal and possible annulation, but neither of these can be confirmed (Fig. 11I). Specimen FHPR 11419 is a shorter segment of a similarly preserved specimen. Specimen FHPR 11420 is smaller and somewhat better preserved; there is a small mid-line canal near the tapered end. The main body at mid-section consists of narrowly spaced, longitudinal tubular structures aligned diagonal to the main axis of the body. The fossil is otherwise featureless and unidentifiable (Fig. 11J).

Discussion. – Many of these specimens are similar to one of Conway Morris & Robison’s (1986) “indeterminate fossil worms” in their figure 11.1, which are also mentioned as “elongate vermiform structures” (pp. 20, 21). Their figured specimen, KUMIP 144852 (Conway Morris & Robison 1986), is broadly similar in proportions and features to FHPR 16652, FHPR 11444, and FHPR 16662 and is from the same locality. Overall, this suite of fossils shares very broad similarities to poorly preserved specimens of scalidophorans or enteropneusts (Conway Morris 1977, Caron *et al.* 2013), or possibly living tubes, burrows, or coprolites of animals of similar size (Conway

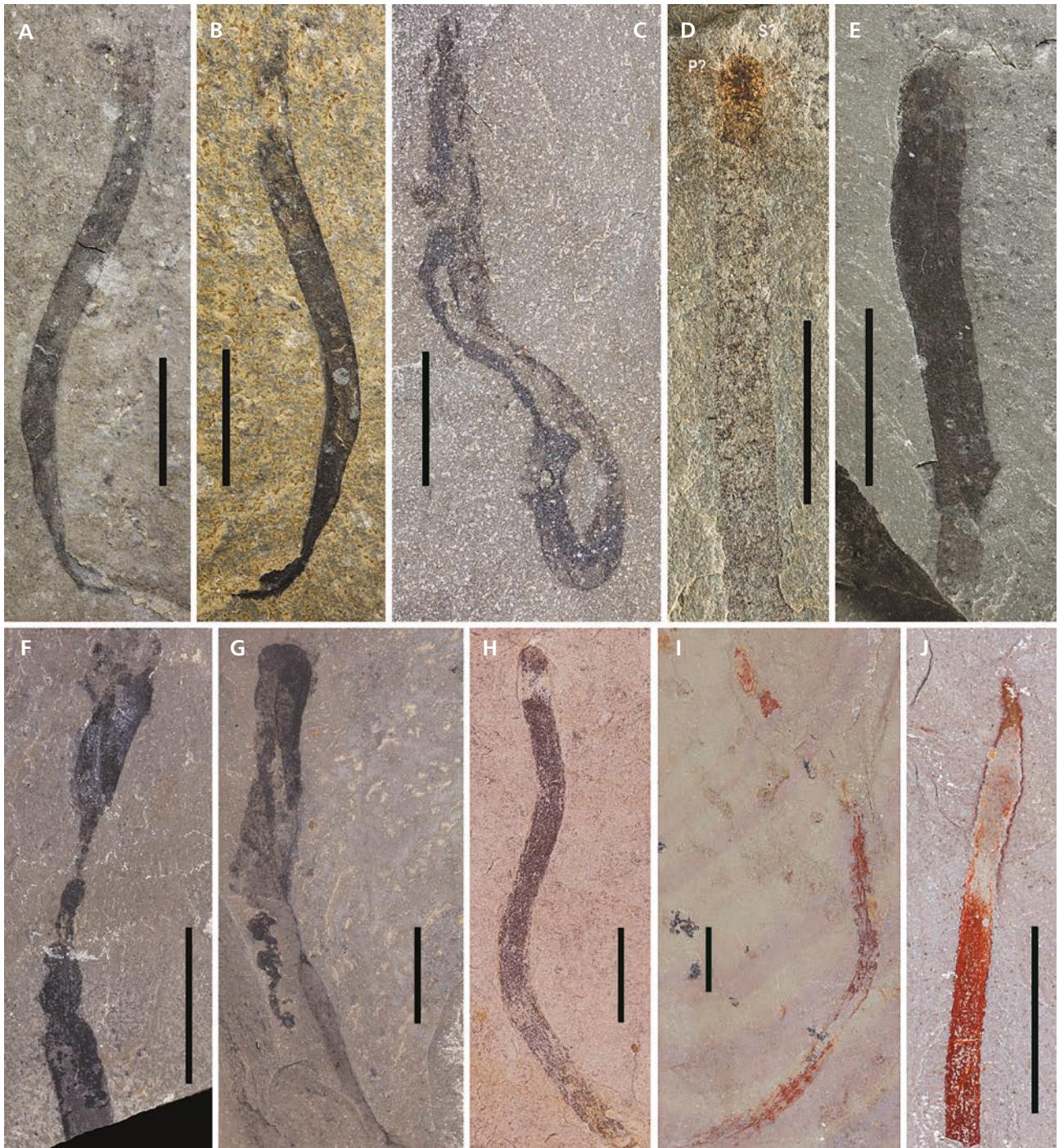


Figure 11. Indeterminate worm-like structures *incertae sedis* from the Wheeler Formation of the Drum Mountains (A–G), Mockingbird Gulch (H), and Antelope Mountains (I–J). A–B – part and counterpart of FHPR 16652. C – FHPR 11444. D – FHPR 11438. E – FHPR 16662. F – FHPR 18286. G – FHPR 18284. H – FHPR 11424. I – FHPR 11418. J – FHPR 11420. Abbreviations: P? = proboscis?; S? = spines? (D). All scale bars = 1 cm.

Morris & Robison 1986, 1988; Kimmig & Strotz 2017, Chen *et al.* 2020, Nanglu & Caron 2021). Scalidophorans demonstrate a range of dietary modes from predatory to generalists that may have ingested some sediment (Martin *et al.* 2016), so those with tubes and/or burrows may also exhibit a range of preservation types. The true nature of

these Wheeler fossils is still elusive due to their poor preservation.

Occurrence. – Mockingbird Gulch, Antelope Mountains locality 116, Drum Mountains, Wheeler Formation, Miaolingian (Drumian).

Discussion

New specimens reported here enhance the known diversity of the Wheeler Formation paleocommunities of the Drum Mountains and House Range. The additional material of *Selkirkia willoughbyi* and the probable occurrence of *S. spencei* suggest that these tubicolous priapulids were more diverse and abundant than previously hypothesized. Among enteropneusts reported here, additional specimens of *Margaretia*, many from one restricted interval in the Drum Mountains, bolster a pattern seen in the Wheeler of both the Drum Mountains and the House Range in which the tubes are ripped at either end and appear to have been possibly transported and/or concentrated in relatively high energy events. Similarly, individual sites and horizons in the Wheeler Formation are often particularly rich in certain taxa. Although the reasons for these richness patterns are not fully understood, it hints at patchy or intermittent monotaxic dominance of enteropneusts and other organisms in some Cambrian seafloor settings.

Selkirkia tubes have been the sole soft-bodied fossils recovered from Spence Shale sites outside of the Wellsville Mountains (e.g., Spence Gulch). The presence of *Selkirkia* now in the Ophir Formation, in addition to the Spence Shale from the Wellsville Mountains, Utah, and Bear River Range, Idaho, demonstrates that the taxon ranged from proximal, relatively shallow settings out to more distal, relatively deep-water settings (Liddell *et al.* 1997), respectively, within the same transects along the Laurentian continental shelf. The first occurrence of *Selkirkia* in the Ophir Formation also indicates the unit's potential for bearing other non-mineralized Cambrian taxa.

Finally, the probable presence of the tubicolous scalidophoran *Selkirkia* in the Bright Angel Formation, if further validated with better-preserved specimens, would extend the geographic range of *Selkirkia* during the Wulian significantly south within the western United States (~650 km), from northern Utah (Spence Shale) to northwestern Arizona.

Conclusions

Among the specimens described here are the first occurrences of the scalidophoran *Selkirkia* in the Ophir and Bright Angel formations and possibly the first occurrence of *S. spencei* in the Wheeler Formation. We acknowledge that preservation of *Spartobranchus*?, possible indeterminate enteropneusts, and indeterminate vermiform specimens from the Wheeler of the Drum Mountains and House Range (Mockingbird Gulch) is marginal, although these specimens are clearly different from most other reported vermiform specimens known

from these units. The additional *Margaretia* specimens described here strengthen indications that the taxon is abundant, possibly in event concentrations, in some beds of the Wheeler in the Drum Mountains as well. With the foregoing in mind, future investigations might benefit from focusing on soft-bodied fossil-bearing intervals in the Ophir and Bright Angel formations, and perhaps also assessing if monotaxic assemblages of tubular fossils and associated vermiform taxa in the Wheeler deposits are tied to specific paleoenvironments or preservational conditions.

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Appendix

Locality details here are listed by site numbers used in Figure 1. Locations given in US Public Land Survey System quarter-quarter sections and by 7.5-minute topographic map quadrangles. (Note: collecting soft-bodied fossils at public land sites requires a permit from the appropriate federal land management agency, if Bureau of Land Management- or Forest Service-administered federal lands, or permission from the land owner, if private land.).

- 1 – Diamond Bar Ranch (Bright Angel Formation, Wulian, *Glossopleura* Assemblage Biozone) – NE1/4, SW1/4, Sec. 24, T29N, R16W, Grapevine Canyon quad.
- 2 – Mockingbird Gulch (Wheeler Formation, Drumian, *Bolaspidella* Zone) – Near center of Sec. 4, T17S, R13W, Marjum Pass quad.
- 3 – Antelope Mountains site RAR 116 (“Red Wheeler locality”; Wheeler Formation, Drumian, *Bolaspidella* Zone) – SE1/4, NE1/4, Sec. 35, T17S, R13W, Marjum Pass quad.
- 4 – Wheeler Amphitheater (Wheeler Formation, Drumian, *Bolaspidella* Zone) – SE1/4, SE1/4, Sec. 2, T17S, R13W, Marjum Pass quad.
- 5 – Drum Mountains (Wheeler Formation, Drumian, upper *Bolaspidella* Zone) – SE1/4, NE1/4, Sec. 20, T15S, R10W, Drum Mtns Well quad.
- 6 – Bowman Gulch (Ophir Formation, Wulian, *Glossopleura* Assemblage Biozone) – N1/2, SW1/4, Sec. 23, T5S, R4W, Ophir quad.
- 7 – Miners Hollow (Spence Shale Member, Langston Formation, Wulian, *Glossopleura* Assemblage Biozone) – NW1/4, SE1/4, Sec. 14, T10N, R2W, Brigham City quad.
- 8 – Spence Gulch (Spence Shale Member, Langston Formation, Wulian, *Glossopleura* Assemblage Biozone) – NE1/4, NE1/4, Sec. 14, T13S, R42E, Midnight Mountain quad.