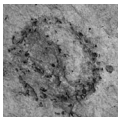


Coprolites in mid-Cambrian (Series 2-3) Burgess Shale-type deposits of Nevada and Utah and their ecological implications

JULIEN KIMMIG & LUKE C. STROTZ



Five types of coprolites, represented by 40 specimens from the Cambrian (Series 2-3) Burgess Shale-type deposits in the Pioche Shale of Nevada and the Spence Shale of Utah, are described. They are preserved in finely laminated deep-water calcareous mudstones. Round to ellipsoid features 13–42 mm in diameter consisting of black carbon film and variable amounts of skeletal fragments are interpreted as coprolites that were originally deposited in a burrow. Two kinds of elongated coprolites are also preserved and either consist of small pellets or skeletal debris. The pellets are typically 0.5 to 2 mm across and have a round to ellipsoid outline. Two different types of pellet-filled burrows are also present. The presence of organic tissue and skeletal fragments in some coprolites provides direct evidence of predatory or scavenging activity, and may advance understanding of the food chain in these Cambrian deposits. • Key words: coprolites, Spence Shale, Pioche Formation, Cambrian, ichnology, burrows, Burgess Shale-type deposit.

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The Burgess Shale-type (BST) deposits of the Great Basin, extending across Western Utah and Nevada, offer significant insight into the ecology of the early to mid-Cambrian (Rigby 1983, Conway Morris & Robison 1986, Lieberman 2003, Briggs *et al.* 2008). Whilst the faunas from the Great Basin BSTs have received focused attention, there have been few studies to date describing the relatively rare bromalites found in those deposits (Robison 1969; Conway Morris & Robison 1986, 1988; English & Babcock 2010). Bromalite is a term that covers all fossils that originated from the digestive tracts of animals, including coprolites (feces), regurgitites (material regurgitated from the oral cavity), *in situ* intestinal contents (cololites) and stomach contents (gastrolites) (Hunt 1992, Aldridge *et al.* 2006). The size and shape of particular bromalites can help to identify the source animal, and the preserved organic matter and fragments in the bromalites indicate what organisms were preyed upon. Early to mid-Cambrian bromalites are rare, as feces often disintegrate or get consumed before they can be preserved (Hollocher & Hollocher 2012, Izumi & Yoshizawa 2016). When preserved though, coprolites are particularly important, as they provide insight into the feeding ecology and biotic interactions of some of the first animal communities (Bengt-

son 2002, Budd 2013), information that body fossils alone cannot provide.

Round, compressed coprolites are the most commonly observed coprolites in the Cambrian BST deposits of North America. They have been reported from the Stephen Formation (Sprinkle 1973, pl. 21, fig. 7), the Wheeler and Marjum Formations (Conway Morris & Robison 1986, fig. 10.2), the Spence Shale (Conway Morris & Robison 1988, fig. 32; and this paper), the Indian Springs Lagerstätte (English & Babcock 2010, fig. 5f), and the Ravens Throat River Lagerstätte (Kimmig & Pratt 2016, unpublished observation). Outside of North America, Cambrian BSTs yield a variety of coprolites, ranging from microscopic size to large pellet-filled burrows. Examples of microscopic phosphatized coprolites are known from the early Cambrian Sirius Passet Lagerstätte in Greenland (Peel 2015), the earliest Cambrian of the Yangtze Gorge in China (Chen & Chen 1980), and the mid-Cambrian Gaotai Formation in southern China (Shen *et al.* 2014). Macroscopic coprolites have been better studied, but the record is still sparse. Specimens have been reported from the early Cambrian Paseky Shale of the Czech Republic (Mikuláš 1995), the early Cambrian Maotianshan Shale of China (Vannier & Chen 2005), the mid-Cambrian Kaili

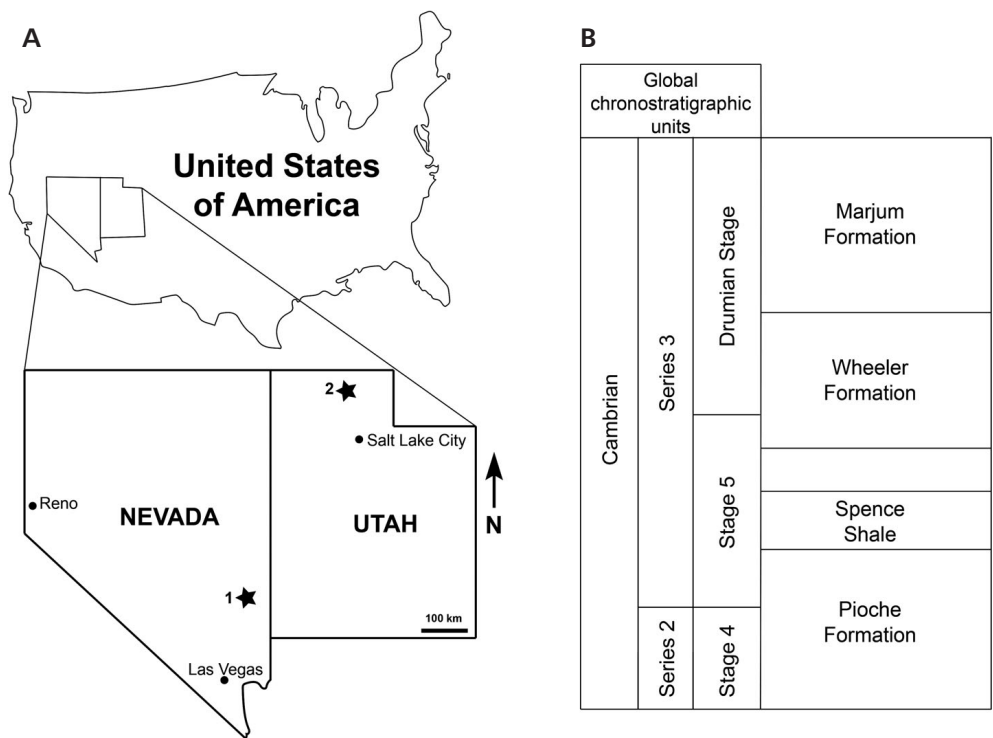


Figure 1. A – map indicating the location of the Chief Range (37° 42' N, 114° 33' W) and Highland Range (37° 53' N, 114° 34' W) localities of the Pioche Formation (1) and the Miner's Hollow (41° 36' N, 112° 02' W) locality of the Spence Shale (2). • B – generalized stratigraphy of the major mid-Cambrian Burgess Shale-type deposits in Nevada and Utah.

Lagerstätte of China (Lin *et al.* 2010), and the mid-Cambrian of Sweden (Eriksson & Terfelt 2007). Despite this growing number of known fossilized coprolites in the Cambrian and the improved knowledge on digestive tracts and feeding habits of several Cambrian animals (Lerosey-Aubril *et al.* 2012, Vannier 2012, Vannier *et al.* 2014) it is often unclear what kind of animal(s) are the source of the coprolites. In most cases though, arthropods or worms are considered to be the producers (Mikuláš 1995, Vannier & Chen 2005, Shen *et al.* 2014).

This paper examines a variety of large coprolites from the late early to mid-Cambrian (Series 2-3) Pioche Formation and Spence Shale of Nevada and Utah. These coprolites occur together with BST soft-bodied fossils and are composed of carbonaceous flakes and films, skeletal debris and, for some Pioche Formation specimens, iron-bearing minerals (Lieberman 2003). Because the coprolites preserve skeletal debris, direct interpretation of predator-prey relationships is possible, as both predator and prey can potentially be identified. Specimens consisting only of carbonaceous films provide some information on the lifestyle of the predator and the preservation of the coprolites in burrows allows the identification of possible producers, by reducing the pool of potential source organisms. As there is some cross-over between the biota of the Pioche Formation/Spence Shale biota and the biotas found in other Cambrian BSTs (Robison *et al.* 2015), these results have broader implications for the interpretation and understanding of coprolites from Cambrian BST deposits.

Geological setting

The coprolites described herein are from the early to mid-Cambrian (Series 2-3, upper *Olenellus* to *Eokochaspis* biozones) Comet Shale Member (Lieberman 2003) of the Pioche Formation in Nevada and the mid-Cambrian (Series 3, *Glossopleura* Biozone) Spence Shale Member of the Langston Formation in Utah (Fig. 1; Liddell *et al.* 1997). Both deposits were likely seaward of a carbonate platform that subsequently planed off and formed part of the fine-grained middle carbonate or outer detrital belt of the Great basin (Robison 1991, Liddell *et al.* 1997, Lieberman 2003).

The Pioche Formation is a deeper water slope deposit, which is separated into six members. At least two horizons containing BST fossils are found in the Comet Shale Member. The first horizon is early Cambrian in age and the second horizon is mid-Cambrian (Moore & Lieberman 2009). The Comet Shale biota is arthropod dominated, including species of olenelloid and ptychoparid trilobites, the carapaced arthropods *Canadaspis*, *?Perspicaris*, and *Tuzoia*, and at least two species of *Anomalocaris* (Lieberman 2003). In addition to arthropods, the priapulid worm *Ottoia*, brachiopods, sponges, hyolithids, gastropods, and eocrinoids are also found. Soft-bodied animals are relatively rare. Olenelloid trilobites are common in the Series 2 parts of the shale, and the ptychoparioid trilobites are common in the Series 3 parts (Lieberman 2003, Webster *et al.* 2008, Moore & Lieberman 2009).

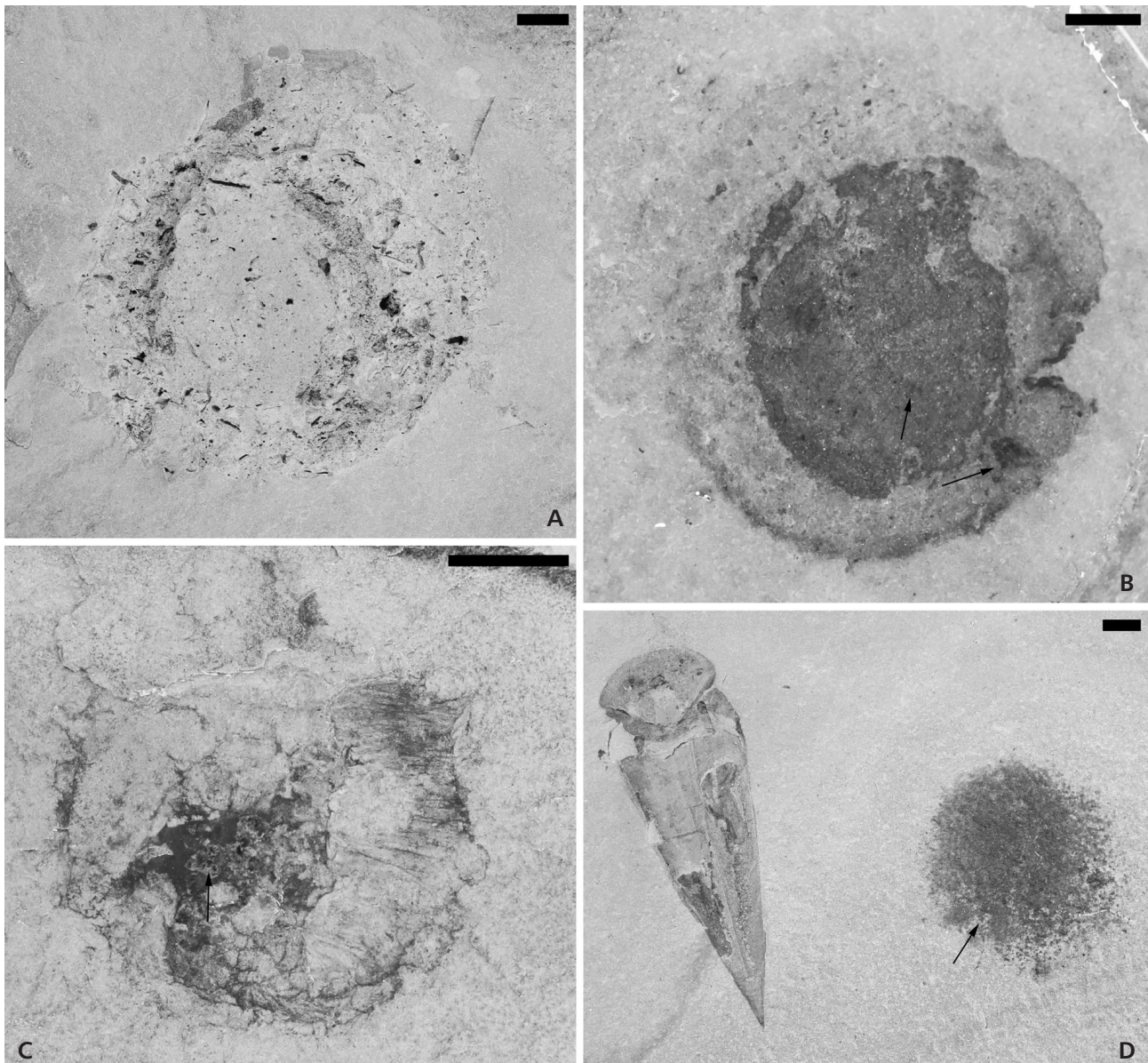


Figure 2. Round disk-shaped coprolites of Morphotype 1. • A – KUMIP 204369 large specimen preserving skeletal fragments. • B – KUMIP 377080 dense aggregate preserving a carbonaceous halo. • C – KUMIP 314126 dense aggregate preserving worm cuticle. • D – KUMIP 314260 dense aggregate with a specimen of *Haplophrentis reesei* on the same slab. Scale bars are 5 mm. Arrows indicate pellets.

The Spence Shale is a regionally extensive deeper water slope deposit found in southeastern Idaho and northeastern Utah (Fig. 1; Liddell *et al.* 1997). The BST fossils occur in several meter-thick calcareous mudstones, and are most abundant on the western flank of the Wellsville Mountains near Brigham City, Utah (Liddell *et al.* 1997, Briggs *et al.* 2008). The Spence Shale biota is one of the more diverse BST biotas and has yielded a wide array of carapaced arthropods, great appendage arthropods, annelid and priapulid worms, hyoliths, brachiopods, sponges, algae and stem group metazoans (Rigby 1983, Briggs *et al.* 2008,

Conway Morris *et al.* 2015, Kimmig & Pratt 2015, Legg & Pates 2017, Kimmig *et al.* in press).

The Spence Shale preserves a diverse ichno fauna of at least 19 species (Hammersburg *et al.* 2013) and the ichnofabric index varies between 1 and 4 through the exposure, with a majority of the layers having an ichnofabric index of 1 (Garson *et al.* 2012; Kloss *et al.* 2015a, b). While most of the traces found in the Spence Shale are shallow burrows, they co-occur with soft-bodied fossils (Garson *et al.* 2012), and some deeper vertical burrows are also present and play an important role in the preservation of the

Table 1. Locality information and size of specimens analyzed in this study. Chief Range is located at 37° 42' N, 114° 33' W, Highland Range is located at 37° 53' N, 114° 34' W and the Miner's Hollow locality in the Wellsville Mountains is located at 41° 36' N, 112° 02' W.

Specimen ID	Morphotype	Locality	Lithostratigraphy	length (mm)	width (mm)	depth (mm)
KUMIP 377064	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	13	12	3
KUMIP 204368	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	29	25	9
KUMIP 204369	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	42	40	1
KUMIP 314124	1	Unrecorded	Spence Shale Mb., Langston Fm.	21	20	1
KUMIP 314126	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	20	19	0.5
KUMIP 314260	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	20	21	0.5
KUMIP 376843	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	20	19	2
KUMIP 376844	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	25	24	6
KUMIP 376845	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	30	27	7
KUMIP 376846	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	17	17	10
KUMIP 376847	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	20	20	5
KUMIP 376848	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	18	16	8
KUMIP 376849	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	24	20	9
KUMIP 376849	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	23	22	8
KUMIP 376850	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	29	27	10
KUMIP 376851	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	22	21	10
KUMIP 377066	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	15	14	2
KUMIP 377077	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	25	19	5
KUMIP 377078	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	25	20	2
KUMIP 377080	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	22	20	0.5
KUMIP 419284	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	19	17	4
KUMIP 419285	1	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	15	7	6
KUMIP 314187	2	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	35	14	3
KUMIP 314195	2	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	25	5	1
KUMIP 377063	2	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	19	12	4
KUMIP 293610	2	Chief Range, Lincoln Co, Nevada	Comet Shale Mb., Pioche Fm.	30	7	1
KUMIP 378577	2	Chief Range, Lincoln Co, Nevada	Comet Shale Mb., Pioche Fm.	25	15	1
KUMIP 378576	3	Highland Range, Lincoln Co, Nevada	Comet Shale Mb., Pioche Fm.	36	12	1
KUMIP 314245	4	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	105	35	0.5
KUMIP 314255	4	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	70	10	0.5
KUMIP 366400	4	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	59	7	0.5
KUMIP 366401	4	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	78	9	0.5
KUMIP 377071	4	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	125	8	0.5
KUMIP 314243	5	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	130	7	1
KUMIP 377075	5	Wellsville Mountains, Box Elder Co, Utah	Spence Shale Mb., Langston Fm.	60	7	0.5

coprolites in this deposit (this paper). The Pioche Formation preserves a variety of trace fossils (Moore & Lieberman 2009), but no detailed studies on their systematics or co-occurrence with the soft-bodied fauna have been attempted to date.

Material

The described coprolites (Tab. 1) are all part of the University of Kansas, Biodiversity Institute, Division of Inverte-

brate Paleontology collections (KUMIP). Pioche Formation specimens were collected between the 1980s and 1990s by the Gunther family, L.B. McCollum, and A.R. Palmer, at the Chief Range (37° 42' N, 114° 33' W) and Highland Range (37° 53' N, 114° 34' W) localities in Lincoln County, Nevada. Spence Shale specimens were collected between the 1970s and 1990s by the Gunther family, P. Rees, and R.A. Robison, at the Miner's Hollow locality (41° 36' N, 112° 02' W) in the Wellsville Mountains, Box Elder County, Utah. Specimens were examined using a Leica S4E binocular microscope. All specimens were

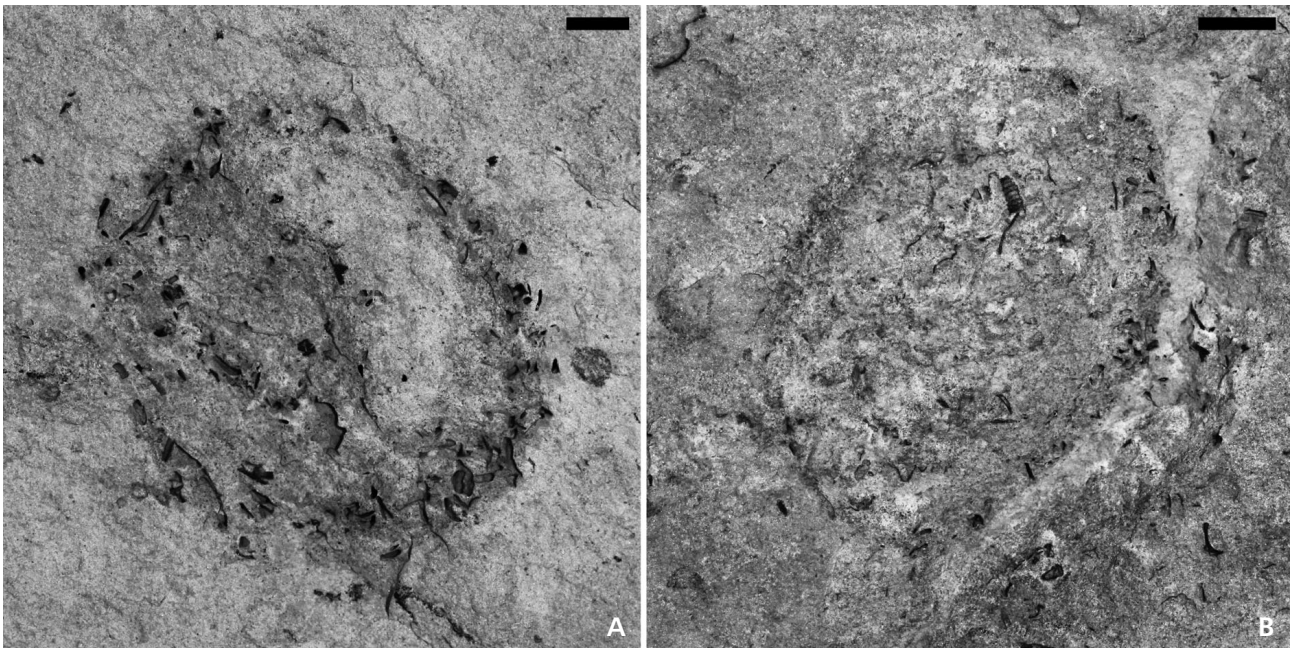


Figure 3. Round disk-shaped coprolite of Morphotype 1. • A – KUMIP 204368 top of specimen preserving skeletal fragments and carbonaceous film. • B – KUMIP 204368 bottom of specimen preserving skeletal fragments and carbonaceous film. Scale bars are 5 mm.

photographed using a Canon EOS 5D Mark II digital SLR camera equipped with a Canon 50 mm macro lens. Pictures were taken submerged in alcohol. The contrast, color and brightness of images were adjusted using Adobe Photoshop.

Description

Coprolite morphotypes

Morphotype 1

The most common coprolite in the Spence Shale is represented by 22 specimens (Spence: KUMIP 204368, 204369, 314124, 314126, 314260, 376844–376851, 377064, 377066, 377077, 377078, 377080, 419284, 419285). Each consists of a round to ellipsoid organic accumulation, ranging from 13 mm to 42 mm in diameter. These have sharp edges and consist of variably dense aggregates composed of up to hundreds of carbonaceous flakes, sometimes with additional worm cuticle, trilobite parts, and/or possible shell fragments (Figs 2A–D, 3A, B, 4A–F). The pellets can be discriminated in the less dense aggregates, where they are dorso-ventrally ovoid to ellipsoid in outline and ~ 0.5 mm. The length-to-width ratio varies between ~ 1:1 to 2:1, variably creating round to ellipsoid pellets. Some aggregates preserve relief up to 3 mm, and six specimens (KUMIP 204368, 376844, 376845, 376848, 376851, 377066) are large enough to be visible on both sides of

their source slab (Figs 3A, B, 4A–F). The thickest coprolites are 10 mm (KUMIP 204368), but the majority range from < 1 mm to 2 mm in size. KUMIP 377080 preserves a 1 mm wide diffuse carbonaceous halo about 2mm from the edge of the inner margin.

Trilobite, brachiopod, and possible eocrinoid (KUMIP 204368 and 204369, Conway Morris & Robison 1988) fragments are preserved in some of the coprolites, and one (KUMIP 314126) also contains worm cuticles. The fossils are always matrix/pellet supported and make up less than 10% of the actual composition of the coprolites. None of the identifiable fossil material appears to be complete.

Morphotype 2

Five specimens (Spence: KUMIP 314187, 314195, 377063, Pioche: KUMIP 293610, 378577) of elongated, ellipsoid coprolites 19 mm to 35 mm in length and 5 mm to 15 mm wide (Fig. 5A–C). All specimens are preserved on the surface of slabs, have sharp, well-defined edges, and consist of round to ellipsoid pellets of about 0.5 mm to 2 mm in diameter. The maximum thickness is 4 mm.

Morphotype 3

One elongated, ellipsoid coprolite (Pioche: KUMIP 378576, Fig. 6) composed of unidentifiable skeletal fragments. It is 36 mm long and 12 mm wide. It has no soft-tissue preserved.

Morphotype 4

Five specimens (Spence: KUMIP 314245, 314255, 366400, 366401, 377071) of pellet-filled burrows (Fig. 7A–C). The pellets are elongate, vary from straight to curved, range from 2 mm to 125 mm in length, and are about 0.5 mm to 1 mm wide. The pellets are aligned parallel to the direction of the burrow and sometimes overlay each other. The wall of the burrow is smooth. The burrows are 59 mm to 105 mm long and between 7 mm and 35 mm wide. The widest part consists of a chamber-like structure at the end of the burrow. Branching is observed twice in KUMIP 314245 (Fig. 7A) and once in KUMIP 366401 (Fig. 7B). The other three specimens do not show any signs of branching.

Morphotype 5

Two specimens (Spence: KUMIP 314243, 377075) representing filled burrows with round pellets (Fig. 7D). The burrows are 60 mm to 130 mm long and 7 mm wide. The wall of the burrow is smooth. No branching is observed in Morphotype 5 burrows. One of the Morphotype 5 burrows (KUMIP 314243) preserves fragments of trilobites, agnostoids, and hyoliths. The fragments range from 2 mm to 7 mm in size and are pellet supported.

Associated faunas

Most of the coprolites are isolated specimens, with no animals represented on the same slab. Two specimens (KUMIP 293610, 314260) have hyoliths associated with them, two specimens (KUMIP 377063, 377071) have agnostoids and trilobites on the same slab, and one specimen (KUMIP 314187) preserves a lingulid brachiopod. The hyoliths were likely not part of the coprolites, as they are not in close proximity and are too large by comparison (Figs 2D, 5B). The agnostoids and trilobites are also entirely separate from the coprolites and in KUMIP 377071 they are articulated, and thus were likely not digested. The lingulid brachiopod is in the center of the coprolite (Fig. 5C) and is a complete valve. This brachiopod likely represents a digested specimen. Because it is complete, the source predator for the associated coprolite was probably not a shell-crushing predator and could potentially only dissolve soft-tissue.

Discussion

Coprolite origin and producers

The large size, circular shape and organic composition of the Great Basin Morphotype 1 coprolites suggest that the

original feces were likely deposited in a burrow, with the circular outline of the coprolite due to the shape of the burrow and not due to compression of a fecal ball. In some cases, the burrows can be observed on both sides of the rock slab. In three cases, this represents a distance of 10 mm. Considering the putative 85% compaction rate for BST deposits (Whittington 1985), this would indicate an original length of the burrow of at least 85 mm. Similar observations have been made in the Ravens Throat River Lagerstätte, where coprolites preserve spreiten structures (unpublished observation). It is unlikely that the structures represent poorly preserved jellyfish, eldonids, or Ediacaran-like discoidal fossils, as no rays, ridges, or circular structures are preserved; typical features of such fossils (Liu *et al.* 2015, Lieberman *et al.* 2017, McMahon *et al.* 2017, Sappenfield *et al.* 2017).

The common hypothesis is that coprolites of the kind found in the Great Basin were produced by large predators or scavengers (Mikuláš 1995, Blau *et al.* 1997, English & Babcock 2010). However, a study of modern worms by Schäfer (1953) suggests either priapulids or large annelids were the potential producers. Schäfer (1953) demonstrated that worms are able to form both isolated pellets and piles of pellets which, when compacted, would form structures similar to the round to ellipsoid specimens typical of Morphotype 1. Alternatively, many round invertebrate coprolites have been previously attributed to crustaceans (Blau *et al.* 1997, Schweigert *et al.* 1997, Senowbari-Daryan & Kube 2003). Large stem group arthropods such as *Anomalocaris* and *Tuzoia* are part of the Great Basin biota and, therefore, could also be the source of Morphotype 1.

The length of at least 85 mm in some of the Morphotype 1 burrows, together with the relatively rare horizontal burrows in both the Pioche and the Spence, indicate the environment in the Great Basin during the Cambrian might have, at times, been well oxygenated and allowed for bioturbation at a larger scale than in some other BST deposits (Garson *et al.* 2012, Kimmig & Pratt 2016). However, it is also possible that individualistic taphonomic or diagenetic pathways present in other BST deposits did not allow for the preservation of the kinds of burrows found in the Great Basin deposits.

The producer of Morphotype 2 was a predator or scavenger that hunted soft-bodied animals, as the specimens are elongated coprolites composed of soft tissue pellets with no skeletal remains. Morphotype 2 has no relief, suggesting that the producer lived on the seafloor or in the water column. Considering the large size of Morphotype 2 (19 to 35 mm) and, given the known animals in the Great Basin Cambrian biota capable of producing a coprolite of that size, a larger arthropod is the only possible progenitor. It could possibly have been derived from one of the anomalocaridids known from both the Pioche and the

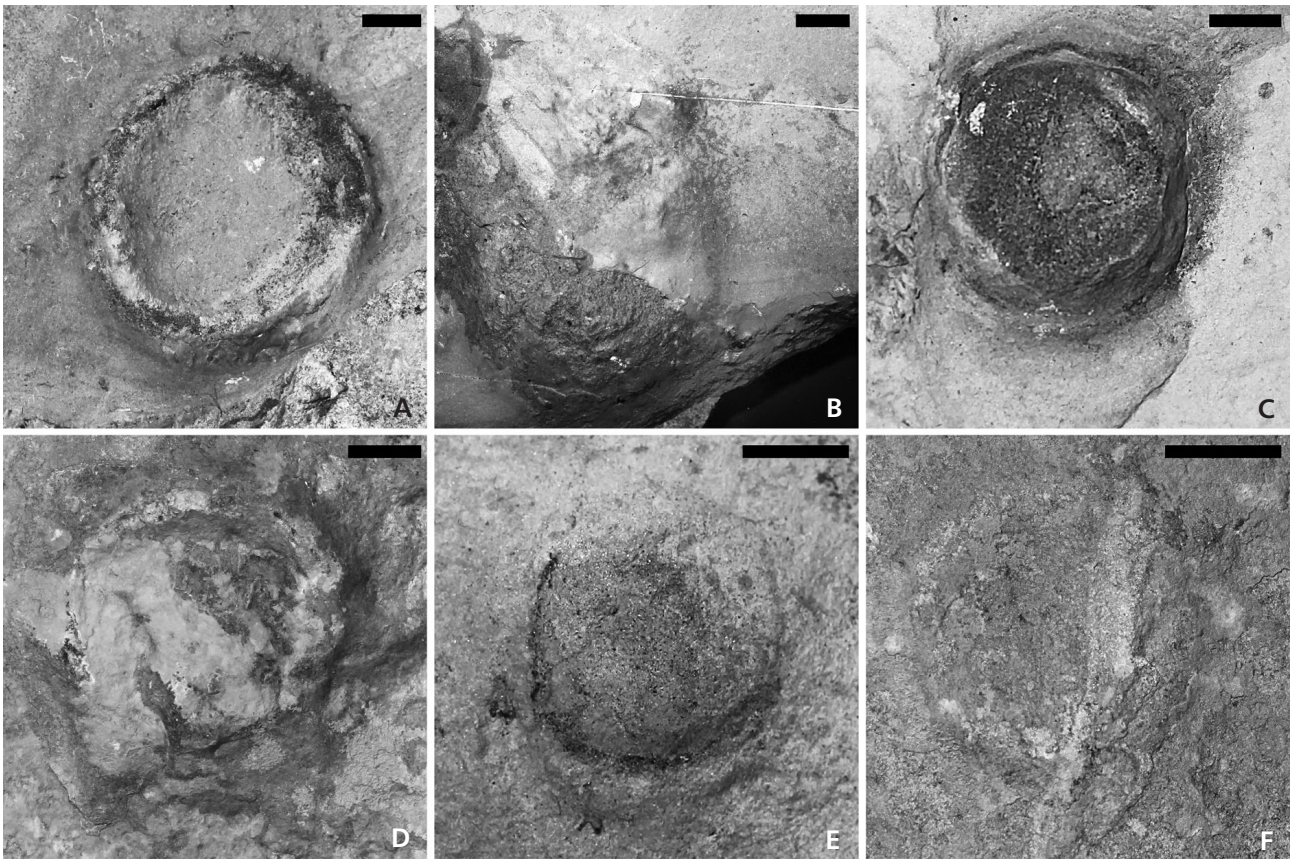


Figure 4. Round carbonaceous disk-shaped coprolites of Morphotype 1 apparent on both sides of the slab. • A – KUMIP 376845 top view, preserving carbonaceous flakes and negative relief. • B – KUMIP 376845 bottom view, preserving carbonaceous film and positive relief. • C – KUMIP 376844 top view, preserving carbonaceous flakes and positive relief. • D – KUMIP 376844 bottom view, preserving carbonaceous film fragments and positive relief. • E – KUMIP 419285 top view, preserving carbonaceous flakes and positive relief. • F – KUMIP 419285 bottom view, preserving positive relief. Scale bars are 5 mm.

Spence, as previous work has determined that some anomalocaridids only fed on soft-bodied animals (Daley *et al.* 2013).

Either a predator or a scavenger must have been the source of Morphotype 3. The dense accumulation of agnostoid and other skeletal fragments indicates that the producer was able to digest most soft tissue associated with the prey and that it was likely their main food source, as omnivores usually produce a coprolite composed of a mix of sediment, organic matter, and exoskeletal fragments (Vannier & Chen 2005, Zacaï *et al.* 2016, Peel 2017). The coprolite shows similarities to the ellipsoid aggregates described from the Maotianshan Shale, which have been attributed to large arthropods (Vannier & Chen 2005), consistent with our predator/scavenger interpretation. A possible producer might be *Tuzoia*, as it has been linked with predation on trilobites in the Jince Formation of the Czech Republic (Fatka *et al.* 2015).

Morphotype 4 likely represents specimens of the ichnogenus *Tomaculum* Groom, 1902. The long slim pellets in the burrows, the curvature, and the arrangement of

the pellets all correspond to the description of the ichnogenus (Eiserhardt *et al.* 2001). Morphotype 4 differs from the type description in two key ways. Firstly, no individual fecal pellets can be observed in the elongated organic structures. Secondly, Morphotype 4 specimens KUMIP 314245 and 366401 are branched. Eiserhardt *et al.* (2001) mentioned that *Tomaculum* specimens were likely not produced by worms, as studies on modern worms showed that they are not able to produce the kind of elongated ribbon-like pellet accumulations found in *Tomaculum*. If this was also the case for Cambrian worms, then the burrows were likely created by arthropods, this might also explain the presence of arthropod and hyolith fragments in one Morphotype 4 specimen. Cambrian trace fossils indicate that trilobites might have been predatory (Tarhan *et al.* 2011, Selly *et al.* 2016) and the size of the burrows associated with Morphotype 4, accounting for compaction, could have housed a variety of different trilobite species. Some bradoriids and other carapaced arthropods would also fit the size of the burrows. Alternatively, palaeoscolid worms do co-occur with *Tomaculum*-like

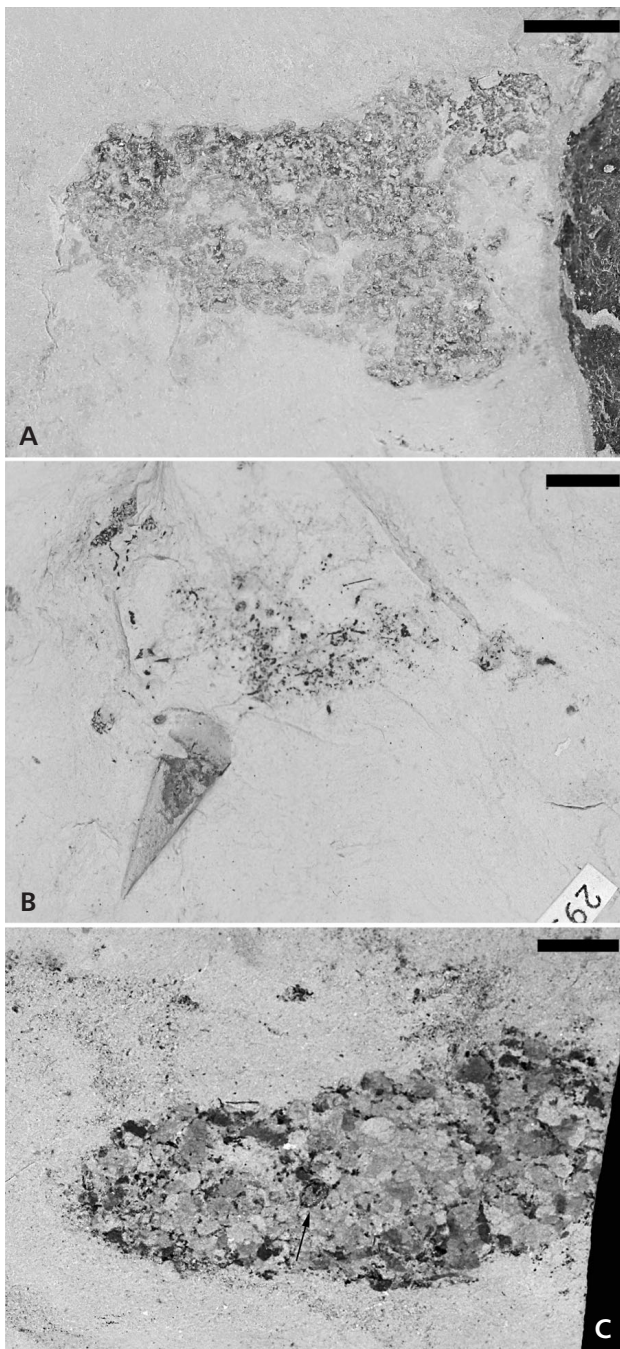


Figure 5. Coprolites of Morphotype 2. • A – KUMIP 378577, elongated coprolite preserving ellipsoid pellets. • B – KUMIP 293610 dispersed elongated coprolite in association with hyolith, with preserved operculum. • C – KUMIP 314187 elongated coprolite in association with a lingulid brachiopod (arrow). Scale bars are 5 mm.

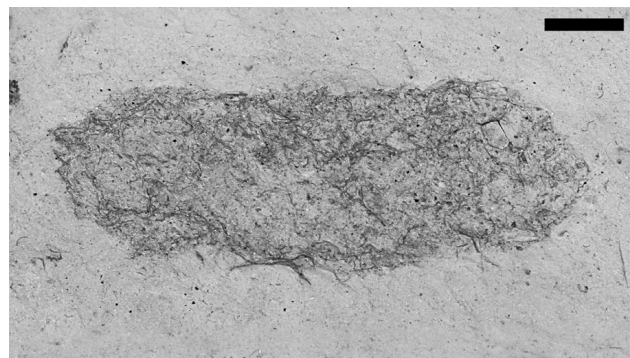


Figure 6. Coprolite of Morphotype 3 (KUMIP 378576): elongated coprolite preserving fragmentary agnostids and skeletal debris. Photographed under alcohol. Scale bar is 5 mm.

structures in the Ordovician Fezouata Lagerstätte in Morocco, indicating a worm could have produced the pellet-filled burrows in this deposit (Martin *et al.* 2016).

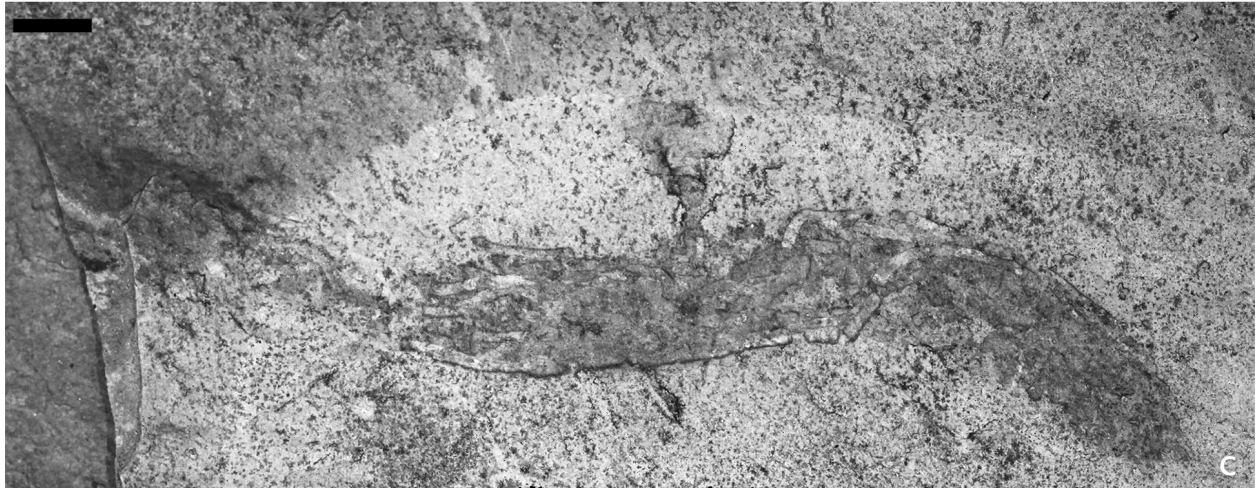
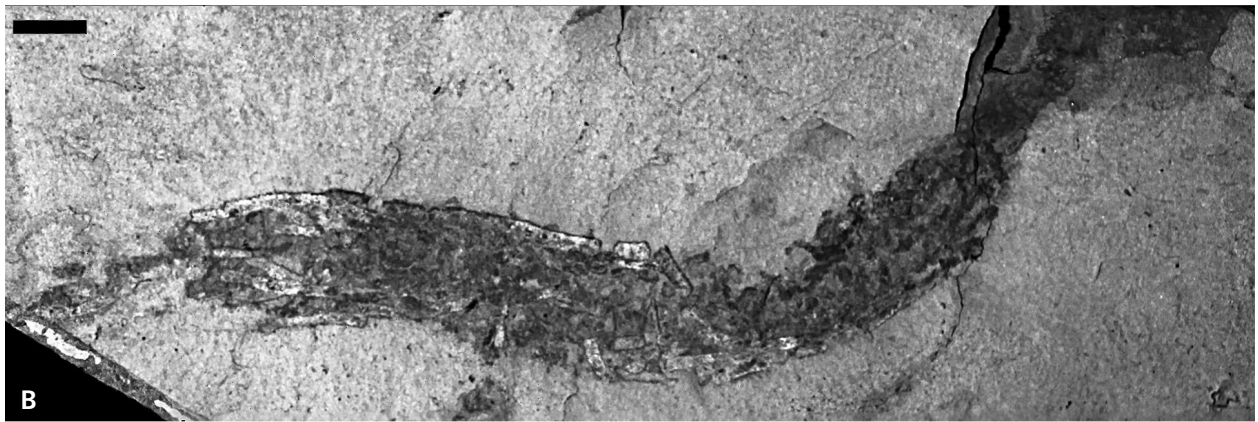
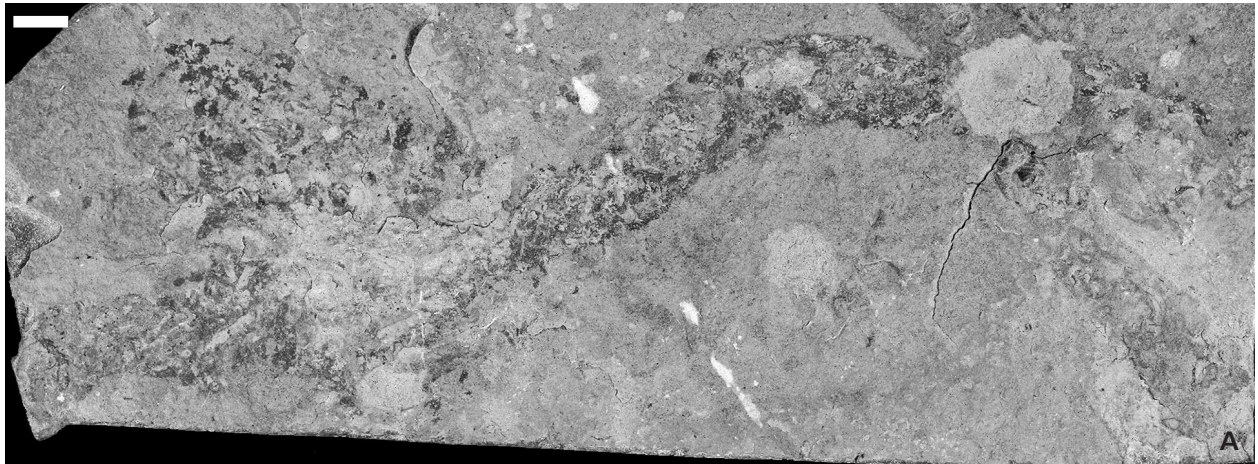
Morphotype 5 specimens are tentatively attributed to the ichnogenus *Planolites?* Nicholson, 1873, based on the smooth walls, the round pellets which fill the burrow, and because no branching is observed in the specimens. The producers of the burrows were likely a range of different worm species (Valentine 1995, Marengo & Bottjer 2008). The presence of priapulids and other worms in the Pioche and Spence (Robison 1969, Conway Morris & Robison 1986, Lieberman 2003) supports this interpretation.

Comparison to other Cambrian coprolites

Invertebrate coprolites have a sparse record in the Paleozoic (English & Babcock 2010, Eriksson *et al.* 2011, Slater *et al.* 2012, Fiorelli *et al.* 2013). Round and elongated coprolites are found in marine and terrestrial environments of the Paleozoic and have been ascribed to a wide variety of producers. In the early Paleozoic they are usually attributed to large arthropods (Conway Morris & Robison 1988, English and Babcock 2010), as these are considered to have been alpha predators.

Round coprolites, similar in shape and size to the ones described herein have also been reported from the Lower Cambrian Paseky Shale in the Czech Republic (Mikuláš 1995). Similar to the Pioche and Spence coprolites, they are variably filled with arthropod fragments and round to oval pellets. Mikuláš (1995) argued that the coprolites were likely produced by large arthropods, but he did not

Figure 7. Pellet-filled burrows. • A – KUMIP 314245, coprolite of Morphotype 4, *Tomaculum?* burrow filled with elongated pellets and 2 branches. • B – KUMIP 366401 coprolite of Morphotype 4, *Tomaculum?* burrow filled with elongated pellets and 1 probable branch. • C – KUMIP 314255 coprolite of Morphotype 4, *Tomaculum?* burrow filled with elongated pellets and 1 probable branch. • D – KUMIP 377075, coprolite of Morphotype 5, *Planolites?* burrow filled with round to ellipsoid pellets. Scale bars are 5 mm.



name any specific producers. It is unclear if those coprolites were deposited in burrows or on the seafloor. However, as many of the coprolites in the Spence Shale inferred to have been produced in burrows are similar in appearance to those in the Paseky Shale, it is perhaps possible that those from the Paseky were also produced in burrows. This would explain their circular outline. If this is the case they would have had to be deposited in shallow burrows, as the Paseky Shale only preserves shallow bioturbation (Mikuláš, personal communication).

Coprolites that have been previously reported from BST deposits (Nedin 1999, Vannier & Chen 2005, English & Babcock 2010, Lin *et al.* 2010) are usually rich in animal fragments and ellipsoid to elongate in shape (Vannier & Chen 2005, English & Babcock 2010). These coprolites are generally attributed to large arthropods or priapulids, but there has been little evidence provided to support these assertions. With few body fossils directly associated with the Pioche and Spence coprolite specimens, our interpretation of possible producers is based on modern analogues and the known fossil record of the source deposits. Priapulids or other worms are a likely producer for many of the Morphotype 1 coprolites in the Pioche and the Spence, as modern relatives are known to dig burrows if the substrate is muddy (Vannier *et al.* 2010, Vannier & Martin 2017), and predatory behavior has been observed in some modern burrowing worms (Lachat & Haag-Wackernagel 2016). Specimens of the priapulid *Ottoia prolifica* from the Burgess Shale preserve guts containing exoskeletal fragments, notably hyolith conches, arthropods, and brachiopod valves. The skeletal elements in the Burgess Shale *Ottoia* specimens are filled with sediment and ribbon-like features, indicating that *Ottoia* was an omnivore (Vannier 2012). Other potential vermiform coprolite producers could be palaeoscolecid. Cambrian palaeoscolecid species were mostly deposit feeders (Martin *et al.* 2016) but some also fed on organic matter, as arthropod remains have been preserved in at least one specimen from Sirius Passet (Conway Morris & Peel 2010).

Trilobites are another possible producer, as they are known to be able to burrow and some species have been identified as potential predators, but their feeding strategies are poorly understood (Chatterton *et al.* 1994, Fortey & Owens 1999, Hughes 2001, Lerosey-Aubril *et al.* 2011, Tarhan *et al.* 2011, Selly *et al.* 2016). Because the burrows in the Pioche and Spence Shale deposits do not preserve any scratch marks, as would be expected for trilobites (Seilacher 2007), it is more likely that worms or other arthropods are the source of the burrows. It is also possible that the fine-grained mudstones did not preserve the scratch marks.

The fecal pellet-filled burrows of Morphotypes 4 and 5 are comparable to structures found throughout the Phanerozoic (Robison 1969, Eiserhardt *et al.* 2001, Marenco

& Bottjer 2008, Buatois & Mángano 2011). These structures have been attributed to a range of producers, including several kinds of arthropods, worms and gastropods (Schäfer 1953, Pickerill & Narbonne 1995, Eiserhardt *et al.* 2001). Similar burrows can be found in other BST deposits, for example, the Wulongqing Formation of the early Cambrian of China (Hu *et al.* 2010, Weber *et al.* 2012) and the mid-Cambrian Kaili biota (Lin *et al.* 2010).

Microscopic coprolites have been described from the Cambrian of China (Shen *et al.* 2014) and Greenland (Peel 2015). In both cases the producers are not known, but brachiopods or mollusks have been suggested. Considering the size and shape of the coprolites from those deposits differ markedly from the Pioche and Spence coprolites, it is unlikely that they have a common provenance.

Conclusions

The relatively rare coprolites in the Pioche Formation and Spence Shale provide information about the enigmatic food chain of the mid-Cambrian. The intact coprolites we assign to Morphotype 1 are typically around 20 mm in size and were likely produced by one or a few closely related species of predators that inhabited burrows in which the fecal pellets were accumulated. Considering coprolites of similar size, shape, and composition from other deposits, as well as the animals that have been recovered in the Pioche Formation and the Spence Shale, it is likely that the producer was a burrowing arthropod or priapulid. Larger animals living on the sediment or in the water column likely produced the coprolites we assign to Morphotypes 2 and 3. Smaller animals produced the pellet-filled burrows of Morphotype 4 and 5. Considering the shape of the fecal matter, as well as comparable traces in the Paleozoic, they were likely produced by worms or possibly trilobites.

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