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Miocene Ichnofaunas and Mammalian Communities in the Great Basin Region, Nevada and California

AnnMarie R. Jones

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MIOCENE ICHNOFAUNAS AND MAMMALIAN COMMUNITIES IN THE GREAT BASIN
REGION, NEVADA AND CALIFORNIA.

By

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A dissertation submitted in partial fulfillment
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Abstract

The purpose of this dissertation is to document and interpret three new ichnofaunas and two fossil assemblages from the Neogene of Nevada and California. Ichnofossils are important for understanding behavior and geographical range of animals in the distant past and are key to locating and preserving sensitive material for future studies. I examined ichnofauna at three localities: two within the Mio-Pliocene Muddy Creek Formation of Nevada, and one within the Miocene China Ranch Beds of California. My research focuses primarily on (1) camelid and ursid ichnotaxa and how these new localities help in understanding the evolutionary history of these taxa within the southwestern United States, and (2) the composition and structure of mammalian communities in the Great Basin region during the Mid-Miocene Climatic Optimum.

Chapter 1 documents a new camelid trackway locality in the Muddy Creek Formation, exposed near Flat Top Mesa in Mesquite, Nevada. Using a combination of field and photogrammetric analysis, I document the presence of 40 prints within a thin layer of limestone. The average length of these prints is 135 mm. I refer these camelid tracks to the ichnotaxon *Lamaichnum* isp. In comparison to older camelid tracks, the Flat Top Mesa tracks are larger on average, which reinforces a previously recognized trend of increasing camelid body size through the Neogene.

In Chapter 2, I document and interpret a more diverse ichnofauna within the Muddy Creek Formation at the informally named Muddy Creek Canyon locality near Overton, Nevada. This ichnofauna consists of camelid, ursid, felid, equid, and avian tracks. While most of the tracks are isolated in float or on the undersides of overhanging ledges, two camelid-trackway bedding-plane exposures are documented and analyzed. The camelid tracks at this locality exhibit extramorphological variation as *Lamaichnum* isp. and are smaller on average than the

camelid tracks at the Flat Top Mesa locality. When combining the Muddy Creek Canyon data with the Flat Top Mesa camelid track length data, the average length is 120 mm for the entirety of the Muddy Creek Formation. The depositional environment is interpreted to be the shoreline of an ephemeral lake.

Chapter 3 documents an ichnofauna consisting of camelid and ursid tracks within the Miocene China Ranch Beds of southeastern California. While camelid tracks are known from these beds, the ursid tracks are new and are possibly some of the oldest ursid tracks within the United States. They document the first known occurrence of a galloping gait in ursids. The depositional environment is interpreted to be similar to that of the Muddy Creek Formation at the shoreline of an ephemeral lake. The Muddy Creek Canyon ichnofauna diversity is typical for Miocene ichnofaunas and is higher than the China Ranch Beds ichnofauna diversity. Therefore, it is possible new tracks in the China Ranch Beds may be exposed in the future and monitoring of this site is suggested.

Chapter 4 analyzes and compares two mammalian assemblages that document species richness through the Mid-Miocene Climatic Optimum. A combination of changing climate and topography influenced the transition from warmer wooded ecosystems to cooler grasslands. In general, mammalian species richness declined after the MMCO. Carnivore species richness was surprisingly high in both faunas while herbivore species richness was not.

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Chapter 1: A Camelid Tracksite in the Mio-Pliocene Muddy Creek Formation Near Mesquite, Nevada

1.1 Abstract

This chapter documents a new camelid trackway locality in the Muddy Creek Formation, exposed near Flat Top Mesa in Mesquite, Nevada. Photogrammetric models are used to analyze and document two exposures. These digital models make it possible for more tracks to be visible than what is seen in the field. Altogether, there are 40 camelid prints at this locality within a thin and friable layer of limestone. With an average track length of 135 mm, I refer these camelid tracks to the ichnotaxon *Lamaichnum* isp. In comparison to older camelid tracks, the Flat Top Mesa tracks are larger on average, which reinforces a previously recognized trend of increasing camelid body size through the Neogene. The Muddy Creek Formation is emerging as an important source of Neogene fossil trackways.

1.2 Introduction

Camelid footprints are abundant in Neogene deposits of North America. They first appear in the Oligocene, and they range from Mexico to Canada (Lucas and Hunt, 2007). They are especially abundant in the Mojave Desert region where camelid morphological evolution is evident in fossil bones and trackways found in the Barstow, Avawatz, Horse Spring, and Muddy Creek formations, among others (Lockley and Hunt, 1995; Sarjeant and Reynolds, 1999; Jones, 2002; Lofgren et al., 2006; Lucas and Hunt, 2007); a gradual increase in average foot size is evident in tracks seen in these formations. In this study, I document a previously undescribed fossil tracksite near Flat Top Mesa near Mesquite, Nevada (Figs. 1.1, 1.2). This new tracksite

contributes to the plethora of North American Neogene camelid footprint occurrences and will help build a more complete picture of camelid autecology and behavior.

Camel evolution is well documented in the Cenozoic fossil record of North America, following trends similar to those seen in horses; Eocene ancestors with small body sizes and undifferentiated morphologies evolved into much larger animals with a reduced number of toes and other specialized features by the end of the Pliocene (Gauthier-Pilters and Dagg, 1981). Rapid radiation in the Miocene transformed camelids into the familiar taxa that we know today (Lucas and Hunt, 2007). The Miocene uptick in evolutionary pressure is generally interpreted to have been driven by the spread of grasslands (Janis, 1993). The camel foot evolved from having five toes to having two toes with nails and two pads connected by a septum (Arnautovic and Abdalla, 1969; Sarjeant and Reynolds, 1999) (Fig. 1.3). Camelid footprints are distinctive in that the anterior tips (or ‘toes’) are either parallel or divergent, whereas the digits of other artiodactyl toes are convergent (Sarjeant and Reynolds, 1999). Camelid footprints are typically heart shaped due to the animals walking on the palms of their feet, not just on their toes, unlike other artiodactyls (Sarjeant and Reynolds, 1999) (Fig. 1.4).

The Flat Top Mesa Tracksite is in the late Miocene Muddy Creek Formation. A total of 40 camelid footprints occur within three exposures of the same bedding plane: Exposures A and B (Fig. 1.2), and Exposure C (Fig. 1.5). Exposure C occurs several meters downslope from Exposures A and B and contains only one truncated print. These exposures occur within a limestone bed that is mostly covered by a soil crust. The friability of this limestone makes removal of the tracks impossible. In this study, I used a combination of 3D photogrammetric models and singular photographs to identify the ichnotaxa and to document and interpret the tracksite.

1.3 Geologic Setting and Previous Work

The Muddy Creek Formation was deposited during the Hemphillian North American Land Mammal Age (Reynolds and Lindsay, 1999), which straddles the Miocene and Pliocene epochs; from about 4.8 Ma to 9 Ma (Lindsay et al., 2002; Tedford et al., 2004). The formation is exposed throughout southeastern Nevada, from Moapa Valley to Mesquite. Age constraints are not precise for individual exposures, given the stratigraphically complex nature of the formation (Muntean, 2012). In some areas, the formation is unconformably capped by a petrocalcic horizon that is typically 2-5 meters thick (Gardner, 1972; Williams, 1996). This interval forms the cap on Flat Top Mesa, near the tracksite. The depositional environment of the Muddy Creek Formation has been interpreted to have been fluvial and lacustrine, with small streams and lakes scattered across an expansive sandy plain (Williams, 1996).

The Flat Top Mesa section consists of deposits within the upper part of the Muddy Creek Formation. The strata in this area have been interpreted to mainly be the products of fluvial processes. The sediments originated in the Caliente Caldera complex, north of the field area, and they filled the Mesquite basin following Basin-and-Range extension (Kowallis and Everett, 1986; Forrester, 2009; Muntean, 2012). Deposition of these sediments occurred in several small basins that eventually combined into one large basin (Reynolds and Lindsay, 1999). Kowallis and Everett (1986) analyzed the sediments in the Mesquite area and described them as basin-fill, immature, poorly to well sorted, coarse to fine grained, light pink to orange, mudstones, siltstones, and sandstones. They interpreted the environment to have fluctuated between dry and wet playas with evaporites and long periods of standing water. Temperatures were slightly cooler with more rainfall than today, and the topography was less hilly. They concluded that correlation of beds over long distances is not possible because beds pinch out

quickly and are not laterally continuous. Analysis of the deposits in this area must be studied in road cuts and washes where they are best exposed.

Fossils within the Muddy Creek Formation include invertebrate trace fossils such as horizontal and vertical burrows, as well as mammal, bird and lizard prints (Kowallis and Everett, 1986). Older exposures of the Muddy Creek Formation contain avian, ursid, camelid, and felid ichnotaxa (Howe, 1997; see Chapter 2). While most footprints in the formation occur in sandstone, this tracksite occurs in a layer of limestone ranging from roughly two to four centimeters thick. Some skeletal fossils have been reported from the Muddy Creek Formation, but none have been formally described (Williams, 1996; Howe, 1997; Reynolds and Lindsay, 1999).

1.4 Methods

A Nikon D750 DSLR camera and Agisoft PhotoScan Professional software were used to take and process photogrammetric images. Photographs were taken of each tracksite following protocol from Faulkingham et al. (2018). Separate photogrammetric models were made for exposures A and B. The single partial track in Exposure C was not examined photogrammetrically. Analysis of each footprint was based on the photogrammetric model, accompanied by individual photographs. Ichnotaxonomic identification is based on Lucas and Hunt (2007).

1.5 Results

When examining this tracksite visually, 19 prints are evident. However, analysis of the photogrammetric models revealed 21 additional prints, making a total of 40 prints (Figs. 1.6,

1.7). By turning the model over and analyzing the underside, print morphology is more easily seen. All footprints are concave epirelief, or molds.

Track lengths range from 60 to 190 mm, with an average length of 135 mm (Fig. 1.8). The truncated print in Exposure C is not included in the size frequency histogram because not enough of the print is preserved to measure its length. The footprints are all subdigitate and bidigital, with slight variations of a general heart shape. Posterior ends are round with a cleft, while anterior ends are pointed with parallel or diverging tips. In some prints, the interdigital sulcus was observed to extend from the anterior cleft to the posterior cleft. While in other prints, the sulcus does not extend from one cleft to the other (Fig. 1.3). These differences are extramorphological variations which in many cases produced suboptimal prints, usually caused by changing characteristics of the substrate or by foot movement of the individual (e.g., walking versus running) (Peabody, 1948). In modern artiodactyls, Murie (1974) demonstrated that extramorphological variation may produce different size and shape prints from the same foot. Two examples of extramorphological variation in the Flat Top Mesa Tracksite camelid footprints are illustrated in Figure 1.4.

1.6 Systematic Ichnology

Ichnogenus *Lamaichnum* Aramayo and Bianco, 1987

Material Referred: 40 Footprints from the Flat Top Mesa Tracksite near Mesquite, NV.

Lucas and Hunt (2007) simplified camel ichnotaxonomy into one ichnogenus and two ichnospecies (*L. guanico* and *L. macropodum*). These two ichnospecies are different only in footprint length, with *L. guanicoe* being shorter than 160 mm and *L. macropodum* ranging in length from 160 to 260 mm. Because size is not a reliable way to differentiate between

ichnospecies, Lucas and Hunt (2007) acknowledged that camelid ichnotaxonomy is a work-in-progress. The Flat Top Mesa Tracksite footprints range in length from 60 mm to 190 mm, with an average length of 135 mm (Fig. 1.8). Differentiating these ichnospecies provides no meaningful distinction in the case of this assemblage of tracks, so I refer them to *Lamaichnum* isp.

1.7 Discussion

By the middle Miocene, North American camelid foot morphology had evolved into the shape that we see in modern camels (Lucas and Hunt, 2007). Following general camel evolution, we would expect to see a slight increase in average footprint size from middle Miocene (Barstow and Avawatz formations) to late Miocene-early Pliocene (Muddy Creek Formation), by which time camels had evolved into the larger body type that is familiar in extant dromedary and bactrian camels. The trend toward generally larger footprints in the Mojave region can be seen in Figure 1.8, with the Muddy Creek Formation having a broader range in size distribution of footprint length than the Barstow and Avawatz formations. These older Barstow and Avawatz formations have normal size distributions with an average footprint length of 90 mm, whereas the Muddy Creek Formation tracks average 135 mm, with a normal distribution of sizes starting to emerge. However, the Muddy Creek sample size ($n = 39$) is much smaller than that of the Barstow ($n = 297$). The number of measured specimens in the Avawatz is not specifically stated (Lucas and Hunt, 2007); the estimation of $n \sim 48$ is derived from their histogram. More Muddy Creek footprints need to be measured to be able to make a more robust comparison (see Chapter 2).

Modern camels have a distinctive walking gait in which they walk with both right legs in succession, followed by both left legs. This is known as a pacing gait (Webb, 1972) and also as a lateral sequence gait (Hildebrand, 1980). This helps conserve energy by permitting longer strides and fewer steps, at the expense of not being able to make quick direction changes (Sarjeant and Reynolds, 1999). The pacing gait produces a trackway with the slightly larger manus in front of the slightly smaller pes (Webb, 1972). This is demonstrated in a famous Barstow Formation trackway made by two camelids pacing side by side, on display at the Raymond Alf Museum (Sarjeant and Reynolds, 1999, figure 9). At the Flat Top Mesa tracksite, there are two possible examples of a pacing gait. One possible example in Exposure A recorded in prints A1/A5/A8 (Fig. 1.6), and a possible example in Exposure B is recorded in prints B1/B2/B3/B4 (Fig. 1.7).

Possible trackmakers for the Flat Top Mesa Tracksite include *Megatylopus* and *Alforjas*. Skeletal fossils of these genera have been reported from the upper Muddy Creek Formation near Mesquite (Howe, 1997; Reynolds and Lindsey, 1999), but are not formally described. *Megatylopus* is also found in the Panaca Formation, a Hemphillian NALMA formation with a large fossil assemblage (Reynolds and Lindsey, 1999; Meyers, 2011).

Ethologically, not much can be said about the behavior of the camelids that left these impressions. However, we can make a few assumptions given the substrate and the orientation of the prints. While both exposures contain tracks headed in different directions, in general, these camelids were traveling in a northward direction. In Exposure A, most of the prints are heading northeastward (Fig. 1.6), while in Exposure B, the prints are generally heading northwestward (Fig. 1.7). Determination of adults vs. juveniles was not attempted due to the extramorphological variation of these camelid prints. Multiple individuals of various ages are

probable because prints occur in a range of sizes. There is only one instance of trampling (one print on top of another) with A11 and A12, which may indicate a relatively low level of activity within the area. The limestone in which these prints were impressed represents a relatively long-standing body of water, possibly making it a reliable water source for animals to return to.

For the preservation of these prints, the water level most likely dropped, prompting the animals to walk about the shoreline to get closer to the lower water levels. The water level stayed low, permitting the sediments to dry out. Soon after, an influx of sediments covered the prints, preserving them.

It is not possible to determine whether these prints were imprinted at the same time. It is possible that different groups passed through, days or even hours apart (Lockley and Hunt, 1995). Therefore, this could be a group of individuals, a pair of individuals passing through at different times, or even several individuals passing through one at a time, separated by hours or days. However, the occurrence of tracks made by multiple individuals headed in the same general direction suggests that these animals were gregarious, and they were members of a small herd. Assuming these prints record a herd of camelids visiting the lake at the same time, the maximum number of individuals at the Flat Top Mesa Tracksite would be around 20. Exposure A has three possible trackways (A1, A5, A8; A2, A4; A22, A14, A15). Exposure B has one possible trackway (B1-B4). All the rest could be separate individuals.

1.8 Conclusions

The Flat Top Mesa Tracksite contributes new data to the Neogene camelid footprint record. The site consists of 40 camelid footprint molds (concave epirelief) identified as

Lamaichnum isp., with an average length of 135 mm. Footprint size follows the general camel evolutionary pattern; on average the tracks are larger than earlier Neogene footprints.

It is probable that the Flat Top Mesa Tracksite records the presence of multiple individuals, probably in a small herd, possibly with juveniles present. I suggest these animals came to a shallow lake, waded around and drank, but did not linger. The Muddy Creek Formation is emerging as an important mammalian ichnology resource similar to other Mojave Desert formations. This fact will be more evident in Chapter 2.

1.9 Figures

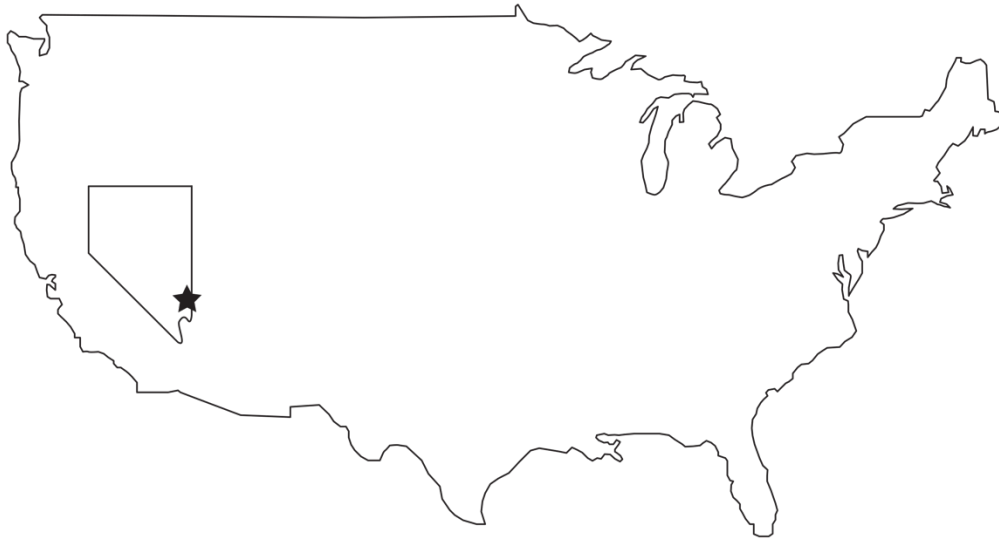


Figure 1.1 Map of United States with inset of Nevada. General location of Mesquite highlighted with star.

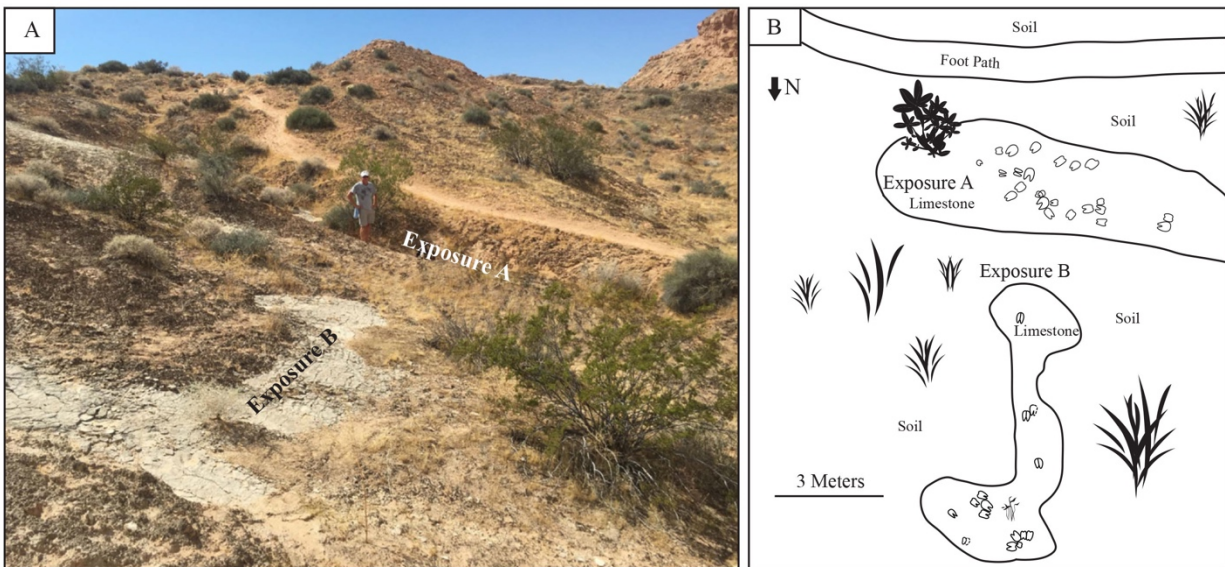


Figure 1.2 Flat Top Mesa Tracksite. A. Photograph, looking South, with the tracksites discoverer, Lloyd Chartrand, standing on Exposure A. B. Map of Exposure A and B. Exposure C is out of viewing to the right, several meters down slope.

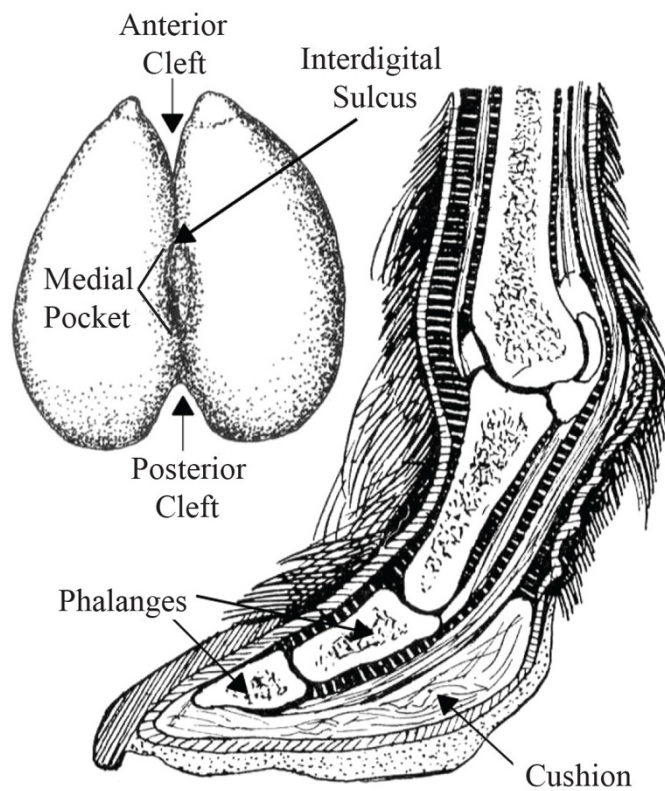


Figure 1.3 Anatomy of a camel foot, modified from Lucas and Hunt (2007), Sergeant and Reynolds (1999) and Weber (1928).

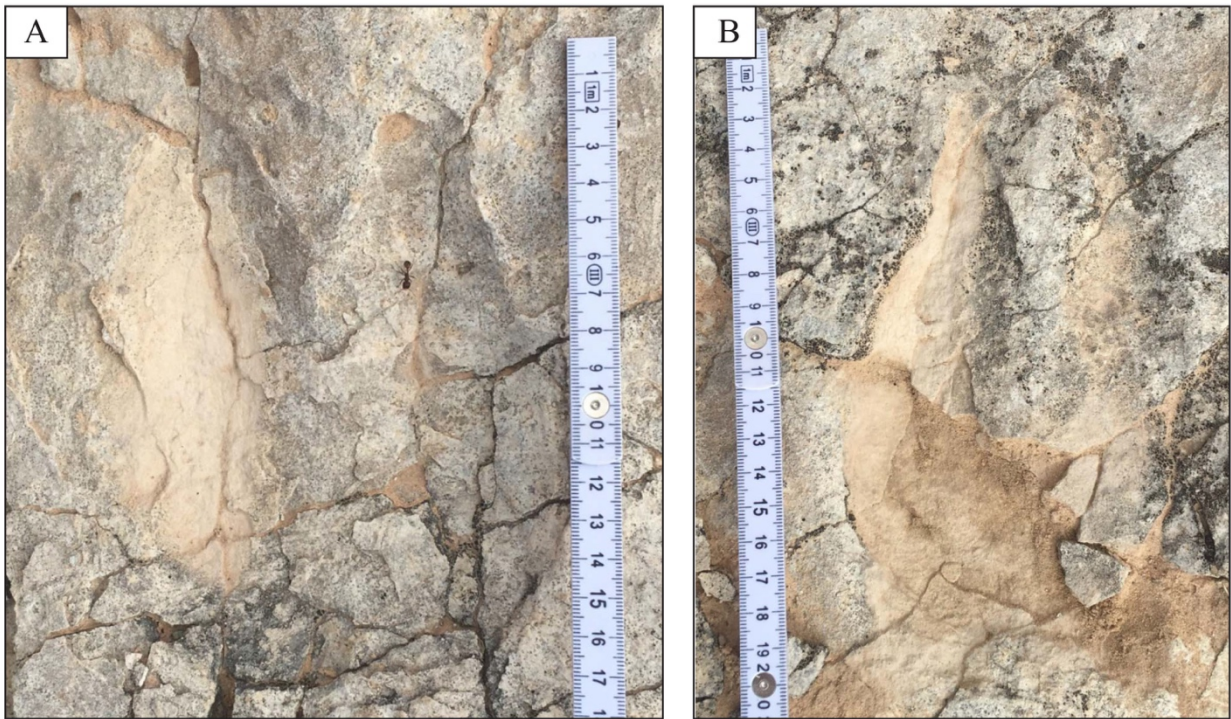


Figure 1.4 Prints from Exposure B to highlight extramorphological variation. Figure 4A: Ichnite B4 has an interdigital sulcus that extends the length of the pad. This track has rounded anterior ends and a wide anterior cleft with a faint posterior cleft. Figure 4B: Ichnite B14 has a short interdigital sulcus, sharp anterior ends, a narrow anterior cleft, but no posterior cleft visible.

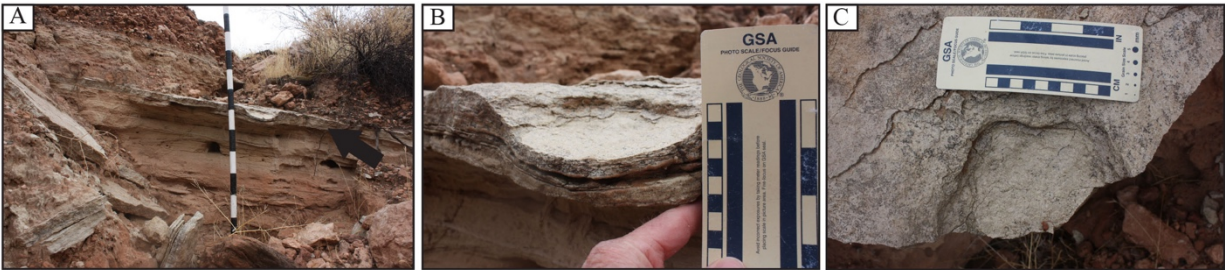


Figure 1.5 Exposure C, a partial print that is much deeper than other prints and occurs within thicker limestone, suggesting deeper water. A: partial print down the slope of the hill from exposures A and B. B: close up of the cross-section of the partial print. C: close up of heel of partial print.

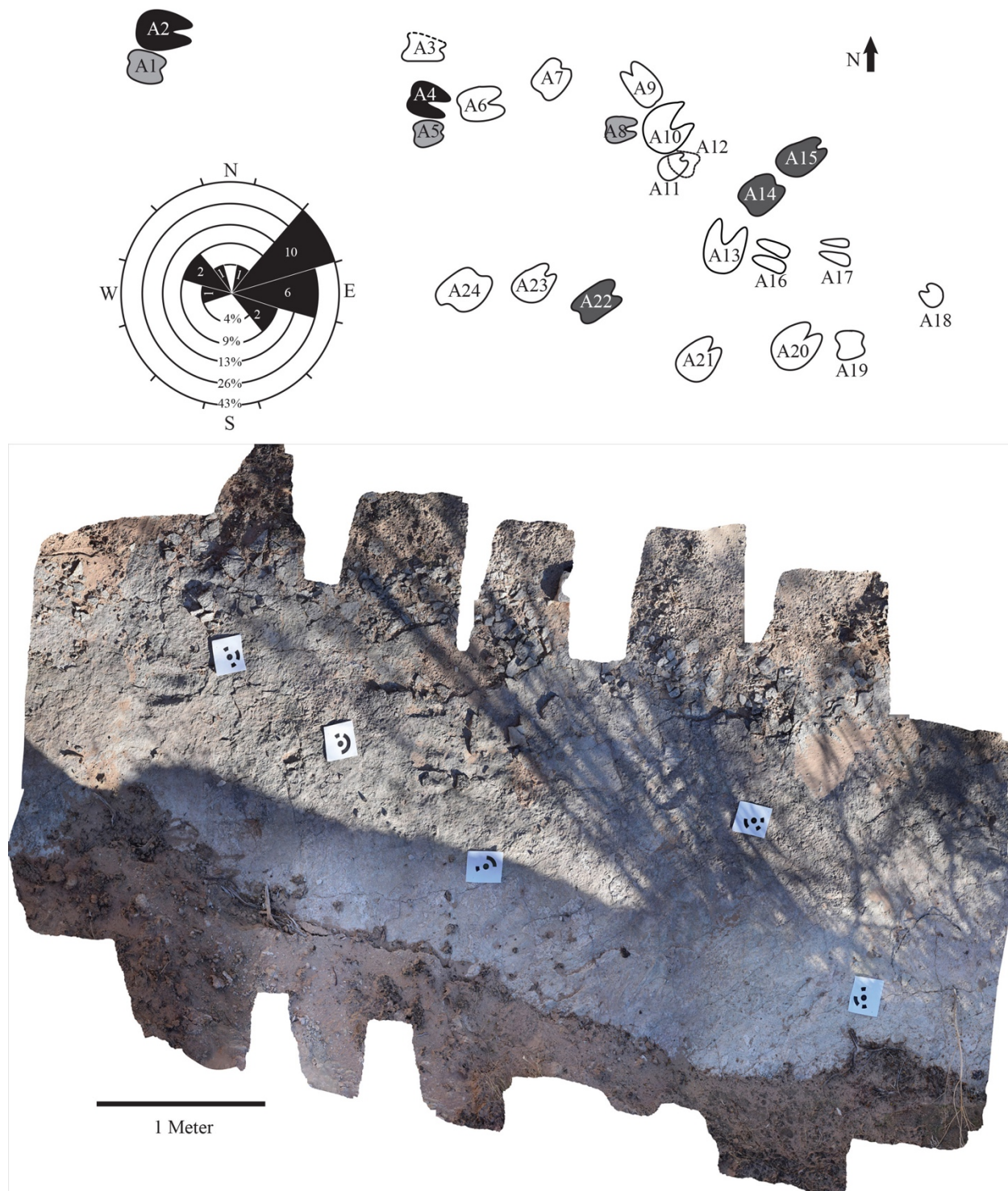


Figure 1.6 2D photogrammetric model of Exposure A, with outline of 24 footprints. Trackways are indicated with colored prints. Rose diagram contains all Exposure A prints minus A12 and shows a dominant direction toward the northeast and east.

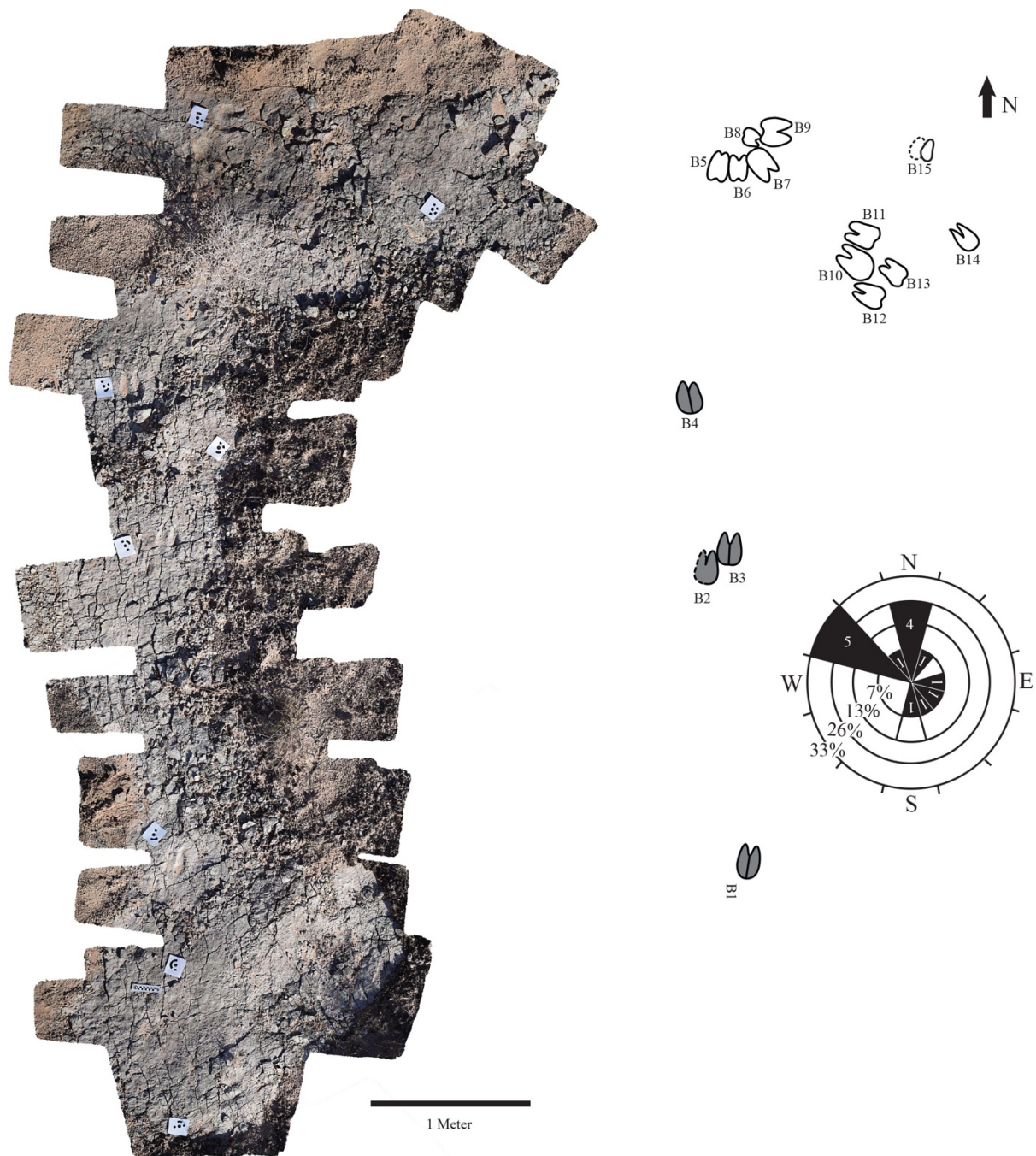


Figure 1.7 2D photogrammetry of Exposure B with 15 ichnite outlines. Trackway indicated with colored print. Rose diagram contains all Exposure B prints and shows a dominant direction toward the northwest and north.

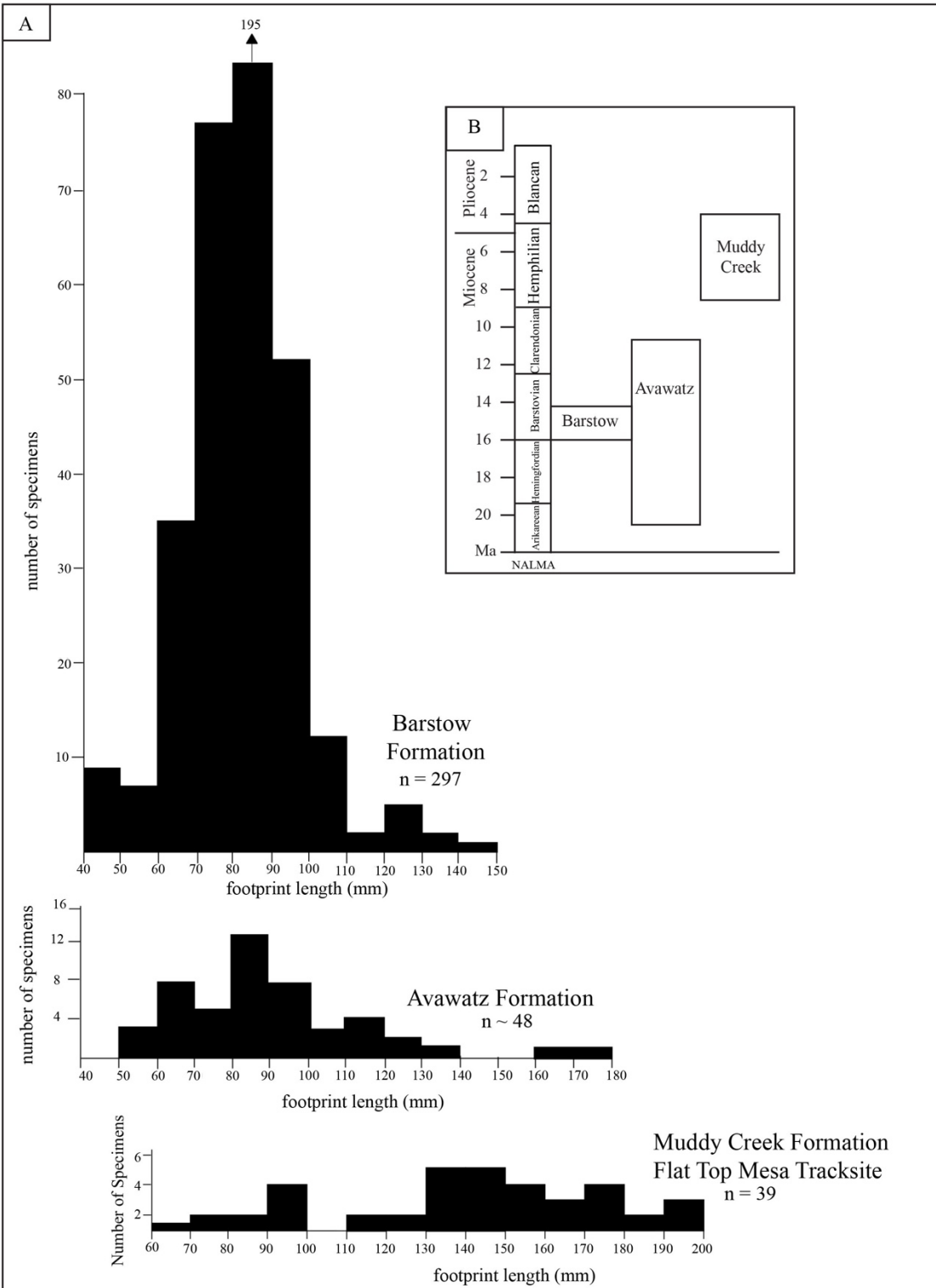


Figure 1.8 A: Flat Top Mesa Tracksite camelid footprint length histogram compared to the Barstow and Avawatz formations footprint length histograms, from Lucas and Hunt (2007). B: Inset shows North American Land Mammal Ages and the ages of formations discussed in the text.

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Chapter 2: A Diverse Late Miocene (Hemphillian) Lake Margin Ichnofauna in the Muddy Creek Formation Near Lake Mead, Nevada

2.1 Abstract

A new diverse ichnofauna of the Muddy Creek Formation consists of camelid, ursid, felid, equid and avian tracks. Tracks are exposed in sediments along a canyon where most tracks are found in float or on the under sides of overhanging sandstone beds throughout the canyon. Two large camelid tracksites exposed on the bottom of the dry canyon, were mapped and analyzed. This ichnofauna also contains 7 ursid tracks, some of the rarest mammalian tracks. Documentation of these tracks is important because they are in a sensitive area and can be weathered easily or taken by anyone. Documenting these mammalian trackways is imperative to understanding ancient ecosystems and geographic range of ancient animals, and most importantly, preserving them for future studies.

2.2 Introduction

Fossil footprints are an important data source for documentation of Cenozoic mammal evolution (Lucas, 2007). Research and interest in such ichnofossils has grown significantly in recent years (McDonald et al., 2007). The western United States in particular, has become the forefront of Neogene ichnology, in rock units such as the Barstow, Avawatz, Muddy Creek, and White Narrows formations. A generalized overview of Neogene western United States track occurrences is shown in Figure 2.1. A comprehensive bibliography of North American Cenozoic vertebrate track studies can be found in Hunt and Lucas (2007). McDonald et al. (2007) contains a bibliography of global occurrences. The most frequently occurring Neogene tracks in North America are those of camelids, which occur in most ichnofaunas (Fig. 2.1).

In Chapter 1 I described a new camelid tracksite (Flat Top Mesa Tracksite) in the upper part of the Muddy Creek Formation near Mesquite, Nevada. In this chapter I describe a more diverse vertebrate ichnofauna within this formation at the informally named Muddy Creek Canyon locality near Lake Mead, Nevada (Fig. 2.2). This locality encompasses roughly 1.5 km of a canyon, exposing flat-lying beds of conglomerate, sandstone and mudstone. The fossil-bearing strata of the Muddy Creek Formation that was deposited between 9-4 Ma (Williams, 1996; Reynolds and Lindsay, 1999; Forester, 2010; Muntean, 2012), places it mostly within the Hemphillian North American Land Mammal Age (NALMA) (Fig. 2.1). I infer that the Muddy Creek Canyon locality is late Miocene, and therefore Hemphillian, but its precise age is not known.

Camelid tracks are ubiquitous in Muddy Creek Canyon, and the analysis of camelid print size (Chapter 1) is continued in this chapter. Unlike the Flat Top Mesa Tracksite, where only one ichnogenus is present, the diversity of trackmakers at this locality is much higher, with ursids, equids, felids, camelids and birds. Modes of footprint preservation are also more diverse, including tracks occurring as casts, molds, singular prints, and extensive trackways. Tracks appear throughout the canyon, including on the undersides of overhanging sandstone beds, on pieces of float, and on exposed beds at the bottom of the dry canyon. Two large camelid tracksites, Tracksite A and Tracksite B, were mapped and analyzed. In this dissertation, the terms tracks and prints are synonymous and indicate a single specimen. The term trackways indicates two or more prints or tracks within one trackway.

This study was conducted under Permit LC-NV-20-04 (Paleo) from the U.S. Bureau of Reclamation (BOR). Collecting tracks was not permitted by the BOR, so they were studied and documented *in situ*. The purpose of this study is to document, describe, interpret, and digitally

preserve the prints within the Muddy Creek Formation at the Muddy Creek Canyon locality.

Ichnology, the study of fossil footprints, is important because prints give us a temporal snapshot of animal behavior. Footprints also give us information about the geographical range of various taxa. This is especially important where there is little or no skeletal material to be found within a formation, as is the case in the Muddy Creek Formation. This site has emerged as one of the most diverse late Neogene localities for mammalian and avian tracks in North America.

2.3 Previous Studies

There have been several previous studies of Muddy Creek Formation vertebrate tracks, including descriptions of camelids, canids, felids, ursids and birds (Sarjeant and Reynolds, 1999; Lofgren et al., 2006a, 2006b; Lockley et al., 2007b). However, the Muddy Creek Canyon exposures have not previously been studied. The most notable, previously reported Muddy Creek Formation tracks are those of the ursid ichnophylotype *Platykopus ilyalcator* (Sarjeant et al., 2002), and large avian tracks attributed to herons and ducks (Lockley and Hunt, 1995). Mapping by Schmidt et al. (1996) revealed that some of the track-bearing strata that previous workers had included within the Muddy Creek Formation (e.g., Gardner, 1968) were contained within a slightly younger stratigraphic interval that had filled a graben within the Muddy Creek Formation. Schmidt et al. (1996) named this graben-fill unit the White Narrows Formation. This resulted in most of the previously recorded “Muddy Creek” tracks being placed into the White Narrows Formation (Reynolds and Lindsay, 1999; Lockley et al., 2007b; Hunt and Lucas, 2007). Both the White Narrows and Muddy Creek formations crop out in the Glendale/Moapa area of southern Nevada, making previously collected tracks from that area ambiguous. Identification of these collection localities is needed to decipher which formation various prints are from.

Skeletal material from the Muddy Creek Formation is scarce. Some material is repositied at the American Museum of Natural History (AMNH) and some at the San Bernardino County Museum (SBCM) (Williams, 1996; Howe, 1997; Reynolds and Lindsay, 1999). Reynolds and Lindsay (1999) described Muddy Creek Formation skeletal fossils from the Mesquite area, which they determined to be within the Hemphillian NALMA (Fig. 2.1). Taxa represented in the skeletal fossil material include carnivores (*Aelurodon* and *Indarctos*), equids (Equinae), and camelids (*Megatylopus* and *Alforjas*) (Stock, 1921; Reynolds and Lindsay, 1999). In an abstract with little detail, Howe (1997) reported the collection of skeletal and trackway material near Mesquite, Nevada, repositied at the San Bernardino County Museum, consisting of three mostly articulated individual camelids, including a nearly complete skull of *Alforjas*. Howe (1997) reported that the trackways indicated three sizes of animals travelling in the northwest and southeast directions.

2.4 Methods

Photographs were taken with a Nikon D3300 DSLR camera. Section measurements were taken with a 1.5 meter staff, calibrated in decimeters. To create maps of the two large tracksites, each tracksite was sectioned into grids; Tracksite A was grided into 0.9 meter by 0.9 meter squares and Tracksite B into 0.3 meter by 0.3 meter squares. Within each square, the position and size of each track was recorded. The maps were then transferred to Adobe Illustrator CS6 and digitized.

2.5 Stratigraphy and Sedimentology

The Muddy Creek Formation crops out in multiple places within the Lake Mead region (Fig. 2.2), with younger outcrops near Mesquite, Nevada (Williams, 1996; Muntean, 2012). The strata at the Muddy Creek Canyon locality, are more exposed, and more accessible than those at

the Flat Top Mesa locality. The petrocalcic cap that caps the Flat Top Mesa sediments (Gardner, 1972a, b) is not present at the Muddy Creek Canyon locality. The absence of the petrocalcic cap at this locality suggests that this locality is older than the Flat Top Mesa locality, although the precise age is not known. Strata in the Mesquite area, which includes the Flat Top Mesa locality, are not continuous. This prevented Kowallis and Everett (1986) from correlating stratigraphic columns. Similarly, the sedimentary layers at the Muddy Creek Canyon locality inconspicuously pinch out within a few tens of meters, making it impossible to precisely correlate across and down the canyon, with one correlation exception discussed below. These layers range in thickness from roughly 1 to 20 cm, with a strong cyclicity of alternating sandstone and mudstone layers. A few conglomeratic layers and green clay marker beds also occur (Fig. 2.3). Unless otherwise stated, the sandstone beds are light tan to orange in color, with homogenous grains of very fine to fine, rounded to subrounded sand grains. The conglomerate beds contain clasts up to 2 cm in diameter. Common sedimentary structures include mudcracks and ripples. Less common sedimentary structures include crossbeds, invertebrate burrows, channels, evaporite casts and soft sediment deformation structures (Fig. 2.4).

Three stratigraphic columns are used to document the stratigraphic sequence of fossil-bearing strata throughout the canyon (Fig. 2.3). Section 1 is the most complete section, with a resistant conglomerate consisting of a white matrix exposed at the bottom and Pleistocene conglomerate at the top. The distinctive conglomerate exposed at the base of section 1 does not occur anywhere else in the canyon. Thus, the base of Column 1 is the stratigraphically lowest point exposed in the Muddy Creek Canyon. Section 2 is located adjacent to camelid Tracksite B, within a small side canyon, down the canyon from camelid Tracksite A. Section 3 is located farther up the canyon, near camelid Tracksite A (Fig. 2.3).

Invertebrate traces fossils are rare and represented by only a few burrows (Fig. 2.4B). The burrows are vertical, non-branching, cylindrical tubes. They were found in float between Columns 2 and 3. Therefore I am unable to place them in a stratigraphic column.

Channels are not abundant. One large, conspicuous channel across the canyon from section 1 is 45 cm thick and three meters wide (Fig. 2.4A). The margin of this channel is oriented due north-south. The sandstone beds, especially in the lower part of the section, become conspicuously thinner from Column 3 to the other columns. Together, with the orientation of the large channel, this indicates that the low point of the basin was in the northward direction.

Soft sediment deformation structures are conspicuous within one layer in sections 1 and 2, yet absent in section 3 (Fig. 2.4G). They are located between two sandstone layers, just below the horizon in which camelid tracksite B occurs (Fig. 2.3). Such features come in many different forms and are produced by water being quickly expelled from the substrate, or sandstone in this case. This liquefaction process can be triggered by many different events (e.g., seismicity and sediment loading) (Shanmugam, 2016). These deformation structures are prominent enough to correlate between columns 1 and 2, making this the only confident correlation between all 3 columns.

Evaporite casts in sandstone are seen in one sample (Fig. 2.4E). These evaporite casts are gypsum crystals, similar to dovetail gypsum crystal aggregates (Bain, 1990). This specimen, which was found in float across the canyon from Column 3, contributes to the interpretation that an arid, evaporite lake basin existed at this site.

2.6 Ichnology

2.6.1 Avian Tracks

Avian prints are very abundant at the Muddy Creek Canyon locality. Mostly seen in float, they occur in a variety of sizes and shapes throughout the entire canyon. Several trampling sites are also present. The bird prints are often difficult to see *in situ* because they are smaller and less conspicuous than the larger mammal prints. In Figure 2.5, a diagram of bird foot morphology illustrates the terminology used.

The most common avian track is an *Avipeda*-like track (Fig. 2.6A and B). These *Avipeda*-like tracks have no visible hallux impression and are possibly partially webbed. Some tracks have no webbing visible (Fig. 2.6B), while others have a visible web, but the web is close to the heel of the foot; it does not extend the length of the digits. An *Anatipeda*-like (small, webbed) trackway of three prints is shown in Figure 2.6C. These prints have a very visible web and hallux (digit I) impressions, but digits II-IV are not impressed deeply enough to show the length of the digits.

Possible trackmakers include small shore birds of the family Scolopacidae, which includes snipes, sandpipers, and dowitchers. Members of this family typically occur on shorelines and in wetlands. Skeletal material of scolopacids has been reported in the Pliocene Panaca Formation (Meyers, 2011), about 200 km north of Muddy Creek Canyon. The White Narrows and Horse Spring formations have bird prints similar to those described above. Large heron-like prints, attributed to *Ardeipeda*, have also been reported from these formations (Lockley and Hunt, 1995; Jones, 2002), however, no such tracks occur at this locality.

2.6.2 An Equid Track

One probable equid print has been identified at this locality (Fig. 2.7A). It was found on a piece of float on the floor of the canyon, so its precise stratigraphic position is not known. It is a convex hyporelief print (cast). For comparison, an outline of a modern horse print is shown in Figure 2.7B. This is the first equid print reported from the Muddy Creek Formation. The overall shape is ovate; it is truncated posteriorly, and it is slightly wider (~9 cm) than long (~7-8 cm), with a wall width of 1 cm. Because this print is wider than long, it is probably the print of a forefoot, which differs from a more elongated hind foot (Sarjeant and Reynolds, 1999).

By the middle Miocene, most equids had become functionally monodactyl; some were tridactyl but typically did not leave a tridactyl trace (Scrivner and Bottjer, 1986). So the use of modern equid terminology in relation to late Miocene fossil prints is therefore appropriate (MacFadden, 1992). Most middle Miocene equid prints do not have a preserved frog (triangular region on the bottom of a modern horse's hoof), which could indicate that the frog was not a primitive feature (Sarjeant and Reynolds, 1999). Because the Muddy Creek Canyon equid print does not display the posterior part of the foot, it is not clear whether a frog was present. This print is most similar to the ichnotaxa *Hippipeda* C of the Pliocene Copper Canyon ichnofauna in Death Valley (Scrivner and Bottjer, 1986; Santucci et al., 2012). Later designated as *Hippipeda gyripeza* by Sarjeant and Reynolds (1999).

With very few characteristics preserved, this equid print is recognized only to the ichnogenus *Hippipeda* (Vyalov, 1966), which is the generic ichnogenus for equid prints. Possible trackmakers include *Dinohippus*, which is found in the Panaca Formation (Reynolds and Lindsay, 1999). *Dinohippus* is closely related to modern equids and was locally common in North America during the Hemphillian NALMA (MacFadden, 1992).

2.6.3 *Felid Tracks*

At this locality, two isolated felid prints have been found (Fig. 2.8), and no canid tracks. Felid prints tend to be wider than long with no claw marks, whereas canid prints tend to be longer than wide, with claw marks present (Reynolds and Milner, 2012). These two felid prints occur as convex hyporelief (molds). All digits are separated from the metapodial pad (Fig. 2.8). Print A is a medium-size felid track, at 5.5 cm long by 5.0 cm wide. It has four, round digits, and a mostly round metapodial pad with only one anterior lobe, whereas most felids of the Hemphillian/Blancan NALMAs have two to three lobes on the larger metapodial pad (Reynolds and Milner, 2012). Print B measures wider than long at 6 cm wide and 4 cm long, which also falls into the range of a medium-size felid track (Reynolds and Milner, 2012). There is also a partial print next to the main print, suggesting overprinting. The pads are more laterally ovate than circular.

These felid prints differ from other Mio-Pliocene felid prints in western North America in that the metapodial pad is not bilobed. These tracks are assigned to the ichnogenus *Felipeda*, the generic ichnogenus for cat prints. The angle and shape of the digits fanning around the metapodial pad were once used to designate ichnospecies. However, as Luebbers et al. (2017) pointed out, these characteristics are affected by substrate hardness and motion of the individual which lead to extramorphological variation (discussed in Chapter 1).

Felid phylogeny and evolution are not well understood mainly due to the homogeneity of skeletal morphology and the scarcity of skeletal fossils (O'Brien and Johnson, 2007). A possible trackmaker of the Muddy Creek Canyon felid tracks is *Felis lacustris* from the Pliocene of Idaho (Gazin, 1933). *F. lacustris* is most likely an ancestor of the puma lineage (Seymour, 1999;

Werdelin et al., 2010), a diverse lineage that evolved from Asian ancestors that immigrated to North America in the late Miocene.

2.6.4 Ursid Tracks

Ursid tracks present within Muddy Creek Canyon include eight footprint specimens (seven casts and one mold) of *Platykopus ilyocator* (Sarjeant et al., 2002) (Fig. 2.9). This diagnosis follows the type and paratype specimen of *Platykopus* from the White Narrows Formation (Sarjeant et al., 2002; Lockley et al., 2007b). These tracks are plantigrade with five digits, each digit having two pads and one nail (Fig 9E). The manus is generally wider and shorter than the pes. The pes is elongated with an oval metatarsal pad (Fig 2.9A, D, E). Digits 1-4 are visible in Figure 2.9A. These tracks range from 13-13.5 cm long by 10.7-11 cm wide (manus) to 13.5-15 cm long by 11-13.7 cm wide (pes). This includes the holotype and paratype specimens (Sarjeant et al., 2002) as well as 13 tracks from a White Narrows Formation trackway specimen described by Martinez and Farke (2018).

Possible trackmakers are *Indarctos* (Reynolds and Lindsay, 1999) and *Agriotherium*, both giant short-faced bears (Tedford et al., 2004). Possible *Indarctos* bone material has been reported, but not verified, from the Muddy Creek Formation by Reynolds and Lindsay (1999). *Indarctos* bone material has also been reported from the Hemphillian Smiths Valley fauna in western Nevada (Macdonald, 1959; Tedford et al., 2004). *Agriotherium*, is reported to have been present in North America during the Hemphillian NALMA (Tedford et al., 2004; Samuels et al., 2009). Both *Indarctos* and *Agriotherium* were larger than modern ursids. Their diets are thought to have diverged from ancestral carnivorous diets to a more omnivorous diet, closer to that of modern ursids (Vrianta, 2004; Pagnac and Reynolds, 2006; Sorkin, 2006; Figueirido et al., 2010). Both taxa immigrated to North America from Eurasia (Qui, 2003).

2.6.5 Camelid Tracks

In Chapter 1 I analyzed the Flat Top Mesa Tracksite, a camelid tracksite in the upper portion of the Muddy Creek Formation, located about 40 km north-northeast of the Muddy Creek Canyon locality (Fig. 2.2). While the Muddy Creek Canyon locality has a much more diverse ichnofauna than the Flat Top Mesa Tracksite, camelid tracks are the most abundant mammalian prints at this locality, with 53 sites recorded, and roughly 400 individual tracks. These camelid tracks are found in many layers throughout the canyon, occurring as casts in float, on the underside of ledge overhangs, as well as molds located at the bottom of the canyon on exposed bedding planes (Fig. 2.3).

Two large tracksites (A and B) were chosen to be analyzed due to exposure and accessibility. Tracksite A is located at the bottom of the main wash (Figs. 2.3, 2.10A). Tracksite B is located on the floor of a side canyon (Figs. 2.3, 2.10B). A map was created for each tracksite to indicate orientation of the prints. There are many different morphologies within each tracksite, as well as throughout the canyon (Fig. 2.11). See Chapter 1 for an explanation of extramorphological variation, and why these tracks are all referred to *Lamaichnum* isp.

Direction of travel, width, and length measurements were documented for each individual print at tracksites A and B, where the quality of preservation permitted. Some prints that are documented on the map are not included in the size or direction information. For example, a shallow print may provide a reliable width measurement, but differentiating between the anterior and posterior ends of the print may not be possible, making the direction the print is facing ambiguous. The prints in Tracksite A occur in different sizes and are headed in numerous directions, with some trampling. The depth of the tracks at this tracksite is highly variable. Some are deep and distinct, while others are extremely shallow, making them difficult to see

with the naked eye. The time of day and sun angle strongly influence which prints are more visible at any given time.

The map of Tracksite A shows 66 prints (Fig. 2.12). This is a minimum number. The rose diagram in Figure 2.12 shows that these prints are generally bidirectional and trend either northeastward or southwestward. Length measurements taken at Tracksite A were added to the camelid footprint histogram created in Chapter 1 and are discussed later in this chapter. Two trackways of more than two prints are highlighted in gray and black in Figure 2.12. The trackway consisting of eight tracks, shown in gray, beginning with track number 12 near the north end of the exposure, records the path of a camel headed south-southeast. Another trackway, shown in black, consists of three tracks headed northeast. In both trackways the tracks are evenly spaced, indicating that these animals were walking. The faster moving pacing gait typically has prints grouped together within a trackway (Webb, 1972).

Tracksite B consist of 21 prints, with two possible trackways (Fig. 2.13). Length and width measurements of the tracks were not taken at this tracksite. These tracks are very deep, making it difficult to measure the dimensions with confidence. The rose diagram indicates that these animals were less consistent in their direction of travel than those recorded in Tracksite A, but with a roughly bimodal pattern. There are two probable trackways of more than two prints each, highlighted in gray. Like tracksite A, the tracks in tracksite B are evenly spaced, indicating the animals were walking.

Possible trackmakers are the same as discussed in Chapter 1: *Alforjas* and *Megatylopus*. Skeletal material of both genera have been found in the Muddy Creek Formation and the Panaca Formation (Howe, 1997; Reynolds and Lindsay, 1999; Meyers, 2011).

2.6.6 Camelid Evolutionary Implications

In Chapter 1, I discussed the evolutionary history of camelids through the Neogene; as body size increased, morphological characteristics became more specialized. For example, camelid ancestors evolved from four toes down to two toes by the middle Miocene. At this time, ungulate taxa underwent rapid radiation, and by the end of the Miocene, camels were morphologically recognizable as modern camels (Lucas and Hunt, 2007). Using print size as a proxy for body size, an increase in print length between older Miocene formations (e.g., Barstow and Avawatz formations) and the younger Muddy Creek Formation can be seen (Chapter 1, Fig. 1.8). To compare print size within the Muddy Creek Formation, prints from Muddy Creek Canyon Tracksite A were added to the size analysis. Muddy Creek Canyon Tracksite B prints are not distinct enough to provide reliable print measurements. Muddy Creek Canyon Tracksite A prints and Flat Top Mesa tracksite prints used for this analysis are all molds from one horizon in their respective formation.

Figure 2.14 is the same Flat Top Mesa print-length histogram from Chapter 1 (denoted with black columns), with the added print length measurements from the Muddy Creek Canyon Tracksite A (denoted with striped columns). The prints from the Muddy Creek Canyon locality range from 80-150 mm and are smaller on average, at 100 mm, than those found at the Flat Top Mesa tracksite, which range from 60-200 mm and average 135 mm. Together, the average size of camelid prints within the Muddy Creek Formation is 120 mm.

This increase in print size can be seen in other late Neogene formations, with some prints even larger than the prints at the Flat Top Mesa locality. For example, the Ogallala Formation in the panhandle of Texas has many camelid tracks (of Blancan age) that vary in length from 100 to 260 mm in length (Lucas and Shultz, 2007). The late Pliocene Santa Fe Camel Trackway in

New Mexico, although highly eroded, has also produced larger camelid prints, from 160 to 200 mm (Morgan et. al., 2007). Another example is the late Pleistocene Wally's Beach site in southern Alberta, Canada, which has large tracks and multiple ichnogenera. The camelid tracks at that locality average 200 mm in length, with the maximum length being 260 mm; *Camelops* was possibly the trackmaker (McNeil et al., 2007). This increase in camelid print size is expected as camelids evolved into larger sizes, culminating in *Camelops*, the largest camelid genus in the North American fossil record. *Camelops* went extinct during the megafauna extinction event near the end of the Pleistocene (Heintzman et al., 2015).

2.7 Discussion

Several lines of evidence indicate a marginal lacustrine depositional environment at the Muddy Creek Canyon locality. Interbedded sandstone and mudstone layers record fluctuating episodes of low and high water levels. The presence of gypsum casts records dry periods; gypsum crystals that grow uninhibited are characteristic of subaerial lacustrine environments (Boggs, 2009). Sandstone units and channels record episodes of fluvial input of sediment into the basin, symmetrical ripples record standing high lake levels, while mud cracks, evaporite crystal casts, and mammalian trace fossils indicate dry periods when the lake level dropped. The flow direction of the channel in Figure 2.4A indicates the low portion of the basin was northward, meaning Column 3 sediments are farther away from the lake while Columns 1 and 2 are closer with increasing amounts of mudstone.

Most tracks at this locality were created in mud, then filled with sand. During the weathering process, the mudstone weathered away, and the sandstone cast was then exposed. The water content of the mud was highly variable. The presence of tracks of small birds indicates that the water content of the substrate was high enough to create a track from a light-

weight animal, but not too wet for the track to be destroyed. The presence of mudcracks with the bird tracks records the drying of the sediments; however, the large camelid tracks on tracksites A and B are sandstone molds. These molds differ in depth depending on the location of the print, not necessarily the size of the animal. For example, in Tracksite A (Fig. 12), print 37 is small, at 9 cm in length, and very deep, while print 35 is larger at 14 cm in length, but is very shallow. These prints are very close together on the same substrate. This suggests that the water content was highly variable within the same layer of sediment, which can influence the number of prints preserved. This, in turn, implies that all of the camelids that left these tracks were not present at the same time. Rather, camelids were present at this site repeatedly, under varying conditions of sediment moisture content.

The camelid ichnotaxon *Lamaichnum*, is the most abundant ichnotaxon within the Muddy Creek Formation. Tracksite A shows tracks heading in many different directions, with two dominant directions (Fig. 2.12). This could record milling behavior, in which individuals walk about with no real direction while they are foraging. A study in Tanzania, observed several species of modern mammals in relation to a lake shoreline (Cohen et al., 1991; 1993). The researchers found that milling, or variable track direction, is seen in animals that are more sedentary, whereas migratory animals tend to leave tracks that are parallel to the shoreline. Migratory animals make long, linear trackways. Multiple parallel trackways are not seen at the Muddy Creek Canyon locality. Even still, observed behavior of modern camels in general shows that camels walk in single-file while traveling back and forth to a water source (Gauthier-Piltars and Dagg, 1981). Since camelid tracks are found in many layers within this locality, and milling behavior is present, it is possible these camelids treated this area as a main source of water and

lived nearby. Or perhaps they migrated and would continually return to this source for a short while.

The Mio-Pliocene Copper Canyon ichnofaunal assemblage in Death Valley (Fig. 2.1) is similar to the Muddy Creek Canyon locality in that it too was deposited along a lake margin, with sedimentary cycles that record alternating low and high-water levels with extensive mudflats. Camelid tracks are also abundant at this locality and are interpreted to record travel to and from the lake because tracks appear in one-way, parallel trackways, not in multiple directions of the milling behavior (trample tracks). Again, whether or not these camelids were migratory is indiscernible (Scrivner and Bottjer, 1986; Nyborg and Buccheim, 2005; Nyborg, 2011; Nyborg et al., 2012; Santucci et al., 2012).

The Muddy Creek Formation compliments other Neogene ichnofaunas in the North American southwest by having a diverse ichnofaunal assemblage. When comparing the ichnofaunal assemblages in Figure 2.1, camelid prints are present within all but one assemblage. Conspicuously, the Muddy Creek ichnofaunal assemblage contains no canids or proboscideans. This does not necessarily mean these trackmakers were not present, just that we have no record of their presence, yet.

I interpret the depositional environment of the Muddy Creek Canyon locality to be lacustrine, with large mudflats and few channels flowing north into an ephemeral lake. The lake level repeatedly rose and covered the study area, causing mud to settle out. The water level would then fall, and the animals would walk across the exposed lakebed and create prints in the mud. The mud would then dry out, preserving the prints, along with large mud cracks. The dried-and-cracked, track-bearing mud would then be covered by fluvial sand as the river delta prograded across the exposed lakebed. The lake level would eventually rise again, flooding the

fluvial sediments and resulting in the deposition of another layer of mud. Green-clay marker beds are clay layers that were deposited during times of high-water levels; diagenetic fluids later reduced the organic material within these clay sediments, turning them green. These green-clay marker beds were suspected to contain datable volcanic ash, but none was found.

2.8 Conclusion

The Muddy Creek Canyon locality records a lake margin environment, with alternating mudflats and deltaic fluvial sedimentation. This area was a semi-permanent source of water to which animals repeatedly returned. The megafauna ecosystem consisted of abundant large camelids, shore birds, rare equids, and two taxa of carnivores. An increase in camelid print size can be seen throughout the Neogene from smaller mid-Miocene (Barstovian) tracks to larger late-Miocene (Hemphillian) Muddy Creek Formation tracks. The diversity and quantity of the Muddy Creek formation ichnofauna is important because skeletal fossils are rare in this formation. The ichnofauna present here documents the fact that these animals lived in this region, even if there are no skeletal fossils. The Muddy Creek Formation has emerged as an important stratigraphic unit for documenting the presence of a diverse mammalian fauna in Neogene arid basins of the southwestern United States.

2.9 Figures

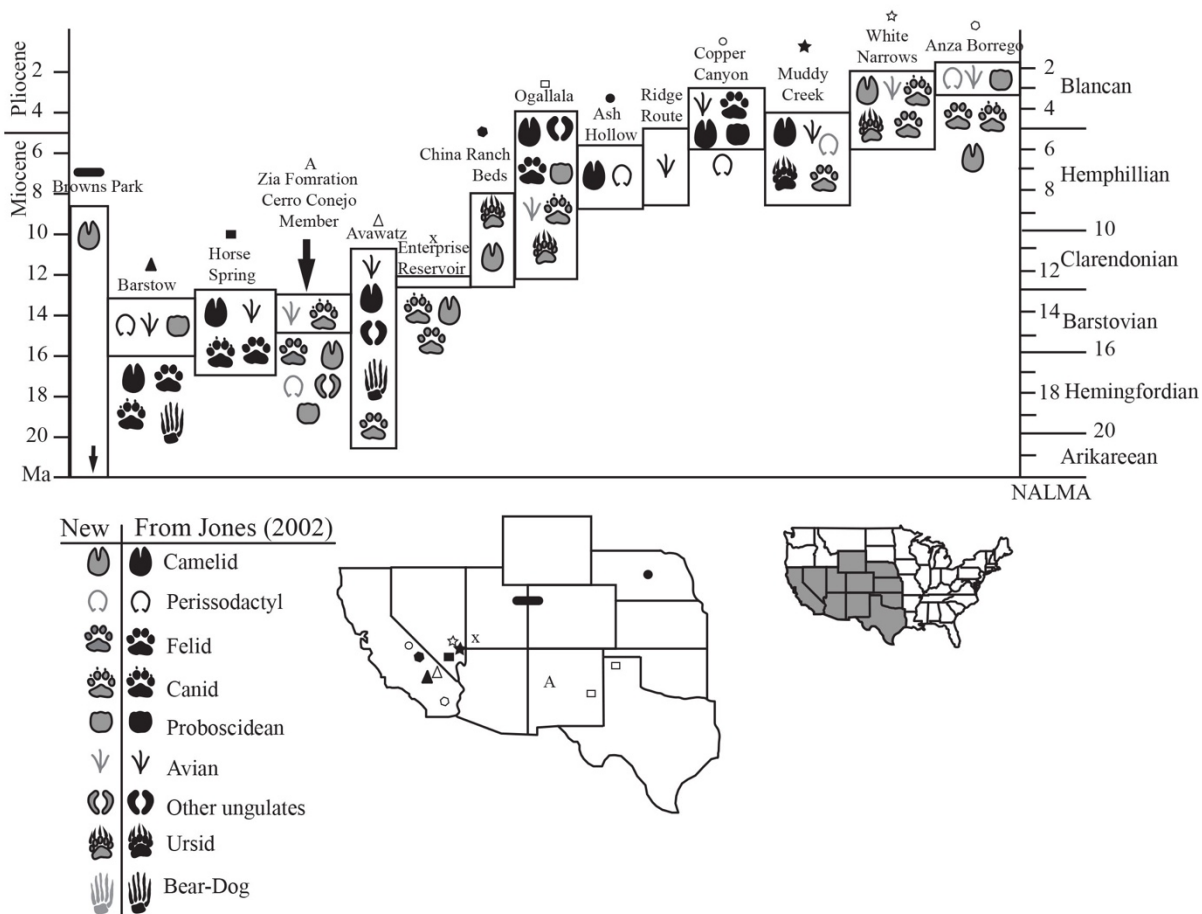


Figure 2.1 Synthesis of Miocene vertebrate tracksites in the United States southwest, not including rodent and invertebrate trace fossils. Modified and updated from Jones (2002). Black prints are from Jones (2002); gray prints are additions. Black boxes represent age range of formation. Print placement within the box does not necessarily define where prints are found within the formation. A more in-depth overview of Cenozoic tracks is in Hunt and Lucas (2007). Anza Borrego: Remeika (2001); Ash Hollow: Lockley and Hunt (1995); Avawatz: Raymond (1959); Sarjeant and Reynolds (1999, 2001); Sarjeant et al. (2002); Lofgren, et al. (2006a, b); Barstow: Alf (1966); Lofgren et al. (2006a, b); Browns Park: Lockley et al. (2007a); Cerro Conejo: Tedford et al. (2004), Morgan and Williamson (2007); China Ranch Beds: Chapter 3; Scott (1985); Lofgren et al. (2006a, b), Sarjeant and Reynolds (1999); Copper Canyon: Scrivner and Bottjer (1986), Nyborg and Buccheim (2005), Nyborg (2011), Santucci et al. (2012), Nyborg et al. (2012); Enterprise: Reynolds and Milner (2007, 2012); Horse Spring: Jones (2002); Muddy Creek: Lofgren (2006 a, b), this dissertation; Ogallala: Texas: Lucas and Schultz (2007); Johnston (1937), New Mexico: Williamson and Lucas (1996); Ridge Route: Hunt and Lucas (2007); White Narrows: Hunt and Lucas (2007), Lockley et al. (2007b).

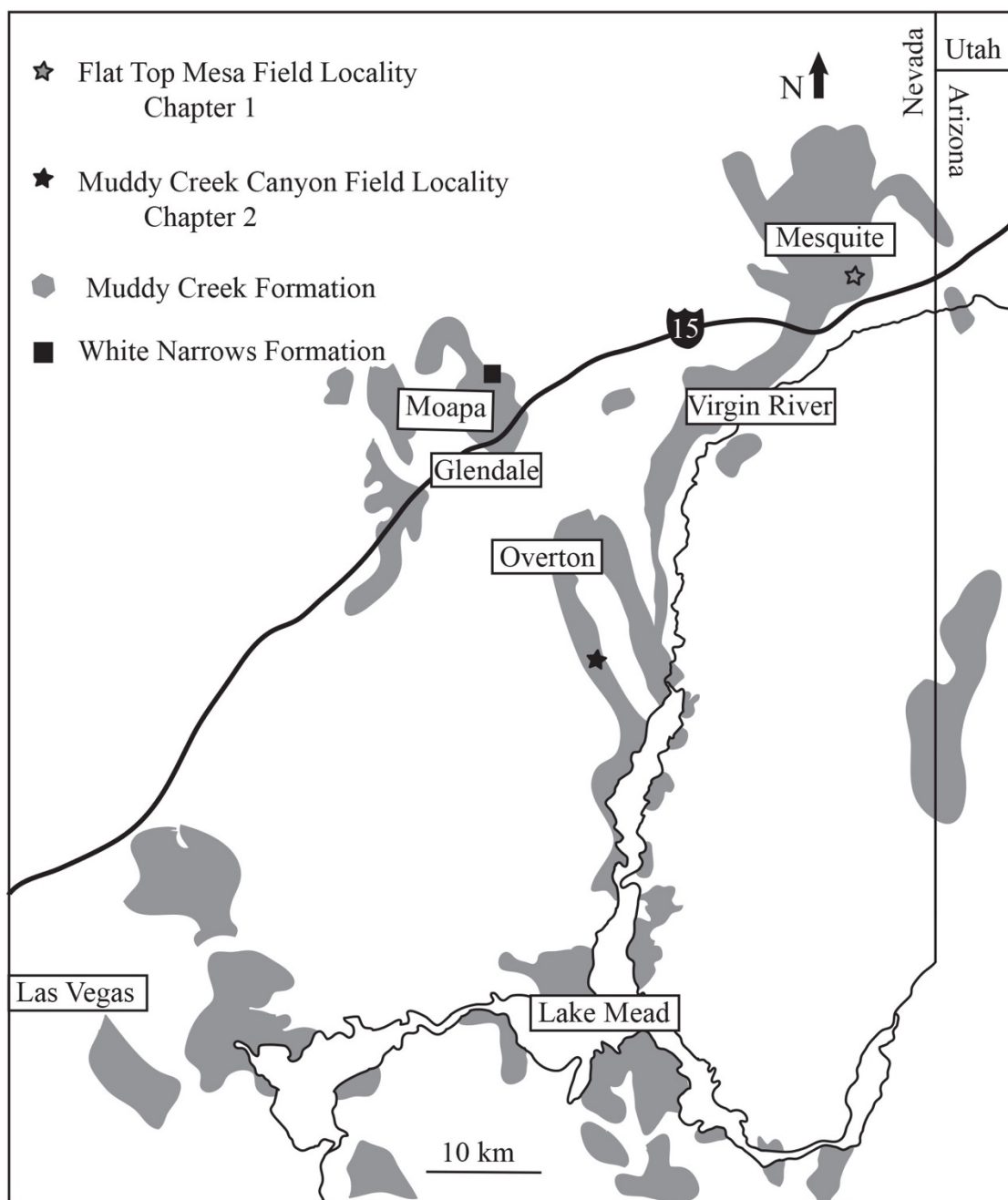


Figure 2.2 Approximate exposure of Muddy Creek Formation showing field localities of this study. The White Narrows Formation location is approximate. Modified from Muntean (2012).

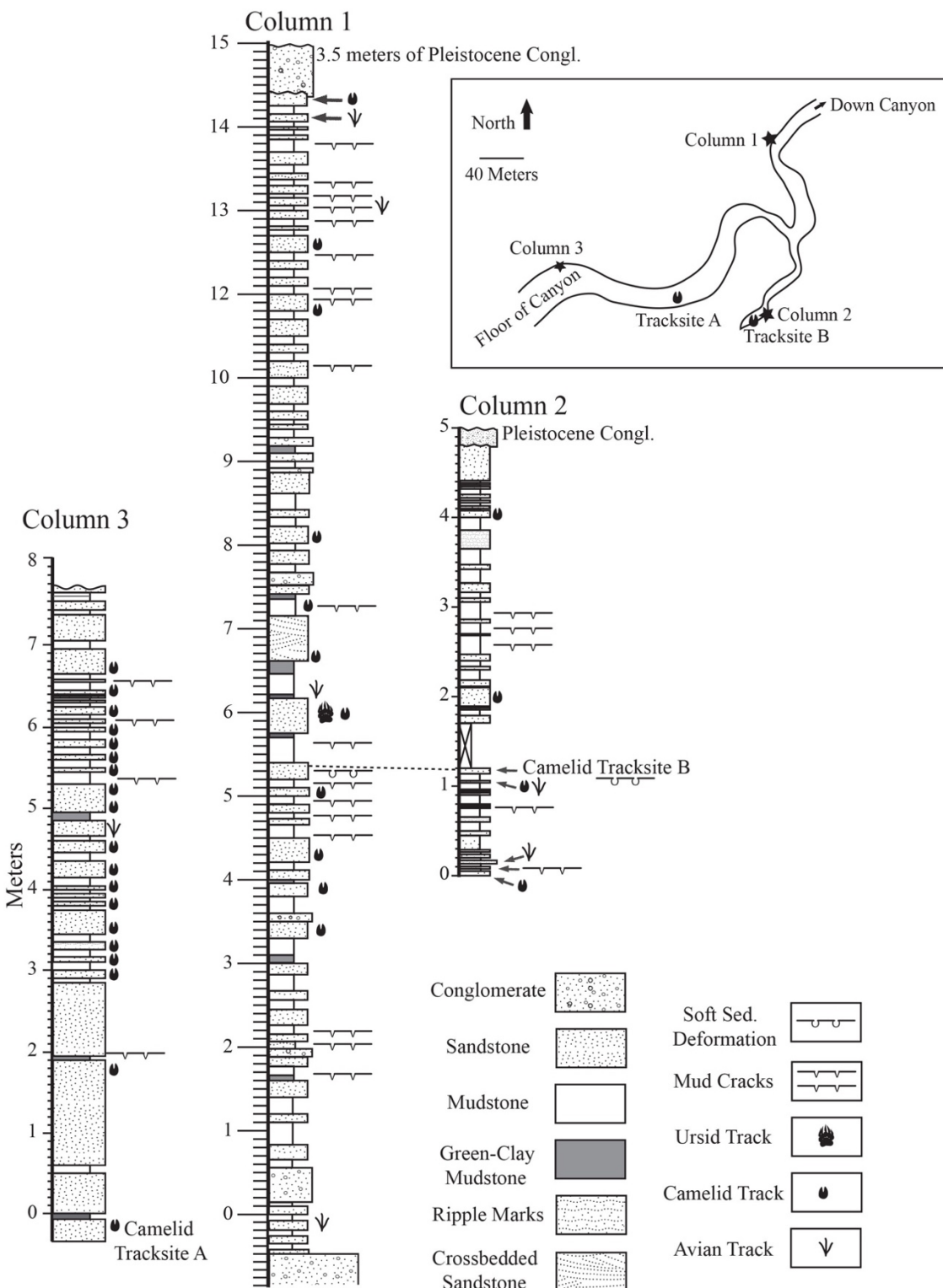


Figure 2.3 Stratigraphic Column 1 (most complete section), 2 section with camelid tracksite B. Column 3 with camelid tracksite A. Inset is a generalized map of the Muddy Creek Canyon locality showing the location of each stratigraphic column and camelid tracksite placement.

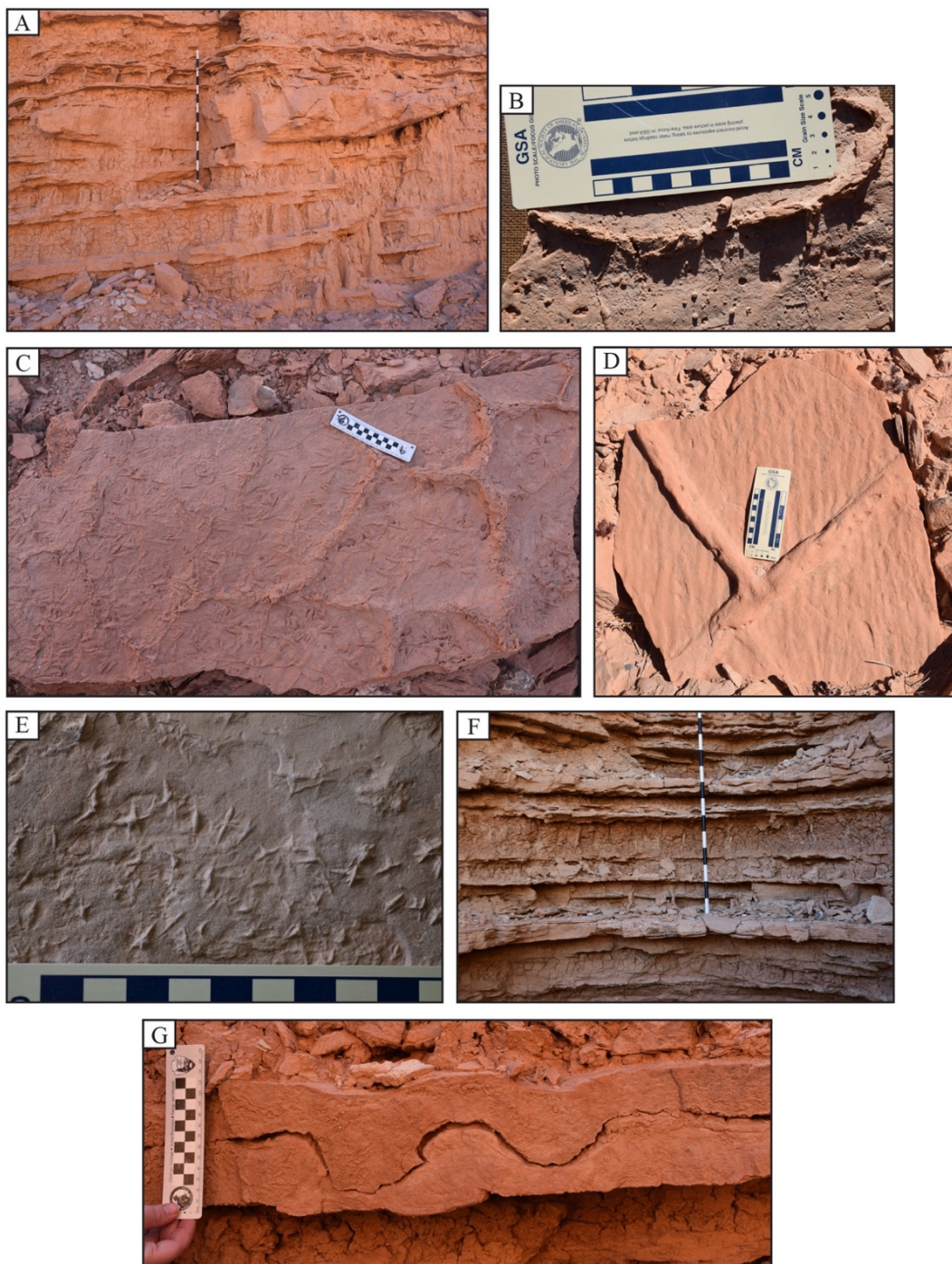


Figure 2.4 Sedimentary Structures: A: Channel in between mudstone and sandstone layers with large mudcracks just above channel, with 1.5 meter staff. B: Vertical, invertebrate burrows with mudcracks with 10 cm scale. C: Large mudcracks with avian trample tracks with 15 cm scale. D: Large mudcrack with ripple marks with 10 cm scale. E: Gypsum crystal casts with 10 cm scale. F: Side of canyon wall with cyclical sandstone and mudstone layers with 1.5 meter staff. G: Soft sediment deformation on Tracksite B sandstone layer, seen in Column B Figure 3 with a 15 cm scale.

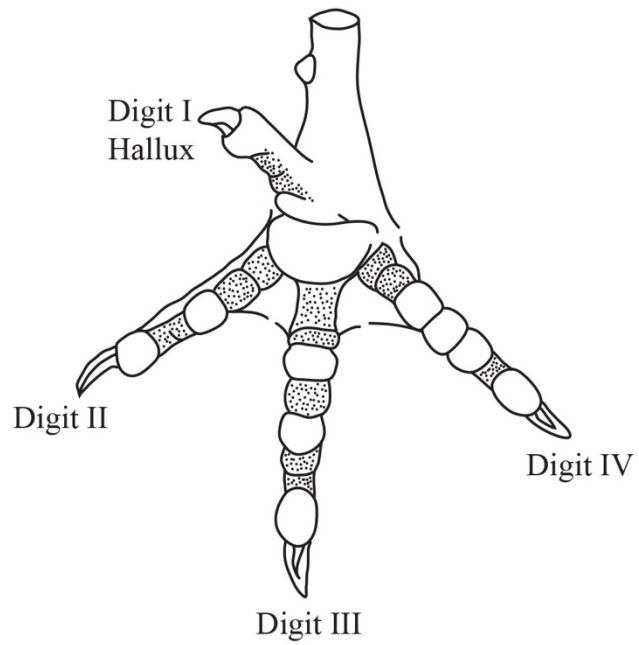


Figure 2.5 Avian foot terminology used in this chapter. Modern bird foot recreated and modified from Clark, 1993 and Lucas et al., 2007.

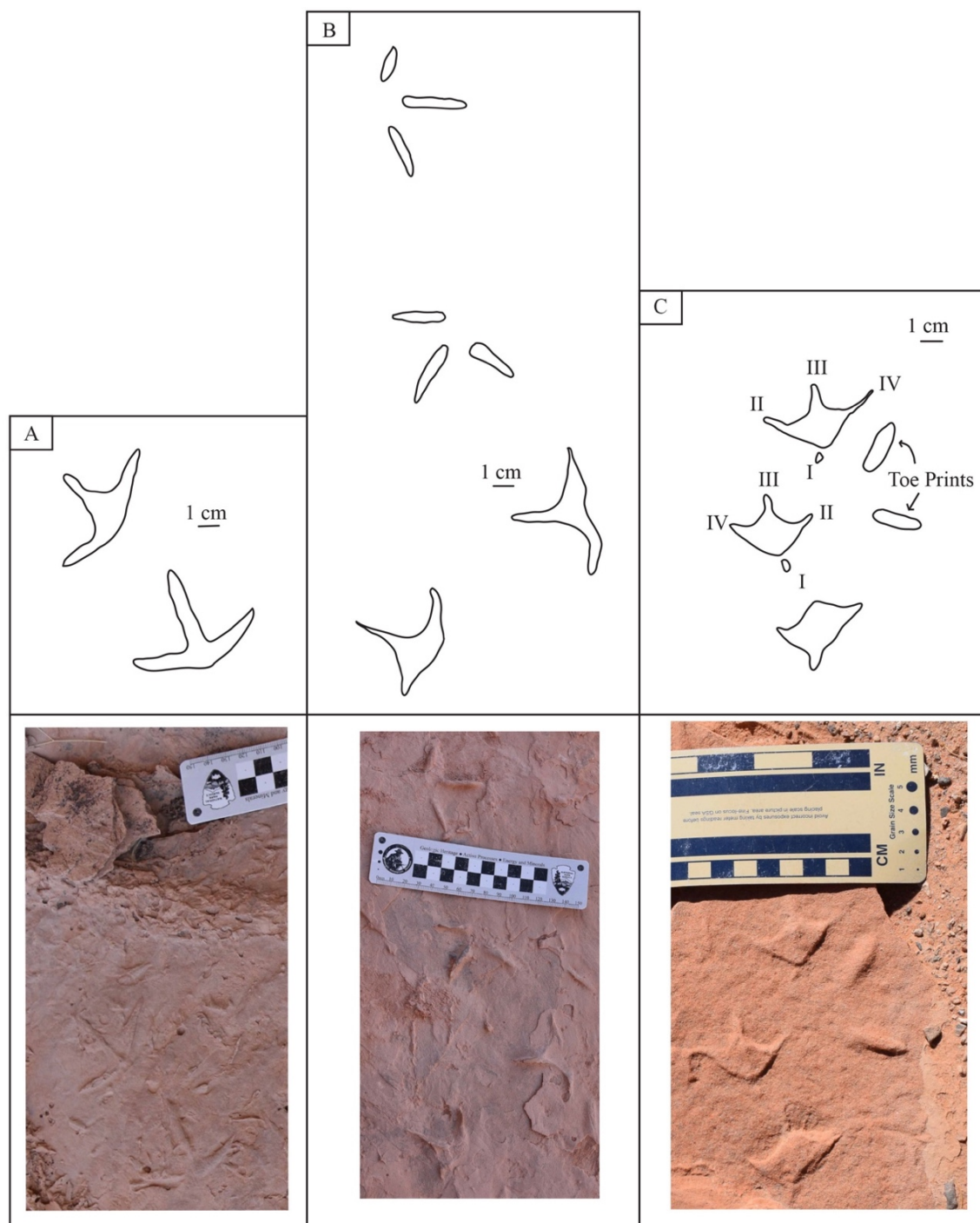


Figure 2.6 Examples of avian prints and trackways from different areas of the canyon. A and B are from same spot in the canyon as float. C is several meters down the canyon, also in float. A: Two full prints with one print having visible webbing. B: 4 prints, two on the bottom are a possible trackway. C: Possible *Anatipeda* (small, webbed prints), 3 prints with visible webbing and hallux. An additional two large toe prints that do not show enough morphology to diagnose an ichnotaxon past *Avipeda* (possibly from one foot of a larger bird?). Outlines with 1 cm scale bars. A and B have 15 cm scales and C has a 10 cm scale.

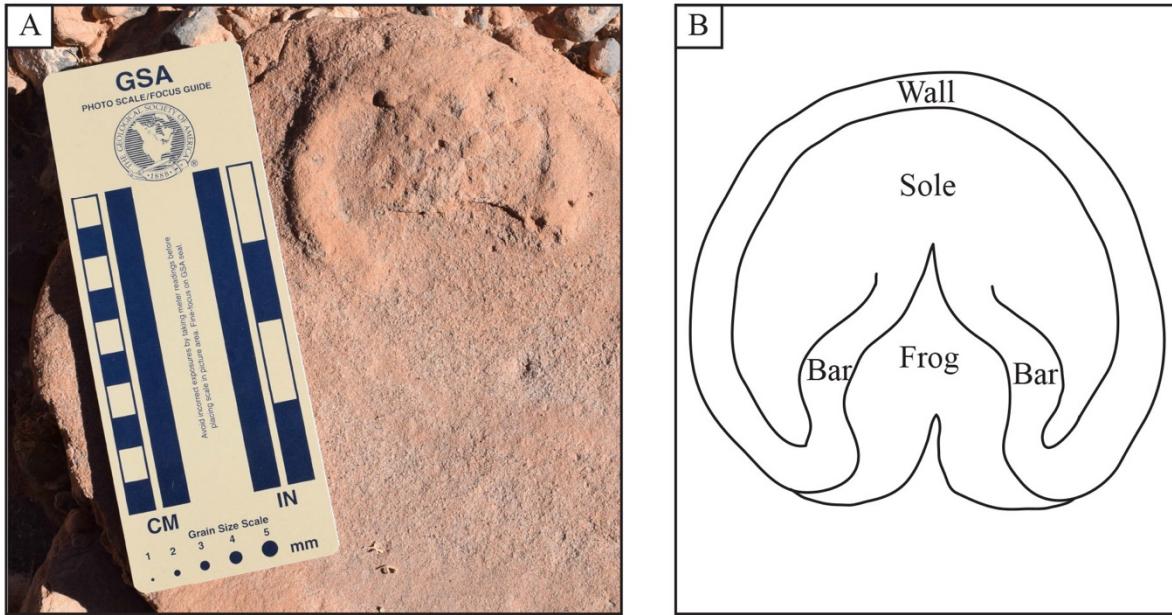


Figure 2.7 Single equid print A: Convex hyporelief (cast) with no frog or bars visible with a 10 cm scale. B: A modern forefront horse hoof with the underside structure, modified from Sarjeant and Reynolds (1999).

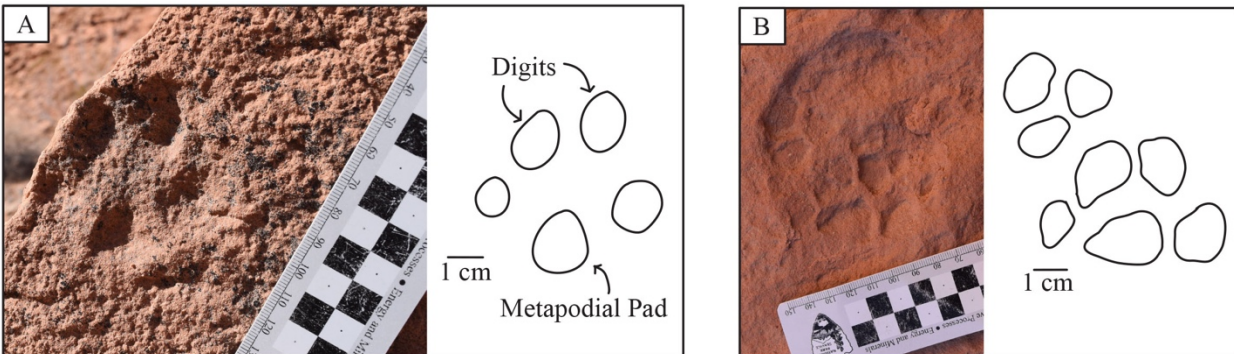


Figure 2.8 Two felid prints in float from different areas of the canyon. A: 5.5 cm long and 5 cm wide. B: One print with second partial print. Scales are 15 cm.

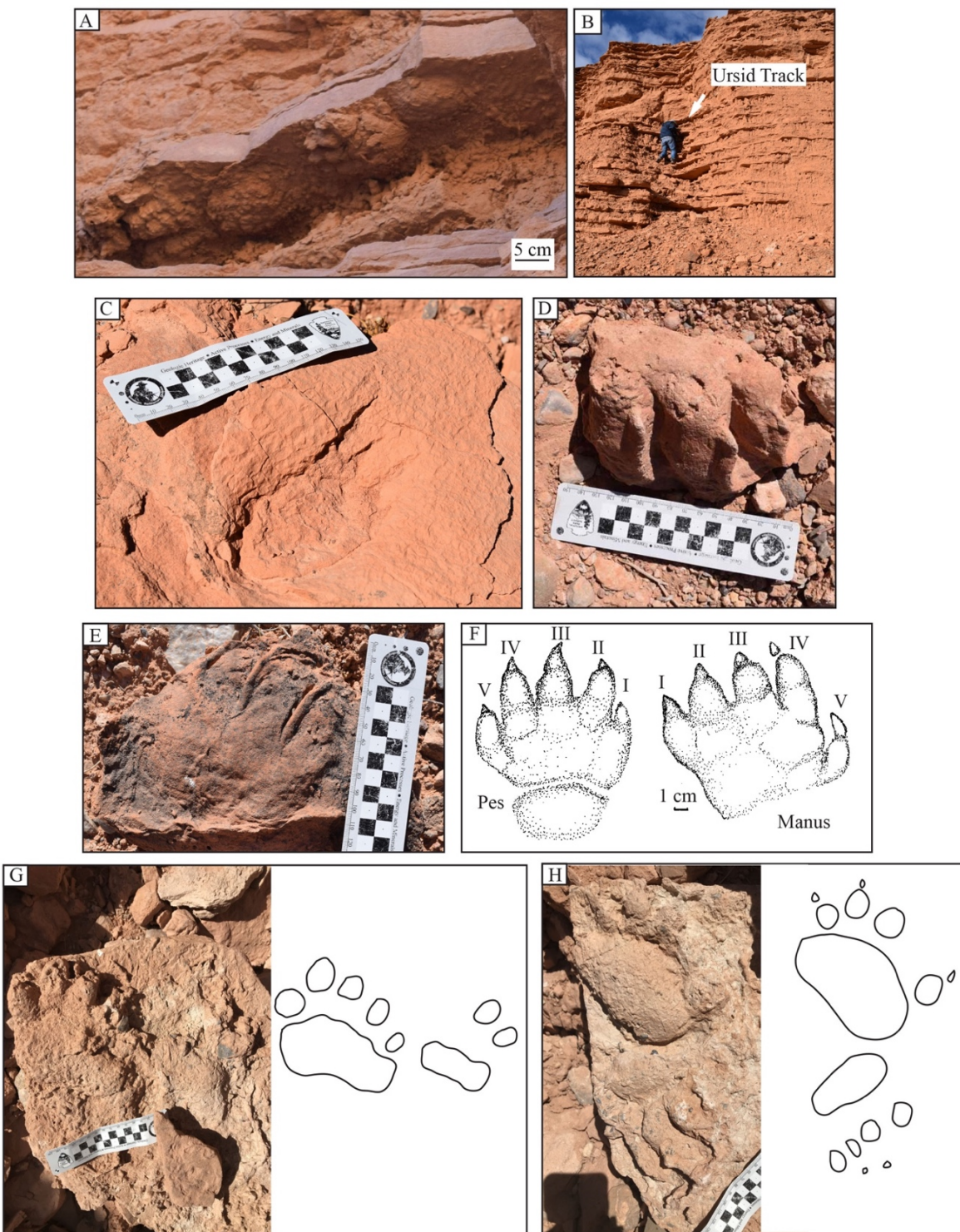


Figure 2.9 There are 8 ursid tracks at this site. All are casts except for D, a mold. A: Bear Tracksite casts with three prints visible with scale of 5 cm. The middle print that has the pads and nails present is a hind foot. B: One cast print in float. C: Three digits with nails. D: Right pes mold with visible nail scrapes. E: *Platykopus ilycalculator* right pes (paratype) and manus (holotype), modified from Sarjeant et al., (2002). Rulers are 15 cm.



Figure 2.10 North facing outcrop pictures of camelid footprint tracksites A and B. A is Tracksite A with field assistant Barry Luchs. B is Tracksite B.

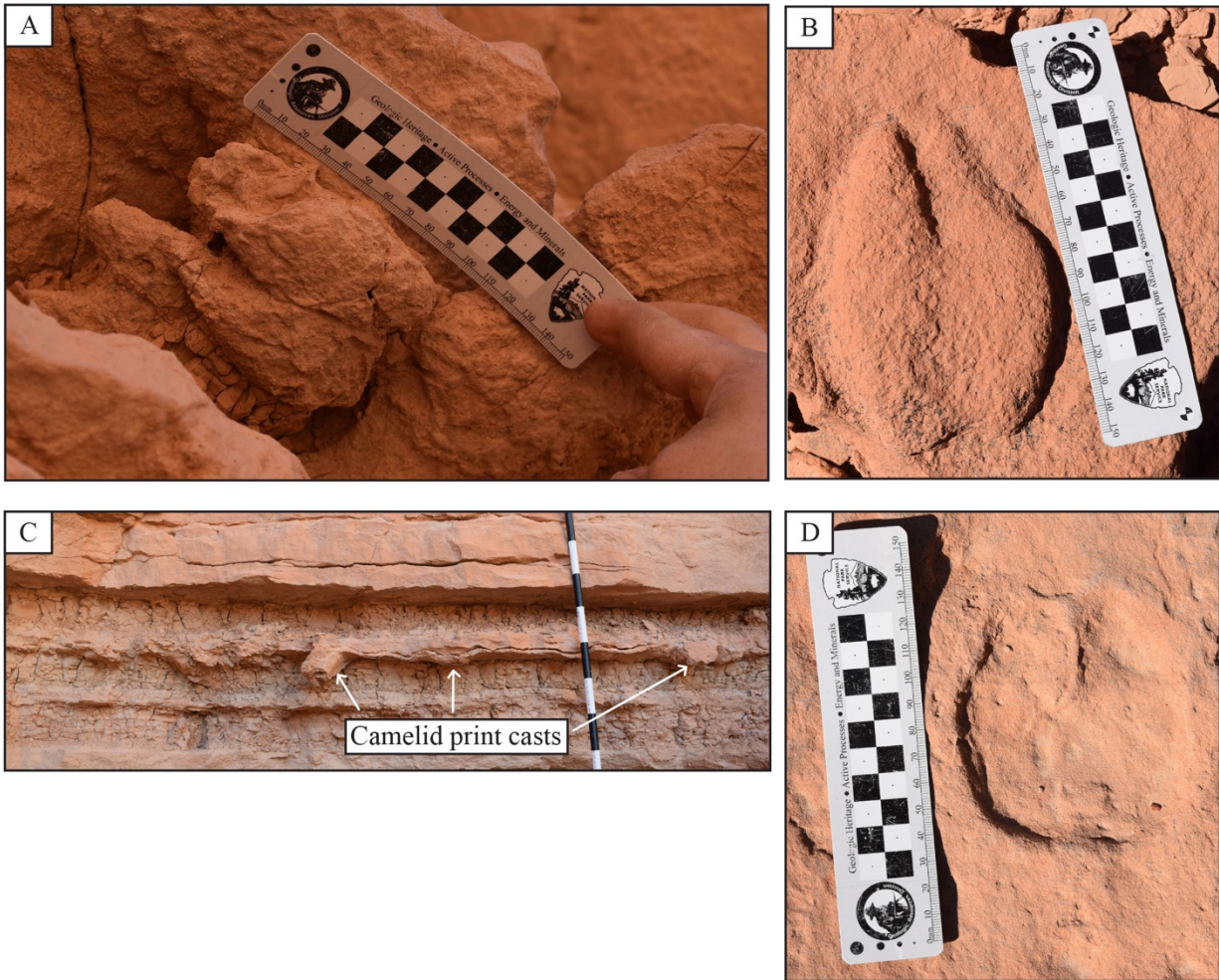


Figure 2.11 Examples of camel prints from different locations and horizons within the Muddy Creek Canyon Tracksite. A: Two prints, possible overprint of manus and pes, on underside of layer at edge of canyon, convex hyporelief (cast) with a 15 cm scale. B: Concave epirelief (cast), with a 15 cm scale. C: Convex hyporelief (cast) camelid prints in situ on side of canyon in Column 3 (Fig. 3), with 1.5 meter staff. D: Single print from Tracksite A, concave epirelief (mold), with a 15 cm scale.

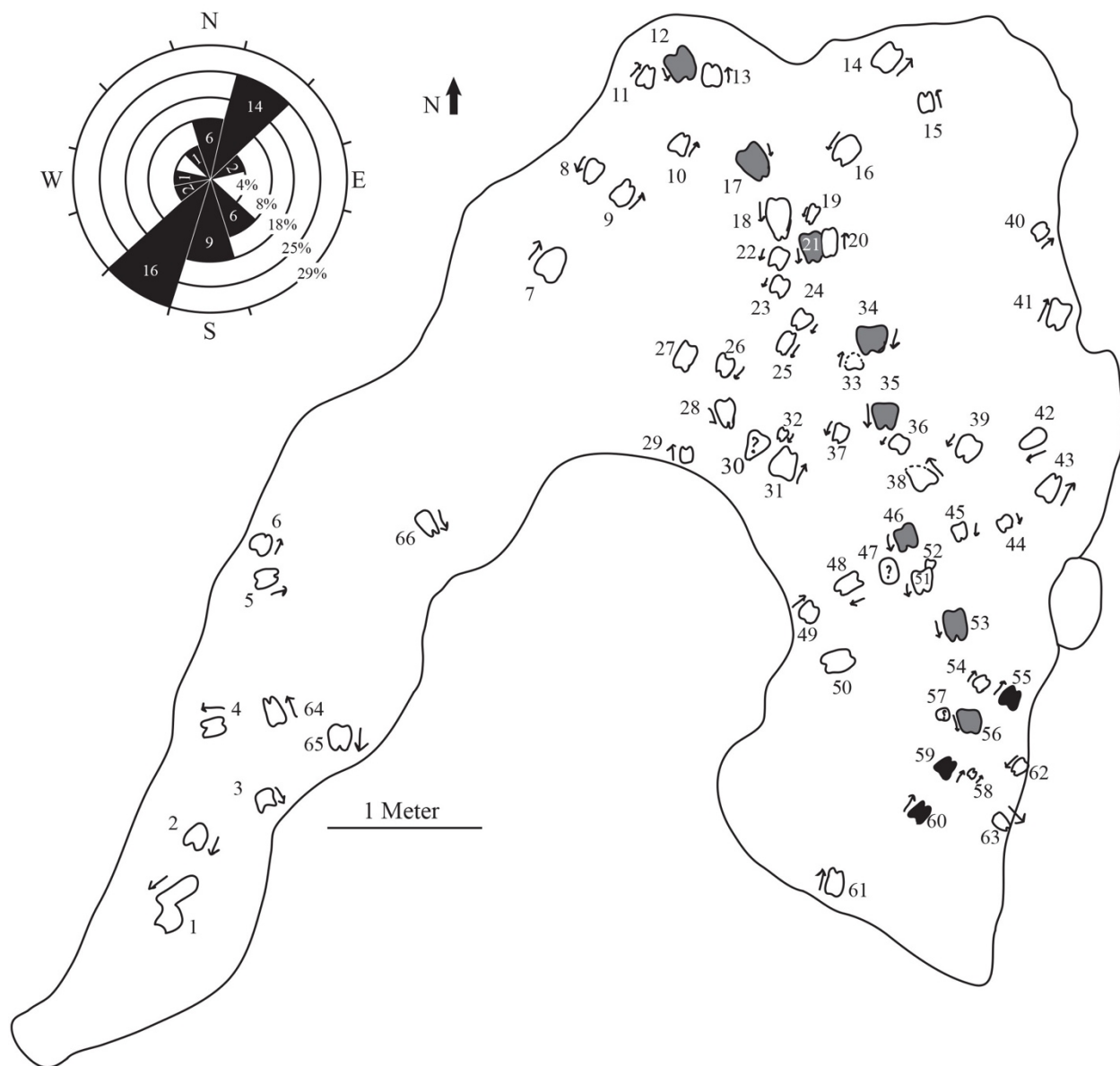


Figure 2.12 Map of Camelid Tracksite A, located on the floor of the main canyon. Some prints are partial prints, which are not included in the footprint size analysis. Arrows indicate the direction of travel. Question marks denote prints in which the features are poorly presented. Trackways with more than two prints are indicated in gray or black. The rose diagram indicates that the tracks are travelling mainly in the southwest and northeast directions. The scale bar is 1 meter.

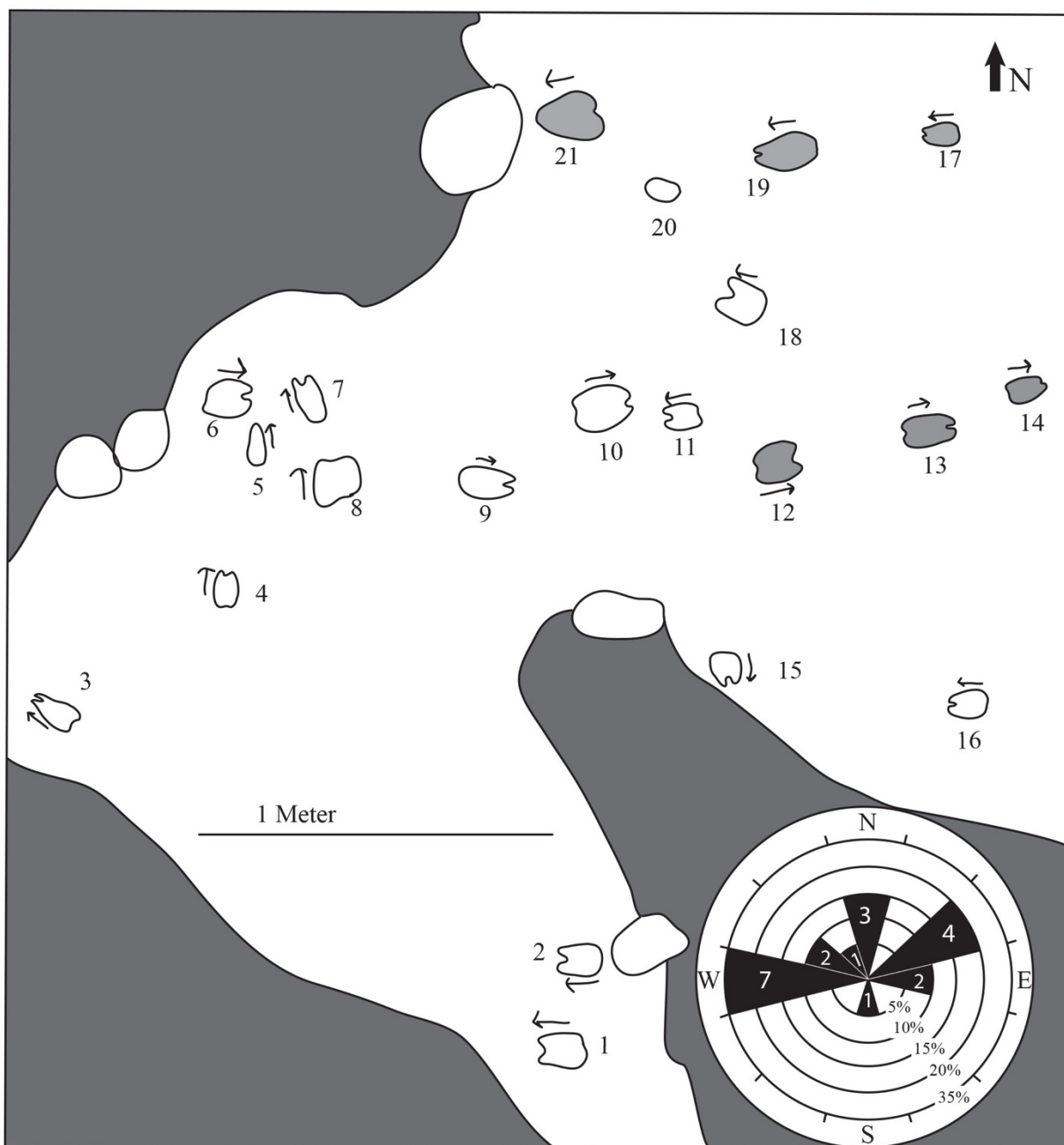


Figure 2.13 Map of Camelid Tracksite B. Arrows indicate direction of travel for each individual print. Gray prints indicate possible trackways of three or more prints. The rose diagram indicates no dominant direction but an approximate bimodality. The scale bar is 1 meter.

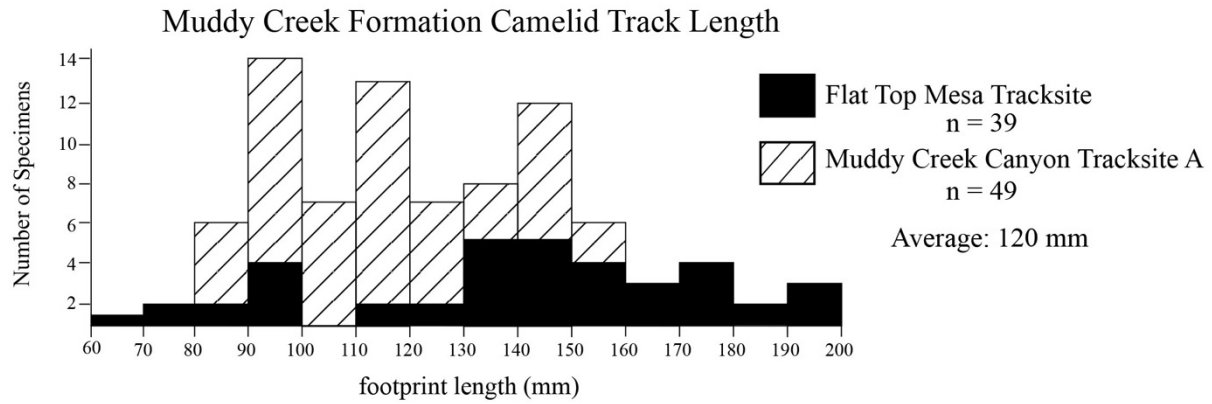


Figure 2.14 Camelid footprint length histogram, modified from Chapter 1. Diagonal lines are prints from Tracksite A of the Muddy Creek Canyon locality. Black columns are prints from the Flat Top Mesa Tracksite from Chapter 1.

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Chapter 3: An Ursid and Camelid Ichnofauna in the Miocene China Ranch Beds Near Tecopa, California

3.1 Abstract

A new ursid trackway has been located in the Miocene China Ranch Beds near Tecopa, California. This increases the ichnofaunal diversity to include camelids and ursids. This ursid track is significant because it is the oldest ursid trackway recorded in North America. It also may record a galloping gait, which is not otherwise documented for ursids in the Neogene. Sixteen camelid tracks are also described and documented. Miocene ichnofaunas are important for understanding the paleogeographic range of mammals in rock units that do not have fossilized bone material. The depositional environment is interpreted to be similar to that of the Muddy Creek Formation, the shoreline of an ephemeral lake. The ichnofaunal diversity of the China Ranch Beds is lower than other Miocene ichnofaunas. With the recent discovery of an ursid trackway, it is important to monitor the China Ranch Beds for more exposures in the future.

3.2 Introduction

A recently discovered ursid trackway, along with previously discovered camelid tracks, occurs in the China Ranch Beds, near the China Ranch Date Farm, southeast of Tecopa, California (Figs. 3.1, 3.2). These are among the oldest known ursid tracks globally. Pre-Miocene ursid tracks are unknown, and Miocene ursid tracks are rare. They have been reported only from North America and Iran (Fig. 3.3). Ursid skeletal fossils are more common than ursid ichnofossils, appearing first in the early Miocene in Eurasia and becoming relatively abundant and diverse in the Pliocene. A synthesis of Miocene North American ursid trackways and skeletal fossils is provided in figure 3.3.

The China Ranch Beds are an important new data point for Neogene ichnotaxa with the discovery of these ursid tracks. Along with previously reported camelid tracks (Scott, 1985; Lofgren et al., 2006a, b), in this chapter I describe 16 more camelid prints. Camelid tracks are common in the Miocene of southwestern North America, as reviewed in Chapters 1 and 2. Understanding the evolutionary history of various mammalian taxa is achieved by using a combination of fossil tracks and skeletal material. Tracks help to elucidate geographic range and behaviors that are not available with skeletal material alone. The purpose of this study is to document and describe the China Ranch Beds ichnofauna.

3.2.1 Brief Overview of Ursid Evolution

Ursid evolution is poorly known and heavily debated due to a dearth of skeletal material. The history of ursid evolution in the Neogene is similar to that of several other mammal groups. Smaller, less differentiated ancestors immigrated to North America from Asia where they thrived, diversified, and became much larger in the Neogene (McLellan and Reiner, 1994). Having evolved from canids in the Oligocene, ursids immigrated to North America in two major pulses, both in the Miocene, across the Bering Land Bridge (Qui, 2003). The first immigration event occurred roughly 20 million years ago during the early Miocene (Burdigalian Age) with the introduction of the genus *Ursavus* (McLellan and Reiner, 1994). The second wave occurred 7-8 million years ago during the late Miocene (Tortonian Age) with the immigration of *Indarctos* and *Agriotherium* (Qui, 2003).

Indarctos and *Agriotherium* are considered large ursids with tooth and skull morphology supporting the hypothesis of a more omnivorous diet in these derived taxa, diverging from the ancestral carnivorous diet (Sorkin, 2007). *Indarctos*, which was the first to show herbivorous tendencies, apparently shifted its habitat preference from closed canopy to open savanna when

needed (Viranta, 2004). In the Pliocene, the giant ursid *Arctodus* appears in the fossil record in North America. These ursids have also been found to have skeletal morphology suggesting herbivory, supporting the hypothesis that late Miocene ursids were more omnivorous than carnivorous (Sorkin, 2007). In addition to the view that late Neogene ursids were omnivorous, Figueirido et al. (2010) hypothesized that the carnivorous component of their diet involved more scavenging than active hunting.

3.3 Geologic Setting and Previous Work

The China Ranch beds were deposited between 12-8 Ma, which straddles the boundary between the Clarendonian and Hemphillian North American Land Mammal Ages (NALMA)(McMakin, 1997). A pumiceous tuff that is interbedded within the upper section of the China Ranch Beds has been dated at 8.5 Ma (John Caskey, personal communication, 2021). The ursid tracks described here are stratigraphically below this tuff. They are probably Hemphillian in age, but their precise age is not known.

The China Ranch Beds are exposed southeast of Tecopa, California, and extend from Sperry Wash to the Amargosa River (Scott, 1985)(Fig. 3.1). The sediments present within these beds are generally light tan to gray conglomerates, sandstones, siltstone-mudstones, and marls. Scott (1985) interpreted the depositional environment to be a small paleobasin with a playa-lake system. Sedimentary structures include ripple marks, mudcracks, and large amounts of gypsum. Gypsum is found in several different forms including lamina, euhedral crystals, and fibrous pods; some of the gypsum was re-worked and used by Scott (1985) as a proxy for an ephemeral lake. Plant fossils include possible palm fronds and roots (Scott, 1985).

The recently discovered ursid trackway is located within shoreline sediments, within member D of Scott (1985). This member consists of very fine-grained marl interbedded with

tuff and mudstone. The marl matrix is composed of calcareous material, with ostracods visible. The tracks crop out as natural casts on the base of a bed of erosion resistant marl. The marl overlies a less resistant layer of mudstone (Fig. 3.4).

The camelid tracks occur on two boulders, so their precise stratigraphic position is unknown. However, the boulders occur approximately in the same stratigraphic section as the ursid tracks. It is presumed, therefore, that the camelid and ursid tracks are roughly the same age and were made in similar environments. Two sets of camelid tracks have previously been reported from the China Ranch Beds. Scott (1985) reported camelid tracks in float by the China Ranch Date Farm, but these have not been relocated. Thirteen camelid tracks were collected along the Amargosa River and repositied in the Raymond Alf Museum of Paleontology (Lofgren et al., 2006 a, b). Two of these tracks (RAM 146, 165) were designated as the syntype for the ichnotaxon *Lamaichnum marcopodum* (Sarjeant and Reynolds, 1999).

3.4 Ichnology

3.4.1 Ursid Tracks

The ursid trackway, consisting of 3 tracks (Fig. 3.5), is located on the underside of an overhanging bed, about twelve meters above ground level on the face of a cliff (Fig. 3.2). These prints are convex hyporelief, or natural casts. These prints meet the characteristics of *Platykopus* isp. described by Sarjeant et al. (2002). They are plantigrade with 5 toes that are spread out in a semi-circle around the metatarsal pad with claw marks visible (Fig. 3.5). The bottom two tracks have shorter metatarsal pads, which is characteristic of manus prints. Print #1 is roughly 13 cm wide, while print #2 is roughly 11 cm wide. Manus prints are typically wider and shorter than pes prints; pes prints are typically more elongate (Fig. 3.3 prints 1 and 2). Print #3 has a more elongate metatarsal pad, which is characteristic of pes pads. It is roughly 12 cm wide and 10 cm

long. These tracks look similar to the modern grizzly bear tracks (Fig. 3.6). Modern grizzly bear prints have five toes that are close together and close to the metatarsal pad (Fig. 3.6D). The largest digit is on the outside of the foot, unlike humans where the largest digit is on the inside of the foot (Murie, 1974). The photograph of modern grizzly bear tracks (Fig. 3.6A) shows the manus print to be deeper than the two pes prints. This is due to the fact that modern bears put more weight on their fore limbs than their hind limbs (Shine et al., 2015). The ursid tracks in the China Ranch Beds also have more well defined manus prints than the one pes print, which I attribute to the same phenomenon. The bedding plane with ursid tracks in the China Ranch Beds contains other bumps and irregularities, but no other conspicuous vertebrate tracks.

The modern grizzly bear trackway in figure 3.6A,B records a walking symmetrical gait, with one manus track, then one pes track, and so forth, approximately symmetrical spaced. However, the China Ranch Bed ursid trackway records a galloping asymmetrical gait (cf. Hildebrand, 1977) in which the front feet were impressed in rapid succession, followed by a time lag, and then the left foot was impressed into the sediment (Fig. 3.5). In the terminology of Hildebrand (1977) this pattern is a gallop. In the terminology of Shine et al. (2015) it would be a canter (slow gallop) or gallop. This is the first demonstration of galloping in a Neogene ursid.

3.4.2 Camelid Tracks

A total of sixteen camelid tracks occur on two boulders roughly 150 meters from the ursid trackway. These tracks are also convex hyporelief, or casts, in marl. Fifteen of those camelid tracks are on a boulder facing south (Fig. 3.7) and one track is on a boulder facing north (Fig. 3.8). These camelid tracks have long been known to local residents. On the south-facing boulder (Fig. 3.7) a mold of the tracks was taken by R.E. Reynolds (Brian Brown, personal communication, 2021). But they have not been documented and described. These prints exhibit

the classic camelid track heart shape, with two digits, and they illustrate extramorphological variation (see Chapter 1). The average length of nine measurable prints is 95 mm. The average width of eight measurable prints is 78 mm. These dimensions place these prints within the ichnogenus *Lamaichnum* (Lucas and Hunt, 2007).

3.5 Discussion

The China Ranch Beds were deposited in a similar depositional environment to that of the Muddy Creek Formation, an ephemeral paleolake with large mudflats. Tracks were imprinted into wet mud that then dried out quickly enough to be covered by an influx of calcareous sediment. The sediments were later lithified, and eventually they were exposed and weathered to reveal the natural casts on the underside of the erosion-resistant marl bed.

One difference is that the China Ranch Bed ursid tracks were imprinted in mud and covered by marl, or calcareous sediments, whereas the Muddy Creek Formation tracks are in siliciclastic sediments only. The depositional environment of the China Ranch Beds marl unit is possibly a bench or platform which occurs at a lake margin. Figure 3.9 illustrates a generalized lake slope margin. The bench is just beneath the water line with some vegetation. This creates a shallow marsh environment adjacent to the mudflats where the bears and camels were walking. The prints dried out before the water level rose and marl was deposited on top.

Another difference between the Muddy Creek Formation and the China Ranch Beds is the presence of palm fossils within the China Ranch Beds (Scott, 1985). The palm fossils, which are not known to occur in the Muddy Creek Formation, help elucidate the type of environment during the time of deposition of the China Ranch Beds. Modern palms tend to be present in environments where water is continuously present (Purcell, 2012). This indicates a somewhat reliable source of water for animals in the China Ranch Basin.

Ichnofaunal diversity between the Muddy Creek Formation and the China Ranch Beds is also quite different. The Muddy Creek ichnofauna, with six ichnogenera, is more diverse than the China Ranch Beds ichnofauna, which has only two ichnogenera. Ichnofaunas of the Miocene that contain tracks of mammals and birds, range in diversity from one to seven ichnogenera (Ch. 2, Fig. 1). The new ursid tracks described in this chapter were apparently only recently exposed, which is why they were not previously reported. More ichnotaxa may eventually become exposed in the China Ranch Beds. In particular, bird tracks are likely to be present.

The most probable ursid trackmaker in the China Ranch Beds is *Indarctos* because it is the most common ursid in North America around the time of deposition. In Europe, *Indarctos* lived in a mixture of habitats through the late Miocene, from forested to open steppe and savannas (Viranta, 2004). As global temperatures started to fall at this time, seasonality increased and grasslands expanded into previously forested areas (Cerling et al., 1997; Janis et al., 2000, 2002; Zachos et al., 2001). Viranta (2004) suggested that *Indarctos* was able to shift back-and-forth between an herbivorous diet and a carnivorous diet when needed. This indicates the ability of ursids to adapt to different diets and environments, perhaps helping them to survive the Pleistocene megafaunal extinction (McLelland and Reiner, 1994).

3.6 Conclusion

The ichnofauna of the China Ranch Beds includes important Miocene ichnotaxa, including camelid tracks and one new ursid trackway of *Platykopus* isp. This ursid trackway is one of the oldest in North America and is also the first Neogene record of a galloping gait in ursids. The depositional environment is similar to that of the Muddy Creek Formation, the shoreline of an ephemeral lake. Because most Miocene ichnofaunas are typically more diverse than two ichnotaxa, it is likely that the China Ranch Beds will reveal more tracks and trackways

in the future, especially bird tracks. Therefore, the China Ranch Beds should be monitored for new track exposures.

3.7 Acknowledgments

Thank you to Matt McMackin for sharing the discovery of these new ursid tracks with us. Thank you to Brian Brown for access to these tracks from the China Ranch Date Farm property and for his interest in this research. And thank you to Cadie Hermansen for providing the photograph of a modern grizzly bear trackway.

3.8 Figures

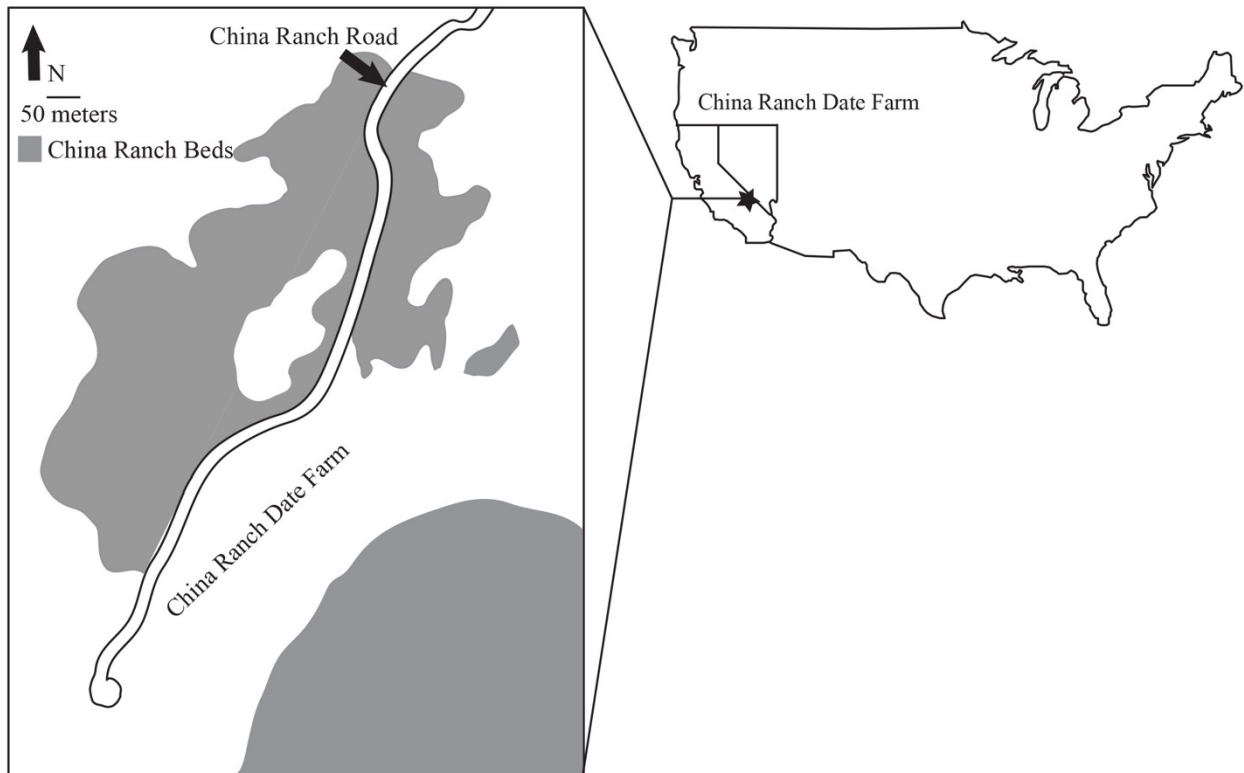


Figure 3.1 China Ranch Date Farm locality, a few miles southeast of Tecopa, California. Inset indicates generalized location of exposure of China Ranch Beds.

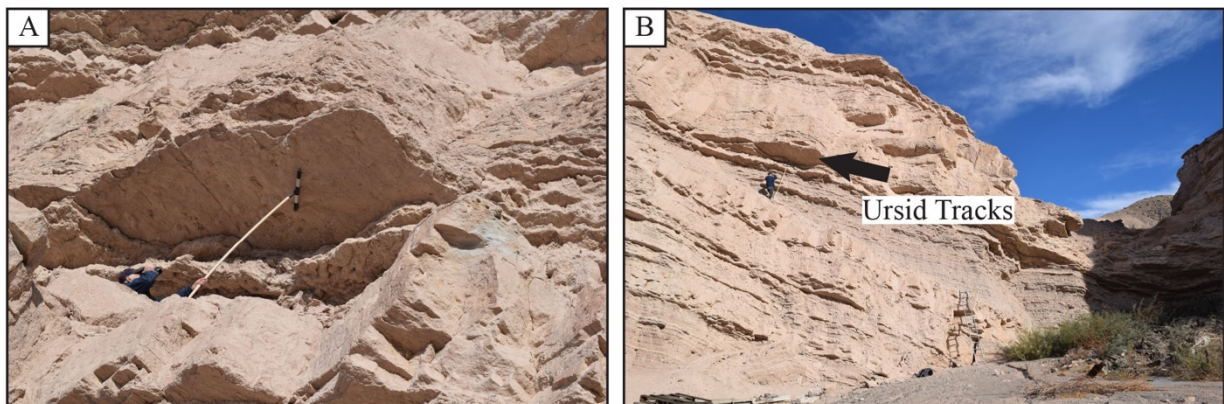


Figure 3.2 Ursid tracks at the China Ranch Date Farm locality. A: Steve Rowland holding a 0.5 m scale adjacent to the ursid tracks. The scale is attached to a white pole. The tracks occur on the bottom of marl bed. B: Location of ursid track exposure within canyon wall.

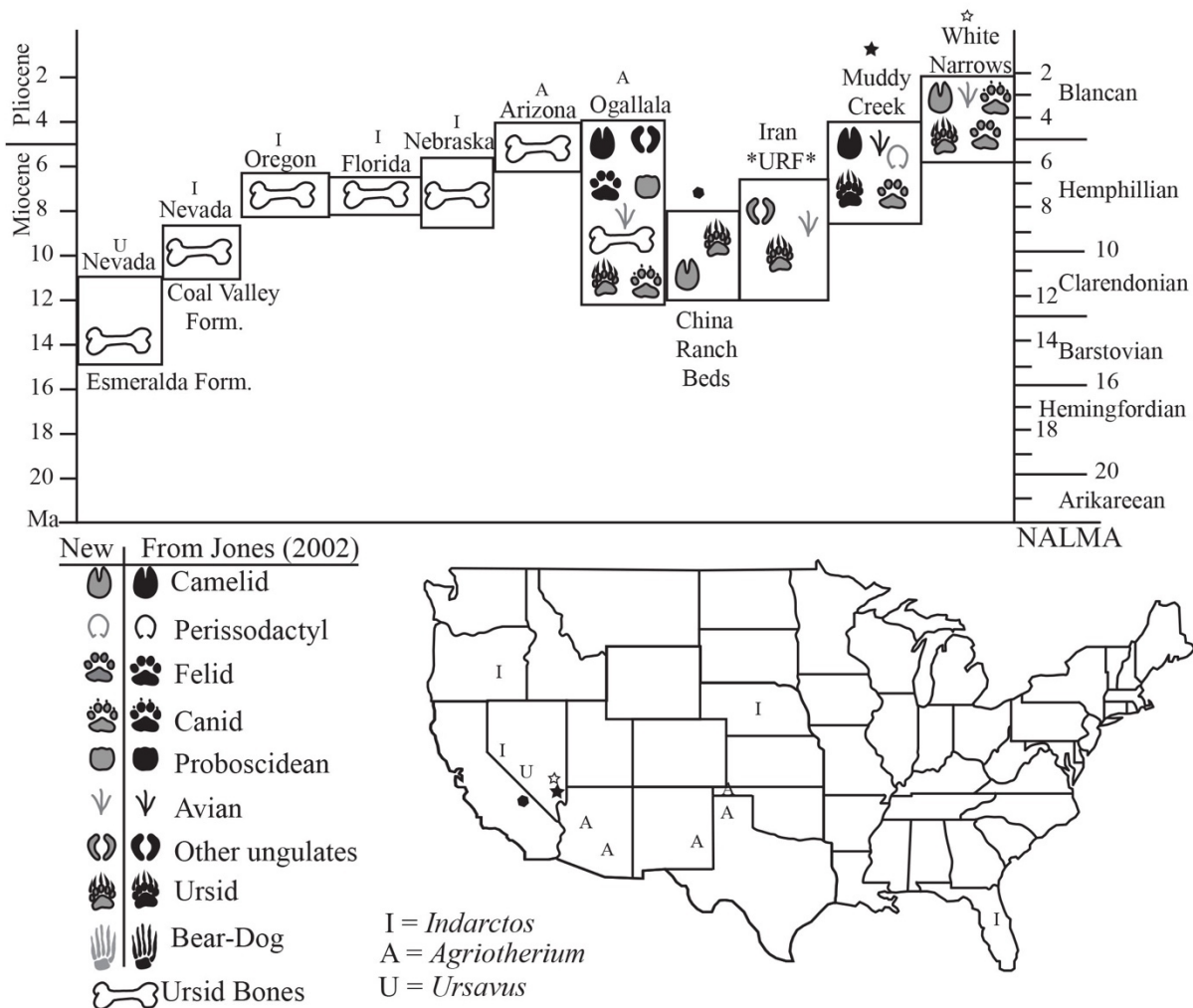


Figure 3.3 Miocene ursid track comparison in the United States with the exception of the URF. URF: Upper Red Formation at the Shokorchchi Area, Zanjan Province, NW Iran estimated to be mid-Miocene to Pliocene (Abbassi, 2010). Arizona: two formations: Big Sandy Formation and the Quiburis Formation (Morgan and White, 2005); China Ranch Beds: Chapter 3; Scott (1985); Lofgren et al. (2006a, b), Sarjeant and Reynolds (1999); Florida: Wolff (1978); Jiangzuo and Hulbert (2021); Muddy Creek Formation: See Chapter 2, Lofgren (2006a, b); Nevada: Esmeralda Formation (Ursavus: Stewart Spring Fauna): Stirton (1940), (Indarctos: Coal Valley Fauna), Macdonald (1959); Nebraska: Ash Hallow locality: Shultz and Martin (1975); Voorhies (1990); Ogallala: Texas: Lucas and Schultz (2007), Johnston (1937), Dalquest and Patrick (1989); New Mexico: Williamson and Lucas (1996); Oklahoma (Bones only): Hesse (1936), Savage (1941); Oregon: Rattlesnake Formation: Merriam et al. (1916); White Narrows Formation: Hunt and Lucas (2007), Lockley et al. (2007).

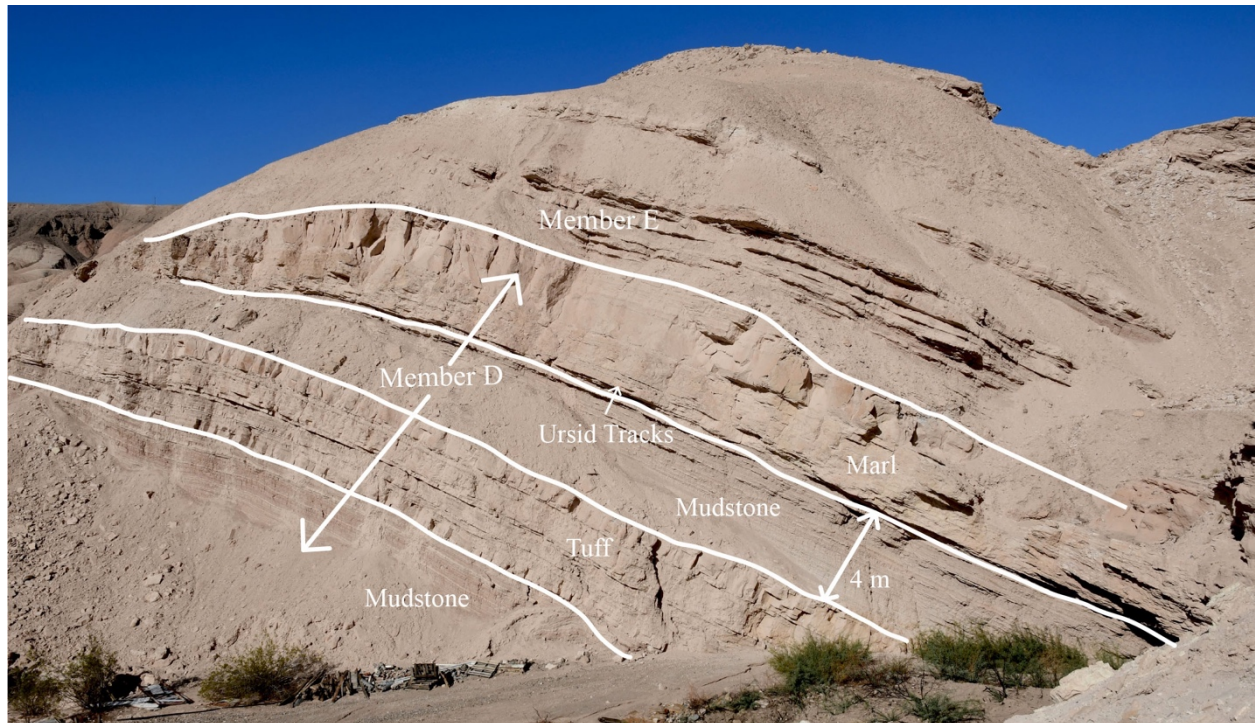


Figure 3.4 Generalized stratigraphy of the China Ranch Beds at the location of where the ursid tracks are exposed.

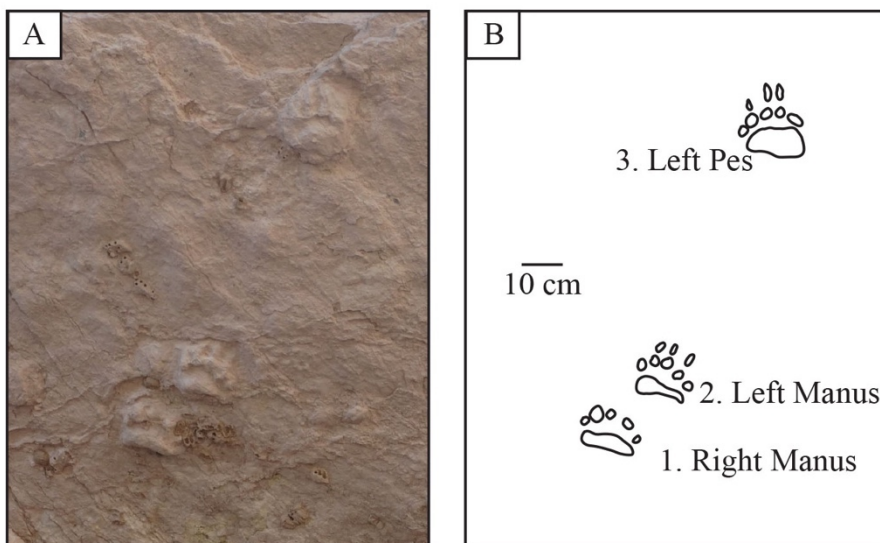


Figure 3.5 A: Photograph of ursid trackway. B: Outline of ursid trackway. Photograph courtesy of Matt McMackin.

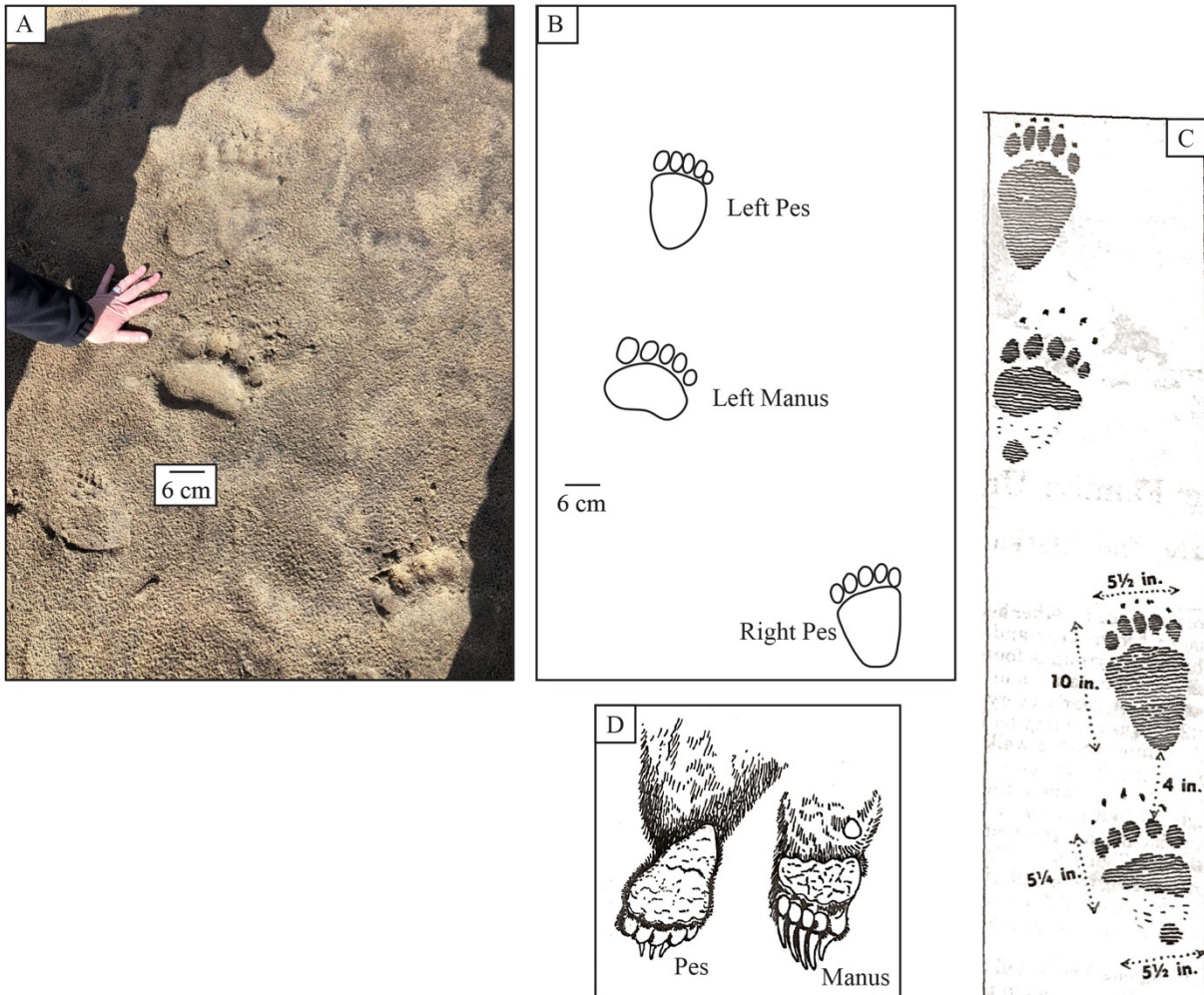


Figure 3.6 Modern ursid tracks. A: Photograph of one manus and two pes tracks of a grizzly bear near the Kustaten River in Alaska, courtesy of Cadie Hermansen. B: Outline of tracks. C: Generalized trackway of grizzly bear walking gait. D: Generalized drawing of modern ursid feet. Both C and D are modified from Murie (1974).



Figure 3.7 A: Fifteen camelid tracks in float on a south-facing boulder near the China Ranch Date Farm. Scale is 15 cm. B: Outline of camelid tracks with 15 cm scale bar.



Figure 3.8 Single camelid track indicated with circle, on north facing boulder near the China Ranch Date Farm. Scale is 15 cm.

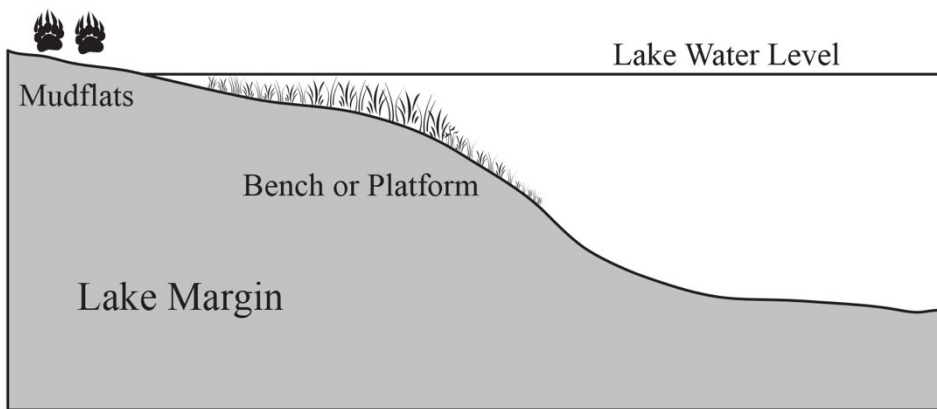


Figure 3.9 A generalized lake margin setting. The shallow bench area, just below the shoreline, is a large enough area for ursids to walk through and indicates possible depositional environment. Modified from James and Jones (2015) and Gierlowski-Kordesch (2010).

3.9 References

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Chapter 4: The Composition and Structure of Terrestrial Mid-Miocene

Mammalian Communities in the Great Basin

4.1 Abstract

The mid-Miocene Climatic Optimum (MMCO) is a brief warming period during a generalized decreasing trend in temperatures through the Neogene. It has been shown that Great Basin mammalian species richness also experienced a peak at the MMCO, followed by a downtrend, mimicking the temperature trends. However, community structure within individual faunas has not been analyzed. This study uses two faunas to compare community structure. The first being the Tonopah Local Fauna in southeastern Nevada, deposited during the MMCO, and the second being the Robbins Quarry Fauna in southern California, deposited just after the MMCO. Species richness of carnivores is surprisingly high compared to herbivore species richness in both faunas. Browsing and grazing herbivore species also occur in both faunas, but browsers give way to grazers, presumably in response to the increase in grassland habitat.

4.2 Introduction

Global temperature generally decreased throughout the Neogene, with a brief warming interval in the Miocene known as the Mid-Miocene Climatic Optimum (MMCO). The MMCO lasted from about 17 to 14 Ma. After about 14 Ma, temperatures declined throughout the remainder of the Neogene and into the Quaternary (Zachos et al. 2001) (Fig. 4.1).

The mammalian taxonomy of the MMCO within terrestrial communities in the Mojave Desert/Great Basin region has been well studied (Badgley et al., 2014, 2015). However, the structure of these communities has not been analyzed. It has been established that during the mid-Miocene in North America, there was an anomalously high species richness of browsing ungulates in the Great Plains, presumably in response to elevated primary productivity and

possibly the spread of C₄ grasses (Janis et al., 2004). This high species richness of browsing ungulates has not been documented in the Great Basin region. It is also not known how the structure of Miocene terrestrial communities in the Great Basin responded to the MMCO.

Ecological models recently derived from the study of modern communities (Carbone and Gittleman, 2002; Hatton et al., 2015; Blanco et al., 2021) now permit a more detailed analysis of the structure of paleocommunities. In this chapter we apply those models to the analysis of the structure of Barstovian communities of the Great Basin to examine how the structure of terrestrial mammalian communities responded to the MMCO in the Mojave/Great Basin region. We hypothesize that MMCO faunas in this region experienced high species richness among both browsing herbivores and carnivores than in post-MMCO and modern communities. To test this, we selected two MMCO fossil faunas from the Mojave/Great Basin region: the Tonopah Local Fauna (TLF) and the Robbins Quarry Fauna (RQF). The TLF of the Siebert Formation was deposited as the MMCO hit its peak, around 15 Ma, and the RQF of the Barstow Formation was deposited at the tail end of the MMCO around 13.5 Ma (Fig. 1) (Bonham and Garside, 1979; Browne, 2002). Both faunas occur within the Barstovian North American Land Mammal Age (NALMA). These two very diverse fossil faunas, both of which have been interpreted to have accumulated in lake-margin settings, are more representative samples of species richness within their respective mid-Miocene communities than faunas that conflate species from different communities.

4.2.1 Mammalian Species Richness in the Mid-to-Late Miocene

Generally speaking, mammalian species richness within the Great Basin peaked during the MMCO. Increases among carnivores, perissodactyls, and rodents accounting for most of this peak (Fig. 4.2A). Proboscideans experienced a brief interval of increasing diversity between 14

Ma and 9 Ma, and then disappeared from this region after 9 Ma (Fig. 4.2A). Ungulate (hooved mammals; perissodactyls and artiodactyls) species richness gradually decreased after the MMCO. These changes in diversity were at least partially driven by the formation of the Basin and Range topography, coinciding with a shift to a more arid climate (Badgley et al., 2014, 2015). Mammalian species richness within the Great Basin has seen a significant shift to large numbers of rodent species, with a corresponding reduction in perissodactyl species richness (Fig. 2). In this study we focus on ungulates and carnivores, which we infer to be the most faithfully represented taxa in the TLF and RQF faunas.

4.2.2 The Tonopah Local Fauna

The Barstovian age Tonopah Local Fauna (TLF) is a Miocene mammal assemblage from a single site that was discovered in 1922 by H. G. Ferguson near Tonopah, Nevada (Fig. 4.3). The formation in which the TLF occurs, has been variously referred to as the Siebert Formation, the Tonopah Formation, and the Esmeralda Formation. We use the name Siebert Formation in this study, following Bonham and Garside (1979). The Siebert Tuff, which lies just below the TLF collection site (Fig. 4.4), has been dated at 15 Ma (Swisher, 1992).

Over several years the assemblage was excavated by paleontologists from the California Institute of Technology as site CIT 172, and then analyzed and described by P. C. Henshaw (Henshaw, 1938, 1940). Later, the collection was transferred to the Natural History Museum of Los Angeles County, where it remains today, consisting of approximately 950 specimens. Since then, the TLF specimens have been largely unstudied, with the exception of a re-examination of carnivore taxonomy (Wang et al., 1999). An updated list of taxa originally identified by Henshaw (1938, 1940) is provided in Table 4.1. The collection site has also been deserted and

the initial excavation of the site has mostly been filled in by cliff collapse, but remnants of collection activity, including a dilapidated picnic table, remain (Fig. 4.5).

The following information about the collection and state of the TLF is summarized from Henshaw (1938, 1940). Fossils were found 3 meters below the surface, within a 1.5-meter-thick vertical section composed of gray-green siltstones and sandstones with interbedded chert (Henshaw, 1940). The assemblage consists mostly of teeth and leg bones, with vertebrae and ribs noticeably absent. The specimens are highly silicified and were found in no consistent orientation. Most of the bones were found within a meter of each other, with some scattering of bones. Henshaw (1940) inferred that minimal transport had occurred. Weathering of bones is also minimal, suggesting rapid burial (except for a few rounded teeth), but slowly enough for some bones to have been lost from the assemblage. Henshaw (1940) inferred that the chert within the fossil-bearing sediment records the mixing of fresh and saltwater. He noted no sedimentary evidence of channels within the collection site, but it is possible that the entire outcrop is a channel fill.

Within 3 km east of the collection site, there is an outcrop of invertebrate-bearing light gray shales and marls (Spurr, 1905)(Fig. 4.6). Henshaw (1940) interpreted this outcrop to be a lake margin that was contemporaneous with the mammal-bearing interval. The molluscs found within this sediment indicate fresh water, with three taxa of gastropods (*Lanx* cf. *L. undulatus*, *Planorbis* cf. *P. cordillerana*, and *Viviparus turneri*) and one bivalve (*Pisidium meeki*) (Henshaw, 1940). Henshaw concluded that the lake was somewhat salty, but with a low enough salinity level to make it tolerable for freshwater molluscs. He also referenced an outcrop with fish scales, allegedly indicating a saline lake. However, we were unable to locate this outcrop. Henshaw (1940) concluded that this area was a large saline lake, with tributary streams in a

delta, surrounded by an arid plain. The bones presumably were transported to the lake by fluvial processes before being buried.

The minimum number of individuals (MNI) represented in the TLF is 231. Of these, 196 are attributed to herbivores, 31 to carnivores, one to a lagomorph, and two to rodents (Table 4.2). Fewer than 20 are juveniles (Henshaw 1938, 1940). Henshaw (1940) concluded that this assemblage represents a normal distribution of mammals in an arid plain habitat adjacent to a saline lake.

4.2.3 *The Robbins Quarry Fauna*

The Robbins Quarry Fauna (RQF) is from a site in the Mud Hills, near Barstow, California (Fig. 4.3). This late Barstovian assemblage is one of the youngest and most diverse assemblages of the Barstow Formation (Reynolds and Browne, 2015). The assemblage sits between two dated beds, the Hemicyon Tuff, dated at 14 Ma, and the Lapilli Sandstone, dated at 13.4 Ma (MacFadden et al., 1990) (Fig. 4.4).

The area from which this assemblage was collected was first excavated in the 1930s by the Frick Laboratory of the American Museum, New York. In the 1960s, a newly discovered bone bed was named the Robbins Quarry bone bed. It was intermittently excavated by the San Bernardino County Museum until 1998 (Reynolds and Browne, 2015). Subsequently, Browne (2002) described the stratigraphy and the fossil material from this quarry. A list of taxa and MNI compiled by Reynolds (2020) is presented in Table 4.2. The majority of the fossil material is equid (Browne, 2002), representing two species of *Scaphohippus*, a genus that is not present in the Tonopah Local Fauna. Reynolds and Browne (2015) summarized the data from this site, concluding that the assemblage was a death assemblage that accumulated at a lake margin, with evidence of predation, transport, and trampling before fossilization. This assemblage has a high

diversity of carnivores, which Reynolds and Browne (2015) attributed to niche partitioning, as described by Behrensmeyer (1975).

The RQF is in the Upper Member of the Barstow Formation. The sedimentology of the site was not described by Browne (2002) or Reynolds and Browne (2015), but the Upper Member of the Barstow Formation in the area of the collection site was described by Woodburne et al. (1990) as fine-grained lacustrine and fluvial claystones, mudstones, and shale. Browne (2002) interpreted the depositional environment of the assemblage as a floodplain. Reynolds (2020) interpreted the environment to have been a wetland with a combination of brush and grasslands, with marginal riparian trees such as palms. During the transition out of the MMCO, when the RQF accumulated, temperatures were dropping and seasonal precipitation was increasing (Zachos et al., 2002; Loughney et al., 2019).

4.3 Assemblage Comparison

The minimum number of individual animals (MNI) is very different between these assemblages, with TLF having an MNI of 231 (Henshaw, 1940) and RQF a value of only 55 (Reynolds and Browne, 2015) (Table 4.2). This difference is mainly due to the abundance of bones of the hypsodont equid *Merychippus* and the hypsodont antilocaprid *Paracosoryx* within the TLF, both of which are medium-size herbivores. However, both assemblages have higher amounts of equid material than those from any other taxon. The rodent content of the TLF is very scant at 2% of the total MNI, while the rodent content within the RQF is much larger at 36% of the total MNI (Fig. 4.7). The large differences in MNI between these two assemblages and their differences with that of the Modern Great Basin fauna, are most likely due in part to differences in depositional environments and methods of collection. Therefore, a more meaningful comparison is the taxonomic similarity.

We used the Simpson coefficient of similarity to assess the taxonomic similarity of the two MMCO faunas (Simpson, 1943, 1960). This is calculated as S/N , with S being the number of co-occurring taxa, and N being the number of taxa within the assemblage with fewer taxa. The result is a value between 0 and 1, with 0 being the least similar and 1 being the most similar. The number of genera in the TLF is 18, with 19 in the RQF. The number of co-occurring genera is 8. Therefore, the Simpson Coefficient of Similarity at the genus level is $8/18 = 0.44$. This means these two faunas are not highly similar at the generic level. However, using the same metric, these assemblages are more similar at the familial level ($10/13 = 0.76$). This suggests that the two communities were very similar in terms of ecological structure, with different genera from some of the same families occupying similar niches.

Neither assemblage includes gomphotheres or ursids, although those groups were present in North America during this time. Both assemblages have been interpreted to occur in fluvial-lacustrine sediments, where a stream flowed into a lake. They both include a high diversity of carnivores, with seven genera in the RQF and nine genera in the TLF.

This carnivore diversity is significant in both assemblages. In general, carnivore diversity is low compared to herbivore diversity (Fig. 4.8). For a normal modern fauna, such as the Amboseli Basin in Kenya, there is commonly a high diversity of small herbivores, a lower diversity of large herbivores, and an even lower diversity of carnivores. The Amboseli Basin is a good modern analogue for Miocene fossil assemblages because of its relatively pristine ecosystem. It is possible that both assemblages are missing a cohort of smaller mammals (as suggested in the cenogram analysis in the next section). It is likely that the lake margin depositional environment of both faunas had a preservation bias against smaller mammals. Such bones may also have been more scavenged.

4.3.1 *Paleoenvironments*

The mid-Miocene (~18–12 Ma) was a very dynamic time in southwestern North America, both tectonically and climatically (DeCells, 2004; Janis et al., 2004; Colgan and Henry, 2009; Badgley et al., 2014). The old Farallon Plate was a motionless slab beneath the Sierra Nevada Batholith and the Nevadaplano (a high plateau in portions of Nevada and adjacent states). At about 17 Ma the Farallon Plate began to delaminate from the overlying continental lithosphere and disintegrate into the mantle (Colgan and Henry, 2009). This led to the collapse of the Nevadaplano and major east-west widening of the Basin-Range geologic province. The result was the creation of north-south-trending ranges and valleys in the Great Basin region.

4.3.2 *Cenogram Analysis*

A cenogram (Fig. 4.9) compares body sizes of herbivore taxa to illustrate community structure and infer ecosystems within a fossil assemblage (Legendre, 1986; Legendre and Hartenberger, 1992). The y-axis is the natural log of body mass, which allows taxa with large size differences to be placed on the same graph. Points representing each taxon are evenly spaced on the x-axis, in descending order of body mass, from left to right. Such a graph allows “missing” sizes to stand out. Cenograms are particularly useful for recognizing the presence or absence of medium-size herbivores. If medium-size herbivores are absent, identified by a gap in the cenogram between values of 5–9, a semi-open environment is indicated. If medium-size herbivores are present, and the cenogram would show a continuous slope with no gaps in body size and a forested environment is indicated (Legendre and Hartenberger, 1992).

A cenogram has been created for both the TLF (Fig. 4.9a) and RQF (Fig. 4.9b) assemblages. Body mass estimates are from Pagnac (2005), which were derived from Voorhies

(1969) and Novak (1999). There is a conspicuous gap in body mass between values 5 and 7 in each cenogram, which suggests a partially open environment. Smaller body sizes between values of 2 and 5 (8–105 kg) are missing in both cenograms, suggesting an incomplete fossil record for these two assemblages.

Recent studies of the vegetation during the deposition of the Barstow Formation indicate that environments during the MMCO varied between woodlands and forested grasslands with the development of dry, wooded grasslands by the time of the RQF (Loughney, 2017; Loughney and Badgley, 2017). The RQF cenogram fits this scenario, with a gap in the slope suggesting an arid environment with a partially open canopy. This interpretation is also supported by the dominance of hypsodont (grazing) ungulates in the RQF (Table 4.2).

The cenogram of Pagnac's (2005) that covers a portion of the Barstow Formation (Fig. 10) also suggests a partially open environment, with gaps between values 5 to 6. The gap between values 2 and 5 (8–105kg) in the TLF and the RQF cenograms (Fig. 4.9) is anomalous, which is not shown in the cenograms of Pagnac (2005). Pagnac (2005) used multiple assemblage data to construct the cenograms in Figure 4.10. Both the TLF and RQF are single-locality assemblages in which herbivores with size-range values between 2 and 5 may have been selectively excluded for unknown reasons.

Based on evidence from published analyses, cenogram analyses, and the relative abundance of browsing and grazing ungulates in the TLF and RQF faunas, we conclude that the environment of the TLF was a savanna-woodland, which became more arid and less wooded by the time of the RQF.

4.3.3 Community Structure

The structure of mid-Miocene mammalian communities of the Great Basin region emerges from the data presented in Tables 4.2, 4.3 and 4.4. These were communities with a diverse ungulate fauna and a diverse carnivore fauna. Hypsodont (having high-crowned teeth) ungulates are inferred to have been grazers, while brachyodont (having low-crowned teeth) ungulates are inferred to have been browsers (Janis et al., 2004).

Among the taxa of horses present in the TLF and RQF, the brachyodont (browsing) horse *Hypohippus* is present only in the TLF, along with the brachyodont rhinoceros *Peroceras*. The hypsodont (grazing) horse *Merychippus* is also present in the TLF and in fact dominates the fauna in terms of MNI (Table 4.2). Among artiodactyls, the TLF is dominated by hypsodonts, with three species of antilocaprids. However, the brachyodont camel *Aepycamelus* is also present (Table 4.2). This distribution of browsers and grazers within the TLF supports the conclusion that the environment included a mixture of grasslands and open-canopy woodland.

Approximately 1.5 million years later, when the RQF fauna was present, the brachyodont ungulates were less abundant. Among the horses, the brachyodont *Hypohippus* was gone, and only the hypsodont genus *Scaphohippus* was present (Table 4.2). However, the brachyodont camel *Aepycamelus* was still present in the RQF fauna, as was the brachyodont rhinoceros *Peraceras* (Table 4.2). The environment was still savanna-woodland, but evidently with more extensive grasslands than during the peak of the MMCO. While grazing and browsing herbivores were present in both faunas, the TLF is mostly dominated by browsers while the RQF is dominated by grazers. This change from TLF to RQF seems to support a transition from wooded to more open grasslands.

The apex predator in the Great Basin region during the MMCO was the giant bear-dog *Amphicyon*, which occurs in the TLF. It is absent from the RQF, although it occurs elsewhere in the Barstow Formation at the time of this fauna (Pagnac, 2005). *Amphicyon*, with a body mass as high as 550 kg, is among the largest mammalian terrestrial predators in Earth history, far exceeding the body mass of large male Siberian tigers (320 kg) (Sorkin, 2006). Bear-dogs were pursuit predators that preyed on ungulates. They probably pursued their prey over long distances and dispatched them by tearing into their neck or ribcage (Sorkin, 2006).

Also among the carnivorans was an astonishing diversity of canids. Six species of canids occurred in the TLF, and four species occurred in the RQF (Table 4.2). Both faunas contain the small wolf-size hypercarnivore *Aelurodon asthenostylus* and the small fox-size canid *Leptocyon*. Among the canids, all but one species are borophagines. The largest of the borophagine canids, *Aelurodon*, with a body mass of 14–18 kg, was described by Wang and Tedford (2008) as a hypercarnivore. There is some speculation that borophagines hunted in packs (Van Valkenburgh et al., 2003). One can imagine a pack of larger borophagines hunting medium-sized equids and antilocaprids. Felids of various sizes were also present in both faunas, including the puma-size *Pseudaelurus intrepidus*, the bobcat-size *Nimravides*, and the small wolverine-size mustelid *Brachypsalis* in the TLF and an indeterminate mustelid in the RQF.

4.3.4 Carnivore-Prey Relationships

A general model for the scaling of predator density among mammalian carnivores indicates that 10,000 kg of prey supports a ~90 kg carnivore (Carbone and Gittleman, 2002). The number of individual carnivores supported on a given biomass of prey increases at a predictable rate with decreasing body size of the carnivores. This relationship is quantified as:

$$(\text{number of carnivores per } 10,000 \text{ kg of prey}) = 89.1(\text{carnivore mass})^{-1.05}$$

This rule for the scaling of carnivore density (Carbone and Gittleman, 2002) was slightly modified by Hatton et al. (2015) who showed that across a wide range of ecosystems, as prey biomass increases, the ratio of predator-to-prey biomass decreases (Fig. 4.11). In other words, the trophic pyramid within an ecosystem becomes relatively more bottom-heavy as the biomass increases (Fig. 4.11).

These relationships between predator and prey biomass are relevant to our understanding of mid-Miocene terrestrial community structure because of the apparent increase in the species richness – and presumably biomass – of browsing ungulates in the mid-Miocene (Janis et al., 2004). As the biomass of ungulates increased in response to an increased level of primary productivity, the biomass of ungulate-supported carnivores would not have increased as fast and the trophic pyramid would have become more bottom heavy.

The body sizes of carnivores represented in the TLF and RQF faunas span more than two orders of magnitude, from the small, foxlike canid *Leptocyon*, with a mass of 2 kg or less (Wang and Tedford, 2008), to the large hypercarnivore bear-dog *Amphicyon*, with a mass of 550 kg (Sorkin, 2006), and the puma-size felid *Pseudaelurus* (Reynolds and Miller, 2002).

A study of predator-prey size relationships in an African large-mammal food web showed that carnivores selectively favor prey species approximately half to twice their mass. Each carnivore species has a preferred size range in its prey (Owen-Smith and Mills, 2008). Moreover, nearly all mortality among ungulate species up to the size of a giraffe (800–900 kg) occurred through the agency of predation. In the African study, only megaherbivores exceeding 1000 kg were exempt, or nearly so, from predation.

With respect to the mid-Miocene communities of the Great Basin, we infer that adult giraffe-camels (*Aepycamelus*), with a mass of approximately 1000 kg, could have been preyed upon by *Amphicyon*. Less massive ungulates were probably fair game for the puma-sized felid *Pseudaelurus*, and the small wolverine-size mustelid *Brachypsalis*.

Borophagine canids were dentally and cranially adapted for cracking bones (Werdelin, 1989; Wang and Tedford, 2008). The unusually high genus-level richness of borophagines in the mid-Miocene, with four genera in the TLF and three genera in the RQF (Table 4.2), can be partly explained by the abundance of ungulate skeletons of varying size. The borophagines presumably partitioned the bone-cracking niche in response to the large range of available bone sizes and densities.

Energetic constraints on the diet of terrestrial carnivores indicate that carnivores with a body mass greater than 21.5 kg fed mostly on prey that is greater than 45% of their own mass (Carbone et al., 1999). Thus, *Aelurodon asthenostylus* was almost certainly a hypercarnivore ($\geq 70\%$ of their diet being of animal origin) that hunted prey 10 kg or greater in size.

The biomass flux diagram in Figure 4.12 displays inferred predator-prey relationships between hypercarnivores and ungulates during the MMCO in the Great Basin region, based on the compositions of the TLF and RQF faunas and insights from modern terrestrial mammalian communities (Carbone et al., Owen-Smith and Mills, 2008). As suggested in Figure 4.12, the smaller borophagine canids are inferred to have been mostly bone-crushing scavengers (Werdelin, 1989; Vann Valkenburgh et al., 2003).

4.4 Conclusions

This study is a preliminary look at the community structure of Great Basin faunas during and after the MMCO. Through the transition out of the MMCO, the environment transitioned

from warmer woodlands to cooler grasslands while the Nevadaplano collapsed into the Basin and Range topography of the Great Basin. The resulting topographic heterogeneity doubtlessly contributed to high species richness in this region during the mid-Miocene (Badgley, 2010). However, our hypothesized high species richness for browsers and carnivores is only partially supported by the data; species richness of carnivores was indeed very high, but species richness of browsers was not particularly high. Both the TLF and RQF have a combination of browsing and grazing herbivores, but grazers are more abundant in the RQF, reflecting the presence of more grassland habitat. Carnivore species richness was surprisingly high in both faunas. In general, species richness declined after the MMCO (Fig. 2A).

4.5 Tables

Table 4.1: Taxa of the Tonopah Local Fauna, updated from Henshaw (1938, 1940).

List of Tonopah Local Fauna Taxonomy with Updates Where Applicable				
Taxonomic Identification			Original Identification by Henshaw	Reference
Artiodactyla	Antilocapridae	<i>Merycodus hookwayi</i>		
		<i>Paracosoryx loxocerus</i>	<i>Merycodus loxocerus</i>	Davis, 2007
	Camelidae	<i>Aepycamelus stocki</i>	<i>Alticamelus stocki</i>	Macdonald, 1956
Carnivora	Amphycionidae	<i>Amphicyon</i>		
	Canidae	<i>Aelurodon asthenostylus</i>	<i>Aelurodon wheelerianus asthenostylus</i>	Wang et al., 1999
		<i>Leptocyon vafer</i>		
		<i>Micromarctus confertus</i>	<i>Tomarctus paulus (type)</i>	Wang et al., 1999
		<i>Paracynarctus kelloggi</i>	<i>Tomarctus kelloggi</i>	Wang et al., 1999
		<i>Tomarctus brevirostris</i>		
		<i>Tomarctus hippophaga</i>		
	Felidae	<i>Pseudaelurus intrepidus</i>		
	Mustelidae	<i>Brachypsalis pachycephalus</i>		
Insectivora	Erinaceidae	<i>Brachyerix incertis</i>	<i>Metechinus fergusonii</i>	Rich, 1981
Lagomorpha	Leporidae	<i>Hypolagus parviplicatus</i>	<i>Hypolagus sp.</i>	Dawson, 1958
Perissodactyla	Equidae	<i>Hypohippus affinis</i>		
		<i>Merychippus calamarius</i>		
	Rhinocerotidae	<i>Peraceras superciliosum</i>	<i>Aphelops cristatus (type)</i>	Prothero, 1998
Rodentia	Muridae	<i>Copemys longidens</i>	<i>Peromyscus longidens</i>	?
	Sciuridae	<i>Tamias ateles</i>	<i>Eutamias ateles</i>	Hall, 1930

Table 4.2 Minimum Number of Individuals (MNI) of taxa between the Tonopah Local Fauna (TLF) and the Robbins Quarry Fauna (RQF) (Henshaw, 1938, 1940; Browne, 2002; Reynolds, 2020).

MNI within the TLF and the RQF					
Order/Family	Genus/Species	Size	Dentition/Diet	TLF	RQF
Artiodactyla					
Antilocapridae	<i>Merycodus</i> sp.		Hypsodont	-	6
	<i>Merycodus hookwayi</i>			3	-
	<i>Paracosoryx loxoceros</i>		Hypsodont	60	-
Camelidae	<i>Aepycamelus</i> sp.	~1000 kg	Brachyodont		3
	<i>Aepycamelus stocki</i>			8	-
Merycoidodontidae	Indeterminate	~220 kg	Hypsodont	1	-
Perissodactyla					
Equidae	<i>Hypohippus</i>	~360 kg	Brachyodont	12	-
	<i>Merychippus calamarius</i>	~220 kg	Hypsodont	110	-
	<i>Scaphohippus intermontanus</i>	Medium	Hypsodont	-	4
	<i>Scaphohippus sumani</i>		Hypsodont	-	5
Rhinocerotidae	<i>Peraceras superciliosum</i>		Brachyodont	3	-
	<i>Peraceras</i> sp.			-	1
Carnivora					
Amphicyonidae	<i>Amphicyon</i>	Large	Hypercamivore	2	-
Canidae	<i>Aelurodon asthenostylus</i>	~14-18 kg	Hypercamivore	4	1
	<i>Cynarctus galushai</i>	<15 kg	Omnivore	-	4
	<i>Leptocyon vafer</i>			6	-
	<i>Leptocyon</i> sp.			-	2
	<i>Microtomarctus conferta</i>	Interm.	Carnivore	5	-
	<i>Paracynarctus kelloggi</i>			3	-
	<i>Paratomarctus temerarius</i>	~20 kg		-	1
	<i>Tomarctus brevirostris</i>			1	-
	<i>Tomarctus hippohaga</i>			1	-
Felidae	<i>Nimravides</i> sp.	~18 kg	Carnivore	-	2
	<i>Pseudaelurus intrepidus</i>	~60-90 kg	Carnivore	5	1
Mustelidae	<i>Brachypsalis pachycephalus</i>	~13-25 kg	Carnivore	3	-
	Indeterminate			-	2
Insectivora					
Erinaceidae	<i>Brachyerix incertis</i>			1	-
Soricidae	<i>Paradomina</i> cf. <i>relictus</i>			-	1
Lagomorpha					
Leporidae	<i>Hypolagus parviplicatus</i>			1	2
Rodentia					
Cricetidae	<i>Copemys barstowensis</i>			-	1
	<i>Copemys longidens</i>			1	8
	<i>Copemys</i> cf. <i>tenuis</i>			-	4
Geomyidae	<i>Mojavemys lophatus</i>			-	1
Heteromyidae	<i>Cupidinimus halli</i>			-	2
	<i>Cupidinimus lindayi</i>			-	1
	<i>Perognathus minutus</i>			-	1
Sciuridae	<i>Miospermophilus</i> sp.			-	1
	<i>Tamias ateles</i>			1	1
Total number of MNI				231	55
Total number of genera				19	18

Table 4.3 Herbivore versus carnivore species diversity between the Tonopah Local Fauna (TLF) and the Robbins Quarry Fauna (RQF). Rodents and lagomorphs are omitted. Data compiled for TLF from Henshaw (1940), and RQF from Browne (2002), Reynolds and Browne (2015), and Reynolds (2020).

Herbivore			Carnivore		
	TLF	RQF		TLF	RQF
Equidae	2	2	Amphicyonidae	1	0
Rhinocerotidae	1	1	Canidae	6	4
Antilocapridae	2	1	Felidae	1	2
Camelidae	1	1	Mustelidae	1	1
Merycoidodontidae	1	0			
Totals	7	5		9	7

Table 4.4 Carnivores and ungulates of the Mid-Miocene Tonopah Local Fauna

Carnivora

Family/Subfamily	Taxon	Body mass (kg)	Paleoguild	Remarks	References
Amphicyonidae	<i>Amphicyon</i> sp.	~500	hypercarnivore	pursuit predator of large prey	Sorkin, 2006
Canidae/Borophaginae	<i>Aelurodon asthenostylus</i>	23	hypercarnivore	solitary ambush hunter of large prey	V V et al., 2003; W & T, 2008
Canidae/Borophaginae	<i>Tomarctus brevirostris</i>	18	hypercarnivore	possibly hunted in packs	V V et al., 2003; W & T, 2008
Canidae/Borophaginae	<i>Tomarctus hippohaga</i>	14	hypercarnivore	possibly hunted in packs	V V et al., 2003; W & T, 2008
Canidae/Borophaginae	<i>Microtomarctus conforata</i>	7	hypercarnivore	possibly hunted in packs	V V et al., 2003; W & T, 2008
Canidae/Borophaginae	<i>Paratomarctus temerarius</i>	11	omnivore/scavenger	"coyote-size, generalized predator"	W & T, 2008
Canidae/Borophaginae	<i>Paracyanarctus kelloggi</i>	?	omnivore/scavenger	"medium-size omnivore"	W & T, 2008
Canidae/Caninae	<i>Leptocyon rafer</i>	<2	omnivore/scavenger	foxlike; hunted small, quick prey	W & T, 2008
Felidae	<i>Pseudaelurus intrepidus</i>	~55		size of a small puma	Rothwell 2003
Mustelidae	<i>Brachypsalis</i>		fossorial carnivore/scavenger	size of large badger/small wolverine	Pagnac, 2005

Perissodactyla

Equidae	<i>Hypohippus</i> sp.	~400	browser (brachiodont)		MacFadden 1986
	<i>Merychippus calamarius</i>	~220	grazer (hypsodont)		MacFadden 1986
Rhinocerotidae	<i>Peraceras superciliosum</i>	1,800	grazer (brachodont)		Pagnac 2005

Artiodactyla

Antilocapridae	<i>Merycodus hookwayi</i>	9	grazer (hypsodont)		Pagnac 2005
	<i>Paracosoryx loxoceros</i>	9	grazer (hypsodont)		Pagnac 2005
Camelidae	<i>Aepycamelus stocki</i>	~1,000	browser (brachyodont)		
Merycoidodontidae	Indeterminate sp.	220	grazer (hypsodont)		

V V et al., 2003 = Van Valkenburgh et al., 2003

W & T, 2008 = Wang and Tedford, 2008

4.6 Figures

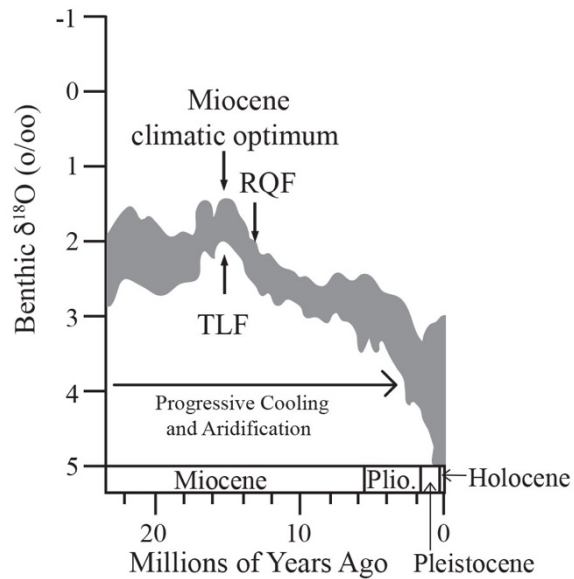


Figure 4.1 Global temperature change from the early Miocene to the present. The X-axis is in millions of years. The Y-axis is $\delta^{18}\text{O}$ ratio values from deep-sea foraminifera. TLF = Tonopah Local Fauna; RQF = Robbins Quarry Fauna. Modified from Badgley et al. (2014).

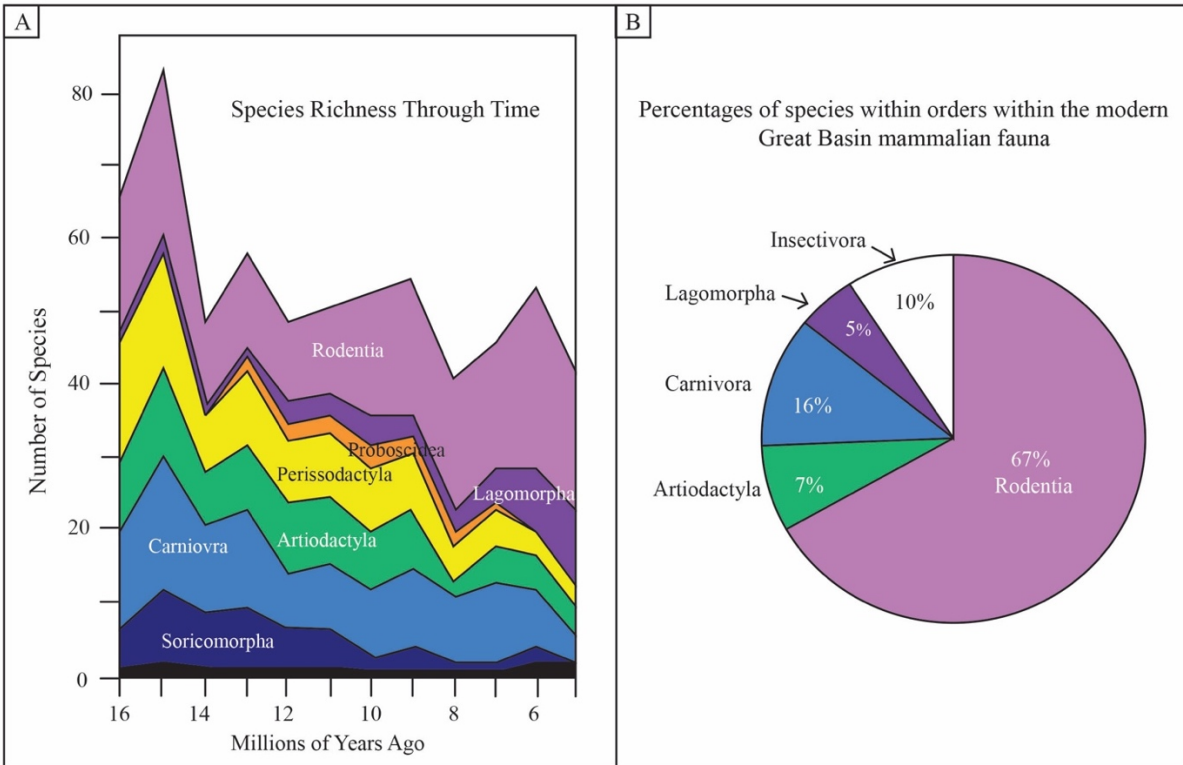


Figure 4.2 A: Species richness through the Miocene between 16-5 Ma in the Great Basin. The black at the bottom represents species in other orders. B: Modern mammal diversity in the Great Basin, in terms of percentages of species within orders. Data are from Badgley et al. (2014, 2015).

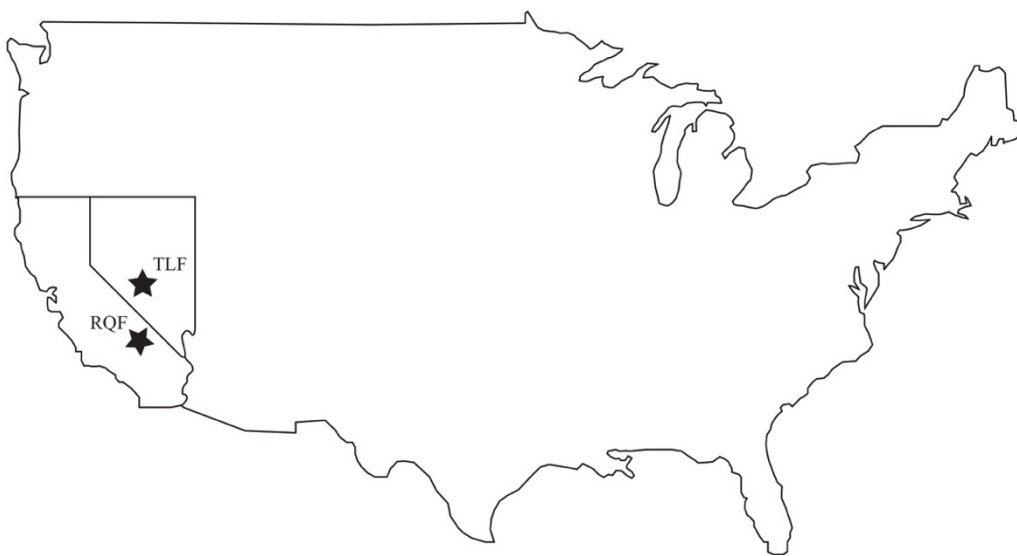


Figure 4.3 Locality of the Tonopah Local Fauna (TLF), near Tonopah, Nevada, and the locality of the Robbins Quarry Fauna (RQF), near Barstow, California.

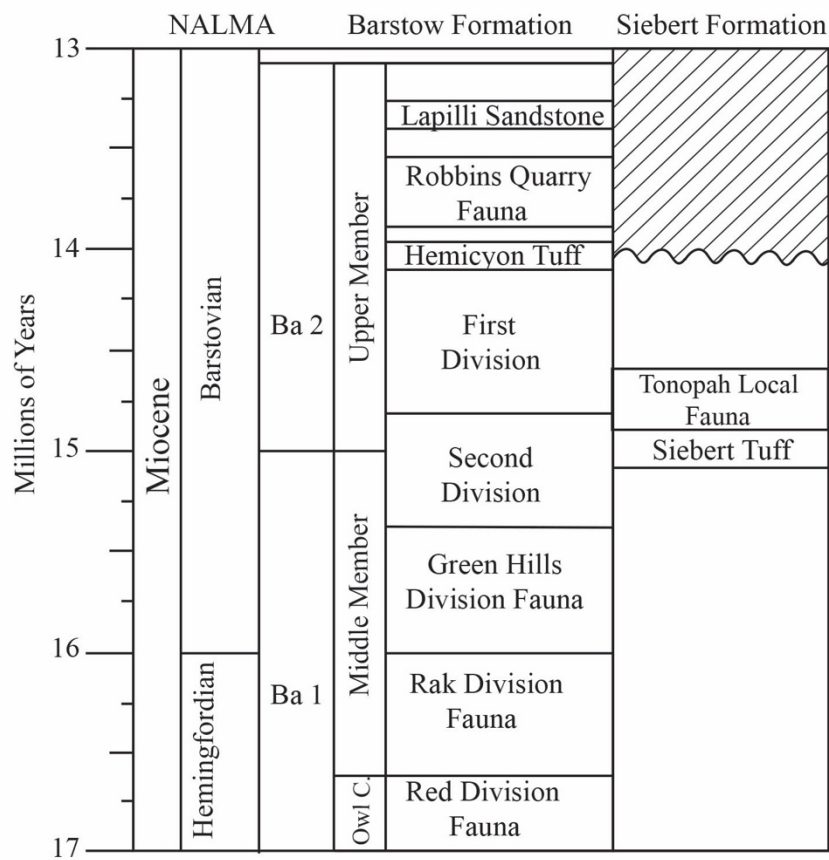


Figure 4.4 Faunal Strat Column. The Lapilli Sandstone dated at 13.4 Ma (MacFadden et al., 1990). The Hemicyon Tuff dated to 14 Ma (MacFadden et al., 1990). The Siebert Tuff, dated at 15 Ma (Swisher, 1992). Modified from Tedford (2004) and Pagnac (2005; 2009).

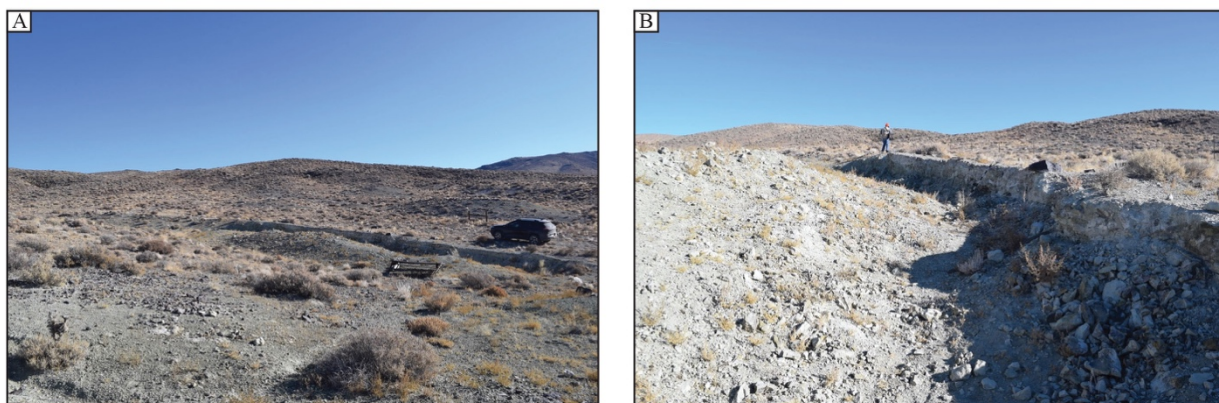


Figure 4.5 Tonopah Local Fauna collection site in the Siebert Formation, showing what the site looks like today. A: View toward the east. B: Close-up view of the excavation site. Photographs taken in October 2019.

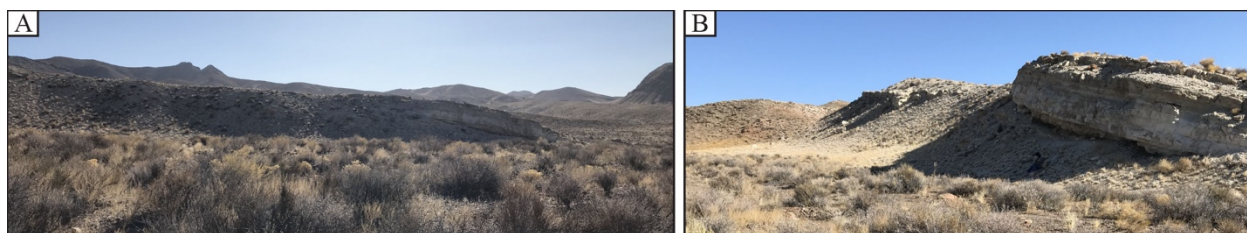


Figure 4.6 The invertebrate collection site near the Tonopah Local Fauna collection site in the Seibert Formation. A: View to the east. B: View to the north. Photographs taken in October 2019.

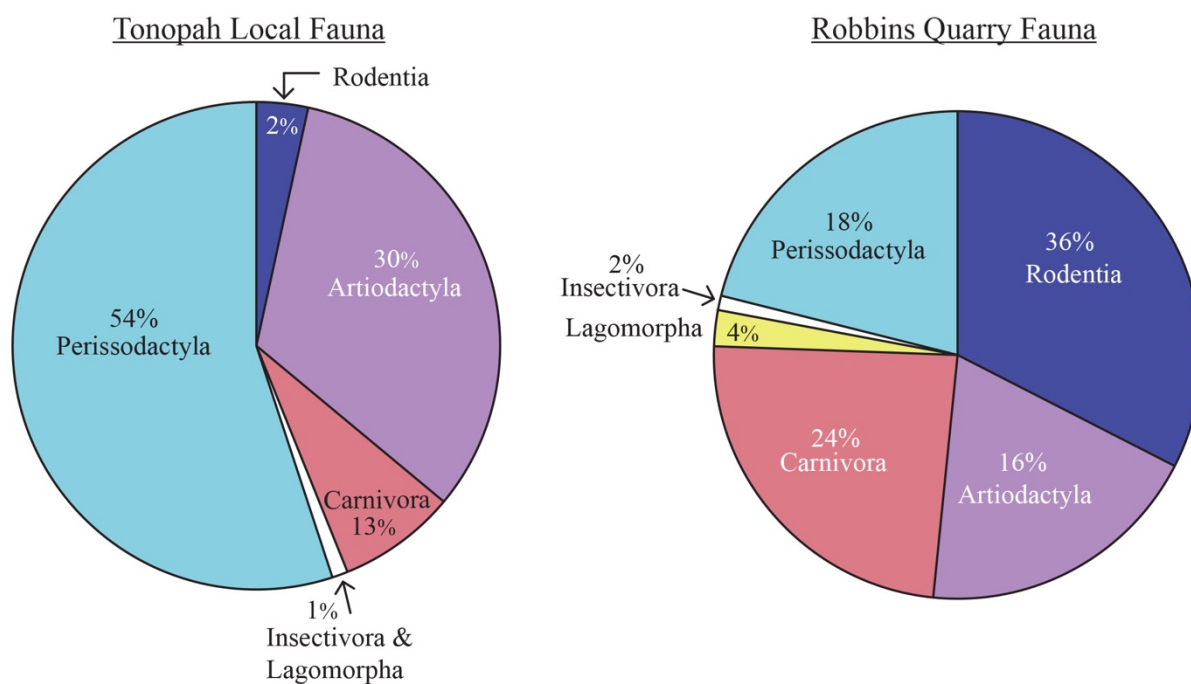


Figure 4.7 Pie charts with MNI percentages for each assemblage. Tonopah Local Fauna data are from Henshaw (1938; 1940); Robbins Quarry data are from Reynolds (2020).

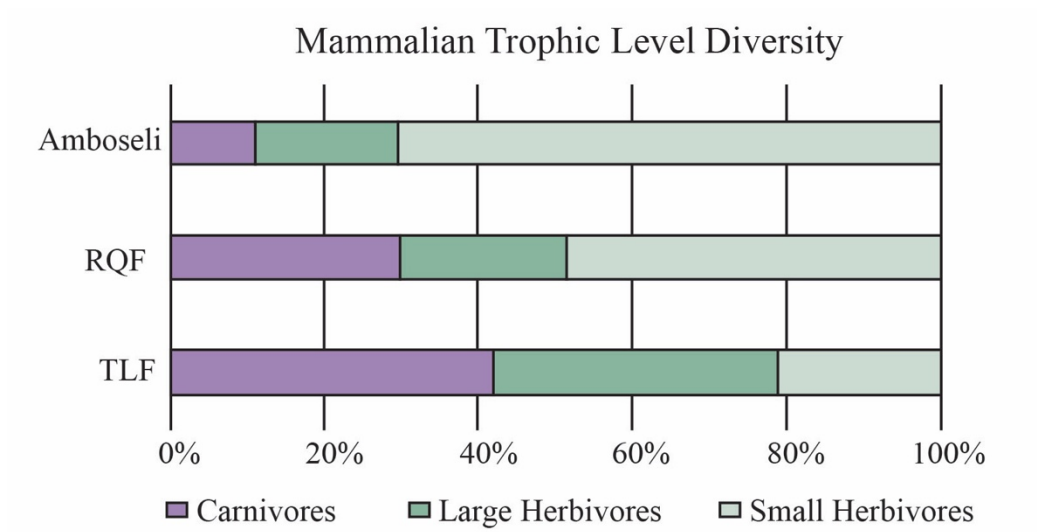
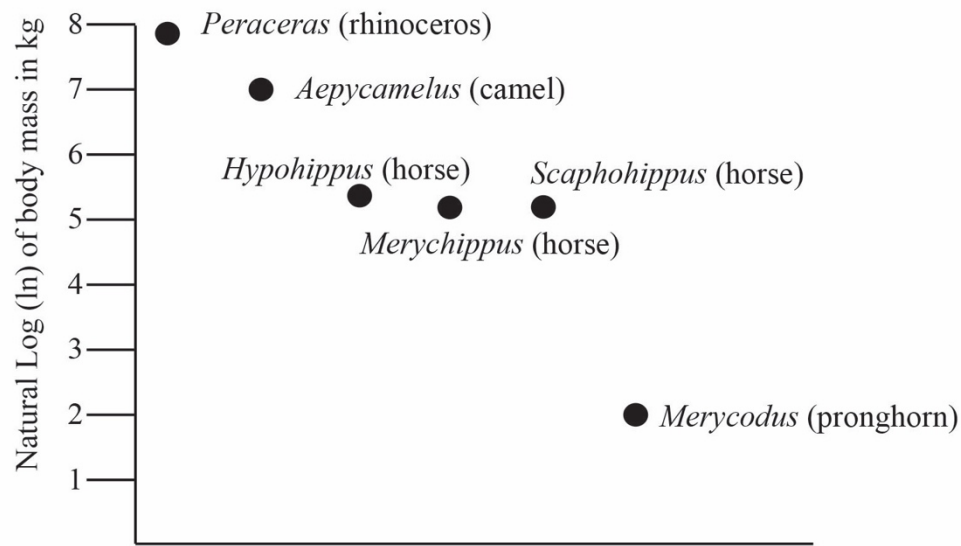
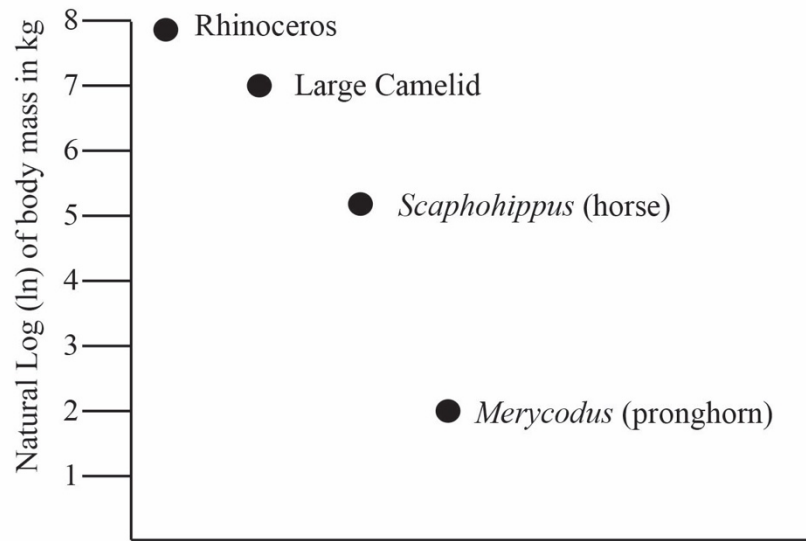


Figure 4.8 Trophic levels based on species diversity. Robbins Quarry Fauna (RQF) and Tonopah Local Fauna (TLF) data are generated from Table 2. Amboseli data are after Meyers (2011) from Grimshaw et al. (1995).



A Cenogram for Tonopah Local Fauna



B Cenogram for Robbins Quarry Fauna

Figure 4.9 Cenograms for the Tonopah Local Fauna (A) and the Robbins Quarry Fauna (B). The x-axis datapoints are evenly spaced in descending order of body mass.

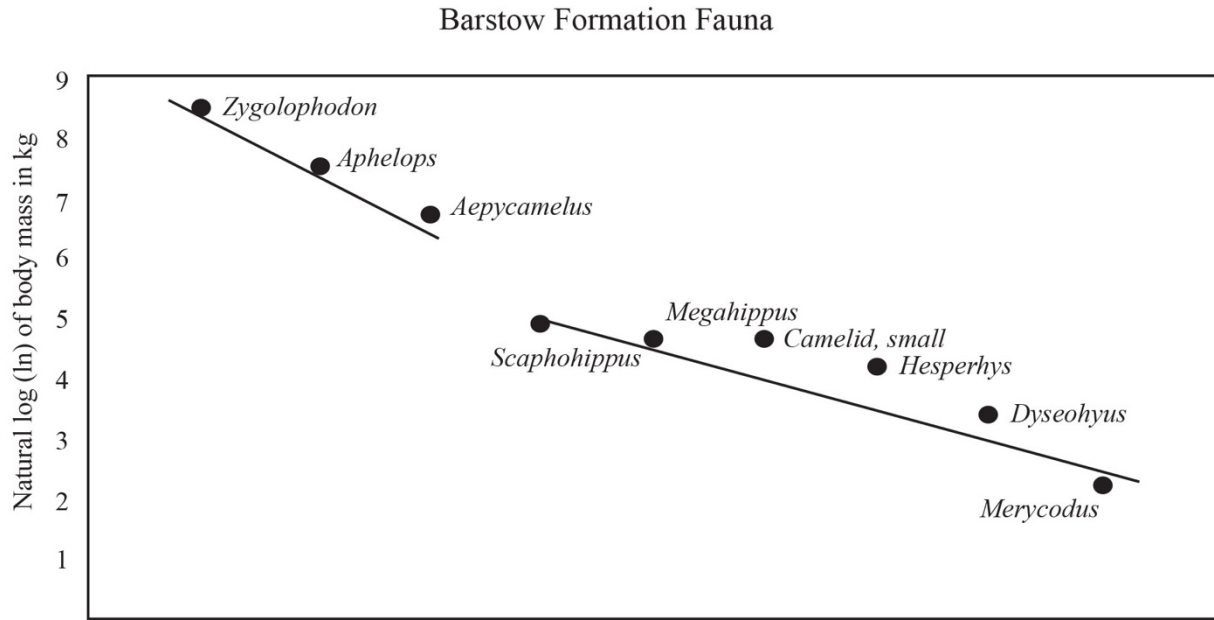


Figure 4.10 Cenogram of a portion of the Barstow Formation fauna, recreated from Pagnac (2005, fig. 58), which is partly correlative with the TLF (Fig. 4).

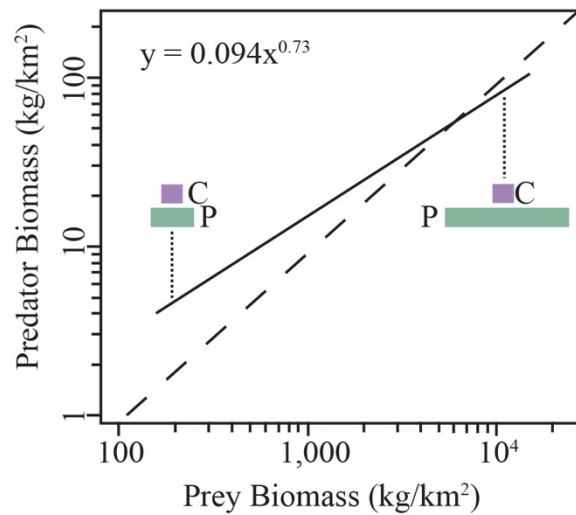


Figure 4.11 Predator/Prey Biomass correlation. C is for carnivore and P is for prey. Dashed line assumes a stable relationship between prey biomass and carnivore biomass. Modified from Hatton et al. (2015).

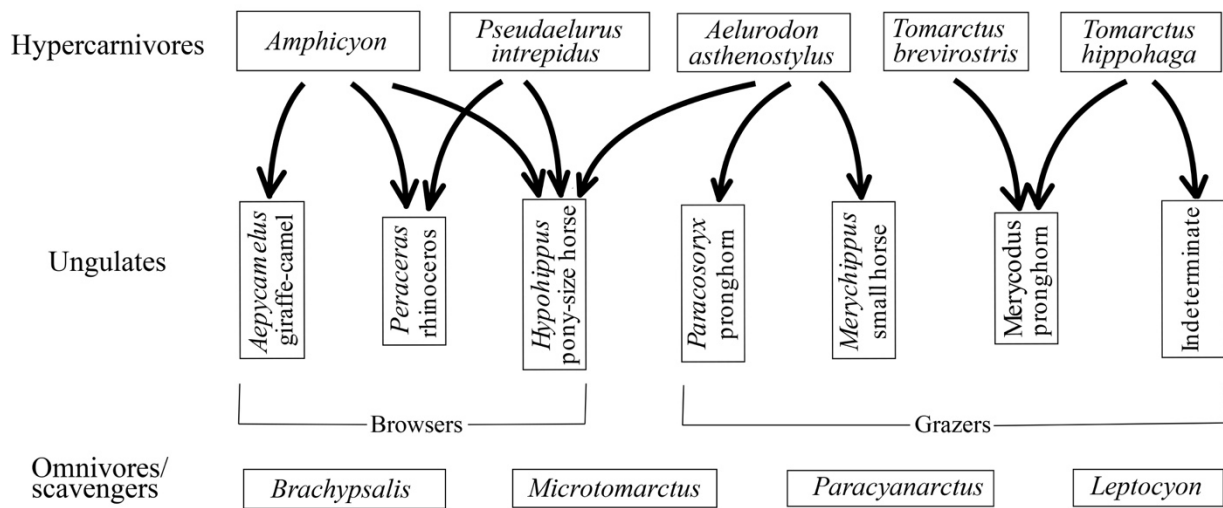


Figure 4.12 Biomass flux of predator (hypercarnivores) and prey (ungulates) relationships within the Great Basin region during the Mid-Miocene-Climatic-Optimum.

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Curriculum Vitae

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Education:

Ph.D. Geoscience, 2022

University of Nevada, Las Vegas

Dissertation: Miocene ichnofaunas of the Muddy Creek Formation, southern Nevada, and the China Ranch Beds, southeastern Nevada.

Master of Science, Geology, 2013

Kent State University, Ohio

Thesis: Population Dynamics of *Dakoticancer overanus* from the Pierre Shale, South Dakota

Bachelor of Science, Marine Biology, 2006

University of Oregon, Eugene

Awards and Acknowledgments:

2021UNLV Geosymposium 4th Place Talk

2017Graduate College: Summer Doctoral Research Fellowship

2014-2017Brenda French Scholarship, UNLV

Experience:

University of Nevada Las Vegas:

Graduate Assistant 2014- 2018; 2020-2021

- Taught introductory Geology labs in person and online to college undergraduates including Physical Geology and Physical Geography
- Taught upper division Paleontology Lab in person to college undergraduates and led fieldtrips to paleontological field sites

Graduate College Mentorship Program 2021-2022

- Learned how to be an effective mentor through group meetings and having mentees

Tule Springs National Monument

Volunteer

- Fossil inventory field work

Great Basin National Park, GeoCorps of America Internship: 2014

Field Assistant

- Fossil Inventory field work

Cleveland Museum of Natural History: 2013

Curatorial Assistant Internship, Invertebrate Paleontology

- Catalogued specimens
- Responded to public inquiries

Santa Cruz Biotechnology Inc: 2008-2011

Laboratory Assistant

- Purified antibodies
- Made and facilitated electrophoresis gels and western blots

University of Oregon 2005-2007

Teaching Assistant 2007

- Assisted in the marine invertebrate laboratory for undergraduates

GK-12 Undergraduate Fellow 2005-2006

- Assistant Science Teacher for grades K and 1

Conference Presentations:

- Jones, A., and Rowland, S.M., 2021, New Muddy Creek Formation Trackways and how to preserve them
 - UNLV Geosymposium: May 2021, Las Vegas, NV
- Jones, A., and Rowland, S.M., 2021, A Miocene camelid tracksite in the Muddy Creek Formation near Mesquite, Nevada
 - Geological Society of America Cordilleran Section Meeting, online

- Jones, A., and Rowland, S.M., Paleocology of the Mid-Miocene Tonopah local fauna of southwestern Nevada
 - Geological Society of America Annual Meeting, September 2019, Phoenix, Arizona
- Jones, A., Schweitzer, C., and Feldmann, R., Intersex specimens of the fossil crab *Dakoticancer overanus* from the Late Cretaceous Pierre Shale of South Dakota
 - Geological Society of America Annual Meeting, 2013, Denver, Colorado
- Jones, A., Schweitzer, C., and Feldmann, R., Population Dynamics of *Dakoticancer overanus*
 - Geological Society of America Annual Meeting, 2012, Charlotte, North Carolina

Publications

- Jones, A., and Rowland, S.M., 2022, A Late Miocene camelid tracksite in the Muddy Creek Formation near Mesquite, Nevada, *in* Miller, D.M., ed., Volcanoes in the Mojave, Desert Symposium Field Guide and Proceedings, p. 200-206.
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