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AN ICHNOTAXONOMIC ASSESSMENT OF THE CRETACEOUS DAKOTA GROUP, FRONT RANGE, COLORADO, USA, AND ITS COMPARISON TO OTHER WESTERN INTERIOR SEAWAY DEPOSITS

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Thalassinoides suevicus and *Zoophycos insignis* in the upper part of the Glencairn Formation in the Dakota Group at Skyline Drive, Cañon City, Colorado. They appear to form a compound burrow system, with *T. Suevicus* representing domichnia (dwelling behavior) and *Z. insignis* representing fodinichnia (deposit-feeding behavior) by the same tracemaker. Photograph by S. T. Hasiotis.

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ABSTRACT

The Aptian-Cenomanian Dakota Group along the Colorado Front Range is known for its dinosaur tracks; however, it also contains extensive invertebrate marine and continental trace fossils. The Dakota Group in Colorado is subdivided into the Lytle, Plainview, Glencairn (Cañon City), Skull Creek Shale (Denver, Fort Collins), and Muddy formations. Thirty-two invertebrate ichnogenera and 34 ichnospecies were identified: *Archaeonassa, Arenicolites, Asterosoma, Asthenopodichnium, Aulichnites, Chondrites, Cochlichnus, Conichnus, Cruziana, Cylindrichnus, Diplocraterion, Gyrolithes, Lockeia, Macaronichnus, Margaritichnus, Naktodemasis, Ophiomorpha, Palaeophycus, Planolites, Protovirgularia, Rhizocorallium, Rosselia, Rusophycus, Schaubcylindrichnus, Scolicia, Skolithos, Taenidium, Teichichnus, Teredolites, Thalassinoides, Treptichnus*, and *Zoophycos*. Six tetrapod ichnogenera and three ichnospecies were identified: *Caririchnium, Dromaeosauripus, Hatcherichnus, Ostendichnus, Magnoavipes,* and *Tetrapodosaurus*. Three tetrapod ichnogenera *Chelonipus, Ignotornis*, and *Mehliella* have been reported at other sites in the Dakota Group, but none were found at our study sites. Rhizohaloes are reported in the Muddy Formation. Three vertebrate ichnogenera and two ichnospecies were previously described elsewhere by other workers. The Dakota Group trace fossils comprise eight ichnocoenoses–*Caririchnium, Diplocraterion, Lockeia, Naktodemasis, Rhizohalo, Scolicia, Skolithos-Teichichnus*, and *Zoophycos*–representing dwelling, deposit- and filter-feeding, and locomotion behaviors of plants, invertebrates, and tetrapods. Twelve previously unreported ichnogenera were identified: *Archaeonassa, Asthenopodichnium, Conichnus, Cylindrichnus, Gyrolithes, Macaronichnus, Naktodemasis, Protovirgularia, Rusophycus, Taenidium, Treptichnus,* and *Zoophycos*. This study is the first systematic ichnotaxonomic assessment of the invertebrate trace fossils of the Dakota Group along the Colorado Front Range, which has the highest reported ichnodiversity when compared to other Western Interior Seaway deposits.

Keywords: Trace fossils, continental, marine, invertebrate, vertebrate, ichnofacies

INTRODUCTION

The objective of this study is to conduct an ichnotaxonomic assessment of the trace fossils within the Dakota Group that can be used to better interpret paleoenvironmental and paleoecological settings of the strata that comprise the members and formations along the Colorado Front Range. Trace fossils are commonly used to reconstruct the depositional settings and paleoenvironments (Gustason & Kauffman, 1985) that are used to help define sandbody and seal geometries in a sequence-stratigraphic framework (Weimer, 1970; Clark, 1978; Savrda, 1991b; Graham & Ethridge, 1995; Gingras & others, 2009; van der Kolk, Flaig, & Hasiotis, 2015; Flaig & others, 2019). Outcrops located in the Colorado Front Range are commonly used as analogs for subsurface reservoirs and seals in the Denver Basin (Ladd, 2001; Higley, Cox, & Weimer, 2003). The Dakota Group is internationally known for its early Late Cretaceous dinosaur tracks, particularly those that are found at Dinosaur Ridge, which is a National Natural Landmark (Lockley & Marshall, 2017). These track sites within the Dakota Group record the interactions of herbivores, omnivores, and carnivores that coexisted in alluvial, coastal plain, and shallow marine environments. For this reason, most ichnotaxonomic research has focused on tetrapods (Matsukawa, Matsui, & Lockley, 2001; Houck

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& others, 2010; Lockley, Cart & others, 2014a; Lockley & Gierlinski, 2014b; Lockley, Honda, & Simmons, 2014d). Invertebrate trace fossils, however, are more accurate indicators of the physicochemical conditions that affected organism distribution within paleoenvironments (MacEachern & Pemberton, 1992; Hasiotis, 2004, 2007, 2008; Hasiotis & Platt, 2012; Hasiotis & others, 2012; MacEachern & others, 2012b). Only a few researchers have used invertebrate trace fossils to help interpret paleoenvironments within Dakota Group outcrops (Weimer, 1970; MacKenzie, 1975; Chamberlain, 1985; Gustason & Kauffman, 1985).

No ichnotaxonomic assessment of trace fossils has been conducted for the Dakota Group. Some of the traces described previously are in open nomenclature (Weimer, 1970), or have been renamed or amended in more recent work (Clark, 1978; Frey & Howard, 1981; Miller III, 1995; Hammersburg, Hasiotis, & Robison, 2018). There is also potential for new discoveries of previously unreported ichnotaxa. The current status of the Dakota Group ichnotaxonomy creates such problems as: 1) misidentification of trace fossils; 2) perpetuating open nomenclature; and 3) misinterpreting depositional environments and paleoecological settings based on the lack of understanding of the ichnotaxa in outcrop and core.

The purpose of this study is to: (1) document the ichnofossils and ichnodiversity of the Dakota Group; (2) establish ichnocoenoses and assign ichnofacies; and (3) compare the Dakota Group ichnotaxa to ichnotaxa present elsewhere in the Western Interior Seaway. Studies on ichnotaxonomy in Dakota Group deposits can allow the interpretation of the physicochemical controls on the types and degrees of bioturbation and the establishment of ichnocoenoses and ichnofacies.

This is the first study to conduct a detailed ichnotaxonomic analysis of the ichnofossils in the Dakota Group along the Colorado Front Range. This study will examine trace fossils across a large geographic area to form a baseline for the ichnotaxonomy of the Dakota Group. There have been numerous studies that have examined the trace fossils in the Western Interior Seaway (e.g., Howard & Frey, 1984; MacEachern & Pemberton, 1992, 1994; Scott & others, 2004; Gani, Bhattacharya, & MacEachern, 2009), only a few of which have systematically described the trace fossils (e.g., Frey & Howard, 1985).

BACKGROUND

The Dakota Group was named by the Hayden Survey in Colorado conducted in 1873 (Hayden, 1873; see also Waage, 1955). The name comes from the Dakota Formation in Nebraska, due to the Dakota Group having similarities to that formation (Hayden, 1873, Waage, 1955). The Colorado strata were briefly named the Dakota Formation, until Walcott (1903) officially referred to those strata as the Dakota Group. In the 1950's the Dakota Group was subdivided by Waage (1953, fig. 2) in the Cañon City area into the Purgatoire Formation and the Dakota Formation. The Purgatoire Formation was further subdivided into the Lytle and Glencairn members. In the northern portion of the Colorado Front Range near Denver and Fort Collins, Colorado, Waage (1955) subdivided the Dakota Group into the Lytle Formation and South Platte Formation. The South Platte Formation was subdivided into the Plainview, Third Shale, Third Sandstone, Second Shale, Kassler Sandstone, Van Bibber Shale, and First Sandstone members, in ascending order. These subdivisions have been contested by other researchers because they are difficult to identify in outcrop (Mackenzie, 1965; Weimer & Land, 1972). In outcrops around Fort Collins, Mackenzie (1965) reorganized the South Platte Formation into the Plainview Formation, Skull Creek Shale, and Muddy Formation. These subdivisions have also been applied to the Dakota Group in the outcrops around Denver (Weimer & Land, 1972; Clark, 1978; Ladd, 2001; Higley, Cox, & Weimer, 2003). The stratigraphic nomenclatures of both Waage (1955) and Mackenzie (1965) are still in use, with some researchers using one or the other or a combination of both (Graham & Ethridge, 1995; Matsukawa, Lockley, & Hunt, 1999; Lockley, Simmons, & Daggett, 2014f). In the southern Colorado Front Range, the Purgatoire Formation was reorganized by Altschuld (1980) into the Lytle, Plainview, Glencairn, and Muddy formations, which are still in use (e.g., Gustason & Kauffman, 1985; Holbrook & Dunbar, 1992; Holbrook, 2001; Kurtz, Lockley, & Engard, 2001). To create a more uniform correlation between the northern (near Fort Collins to Denver) and southern (near Cañon City) outcrops of the Dakota Group, this study uses stratigraphic nomenclature proposed by Mackenzie (1965) and Altschuld (1980).

Most of the past researchers of the Dakota Group focused on stratigraphic correlations of interest to the petroleum industry, whereas others concentrated on paleoenvironmental interpretations (Waage, 1961; Weimer, 1970; Clark, 1978; Altschuld, 1980; Gustason & Kauffman, 1985; Weimer & Sonnenberg, 1989; Holbrook & Dunbar, 1992; Odien, 1997; Ladd, 2001; Higley, Cox, & Weimer, 2003). Invertebrate trace fossils have been identified by some of these researchers (Table 1), with only Odien (1997) examining the trace fossils in any detail. Whereas more recent researchers have shifted toward studying trace fossils, their focus is only on tetrapod ichnology with an emphasis on dinosaur footprints and trackways (Matsukawa, Lockley, & Hunt, 1999; Kurtz, Lockley, & Engard, 2001; Lockley & others, 2016a, 2016b; Lockley & others, 2018a).

Some trace fossils named in the Dakota Group, such as *Asterosoma zoned, Micatuba, Syphanites,* and *Terebellina,* are examples of problematic ichnotaxa. *Micatuba* and *Terebellina* have been either renamed or made junior synonyms of other ichnogenera. *Micatuba* (Chamberlain, 1971) was renamed *Arenituba* by Stanley and Pickerill (1995) because *Micatuba* was already applied to a genus of an agglutinated foraminifer. *Terebellina* is no longer considered as a valid ichnogenus, due to the name being used for an annelid body fossil, aside from its similarities to *Palaeophycus* and *Schaubcylindrichnus* (e.g., Miller III, 1995). The ichnotaxon *Asterosoma zoned* (Holbrook & Ethridge, 1996) does not exist in the literature. The ichnotaxon *Syphanites* was not figured by Holbrook (2001). It also does not exist elsewhere in the literature, and may be a misspelling of *Siphonites* (e.g., Häntzchel, 1975).

GEOLOGIC SETTING

The Dakota Group in the Colorado Front Range was deposited during the Aptian–Cenomanian ages (Lower to Upper Cretaceous) along the western edge of the Western Interior Seaway (Fig. 1)

Formation	Invertebrate Trace Fossil	Vertebrate Trace fossils	Plant traces	References
Lytle Formation	*Arenicolites, Skolithos*			Basan & Scott, 1979; Altschuld, 1980; Gustason & Kauffman, 1985
Plainview Formation	*Arenicolites, Margaritichnus, Ophiomorpha, Palaeophycus, Planolites montanus, Planolites* isp., *Rhizocorallium jenense, Skolithos, Teredolites, Thalassinoides, Trichichnus*	*Magnoavipes caneeri, Dromaeosauripus* isp. *Tetrapodosaurus* isp.	Plant roots	Basan & Scott, 1979; Altschuld, 198 Grube, 1984; Gustason & Kauffman 1985; Odien, 1997; Kurtz, Lockley, & Engrad, 2001
Glencairn Formation	*Arenicolites, Aulichnites, Chordites, Crossopodia, Micatuba, Ophiomorpha, Palaeophycus, Paleodictyon, Planolites, Rosselia, Rhizocorallium, Schaubcylindrichnus, Scolicia, Skolithos, Thalassinoides, Trichichnus*			Altschuld, 1980; Gustason & Kauffman, 1985; Odien, 1997
Skull Creek Shale	*Anchonichnus anchonichnus, Anchonichnus horizontalis, Arenicolites curvatus, Arenicolites sparsus, Arenicolites* isp., *Asterosoma zoned, Asterosoma* isp., *Crossopodia scotia, Ophiomorpha irregularis, Palaeophycus herberti, Planolites beverleyensis, Planolites* isp., *Terebellina, Schaubcylindrichnus coronus, Teichichnus rectus*			Graham & Ethridge, 1995; Holbrook, 1996
Muddy Formation	*Arenicolites, Asterosoma, Cochlichnus, Corophioides, Cruziana, Diplocraterion parallelum, Lockeia, Ophiomorpha nodosa, Ophiomorpha* isp., *Planolites beverleyensis, Planolites* isp., *Rhizocorallium, Rosselia, Terebellina, Skolithos, Syphanites, Teichichnus, Teredolites, Thalassinoides, Trichichnus*	*Caririchnium leonardii, Hatcherichnus* isp., *Ignotornis* isp., *Magnoavipes caneeri, Mehliella jeffersonensis, Ostendichnus bilobatus,* Pterosaur swim tracks	Rhizoliths	Clark, 1978; Altschuld, 1980; Grube, 1984; Chamberlain, 1985; Gustason & Kauffman, 1985; Holbrook, 1996; Odien, 1997; Lockley & others, 2009; Lockley & Schumacher, 2014; Lockley & others 2016

Table 1. Previously documented trace fossils from the Dakota Group.

(e.g., Nazworth, 2019; Singer & others, 2020). In southern Colorado, near Cañon City, the Dakota Group consists of the Lytle, Plainview, Glencairn, and Muddy formations, in ascending order. In central and northern Colorado (Fig. 2) (from Denver to Fort Collins) the Dakota Group consists of the Lytle, Plainview, Skull Creek Shale, and Muddy formations (Fig. 2) (e.g., Mackenzie, 1965; Weimer & Land, 1972).

The Lytle Formation is a 3.4–33-m-thick succession that is reddish yellow (7.5YR 7/8) to strong brown (7.5YR 5/8), red (2.5YR 4/8), and dark red (10R 3/6). The Lytle Formation fines upward from medium- to coarse-grained sandstones into fine- to very fine-grained sandstones. Grains are subrounded to rounded, with some sandstones being poorly sorted and others being moderately well sorted. The sandstones are interbedded with siltstone and mudstone. Outcrops at Horsetooth Reservoir, Grape Creek, I-70, and Skyline Drive have a basal conglomerate layer. Trough-cross-stratification, tabular-cross-stratification, and planar bedding are present throughout the Lytle Formation (Fig. 3). The Lytle Formation represents a series of braided fluvial environments (Weimer & Land, 1972; Altschuld, 1980; Grube, 1984; Gustason & Kauffman, 1985; Holbrook & Ethridge, 1996).

The Plainview Formation is a 4–17.7-m-thick succession that is reddish yellow (7.5YR 7/8), white (10R 8/1), and light red (2.5YR 6/8) with very fine- to medium-grained, subrounded to rounded, moderately well-sorted sandstones. The sandstones in the lower part of the formation are commonly interbedded with intervals of mudstone and siltstone. The Plainview Formation fines upward in most outcrops. In the lower parts of the Plainview Formation, trough-crossbedding and planar bedding are present, whereas the middle and upper parts can have tabular-crossbedding, planar bedding, ripple marks, herringbone cross stratification, and flaser, wavy, and lenticular bedding (Fig. 3). At Cañon City, the lower part has several conglomerate beds that alternate with sandstone (Fig. 3; Waage, 1953; Odien, 1997). The upper part of the Plainview Formation at Cañon City is highly bioturbated and truncated by a disconformity (e.g., Waage, 1953; Odien, 1997). At Horsetooth Reservoir, the upper part of the Plainview Formation locally contains syndepositional deformation of heterolithic bedsets. The lower parts of the Plainview Formation represent mostly fluvial-dominated environments, whereas the upper parts represent intertidal or subtidal marine environments (Weimer & Land, 1972; Wescott, 1979; Altschuld, 1980; Grube, 1984; Gustason & Kauffman, 1985; Holbrook & Ethridge, 1996; Odien, 1997).

The Glencairn Formation is a 19.2–21.2-m-thick succession consisting of four to seven coarsening-upward sequences. Each sequence consists of laminated very dark gray (7.5YR 3/1) to black (7.5YR 2.5/1) shale interbedded with white (10R 8/1), very fine-grained sandstone to siltstone that grades upward into a reddish yellow (7.5YR 7/8) to strong brown (7.5YR 5/8), very fine- to fine-, moderate- to well-sorted, subrounded- to well-rounded sandstone beds (Fig. 3). The shale beds have an overall decrease in thickness up-section, whereas sandstones have an overall increase in thickness up-section. The shales lack visible bedding, whereas small symmetrical ripple marks are present in the sandstone beds (Fig. 3). The body fossil *Inoceramus comancheanus* occurs in some intervals and has been used to date this formation to the Albian. The Glencairn Formation represents the Kiowa-Skull Creek cyclothem and is interpreted as a progradational deltaic succession (e.g., Waage, 1953; Altschuld, 1980; Gustason & Kauffman, 1985; Odien, 1997).

The Skull Creek Shale is a 6.5–30-m thick, black (5YR 2.5/1) shale interbedded with white (10R 8/1), reddish yellow (7.5YR

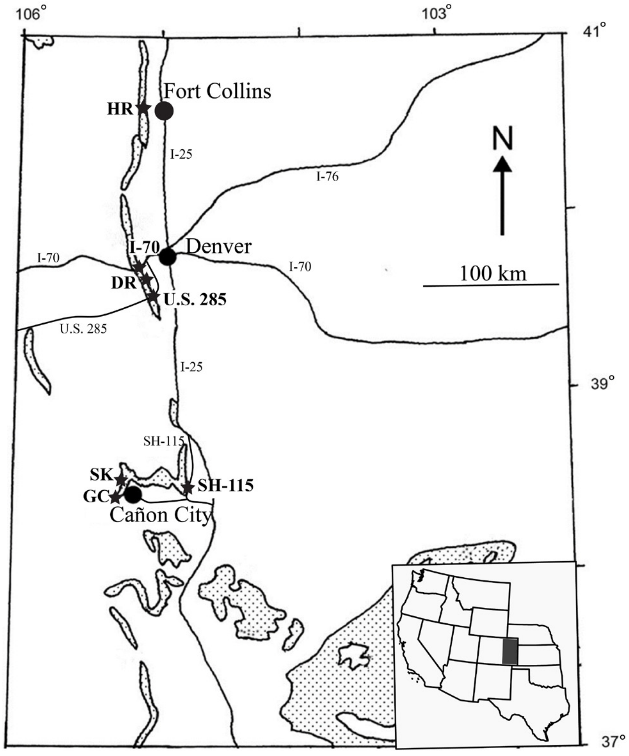


Figure 1. Map of study localities of the Dakota Group along the Colorado Front Range. Inset map of western U.S. with black area highlighting of eastern Colorado. Stars are localities: Cañon City, Denver, and Fort Collins areas: GC (Grape Creek); SK (Skyline Drive); Colorado State Highway-115; U.S. Route 285; DR (Dinosaur Ridge); I-70; and HR (Horsetooth Reservoir). Modified from Lockley & others (2006).

7/8), to yellowish red (5YR 5/8), fine- to very fine-grained sandstone and siltstone (Fig. 3). Intervals of kaolinite are common in several outcrops near Denver. At Dinosaur Ridge, I-70, and U.S. Route 285, the Skull Creek Shale exhibits very little bedding. In outcrops near Fort Collins, gutter casts and hummocky cross-stratification are common in sandstones (e.g., Fig. 3; Graham & Ethridge, 1995), and bentonite beds are common in fine-grained deposits (e.g., Graham & Ethridge, 1995). *Inoceramus comancheanus* is commonly present in fine-grained deposits (e.g., Holbrook & Ethridge, 1996). At Dinosaur Ridge, I-70, and U.S. Route 285, the Skull Creek Shale represents a marine embayment, whereas it represents a middle to lower shoreface environment at Horsetooth Reservoir (Weimer & Land, 1972; Grube, 1984; Graham & Ethridge, 1995; Holbrook & Ethridge, 1996).

The Muddy Formation ranges from 8–44 m thick and is subdivided into several members along the Colorado Front Range (Fig. 2). Outcrops near Fort Collins are subdivided into the Fort Collins and Horsetooth members in ascending order (e.g., MacKenzie, 1965). Outcrops near Cañon City are subdivided into the Channel Sandstone Member and Upper Transitional Member in ascending order (e.g., Altschuld, 1980). Outcrops near Denver have not been subdivided (Clark, 1978). At Cañon City, plant fragments are present in both members. The Channel Sandstone Member is a reddish yellow (7.5YR 7/8), medium- to fine-grained, subrounded to moderately well-sorted sandstone, with tabular and trough cross-stratified beds (Fig. 3). The Upper Transitional Member is a reddish yellow (7.5YR 7/8), fine-grained, well-rounded and well-sorted sandstone and interbedded with gray (7.5YR 5/1) shales (Fig. 3). Trough cross-stratification, asymmetrical ripple marks, desiccation cracks, and syneresis cracks are present. The upper part of this member at Skyline Drive has a sulfur smell. The Channel Sandstone Member represents a fluvial environment, whereas the Upper Transitional Member represents an intertidal environment (e.g., Altschuld, 1980; Gustason & Kauffman, 1985; Odien, 1997).

In the Denver area, the lower parts of the Muddy Formation are a reddish yellow (7.5YR 6/8) very fine- to fine-grained, subrounded to rounded, moderately well-sorted sandstone. In lower part of the Muddy Formation, symmetrical ripple marks with syneresis cracks are present, which are over- or underlain by medium-grained sandstones with asymmetrical ripple marks (Fig. 3). The middle part of the Muddy Formation consists of reddish yellow (7.5YR 7/8), strong brown (7.5Y 5/8), white (10R 8/1), very fine- to fine-grained, well-rounded, and moderately well-sorted sandstone with symmetrical ripple marks. A thin paleosol and an interval bearing dinosaur tracks (Fig. 3) is present in the middle part of the Muddy Formation. The upper parts of this formation contain reddish yellow (7.5YR 7/8), white (10R 8/1), very fine- to fine-grained, well-rounded, and moderately well-sorted sandstones consisting of tabular and trough-crossbed sets and symmetrical ripple marks with syneresis cracks (Fig. 3). Some of the sandstone beds in the upper part of the Muddy Formation are interbedded with mudstones. Plant fragments are present in each of the different parts of the Muddy Formation. The Muddy Formation represents paralic and transitional environments, such as intertidal and coastal plain (e.g., Weimer & Land, 1972; MacKenzie, 1975; Clark, 1978; Chamberlain, 1985).

At Fort Collins, the Fort Collins Member of the Muddy Formation is a white (10R 8/1), very fine-grained, well-rounded, and well-sorted sandstone with planar bedding (Fig. 3). The Horsetooth Member is a red (2.5Y 4/8), fine- to medium-grained sandstone with planar-tabular and trough-cross-stratified beds (Fig. 3). The Fort Collins Member represents a deltaic environment deposited during sea-level highstand, whereas the Horsetooth Member represents fluvial and estuarine deposits that infilled an incised valley (e.g., MacKenzie, 1965; Holbrook & Ethridge, 1996).

MATERIAL AND METHODS

Material for this study comes from Dakota Group outcrops in Colorado at: 1) Skyline Drive and Grape Creek near Cañon City; 2) Horsetooth Reservoir near Fort Collins; 3) I-70, Dinosaur Ridge, and U.S. Route 285 near Golden and Morrison; and 4) Colorado State Highway 115 near Penrose (Fig. 1). Specimens were measured using a metric scale ruler and tape. Winding traces were measured along the length of the trace using string, which was measured longitudinally with the tape. Photographs were taken using a Canon EOS Rebel T7 and processed with Adobe Photoshop^{TM} Creative Cloud version.

Strata at each outcrop were described by thickness, color, grain size, grain type, degree of sorting, sedimentary structures, and bedding morphology (e.g., Riese, Hasiotis, & Odier, 2011; van der Kolk, Flaig, & Hasiotis, 2015; Fischer & Hasiotis, 2018).

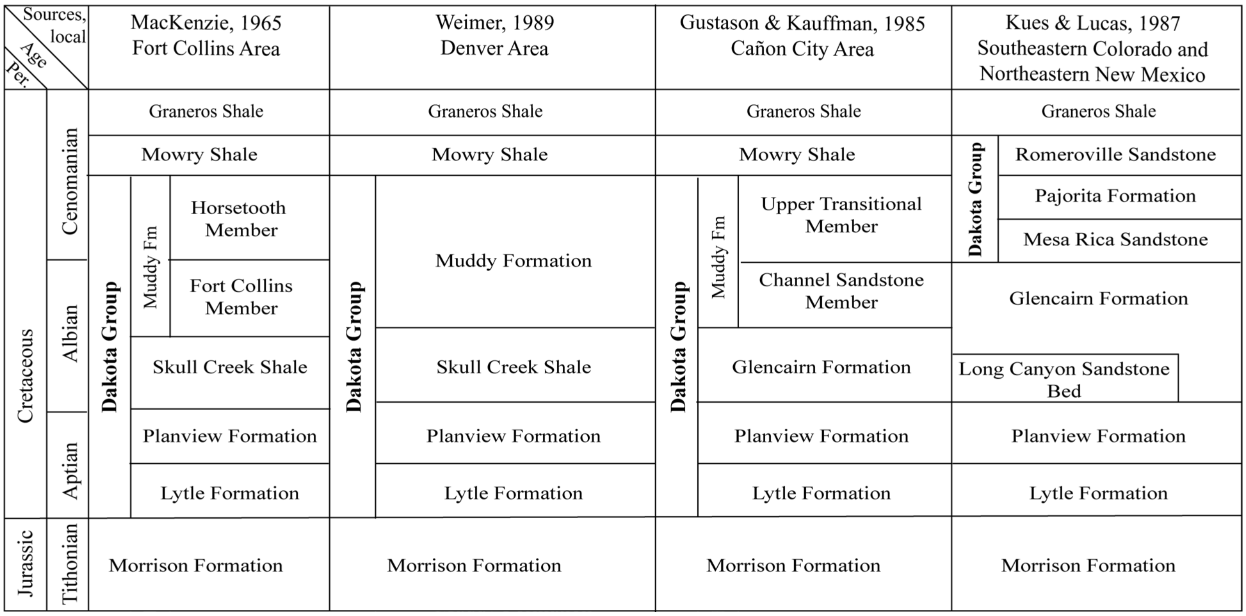


Figure 2. Stratigraphic correlation chart of the Dakota Group within eastern and southeastern Colorado and northeastern New Mexico.

Lithofacies were characterized by grain size, dominant sedimentary structures, and trace fossils and grouped into lithofacies associations to interpret depositional environments (e.g., Gustason & Kauffman, 1985; Graham & Ethridge, 1995; Fischer & Hasiotis, 2018; Flaig & others, 2019). Color was characterized by Munsell Soil Color Charts, 1994 Revised Edition. Formations and members were identified in outcrop according to MacKenzie (1965) and Altschuld (1980).

Invertebrate traces were described by their architectural and surficial morphologies and fill pattern to identify key characteristics to assign them to an ichnotaxon (e.g., Hasiotis & Mitchell, 1993; Bromley, 1996). Outcrops with bioturbation were characterized with the ichnofabric index (ii; Droser & Bottjer, 1986): ii1=0% disruption; ii2=0–10% disruption; ii3=10–40% disruption; ii4=40–60% disruption; ii5=60–100% disruption, burrows still discrete in places, fabric not mixed; ii6=>100% disruption, bedding is homogenized.

Bedding planes were characterized with the bedding-plane bioturbation index (BPBI; Miller & Smail, 1997): BPBI 1=0% disruption; BPBI 2=0–10% disruption; BPBI 3=10–40% disruption; BPBI 4=40–60% disruption; BPBI 5=60–100% disruption. Rhizoliths were described by morphology, size, color(s), lithology, and the enclosing matrix (e.g., Kraus & Hasiotis, 2006).

Ichnocoenoses were determined through immediate horizontal and vertical associations of the trace fossils and named according to the most abundant trace(s) (Hasiotis, 2004, 2008; Fischer & Hasiotis, 2018; Hammersburg, Hasiotis, & Robison, 2018). Paleoenvironments were determined by the lithofacies, physicochemical characteristics recorded by the traces in the ichnocoenoses, and their occurrence in facies associations (Reineck & Singh, 1980; Bown & Kraus; 1983; MacEachern & Pemberton, 1992; Hasiotis & Dubiel, 1994; Holbrook, 1996; Hasiotis 2004, 2007, 2008; MacEachern & others, 2005; Kraus & Hasiotis, 2006; Hasiotis, McPherson, & Reilly, 2013; Fischer & Hasiotis, 2018; Hammersburg, Hasiotis, & Robison, 2018). Ichnofacies were determined by the association of recurrent ichnocoenoses and lithofacies associations (Pemberton & MacEachern, 1995; MacEachern & others, 2012a; Flaig & others, 2019).

SYSTEMATIC ICHNOLOGY

TRACES OF PLANTS

RHIZOHALOES

Figure 4.1, 4.2

Description.—Subhorizontal to subvertical, straight to winding, simple to branching traces light bluish gray (Gley 8/1) in color vs bluish gray (Gley 5/1) matrix. Preserved in epirelief. Traces are 10–60 mm long (exposed length) and 2–3 mm wide. Width of traces slightly decreases between the main trace and side branches.

Occurrence.—Bluish gray, silty, pedogenically modified mudstone. Traces are present in the middle part of the Muddy Formation at Dinosaur Ridge.

Associated ichnotaxa.—None.

Discussion.—Traces are interpreted as rhizohaloes (traces of plant roots) based on the color contrast between the trace and matrix, absence of original root material or fill material within the root channels, changes in diameter between orders of branches, and distal tapering of terminal segments (e.g., Kraus & Hasiotis, 2006; Fischer & Hasiotis, 2018). Roots are used by plants as a holdfast as well as to obtain water and macro- and micronutrients from the surrounding soil (e.g., Brady & Weil, 2002; Schaetzl & Anderson, 2005). Rhizohaloes, as well as rhizoliths and rhizocretions, remain in open nomenclature because of the labile morphologic expression and response of moisture- and nutrient-seeking behaviors in sediment at the time of growth due to local physicochemical conditions (e.g., Hasiotis, 2002, 2004, 2008; Kraus & Hasiotis, 2006; Hasiotis & others, 2012, Hasiotis, McPherson, & Reilly, 2013; Fischer & Hasiotis, 2018).

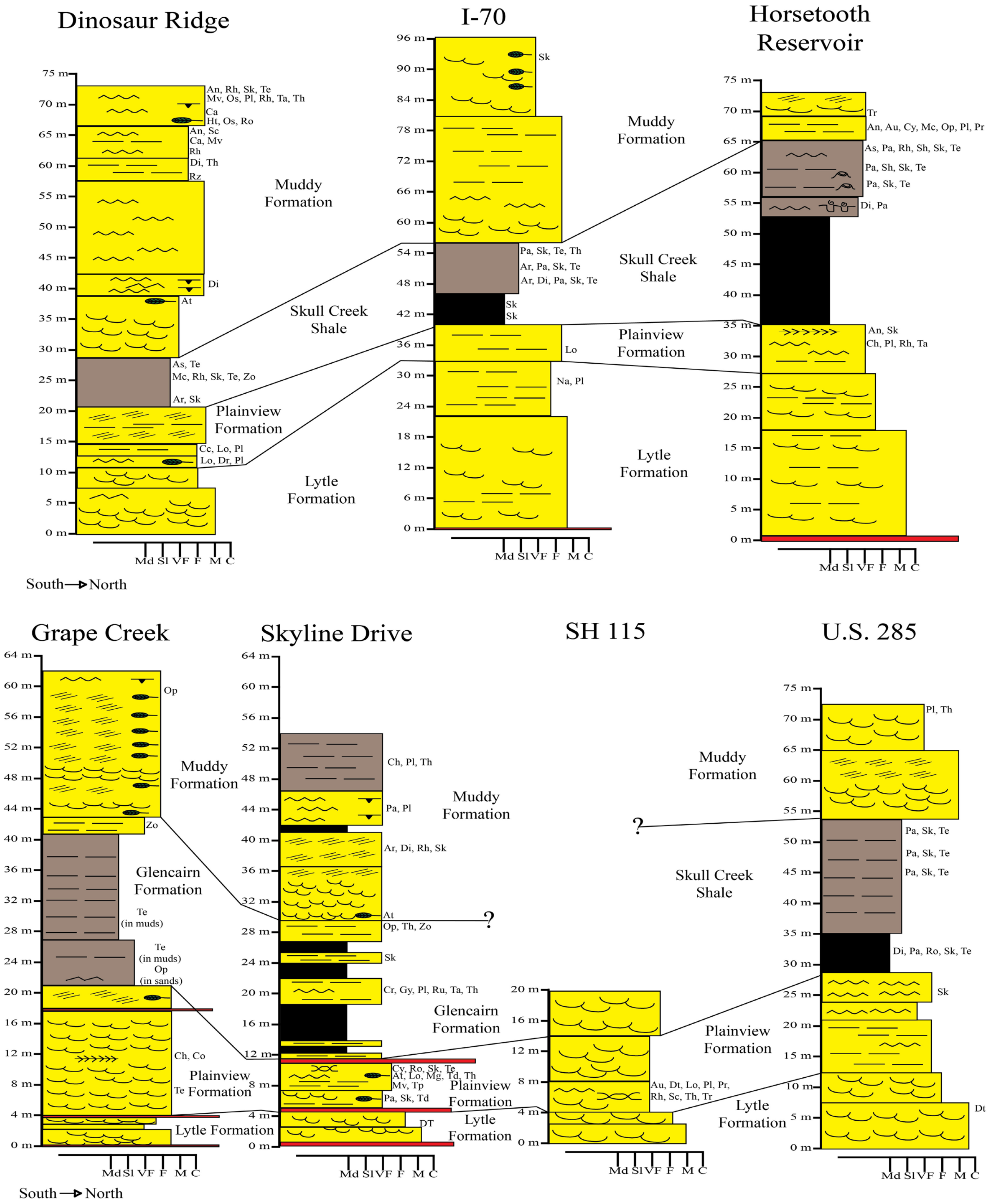
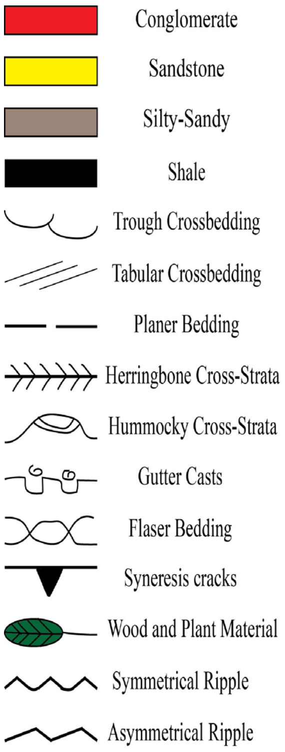


Figure 3. Measured sections and key for the Dakota Group study area. From lower left is the southernmost study site to the upper right being the northernmost study site. Figure key on facing page.



Grain Size	
Md	Mud
Sl	Silt
VF	Very Fine-Grained Sandstone
F	Fine-Grained Sandstone
M	Medium-Grained Sandstone
C	Corase-Grained Sandstone

Trace fossil Assemblage	
An	*Archaeonassa*
Ar	*Arenicolites*
As	*Asterosoma*
At	*Asthenopodichnium*
Au	*Aulichnites*
Ca	*Caririchnium*
Ch	*Chondrites*
Cc	*Cochlichnus*
Co	*Conichnus*
Cr	*Cruziana*
Cy	*Cylindrichnus*
Dt	Dinosaur tracks
Di	*Diplocraterion*
Dr	*Dromaeosauripus*
Gy	*Gyrolithes*
Ht	*Hatcherichnus*
Lo	*Lockeia*
Mc	*Macaronichnus*
Mv	*Magnoavipes*
Mg	*Margaritichnus*
Na	*Naktodemasis*
Op	*Ophiomorpha*
Os	*Ostendichnus*
Pa	*Palaeophycus*
Pl	*Planolites*
Pr	*Protovirgularia*
Rh	*Rhizocorallium*
Rz	Rhizohaloes
Ro	*Rosselia*
Ru	*Rusophycus*
Sh	*Schaubcylindrichnus*
Sc	*Scolicia*
Sk	*Skolithos*
Ta	*Taenidium*
Te	*Teichichnus*
Td	*Teredolites*
Tp	*Tertrapodosaurus*
Th	*Thalassinoides*
Tr	*Treptichnus*
Zo	*Zoophycos*

Figure 3. Key for the Dakota Group study area (facing page).

Rhizohaloes represent plants at the time of deposition within an ecosystem and are indicative of a terrestrial environment that had fluctuating soil moisture in the vadose zone (e.g., Kraus & Hasiotis, 2006; Dubois, Goldstein, & Hasiotis, 2012; Fischer & Hasiotis, 2018). Terrestrial plants range from the Ordovician to Holocene, with aquatic plants ranging from Cretaceous to Holocene (e.g., Hasiotis, Cressler, & Beerbower, 1999; Retallack, 2001). These rhizohaloes occur in a paleosol ~25–30 cm thick with sparse, iron-rich masses of goethite within the surrounding matrix that associate with the rhizohaloes. The drab color, iron masses, and mostly horizontal roots indicate that the paleosol was poorly drained (e.g., Kraus & Hasiotis, 2006). The rhizohalo-bearing mudstone unit overlies a very fine-grained sandstone with *Diplocraterion* isp. and *Thalassinoides suevicus* deposited in shallow intertidal to subtidal marine settings (MacKenzie, 1975; Chamberlain, 1985). This paleosol was developed in a coastal plain environment with high water table and poorly drained conditions based on the rhizohaloes and corresponding pedogenic features and lithology.

TRACE FOSSILS OF INVERTEBRATES

Ichnogenus ARCHAEONASSA
Fenton & Fenton, 1937a

non *Scolicia* de Quatrefages, 1849, p. 265.
non *Palaeobullia* Götzinger & Becker, 1932.
Archaeonassa fossulata Fenton & Fenton, 1937a, p. 455, pl. 1, fig. 1, 2.
Scolicia vada Chamberlain, 1971, fig 4i, pl. 29, fig. 8.
non *?Scolicia prisca* de Quatrefages; Chamberlain, 1971, p. 225.
Archaeonassa Buckman, 1994, fig. 2, 3, 5.
Archaeonassa Yochelson & Fedonkin, 1997, fig. 1–7.
Archaeonassa Hammersburg, Hasiotis, & Robison, 2018, p. 7, fig. 6.1, 6.2.

Type Ichnospecies.—*Archaeonassa fossulata* Fenton & Fenton, 1937a.

Diagnosis.—Short, ovoid to round or elongate trail that is commonly deeper at one end, and may grade into an indistinct V-shaped trail. Trace can be straight or curving with concave to slightly convex furrow flanked by a pair of convex lateral ridges, with the central furrow wider than the ridges. Lateral ridges are smooth or ornamented with oblique to transverse striate or smaller lobes (after Hammersburg, Hasiotis, & Robison, 2018).

Discussion.—According to Häntzschel (1975), *Archaeonassa* can be placed within the *Scolicia* Group, however, it lacks the diagnostic backfill associated with that group (e.g., Buckman, 1994). In a review of *Archaeonassa,* Buckman (1994), synonymized *Scolicia vada* Chamberlain, 1971, along with some specimens of *Palaeobullia* Götzinger & Becker, 1932, within *Archaeonassa*. This synonymization has been rejected by Yochelson and Fedonkin (1997) because Buckman (1994) did not examine the original type material of *Archaeonassa* before placing *Palaeobullia* within *Archaeonassa. Palaeobullia* is clearly distinct from *Archaeonassa* (Yochelson & Fedonkin, 1997).

Archaeonassa has been interpreted as a gastropod locomotion or grazing trace (Fenton & Fenton, 1937a; Buckman, 1994; Singh & others, 2015; Hammersburg, Hasiotis, & Robison, 2018). This was rejected by Yochelson and Fedonkin (1997), who did not offer other tracemakers as an explanation for *Archaeonassa*. The ichnotaxon is reported from a wide range of marine and continental environments including intertidal, shoreface, offshore, channel, floodplain, and lacustrine settings (Buckman, 1994; Buatois & Mángano, 2002; Singh & others, 2015; Hammersburg, Hasiotis, & Robison, 2018). The geologic range of *Archaeonassa* is Ediacaran to Holocene (Buckman, 1994; Jensen, Droser, & Gehling, 2005).

ARCHAEONASSA FOSSULATA Fenton & Fenton, 1937a

Scolicia isp.—Hasiotis, 2004, p. 212, fig. 15e.
Scolicia isp.—Bohacs, Hasiotis, & Demko, 2007, p.88, 102, fig. 6b, 18a, 18d.
Scolicia prisca—Ash & Hasiotis, 2013, p. 77, fig. 8g.
Crossopodia isp.—Jackson, Hasiotis, & Flaig, 2016, p. 273, fig. 4a.
Scolicia isp.—Jackson, Hasiotis, & Flaig, 2016, p. 281, fig. 9a.

Figure 4.3, 4.4

Diagnosis.—Same as for the ichnogenus.

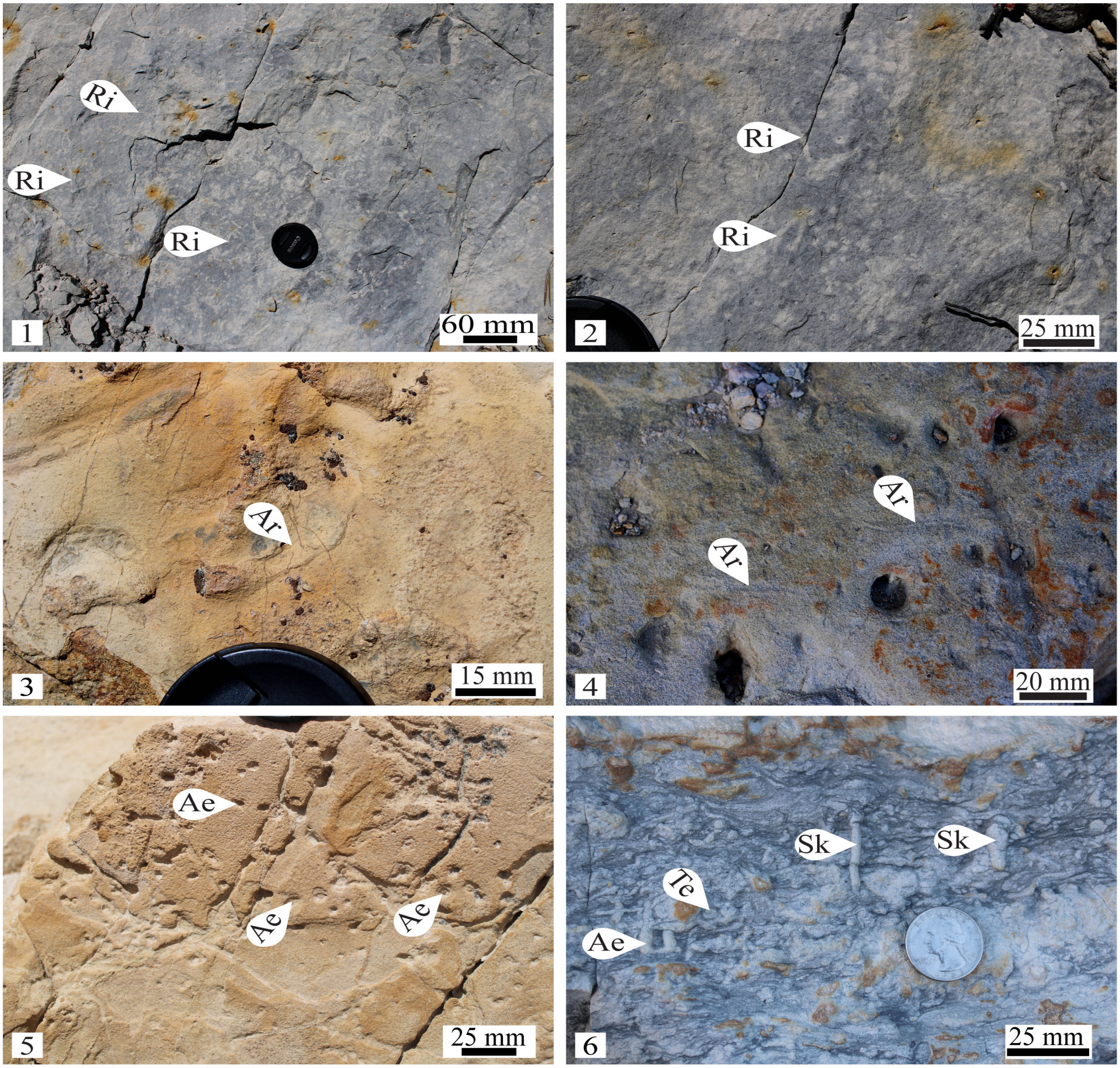


Figure 4. *Archaeonassa* (Ar), *Arenicolites* (Ae), Rhizohaloes (Ri), *Skolithos* (Sk), and *Teichichnus* (Te) from the Dakota Group. *1*, Rhizohaloes in full relief, with goethite masses in a bluish gray matrix from the Muddy Formation at Dinosaur Ridge. *2*, Rhizohaloes in full relief, within a bluish gray matrix from the Muddy Formation at Dinosaur Ridge. *3*, *Archaeonassa fossulata* in convex epirelief, from the upper part of the Muddy Formation at Dinosaur Ridge. *4*, *Archaeonassa fossulata* in convex epirelief, from the Fort Collins Member of the Muddy Formation at Horsetooth Reservoir. *5*, Plan view of *Arenicolites carbonaria* from the middle part of the Muddy Formation at Skyline Drive. *6*, *Arenicolites variabilis* along with *Skolithos linearis* and *Teichichnus rectus* in vertical section within the middle part Skull Creek Shale at I-70.

Description.—Concave furrow in epirelief flanked by smooth, convex ridges that are either straight or curving. Trails are 3–10 mm wide; ridges are <1 mm tall and <1 mm wide, and overall length is 10–180 mm.

Occurrence.—(1) Reddish yellow (7.5YR 7/8) to strong brown (7.5YR 5/8), fine-grained, subrounded and moderately well-sorted sandstone; (2) white (10R 8/1), very fine-grained planar laminated sandstone; (3) white (10R 8/1), very fine-grained ripple-laminated sandstone, with BPBI 1–2; (4) strong brown (7.5YR 5/8), fine- to very fine-grained, moderately well-sorted, well-rounded sandstone, with BPBI 2. Specimens are present in the middle part of the Plainview Formation and lower part of the Muddy Formation at Horsetooth Reservoir and in the middle and upper part of the Muddy Formation at Dinosaur Ridge.

Associated ichnotaxa.—Rhizocorallium commune and *Scolicia* isp.

Discussion.—Specimens are placed in *Archaeonassa fossulata* based on the morphology of simple, smooth furrows with lateral ridges in epirelief (Fenton & Fenton, 1937a; Buckman, 1994; Hammersburg, Hasiotis, & Robison, 2018). The tracemaker for *Archaeonassa fossulata* in the Dakota Group are likely gastropods (e.g., Fenton & Fenton, 1937a; Buckman, 1994; Singh & others, 2015; Hammersburg, Hasiotis, & Robison, 2018). At Horsetooth Reservoir *Archaeonassa fossulata* is monospecific in both the Plainview Formation and the Fort Collins Member of the Muddy Formation. The Plainview Formation at Horsetooth Reservoir was deposited in an intertidal to subtidal environment, based on lithology and bedforms (Wescott, 1979). The Fort Collins Member was deposited in a deltaic environment based on lithology, bedforms present, and sedimentary succession (MacKenzie, 1965).

In the middle part of Dinosaur Ridge, *Archaeonassa fossulata* is present on a surface of wave-ripple sets with *Scolicia* isp., which overlie the bed that contains the tetrapod tracks *Caririchnium leonardii*, *Hatcherichnus* isp., and *Magnoavipes caneeri*. These wave-ripple sets are microbially induced sedimentary structures (MISS), which are created when cyanobacterial film or mats attach to the surface of depositional grains (e.g., Noffke & others, 2001a; Noffke, Hagadorn, & Bartlett, 2019). These mats protect the sedimentary structures from weathering and erosion and are commonly located in intertidal and supratidal zones (Noffke & others, 2001a, 2001b). The presence of *Archaeonassa fossulata* and *Scolicia* isp. on these structures suggests that the tracemakers could have been feeding on these microbial mats. This interval of the Muddy Formation was an intertidal environment based on lithology and bedforms (MacKenzie, 1975; Chamberlain, 1985). In the upper part of the Muddy Formation at Dinosaur Ridge, *Archaeonassa fossulata* co-occurs with *Rhizocorallium commune*. The bed in which *Archaeonassa fossulata* is present overlies the bed with *Rhizocorallium jenense, Skolithos linearis, Teichichnus rectus, Taenidium serpentinum,* and *Thalassinoides suevicus*. *Archaeonassa fossulata* within the upper part of the Muddy Formation were produced in a subtidal environment, based on lithology and bedforms (Weimer & Land, 1972; MacKenzie, 1975; Chamberlain, 1985).

Ichnogenus ARENICOLITES Salter, 1857

Arenicola Binny, 1852, p. 192.

Arenicolites Salter, 1857, p. 204.

Arenicolites Chamberlain, 1977, p. 8.

Arenicolites Rindsberg & Kopaska-Merkel, 2005, p. 129, fig. 2–4.

Arenicolites Bradshaw, 2010, p. 68, fig. 6a–f.

Arenicolites Hammersburg, Hasiotis, & Robison, 2018, p. 9, fig 6.3, 6.4

Type Ichnospecies.—Arenicola carbonaria Binney, 1852

Diagnosis.—Vertical, U-shaped burrows without spreite, and visible as paired openings in plan-view (after Hammersburg, Hasiotis, & Robison, 2018).

Discussion.—Arenicolites is a U-shaped, vertical burrow that differs from *Diplocraterion* Torell, 1870, in its lack of spreite (Fillion & Pickerill, 1990). There are currently nine recognized ichnospecies of *Arenicolites*: *Arenicolites compressus* Sowerby, 1829; *Arenicolites carbonaria* Binney, 1852; *Arenicolites subcompressus* Eichwald, 1860; *Arenicolites brevis* Matthew, 1890; *Arenicolites statheri* Bather, 1925; *Arenicolites curvatus* Goldring, 1962; *Arenicolites variabilis* Fürsich, 1974a; *Arenicolites naraensis* Badve & Ghare, 1978; and *Arenicolites longistriatus* Rindsberg & Kopaska-Merkel, 2005. *Arenicolites longistriatus* is subhorizontal due to compaction and has longitudinal striate along the length of the burrow (Rindsberg & Kopaska-Merkel, 2005; Hammersburg, Hasiotis, & Robison, 2018). *Arenicolites curvatus* has inclined limbs and, along with *Arenicolites compressus* and *Arenicolites subcompressus,* is elliptical in cross section (Fürsich, 1974a; Chamberlain, 1977; Fillion & Pickerill, 1990; Hammersburg, Hasiotis, & Robison, 2018). *Arenicolites statheri* and *Arenicolites naraensis* have thick wall linings, and *Arenicolites statheri* has narrow, parallel, vertical limbs (Fürsich, 1974a; Chamberlain, 1977; Fillion & Pickerill, 1990; Schlirf, 2000; Hammersburg, Hasiotis, & Robison, 2018). *Arenicolites carbonaria* has relatively narrow limbs with a thin lining and funnel-shaped apertures (e.g., Fürsich, 1974a; Fillion & Pickerill, 1990; Hammersburg, Hasiotis, & Robison, 2018).

Arenicolites is considered as a dwelling burrow of a suspension-feeding organism, such as a polychaete or crustacean (Fillion & Pickerill, 1990; Davies, Sansom, & Albanesi, 2007). Though typically present in shallow-marine environments, *Arenicolites* is also known both in continental (fluvial and lacustrine) and deep-marine environments (Crimes, 1977; Pickerill & Keppie, 1981; Ash & Hasiotis, 2013; Fischer & Hasiotis, 2018; Flaig, Hasiotis, & Jackson, 2016, Flaig & others, 2019). *Arenicolites* ranges from the Cambrian to Holocene (Binney, 1852; Pickerill & Keppie, 1981; Hammersburg, Hasiotis, & Robison, 2018).

ARENICOLITES CARBONARIA Bather, 1925
Figure 4.5

Diagnosis.—Vertical, U-shaped burrow with narrow limbs and funnel-shaped apertures (after Hammersburg, Hasiotis, & Robison, 2018).

Description.—Single vertical, J-shaped burrow, seen in both concave epirelief and full relief. The complete size of the trace is difficult to determine due to missing portions of the U-shaped burrow, resulting in a J shape or a partial U shape. Other specimens are found in concave epirelief. Specimens range from 10 to 30 mm wide (measured from outside of the limbs) and up to ~55 mm deep. In concave epirelief the funnel-shaped opening has a lining, ~1 mm thick. The diameter of the openings is from 2 to 4 mm.

Occurrence.—Reddish yellow (7.5YR 7/8), very fine-grained, well-sorted and rounded, planar-bedded sandstone, with BPBI 2. Present in the middle part of the Muddy Formation along Skyline Drive.

Associated ichnotaxa.—Skolithos linearis.

Discussion.—Traces are assigned to *Arenicolites carbonaria* based on the presence of funnel-shaped apertures and the thickness of the wall lining (e.g., Chamberlain, 1977; Fillion & Pickerill, 1990; Hammersburg, Hasiotis, & Robison, 2018). The tracemaker for *Arenicolites carbonaria* were most likely either polychaete worms or crustaceans (Fillion & Pickerill, 1990; Davies, Sansom, & Albanesi,

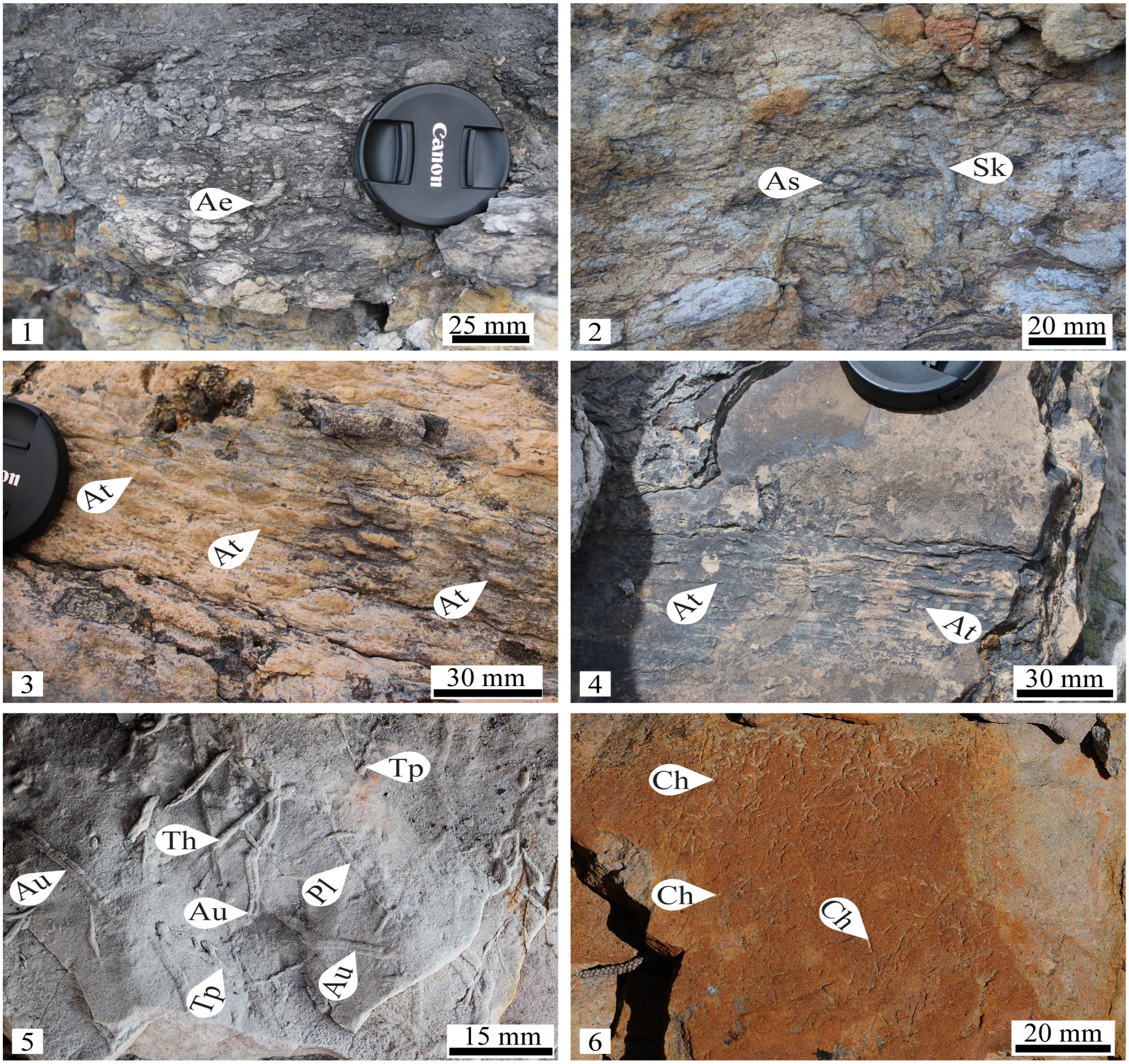


Figure 5. *Arenicolites* (Ae), *Asterosoma* (As), *Asthenopodichnium* (At), *Aulichnites* (Au), *Chondrites* (Ch), *Planolites* (Pl), *Skolithos* (Sk), *Thalassinoides* (Th), and *Treptichnus* (Tp) from the Dakota Group. *1,* J-shaped *Arenicolites* isp. in vertical section within the lower part of the Skull Creek Shale at Dinosaur Ridge. *2, Asterosoma* isp. with *Skolithos* linearis in vertical section, within the upper part of the Skull Creek Shale at Horsetooth Reservoir. *3, Asthenopodichnium xylobiontum* in convex hyporelief within the lower part of the Muddy Formation at Skyline Drive. *4, Asthenopodichnium xylobiontum* in convex epiorelief within the lower part of the Muddy Formation at Dinosaur Ridge. *5, Aulichnites parkerensis* with *Planolites montanus*, *Thalassinoides horizontalis,* and *Treptichnus bifurcus* in convex epirelief, within the Plainview Formation at Colorado State Highway 115. *6, Chondrites intricatus* in full relief, within the middle part of the Plainview Formation at Grape Creek.

2007). Most specimens in outcrop were only partially preserved. These specimens overlie a planar-bedded-bearing *Skolithos linearis*. These traces were constructed in an intertidal environment based on bedforms and lithology (Gustason & Kauffman, 1985).

ARENICOLITES VARIABILIS Fürsich, 1974a

Figure 4.6

Diagnosis.—Variably narrow to wide, vertical to slightly oblique, mainly straight, cylindrical U-shaped burrow without spreite (after Fürsich, 1974a).

Description.—Single vertical, incomplete U-shaped burrow in full relief. Burrow limbs are not symmetrical. Specimen is 10 mm wide (measured from outside of the limbs) and 17 mm deep. Each limb is 3 mm in diameter.

Occurrence.—Black (7.5YR 2.5/1) to very dark gray (7.5YR 3/1) siltstone to shale, interbedded with a white (10R 8/1), very fine-grained clayey sandstone, with moderate bioturbation (ii3). Present in the middle part of the Skull Creek Shale at I-70.

Associated ichnotaxa.—Palaeophycus tubularis, Skolithos linearis, and *Teichichnus rectus*.

Discussion.—The specimen is assigned to *Arenicolites variabilis* based on the 1) asymmetry between the U-shaped burrow limbs; 2) no lining; and 3) no funnel-shaped aperture (e.g., Fürsich, 1974a; Pickerill & Keppie, 1981). The tracemaker for *Arenicolites variabilis* were either polychaete worms or crustaceans (Fillion & Pickerill, 1990; Davies, Sansom, & Albanesi, 2007). The lack of a visible lining precludes its assignment to *Arenicolites curvatus* (Goldring, 1962). The occurrence of *Arenicolites variabilis* with the associated traces in the Skull Creek Shale represents a marine embayment based on the lithofacies succession, bedforms, and bioturbation (Weimer & Land, 1972).

ARENICOLITES isp.
Figure 5.1

Description.—Vertical J-shaped to partially U-shaped burrows in full relief. Specimens have smooth walls and lack visible lining on the burrow limbs. Specimens ranged from 17 to 25 mm wide (measured from outside the limbs) and up to ~30 mm deep, with each limb having a diameter of 2–5 mm.

Occurrence.—Black (7.5YR 2.5/1) to very dark gray (7.5YR 3/1) , siltstone to shale interbedded with a white (10R 8/1), very fine-grained clayey sandstone with varying degrees of bioturbation (ii2–3). Present in the upper part of the Skull Creek Shale at I-70 and the middle part of the Skull Creek Shale at Dinosaur Ridge.

Associated ichnotaxa.—Palaeophycus tubularis, Skolithos linearis, and *Teichichnus rectus*.

Discussion.—The specimens are placed in *Arenicolites* due to the partially U-shaped morphology. The tracemaker for *Arenicolites* isp. were either polychaete worms or crustaceans (e.g., Fillion & Pickerill, 1990; Davies, Sansom, & Albanesi, 2007). The level of preservation, however, precludes assignment to an ichnospecies due to the degree of bioturbation. The specimens at Dinosaur Ridge were constructed in a marine embayment environment based on lithology and bedforms (Weimer & Land, 1972).

Ichnogenus ASTEROSOMA von Otto, 1854

Asterosoma von Otto, 1854, p. 15.

Asterosoma Chamberlain, 1971, p. 225, pl. 29, fig. 6b–e, 8h–i, 14.

Asterosoma Häntzschel, 1975, p.43, fig. 25, 1a, 1b.

Asterosoma Chamberlain, 1978, p. 142, fig. 8–10, 79–83.

Asterosoma Schlirf, 2000, p. 166, pl. 3, fig. 1–11, 19a–b.

Asterosoma Bradshaw, 2010, p. 71, fig. 8a–d.

Type Ichnospecies.—Asterosoma radiciforme von Otto, 1854.

Emended Diagnosis.—Horizontal to inclined burrows, either with star-like arranged bulbs or bulbs that originate from a circular to elliptical tube dichotomously or in a fan-like pattern. Bulbs taper at one end or at both ends and are concentrically to irregularly laminated internally with a small cylindrical, inner tube that lies in a center to off-centered position. Burrow walls with or without longitudinal, subangular furrows and striae (modified from Chamberlain, 1971; Schlirf, 2000).

Discussion.—Chamberlain (1971) made *Asterophycus* Lesquereux, 1876, a junior synonym of *Asterosoma* von Otto, 1854, due to their similar morphology and interpreted behaviors. This was seemingly questioned by Häntzschel (1975) who kept both ichnogenera separate in the treatise. In a personal correspondence with Rindsberg (2021), he stated that Häntzschel (1975) passed away before the treatise was complete, so it is possible that he never got to examine the type material for *Asterophycus* and *Asterosoma* to determine their ichnotaxonomic status. When examining the descriptions and photographs of both *Asterophycus* and *Asterosoma*, we agree with the ichnotaxonomic assessment of made by Chamberlain, (1971). Chamberlain (1971) described the bulb structures of *Asterosoma* as having a concentric lamina around a central tube. Other researchers have subsequently described concentric lamina within the bulbs (Chamberlain, 1978; Howell, Flint, & Hunt, 1996; Bromley & Uchman, 2003), with Schrlif (2000) adding this feature to the diagnosis of *Asterosoma*. Recently, Knaust (2021) stated that the original diagnosis of *Asterosoma* described the bulbs as passively filled, with no concentric laminae. For this reason, Knaust (2021) assigned *Asterosoma ludwigae* Schrlif, 2000, which is described as being fanlike in shape with concentric laminated bulbs, into *Lamellaecylindrica* Knaust (2020). This synonymy is questionable, however, as the type ichnospecies *Asterosoma radiciforme* was described by Chamberlain (1971) as having concentric laminae within its bulb structures. Bromley and Uchman (2003) have similar laminae in examples of *Asterosoma* that are similar to the type ichnospecies. For this reason, we reject the ichnotaxonomic assessment of Knaust (2021). We suggest, as other researchers have suggested (e.g., Bromley & Uchman, 2003; Bradshaw, 2010), that *Asterosoma* undergo further taxonomic assessment, based on the present confusion within the literature.

Asterosoma is present in such shallow marine environments as tidal, deltaic, estuarine, and lower shoreface settings, as well as in deep-marine environments (Greb & Chesnut, Jr, 1994; Bromley & Uchman, 2003; Bradshaw, 2010). *Asterosoma* is interpreted to be the burrow of deposit-feeding organisms, such as worms (Chamberlain 1971; Niebuhr & Wilmsen, 2016; Callow & others, 2013) or decapod crustaceans (Häntzschel 1975; Niebuhr & Wilmsen, 2016; Joseph, Patel, & Bhatt, 2012). *Asterosoma* occurs from the Silurian to Holocene (Häntzschel, 1975; Chamberlain, 1978; Bromley & Uchman, 2003; Bradshaw, 2010).

ASTEROSOMA isp.
Figure 5.2, 11.3, 14.3

Description.—Oval-shaped burrows in full relief that have a concentric laminae enclosing a central tunnel. Only arm or bulb of the *Asterosoma* is visible in the beds. The specimens have a width of 15–20 mm and height of 6–9 mm.

Occurrence.—(1) Black (7.5YR 2.5/1) to very dark gray (7.5YR 3/1) siltstone to shale, interbedded with a white, (10R 8/1) very fine-grained clayey sandstone with moderate bioturbation (ii2–3); and (2) black (7.5YR 2.5/1) to very dark gray (7.5YR 3/1) shale interbedded with reddish yellow (7.5YR 7/8) to red (10R 4/8) very fine-grained sandstone to siltstone with significant bioturbation (ii3–4). Present in the upper part of the Skull Creek Shale at Horsetooth Reservoir and Dinosaur Ridge.

Associated ichnotaxa.—*Rhizocorallium commune, Schaubcylindrichnus freyi, Skolithos linearis,* and *Teichichnus rectus.*

Discussion.—Specimens are assigned to *Asterosoma* due to the oval shape and the concentric laminae that surround a centered or off-centered tube (Chamberlain, 1978; Schlirf, 2000). The tracemaker for *Asterosoma* isp., were most likely polychaetes (Niebuhr & Wilmsen, 2016). The specimens lack the characteristics needed to properly identify the ichnospecies. At Horsetooth Reservoir, *Asterosoma* isp. co-occurs with all the associated ichnotaxa, whereas at Dinosaur Ridge it only occurs with *Teichichnus rectus*. These specimens were constructed in a lower shoreface environment based on the lithology and facies succession (Graham & Ethridge, 1995).

Ichnogenus ASTHENOPODICHNIUM von Thenius, 1979

Asthenopodichnium von Thenius, 1979, p. 185, fig. 1, 2.

Asthenopodichnium von Thenius, 1988, p. 9, fig. 3, pl. 3, fig. 1, 2.

Asthenopodichnium Uchman & others, 2007, p. 331, fig. 2c, 4, 6.

Asthenopodichnium Genise & others, 2012, p. 185, fig. 2, 3.

Asthenopodichnium Francischini & others, 2016, p. 33, fig. 6.

Type Ichnospecies.—*Asthenopodichnium xylobiontum* von Thenius, 1979.

Emended Diagnosis.—Traces with hemiellipsoid (U-shaped pouchlike) structures aligned parallel to each other; structures are produced in wood, organic-rich sediment, bone, or hardground media (modified from von Thenius, 1979; Uchman & others, 2007).

Discussion.—*Asthenopodichnium* was named by von Thenius (1979) for "U-förmige Spreitenbauten in Holz, senkrecht zur Stammoberfläche angeordnet" or "U-shaped wooden structures, arranged perpendicular to the trunk surface." A mistranslation of "Spreitenbauten" as being spreite or U-shaped packets of sediment, rather than a spreading structure by Uchman and others (2007) produced misinterpretations of the diagnosis of von Thenuis (1979) by several workers. For example, Uchman and others (2007) mentioned that spreite is "present" but not obvious in the type material (Moran & others, 2010). We emend the diagnosis to include the proper translation of the original diagnosis and use the term hemiellipsoid as a more appropriate description of the 3D geometric shape of the trace. Other researchers have used pouchlike or tongue shape (e.g., Uchman & others, 2007) to describe the morphology of *Asthenopodichnium;* however, we prefer a standardized 3D geometric shape to diagnosis the morphology. We also include the occurrence of *Asthenopodichnium* in hardgrounds in the emended diagnosis as observed by Francischini and others (2016). The structures were interpreted to be made by mayfly nymphs.

The ichnospecies of *Asthenopodichnium* are defined by the preferred medium into which the tracemakers bored: *Asthenopodichnium xylobiontum* is constructed in wood; *Asthenopodichnium ossibiontum* is constructed in bone (von Thenius, 1988); *Asthenopodichnium lithuanicum* (Uchman & others, 2007) is constructed in brown coal or organic-rich siltstone; and *Asthenopodichnium fallax* is constructed in hardgrounds (Francischini & others, 2016). Genise and others (2012) named a new ichnospecies, *Asthenopodichnium lignorum,* as small, shallow groovelike patterns in wood produced by fungi. The validity of this ichnospecies is questionable, as the forms and behaviors described do not match the original description of the ichnotaxon. First, the original description of *Asthenopodichnium* was that of "U-shaped wooden structures arranged perpendicular to the trunk surface" (von Thenius, 1979, p. 185) present on the outer surface of the wood. The diagnosis of *Asthenopodichnium xylobiontum* only had a maximum depth given by von Thenius (1979) as up to 20 mm. The purported new ichnospecies actually occurs within the cambium itself and not on the surface as originally defined. The structures described by Genise and others (2012), however, are produced by fungi dissolving wood with enzymes following the path of least resistance through the xylem and phloem (Blanchette, 1984, 1991; Blanchette & others, 1985; Leonowicz & others, 1999; Schmidt, 2006). This results in multiple layers of eye- or almond-shaped patterns aligned along the tubular internal plant structures, which are commonly accentuated by silicification. Genise and others (2012) also conflated the fungal structures with that of reproductive pupal structures by *Pissodes castaneus* (Coleoptera, Curculionidae), a wood-boring beetle, possibly suggesting that some of almond-shaped structures have a beetle origin. However, this conclusion is unwarranted. Lastly, *Asthenopodichnium* is produced from wood removal on the surface of a log by an insect nymph and used as a place to suspension-feed, whereas the fungal structures are produced by digestion of wood by dissolution of cellular tissues through chemical reaction. We, therefore, reject the validity of *Asthenopodichnium lignorum* (Genise & others, 2012; Abu Hamad & Uhl, 2015), and consider it a *nomen dubium* as the morphology of those specimens do not belong to *Asthenopodichnium*.

The tracemakers of *Asthenopodichnium* are interpreted to be mayfly nymphs boring into a medium (von Thenius, 1979) to produce dwellings for suspension feeding. Possible behaviors of crustaceans and beetles have not been ruled out by others (von Thenius, 1979; Uchman & others, 2007; Moran & others, 2010; Francischini & others, 2016), although they have not been demonstrated to create similar structures in recent media. *Asthenopodichnium* is present in fluvial and lacustrine continental environments (von Thenius, 1979; Uchman & others, 2007; Moran & others, 2010). *Asthenopodichnium* ranges from the Middle Jurassic to Holocene (Moran & others, 2010; Abu Hamad & Uhl, 2015; Francischini & others, 2016).

ASTHENOPODICHNIUM XYLOBIONTUM
von Thenius, 1979
Figure 5.3, 5.4

Diagnosis.—Structures with a hemiellipsoid (U-shaped pouchlike) morphology of narrow diameter and shallow to deep within the woody structure (after von Thenius, 1979; Uchman & others, 2007).

Description.—Specimens are in convex hyporelief as sediment-filled impressions cast from the surface of wood. Structures range from 8 to 12 mm long, 2 to 3 mm wide, and 1 to 2 mm deep.

Occurrence.—Tree log impressions occur in: (1) reddish yellow (7.5YR 6/8) fine- to very fine-grained, subrounded, moderately well-sorted sandstone, with some ripple marks and flaser bedding, and significant bioturbation (ii4); (2) reddish yellow (7.5YR 7/8) gray (7.5YR 5/1) very fine- to fine-grained sandstone; and (3) strong brown (7.5YR 5/8), fine-grained sandstone, with some trough crossbeds. Present in the upper part of the Plainview Formation along Skyline Drive and lower parts of the Muddy Formation at Skyline Drive and Dinosaur Ridge.

Associated ichnotaxa.—Lockeia isp.*, Margaritichnus mansfieldi, Teredolites clavatus,* and *Thalassinoides suevicus*.

Discussion.—Specimens are placed in *Asthenopodichnium xylobiontum* based on their hemiellipsoid shape in woody media (von Thenius, 1979; Uchman & others, 2007; Moran & others, 2010). The tracemaker for *Asthenopodichnium xylobiontum* were mayfly nymphs (von Thenius, 1979). Specimens at Skyline Drive are constructed close together with some tightly clustered. Specimens at Dinosaur Ridge are not as closely constructed in the woody medium and are more worn in appearance based on the preservation of their size and shape. Even though *Asthenopodichnium xylobiontum* was constructed in a freshwater setting, the log in which it was bored was deposited in the intertidal settings of the Plainview Formation at Skyline Drive and Muddy Formation at Dinosaur Ridge (Weimer & Land, 1972; MacKenzie, 1975; Chamberlain, 1985; Gustason & Kauffman, 1985). Only the example deposited in a fluvial setting was in the Muddy Formation at Skyline Drive (Gustason & Kauffman, 1985), suggesting that the other *Asthenopodichnium xylobiontum*-bearing wood was transported from a freshwater to marine setting. *Teredolites clavatus* and *Asthenopodichnium xylobiontum* are not present in the same woody media, suggesting either that *Asthenopodichnium*-bearing woody media were not appealing to the tracemakers of *Teredolites,* or that *Asthenopodichnium*-bearing woody media was rapidly buried in the marine setting before it could be bored. The presence of two types of wood borings in these beds suggests a source of wood was present nearby.

Ichnogenus AULICHNITES Fenton & Fenton, 1937b

Aulichnites Fenton & Fenton, 1937b, p. 1080, pl. 1, fig. 1, 2.
Scolicia parkerensis Chamberlain, 1971, p. 220, pl. 29, fig. 4.
Aulichnites Hakes, 1977, p. 216, pl. 1b.
Psammichnites D'Alessandro & Bromley, 1987, p. 749.
Aulichnites Maples & Suttner, 1990, p. 865, fig. 9.4.
Psammichnites Mángano, Buatois, & Rindsberg, 2002, p. 3.
Aulichnites Hammersburg, Hasiotis, & Robison, 2018, p. 10, fig. 6.5.

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

Diagnosis.—Preserved in convex epirelief with a bilobate upper surface. May be a unilobate, convex-downward lower surface, in which case lateral margins of both surfaces intersect. Upper surface may have transverse, concave-convex striations. Lobes are separated by a median furrow (after Hammersburg, Hasiotis, & Robison, 2018).

Discussion.—Aulichnites is similar to other bilobate ichnotaxa, such as *Olivellites* Fenton & Fenton, 1937c, *Psammichnites* Torell, 1870, and *Scolicia* de Quatrefages, 1849. *Aulichnites* was synonymized under *Scolicia* by Chamberlain (1971), with no explanation provided. This synonymy was rejected by Häntzschel (1975). D'Alessandro and Bromley (1987) synonymized *Aulichnites* under *Olivellites*, based on a description provided by Hakes (1977), who examined the holotype of *Aulichnites*. Hakes (1977) observed the presence of a unilobate structure within the sediment below the bilobated upper surface of *Aulichnites*. Hakes (1977) stated that the unilobate structure is visible in cross-section and does not have a medial ridge or groove corresponding to the upper surface medial furrow. D'Alessandro and Bromley (1987), based on this description, inferred that *Aulichnites* and *Olivellites* are preservational variants of each other and synonymized *Aulichnites* under *Olivellites*. Additionally, they considered *Olivellites* morphologically similar to *Psammichnites* and synonymized *Olivellites* under *Psammichnites*, making *Aulichnites* a junior synonym of *Psammichnites*. This synonymy was contested by Maples and Suttner (1990), who stated that the absence of a medial ridge for *Aulichnites* separates it from *Psammichnites*; other researchers have agreed with this argument (e.g., Buckman, 1992; Stanley & Pickerill, 1996). Mángano, Buatois, and Rindsberg (2002) reexamined the type material of *Aulichnites* and agreed with the synonym proposed by D'Alessandro and Bromley (1987). This synonymy is problematic, however, because detailed photographic evidence for the preservational variation between *Aulichnites* and *Olivellites* was not provided to support the observations and subsequent synonymy by Mángano, Buatois, and Rindsberg, (2002). Additionally, the synonymy of these ichnotaxa oversimplify the morphological variation as being due to preservational variation rather than the interpretation as a result of behavioral differences. Therefore, we reject this synonymy of *Aulichnites* into *Olivellites* and *Psammichnites* and follow the original diagnosis of *Aulichnites*.

Aulichnites has been interpreted to be the grazing or locomotion trail of a gastropod (Fenton & Fenton, 1937b; Fillion & Pickerill, 1990). Other interpretations include the burrows of xiphosurids (horseshoe crabs) or mollusks (Fillion & Pickerill, 1990; Yiming, 1999; Hammersburg, Hasiotis, & Robison, 2018). *Aulichnites* has been reported in shallow (delta fronts, lower shoreface, lower tidal flats) to deep marine (flysch), brackish water, and fluvial continental environments (Fenton & Fenton, 1937b; Pollard, 1988; Martino, 1989; Fillion & Pickerill, 1990; MacEacheren & Pemberton, 1992; MacNaughton & Pickerill, 1995; Yiming, 1999). *Aulichnites* ranges from the Ediacaran to Holocene (Häntzschel, 1975; Hill, 1981; Hammersburg, Hasiotis, & Robison, 2018).

AULICHNITES PARKERENSIS
Fenton & Fenton, 1937b

Psammichnites parkerensis—de Gibert & others, 2011, p. 33, fig. 4d.

Figure 5.5

Diagnosis.—Same as for ichnogenus.

Description.—Traces are seen in convex epirelief, with smooth lobes. Traces are 3 mm wide, and 20–30 mm long, and approximately 1 mm high.

Occurrence.—(1) White (10R 8/1), fine-grained sandstone, ripple marks present in bedding surface with BPBI 2; and (2) white (10R 8/1), very fine-grained sandstone. Present in the upper part of the Plainview Formation along Colorado State Highway 115 and in the middle part of the Fort Collins Member of the Muddy Formation at Horsetooth Reservoir.

Associated ichnotaxa.—Planolites montanus, Thalassinoides horizontalis, and *Treptichnus bifurcus*.

Discussion.—Specimens are assigned to *Aulichnites parkerensis* based on the bilobate, convex epirelief, and smooth surface of the traces (Fenton & Fenton, 1937b). The tracemaker for *Aulichnites parkerensis* was most likely a gastropod (Fenton & Fenton, 1937b; Fillion & Pickerill, 1990; Hammersburg, Hasiotis, & Robison, 2018). At Colorado State Highway 115, a specimen of *Aulichnites parkerensis* is being crosscut by *Thalassinoides horizontalis,* suggesting *Thalassinoides horizontalis* was produced after the surface that bears *Aulichnites parkerensis* was buried. These traces were constructed in an intertidal to subtidal environment based on bedforms and lithology (Weimer, 1970; Gustason & Kauffman, 1985).

Ichnogenus CHONDRITES von Sternberg, 1833

Chondrites von Sternberg, 1833, p. 25.

Chondrites Osgood, 1970, p. 384, pl. 7, fig. 2–5, pl. 8, fig. 2–8, pl. 9, fig. 8, pl. 11, fig. 4, pl. 13, fig. 1, 8, pl. 23, fig. 5, 6, pl. 26, fig. 4, pl. 27, fig. 4, fig. 14–17, 22, 25.

Chondrites Fu, 1991, p. 21, fig. 14a–b.

Chondrites Uchman, 1999, p. 88, pl. 4, fig. 6, 7, pl. 5, fig. 1–7, pl. 6, fig. 1–8, pl.7, fig. 1–5, pl. 15, fig. 3.

Chondrites Donovan, Fearnhead, & Clarkson, 2009, p. 84, fig. 1.

Chondrites Baucon & others, 2020, p. 3.

Type Ichnospecies.—*Fucoides antiquus* Brongniart, 1828.

Diagnosis.—Regularly branching tunnel systems consisting of a small number of subvertical master shafts, connected to the ancient sediment-water interface, that branch at depth to from a dendritic system. The branches rarely interpenetrate or interconnect with each other. Fill can be active or passive (after Donovan, Fearnhead, & Clarkson, 2009; Baucon & Others, 2020).

Discussion.—Over 170 ichnospecies of *Chondrites* have been described in the literature (von Sternberg 1833; Baucon & others, 2020). This number, however, was reduced to four ichnospecies—*Chondrites intricatus* Brongniart, 1823; *Chondrites targionii* Brongniart, 1828; *Chondrites patulus* Fischer-Ooster, 1858; *Chondrites recurvus* Brongniart, 1823—by Fu (1991), who synonymized them based on the mode of branching as the only useful morphological criterion. Not all morphotypes of *Chondrites* can be synonymized into these four ichnospecies. For example, *Chondrites aequalis* Schafhäutl, 1851 does not conform to any of the diagnoses of the four ichnospecies (Uchman, 1999; Uchman, Caruso, & Sonnino, 2012; Baucon & others, 2020).

The tracemaker of *Chondrites* is interpreted to be an infaunal deposit feeder, most likely a sipunculoid worm (Fürsich, 1974a; Pemberton & Frey, 1984; Uchman, 1999). Other researchers have noted that *Chondrites* lived at the aerobic-anoxic interface, which suggests that some of the tracemakers might have been chemosymbiotic organisms (e.g., Seilacher, 1990a; Fu, 1991). *Chondrites* occurs in shallow-marine (bays, tidal flats, lower shoreface, offshore) and deep-marine environments (flysch) (Wetzel & Uchman, 1997; Hubbard, Gingras, & Pemberton, 2004; Vaziri & Fürsich, 2007; Joseph, Patel, & Bhatt, 2012; Uchman, Caruso, & Sonnino, 2012; Fiah & Lambiase, 2014; Fürsich & others, 2018). *Chondrites* ranges from the Cambrian to Holocene (Crimes, 1987; Uchman, 1999).

CHONDRITES INTRICATUS Brongniart 1823
Figure 5.6, 6.1, 13.6

Diagnosis.—Small burrow network comprised of numerous downward radiating, mostly straight branches. The angle of branching is typically <45°. Branches are very narrow, with the burrow system being broad in width (after Uchman, 1999).

Description.—Specimens are in convex hyporelief and concave epirelief. Tunnels form a dendritic pattern. The source from which the traces radiate is absent or not preserved. Specimens are 1.5–2 mm wide and 10–26 mm long.

Occurrence.—(1) Reddish gray (10R 5/1), fine- to very fine-grained sandstone with BPBI 3; and (2) reddish yellow (7.5YR 6/8) fine- to very fine-grained sandstone with BPBI 2. Specimens are present in the middle parts of the Plainview Formation at Horsetooth Reservoir and Grape Creek, and in the upper part of the Muddy Formation at Skyline Drive.

Associated ichnotaxa.—*Planolites montanus, Taenidium serpentinum,* and *Thalassinoides suevicus.*

Discussion.—Specimens are placed in *Chondrites intricatus* based on their dendritic branching patterns with branching angles of 45° or less (Fu, 1991; Uchman, 1999). The size of the traces for *Chondrites intricatus* suggest the tracemaker was an infaunal worm (Fürsich, 1974a; Uchman, 1999). At Horsetooth Reservoir, in the Plainview Formation *Chondrites intricatus* co-occurs with *Planolites montanus* and *Taenidium serpentinum*. These traces were constructed in a subtidal environment based on lithology and bedforms (Wescott, 1979). At Grape Creek *Chondrites intricatus* forms a monospecific occurrence within the Plainview Formation and was constructed in a subtidal environment based on lithology and bedforms (Gustason & Kauffman, 1985). At Skyline Drive *Chondrites intricatus* is occurs with *Thalassinoides suevicus* in the Muddy Formation and was constructed in an intertidal environment (Gustason & Kauffman, 1985).

Ichnogenus COCHLICHNUS Hitchcock, 1858

Cochlichnus Hitchcock, 1858, p. 61.

Sinusites Krestew, 1928, p. 574.

Sinusites Demanet & Van Straelen, 1938, p. 107.

Cochlichnus Häntzschel, 1975, p. 52, fig. 31.a, 31b.

Cochlichnus Fillion & Pickerill, 1990, p. 23, pl. 3, fig. 3.

Cochlichnus Głuszek, 1995, p. 184, fig. 5, 7, 8, 15a.

Cochlichnus Stanley and Pickerill, 1996, p. 8, pl. 2, fig. 1, 2, pl. 11, fig. 4.

Cochlichnus Uchman, 1998, p. 173, fig. 76.

Cochlichnus Gámez Vintaned & others, 2006, p. 451, fig. 8(9d), 9(9b), 10(1a).

Type Ichnospecies.—*Cochlichnus anguineus* Hitchcock, 1858.

Diagnosis.—Smooth trails, regularly meandering, resembling a sine curve (after Häntzschel, 1975).

Discussion.—*Cochlichnus* was incorrectly considered synonymous with *Belorhaphe* Fuchs, 1895 by Michelau (1956). This is incorrect due to *Belorhaphe* having zigzaglike angular bends, which differ from the smoother sine-curve bends of *Cochlichnus* (Fillion & Pickerill, 1990; Hogue & Hasiotis, 2018). Häntzschel (1975) placed *Sinusia* Krestew, 1928 and *Sinusites* Demanet & Van Straelen, 1938 within *Cochlichnus*. *Sinusia* and *Sinusites* were originally placed under *Belorhaphe* Michelau (1956) but were

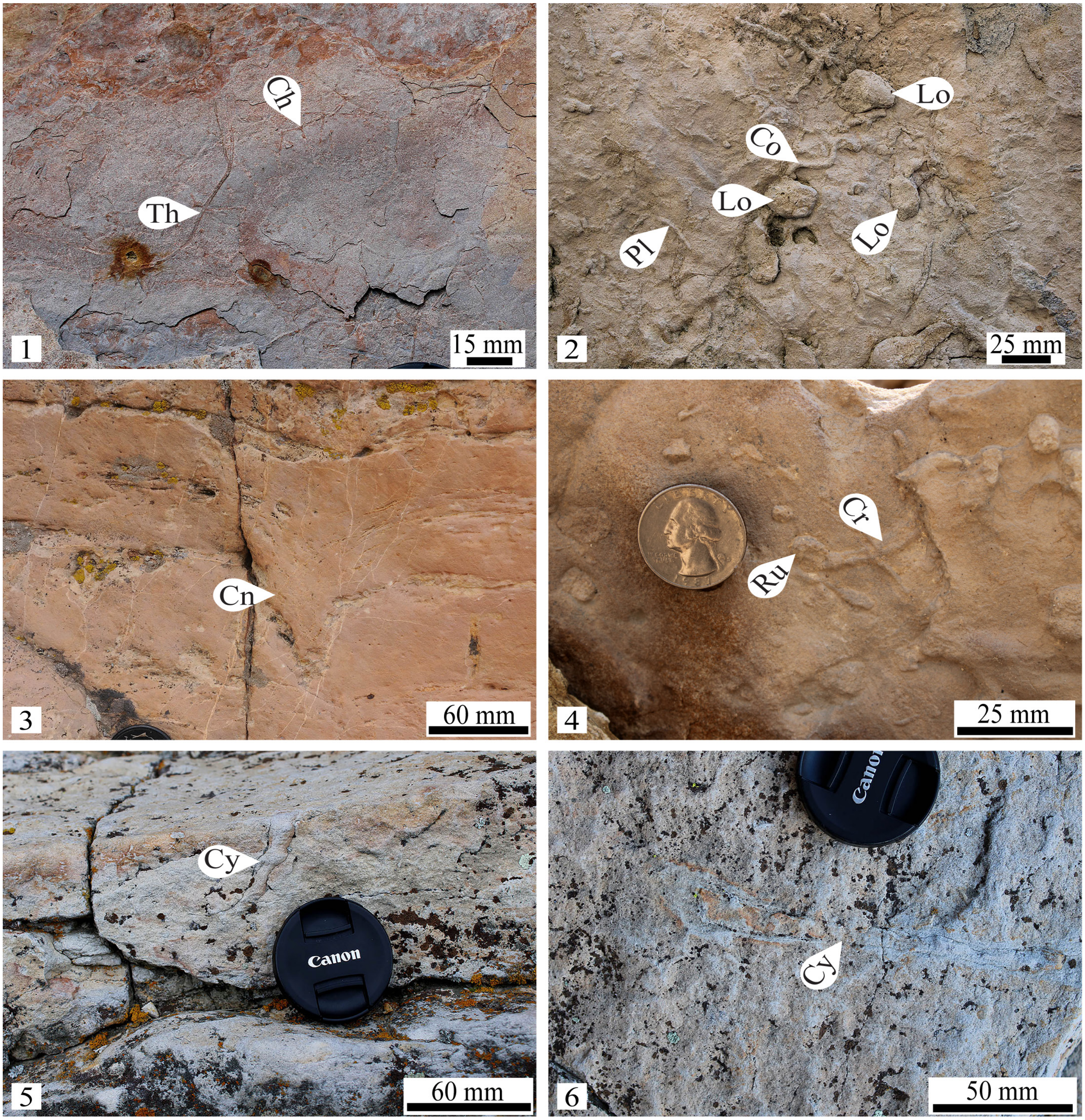


Figure 6. *Chondrites* (Ch), *Cochlichnus* (Co), *Conichnus* (Cn), *Cruziana* (Cr), *Cylindrichnus* (Cy), *Lockeia* (Lo), *Planolites* (Pl), *Rusophycus* (Ru), and *Thalassinoides* (Th) from the Dakota Group. *1*, *Chondrites intricatus* with *Thalassinoides suevicus* in convex epirelief, within the upper part of the Muddy Formation at Skyline Drive. *2, Cochlichnus anguineus, Lockeia siliquaria,* and *Planolites montanus* in convex hyporelief within the middle part of the Plainview Formation at Dinosaur Ridge. *3, Conichnus conicus* in vertical section within the middle part of the Plainview Formation at Grape Creek. *4, Cruziana* isp. transitioning into *Rusophycus* isp., in convex hyporelief within the middle part of the Glencairn Formation at Skyline Drive. *5, Cylindrichnus concentricus* in vertical section within the upper part of the Fort Collins Member of the Muddy Formation at Horsetooth Reservoir. *6, Cylindrichnus concentricus* in concave epirelief within the middle part of the Fort Collins Member of the Muddy Formation at Horsetooth Reservoir.

moved by Häntzschel (1975) due to their trails consisting of being more smooth sine curves than sharp corners. Fillion and Pickerill (1990) changed the diagnosis of *Cochlichnus* to include trails and burrows. Rindsberg (1994) established *Cymataulus undulatus* for sinusoidal burrows with thin linings and placed specimens of *Cochlichnus* described as burrows within it. Rindsberg (1994) stated that Hitchcock (1858) was capable of distinguishing between trails and burrows, based on the establishment of *Cunicularius* for shallow, subterranean, horizontal burrows. Stanley and Pickerill (1996) argued against the establishment of *Cymataulus*, stating that distinguishing between trails and burrows is difficult due to preservation, and therefore synonymized *Cymataulus* into *Cochlichnus*. Rindsberg (2014) argued that previous work has shown that distinguishing burrows and trails is possible, and rejected the synonymy. Some researchers still follow the synonym by Fillon and Pickerill (1990) (e.g., Buatois, Jalfin, & Aceñolaza, 1997; Gámez Vintaned & others, 2006; Minter & Braddy, 2009). We agree with Rindsberg (2014) that distinguishing between trails and burrows is possible, however, we synonymize *Cymataulus undulatus* with *Palaeophycus*, based on the thin lining of the burrow, resulting in the ichnotaxon *Palaeophycus undulatus*. Similarly, *Cochlichnus* described as burrows without linings could be placed within *Planolites* (Stanley & Pickerill, 1996). We follow the diagnosis provided by Häntzschel (1975) because it clearly defines *Cochlichnus* as a regularly meandering sinusoidal trail. We recommend a review of the architectural morphologies that have been assigned to the ichnotaxon *Cochlichnus* to determine the need, if any, for erection of new ichnotaxa to accommodate any morphologies that cannot be placed within existing ichnotaxa.

Cochlichnus is interpreted as a locomotion trail produced by annelids, nematodes, or insect larvae in continental settings and annelids in marine settings (Metz, 1987; Schlirf, 2003; Hasiotis, 2002, 2004; Tiwari & others, 2011). *Cochlichnus* is present in channel, floodplain, and lacustrine continental settings and delta front, lagoonal, offshore marine settings (Fordyce, 1980; Pemberton & Frey, 1984; Fillion & Pickerill, 1990; Hasiotis, 2002, 2004; Hogue & Hasiotis, 2018). *Cochlichnus* ranges from the Ediacaran to Holocene in marine settings, and Carboniferous to Holocene in continental settings (Gibbard & Stuart, 1974; Fillion & Pickerill 1990; Hogue & Hasiotis, 2018).

COCHLICHNUS ANGUINEUS Hitchcock, 1858

Figure 6.2

Diagnosis.—Smooth trail with regular to irregular meanders, generally resembling a sine curve (after Hogue & Hasiotis, 2018).

Description.—Single specimen is in convex hyporelief with smooth walls; ~3 mm wide and ~45–50 mm long.

Occurrence.—Reddish yellow (7.5YR 6/8) fine-grained, well-rounded and sorted sandstone, with BPBI 2. Present in the middle part of the Plainview Formation at Dinosaur Ridge.

Associated ichnotaxa.—*Dromaeosauripus* isp*., Lockeia siliquaria,* and *Planolites montanus*.

Discussion.—The specimen are assigned to *Cochlichnus anguineus* based on the uniform sine-curve pattern, smooth walls, and lack of helical form (Pemberton & Frey, 1984; Hogue & Hasiotis, 2018). The tracemaker for *Cochlichnus anguineus* is oligochaete worms, based on the large width of the trail (Hasiotis 2004). *Cochlichnus anguineus* is present with several *Lockeia siliquaria*. The bed bearing *Cochlichnus anguineus* is overlain by planar tabular crossbedded sandstone and is underlain by a bed with tracks assigned to *Dromaeosauripus* isp.; these traces and facies indicate a fluvial environment with variable flow regime (Weimer & Land, 1972).

Ichnogenus CONICHNUS Männil, 1966

Conichnus Männil, 1966, p. 201.

Amphorichnus Männil, 1966, p. 202.

Plug-Shaped burrows, Howard, 1966, p. 48, fig. 15.

Conichnus Frey & Howard, 1981, p. 800, fig., 1a, 2a–e.

Conichnus Hammersburg, Hasiotis, & Robison 2018, p. 12, fig. 8.2–8.4.

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

Diagnosis.—Short to long, vertical, conical to subcylindrical burrows with a smooth, rounded base or oriented papillar protuberances on base; burrow infill may be unstructured or have V-shaped laminae (after Hammersburg, Hasiotis, & Robison, 2018).

Discussion.—*Conichnus* and *Amphorichnus* were established for simple conical burrows by Männil, 1966, the only difference between the ichnogenera being minor differences in morphology. Accordingly, Frey and Howard (1981) considered these ichnogenera to be synonymous, with *Conichnus* having priority. In another study by Pemberton, Frey, and Bromley (1988), *Conichnus* was compared to 14 other plug-shaped ichnogenera, which resulted in only five ichnogenera being recognized as valid: *Astropolichnus* Crimes & Anderson, 1985; *Bergaueria* Prantl, 1945; *Conichnus* Männil, 1966; *Conostichnus* Lesquereux, 1876; and *Dolophichnus* Alpert & Moore, 1975. They synonymized *Amphorichnus* with *Conichnus* based on the conical to subcylindrical shape with a rounded base, with or without a protuberance. These assessments have recently been disputed based on the amphoralike shape and papillate termination of *Amphorichnus* (Vinn, Wilson, & Toom, 2015).

Conichnus is interpreted be to a resting, equilibrium, or escape trace with the tracemakers being sea anemones in marine settings (Pemberton & Jones, 1988; Savrda, 2002; Desai & Saklani, 2015; Klug & Hoffman, 2018). *Conichnus* is present in high-energy, shallow marine, deltaic, and tidal settings (Howard & Frey, 1984; Eisawi, Babikir, & Salih, 2011; Vinn, Wilson, & Toom, 2015; Hammersburg, Hasiotis, & Robison, 2018). *Conichnus* ranges from the early Cambrian to Holocene (Schäfer, 1972; Savrda, 2002; Darroch & others, 2016; Hammersburg, Hasiotis, & Robison, 2018).

CONICHNUS CONICUS Männil, 1966

Figure 6.3

Diagnosis.—Short cone- to plug-shaped depression with smooth, rounded bottom, and a vertical tube penetrates some (after Hammersburg, Hasiotis, & Robison, 2018).

Description.—Single specimen is present in full relief; ~115 mm wide and 150 mm tall.

Occurrence.—Reddish yellow (5YR 7/8) fine- to very fine-grained sandstone with planar bedding. Specimen was present in the middle part of the Plainview Formation at Grape Creek.

Associated ichnotaxa.—None.

Discussion.—The specimen is assigned to the ichnospecies *Conichnus conicus* based on the conical plug shape, rounded base, absence of a visible central shaft, and lack of a protuberance (Pemberton, Frey, & Bromley, 1988; Hammersburg, Hasiotis, & Robison, 2018). The tracemaker for *Conichnus conicus* was a sea anemone (Pemberton & Jones, 1988). *Conichnus conicus* was constructed in a subtidal environment based on lithology and bedforms (Gustason & Kauffman, 1985).

Ichnogenus CRUZIANA d'Orbigny, 1842

Cruziana d'Orbigny, 1842, p. 30.

Cruziana Seilacher, 1970, p. 454.

Isopodichnus Bromley & Asgaard, 1979, p. 66.

Cruziana Hammersburg, Hasiotis, & Robison, 2018, p. 13, fig. 9.1–9.4, 10.1–10.5, 16.5.

Type Ichnospecies.—*Cruziana rugosa* d'Orbigny, 1842.

Diagnosis.—Elongate, bilobate, ribbonlike furrows with medial ridges (concave epirelief) or grooves (convex hyporelief). Furrows are commonly covered by herringbone-like, transverse, or longitudinal striate (after Hammersburg, Hasiotis, & Robison, 2018).

Discussion.—*Cruziana* was synonymized with *Rusophycus* by Seilacher (1970) due to their similar striation patterns and having the same interpreted tracemaker. This synonymy has been rejected by most researchers based on each of the ichnogenera representing distinct behavior and having recognizable morphological differences (Crimes, 1975; Fillion & Pickerill, 1990; Pickerill, 1995; Jensen, 1997). Several researchers have noted that *Cruziana* can transition into such ichnogenera as *Diplichnites*, *Diplopodichnus*, and *Rusophycus* (Crimes, 1970b; Bromley & Asgaard, 1979; Jensen, 1997; Zonneveld & others, 2002).

Cruziana is interpreted to be deposit-feeding, grazing, locomotion, or predation behaviors (Crimes 1970a, 1970b; Seilacher 1970; Pickerill, 1995; Jensen, 1997; Zonneveld & others, 2002; Gingras & others, 2007; Hammersburg, Hasiotis, & Robison, 2018). The tracemakers of *Cruziana* are commonly interpreted to be trilobites (Paleozoic), with horseshoe crabs, branchiopods, and notostracan arthropods being suggested for post-Paleozoic *Cruziana* (Crimes, 1970a; Fillion & Pickerill, 1990; Pickerill, 1995; Zonneveld & others, 2002; Hammersburg, Hasiotis, & Robison, 2018). *Cruziana* has been reported in continental (fluvial, lacustrine, and brackish), shallow-marine (deltaic, foreshore, lagoonal, offshore, and tidal-flat) and deep-marine (flysch) environments (Crimes, 1970a, 1970b; Bromley & Asgaard, 1979; Seilacher, 1985; Fillion & Pickerill, 1990; Pickerill, 1995). *Cruziana* ranges from the early Cambrian to Cretaceous (Crimes, 1970a, 1970b, 1987, 1992; Mángano & others, 2002; Hasiotis, 2012).

CRUZIANA isp.

Figure 6.4

Description.—Single trace in convex hyporelief with the bilobate furrows lacking any surficial morphology. Trace is ~25 mm long and ~3 mm wide, with the lobes ~1 mm wide.

Occurrence.—Reddish yellow (7.5YR 6/8), very fine-grained, subrounded and well-sorted sandstone, with planar bedding with a BPBI 4. Specimen is present in the middle part of the Glencairn Formation at Skyline Drive.

Associated ichnotaxa.—*Gyrolithes lorcaensis, Lockeia siliquaria, Rusophycus* isp.*, Planolites montanus, Taenidium serpentinum,* and *Thalassinoides suevicus*.

Discussion.—The specimen is assigned to *Cruziana* based on its elongate bilobate furrows with a medial groove (e.g., Hammersburg, Hasiotis, & Robison, 2018). The tracemakers was most likely an arthropod (Fillion & Pickerill, 1990; Hammersburg, Hasiotis, & Robison, 2018). The worn surface of the specimen prevents proper placement into an ichnospecies. The specimen grades into a *Rusophycus* isp. This specimen occurs in the 2nd sandstone bed of the Glencairn Formation, which, based on the lithology and succession of beds, was constructed in a deltaic environment (Gustason & Kauffman, 1985).

Ichnogenus CYLINDRICHNUS Toots in Howard, 1966

Cylindrichnus Toots, 1962, p. 94.

Cylindrichnus Howard, 1966, p. 44, fig. 10.

Cylindrichnus Frey & Howard, 1985, p. 378, fig. 8.1, 10.3, 10.4, 10.9, 16.11.

Cylindrichnus Ekdale & Harding, 2015, p. 429.

Type ichnospecies.—*Cylindrichnus concentricus* Toots in Howard, 1966.

Emended Diagnosis.—Long, subcylindrical to subconical, vertical to horizontal, straight to gently curved, sometimes U-shaped, or rarely helicoidal or branched burrows having multiple concentrically layered laminae around a central core; surficial morphology may be present on the burrow surface (modified after Frey & Howard, 1985; Ekdale & Harding, 2015).

Discussion.—*Cylindrichnus* was introduced in an unpublished thesis by Toots (1962), who proposed *Cylindrichnus concentricus* as the type ichnospecies, which was reported subsequently by Howard (1966). *Cylindrichnus* was named for nearly horizontal to vertical burrows with an exterior wall that was concentrically layered around a central core (e.g., Howard, 1966). A formal diagnosis was provided by Howard and Frey (1984) as "long, subcylindrical to subconical burrows, straight to gently curved, vertical to horizontal, having concentrically layered walls". A slight modification appeared in Frey and Howard (1985) with the addition of "rarely branched". Currently seven ichnospecies of *Cylindrichnus* are recognized: *Cylindrichnus concentricus* Toots, 1962 in Howard, 1966; *Cylindrichnus elongatus* Noda, 1984; *Cylindrichnus pustulosus* Frey & Bromley, 1985; *Cylindrichnus errans* D'Alessandro & Bromley, 1986; *Cylindrichnus operosus* Orłowski, 1989; *Cylindrichnus candelabrus* Głuszek, 1998; and *Cylindrichnus helix* de Gibert & others, 2006. *Cylindrichnus candelabrus* and *Cylindrichnus concentricus* were described as having a U shape with *Cylindrichnus candelabrus* being branched at one end. *Cylindrichnus errans* possesses causative shafts with vertically oriented spreite. *Cylindrichnus elongatus* and *Cylindrichnus operosus* are vertical burrows with the only difference between them being size. For this reason, we regard *Cylindrichnus operosus* as a junior synonym of *Cylindrichnus elongatus* as size is not an ichnotaxonomic criterion (Bertling & others, 2006). The burrows of *Cylindrichnus helix* are helicoidal rather than straight, and *Cylindrichnus pustulosus* has surficial morphology in the form of ridges or nodes on its outer surface. Ekdale and Harding (2015) emended the diagnosis of *Cylindrichnus* to account for the reexamination of the original type material. This emended diagnosis, however, failed to take into account the various morphologies of *Cylindrichnus* ichnospecies, including those of *Cylindrichnus concentricus,* whose diagnosis was also emended. For this reason, we emended the diagnosis of *Cylindrichnus* to account for the various forms of its ichnospecies.

Cylindrichnus bears similarities to *Rosselia,* but the lack of a bulbous form in the upper parts of *Cylindrichnus* and the uniform concentric cone-in-cone arrangement of laminae make it distinct (Frey & Howard, 1985; Nara & Ekdale, 2006; Ekdale & Harding, 2015). Goldring (1996) called into question the validity of *Cylindrichnus* and considered it a *nomen dubium* based on the construction of its concentric laminae and sediment infill. However, several researchers have examined the sediment infill and concentric laminae of *Cylindrichnus* including the type specimen and concluded that *Cylindrichnus* was still a valid ichnogenus based on its architectural and surficial morphology (Nara & Ekdale, 2006; Belaústegui & de Gibert, 2013; Ekdale & Harding, 2015).

Cylindrichnus is interpreted variously as the dwelling burrow of a sessile suspension feeder such as a polychaete worm, a surface-deposit feeder, or an active ambush predator (Howard, 1966; Głuszek, 1998; Belaústegui & de Gibert, 2013; Ekdale & Harding, 2015). *Cylindrichnus* was present in brackish, lower to middle shoreface, and offshore marine environments (Frey & Bromley, 1985; Frey & Howard, 1985; D'Alessandro & Bromley, 1986; Głuszek, 1998; Ekdale & Harding, 2015; Gingras & others, 2016). *Cylindrichnus* ranges from the early Cambrian to Holocene (D'Alessandro & Bromley, 1986; Głuszek, 1998).

CYLINDRICHNUS CONCENTRICUS
Toots, in Howard, 1966
Figure 6.5, 6.6, 11.6, 13.1

Diagnosis.—Downward tapering burrow, longer than deep, with vertical to slightly inclined orientation. Fill is concentrically lined throughout (after Ekdale & Harding, 2015).

Description.—Specimens are seen in concave epirelief, convex epirelief and full relief. Concentric circular laminae are present in some of the specimens, whereas others are recognized by their downward tapering forms. Specimens range from 3 to 8 mm wide, 30 to 50 mm tall, and 10 to 68 mm long.

Occurrence.—(1) Reddish yellow (7.5YR 6/8), fine- to very fine-grained sandstone that is significantly bioturbated (ii4); and (2) white (10R 8/1), very fine- to fine-grained sandstone, with BPBI 1–3. Present in the upper part of the Plainview Formation along Skyline Drive and the middle and upper parts of the Fort Collins Member of the Muddy Formation at Horsetooth Reservoir.

Associated ichnotaxa.—*Ophiomorpha nodosa, Ophiomorpha* isp., *Rosselia socialis, Skolithos linearis,* and *Teichichnus rectus.*

Discussion.—Specimens are assigned to *Cylindrichnus concentricus* based on their downward tapering curvature, presence of concentric layers, and smooth burrow surface (e.g., Frey & Bromley, 1985; Głuszek, 1998; Ekdale & Harding, 2015). The tracemaker for *Cylindrichnus concentricus* is an infaunal worm (Ekdale & Harding, 2015). The specimens in the Plainview Formation are clustered together, whereas those at Horsetooth Reservoir occur individually. The concentric layers of the specimens in the Muddy Formation are better preserved than those in the Plainview Formation. In the Plainview Formation, *Cylindrichnus concentricus* was constructed in a subtidal environment based on the lithology and the presence of both suspension-feeding and deposit-feeding trace fossils in which suspension feeders are dominant (Gustason & Kauffman, 1985). *Cylindrichnus concentricus* in the Muddy Formation were constructed in a deltaic environment, based on the grain size of the sand and the presence of planar bedding (MacKenzie, 1965).

Ichnogenus DIPLOCRATERION Torell, 1870

Diplocraterion Torell, 1870, p. 13.

Polyupsilon Knox, 1973, p. 133.

Corophioides Fürsich, 1974b , p. 957.

Diplocraterion Fürsich, 1974b, p. 957.

Type Ichnospecies.—Diplocraterion parallelum Torell, 1870.

Diagnosis.—Vertical U-shaped burrow with spreite between limbs (after Fürsich, 1974b).

Discussion.—Diplocraterion was grouped with the U-shaped spreite burrows *Corophioides* and *Polyupsilon* in the Rhizocoralliidae by Richter (1926) (e.g., Fürsich, 1974b; Fillion & Pickerill, 1990). In a study by Knox (1973), *Polyupsilon* was made a junior synonym of *Corophioides*. Fürsich (1974b) made *Corophioides* a junior synonym of *Diplocraterion* based on similar morphological features. This synonymy has been disputed by some authors based on *Corophioides* possessing a different spreite pattern than *Diplocraterion*, as well as *Corophioides* lacking funnel-shaped limb openings (e.g., McCarthy, 1979; Benton & Gray, 1981). Fürsich (1974b) argued, however, that the presence of a funnel for *Diplocraterion* is not a proper diagnostic characteristic because funnels can be removed by erosion prior to burial and weathering due to exposure. Fürsich (1974b) also argued that the differences in spreite morphology are not distinctive enough to warrant a distinct ichnogenus. Additionally, these different spreite morphology have been found together in specimens of *Diplocraterion* (Fürsich, 1974b).

Diplocraterion is interpreted to be the dwelling of such suspension feeders as polychaete annelids or crustaceans (Fürsich, 1974b; Fillion & Pickerill, 1990; Bradshaw, 2010). *Diplocraterion* occurs in shallow-marine (estuarine, deltaic, intertidal, lagoonal, middle shoreface, subtidal, and tidal flat) and deep-marine (distal shelf, flysch, and sea fan) environments (Crimes, 1977; Crimes & others, 1981; Cornish, 1986; Pemberton & Frey, 1984; Fillion & Pickerill, 1990; MacEachern & Pemberton, 1992; Schlirf, 2003; Talyor, Goldring, & Gowland, 2003; Hubbard, Gingras, & Pemberton, 2004; Bradshaw, 2010; Hasiotis, McPherson, & Reilly, 2013; Flaig, Hasiotis, & Jackson, 2016, Flaig & others, 2019). *Diplocraterion* ranges from the early Cambrian to Holocene (Orłowski, 1989; D'Alessandro & Bromley, 1986).

DIPLOCRATERION HABICHI Lisson, 1904
Figure 7.1, 7.2

Emended Diagnosis.—Vertical, U-shaped burrow with discontinuous spreite between limbs with the width between the limbs narrow; uppermost part of limbs can diverge outward in complete specimens (modified from Fürsich, 1974b).

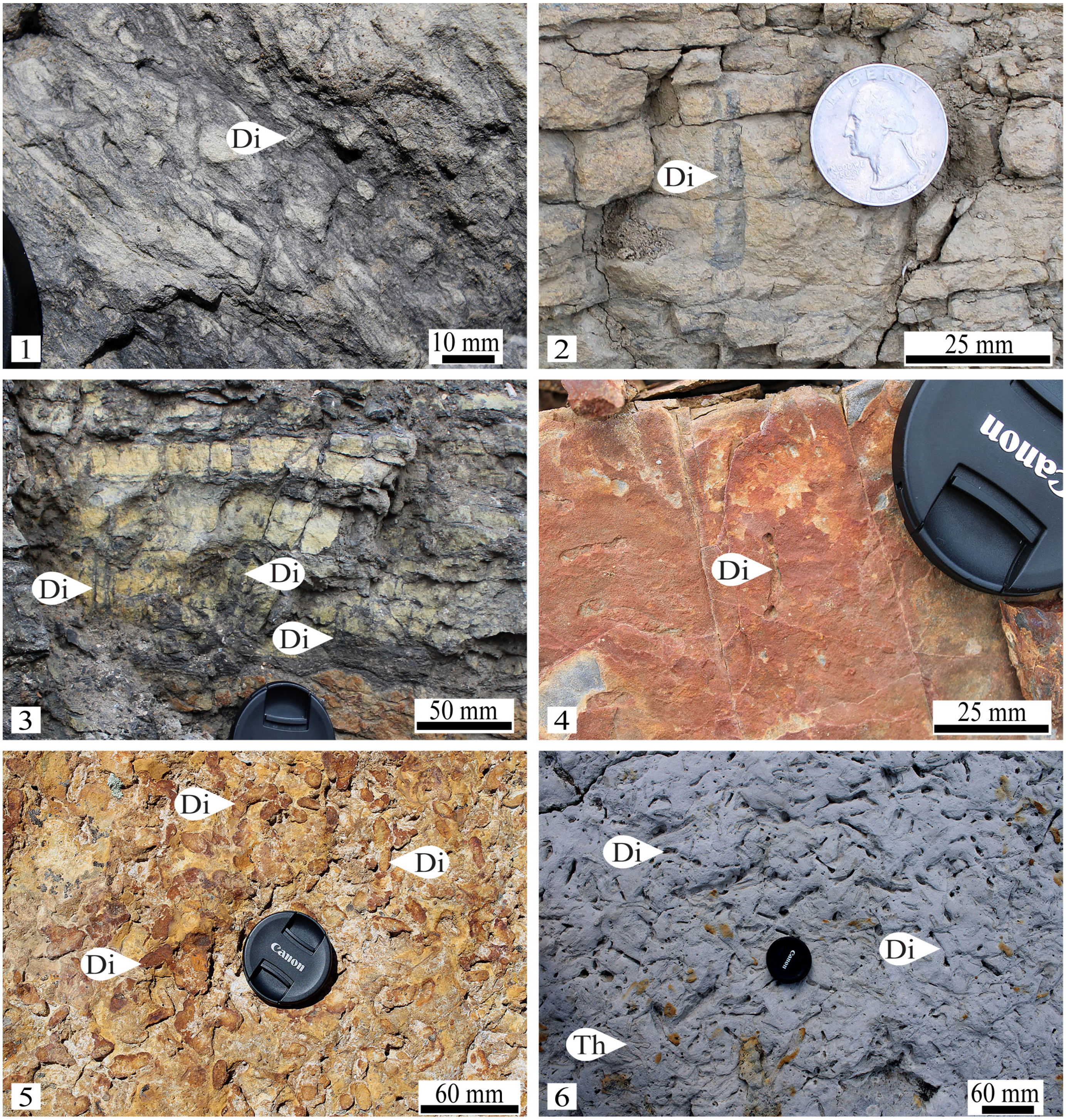


Figure 7. *Diplocraterion* (Di) and *Thalassinoides* (Th) from the Dakota Group. *1, Diplocraterion habichi* in vertical section within the middle part of the Skull Creek Shale at I-70. *2, Diplocraterion habichi* in vertical section within the middle part of the Skull Creek Shale at Horsetooth Reservoir. *3, Diplocraterion parallelum* in vertical section within the lower part of the Skull Creek Shale at U.S Route 285. *4, Diplocraterion* isp. in concave epirelief within the upper part of the Muddy Formation at Skyline Drive. 5*, Diplocraterion* isp. in concave epirelief within the lower part of the Muddy Formation at Dinosaur Ridge. 6*, Diplocraterion* isp. and *Thalassinoides suevicus* in concave epirelief within the middle part of the Muddy Formation at Dinosaur Ridge.

Description.—Specimens are in full relief, with protrusive spreite faint in the narrow space between the limbs of each specimen. Specimens range from 5 to 29 mm high, 2.5 to 6 mm wide (measured outside the limbs), with the limbs of the larger specimens ~2 mm in diameter.

Occurrence.—(1) Very dark gray (7.5YR 3/1) shale interbedded with a white (10R 8/1) siltstone to very fine-grained sandstone with varying degrees of bioturbation (ii2–4); and (2) very dark gray (7.5YR 3/1) shale interbedded with strong brown (7.5YR 5/8) very fine-grained sandstone, with little bioturbation (ii2). Present in the middle part of the Skull Creek Shale at I-70 and Horsetooth Reservoir.

Associated ichnotaxa.—Palaeophycus tubularis and *Teichichnus rectus.*

Discussion.—Specimens are assigned to *Diplocraterion habichi* based on the U shape of the burrows, the presence of discontinuous spreite, and narrow width between the limbs (e.g., Fürsich, 1974b). We emended the diagnosis to include the morphology described by Fürsich (1974b), that distinguishes *Diplocraterion habichi* from other *Diplocraterion* ichnospecies. The limbs do not have signs of diverging outward at their uppermost part; however, this characteristic could be missing due to preservation of the specimens. This is not uncommon as other researchers have reported *Diplocraterion habichi* without the diverging upward limbs (e.g., Fürsich, 1974b; Martin & Pollard, 1996; Bann & others, 2004; MacEachern & others, 2007a, 2007b, 2007c). At I-70, *Diplocraterion habichi* are much smaller compared to those at Horsetooth Reservoir. The tracemaker for *Diplocraterion habichi* at I-70 was most likely a polychaete based on the size of the specimen (Fillion & Pickerill, 1990). At Horsetooth reservoir the tracemaker for *Diplocraterion habichi* was most likely a polychaete or crustacean (Fillion & Pickerill, 1990). *Diplocraterion habichi* at I-70 were constructed in a marine embayment based on the presence of both suspension- and deposit-feeding trace fossils and the increasing presence of mudstone (Weimer & Land, 1972); at Horsetooth Reservoir they were constructed in a middle to lower shoreface environment, based on the lithology and sedimentary structures, and degree bioturbation of the beds (Graham & Ethridge, 1995).

DIPLOCRATERION PARALLELUM Torell, 1870

Figure 7.3

Diagnosis.—Vertical U-shaped burrow, with parallel limbs and spreite (after Fürsich, 1974b).

Description.—Specimens of U-shaped burrows in full relief with protrusive spreite faintly visible between the limbs. Specimens are ~30 mm tall, 9 mm wide (measured outside the limbs), with the limbs ~2 mm in diameter.

Occurrence.—Reddish yellow (7.5YR 6/8) to light olive brown (10Y 5/4) shale, interbedded with white (10R 8/1) siltstone, heavily bioturbated (ii5). Present in the lower part of the Skull Creek Shale at U.S. Route 285.

Associated ichnotaxa.—None.

Discussion.—Specimens are assigned to *Diplocraterion parallelum* based on the U shape of the burrows, smooth surface of the limbs, parallel orientation of the limbs, the wide width between the limbs, and spreite between the limbs (Fürsich, 1974b; Fillion & Pickerill, 1990). The tracemaker for *Diplocraterion parallelum* was most likely a polychaete or crustacean (Fillion & Pickerill, 1990). The beds in which *Diplocraterion parallelum* occur were deposited in an interdistributary bay (marine embayment) based on lithology and bioturbation (Weimer & Land, 1972).

DIPLOCRATERION isp.

Figure 7.4, 7.5, 7.6, 8.1

Description.—Specimens are in concave epirelief with some having a slight curve, which exhibits a dumbbell shape. Distance between limbs of the U-shaped burrow ranges from 24 to 60 mm (measured from the outside), each limb being 2–8 mm in diameter.

Occurrence.—(1) Reddish yellow (7.5YR 6/8) mudstone with desiccation cracks and a sulfurous smell, with BPBI 2; (2) reddish yellow (7.5YR 7/8), very fine- to fine-grained sandstone with BPBI 2–3; (3) reddish yellow (7.5YR 7/8) to strong brown (7.5YR 5/8), fine- to very fine-grained sandstone with BPBI 2–3; and (4) white (10R 8/1), very fine- to fine-grained sandstone with BPBI 3–5. Present in the middle and upper parts of the Muddy Formation along Skyline Drive and in the lower and middle parts of the Muddy Formation at Dinosaur Ridge.

Associated ichnotaxa.—Rhizocorallium commune and *Thalassinoides suevicus.*

Discussion.—Specimens are assigned to *Diplocraterion* based on the dumbbell shape being a common characteristic of *Diplocraterion* in epirelief (Fillion & Pickerill, 1990). The tracemaker for *Diplocraterion* isp. was most likely a polychaete or crustacean (Fillion & Pickerill, 1990). *Diplocraterion* isp. at Skyline Drive have a curved shape to the dumbbell (Fig. 7.4, 8.1). At Skyline Drive *Diplocraterion* isp. is present with a single specimen of *Rhizocorallium commune*. *Diplocraterion* isp. in the middle part of Skyline Drive were produced in a subtidal environment based on the lithology, presence of ripple marks, and bioturbation pattern (Gustason & Kauffman, 1985). *Diplocraterion* isp. in the upper part of the Muddy Formation at Skyline Drive were constructed in an intertidal environment based on the presence of ripple marks and desiccation cracks (Gustason & Kauffman, 1985). At Dinosaur Ridge *Diplocraterion* isp. in the lower part of the Muddy Formation are overlain and underlain both by wave ripples with syneresis cracks and by current ripples, indicating they were constructed in a subtidal environment associated with a tidal channel (MacKenzie, 1975; Chamberlain, 1985). In the middle part at Dinosaur Ridge *Diplocraterion* isp. co-occurs with and crosscuts *Thalassinoides suevicus,* suggesting that at least some of *Diplocraterion* isp. were constructed after *Thalassinoides suevicus*. These traces were likely constructed in a subtidal environment based on the lithology and bedforms (MacKenzie, 1975; Chamberlain, 1985).

Ichnogenus GYROLITHES de Saporta, 1884

Spiroscolex Torrell, 1870, p. 12.
Gyrolithes de Saporta, 1884, p. 27.
Xenohelix Mansfield, 1927, p. 7, pl. 2, 3.
Conispiron Vialov, 1969, p. 108.
Spirocircus Mikuláš & Pek, 1994, p. 76, fig. 2.
Gyrolithes Uchman & Hanken, 2013, p. 315.

Type Ichnospecies.—Gyrolithes davreuxi de Saporta, 1884.

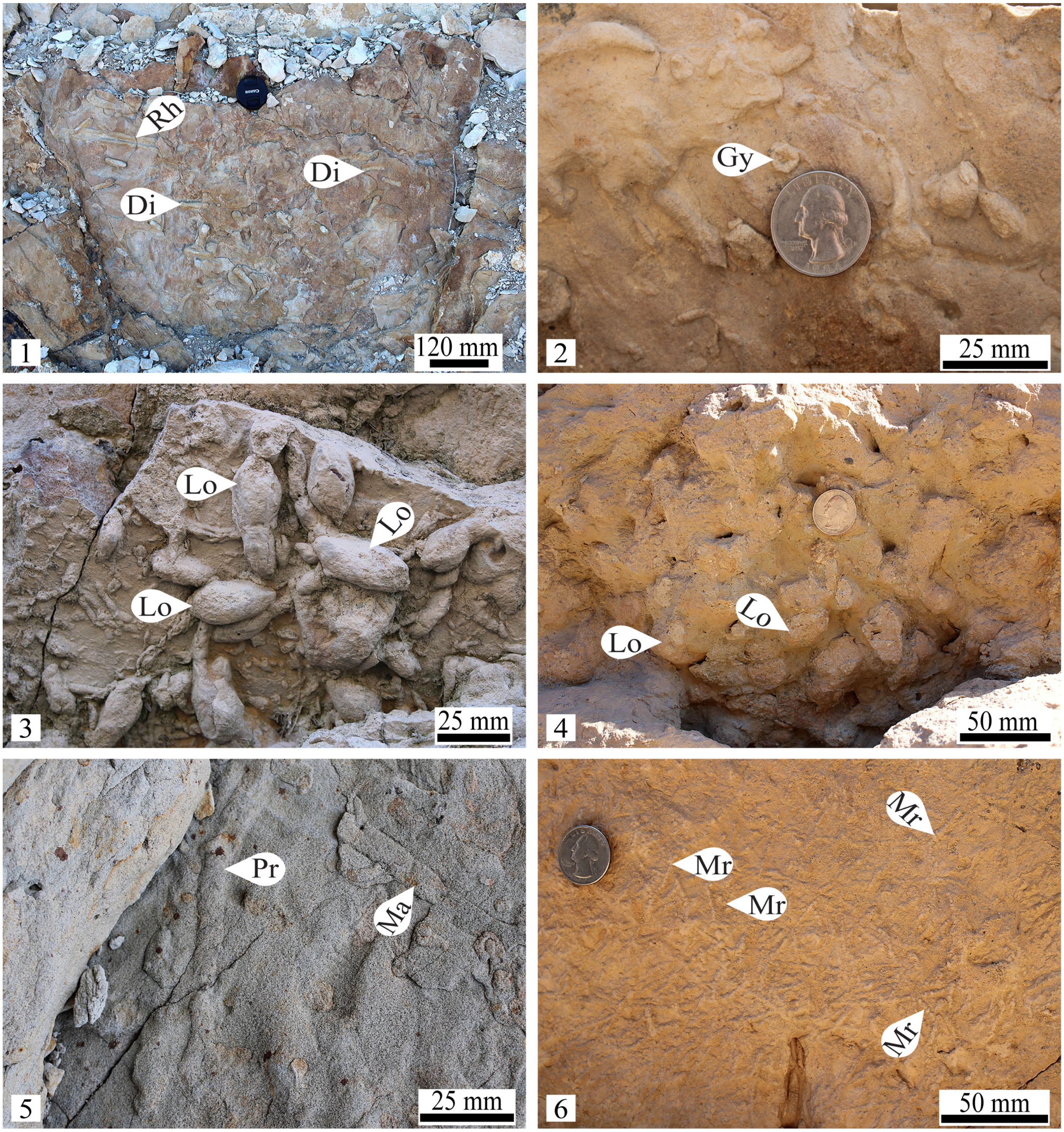


Figure 8. *Diplocraterion* (Di), *Gyrolithes* (Gy), *Lockeia* (Lo), *Macaronichnus* (Ma), *Margaritichnus* (Mr), *Protovirgularia* (Pr), and *Rhizocorallium* (Rh) from the Dakota Group. *1, Diplocraterion* isp. and *Rhizocorallium commune* in convex epirelief within the middle part of the Muddy Formation at Skyline Drive. *2, Gyrolithes lorcaensis* in convex hyporelief within the middle part of the Glencairn Formation at Skyline Drive. *3, Lockeia siliquaria* in convex hyporelief within the lower part of the Plainview Formation at Dinosaur Ridge. *4, Lockeia* isp. in convex hyporelief within the middle part of the Plainview Formation at Skyline Drive. *5, Macaronichnus segregatis* and *Protovirgularia pennatus* in concave epirelief, within the middle part of the Fort Collins Member of the MuddyFormation at Horsetooth Reservoir. *6, Margaritichnus mansfieldi* in convex hyporelief within the middle part of the Plainview Formation at Skyline Drive.

Emended Diagnosis.—Helical burrow, essentially vertical, consisting of dextral, sinistral or reversing coils, that are not in contact; surface with or without sculpture; burrows terminating with or without expanded chamber (modified after Uchman & Hanken, 2013).

Discussion.—Bromley and Frey (1974) redescribed *Gyrolithes* to separate it from *Ophiomorpha* and *Thalassinoides*, due to *Gyrolithes* sometimes forming a compound burrow system with those trace fossils. Jensen (1997) examined the poorly known spiral ichnotaxon *Spiroscolex* Torell, 1870. The diagnosis of *Spiroscolex* is "Vermis per totum corpus aequalem latitudinem exhibens, annulatus, statu quiescenti spiraliter convolutes", which roughly translates into "The worm along its entire body exhibiting equal width, annulus, convolutes spirally in a quiescent state". Examining the type material, Jensen (1997) noted that the type material can be described as a vertical spiral burrow similar to *Gyrolithes*. From this, he determined that *Spiroscolex* was a senior synonym to *Gyrolithes.* However, because of it not being heavily used in the literature he proposed that it be suppressed for reasons of taxonomic stability based on the International Code of Zoological Nomenclature (ICZN, Article 23b). Uchman and Hanken (2013) reexamined the morphological characteristics used to separate the 19 ichnospecies of *Gyrolithes*. They argued that features such as a basal chamber should be removed as a morphological characteristic, due to the chamber either being absent or not being properly observed. Raisanen and Hasiotis (2018), however, argued that the basal chamber of this burrow morphology is a significant morphological characteristic, and should be included when erecting an ichnotaxon regardless of the preservation of that feature.

Gyrolithes is interpreted to be the dwelling of a thalassinidean shrimp, such as those in the genus *Axianassa,* and/or polychaete worms (Bromley & Frey, 1974; Powell, 1977; Gingras & others, 2007; Wetzel, Tjallingii, & Stattegger, 2010). *Gyrolithes* occurs in brackish, tidal flat, estuarine, intertidal, and shoreface environments (Fillion & Pickerill, 1990; Jensen, 1997; Hubbard, Gingras, & Pemberton 2004; Morshedian, MacEachern, & Dashtgard, 2009; Gingras & others, 2016). *Gyrolithes* ranges from the early Cambrian to Holocene (Jensen, Droser, & Gehling, 2006; Wetzel, Tjallingii, & Stattegger, 2010; Hasiotis, 2012; Laing & others, 2018; Muñiz & Belaústegui, 2019).

GYROLITHES LORCAENSIS Uchman & Hanken, 2013

Figure 8.2

Diagnosis.—Smooth spiral burrow without a wall lining, whose burrow width ranges from 3 to 8 mm, and whose whorl radius ranges from 4 to 8 mm (after Uchman & Hanken, 2013).

Description.—Single specimen is in convex hyporelief, the whorl is smooth. One and a half whorls are preserved with ~1 mm space between whorls. Whorl is 8 mm wide (measured from the outside), burrow diameter is ~3 mm, and space within the helix of the whorl is ~2 mm.

Occurrence.—Reddish yellow (7.5YR 6/8), very fine-grained subrounded and well-sorted sandstone, with planar bedding with BPBI 3. Specimen is present in the middle part of the Glencairn Formation at Skyline Drive.

Associated ichnotaxa.—*Cruziana* isp., *Lockeia siliquaria*, *Planolites montanus*, *Rusophycus* isp., *Taenidium serpentinum*, and *Thalassinoides suevicus*.

Discussion.—The specimen is assigned to *Gyrolithes lorcaensis* based on the whorl pattern of the burrow, its vertical nature, smooth surface, and width of the burrow and whorl (e.g., Uchman & Hanken, 2013). The tracemaker for *Gyrolithes lorcaensis* was most likely a polychaete worm (Wetzel, Tjallingii, & Stattegger, 2010). The specimen is present in the 2nd sandstone bed of the Glencairn Formation (Fig., 8.2). *Gyrolithes lorcaensis* was constructed in a deltaic environment (Gustason & Kauffman, 1985).

Ichnogenus LOCKEIA James, 1879

Lockeia James, 1879, p. 17.

Pelecypodichnus Seilacher, 1953, p. 105, pl. 10, fig. 1, pl. 12, fig. 1, 2.

Lockeia Osgood, 1970, p. 368, pl. 1, fig. 7, pl. 2, fig. 10, pl. 3, fig. 1, 7, pl. 7, fig. 6, fig. 27.

Pelecypodichnus Eager, 1974, p. 230, fig. 8.

Lockeia Hakes, 1976, p. 29, pl. 6, fig. 3.

Pelecypodichnus Hakes, 1977, p. 222, pl. 1d.

Lockeia Maples & West, 1989, p. 694.

Lockeia Seilacher & Seilacher, 1994, p. 9.

Lockeia Hammersburg, Hasiotis, & Robison, 2018, p. 23, fig. 6.5, 19.2.

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

Diagnosis.—Almond-shaped to ovoid features in convex hyporelief or depressions in concave epirelief that taper at one or both ends; surface is typically smooth but may be irregular, and may have a medial, longitudinal crest (hyporelief) or groove (epirelief) (after Hammersburg, Hasiotis, & Robison, 2018).

Discussion.—Osgood (1970) considered *Lockeia* to be the senior synonym of *Pelecypodichnus* Seilacher, 1953 based on their similar morphologies. Eagar (1974), rejected this synonym, due to James (1879) not supplying a figure with his original description. Hakes (1976) countered this argument by citing Article 12 (e.g., ICZN, 2000) that type species assembled prior to 1931 only needed a description. In another study, Hakes (1977) considered *Lockeia* to be a *nomen oblitum* under the 50-year rule of the ICZN, because *Lockeia* had not been in use prior to 1960. This made *Lockeia,* according to Hakes (1977), synonymous with *Pelecypodichnus* under the Principle of Priority Article 23) (e.g., ICZN, 2000). Maples and West (1989) found this claim to be inaccurate due to Twenhofel (1927) creating the ichnospecies *Lockeia anticostiana*, which meant *Lockeia* had not undergone a 50-year hiatus. Additionally, the Commission on Zoological Nomenclature was not petitioned by Hakes (1977) to declare *Lockeia nomen oblitum*. For a recent review of the ichnospecies of *Lockeia*, see Hammersburg, Hasiotis, & Robison (2018).

Lockeia is interpreted to be the resting trace of bivalves (e.g., Osgood, 1970; Hakes, 1976; Fillion & Pickerill, 1990; Seilacher & Seilacher, 1994; Schlirf & others, 2001; Hammersburg, Hasiotis, & Robison, 2018). *Lockeia* is present in continental (fluvial and lacustrine), shallow marine (lagoonal, tidal flat, intertidal, and subtidal) and deep marine (flysch) environments (Bromley & Asgaard, 1979; Crimes & others, 1981, Fillion & Pickerill, 1990; Kim, 1994; Schlirf, & others, 2001; Hasiotis, 2002, 2004, 2007, 2008; Mángano, Buatois, & Rindsberg, 2002; Hasiotis & others, 2012). *Lockeia* ranges from the Ediacaran to Holocene in marine settings and Carboniferous to Holocene in continental settings (Crimes, 1987, 1992; Pemberton & Jones, 1988; Fillion & Pickerill 1990; Narbonne & Aitken, 1990; Głuszek, 1995; Hasiotis, 2002; Jensen, Droser, & Gehling, 2006; Carmona, Ponce, & Wetzel, 2018).

LOCKEIA SILIQUARIA James, 1879

Figure 6.2, 8.3

Diagnosis.—Almond-shaped to ovoid trace, with both or one of the ends tapering to a point or rounded surface. May be smooth or have a sharp longitudinal keel (after Fillion & Pickerill, 1990).

Description.—Traces are in convex hyporelief, almond-shaped with one of the ends tapering to a point or both being rounded, with medial ridges present on some. Surfaces are typically smooth. Specimens occur in clusters in random orientation or as individuals. Traces are 20–30 mm long and 10–15 mm wide, with few being smaller at 5 mm long and 3 mm wide.

Occurrence.—(1) Reddish yellow (7.5YR 6/8), fine-grained, well-rounded and well-sorted sandstone, with BPBI 2–3; (2) white (10R 8/1), very fine-grained, ripple-laminated sandstone interbedded with mudstone, with BPBI 2; and (3) reddish yellow (7.5YR 6/8), very fine-grained, subrounded and well-sorted sandstone with planar bedding and BPBI 4. Specimens are present in the lower part of the Plainview Formation at I-70, the lower part of the Plainview Formation at Dinosaur Ridge, at the upper part of the Plainview Formation at Colorado State Highway 115, and in the middle part of the Glencairn Formation at Skyline Drive.

Associated ichnotaxa.—Cochlichnus anguineus, Cruziana isp., *Dromaeosauripus* isp.*, Gyrolithes lorcaensis, Planolites montanus, Rusophycus* isp.*, Taenidium serpentinum,* and *Thalassinoides suevicus*.

Discussion.—Specimens are assigned to *Lockeia siliquaria* based on their almond shape and the tapering and rounding of the ends (Fillion & Pickerill, 1990; Seilacher & Seilacher, 1994). The tracemaker for *Lockeia siliquaria* were bivalves (Fillion & Pickerill, 1990). *Lockeia siliquaria* at Dinosaur Ridge are present in bedding planes with other trace fossils or by themselves. The *Lockeia*-bearing beds at Dinosaur Ridge and at I-70 represent a freshwater fluvial environment with variable flow regime (Weimer & Land, 1972). Specimens at Colorado State Highway 115 are smaller than those at other localities, co-occurring with *Thalassinoides suevicus*. They were produced in an intertidal to subtidal environment (Gustason & Kauffman, 1985).

LOCKEIA isp.

Figure 8.4

Description.—Specimens are in convex hyporelief with oval to almond-like shape, occurring in clusters in random orientation. External surfaces are worn. Specimens are ~25 mm wide and 30–35 mm long.

Occurrence.—Reddish yellow (7.5YR 6/8), fine- to very fine-grained, subrounded, moderately well-sorted sandstone, with some minor ripple marks and flaser bedding with significant bioturbation (ii4). Present in the middle part of the Plainview Formation along Skyline Drive.

Associated ichnotaxa.—Asthenopodichnium xylobiontum, Margaritichnus mansfieldi, Teredolites clavatus, and *Thalassinoides suevicus*.

Discussion.—Specimens are assigned to *Lockeia* based on their oval to almond shape (e.g., Fillion & Pickerill, 1990; Hammersburg, Hasiotis, & Robison, 2018). The tracemaker for *Lockeia* isp. were bivalves (Fillion & Pickerill, 1990). The worn surface of the specimens prevents proper placement within an ichnospecies. *Lockeia* are present in a bed that overlie the bed containing the tetrapod tracks *Magnoavipes caneeri* and *Tetrapodosaurus* isp. *Lockeia* were constructed in an intertidal to subtidal environment based on lithology and structures (Gustason & Kauffman, 1985; Kurtz, Lockley, & Engard, 2001).

Ichnogenus MACARONICHNUS Clifton & Thompson, 1978

Macaronichnus Clifton & Thompson, 1978, p. 1294, fig. 1–3.

Macaronichnus Bromley & others, 2009, p. 116, fig. 4–7, 13, 15.

Type Ichnospecies.—*Macaronichnus segregatis* Clifton & Thompson, 1978.

Emended Diagnosis.—Variably sinuous and looping, subhorizontal to subvertical, cylindrical, unbranched burrows commonly with a core lighter in color compared to host rock, sometimes surrounded by a mantle of dark grains; commonly densely packed and interpenetrating; fill may be meniscate (modified from Clifton & Thompson, 1978; Bromley & others, 2009; Nara & Seike, 2019).

Discussion.—*Macaronichnus* was named by Clifton and Thompson (1978) for cylindrical, smooth, sinuous intrastratal trails, with an infill slightly different than the surrounding lithology. These trails are enclosed by an outer rim that consists of mica, giving the trace a lined appearance. Bromley and others (2009) defined *Macaronichnus* as having horizontal orientation and a color difference between the burrow fill and surrounding host rock. We further emend the diagnosis to account for its variable orientation (Seike & others, 2015; Uchman & others, 2016), degree of interpenetration (Clifton & Thompson, 1978; Gingras & others, 2002; Savrda & Uddin, 2005; Carmona & others, 2009; Seike & others, 2011, 2015; Uchman & others, 2016; Nara & Seike, 2019), and meniscate backfill observed in some cases (Clifton & Thompson, 1978; Uchman & others, 2016). Studies of the infill of *Macaronichnus* suggest that the tracemaker had some preference for the sand it ingested, resulting in the infill being richer in felsic minerals than mafic (Clifton & Thompson, 1978; Gingras & others, 2002; Savrda & Uddin, 2005; Dafoe, Gingras, & Pemberton, 2008; Seike & others, 2011). This creates a contrast in which *Macaronichnus* is lighter in color than the surrounding host rock (Savrda & Uddin, 2005; Seike, 2007; Dafoe, Gingras, & Pemberton, 2008; Seike & others, 2015; Uchman & others, 2016). The outer rim or mantle (that comes from the selective feeding behavior of the tracemaker) results from mafic minerals being separated out and pushed to the sides (Clifton & Thompson, 1978; Maples & Suttner, 1990; Gingras & others, 2002; Savrda & Uddin, 2005; Dafoe, Gingras, & Pemberton, 2008).

Macaronichnus is interpreted to result from the deposit-feeding behavior of polychaete worms such as *Euzonis* and *Ophelia* (Clifton & Thompson, 1978; Maples & Suttner, 1990; Gingras & others, 2002). The ichnogenus is present in high-energy, shallow-marine (intertidal, subtidal, foreshore, shorefaces, distal delta front, and prodelta), sand-rich environments (Clifton & Thompson, 1978; MacEachern & Pemberton, 1992; Taylor & Lowell, 1995; Gingras, MacEachern & Pemberton, 1998; Carmona & others, 2009; Seike & others, 2011, 2015; Flaig & others, 2019). *Macaronichnus* occurs in marine waters of tropical, subtropical, temperate, and cold conditions (Clifton & Thompson, 1978; Maples & Suttner, 1990; Pemberton & others, 2006; Bromley & others, 2009; Seike & others, 2015; Flaig & others, 2019). *Macaronichnus* ranges from the Pennsylvanian to Holocene (Clifton & Thompson, 1978; Maples & Suttner, 1990; Seike, 2007). Poorly preserved traces from the Cambrian (Knaust, 2004b) may be *Macaronichnus,* however, the morphology and thus attribution to this ichnotaxon are suspect.

MACARONICHNUS SEGREGATIS

Clifton & Thompson, 1978

Figure 8.5, 11.4

Diagnosis.—Same for as ichnogenus.

Description.—Subhorizontal to subvertical, cylindrical, unbranched burrows 2–5 mm wide and 10–15 mm long (exposed length) in concave epirelief and full relief. The burrow core is slightly lighter in color in contrast to the host rock. Burrows exhibit a thin, <1 mm wide mantle of grains. Burrows occur as individual to densely packed and interpenetrated groupings.

Occurrence.—(1) White (10R 8/1), very fine-grained sandstone with bioturbation BPBI 1–3; and (2) dark gray (7.5YR 3/1) shale interbedded with white (10R 8/1) siltstone to very fine-grained sandstone, with bioturbation present (ii2–3). Specimens are present in the lower part of the Skull Creek Shale at Dinosaur Ridge and middle part of the Fort Collins Member of the Muddy Formation at Horsetooth Reservoir.

Associated ichnotaxa.—*Cylindrichnus concentricus, Ophiomorpha nodosa, Ophiomorpha* isp., *Protovirgularia pennatus, Rhizocorallium commune, Skolithos linearis, Teichichnus rectus,* and *Zoophycos* isp.

Discussion.—Specimens are assigned to *Macaronichnus segregatis* based on their morphology, color contrast between the burrow and the surrounding host rock, and presence in sandy beds (Clifton & Thompson, 1978; Maples & Suttner, 1990; Bromley & others, 2009; Nara & Seike, 2019). The tracemaker for *Macaronichnus segregatis* are polychaetes (Clifton & Thompson, 1978). *Macaronichnus segregatis* in the Fort Collins Member co-occurs with *Protovirgularia pennatus* and *Ophiomorpha nodosa*, whereas those in the Skull Creek Shale are present in the sandstone intervals that overlie and underlie *Rhizocorallium commune* and *Zoophycos* isp. The occurrences of *Macaronichnus segregatis* represent zones of well circulated marine waters produced by high-energy conditions in tidally influenced bay (Skull Creek Shale) and deltaic (Fort Collins Member) environments (MacKenzie, 1965; Weimer & Land, 1972).

Ichnogenus MARGARITICHNUS Bandel, 1973

Cylindrichnus Bandel, 1967, p. 6, pl. 3, fig. 2, pl. 4, fig. 1, 5, fig. 2.2.

Margaritichnus Bandel, 1973, p. 1002.

Margaritichnus Häntzchel, 1975, p. W82, fig. 51.5.

Margaritichnus Pemberton, Frey, & Bromley, 1988, p. 887, fig. 12.

Parataenidium Buckman, 2001, p. 86, fig., 5, 6, 8.

Margaritichnus Garvey & Hasiotis, 2008, p. 265, fig. 4.

Type Ichnospecies.—*Margaritichnus reptilis* Bandel, 1973.

Emended Diagnosis.—Vertically compressed, spherical to hemielliptical, ball-like structures in convex epirelief and occasionally convex hyporelief. Ball structures have structureless fill and a smooth surface and are arranged like a string of pearls commonly connected by a ridge. In cross-section when upper and lower ball structures are present, they are connected by a poorly defined cylindrical shaft (modified after Bandel, 1967; Hakes, 1976; Pemberton, Frey, & Bromley, 1988; Garvey & Hasiotis, 2008).

Discussion.—Originally named *Cylindrichnus reptilis* by Bandel (1967), the name was replaced by *Margaritichnus* in 1973, due to *Cylindrichnus concentricus* having already been established for a different ichnotaxon (Bandel, 1973). *Margaritichnus* was erected by Bandel (1967) for vertically compressed ball-like or oblate structures originally spherical that are laterally compressed and arranged like a string of pearls. Pemberton, Frey, and Bromley (1988) emended the diagnosis to include cross-section descriptions of *Margaritichnus*. We emended the diagnosis to account for the range of morphologies described within the literature (Bandel 1967, Hakes, 1976, Pemberton, Frey, & Bromley, 1988; Garvey & Hasiotis, 2008).

Confusion is present in the literature with respect to assigning traces with subspherical ball-like structures to an ichnotaxon. *Margaritichnus*, *Parataenidium* Buckman, 2001, and *Neoeione* Boyd & McIlroy, 2018 have been confused for each other based on their similar morphologies (Mángano & Droser, 2004; Uchman & Gaździcki, 2006; Baucon & Carvalho, 2008; Garvey & Hasiotis, 2008; Joseph, Patel, & Bhatt, 2012; Jackson, Hasiotis, & Flaig, 2016; Parihar & others, 2016; Boyd & McIlroy, 2018). Buckman (2001) created *Parataenidium* for backfilled burrows that were comprised of an upper and lower section and established two ichnospecies: *Parataenidium mullaghmorensis* and *Parataenidium moniliformis*. He synonymized *Margaritichnus reptilis* within *Parataenidium moniliformis* because both appear to possess similar morphology. *Parataenidium moniliformis* was originally described as *Eione* Tate, 1859, but was declared a *nomen nudum* by Häntzschel (1975) due to it being a junior homonym of the mollusk *Eione* Rafinesque, 1814.

Uchman and Gaździcki (2006) agreed that some specimens previously placed within *Margaritichnus* (Lockley, Rindsberg, & Zeiler, 1987) belonged in *Parataenidium* and stated that *Margaritichnus* required further study. Boyd and McIlroy (2018) reexamined the formation from which *Eione* was originally described. From specimens within that formation, they established *Neoeione* for a horizontal structure with inclined backfilled sediment packages that crosscut one other creating the appearance of an upper and lower section. When comparing *Neoeione* to *Parataenidium*, Boyd and McIlroy (2018) synonymized *Parataenidium moniliformis* and *Parataenidium seymourensis* within *Neoeione*.

According to Principle of Priority (Article 23) in the International Code of Zoological Nomenclature, the valid name for a taxon is the oldest available name applied to it. *Margaritichnus* Bandel, 1973, was established before *Parataenidium* Buckman,

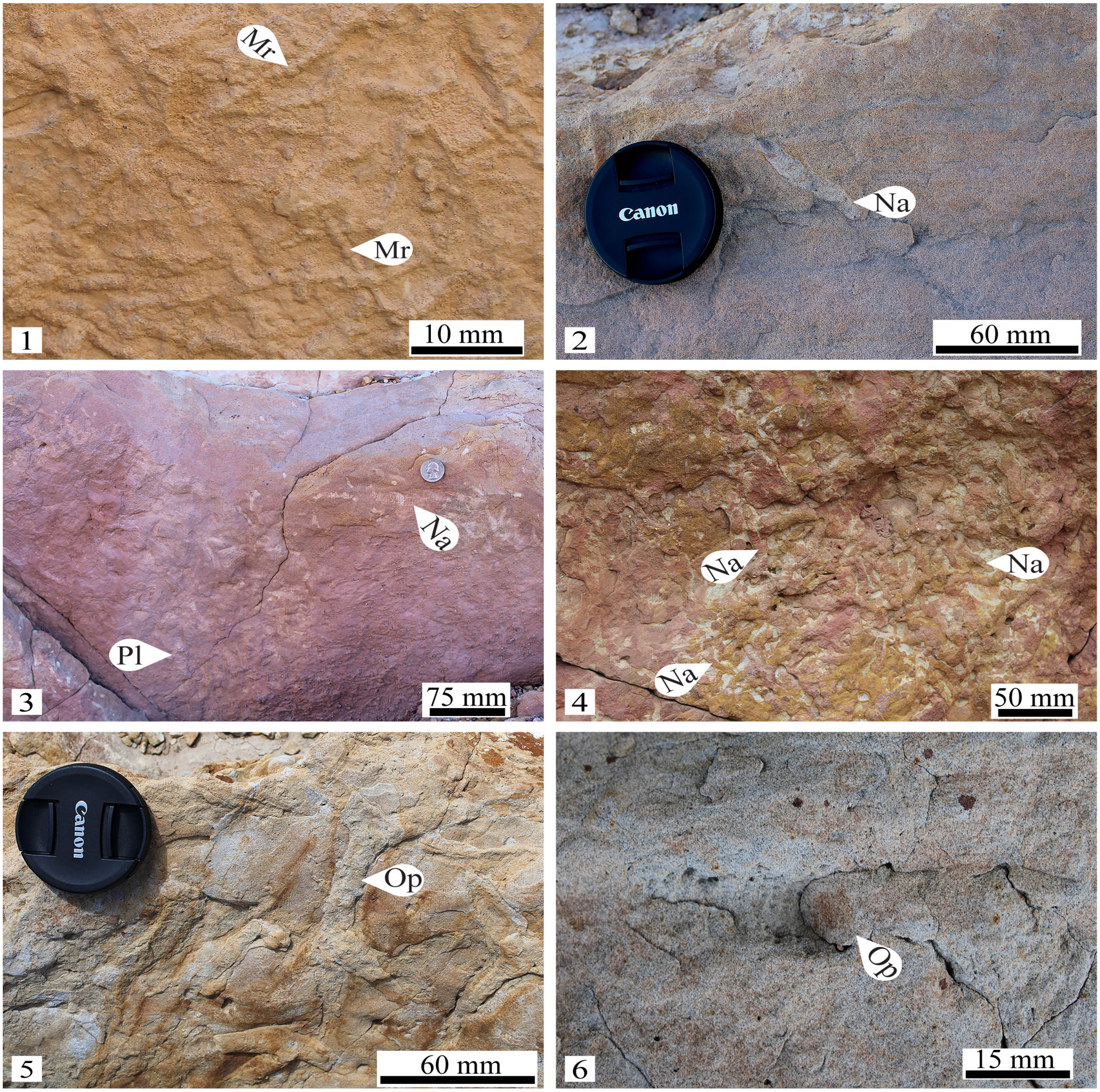


Figure 9. *Margaritichnus* (Mr), *Naktodemasis* (Na), *Ophiomorpha* (Op), and *Planolites* (Pl) from the Dakota Group. *1, Margaritichnus mansfieldi* in convex hyporelief within the middle part of the Plainview Formation at Skyline Drive. *2, Naktodemasis bowni* in vertical section within the upper part of the Lytle Formation at I-70. *3, Naktodemasis bowni* and *Planolites montanus* in vertical section within the upper part of the Lytle Formation at I-70. *4, Naktodemasis bowni* in concave hyporelief with evidence of horizontal and vertical movement within the upper part of the Lytle Formation at I-70. *5, Ophiomorpha nodosa* boxwork system in convex epirelief in the upper part of the Glencairn Formation at Skyline Drive. *6, Ophiomorpha nodosa* in full relief epirelief burrow within the middle part of the Fort Collins Member of the Muddy Formation at Horsetooth Reservoir.

2001, and therefore *Parataenidium* does not have priority over *Margaritichnus.* Similarly, *Neoeione* Boyd and McIlroy, 2018, was established after *Margaritichnus* and *Parataenidium,* and therefore *Neoeione* does not have priority over them.

Furthermore, the architectural morphologies of *Margaritichnus* and *Parataenidium,* though grossly similar, differ significantly enough to warrant two separate and valid ichnotaxa. The architectural morphology of *Margaritichnus* records an organism periodically shifting its position through time to produce closely-spaced or adjacent ball-like structures (Bandel, 1967; Hakes, 1976; Garvey & Hasiotis, 2008; Joseph, Patel, & Bhatt, 2012; Jackson, Hasiotis, & Flaig, 2016; Parihar & others, 2016). This morphology is interpreted as a resting trace (cubichnia) of a motile, suspension-feeding organism living in the sediment and protruding from the sediment-water interface. This differs from the architectural morphology of *Parataenidium* and *Neoeione*, which resulted from the horizontal to subhorizontal, continual locomotion of an organism that produced wedge- to ovoid-shaped, backfilled structures, some of which give the appearance of two layers (Buckman, 2001; Baucon & Carvalho, 2008; Boyd & McIlroy, 2018). This morphology is interpreted as a deposit-feeding trace (fodinichnia) of a highly motile organism burrowing at or beneath the sediment-water interface.

We, therefore, recognize *Margaritichnus* as a valid ichnotaxon based on the closely-spaced to adjoining subspherical structures and their vertical construction, produced by a suspension-feeding organism readjusting its position in the sediment (cubichnia) that produced *Margaritichnus reptilis* and *Margaritichnus mansfieldi*. We recognize *Parataenidium* as a valid ichnotaxon for its numerous backfilled structures composed of a variably distinguishable upper section of oblate or globular backfill and a lower section of wedge-shaped to structureless backfill, produced by a deposit-feeding organism moving through the sediment (fodinichnia) that produced *Parataenidium mullaghmorensis* and *Parataenidium moniliformis* by Buckman (2001), and *Parataenidium seymourensis* by Uchman & Gaździcki (2006). *Neoeione* (Boyd & McIlroy, 2018) is synonymized under *Parataenidium* as a junior synonym by the principle of priority.

Margaritichnus has been interpreted as: (1) the work of deposit-feeding worms with the spherical structures as fecal pellets (Bandel, 1967; Häntzschel, 1975); (2) dwelling and resting structures of a soft-bodied anemone-like organism or hydrozoan (Hakes, 1976; Davies, Sansom, & Turner, 2006); and (3) locomotion traces, resting, and/or feeding traces of a subspherical organism, such as a bivalve or gastropod (Garvey & Hasiotis, 2008; Parihar & others, 2016). *Margaritichnus* is present in fluvial channel and marine intertidal, subtidal, foreshore, and deltaic environments (Bandel, 1967; Davies, Sansom, & Turner, 2006; Garvey & Hasiotis, 2008; Parihar & others, 2016). *Margaritichnus* ranges from the Ediacaran to Holocene (Glaessner, 1969; Narbonne, 1984; Garvey & Hasiotis, 2008; Parihar & others, 2016).

MARGARITICHNUS MANSFIELDI
Garvey & Hasiotis, 2008
Figure 8.6, 9.1

Diagnosis.—Small, flattened, subspherical, aligned structures, circular to slightly elliptical in cross section, with unornamented walls, structureless filling, and a median longitudinal groove in aligned structures (after Garvey & Hasiotis, 2008).

Description.—Specimens preserved in convex hyporelief, with the surface of the spherical structures smooth. Spherical structures are connected in a manner similar to a string of pearls. The spherical structures are 2–3 mm in diameter, the number of connected spheres ranges from 3 to 10, with lengths up to 40 mm long. Specimens crosscut one another on the bedding surface.

Occurrence.—Yellowish red (5YR 5/8), fine- to very fine-grained, subrounded, moderately well-sorted sandstone, with some minor ripple marks and flaser bedding, BPBI 4. Specimens are present in the middle part of the Plainview Formation along Skyline Drive.

Associated ichnotaxa.—Asthenopodichnium xylobiontum, Lockeia isp., *Teredolites clavatus,* and *Thalassinoides suevicus*.

Discussion.—Specimens are assigned to *Margaritichnus mansfieldi* based on their string of pearl-like trail, the presence of flattened spheres, and the smooth surface of the spheres (Garvey & Hasiotis, 2008). The tracemakers of *Margaritichnus mansfieldi* are bivalves (Garvey & Hasiotis, 2008). *Margaritichnus mansfieldi* form a monospecific occurrence, however, *Asthenopodichnium xylobiontum, Lockeia* isp., *Teredolites clavatus,* and *Thalassinoides suevicus* occur in directly overlying beds. The bed bearing *Margaritichnus mansfieldi* overlies a bed with the tetrapod tracks *Magnoavipes* and *Tetrapodosaurus*. *Margaritichnus mansfieldi* were produced in an intertidal to subtidal environment based on lithology and bed forms (Gustason & Kauffman, 1985; Kurtz, Lockley, & Engard, 2001).

Ichnogenus NAKTODEMASIS Smith, Hasiotis, Kraus, & Woody, 2008

Naktodemasis Smith & others, 2008, p. 276, fig., 4, 6.

Taenidium Krapovickas & others, 2009, p. 138.

Naktodemasis Counts & Hasiotis, 2009, p. 86, fig. 9.

Type Ichnospecies.—Naktodemasis bowni Smith, Hasiotis, Kraus, & Woody, 2008.

Diagnosis.—Straight to sinuous, unlined and unbranched burrows comprised of nested ellipsoidal packets of meniscate backfill, with thin tightly spaced menisci that are subparallel to bounding edges of burrow. Burrows have the same grain size as the surrounding medium (after Counts & Hasiotis, 2009).

Discussion.—Naktodemasis was named by Smith and others (2008) for traces previously described as “adhesive meniscate burrows” in paleosols (Bown & Kraus, 1983; Hasiotis 2002, 2004, 2008). *Naktodemasis* is distinguished from other meniscate backfill burrows such as *Ancorichnus, Beaconites, Laminites, Scoyenia,* and *Taenidium* by having its backfilled material organized into a nested series of discrete packets containing thin, subparallel menisci (Smith & others, 2008; Counts & Hasiotis, 2009). Some researchers make *Naktodemasis* a junior synonym of *Taenidium,* based on both ichnogenera having “unwalled” lining (Krapovickas & others, 2009; Díez-Canseco & others, 2016). This proposed synonymy fails to acknowledge the presence of a wall between the burrow and surrounding matrix (Smith & others, 2008, fig. 4; Smith & Hasiotis, 2008, fig. 8; Counts & Hasiotis, 2009, fig. 9), as well as the strong morphological differences between *Naktodemasis* and other burrow morphologies incorrectly lumped into *Taenidium* as discussed by Smith and others (2008), Counts and Hasiotis (2009), and Hammersburg, Hasiotis, and Robison (2018). Thus, *Naktodemasis* and *Taenidium* are separate valid ichnogenera, with *Naktodemasis* representing burrows with nested, ellipsoidal, and asymmetrical packets of thin, tightly spaced meniscate backfill subparallel to bounding edges, whereas *Taenidium* represents evenly spaced, uniformly thick, meniscate backfilled burrow segments (D’Alessandro & Bromley, 1987; Smith & others 2008; Counts & Hasiotis, 2009; Hammersburg, Hasiotis, & Robison, 2018). *Ancorichnus, Beaconites, Laminites,* and *Scoyenia* are also valid ichnogenera due to their distinct morphological features (Smith & others 2008; Counts & Hasiotis, 2009).

Naktodemasis is interpreted to be the locomotion, resting, and deposit-feeding traces of insect nymphs and larvae belonging to the families Cydnidae, Cicadea, and Scarabaeidae (e.g., Smith & Hasiotis, 2008; Smith & others 2008; Counts & Hasiotis, 2009, 2014; Fischer & Hasiotis, 2018). *Naktodemasis* is present in terrestrial settings in the vadose zone of continental environments (Hasiotis & Dubiel, 1994; Xing & others, 2012; Chakraborty & others, 2013; Woodburn, 2013; Counts & Hasiotis, 2014; Wiest & others, 2018). *Naktodemasis* ranges from Upper Pennsylvanian to Holocene (Smith & others, 2008; Counts & Hasiotis, 2009, 2014; Golab, Smith, & Hasiotis, 2018).

NAKTODEMASIS BOWNI
Smith, Hasiotis, Kraus, & Woody, 2008

Muensteria—Dubiel, Skipp, & Hasiotis, 1992, p. 30.

Taenidium isp.—Sarkar & Chaudhuri, 1992, p. 11–12, fig. 4.

Taenidium—Savrda & others, 2000, p. 230, fig. 2e–f.

Taenidium—Rebata & others, 2006, p. 104–110, fig. 8, 9d, 12b, 14b–c.

Taenidium—Hovikoski & others, 2007, p. 1515, fig. 6g.

Taenidium bowni—Krapovickas & others, 2009, p. 138.

Taenidium bowni—MacEachern & others, 2012a, p. 124, fig. 7b.

Taenidium bowni—Baraboshkin, 2013, p.67-68, fig. 2.

Taenidium bowni—Knaust, 2015, p.488.

Taenidium bowni—Buatois & others, 2016, p. 242.

Taenidium bowni—Díez-Canseco & others, 2016, p. 258, fig. 6.4.

Taenidium bowni—Moreira & others, 2018, p.110, fig. 5.

Taenidium isp.—Polo & others, 2019, p. 6–20, fig. 6c–e, 6g–i, 10.

Taenidium barretii, T. satanassi.—Zou & others, 2019, p. 396–397, fig. 3.

Taenidium isp.—Buatois, Wetzel, Mángano, 2020, p. 6, fig. 5d–e

Taenidium isp.—Sedorko & others, 2020, p. 255–256, fig. 5f, 6b.

Taenidium barretii—Cabral, Mescolotti, Varejaö, 2021, p. 4, fig. 4, 11.

Taenidium barretii—Sciscio & others, 2021, p. 133–135, fig. 4.

Taenidium barretii—Silva & others, 2022, p. 5–6, fig. 4.

Taenidium isp.—Hembree, 2022, p. 678–679, fig. 7i.

Figure 9.2, 9.3, 9.4

Diagnosis.—As for the ichnogenus.

Description.—Traces present in full relief and concave hyporelief, consisting of unlined burrows with nested, asymmetrical packets of thin, tightly packed menisci. Individual packets range from 4 to 10 mm long. Several packets have clear menisci within them, whereas others exhibit faint menisci or are absent due to preservation. Menisci within packets are <1 mm wide, discontinuous and irregular, commonly overlapping each other. Traces range from 30 to 70 mm long and 9 to 12 mm wide.

Occurrence.—Reddish yellow (7.5YR 7/8) to red (10R 4/8), fine- to very fine-grained sandstone; beds show varying degrees of bioturbation (ii2–4). Specimens are present in the upper part of the Lytle Formation at I-70.

Associated ichnotaxa.—Planolites montanus.

Discussion.—Traces are assigned to *Naktodemasis bowni* based on the presence of asymmetrical packets of menisci, with menisci being thin and irregular, and absence of a visible wall lining (e.g., Smith & others, 2008; Counts & Hasiotis, 2009, 2014). The tracemaker for *Naktodemasis bowni* was an insect nymph or larva (Smith & others, 2008; Counts & Hasiotis, 2009). The more distinct *Naktodemasis bowni* are present by themselves or in small groups. *Naktodemasis bowni* that have less distinct packets and menisci, are present in the base of a bed with a high degree of bioturbation (Fig. 9.4). Sarkar and Chaudhuri (1992) identified meniscate backfill burrows within a fluvial setting as *Taenidium*; however, the burrow morphology is unlike that of *Taenidium* but more similar to *Beaconites* or *Naktodemasis*. Quality of the photographs makes discernment between the two for those samples difficult. *Naktodemasis bowni* with *Planolites montanus* have both horizontal and vertical movement in the vadose zone, but with different behaviors, one producing meniscate backfill and the other producing an open passively filled burrow. *Naktodemasis bowni* was constructed within the vadose zone in a fluvial floodplain environment based on lithology, lack of internal bedding, and red to mottled coloration (Weimer & Land, 1972).

Ichnogenus OPHIOMORPHA Lundgren, 1891

Ophiomorpha Lundgren, 1891, p. 115.

Spongeliomorpha Fürsich, 1973, p. 729.

Ophiomorpha Bromley & Frey, 1974, p. 329.

Ophiomorpha Frey, Howard, & Pryor, 1978, p. 222, fig., 1b, f, 2h, 4a, 12a, b, 13a, b, 14a, b.

Spongeliomorpha Schlirf, 2000, p. 158, pl. 4, fig. 2–4, 6–9.

Ophiomorpha de Gibert & others, 2006, p. 81, fig. 4–9.

Type Ichnospecies.—Ophiomorpha nodosa Lundgren, 1891.

Diagnosis.—Simple to complex burrow systems distinctly lined with agglutinated pelletoidal sediment. Burrow lining is smooth interiorly, densely to sparsely mammilated or nodose exteriorly. Individual pellets or pelletal masses may be discoid, ovoid, mastoid, bilobate, or irregular in shape. Characteristics of the lining may vary within a single specimen (after Frey, Howard, & Pryor,1978; de Gibert & others, 2006).

Discussion.—*Ophiomorpha* has been compared to *Gyrolithes* de Saporta, 1884, *Spongeliomorpha* de Saporta, 1887, and *Thalassinoides* Ehrenberg, 1944 due to its similar structure and interconnective nature of these trace fossils. Fürsich (1973) synonymized *Ophiomorpha* and *Thalassinoides* with *Spongeliomorpha* due to similarities in their morphology and confusion in the literature. Schlirf (2000) agreed with this assessment, stating that the morphological differences could be due to the medium in which the trace is constructed. The assessment of Fürsich (1973) was contested by Bromley and Frey (1974), who stated that morphological differences between these ichnogenera prevent them from being synonymized with one another. They also stated that any synonymy among them would require the inclusion of *Gyrolithes,* which would have priority over the other ichnogenera and would be inappropriate

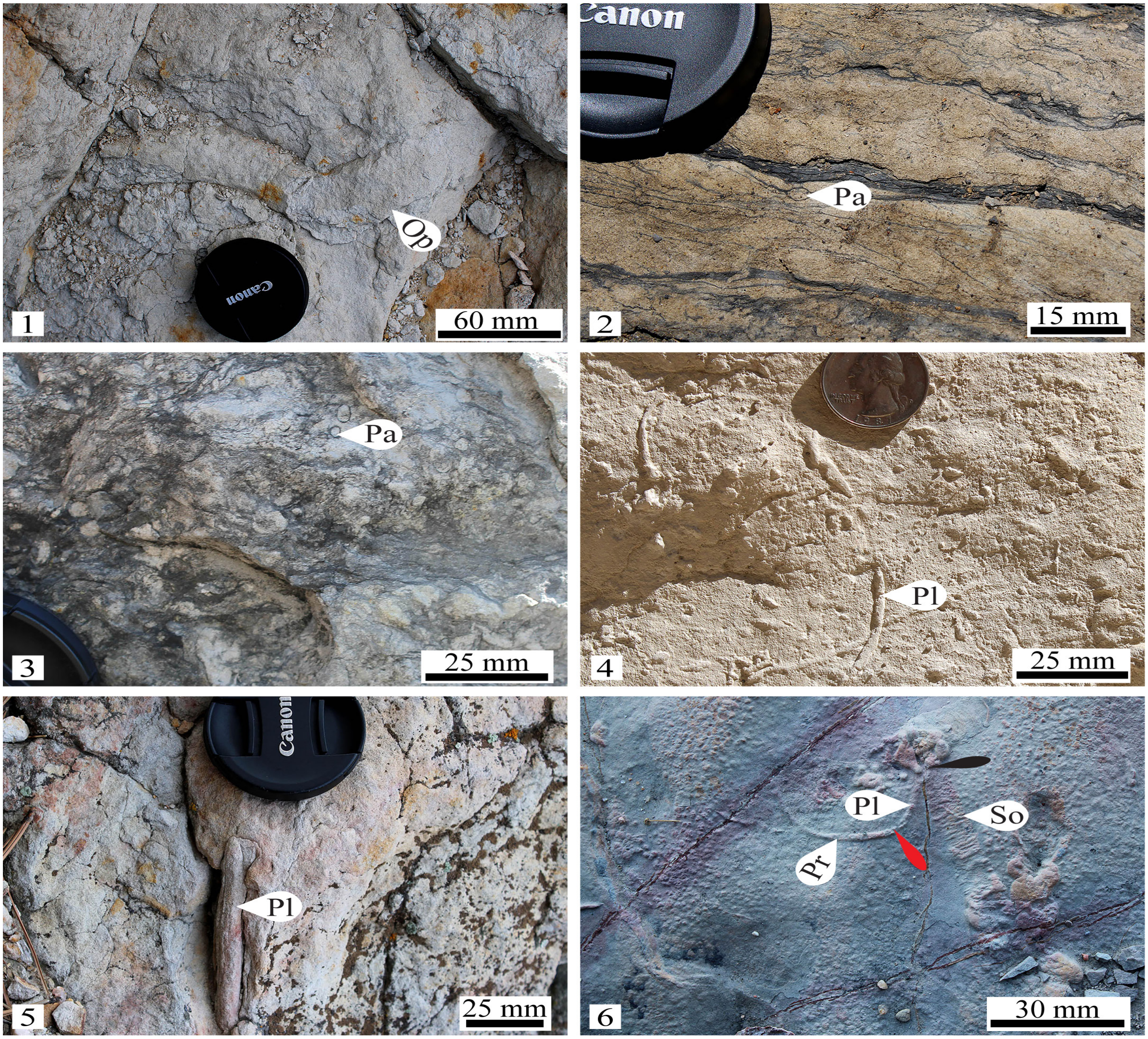


Figure 10. *Ophiomorpha* (Op), *Palaeophycus* (Pa), *Planolites* (Pl), *Protovirgularia* (Pr), and *Scolicia* (So) from the Dakota Group. *1, Ophiomorpha* isp. in full relief within the middle part of the Fort Collins Member of the Muddy Formation at Horsetooth Reservoir. *2, Palaeophycus tubularis* in vertical section within the lower part of the Skull Creek Shale at U.S. Route 285. *3, Palaeophycus tubularis* in vertical section within the upper part of the Skull Creek Shale at I-70. *4, Planolites montanus* in convex hyporelief within the middle part of the Plainview Formation at Dinosaur Ridge. *5, Planolites terraenovae* in full relief within the lower part of the Fort Collins Member of the Muddy Formation at Horsetooth Reservoir. *6, Planolites montanus* transitioning into *Protovirgularia pennatus* at the red arrow, then terminating at *Scolicia plana* at the black arrow, in convex epirelief present within middle part of the Plainview Formation at Colorado State Highway 115.

due to the helical architectural morphology of *Gyrolithes*. Bromley and Frey (1974) further argued that *Spongeliomorpha* should be declared as a *nomen dubium* due to lacking a proper description. Whereas Bromley and Frey (1974) saw similar characteristics in both *Ophiomorpha* and *Thalassinoides,* they kept these ichnogenera separate based on *Ophiomorpha* having a pelleted lining on its outer surface and *Thalassinoides* having a smooth exterior wall. The assessment by Bromley and Frey (1974) has been followed within the literature, with some researchers stating that the differences are not "ideal" taxonomic criteria (Frey, Howard, & Pryor, 1978; Cherns, Wheeley, & Karis, 2006; de Gibert & others, 2006; de Gibert & Ekdale, 2010; Tiwari & others, 2011; Chrząstek, 2013; Nagy, Rodríguez-Tovar, & Reolid, 2016; Parihar & others, 2016).

Ophiomorpha is interpreted to be the dwelling burrow system of suspension or deposit-feeding decapod crustaceans comparable to modern callianassids (Pryor, 1975; Frey, Howard & Pryor, 1978; de Gibert & others, 2006; Nagy, Rodríguez-Tovar, & Reolid, 2016; Parihar & others, 2016). *Ophiomorpha* is present in shallow-marine (brackish, subtidal, deltaic, shoreface, and offshore) and deep-marine (flysch) deposits (MacEachern & Pemberton, 1992; Uchman, 1995; Tchoumatchenco & Uchman, 2001; de Gibert & others, 2006; MacEachern & Gingras, 2007a; Vaziri & Fürsich, 2007; Nagy, Rodríguez-Tovar, & Reolid, 2016; Parihar & others, 2016; Flaig & others, 2019). *Ophiomorpha* ranges from the Permian to Holocene (Bromley & Frey, 1974; de Gibert & others, 2006; Baucon & others, 2014; Flaig & others, 2019).

OPHIOMORPHA NODOSA Lundgren, 1891

Figure 9.5, 9.6

Diagnosis.—Burrow walls consisting predominantly of dense, regularly distributed discoid, ovoid, or irregular polygonal pellets (after Frey, Howard & Pryor, 1978).

Description.—Specimens in concave and convex epirelief. The pattern of pellets on burrow walls are fairly regular, pellets range little in size, from ~2 to 3 mm in diameter. Specimens are present in unbranched, branched, or boxwork burrow systems. Visible burrow segments range from 60 to 120 mm long and 10 to 15 mm wide. The angle between branching burrow elements range from ~60° to ~120°.

Occurrence.—(1) Reddish yellow (7.5YR 6/8), very fine-grained sandstone with BPBI 2; and (2) white (10R 8/1), very fine-grained sandstone, with BPBI 2–3. Specimens are present in the upper part of the Glencairn Formation along Skyline Drive and the middle and upper parts of the Fort Collins Member of the Muddy Formation at Horsetooth Reservoir.

Associated ichnotaxa.—Cylindrichnus concentricus, Macaronichnus segregatis, Ophiomorpha isp., and *Protovirgularia pennatus*.

Discussion.—Specimens are assigned to *Ophiomorpha nodosa* based on the pelleted lining, regular distribution of pellets, and uniform size of pellets (Frey, Howard & Pryor, 1978; de Gibert & others, 2006). The tracemaker for *Ophiomorpha nodosa* are decapod crustaceans (de Gibert & others, 2006). In the Glencairn Formation, *Ophiomorpha nodosa* are present in the upper sandstone bed either as a boxwork or in unbranched burrow arrangements. In the Fort Collins Member, *Ophiomorpha nodosa* are present as unbranched and branched burrow segments. *Ophiomorpha nodosa* in the Fort Collins Member co-occur with other trace fossils, whereas those in the Glencairn Formation do not. *Ophiomorpha nodosa* in both the Glencairn Formation and Fort Collins Member were constructed in a deltaic environment, based on lithology, bedforms, and succession of beds (MacKenzie, 1965; Gustason & Kauffman, 1985).

OPHIOMORPHA isp.

Figure 10.1

Description.—Traces in convex epirelief with burrows having faint pelleted walls. Burrows are winding or straight with either an unbranched or branched burrow segment 60–200 mm long and 10–40 mm wide.

Occurrence.—(1) Reddish yellow (7.5YR 7/8), very fine- to fine-grained sandstone with BPBI 2; (2) gray (7.5YR 5/1), very fine-grained sandstone, beds moderately bioturbated (ii3); and (3) white (10R 8/1), very fine-grained sandstone with BPBI 2–3. Specimens are present in the lower part of the Glencairn Formation and upper part of the Muddy Formation at Grape Creek, and the upper and middle parts of the Fort Collins Member of the Muddy Formation at Horsetooth Reservoir.

Associated ichnotaxa.—Cylindrichnus concentricus, Macaronichnus segregatis, Ophiomorpha nodosa, and *Protovirgularia pennatus*.

Discussion.—Specimens are assigned to *Ophiomorpha* based on their shape and the presence of faint pellets on the outer walls of the burrow (Frey, Howard, & Pryor, 1978; Vaziri & Fürsich, 2007). The tracemaker for *Ophiomorpha* isp. are decapod crustaceans (de Gibert & others, 2006). The worn and/or bioturbated surface of the specimens makes proper placement of the ichnospecies difficult, due to specimens bearing the characteristics of both *Ophiomorpha irregulaire* and *Ophiomorpha nodosa*. *Ophiomorpha* in both formations at Grape Creek do not occur with other trace fossils. *Ophiomorpha* isp. from the Grape Creek in the Glencairn Formation were constructed in a deltaic environment, whereas those in the Muddy Formation at Grape Creek were constructed in a subtidal environment based on the lithology, bedforms, and succession of strata (Gustason & Kauffman, 1985).

At Horsetooth Reservoir in the Fort Collins Member, beds with *Ophiomorpha* isp. overlie and underlie beds with *Cylindrichnus concentricus, Macaronichnus segregatis, Ophiomorpha nodosa,* and *Protovirgularia pennatus*. These traces were produced in a deltaic environment based on the lithology and succession of bedforms (MacKenzie, 1965).

Ichnogenus PALAEOPHYCUS Hall, 1847

Palaeophycus Hall, 1847, p. 7, pl. 2, fig. 1–5, pl. 21, fig. 1.

Palaeophycus Pemberton & Frey, 1982, p. 850, pl. 1, fig. 1–10, pl. 2, fig. 1–9, pl. 3, 3–6, pl. 4, 1–5.

Palaeophycus Buckman, 1995, p. 133, fig. 2–3.

Type Ichnospecies.—Palaeophycus tubularis Hall, 1847.

Diagnosis.—Straight to slightly curved, simple or occasionally branched, smooth or with other surficial morphology, thinly lined, essentially cylindrical, predominantly horizontal burrows of variable diameter; burrow fill typically massive and similar to host rock, although substantial fill may be absent to produce flattened lined tubes. When present, bifurcation is not systematic, nor does it result in widening at the location of branching (after Pemberton & Frey, 1982; Buckman, 1995).

Discussion.—Palaeophycus is similar to and has commonly been confused with the ichnogenus *Planolites* (Pemberton & Frey, 1982; Keighley & Pickerill, 1995; Hammersburg, Hasiotis, & Robison, 2018). According to Pemberton and Frey (1982), problems in differentiating the two ichnogenera stem from a lack of detailed examination of specimens and perpetuation of ichnotaxonomic inconsistencies. Other issues are that *Palaeophycus* and *Planolites* both range from the Ediacaran to Holocene. They are both facies-crossing trace fossils and occur in marine and continental deposits, including aquatic (i.e., saturated sediment) and terrestrial (vadose zone sediment) settings (Hasiotis & others, 2012; Hasiotis, MacPherson, & Reilly, 2013). Pemberton and Frey (1982) defined *Palaeophycus* as a lined burrow whose fill is texturally similar to the host rock (i.e., passive fill), and *Planolites* as an unlined burrow whose fill is texturally different than the host rock (i.e., active fill). Keighley and Pickerill (1995) recommended that the passive or active fill diagnostic criteria of Pemberton and Frey (1982) be removed, as it is an interpretation rather than a description of morphology, as well as retaining ambiguities of the descriptions and discussions of these traces originally described (see sources in Pemberton & Frey, 1982; Keighley & Pickerill, 1995). This recommendation has been largely ignored in the literature because burrow fill can be objectively described based on the morphological characteristics (Jensen, 1997; Uchman, 1998; Davies, Sansom, & Albanesi, 2007; Garvey & Hasiotis, 2008; Mørk & Bromley, 2008; Bradshaw, 2010; Chrząstek, 2013; Jackson, Hasiotis, & Flaig, 2016; Rindsberg, 2018).

Palaeophycus is interpreted to be the dwelling of a suspension-feeding or predatory annelid worm or other invertebrate animal (Fillion & Pickerill, 1990; Davies, Sansom, & Albanesi, 2007; Mørk & Bromley, 2008; Garvey & Hasiotis, 2008; Chrząstek, 2013) or a dwelling of a terrestrial or aquatic invertebrate organism. *Palaeophycus* is present in continental (fluvial and lacustrine; vadose or subaqueous), shallow-marine (lagoonal, tidal flat, bay, shoreface, and offshore), and deep-marine (flysch) environments (Fillion & Pickerill, 1990; Frey & Howard, 1990; MacEachern & Pemberton, 1992; Gingras, MacEachern, & Pemberton 1998; Jensen, 1997; Yiming, 1999; Hasiotis, 2004, 2008; Hubbard, Gingras, & Pemberton, 2004; Garvey & Hasiotis, 2008; Bradshaw, 2010; Tiwari & others, 2011; Chrząstek, 2013; Flaig & others, 2019). *Palaeophycus* ranges from the Ediacaran to Holocene (Pemberton & Frey, 1982; Narbonne & Hofmann, 1987; Uchman, 1995; Garvey & Hasiotis, 2008; Jackson, Hasiotis, & Flaig, 2016).

PALAEOPHYCUS TUBULARIS Hall, 1847

Figure 10.2, 10.3

Diagnosis.—Smooth, unornamented burrows of variable diameter, but distinctly lined (after, Pemberton & Frey, 1982).

Description.—Specimens are in concave epirelief, convex hyporelief, and full relief, with a thin, visible lining <1 mm thick. Infill of the specimens are similar to the host rock. Burrows are 3–4 mm wide and 24–40 mm long.

Occurrence.—(1) Reddish yellow (7.5YR 7/8), fine- to very fine-grained sandstone, with BPBI 2; (2) very dark gray (7.5YR 3/1) shale, interbedded with white (10R 8/1) siltstone to very fine-grained sandstone, in beds having varying degrees of bioturbation (ii2–4); (3) very dark gray (7.5YR 3/1) shale interbedded with strong brown (7.5YR 5/8), very fine-grained sandstone, with bioturbation present (ii3); (4) light olive brown (10Y 5/4) shale interbedded with reddish yellow (7.5YR 7/8) sandy siltstone, with some bioturbation present (ii2); and (5) white (10R 8/1), fine-grained sandstone with BPBI 2. Specimens are present in the lower part of the Plainview Formation at Skyline Drive, in the middle and upper parts of the Skull Creek Shale at I-70, the middle and upper parts of the Skull Creek Shale at Horsetooth Reservoir, the middle and upper parts of the Skull Creek Shale at U.S. Route 285, and the upper parts of the Muddy Formation at Skyline Drive.

Associated ichnotaxa.—Arenicolites variabilis, Arenicolites isp., *Asterosoma* isp., *Diplocraterion habichi, Schaubcylindrichnus freyi, Skolithos linearis, Teichichnus rectus,* and *Thalassinoides suevicus.*

Discussion.—Specimens are assigned to *Palaeophycus tubularis* based on the smooth burrow surface, the presence and thickness of the lining, and infill similar to the host rock (Pemberton & Frey, 1982; Fillion & Pickerill, 1990). The tracemaker of *Palaeophycus tubularis* is an annelid worm (Pemberton & Frey, 1982). *Palaeophycus tubularis* is only present in full relief in the Skull Creek Shale, where it is more prominent than in the other formations. Specimens in the Plainview Formation at Skyline Drive overlie the beds that contain *Skolithos linearis* and *Teredolites clavatus*. Traces in the Plainview Formation at Skyline Drive were constructed in an intertidal environment based on the lithology and succession of bedforms (Gustason & Kauffman, 1985). In the Skull Creek Shale, *Palaeophycus tubularis* occurs with *Arenicolites*, *Asterosoma*, *Diplocraterion*, *Schaubcylindrichnus*, *Skolithos*, *Teichichnus*, and *Thalassinoides*. At I-70 *Palaeophycus tubularis* was constructed in a marine embayment (Weimer & Land, 1972), whereas those at Horsetooth Reservoir were constructed in a lower shoreface (Graham & Ethridge, 1995). *Palaeophycus tubularis* in the Muddy Formation at Skyline Drive form a monospecific occurrence and were constructed in an intertidal environment (Gustason & Kauffman, 1985).

Ichnogenus PLANOLITES Nicholson, 1873

Planolites Nicholson, 1873, p. 289.

Planolites Pemberton & Frey, 1982, p. 864, pl. 1, fig. 7, 11, pl. 2, fig. 4, 5, 7, 8, 9, pl. 3, fig. 1, 2, 7, 8, 9, pl. 5, fig., 1, 2.

Type Ichnospecies.—Planolites vulgaris Nicholson & Hinde, 1875.

Diagnosis.—Unlined, rarely branched, straight to tortuous, smooth to irregularly walled, horizontal to slightly inclined burrows; burrows circular to elliptical in cross section with variable dimensions and configurations; infill lithology differing from host rock (after Pemberton & Frey, 1982).

Discussion.—The ichnotaxonomy of *Palaeophycus* and *Planolites* has created confusion, with several researchers attempting to resolve this by establishing diagnostic criteria (e.g., Pemberton & Frey, 1982; Keighley & Pickerill, 1995). Pemberton and Frey (1982) established several diagnostic criteria that have been used to separate *Palaeophycus* and *Planolites* (see discussion in *Palaeophycus* section). Fillion and Pickerill (1990) suggested that another diagnostic criterion to identify *Planolites* is its lack of branching or enlargements around branch junctions.

Planolites beverleyensis was distinguished by Pemberton and Frey (1982) as being relatively large compared to *Planolites montanus* which was characterized as being relatively small, however, no scale was provided to define this difference. Fillion and Pickerill (1990) addressed the size issue by formalizing *Planolites montanus* as < 5 mm in width; however, this recommendation has not always been followed by authors who placed specimens smaller than this into *Planolites beverleyensis* (Keighley & Pickerill, 1997; Uchman, 1999; Gingras & others, 2011). This recommendation is also invalid because size criteria should be avoided, although proportions or ratios of burrow measurements is valid (Bertling & others, 2006; Raisanen & Hasiotis, 2018). Keighley and Pickerill (1997) recommended that *Planolites montanus* be synonymized within *Planolites beverleyensis*, as they lacked any difference in morphology expect for size. This recommendation, however, has not been followed in the literature (Pickerill & Fyffe, 1999; Uchman, 1999; Davies, Sansom, & Albanesi, 2007; Giannetti & McCann, 2010; Gingras & others, 2011; Hofmann & others, 2012; Hammersburg, Hasiotis, & Robison, 2018).

Planolites is interpreted as deposit-feeding or grazing traces of polychaete worms, isopod crustaceans, arthropods, oligochaetes, and a variety of insects (Fillion & Pickerill, 1990; Hasiotis, 2004, 2008; Rodríguez-Tovar & Uchman, 2010; Tiwari & others, 2011; Virtasalo & others, 2011; Hammersburg, Hasiotis, & Robison, 2018). *Planolites* is a facies-crossing ichnogenus and has been reported in continental (terrestrial and aquatic; vadose and subaqueous) and shallow- and deep-marine environments (Fillion & Pickerill, 1990; Keighley & Pickerill, 1997; Kim, Kim, & Pickerill, 2002; Hasiotis 2004, 2007, 2008; Uchman & others, 2004; Ekdale, Bromley, & Loope, 2007; Smith & others, 2009; Gingras & others, 2011; Hammersburg, Hasiotis, Robison, 2018). *Planolites* ranges from the Ediacaran to Holocene (Narbonne & Hofmann, 1987; Crimes, 1992; Kundal & Dharashivkar, 2006; Hasiotis, 2012; Hammersburg, Hasiotis, Robison, 2018).

PLANOLITES MONTANUS Richter, 1937

Figure 5.5, 6.2, 9.3, 10.4, 10.6

Diagnosis.—Relatively small, curved to tortuous burrow that lack a lining (after Hammersburg, Hasiotis, & Robison, 2018).

Description.—Specimens are present in concave epirelief and convex hyporelief, with some crosscutting one another. Specimens are 3–4 mm wide and 10–20 mm long with no lining and an infill that differs from the surrounding host rock.

Occurrence.—(1) Gray (10YR 5/1), very fine-grained sandstone with BPBI 2, interbedded with mudstone. Beds have a sulfur smell; (2) white (10R 8/1), very fine-grained sandstone; (3) gray (10YR 5/1), fine- to very fine-grained sandstone with BPBI 3; (4) reddish yellow (7.5YR 6/8), very fine-grained sandstone with BPBI 2, interbedded with mudstone; (5) white (10R 8/1), fine-grained, ripple-laminated sandstone with BPBI 2; (6) reddish yellow (7.5YR 7/8), fine-grained, well-rounded and -sorted sandstone with BPBI 2; (7) reddish yellow (7.5YR 6/8), very fine-grained, subrounded and well-sorted sandstone, with planar bedding and BPBI 4; and (8) red (10R 4/8), very fine- to fine-grained sandstone with BPBI 4. Specimens are present in the upper part of the Lytle Formation at I-70, in the upper part Plainview Formation at Colorado State Highway 115, in the upper part of the Plainview Formation at Horsetooth Reservoir, the lower part of the Plainview Formation at Dinosaur Ridge, the middle part of the Glencairn Formation at Skyline Drive, and the upper part of the Muddy Formation at Dinosaur Ridge, Skyline Drive, and U.S. Route 285.

Associated ichnotaxa.—Aulichnites parkerensis, Chondrites intricatus, Cochlichnus anguineus, Cruziana isp.*, Dromaeosauripus* isp.*, Gyrolithes lorcaensis, Lockeia siliquaria, Naktodemasis bowni, Protovirgularia pennatus, Rusophycus* isp.*, Scolicia plana, Taenidium serpentinum, Thalassinoides horizontalis,* and *Thalassinoides suevicus*.

Discussion.—Specimens are assigned to *Planolites montanus* based on the absence of a lining, infill differing from the host rock, and their relatively small diameter (Pemberton & Frey, 1982; Kim, Kim, & Pickerill, 2002). The tracemaker for *Planolites montanus* were most likely polychaete worms (Hammersburg, Hasiotis, & Robison, 2018). *Planolites montanus* commonly co-occurs with the other trace fossils, and it rarely occurs by itself. Within these co-occurrences *Planolites montanus* occasionally crosscuts or interpenetrates *Naktodemasis* and *Thalassinoides*, typically in beds with a high degree of bioturbation. *Planolites montanus* co-occurs with *Naktodemasis bowni* in the Lytle Formation and was produced in a fluvial floodplain environment in the vadose zone based on lithology, lack of internal bedding, and red to mottled coloration (Weimer & Land, 1972). *Planolites montanus* in the Plainview Formation at Horsetooth Reservoir were constructed in a subtidal environment, based on lithology and succession of bedforms (Wescott, 1979). In the Plainview Formation at Dinosaur Ridge, *Planolites montanus* co-occurs with *Cochlichnus* and *Lockeia* and was constructed in a fluvial environment with variable flow regime (Weimer & Land, 1972). In the Glencairn Formation *Planolites montanus* co-occurs with *Cruziana, Gyrolithes, Rusophycus, Taenidium,* and *Thalassinoides*. These traces are present in the 2nd sandstone bed in the Glencairn Formation, which was deposited in a deltaic environment based on lithology and succession of bedforms (Gustason & Kauffman, 1985). *Planolites montanus* in the upper parts of the Muddy Formation at Dinosaur Ridge and U.S. Route 285 were constructed in intertidal to subtidal environments, based on lithology and succession of bedforms (Weimer & Land, 1972; MacKenzie, 1975; Chamberlain, 1985).

PLANOLITES TERRAENOVAE Fillion & Pickerill, 1990

Figure 10.5

Diagnosis.—Relatively straight horizontal burrow lacking a lining with surficial morphology consisting of longitudinal striae or ridges parallel and continuous. Infill different than surrounding lithology (after Fillion & Pickerill, 1990).

Description.—Single trace in convex epirelief, with several longitudinal striae that extend most of the length on the surface of the burrow. Burrow is 10 mm wide and 30 mm long.

Occurrence.—White (10R 8/1), very fine-grained sandstone with BPBI 2–3. Specimen is present in the lower part of the Fort Collins Member of the Muddy Formation at Horsetooth reservoir.

Associated ichnotaxa.—None.

Discussion.—This trace is assigned to *Planolites terraenovae* based on the longitudinal striation, lack of a lining, and infill differing from the host rock (e.g., Fillion & Pickerill, 1990). The tracemaker for *Planolites terraenovae* were most likely polychaete worms (Hammersburg, Hasiotis, & Robison, 2018). *Planolites terraenovae* occurs monospecifically in the Fort Collins Member. This trace was constructed in a deltaic environment, based on lithology and succession of bedforms (MacKenzie, 1965).

Ichnogenus PROTOVIRGULARIA M'Coy, 1850

Protovirgularia M'Coy, 1850, p. 272, pl. 1b, figs. 11, 12.
Walcottia Miller & Dyer, 1878, p. 39, pl. 2, fig. 11.
Pennatulites De Stefani, 1885, p. 99, pl. 2, fig. 2.
Paleosceptron De Stefani, 1885, p. 101, pl. 2, fig. 2.
Biformites Linck, 1949, p. 40, pl. 4, fig. 1, 2.
Uchirites Macsotay, 1967, p. 37, fig. 15, 15a.

Imbrichnus Hallam, 1970, p. 197, pl. 2a–c.

Sustergichnus Chamberlain, 1971, p. 231, pl. 31, fig. 8, 11.

Protovirgularia Han & Pickerill, 1994b, p. 236, fig. 7g.

Protovirgularia Seilacher & Seilacher, 1994, p. 10, pl. 1f–h, pl. 2a–c.

Protovirgularia Uchman, 1998, p. 162, fig. 67a, c, d, 68b–d, 69, 70, 71.

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

Diagnosis.—Horizontal to subhorizontal cylindrical burrows, distinctly or indistinctly bilobate, internal structure, where preserved, formed by successive pads of sediment that may be expressed as ribs on the exterior; ribs arranged in a chevron-shaped, biserial pattern along the external or internal dorsal part; occasionally trace is covered by a smooth mantle and/or ovular mound-like terminations (after Uchman, 1998).

Discussion.—Seilacher and Seilacher (1994) demonstrated through neoichnological experiments that protobranch bivalves and scaphopods could be tracemakers of *Protovirgularia*. They also synonymized the ichnogenera *Crossopodia* M'Coy, 1851, *Walcottia* Miller & Dyer, 1878, *Paleosceptron* De Stefani, 1885, *Pennatulites* De Stefani, 1885, *Biformites* Linck, 1943, *Uchirites* Macsotay, 1967, *Imbrichnus* Hallam, 1970, and *Sustergichnus* Chamberlain, 1971 within *Protovirgularia* to reduce the number of ichnogenera with similar morphologies thought to be produced by the same behavior (Seilacher & Seilacher, 1994; also Bradshaw, 2010). Han and Pickerill (1994) reevaluated four ichnospecies of *Protovirgularia,* resulting in *Protovirgularia nereitarum* Richter, 1871 and *Protovirgularia mongraensis* Chiplonkar & Badve, 1970 being made junior synonyms of *Protovirgularia dichotoma* M'Coy, 1850, because the original description of *Protovirgularia dichotoma* accounted for the differences in the chevron angles of those ichnospecies. Han and Pickerill (1994) also declared *Protovirgularia harknessi* Lapworth, 1870 a *nomen nudem,* due to it lacking a proper description. Uchman (1998) synonymized ichnospecies from *Gyrochorte* Heer, 1865, *Nereites* MacLeay, 1839, *Rhabdoglyphus* Vassoevich, 1951, and *Tuberculichnus* Ksiażkiewicz, 1977 into *Protovirgularia*.

Protovirgularia is interpreted to represent the push-pull locomotion of protobranch bivalves and scaphopods in marine settings and dragonfly nymphs and bivalves in freshwater settings (Seilacher & Seilacher, 1994; Uchman, 1998; Ekdale & Bromley, 2001; Metz, 2002; Hammersburg, Hasiotis, & Robison, 2018). *Protovirgularia* is present in continental (fluvial and lacustrine), shallow-marine (tidal flat, estuarine, and deltaic) and deep-marine (flysch) environments (Han & Pickerill, 1994; Uchman, 1998; Kim, Kim, & Pickerill, 2000; Metz, 2002; Mángano & Buatois, 2004; Uchman & Gaździcki, 2006; Carmona & others, 2010; Nara & Ikari, 2011; Jackson, Flaig, & Hasiotis, 2016; Hammersburg, Hasiotis, & Robison, 2018; Flaig & others, 2019). *Protovirgularia* ranges from the early Cambrian to Holocene (Seilacher & Seilacher, 1994; Orłowski & Ylińska, 2002; Hammersburg, Hasiotis, & Robison, 2018).

PROTOVIRGULARIA PENNATUS Eichwald, 1860.

Figure 8.5, 10.6

Diagnosis.—Straight to winding trail with biserial chevron markings, faint and densely spaced, with or without a medial ridge (after Hammersburg, Hasiotis, & Robison, 2018).

Description.—Specimens are convex epirelief, with the chevron pattern of the specimens faint, but still visible. Specimens range from 4 to 7 mm wide and 40 to 60 mm long.

Occurrence.—(1) White (10R 8/1), very fine-grained sandstone with BPBI 2–3; and (2) white (10R 8/1), fine-grained ripple-laminated sandstone with BPBI 2, interbedded with mudstone. Specimens are present in the upper part of the Plainview Formation at Colorado State Highway 115 and the middle part of the Fort Collins Member of the Muddy Formation at Horsetooth Reservoir.

Associated ichnotaxa.—*Macaronichnus segregatis, Ophiomorpha nodosa, Planolites montanus,* and *Scolicia plana*.

Discussion.—Specimens are assigned to *Protovirgularia pennatus* based on the spacing of the chevrons, their distinct biserial pattern, and the absence of a visible medial furrow (Uchman, 1998; Hammersburg, Hasiotis, & Robison, 2018). The tracemaker for *Protovirgularia pennatus* are bivalves (Hammersburg, Hasiotis, & Robison, 2018). In the Plainview Formation at Colorado State Highway 115, a specimen of *Planolites montanus* transitions into *Protovirgularia pennatus* (red arrow, Fig. 10.6) after which it terminates at *Scolicia plana* (black arrow, Fig. 10.6). The termination of one trace by other can suggest predation (e.g., Hammersburg, Hasiotis, & Robison, 2018). However, the interpreted tracemakers of *Scolicia* from the Cretaceous are thought to be detritivores, which makes predation of *Planolites-Protovirgularia* tracemaker by the *Scolicia* tracemaker unlikely. One explanation for the termination of the trail of *Protovirgularia pennatus* is that it was removed by the grazing behavior of *Scolicia plana*. Another possibility is that the missing trail of *Protovirgularia pennatus* was removed through weathering. The trails in the Plainview Formation were constructed in an intertidal to subtidal environment based on the lithology and succession of bedforms (Gustason, Kauffman, 1985). In the Fort Collins Member, *Protovirgularia pennatus* co-occurs with *Ophiomorpha nodosa* and *Macaronichnus segregatis*. These traces were constructed in a deltaic environment, based on lithology and succession of bedforms (MacKenzie, 1965).

Ichnogenus RHIZOCORALLIUM Zenker, 1836

Rhizocorallium Zenker, 1836, p. 216.

Fucoides Hall, 1852, p. 47.

Lithochela Gümbel, 1861, p. 411.

Rhizocorallium Schmid, 1876, p. 17.

Rhizocorallium Hecker, 1930, p. 156, pl. 16.

Rhizocorallium Mayer, 1954, p. 82, pl. 2, 3.

Rhizocorallium Firtion, 1958, p. 107, pl. 1, 2, fig. 1, 3.

Rhizocorallium Hofmann, 1979, p. 40, pl. 13a.

Rhizocorallium Fürsich, 1974c, p. 16, pl. 4.

Rhizocorallium Häntzschel, 1975, p. W101, fig. 63.

Ilmenichnus Hecker, 1980, p. 20, pl. 3, fig. 2.

Ilmenichnus Schlirf, 2011, p. 41, fig. 7–12.

Rhizocorallium Knaust, 2013, p. 7, fig. 5–10, 13, 17, 18, 21, 22, 23, 25, 26, 29, 31, 32.

Type Ichnospecies.—*Rhizocorallium jenense* Zenker, 1836.

Diagnosis.—Horizontal to oblique, U-shaped burrow with spreite, mostly protrusive or somewhat oblique to bedding (after Häntzschel, 1975).

Discussion.—*Rhizocorallium* has been reviewed several times with the goal to create better diagnostic criteria for its ichnospecies.

Fürsich (1974c) validated three ichnospecies of *Rhizocorallium*: *Rhizocorallium jenense* Zenker, 1836, *Rhizocorallium irregulare* Mayer, 1954, and *Rhizocorallium uliarense* Firtion, 1958, which were characterized by their length and dimensional shape. The presence of scratches and fecal pellets as an ichnotaxonomic criterion was dismissed by Fürsich (1974c), due to these being too reliant on preservation. Hecker (1980, 1983) criticized this classification scheme in that it was too broad a grouping and did not follow Zenker's (1836) original description of *Rhizocorallium*. Hecker (1980, 1983) regarded the morphological differences between *Rhizocorallium jenense* and *Rhizocorallium devonicum* Hecker, 1930 to be great enough to justify the erection of a new ichnogenus *Ilmenichnus,* to account for large horizontal U-shaped burrows, but this was later rejected by Jensen (1997) and Knaust (2013). Schlirf (2011) created the diagnostic criteria of single-spreite laminae (one spreite between the U-limbs resulting from the displacement of the U-limb either proximal or distal) for *Ilmenichnus* and double-spreite laminae (combination of a spreite laminae between the U-limbs plus an additional, predominantly retrusive shift of the U limb) for *Rhizocorallium*. *Rhizocorallium* possesses a double-spreite laminae or subvertical orientation, whereas *Ilmenichnus* possesses a single-spreite laminae or horizontal orientation (e.g., Schlirf, 2011). These criteria, however, are questionable as: (1) a double-spreite is absent in most specimens of *Rhizocorallium jenense,* including specimens from the type stratum (Knaust, 2013), and (2) double-spreite laminae have not been described in that manner previously in the literature, creating confusion (Fürsich, 1974c; Pemberton & Frey, 1984; Jensen, 1997; Worsley & Mørk, 2001; Uchman & Gaździcki. 2006; Mørk & Bromley, 2008; Knaust, 2013; Savrda, Bingham, & Daymond, 2016). Also, the morphologic pattern produced by the double movement of the whole U tube and spreite of *Rhizocorallium* was previously designated as *Lithochela problematica* by Gümbel (1861) and transferred to *Rhizocorallium* by Fürsich (1974c). For these reasons, we suggest *Ilmenichnus* be made a junior synonym of *Rhizocorallium*.

Knaust (2013) synonymized *Rhizocorallium devonicum* and *Rhizocorallium irregulare* within *Rhizocorallium commune* based on their similar described morphologies, with *Rhizocorallium commune* having priority (Schmid, 1876; Schmidt, 1928; Helms, 1995). After examining the literature sources presented by Knaust (2013), we agree with this synonymy.

Rhizocorallium auriforme originally called *Fucoides auriforme* by Hall (1843, 1852), has questionable ichnotaxonomic affinity, as Hall did not provide a description of *Fucoides auriforme,* only a drawing. Hofmann (1979) examined material from the same region *Fucoides auriforme* was identified. When he examined the material, he renamed it *Rhizocorallium auriforme* based on its morphological similarities to *Rhizocorallium*. When examining the description and photograph of *Rhizocorallium auriforme* provided by Hofmann (1979), the traces resemble *Rhizocorallium jenense* (Fürsich 1974c; Worsley & Mørk, 2001; Uchman & Gaździcki, 2006). For this reason, we suggest synonymizing *Rhizocorallium auriforme* within *Rhizocorallium jenense*.

Knaust (2013) reworked *Rhizocorallium* into two ichnospecies *Rhizocorallium jenense* and *Rhizocorallium commune*, with *Rhizocorallium commune* be broken down even further into ichnosubspecies and varieties. This classification of ichnospecies, ichnosubspecies, and varieties for *Rhizocorallium* was done based on their surficial morphology, media firmness, orientation, and size. This classification is problematic for several reasons. First, varieties are not allowed under the Zoological Code of Nomenclature (A. Ringsberg, personal communication, 2021). Second, the use of surficial morphologies to justify the separation of ichnospecies relies on specimen preservation and media consistency (= degree of firmness or stiffness). This creates unnecessary confusion for the assignment of specimens to an ichnospecies due to preservation variance. Also, the establishment of ichnosubspecies is not common in ichnology and constitutes a high degree of ichnotaxonomic splitting, which creates further confusion. Therefore, we reject splitting *Rhizocorallium* into ichnosubspecies and varieties and recommend that the ichnotaxonomic assessment by Fürsich (1974c) be followed.

Rhizocorallium is interpreted as a dwelling of (1) a suspension feeder for specimens with short and subvertical morphologies, and (2) a deposit feeder for specimens with large and horizontal morphologies (Fürsich, 1974c; Pemberton & Frey, 1984; Mørk & Bromley, 2008; Knaust, 2013). *Rhizocorallium* tracemakers are interpreted to be polychaetes and/or crustaceans (Pemberton & Frey, 1984; Worsley & Mørk, 2001; Uchman & Gaździcki. 2006; Savrda, Bingham, & Daymond, 2016). *Rhizocorallium* is present in marine intertidal, subtidal, estuarine, deltaic, lower shoreface, upper offshore, and flysch environments (Fürsich & Mayr, 1981; MacEachern & Pemberton, 1992; Uchman, 1992; Tiwari & others, 2011; Knaust, 2013; Van der Kolk, Flaig, & Hasiotis, 2015; Savrda, Bingham, & Daymond, 2016). *Rhizocorallium* ranges from the early Cambrian to Holocene (Orłowski, 1989; Bromley & Allouc, 1992; Hasiotis, 2012; Knaust, 2013).

RHIZOCORALLIUM COMMUNE Schmid, 1876

Figure 8.1, 11.1, 11.2, 11.3, 11.4

Diagnosis.—Large U-shaped, spreite burrows, rarely branched, with a horizontal to subhorizontal orientation; burrows elongate, bandlike, straight or winding, some with subparallel longitudinal scratches on the burrow; fecal pellets in some cases common within the spreite and within the burrow (after Knaust, 2013).

Description.—Specimens are in convex epirelief, concave epirelief, and full relief. Traces are horizontal and smooth walled. Diameter of the burrow limbs ranges from 5 to 10 mm, with the burrow limbs 45 to 100 mm apart (measured from the outside of the burrow limbs), and 70–430 mm long.

Occurrence.—(1) White (10R 8/1), fine- to very fine-grained ripple-laminated sandstone with BPBI 2–3; (2) very dark gray (YR 7.5 3/1) shale interbedded with reddish yellow (7.5YR 7/8), very fine-grained sandstone, with moderate bioturbation (ii3); (3) reddish yellow (7.5YR 7/8) to gray (7.5YR 5/1), very fine- to fine-grained sandstone with some chert clasts present; (4) reddish yellow (7.5YR 7/8), very fine- to fine-grained sandstone with BPBI 2; (5) very dark gray (YR 7.5 3/1) shale interbedded with white siltstone to very fine-grained sandstone, with low to moderate bioturbation (ii2–3); and (6) reddish yellow (7.5YR 7/8), very fine- to fine-grained sandstone with BPBI 2–3. Specimens are present in the middle part of the Planview Formation at Colorado State Highway 115, in the lower part of the Skull Creek Shale at Dinosaur Ridge, in the upper part of the Skull Creek Shale at

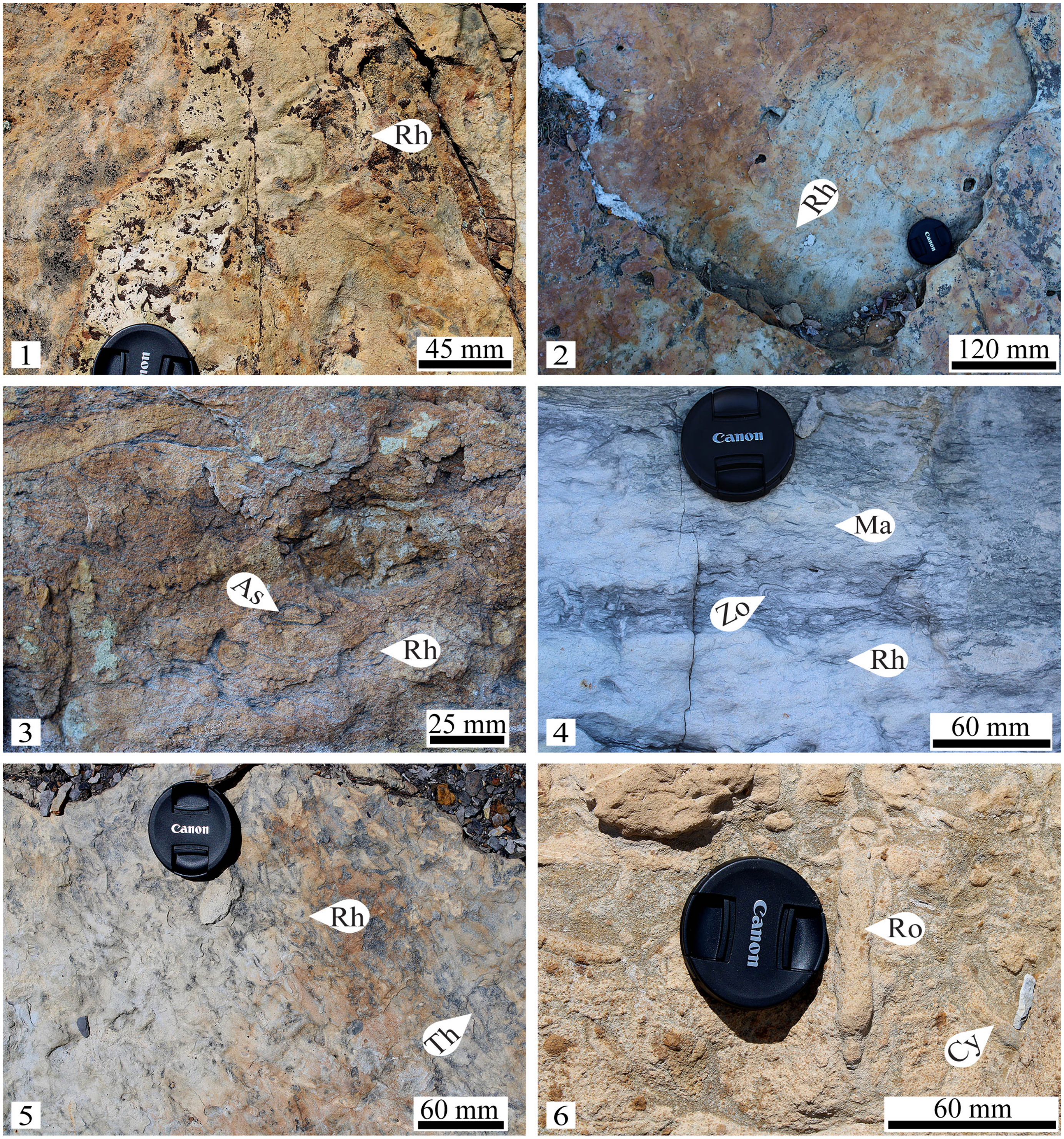


Figure 11. *Asterosoma* (As), *Cylindrichnus* (Cy), *Macaronichnus* (Ma), *Rhizocorallium* (Rh), *Rosselia* (Ro), *Thalassinoides* (Th), and *Zoophycos* (Zo) from the Dakota Group. *1, Rhizocorallium commune* in concave epirelief within the upper part of the Muddy Formation at Dinosaur Ridge. *2, Rhizocorallium commune* (red circle) in convex epirelief within the middle part of the Muddy Formation at Dinosaur Ridge. *3, Asterosoma* isp. and *Rhizocorallium commune* in vertical section within the upper part of the Skull Creek Shale at Horsetooth Reservoir. *4, Macaronichnus segregatis, Rhizocorallium commune,* and *Zoophycos* isp. in vertical section within the middle part of the Skull Creek Shale at Dinosaur Ridge. *5, Rhizocorallium jenense* and *Thalassinoides suevicus* in concave epirelief within the upper part of the Muddy Formation at Dinosaur Ridge. *6, Cylindrichnus concentricus* and *Rosselia socialis* in vertical section within the upper part of the Plainview Formation at Skyline Drive.

Horsetooth Reservoir, in the middle part of the Muddy Formation at Dinosaur Ridge and Skyline Drive, and in the upper part of the Muddy Formation at Dinosaur Ridge.

Associated ichnotaxa.—Archaeonassa fossulata, Asterosoma isp., *Diplocraterion* isp., *Macaronichnus segregatis, Schaubcylindrichnus freyi, Skolithos linearis, Teichichnus rectus,* and *Zoophycos isp*.

Discussion.—Specimens are assigned to *Rhizocorallium commune* based on their horizontal U-shaped burrow, the presence of a spreite between the burrow limbs, and relatively large overall size (Fürsich, 1974c; Knaust, 2013; Chrząstek, 2013; Savrda, Bingham, & Daymond, 2016). *Rhizocorallium commune* is interpreted to be a deposit-feeding burrow, with the tracemakers being crustaceans and polychaetes (Fürsich, 1974c; Chrząstek, 2013; Knaust, 2013; Savrda, Bingham, & Daymond, 2016).

In the Plainview Formation at Colorado State Highway 115, *Rhizocorallium commune* forms a monospecific occurrence, with the single trace being constructed in an intertidal to subtidal environment based on lithology and succession of bedforms (Weimer, 1970; Gustason & Kauffman, 1985). In the Skull Creek Shale at Dinosaur Ridge *Rhizocorallium commune* co-occurs with *Macaronichnus segregatis*, *Teichichnus rectus*, and *Zoophycos* isp, with these traces being constructed in a marine embayment (Weimer & Land, 1972). *Rhizocorallium commune* in the Skull Creek Shale at Horsetooth Reservoir co-occurs with a few *Asterosoma* isp. and *Teichichnus rectus,* all of which were constructed in a lower shoreface environment, based on lithology and succession of bedforms (Graham & Ethridge, 1995). A large specimen of *Rhizocorallium commune* (101 mm wide and 430 mm long) occurs by itself in the middle part of the Muddy Formation at Dinosaur Ridge (Fig. 11.2), whereas those in the upper part of the Muddy Formation at Dinosaur Ridge co-occur with *Archaeonassa fossulata*. *Rhizocorallium commune* in both parts of the Muddy Formation at Dinosaur Ridge were constructed in a subtidal environment based on lithology and succession of bedforms (MacKenzie, 1975; Chamberlain, 1985). At Skyline Drive *Rhizocorallium commune* co-occurs with *Diplocraterion* isp., both having been produced in a subtidal environment based on lithology and succession of bedforms (Gustason & Kauffman, 1985).

RHIZOCORALLIUM JENENSE Zenker, 1836

Figure 11.5

Emended Diagnosis.—Unbranched, short, straight U-shaped burrow, commonly with horizontal to oblique orientation to the bedding plane; burrow and spreite vertically retrusive in some cases; with or without subparallel to netlike scratches on the burrow wall; fecal pellets sometimes present within the spreite and within the burrow (modified after Knaust, 2013).

Description.—Traces are horizontal to the bedding plane and are preserved in concave epirelief. Faint spreite are present between the burrows, which are smooth and lack surficial morphology. Diameter of the limbs of the burrow are ~3 mm, with the limbs are 14–25 mm apart (measured from the outside of each limb) and 17–70 mm long.

Occurrence.—(1) Strong brown (7.5YR 5/8) to gray (7.5YR 5/1), very fine- to fine-grained sandstone with BPBI 4, with some chert clasts present in the sandstone; and (2) black (7.5YR 2.5/1), very fine-grained sandstone to siltstone with BPBI 2. Specimens are present in the middle part of the Plainview Formation at Horsetooth Reservoir and in the upper part of the Muddy Formation at Dinosaur Ridge.

Associated ichnotaxa.—Taenidium serpentinum and *Thalassinoides suevicus*.

Discussion.—We emend the diagnosis to account for surficial morphological descriptions of *Rhizocorallium jenense* (Schlirf, 2003; Knaust, 2013; Hofmann, & others, 2015; Zhang, Knaust, & Zhao, 2016), and use the terms shafts and tunnels to describe the elements that comprise the U-shaped burrow. Traces are assigned to *Rhizocorallium jenense* based on U-shaped burrow, horizontal orientation, the presence of spreite between the limbs of the burrow, and relatively small overall size (Fürsich, 1974c; Chrząstek, 2013; Knaust, 2013; Savrda, Bingham, & Daymond, 2016). *Rhizocorallium jenense* is interpreted to represent suspension- and/or deposit-feeding behavior, with the tracemaker being polychaetes or crustaceans (Fürsich, 1974c; Knaust, 2013; Chrząstek, 2013; Savrda, Bingham, & Daymond, 2016).

In the Plainview Formation *Rhizocorallium jenense* is present in float, which makes its orientation and stratigraphic position within the Plainview Formation difficult to place. A nearby float block with similar lithology and bedforms contained *Chondrites intricatus, Planolites montanus,* and *Taenidium serpentinum* suggesting they are from the same interval as *Rhizocorallium jenense*. *Rhizocorallium jenense* in the Plainview Formation were constructed in an intertidal to subtidal environment, based on lithology and succession of bedforms (Wescott, 1979). In the Muddy Formation *Rhizocorallium jenense* co-occurs with *Taenidium serpentinum* and *Thalassinoides suevicus,* overlying wave-ripple marks with syneresis cracks and underlying a thin mudstone bed with *Skolithos linearis* and *Teichichnus rectus*. *Rhizocorallium jenense* in the Muddy Formation were constructed in an intertidal environment, based on lithology and succession of bedforms (MacKenzie, 1975; Chamberlain, 1985).

Ichnogenus ROSSELIA Dahmer, 1937

Rosselia Dahmer, 1937, p. 532, pl. 31, fig. 2, 4, pl. 32, fig. 1, fig. 2.

Rosselia Uchman & Krenmayr, 1995, p. 507, fig. 2, 3b–h, 4a–g, 5b.

Rosselia Knaust, 2021, p. 4, fig. 3–6.

Type Ichnospecies.—*Rosselia socialis* Dahmer, 1937.

Diagnosis.—Vertical to inclined, downward tapering, straight or curved burrow with a funnel-shaped, bulbous or fusiform aperture containing a thick concentric, spiraled or eccentric lining around one or several, passively filled, cylindrical tube(s). Secondary successive branching may occur (after Knaust, 2021).

Discussion.—Previous researchers have noted that the morphologies of *Rosselia* can create confusion when compared to other conical or funnel-shaped ichnogenera (Frey & Howard, 1985; Fillion & Pickerill, 1990; Uchman & Krenmayr, 1995; Jensen, 1997; Schlirf, 2000; Bradshaw, 2010). Frey and Howard (1985) noted that the basal stems of *Rosselia* appear similar to *Cylindrichnus,* whereas *Rosselia* has concentric layers around a central tube and a bulblike shape that appears similar to *Asterosoma*. Fillion and

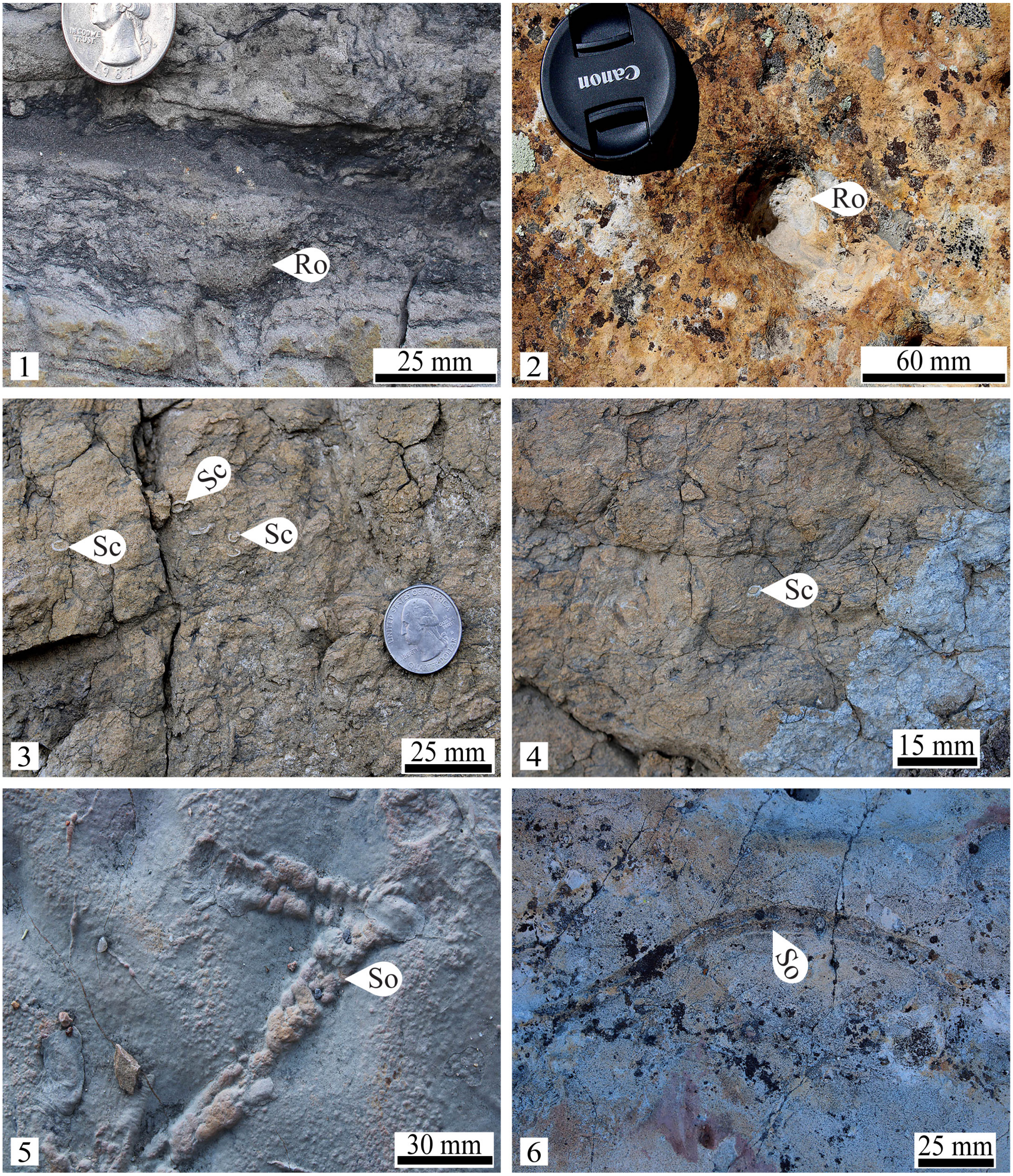


Figure 12. *Rosselia* (Ro), *Schaubcylindrichnus* (Sc), and *Scolicia* (So) from the Dakota Group. *1,* Stacked *Rosselia socialis* in vertical section within the lower part of the Skull Creek Shale at U.S. Route 285. *2, Rosselia* isp. in concave epirelief within the upper part of the Muddy Formation at Dinosaur Ridge. *3, Schaubcylindrichnus freyi* in vertical section with broken lining within the upper part of the Skull Creek Shale at Horsetooth Reservoir. *4, Schaubcylindrichnus freyi* within the upper part of the Skull Creek Shale at Horsetooth Reservoir. *5,* Two *Scolicia plana* crosscutting each other in convex epirelief within the middle part of the Plainview Formation at Colorado State Highway 115. *6, Scolicia* isp. in concave epirelief within the middle part of the Muddy Formation at Dinosaur Ridge.

Pickerill (1990) stated that the confusion primarily stems from lack of understanding about the diagnoses of these ichnogenera. To address this issue, researchers have provided criteria to distinguish *Rosselia* from other similar ichnogenera. *Asterosoma* is differentiated based on its star-shaped pattern and horizontal orientation, whereas *Cylindrichnus* is differentiated based on its tapering orientation and lack of a bulb (Frey & Howard, 1985; Fillion & Pickerill, 1990; Uchman & Krenmayr, 1995; Schlirf, 2000). Several researchers have identified seafloor surface material within the laminae of *Rosselia*, suggesting that the tracemakers collected the material from there (e.g., Nara, 1995; Zorn & others, 2007). Researchers have also found vertically stacked bulbs of *Rosselia* in which a central shaft is shared between the different segments. These stacked segments are interpreted to be the tracemaker attempting to maintain equilibrium with the seafloor (MacEachern & Pemberton, 1994; Nara, 1995, 2002; MacEachern & others, 2005; MacEachern & Gingras, 2007a; Netto & others, 2014; Campbell & others, 2016).

Rosselia is interpreted to be a dwelling or equilibrium trace of suspension-feeding of annelids, terebellid polychaetes, crustaceans or sea anemones (Nara, 1995; Schlirf, 2000; Frieling, 2007; Hofmann, & others, 2012). *Rosselia* is present in lagoonal, tidal flat, estuarine, bay, deltaic, middle and lower shoreface, offshore, and flysch environments (Książkiewicz, 1977; Pemberton & Frey, 1984; Pemberton, Wagoner, & Wach, 1992; MacEachern & Pemberton, 1994; Jensen, 1997; Nara, 2002; Hubbard, Gingras, & Pemberton, 2004; Frieling, 2007; MacEachern & Gingras, 2007a; Nara & Haga, 2007; Zorn & others, 2007; Bradshaw, 2010; Paz & others, 2020). *Rosselia* ranges from the early Cambrian to Holocene (Jensen, 1997; Gibert & others, 2006; Frieling, 2007).

ROSSELIA SOCIALIS Dahmer, 1937
Figure 11.6, 12.1

Diagnosis.—Unbranched, inclined to vertical burrow concentrically layered around a central core, with a funnel-shaped or bulbous aperture with passively filled cylindrical tube(s) occupying a minor fraction of the funnel (after Knaust, 2021).

Description.—Specimens are in full relief, with the trace either displaying concentric lining around a central shaft and/or a bulb shaped structure (Fig. 11.6), that can form stacked and offset structures (Fig. 12.1). Specimens are 10 mm wide and 40–86 mm tall.

Occurrence.—(1) Strong brown (7.5YR 5/8), fine- to very-fine grained sandstone, beds highly bioturbated (ii4); and (2) reddish yellow (7.5YR 6/8) to light olive brown (10Y 5/4), interbedded with white (10R 8/1) siltstone with little bioturbation (ii2). Specimens are present in the upper part of the Plainview Formation at Skyline Drive, and in the lower part of the Skull Creek Shale at U.S. Route 285.

Associated ichnotaxa.—Cylindrichnus concentricus, Skolithos linearis, and *Teichichnus rectus.*

Discussion.—Specimens are assigned to *Rosselia socialis* based on the bulblike vertically oriented structure of the proximal part of burrow, presence of a central vertical shaft, and concentric layers (Frieling, 2007; Bradshaw, 2010; Knaust, 2021). The tracemakers for *Rosselia socialis* were most likely an infaunal worm (Nara, 1995). Although the specimen in the Skull Creek Shale might have been considered as *Conichnus,* the presence of the central vertical shaft places it in *Rosselia* (Pemberton & Frey, 1984; Bradshaw, 2010). In the Plainview Formation, *Rosselia socialis,* along with other trace fossils, are present near the contact with the Glencairn Formation. Traces in the Plainview Formation were constructed in a subtidal environment, based on lithology and bedforms (Weimer, 1970; Gustason & Kauffman, 1985). A specimen having three stacked bulblike structures (Fig. 12.1) suggests that the tracemaker maintained equilibrium with the seafloor (e.g., Nara, 1995, 2002; Netto & others, 2014; Campbell, & others, 2016). In the Skull Creek Shale, *Rosselia socialis* occurs by itself and was constructed in a marine embayment, based on lithology and succession of bedforms (Weimer & Land, 1972).

ROSSELIA isp.
Figure 12.2

Description.—Specimens are ovoid in concave epirelief. Some of the specimens have a visible circular depression in the middle, surrounded by other concentric depressions or laminae. These laminae are faint due to weathering, making their identification difficult. Specimens range from 20 to 35 mm wide and 20 to 40 mm long, and ~10 mm deep; total depth is unknown due to its epirelief expression in outcrop.

Occurrence.—Reddish yellow (7.5YR 6/8), very fine- to fine-grained sandstone, with BPBI 2. Specimens are present in the upper part of the Muddy Formation at Dinosaur Ridge.

Associated ichnotaxa.—None.

Discussion.—Specimens are assigned to *Rosselia* due to their circular outline, faint concentric laminae, and presence of a central shaft in some specimens (see Uchman & Krenmayr, 1995; Jensen, 1997). The tracemakers of *Rosselia* isp. were infaunal worms (Nara, 1995). Due to the level of weathering, specimens could not be properly placed within an ichnospecies. Specimens occur sporadically on the bedding surface, with some clustered. The beds bearing *Rosselia* are overlain by plant impressions and *Ostendichnus bilobatus*, indicating this area was close to a terrestrial environment. *Rosselia* isp. in the Muddy Formation were constructed in an intertidal environment, based on lithology and succession of bedforms (MacKenzie, 1975; Chamberlain, 1985).

Ichnogenus RUSOPHYCUS Hall, 1852

Rusophycus Hall, 1852, p. 23.

Rusophycus Osgood, 1970, p. 346, pl. 1, fig. 1, 5, 6, pl. 2, fig. 1–10, pl. 3, fig. 4–6, pl. 4, fig. 3, pl. 10, fig. 3, pl. 15, fig. 1, pl. 26, fig. 9.

Cruziana Seilacher, 1970, p. 454.

Rusophycus Keighly & Pickerill, 1996, p. 278, fig. 1a–c, 1g, 2b–d.

Rusophycus Hammersburg, Hasiotis, & Robison, 2018, p. 20, fig. 15.5, 18.1–18.6.

Type Ichnospecies.—Rusophycus clavatus Hall, 1852.

Diagnosis.—Small to large bilobate depressions with parallel lobes separated by a median furrow that sometimes merge near the posterior; traces with or without parallel to oblique to transverse striation; may be smooth (after Hammersburg, Hasiotis, & Robison, 2018).

Discussion.—Seilacher (1970) synonymized *Rusophycus* within *Cruziana* based on their morphological similarity and identical interpreted tracemakers. This synonymy has been rejected by researchers (see discussion in *Cruziana*). The ichnospecies of *Rusophycus* are distinguished primarily by striation pattern, as in *Cruziana*; however, size, lobe morphology, and tracemaker remnants are sometimes used as well (Crimes, 1970b; Osgood, 1970; Seilacher, 1970; Hammersburg, Hasiotis, & Robison, 2018).

Rusophycus is commonly interpreted as a resting trace, with hunting and nesting behaviors also suggested based on its morphology (Fenton & Fenton, 1937d; Crimes, 1970b; Osgood, 1970; Seilacher, 1970; Jensen, 1990; Garvey & Hasiotis, 2008; Tarhan, Jensen, & Droser, 2011; Hammersburg, Hasiotis, & Robison, 2018). The tracemakers of *Rusophycus* are interpreted to be arthropods (trilobites and crustaceans) along with gastropods and some tetrapods (Crimes, 1970a; Seilacher, 1970; Bromley & Asgaard, 1979; Hammersburg, Hasiotis, & Robison, 2018). *Rusophycus* is present in continental (fluvial and lacustrine), shallow-marine (lagoonal, intertidal, tidal flat, foreshore, deltaic, lower shoreface, and middle shoreface), and deep-marine (offshore, slope and basin) environments (Crimes, 1970b; Seilacher, 1970; Hakes, 1976, 1985; Bromley & Asgaard, 1979; Pollard, 1985; Fillion & Pickerill, 1990; Pickerill, 1995; Davies, Sansom, & Albanesi, 2007; Garvey & Hasiotis, 2008; Bradshaw, 2010; Jackson, Hasiotis, & Flaig, 2016). *Rusophycus* ranges from the Cambrian to Holocene (Crimes, 1987; Hasiotis, 2012; Hammersburg, Hasiotis, & Robison, 2018).

RUSOPHYCUS isp.
Figure 6.4

Description.—The single specimen is in convex hyporelief with a bilobate structure; the median furrow is present but faint. The bilobate structure is smooth, lacking visible striation. Specimen is ~8 mm long and ~5 mm wide.

Occurrence.—Reddish yellow (7.5YR 6/8), very fine- to fine-grained subrounded and well-sorted sandstone with planar bedding and BPBI 4. Specimen is present in the middle part of the Glencairn Formation at Skyline Drive.

Associated ichnotaxa.—*Cruziana* isp., *Gyrolithes lorcaensis, Lockeia siliquaria, Planolites montanus, Taenidium serpentinum,* and *Thalassinoides suevicus.*

Discussion.—This specimen is assigned to *Rusophycus* based on its short length and bilobate structure (see Hammersburg, Hasiotis, & Robison, 2018). The tracemaker for *Rusophycus* isp. was most likely an arthropod (Hammersburg, Hasiotis, & Robison, 2018). The worn surface of the specimen prevents proper placement within an ichnospecies. *Cruziana* transitions into this specimen, suggesting the tracemaker stopped and rested. The specimen is present in the 2nd sandstone bed in the Glencairn Formation, which was deposited in a deltaic environment based on lithology and succession of bedforms (Gustason & Kauffman, 1985).

Ichnogenus SCHAUBCYLINDRICHNUS
Frey & Howard, 1981

Schaubcylindrichnus Frey & Howard, 1981, p. 801, fig. 1b, 3a–c.
Schaubcylindrichnus Miller, 1995a, p. 143, fig. 3–5.
Schaubcylindrichnus Nara, 2006, p. 451, fig. 2, 3, 7, 8, 11, 12, 14, 15.

Type Ichnospecies.—*Schaubcylindrichnus coronus* Frey & Howard, 1981.

Diagnosis.—Distinct, thickly, sometimes twofold-lined, cylindrical tubes. Tubes are isolated or bundled and do not branch or interconnect (after Frey & Howard, 1981; Nara, 2006).

Discussion.—*Schaubcylindrichnus* was named for bundled, lined tubes that do not interconnect and are considered to be different from other "bundled" burrows due to what is described as a lack of communication between the tubes (Frey & Howard, 1981). Miller (1995) recommended that the use of the ichnogenus *Terebellina* be discontinued due to the type species being referred to the large agglutinated foraminiferid *Bathysiphon,* and that most identified *Terebellina* can be accommodated in *Palaeophycus* or *Schaubcylindrichnus*. This suggestion has not always been followed by researchers (MacEachern & others, 2007b; Buatois & Mángano, 2013). Other researchers have noted morphological similarities between *Palaeophycus* and *Schaubcylindrichnus* based on their lining, noting that the ichnogenera should remain separate based on *Schaubcylindrichnus* having a thick, sometimes twofold lining, and *Palaeophycus* having a thin lining (e.g., Nara, 2006; Evans & McIlroy, 2016). Evans and McIlroy (2016) placed *Palaeophycus heberti* in *Schaubcylindrichnus* due to it being the only *Palaeophycus* with a thick lining.

Schaubcylindrichnus freyi Miller, 1995 was synonymized within *Schaubcylindrichnus coronus* by Nara (2006), based on the lack of morphological differences between the ichnospecies. We suggest that *Schaubcylindrichnus freyi* be retained as it was defined for isolated tubes, whereas *Schaubcylindrichnus coronus* was defined for bundles or rows of tubes. Such a distinction communicates clearly which morphotype of *Schaubcylindrichnus* is observed in outcrop or core.

Schaubcylindrichnus is interpreted to be a dwelling of such filter feeders or deposit feeders as polychaetes and/or enteropneusts worms (Frey & Howard, 1981; Löwemark & Hong, 2006). A current interpretation of the feeding strategy of the tracemaker of *Schaubcylindrichnus* is funnel-feeding, in which a funnel opens to the sea floor that traps organic detritus that is then filtered out by the tracemaker (Nara, 2006; Löwemark & Nara, 2010; Evans & McIlroy, 2016). *Schaubcylindrichnus* has been reported from estuarine, foreshore, delta-front, lower shoreface, and offshore environments (MacEachern & Pemberton, 1992; Savrda & others, 1998; Van der Kolk, Flaig, & Hasiotis, 2015; Evans & McIlroy, 2016; Paz & others, 2020). *Schaubcylindrichnus* ranges from the Lower Cretaceous to Holocene (Nara, 2006; MacEachern & others, 2012b).

SCHAUBCYLINDRICHNUS FREYI Miller, 1995
Figure 12.3, 12.4, 13.2

Emended Diagnosis.—Cylindrical, thickly lined, sometimes twofold-lined, arcuate tube; commonly oblique to the bedding plane but occasionally oriented subvertical to subhorizontal. Burrows may be isolated or in unattached groups (modified from Miller, 1995; Nara, 2006).

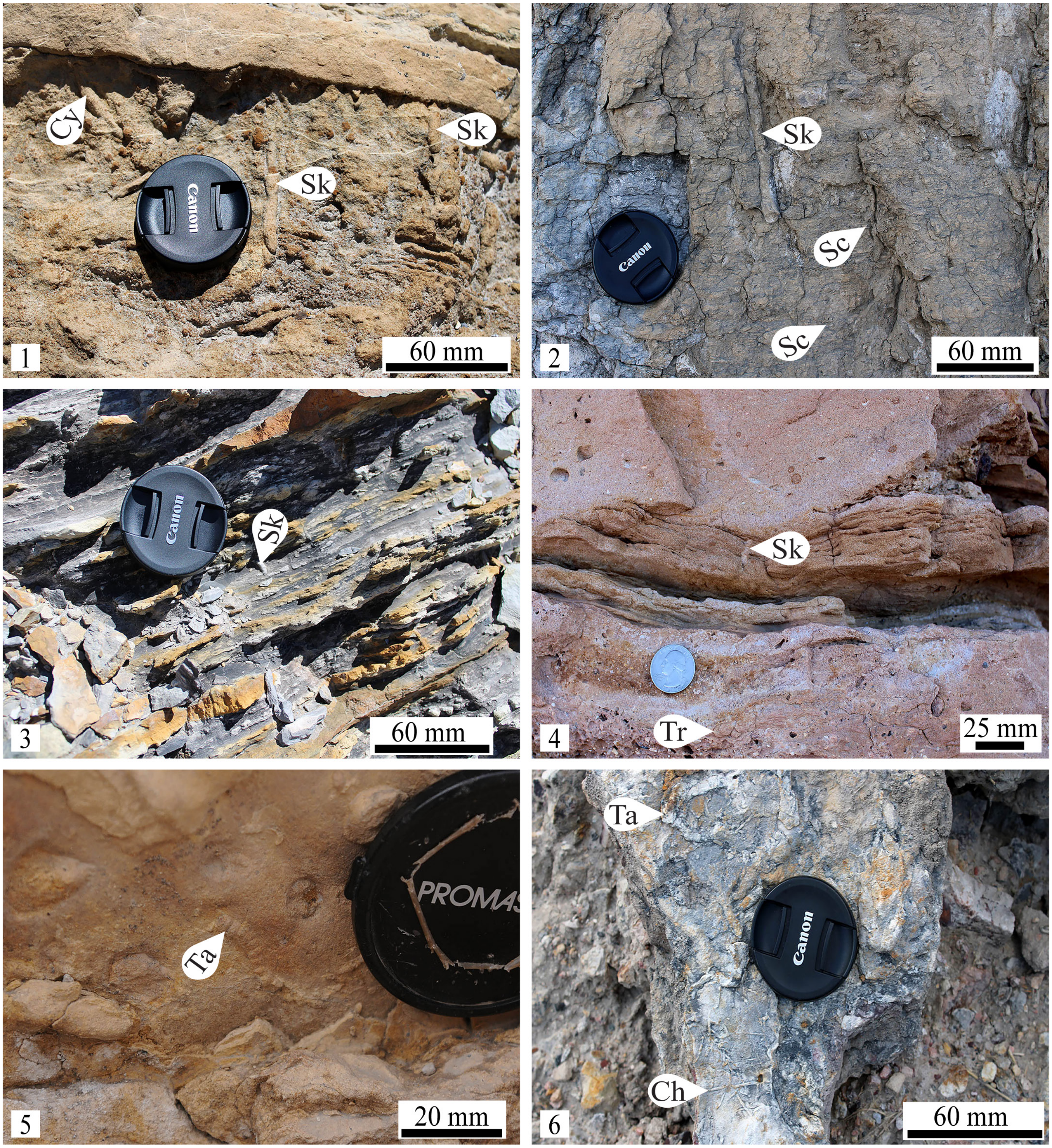


Figure 13. *Chondrites* (Ch), *Cylindrichnus* (Cy), *Schaubcylindrichnus* (Sc), *Skolithos* (Sk), *Taenidium* (Ta), and *Teredolites* (Tr) from the Dakota Group. *1, Cylindrichnus concentricus* and *Skolithos linearis* in vertical section within the upper part of the Plainview Formation at Skyline Drive. *2, Skolithos linearis* (Sk) with *Schaubcylindrichnus freyi* (Sh) in vertical section within the upper part of the Skull Creek Shale at Horsetooth Reservoir. *3, Skolithos linearis* in vertical section within the lower part of the Skull Creek Shale at I-70. *4, Skolithos linearis* and *Teredolites clavatus* in vertical section within the lower part of the Plainview Formation at Skyline Drive. *5, Taenidium serpentinum* convex hyporelief within the middle part of the Glencairn Formation at Skyline Drive. *6, Chondrites intricatus* and *Taenidium serpentinum* float blocks from the upper part of the Plainview Formation at Horsetooth Reservoir.

Description.—Specimens may be in full relief, sometimes with an apparent twofold lining, with the lining of some specimens having fractures. The lining of the traces is constructed of a different material than the surrounding rock. Traces are present singularly or in unattached groups. Traces range from 15 to 30 mm long and 2 to 3 mm in diameter.

Occurrence.—Very dark gray (7.5YR 3/1), shale interbedded with strong brown (7.5YR 5/8) to red (10R 4/8), very fine-grained sandstone to siltstone with moderate to high bioturbation (ii3–4). Specimens are present in the upper part of the Skull Creek Shale at Horsetooth Reservoir.

Associated ichnotaxa.—Asterosoma isp.*, Skolithos linearis, and Teichichnus rectus.*

Discussion.—We emend the diagnosis to account for the new descriptions of the sometimes apparent twofold lining of the thick tube that defines *Schaubcylindrichnus* (Löwemark & Hong, 2006; Nara, 2006; Löwemark & Nara, 2010). Specimens are assigned to *Schaubcylindrichnus freyi* based on the unattached groups or singular occurrence of tubes, thickness of the lining, the sometimes apparent twofold appearance of the lining, and the lining being constructed of a different material than the surrounding lithology (Miller III, 1995; Nara, 2006). The tracemaker for *Schaubcylindrichnus freyi* was an infaunal worm (Nara, 2006). The lining of some specimens of *Schaubcylindrichnus freyi* is fractured (Fig. 12.3). Other researchers have reported cracked and broken linings in *Schaubcylindrichnus*, which they attributed to bioturbation of the surrounding bed or interpenetration by younger *Schaubcylindrichnus* (Löwemark & Hong, 2006; Nara, 2006). *Schaubcylindrichnus freyi* was constructed in a lower shoreface environment, based on lithology and bedforms (Graham & Ethridge, 1995).

Ichnogenus SCOLICIA de Quatrefages, 1849

Scolicia de Quatrefages, 1849, p. 265.

Taphrhelminthopsis Sacco, 1888, p. 24, pl. 1, fig. 20, pl. 2 fig. 3.

Subphyllochorda Götzinger & Becker, 1932, p. 380, pl. 8, fig. a, pl. 9, fig. a, b, fig. 4, 5, 4.11.

Laminites Ghent & Henderson, 1966, p. 158, pl. 1, 2.

Scolicia Häntzschel, 1975, p. 106, fig. 66.

Scolicia Uchman, 1995, p. 34, pl. 9, fig. 5, 6, pl. 10, fig. 1–3.

Scolicia Hammersburg, Hasiotis, & Robison, 2018, p. 36, fig. 20.1–20.6.

Type Ichnospecies.—Scolicia prisca de Quatrefages, 1849.

Diagnosis.—Simple, winding to meandering to coiling, bilobate to trilobate backfilled burrows, which may have one or two parallel, locally discontinuous sediment furrows or sand-filled cylinders along their base, the area between the sand-filled cylinders being flat to slightly convex; cross sections are circular to oval; geopetal meniscate backfill and massive burrow infill both common (after Uchman, 1995; Hammersburg, Hasiotis, & Robison, 2018).

Discussion.—Owing to the number of ichnogenera with morphologies similar to *Scolicia,* Häntzschel (1962, 1975) created the *Scolicia* group, which contains ichnogenera with similar morphologies and behaviors as *Scolicia*. Ichnotaxa within this group over the years have been synonymized within *Scolicia* or other members of the group (Uchman, 1995; Mángano, Buatois, & Rindsberg, 2002). Plaziat and Mahmoudi (1988) suggested separating *Scolicia* and *Subphyllochorda* Götzinger & Becker, 1932, based on *Scolicia* being in concave epirelief and *Subphyllochorda* in convex hyporelief. This was rejected by Uchman (1995), who synonymized *Taphrhelminthopsis* Sacco, 1888, *Subphyllochorda,* and *Laminites* Ghent & Henderson, 1966 within *Scolicia* based on the differences between them being their toponomic position and preservation. Smith and Crimes (1983) stated that true *Scolicia* ranges from the Mesozoic to Cenozoic based the complexity of those traces and on the interpreted. Surface trails with furrows reported from Paleozoic deposits were simplistic in their construction and lacked the morphologies that would have placed them within "*Scolicia* group". Other researchers have stated that Paleozoic *Scolicia* could be made by gastropods and that examples of *Scolicia* in the Paleozoic are morphologically more similar to Mesozoic to Cenozoic *Scolicia* than to other ichnotaxa in the "*Scolicia* group" (Fillion & Pickerill, 1990; Zhu, 1997, Mángano, Buatois, & Rindsberg, 2002). *Scolicia* differs from *Archaeonassa,* which has a wide central medial furrow bounded by narrow convex ridges, and from *Aulichnites,* which has two lobes separated by a deep furrow (Fillion & Pickerill, 1990; Uchman, 1995; Hammersburg, Hasiotis, & Robison, 2018).

Scolicia is interpreted to be a locomotion, deposit-feeding, or grazing trace of irregular echinoids (marine and Mesozoic-Cenozoic) and gastropods (Paleozoic) (Smith & Crimes, 1983; Plaziat & Mahmoudi, 1988; Uchman, 1995; Fu & Werner, 2000; Donovan, Renema, & Pickerill, 2005; Heard & Pickering, 2008; Zonneveld, Gingras, & Beatty, 2010; Hammersburg, Hasiotis, & Robison, 2018). *Scolicia* is present in tidal flat, deltaic, lower shoreface, offshore, and deep-sea (flysch) environments (Fillion & Pickerill, 1990; Frey & Howard, 1990; MacEachern & Pemberton, 1992; Pemberton, Wagoner, & Wach, 1992; Uchman, 1998; Tchoumatchenco & Uchman, 2001; Uchman & others, 2004; Flaig & others, 2019). *Scolicia* has been reported from the Cambrian to Holocene, with most researchers interpreting the true *Scolicia* as starting in the Jurassic (Fu & Werner, 2000; Donovan, Renema, & Pickerill, 2005; Jensen, Droser, & Gehling 2006).

SCOLICIA PLANA Książkiewicz, 1970

Figure 10.6, 12.5

Diagnosis.—Epichnial trilobate furrow with low, flat median trail ("lobe" of Książkiewicz, 1970, p. 289), densely striated and bordered by lateral, less densely ribbed fringes; median lobe bordered in some specimens by narrow rims and longitudinally transected by a very narrow furrow (after Książkiewicz, 1970).

Description.—Trails are either winding or straight in convex epirelief. The trails are nearly flat and covered with riblike structures perpendicular to trail that are sometimes transected by a narrow medial furrow. Specimens range from 15 to 20 mm wide and 40 to 180 mm long.

Occurrence.—Float block of white (10R 8/1), fine to very fine-grained, ripple-laminated sandstone, with BPBI 2. Specimens are present in the upper part of the Plainview Formation at Colorado State Highway 115.

Associated ichnotaxa.—Planolites montanus and *Protovirgularia pennatus.*

Discussion.—Specimens are assigned to *Scolicia plana* based on their densely ribbed, nearly flat trail, straight ribs, and narrow medial furrow (Książkiewicz, 1970; Uchman, 2004). The tracemaker for *Scolicia plana* was an irregular echinoid (Smith & Crimes, 1983; Hammersburg, Hasiotis, & Robison, 2018). These traces co-occur on the surface of wave-ripple sets with *Planolites montanus* and *Protovirgularia pennatus*. Some *Scolicia plana* crosscut specimens of *Scolicia plana,* whereas *Protovirgularia pennatus* is truncated by *Scolicia plana*. Where *Protovirgularia pennatus* is terminated by *Scolicia plana*, predation of the *Protovirgularia* tracemaker can be inferred, although this is unlikely based on the diet of modern irregular echinoids. These traces in the float block are likely from the middle part of the Plainview Formation at Colorado State Highway 115, based on comparison to the stratigraphic section. These traces in the Plainview Formation were constructed in an intertidal to subtidal environment, based on lithology and succession of bedforms (Weimer, 1970; Gustason & Kauffman, 1985).

SCOLICIA isp.
Figure 12.6

Description.—Trails are in concave epirelief with a flat, narrow floor, exhibiting a faint bilobate structure. The floor of the trail is smooth with a medial ridge. Traces are 10 mm wide and 60–180 mm long, with the ridge ~2 mm wide.

Occurrence.—White (10R 8/1), very fine-grained, ripple-laminated sandstone, with BPBI 2. Traces are present in the upper part of the Muddy Formation at Dinosaur Ridge.

Associated ichnotaxa.—Archaeonassa fossulata.

Discussion.—Traces are placed in *Scolicia* based on the bilobate structure of the floor of the trail (Hammersburg, Hasiotis, & Robison, 2018). The tracemakers for *Scolicia* isp. were irregular echinoids (Smith & Crimes, 1983; Hammersburg, Hasiotis, & Robison, 2018). Traces lacked any diagnostic characteristics for proper placement within an ichnospecies. *Scolicia* are present on top of wave-ripple sets co-occurring with *Archaeonassa fossulata*. These traces overlie fine-grained sandstone beds bearing the tetrapod tracks *Caririchnium leonardii, Hatcherichnus* isp., and *Magnoavipes caneeri*. *Scolicia* isp. were constructed in an intertidal environment based on lithology and succession of bedforms (MacKenzie, 1975; Chamberlain, 1985).

Ichnogenus SKOLITHOS Haldeman, 1840

Fucoides Haldeman, 1840, p. 3.

Scolithus Hall, 1847, p. 2.

Skolithos Alpert, 1974, p. 661.

Skolithos Fillion & Pickerill, 1990, p. 59–60, pl. 16, fig. 3–6.

Skolithos Schlirf, 2000, p. 151, pl. 1, fig. 2, 3.

Type Ichnospecies.—Fucoides (*Skolithos) linearis* Haldeman, 1840.

Diagnosis.—Single, unbranched, vertical or steeply inclined, cylindrical or subcylindrical, lined or unlined burrows. Walls distinct or indistinct, smooth to rough, possibly annulate; fill massive; burrow diameter may vary along its length (after Alpert 1974; Fillion & Pickerill, 1990).

Discussion.—Alpert (1974) examined *Skolithos* in order to simplify its numerous ichnospecies. From 35 named ichnospecies, Alpert (1974) validated five: *Skolithos linearis* Haldeman, 1840, *Skolithos verticalis* Hall, 1843, *Skolithos magnus* Howell 1944, *Skolithos ingens* Howell, 1945, and *Skolithos annulatus* Howell, 1957. *Skolithos annulatus* and *Skolithos ingens* are characterized by surficial morphology of ringlike undulations and slight bulges at irregular intervals along the burrow wall, respectively. *Skolithos linearis*, *Skolithos magnus,* and *Skolithos verticalis* are characterized by the diameter of the burrow and distinctness of the wall structure (*Skolithos verticalis* = 1–4 mm, smooth; *Skolithos linearis* = 3–7 mm, distinct to indistinct, may be annulated; *Skolithos magnus* = 7–12 mm, indistinct, somewhat irregular) (e.g., Alpert, 1974; Fillion & Pickerill, 1990; Frey & Howard, 1990). Schlirf (2000) suggested there is no significant difference between *Skolithos linearis* and *Skolithos verticalis*, and that *Skolithos verticalis* should be synonymized within *Skolithos linearis*. This suggestion has been ignored with authors citing *Skolithos linearis* as larger and more vertical, whereas *Skolithos verticalis* is smaller and with a stronger curve (Knaust & Hauschke, 2005; Carmona & others, 2008; Joseph, Patel, & Bhatt, 2012; Mude & others, 2012). This has created confusion due to authors placing specimens into the incorrect ichnospecies or ignoring diameter size and relying on other diagnostic criteria to separate the ichnospecies (e.g., Tiwari & others, 2011; Joseph, Patel, & Bhatt, 2012; Mude, 2012; Chrząstek, 2013; Darngawn & others, 2018). Several researchers have placed J-shaped and strongly inclined vertical burrows within *Arenicolites,* based on the strong curving nature of the burrows and how the base of some burrows begins to curve in an upward direction (Maples & Suttner, 1990; Knaust & Bromley, 2012; Netto, & others, 2014; Gingras & others, 2016). We follow the synonymy of *Skolithos verticalis* within *Skolithos linearis* as suggested by Schlirf (2000).

Skolithos is interpreted to be a dwelling of suspension-feeding annelids, phoronids, and/or crustaceans in marine settings and insect adults, larvae, and nymphs and other arthropods (e.g., spiders) in continental settings (Alpert, 1974; Schlirf & others, 2001; Davies, Sansom, & Albanesi, 2007; Tiwari & others, 2011; Mude & others, 2012; Chrząstek, 2013; Fischer & Hasiotis, 2018). *Skolithos* are reported from fluvial, playa lake, bay, deltaic, upper and lower offshore, and deep marine environments (Fillion & Pickerill, 1990; MacEachern & Pemberton, 1992; Schlirf & others, 2001; Melchor, Bellosi, & Genise, 2003; Uchman & others, 2004; Hasiotis & others, 2012; Mude & others, 2012; van der Kolk, Flaig, & Hasiotis, 2015; Flaig & others, 2019; Paz & others, 2020). *Skolithos* ranges from the Ediacaran to Holocene (Jensen, Droser, & Gehling, 2006; Virtasalo & others, 2011).

SKOLITHOS LINEARIS Haldeman, 1840
Figure 4.6, 5.2, 13.1, 13.2, 13.3, 13.4

Diagnosis.—Vertical to slightly inclined, cylindrical to subcylindrical, straight to slightly curved, unbranched burrow, with or without lining, with homogeneous fill (after Schlirf, 2000; Knaust, Thomas, & Curran, 2018).

Description.—Specimens are present in full relief, with smooth walls. Most of the traces are straight with only the larger specimens being slightly bowed. Specimens range from 3 to 5 mm wide and 8 to 120 mm deep.

Occurrence.—(1) Reddish yellow (7.5YR 6/8), fine- to very fine-grained sandstone, subrounded and moderately well-sorted

TO HERE ON TUES

sandstone, highly bioturbated (ii4); (2) black (7.5YR 2.5/1) to very dark gray (7.5YR 3/1), shale interbedded with white (10R 8/1) very fine-grained clayey sandstone moderately to highly bioturbated (ii3–4); (3) reddish yellow (7.5YR 7/8), fine- to very-fine grained sandstone; (4) black (7.5YR 2.5/1) to very dark gray (7.5YR 3/1), shale interbedded with reddish yellow (7.5YR 6/8) to red (10R 4/8) very fine-grained sandstone to siltstone, with weak to moderate bioturbation (ii2–3); (5) reddish yellow (7.5YR 6/8), fine- to very fine-grained sandstone, weakly bioturbated (ii2), interbedded with conglomerate; (6) black (7.5YR 2.5/1) shale interbedded with reddish yellow (7.5YR 6/8), very fine-grained sandstone weakly bioturbated (ii2); and (7) reddish yellow (7.5YR 6/8), very fine-grained, well-sorted and rounded planar bedded sandstone, weakly bioturbated (ii2). Specimens are present in the lower part of the Plainview Formation at Skyline Drive, upper parts of the Plainview Formation at U.S. Route 285, Horsetooth Reservoir and Skyline Drive, the middle parts of the Glencairn Formation at Skyline Drive, the middle and upper parts at Skull Creek Shale at I-70, lower part of the Skull Creek Shale at Dinosaur Ridge, the lower and middle parts of the Skull Creek Shale at U.S. Route 285, the upper part of the Skull Creek Shale at Horsetooth Reservoir, the middle part of the Muddy Formation at Skyline Drive, and upper part of the Muddy Formation at Dinosaur Ridge.

Associated ichnotaxa.—Arenicolites carbonaria, Arenicolites variabilis, Arenicolites isp*., Asterosoma* isp*., Cylindrichnus concentricus, Palaeophycus tubularis, Rosselia socialis, Schaubcylindrichnus freyi, Teichichnus rectus, Teredolites clavatus,* and *Zoophycos isp*.

Discussion.—Specimens are assigned to *Skolithos linearis* based on their predominantly vertical nature and smooth burrow surface (Schlirf, 2000; Knaust, Thomas, & Curran, 2018). The tracemakers for the smaller *Skolithos linearis* specimens were most likely infaunal worms, whereas the tracemakers for the larger specimens were infaunal worms or crustaceans (Chrząstek, 2013). *Skolithos linearis* in the Plainview Formation at U.S. Route 285 do not occur with any other trace fossils and were constructed in an intertidal environment, based on lithology and bedforms (Weimer & Land, 1972). In the Plainview Formation at Skyline Drive, *Skolithos linearis* is present near the upper and lower contacts of the formation, with those at the lower contact in beds overlying *Teredolites clavatus*. *Skolithos linearis* in the upper part of Plainview Formation co-occur with *Cylindrichnus concentricus, Rosselia socialis,* and *Teichichnus rectus*. Traces in the lower part of the Plainview Formation were constructed in an intertidal environment, whereas those in the upper part were constructed in a subtidal environment, based on lithology and succession of bedforms present in each interval (Gustason & Kauffman, 1985). In the Glencairn Formation at Skyline Drive, *Skolithos linearis* forms a monospecific occurrence, with the traces being produced in a deltaic environment based on lithology and succession of bedforms (Gustason & Kauffman, 1985). In the Skull Creek Shale at Horsetooth Reservoir, *Skolithos linearis* are larger than those at other localities, and co-occur with *Asterosoma* isp., *Palaeophycus tubularis, Schaubcylindrichnus freyi,* and *Teichichnus rectus*. These traces were produced in a lower shoreface environment, based on lithology and succession of bedforms (Graham & Ethridge, 1995). In the Skull Creek Shale at I-70, *Skolithos linearis* co-occurs with *Arenicolites variabilis, Palaeophycus tubularis,* and *Teichichnus rectus*. These traces were constructed in a marine embayment, based on lithology and succession of bedforms (Weimer & Land, 1970). In the Muddy Formation at Skyline Drive, *Skolithos linearis* is overlain by *Arenicolites carbonaria,* with the traces constructed in an intertidal to subtidal environment based on lithology and succession of bedforms (Gustason & Kauffman, 1985). In the Muddy Formation at Dinosaur Ridge, *Skolithos linearis* co-occurs with *Teichichnus rectus* in a mudstone overlain by a sandstone bearing *Rhizocorallium commune* and *Archaeonassa fossulata*. *Skolithos linearis* in the Muddy Formation were constructed in an intertidal environment based on lithology and succession of bedforms (MacKenzie, 1975; Chamberlain, 1985).

Ichnogenus TAENIDIUM Heer, 1877

Muensteria von Strenberg, 1833, p. 31, pl. 6, fig. 4, pl. 7, fig. 3.

Taenidium Heer, 1877, p. 117, pl. 45, fig. 9, 10b, pl. 50, fig. 1, 2.

Taenidium D'Alessandro & Bromley, 1987, p. 750, fig. 2, 3, 6a–c, 7, 8a–d, 9.

Taenidium Hammersburg, Hasiotis, & Robison, 2018, p. 38, fig. 19.3, 19.4.

Type Ichnospecies.—Taenidium serpentinum Heer, 1877.

Diagnosis.—Unlined, unbranched, straight to sinuous, cylindrical burrows with evenly spaced, uniformly thick meniscate backfill (after D'Alessandro & Bromley, 1987; Hammersburg, Hasiotis, & Robison, 2018).

Discussion.—Prior to being reevaluated, the ichnogenus *Muensteria* von Sternberg, 1833 referred to unbranched meniscate burrows, whereas *Taenidium* referred to branched meniscate burrows (D'Alessandro & Bromley, 1987; Hammersburg, Hasiotis, & Robison, 2018). D'Alessandro and Bromley (1987) reexamined *Muensteria* and *Taenidium,* and determined that *Muensteria* was invalid as it was poorly defined. Instead, they assigned unbranched meniscate burrows to *Taenidium* because its type material matched the description of *Muensteria*. They erected *Cladichnus* to accommodate branching or radiating meniscate burrows.

In a review of backfilled burrows, Keighley and Pickerill (1994) defined a wall as a feature actively constructed by an organism to protect itself from the external environment, whereas a lining is a type of wall structure produced by active or passive attachment of fine-grained material. They argued that backfill burrows do not have true walls or linings because they are simple excavations and not a form of active construction. Keighley and Pickerill (1994), based on their definition, placed *Beaconites barretti* Bradshaw, 1981, in *Taenidium* based on the ends of its menisci not forming a true wall or lining. Some researchers have followed this interpretation of a wall and synonymy by Keighley and Pickerill (1994) (Schlirf, & others, 2001; Keighley & Pickerill, 2003; Buatois & Mángano, 2007), whereas others do not agree with their definitions and interpretations, which has resulted in unnecessary lumping of morphologically distinct ichnotaxa (Morrissey & Braddy, 2004; Smith & Hasiotis, 2008; Smith & others, 2008; Counts & Hasiotis, 2009; Fischer & Hasiotis, 2018; Hammersburg, Hasiotis, & Robison, 2018). These other researchers argued that Keighley and Pickerill (1994) interchanged and integrated the terms of wall and lining, muddling the definitions and usage (for discussion see Hammersburg, Hasiotis, & Robison, 2018). For example, the overlapping of menisci in *Beaconites barretti* form a crenulated but unlined burrow wall, based on the boundary of the menisci (Smith & others, 2008; Counts & Hasiotis, 2009; Hammersburg, Hasiotis, & Robison, 2018). As a result of lumping all meniscate backfilled burrows into *Taenidium,* this ichnotaxon has been reported in both continental and marine settings. Current studies, however, place *Taenidium* only in marine settings, with the continental traces belonging to *Ancorichnus, Beaconites*, and *Naktodemasis* (Smith & others, 2008; Counts & Hasiotis, 2009; Morshedian, MacEachern, & Dashtgard, 2012; Chakraborty & others, 2013; Gingras & others, 2016; Harris & others, 2016; Fischer & Hasiotis, 2018; Golab, Smith, & Hasiotis, 2018; Hammersburg, Hasiotis & Robison, 2018; Raisanen & Hasiotis, 2018; Wiest & others, 2018).

Taenidium is interpreted to be a deposit-feeding trace of polychaetes (Książkiewicz, 1977; Stachacz, 2012; Fürsich & others, 2018). *Taenidium* is reported in shallow- to deep-marine environments (MacEachern & Pemberton, 1992; Uchman, 1998; Tiwari & others, 2011; Jackson, Hasiotis, & Flaig, 2016; Pearson & Gooday, 2019). *Taenidium* ranges from the Ediacaran to Holocene (Uchman, 1998; Jensen, Droser, & Gehling, 2006; Tiwari & others, 2011; Jackson, Hasiotis, & Flaig, 2016).

TAENIDIUM SERPENTINUM Heer, 1877

Figure 13.5, 13.6

Diagnosis.—Serpentiform, unlined, unbranched burrows with evenly spaced, uniformly thick, weakly arcuate menisci; distance between menisci about equal or a little less than burrow width. External molds may have slight annulation corresponding to menisci or fine transverse wrinkling. Secondary subsequent branching and intersections may occur. Boundary is sharp and lacks lining (after D'Alessandro & Bromley, 1987).

Description.—Burrows are straight to curving with no lining; present in convex epirelief and hyporelief. Menisci are evenly spaced and uniformly thick with some specimens exhibiting faint menisci due to weathering. Specimens are ~7 mm wide and 40–60 mm long.

Occurrence.—(1) White (10R 8/1), very fine-grained sandstone with BPBI 3; (2) black (7.5YR 2.5/1), very fine-grained sandstone to siltstone, with BPBI 2; and (3) reddish yellow (7.5YR 6/8), very fine- to fine-grained, subrounded, and well-sorted sandstone with planar bedding and BPBI 4. Specimens are present in the middle parts of the Plainview Formation at Horsetooth Reservoir, the middle part of the Glencairn Formation at Skyline Drive, and the upper part of the Muddy Formation at Dinosaur Ridge.

Associated ichnotaxa.—*Cruziana* isp., *Chondrites intricatus, Gyrolithes lorcaensis, Lockeia siliquaria, Planolites montanus, Rhizocorallium jenense, Rusophycus* isp., and *Thalassinoides suevicus*.

Discussion.—Specimens are assigned to *Taenidium serpentinum* based on the lack of a lining, spacing and uniform thickness of menisci, and the weakly arcuate backfill (D'Alessandro & Bromley, 1987). The tracemakers for *Taenidium serpentinum* were infaunal worms (Fürsich & others, 2018). In the Plainview Formation at Horsetooth Reservoir, *Taenidium serpentinum* co-occurs with *Chondrites intricatus* and *Planolites montanus*. These traces are present in float blocks that likely originated from the middle part the Plainview Formation, based on comparison to the stratigraphic section. *Rhizocorallium jenense* is present in a nearby float block with a similar lithology as *Taenidium serpentinum,* suggesting that it, too, came from the same stratigraphic context. These traces were constructed in an intertidal to subtidal environment, based on lithology and succession of bedforms (Wescott, 1979). At Skyline Drive, *Taenidium serpentinum* is present in the second sandstone bed in the Glencairn Formation, where it co-occurs with *Cruziana* isp., *Gyrolithes lorcaensis, Lockeia siliquaria, Planolites montanus, Rusophycus* isp., and *Thalassinoides suevicus*. These trace fossils were deposited in a deltaic environment based on lithology and succession of bedforms (Gustason & Kauffman, 1985). *Taenidium serpentinum* in the Muddy Formation at Dinosaur Ridge are present near the upper contact with the Mowry Shale and co-occur with *Rhizocorallium jenense* and *Thalassinoides suevicus*. The beds with *Taenidium serpentinum* are overlain by a thin mudstone with *Skolithos linearis* and *Teichichnus rectus*. Beds that underlie those with *Taenidium serpentinum* contain wave-ripple lamination with syneresis cracks. *Taenidium serpentinum* were constructed in an intertidal environment, based on lithology and succession of bedforms (MacKenzie, 1975; Chamberlain, 1985).

Ichnogenus TEICHICHNUS Seilacher, 1955

Teichichnus Seilacher, 1955, p. 378, pl. 24, fig. 1.
Teichichnus Häntzschel, 1975, p. 114, fig. 71.
Teichichnus Frey & Howard, 1985, p. 392, fig. 19.6, 21–23.
Teichichnus Orłowski, 1989, p. 222, pl. 17, fig. 1–4.
Teichichnus Buckman, 1992, p. 234.
Teichichnus Schlirf & Bromley, 2007, p. 135, fig. 4–7, 8a–e.
Teichichnus Knaust, 2018, p. 387, fig. 2, 3, 7–11.

Type Ichnospecies.—*Teichichnus rectus* Seilacher, 1955.

Emended Diagnosis.—Vertical to oblique, singular to interpenetrated, elongated to arcuate spreite burrows with individual spreiten stacked concavely upward (retrusive) or convexly downward (protrusive), with or without passively filled terminal causative burrow preserved, oriented at various angles with respect to bedding (modified after Frey & Howard, 1985; Knaust, 2018).

Discussion.—*Teichichnus* was named for vertically stacked, horizontal burrows with gutter-shaped spreite (Seilacher, 1955; Fillion & Pickerill, 1990). Convex-down laminae are interpreted as protrusive spreite, whereas convex-up laminae are interpreted as retrusive spreite. Schlirf and Bromley (2007) established *Teichichnus duplex* to account for side-by-side gutter-shaped spreite with surficial morphology. This ichnotaxonomic assignment, however, is questionable as *Teichichnus duplex* is similar in architecture and surficial morphology to *Arthrophycus parallelus,* which is described as having well-developed paired, transverse ridges, and medial groove developed locally with surficial morphology (Brandt & others, 2010, 2012). Both traces develop within a single plane, with specimens seeming to overlap with each other (Schlirf & Bromley, 2007; Brandt & others, 2010, 2012). When examined in full relief, *Teichichnus duplex* lacks visible side-by-side, gutter-shaped spreite (Schlirf & Bromley, 2007, fig. 4), with these spreite only visible in plan-view. Additionally, the majority of the *Teichichnus duplex* specimens are from the Cambrian, which falls within the range of *Arthrophycus*. *Teichichnus duplex* is a trace that was likely constructed by the behavior of the tracemaker of both *Arthrophycus*

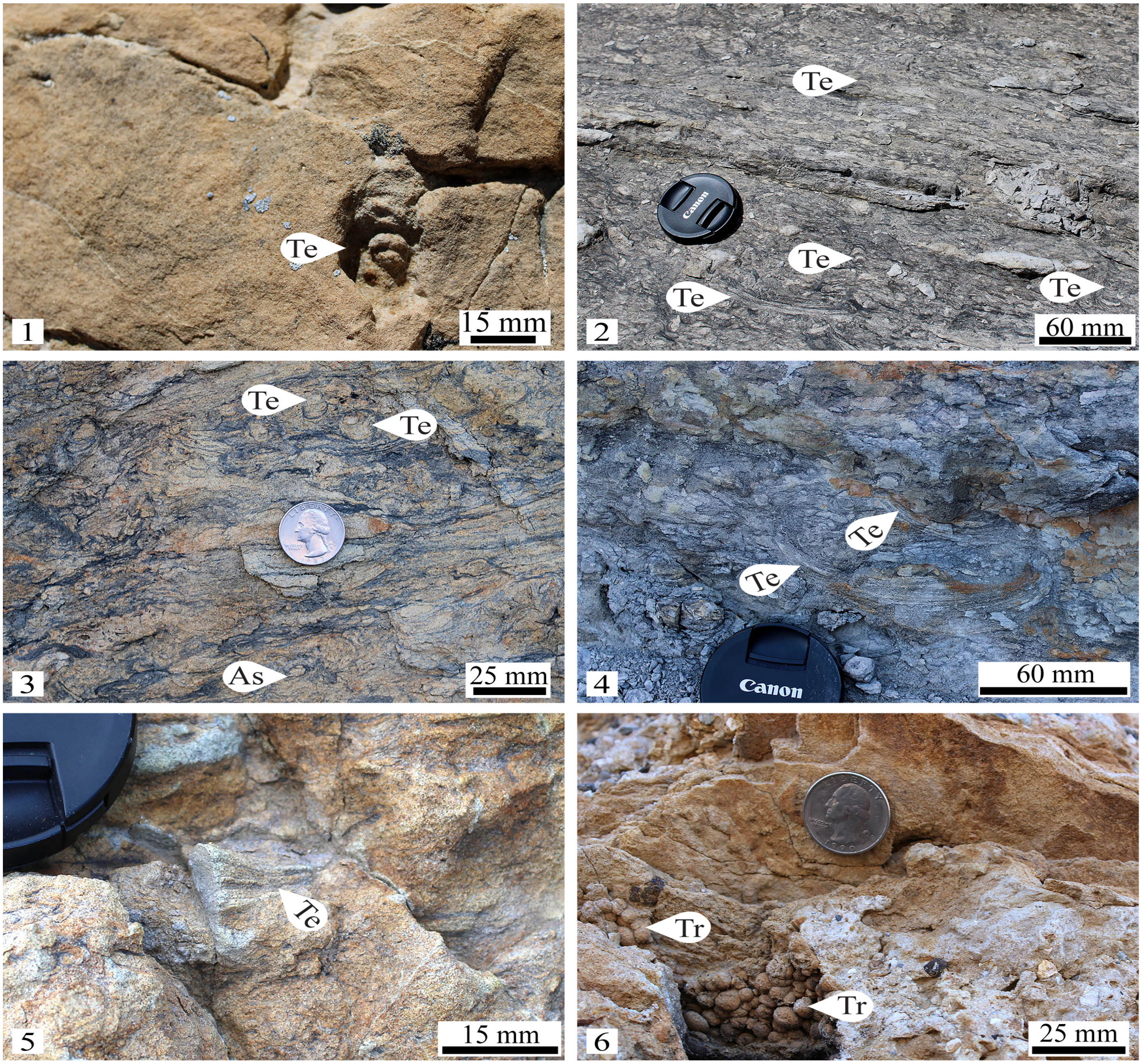


Figure 14. *Asterosoma* (As), *Teichichnus* (Te), and *Teredolites* (Tr) from the Dakota Group. *1, Teichichnus rectus* in vertical section with protrusive laminae in the upper part of the Plainview Formation at Skyline Drive. *2, Teichichnus rectus* in vertical section within the middle part of the Skull Creek Shale at I-70. *3, Asterosoma* isp. and *Teichichnus rectus* in vertical section within the upper part of the Skull Creek Shale at Horsetooth Reservoir. *4, Teichichnus rectus* in vertical section within the lower part of the Skull Creek Shale at Dinosaur Ridge. *5, Teichichnus rectus* in full relief within the upper part of the Skull Creek Shale at Horsetooth Reservoir. *6, Teredolites clavatus* in convex hyporelief within the lower part of the Plainview Formation at Skyline Drive.

parallelus and *Teichichnus rectus,* which accounts for the paired transverse ridges with a medial groove, surficial morphology of variably oriented scratches, and vertical stacking of spreite. We recommend that *Teichichnus duplex* be regarded as a synonym of *Arthrophycus parallelus*. Thus, we emend the emended diagnosis of Knaust (2018) to remove the double gutter-cast spreite and presence of surficial morphology in *Teichichnus*.

Whereas *Teichichnus* is considered to be a stand-alone ichnogenus, several researchers have reported *Teichichnus* behavior integrated into specimens of *Cruziana, Ophiomorpha, Phycodes, Rhizocorallium,* and *Thalassinoides* to form compound burrow morphologies (Bromley & Frey, 1974; Fillion & Pickerill, 1990; Knaust, 2013). *Teichichnus* bears some morphological similarities to *Trichophycus* Miller & Dyer, 1878, due to both having gutter-shaped spreite. *Teichichnus,* however, is differentiated from *Trichophycus* by its more planar spreite and lack of fine scratches on the exterior of the burrow (Osgood, 1970; Frey & Howard, 1985; Fillion & Pickerill, 1990; Geyer & Uchman, 1995). Knaust

(2018) reevaluated *Teichichnus,* resulting in the validation of only four of ichnospecies: *Teichichnus rectus*; *Teichichnus zigzag* Frey & Bromley, 1985; *Teichichnus patens* Schlirf, 2000; and *Teichichnus duplex*, Schlirf & Bromley, 2007. *Teichichnus rectus* is characterized by a single vertical burrow with protrusive or retrusive gutter-cast spreite. *Teichichnus zigzag* is characterized by a single vertical burrow with zigzag gutter-cast spreite. *Teichichnus patens* is characterized by being branched.

Teichichnus is interpreted to be a deposit-feeding or dwelling trace with the tracemaker being either polychaetes or arthropods (Dam, 1990; MacEachern & Pemberton, 1994; Uchman & others, 2004; Davies, Sansom, & Albanesi, 2007; Knaust, 2018). *Teichichnus* is found in shallow-marine (lagoon, estuarine, deltaic, lower shoreface, and offshore) and deep-marine (submarine fan and abyssal plain) environments (Fürsich, 1975; Fillion & Pickerill, 1990; Maples & Suttner, 1990: Pemberton & Wightman, 1992; Gingras, MacEachern, & Pemberton, 1998; Schlirf, 2000; Gingras & others, 2011; Tiwari & others, 2011; Jackson, Hasiotis, & Flaig, 2016). *Teichichnus* ranges from the early Cambrian to Holocene (Narbonne & others, 1987; Uchman & others, 2004; Hasiotis, 2012; Stachacz, 2012).

TEICHICHNUS RECTUS Seilacher, 1955

Figure 4.6, 14.1, 14.2, 14.3, 14.4, 14.5

Diagnosis.—Straight to unbranched, variably inclined, stacked concave and/or convex spreite, with or without passively filled terminal causative burrow preserved. Morphology varies between and within individual burrows; burrows L- or U-shaped in vertical section parallel to burrow axis (after Knaust, 2018).

Description.—Specimens are present in full relief and convex epirelief. Both protrusive (convex) and retrusive (concave) forms of the spreite are present, with the retrusive forms being the most common, and protrusive forms being larger. Specimens range from 5 to 12 mm wide, 5 to 60 mm tall and 25 to 70 mm long.

Occurrence.—(1) Black (7.5YR 2.5/1) to very dark gray (7.5YR 3/1), shale interbedded with a white (10R 8/1), very fine-grained clayey sandstone of moderate bioturbation (ii3); (2) black (7.5YR 2.5/1) shale interbedded with reddish yellow (7.5YR 7/8) very fine-grained sandstone of moderate bioturbation (ii3); (3) reddish yellow (7.5YR 6/8), fine-grained, subrounded and moderately well-sorted sandstone, with weak to strong bioturbation (ii2–4); and (4) very dark gray (7.5YR 3/1), shale interbedded with strong brown (7.5YR 5/8) to red (10Y 4/8), very fine-grained sandstone to siltstone, beds being moderately to strongly bioturbated (ii3–4). Specimens are present in the middle part of the Plainview Formation at Grape Creek, in the upper part of the Plainview Formation at Skyline Drive, in the lower and middle parts of the Glencairn Formation at Grape Creek, in the middle and upper parts of the Skull Creek Shale at I-70, in the middle part of the Skull Creek Shale at Dinosaur Ridge, in the middle part of the Skull Creek Shale at U.S. Route 285, in the upper part of the Skull Creek Shale at Horsetooth Reservoir, and in the upper part of the Muddy Formation at Dinosaur Ridge.

Associated ichnotaxa.—*Arenicolites* isp., *Arenicolites variabilis, Asterosoma* isp., *Cylindrichnus concentricus, Diplocraterion habichi, Macaronichnus segregatis, Palaeophycus tubularis, Rhizocorallium commune, Rosselia socialis, Schaubcylindrichnus freyi, Skolithos linearis, Thalassinoides suevicus,* and *Zoophycos* isp.

Discussion.—Specimens are assigned to *Teichichnus rectus* based on their vertically stacked concave and convex spreite (MacEachern & Pemberton, 1994; Knaust, 2018). The tracemaker for *Teichichnus rectus* were infaunal worms or arthropods (MacEachern & Pemberton, 1994; Knaust, 2018). The abundance of *Teichichnus rectus* in the Skull Creek Shale is moderate to high, whereas in other formations its abundance ranges from being rare (Plainview Formation and Muddy Formation) to moderate (Glencairn Formation). In the Plainview Formation at Skyline Drive, *Teichichnus rectus* is present as protrusive forms (Fig. 14.1) and co-occurs with *Cylindrichnus concentricus, Rosselia socialis,* and *Skolithos linearis*. In the Plainview Formation at Grape Creek, *Teichichnus rectus* is monospecific. *Teichichnus rectus* in the Plainview Formation at Grape Creek were constructed in an intertidal environment, whereas those at Skyline Drive were constructed in a subtidal environment, based on lithology and succession of bedforms (Gustason & Kaufmann, 1985). *Teichichnus rectus* in the Glencairn Formation at Grape Creek form a monospecific assemblage and were constructed in a deltaic environment, based on lithology and succession of bedforms (Gustason & Kaufmann, 1985). In the Skull Creek Shale at Horsetooth Reservoir, *Teichichnus rectus* co-occurs with *Asterosoma* isp., *Palaeophycus tubularis, Rhizocorallium commune, Schaubcylindrichnus freyi,* and *Skolithos linearis* and was constructed in a lower shoreface environment, based on lithology and succession of bedforms (Graham & Ethridge, 1995). *Teichichnus rectus* in the Skull Creek Shale at I-70, co-occurs with *Arenicolites variabilis, Diplocraterion habichi, Palaeophycus tubularis,* and *Skolithos linearis*. At Dinosaur Ridge in the Skull Creek Shale, *Teichichnus rectus* co-occurs with *Arenicolites* isp., *Macaronichnus segregatis, Rhizocorallium commune, Skolithos linearis,* and *Zoophycos* isp., whereas at U.S. Route 285, *Teichichnus rectus* co-occurs with *Palaeophycus tubularis* and *Skolithos linearis*. *Teichichnus rectus* in the Skull Creek Shale at I-70, Dinosaur Ridge, and U.S. Route 285 were constructed in a marine embayment, based on lithology and succession of bedforms (Weimer & Land, 1972). In the Muddy Formation at Dinosaur Ridge, *Teichichnus rectus* co-occurs with *Skolithos linearis* in a thin mudstone interval that is overlain by *Rhizocorallium commune* and *Archaeonassa fossulata* and underlain by *Rhizocorallium jenense, Taenidium serpentinum,* and *Thalassinoides suevicus*. *Teichichnus rectus* in the Muddy Formation at Dinosaur Ridge were constructed in an intertidal environment, based on lithology and succession of bedforms (MacKenzie, 1975; Chamberlain, 1985).

Ichnogenus TEREDOLITES Leymerie, 1842

Teredolites Leymerie, 1842, p. 2, pl. 2, fig. 4, 5.

Martesites Vitalis, 1961, p. 124, pl. 1, 2.

Teredolites Kelly & Bromley, 1984, p. 803, fig. 9a–b, 10, 11a–b.

Type Ichnospecies.—*Teredolites clavatus* Leymerie, 1842.

Diagnosis.—Flask-shaped borings in woody media, acutely turbinate, evenly tapered from the aperture to base of main chamber; neck region connected to the main chamber; cross sections at all levels more or less circular; elongate to short (after Kelly & Bromley, 1984).

Discussion.—Kelly and Bromley (1984) reexamined flask-shaped borings and placed those in woody media in *Teredolites,* whereas they placed those in hardground media in *Gastrochaenolites*. One of the characteristics noted by Kelly and Bromley (1984) for flask-shaped borings is the presence of a calcite lining. This lining is created around the siphonal region of the aperture and neck and is thought to provide attachment sites for the retractor muscles of the tracemaker. They noted, however, that the calcite lining should be treated as a part of the shell of the tracemaker as it is a mineral secretion of the bivalve. The presence or absence of the calcite lining can have zootaxonomic significance, as some species can secrete the lining and others cannot. Savrda and Smith (1996) interpreted that the lining reflected behavior, based on the position of the lining within boring, which led them to conclude that the presence of a lining should be included in the description of *Teredolites* but not as an ichnotaxonomic criterion. We follow the criteria developed by Kelly and Bromley (1984), as the assessment of Savrda and Smith (1996) is not widely discussed or accepted in the literature (Schlirf, 2000; Pickerill, Donovan, & Portell, 2003; Kříž & Mikuláš, 2006; Villegas-Martín & others, 2012).

Donovan's (2018) analysis of *Teredolites* resulted in the transfer of *Teredolites longissimus* to the monotypic genus *Apectoichnus*. He reasoned that the qualitative relationships in the systematic diagnosis negate the difference in morphology, and that media type is not a significant ichnotaxonomic character, which would separate *Teredolites clavatus* and *Teredolites longissimus* at the ichnogeneric level. We do not agree with this assessment of *Teredolites* and follow Buntin and Hasiotis (in press) in recognizing *Apectoichnus* as a junior synonym of *Teredolites* and recognize *Teredolites clavatus* and *Teredolites longissimus* as valid ichnopecies. Separation of *Teredolites longissimus* from *Teredolites* ignores several important ichnotaxonomic characters shared by both ichnospecies of *Teredolites,* including media character, shared and overlapping architectural and surficial morphology, and shared behavior early in the ontogenetic stages (Buntin, 2020).

Teredolites is interpreted to be a dwelling or possibly feeding trace of teredinid and pholadid bivalves (Kelly & Bromley, 1984; Savrda & Smith, 1996; Schlirf, 2000; Villegas-Martín & others, 2012). *Teredolites* is present in tidal, marsh, intertidal, bay, and fully marine environments (Savrda, 1991a; Gingras, MacEachern, & Pickerill, 2004; Kříž & Mikuláš, 2006; Paz & others, 2020). *Teredolites* ranges from the Lower Jurassic to Holocene (Gingras, MacEachern, & Pickerill, 2004; Villegas-Martin & others, 2012).

TEREDOLITES CLAVATUS Leymerie, 1842
Figure 13.4, 14.6

Diagnosis.—Flask-shaped boring predominantly perpendicular to the grain in woody media in full relief or as ovoid to hemispherical in convex epirelief and hyporelief, having length/width ratios typically <5 (after Kelly & Bromley, 1984).

Description.—Specimens are present in convex hyporelief and full relief. Specimens are typically clustered with no visible signs of overlap or branching. In hyporelief, specimens are flask to ovaloid in shape, whereas those in full relief are practically flask-shaped as the neck region is absent or reduced in these specimens. Specimens are 5–7 mm wide and 7 mm tall.

Occurrence.—(1) Reddish yellow (7.5YR 6/8), fine- to very fine-grained sandstone, interbedded with conglomerate beds, with weak bioturbation (ii2); and (2) reddish yellow (7.5YR 6/8), fine- to very fine-grained, subrounded, moderately well-sorted sandstone, with some minor ripple marks and flaser bedding, and intense bioturbation (ii4). Specimens are present in the lower and upper parts of the Plainview Formation at Skyline Drive.

Associated ichnotaxa.—*Asthenopodichnium xylobiontum, Lockeia* isp*., Margaritichnus mansfieldi, Skolithos linearis,* and *Thalassinoides suevicus*.

Discussion.—Specimens are assigned to *Teredolites clavatus* based on the flask shape of the specimens, their presence in woody media or carbon-rich layers, and the length/width ratio of the specimens being <5 (see Kelly & Bromley, 1984). The tracemaker for *Teredolites clavatus* was most likely a pholadid bivalve (Kelly & Bromley, 1984; Savrda & Smith, 1996). *Teredolites clavatus* do not reside in the same woody media as *Asthenopodichnium xylobiontum*. The good preservation of the *Asthenopodichnium xylobiontum*-bearing wood fragments suggests that they underwent rapid burial, preventing *Teredolites clavatus* tracemakers from boring into them. In the lower part of the Plainview Formation, *Teredolites clavatus* co-occur with *Skolithos linearis* and in the upper part, *Teredolites clavatus* co-occurs with *Asthenopodichnium xylobiontum, Lockeia* isp*., Margaritichnus mansfieldi,* and *Thalassinoides suevicus*. Traces in the lower part of the Plainview Formation were constructed in an intertidal environment, whereas those in the upper part were constructed in an intertidal to subtidal environment, based on lithology and succession of bedforms (Gustason & Kauffman, 1985).

Ichnogenus THALASSINOIDES Ehrenberg, 1944

Thalassinoides Ehrenberg, 1944, p. 358.

Spongeliomorpha Fürsich, 1973, p. 729.

Ophiomorpha Bromley & Frey, 1974, p. 329.

Thalassinoides Howard & Frey, 1984, p. 212, fig. 23, 24.

Thalassinoides Uchman, 1998, p. 128, fig. 28.

Spongeliomorpha Schlirf, 2000, p. 158, pl. 4, fig. 2–4, 6–9.

Thalassinoides Ekdale & Bromley, 2003, p. 224, fig. 2.

Type Ichnospecies.—*Thalassinoides callianassae* Ehrenberg, 1944.

Diagnosis.—Large, branched burrow systems consisting of smooth-walled, essentially cylindrical components; branch junctions Y to T shaped, typically wider at points of bifurcation; burrow dimensions variable within a given system (after Frey & Howard, 1985; Uchman, 1998; Ekdale & Bromley, 2003).

Discussion.—Several researchers have evaluated the ichnotaxonomic differences between *Thalassinoides* and *Ophiomorpha,* and have determined that both should remain separate ichnotaxa, with *Ophiomorpha* having a pelleted lining on its outer surface and *Thalassinoides* have a smooth exterior wall (see full discussion under *Ophiomorpha*). Currently, four valid ichnospecies of *Thalassinoides* are recognized: *Thalassinoides paradoxicus* Woodward, 1830; *Thalassinoides suevicus* Rieth, 1932; *Thalassinoides horizontalis* Myrow, 1995; and *Thalassinoides bacae* Ekdale & Bromley, 2003. *Thalassinoides paradoxicus* is characterized by its irregular branching and with branching occurring at T-shaped junctions (Kennedy, 1967; Frey & Bromley, 1985; Tiwari & others, 2011).

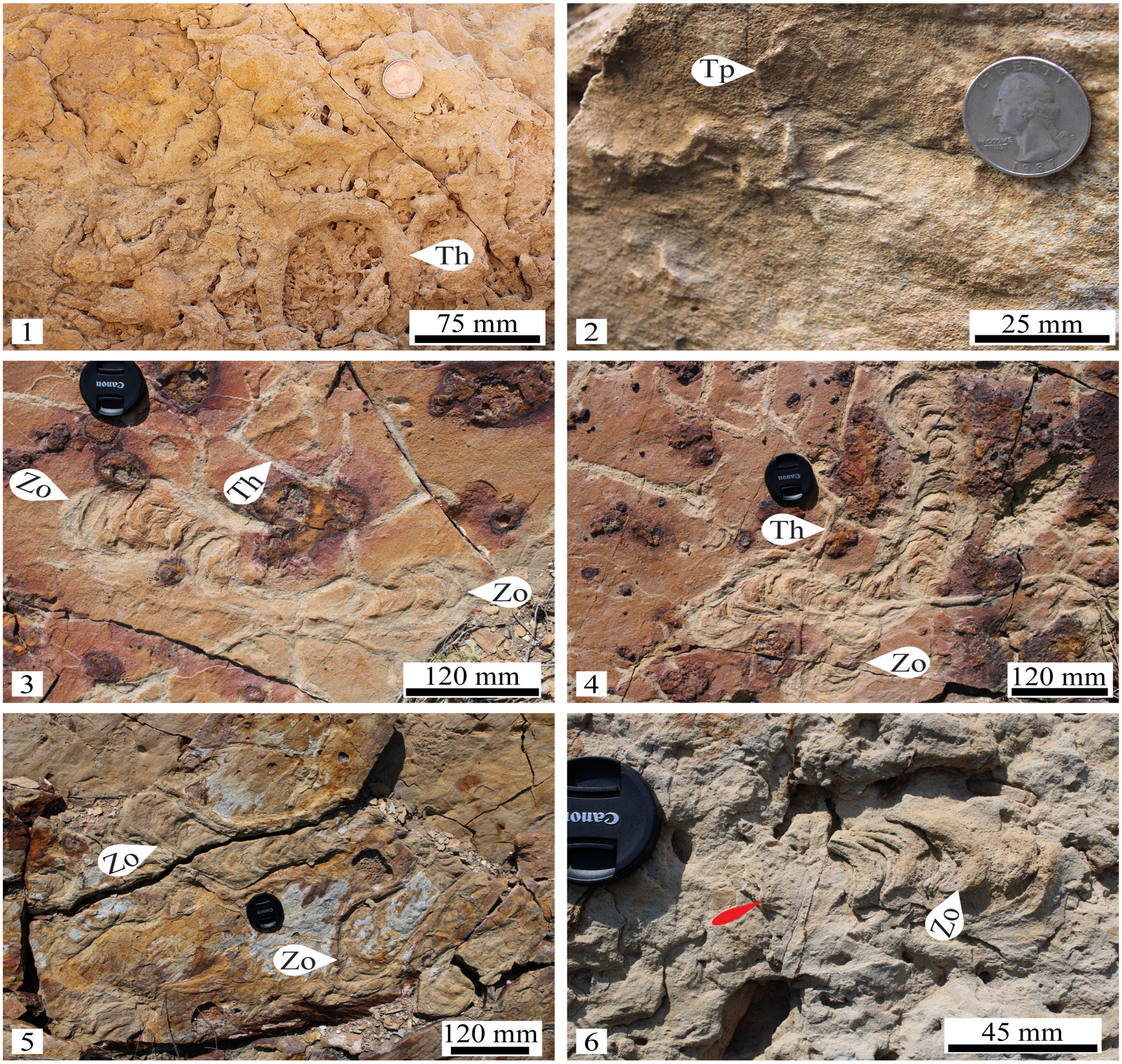


Figure 15. *Thalassinoides* (Th), *Treptichnus* (Tp), and *Zoophycos* (Zo) from the Dakota Group. *1, Thalassinoides suevicus* in convex hyporelief within the upper part of the Glencairn Formation at Skyline Drive. *2, Treptichnus bifurcus* convex hyporelief within the lower part of the Horsetooth Member of the Muddy Formation at Horsetooth Reservoir. *3, Thalassinoides suevicus* and *Zoophycos insignis* in concave epirelief within the upper part of the Glencairn Formation at Skyline Drive. *4, Thalassinoides suevicus* and *Zoophycos insignis* in concave epirelief within the upper part of the Glencairn Formation at Skyline Drive. *5, Zoophycos insignis* in full relief with two lobes attached to a central whorl, upper part of the Glencairn Formation at Skyline Drive. *6, Zoophycos insignis* with a whorl structure (red arrow) in full relief within the upper part of the Glencairn Formation at Skyline Drive.

Thalassinoides suevicus is characterized by its regular branching and with branching occurring at dichotomous or Y-shaped junctions (Frey & Howard, 1985; Uchman, 1998; Chrząstek, 2013). *Thalassinoides horizontalis* and *Thalassinoides bacae* are characterized by their dominantly horizontal orientation and small diameter. *Thalassinoides bacae* is characterized by having vertical shafts, which *Thalassinoides horizontalis* lacks (Myrow, 1995; Ekdale & Bromley, 2003; Tiwari & others, 2011). Some authors consider *Thalassinoides saxonicus* Geinitz, 1842 in 1839–1842 and *Thalassinoides ornatus* Kennedy, 1967 to be valid (e.g., Kim, Kim, & Pickerill, 2002). The mamillated or pelleted surface of *Thalassinoides saxonicus,* however, places it within *Ophiomorpha*, whereas the ridge structures on the surface of *Thalassinoides ornaus* places it within *Spongeliomorpha* (e.g., Fürsich, 1973; Schlirf, 2000).

Thalassinoides is interpreted to be a dwelling and/or feeding burrow of decapod crustaceans, worms, or trilobites (Frey & Howard, 1985; Myrow, 1995; Uchman, 1998; Cherns, Wheeley, & Karis, 2006; Chrząstek, 2013). *Thalassinoides* is reported in intertidal, lagoon, subtidal, marine bays, deltaic, and flysch environments (Pryor, 1975; Kamola, 1984; Miller & Byers, 1984; Frey & Howard, 1985, 1990; Myrow, 1995; Uchman, 1995; Gingras, MacEachern, & Pemberton, 1998; El-Sabbagh, El-Hedeny, & Al Farraj, 2017). *Thalassinoides* ranges from the Cambrian to Holocene (Zhu, 1997; Gingras, MacEachern, & Pickerill, 2004; Tiwari & others, 2011).

THALASSINOIDES HORIZONTALIS Myrow, 1995

Figure 5.5

Diagnosis.—Branching network of horizontal, smooth-walled, unlined burrows with a relatively small diameter; lack vertical burrow components; inner and outer burrow walls of consistent width, with no constrictions or widenings at junctions and interjunction segments (after Myrow, 1995).

Description.—The single specimen is in convex epirelief and consists of two horizontal burrow segments intersecting at a T-shaped junction. The walls of the burrow are smooth, with the junction lacking a notable widening. The burrow segments are 2 mm in diameter and ~20 mm long.

Occurrence.—White (10R 8/1), fine-grained, ripple-laminated sandstone interbedded with mudstone, with BPBI 2. Specimen is in the upper part of the Plainview Formation at Colorado State Highway 115.

Associated ichnotaxa.—Aulichnites parkerensis, Planolites montanus and *Treptichnus bifurcus*.

Discussion.—The specimen is assigned to *Thalassinoides horizontalis* based on its horizontal orientation, apparent lack of vertical branching, relative small diameter, and lack of widening at the junction (Myrow, 1995). The tracemakers were likely worms, other soft-bodied organisms, or crustaceans (Myrow, 1995; Uchman 1998). *Thalassinoides horizontalis* crosscuts a specimen of *Aulichnites parkerensis,* suggesting that it was constructed after *Aulichnites parkerensis* was buried beneath the seafloor. *Thalassinoides horizontalis* was constructed in an intertidal to subtidal environment based on lithology and succession of bedforms (Weimer, 1970; Gustason & Kauffman, 1985).

THALASSINOIDES SUEVICUS Rieth, 1932

Figure 6.1, 7.6, 11.5, 15.1, 15.3, 15.4, 16.1

Diagnosis.—Predominantly horizontal, more or less regularly branched, essentially cylindrical components forming large burrow systems; dichotomous bifurcations more common than T-shaped branches (after Howard & Frey, 1984).

Description.—Specimens are in convex and concave epirelief and convex hyporelief. Junctions are common, Y-shaped, and regularly spaced along the burrow. Burrows can either be present by themselves or as network systems. Those within a network that is closely spaced and interconnected in three-dimensional (3D) space form a boxwork, whereas those that are horizontal (i.e., in one plane) form a maze system. Specimens range from 3 to 28 mm in diameter and 50 to 360 mm long.

Occurrence.—(1) Gray (7.5YR 5/1), very fine-grained sandstone interbedded with a mudstone having a sulfurous smell in outcrop, with BPBI 2; (2) red (2.5YR 4/8), very fine-grained sandstone with BPBI 3; (3) reddish yellow (7.5YR 6/8), very fine-grained sandstone with BPBI 3; (4) very dark gray (7.5YR 3/1) shale interbedded with either a white (10R 8/41) siltstone to very fine-grained sandstone with moderate bioturbation (ii2–3); (5) white (10R 8/41), fine-grained ripple-laminated sandstone interbedded with a mudstone, with BPBI 2; (6) reddish yellow (7.5YR 6/8), fine- to very fine-grained sandstone, with some large clasts, in intensity bioturbated beds (ii4); (7) reddish yellow (7.5YR 7/8), very fine- to fine-grained sandstone, with BPBI 2; (8) white, very fine- to fine-grained sandstone, with BPBI 3–5; and (9) reddish yellow (7.5YR 6/8) to gray (7.5YR 5/1), very fine- to fine-grained sandstone with some chert clasts, with BPBI 4. Specimens are present in the upper parts of the Plainview Formation at Skyline Drive and Colorado State Highway 115, the middle and upper parts of the Glencairn Formation at Skyline Drive, the upper part of the Skull Creek Shale at I-70, the upper part of the Muddy Formation at Skyline Drive, the middle and upper parts of the Muddy Formation at Dinosaur Ridge, and the upper part of the Muddy Formation at U.S. Route 285.

Associated ichnotaxa.—Asthenopodichnium xylobiontum, Chondrites intricatus, Cruziana isp.*, Diplocraterion* isp.*, Gyrolithes lorcaensis, Lockeia siliquaria, Lockeia* isp.*, Margaritichnus mansfieldi, Palaeophycus tubularis, Planolites montanus, Rhizocorallium jenense, Rusophycus* isp.*, Taenidium serpentinum, Teichichnus rectus, Teredolites clavatus,* and *Zoophycos insignis.*

Discussion.—Specimens are assigned to *Thalassinoides suevicus* based on their horizontal orientation, smooth burrow surface, regular branching, and presence of Y-shaped junctions (see Frey & Howard, 1985). The tracemakers were likely decapod crustaceans (Uchman, 1998). Within the Plainview Formation at Colorado State Highway 115, *Thalassinoides suevicus* co-occur with *Lockeia siliquaria* and are overlain by beds with *Aulichnites parkerensis, Planolites montanus, Thalassinoides horizontalis,* and *Treptichnus bifurcus*. These traces were constructed in an intertidal to subtidal environment based on lithology and succession of bedforms (Weimer, 1970; Gustason & Kauffman, 1985). In the Plainview Formation at Skyline Drive, *Thalassinoides suevicus* co-occurs with *Asthenopodichnium xylobiontum, Lockeia* isp.*, Margaritichnus mansfieldi,* and *Teredolites clavatus*. These traces were constructed in an intertidal to subtidal environment, based on lithology and succession of bedforms (Gustason & Kauffman, 1985). In the middle part of the Glencairn Formation at Skyline Drive, *Thalassinoides suevicus* co-occurs with *Cruziana* isp.*, Gyrolithes lorcaensis, Planolites montanus, Rusophycus* isp., and *Taenidium serpentinum,* whereas in the upper part it occurs either by itself or with *Zoophycos insignis*. *Thalassinoides suevicus* in the upper part of the Glencairn Formation are present in a boxwork with both horizontal and vertical connections (Fig. 15.1) and as a maze system. In parts of the maze, specimens of *Zoophycos insignis* appear to be intergraded into the maze, creating a compound burrow system (Fig. 15.3). This suggests that the tracemaker created a maze system with dual purposes, with *Thalassinoides suevicus* representing the dwelling of the tracemaker and *Zoophycos insignis* representing its deposit feeding (see Miller III, 2001; Carvalho & others, 2010). In other parts of the maze system, however, *Zoophycos insignis* is constructed separately from *Thalassinoides suevicus*. These *Zoophycos insignis* crosscut the *Thalassinoides suevicus* maze system, suggesting they were constructed after *Thalassinoides suevicus* (Fig. 15.4). The number of *Zoophycos insignis* specimens that appear to be separate constructions is greater than those that appear to be apart of a compound burrow system, suggesting that *Thalassinoides suevicus* and *Zoophycos insignis* represent a composite burrow. The relationship between *Thalassinoides suevicus* and *Zoophycos insignis* requires further research to fully understand the nature of their relationship, which is outside the scope of this study. *Thalassinoides suevicus* in the Glencairn Formation were constructed in a prodelta environment based on lithology and succession of bedforms (Gustason & Kauffman, 1985). In the Skull Creek Shale at I-70, *Thalassinoides suevicus* is rare and co-occurs with *Palaeophycus tubularis* and *Teichichnus rectus*. In the upper part of the Muddy Formation at Skyline Drive, *Thalassinoides suevicus* co-occurs with *Chondrites intricatus* and *Planolites montanus*. These traces were constructed in an intertidal environment based on lithology and succession of bedforms (Gustason & Kauffman, 1985). In the middle part of the Muddy Formation at Dinosaur Ridge, *Thalassinoides suevicus* co-occurs with *Diplocraterion* isp., with *Diplocraterion* interpenetrating some of the *Thalassinoides suevicus,* indicating that *Diplocraterion* was constructed after *Thalassinoides suevicus*. In the upper part of the Muddy Formation, *Thalassinoides suevicus* co-occurs with *Rhizocorallium jenense* and *Taenidium serpentinum*. These traces were constructed in an intertidal environment based on lithology and succession of bedforms (MacKenzie, 1975; Chamberlain, 1985).

Ichnogenus TREPTICHNUS Miller, 1889

Treptichnus Miller, 1889, p. 581, fig. 1095.

Trepticynus Archer & Maple, 1984, p. 455.

Treptichnus Maples & Archer, 1987, p. 893, fig. 2.4, 2.5, 3.2, 5.3.

Treptichnus Buatois & Mángano, 1993b, p. 250, fig. 4d.

Treptichnus Uchman, Bromley, & Leszczyński, 1998, p. 272, fig. 5, 6.

Treptichnus Schlirf, 2000, p. 156, pl. 2, fig. 7–10, fig. 11, 12a–b.

Treptichnus Rindsberg & Kopaska-Merkel, 2005, p. 130, fig. 1, 4–8, 10, 11.

Treptichnus Hammersburg, Hasiotis, & Robison, 2018, p. 40, fig. 10.5, 13.5, 21.1–21.6, 22.1–22.3.

Type Ichnospecies.—*Treptichnus bifurcus* Miller, 1889.

Diagnosis.—Chains of horizontal to subhorizontal, straight to curved, zigzagging burrow segments associated with vertical to oblique tunnels producing a three-dimensional burrow structure; pits and nodules may occur near the top or base of burrow segments at sediment interfaces (after Hammersburg, Hasiotis, & Robison, 2018).

Discussion.—Miller (1889) named three ichnogenera (*Haplotichnus*, *Plangtichnus*, and *Treptichnus*) that were similar in their size, morphology, and interpreted tracemakers. Maples and Archer (1987) examined the morphological differences among these ichnogenera and stated that *Treptichnus* and *Plangtichnus* represented the same trace structure, but in different bedding planes. However, Maples and Archer (1987) suggested that *Treptichnus* and *Plangtichnus* should remain separate ichnotaxa based on *Plangtichnus* lacking burrow-end projections that yield a highly angular zigzag form. This was rejected by researchers who argued that the minor morphological differences between the two ichnotaxa are not significant enough to warrant the separation, with erosion being the most likely explanation for the morphological differences between them (Buatois & Mángano, 1993a; Rindsberg & Kopaska-Merkel, 2005). Researchers have suggested that these ichnotaxa are synonymous because of the similar morphology and interpreted behaviors (Buatois & Mángano, 1993a; Rindsberg & Kopaska-Merkel, 2005). Buatois and Mángano (1993a) retained *Treptichnus* due to its heavy use in Cambrian literature, whereas *Plangtichnus* was considered to be a *nomen oblitum* due to lack of use.

Treptichnus also occurs in continental terrestrial and semi-aquatic environments (Maples & Archer, 1984; Getty & others, 2016; Hogue & Hasiotis, 2018). Extant dipteran larvae and pupae (family Limoniidae) were observed by Muñiz and others (2014) to produce surface and shallow surface burrows (just below the surface) very similar to ancient *Treptichnus.* The burrows were found in an irrigated, wet, sandy medium, occurring on and/or just below the sediment surface at the sediment-water-air interface. Other modern *Treptichnus*-like burrows constructed by dipteran larva have been observed by other researchers (Uchman, 2005).

Treptichnus is interpreted to be a deposit-feeding trace, with agricultural, grazing, reproduction, predation, or scavenging being suggested as well (Buatois & Mángano, 1993a; Uchman, Bromley, & Leszczyński, 1998; Rindsberg & Kopaska-Merkel, 2005; Seilacher, 2007; Vannier & others, 2010; Wilson & others, 2012; Getty & others, 2016; Hammersburg, Hasiotis, & Robison, 2018). In marine settings the tracemakers of *Treptichnus* are annelid worms, whereas in continental settings tracemakers are insect larvae and nymphs (Miller, 1889; Buatois & Mángano, 1993a; Uchman, Bromley, & Leszczyński, 1998; Rindsberg & Kopaska-Merkel, 2005; Vannier & others, 2010; Getty & others, 2016; Hammersburg, Hasiotis, & Robison, 2018). *Treptichnus* is found in proximal floodplain, lake-margin, brackish tidal flat, flysch, and submarine fan deposits (Archer & Maples, 1984; Buatois & Mángano, 1993b; Jensen, 1997; Uchman, Bromley, & Leszczyński, 1998 Wilson & others, 2012; Getty & others, 2016; Hammersburg, Hasiotis, & Robison, 2018). *Treptichnus* has been reported from the Cambrian to Holocene (Germs, 1972; Buatois & Mángano, 1993a; Uchman, Bromley, & Leszczyński, 1998; Vannier & others, 2010; Hasiotis, 2012; Hammersburg, Hasiotis, & Robison, 2018), with some possible examples being reported in the Ediacaran (Jensen & others, 2000; Gehling & others, 2001; Droser & others, 2002).

TREPTICHNUS BIFURCUS Miller, 1889

Figure 5.5, 15.2

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 a central axis forming a zigzag pattern (after Hammersburg, Hasiotis, & Robison, 2018).

Description.—Specimens are present in convex epirelief and hyporelief. The chains form a zigzag pattern, with angles between burrow segments within the chain <45 °. Specimens are 1.5–2 mm in diameter with individual segments 5–9 mm long, with chains 17–24 mm long.

Occurrence.—(1) Strong brown (7.5YR 5/8), fine- to very fine-grained trough-crossbedded sandstone, with BPBI 2; and (2) white (10R 8/1), fine-grained, ripple-laminated sandstone interbedded with mudstone, with BPBI 2. Specimens are present in the upper part of the Plainview Formation at Colorado State Highway 115 and in the lower part of the Horsetooth Member of the Muddy Formation at Horsetooth Reservoir.

Associated ichnotaxa.—Aulichnites parkerensis, Planolites montanus, and *Thalassinoides horizontalis.*

Discussion.—Specimens are assigned to *Treptichnus bifurcus* based on their horizontal orientation, presence of zigzagged chains, and short projections at the ends of those chains (Hammersburg, Hasiotis, & Robison, 2018). At Colorado State Highway 115, *Treptichnus bifurcus* co-occurs with *Aulichnites parkerensis, Planolites montanus,* and *Thalassinoides horizontalis*. The tracemaker for *Treptichnus bifurcus* at Colorado State Highway 115 was an annelid (Hammersburg, Hasiotis, & Robison, 2018). These traces were constructed in an intertidal to subtidal environment based on lithology and succession of bedforms (Weimer, 1970; Gustason & Kauffman, 1985). In the Horsetooth Member of the Muddy Formation, *Treptichnus bifurcus* forms a monospecific occurrence and was constructed in a fluvial environment, possibly an incised valley, based on the lithology and succession of bedforms (MacKenzie, 1965). The tracemaker for *Treptichnus bifurcus* at in the Horsetooth Member was an insect larva (Hammersburg, Hasiotis, & Robison, 2018).

Ichnogenus ZOOPHYCOS Massalongo, 1855

Zoophycos Massalongo, 1855, p. 48.

Zoophycos Frey, 1970, p. 22, pl. 4, fi. 5, pl. 7, fig. 1–3, fig. 4d.

Zoophycos Häntzschel, 1975, p. W120, fig. 75.

Zoophycos Fillion & Pickerill, 1984, p. 32, fig. 10b.

Zoophycos Uchman, 1998, p. 148, fig. 51.

Zoophycos Olivero, 2007, p. 226, fig. 13.9–13.12.

Type Ichnospecies.—Zoophycos brianteus Massalongo, 1855.

Diagnosis.—Spreite structures consisting of numerous J- or U-shaped protrusive burrows of variable length and width. The spreite form laminae bordered by a marginal tunnel, spirally coiled around a central axis, constructed upward or downward, furrowed by numerous lamellae (primary and secondary). Whorls or lobes in cross section show laminae as pseudobackfill structures, which are actually spreite, formed during the lateral displacement of the marginal tunnel (after Olivero, 2007).

Discussion.—The type ichnospecies of *Zoophycos* was considered questionable by Häntzschel (1975), because it lacked a proper description to separate the ichnogenus accurately from other ichnogenera. Moreover, the original type ichnospecies, *Zoophycos caput medusae,* is a fossil plant (Olivero, 2007). Olivero (2007) reexamined the collection of Massalongo (1855) to designate a new type ichnospecies. He identified only two specimens within the collection as actual trace fossils, resulting in the designation of *Zoophycos brianteus* as the new type ichnospecies.

Several researchers have noted that the morphology of *Zoophycos,* its position within the medium, and its preferred water depth changed through geologic history (Olivero, 1994, 2003; Seilacher, 2007; Uchman & Wetzel, 2012; Zhang, Fan, & Gong, 2015; Vinn & others, 2020). Specimens of *Zoophycos* from the Paleozoic are described as helicoidal with circular to elliptical spreite and pronounced primary lamellae (Olivero, 1994; Zhang, Fan, & Gong, 2015). Paleozoic *Zoophycos* are shallow-tiered in media and were more prominent in shallow-marine settings (Olivero, 1994; Zhang, Fan, & Gong, 2015). Mesozoic *Zoophycos* became more lobate in form with primary and secondary laminae, and shifted into deeper tiers, and more prominent in offshore to abyssal settings (Olivero, 1994, 2003; Zhang, Fan, & Gong, 2015). *Zoophycos* in the Cenozoic developed multiwhorl patterns and extended into even deeper tiers with increased presence in abyssal marine settings (Wetzel & Werner, 1980; Olivero, 1994; Zhang, Fan, & Gong, 2015). The branching, whorl pattern, three-dimensional architecture, and less uniform spreite of *Zoophycos* differentiates it from *Rhizocorallium* (Miller, 1991; Knaust, 2013).

Zoophycos is interpreted to be a deposit-feeding trace made by polychaetes, sipunculids, and/or arthropods (Książkiewicz, 1977; Fillion & Pickerill, 1984; Uchman, 1999; Olivero, 2003; Knaust, 2004a; Vinn & others, 2020). *Zoophycos* has been reported in shallow-marine (subtidal, deltaic, and offshore) paleoenvironments, but is more common in deep-marine (flysch and abyssal) settings (Książkiewicz, 1977; Fillion & Pickerill, 1984; Miller, 1991; Knaust, 2004a; Giannetti & McCann, 2010; Zhang, Fan, & Gong, 2015). *Zoophycos* ranges from the Cambrian to Holocene (Bromley, 1991; Sappenfield & others, 2012; Zhang, Fan, & Gong, 2015).

ZOOPHYCOS INSIGNIS Squinabol, 1890
Figure 15.3, 15.4, 15.5, 15.6, 16.1

Diagnosis.—Spreite structures consisting of numerous distinct U-shaped, protrusive lobes of variable length, bordered by a marginal tunnel (i.e., causative burrow). Lobes coil spirally around a central axis, which may be a spreite whorl structure (after Książkiewicz, 1977; Uchman, 1999).

Description.—Specimens are in concave and convex epirelief. Lobes are branched or unbranched, with a central whorl associated with some of the lobes. Marginal tunnels (i.e., causative burrow) border the lobes of some specimens. Spreite within the lobes have variable width between one another creating a rooster tail-like pattern. Spreite within the posterior sections of some lobes have a greater width between each other, than those within the anterior section. Lobes of some specimens appear to have resulted in a change in direction (Fig. 15.3, 15.4, 15.5). These change in direction resulted in the overall lobe width variation. Some lobes show expansion of the posterior section of the lobe causing it to be wider than anterior sections of the lobe. Specimens range from 40 to 130 mm wide and 90 to 180 mm long; marginal tunnel diameter ranges from 10 to 25 mm.

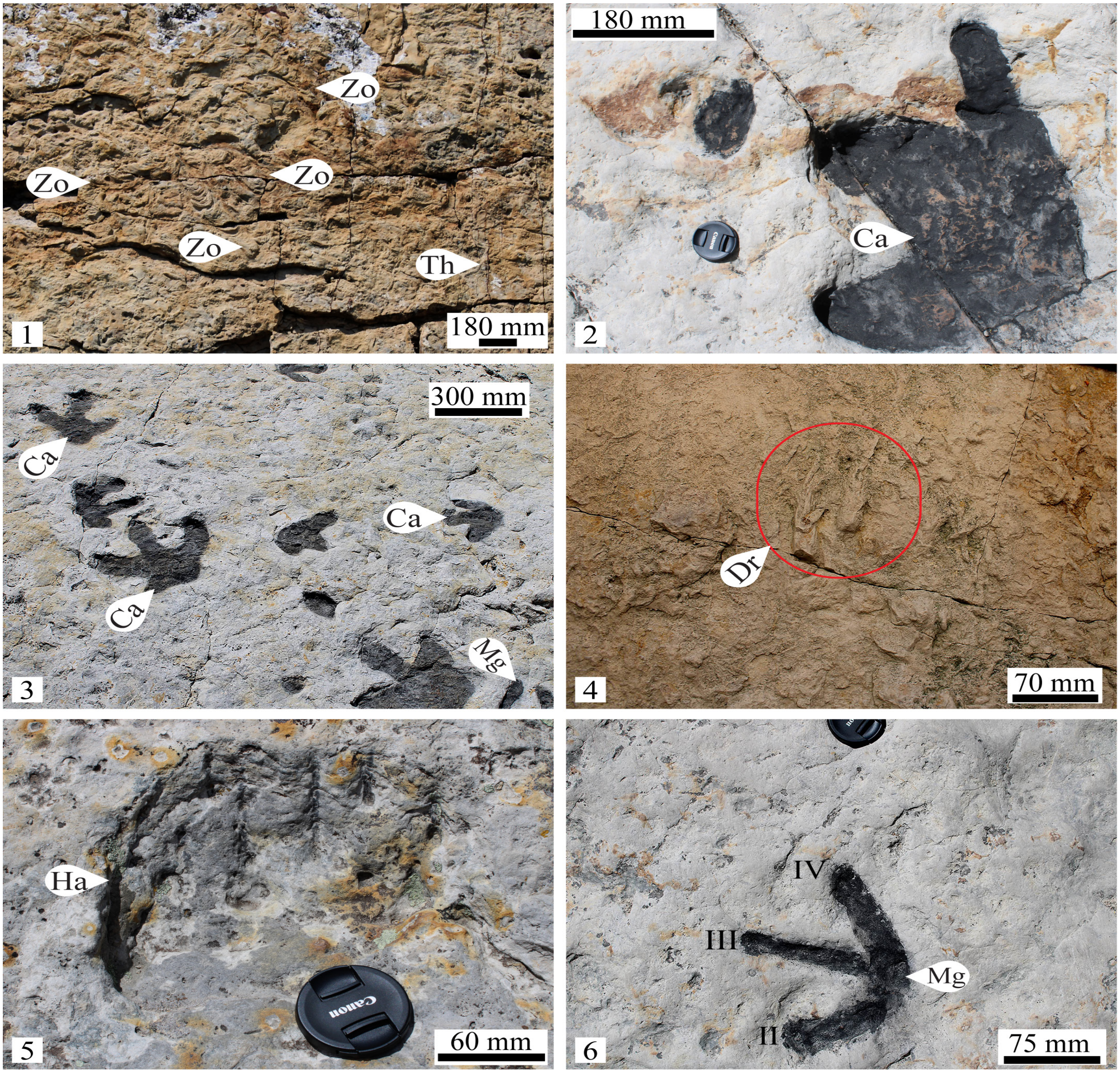


Figure 16. *Caririchnium* (Ca), *Dromaeosauripus* (Dr), *Hatcherichnus* (Ha), *Magnoavipes* (Mg), *Thalassinoides* (Th), and *Zoophycos* (Zo) from the Dakota Group. *1, Thalassinoides suevicus* and *Zoophycos insignis* in full relief, within the upper part of the Glencairn Formation at Skyline Drive. *2,* Adult *Acridinium leonardii* in concave epirelief with both manus and pes present, in the middle of the Muddy Formation at Dinosaur Ridge. *3,* Adult and juvenile *Caririchnium leonardii* along with *Magnoavipes caneeri* in concave epirelief within the middle part of the Muddy Formation at Dinosaur Ridge. *4, Dromaeosauripus* isp. in convex hyporelief (red oval), in the lower part of the Plainview Formation at Dinosaur ridge. *5, Hatcherichnus* isp. in concave epirelief, present within in the middle part of the Muddy Formation at Dinosaur Ridge. *6, Magnoavipes caneeri* in concave epirelief with digit numbers indicated, within the middle part of the Muddy Formation at Dinosaur Ridge.

Occurrence.—(1) Red (2.5YR 4/8), very fine-grained sandstone, with BPBI 3; and (2) white (10R 8/1), fine-grained sandstone, with BPBI 3. Specimens are present in the upper part of the Glencairn Formation along Grape Creek and Skyline Drive.

Associated ichnotaxa.—*Thalassinoides suevicus*.

Discussion.—Specimens are assigned to *Zoophycos insignis* based on the branching U-shaped lobes, marginal tunnels of the lobes, lobes extending from a central axis, variable width of the spreite, and the presence of a whorl at the central axis (Książkiewicz, 1977; Miller, 1991, Uchman 1999; Olivero, 2003). Tracemakers were most likely polychaetes or decapod crustaceans (Fillion & Pickerill, 1984). Previous interpretations of these specimens have placed them in *Rhizocorallium* due to their U-shaped horizontal nature (Basan & Scott, 1979); however, the morphology of the specimens are more indicative of *Zoophycos* (Häntzschel, 1975; Książkiewicz, 1977; Fillion & Pickerill, 1984; Miller, 1991; Uchman, 1998, 1999; Bromley & Hanken, 2003; Olivero, 2003). The morphology of the spreite within the lobes is similar to what has been described in *Zoophycos* by Miller (1991, figs. 5a–c) and by other researchers (Książkiewicz, 1977; Uchman 1999; Olivero, 2003). Some specimens at Skyline Drive have spreite within the lobes that are clustered in the anterior section and more spaced out in the posterior section (Fig. 15.4).

This spreite morphology could be deviation spreite or spreite that forms when the tracemaker transitions from the central shaft to the feeding structure (Wetzel & Werner, 1980). In Miller (1991) and Uchman (1999), lobes can be seen crosscutting one another (Fig 15.5). Crosscutting occurs when the tracemaker withdraws into the axial part of the burrow and constructs a new lobe (Uchman, 1999). This behavior can be repeated vertically at several levels, which could explain why some lobes exhibit changes in thickness (Fig. 15.4, 15.5).

In the Late Cretaceous, *Zoophycos* had a dominate radiating behavior with lobes extending from a whorl or central point. This is visible in *Zoophycos* present in Europe and North America Cretaceous strata (Olivero, 2003; Rodrígueiz-Tovar & Uchman, 2008; Challow & others, 2013; Zhang, Fan, & Gong, 2015). At Skyline Drive, some of the lobes are associated with a central whorl or appear to extend from a central axis (Fig. 15.5, 15.6, 16.1). The proximity of the posterior sections of the lobes to a central axis or whorl suggests that they were constructed outward from a central axis.

Zoophycos insignis co-occurs with *Thalassinoides suevicus,* in two different interactions. The first appears to be as a compound burrow system (Fig. 15.3), with *Thalassinoides suevicus* representing a dwelling and *Zoophycos insignis* representing deposit feeding of the tracemaker. The second interaction is as composite traces with *Zoophycos insignis* crosscutting the maze system of *Thalassinoides suevicus* (Fig. 15.4). The burrow and tunnel diameter of both *Zoophycos insignis* and *Thalassinoides suevicus* are similar, which suggests that they may have had the same tracemaker. The presence of *Thalassinoides suevicus* and *Ophiomorpha nodosa* in beds over and underlying those with *Zoophycos insignis* suggest that *Thalassinoides suevicus* was constructed first, with *Zoophycos insignis* being constructed later. This relationship requires further research. These traces were constructed in a prodelta environment based on lithology and succession of bedforms (Gustason & Kauffman, 1985).

ZOOPHYCOS isp.

Figure 11.4

Description.—Single specimen in full relief, with the primary spreite alternating between light and dark sediments. The shape of chevron-shaped spreite ranges from rounded to triangular and elongate, with the spacing between them variable. Specimen is 110 mm wide and 20 mm tall.

Occurrence.—Black (7.5YR 2.5/1) to very dark gray shale (7.5YR 3/1) interbedded with white (10R 8/1), very fine-grained clayey sandstone, with moderate bioturbation (ii2-3). Specimen is present in the lower part of the Skull Creek Shale at Dinosaur Ridge.

Associated ichnotaxa.—Macaronichnus segregatis, Rhizocorallium commune, Skolithos linearis, and *Teichichnus rectus.*

Discussion.—The specimen is assigned to *Zoophycos* based on the varying shapes of chevron-shaped laminae within the burrow (Chamberlain, 1975; Wetzel & Werner, 1980; Bromley & Hanken, 2003; Olivero, 2007). It lacks sufficient morphological features to allow proper placement within an ichnospecies. The tracemaker was most likely a polychaete (Fillion & Pickerill, 1984). This *Zoophycos* was constructed in a marine embayment, based on lithology and bedforms (Weimer & Land, 1972). *Zoophycos* within the Skull Creek Shale occurs in relatively shallow-marine environments compared to others reported in the Cretaceous (Olivero, 1994, 2003; Zhang, Fan, & Gong, 2015). This shows that the *Zoophycos* makers still resided within shallow-marine environments, despite previous interpretations that it was no longer present there.

TRACE FOSSILS OF TETRAPODS

Ichnogenus CARIRICHNIUM Leonardi, 1984

Caririchnium Leonardi, 1984, p. 177, fig. 8.

Caririchnium Lockley, 1987, p. 113, fig. 5, 6.

Type Ichnospecies.—Caririchnium magnificum Leonardi, 1984.

Diagnosis.—Quadrupedal trackway characterized by the remarkable difference between large tridactyl pes footprints and small subelliptical hooflike manus footprints. High pace angulation, trackway quite narrow, inner width with negative value (pace of tracks overlap with respect to the midline). Small elliptical manus print with long axis directed antero-posteriorly or slightly antero-medialy to postero-laterally. Pes footprints large, tridactyl with a plantar pad separated from the digits by skin wrinkles. Digits thick and stumpy with feet showing negative inward rotation (after Leonardi, 1984; Lockley, 1987).

Discussion.—There are currently five valid tracks attributed to ornithopod dinosaurs: *Amblydactylus* Sternberg, 1932; *Caririchnium* Leonardi, 1984; *Iguanodontipus* Sarjeant, Delair, & Lockley, 1998; *Hadrosauropus* Lockley & others, 2003; *Hypsiloichnus* Stanford, Weems, & Lockley, 2004. *Amblydactylus*, *Caririchnium*, *Hypsiloichnus, and Iguanodontipus* have only been identified in Lower Cretaceous strata, whereas *Hadrosauropus* has only been identified in Upper Cretaceous strata. *Amblydactylus* is characterized by an interdigital web for the pes (i.e., hindfoot, backfoot); the manus (i.e., forefoot, frontfoot) has been reported with some trackways but it is rare (Currie, 1983; Currie, 1995; Hunt & Lucas, 1998; Lockley & others, 2014h). *Caririchnium* is characterized by a well-developed digital pad, no interdigital web, a bilobed heel, and the manus being common and irregular in shape (Lockley, 1987, Lee, 1997; Lockley & others, 2014h). *Iguanodontipus* is characterized by having a slightly curving to flat sole and lacking a manus (Sarjeant, Delair, & Lockley, 1998; Diedrich, 2004; Lockley & others, 2014h). *Hadrosauropus* is characterized by having a large bilobed heel, which makes up 2/3 of the pes width, and present of a manus (Lockley, Nadon, & Currie, 2003; Lockley & others, 2014h). *Hypsiloichnus* is characterized by having a pentadactyl manus and a tetradactyl pes (Stanford, Weems, & Lockley, 2004).

Caririchnium is interpreted to be a locomotion trackway of ornithopod (iguanodontid or hadrosaurid) dinosaurs (Lockley, 1987; Lee, 1997; Hunt & Lucas, 1998; Lockley & others, 2014h). *Caririchnium* is found in continental settings in Asia, North America, and South America (Leonardi, 1984; Lockley, 1987; Díaz-Martínez & others, 2012; Xing & others, 2014). *Caririchnium* has only been reported in the Early Cretaceous (Lockley, 1987; Lee, 1997; Hunt & Lucas, 1998; Lockley & others, 2014h).

CARIRICHNIUM LEONARDII Lockley, 1987

Figure 16.2, 16.3

Diagnosis.—Quadrupedal trackway characterized by the remarkable difference between the large tridactyl pes footprints and the small, subelliptical, hooflike manus tracks. Manus has a medially directed impression of a digit that is shallower than the remainder of the manus impression. Manus impressions situated anteriorly and slightly lateral to the pes impression resulting in pace angulation values of ~145 ° that are less than those obtained for the pes (after Lockley, 1987).

Description.—Tracks are in concave epirelief, with both manus and pes present. Tracks are present as a singular track or as part of a trackway (multiple tracks oriented in the same direction). The trackways indicate the direction of movement of the tracemaker. Two sets of trackways are present with one possessing larger tracks with both manus and pes present, and the other containing smaller tracks with only the pes present. Pace length for the trackways range from 78 to 150 cm. For the larger tracks, the manus ranges from 114 to 152 mm wide and 63.5 to 127 mm long, with the pes ranging from 343 to 406 mm wide and 330 to 508 mm wide. In the smaller tracks, the pes ranges from 203 to 279 mm long and 254 to 279 mm wide.

Occurrence.—White (10R 8/1), very fine-grained, well-rounded, well-sorted sandstone. Tracks are present in the middle part of the Muddy Formation at Dinosaur Ridge.

Associated ichnotaxa.—*Magnoavipes caneeri*.

Discussion.—Tracks include the holotype trackway for the ichnospecies *Caririchnium leonardii* (Lockley, 1987). The difference in the sizes of *Caririchnium leonardii* trackways is attributed to the presence of both adult and juvenile tracemakers. The tracemaker for *Caririchnium leonardii* is an ornithopod dinosaur (Lockley, 1987). *Caririchnium leonardii* show locomotion in multiple directions on the track site, with the greatest number of *Caririchnium leonardii* heading in a southeastern direction. The stride length of the tracks suggests that the tracemaker was walking (Lockley, 1987). Trackways of juvenile trackmakers lack the manus, suggesting that either they were walking on their hindlegs or lacked the weight needed for the manus trace to be preserved in the sediment. The tracemakers likely traveled in groups based on the number of tracks at this location and the dominate direction in which they are heading (Lockley & others, 1992; Matsukawa, Lockley, & Hunt, 1999). These tracks are underlying wave ripple sets that have *Archaeonassa fossulata* and *Scolicia* isp within them. These tracks were constructed in a continental environment in the coastal plain, based on lithology and succession of bedforms (MacKenzie, 1975; Chamberlain, 1985; Lockley, 1987).

Ichnogenus DROMAEOSAURIPUS J. Kim, K. Kim, Lockley, Yang, Seo, Choi, & Lim, 2008

Dromaeosauripus J. Kim & others, 2008, p. 74, fig. 3a–d, 3f, 4d.

Type Ichnospecies.—*Dromaeosauripus hamanensis*, J. Kim, K. Kim, Lockley, Yang, Seo, Choi, & Lim, 2008.

Diagnosis.—Medium-sized didactyl tracks with slender digit impressions, very narrow (5°–10°) divarication angles between digits III and IV. Digit III slightly longer than IV. Digital pad impressions well-developed, sharp claw impressions distinct. Individual pes impressions with little rotation with respect to the trackway axis, i.e., digit III is directed cranially and nearly parallel to the trackway axis (Kim & others, 2008).

Discussion.—There are currently three valid trackways attributed to dromaeosaurid theropods: *Velociraptorichnus* Zhen & others, 1994; *Dromaeopodus* Li & others, 2008; and *Dromaeosauripus*. *Velociraptorichnus* is characterized by its relatively smaller size and the digits united at a heel pad (Zhen & others, 1994; Kim & others, 2008). *Dromaeopodus* is characterized by its narrow digits, with a third digit as the heel pad (Li & others, 2008; Kim & others, 2012b). *Dromaeosauripus* is characterized by a higher length to width ratio, the two digits being nearly parallel, and lacking a heel impression (Kim & others, 2008, 2012b). *Dromaeosauripus* are interpreted to be the locomotion trackways of dromaeosaurid dinosaurs (Kim & others, 2008; Lockley & others, 2016b). *Dromaeosauripus* are present in continental settings and have been only reported in the Early to Late Cretaceous (Kim & others, 2008, 2012b; Lockley & others, 2016b).

DROMAEOSAURIPUS isp.

Figure 16.4

Description.—The single track is present in convex hyporelief. The digits of the track are parallel to each other and are not connected by a heel impression. Digit III is ~100 mm long, whereas digit IV is ~110 mm long, the track is 68 mm wide (measured from digit III to digit IV).

Occurrence.—Reddish yellow (7.5YR 7/8), fine-grained, well-rounded and well-sorted sandstone. Present in the middle part of the Plainview Formation at Dinosaur Ridge.

Associated ichnotaxa.—*Cochlichnus anguineus, Lockeia siliquaria,* and *Planolites montanus*.

Discussion.—The track is assigned to *Dromaeosauripus* based on the relative size of the digits, the parallel nature of the digits, and the absence of a visible heel (Kim & others, 2008; Lockley & others, 2016b). The tracemaker for *Dromaeosauripus* was a dromaeosaurid dinosaur (Kim & others, 2008). The lack of morphological features of the track prevents proper placement within an ichnospecies. *Dromaeosauripus* is overlain by beds containing *Lockeia siliquaria* and *Planolites montanus;* underlying beds contain *Cochlichnus anguineus, Lockeia siliquaria,* and *Planolites montanus*. These traces were constructed in a fluvial environment with a variable flow regime, based on lithology and bedforms (Weimer & Land, 1972; Lockley & others, 2016b).

Ichnogenus HATCHERICHNUS Foster & Lockley, 1997

Hatcherichnus Foster & Lockley, 1997, p. 124, fig. 3, 4, 5, 6, 9

Type Ichnospecies.—*Hatcherichnus sanjuanensis* Foster & Lockley, 1997.

Diagnosis.—Tetradactyl pes impression consisting of digit impressions only (no heel impression), with digit III being the longest, digit II second longest, digits I and IV nearly equal in length and shorter then II and III by ~25%. Digit I and II impressions are slightly recurved laterally. Claw impressions are present on the digits. Total divarication between I and IV ~70 degrees. Manus impressions have only digits I–III preserved. Digit impressions laterally recurved, and digit II showing a claw impression (after Foster & Lockley, 1997).

Discussion.—*Hatcherichnus* was named for relatively large tetradactyl pes and tridactyl manus tracks interpreted as tetrapod swimming traces found within a uranium mine (Foster & Lockley, 1997). *Characichnos* Whyte & Romano, 2001 and *Albertasuchipes* McCrea, Pemberton, & Currie, 2001 are trackways that have a similar morphology and interpretations as *Hatcherichnus*. They differ from *Hatcherichnus* in that *Characichnos* is a tridactyl pes and lacks a manus, whereas *Albertasuchipes* is characterized by its tridactyl manus and tridactyl pes (Foster & Lockley, 1997; Whyte & Romano, 2001; McCrea, Pemberton, & Currie, 2001). *Characichnos* is interpreted to have been made by a dinosaur, whereas *Hatcherichnus* is interpreted as a crocodilian trackway (Foster & Lockley, 1997; Whyte & Romano, 2001; Lockley & others, 2010). *Albertasuchipes* occurs in Paleocene strata, whereas *Hatcherichnus* occurs in Mesozoic strata (Foster & Lockley, 1997; McCrea, Pemberton, & Currie, 2001; Lockley & others, 2010).

Hatcherichnus is interpreted to be a locomotion (swimming) trackway of neosuchian crocodiles (Foster & Lockley, 1997; Avanzini & others, 2010; Kukihara & Lockley, 2012; Lockley & others, 2014e). It is reported from fluvial, marsh, and coastal plain paleoenvironments (Foster & Lockley, 1997; Avanzini & others, 2010; Kukihara, Lockley, & Houck, 2010). *Hatcherichnus* ranges from the Middle Jurassic to Cretaceous (Foster & Lockley, 1997; Kukihara, Lockley, & Houck, 2010).

HATCHERICHNUS isp.

Figure 16.5

Description.—Two tracks are in concave epirelief, with the digits being slightly distorted, likely due to locomotion of the tracemaker. Within the pes of one footprint, digits I and IV are shorter than digits II and III. Pes ranges from 100 to 150 mm wide, 150 to 177 mm long, with digits ranging from 40 to 65 mm long. Another footprint consisting of three digits is represented by elongated grooves. Digit II is ~15 cm long, digit III is ~19 cm long, and digit IV is ~11 cm in length. The track is ~13 cm wide (measured from outside digits II and IV).

Occurrence.—(1) White (10R 8/1), very fine-grained sandstone, with BPBI 2; and (2) Reddish yellow (7.5YR 6/8), very fine-grained sandstone, with BPBI 2. Tracks are present in the middle part of the Muddy Formation at Dinosaur Ridge.

Associated ichnotaxa.—*Caririchnium leonardii* and *Magnoavipes caneeri*.

Discussion.—Tracks are assigned to *Hatcherichnus* based on the size and length of the groove impressions (Foster & Lockley, 1997). The lack of a manus immediately anterior of the pes prevents its placement within *Albertasuchipes* (McCrea, Pemberton, & Currie, 2001). The length of each track, along with the shallow depression of the grooves, prevents their placement within *Characichnos* (Whyte & Romano, 2001). The tracemaker for *Hatcherichnus* was a neosuchian crocodile (Foster & Lockley, 1997). The condition of the tracks makes proper placement within an ichnospecies difficult. Due to the size of the individual scratch marks and its similarities to other *Hatcherichnus* track sets found within Dakota Group, we are confident that these traces belong in *Hatcherichnus* (see, Kukihara, Lockley, & Houck, 2010). These tracks were constructed in a coastal plain environment, based on lithology and succession of bedforms (MacKenzie, 1975; Chamberlain, 1985; Lockley, 1987).

Ichnogenus MAGNOAVIPES Lee, 1997

Magnoavipes Lee, 1997, p. 853, fig. 3a, 5a.

Magnoavipes Lockley, Wright, & Matsukawa, 2001, p. 138, fig. 1–3.

Type Ichnospecies.—*Magnoavipes lowei* Lee, 1997.

Diagnosis.—Bipedal trackway consisting of narrow-toed, tridactyl tracks. Track length to width ratio is 4:5 (0.8:1.0). Digit divarication angles wide (average 85°) but highly variable (65–105°). Trackway slightly asymmetric (after Lockley, Wright, & Matsukawa, 2001).

Discussion.—*Magnoavipes* were named for narrow tridactyl tracks from the Upper Cretaceous Woodbine Formation in Texas (Lee, 1997). Lockley, Wright, and Matsukawa (2001) emended the diagnosis, because Lee (1997) did measure the divarication of the digits using the standard methodology, resulting in a difference of 20°. Within their emended diagnosis, however, an error is present involving the ratio between the length and width of the track. The original ratio was 1.0:0.8, making the track slightly longer than it is wide. The description of *Magnoavipes,* however, states that the track is slightly wider than long. For this reason, we have emended the diagnosis to clearly state the ratio and its meaning [footprint length to width ratio is 4:5 (0.8:1.0)]. Lee (1997) originally determined that the tracemakers of *Magnoavipes* were large birds, but Lockley, Wright, and Matsukawa (2001) argued that birds of this size have not been recorded from this particular time in the Cretaceous and that the tracemakers were most likely theropod dinosaurs.

Magnoavipes is thus interpreted to be a locomotion trace of a theropod dinosaur, most likely an ornithomimid (Lockley, Wright & Matsukawa, 2001; Matsukawa & others, 2014). *Magnoavipes* are reported in continental (fluvial, lacustrine, and montane) settings in North America and Asia (Lee, 1997; Lockley, Wright, & Matsukawa, 2001; Fiorillo & others, 2011; Matsukawa & others, 2014). *Magnoavipes* ranges from the Lower to Upper Cretaceous (Lee, 1997; Lockley, Wright & Matsukawa, 2001; Matsukawa & others, 2014).

MAGNOAVIPES CANEERI

Lockley, Wright, & Matsukawa, 2001

Figure 16.3, 16.6, 17.3

Diagnosis.—Shallow, well-defined digit pad impressions with digits II, III, and IV present. Footprints are subparallel to trackway midline (after Lockley, Wright, & Matsukawa, 2001).

Description.—Tracks are in concave epirelief (Fig. 16.3, 16.6) and convex hyporelief (Fig. 17.3). The heel impression is preserved in some specimens and absent in others. Digit II is absent in some

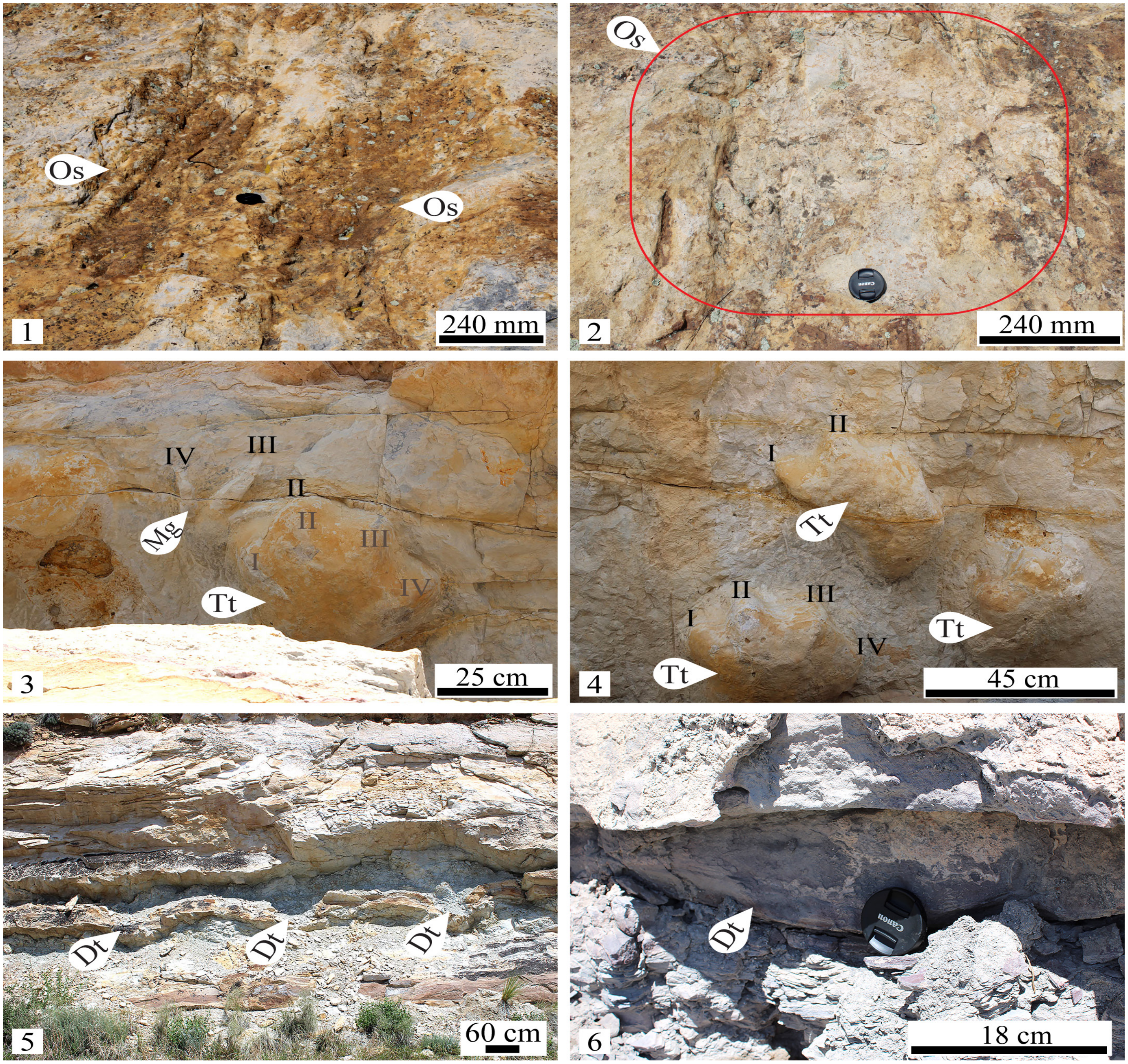


Figure 17. *Ostendichnus* (Os), *Magnoavipes* (Mg), and *Tetrapodosaurus* (Tt) from the Dakota Group. *1, Ostendichnus bilobatus* present in concave epirelief in the middle part of the Muddy Formation at Dinosaur Ridge. *2, Ostendichnus bilobatus* present in concave epirelief (red oval) in the upper part of the Muddy Formation at Dinosaur Ridge. *3, Magnoavipes caneeri* and *Tetrapodosaurus* isp. in convex hyporelief with digit numbers indicated for each trace fossil, within the middle part of the Plainview Formation at Skyline Drive. *4, Tetrapodosaurus* isp. pes and manus tracks in convex hyporelief, with digit numbers indicated within the middle part of the Plainview Formation at Skyline Drive. *5,* Unidentified dinosaur tracks (Dt) within the middle part of the Lytle Formation at Skyline Drive. 6, Unidentified dinosaur track (Dt) within the middle part of the Plainview Formation at Colorado State Highway 115.

samples (Fig. 16.3). Divarication between the digits within the tracks averages 83°. The stride length ranges from 180 to 280 cm. The tracks are ~177 mm wide (measured from the tip of digit II to the tip of digit IV) and 228 mm long (measured from the tip of digit III to the heel).

Occurrence.—(1) White (10R 8/1), very fine-grained sandstone, with BPBI 3; and (2) reddish yellow (7.5YR 6/8), fine- to very fine-grained sandstone, with BPBI 3. Tracks are present in the middle part of the Plainview Formation at Skyline Drive, and the middle part of the Muddy Formation at Dinosaur Ridge.

Associated ichnotaxa.—*Caririchnium leonardii, Ostendichnus bilobatus,* and *Tetrapodosaurus* isp.

Discussion.—The tracemaker is likely a ornithomimid dinosaur (Lockley, Wright, & Matsukawa, 2001). *Magnoavipes caneeri* co-occurs with large herbivore tracks in the Plainview and Muddy formations and have the same orientation as the herbivore tracks.

In the Plainview Formation at Skyline Drive, a single track was assigned to *Magnoavipes caneeri* based on the thickness of its digits, relative size of the track, and divarication of the digits in the track (Lockley, Wright, & Matsukawa, 2001). *Magnoavipes caneeri* is present side-by-side with the pes of a *Tetrapodosaurus* (Fig. 17.3). These tracks are overlain by a bed containing *Asthenopodichnium xylobiontum, Lockeia* isp., *Margaritichnus mansfieldi, Teredolites clavatus,* and *Thalassinoides suevicus*. These tracks were constructed in a coastal plain environment close to the shoreline, based on lithology, bedforms, and overlying trace-fossil-bearing strata (Gustason & Kauffman, 1985).

In the Muddy Formation at Dinosaur Ridge, tracks include the holotype trackway of *Magnoavipes caneeri* (Lockley, Wright, & Matsukawa, 2001). In some *Magnoavipes caneeri*, digit II is absent (Fig. 16.3); however, based on the number of morphologically similar tracks, these tracks are still considered *Magnoavipes caneeri*. The spacing between the tracks suggests that the tracemaker was not running, but rather moving at a walking pace (Lockley, Wright & Matsukawa, 2001). *Magnoavipes caneeri* co-occurs with *Caririchnium leonardii*. These tracks were produced in a coastal plain environment near the shoreline, based on lithology and succession of bedforms (MacKenzie, 1975; Chamberlain, 1985; Lockley, 1987).

Ichnogenus OSTENDICHNUS Lockley, McCrea, Buckley, Lim, Matthews, Breithaupt, Houck, Gierliński, Surmik, Kim, Xing, Kong, Cart, Martin, & Hadden 2016

Ostendichnus Lockley & others, 2016a, p. 2, fig. 3.

Type Ichnospecies.—*Ostendichnus bilobatus* Lockley, McCrea, Buckley, Lim, Matthews, Breithaupt, Houck, Gierliński, Surmik, Kim, Xing, Kong, Cart, Martin, & Hadden, 2016.

Diagnosis.—Large, bilaterally-symmetrical, bilobed to oval impressions with multiple, well-defined digital scratch marks aligned parallel or subparallel to long axis of the whole trace. Up to 10–15% as deep as long. Traces mostly with a single raised central ridge, separating left and right sides of the impressions, which may include complete or partial diagnostic tridactyl theropod tracks (after Lockley & others, 2016a).

Discussion.—*Ostendichnus* was named for large bilateral scrapes found at four different localities in Colorado (Lockley & others, 2016a). This trace is interpreted as a ceremonial display, likely produced during the breeding season (Lockley & others, 2016a, 2018a). The tracemaker was likely a theropod dinosaur, due to the presence of theropod dinosaur tracks at other localities. *Ostendichnus* are present in Lower Cretaceous continental deposits (Lockley & others, 2016a; Lockley & others, 2018a).

OSTENDICHNUS BILOBATUS Lockley & others, 2016a

Figure 17.1, 17.2

Diagnosis.—Same as for the ichnogenus.

Description.—Traces are present as a bilobate impressions with multiple grooves with a raised central ridge of variable width between each side of the impression. Within one side of the bilobate impression, the scratches are well defined, whereas within the other the scratches are poorly defined due to weathering. Both have an east-to-west orientation on the outcrop. Each side of the bilobate impressions ranges from 154.4 cm to 61 cm long, to 43.2 cm to 28 cm wide. The depth of each side of the impression ranges from 12 cm to 8 cm.

Occurrence.—Reddish yellow (7.5YR 6/8), fine- to very fine-grained, rounded, moderately well-sorted sandstone. Scrapes are present in the upper part of the Muddy Formation at Dinosaur Ridge.

Associated ichnotaxa.—*Magnoavipes caneeri*.

Discussion.—The bilobate impressions are assigned to *Ostendichnus bilobatus*, based on the bilobate impressions and the presence of multiple, parallel grooves within each side of the bilobate impression (Lockley & others, 2016a, 2018a). The tracemaker was a theropod dinosaur (Lockley & others, 2016a). The first occurrence of *Ostendichnus bilobatus* forms a monospecific occurrence in the lower part of the section representing the upper Muddy Formation. The second occurrence of *Ostendichnus bilobatus* is present near the contact with the Mowry Shale and co-occurs with *Magnoavipes caneeri*. These tracks were constructed in a coastal plain environment near the shoreline of the ocean, based on lithology and succession of bedforms (MacKenzie, 1975; Chamberlain, 1985; Lockley, 1987).

Ichnogenus TETRAPODOSAURUS Sternberg, 1932

Tetrapodosaurus Sternberg, 1932, p. 73, pl. 5, fig. 9.

Tetrapodosaurus McCrea, Lockley, & Meyer, 2001, p. 422, fig. 20.5–20.13.

Tetrapodosaurus Gangloff, May, & Storer, 2001, p. 308, fig. 4e.

Type Ichnospecies.—*Tetrapodosaurus borealis* Sternberg, 1932.

Emended Diagnosis.—Quadrupedal tracks with a tetradactyl pes and a pentadactyl manus. The manus can be approximately 2/3 the size of the pes. Manus has a greater width than length; the divarication between digits I and II is ~73°; II and III is ~42°; III and IV is ~33°; and IV and V is ~50°. The pes has a greater length than width, and toes are elongated with the divarication between digits being <40 ° (modified from McCrea, Lockley, & Meyer, 2001; Gangloff, May, & Storer, 2001).

Discussion.—*Tetrapodosaurus* was originally named for trackway of a quadruped with a short and broad, five-digit manus and four-digit pes, in which the digits were enclosed by a web or pad (Sternberg, 1932; Gangloff, May, & Storer, 2001; Lockley & Gierlinski, 2014b). Recent studies, however, have interpreted these pads and/or webs as being poorly preserved due to deformation during trackmaking (McCrea, Lockley, & Meyer, 2001; Gangloff, May, & Storer, 2001). We emend the diagnosis to account for the lack of enclosing webbing or pad based on new observations in the literature of well-preserved track specimens (McCrea, Lockley, & Meyer, 2001; Gangloff, May, & Storer, 2001). *Tetrapodosaurus* is interpreted to be locomotion tracks of nodosaurid ankylosaurs (Kurtz, Lockley, & Engard, 2001; Rodríguez-de la Rose & others, 2018). *Tetrapodosaurus* is present in continental deposits that range from the Jurassic to Upper Cretaceous (Sternberg, 1932; Kurtz, Lockley, & Engard, 2001; Rodríguez-de la Rosa & others, 2018).

TETRAPODOSAURUS isp.
Figure 17.3, 17.4

Description.—Tracks are in convex hyporelief. The divarication between digits within a pes is <40°. The digits of the manus vary in preservation, with digits I and II being the better preserved and digits III, IV, and V being rarely preserved or absent. The divarication between digit I and II is ~70°, and digit II and III is ~45°. The manus is close in size to the pes. Pedes are ~457 mm wide and ~460–480 mm long, the manus is ~457 mm wide and 304 mm long.

Occurrence.—Reddish yellow (7.5YR 7/8), fine- to very fine-grained sandstone, with BPBI 3. Tracks are present in the middle part of the Plainview Formation at Skyline Drive.

Associated ichnotaxa.—Magnoavipes caneeri.

Discussion.—Tracks are assigned to *Tetrapodosaurus* based on the five toes on the manus and four on the pes, and the size ratio between the manus and pes of 2:3 (Sternberg, 1932; Kurtz, Lockley, & Engard, 2001; McCrea, Lockley, & Meyer, 2001). The tracemaker is interpreted to be a nodosaurid ankylosaur (Kurtz, Lockley, & Engard, 2001). The lack of clear diagnostic morphology prevents proper placement within an ichnospecies. Digits III, IV, and V on the manus are not well preserved, with only a few tracks having an identifiable digit III. Digit I and II on the manus are more distinct, possibly due to the higher divarication angle between them. The digits on the pes are identifiable; however, the pes has a greater degree of variation than the manus in terms of overall size. The tracks indicate the tracemakers moved in a southwestern direction. These tracks underlie a bed containing *Asthenopodichnium xylobiontum, Lockeia* isp.*, Margaritichnus mansfieldi, Teredolites clavatus,* and *Thalassinoides suevicus*. They were constructed in a coastal plain environment, based on lithology and succession of bedforms (Gustason & Kauffman, 1985; Kurtz, Lockley, & Engard, 2001).

DINOSAUR TRACKS
Figure 17.5, 17.6

Description.—Tracks are present in full relief. Vertical, asymmetrical, hemielliptical depressions that deform the enclosing and underlying beds. Depressions are smooth and infilled with sediment from the overlying beds (Engelmann & Hasiotis, 1999; Hasiotis, 2004; Platt & Hasiotis, 2006; Flaig, Hasiotis, & Fiorillo, 2018). Beds overlying the depressions are horizontal and undeformed, a trait commonly seen in tracks preserved in full relief (Engelmann & Hasiotis, 1999; Hasiotis, 2004; Platt & Hasiotis, 2006; Flaig, Hasiotis, & Fiorillo, 2018). Depressions are present in groups or are by themselves. Depressions range from 36 to 94 cm long and 12 to 66 cm deep.

Occurrence.—(1) Reddish yellow (7.5YR 7/8), medium- to coarse-grained, well-rounded, poorly sorted sandstone; and (2) white (10R 8/1), fine-grained ripple-laminated sandstone. Tracks are present in the middle part of the Lytle Formation at Skyline Drive and U.S. Route 285, and the upper part of the Plainview Formation at Colorado State Highway 115.

Discussion.—These depressions are interpreted as tracks based the deformation of the enclosing and underlying beds, and the infill within the depression matching the lithology of the overlying beds (Engelmann & Hasiotis, 1999; Hasiotis, 2004; Platt & Hasiotis, 2006; Flaig, Hasiotis, & Fiorillo, 2018). Although other tetrapod animals were present during this time, the only animals that were large enough to have made these tracks were dinosaurs of the Ankylosauria, Ceratopsia, Ornithopoda, and Sauropoda. The size and morphology of the track within the Plainview Formation prevent more exact identification of the tracemaker. The single track within the Plainview Formation was produced in a coastal plain environment based on lithology and succession of bedforms (Weimer, 1970; Gustason & Kauffman, 1985). Tracks within the Lytle Formation are large, ranging from 79 to 94 cm long with a depth of 58 to 66 cm, and were most likely produced by sauropods based on the length and depth of the tracks (Engelmann & Hasiotis, 1999; Hasiotis, 2004; Platt & Hasiotis, 2006). These tracks occur in a continental fluvial environment based on lithology and succession of bedforms (Weimer & Land, 1972; Gustason & Kauffman, 1985).

OTHER TETRAPOD TRACKS PRESENT IN THE DAKOTA GROUP

In addition to the tetrapod tracks found within our study sites, four other tetrapod tracks have been identified by researchers at other localities in the Dakota Group. These localities were not included in this study because they are on private property, and the exact location of one of the tetrapod track localities has been lost (Lockley & others, 2009, 2010). We discuss these previously described tetrapod tracks here in order to be thorough with our ichnotaxonomic analysis of the Dakota Group along the Colorado Front Range.

Ignotornis mcconnelli are avian tracks that were first reported in the 1930s from a locality near Golden, Colorado (Mehl, 1931; Lockley & others, 2009). Currently five localities are found in Colorado, three in the Golden area and two in Roxborough State Park, south of Morrison, Colorado, with the tracks being located in the middle part of the Muddy Formation (Lockley & others, 2009; Lockley, Honda, & Simmons, 2014d). In total these five localities contain over 300 footprints and 50 trackways (Lockley & others, 2009; Lockley & others, 2014e). *Ignotornis* is diagnosed by its four digits with a hind hallux digit. The *Ignotornis* footprints are small, ranging from 5.5 to 3.7 cm wide and 6.4 to 4.9 cm long with the hallux (Lockley & others, 2009). The divarication between the digits varies with the largest being between digits II-IV (95° to 146°), whereas the smallest being between digits II-III and III-IV (37° to 105°) (Lockley & others, 2009). *Ignotornis* is interpreted to be the locomotion track of a bird; it has only been found in continental environments in Asia and North America in the Early Cretaceous (Lockley & others, 2009; Lockley, Honda, & Simmons, 2014d; Kim & others, 2012a; Kang & others, 2021).

Mehliella jeffersonensis are crocodilian locomotion (walking) trackways in which the pes, manus, and tail of the tracemaker are preserved. *Mehliella jeffersonensis* was discovered near Golden, Colorado, in the 1930's (Mehl, 1931; Lockley, 2010). Mehl (1931) stated that the tracks occurred in the massive sandstone in the upper part of the Dakota Sandstone, which suggests they could possibly have been in the Muddy Formation. The locality for *Mehliella* has been lost, with only the drawings and two molds of the tracks made by Mehl (1931) reported. Currently only one of these molds has been found (Lockley, 2010). Identified by Mehl (1931), the trackways were originally named *Walteria jeffersonensis;* however, this was changed by Strand (1932) due to *Walteria* already being used for a sponge (Lockley, 2010). The mold of *Mehliella jeffersonensis* only has a four-digit left pes present and has a length of 23.5 cm and a width of 15 cm (Lockley, 2010). Lockley (2010) inferred that the stride of *Mehliella jeffersonensis* was 57 cm and the width of the tail trace was 10 cm, based on the size of the track and descriptions of the trackway by Mehl (1931). *Mehliella jeffersonensis* has only been found in continental deposits in North America from the Early Cretaceous (Lockley, 2010).

Chelonipus is an ichnogenus named for locomotion tracks of turtles (Lockley & others, 2010; Lichtig & others, 2017). There are three localities in Colorado with turtle trackways that could be placed within this ichnogenus. Only one of these localities are found in the Dakota Group (Lockley & Foster, 2006; Lockley & others, 2010). *Chelonipus* exhibits a pentadactyl morphology, in which digits I and V are shorter than digits II–IV (Lockley & Foster, 2006; Lockley & others, 2010; Lichtig & others, 2017). The difference in length between the outer digits (I and V) and the inner digits (II–IV), has resulted in either one or both of the outer digits not being persevered in the trackway (Lockley & Foster, 2006; Lockley & others, 2010; Lichtig & others, 2017). The *Chelonipus* tracks within the Dakota Group have a mean length of 3.6 cm and a mean width of 4.1 cm (Lockley & others, 2010). *Chelonipus* is interpreted to be the swimming locomotion of turtles and is found in continental environments in Asia, Europe, and North America (Lockley & Foster, 2006; Lockley & others, 2010; Lockley, Xing, & Xu, 2019; Lichtig & others, 2017; Xing & others, 2019). *Chelonipus* ranges from the Triassic to Cretaceous (Lockley & others, 2010; Lichtig & others, 2017; Lockley, Xing, & Xu, 2019; Xing & others, 2019).

Pterosaur swim trackways are also found in the Dakota Group. These trackways are present at several different localities, with one located in the Muddy Formation near Golden, Colorado, and two others in southeastern Colorado in outcrops of the Mesa Rica and Pajarito formations (Kukihara, Lockley, & Houck, 2010; Lockley & Schumacher, 2014g). The tracks are characterized by digits II and III being longer, with digits I and IV being shorter. The width of the digits is narrow with most of the tracks having a width ranging from 4 to 12 cm (Lockley, Simmons, & Daggett, 2014f; Lockley & Schumacher, 2014g). These pterosaur swim trackways occur in continental environments in Asia and North America (Kim & others, 2006; Lockley & Schumacher, 2014g). Pterosaur swim trackways range from the Late Jurassic to Early Cretaceous (Lockley & Wright, 2003; Lockley & Schumacher, 2014g).

DISCUSSION

Within this section we summarize the ichnotaxa identified in the Dakota Group and the behaviors they represent. The ichnotaxa and paleoenvironmental occurrences are used to construct ichnocoenoses within the Dakota Group. These ichnocoenoses are used to assign ichnofacies after which we discuss the stratigraphic distribution and paleoecology of the ichnofacies. The ichnotaxa, ichnocoenoses, and ichnofacies of the Dakota Group are compared to other formations: (1) within the Dakota Group but outside the Colorado Front Range; and 2) deposits from the Western Interior Seaway. The objective here is to determine how similar or dissimilar the ichnology of the Dakota Group along the Colorado Front Range is to other Western Interior Seaway transitional and marine paleoenvironments.

Ichnotaxa

The Dakota Group contains a relatively diverse suite of trace fossils (Table 2, p. 60–61). Rhizohaloes were identified from outcrops and samples. Thirty-four ichnospecies of thirty-two invertebrate ichnogenera were identified: *Archaeonassa, Arenicolites, Asterosoma, Asthenopodichnium, Aulichnites, Chondrites, Cochlichnus, Conichnus, Cruziana, Cylindrichnus, Diplocraterion, Gyrolithes, Lockeia, Macaronichnus, Margaritichnus, Naktodemasis, Ophiomorpha, Palaeophycus, Planolites, Protovirgularia, Rhizocorallium, Rosselia, Rusophycus, Schaubcylindrichnus, Scolicia, Skolithos, Taenidium, Teichichnus, Teredolites, Thalassinoides, Treptichnus,* and *Zoophycos*. Three ichnospecies were identified in six tetrapod ichnogenera: *Caririchnium, Dromaeosauripus, Hatcherichnus, Magnoavipes, Ostendichnus,* and *Tetrapodosaurus*.

Behavior

Ichnofossils from the Dakota Group represent a range of behaviors that are grouped into ethological categories (Seilacher, 1953, 1964; Bromley, 1996): Cubichnia (resting); domichnia (dwelling); equilibrichnia (adjusting, stabilizing); fodinichnia (feeding); pascichnia (grazing); and repichnia (locomotion). Cubichnia are represented by *Conichnus, Lockeia, Margaritichnus,* and *Rusophycus*. Domichnia are represented by *Arenicolites, Asthenopodichnium, Cylindrichnus, Diplocraterion, Ophiomorpha, Rhizocorallium, Rosselia, Skolithos, Teredolites,* and *Thalassinoides*. Equilibrichnia are represented by *Rosselia*. Trace fossils representing fodinichnia are *Asterosoma, Chondrites, Macaronichnus, Margaritichnus, Planolites, Rhizocorallium, Schaubcylindrichnus, Taenidium, Teichichnus, Treptichnus,* and *Zoophycos*. The behavior of pascichnia is present in *Archaeonassa, Aulichnites, Cochlichnus,* and *Scolicia*. Repichnia are represented by *Caririchnium, Cruziana, Dromaeosauripus, Hatcherichnus, Magnoavipes, Margaritichnus, Protovirgularia,* and *Tetrapodosaurus*. *Naktodemasis* represents repichnia and domichnia equally and fodinichnia as a secondary behavior (Smith & others, 2008; Counts & Hasiotis, 2009). *Ostendichnus* represents a courtship behavior (Lockley & others, 2016a). The compound burrow structures of *Thalassinoides-Zoophycos* represent both domichnia (*Thalassinoides*) and fodinichnia (*Zoophycos*) behaviors. The *Protovirgularia-Planolites* compound structure represents a tracemaker transitioning from a fodinichnia (*Planolites*) to repichnia (*Protovirgularia*) behavior.

Ichnocoenoses

An ichnocoenosis is an assemblage of ichnofossils that results from the activity of a single community of tracemaking organisms, which can be used to interpret various physicochemical controls present during deposition (Ekdale, 1988; Frey, Pemberton, & Saunders, 1990; MacEachern & Pemberton, 1994; Bromley, 1996; Taylor, Goldring, & Gowland, 2003; Hasiotis 2004, 2008; Hammersburg, Hasiotis, & Robison, 2018). Eight ichnocoenoses are established for the Dakota Group, with varying degrees of stratigraphic occurrence: *Caririchnium, Diplocraterion, Lockeia, Naktodemasis,* Rhizohalo, *Scolicia, Skolithos-Teichichnus,* and *Zoophycos* ichnocoenoses (Table 3). These ichnocoenoses reflect how paleoenvironments recorded by various stratigraphic intervals in the Dakota Group were controlled by depositional energy, sedimentation rate, oxygenation, salinity, medium, and other factors (Hasiotis & Platt 2012).

The *Caririchnium* ichnocoenosis occurs in fine- to very fine-grained sandstones. The *Caririchnium* ichnocoenosis is only present in the middle part of the Muddy Formation at Dinosaur Ridge. The ichnodiversity of the *Caririchnium* ichnocoenosis is low, with *Caririchnium* and *Magnoavipes* being the only ichnogenera present. The behavior represented by the *Caririchnium* ichnocoenosis is repichnial. The bedding-plane bioturbation ranges from 2 to 3 BPBI. The *Caririchnium* ichnocoenosis overprints the top of a *Diplocraterion* ichnocoenosis. This ichnocoenosis represents the subaerial exposure of an intertidal environment at low tide (see, MacEachern & Pemberton, 1992; Hasiotis, McPherson, & Reilly, 2013).

The *Diplocraterion* ichnocoenosis occurs in fine- to very fine-grained sandstones, with wave and current ripples, along with syneresis cracks on some of the ripple surfaces. Four beds at three localities are assigned to the *Diplocraterion* ichnocoenosis: the middle part of the Skull Creek Shale at Horsetooth Reservoir, and the lower and middle parts of the Muddy Formation at Skyline Drive and Dinosaur Ridge. The ichnodiversity of the *Diplocraterion* ichnocoenosis is low, with two other ichnogenera present: *Rhizocorallium* and *Thalassinoides*. The dominant behavior is domichnial, with fodinichnia being a secondary behavior. The bedding-plane bioturbation ranges from BPBI 2 to 5. This ichnocoenosis represents deposition in an intertidal to subtidal environment (seevMacEachern & Pemberton, 1992; Hasiotis, McPherson, & Reilly, 2013) with: (1) low to moderate, variable depositional energy; (2) moderate and nonsteady sedimentation rate; (3) normal benthic oxygen; and (4) reduced to normal marine salinity.

The *Lockeia* ichnocoenosis occurs in fine-grained, planar-tabular sandstone, at a single locality in the middle part of the Plainview Formation at Dinosaur Ridge. This ichnocoenosis has the third highest ichnodiversity with three other ichnogenera present: *Cochlichnus*, *Dromaeosauripus,* and *Planolites*. The behaviors represented in this ichnocoenosis are repichnial and domichnial. The bedding-plane bioturbation ranges from BPBI 2 to 4. This ichnocoenosis represents deposition in a fluvial environment with a variable salinity (Weimer & Land, 1972; Hasiotis, McPherson, & Reilly, 2013) with: (1) moderate, variable depositional energy; (2) moderate and nonsteady sedimentation rate; (3) normal benthic oxygen; and (4) freshwater conditions.

The *Naktodemasis* ichnocoenosis occurs in fine- to very fine-grained sandstone, at a single locality in the upper part of the Lytle Formation at I-70. The *Naktodemasis* ichnocoenosis has only two ichnogenera: *Naktodemasis* and *Planolites*. The behaviors represented in this ichnocoenosis are repichnial and domichnial, with fodinichnia being a secondary behavior. The degree of bioturbation of the *Naktodemasis* ichnocoenosis is moderate to high (ii2–4). The *Naktodemasis* ichnocoenosis represents a fluvial floodplain environment in the vadose zone (see, Hasiotis, 2002, 2004, 2007, 2008) with: (1) variable depositional energy; (2) low and nonsteady sedimentation rate; (3) low to moderate soil moisture; and (4) weak soil development.

The Rhizohalo ichnocoenosis occurs in a silty, pedogenically modified mudstone. The Rhizohalo ichnocoenosis is present in the middle part of the Muddy Formation at Dinosaur Ridge and is the only trace fossil present in its ichnocoenosis. It represents domichnial and fodinichnia as plant roots record the location of plant and are used to gather nutrients and water from the soil. The bioturbation of the Rhizohalo ichnocoenosis has a range of 4–6 BPBI. The Rhizohalo ichnocoenosis represents a coastal plain environment with high water table and poorly drained conditions (see, MacKenzie, 1975; Reineck & Singh, 1980; Chamberlain, 1985; Kraus & Hasiotis, 2006; Hasiotis, McPherson, & Reilly, 2013).

The *Scolicia* ichnocoenosis occurs in very fine- to fine-grained sandstones, with wave ripples and flaser bedding. Two beds at two localities were assigned to this ichnocoenosis: the upper part of the Plainview Formation at Colorado State Highway 115 and the upper part of the Muddy Formation at Dinosaur Ridge. The *Scolicia* ichnocoenosis has the second highest ichnodiversity, with nine ichnogenera: *Aulichnites, Archaeonassa, Lockeia, Planolites, Protovirgularia, Rhizocorallium, Scolicia, Thalassinoides,* and *Treptichnus*. The dominate behavior is pascichnial, with domichnia and cubichnia being secondary behaviors. Bioturbation within this ichnocoenosis varies from BPBP 2 to 3. This ichnocoenosis represents a subtidal environment (see, Reineck & Singh, 1980; MacEachern & Pemberton, 1992; Hasiotis, McPherson, & Reilly, 2013) with: (1) moderate and variable depositional energy; (2) moderate and nonsteady sedimentation rate; (3) normal benthic oxygen; and (4) normal marine salinity.

The *Skolithos-Teichichnus* ichnocoenosis occurs in shales interbedded with very fine-grained sandstones to siltstones with some ripple marks, and in fine- to very fine-grained sandstones. Six beds at five localities are assigned to the *Skolithos-Teichichnus* ichnocoenosis: the upper part of the Plainview Formation at Skyline Drive, in the middle and upper parts of the Skull Creek Shale at I-70, in the middle part of the Skull Creek Shale at Dinosaur Ridge, in the middle part of the Skull Creek Shale at U.S. Route 285, and in the upper part of the Skull Creek Shale at Horsetooth Reservoir. The *Skolithos-Teichichnus* ichnocoenosis has the highest biodiversity with twelve ichnogenera: *Arenicolites, Asterosoma, Cylindrichnus, Macaronichnus, Palaeophycus, Rhizocorallium, Rosselia, Schaubcylindrichnus, Skolithos, Teichichnus, Thalassinoides*, and *Zoophycos*. The dominant behavior is fodinichnial, with domichnia being a secondary behavior. The degree of bioturbation for the *Skolithos-Teichichnus* ichnocoenosis is moderate to high (ii3–4). The *Skolithos-Teichichnus* ichnocoenosis represents subtidal, embayment, and lower shoreface environments (see, MacEachern & Pemberton,

Trace Fossil	Formation									Lithology			Environment							
	LF	PF	GF	SKS	MF(CSM)	MF(UTM)	MF	MF(FC)	MF(HM)	Ss	Slt	Sh	F	CP	IT	ST	ME	D	MS	LS
Archaeonassa fossulata		X					X	X		X					X	X		X		
Arenicolites carbonaria						X				X					X					
Arenicolites variabilis				X								X					X			
Arenicolites isp				X								X					X			
Asterosoma isp.				X								X								X
Asthenopodichnium xylobontum		X			X		X			X			X		X					
Aulichnites parkerensis		X								X					X	X				
Chondrites intricatus		X				X				X	X				X	X				
Cochlichnus anguineus		X								X			X							
Conichnus conicus		X								X						X				
Cruziana isp.			X							X								X		
Cylindrichnus concentricus		X						X		X						X		X		
Diplocraterion habichi				X							X	X					X		X	
Diplocraterion parallelum				X								X					X			
Diplocraterion isp						X	X			X					X	X				
Gyrolithes lorcaensis			X							X								X		
Lockeia siliquaria		X	X							X			X		X	X		X		
Lockeia isp.		X								X					X	X				
Macaronichnus segregatis				X				X		X		X					X	X		
Margaritichnus mansfieldi		X								X					X	X				
Naktodemasis bowni	X									X			X							
Ophiomorpha nodosa			X					X		X								X		
Ophiomorpha isp.						X		X		X						X		X		
Palaeophycus tubularis		X		X		X				X		X			X	X	X			
Planolites montanus	X	X	X			X	X			X			X		X	X		X		
Planolites terraenovae								X		X								X		
Protovirgularia pennatus		X						X		X					X	X		X		
Rhizocorallium commune		X		X		X	X			X		X				X				X
Rhizocorallium jenense		X					X			X	X				X	X				
Rosselia socialis		X		X						X		X				X	X			
Rosselia isp.							X			X					X					
Rusophycus isp.			X							X								X		
Schaubcylindrichnus freyi				X								X								X
Scolicia plana		X								X					X	X				
Scolicia isp.							X			X					X					
Skolithos linearis		X	X	X		X	X			X		X			X		X			X
Taenidium serpentinum		X	X				X			X					X	X		X		
Teichichnus rectus		X	X	X			X			X		X			X	X	X	X		X
Teredolites clavatus		X								X					X	X				

Table 2. Distribution of trace fossils in the Dakota Group with respect of stratigraphic units, lithology, and paleoenvironmental context: LF (Lytle Fm), PF (Plainview Fm), GF (Glencairn Fm), SKS (Skull Creek Shale), MF (Muddy Fm, Denver area), MF (CSM; Channel Sandstone Member), MF (UTM; Upper Transitional Member), MF (FC) (Fort Collins Member), MF (HM; Horsetooth Member); Ss (Sandstone), Slt (Siltstone), Sh (Shale); F (Fluvial), CP (Coastal Plain), IT (Intertidal), ST (Subtidal), ME (Marine Embayment), D (Deltaic), MS (Middle Shoreface), LS (Lower Shoreface).

Table 2. Continued on next page.

Trace Fossil	Formation									Lithology			Environment									
	LF	PF	GF	SKS	MF(CSM)	MF(UTM)	MF	MF(FC)	MF(HM)	Ss	Slt	Sh	F	CP	IT	ST	ME	D	MS	LS
Thalassinoides horizontalis		X													X	X				
Thalassinoides suevicus		X	X	X		X	X			X	X				X	X	X	X		
Treptichnus bifurcus		X							X	X			X		X	X				
Zoophycos insignis			X							X								X		
Zoophycos isp.				X								X					X			
Rhizohaloes							X				X			X						
Caririchnium leonardii							X			X				X						
Chelonipus isp.							X			X				X						
Dromaeosauripus isp.		X								X			X							
Hatcherichnus isp.							X			X				X						
Ignotornis mcconnelli							X			X				X						
Magnoavipes caneeri		X					X			X				X						
Mehliella jeffersonensi							X			X				X						
Ostendichnus bilobatus							X			X				X						
Pterosaur swim tracks							X			X				X						
Tetrapodosaurus isp.		X								X				X						
Dinosaur tracks	X	X								X			X	X						

Table 2. (continued from facing page). See description on p. 60.

Ichnocoenoses	Minor Traces	Dominant Behaviors	Environmental Interpretations
Caririchnium	*Magnoavipes*	Repichnia	Subaerial exposure of an intertidal environment at low tide
Diplocraterion	*Rhizocorallium, Thalassinoides*	Domichnia, Fodinichnia	Moderate depositional energy; moderate sedimentation rate; moderate benthic oxygen; moderate to high nutrients
Naktodemasis	*Planolites*	Repichnia, Domichnia	Variable depositional energy; low and nonsteady sedimentation rate; low to moderate soil moisture; and weak soil development.
Rhizohaloe	NA	Fodinichnia, Domichnia	High water table and poorly drained conditions
Scolicia	*Aulichnites, Archaeonassa, Lockeia, Planolites, Protovirgularia, Thalassinoides, Treptichnus*	Pasichnia, Domichnia, Cubichnia	Moderate to high depositional energy; high sedimentation rate; high benthic oxygen; moderate nutrient levels
Teichichnus-Skolithos	*Asterosoma, Cylindrichnus, Macaronichnus, Palaeophycus, Rhizocorallium, Rosselia, Schaubcylindrichnus, Thalassinoides, Zoophycos*	Fodinichnia, Domichnia	Moderate to low depositional energy; moderate to low sedimentation rate; moderate oxygen; moderate nutrient levels
Zoophycos	*Thalassinoides*	Fodinichnia, Domichnia	Moderate depositional energy; low sedimentation rate; low oxygen; low nutrients

Table 3. Ichnocoenoses of the Dakota Group with minor associated traces, dominant behavior, and environmental interpretations.

1992; Hasiotis, McPherson, & Reilly, 2013) with: (1) variably low to moderate depositional energy; (2) low to moderate, nonsteady sedimentation rate; (3) moderate to low benthic oxygen; and (4) normal marine salinity.

The *Zoophycos* ichnocoenosis occurs in very fine-grained sandstones. Two beds in the upper part of the Glencairn Formation at Skyline Drive and Grape Creek were assigned to the *Zoophycos* ichnocoenosis. This ichnocoenosis has a low biodiversity with *Thalassinoides* being the only other ichnogenus present. The dominant behavior of this ichnocoenosis is fodinichnial with domichnia being a secondary behavior. The bioturbation of the *Zoophycos* ichnocoenosis has a range of 2–3 BPBI. The *Zoophycos* ichnocoenosis represents a prodelta environment (see, MacEachern & Pemberton, 1992; Hasiotis, McPherson, & Reilly, 2013) with: (1) low to moderate depositional energy; (2) low, nonsteady sedimentation rate; (3) moderate to 1ow benthic oxygen; and (4) moderate nutrient availability.

Ichnofacies

The trace-fossil and lithofacies associations that occur in the formations of the Dakota Group are assigned to three ichnofacies: Cruziana, Skolithos, and Scoyenia. The Cruziana Ichnofacies is represented in the upper part of the Plainview Formation at Skyline Drive, the middle and upper parts of the Glencairn Formation at Grape Creek and Skyline Drive, the middle and upper parts of the Skull Creek Shale at Horsetooth Reservoir, the middle and upper parts of the Skull Creek Shale at I-70, the lower and middle parts of the Skull Creek Shale at Dinosaur Ridge, and the lower and middle parts of the Skull Creek Shale at U.S. Route 285. *Asterosoma, Arenicolites, Cruziana, Gyrolithes, Rusophycus, Schaubcylindrichnus, Skolithos, Taenidium, Teichichnus,* and *Zoophycos* in the *Skolithos-Teichichnus* and *Zoophycos* ichnocoenoses are the most indicative of this ichnofacies (MacEachern & Pemberton, 1992; Bromley, 1996). The moderate abundance of domichnia suggests that these traces are present in a more proximal setting than the archetypal Cruziana Ichnofacies. The presence of shale interbedded with very fine-grained sandstone or siltstone is another common feature for this ichnofacies (see, MacEachern & Pemberton, 1992; Hasiotis, McPherson, & Reilly, 2013).

The Skolithos Ichnofacies is represented in the middle part of the Plainview Formation at Grape Creek; lower and middle part of the Plainview at Skyline Drive; middle part of the Plainview at Colorado State Highway 115; middle and upper parts of the Plainview at Horsetooth Reservoir; the middle and upper parts of the Muddy Formation at Grape Creek and Skyline Drive, the lower, middle and upper parts of the Muddy Formation at Dinosaur Ridge, U.S. Route 285, and I-70; and the lower part of the Muddy Formation at Horsetooth Reservoir were deposited in the Skolithos Ichnofacies. The *Diplocraterion* and *Scolicia* ichnocoenoses are the most indicative of this ichnofacies, with a high abundance of trace fossils representing domichnia compared to those representing fodinichnia. The presence of trace fossils representing cubichnia are also indicative of the Skolithos Ichnofacies. *Aulichnites, Asthenopodichnium, Diplocraterion, Margaritichnus, Ophiomorpha, Rhizocorallium, Protovirgularia, Scolicia, Teredolites, Thalassinoides,* and *Treptichnus* are common within the Skolithos Ichnofacies. The lithology of the strata representing the Skolithos Ichnofacies consists of fine- to medium-grained sandstone, with the presence of ripple marks, syneresis cracks, and flaser bedding (see, MacEachern & Pemberton, 1992; Hasiotis, McPherson, & Reilly, 2013).

The Scoyenia Ichnofacies is represented in the upper part of the Lytle Formation at I-70, middle part of the Plainview Formation at Dinosaur Ridge and Skyline Drive, and the middle part of the Muddy Formation at Dinosaur Ridge. The continental *Caririchnium, Lockeia, Naktodemasis,* and Rhizohalo ichnocoenoses are present within this ichnofacies. *Caririchnium, Dromaeosauripus,* and *Magnoavipes* (i.e., footprints), *Naktodemasis* (i.e., meniscate backfilled burrows), and Rhizohaloes (i.e., roots) are indicative of the Scoyenia Ichnofacies (see, Seilacher, 1967; Ekdale, Bromley, & Pemberton, 1984; Hasiotis, 2002, 2004, 2007, 2008; Fischer & Hasiotis, 2018). The lithology of the strata representing the Scoyenia Ichnofacies consists of fine- to very fine-grained, trough-crossbedded and planar sandstones and pedogenically modified mudstones (see, Hasiotis, McPherson, & Reilly, 2013; Fischer & Hasiotis, 2018).

Other researchers have used tetrapod ichnofacies (Lockley, Hunt, & Meyer, 1994; Hunt & Lucas, 2006) to the Dakota Group; however, this should be avoided because tetrapods lack the same sensitivity to physicochemical conditions exhibited by invertebrates, which have life histories and behaviors much more intimately associated the environment (Hasiotis, 2004, 2007, 2008; Hasiotis & Platt, 2012; Hasiotis & others 2012). Tetrapods have greater mobility in that they can move from one environment to another, crossing environments with different physicochemical conditions.

Paleoecology

Trace fossils in the Dakota Group provide a record of the paleoecologic relationships in continental and marine paleoenvironments not represented by body fossils. The limited amount of body fossils within the Dakota Group makes reconstructing ecological relationships difficult and preservational bias is recognized due to the degree of bioturbation, preservation potential of organisms, and the physicochemical factors operating in the environment (Ekdale, Bromley, & Pemberton, 1984; Bromley 1996; Hasiotis, 2004, 2008; MacEachern & others, 2007a; Hasiotis & Platt, 2012; Counts & Hasiotis, 2014).

The paleoecologic relationships of tracemaking organisms in continental paleoenvironments in the Lytle, Plainview, and Muddy formations is recorded by the Scoyenia Ichnofacies, which contains the *Caririchnium, Lockeia, Naktodemasis,* and Rhizohalo ichnocoenoses. The primary producers in these paleoenvironments are represented by rhizohaloes, branch impressions, and wood fragments. The types of plants cannot be inferred but likely represent angiosperms and gymnosperms. The rhizohaloes indicate plants growing in poorly-drained, wetland conditions (Kraus & Hasiotis, 2006; Hasiotis, Kraus, & Demko, 2007). The great abundance of *Naktodemasis* suggests the one-time-presence of abundant plant roots and plant detritus in the soils that were better drained than those with drab-colored rhizohaloes (Smith & Hasiotis, 2008; Counts & Hasiotis, 2009, 2014). Above ground plants of various sizes supported such primary consumers (herbivores) as nodosaurid ankylosaurs (tracks, *Tetrapodosaurus*), ornithopods (tracks, *Caririchnium*), and sauropods (unnamed dinosaur tracks) that required large amounts of vegetation for their diets (Barrett, 2014; Gill & others, 2018). Other primary consumers are represented by burrowing insect adults (*Planolites*) and nymphs and larvae (*Naktodemasis*), which fed on plants and plant roots. The turtles (tracks, *Chelonipus*) were either primary or secondary consumers (Spencer, Thompson, & Hume, 1998). Secondary consumers represented by tracks and trackways include birds (tracks, *Ignotornis*), crocodiles (tracks, *Hatcherichnus, Mehliella*), pterosaurs (unnamed tracks), and dromaeosaurid and ornithomimid theropod dinosaurs (tracks, *Dromaeosauripus*, *Magnoavipes*) (Barrett, 2005). The top consumer was possibly a large carcharodontosaurid therapod dinosaur (traces, *Ostendichnus*) (Lockley & others 2014c; 2016a). Freshwater settings contain deposit-feeding annelid worms (traces, *Cochlichnus*) on bedding surfaces, and filter-feeding, shallow tiered bivalves (traces, *Lockeia*) (Hasiotis, 2004, 2008; Giere, 2006). Terrestrial environments with a high, near-surface water table contain feeding or pupation traces produced by insect larvae or pupae (traces, *Treptichnus*) (Uchman, 2005; Muńiz Guinea & others, 2014; Hogue & Hasiotis, 2018), Detritivores are represented by detritophagous- and rhizophagous-feeding behavior of beetle larvae interpreted as also recorded by *Naktodemasis* in well-drained paleosols and the destructive wood-boring behavior of mayflies represented by *Asthenopodichnium* in freshwater aquatic settings (Hasiotis 2002; Counts & Hasiotis, 2014).

The paleoecologic relationships of tracemaking organisms in shallow marine paleoenvironments in the Plainview and Muddy formations are recorded by the Skolithos Ichnofacies, which contains the *Diplocraterion* and *Scolicia* ichnocoenoses. Trace fossil evidence of primary producers include cyanobacteria based on the presence of microbially induced sedimentary structures (Noffke & others, 2001a); diatoms, dinoflagellates, and marine algae also likely were present (White, Witzke, & Ludvigson, 2000; Witkowski, Harwood, & Chin, 2011). Gastropod (*Aulichnites, Archaeonassa*) and echinoid (*Scolicia*) traces represent grazers and deposit feeders that were likely primary consumers (Gaines & Lubchenco, 1982; McClintock, 1994). Secondary consumers (carnivores and omnivores) are represented by a variety of trace fossils. Traces produced by bivalves represent filter feeders (*Lockeia, Margaritichnus, Protovirgularia*) in sediment and in wood (*Teredolites*) (Page & Lastra, 2003). Traces produced by decapods represent filter feeders and deposit feeders (*Ophiomorpha, Rhizocorallium, Teichichnus, Thalassinoides*) (Pinn & others, 1999; Kinoshita, 2002). Traces produced by polychaetes represent filter feeders (*Arenicolites, Cylindrichnus, Diplocraterion, Palaeophycus, Skolithos*) and deposits feeders (*Chondrites, Macaronichnus, Planolites, Rhizocorallium, Taenidium, Teichichnus, Treptichnus*) (Jumars, Dorgan, & Lindsay, 2015). Traces produced by sea anemones represent filter feeders (*Conichnus, Rosselia*) (Kruger & Griffiths, 1996). Traces produced by echinoids represent deposit feeders (*Scolicia*) (McClintock, 1994). Tiering within the Skolithos Ichnofacies was likely shallow to deep based on the distribution of the trace-fossil assemblage within the strata, with *Arenicolites, Conichnus, Cylindrichnus, Diplocraterion, Macaronichnus, Palaeophycus, Planolites, Rosselia, Rhizocorallium, Skolithos, Taenidium,* and *Teichichnus* occupying shallow tiers, *Ophiomorpha* and *Thalassinoides* occupying intermediate tiers, and *Chondrites* occupying deep tiers within the sediment (MacEachern & others, 2007a; Gingras & others, 2008; Hasiotis, MacPherson, & Reilly, 2013).

The paleoecologic relationships of tracemaking organisms in lower shoreface and offshore marine paleoenvironments in the Plainview, Glencairn, and Skull Creek Shale formations is recorded by the Cruziana Ichnofacies, which includes the *Skolithos-Teichichnus* and *Zoophycos* ichnocoenoses. Filter feeders (primary consumers) are likely represented by traces of bivalves (*Lockeia*) and polychaetes (*Arenicolites, Diplocraterion, Gyrolithes, Palaeophycus, Skolithos*) (Page & Lastra, 2003; Jumars, Dorgan, & Lindsay, 2015. Surface feeders (primary consumers and detritivores) are likely represented by arthropods (*Cruziana, Rusophycus*) (Robertson & Mann, 1980; Goecker & Kåll, 2003). Traces produced by decapods represent filter feeders (*Ophiomorpha, Thalassinoides*) and deposit feeders (*Ophiomorpha, Rhizocorallium, Teichichnus, Thalassinoides, Zoophycos*) (Pinn & others, 1999; Kinoshita, 2002). Traces produced by oligochaetes represent deposit feeders (*Asterosoma, Planolites*) (Giere, 2006). Traces produced by polychaetes represent filter feeders (*Arenicolites, Cylindrichnus, Diplocraterion, Gyrolithes, Palaeophycus, Rosselia, Schaubcylindrichnus, Skolithos*) and deposit feeders (*Macaronichnus, Planolites, Taenidium, Teichichnus, Zoophycos*) (Jumars, Dorgan, & Lindsay, 2015). The Skull Creek Shale is dominated by deposit feeders with only a minor abundance of filter feeders, whereas the Glencairn Formation is dominated by filter feeders and deposit feeders within the sand-rich beds. Tiering in the Cruziana Ichnofacies likely ranged from shallow to deep based on the distribution of the trace-fossil assemblage within the strata, with *Arenicolites, Asterosoma, Cylindrichnus, Diplocraterion, Gyrolithes, Lockeia, Macaronichnus, Rhizocorallium, Rosselia, Palaeophycus, Planolites, Schaubcylindrichnus, Skolithos, Taenidium,* and *Teichichnus* occupying the shallow tiers, *Ophiomorpha* and *Thalassinoides* occupying intermediate tiers, and *Thalassinoides* with *Zoophycos* occupying deeper tiers within the sediment (MacEachern & others, 2007a; Gingras & others, 2008; Hasiotis, MacPherson, & Reilly, 2013).

Stratigraphic Distribution of Dakota Group Ichnotaxa, Ichnocoenoses, and Ichnofacies

The ichnotaxa, ichnocoenoses, and ichnofacies present within each formation of the Dakota Group are discussed herein (Table 4). The purpose is to understand how uniformly distributed the ichnotaxa are throughout the Dakota Group along Colorado Front Range, as well as to determine which formation and location has the greatest ichnodiversity. This will allow a better understanding of the distribution of paleoenvironmental conditions during deposition of the Dakota Group.

The Lytle Formation.—The Lytle Formation contains only two ichnotaxa and one morphotype in open nomenclature (Table 4). The Denver area has the greatest ichnodiversity, with two invertebrate ichnotaxa and one tetrapod morphotype. In contrast, in the Cañon City area, The Lytle Formation only contains one tetrapod track morphotype, whereas the Fort Collins area has no trace fossils. The very low ichnodiversity of this Formation results from the predominance of channel deposits, which support far fewer tracemakers and preserve fewer traces due to their high energy (see Hasiotis 2004, 2007, 2008; Hasiotis & others 2012; Hasiotis, MacPherson, & Reilly, 2013). Most trace fossils in fluvial environments occur in floodplain deposits (Hasiotis 2004, 2007, 2008; Hasiotis & others 2012), which have been removed by channel reworking in the Lytle Formation.

The Plainview Formation.—The Plainview Formation contains 25 ichnotaxa overall (Table 4), with the highest diversity in the Cañon City area (18 invertebrate ichnotaxa and three tetrapod ichnotaxa). Only six invertebrate ichnotaxa have been recognized in the Fort Collins area, and only five ichnotaxa (four invertebrate and one tetrapod) observed in the Denver area. *Skolithos* and *Planolites* were present in all three areas, with *Chondrites* and *Rhizocorallium* being present in the Cañon City and Fort Collins areas. *Lockeia* is present only in the Cañon City and Denver areas, whereas *Conichnus* is only present in the Cañon City area, and *Cochlichnus* is only present in the Denver area. The high ichnodiversity of the Plainview Formation results from its three ichnocoenoses (*Lockeia, Scolicia* and *Skolithos-Teichichnus*) and three ichnofacies (Cruziana, Scoyenia, and Skolithos). These environments range from fluvial to mostly intertidal and subtidal with physicochemical conditions that reflect shallow marine processes that operated in environments

Fort Collins Area	Muddy Formation (8)	*Archaeonassa, Aulichnites, Cylindrichnus, Macaronichnus, Ophiomorpha, Planolites, Protovirgularia, Treptichnus*
	Skull Creek Shale (7)	*Asterosoma, Diplocraterion, Palaeophycus, Rhizocorallium, Schaubcylindricnus, Skolithos, Teichichnus*
	Plainview Formation (6)	*Archaeonassa, Chondrites, Planolites, Rhizocorallium, Skolithos, Taenidium*
	Lytle Formation (0)	None
Denver Area	Muddy Formation (21)	*Archaeonassa, Asthenopodichnium, Caririchnium, Chelonipus, Diplocraterion, Hatcherichnus, Ignotornis, Magnoavipes, Mehliella, Ostendichnus, Palaeophycus, Planolites,* Pterosaur swim tracks, *Rhizocorallium, Rhizohaloes, Rosselia, Scolicia, Skolithos, Taenidium, Teichichnus, Thalassinoides*
	Skull Creek Shale (11)	*Arenicolites, Asterosoma, Diplocraterion, Macaronichnus, Palaeophycus, Rhizocorallium, Rosselia, Skolithos, Teichichnus, Thalassinoides, Zoophycos*
	Plainview Formation (5)	*Cochlichnus, Dromaeosauripus, Lockeia, Planolites, Skolithos*
	Lytle Formation (3)	*Naktodemasis, Planolites,* Dinosaur tracks
Cañon City Area	Muddy Formation (10)	*Arenicolites, Asthenopodichnium, Chondrites, Diplocraterion, Ophiomorpha, Palaeophycus, Planolites, Rhizocorallium, Skolithos, Thalassinoides*
	Glencairn Formation (11)	*Cruziana, Gyrolithes, Lockeia, Ophiomorpha, Planolites, Rusophycus, Skolithos, Taenidium, Teichichnus, Thalassinoides, Zoophycos*
	Plainview Formation (21)	*Asthenopodichnium, Aulichnites, Chondrites, Conichnus, Cylindrichnus, Lockeia, Magnoavipes, Margaritichnus, Palaeophycus, Planolites, Protovirgularia, Rhizocorallium, Rosselia, Scolicia, Skolithos, Teichichnus, Teredolites, Tetrapodosaurus, Thalassinoides, Treptichnus,* Dinosaur tracks
	Lytle Formation (1)	Dinosaur tracks

Table 4. Distribution of trace fossils by formation and area in the Dakota Group along the Colorado Front Range.

inhabited by a variety of marine organisms (see, MacEachern & Pemberton, 1992; Hubbard, Gingras, & Pemberton, 2004; Harris & others, 2016; Bhatt & Patel, 2017).

The Skull Creek Shale and the Glencairn Formation.—The Skull Creek Shale in the Denver area and the Glencairn Formation in the Cañon City area have the same ichnodiversity with 11 ichnotaxa. In contrast, the Skull Creek Shale in the Fort Collins area has seven ichnotaxa (Table 4). *Skolithos* and *Teichichnus* are present in all three areas, with *Asterosoma, Diplocraterion, Palaeophycus,* and *Rhizocorallium* occurring only in the Skull Creek Shale. *Thalassinoides* and *Zoophycos* are present in Glencairn Formation and the Skull Creek Shale in the Denver area. The ichnodiversity of the Glencairn Formation and the Skull Creek Shale are similar, with the Skull Creek Shale having one more ichnotaxa overall. The Cruziana Ichnofacies are represented in both formations, with the Skull Creek Shale recording two ichnocoenoses (*Diplocraterion* and *Skolithos-Teichichnus*) and the Glencairn Formation recording only the *Zoophycos* ichnocoenosis. The ichnodiversity of these formations are likely lower than that of the Plainview and Muddy formations due to the lower availability of oxygen and nutrients in the sediments (see, MacEachern & Pemberton, 1992; Gingras, MacEachern, & Pemberton, 1998; Olariu, Steel, & Petter, 2010; Van der Kolk, Flaig, & Hasiotis, 2015).

The Muddy Formation.—The Muddy Formation has 24 ichnotaxa (Table 4). In the Denver area, the Muddy Formation has the greatest ichnodiversity with 11 invertebrate and seven tetrapod ichnotaxa, one morphotype of plant roots in open nomenclature, and one tetrapod morphotype of pterosaur swim tracks in open nomenclature. Cañon City area has the second highest ichnodiversity with 10 ichnotaxa, followed by eight ichnotaxa in the Fort Collins area. *Planolites* is the only ichnogenus occurring in all areas; *Asthenopodichnium, Diplocraterion, Palaeophycus, Rhizocorallium,* and *Thalassinoides* are found in the Cañon City and Denver areas. *Archaeonassa* occur in the Muddy Formation in the Denver and Fort Collins areas, whereas *Ophiomorpha* occurs in the Muddy Formation in the Cañon City and Fort Collins areas. Similar to

Formation	Shared Ichnotaxa	Ichnofacies	Depositional environment	References
Mesa Rica Sandstone	*Arenicolites, Caririchnium, Chondrites, Conichnus, Macaronichnus, Ophiomorpha, Palaeophycus, Planolites, Rhizocorallium, Rosselia, Skolithos, Teichichnus, Thalassinoides*		Fluvial, with minor marine influence	Kues & Lucas, 1987; Holbrook, 1996; Scott & others, 2004; van Yperen & others, 2020
Pajarito Formation	*Arenicolites, Caririchnium, Hatcherichnus, Magnoavipes, Rhizocorallium, Skolithos, Planolites, Thalassinoides*	Skolithos, Scoyenia	Coastal plain to intertidal	Holbrook, 1996, Matsukawa, Lockley, & Hunt, 1999; Scott & others, 2004; Kukihara & Lockley, 2012

Table 5. Shared ichnotaxa, ichnofacies and depositional environments of other Dakota Group formations.

the Plainview Formation, the Muddy Formation has high ichnodiversity due to its multiple depositional environments. Although only two ichnofacies (Scoyenia and Skolithos) are present in the Muddy Formation, four ichnocoenoses (*Caririchnium*, *Diplocraterion*, Rhizohalo, and *Scolicia*) occur therein. These ichnocoenoses record communities in coastal plain to intertidal and subtidal paleoenvironments. Salinity fluctuations within the Muddy Formation were variable, based on the fact that some intervals have higher ichnodiversity that likely reflect mesohaline to polyhaline salinities, whereas other intervals exhibit lower ichnodiversity that likely reflect oligohaline to mesohaline conditions (see, MacEachern & Pemberton, 1992; Hubbard, Gingras, & Pemberton, 2004; Paz & others, 2020).

Comparative Ichnotaxonomy

The Dakota Group contains numerous, common facies-crossing ichnotaxa, which represent multiple depositional environments. Similarities between the Dakota Group ichnotaxa and the ichnotaxa of other Western Interior Seaway deposits reflect the environments in which they were deposited. The Lytle Formation was deposited in a fluvial environment. The Plainview Formation was deposited in a shallow-marine environment, similar to an estuary. The Glencairn Formation was deposited in a marine delta-front to prodelta environment. The Skull Creek Shale was deposited in shallow-marine embayments at Dinosaur Ridge, I-70, and U.S. Route 285, as well in middle and lower shoreface environments at Horsetooth Reservoir. The Muddy Formation was deposited in both continental and marine environments, in settings ranging from fluvial and coastal plain to estuarine and deltaic.

Ichnotaxonomy of other Dakota Group deposits.—Other formations also included in the Dakota Group are located in southeastern Colorado, New Mexico, Oklahoma, and Texas. No ichnotaxonomic studies of the invertebrate trace fossils exist, as researchers focused on stratigraphy or tetrapod ichnology (Kues & Lucas, 1987; Holbrook, 1996; Holbrook & Ethridge, 1996; Matsukawa, Lockley, & Hunt, 1999; Scott & others, 2004; Oboh-Ikuenobe & others, 2008; Kukihara & Lockley, 2012; Van Yperen & others, 2020). In ascending order, the Mesa Rica Sandstone, Pajarito, and Romeroville formations have stratigraphic equivalency to the Muddy Formation in the Colorado Front Range. With the exception of the Romeroville Formation, previous studies have identified ichnogenera in these units (Kues & Lucas, 1987; Scott & others, 2004).

The Mesa Rica Sandstone of the Lower Cretaceous of southeastern Colorado, New Mexico, Oklahoma, and Texas, shares 13 of its 15 ichnogenera with the Muddy Formation in the Colorado Front Range (Table 5) (Holbrook, 1996; Scott & others, 2004; Van Yperen & others, 2020). *Helminthopsis* and *Phycosiphon* are not shared with the Muddy Formation. The Mesa Rica Sandstone is interpreted as representing a fluvial to river dominated-deltaic system (Kues & Lucas, 1987; Holbrook, 1996; Scott & others, 2004; Van Yperen & others, 2020). Invertebrate trace fossils are present in marine intervals interfingering with fluvial deposits. Within the deltaic system, ichnodiversity is higher in deposits with a more dominant marine influence than under fluvial influence. This suggests that salinity was a physiochemical control in the Mesa Rica Sandstone. No ichnofacies were assigned to the Mesa Rica Sandstone trace-fossil assemblages, but intervals with invertebrate trace fossils and a strong marine influence likely belong to the Skolithos Ichnofacies, whereas those with tetrapod trace fossils in fluvially dominant deposits belong to the Scoyenia Ichnofacies.

The Pajarito Formation, reported to represent coastal plain to intertidal environments, shares eight of its 12 ichnogenera with the Muddy Formation (Table 5) (Holbrook, 1996; Holbrook & Ethridge, 1996; Matsukawa, Lockley, & Hunt, 1999; Scott & others, 2004; Kukihara & Lockley, 2012). *Lockeia,* pterosaur swim tracks, *Siphonites,* and *Teredolites* are recorded in the Pajarito Formation but are not present in the Muddy Formation at localities in our study. Although no ichnofacies have been assigned to the Pajarito Formation trace-fossil assemblages, its marine intervals therein likely belong to the Skolithos Ichnofacies, whereas its coastal plain intervals belong to the Scoyenia Ichnofacies (see, Kues & Lucas, 1987; Holbrook, 1996; Holbrook & Ethridge, 1996; Scott & others, 2004; Oboh-Ikuenobe & others, 2008).

Ichnotaxonomy of Western Interior Seaway deposits.—The Dakota Group shares ichnotaxa with multiple other formations along the Western Interior Seaway (Table 6). The Upper Cretaceous Cardium Formation in Alberta, Canada, has 20 ichnogenera (Pemberton & Frey, 1984; Vossler & Pemberton, 1989) of which 17 are shared with the Dakota Group (Table 5). *Ancorichnus, Bergaueria,* and *Helminthopsis* are not shared with the Dakota Group. The Cardium Formation was deposited in upper shoreface to offshore environments, with the deposits influenced by storm events (Pemberton & Frey, 1984; Vossler & Pemberton, 1989). The Cardium Formation has been assigned to Skolithos and Cruziana ichnofacies (Pemberton & Frey, 1984). The traces within the Skolithos Ichnofacies (*Cylindrichnus, Diplocraterion, Ophiomorpha, Rosselia,* and *Skolithos*) evidently had opportunistic makers that colonized after storm events (Pemberton & Frey, 1984). The traces of the Cruziana

Formation	Shared Ichnotaxa	Ichnofacies	Depositional environments	References
Cardium Formation	*Asterosoma, Chondrites, Cochlichnus, Conichnus, Cylindrichnus, Diplocraterion, Ophiomorpha, Palaeophycus, Planolites, Rhizocorallium, Rosselia, Schaubcylindrichnus, Skolithos, Taenidium, Teichichnus, Thalassinoides, Zoophycos*	Cruziana	Upper shoreface and offshore	Pemberton & Frey, 1984; Vossler & Pemberton, 1989
Star Point Formation, Panther Member	*Chondrites, Cylindrichnus, Ophiomorpha, Palaeophycus, Planolites, Protovirgularia, Rosselia, Scolicia, Schaubcylindrichnus, Skolithos, Taenidium, Teichichnus, Teredolites*	Cruziana	Offshore to middle shoreface	Frey & Howard, 1985; Olariu, Steel, & Petter, 2010
Dunvegan Formation	*Arenicolites, Asterosoma, Chondrites, Cylindrichnus, Diplocraterion, Macaronichnus, Ophiomorpha, Palaeophycus, Planolites, Rosselia, Rhizocorallium, Schaubcylindrichnus, Skolithos, Teichichnus, Thalassinoides, Zoophycos*	Skolithos, Cruziana, Zoophycos	River- and wave-dominated delta	Bhattacharya & Walker, 1991; Gingras, MacEachern, & Pemberton, 1998
Blackhawk Formation, Spring Canyon Member	*Arenicolites, Chondrites, Cylindrichnus, Lockeia, Ophiomorpha, Palaeophycus, Planolites, Rosselia, Schaubcylindrichnus, Skolithos, Teichichnus, Teredolites, Thalassinoides*	Cruziana, Skolithos	Offshore to middle shoreface and near shore deposits transitioning into a delta	Kamola, 1984; Frey, 1990
Viking Formation	*Arenicolites, Asterosoma, Aulichnites, Chondrites, Conichnus, Cylindrichnus, Diplocraterion, Lockeia, Macaronichnus, Ophiomorpha, Palaeophycus, Planolites, Rhizocorallium, Rosselia, Schaubcylindrichnus, Scolicia, Skolithos, Teichichnus, Thalassinoides, Zoophycos*	Glossifungites, Skolithos, Cruziana, Zoophycos	Progradational, transgressive events	MacEachern, Bechtel, & Pemberton, 1992; Raychaudhuri & others, 1992; MacEachern & Pemberton, 1994; MacEachern, Zaitlin, & Pemberton, 1999
Peace River Formation, Paddy Member	*Arenicolites, Asterosoma, Chondrites, Conichnus, Cylindrichnus, Diplocraterion, Lockeia, Macaronichnus, Ophiomorpha, Palaeophycus, Planolites, Rosselia, Schaubcylindrichnus, Skolithos, Teichichnus, Teredolites, Thalassinoides, Zoophycos*	Skolithos, Cruziana	Estuarine, restricted bay	Leckie & Singh, 1991; MacEachern & Gingras, 2007
Grand Rapids Formation	*Asterosoma, Chondrites, Cylindrichnus, Gyrolithes, Palaeophycus, Planolites, Rosselia, Skolithos, Teichichnus*	Skolithos, Cruziana	River-dominated delta, restricted bay	Beynon & others, 1988; MacEachern & Gingras, 2007
McMurry Formation	*Arenicolites, Asterosoma, Conichnus, Cylindrichnus, Gyrolithes, Lockeia, Naktodemasis, Ophiomorpha, Palaeophycus, Planolites, Rosselia, Rhizocorallium, Schaubcylindrichnus, Skolithos, Teichichnus, Thalassinoides*	Skolithos, Cruziana	Estuarine, open bay	MacEachern & Gingras, 2007; Gingras & others, 2016
Frontier Formation, Wall Creek Member	*Arenicolites, Asterosoma, Chondrites, Conichnus, Cylindrichnus, Diplocraterion, Macaronichnus, Ophiomorpha, Palaeophycus, Planolites, Rhizocorallium, Rosselia, Schaubcylindrichnus, Scolicia, Taenidium, Teichichnus, Thalassinoides, Zoophycos*	Skolithos, Cruziana	River-dominated delta to a wave-dominated delta to a tide-influenced delta	Gani, Bhattacharya, & MacEachern, 2008; Sadeque & others, 2009
Fort Hays Member, Niobrara Chalk	*Asterosoma, Cylindrichnus, Chondrites, Planolites, Protovirgularia, Teichichnus, Thalassinoides, Zoophycos*	Cruziana, Zoophycos	Offshore	Frey, 1970
Bluesky Formation	*Arenicolites, Asterosoma, Chondrites, Cylindrichnus, Diplocraterion, Planolites, Gyrolithes, Macaronichnus, Palaeophycus, Rosselia, Schaubcylindrichnus, Skolithos, Teichichnus, Teredolites, Thalassinoides*	Skolithos, Cruziana	Estuarine	Hubbard, Gingras, & Pemberton, 2004
Mannville Group	*Arenicolites, Asterosoma, Chondrites, Cylindrichnus, Gyrolithes, Lockeia, Palaeophycus, Planolites, Rhizocorallium, Rosselia, Schaubcylindrichnus, Skolithos, Teichichnus, Thalassinoides*	Skolithos, Cruziana	Bay-head deltas and estuarine	Morshedian, MacEachern, & Dashtgrad, 2009
Loyd Sandstone	*Arenicolites, Aulichnites, Conichnus, Cylindrichnus, Diplocraterion, Lockeia, Macaronichnus, Ophiomorpha, Palaeophycus, Planolites, Protovirgularia, Rhizocorallium, Schaubcylindrichnus, Scolicia, Skolithos, Taenidium, Teichichnus, Teredolites, Thalassinoides*	Skolithos, Cruziana	Delta front, prodelta, and offshore	Flaig & others, 2019

Table 6. Shared ichnotaxa, ichnofacies and depositional environments of related Western Interior Seaway deposits.

Ichnofacies (*Chondrites, Cochlichnus, Rhizocorallium, Taenidium, Thalassinoides,* and *Zoophycos*) are interpreted to have had resident tracemakers that inhabited media above the fair-weather wave base (e.g., Pemberton & Frey, 1984).

The Upper Cretaceous Panther Member of the Star Point Formation in eastern Utah, USA, has 16 ichnogenera (Frey & Howard, 1985; Olariu, Steel, & Petter, 2010) of which 13 are shared with the Dakota Group (Table 6). *Ancorichnus, Helminthopsis,* and *Phycosiphon* are not shared with the Dakota Group. The Panther Member was deposited in a river-dominated deltaic system (Olariu, Steel, & Petter, 2010). Trace fossil abundance and diversity increase as the deposits transition from shallow marine (*Palaeophycus* and *Teredolites*) to distal delta-front (*Cylindrichnus, Ophiomorpha, Rosselia, Schaubcylindrichnus,* and *Teichichnus*) environments. No ichnofacies were assigned to the trace-fossil assemblages in the Panther Member, but they likely belongs to the Skolithos and Cruziana ichnofacies (Frey & Howard, 1985; Olariu, Steel, & Petter, 2010).

The Upper Cretaceous Dunvegan Formation in northwestern Alberta, Canada, has 20 ichnogenera (Bhattacharya & Walker, 1991; Gingras, MacEachern, & Pemberton, 1998) of which 16 are shared with the Dakota Group (Table 6). *Ancorichnus, Helminthopsis, Siphonichnus,* and *Trichichnus* are not shared with the Dakota Group. The Dunvegan Formation is subdivided into numerous facies associations that represent offshore, distal and proximal delta-front, prodelta, distributary mouth bar, and delta-plain environments (Bhattacharya & Walker, 1991; Gingras, MacEachern, & Pemberton, 1998). The deltas of the Dunvegan Formation are interpreted to have transitioned from river-dominated to wave-dominated deltaic systems (Bhattacharya & Walker, 1991; Gingras, MacEachern, & Pemberton, 1998). The wave-dominated deltaic systems have a higher overall ichnodiversity and abundance than the river-dominated deltaic systems. Facies associations within both deltaic systems have been assigned to the Skolithos, Cruziana, and Zoophycos ichnofacies (Bhattacharya & Walker, 1991; Gingras, MacEachern, & Pemberton, 1998).

The Upper Cretaceous Spring Canyon Member of the Blackhawk Formation in east-central Utah has 15 ichnogenera (Kamola, 1984; Frey, 1990) of which 13 are shared with the Dakota Group (Table 6). *Ancorichnus* and *Pholeus* are not shared with the Dakota Group. At one locality, the Spring Canyon Member records several transitions from an offshore to a middle shoreface environments, whereas another locality exposure records nearshore deposits transitioning into a deltaic deposit. Ichnogenera reported from these localities are dominated by domichnia, with only a few ichnospecies of fodinichnia and cubichnia reported. Within the nearshore deposits in the upper part of the Spring Canyon Member, evidence of plants, either as plant debris or as coal seams, is reported (Kamola, 1984). Coal seams indicate that those parts of the Spring Canyon Member were deposited in continental settings. The marine deposits of the Spring Canyon Member have been assigned to the Cruziana and Skolithos ichnofacies (Kamola, 1984; Frey, 1990). Continental deposits were not previously assigned an ichnofacies, but they evidently belong to the Scoyenia Ichnofacies.

The Viking Formation of Albian age in Alberta, Canada, has 26 ichnogenera (MacEachern, Bechtel, & Pemberton, 1992; Raychaudhuri & others, 1992; MacEachern & Pemberton, 1994; MacEachern, Zaitlin, & Pemberton, 1999) of which 20 are shared with the Dakota Group (Table 6). *Bergaueria, Gastrochaenolites, Helminthopsis, Phycosiphon, Polykladichnus,* and *Siphonichnus* are not shared with the Dakota Group. Overall, the Viking Formation records several progradational and transgressive events, resulting in deposition in incised valleys, estuaries, bay-head deltas, and channel complexes (MacEachern, Bechtel, & Pemberton, 1992; Raychaudhuri & others, 1992; MacEachern & Pemberton, 1994; MacEachern, Zaitlin, & Pemberton, 1999). Shoreface environments contain *Asterosoma, Arenicolites, Chondrites, Cylindrichnus, Diplocraterion, Helminthopsis, Ophiomorpha, Rosselia, Rhizocorallium, Schaubcylindrichnus, Skolithos,* and *Teichichnus,* indicating the presence of both the Skolithos and Cruziana ichnofacies. Offshore environments contain *Asterosoma, Chondrites, Cylindrichnus, Helminthopsis, Teichichnus,* and *Zoophycos,* suggesting a Cruziana Ichnofacies (MacEachern, Bechtel, & Pemberton, 1992; Raychaudhuri & others, 1992; MacEachern & Pemberton, 1994; MacEachern, Zaitlin, & Pemberton, 1999). The incised valley deposits and surfaces were reworked during transgression and little to no fluvial deposits remain. Trace fossils reported in these surfaces are *Arenicolites, Diplocraterion, Gastrochaenolites, Rhizocorallium, Skolithos,* and *Thalassinoides* and are assigned to the Glossifungites Ichnofacies. Estuary deposits show few signs of salinity-stressed conditions with the trace fossils *Arenicolites, Diplocraterion, Helminthopsis, Ophiomorpha, Palaeophycus, Rosselia, Schaubcylindrichnus,* and *Teichichnus* being abundant. Trace fossils within tidal channel complexes are rare to moderate in abundance, with *Ophiomorpha* and *Skolithos* being the most common. The Viking Formation was assigned mostly to the Skolithos and Cruziana ichnofacies, with part assigned to the Glossifungites Ichnofacies, and deep marine deposits assigned to the Zoophycos Ichnofacies (MacEachern, Bechtel, & Pemberton, 1992; Raychaudhuri & others, 1992; MacEachern & Pemberton, 1994; MacEachern, Zaitlin, & Pemberton, 1999).

The Paddy Member of the Albian Peace River Formation in Alberta, Canada, has 19 ichnogenera (Leckie & Singh, 1991; MacEachern & Gingras, 2007) of which 18 are shared with the Dakota Group (Table 6). *Trichichnus* is the only trace fossil not shared with the Dakota Group. The Paddy Member was deposited in an estuary that emptied into a restricted bay (Leckie & Singh, 1991; MacEachern & Gingras, 2007). Deposits within the Paddy Member represent salinity-stressed conditions with reduced trace-fossil abundance; most of the trace fossils are reported in deposits with a greater marine influence. Trace-fossil assemblages in the Paddy Member has been assigned to the Skolithos and Cruziana ichnofacies (Leckie & Singh, 1991; MacEachern & Gingras, 2007).

The Grand Rapids Formation of lower Albian age in Alberta, Canada, has 10 ichnogenera (Beynon & others, 1988; MacEachern & Gingras, 2007) of which nine are shared with the Dakota Group (Table 6). The trace fossil *Monocraterion* is not shared with the Dakota Group. The Grand Rapids Formation has six recorded shoaling-upward parasequences that represent restricted bays and river-dominated delta complexes (Beynon, & others, 1988; MacEachern & Gingras, 2007). The conditions within these environments were controlled by salinity, as reflected in the low ichnodiversity and reduced sizes of the trace fossils (Beynon, & others, 1988). Trace-fossil assemblages in the Grand Rapids Formation has been assigned to the Skolithos and Cruziana ichnofacies (MacEachern & Gingras, 2007).

The McMurry Formation of Albian Age has 25 ichnogenera (MacEachern & Gingras, 2007; Gingras & others, 2016; Harris & others, 2016) of which 16 are shared with the Dakota Group (Table 6). Trace fossils reported in the McMurry Formation, but not in the Dakota Group, are present within both continental and marine deposits. Within the continental deposits *Beaconites, Camborygma, Daimonelyx,* and *Scoyenia* are reported, whereas the marine deposits contain *Bergaueria, Helminthopsis, Siphonichnus, Phycosiphon,* and *Psilonichnus*. The depositional history of the McMurry Formation has been reinterpreted several times over the decades, with current interpretations of its depositional environment being an estuary that emptied into an open bay (MacEachern & Gingras, 2007; Gingras & others, 2016). The upper part of the McMurry Formation consists of several parasequences that contain marine to brackish water trace-fossil assemblages. The lower McMurry Formation contains fluvial pointbar successions with continental traces from produced by invertebrates and tetrapods (Gingras & others, 2016). The marine deposits of the McMurry Formation are assigned to the Skolithos and Cruziana ichnofacies. The continental deposits have not previously been assigned an ichnofacies, but evidently belong in the Scoyenia Ichnofacies (MacEachern & Gingras, 2007).

The Wall Creek Member of the Upper Cretaceous Frontier Formation in Wyoming, USA, has 24 ichnogenera (Sadeque & others, 2008; Gani, Bhattacharya, & MacEachern, 2009) of which 18 are shared with the Dakota Group (Table 6). *Bergaueria, Helminthopsis, Phoebichnus, Phycosiphon, Siphonichnus,* and *Trichichnus* are not shared with the Dakota Group. The Wall Creek Member records three deltaic successions, with the first being a river-dominated delta, followed by a wave-dominated delta, and then a tide-dominated delta (Sadeque & others, 2008; Gani, Bhattacharya, & MacEachern, 2009). The river-dominated delta deposits have low to moderate bioturbation, suggesting that physicochemical controls on ichnodiversity were affected by both freshwater and marine conditions. The wave-dominated delta deposits have moderate to high bioturbation, indicating that physicochemical controls on the ichnodiversity were dominated by marine conditions. The tidal-dominated delta deposits exhibit low bioturbation, with synaeresis cracks, suggesting that salinity was the dominant physicochemical control within the delta. The Wall Creek Member has been assigned to the Skolithos and Cruziana ichnofacies (Sadeque & others, 2008; Gani, Bhattacharya, & MacEachern, 2009).

The Fort Hays Member of the Upper Cretaceous Niobrara Chalk in western Kansas, USA, has nine ichnogenera (Frey, 1970) of which eight are shared with the Dakota Group (Table 6). *Ancorichnus* is the only trace fossil not shared with the Dakota Group. The carbonate units of the Fort Hays Member consist of chalk, limestone, and shale deposited in an offshore environment. Within these units, channels indicate low to moderate currents, which were inferred to have kept benthic oxygen moderate to high. The Fort Hays Member of the Niobrara Chalk has been assigned to the Cruziana and Zoophycos ichnofacies (Frey, 1970).

The Lower Cretaceous Bluesky Formation Alberta, Canada, has 18 ichnogenera (Hubbard, Gingras, & Pemberton, 2004), of which 16 are shared with the Dakota Group (Table 6). *Ancorichnus* and *Helminthopsis* are not shared with the Dakota Group. The Bluesky Formation was deposited in lower, middle, and upper estuarine environments. Ichnodiversity was lowest within the upper estuary and highest within the lower estuary. Rhizoliths are present within both the upper and middle estuary environments and may represent mangroves and other seawater-tolerant conditions. *Teredolites* is present in the middle and lower estuary deposits. The Bluesky Formation has been assigned to the Skolithos and Cruziana ichnofacies (Hubbard, Gingras, & Pemberton, 2004).

The Lower Cretaceous Mannville Group in west-central Saskatchewan, Canada, has 16 ichnogenera (Morshedian, MacEachern, & Dashtgard, 2009), of which 14 are shared with the Dakota Group (Table 6). *Lingulichnus* and *Phycosiphon* are not shared with the Dakota Group. The Mannville Group contains three formations: Sparky, Waseca, and McLaren formations, in which 10 recurring facies are reported. These facies record physiochemically stressed conditions typically found in brackish environments such as bay-head deltas and estuaries. The Mannville Group has been assigned to the Skolithos and Cruziana ichnofacies (Morshedian, MacEachern, & Dashtgard, 2009).

The Upper Cretaceous Loyd Sandstone Member of the Mancos Shale in western Colorado, USA, has 26 ichnogenera (Flaig & others, 2019), of which 19 are shared with the Dakota Group (Table 6). *Bergaueria, Gyrochorte, Helminthopsis, Monocraterion, Phycodes, Piscichnus,* and *Sagittichnus* are not shared with the Dakota Group. The Loyd Sandstone Member is interpreted to have been deposited in distal and proximal delta fronts, prodelta, and offshore environments (Flaig & others, 2019). The distal delta front and prodelta deposits have high ichnodiversity and abundance, suggesting that the physicochemical controls were dominated by marine conditions. Proximal delta-front deposits contain abundant *Ophiomorpha* along with *Palaeophycus, Planolites, Scolicia,* and *Thalassinoides*. The physicochemical controls on the proximal delta front were depositional energy and/or sedimentation rate, as is interpreted from medium-grained sandstones with trough-cross stratification infilling erosional surfaces. Offshore deposits have a less diverse ichnofauna consisting of *Helminthopsis, Palaeophycus, Planolites, Phycosiphon,* and *Teichichnus,* suggesting that benthic oxygen was a physicochemical control in that environment. The trace-fossil assemblages of the Loyd Sandstone Member have been assigned to the Skolithos and Cruziana ichnofacies (Flaig & others, 2019).

SUMMARY

The ichnofauna of the Lytle Formation occurs in medium- to fine-grained sandstones, with trough-crossbedding indicative of a fluvial environment, similar to the lowest stratigraphic units of the McMurry Formation. The lack of ichnofauna in most of the Lytle Formation suggests that the major physicochemical controls were high depositional energy, low sedimentation rate, and groundwater profile (soil moisture content). The presence of dinosaur tracks suggests that large dinosaurs lived periodically along the fluvial systems of the Lytle Formation. The presence of invertebrates is seen in both the McMurry and Lytle formations; however, the presence of non-dinosaur tetrapods is only seen in the McMurry Formation, with the Lytle Formation lacking evidence for these tracemakers.

The ichnofauna of the Plainview Formation occur in intertidal to subtidal environments, similar to the ichnofauna reported in the Bluesky, McMurry, and Peace River (Paddy Member) formations and Mannville Group. Only the Planview and McMurry formations have continental trace fossils. The physicochemical controls for the marine ichnofauna in the Plainview Formation were, highly variable depositional energy, moderate, unsteady sedimentation rate, moderate to high oxygen, and variable salinity. The overall abundance of shallow-marine domichnia (e.g., *Lockeia, Margaritichnus, Rosselia, Skolithos, Teredolites,* and *Thalassinoides*), places the Plainview Formation within the Skolithos Ichnofacies. The presence of dinosaur tracks suggests that a few intervals within the Plainview Formation were continental fluvial environments (Dinosaur Ridge, Skyline Drive, and Colorado State Highway 115).

The ichnofauna of the Glencairn Formation occurs in fine-grained sandstones of coarsening upward parasequences in a wave- or tide-influenced deltaic system similar to the Dunvegan, Grand Rapids, and Frontier (Wall Creek Member) formations. The physiochemical controls on the Glencairn Formation were low to moderate depositional energy, low to moderate sedimentation rate, and aerobic to dysaerobic benthic oxygen levels. This is based on the presence of domichnia and fodinichnia within the Glencairn Formation (e.g., *Cruziana, Gyrolithes, Ophiomorpha, Rusophycus, Thalassinoides,* and *Zoophycos*).

The ichnofauna of the Skull Creek Shale occur in shales interbedded with very fine-grained sandstones and siltstones, similar to the Cardium, Star Point (Panther Member), Blackhawk (Spring Canyon Member), and Viking formations. The Skull Creek Shale was deposited in a marine embayment (Dinosaur Ridge, I-70, U.S. Route 285) and in middle and lower shoreface environments (Horsetooth Reservoir). The dominant controlling physicochemical factors on the Skull Creek Shale ichnofauna were low to moderate depositional energy, low to moderate nonsteady sedimentation rate, and aerobic to dysaerobic benthic oxygen, based on the moderate abundance of domichnia (e.g., *Arenicolites, Diplocraterion, Schaubcylindrichnus,* and *Skolithos*) and high abundance of fodinichnia (e.g., *Asterosoma, Rhizocorallium,* and *Teichichnus*). The low abundance of domichnia in intervals from the lower parts of the Skull Creek Shale at Horsetooth Reservoir, I-70, and U.S. Route 285 suggests that intermittent shifts in salinity may have been a controlling physicochemical factor for the Skull Creek Shale.

The ichnofauna of the Muddy Formation occur in fine- to very fine-grained sandstones with bedding indicative of shallow-marine to coastal plain environments, similar to the Bluesky, McMurry, Mesa Rica, Pajarito, and Peace River (Paddy Member) formations, and the Mannville group. The physicochemical controls on the Muddy Formation ichnofauna were low to moderate depositional energy, moderate and nonsteady sedimentation rate, normal benthic oxygen, and variable marine salinity The low ichnodiversity of abundant domichnia within multiple intervals, presence of syneresis cracks, asymmetrical ripple marks, and fluvial deposits within the Channel Sandstone Member (Cañon City) and Horsetooth Member (Horsetooth Reservoir) suggest variable changes in marine salinity. The tetrapod tracks suggest that the coastal plain intervals in the middle part of the Muddy Formation may have been frequented by large herbivores and carnivores.

The Dakota Group ichnofauna is similar to ichnofaunas from fluvial, estuarine, and shoreface deposits of other Cretaceous deposits in the Western Interior Seaway. However, the Dakota Group along the Colorado Front Range has the greatest ichnodiversity with 41 ichnogenera and 39 ichnospecies. Possible reasons for this are the overall size of field area in which this study was conducted (seven localities total), larger area of outcrop examined, and the high number of different paleoenvironments. From Cañon City (south) to Fort Collins (north) the study area is ~235 km long, with outcrops averaging 70 m thick. This would allow for a great range of trace fossils to be identified in outcrops of varying degrees of exposure and conditions. The wide range of paleoenvironments represented in the Dakota Group exposures in the Front Range of Colorado—from fluvial to lower shoreface—allow for greater occurrence and preservation potential of the diversity of organisms and their behaviors recorded in these Cretaceous strata.

CONCLUSIONS

The Dakota Group contains an abundant and diverse trace-fossil assemblage with 41 ichnogenera and 39 ichnospecies. Trace fossils within the Dakota Group occur in either fine- to very fine-grained sandstones or shales interbedded with very fine-grained sandstones to siltstones, and represent a broad range of behaviors represented by cubichnia, domichnia, equilibrichnia, fodinichnia, pascichnia, and repichnia.

Within the Dakota Group, the Plainview and Muddy formations have the highest ichnodiversity due to their wide range of depositional environments and favorable physicochemical conditions in coastal plain, intertidal, and subtidal settings. The Glencairn Formation and the Skull Creek Shale have intermediate ichnodiversity representing less favorable physicochemical conditions in lower shoreface settings. The predominantly fluvial Lytle Formation has the lowest diversity of tracemaking organisms owing to the low trace-fossil preservation potential associated with high hydraulic energy and reworking of previously deposited fluvial and overbank sediments.

Previously unreported ichnogenera were identified in the Dakota Group include the following: *Archaeonassa, Asthenopodichnium, Conichnus, Cylindrichnus, Gyrolithes, Macaronichnus, Naktodemasis, Protovirgularia, Rusophycus, Taenidium, Treptichnus,* and *Zoophycos*.

Eight ichnocoenoses were constructed and three ichnofacies were assigned to the deposits of the Dakota Group: (1) Skolithos Ichnofacies representing variable depositional energy, low to moderate sedimentation rate, high to moderate benthic oxygenation, and normal to reduced salinity (*Diplocraterion* and *Scolicia* ichnocoenoses); (2) Cruziana Ichnofacies representing low to moderate depositional energy, low to moderate sedimentation rate, moderate to low benthic oxygenation, moderate nutrient availability, and normal salinity (*Skolithos-Teichichnus* and *Zoophycos* ichnocoenoses); and (3) Scoyenia Ichnofacies representing variable fluvial depositional energy, moderate to poorly drained soils, and moderate to high soil moisture content (*Caririchnium*, *Lockeia, Naktodemasis*, and Rhizohalo ichnocoenoses). All of these were used to reconstruct the paleoecological relationships recorded in continental and marine paleoenvironments of the Dakota Group.

The Dakota Group contains numerous trace fossils also identified in other Cretaceous deposits in the Western Interior Seaway and elsewhere, and has the highest known ichnodiversity in the Western Interior with 41 ichnogenera and 39 ichnospecies.

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