The Spence Shale Lagerstätte: an important window into Cambrian biodiversity

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Abstract: The Spence Shale Member of the Langston Formation is a Cambrian (Miaolingian: Wuliuan) Lagerstätte in northeastern Utah and southeastern Idaho. It is older than the more well-known Wheeler and Marjum Lagerstätten from western Utah, and the Burgess Shale from Canada. The Spence Shale shares several species with these younger deposits, yet it also contains a remarkable number of unique species. Because of its relatively broad geographical distribution, and the variety of palaeoenvironments and taphonomy, the fossil composition and likelihood of recovering weakly skeletonized (or soft-bodied) taxa varies across localities. The Spence Shale is widely acknowledged not only for its soft-bodied taxa, but also for its abundant trilobites and hyoliths. Recent discoveries from the Spence Shale include problematic taxa and provide insights about the nature of palaeoenvironmental and taphonomic variation between different localities.

Supplementary material: A generic presence–absence matrix of the Spence Shale fauna and a list of the Spence Shale localities are available at: https://doi.org/10.6084/m9.figshare.c.4423145

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The Early Paleozoic has yielded a remarkable number of fossil-bearing sediments preserving weakly skeletonized (or soft-bodied) fossil taxa (Gaines 2014; Van Roy et al. 2015; Muscente et al. 2017; Pates & Daley in press). The Great Basin of the western USA preserves a significant number of Cambrian Burgess Shale-type deposits including the Pioche Formation of Nevada (Lieberman 2003), the Wheeler, Marjum and Weeks formations of western Utah (Robison 1991; Robison et al. 2015; Foster & Gaines 2016; Lerosey-Aubril et al. 2018), and the Spence Shale of northeastern Utah and southeastern Idaho (Robison 1991; Liddell et al. 1997; Robison et al. 2015). These deposits contain an exceptional number of soft-bodied fossils, preserved as 2D mineral films, and thus greatly extend our knowledge of Cambrian evolution and palaeoecology.

The Spence Shale is one of five Cambrian Konservat-Lagerstätten that occurs in Utah; the others comprise the (‘deep’) Wheeler, Marjum and Weeks formations in the House Range and the (‘shallow’) Wheeler Formation in the Drum Mountains (Robison 1991; Briggs et al. 2008; Robison et al. 2015; Foster & Gaines 2016; Lerosey-Aubril et al. 2018). The Spence Shale preserves a diverse fauna of soft-bodied and skeletonized taxa, and each of these are dominated by arthropods (Robison et al. 2015); it is also the oldest of the Cambrian Lagerstätten of Utah, dating back to the early Wuliuan Stage (Robison & Babcock 2011). The Lagerstätten in the Wheeler, Marjum and Weeks formations of western Utah are younger (Bolaspidella-Cedaria trilobite biozones) but have several taxa in common with the Spence Shale Member (Liddell et al. 1997; Robison & Babcock 2011; Robison et al. 2015; Lerosey-Aubril et al. 2018; Pates et al. 2018). Thus far, the two Lagerstätten of the Wheeler Formation (House Range and Drum Mountains) have been the most intensively studied Cambrian units containing soft-bodied taxa in Utah (Gaines & Droser 2005; Gaines et al. 2005; Brett et al. 2009; Haldedahl et al. 2009; Kloss et al. 2015; Foster & Gaines 2016); thus, the depositional environments, ichnology and taxonomy are known to an exceptional degree of detail. The slightly younger Marjum Formation has also received a significant amount of attention (Elrick & Snider 2002; Brett et al. 2009; Robison et al. 2015). The Weeks Formation Lagerstätte is the youngest of the Burgess Shale-type deposits of Utah (Proagnostus bulbus biozone) and has received relatively little study (Robison & Babcock 2011; Lerosey-Aubril et al. 2012, 2018; Robison et al. 2015), although it contains some soft-bodied animals (Lerosey-Aubril et al. 2013, 2014, 2018; Lerosey-Aubril 2015; Ortega-Hernández et al. 2015). The Spence Shale occupies an intermediate position between these three formations. Several comprehensive studies of Spence palaeontology exist such that there is a good knowledge of the biota contained within (for a recent review see Robison et al. 2015). However, new taxonomic discoveries continue to be made from the Spence Shale (e.g. Kimmig et al. 2017). In a similar vein, Spence sedimentology and geochemistry have been studied (e.g. Liddell et al. 1997; Garson et al. 2012; Kloss et al. 2015), but recent fieldwork conducted by Kimmig and Strotz and associated taphonomic and sedimentological analyses (Kimmig et al. 2018) have revealed new and distinctive patterns of palaeoenvironmental and taphonomic variation across the geographical and temporal breadth of the Spence Shale.

The Spence Shale occupies a distinctive position among the Lagerstätten of Utah, as it preserves a range of environments from shallow water carbonates to deep shelf dark shales. Although this by itself is not unique, the fact that soft-bodied organisms are found in the mudstones of the Wellsville Mountains and the deeper water sediments of Idaho allows for a unique opportunity to understand the taphonomic pathways of soft-bodied preservation in different environments within one member. In addition, the presence of several laminae and beds preserving soft-bodied fossils in different...
carbonate cycles within each outcrop of the Wellsville Mountains offers the chance to study changes in taphonomic pathways and diagenetic effects on soft-tissue preservation within one locality.

**Material and methods**

Skeletonized fossils were photographed dry, and all soft-bodied fossils were photographed submerged in ethanol, using a Canon EOS 5D or 7D Mark II digital SLR camera equipped with Canon 50 mm macro lens, or a Leica DMS 300 digital microscope. The contrast, colour and brightness of images were adjusted using Adobe Photoshop. All figured fossils are part of the University of Kansas, Biodiversity Institute, Division of Invertebrate Paleontology collections (KUMIP).

Sedimentological analyses are based on macroscopic and microscopic observations. Thirty ultrathin (<20 µm) polished thin sections of the shale and limestone stratigraphic intervals were analysed. Samples for thin sections were taken at c. 1 m intervals along the Spence Shale exposure at Miners Hollow (Fig. 1). This is perhaps the best-known Spence Shale locality and has also yielded the most diverse soft-bodied biota.

Data for the generic presence–absence matrix in the major Spence Shale locations were collected from literature (Robison et al. 2015, and references therein; Conway Morris et al. 2015a, b; Kimmig et al. 2017; Pates & Daley 2017; Hammersburg et al. 2018; Pates et al. 2018) and museum databases (KUMIP; Yale University Peabody Museum (YPM); Harvard University Museum of Comparative Zoology (MZC); and United States National Museum of Natural History (USNM)) and iDigBio (www.idigbio.org).

**Locality, geological setting and depositional environment**

The Spence Shale Member is the middle member of the Langston Formation (Fig. 1c; sometimes referred to as the Twin Knobs...
Box 1. Sedimentology of the Spence Shale in the Wellsville Mountains

The Spence Shale consists of carbonate mudstones to carbonate-rich siliciclastic mudstones that are sub-millimetre- to several centimetre-scale laminated and bedded, and contain abundant millimetre- to decimetre-scale carbonate beds and laminae. Wackestones occur as millimetre-thick lenses. The mudstones are also irregular in thickness, and in some places, lenticular. In several portions throughout the succession, millimetre-thick accumulations of biogenic carbonate debris are intercalated into the succession that have sharp, irregular bases in places and pinch out laterally. Isolated biogenic carbonate debris is common throughout the succession and is generally oriented parallel to subparallel to bedding. Organic matter in this unit consists of sub-millimetre wide flattened flakes, in many places associated with pyrite, which is generally concentrated in distinct laminae. Locally, it forms lens-shaped slightly inclined accumulations directly adjacent to biogenic debris. All siliciclastic mudstones contain abundant silt-size carbonate grains that are generally rounded to some degree, as well as plathy clay minerals. In places, macroscopically visible burrows are common in these rocks.

The carbonate beds are irregularly thickened laterally, and can be nodular. They consist of either carbonate mudstones with lenses of silty packstones composed of peloids, or up to decimetre-thick carbonate wacke- to packstones made up of biogenic debris and aggregate grains. Grains in this facies are poorly sorted, generally recrystallized, and contain a micritic outer rim. Burrows with varying orientations are common in these rocks. Fractures showing a clear zigzag pattern occur in both the carbonates and the siliciclastic mudstones but are more common in the mudstones, and are filled with a clear carbonate cement that is structureless.

The abundance of carbonate mud and grains suggests that the Spence Shale was the distal equivalent of a carbonate system, probably a rimmed carbonate platform based on laggonal components such as the aggregate grains and peloids. The depositional environment shows a transition from carbonate-rich shales in proximal areas to siliciclastic shales distally. High-energy events, probably storms, must have been abundant in all environments as reflected in sharp irregular bases, here interpreted as scour. At the base of carbonate and siliciclastic mudstone beds, lens-shaped bedding indicating bed-load transport, and carbonate debris forming lags. The great quantity of burrows in the carbonates indicates abundant benthic life during deposition of this unit in carbonate facies; the same appears partly true with the siliciclastic mudstones. The cement-filled fractures are here interpreted as recrystallized, originally mud-filled clastic dykes probably reflecting synsedimentary earthquakes in the Spence Shale.

The Spence Shale preserves carbonate mudstones (these predominate) to carbonate-rich siliciclastic mudstones (Box 1; Fig 2) and has been interpreted to have been deposited in the middle carbonate to outer detrital belt of a now west-facing carbonate platform (Palmer 1971; Robison 1991; Liddell et al. 1997). The Spence Shale shows excellent geographical and stratigraphic exposure over broad areas in northeastern Utah and southeastern Idaho (see supplementary material). It is assigned to the *Albertella–Glossopleura* trilobite biozones, and is interpreted to represent sedimentation on a shelf, although no details are currently known about depositional depth relative to wave base (Liddell et al. 1997). Exposures vary from c. 9 m at Blacksmith Fork (Walcott 1908; Deiss 1938) to c. 120 m at Oneida Narrows (Liddell et al. 1997), and the most important localities to date are Miners Hollow, Antimony Canyon and Cataract Canyon (all in the Wellsville Mountains) and High Creek, Spence Gulch and Oneida Narrows in the Bear River Range (Fig. 1b). However, other localities have also yielded a variety of skeletonized and soft-bodied fossils.

The palaeontological significance of the Spence Shale has been recognized for over 100 years (Box 2; Walcott 1908; Robison 1965, 1969, 1991; Gunther & Gunther 1981; Conway Morris & Robison 1982, 1986, 1988; Briggs et al. 2008; Robison & Babcock 2011; Robison et al. 2015), and important efforts have also focused on characterizing the depositional environments within this member (Liddell et al. 1997; Garson et al. 2012; Kloss et al. 2015). The Spence Shale contains up to eight parasequences, or carbonate cycles (Maxey 1958; Liddell et al. 1997; Garson et al. 2012). The Wellsville Mountain localities are considered the most proximal Spence deposits, and contain extensive soft-bodied fossils (Liddell et al. 1997; Garson et al. 2012); the depositional setting becomes more distal towards the NE. This is indicated by the reduced presence of dolomites and limestones, and the number of soft-

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Fig. 2. Sedimentology of the Spence Shale. (a) Lag deposit near base of ‘cycle 3’, consisting of biogenic debris, probably of echinoderm, brachiopod and trilobite remains. It should be noted how bedding bends around the millimetre-size echinoderm bioclasts. The matrix is carbonate-rich siliciclastic mudstone with varying amounts of sub-millimetre carbonate debris. (b) Carbonate-rich siliciclastic mudstone near top of ‘cycle 3’, with several millimetre-long black organic-rich flakes oriented parallel to bedding. Abundant silt-size carbonate particles in the matrix should be noted. Scale bar is 1 mm.
Box 2. Collections history of the Spence Shale

The Spence Shale was first described by Charles Walcott (1908) from Spence Gulch in Idaho (Fig. 1b). Since then, palaeontologists have unearthed a treasure trove of fossils from the unit, especially in the Wellsville Mountains north of Brigham City, Utah. Its potential scientific value was already recognized by Walcott (1908, p. 8), who called it ‘an extremely abundant and varied lower Middle Cambrian fauna’. The scientific merit of the Spence Shale began to come to fruition through the work of Deiss (1938), Resser (1939) and Maxey (1958), and especially in publications by Dick Robison and colleagues that highlighted the soft-bodied biota (Robison 1969, 1991; Robison & Richards 1981; Briggs & Robison 1984; Conway Morris & Robison 1986, 1988; Babcock & Robison 1988). One of the chief reasons for the Spence Shale becoming a deposit so well known for soft-bodied preservation was the extensive and diligent efforts by several private collectors, which tremendously aided and facilitated the work by Robison and colleagues, as well as of subsequent researchers (e.g. Briggs et al. 2005, 2008; Robison & Babcock 2011; Conway Morris et al. 2015a, b; Kimmig et al. 2017; Pates et al. 2018).

In particular, the contributions of the famous Gunther family (Lloyd, Val and Glade; Fig. 3a and b) of Brigham City, UT, winners of the prestigious Strimple Award from the Paleontological Society (USA), stand out, including their scientific publications (e.g. Gunther & Gunther 1981). They started collecting in the Spence Shale, as well as in the Wheeler, Marjum and Weeks formations, around 1965, and their efforts have contributed over 75% of all known Spence Shale specimens to museum collections, a remarkable legacy. The Gunther family was later joined by Phil Reese and Paul Jamison (Fig. 3c), and they extended the tradition of giving scientifically important specimens to museums. Indeed, it is no exaggeration to state that these collectors are the major reason the diversity of the Spence Shale is so well understood; without their contributions the many taxonomic studies of Spence Shale fossils would not have been possible. In many respects this legacy continues, as these enthusiastic private collectors are still one of the driving forces behind the exploration of the Cambrian deposits of Utah. The majority of soft-bodied fossils would probably never have been found were it not for the passion of these people. Given that new species are still being described from this unit, and that there are several specimens in museum collections that are currently unidentifiable, palaeontologists can only hope that such collection efforts continue, further contributing to our knowledge of Cambrian biodiversity.

bodied fossils also declines in this direction (Liddell et al. 1997; Garson et al. 2012). Recent investigations of the Langston Formation type locality at Blacksmith Fork, Utah (Bear River Range) suggest that it might represent an even more proximal environment than the Wellsville Mountains, as it preserves large amounts of dolomites, indicating shallow water conditions (Maxey 1958; J. Kimmig, pers. obs.). The Blacksmith Fork locality has yielded few soft-bodied fossils to date, but is valuable for inferring how ecological communities varied along the Cambrian Spence Shale shelf from shallow to deep water. Although fossils are in places well preserved in the Spence Shale, burrows are also ubiquitous, both in proximal and distal shelf sediments. The presence of trace fossils indicates that dynamic redox conditions may have prevailed during the deposition of the shelf-bearing distal Spence environment (Garson et al. 2012; Hammersburg et al. 2018). However, the fine-scale distribution of burrows and fecal strings can be deduced only via thin sections, and although these were recently collected (Kimmig et al. 2018) they have not yet been studied in sufficient quantity to ascertain the precise prevalence and distribution of dynamic redox states (Egenhoff & Fishman 2013).

Taphonomy

There have been numerous hypotheses offered to account for the type of soft-bodied preservation seen in the Spence Shale. Some have suggested it is the result of an oxygen-depleted environment in conjunction with rapid burial (e.g. Gaines et al. 2012; Garson et al. 2012), although oxygen depletion in and of itself cannot account for soft-tissue preservation (Allison 1988). Intriguingly, the Spence Shale does not record evidence of constant anoxia (Garson et al. 2012; Kloss et al. 2015; Hammersburg et al. 2018). In fact, in the Spence Shale, soft-bodied fossils are also found in association with bioturbated sediments (Garson et al. 2012; Kimmig & Strotz 2017), and geochemical analysis of some intervals indicates oxygenated bottom waters (Kloss et al. 2015). One of the notable aspects of the Spence Shale is that there appears to be significant variation in the degree of soft-bodied preservation and also the range of taxa preserved within any given exposure and across localities (supplementary material; Liddell et al. 1997; Garson et al. 2012; Robison et al. 2015). For instance, Broce & Schiffbauer (2017) analysed 10 vermiform fossils from the Spence Shale (eight from
Miners Hollow, one from Antimony Canyon and one from an indeterminate locality in the Wellsville Mountains) and found a variety of preservational modes associated with these fossils. The most common form of preservation in these fossils was pyritization, but several fossils showed kerogenization and aluminosilicification; further, phosphatization, as well as barite, monazite and calcite associations were found (Broce & Schiffbauer 2017).

The different preservational styles in the Spence Shale have unfortunately not yet been fully explored at the millimetre-scale but are probably due to changes in ocean water chemistry and sedimentology. This will be important to more precisely ascertain depositional environments as has been done for other well-known soft-bodied deposits (e.g. Gabbott et al. 2008). The role that diagenesis plays in mediating soft-bodied preservation (e.g. Butterfield et al. 2007) has also yet to be unravelled. Thus, additional work is required to tease apart the various taphonomic pathways involved in soft-bodied preservation in the Spence Shale. This would have the added benefit of helping elucidate the factors generally responsible for soft-bodied preservation in shales. Further studies currently under way (e.g. Kimmig et al. 2018) will be a valuable step forward.

**Overview of the Spence Shale biota**

To date, 87 species in 71 genera that belong to at least 10 phyla have been described from the Spence Shale (Figs 4a–l and 5a–l; supplementary material). Two-thirds of the species in the Spence Shale are well skeletonized and such taxa are not only more diverse but also significantly more abundant than the co-occurring soft-bodied taxa. The greatest diversity of soft-bodied taxa is found at Miners Hollow, followed by Antimony Canyon: 20 and 14 soft-bodied species, respectively. More information on the fauna, algae, cyanobacteria and trace fossils is provided in the subsequent sections, and the soft-bodied arthropods are discussed in Box 3.

**Arthropods**

**Trilobites and agnostoids**

Trilobites are the most diverse group in the Spence Shale and are represented by 41 species in 25 genera. Agnostoid trilobites can be abundant locally, but are generally less common and only two species are known: *Peronopsis bonnernensis* and *P. brighamensis*. Such a low diversity of agnostoids is among Cambrian soft-bodied deposits from Utah unique to the Spence Shale, and might suggest a more restricted and/or proximal environment compared with the other Utah Lagerstätten. Trilobite diversity is the highest at Spence Gulch (16 genera) in Idaho, and the Wellsville Mountain localities in Utah (17 genera). Because of the lack of available collections from High Creek and Blacksmith Fork, it is unclear how many genera are present in these deposits.

Psychoparid and corynexochid trilobites are the most common types of trilobites in the Spence Shale and can be found throughout most of the exposures. Recent comprehensive discussions on these have been provided by Robison & Babcock (2011) and Robison et al. (2015). Distinctive biostratigraphic patterns among Spence trilobites were described by Campbell (1974), who argued that there may be some turnovers preserved in the trilobite fauna at Antimony Canyon. Further study is needed to confirm whether these turnovers appear at other Spence Shale locations.

In the Wellsville Mountains the trilobites usually appear as isolated specimens, with only one to a few, often complete exoskeletons preserved per slab. Preserved soft parts have not been described to this point, but a few unpublished specimens from Miners Hollow actually display gut structures. In Spence Gulch, isolated trilobites are present, but ‘trilobite-hash’ containing dozens to hundreds of broken specimens is dominant. Some of the hash is deposited in ribbon-like and circular forms, resembling coprolites.

**Soft-bodied arthropods**

Soft-bodied arthropods are the most diverse clade, other than trilobites, from the Spence Shale, with currently 14 species identified. Fossils of this type are mostly limited to the Wellsville Mountains (Box 3, Fig. 4a–l).

**Lobopodians**

*Acinocricus stichus* Conway Morris & Robison 1988 is the only lobopodian species known from the Spence Shale (Robison et al. 2015). Specimens can be easily identified by their prominent spines (Fig. 5g) and are fairly common, with at least 50 specimens known from Miners Hollow, Antimony Canyon and Donation Canyon in the Wellsville Mountains. Complete (or largely complete) specimens are rare, however, and most of the time only isolated segments are preserved. Previous studies have concluded that *Acinocricus* is a luolishanid, a group of ecologically specialized lobopodians with a worldwide distribution (Spence Shale, Burgess Shale, Chengjiang, Emu Bay and Xiaoshiba) (Yang et al. 2015).

**Scalidophorans**

Vermiform fossils are abundant in the Spence Shale, but they usually do not preserve diagnostic characteristics. However, the few specimens that are well enough preserved retain extensive detail (Fig. 5c and d). For instance, a palaeoascolocid is known from Miners Hollow, *Waronascolepis* ratcliffi (Robison 1969; Conway Morris & Robison 1986; Garcia-Bellido et al. 2013) and is represented by two specimens, the holotype (KUMIP 204390, UU1020) and a recently collected specimen with an everted proboscis (KUMIP 490902, Fig. 5c). *Ottoia prolifica* and two species of *Selikirka*, *S. spencei* and *S. cf. columbica*, represent the only other scalidophorans in the Spence Shale (Robison et al. 2015). *Ottoia* has been reported only from Miners Hollow and Antimony Canyon (supplementary material), whereas *Selikirka* has also been found in the Langston Formation type section at Blacksmith Fork (Resser 1939). The specimen from Blacksmith Fork comprises solely the external tube.

**Lophophorates**

Brachiopods and hyoliths are some of the most common fossils in the Spence Shale, and can be preserved in concentrations containing dozens of specimens. Despite the high abundance, the brachiopods have received little attention, and the six species known from the Spence Shale (Resser 1939; Robison et al. 2015; supplementary material) probably represent only a fraction of overall diversity. A few of the specimens from High Creek preserve chaetae (Fig. 5h). Some of the hyoliths in the Wellsville Mountains, referable to *Haplophrentis reesei*, preserve soft tissues, and these have been interpreted as evidence of a lophophore and pharynx (Moyssiak et al. 2017). The other two genera of hyoliths, *Hyolithellus* and *Hyolithes*, are less common; no specimens with soft-bodied preservation are known.

**Molluscs**

Molluscs are extremely rare in the Spence Shale and are found only in the Wellsville Mountains. Only two species have been described, *Latoschella arguata* and *Scenella radians* (Babcock & Robison 1988), and little material has been added since the initial descriptions. The soft-bodied *Wiwaxia herka* (Fig. 5b) is the most common mollusc in the Wellsville Mountains. In addition, an undescribed halkieriid has recently been discovered in Miners Hollow by Paul Jamison.
Sponges

Sponges are a rare element of the Spence Shale fauna and only three species have been described, two of which, *Vauxia gracilenta* and *Vauxia magna* (Fig. 5a), are known from only four specimens total from the Wellsville Mountains (Rigby 1980; Robison et al. 2015). This is different from other Utah Lagerstätten, where sponges are typically the most diverse phylum after arthropods. There are other sponges from the Bear River Range: *Protospongia hicksi* has been reported from the Oneida Narrows locality (Fig. 1b), where hundreds of specimens have been recovered from a 2 m interval (Church et al. 1999).

Echinoderms

Echinoderms are fairly common in the Spence Shale and can be found at most localities. They are represented by at least six species, the most common being *Ctenocystis utahensis*, which often appears in mass assemblages, and three species of *Gogia*: *G. granulosa*, *G. guntheri* and *G. palmeri*. Robison et al. (2015) also mentioned new *Gogia* and totiglobid species, but they have not yet been described. *Lyracystis reesei* and *Ponticulocarpus robisoni* are relatively rare and have thus far been reported from only the Wellsville Mountains (Sumrall & Sprinkle 1999; Sprinkle & Collins 2006).
Fig. 5. Selected fossils from the Spence Shale. (a) KUMIP 491902 and KUMIP 491903, *Vauxia magna* from Miners Hollow, collected by Rhiannon LaVine. (b) KUMIP 287449, holotype of *Wiwaxia herka* from Miners Hollow, collected by Phil Reese and the Gunther family. (c) KUMIP 490902, *Wronascolex? ratcliffi* from Miners Hollow, collected by Riley Smith. (d) KUMIP 314115, *Selkirkia spencer* from the Wellsville Mountains, collected by the Gunther family. (e) KUMIP 204370, *Eldonius ludwigi* from Antimony Canyon, collected by Lloyd and Val Gunther. (f) KUMIP 339907, *Sphenoecium wheelerensis* from Miners Hollow, collected by the Gunther family. (g) KUMIP 491080, *Acinocricus stichus* from Miners Hollow, collected by Paul Jamison. (h) KUMIP 490932, *Micromitra*? sp. from High Creek, with chaetae preserved, collected by Paul Jamison. (i) KUMIP 491805, *enrolled* *Amecephalus laticaudum* from Miners Hollow, collected by Paul Jamison. (j) KUMIP 491808, *Zacanthoides liddellii* from High Creek, collected by Paul Jamison. (k) KUMIP 491853, *Oryctocephalus walcotti* from Oneida Narrows, collected by the Gunther family. (l) KUMIP 135150, holotype of *Siphusanctum lloydguntheri* from Antimony Canyon, collected by Lloyd Gunther. Scale bars represent 5 mm.
Spence Shale; it has been reported from Antimony Canyon.

Marpolia spissa

Algae and cyanobacteria

The majority of the species are trilobites and agnostoids, comprising 43 species. The most abundant trilobites in the Wellsville Mountains are Amecophalus, Athabaskia and Oogygopsis, and other trilobita genera co-occur. At Oneida Narrows Ortygocephalus, Oryctocephalus and Pentagnostus represent over 90% of the diversity and several dozen specimens can appear on one slab, possibly indicating a restricted environment. The 14 species of soft-bodied arthropods, with the exception of some carapaces, are restricted to localities in the Wellsville Mountains north of Brigham City, Utah, in particular Miners Hollow and Antimony Canyon (supplementary material). Many of the Spence Shale taxa are otherwise known only from the Burgess Shale (e.g. Waptia, Toehisia) or are endemic to the Spence Shale, like the probable stem-chelicerate Uthacaris orion (Conway Morris & Robison 1988; Legg & Pates 2017). Fully articulated, well-preserved specimens are rare when compared with deposits such as the Burgess Shale, but when they are present, they can preserve fine details of the appendages, limbs and other parts of the body (Fig. 4a–i). Four bivalved arthropods have been described from the Spence Shale, Canadaspis cf. C. perfecta, Diosycaris argenta, Isosyx sp. and Tuzosia retifera. They rarely have body parts associated, and often are isolated carapaces, which is indicative of decomposition before burial or possible predation (Kimmig & Pratt 2016, 2018; Kimmig & Strotz 2017). Tuzosia represents the largest bivalved arthropod from the Spence Shale, with some valves reaching 12 cm long by 8 cm wide. Radiodonts are also fairly common in the Spence Shale and at least three species are known, an indeterminate Anomalocaris species (Briggs et al. 2008), Caryosyntrips camurus (Pates & Daley 2017) and at least one species of Hurdia, H. victoria (Pates et al. 2016). It is likely that there are more species present, as some specimens have not yet been assigned to species or genus (Fig. 4g and h; Pates et al. 2018). Anomalocaris appears to have been the largest radiodont, whereas most horduroids were fairly small (Briggs et al. 2008; Pates et al. 2018). The radiodonts of the Spence Shale have a variety of interpreted feeding habits, including grasping, grasping–slicing and sediment sifting.

Hemichordates

Hemichordates are represented by two species, the proposed enteropneust tube Margaretia dorus (see Nanglu et al. 2016) and the pterobranch Sphenoecium wheelerensis (Maletz & Steiner 2015). Both species are common in the Wellsville Mountains but have not yet been found in Idaho, or in the more eastern exposures in Utah (supplementary material).

Problematica

Three species of problematic taxa have been described from the Spence Shale, Banffia episwa, Eldonia ludwigi and Siphusauctum lloydguntheri (Fig. 5e and i) (Conway Morris & Robison 1988; Conway Morris et al. 2015a, b; Kimmig et al. 2017); two of the three were species originally described from the Burgess Shale. Siphusauctum lloydguntheri (Fig. 5i) is known from a single specimen from near the top of Antimony Canyon (Kimmig et al. 2017); it is a congener of the species described from the Burgess Shale. The other two species are all known from multiple specimens and Eldonia can be found in several localities within the Spence Shale (supplementary material).

Algae and cyanobacteria

Marpolia spissa is the only alga currently recognized from the Spence Shale; it has been reported from Antimony Canyon (Conway Morris & Robison 1988). Its precise affinities among algae have been debated, and it has even been interpreted as a prokaryote (see LoDuca et al. 2017). The possible cyanobacterium Morania fragmenta has been reported from the Wellsville Mountains, although its biological affinities are also questionable (Handle & Powell 2012), and it might actually represent fecal pellets (Robison et al. 2015).

Box 3. Soft-bodied arthropods of the Spence Shale

Arthropods are the dominant component throughout the Spence Shale and are currently represented by 57 species in 40 genera (Conway Morris et al. 2015a; Robison et al. 2015; Pates & Daley 2017; Pates et al. 2018). The Spence Shale museum collections. The diverse echinoderm fauna is unique relative to other Cambrian Lagerstätten of Laurentia, as usually sponges are the second most dominant phylum (e.g. Caron & Jackson 2008; Kimmig & Pratt 2015; Foster & Gaines 2016; Paterson et al. 2016; Hou et al. 2017; Lerosey-Aubril et al. 2018). When considering well-skeletonized taxa, trilobites outnumber all the other groups in terms of specimens in museums by a factor of c. 9:1; echinoderms and hyoliths are the next most abundant groups in Spence Shale museum collections. The diverse echinoderm fauna is unique relative to other Cambrian Lagerstätten of Laurentia, as usually sponges are the second most dominant phylum (e.g. Caron & Jackson 2008; Robison et al. 2015). The Spence Shale may represent a distinct environment, perhaps more oxygenated based on the presence of these as well as the abundant trace fossils. Trilobites also seem to dominate in field samples (J. Kimmig, pers. obs.). Notably, there are some well-skeletonized groups that are quite rare in museum collections from the Spence Shale, such as molluscs, and this rarity probably represents true rarity in the field, but the relative paucity of brachiopods in museum collections seems to be a matter of sampling (J. Kimmig, pers. obs.). This is something that has to be considered for future palaeoecological analyses (e.g. Lieberman & Kimmig 2018).

Trace fossils

Trace fossils are common in the Wellsville Mountains and more than 35 ichnospicies have been described. These range from burrows to moving and resting traces to a variety of coprolites (Fig. 4c; Kimmig & Strotz 2017; Hammersburg et al. 2018). Ichnofossils have the highest diversity in the Wellsville Mountains, but Planolites and Diplichnites can be found in Oneida Narrows, and Diplichnites, Rusophycus and Treptichnus have been reported from High Creek (supplementary material; Hammersburg et al. 2018).

Palaeoecology

The Spence biota is similar to other Cambrian Burgess Shale-type biotas in that the fauna is dominated by arthropods (e.g. Caron & Jackson 2008; Kimmig & Pratt 2015; Foster & Gaines 2016; Paterson et al. 2016; Hou et al. 2017; Lerosey-Aubril et al. 2018). When considering well-skeletonized taxa, trilobites outnumber all the other groups in terms of specimens in museums by a factor of c. 9:1; echinoderms and hyoliths are the next most abundant groups in Spence Shale museum collections. The diverse echinoderm fauna is unique relative to other Cambrian Lagerstätten of Laurentia, as usually sponges are the second most dominant phylum (e.g. Caron & Jackson 2008; Robison et al. 2015). The Spence Shale may represent a distinct environment, perhaps more oxygenated based on the presence of these as well as the abundant trace fossils. Trilobites also seem to dominate in field samples (J. Kimmig, pers. obs.). Notably, there are some well-skeletonized groups that are quite rare in museum collections from the Spence Shale, such as molluscs, and this rarity probably represents true rarity in the field, but the relative paucity of brachiopods in museum collections seems to be a matter of sampling (J. Kimmig, pers. obs.). This is something that has to be considered for future palaeoecological analyses (e.g. Lieberman & Kimmig 2018).

Box 4. Outstanding questions

1. What factors make the Wellsville Mountains localities more likely to preserve soft-bodied fossils than other Spence Shale localities?

2. What are the patterns of ecological association in the Spence Shale?

3. What are the stratigraphic relationships among the various Spence Shale localities?

4. How does the Spence Shale correlate with other deposits within and outside the Great Basin?
In terms of soft-bodied fossils, the Spence Shale again is similar to other lower and middle Cambrian Lagerstätten (e.g. Caron & Jackson 2008; Kimmig & Pratt 2015; Foster & Gaines 2016; Paterson et al. 2016; Hou et al. 2017; Leresy-Aubril et al. 2018), as it is dominated by arthropods (Box 3; supplementary material), which make up about half of the soft-bodied genera. In terms of abundance, only vermiform fossils exceed arthropods. Echinoderms are locally abundant in the Spence Shale and can occur on slabs with dozens of specimens at Miners Hollow and Cataract Canyon. Many soft-bodied taxa comprise autochthonous benthic species, such as hemichordates, scaliodophorans, lobopodians, Wittwaxia, sponges, rare stalked filter feeders, some arthropods and various trace makers, supporting the notion of tolerably well-oxygenated bottom waters (Church et al. 1999; Robison et al. 2015; Kimmig & Strotz 2017; Kimmig et al. 2017; Kimmig & Pratt 2018; Pratt & Kimmig 2019).

There were, however, also many putatively nektonic (or even pelagic) taxa such as Banfia, radiodonts and Tuozia (Conway Morris et al. 2015a, b; Robison et al. 2015; Pates et al. 2018), and Marpolia spissa is a possible denizen of the plankton (Kimmig et al. 2017).

Based on the generic presence–absence list of Leresy-Aubril et al. (2018) and the list generated for this paper (supplementary material) there are at least 26 genera found in the Spence Shale that have not been reported from other Utah Lagerstätten. Although part of this might be due to the older age of the deposit, several of the taxa have been reported from younger Burgess Shale, suggesting that at least part of it might be due to different environmental conditions when compared with the other Cambrian Utah Lagerstätten; that is, better oxygenation, shallower water and possibly higher productivity.

Summary

The Spence Shale of northeastern Utah and southeastern Idaho preserves a diverse, well-skeltonalized and soft-bodied biota of early middle Cambrian (Miaolingian; Wulian) age. It provides insight into marine life in Laurentia just before the time of the Walcott Quarry of the Burgess Shale. Notably, although older than the Burgess Shale and the Wheeler, Marjum and Weeks formations, the Spence Shale shares several taxa with these deposits, as well as with the older Poche Formation in Nevada (supplementary material). It seems that during this interval, soft-bodied arthropods (Hendricks et al. 2008) and soft-bodied taxa in general (Hendricks 2013) showed less evolutionary volatility (sense Lieberman & Melott 2013) than trilobites. Let us consider the trilobites, which show a very high degree of turnover of 128 species that occur in soft-bodied deposits globally, not a single species persists for more than one stage (Hendricks et al. 2008). By contrast, among 156 species of soft-bodied arthropods, 16 species persist for more than one stage, and some of these persisted for several stages (Hendricks et al. 2008). Ultimately, unravelling macroevolutionary patterns in taxa occurring in soft-bodied deposits such as the Spence Shale will probably prove useful for evaluating various hypotheses about the nature and timing of the Cambrian radiation (for discussion of some of these hypotheses, see Lieberman & Cartwright 2011; Daley et al. 2018). In addition, progress recently has been made in understanding the geographical distribution of various fossils in the Spence Shale, but much more information is needed about the stratigraphic and sedimentological context of fossils within and across localities (Box 4). Only then will it be possible to work out the various taphonomic pathways that allowed soft-bodied preservation in this key window of Cambrian life.

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Correction Notice: Error bars have been added to Fig. 5g and h. The Editorial Office apologizes for this error.

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