

ICHTHOLOGY AND SEDIMENTOLOGY OF THE NON-MARINE FRONTIER FORMATION
(UPPER CRETACEOUS) OF SOUTHWESTERN MONTANA

by
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ABSTRACT

The Frontier Formation of southwestern Montana (USA) is comprised of rocks assigned to the early Upper Cretaceous (Cenomanian- Santonian), and has recently yielded a notable fossil record, mostly comprised of dinosaur tracks and invertebrate trace fossils. This fossil record lays within a poorly understood period of the Upper Cretaceous, also known as the middle Cretaceous, valued as critical to understand the evolution of terrestrial ecosystems in North America at the end of the Mesozoic Era. This study aims to describe and analyze preservation and distribution of the Frontier trace fossils record. Twelve stratigraphic sections are measured and sedimentology, taphonomy, and stratigraphic framework described for the main fossiliferous sites. Sixty-five dinosaur tracks and associated invertebrate traces are described. Three tracks are further analyzed by combining anatomical characters and track morphological features to infer a more specific producer. Photogrammetry, tridimensional models, and color elevation maps are generated to document significant specimens and to map two excavated track sites. A concise description and classification of a freshwater turtle is also included to enhance paleoecological and paleodepositional reconstructions. A Coniacian age is provided for the Frontier Formation, main fossiliferous sites. Sedimentology and fossil record suggest the establishment of a rich ecosystem in alluvial plains and wetlands extending between the offshoots of the uplifting Rocky Mountains to the east and the Cody Sea to the east. Facies distribution across the southwest-northeast transect suggests that fossil distribution and preservation is mainly controlled by autogenic and allogenic processes seen in foreland basin systems. Tracks and invertebrate trace fossils preservation was likely favored by high sedimentation rates and variations of the ground water table. Dinosaur track assemblage is comparable to those reported in other middle Cretaceous formations of western North America and include derived hadrosauriform ornithopods, ankylosaurians, and theropods. The integration of body fossil data would suggest the presence of a fauna that included elements (i.e. *Neurankylus* sp.) shared with Campanian and Maastrichtian formations, suggesting that the Coniacian ecosystems across southwestern Montana was likely undergoing a process of provincialisms as seen in North America at the end of the Cretaceous.

CHAPTER ONE

INTRODUCTION

The Cretaceous is a geological period that spans about 80 million years of the Earth's history and is marked by important ecological events related to high sea level rise, land masses' fragmentation, anoxic oceanic events, and mass extinctions occurred over a time of global warming and greenhouse climatic conditions (Wendler and Wendler, 2015; Dunhill et al, 2016; Hay et al., 2019; Schoene et al., 2019; Matsumoto et al., 2022). During the late Lower Cretaceous (Aptian-Albian) the terrestrial ecosystems of North America underwent an important biotic interchange and consequent ecologic reorganization (Wolf et al., 1998; Zanno and Makovicky, 2011). Faunas dispersed from Asia to the North American continent crossing the land bridge known as Beringia, and here they greatly diversified, forming by the end of the Cretaceous a distinctive and rich ecosystem. This biotic interchange contributed to shape the iconic Late Cretaceous biota of North America (Nesbit et al., 2019). Nevertheless, understanding this transitional period is still challenging. Besides the abundant pre-Cenomanian and Campanian-Maastrichtian fossil record, only a few Cretaceous fossiliferous sites are known from Turonian, Coniacian, and Santonian stages (Dean et al., 2020). These stages cover a period of about 20 million years, also known as the middle Cretaceous, and represent the cornerstone to decipher the evolution of terrestrial ecosystems of North America at the end of the Mesozoic Era (Cilliers et al., 2021).

In recent years, efforts have been made to fill this temporal gap and collect new information from unexplored regions of the Rocky Mountains in Idaho and Montana. This research has extended the Cenomanian fossil record distribution to western Idaho and

southwestern Montana with the discovery of microsites (Ullmann et al., 2011), dinosaur egg clutches (Simon et al., 2018), and the description of partial and fragmentary skeletal remains assigned to the burrowing dinosaur *Oryctodromeus cubicularis* (Varricchio et al., 2007; Krumenacker et al., 2019). Post-Cenomanian formations exposed across this studied area have been so far considered scarcely fossiliferous until recent discoveries reported a rich record of dinosaur tracks and invertebrate traces from the Frontier Formation exposed in southwestern Montana. Likewise other Cretaceous formations of western North America (Lockley and Hunt, 1999), the Frontier Formation is dominated by trace fossils rather than body fossils and, in contrast to the older Blackleaf and Wayan Formations, they represent the major source of evidence to investigate the terrestrial fauna inhabiting these regions during the early Upper Cretaceous. The study of trace fossils involves a comprehensive approach combining sedimentological, anatomical, and ethological inquiries that provide a wealth of information for paleoenvironmental and paleoecological reconstruction (Buatois and Mangano, 2011), otherwise limited by the scarce and fragmentary body fossil record available.

This dissertation aims to describe the ichnology and sedimentology of the non-marine Frontier Formation exposed in the Beaverhead and Madison County of Montana. It provides the first study on dinosaur tracks and invertebrate trace fossils preservation and distribution in the formation. Additionally, it will present a concise discussion upon the limited body fossils reported and their importance in constraining the paleodepositional environment of the Frontier Formation. The following chapters consists of five contributions. The second chapter discusses the sedimentology and stratigraphic framework of the Frontier fossil record and provides interpretations on its preservation and distribution. The third chapter provides the description of a

dinosaur track site and its implications to interpret depositional environments and preservation of the track-bearing horizons in the Frontier Formation. I will then present a concise description and classification of a freshwater turtle and its value for constraining the depositional environments of Frontier track sites and reconstructing the paleocommunity. The fifth chapter is focused on the description of three ornithopods tracks and discusses the importance of combining osteological features with morphological characters of tracks to identify different ornithopod producers. Lastly, I will present a comprehensive study on the dinosaur track record, paleoenvironments, and paleocommunity of the Frontier Formation of southwestern Montana, and its importance to understand the evolution of middle Cretaceous terrestrial ecosystems of North America.

Paleontological studies in southwestern Montana have been mainly focused on body fossil-rich formations, and so far, have largely overlooked the possibility to expand the investigation to potentially rich track-bearing formations. The discovery of abundant ichnoassemblages in Frontier Formation deposits of southwestern Montana shows how integrating trace fossils into paleontological inquiries may be critical to understand ancient ecosystems and their evolution. This study will confirm that track and trace fossils represent a key to unlocking the potential for novel investigations on unexplored Cretaceous formations of North America, as well as expanding the knowledge on well-known formations primarily studied for their body fossil record.

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CHAPTER TWO

SOUTHWEST-NORTHEAST FACIES DISTRIBUTION OF NON-MARINE FRONTIER
FORMATION (UPPER CRETACEOUS), SOUTHWESTERN MONTANA: IMPLICATIONS
FOR FOSSIL PRESERVATION.

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Abstract

The non-marine Frontier Formation of southwestern Montana yields a rich fossil record newly reported from different localities across Beaverhead and Madison Counties, Montana, but only a few of these sites have been constrained sedimentologically and stratigraphically. To provide a more rigorous geologic framework and to better understand fossil distribution and preservation, we describe the sedimentology and stratigraphy of five fossiliferous localities along a southwest-northeast transect, from the Lima Peaks area to the western Centennial Mountains, and upper Ruby River valley. Near Lima Peaks, the Frontier is characterized by a coarse-grained succession representing proximal alluvial environments extending nearby the fold-and-thrust belt. In the Lima Peaks area, fossiliferous sites of the lower Frontier are Cenomanian-Coniacian in age and contain bone and eggshell concentrations in calcareous paleosols associated with fine-grained floodplain lithofacies, thick conglomerate horizons, and volcanoclastic and bentonitic deposits. Other nearby fossil localities in the Lima Peaks area are assigned either to the informal middle fine-grained or upper coarse-grained units of the Frontier Formation and are Coniacian or early Santonian. Eastern and northeastern fossil-bearing strata of the middle and upper Frontier in the western Centennial Mountains and upper Ruby River valley are Coniacian in age, finer-grained, and are interpreted as distal alluvial plain environments. The Frontier Formation of southwestern Montana represents regional non-marine deposition across an extensive, Late Cretaceous alluvial plain. Eggshell and bone concentrations occur in western, coarse successions of the lower Frontier Formation within calcareous paleosols, where more proximal fluvial systems were likely less affected by avulsion and reworking processes, thus favoring pedogenesis. The sedimentologic context of eastern, Coniacian successions indicates high

sedimentation and reworking rates, that may have favored fossil concentrations in low-energy aquatic environments. Variations in the ground water table and consequent changes in substrate conditions also aided in dinosaur track preservation. Facies distribution across our southwest-northeast transect is consistent with a general proximal-distal trend observed in alluvial coastal plains in other foreland basin systems. This pattern of distribution may be useful in reconstructing the taphonomic modes and paleodepositional environments of non-marine Upper Cretaceous successions exposed in southwestern Montana.

Introduction

The Cenomanian to early Santonian rock record in southwestern Montana is discontinuously exposed within and east of the fold -and- thrust belt, and is in large part comprised of thick fluvial and coastal successions assigned to the Frontier Formation. These successions document the tectonic history, paleogeography, and terrestrial ecosystems of the region during the early stages of the Late Cretaceous. The Frontier Formation is a thick, sedimentary wedge consisting of siltstone, sandstone, mudstone, limestone, coal lenses, shale, and conglomerate. Knight (1902) was the first to describe coastal and marine rocks of the Frontier Formation in western Wyoming. In southwestern Montana, the Frontier crops out in the Madison Range, upper Ruby River valley of the Snowcrest and Gravelly Ranges, western Centennial Mountains, and Lima Peaks area (Fig 2.1). Deposition occurred within a rapidly subsiding foreland basin during a period of global highstand and regional orogenic deformation (Ryer, 1977; Kauffman, 1984; Kauffman and Caldwell, 1993; Scott et al., 2018). Sediment was profusely supplied by volcanic activity, erosion of the western Cordillera, and incipient unroofing of the foreland Blacktail-Snowcrest up-lift likely initiated during the Coniacian (Perry

et al., 1988; Orme, 2020). In contrast to successions reported in Wyoming, the Frontier Formation of the foreland in southwestern Montana is thicker, partially or completely non-marine, and includes strata as young as early Santonian (Zartman et al., 1995; Dyman et al., 2008). Thus, the Frontier is comprised of strata regionally equivalent to the Marias River Shale, Cody Shale, Telegraph Creek Formation, and Niobrara Formation (Cobban et al., 1976; Finn, 2019).

The stratigraphy and sedimentology of the Frontier Formation have been broadly described over the last thirty years in different localities including the Pioneer Mountains northeast of Dillon (Tysdal and Dyman, 1998), Lima Peaks area (Dyman and Nichols, 1988; Dyman et al., 1990; Dyman et al., 1995), western Centennial Mountains (Dyman et al., 2008; Roseblume et al., 2018), upper Ruby River valley (Tysdal et al., 1990), and Madison Range (Tysdal, 1990). Other reports also addressed sediment provenance and paleogeography (Garber et al., 2020). The non-marine Frontier in southwestern Montana has recently received more attention due to the discovery of plants, dinosaurian and non-dinosaurian bone remains, eggshells, gastropods, bivalves, invertebrates trace fossils, and dinosaur tracks (Panasci et al., 2020, 2021). Much of this fossil record has been assigned to the informal Coniacian middle fine-grained unit and equivalent strata of the Frontier Formation (Dyman et al., 1989, 1997, 2008; Panasci et al., 2021). This is particularly important since these fossil collections reside within a poorly sampled interval of the Upper Cretaceous of North America. In addition, new fossiliferous localities have been identified, and require further studies to contextualize paleodepositional environments and stratigraphic framework. This paper describes and discusses the sedimentology and stratigraphy of five localities along a southwest-northeast transect from

the Lima Peaks area eastward, to the western Centennial Mountains, and upper Ruby River valley. To understand the nature, distribution, and preservation of the palaeontologic record, we outline the depositional setting and stratigraphic position of these localities by describing eleven stratigraphic sections and lithofacies (Table 1).

Lima Peaks area

The thickest non-marine Frontier succession occurs south of Lima Peaks where it is underlain by the Vaughn Member of the Blackleaf Formation and overlain by the Beaverhead Group (Fig. 2.2). The age of the Frontier Formation in this area has been constrained by biostratigraphic and radiometric data, and ranges from middle Cenomanian to early Santonian (Nichols et al., 1985; Dyman and Nichols, 1988; Zartman et al., 1995). Lithofacies are alluvial and vary laterally and vertically. Dyman et al. (1989) first subdivided the Frontier south of Lima Peaks into lower mixed clastic, middle mudstone-siltstone, and upper mixed clastic units. A similar subdivision was also provided by Dyman et al. (2008). They recognized a lower coarse, a middle fine, and a upper coarse grained unit in a larger study area including the western Centennial Mountains. We here adopt the tripartite subdivision by Dyman et al. (2008) to distinguish general lithologic differences and relative stratigraphic position of the rock units at Lima Peaks and along our entire transect. Frontier strata south of Lima Peaks may exceed 5,000 feet in thickness (Dyman et al, 1989). The best exposures occur along Sawmill, Shineberger, and Middle Creeks.

The lower coarse-grained unit is well exposed along Sawmill Creek and is characterized by lithic-rich and felspathic volcanoclastic sandstones, conglomerates, mudstones, shales, with an abundant volcanoclastic component. The contact with the underlying Vaughn Member of the

Blackleaf Formation is formally identified at the base of the first shale horizon overlying volcanoclastic, pastel-colored strata assigned to the Vaughn Member (Dyman and Nichols, 1988). This likely represents an unconformity, as suggested by the presence of a dark shale and the abrupt change in color marking the base of the overlying Frontier Formation.

The lower coarse-grained unit consists of fine-to-coarse grained sandstones, conglomerates, siltstones, and mudstones. Lowermost strata are intercalated with porcellanites that are useful marker beds. Fine-grained sandstones are tan, gray, or olive green in color, can be locally bioturbated, and contain plant material. Mudstones and shales are bentonitic, and characteristically gray-to-olive in color. Thick conglomerates are comprised of dominantly rounded to subrounded, chert, quartzite, and rare volcanic clasts (Dyman and Nichols, 1988). They can form prominent clast supported ridge-forming beds 10-25 m in thickness. Conglomerates may also form lenses or intraformational lags in coarse-grained sandstones and can be associated with carbonaceous plant material and rip-up clasts. Paleosols are characterized by oxidized horizons, and calcareous nodules. The lower coarse-grained unit has so far produced a paleontological record comprised of invertebrate trace fossils, leaves, petrified wood, and carbonaceous plant material. Body fossils consisting of dinosaur eggshell fragments, turtles bone fragments, and crocodile teeth are found primarily in gray mudstones.

The middle fine-grained unit is well exposed along Shineberger and Middle Creeks, but exposures are also reported south of Shine Hill. The unit is comprised of mudstones, siltstones, sandstones, and minor conglomerates. Sandstones and siltstones are yellow, reddish, green, or gray in color and are highly calcareous. They are finely laminated, cross-bedded, and normally graded, whereas siltstones may be rippled, planar-laminated, or massive and associated with

abundant carbonaceous debris. Mudstones are gray, calcareous, and usually highly carbonaceous. These fine-grained lithologies typically form beds showing sharp lower and upper contacts and tend to grade laterally into one another defining lenticular geometries. The middle fine-grained unit of the Frontier Formation is highly calcareous, and volcanoclastic rich strata increase up-section where green porcellanitic horizons form distinctive marker beds. The fossil assemblage of the middle fine-grained unit is comprised of abundant trace fossils consisting of vertical and horizontal burrows, trails, and plant material, preserved in sandstone and siltstone beds. Dinosaur tracks preserved as isolated tridimensional casts have also been reported but they are not abundant.

The upper coarse-grained unit consists of conglomerates, coarse-grained sandstones, siltstones, and mudstones. Conglomerates are of mixed provenance with locally sourced limestones clasts derived from Jurassic and Lower Cretaceous formations, and extra-basinal chert and quartz clasts. This unit can be examined along Shineberger Creek, but notable exposures occur along Modoc Creek on the Idaho side of the Continental Divide. Conglomerates comprised mainly of sub-angular limestone clasts with a maximum diameter of 5 cm locally form laterally discontinuous channel-like beds (Dyman et al., 1991). Limestone pebbles and grains were derived from the Jurassic Rierdon Formation and the Lower Cretaceous Kootenai Formation. The upper Frontier Formation contact is placed at the uppermost green porcellanite overlain by quartzite and chert-rich conglomerates assigned to the Beaverhead Group. Carbonaceous plant material, and invertebrate trace fossils consisting of vertical and horizontal burrows are the only fossils reported so far from the upper coarse-grained unit.

The Frontier Formation in the Lima Peaks area consists of alluvial lithofacies deposited along the westernmost portion of an extensive coastal plain. Conglomerates are a distinctive feature of the lower and upper coarse-grained units and are suggestive of deposition under high hydraulic energy. Clast-supported conglomerates of the lower coarse-grained unit are here assigned to the Gh lithofacies of Miall (1996) and likely represent the product of transport and deposition by traction with very limited suspension. Limestone clast conglomerates of the upper coarse-grained unit are poorly sorted, they often appear massive and are interbedded with medium-to-coarse, cross-bedded sandstones, siltstones, and mudstones. Upper limestone paraconglomerates are assigned to Gmm lithofacies and are interpreted as high-strength debris flows (Miall, 1996). The fine grained lithofacies of the middle fine-grained unit are comprised of cross-bedded sandstones, ripple-laminated siltstones, mudstones, limestones, and paleosols. They are here assigned to lithofacies Fl and P (Miall, 1996) and represent deposits formed by traction, suspension, decanting, and pedogenesis in floodplain environments.

Shine Hill

Frontier Formation lithologies at Shine Hill consist of conglomerate, conglomeratic sandstone, siltstones, and mudstones. Thick conglomerate and coarse-grained sandstone strata form prominent ridges, whereas finer-grained rocks are exposed primarily in drainages (Fig 2.3). Mudstones form badlands characterized by gullies and hogback hills with little or no vegetation that are easily recognizable from a distance. A well-exposed, 30 m thick section comprised mainly of mudstones and medium-to-coarse, conglomeratic sandstones was measured (Fig 2.4). The base of the section consists of a thin, lenticular, fine-grained, and ripple-laminated sandstone bed about 15 cm thick, locally displaying invertebrate burrows (Fig 2.5.1,2). This bed thins

laterally passing into silty mudstones. Gray mudstones typically exhibit popcorn texture and overlie this thin basal bed. The lower three meters of the mudstones are highly fossiliferous, and have yielded dinosaur eggshell fragments, turtle bones, and crocodile teeth. Selenite gypsum crystals are occasionally present. A red-to-pink, oxidized paleosol horizon occurs 4 m above the base of the section and is associated with calcareous concretions (Fig 2.5.3,4). It has a maximum thickness of 120 cm but laterally thins to just a few centimeters. Mudstones are abruptly overlain by a conglomerate lag that forms the base of a 20 m thick, coarse-grained, cross-bedded sandstones unit associated with lenses of matrix-supported conglomerate. (Fig 2.5.5,6)

Fine-grained lithofacies observed in the measured section are calcareous and characterized by ripple lamination, lenticular geometries, bioturbation, and oxidized horizons. They are interpreted as lithofacies Fl and P (Miall, 1996). Processes connected to carbonate precipitation and formation of calcareous nodules are generally observed in well drained soils formed under subhumid to arid climates when evaporation tends to exceed meteoric water accumulation (Bockheim and Gennadiyev, 2000; Therrien, 2005). Oxidized horizons may develop when arid conditions favor the formation of iron oxides in sub-aerial environments (Retallack, 1988). These features likely suggest alternation of humid and arid conditions.

Coarse-grained lithofacies consist of medium-to-coarse, cross-bedded sandstones and conglomerates. Trough cross-bedded sandstones form lateral accretionary bodies 150 to 560 m thick, are associated with basal conglomerate lags and matrix-supported conglomeratic sandstone lenses. These beds are here assigned to St lithofacies and represents multi-story channel deposits (Miall, 1996).

Frontier Formation lithologies at Shine Hill are considered middle Cenomanian-Turonian in age based on palynologic data and absolute age dating (Ryder and Ames, 1970; Nichols et al., 1985; Dyman and Nichols, 1988; Zartman et al., 1995). Recent work by Rosenblume (2021) alternatively suggests a lower Coniacian maximum depositional age based on U-Pb detrital zircon geochronology.

Middle Creek

At this locality, the Frontier Formation consists primarily of sandstones, siltstones, and mudstones. Lithofacies are comprised of planar and ripple-laminated sandstones and siltstones, carbonaceous mudstones, and rare thin limestone lenses. Olive green, volcanoclastic sandstones and siltstones are common throughout this succession, whereas gray, popcorn textured mudstones are rare. Coarse-grained lithofacies consist of lithic-rich, trough-crossed, and ripple laminated conglomeratic sandstones. Trace fossils associated with sandstones and siltstones may be abundant and are characterized by sinusoidal trails, and horizontal and vertical burrows. Gray mudstone beds also yielded a sparse fossiliferous assemblage of eggshell fragments. Although the Frontier Formation is discontinuously exposed at Middle Creek, it is possible to provide a detailed description of lithologies by trenching and prospecting drainages and incisions along slopes flanking the creek.

Section MC 1 was measured east of Middle Creek where about 24 m of the Frontier Formation is exposed on the top of a hill crest (Fig 2.6). The succession is comprised of yellow, tan, olive, and grey, fine-grained, ripple-laminated sandstones; yellow-to-olive, massive and ripple-laminated carbonaceous siltstones; and gray carbonaceous mudstones. The top of this section is primarily comprised of calcareous silty sandstones and siltstones. Several ripple-

laminated horizons preserve abundant horizontal and vertical burrows associated with sinusoidal trails (Fig 2.7). Horizontal and vertical burrows display alternation of fine and coarse-grained, 0.5-1 mm asymptotic menisci, and no distinctive wall. These structures do not show branching although they often tend to crosscut each other producing apparent splitting (Fig 2.7.2). Based on morphological features, these trace fossils may be assigned to *Taenidium barretti* (Keighley and Pickerill, 1994; Rodríguez-Tovar et al., 2016). Sinusoidal trails, when present, are usually not well preserved, but considering the regular wavelength (about 10 mm) and height (2-3 mm), they can be assigned to the ichnogenus *Cochlichnus* isp. (Buatois and Mángano, 1993) (Fig 2.7.3). In several instances, cross-cutting burrows obliterate their internal structure (Fig 7.4). Sinusoidal trails and meniscated burrows may show different preservation states on the same horizon and menisci may be well-to-poorly defined moving to different sections of the same burrow (Fig 2.7.5). In addition, vertical burrows generally do not deform rippled and parallel laminae (Fig 2.7.6).

Section MC 2 was measured on a hill west of a tributary of Middle Creek (Fig 2.8). It is comprised of olive, medium-grained, cross-bedded sandstones overlain by thin horizons of ripple-laminated siltstones, carbonaceous mudstones, and massive siltstone beds containing abundant carbonaceous plant material. The remaining section is mainly comprised of alternating, ripple-laminated siltstones, and sandstones varying in thickness from 30 to 120 cm. Locally exposed carbonaceous mudstones may be present. A thick, medium-to-coarse grained, trough cross-bedded sandstone with intraformational conglomeratic lags and plant material, extends laterally for about 30 m. The base of the sandstone is not exposed but the upper contact appears to be transitional, passing upward into ripple-laminated siltstones. We identified three poorly

preserved dinosaur tracks while measuring section MC 2, but since they are isolated casts, their exact stratigraphic position is unknown.

Sandstones of the Frontier Formation at Middle Creek are highly calcareous but lack thick conglomeratic units. Coarse-grained trough cross-bedded conglomeratic sandstones are interpreted as St and Gh lithofacies deposited in channel settings. Ripple-laminated sandstones and siltstones, planar laminated siltstones, massive carbonaceous siltstones, and carbonaceous mudstones are assigned to floodplain lithofacies Fl (Miall, 1996). The dominantly fine-grained, highly calcareous succession, combined with the lack of thick conglomerate beds observed at Middle Creek, suggests that these sections are transitional between the middle fine-grained unit and the upper coarse-grained unit of the Frontier Formation. These deposits are in fact similar to the middle fine-grained unit described in nearby sections exposed at Shineberger Creek (Dyman et al., 1991; Dyman et al., 2008), but lack noticeable porcellanitic marker beds. However, absence of porcellanitic horizons, and thick conglomerate beds may be connected to lateral facies variations, stratigraphic position, exposure quality, or a combination of the three. Given the absence of definitive diagnostic characteristics, we consider the Frontier Formation at Middle Creek either Coniacian or early Santonian in age.

Western Centennial Mountains

The Frontier Formation in the western Centennial Mountains is discontinuously exposed. Lithologies can be studied by prospecting small trenches and gullies where erosion has removed most of the talus covering the unaltered underling rock. Strata are comprised of fine-grained lithofacies including ripple-laminated sandstones, siltstones, and carbonaceous mudstone associated to limestones. Medium-to-coarse lithofacies are less abundant. Fine-grained, cross-

bedded sandstones, ripple-laminated siltstones, and carbonaceous mudstones form fining-upward sequences a few centimeters up to 2 m thick, occasionally associated with thin limestone horizons. Fine-grained sandstone and siltstone lithofacies are tan or olive green in color and contain abundant invertebrate fossil traces and dinosaur tracks. Mudstones are rich in carbonaceous plant material and may contain limestone nodules. Bone fragments assigned to fresh-water turtles, crocodilians, and dinosaurs have been collected from carbonaceous mudstones. Coarse-grained lithofacies are generally unfossiliferous, and comprised of cross-bedded, ripple laminated sandstones and pebbly sandstones.

The Frontier Formation in the western Centennial Mountain has been largely assigned to strata equivalent to the middle fine-grained unit (Dyman et al., 2008). Beds exposed near the town of Monida, previously assigned by Dyman et al., (1989) to the upper Frontier Formation, are actually equivalent to the lower coarse-grained unit based on lithologic and palynologic data. The Frontier Formation at Monida is unconformably overlain by the Monida Sandstone (Dyman et al., 1991) indicating tectonism and substantial erosion of younger Frontier strata. Nichols and Sweet (1993) collected shale samples yielding Coniacian palynomorphs from Peet Creek and nearby areas of the western Centennial Mountains including localities nearby in Idaho. This age is further supported by U-Pb detrital zircon geochronology (Rosenblume et al., 2018). Panasci et al. (2021) assigned beds at Price Creek to the Coniacian fine-grained middle unit of the Frontier Formation.

Sand Creek

At this locality the Frontier Formation is comprised of an heterolithic succession of fine-to-medium sandstones, siltstones, carbonaceous mudstones, shales, and limestones. Thin,

discontinuous coaly lenses are occasionally present. From a distance, exposures have a distinctive light yellow appearance which makes them easy to identify in the field (Fig 2.9). At Sand Creek, coarse-grained lithofacies are mainly comprised of trough-crossed bedded, laterally extensive sandstones, but they are less abundant and thinner than at Price Creek.

The measured section, which is about 15 m thick, is exposed along a deeply incised drainage. Strata are overturned and comprised of fine-grained sandstones, carbonaceous sandy siltstones, ripple-laminated siltstones, and carbonaceous mudstones. Medium and coarse-grained, salt-and-pepper, trough cross-bedded sandstones are less abundant than fine-grained lithofacies (Fig 2.10). Siltstones are dominant and form beds up to 200 cm thick. Thin olive-to- gray sandy siltstones are ripple-laminated and normally graded, whereas thicker strata are massive and highly carbonaceous. Fine-grained, ripple-laminated sandstones are tan to reddish-brown in color and vary from about 10 to 20 cm in thickness. Trace fossils were observed at the base of sandstones and consist of horizontal and vertical burrows associated with dinosaur tracks (Fig 2.11.1,2). Invertebrate trace fossils are preserved both as positive and negative hyporeliefs. Horizontal burrows typically average about 1 mm in diameter (Fig 2.11.3), but larger meniscated burrows up to 1 cm in diameter are present and display alternating coarser and finer menisci (Fig 2.11.4). Vertical and horizontal burrows form circular or subcircular structures 0.7-1.5 cm in diameter. Fine grained lithofacies form fining upward sequence characterized by ripple lamination, plant debris, and thin mudstones beds evidently formed by decelerating flows. We interpret the alternation of ripple-laminated sandstones, siltstones, and mudstones, that comprise much of this section as Fl lithofacies. Sandstones and sandy siltstones characterizing the top of

the measured section are likely the product of flood and channel deposition and interpreted respectively as Sm and St lithofacies (Miall, 1996).

Price Creek

At Price Creek, the Frontier Formation is comprised of fine-grained sandstones, siltstones, mudstones, and limestones, with less abundant coarse-grained sandstones and pebbly sandstones. Sandstones are lithic-rich and may be associated with vertical and horizontal burrows. Gray mudstones characterized by calcareous concretions may also be present. Abundant fossils, especially dinosaur tracks, bone fragments, invertebrate shells, and plant material are present in fine-grained lithofacies. Bone fragments of the fresh-water turtle *Neurankylus* sp. were identified (Panasci et al., 2020). Two stratigraphic sections, PC 1 and PC 2, were measured on the east side of Price Creek.

PC 1 is 30 m thick and comprised of fine-grained, ripple-laminated sandstones, ripple-laminated siltstones, carbonaceous mudstones, and limestones (Fig 2.12). Fine-grained sandstones are 10-200 cm thick (Fig 2.13.1). Siltstones beds vary from 20 to 50 cm in thickness, they are ripple laminated, often massive, and well indurated, and rich in carbonaceous debris. Carbonaceous mudstones may be up to 60 cm in thickness, they appear crumbly on fresh surfaces, and laterally and vertically grade into fine siltstones (Fig 2.13.2). Carbonaceous mudstones may contain calcareous concretions. (Fig 2.13.3,4). Medium-to-coarse sandstones were absent in PC 1 although they are exposed nearby. Fossils are abundant in finer-grained lithologies, especially in fine-grained sandstones where dinosaur tracks, invertebrate trace fossils, and plant material are observed. Leaves, gastropods, bivalves, and bone fragments are reported from carbonaceous mudstones.

PC 2 was measured about 1 km north of PC 1 (Fig 2.14). Here the Frontier Formation is predominantly comprised of fine-grained sandstones and siltstones. Sandstones range in thickness from 20-130 cm, while siltstones form thicker beds ranging from 60-300 cm. Sandstones and siltstones may be either cross-bedded and ripple-laminated, or massive. Individual beds are laterally extensive, but ultimately tend to thin, grading into coarser or finer lithologies. Alternating sandstone and siltstone strata may contain exquisitely preserved plant material. Dinosaur bones, gastropods, and bivalves have been collected from carbonaceous mudstones.

The base of the section consists of thick beds of medium-to-coarse, trough-cross bedded, and ripple laminated sandstones, each extending laterally about 30 m. These sandstones are overlain by carbonaceous siltstones and mudstones. Alternating beds of poorly exposed yellow-to-gray, cross-bedded, ripple-laminated sandstones, and siltstones, form depositional units about 10 m thick. Several beds are massive, while others are ripple laminated and associated with vertical burrows. Plant material consisting of leaves are particularly abundant in finer units; logs and carbonaceous horizons occur in massive sandstone beds intercalated with finer, rippled sandstones (Fig 2.15). The uppermost 10 m of section PC 2 is very well exposed and consists of fine-to-medium grained sandstones, ripple-laminated siltstones, and mudstones. Thick fine-grained sandstones with sharp lower contacts define single-story, fining upward sequences up to 130 cm thick (Fig.2.16.1). Sandstones thin laterally, grading upward into convoluted siltstone and mudstone beds that range from a few centimeters up to 30 cm thick (Fig 2.16.2,3). Trace fossils are abundant and consist mainly of dinosaur tracks, and vertical and horizontal burrows. Dinosaur tracks are preserved as positive hyporeliefs at the base of fine-grained sandstone units

and may be associated with vertical, meniscated, and walled burrows (Fig 2.16.4). Several, vertical or highly inclined, burrows crosscut multiple horizons.

Calcareous concretions were identified in gray mudstones beds near the measured section. These gray mudstones are underlain and overlain by a sequence of poorly sorted, ripple-laminated sandstones, and carbonaceous siltstones with abundant plant debris, rip-up clasts, root traces, and mottling (Fig 2.17). Concretions form localized horizons about 25 cm thick.

The Frontier Formation exposed at Price Creek is characterized by fine-grained sandstones, siltstones and carbonaceous mudstones assigned to Fl lithofacies (Miall, 1996). Carbonaceous sandstones and silty sandstones either massive or ripple laminated are assigned to Sm and Sr lithofacies. Thick, massive, poorly sorted sandstones, are rich in plant debris, have erosive lower contacts, and fine upward. These sandstones may represent crevasse splay deposits. Poorly sorted, fine-grained sandstones and siltstones, associated with abundant carbonaceous plant material, root traces and mottling are assigned to lithofacies P. Medium-to-coarse, cross-bedded and ripple laminated sandstones represent channel deposits and are assigned to St and Sr lithofacies (Miall, 1996).

Upper Ruby River valley

The Frontier Formation exposed in the upper Ruby River valley consists of sandstones, siltstones, mudstones, limestones, carbonaceous shales, and local coal horizons. Based on lithologic data in Tysdal et al. (1990) and from this study, we broadly subdivided the formation into two informal units, each with distinctive facies associations. The lower unit primarily consists of marine and brackish water lithofacies underlain disconformably by the Vaughn Member of the Blackleaf Formation, whereas the upper unit is comprised of alluvial lithofacies.

Both units contain olive-to-gray sandstones, siltstones, and mudstones, but thick carbonaceous shales and coal horizons are common in marine and brackish-water deposits of the lower unit. Well-exposed non-marine strata in the upper unit can be observed along the banks of the upper Ruby River following its course upstream to the south. These deposits are characterized by calcareous, fine-grained sandstones, siltstones, mudstones, limestones, and less abundant medium-to-coarse grained sandstones and conglomerates. They can be associated with bentonitic and volcanoclastic-rich strata. Plant remains, and invertebrate and vertebrate traces are common, but bone fragments are rare.

Previous studies have provided only general lithological descriptions for the upper Frontier Formation along the upper Ruby River (Mann, 1960), or focused on lower marine sequences (Hadley, 1980; Tysdal et al., 1990). Age of the lower marine Frontier unit is Cenomanian-Turonian (Dyman and Nichols, 1988; Tysdal et al., 1990), but less is known of the upper non-marine unit. Consequently, it will be discussed in the following paragraphs.

Basin and Coal Creek

One of the best exposed non-marine Frontier successions lies between two eastern tributaries of the Ruby River, Basin Creek and Coal Creek. Here the Frontier Formation is mainly comprised of fine-grained lithologies exposed on the west bank of the Ruby River. About 86 m of the Frontier Formation has been described, but notable outcrops are locally exposed on the banks of Coal Creek. They will also be discussed.

This succession was described along strike by subdividing it into five measured sections (Fig 2. 18). Section UR 1 forms the base of our lowest stratigraphic datum: a medium-to-coarse grained, cross stratified sandstone bed overlain by a thick sequence of carbonaceous siltstones

and mudstones, fine-grained sandstones, and minor limestone lenses (Fig 2.19). Siltstones are yellow, green, or reddish in color, are ripple-laminated or massive, and form beds from a few centimeters up to 130 cm thick. Sandstones are gray, reddish brown, or tan, and form ripple-laminated depositional units up to 150 cm thick. Mudstones appear to be less abundant and form thin carbonaceous strata up to 25 cm thick. Sandstones and siltstones show mottling, slickensides, and contains vertical and horizontal burrows. Carbonaceous plant material is also abundant, especially in sandstone and siltstone lithologies (Fig 2.20.1). Two fine-grained dinosaur track-bearing sandstone horizons were identified approximately 20 m above the base of the section (Fig 2.20.2).

UR 2 consists of fine-grained, ripple-laminated sandstones, carbonaceous, rippled and planar-laminated siltstones, and carbonaceous mudstones (Fig 2.21). The base of the section is marked by laterally extensive, fine-to-medium grained, cross-bedded sandstones, each averaging 80 cm thick. Sandstones are overlain by thick units comprised of laminated siltstones with plant debris, vertical and horizontal burrows, and trace fossils assigned to *Cochlichnus* isp., and *Lockeia* isp. (Fig 2.22). Thin, fine-grained ripple-laminated sandstones may be interbedded with siltstones, especially in the upper part of the section. Sandstones may be mottled and contain vertical burrows and dinosaur tracks. A 300 cm thick carbonaceous mudstone unit was identified at the top of the section.

Lower contacts between a sandstone channel and fine-grained floodplain lithofacies are exposed at the base of UR 3. This section is comprised of interbedded thin, fine-grained sandstones and siltstones, about 400 cm thick. They are overlain by medium-to-coarse, planar, and trough-crossed bedded, conglomeratic sandstones (Fig 2.23). Siltstones are green or

violaceous in color, whereas fine-grained sandstones are usually gray, yellow, or red. These lithologies are highly carbonaceous, mottled, and preserve thin root traces and vertical burrows. Sandy siltstones are associated with centimeter-scale coal lenses and carbonaceous material. Carbonaceous mudstones, highly rich in plant material, form thin continuous horizons or localized lenses. Fine-grained sandstones may be mottled, and display vertical burrows, millimeter scale root traces, and calcareous concretions (Fig 2.24.1,2). In some instances, crossbedding and ripple lamination may be poorly preserved due to pervasive mottling. An erosive contact separates the fine-grained lithologies by overlaying thick coarse-grained sandstones and conglomeratic sandstones. The base of the upper coarse-grained unit consists of a matrix-supported conglomerate, about 15 cm thick, that incorporates plant fragments, sandstone, and siltstone clasts from lithologies seen in the lower part of the section (Fig 2.24.3). The conglomerate is poorly indurated, and laterally varies in thickness. No stratification or imbrication is present and contact with the lower units is sharp (Fig 2.24.4). The conglomerate grades upward into coarse-grained, planar-laminated and trough-cross bedded conglomeratic sandstones (2.24.5,6). The upper contact of this coarse unit is covered.

Measured section UR 4 is comprised of lithologies similar to those observed in UR 1 (Fig 2.25). Sandstones fine upward and display thicker beds (60-100 cm) than siltstones (10-30 cm). Ripple-laminated sandstones and siltstones, overlain by mottled, concretionary, silty-sandstones form alternating sequences. Alternating beds of ripple-laminated, carbonaceous siltstones and silty mudstones were also observed. Plant material is generally abundant and found preserved at the base of sandstones. Invertebrate trace fossils are found scattered as tubular casts along the slope or preserved on isolated sandstone slabs.

Measured section UR 5 is 35 m thick, and it is comprised of alternating beds of fine-grained, ripple-laminated sandstones, carbonaceous siltstones, and mudstones (Fig 2.26). The section is not well exposed, and fine-grained units are poorly visible in the field. In general, sandstone-rich units are yellow, whereas siltstones and subordinate mudstones are gray. Mudstones increase in frequency up-section and are overlain by a 16 m thick, coarse-grained, conglomeratic sandstone bed containing sizable fragments of petrified wood (Fig 2.27.1,2). Nicely exposed contact between channel and floodplain lithofacies can be observed along the bank of Coal Creek. The succession consists of a medium-to-coarse grained, trough-crossed sandstone bed overlain by fining-upward units of fine-grained sandstones, siltstones, and mudstones (Fig 2.28.1). Coarse-grained sandstones are comprised of co-sets of trough-crossed beds. They have sharp contacts with overlying finer grained units (Fig 2.28.2) of ripple-laminated silty sandstones grading upward into ripple-laminated siltstones, and gray, calcareous mudstones (Fig 2.28.3). Fine-grained sandstone beds and siltstones are generally not thicker than 10 cm, whereas mudstones may be as thick as 30 cm. Fine-grained sandstones may also display deformed ripples and cut-and-fill structures. Mudstones are nodular and highly calcareous. These fine-grained lithofacies display lenticular geometries (Fig 2.27.4).

The succession exposed between Basin and Coal Creeks is primarily comprised of alternating fine-grained beds of sandstones, siltstones, and mudstones. Laminated siltstones and mudstones define sequences up to 5 m in thickness and display sharp or transitional contacts. Mottling, root traces, and centimeter scale calcareous concretions are reported in sandstone and siltstone lithofacies across the interval. Bioturbation, dinosaur tracks, and carbonaceous plant material are common. Coarser sandstone units are also present, but they are less abundant, may

form multistory units up to 15 m thick and have basal conglomerate lags, parting lineation, and trough-crossed bedding. Lower contacts with fine-grained beds are sharp and associated with intraformational lags comprised of Frontier Formation clasts dispersed into a coarse-grained, poorly sorted, sandstone matrix. The lower fine-grained beds were formed by traction current, suspension and pedogenesis in floodplain environments, and are overlined by avulsion and channel deposits. We assign floodplain deposits to Fl and P lithofacies, whereas coarse grained units are here interpreted as St, Sh, and Gmm, lithofacies (Miall, 1996).

The lower marine to brackish water unit of the Frontier Formation in the Ruby River valley is Cenomanian to Turonian (Tysdal et al., 1990). The age of the non-marine upper unit is likely Coniacian, based on lithological affinities with successions exposed in the western Centennial Mountains and Lima Peaks (Panasci et al., 2021), as well as ages derived from U-Pb detrital zircon geochronology (Rosenblume et al., 2021). The upper contact with the Beaverhead Group is covered in the upper Ruby River valley, but a transition in lithologies is observed in discontinuous exposures east of the Divide Guard Station (see Fig 2.1) near the headwaters of the Ruby River. The Frontier Formation is here overlain by quartz-rich sandstones that weather reddish brown and resemble the Monida Sandstone near Monida, MT, and at Clover Divide in the central Snowcrest Range (Ryder and Scholten, 1973; Nichols et al., 1985). Whether deposition is continuous through this covered interval, or an unconformity separates the Frontier Formation and overlying quartz-rich sandstones is unknown.

Discussion

Sedimentology and absolute age dating was used to outline a general stratigraphic framework of the Frontier Formation exposed at our localities along the transect. Stratigraphic

correlation between the middle fine-grained successions examined in the Lima Peaks area, with those in the western Centennial Mountains, and upper Ruby River valley have been provided by Dyman et al. (2008) and more recently by Panasci et al. (2021). These studies indicate a Coniacian age for the upper non-marine Frontier and are corroborated by U-Pb detrital zircon geochronology (Rosenblume et al., 2018; Rosenblume et al., 2021). According to Rosenblume et al. (2021), strata exposed near Lima Peaks at Shine Hill are no younger than the early Coniacian. A shale sample from the northern flank of Shine Hill provided palynomorphs assemblages indicating an older Cenomanian and possibly Turonian age (Nichols et al., 1985; Dyman et al., 1989, p. 109). Based on lithology and palynomorphs these strata are older than the Frontier at Sand, Price, Basin and Coal Creeks. The Frontier Formation at Middle Creek has no definitive marker beds, and consequently is broadly assigned to a Coniacian-early Santonian age based on lithological affinities.

The successions examined are comprised of floodplain lithofacies Fl, P, St, Sh, Gh, and Gmm and are interpreted as alluvial plain in origin. Lithofacies and grain-size vary substantially moving from western to eastern successions. In the western successions of the Lima Peaks area, Fl lithofacies are associated with thick, coarse-grained lithologies that are lacking in eastern successions of the western Centennial Mountains and the upper Ruby River valley. These conglomerates are comprised predominantly of Proterozoic and Paleozoic metasedimentary clasts derived from erosion of the thrust belt. Rare volcanic clasts were derived from the western Cordilleran Magmatic Arc (Dyman et al., 1991; Laskowski et al., 2013). Conglomerates and sandstones at Lima Peaks form thick, incised channel deposits representative of an extensive fluvial system spread across what is now eastern Idaho and southwestern Montana (Dyman et al.,

1989; Rosembume, 2021). Paleosols reported from the fossiliferous sites suggest a longer period of stability connected to less frequent avulsion events and low reworking rates (Bown and Kraus, 1987; Kraus, 1999). Fine-grained lithofacies are dominant, but sandstone channels are characteristically medium-to-coarse grained and commonly associated with intraformational conglomerates.

Eastern successions exposed in the western Centennial Mountains and the upper Ruby River valley, in contrast, are dominantly fine-grained and likely represent more distal alluvial environments. Strata show lenticular geometries, sharp contacts, convoluted stratification, abundant plant material, and trace fossils. Thin limestone horizons associated with carbonaceous mudstones and siltstones were deposited during ponding events. Floodplain lithofacies are often laterally extensive, indicating that floods were unconfined, and the presence of fining upward units and massive mudstone beds is supportive of deposition caused by decelerating flows in subaqueous environments. Mudstones also indicate low energy aquatic environments, with possible instances of pedogenesis as suggested by the presence of granular ped structures and calcareous nodules (Retallack, 1988; Bellosi et al., 2021). Mudstones commonly contain gastropods, bivalves, eggshells, bone fragments, and abundant plant debris. Limestones lenses may be thinly laminated, or structureless and not fossiliferous. The presence of low energy aquatic environments is further suggested by laminated siltstones with invertebrate trace fossils assigned to nematode worms and bivalves. Notably, the presence of trace fossils in sandstones and siltstones with differential preservation suggests taphonomic pathways influenced by variations in the groundwater table and changes in substrate consistency (Carmona et al., 2010). Calcareous nodules in gray mudstones may have resulted from precipitation of minerals from

phreatic water due to seasonal fluctuations in the water table (Therrien et al., 2015; Freimuth and Varricchio, 2019). Eastern successions are characterized by channel deposits comprised of multistory sandstones showing sharp, erosive contacts, and intraformational conglomeratic lags. They migrated by avulsion, resulting in scouring and substantial erosion of preexisting alluvial deposits (Allen, 1970; Miall, 1988). Channel abandonment is marked by either transitional or abrupt passage to Fl lithofacies. A clear transition is evident in deposits observed at Coal Creek where channel sandstones are overlain by silty, ripple-laminated sandstones, fining upward into ripple-laminated siltstones and mudstones. This sequence is similar to those reported in meandering systems where channel abandonment is marked by vertical accretion of sand, silt, and mud, later affected by ground water fluctuations and incipient pedogenesis (Walker and Cant, 1984).

It is worth noting that western and eastern successions reflect distinct taphonomic characteristics. The Frontier Formation in the Lima Peaks area includes calcareous paleosols, that provided adequate alkaline conditions to preserve eggshell and bone fragments (Smith, 1990; Martin, 1999; Patra et al., 2018; Rogers et al., 2010). Alternatively, paleosols reported from strata in the western Centennial Mountains and upper Ruby River valley yielded dinosaur tracks, invertebrate trace fossils and plant material, while bone remains and eggshells are rare or absent. Bone and eggshell concentrations characterize carbonaceous mudstones in eastern Frontier successions, where they are comprised of disarticulated and fragmentary elements, associated with invertebrates and plant remains. Eggshell and bone concentrations in paleosols provide a strong terrestrial signature due to the reproductive constraints and ecological requirements of terrestrial organisms (Rogers, 1993), thus strongly suggesting upper alluvial

plain environments. In fact, proximal alluvial plains are characterized by coarser-grained sediments, deep ground water level position, and relative drier conditions of the substrate (Smith, 1990; Patra et al., 2018). Preservation in these environments was likely controlled by passive attritional processes under low sedimentation settings that favored accumulation of articulated and/or dissociated and fragmentary bone material (Behrensmeyer, 2007). Alternatively, in the western Centennial Mountains and upper Ruby River valley, paleosols lack bone and eggshell fragments, and sedimentological characteristics indicate more saturated conditions as typically observed in more distal alluvial environments (Retallack, 1988). Sedimentologic data from this study suggest that bone and plant concentrations accumulated in subaqueous floodplain environments, reflecting similarities with modern distal alluvial wetlands characterized by seasonal variations in water regime, groundwater fluctuations, and a freshwater fauna comprised of invertebrates and reptiles (Mitch and Gosselink, 2015). Processes affecting bone, eggshell, and plant accumulations include traction currents and high sedimentation and reworking rates. Deposition of floodplain sequences under high sedimentation rates and variations of the ground water table may have also aided in preservation of trace fossils, especially dinosaur tracks. In addition to the importance of these fossils in refining the reconstruction of depositional environments, they are particularly significant for their stratigraphic distribution. The Frontier Formation includes Coniacian and possibly early Santonian fossil localities, that would expand our understanding of terrestrial ecosystems and their evolution in this region during the Late Cretaceous.

Conclusions

The non-marine Frontier Formation exposed in southwestern Montana was deposited in a broad alluvial plain extending from the Cordillera eastward to the Western Interior Seaway during the Cenomanian to early Santonian. Western successions are coarser grained than eastern successions reflecting a trend from proximal to distal alluvial plain environments. Southwestern fossil localities in the Lima Peaks area are assigned to Coniacian and possibly early Santonian in age. Eastern fossiliferous localities in the western Centennial Mountains and upper Ruby River valley, respectively, are Coniacian in age. Strata are time equivalent to the middle fine-grained unit of the Frontier Formation in the Lima Peaks area. The western, Frontier Formation successions at Lima Peaks includes calcareous paleosols yielding a rich assemblage of bone remains and eggshells, providing a strong terrestrial taphonomic signature, and suggesting a relatively stable channel system with infrequent avulsion events and low reworking rates. Eastern successions yielded an abundant, Coniacian fossil assemblage from poorly developed, hydromorphic paleosols, fine-grained sandstones, and carbonaceous mudstones. This fossil record is comprised of invertebrate trace fossils, dinosaur tracks, plant material remains, gastropods, bivalves, bone remains, and eggshells primarily preserved in overbank deposits. The successions were likely deposited in a low gradient distal alluvial plain characterized by high sedimentation and reworking rates, unconfined flood events, formation of low energy aquatic environments, and fluctuating ground the water table.

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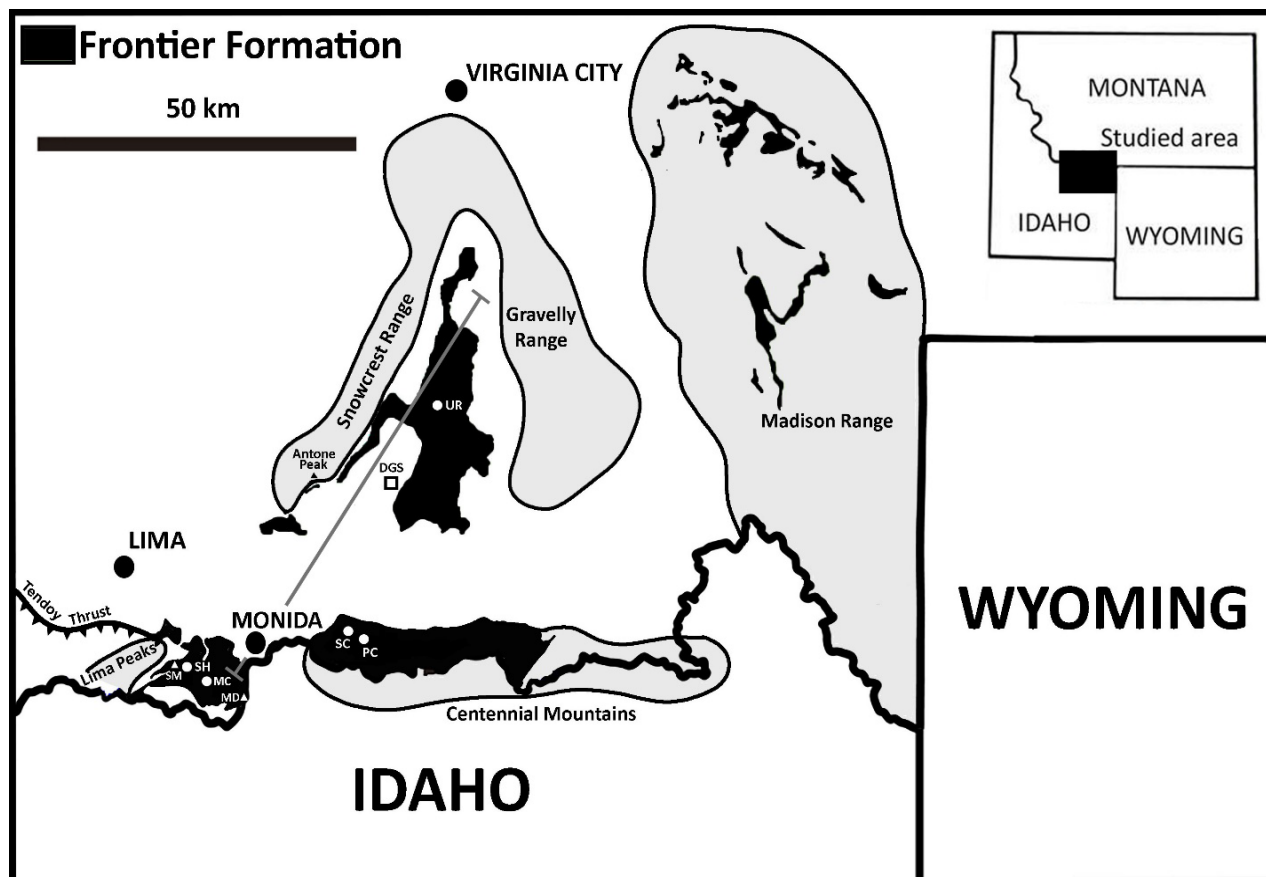


Figure 2.1. Generalized map of southwestern Montana showing the distribution of the Frontier Formation and the localities studied; gray line indicates the southwest-northeast transect; white dots indicate localities where stratigraphic sections were measured: Shine Hill (SH), Middle Creek (MC), Modoc Creek (MD), Sand Creek (SC), Price Creek (PC), Basin Creek and Coal Creek (UR); white triangles denote sites additionally described without measured sections; square indicates Divide Guard Station (DGS); Antone Peaks (black triangle).

[illegible]

Figure 2.2. Chronostratigraphic section of the Frontier Formation in southwestern Montana at the localities examined: Shine Hill (SH), Middle Creek (MD), Sand Creek (SC), Price Creek (PC), Basin Creek and Coal Creek (UR). Absolute ages for Lima Peaks area are from Dyman et al. (1989, 2008) and measurement reflects uncertainty values indicated by Zartman et al. (1995); ages marked by asterisk are provided by Rosenblume et al. (2018) and Rosenblume (2021); ammonite symbols indicate biostratigraphic constraints provided by *Collignonicerias woollgari* (Cw), *Prionocyclus hyatti* (Ph); *Scaphites ventricosus* (Sv), (Dyman et al., 1997). Shaded areas represent missing time; dashed lines indicate uncertainty in correlation.



Figure 2.3. Panorama of Shine Hill seen from west and showing the south flank with vertical conglomerate strata defining the elevated, and vegetated topographies.

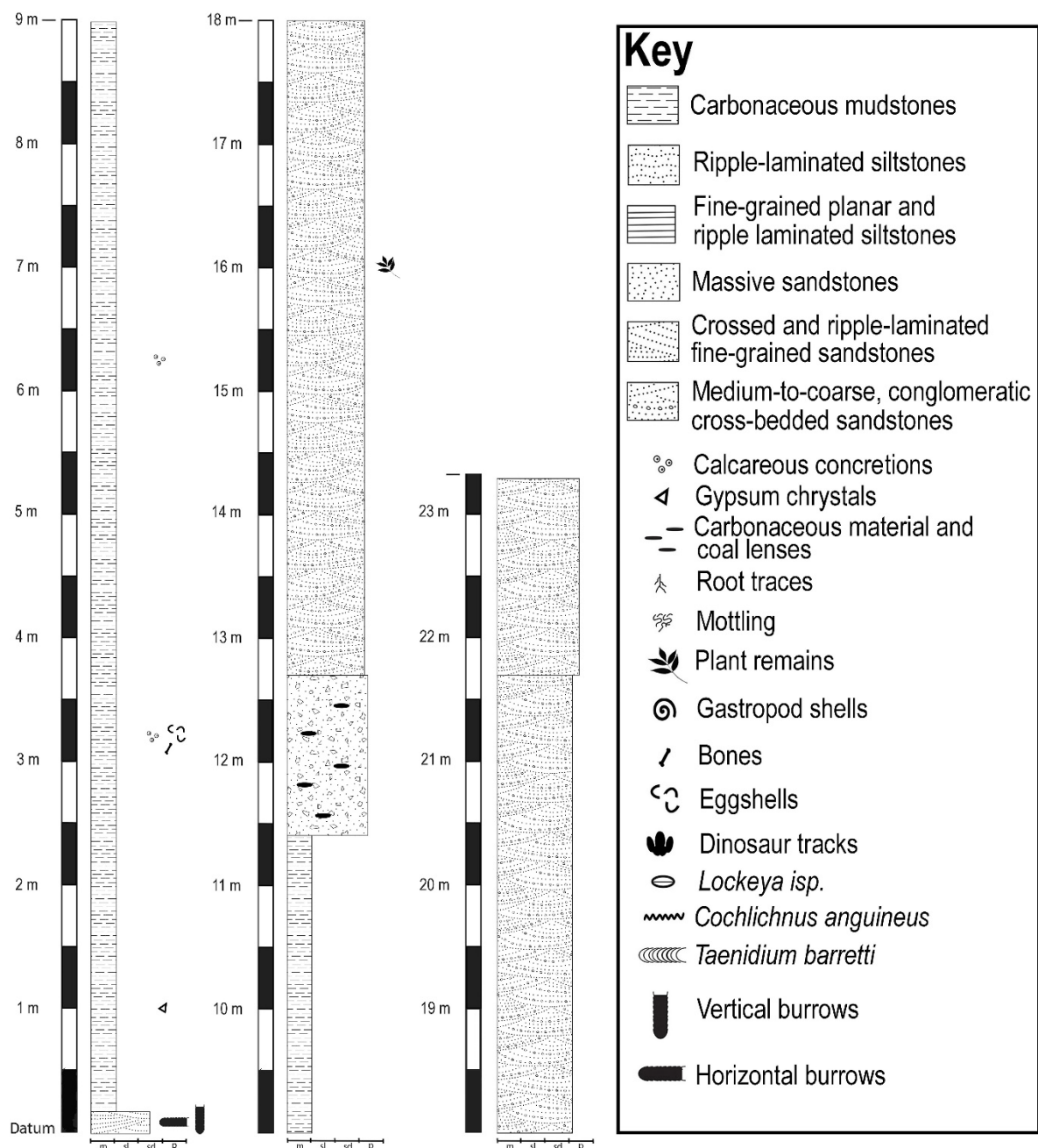


Figure 2.4. Shine Hill stratigraphic section SH.



Figure 2.5. Lithofacies exposed at Shine Hill: 2.5.1,2) fine-grained bioturbated sandstones, siltstones and mudstones; 2.5.3) gray mudstones with popcorn texture forming characteristic badlands features with red oxidized horizon marked by the rock hammer (black arrow) associated with 2.5.4) calcareous nodules; 2.5.5) St lithofacies comprised of medium-to-coarse grained sandstones, and 2.5.6) conglomeratic lenses.

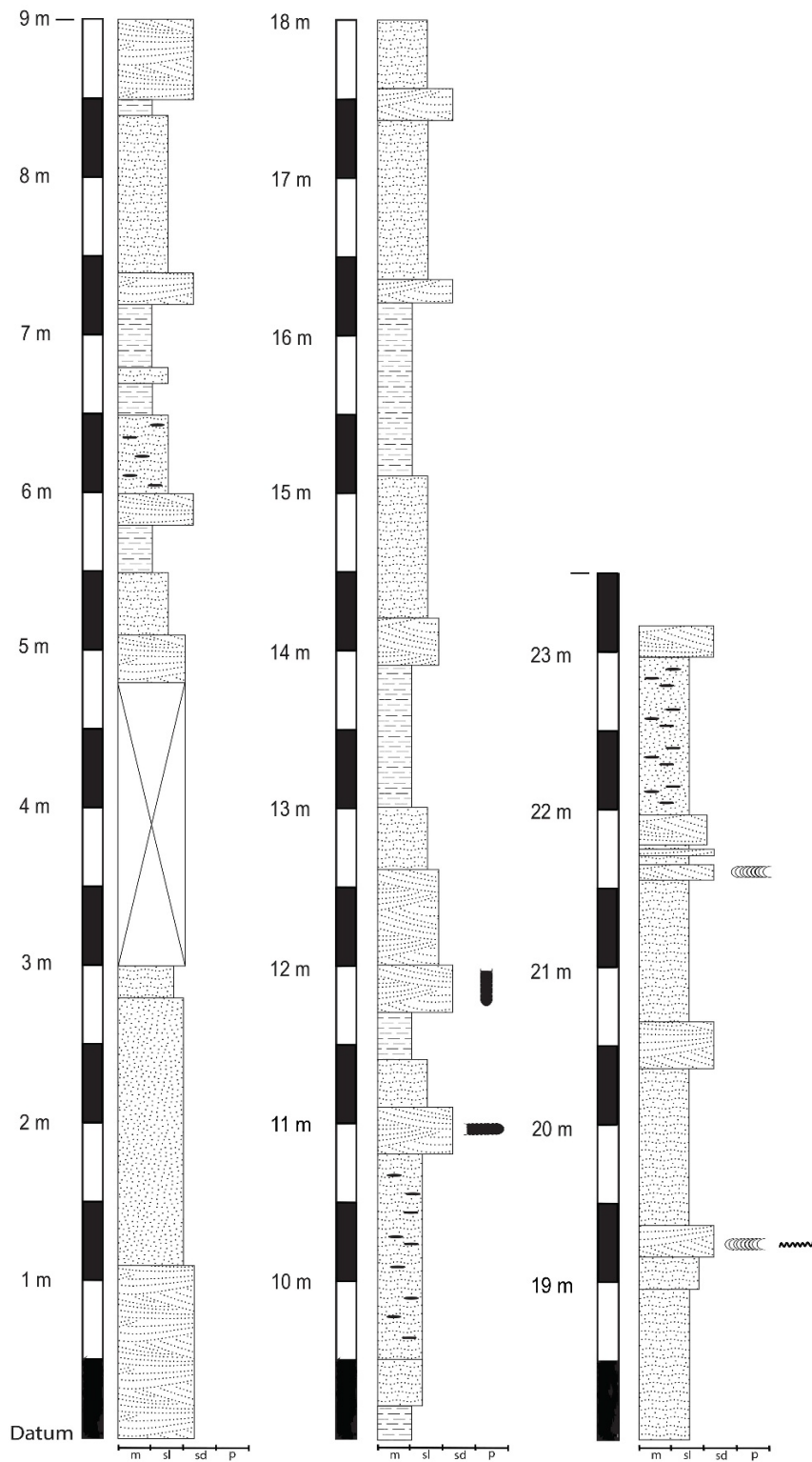


Figure 2.6. Middle Creek stratigraphic section MC 1 (see Figure 2.2.4 for key).

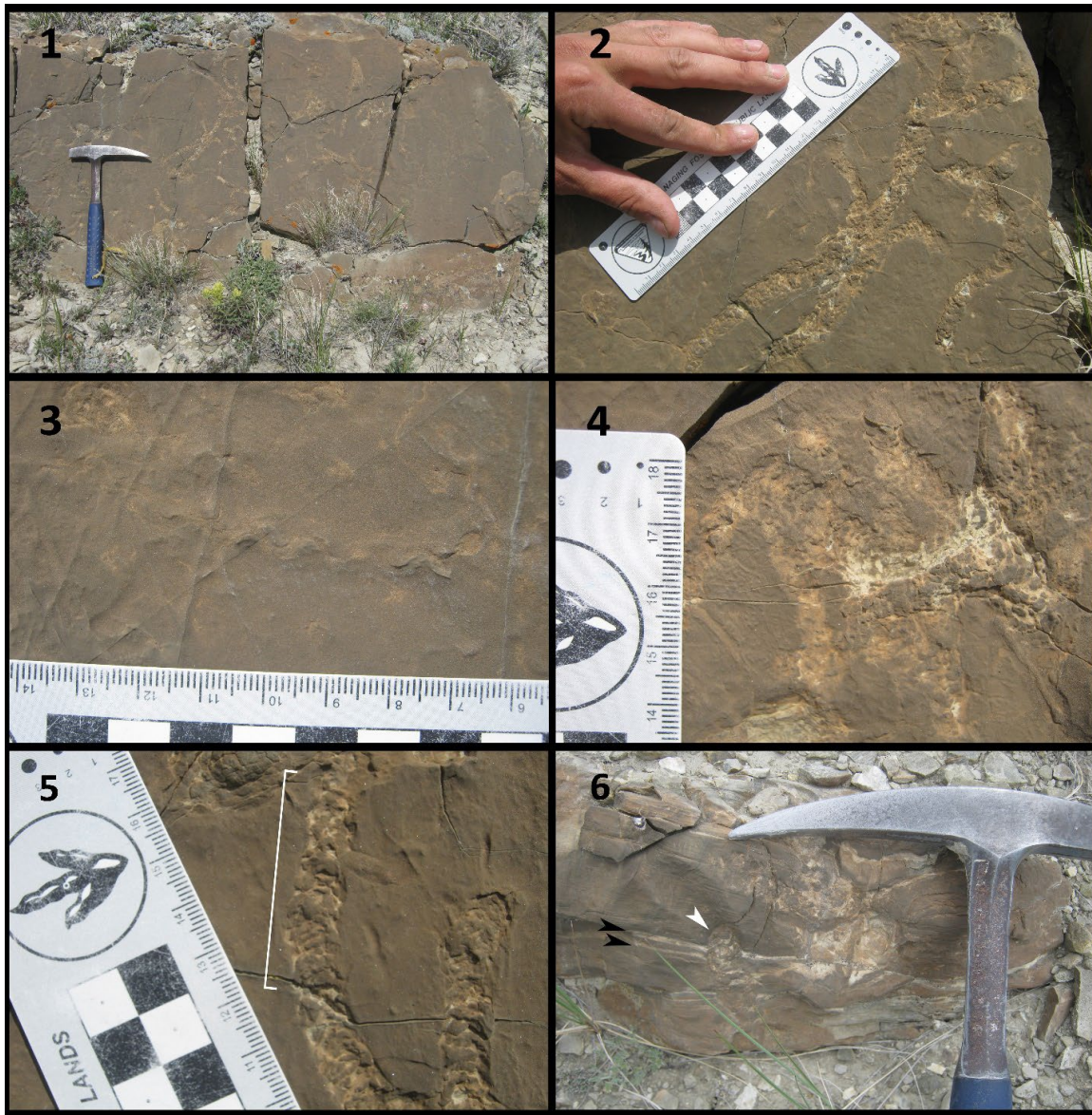


Figure 2.7. Trace fossils reported at the top of section MC 1 on a bedding surface 2.7.1) with details of : 2.7.2) *Taenidium barretti* and 2.7.3) *Cochlichnus* isp.; 2.7.4) crosscutting burrows assigned to *Taenidium* isp.; 2.7.5) variable preservation of menisci in two sections of the same horizontal burrow; white bracket indicates the area where menisci are poorly preserved; 2.7.6) undeformed parallel lamination (black arrows) crosscut by a nearly vertical burrow (white arrow).

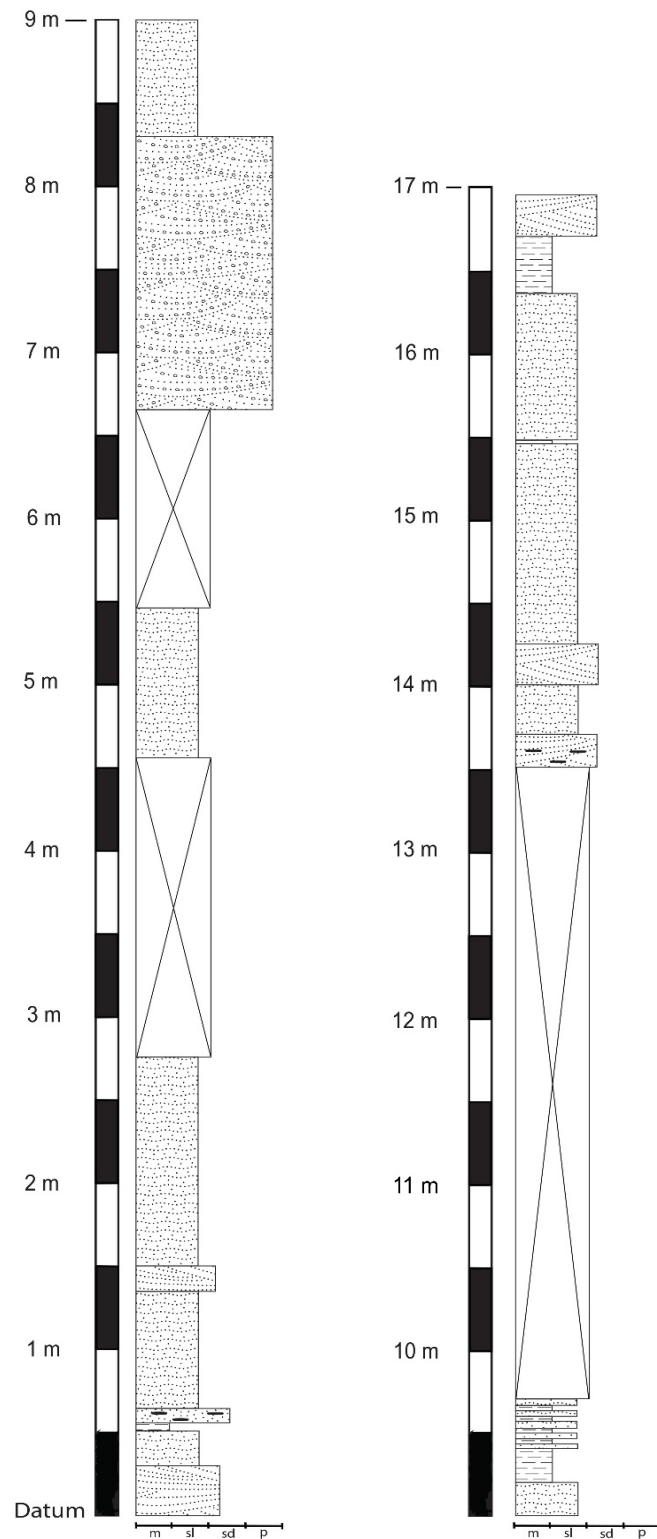


Figure 2.8. Middle Creek stratigraphic section MC 2 (see Figure 2.4 for key).



Figure 2.9. Frontier Formation exposures near Sand Creek looking north.

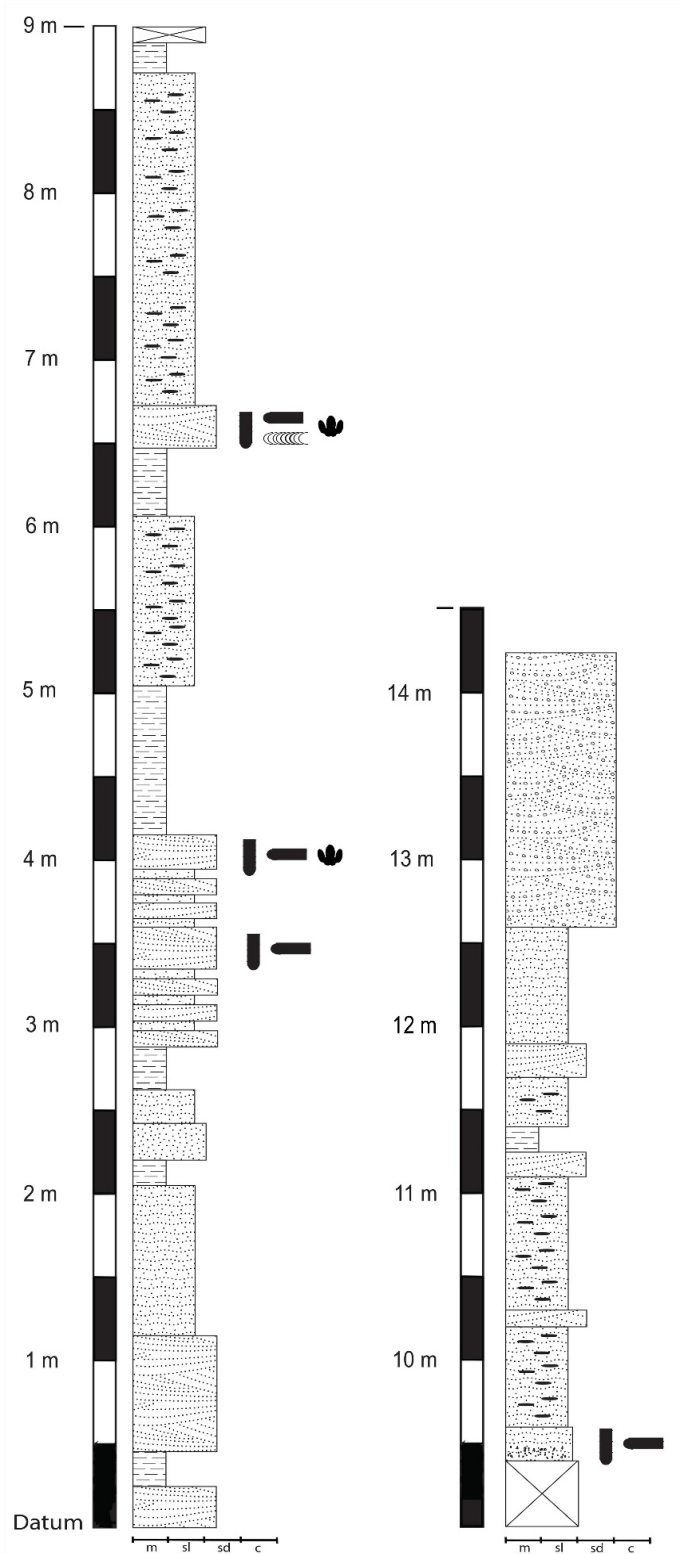


Figure 2.10. Sand Creek stratigraphic section SC (see Figure 2.4 for key).

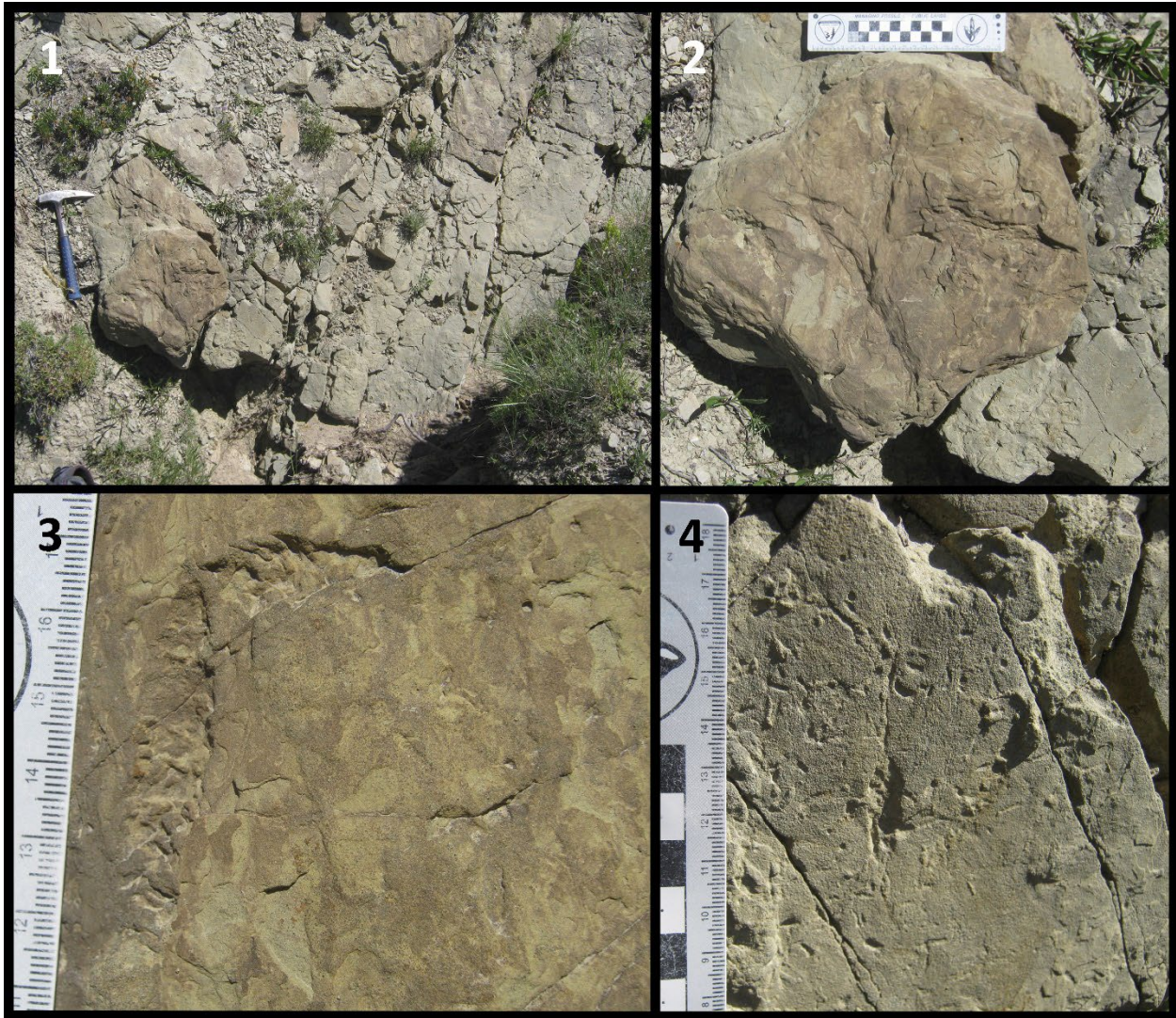


Figure 2.11. Trace-bearing sandstone horizons seen in strike view at Sand Creek (SC) showing 2.11.1,2) an ornithopod dinosaur track, 2.11.3) and meniscated horizontal burrows on a same bedding surface; 2.11.4) small millimeter-scale horizontal burrows.

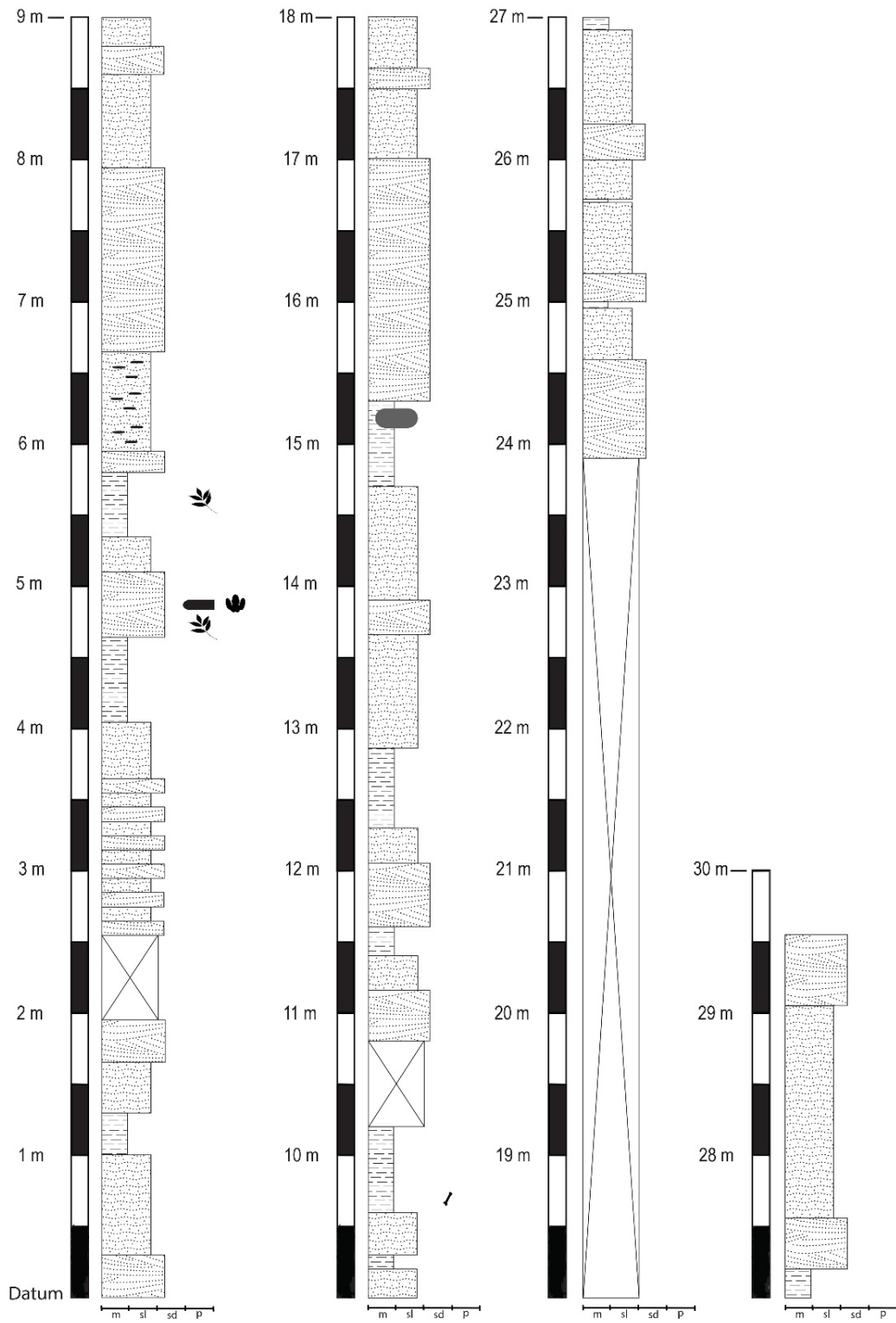


Figure 2.12. Sand Creek stratigraphic section PC 1 (see Figure 2.4 key).

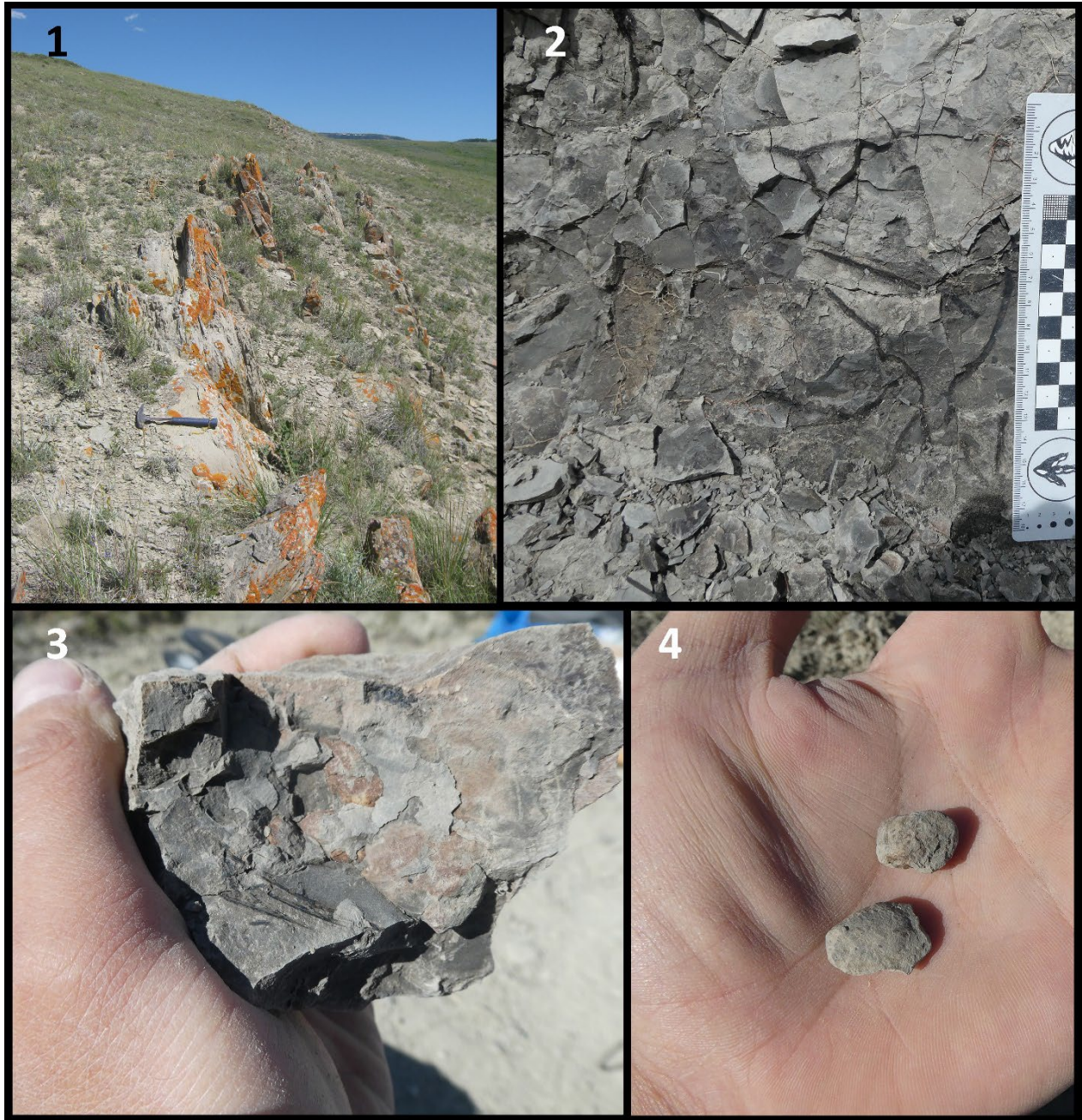


Figure 2.13. Lithofacies F1 exposed at Price Creek (PC 1): 2.13.1) overturned, steeply dipping, fine-grained, ripple-laminated sandstones (section becomes younger moving toward left; 2.13.2) carbonaceous mudstones; 2.13.3) fresh block of carbonaceous mudstones showing nodular appearance and 2.13.4) isolated calcareous concretions.

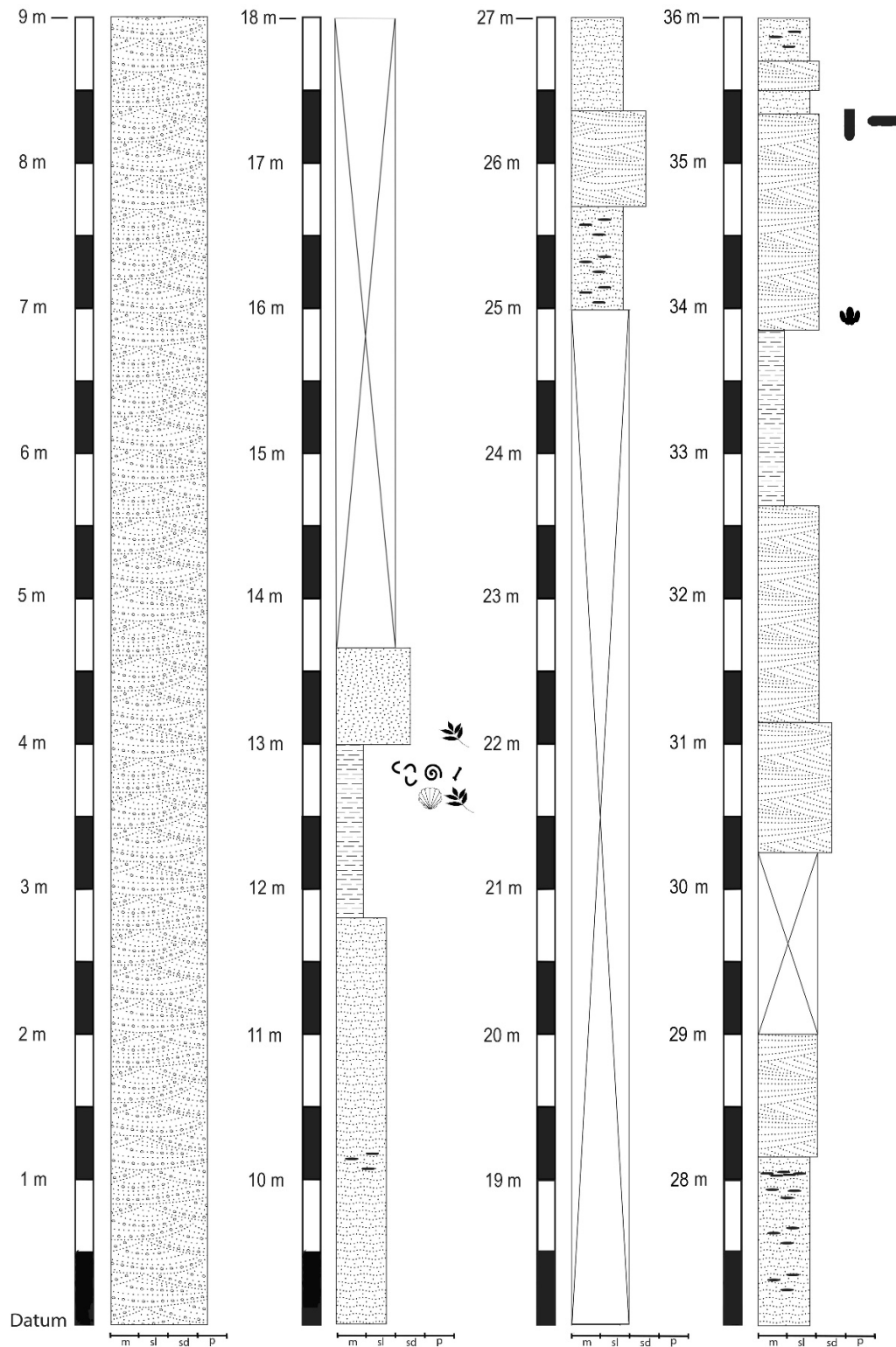


Figure 2.14. Price Creek stratigraphic section PC 2 (see Figure 2.4 for key).

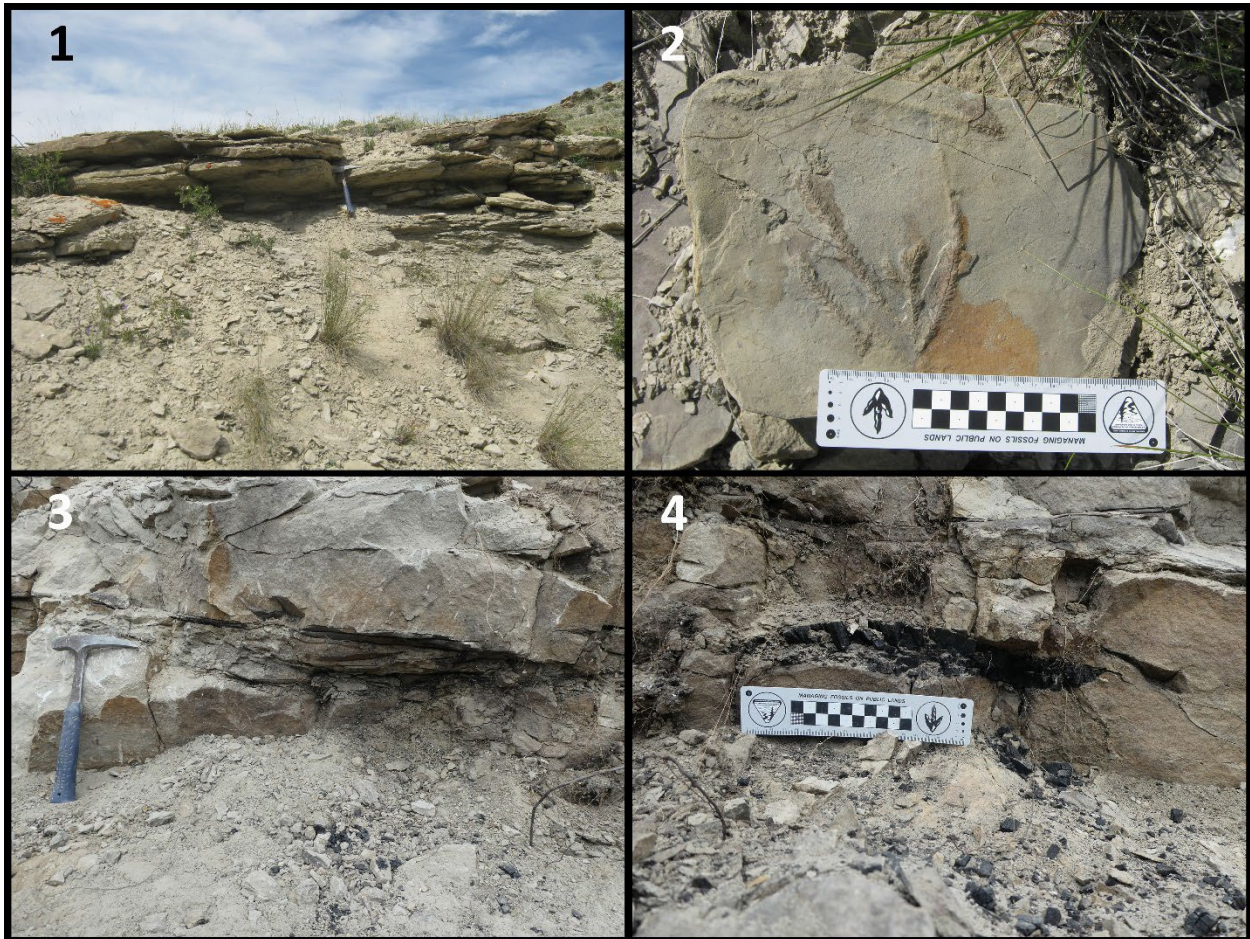


Figure 2.15. Lithofacies exposed at Price Creek (PC 2): 2.15.1) alternation of fine-grained, ripple-laminated sandstones and siltstones with 2.14.2) isolated siltstone block preserving conifer leaves; 2.15.3) massive or crudely stratified sandstones and ripple laminated sandstones with abundant carbonaceous debris, and detail of 2.15.4) log preserved as carbonaceous fragment.

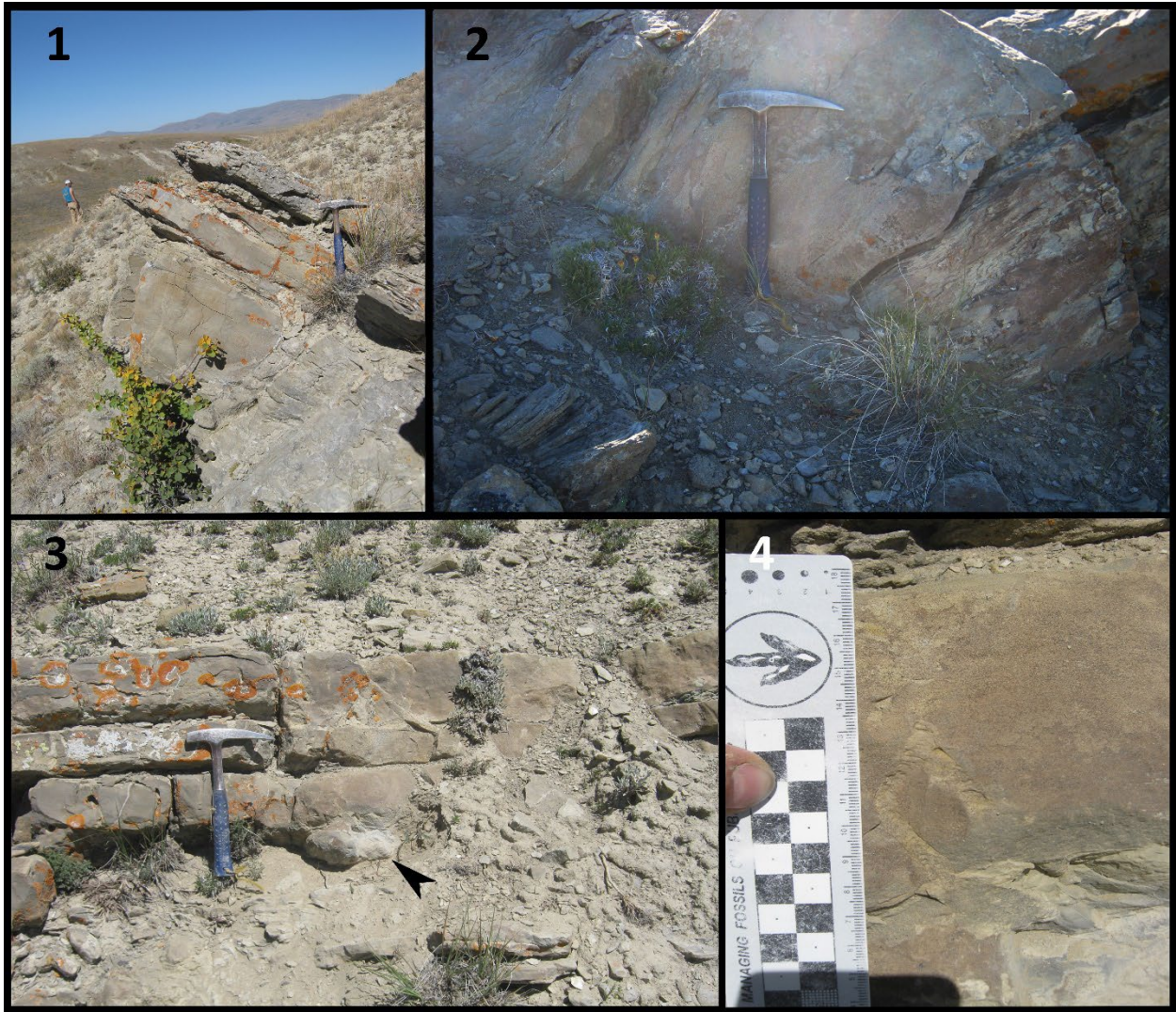


Figure 2.16. Lithofacies F1 exposed at top of section PC 2: 2.16.1) fine-grained ripple laminated sandstones, siltstones and mudstones forming repeating fining upward cycles; 2.16.2) convoluted siltstones and mudstones overlain by cross-bedded sandstones (note the sharp erosive contact); 2.16.3) alternation of fine-grained ripple laminated, sandstones, siltstones, and mudstones with dinosaur track (black arrow) associated with 2.16.4) vertical, walled, meniscated burrows.



Figure 2.17. Frontier Formation succession at Price Creek showing: 2.17.1) overturned fine-grained sandstones, siltstones and gray mudstones strata with close-up of 2.17.2) calcareous concretions observed in gray mudstones, and 2.17.3) overlying sandstones with rip-up clasts and plant debris.



Figure 2.18. Composite panorama showing: 2.18.1) Frontier Formation exposed near Basin and Coal Creeks along bank of the Ruby River, and 2.18. 2) generalized lithologies exposed and location of measured sections.

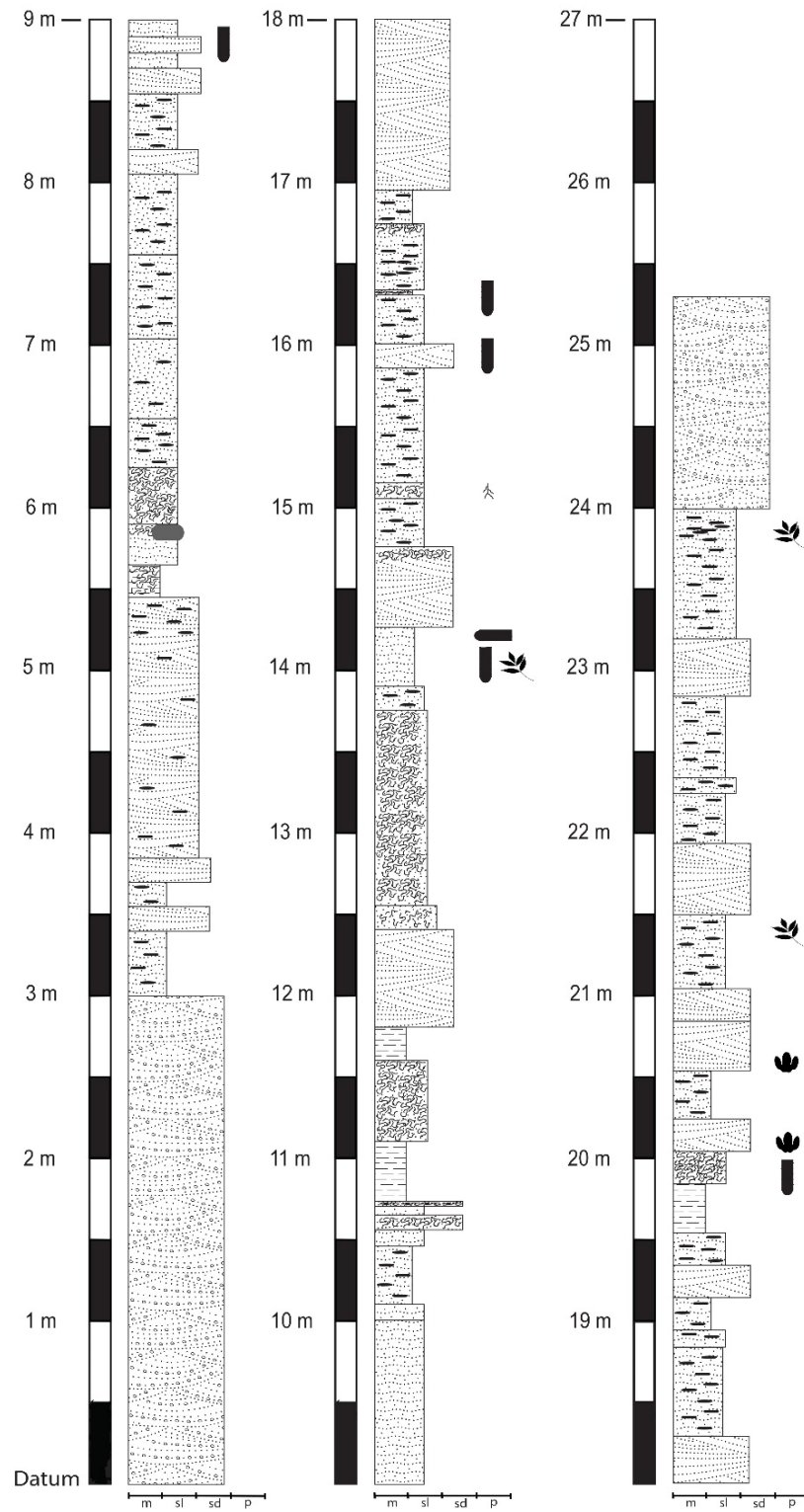


Figure 2.19. Stratigraphic section UR 1 (see Figure 2.4 for key).

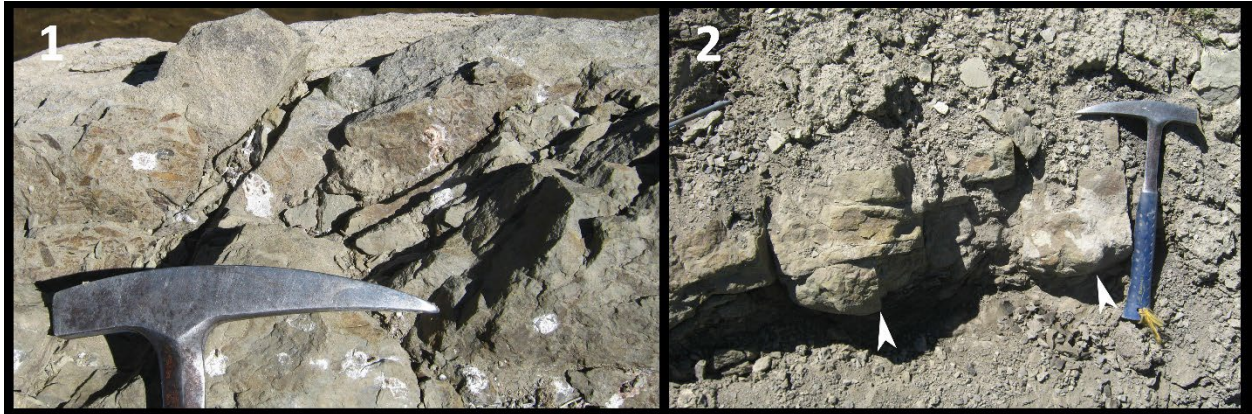


Figure 2.20. Sandstone lithofacies Sr and Fl at UR 1 showing: 2.20.1) abundant carbonaceous plant debris and 2.20.2) two dinosaur tracks preserved as convex hyporeliefs (white arrows).

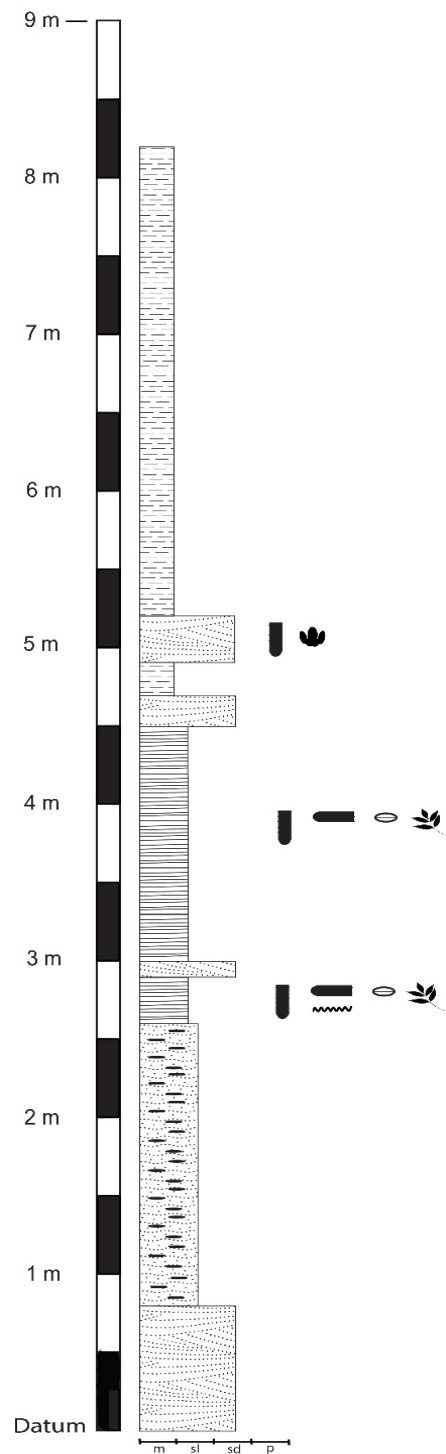


Figure 2.21. Stratigraphic section UR 2 (see Figure 2.4 for key).

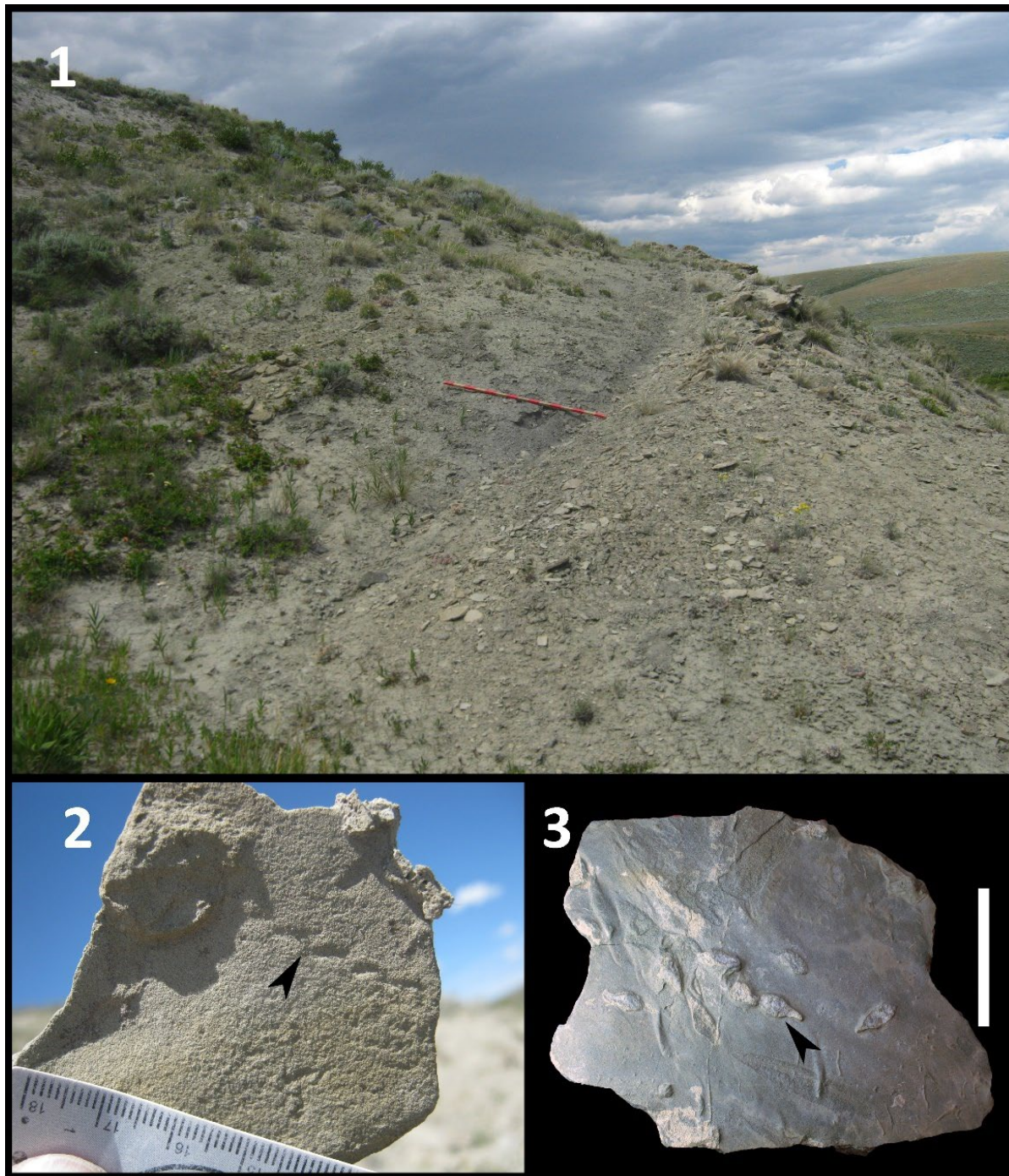


Figure 2.22. Siltstone and mudstone lithofacies exposed at top of section UR 2: 2.22.1) overview of gray carbonaceous mudstones overlying laminated siltstones, and closeup images of 2.22.2) *Cochlichnus* isp. and 2.22.3) *Lockeia* isp. in laminated sandy siltstones (black arrow). Jacob Staff for scale is 150 cm.

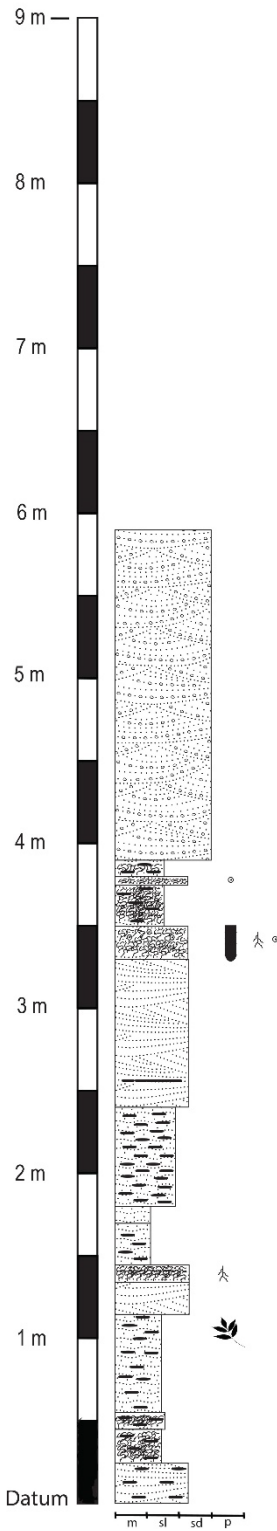


Figure 2.23. Stratigraphic section UR 3 (see Figure 2.4 for key).

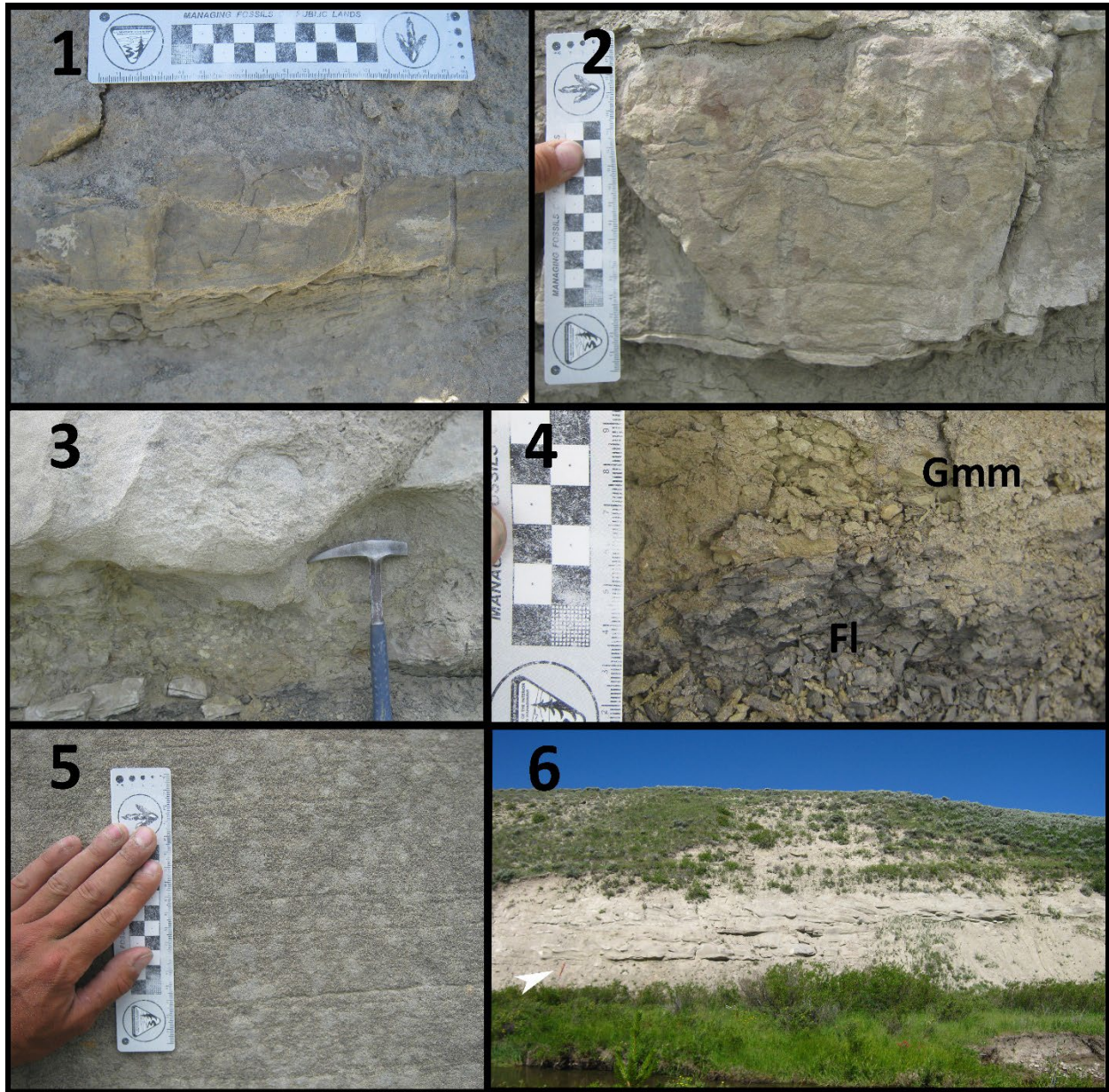


Figure 2.24. Lithologies exposed at UR 3: 2.24.1) Fine-grained sandstones associated with vertical burrows and millimeter scale root traces; 2.24.2) Mottled, nodular, fine-grained sandstones with poorly preserved laminations; top 5 cm of the bed lacks its original sedimentary structures; 2.24.3) Conglomerates comprised of para-autochthonous clasts derived from fine-grained Frontier Formation lithologies, and 2.24.4) closeup image of lower sharp contact between conglomerate bed (Gmm) and overlying carbonaceous mudstone (Fl); 2.24.5) parting lamination at base of medium-to-coarse grained sandstones; 2.24.6) Overview of the coarse grained sandstone unit showing distinctive cross-bedding in upper part. Jacob Staff for scale (white arrow) on the bottom left of the picture is 150 cm.

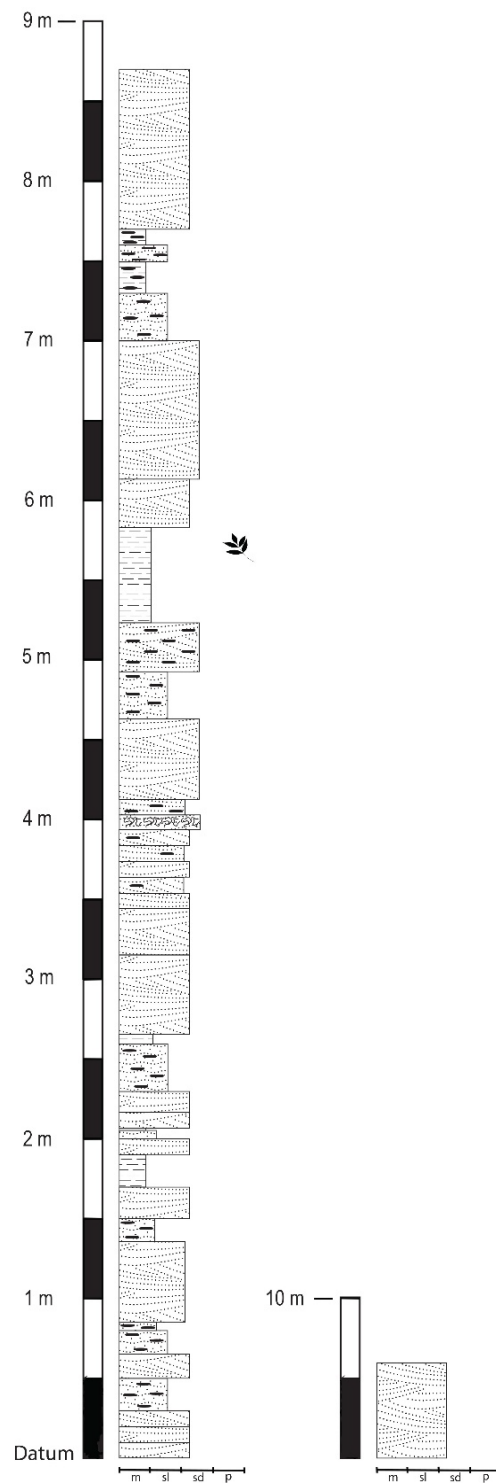


Figure 2.25. Stratigraphic section UR 4 (see Figure 2.4 for key).

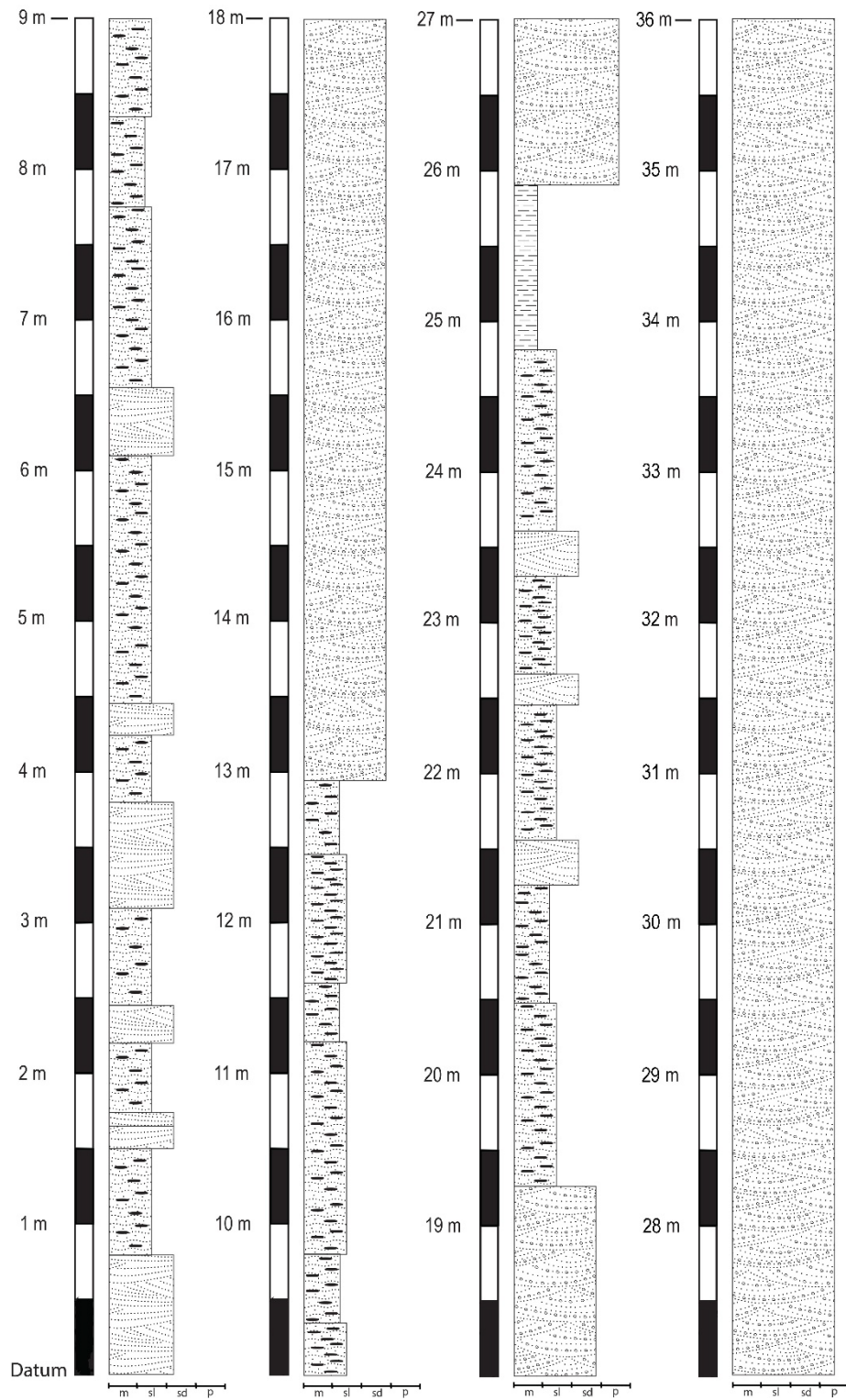


Figure 2.26. Stratigraphic section UR 5 (see Figure 2.4 for key).

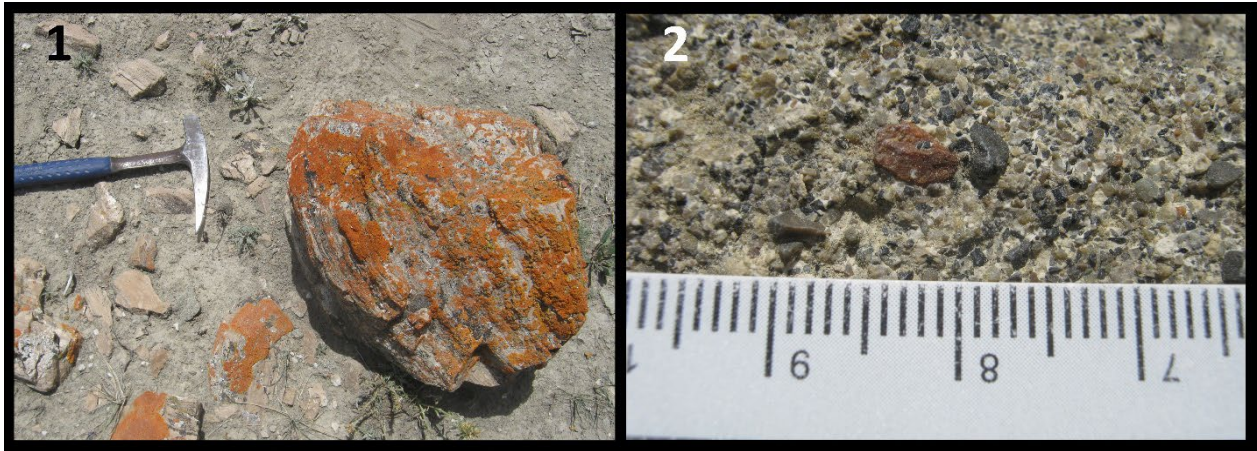


Figure 2.27. Coarse-grained St and Sr lithologies exposed at top of section UR 5 comprised of conglomerate and cross-bedded sandstone. 2.27.1) Large fragment of petrified wood and small weathered fragments; 2.27.2) close-up of a conglomeratic sandstone unit.

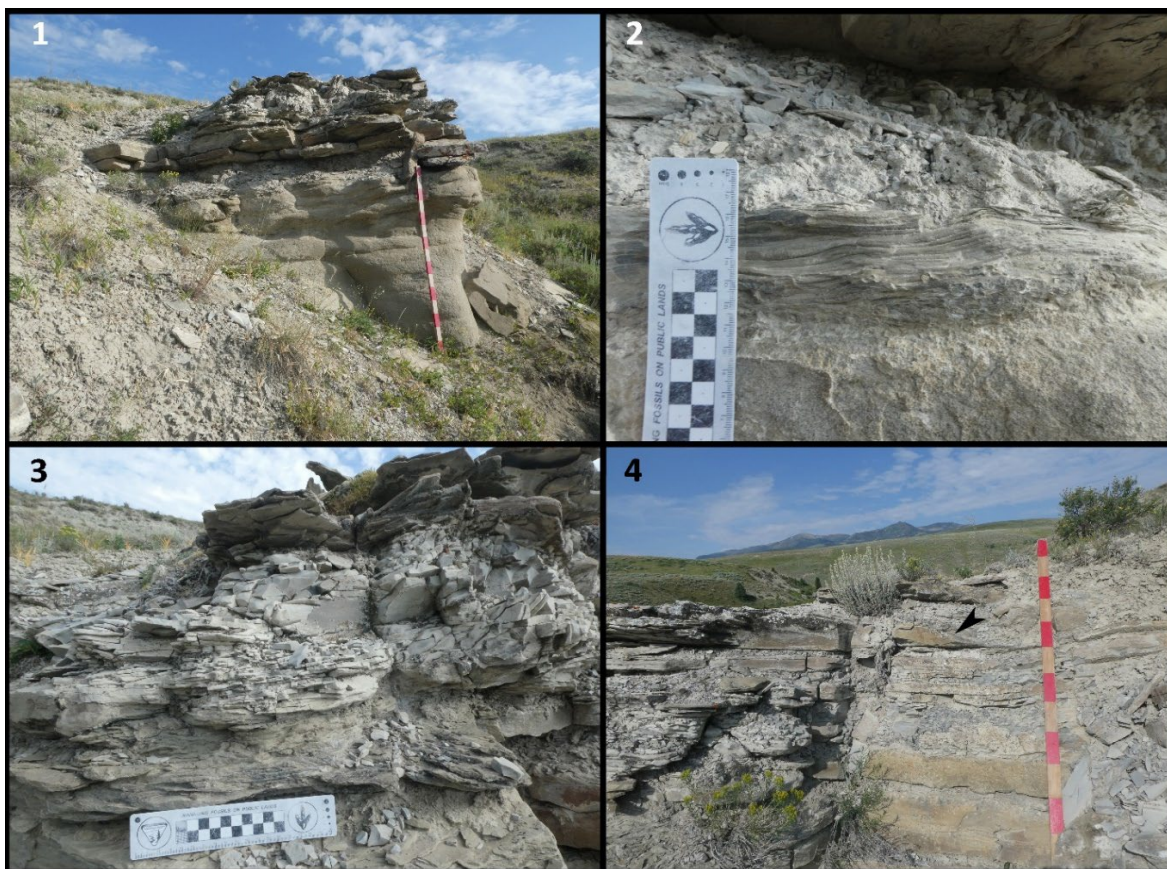


Figure 2.28. Abandonment channel sequence exposed at Coal Creek showing: 2.28.1) transition from coarser-grained channel lithofacies to floodplain lithofacies; 2.28.2) contact between coarse-grained channel sandstone and floodplain lithofacies consisting of ripple-laminated siltstones and mudstones; 2.28.3) fining upward cycles capped by massive gray mudstone; 2.28.4) fining upward-units showing lateral variation in thickness; note the uppermost sandstone bed (black arrow) pinching out from left to right. Jacob's Staff is 150 cm.

Sedimentary Facies	Description	Interpretation
Gh	Clast supported conglomerate with rounded to subrounded clasts, rip-up clasts when present are angular to sub-angular; thickness varies from 10 to 25 m.	Transport and deposition by traction with very limited suspension
Gmm	Matrix supported conglomerates; crudely stratified or massive clasts includes black chert and limestones; units may contain intraformational clasts; thickness laterally variable; intraformational conglomerates may be up to 15 cm thick.	High-strength debris flows
St	Medium to coarse, trough cross-bedded, sandstones; yellow to tan, grey, or greenish in color; conglomeratic lenses may be present; foresets show asymptotic downlaps; common carbonaceous plant material and petrified wood; rare vertical invertebrate burrows and bone fragments; thickness varies 5 to 16 m and they can be 30 to 100 m in extent.	Migration of 3-D dunes
Sh	Horizontally laminated, fine to conglomeratic sandstones; thickness is highly variable from few centimeters up to 50 cm.	Parting lineations, plane-bed flow
Sm	Poorly sorted, fine to medium sandstones, massive or with poorly discernable laminations, display abundant carbonaceous material, rip up clasts and rare bone fragments; thickness varies from 25 to 50 cm.	Sedimentary gravity flows
Sr	Fine to medium grained, ripple laminated sandstones, tan to gray in color; may be normal graded. Thickness varies from few centimeters up to 150 cm.	Traction currents
Fl	<i>Sandstones</i> Gray, rusty or olive in color, may display normal grading, and soft deformation structures; fossil content consists of vertical and horizontal invertebrate burrows and dinosaur tracks; occasional bones may be present; thickness varies from 10 to 40 cm.	Traction currents and decanting
	<i>Siltstones</i> Tan, gray, or green in color; rippled, planar-laminated, or massive; several strata may also display convoluted stratification; carbonaceous plant material is abundant; gray to reddish thinly laminated siltstone units can be bioturbated and preserve abundant plant material; thickness varies from 3 to 150 cm.	
	<i>Mudstones</i> Massive, nodular, sometimes laminated or associated to convoluted stratification; carbonaceous mudstones are very common, characteristically gray or dark gray in color, and associated to centimetric coal lenses; massive and nodular mudstones may contain invertebrate trace fossils; carbonaceous mudstones may contain plant material, bone fragments, and invertebrate shells; thickness varies from few centimeters up to 200 cm.	
	<i>Limestones</i> Lentiform beds; grey in color; either structureless or laminated; well-preserved plant material is common; thickness varies from centimeter-scale veneers up to 20 cm.	
P	Mudstones, siltstones and sandstones associated to mottling, slickensides, caliche nodules, calcareous concretions, and oxidized horizons; gypsum crystals may be occasionally present; deposits can be massive or preserving sedimentary structures; fossil content include invertebrate trace fossils, root traces, bone fragments, and eggshells; thickness varies from 0.05 to 10 m	Paleosols

Table 2.1. Frontier Formation lithofacies and relative depositional environment interpretation according to Miall (1996)

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CHAPTER THREE

ICHTHOLOGY AND SEDIMENTOLOGY OF THE CONIACIAN NON-MARINE FRONTIER
FORMATION, WESTERN CENTENNIAL MOUNTAINS, SOUTHWESTERN MONTANA.

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Manuscript in Chapter 3

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Contributions: Conceived the study, performed the analyses discussed results and implications, and edited earlier manuscripts.

Co-Author: John P. Wilson

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Co-Author: Thaddeus Dyman

Contributions: Conceived the study, performed the analyses, discussed results and implications, and edited earlier manuscripts.

Manuscript Information

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Abstract

The Coniacian non-marine portion of the Frontier Formation in southwestern Montana has been primarily studied stratigraphically, whereas its trace fossil record and relative sedimentological significance have remained so far overlooked. We present the first description of a trace fossil assemblage reported from Frontier Formation deposits exposed in the western Centennial Mountains, Beaverhead County, Montana. Three main lithofacies groups with distinctive trace fossil assemblages have been recognized at the locality of Price Creek: 1) coarse-grained, thin and laterally extensive cross bedded sandstone channel bodies characterized by rare vertical, passively filled burrows; 2) fine-grained overbank sandstones and siltstones, with abundant horizontal, meniscated, and unwallled burrows, sinusoidal trails, vertical burrows, and dinosaur tracks, and 3) fining-upward, planar cross-bedded silty sandstones, associated with carbonaceous plant material and bone fragments. The trace fossil assemblage is ascribed to the pre-desiccation suit of the *Scoyenia* ichnofacies. The occurrence of theropod, ornithopod, and thyreophoran dinosaur tracks, and invertebrate trace fossils suggests considerable diversity of terrestrial and aquatic fauna. Tracks described here represent the first dinosaurian record reported from Coniacian deposits in Montana and one of the few fossil records reported from non-marine Coniacian deposits in North America.

Introduction

The Frontier Formation is a thick siliciclastic sedimentary succession deposited during the early Late Cretaceous in western North America, and extends across Wyoming, Colorado, Utah, New Mexico, Idaho, and Montana (Masters, 1952). Westernmost non-marine facies of the

Frontier have been studied mostly from a stratigraphic standpoint, whereas paleontological and detailed sedimentologic works are scarce (Marsh, 1889; Knowlton, 1917; Lull, 1921; Hamblin et al., 2000; Eaton, 2004). One of the thickest non-marine Frontier successions is exposed in southwestern Montana and was formally described by Tysdal et al. (1997), Dyman et al. (1997), and Dyman et al. (2008), but no detailed body and trace fossil descriptions have been provided so far (Panasci et al., 2020). Studying the non-marine Frontier successions is rather challenging in southwestern Montana because outcrops are poorly and discontinuously exposed. Nonetheless, during the last fifteen years a research team from Montana State University and the Museum of the Rockies has conducted several preliminary investigations of Cretaceous deposits in southern Beaverhead County. These investigations resulted in the collection of isolated bone fragments and teeth, plant material and nine isolated dinosaur tracks from the Coniacian middle Frontier of the Price Creek area, in the western Centennial Mountains (Fig 3.1). This work was systematically expanded between 2018 and 2019, revealing a substantial assemblage of invertebrate trace fossils and dinosaur footprints. The abundance of ichnofossils in these strata is unprecedented. The aim of this study is to provide a comprehensive sedimentological and paleontological analysis of these deposits. We describe lithofacies and trace fossil assemblages and introduce an interpretation of the paleodepositional environment and paleohydrogeologic framework. Additionally, the first dinosaur track-bearing horizon from the Frontier Formation of southwestern Montana will be presented. This report is part of a larger regional study to characterize the paleontology and sedimentology of the Frontier Formation along the western margin of the Western Interior Seaway in the northern Rocky Mountain region. We have observed the Frontier Formation in several mountain ranges in southwest Montana including the

Pioneer Mountains, Lima Peaks, and the Snowcrest and Gravelly Ranges, but have focused this first detailed report on our work in the western Centennial Mountains. Future studies will expand the investigation to other areas and will provide more detailed analysis on the vertebrate and invertebrate ichnoassemblage.

Materials and methods

The field study was carried out between July and August 2019 at the Price Creek locality, in the western Centennial Mountains, Beaverhead County of Montana. The area was chosen for exposure quality and the abundant fossil assemblage including in situ and isolated dinosaur footprints, as well as invertebrate burrows. The area of study extends along the east side of Price Creek where a continuous section of Frontier Formation strata is exposed for several hundred meters. We focused on about 65 m of this section, representing the best exposures for measurement and analysis. The succession was measured using a Jacob staff and measuring tape. Lithofacies and invertebrate and vertebrate trace fossils were described. Lithofacies were defined according to the classification proposed by Miall (1996) and combined into packages based on the characteristics of the fluvial system. A portion of the stratigraphic section was excavated revealing the lower surface of a thin sandstone horizon bearing six dinosaur tracks preserved as convex hyporeliefs. The process initially involved the removal of about 3 m of siltstone and claystone using axe picks and shovels. Subsequently, the uncovered surface was cleaned using brushes and dental picks.

Because the trackway could not be collected, the track-bearing horizon was documented using standard photogrammetry techniques to document and preserve its 3D morphology and geological context (Mallison and Wings, 2014; Wilson and Varricchio, 2019). The tracks were

documented with 204 photographs using a 24-megapixel Canon 760D DSLR camera. The photographs were processed using Agisoft Metashape Professional (64 bit) utilizing standard paleontological photogrammetry workflow (Mallison and Wings, 2014; Wilson and Varricchio, 2019). Tridimensional models are all provided as supplement material. A sparse point cloud was generated with high accuracy and allowed to determine the actual maximum number of tie and key points. Sparse cloud optimization eliminated inaccurately placed points, and camera alignment was optimized. A dense point cloud was constructed with high accuracy, and a mesh was generated from the dense point cloud and allowed to construct the maximum number of faces and vertices. Texture was mapped onto the mesh at a size of 9,000 pixels to minimize final output file size and compatibility. The final model was cropped to remove extraneous points, and the mesh was decimated to 280,000 faces to reduce file size. The model was also processed using the software ParaView 5.9.0. to produce false-color elevations of the track site and of the most relevant tracks herein discussed. One individual, isolated track was documented in 64 photographs likewise using a 24-megapixel Canon 760D DSLR camera. Photogrammetric processing was conducted in Agisoft Metashape Professional (64 bit) using identical workflow to the in situ trackway, though the photos were processed in two chunks. Highest accuracy was utilized for sparse cloud construction, and aggressive depth filtering used for dense cloud construction. The two chunks were merged using markers placed on common points to completely model the specimen. The model was decimated to 200,000 faces to reduce file size. Finally, the site was back filled according to Bureau of Land Management regulations using the overburden previously removed and restoring the original slope of the drainage.

Because of the rarity of well-preserved bedding surfaces, no collection of invertebrate trace fossils was attempted and specimens were described in situ to preserve the outcrops intact. Twenty-three dinosaur tracks, preserved as in situ and ex situ concave hyporeliefs, were identified from Price Creek. They are listed in two separate tables providing: specimen catalog number, track producer, measurements, as well as collected and uncollected specimens. In situ tracks reported from the track-bearing horizon are listed separately. Due to track preservation, recognition of left and right limb impressions was not possible. Thus, digit impressions are here conventionally counted clockwise, in plantar view, and using Arabic numerals. Measurements were taken according to Thulborn (1990) and include length and width of tracks as well as digit width and length. Digit divarication is calculated assuming that the digit axes represent lines of best fit. For tridactyl tracks this usually correspond to axes converging at or in proximity of the rear margin of the track. Depth of in situ tracks was estimated considering the maximum thickness measured from the base of the track-bearing horizon to the deepest point of the pad impression. When tracks were preserved as isolated casts, a minimum thickness was approximated using the maximum depth observed. Specimens collected are curated at the Museum of the Rockies, Bozeman, Montana, with repository number MOR 1644.

Stratigraphic and sedimentologic settings

The Frontier Formation is a thick and extensive synorogenic clastic wedge deposited during the Late Cretaceous in a rapidly subsiding foreland basin along the western margin of the Western Interior Seaway (Dyman et al, 2008). Deposition of the Frontier Formation occurred during a global sea level rise that reached its maximum extent during the Turonian (Eaton et al., 1997). Abundant sediment supply was provided by increased thrusting, regional uplift, and

erosion related to formation of the western Cordillera (Jordan, 1981; Yonkee and Weil, 2015; Miall and Catuneanu, 2019). Sediment was also provided by regional volcanic activity as indicated by abundant volcanoclastic horizons observed in regional Frontier successions (Roberts, 1972; Dyman et al., 1997).

In southwestern Montana, the Frontier Formation consists of carbonaceous shales and mudstones, limestones, siltstones, sandstones and conglomerates. Volcanically-derived porcellanitic rocks are common in the middle and upper parts of the Frontier in the region. Westernmost facies are thick and entirely non-marine, whereas equivalent rocks become increasingly thinner and marine-influenced eastward (Cobban, 1951; Roberts, 1972; Dyman et al., 1997). In westernmost areas, near Lima Peaks, the Frontier Formation is estimated to be at least 2,000 m thick and is comprised of siltstones, mudstones, sandstones and conglomerates, representing a proximal western facies deposited in fluvial and coastal settings. The succession in the Lima Peaks area has been subdivided into: 1) a lower coarse unit characterized by fine- to coarse-grained sandstones, siltstones, mudstones, and conglomerates, 2) a middle fine-grained unit consisting of fine to medium-grained sandstones, siltstones, limestones, and mudstones, and 3) a coarse upper unit containing porcellanites, volcanoclastic sandstones, and conglomerates (Fig 3.2) (Dyman et al., 1997; Dyman et al., 2008). Here the Frontier Formation overlies the Vaughn Member of the Blackleaf Formation disconformably, whereas the contact with the overlying Upper Cretaceous Beaverhead Group may be transitional or unconformable. Both the lower and the upper Frontier Formation strata in the Lima Peaks area have been time-constrained by radiometric dates from porcellanites that indicate an age no older than middle Cenomanian, and as young as early Santonian (Dyman et al., 1997). Frontier strata comprise facies younger

than those reported from the type section in southwestern Wyoming (Knight, 1902; Cobban and Reeside, 1952). The upper part of the succession in the Lima area is stratigraphically equivalent to easternmost Coniacian and Santonian deposits assigned respectively to the overlying Cody Shale, and the Telegraph Creek Formation (Tysdal, 1991; Dyman et al. 1997; Dyman et al., 2008).

The deposits under examination are located about 30 km southeast of Lima, Montana, in the western Centennial Mountains. Only the Coniacian middle unit of the Frontier is exposed here. The lower and upper parts of the formation are missing due to Late Cretaceous to Cenozoic thrusting, volcanism, and extensional faulting. (Dyman et al., 2008). This sequence is comprised of fine to coarse sandstones, siltstones, and mudstones respectively interpreted as laterally extensive fluvial sandstone channel and fine overbank deposits. Evidence from sedimentology, palynomorphs, and fresh-water vertebrate fossils suggests that the middle Frontier of the western Centennial Mountains was deposited in a distal coastal plain setting (Dyman et al., 2008; Panasci et al., 2020).

Sedimentary facies and paleodepositional environment

The stratigraphic section herein described is located along the east side of the Price Creek drainage and consists of 65 m of fine to coarse grained sandstones, silty sandstones, siltstones, mudstones, shales and limestones. The Price Creek section is part of the Peet Creek anticlinorium, delimited to the north by the Centennial fault and extending for about 248 square kilometers (Honkala, 1960). Strata are overturned and steeply inclined, dipping about 74 degrees to the southwest, and with optimal exposures mainly visible along incised drainages. Medium- to coarse-grained sandstones form bodies that can reach tens of meters in apparent lateral extent.

They are encased in packages of fine- to medium-grained sandstones, siltstones, mudstones, and limestones forming multiple fining up-ward sequences. The top 25 m of section (Fig 3.3), which preserves an abundant invertebrate and vertebrate ichnoassemblage, was described in detail and includes three main lithofacies groups of Miall (1996).

Lithofacies St and Sr

Units are comprised of yellow to tan, gray, and greenish gray salt and pepper, coarse to medium, trough cross-bedded sandstones. These sandstone bodies are 110 to 500 cm thick and may extend laterally up to about 30 m or more (Fig 3.4). The coarser and thicker sandstone units form distinctive reliefs appearing light blue, or gray to yellow. Units fine upward and contain trough co-sets, each typically about one meter thick, and dipping between 10-16°.

Intraformational lag deposits comprised of coarse, sometimes conglomeratic sandstones may also be present, forming a well indurated massive or sometimes crudely cross-stratified stratum at the base of the sandstone bodies. These horizons are characteristically rusty in color and display sharp contacts with the underlying units. These sandstones grade upward from trough-cross bedding into ripple cross-laminated units.

Thinner sandstone units are finer grained and lack conglomeratic lags, but can be as laterally extensive as the thicker, coarser units. Stratification consists of co-sets of gently dipping trough beds, sometimes grading upward into centimeter scale sets of ripple laminae.

Sandstone bodies comprising these lithofacies usually lack fossils, but carbonaceous plant material and less frequent bioturbation may be present. Individual sandstones are relatively thin, but laterally extensive, with small-scale, lateral accretion geometries. Trough bedded and ripple

laminated sandstones units can be associated respectively to lithofacies St and Sr observed in channels architectural elements and are interpreted as channel deposits (Miall, 1996).

Lithofacies Fl

Lithofacies Fl comprises about 80 % of the section analyzed, and its lithologies define multiple fining upward cycles, forming packages from few tens of centimeters up to 2 m. Each package generally consists of fine-grained, cross-bedded sandstones, ripple-laminated siltstones, carbonaceous mudstones, and limestones (Fig 3.5). Fine-grained cross-bedded sandstones typically form the base of each fining upward unit, they usually become ripple laminated at the top, and may display normal grading. They are calcareous and characteristically weather with a brown or reddish color. The fresh color is typically gray or green. Sandstone beds vary from 10-40 cm in thickness and can be a few meters up to tens of meters in lateral extent. Strata are lenticular and have sharp upper and lower contacts. Siltstones are olive to yellow in color and form ripple laminated beds. They are often rich in layers of carbonaceous plant material and range from 10-100 cm in thickness. They are usually overlain by gray organic-rich mudstones, but fine-grained sandstones may also overlie siltstone strata. Gray organic mudstones may occur as thin drapes overlying siltstone beds, and form units up to 2 m thick. Thicker units contain abundant plant material, gastropod shells, and occasional thin coal lenses (Fig 3.5.4). Gray limestones may be present, forming laterally continuous, or discontinuous lentiform beds about 20 cm thick. Limestones can be either structureless or laminated and contain well preserved plant material.

A 5-30 cm thick unit of rusty to gray, laminated, fine-grained siltstone was observed at the base of the section, but contacts with the lower units could not be determined since it is not

visible on the outcrop. The contact with the overlying fine sandstone unit, on the other hand appears to be sharp. It consists of sets of 0.5-1 cm thick laminae, with frequent burrowing, bioturbation and abundant plant material often found in exquisite state of preservation (Fig 3.6). Oscillatory ripples and soft deformation structures may be occasionally observed, suggesting that this laminated siltstone unit was deposited in very low-energy environments such as ponds or pools. Lithofacies Fl is interpreted as overbank fines generated by traction currents and suspension (Miall, 1996).

Lithofacies St, Sh, and Sr

These lithofacies comprise about 7 m of section measured and are characterized by 50-150 cm thick units of: 1) normally graded, cross-bedded, fine-grained sandstones, and 2) silty sandstones, containing abundant carbonaceous plant material and occasional bone fragments (Fig 3.7). Together, these units form a distinctive coarsening upward sequence, with multiple thin units at the base that pass upward to thicker and coarser units associated with increasingly abundant carbonaceous material. Lower units are composed by fine grained sandstones, sometimes planar laminated at the base and passing to ripple lamination at the top, overlain by thin beds of ripple laminated siltstones and mudstones. The lower units grade upward into coarser and increasingly thicker units of fine-grained, cross bedded and normally graded sandstones and silty sandstones. Silty sandstones are poorly sorted and usually have a massive appearance. Presence of planar and ripple lamination, normal gradation, and abundant carbonaceous plant fragments suggests that these units were emplaced by decelerating flows (Jones and Rust, 1983; Burns et al., 2017). Lithofacies St, Sh, and Sr are interpreted as crevasse splay deposits.

Invertebrate trace fossils

Cochlichnus anguineus Hitchcock 1858

Description. These small sinusoidal trails are preserved as concave hyporeliefs. Each trail may be up to 10 cm long, displaying waves with a consistent wavelength of 3-5 mm, and amplitude from 2-3 mm (Fig 3.8.5). Trails vary in shape from straight to slightly curved, and do not display second-order meanders. Cross cutting trails are sometimes observed.

Remarks. The ichnogenus *Cochlichnus* is characterized by sinusoidal forms and comprises three valid ichnospecies, including *C. anguineus*, *C. annulatus* and *C. antarcticus* (Fillion and Pickerill, 1990; Buatois and Mángano, 1993). Specifically, *C. anguineus* is differentiated by the absence of annulations or lateral markings. These trails have been interpreted as grazing, locomotion, feeding traces, or as a result of a combination of locomotion and feeding behavior (Buatois and Mángano, 1993; Eagar et al., 1984; Buatois et al., 1997). Several possible trace makers have been suggested for *Cochlichnus* isp., but experiments have demonstrated that the most probable producers likely are nematode worms (Uchman et al., 2004).

cf. *Skolithos* isp.

Description. These structures have been observed in situ as passively filled, distinctively walled or unwallled burrows with circular cross section, and highly inclined or vertical orientation (Fig 3.8.3). Diameters may vary from 0.5-2 cm. They are typically preserved in fine grained sandstone beds of the Fl lithofacies as full reliefs, with passive filling consisting of the same lithology of the host rock. They can also be preserved as empty circular cross sections on

bedding surfaces. Several burrows may extend downward, forming a vertically or steeply inclined shaft, that curves and becomes parallel to the bedding plane. A burrow was reported forming a vertical shaft about 6 cm long into a fine-grained sandstone sheet, crosscutting an underlying thin, ripple laminated silty sandstone horizon, and then curving and becoming almost horizontal approaching the base of a lower fine sandstone sheet (Fig 3.8.4). Rare vertical burrows have also been observed in cross section at the base of medium and coarse-grained sandstone channels.

Remarks. Simple vertical, unbranched and passively filled burrows are typically assigned to the ichnogenus *Skolithos* isp. Knaust et al. (2018) revised the diagnosis of this ichnogenus, pointing out the homogeneous fill, the vertical or slightly inclined orientation associated with high length to diameter ratio, the absence of branching, and the presence of lining. Vertical burrows observed in medium and coarse-grained sandstones may be tentatively assigned to *Skolithos* isp., as they seem to present a lined areola along the border of the structure and display passive infilling and vertical orientation. On the other hand, other vertical burrows reported in finer deposits of lithofacies F1 seem to be quite different in that they vary in inclination with increasing depth, sometimes becoming almost horizontal with respect to the bedding plane. These trace fossils are here interpreted as structures produced by suspension feeders or as burrows constructed by otherwise dwelling invertebrates (Knaust et al., 2018).

cf. *Taenidium barretti* (Bradshaw, 1981)

Description. These are horizontal, cylindrical, meniscated burrows, straight- to slightly-curved, or wavy in orientation, and lacking a wall (Fig 3.8.1). Specimens are typically preserved as epichnial and hypichnial structures on fine sandstone units of the F1 lithofacies, with several

burrows that may be gently inclined and descending into the sandstone bed. Although crosscutting can be observed, true branching is absent. Diameters may vary from 0.5-1.5 cm, and internal structures are composed by menisci with alternating sandy and silty sediment. Meniscated fillings are often evident due to weathering. They produce a characteristic color contrast and differential erosion between finer and less resistant material, and the coarser sediment comprising the burrow's filling. Menisci form sets of hemispherical, closely spaced nesting patterns, asymptotic with respect to the burrow's border. Each meniscus is about 1 mm thick in small specimens and can reach 3-5 mm in several larger specimens observed (Fig 3.8.2).

Remarks. The ichnogenus *Taenidium* was revised by Kingsley and Pickerrill (1994). They defined it as an unwalled, unbranched, meniscated, horizontal burrow with a circular or elliptical cross-section, and a straight to curved, or wavy orientation. *Taenidium* ichnospecies are differentiated by morphology and variation of the meniscated infill. For example, in *T. serpentinum* the menisci are widely spaced and with homogeneous filling (D'Alessandro and Bromley, 1987); *T. irregularis* displays more curved menisci staked in a nest fashion (Li, 1993). Different morphotypes displaying variation in dimension and burrow orientation have been also reported by de Gibert and Saez (2009), in specimens assigned to *T. barretti*. The specimens differ from *T. serpentinus* in the absence of broadly spaced, arcuate menisci (Kighley and Pickerill, 1994). They are similar to *T. irregularis* in the presence of asymptotic menisci (Li, 1993), but the structures here described are assigned to *T. barretti*, according to presence of hemispherical menisci that display two different materials (Rodríguez-Tovar et al., 2016). The characteristic backfilling observed in *Taenidium* may either indicate a series of ingestion and excretion of

detritus, typical of worm-like organisms processing the sediment, or sediment manipulation as observed in arthropods (Bromley, 1996; Melchor et al., 2006).

Enigmatic structures

Several structures represented by depressions and knobs with a hemispherical, concave shape, are preserved as convex hyporeliefs on laminated siltstones assigned to lithofacies Fl (Fig 3.8.5). They are about 2-5 mm in diameter, and sometimes appear to form clusters on bedding surfaces. Some bed surface depressions also correspond to knobs on opposite sides of the rock slabs (Fig 3.8.6). These structures are common, but their interpretation is problematic. Spherical, knobby structures forming similar patterns may be produced by microbial activity (Fillmore et al., 2017), but they differ drastically from the structure here described since they consist of coarser spherical or ellipsoidal units that contrast with the surrounding finer sediment. It seems also highly doubtful that they represent feeding probe marks such as those observed in association with bird footprints as these structures are both preserved in proximity (Falk et al., 2010).

Vertebrate trace fossils

Dinosaur footprints

Dinosaur tracks are preserved as convex hyporeliefs in fine-grained sandstone units, or more commonly as isolated casts detached from the parental bed. Given their preservation, a confident ichnotaxonomical attribution could not be attempted, but a broad assignment to a possible producer is here provided according to several morphological features. At least thirteen tracks have been assigned to ornithopod track makers, followed by two theropod and two possible thyreophoran footprints (Fig 3.9). Ornithopod tracks are tridactyl, wider than longer

footprints, and lack claw impressions, while theropod tracks are longer than wider, with distinctively tridactyl claw-bearing impressions. Tracks were tentatively ascribed to ankylosaurian or nodosaurian pes footprints, according to the elongated impressions of digits (Carpenter, 2001, p. 414). Other poorly preserved irregular structures and isolated fragmentary material were confidently ascribed to dinosaur footprints, according to the presence of diagnostic taphonomic attributes comparable to those observed in other well-preserved specimens, such as scale-scratch marks, hoof and claw impressions, and skin impressions. Most of the tracks were found detached from the parental bed and collected at Price Creek can be confidently ascribed to the excavated track-bearing horizon that corresponds to the top of the section measured. Other tracks have been found as isolated casts or convex hyporeliefs in stratigraphically lower, fine sandstone horizons of the measured section (Table 1,2).

Track-bearing horizon

The track-bearing horizon herein described consists of a 20 cm thick, fine-grained, cross bedded sandstone, extending laterally about 15 m. Excavation exposed a triangular section in this horizon that is about 300 cm long and 90 cm high. The sediment removed during excavation also revealed 220 cm of the lower succession, consisting from the bottom-up of: 1) yellow, ripple laminated siltstones, and 2) gray organic mudstones associated to a laterally continuous limestone horizon. These lithologies are all assigned to lithofacies F1 (Fig 3.10). Six tracks preserved as convex hyporeliefs and with variable preservation styles are described, of which one track has possible ornithopod affinity, and the other one is likely assigned to a theropod dinosaur (Fig 3.11; see also supplemental material).

Track 1 (Fig 3.12) is oriented parallel to the ground surface of the quarry. Poorly preserved tridactyl digit impressions suggest a possible ornithopod or theropod affinity, but the track is no more than 2 cm shallow and poorly defined, thus precluding its identification with confidence. Track 2 is the best preserved on the bedding surface, and represents a well-defined tridactyl footprint, with the middle digit forming a larger and deeper impression than those formed by the lateral digits (Fig 3.13). The heel is characterized by a “W” shaped outline and appears to be less impressed than the anterior side of the track. A lateral digit displays distinctive linear marks at the extremity of the digit impression, possibly produced by the ungual. The track is 27 cm long and 33 cm wide, with a length/width ratio of 0.81. Considering the overall morphology observed, this track is confidently assigned to an ornithopod dinosaur due to the short, broad digits and wide heel pad, as well as the low pes length/width ratio (Kim et al., 2009). Track 3 is an elongated impression, pinching out toward the superior side of the bedding plane, and is oriented perpendicular to the floor of the quarry (Fig 3.14). The track is approximately 30 cm long and 20 cm wide and displays three poorly preserved digit impressions. Adjacent to track 3 lies another elongated tridactyl track (track 4), bearing deep claw impressions on the digits, and metatarsal impressions on the posterior side (Fig 3.15). The total length estimated, including the metatarsal impressions, is about 27 cm, and it is about 15 cm wide. A lateral digit seems to be absent, but a closer inspection reveals that it is partially obscured by track 3, and only the tip of the claw impression is visible. This digit impression is 9.5 cm long and seems slightly diverging from the middle digit. The other lateral digit is also partially covered by track 5 and its length cannot be estimated, although it appears to have approximately the same length of the other lateral digit impression. The pad impression of track 4 has a knotted texture, and three wrinkled

parallel structures can be observed on the posterior side. Digits are overall not splayed and suggest low interdigit angle. This track is likely assigned to a theropod producer according to presence of claw impressions and relatively low length/width ratio. It also appears that a second set of irregular impressions, consisting of a claw-bearing track, and an elongated impression with distinctive lateral scratch marks (Track 5 and 6), laterally overlap track 4.

Biogenic structures

Two additional structures of biogenic origin observed on the same bedding surface do not display evident diagnostic features assignable to a footprint, and their description are treated separately. One structure can be observed very close to track 4 and consists of a patch about 4 x 2 cm characterized by small rounded, regular or elongated knobs, tightly spaced, and preserved as convex hyporeliefs (Fig 3.16). Each knob is about 2-4 mm in diameter and has a rounded or somewhat polygonal shape. Individual knobs are separated from adjacent knobs by a thin groove about 1 mm wide. On the left side of the patch, knobs seem to merge forming two elongated ridges about 1 cm long.

In the left lateral corner of the exposed track bearing horizon, an irregular, somewhat crescent-shaped structure was observed (Fig 3.17). The structure is preserved as a positive hyporelief about 25 cm long, with a concave side facing toward the base of the quarry. Several ridges-and-furrows features observed on the convex hyporelief structure appear to form small lobes, arranged somewhat in a nesting pattern and become increasingly elongated following the curvature of the crescent-shaped structure. A set of thin sandstone laminae is also visible on the lateral side of this structure.

Remarks. The occurrence of knobby clusters, or irregular hyporeliefs in fine-grained alluvial deposits may be caused by a wide array of sedimentary processes such as soft sediment deformation, rain drops and traction currents, or they may be associated with organic causes such as invertebrate and vertebrate bioturbation (Paik et al., 2010). Discriminating organic from inorganic sedimentary structures related to physical and chemical sedimentary processes is challenging since these structures often closely mimic invertebrate bioturbation or dinosaur tracks (Thulborn, 1990 p. 232; Buck and Goldring, 2003). The knobby structures observed near track 4 form an isolated, tightly packed cluster of regular convex hyporeliefs, relatively uniform in morphology. It seems doubtful that these structures were produced by raindrops, since they are usually more widely spaced, variable in size, and typically characterize more extensive surfaces (Metz, 1981). Several trace fossils such as *Paleodyction* and graphoglyptid traces may also show similar structures. However, they all have a tridimensional, hexagonal shape, and are typically reported from strata assigned to deep marine environments (Wetzel and Uchman, 1997; Monaco, 2008). Morphology, shape, and circumstantial presence of dinosaur tracks on the same horizon, on the other hand, may reasonably suggest that these structures represent skin impressions, likely produced by a dinosaurian trace maker (Kim et al., 2010). Unfortunately, there seems to be no definitive pattern to categorize different makers for skin impressions, especially when they are found as isolated patches. Additionally, identification is often circumstantial to other tracks observed in association with them. Independent criteria such as dimension and morphology have been used to identify skin impressions produced by sauropod dinosaurs (Foster and Hunt-Foster, 2011). In this specific case, however, arrangement and morphology appear to be more congruent with the polygonal smooth basement scales observed in ornithopod dinosaurs (Bell, 2014). In

fact, similar morphologies have been also observed in ornithopod skin impressions associated with deep footprints preserved in overbank deposits (Shillito and Davies, 2019). Whether these impressions represent a partial footprint or an isolated patch from a different part of the trace maker's body also remains unclear. Even though specific patterns in scale dimension and morphology have been reported from specific parts of the body (Bell, 2014), it was also pointed out that morphology observed on pad impressions in tracks assigned to ornithopod dinosaurs may also be very similar to other integumentary impressions produced by the rest of the body (Currie et al., 1991). So far, ornithopod dinosaurs are the most abundant trace makers in middle Frontier strata. Similar tracks have also been recognized on the track-bearing horizon here described, suggesting a potential ornithopod affinity.

The crescent-shaped hyporelief structure observed on the track-bearing horizon here described displays features likely comparable to those produced by deformation in fine-grained soft sediments (Van Loon, 2009). Similar features have also been reported from dinosaur tracks preserved as isolated casts and displaying high distortion of pad and digit impressions. An irregular tridactyl track collected from the same area clearly displays deformed laminae at the top of the structure, and distortion of digits with concurrent association of longitudinal ridges-and-furrows structures (see supplemental material). Ridges and furrows structures at the base of tracks may be also associated with linear or curved, elongated lobes 3-5 mm in size. They are rounded and elongated, and may form bifurcated arrow-shaped lineations, pointing toward the distal end of the digit impression. The co-occurrence of such features seems reasonably consistent with preservation of other dinosaur tracks observed in the same area.

Discussion

As earlier defined, three groups of lithofacies have been reported in the Frontier Formation deposits of Price Creek locality. These lithofacies show distinct trace fossil assemblages. Channel sandstones, lithofacies St and Sr, are mainly characterized by sparse, vertically orientated, passively filled, and lined *Skolithos*-like burrows. Interpretation of the *Skolithos* burrows depends on the specific sedimentological context and may vary from suspension-feeding organisms to terrestrial arthropods, or even root traces (Kim and Pickerrill, 2003; Gregory et al., 2006; Netto, 2007; Baucon et al., 2014). Burrows observed in coarse-grained, cross-bedded sandstone bodies may therefore be more reconcilable with structures produced by organisms capable of exploiting suspended food particles in high-energy fluvial settings (Knaust et al., 2018). In contrast, Fl floodplain lithofacies are almost exclusively represented by *T. barretti* burrows, with subordinate dinosaur tracks, and vertical burrows preserved in fine grained sandstones units.

Sedimentological and ichnological evidence indicates that water bodies occupying this sector of the floodplain basin underwent subsequent lowering after a flood event, but the water table overall remained sufficiently high to maintain the substrates in a saturated to cohesive state. Overbanks were unconfined and deposited fine-grained sediments mostly via decelerating flows and decanting as shown by their lateral extension, normal grading, parallel and ripple lamination, and the emplacement of mudstone and limestone units. Siltstones, mudstones, and limestones also form units of transitional composition suggesting variation in hydraulic competence. Settling of low-energy aquatic environments, such as ponds or pools was likely facilitated by the presence of natural depressions and by the abundance of silt and mud sediment preventing

immediate draining of water after a flood event (Williams et al., 2001). Trace fossil preservation observed in Fl lithofacies is distinctively variable and reflects differential substrate conditions established in the sedimentary basin. Horizontal burrows emplaced in waterlogged substrates may be abundant but poorly defined. The high concentration of horizontal meniscated burrows may suggest an opportunistic behaviour of the trace makers, exploiting new favourable substrates following a flood event (Rodríguez-Tovar et al., 2016). In more cohesive conditions, horizontal trace fossils display well-defined morphologies with more definite menisci, and they may be crosscut by distinctive vertical passively filled burrows. Vertical and inclined burrows do not deform the bedding laminations suggesting that they were emplaced when the substrate was less hydrated and more cohesive (Buatois and Mángano, 2004). They may represent possible domichnia structures produced by invertebrates during low stages of the ground water table, likely in search of shelter to reach better temperature and moisture conditions of the substrate (Bown and Kraus, 1983; d'Alessandro et al., 1987).

Variation in substrate conditions is also suggested by the variable preservation observed on in situ dinosaur tracks as well as on tracks detached from the parent horizon. Several dinosaur tracks are well preserved throughout the Price Creek section. They bear scale-scratch marks, hoof, claw, and metatarsal impressions. Others are scarcely preserved and characterized by poorly defined digit impressions, and an irregular morphology. Tracks are all preserved as convex hyporeliefs impressed on a muddy substrate that corresponds to the carbonaceous mudstone unit reported in the Fl lithofacies. A subsequent flooding event filled the impressions with fine-grained sand. In situ tracks 2 and 4 reported on the excavated track-bearing horizon display fine preservation of ungual and metatarsal impressions allowing a confident assignment

respectively to ornithopod (track 2) and theropod (track 4) producers. Alternatively, tracks 1, 3, 5, and 6 are very poorly defined suggesting that the substrate likely underwent changes in water content over time but generally remained in a hydrated condition. Several of the poorly preserved tracks observed may have been emplaced under shallow subaqueous conditions. Nonetheless, subaerial exposure may have also occurred as indicated by preservation of skin impressions on the same horizon (Paik et al., 2010). Another indicator of subaerial exposure may be the emplacement of limestone units associated with carbonaceous mudstones likely formed by concentration of calcium carbonate during evaporative processes.

A distinctive character of the ichnoassemblage observed is the absence of striated meniscated burrows, consistent with the pre-desiccation suite of the *Scoyenia* ichnofacies, which is dominantly represented by unwallled, horizontal, meniscated burrows (Buatois and Mángano, 1995). The absence of mud cracks and scarce pedogenetic features would corroborate the overall hydrated condition characterizing the substrates emplaced in this floodplain environment.

Deposition of a thick sedimentary succession of overbank fines and associated substrates subjected to dehydration, but not desiccation, also suggests a lower coastal plain setting. In such depositional environments, the extensiveness and relative thickness of floodplain fines relative to channel deposits, and the high-water table may inhibit desiccation and soil formation (Weissmann et al., 2013). The middle Frontier at Price Creek displays an overall fining upward tendency, with a relative increase of trace fossil abundance up section. The thickest and most laterally continuous sandstone channel units ascribed to lithofacies St and Sr are reported in the lower part of the measured section. They are generally coarser than units observed in the upper part of the measured section and all display small-scale, lateral accretion geometries, small

thickness, and define isolated bodies incised into finer overbank units. Alternatively, overbank fines form vertically aggrading packages that display relatively homogeneous thicknesses. They may be characterized by sudden lateral lithological variations, especially in proximity to channel sandstones. Deposition in this sector of the flood plain was episodic and accompanied by fluctuation of the water table. Substrates remained inundated or saturated in variable proportions even during low stages of the ground water table. These deposits are similar to those described by Dyman et al. (2008) elsewhere in the western Centennial Mountains, but we have not yet found root traces and calcareous concretions reported in siltstones and mudstone units. Presence of root traces and calcareous concretions indicates that pedogenesis could have occurred in more dehydrated substrate or in topographically higher and better drained areas.

Contextualizing this succession into a general fluvial coastal plain system is preliminary, since it only represents a small portion of the thick succession exposed in the western Centennial Mountains. In addition, good exposures in this area are scarce, limiting data collection, especially in the fine-grained sequences. Additional data will add to the morphological characterization of channel bodies and their relationship with overbank deposits. Channel bodies described in this study are often poorly exposed, and the apparent geometrical relationships with encasing overbank fines is limited to few well exposed outcrops. Generally, channel sandstones observed in two dimensions form relatively thin rock bodies, with an overall thickness less than 10 m, that contrasts with a larger lateral extension reaching at least 30 m. They are composed by medium- to coarse-grained, often pebbly sandstones, forming asymmetric bodies enclosed into thick sequences of floodplain fines. The lower contacts with overbank fines are distinctively sharp, likely suggesting an erosive origin. The prevalent vertical aggradation of floodplain

deposits, coupled with evidence of water table fluctuations, are all features that may be representative of a lower alluvial plain channel system emplaced on very low gradient slopes, where sandstones form vertically and laterally isolated channel bodies separated by extensive fine-grained overbank deposits (Zwoliński, 1992; Currie, 1997). Prevalence of fines to coarse-grained sandstone also suggests that the fluvial system transported abundant suspension load. That may have favoured deposition of abundant floodplain successions capable of isolating channels fills (Friend, 1983 in Miall 1996, p. 94). Lateral accretion of channel bodies is indicated by the asymmetric internal geometries and presence of prevalent trough cross bedding (Miall, 1996). The sharp erosive contacts at the base of channel sandstone suggests that the fluvial system migrated primarily by avulsion.

The definition of a fluvial style is difficult to assess. According to the lithofacies here described there may be resemblances with the fine-grained fluviolacustrine successions observed in meandering fluvial systems described by Fielding (1984). Meandering fluvial systems in distal alluvial plains commonly display an aggrading alluvial record, with sediment reworking that mostly occurs by slow lateral migration and occasional erosion during avulsion events (Keen-Zebert et al., 2013). This seems to agree with a river system where discharges are controlled by seasonal fluvial flow rate variations and relative ground water table fluctuations, as for example, observed in seasonal wetlands (Wright et al., 2000). However, without a rigorous definition of channel geometries, hypotheses remain highly uncertain.

A Coniacian age for the middle Frontier deposits of the western Centennial Mountains is suggested by lithological and paleontological evidence. A distinctive feature of the Price Creek succession is the presence of thin olive to green sandstone and siltstone units. These ripple-

laminated, often bioturbated strata are observed in Fl lithofacies are likely volcanoclastic, possibly equivalent to Coniacian porcellanitic units of the middle and upper Frontier in the Lima Packs area (Dyman et al., 2008). If these deposits are equivalent, they could be considered distinctive marker beds of the Coniacian-aged middle and upper Frontier Formation in southwestern Montana. Further work needs to be done to establish this relationship.

The Frontier Formation deposits of the western Centennial Mountains represent part of a broad, wet, lower alluvial coastal plain environment that existed west of the Coniacian Cody Sea. Extensive alluvial plains were dominated by fine-grained sediments supplied by the erosion of Palaeozoic limestones and Proterozoic and Paleozoic sedimentary and igneous rocks from the thrust belt. Tectonic subsidence contributed to the emplacement of this thick Coniacian succession, during a period of general high stand (Roberts and Kirschbaum, 1995, p. 27).

Distal alluvial deposits of the western Centennial Mountains are characterized by a rich fossil record comprised of dinosaurs, freshwater turtles, crocodilians, abundant invertebrates and vegetation (Panasci et al., 2020). Although a taxonomical analysis of dinosaur tracks is not the scope of this study, a broad definition of track producers and relative abundance is worth mentioning for their paleoecological significance. At least thirteen dinosaur tracks represent ornithomimid producers whereas tracks ascribed to thyrophorid and theropod dinosaurs are relatively less abundant. This association seems consistent with other ancient fluvial systems reported in Upper Cretaceous deposits of western North America, where similar distal alluvial plains are dominated by ornithomimid dinosaurs (Lucas et al., 1989, p. 217-221; Lockley and Hunt, 1999, p. 192-197; Lockley, 2014; McCrea et al. 2014). The relative abundance of ornithomimid tracks in such environments has been particularly emphasized in lower alluvial plains and may

be indicative of survival strategies related to abundant vegetation, offspring nursing, and protection against predators (Nadon, 1993; Difley and Ekdale, 2002; Fiorillo et al., 2019). This behaviour seems to be also supported by a series of anatomical adaptations that may have improved stability during locomotion on variably consolidated substrates (Xing et al., 2012). Alluvial plain settings, with ponds and pools, and cohesive substrates in the floodplain basins may have also been ideal environments for sustaining freshwater organisms such as turtles and crocodilians, as well as a variety of invertebrates including insects, molluscs, crustaceans, and nematode worms. Overall, this indicates a complex living community with substantial diversity in distal alluvial coastal plains spread across southwestern Montana during the Coniacian.

Conclusions

The Coniacian Frontier Formation deposits at Price Creek locality are characterized by a fine-grained succession consisting of relatively thin but laterally extensive sandstone channels encased into thick overbank fine deposits associated to abundant trace fossil assemblage. Three lithofacies groups are recognized: Lithofacies St and Sr, comprised by medium to coarse grained, cross bedded sandstones, interpreted as channel sandstones. Lithofacies Fl, comprised by fine to medium cross-bedded sandstones, laminated siltstones, carbonaceous mudstones and limestones, interpreted as overbank fines. Lithofacies St, Sh, and Sr, composed by fining-upward, planar cross bedded sandstones, associated to carbonaceous silty sandstones and bone fragments, representing crevasse splay deposits. Trace fossil record includes *Taenidium barretti*, *Cochlichnus anguineus*, vertical and passively filled burrows likely assigned to *Skolithos* isp., and dinosaur tracks. Rare vertical burrows have been reported in sandstone channel bodies, whereas meniscated, unwalled, horizontal traces abound in overbank deposits, associated with

dinosaur tracks, and vertical burrows. Laminated siltstones units interpreted as pond or pool environments are associated to sinusoidal trails and finely preserved plant material. The abundance of mudstone and siltstone deposits, rarity of root traces, and absence of mud cracks, suggests that this succession was deposited on a low gradient slope where sediment was primarily transported in suspension, and that the ground water table perennially remained shallow, maintaining the substrates in a saturated to cohesive state, inhibiting desiccation and limiting pedogenesis. The abundance of meniscated, unwalled burrows, assigned to *Taenidium barretti* and absence of striated burrows in overbank fines are suggestive of a pre-desiccation trace fossil suite of the *Scoyenia* ichnofacies. Sedimentological and ichnological data corroborate previous works, indicating that the Coniacian middle Frontier succession exposed in the western Centennial Mountains was deposited in a distal alluvial coastal plain setting adjacent to the Cody Sea. Trace fossils provide the first evidence of dinosaurs in middle Frontier Formation deposits of southwestern Montana, mostly comprised of ornithopods and less abundant theropod and thyreophoran dinosaurs. Invertebrate and vertebrate trace fossils are associated with a body fossil record comprised of crocodilians, and freshwater turtles, and abundant plant material indicating that these Cretaceous alluvial environments could sustain considerable biologic diversity.

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Figure 3.1. Map showing the location of the site studied at the Price Creek locality (black dot).

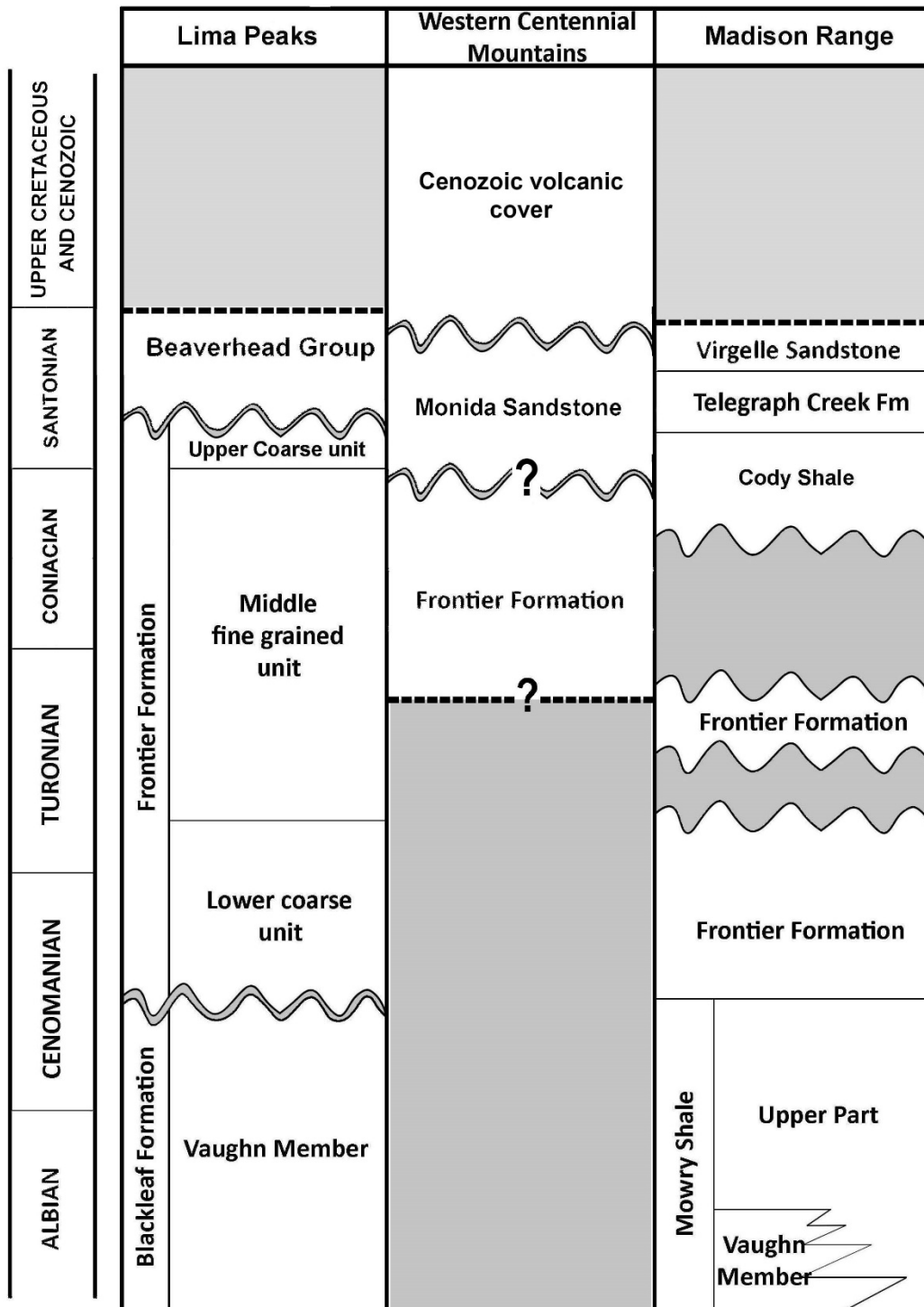


Figure 3.2. Chart showing stratigraphic correlation between the Frontier Formation units in southwestern Montana, in the Lima Peaks area, the western Centennial Mountains and the Madison Range; grey blocks indicated no exposure or erosion (modified from Dyman and Tysdal, 1998).

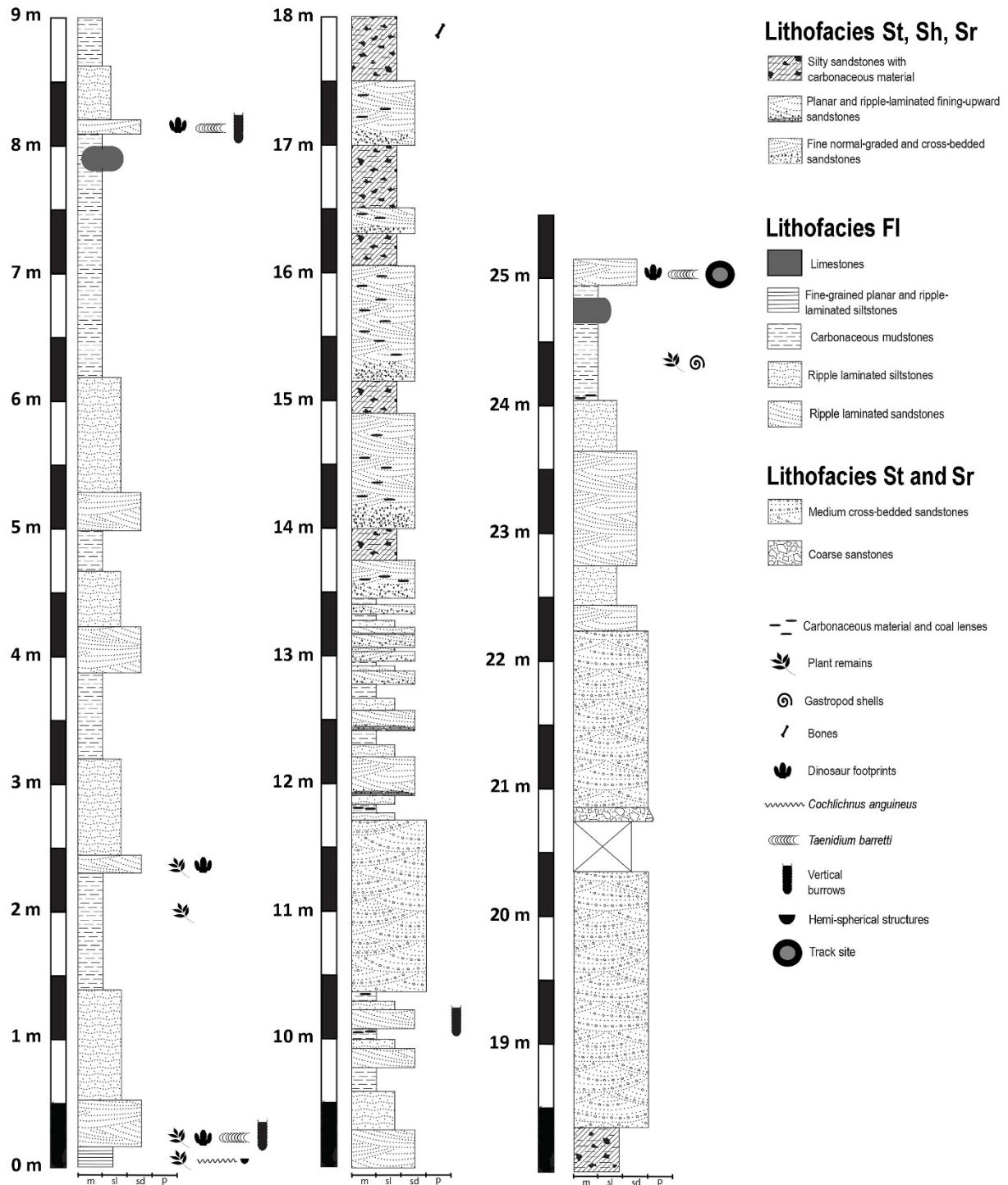


Figure 3.3. Detailed stratigraphic log of the uppermost 25 m of section measured at Price Creek.

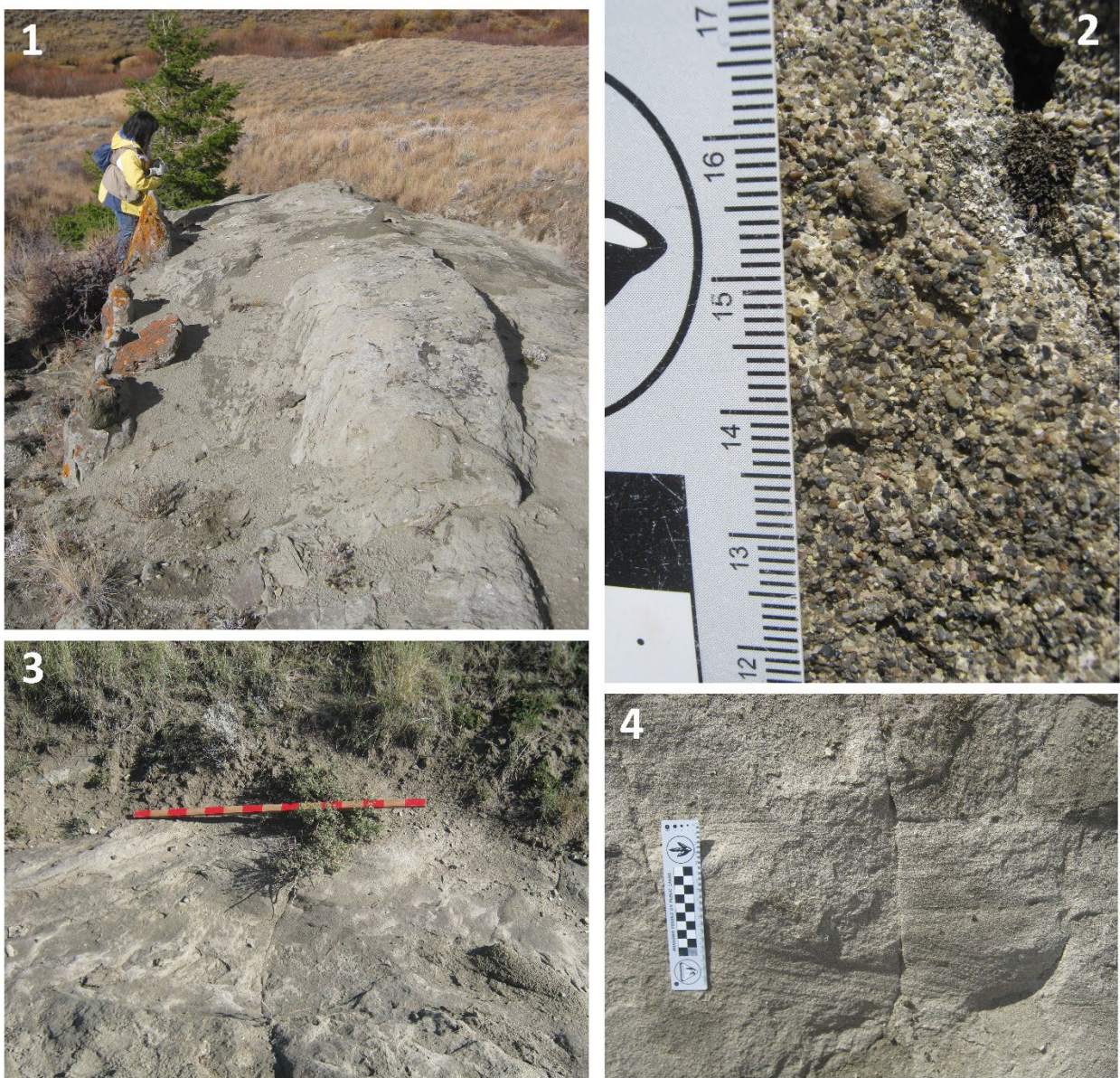


Figure 3.4. Coarse-grained sandstones of lithofacies Sr as observed on outcrop: 3.4.1) sandstone channel body with basal conglomeratic sandstone; 3.4.2) detail of basal conglomeratic sandstone; 3.4.3) overview of cross bedded strata; and 3.4.4) co-set of trough cross bedding. Jacob staff in figure 5.3 is 150 cm.

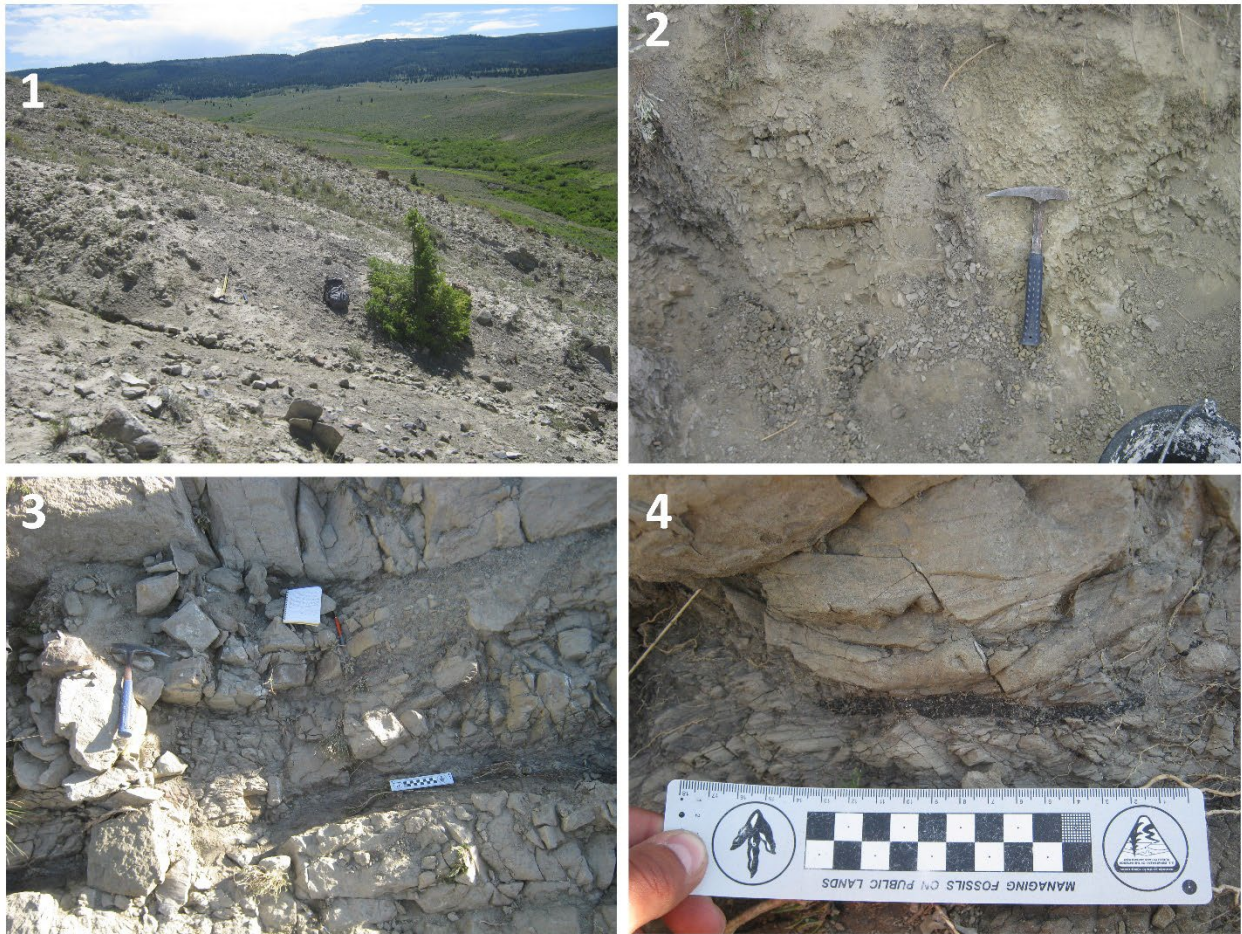


Figure 3.5. Lithofacies F1 outcrop photographs: 3.5.1) Frontier Formation strata eroded preferentially along fine-grained units representing overbank deposits, and forming drainages dipping downslope; 3.5.2) alternation of ripple laminated siltstone and carbonaceous mudstones units; 3.5.3) alternation of lentiform fine-grained sandstone, ripple laminated siltstones, and carbonaceous mudstones, capped by medium-grained sandstones; note the sharp contact with the overlying sandstone unit located right above the notebook; 3.5.4) detail of carbonaceous plant material within a thin mudstone unit.



Figure 3.6. Strata assigned to lithofacies Fl exposed on outcrop: 3.6.1) in the upper part of the picture, strata are composed by fine, cross bedded sandstones; a dinosaur track preserved as hyporelief at the base of the unit. Laminated siltstones can be observed in the lower part of the picture, and are characterized by 3.6.2) rusty, bioturbated, siltstone units, containing 3.6.3) exquisitely preserved plant material.

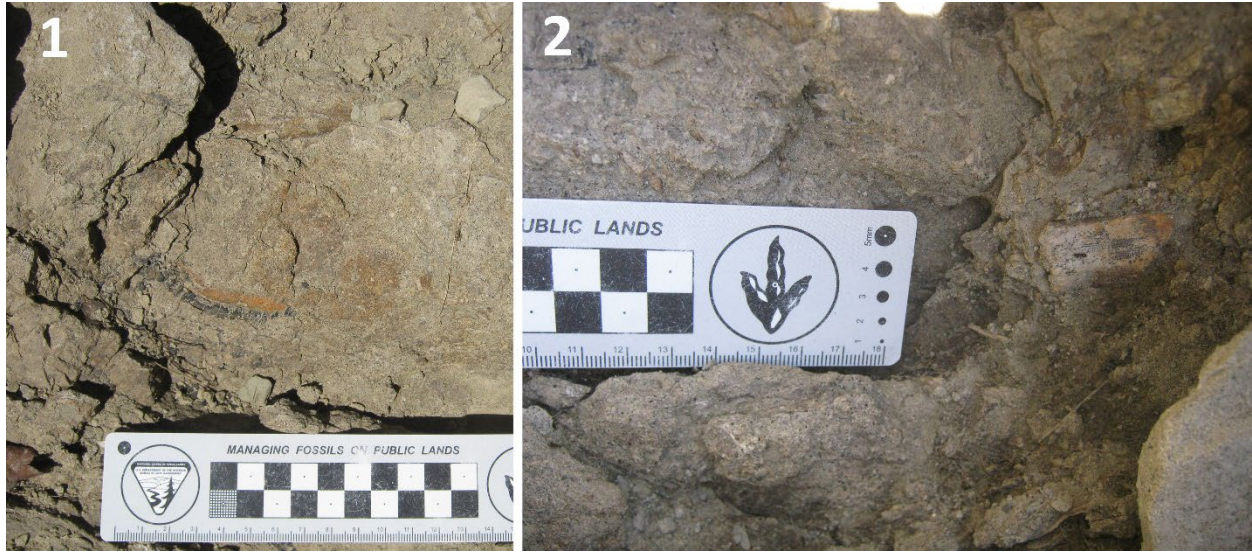


Figure 3.7. Poorly sorted silty sandstones of lithofacies with details of: 3.7.1) abundant carbonaceous plant material; and 3.7.2) bone fragments.

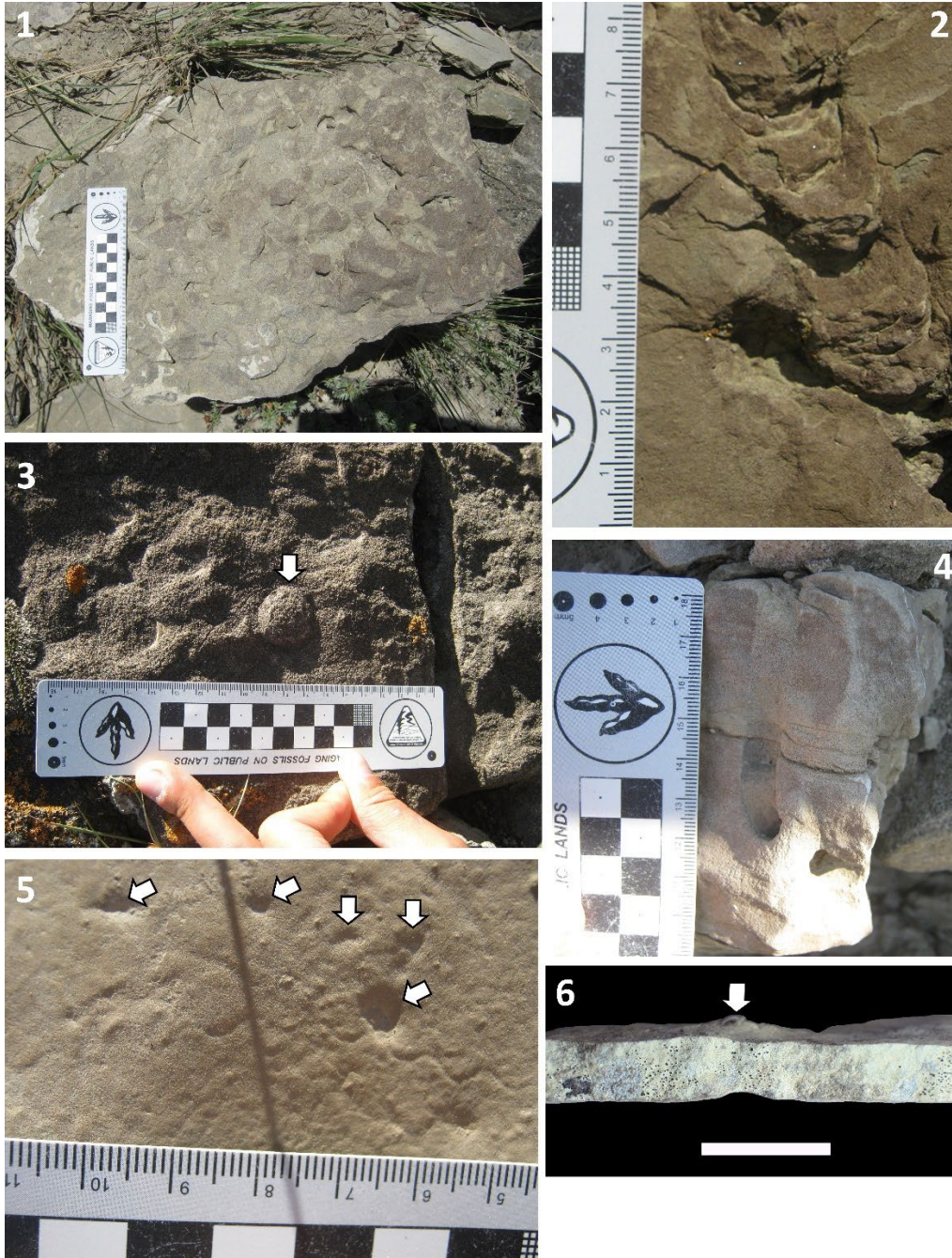


Figure 3.8. Invertebrate trace fossil assemblage: 3.8.1) isolated sandstone slab with high concentration of *Taenidium barretti*; 3.8.2) detail of the meniscated structure in a specimen of *Taenidium barretti*; 3.8.3) vertical burrow (white arrow) assigned to *Skolithos* isp. preserved in cross section at the base of a coarse sandstone unit assigned to lithofacies St and Sr; 3.8.4) vertical burrow with variable inclination reported in fine-grained sandstone units of lithofacies Fl; 3.8.5) *Cochlichnus anguineus* associated with a cluster of concave hemispherical structures (white arrows) preserved as concave hyporeliefs; 3.8.6) cross section of an hemispherical structure associated with a knob on the opposite side of the rock slab.



Figure 3.9. Dinosaur tracks: 3.9.1) two tracks preserved as convex hyporeliefs (white arrows) on the uppermost fine-grained, track-bearing sandstone horizon; 3.9.2) dinosaur track assigned to an ornithopod dinosaur; 3.9.3) isolated track assigned to an ornithopod dinosaur; 3.9.4) tetradactyl track preserved as isolated cast and assigned to a possible thyreophoran trace maker.



Figure 3.10. Lithologies exposed during the excavation of the track-bearing horizon and interpreted as overbank fines showing from right to left: slt) yellow, ripple laminated siltstones; cls) gray, organic mudstones associated with lms) a laterally continuous limestone horizon, and sdt) fine-grained cross-bedded sandstones comprising the track bearing horizon.

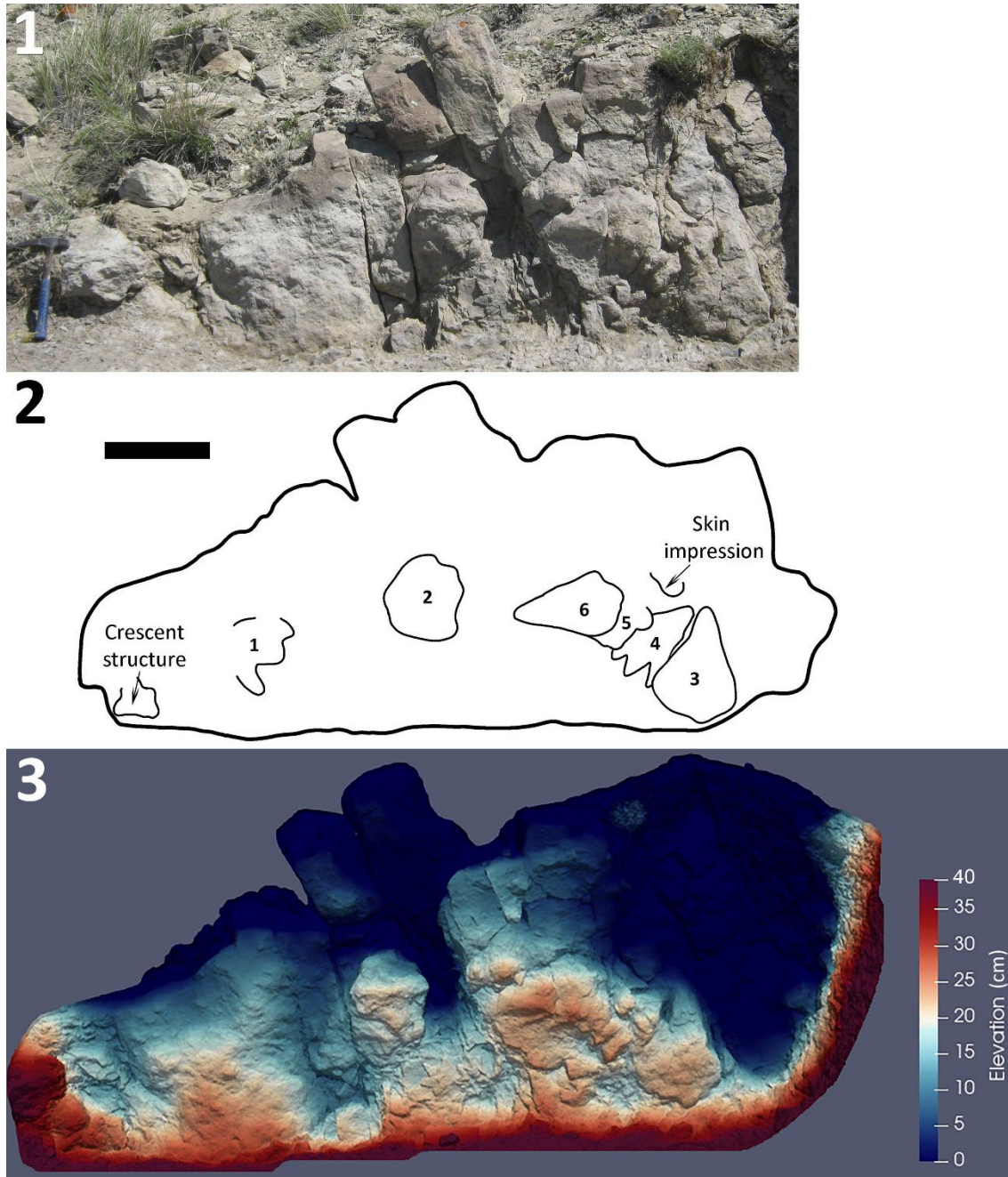


Figure 3.11. Track-bearing horizon: 3.11.1) overview of the quarry after excavation; 3.11.2) relative schematic map showing track locations; 3.11.3) false-colour elevations. Track numbers correspond to those reported in the text. Scale bar = 30 cm.



Figure 3.12. Track 1: undetermined tridactyl impression. Scale bar = 7 cm.

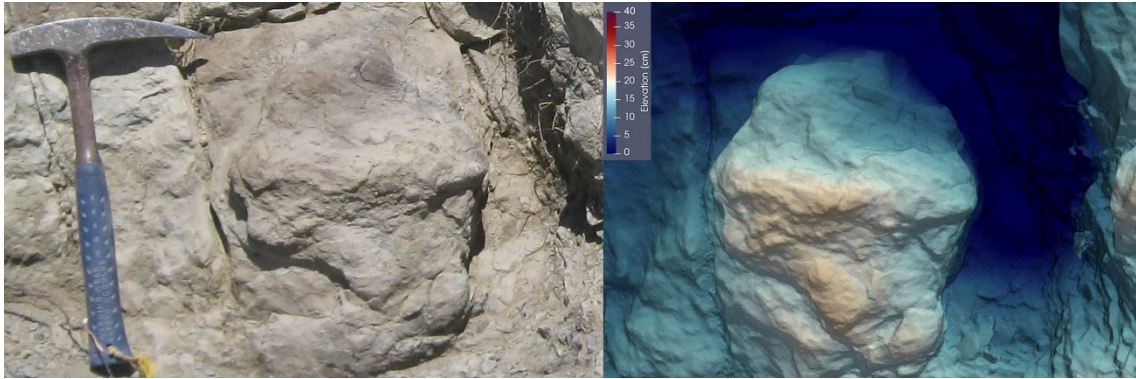


Figure 3.13. Track 2: ornithopod track impression. Rock hammer for scale about 31 cm.

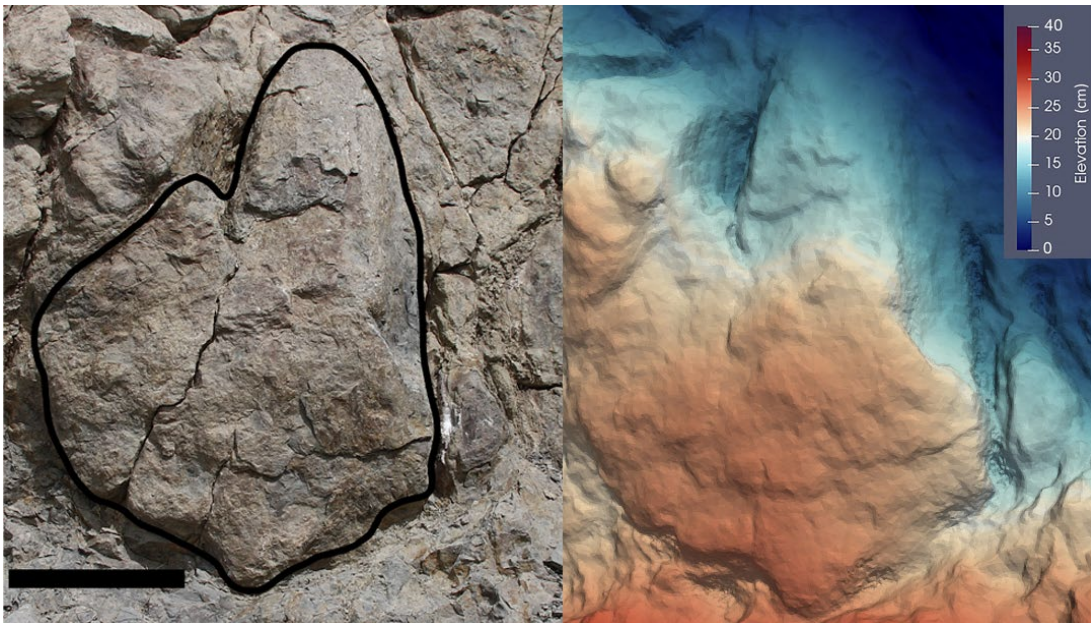


Figure 3.14. Track 3: deep impression assigned to a dinosaurian producer.

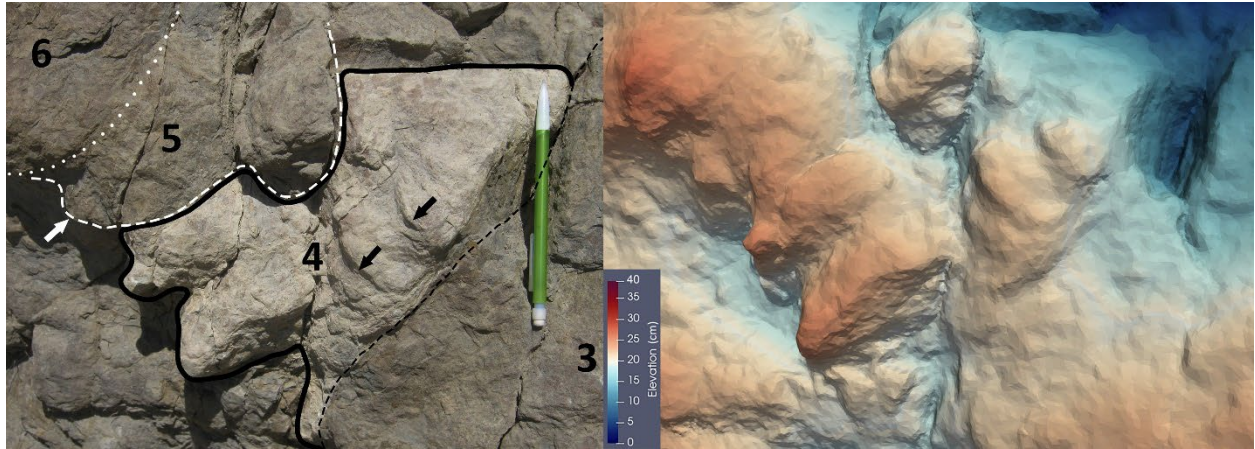


Figure 3.15. Track 4 emphasized by a black contour assigned to a theropod dinosaur and bearing evident metatarsal and claw impressions; black arrows indicate three wrinkled parallel structures on the pad impression. Black and white paths and dashed lines indicate borders respectively of tracks 3, 5, and 6. White arrow shows a possible claw impression associated with track 5. Pencil for scale is 15 cm long.

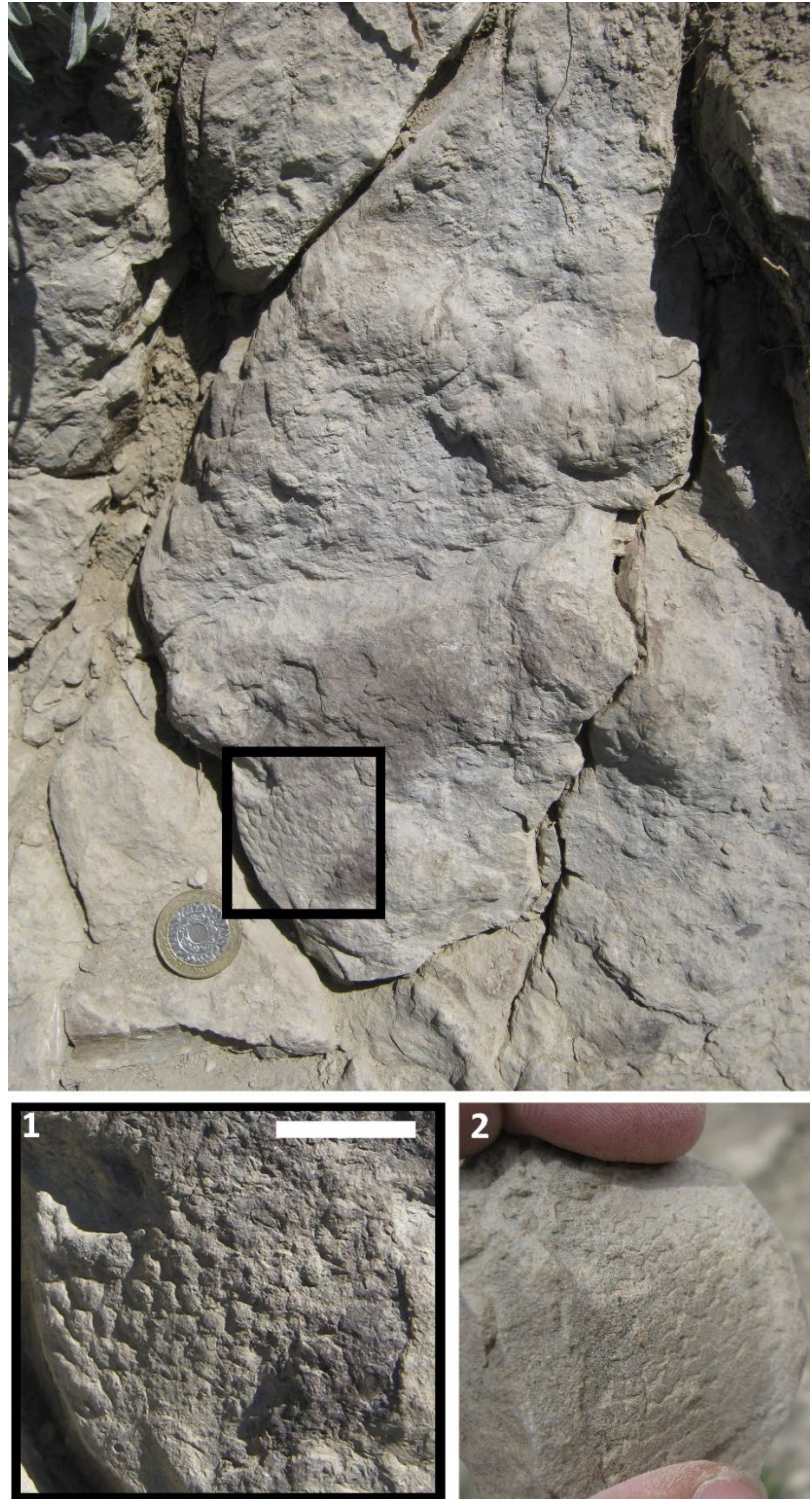


Figure 3.16. Skin impressions preserved on the track bearing horizon with: 3.15.1) detail of scales morphology and arrangement (black box); scale bar = 2 cm; 3.15.2) skin impression reported on fragmentary, isolated material from the same site and likely assigned to a possible dinosaur track.

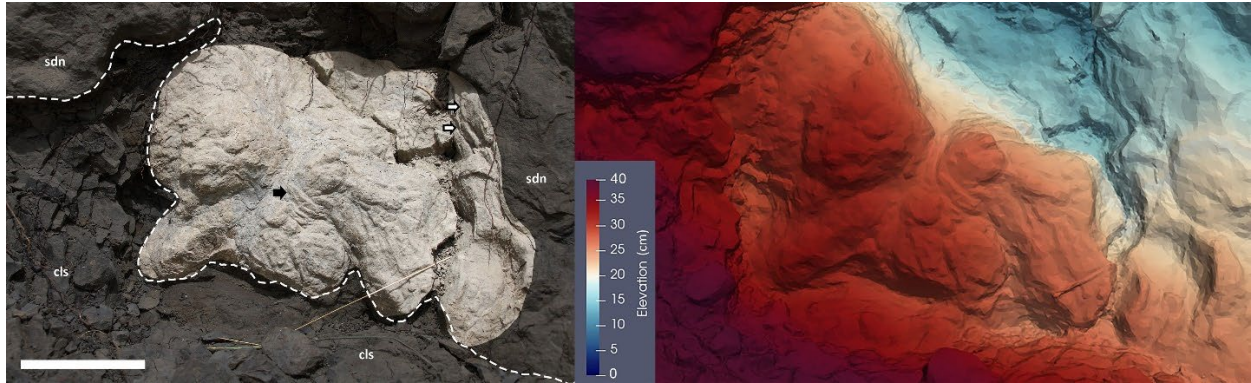


Figure 3.17. Crescent, convex hyporelief structure preserved on the track-bearing horizon; black arrow indicates a set of small lobes, arranged in a nesting pattern; white arrows indicate thin, deformed laminae preserved on the lateral side of the crescent structure; cls= mudstones, sdn= sandstones. Scale bar 7 cm.

Catalog Number	Taxon	D1 W	D1 L	D2 W	D2 L	D3 W	D3 L	D4 W	D4 L	Div 1	Div 2	Div 3	Div 4	Width	Length	PL/PW	Depth
MOR 1644-1	*Ornithopod?	6.5	10	6.5	8.5	?	?	-	-	48	-	?	-	?	7	?	5
MOR 1644-2	*Thyreophoran	4.5	10	7	12	7	13	9	~10.5	60	33	11	40	29	31	1.06	15
MOR 1644-4	*Thyreophoran	5.8	~7.5	6	~9	7.5	9	10	?	52	25	71	11	18	16	0.88	16
MOR 1644-3	*Theropod	?	?	8	~12	5.5	11	-	-	?	-	44	-	?	~18	?	13
MOR 1644-5	*Ornithopod	7.5	8	9	10	?	?	-	-	36	-	35	-	~22	21	0.95	11
MOR 1644-6	*Ornithopod	5	7	9	12	5.5	11	-	-	35	-	27	-	22	22	1	12
MOR 1644-7	*Ornithopod	?	?	?	?	?	?	-	-	?	?	?	-	~9	~21	?	8.5
MOR 1644-8	*Ornithopod	?	?	?	?	?	?	-	-	?	?	?	-	23	21	0.91	19
MOR 1644-9	*Ornithopod	9.9	15	~12	17	~7	~7	-	-	44	-	40	-	31	30	0.96	6
MOR 1644-10	*Ornithopod	11	10	13	10	12	~9	-	-	55	-	47	-	26	~22	~0.83	~16
MOR 1644-11	*Ornithopod	?	?	?	?	?	?	-	-	?	-	?	-	28	27	0.96	16
MOR 1644-12	*Ornithopod	10	7.5	16.5	10.5	13	6.9	-	-	45	-	50	-	25	26	0.96	15
MOR 1644-13	*?	?	?	?	?	?	?	-	-	?	-	?	-	26	~20	~0.76	14
-	Ornithopod	?	?	?	?	?	?	-	-	44	?	?	-	~27.5	27.4	~0.98	~10

-	?	?	?	?	?	?	?	-	-	?	?	?	-	25.7	~23	~ 0.8 8	21
-	Ornitho pod	7.9	11. 1	8.4	13.2	5.1	10. 4	-	-	24	-	31	-	34.4	32.9	0.93	~2
-	Ornitho pod	?	?	?	?	?	?	-	-	44	?	?	-	$\sim 27.$ 5	27.4	~ 0.9 8	~10

Table 3.1. Dinosaur track measurements from Price Creek measured section; dimensions are in centimeters and degrees: DW=digit width, DL= digit length, Div= digit divarication; PL/PW= pes length to width ratio. Ex situ tracks derived from the track bearing horizons are in grey. Asterisk indicates collected tracks.

#	Taxon	D 1 W	D 1 L	D 2 W	D 2 L	D 3 W	D 3 L	D 4 W	D 4 L	Di v 1	Div 2	Div 3	Div 4	Wi dth	Len gth	PL/ PW	Depth
1	?	?	?	?	?	?	?	-	-	?	?	?	-	-	-	-	~2
2	Ornitho pod	?	?	5.5	?	?	~13	-	-	31	-	52	-	33	27	0.81	19.5
3	?	?	?	?	?	?	?	-	-	?	?	?	-	20	30	?	13
4	Therop od	3.8	?	4	9.5	?	?	-	-	?	?	?	-	15	27	-	16.7
5	?	?	?	?	?	?	?	?	?	?	?	?	?	~16	~17	?	?
6	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table 3.2. Measurements on in situ dinosaur tracks from the Price Creek track-bearing horizon. Dimensions in centimeters: DW=digit width, DL= digit length, Div= digit divarication, PL/PW= pes length to width ratio.

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CHAPTER FOUR

NEW OCCURRENCE OF NEURANKYLUS SP. (TESTUDINES: PARACRYPTODIRIA:
BAENIDAE) IN THE UPPER CRETACEOUS FRONTIER FORMATION OF
SOUTHWESTERN MONTANA (USA)

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Abstract

An incomplete specimen assigned to the genus *Neurankylus* sp. was collected from Coniacian deposits of the Frontier Formation of Montana (USA). The material consists of anterior plastron, a costal plate and neural plate fragment, and several undetermined skeletal elements. The identification is based on the relatively large size of the specimens, scute elements joining along the mid-line of the plastron with the intergulars reaching the humerals, and complete fusion of the sutures. The specimen represents the first baenid turtle reported from non-marine Frontier Formation deposits and is particularly relevant for understanding stratigraphical and paleogeographical distribution of the Family Baenidae. This will have important implications for phylogenetic studies and paleoenvironmental interpretation of non-marine Frontier Formation deposits of south-western Montana.

Introduction

Baenids are a group of turtles endemic to North America with a fossil record spanning from the mid-Cretaceous to the Eocene (Lichtig and Lucas, 2016; Gaffney, 1972). Their record is known since the Aptian-Albian and includes species with a geographic distribution extended to both the Appalachia and Laramidia provinces (Gilmore, 1920; Lipka et al., 2006; Joyce and Lyson, 2015). Baenids are one of the most common group of turtles in “middle” and Late Cretaceous deposits, and their frequent occurrence in aquatic non-marine deposits is considered important for depositional environment interpretation and stratigraphic correlations (Lichtig and Lucas, 2016). However, the evolution and geographic distribution of baenid turtles during the early Late Cretaceous is poorly known. The fossil record is for the most part restricted to

uppermost Cretaceous deposits, with only one report from Coniacian deposits (Larson et al., 2013; Joyce and Lyson, 2015; Lichting and Lucas, 2016). The underrepresented fossil record observed in early Late Cretaceous non-marine deposits has been traditionally connected to the reduced extension of terrestrial habitats during the transgression phase that culminated in the Turonian with the maximum expansion of the Western Interior Seaway (Hancock and Kauffman, 1979; Eaton et al., 1997; Blakey, 2014; Slattery et al., 2015). Furthermore, sedimentary successions underwent important compressional and extensional regimes during the Sevier and Laramide orogenesis, resulting in significant up-lifting and erosional processes. Therefore, the non-marine fossil record was either considerably diminished or it was not preserved.

In recent years paleontological expeditions in south western Montana have reported a notable fossil assemblage from the middle Cenomanian-Early Santonian Frontier Formation deposits. The assemblage consists of vertebrate and plant remains associated with abundant trace fossils, and it represents an important addition to the poorly known fossil record so far described in early Late Cretaceous deposits of western North America. The aim of this study is to report the first description of a baenid turtle from non-marine Frontier Formation deposits of Montana, representing the first occurrence of the genus *Neurankylus* from the early Upper Cretaceous deposits of Southwestern Montana.

Geological setting

The Frontier Formation is a thick siliciclastic succession deposited along the western margin of the Western Interior Seaway, an epicontinental sea that during most of the Late Cretaceous extended from the Arctic Ocean to what is presently known as the Gulf of Mexico. The Frontier Formation deposited in a highly subsiding tectonic setting related to the

establishment of a foreland basin during the Late Cretaceous (Ryer, 1994). Thrust loading and erosion of the Sevier thrust and fold belt, associated with volcanic activity, largely contributed to accommodation and sediment supply (Jordan, 1980; Dyman et al., 1997; Dyman et al., 2008). In Montana the Frontier Formation crops out in the southwestern and south-central areas of the state and consists of siltstone, mudstone, sandstone, conglomerate, and shale lithologies, associated to coaly and carbonaceous horizons (Tysdal et al., 1990; Tysdal and Nichols, 1989). Bentonitic horizons and porcellanitic tuffs may also be abundant throughout the succession (Robert, 1972). The Frontier Formation of Montana has a typical stratigraphic range spanning from the middle Cenomanian up to the Turonian in the eastern area, but it may include also younger facies than those reported in the type section of Wyoming (Dyman et al. 1997). The thickest western succession reported near the Lima Peaks area contains non-marine strata stratigraphically correlated to the eastern marine succession attributed to the Coniacian Cody Shale, and Santonian Telegraph Creek formations (Tysdal et al. 1990; Tysdal, 1990; Dyman et al. 1997; Dyman et al. 2008).

Studied area

The studied area is located in Beaverhead County, east from the town of Monida in the western Centennial Mountains. The Frontier Formation succession extends between the town of Monida and Lake View and comprises distal facies equivalent to those reported in the western Lima Peaks area Frontier strata (Fig 4.1). In the Western Centennial Mountains, the Frontier Formation is entirely non-marine and deposited in fluvial and costal setting (Dyman et al., 2008). Strata consist of mudstone, siltstone, and sandstone lithologies stratigraphically equivalent to the Coniacian middle mudstone/siltstone unit reported in the close Lima Peaks area (Dyman et al.

2008). Medium-to coarse-grained trough-cross bedded sandstones form poorly channelized bodies 150 to 500 cm thick and may be associated with intraformational lag deposits rich in plant debris and in some cases in bone material. These sandstone bodies are encased in a succession composed by an alternation of lentiform, fine cross-bedded sandstones, rippled siltstones and mudstones units displaying erosive basal contacts, soft deformation, and convoluted bedding. Invertebrate bioturbation is frequent and occurs mostly at the top and at the base of the fine-grained sandstones units. Fine-grained sandstone sheets may also bear deep dinosaur tracks preserved as natural casts. No evidence of desiccation structures or pedogenetic features have been observed suggesting that these deposits likely represent part of a floodplain subjected to inundation and persistent saturation of the substrates over time.

Institutional abbreviations

MOR, Museum of the Rockies, Bozeman, Montana (USA)

Systematic paleontology

TESTUDINES Linnaeus, 1758

PARACRYPTODIRA Gaffney, 1975

BAENIDAE Cope, 1882

Neurankylus sp. Lambe, 1902

Referred material

MOR 1646, partial anterior plastron and costal plate, associated with a neural plate fragment and several undetermined carapace and plastron bone fragments.

Description

The plastron consists of epiplastra, entoplastron, and hyoplastra, and is approximately 19 cm width and 17 cm long with the right side better preserved than the left side (Fig 4.2). Sutures are completely fused, as typically observed in the family Baenidae. All scutes but the intergulars form a mosaic of elements joining along the mid-line of the plastron. The anteriormost margin of the plastron is slightly curved dorsally with the gulars forming a robust swelled border. Humerals and pectorals are well developed, forming an expanded surface, and the intergulars reach the humerals as observed in *Neurankylus* (Gaffney, 1972). The left and right pectorals are rather asymmetrical, possibly due to post-burial deformation. A portion of the axillary may be still attached to the right pectoral. The costal plate fragment concordant with the overall plastron suggests that the turtle could have a carapace approximately 50 cm long. Based on the fusion of sutures, scutes' configuration, and relatively large size, the specimen is accordingly identified as a baenid turtle and assigned to *Neurankylus* sp.

Discussion

Larson et al. (2013) first reported the possible occurrence of *Neurankylus wyomingensis* from marine deposits of the Cody Shale Formation in Colorado, providing an estimate age comparable to that reported by Dyman et al. (2008) for the Frontier Formation deposits of the western Centennial Mountain. This stratigraphic attribution was based on conservative speculations regarding the provenance of the material, and first suggested that the genus *Neurankylus* sp. could be expanded including Coniacian deposits. Later, Lichting and Lucas (2016) reported the first occurrence of *Neurankylus* from Coniacian deposits of the Crevasse Canyon Formation in New Mexico. The material herein reported can be confidently constrained

to Coniacian deposits, and extends the geographical distribution of the genus *Neurankylus* to southwestern Montana.

Most importantly, the specimen helps in the definition of a coherent depositional environment for the Frontier Formation deposits of the western Centennial Mountains. Baenid turtles have been traditionally considered inhabitants of fresh-water environments since they are characteristically found in fluvial and lacustrine deposits, and display several anatomical adaptations including hydrodynamic shell shape and elongated pes (Joyce and Larson, 2015). Palynological studies and macrofossils would indicate that the Frontier Formation in the Western Centennial Mountain is entirely non-marine (Dyman et al., 1997). Fossils here collected comprise conifer leaves, petrified wood, dinosaurian and non-dinosaurian remains and dinosaur tracks. The Frontier Formation succession from the western Centennial Mountain is composed of strata representing distal facies equivalent to western non-marine deposits near Lima Peaks (Dyman et al., 2008). Their precise collocation into the fluvial system in respect to proximal and distal facies is however difficult to assess since the outcrops are laterally discontinuous due to poor quality of the exposures and structural complications. Sedimentological evidence coupled with the ecological requirements dictated by baenid turtles would constrain these deposits to fresh-water aquatic environments, thus positioning the Frontier Formation of the western Centennial Mountains in distal fluvial settings, not yet subjected to marine influence.

Conclusions

Here we reported the first occurrence of the genus *Neurankylus* sp. from non-marine Frontier Formation deposits of southwestern Montana. The association of baenid turtle with dinosaurian, non-dinosaurian, invertebrate and plant fossil remains argues for a notable diversity

occurring in terrestrial and aquatic habitat of Southwestern Montana. The occurrence of baenid turtles would confirm that the Frontier Formation in the western Centennial Mountains were deposited in aquatic fresh-water environments. Baenid turtles allow for a better understanding of the depositional setting and paleogeographical collocation of the Frontier Formation successions outcropping in southwestern Montana.

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Figure 4.1. Schematic and satellite maps showing location of the site.

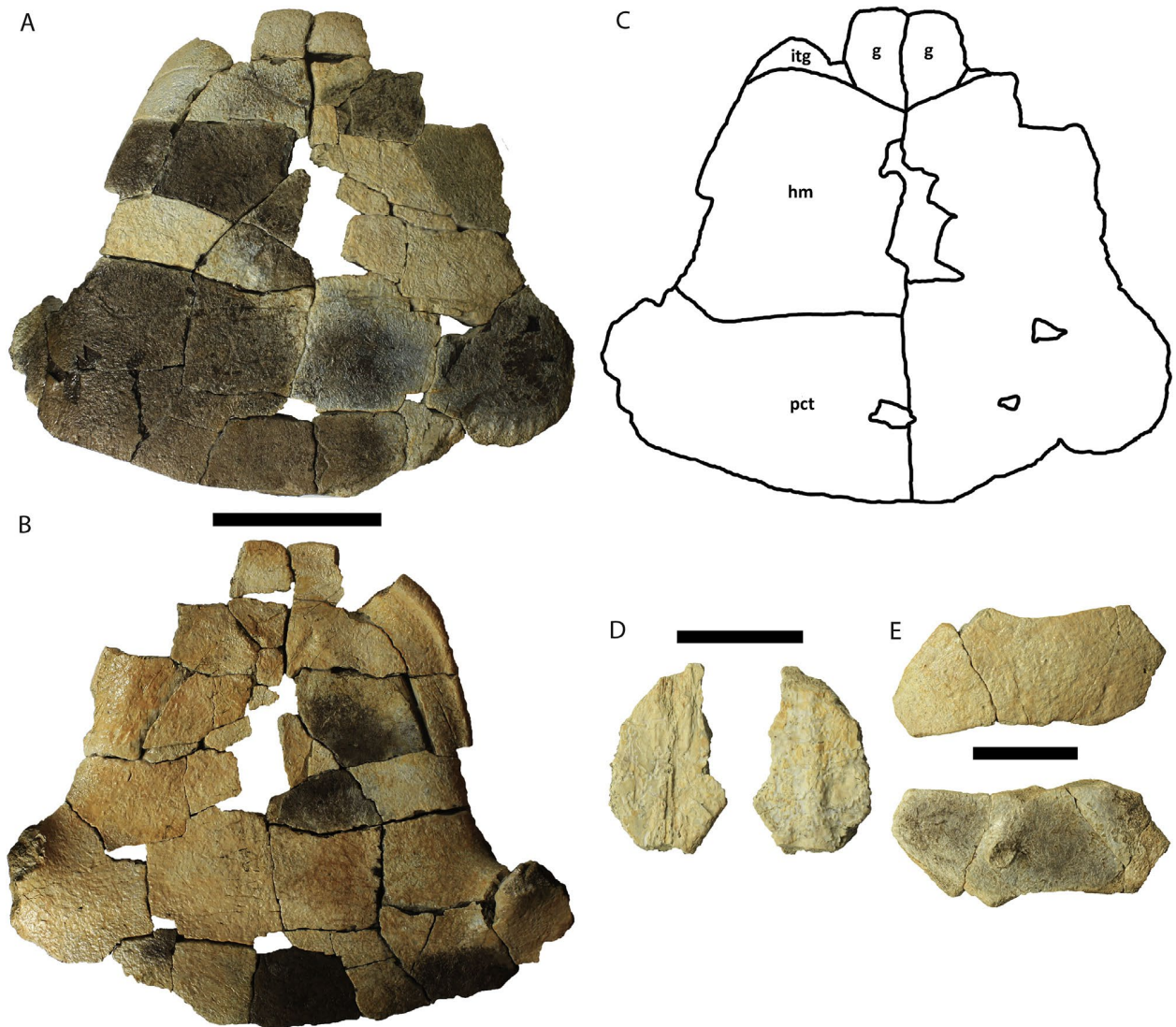


Figure 4.2. Specimen MOR 1646: anterior plastron in (A) ventral and (B) dorsal view. C, outline of the plastron shown in ventral view with sulci delineated: g, gular; itg, intergular; hm, humeral; pct, pectoral. Scale bar for A, B, and C= 6 cm. D, neural fragment in ventral view (right) and dorsal view (left). Scale bar = 4 cm. E, costal plate fragment respectively in dorsal view (up) and ventral view (down). Scale bar=4 cm.

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CHAPTER FIVE

AUTOPOD AND TRACK MORPHOLOGY ELUCIDATE ON THE PUTATIVE PRODUCER
IN HADROSAURIFORM ORNITHOPODS: A CASE STUDY OF MANUS TRACKS FROM
THE FRONTIER FORMATION (CONIACIAN), MONTANA.

Contribution of Authors and Co-Authors

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Abstract

Hadrosauriformes is a group of ornithopod dinosaurs with a rich and extensive Cretaceous tracks record. However, their rear foot (pes) anatomy is rather conservative. Thus, distinguishing different putative track producers from morphological differences is often impeded unless their identification is corroborated by stratigraphic and geographic distribution. On the contrary, the forefoot (manus) anatomy of hadrosauriform taxa reflects distinctive characters that, when preserved in tracks, may be critical for identifying their trackmakers. In this study, we examined three manus tracks preserved as sandstone casts, collected from Coniacian deposits of the Frontier Formation, southwestern Montana, USA. Tracks are assigned to Hadrosauriformes according to their steeply inclined morphology, functionally tridactyl condition, presence of hoof-like impressions, and crescentic cross-sectional shape. Track preservation suggests that digit II could be extended medially, whereas movements for digits III and IV were limited. The dorsally curved digit II and III impressions indicate that these digits could be hyperextended. One track shows a short, spade-like ungual II impression, suggesting a closer affinity of its producer to hadrosauroid or hadrosaurid ornithopods. Osteological characters of the manus combined with track morphology can help with discerning different hadrosauriform producers, providing important implication for paleoecological and palaeogeographical reconstructions.

Introduction

Hadrosauriformes (Sereno, 1997) is a highly diverse and widespread group of Cretaceous ornithopods that include large forms such as the iconic *Iguanodon* and the celebrated “duck-billed” dinosaurs. Tracks assigned to these groups are often abundant in continental deposits (Lockley and Hunt, 1998, p.192-209) and represent distinctive biogenic sedimentary structures in

the rock record. As their name suggests, ornithopod dinosaurs are renowned for their tridactyl, bird-like feet (Marsh, 1881); identification of their footprints mainly relies on proportions, shape of individual digit impressions, morphology of digital extremities (i.e. presence/absence of claw impressions), and angle of divarication of the digit impressions (Castanera et al., 2013).

Despite their distinct characteristics, ascribing hadrosauriform ornithopod tracks to more specific trackmakers is nonetheless challenging. Foot anatomy within hadrosauriforms remains rather conservative (Moreno et al., 2007; Lockley, 2009), meaning that different groups tend to produce similar footprints. Consequently, circumstantial data, such as the body fossil record and paleogeographic distributions of potential trackmakers, are frequently applied for trackmaker identification. For example, Lower Cretaceous tracks are usually credited to basal hadrosauriforms, whereas uppermost Cretaceous tracks are ascribed to hadrosaurid ornithopods, according to the relative abundance and stratigraphic distribution of their body fossils (Lockley et al., 2014). This methodology, however, reflects considerable limits, particularly when the body fossil record for a specific trackmaker is scarce or unknown, or when the stratigraphic and geographic distributions of several potential track producers temporally overlap (Tsukiji et al., 2018).

An alternative method of identification relies on the use of autopodia characters, that is the anatomy of the distal appendicular skeleton. The advantage of this method is that track morphology may be linked to taxonomically diagnostic features, rather than complementary data (Carrano and Wilson, 2001; Brusatte et al., 2010). This method has been validated for tracks assigned to non-dinosaurian and dinosaurian trackmakers. For instance, late Permian tracks of the ichnospecies *Pachypes dolomiticus* were assigned to pareiasaurs of the clade Therischia

according to their track morphology and biodynamics (Valentini et al., 2008). Autopod anatomy and biodynamics has also been used to infer tracemaker identities for theropod (Romano and Citton, 2017), ornithopod (Moratalla et al., 1992; Currie et al., 1991) and sauropod tracks (Wilson, 2005; Lallensack et al., 2017), respectively.

Nevertheless, the acquisition of detailed morphological characters from tracks can prove arduous. For instance, tracks preserved as shallow impressions rarely show details of the limb excursion within the substrate (Gatesy et al., 1999). On the other hand, tridimensional casts may provide exceptional insights into anatomy and biodynamics of the distal limbs, as they represent volumetric records of the interaction between an autopod and a substrate (Falkingham et al., 2020).

In contrast to the more conservative pes anatomy, manus anatomy varies across taxonomic groups within Hadrosauriformes, showing distinctive morphological characters related to digit configuration, morphology, biomechanics, and posture (Norman, 1980; Maryanska and Osmolska, 1984; Prieto-Marquez, 2014). These characters may be detected and used to discriminate the possible trackmaker. To date, most morphological description of tracks assigned to hadrosauriform ornithopods have been based on shallow positive or negative impressions, whereas footprints preserved as tridimensional casts have received little attention (Xing et al., 2012, 2017; Cobos et al., 2016; Nakajima et al., 2018). Similarly, manus tracks assigned to hadrosauriform ornithopods have been mostly described as positive or negative shallow impressions, and only rarely described as tridimensional casts (Vila et al., 2013; Cobos et al., 2016; García-Cobeña et al., 2023).

Here we provide a description of three purported hadrosauriform manus tracks preserved as tridimensional casts from the Coniacian deposits of the Frontier Formation in Montana (USA). We suggest that morphological features exhibited by these tracks, when compared to diagnostic osteological characters, may serve as a helpful model for differentiating among possible hadrosauriform trackmakers.

Material and methods

Material consists of three tracks collected in Frontier Formation deposits exposed in the western Centennial Mountains of Beaverhead County, and in the upper Ruby River valley of Madison County, southwestern Montana (Fig 5.1). Digit impressions were counted using Roman numerals, but when recognition of a left or right track was not possible, digits were counted clockwise using Arabic numerals. Manus characters used for track-producer identification are based on the studies of Norman (1980), Norman et al. (2004), Norman (2014), Brett-Surman and Wagner (2007), and Prieto-Márquez (2010, 2014). The term “palmar” is used to describe the manus track in caudal view. One tridimensional model is produced using the software Agisoft Metashape Professional (64 bit). The model is generated by merging two separate chunks using a total of 242 photographs, following the turntable method described by Mallison and Wings (2014), and standard photogrammetric procedures described by Romilio (2020). The model is presented as supplemental material. Tracks are curated with numbers MOR 11769 GP 33, MOR 11770 GP 65, and MOR 11768 RR 98, at the Museum of the Rockies, Bozeman, Montana.

Ornithopod manus anatomy

Ornithopoda refers to a group of bipedal and facultatively quadrupedal dinosaurs that originated in the late Triassic. This group underwent a striking evolutionary radiation during the Mesozoic, and by the end of the Cretaceous became one of the most successful herbivorous groups on land (Strickson et al., 2016). Important adaptations reflecting their evolutionary success involved the masticatory apparatus and the appendicular skeleton, among others (Norman et al., 2004; Butler and Barrett, 2012). The manus in particular shows significant anatomical and biomechanical changes (Fig 5.2). Basal ornithopods were small, bipedal, cursorial organisms capable of quadrupedal locomotion. The manus in *Heterodontosaurus* was pentadactyl and manipulation was accomplished by peculiar articulations between metacarpals and carpal elements (Norman et al., 2004). The distal metacarpal joints extend dorsally and proximally (Fig 5.2.1), producing an atypical digit I-III hyperextension on the metacarpals (Santa Luca et al., 1976). In contrast, the manus of more derived Cretaceous iguanodontian ornithopods lost much of its digit mobility in favor of a more rigid anatomy, which likely reflects the increased importance of the manus in supporting body weight during quadrupedal locomotion. For instance, Forster (1990) provided evidence for facultative quadrupedalism in the iguanodontian *Tenontosaurus tilletti*. This includes a broad distal articular surface on the metacarpals that extends onto the dorsal surface, as well as diverging manual digits (Fig 5.2.2). These anatomical assets would favor digit hyperextension and a more beneficial distribution of body weight during quadrupedal progression. Apparently, *T. tilletti* also displays unossified distal carpal elements, a unique feature among ornithopods (Hunt et al., 2021).

Further modifications occurred in Hadrosauriformes. The manus of *Iguanodon* (Fig 5.2.3) is one of the most iconic structures among dinosaurs, and it is best exemplified by the Lower Cretaceous *I. bernissartensis* (Norman, 1980). The *Iguanodon* manus is functionally tridactyl; the ossified carpals form a compact structure, whereas the broad distal condyles of the metacarpals favored digit hyperextension. The manus phalangeal formula is 2-3-3-2-4, with the first digit strongly reduced into a single spike-like pollex. Metacarpals III and IV have similar dimensions and form a tightly bounded carpal complex. Digit III bears two symmetrical phalanges and a prominent, broad hoof-like ungual. Digit IV is equipped with a vestigial phalanx 2 and lacks phalanx 3 and ungual. In contrast, metacarpal II is proportionally shorter in respect to those observed in digit III and IV, but bears a long, somewhat spatula-like, ungual that diverges laterally from digit III. Digit V is slender and composed of phalangeal elements with joints indicating greater ranges of movement. Compared with other digits, phalangeal articulation surfaces suggest that digit V could be flexed more efficiently and was thus more likely used for grasping rather than for weight support (Norman, 1980).

More derived groups retain a similar plan to *Iguanodon* but show a distinctive reduction in digits and different proportion of manual elements (Brett-Surman and Wagner, 2007). The metacarpals in hadrosauroid and hadrosaurid ornithopods are proportionally longer with respect to the phalanges (Prieto-Marquez, 2010). The spike-like pollex may be lost in several hadrosauroid groups (Della Vecchia, 2009) and is absent in hadrosaurids (Prieto-Marquez, 2014). Phalangeal configuration in more basal hadrosauroid ornithopods is less known owing to a lack of complete appendicular remains. However, complete and articulated manus elements are reported from the hadrosauroids *Mantellisaurus atherfieldensis* and *Gobihadros mongoliensis*,

showing a phalangeal formula 2-3-3-3-4 (Norman 1980; Tsogtbaatar et al., 2019). In contrast, the hadrosauroid *Tethyshadros insularis* displays an unusual phalangeal configuration 0-3-3-2-0 (Della Vecchia, 2009). In hadrosaurids such as *Edmontosaurus annectens* (Fig 5.2.4), the manus acquires an overall phalangeal formula 0-3-3-3-4 (Prieto-Marquez, 2014). An important change observed among hadrosauroid and hadrosaurid ornithopods is in ungual morphology and proportions (Paul, 2007), which acquire an ungual II subequal or shorter than phalanx II-1 (Fig 5.3). By contrast, ungual II in *Iguanodon bernissartensis* is about twice the length of phalanx II-1 and ungual III (Norman, 1980). Interestingly, the manus of several hadrosauroids retains a long, spatula-like ungual, although it is reduced to about the same size of phalanx II-1 (McDonald et al. 2012, p. 29, figure 30; Tsogtbaatar et al., 2019, p. 32, figure 26). In *Probactrosaurus gobiensis*, ungual II is spade-like and proportionally shorter than phalanx II-1 (Norman, 2002), a condition also observed in hadrosaurids such as *Edmontosaurus*, *Brachilophosaurus*, *Nipponosaurus*, and *Lambeosaurus*, (Nago, 1938; Hohloch, 2013; Evans and Reisz, 2007; Prieto-Marquez, 2014). Anatomy of digit IV is poorly known in hadrosauroids but in several groups it is distally “bent” (Norman, 2004). This arthrological feature was first reported in hadrosaurid ornithopods (Maryanska and Osmolska, 1984), where digit IV was likely capable of movement thanks to the lateral twisting of metacarpal IV and its anteroposteriorly convex articular surface (Brett-Surman and Wagner, 2006). When present, digit V in hadrosauroid and hadrosaurids retains the same overall functionality observed in more basal hadrosauriform ornithopods. In hadrosauroids, the phalangeal formula for digit V is not well known, but in hadrosaurids it may consist either of four or three phalangeal elements (Prieto-Marquez, 2007; Prieto-Marquez, 2014). We remain unsure whether the number of phalanges on this digit can be

attributed to taphonomic biases, or it may instead represent a genuine character differentiating hadrosaurid groups.

Geological setting

The Frontier Formation is an extensive synorogenic clastic wedge consisting of continental and marine sediments deposited during the early Late Cretaceous (Coniacian) in the western interior of North America (Dyman et al., 1997). Frontier-type sections are exposed in Wyoming and are comprised of strata spanning from the middle Cenomanian up to the Turonian (Cobban and Reeside, 1952). However, in southwestern Montana the Frontier Formation successions are thicker and include Coniacian and early Santonian deposits equivalent to the marine Cody Shale and Telegraph Creek Formation (Tysdal et al., 1990; Dyman et al., 1997; Dyman et al., 2008). In southwestern Montana, the best exposed continental Frontier successions are in the Pioneer Mountains, Lima Peaks area, western Centennial Mountains, and the upper Ruby River valley. Klepper (1951), Sholten et al. (1955) and Honkala (1960) provided a first general structural and sedimentological descriptions of these areas. Subsequent more detailed studies have been presented by Tysdal et al. (1990), Tysdal and Dyman (1998), Dyman et al. (2008), and Panascí et al. (2021). We refer to these works for general sedimentological and stratigraphic descriptions of the area where tracks were collected.

The Frontier Formation deposits examined in this study are exposed in the western Centennial Mountains and upper Ruby River valley. They are part of thick continental sequences of fine-grained sandstones, siltstones, mudstones, and less abundant medium- to coarse-grained sandstones and conglomerates deposited in a rapidly subsiding foreland basin (Tysdal et al., 1990; Dyman et al., 2008). Deposits in the study area are composed of fine-grained, planar-

laminated and ripple-laminated sandstones, laminated siltstones, carbonaceous mudstones, and limestones. Fine-grained sandstones and siltstones may be characterized by normal gradation, and mudstones by convoluted stratification. Carbonaceous plant debris is common, and deposits are frequently bioturbated. Pedogenic features represented by mottling, root traces, and calcareous nodules may also be present. Fine-grained units compose multiple fining upward cycles and were interpreted by previous authors as flood deposits emplaced by traction current, suspension, and decanting in alluvial coastal plain settings (Panascí et al., 2021). Subordinate medium-to-coarse, trough-crossed sandstones assigned to channel deposits define isolated, relatively thin, and laterally extensive bodies within these thick fine-grained successions (Dyman et al., 2008).

Frontier Formation dinosaur tracks occur either as convex hyporeliefs at the base of fine-grained, ripple-laminated sandstones units, or more commonly as fine-grained sandstone casts detached from the original track-bearing bed. Lithology and preservation indicate that tridimensional casts formed after flood events by filling of impressions left on floodplain substrates, either corresponding to silty mudstones or carbonaceous mudstones (Fig 5.4).

Tracks MOR 11769 GP 33 and MOR 11770 GP 65 were collected in the western Centennial Mountains, whereas MOR 11768 RR 98 was collected in the upper Ruby River valley. Based on lithology, palynostratigraphy, and U-Pb detrital zircon geochronology, the Frontier Formation at these localities is considered Coniacian (Dyman et al, 2008; Rosenblume et al., 2018; Panascí et al., 2021; Rosenblume, 2021).

Description

The three tracks are all preserved as tridimensional casts showing a crescentic outline in plan view and bearing three digit impressions (Table 5.1). Track MOR 11769 GP 33 (Fig 5; supplemental material) displays well-defined vertical digit impressions in dorsal view. The middle digit impression is the biggest, curving slightly forward and ending with a prominent subcircular, flat base, corresponding to the ungual. One lateral digit impression, here interpreted as digit II, is slightly shorter and distally thicker compared to the middle digit. It curves dorsally and bears a short ungual impression that diverges from the middle digit with an angle of about 35 degrees. The other side digit impression is comparatively shorter than the others and terminates with a blunt, rounded extremity.

Track MOR 11770 GP 65 is an isolated, tridactyl, fine-grained sandstone cast with two short but broader lateral digit impressions and an elongated middle-digit impression (Fig. 5.6). One lateral digit impression is fractured, lacking the distal portion. Nevertheless, it bears curved scale lineations visible on the lateral side. Digit impressions are vertical overall, but they also display some translational components. In particular, the middle digit is anomalously elongated compared to the lateral digits and is slightly curved forward, bearing characteristic longitudinal ridges-and-furrows structures along its length. Panasci et al. (2021) first provided a tridimensional model for MOR 11770 GP 65 and compared several morphological features to other Frontier Formation dinosaur tracks. Scale traces and ridge-and-furrows structures are not uncommon in Frontier dinosaur tracks of the same study area. In MOR 11770 GP 65, they are present on the dorsal side and in palmar view, measuring 3 to 5 mm wide and curving slightly along the digit impression.

Track MOR 11768 RR 98 is a convex hyporelief cast dipping at a high angle with respect to the fine-grained sandstone horizon, to which it is still attached (Fig 5.7). The surface has a bumpy appearance characterized by elongated and crosscutting knobs, forming a prominent, laminated surface texture. This feature is particularly evident at the base of digit impressions and in palmar view. Single-digit morphology is poorly preserved, but the middle digit is seemingly the widest. A side digit impression is considerably thick and protrudes forward, diverging from the other digit impressions (Fig 5.8). In dorsal view a distinct groove separates this thick protuberance from the middle digit trace that, together with the other side digit, form a single and uniform impression.

Discussion

Although preservation varies and tracks were found dissociated from pes tracks or trackways, these tridimensional casts share several common features, such as: steeply inclined morphology, three functional digits, presence of hoof-like impressions, and crescentic cross-sectional shapes. These features are akin to manus tracks assigned to hadrosauriform ornithopods (Thulborn, 1990). Theropod trackways showing either bipedal or quadrupedal progression show clawed pes and manus impressions (Li et al., 2020), whereas tracks assigned to thyreophorans, such as nodosaurians and ankylosaurians, display crescentic pentadactyl manus and broad tetradactyl pes impressions, respectively (Thulborn, 1990, p. 205; McCrea et al., 2001, p. 414). Therefore, these dinosaurs seem unlikely as possible candidates for the track producers. A ceratopsian producer is also questionable, as manus and pes tracks assigned to this group are both broad and functionally pentadactyl and tetradactyl (Lockley and Hunt, 1995).

Iguanodontian ornithopods were present in North America starting in the Early Cretaceous (Kirkland et al., 1998), with the oldest confident occurrences of hadrosauroid ornithopods reported in lower Cenomanian deposits of the Cedar Mountain Formation (McDonald et al., 2012) and Woodbine Formation (Head, 1998). Hadrosauroid dispersal to North America was supposedly from Asia, and occurred passing across the Beringia corridor during Albian-Cenomanian time (Kirkland et al., 1998), as the eastern connection with Eurasia was already terminated by the end of the Barremian (Brikiatis, 2016). The age of the Frontier Formation in southwestern Montana spans from the middle Cenomanian up to the early Santonian (Dyman et al., 2008), whereas the tracks herein described were assigned to the Coniacian. Although the Frontier Formation has produced only fragmentary and non-diagnostic ornithopod skeletal remains, the Moreno Hill Formation in west-central New Mexico confirms the presence of hadrosauroid ornithopods in Turonian deposits (McDonald et al., 2010). Moreover, hadrosaurid remains have also been reported in upper Coniacian deposits of the Niobrara Formation (Everhart and Ewell, 2006).

Although they were most probably impressed on substrates with different consistencies, as indicated by the different states of preservation, tracks still retain details of digit anatomy and morphologic features that may give insights on the potential track producer. Preservation of digit impression II in MOR 11769 GP 33 and MOR 11768 RR 98 is quite characteristic, because it is distinctly thicker distally than digit impressions III and IV, and clearly separated from digit trace III by a groove. Possible explanations for this morphology may be related to: 1) rotation of the manus; 2) soft-sediment deformation; 3) extension of digit II; or 4) any combination of these factors.

Although the wrist mobility in dinosaurs was limited and the manus was obligated to a semi-supinate posture (Fujiwara, 2009), a rotation of the manus would have been possible if shoulder rotation was involved, more so if movements were affected by substrate instability. A subsequent distortion of the track, however, should affect all the digit impressions, and not just digit II, thus leading to an alternative hypothesis. A common cause of distortion may also be connected to soft-sediment deformation and collapsing of the track's walls after withdrawal of the autopod (Farlow et al., 2012). If so, this would imply that tracks underwent differential collapsing, because only digit II appears distally thicker than the other digit impressions. Although the same sedimentary processes and similar effects for all the tracks are possible, these are unlikely for tracks that show different states of preservation and were likely generated under different substrate consistency. Track MOR 11768 RR 98 and MOR 11769 GP 33 both show the ungual II clearly drawing an arch that diverges with an angle of about 35 degrees from the middle digit. In MOR 11769 GP 33, this feature is quite evident thanks to the pristine preservation of the ungual impression. Although minimal deformation may be possible, such preservation would be more coherent with a sideward movement of digit II, rather than manus rotation or collapsing of the track's wall (Fig 5.9). This movement could have resulted from a passive response from ground reaction forces during the bearing-weight phase of track formation. Digit II likely began to impress on the substrate in a flexed position, close to the middle digit III, and then was abducted and extended after touchdown (Fig 5.10). A flexion before kick-off would also explain the retention of both the ungual impression and the dorsal curvature of the digit, as observed in MOR 11769 GP 33. Similarly, a certain degree of flexion before kick-off may be possible for digits III and IV, given their crisply defined forms.

In contrast, several morphological distortions attributed to substrate rheology and autopod movement are likely for MOR 11770 GP 65. The dorsal curving of the middle digit impression is exaggerated so that instead of facing dorsally, as seen in track MOR 11769 GP 33, it is somewhat curved upward. This irregular morphology could be the result of translational movements during the bearing-weight phase, possibly caused by sliding on an unstable substrate.

The displaced digit impressions observed in tracks MOR 11769 GP 33 and MOR 11768 RR 98 likely represent the medial digit II, thus they may be considered as left manus impressions (Fig 11). This morphology would support the hypothesis that the manus in Hadrosauriformes was a fleshy appendage with limited movements of digit III and IV (Osborn, 1912; Currie et al., 1991). In contrast, digit II was likely capable of medial divergence as suggested by osteological and ichnological evidence (Norman, 1980; Moratalla et al., 1992; Currie, 1995). Interestingly, the dorsal curvature observed on digit II and III may be also suggestive of digit hyperextension, as observed in hadrosauriform ornithopods (Norman, 1980; Prieto-Márquez, 2014). This curvature would define the approximate location where phalanx and ungual are articulated. Medial divergence of digit II is also suggested by shallow positive and negative manus impressions in trackways that reflect quadrupedal progression. For example, out of six valid Cretaceous ichnogenera assigned to iguanodontian track makers, four – *Amblydactylus*, *Caririchnium*, *Hadrosauropodus*, and *Iguanodontipus* – include manus tracks (Stenberg, 1932; Leonardi, 1984; Meyer and Thüring, 2003; Lockley et al., 2004) (Table 5.2). Each manus track is preserved as crescent-shaped or sub-circular impressions located anteriorly to the pes track (Fig 5.12,13), and all ichnogenera but *Iguanodontipus* display a medially diverging digit II. Currie (1984, 1995) provided one of the most detailed descriptions of hadrosauriform manus tracks for

the ichnospecies *Amblidactylus kortmeyeri*. The manus of this ichnotaxon is characterized by three digit impressions with a rounded and larger margin corresponding to digits III and IV and directed postero-laterally; in contrast, the smaller innermost digit II impression is directed medially. In *Caririchnium*, the manus tracks display an elliptical shape that may also bear a small, shallow digit impression directed medially as in *C. leonardi* and *C. lotus* (Lockley, 1987; Xing et al., 2007). Likewise, manus tracks in *Hadrosauropodus* (Currie et al., 1991; Lockley et al., 2004) show a crescent shape with a medially directed projection. Quality of preservation and retention of all digit impressions in large ornithopod tracks are seemingly controlled by the penetration's depth of the autopod within the substrate (García-Cobeña et al., 2023). Very simply, the deeper the manus track, the more likely that its digit impressions are preserved. Considering the morphological features observed and the arthrological characters reported in Hadrosauriformes, we suggest that the medial divergence of digit II reported in the manus tracks of the Frontier Formation could be related to medial extension of the digit.

Although the manus anatomy of hadrosauriforms is poorly known because elements of their appendicular skeletons are often disarticulated and fragmentary and rarely preserved intact, a comparison between track morphology and the most completely described manus specimens allow for discussing their taxonomic assignment. In Hadrosauriformes, several important differences in the manus include carpal proportions and ungual morphology. Previous researchers emphasized that – in contrast to basal hadrosauriforms – the manus in hadrosauroid and hadrosaurid ornithopods has proportionally longer metacarpals and is characterized by hoof-like unguals on digit II and III (Prieto-Marquez, 2010). Unfortunately, an estimate of metacarpal proportions is not possible from the manus tracks described here because only digit impressions

are preserved. The best digit impressions observed are in MOR 11769 GP 33, where the middle digit III is well developed and forms a wide, hoof-like impression with a subrounded flat base. Impression of digit II is clearly curved dorsally and shows evidence of a spade-like ungual. This impression seems short when compared to those observed in basal hadrosauriform and several hadrosauroid ornithopods, in which digit II has a long and spatula-like ungual (Norman, 1980; Carrano and Wilson, 2001; Wenhao and Godefroit, 2012; Norman, 2014, p. 32, 41; McDonald et al., 2012; Tsogtbaatar et al., 2019). The ungual impression II in MOR 11769 GP 33 is reduced and about the same length of ungual impression III. A short and spade-like ungual II is a characteristic feature reported in hadrosauroid and hadrosaurid ornithopods (Norman, 2002; Prieto-Marquez, 2014), likely suggesting a closer affinity of the producer to these groups than to more basal hadrosauriform ornithopods (Table 5.3). Lateral extension of digit IV was not detected in any of the three specimens. This character seems peculiar to Saurolophine hadrosaurs (Maryanska and Osmólska, 1984), but owing to the rarity of complete appendicular skeleton elements, it may also be shared by all hadrosauroids and hadrosaurids ornithopods (Gilpin et al., 2006; Hailu et al., 2011; McDonald et al., 2014). Regardless, we point out that lateral extension of digit IV may well represent a predictable character in manus tracks.

Conclusion

The Frontier Formation ornithopod tracks examined in this study are identified as hadrosauriform manus tracks because of their steeply inclined morphology, three functional digits, presence of hoof-like impressions, and crescentic cross-sectional shapes. Preservation indicates that digit II could be extended and abducted, whereas digits III and IV were likely incapable of a wide range of movements. These features have been reported in other ornithopod

manus tracks ascribed to hadrosauriform producers and are confirmed here by morphological and arthrological evidence. Based on morphological features, we interpret the short, spade-like ungual II impression, as a character identifying a possible hadrosauroid or hadrosaurid producer. If so, this track record extends the distribution of derived hadrosauriforms to Coniacian, Frontier Formation deposits of southwestern Montana.

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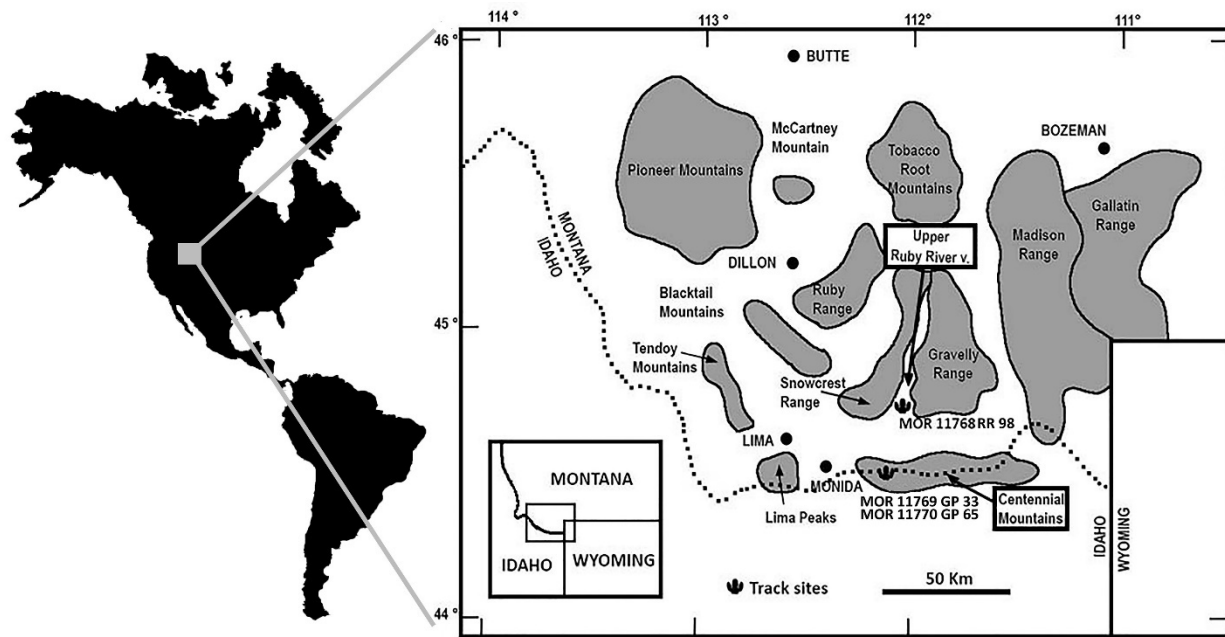


Figure 5.1. Location of the track sites.

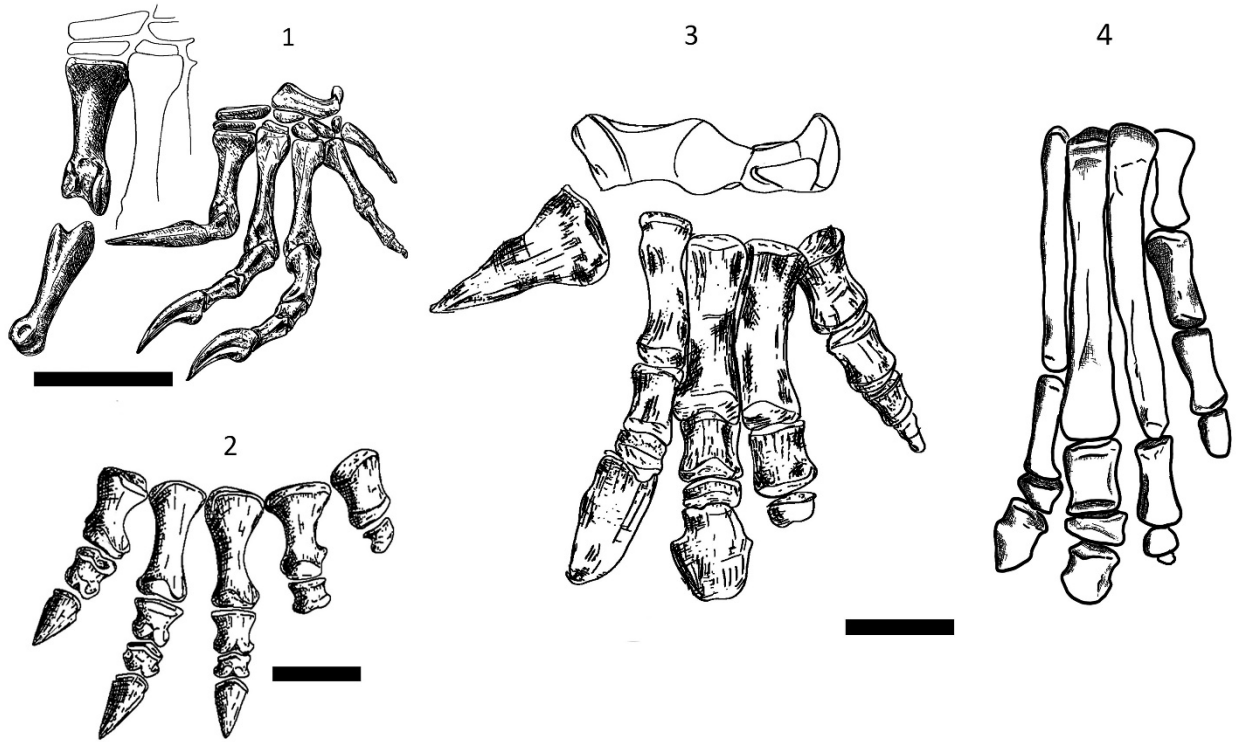


Figure 5.2. Ornithomimid manus: 5.2.1) *Heterodontosaurus*, with detail of the digit I articulation, scale bar 1.5 = cm; 5.2.2) *Tenontosaurus*, scale bar 5 = cm; 5.2.3) *Iguanodon* and 5.2.4) *Edmontosaurus*, scale bar 5 cm. All drawings represent left manus (modified from Norman, 1980; Brett-Surman et al., 2012; Prieto-Márquez, 2014).

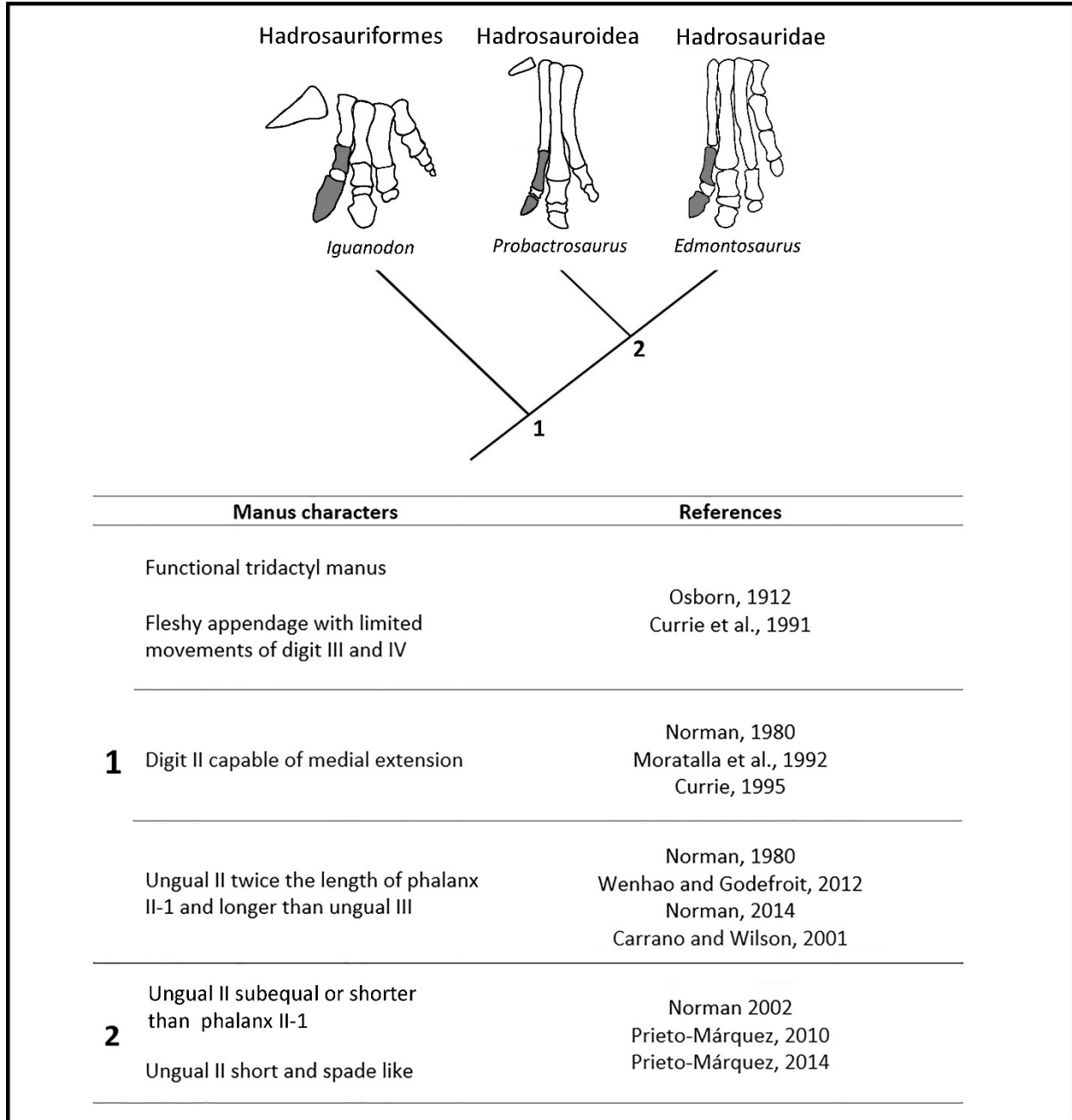


Figure 5.3. Osteological characters for Hadrosauriformes, Hadrosauroidea, and Hadrosauridae. Shaded areas emphasize the shape and proportions of phalanx II-1 and ungual II. Drawings are modified from Norman (1980), Norman (2002), Prieto-Márquez (2014).



Figure 5.4. Characteristic convex hyporeliefs preservation of a Frontier Formation dinosaur track; the in-situ track likely represents a pes track of an ornithopod producer. Sandstone bed is dipping toward the left side of the picture; note the gray, mudstones at the base of a buff sandstone horizon.

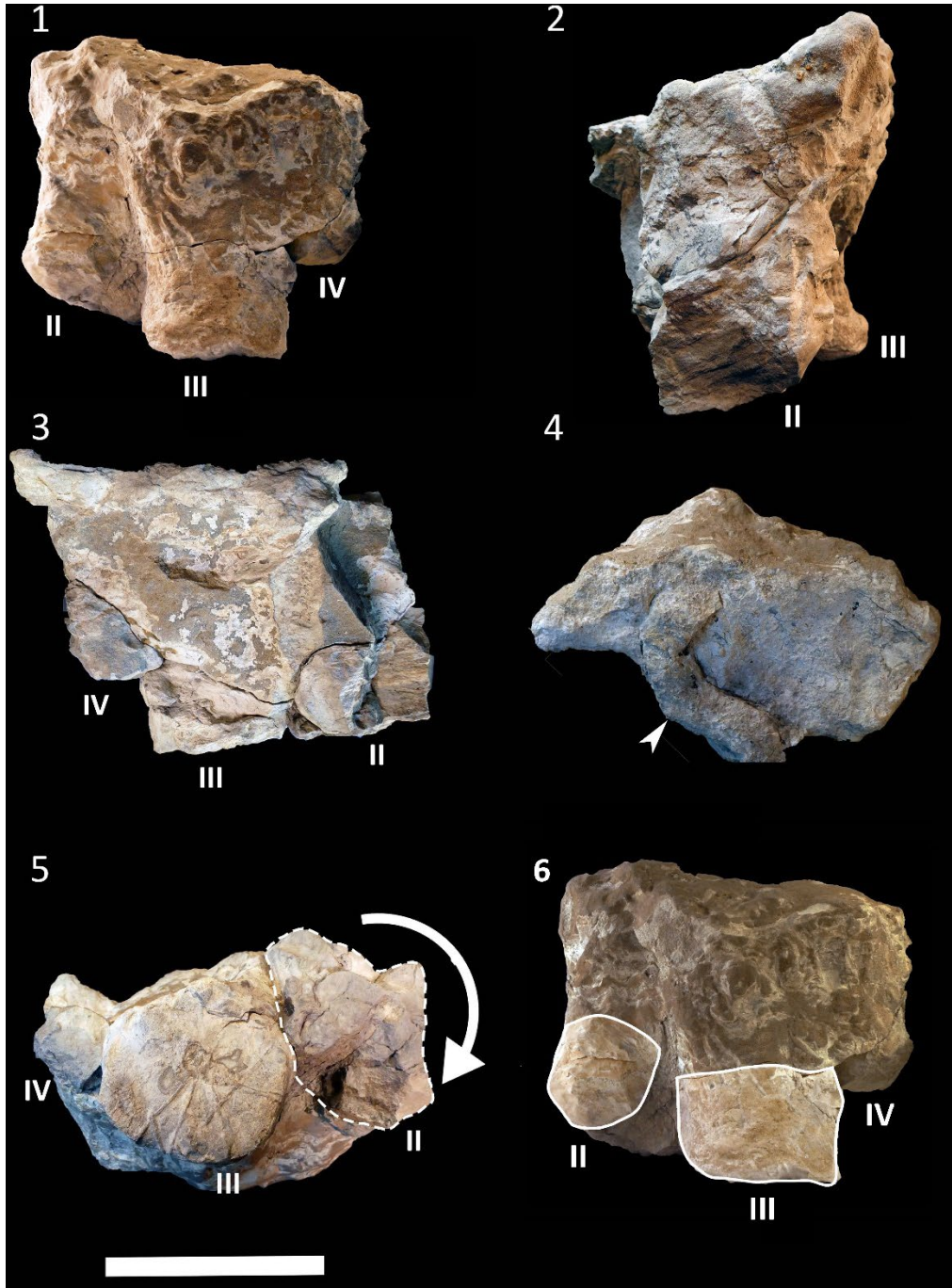


Figure 5.5. Track MOR 11769 GP 33: 5.5.1) dorsal view; 5.5.2) medial view; 5.5.3) palmar view; 5.5.4) plan view showing the clear crescent, cross section; dorsal side is directed up-ward; note the horizontal burrow cross-cutting the upper surface (white arrow); 5.5.5) distal view: white dashes mark the thick digit II impression, white arrow indicates movement direction of the digit; 5.5.6) track in dorsal view with interpretation of ungual impressions II and III. Scale bar = 10 cm.

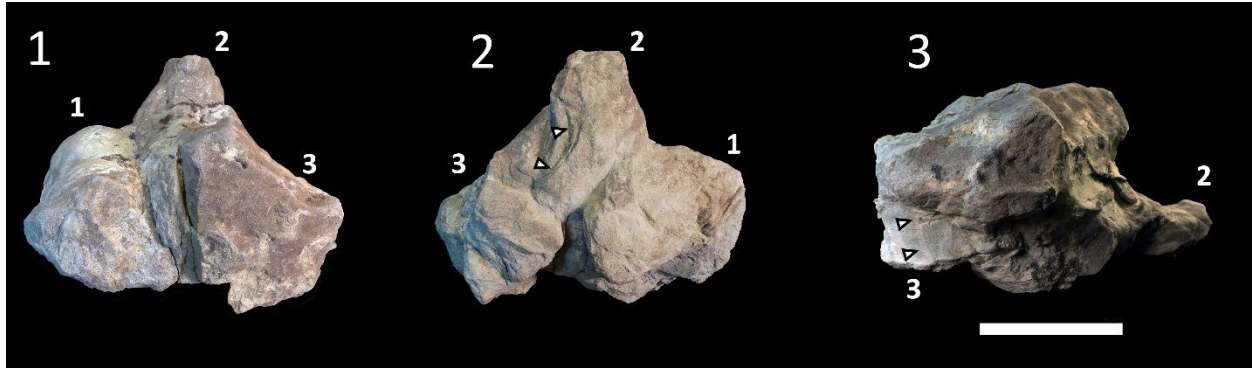


Figure 5.6. Track MOR 11770 GP 65: 5.6.1) plan view; 5.6.2) distal view with lineation (white arrows) running along the middle digit impression; 5.6.3) lateral view with scale-scratch traces on the incomplete digit 3 impression. Scale bar = 10 cm.

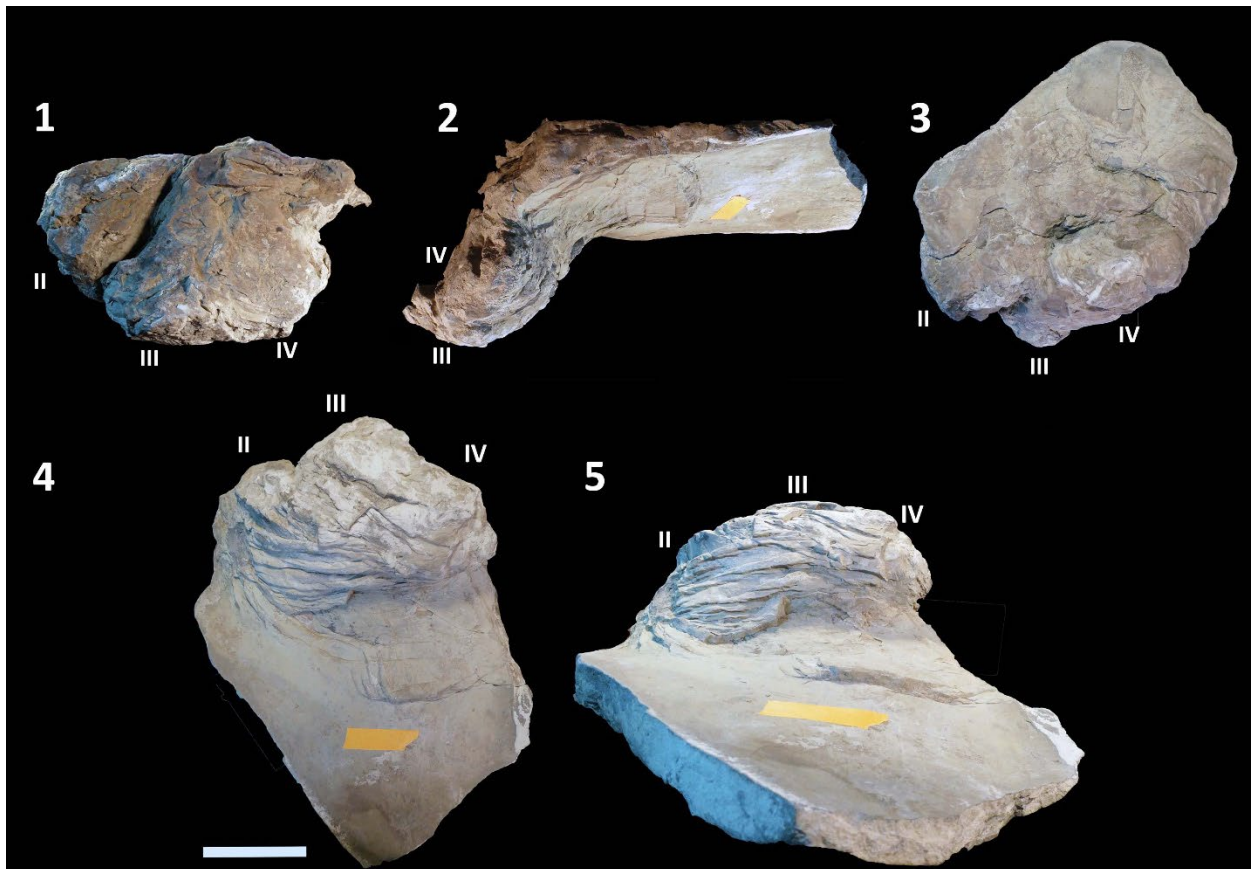


Figure 5.7. Track MOR 11768 RR 98: 5.7.1) dorsal view; 5.7.2) lateral view; 5.7.3) plan view; 5.7.4) distal view; 5.7.5) palmar view. Scale bar = 10 cm.



Figure 5.8. Close-up of track MOR 11768 RR 98 in dorsal view showing three digit impressions. Scale bar 9 cm.

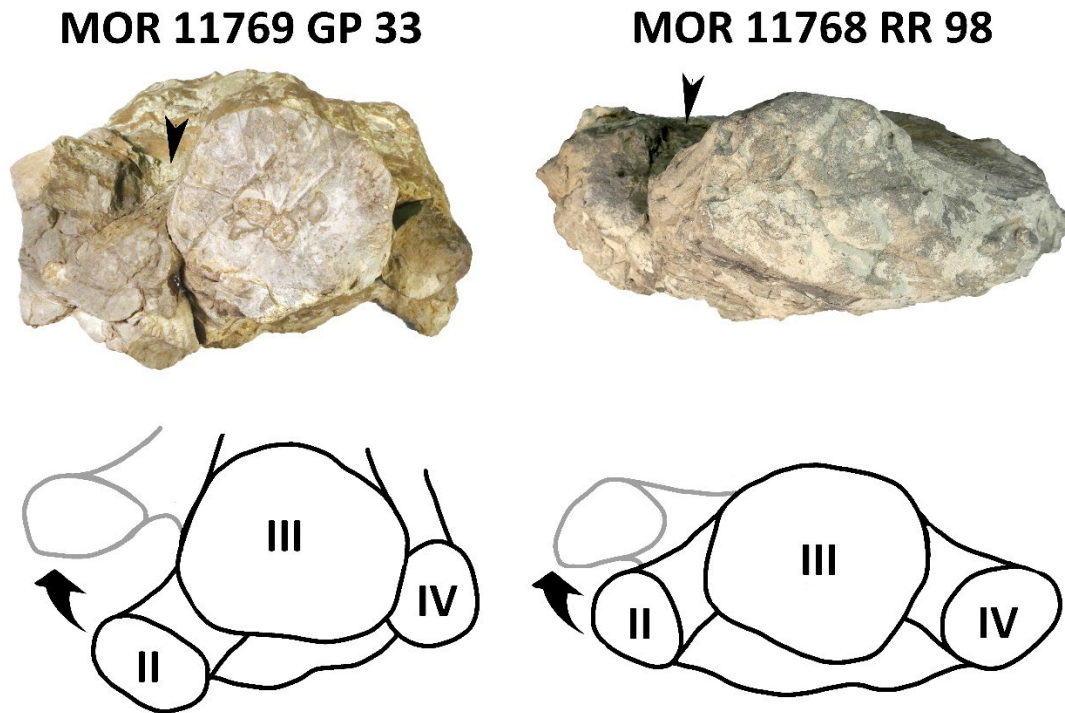


Figure 5.9. Distal view of tracks MOR 11769 GP 33 and MOR 11768 RR 98. Above are pictures depicting the groove separating digit impression II from digit impression III (black arrow); below is the block diagram showing location of ungual impressions and digit kinematic; final position of digit II after weight-bearing phase is emphasized in gray.

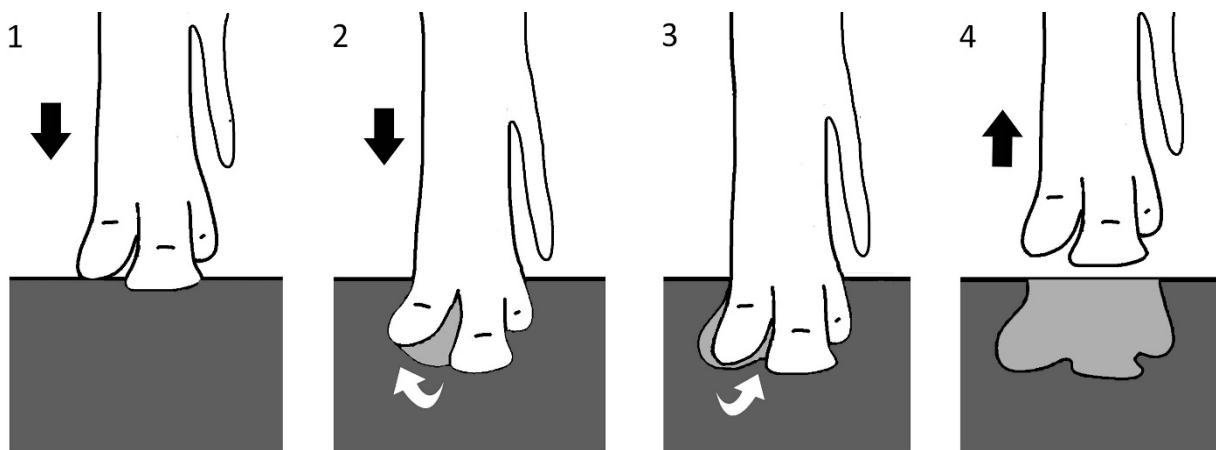


Figure 5.10. Block diagram showing track producer-substrate interaction during 5.10.1) touchdown phase; 5.10.2) weight-bearing phase and lateral extension with rotation of digit II; 5.10.3) digit II flexion and 5.10.4) kick-off phase.

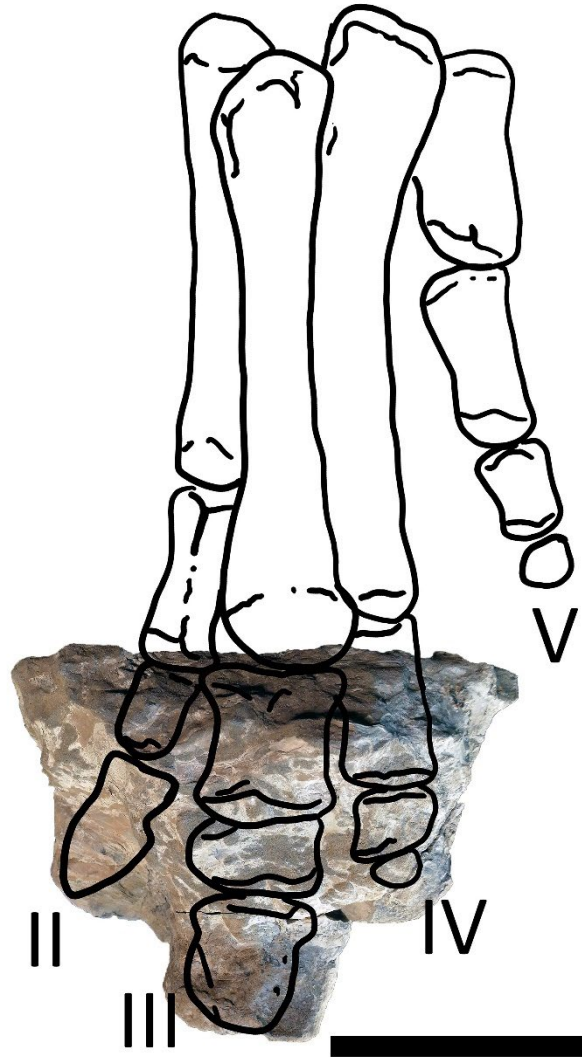


Figure 5.11. Left hadrosaurid manus overlapping track MOR 11769 GP 33 (modified from Brown 1912). Scale bar =10 cm.

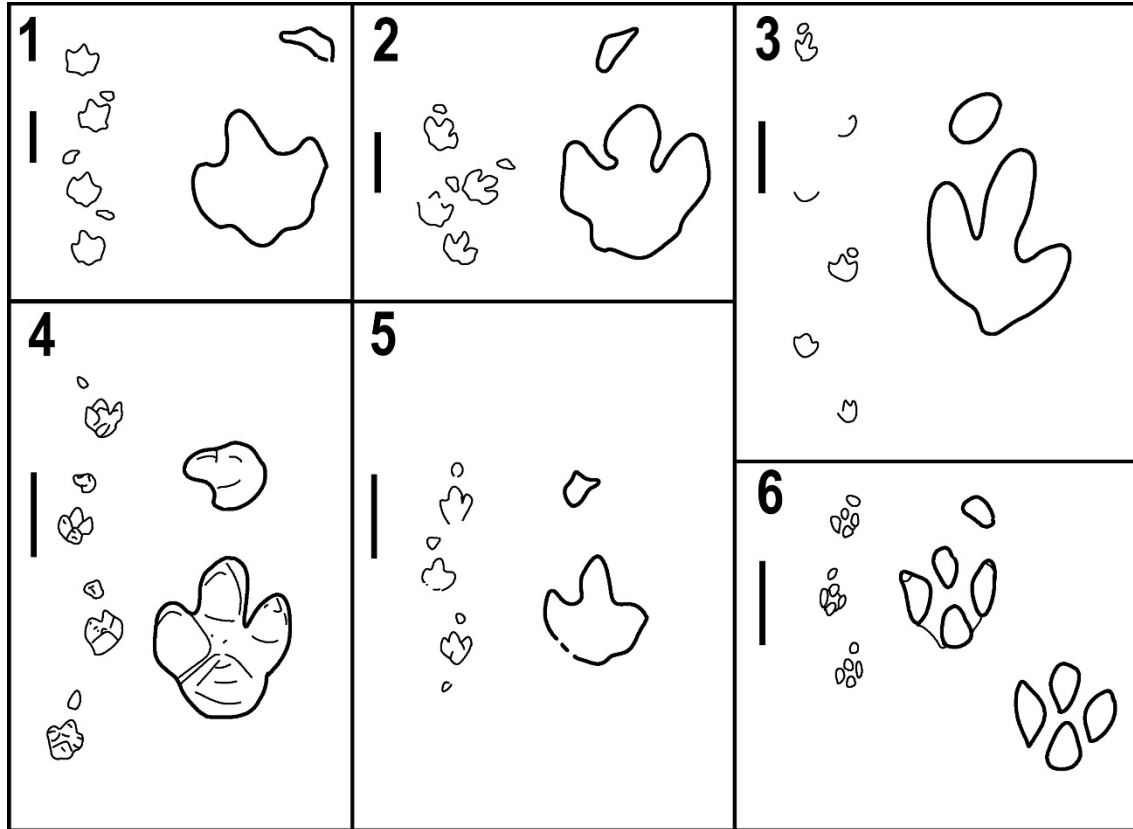


Figure 5.12. Cretaceous trackways assigned to hadrosauriform producers and displaying quadrupedal progression; each trackway is associated to a schematic outline of pes and manus impressions based on holotypes: 5.12.1) *Amblydactylus kortmeyeri*; 5.12.2) *Hadrosauropodus longstoni*; 5.12.3) *Iguanodontipus billsarjeanti*. 5.12.4) *Caririchnium magnificum*; 5.12.5) *Caririchnium leonardi*; 5.12.6) *Caririchnium lotus*. Scale bar for trackways = 1 m.

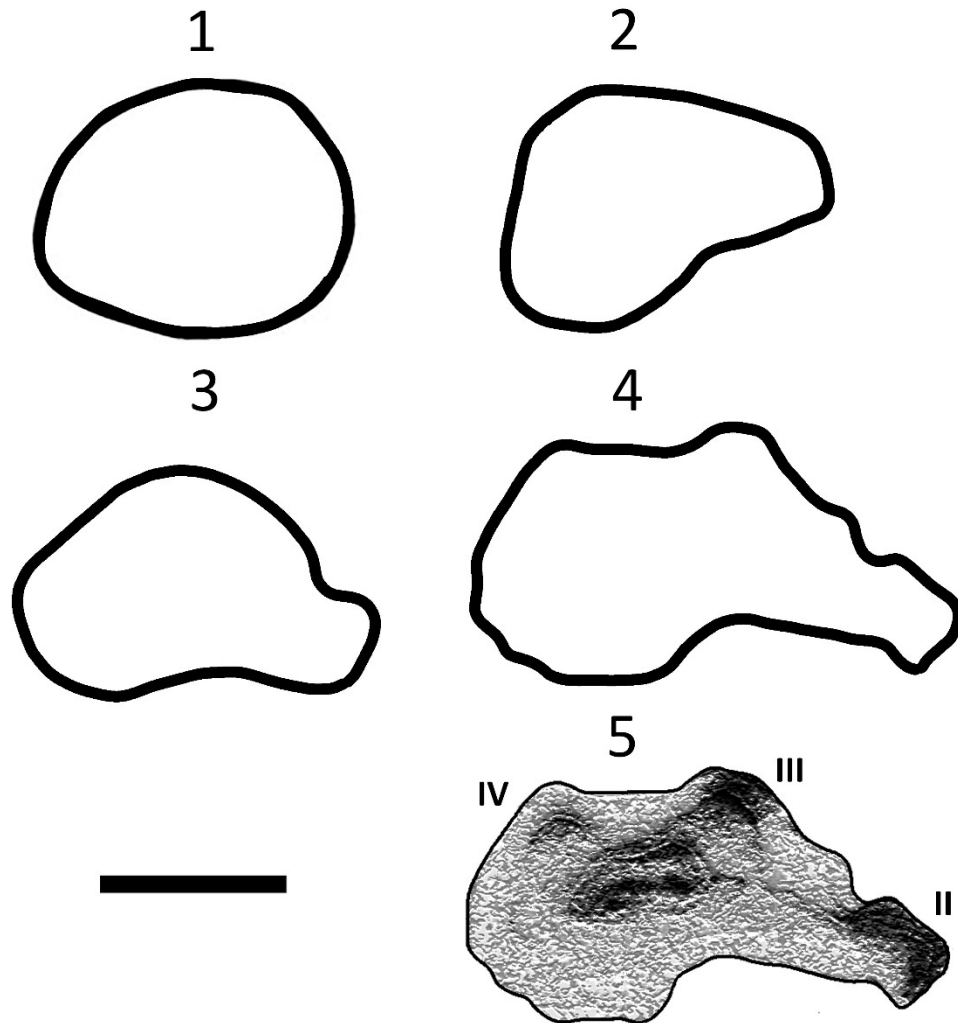


Figure 5.13. Manus outlines of 5.13.1) *Iguanodontipus* isp., 5.13.2) *Caririchnium* isp., 5.13.3) *Hadrosauropodus* isp., 5.13.4-5) *Amblydactylus* isp. All outlines are represented as left manus impressions. Scale bar=5 cm (modified from Meyer and Thüring, 2003; Tsukiji et al., 2018; Lockley et al., 2004; Currie, 1995).

	DII W	DII L	DIII W	DIII L	DIV W	DIV L	Width	Length	Depth
MOR 11769 GP 33	5.5	9	6.7	10.1	4	7.5	15.5	13.2	7.5
MOR 11768 RR 98	15.3	12	?	17.4	?	?	26.7	~18	17.5
	D1W	D1L	D2W	D2L	D3W	D3L	Width	Length	Depth
MOR 11770 GP 65	?	?	7.5	10.2	~8	8.7	22.1	17.2	7.9

Table 5.1. Tracks measurement: DW=digit width, DL= digit length. Dimensions are in centimeters

Age	Ichnogenus	Manus tracks	References
Maastrichtian	<i>Hadrosauropodus</i>	Yes	Lockley et al. 2004a
Cenomanian	<i>Jiayinosauripus</i>	No	Dong et al. 2003
Albian	<i>Ornithopodichnus</i>	No	Kim et al. 2009
Albian	<i>Amblydactylus</i>	Yes	Sternberg 1932
Valanginian-Albian	<i>Caririchnium</i>	Yes	Leonardi 1984
Berriasian-Albian	<i>Iguanodontipus</i>	Yes	Meyer and Thüring (2003)

Table 5.2. List of valid ichnogenera assigned to ornithopod track makers.

Manus characters	Track features	References
Functional tridactyl manus		
	Crescentic shape	Osborn, 1912
Fleshy appendage with limited movements of digit III and IV		Currie et al., 1991
Digit II capable of medial extension	Digit II medially divergent	Norman, 1980 Moratalla et al., 1992 Currie, 1995
Hyperextension of digit II and III	Digit impressions dorsally curved	Norman, 1980
Ungual II twice the length of phalanx II-1 and longer than ungual III	Ungual impression II longer then ungual impression III	Norman, 1980 Wenhao and Godefroit, 2012 Norman, 2014 Carrano and Wilson, 2001
Ungual II subequal or shorter than phalanx II-1	Ungual impression II subequal or shorter then ungual impression III	Norman 2002 Prieto-Márquez, 2010
Ungual II subequal or shorter than ungual III		Prieto-Márquez, 2014

Table 5.3. Manus characters with relative morphological features observed in hadrosauriform manus tracks.

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CHAPTER SIX

DINOSAUR TRACKS FROM THE FRONTIER FORMATION, MONTANA:
PRESERVATION, DISTRIBUTION AND PALEOECOLOGICAL SIGNIFICANCE FOR THE
MIDDLE CRETACEOUS TERRESTRIAL ECOSYSTEMS OF NORTH AMERICA

Contribution of Authors and Co-Authors

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Abstract

The Coniacian-Santonian stages in western North America are characterized by a sparse fossil record. We present here the first account of dinosaur tracks from nine sites in the Frontier Formation (Coniacian-Santonian) of southwestern Montana. Tracks are largely preserved in distal alluvial facies as sandstone casts, with a single example of shallow epirelief impression interpreted as undertrack. Sandstone casts show significant relief, kinematic features (i.e., scale marks), and variable morphologies, arguing for a strong substrate control on their preservation. Putative producers are assigned to ornithopod, ankylosaurian, and theropod dinosaurs in decreasing order of abundance. This record reflects a composition similar to those of other middle Cretaceous formations in North America. Moreover, ankylosaurian tracks of the Frontier Formation represent the first known from Coniacian strata in North America. The incorporation of body and trace fossils yielded by the Frontier Formation indicates the presence of a fauna with North American endemic elements. The establishment of Coniacian-Santonian dinosaurian paleocommunities akin to those observed in Campanian and Maastrichtian formations may reflect the trend toward provincialism attested for the end of the Mesozoic in North America.

Introduction

The informal term “middle” Cretaceous refers to a time interval spanning the Albian through the Santonian stages (Cilliers et al., 2021) and is considered important for understanding the evolution of terrestrial ecosystems in western North America near the end of the Mesozoic (Avrahami et al., 2018; Nesbitt et al., 2019; Tucker et al., 2020). The middle Cretaceous dinosaur fossil record in North America is stratigraphically, geographically, and temporally

heterogeneous, mainly reported from Aptian-Cenomanian and, to a lesser degree, from Turonian deposits; in contrast, only scarce information is available from the Coniacian and Santonian stages (Mannion et al., 2011; McCrea et al., 2014). Important fossiliferous horizons in the western USA occur primarily in: the Aptian-Cenomanian Cedar Mountain Formation (Kirkland et al. 1999); Albian deposits of the Cloverly (Oreska et al., 2013; Carrano et al. 2016), Wayan (Krumenacker et al., 2016), and Blackleaf Formations (Varricchio et al., 2007; Ulman et al., 2011); and from Turonian deposits of the Moreno Hill Formation (Wolfe et al., 1998; Zanno et al., 2019). Ultimately, this uneven distribution of middle Cretaceous strata strongly affects our perception of its biodiversity and hamper analyses of Mesozoic terrestrial ecosystems and their evolution.

In this regard, trace fossils may play a crucial role in the study of this time interval, especially where body fossils are scarce or absent. Dinosaur tracks have been extensively used in paleoenvironmental and paleoecological reconstructions to define depositional environments (Petti et al., 2011), paleocommunity composition (Fiorillo et al., 2011; Fanti et al., 2013), trackmaker behavior (García-Ortiz and Pérez-Lorente, 2014), and sedimentologic and paleogeographic constraints (Nicosia et al., 2007; Noè et al., 2020). Most importantly, dinosaur tracks usually occur in far greater abundance than body fossils, and thus are critical in resolving gaps in the fossil record (Lockley and Hunt, 1998, p. 19; Difley and Ekdale, 2002; Willson, 2005).

Recent discoveries in southwestern Montana have yielded a rich record of dinosaur tracks attested in Frontier Formation deposits of Coniacian and likely Santonian age. This ichnoassemblage represents one of the few fossil records reported in North America from these

stages (Panasci et al., 2021). We aim to provide a comprehensive account of these ichnofossils by examining their preservation, possible track producers, and dinosaur diversity in the Frontier Formation. A comparison of this fossil record with that reported from other Albian-Maastrichtian formations of western USA will also be provided.

Previous studies

The first formal description of the Frontier Formation was by Knight (1902), who analyzed exposures located near the mining town of Frontier in southwestern Wyoming. Since then, the Frontier Formation has been widely studied from a stratigraphic, sedimentologic, and paleontologic standpoint with particular emphasis on marine deposits in Wyoming (Masters, 1952; Merewether et al., 1979; Tillman and Almon, 1979; Winn, 1991; White et al., 2004; Hutsky et al., 2012; Feldman et al., 2014). The non-marine fossil record in western Wyoming and southwest Montana is scarce, and the Frontier Formation has been primarily studied sedimentologically and stratigraphically (Dyman and Nichols, 1988; Tysdal et al., 1990; Dyman and Tysdal, 1998; Dyman et al., 2008), with limited paleontological accounts published (Marsh, 1889; Lull, 1920; Knowlton, 1917; Andrews and Pearsall, 1941). In recent decades the non-marine paleontological record has, however, gained more attention. For example, Eaton (2004) reported a Cenomanian fossil record from non-marine deposits comprising gastropods, eggshell, and vertebrate bone fragments. Dinosaur tracks were reported by Hamblin et al. (2000) from the Turonian part of the Frontier Formation in the Uinta Basin of Utah. Novel papers on the non-marine Frontier Formation have focused on alluvial deposits exposed in southwestern Montana and reported bone fragments assigned to ornithopod and theropod dinosaurs, crocodilian and

freshwater turtles, as well as an abundant invertebrate and vertebrate ichnoassemblage (Panasci et al., 2020; Panasci et al., 2021).

Geological setting

The Frontier Formation is a siliciclastic succession consisting of siltstones, mudstones, sandstones, coal, carbonaceous shales, limestones, and associated bentonites and porcellanites (Cobban and Reeside, 1952). Its sediments were deposited during the early Late Cretaceous in a foreland basin formed in western North America by eastward thrusting, flexural crustal loading, and tectonic subsidence during the Sevier orogeny (DeCelles and Currie, 1996). Frontier sediments were deposited in alluvial and coastal plain settings along the western margin of the Western Interior Seaway (Roberts and Kirshbaum, 1995), when the North American continent was divided into western Laramidia and eastern Appalachia provinces (Brownstein, 2018).

In southwestern Montana the non-marine Frontier Formation is comprised of siltstones, mudstones, limestones, sandstones, shales, minor coal lenses, and conglomerates. Volcanoclastic beds are particularly abundant in the lower and upper Frontier Formation (Roberts, 1972; Tysdal et al., 1990; Dyman et al., 2008). The succession is often complicated by thrusting, Cenozoic volcanism, and more recent alluvial cover (Haley and Perry, 1991; Dyman et al., 2008). Moreover, Frontier sections are usually incomplete and poorly exposed due to the prevalence of fine-grained rocks and their preferential erosion. The thickest and most complete non-marine succession is exposed near Lima Peaks in southern Beaverhead County, where it is underlain by the Albian-Cenomanian Vaughn Member of the Blackleaf Formation and overlain by the Beaverhead Group (Fig. 6.1) (Dyman et al., 1991; Dyman et al., 2008). The Lima Peaks

sequence is entirely non-marine, and was informally subdivided by Dyman et al., (2008) into lower coarse, middle fine, and upper coarse units.

To the east and northeast, the Frontier is thinner, and composed of more marine strata. In the western Centennial Mountains non-marine deposits equivalent to the middle fine-grained unit are exposed (Dyman et al., 2008). Northeastward in the Snowcrest Range, Ruby River valley, and Gravelly Range, lower Frontier Formation deposits are mainly marine (Tysdal et al., 1989), whereas units higher in the section are non-marine. Farther to the east in the Madison Range, the Frontier Formation is predominantly marine (Tysdal, 1991).

Dinosaur tracks are reported here from the Lima Peaks area (MC), western Centennial Mountains (WCM), and upper Ruby River valley (URR) (Fig. 6.2). The Frontier Formation in these areas is comprised of thick siltstone and mudstone-dominated successions deposited in alluvial plain settings. Sandstones, siltstones, and mudstones form recurrent, fining-upward depositional units, often associated with thin limestone horizons. Paleosols lithofacies display mottling, bioturbation, root traces, and calcareous concretions (Panascí et al., 2021; Panascí et al., in review).

Coarse conglomeratic units are mainly observed in the Lima Peaks area. Conglomerates are rare at the WCM and URR localities where the successions are dominated by fine-to-medium grained, cross-bedded sandstones, ripple-laminated siltstones, and mudstones. Medium-to-coarse grained, trough-crossed bedded and ripple-laminated sandstones form relatively thin and extensive channel bodies isolated by thick sets of fine grained, overbank lithofacies (Dyman et al., 2008). WCM and the URR deposits have yielded most of the dinosaur tracks reported in this

paper. In contrast, the MC site in the Lima Peaks area has so far produced only three dinosaur tracks.

Age of the track-bearing horizons

Porcellanitic horizons provided an age for the Frontier Formation in southwestern Montana as old as middle Cenomanian and as young as early Santonian (Dyman and Tysdal, 1997; Dyman et al., 2008). Absolute ages obtained from volcanically derived beds yield dates spanning from about 95 to 85.81 Ma (Zartman et al., 1995; Dyman et al., 2008). Palynomorphs collected from the lower Frontier Formation deposits indicate a Cenomanian-Turonian age (Dynam and Nichols, 1988). Data obtained from lowermost Frontier beds exposed in the Pioneer Mountains provided a congruent age of 93-95 Ma, and equivalent deposits near Drummond in west-central Montana indicate a similar range of 95-96 Ma, thus corroborating a middle Cenomanian age (Zartman et al., 1995). Therefore, the non-marine Frontier Formation includes strata equivalent to the marine Marias River Shale, Cody Shale, Niobrara Formation, and Telegraph Creek Formation (Cobban and Reeside, 1952; Cobban et al., 2005; Finn, 2019). At MC both middle and upper units of the Frontier Formation are exposed (Panasci et al., in review). Their differentiation is based mainly on relative position with respect to tuffaceous marker beds and overall lithology (Dyman et al., 1990). The middle unit of the Frontier Formation is comprised of fine-grained rocks with abundant volcanoclastic and calcareous components. In the Lima Peaks area, the upper strata of the middle unit are marked by green porcellanitic horizons that provided an early Santonian age (Dyman et al., 2008). The uppermost Frontier Formation is overall coarser and can be characterized by limestone conglomerates derived from exhumation and erosion of older middle-to-late Jurassic and Cretaceous rock units.

Exhumation of older Mesozoic formations likely took place close to the thrustured hinterland uplifts during late Frontier deposition (Dyman et al., 1990). The upper boundary of the Frontier is conventionally identified at the presence of the uppermost porcellanitic horizon below the quartzite clast conglomerates of the lower Beaverhead Group (Dyman et al., 1990).

Lithofacies exposed at MC are fine-grained and rich in calcareous detritus. Green volcanoclastic sandstones are also exposed there, although no porcellanitic bed are reported at the site. However, these deposits do display typical lithologies of the middle fine-grained unit observed in deposits about 3 km west at Shineberger Creek and in the western Centennial Mountains area (Dyman et al., 1991; Dyman et al., 2008). Still, exposures at MC are limited and porcellanitic horizons could not be identified in the field, thus the track-bearing horizons could be either Coniacian or early Santonian in age.

The Frontier Formation at WCM is only partially exposed and comprises strata equivalent to the middle fine-grained unit observed in the Lima Peaks area (Dyman et al., 2008). Track-bearing horizons are assigned to the Coniacian based on lithological affinity with equivalent middle Frontier units exposed in the Lima Peaks area, as well as occurrence of the palynomorphs *Tschudypollis* (= *Proteacidites*) *retusus*, indicating an age not older than Coniacian (Dyman et al., 2008). This age is also corroborated by geochronological data provided by Rosenblume et al. (2018).

Stratigraphic and sedimentologic studies on the track-bearing successions exposed in the upper Ruby River valley (URR) are few. An initial account of lower Frontier Formation units was provided by Mann (1960), though he correlated these deposits with the Colorado Formation. He recognized a lower shaley unit and an upper volcanoclastic, sandstone unit, both later

emended by Tysdal et al. (1990) to the Frontier Formation. Tysdal and others described an 881 m thick section comprising the entire lower marine unit of the lower Frontier Formation and part of the non-marine upper unit. Lithofacies were interpreted as marine or marginal marine, passing up section into brackish and coastal plain lithofacies (Tysdal et al., 1990). The remaining upper units exposed in the upper Ruby River valley are entirely non-marine (Panascí et al., in review) and have produced dinosaur tracks. The lower marine unit of the Frontier Formation exposed in the URR are considered Cenomanian-Turonian based on marine fossil content and palynomorphs (Dyman et al., 1988; Tysdal et al., 1990). The non-marine strata surveyed for dinosaur tracks are located higher in the section and seemingly equivalent to the middle volcanoclastic-rich units reported in the western Centennial Mountains and Lima Peaks areas (Panascí, et al., 2021). U-Pb detrital zircon geochronological data reported a Coniacian age for sandstone samples collected at URR-1 (Rosenblume, 2021). We therefore interpreted the track-bearing successions in URR as more likely Coniacian in age.

Material and methods

A total of 65 dinosaur tracks were documented in southwestern Montana from field work between 2018 and 2021. Among these tracks, 56 are reasonably assignable to a track producer, 33 were collected, and three isolated manus tracks of possible ornithopod producers were described separately (Panascí et al., in review). Dinosaur track measurements include: width and length of digit impressions, angle of divarication between digit impressions, track length, width, and depth (Fig. 6.3). Data also include additional measurements reported by Panascí et al. (2021). The term “plantar” is used here to define a pedal track seen in pad view. Divarication between digit impressions is calculated according to Thulborn (1990), which consider digit axes

as lines of best fit. Since most tracks were found as isolated casts, recognition of right or left impression was often not possible, and thus for the sake of simplicity we count digits clockwise in plantar view using Arabic numerals unless specified otherwise. However, we implicitly consider that the central digit of tridactyl ornithopod and theropod tracks are assigned to digit III. Depth for in-situ tracks was defined as the maximum thickness calculated from the base of the track-bearing horizon to the deepest point of the pad impression. Whenever the track was preserved as an isolated cast, a minimum thickness was estimated using the maximum depth observed (Panasci et al., 2021). Standard photogrammetry techniques were used to document relevant specimens. Photos are taken using a Panasonic Lumix ZS70 camera equipped with a Leica optical zoom. The photographs were processed using Agisoft Metashape Professional (64 bit) utilizing standard photogrammetry workflow (Romilio, 2020; Mallison and Wings 2014). False-color elevations of the tracks were obtained using the software ParaView 5.9.0. A cast was prepared using Plaster of Paris to collect an in situ track preserved as concave epirelief. Specimens are now curated at the Museum of the Rockies (MOR), Bozeman, Montana, USA, with catalog numbers MOR 1644, MOR 11770, MOR 11772, MOR 11768, and MOR 11766.

Dinosaur tracks

The bulk of the Frontier dinosaur track record has been reported from WCM and URR with a total of nine track sites. In contrast, only one site has been reported from MC. Dinosaur tracks are primarily found along slopes or drainages as isolated tridimensional casts, and the lack of well exposed outcrops complicates the exact location of the original track-bearing horizon. Only in few instances could their exact stratigraphic position be identified. Sites on the maps provide the approximate locations where tracks are found (Table 6.1; Fig. 6.4,5).

Track preservation is highly variable, with ichnites either featuring undefined digit and pad impressions, or having highly detailed digit, ungual, pad, and metatarsal impressions. Soft deformation structures, plant material, and invertebrate trace fossils may also be associated with dinosaur tracks. The ichnites can be broadly assigned to ornithopod, theropod, and ankylosaurian producers, but due to preservation their morphology is not sufficient for an ichnotaxonomical attribution.

Ornithopod tracks

The Frontier Formation is dominated by ichnites assigned to ornithopod producers (Fig. 6.6). These tracks can be readily identified based on their tridactyl configuration, absence of claw impressions, and overall proportions (i.e., tracks are wider than longer) (Table 6.2). Accordingly, fifty tracks have been assigned to this group, and four morphotypes can be broadly distinguished based on their preservation (Fig. 6.7). Morphotype 1 is characterized by tracks with short and sometimes pointy digits, and with a dominant pad impression, giving an overall triangular shape. Several tracks assigned to this morphotype may also be associated with metatarsal impressions. Morphotype 2 is distinguished by tracks with a characteristic curved middle digit. Morphotype 3 is defined by tracks with well-preserved digit and pad impressions, ungual traces are blunt with subrounded or subtriangular extremities; the metatarsophalangeal pad, as reported by Panasci et al. (2021), may also be caudally bilobed. Tracks assigned to this morphotype may also be associated to soft-sediment deformation structures, such as deformed laminae and load casts, indicating water saturation and hydroplastic rheology of the substrate (Fig. 6.8). Well preserved hoof impressions and scale marks are in several deep casts, aiding in the recognition of autopodial kinematic. In general, kinematic markers observed on deep casts

suggest dominantly vertical movements during weight-bearing and kick-off phases (Fig. 6.9). Interestingly, these kinematic marks are notably featured in tracks assigned to ornithopod dinosaurs (Cobos et al., 2016). In contrast, morphotype 4 is comprised of tracks often preserved as deep casts with irregular pad morphology. Preservation of kinematic markers and digit traces are effective morphological features used in their assignment.

Preservation state limited morphometric analysis to only 30 specimens (Table 6.3). Among them, the majority show widths ranging from 20 to 30 cm, seven specimens are between 30 and 40 cm, and three between 40 and 50 cm. The least frequent classes are represented by specimens less than 20 cm wide. Considering a length average of 22.5 cm for the most frequent class (n=17), the approximate hip height for these track producers is estimated as 90 cm, according to Henderson (2003). For the longest tracks, the height to the hip may reach about 176 cm.

The bilobed heel impression observed in several specimens is comparable to that seen in uppermost Cretaceous ornithopod tracks assigned to hadrosaurid producers (Nakajima et al., 2018). Based on this morphological character alone, designation is nonetheless questionable since bilobed heel impressions have been also reported in other Upper Cretaceous ornithopod tracks, regardless of their temporal distribution (Currie, 1995; Lockley et al., 2004; Lockley et al., 2006; Lockley, 2014; Díaz-Martínez et al., 2015; Tsukiji et al., 2018). Equivalent Frontier Formation deposits of the Moreno Hill (McDonald et al., 2010) and Niobrara Formations (Everhart and Ewell, 2006) have yielded respectively hadrosauroid and hadrosaurid ornithopod bone material. Thus, even though a hadrosaurid producer may not be ruled out, footprints may be equally assigned to a possible hadrosauroid ornithopod. Panasci and others (in review) describe

three tracks preserved as sandstone casts with steeply inclined and hoofed digit impressions in Coniacian deposits, proposing a hadrosauroid or hadrosaurid ornithopod producers based on morphological and osteological evidence. As a result, the presence of derived hadrosauriform ornithopods could be extended to Coniacian Frontier Formation deposits of southwestern Montana.

Ankylosaurian tracks

Four tracks are assigned to this group and are distinguished by an enlarged pad and four blunt digit impressions (Fig. 6.10; supplemental materials). Measurements are reported in Table 4. Dimensions are variable among specimens, but two morphotypes may be recognized. The first morphotype comprises tracks with relatively elongated digit impressions. MOR 1644 2 possesses digit traces with blunt extremities, and a side digit impression here interpreted as digit I that seems to diverge medially, whereas digit traces II, III, and IV point overall forward (Fig. 6.11). The pad impression is well-developed and shows a somewhat triangular outline. In MOR 1644 4 the distal impression of digit traces 1,2 and 4 are missing, thus length can only be approximated (Fig. 16.2). The pad impression is well developed and shows a posterior, rounded outline. Several scale traces forming short, curved striations are on the proximal impression of digit 4.

The second morphotype comprises tracks showing relatively short digit traces compared to the other specimens reported. MOR 11770 GP 64 (Fig. 6.13) is poorly preserved due to weathering, thus its short-digit morphology can be considered circumstantial. It displays shallow pad and digit traces, the latter characterized by blunt extremities. In MOR 11768 2 the pad and rear impressions are dominant, whereas digit traces define short and deep buttresses (Fig. 6.14). Digit traces do not form vertical and symmetrical impressions, but seem obliquely

directed and are deeper on the left than on the right side of the track in plantar view. This asymmetry may suggest a major body weight load on the side where the track was shifting its weight and thus impressing more deeply into the substrate.

Four-digit footprints from the Frontier Formation have been assigned by Panasci et al. (2021) to possible ankylosaurian pedal impressions based on this number of digits, as well as relatively long and blunt morphology of digit impressions. This designation seems to be corroborated by several synapomorphies observed in Ankylosauria that include loss of pedal digit V and rounded unguals (Riguetti et al., 2021). Apparently, digit morphology is particularly important to differentiate ankylosaurian pes tracks from other tetradactyl pedal impressions, such as those assigned to purported ceratopsians. Ankylosaurians also have proportionally shorter metatarsals in respect to the toes, thus producing relatively longer digit traces (McCrea et al., 2001, p. 414). In this regard, morphology of MOR 1644 2 and MOR 1644 4 may be comparable to pedal impressions described for the ichnogenus *Tetrapodosaurus*, also assigned to ankylosaurian producers (McCrea, 2000).

Aside from the possible track maker, digit morphology and angle of divarication may also be used to further assess whether these four-digit tracks represent left or right pedal impressions. A useful character to designate ankylosaurian pedal impressions is the reduction of digits I and IV, a feature typically observed in ankylosaurians (Butler et al., 2008). In purported ankylosaurian tracks the first digit is divergent, whereas digits II, III and IV point overall forward in respect to the pes axis (McCrea, 2000; Milner et al., 2006). Even though some degree of distortion is not excluded, in MOR 1644 2 the side digit I is comparatively short and diverges with a higher angle with respect to the other digit traces; thus we likely interpret MOR 1644 2 as

a possible ankylosaurian left pedal impression. Similarly, in MOR 1644 4 the digit impressions are elongated overall, also supporting an ankylosaurian producer. The side digit 4 seems to diverge laterally, but is incomplete, thus hindering the designation to a left or right pedal impression.

Tracks MOR 11768 2 and MOR 11770 GP 64 have short digit impressions and digit trace 4 diverges laterally, indicating a possible ankylosaurian producer. A ceratopsian producer may also be possible for these four-digit tracks, as ceratopsian pedal impressions are differentiated from those assigned to ankylosaurians mainly on the short digit traces enclosed in the pad impression (Lockley and Hunt, 1995). As previously observed, the form of MOR 11768 2 is likely the product of weathering, and thus digit morphology can be considered merely circumstantial. It is worth mentioning that short-digit morphologies have also been reported in pedal impressions assigned to ankylosaurian track makers (Lockley et al., 2006). This morphology may result from substrate deformation under the animal body weight (McCrea, 2000), a scenario that cannot be excluded for deep tracks such as MOR 11768 2. Moreover, in purported ceratopsian pedal traces, all digit traces point forward in respect to the pes axis (Lockley and Hunt, 1995; Milner et al., 2006), whereas in MOR 11770 GP 64 and MOR 11768 2 digit 4 seems divergent from the other digit traces.

The occurrence of purported ankylosaurian tracks in Frontier deposits is congruent with the ankylosaurian fossil record of North America (Arbour and Currie, 2016). Notably, ankylosaurian fossil remains were originally reported from Frontier Formation deposits by Marsh (1889). The oldest body fossil evidence in the ceratopsian fossil record of North America is reported from Albian deposits of the Cloverly Formation (Farke et al., 2014). Turonian

deposits of the Moreno Hill Formation have also yielded basal ceratopsian remains (Wolfe et al., 1998). Although a single track of possible ceratopsian origin was reported from Albian deposits of the Nanushuk Formation (Fiorillo et al., 2010), other more plausible ceratopsian tracks have been described primarily from Santonian and younger Cretaceous formations (Parker and Rowley, 1989; Lockley and Hunt, 1995; Milner et al., 2006; Lockley, 2014). Thus, though a possible ceratopsian producer may be likely, we prefer to adopt a more conservative approach considering all tetradactyl tracks as more probably ankylosaurian in origin.

Theropod tracks

Theropod tracks are the least abundant ichnites from the Frontier Formation. Two specimens were reported at PCr 1 in the western Centennial Mountains, and they are derived from the same track-bearing horizon described by Panasci et al. (2021). The tracks are preserved as deep, fine-grained sandstone casts, bearing distinctive claw-mark impressions on the tip of the digit traces, and a posterior metatarsal impression that makes them overall longer than wider (Table 6.5).

Track MOR 1644 3 is an isolated, tridimensional cast about 18 cm long, with an evident metatarsal impression (Fig. 6.15; see supplemental material). Notable linear scale impressions were observed on the lateral side of the tracks forming parallel corrugations 0.1 - 0.4 mm wide, inclined in two opposite directions with an angle of approximately 60 degrees. These grooves define a characteristic “V-shaped” configuration on the both side of the digit 1 impression, which is unfortunately incomplete. The middle digit is also partially preserved but maintains its overall form when observed in pad view. Scale traces, dipping about 60 degrees, can be seen on the distal middle digit impression, but they are less consistent in shape and pattern than those

observed for the missing digit 1. These scale marks are short, curved, and seem to converge towards the tip of the claw impression. Digit 3 is the best-preserved impression and displays wide divarication. An almost vertically directed claw striation can be followed across the entire depth of digit impression 3. Well-developed vertical scale traces can also be seen between digit 2 and 3 impressions. Digit 3 shows two different orientations if observed in pad or dorsal view (Fig. 6.16). In dorsal view the claw impression is oriented inward, thus pointing towards the middle axis of the track. Seen in pad view, the claw impression is in contrast oriented sideways. Kinematic markers strongly suggest considerable digit mobility. During substrate penetration movement was dominantly vertical, but digit 3 was likely abducted and rotated during the weight-bearing phase. Torsion and abduction of the digit may have compensated for the forces transmitted outward and upward during weight-bearing phase (Allen, 1989, 1997). Notably, digit impressions retain their original morphology, suggesting that the heel was likely the first to be retracted during kick-off phase, and then was followed by the digits.

The second theropod track reported at PCr 1 was previously described on the track-bearing horizon by Panasci et al. (2021). The track is preserved at the base of a fine-grained sandstone bed and is partially obscured by two other dinosaur tracks possibly overstepping it. Nevertheless, a metatarsal impression and three, clawed digit traces are clearly visible. In contrast to MOR 1644 3, digit traces are only slightly diverged and point forward.

Epirelief track

MOR 11767 RR 97 represents the only dinosaur track from the Frontier Formation reported as concave epirelief (Fig. 6.17; see supplemental material). This track was reported in

situ from URR 4 in an interval of fine-grained sandstone and carbonaceous siltstone. Given the uncommon preservation, a plaster cast was made to permit the collection of the specimen.

The track-bearing horizon is comprised of a 4 cm-thick, fine-grained, ripple-laminated sandstone bed with a characteristically gray-to-reddish color. Ripple laminae distinctively flake off from the upper surface. Fine-grained sandstone horizons are locally bioturbated, though the interval that bears the track does not show evidence of it. This horizon is overlain by a carbonaceous silty bed forming a 3.5 cm-thick, bioturbated, veneer. Generally, the amount of carbonaceous plant material in the siltstones is more abundant at the base of the unit. The siltstone horizon is overlain by another ripple-laminated sandstone characterized at the base by centimeter-scale load casts, suggesting an overall saturated condition of the underlining sediments during deposition (Fig. 6.18).

MOR 11767 RR 97 is a shallow, tridactyl impression about 1 cm deep, with the distal digit traces more deeply impressed than the rest of the track (Table 6.6). The middle digit trace is the deepest, especially in the distal portion. Sandstone laminae visibly flaked off the internal surface of the track across the entire surface of the track-bearing horizon. A second, deeper epirelief structure is closely associated with MOR 11767 RR 97. It is elongated and terminates with a deep, pointy morphology. This structure may represent a partial digit impression corresponding to another track.

Color elevation maps indicate that the distal digit impressions of MOR 11767 RR 97 are relatively deeper, and their morphology better defined than the rear impression of the track. On one hand, this may indicate that such preservation resulted from a deeper digit penetration into the substrate horizons where consistency was greater, therefore improving the overall

preservation (Seilacher, 2007; Shibata and Varricchio, 2020). However, the upper surface of the track-bearing horizon is partially missing from erosion, and thus MOR 11767 RR 97 likely represents an undertrack. Possibly, the true track was impressed on the overlain veneer of carbonaceous siltstones and transmitted on the lower unconsolidated sandy horizon (Fig. 6.19.6-10). When compared to the original tracks, undertracks generally display an increasing degradation of morphologies moving towards deeper horizons (Milàn and Bromley, 2006), and proportions usually are not affordable to distinguish the possible producer. Consequently, the track maker designation for MOR 1767 RR 97 remains unsolved.

Discussion

The dinosaur body fossil record is overall scarce in Frontier Formation deposits of southwestern Montana and only represented by fragmentary material of theropod and ornithopod dinosaurs. However, the abundant dinosaur track assemblage reported here provides further insights into the Frontier Formation terrestrial paleocommunity.

The track record is largely reported in middle, fine-grained Frontier Formation units, whereas it seems absent in the lower and upper coarse-grained units. The most abundant assemblage comes from the Coniacian Frontier Formation deposits of WCM, comprising a reported total of 44 tracks (Fig. 6.20). A less abundant yet consistent assemblage is represented by tracks reported in stratigraphically equivalent deposits at URR, with a total number of 18 tracks. The prolific ichnofossil assemblage observed may have resulted from the dominant fine-grained floodplain lithofacies attested in these areas. In general, preservation potential in fine-grained floodplain deposits is enhanced due to the alternate deposition of coarse and fine sediments typical of overbank processes (Maple and Archer, 1989; de Souza Carvalho and

Leonardi, 2021). The middle unit of the Frontier Formation was deposited in low-gradient, alluvial coastal plains (Dyman et al., 2008), and may reflect features typical of wetland deposits based on sedimentological and ichnological evidence (Panascí et al., 2021). Such depositional environments could have provided highly suitable conditions for track emplacement and preservation. In this regard, the low abundance of dinosaur tracks observed in Frontier lithofacies at MC may be due to the overall coarser sedimentology observed in the Lima Peaks area. Based on this assumption, track distributions and abundances may thus reflect an increasing trend of preservation potential moving from western proximal to eastern distal alluvial plain successions. However, more data are needed to verify this interpretation.

Most tracks are preserved as natural sandstone casts, indicating the importance of cyclical sand deposition across floodplain setting for track preservation (Foster et al., 2006). Dinosaur tracks generally display considerable relief suggesting that producers impressed deeply into the substrate, and most of the tracks can be defined as penetrative tracks (Falkingham et al., 2020). Moreover, preservation variability suggests that substrate consistency strongly impacted track taphonomy. Interestingly, there is a consistent disparity between tracks preserved as convex hyporeliefs and those preserved as concave epireliefs (i.e, tracks preserved on bedding plains), the latter reported only once. The depositional environment, as noted by Panascí et al. (2021), favors hyporelief preservation. Tracks were emplaced on muddy and silty substrates, and the impressions were then filled by fine-grained sands deposited during subsequent floods. Preferential erosion of fine-grained deposits underlining the track-bearing horizon would consequently favor track detachment by mass failure. However, low abundance of tracks preserved as epireliefs may be likely the result of outcrop quality, since extensive bedding planes

are infrequent in the studied areas and this would considerably decrease the opportunity to observe epirelief structures (Marenco and Hagadorn, 2019).

Dinosaur tracks sites are generally rare in Turonian-to-Santonian deposits of western USA (Wolfe, 2006; Gerlinski and Lockley 2013), but abundantly reported from Albian-Cenomanian and Campanian-Maastrichtian formations (Fig. 6.21, 22). A similar situation is also observed in western Canada and Mexico where track sites are scarce or absent in Turonian, Coniacian, and Santonian deposits (McCrea et al., 2014; Ortíz-Mendieta, 2001; Rodríguez-de la Rosa, 2001; Rodríguez-de la Rosa, 2003; Kappuss et al., 2011; Bravo-Cuevas and Rodríguez-de la Rosa, 2014; Vogt et al., 2016). The Frontier Formation in southwestern Montana and northeastern Utah has yielded eleven track sites that include track-bearing horizons assigned to Turonian (Hamblin et al., 2000), and Coniacian deposits (Panasci et al., 2021; Panasci et al., in review). Data from this study indicates that the fossil record in southwestern Montana is dominated by tracks assigned to ornithopod dinosaur producers followed by ankylosaurians and theropods. The overall track-maker composition compares well with ichnoassemblages described in the Albian-Cenomanian Dakota Group, where ornithopod tracks are profuse (Lockley et al., 1983; Parker and Balsley, 1989; Parker and Rowley, 1989; Lockley and Hunt, 1998 p. 192-197; Lockley et al., 2006; Lockley et al., 2011; Simpson et al., 2011; Lockley, 2018; Lockley et al., 2021). Deposits of the Moreno Hill (Wolfe, 2006), Ferron Sandstone (Gerlinski and Lockley, 2013) and Toreva Formations (Irby and Albright, 2002) are likewise akin to these, although they reported a smaller number of track sites. Notably, the Frontier Formation is unique in yielding ankylosaurian tracks from Coniacian deposits, previously found exclusively in Turonian deposits of the Kaskapau Formation (Rylaarsdam et al., 2006) and older Cretaceous formations of Canada

and USA (McCrea, 2000; Lockley et al., 2006; McCrea et al., 2014; Lockley et al., 2021; Plint et al., 2022).

The Frontier Formation provides an abundant dinosaur track record from Turonian and especially Coniacian deposits of western USA. The scarce regional Turonian, Coniacian, and Santonian track record previously reported has been variously associated with a recipe of sea level rise, paleoenvironmental changes, and non-preservation of the fossil record (Lockley and Hunt, 1998, p. 192; Lockley et al., 2014). High sea level has also been indicated as a possible explanation to interpret the scarce dinosaur body fossil reported in Turonian-to-Santonian continental successions (Nesbitt et al., 2019). During the Turonian and Coniacian, the Western Interior Seaway reached a maximum expansion, likely resulting in a limited land mass extent that could have hampered fossil preservation in non-marine environments. Track site abundance in western USA formations shows an increased abundance corresponding to the Albian-Cenomanian stages, followed by a striking decrease between the Turonian and Santonian, and finally an increase in the abundance corresponding to Campanian and Maastrichtian stages. Although the trend observed seems consistent with relative sea-level base variations, this may however not be a ubiquitous explanation for the heterogeneously distributed fossil record observed in Upper Cretaceous formations. In fact, besides possible ecological constraints likely impacting organism distribution on land, several authors also recognized the importance of sampling biases, in particular the limited number of studies available (Mannion and Upchurch, 2011; Arbour et al., 2016). Possible sampling biases may be invoked to explain the richer abundances of sites reported in Campanian and Maastrichtian formations. For example, Campanian and Maastrichtian dinosaur track sites are relatively abundant, likely because of the

systematic research done on important fossiliferous formations (Lockley et al., 1983; Parker and Rowley, 1989; Nadon, 1993; Lockley and Hunt, 1998; Lockley and Foster, 2003; Lockley et al., 2011; McCrea et al., 2014; Lockley et al., 2014; Therrien et al., 2015; Lockley et al., 2018). It is also possible that biases occurring in data collection may reflect academic preferences that favored certain localities, or focused on body fossils and neglected trace fossils. For example, invertebrate and vertebrate trace fossils have been widely identified from the Two Medicine Formation (Horner, 1984; Horner, 1987, p. 60; Nadon, 1993; Chin and Gill, 1996), but only more recent studies have indicated the abundance and paleoecological value of this ichnoassemblage (Martin and Varricchio, 2011; Lockley et al., 2014; Freimuth and Varricchio, 2019). Recognition may have also been limited in areas where access to outcrops is minimal due to erosion, harsh topography, and collection permit limitations. The importance of human factors affecting data collection is a topic still poorly treated when dealing with fossil record distribution and abundance. Further studies are needed to better understand the relationship between collection biases and fossil record distribution.

As mentioned above, ornithopod tracks are the most abundant ichnites reported in Frontier Formation deposits of southwestern Montana. Accordingly, the habitat provided suitable ecological conditions for sustaining such an abundance of herbivore dinosaurs. Presence of ornithopod tracks in fluvio-lacustrine settings is widely reported (Carpenter, 1984; Houck and Lockley, 2006; Gasca et al., 2017), and their association with lower alluvial coastal plains and especially vegetated wetlands lead several authors to suggest possible ecological constraints including food supply, nesting and nursing, as well as protection from predators (Nadon 1993; Difley and Ekdale 2002; Fiorillo et al. 2019). Body (Carpenter et al., 2001; Ebert, 2005;

Carpenter et al., 2008; Arbour and Currie, 2016; Arbur and Mallon, 2017) and trace fossil evidence (Carpenter, 1984; McCrea and Currie, 1998; McCrea et al., 2001; Gangloff et al., 2004; Hornung and Reich, 2014) would also suggest a similar association for ankylosaurian dinosaurs, which seems to have preferred vegetated, freshwater- dominated environments. Ankylosaurian tracks are less abundant than those assigned to ornithopods, but their co-occurrence seems to be consistent with the general paleodepositional environment proposed for middle fine-grained unit and equivalent strata of the Frontier Formation, characterized by wetlands with freshwater, ponded areas and abundant vegetation (Dyman et al., 2008; Panasci et al., 2021). Given the abundant plant material reported in Frontier Formation deposits, food supply could be a valid ecological factor explaining presence of herbivores dinosaurs in such alluvial environments. However, paleoecological generalizations on ecological constraints exclusively based on track record may be misleading, because ankylosaurian and ornithopod remains are also reported in arid and semiarid environments, suggesting broader ecological distributions for these dinosaur groups (Varricchio and Horner, 1992; Jerzykiewicz et al., 2021; Botfalvai et al., 2021). Tracks rarely provide a specific taxonomical identification of the track producer and caution should also be taken when local and regional stratigraphic correlations cannot be carried out with precision (Fowler, 2017). In addition, abundant track records are typically reported in sedimentary successions with high preservation potential, such as those deposited in lower alluvial coastal plains (Lockley et al., 1992; Lockley et al., 2006). Thus, ecological constraints inferred only from the track record would be biased against those environments that are less likely to be preserved. Even though correlation between several ornithopod and ankylosaurian groups in

these environments is possible, paleoecological studies should prioritize a comprehensive approach to define the actual distribution and relative abundance of various dinosaur groups. The Frontier Formation fossil record reflects similarities with other middle Cretaceous dinosaurian paleocommunities (Table 6.7). The Mussentuchit Member of the Cedar Mountain Formation includes theropods, sauropods, iguanodontians, hadrosauroids, orodromines, and ankylosaurians (Kirkland et al., 1999; McDonald et al., 2017). Except for sauropods, the Wayan and Blackleaf Formations also display a similar assemblage (Ulmann et al., 2011; Krumenacher et al., 2016; Krumenacher, 2019). The Moreno Hill Formation also includes neoceratopsians (Wolfe et al., 1998), therizinosaurid, hadrosauroids (McDonald et al., 2010), theropods, and ankylosaurian remains (Nesbitt et al., 2019), whereas iguanodontian ornithopods are apparently absent. The presence of derived hadrosauriform ornithopods as well as ankylosaurian, and theropod dinosaurs would make the Frontier Formation composition overall similar to the previously mentioned middle Cretaceous formations. Remarkably, if the Frontier fossil record is considered in its entirety, the occurrence of the freshwater turtle *Neurankylus* sp. (Panasci et al., 2020), mainly a characteristic component of uppermost Cretaceous formations, is also significant, as this genus of baenid turtles has a restricted geographical distribution, only known from Coniacian-to Paleocene deposits of western North America (Joyce and Lyson, 2015; Lichtig and Lucas, 2016). This preliminary analysis suggest that the Frontier Formation retains components typical of middle Cretaceous formations, such as derived hadrosauriforms, theropod, and ankylosaurian dinosaurs, and yet it concurrently reflects unique Campanian and Maastrichtian elements. This fossil record may suggest the setting of paleocommunities more similar to those observed in uppermost Cretaceous formations, and likely reflecting the North

American provincialism established during the end of the Mesozoic era (Sereno, 1997; Hirayama et al., 2000).

Conclusions

Dinosaur tracks represent the primary vertebrate fossil record of the non-marine Frontier Formation in southwestern Montana. Deposits were likely favorable for track preservation due to the dominant fine-grained nature and consistency of sediments deposited in floodplain alluvial settings. This depositional setting generally allowed for deep penetration within the substrate, leaving impressions that subsequently were filled with coarser sediments. Sixty-five dinosaur tracks have been reported and can be assigned to ornithopods, ankylosaurians, and theropods producers. Among dinosaur track producers, most are assignable to ornithopod dinosaurs. Most of the dinosaur track assemblage come from the Coniacian deposits of the Frontier Formation and is comparable to those reported in other middle Cretaceous formations of western North America including ornithopod, ankylosaurian, and theropod dinosaurs. The integration of body fossil data would suggest the presence of a fauna that included elements in common with Campanian and Maastrichtian formations, suggesting that North American faunal provincialisms was likely taking place across southwestern Montana during the Coniacian.

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research could not have been possible without the assistance of the staff of US Forest Service and Bureau of Land Management that provided us with assistance and accesses to the areas studied in this paper.

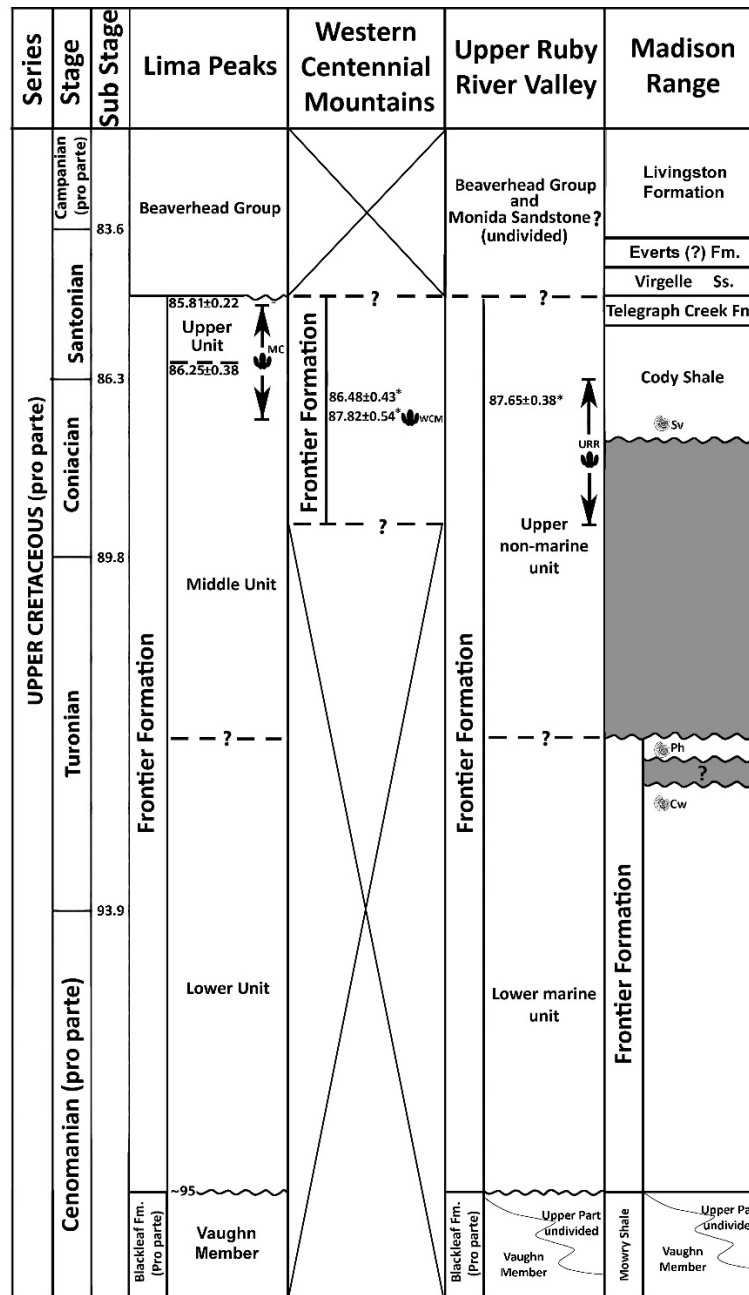


Figure 6.1. Chronostratigraphy of the Frontier Formation in southwestern Montana for the localities examined: Middle Creek (MC), western Centennial Mountains (WCM), and upper Ruby River valley (URR); arrows indicate maximum temporal ranges in the stratigraphic position. Shaded areas and crosses indicate missing time and covered intervals, respectively. Ages for the Lima Peaks area are from Dyman et al. (2008); lower contact age reflects uncertainty values indicated by Zartman et al. (1995); ages marked by asterisk and are provided by Rosenblume et al. (2018); ammonite symbols indicate biozone constraints for *Collignonicerus woollgari* (Cw), *Prionocyclus hyatti* (Ph); *Scaphytes ventricosus* (Sv), according to Dyman et al. (1997).

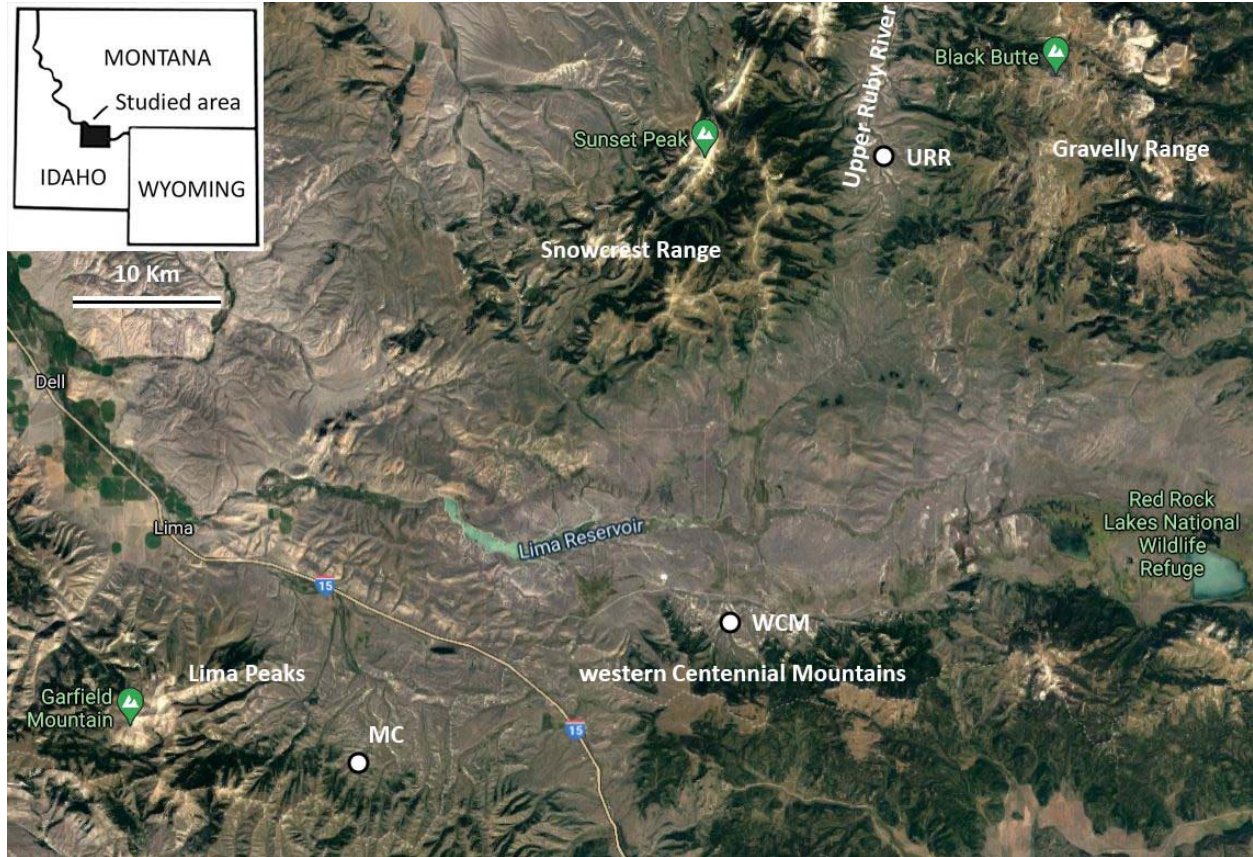


Figure 6.2. Area of study. Middle Creek (MC), western Centennial Mountains (WCM), upper Ruby River valley (URR).

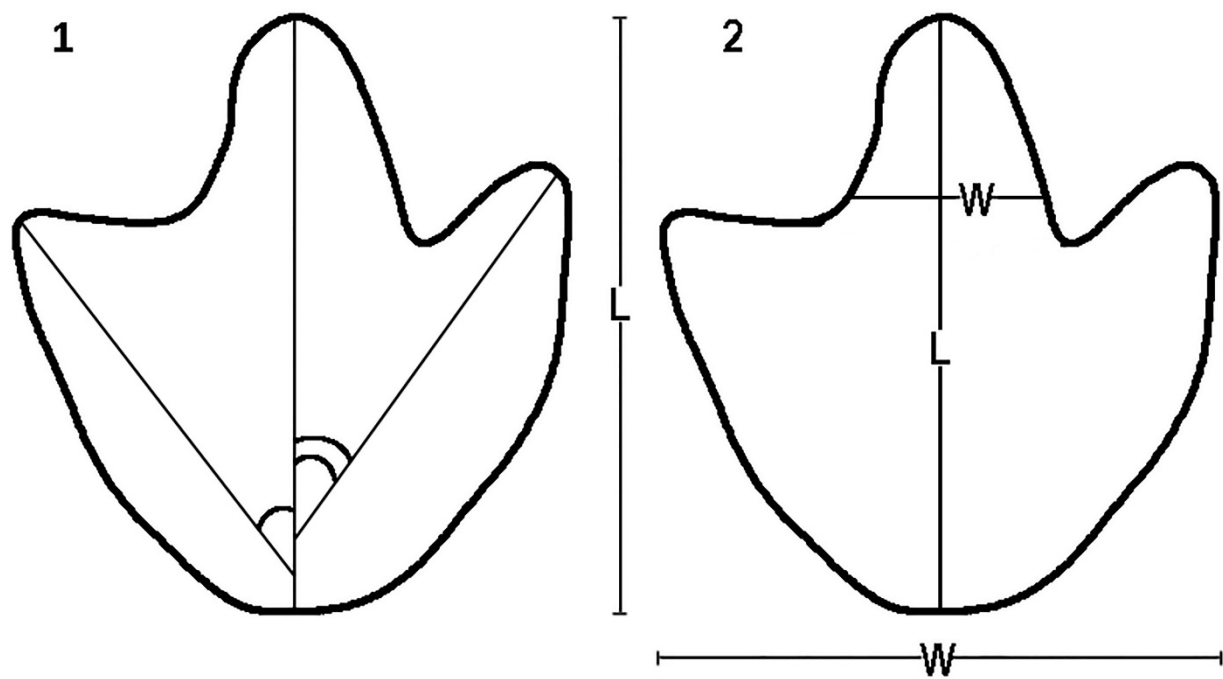


Figure 6.3. Diagram showing track measurements adopted: 6.3.1) interdigital angle (DIV); 6.3.2) Width (W) and length (L) of track and digits.

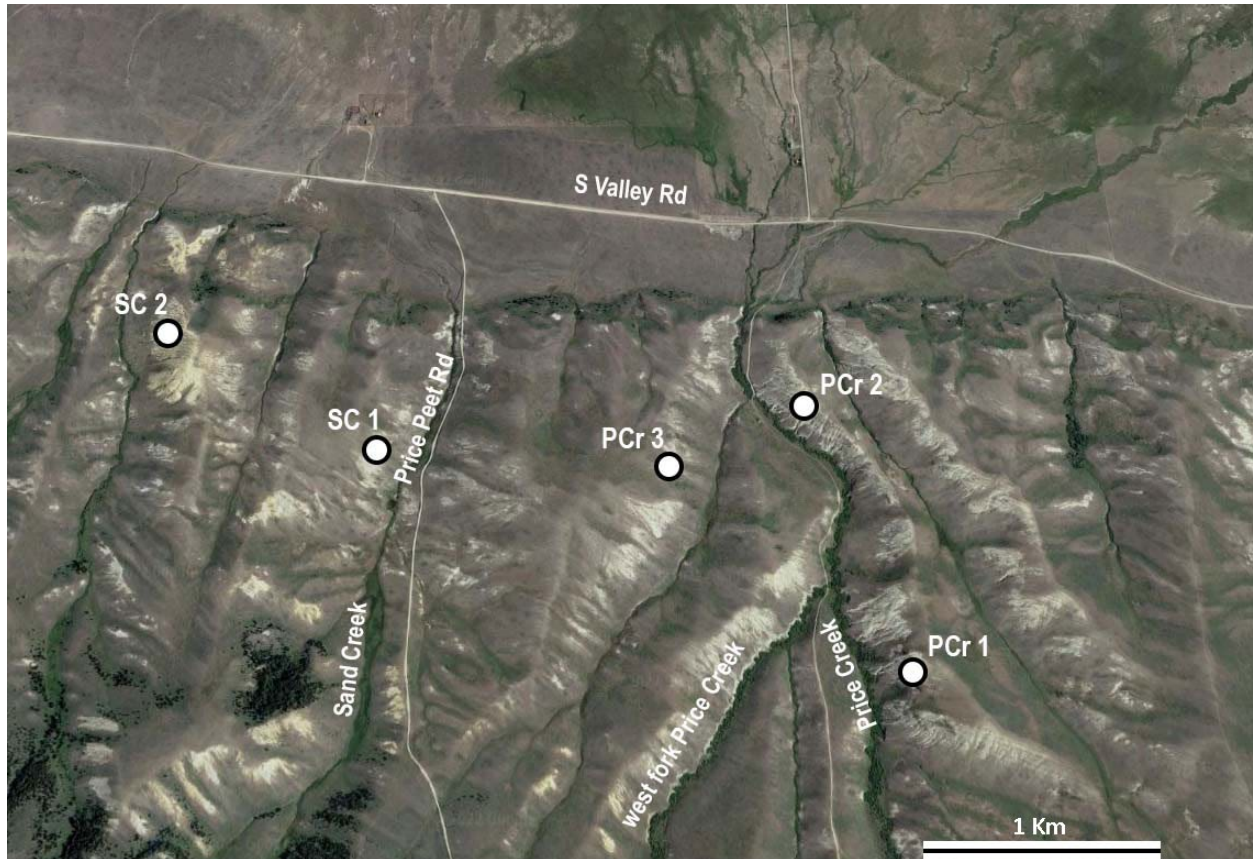


Figure 6.4. Collection site locations in the western Centennial Mountains (WCM); PCr and SC represent Price Creek and Sand Creek.



Figure 6.5. Map of site locations in the upper Ruby River valley (URR 1-4).

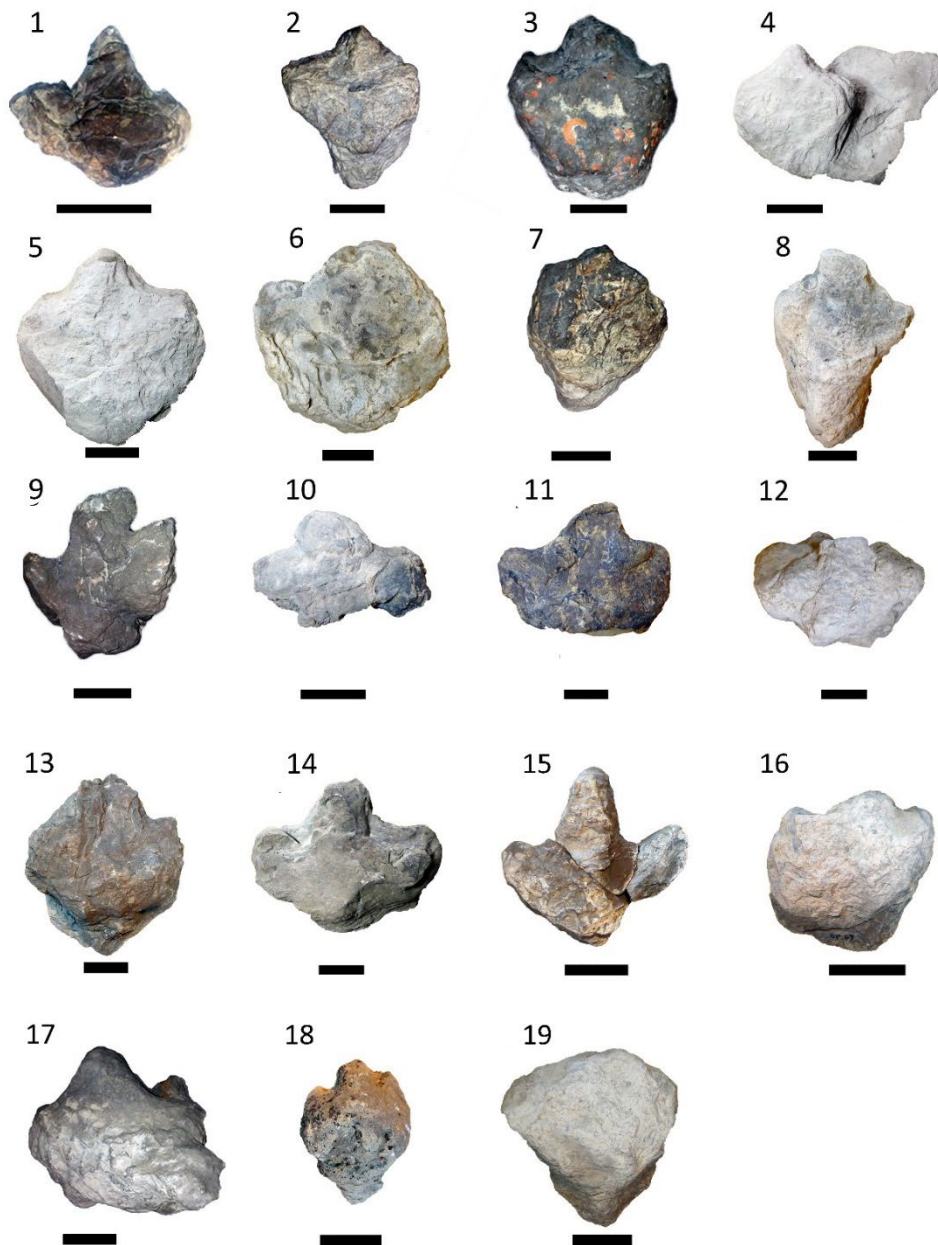


Figure 6.6. Ornithopod tracks from the Frontier Formation: 6.6.1) MOR 1644 1; 6.6.2) MOR 1644 5; 6.6.3) MOR 1644 9; 6.6.4) MOR 11766 RR 93; 6.6.5) MOR 11768 7; 6.6.6) MOR 11768 5; 6.6.7) MOR 1644 7; 6.6.8) MOR 11772 GP 66; 6.6.9) MOR 1644 6; 6.6.10) MOR 11768 4; 6.6.11) MOR 11768 3; 6.6.12) MOR 11766 RR 58; 6.6.13) MOR 1644 11; 6.6.14) MOR 11768 1; 6.6.15) MOR 1644 12; 6.6.16) MOR 1644 14; 6.6.17) MOR 11773 GP 72 ; 6.6.18) MOR 11773 GP 71; 6.6.19) MOR 1644 13. Scale bar=10 cm

Figure 6.7. Ornithopod track morphotypes based on tracks: 6.7.1) MOR 1644 5; 6.7.2) MOR 1644 5; 6.7.3) MOR 1644 9; 6.7.4) MOR 11768 4; 6.7.5) MOR 11768 3; 6.7.6) MOR 11768 1; 6.7.7) MOR 1644 12; 6.7.8) MOR 1644 10. Scale bar= 10 cm.

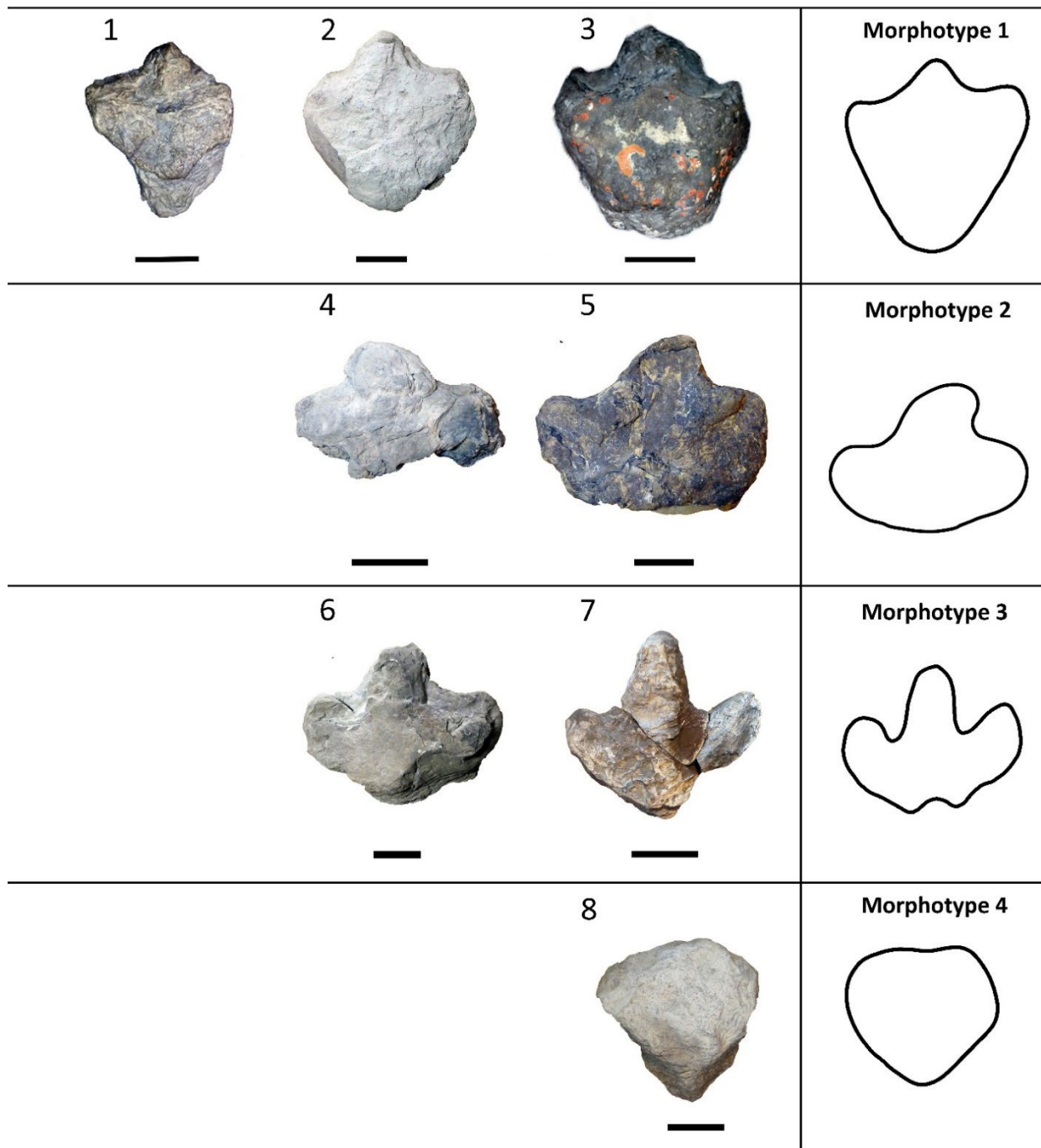


Figure 6.7. Ornithopod track morphotypes based on tracks: 1) MOR 1644 5; 2) MOR 1644 5; 3) MOR 1644 9; 4) MOR 11768 4; 5) MOR 11768 3; 6) MOR 11768 1; 7) MOR 1644 12; 8) MOR 1644 10. Scale bar= 10 cm.

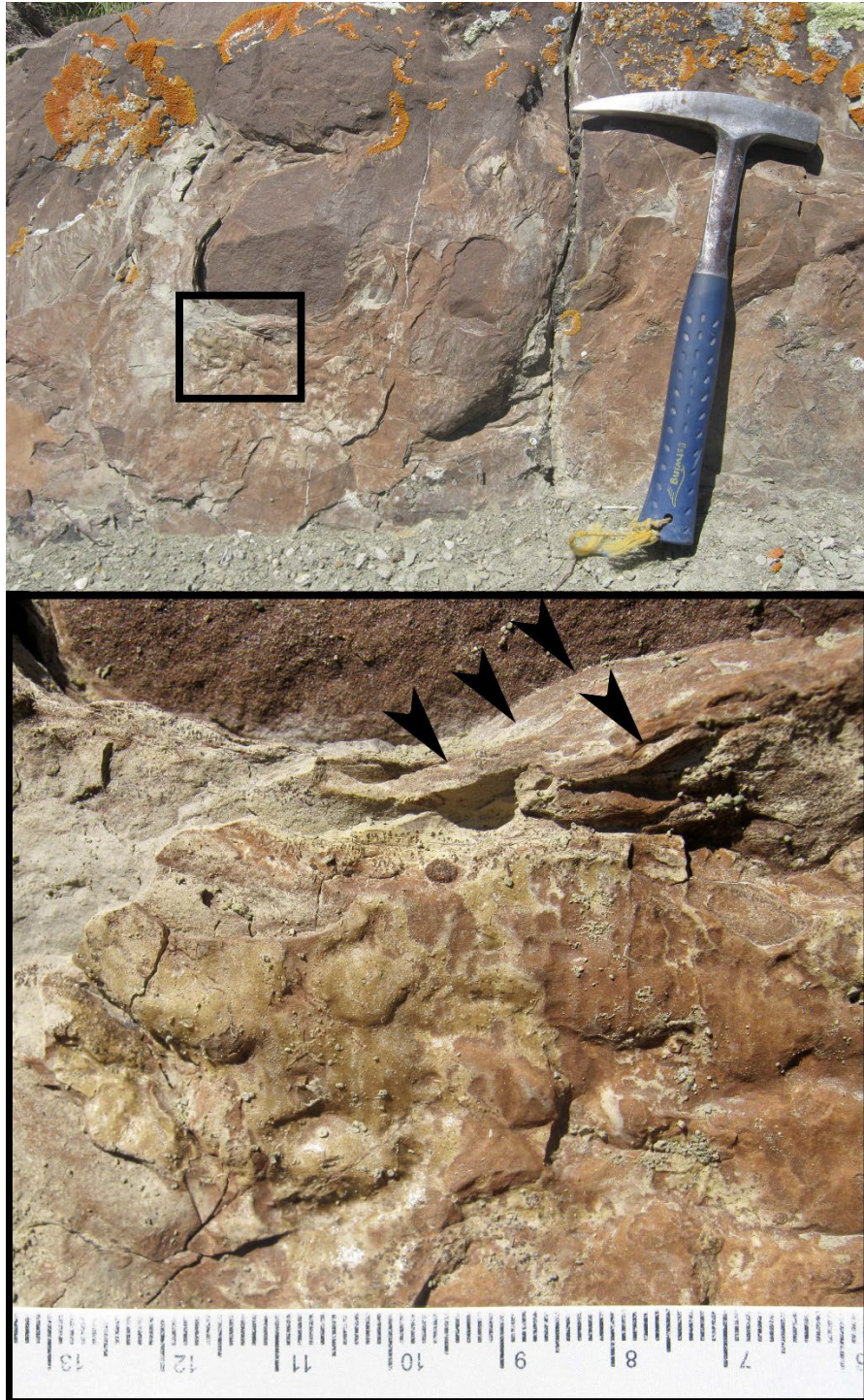


Figure 6.8. Track associated with soft sediment deformation structures. Note the thin, deformed laminae (black arrows) and the centimeter-scale load casts associated to the track outline.

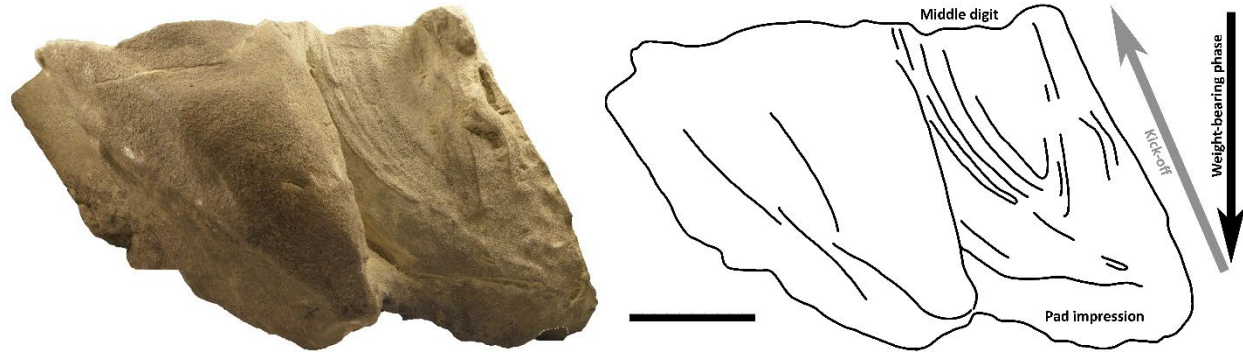


Figure 6.9. Ornithopod track MOR 1644 12 on side view displaying characteristic scale marks indicating vertically and highly inclined weight-bearing and kick-off phase movement of the autopod. Scale bar = 5 cm.



Figure 6.10. Ankylosaurian tracks: 1) MOR 1644 2; 2) MOR 1644 4; 3) MOR 11768 2; 4) MOR 11770 GP 64. Scale bar=10 cm.

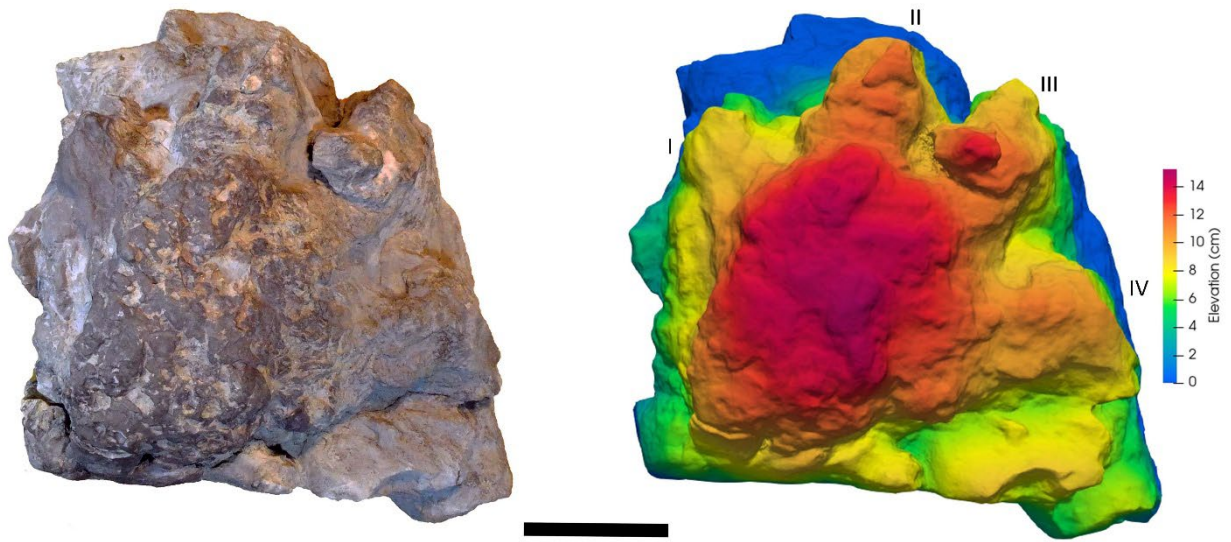


Figure 6.11. Color elevation map of track ankylosaurian MOR 1644 2. Scale bar 10 cm.

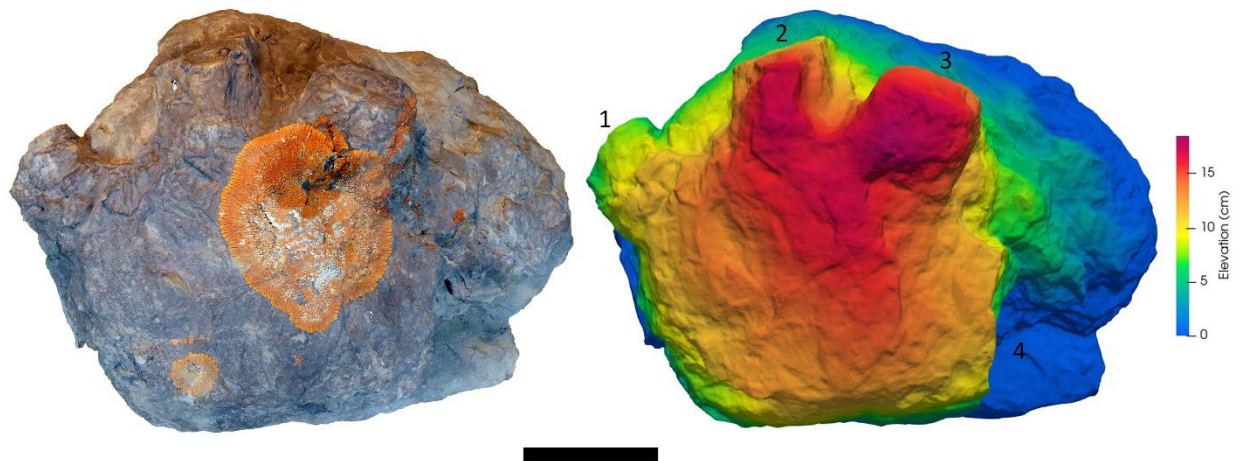


Figure 6.12. Color elevation map of track ankylosaurian MOR 1644 4. Scale bar 10 cm.

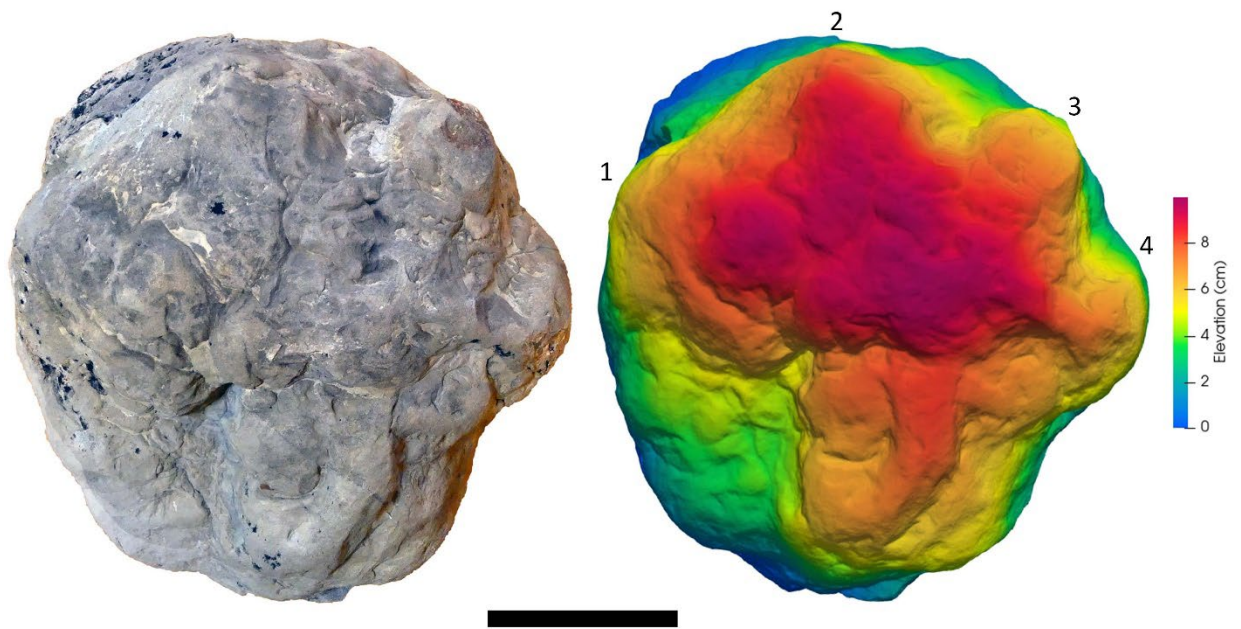


Figure 6.13. Color elevation map of ankylosaurian track MOR 11770 GP 64. Scale bar 10 cm.

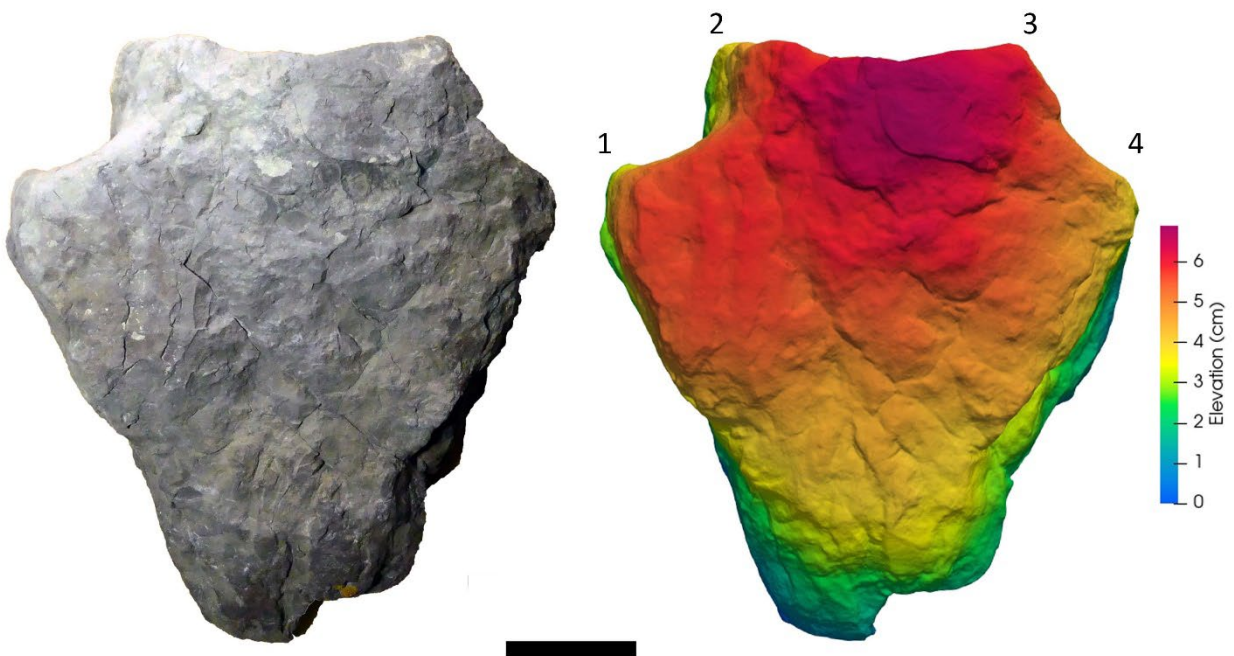


Figure 6.14. Color elevation map of ankylosaurian track MOR 11768 2. Scale bar 10 cm.

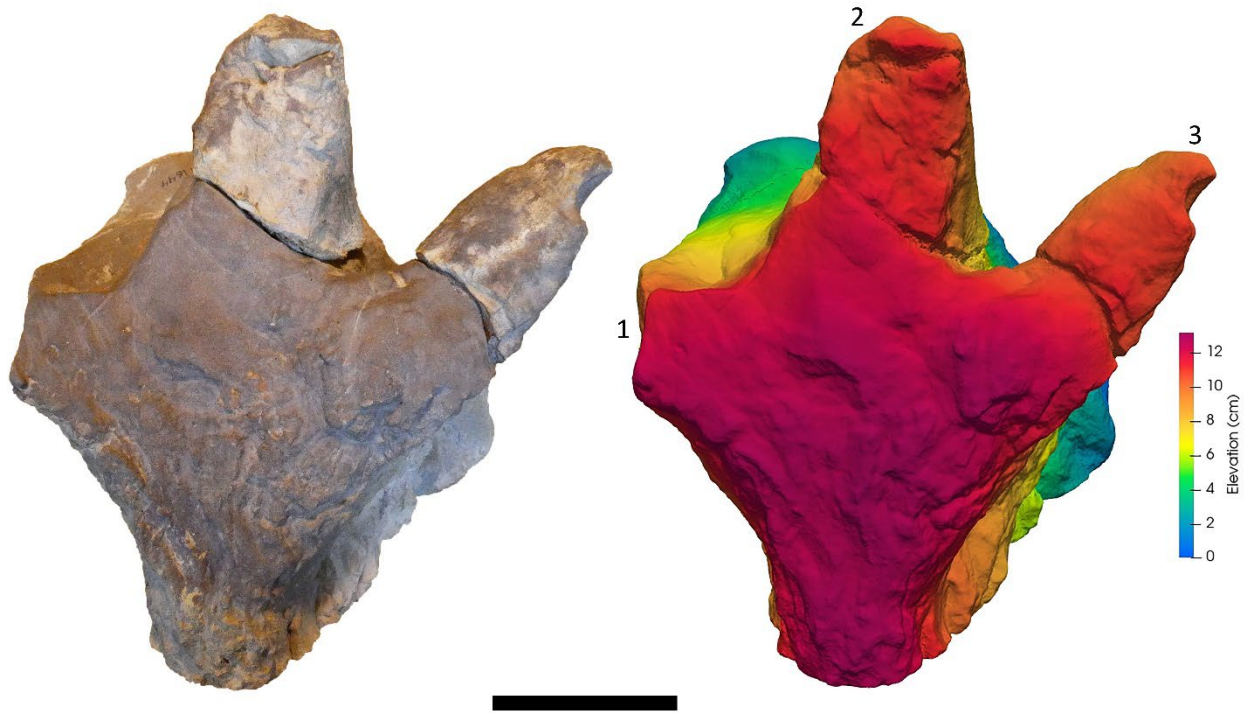


Figure 6.15. Color elevation map of theropod track MOR 1644 3. Scale bar 10 cm.

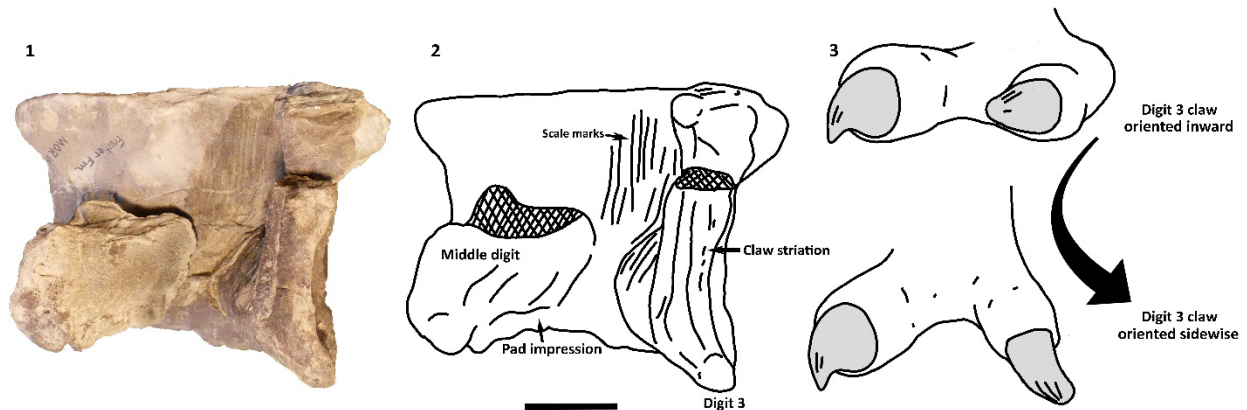


Figure 6.16. Block diagram showing 1) theropod track MOR 1644 3 in lateral view; 2) location of middle digit 2 (digit III) and side digit 3; 3) interpretation of digit 3 movement during weight-bearing phase. Black arrow indicates movement direction. Since the right or left nature of the foot is unknown this kinematic explanation accounts for two mutually possible scenarios considering digit 3 as being the medial digit II or the lateral digit IV. Scale bar= 10 cm.

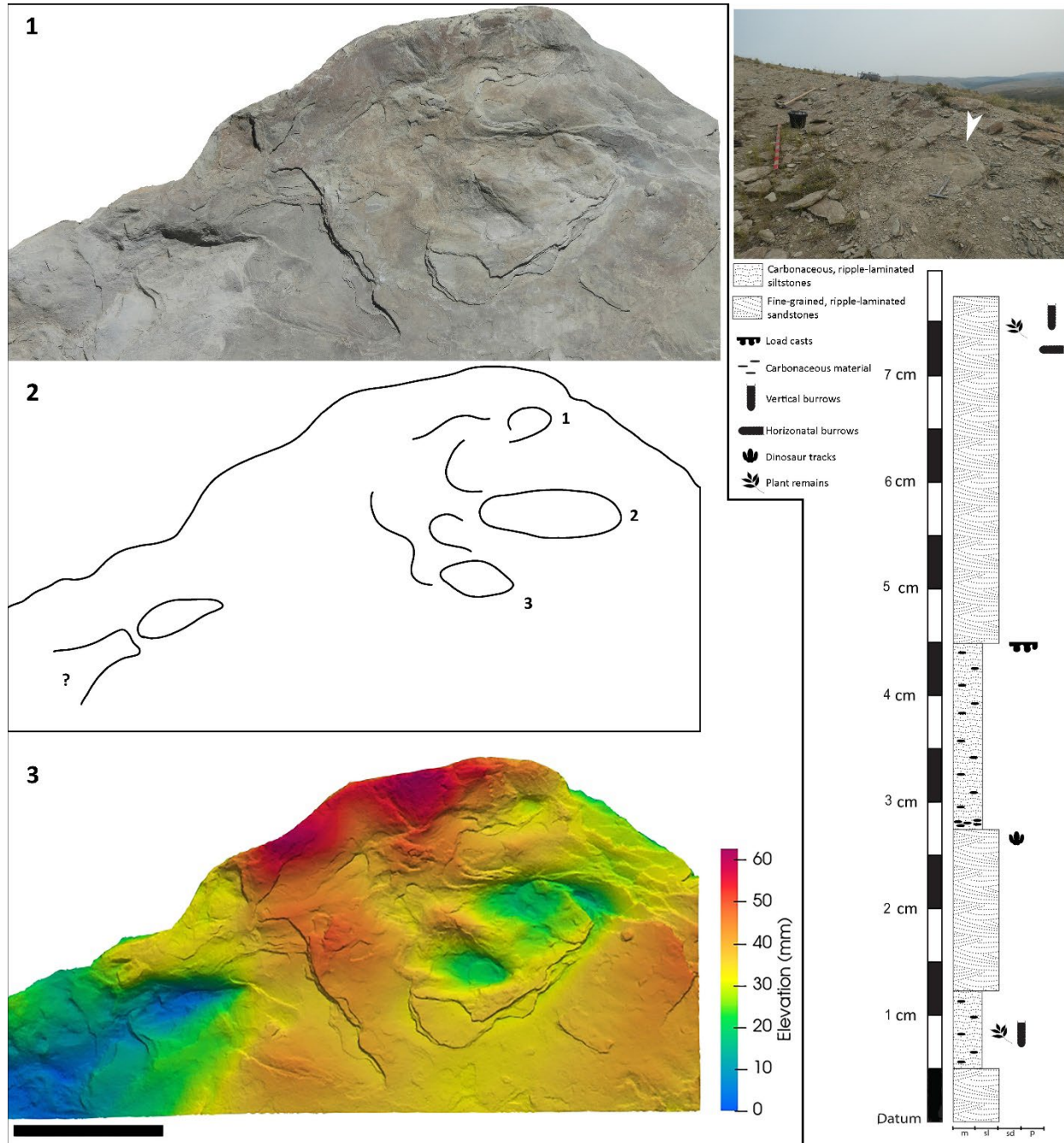


Figure 6.17. Track MOR 11767 RR 97 (white arrow) at UUR 4 with relative stratigraphic and lithological context. 6.17.1) Overview of track MOR 11767 RR 97 ; 6.17.2) interpretation map; 6.17.3) color elevation map. Scale bar= 15 cm.



Figure 6.18. Fragment of a thin, ripple-laminated sandstone showing centimeter-scale load cast structure at the base. The fragment derives from a bed directly overlaying the track-bearing horizon and the siltstone veneer.

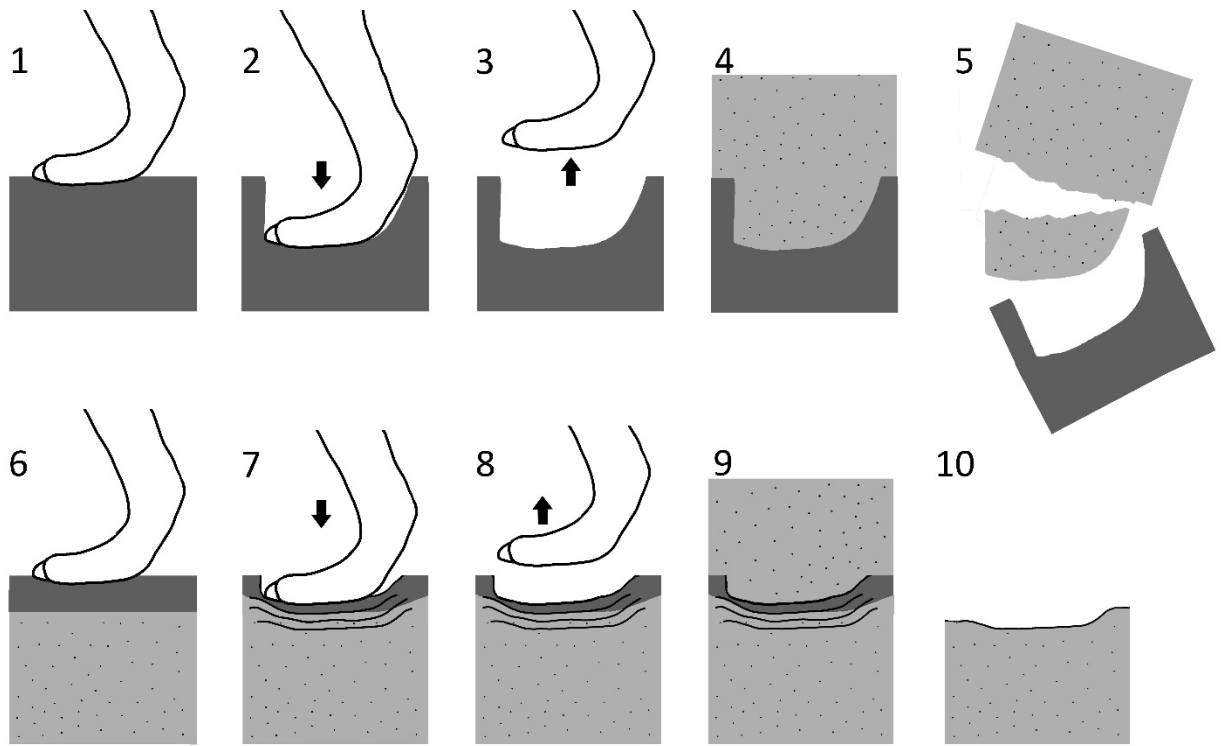
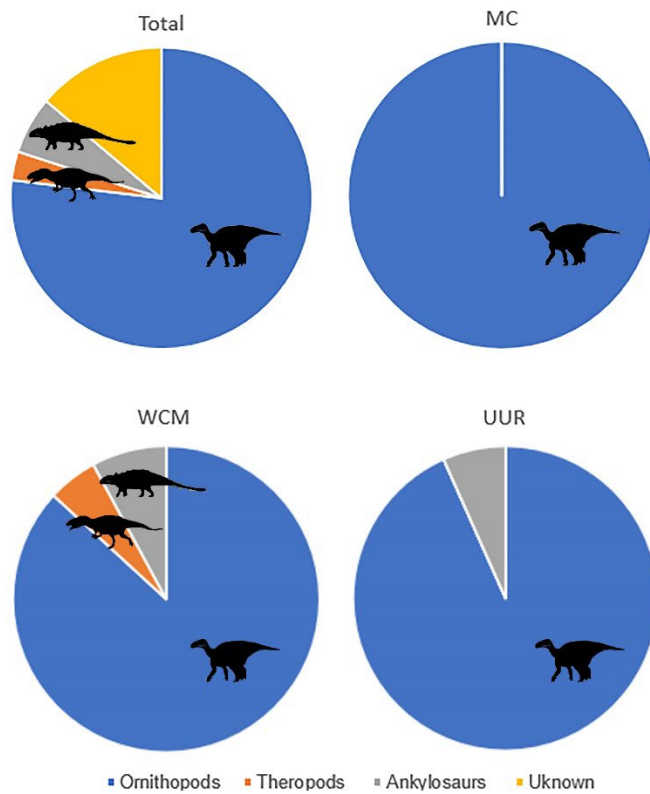


Figure 6.19. Block diagram showing preservation styles for Frontier Formation dinosaur tracks: 6.19.1-5) tridimensional casts; 6.19.6-10) epirelief undertracks; light gray dotted blocks indicate sandstone lithologies, dark gray blocks designate either mudstone or siltstones.



	MC	WCM	UUR
Ornithopods	3	33	14
Theropods	0	2	0
Ankylosaurs	0	3	1
Unknown	0	6	3
Total	3	44	18

Figure 6.20. Track maker abundance by number of tracks. Middle Creek (MC), western Centennial Mountains (WCM), upper Ruby River valley (URR).

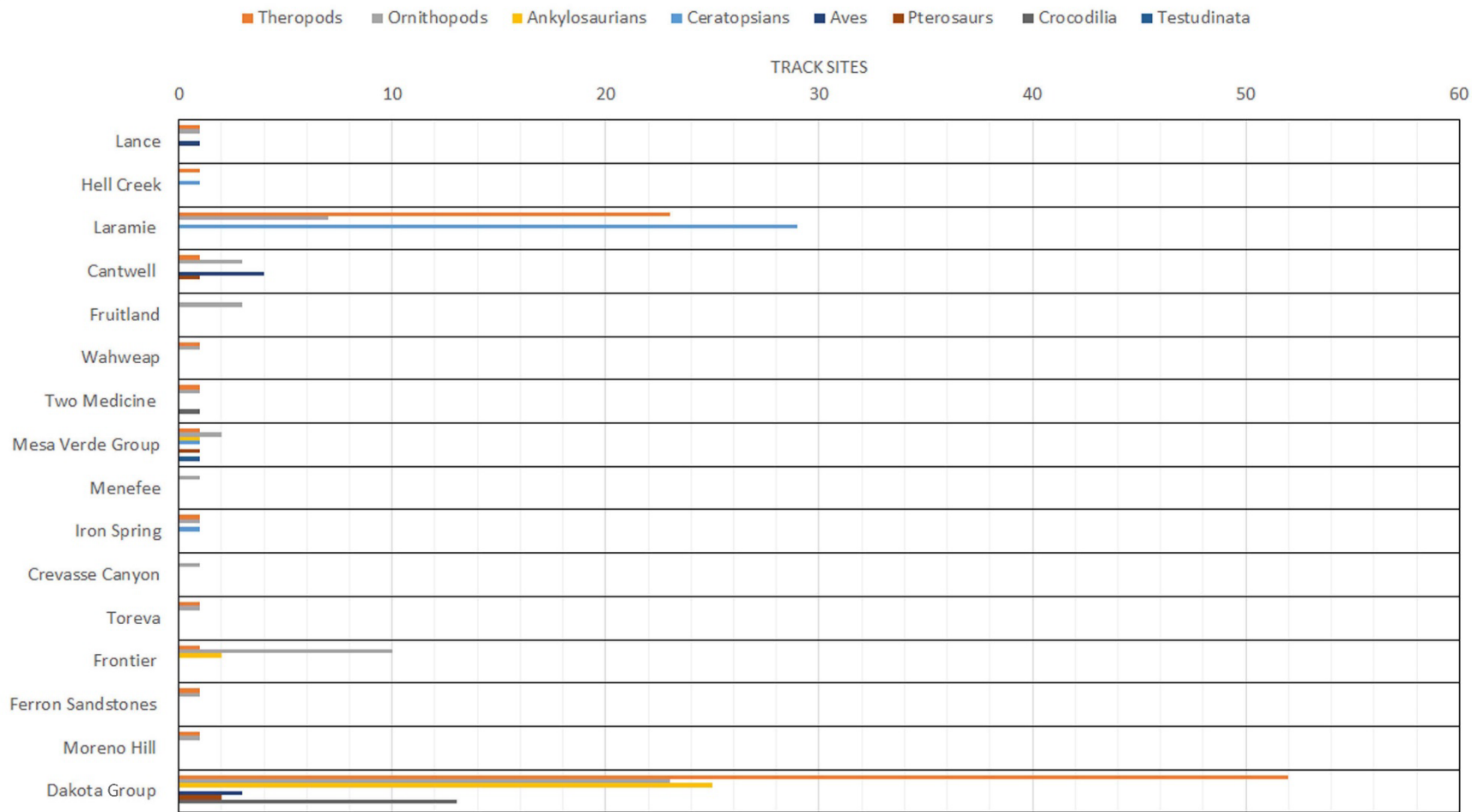


Figure 6.21. Track producer abundance by number of track sites. Data are from Albian-Maastrichtian formations of western USA.

Formation	Age	Theropods	Ornithopods	Ankylosaurians	Ceratopsians	Aves	Pterosaurs	Crocodylia	Testudinata	Reference
Lance	Maastrichtian	1	1	0	0	1	0	0	0	Lockley et al.,2004
Hell Creek	Maastrichtian	1	0	0	1	0	0	0	0	Lockley, 2014; Manning et al., 2008
Laramie	Maastrichtian	23	7	0	29	0	0	0	0	Lockley and Hunt, 1995
Cantwell	Maastrichtian	1	3	0	0	4	1	0	0	Fiorillo et al., 2009; Fiorillo et al., 2011; Fiorillo et al., 2014; Fiorillo et al., 2018
Fruitland	Campanian-Maastrichtian	0	3	0	0	0	0	0	0	Wolberg et al., 1988; Williamson, 2000; Hunt and Lucas, 2003; Lucas et al., 2011
Wahweap	Campanian	1	1	0	0	0	0	0	0	Simpson et al.,2011
Two Medicine	Campanian	1	1	0	0	0	0	1	0	Lockley, 2014;
Mesa Verde Group	Campanian	1	2	1	1	0	1	0	1	Parker and Balsley, 1989; Parker and Rowley, 1989; Lockley and Hunt, 1998; Lockley et al., 1983; Carpenter, 1992; Lockley et al., 2011; Simpson et al., 2011; Lockley et al., 2018
Menefee	late Santonian-early Campanian	0	1	0	0	0	0	0	0	Lucas et al.,2006
Iron Spring	Santonian	1	1	0	1	0	0	0	0	Milner et al., 2006
Crevasse Canyon	Santonian	0	1	0	0	0	0	0	0	Lucas et al.,2016
Toreva	Coniacian	1	1	0	0	0	0	0	0	Irby and Albright, 2002
Frontier	Turonian-Coniacian-Santonian	1	10	2	0	0	0	0	0	Hamblin et al.,2000; Panascí et al. 2021; This paper
Ferron Sandstones	Turonian	1	1	0	0	0	0	0	0	Gierlinski and Lockley,2013
Moreno Hill	Turonian	1	1	0	0	0	0	0	0	Wolf,2006
Dakota Group	late Albian-early Cenomanian	52	23	25	0	3	2	13	0	Lockley et al.,2006a; Noffke et al.,2019; Lockley et al., 2021

Figure 6.22. Abundances break down from middle and Upper Cretaceous formations exposed in western USA.

Location	Site	Catalog Number	Field number
MC	-	-	LP 73
MC	-	-	LP 74
MC	-	-	LP 75
WCM	PCr1	MOR 1644 1	-
WCM	PCr1	MOR 1644 2	-
WCM	PCr1	MOR 1644 3	-
WCM	PCr1	MOR 1644 4	-
WCM	PCr1	MOR 1644 5	-
WCM	PCr1	MOR 1644 6	-
WCM	PCr1	MOR 1644 7	-
WCM	PCr1	MOR 1644 8	-
WCM	PCr1	MOR 1644 9	-
WCM	PCr1	MOR 1644 10	GP 40
WCM	PCr1	MOR 1644 11	GP 41
WCM	PCr1	MOR 1644 12	GP 54
WCM	PCr1	MOR 1644 14	GP 69
WCM	PCr1	MOR 1644-13	GP 70
WCM	PCr1	MOR 1644-15	GP 68
WCM	PCr1	-	GP 42
WCM	PCr1	-	GP 53
WCM	PCr1	-	GP 84-1
WCM	PCr1	-	GP 38
WCM	PCr1	-	GP 61
WCM	PCr1	-	GP 80-1
WCM	PCr1	-	GP 80-2
WCM	PCr1	-	GP 80-3
WCM	PCr1	-	GP 83
WCM	PCr1	-	GP 35
WCM	PCr1	MOR 11773 GP 71	GP 71
WCM	PCr1	MOR 11773 GP 72	GP 72
WCM	PCr2	-	GP 84-2
WCM	PCr2	MOR 11769 GP 33	GP 33
WCM	PCr2	-	GP 14
WCM	PCr2	MOR 11774 GP15	GP 15
WCM	PCr2	MOR 11774 GP 16	GP 16
WCM	PCr2	MOR 11771 GP 18	GP 18
WCM	PCr1	-	GP 19
WCM	PCr3	MOR 11770 GP 64	GP 64
WCM	PCr3	MOR 11770 GP 65	GP 65
WCM	PCr3	MOR 11772 GP 66	GP 66
WCM	SC1	-	GP 76
WCM	SC1	-	GP 77
WCM	SC1	MOR 11938 GP 1	GP 1
WCM	SC2	-	GP 6
WCM	SC2	-	GP 78
URR	URR1	MOR 11766 RR 58	RR 58

URR	URR1	MOR 11766 RR 93	RR 93
URR	URR2	-	RR 85
URR	URR2	-	RR 86
URR	URR2	-	RR 87
URR	URR2	-	RR 88
URR	URR2	-	RR 89
UUR	URR3	-	RR 92
URR	URR3	MOR 11768 1	RR 90
URR	URR3	MOR 11768 2	RR 94
URR	URR3	MOR 11768 3	RR 95
URR	URR3	MOR 11768 4	RR 96
URR	URR3	MOR 11768 RR 98	RR 98
URR	URR3	MOR 11768 5	RR 100
URR	URR3	MOR 11768 6	RR 101
URR	URR3	MOR 11768 7	RR 102
URR	URR4	MOR 11767 RR 97	RR 97
URR	URR4	-	RR 99
URR	URR4	-	RR104

Table 6.1. Track location list: Lima Peaks (LP), Western Centennial Mountains (WCM), upper Ruby River valley (URR), Middle Creek (MC), Price Creek PCr, Sand Creek (SC). Specimens that are collected have a MOR (Museum of the Rockies) catalog number.

Catalog Number	Field Number	D1W	D1 L	D2 W	D2 L	D3 W	D3 L	Div1	Div 3	Width	Length	PL/PW	Depth
MOR 1644 1	-	6.50	10.00	6.50	8.50	?	?	48.00	?	?	7.50	?	5.00
MOR 1644 5	-	7.5	8	9	10	?	?	36	35	~22	21	0.95	11
MOR 1644 6	-	5	7	9	12	5.5	11	35	27	22	22	1	12
MOR 1644 7	-	?	?	?	?	?	?	?	?	~9	~21	?	8.5
MOR 1644 8	-	?	?	?	?	?	?	?	?	23	21	0.91	19
MOR 1644 9	-	9.9	15	~12	17	~7	~7	44	40	31	30	0.96	6
MOR 1644 10	-	11	10	13	10	12	~9	55	47	26	~22	~0.83	~16
MOR 1644 11	-	?	?	?	?	?	?	?	?	28	27	0.96	16
MOR 1644 12	-	10	7.5	16.5	10.5	13	6.9	45	50	25	26	0.96	15
MOR 1644 13	-	?	?	?	?	?	?	?	?	26	~20	~0.76	14
MOR 1644 14	-	?	?	?	?	?	?	?	?	23	~20	~0.86	28.7
MOR 11772 GP 66	GP 66	10.3	~13	8.9	~16	7.5	~13	45	60	26.1	~23	0.80	14.2
MOR 11938 GP 1	GP 1	?	?	?	?	?	?	~43	~44	31.2	30.0	0.95	~19
MOR 11733 GP 71	GP 71	?	?	?	?	?	?	?	?	25.1	21.3	0.84	10.4
MOR 11733 GP 72	GP 72	?	?	?	?	?	?	?	?	19.9	18.9	0.95	15.9
see (Panasci et al., 2021)	Track 2	?	?	5.5	?	?	~13	31	52	33	27	0.81	19.5
-	GP 19	?	?	?	?	?	?	?	?	?	31.4	?	~11
-	GP 42	?	?	?	?	?	?	?	?	25.7	~23	~0.88	21
-	GP 53	7.9	11.1	8.4	13.2	5.1	10.4	24	31	34.4	32.9	0.93	~2
-	GP 84-1	?	?	?	?	?	?	44	?	~27.5	27.4	~0.98	~10
-	GP 14	?	?	?	?	?	?	?	?	~20	22.2	?	?
-	GP 38	?	?	?	?	?	?	?	?	26.6	~25	?	~17
-	GP 80-2	?	?	?	?	?	?	?	?	~30	~24	?	~18
-	GP 80-3	?	?	?	?	?	?	?	?	26.5	26.0	0.98	19
-	GP 83	?	?	?	?	?	?	?	?	~24	~21	?	~2
-	GP 35	?	?	?	?	?	?	?	?	~40	35.5	?	19
-	GP 84-2	?	?	?	?	?	?	?	?	~30	?	?	~9
-	GP 77	?	?	?	?	?	?	?	?	33.0	22.5	?	~12
-	GP 6	?	?	?	?	?	?	?	?	~44	~40	~0.90	~15
-	GP 78	?	?	?	?	?	?	?	?	~24	~22	?	9
-	LP 73	?	?	?	?	?	?	?	?	~28	~22	~0.78	~10
-	LP 74	?	?	?	?	?	?	?	?	~14	~20	~0.70	~19
-	LP 75	?	?	?	?	?	?	?	?	~20	~31	?	~7
MOR 11766 RR 58	RR 58	?	?	?	?	?	?	?	?	27.6	?	?	11.1
MOR 11766 RR 93	RR 93	?	?	?	?	?	?	50.1	60.0	25.0	23.5	0.92	10.7
MOR 11768 1	RR 90	?	?	?	?	?	?	?	?	~37	?	?	~13
MOR 11768 3	RR 95	?	?	?	?	?	?	?	?	37.40	~25	0.66	~14
MOR 11768 4	RR 96	?	?	?	?	?	?	?	?	?	?	?	?
MOR 11769 5	RR 100	?	?	?	?	?	?	?	?	~37.5	37	?	8.9

MOR 11768 6	RR 101	?	?	?	?	?	?	?	?	44.0	34.30	0.77	18.0
MOR 11768 7	RR 102	?	?	?	?	?	?	?	?	32	25.3	0.78	~11
-	RR 85	?	?	?	?	?	?	?	?	~25	?	?	17.1
-	RR 86	?	?	?	?	?	?	?	?	~22	?	?	~9
-	RR 87	?	?	?	?	?	?	?	?	~28	?	?	17.9
-	RR 88	?	?	?	?	?	?	?	?	~23.5	?	?	12.4
-	RR 89	?	?	?	?	?	?	?	?	?	~28	?	17.9
-	RR 99	?	?	?	?	?	?	?	?	23	19	0.82	~4

Table 6.2. Ornithopod track measurement.

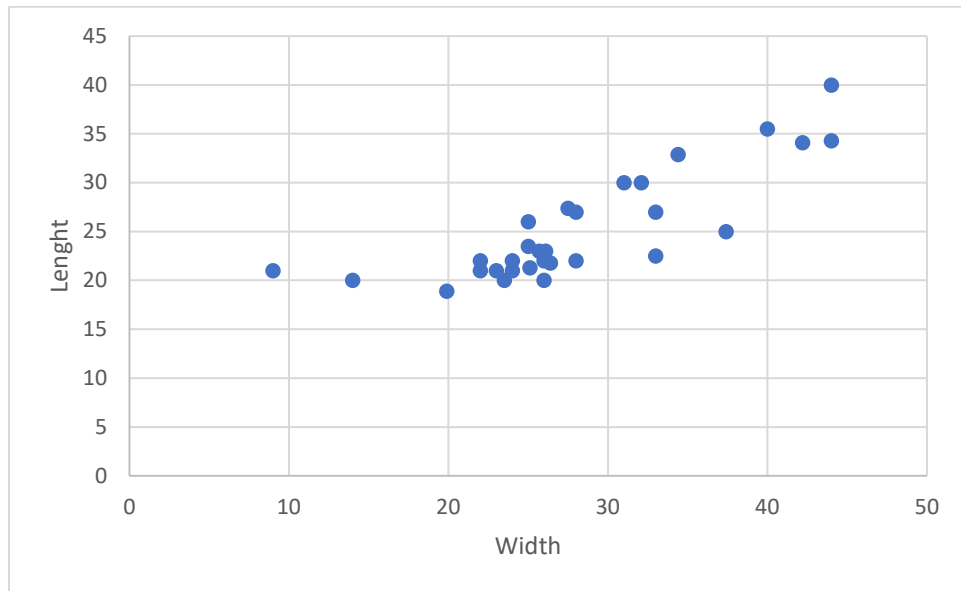


Table 6.3. Frequency distribution of ornithopod tracks from the Frontier Formation with respect to width and length (N = 30). Measurements are in centimeters.

#	D I W	D I L	D II W	D II L	D III W	D III L	D IV W	D IV L	Div I	Div II	Div III	Div IV	Wid th	Leng th	PL/P W	Dept h
MOR 1644 2	4.5	10	7	12	7	13	9	~10.5	60	33	11	40	29	31	-	15
	D I W	D I L	D 2 W	D 2 L	D 3 W	D 3 L	D 4 W	D 4 L	Div 1	Div 2	Div 3	Div 4	Wid th	Leng th	PL/P W	Dept h
MOR 1644 4	5.8	~7.5	6	~9	7.5	9	10	?	52	25	71	11	18	16	-	16
MOR 11770 GP 64	~9	~13.7	~8	~16.5	7.3	17	~6	11	53	13	35	80	31	28	-	9.30
MOR 11768 8 2	~11	~10	~15.5	~13	?	~8	?	?	40	22	30.8	60.5	43.4	46.4	-	7.9

Table 6.4. Ankylosaurian track measurements.

Catalog Number	D 1 W	D 1 L	D 2 W	D 2 L	D 3 W	D 3 L	Div 1	Div 3	Width	Length	PL/PW	Depth
Track 4 see (Panasci et al., 2021)	3.8	?	4	9.5	?	?	?	?	15	27	1.8	16.7
MOR 1644 3	?	?	8	~12	5.5	11	?	44	?	~18	?	13

Table 6.5. Theropod track measurements.

Table 6.6. Epi-relief track measurements.

Catalog Number	D 1 W	D 1 L	D 2 W	D 2 L	D 3 W	D 3 L	Div 1	Div 3	Width	Length	PL/PW	Depth
MOR 11767 RR 97	~3.5	12.4	5.9	~15	5.4	11.6	35	26	18.9	~21	1.11	~1

	Albian- Cenomanian	Albian- Cenomanian	Cenomanian	Albian- Cenomanian	Turonian	Turonian- Coniacian	Upper Coniacian
	Blackleaf Fm. (Vaughn Member)	Wayan Fm.	Willow Tank Fm.	Cedar Mtn Fm. (Mussentuchit Member)	Moreno Hill Fm.	Frontier Fm.	Niobrara Fm. (Lower Smoky Hill Member)
Dinosaurs							
Theropoda						X*	
Dromeosaurids	X	X	X	X			
Tyrannosauroids	X	X	X	X	X		
Terizynosaurus					X		
Ornithopoda							
Hadrosauroids				X	X	X*	
Hadrosaurids						X*	X
Orodrominae	X			X			
Iguanodontid ind.		X	X	X			
Thyreophorans							
Ankylosaurian	X	X	X	X		X*	X
Sauropoda			X	X			
Ceratopsians				X	X		
Crocodylians		X	X		X	X	
Bernissartia	X			X			
Goniopholidids							
Atoposaurids				X			
Pholidosaurids				X			
Pterosaurs							X
Turtles							
Glyptops	X						
Chelydrids	X						
Naomichelys			X				
Neurankylus						X	
Testudines ind.		X			X		
Amphibians							
Lissamphibians				X			
Fish							
Neopterygiians	X	X		X			
Amiiforms				X			
Mylobatiforms				X			
Semionotiforms				X			
Lepisosteiforms				X			
Pycnodontiforms				X			
Ceratodus			X				
Mammals		X		X			

Table 6.7. Fossil record comparison between the Frontier Formation and middle Cretaceous Formation from western USA. Asterisks indicate ichnofossil record.

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CONCLUSIONS

The Frontier Formation in southwestern Montana is comprised of a thick, non-marine, fluvial succession deposited in a broad alluvial plain during the Late Cretaceous. Coniacian deposits of the middle and upper Frontier Formation are rich in both assigned to vertebrate and invertebrate trace fossils, but body fossils are relatively. Vertebrate trace fossils include dinosaur tracks. Invertebrate traces include vertical and horizontal meniscated burrows, vertical non-meniscated burrows, sinusoidal trails, and resting traces. Body fossils are comprised of gastropods and bivalve shells, dinosaur eggshells, plant remains, dinosaurian and non-dinosaurian bone material. Lithofacies distribution and fossil preservation varies from southwest to northeast in the studied area. In the west, in the Lima Peaks area, body fossils occur in mudstone lithofacies interpreted as calcareous paleosols that characterize dominantly coarse successions. In the east, body fossils are primarily preserved in floodplain overbank lithofacies from deposits set by traction currents, suspension, and decanting.

Dinosaur tracks and invertebrate traces occur in both western and eastern localities in fine-grained, sandstone, siltstone, and mudstone lithofacies. Dinosaur tracks are particularly abundant in more eastern facies of the western Centennial Mountains and the upper Ruby River valley. Lithofacies distribution and fossil content suggest that the Coniacian deposits of the Frontier Formation was deposited in more proximal and distal settings of a broad coastal alluvial plain extending from the thrust belt in the west to the Cody Sea in the east. Rapid sedimentation and subsidence rates, avulsion, sediment reworking, and emplacement of local low-energy, ponding environments characterized the Frontier Formation deposition, especially in more eastern distal alluvial settings. The trace fossil record suggests a diverse fauna consisting of derived

hadrosauriform, ankylosaurian, and theropod dinosaurs that inhabited a lush, seasonal, coastal plain. Freshwater ponds and pools provided suitable environments for turtles, crocodilians, insects, bivalves, gastropods, crustaceans, and nematode worms. The Coniacian Frontier Formation paleocommunity reflects a diverse middle Cretaceous fauna with endemic elements observed in Campanian and Maastrichtian formations of western North America. The Frontier Formation fauna represents one of the few Coniacian non-marine fossil records reported from North America. The presence of endemic groups of turtles in the Frontier Formation suggest a trend towards endemism and faunal provincialism taking place in southwestern Montana during Coniacian.

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