A new middle Paleocene mammalian fauna from the Fort Union Formation, Great Divide Basin, Wyoming

by

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A new middle Paleocene mammalian fauna from the Fort Union Formation, Great Divide Basin, Wyoming

Thesis directed by Associate Professor & Curator of Fossil Vertebrates Jaelyn J. Eberle

Over the last three decades, mammalian faunas that span the Torrejonian-Tiffanian boundary have been reported by others from the Hanna and Bighorn Basins, and are important for assessing mammalian diversity and evolution during middle Paleocene time. Reported here is a Torrejonian – Tiffanian transitional fauna from the Overland Member of the Fort Union Formation in the Great Divide Basin, south-central Wyoming. The fauna, which is primarily comprised of isolated teeth, includes 20 species in five mammalian orders. The taxa identified from the Overland Member include the pantodont *Pantolambda cavirictis*; 'condylarths' *Mimotricentes* sp., *Haplaletes disceptatrix, Haplaletes pelicatus, Litomylus dissentaneus, Litaletes disjunctus, Promioclaenus acolytus, Promioclaenus* sp., *Phenacodus* and *Ectocion*; cimolestids *Acmeodon hyoni, Acmeodon secans, Gelastops parcus and Gelastops joni;* pantolestids *Paleotomus junior* and *Paleotomus senior* as well as *Bessoecetor;* leptictids *Prodiacodon concordiarcensis and Prodiacodon puercensis;* and the primate *Nannodectes intermedius*.

The Overland fauna is similar to latest Torrejonian faunal assemblages elsewhere in containing *Acmeodon hyoni, Pantolambda cavirictis* and *Litaletes disjunctus*. However, it also contains the plesiadapid *Nannodectes intermedius,* an index taxon for the earliest Tiffanian (Ti1) lineage zone, and *Ectocion*, which first appears in Ti1 as well. Surprisingly, *Plesiadapis praecursor*, the index species on which Ti1 is defined, has not yet been recovered in the Overland fauna. Nevertheless, based upon presence of *N. intermedius* and *Ectocion*, as well as similarities to earliest Tiffanian fauna in the Hanna Basin, I suggest the Overland fauna is earliest Tiffanian (Ti1) in age.

With regard to geographic range extensions, the largest occurs for *Paleotomus junior*, previously documented only from localities in Alberta, Canada. Reported temporal range extensions include

Haplaletes pelicatus, whose range is extended from Ti2-3 into Ti1, and *Acmeodon hyoni* is extended from To3 to Ti1. While the Overland fauna is not as diverse as the earliest Tiffanian fauna in the Hanna Basin, it is comparable to other earliest Tiffanian faunas.

DEDICATION

For my parents Kathy and Wayne,

who instilled in me determination and the importance of knowledge

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I would also like to thank staff at the University of Colorado, including the vertebrate paleontology section for the specimens used in the research, and especially Toni Culver, who was always available and willing to help give me information and associated documentation for this faunal analysis, as well giving me the best training for my future as a collections manager. The Entomology section also helped facilitate this thesis research through the use of their imaging station, and I thank Katie Wolfson for her time and expertise.

This analysis was greatly enhanced by the generous loans of comparative material from the Smithsonian Institution, the Yale Peabody Museum of Natural History, and the University of Wyoming Geology Museum, whose collections manager Laura Vietti, hosted me on a recent visit to the collection and provided me with multiple loans for comparative research.

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INTRODUCTION

While the Paleocene Epoch is relatively well studied, considerable research has focused on faunal turnover at the Cretaceous-Paleogene (K-Pg) boundary and early Paleocene, as well as at the Paleocene-Eocene Thermal Maximum (PETM) and early Eocene time which saw the height of global warming during the Cenozoic Era. Few studies have focused on the middle Paleocene, and specifically the Torrejonian and Tiffanian North American Land Mammal Ages (NALMA), which span from ca. 64-56 Ma (Lofgren et al., 2004), are not well understood. Few fauna are known from the middle Paleocene, but assemblages can be found occurring in the San Juan Basin, New Mexico; Lebo Formation, Crazy Mountain Area, Montana; Paskapoo Formation, Alberta; Hanna Formation, Wyoming and throughout the Fort Union Formation (Williamson and Lucas, 1993; Simpson, 1938; Higgins, 2000; Scott et al., 2002; Hartman, 1986). However, the middle Paleocene marks an important time in mammalian evolution and dispersal throughout North America.

Archibald et al. (1987) noted that Tiffanian mammals were likely derived from mammals in North America that were present in the Torrejonian, therefore making fauna from the Tiffanian the result of local evolution. The Tiffanian represents more advanced forms of species than those found in the Torrejonian (Rigby, 1980) but they are clearly still related. Furthermore, this is contrary to what occurred in the late Tiffanian and across the Tiffanian-Clarkforkian boundary, where the fauna began to be heavily influenced by mammals dispersing from Asia into North America (including the orders Rodentia and Tillodontia at the onset of the Clarkforkian NALMA approximately 56 million years ago). These immigrants interspersed with the local fauna, and multiple new orders and families appeared in North America in late Paleocene and early Eocene time (Archibald et al., 1987; Beard and Dawson, 1998).

This study is a faunal analysis of a middle Paleocene mammalian assemblage from the Fort Union Formation in Wyoming's Great Divide Basin that was initially discovered in 1985 by James and Jeannie Honey and Malcolm McKenna. My study focuses on mammals of late Torrejonian-early Tiffanian time (further discussed below), and is the first fauna of this age to be described from the Great Divide Basin. My study includes only the Eutheria from this assemblage, although it should be noted that a diverse multituberculate fauna is being identified and studied by Donald Lofgren at the Raymond M. Alf Museum of Paleontology. Further, I have not included the non-mammalian vertebrates from the faunal assemblage in my study, and specifically Crocodylia, Anguidae and Squamata, as well as the fishes Lepisosteidae and Osteichthyes. However, presence of these taxa is consistent with a fluvial depositional environment for the localities utilized in this study.

Background to North American Land Mammal Ages (NALMA)

To refine the relative dating and correlation among Cenozoic fossil-bearing strata in North America, Wood et al. (1941) formulated the North American Land Mammal Ages (NALMA) by using mammalian biostratigraphy. NALMA are biochronologic units used to describe the subset of ages for the succession of mammalian evolution within the last ca. 66 million years of geologic history (Woodburne, 2004). Wood et al. (1941) defined 18 NALMA, using known index taxa from deposits within the assigned age, first and last appearances of mammalian species, and characteristic fossils from that age. In more recent decades, Woodburne et al. (1987; 2004) revised the NALMA based upon updated biostratigraphy and new localities and discoveries, lithostratigraphy, and magnetostratigraphy. The more recent revision of NALMA (Woodburne et al., 2004 and chapters within) now places the Dragonian within the Torrejonian NALMA as the Torrejonian 1 Interval Zone (To1), and two additional NALMA have been added to the Pleistocene - the Irvingtonian and Rancholabrean - bringing the total number of NALMA to 19. The fossil localities used in my mammalian faunal analysis correlate best with the Torrejonian and Tiffanian NALMA (Figure 1; age is further discussed below).



Figure 1. Paleocene North American Land Mammal Ages (NALMA). Figure adapted from Higgins (2000).

Torrejonian NALMA

The Torrejonian NALMA is correlative with early to middle Paleocene time, lasting from ca. 64-61 Ma (Lofgren et al., 2004). It was named for the Torrejon Formation in the San Juan Basin, New Mexico, which comprises the type locality, the heads of Arroyo Torrejon (Wood et al. 1941). The Torrejonian NALMA is subdivided into three interval zones, defined by characteristic fossils from each zone (Lofgren et al., 2004). The Torrejonian NALMA is defined by the first appearance of the periptychid 'condylarth' *Periptychus carinidens* which also defines the onset of the first interval zone, previously known as the Dragonian NALMA (Wood et al. 1941; Woodburne, 2004). The Torrejonian ends with the first appearance of the primate *Plesiadapis* (which identifies the onset of the subsequent Tiffanian NALMA) (Lofgren et al., 2004). The Torrejonian marks the first appearances for several mammals such as *Acmeodon, Anconodon, Aphronorus, Baiotomeus, Besseocetor Coriphagus, Gelastops, Ignacius,* Jepsenella, Myrmecoboides, Paleotomus, Pantolambda, Paromomys, Phenacodus, Pronothodectes, Protictis and Simpsonictis; it also marks last appearances for genera such as Ellipsodon, Goniacodon, Haploconus, Ictidopappus, Loxolophus, Oxyclaenus, Stygimyus, and Xyronomys (Lofgren et al., 2004). Index taxa for the Torrejonian include Ankalagon, Avunculus, Conoryctella, Escavadodon, Huerfanodon, Draconodus, Leptonysson, Microclaenodon, Mioclaenus, Mixodectes, Triisodon and Xanoclomys (Lofgren et al., 2004). Torrejonian faunas are well represented, stretching from the U. S. Western Interior to Western Canada, and including localities from the Tullock Formation, Montana; Porcupine Hills Formation, Alberta; Fort Union Formation, Wyoming; Nacimiento Formation, New Mexico; Tornillo Formation, Texas; North Horn Formation, Utah; Hanna Formation, Wyoming; Crazy Mountain area, Montana; Ludlow Formation, North Dakota; and Coalspur Formation, Alberta (Lofgren et al., 2004).

The Puercan-Torrejonian boundary falls near the boundary of magnetic polarity chrons C28r and C28n, and the earliest Torrejonian (To1) faunal assemblages fall within magnetic polarity chron C28n as well (Lofgren et al., 2004). Near the end of the To1 interval zone, magnetic polarity chron C27r begins and extends through the entire To2 interval zone and into the beginning of To3. Finally, the onset of magnetic polarity chron C27n begins just after the onset of the To3 interval zone and ends before the Torrejonian-Tiffanian boundary; the boundary occurs within strata of reversed polarity that correlate with magnetic polarity chron C26r (Lofgren et al, 2004; Secord, 2006).

Tiffanian NALMA

The Tiffanian is a late Paleocene NALMA, lasting from ca. 61-56 million years ago (Lofgren et al. 2004), and was named for the Tiffany local fauna discovered on the northern rim of the San Juan Basin in southwestern Colorado (Wood et al., 1941). The onset of the Tiffanian NALMA has been defined at the first appearance of *Plesiadapis* and ends with the first appearance of Rodentia (which marked the onset of the subsequent Clarkforkian NALMA) (Lofgren et al., 2004). *Plesiadapis* occurs throughout the

Tiffanian and the various species are used to subdivide the NALMA into six lineage-based zones (Archibald et al. 1987). The Tiffanian marks the first appearances of mammals, such as *Aletodon*, *Anacodon*, *Apatemys*, *Carpolestes*, *Chiromyoides*, *Didymictis*, *Ectocion*, *Haplolambda*, *Lambertocyon*, *Oxyaena*, *Paleosinopa*, *Plesiadapis*, *Thryptacodon*, *Titanoides* and *Viverravus* (Lofgren et al., 2004). Last appearances for species include *Acmeodon*, *Bessoecetor*, *Gelastops*, *Haplaletes*, *Litaletes*, *Litomylus*, *Mimotricentes*, *Paleotomus*, *Pantolambda*, and *Promioclaenus*, all of which are found in this fauna (Lofgren et al., 2004). Index taxa for the Tiffanian include *Amelotabes*, *Bisonalveus*, *Caenolambda*, *Carpodaptes*, *Copecion*, *Dorraletes*, *Fractinus*, *Liotomus*, *Litolestes*, *Nanodectes*, *Navajovius*, *Pristinictis*, *Raphictis*, *Saxonella*, *Utemylus*, *Xenacodon* and *Zanycteris* (Lofgren et al., 2004). Tiffanian faunas are well represented from the Fort Union Formation, Wyoming and Montana; Paskapoo Formation, Alberta; Tongue River Formation, Montana; Tongue River and Sentinel Butte Formations, North Dakota; Hoback Formation, Wyoming; Togwotee Pass area, Wyoming; Wasatch Formation, Wyoming; Evanston Formation, Wyoming and Black Peaks Formation, Wyoming (Lofgren et al., 2004).

The Torrejonian – Tiffanian boundary is thought to fall near the boundary between magnetic polarity chrons C27n and C26r, and an ash near this is dated at 61.65±0.2 Ma (Secord et al., 2006; Lofgren et al., 2004). Early Tiffanian (Ti1) is estimated to be about one million years in duration, and falls within a reversed magnetic polarity chron (C26r), which lasts until the beginning of the middle of Tiffanian lineage zone 4 (Ti4b), where normal polarity ensues (C26n). Polarity reverses again by the beginning of the Tiffanian lineage zone 5 (Ti5) (Secord et al., 2006). At the end of the Tiffanian (Ti6) and into the Clarkforkian NALMA, the polarity is normal (C25n) (Secord et al., 2006).

Paleocene Paleoclimate and Environment

During the early Paleocene (Torrejonian), the climate is hypothesized to have been subtropical at mid-latitudes (Secord, 2008), followed by a cooling of temperatures and a more temperate climate by

the late Paleocene (Tiffanian). That, in turn, was followed by significant warming events in the latest Paleocene (late Tiffanian-Clarkforkian) and early Eocene (Secord, 2008; Krause and Mass, 1990). Krause and Maas (1990) also suggested that there were broad-leaved evergreen forests occurring up to 60°N latitude during the Paleocene, with a mean annual temperature between 13° to 20°C.

Based on species diversity from the Bighorn and Crazy Mountain Basins, Secord (2008) correlated mean annual temperature with mammalian diversity and found that diversity is strongly dependent on mean annual temperature (MAT). Secord (2008) noted a decrease in mammalian diversity during the Torrejonian and early Tiffanian, in contrast to Krause and Maas (1990), who found no diversity change until the middle Tiffanian (Ti2). Secord (2008) also found that there was a steady increase in mammalian diversity from Ti3 into the Clarkforkian, whereas Krause and Maas found higher diversity in the late Tiffanian (Ti5) than in the Clarkforkian.



Figure 2. Map of the Greater Green River Basin and shaded area showing the study area (modified from Hettinger et al., 2008). See Figure 3 for detailed geologic map.



Figure 3. Geologic Map showing the location of fossil localities UCM 2011056, 2011057, 2011058 and 2011062 (adapted from Hettinger et al., 2008).

GEOLOGIC SETTING

The Great Divide Basin is in the eastern portion of the greater Green River Basin (Honey and Hettinger, 2004) in south-central Wyoming. It is located to the northeast of the Rock Springs uplift and north of the Washakie Basin (Kirschbaum et al., 1993). Fossils used in my study are from localities in the Overland Member of the Fort Union Formation cropping out in the southeastern part of the Great Divide Basin in Sweetwater County, Wyoming (Honey and Hettinger, 2004; see Figure 3).

The geology and stratigraphy of the Fort Union Formation was summarized by Hettinger et al., (2008; see Figure 3). The formation is divided into three members: the Overland Member (upper middle and upper Paleocene), Blue Gap Member (lower Paleocene), and the China Butte Member (lower Paleocene). The fauna described here occurs in the Overland Member, which consists of the Cherokee coal zone, a fine-grained middle unit and a basal sandstone (Hettinger et al., 2008). The Overland Member has a distinct succession of light-gray sandstone, siltstone and mudstone that occurs between the overlying mudstone of the Wasatch Formation and underlying claystones of the Blue Gap Member. In the northern section of the Fort Union Formation, the Overland Member flanks the Wasatch Formation and the underlying China Butte Member of the Fort Union Formation (Honey and Hettinger, 2004).

The Overland Member is thinner in the south, near the Washakie Basin (~425 feet thick), and thicker in the north, up to 2,271 feet (Honey and Hettinger, 2004). All of the fossil localities are in the northern part of the Overland Member (See Figure 3). The fauna described below is from fossil localities that are approximately 280 feet stratigraphically above the base of the Overland Member (Hettinger, pers. comm., 2014), specifically from the basal sandstone, which consists of coarse-grained sandstone with pieces of quartz and feldspar granules and chert pebbles (Hettinger et al., 2008).

All of the specimens were collected from UCM localities 2011056, 2011057, 2011058 and 2011062. These localities represent assemblages that were collected from anthills, as well as surface

collected; however, all appear to be on the same dip-slope (Hettinger, pers. comm., 2014). The specimens in this fauna are isolated teeth with the exception of one specimen of *Ectocion* which consists of a dentary fragment containing p4-m1 and a specimen of *Pantolambda* that includes multiple associated teeth and bone fragments from one individual. Since many of the specimens were collected from anthills, the taxonomic composition of the fauna is largely skewed towards smaller-bodied mammals. This probably represents a collecting bias, both by ants and then subsequently by paleontologists.

The anthills are gravel-covered, conical hills produced by the western harvester ant, *Pogonomyrmex occidentalis* (McCook, 1881; Matthias and Carpenter, 2004). The range of *P. occidentalis* largely overlaps with fossiliferous late Cretaceous and Cenozoic exposures, and these ants (and their anthills) are very common in Wyoming. Therefore, this species is a very useful facilitator of microvertebrate collection because they often incorporate fossils while building their mounds (Matthias and Carpenter, 2004). At their largest, the anthills can be two feet high and three feet in diameter, but hills are variable depending on the size of the colony (Scott, 1951). Ants collect fossils to build their mounds from up to three meters below ground (McCook, 1881), as well as from within the clearing around their hills of up to about 15 meters (Robinson and Kron, 1998). Anthills are meticulously selected by paleontologists, based on known stratigraphy within the area that the ants are collecting material (Robinson and Kron, 1998).

MATERIALS AND METHODS

The specimens described in this analysis are from the Fossil Vertebrate Collection at the University of Colorado Museum of Natural History (UCM). Identifications were made via comparison to specimens and casts at the UCM as well as specimens on loan from the Smithsonian Museum of Natural History (USNM), University of Wyoming (UW), and Yale Peabody Museum of Natural History (YPM). Casts of holotypes were utilized for comparison when available, as were descriptions, images and measurements in the literature. Taxonomic classification follows Thewissen (1990) for Phenacodontidae and Janis et al. (1998; 2008) for all other taxa.

Teeth were measured using an Ehrenreich Photo-Optical Industries Shopscope on loan from J. A. Lilligraven (University of Wyoming) and for larger specimens, Mitutoyo digital calipers (*Pantolambda, Phenacodus* and *Ectocion* specimens). Measurements for Phenacodontidae follow Thewissen (1990).

Images of large specimens were taken using a Canon 5D Mark II camera, a Canon MP-E 65mm Macro Photo Lens, and Helicon Focus 5.3 focus stacking software, located in the Entomology Section of the UCM. All other images were taken using a Leica MZ16 microscope with attached Spot Insight camera.

The Rarefaction software, Analytic Rarefaction 1.3 was used to conduct biodiversity comparisons between documented faunas (Hartman, 1986 and Higgins, 2000) and the fauna described below in this analysis.

Institutional Abbreviations - AMNH, American Museum of Natural History, New York, New York; UCM, University of Colorado Natural History Museum, Boulder, Colorado; USNM, United States National Museum, Smithsonian Institution, Washington, D.C.; UW, University of Wyoming, Laramie, Wyoming; YPM-PU, Yale Peabody Museum of Natural History, New Haven, Connecticut

Dental Terminology and Measurements - L, assigned to a left tooth (e.g., L m1); R,

assigned to a right tooth (e.g., R m1). **M/m,** assigned to upper/lower molars; **P/p,** assigned to upper/lower premolars. **A-P length**, anteroposterior length; **WTri**, width of trigonid; **WTal**, width of talonid; **Wtrans**, tranverse width.



Figure 4. Diagram of molar measurements. Diagram of upper (top) and lower (bottom) molar measurements (modified from Archibald, 1982).

SYSTEMATIC PALEONTOLOGY

Class: Mammalia Linnaeus, 1758 Infraclass Eutheria Gill, 1872 Order: Pantodonta Cope, 1873 Family: Pantolambdidae Cope, 1883d Genus: *Pantolambda* Cope, 1882c *Pantolambda cavirictis* Cope, 1883c (Table 1, Figure 5)

Referred Specimen – UCM 105371 LP4, LM2 and RM3 from UCM locality 2011057; locality from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution - Nacimiento Formation, San Juan Basin, New Mexico (Torrejonian 3-Tiffanian 1); Fort Union Formation, Bighorn Basin, Wyoming (Torrejonian 3); Fort Union Formation, Shotgun Member, Wind River Basin, Wyoming (Tiffanian 1) (Janis et al., 1998).

Description and Discussion- *Pantolambda cavirictis* was well described by Matthew (1937), and the UCM specimen falls within the size range of *Pantolambda cavirictis*, based upon measurements provided by Simons (1960). Higgins (2000) noted that the difference between *Caenolambda* and *Pantolambda* is the presence of a continuous lingual cingulum around the protocone on upper molars of *Pantolambda*, whereas *Caenolambda* has cingula only on the lateral sides of the protocone. The continuous lingual cingulum around the protocone is observed on UCM 105371 (See Figure 5), and therefore it is identified as *Pantolambda cavirictis*.

Tooth position	UCM Locality	A-P length	Wtrans
P4	2011057	14.38	21.81
M2	2011057	18.04	22.18
M3	2011057	15.39	24.92

TABLE 1. Measurements (in mm) of upper molars of *Pantolambda cavirictis* from the Great Divide Basin.



Figure 5. Occlusal view of *Pantolambda cavirictis*, UCM 105371. A, LP4. B, LM1. C, RM3.

Order: 'Condylarthra' Cope, 1881e Family: Arctocyonidae (Giebel, 1855) Murray, 1866 *Mimotricentes* Simpson, 1937 *Mimotricentes* sp. (Table 2)

Tricentes Cope, 1884a

Referred Specimens: UCM 103726 Rm2 from UCM locality 2011058, UCM 106381 Rm3 from UCM locality 2011056, and UCM 103899 Rm3 from UCM locality 2011057; all localities are from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution –*Mimotricentes* ranged temporally from the early Torrejonian through mid-Tiffanian within the Western Interior of North America, including at localities in Alberta, Montana, New Mexico, Utah, and Wyoming (Janis et al., 1998).

Description and Discussion -The two species of *Mimotricentes, M. subtrigonus* and *M. fremontensis,* are very similar in size and morphology based on the original description of *M. fremontensis* by Gazin (1956). Specifically the two species' lower molars are differentiated based on the size and placement of the paraconid. In *M. fremontensis* the paraconid on the m2 and m3 is low on the trigonid and weaker than in *M. subtrigonus* (Gazin, 1956). UCM 103726 and UCM 103899 are both worn specimens, and consequently the position of the paraconid cannot be determined. The third specimen, UCM 106381, does not have a paraconid, as would be expected in the species *M. fremontensis*. However, Gazin (1956) noted that in both species, morphology is highly variable and some specimens of *M. subtrigonus* have a very weak paraconid, and therefore species cannot be determined based on the isolated m3.

Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 103726	2011056	m2	5.57	3.85	4.30
UCM 103899	2011057	m3	5.05	3.81	-
UCM 106381	2011056	m3	5.52	3.76	-

Table 2. Measurements (in mm) for lower molars of *Mimotricentes* sp. from the Great Divide Basin.

Family: Hyopsodontidae Trouessart, 1879 Genus: *Haplaletes* Simpson, 1935 *Haplaletes disceptatrix* Simpson, 1935a

(Table 3, Figure 6)

Referred Specimens – UCM 103907 RM2 and UCM 103958 RM2 from UCM locality 2011057; UCM 104003 RM1, UCM 104004 RM1, UCM 104013 LM1, UCM 104028 LM1, UCM 104030 RM1 and UCM 104010 RM2 from UCM locality 2011058; UCM 103767 LM2 and UCM 103939 RM2 from UCM locality 2011062; all localities are from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution – Nacimiento Formation, San Juan Basin, New Mexico (Torrejonian 3-Tiffanian 1); Black Peaks Formation, Texas (Tiffanian 5); Fort Union (Polecat Bench) Formation, Bighorn and Clark's Fork Basins, Wyoming (Torrejonian 3 and Tiffanian 2); Fort Union Formation, Washakie Basin, Wyoming (Torrejonian 3); Hoback Formation, Hoback Basin, Wyoming (Tiffanian 3); Lebo Formation, Crazy Mountain Area, Montana (Torrejonian 3); Tongue River Formation, Powder River Basin, Montana (Tiffanian 1 and Tiffanian 3) (Janis et al., 1998).

Description and Discussion – Upper molars of *Haplaletes disceptatrix* were compared to specimens on loan from USNM and YPM-PU and identified based on very comparable morphology and size. Upper molars of *Haplaletes* fall in to two distinct groups based on size; the smaller group is comprised of teeth that have smaller anteroposterior lengths but are also wider and range in width (from 3.11 to 4.49 in M2s), which is consistent with upper molar measurements taken from specimens of *H. disceptatrix* (USNM 9555 and 9556; YPM-PU 17489, 17495 and 17520).

Specimen	UCM Locality	Tooth position	A-P length	Wtrans
UCM 104003	2011058	M1	2.83	3.45
UCM 104004	2011058	M1	3.05	4.07
UCM 104013	2011058	M1	2.62	3.70
UCM 104028	2011058	M1	3.12	4.04
UCM 104030	2011058	M1	2.95	3.87
UCM 103767	2011062	M2	3.21	4.18
UCM 103907	2011057	M2	3.05	4.32
UCM 103939	2011062	M2	3.23	4.00
UCM 103958	2011057	M2	2.83	3.14
UCM 104010	2011058	M2	3.18	4.46

TABLE 3. Measurements (in mm) of upper molars of *Haplaletes disceptatrix* from the Great Divide Basin.





Figure 6. Upper molar measurements for *Haplaletes*. A, upper M1s. B, upper M2s.

Haplaletes pelicatus Gazin, 1956

(Table 4 and 5; Figure 7)

Referred Specimens: UCM 103495 RM2 and UCM 103978 RM2, UCM 103980 RM2 from UCM locality 2011056; UCM 103968 RM1, UCM 103969 LM1, and UCM 103938 LM2 from UCM locality 2011057; UCM 103801 Rp4, UCM 104025 LM1, UCM 104027 LM1, UCM 103890 RM2, UCM 104001 LM2, UCM 104002 LM2, UCM 104014 RM2, UCM 104022 RM2, UCM 104029 RM2, and UCM 104031 LM2 from UCM locality 2011058; all localities are from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution – Fort Union Group, Bison Basin, Wyoming (Tiffanian 2) and Evanston Formation, Fossil Basin, Wyoming (Tiffanian 3) (Janis et al., 1998); Ohio Creek Formation, Piceance Creek Basin, Colorado (Tiffanian 3) (Burger, 2007).

Description and Discussion – There is currently a lack of published material describing and documenting the measurements of upper molars of *Haplaletes pelicatus*. However, as noted above under the description of *Haplaletes disceptatrix*, the upper molars of UCM specimens of *Haplaletes* from the Great Divide Basin fall into two size classes. The larger teeth have greater anteroposterior lengths, but are consistently narrower in width than UCM specimens identified above as *H. disceptatrix*. Because the lower molars of the two species of *Haplaletes* are differentiated on size, the upper molars also assumed to be differentiated by size, and consequently I identified the larger upper molars as *H. pelicatus*. One lower premolar was identified as *Haplaletes pelicatus* because its measurements fell directly within the measurements given by Gazin (1956) for lower premolars, including the holotype of *H. pelicatus* (USNM 21008).

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Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 103801	2011058	p4	3.28	-	1.94

TABLE 4. Measurements (in mm) of lower premolar of *Haplaletes pelicatus* from the Great Divide Basin.

TABLE 5. Measurements (in mm) of upper molars of *Haplaletes pelicatus* from the Great Divide Basin.

Specimen	UCM Locality	Tooth position	A-P length	Wtrans
UCM 103968	2011057	M1	3.32	2.89
UCM 103969	2011057	M1	3.39	2.82
UCM 104025	2011058	M1	3.51	2.85
UCM 104027	2011058	M1	3.63	2.92
UCM 103495	2011056	M2	4.23	3.16
UCM 103890	2011058	M2	4.30	3.01
UCM 103938	2011057	M2	3.60	2.98
UCM 103978	2011056	M2	3.84	3.00
UCM 103980	2011056	M2	3.85	3.08
UCM 104001	2011058	M2	4.00	3.14
UCM 104002	2011058	M2	3.92	3.00
UCM 104014	2011058	M2	3.85	3.11
UCM 104022	2011058	M2	3.90	3.02
UCM 104029	2011058	M2	4.08	3.06
UCM 104031	2011058	M2	3.55	2.73



Figure 7. Occlusal view of *Haplaletes pelicatus*, UCM 103938 LM2.

Haplaletes sp. indet.

(Table 6 and Table 7; Figure 8, Figure 9 and Figure 10)

Referred Specimens – UCM 103510 LM1, UCM 103508 RM2, UCM 103779 Lm2, UCM 103781 Lm2, UCM 103783 Lm2, UCM 103785 Rm2, UCM 103794 Rm2, UCM 103796 Rm2, UCM 103480 Lm3, UCM 103788 Lm3, and UCM 103798 Rm3 from UCM locality 20110256; UCM 103903 Lm1, UCM 103944 Rm2 from UCM locality 2011057; UCM 104005 RP4, UCM 104006 LP4, UCM 104007 RP4, UCM 104008 RP4, UCM 104009 RP4, UCM 104011 RP4, UCM 104012 RP4, UCM 104015 RP4, UCM 104016 LP4, UCM 104017 LP4, UCM 104018 RP4, UCM 104019 RP4, UCM 104020 LP4, UCM 104021 LP4, UCM 104023 RP4, UCM 103888 LM1, UCM 103892 RM1, UCM 104024 RM1, UCM 103886 LM2, UCM 104026 RM2, UCM 103803 Lm1, UCM 103805 Rm1, UCM 103806 Rm1, UCM 103807 Rm1, UCM 103808 Rm1, UCM 103810 Rm1, UCM 103813 Lm1, UCM 103817 Rm1, UCM 103823 Lm1, UCM 103883 Lm1, UCM 103802 Rm2, UCM 103804 Rm2, UCM 103809 Lm2, UCM 103812 Lm2, UCM 103814 Lm2, UCM 103815 Lm2, UCM 103818 Rm2, UCM 103819 Rm2, UCM 103820 Lm2, UCM 103821 Lm2, UCM 103822 Rm2, UCM 103825 Rm2, UCM 103879 Lm2, UCM 103811 Lm3, UCM 103826 Rm3, UCM 103827 Rm3, UCM 103873 Lm3, UCM 103874 Rm3, UCM 103875 Rm3, UCM 103876 Rm3, UCM 103877 Rm3, UCM 103878 Lm3, UCM 103880 Rm3, UCM 103881 Lm3, UCM 103882 Lm3, UCM103884 Rm3 from UCM locality 2011058; UCM 103772 RM1, UCM 103839 Rm2, from UCM locality 2011062; all localities are from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution –*Haplaletes* ranges temporally from the late Puercan through late Tiffanian within the Western Interior of the United States, including localities in Montana, New Mexico, Texas, Utah, and Wyoming (Janis et al., 1998).

Description and Discussion – As stated above, *Haplaletes disceptatrix* and *Haplaletes pelicatus* are differentiated based on size (Gazin, 1956), and specifically *H. pelicatus is* 20% larger than *H.*

disceptatrix. The morphology of the UCM specimens is very comparable to *Haplaletes* material on loan from the USNM and YPM-PU. However, the lower molar measurements fall along a continuum. While it is probable that the referred UCM specimens represent both species of *Haplaletes*, it is challenging to distinguish between the species based on size of the lower molars, as there is no clear-cut distinction, as was seen in the upper molars of *Haplaletes*. The observation of a continuum in the UCM specimens that captures the range of sizes of both *H. disceptatrix* and *H. pelicatus*, in the absence of any observed morphologic difference in lower molars, may represent the presence of only a single species of *Haplaletes* with a larger size variation. However, without more material, and in particular dentaries with multiple teeth (as opposed to isolated teeth), I conservatively assign all of the lower molars to *Haplaletes* sp. indet. Upper premolars of *Haplaletes* also show a size variation and could not be determined to species, especially since there is little for published measurements of upper molars for these species.

Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 103805	2011058	m1	2.86	2.08	2.24
UCM 103806	2011058	m1	2.95	2.29	2.25
UCM 103807	2011058	m1	2.75	2.01	2.15
UCM 103808	2011058	m1	2.78	2.08	2.16
UCM 103810	2011058	m1	3.13	2.33	2.46
UCM 103813	2011058	m1	2.81	2.26	2.46
UCM 103817	2011058	m1	2.77	2.02	2.15
UCM 103823	2011058	m1	2.95	2.15	2.42
UCM 103883	2011058	m1	2.94	2.05	2.22
UCM 103903	2011057	m1	3.17	2.33	2.45
UCM 103779	2011056	m2	2.87	2.19	2.28
UCM 103781	2011056	m2	3.14	2.48	2.58
UCM 103783	2011056	m2	2.72	2.01	2.11
UCM 103794	2011056	m2	3.13	2.60	2.68
UCM 103796	2011056	m2	3.04	2.54	2.62
UCM 103802	2011058	m2	3.37	2.75	2.78
UCM 103804	2011058	m2	2.93	2.40	2.51

TABLE 6. Measurements (in mm) of lower molars of *Haplaletes* sp. from the Great Divide Basin.

UCM 103809	2011058	m2	2.90	2.32	2.35
UCM 103812	2011058	m2	3.05	2.65	2.68
UCM 103814	2011058	m2	2.94	2.60	2.76
UCM 103815	2011058	m2	2.98	2.33	2.45
UCM 103818	2011058	m2	2.94	2.35	2.42
UCM 103819	2011058	m2	3.24	2.70	2.64
UCM 103820	2011058	m2	3.21	2.74	2.79
UCM 103821	2011058	m2	2.90	2.36	2.39
UCM 103822	2011058	m2	3.11	2.73	2.76
UCM 103825	2011058	m2	3.18	2.40	2.55
UCM 103839	2011062	m2	3.21	2.50	2.71
UCM 103879	2011058	m2	3.15	2.65	2.82
UCM 103944	2011057	m2	3.10	2.64	2.75
UCM 103480	2011056	m3	3.06	-	2.01
UCM 103788	2011056	m3	3.06	-	2.01
UCM 103798	2011056	m3	3.05	-	2.16
UCM 103811	2011058	m3	3.05	-	2.38
UCM 103826	2011058	m3	3.17	-	2.48
UCM 103827	2011058	m3	3.29	-	2.36
UCM 103873	2011058	m3	3.18	-	2.34
UCM 103874	2011058	m3	3.20	-	2.49
UCM 103875	2011058	m3	3.31	-	2.62
UCM 103876	2011058	m3	3.23	-	2.15
UCM 103877	2011058	m3	3.10	-	2.35
UCM 103878	2011058	m3	3.20	-	2.80
UCM 103880	2011058	m3	3.18	-	2.64
UCM 103881	2011058	m3	3.27	-	2.57
UCM 103882	2011058	m3	3.00	-	2.39

TABLE 7. Measurements (in mm) of upper premolars of *Haplaletes* sp. from the Great Divide Basin.

Specimen	UCM Locality	Tooth position	A-P length	Wtrans
UCM 104005	2011058	P4	2.97	3.33
UCM 104006	2011058	P4	3.48	3.42
UCM 104007	2011058	P4	2.58	3.05
UCM 104008	2011058	P4	3.25	2.66
UCM 104009	2011058	P4	3.24	2.77
UCM 104011	2011058	P4	3.37	2.78
UCM 104012	2011058	P4	3.20	2.71
UCM 104015	2011058	P4	3.31	2.75
UCM 104016	2011058	Ρ4	3.33	2.86
UCM 104017	2011058	P4	3.25	2.82
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UCM 104018	2011058	P4	3.00	2.60
UCM 104019	2011058	P4	3.08	2.81
UCM 104021	2011058	P4	3.14	2.88
UCM 104023	2011058	P4	3.60	3.05



Figure 8. Occlusal view of *Haplaletes* sp., UCM 103808 Rm1.





Figure 9. Lower molar measurements for *Haplaletes*. A, lower m1s. B, lower m2s.



Figure 10. Lower molar measurements for *Haplaletes*. C, lower m3s.

Genus: *Litomylus* Simpson, 1935 *Litomylus dissentaneus* Simpson, 1935 (Table 8 and 9; Figure 11)

Litomylus scaphiscus Gazin, 1956

Litomylus scaphicus Gazin, 1956

Referred Specimens - UCM 105807 RM2, UCM 105808 Lm2 and UCM 103509, Lm3 from UCM locality 2011056; UCM 103905 Rm1 from UCM locality 2011057; all localities are from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution - Nacimiento Formation, San Juan Basin, New Mexico (Torrejonian 3-Tiffanian 1); Fort Union Formation, Bighorn and Clark's Fork Basin, Wyoming (Torrejonian 3 and Tiffanian 2); Fort Union Formation, Washakie Basin, Wyoming (Torrejonian 3); Fort Union Group, Bison Basin, Wyoming (Tiffanian 2-3); (Torrejonian 3 and Tiffanian 2); Porcupine Hills Formation, Alberta, Canada (Tiffanian 1); Lebo Formation, Crazy Mountain Basin, Montana (Torrejonian 3); Melville Formation, Montana (Tiffanian 1 and 3) (Janis et al., 1998).

Description and Discussion – Tooth size and morphology are identical to comparative material of *Litomylus dissentaneus* (AMNH 87543; YPM-PU 17408), with which the UCM specimens were compared, and they fit the as description of *Litomylus dissentaneus* given by Simpson (1935).

TABLE 8. Measurements (in mm) of lower molars of *Litomylus dissentaneus* from the Great Divide Basin.

Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 103905	2011057	m1	3.26	2.00	2.18
UCM 105808	2011056	m2	3.70	2.77	2.98
UCM 103509	2011056	m3	3.15	-	2.29

Specimen	UCM Locality	Tooth position	A-P length	Wtrans
UCM 105807	2011056	M2	3.14	4.15

TABLE 9. Measurement (in mm) of upper molar of *Litomylus dissentaneus* from the Great Divide Basin.



Figure 11. Occlusal view of *Litomylus dissentaneus*, UCM 103509 Lm3 and UCM 105807 RM2.

Family: Mioclaenidae Osborn and Earle, 1895 Genus: *Litaletes* Simpson 1935 *Litaletes disjunctus* Simpson, 1935 (Table 10 and 11; Figure 12)

Referred Specimens – UCM 103901 Lm2 from UCM locality 2011057; UCM 104959 RM2, UCM 103990 Lm1, UCM 103997 Lm1, UCM 103999 Rm1, UCM 104036 Lm1, UCM 104964 Lm1, UCM 104984 Rm2, UCM 103998 Rm3, UCM 104973 Rm3, UCM 104976 Rm3 from UCM locality 2011058; all localities are from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution - North Horn Formation, Wasatch Plateau, Utah (Torrejonian 1); Fort Union Formation, Bighorn and Clark's Fork Basin, Wyoming (Torrejonian 3); Evanston Formation, Fossil Basin, Wyoming (Tiffanian 1); Lebo Formation, Crazy Mountain Basin, Montana (Torrejonian 3) (Janis et al., 1998).

Description and Discussion –*Litaletes* was adequately described by Simpson (1937), and according to Higgins (2000) and Rigby (1980), lower molars of *Litaletes* differ from those of *Promioclaenus* in that the paraconid is more separated from the metaconid in *Litaletes*, which was observed in the UCM specimens. Also observed in a cast of *Litaletes mantiensis* (AMNH 87581), as well as mentioned in Rigby (1980) were "three distinct swellings in addition to the large hypoconid", which infers the presence of an entoconulid anterior to the entoconid. The entoconulid also occurs in two UCM specimens, UCM 103997 and 103901. Additionally, UCM 103997 has twinned cups on the hypoconulid, which was also observed in the cast of *Litaletes mantiensis*. Upper molars are differentiated based on *Litaletes* having a more distinct hypocone than *Promioclaenus* (Simpson, 1937). I assigned the UCM specimens to *Litaletes disjunctus* based on size; all of the UCM specimens are smaller than *Litaletes ondolinae* and *L. mantiensis*. See Table 7 and Table 8 for measurements.

Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 103990	2011058	m1	3.14	2.57	2.51
UCM 103997	2011058	m1	3.65	2.71	2.84
UCM 103999	2011058	m1	3.77	2.44	2.76
UCM 104036	2011058	m1	3.59	2.63	2.86
UCM 103901	2011057	m2	3.60	2.73	2.95
UCM 104984	2011058	m2	3.55	2.78	2.88
UCM 103998	2011058	m3	3.84	-	2.75
UCM 104973	2011058	m3	4.20	-	2.78
UCM 104976	2011058	m3	4.12	-	2.87

TABLE 10. Measurements (in mm) of lower molars of *Litaletes disjunctus* from the Great Divide Basin.

TABLE 11. Measurement (in mm) of upper molar of *Litaletes disjunctus* from the Great Divide Basin.

Specimen	UCM Locality	Tooth position	A-P length	Wtrans
UCM 104959	2011058	M2	3.53	4.62



Figure 12. Occlusal view of *Litaletes disjunctus*, UCM 103997 Lm1 and UCM 104959 RM2.

Genus: Promioclaenus Trouessart, 1904 Promioclaenus acolytus Cope, 1882c (Table 12 and 13; Figure 13)

Hyopsodus acolytus Cope, 1882c Mioclaenus minimus Cope, 1882 Mioclaenus acolytus (Cope) Osborn, 1902 Ellipsodon acolytus (Cope) Matthew, 1937 Promioclaenus aquilonius Simpson, 1935

Referred Specimens - UCM 106704 RM1, UCM 106329 RM2, UCM 106330 RM2 and UCM 103451 Rm3 from UCM locality 2011056; UCM 103963 Lm3 from UCM locality 2011057; UCM 104951 LM1, UCM 103993 Lm1, UCM 104055 Lm3, UCM 104955 Rm3, and UCM 104963 Lm3 from UCM locality 2011058; UCM 103762 RM1, and UCM 103863 Lm3 from UCM locality 2011062; all localities are from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution - Nacimiento Formation, San Juan Basin, New Mexico (Torrejonian 2-Tiffanian 1); Black Peaks Formation, Texas (Tiffanian 1); North Horn Formation, Wasatch Plateau, Utah (Puercan 2); Fort Union Formation (Polecat Bench) Formation, Bighorn and Clark's Fork Basins, Wyoming (Torrejonian 3 and Tiffanian 2); Fort Union Formation, Washakie Basin, Wyoming (Torrejonian 3); Evanston Formation, Fossil Basin, Wyoming (Tiffanian 1); Togwotee Pass Area, Wind River Basin, Wyoming (Tiffanian 3); and Lebo Formation, Crazy Mountain Area, Montana (Torrejonian 3) (Janis et al., 1998); Ohio Creek Formation, Piceance Creek Basin, Colorado (Tiffanian 3) (Burger, 2007).

Description and Discussion – In my previous description of specimens of *Litaletes* (above), I discussed how to differentiate *Promioclaenus* from *Litaletes*. Specifically, the UCM specimens referred here to *Promioclaenus* have the paraconid placed rather close to the metaconid and are lingual,

compared to specimens of *Litaletes* where the paraconid tends to be more medial (Hartman, 1986). Species of *Promioclaenus* are primarily differentiated on the basis of size. Specifically, *Promioclaenus acolytus* is about 20% smaller than *Promioclaenus lemuroides* and *Promioclaenus pipiringosi* (Williamson and Lucas, 1993). The UCM specimens fall within the size range for *P. acolytus* given by Rigby (1980).

TABLE 12. Measurements (in mm) of lower molars of *Promioclaenus acolytus* from the Great Divide Basin.

Specimen UCM Locality Tooth position A-P length Wtri	Wtal
UCM 103933 2011058 m1 3.73 2.55	2.9
UCM 103451 2011056 m3 4.08 -	2.72
UCM 103863 2011062 m3 3.82 -	2.74
UCM 103963 2011057 m3 3.93 -	2.73
UCM 104055 2011058 m3 4.01 -	2.67
UCM 104955 2011058 m3 3.88 -	2.80
UCM 104963 2011058 m3 3.80 -	2.78

TABLE 13. Measurements (in mm) of upper molars of *Promioclaenus acolytus* from the Great Divide Basin.

Specimen	UCM Locality	Tooth position	A-P length	Wtrans
UCM 103762	2011062	M1	3.36	4.21
UCM 104951	2011058	M1	3.36	4.24
UCM 106329	2011056	M2	3.35	4.60



Figure 13. Occlusal view of *Promioclaenus acolytus*, UCM 104955 Rm3 and UCM 106329 RM2.

Promioclaenus sp. indet.

(Table 14; Figure 14)

Referred specimens – UCM 103989 Lm3 from UCM locality 2011058; locality is from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution –*Promioclaenus* ranges temporally from the Puercan to mid-Tiffanian within the Western Interior of North America, including localities in Montana, New Mexico, Texas, Utah and Wyoming (Janis et al., 1998).

Description and Discussion – UCM 103989 is larger than the other UCM specimens of

Promioclaenus and it falls within measurements of both *Promioclaenus lemuroides* and *Promioclaenus pipiringosi*. These two species were characterized by Gazin (1956) as being very similar in size, but differing from one another in that *P. pipiringosi* has noticeably smaller lower premolars. Because UCM 103989 is an isolated molar, it could not be identified to species.

TABLE 14. Measurement (in mm) of lower molar of *Promioclaenus* sp. from the Great Divide Basin.SpecimenUCM LocalityTooth positionA-P lengthWtriWtal

4.4

_

m3

UCM 103989

2011058



Figure 14. Occlusal view of Promioclaenus sp., UCM 103989 Lm3.

2.96

Family: Phenacodontidae Cope, 1881e Genus: *Phenacodus* Cope 1873 *Phenacodus* sp. indet. (Table 15; Figure 15)

Opisthotomus Cope, 1875

Eohyus (in part) marsh, 1894

Almogaver Crusafont and Villalta, 1955

Referred specimens - UCM 105395 Rm2 from UCM locality 2011056; locality is from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution- *Phenacodus* ranges temporally from the late Torrejonian through the Bridgerian in North America, including localities in Alberta, California, Colorado, New Mexico, North Dakota, Saskatchewan, Texas, and Wyoming (Janis et al., 1998).

Description and Discussion –UCM 105395, a lower right m2, is bunodont and compares well in morphology to *Phenacodus* (UCM 73817). Specifically, it falls within the range of size for *Phenacodus bisonensis* and *Phenacodus vortmani*, which are both very similar in morphology and size. According to Thewissen (1990), *P. vortmani* differs from *P. bisonensis* in that the talonid basin of the p4 is narrower, and there is usually an entoconid. Since UCM 105395 is an isolated lower molar, the species cannot be determined.

TABLE 15. Measurement (in mm) of lower molar of *Phenacodus* sp. from the Great Divide Basin.

Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
105395	2011056	m2	8.57	7.02	-



Figure 15. Occlusal view of *Phenacodus* sp., UCM 105395 Rm2.

Genus: Ectocion Cope, 1882d *Ectocion* sp. indet.

(Table 16 and 17; Figure 16)

Oligotomus (in part) Cope, 1882a

Ectocion Cope, 1882c

Gidleyina Simpson, 1935a

Prosthecion Patterson and West, 1973; West, 1976

Referred specimens – UCM 105398 LM1, UCM 103535 Rp4-m1, UCM 103531 Rm1, UCM 105815 Rm2, and UCM 109150 Lm2 from UCM locality 2011056; locality is from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution - *Ectocion* ranges temporally from the early Tiffanian through Early Bridgerian throughout North America, including localities in Alberta, California, Colorado, Mississippi, Montana, North Dakota, Saskatchewan, Texas, and Wyoming (Janis et al., 1998).

Description and Discussion- The UCM specimens referred here to *Ectocion* sp. indet. are more lophodont than *Phenacodus* and fit the morphology of *Ectocion* given by Thewissen (1990) and as seen in comparative cast material (UW 10269 and 10270). In the referred UCM specimens and observed by Thewissen (1990), the lower molars lack a paraconid and upper molars have a distinct parastyle. Lower molar specimens (UCM 103535, 103531, 105815 and 109150) are larger (based on Thewissen, 1990) than most species of *Ectocion* and therefore were not assigned to a species.

TABLE 16. Measurements (in mm) of lower molars of *Ectocion* sp. from the Great Divide Basin.

Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
103535	2011056	p4	7.55	5.25	5.05
103531	2011056	m1	8.03	5.95	6.28
103535	2011056	m1	7.58	6.24	6.22
109150	2011056	m1	7.84	6.56	6.52
105815	2011056	m2	7.95	6.13	6.14

Specimen	UCM Locality	Tooth position	A-P length	Wtrans
105398	2011056	M1	7.4	8.35

TABLE 17. Measurement (in mm) of upper molar of *Ectocion* sp. from the Great Divide Basin.



Figure 16. Occlusal view of *Ectocion* sp., UCM 103531 Rm1 and UCM 105398 LM1.

Order: "Proeutheria" Romer, 1966 Suborder: Didelphodonta McKenna, 1975 Family: Cimolestidae Marsh, 1889 Genus: *Acmeodon* Matthew and Granger, 1921 *Acmeodon hyoni* Rigby, 1980 (Table 18; Figure 17)

Referred Specimens – UCM 104050 Rm1 and UCM 104953 Rm1 from UCM locality 2011058; locality is from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution – Fort Union Formation, Washakie Basin, Wyoming (Torrejonian 3) (Janis et al., 2008).

Description and Discussion –*Acmeodon* was described by Van Valen (1966). Referred UCM specimens were identified by the slit at the end of the lowest point of the cristid obliqua which distinguishes this genus from *Gelastops;* UCM specimens also have lingually-placed paraconids (Hartman, 1986; Winterfield, 1982). The UCM specimens are larger than known measurements for *Acmeodon secans,* but fit within the size range of lower molars of *Acmeodon hyoni*.

It should be noted that Williamson and Lucas (1993) considered *A. hyoni* to be a junior synonym of *A. secans*, which may be plausible in that there are few morphological differences, and the size differences are not large. However, Gunnell et al., (2008) recognized them as separate species, so I follow these authors in recognizing both *A. hyoni* and *A. secans* based upon size differences.

TABLE 18. Measurement (in mm) of lower molars of Acmeodon hyoni from the Great Divide Basin.

Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 104050	2011058	m1	3.92	2.14	2.33
UCM 104953	2011058	m1	3.84	2.27	2.34





Acmeodon secans Matthew and Granger, 1921

(Table 19)

Referred Specimens – UCM 104032 Lm2, UCM 104960 Rm2 and UCM 104035 Lm3 from UCM locality 2011058; locality is from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution – Nacimiento Formation, San Juan Basin, New Mexico (Torrejonian 2-3); Fort Union (Polecat Bench) Formation, Bighorn and Clark's Fork Basins, Wyoming (Torrejonian 3 and Tiffanian 2); Hanna Formation (Carbon County), Wyoming (Tiffanian 1); Fort Union Formation, Washakie Basin, Wyoming (Torrejonian 3) (Janis et al., 2008).

Description and Discussion – *Acmeodon secans* is distinguished from *A. hyoni* by size, and specifically the lower m2s are shorter in anteroposterior length and are generally wider (Ribgy, 1980). The referred UCM specimens are smaller than UCM specimens referred above to *A. hyoni*, and fall within the size range of *A. secans* (Rigby, 1980); therefore these specimens were referred to this species.

Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 104032	2011058	m2	3.03	1.95	2.54
UCM 104960	2011058	m2	3.43	1.86	2.33
UCM 104035	2011058	m3	2.99	1.48	2.19

Genus: *Gelastops* Simpson, 1935a *Gelastops parcus* Simpson, 1935a (Table 20 and 21; Figure 18)

Emperodon acmeodontoides Simpson 1935

Referred Specimens – UCM 103868 RM1 and UCM 104051 Rm2 from UCM locality 2011058; UCM 104692 RM1 from UCM locality 2011057; all localities are from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution – Fort Union (Polecat Bench) Formation, Bighorn and Clark's Fork Basins, Wyoming (Torrejonian 3 and Tiffanian 2); Fort Union Formation, Washakie Basin, Wyoming (Torrejonian 3); Lebo Formation, Crazy Mountain area, Montana (Torrejonian 3) (Janis et al., 2008); Ohio Creek Formation, Piceance Creek Basin, Colorado (Tiffanian 3) (Burger, 2007).

Description and Discussion – UCM lower molars were compared to casts of *Gelastops* (AMNH 100378; UCM 48917), and are referred to *Gelastops* because they did not have a slit at the lowest point of the cristid obliqua, like that of *Acmeodon* (Van Valen, 1966). The cristid obliqua is often much more developed, especially at the anterior end where it meets the trigonid. Lower m1s were differentiated from m2s by having a longer trigonid with the paraconid and metaconid separated more than in the m2s. UCM specimens were designated as *G. parcus* based on their smaller size and are within the range of known measurements of that species (Van Valen 1966). Upper molar characters of *Gelastops* include the absence of a hypocone, and presence of a small paraconule and a vestigial metaconule, whereas *Acmeodon* has large conules (Van Valen, 1966; Hartman, 1986). Upper molars were also identified as *G. parcus* based on their smaller size also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars were also identified as *G. parcus* based on their solver molars we

Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 104051	2011058	m2	3.14	2.3	1.81

TABLE 20. Measurement (in mm) of lower molar of *Gelastops parcus* from the Great Divide Basin.

TABLE 21. Measurement (in mm) of upper molars of *Gelastops parcus* from the Great Divide Basin.

Specimen	UCM Locality	Tooth position	A-P length	Wtrans
UCM 103868	2011058	M1	3.33	4.65
UCM 104692	2011057	M1	3.63	5.72



Figure 18. Occlusal view of Gelastops parcus, UCM 103868 M1.

Gelastops joni Rigby, 1980

(Table 22 and 23)

Referred Specimens – UCM 103869 RM2, UCM 103872 RM3, UCM 103985 Lm2 from UCM locality 2011058; UCM 103760 Rm2 and UCM 103761 Rm2 from UCM locality 2011062; all localities are from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution – Hanna Formation (Carbon County), Wyoming (Torrejonian 3-Tiffanian 1); Fort Union Formation, Washakie Basin, Wyoming (Torrejonian 3) (Janis et al., 2008).

Description and Discussion – In my previous description of *Gelastops parcus* (above), I discuss the identification characters for *Gelastops*. Lower molars of UCM specimens were compared to casts of the type specimen (AMNH 100378) and assigned based on proper morphology and size. *G. joni is* the larger of the two species, specifically in length of lower m2s, according to Rigby (1980). Upper molars were also identified as *G. joni* due to their larger size, however there is little published data on measurements of upper molars for this species.

TABLE 22. Measurement (in mm) of lower molars of *Gelastops joni* from the Great Divide Basin.

Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 103760	2011062	m2	3.87	2.27	2.09
UCM 103761	2011062	m2	3.36	2.41	1.8
UCM 103985	2011058	m2	3.39	2.65	1.97

TABLE 23. Measurement (in mm) of upper molars of *Gelastops joni* from the Great Divide Basin.

Specimen	UCM Locality	Tooth position	A-P length	Wtrans
UCM 103869	2011058	M2	3.15	4.49
UCM 103872	2011058	M3	4.22	2.45

Gelastops sp.

(Table 24)

Emperodon Simpson, 1935

Referred Specimens – UCM 103513 Rm1 from UCM locality 2011056; UCM 103956 Rm1 from UCM locality 2011058; UCM 103981 Lm1, UCM 103982 Lm1, UCM 104043 Lm1, UCM 104049 Lm1, UCM 104053 Lm1 from UCM locality 2011058; all localities are from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution –*Gelastops* ranges temporally from the late Torrejonian through early Tiffanian within the Western Interior of the United States, including localities in Montana and Wyoming (Janis et al., 2008).

Description and Discussion – Lower m1s match the proper morphology for the genus *Gelastops*. However, the two species were separated by Rigby based on the size differences; the m1s were identified as distinctly wider and the m2s distinctly longer. In the case of the referred specimens of lower m1s, they are larger both in length and width and therefore were not identified to a species. This simply may represent a single species of *Gelastops* with a larger size variation then previously known, since some measurements are very close to both species. It is also possible the two species of *Gelastops* are not clearly defined, and therefore *G. joni* should be considered a junior synonym. Since there is little published data on the species, and all referred specimens are isolated teeth, all specimens are identified based on size at this time.

Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 103513	2011056	m1	3.72	2.39	2.21
UCM 103956	2011057	m1	3.63	2.27	2.02
UCM 103981	2011058	m1	3.63	2.37	2.11
UCM 103982	2011058	m1	4.02	2.32	2.1
UCM 104043	2011058	m1	3.85	2.35	2.19
UCM 104049	2011058	m1	3.83	2.48	2.2
UCM 104053	2011058	m1	4.05	2.53	2.25

TABLE 24. Measurement (in mm) of lower molars of *Gelastops* sp. from the Great Divide Basin.

Suborder: Pantolesta McKenna, 1975 Family: Pantolestidae Cope, 1884a Genus: *Paleotomus* Van Valen, 1967 *Paleotomus junior* Scott et al., 2002 (Table 25; Figure 19)

Referred Specimen – UCM 104949 Lm2 from UCM locality 2011058; locality is from the basal

Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution – Porcupine Hills Formation, Alberta (Tiffanian 1); and Paskapoo Formation, Alberta (Torrejonian 3) (Janis et al., 2008).

Description and Discussion – Based on comparisons with cast material of *Paleotomus milleri* (AMNH 100644, 100422 and 100423), UCM 104949, a left m2, fits the morphology for the genus *Paleotomus*. Based on the small size of this specimen, it was identified as *Paleotomus junior* (Scott et al., 2002), the smallest species in the genus.

TABLE 25. Measurement (in mm) for the lower molar of Paleotomus	junior from the Great Divide Basin.
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Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 104949	2011058	m2	3.30	2.14	1.60



Figure 19. Occlusal view of Paleotomus junior, UCM 104949 Lm2.

Paleotomus senior Simpson, 1937a

(Table 26; Figure 20)

Palaeosinopa senior Simpson, 1937a

Palaeosinopa simpsoni Van Valen, 1967

Referred Specimen – UCM 103758 Lm1 from UCM locality 2011062; locality is from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution – Black Peaks Formation, Texas (Tiffanian 1); Hoback Formation, Hoback Basin, Wyoming (Tiffanian 5); Porcupine Hills Formation, Alberta (Tiffanian 1); Melville Formation, Montana (Tiffanian 1 and 3); Tongue River Formation, Williston Basin, North Dakota (Torrejonian 3-Tiffanian 1, and Tiffanian 3) (Janis et al., 2008).

Description and Discussion – Based on comparisons of cast material for this species, the referred specimen is identical in size and morphology to *Paleotomus senior*. This specimen is of much larger size than the specimen referred to *Paleotomus junior*, and fits within the proper size range for *Paleotomus senior*.

TABLE 26. Measurements (in mm) for lower molar of *Paleotomus senior* from the Great Divide Basin.

Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 103758	2011062	m1	4.56	2.52	2.50



Figure 20. Occlusal view of Paleotomus senior, UCM 103758 m1.

Genus: Bessoecetor Simpson 1936

Bessoecetor sp.

(Table 27)

Propalaeosinopa Simpson, 1927

Thylacondon, (Matthew and Granger, 1921 in part); Russell in Rutherford, 1927 *Palaeosinopa*, Matthew, 1901 (in part); Simpson, 1935a *Palaeictops*, Matthew, 1899 (in part); Van Valen, 1967

Referred Specimens – UCM 103464 Lm3 and UCM 103465 Rm3 from UCM locality 2011056; locality is from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution –*Bessoecetor* ranges temporally from the late Puercan through late Tiffanian throughout North America, including localities in Alberta, Montana, North Dakota, Saskatchewan, Utah and Wyoming (Janis et al., 2008).

Description and Discussion – UCM specimens are very similar in morphology for *Bessoecetor* when compared to cast material (AMNH 35701 and 35702). The UCM specimens have narrow, elongated talonids with a further extended, medial and posterior-directed hypoconulid, as noted by Hartman (1986) for *Bessoecetor*. The UCM specimens were not assigned to species because while they could represent a small individual of *Bessoecetor septentrionalis*, the material is incomplete, isolated teeth. The referred specimens are smaller than *Bessoecetor septentrionalis* and *Bessoecetor thomsoni* and larger than *Bessoecetor krausei*. The UCM specimens may represent a different species because they are intermediate in size.

TABLE 27. Measurements (in mm) for lower molars of <i>Bessoecetor</i> sp	p. from the Great Divide Basin.
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Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 103464	2011056	m3	2.37	1.44	1.16
UCM 103465	2011056	m3	2.46	1.46	1.35

Superorder: Leptictida McKenna, 1975 Family: Leptictidae Gill, 1872 Genus: *Prodiacodon* Matthew, 1929 *Prodiacodon concordiarcensis* Simpson, 1935a (Table 28; Figure 21)

Diacodon concordiarcensis (Gazin, 1956) Van Valen, 1967

Diacodon pearcei Gazin, 1956

Referred Specimens – UCM 103959 Lp5 from UCM locality 2011057; UCM 103986 Rp5 from UCM locality 2011058; all localities are from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution – Fort Union (Polecat Bench) Formation, Bighorn and Clark's Fork Basins, Wyoming (Tiffanian 5); Fort Union Formation, Washakie Basin, Wyoming (Torrejonian 3); Fort Union Group, Bison Basin, Wyoming (Tiffanian 2); Wasatch Formation, Chappo Member, Wyoming (Tiffanian 3); Porcupine Hills Formation, Alberta (Tiffanian 1); Lebo Formation, Crazy Mountain area, Montana (Torrejonian 3); Melville Formation, Montana (Tiffanian 3) (Janis et al., 2008).

Description and Discussion – Novacek (1977) has described leptictids in detail. Based on the description given by Novacek and McKenna (1975), the dental formula within the leptictid lineage included five premolars, but all Tertiary specimens have four premolars. McKenna (1975) identified the dental formula for the lower molars as i1, i2, i3, c1, p1, p2, p4, p5, m1, m2, m3; the lower p3 has been lost, resulting in four lower premolars, with the fourth in the third position and fifth in the fourth position. For the purposes of identification, premolars are identified based on this dental formula, so all p5 molars are in the fourth premolar location (Novacek, 1977).

The referred UCM specimens were compared to cast material (AMNH 35693, 35291 and 16748), and they fit the size and morphology of *Prodiacodon concordiarcensis*. This species is the smallest

species of *Prodiacodon* (smaller than the *P. puercensis* and *P. tauricinerei*), and the UCM specimens are distinguished from other species by having three cusps on the talonid basin of the lower p5, instead of four, as is seen in *P. puercensis, P. tauricinerei* and *P. furor* (Novacek, 1977).

TABLE 28. Measurements (in mm) for lower molars of *Prodiacodon concordiarcensis* from the Great Divide Basin.

Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 103959	2011057	р5	2.44	1.2	1.12
UCM 103986	2011058	р5	2.66	1.4	1.17



Figure 21. Occlusal view of *Prodiacodon concordiarcensis,* UCM 103959 Lp5.

Prodiacodon cf. P. puercensis

(Table 29; Figure 22)

Diacodon (Palaeolestes) puercensis Matthew, 1918

Referred Specimens – UCM 104937 Rm2, UCM 106343 Lm3 from UCM locality 2011056; UCM 104972 Rm1, UCM 104058 Lm2 from UCM locality 2011058; all localities are from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution – Nacimiento Formation, San Juan Basin, New Mexico (Torrejonian 1-3); Fort Union Formation, Washakie Basin, Wyoming (Torrejonian 3); Porcupine Hills Formation, Alberta (Tiffanian 1) (Janis et al., 2008).

Description and Discussion – Lower molars of *Prodiacodon* have sharp cusps, high trigonids, the paraconid is well separated from the metaconid, and *Prodiacodon puercensis* has an entoconulid present on the talonid basin (Novacek, 1977). The size and morphology of UCM specimens are nearly indistinguishable from the cast material of *P. puercensis* (AMNH 16748). Lower m3s have five cusps, including the entoconulid. While the lower m3, UCM 106343, does have an entoconulid present, due to condition, it is unclear whether there are a total of four additional cusps on the talonid, because one, located between the hypoconulid and entoconid, may be either broken or worn. Because the morphology of the lower m3, UCM 106343 is tentatively identified to *Prodiacodon puercensis*.

TABLE 29. Measurements (in mm) for lower molars of *Prodiacodon* cf. *P. puercensis* from the Great Divide Basin.

Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 104937	2011056	m1	3.59	3.01	2.33
UCM 104972	2011058	m1	3.41	2.77	2.24
UCM 104058	2011058	m2	3.62	2.45	2.3
UCM 106343	2011056	m3	3.9	2.52	2.12



Figure 22. Occlusal view of *Prodiacodon* cf. *P. puercensis,* UCM 104058 Lm2.

📕 1 mm

Order: Primates Linnaeus, 1758 Family: Plesiadapidae Trouessart, 1897 Genus: *Nannodectes* Gingerich, 1975 *Nannodectes intermedius* Gazin, 1971 (Table 30 and 31; Figure 23)

Pronothodectes intermedius Gazin, 1971

Referred Specimens – UCM 104827 LM1, UCM 104831 RM2, UCM 104826 Lm2, UCM 105399 Lm2, UCM 104828 Rm3 and UCM 104830 Lm3 from UCM locality 2011056; UCM 104063 Rm1, UCM 104071 Rm1, UCM 104080 Rm1, UCM 104083 Rm1, UCM 104089 Rm1, UCM 104091 Rm1, UCM 104066 Lm2, UCM 104073, UCM 104074 Lm2, UCM 104078 Rm2, UCM 104084 Rm2, UCM 104088 Rm2, UCM 104090 Rm2, UCM 104081 Lm3, and UCM 104086 Lm3 from UCM locality 2011058; all localities are from the basal Overland Member, Fort Union Formation, Great Divide Basin, Wyoming.

Known Distribution – Fort Union (Polecat Bench) Formation, Bighorn and Clark's Fork basins, Wyoming (Tiffanian 2); Hanna Formation (Carbon County), Wyoming (Tiffanian 1); Fort Union Formation, Shotgun member, Wind River Basin, Wyoming (Tiffanian 1); Porcupine Hills formation, Alberta (Tiffanian 1); Melville Formation, Montana (Tiffanian 1 and 3); Tongue River Formation, Powder River Basin, Montana (Tiffanian 1) (Janis et al., 2008).

Description and Discussion – Higgins (2000) observed a noticeable anterior tilt of the trigonid in lower molars of *Nannodectes;* the referred UCM specimens exhibit the same tilt. The UCM specimens also show the squared entoconid reported by Gingerich (1976) for *Nannodectes*, and they especially show inclined labial walls (Hartman, 1986) in contrast to *Plesiadapis* lower molars which exhibit less steep labial walls. The UCM specimens were compared with a *Nannodectes intermedius* cast (UW 3223), which shows the paraconid and metaconid to be closer together. This was also true for the referred UCM specimens, where twinning of the paraconid and metaconid was observed, whereas specimens of *Plesiadapis* appear to have more spaced paraconids and metaconids (UW 3223 and PU 14512). The upper molars were identified to *Nannodectes* by the presence of a small mesostyle, which is not observed in *Plesiadapis* (Secord, 1998). Overall, the size of the UCM specimens falls within the size range of *Nannodectes*, and the morphology is correct so these specimens were identified as *Nannodectes intermedius*.

Specimen	UCM Locality	Tooth position	A-P length	Wtri	Wtal
UCM 104063	2011058	m1	2.62	2.08	2.44
UCM 104080	2011058	m1	2.54	1.93	2.27
UCM 104083	2011058	m1	2.49	1.88	2.13
UCM 104089	2011058	m1	2.44	2.15	2.36
UCM 104090	2011058	m1	2.56	2.20	2.21
UCM 104091	2011058	m1	2.68	2.00	2.34
UCM 104066	2011058	m2	2.64	2.34	2.60
UCM 104073	2011058	m2	2.63	2.31	2.49
UCM 104074	2011058	m2	2.50	2.38	2.52
UCM 104078	2011058	m2	2.57	2.49	2.63
UCM 104084	2011058	m2	2.68	2.59	2.70
UCM 104826	2011056	m2	2.74	2.37	2.52
UCM 105399	2011056	m2	2.93	2.53	2.68
UCM 104081	2011058	m3	3.67	-	2.31
UCM 104086	2011058	m3	3.58	-	2.39
UCM 104828	2011056	m3	3.03	2.13	2.36
UCM 104830	2011056	m3	3.58	2.09	2.31

TABLE 27. Measurements (in mm) for lower molars of *Nannodectes intermedius* from the Great Divide Basin.

TABLE 28. Measurements (in mm) for lower molars of *Nannodectes intermedius* from the Great Divide Basin.

Specimen	UCM Locality	Tooth position	A-P length	Wtrans
UCM 104827	2011056	M1	2.31	3.41
UCM 104831	2011056	M2	2.49	3.9



Figure 23. Occlusal view of Nannodectes intermedius, UCM 104084 Rm2 and UCM 104827 LM1.

Faunal List

Order Pantodonta Family Pantolambdidae Pantolambda cavirictis Order 'Condylarthra' Family Arctocyonidae Mimotricentes sp. Family Hyopsodontidae Haplaletes disceptatrix Haplaletes pelicatus Haplaletes sp. Litomylus dissentaneus Family Mioclaenidae Litaletes disjunctus Promioclaenus acolytus Promioclaenus sp. Family Phenacodontidae Phenacodus sp. Ectocion sp. Order "Proeutheria" Suborder Didelphodonta Family Cimolestidae Acmeodon hyoni Acmeodon secans Gelastops parcus Gelastops joni Gelastops sp. Suborder Pantolesta Family Pantolestidae Paleotomus junior Paleotomus senior Bessoecetor sp. Order Leptictida **Family Leptictidae** Prodiacodon concordiarcensis Prodiacodon cf. P. puercensis **Order Primates** Family Plesiadapidae Nannodectes intermedius

RESULTS AND DISCUSSION

In total, 189 fossil teeth from four UCM localities on same stratigraphic horizon were identified and used in this study. The taxa fall within 14 different genera and five mammalian orders. The mammalian fauna from the Great Divide Basin is comparable to late Torrejonian faunas (See Figure 24) and is consistent with known first and last appearances of species within the late Torrejonian and early Tiffanian NALMA (Lofgren et al., 2004). Further, the absence of *Plesiadapis precursor* would also suggest a late Torrejonian age, as the first appearance of this species defines the onset of the Tiffanian NALMA and specifically the Tiffanian 1 lineage zone (Lofgren et al., 2004). The presence of the cimolestid, Acmeodon hyoni also suggests that this fauna is of late Torrejonian age. However, neither of these indicators can conclusively indicate a late Torrejonian age. Acmeodon hyoni is not well represented in the literature and has been considered a junior synonym of A. secans by Williamson and Lucas (1993), a species known to extend into the early Tiffanian (Hartman, 1986; Higgins, 1990). The absence of Plesiadapis is suspect as well, because the earliest occurrence of that species may in fact be part of a transitional fauna between the late Torrejonian and early Tiffanian NALMA, suggested by Higgins' (2000) transitional fauna in the Hanna Basin to the northeast of the Great Divide Basin. Based upon a comparable fauna described by Higgins (2000), as well as the presence of *Ectocion* (which first occurs in earliest Tiffanian time) and the early Tiffanian index taxon Nannodectes intermedius, the faunal assemblage from the Great Divide Basin is best referred to the early Tiffanian lineage zone 1.

It seems probable that the Overland fauna represents a transitional fauna between the end of the Torrejonian and beginning of the Tiffanian NALMA, not unlike what Higgins (2000) identified in the Hanna Formation of the Hanna Basin (see also Lofgren at al., 2004 for a discussion). The absence of *Plesiadapis* from the Great Divide Basin localities may be a sampling bias, although it seems unlikely that

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Figure 24. Documented Temporal distribution of Mammalia taxa that have also been identified from the Great Divide Basin, Wyoming. Temporal ranges of these taxa are based on Janis et al., (1998; 2008).

Plesiadapis teeth (if present in the assemblage) would not have been collected by the ants and incorporated into their hills, as the teeth are not very different in size from *Nannodectes* and are certainly not out of the size range for ants to collect. Higgins (2000) identified her overlap zone as Tiffanian 1 due to the presence of *Plesiadapis praecursor* and *Nannodectes intermedius* (2000).

However, Higgins' overlap zone also comprises last appearances of *Gelastops joni* and *Litaletes disjunctus*, and with characteristic species of Tiffanian 1, such as *Mimotricentes subtrigonus*. She also noted that most of the species within the overlap zone are largely considered Torrejonian in age, which is consistent with the findings in my faunal analysis. Further, the Overland fauna appears to represent only fauna from Tiffanian 1 (as opposed to younger Tiffanian lineage zones), because species such as *Pantolambda cavirictis, Litaletes disjunctus, Gelastops joni, Paleotomus senior* and *Prodiacodon puercensis* are known to have made their last appearances during Tiffanian 1 (Janis et al., 1998, 2008; Lofgren et al., 2004).

Geographic and Temporal Range Extensions

All species included in this faunal analysis represent slight geographic range extensions in that they are now represented in the Great Divide Basin of south-central Wyoming, about 50 miles southwest of the Hanna Basin. The largest geographic range extension is for *Paleotomus junior*, which has previously only been documented from localities in the Porcupine Hills and Paskapoo Formations in Alberta, Canada (Gunnell et al., 2008; Scott et al., 2002; Scott, 2003).

The largest temporal range extension is for *Haplaletes pelicatus*, which was previously only known from the mid-Tiffanian (Tiffanian 2 and 3) (Gazin, 1956a). Another temporal range extension into the early Tiffanian is for *Acmeodon hyoni*, which is currently documented only from Torrejonian 3 (Rigby, 1980; Janis et al., 2008). *Gelastops parcus* is documented as occurring in the late Torrejonian and Tiffanian 2 and 3 (but not in Tiffanian 1). With its presence in the fauna from the Great Divide Basin, it is now known to occur in the Tiffanian 1 as well. This fauna also confirms the presence of many species found within the transitional zone between the late Torrejonian and early Tiffanian, including *Phenacodus*, which was previously thought to first appear at the beginning of the Tiffanian but have since been documented from the late Torrejonian (Janis et al., 1998).
RAREFACTION

By conducting rarefaction, species diversity can be compared among faunal assemblages that have different abundance data; specifically larger samples are used to estimate the richness of a smaller sample (Magurran, 2004). However, in order to conduct rarefaction, a number of assumptions are made, based on the compared faunal assemblages. These assumptions include similar collecting techniques, faunal assemblages are similar, individuals are randomly dispersed, and that there is a sufficient sample size (Magurran, 2004). In this study, these assumptions are not sufficiently satisfied for the faunal assemblages that were compared. Specifically, while the UCM localities were from a single stratigraphic horizon and many of the teeth were collected from anthills, the other earliest Tiffanian faunal assemblages with which the UCM localities were compared included more than one stratigraphic horizon (in the case of the Hanna Basin, localities spanning 150 meters of stratigraphic section) and the fossils were collected by a variety of methods (anthills, surface collecting, quarrying and screen washing). However, while the assumptions of rarefaction are not satisfied, this technique does allow us to gauge the diversity of an admittedly skewed faunal assemblage.

Analytic Rarefaction 1.3 software (Holland, 2003) was used to compare biodiversity between the fauna from the Great Divide Basin with other faunas, including fauna from the Hanna Formation documented by Higgins (2000) and the Polecat Bench Formation in the south Bighorn Basin, documented by Hartman (1986). Because multituberculates were not included in this faunal analysis (as they are being studied by D. Lofgren), they were also omitted from both Higgins' and Hartman's fauna for the purposes of the rarefaction analysis. Compared fauna from the Hanna Formation assemblage only include species found in the overlap zone (Tiffanian 1) or in the Tiffanian 1 zone of her stratigraphic sections, totaling a sample from about 150 meters of section (Higgins, 2000). The comparative faunal assemblage from the Polecat Bench Formation includes nine localities from the earliest Tiffanian, and spanning approximately 40 meters of section (Hartman, 1986).

The rarefaction analysis shown in Figure 25 (in blue) infers that the fauna from the Great Divide Basin is not as diverse compared to early Tiffanian faunas from the Hanna Formation (Higgins, 2000). However the fauna included from the Hanna Formation includes many more localities, collected from anthills, quarrying and screen-washing, and were sampled from a much thicker stratigraphic section (Higgins, 2000). The Polecat Bench Formation faunal assemblage (Hartman, 1986) incorporates nine fossil localities and has a lower number of specimens (N=164), but this may be due to the fact that fossils were collected predominantly from anthills (and therefore the assemblage is skewed towards smaller mammals).



Figure 25. Results of rarefaction analysis comparing earliest Tiffanian faunal assemblages from the Great Divide Basin, Hanna Basin (Higgins, 2000), and Bighorn Basin (Hartman, 1986). Dashed lines represent 95% upper and lower confidence intervals for each faunal assemblage.

When compared to the fauna from the Polecat Bench Formation, which is similar to the fauna from the Great Divide Basin in that is was largely sampled from anthills, it shows the fauna from the Great Divide Basin is comparable, but slightly more diverse (Figure 25). Because many of the specimens utilized in both of these faunal analyses were collected from anthills, it is predicted that the ants will produce a sampling bias (skewed towards smaller-bodied mammals that have tiny teeth), and the assemblages do not preserve the full biologic diversity. The lower diversity may also represent a preservation bias, in that very few fossils were found on the ground in Hartman's fossil sites.

Other factors that probably contribute to the lower diversity of the Great Divide Basin Tiffanian faunal assemblage is that fossils are from a single stratigraphic horizon. Many would consider this to represent a single fossil locality, as opposed to multiple sites. In contrast, Higgins' (2000) total fauna contains over 2000 specimens of fossil vertebrates that were collected from 57 different localities spanning Torrejonian 3-Tiffanian 1 and almost 500 meters of section. Although there is lower species diversity, Hartman's (1986) fossil localities from the earliest Tiffanian represent sampling from about 40 meters of section. Overall, considering that the early Tiffanian fauna from the Great Divide Basin is from one stratigraphic horizon, it does capture considerable diversity.

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CONCLUSION

The fauna from the Overland Member of the Fort Union Formation in the Great Divide Basin is best referred to the earliest Tiffanian lineage zone 1, and is especially comparable to, and confirms the presence of, a transitional fauna between the late Torrejonian and early Tiffanian NALMA, as described in the nearby Hanna Basin by Higgins (2000). While the Great Divide Basin fauna was referred to Tiffanian 1, it is missing the index taxon *Plesiadapis praecursor*. The absence of this species is surprising because the sampling bias by ants would not be predicted to affect that species because it is rather small and comparable in size to teeth of *Nannodectes*. However, the Great Divide Basin fauna supports Higgins' (2000) transitional zone in that the assemblage is heavily influenced by Torrejonian species, but the presence of *Nannodectes intermedius* infers an early Tiffanian age for the fauna.

This faunal analysis provides temporal range extensions for species such as *Haplaletes pelicatus, Gelastops parcus* and *Acmeodon hyoni* as well as a large geographic range extension for *Paleotomus junior* (previously only known from western Canada). My study also provides valuable measurements for each recorded species, which previously had been lacking in publications of other faunal assemblages and should greatly assist to differentiate species, as many of the species are separated by size.

Mammalian faunas from the middle Paleocene are not well known, and therefore the early Tiffanian fauna reported here provides valuable information not only for species presence in the Great Divide Basin, but also from the early Tiffanian. My study also extends Higgins' (2000) transitional zone between the late Torrejonian and early Tiffanian to areas outside of the Hanna Basin. Based on my results, more is known from the early Tiffanian and can be used as framework for future studies within the Great Divide Basin.

Future Research

The stratigraphic relationship of fossil-bearing horizons within the Great Divide Basin are well established by Hettinger et al. (2008), so suggested future research would be to collect more fossils from this area, including if possible, more complete fossil mammal specimens. It is probable that this would increase the known diversity and provide further corroboration to the transitional fauna that exists, as well as have more material with which to compare and identify species. Through the collection of more fossil mammals, it will also be more likely to increase documented diversity found within the Great Divide Basin, which, in turn, would provide a better understanding of middle Paleocene mammalian diversity in the Western Interior.

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