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EOCENE AND OLIGOCENE MAMMALS FROM THE GRAVELLY RANGE OF SOUTHWEST MONTANA

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ABSTRACT

High elevation outcrops of Tertiary strata in the Gravelly Range of southwest Montana yield late Uintan to Whitneyan vertebrates that comprise five mammalian assemblages; *Rapamys* Site, Black Butte Low, Teepee Mountain, Black Butte High, and Lion Mountain High. The *Rapamys* Site and Black Butte Low are late Uintan or early Duchesnean. Two new species are present at the *Rapamys* Site (the carnivore *Lycophocyon tabrumi* and the rodent *Pareumys muffleri*). Small mammalian assemblages from Teepee Mountain and Black Butte High are late Duchesnean-early Chadronian and Chadronian, respectively. The most diverse assemblage is from Lion Mountain High, which is correlative with Whitneyan faunas from Wyoming, Nebraska, and South Dakota. The Whitneyan age of the Lion Mountain High assemblage is further age constrained by an underlying tuff with a weighted mean ^{40}Ar/^{39}Ar age of 31.7 ± 0.02 Ma and an overlying basalt flow with a K/Ar age of 30.8 ± 0.7 Ma. Paleogeographic range extensions into Montana for Lion Mountain High taxa include *Diceratherium tridactylum* and *Oxetocyon cuspidatus*. The taxonomic composition of the combined *Rapamys* Site/Black Butte Low mammalian assemblage is most similar to those from southern California, rather than geographically closer assemblages found in Wyoming and Utah. Comparison of undescribed middle Eocene mammalian assemblages from southwest Montana to those from southern California will further elucidate the middle Eocene Montana-California paleobiogeographic affinity.

INTRODUCTION

Earl Douglass (1909) initially reported the presence of Tertiary vertebrate fossils in the Gravelly Range of southwest Montana, but the first collections of vertebrate fossils were made in the late 1940s when J. Mann (1954) recovered vertebrate fossils in the Black Butte and Lion Mountain areas (Figure 1). These specimens were tentatively identified as *Trigonias*, *Leptomeryx*, titanothere, and agriochoerid by Princeton vertebrate paleontologist G. Jepsen who estimated that the fossils were early Oligocene in age (Mann, 1954). This unusually high elevation occurrence of vertebrate fossils caught the interest of paleontologists at the Museum of Comparative Zoology (MCZ) who sent A. Lewis to the area in 1952 and 1958 (Luikart, 1997) when specimens were recovered from three sites; Black Butte I, Black Butte II, and Black Butte III. Based on MCZ locality data, Black Butte II was located low on the southeast flank of Black Butte adjacent to and north of the west fork of Rossiter Creek. Black Butte III was directly east of Black Butte, and Black Butte I was adjacent to the east fork of Rossiter Creek about 1 km east of Black Butte II. Many of the MCZ specimens were identified and catalogued but none were described for publication.

In the 1980s, M. McKenna and others representing the American Museum of Natural History (AMNH) visited the Gravelly Range to search for vertebrate fossils (Luikart, 1997) and found late Orellan-Whitneyan mammalian taxa (*Diceratherium tridactylum*, *Oxetocyon*, *Nanodelphys*, *Palaeolagus* cf. *P. burkei*) in channel fillings about 20 m below a basalt flow with a K-Ar age of 30.8+/- 0.7 Ma that caps the approximately 270 m thick Tertiary section at Lion Mountain (Gutmann et al., 1989). An Eocene titanothere jaw was also found in a tuffaceous mudstone 90 m above the base of the exposed section at Lion Mountain, about 60 m below an ashfall tuff that has a weighted mean ^{40}Ar/^{39}Ar age of 31.7 ± 0.02 Ma (W. McIntosh personal communication, 2018). AMNH crews also collected at MCZ Black Butte I, a locality they called the *Rapamys* Site after a new species of *Rapamys* (*Rapamys atramontis*) recovered there and described by Wahlert et al. (2006). The holotype and hypodigm of *R. atramontis* are the only described specimens from the Gravelly Range.

In the 1990s, E. Luikart thesis (1997) focused partly on the vertebrate biostratigraphy of the south-central part of the Gravelly Range, an area that included the vertebrate sites visited by Mann (1954), the MCZ, and the AMNH, and included the first attempt to establish a biostratigraphic and biochonologic treatment

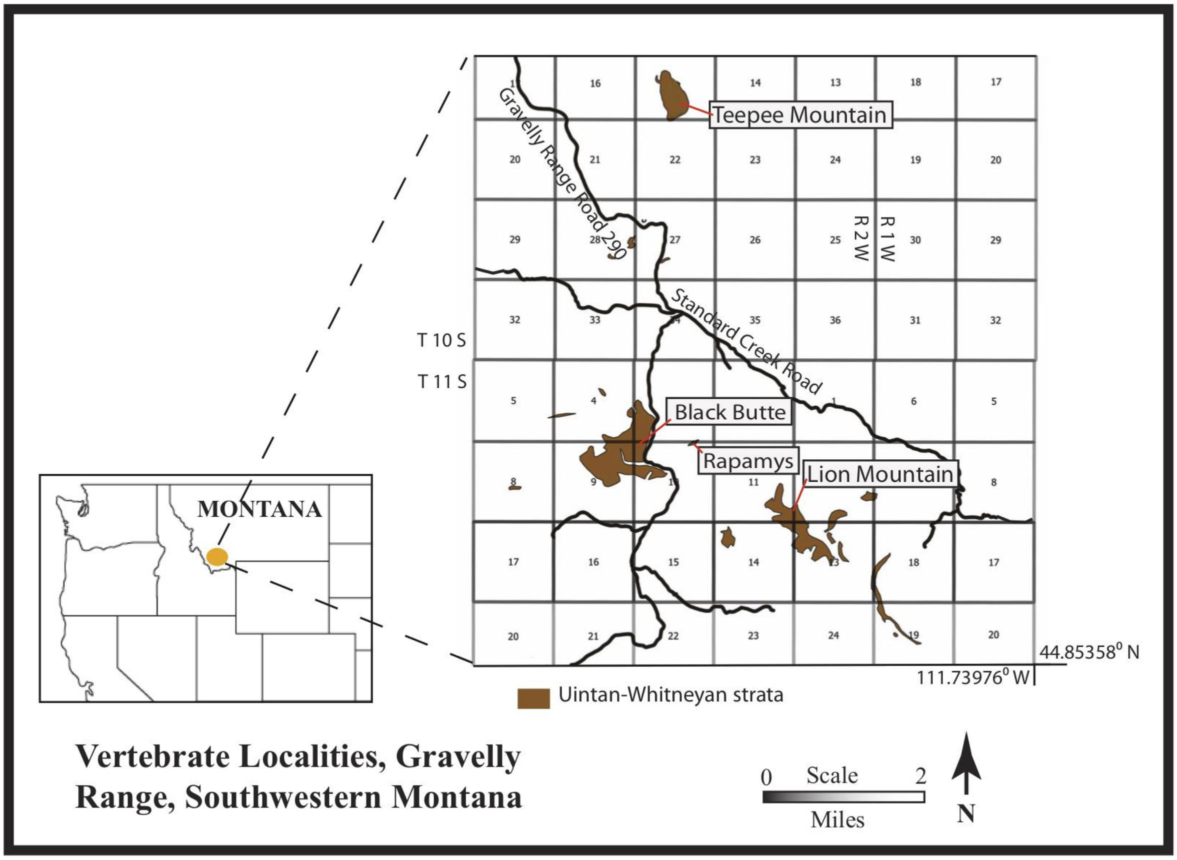

FIGURE 1. Exposures of Middle Eocene to Early Oligocene strata (Uintan to Whitneyan North American Land Mammal Ages) in the south-central Gravelly Range of southwest Montana. Outcrops yielding mammalian assemblages are located in the Teepee Mountain, Black Butte, *Rapamys*, and Lion Mountain areas.

of Gravelly Range mammalian assemblages. In addition to recovering fossils from MCZ and AMNH sites, Luikart (1997) discovered a new locality called Teepee Mountain (Figure 1; Luikart's fossils were deposited at the AMNH). Luikart (1997) made tentative identifications of many Gravelly Range mammalian specimens and provided faunal lists for four sites; *Rapamys* Site, Black Butte, Teepee Mountain, and Upper Lion Mountain. Based on stratigraphic position and mammalian assemblage, Luikart (1997) thought that the Black Butte, Teepee Mountain, and *Rapamys* sites were approximately equivalent in age and that their mammalian assemblages represent a Duchesnean age local fauna. Luikart (1997) also considered the Upper Lion Mountain locality as Whitneyan following Gutmann et al. (1989).

Starting in 2016, D. Hanneman remapped the south-central Gravelly Range and measured sections of fossil-bearing Tertiary strata, while crews from the Raymond M. Alf Museum of Paleontology (RAM) led by D. Lofgren collected additional specimens at Teepee Mountain and the MCZ and AMNH sites (fossils now housed at the RAM). Based on this work and study of the MCZ and AMNH collections, we present a description of Gravelly Range mammals and provide a biostratigraphic and biochronologic analysis of five mammalian assemblages. We also correlate our analysis with the regional biostratigraphic framework for middle Eocene to Pliocene strata in southwest Montana developed by Tabrum et al. (1996, 2001) and briefly discuss the paleobiogeographic implications of Gravelly Range mammalian assemblages. Detailed geologic work on Eocene-Oligocene depositional environments and the determination of paleoelevation for Cenozoic strata of the Gravelly Range are currently under investigation by Hanneman and Lofgren (in preparation).

GEOLOGIC SETTING

Tertiary strata that yield significant assemblages of mammals are exposed at four high elevation areas

(9,200-9,800 feet or approximately 3,000 m) in the south-central part of the Gravelly Range (Figure 1). These rocks are part of the informal Sequence 2 of Hanneman and Wideman (1991, 2006) and a lithostratigraphic proxy, the Renova Formation of Kuenzi and Fields (1971). The strata include fluvial, debris flow, aeolian, and travertine deposits, with clastic rocks ranging in grain size from mudstone to conglomerate. As documented here, Uintan to Whitneyan vertebrates occur within the finer-grained units. Also, travertine deposits located in the northern part of the study area contain Eocene-Oligocene plant remains. Early Oligocene basalt to basaltic-andesitic flows and minor mafic intrusive rocks also occur throughout the study area.

Measured stratigraphic sections (Figure 2) include the five major vertebrate-bearing sites and typify the main Tertiary lithologies of the south-central Gravelly Range. These sections also contain volcanic rock units that provide age constraints on some assemblages of fossil mammals. Furthermore, the measured sections illustrate that Tertiary sediment deposition occurred on a surface of at least moderate relief, based upon the various elevations for the base of each section and the different stratigraphic units that underlie each Tertiary section.

The thickest Tertiary stratigraphic sections are exposed at Lion Mountain and Black Butte (Figures 1-2). The Lion Mountain section is approximately 270 m thick and unconformably overlies Mississippian Madison Group strata. The lower half of the section is predominantly aeolian deposits which yielded a titanothere jaw fragment Duchesnean or Chadronian in age. Fluvial units, both channel and floodplain deposits, occur in portions of the upper half of the section. The uppermost 20 m contains Whitneyan vertebrates and is capped by a 50 m thick basalt that produced a K-Ar groundmass feldspar concentrate age of 30.8±0.7 Ma (Gutmann et al., 1989). A tuff that occurs on the east side of Lion Mountain has a weighted mean ^{40}Ar/^{39}Ar single crystal sanidine age of 31.7 ± 0.02 Ma (W. McIntosh personal communication, 2018) and is shown at its approximate stratigraphic position in the section measured on the west side of Lion Mountain (Figure 2).

The Black Butte stratigraphic section is about 140 m thick and unconformably overlies Permian Shedhorn Sandstone. The basal 30 m contains minor fluvial sand lenses, but much of the remaining section is largely aeolian in origin. Immature Stage II calcic paleosols containing non-coalesced calcic nodules up to 10 cm in diameter occur in several horizons throughout the section. Uintan-Duchesnean vertebrate remains are found within nodules associated with paleosols in the lowest 30 m of the section (Figure 2). The uppermost unit yields a sparse Chadronian mammalian fauna that is associated with calcic nodules and isolated lenses of shelly, bivalve-rich siltstone that are interpreted as isolated, small ponded areas. Extensive burrows are also present within Tertiary strata at Black Butte.

Exposed Tertiary strata thin rapidly away from the Black Butte and Lion Mountain areas, with other vertebrate-bearing strata having a maximum thickness of about 20 m. The *Rapamys* Site section, the thinnest at about 8 m, is an isolated pocket of mudstone of probable floodplain origin, that unconformably overlies Permian Shedhorn Sandstone (Figure 2). The section exhibits immature, Stage II calcareous paleosols, trace fossils (possibly invertebrate pellets), and Uintan-Duchesnean vertebrates within calcareous nodules.

The Teepee Mountain stratigraphic section contains late Duchesnean-early Chadronian vertebrates and is capped by a meter-thick basalt with an ^{40}Ar/^{39}Ar whole rock age of 32.38 ± 0.64 Ma (Luikart, 1997). The section overlies Triassic Dinwoody Formation strata and consists of mudstone, that in the basal 3 m, contains approximately 5% quartz, granitic, and mafic floating clasts representing debris flow material. The remainder of the section exhibits Stage II calcic paleosols and extensively bioturbated horizons (Figure 2) representing floodplain deposition.

Travertine deposits present along the west-central edge of the Gravelly Range are associated with previously mapped thrust faults (Mann, 1954; Luikart, 1997; Kellogg and Williams, 2000; O'Neill and Christiansen, 2004) and recently recognized and mapped extensional faults (Hanneman and Lofgren, in preparation). The travertines are up to 52.5 m thick and are exposed in three main areas that occur along a northwest trending ridgeline for about 2.5 km. Leaf imprint assemblages in the travertines contain *Metasequoia*, *Sequoia*, Gingko, *Quercus*?, *Fagopsis*, *Tilia*?, Amelanchier/Rosa, *Plafkeria*?, and *Cornus* and are Eocene-Oligocene in age (H. Meyer personal communication, 2018). These travertines, previously mapped as Upper Cretaceous-Paleocene Beaverhead Formation, are here reassigned to the southwestern Montana informal Cenozoic Sequence 2 of Hanneman and Wideman (1991, 2006).

MATERIALS AND METHODS

Gravelly Range specimens described here are housed at the AMNH, MCZ, and RAM. Specimens were studied during 2017-2019 on visits to the AMNH and MCZ and both institutions loaned specimens for detailed analysis and photography.

At the MCZ, nearly all dentigerous specimens from the Gravelly Range are labelled as being from the Black Butte I, II, and III localities. On a topographic map of the Black Butte area in the MCZ collections archives, Black Butte I is plotted at the identical location of the AMNH *Rapamys* Site. The plot of Black Butte II

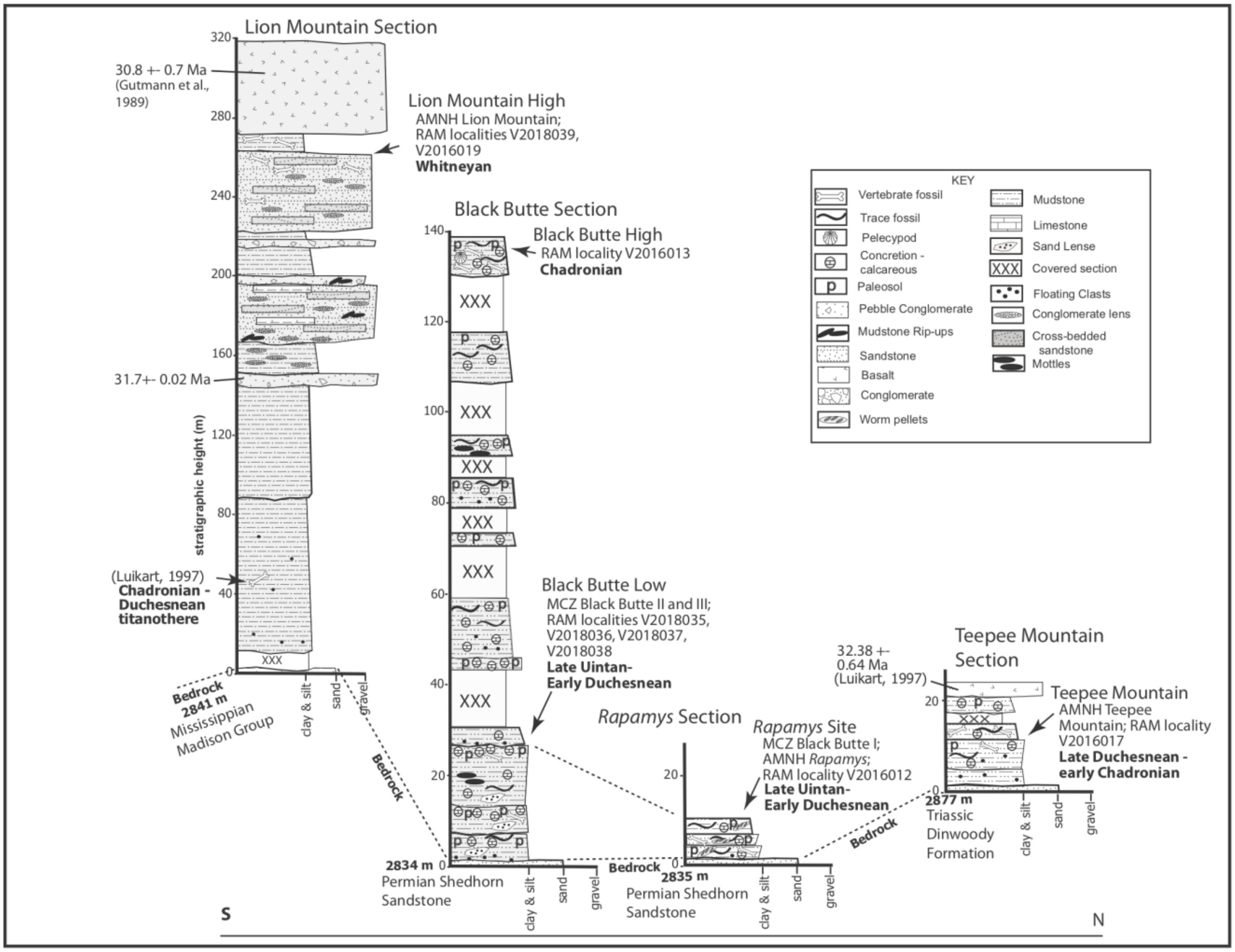

FIGURE 2. Uintan to Whitneyan fossil assemblage locations within measured Tertiary stratigraphic sections in the south-central Gravelly Range, southwest Montana. Measured sections are shown in a general south to north transect; specific location areas for each section are plotted in Figure 1.

covers about 1 square km of outcrop on the lower southeast flank of Black Butte and appears to closely correspond to the lower 30 m of Tertiary strata depicted in the Black Butte stratigraphic section in Figure 2, which includes RAM localities V2018035, V2018036, V2018037 and V2018038. The plot for Black Butte III is at the same stratigraphic level as Black Butte II, but about 1 km further north. However, a photograph of Black Butte (taken from about 1 km south of Black Butte, looking north) in the MCZ archives has locality numbers written on it and shows Black Butte I as occurring on the southeast flank of Black Butte. This may have caused some confusion as, for example, MCZ 20120 is a dentary labeled *Mesohippus* from Black Butte I that is partly encased in highly indurated gray rock, unlike all other MCZ specimens labelled Black Butte 1. Concretions from Black Butte II and III are gray and highly indurated while those from the *Rapamys* Site (correct location of Black Butte I) are beige and only moderately indurated. Thus, MCZ 20120 (*Mesohippus*) must be from Black Butte II or III. Another problematic specimen is MCZ 7348, identified here as *Hesperaletes borineyi*, a rare taxon previously only known from Uintan strata in southern California (Colbert, 2006a). The specimen label for MCZ 7348 reads from the "highest exposures below Black Butte west of road," and the highest exposures at Black Butte are Chadronian (this paper). Based on its Uintan age in California, MCZ 7348 probably was recovered from the lowermost 30 m of strata shown in Figure 2 (a level where RAM crews found late Uintan or early Duchesnean mammals in gray, highly indurated concretions). Thus, in a few cases we had to decide if we should include poorly constrained MCZ specimens in our biostratigraphic analysis of Gravelly Range mammals. An example of inclusion is MCZ 7348 (*Hesperaletes borineyi*), which we assume was recovered from the upper part of the lowest 30 m of strata at Black Butte because *H. borineyi* is limited elsewhere to Uintan strata. Other poorly constrained MCZ specimens were excluded from this study, including the partial dentary of *Mesohippus* (MCZ 20120).

At the AMNH, only those specimens from the Gravelly Range that were the holotype or hypodigm of *Rapamys atramontis* were cataloged. The remaining AMNH Gravelly Range specimens were stored on floor five of the Frick collections in two drawers labelled "field collections of M. McKenna." These drawers contained mammalian specimens and some of them were labelled with preliminary identifications by McKenna. The most diagnostic and complete of these specimens were included in this study after they were cataloged in 2018.

For each mammal specimen described, a specific locality name or site number is provided in Systematic Paleontology. A mammalian assemblage from a specific site (example, *Rapamys* Site) or assemblages from stratigraphically equivalent sites in the same area (example, Black Butte Low) comprise a local fauna. The names of the local faunas are used in the text and the sites they represent are listed below and shown in Figure 2.

--*Rapamys* Site (MCZ Black Butte I, AMNH *Rapamys* Site, RAM locality V2016012)
--Black Butte Low (MCZ Black Butte II and III, RAM localities V2018035, V2018036, V2018037, and V2018038)
--Black Butte High (RAM locality V2016013)
--Teepee Mountain (AMNH Teepee Mountain, RAM locality V2016017)
--Lion Mountain High (AMNH Lion Mountain, RAM localities V2016019 and V2018039)

Dimensions of mammalian teeth were recorded in mm using a Carrera Precision digital caliper and were photographed using a high-resolution Canon camera system.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York; ANSP, Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania; CIT, California Institute of Technology, Pasadena, California (collections now housed at the Natural History Museum of Los Angeles County, Los Angeles, California); CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; FMNH, The Field Museum, Chicago, Illinois; MB.Ma, Museum Fur Naturkunde Berlin, Berlin, Germany; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts; OU, University of Oregon Museum of Natural History, Eugene, Oregon; PU, Princeton University, Princeton, New Jersey (collections now housed at the YPM); RAM, Raymond M. Alf Museum of Paleontology, Claremont, California; SDSM, South Dakota School of Mines, Rapid City, South Dakota; SDSNH, San Diego Society of Natural History, San Diego, California; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut; UA, University of Alberta Laboratory of Vertebrate Paleontology, Edmonton, Alberta, Canada; UCMP, University of California Museum of Paleontology, Berkeley, California; USNM, Department of Paleobiology, United States National Museum of Natural History, Washington D. C.

SYSTEMATIC PALEONTOLOGY

Order Didelphimorphia Gill, 1872
Family Didelphidae Gray, 1821
Herpetotherium Cope, 1873a
*Herpetotherium fugax C*ope, 1873a
Figures 3A-G, Tables 1-2

Holotype—AMNH 5254, right dentary fragment with m1-4 (Cope, 1884: pl. LXII, fig. 7; Korth, 1994: fig. 3.1).

Referred Specimens—RAM 25532 nearly complete, partially crushed skull with articulated dentaries (Figure 3A-C, E-G) missing the occipital condyle, posterior 10% of braincase and basicranium, and part of left maxilla with M3-4 from RAM locality V2018039 (Lion Mountain High); AMNH 145517 right dentary with p1-3, m1-4, and roots of canine and i2-4 (Figure 3D); AMNH 145516 right m2 from AMNH Lion Mountain.

Description—RAM 25532 is an extraordinary specimen because it is the first to preserve the entire dentition of *Herpetotherium fugax* (dental formula: I5/4, C1/1, P3/3. M4/4). Description of the lower dentition of *H. fugax* is based on AMNH 145517 and the dentaries of RAM 25532. Molars and premolars of AMNH 145517 are slightly worn and the single-rooted canine and incisors lack crowns due to breakage. Premolars have two roots and a single main cusp. A minute heel is present in p1, the smallest premolar. A diastema is present between p1 and p2. Subequal in size, p2-3 have small talonid basins. The lower molars of AMNH 145517 have a large paraconid, metaconid, protoconid, and hypoconid, and a small hypoconulid twinned with a larger entoconid (Figure 3D).

The dentaries of RAM 25532 preserve a complete lower dental battery. There are four spatulate lower incisors, with i1-2 slightly larger in size and height than i3-4 (Figure 3C, 3G). The size difference between i1-2 and i3-4 in RAM 25532 is significantly less than that of UA 8572, a skull and dentaries of *Herpetotherium fugax* described and illustrated by Fox (1983: figs. 1c, 2c). Also, MB.Ma.50671, a skull of *H. fugax* illustrated by Horowitz et al. (2008: pl. 1, fig. b) preserves i2-4, and the slight difference in size between i2 and i3-4 appears to be more similar to that of RAM 25532 than UA 8572.

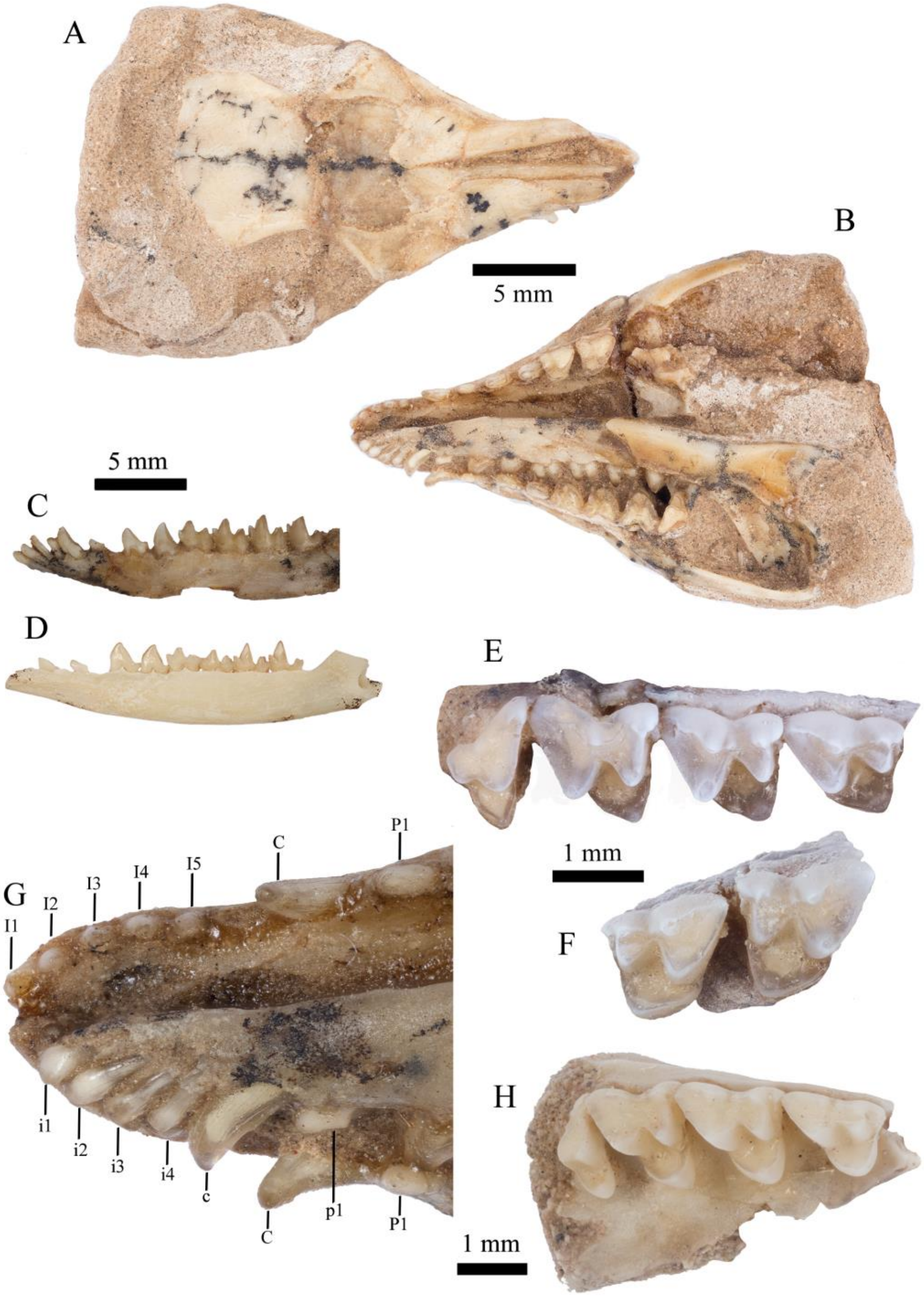

FIGURE 3: *Herpetotherium fugax* and *Nanodelphys* cf. *N. hunti* from Lion Mountain High. **A.** Dorsal and **B.** Ventral views of RAM 25532 skull with right dentary of *Herpetotherium fugax* (left dentary in C, upper molars in E and F, incisors in G). **C.** Labial view of left dentary of RAM 25532 with i1-4, c, p1-m4 (5 mm scale applies also to D). **D.** Lingual view of AMNH 145517 right dentary of *Herpetotherium fugax* with p1-3, m1-4 and roots of canine and i2-4. **E.** Occlusal view of right M1-4 of RAM 25532. **F.** Occlusal view of left M1-2 of RAM 25532. **G.** Ventral view of the anterior part of Figure 3B, with the right dentary covering part of skull and lower and upper dentitions labelled where visible (1 mm scale applies to G and H). **H.** Occlusal view of RAM 25531 right maxilla fragment of *Nanodelphys* cf. *N. hunti* with M1-M4.

In RAM 25532 the canine is much larger in size and height compared to i1-4 (Figure 3C, 3G). The lower premolars and molars of RAM 25532 are very similar to those AMNH 145517, except p3 is larger than p2, and the talonid basin in p2-3 is less developed compared to the p2-3 of AMNH 144517 (Figure 3C-D).

The rostrum of RAM 25532 is mostly intact and there are five incisors (Figure 3G), the first documented complete set of upper incisors of *Herpetotherium fugax*. The crown of I1 is missing but a single root is clearly present, as are four additional closely spaced and small, single-rooted incisors with conical crowns. There is a sizable diastema between I5 and the canine, which is large and has a slightly recurved apex. The upper premolars of RAM 25532 are two-rooted, each with a single main cusp, and P2 is smaller than P3 and there is a small diastema between P1-P2 and a smaller one between P2-P3 (Figure 3B).

TABLE 1. Measurements in mm of the P1-M4 of RAM 25532 compared to the means of the P1-M4 of *Herpetotherium fugax* from Cedar Creek, Colorado (Korth, 1994, table 4).

Tooth Site		RAM 25532	*H.fugax*
P1	L	0.7-0.8	0.9
	W	0.4	0.4
P2	L	1.2-1.3	1.5
	W	0.6-0.7	0.6
P3	L	1.3-1.4	—
	W	0.6-0.7	—
M1	L	1.9-2.0	1.8
	W	1.7-1.8	1.6
M2	L	2.0	1.8
	W	1.9-2.2	1.8
M3	L	2.1	1.7
	W	2.0	2.1
M4	L	1.4	1.2
	W	1.9	2.0

The M1-3 of RAM 25532 have a well-developed centrocrista and a metacone that is much larger than the paracone (difference most prominent in M1), and a large protocone with a well-developed pre-and postprotocrista (Figure 3E-F). The M1 of RAM 25532 has a small parastyle with a minute stylar A cusp, a small B cusp connected to the paracone by a paracrista, a large D cusp (larger than B cusp), and a slight ectoflexus. There is a minute C cusp high on the anterior slope of the D cusp in the right M1, but no trace of the C cusp on the left M1. The paracone, protocone and stylar B cusp are transversely aligned on the M1 and a minute metaconule and protoconule are evident on their respective pre-and postprotocrista.

The M2 of RAM 25532 is similar to the M1, but has a more defined ectoflexus, a relatively larger B cusp, and a distinct C cusp on the anterior slope of a large D cusp (on both left and right M2; Figure 3E-F). The M3 differs from M1-2 in having a strong ectoflexus, a minute parastyle with a large A cusp, a well-developed C cusp, and in lacking conules and B and D cusps (Figure 3E). In M4, the paracone is relatively massive compared to the metacone and the protocone is also large. The M4 has a parastyle with a small A cusp, a C cusp defined by an area of thickened enamel on the labial edge of the stylar shelf and lacks B and D cusps (Figure 3E).

TABLE 2. Measurements in mm of the p1-m4 of AMNH 145517 and RAM 25532 compared to means of the m1-m4 of *Herpetotherium fugax* from Cedar Creek, Colorado (Korth, 1994, table 4).

Tooth Site		AMNH 145517	RAM 25532	*H. fugax*
p1	L	1.1	0.9	0.8
	W	0.4	0.4	0.4
p2	L	1.8	1.3	1.6
	W	0.6	0.6	0.6
p3	L	1.5	1.2	1.6
	W	0.7	0.7	0.8
m1	L	1.8	1.6	1.8
	W	1.0	1.0	1.1
m2	L	1.9	1.7	1.9
	W	1.2	1.2	1.2
m3	L	1.8	1.9	1.9
	W	1.1	1.4	1.2
m4	L	1.8	1.7	1.9
	W	1.0	1.2	1.1

Discussion—*Herpetotherium fugax* is distinguished from other species of *Herpetotherium* by its intermediate size, fusion of the C and D cusps on M1-2, presence of a large C cusp on M3-M4, and having a larger D cusp than B cusp on M1-2 (Korth, 1994). RAM 25532 shares these stylar cusp features and measurements of the upper dentition of RAM 25532 are also similar to those of *H. fugax* (Table 1). For the lower dentition, molars of species of *Herpetotherium* differ only in size (Korth, 1994) and the lower dentition of RAM 25532 is most similar in size to that of *H. fugax* (Table 2). AMNH 145516 and AMNH 145517 are from the same site as RAM 25532 and represent additional examples of the lower dentition of *H. fugax*.

There is significant variation in the dentition of specimens referred to *H. fugax*. In AMNH 145517, p2-3 are subequal in size, whereas in RAM 25532, p3 is larger than p2. Also, based on the i1-4 of UA 8572, a dentary from southeast Wyoming (Fox, 1983), i1-2 of *H. fugax* are significantly larger than i3-4. But in RAM 25532 from southwest Montana, i1-2 are only slightly larger than i3-4. Also, there is considerable variation in the development of stylar cusps within species of *Herpetotherium* (Korth, 1994). Thus, a reassessment of *H. fugax* that includes newly discovered specimens like RAM 25532 might result in recognition of an additional taxon.

Family Peradectidae Crochet, 1979
Nanodelphys McGrew, 1937
Nanodelphys cf. *N. hunti* Cope, 1873b
Figure 3H, Table 3

Holotype—AMNH 5266, left dentary fragment with m2-m4, Cedar Creek Beds, Logan County, Colorado (Orellan) (Korth, 1994: fig. 6.4).

Referred Specimen—RAM 25531, right maxilla fragment with M1-M4 (Figure 3H), from RAM locality V2018039 (Lion Mountain High).

Description—The M1-4 of RAM 25531 lack both a V-shaped centrocrista and conules and the molars are wider than long (Figure 3H). The metacone is slightly larger than the paracone in M1, but the metacone is significantly larger than the paracone in M2-3. Development of stylar cusps in RAM 25531 is reduced, as M1-3 have a well-defined conical B cusp that is small and confluent with the labial terminus of the paracrista, and a D cusp that is an elongated thickening of the labial rim of the stylar shelf rather than a conical cusp (less developed in M1 compared to M2-3; Figure 3H). A minute C cusp is present on M1-M3 and an ectoflexus is well developed only on M3. The M4 of RAM 25531 is transversely elongate, lacks stylar cusps, and has a large paracone and an anteriorly expanded parastyle.

Discussion—*Nanodelphys* is a small peradectid whose upper molars are wider than long and whose B cusp is the only well-developed stylar cusp, features that separate it from *Peradectes* (Korth, 1994). The M1-3 of RAM 25531 are wider than long (Table 3) and B cusp is the only well-defined stylar cusp, although the D cusp is also present on the labial rim of the stylar shelf, as is a minute C cusp (Figure 3H), features that match the description by Korth (1994) of the M1-3 of *Nanodelphys hunti*. Also, the ratio of length versus width of the molars of RAM 25531 are similar to those of *N. hunti* (Table 3).

One significant feature that differentiates *Nanodelphys hunti* from RAM 25531 is the relative size of the metacone. The metacone significantly exceeds the size of paracone in the M2-3 of RAM 25531, and in *Nanodelphys*, the metacone and paracone of M1-3 are subequal in size (Korth, 1994) (a condition present in the M1 of RAM 25531). Although similar to *N. hunti* in nearly all respects, the relatively large metacone in the M2-3 of RAM 25531 makes its referral to *N. hunti* tentative.

TABLE 3. Measurements in mm and ratios of length versus width of the M1-M4 of RAM 25531 compared to length versus width ratios of upper molars of *Nanodelphys hunti* from North America (Korth, 1994, table 8).

Tooth Site		RAM 25531	RAM 25531	*N. hunti*
M1	L	1.4	1.0	0.91
	W	1.4		
M2	L	1.4	0.93	0.86
	W	1.5		
M3	L	1.3	0.81	0.75
	W	1.6		
M4	L	0.8	0.57	—
	W	1.4		

Order Lagomorpha Brandt, 1855
Family Leporidae Fischer von Waldheim, 1817
Megalagus Walker, 1931
Megalagus cf. *M. brachyodon* Matthew, 1903
Figure 4A

Holotype—AMNH 9652, left maxilla with P2-M2 from Pipestone Springs, Montana (Matthew, 1903; illustrated by Wood, 1940: fig. 106).

Referred Specimen—AMNH 145521 crushed partial skull with right and left P3-M2 (Figure 4A) from AMNH Teepee Mountain.

Description-Discussion—AMNH 145521 represents a lagomorph larger than *Palaeolagus* which has moderately worn cheek teeth and broken incisors. The skull is laterally crushed and is missing most of the braincase, basicranium, and the left zygomatic arch (Figure 4A). The cheek teeth of AMNH 145521 were compared to those of *Megalagus brachyodon* in the RAM collections from Pipestone Springs, where *M. brachyodon* is a rare component. The length of the P3-M2 of AMNH 145521 from AMNH Teepee Mountain is 9.7 mm (for both right and left) and the P3-M2 of the holotype of *M. brachyodon* (AMNH 9652) measures 10.6 mm in length (Wood, 1940, 344). A maxilla with P3-M2 (RAM 9207) from Pipestone Springs of *M. brachyodon* has a length of 11.1 mm. Thus, AMNH 145521 is smaller than the holotype and significantly smaller than RAM 9207 from the type locality. The range of variation in *M. brachyodon* from Pipestone Springs is unknown, but the range in length of the P3-

M2 of *M. brachyodon* from Flagstaff Rim (Wyoming) is 11.0-12.1 mm (Gawne, 1978: table 1). AMNH 145521 is tentatively referred to *M. brachyodon* because it is small in relation to the documented size of the species.

Palaeolagus Leidy, 1856
Palaeolagus burkei Schlaikjer, 1935
Figure 4B-E

Holotype—AMNH 8704, skull with complete dentition from the White River Formation, Castle Rock, Colorado (Wood, 1940: fig. 97).

Referred Specimens—AMNH 145519 crushed skull missing part of braincase, most of basicranium, and entire occipital condyle, with left I1-2, P2-M2 and right I1-2, P2-M3; AMNH 145512 right maxilla fragment with P2-M2 with root of M3 (Figure 4B); AMNH 145514 left maxilla fragment with a partial P3 and P4-M2 (Figure 4C); AMNH 145508 right dentary fragment with p2-3; AMNH 145509 left dentary fragment with p2-m1 from AMNH Lion Mountain. RAM 18637 anterior half of skull with left I1-2, P2-M1 and right I2, P2-M3 (Figure 4D-E) from RAM locality V2016019 (Lion Mountain High).

Description-Discussion—These specimens represent a small lagomorph, smaller than *Palaeolagus hypsodus*. *P. haydeni*, and *P. temnodon*. Lengths of the P3-M2 of AMNH 145512, AMNH 145514, AMNH 145519 and RAM 18637 vary from 6.3-7.0 mm and are very similar in size to those of *P. burkei* (5.7-7.4 mm, Gawne, 1978: table 1). The P3s of RAM 18637, AMNH 145519, AMNH 145512 and AMNH 145514 have a labial reduction in the width of the protoloph (Figure 4B-E), a distinguishing feature of *P. burkei* (Wood 1940: fig. 97) and *P. hypsodus* (Dawson, 1958, fig. 10a) not seen in *P. haydeni* or *P. temnodon*. *Palaeolagus hypsodus* is more hypsodont than *P. burkei* (Dawson, 1958), and RAM 18637, AMNH 145519, AMNH 145512, and AMNH 145514 are more similar to *P. burkei* in this regard. Two lower dentitions (AMNH 145508 and AMNH 145509) also from AMNH Lion Mountain compare closely to *P. burkei* in size and represent that species.

Palaeolagus sp.
Figure 4F-G

Referred Specimen—AMNH 145529 right dentary with i1, p2-m3, and partially prepared left dentary with i1, p2-4 (m1-m3 still encased in matrix; Figure 4F-G) from AMNH Teepee Mountain.

Description-Discussion—AMNH 145529 was compared directly to RAM specimens of *Palaeolagus temnodon* from Pipestone Springs and it represents a smaller species. The dentition of AMNH 145529 is similar in size to AMNH 145508 and AMNH 145509

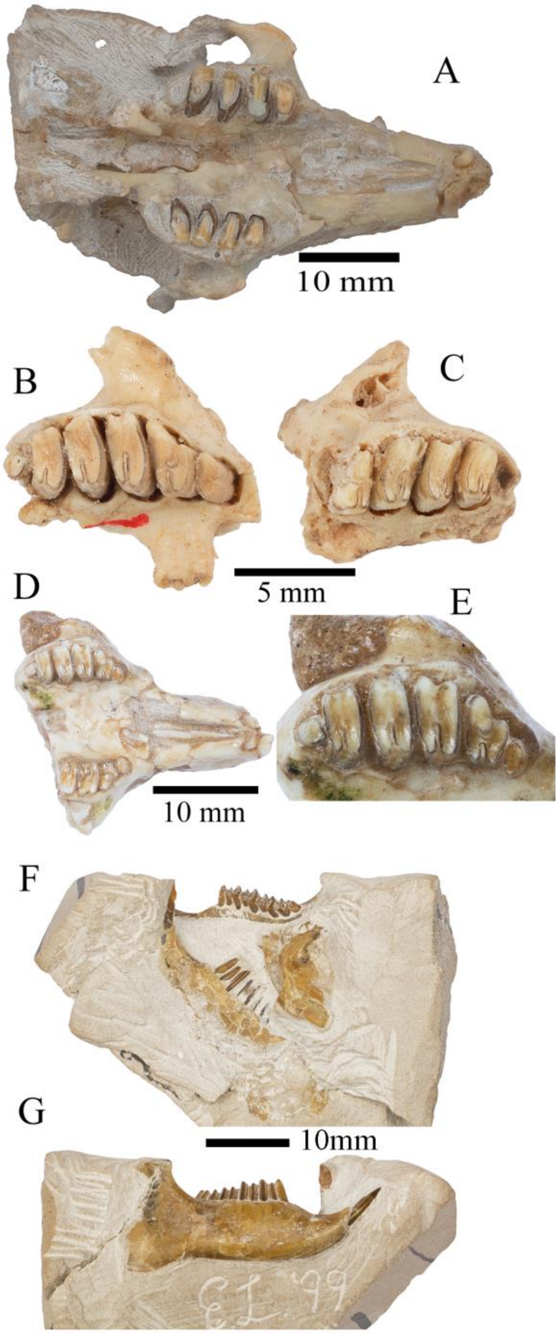

FIGURE 4: Lagomorphs from Lion Mountain High and Teepee Mountain. **A.** Occlusal view of AMNH 145521 crushed partial skull of *Megalagus* cf. *M. brachyodon* with right and left P3-M2 from Teepee Mountain. **B.** Occlusal view of AMNH 145512 right maxillary fragment with P2-M2 and M3 root of *Palaeolagus burkei* from Lion Mountain High (5 mm scale applies to B, C, and E). **C.** Occlusal view of AMNH 145514, left maxilla fragment with partial P3 and P4-M2 of *P. burkei* from Lion Mountain High. **D**. Occlusal view of RAM 18637 anterior half of skull of *P. burkei* with left I1-2, P2-M1, and right I2 and P2-M3 from Lion Mountain High. **E.** Occlusal view of right P2-M3 of RAM 18637. **F.** Lingual view of AMNH 145529 left dentary with i1 and p2-4 partially exposed and crowns of p2-m3 of right dentary of *Palaeolagus* sp. from Teepee Mountain. **G**. Labial view of right dentary with i1 and p2-m3 of AMNH 145529.

from Lion Mountain High referred to *P. burkei*, but the Lion Mountain specimens are higher crowned and the p2 metaloph of AMNH 145529 (Figure 4F-G) is not as well-developed as the more molariform p2 of AMNH 145508 and AMNH 145509. AMNH 145529 could not be confidently referred to a specific species of *Palaeolagus.*

Order Rodentia Brandt, 1855
Family Ischyromyidae Alston, 1876
Ischyromys Leidy, 1856
Ischyromys douglassi Black, 1968
Figure 5A-C, Table 4

Holotype—CM 1122, partial skull lacking parietals, left bulla, occiput, with left P3 and M3, from McCarty's Mountain, Montana (Black, 1968: figs. 7-9, 16).

Referred Specimens—AMNH 145522 partial skull with large bullae, broken incisors, and left M1 and M3, and heavily damaged left P4 and right M3 (Figure 5A) from AMNH Teepee Mountain. RAM 25137 left maxilla fragment with M1-3 (Figure 5B); RAM 23638 left dentary with m1-2 (Figure 5C) from RAM locality V2016017 (Teepee Mountain).

Description-Discussion—The M1 of AMNH 145522 and the M1-3 of RAM 25137 each have a large protocone connected to a small hypocone, a distinct metaconule, a metacone, and a metaloph that is low and incompletely connected to the hypocone. These features closely align the upper molars of AMNH 145522 and RAM 25137 with those of *Ischyromys douglassi* described by Black (1968). The M3 of AMNH 145522 has a metaconule but lacks a metacone, similar to some M3s of *I. douglassi* that also have a distinct metaconule but no metacone (Black, 1968). The diagnosis of *I. douglassi* notes the presence of a shallow lingual notch between the protocone and hypocone (Black, 1968), a feature seen in the M1 of AMNH 145522 and M1-2 of RAM 25137 (Figure 5A-B).

Compared to *Ischyromys veterior*, the M1 and M3 of AMNH 145522 and the M1-3 of RAM 25137 are significantly larger based on specimens from Pipestone Springs. Also, the M1-M3 of *I. veterior* have a deeper lingual grove between the protocone and hypocone and a more distinct hypocone than the M1 and M3 of AMNH 145522 and the M1-3 of RAM 25137. Upper molars of *I. typus* are comparable in size to AMNH 145522 and RAM 25137 (Table 4), but they lack metaconules (Black, 1968).

A partial dentary with m1-2 (RAM 23638) was also recovered from Teepee Mountain and its molars match the diagnosis of *I. douglassi* (Black, 1968), as the hypolophid of m1-2 is complete, but low and narrow, and a small low cusp is located on the posterior slope of the metalophid (Figure 5C).

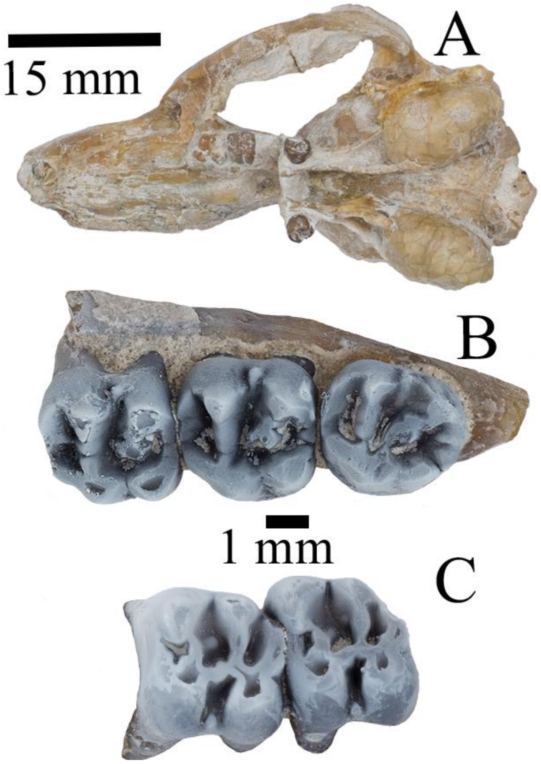

FIGURE 5: *Ischyromys douglassi* from Teepee Mountain. **A.** Ventral view of AMNH 145522 partial skull of *I. douglassi* with left M1 and M3 and damaged left P4 and right M3. **B.** Occlusal view of RAM 25137 left maxilla fragment with M1-3 of *I. douglassi*. **C.** Occlusal view of RAM 23638 left dentary fragment with m1-2 of *I. douglassi*.

Rapamys Wilson, 1940a
Rapamys atramontis Wahlert et al., 2006
Figures 6A-D, Table 5

Holotype—AMNH 128706, skull and mandibles with all cheek teeth, AMNH *Rapamys* Site, Renova Formation, Montana (Wahlert et al., 2006: figs. 1-2).

Referred Specimens—RAM 18618 partial skull with right and left P4-M3 (Figure 6A-B); RAM 18620 left dentary fragment with m1-3 (Figure 6C) from RAM locality V2016012 (*Rapamys* Site). AMNH 145922 left maxilla fragment with P4-M1 (Figure 6D) from AMNH *Rapamys* Site.

Description-Discussion—The partial skull (RAM 18618), dentary (RAM 18620), and P4-M1 (AMNH

TABLE 4. Measurements in mm of the length and width of the m1-2 of RAM 23638, M1-3 of RAM 25731, and M1 and M3 of AMNH 145522 compared to the m1-2 and M1-M3 of *Ischyromys typus* from the Brule Formation, Nebraska (Howe, 1966, tables 2-3), and *I. douglassi* from McCarty's Mountain, Montana (Black, 1968, tables 1-2).

Tooth Site		*Ischyromys typus*	*Ischyromys douglassi*	AMMH 145522	RAM 23638	RAM 25731
m1	L	3.1-3.9	3.4-3.8	—	3.5	—
	W	2.8-4.0	3.1-3.9	—	3.7	—
m2	L	2.9-4.0	3.5-3.9	—	3.4	—
	W	2.9-4.0	3.2-4.1	—	3.9	—
M1	L	3.3-3.7	3.1-3.8	3.6	—	3.3
	W	2.9-4.2	3.6-4.5	3.7	—	3.6
M2	L	3.1-3.7	2.6-3.8	—	—	3.5
	W	3.0-4.0	3.3-4.1	—	—	3.8
M3	L	3.2-3.7	2.9-3.9	3.6	—	3.7
	W	2.5-3.6	2.9-3.6	3.4	—	3.5

145922, Figures 6A-D) are from the same locality as the holotype and the hypodigm of *Rapamys atramontis* and add little to the original morphological description of the species by Wahlert et al., (2006). However, upper molars of RAM 18618 and m1-2 of RAM 18620 are narrower, and the P4-M1 of AMNH 145922 are wider than the respective teeth of *R. atramontis* measured by Wahlert et al. (2006) (Table 5). Thus, these three specimens document additional variation in the size of the dentition of *R. atramontis.*

Family Cylindrodontidae Miller and Gidley, 1918
Pareumys Peterson, 1919
Pareumys muffleri n. sp.
Figure 7A-B, Table 6

Holotype—AMNH 145526, left dentary fragment with p4-m3 (Figure 7A), from AMNH *Rapamys* Site, Renova Formation, Madison County, Montana.

Referred Specimen—MCZ 20119 left maxilla fragment with P4-M2 (Figure 7B) from MCZ Black Butte I (*Rapamys* Site).

Etymology—Named in honor of L. J. Patrick Muffler for his guidance and support of the Raymond M. Alf Museum of Paleontology and his contributions to the study of North American geology over many decades as a geoscientist and administrator for the United States Geological Survey.

Diagnosis—Differs from all other species of *Pareumys* in having a strongly molariform p4 that is slightly larger than the m1, and a short posterolophulid in p4-m2 that does not extend to the posterolingual tooth margin.

Description—The p4-m3 of ANNH 145526 are undamaged and exhibit slight wear. The p4 of AMNH 145526 has a large metaconid and protoconid which are connected anteriorly by a relatively low anterolophid (Figure 7A). Posteriorly, a relatively high metalophid, extending lingually from the protoconid, does not reach the metaconid, and the space between the anterolophid and metalophid forms a small enamel lake with an incomplete posterior margin. The ectolophid and hypolophid of the p4 are well developed, with the ectolophid extending posteriorly from the protoconid to terminate labially at a distinct hypoconid. The hypolophid is also well-developed and begins just posterolabial to the metaconid and terminates posterolingual at a distinct entoconid. A short posterolophulid, without a distinct hypoconulid, branches posterolingual from the ectolophid but does not reach the lingual margin of the p4 (Figure 7A).

The m1 of AMNH 145526 is similar to the p4 but is slightly smaller and has a wider trigonid and a more prominent anterolophid and enamel lake. The m2 is very similar to the m1, but the posterolabial terminus of the ectolophid is deflected more anteriorly than in m1. Compared to the m1-2, the m3 of the holotype is distinctly longer than wide, the metalophid is not as distinct, and the enamel lake is smaller (Figure 7A). Also, the posterolophulid of the m3 extends to the lingual margin of the tooth unlike p4-m2, and the entoconid and hypoconid of m3 are relatively larger in comparison to the entoconid of m1-2.

Discussion—A survey of reported species of *Pareumys* indicates that AMNH 145526 represents a new species. The holotype of *P. milleri* (CM 2938) lacks a p4, but the m1 has a prominent posterolophulid that extends to the posterolingual margin of the m1 (Peterson, 1919: fig. 7) unlike AMNH 145526. In a dentary (CM 12062) referred to *P. milleri* by Burke

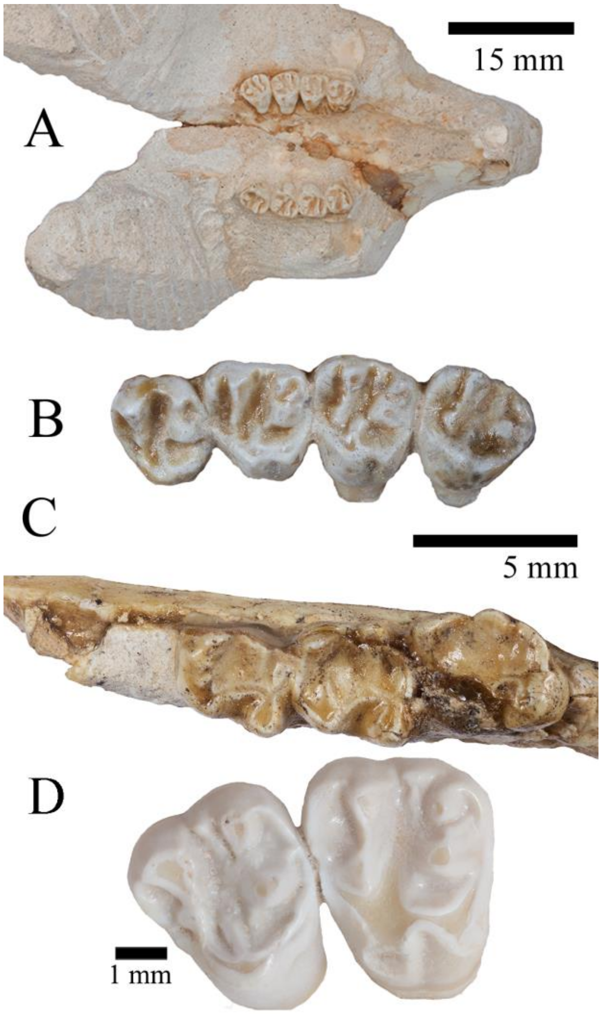

FIGURE 6: *Rapamys atramontis* from the *Rapamys* site. **A.** Ventral view of RAM 18618 partial skull of *R. atramontis* with right and left P4-M3. **B.** Occlusal view of left P4-M3 of RAM 18618. **C.** Occlusal view of RAM 18620 left dentary fragment with m1-3 of *R. atramontis*. **C.** Occlusal view of AMNH 145922 left maxilla fragment with P4-M1 of *R. atramontis*.

(1935: fig. 3), p4 is smaller than the m1 and is not as molariform as the p4 of the holotype of *P. muffleri*. Similarly, the p4 of CIT 2209 referred to *P.* near *milleri* by Wilson (1940b: pl. 2, fig. 1) is relatively small and not molariform, while the m1-m2 of CIT 2210 of *P.* near *milleri* have large posterolophulids (Wilson, 1940b: pl. 1, fig. 6).

Two species of *Pareumys*, *P. grangeri* and *P. troxelli*, were described by Burke (1935). The holotype of *P. grangeri* (AMNH 1869) has a p4 that is small and less molariform than the p4 of AMNH 145526 and the m1-2 posterolophulids of AMNH 1869 are well developed and extend posterolingual to their tooth margins (Burke, 1935: fig. 2). Also, posterolophulids of the m1-2 of CIT 2225 referred to *P.* near *grangeri* by Wilson (1940b: pl. 1, fig. 9) are strongly developed, unlike the m1-2 of the holotype of *P. muffleri* (AMNH 145526). The holotype of *P. troxelli* (AMNH 2021) lacks a p4, but posterolophulids of the m1-2 (Burke, 1935: fig. 4) are also more strongly developed than those of AMNH 145526.

TABLE 5. Measurements in mm of the m1-3 of RAM 18620, the P4-M3 of RAM 18618, and the P4-M1 of AMNH 145922 compared to the dentition of *Rapamys atramontis* (Wahlert et al., 2006, table 1).

Tooth Site		RAM 18620	RAM 18618	AMNH 145922	*Rapamys atramontis*
p4	L	—	—	—	3.7-3.8
	W	—	—	—	3.5
m1	L	3.5	—	—	3.4-3.6
	W	3.1	—	—	3.5-3.6
m2	L	3.8	—	—	3.5-3.8
	W	3.4	—	—	3.8
m3	L	4.1	—	—	4.4-4.5
	W	3.6	—	—	3.6
P4	L	—	3.1-3.1	3.4	3.0-3.5
	W	—	3.4-3.5	4.5	4.0-4.2
M1	L	—	3.2-3.2	3.3	3.1-3.3
	W	—	3.5-3.7	4.6	3.8-4.0
M2	L	—	3.3-3.4	—	3.2-3.7
	W	—	3.7-3.8	—	4.1-4.2
M3	L	—	3.3-3.4	—	3.6-3.9
	W	—	3.4-3.5	—	3.9-4.1

The holotype of *P. guensbergi* (FMNH 14978) is significantly larger than AMNH 145526 (Table 6) and the p4 of FMNH 14978 is significantly smaller than the m1, and the posterolophulid of m2 is large and extends strongly posterolingual (Black, 1970: fig. 1; posterolophulid of m1 of FMNH 14978 obscured by wear). A second m2 (FMNH 14979) figured by Black (1970: fig. 2C) has a large posterolophulid and a very weakly developed metalophid, unlike the m2 of AMNH 145526.

The holotype of *Pareumys boskeyi* ("*Mysops*" *boskeyi*) is an isolated M1, but one p4 and m1, and three m2s are included in the hypodigm (Wood, 1973). The p4 is smaller than the m1 and is not strongly molariform like the p4 of AMNH 145526, and the m1 and the m2s of *P. boskeyi* have well developed posterolophulids (Wood, 1973: fig. 4).

The holotype of *Pareumys muffleri* (AMNH 145526) and a heavily worn and damaged P4-M2 of *Pareumys* (MCZ 20119; Figure 7B) were recovered from the *Rapamys* Site. MCZ 20119 was identified as *Pareumys* because the orientation of its cusps and lophs were very similar to those of *Pareumys*. MCZ 20119 probably represents the upper dentition of *P. muffleri*, and the respective lengths and widths of the P4-M2 are: P4, 2.0 and 1.9 mm; M1 1.9 and 2.2 mm; M2, 1.9 and 1.7 mm.

TABLE 6. Measurements in mm of the p4-m3 of AMNH 145526 compared to the holotypes of *Pareumys troxelli* (AMNH 2021) and *P. grangeri* (AMNH 1869) from Burke (1935, 9), *P. guensbergi* (FMNH 14978) from Black (1970, 456), and *P. milleri* (CM 2938) from Peterson (1919, 66), and the means of the p4-m3 of *P. boskeyi* from Wood (1973, table 5).

Tooth Site		AMNH 145526	*P. troxelli*	*P. guensbergi*	*P. milleri*	*P. boskeyi*	*P. grangeri*
p4	L	2.0	–	1.9	–	1.6	1.7
	W	1.8	–	1.9	–	1.5	1.5
m1	L	1.9	2.0	2.3	–	1.9	1.7
	W	1.7	1.8	2.1	–	1.7	1.7
m2	L	2.2	2.0	2.6	1.6	1.8	1.8
	W	1.9	2.0	2.5	1.6	1.8	1.9
m3	L	2.3	–	2.4	2.0	2.2	2.5
	W	1.8	–	2.5	1.2	1.7	1.9

Family Eomyidae Winge, 1887
Paradjidaumo Burke, 1934
Paradjidaumo disjunctus Korth, 2013
Figure 7C-D, Table 7

Holotype—CM 71450, left dentary with p4-m3 from Diamond O Ranch, Beaverhead County, Montana (Korth, 2013: fig. 2b).

Referred Specimen—AMNH 145524 right dentary with i1 and p4-m3 (Figure 7D) and damaged skull with right side mostly intact, with left I1, right P4-M3 (Figure 7C) and broken right I1 from AMNH Teepee Mountain.

Description-Discussion—The dentition of AMNH 145524 is moderately worn and well preserved. The cheek teeth of AMNH 145524 are similar in size to *Paradjidaumo disjunctus* (Table 7) and *P. hansonorum*, but *P. disjunctus* is separated from *P. hansonorum* by having a P4 and p4 that are shorter or equal in length to their respective M1 and m1 (Korth, 2013). The relative dimensions of these teeth in AMNH 145524 are more similar to those of *P. disjunctus* (Table 7). A character diagnostic of *P. disjunctus* is the mesolophs and mesolophids of the cheek teeth do not extend the entire width of each tooth, a feature seen in the p4-m2 and P4-M2 of AMNH 145524 (Figure 7C-D). Thus, there is little doubt that AMNH 145524 represents *P. disjunctus.*

Family Cricetidae Fischer von Waldheim, 1817
Eumys Leidy, 1856
Eumys elegans Leidy, 1856
Figure 7E, Table 8

Holotype—ANSP 11027, left dentary with m2 and partial m1, Bear Creek, Scenic Member, Brule Formation, South Dakota (Leidy, 1856).

Referred Specimen—AMNH 145511 left dentary with m1-m3 (Figure 7E) from AMNH Lion Mountain.

Description-Discussion—AMNH 145511 is a well-preserved dentary of *Eumys* with moderately worn molars, of which m1 is the longest and m3 is greater in length than m2 (Figure 7E; Table 8). *Eumys* "*parvidens*" was the smallest known species of *Eumys* (Wood, 1937; Martin, 1980; Korth, 2011), but specimens referred to *E.* "*parvidens*" are now considered smaller individuals of *E. elegans* based on the study of large samples of *Eumys* from the Orellan of South Dakota (Korth, 2018, see fig. 2). AMNH 145511 is referred to *E. elegans* because the size of the m1-3 is very similar to the m1-3 of *E. elegans*.

Leidymys Wood, 1936
Leidymys sp.
Figure 7F-G, Table 9

Referred Specimen—AMNH 145510 partial skull with left and right M1-M (Figure 7F-G) from AMNH Lion Mountain.

Description—AMNH 145510 is a skull fragment with heavily worn left and right M1-2 and alveoli for M3 (Figure 7F), with infraorbital foramina (Figure 7G), but missing the anterior part of the rostrum and nasals, 90% of the zygomatic arches, and the posterior third of the cranium.

Discussion—Severe wear on the crown of the M1-2 of AMNH 145510 has erased most details of cusp morphology (Figure 7F), making it difficult to determine which species of *Leidymys* AMNH 145510 represents. However, molar size is useful as the M1-2 of *L. juxtaparvulus*, *L. korthi*, and *L. blacki* are significantly smaller than the M1-2 of AMNH 145510 (compare Table 9 to Macdonald, 1963: table 32 for *L. blacki*; Williams and Storer, 1998: table 2 for *L. korthi*; Korth, 2014: table 14 for *L. juxtaparvulus*). Also, *L. alicae* is small (Martin, 1980), similar to *L. korthi* in size

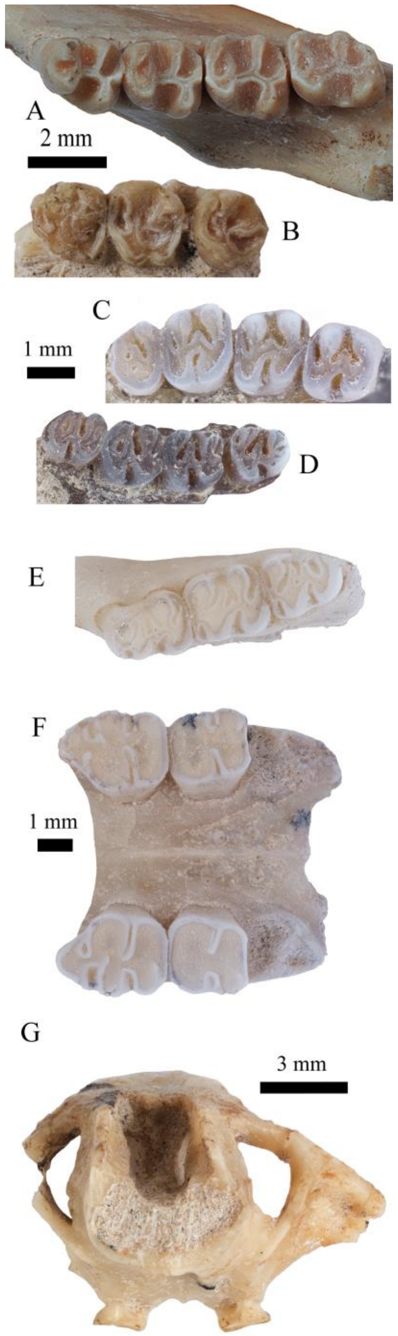

FIGURE 7: Various rodents from the Gravelly Range. **A.** Occlusal view of AMNH 145526 left dentary with p4-m3, holotype of *Pareumys muffleri* (new species) from the *Rapamys* Site. **B.** Occlusal view of MCZ 20119 left maxilla fragment with P4-M2 of *Pareumys muffleri* from the *Rapamys* Site. **C.** Occlusal view of right P4-M3 of AMNH 145524 a partial skull of *Paradjidaumo disjunctus* from Teepee Mountain. **D.** Occlusal view of right dentary with p4-m3 of AMNH 145524 of *P. disjunctus*. **E.** Occlusal view of AMNH 145511 left dentary with m1-3 of *Eumys elegans* from Lion Mountain High. **F.** Ventral view of AMNH 145510 partial skull with left and right M1-M2 of *Leidymys* sp. from Lion Mountain High. **G.** Anterior view of AMNH 145510 showing left (intact) and right (damaged) infraorbital foramen.

(Williams and Storer, 1998). Thus, the M1-2 of AMNH 145510 are most similar in size to that of *L. cerasus*, *L. nematodon* and *L. lockingtonianus* (Table 9). However, *L. cerasus* and AMNH 145510 differ in the development of the anterocone of M1 because the large anterocone of *L. cerasus* extends anteriorly more than any other species of *Leidymys* (Korth, 2014). The M1 anterocone in AMNH 145510 is relatively small in terms of size and anterior extension (Figure 7F), more like the M1 of *L. nematodon* and *L. lockingtonianus* (see Wood, 1936: figs. 2-3).

Features of the upper molars described by Martin (1980) that separate *L. nematodon* and *L. lockingtonianus* cannot be seen in the M1-2 of AMNH 145510 because of wear. However, Martin (1980) notes the presence of very large infraorbital foramina in *L. lockingtonianus* and the left infraorbital foramen preserved in AMNH 145510 is large (Figure 7G), but does not appear to equal the size of the foramina of the holotype of *L. lockingtonianus* (see Martin, 1980: fig. 15b). Thus, AMNH 145510 could represent *L. nematodon* or *L. lockingtonianus* and is referred to *Leidymys* species indeterminate.

Order Carnivora Bowdich, 1821
Caniformia sensu Bryant, 1996
Lycophocyon Tomiya, 2011
Lycophocyon tabrumi n. sp.
Figure 8A-C; Table 10

Holotype—RAM 18619, partial skull with right I1-3, P2-M3 and left I1, P2, P4-M2 (Figure 8A-C) from RAM locality V2016012 (*Rapamys* Site), Renova Formation, Madison County, Montana; holotype only known specimen.

Diagnosis—*Lycophocyon tabrumi* similar to *L. hutchisoni* in nearly all respects, except M1 and M2 of *L. tabrumi* have a less developed cingulum, lingual and posterior to the protocone apex; M2 of *L. tabrumi* transversely rectangular in occlusal view, lacks a paraconule, and has a relatively smaller protocone in comparison to M2 of *L. hutchisoni*; and M3 of *L. tabrumi* significantly shorter and wider than M3 of *L. hutchisoni*.

Etymology—Named after the late Alan R. Tabrum in honor of his many contributions to the study of mammals from Tertiary strata in southwest Montana.

Description-Discussion—RAM 18619 is a partial skull missing part of the right basicranium, the right glenoid fossa, the posterior half of the right zygomatic arch, and the entire left zygomatic arch (Figure 8A-B). The upper dentition of RAM 18619 is not complete, but an example of each tooth site is present except for the canine and P1. RAM 18619 was compared directly to SDSNH 107659, a paratype of *L. hutchisoni* and the morphology and dimensions of the pre-molariform

TABLE 7. Measurements in mm of the dentition of AMNH 145524 compared to the means of the dentition of *Paradjidaumo disjunctus* from the Diamond O Ranch and McCarty's Mountain sites in southwest Montana from Korth (2013, table 4).

Tooth Site		AMNH 145524	*Paradjidaumo disjunctus*
p4	L	1.3	1.2
	W	1.4	1.3
m1	L	1.4	1.3
	W	1.3	1.4
m2	L	1.2	1.2
	W	1.4	1.4
m3	L	1.3	1.3
	W	1.2	1.2
p4-m3	L	5.2	5.3
P4	L	1.3	1.2
	W	1.1	1.4
M1	L	1.3	1.3
	W	1.4	1.5
M2	L	1.3	1.2
	W	1.4	1.4
M3	L	0.9	0.9
	W	1.2	1.1
P4-M3	L	4.7	4.8

dentition of RAM 18619 are nearly identical to that of SDSNH 107659, but significant differences are evident when comparing the molars.

RAM 18619 has three small incisors, with I3 approximately twice the size of either I1 or I2. The alveolus of the left canine and a single rooted P1 are present and indicate a small diastema separated them. A larger diastema is developed between P1 and P2 (Figure 8B). Separated by a small diastema, P2 and P3 each have a large primary cusp, but P3 is larger than P2 and has two subequal posterior cusps compared to the single ancillary posterior cusp of P2. Triangular in occlusal outline, P4 of RAM 18619 has a small protocone, a large paracone, and a well-developed metastylar blade that is separated from the paracone by a carnassial notch (Figure 8C). Also, a faint but continuous cingulum is developed anterior and labial to the paracone that extends posteriorly to the labial edge of the metastylar blade.

In occlusal view, the area of the M1 of RAM 18619 approximates that of the P4 and has a well-developed parastylar blade, a distinct paraconule, a labial cingulum, a shallow ectoflexus, and a large paracone, metacone, protocone, with the paracone slightly larger than the metacone (Figure 8C), features it shares with *L. hutchisoni*. The cingulum lingual and posterior to the apex of the protocone in the M1 of RAM 18619, is less developed than that of *L. hutchisoni*, whose lingual cingulum forms a shelf that bulges posterolingual and gives that part of the M1 an asymmetrical appearance (Tomiya, 2011: fig. 4G).

The M2 of RAM 18619 is smaller and much narrower than the M1 and has a well-defined paracone, metacone and protocone, but lacks a protoconule (Figure 8C). Also, a weak cingulum is present posterior to the protocone apex. In contrast, the M2 of *L. hutchisoni* has a protoconule and a broad, bulbous lingual cingulum posterior to the protocone (Tomiya, 2011: fig. 4G), and is more squared in occlusal outline compared to the narrow rectangular occlusal outline of the M2 of RAM 18619.

The vestigial M3 of RAM 18619 is approximately one fourth the area of the adjacent M2 and has a narrow rectangular shape with undulating crown enamel, so a distinct paracone, metacone or protocone is not evident (Figure 8C). Compared to the only known M3 of *L. hutchisoni* (UCMP 170713), the M3 of RAM 18619 is shorter and wider (Table 10). Although RAM 18619 is certainly referable to *Lycophocyon*, differences in the morphology and dimensions of the molars indicates it represents a species distinct from *L. hutchisoni*, and RAM 18619 is designated as the holotype of *L. tabrumi*.

TABLE 8. Measurements in mm of the m1-3 of AMNH 145511 compared to *Eumys elegans* from Orellan strata in Sioux County, Nebraska, from Korth (2018, table 1).

Tooth Site		AMNH 145511	*Eumys elegans*
m1	L	1.9	1.8-2.6
	W	1.5	1.3-1.9
m2	L	1.7	1.7-2.3
	W	1.6	1.5-2.1
m3	L	1.8	1.5-2.4
	W	1.5	1.3-2.2

Family Canidae Gray, 1821
Hesperocyon Scott, 1890
Hesperocyon gregarius (Cope, 1873a)
Figure 8D-E, Table 11

Holotype—AMNH 5297a, fragment of left dentary with p2-m1 and alveolus for p1, White River Formation, Colorado (Wang, 1994: figs. 11D-E).

Referred Specimen—RAM 18623 right m1 (Figure 8D-E) from RAM locality V2016013 (Black Butte High).

Description-Discussion—RAM 18623 is a slightly worn m1 that has features indicative of *Hesperocyon*; a large protoconid separated by a notch from a smaller, anteriorly positioned paraconid, a small metaconid that is positioned slightly posterior to the protoconid, and a well-developed talonid basin (Figure 8D-E). *Hesperocyon* is represented by three morphologically similar species, *H. gregarius*, *H. pavidus*, and *H. coloradensis* which can be differentiated by size (Wang, 1994). The m1 of *H. coloradensis* is 18% larger, and the m1 of *H. pavidus* is 10-30% smaller than the m1 of *H. gregarius* (Wang, 1994). RAM 18623 is too small to represent *H. coloradensis* and too large to represent *H. pavidus* (Table 11) but falls within the range of variation for the m1 of *H. gregarius* and is referred to that species.

TABLE 9. Measurements in mm of AMNH 145510 compared to the holotype of *Leidymys cerasus* (USNM 24105) from Korth (1992, table 12) and the holotypes of *L. nematodon* (AMNH 7018) and *L. lockingtonianus* (AMNH 7028) from Wood (1936, table 1).

Tooth Site		AMNH 145510	USNM 24105	AMNH 7018	AMNH 7028
M1	L	2.8	2.5	2.6	2.8
	W	2.1	1.7	1.8	2.0
M2	L	1.9	1.8	2.0	2.1
	W	1.9	1.8	1.9	2.1

Oxetocyon Green, 1954

Oxetocyon cuspidatus Green, 1954

Figure 8F

Holotype—SDSM 2980, left maxillary fragment with M1 and broken alveoli of P4 and M2, *Protoceras* Channels, Poleslide Member, Brule Formation (Whitneyan), South Dakota (Green 1954: fig. 1; stratigraphic assignment from Wang et al., 1999).

Referred Specimen—AMNH 145515 right maxilla fragment with M1 and roots of P4 (Figure 8F) from Lion Mountain High.

Description/Discussion—The P4 of AMNH 145515 lacks a crown due to breakage, but three roots are preserved in their alveoli. The M1 is slightly worn, quadrate in occlusal outline. and is ringed by cingula, weakest posteriorly, well developed labially and anteriorly, and massive and cuspidate lingually (Figure 8F). On the labial edge of the M1, a parastyle and ectoflexus are present, the latter weakly developed, and a mesostyle is absent.

The M1 of AMNH 145515 has six main cusps oriented in two transverse rows in what Wang et al. (1999) described as transverse cleavage. The anterior row has a large paracone and protocone with a third smaller cusp positioned on the lingual cingulum. The posterior row has a large metacone and metaconule and smaller hypocone positioned partly on the lingual cingulum (Figure 8F). In the description of the holotype of *Oxetocyon cuspidatus* (SDSM 2980), Green (1954) identified the hypocone as the cusp Wang et al. (1999) refer to as the metaconule. Green (1954) noted that the holotype had three cusps on the lingual cingulum, the posterior and largest of which was identified by Wang et al. (1999) as the hypocone. As noted by Wang et al. (1999), in *O. cuspidatus*, a distinct valley labial and anterior to the hypocone separates it from the protocone and metaconule; AMNH 145515 shares this feature. AMNH 145515 has two additional very small circular M1 cusps. One is heavily worn, positioned on the posterior cingulum, and connected to the hypocone by a wear facet. The other cusp, which we identify as the protoconule, is positioned between the paracone and protocone (Figure 8F). The M1 of AMNH 145515 has a length of 5.6 mm and a width of 7.3 mm. The range of known M1s of *O. cuspidatus* have lengths of 4.9-6.2 mm and widths of 6.0-7.6 mm (Wang et al., 1999; appendix III). The size and the distinctive features of the M1 of AMNH 145515 indicate it represents *O. cuspidatus*, the only described species of the genus (Wang et al., 1999).

TABLE 10. Measurements in mm of the P2-M3 of RAM 18619 compared to the P2-M3 of *Lycophocyon hutchisoni* from southern California (Tomiya, 2011, table 1).

Tooth Site		RAM 18619	*Lycophocyon hutchisoni*
P2	L	5.4–5.9	5.5-6.4
	W	2.5–2.8	2.4-2.6
P3	L	7.3	6.4-7.6
	W	3.5	3.5-4.3
P4	L	9.4–9.8	9.4-10.9
	W	6.6–7.0	6.4-7.6
M1	L	6.5–6.9	6.5-8.1
	W	10.1–10.3	9.9-11.9
M2	L	3.7–3.6	3.8-4.9
	W	6.8–6.8	6.6-8
M3	L	1.4	1.8
	W	4.2	2.9

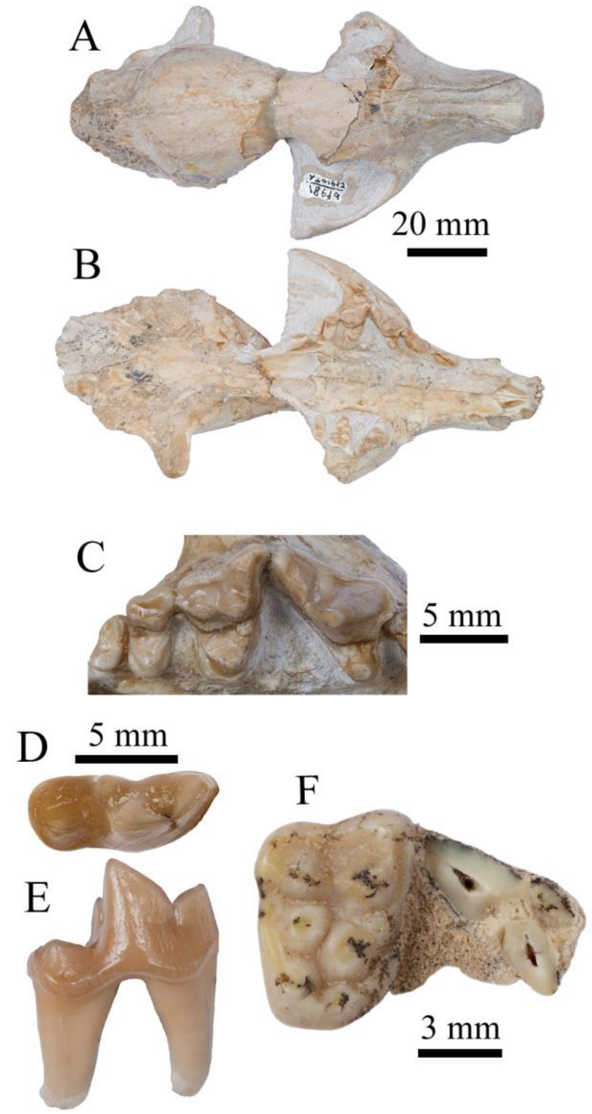

FIGURE 8: Carnivora from the Gravelly Range. **A.** Dorsal and **B.** Ventral views of RAM 18619 nearly complete skull of *Lycophocyon tabrumi* (new species) from the *Rapamys* Site. **C.** Occlusal view of part of the left maxilla with P4-M3 of RAM 18619. **D.** Occlusal and **E.** Labial views of RAM 18623 right m1 of *Hesperocyon gregarius* from Black Butte High. **F.** Occlusal view of AMNH 145515 right maxilla with M1 and roots of P4 of *Oxetocyon cuspidatus* from Lion Mountain High.

Order Lipotyphla Haeckel, 1866
Family Geolabididae McKenna,1960
Centetodon Marsh, 1872
Centetodon magnus Clark, 1936
Figure 9A-C, Table 12

Holotype—PU 13835, right dentary fragment with p4-m3 from the White River Formation, Flagstaff Rim, Wyoming (Clark, 1936, in Scott and Jepsen 1936: pl. 2, fig. 5-5a).

Referred Specimen—RAM 25545 left dentary fragment with p4-m3 (Figure 9A-C) from RAM locality V2018039 (Lion Mountain High).

Description-Discussion—The p4-m3 of RAM 25545 exhibit slight apical wear and the p4 is indicative of *Centetodon* as it has a highly elevated trigonid (higher than m1-3) with a prominent protoconid transversely adjacent to a small and low metaconid, and a paraconid that is low, small, and anteriorly positioned (Figure 9A-C). The morphology of the molars of RAM 25545 also closely match those of *Centetodon*. Measurements of the p4-m3 of RAM 25545 are consistent with the ranges of the p4-m3 for *C. magnus*, and the p4 of RAM 25545 is slightly larger than the p4 of either *C. kuenzii* or *C. chadronensis* (Table 12). Also, a labial cingulum is usually developed in m1-3 of *C. kuenzii* (Lillegraven and Tabrum, 1983) and molars of RAM 25545 lack this feature. RAM 25545 appears to represent *C. magnus* based on the size of the p4 and the lack of a labial cingulum in m1-3.

TABLE 11. Measurements in mm of the m1 of RAM 18623 compared to m1s of *Hesperocyon gregarius, H. coloradensis, and H. pavidus* from Wang (1994, appendix III).

Tooth Site		*H. gregarius*	*H. coloradensis*	*H. pavidus*	RAM 18623
m1	L	7.7-11.3	10.4-11.5	6.7-7.8	9.6
	W	3.3-5.7	4.8-5.3	3.0-3.6	4.0

Family Soricidae Fischer von Waldheim, 1817
Domnina Cope, 1873a
Domnina thompsoni Simpson, 1941
Figure 9D-E, Table 13

Holotype—AMNH 32647, partial left dentary with m1-3 and alveoli of p2-4 and i3, Pipestone Springs, Renova Formation, Montana (Simpson, 1941, fig. 1).

Referred Specimen—RAM 21925 right dentary fragment with m1 (Figure 9D-E) from RAM locality V2016013 (Black Butte High).

Description-Discussion—The protoconid of the m1 of RAM 21925 is the tallest and largest trigonid cusp and the metaconid and paraconid are smaller and subequal in size. The trigonid has a well-developed paracrista, metacrista, and anterolabial cingulum and the hypoconid and entoconid of the talonid are also subequal in size (Figure 9D-E). RAM 21925 was compared directly to m1s of *Domnina thompsoni* from Pipestone Springs (type locality of species) and the m1s were almost identical in morphology. RAM 21925 is also similar in size to the holotype of *D. thompsoni*

(AMNH 32647) and other specimens from Pipestone Springs (Table 13).

TABLE 12. Measurements in mm of the p4-m3 of RAM 25545 compared to measurements of *Centetodon magnus, C, kuenzii,* and *C. chadronensis* provided by Lillegraven et al. (1981, table 7) and Lillegraven and Tabrum (1983, tables 1-2).

Tooth Site		RAM 25545	*C. magnus*	*C. kuenzii*	*C. chadronensis*
p4	L	1.7	1.5-2.0	1.3-1.6	1.4-1.6
	W	0.9	0.9-1.1	0.8-0.9	0.8-0.9
m1	L	1.8	1.9-2.2	1.6-1.9	1.6-1.8
	W	1.0	1.2-1.3	1.0-1.2	0.9-1.2
m2	L	1.6	1.6-2.1	1.4-1.8	1.5-1.7
	W	1.1	1.1-1.5	1.0-1.3	0.9-1.2
m3	L	1.5	1.5-2.0	1.4-1.7	1.4-1.6
	W	0.9	1.0-1.3	0.9-1.1	0.9-1.0

?Talpidae
Figure 9F-H

Referred Specimen—AMNH 145513, right dentary fragment with m3 (Figure 9F-H) from AMNH Lion Mountain.

Description—AMNH 145513 has an undamaged m3 that is unworn (Figure 9F-H). The trigonid is V-shaped in occlusal view and much higher and wider than the talonid. The paraconid and metaconid appear equal in size and height, but the base of the metaconid is broader than that of the paraconid. The protoconid is significantly higher than the metaconid and paraconid whose apexes are symmetrically equidistant along a well-developed and very thin paralophid and protolophid that extend lingually from the slightly recurved apex of the protoconid (Figure 9F-H). The height and positioning of the trigonid cusps and lack of a metacristid results in the development of a deep and narrow prefossid that opens lingually. The anterior cingulid is prominently developed along the entire anterior face of m3 and a small cuspule is present on its lingual terminus.

Like the trigonid, talonid crests form a distinct V-shape bordering a well-developed postfossid (Figure 9F). The entoconid and hypoconid are large and subequal in size and are positioned on the posterolingual and posterolabial corners of the m3, respectively. A postcristid that is concave in posterior view connects the hypoconid and entoconid and the cristid obliqua is prominent and widens as it merges with the base of the metaconid. AMNH 145513 has a weakly developed entocristid and lacks a metastylid, so its deep and narrow postfossid opens lingually. AMNH 145513 is 2.2 mm in

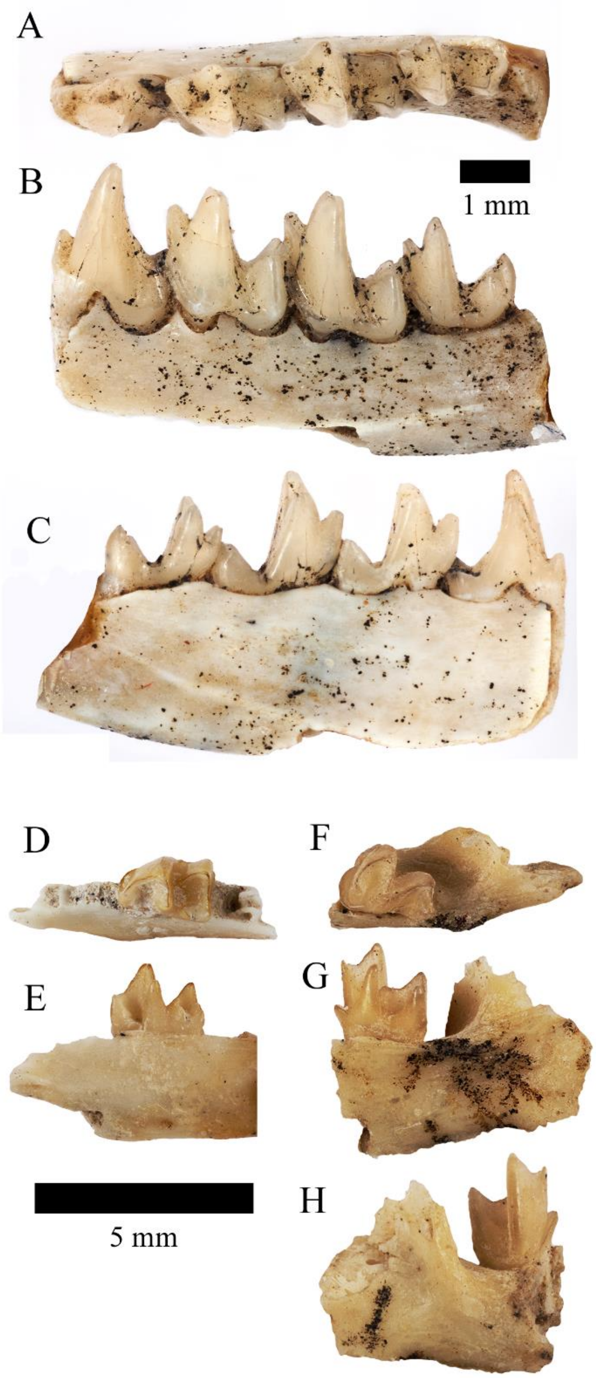

FIGURE 9: Lipotyphla from the Gravelly Range. **A.** Occlusal, **B.** Labial, and **C.** Lingual views of RAM 25545 left dentary fragment with p4-m3 of *Centetodon magnus* from Lion Mountain High. **D.** Occlusal and **E.** Lingual views of RAM 21925 right dentary fragment with m1 of *Domnina thompsoni* from Black Butte High. **F.** Occlusal, **G.** Lingual and **H.** Labial views of AMNH 145513 of right m3 of ?Talpidae from Lion Mountain High.

length, with a trigonid width of 1.6 mm and talonid width of 1.1 mm.

Discussion—AMNH 145513 is a dilambdodont m3 that represents some type of lipotyphlan whose morphology suggests an affinity with talpids. A survey of known talpids indicates that AMNH 145513 appears to be most similar to Miocene talpid m3s from Oregon described by Hutchison (1968), particularly an m3 of *Scalopiodes* and an m3 referred to ?Talpidae incertae sedis. The sample of *S. ripafodiator* includes an m3 (OU 22490) (Hutchison 1968: fig. 51C) whose general morphology resembles that of AMNH 145513, but OU 24490 has a more robust entocristid so the postfossid is not as open lingually and the orientation of paraconid and metaconid are not symmetrical in relation to protoconid as in AMNH 145513. The apex of the paraconid in OU 24490 is directed anteriorly so its base extends lower on the lingual wall of the trigonid than does the metaconid, unlike AMNH 145513.

An m3 (OU 25105) questionably referred to Talpidae (Hutchison 1968: fig. 97), is also generally similar to the m3 of AMNH 145513, but has a robust entocristid and a distinct metastylid, and the orientation of the paraconid and metaconid resembles that of OU 24490, features unlike the m3 of AMNH 145513. Thus, AMNH 145513 appears to represent an unreported talpid-like lipotyphlan.

TABLE 13. Measurements in mm of the m1 of RAM 21925 compared to m1s of *Domnina thompsoni* from Pipestone Springs (RAM 7275, RAM 7274, RAM 7273) and the m1 of the holotype of *D. thompsoni* (AMNH 32647) from Simpson (1941).

Tooth Site		RAM 21925	Pipestone Springs	AMNH 32647
m1	L	2.1	1.9-2.0	1.8
	W	1.3	1.1-1.2	1.2

Order Artiodactyla Owen, 1848
Family Agriochoeridae Leidy, 1869
Diplobunops Peterson, 1919
Diplobunops matthewi Peterson, 1919
Figure 10A-E, Table 14

Holotype—CM 2974, numerous fragments of the skeleton, Uinta Formation, Horizon C, six miles east of Myton, Utah (Peterson 1919: pl. XXXVIII, figs. 1-23; paratype is CM 3394, foot-bones and other fragments of the skeleton, with fragments of the skull and lower jaws provisionally included, pl. XXXVIII, figs. 24-27).

Referred Specimens—RAM 18622 left dentary fragment with i3, p2-p3, dp4, partial m1-2, and right dentary fragment with i1-3, p2-3, dp4, m1; RAM 18621 left maxillary fragment with dP3-dP4 from RAM locality V2016012 (*Rapamys* Site). AMNH 145523 right maxillary fragment with P4-M3 from AMNH Teepee Mountain. AMNH 145525 left p3, dp4, m1, and broken m2 from AMNH *Rapamys* Site. MCZ 19716 skull and dentaries, right maxilla with P2-3, M1, M3, and broken P4 and M2 and left maxilla with P1-2, P4, M1-3, and broken P3, right dentary with p3-m3, left dentary with c, p3-m3; MCZ 19717 skull and dentaries, right and left maxilla with P2-M3, right dentary with m2-3, left dentary with damaged teeth; MCZ 19719 partial skull with left maxilla with dP2-4 and M1 and right maxilla with dP4 and M1-3; MCZ 19720 left dentary with p3-m2 and damaged m3, right dentary with p2-m3; MCZ 19722 right dentary with p2-m2 and anterior half of m3; MCZ 19725 right maxilla with dP3-4, M1, and broken M2; MCZ 19726 left dentary with p2-4 and m2-3 from MCZ Black Butte II (Black Butte Low). MCZ 19727 skull and dentaries, right and left maxilla with P1-M3, right dentary with c-m3, left dentary with p2-m3; MCZ 19728 left maxillary fragment with P4-M2 and damaged M3 from MCZ Black Butte III (Black Butte Low). MCZ 19729 skull and dentaries, right maxilla with P1-M3 and left maxilla with C and P1-M3, right dentary with p1-m2 and partial m3, left dentary with p4-m3 (Figure 10A-E); MCZ 19730 left dentary fragment with p1-3; MCZ 19731 partial skull with damaged right and left P3-4; MCZ 19732 maxilla fragment with left P2 and right P1; MCZ

TABLE 14. Measurements of the M1-3 and m1-3 of *Diplobunops matthewi* from Badwater Creek, Wyoming (Black, 1978, 237-238) compared to MCZ 19716, MCZ 19727, MCZ 19729, MCZ 19717, MCZ 19726, and AMNH 145523 from Black Butte Low, Teepee Mountain, and the *Rapamys* Site.

	M1-M3	m1-m3
Black 1978	35.4-41.1 N=7	43.4-45.6 N=3
MCZ 19716	39.4	42.4
MCZ 19727	37.2	43.7
MCZ 19729	39.5	40.8
MCZ 19717	41.4	—
MCZ 19726	—	43.7
AMNH 145523	36.3	—

N is number of specimens.

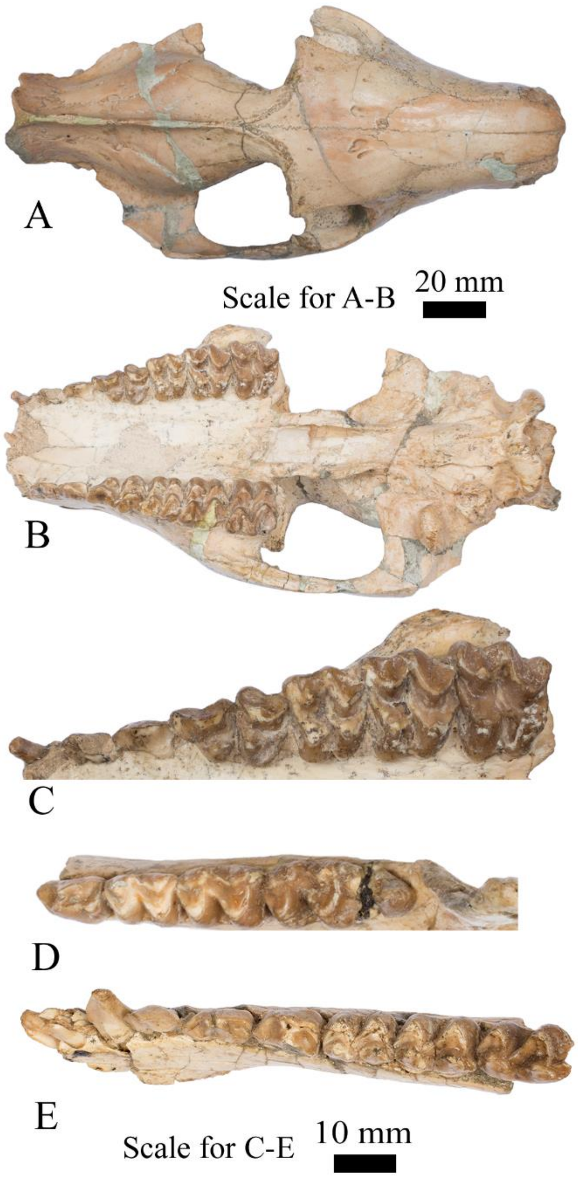

FIGURE 10: MCZ 19729, skull of *Diplobunops matthewi* with dentaries from the *Rapamys* Site. **A.** Dorsal and **B.** Ventral views of the skull. **C.** Occlusal view of left maxilla with C, P1-M3. **D.** Occlusal view of left dentary with p4-m3. **E.** Occlusal view of right dentary with p1-m2 and partial m3.

19733 right maxilla fragment with P2, dP3, and broken dP4 from MCZ Black Butte I (*Rapamys* Site).

Description/Discussion—These skulls and dentaries of a large agriochoerid represent the mammal most commonly recovered from the Gravelly Range. This taxon can be distinguished from *Protoreodon* (except "*Protoreodon pearcei*") by its large size, lack of a divided paracone and metacone on P4, and presence of a well-developed diastema between C and P1 (Golz, 1976). When Gazin (1956) erected "*P. pearcei*," he noted that the holotype (USNM 20305) from the Teepee Trail Formation at Badwater Creek, Wyoming, was very similar in size to *Diplobunops matthewi*, but differed in the morphology of the rostrum and in having a diastema between C and P1. Based on a larger sample of *D. matthewi* from Badwater Creek than what was available to Gazin (1955, 1956), Black (1978) argued that differences in the holotype of "*Protoreodon pearcei*" and the sample of *Diplobunops matthewi* were due to sexual dimorphism, a tenet noted by Theodor (1999). We follow Black (1978) and recognize *Protoreodon pearcei* as a junior synonym of *Diplobunops matthewi*.

A relatively complete representative of *Diplobunops matthewi* from the Gravelly Range is provided by MCZ 19729 from the *Rapamys* Site (MCZ Black Butte 1) whose skull morphology (Figure 10A-B) and dentition (Figure 10C-E) indicate a close affinity to that taxon. The size of the dentition of *D. matthewi* from the Gravelly Range is consistent with that of specimens from Badwater Creek, Wyoming (Table 14) and is smaller than the dentition of *D. kardoula* from the Hancock Mammal Quarry (Clarno Formation) in Oregon (Emery et al., 2015: table 2).

TABLE 15. Measurements in mm of the p3-m3 of the holotype of *Protoreodon pumilus* (YPM 11890) and USNM 20352 (from Gazin 1955, 51-52) compared to the p3-m3 of MCZ 19721, MCZ 19724, and RAM 23758 from Black Butte Low.

Tooth Site		MCZ 19721	MCZ 19724	RAM 23758	YPM 11890	USNM 20352
p3	L	6.8	7.2	8.3	—	9.9
	W	3.6	4.0	5.1	—	4.9
p4	L	8.2	—	9.3	—	10.0
	W	5.2	—	7.4	—	6.9
m1	L	9.6	9.2	9.4	9.5	9.7
	W	7.1	6.9	8.0	7.1	7.5
m2	L	—	9.3*	11.6	10.0	11.4
	W	—	8.0	9.5	7.8	8.1
m3	L	—	—	16.7	—	17.8
	W	—	—	8.0	—	7.8

Protoreodon Scott and Osborn, 1887
Protoreodon pumlius Marsh, 1875
Figure 11A-C, Tables 15-16

Holotype—YPM 11890, dentary fragments with right m1 and partial m2-3, left m2, and other skeletal fragments, White River, Uinta Basin, Utah, probably Uinta C (Thorpe, 1937; not figured by Marsh, 1875; see Gazin, 1955: pl. 6, fig. 2).

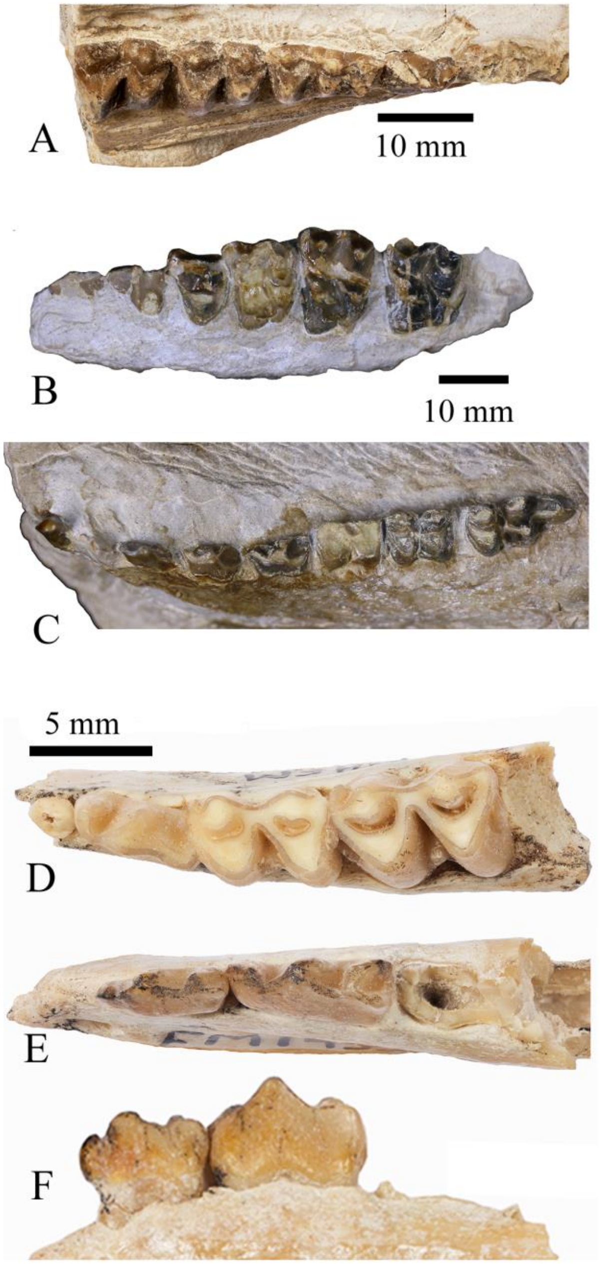

FIGURE 11: Various other artiodactyls from the Gravelly Range. **A,** Occlusal view of MCZ 19724 right dentary with p3, dp4, m1-2 of *Protoreodon pumilus* from Black Butte Low. **B.** Occlusal view of left maxilla with P3-M3 of RAM 23757 of *Protoreodon pumilus* from Black Butte Low. **C.** Occlusal view of left dentary with p1-m3 of RAM 23757. **D.** Occlusal view of AMNH 145528 left dentary with p4-m2 of *Hypertragulus calcaratus* from Lion Mountain High (5 mm scale also applies to E-F). **E.** Occlusal and **F.** Labial views of AMNH 145518 left dentary fragment with p2-p3 of *Leptomeryx*? from Lion Mountain High.

Referred Specimens—MCZ 19721 right dentary with p3-m1 and m2 erupting; MCZ 19723 juvenile left dentary with dp4-m1; MCZ 19724 right dentary with p3, dp4, m1-2 (Figure 11A) from MCZ Black Butte II (Black Butte Low). RAM 23757 partially prepared skull with dentaries, left maxilla with P2-M3 (Figure 11B), right maxilla with P3-M3, left dentary with p1-m2 (Figure 11C) and right dentary with p1-m3 from RAM locality V2018037 (Black Butte Low). RAM 23758 left and right dentaries with incisor fragments and left p1-m3 (p1-2 damaged) and right p1-m3 (p1-m1 severely damaged, m2-3 damaged) from RAM locality V2018038 (Black Butte Low).

Description/Discussion—These agriochoerid specimens represent a species of *Protoreodon* that is comparable in size to *Protoreodon pumilus* and *P. walshi* (Tables 15-16) and too small to represent *P. minor*, *P. pacificus*, *P. minimus*, *P. paradoxicus*, *P. parvus*, *P. transmontanus* and *P. petersoni*; measurements of taxa provided by Golz (1976) and Theodor (1999). The only upper dentition recovered from the Gravelly Range of *Protoreodon* is RAM 23757, whose P4 paracone and metacone are twinned (Figure 11B) like the P4 of *P. pumilus*, and not distinctly divided like P4s of *P. pacificus*, *P. transmontanus*, and *P. minimus* (Golz, 1976). Although the upper dentition of RAM 23757 is similar in size to that of *P. pumilus* and *P. walshi* (Table 16), the latter has an undivided paracone and metacone on P4 (Theodor, 1999), while the paracone and metacone are distinctly twinned in RAM 23757.

The lower dentition of RAM 23757 (Figure 11C) and other lower dentitions like MCZ 19724 (Figure 11A) are also similar in size to *Protoreodon pumilus* (Table 15) and support the referral of the Gravelly Range specimens to this species.

Family Hypertragulidae Cope, 1879
Hypertragulus Cope, 1873a
Hypertragulus calcaratus Cope, 1873a
Figure 11D, Table 17

Referred Specimen—AMNH 145528 left dentary fragment with p4-m2 and the anterior root of p3 from AMNH Lion Mountain.

Description-Discussion—AMNH 145528 has low crowned and narrow molars with simple selenodont crests and the p4 has a distinct talonid basin. The p4 also has a labial margin that consists of a high ridge connecting a small paraconid and hypoconid, and large protoconid connected by a wear facet to a posteriorly directed metaconid (Figure 11D), features similar to those of *Hypertragulus*. *Hypertragulus calcaratus* is a commonly reported species from Orellan to Arikareean strata in South Dakota and Nebraska (Scott, 1940; Webb, 1998) and AMNH 145528 was compared directly to dentaries of *H. calcaratus* at the AMNH and they were very similar in morphology and size (Table 17).

Family Leptomerycidae Zittel, 1893
Leptomeryx Leidy, 1853
Leptomeryx?
Figure 11E-F

Referred Specimen—AMNH 145518 left dentary fragment with p2-3 and anterior root of p4 from AMNH Lion Mountain.

Discussion—The premolars of AMNH 145518 each have three cuspids (Figure 11E-F) and document the occurrence of a leptomerycid at Lion Mountain High, but AMNH 145518 is too incomplete to be identified confidently to taxon.

TABLE 16. Measurements in mm of the P2-M3 of *Protoreodon pumilus* (AMNH 1818, USNM 230352 from Gazin, 1955, 51-52) and the holotype of *P. walshi* (SDSNH 40809 from Theodor, 1999, table 1) compared to RAM 23757 from Black Butte Low.

Tooth Site		AMNH 1818	USNM 20352	RAM 23757	SDSNH 40809
P2	L	10.0	9.4	7.7	7.5-7.8
	W	5.1	5.0	4.7	5.7-5.8
P3	L	9.5	9.7	8.7	7.9
	W	10.3	8.5	7.2	8.0
P4	L	8.0	8.2	8.1	7.8-7.9
	W	10.5	11.0*	10.9	10.2-10.3
M1	L	—	10.7*	10.6	9.7-9.8
	W	—	—	12.8	11.6-11.8
M2	L	13.3	13.0	11.0	11.2
	W	15.8	14.2	15.3	14.0-14.1
M3	L	13.4	13.7	11.6	11.3-11.6
	W	17.4	16.0	14.2	14.3-14.4

TABLE 17. Measurements in mm of the p4-m2 of AMNH 145528 compared to the p4-m2 of *Hypertragulus calcaratus* (AMNH 1341) from Scott (1940, 522).

Tooth Site		AMNH 145528	AMNH 1341
p4	L	5.4	5.0
	W	2.3	2.0
m1	L	5.6	5.0
	W	4.0	3.5
m2	L	6.4	6.0
	W	4.9	4.5

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Miohippus Marsh, 1874
Miohippus sp.
Figure 12A-B, Table 18

Referred Specimens—RAM 18625 right dentary with p3-m2 (Figure 12A); RAM 18624 right P2 (Figure 12B) from RAM locality V2016013 (Black Butte High).

Description-Discussion—RAM 18625 is a well-preserved partial dentary with a slightly worn p3-4, an unworn m1 and an erupting m2; RAM 18624 is an isolated P2 that exhibits slight wear on the protoloph and hypoloph (Figure 12A-B). The anterior ridge of the hypostyle is worn, but RAM 18624 appears to have the type 2 hypostyle (a small spur projecting anteriorly from the hypostyle ridge) of Prothero and Shubin (1989: fig. 10.1).

Mesohippus and *Miohippus* are morphologically similar genera and methods for differentiating them discussed by Osborn (1918), Stirton (1940), and Forstén (1970) are considered problematic (Emry et al., 1987; Prothero and Shubin, 1989). To differentiate the two genera, the shape and complexity of the hypostyles in the upper cheek teeth of *Mesohippus* and *Miohippus* were divided into three types by Prothero and Shubin (1989: fig. 10.1). However, this methodology has limitations because although *Miohippus* usually has a type three mesostyle, *Mesohippus* can have a type 1 (*M. westoni*), type 2 (*M. bairdi*), or type 3 (*M. exoletus*) hypostyle, depending on the species (Prothero and Shubin, 1989). The hypostyle of the P2 of RAM 18624 appears to be type 2, but wear obscures morphological details. However, there does appear to be a recognizable size difference (with some overlap) between *Mesohippus* and *Miohippus* (Prothero and Shubin, 1989) and measurements of the p3-m1 of RAM 18624 and the P2 of RAM 18625 compare much more favorably with species of *Miohippus* (Table 18). Thus, RAM 18624 and RAM 18625 are referred to *Miohippus* species indeterminate.

Family Hyracocontidae Cope, 1879
Trilophus Cope, 1880
Trilophus cf. *T. rhinocerinus* Wood, 1927
Figure 12C, Table 19

Holotype—YPM 13331, left and right maxillae and dentaries, from near mouth of Lake Fork, Uinta Basin, Utah (Wood 1927: pl. 4, figs. 17-19; Uinta C according to Wood, 1929).

Referred Specimen—RAM 23756 left maxilla fragment with P2-M3 (Figure 12C) from RAM locality V2018035 (Black Butte Low).

Description—The P2-M3 of RAM 23756 exhibit moderate wear and are well preserved except for the

TABLE 18. Measurements in mm of p3-m1 and P2 of *Mesohippus. bairdi*, *M. westoni*, *M. barbouri*, *Miohippus assiniboiensis*, and *M. gidleyi* (Prothero and Shubin, 1989; table 10.2 and 10.3) compared to RAM 18625 and RAM 18624.

Tooth Site		*Mesohippus bairdi*	*M. westoni*	*M. barbouri*	*Miohippus assiniboiensis*	*M. gidleyi*	RAM 18625	RAM 18624
p3	L	11.8-12.3	11.4-11.8	11.8-13.4	13.9-14.1	16.3–16.7	14.2	–
	W	8.2-8.3	7.1-8.3	7.4-7.6	8.7-10.5	10.0-10.1	9.8	–
p4	L	11.9-12.4	11.2-12.4	11.6-13.4	13.5-14.5	16.3-17.7	13.2	–
	W	9.1	8.7-9.0	7.8-8.2	10.1-11.3	13.3-13.7	9.6	–
m1	L	11.0-11.4	11.6-11.8	12.0-13.0	12.3-14.5	16.2-16.9	13.3	–
	W	7.8	7.4-8.0	7.1-7.3	9.2-9.3	11.6-12.3	9.7	–
P2	L	10.8-12.2	10.3-11.9	10.6-11.4	11.9-14.1	14.3-15.3	–	15.7
	W	12.7-12.9	11.8-13.4	11.2-13.0	13.2-14.4	15.5-16.9	–	13.5

absence of small sections of enamel on the lingual edge of the metaloph of M1, the lingual edge of the protoloph of M2, and the labial edge of the ectoloph of M3 (Figure 12C). The P2-4 are rectangular in occlusal outline and have well-developed protolophs, ectolophs, and distinct paracones, metacones, and protocones. In comparison, the metalophs of P2-4 are much less developed (particularly P2), lack a distinct hypocone, and with moderate wear the metaloph merges labially with the apex of the protocone. A distinct cingulum is developed anterior, lingual, and posterior to the protocone of P2-4; most robust in P4. The least molariform of the premolars in RAM 23756 is P2.

The M1-2 of RAM 23756 are square in occlusal outline and have well-developed parastyles, ectolophs, and protolophs, and metalophs with a distinct protocone and hypocone (Figure 12C). The ectoloph extends posteriorly past the metaloph in both M1-2, but more so in M2. In contrast, M3 is more triangular in occlusal outline, primarily because it has a short ectoloph that does not extend posteriorly past the metaloph, a condition referred to as the absence of a metacone by Radinsky (1967a). The M3 has a small parastyle and a well-developed protoloph and metaloph, but is significantly smaller than M2, the largest tooth of RAM 23756.

Discussion—RAM 23756 is most similar to the tapiroid *Hyrachyus* and the rhinocerotoid *Triplopus* in terms of the development of the P2-4 and M1-2. But the M3 of RAM 23756 lacks a metacone, so its ectoloph is short and thus the orientation of protoloph-ectoloph-metaloph in M3 is more like a hyracodontid rhinocerotoid than a tapiroid. *Triplopus* is the most common rhinocerotoid from the Uintan of North America (Prothero, 1998) and specimens of it are easily confused with those of *Hyrachyus* (a mostly Bridgerian taxon) when they lack the M3 (Radinsky, 1967b). The only described specimen of *Hyrachyus* from Eocene strata in southwest Montana is the holotype of *H. douglassi* (CM 784) from the Sage Creek Basin (Douglass, 1903; Tabrum et al., 1996), which is only 60 km west of Black Butte. CM 784 has a hypocone and a well-developed metaloph on P2, unlike any other species of *Hyrachyus* (Douglass, 1903; Wood, 1934). In addition to CM 784, a few lower dentitions and a deciduous upper dentition from the Uinta Formation (Uinta B strata) were referred to *H. douglassi* by Wood (1934). But according to Radinsky (1967b), specimens referred to *H. douglassi* could represent *Triplopus* because an M3 or unworn upper molars are needed to distinguish *Hyrachyus* from *Triplopus*. RAM 23756 lacks a hypocone on P2 and thus cannot be the same taxon as CM 784 (i.e. *Hyrachyus douglassi*). Also, the P3-M3 of RAM 23756 appear to represent the hyracodontid *Triplopus* because they are similar to *T. rhinocerinus* from the Uintan Basin. Particularly important in this comparison is the morphology of the M3. In YPM 13331, the holotype of *Triplopus rhinocerinus*, the M3 has just a vestige of a metacone (Wood, 1927: pl. 4, fig. 17; Radinsky, 1967a: fig. 4B) and the M3 of RAM 23756 lacks a metacone (Figure 12C). *Hyrachyus* has a metacone on M3 as do all species of *Triplopus*, except for the tiny metacone of *T. rhinocerinus* (Radinsky, 1967a).

However, there are significant differences between YPM 13331 and RAM 23756 in the morphology of the P2 and the size of the dentition. Unlike the absence of a P2 hypocone in RAM 23756, the P2 of YPM 13331 has a small hypocone as figured by Wood (1927: pl. 4, fig. 17) and a somewhat larger hypocone as figured by Radinsky (1967a: fig. 4B). There is a lot of variation in the development of the P2 in *Triplopus*, as *T. cubitalis*

TABLE 19. Measurements in mmof the P2-M3 of RAM 23756 compared to the P2-M3 of the holotype of *Triplopus rhinocerinus* (YPM 13331) from the Uinta Basin (Utah) from Wood (1927, table 1a).

Tooth Site		RAM 23756	YPM 13331
P2	L	12.5	10.0
	W	17.5	11.0
P3	L	14.1	10.5
	W	19.8	14.0
P4	L	14.7	11.7
	W	22.7	16.4
M1	L	19.1	16.0
	W	22.5	17.6
M2	L	21.5	16.6
	W	25.8	19.3
M3	L	17.2	17.2
	W	24.5	19.6

has a primitive P2, the P2 of *T. implicatus* is unknown, and the degree of molarization of the P2 of *T. obliquidens* varies (Radinsky 1967a). Because the P2 of *T. rhinocerinus* is only known from a single specimen, there is some uncertainty concerning the variation in hypocone development of the P2 in that species. In size, RAM 23756 and YPM 13331 differ by 17% in the length of the M1-3 (50 mm in YPM 13331, Radinsky, 1967a; 60 mm in RAM 23756) and by approximately 20-25% in the size of individual cheek teeth (Table 19). Therefore, RAM 23756 is tentatively referred to *T. rhinocerinus*, a referral based primarily on M3 morphology. However, differences in the size of the dentition and the morphology of the P2 between RAM 23756 and the known sample of *T. rhinocerinus* indicate that RAM 23756 might represent a new species of *Triplopus.*

Family Rhinocerotidae Gray, 1821
Diceratherium Marsh, 1875
Diceratherium tridactylum Osborn, 1893
Figure 12D, Table 20

Holotype—AMNH 538, a complete articulated skeleton from the *Protoceras* Beds (late Whitneyan) of South Dakota (Osborn, 1893; figured in Osborn, 1898: pl. XIII fig. 8, pl. XVII fig. 21-22; pl. XIX fig. 30; pl. XX).

Referred Specimen—AMNH 145520 left dentary fragment with p3-m3 (Figure 12D) from AMNH Lion Mountain.

Description-Discussion—AMNH 145520 is a heavily worn fragment identified and labelled *Diceratherium tridactylum* by M. McKenna in the 1980s. AMNH 145520 is very similar in size to the lower dentition of *D. tridactylum* (Table 20). *Diceratherium armatum* and *D. annectens* have been reported from late Oligocene and early Miocene strata in Montana (Douglass, 1903; Wood, 1933; Rasmussen, 1989; Prothero, 2005), but the molars of AMNH 145520 are too small to represent *D. armatum* and are larger than *D. annectens* (Table 20).

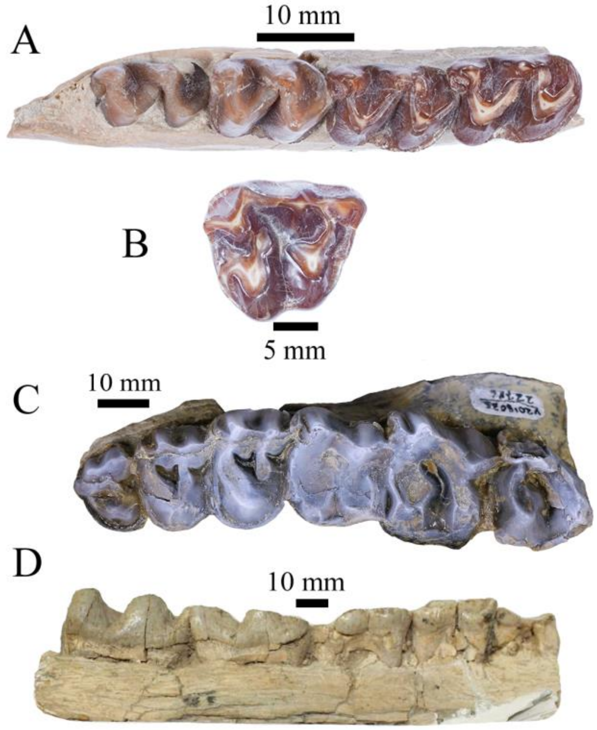

FIGURE 12: Perissodactyls from the Gravelly Range. **A.** Occlusal view of RAM 18625 right dentary p3-m2 of *Miohippus* sp. from Black Butte High. **B.** Occlusal view of RAM 18624 right P2 of *Miohippus* sp. from Black Butte High. **C.** Occlusal view of RAM 23756 left maxilla fragment with P2-M3 of *Triplopus* cf. *T. rhinocerinus* from Black Butte Low. **D.** Labial view of AMNH 145520 left dentary fragment with p3-m3 of *Diceratherium tridactylum* from Lion Mountain High.

Tapiroidea sensu Colbert, 2005
Hesperaletes Colbert, 2006a
Hesperaletes borineyi Colbert, 2006a
Figure 13A-C, Table 21

Holotype—SDSNH 31326, partial skull with left and right C, p2-4, and M1-3 from SDSNH Locality 3378, Santiago Formation, San Diego County, California (Colbert, 2006a: figs.1-2).

Referred Specimen—MCZ 7348 partial left dentary with p2-m3 with right dentary fragment anterior to symphysis (Figure 13A-C) probably from MCZ Black Butte II (Black Butte Low).

Description—The anterior and posterior parts of the left dentary are missing due to breakage, but all cheek teeth are present except for p1 (Figure 13A-C). The posterior edge of the symphysis is transversely positioned parallel to the boundary of p2 and p3. The crown of p2 is heavily damaged and no cusps can be discerned, but p2 is clearly the smallest premolar. The p3 and p4 are similar in morphology and have a reduced trigonid with a transversely parallel metaconid and protoconid, and a small, anterolingual positioned paraconid. The talonid of p3 and p4 are lower than the trigonid and have a distinct basin that is bordered posteriorly by a well-developed hypoconid and a small entoconid. The p3 is relatively narrower than the p4 and wear facets of the metaconid, protoconid and hypoconid of the p3 are larger than those on respective cusps of the p4. Two well-developed transverse lophs are present on m1-m3. The m1 of MCZ 7348 is heavily worn and the m2 is damaged, missing parts of the anterior and posterior lophs. The m3 is unworn and the vertical depth of the dentary below the m2 is 18.6 mm.

Discussion—*Hesperaletes* is represented by *H. borineyi* and *H. walshi*, which are distinguished by features of the dentary and the size of cheek teeth. *Hesperaletes walshi* has a significantly shorter m1 length and width, a shorter m2 length, and a greater p2 length and width than *H. borineyi* (Colbert, 2006a). The m1 and p2 lengths of MCZ 7348 are smaller than the range of lengths of these teeth for either *H. walshi* or *H. borineyi* but fall closer to the minimum value of *H. borineyi* (Table 21); m1, m2, and p2 widths and the m2 length of MCZ 7348 fall within the range of variation of both species.

Also useful for distinguishing the two species is the posterior border of the symphysis of the dentary. In *H. borineyi* it is positioned posterior to p1, whereas in *H. walshi* it is anterior to p1 (Colbert, 2006a). The posterior border of the symphysis of the dentary of MCZ 7348 is positioned posterior to p1. *Hesperalates walshi* and *H. borineyi* can be differentiated also by the ratio between the depth of the dentary below m2 and the length of m2, with a percentage greater than 45% corresponding to *H. walshi*, a percentage less than 45% to *H. borineyi* (Colbert, 2006a). MCZ 7348 has a ratio of 43%, which indicates an affinity with *H. borineyi*. Thus, MCZ 7348 appears to represent *H. borineyi*. In addition, MCZ 7348 was compared directly to the left dentary of *H. borineyi* (SDSNH 35220) and it was identical in morphology and size.

MAMMALIAN BIOSTRATIGRAPHY AND BIOCHRONOLOGY

The presence of only widely spaced erosional remnants of Tertiary strata in the south-central Gravelly Range (Figure 1) make lithostratigraphic correlation of vertebrate-bearing strata extremely difficult. Even though there are examples of superpositional relationships between vertebrate-bearing strata in the Lion Mountain and Black Butte sections, the relative ages of mammalian assemblages in the Gravelly Range study area are based on mammalian biochronology in the absence of lithostratigraphic correlations between measured sections.

Black Butte Low and the *Rapamys* Site (late Uintan or early Duchesnean)**—**The oldest Gravelly Range mammalian assemblages are from the *Rapamys* Site and Black Butte Low (basal 30m of Black Butte section) and are late Uintan or early Duchesnean in age. These assemblages consist of only four taxa each, with *Diplobunops matthewi* present at both sites. The two sites occur at the base of their respective sections (1 km apart) and differ in that vertebrate fossils in the 8 m thick *Rapamys* section were recovered from moderately indurated, beige-colored calcareous nodules that occur within strata containing abundant pod-shaped invertebrate (?) trace fossils 2-4 mm in length. Vertebrate fossils from Black Butte Low also occur in calcareous nodules, but they are gray and highly indurated, and the trace fossils found so abundantly at the *Rapamys* Site are absent from Black Butte Low strata. Thus, the bed that yields fossils at the *Rapamys* Site could not be traced to the section at Black Butte (Figure 2). However, based on mammalian biochronology, the mammalian assemblages from the *Rapamys* Site and Black Butte Low appear to be approximately age equivalent.

The faunal list for the *Rapamys* Site is *Diplobunops matthewi*, *Rapamys atramontis*, and two new species, *Lycophocyon tabrumi* and *Pareumys muffleri*. *Diplobunops matthewi* is only known from Uintan and Duchesnean strata in Montana, Utah, and Wyoming, and first occurs in the late Uintan (Robinson et al., 2004). *Rapamys atramontis* has only been reported from the *Rapamys* Site (Wahlert et al., 2006), but two other species have been described, *R. fricki* from southern California (Wilson, 1940a) and *R. wilsoni* from Badwater, Wyoming (Black, 1971). *Rapamys fricki* was recovered from Uintan strata in San Diego County (Walsh, 1996; Robinson et al., 2004) and the early Duchesnean Pearson Ranch locality in the Sespe Formation in Ventura County (Golz and Lillegraven, 1977; Walsh, 1996). The Badwater sites in Wyoming that yield *R. wilsoni* are late Uintan (Walsh, 1996; Robinson et al., 2004).

Lycophocyon tabrumi and *L. hutchisoni* are the only known species of *Lycophocyon,* and the latter is known from late Uintan and early Duchesnean sites in southern California (Tomiya, 2011). The new species, *Pareumys muffleri* from the Gravelly Range, may also be present at Hough Draw (late Uintan) in the Sage Creek Basin (*Pareumys*? new species, in Tabrum et al.,

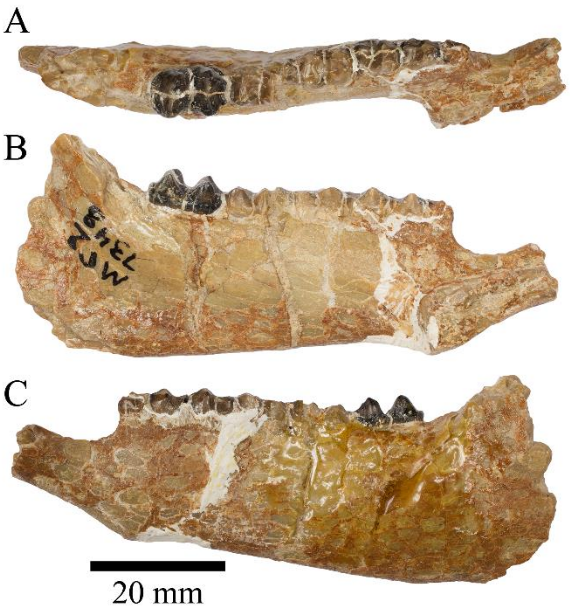

FIGURE 13: *Hesperaletes borineyi* from Black Butte Low. **A.** Occlusal, **B.** Lingual and **C.** Labial views of MCZ 7348 left dentary fragment with p2-m3.

known from Uintan and Duchesnean sites in California, Wyoming, Texas, and Utah (Wilson, 1986; Walsh, 1996; Kelly et al., 2012; Walsh and Storer, 2008) and last occurs in the Duchesnean (Robinson et al., 2004).

In addition to *Diplobunops matthewi*, other taxa known from Black Butte Low are *Protoreodon pumilus*, *Triplopus* cf. *T. rhinocerinus*, and *Hesperaletes borineyi*. *Protoreodon pumilus* is known from Uintan sites in Wyoming and Utah (Prothero, 1996), as well as Uintan and Duchesnean strata in California, Texas, and New Mexico (Wilson, 1971; Golz and Lillegraven, 1977; Schiebout and Schrodt, 1981; Kelly, 1990; Walsh, 1996). *Protoreodon pumilus* has also been recovered from late Uintan rocks from the Sage Creek Basin in Montana (Tabrum et al., 1996) (only 60 km west of Black Butte) and *Protoreodon* last occurs in Duchesnean strata (Robinson et al., 2004).

Hesperaletes borineyi is only confidently known from late Uintan rocks in San Diego County, California, but specimens of cf. *Hesperaletes* of Duchesnean age might also represent *H. borineyi* if more complete material was recovered (Colbert, 2006a, 2006b). *Triplopus rhinocerinus* is known from the late Uintan Myton Pocket site in Utah (Radinsky, 1967b) and the lower Dell Beds (late Uintan) of the Sage Creek Basin (Tabrum et al., 1996, 2001). *Triplopus* is known from Uintan rocks, and in a few cases Duchesnean strata, in Utah, Texas, California, Wyoming, and Colorado (Wilson, 1986; MacCarroll et al., 1996; Stucky et al., 1996; Prothero 1996, 1998; Walsh, 1996) and last appears in the Duchesnean (Robinson et al., 2004).
Because all mammalian genera recovered from the *Rapamys* site and Black Butte Low have strong late Uintan and early Duchesnean affinities, these two approximately age equivalent sites are late Uintan or early Duchesnean in age.

Teepee Mountain (late Duchesnean or early Chadronian)—The sample from Teepee Mountain consists of seven specimens identified to genus or species (*Megalagus* cf. *M. brachyodon*, *Palaeolagus* sp., *Ischyromys douglassi*, *Paradjidaumo disjunctus*, and *Diplobunops matthewi*). In addition, fragmentary postcranial elements of brontotheres were also recovered. These specimens cannot be identified to

TABLE 20. Measurements in mm of the p4-m3 of AMNH 145520 compared to the means of the p4-m3 of *Diceratherium tridactylum*, *D. armatum*, and *D. annectens* from Prothero (2005, table 4.4).

Tooth Site		AMNH 145520	*D. tridactylum*	*D. armatum*	*D. annectens*
p4	L	31	32	33	28
	W	24	24	27	22
m1	L	36	31	41	30
	W	25	24	29	23
m2	L	41	38	45	35
	W	28	25	30	24
m3	L	44	45	58	38
	W	27	29	30	23

TABLE 21. Measurements in mm of the p2-m3 of MCZ 7348 compared to the p2-m3 of *Hesperaletes walshi* and *H. borineyi* from Colbert (2006a, fig. 5).

Tooth Site		MCZ 7348	*H. walshi*	*H. borineyi*
p2	L	3.9	5.0-5.4	4.0-4.8
	W	3.5	3.2-3.8	2.6-3.2
p3	L	5.0	5.0-6.0	5.0-5.8
	W	4.3	3.2-3.8	2.6-3.2
p4	L	6.0	6.4	5.8-7.2
	W	4.6	—	4.2-5.6
m1	L	6.7	7.2-7.6	7.0-8.6
	W	5.2	5.0-5.4	4.6-6.2
m2	L	8.1	8.4-8.6	8.4-10.2
	W	5.6	6.2	5.2-6.8
m3	L	10.1	8.6-10.0	8.8-11.1
	W	6.3	5.2-6.6	5.8-7.0

genus, but the presence of brontotheres indicates that Teepee Mountain is not younger than Chadronian because brontothere remains last occur in Chadronian strata (Emry et al., 1987; Mader, 1998).

Teepee Mountain yielded three specimens of *Ischyromys douglassi*, whose holoype is from McCarty's Mountain (Black, 1968), an early Chadronian site in southwest Montana (Tabrum et al., 1996, 2001; Prothero and Emry, 2004). *Ischyromys douglassi* is also known from three other Chadronian sites, Raben Ranch, Nebraska (Ostrander, 1985), Florissant, Colorado (Lloyd et al., 2008), and Diamond O Ranch (Korth and Tabrum, 2017), the latter of which could be late Duchesnean (Fostowicz-Frelik and Tabrum, 2009). *Paradjidaumo disjunctus* is known from only Diamond O Ranch and McCarty's Mountain (Korth, 2013) which suggests a late Duchesnean or early Chadronian age. The presence of *Diplobunops matthewi* supports a late Duchesnean age assignment because it is only known from late Uintan to Duchesnean strata and last occurs in the Duchesnean (Robinson et al., 2004). Finally, a lagomorph skull from Teepee Mountain was tentatively identified as *Megalagus* cf. *M. brachyodon*, and *Megalagus* is widely known from Chadronian strata in western Canada, North Dakota, Montana, and Nebraska (Ostrander, 1985; Storer, 1996; Tabrum et al., 1996, 2001; Dawson, 2008). Because there is both a significant Chadronian and Duchesnean affinity to the mammalian assemblage from Teepee Mountain, the site is either late Duchesnean or early Chadronian in age.

Black Butte High (Chadronian)—This site is located at the top of the Black Butte section, about 100 m above Black Butte Low (Figure 2). Black Butte High has yielded four identifiable mammalian specimens that represent three taxa, *Hesperocyon gregarius*, *Miohippus*, and *Domnina thompsoni*. *Hesperocyon gregarius* and *Miohippus* have broad biochronologic occurrences; Duchesnean to Whitneyan for *Hesperocyon gregarius* (Wang, 1994) and Chadronian to Arikareean for *Miohippus* (MacFadden, 1998). However, *Domnina thompsoni* is only well known from Chadronian strata in Nebraska, Montana, and Colorado (Ostrander, 1985; Tabrum et al., 1996, 2001; Lloyd et al., 2008), and has also been reported from the late Duchesnean or early Chadronian Diamond O Ranch site in southwest Montana (Tabrum et al., 1996, 2001). Based on limited biochronologic data, the Black Butte High mammalian assemblage is most likely Chadronian in age.

Lion Mountain High (Whitneyan)—Strata on the west face of Lion Mountain that yield this mammalian assemblage are capped by basalt that yielded a date of 30.8+-0.7 Ma (Gutmann et al., 1989). A tuff from the east flank of Lion Mountain was dated at 31.7 +- 0.02 Ma **(**W. McIntosh personal communication, 2018) and this tuff, as correlated in Figure 2, would be approximately 100 m below the level of Lion Mountain High. These dates suggest that Lion Mountain High is Whitneyan in age as the Whitneyan occurs in strata 32-30 Ma (Prothero and Emry, 2004, fig. 5.2). Fragmentary vertebrate fossils have been found much lower in the section than Lion Mountain High, below the dated tuff (Figure 2) and include a titanothere jaw (Luikart, 1997) which indicates an age no younger than Chadronian for the strata. The lower 150 m of the Lion Mountain section is composed of steep slopes or cliffs of indurated ash-rich mudstone, strata with the potential to yield additional identifiable specimens. However, very few have been recovered to date so the age of the base of the Lion Mountain section is unknown.

Biochronological analysis of the mammalian assemblage recovered from Lion Mountain High agrees with the isotopic age constraints noted above as the assemblage includes *Herpetotherium fugax*, *Nanodelphys* cf. *N. hunti*, *Palaeolagus burkei*, *Eumys elegans*, *Leidymys*, *Ocetocyon cuspidatus*, *Centetodon magnus*, *Hypertragulus calcaratus*, and *Diceratherium tridactylum*. *Ocetocyon cuspidatus* and *Diceratherium tridactylum* strongly suggest a Whitneyan age as the latter is restricted to Whitneyan strata in South Dakota, North Dakota, Nebraska, Colorado, and Wyoming (Prothero, 2005) and *Ocetocyon cuspidatus* is a rare taxon only known from Whitneyan strata in South Dakota and Whitneyan to early Arikareean rocks in Nebraska (Wang, et al., 1999).

All other taxa from Lion Mountain High also support the proposed Whitneyan age determination. *Palaeolagus burkei* is known from Orellan and Whitneyan rocks in Wyoming, Montana, Nebraska, South Dakota, and Colorado (Galbreath, 1953; Simpson, 1985; Korth and Hageman, 1988; Tabrum et al., 1996) and *Hypertragulus calcaratus* is best known from Orellan to Arikareean strata in South Dakota and Nebraska (Scott, 1940; Webb, 1998). *Leidymys* has been reported from Whitneyan to Hemingfordian aged rocks in California, South Dakota, Oregon, Nebraska, and Montana (Macdonald, 1970; Martin, 1976; Rasmussen, 1989; Whistler and Lander, 2003; Bailey, 2004; Korth, 2014; Lindsay, 2008) and *Eumys elegans* is known from Orellan and Whitneyan strata in Colorado, Montana, Wyoming, South Dakota, and Nebraska (Tabrum et al. 1996; Kuenzi and Fields, 1971; Lindsay, 2008; Korth, 2010, 2011, 2018). *Centetodon magnus* is known from Uintan to Arikareean strata throughout western North America (Lillegraven et al., 1981) and *Herpetotherium fugax* is the most common Orellan species of *Herpetotherium* and is well-known from middle Chadronian to early Arikareean strata throughout the Great Plains and Rocky Mountain states (Galbreath, 1953; Simpson,

TABLE 22. Paleobiogeographic comparisons of mammalian assemblages from the *Rapamys* Site and Black Butte Low compared to Uintan and Duchesnean assemblages from California (San Diego and Ventura counties), Utah (Uinta Basin), and Wyoming (primarily Badwater) (Golz, 1976; Walsh, 1996, tables 4 and 6; Colbert, 2006a; Tomiya, 2011) (S= species, G= genus). Notable paleobiogeographic aspects of the Teepee Mountain, Black Butte High, and Lion Mountain High are provided.

Taxon and Locality	California	Utah	Wyoming
Rapamys Site/ Black Butte Low			
Diplobunops matthewi	–	S	S
Protoreodon pumilus	S	S	S
Triplopus cf. T. rhinocerinus	G	S	G
Hesperaletes borineyi	S	–	–
Lycophocyon tabrumi	G	–	–
Pareumys muffleri	G	G	G
Rapamys atramontis	G	–	G
Teepee Mountain *Megalagus cf. M. brachyodon* *Palaeolagus* *Ischyromys douglassi* *Paradjidaumo disjunctus* *Diplobunops matthewi*	*Paradjidaumo disjunctus* endemic to southwest Montana		
Black Butte High *Hesperocyon gregarius* *Miohippus* *Domnina thompsoni*	*Hesperocyon* and *Miohippus* are cosmopolitan taxa		
Lion Mountain High *Herpetotherium fugax* *Nanodelphys cf. N. hunti* *Palaeolagus burkei* *Eumys elegans* *Leidymys* *Ocetocyon cuspidatus* *Centetodon magnus* *?Talpidae* *Hypertragulus calcaratus* *Leptomeryx?* *Diceratherium tridactylum*	Diverse assemblage similar to Whitneyan faunas from Wyoming, Nebraska, and South Dakota Range extensions of *Ocetocyon cuspidatus* and *Diceratherium tridactylum* to southwest Montana		

1985; Korth, 1994, 2008; Hayes, 2007). Finally, *Nanodelphys hunti* occurs in Orellan to Arikareean strata in Colorado, Nebraska, South Dakota, Montana, and Wyoming (Korth, 1994, 2008). Thus, the biochronologic ranges of all of these taxa include Whitneyan occurrences and support the Whitneyan age of Lion Mountain High indicated by co-occurrence of *Ocetocyon cuspidatus* and *Diceratherium tridactylum* and the tuff and basalt age analyses.

PALEOBIOGEOGRAPHY

The mammalian sample from each Gravelly Range local fauna is small, with the 11 taxa at Lion Mountain High the largest number of taxa recovered. The combined age equivalent *Rapamys* Site/Black Butte Low assemblage has seven taxa (Table 22), while Teepee Mountain and Black Butte High have only five and three taxa respectively. In addition to being too small for meaningful paleobiogeographical analysis, the Black Butte High sample includes *Hesperocyon gregarius* and *Miohippus*, which have very broad geographic and biochronologic ranges, and the Teepee Mountain sample includes *Paradjidaumo disjunctus*, a species endemic to southwest Montana because it occurs only at Diamond O Ranch and McCarty's Mountain (Korth, 2013).

The Black Butte Low and *Rapamys* Site mammalian assemblages are combined for paleobiogeographic analysis because they are approximately age equivalent. When compared to similar age assemblages from central Wyoming, northern Utah and southern California, the late Uintan to early Duchesnean *Rapamys* Site/Black Butte Low assemblage has the strongest affinity to southern California (Table 22), as six of seven Gravelly Range taxa are shared with southern California localities and two of the taxa represent unique occurrences (*Hesperaletes borineyi* and *Lycophocyon*). Similar age sites in central Wyoming and northern Utah share five and four taxa respectively with *Rapamys* Site/Black Butte Low, but none are uniquely shared with the Gravelly Range assemblage. These results, based on limited faunal data from southwest Montana, are unexpected because the distance between California and Montana significantly exceeds that between Montana and Utah or Wyoming. The late Uintan-early Duchesnean sample from the Gravelly Range is too small for an effective statistical comparison to the much larger late Uintan-early Duchesnean mammalian assemblages from Wyoming, Utah and California. However, description of the more diverse late Uintan mammalian assemblage from the Dell Beds in the Sage Creek Basin (Tabrum et al., 1996, 2001) only 60 km west of Black Butte, is in progress (Lofgren et al. in preparation). This middle Eocene mammalian assemblage can then be compared to those from Wyoming, Utah, and California to test whether the California to Montana affinity will remain most robust.

Lion Mountain High has the largest and most taxonomically diverse mammalian assemblage (Table 22) and these taxa are all present in Whitneyan faunas from Wyoming, Nebraska, and South Dakota (except the taxon represented by a talpid-like m3 which could be new). Unfortunately, because Whitneyan mammals are not known from southern California (Prothero and Emry, 2004), the intriguing similarity of the late Uintan-early Duchesnean assemblage from the Gravelly Range (Black Butte Low/*Rapamys* Site) to similar age assemblages in southern California cannot be evaluated with regard to the mammalian assemblage from Lion Mountain High. Significant paleobiogeographic range extensions of taxa present at Lion Mountain High include *Diceratherium tridactylum* and *Ocetocyon cuspidatus*, because *O. cuspidatus* was only known from the Whitneyan in South Dakota and Nebraska (Wang, et al., 1999), and *Diceratherium tridactylum* from the Whitneyan in South Dakota, North Dakota, Nebraska, Colorado, and Wyoming (Prothero, 2005).

SUMMARY

Isolated outcrops of Tertiary strata that yield late Uintan to Whitneyan vertebrate fossils are located at high elevation in the south-central Gravelly Range of southwest Montana. Recovery of mammalian fossils from this area began in the late 1940s, with renewed efforts in the 1980-1990s and from 2016 to 2019, the latter of which included detailed geologic mapping and lithostratigraphic study of fossil-producing outcrops. This resulted in the identification of five mammalian assemblages from four areas; Black Butte, Lion Mountain, Teepee Mountain, and the *Rapamys* Site. The *Rapamys* Site yielded four taxa, including two new species, the caniform *Lycophocyon tabrumi* and the cylindrodontid *Pareumys muffleri*. Black Butte Low also yielded four taxa, of which *Diplobunops matthewi* also occurs at the *Rapamys* Site. The Black Butte Low and *Rapamys* Site assemblages are approximately age equivalent and are late Uintan or early Duchesnean in age.

The Teepee Mountain assemblage consists of five taxa (including *Diplobunops matthewi*) that indicate a late Duchesnean or early Chadronian age for the site. The sample from Black Butte High includes only three taxa, including *Domnina thompsoni*, which suggests the site is most likely Chadronian.

Lion Mountain High yielded the youngest Gravelly Range mammalian assemblage and is Whitneyan in age. The site lies just below a basalt with an age of 30.8 +- 0.7 Ma and about 100 m above a tuff with an age of 31.7+-.02 Ma. The Whitneyan occurred about 30-32 Ma (Prothero and Emry, 2004), an interval that matches the geochronologic age of the Lion Mountain High assemblage based on the dated extrusive igneous units at Lion Mountain. The composition of the mammalian assemblage from Lion Mountain High also indicates a Whitneyan age as the fauna is similar to Whitneyan assemblages from Wyoming, Nebraska, and South Dakota. Significant paleobiogeographic range extensions of taxa present at Lion Mountain High include *Diceratherium tridactylum* and *Ocetocyon cuspidatus*.

When compared to similar age sites in southern California, northern Utah, and central Wyoming, the taxonomic composition of the *Rapamys* Site/Black Butte Low mammalian assemblage is most similar to those from southern California with two shared unique occurrences (*Hesperaletes borineyi* and *Lycophocyon*). The southern California paleobiogeographic affinity of the Black Butte Low/*Rapamys* Site mammalian assemblage is surprising as the distance between California and southwest Montana is much greater than the distance between Montana and Wyoming or Utah. The mammalian assemblage from Black Butte Low/*Rapamys* Site is small so its California affinity is not statistically robust, but additional comparisons of middle Eocene mammalian assemblages from the Dell Beds in the Sage Creek Basin in southwest Montana would further elucidate this tentative late Uintan or early Duchesnean paleobiogeographic affinity.

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