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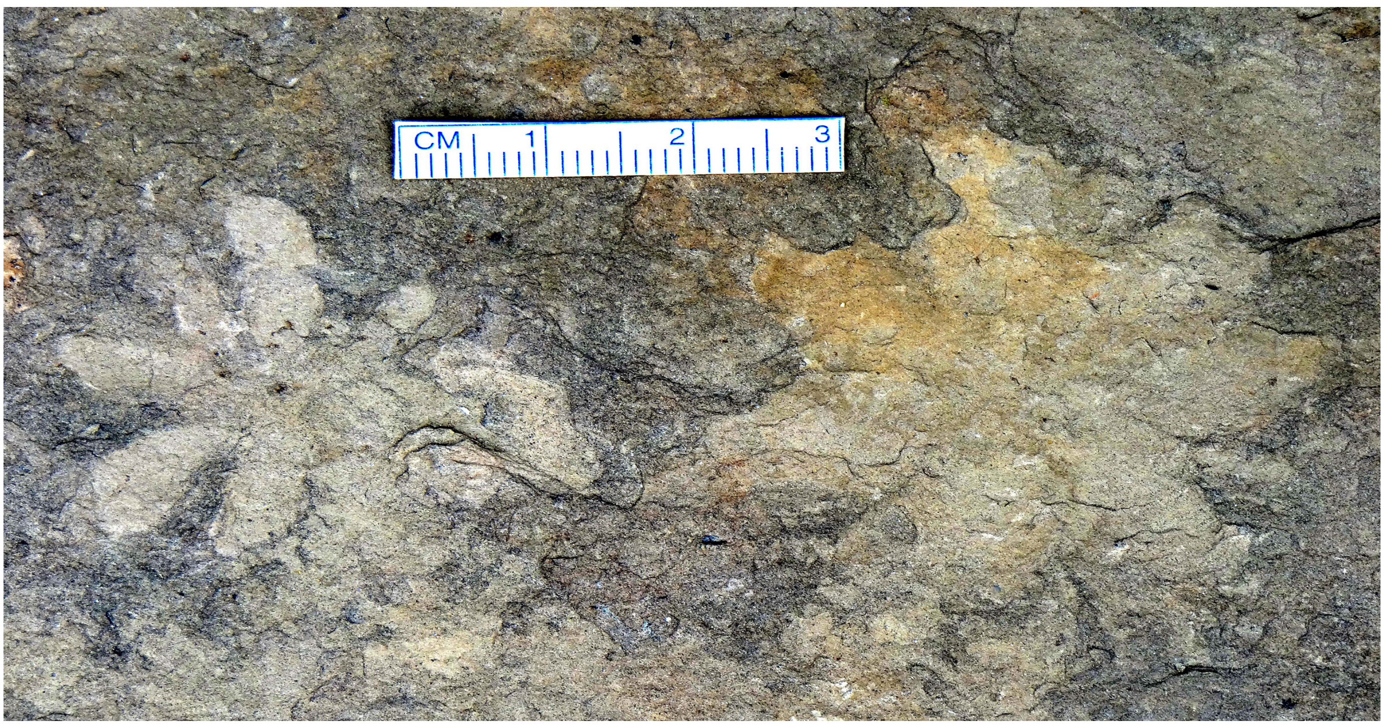

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Cover Figure: Endoreliefs of *Gyrophyllites kwassizensis,* False color image, KUMIP 314143, Cataract Canyon.

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ICHNOTAXONOMY OF THE CAMBRIAN SPENCE SHALE MEMBER OF THE LANGSTON FORMATION, WELLSVILLE MOUNTAINS, NORTHERN UTAH, USA

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ABSTRACT

The Spence Shale of northern Utah is the oldest North American middle Cambrian (~506–505 Ma) Burgess Shale-type (BST) deposit and, unlike previously thought for BST deposits, has a very diverse ichnofauna. Twenty-four ichnogenera and 35 ichnospecies were identified: *Archaeonassa* (*A. fossulata* and *A. jamisoni* isp. nov.), *Arenicolites carbonaria*, *Aulichnites*, *Bergaueria* (*B. hemispherica* and *B.* aff. *perata*), *Conichnus conicus*, *Cruziana* (*C. barbata* and *C. problematica*), *Dimorphichnus*, *Diplichnites (D.* cf. *binatus, D. gouldi*, and *D.* cf. *govenderi)*, *Gordia marnia*, *Gyrophyllites kwassizensis*, *Halopoa* aff. *imbricata*, *Lockeia siliquaria*, *Monomorphichnus* (*M. bilinearis*, *M. lineatus*, and *M.* cf. *multilineatus*), *Nereites* cf. *macleayi*, *Phycodes curvipalmatum*, *Phycosiphon incertum*, *Planolites* (*P. annularius*, *P. beverleyensis*, and *P. montanus*), *Protovirgularia* (*P. dichotoma* and *P.* cf. *pennatus*), *Rusophycus* (*R. carbonarius*, *R.* cf. *pudicus,* and *R.* cf. *cerecedensis*), *Sagittichnus lincki*, *Scolicia*, *Taenidium* cf. *satanassi*, *Teichichnus* cf. *nodosus*, and *Treptichnus* (*T. bifurcus*, *T. pedum*, and *T. vagans*). The ichnofossils comprise three ichnocoenoses—*Rusophycus-Cruziana, Sagittichnus*, and *Arenicolites-Conichnus*—representing dwelling, deposit- and filter-feeding, grazing, locomotion, and predation behaviors of organisms (e.g., annelid worms and trilobites). Two ichnofossil associations are suggestive of predation: (1) *Planolites* terminating at a *Rusophycus*; and (2) *Archaeonassa* crosscutting a *Taenidium*. The Spence Shale ichnofauna represent a distal Cruziana Ichnofacies and depauperate, distal Skolithos Ichnofacies. A new ichnospecies of *Archaeonassa* is proposed, *A. jamisoni* isp. nov., and *Ptychoplasma* (*Protovirgularia*) *vagans* is herein transferred to *Treptichnus*. This study is the first ichnotaxonomic study of the Spence Shale and North American BST deposits and shows highly diverse ichnofaunas can be present in BST deposits.

Keywords: *Archaeonassa*, *Cruziana*, *Gyrophyllites*, ichnofossil, *Rusophycus*

INTRODUCTION

Although rare in the fossil record, soft-tissue preservation has provided paleontologists with a detailed glimpse into unique paleoenvironments with even more unique and sometimes bizarre faunas not seen elsewhere. Soft tissues are most commonly preserved as kerogenized carbonaceous films, known as Burgess Shale-type (BST) preservation (e.g., Gaines, Kennedy, & Droser, 2005). A fossilization mode still not well understood, numerous studies of BST deposits (e.g., Butterfield, 1990, 1995; Allison & Brett, 1995; Petrovich, 2001) have tried to delineate and understand the mechanics and paleoenvironmental conditions necessary for BST production, including whether or not the absence of ichnofossils is necessary. Understanding the physicochemical controls can help refine depositional, paleoenvironmental, and paleoecological interpretations of BST deposits. Ichnofossils, however, can be used as proxies for paleoenvironmental and physicochemical conditions (e.g., sedimentation rate, benthic paleooxygenation, nutrients, depositional energy, etc.) present during and after deposition, even when body fossils are absent (e.g., Bromley, 1996; Hasiotis & Platt, 2012), and, therefore, can aid in understanding BST production.

Rare throughout the middle and upper Proterozoic and lower Phanerozoic, most BST deposits occur globally in lower and middle Cambrian (Terreneuvian–Series 3) rocks with most middle Cambrian BST deposits confined to North America (Conway Morris, 1992; Butterfield, 1995; Garson & others, 2012). The most well-

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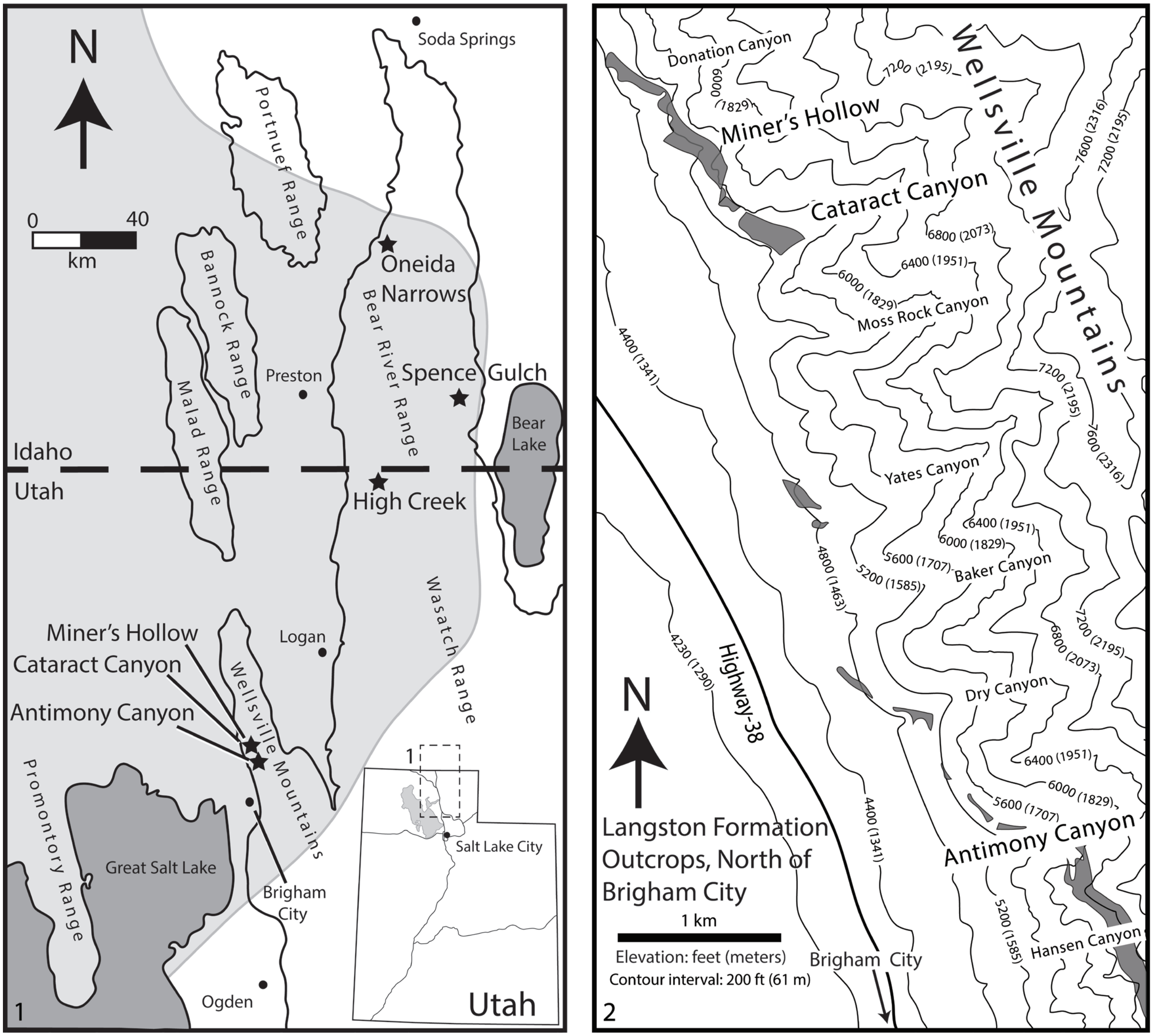

Figure 1. Map of study area and collection sites from the Spence Shale. *1*, Spence Shale collection localities in northern Utah and southern Idaho, shaded area denotes presence of the Spence Shale (modified from Liddell, Wright, & Brett, 1997); *2*, Topographic map of the Wellsville Mountain area, north of Brigham City with Langston Formation outcrops shaded (modified from Jensen & King, 1999).

known North American BST deposits include (by age), the Spence Shale (~506–505 Ma), Burgess Shale, Wheeler Formation, and Marjum Formation (Gaines & Droser, 2005; Garson & others, 2012). The Spence Shale of northern Utah (Fig. 1) is the oldest among North American BST deposits with unique preservation of both soft tissues and numerous ichnofossils sometimes in the same stratigraphic intervals or in direct contact (Garson & others, 2012).

The purpose of this study is to: (1) document the ichnofossils and ichnodiversity of the Spence Shale; (2) establish ichnocoenoses and assign ichnofacies; and (3) compare the Spence Shale ichnofauna to ichnofaunas present in other BST and Cambrian-aged deposits. Detailed ichnotaxonomic studies on BST deposits are necessary so that ichnocoenoses and ichnofacies can be established to further interpret the physicochemical controls that determined faunal types and the type and degree of bioturbation.

This is the first study to conduct a detailed ichnotaxonomic examination of ichnofossils in a North American BST deposit, which will help form a baseline for BST deposits. No significant ichnotaxonomic work exists and only a few reports of ichnofossils are available for the Wheeler and Marjum formations (Ubaghs & Robison, 1985; Robison, 1991; Gaines & Droser, 2005; Gaines, Kennedy, & Droser, 2005). Similarly, very little ichnotaxonomic work exists from the Burgess Shale (e.g., Caron & others, 2010; Mángano, 2011; Minter, Mángano, & Caron, 2012). There are several ichnotaxonomic studies from lower and middle Cambrian BST deposits of China: the Chengjiang Formation (e.g., Zhang

& others, 2007; Huang & others, 2014) and the Kaili Formation (e.g., Yang, 1994; Yang & Zhao, 1999; Wang & others, 2004, 2009; Lin & others, 2010). Ichnotaxonomic comparisons between Chinese and North American BST deposits, as well as others, help establish the range of paleoenvironments and physicochemical conditions in which BST fossils had been produced.

BACKGROUND

The Spence Shale was first described by Walcott (1908) from the Spence Gulch, southeastern Idaho, after a Bear River Range resident, R.S. Spence, began a 10-year correspondence in 1896 sending numerous well-preserved fossils to Walcott (Resser, 1939). Described as a 30-foot-thick (9.1 m) "argillaceous shale with sandy shale," the Spence Shale was interpreted as the basal member of the Ute Formation of Idaho (Walcott, 1908; Resser, 1939). Maxey (1958) later placed the Spence Shale as the middle member of the Langston Formation between the Naomi Peak Limestone (basal) and High Creek Limestone (upper) members. Oriel and Armstrong (1971), however, placed the Spence Shale as a tongue deposit within the Lead Bell Shale of Idaho. Subsequent authors have followed Maxey (1958) for units outcropping within Utah (e.g., Hintze & Robison, 1975; Robison, 1976; Conway Morris & Robison, 1988; Liddell, Wright, & Brett, 1997; Garson & others, 2012); whereas, Oriel and Armstrong (1971) has remained in use for outcrops in Idaho (e.g., Palmer & Campbell, 1976; Liddell, Wright, & Brett, 1997). Robison (1991) proposed that the Spence Shale be elevated to formation rank, but to date, no author has accepted this proposal (Liddell, Wright, & Brett, 1997; Garson & others, 2012).

Middle and upper Cambrian units of the Great Basin of Utah were deposited in a north–south-trending (present-day orientation) carbonate belt, flanked by inner (eastern) and outer (western) detrital belts (Palmer, 1960; Robison, 1960) (Fig. 2). The Spence Shale was deposited mostly within the outer detrital belt and some of the middle carbonate belt (Robison, 1960; Liddell, Wright, & Brett, 1997; Garson & others, 2012). Palmer and Campbell (1976) proposed three biofacies for the Langston Formation and equivalent strata: (1) low-diversity, restricted-shelf biofacies corresponding to deposition in the inner detrital belt; (2) high-diversity, platform-margin to open-shelf biofacies corresponding to deposition in the middle carbonate belt; and (3) deep-shelf or basinal, low-diversity biofacies characterized by agnostoid and oryctocephalid trilobites. Robison (1976) showed that the agnostoid and polymeroid trilobite distributions of the Langston Formation correlated with the carbonate and detrital belts similar to the Palmer and Campbell (1976) biofacies. The restricted-shelf biofacies includes the sandy units of the Naomi Peak Limestone Member (also known as Twin Knobs Formation of Idaho), whereas, the platform-margin to open-shelf biofacies corresponds to most of the limestones and shales of the Langston Formation, and the deep-shelf biofacies corresponds to the shales at the Oneida Narrows locality (Liddell, Wright, & Brett, 1997).

Several models have been proposed for the production of BST and each suggests a dominant environmental physicochemical factor(s): (1) rapid burial and benthic anoxia (Conway Morris, 1986); (2) clay-rich sediment to allow adsorption of enzymes into surrounding clays and inhibit decomposition (Butterfield, 1990, 1995); (3) oscillations between benthic anoxia and dysoxia (Allison & Brett, 1995); or (4) iron mineral-rich sediment to allow iron (II) adsorption and inhibit bacterial decomposition (Petrovich, 2001). Gaines and Droser (2005) and Gaines, Kennedy, and Droser (2005) developed a new model for BST from the Wheeler Formation of central Utah requiring siliciclastic clay-dominant, mixed siliciclastic-carbonate sediment with low original porosity, proximity to both oxic and anoxic bottom waters, and little to no bioturbation. Gaines and Droser (2010) used ichnofabric indices to confirm the Gaines, Kennedy, and Droser (2005) model for the Wheeler and Marjum formations and found that benthic anoxia was necessary for BST production. Similarly, Garson and others (2012) used bioturbation patterns via ichnofabric indices to interpret the Spence Shale benthic paleooxygenation and found that significant bottom-water oxygenation occurred and was persistent for some periods and rapidly alternated between anoxic and oxic conditions during others.

GEOLOGIC SETTING

During the middle Cambrian, present-day northern Utah was located on the northwestern margin of Laurentia (Fig. 3; Liddell, Wright, & Brett, 1997). The Spence Shale is the early middle Cambrian (Series 3, Stage 5), middle member of the Langston Formation in northern Utah stratigraphy (Maxey, 1958; Liddell, Wright, & Brett, 1997; Garson & others, 2012; Peng, Babcock, & Cooper, 2012). In Utah, the Langston Formation is underlain by the Geertsen Canyon Quartzite of the Neoproterozoic–lower Cambrian Brigham Group and overlain by the Ute Formation (Fig. 4; Maxey, 1958; Liddell, Wright, & Brett, 1997). In the Wellsville Mountain area, the Spence Shale is underlain by the Naomi Peak Limestone Member (Twin Knobs Formation of Idaho) and overlain by the High Creek Limestone Member (Maxey, 1958; Liddell, Wright, & Brett, 1997).

The Spence Shale is a 50–65-m-thick, gray to black, calcareous shale interbedded with peloidal–oolitic limestone intervals and sandy stringers (Fig. 5) deposited on a ramp setting, shifting from proximal to distal as time progressed (Liddell, Wright, & Brett, 1997; Garson & others, 2012) (see Fig. 2). The Spence Shale contains several stacked, shallowing parasequences that lead to deposition of peloidal, oolitic, and nodular limestone intervals (Liddell, Wright, & Brett, 1997).

The Spence Shale has an abundant and diverse hard-bodied fauna, including, agnostoid and polymeroid trilobites, articulate and inarticulate brachiopods, eocrinoids, mollusks, and sponges (Walcott, 1908; Resser, 1939; Gunther & Gunther, 1981; Babcock & Robison, 1988; Robison, 1991; Liddell, Wright, & Brett, 1997; Sprinkle & Collins, 2006; Briggs & others, 2008). It also contains a diverse soft-bodied fauna, including, algae, annelids, and soft-shelled arthropods (Robison, 1969, 1991; Briggs & Robison, 1984; Conway Morris & Robison, 1988; Liddell, Wright, & Brett, 1997). Traditionally, ichnofossils and BST fossils are not thought to normally occur in close proximity to each other but to be deposited in exclusive zones of oxia–dysoxia and anoxia, respectively (Allison & Brett, 1995). There are, however, increasing reports of ichnofossils and BST fossils occurring together,

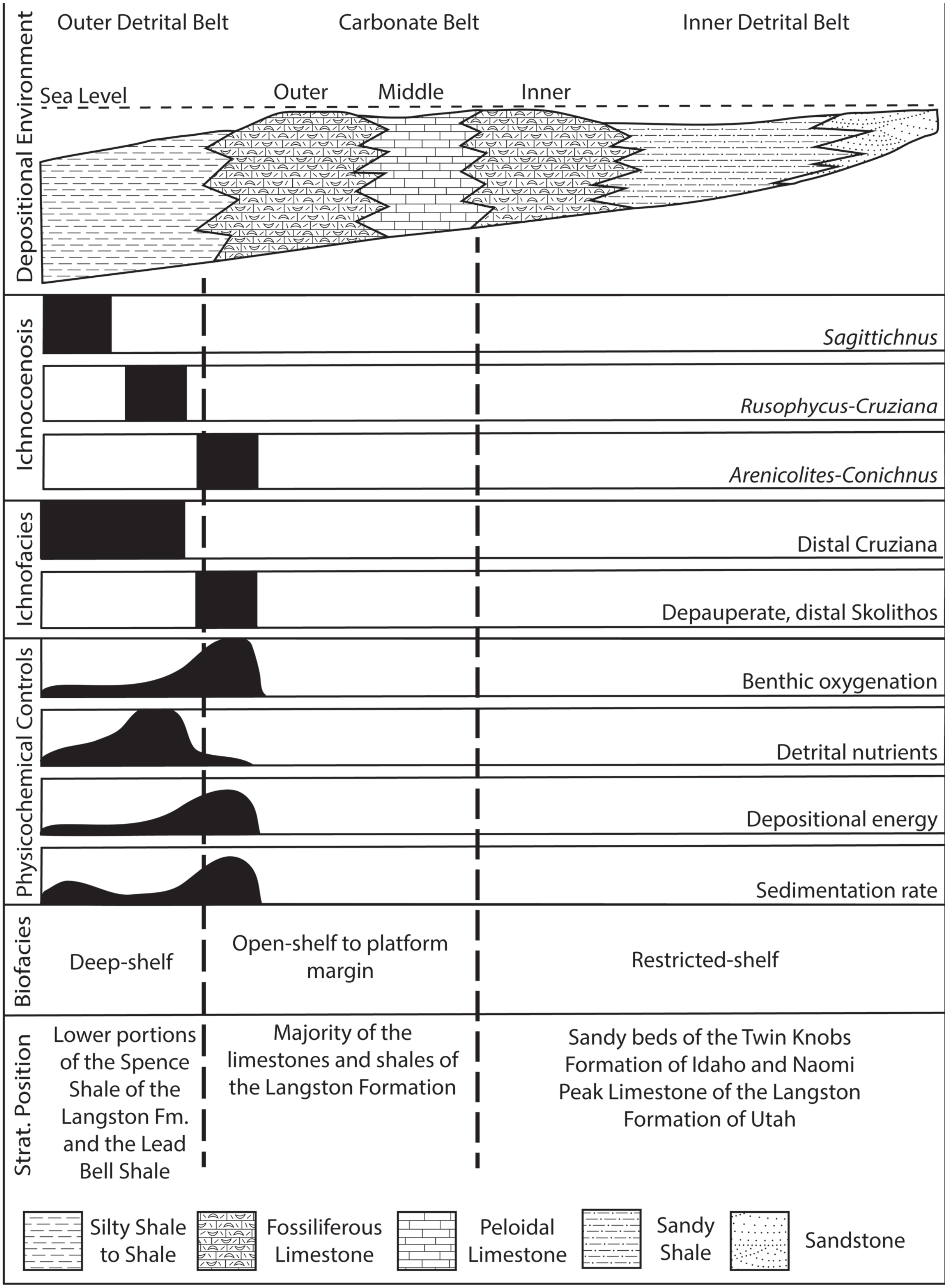

Figure 2. Depositional and biofacies models, ichnocoenoses, ichnofacies, and physicochemical controls of the Langston Formation and equivalent units (modified from Palmer & Campbell, 1976; Robison, 1976; Liddell, Wright, & Brett, 1997).

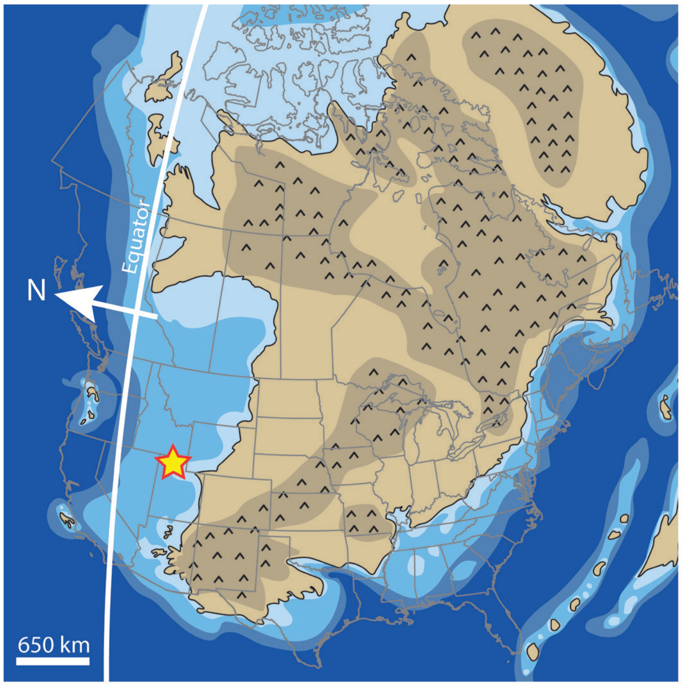

Figure 3. Middle Cambrian paleogeography of Laurentia with Spence Shale location (star) (modified and redrawn with permission from Colorado Plateau Geosystems ©2007).

recording interactions between tracemaking organisms and BST fossils, suggesting more dynamic paleoenvironmental conditions during deposition (e.g., Zhang & others, 2007; Wang & others, 2009). Prior to this study, only a few ichnofossils were reported or described from the Spence Shale, including *Brooksella*, coprolites, *Cruziana*, *Gyrophyllites*, *Neonereites*, *Palaeophycus*, *Planolites*, *Rusophycus*, *Tasmanadia*, and *Treptichnus* (Robison, 1969, 1991; Willoughby & Robison, 1979; Ubaghs & Robison, 1985; Conway Morris & Robinson, 1986).

ABBREVIATIONS

The abbreviations used in this study include: **KUMIP**, University of Kansas Museum of Invertebrate Paleontology; **IBGS**, IchnoBioGeoScience Research Group (University of Kansas). Key to fossil collection naming: **YY-A-XXX** [**YY**: collector and donor (LG: Lloyd Gunther, PJ: Paul Jamison); **A**: depositional realm (C: continental, M: marine); **XXX**: three-digit specimen number].

MATERIALS AND METHODS

Material for this study (Fig. 6–24) comes from Spence Shale outcrops in the Wellsville Mountains of northern Utah, USA. Specimens were collected and donated to the KUMIP and IBGS collections by Lloyd and Val Gunther, Paul Jamison, Phillip Reese, and Richard A. Robison. Specimens were measured using

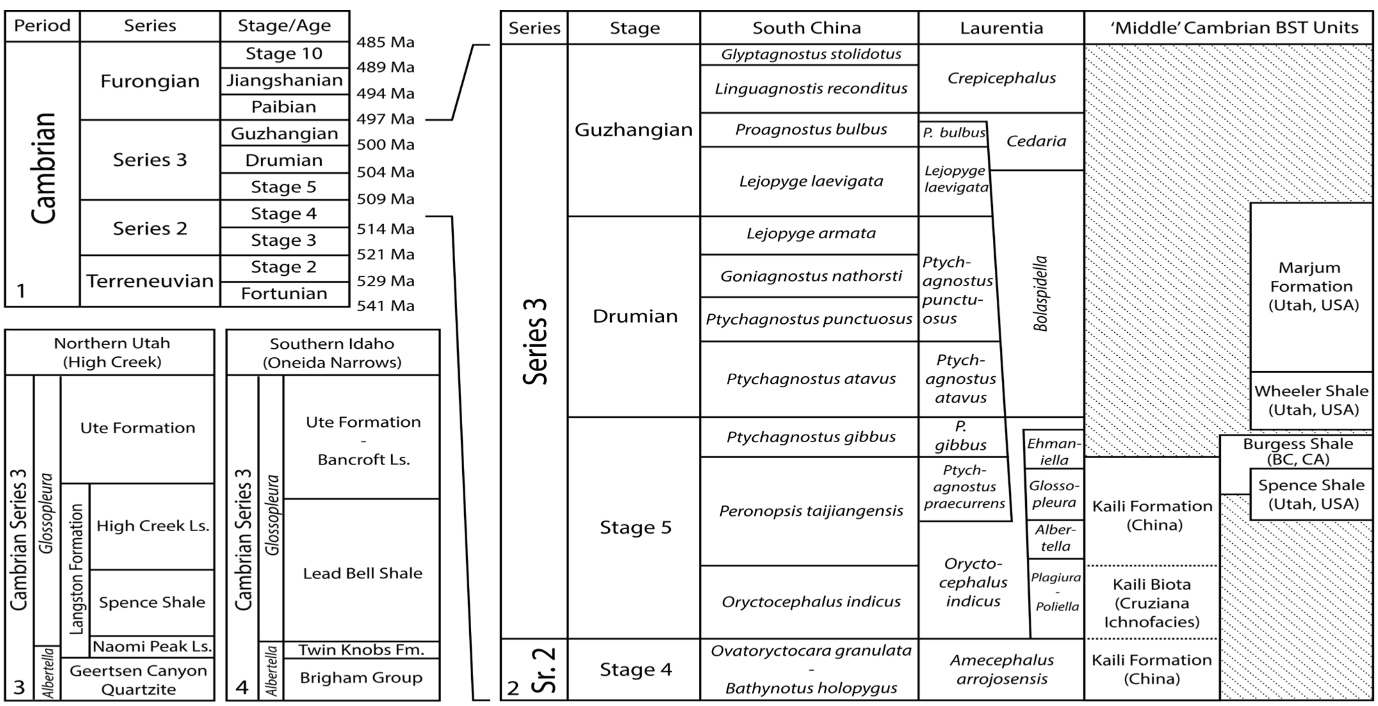

Figure 4. Cambrian geologic time scale and correlated biostratigraphy of Series 3 Cambrian Burgess Shale-type units of China and North America. *1,* Cambrian Period geologic time scale with series and stages/ages (redrawn from Peng, Babcock, & Cooper, 2012); *2,* Cambrian Series 2–3 trilobite biozonation correlation between South China and North America (i.e., Laurentia) with Burgess Shale-type deposits; BC, CA=British Columbia, Canada (modified from Liddell, Wright, & Brett, 1997; Collom, Johnston, & Powell, 2009; Lin & others, 2010; Robison & Babcock, 2011; Peng, Babcock, & Cooper, 2012); *3–4,* Northern Utah and southern Idaho stratigraphic correlation (modified from Liddell, Wright, & Brett, 1997).

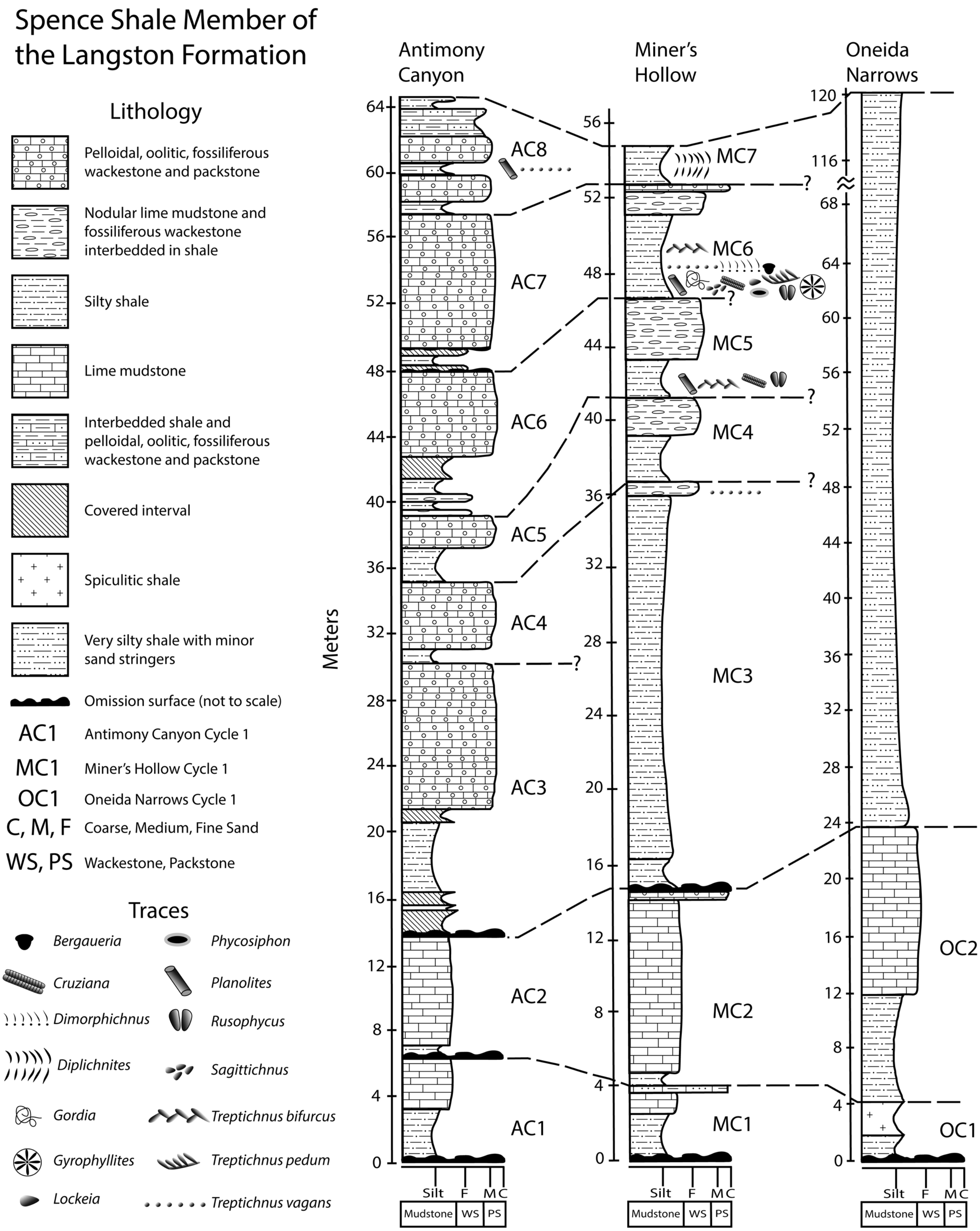

Figure 5. Stratigraphy of the Spence Shale with ichnofossil placement (modified from Liddell, Wright, & Brett, 1997).

nondigital Vernier calipers (0.1 mm accuracy). Long or winding traces were measured by a waxed string, which was then measured with calipers. ImageJ (v. 1.48; USNIH, 2015) analysis software was used to measure V-shaped angles of striation patterns, dimensions of smaller specimens, and grain sizes. Several specimen slabs were prepared for in-laboratory examination and photography with a 2.0% HCl acid solution to dissolve thin surficial carbonate deposits obscuring underlying traces. Unpolished sections of cut samples were wetted with glycerin and photographed. Specimens were examined in hand sample and using a Nikon SMZ1000 binocular light microscope. Specimen photographs were taken with a mounted Sony Cyber-shot DSC-HX200V camera or a Nikon DXM1200 digital camera attached to the Nikon SMZ1000 microscope. Photographs were processed with Adobe Photoshop™ Creative Cloud (CC) version.

Ichnological assessments were made following several methodologies. Descriptions of architectural and surficial morphology follow Hasiotis and Mitchell (1993), Bromley (1996), and Hasiotis (2004, 2008). Trackways were described using the terminology of Trewin (1994), Keighley and Pickerill (1998), and Minter, Braddy, and Davis (2007). Samples with visible bedding or laminations and bioturbation were analyzed via the Ichnofabric Index (*ii*; Droser & Bottjer, 1986). Bedding planes were analyzed with the Bedding-Plane Bioturbation Index (BPBI); Miller & Smail, 1997). Since this material was collected and donated by private collectors, the establishment of truly representative ichnocoenoses is difficult. Each examined slab specimen is itself a unique ichnocoenosis and represents a single community of traces. Overarching ichnocoenoses were constructed via reoccurring ichnofossil associations following Pemberton and others (2001) and Jackson, Hasiotis, and Flaig (2016).

SYSTEMATIC ICHNOLOGY

Ichnogenus ARCHAEONASSA Fenton & Fenton, 1937a

Type ichnospecies.—Archaeonassa fossulata Fenton & Fenton, 1937a.

Emended Diagnosis.—Short, round- to ovoid-shaped or elongated trails or burrows commonly deeper at one end, and may grade into indistinct V-shaped trails; concave to slightly convex furrow flanked by pair of convex ridges, central furrow typically wider than ridges; lateral convex ridges may be smooth or ornamented with oblique to transverse striations or smaller lobes (Fenton & Fenton, 1937a; Buckman, 1994).

Discussion.—Fenton and Fenton (1937a) established *Archaeonassa* for elongate, concave furrows with flanking convex ridges produced by snails and other gastropods from the lower Cambrian Mount Whyte Formation of British Columbia. Häntzschel (1975) placed *Archaeonassa* in the Scolicia Group, but was not placed in synonymy with *Scolicia* because *Archaeonassa* lacks any complex backfill diagnostic to *Scolicia* (Buckman, 1994). Buckman (1994) reviewed *Archaeonassa* and considered it the senior synonym of *Scolicia vada* Chamberlain, 1971, and some specimens of *Palaeobullia* Götzinger & Becker, 1932. Yochelson and Fedonkin (1997) rejected this synonymy, however, partly because Buckman (1994) did not include the original type material of *Archaeonassa* while also including ornamented lateral ridges.

Archaeonassa is generally interpreted as a gastropod locomotion or grazing trace (Fenton & Fenton, 1937a; Buckman, 1994; Jensen, Droser, & Gehling, 2005). Yochelson and Fedonkin (1997), however, suggested that *Archaeonassa* was not produced by mollusks but did not suggest any other producers. Trilobites and echinoids have also been suggested as possible tracemakers (Buckman, 1994). Jensen, Droser, and Gehling (2005) pointed out that such protists as foraminifera can make traces similar to *Archaeonassa* but are rarely considered as producers. Buchanan and Hedley (1960, p. 557–558) did not figure any ichnofossils (i.e., only provided drawings of the pseudopodial systems used by forams), but provided a description of foram-produced furrows: "… a furrow is left in the sand as a result of the leading edge of the test being preceded by a raised mound or 'bow-wave' of sand." This description, however, does match most *Archaeonassa* descriptions. *Archaeonassa* has mostly been reported from shallow-marine deposits (e.g., tidal flats), as well as from continental deposits (e.g., delta front, fluvial, and lacustrine; e.g., Fenton & Fenton, 1937a; Buatois & Mángano, 2002, 2007; Mángano, Buatois, & Muñiz Guinea, 2005). *Archaeonassa* was recently reported from flysch deposits from India (Khaidem, Rajkumar, & Soibam, 2015); however, those specimens are overlapping, bilobate, convex epireliefs, likely *Crossopodia* M'Coy, 1851 or *Gyrochorte* Heer 1865 in Heer 1864–1865. *Archaeonassa* ranges from the Ediacaran to recent (e.g., Fenton & Fenton, 1937a, Jensen, Droser, & Gehling, 2005; Buckman, 1994; Martin, 2013).

ARCHAEONASSA FOSSULATA (Fenton & Fenton, 1937a)
Figure 6.1

Material.—IBGS PJ-M-027: one specimen, Miner's Hollow; IBGS PJ-M-033: one specimen (part and counterpart), Miner's Hollow.

Diagnosis.—Concave to slightly convex furrow flanked by pair of convex ridges; central furrow wider than flanking ridges; the lateral convex ridges may be smooth or ornamented with oblique to transverse striations or smaller lobes (Fenton & Fenton, 1937a; Buckman, 1994).

Description.—Convex furrow with concave lateral ridges in hyporelief (IBGS PJ-M-027) and concave furrow with convex lateral ridges in epirelief (IBGS PJ-M-033). Furrows 37.4–40.2 mm long, 3.7–5.4 mm wide, and 1.4 mm deep; lateral ridges 0.6–2.8 mm wide.

Occurrence.—Gray to slightly blue-gray (weathered to tan), calcareous and micaceous silty shale.

Associated ichnotaxa.—Gyrophyllites kwassizensis, *Nereites* cf. *macleayi*, *Planolites montanus*, and *Treptichnus pedum*.

Discussion.—Specimens were assigned to *Archaeonassa fossulata* based on the simple and smooth furrows flanked by lateral ridges in epirelief (Fig. 6.1). The specimen of *Archaeonassa* on IBGS PJ-M-027 occurs as a convex furrow with concave lateral ridges in hyporelief. The width and depth of the furrow and lateral ridges are not uniform. The furrow and ridges are narrower and shallower on one end than on the other, suggesting the tracemaker may have been burrowing obliquely through the sediment. The specimen on IBGS PJ-M-033 occurs as a concave furrow with convex lateral ridges (in part and counterpart).

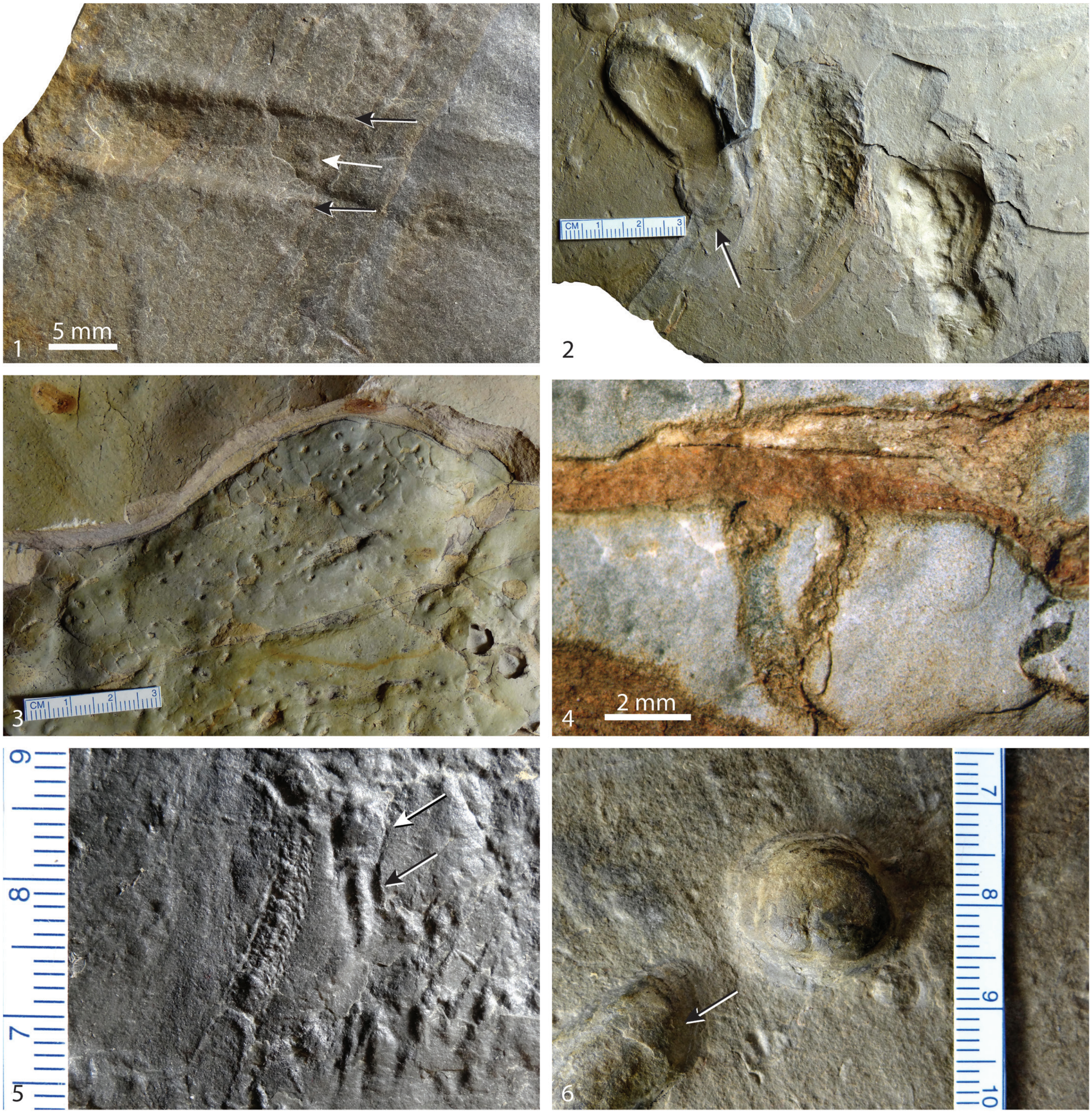

Figure 6. *Archaeonassa*, *Arenicolites*, *Aulichnites*, and *Bergaueria* specimens from the Spence Shale. *1, Archaeonassa fossulata* with convex ridges (black arrows) and concave furrow (white arrow) in concave epirelief, IBGS PJ-M-033; *2, Archaeonassa jamisoni* isp. nov. with holotype (arrow), in convex and concave epirelief, IBGS PJ-M-005, Miner's Hollow float; *3–4, Arenicolites carbonaria*, IBGS PJ-M-003, Cataract Canyon; *3, Arenicolites carbonaria* apertures in concave epirelief; *4, Arenicolites carbonaria* in full relief; *5,* Concave hyporelief of *Aulichnites* isp. (black arrow) terminating at *Lockeia siliquaria* (white arrow) and *Protovirgularia* cf. *pennatus* (left center) in convex hyporelief, IBGS PJ-M-019, Miner's Hollow; *6, Bergaueria hemispherica* near the termination of *Teichichnus* c.f. *nodosus* (arrow) in convex hyporelief, IBGS PJ-M-025, Cataract Canyon; scales in cm.

ARCHAEONASSA JAMISONI new ichnospecies
Figure 6.2, Figure 19.3–19.4

Material.—IBGS PJ-M-002: two specimens, Miner's Hollow; IBGS PJ-M-005: three specimens, Spence Shale float, Cataract Canyon.

Diagnosis.—Smooth, curved, asymmetrical furrow in concave epirelief with or without paired convex lateral ridges along sides of furrow that may merge at furrow terminations with massive fill; infill and lateral ridges may be absent, forming depressions with terracing on trace wall.

Description.—Curved, asymmetrical furrow with convex lateral ridges in epirelief. Furrows 47.2–52.6 mm long, 11.2–38.2 mm wide, and 1.4–5.7 mm deep; lateral ridges 2.7–5.2 mm wide and 2.1–3.8 mm thick, merged at furrow terminations.

Etymology.—After Paul Jamison, who collected and donated a large number of fossil specimens used in this study.

Types.—Holotype: IBGS PJ-M-005; Paratype: IBGS PJ-M-002.

Type stratum.—Cambrian, Series 3, Spence Shale Member of the Langston Formation.

Type locality.—Miner's Hollow, west side of Wellsville Mountains: T10N, R2W, Sec. 14, NE1/4 SW1/4 and NW1/4 SE1/4 (41° 36′ 4.8″N, 112° 2′ 12.5″W).

Repository.—Division of Invertebrate Paleontology, Museum of Natural History and Biodiversity Research Center, University of Kansas, Lawrence, Kansas, USA.

Occurrence.—Two lithologies: (1) Tan to light brown, siliciclastic silty shale; and (2) gray, calcareous shale.

Associated ichnotaxa.—*Phycodes curvipalmatum* and *Taenidium* cf. *satanassi.*

Discussion.—Until now, *Archaeonassa* was monotypic. The closest published morphotype resembling *A. jamisoni* was from a neoichnological experiment by Jensen, Droser, and Gehling (2005, fig. 2C) that produced asymmetrical undertraces via locomotion of a marine gastropod, *Nassarius* (*Hinia*) *reticulata* (Linnaeus, 1758). They compared the experimental traces to specimens of *Archaeonassa* from the Ediacaran Ust' Pinega Formation of northwest Russia and the Ediacara Member of the Rawnsley Quartzite, Flinder's Ranges, South Australia. Jensen, Droser, and Gehling (2005) suggested that the Neoproterozoic *Archaeonassa* represented movement over sandy media and were analogous to the specimens generated by creeping gastropods during their experiment. Sören Jensen (personal communication, 2014) suggested that the *A. jamisoni* specimens were likely produced by a similar behavior. Martin (2013, fig. 6.6b, p. 266) illustrated a modern moon-snail trace that consisted of a short, concave, asymmetrical furrow flanked by lateral ridges and greatly resembled *A. jamisoni* (Fig. 6.2). Jean-Bernard Caron (personal communication, 2016) suggested, however, that an ichnofossil interpretation of *A. jamisoni* is highly dubious due to the wide range of morphology between specimens and may actually be nodular concretions. We disagree with the nodular-concretion interpretation due to the presence of several shallow furrows that widen and deepen proximal to the specimens and taper and shallow out away from them (see Fig. 19.3). We interpret the shallow furrows to be short, entry furrows of a biogenic affinity.

Yochelson and Fedonkin (1997) noted that the original description of *Archaeonassa* contained two morphologies (elongate ribbon traces and rimmed pits) but restricted *Archaeonassa* to elongate ribbon traces and did not discuss the rimmed pits (resting traces) mentioned by Fenton and Fenton (1937a, p. 454). The rimmed pits of *Archaeonassa jamisoni* differ from *A. fossulata* due to the lack of elongate, ribbonlike furrow morphology typical of the ichnospecies. The Spence Shale material presented herein is, therefore, assigned to *Archaeonassa* based on comparisons to material described in Fenton and Fenton (1937a) and Buckman (1994) and discussions with S. Jensen. We interpret *A. jamisoni* to represent a combined locomotion and resting trace and possibly even a hunting trace of a gastropod.

Ichnogenus ARENICOLITES Salter, 1857

Type ichnospecies.—*Arenicola carbonaria* Binny, 1852 by subsequent designation (Richter, 1924, p. 137).

Diagnosis.—Vertical, U-shaped burrows without spreiten, and visible as paired openings in plan view (Fürsich, 1974a; Fillion & Pickerill, 1990).

Discussion.—*Arenicolites* is a U-shaped burrow similar to *Diplocraterion* Torell, 1870, but lacks spreite between tubes (Hakes, 1976; Fillion & Pickerill, 1990). Ten ichnospecies of *Arenicolites* are recognized: *A. brevis* Matthew, 1890; *A. carbonaria* Binney, 1852; *A. compressus* (Sowerby, 1829); *A. curvatus* Goldring, 1962; *A. longistriatus* Rindsberg & Kopaska-Merkel, 2005; *A. naraensis* Badve & Ghare, 1978; *A. sparsus* Salter, 1857; *A. statheri* Bather, 1925; *A. subcompressus* (Eichwald, 1860); and *A. variabilis* Fürsich, 1974a. *Arenicolites compressus*, *A. curvatus*, and *A. subcompressus* have elliptical cross sections, and *A. curvatus* also has inclined limbs (Fürsich, 1974a; Chamberlain, 1977; Fillion & Pickerill, 1990). *Arenicolites statheri* has narrow, parallel and vertical limbs, and both *A. statheri* and *A. naraensis* have a thick wall lining (Fürsich, 1974a; Chamberlain, 1977; Fillion & Pickerill, 1990). *Arenicolites sparsus* typically lacks a wall lining but usually occurs only as paired openings on the tops of beds (Fürsich, 1974a). *Arenicolites carbonaria* consists of a small-diameter U-shaped tube with a very thin wall lining and funnel-shaped apertures (Fürsich, 1974a; Fillion & Pickerill, 1990). *Arenicolites longistriatus* is a U-shaped burrow that is subhorizontal after compaction and has longitudinal striations along the length of the burrow, most commonly at the base of the U-shaped tube (Rindsberg & Kopaska-Merkel, 2005).

The ichnotaxonomic status of some *Arenicolites* ichnospecies is currently debated. Recently, McIlroy, Crimes, and Pauley (2005) and Callow, McIlroy, and Brasier (2011) reexamined the type material of *Arenicolites sparsus*, the first ichnospecies established, and found that the depressions Salter (1857) interpreted as paired burrow apertures were in fact not paired and not connected together by a U-shaped tube. *Arenicolites sparsus* was reinterpreted as body fossils of small microbial mats and transferred to *Beltanelliformis* Menner in Keller & others, 1974 (McIlroy, Crimes, & Pauley, 2005; Callow, McIlroy, & Brasier, 2011). Menon and others (2015) later reinterpreted *Beltanelliformis* as a pseudofossil formed from fluid injection through the sediment and, therefore, *A. sparsus* is also likely a pseudofossil.

Arenicolites is considered a dwelling or suspension-feeding burrow of annelid worms or small arthropods (e.g., Hakes, 1976; Bromley & Asgaard, 1979; Fillion & Pickerill, 1990). *Arenicolites* has been reported mostly from shallow marine deposits, but freshwater-aquatic and deep-marine deposits have been reported as well (e.g., Crimes & others, 1977; Bromley & Asgaard, 1979; Fillion & Pickerill, 1984; Hasiotis, 2002, 2004, 2008; Ash & Hasiotis, 2013). *Arenicolites* ranges from the early Cambrian to recent (e.g., Crimes, 1987, 1992) with problematic specimens reported from the Neoproterozoic (e.g., Fillion & Pickerill, 1990).

ARENICOLITES CARBONARIA (Binney, 1852)
Figure 6.3–6.4

Material.—IBGS PJ-M-003: multiple specimens, Spence Shale float, Cataract Canyon.

Diagnosis.—Vertical, U-shaped tubes expressed in plan view as paired depressions (concave epirelief) with small diameter limbs and funnel-shaped apertures in cross section (Fürsich, 1974a; Fillion & Pickerill, 1990).

Description.—Specimens are preserved as paired openings in concave epirelief. Apertures 1.0–2.2 mm wide, 0.7–1.1 mm deep, with variable spacing 0.7–4.1 mm. Burrow limbs are narrower than burrow openings and range 0.2–0.9 mm wide. Most limbs lack or have very thin wall linings (> 0.1 mm).

Occurrence.—Gray, massive, peloidal carbonate wackestone and packstone to mudstone with thin continuous and discontinuous laminations of tan to brown, very fine-grained siliciclastic sandstone and siltstone. Soft-sediment deformation is present, but limestone and laminations are extensively bioturbated (*ii*3–4).

Associated ichnotaxa.—Conichnus conicus.

Discussion.—Specimens were assigned to *Arenicolites carbonaria* due to their small, paired depression morphology. These specimens occur on the same slab as the *Conichnus conicus* described herein, but in a horizon ~1 cm below the *Conichnus* specimens (Fig. 6.3). Since *Arenicolites* is usually indicative of shallow-marine settings (e.g., Fillion & Pickerill, 1990) and due to its close vertical proximity to the *Conichnus*, sample IBGS PJ-M-003 is interpreted to have been deposited in shallower water and/or higher energy settings than the other Spence Shale ichnofossils. Though complete U-shaped tubes connecting surficial depressions are not visible in areas of the massive limestone in cut slabs, one complete U-shaped tube and several partial tubes are visible in weathered sections connecting funnel shapes in the thin laminations of very fine sandstone and siltstone (Fig. 6.4).

Ichnogenus AULICHNITES Fenton & Fenton, 1937b

Type ichnospecies.—Aulichnites parkerensis Fenton & Fenton, 1937b.

Diagnosis.—Convex epirelief, bilobate, ribbon trail with a medial furrow separating lobes; lower surface may show a unilobate, convex-downward shape, or as concave furrows with convex medial ridge (Fenton & Fenton, 1937b; Fillion & Pickerill, 1990).

Discussion.—Aulichnites is similar to other convex bilobate epirelief ichnotaxa, including *Gyrochorte*, *Olivellites* Fenton & Fenton, 1937c, *Psammichnites* Torell, 1870, and *Scolicia* de Quatrefages, 1849. *Aulichnites* and *Gyrochorte* are composed of paired convex ridges with a medial furrow (epirelief); however, the ridges of well-preserved *Gyrochorte* have a biserial-plaited ornamentation (Häntzschel, 1975), and may occur as vertical stacks of bilobate, concave-down spreite (Heinberg, 1973, p. 231, fig. 6). *Aulichnites* may be similar to poorly preserved *Gyrochorte* specimens that lack the plaited ornamentation, like those illustrated by Heinberg (1973). D'Alessandro and Bromley (1987) and Mángano, Buatois, and Rindsberg (2002) synonymized *Aulichnites* under *Psammichnites* after interpreting *Aulichnites* to be a preservational variant of *Olivellites,* which was also considered a junior synonym of *Psammichnites*. Though similar, *Aulichnites* and *Olivellites* were established separately by Fenton and Fenton (1937b, 1937c) due to the presence of a medial furrow or ridge in epirelief, respectively. Chamberlain (1971) synonymized *Aulichnites* under *Scolicia* with no reason given; however, Häntzschel (1975) rejected the Chamberlain (1971) synonymy and most subsequent authors (e.g., Hakes, 1976, 1977; Fillion & Pickerill, 1990) have followed Häntzschel's rejection.

Aulichnites is interpreted as the locomotion or grazing trail of a gastropod (Fenton & Fenton, 1937b; Fillion & Pickerill, 1990); however, some authors considered them to have been produced by xiphosurids (i.e., horseshoe crabs; Yochelson & Schindel, 1978; Chisholm, 1985; Fillion & Pickerill, 1990). *Aulichnites* occurs in shallow- and deep-marine as well as brackish water deposits (e.g., Fenton & Fenton, 1937b; Fillion & Pickerill, 1990). *Aulichnites* ranges from the Ediacaran to recent (e.g., Häntzschel, 1975; Narbonne & Aitken, 1990; Crimes, 1992; Buatois & Mángano, 1993b; Jenkins, 1995; MacNaughton, 2003).

AULICHNITES isp.
Figure 6.5

Material.—IBGS PJ-M-019: one specimen, Miner's Hollow.

Diagnosis.—Paired concave furrows separated by a medial ridge in hyporelief.

Description.—Bilobate, concave furrows separated by convex ridge in hyporelief, 7.0 mm long and 3.4 mm wide.

Occurrence.—Gray, laminated, siliciclastic or calcareous silty shale. Laminations are continuous with very little bioturbation occurring to disrupt them, indicating an *ii*2. The exposed bedding plane has extensive bioturbation with overprinting, indicating a (BPBI)3–4.

Associated ichnotaxa.—Dimorphichnus isp., *Lockeia siliquaria*, *Phycosiphon incertum*, *Protovirgularia* cf. *pennatus*, and *Treptichnus vagans*.

Discussion.—This specimen occurs as a short bilobate trail of paired concave ridges. The *Aulichnites* specimen terminates at a unilobate convex hyporelief mound. This mound is likely a short amygdaloidal (almond-shaped) resting trace assigned herein as *Lockeia siliquaria*. We consider the *Aulichnites* and *Lockeia* specimens to represent a compound trace (*sensu* Bertling & others, 2006) with the tracemaker having burrowed through the sediment (*Aulichnites*) and then stopped to rest (*L. siliquaria*).

Ichnogenus BERGAUERIA Prantl, 1945

Type ichnospecies.—Bergaueria perata Prantl, 1946.

Diagnosis.—Vertical, cylindrically to hemispherically shaped, lined or unlined protrusions (convex hyporelief) or depressions (concave epirelief) that may have central, circular depression, or raised bump at base; may be surrounded by tubercles or ledge-

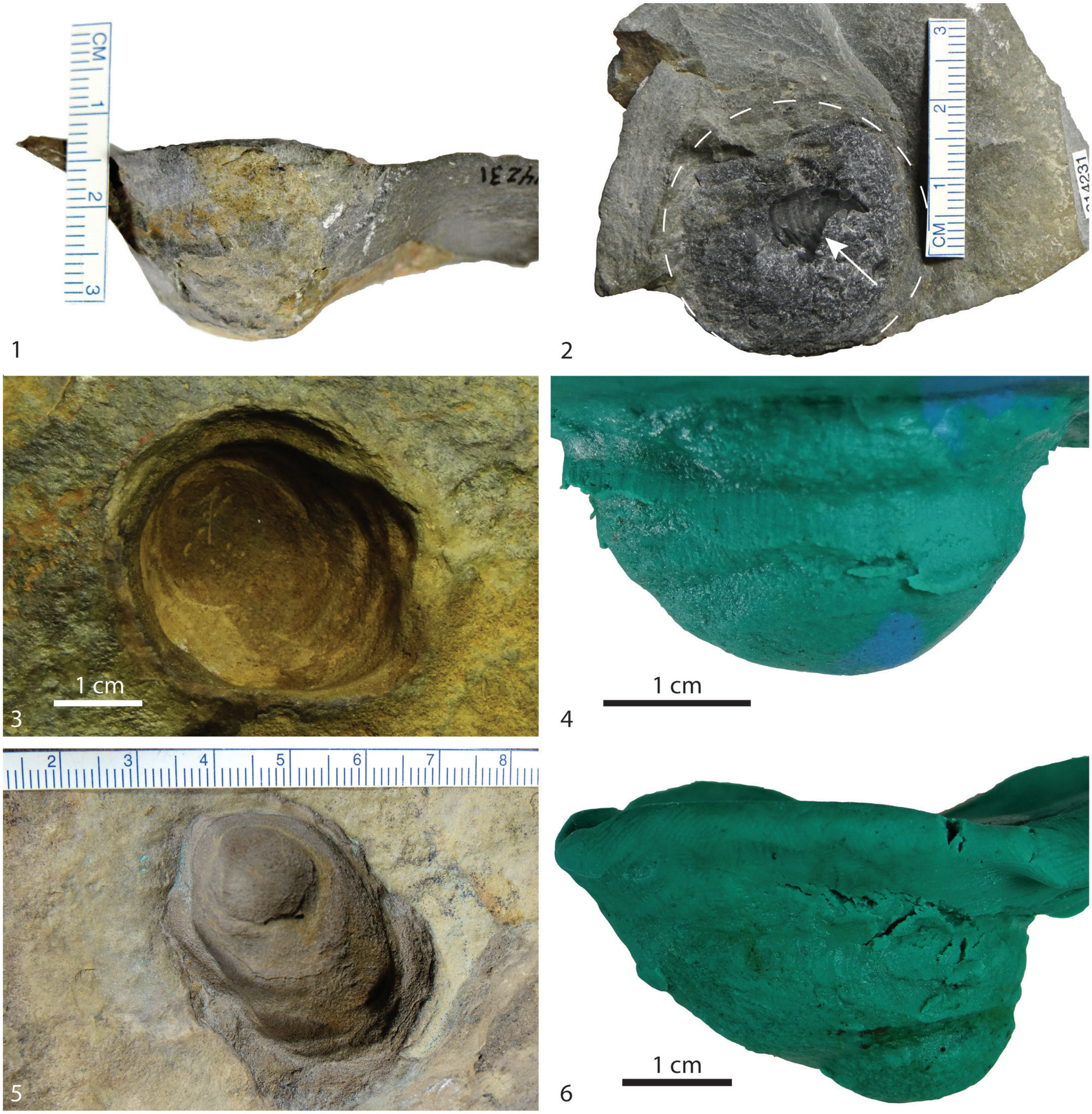

Figure 7. Plug-shaped ichnofossil specimens from the Spence Shale. *1–2, Bergaueria hemispherica* in convex hyporelief, (*1*) profile view and (*2*) upper plan view with coarse infill (circle) and a trilobite pygidium fragment (arrow), KUMIP 314231; *3–4, Bergaueria hemispherica* in concave epirelief (*3*) and cast (*4*), IBGS PJ-M-021, Miner's Hollow; *5–6, Bergaueria hemispherica* in concave epirelief (*5*) and cast (*6*) with asymmetric shape and transverse constrictions, IBGS PJ-M-029, Miner's Hollow; scales in cm.

like constrictions; vertical cross section typically U shaped with massive and unstructured fill (Prantl, 1945, 1946; Alpert, 1973; Fürsich, 1974a; Häntzschel, 1975; Pemberton, Frey, & Bromley, 1988; Fillion & Pickerill, 1990).

Discussion.—The lining type or lack of lining can determine the behavior, either cubichnia or domichnia; lined specimens represent domichnia, whereas unlined specimens represent cubichnia (Pemberton, Frey, & Bromley, 1988). *Bergaueria* is similar to several other plug-shaped ichnofossils: *Astropolichnus* Crimes & Anderson, 1985; *Conichnus* Männil, 1966; *Conostichus* Lesquereux, 1876; and *Dolopichnus* Alpert & Moore, 1975. *Bergaueria* is distinguished from them by the presence of wall linings, smooth outer walls, with or without radial ridges or a circular depression on the base, and a diameter twice its height (Pemberton, Frey, & Bromley, 1988).

Bergaueria is interpreted as a dwelling or resting trace of suspension-feeding organisms, usually actinians (e.g., Alpert, 1973;

Häntzschel, 1975; Pemberton, Frey, & Bromley, 1988; Fillion, & Pickerill, 1990). *Bergaueria* is commonly found in shallow-marine deposits (e.g., tidal or shoreface), but has been reported from deep-marine and brackish deposits as well (e.g., Crimes & others, 1977; Fillion & Pickerill, 1990; Uchman, 1998; Jackson, Hasiotis, & Flaig, 2016). *Bergaueria* ranges from the Ediacaran to recent (e.g., Crimes & others, 1977; Pemberton & Jones, 1988; Crimes, 1992; Uchman, 1998; Jackson, Hasiotis, & Flaig, 2016).

BERGAUERIA HEMISPHERICA Crimes & others, 1977

Figure 6.3–6.6, Figure 7.1–7.6

Material.—KUMIP 314229, KUMIP 314231, IBGS PJ-M-020, IBGS PJ-M-021, IBGS PJ-M-029: one specimen each, Miner's Hollow; IBGS PJ-M-025, two specimens, float from Cataract Canyon.

Diagnosis.—Vertical, hemispherical, plug-shaped burrow lacking shallow, central depression at apex of the burrow (Crimes & others, 1977).

Description.—Circular to elliptical plug-shaped depressions (concave epirelief) and mounds (convex hyporelief), diameter 15.8–40.8 mm, 4.3–17.2 mm thick, and diameter/thickness (D/T) ratio 1.5–3.5. Some epirelief specimens have transverse, ledgelike constrictions along burrow wall, hyporelief specimens have smooth walls; and lack both radial ridges and a central depression (hyporelief) or knob (epirelief) on base.

Occurrence.—Gray (weathered to brown), laminated calcareous or siliciclastic silty shale and sandy shale.

Associated ichnotaxa.—*Cruziana barbata*, *Planolites annularis*, *Rusophycus carbonarius, Sagittichnus lincki*, and *Teichichnus* cf. *nodosus*.

Discussion.—The majority of specimens assigned to this ichnospecies occur in concave epirelief on individual slab samples. *Bergaueria hemispherica* specimens have smooth rounded bases that lack small knobs (concave epirelief) or depressions (convex hyporelief) characteristic to other *Bergaueria* ichnospecies (Pemberton, Frey, & Bromley, 1988). Ledgelike constrictions (Fig. 7.3–7.6) occur transversely along burrow wall and are similar to constrictions associated with *Conostichus*. Crimes and others (1977) noted a similar concentric ornamentation and suggested it represents mud-rich laminations not related to tracemaker morphology. Specimens lack radial ridges that would justify assignment to *B. radiata, B. perata*, or even *Conostichus*. One *B. hemispherica* specimen (Fig. 7.5–7.6) does bear a strong resemblance to *Conostichus broadheadi* due to the presence of a well-developed conical shape and narrow apical disc but lacks the distinctive longitudinal fluting. The 1.5–3.5 D/T ratios fit with those suggested by Pemberton, Frey, and Bromley (1988) for *Bergaueria*.

BERGAUERIA aff. PERATA (Prantl, 1945)

Figure 8.1

Material.—IBGS PJ-M-026: one specimen (part and counterpart), Miner's Hollow.

Diagnosis.—Smooth walled, unlined or thinly lined, cylindrical mounds in convex hyporelief; faint ridges present radiating from a central depression may be present; diameter is generally equal to or greater than thickness (height) (Prantl, 1945; Pemberton, Frey, & Bromley, 1988).

Description.—Smooth, low relief depression (mound in convex hyporelief), 10.0 mm in diameter, 1.2 mm thick (height), and has a diameter-thickness ratio (D/T) of 8.33. No discernable radial ridges or central depressions are present.

Occurrence.—Gray (weathered to brown), calcareous silty shale.

Associated ichnotaxa.—None.

Discussion.—Only one specimen was collected and described from the Spence Shale. *Bergaueria perata* Prantl, 1945, was erected for unlined or thinly lined plug-shaped ichnofossils that may have diameters significantly greater than its thickness. Shallow and smooth *B.* aff. *perata* specimens may also be similar to *Bergaueria sucta* Seilacher, 1990—smooth, low relief, disclike basal impressions of actinians in laterally repeated sets that indicate lateral movement or creeping (Jensen, 1997). The smooth low relief and high D/T ratio is suggestive of an affinity to *B. sucta*, but the lack lateral repetition would preclude assignment as such.

Ichnogenus CONICHNUS Männil, 1966

Type ichnospecies.—*Conichnus conicus* Männil, 1966.

Diagnosis.—Short to long, vertical, cone-shaped to subcylindrical burrows with smooth, rounded base or randomly oriented papillalike protuberances on base; burrow infill may be unstructured or have V-shaped laminations (Männil, 1966; Pemberton, Frey, & Bromley, 1988).

Discussion.—*Conichnus* is similar to several plug-shaped ichnofossils. Pemberton, Frey, and Bromley (1988) conducted a detailed review of 15 plug-shaped ichnogenera and synonymized them together into five ichnogenera: *Astropolichnus*, *Bergaueria*, *Conichnus*, *Conostichus*, and *Dolopichnus*. *Conichnus* is a conical to subcylindrical burrow with smooth walls and rounded base (*C. conicus*), but the base may have protuberances (*C. papillatus*) (e.g., Männil, 1966; Frey & Howard, 1981; Pemberton, Frey, & Bromley, 1988). *Conostichus* is distinguished by transverse constrictions and longitudinal fluting of the burrow wall, a basal apical disc, and a burrow diameter approximately twice its height. *Bergaueria* is characterized by a cylindrical to hemispherical shape, thick to thin wall linings, a central depression and/or radial ridges on the base, and a diameter twice its height. *Dolopichnus* is distinguished by a larger size, a central cylindrical core typically with coarser infill, bulb-shaped terminations in some, and a diameter roughly one quarter its height. *Astropolichnus* is a short cylinder with a diameter over three times its height, radial ridges, and a central core (Pemberton, Frey, & Bromley, 1988).

Conichnus is commonly interpreted as dwelling or resting traces of actinians (e.g., sea anemones) (e.g., Pemberton, Frey, & Bromley, 1988; Mángano & others, 2002). Most *Conichnus* are reported from shallow-marine deposits and tidal deposits (e.g., Frey & Howard, 1981; Hiscott, James, & Pemberton, 1984; Mángano & others, 2002). *Conichnus* ranges from the early Cambrian to recent (e.g., Curran & Frey, 1977; Hiscott, James, & Pemberton, 1984; Jackson, Hasiotis, & Flaig, 2016).

CONICHNUS CONICUS Männil, 1966

Figure 8.2–8.4

Material.—IBGS PJ-M-003: 12 specimens, Spence Shale float, Cataract Canyon.

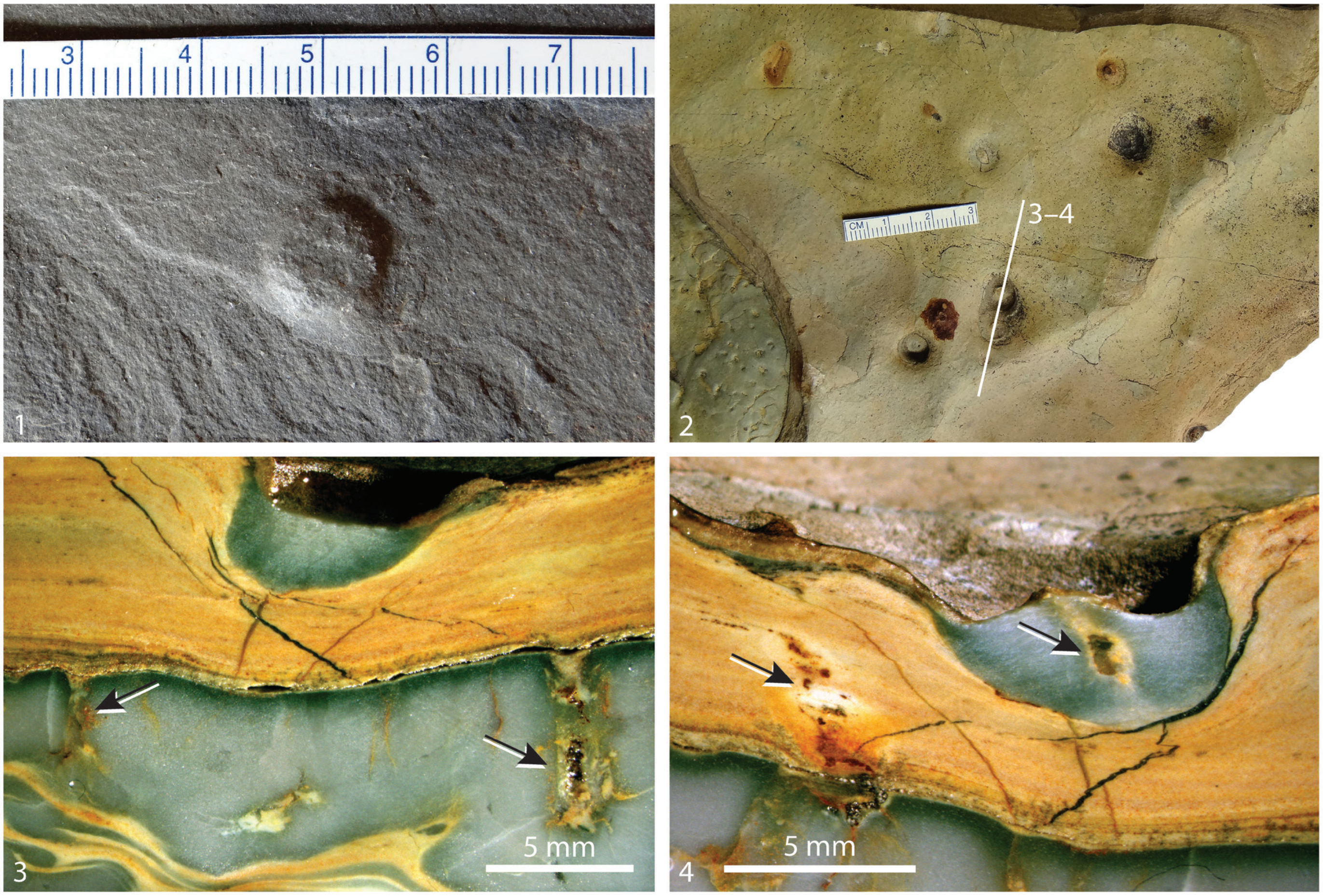

Figure 8. Plug-shaped ichnofossil specimens from the Spence Shale (continued). *1, Bergaueria* aff. *perata* in convex hyporelief, IBGS PJ-M-026, Miner's Hollow; *2,* plan view of *Conichnus conicus* in concave epirelief, IBGS PJ-M-003, Cataract Canyon; *3–4,* Cross-sections of *C. conicus* and *Skolithos*-like vertical tubes (arrows); scales in cm.

Diagnosis.—Short cone- to plug-shaped depression with smooth, rounded bottom, some penetrated by vertical tube.

Description.—Short, plug-shaped depression with smooth base filled with massive, gray calcareous mudstone; 4–10 mm in diameter and 1–4 mm deep. Central-plug diameter 2.6–2.9 mm.

Occurrence.—Tan to brown, very fine-grained sandstone with ripple marks above a layer of gray peloidal carbonate wackestone and packstone to mudstone with thin, tan to brown silty to sandy laminations and soft-sediment deformation; however, no *Conichnus* specimens are present in the lower layer.

Associated ichnotaxa.—Arenicolites carbonarius.

Discussion.—Specimens were assigned to *C. conicus* for their small, pluglike morphology with smooth, rounded bottoms and lack of basal protuberances (Fig. 8.2–8.4). *Conichnus conicus* specimens occur on the same sample with *Arenicolites carbonarius* but are restricted to a higher layer. Most *C. conicus* specimens occur close to another specimen and falsely appear as openings to U-shaped burrows (e.g., *Arenicolites* or *Diplocraterion*; Fig. 8.2). A cut section of one specimen revealed a massive, carbonate mudstone infill penetrated by a central vertical tube (e.g., possible *Skolithos;* Fig. 8.3–8.4) suggesting that some *C. conicus* may be composite traces (i.e., two or more unrelated ichnotaxa occurring within each other; *sensu* Bertling & others, 2006).

Ichnogenus CRUZIANA d'Orbigny, 1842

Type ichnospecies.—Cruziana rugosa d'Orbigny, 1842, by subsequent designation in Miller (1889).

Diagnosis.—Elongate, bilobate, ribbonlike furrows with medial ridges (concave epirelief) or grooves (convex hyporelief): furrows commonly covered by herringbonelike, transverse, or longitudinal striations (Crimes, 1970a, 1970b; Seilacher, 1970; Häntzschel, 1975).

Discussion.—Seilacher (1970) united both bilobate long furrows and short excavations (=*Rusophycus*) under *Cruziana* due to similar striation patterns (interpreted as scratch marks) attributed to the same organism, trilobites; however, this proposal was rejected by numerous authors (e.g., Crimes, 1970a, 1970b, 1975; Fillion & Pickerill 1990; Pickerill, 1995; Jensen, 1997) due to significant morphologic differences between the two ichnogenera. Bromley and Asgaard (1979) included ribbonlike *Isopodichnus* Bornemann, 1889, under *Cruziana* because the two ichnogenera differ only in accessory features (e.g., size), which is suggested for use only in ichnospecific designation (*sensu* Fürsich 1974b). The *Cruziana*-

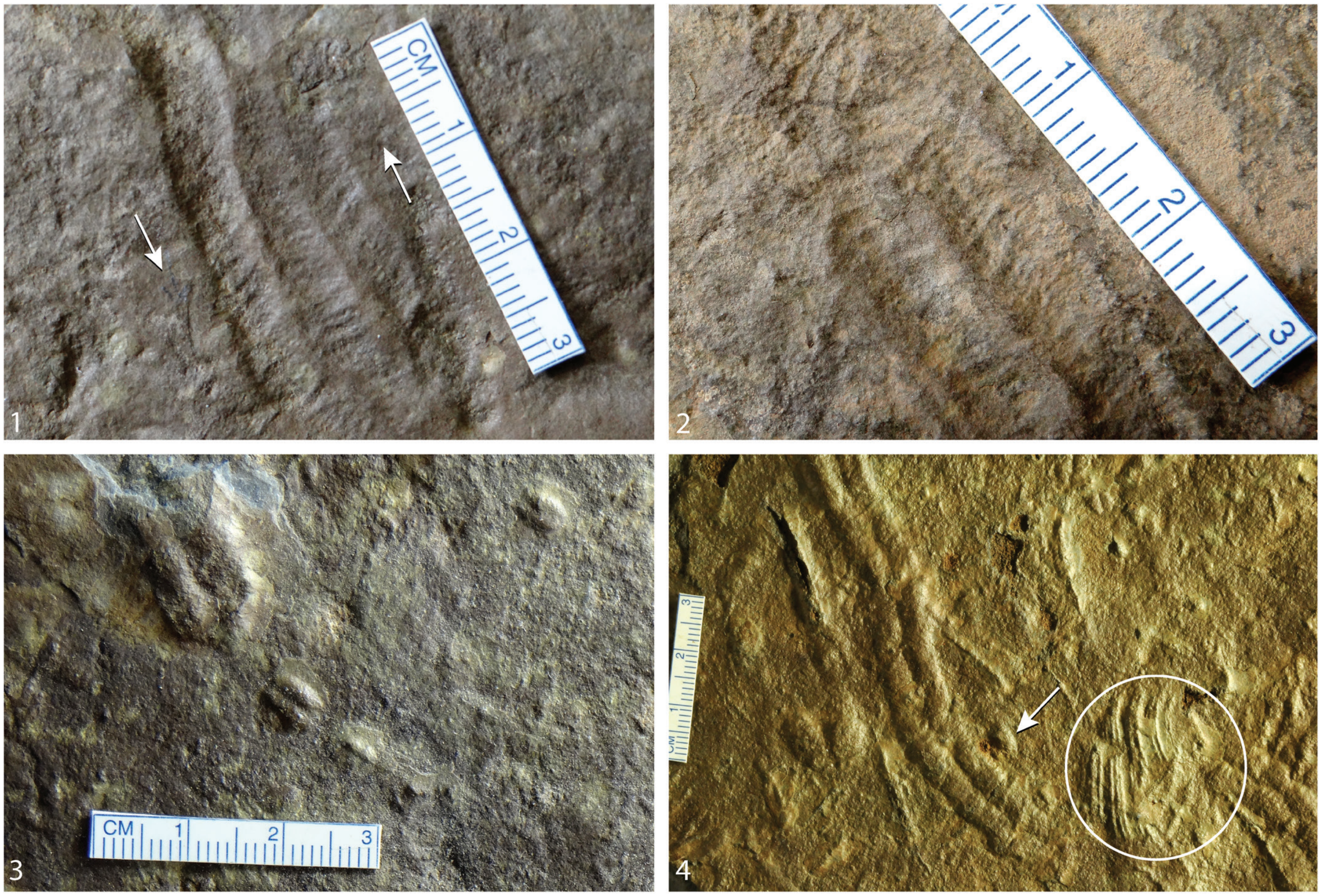

Figure 9. *Cruziana* specimens from Spence Shale. *1–2, Cruziana barbata* in concave epirelief, KUMIP 314229, Miner's Hollow; *1,* two specimens of *C. barbata* overlapped in opposite directions (arrows); *3,* Rusophycid *C. problematica* with small *Rusophycus carbonarius* in convex hyporelief, IBGS PJ-M-007, Miner's Hollow; *4, Cruziana problematica* with *Lockeia siliquaria* (arrow) and *Monomorphichnus* cf. *multilineatus* (circle) in convex hyporelief, KUMIP 314228, Miner's Hollow; scale in cm.

Isopodichnus synonymy, though rejected by Hakes (1985), Pollard (1985), and Seilacher (1985), is still followed by most authors. Crimes (1970b) noted that *Cruziana* can grade into other ichnogenera (e.g., *Diplichnites*, *Diplopodichnus* Brady, 1947, and *Rusophycus*) and that the V-shaped striations open in the direction of movement as with *Diplichnites*.

Cruziana is commonly interpreted as a surficial to shallow deposit-feeding, dwelling, grazing, locomotion, or predation trace (e.g., Crimes, 1970a, 1970b; Seilacher, 1970; Zonneveld & others, 2002; Gingras & others, 2007). Most *Cruziana* have been interpreted as the product of trilobites but other tracemakers have been suggested: nontrilobite arthropods (e.g., horseshoe crabs, branchiopods, aglaspidids), or even some vertebrates (e.g., Seilacher, 1970; Fisher, 1978; Shone, 1978, 1979; Bromley & Asgaard, 1979, Pollard, 1985). *Cruziana* has been reported in deep- and shallow-marine and continental deposits (e.g., fluvial, lacustrine, and brackish) (e.g., Crimes, 1970a, 1970b; Bromley & Asgaard, 1979; Seilacher, 1985; Fillion & Pickerill, 1990; Pickerill, 1995). *Cruziana* ranges from the early Cambrian to the Cretaceous (e.g., Crimes, 1987, 1992; Mángano & others, 2002; Hasiotis, 2012).

CRUZIANA BARBATA Seilacher, 1970
Figure 9.1–9.2

Material.—KUMIP 314229; eight specimens, Spence Shale, Miner's Hollow, Wellsville Mountains, Utah, USA.

Diagnosis.—Small to medium, straight to curved, bilobate ribbonlike furrow with medial ridge and curved V-shaped striations angled ~160° (Seilacher, 1970; Legg, 1985).

Description.—Bilobate, concave epirelief, ribbon trails; 27.0–94.4 mm long and 9.8–11.9 mm wide. Curved striations are visible in several specimens and have a V-shaped angle 142–163°.

Occurrence.—Greenish gray (weathered to brown) calcareous, micaceous silty shale.

Associated ichnotaxa.—*Bergaueria hemispherica*, *Planolites annularis*, and *Rusophycus carbonarius*.

Discussion.—Specimens assigned to *C. barbata* partly crossover other *C. barbata* specimens on the same sample along their lengths causing some lobes to be lost and give the appearance of a trilobate form, but the specimens can be differentiated, as the V-shaped striations are oriented opposite to the overlapping furrow (Fig. 9.1). Several trilobite pygidia are present on the sample;

however, their widths are greater than the widths of the *C. barbata* specimens indicating that those trilobites were not the producers (*sensu* Fortey & Seilacher, 1997). Spence Shale specimens of *C. barbata* are significantly smaller (~1 cm) than most previously recorded specimens (~3–9 cm; Legg, 1985; Orłowski, 1992). The decreased size is likely the result of lower available oxygen near the sediment-water interface (e.g., Garson & others, 2012).

CRUZIANA PROBLEMATICA (Schindewolf, 1921)
Figure 9.3–9.4, Figure 10.1–10.5, 16.5

Material.—KUMIP 204523 A (part) and B (counterpart): 31 specimens, Miner's Hollow; KUMIP 314228: two specimens, Miner's Hollow; IBGS PJ-M-007: five specimens, Miner's Hollow; IBGS PJ-M-016: two specimens, Miner's Hollow; IBGS PJ-M-017: one specimen, Miner's Hollow float.

Diagnosis.—Small to large, straight to curved, bilobate ribbonlike furrow with medial ridge and transverse striations (Bromley & Asgaard, 1979; Fillion & Pickerill, 1990; Jensen, 1997).

Description.—Concave or convex, bilobate, ribbonlike burrows with a medial ridge (epirelief) or furrow (hyporelief) and transverse striations; Burrows 11.4–95.1 mm long and 8.0–15.4 mm wide. Striation V-shaped angle ~180° but some range from 145–160°. Burrow paths are typically slightly curved to straight, but several burrows are highly curved and overlap or crosscut each other.

Occurrence.—Greenish gray to gray laminated, calcareous silty to sandy shale; sometimes weathered to brown or brownish yellow.

Associated ichnotaxa.—*Lockeia siliquaria*, *Monomorphichnus lineatus*, *M.* cf. *multilineatus*, *Planolites beverleyensis*, *P. montanus*, *Rusophycus carbonarius*, *Rusophycus* cf. *cerecedensis*, *Treptichnus bifurcus*, and *T. pedum*.

Discussion.—Bromley and Asgaard (1979) placed ribbonlike *Isopodichnus* Bornemann, 1889, under *Cruziana problematica* because size was not enough to warrant a separate ichnogenus. Some authors, however, retain *Isopodichnus* for use as a salinity indicator in fresh- and brackish-water settings (e.g., Hakes 1985; Pollard 1985; Seilacher 1985, 2007). Bromley and Asgaard (1979) also noted that *Isopodichnus* was reported from marine deposits by Alpert (1976a) and Trewin (1976), thus, making retention of *Isopodichnus* as a salinity indicator invalid. Jensen (1997) attempted to distance the ichnospecies from the common interpretation as a salinity indicator by placing it under a resurrected name, *Cruziana tenella* (Linnarsson, 1871) (for discussion, see Jensen, 1997). Reassignment of *C. problematica* to *C. tenella* has been accepted by some authors (e.g., MacNaughton & Narbonne 1999; Jensen, Droser, & Heim, 2002; Zonneveld & others, 2002; Sadlok, 2010), but rejected by others for nomenclatural stability (e.g., Mángano & others, 2002; Schatz & others, 2011). We reject the renaming of *C. problematica* to *C. tenella* in favor of nomenclatural stability, even though the use of ichnotaxa as environmental stress indicators is not valid to establish, rename, or retain ichnotaxa.

Cruziana problematica specimens show some meandering, suggesting they were produced via grazing, and are noticeably larger than *R. carbonarius* (Fig. 9.3–9.4, Fig. 10.1–10.5). The average width of *C. problematica* is 10 mm, whereas *R. carbonarius* averages ~5 mm wide. The width difference suggests that *C. problematica* tracemakers were not the same as the tracemakers of *R. carbonarius* (*sensu* Fortey & Seilacher, 1997), which could be juveniles of the adult form (*Cruziana* producers). *Cruziana problematica* and *C. problematica*-sized *Rusophycus* specimens do not occur together on KUMIP 204523, although one association does occur on KUMIP 314228 (see Fig. 9.4). The specimens of *Cruziana problematica* on KUMIP 204523 co-occur with *Rusophycus carbonarius*, *Planolites montanus*, and *Treptichnus bifurcus* and were likely not constructed at the same time and may have been affected by sudden changes in available oxygen or nutrients. *Rusophycus carbonarius* specimens crosscut both *C. problematica* and other *R. carbonarius* (Fig. 10.1), whereas *Cruziana problematica* specimens only crosscut each other (Fig. 10.3). *Planolites montanus* crosscuts both *C. problematica* and *R. carbonarius* (Fig. 10.4). The crosscutting relationships suggest that *C. problematica* were constructed and abandoned first, followed by *R. carbonarius*, and then finally, *P. montanus*. The *T. bifurcus* specimen was constructed sometime after the *C. problematica* as the latter was cross cut by the former (Fig. 10.5), but its placement in the aforementioned crosscutting timeline is unknown because the *T. bifurcus* specimen has no interaction with any other specimen.

Ichnogenus DIMORPHICHNUS Seilacher, 1955a

Type ichnospecies.—*Dimorphichnus obliquus* Seilacher, 1955a.

Diagnosis.—Asymmetrical trackways with two types of impressions, typically of equal width: (1) long, thin, straight to sigmoidal striations; and (2) short, punctate to elliptical impressions at end of long striations; both types occur oblique to direction of movement (Seilacher, 1955a; Fillion & Pickerill, 1990).

Discussion.—Seilacher (1955a) named *Dimorphichnus* for oblique sets of elongate striations with punctate impressions produced by trilobites. The movement of the *Dimorphichnus* tracemaker was oblique to fully sideways with the short, punctate impressions formed by one set of legs acting as a holdfast to keep the tracemaker in place, while the sigmoidal striations were formed by the other set of legs sweeping through the medium returning to their starting position (Seilacher, 1955a, 2007). Crimes (1970a, 1970b) suggested the oblique to sideways orientation of *Dimorphichnus* was due to increased current energy forcing the tracemaker to reorient itself to remain stable while moving or grazing. After *Monomorphichnus* was described by Crimes (1970b), Seilacher (1985) argued that *Monomorphichnus* was a junior synonym of *Dimorphichnus* and the *Monomorphichnus* holotype contained punctate impressions consistent with *Dimorphichnus.* Most authors have rejected this suggestion and maintain both as separate ichnogenera (e.g., Walter, Elphinstone, & Heys, 1989; Fillion & Pickerill, 1990; Orłowski, 1992; Jensen, 1997; Hofmann & others, 2012). More recently, Seilacher (2007) proposed that *Dimorphichnus* and *Monomorphichnus* should be considered as a behavioral and preservational variant of *Diplichnites,* respectively. Jensen (1997) and Hofmann and others (2012) suggested that *Dimorphichnus* and *Monomorphichnus* should remain separate due to each representing a separate behavior.

Dimorphichnus is interpreted as a locomotive, deposit feeding, or grazing trace (Seilacher, 1955a, 1985; Crimes, 1970b; Fillion & Pickerill, 1990). Proposed producers of *Dimorphichnus* include marine and continental arthropods (e.g., trilobites, decapods, centipedes, millipedes) (Fillion & Pickerill, 1990). *Dimorphichnus* has

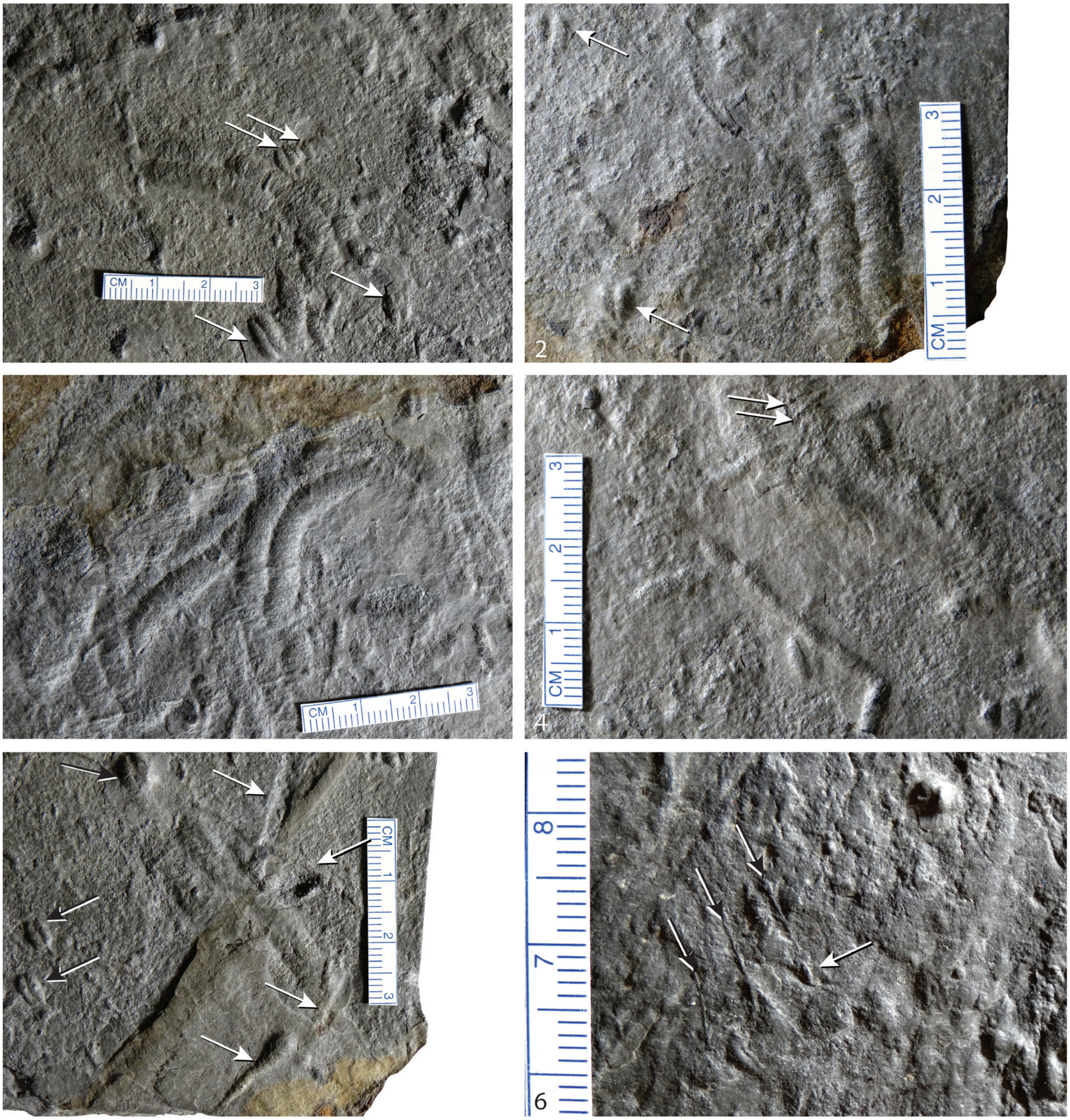

Figure 10. *Cruziana problematica* and *Dimorphichnus* specimens from the Spence Shale. *1–5, Cruziana problematica,* KUMIP 204523A and B, Miner's Hollow; *1–2, Cruziana problematica* with several *Rusophycus carbonarius* (arrows), convex hyporelief; *3, Cruziana problematica* with transverse striations, crosscut by *Planolites montanus* and *R. carbonarius*; *4,* overlapping *C. problematic*a with grazinglike scribble paths; *5,* convex hyporelief of *C. problematica* with several *R. carbonarius* (black arrows) and *Treptichnus bifurcus* (white arrows) in both convex and concave hyporelief; *6, Dimorphichnus* isp., rakes (black arrows) and pusher (white arrow), in convex hyporelief, IBGS PJ-M-019, Miner's Hollow; scale in cm.

been reported from shallow-marine, deep-marine, and continental deposits (e.g., alluvial, lacustrine, and eolian) (e.g., Seilacher, 1955a; Fillion & Pickerill, 1990). *Dimorphichnus* ranges from the Cambrian to recent (e.g., Crimes, 1970b).

DIMORPHICHNUS isp.
Figure 10.6

Material.—IBGS PJ-M-019: one specimen, Miner's Hollow; IBGS PJ-M-024: one specimen, Miner's Hollow.

Diagnosis.—Small, thin, laterally repeated sets of elongate, sigmoidal striations (convex hyporelief) with separate blunt, ovoid to circular mounds occurring near end of elongate striations.

Description.—Specimens consist of thin convex ridges and separate ovoid to punctate mounds near the ridge ends. Trackways 19.6 mm long, 7.1 mm wide. Sigmoidal striations 4.0–6.2 mm long, 0.2–0.4 mm wide. The blunt mounds 0.8–2.0 mm long, 0.4–0.6 mm wide.

Occurrence.—Gray, laminated, siliciclastic or calcareous silty shale. Laminations are continuous with very little bioturbation occurring to disrupt them, indicating an *ii*2. The exposed bedding plane has extensive bioturbation with some overprinting, indicating a BPBI 3–4.

Associated ichnotaxa.—Aulichnites isp., *Lockeia siliquaria*, *Phycosiphon incertum*, *Planolites annularis*, *P. montanus*, *Protovirgularia* cf. *pennatus*, *Rusophycus carbonarius*, *Sagittichnus lincki*, and *Treptichnus vagans*.

Discussion.—The specimens of *Dimorphichnus* are very diminutive in size with sigmoidal striation. Pusher mound widths are < 1.0 mm (Fig. 10.6). The *Dimorphichnus* isp. on IBGS PJ-M-019 does not crosscut any recognizable traces. The extensive bioturbation of the base of IBGS PJ-M-019 makes identification of ichnotaxa difficult and suggests a more oxygenated environment than the shallower laminations yielding *Phycosiphon incertum*.

Ichnogenus DIPLICHNITES Dawson, 1873

Type ichnospecies.—Diplichnites aenigma Dawson, 1873.

Diagnosis.—Simple trackways of punctate to elongate track impressions in parallel track rows; track impressions closely and regularly spaced, and normal or oblique to trackway axis (Häntzschel, 1975; Briggs, Rolfe, & Brannan, 1979; Fillion & Pickerill, 1990).

Discussion.—Originally interpreted as trails of large myriapods or annelids by Dawson (1873), recent authors have used *Diplichnites* to describe smaller-scaled trackways thought to be produced by trilobites (Fillion & Pickerill, 1990). Briggs, Rolfe, and Brannan (1979) suggested that *Diplichnites* be restricted to continental arthropod trackways because they noted that workers were departing from the original diagnosis of *Diplichnites* as a continental trackway and suggested using some junior synonyms of *Diplichnites* from Osgood (1970) to place the trilobite-produced trackways.

Nine ichnospecies are currently recognized within the literature (e.g., Buatois & others, 1998; Smith & others, 2003): *Diplichnites aenigma* Dawson, 1873; *D. binatus* Webby, 1983; *D. cuithensis* Briggs, Rolfe, & Brannen, 1979; *D. govenderi* Savage, 1971; *D. gouldi* (Gevers in Gevers & others, 1971); *D. incertipes* (Matthew, 1910); *D. minimus* Walter & Gaitzsch, 1988; *D. minor* (Matthew, 1910), and *D. triassicus* (Linck, 1943). Track orientation and shape, number of tracks per track series, and number of track series per track row are generally used to differentiate ichnospecies (e.g., Savage, 1971; Trewin & McNamara, 1995). Trewin and McNamara (1995) divided *D. gouldi* into three morphotype end-members (types A, B, and C) based on trackway width and the number of tracks per track series.

Diplichnites is generally interpreted as a locomotion trace of trilobites but other arthropods, including myriapods, and some annelids have been suggested (e.g., Dawson, 1873; Osgood, 1970; Briggs, Rolfe, & Brannen, 1979). *Diplichnites* is found in shallow- and deep-marine, and continental deposits (e.g., Crimes & others, 1977; Fillion & Pickerill, 1990; Crimes & Fedonkin, 1994). Deep-marine *Diplichnites* is mostly reported from the lower and middle Cambrian and only rarely after the Cambrian (Pickerill, 1981; Crimes & Fedonkin, 1994). *Diplichnites* ranges from the Cambrian to recent (e.g., Briggs, Rolfe, & Brannen, 1979; Crimes, 1987, 1992; Fillion & Pickerill, 1990; Hasiotis, 2012).

DIPLICHNITES GOULDI (Gevers in Gevers & others, 1971)
TYPE A Trewin & McNamara, 1995
Figure 11.1–11.3

Material.—KUMIP 204522: one specimen, Antimony Canyon; IBGS PJ-M-011: one specimen, Spence Tongue of the Lead Bell Shale, Oneida Narrows, Bear River Range, Idaho, USA; IBGS PJ-M-014 (part and counterpart) and IBGS PJ-M-015: one specimen, Miner's Hollow.

Diagnosis.—Paired rows of punctate to ellipsoidal or elongated straight impressions oriented perpendicular or oblique to trackway axis; track series consist of 5–9 tracks in opposition. Within track rows, multiple sets of track impressions may overlap previous sets (Trewin & McNamara, 1995; Buatois & others, 1998; Smith & other, 2003).

Description.—Trackways 32.1–49.0 mm long; outer trackway 10–15 mm wide, inner trackway 8.4–9.5 mm wide. Punctate to ellipsoidal tracks 2–4 mm wide, spaced 2.5–4.0 mm apart. Specimens with overlapping track series, overlap occurs by 2–3 tracks, overlap distance 1.5–2.9 mm.

Occurrence.—Two lithologies: (1) gray to dark gray (weathered to tan), very fine to fine carbonate sand to silty shale; and (2) pale greenish gray, mica-rich, silty to sandy shale. Thin to thick laminations are present, but are unbroken or have rare traces in slab samples (*ii*1–2). Bedding plane is only disrupted by *D. gouldi* (BPBI 2).

Associated ichnotaxa.—Planolites montanus and *Treptichnus vagans*.

Discussion.—Diplichnites gouldi was originally described by Gevers in Gevers and others (1971) for paired, parallel rows of punctate to ellipsoidal track impressions under the name *Arthropodichnus gouldi*. Gevers (1973) changed the name from *Arthropodichnus* to *Beaconichnus* since *Arthropodichnus* was already proposed for another ichnogenus. Bradshaw (1981) transferred *Beaconichnus gouldi* into *Diplichnites* as *D. gouldi*. Trewin & McNamara (1995) recognized three end-members (types A, B, and C) with material assigned to *D. gouldi* based on trackway widths and tracks per series. Buatois and others (1998), however, considered that *D. gouldi* type A did not belong in *Diplichnites* and viewed

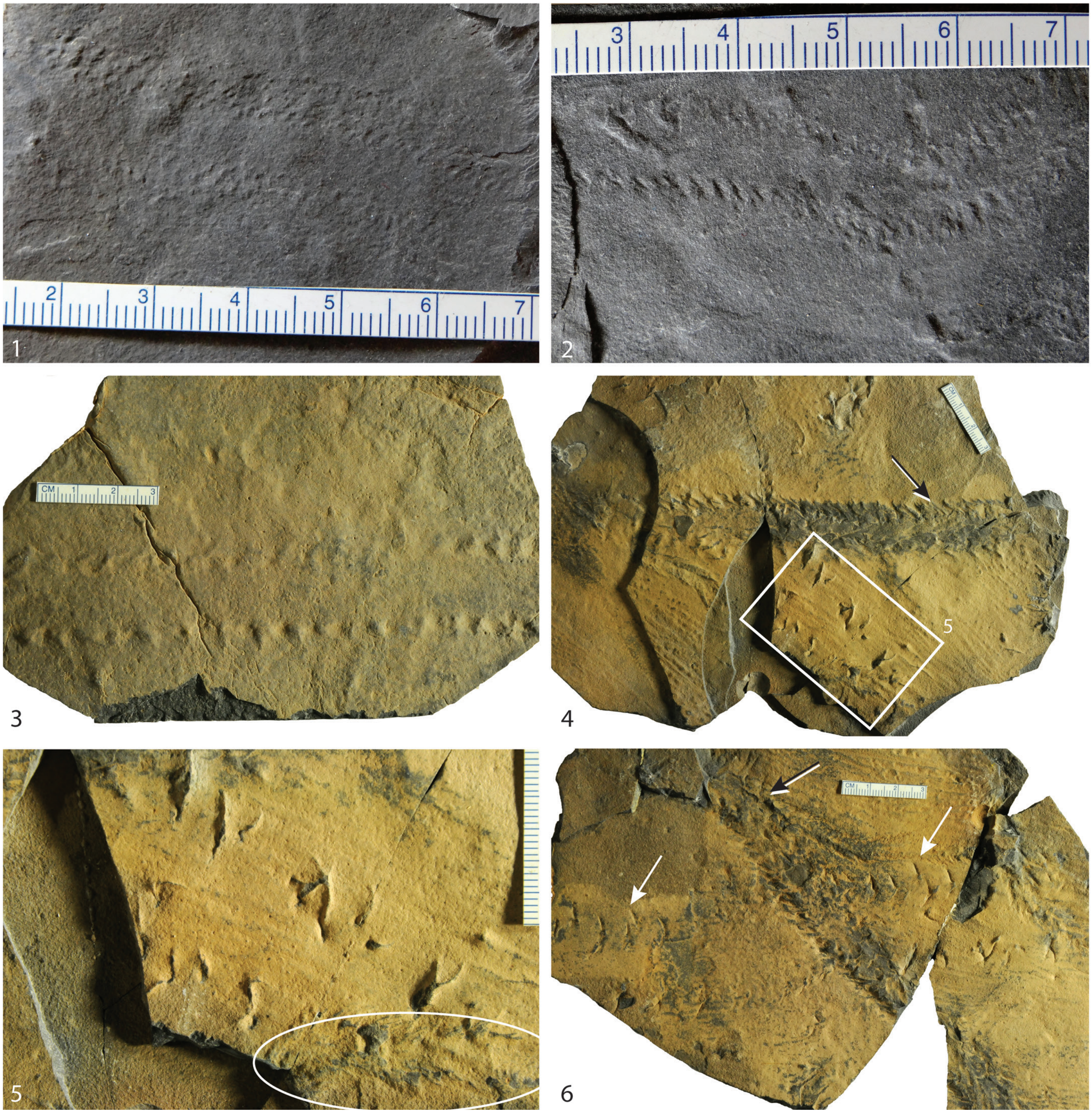

Figure 11. Trackway ichnofossil specimens from the Spence Shale. *1, Diplichnites gouldi* in concave epirelief, IBGS PJ-M-015, Miner's Hollow; *2, Diplichnites gouldi* in convex hyporelief, IBGS PJ-M-014, Miner's Hollow; *3, Diplichnites gouldi* in concave epirelief, KUMIP 204522, Antimony Canyon; *4, Diplichnites* cf. *binatus* with paired impressions (arrows) in convex hyporelief, KUMIP 204521 A and B, Miner's Hollow; *5,* close up of *D.* cf. *govenderi* track impressions with *Protovirgularia* cf. *pennatus* in convex hyporelief, KUMIP 204521 A and B; *6, Diplichnites* cf. *govenderi* (white arrows) crosscut by *D.* cf. *binatus* (black arrow) in concave epirelief, KUMIP 204521 A and B. *1–4, 6,s* Scale in cm; *5,* scale in mm.

it as a form of *Umfolozia* Savage, 1971, while retaining *D. gouldi* types B and C. Smith and others (2003) suggest retaining all three end-members of *D. gouldi*, with which we agree.

Häntzschel (1975) placed *Acripes* Matthew, 1910, within *Diplichnites* due to similar morphology. Miller (1996) reviewed type material of *Acripes* and confirmed its placement in *Diplichnites* but made no reference or recommendation on whether all three *Acripes* ichnospecies should remain valid under *Diplichnites*. Some authors have included *A. incertipes*, *A. leavitti*, and *A. minor* as valid ichnospecies within *Diplichnites* (e.g., Keighley & Pickerill, 1998; Smith & others, 2003). Keighley and Pickerill (1998) recommended that *A. incertipes* (Matthew, 1910, pl. III, fig. 1–2) should not be included in *Diplichnites* due to significantly different track impression shapes of each track row similar to *Dimorphichnus*, *Petalichnus*, and *Ptilichnus*.

The ichnospecies of Matthew (1910), *Acripes incertipes* (*sensu stricto;* plate III, fig. 1), *A. leavitti*, and *A. minor,* are morphologically almost identical to *Diplichnites gouldi.* Each ichnospecies are paired, parallel trackways with punctate, opposite track impressions in series that may overlap and are differentiated primarily by size. We suggest that they should be grouped under a single ichnospecies, *Diplichnites gouldi*, as it: (1) has the most similar morphology to *Acripes*; (2) is the most commonly used in the literature; and (3) would help stabilize the nomenclature regarding *Diplichnites*.

Specimens assigned to *Diplichnites gouldi* type A consist of small, punctate to ellipsoidal track impressions. Most *D. gouldi* type A specimens occur with specimens of *Planolites montanus*, but one specimen is present alongside *Monomorphichnus bilinearis* as well as *P. montanus* (IBGS PJ-M-011). Most trackways are straight to gently curved, with the track series being most apparent in the curved sections. Some specimens have punctate tracks (Fig. 11.1); however, tracks are typically ellipsoidal and oriented ~45–90° from the trace axis (Fig. 11.2–11.3). Several of the ellipsoidal-track specimens show track impressions of both track rows that are oriented parallel in a single direction suggesting bottom currents influenced the movement of the tracemakers (Trewin & McNamara, 1995; Smith & others, 2003; Seilacher, 2007).

DIPLICHNITES cf. BINATUS Webby, 1983
Figure 11.4, 11.6

Material.—KUMIP 204521: one specimen (part and counterpart), Miner's Hollow.

Diagnosis.—Paired rows of thin, straight, elongated striations grouped in pairs or triplets oriented obliquely to the trackway axis; track impression morphology may be asymmetric (Webby, 1983; Buatois & others, 1998).

Description.—The left track row (relative to inferred tracemaker movement) is poorly preserved compared to the right track row. Trackway 153 mm long; outer trackway 23.8 mm wide, and inner trackway 18.4 mm wide. Thin, elongate striations 7.6–12.2 mm long, 0.6–1.6 mm wide, and spaced 1.2–5.9 mm apart. Track impressions oriented 45° from the central axis with a ~90° V-shaped angle.

Occurrence.—Dark gray (weathered to tan) to pale greenish gray, very fine- to fine-grained carbonate silty shale.

Associated ichnotaxa.—Diplichnites cf. *govenderi* and *Protovirgularia* cf. *pennatus*.

Discussion.—The specimen assigned to *Diplichnites* cf. *binatus* occurs with other surficial arthropod trackways. The specimen is crosscut by a paired-row trackway with highly variable track impression morphologies, which ranges between punctate to apostrophelike to bifid to trifid morphologies of Keighley and Pickerill (1998) that is herein assigned to *D.* cf. *govenderi*. The *D.* cf. *binatus* specimen is poorly preserved and only one track row is clearly visible (Fig. 11.4), but shows a clear V-shape angle to indicate the tracemaker moved from right to left (relative to the image). Some of the elongate tracks occur in close pairs, which justify placement under *D. binatus;* however, some impressions are singular and others are in groups of three.

Diplichnites cf. *binatus* bears a resemblance to *Pterichnus* Hitchcock, 1865, as both ichnospecies have track impressions that are elongate and thin; however, *D.* cf. *binatus* commonly has asymmetrical impressions (Buatois & other, 1998), whereas the impressions of *P. tardigradus* are usually always symmetrical (Hitchcock, 1858, 1865; Gaillard & others, 2005). Minter, Mángano, and Caron (2012) suggested that *Pterichnus* and other similar V-forming trackways described by Hitchcock (1858, 1865) were actually undertracks and should be considered junior synonyms of *Lithographus* Hitchcock, 1858.

DIPLICHNITES cf. GOVENDERI Savage, 1971
Figure 11.4–11.6

Material.—KUMIP 204521 A and B: two specimens, Miner's Hollow.

Diagnosis.—Paired rows of lunate to tapered to bifid track impressions oriented perpendicular to oblique to trackway axis; tracks may be opposite or staggered.

Description.—Trackways 47–190 mm long; outer trackways 30.6–45.3 mm wide, and inner trackway 9.5–15.8 mm wide. Lunate to tapered, bifid track impressions 3.6–12.2 mm long, 0.8–1.6 mm wide, and spaced 2.6–13.0 mm apart. Specimens lack overlapping series and form single-series track rows.

Occurrence.—Dark gray (weathered to tan) to pale greenish gray, very fine- to fine-grained calcareous silty shale. No visible bedding or laminations are present. Low to moderate bedding plane disruption by traces indicating BPBI 2.

Associated ichnotaxa.—Diplichnites cf. *binatus* and *Protovirgularia* cf. *pennatus*.

Discussion.—The specimen assigned to this ichnospecies has highly variable track impressions that make classification difficult; however, the closest ichnotaxa to which the Spence Shale material can be assigned are *Diplichnites govenderi*, *Incisifex* Dahmer, 1937, *Lithographus* or *Permichnium* Guthorl, 1934. The specimens differ from *Incisifex* because the track impressions are typically straight and elongate, whereas *D.* cf. *govenderi* have a mix of bifid, lunate, and elongate impressions (Häntzschel, 1975). The specimen differs from *Lithographus* because none of the track impressions have the trifid to J-shaped track impressions, whereas the holotype of *D. govenderi* (Savage, 1971, fig. 7A) shows lunate-shaped track impressions similar to those seen in the Spence Shale specimens. *Permichnium* differs from *D.* cf. *govenderi* as the track impressions are typically bifid and open either to the outside or inside of the trackway (Kramer & others, 1995), whereas *D.* cf. *govenderi* has multiple impression shapes.

A "quadrifid" track impression is present and is likely two tracks overprinting each other, composed of two bifid grooves that intersect near the outer margin of the trackway (Fig. 11.5). The quadrifid impression was likely produced via a two-part limb motion. First, an insertion of a bifid limb into the medium, which moved obliquely inward and to the posterior of the trackway, as indicated by a raised sediment mound near the end of the impression. Later, a second insertion that shifted obliquely inward

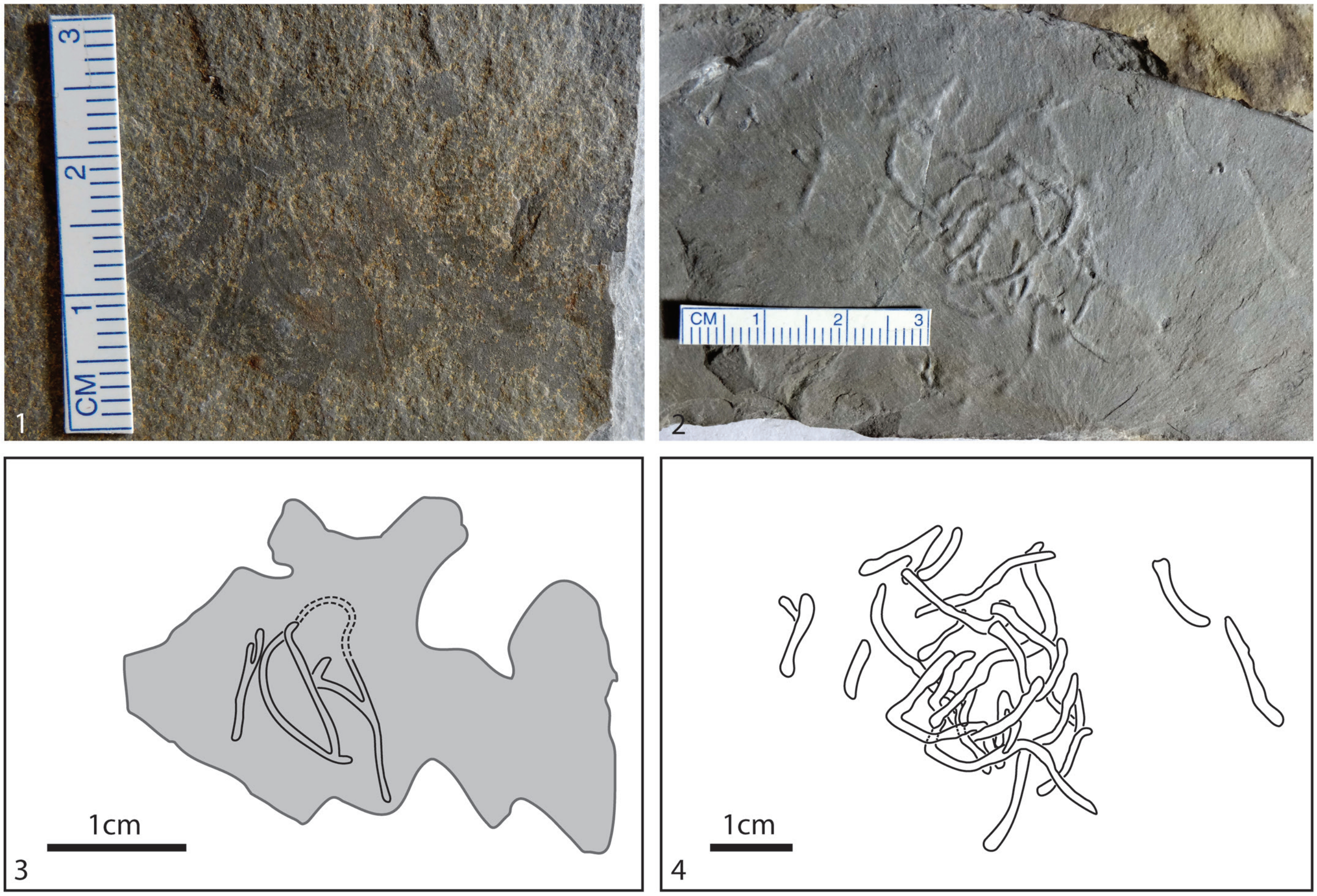

Figure 12. *Gordia marnia* specimens from the Spence Shale. *1, Gordia marnia* in *Banffia* sp. BST carbon film in convex and concave hyporelief, IBGS LG-M-006; *2, Gordia marnia* in convex hyporelief and endorelief, IBGS PJ-M-004, Miner's Hollow; *3,* line drawing of *G. marnia* on IBGS LG-M-006; *4,* line drawing of overlapping *G. marnia* burrows on IBGS PJ-M-004.

toward the anterior of the trackway, which resulted in overlapping bifid impressions.

Ichnogenus GORDIA Emmons, 1844

Type ichnospecies.—*Gordia marnia* Emmons, 1844, by original monotypy.

Diagnosis.—Smooth, winding but not meandering, unbranched, cylindrical burrows with common overcrossings and massive infill (Fillion & Pickerill, 1990; Wang & others, 2009).

Discussion.—*Gordia* was originally described and named for its resemblance to the freshwater hairworm, *Gordius* Linnaeus, 1758, but a poor definition caused some authors to view *Gordia* as *nomen nudum* (Emmons, 1844; Fillion & Pickerill, 1990). Hall (1847) provided a new description, which provided the diagnosis for *Gordia* as an ichnofossil (Fillion & Pickerill, 1990). Buatois and others (1998) suggested the synonymy of *Haplotichnus* Miller, 1889, under *Gordia* due to similar path irregularity and burrow overlap, even though *Haplotichnus* has frequent sharp bends in the burrow and rarely crosses itself. They considered the sharp bends in *Haplotichnus* to represent only a minor behavioral difference that yielded only an accessory feature (*sensu* Fürsich, 1974b; Buatois & others, 1998) and did not warrant separation. The sharp, irregular bends, however, are major architectural differences (*sensu* Hasiotis & Mitchell, 1993; Hasiotis, Mitchell, & Dubiel, 1993), as the sharp-angle bends and rare self-crossings are ichnotaxonomically significant at the ichnogeneric level. We, therefore, reject the synonymy of *Haplotichnus* within *Gordia*, and retain *Haplotichnus* as a separate ichnotaxon.

Gordia is commonly interpreted as a locomotion, deposit-feeding, or grazing trace of annelid worms or other wormlike organisms, arthropods, or nematodes (e.g., Emmons, 1844, Buatois & Mángano, 1993b). *Gordia* is a one of most common facies-crossing ichnofossils known and has been reported from almost every depositional environment in deep and shallow marine, as well as, from estuarine, fluvial, and lacustrine deposits (e.g., Fillion & Pickerill, 1990; Buatois & Mángano, 1993b; Uchman, Kazakauskas, & Gaigalas, 2009; Jackson, Hasiotis, & Flaig, 2016). *Gordia* ranges from the Ediacaran to recent (Crimes & Anderson, 1985; McCann & Pickerill, 1988; Fillion & Pickerill, 1990; Wang & others, 2009; Hasiotis & others, 2012).

GORDIA MARNIA Emmons, 1844
Figure 12.1–12.4

Material.—IBGS LG-M-006: one specimen; IBGS PJ-M-004: one specimen, Miner's Hollow.

Diagnosis.—Thin, arcuate to winding burrows or trails with self-overcrossing patterns (De Gibert & others, 2000).

Description.—Winding burrows in convex epi- or hyporelief or in concave epirelief with multiple, arcuate, self-overcrossing trails. Burrows 4.2–38.4 mm long, 0.3–1.1 mm wide.

Occurrence.—Laminated, greenish gray (weathers to brown or yellowish brown), mica-rich siliciclastic shale with thin laminations of dark gray sandy shale. One specimen occurs in a BST carbonaceous film of *Banffia* sp. (J.B. Caron, personal communication, 2016).

Associated ichnotaxa.—None.

Discussion.—The occurrence *G. marnia* within the BST film (Fig. 12.1, 12.3) suggests that anoxic conditions were present for a period long enough to allow the *Banffia* sp. to decay into a BST carbon film before oxic or dysoxic conditions returned, allowing the *Gordia* tracemaker to feed off the remaining organic matter (*sensu* Wang & others, 2009; Garson & others, 2012). The numerous overlapping burrow segments on IBGS PJ-M-004 suggests a high concentration of detrital organics in the sediment (Fig. 12.2, 12.4).

Ichnogenus GYROPHYLLITES Glocker, 1841

Type ichnospecies.—Gyrophyllites kwassizensis Glocker, 1841.

Diagnosis.—Vertical to oblique shaft with numerous radiating club- to leaf-shaped tunnels or lobes on staggered levels and usually unbranched; each lobe may have been backfilled (Uchman, 1998).

Discussion.—Gyrophyllites is very similar to numerous rosette-shaped ichnofossils. Głuszek (1998) noted that *Gyrophyllites* bears a strong resemblance to *Asterosoma* Otto, 1854, when viewed in plan view where only one level of *Gyrophyllites* is viewed. Some authors have noted that *Gyrophyllites* looks similar to both *Asterichnus* Bandel, 1967, and *Stelloglyphus* Vialov, 1964 (e.g., Uchman, 1998, Le Roux, Nielson, & Henríquez, 2008). Similarities between *Atollites* Maas, 1902, and *Gyrophyllites* have been noted as both have radiating lobes and a theorized helical structure (Seilacher, 1977; Serpagli, 2005). However, the lobe terminations in *Atollites* are more spherical than club shaped or straight compared to *Gyrophyllites*. *Lorenzinia* Gabelli, 1900, is composed of radiating burrows with a large flat central area separating the inner burrow terminations and has no apparent central shaft (Häntzschel, 1975). Fürsich and Bromley (1985) reinterpreted *Dactyloidites* Hall, 1886, and remarked on its superficial similarity to *Gyrophyllites* and other rosette ichnofossils, but noted that *Dactyloidites* contained radial spreiten. The figures in Fürsich and Bromley (1985, fig. 7, 8, & 10), however, show vertically to subvertically stacked spreiten with the exception of *D. asterioides*. Though commonly illustrated as a three-dimensional helical structure (e.g., Häntzschel, 1975, p. 66, fig. 40.2b), *Gyrophyllites* is thought by some to be a rosette trace occurring in multiple stories, with each restricted to a single bedding plane and connected by a central tube (e.g., Fürsich & Kennedy, 1975; Le Roux, Nielson, & Henríquez, 2008; Strzeboński & Uchman, 2015).

Gyrophyllites is interpreted as the feeding burrow system of a wormlike deposit feeder, such as polychaete and echiuran worms (e.g., Chamberlain, 1975; Fürsich & Kennedy, 1975; Mángano, Buatois, & Muñiz Guinea, 2005; Le Roux, Nielson, & Henríquez, 2008; Strzeboński & Uchman, 2015). Fürsich and Kennedy (1975) suggested that *Gyrophyllites* was produced preferentially in silty and clayey layers as the tracemaker mined sediment for food and stopped excavation when sand-rich layers were encountered. *Gyrophyllites* is most commonly reported from deep-marine flysch and fan overbank deposits but has also been reported from shallow-marine deposits (e.g., Wetzel & Uchman, 1997; Uchman, 1998; Seilacher, 2007; Strzeboński & Uchman, 2015). *Gyrophyllites* ranges from the Cambrian to Eocene (Mángano, Buatois, & Muñiz Guinea, 2005; Strzeboński & Uchman, 2015).

GYROPHYLLITES KWASSIZENSIS Glocker, 1841
Figure 13.1–13.6

Material.—KUMIP 314143: two specimens, Cataract Canyon; KUMIP 314162: one specimen, Miner's Hollow; KUMIP 314223: one specimen, Antimony Canyon; IBGS PJ-M-022: one specimen, High Creek Canyon, Bear River Range, Utah, USA; IBGS PJ-M-033: one specimen, Miner's Hollow.

Diagnosis.—Horizontal, straight to club-shaped lobes radiating from single point; may have burrow fills of different color from host lithology, thin ring of disturbed sediment surrounding radiating lobes, and/or lobes that appear bifurcated.

Description.—Endorelief, concave epirelief, and convex hyporelief rosettes with 7–19 straight to club-shaped lobes radiating from a central shaft. Rosettes 16.4–42.5 mm diameter: Lobes 3.9–20.8 mm long, 1.4–11.0 mm wide. Lobes commonly separate but may bifurcate, overlap, or be amalgamated together. Central shaft is only visible on one specimen as a small dark circle, 1.1 mm diameter.

Occurrence.—Two lithologies: (1) greenish gray (weathered to brown) siliciclastic silty to sandy shale and may have black to brown dendrites; and (2) dark gray (weather to brown), laminated calcareous silty shale. No visible bedding or laminations present; low to moderate bedding plane disruption (BPBI 2).

Associated ichnotaxa.—Planolites beverleyensis, Rusophycus carbonarius, Sagittichnus lincki, and *Treptichnus bifurcus*.

Discussion.—Most specimens assigned to *G. kwassizensis* occur individually; however, on one slab sample, two endorelief specimens are present and in close proximity (Fig. 13.1–13.2). Only two slab specimens have *G. kwassizensis* with other ichnotaxa (Fig. 13.3–13.5). Two specimens occur as flat endoreliefs (see Fig. 13.1–13.2). Fill of both rosettes is slightly finer and a lighter color than the surrounding matrix. The lobe shape of each specimen is variable. One specimen has wide lobes with indistinct margins, whereas the other has thinner lobes with distinct margins. At the center of the thin-lobed specimen is a small dark circle, which we interpret as the central tube that would have connected to the next tier and where the tracemaker resided.

One collector and donor, Phillip Reese, originally identified a medusoid fossil specimen (Fig. 13.6) as *Brooksella* Walcott, 1896, which was stored in the KUMIP since 1989 and only recently was reinterpreted as *Gyrophyllites* by R. A. Robison. Most authors follow the suggestion of Häntzschel (1975) and consider *Brooksella* to be a body fossil, rather than an ichnofossil. Some authors have retained *Brooksella* as a valid medusoid ichnogenus (e.g., Willoughby & Robison, 1979; Jensen, 1997), whereas others (e.g., Fürsich & Bromley, 1985) consider *Brooksella* to be a junior synonym of *Dactyloidites* Hall, 1886. This specimen has a

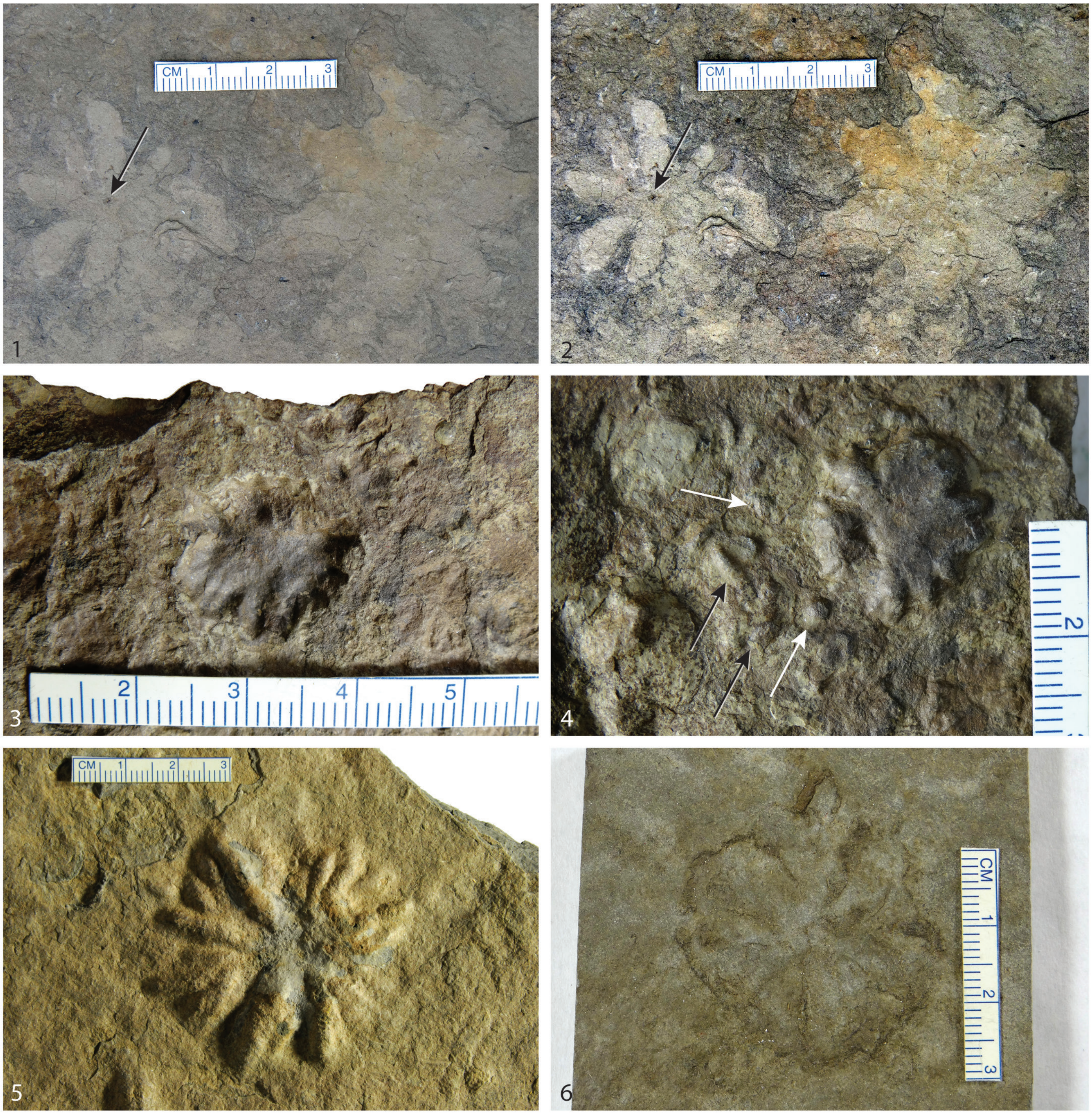

Figure 13. *Gyrophyllites kwassizensis* specimens from the Spence Shale. *1–2,* Endoreliefs of *G. kwassizensis,* KUMIP 314143, Cataract Canyon; *1,* True color image; *2,* False color image; (Arrows indicate central shaft); *3–4, Gyrophyllites kwassizensis* preserved in epirelief (*3*) and hyporelief (*4*) with *Sagittichnus lincki* (white arrows) and *Treptichnus bifurcus* (black arrows), IBGS PJ-M-022, High Creek Canyon, Wasatch Range; *5, Gyrophyllites kwassizensis* KUMIP 314223, Antimony Canyon; *6, Gyrophyllites kwassizensis,* KUMIP 314162, Miner's Hollow; scale in cm.

sandy outer rim surrounding the central, radiating lobes, likely due to the organism having made contact with a sandier layer and stopped excavation (Fürsich & Kennedy, 1975).

Willoughby and Robison (1979) reported four specimens of *Brooksella* from the Spence Shale (Spence Tongue of the Lead Bell Shale of Idaho). Three specimens (Willoughby & Robison, 1979, fig. 1A–C) belong to *Gyrophyllites*. The fourth (Willoughby & Robison, 1979, fig. 1D) belongs to *Dactyloidites* as it consists of six radiating lobes with small tubes or tube plugs in the distal ends of the lobes, similar to the specimen of *Dactyloidites asterioides* Fitch, 1850, figured by Häntzschel (1975, p. 145, fig. 88).

Ichnogenus HALOPOA Torell, 1870

Type ichnospecies.—Halopoa imbricata Torell, 1870, designated by Häntzschel, 1975.

Diagnosis.—Long, horizontal burrows covered with irregular longitudinal ridges or wrinkles; may include multiple overlapping cylindrical probes (Uchman, 1998).

Discussion.—*Halopoa* is considered by multiple authors to be very similar to *Fucusopsis* Palibin in Vasseoevich, 1932, causing each ichnogenus to be transferred back and forth into the other (e.g., Hakes, 1976; Jensen, 1997; Uchman, 1998). Both ichnogenera are described as long, straight to curved, horizontal burrows with longitudinal striations or wrinkles. Hakes (1976) compared and noted that poorly preserved specimens of *Fucusopsis*, *Halopoa*, and *Scoyenia* White, 1929, would be difficult to differentiate. *Fucusopsis* was synonymized with *Palaeophycus* and split between *P. striatus* and *P. sulcatus* (Pemberton & Frey, 1982). Jensen (1997) argued that *Halopoa imbricata* was similar to both *Fucusopsis* and *P. sulcatus* and partially followed the synonymy of Pemberton and Frey (1982), regarding *H. imbricata* as a valid ichnospecies within *Palaeophycus* (i.e., *P. imbricatus*). Jensen (1997) agreed with the Osgood (1970) interpretation that longitudinal striations on the burrow were caused by sediment deflection and lamination rupture as the tracemaker burrowed through the medium. Jensen (1997) considered them not very useful for ichnotaxonomic assessment as the surficial morphology reflected properties of the sediment. He also noted that there were (rare) spreiten present in *H. imbricata* but disregarded the fact that spreite are usually an indicator of active burrowing (*sensu* Fürsich, 1974b).

Uchman (1998) argued for the retention of *Halopoa*, noting the striations of *Fucusopsis* and *Halopoa* were likely produced by active digging, passive dragging of body parts due to body shape, or the sediment deflection-lamina rupture method proposed by Osgood (1970). He considered each to represent unique behaviors that generated a unique morphology. Uchman also noted several *Halopoa* specimens had *Teichichnus*-like, vertically stacked, overlapping probes (spreiten), but maintained *Halopoa* and *Teichichnus* as separate, arguing that *Teichichnus* generally lacks external ornamentation and that the spreiten in *Halopoa* were not as developed. He argued against the Pemberton and Frey (1982) synonymy, noting *Halopoa* lacked any type of wall or lining that would warrant placement within *Palaeophycus*. We herein follow the Uchman (1998) retention of *Halopoa*.

Three ichnospecies of *Halopoa* are known: *H. annulata* (Książkiewicz, 1977), *H. imbricata*, and *H. storeana* Uchman, 2001. The primary feature that separates *H. imbricata* from *H. storeana* is the orientation of the surficial wrinkles (ridges). The wrinkles of *H. imbricata* are parallel to subparallel to the trace axis, whereas the wrinkles on *H. storeana* have a plaited pattern (Uchman, 2001). *Halopoa annulata* is differentiated from *H. imbricata* and *H. storeana* by occasional branching and the presence of transverse annulations producing an undulatory pattern along the burrow (Uchman, 1998, 2001).

Commonly interpreted as the feeding burrow of an infaunal deposit feeder, *Halopoa* tracemakers may include annelid worms, enteropneusts, echiurans, and holothurians (e.g., Hakes, 1976; Uchman, 1998; Zonneveld, Gingras, & Beatty, 2010). Uchman (2001) interpreted *Halopoa* as a grazing trace. *Halopoa* is most commonly found in sandstone turbidites of deep-marine flysch deposits (e.g.. Uchman, 1998); however, some have been reported from shallow-marine deposits (e.g., Jensen, 1997) and tidal flats (e.g., Mángano & others, 2002). *Halopoa* ranges from the early Cambrian to middle Miocene (Jensen, 1997; Uchman, 1998).

HALOPOA aff. IMBRICATA Torell, 1870
Figure 14.1

Material.—IBGS LG-M-012: three specimens, Box Elder Canyon, Wellsville Mountains, Utah, USA

Diagnosis.—Long, horizontal burrows covered with irregular, longitudinal ridges (Uchman, 1998).

Description.—Horizontal, convex hyporelief burrows with irregular-shaped ridges and furrows or wrinkles along the length of the burrow. Burrows 11.0–70.0 mm long, 1.6–2.7 mm wide. Burrows overlap each other to form pseudobranching.

Occurrence.—Gray (weathered to brown) calcareous silty shale.

Associated ichnotaxa.—*Planolites montanus* and *Treptichnus vagans*.

Discussion.—Ichnofossils are primarily assigned to *Halopoa* aff. *imbricata* due to the longitudinally wrinkled texture of the outer burrow margins and the lack of transverse annulations or a plaited pattern (Fig. 14.1). The nature of the burrow fill is unknown, and the burrows are poorly preserved, convex hyporeliefs. Burrows show overlapping to form pseudobranching, but some possible branching (i.e., secondary successive branching; *sensu* Keighley & Pickerill, 1995) may be present. Analysis of the fill is needed to confirm the type of branching, if present.

Ichnogenus LOCKEIA James, 1879

Type ichnospecies.—*Lockeia siliquaria*, James 1879.

Diagnosis.—Amygdaloidal- to ovoid-shaped mounds (convex hyporelief) or depressions (concave epirelief) that taper at one or both ends; surface usually smooth but may be irregular; may have a medial longitudinal crest (hyporelief) or groove (epirelief) (Osgood, 1970; Fillion & Pickerill, 1990; Mángano & others, 2002).

Discussion.—*Lockeia* was the subject of much debate when reintroduced into ichnotaxonomy. Osgood (1970) considered *Lockeia* as the senior synonym for almond-shaped resting traces and considered *Pelecypodichnus* Seilacher, 1953a, to be a subjective junior synonym. Numerous authors have followed this suggestion (e.g., Häntzschel, 1975, Hakes 1976, Mángano & others, 2002). Other authors, however, continued to used *Pelecypodichnus* after Eagar (1974) argued that *Lockeia* was *nomen oblitum* citing the International Code of Zoological Nomenclature rule (ICZN 1964, 2nd edition, Article 31) requiring a figure or illustration, alongside the original description, to be a valid taxon (Hakes, 1976; Bromley & Asgaard, 1979; Fillion & Pickerill, 1990). Hakes (1976) retained *Lockeia* because Article 12 of the ICZN did not require figures for taxa established before 1931 if the original author provided a description or definition. Hakes (1977) later regarded *Lockeia* as *nomen oblitum* citing the 50-year rule (ICZN, Article 79) of non-use of a taxon. Maples and West (1989) noted that *Lockeia* was used once to validly erect an ichnospecies, *Lockeia anticostiana,* by Twenhofel (1927) during the supposed 50-year hiatus and, thus, invalidated the argument of Hakes (1977).

At least 13 ichnospecies of *Lockeia* have been proposed: *L. amygdaloides* (Seilacher, 1953a); *L. anticostiana* Twenhofel, 1927;

Figure 14. *Halopoa, Monomorphichnus,* and *Nereites* specimens from the Spence Shale. *1, Halopoa* aff. *imbricata* (black arrows) in convex hyporelief, IBGS LG-M-012, Box Elder Canyon; *2, Monomorphichnus bilinearis* (arrow) in convex hyporelief with *Treptichnus vagans,* IBGS PJ-M-031; *3, Monomorphichnus lineatus,* convex hyporelief, IBGS PJ-M-012, Miner's Hollow; *4, Monomorphichnus lineatus* in concave epirelief, IBGS LG-M-008; *5, Monomorphichnus* cf. *multilineatus* with *Cruziana problematica* and *Lockeia siliquaria* convex hyporelief, KUMIP 314228, Miner's Hollow; *6, Nereites* cf. *macleayi* (white arrow) in concave epirelief with *Planolites montanus* (black arrow), IBGS PJ-M-033, Miner's Hollow; scale: *2* and *6,* in mm; *1, 3–5,* scale in cm.

L. avalonensis Fillion & Pickerill, 1990; *L. cordata* Rindsberg, 1994; *L. cunctator* Schlirf & Uchman in Schlirf, Uchman, & Kümmel, 2001; *L. czarnockii* (Karaszewski, 1975); *L. elongata* Yang, 1984; *L. gigantus* Kim & Kim, 2008; *L. hunanensis* Zhang & Wang, 1996; *L. ornata* (Bandel, 1967); *L. serialis* Seilacher & Seilacher, 1994; *L. siliquaria* James, 1879; and *L. triangulichnus* Kim, 1994. Schlirf, Uchman, and Kümmel (2001) and Mángano and others (2002) recently reviewed and compared most of the ichnospecies of *Lockeia* except for *L. gigantus*. *Lockeia anticostiana* was considered as *Planolites* (Hakes, 1977). *Lockeia cunctator* is considered a repichnia version of *Lockeia* similar to and partly as a replacement for *L. serialis*—considered *nomen nudum* due to lack of holotype designation and not figured by Seilacher and Seilacher (1994)—but *L. cunctator* is more similar to *Treptichnus bifurcus* from where it was transferred by Schlirf, Uchman, and Kümmel (2001)—due to its feather-stitch morphology. *Lockeia gigantus* was proposed for extremely large, almond-shaped ichnofossils (up to 70 mm long and 30 mm wide) from the Lower Cretaceous lacustrine deposits of Korea (Kim & Kim, 2008).

Lockeia is considered a dwelling or resting trace of a bivalve or bivalve-like organism (Seilacher & Seilacher, 1994; Mángano & others, 2002). *Lockeia* has been reported from shallow marine (e.g., lower delta fronts, and subtidal and intertidal flats), deep marine, and continental lacustrine and fluvial deposits (e.g., Seilacher, 1953a; Hakes, 1976; Bromley & Asgaard, 1979; Crimes & others, 1981; Fillion & Pickerill, 1990; Głuszek, 1995; Hasiotis, 2002, 2004, 2007, 2008; Mángano & others, 2002; Hasiotis & others, 2012). Precambrian *Lockeia* specimens have been reported (e.g., Narbonne & Aitken, 1990; Jenkins, 1995; McMenamin, 1996), however, Mángano and others (2002) and Jensen, Droser, and Gehling (2006) noted that the traces did not possess the diagnostic characteristics of *Lockeia* and were likely dubiofossils or body fossils, respectively. The Narbonne and Aitken (1990) specimens show the oval to almond shape characteristic of *Lockeia,* and, thus, the assignment is justified. Some of the specimens illustrated by McMenamin (1996) may actually be a form of *Treptichnus,* as they appear to have a feather-stitch morphology characteristic to *Treptichnus*. *Lockeia* ranges from the Ediacaran to recent (e.g., Crimes, 1987, 1992; Narbonne & Aitken, 1990; Hasiotis, 2002; Mángano & others, 2002; Jensen, Droser, & Gehling, 2006).

LOCKEIA SILIQUARIA James, 1879
Figure 6.5, Figure 19.2

Material.—KUMIP 314228: one specimen, Miner's Hollow; IBGS LG-M-003: one specimen; IBGS PJ-M-019; one specimen, Miner's Hollow.

Diagnosis.—Amygdaloidal (almond-shaped) convex hyporeliefs, with one or both ends usually tapered to a point, some may be round.

Description.—Amygdaloid-shaped (almond-shaped) mound in convex hyporelief; 4.1–6.3 mm long and 2.6–4.4 mm wide.

Occurrence.—Two lithologies: (1) Light to dark gray, laminated silty shale with continuous laminations indicating an *ii*2; and (2) medium to dark gray calcareous, micaceous silty to sandy shale. Bedding planes are highly disrupted with numerous traces indicating BPBI 4–5.

Associated ichnotaxa.—*Aulichnites* isp., *Cruziana problematica*, *Dimorphichnus* isp., *Monomorphichnus lineatus*, *M.* cf. *multilineatus*, *Phycosiphon incertum*, *Planolites beverleyensis*, *P. montanus*, *Protovirgularia* cf. *pennatus*, *Rusophycus carbonarius*, *Rusophycus* cf. *cerecedensis*, *Sagittichnus lincki,* and *Treptichnus vagans*.

Discussion.—The *Lockeia siliquaria* specimen on IBGS PJ-M-019 occurs at the termination of a bilobate concave hyporelief burrow assigned to *Aulichnites*. The close linear association of the two ichnotaxa suggests they were produced by the same tracemaker. The depth of the *L. siliquaria* increases toward the opposite side of the intersection of the two ichnotaxa, suggesting the tracemaker produced the *Aulichnites* and then the *Lockeia* (see Fig. 6.5). On IBGS LG-M-003, a *L. siliquaria* specimen is found alongside specimens of *Sagittichnus lincki*, which are similarly shaped, small ovoid-shaped convex mounds (for discussion see *Sagittichnus,* p. 36). The two morphologies can be distinguished by size, as *L. siliquaria* is larger than the *Sagittichnus lincki* specimens.

Ichnogenus MONOMORPHICHNUS Crimes, 1970b

Type ichnospecies.—Monomorphichnus bilinearis Crimes, 1970b.

Diagnosis.—Series of straight to sigmoidal, parallel or intersecting, laterally repeating striations in isolated or grouped sets; typically preserved in convex hyporelief (Crimes, 1970b; Fillion & Pickerill, 1990; Keighley & Pickerill, 1998).

Discussion.—Crimes (1970b) established *Monomorphichnus* for surficial striations produced by bottom-current-propelled trilobites raking the sediment surface with their endopodite claws. He noted that these striations were similar to *Dimorphichnus* but lacked the characteristic blunt impressions (Crimes, 1970b; Fillion & Pickerill, 1990; Jensen, 1997). *Monomorphichnus* maybe a junior synonym of *Ctenichnites* Matthew, 1891, *Eoichnites* Matthew, 1891, *Medusichnites* Matthew, 1891, or *Taonichnites* Matthew in Selwyn, 1890; however, their ichnotaxonomic status is unclear as some authors have considered them dubiofossils or pseudofossils, whereas others considered them valid ichnotaxa (see Fillion & Pickerill, 1990, for full discussion).

Since *Monomorphichnus* was established at least 15 ichnospecies have been proposed and differentiated by the number of striations present: *M. bilinearis* Crimes, 1970b; *M. biserialis* Mikuláš, 1995; *M. cretacea* Badve & Ghare, 1980; *M. devonicus* Yang & Hu in Yang, Hu, & Sun, 1987; *M. gaopoensis* Yang, Yin, & He, 1982; *M. gregarius*, Pandey & others, 2014; *M. henanensis* Yang & Wang, 1991; *M. intersectus* Fillion & Pickerill, 1990; *M. lineatus* Crime & others, 1977; *M. monolinearis* Shah & Sudan, 1983; *M. multilineatus* Alpert, 1976a; *M. pectenensis* Legg, 1985; *M. podolicus* Uchman & others, 2004; *M. semilineatus* Mikuláš, 1995; and *M. sinus* Gibb, Chatterton, & Pemberton, 2009. *Monomorphichnus cretacea* and *M. gaopoensis* are considered inorganic tool marks or a combination of organic and inorganic structures (e.g., Fillion & Pickerill, 1990; Uchman & others, 2004). Fillion and Pickerill (1990) found *M. monolinearis* to be a junior synonym of *M. lineatus*. *Monomorphichnus podolicus* was synonymized with *Cruziana omanica* Seilacher, 1970, due to its tendency to occur bilobate (Gibb, Chatterton, & Pemberton, 2009). *Monomorphichnus gregarius* was introduced by Pandey and others (2014) for highly overlapping sets of 4 striations; however, the holotype has sets of 4–6 striations, most of which occur in sets of 6, with central striations being more prominent, and crosscut other sets, which suggests affinities to both *M. multilineatus* and *M. intersectus*. We, therefore, regard *M. gregarius* and *M. intersectus* as subjective junior synonyms of *M. multilineatus*.

Monomorphichnus is considered a locomotion or grazing trace (Crimes, 1970b; Crimes & others, 1977), and often has been attributed to trilobites (e.g., Crimes, 1970b; Alpert, 1976a), but other arthropods (e.g., eurypterids and xiphosurids) have also been proposed as possible tracemakers (Romano &

Meléndez, 1985; Jensen, 1997). Osgood (1970) suggested the grazing interpretation was an inefficient feeding strategy and that *Monomorphichnus* was likely produced by an arthropod trying to stabilize itself while caught in turbulent bottom-water currents. A recent neoichnological study by Jones (2016) has shown several *Monomorphichnus*-like traces produced by bats via ground-based locomotive and searching behaviors. *Monomorphichnus* has been reported from shallow- and deep-marine, and continental deposits (e.g., Crimes, 1970b; Crimes & others, 1977; Keighley & Pickerill, 1998). The earliest occurrence of *Monomorphichnus* has been thought to be in units previously referred to as Vendian—now known as the Ediacaran—by Crimes (1987, 1992). Reports of *Monomorphichnus* from latest Neoproterozoic strata by Jenkins (1995) and Waggoner and Hagadorn (2002) were reinterpreted by Jenson, Droser, and Gehling (2006) as *Radulichnus* and tool marks or a trace fossil(?), respectively. However, the redefinition of the Ediacaran (Neoproterozoic)-Cambrian (Paleozoic) boundary based on the occurrence of *Treptichnus pedum* may define the range of *Monomorphichnus* as Cambrian to recent (e.g., Jensen, 1997; MacNaughton & Narbonne, 1999; Jenson, Droser, & Gehling, 2006; Landing & others, 2007; Hasiotis, 2012).

MONOMORPHICHNUS BILINEARIS Crimes, 1970b
Figure 14.2, Figure 23.5

Material.—IBGS PJ-M-031; five specimens, Miner's Hollow.

Diagnosis.—Pairs of parallel, straight to slightly sigmoidal striations with one striation more prominent than the other, and sometimes repeated laterally (Crimes 1970b; Fillion & Pickerill, 1990).

Description.—Paired sigmoidal striations in convex hyporelief. Striations 12.1–45.2 mm long, 0.6–1.7 mm wide, and spaced 1.0–1.3 mm apart.

Occurrence.—Gray (weathered to brown), micaceous silty shale.

Associated ichnotaxa.—*Treptichnus vagans*.

Discussion.—*Monomorphichnus bilinearis* are only present on IBGS PJ-M-031 alongside *Treptichnus vagans*. The striations were assigned to this ichnogenus due to their sigmoidal shape and tendency to occur in pairs. Some *M. bilinearis* specimens are cross cut by *Treptichnus vagans* specimens (Fig. 14.2), thus, indicating the striations were produced first, followed by the construction of the *Treptichnus vagans*.

MONOMORPHICHNUS LINEATUS Crimes, & others, 1977
Figure 14.3–14.4

Material.—KUMIP 314228: one specimen, Miner's Hollow; IBGS LG-M-008 and LG-M-009 (part and counterpart): one specimen, Spence Shale; IBGS PJ-M-012: one specimen, Miner's Hollow.

Diagnosis.—Individual, straight to slightly sigmoidal striations that can be repeated laterally (Crimes & others, 1977; Fillion & Pickerill, 1990).

Description.—Sigmoidal to slightly curved striations, some may be bifid, in convex hyporelief and concave epirelief. Striations 5.4–36.1 mm long, 0.5–2.1 mm wide. One row of repeated striations is 50.6 mm long, 9.7 mm wide, and spaced 1.5–1.9 mm apart. Striations may have blunt ends and sharply taper on the other.

Occurrence.—Two lithologies: (1) greenish gray (weathered to tan or brown), micaceous silty shale; and (2) gray, silty shale with laminations of light and dark gray, silty to sandy, siliciclastic to carbonate shale.

Associated ichnotaxa.—*Cruziana problematica*, *Lockeia siliquaria*, *Monomorphichnus* cf. *multilineatus*, *Planolites beverleyensis*, *P. montanus*, *Protovirgularia dichotoma*, *Rusophycus carbonarius*, *Rusophycus* cf. *cerecedensis*, *Treptichnus bifurcus*, and *T. vagans*.

Discussion.—The specimen on IBGS PJ-M-012 is differentiated from *Cruziana billingsi* Fillion & Pickerill, 1990, by the arrangement of striations in a single track row—whereas *C. billingsi* is bilobate—and is almost identical to the holotype illustrated by Crimes and others (1977, p. 107, pl. 3b) (Fig. 14.3). Specimens on IBGS LG-M-008 and LG-M-009 occur with no other traces (Fig. 14.4).

MONOMORPHICHNUS cf. MULTILINEATUS Alpert, 1976a
Figure 14.5

Material.—KUMIP 314228: one specimen, Miner's Hollow.

Diagnosis.—Parallel, straight to sigmoidal striations grouped in sets of 5 to 6, with deeper and thicker striations in center of group (Alpert, 1976a).

Description.—Horizontal, sigmoidal striations (convex hyporelief) grouped in sets of 2–4, spaced 1.6–1.8 mm apart with one striation more prominent than the others. Striations 3.0–14.2 mm long, 0.3–0.7 mm wide, and spaced 0.5–1.1 mm apart.

Occurrence.—Greenish gray (weathered to tan or brown), micaceous silty shale.

Associated ichnotaxa.—*Cruziana problematica*, *Lockeia siliquaria*, *Monomorphichnus lineatus*, *Planolites beverleyensis*, *P. montanus*, *Rusophycus carbonarius*, *R.* cf. *cerecedensis*, and *Treptichnus bifurcus*.

Discussion.—The specimen has striations grouped in pairs assignable to *M. bilinearis*, but others grouped in triplets and quadruplets, which are assignable to *M. multilineatus*. A specimen illustrated by Fillion and Pickerill (1990, pl. 10, fig. 3) has several bundles of 2–3 striations mixed with the typical 4–6 striation bundles. The similarity between the Spence Shale specimen and the Fillion and Pickerill (1990) specimen justifies assignment to *M. multilineatus*. Another *Monomorphichnus* ichnospecies that the Spence Shale specimen resembles is *M. semilineatus* Mikuláš, 1995, which is characterized as curved to straight sigmoidal striations in groups of 2–10 (Mikuláš, 1995, pl. 1 & 3, fig. 1C). *Monomorphichnus semilineatus*, however, appears to be morphologically variable with bundle sets that are indistinguishable from other *Monomorphichnus* ichnospecies. We, therefore, consider *M. semilineatus* to be an amalgam of several *Monomorphichnus* ichnospecies and no valid use to ichnotaxonomy. *Monomorphichnus multilineatus* also resembles the coarse striations of *Rusophycus dispar* Linnarsson, 1869, like those figured by Jensen (1990, fig. 1) (Fig. 14.5); however, the specimen lacks the bidirectionality and bilobate shape typical of *R. dispar*.

Ichnogenus NEREITES MacLeay in Murchison, 1839

Type ichnospecies.—*Nereites cambrensis* MacLeay 1839 in Murchison (1839, p. 700).

Diagnosis.—Curved, winding to regularly meandering, unbranched, horizontal trails, with a medial backfilled tunnel flanked by an even to lobate zone of reworked sediment (Uchman, 1995; Mángano & others, 2000, 2002).

Discussion.—A long-lasting debate in ichnotaxonomy has been raging regarding status of the ichnotaxa *Nereites* MacLeay, 1839 in Murchison, 1839; *Neonereites* Seilacher, 1960; and *Scalarituba* Weller, 1899. Numerous authors have suggested that *Nereites* is the senior synonym of *Neonereites* and *Scalarituba*, arguing that both are preservational variants of *Nereites* (e.g., Chamberlain, 1971; Chamberlain & Clark, 1973; D'Alessandro & Bromley, 1987; Devera, 1989; Rindsberg, 1994; Uchman 1995; Mángano & others, 2000, 2002). Some authors, however, retain or advocate for the retention of *Neonereites* as a separate ichnotaxon (e.g., Benton, 1982; Fillion & Pickerill, 1990; Pickerill, 1991).

Though long suggested, Uchman (1995) was one of the few to formally place *Neonereites* and *Scalarituba* within *Nereites*. He also suggested that the three *Neonereites* ichnospecies (*N. biserialis* Seilacher, 1960; *N. multiserialis* Pickerill & Harland, 1988; and *N. uniserialis* Seliacher, 1960) should be used informally as subichnospecies to describe associated preservational variation. *Helminthoida* Schafhäutl, 1851, was also synonymized under *Nereites* because Uchman (1995) noted *Nereites*-like marginal lobes in the type specimen. Seilacher (1962) suggested that *Helminthoida* and *Neonereites* were related with *Neonereites* being a preservational variant of *Helminthoida* in sand-rich environments. We, however, suggest retaining *Helminthoida* due to its high-sinuosity, tightly meandering, and repetitive pattern in morphology that is distinctive and diagnostic of this ichnotaxon, which is morphologically related to *Helminthopsis* Heer, 1877.

Nereites is interpreted as a deposit-feeding or grazing trace (e.g., Uchman, 1995; Mángano & others, 2000, 2002). Commonly proposed tracemakers include annelid, enteropneust, and polychaete worms (e.g., Seilacher, 1960; Rindsberg, 1994; Uchman 1995; Mángano & others, 2000, 2002); however, gastropods, arthropods, and echinoderms (e.g., holothurians) have also been proposed (e.g., Rindsberg, 1994). Although the namesake of the deep marine Nereites Ichnofacies, *Nereites* has been reported from shallow-marine (e.g., lagoon, shoreface, tidal flats) and deep-marine settings (e.g., flysch) (e.g., Hakes, 1976; McCann & Pickerill, 1988; Uchman, 1995, 1998; Mángano & others, 2000). *Nereites* is common in both shallow- and deep-marine Paleozoic deposits but became almost exclusively deep marine in Mesozoic and Cenozoic deposits (e.g., Uchman, 1995; Mángano & others, 2000). Mángano and others (2002) argued that the lacustrine *Nereites* specimens figured by Hu, Wang, and Goldring (1998) did not fit the diagnostic criteria for *Nereites* and belong in *Vagorichnus* Buatois and others, 1995. We, however, consider *Vagorichnus* to be a junior synonym of *Walpia* White, 1929, based on morphologic similarities. We suggest that the specimens figured by Hu, Wang, and Goldring (1998) have morphologic features assignable to *Walpia*, which are typical of burrows produced by modern mud-loving beetles and some spiders just above the sediment-water interface (Hasiotis, 2002, 2004, 2008). *Nereites* has been reported from the Vendian (i.e., Edicaran) (e.g., Crimes & Germs, 1982; Jenkins, 1995); however, Jensen, Droser, and Gehling (2006) considered those specimens to be a form of *Archaeonassa*. Yet the photograph of the *Nereites* specimen in Crimes and Germs (1982) does show a central furrow flanked by ridges that are subtly lobate that grade into strongly hemispherical lobes typical of several *Nereites* ichnospecies; thus, we consider this specimen to be *Nereites*. The stratigraphic position of this specimen, however, is in the Vingerbreek Member of the Nudaus Formation of the lower part of the Schwarzrand Subgroup, which is Ediacaran in age, based on the co-occurrence of body fossils (e.g., Cohen & others, 2009). *Nereites*, therefore, ranges from the Ediacaran to recent (e.g., Crimes & Germs, 1982; Crimes, 1992; Mángano & others, 2000; Uchman, 1995).

NEREITES cf. MACLEAYI MacLeay in Murchison, 1839
Figure 14.6

Material.—IBGS PJ-M-033: one specimen (part and counterpart), Miner's Hollow.

Diagnosis.—Small, straight to meandering, concave furrow (epirelief) or convex burrow (hyporelief) flanked by small, semicircular lobes along furrow margin (McCann & Pickerill, 1988).

Description.—Straight, concave furrow flanked by small, semicircular lobes 24.1 mm long, 2.5–4.5 mm wide. Furrow 1.1–3.0 mm wide, and lobes 1.4–1.8 mm wide (from furrow margin). Furrow has a serial, spherical-chambered expression, chamber diameter 1.4–3.0 mm.

Occurrence.—Gray (weathered to brown), siliciclastic silty to sandy shale.

Associated ichnotaxa.—*Archaeonassa fossulata*, *Gyrophyllites kwassizensis*, and *Planolites montanus.*

Discussion.—The assignment to *Nereites* cf. *macleayi* was based primarily on the presence of small, semicircular lobes present along the furrow margin (Fig. 14.6). The furrow also has a serial-chamberlike appearance similar to *Neonereites uniserialis;* however, since *Neonereites* was synonymized under *Nereites*, assignment to *Neonereites* is untenable. Assignment to *Nereites missouriensis* may be justified by the presence of the serial chambers; yet, no meniscate backfill typical of *N. missouriensis* is observed in the specimen.

Ichnogenus PHYCODES Richter, 1850

Type ichnospecies.—*Phycodes circinatus* Richter, 1853.

Diagnosis.—Horizontal to subhorizontal, cylindrical to U-shaped burrows with dichotomously branched tunnels forming bundles (Fillion & Pickerill, 1990; Knaust, 2007).

Discussion.—Since Richter (1850) originally designated *Phycodes* for bundled structures regarded as fucoids, *Phycodes* has undergone several revisions to its present-day status as an ichnofossil (see Fillion & Pickerill, 1990; Han & Pickerill, 1994b; Jensen, 1997). *Phycodes* has been interpreted as a deposit-feeding trace of annelid worms (Fillion & Pickerill, 1990). *Phycodes* has been considered to be a good indicator for shallow-marine settings and indicative of the Cruziana Ichnofacies, but *Phycodes* has been reported from brackish and deep-water deposits as well (e.g., Hakes, 1985; Fillion & Pickerill, 1990; Han & Pickerill, 1994a; Jackson, Hasiotis, & Flaig, 2016). *Phycodes* ranges from the early Cambrian to the Miocene (Crimes, 1987, 1992; Han & Pickerill, 1994a).

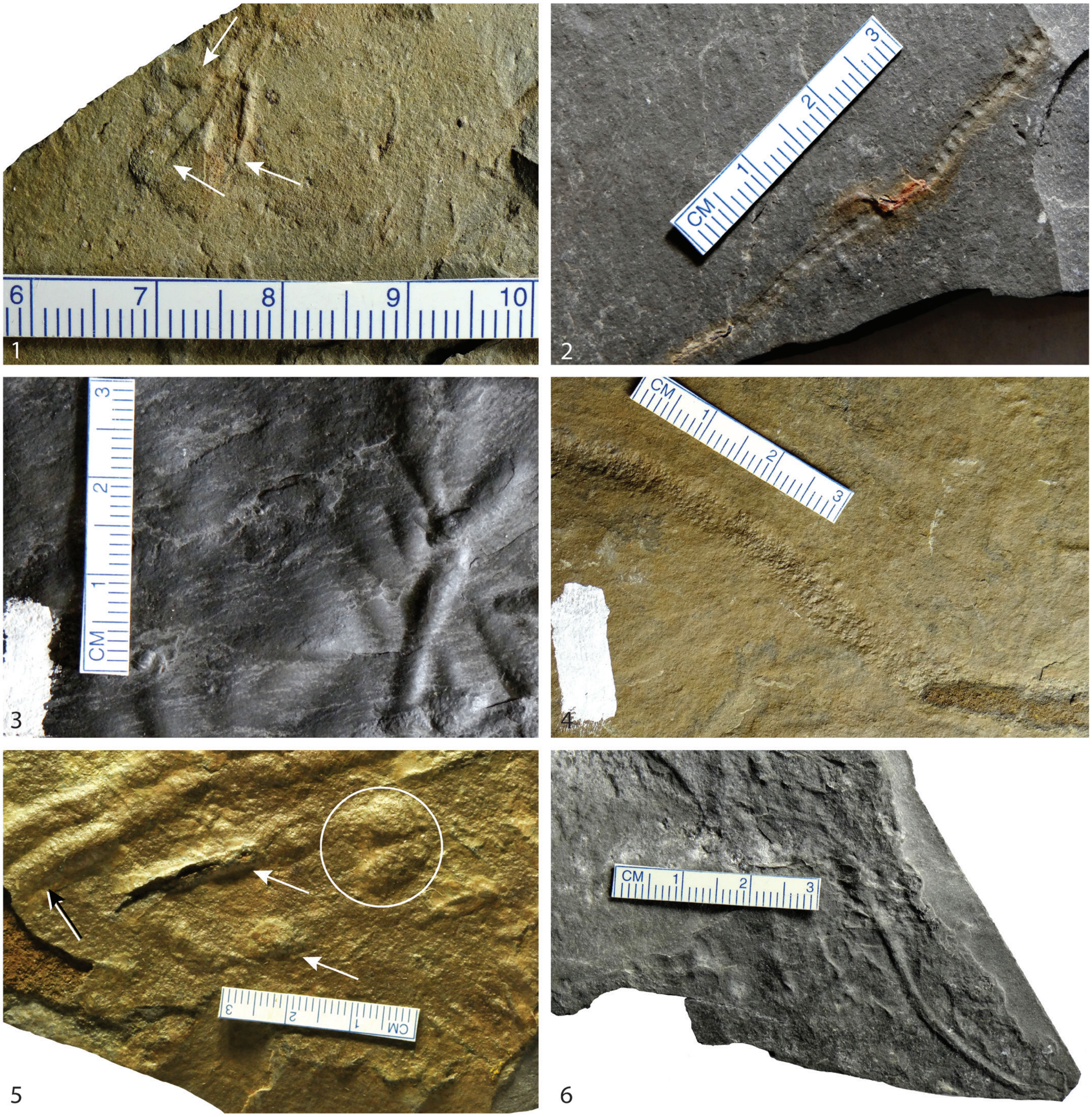

Figure 15. *Phycodes* and *Planolites* specimens from the Spence Shale. *1, Phycodes curvipalmatum,* in partial convex hyporelief and endorelief, IBGS PJ-M-005, Miner's Hollow; *2, Planolites annularis* in concave epirelief, IBGS PJ-M-001, Miner's Hollow; *3–5, Planolites beverleyensis: 3,* Convex hyporelief, IBGS LG-M-005; *4,* Concave hyporelief, IBGS LG-M-001; *5,* Self-crossing specimen (white arrows) with *Cruziana problematica* (black arrow) and *Rusophycus* cf. *cerecedensis* (circle) in convex hyporelief, KUMIP 315228, Miner's Hollow; *6, Planolites montanus* in convex hyporelief, IBGS LG-M-012, Box Elder Canyon; scale in cm.

PHYCODES CURVIPALMATUM Pollard, 1981
Figure 15.1

Material.—IBGS PJ-M-005: one specimen, Miner's Hollow float.

Diagnosis.—Thin, short, rounded, horizontal palmate or digitate burrows that originate from the same point (Pollard, 1981).

Description.—Small trifid-branched system of short burrows in convex epirelief and partial endorelief. Burrows range from 4.6–16.9 mm long and 2.0–2.5 mm wide. Burrow fill of two branches are exposed with burrow walls 0.3–0.8 mm thick and is similar to the host lithology.

Occurrence.—Tan to light brown, siliciclastic silty shale.

Associated ichnotaxa.—*Archaeonassa jamisoni* and *Taenidium* cf. *satanassi*.

Discussion.—The specimen consists of a triplet of burrows exhibiting primary successive branching (*sensu* D'Alessandro & Bromley, 1987; Keighley & Pickerill, 1995). (Fig. 15.1). The specimen is assigned to *P. curvipalmatum* and not *P. palmatus* because the burrows are both short and narrow, whereas *P. palmatus* Hall, 1852 has long and wide burrows. Two branches are preserved mostly as endoreliefs with the burrow walls as the only significant structures remaining, whereas one branch is in convex epirelief.

Ichnogenus PHYCOSIPHON Fischer-Ooster, 1858

Type ichnospecies.—*Phycosiphon incertum* Fischer-Ooster, 1858, by original monotypy.

Diagnosis.—Small, oblique or parallel to bedding, spreiten-filled burrow systems comprised of protrusive U-shaped lobes with dark, finer grained cores and light, coarser grained mantles; lobes may be nearly vertical to bedding; spreiten may not be visible (Wetzel & Bromley, 1994; Głuszek, 1998; Uchman, 1998).

Discussion.—Like most ichnofossils, *Phycosiphon* was originally interpreted as fossilized algae. More recently, however, it was interpreted as a complex burrow system of a deposit feeder, typically in dysoxic sediments (e.g., Ekdale & Mason, 1988; Uchman, 1998; Naruse & Nifuku, 2008). Wetzel and Bromley (1994) noted two general lobe arrangements occur in *Phycosiphon,* influenced by the host lithology: (1) lobes are parallel or subparallel to bedding in laminated sands and silts (exaggerated by compaction); and (2) lobes are randomly to vertically oriented in muddy and homogenous sediments. Wetzel and Bromley (1994) also compared *Phycosiphon* to *Anconichnus* Kern, 1978, because both are mantled, spreiten-filled, U-shaped burrow systems, and they decided that *Anconichnus* was a junior synonym of *Phycosiphon*.

Phycosiphon was monotypic with *P. incertum* as its sole ichnospecies until Uchman (1998) synonymized *Muensteria hamata* Fischer-Ooster, 1858, under *Phycosiphon* as *P. hamata*, and later joined by *Muensteria geniculata* Sternberg, 1833 by Uchman (1999) as *P. geniculatum*. *Phycosiphon hamata* differs from *P. incertum* with its more regularly shaped lobes, larger size, and J- to U-shaped lobes. Uchman (1998) also warned that *P. hamata* should not confused with *Zoophycos*, which occur in multiple levels, whereas *P. hamata* occurs on only one. *Phycosiphon geniculatum* differs from *P. hamata* and *P. incertum* by having radially arranged lobes with one margin well defined, usually concave, and the other margin is convex and highly lobate and indistinct. Naruse and Nifuku (2008) demonstrated that the elliptical burrow cross-sections of *Phycosiphon* could be used to determine the paleoslope inclination of a deposit.

Phycosiphon is interpreted a trace of a deposit-feeding, worm-like organism (Wetzel & Bromley, 1994). *Phycosiphon* occurs in continental-shelf slopes, submarine fans, turbidites, and flysch deposits (e.g., Uchman, 1998; Naruse & Nifuku, 2008; Rajchel & Uchman, 2012). Recent studies have found that *Phycosiphon* tracemakers are early colonizers of the upper portions of turbidite deposits when bottom waters are fully oxygenated (e.g., Wetzel & Uchman, 2001; Naruse & Nifuku, 2008). *Phycosiphon* ranges from the early Cambrian to recent (Fu, 1991; Naruse & Nifuku, 2008).

PHYCOSIPHON INCERTUM Fischer-Ooster, 1858
Figure 16.1–16.6

Material.—IBGS LG-M-007: seven specimens; IBGS PJ-M-019: five specimen, Miner's Hollow.

Diagnosis.—Small, oblique or parallel to bedding, spreiten-filled burrow systems comprised of protrusive U-shaped lobes with dark, fine-grained cores and light, coarse-grained mantles (Wetzel & Bromley, 1994; Głuszek, 1998; Uchman, 1998).

Description.—Mantled, endorelief burrows with elliptical to U-shaped cross sections. Light gray mantles 0.1–0.4 mm thick, average thickness 0.2 mm. Dark gray cores 0.3–1.0 mm thick, 1.1–7.8 mm wide.

Occurrence.—Two lithologies: (1) green, fine-grained siliciclastic sandstone, weathered to tan; and (2) laminated mudstone of alternating light-gray and dark-gray laminations. Laminations on IBGS PJ-M-019 are continuous with very little bioturbation occurring to disrupt them (*ii*2), but on IBGS LG-M-007, the laminations are moderately disrupted (*ii*3–4).

Associated ichnotaxa.—*Aulichnites* isp., *Dimorphichnus* isp., *Lockeia siliquaria*, *Protovirgularia* cf. *pennatus*, and *Treptichnus vagans*.

Discussion.—*Phycosiphon incertum* present on IBGS LG-M-007 in cross section show a light gray to white mantle and some spreite within the burrow fill (Fig. 16.1–16.4). Some spreiten are visible in longitudinal cross section (Fig. 16.1–16.2), but are most visible in specimens with transverse cross sections (Fig. 16.3–16.4). The sediment of IBGS LG-M-007 is mostly pale green to white fine-grained sandstone, while the burrow fill is composed of fine- to very fine-grained, gray to black sandstone. Sample IBGS PJ-M-019 has several specimens of *P. incertum* on the cut side of the samples (Fig. 16.5–16.6). The mantle surrounding some of the IBGS PJ-M-019 burrows is not very noticeable, possibly due to their small size and compaction.

Ichnogenus PLANOLITES Nicholson, 1873

Type ichnospecies.—*Planolites beverleyensis* Billings, 1862 (=*Planolites vulgaris* Nicholson & Hinde, 1875, junior synonym, Pemberton & Frey, 1982).

Diagnosis.—Unlined to rarely lined, rarely branching, straight to tortuous burrows with smooth to irregular walls and circular to elliptical cross sections; infill unstructured and may differ from host-rock lithology (Pemberton & Frey, 1982; Fillion & Pickerill, 1990; Uchman, 1998).

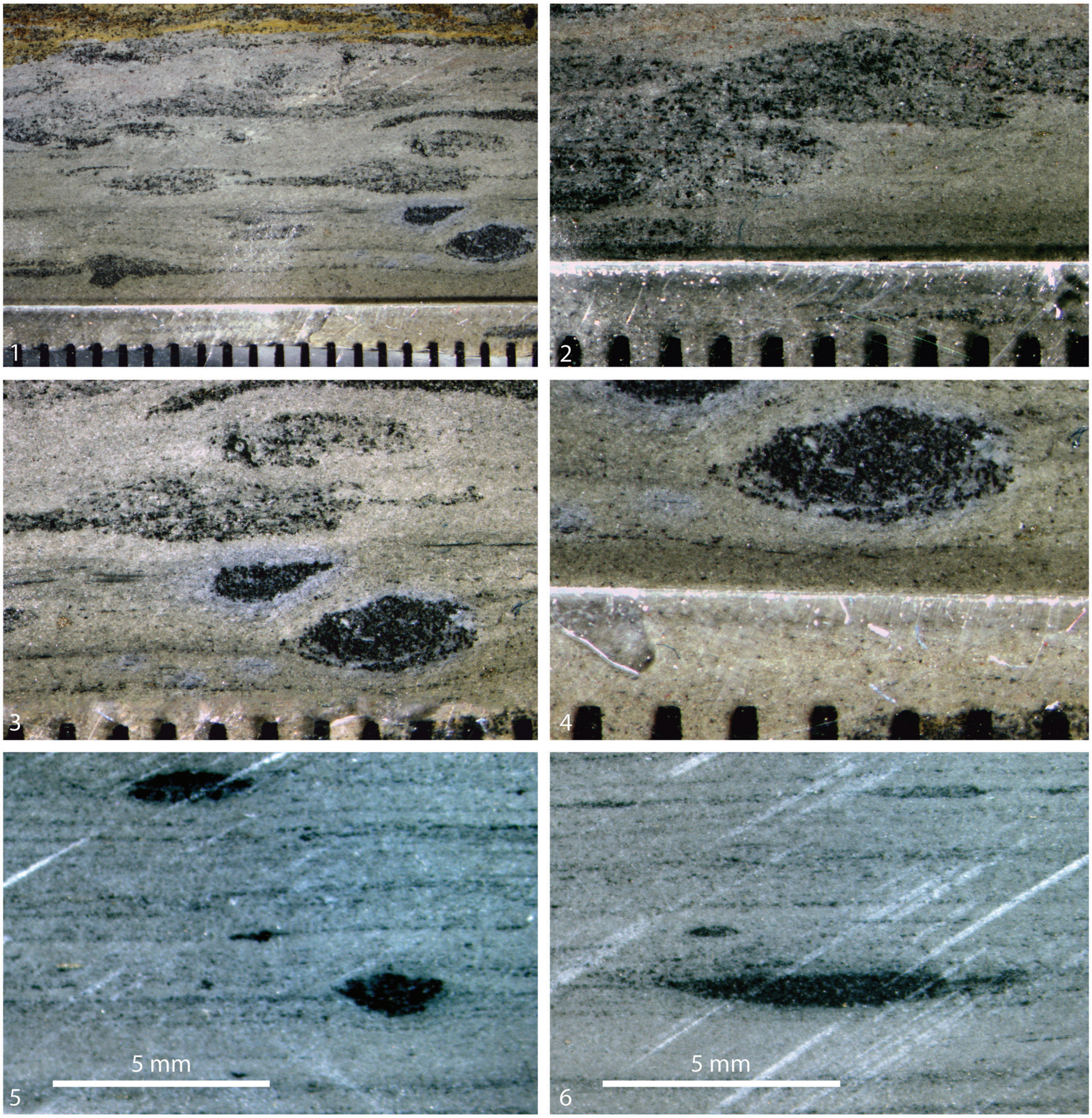

Figure 16. *Phycosiphon incertum* specimens from the Spence Shale. *1–4,* Full relief and cross sections of *P. incertum,* IBGS LG-M-007; *5–6,* Cross sections of *P. incertum,* IBGS PJ-M-019, Miner's Hollow; scale bars in mm.

Discussion.—Ichnotaxonomy still has numerous problems with differentiating between certain ichnotaxa, including *Palaeophycus* Hall, 1847, and *Planolites* (e.g., Osgood, 1970; Häntzschel, 1975; Pemberton & Frey, 1982). In an attempt to resolve those problems, Pemberton and Frey (1982) reexamined both ichnogenera and established standard diagnostic criteria for differentiating them: (1) burrows lack wall linings; and (2) burrows have different color and texture from host-rock lithology that indicate active infilling. Another criterion suggested to help identify *Planolites* is the lack of systematic branching or enlargements around branch sites (Fillion & Pickerill, 1990). Keighley and Pickerill (1995) argued against the use of active vs. passive infill and suggested that the presence or lack of a wall lining should be the primary diagnostic criterion for *Palaeophycus* and *Planolites*, respectively. Keighley and Pickerill (1997) also recommended synonymizing *P. montanus* under *P. beverleyensis* and argued that the size criterion used to separate the two ichnospecies was invalid; however, most authors have ignored the Keighley and Pickerill (1997) recommendation and continue to use both *P. beverleyensis* and *P. montanus* (e.g., Pickerill & Fyffe, 1999; Uchman, 1999; Hofmann & others, 2012).

Planolites is typically interpreted as the trace of a deposit-feeding marine or freshwater worm (e.g., Häntzschel, 1975; Fillion & Pickerill, 1990); however, soil arthropods and worms have been suggested as possible tracemakers in continental deposits (e.g., Ekdale, Bromley, & Loope, 2007; Hasiotis, 2004, 2008; Smith & others, 2008a, 2009). *Planolites* is a facies-crossing ichnogenus and has been report from shallow- to deep-marine and continental deposits (e.g., alluvial, fluvial, lacustrine, and eolian) (e.g., Chamberlain, 1971, 1975, 1977; Fillion & Pickerill, 1990; Keighley & Pickerill, 1997; Kim & others, 2005; Ekdale, Bromley, & Loope, 2007; Bohacs, Hasiotis, & Demko, 2007; Hembree & Hasiotis, 2007; Hofmann & others, 2012). *Planolites* ranges from the Ediacaran to recent (Häntzschel, 1975; Crimes, 1987, 1992; Uchman, 1998).

PLANOLITES ANNULARIUS Walcott, 1890
Figure 15.2

Material.—KUMIP 314229: two specimens, Miner's Hollow; IBGS PJ-M-001: four specimens, Miner's Hollow.

Diagnosis.—Horizontal, straight to curved, subcylindrical burrows with pronounced annulations (Pemberton & Frey, 1982; Fillion & Pickerill, 1990).

Description.—Simple, straight to curved burrows in concave epirelief or convex hyporelief with transverse constrictions forming numerous short chambers (1.1–2.0 mm long). Burrows 17.1–125.2 mm long, 0.8–1.5 mm wide. On IBGS PJ-M-001, a reddish brown halo is present along some burrows and extends 0.9–2.3 mm from burrow margin.

Occurrence.—Gray to dark gray, massive siliciclastic shale.

Associated ichnotaxa.—*Bergaueria hemispherica*, *Cruziana barbata*, and *Rusophycus carbonarius*.

Discussion.—The burrows were formed by peristaltic movement of a wormlike tracemaker that resulted in the serial-chambered expression (Pemberton & Frey, 1982). Most *P. annularius* specimens have a reddish brown oxidation halo surrounding the burrow, indicating poorly oxygenated sediments near the time of construction (e.g., Ekdale, Bromley, & Pemberton, 1984; Bromley, 1996; Forster, 1996) (see Fig. 15.2). One burrow has the reddish brown halo for about half its length and the entire width extending to ~3 mm from the burrow center, but also loses the annulated chambers where the halo is present. The change from an annulated burrow with or without a halo to a fully haloed, smooth burrow could be a transition from *P. annularius* to *P. montanus* representing a change in oxygen and nutrient availability in the sediment (e.g., Pemberton & Frey, 1982; Forster, 1996).

PLANOLITES BEVERLEYENSIS (Billings, 1862)
Figure 15.3–15.5

Material.—KUMIP 314223: one specimen, Antimony Canyon; KUMIP 314228: one specimen, Miner's Hollow;s IBGS LG-M-001: one specimen; IBGS LG-M-005: four specimens.

Diagnosis.—Large, smooth, straight to gently curved or undulated cylindrical burrows with unstructured backfill and lacking wall linings (Pemberton & Frey, 1982; Fillion & Pickerill, 1990; Keighley & Pickerill, 1995).

Description.—Convex hyporelief or concave epirelief, straight to gently curved cylindrical burrow; however, some are contorted and overlap. Burrows 10.3–50.4 mm long and 3.0–6.3 mm wide. No wall lining is visible.

Occurrence.—Light to dark gray (weathered to light brown or tan), siliciclastic silty shale.

Associated ichnotaxa.—*Cruziana problematica*, *Gyrophyllites kwassizensis*, *Lockeia siliquaria*, *Monomorphichnus lineatus*, *M.* cf. *multilineatus*, *Planolites montanus*, *Rusophycus carbonarius*, and *Treptichnus bifurcus*.

Discussion.—*Planolites beverleyensis* is typically differentiated from others ichnospecies of *Planolites* by its larger burrow diameter (> 5 mm), its generally straighter course, and a lack of annulations (Billings, 1862; Pemberton & Frey, 1982). Though most burrow diameters are < 5 mm, specimens assigned to *P. beverleyensis* are significantly larger and straighter than any specimen assigned to *P. montanus*. One specimen of *P. beverleyensis* appears to record a predation-prey interaction with a *Rusophycus* cf. *cerecedensis* (Fig. 15.5) (for discussion see *Rusophycus* cf. *cerecedensis* p. 34).

PLANOLITES MONTANUS Richter, 1937
Figures 10.3, 14.6, 15.6, 18.3, 18.6, 22.3

Material.—KUMIP 204523 A and B: four specimens, Miner's Hollow; KUMIP 314122: one specimen, Antimony Canyon; KUMIP 314222 B: 13 specimens, Miner's Hollow; KUMIP 314228: 11 specimens, Miner's Hollow; IBGS LG-M-010: four specimens; IBGS LG-M-011: four specimens; IBGS LG-M-012: two specimens; IBGS LG-M-013: three specimens; IBGS PJ-M-001: one specimen, Miner's Hollow; IBGS PJ-M-004: two specimens, Miner's Hollow; IBGS PJ-M-005: five specimens, Miner's Hollow float; IBGS PJ-M-007: six specimens, Miner's Hollow; IBGS PJ-M-010: three specimens, Miner's Hollow IBGS PJ-M-011: three specimens, Spence Tongue of the Lead Bell Shale, Oneida Narrows, Idaho; IBGS PJ-M-013: one specimen, Miner's Hollow; IBGS PJ-M-014: one specimen, Miner's Hollow; IBGS PJ-M-016: two specimens, Miner's Hollow; IBGS PJ-M-020: one specimen, Miner's Hollow; IBGS PJ-M-023: two specimens, Miner's Hollow; IBGS PJ-M-024: one specimen, Miner's Hollow; IBGS PJ-M-027: two specimens, Miner's Hollow; IBGS PJ-M-030: one specimen, Miner's Hollow; IBGS PJ-M-033: two specimens.

Diagnosis.—Relatively small, curved to tortuous, cylindrical to subcylindrical burrows lacking wall linings (Pemberton & Frey, 1982; Fillion & Pickerill, 1990; Keighley & Pickerill, 1995).

Description.—Small, smooth burrows that are generally straight but sometimes sharply bent, curved, or contorted. Burrows 12.5–73.2 mm long and 0.7–5.4 mm wide.

Occurrence.—Laminated light to dark gray or dark gray (weathered to tan or brown) to pale greenish gray, calcareous or siliciclastic silty shale.

Associated ichnotaxa.—*Archaeonassa fossulata*, *Cruziana problematica*, *Halopoa* aff. *imbricata*, *Lockeia siliquaria*, *Monomorphichnus lineatus*, *M.* cf. *multilineatus*, *Nereites* cf. *macleayi*, *Planolites beverleyensis*, *Rusophycus carbonarius*, *R.* cf. *cerecedensis*, *Treptichnus bifurcus*, and *Treptichnus vagans*.

Discussion.—*Planolites montanus* is one of the most common ichnofossils from the Spence Shale. Burrows assigned to this ichnotaxon exhibit simple, smooth margins, fill different from the host rock, a lack of distinct walls, and diameters typically < 5 mm. Some specimens of *P. montanus* occur in a *Treptichnus*-like morphology of short burrows that alternate very loosely around a central axis.

Ichnogenus PROTOVIRGULARIA M'Coy, 1850

Type ichnospecies.—*Protovirgularia dichotoma* M'Coy, 1850.

Diagnosis.—Unbranched, straight to slightly curved trails with medial ridge or furrow and paired, wedge-shaped, lateral projections from ridge or furrow (Han & Pickerill, 1994b).

Discussion.—*Protovirgularia* was originally interpreted by M'Coy (1850) as a body fossil of octocoral and graptolites. Han and Pickerill (1994b), Seilacher and Seilacher (1994), and Uchman (1998) have reviewed *Protovirgularia.* Han and Pickerill (1994b) reassessed the four previously established ichnospecies of *Protovirgularia*, and found that: (1) *P. dichotoma* M'Coy, 1850 was the only valid ichnospecies; (2) *P. mongraensis* Chiplonkar & Badve, 1970, and *P. nereitarum* (Richter, 1871) as junior synonyms of *P. dichotoma*; and (3) *P. harknessi* Lapworth, 1870, was *nomen nudum* and not valid because it was not described or figured when originally proposed. Seilacher and Seilacher (1994) demonstrated via neoichnological experiments that protobranch bivalves and scaphopods were the primary producers of *Protovirgularia* and also synonymized *Imbrichnus* Hallam, 1970, *Pennatulites* De Stefani, 1885, *Uchirites* Macsotay, 1967, and *Walcottia* Miller & Dyer, 1878, under *Protovirgularia*. Uchman (1998) also expanded *Protovirgularia* to include some ichnospecies of *Gyrochorte, Nereites, Rhabdoglyphus* Vassoevich, 1951, and *Tuberculichnus* Książkiewicz, 1977, as junior synonyms.

Protovirgularia is interpreted as a push-pull locomotion and feeding trace of bivalves and scaphopods (e.g., Han & Pickerill, 1994b; Seilacher & Seilacher, 1994). *Protovirgularia* has been reported from shallow marine, deep marine (e.g., turbidites), and brackish water deposits (e.g., deltas, estuaries, and tidal flats) (e.g., Han & Pickerill, 1994b; Seilacher & Seilacher, 1994; Carmona & others, 2010; Jackson, Hasiotis, & Flaig, 2016). *Protovirgularia* is sometimes suggestive of salinity, sedimentation rate, and turbidity fluctuations as well as possible oxygen depletion (Carmona & others, 2010). *Protovirgularia* ranges from the early Cambrian to recent (Seilacher & Seilacher, 1994; Orłowski & Zylińska, 2002).

PROTOVIRGULARIA DICHOTOMA M'Coy, 1850
Figure 17.1

Material.—KUMIP 314233: one specimen.

Diagnosis.—Straight, bilobate trails with medial furrow and paired, convex, chevronlike, wedge-shaped projections oblique from furrow.

Description.—Specimen 29.1 mm long and 4.1 mm wide. The chevronlike, wedge-shaped projections range 2.7–4.2 mm long and 1.5–2.3 mm wide. Projection sets have a 45–55° V-shaped angle. Faint striations are present on projections.

Occurrence.—Dark gray (weathered to tan), calcareous silty shale with very thin siliciclastic mud with possible swaley cross-stratification.

Associated ichnotaxa.—*Monomorphichnus lineatus* and *Treptichnus vagans*.

Discussion.—Though similar to *Didymaulichnus* Young, 1972, due to its bilobate shape and seemingly smooth projections, the *P. dichotoma* specimen has a chevronlike morphology most similar to *Protovirgularia* morphologic variant 5 of Carmona and others (2010, fig. 3.8 & 4) and experimental undertraces analogous to *P. dichotoma* illustrated by Seilacher and Seilacher (1994, pl. 1, fig. a) (Fig. 17.1). *Protovirgularia* specimens illustrated by Fernández, Pazos, and Aguirre-Urreta (2010) show intergradation between *P. dichotoma* and *P. rugosa*, and the lateral projections of the Spence Shale *P. dichotoma* are more oblique and wedgelike, and thus are more similar to *P. dichotoma*. However, the morphologic characteristic that separates *P. dichotoma* and *P. rugosa* is the presence of a *Lockeia*-like object at the termination of *P. rugosa* (*sensu* Seilacher & Seilacher, 1994; Uchman, 1998), which the Spence Shale *P. dichotoma* specimen lacks.

PROTOVIRGULARIA cf. PENNATUS (Eichwald, 1860)
Figure 6.5, Figure 17.2–17.4

Material.—KUMIP 204521 A and B: one specimen; IBGS PJ-M-019: Miner's Hollow.

Diagnosis.—Straight to winding, bilobate, chevronlike ribbon trace with medial ridge.

Description.—Chevronlike ribbon trace in convex hyporelief. Specimens 23.5–254 mm long and 2.9–11.2 mm wide. The lobes consist of thin, commalike to arcuate striations or may be plumoselike.

Occurrence.—Two lithologies: (1) laminated light to dark gray silty shale; and (2) dark gray (weathered to tan) to pale greenish gray, calcareous silty to sandy shale.

Associated ichnotaxa.—*Aulichnites* isp., *Dimorphichnus* isp., *Diplichnites* cf. *binatus*, *Diplichnites* cf. *govenderi*, *Lockeia siliquaria*, *Phycosiphon incertum*, and *Treptichnus vagans*.

Discussion.—*Protovirgularia* cf. *pennatus* specimen on IBGS PJ-M-019 has characteristics similar to two ichnospecies of *Protovirgularia* illustrated by Nara and Ikari (2011, fig. 3): *P. dichotoma* and *P. pennatus* (Fig. 17.2–17.4). The *Protovirgularia* cf. *pennatus* specimen has a medial ridge (convex hyporelief) along the length of the trace, which becomes more prominent near the open end of the trace, characteristic of most *Protovirgularia*, including *P. dichotoma*. The striations that form the lateral lobes are very thin and arcuate and similar to the striations of the *P. pennatus* that form the lateral appendages. The specimen on KUMIP 204521 is winding and has a plumoselike, arcuate striation pattern similar to specimens of *P. pennatus* (Uchman, 1998, fig. 67A) and *Protovirgularia* isp. (Knaust, 2007, fig. 7B).

Ichnogenus RUSOPHYCUS Hall, 1852

Type ichnospecies.—*Rusophycus clavatus* Hall, 1852, subsequent designation by Miller (1889, pg. 138).

Diagnosis.—Small to large bilobate mounds or depressions with parallel or merged lobes near the posterior; parallel to oblique to transverse striations; however, some specimens may be smooth (Crimes, 1970b, Osgood, 1970; Alpert, 1976a; Fillion & Pickerill, 1990; Keighley & Pickerill, 1996).

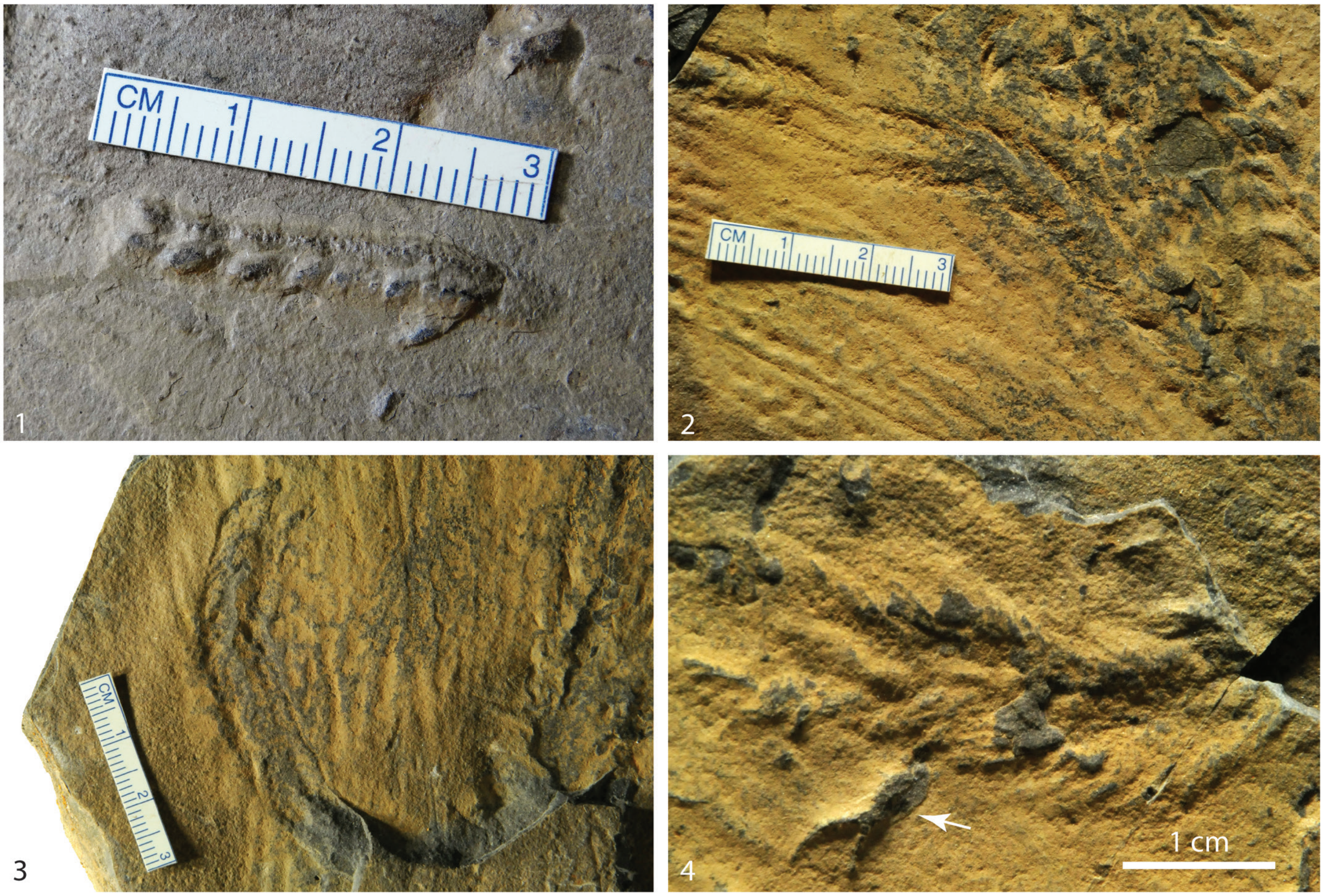

Figure 17. *Protovirgularia* specimens from the Spence Shale. *1, Protovirgularia dichotoma* in convex hyporelief, KUMIP 314233; *2–4*, *Protovirgularia* cf. *pennatus* in concave epirelief (*2–3*), in convex hyporelief (*4*) with *Diplichnites* cf. *govenderi,* KUMIP 204521 A and B; scale bar in cm.

Discussion.—Seilacher (1970) grouped *Rusophycus* under *Cruziana* and argued that they should be considered synonymous due to both being produced by the same tracemaker, trilobites. Seilacher also suggested retaining *Isopodichnus*—morphologically similar to both *Cruziana* and *Rusophycus*—for use as a facies indicator for brackish water. Most workers disagree with the Seilacher (1970) suggestion and maintain *Rusophycus* and *Cruziana* as separate ichnogenera (See *Cruziana* for full discussion p. 13). Similar to *Cruziana*, *Rusophycus* ichnospecies are separated primarily by striation pattern, but size, lobe morphology (i.e., orientation, ornamentation, shape), and tracemaker morphologic remnants are other criteria sometimes used (Crimes, 1970b; Osgood, 1970; Seilacher, 1970, 2007).

Rusophycus is generally interpreted as a resting or hiding trace (e.g., Crimes 1970b; Osgood, 1970; Seilacher, 1970), but also suggested to be a hunting (e.g., Jensen, 1990; Tarhan, Jensen, & Droser, 2011) or nesting (brooding) trace (e.g., Fenton & Fenton, 1937d). Tracemakers of *Rusophycus* are commonly interpreted as arthropods, such as trilobites and crustaceans, but gastropods, and even some vertebrates have been proposed (e.g., Crimes, 1970a; Seilacher, 1970; Bromley & Asgaard, 1979; Seilacher, 2007). Post-Triassic *Rusophycus* are not considered produced by trilobites (Fillion & Pickerill, 1990). Jones (2016) showed small bilobate modern bat manus and pes track impressions similar to small, smooth *Rusophycus* (e.g., *R. carbonarius*), meaning that bats may have produced some *Rusophycus* in Cenozoic water-margin environments (e.g., fluvial, lake plain, crevasse-splay deposits). *Rusophycus* is a facies-crossing ichnogenus reported from shallow marine (e.g., intertidal, lagoon), deep marine (e.g., slope, basin), brackish, lacustrine, and fluvial deposits (e.g., Crimes, 1970b; Seilacher, 1970; Hakes, 1976, 1985; Bromley & Asgaard, 1979; Pollard, 1985; Pickerill, 1995; Garvey & Hasiotis, 2008; Jackson, Hasiotis, & Flaig, 2016). *Rusophycus* ranges from the Cambrian to recent (e.g., Crimes, 1987; Hasiotis, 2012).

RUSOPHYCUS CARBONARIUS (Dawson, 1864)
Emended by Keighley & Pickerill, 1996
Figure 18.1–18.3, 18.5

Material.—KUMIP 204523 A and B (part and counterpart); 39 specimens, Miner's Hollow; KUMIP 314222 B: one specimen, Miner's Hollow; KUMIP 314223: two specimens, Antimony Canyon; KUMIP 314228: eight specimens, Miner's Hollow; KUMIP 314229: three specimens, Miner's Hollow; IBGS LG-M-011: one specimen; IBGS PJ-M-007: 13 specimens, Miner's Hollow; IBGS PJ-M-008: one specimen, Miner's Hollow; IBGS PJ-M-013: one specimen, Miner's Hollow; IBGS PJ-M-018: two specimens, Miner's Hollow; IBGS PJ-M-023: two specimens, Miner's Hollow.

Diagnosis.—Small, bilobate depressions (concave epirelief) or mounds (convex hyporelief) with parallel to slightly gaping lobes; transverse to oblique, fine striations that do not extend beyond the lobe margin, or may be smooth (modified from Keighley & Pickerill, 1997, 1998).

Description.—Small bilobate depressions and mounds with a central furrow, typically smooth but may have fine, oblique striations. Burrows 3.0–11.2 mm long and 2.5–6.5 mm wide at the widest point. Only one specimen has fine striations with a 97–120° V-shaped angle.

Occurrence.—Two lithologies: (1) gray (weathered to brown), laminated calcareous sometimes with brown siliciclastic sand; and (2) gray, siliciclastic silty shale, sometimes with brown carbonate sand.

Associated ichnotaxa.—*Bergaueria hemispherica*, *Cruziana barbata*, *C. problematica*, *Gyrophyllites kwassizensis*, *Lockeia siliquaria*, *Monomorphichnus lineatus*, *M.* cf. *multilineatus*, *Planolites annularis*, *P. beverleyensis*, *P. montanus*, *Rusophycus* cf. *cerecedensis*, *Sagittichnus lincki*, *Treptichnus bifurcus*, and *T. vagans*.

Discussion.—For a full list of synonymy, refer to Keighley and Pickerill (1996). Most *Rusophycus* specimens from the Spence Shale were assigned to *R. carbonarius* due to their small size, coffee bean-like shape, and the smoothness of the paired lobes. Normally, the main criterion for classifying ichnospecies of *Rusophycus* is the surficial striations present on the lobes. *Rusophycus carbonarius* is characterized by thin, transverse to oblique striations, but Keighley and Pickerill (1996) included small, smooth forms under *R. carbonarius* because they noted smooth and striated forms on the same samples. Keighley and Pickerill (1997) suggested that the difference between the two forms was taphonomic, rather than ethologic. Supporters of the Seilacher (1970) suggestion to include *Rusophycus* under *Cruziana* and the retention of *Isopodichnus* would likely identify *R. carbonarius* as *Isopodichnus problematicus* due to its small size and the lack of striations.

Rusophycus carbonarius specimens present in the Spence Shale are significantly smaller than any *C. problematica* specimen. This is most noticeable on KUMIP 204523 and PJ-M-007 (see Fig. 10.1), where significant differences in width between the two ichnogenera suggest that the same organism did not produce the two ichnofossils (*sensu* Fortey & Seilacher, 1997). We propose that agnostoid trilobites or small (juvenile) polymeroid trilobites likely produced the *Rusophycus carbonarius* specimens, whereas medium-sized (adult) polymeroid trilobites likely produced *C. problematica* specimens. Specimens are oriented in a nearly single direction between 315–350° (relative to the longer cut side of KUMIP 204523B), whereas the *C. problematica* show an overlapping, curvilinear pattern, suggesting that the bottom currents were relatively strong for smaller organisms and the *R. carbonarius*-tracemakers had to orient themselves to the current to remain stable (*sensu* Pickerill, 1995). Pickerill (1995) illustrated multiple oriented *Rusophycus* and interpreted their alignment was due to maintaining a rheotactic orientation in waters with significant bottom currents. Multiple specimens of *R. carbonarius* crosscut several *C. problematica* specimens suggesting that the *R. carbonarius* tracemakers may have occupied the area of KUMIP 204523 after the excavation of the *C. problematica.*

RUSOPHYCUS cf. PUDICUS Hall, 1852

Figure 18.4

Material.—IBGS PJ-M-009: one specimen, Spence Shale float, High Creek Canyon, Bear River Range, Utah, USA

Diagnosis.—Small- to medium-sized bilobate depressions (concave epirelief) or mounds (convex hyporelief) with parallel to slightly gaping lobes, which widen anteriorly, and transverse to oblique, fine to well-developed striations; the medial furrow well developed and increases in depth and width toward one end, generally extending to entire length of the trace (Osgood, 1970; Fillion & Pickerill, 1990).

Description.—Convex, bilobate hyporelief mound with a central furrow, an anterior gape, and a merged posterior. Specimen 14.6 mm long, 9.7 mm wide, and 4.3 mm deep. Central furrow 1.4 mm wide.

Occurrence.—Tan to brown, siliciclastic shale with brown, dark gray, or black dendrites.

Associated ichnotaxa.—*Sagittichnus lincki* and *Treptichnus bifurcus.*

Discussion.—Only a single specimen of *Rusophycus* cf. *pudicus* was found in the Spence Shale. Like specimens of *R. carbonarius*, the *R.* cf. *pudicus* specimen has smooth lobes. The assignment to *R.* cf. *pudicus* is based on the depth increase of the medial furrow, length of furrow equaling the length of the trace, and the wide, well-developed lobes that taper to one end. Within the anterior gape of the central furrow, there is a raised area that may be a poorly preserved impression of the tracemaker coxa. The *R. pudicus* specimens illustrated by Osgood (1970) were much larger than the specimens shown here, but the size difference in the Spence Shale material could be due to decreased oxygenation or just a smaller tracemaker.

RUSOPHYCUS cf. CERECEDENSIS Crimes & others, 1977

Figure 15.5, Figure 18.6

Material.—KUMIP 314228: two specimens, Miner's Hollow; IBGS PJ-M-023: one specimen, High Creek Canyon, Bear River Range, Utah, USA.

Diagnosis.—Medium-sized bilobate mound (convex hyporelief); lobes may be rounded or tapered to points and gape anteriorly; individual lobes may be smooth or with oblique to transverse striations.

Description.—Convex bilobate hyporelief mounds 12.5–28.9 mm long, 10.4–15.4 mm wide, and 1.5 mm deep. Medial furrow 1.9 mm wide but widens to 6.5 mm anteriorly with a ~60° V-shaped angle. Oblique striations form ~100° V-shaped angles.

Occurrence.—Brown to gray siliciclastic silty to sandy shale.

Associated ichnotaxa.—*Cruziana problematica*, *Lockeia siliquaria*, *Monomorphichnus lineatus*, *M.* cf. *multilineatus*, *Planolites beverleyensis*, *P. montanus*, and *R. carbonarius*.

Discussion.—Specimens assigned herein to *Rusophycus* cf. *cerecedensis* are distinguished from *R. carbonarius* and *R.* cf. *pudicus* by their larger size and rounded to tapered lobe shape. One specimen possibly records a predator-prey interaction with *P. beverleyensis* (see Fig. 15.5), similar to the association of *R. carbonarius* and *P. montanus* (see Fig. 18.3) and to other such associations of *Rusophycus* and simple burrows (e.g., *Helminthopsis*, *Palaeophycus*, or

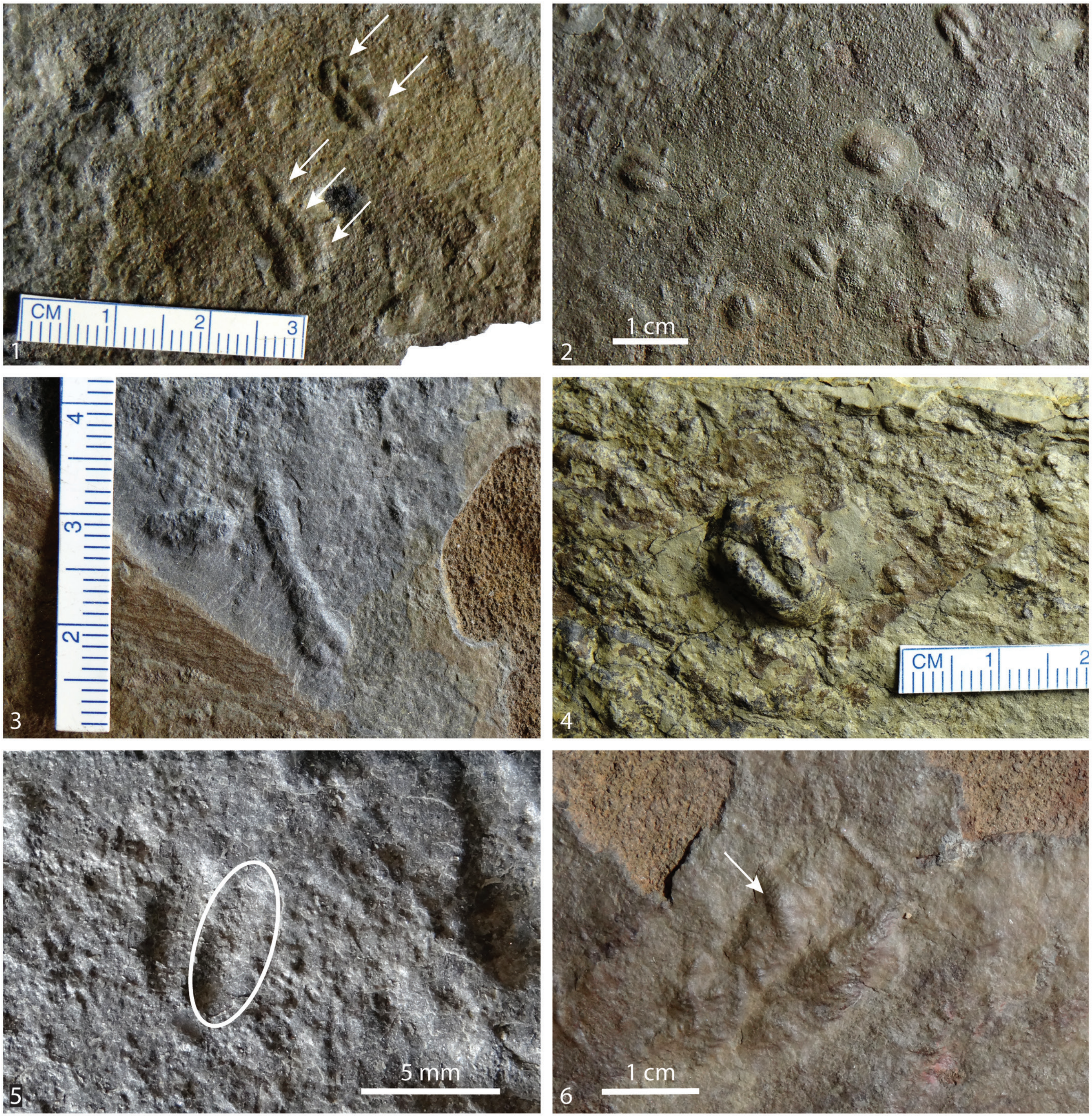

Figure 18. *Rusophycus* specimens from the Spence Shale. *1,* Overlapped, individual *R. carbonarius* (arrows) forming pseudoribbonlike morphology, KUMIP 204523 A and B, Miner's Hollow; *2, Rusophycus carbonarius* in convex hyporelief, IBGS PJ-M-007, Miner's Hollow; *3, Planolites montanus* terminating at a *R. carbonarius* in convex hyporelief, IBGS PJ-M-023, Miner's Hollow; *4, Rusophycus* cf. *pudicus* in convex hyporelief, IBGS PJ-M-009, Miner's Hollow; *5, Rusophycus carbonarius* with faint striations (circle) on one lobe in concave epirelief, IBGS PJ-M-023, Miner's Hollow; *6, Rusophycus* cf. *cerecedensis* with *P. montanus* on lobe (arrow), IBGS PJ-M-023, Miner's Hollow; scale *1–4, 6* in cm; *5* in mm.

Planolites) (e.g., Jensen 1990; Tarhan, Jensen, & Droser, 2011). Another specimen has a *P. montanus* burrow oriented at an oblique angle on one lobe (Fig. 18.6), but since the burrow extends into the surrounding host rock, the association is likely not predation.

Ichnogenus SAGITTICHNUS Seilacher, 1953b

Type ichnospecies.—*Sagittichnus lincki* Seilacher, 1953b.

Diagnosis.—Small, subcircular to ovoid to arrowhead-shaped, convex mounds (hyporelief) or concave pits (epirelief), usually with medial keel; occurring in small to large groups; medial keel may or may not be present (Häntzschel, 1975; Głuszek, 1995; Garvey & Hasiotis, 2008).

Discussion.—*Sagittichnus* is described as small, keeled arrowhead-shaped pits and mounds that are usually interpreted as resting traces of an unknown tracemaker (Seilacher, 1953b; Głuszek, 1995; Garvey & Hasiotis, 2008). Bromley and Asgaard (1979) reported specimens from Triassic fresh to brackish lacustrine deposits of Greenland that resembled *Sagittichnus* but interpreted them as inorganic tool marks, and thus invalid; however, other authors disagree and maintain *Sagittichnus* as a valid ichnogenus (e.g., Głuszek, 1995; Garvey & Hasiotis, 2008). A recent neoichnological study by Retrum, Hasiotis, and Kaesler (2011) showed freshwater ostracodes producing *Sagittichnus*-like morphologies. *Sagittichnus* has also been associated with small arthropod trackways (Głuszek, 1995). *Sagittichnus* is similar to manus and pes track impressions of modern bat trackways (Jones, 2016). *Sagittichnus* may occur with or grade into deposit feeding, hiding, or resting traces like *Rusophycus* (Garvey & Hasiotis, 2008). *Sagittichnus* has been reported from shallow marine and freshwater to brackish continental deposits (e.g., estuarine, fluvial, lacustrine) (e.g., Bromley & Asgaard, 1979; Głuszek, 1995; Garvey & Hasiotis, 2008; Jackson, Hasiotis, & Flaig, 2016). *Sagittichnus* ranges from the Cambrian to recent (Bednarczyk & Przybyołwicz, 1980; Retrum, Hasiotis, & Kaesler, 2011; Jackson, Hasiotis, & Flaig, 2016).

SAGITTICHNUS LINCKI Seilacher, 1953b
Figure 13.4, Figure 19.1–19.2

Material.—IBGS LG-M-002: five specimens, Winter Hollow, Box Elder Mountain; IBGS LG-M-003: 20 specimens; IBGS LG-M-013: 15 specimens, Antimony Canyon; IBGS PJ-M-025: 15 specimens, Spence Shale Float, Cataract Canyon.

Diagnosis.—Small, subcircular to ovoid to arrowhead-shaped, convex mounds lacking discrete medial keels (Garvey & Hasiotis, 2008).

Description.—Small, convex hyporelief mounds without medial keel or furrow. Specimens 1.0–2.7 mm long and 0.7–4.6 mm wide.

Occurrence.—Tan to dark gray, carbonate or siliciclastic shale.

Associated ichnotaxa.—*Bergaueria hemispherica, Gyrophyllites kwassizensis*, *Lockeia siliquaria*, *Teichichnus* cf. *nodosus*, and *Treptichnus bifurcus.*

Discussion.—Specimens were assigned to *Sagittichnus* due to their small, subrounded to ovoid-shaped, convex-mound (hyporelief) morphology, and their highly concentrated groupings (Fig. 19.1–19.2). No specimen had the characteristic medial keel (finlike structure) preserved in either epi- or hyporelief. Most specimens are ovoid in shape, but some show a subrounded to arrowhead shape. Also present on IBGS LG-M-003, alongside some *S. lincki,* is an ovoid-shaped, convex mound that we consider *Lockeia* for its noticeably larger size than the surrounding *Sagittichnus*, the lack of a medial keel, and its tapered ends.

Ichnogenus SCOLICIA de Quatrefages 1849

Type ichnospecies.—*Scolicia prisca* de Quatrefages, 1849.

Diagnosis.—Variable and selectively preserved, simple, winding to meandering to coiling, bilobate or trilobate backfilled burrows; may have one or two parallel, locally discontinuous strings along base; area between strings flat to slightly convex; cross sections circular to oval; geopetal meniscate backfill common but massive burrow infill also common (Häntzschel, 1975; Uchman, 1995).

Discussion.—There are many ichnogenera with morphologies similar to *Scolicia*, informally grouped in the Scolicia Group by Häntzschel (1975, p. 106). Many ichnotaxa from the Scolicia Group were later synonymized with *Scolicia* (e.g., Uchman, 1995). Plaziat and Mahmoudi (1988) suggested restricting *Scolicia* to concave epirelief expressions and retaining *Subphyllochorda* Götzinger & Becker, 1932 for convex hyporeliefs of echinoid traces; however, this complicates ichnotaxonomy more than it helps, and thus, subsequent authors have rejected this suggestion (e.g., Uchman, 1995, 1998; Fu & Werner, 2000).

Scolicia is commonly interpreted as a locomotion or deposit-feeding trace (e.g., Fu & Werner, 2000); however, some authors have interpreted *Scolicia* to be a grazing trace (e.g., Uchman, 1995). *Scolicia* is commonly interpreted as the product of irregular echinoids in the Mesozoic and Cenozoic (Plaziat & Mahmoudi, 1988; Uchman, 1995, 1998), whereas Paleozoic producers were likely gastropods (e.g., Götzinger & Becker, 1932; Häntzschel, 1975; Książkiewicz, 1977). In continental environments since the Devonian, producers were also likely gastropods (e.g., Hasiotis, 2004, 2008; Ash & Hasiotis, 2013). *Scolicia* has been reported from shallow marine as well as deep marine deposits, including turbidites (Uchman, 1995; Fu & Werner, 2000); however, Fu and Werner (2000) suggested that most shallow marine *Scolicia* are commonly destroyed by overprinting of deep-penetrating traces. *Scolicia* tracemakers preferred fine sandy to coarse silty settings, suggesting a preference for lower energy environments (Fu & Werner, 2000). *Scolicia* ranges from the Cambrian to recent (e.g., Häntzschel, 1975; Fu & Werner, 2000).

SCOLICIA isp.
Figure 20.1–20.6

Material.—IBGS PJ-M-032: four specimens, Miner's Hollow, Wellsville Mountains, Utah, USA.

Diagnosis.—Short to elongated, cylindrical to subcylindrical burrows in endorelief; undertrace in concave epirelief and convex hyporelief, some may be bilobate with basal medial furrow.

Description.—Light to medium brown to gray burrows 17.6–33.1 mm wide, 5.0–14.6 mm thick, with dark gray burrow margins 0.8–2.7 mm thick. Burrow infills are subangular to subrounded, moderately well-sorted, fine to medium carbonate sand with small reddish brown to red grains and large, very euhedral, dark grains with penetration twinning.

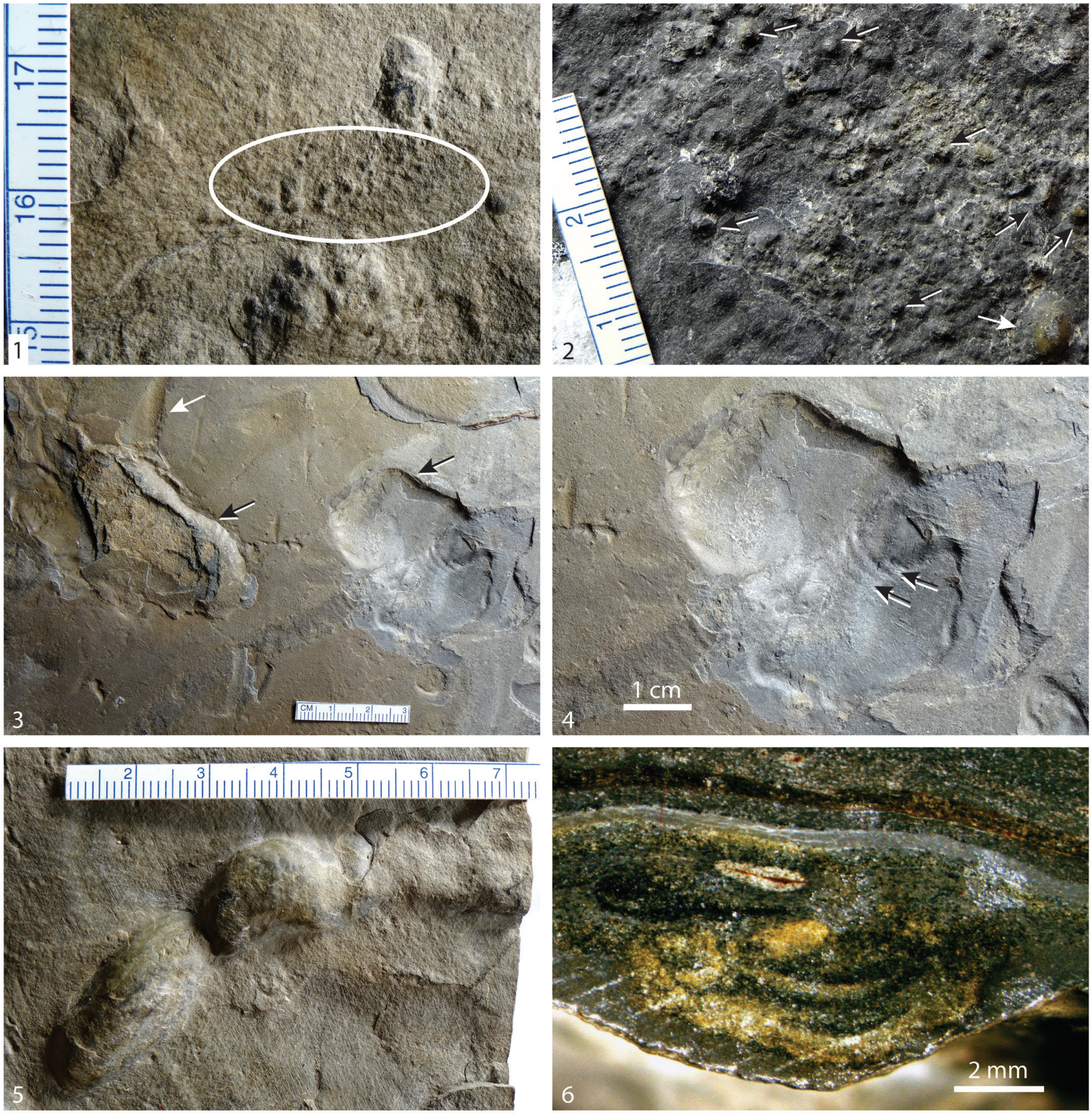

Figure 19. *Sagittichnus, Taenidium,* and *Teichichnus* specimens from the Spence Shale. *1,* Small field of *Sagittichnus lincki,* convex hyporelief, IBGS PJ-M-025; *2,* field of *Sagittichnus lincki* (black arrows) with *Lockeia siliquaria* (white arrow) in convex hyporelief, IBGS LG-M-003; *3, Taenidium* cf. *satanassi* crosscut by *Archaeonassa jamisoni* isp. nov. (black arrows) and insertion furrow (white arrow) in partial endorelief, IBGS PJ-M-002, Miner's Hollow; *4, Taenidium* cf. *satanassi* with meniscate backfill (arrows) in partial endorelief, IBGS PJ-M-002, Miner's Hollow; *5,* Segmented *Teichichnus* cf. *nodosus* in convex hyporelief, IBGS PJ-M-029; *6,* Cross section of *Te.* cf. *nodosus* (*5*) showing characteristic gutter-shaped spreite; scale *1–5* in cm; *6* in mm.

Occurrence.—Light to dark gray, laminated siliciclastic mudstone. Laminations are < 3 mm thick. Soft-sediment deformation is present locally around the burrow with flame structures penetrating or deforming the burrow margin. Laminations above and below the *Scolicia* isp. lack significant bioturbation but several small burrows are present indicating an *ii*2, whereas the layer with the *Scolicia* specimen has an *ii*4–5.

Associated ichnotaxa.—None.

Discussion.—Specimens assigned to *Scolicia* (Fig. 20.1–20.2) lack the diagnostic basal bilobate or trilobate shape or double drainage furrows. Cross sections reveal four elliptical burrows with irregularly shaped margins filled with a light to medium brown to gray, fine to medium sand in a matrix of laminated, light gray silt to fine sand (Fig. 20.3–20.6). The burrow margins are composed of dark gray, fine to medium sand (Fig. 20.3). One burrow appears bilobate from presence of a possible medial furrow composed of a wedge of light gray mud partially separating the burrow into two lobes (Fig. 20.4); however, the medial ridge may be due to compaction and soft-sediment deformation (e.g., flame structures) as other burrows have similar structures penetrating them from the sides. Also present is possible fecal-drainage canal near the base of one lobe, formed by a circle of dark sand grains with a brown core (Fig. 20.4). The irregularity of the dark burrow margins may also be the result of soft-sediment deformation and postdepositional diagenesis. The burrow infill has multiple coarse, angular, dark grains that may have resulted from recrystallization during diagenesis, as some of the grains are very euhedral and one grain appears to exhibit penetration twinning (Fig. 20.5–20.6).

Ichnogenus TAENIDIUM Heer, 1877

Type ichnospecies.—*Taenidium serpentinum* Heer, 1877.

Diagnosis.—Unlined to thinly lined, unbranched, straight to sinuous, cylindrical burrows with meniscate segmented burrow fill (D'Alessandro & Bromley, 1987).

Discussion.—Prior to D'Alessandro and Bromley (1987) reexamining the original descriptions and type material of *Muensteria* Sternberg, 1833 and *Taenidium* Herr*,* 1877, most workers used *Muensteria* for unbranched, unlined meniscate burrows, whereas *Taenidium* was used for branching meniscate burrows. *Muensteria* was considered invalid as the original description was confusing and included algae, coprolites, and several forms of *Chondrites* Sternberg, 1833 (D'Alessandro & Bromley, 1987). *Taenidium* was recommended for unbranched meniscate burrows previously described as *Muensteria* and a new ichnogenus, *Cladichnus*, was erected for meniscate burrows with primary successive branching or radiating systems (D'Alessandro & Bromley, 1987).

Keighley and Pickerill (1994) reviewed *Beaconites* Vialov, 1962, and compared it to other meniscate-backfilled burrows, *Ancorichnus* Heinberg, 1974, and *Taenidium*. They considered *Beaconites barretti* Bradshaw, 1981, as an unlined, unwalled meniscate burrow belonging to *Taenidium* and argued that the ends of the menisci do not form a wall or lining. Many authors followed Keighley and Pickerill (1994) for the use of *Taenidium barretti* (e.g., Schlirf, Uchman, & Kümmel, 2001; Keighley & Pickerill, 2003; Buatois & others, 2007).

Beaconites barretti is valid and still retained by many authors (e.g., Morrissey & Braddy, 2004; Smith & Hasiotis, 2008; Smith & others, 2008b; Counts & Hasiotis, 2009) because its architectural morphology is clearly distinct from *Taenidium*, rejecting the synonymy of most backfilled burrows into *Taenidium* by Keighley and Pickerill (1994). *Beaconites* is an unlined, tightly spaced backfilled meniscate burrow where the backfills merge laterally to form a crenulated burrow wall, representing the remnant of an open cell as it was moved through the sediment. We find the Keighley and Pickerill (1994) definitions of walls and linings to be confusing and inappropriate to all backfilled-burrow morphologies. Keighley and Pickerill (1994) considered backfilled burrows to not have true walls or linings as they considered simple excavation to not be a form of active construction, their requirement for walls and linings. They also interchanged the terms wall and lining, causing their definitions and usage to become muddled. Linings are only one possible type of wall structure (*sensu* Bromley, 1996), whereas Keighley and Pickerill (1994, fig. 1) considered all walled ichnofossils to have linings or mantles. A wall is the outermost margin of the area the tracemaker occupied—regardless of its active or passive excavation or construction (*contra* Keighley & Pickerill, 1994)—where the burrow infill contacts the matrix (*sensu* Morrissey & Braddy, 2004). Smith and others (2008b) argued that the overlapping of menisci form a crenulated, but unlined, wall in *B. barretti* reflecting active excavation of the sediment by the tracemaker, relocating it to the rear of the active cell, and compacting it to form the rear wall. We, therefore, follow Smith and others (2008b) for the retention of *Beaconites barretti* and definitions of walls vs. lining. *Taenidium* should be restricted to burrows that exhibit thick, regularly spaced meniscate backfill that is symmetrical about the axis of the burrow, which is unlined and unbranched (D'Alessandro & Bromley, 1987; Smith & others, 2008b). Prior to the inclusion of *B. barretti* by Keighley and Pickerill (1994), *Taenidium* was only described from marine deposits. *Taenidium* reported from continental deposits (e.g., Savrda & others, 2000; Buatois & Mángano, 2002, 2007, 2011; Krapovickas & others, 2009; Scott & Smith, 2015) actually belong to: (1) *Naktodemasis* Smith & others, 2008b, if the thin meniscate backfill are organized into discreet packages; (2) *Beaconites*, if the menisci are uneven, alternate around a central axis, and not organized into discreet packages; or (3) *Ancorichnus* Heinberg, 1974, if a mantle is present (e.g., Smith & others, 2008b; Counts & Hasiotis, 2009; Morshedian, MacEachern, & Dashtgard, 2012; Gingras & others, 2016; Harris & others, 2016).

Taenidium is interpreted as a deposit-feeding trace of marine worms (Gevers & others, 1971; Keighley & Pickerill, 1994; Smith & others, 2008b). *Taenidium* has been reported from shallow- to deep-marine deposits (Keighley & Pickerill, 1994, fig. 5; Smith & others, 2008b; Jackson, Hasiotis, & Flaig, 2016). *Taenidium* has been reported from the Vendian (i.e., Ediacaran) by Germs (1972) and Jenkins (1995); however, Jensen, Droser, and Gehling (2006), considered them as a cast of *Cloudina* and a tubular fossil, respectively. We follow the interpretation of Germs (1972) and Jenkins (1995) based on the similarity of the morphologies to *Taenidium*. Therefore, *Taenidium* ranges from the Ediacaran to recent (e.g., Germs, 1972; Crimes, 1992; Jenkins, 1995; Uchman, 1998; Jackson, Hasiotis, & Flaig, 2016).

TAENIDIUM cf. SATANASSI D'Alessandro & Bromley, 1987

Figure 19.3–19.4

Material.—IBGS PJ-M-002: one specimen, Miner's Hollow; IBGS PJ-M-005: one specimen, Spence Shale float, Miner's Hollow.

Diagnosis.—Long, slightly sinuous to straight burrow with uniform, evenly spaced, meniscate backfill; meniscate packages shorter than burrow diameter and filled with alternating sediment types (D'Alessandro & Bromley, 1987).

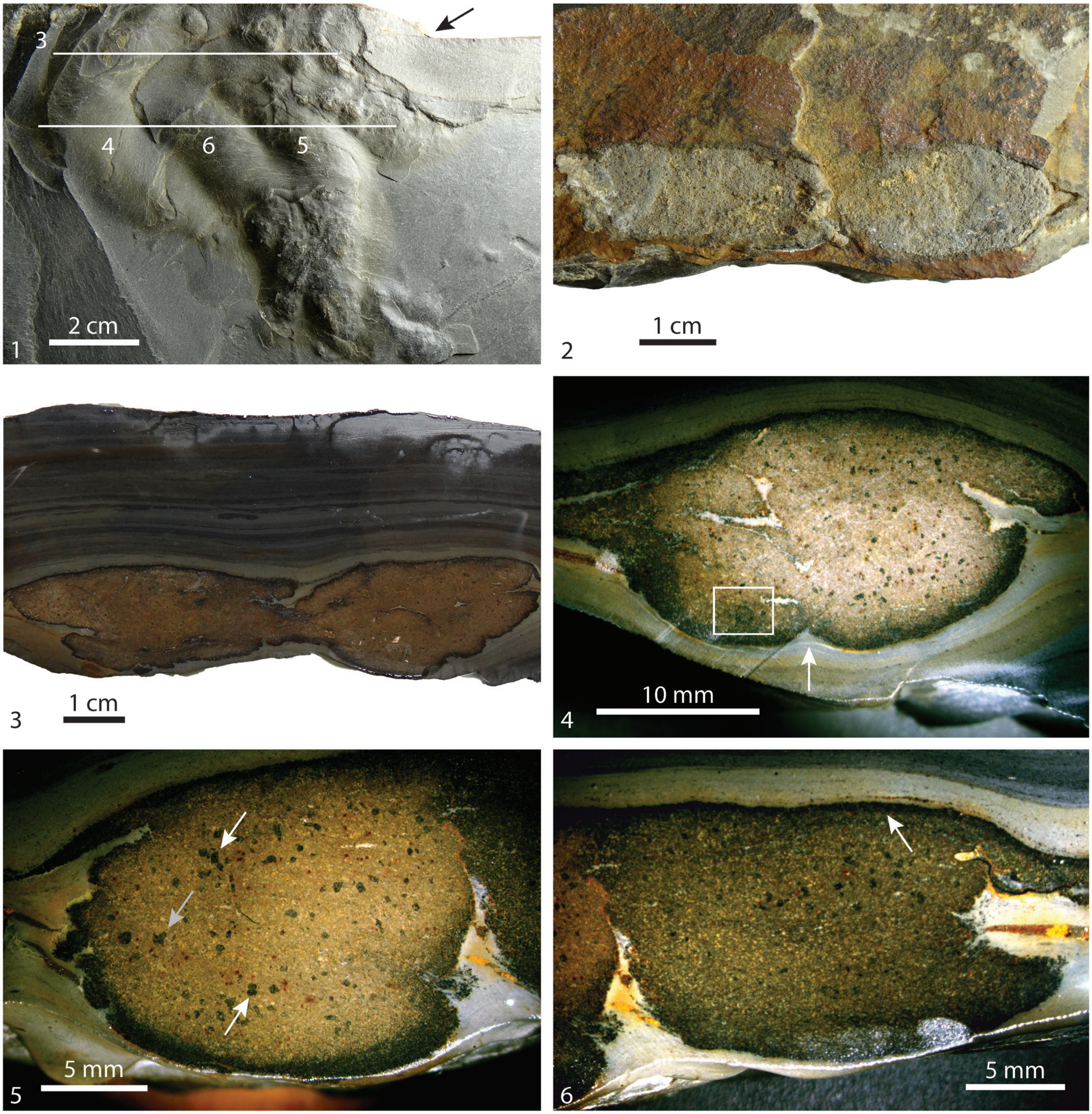

Figure 20. *Scolicia* specimens from the Spence Shale. *1,* Plan view of *Scolicia* isp. specimens with cross-section axis (lines) and weathered edge (arrow), PJ-M-032, Miner's Hollow; *2,* weathered edge of specimen with two *Scolicia* isp. burrows exposed; *3,* cross section of burrows near the weathered edge, note irregular burrow margins; *4–6, Scolicia* isp. cross-sections with variably colored infill and associated soft-sediment deformation; *4, Scolicia* isp. with light tan infill with possible basal medial furrow (arrow) and interpreted fecal drainage canal (box); *5, Scolicia* isp. with tan infill, thick dark-gray burrow margin, and coarse euhedral grains (white arrows) with possible twinning (gray arrow); *6,* gray-brown *Scolicia* isp. with thin burrow margin (arrow) and coarse grains.

Description.—Straight to gently curved, endorelief burrow with gray meniscate backfill and brown to purple weathered infill. Burrows 152.2–159.4 mm long, 6.3 mm wide; burrow menisci ~1.5 mm thick and uniform.

Occurrence.—Two lithologies: (1) tan to light brown, siliciclastic silty shale; and (2) gray, calcareous shale.

Associated ichnotaxa.—*Archaeonassa jamisoni*, *Phycodes curvipalmatum*, and *Planolites montanus*.

Discussion.—The long, mostly straight burrow on IBGS PJ-M-002 was assigned to *Taenidium* cf. *satanassi* due to the presence of meniscate backfill exposed by a large ovoid depression, herein designated as *Archaeonassa jamisoni*. Exposed menisci are shorter than the burrow diameter but lack the sediment alternation characteristic of *T. satanassi* (Fig. 19.3–19.4). The rest of the specimen occurs in endorelief and shows no clear internal structure; however, the purple coloration of the weathered burrow infill has a slight serrated pattern near the burrow margins, possibly a diagenetic remnant of the meniscate backfill. The specimen of *Taenidium* cf. *satanassi* on IBGS PJ-M-005 is completely in endorelief, revealing no internal morphology, and is in close proximity to several *A. jamisoni* specimens.

Ichnogenus TEICHICHNUS Seilacher, 1955b

Type ichnospecies.—*Teichichnus rectus* Seilacher, 1955b, by original monotypy.

Diagnosis.—Long, wall-shaped, septate structures consisting of stacks of gutter-shaped laminations (Seilacher, 1955b; Fillion & Pickerill, 1990).

Discussion.—*Teichichnus* was introduced for vertically stacked, horizontal burrows with spreiten and thought to be produced by upwardly shifting deposit feeders (Seilacher, 1955b; Fillion & Pickerill, 1990). *Teichichnus* has been reported to intergrade with multiple ichnofossils: *Cruziana*, *Ophiomorpha* Lundgren, 1891, *Phycodes*, *Rhizocorallium* Zenker, 1836, and *Thalassinoides* Ehrenberg, 1844 (e.g., Fillion & Pickerill, 1990; Loope & Dingus, 1999). *Teichichnus* has been noted for its similarity to *Trichophycus* Miller & Dryer, 1878, due to the presence of gutter-shaped spreite (e.g., Osgood, 1970; Frey & Howard, 1985; Geyer & Uchman, 1995), but can be typically distinguished by the more planar shape of the spreite and a lack of fine striations present on the outside of the burrow (e.g., Fillion & Pickerill, 1990; Jensen, 1997). Some *Teichichnus* have been reported to have surficial striations (e.g., Jensen, 1997).

Teichichnus is typically interpreted as a deposit-feeding or grazing trace of annelids and arthropods (e.g., Chisholm, 1970; Fillion & Pickerill, 1990). *Teichichnus* primarily occurs in shallow-marine deposits (e.g., tidal flats and deltas) but some have been reported from deep-marine (e.g., submarine fans and abyssal plain) and brackish-marine (meso- to polyhaline) water deposits (e.g., Fürsich, 1975; Fillion & Pickerill, 1990; Pemberton & Wightman, 1992; Gingras, MacEachern, & Pemberton, 1998; Jackson, Hasiotis, & Flaig, 2016). *Teichichnus* ranges from the early Cambrian to recent (e.g., Narbonne & others, 1987; Fillion & Pickerill, 1990; MacNaughton & Narbonne, 1999).

TEICHICHNUS cf. NODOSUS Fillion & Pickerill, 1990
Figure 19.5–19.6

Material.—IBGS PJ-M-025: one specimen, Spence Shale Float, Cataract Canyon.

Diagnosis.—Large, curved, undulating burrow with spreiten forming chain of irregularly spaced nodes preserved in convex hyporelief (Fillion & Pickerill, 1990).

Description.—Curved, undulating, segmented burrow with retrusive spreite. Burrow 73.4 mm long, 7.2–12.5 mm wide, and burrow segments and internodes 2.8–4.3 mm thick. Light to dark gray spreite 0.3–0.6 mm thick, and composed of fine to very fine sand.

Occurrence.—Light to dark gray (weathered to tan), laminated fine to very fine sand.

Associated ichnotaxa.—*Bergaueria hemispherica* and *Sagittichnus lincki.*

Discussion.—*Teichichnus* cf. *nodosus* (Fig. 19.5) was assigned due to its similarity to the undulating and nodular morphology of *T. nodosus* Fillion & Pickerill, 1990. This specimen also occurs with a partial eocrinoid, *Gogia granulosa* Robison, 1965. The specimen of *Teichichnus* cf. *nodosus* terminates near a *B. hemispherica* (see Fig. 6.6). A cross section of *T.* cf. *nodosus* reveals several gutter-shaped spreiten that alternate between brown, light gray, and dark gray fine-grained sand (Fig. 19.6).

Ichnogenus TREPTICHNUS Miller, 1889
Emended by Buatois & Mángano, 1993a

Type ichnospecies.—*Treptichnus bifurcus* Miller, 1889 (p. 581).

Diagnosis.—Chains of horizontal to subhorizontal, straight to curved, zigzagging burrow segments associated with vertical to oblique tubes producing a three-dimensional burrow structure; pits and nodules may occur near top or base of burrow segments at sediment interfaces (Buatois & Mángano, 1993a; Uchman, Bromley, & Leszczyński, 1998).

Discussion.—Miller (1889) named *Treptichnus* for forked, zigzagging burrows with projected burrow ends; Miller interpreted the burrow projections as indicating the direction of tracemaker movement and were produced by insect larvae or pupa. Along with *Treptichnus*, Miller (1889) also described and commented on *Haplotichnus* and *Plangtichnus* as being very similar to *Treptichnus* in terms of size, tracemaker, and morphology. *Plangtichnus* is similar to *Treptichnus* and was originally described as a zigzag trail with pits deeper than the rest of the trail (Miller 1889, p. 580). Archer and Maples (1984) and Maples and Archer (1987) argued that *Plangtichnus* is distinguishable from *Treptichnus* by the lack of burrow-end projections that yields a highly angular zigzagging form; however, Buatois and Mángano (1993a) argued that the projections of *Treptichnus* and the pits of *Plangtichnus* represented morphologically similar vertical shafts along the burrow system and that the lack of the burrow-end projections was likely caused by erosion. Buatois and Mángano (1993a) claimed that, since both ichnogenera had similar morphology and represented similar behaviors, *Plangtichnus* and *Treptichnus* should be considered synonymous. They retained *Treptichnus* for nomenclatural stability and considered *Plangtichnus* to be *nomen oblitum*, citing relative nonuse of the name. *Treptichnus pollardi* was, therefore, erected as a new ichnospecies to replace the name for the morphology previously associated with *Plangtichnus erraticus* (Buatois & Mángano, 1993a).

Treptichnus is commonly interpreted as a deposit-feeding trace (Buatois & Mángano, 1993a, 1993b; Uchman, Bromley, & Leszczyński, 1998), but has also been interpreted to be an agricultural, grazing, reproduction, and predation or scavenging trace (e.g., Rindsberg & Kopaska-Merkel, 2005; Seilacher, 2007; Vannier & others, 2010; Wilson & others, 2012; Getty & others, 2016). *Treptichnus* is interpreted as being produced by marine annelid worms (e.g., Buatois & Mángano, 1993a, 1993b; Uchman, Bromley, & Leszczyński, 1998; Vannier & others, 2010) and some insect larvae in continental environments since the Pennsylvanian (e.g., Miller, 1889; Rindsberg & Kopaska-Merkel, 2005; Getty & others, 2016). *Treptichnus* has been reported from shallow- and deep-marine, and continental proximal floodplain and proximal lacustrine deposits (e.g., Archer & Maples, 1984; Buatois & Mángano, 1993b; Jensen, 1997; Uchman, Bromley, & Leszczyński, 1998; Wilson & others, 2012; Getty & others, 2016). *Treptichnus* ranges from the Cambrian to recent (e.g., Buatois & Mángano, 1993a, 1993b; Uchman, Bromley, & Leszczyński, 1998; Vannier & others, 2010; Hasiotis, 2012); however, some *Treptichnus* have been reported from the Edicaran and were suggested to represent a gradual increase in ichnofossil complexity until the first occurrence of *T. pedum* at the Precambrian-Cambrian boundary (e.g., Germs, 1972; Jensen & others, 2000; Gehling & others, 2001; Droser & others, 2002).

TREPTICHNUS BIFURCUS (Miller, 1889)
Figures 10.5; 13.5; 21.1–21.6; and 22.1–22.3

Material.—KUMIP 204523 A+B: one specimen, Miner's Hollow; KUMIP 314230: one specimen, Antimony Canyon; KUMIP 314250: three specimens, Miner's Hollow; KUMIP 314283: one specimen; IBGS PJ-M-006: one specimen, Miner's Hollow; IBGS PJ-M-008: one specimen, Miner's Hollow; IBGS PJ-M-009: one specimen, Spence Shale float, High Creek Canyon, Bear River Range, Utah, USA; IBGS PJ-M-028: one specimen, Spence Shale Float, Miner's Hollow; IBGS PJ-M-030 (part and counterpart): one specimen, Miner's Hollow.

Diagnosis.—Burrow system with short projections between elongate, thin, and horizontal burrow segments forming straight to slightly curved, zigzagged chains; may occur as chains of evenly spaced beads or depressions alternating around central axis, forming zigzag pattern (Buatois & Mángano, 1993a; Uchman, Bromley, & Leszczyński, 1998).

Description.—A zigzag-segmented burrow system 30.2–120.3 mm long, 8.6–18.4 mm wide with burrow projections. Segments 7.4–33.2 mm long, 1.1–4.7 mm wide; circular to subrounded, depression or bead diameter 1.9–3.9 mm, nonalternating beads spaced 10.7–23.7 mm; whereas alternating beads spaced 5.5–21.0 mm. Angles between burrow segments range from 66–129°, average 99°. Specimens occur in concave and convex hyporelief and epirelief.

Occurrence.—Thickly laminated to massive, medium to dark gray or tan to light brown, siliciclastic silty or calcareous shale.

Associated ichnotaxa.—Cruziana problematica, *Gyrophyllites kwassizensis, Lockeia siliquaria, Monomorphichnus lineatus, M.* cf. *multilineatus, Planolites beverleyensis*, *P. montanus*, *Rusophycus carbonarius*, *Rusophycus* cf. *pudicus*, *Sagittichnus lincki*, and *Treptichnus vagans*.

Discussion.—Treptichnus bifurcus is the most common form of *Treptichnus* from the Spence Shale. Specimens exhibit two primary morphologies with most occurring as chains of simple, short, straight zigzagging burrow segments with short projections of the older segment past the start of new segment (Fig. 21.1, 21.3–21.5). The other *T. bifurcus* morphology has more curved or slightly meandering burrow segments (Fig. 21.2, 21.6). The projections at the end of burrow segments have been interpreted as compressed portions of the oblique shafts (Maples & Archer, 1987). Getty and others (2016), however, recently argued that burrow projections in *Treptichnus* were not formed by compression and resulted from the tracemaker backing into the previous segment, changing directions, and constructing a new segment within the same plane. *Treptichnus bifurcus* is one of the few traces previously reported from the Spence Shale by Robison (1969, pl. 138, fig. 5) as "burrow type A" and "feather-stitch burrow". The term "feather-stitch trail" was widely used in the literature prior to the 1970s before the rediscovery of the Miller (1889) paper (Buatois & Mángano, 1993a; Uchman, Bromley, & Leszczyński, 1998).

Alternating beaded *T. bifurcus* specimens (Fig. 22.1–22.3) are similar to the upper surface features of *T. bifurcus* and *T. pollardi* in Buatois and Mángano (1993a, fig. 2B, 3B). Reconstructions of *T. bifurcus* and *T. pollardi* show both ichnospecies may occur as a series of pits alternating along a central axis in the upper portions of *Treptichnus* systems and were interpreted as the burrow apertures of vertical to oblique shafts (Buatois & Mángano, 1993a). Since both *T. bifurcus* and *T. pollardi* may occur as alternating pits, assignment of alternating beaded specimens to any one *Treptichnus* ichnospecies is usually not possible. Specimens present on IBGS PJ-M-006, however, occur in very close proximity to a long *T. bifurcus* specimen with similar diameters of burrow segments, suggesting the specimen could be part of the *T. bifurcus* and, thus, included within the type ichnospecies.

Alternating beaded *T. bifurcus* specimens also bear a resemblance to *Treptichnus* isp. 5 from Buatois and Mángano (1993a, fig. 4), which also occurs as a chain of alternating pits. *Treptichnus* isp. 5 pits, however, are connected into pairs by burrow segments that do not connect to another pit-burrow segment pair, whereas alternating beaded *T. bifurcus* specimens are not connected into pairs. *Treptichnus* specimens from the Eocene Green River Formation (Hogue & Hasiotis, in review) share the alternating beaded *T. bifurcus* morphology and grade into a single-chain, beaded morphology, which in turn grades into a pitted furrow *Ptychoplasma* (*Protovirgularia*) *vagans*-like morphology (for discussion see *Treptichnus vagans* p. 43).

TREPTICHNUS PEDUM (Seilacher, 1955b)
Figure 23.1

Material.—IBGS PJ-M-017: one specimen, Spence Shale Float, Miner's Hollow; IBGS PJ-M-027: one specimen, Miner's Hollow.

Diagnosis.—Treptichnus burrow system consisting of subhorizontal, straight to curved primary burrow with multiple successive burrow segments branching off in regular intervals (Fillion & Pickerill, 1990; Jensen, 1997).

Description.—Winding burrow system with systematic projection of burrow segments from a primary burrow. Burrow system 26.6–131.5 mm long, 10.2–18.8 mm wide. Burrow segments 6.4–41.8 mm long, 0.6–4.9 mm wide.

Occurrence.—Laminated light gray and medium gray or medium gray and dark gray calcareous silty shale.

Discussion.—Originally, the epithet "*pedum*" was assigned to *Phycodes* by Seilacher (1955b) for a system of burrow segments that successively branch off along a primary tunnel. Jensen (1997) transferred *Phycodes pedum* to *Treptichnus* (see Jensen, 1997 for discussion). Geyer and Uchman (1995) transferred *P. pedum* to *Trichophycus* due to the presence of *Teichichnus*-like spreiten in some burrow segments; however, most authors currently follow

Figure 21. *Treptichnus bifurcus* specimens from the Spence Shale. *1,* Convex hyporelief, KUMIP 314230, Antimony Canyon; *2–3,* convex hyporelief (*2*) and concave hyporelief (*3*), KUMIP 314250, Miner's Hollow; *4,* concave epirelief, KUMIP 314283; *5,* concave epirelief, IBGS PJ-M-028, Miner's Hollow Float; *6,* convex epirelief with yellow-brown burrow infill (black arrow) and concave epirelief *Rusophycus carbonarius* (white arrow), IBGS PJ-M-008, Miner's Hollow; scale bars in cm.

Jensen (1997) on the use of *Treptichnus pedum* (e.g., Jensen & others, 2000; Seilacher, 2007; Wilson & others, 2012; Buatois, Almond, & Germs, 2013). In an attempt to make ichnotaxonomy follow the rules of parsimony common in other areas of science, Dzik (2005) proposed that ichnofossils should be viewed as body fossils and split *Treptichnus* and placed *T. pedum* into one of two new worm genera, *Manykodes*. We disagree with the Dzik (2005) proposal, as parsimony is not always applicable to ichnotaxonomy and to consider ichnofossils as biological taxa would greatly diminish their usefulness in sedimentology and stratigraphy.

Treptichnus pedum specimens occur as convex hyporeliefs on samples IBGS PJ-M-017 and IBGS PJ-M-027. On IBGS PJ-M-017, *T. pedum* occurs in hyporelief and most burrow segments are convex, whereas others are concave (Fig. 23.1). *Treptichnus*

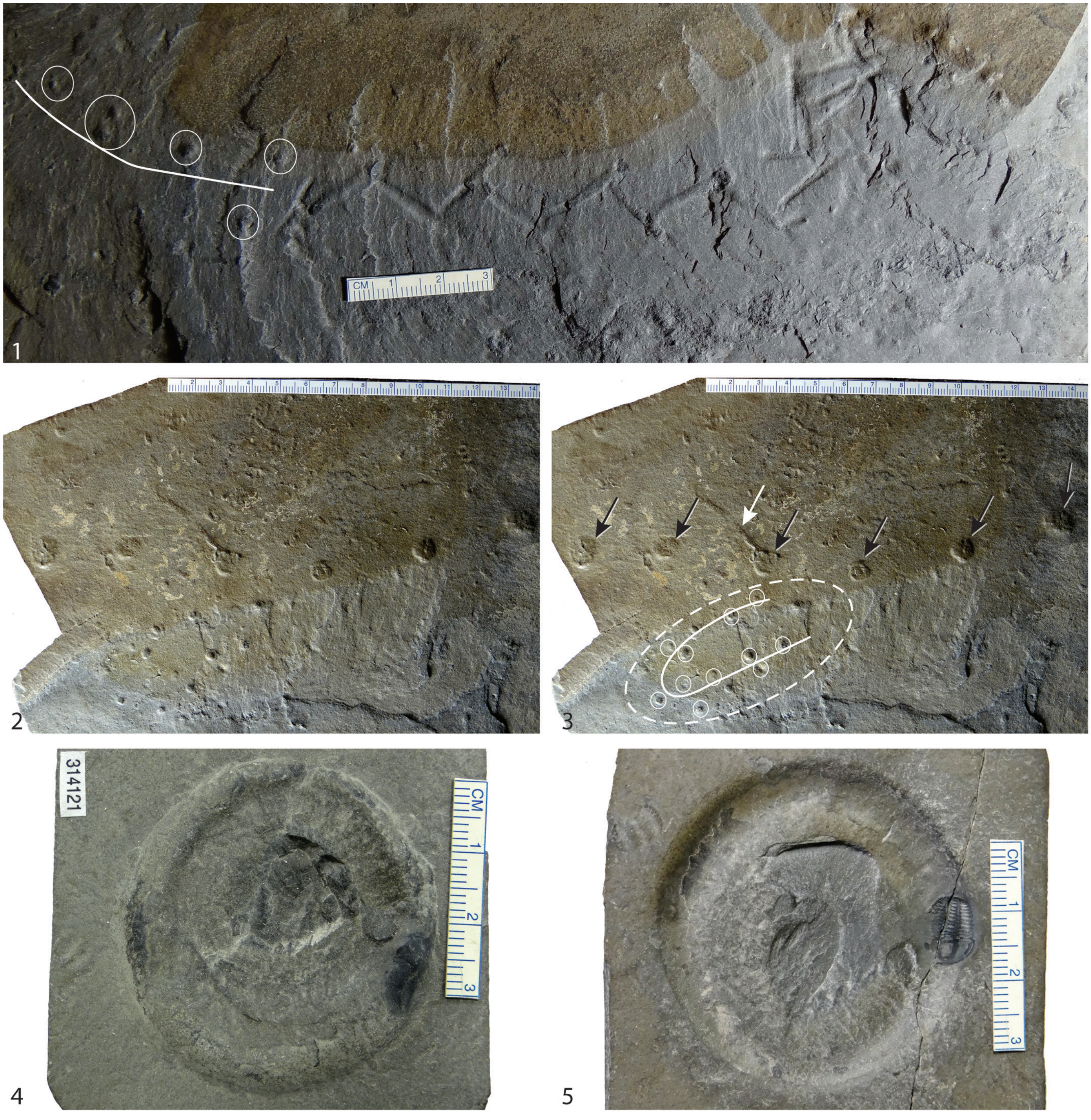

Figure 22. *Treptichnus bifurcus* specimens from the Spence Shale (continued). *1, Treptichnus bifurcus* with eroded shaft bases (circles), IBGS PJ-M-006, Miner's Hollow; *2–3,* Eroded shaft bases of *T. bifurcus* (circles) with trace axis (line), specimens of coprolite chain (black arrows), and *Planolites montanus* (white arrow) in convex hyporelief, IBGS PJ-M-030, Miner's Hollow; *4–5,* Jellyfish? impression with *Elrathia?* sp. trilobite in part (*4*) in convex epirelief and counterpart (*5*) in concave hyporelief, KUMIP 314121; scale bars in cm.

pedum also occurs with some specimens of *Cruziana problematica*. The burrow segments are elongated and straight to curved extending from a master tunnel (Maples & Archer, 1987). Some of the straighter segments widen at one end, which suggest the segments were oriented obliquely to bedding and later flattened during compaction like in specimens of *T. bifurcus*.

TREPTICHNUS VAGANS (Książkiewicz, 1977)
Figure 23.2–23.5, Figure 24.1–24.6

Thin, threadlike discontinuous trails—Germs, 1972, p. 866, pl. 1, fig. 5, 7, pl. 2, fig. 1.

**Tuberculichnus vagans*—Książkiewicz, 1977, p. 140, pl. 13, fig. 4, text-fig. 27C–G.

Figure 23. *Treptichnus pedum* and *T. vagans* "string of beads" specimens from the Spence Shale. *1, Treptichnus pedum* in convex hyporelief, IBGS PJ-M-017, Miner's Hollow Float; *2, Treptichnus vagans* with pitted furrow morphology, pits (arrows), in concave epirelief, IBGS LG-M-013, Antimony Canyon; *3, T. vagans* with *Planolites montanus* (white arrow), *Treptichnus*-like *P. montanus* (white circle), and *Rusophycus carbonarius* (black arrow) in convex hyporelief, KUMIP 314222 B, Miner's Hollow; *4,* Eocene *Treptichnus* from the Green River Formation (Photo courtesy of Joshua Hogue, used with permission): (A) Concave epirelief, alternating beaded morphology (=beaded *Treptichnus bifurcus*); (B) transition to beaded single-chain morphology; and (C) pitted furrow morphology (=*T. vagans*); *5, Treptichnus vagans* with *Monomorphichnus bilinearis* (arrows) in convex hyporelief, IBGS PJ-M-031, Miner's Hollow; scale bars in cm.

Tuberculichnus meandrinus—Książkiewicz, 1977, p. 141, pl. 13, fig. 5–6, text-fig. 27A–B.

Hormosiroidea canadensis—Crimes & Anderson, 1985, p. 325, fig. 8.1, 9.

Hormosiroidea arumbera—Walter, Elphinstone, & Heys, 1989, p. 244, fig. 14D–E, 15B, 15D.

Hostynichnium duplex—Plička & Siránová, 1989, p. 110, pl. 63.

Tuberculichnus vagans Książkiewicz—Uchman, 1991, p. 209.

Tuberculichnus vagans Książkiewicz—Uchman, 1992, p. 432.

String pits—Buatois & Mángano, 1993b, p. 246, fig. 4G.

non *Tuberculichnus vagans* Książkiewicz—Löffler & Geyer, 1994, p. 513, fig. 4E (=*Margaritichnus* or *Microsphaerichnus*).

Tuberculichnus meandrinus Książkiewicz—Pacześna, 1996, p. 67, pl. 29, fig. 5.

Tuberculichnus vagans Książkiewicz—Pacześna, 1996, p. 67, pl. 29, fig. 8, [non pl. 30, fig. 1, 3].

Tuberculichnus vagans Książkiewicz—Buatois & others, 1995, p. 268, fig. 6A,B, 7–8.

Tuberculichnus vagans Książkiewicz—Buatois & others, 1996, p. 296, fig. 10C–D.

Protovirgularia vagans (Książkiewicz)—Uchman, 1998, p. 166, fig. 70.

Treptichnus pedum triplex (Seilacher)—Seilacher, 2007, p. 182, pl. 64, fig. A–B.

Protovirgularia vagans (Książkiewicz)—Uchman, 2007, p. 230, pl. 3, fig. 10, pl. 4, fig. 1.

Tuberculichnus vagans (Książkiewicz)—Uchman, 2008a, p. 64, fig. 120.

Protovirgularia vagans (Książkiewicz)—Uchman, 2008b, p. 130, fig. 8.8 B–C.

Ptychoplasma vagans (Książkiewicz)—Uchman, Mikuláš, & Rindsberg, 2011, p. 394, fig. 3A–G, 4A–B.

Linear rosary structures—Caron and others, 2010, Supplementary material 8, p. 16, fig. DR6 A–B.

Rosary-like structures—Mángano, 2011, p. 98, text-fig. 3, 4C–D, 5, 6A–F.

Ptychoplasma vagans (Książkiewicz) (as Fenton & Fenton, 1937b)—Alonso-Muruaga, Buatois, & Limarino, 2013, p. 232, fig. 3E.

non *Ptychoplasma vagans* (Książkiewicz)—Paranjape, Kulkarni, & Gurav, 2013, p. 1366, pl. 3, fig. G–I (=*Halopoa* or *Palaeophycus*).

non *Ptychoplasma vagans* (Książkiewicz)—Hagdorn, 2014, p. 268, fig. 12.2. (=*Lockeia*).

non *Ptychoplasma vagans* (Książkiewicz)—Knaust, Warchoł, & Kane, 2014, p. 2252, fig. 6D (=*Palaeophycus* or *Planolites*).

Ptychoplasma vagans (Książkiewicz)—Stachacz, 2016, p. 316, fig. 17G.

Treptichnus bifurcus Miller—Getty & others, 2016, p. 273, fig. 4.5.

Material.—KUMIP 314122: one specimen, Antimony Canyon; KUMIP 314217: one specimen, Miner's Hollow; KUMIP 314222 A–C: five specimens, Miner's Hollow; KUMIP 314233: one specimen; KUMIP 314235: one specimen; IBGS LG-M-004: one specimen; IBGS LG-M-012: one specimen; IBGS LG-M-013: two specimens; IBGS PJ-M-008: one specimen, Miner's Hollow; IBGS PJ-M-014: one specimen, Miner's Hollow; IBGS PJ-M-019: two specimens, Miner's Hollow; IBGS PJ-M-031: four specimens.

Emended Diagnosis.—Irregularly meandering or looping, discontinuous trail of variably spaced, short to elongate, ovoid to irregular to circular beads (hyporelief) or depressions (epirelief).

Description.—Trails 16–314 mm long, may overlap and cross each other. Beads 0.6–7.0 mm long, 0.6–3.3 mm wide, spaced 0.7–7.0 mm apart. Most specimens are convex hyporelief; however, two specimens are concave epirelief (KUMIP 314122 and KUMIP 314235), and one specimens is preserved as part and counterpart (KUMIP 314233).

Occurrence.—Three lithologies: (1) gray (weathers to brown), mica-rich silty shale; (2) dark gray calcareous shale; and (3) gray to dark gray siliciclastic shale.

Associated ichnotaxa.—*Dimorphichnus* isp., *Diplichnites gouldi*, *Halopoa* aff. *imbricata*, *Lockeia siliquaria*, *Monomorphichnus bilinearis*, *Phycosiphon incertum*, *Planolites montanus*, *Protovirgularia* cf. *pennatus*, *Rusophycus carbonarius*, *Sagittichnus lincki*, and *Treptichnus bifurcus*.

Discussion.—Originally, the epithet "*vagans*" was assigned to *Tuberculichnus* by Książkiewicz (1977) for irregularly winding chains of ridgelike knobs. Uchman (1998) moved *Tuberculichnus vagans* to *Protovirgularia* for the amygdaloidal shape of said knobs. Uchman, Mikuláš, and Rindsberg (2011) later transferred *Protovirgularia vagans* to *Ptychoplasma* Fenton & Fenton, 1937b, for the carinate shape of the knobs. Mángano and others (2002) suggested *P. vagans* should be considered a form of *Lockeia* due to its amygdaloidal, carinate shape, and lack any chevronate patterns. *Ptychoplasma vagans* from Paranjape, Kulkarni, and Gurav (2013) closely resemble *Halopoa* or *Palaeophycus* and lack the diagnostic beaded morphology. Hagdorn (2014) illustrated *P. vagans* specimens occurring in short chains and not winding chains as in the type material. The *P. vagans* specimens illustrated by Knaust, Warchoł, and Kane (2014) do not form chains, and the ridgelike knobs do not appear connected. The repeated transfer of *P. vagans* and wide range of reported morphologies has caused a significant problem regarding its identification and ichnotaxonomic status.

Herein, we transfer *P. vagans* to *Treptichnus* based on morphological similarities to this ichnotaxon in an attempt to stabilize the nomenclature. The morphology of *P. vagans* is ill suited for inclusion in *Protovirgularia*, *Ptychoplasma*, and *Lockeia* due to the lack of chevronate and bilobate morphology and the beaded morphology that does not match the type material, respectively. Spence Shale specimens are most similar to *P. vagans* as both share a winding, single-chain beaded morphology in convex hyporelief. *Ptychoplasma vagans*, however, sometimes forms irregularly shaped furrows in concave epirelief, which some Spence Shale specimens do as well (Fig. 23.2). Similar to both ichnotaxa is a specimen of *Treptichnus* from the Eocene Green River Formation (Fig. 23.4), which incorporates aspects of Spence Shale chain specimens, alternating beaded *Treptichnus bifurcus*, and *P. vagans* to form: (1) a concave epirelief, alternating beaded morphology (=beaded *Treptichnus bifurcus*); (2) transitions to a beaded single-chain morphology (=beaded *Treptichnus pedum*); and then to (3) a pitted furrow morphology (=*P. vagans sensu* Uchman, Mikuláš, & Rindsberg, 2011) (Hogue & Hasiotis, in review). Due to the similar morphology between ichnotaxa, we, therefore, place *Ptychoplasma* (*Protovirgularia*) *vagans* within *Treptichnus* as a valid

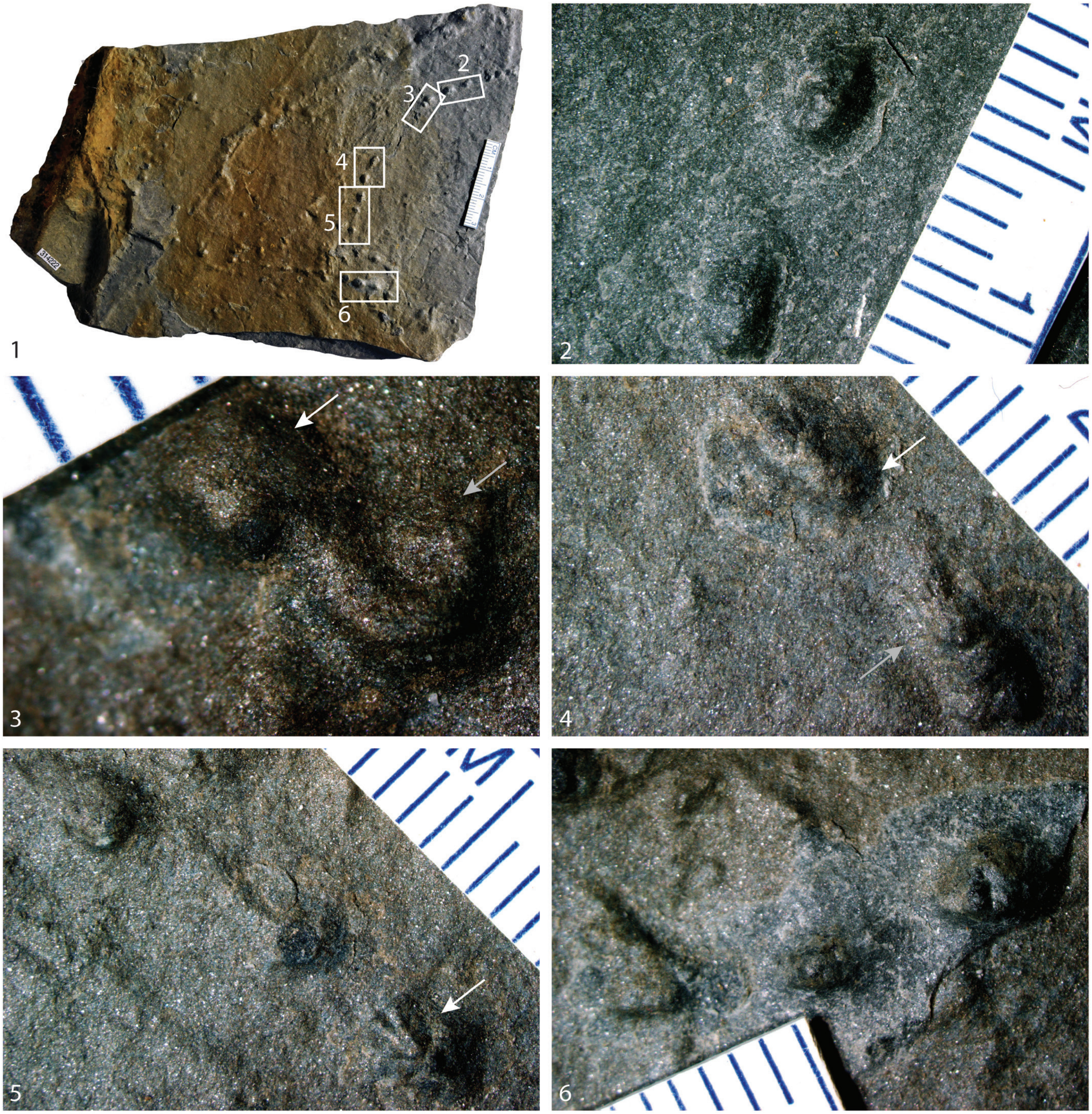

Figure 24. *Treptichnus vagans* with variable bead morphology, including circular, fluted, imbricated, ovoid, and triangular morphologies from the Spence Shale. *1,* Treptichnus vagans with showcased beads highlighted, KUMIP 314222 A, Miner's Hollow; *2,* pair of smooth ovoid beads; *3,* Circular (white arrow) and fluted (grey arrow) beads; *4,* fluted circular bead (white arrow) and imbricated ovoid bead (black arrow); *5,* circular and triangular beads (arrow); and *6,* smooth ovoid beads; scale bar in (*1*) cm; scale bar (*2–6*) in mm.

ichnospecies, and it should be referred to as *Treptichnus vagans*. We interpret the nodes or pits at the base or top of vertical to subvertical shafts as similar to those in *T. bifurcus* and *T. pollardi*, as well as a *Treptichnus* where the tracemaker probed through the sediment interface in a relatively straight line. Erosion of the upper part of the trace would leave an apparent string of beads, with or without remnants of the associated shafts.

Treptichnus vagans is composed of long, winding trails of beads that vary in shape from circular to ovoid to irregular (Fig. 23.2–23.3,5, Fig. 24.1). Most specimens with circular beads cross themselves (Fig. 23.2,5); whereas, only one specimen with ovoid-shaped beads does (Fig. 24.1). The individual bead shape in a single chain is not always morphologically uniform. One specimen with ovoid-shaped beads has short "drag" marks on one end of the beads extending in the same direction, which are interpreted as insertion furrows (see Fig. 23.3). Another specimen has a mix of different bead morphologies: ovoid, fluted (grooves), imbricated, and triangular (Fig. 24.2–24.6). The fluted and triangular bead morphologies may have been produced by protobranch mollusks due to their V shape (*sensu* Seilacher & Seilacher, 1994).

Treptichnus vagans is similar to numerous "string-of-pearls" ichnotaxa, such as *Margaritichnus* Bandel, 1973, and *Microspherichnus* Hakes, 1976. Both ichnotaxa consist of long, sometimes meandering, trails of circular to oval-shaped depressions or mounds. *Margaritichnus* is usually preserved in convex epirelief with mounds closely spaced that are commonly in contact with each other (Hakes, 1976). *Microspherichnus* is also preserved in convex epirelief with irregularly spaced beads that may or may not be in contact with each other (Hakes, 1976; Fillion & Pickerill, 1990). *Treptichnus vagans* specimens also resemble the "string pits" of Buatois and Mángano (1993b, fig. 4G). The "string pits" were described as a hypichnial chain of small, subrounded to oval mounds (< 1 mm) spaced 0.5–4.0 mm apart (max. length = 100 mm) and originally interpreted as locomotion traces of an unknown arthropod. The Buatois and Mángano (1993b) "string pits" are included within *T. vagans*.

Some *Treptichnus pedum* specimens have been reported with a beadlike morphology similar to *T. vagans*. *Treptichnus pedum* specimens from the lower Cambrian of Namibia commonly occur in long, sinuous chains with ovoid to subrounded to circular beads (e.g., Germs, 1972; Jensen & others 2000; Seilacher, 2007; Wilson & others, 2012). Germs (1972) described long, sinuous chains of discontinuous ridges that were later regarded as *Treptichnus pedum triplex* by Seilacher (2007). The discontinuous ridges of Germs (1972) are almost identical to the Książkiewicz (1977) type material and are included in *T. vagans*. Multiple specimens of *T. pedum* with subrounded to circular beads were reported from the lower Cambrian of Namibia (Wilson & others, 2012, fig. 10–12). Some of the Namibian *T. pedum* specimens with beads are amalgamated together to form recognizable burrow segments (Wilson & others, 2012, fig. 12e–g). Jensen and others (2000) also presented chains of beaded trails assigned to *T. pedum* that may be better assigned to *T. vagans*. The Jensen and others (2000) and Wilson and others (2012) specimens likely represent an intergradation between *T. pedum* and *T. vagans*.

Treptichnus vagans specimens are similar to *Hormosiroidea canadensis* Crimes & Anderson, 1985 and *H. arumbera* Walter, Elphinstone, & Heys, 1989. Uchman (1995) later transferred *H. canadensis* to *Saerichnites* Billings, 1866, arguing that the vertical-tube expression was inconsistent with the diagnosis and type ichnospecies of *Hormosiroidea. Hormosiroidea* Schaffer, 1928, is characterized as a horizontal chain of spheres or depressions connected by a central tube, whereas *Saerichnites* was established as a trackway of paired, parallel rows of alternating semicircular to subquadrate pits (Häntzschel, 1975). Crimes and Anderson (1985) considered the beads and depressions of *H. canadensis* to be expressions of a vertical meandering method or vertical shafts that were connected by a horizontal tube. Walter, Elphinstone, and Heys (1989) thought *H. arumbera* was constructed in the same manner as *H. canadensis*. Uchman (1995), however, interpreted *Saerichnites* as an interconnected, zigzag-branching burrow system, similar to *Treptichnus*. We disagree with the Uchman (1995) synonymy, and tentatively place *H. canadensis* and *H. arumbera* within *Treptichnus vagans* due to their beaded-chain morphology and the synonymization of *Hormosiroidea* under *Halimedides* Lorenz von Liburnau, 1902 (Uchman, 1998, 1999; Gaillard & Olivero, 2009).

Treptichnus vagans is also similar to "rosary-like structures" from the middle Cambrian Burgess Shale (Caron & others, 2010; Mángano, 2011) and linear *Treptichnus bifurcus* from the Lower Jurassic East Berlin Formation of Massachusetts (Getty & others, 2016). The Burgess Shale "rosary structures" are short to long, meandering to winding to zigzagging chains of small, beadlike mounds or pits with connecting tunnels and interpreted as chains of globular to spherical chambers used as agrichnia to farm bacteria (Mángano, 2011). Most *Treptichnus vagans* specimens lack tunnels connecting the beads. Some "rosary" chambers were filled with pyrite—which the *T. vagans* specimens lack—and were noted to support an agrichnial interpretation in dysoxic waters and near-anoxic sediments (Mángano, 2011). The "rosary structures" were also noted for their similarity to *T. pollardi* and its associated vertical shaft nodes (Jensen in Mángano, 2011) and are included in *T. vagans*. Specimens of linear *T. bifurcus* reported from the Lower Jurassic East Berlin Formation (Getty & others, 2016, fig. 4.5), described as "string of beads" and composed of linearly oriented burrow segments and swelled projection occurring end on end, are morphologically similar to the Burgess Shale rosary structures, *Ptychoplasma*, *T. pollardi*, and *T. vagans*. We, therefore, include the linear *T. bifurcus* specimens of Getty and others (2016) within *T. vagans*.

Miscellanea

Jellyfish Impression?

Figure 22.4–22.5

Material.—KUMIP 314121: one specimen (part and counterpart), Wellsville Mountains, Utah, USA.

Diagnosis.—Circular, convex mound (part) with broad, shallow depression near center.

Description.—Convex mound: 43.9–46.6 mm wide; 11.7 mm thick; depression is 2.8 mm deep. *Elrathia*? sp. trilobite mold on counterpart: 10.1 mm long, 7.2 mm wide; corresponds to dark gray ovoid-shaped area on part specimen.

Occurrence.—Gray, siliciclastic silty shale.

Associated ichnotaxa.—None.

Discussion.—The exact nature of this specimen is unknown but we propose several possible interpretations: (1) a body fossil and ichnofossil of an unknown cnidarian jellyfish (likely a scyphozoan) perhaps with and the *Elrathia*? sp. trilobite feeding off the remains of the jellyfish (i.e., Mortichnia and Praedichnia); (2) a resting trace of a suspension-feeding cnidarian, for instance, an upside-down jellyfish (Rhizostomeae, Cassiopeidae) or sea anemone; or (3) the nesting trace of an unknown tracemaker, similar to modern-day fish nests.

A cnidarian body fossil and ichnofossil interpretation is the most likely as there are reports of similar circular-shaped fossils interpreted as jellyfish body fossils (e.g., Hagadorn, Dott, & Damrov, 2002; Gaillard & others, 2006; Oosterink & Winkelhorst, 2013). Hagadorn, Dott, and Damrov (2002) and Gaillard and others (2006) illustrated jellyfish specimens with some of the internal morphology (e.g., gonads) and tentacles preserved, whereas other specimens only had concentric rings or slight deformation attributed to shrinkage and/or locomotive pulsation and localized downslope sliding, respectively. Oosterink and Winkelhorst (2013) specimens had concentric rings attributed to shrinkage and appeared to exhibit some internal morphology. The Spence Shale specimen lacks concentric rings to indicate pulsation, no deformation to indicate downslope sliding, or any discernible internal morphology. The central depression, however, may have been formed by the collapse of the jellyfish bell during decay. Trilobites are also known for being predators and/or scavengers of soft-bodied faunas (e.g., Jensen, 1990; Tarhan, Jensen, & Droser, 2011) and there is a report of a complex *Rusophycus* association that was interpreted as trilobites consuming possible jellyfish remains (Brandt & Rudkin, 2011). The close association of the jellyfish body impression and the *Elrathia*? sp. may represent predation or scavenging by the trilobite.

The second proposed interpretation of the mound is as a resting and/or suspension-feeding trace of an unknown species of upside-down jellyfish (i.e., Cassiopeidae) or actinian (e.g., sea anemone). The upside-down jellyfish, *Cassiopeia* Péron & Lesueur, 1810, has a flat to concave, broad bell with tentacles extended upward to capture prey, and it commonly rests on the seafloor (Hummelinck, 1968; DeFelice, Eldridge, & Carlton, 2001; Schembri, Deidun, & Vella, 2010). The concave bell of *Cassiopeia* could possibly form a short, broad mound while resting on the sediment-water interface. An actinian tracemaker could also produce a similar shallow-mound form (e.g., *Bergaueria sucta*); however, the orientation of the specimen would be opposite of the current interpretation.

A third, proposed interpretation is that the mound is a nestlike excavation of an unknown tracemaker, possibly the *Elrathia*? sp. trilobite. Nestlike excavations of known and unknown tracemakers are not unheard of in ichnotaxonomy. Fenton and Fenton (1937d) established and interpreted *Rusophycus jenningsi* as a trilobite brooding nest. Ancient and modern fish produce simple to intricate, radially symmetric mounds or depressions (e.g., *Piscichnus*) to attract mates and spawn (e.g., Feibel, 1987; Hasiotis & others, 2012; Kawase, Okata, & Ito, 2013). The *Elrathia*? trilobite may have produced the mound in an attempt to attract a mate with whom to reproduce.

DISCUSSION

Ichnotaxa

Thirty-five ichnospecies were identified from 24 ichnogenera on slab specimens from the Spence Shale: *Archaeonassa*, *Arenicolites*, *Aulichnites*, *Bergaueria*, *Conichnus, Cruziana, Dimorphichnus*, *Diplichnites*, *Gordia*, *Gyrophyllites*, *Halopoa*, *Lockeia*, *Monomorphichnus*, *Nereites*, *Phycodes*, *Phycosiphon*, *Planolites*, *Protovirgularia*, *Rusophycus*, *Sagittichnus*, *Scolicia*, *Taenidium*, *Teichichnus*, and *Treptichnus* (Table 1).

Behaviors

Ichnofossils from the Spence Shale represent a variety of behaviors grouped into ethological categories (e.g., Bromley, 1996; Gingras & others, 2007) (Table 1): cubichnia (resting), domichnia (dwelling), fodinichnia (feeding), pascichnia (grazing), praedichnia (predation), and repichnia (locomotion). Cubichnia is represented by *Lockeia*, *Rusophycus*, and *Sagittichnus.* The ichnogenera of *Arenicolites, Bergaueria*, and *Conichnus* are commonly interpreted as domichnia. Traces commonly interpreted as fodinichnia include *Gordia, Gyrophyllites*, *Halopoa*, *Phycodes*, *Planolites*, *Scolicia*, *Taenidium*, *Teichichnus*, and *Treptichnus*. Pascichnia is represented by *Cruziana, Gordia, Nereites,* and *Phycosiphon*. Praedichnia are represented by compound ichnofossil associations of *Rusophycus* with *Planolites* and *Archaeonassa jamisoni* with *Taenidium* cf. *satanassi*, which represent epifaunal traces superimposed over the infaunal traces. Repichnia include *Archaeonassa*, *Aulichnites*, *Cruziana*, *Dimorphichnus*, *Diplichnites*, *Monomorphichnus*, and *Protovirgularia.*

Ichnocoenoses

An ichnocoenosis is an assemblage of ichnofossils that is the result of a single community of tracemaking organisms and can be used to interpret various physicochemical controls present during deposition (e.g., Ekdale, Bromley, & Pemberton, 1984; Bromley, 1996). Three ichnocoenoses are established for the Spence Shale, with a varying degree of stratigraphic occurrence: *Rusophycus-Cruziana*, *Sagittichnus*, and *Arenicolites-Conichnus* (Table 2). The ichnocoenoses suggest the Spence Shale was predominantly controlled by benthic oxygenation (Fig. 25–26).

The *Rusophycus-Cruziana* (RC) ichnocoenosis occurs in gray to greenish gray, calcareous or siliciclastic silty shale. Four slab samples were assigned to the RC ichnocoenosis, but only two slabs (KUMIP 204523A+B and IBGS PJ-M-007) could be stratigraphically placed within the Spence Shale, and both occur near the base of Miner's Hollow Cycle 6 (see Fig. 5). The RC ichnocoenosis has the second highest ichnodiversity with seven ichnogenera present: *Bergaueria*, *Cruziana*, *Lockeia*, *Monomorphichnus*, *Planolites*, *Rusophycus*, and *Treptichnus*. The dominant behaviors represented are cubichnia, pascichnia, and repichnia with minor behaviors including fodinichnia, domichnia, and praedichnia. Ichnofabric indices range from *ii*1–2; whereas, bedding-plane bioturbation indices range from BPBI 2–4. The ichnocoenosis represents deposition in a proximal position on the outer detrital belt (see Fig. 2) (e.g., Robison, 1976, 1991; Liddell, Wright, & Brett, 1997) with: (1) low to moderate depositional energy; (2) low sedimentation rate; (3) low to moderate benthic oxygen but poorly oxygenated sediment; (4) moderate to high nutrients; and (5) minor bottom water currents (Fig. 26.1).

The *Sagittichnus* ichnocoenosis is found in gray to greenish gray, siliciclastic silty shale with black dendrites and rarely interlaminated with calcareous shale. None of the assigned slab samples could be stratigraphically placed but are known from Antimony and Cataract canyons, Wellsville Mountains, and High Creek Canyon, Bear River Range. This ichnocoenosis has the highest ichnodiversity in the Spence Shale with eight ichnogenera represented: *Bergaueria*, *Gyrophyllites*, *Lockeia*, *Planolites*, *Rusophycus*, *Sagittichnus*, *Teichichnus*, and *Treptichnus*. The dominant behavior represented is cubichnia, and minor behaviors include fodinichnia and repichnia. The *Sagittichnus* ichnocoenosis represents deposition in a medial position on the outer detrital belt (e.g., Robison, 1976,

Ichnofossil	Frequency	Preservation	Ethology (Behavior)	Tracemaker	References
Archaeonassa fossulata	R	P & CP	Pascichnia, Repichnia	Gastropods	Fenton & Fenton (1937a)
A. jamisoni	R	Epirelief	Cubichnia, Pascichnia, Praedichnia	Gastropods	Fenton & Fenton (1937a)
Arenicolites carbonaria	A	Epirelief	Domichnia, Praedichnia	Annelid worms	Hakes (1976)
Aulichnites isp.	VR	Hyporelief	Pascichnia, Repichnia	Gastropods	Fenton & Fenton (1937b)
Bergaueria hemispherica	C	Epirelief, Hyporelief	Cubichnia, Domichnia	Actinians	Pemberton, Frey, & Bromley (1988)
B. aff. *perata*	VR	P & CP	Cubichnia, Domichnia	Actinians	Pemberton, Frey, & Bromley (1988)
Conichnus conicus	C	Epirelief	Cubichnia, Domichnia	Actinians	Pemberton, Frey, & Bromley (1988)
Cruziana barbata	R	Epirelief	Pascichnia	Trilobites	Seilacher (1970)
C. problematica	C	P & CP	Pascichnia	Trilobites	Bromley & Asgaard (1979)
Diplichnites cf. *binatus*	VR	P & CP	Repichnia	Trilobites	Webby (1983)
D. gouldi	R	P & CP	Repichnia	Trilobites	Trewin & McNamara (1995)
D. cf. *govenderi*	R	P & CP	Repichnia	Trilobites	Savage (1971)
Dimorphichnus isp.	R	Hyporelief	Pascichnia, Repichnia	Trilobites	Fillion & Pickerill (1990)
Gordia marnia	R	Epirelief, Hyporelief	Pascichnia, Repichnia	Annelid worms	Buatois & Mángano (1993b)
Gyrophyllites kwassizensis	R	P & CP, Endorelief	Domichnia, Fodinichnia	Annelid worms	Fürsich & Kennedy (1975)
Halopoa aff. *imbricata*	R	Hyporelief	Pascichnia	Annelid worms	Uchman (1998)
Lockeia siliquaria	R	Hyporelief	Cubichnia	Bivalves	Seilacher & Seilacher (1994)
Monomorphichnus bilinearis	R	Hyporelief	Pascichnia, Repichnia	Trilobites	Crimes (1970b)
M. lineatus	R	P & CP, Hyporelief	Pascichnia, Repichnia	Trilobites	Crimes & others (1977)
M. cf. *multilineatus*	R	Hyporelief	Pascichnia, Repichnia	Trilobites	Alpert (1976a)
Nereities cf. *macleayi*	VR	P & CP	Fodinichnia, Repichnia	Annelid worms	Uchman (1995)
Phycodes curvipalmatum	VR	Epirelief, Endorelief	Fodinichnia	Annelid worms	Pollard (1981)
Phycosiphon incertum	R	Hyporelief	Pascichnia	Annelid worms	Uchman (1998)
Planolites annularis	R	Epirelief	Fodinichnia, Repichnia	Annelid worms	Pemberton & Frey (1982)
P. beverlyensis	R	P & CP	Fodinichnia, Repichnia	Annelid worms	Pemberton & Frey (1982)
P. montanus	C	P & CP, Hyporelief	Fodinichnia, Repichnia	Annelid worms	Pemberton & Frey (1982)
Protovirgularia dichotoma	VR	Hyporelief	Pascichnia, Repichnia	Bivalves, Gastropods	Seilacher & Seilacher (1994)
P. cf. *pennatus*	R	P & CP, Hyporelief	Pascichnia, Repichnia	Bivalves, Gastropods	Uchman (1998)
Rusophycus carbonarius	A	P & CP	Cubichnia, Praedichnia	Trilobites	Keighley & Pickerill (1996)
R. cf. *pudicus*	VR	Hyporelief	Cubichnia	Trilobites	Osgood (1970)
R. cf. *cerecedensis*	R	Hyporelief	Cubichnia, Praedichnia	Trilobites	Crimes & others (1977)
Sagittichnus lincki	A	Hyporelief	Cubichnia	Small arthropods	Retrum, Hasiotis, & Kaesler (2011)
Scolicia isp.	VR	P & CP, Endorelief	Pascichnia, Repichnia	Annelid worms, Gastropods	Uchman (1995)
Taenidium cf. *satanassi*	VR	Epirelief, Endorelief	Pascichnia, Repichnia	Annelid worms	D'Alessandro & Bromley (1987)
Teichichnus cf. *nodosus*	VR	Hyporelief	Fodinichnia	Annelid worms	Fillion & Pickerill (1990)
Treptichnus bifurcus	C	Epirelief, Hyporelief	Pascichnia	Annelid worms	Uchman (1998)
T. pedum	R	Hyporelief	Pascichnia	Annelid worms	Jensen (1997)
T. vagans	C	Hyporelief	Agrichnia, Pascichnia, Repichnia	Annelid worms, Bivalves, Gastropods	Mángano (2011)

Table 1. Frequency, preservation, behavioral ethologies, and tracemakers of Spence Shale ichnofossils. Frequency key: A=abundant (> 20 specimens); C=common (6 to 20 specimens); R=rare (2 to 5 specimens); VR=very rare (1 specimen); P=part, CP=counterpart.

1991; Liddell, Wright, & Brett, 1997) (see, Fig. 2) with: (1) low to moderate depositional energy; (2) rapid sedimentation pulses with some tempestites; (3) low to moderate benthic oxygen; and (4) moderate nutrients (Fig. 26.2).

The *Arenicolites-Conichnus* (AC) ichnocoenosis is the most unique ichnocoenosis from the Spence Shale as it represents different dominant behaviors and an entirely different ichnofacies. The AC ichnocoenosis is from a float sample from Cataract Canyon and could not be stratigraphically placed. The dominant behaviors represented are domichnia and cubichnia. The AC ichnocoenosis also has a low ichnodiversity with only two ichnogenera represented: *Arenicolites* and *Conichnus*. The AC ichnocoenosis represents deposition in a proximal position near the boundary between the outer detrital belt and outer carbonate belt (e.g., Robison, 1976, 1991; Liddell, Wright, & Brett, 1997) (see Fig. 2) with: (1) moderate to high depositional energy; (2) moderate to high sedimentation; (3) moderate to high oxygen; and (4) medium (Fig. 26.3).

Ichnofacies

The majority of the ichnotaxa suggests that a significant portion of the Spence Shale was deposited in a distal Cruziana Ichnofacies. *Bergaueria*, *Cruziana*, *Diplichnites*, *Monomorphichnus*,

Ichnocoenoses	Minor Traces	Dominant Behaviors	Environmental Interpretation
Rusophycus–Cruziana	*Bergaueria*, *Lockeia*, *Monomorphichnus*, *Planolites*, and *Treptichnus*	Cubichnia, Pascichnia, and Repichnia	Low–moderate energy; low–moderate benthic oxygen but poorly oxygenated sediment; low sedimentation; moderate–high nutrients; minor bottom currents
Sagittichnus	*Bergaueria*, *Gyrophyllites*, *Lockeia*, *Planolites*, *Rusophycus*, *Teichichnus*, and *Treptichnus*	Cubichnia	Low–moderate energy and oxygen; rapid, pulsed sedimentation; moderate nutrients
Arenicolites–Conichnus	N/A	Domichnia, Cubichnia	Moderate–high energy sedimentation, and oxygen; silty–sandy media

Table 2. Ichnocoenoses of the Spence Shale with minor associated traces, dominant behaviors, and environmental interpretations.

and *Rusophycus* in the *Rusophycus-Cruziana* and *Sagittichnus* ichnocoenoses are the most indicative of this ichnofacies (Bromley, 1996; MacEachern & others, 2007a). The high number of pascichnial ichnofossils, small burrow diameters (e.g., *Cruziana* and *Rusophycus*), shallow sediment penetration, and low *ii* suggest that bottom-water oxygenation (likely dysoxia) influenced the biota and their behavior (e.g., Ekdale & Mason, 1988; MacEachern & others, 2007b; Garson & others, 2012). Specimens assigned to the Cruziana Ichnofacies occur mostly in the silty shales near the base of Miner's Hollow Cycle 5 and 6 between 42–49 m above the Spence Shale base (see Fig. 5).

The second ichnofacies proposed for the Spence Shale—based on a sample containing *Arenicolites*, *Conichnus,* ripple marks, and soft-sediment deformation—is a depauperate, distal Skolithos Ichnofacies indicating a higher energy environment with shifting media (MacEachern & others, 2007a, 2007b) (see Fig. 2). The depauperate, distal Skolithos Ichnofacies is present in peloidal carbonate wackestone to packstone to mudstone and silty siliciclastic shale of the Spence Shale at the Cataract Canyon locality. The stratigraphic position of the Skolithos Ichnofacies is not known, as no stratigraphic data exists for the assigned sample.

Comparative Ichnotaxonomy

The Spence Shale ichnofauna is composed of numerous common facies-crossing ichnotaxa, which are represented in multiple depositional environments throughout the Phanerozoic. Similarities between the Spence Shale ichnotaxa and the ichnotaxa of other Cambrian-aged deposits suggest that shaley portions of the Spence Shale may have been deposited in shallow marine as well as deep settings following a fluctuating oxycline (*sensu* Garson & others, 2012).

Ichnotaxonomy of BST Deposits.—Since there have been no ichnological studies of the Wheeler and Marjum formations, a comparison between Utah BST deposits is not possible. The Kaili Biota, Kaili Formation of China is the only other middle Cambrian BST deposit that has been extensively studied ichnologically. Other Cambrian BST deposits with reported ichnofossils include the early Cambrian Sirius Passet Biota, Buen Formation of Greenland and Chengjiang Biota, Yu'anshan Formation of China, and middle Cambrian Burgess Shale of British Columbia (Table 3).

The Kaili Biota (*Oryctocephalus indicus* Biozone) (see Fig. 4.2) of the lower–middle Cambrian Kaili Formation in Guizhou Province, China, contains 26 ichnogenera (see Lin & others, 2010, appendix A, for complete list and references) and shares 10 ichnogenera in common with the Spence Shale (Table 3). Yang (1994) assigned the Kaili Biota to the Cruziana Ichnofacies and suggested that the Kaili Formation was deposited during near normal marine conditions in a shallow, nearshore setting under moderate to low energy. Lin and others (2010) suggested that the major sedimentation events of the Kaili Formation occurred due to episodic distal tempestites with relatively low background sedimentation. The Kaili Formation distal tempestite deposition is similar to the Robison (1991) suggestion that many of the Spence Shale Lagerstätten were deposited by tempestites in the distal ramp setting of the Spence Shale. Sudden burial by tempestites (i.e., obrusion) may produce anoxic–dysoxic conditions in the underlying sediment, enabling the production of BST fossils until oxic conditions returned, allowing organisms to burrow, mix sediments, and even feed on the preserved soft tissues (Garson & others, 2012).

The Sirius Passet Biota (SPB) from the early Cambrian (Series 2, Stage 3) (see Fig. 4.1) of Greenland is a remote but rich BST deposit with only six ichnogenera, sharing three with the Spence Shale (Ineson & Peel, 2011). Most of the traces reported from the Sirius Passet were simple, horizontal meandering burrows (likely *Gordia*, *Helminthoidichnites*, and *Planolites* based on photographs) with some specimens of *Chondrites*, *Cosmorhaphe?*, *Megagrapton?*, *Palaeophycus*, *Planolites*, *Spirorhaphe*?, and *Teichichnus* (Table 3) (Ineson & Peel, 2011). Mángano and others (2012) examined narrow, filamentlike structures similar to *Pilichnus* yet no formal assignment was made; however, the SPB "*Pilichnus*" is more likely to be a tubular body fossil similar to *Vendotaenia antiqua* (e.g., Cohen & others, 2009), which is considered analogous to a green or red alga. The SPB was deposited in the deep-water shales of the Buen Formation as part of an outer shelf and slope environment (Peel, 2010). Pyrite is present in the burrow fill of some SPB ichnofossils, suggesting an oxygen-depleted environment (*sensu* Martin, 2004; Ineson & Peel, 2011). No ichnofacies has been assigned to the Buen Formation but likely contains a Zoophycos or Nereites Ichnofacies.

The Chengjiang Biota of the Yu'anshan Formation of the early Cambrian of Yunnan Province, China, has had several reports of ichnofossils in close association with BST fossils (e.g., Zhang & others, 2007; Huang & others, 2014) (Table 3). Zhang and others (2007) reported small (< 2.0 mm diameter), unidentified ichnofossils that burrowed through and beneath BST films, similar to *Gordia* specimens in Wang and others (2009), and suggested they may be forms of *Helminthoidichnites* or *Pilichnus*. Huang and others (2014) had several worm specimens interpreted to have

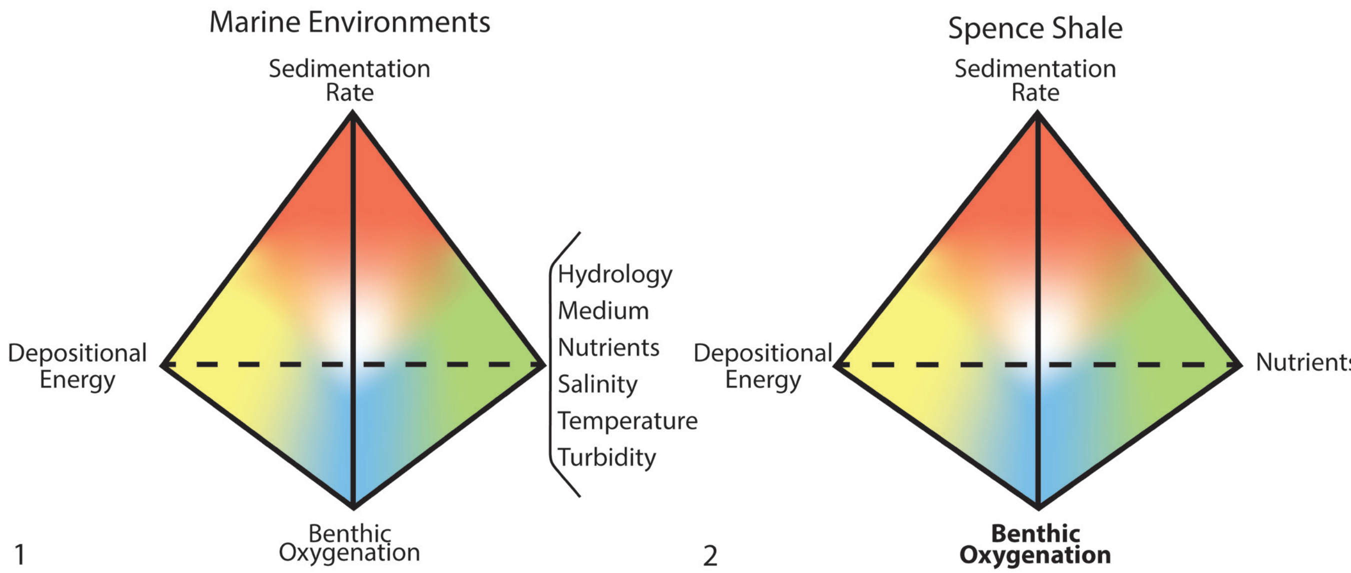

Figure 25. Primary physicochemical controls on organism behavior. *1,* Established primary physicochemical controls in marine depositional systems; *2,* interpreted physicochemical controls for the Spence Shale (modified from Hasiotis & Platt, 2012).

died within thinly lined, horizontal to subvertical burrows—some of which were reported as U shaped with paired openings—but no ichnogeneric names were assigned. These morphologies could represent specimens of *Arenicolites*, *Palaeophycus*, *Planolites*, or *Skolithos*. The Chengjiang ichnofossils suggest a distal Cruziana Ichnofacies.

The Burgess Shale of the middle Cambrian of British Columbia has had few ichnofossils reported—most reported in open nomenclature (e.g., "[U]-shaped tube trace" and "vertical-pipe morphology") by Allison and Brett (1995, fig. 4)—and shares five of eleven ichnogenera with the Spence Shale (Table 3). Hagadorn (2002) assigned the Allison and Brett (1995) ichnofossils to *Arenicolites*, *Cruziana*, *Monocraterion*, and *Planolites*; however, the U-shaped tubes were also described as having reworked sediment between the arms, which would place them in *Diplocraterion*. Caron and others (2010) reported the first ichnotaxonomically assigned ichnofossils from the Burgess Shale (as the "thin" Stephen Formation), including *Cruziana problematica*, *Diplichnites*, *Gordia*, *Helminthoidichnites*, and a pellet-filled burrow, *Alcynidiopsis*, filled with coprolites (possibly *Tibikoia* or *Tomaculum*) associated with an arthropod carapace. These ichnofossils, however, are only illustrated in the supplementary materials (see Caron & others, 2010, supplementary material 8 GSA Data Repository 2010228). Mángano (2011) reexamined the material of Caron and others (2010) and reported specimens of *Diplopodichnus* and *Helminthopsis*. Several large arthropod trackway sets were described from the Kicking Horse Member (*Glossopleura* biozone) of the Burgess Shale Formation as *Diplichnites* (Minter, Mángano, & Caron 2012). *Cheiichnus*, *Fuersichnus*, and arthropod trackway specimens were reported from near the base of the Stephen Formation (Caron & others, 2014, supplementary fig. 3–5). The *Fuersichnus* specimens are more likely specimens of *Palaeophycus* or *Phycodes* due to similar morphologies and lack of retrusive spreiten (e.g., Bromley & Asgaard, 1979; Ekdale, Bromley, & Pemberton, 1984; Hasiotis, 2002; Garvey & Hasiotis, 2008). Mángano (2011) interpreted media consistency (substrate control) and benthic oxygenation as the primary physicochemical controls on the Burgess Shale ichnofauna. The Burgess Shale ichnofauna likely represent shifts between a distal Cruziana and Zoophycos ichnofacies.

Ichnotaxonomy of Non-BST Cambrian deposits.—The Spence Shale shares ichnotaxa with multiple non-BST-bearing Cambrian deposits (Table 4).

The Cándana Quartzite of the Ediacaran–early Cambrian of northern Spain has reported 18 ichnogenera (Crimes & others, 1977) and shares 11 ichnogenera in common with the Spence Shale (Table 4). The Cándana Quartzite was deposited in tidal channels, and intertidal and subtidal sand bars (Crimes & others, 1977). No ichnofacies was assigned, but the ichnofossils present suggest a Cruziana Ichnofacies.

The Chapel Island and Random formations of the Ediacaran–early Cambrian in Canada has 27 ichnogenera (e.g., Crimes & Anderson, 1985; Droser & others, 2002) with 11 ichnogenera in common with Spence Shale (Table 4). The Cambrian-aged sections of the Chapel Island and Random formations record a transition from an offshore to prograding delta front to tidal-channel and tidal-flat setting. No ichnofacies was assigned to either the Chapel Island or Random formation, but likely contains a shift from a Cruziana Ichnofacies to Skolithos Ichnofacies. Most of the ichnogenera shared with the Spence Shale occur in the upward-thickening siltstones, mudstones, and thinly bedded sandstones of the prograding delta front, shoreface rippled siltstones and sandstone, or shifting sand bars and channels.

The Arumbera Sandstone of the Ediacaran–early Cambrian of central Australia contains 24 ichnogenera and shares 11 in common with the Spence Shale (Wells & others, 1970; Walter,

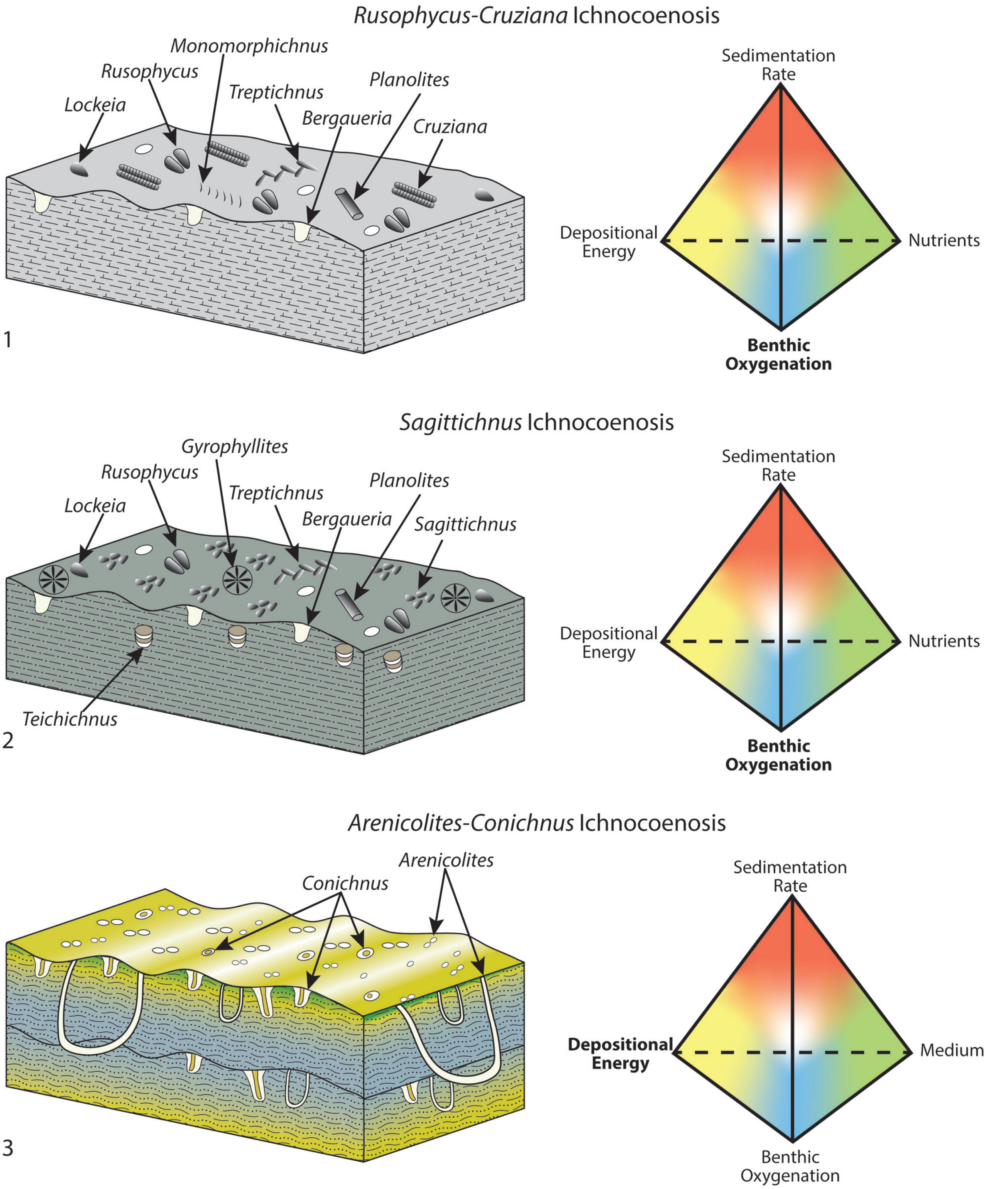

Figure 26. Spence Shale ichnocoenosis models and interpreted physicochemical controls. *1, Rusophycus-Cruziana* ichnocoenosis, dominant control: benthic oxygenation; *2, Sagittichnus* ichnocoenosis, dominant control: benthic oxygenation; *3, Arenicolites-Conichnus* ichnocoenosis, dominant control: depositional energy.

Formation	Age	Depositional Environment and Ichnofacies	Shared Ichnotaxa	References
Buen Formation, Sirius Passet Biota (Greenland)	early Cambrian	Deep marine: outer shelf and slope; Zoophycos or Nereites	*Gordia*, *Planolites*, and *Teichichnus*	Peel (2010); Ineson & Peel (2011)
Yu'anshan Formation, Chengjiang Biota (China)	early Cambrian	Shallow marine: continental shelf; distal Cruziana	*Arenicolites*?, *Gordia*?, *Planolites*? (no ichnotaxa were formally identified)	Zhang & others (2007); Huang & others (2014)
Kaili Formation, Kaili Biota (China)	early–middle Cambrian	Shallow marine: nearshore–continental shelf; Cruziana	*Arenicolites*, *Cruziana*, *Dimorphichnus*, *Diplichnites*, *Gordia*, *Monomorphichnus*, *Phycodes*, *Planolites*, *Rusophycus*, and *Treptichnus*	Yang (1994); Yang & Zhao (1999); Wang & others (2004, 2009); Lin & others (2010)
Burgess Shale (Canada)	middle Cambrian	Deep marine: outer shelf and slope; distal Cruziana–Zoophycos	*Cruziana*, *Diplichnites*, *Gordia*, *Planolites*, and *Treptichnus* (as '*Hormosiroidea*')	Allison & Brett (1995); Hagadorn (2002); Caron & others (2010, 2014); Mángano (2011)

Table 3. Ages, depositional environments, ichnofacies, and shared ichnotaxa of Cambrian BST deposits.

Elphinstone, & Heys, 1989) (Table 4). The Cambrian-aged upper half of the Arumbera Sandstone—which contains the majority of the ichnotaxa—was deposited in a shallowing, marine basinal to shoreface to prograding coastal delta-plain setting. While no ichnofacies was assigned, the Arumbera Sandstone likely contains two ichnofacies, Cruziana and Skolithos ichnofacies, and possibly a third, Nereites Ichnofacies. The Cruziana (and possible Nereites) Ichnofacies likely occurs in the gray-green shales interbedded with thin sandstones interpreted as basinal deposits. The Skolithos Ichnofacies likely occurs in the thick sandstones of the shoreface and prograding delta-plain deposits.

The Holy Cross Group (HCG) of the early Cambrian–Early Ordovician of the Polish Holy Cross Mountains contains nine formations ranging from shallow to deep marine and shares 16 of 43 ichnogenera with the Spence Shale (e.g., Orłowski, 1989, 1992; Orłowski & Żylińska, 2002; Stachacz, 2016) (Table 4). Six formations of the HCG were deposited during the middle Cambrian, but most units had low ichnodiversity (1–5 ichnogenera) except the early–middle Cambrian Ociesęki Sandstone Formation with a high ichnodiversity (43 ichnogenera; e.g., Orłowski, 1989, 1992; Orłowski & Żylińska, 2002; Stachacz, 2016). Middle Cambrian HCG units are composed mostly of clayey to silty shales and siltstones intercalated in fine-grained sandstones (Orłowski, 1989). The majority of ichnofossils from the HCG were assigned to the Cruziana Ichnofacies (e.g., Orłowski, 1989, 1992; Orłowski & Zylińska, 2002; Stachacz, 2012), whereas some specimens are representative of the Nereites Ichnofacies (Orłowski & Zylińska, 2002) and the Skolithos Ichnofacies in the upper portions Ociesęki Sandstone Formation (Stachacz, 2016).

The Mickwitzia Sandstone Member of the File Haidar Formation of the early Cambrian in Sweden is a shallow-marine unit deposited over a Precambrian basement and shares 8 of 24 ichnogenera with the Spence Shale (Table 4). The Mickwitzia Sandstone is composed mostly of thin-bedded, fine- to coarse-grained sandstones and siltstones interbedded with claystone, and a conglomeritic base. The majority of Mickwitzia ichnofossils (e.g., *Cruziana*, *Gyrolithes*, *Rosselia*, *Rusophycus*, and *Zoophycos*) occur in thinly bedded sandstone and siltstone on a mud-dominated shallow shelf assigned to the Cruziana Ichnofacies. Some intervals were assigned to the Skolithos Ichnofacies. Intervals assigned to the Cruziana Ichnofacies typically had an *ii*2–3; whereas, intervals assigned to the Skolithos ichnofacies had an *ii*3–4 (Jensen, 1997).

The Paseky Shale of the early Cambrian of the Czech Republic is a restricted shallow-marine, brackish lagoon or estuary, and shares all five ichnogenera with the Spence Shale (Table 4). The Paseky Shale is composed of alternating claystone and siltstone with fine-grained graywacke intercalations and numerous adhesion structures and wrinkle marks (Kukal, 1995). Paseky ichnofossils are restricted to a 3-m-thick section of light green, olive-, or gray-green laminated shale (Mikuláš, 1995). Most marine ichnotaxa are missing from the Paseky Shale indicating a continental or restricted marine environment (Mikuláš, 1995). Though not discussed by Mikuláš (1995), the reported ichnotaxa are suggestive of the Cruziana Ichnofacies.

The lower Cambrian (Terreneuvian–Series 2) of the White-Inyo Mountains, eastern California, USA, consists of five formations (Deep Spring, Campito, Poleta, Harkless, Saline Valley, and Mule Spring formations) of alternating terrigenous-clastic and carbonate sandstones and shales deposited on a shallow, subtidal shelf (e.g., Marenco & Bottjer, 2008). The White-Inyo Mountains contain 28 ichnogenera with 11 ichnogenera in common with the Spence Shale (e.g., Alpert, 1973, 1976a, 1976b; Alpert & Moore, 1975; Marenco & Bottjer, 2008) (Table 4). The majority of ichnofossils occur in micaceous siltstone and cross-bedded sandstones. The Alpert (1976a, 1976b) ichnofossils suggest multiple ichnofacies are recorded in the White-Inyo Mountains: (1) the Deep Spring Formation likely contains a distal Skolithos Ichnofacies due to the presence of *Diplichnites*, *Monocraterion* (rare), *Monomorphichnus*, *Planolites* (common), *Rusophycus*, and *Skolithos* (rare); (2) the Campito Formation likely records a shift from a distal Cruziana to proximal Cruziana Ichnofacies due to a shift in the ichnofossil suite from *Archaeonassa*, *Belorhaphe*, *Bergaueria*, *Cochlichnus*, *Helminthopsis*, *Rusophycus*, and *Scolicia* in the Andrews Mountain Member to *Archaeonassa*, *Astropolithon*?, *Dactyloidites*, *Monocraterion*, *Planolites*, *Skolithos*, and *Teichichnus* in the Montenegro Member; (3) the Poleta Formation likely contains a distal Skolithos Ichnofacies due to the presence of *Archaeonassa*, *Arthrophycus*?, *Bergaueria*, *Dolopichnus*, *Laevicyclus*, *Monocraterion*,

Formation	Age	Depositional Environment and Ichnofacies	Shared Ichnotaxa	References
Cándana Quartzite (Spain)	Ediacaran–early Cambrian	Shallow marine: intertidal; Cruziana	*Diplichnites*, *Gordia*, *Monomorphichnus*, *Nereites*, *Planolites*, and *Treptichnus*	Crimes & others (1977)
Chapel Island and Random formations (Canada)	Ediacaran–early Cambrian	Shallow marine: offshore–delta–tidal–coastal transition; shift from Cruziana to Skolithos	*Arenicolites*, *Bergaueria*, *Cruziana*, *Gordia*, *Monomporphichnus*, *Nereites*, *Phycodes*, *Planolites*, *Rusophycus*, *Scolicia*, and *Treptichnus*	Crimes & Anderson (1985)
Arumbera Sandstone (Australia)	Ediacaran–early Cambrian	Deep–Shallow marine: offshore–shoreface–coastal delta plain; Cruziana and Skolithos (possible Nereites)	*Arenicolites*, *Bergaueria*, *Diplichnites*, *Gordia*, *Monomorphichnus*, *Nereites*, *Phycodes*, *Planolites*, *Rusophycus*, *Taenidium* (as *Muensteria*), and *Treptichnus*	Wells & others (1970); Walter, Elphinstone, & Heys (1989)
Holy Cross Group (Poland)	early Cambrian–Early Ordovician	Deep marine: flysch; Skolithos, Cruziana, and Nereites	*Arenicolites*, *Bergaueria*, *Cruziana*, *Dimorphichnus*, *Diplichnites*, *Gordia*, *Halopoa*, *Monomorphichnus*, *Nereites*, *Phycodes*, *Planolites*, *Protovirgularia*, *Rusophycus*, *Scolicia*, *Teichichnus*, and *Treptichnus*	Orłowski (1989, 1992); Orłowski & Żylińska (2002); Stachacz (2016)
Mickwitzia Sandstone Member, File Haidar Formation (Sweden)	early Cambrian	Shallow marine: offshore–foreshore, intertidal, shelf; Glossifungites, Skolithos, Cruziana	*Bergaueria*, *Cruziana*, *Halopoa* (as *Palaeophycus*), *Monomorphichnus*, *Phycodes*, *Rusophycus*, *Teichichnus*, and *Treptichnus*	Jensen (1997)
Paskey Shale (Czech Republic)	early Cambrian	Terrestrial–Marine: Brackish Lagoon–Estuarine; Cruziana	*Bergaueria*, *Dimorphichnus*, *Diplichnites*, *Monomorphichnus*, and *Rusophycus*	Mikuláš (1995)
White-Inyo Mountian group (California, USA)	early Cambrian	Shallow marine: continental shelf; shift from distal Skolithos–distal Cruziana–proximal Cruziana–distal Skolithos–Cruziana	*Archaeonassa*, *Arenicolites*, *Bergaueria*, *Cruziana*, *Diplichnites*, *Monomorphichnus*, *Planolites*, *Rusophycus*, *Scolicia*, and *Teichichnus*	Alpert (1973, 1976a, 1976b); Marneco & Bottjer (2008)
Bright Angel Shale (Arizona, USA)	middle Cambrian	Shallow–Coastal marine: continental shelf–estruine; mixed Skolithos and Cruziana	*Bergaueria*, *Cruziana*, *Diplichnites*, *Dimorphichnus*, *Monomorphichnus*, *Phycodes*, *Rusophycus*, *Nereites* (as *Scalarituba*), *Scolicia*, *Teichichnus*, and *Treptichnus*	Elliot & Martin (1987); Lane & others (2003); Baldwin & others (2004)
Hanneh Member, Burj Formation (Jordan)	middle Cambrian	Shallow marine: prodelta–delta front–tidal-flat transition; Glossifungites and Cruziana	*Archaeonassa*, *Arenicolites*, *Bergaueria*, *Cruziana*, *Dimorphichnus*, *Diplichnites*, *Gordia*, *Monomorphichnus*, *Phycodes*, *Planolites*, *Rusophycus*, and *Treptichnus*	Hofmann & others (2012); Mángano & others (2013)
Bell Island and Wabana groups (Canada)	late Cambrian?–Early Ordovician	Shallow marine: offshore–delta–tidal–coastal transition; Skolithos and Cruziana	*Arenicolites*, *Aulichnites*, *Bergaueria*, *Cruziana*, *Dimorphichnus*, *Diplichnites*, *Gordia*, *Lockeia*, *Monomorphichnus*, *Nereites* (as *Neonereites*), *Phycodes*, *Planolites*, *Protovirgularia* (as *Uchrites*), *Rusophycus*, *Scolicia*, *Teichichnus*, and *Treptichnus* (as *Phycodes pedum*)	Fillion & Pickerill (1990)

Table 4. Ages, depositional environments, ichnofacies, and shared ichnotaxa of Cambrian non-BST deposits.

Planolites, *Psammichnites*, *Rusophycus*, *Scolicia*, *Skolithos* (common), and *Teichichnus*; and (4) the Harkless Formation likely contains an archetypal Cruziana Ichnofacies due to the presence of *Archaeonassa*, *Asteriacites*?, *Bergaueria*, *Cruziana*, *Diplichnites*, *Monocraterion*, *Monomorphichnus*, *Planolites*, *Rusophycus*, *Scolicia*, *Skolithos*, and *Teichichnus*. Alpert (1976a, 1976b) reported only a few ichnofossils from the Saline Valley (i.e., *Cruziana*, *Planolites*, and *Teichichnus*), and did not mention any from the Mule Spring Formation. Mount (1982) later assigned the Andrews Mountain Member of the Campito Formation to the Cruziana Ichnofacies.

The Bright Angel Shale (BAS) of the Grand Canyon area was deposited approximately at the same time as the Spence Shale (Cambrian, Series 3), and has been assigned to the *Glossopleura* trilobite biozone (Baldwin & others, 2004). The age and location of the BAS places it within the inner detrital belt of Robison (1960; see Fig. 2). The BAS shares 11 of 21 ichnogenera with the Spence Shale (Table 4). Low energy, silty and muddy laminated beds of the BAS dominated by *Cruziana* and *Diplichnites* are similar to Spence Shale beds containing *C. problematica*. There is still some debate, however, concerning the depositional environment of the BAS. Elliot and Martin (1987) and Lane and others (2003) proposed the BAS was deposited in a shelf environment influenced by both tides and storms; whereas, Baldwin and others (2004) argued the BAS is an estuarine deposit due to high concentrations of freshwater palynomorphs in the heterolithic sandstones and shales. While no ichnofacies was formally assigned to the BAS, Baldwin and others (2004) noted that elements of the Skolithos and Cruziana ichnofacies tend to mix and are juxtaposed within the same beds and could be assigned to a mixed Skolithos-Cruziana ichnofacies.

The Hanneh Member of the Burj Formation of the middle Cambrian in the Dead Sea Basin, Jordan, contains 19 ichnogenera and was deposited in a shallow marine prodelta–delta-front to tidal-flat system (Hofmann & others, 2012; Mángano & others, 2013). The Hanneh Member is composed mostly of siliciclastic mudstone and crossbedded to laminated, fine- to medium-grained sandstone with a limestone base, with ichnofossils present in mudstone and sandstone. Twelve of the 19 Hanneh ichnogenera are also present in the Spence Shale (Table 4). Two ichnofacies were assigned to the Hanneh Member: a Glossifungites Ichnofacies represented by *Diplocraterion*—suggesting high depositional energy and significant erosion—and a Cruziana Ichnofacies represented by *Cruziana*, *Diplichnites*, *Gyrolithes*, and *Rusophycus*—suggesting soft to firmground media in low-energy settings.

The upper Cambrian?–Lower Ordovician Bell Island and Wabana groups of Newfoundland, Canada, is well-studied shallow marine (e.g., onshore lagoon, tidal flat, delta front, etc.) to offshore transition zone deposits. The Bell Island and Wabana groups contain 39 ichnogenera and share 17 ichnogenera with the Spence Shale (Table 4). Many of the shared ichnofossils occur in delta front, middle tidal flat, and lagoonal deposits. The domichnia-dominated sandstones of the subtidal, shoreface, foreshore, and sandbar deposits were assigned to the Skolithos Ichnofacies; whereas the fodinichnia-dominated thin sandstones and shales of the intertidal-flat, lagoonal, and delta-front deposits were assigned to the Cruziana Ichnofacies (Fillion & Pickerill, 1990).

Summary.—The Spence Shale shares more ichnogenera in common with shallow-marine BST deposits than with most deep-marine BST deposits. The moderate number of domichnia and repichnia ichnofossils present and higher ichnodiversity of the Spence Shale is more similar to shallow-marine BST deposits (i.e., Kaili Biota), suggesting that the ichnofossil-bearing beds of the Spence Shale were deposited in a shallower environment on the distal ramp than previously thought. Low *ii* (*ii*2–3) but low to high BPBI (BPBI 2–5) suggest the Spence Shale ichnofauna was predominantly controlled by fluctuating benthic oxygenation (*sensu* Garson & others, 2012). Periodic tempestite deposition (Robison, 1991) and soft-sediment deformation, orientated *Rusophycus* and ripple marks, and frequent pascichnia suggest sedimentation rate, depositional energy, and nutrient availability also had significant influence on the Spence Shale ichnofauna, respectively. The degree of similarity between the Spence Shale and Kaili Biota ichnofaunas, however, may also be to due to the fact that deep-marine BST deposits are more understudied ichnotaxonomically than their shallow-marine counterpart. When more ichnotaxonomic research on deep-marine BST deposits is available, a better comparison can be made.

The Spence Shale ichnofauna is similar to both shallow- and deep-marine, non-BST Cambrian ichnofaunas. The Spence Shale ichnofauna occurs in calcareous to siliciclastic, silty to sandy shales to sandstone like the BAS, Chapel Island and Random, HCG, Mickwitzia Sandstone, and Paseky Shale ichnofaunas. The similarity between the non-BST shallow- and deep-marine ichnofauna and lithofacies associations suggests the Spence Shale was deposited, in part, on a middle section of the distal ramp, where controlling physicochemical factors from shallow and deep settings (e.g., benthic oxygenation, depositional energy, and nutrient availability) could influence the Spence Shale ichnofauna (see Fig. 2). The lack of extensive endobenthic fodinichnia (e.g., *Chondrites*, *Cosmorhaphe*, or *Zoophycos*) or agrichnia (e.g., *Paleodictyon*)—suggestive of low energy and high dysoxia—suggests the studied shales of the Spence Shale were not basinal deposits. The lack of extensive or reinforced domichnia (e.g., *Palaeophycus*, *Skolithos*, or *Thalassinoides*) or reworked equilibrichnia (e.g., *Diplocraterion*)—suggestive of high depositional energy and/or rapidly shifting media—suggests the studied shales were not deposited proximally to the carbonate platform.

CONCLUSIONS

1. The Spence Shale is most known for its numerous and highly well-preserved body fossils, especially trilobites. The Spence Shale is now also known for its numerous ichnofossils and highly diverse ichnofossil assemblage with 24 ichnogenera and 35 ichnospecies. Ichnofossils of the Spence Shale primarily occur in light to dark gray, calcareous or siliciclastic shale, and represent cubichnia, domichnia, fodinichnia, pascichnia, praedichnia, and repichnia behaviors.

2. A new ichnospecies, *Archaeonassa jamisoni*, is proposed for short, downward excavations with rimmed margins. *Ptychoplasma* (*Protovirgularia*) *vagans* is emended and transferred to *Treptichnus* as *T. vagans*.

3. Three ichnocoenoses were constructed and two ichnofacies were assigned to the Spence Shale: (1) a distal Cruziana Ichnofacies representing low- to moderate-energy deposition in oxygen- and nutrient-controlled ichnocoenoses (e.g., *Rusophycus-Cruziana* and *Sagittichnus*); and (2) a depauperate, distal Skolithos Ichnofacies representing moderate- to high-energy deposition with *Arenicolites* and *Conichnus* as representative ichnotaxa (i.e., *Arenicolites-Conichnus* ichnocoenosis). The Spence Shale ichnofauna was controlled by benthic oxygenation, depositional energy, and nutrient availability.

4. The Spence Shale contains numerous BST fossils and ichnofossils and has the second highest known ichnodiversity of BST deposits, and shares more ichnotaxa in common with shallow-marine systems (~11–12 ichnogenera; e.g., Kaili Biota, Hanneh Member of the Burj Formation) than deep-marine systems (~2–4 ichnogenera; e.g., Burgess Shale, Sirius Passet Biota of the Buen Formation), suggesting deposition on shallower parts of the distal ramp setting.

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DEDICATION

This paper is dedicated to the memory of Lloyd Gunther (1917–2013), the patriarch of the generous fossil-collecting Gunther family, whose large contributions and donations of fossil specimens to numerous museums and universities have enabled a significant portion of Earth's past biodiversity to come alive again.

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