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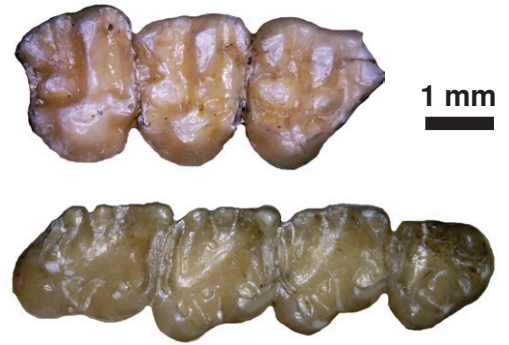
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# Rodents (Mammalia) from Fitterer Ranch, Brule Formation (Oligocene), North Dakota

*William W. Korth, Robert J. Emry, Clint A. Boyd,  
and Jeff J. Person*

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Smithsonian Institution  
Scholarly Press

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## ABSTRACT

Korth, William W., Robert J. Emry, Clint A. Boyd, and Jeff J. Person. Rodents (Mammalia) from Fitterer Ranch, Brule Formation (Oligocene), North Dakota. *Smithsonian Contributions to Paleobiology*, number 103, vi + 45 pages, 17 figures, 15 tables, 1 appendix, 2019.—Eighteen rodent species are recognized from the Fitterer Ranch fauna of North Dakota on the basis of more than a thousand collected specimens. Of the species recognized, four are new: the prosciurine aplodontids *Prosciurus hogansoni* and *Altasciurus leonardi*, the heliscomyid *Heliscomys borealis*, and the cricetid *Eumys lammersi*. A previously described castorid from this fauna, *Oligotheriomys primus* Korth, 1998, is considered a synonym of “*Eutypomys*” *magnus* Wood, 1937, on the basis of the recovery of lower dentitions but is retained in the genus *Oligotheriomys*. A single specimen is questionably referred to *Microparamys*, a genus elsewhere limited to the Eocene (Clarkforkian-Chadronian land mammal ages). The rodent fauna appears to be a combination of predominantly Orellan and Whitneyan species (early Oligocene), suggesting that the section might transcend the Orellan-Whitneyan boundary. However, the rodent fauna does not alter significantly from the lowest to the highest horizons.

Cover images, left to right: Brule Formation at Fitterer Ranch paleontological site in southwest North Dakota (photo by Clint A. Boyd); prehistoric rodent *Prosciurus hogansoni* molars (photo by William W. Korth).

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# Rodents (Mammalia) from Fitterer Ranch, Brule Formation (Oligocene), North Dakota

William W. Korth,<sup>1\*</sup> Robert J. Emry,<sup>2</sup> Clint A. Boyd,<sup>3</sup> and Jeff J. Person<sup>3</sup>

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## INTRODUCTION

Murphy et al. (1993) described the geology of the Little Badlands area of North Dakota, including that of Fitterer Ranch and other localities. Stratigraphically, the Fitterer Ranch locality was assigned to the Brule Formation, which, in turn, was recognized as being Orellan (early Oligocene) in age. Kihm (1990) suggested that much of the Brule Formation in the Little Badlands area of Stark County, North Dakota (including Fitterer Ranch), may be Whitneyan (late Early Oligocene) in age on the basis of the recognition of *Eumys brachyodus*, a rodent species limited elsewhere to the Whitneyan (Wood, 1937; Lindsay, 2008; Korth, 2011), and the absence of *Eumys elegans*. In the faunal list provided for Fitterer Ranch (Murphy et al., 1993: appendix C) 23 species of rodents were identified, the majority of which were typical Orellan species. However, among the species previously reported, one (*Adjidaumo minimus*) is limited at other localities to the latest Eocene Chadronian, three (*Agnotocaster praetereadens*, *Adjidaumo* (= *Leptodontomys*) *douglassi*, *Eumys brachyodus*) are known from the Whitneyan, and one (*Palaeocaster complexus*) is limited to the latest Oligocene, the Arikareean. Part of this confusion may be related to the preliminary nature of those species identifications, or it might reflect a mixing of faunas due to a greater time range represented in the rocks, as suggested by Kihm (1990).

The bulk of the specimens from Fitterer Ranch discussed by Murphy et al. (1993) was surface collected in the 1940s into the 1960s by workers from the Frick Laboratory at the American Museum of Natural History and is currently housed at that institution. Since that time, additional collections have been made by the Smithsonian Institution's National Museum of Natural History, Manitoba Museum of Man and Nature (now Manitoba Museum), Dakota Dinosaur Museum (now Badlands Dinosaur Museum), and North Dakota Geological Survey, including screen washing for smaller specimens. Many of the rodent specimens examined in this study were associated with well-constrained stratigraphic data. As a result, a detailed description of the rodent fauna from Fitterer Ranch should clarify whether there is a mixing of faunas of different ages at the site or if a progression of distinct faunas is noted from different stratigraphic intervals.

## DENTAL TERMINOLOGY

Dental terminology for rodents generally follows that of Wood and Wilson (1936), with specialized terminology for castorids (Stirton, 1935) and geomyoids (Korth and

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Branciforte, 2007). Upper teeth are designated by capital letters; lower teeth are designated by lowercase letters (e.g., upper molar M1 and lower molar, m1). All measurements were taken with an optical micrometer to the nearest 0.01 mm.

#### ABBREVIATIONS

##### *Teeth*

dP	deciduous upper premolar
dp	deciduous lower premolar
M	upper molar
m	lower molar
P	upper premolar
p	lower premolar

##### *Institutions*

AMNH	American Museum of Natural History
FAM	Frick Collections, American Museum of Natural History
NDGS	North Dakota Geological Survey
USNM PAL	Department of Paleobiology, National Museum of Natural History, Smithsonian Institution (formerly United States National Museum)
YPM-PU	Princeton University Collection, Yale Peabody Museum of Natural History

##### *Measurements*

L	maximum anteroposterior length
W	maximum transverse width

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## GEOLOGIC SETTING

The contiguous main body of White River deposits in the Great Plains region is centered in western Nebraska and southwestern South Dakota and extends into the adjacent parts of

eastcentral Wyoming and northeastern Colorado (Prothero and Emry, 2004: fig. 5.1). Well to the north of this main body are scattered remnants in the northwestern corner of South Dakota, southeastern Montana, and southwestern North Dakota. A more detailed accounting of the North Dakota occurrences (Murphy et al., 1993) shows that White River deposits (Chadron and/or Brule Formations) occur as remnants in the upper portions of more than a dozen buttes and other higher elevations throughout the southwestern portion of the state.

The Fitterer Ranch paleontological locality is along the southern margin of the area generally referred to as the Little Badlands, southwest of the city of Dickinson in Stark County, North Dakota (T137N, R97W, sections 6, 7, and 16 to 18). Skinner (1951) was the first to document the stratigraphy and paleontology of the White River Group exposures at Fitterer Ranch, dividing the rocks into six discrete units and various sub-units. Stone (1973) informally divided the Brule Formation into two members, the lower "Dickinson Member" and the upper "Scheffield Member," with proposed type sections for both units located at Fitterer Ranch. The contact between those proposed members roughly corresponds to the contact between units 5 and 6 of Skinner (1951). Murphy et al. (1993), in their review of the White River Group of North Dakota, did not formalize this division of the Brule Formation, stating that the identification of the two proposed members was difficult outside of the type area at Fitterer Ranch. Skinner (1951) was the first to note the presence of a "white marker zone" at the contact between units 4 and 5 that could be traced through much of the Little Badlands area, providing a useful marker bed for stratigraphic correlations. Murphy et al. (1993) identified that marker bed as a tuff, informally naming it the "Antelope Creek tuff," and confirmed via trace element content that it can be correlated between locations within the Little Badlands area.

One of the most fossiliferous deposits at Fitterer Ranch is located within a localized paleovalley that downcuts through the Antelope Creek tuff and into the underlying rocks of the Brule Formation. The base of that paleovalley, which Skinner (1951) called the "Fitterer Channel," is filled by a gray to green, very fine to coarse-grained sandstone that averages several meters in thickness (Murphy et al., 1993). These basal sands, termed the "Fitterer Bed" by Murphy et al. (1993), typically preserve stacked sets of foreset beds at least .6 m (2 feet) in thickness. In most places at Fitterer Ranch, the Fitterer Bed is exposed as the caprock on small hills and plateaus, resulting in erosion of the upper portion of these sands. Within the most fossiliferous and most heavily sampled area of Fitterer Ranch, the Fitterer Bed forms the floor of a small area of badlands outcrop, revealing the upper portion of the sandstone interval. At that location the prominent foreset beds emerge from the subsurface and connect to nearly horizontal topset beds. Those beds could have been formed along a point bar on the inside of a curve in a meandering stream channel. However, the morphology of the cross-bedding more closely resembles that typically seen in a prograding delta, where a stream with sediment-laden water flows into a larger body of standing water, in this case likely an oxbow lake.

The timing of the downcutting of the Fitterer Channel appears to roughly correspond to a pronounced paleoecological change at Fitterer Ranch. Paleontological localities situated below the Fitterer Channel (unit 4 of Skinner, 1951) typically preserve endocarps (likely from the hackberry *Celtis*) and often preserve rhizoliths, whereas those types of fossils are less common in the rocks forming unit 5 of Skinner (1951). Fossils of oreodonts and tortoises are more common in rocks below the Fitterer Channel, whereas they are nearly absent within the Fitterer Bed and the overlying mudstones and siltstones. Within the Fitterer Channel, fossils of various species of fish, anuran amphibians, pond turtles, and aquatic snails are common components of the fauna. This change in paleoecology appears to be represented in the rocks at least until the top of unit 5 (see Figure 1), at which point fossils are sparsely known from Fitterer Ranch, making it difficult to assess the paleoecology. Overall, the Fitterer Channel represents a lithologic facies and associated paleoecology that is atypical for White River rocks in southern South Dakota and Nebraska and requires further study to fully elucidate the conditions under which it formed.

## SAMPLING METHODS

In this study, the stratigraphic column at Fitterer Ranch was broken into seven discrete sampling intervals, and all of the rodent specimens analyzed were assigned to a particular sampling interval. To facilitate the inclusion of earlier collections made at Fitterer Ranch, these sampling intervals correspond to portions of the units defined by Skinner (1951). This methodology allowed the distribution of taxa within the Brule Formation at Fitterer Ranch to be tracked to assess the biostratigraphic age of the fauna preserved within each sampling interval and to identify the stratigraphic position of any transitions between faunas of different biostratigraphic ages, if present. Descriptions of the upper and lower boundaries of each sampling interval and a discussion of important sedimentary units follow and are illustrated in Figure 1. It should be noted that these sampling intervals were defined on the basis of ease of recognition in the field and the ability to collect from rocks of one sampling interval with minimal risk of contamination by fossils of the other sampling intervals and do not necessarily correspond to lithosomes or discrete sedimentary packages. This study should not be interpreted as an attempt to redefine or propose a new stratigraphic framework of the Brule Formation at Fitterer Ranch. Work on that topic remains an ongoing project by some of the authors of the present study.

### SAMPLING INTERVAL 1

The base of sampling interval 1 begins at the base of unit 4 of Skinner (1951), which consists of pink to brown mudstones and nodular siltstones that differ in color, lithology, and weathering profile from the underlying rocks. In defining the South Heart Member of the Chadron Formation, Murphy et al. (1993:101) placed the contact between the Chadron and Brule

Formations at the change from the lower medium brown to gray-brown smectitic claystones to the higher pink-brown siltstones and mudstones. In some places this contact is also marked by the presence of a limestone bed up to 30 cm (1 foot) in thickness (Murphy et al., 1993). Under that definition, the contact between these formations would be placed between units 3 and 4 of Skinner (1951), an interpretation that is supported by the presence of spring seeps at or just below this contact that were noted at the top of unit 3 by Skinner (1951). Although Skinner (1951) suggested the greenish to gray clays composing his unit 3 “transitional zone” may be best referred to the Brule Formation, subsequent studies on the stratigraphy of the White River Group at Fitterer Ranch consistently place the contact between the Chadron and Brule Formations at the base of pink to brown mudstones and siltstones and not below a greenish to gray clay (e.g., Stone, 1973; Murphy et al., 1993).

The upper boundary of sampling interval 1 is placed at the base of the unconformity created by the gray to green channel sandstones of the Fitterer Bed. The entirety of the rocks here included in sampling interval 1 usually corresponds to subunit 4A of Skinner (1951), but the depth of downcutting of the Fitterer Bed is variable at Fitterer Ranch, and in some places rocks of the other subunits of unit 4 may still be present. All specimens included in this study from sampling interval 1 were surface collected.

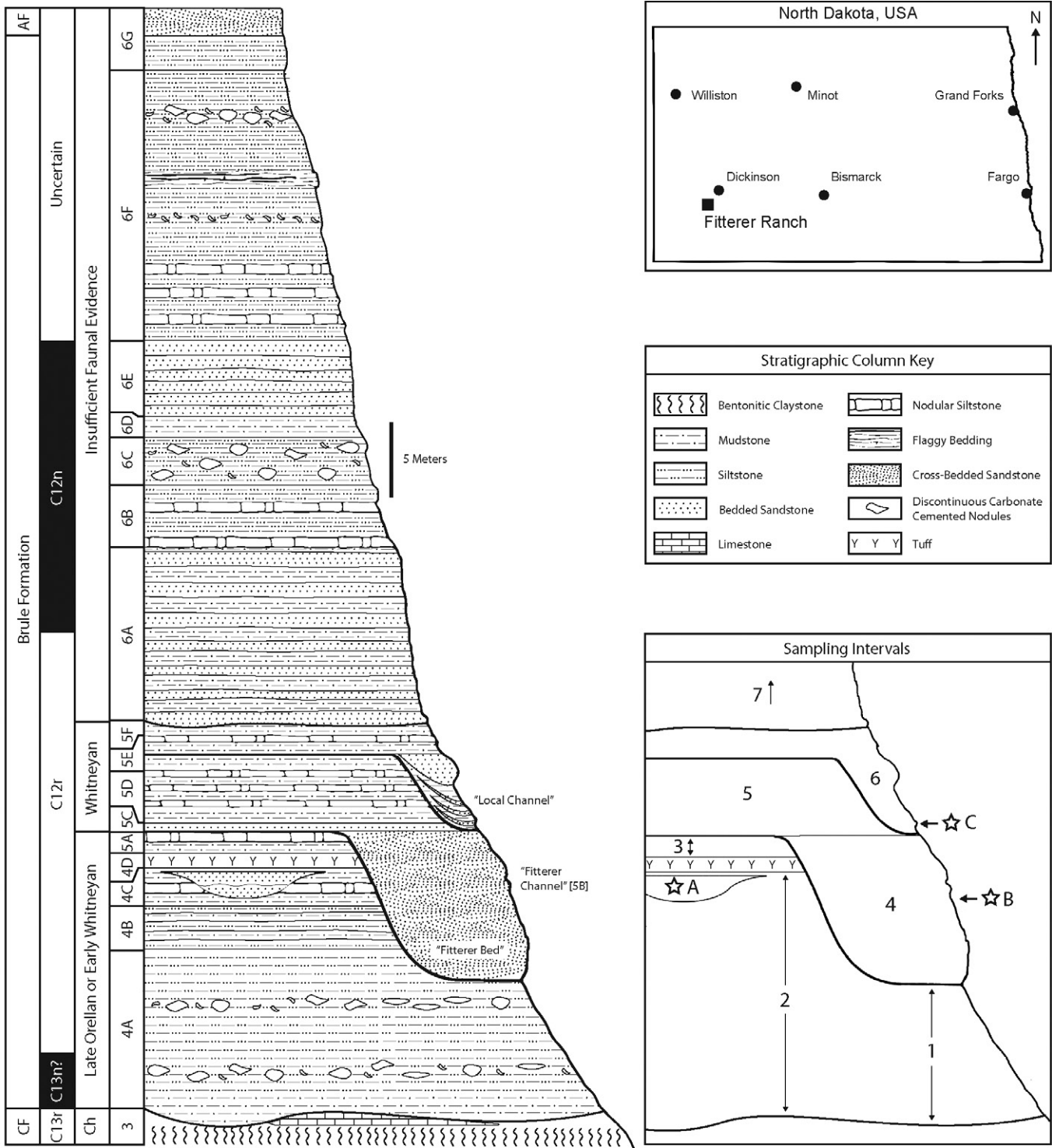
### SAMPLING INTERVAL 2

The base of sampling interval 2 is again placed at the contact between the Chadron and Brule Formations as defined above. The upper contact of sampling interval 2 is placed at the top of the Antelope Creek tuff, so that sampling interval 2 corresponds to the entirety of unit 4 of Skinner (1951). Sampling intervals 1 and 2 were separated in this study to assess whether or not the truncation of the uppermost rocks of unit 4 impacted the interpreted biostratigraphic age of the lower beds of the Brule Formation.

Multiple ribbons of a distinct gray to green, fossiliferous channel sandstone were identified in June of 2017 within subunit 4C of Skinner (1951) that are similar in general appearance to the Fitterer Bed but average only a few meters thick and are positioned below a few meters of mudstone that is capped by the Antelope Creek tuff. This is a separate channel complex older than the Fitterer Channel, here termed the “Fawn Channel.” The preservation within the latter channel sandstone is also distinct from that noted elsewhere at Fitterer Ranch, with fossils from the channel sandstone facies typically having a deep black coloration. Sediments from both the channel sandstone and the overlying mudstone at a single location (NDGS L244) were screen washed, producing the majority of the specimens studied from sampling interval 2.

### SAMPLING INTERVAL 3

The base of sampling interval 3 is the upper surface of the Antelope Creek tuff. The upper boundary is placed at the base of the sandstone of subunit 5C. Sampling interval 3 is present only in areas where the Fitterer Channel is absent; thus, exposures are



**FIGURE 1.** Generalized stratigraphic column for the Fitterer Ranch area of Stark County, North Dakota. Stratigraphic data are derived from personal observations of the authors, unpublished field notes of former curator of vertebrate paleontology Richard Tedford (provided courtesy of the American Museum of Natural History), and published data (Skinner, 1951; Stone, 1973; Murphy et al., 1993). On the left-hand side of the stratigraphic column are the lithostratigraphic boundaries, the magnetostratigraphic data of Prothero (1996: fig. 5), the inferred North American Land Mammal Ages (NALMAs) from this study, and the unit and subunit numbers defined by Skinner (1951). The geographic location of the Fitterer Ranch study area is shown in the upper right inset map. A key to lithologies and sedimentary structures is provided in the center right. The stratigraphic ranges of the seven sampling intervals used in this study are detailed in the lower right inset, with stars indicating the placement of the screen-washed localities (A) NDGS L244, (B) NDGS L245 and (C) NDGS L237. Abbreviations: AF, Arikaree Formation; C13r, Chron 13 reverse polarity interval; C13n, Chron 13 normal polarity interval; C12r, Chron 12 reverse polarity interval; C12n, Chron 12 normal polarity interval; CF, Chadron Formation; Ch, Chadronian NALMA; n, normal polarity; r, reverse polarity. Illustration by Clint Boyd and Becky Barnes.

limited, and few specimens were collected from this sampling interval. All specimens from this sampling interval were surface collected.

#### SAMPLING INTERVAL 4

This sampling interval consists entirely of the gray to green sandstones and conglomerates of the Fitterer Bed that infill the base of the Fitterer Channel. Multiple macrovertebrate quarries have been opened in different locations on Fitterer Ranch within the Fitterer Bed because those rocks tend to preserve dense accumulations of rhinocerotid bones, and microvertebrates can be surface collected in many locations. A single locality within the Fitterer Bed is being screen washed (NDGS L245) and has produced several specimens included in this study. These sandstones and conglomerates correspond to a portion of subunit 5B of Skinner (1951) and are not present in all areas of Fitterer Ranch.

#### SAMPLING INTERVAL 5

This sampling interval consists of either the mudstones, siltstones, and scattered sandstones deposited within the upper portion of the Fitterer Channel paleovalley or beds of similar lithology deposited above the sandstone bed that defines the top of sampling interval 3 (Figure 1). The upper contact is placed either below the local channel cut described in sampling interval 6 (where present) or within the muds below the greenish nodular siltstone that forms the upper portion of subunit 5E. These beds correspond to subunit 5C through the lower portion of subunit 5E of Skinner (1951). Several fossiliferous layers are present within this interval, making it the most productive sampling interval included in this study for surface collection of fossils. Nearly all of the specimens in this study from this sampling interval were surface collected. Attempts to screen wash several of the layers from sampling interval 5 produced limited results as many of the fossiliferous layers are nodular siltstones that are well indurated by carbonate cement and are difficult to break down.

#### SAMPLING INTERVAL 6

This sampling interval is confined largely to a localized channel downcut that is positioned stratigraphically above the paleovalley of the Fitterer Channel (Figure 1). The inset of this channel is between 6 and 9 m (20 and 30 feet), depending on the position within the channel. After initial erosion of the underlying rocks, it appears this was an abandoned channel that was slowly filled mainly with mudstone. Occasional reactivation of the channel is indicated by irregularly spaced, thin beds of siltstone to very fine grained sandstone. One of these thin sandstone beds near the base of the channel is highly fossiliferous, containing a dense accumulation of microvertebrate fossils as well as several species of aquatic snails. That layer was independently identified by the Smithsonian Institution and the North Dakota Geological Survey (NDGS L237), both of which collected the layer for screen washing. That work produced the vast majority

of specimens studied from sampling interval 6. The central portion of the upper part of the channel is filled by a few meters of white to tan, moderately indurated sandstone. Attempts to recover fossils within that upper sandstone have thus far been unsuccessful. This local channel is situated within subunit 5E of Skinner (1951). The top of subunit 5E is marked by a greenish nodular siltstone, and that siltstone and the mudstones immediately above and below extend over the localized channel described above and are fossiliferous in places. Thus, the upper portion of subunit 5E and all of subunit 5F are included in sampling interval 6 since they are situated above the prominent local channel and extend farther geographically than the localized channel at Fitterer Ranch. It is uncertain if this is the same localized channel identified by Skinner (1951) given that it is clearly situated within subunit 5E and not at the base of subunit 6A as shown in the stratigraphic diagram provided by Skinner (1951).

#### SAMPLING INTERVAL 7

The base of sampling interval 7 is placed at the bottom of a thick package of interbedded mudstones and siltstones that typically weather into vertical faces, creating a clear change in slope on weathering profiles. The top of sampling interval 7 is placed at the contact between the Brule Formation and the overlying Arikaree Formation, which at Fitterer Ranch is placed at the base of a gray to green, moderately to well-indurated, silica-cemented sandstone above a brown siltstone (Murphy et al., 1993). Sampling interval 7 of this study corresponds to the “Scheffield Member” of Stone (1973) and nearly all of unit 6 of Skinner (1951), excepting the upper portion of subunit 6G, which is included in the Arikaree Formation. Overall, these rocks tend to be highly resistant to erosion, creating steep faces that are difficult to prospect in most areas. As a result, few paleontological localities are identified within that portion of the Brule Formation at Fitterer Ranch at this time, and few rodent specimens were available for inclusion in this study. No rocks from this sampling interval have been screen washed to our knowledge.

#### POTENTIAL BIASES

Some of the observed stratigraphic distributions of rodent species at Fitterer Ranch are clearly influenced by collecting bias. Overall, the lowest sampling intervals (sampling intervals 1 to 3) have produced many fewer specimens than sampling interval 5, from which most of the surface-collected material comes. Most of the specimens from sampling interval 6 come from a small channel deposit (NDGS L237) that was extensively screen washed. As a result, the majority of specimens recovered from sampling interval 6 are of the smaller rodent species (e.g., eomyids and heteromyids), whereas those surface collected from the other sampling intervals are generally of the larger species (e.g., *Eumys* and *Ischyromys*). Screen washing was recently begun on channel sandstone deposits within sampling interval 2 (NDGS L244) and sampling interval 4 (NDGS L245), but very little rock has been washed thus far, and most of the fossils recovered have not yet been identified.

However, early work on specimens from NDGS L244 conducted in 2017 provided the only records of five of the 11 rodent taxa reported from sampling interval 2 in this study (*Altasciurus leonardi*, *Heliscomys borealis*, *Hesperopetes* cf. *blacki*, cf. *Microparamys* sp., and *Prosciurus hogansoni*), demonstrating the impact screen washing has on elucidating the rodent fauna from a given sampling interval. Without the specimens recovered from NDGS L244, the diversity of the rodent fauna would appear to increase from five species in the lower sampling intervals (sampling intervals 1 to 3) to 18 species in the upper sampling intervals (sampling intervals 4 to 6). Continued screen-washing efforts in the lower sampling intervals at Fitterer Ranch may eventually extend downward the stratigraphic ranges of other taxa currently reported from only the upper sampling intervals. Additionally, the absence of screen-washing efforts within sampling interval 3 likely accounts for the occurrence of several rodent species in sampling intervals 2, 4, and 6 but not within sampling interval 3.

Given that the screen-washed localities in sampling intervals 2, 4, and 6 are within channel sandstone facies, there is some possibility that a portion of the fossils those rocks contain could be reworked. Such reworking could explain the observed mix of typically Orellan and Whitneyan taxa noted in this study, with the Orellan taxa being reworked into an otherwise Whitneyan fauna. Some arguments can be made against widespread reworking of specimens in the channel sandstone facies. Nearly all of the rodent specimens collected via screen washing are isolated teeth, and many are well preserved and have partial to full roots still attached, suggesting those specimens are unlikely to be reworked from older rocks, nor is it likely they were transported a substantial distance prior to burial. Additionally, most of the rodent taxa identified in this study from the screen-washed localities are also represented by partial or complete jaws that were surface collected from outside the channel sandstone facies within the same or higher sampling intervals. Although the presence of some of the extremely rare taxa noted at Fitterer Ranch may be the result of reworking from older rocks that were previously deposited outside of the study area (e.g., the lone specimen of cf. *Microparamys* sp. from sampling interval 2), most of the taxa identified in this study are likely preserved within the correct stratigraphic context.

## SYSTEMATIC PALEONTOLOGY

### ORDER RODENTIA BOWDICH, 1821

### FAMILY ISCHYROMYIDAE ALSTON, 1876

### Genus *Ischyromys* Leidy, 1856

### *Ischyromys typus* Leidy, 1856

FIGURE 2; TABLE A1

REFERRED SPECIMENS. NDGS 1853, fragment of right rostrum with I1, palate with left P3–M2 and right P4, and

dentary fragment with left p4; FAM 145538, palate with right M1–M3 and left dP4–M3; NDGS 1851, dP4; NDGS 2604, M1 or M2; USNM PAL 642971, FAM 96861, 145536, NDGS 2714, 2716, dentaries with p4–m3; FAM 145537, NDGS 2706, dentaries with p4–m2; NDGS 1854, 2570, 2601, dentaries with m1–m3; FAM 94845, USNM PAL 642972, NDGS 1852, 2520, 2582, dentaries with m1–m2; FAM 94846, 94997, 96862, NDGS 2704, partial dentaries with m2–m3; FAM 94848, 96889A, m1s.

OCCURRENCE. Sampling intervals 1 to 6.

DISCUSSION. In dental dimensions, the sample from Fitterer Ranch is nearly identical to the sample from the nearby Little Badlands, North Dakota, with a mean size slightly greater than that of samples of *Ischyromys typus* from the Orellan of the Pine Ridge, Nebraska; northeastern Colorado; and Big Badlands, South Dakota (see Heaton, 1996: figs. 4–7). The anterior medial cusp on the posterior side of the metalophid on the lower molars is variably present (Heaton, 1996: fig. 1), from absent to strongly developed (Figure 2B,C). The molariform

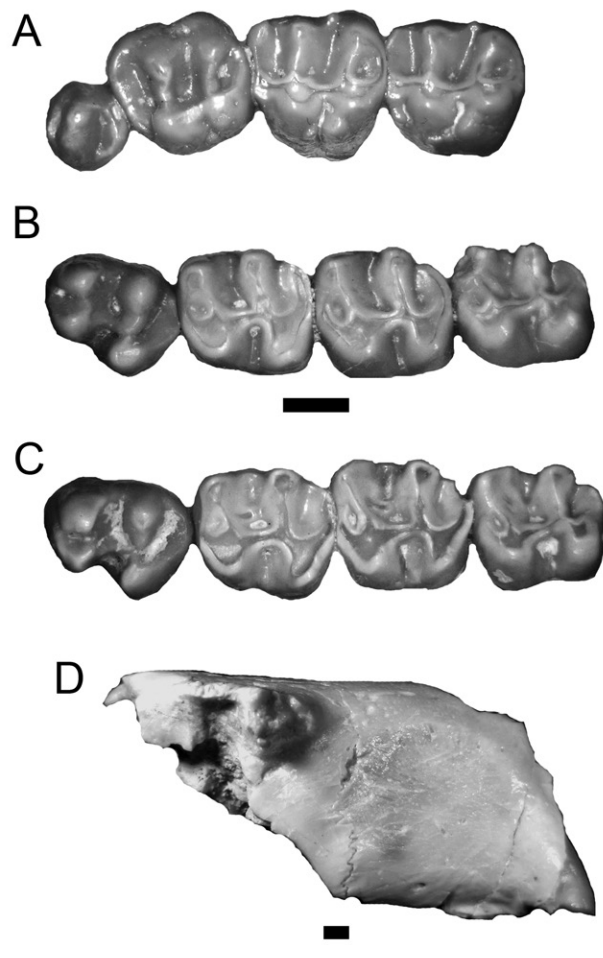


FIGURE 2. Dentitions and partial cranium of *Ischyromys typus* from Fitterer Ranch: (A) NDGS 1853, left P3–M2; (B) FAM 94847, left p4–m3; (C) FAM 96861, left p4–m3; and (D) NDGS 1853, lateral view of rostrum (anterior to right). Bar scales = 2 mm; note different bar length in D.

P4 (Figure 2A) is also characteristic of *I. typus* (Wood, 1937; Black, 1968). The species of *Ischyromys* have been separated into two genera or subgenera, *Ischyromys* Leidy, 1856 and *Titanotheriomys* Matthew, 1910, by some authors on the basis of the morphology of the zygomassteric structure of the skull (Wood, 1937, 1976; Heaton, 1996). The single rostrum from Fitterer Ranch, NDGS 1853 (Figure 2D), does not show the attachment of the masseter onto the rostrum that is described for *Titanotheriomys*.

Although *Ischyromys* specimens occur in nearly all sampling intervals at Fitterer Ranch, there is no discernible difference in the size or morphology from any of the sampling intervals. The rarity of *I. typus* specimens from sampling interval 6 (only one specimen of an immature individual) may be due to the depositional environment that selected for specimens of only the smallest species.

### Genus *Microparamys* Wood, 1959

#### cf. *Microparamys* sp. indet.

FIGURE 3A

REFERRED SPECIMEN. NDGS 2282, right m1 or m2.

OCCURRENCE. Sampling interval 2.

MEASUREMENTS. L = 1.15 mm; W = 1.06 mm.

DESCRIPTION. The tooth is rectangular in occlusal outline, slightly longer than wide, and brachydont. The anterior cingulid is very low, running from the base of the metaconid along the anterior margin of the tooth, ending in a small anterostylid that is anterior and slightly lingual to the protoconid. A distinct valley separates the anterostylid from the metalophid, but a low ridge extends posterolingually from the anterostylid, ending at the base of the metaconid. The metalophid is complete from the protoconid to the metaconid, forming a broad V shape. Both the metaconid and protoconid are anteroposteriorly compressed. The hypoconid is circular to slightly crescentic in shape. There is no ectolophid, but there is a short loph extending anterolingually from the hypoconid toward the center of the tooth for a short distance (=mesolophid?). The entoconid is also anteroposteriorly compressed. The posterolophid extends lingually from the posterior side of the hypoconid for the entire width of the tooth. A low hypolophid extends posterobuccally from the entoconid, meeting the posterolophid near its center.

DISCUSSION. This specimen is tentatively referred to the otherwise exclusively Eocene genus *Microparamys* on the basis of its small size and unique feature of the anterostylid separated from the metalophid, a diagnostic feature of the genus (Wood, 1959, 1962; Anderson, 2008). It differs from other species of *Microparamys* in that it has the combination of (1) smaller size, (2) an incomplete ectolophid, (3) a short hypolophid, and (4) a complete metalophid and therefore cannot be readily assigned to any previously recognized species of *Microparamys*. It

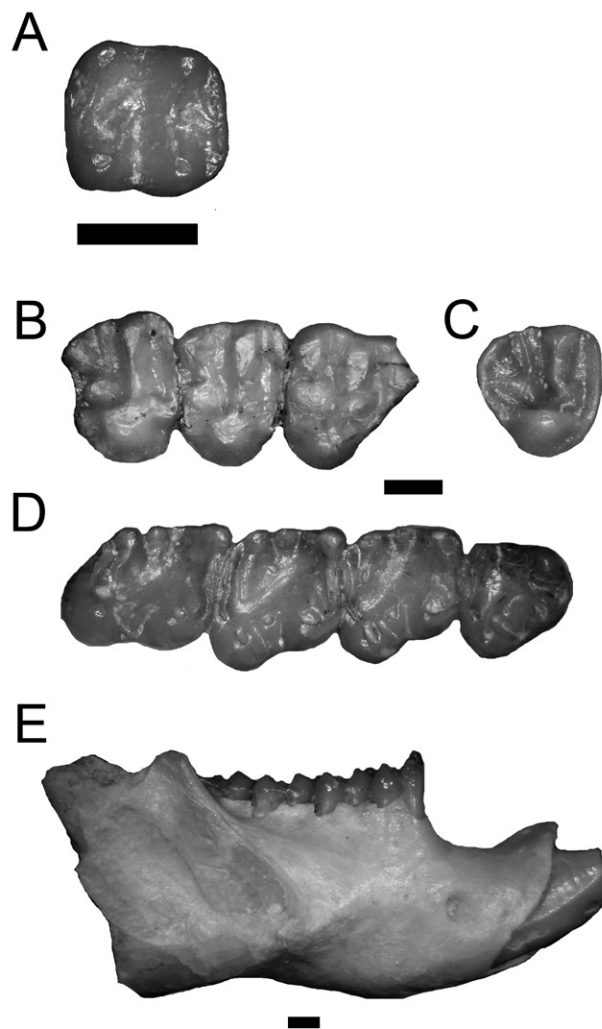


FIGURE 3. Dentition and dentary of cf. *Microparamys* sp. and *Prosciurus hogansoni* from Fitterer Ranch: (A) cf. *Microparamys* sp., NDGS 2282, right m1 or m2; (B)–(E) *P. hogansoni*; (B) NDGS 2720, right P4–M2 (holotype); (C) NDGS 2233, right M3; and (D) NDGS 1855, right p4–m3; (E) NDGS 1855, lateral view of dentary. Bar scales = 1 mm; note different bar lengths in A, B–D, and E.

most closely approaches the size and morphology of *Microparamys* sp. cf. *M. minutus* from the Uintan of Southern California (Wilson, 1940 [= *Paramys* cf. *minutus*]; Wood, 1962 [= *Microparamys* sp. D]; Lillegraven, 1977). This latter species has the unique features of the Fitterer Ranch specimen occurring variably in the sample from California but never develops the mesolophid present in NDGS 2282 (Lillegraven, 1977). This is the latest occurrence of *Microparamys* ever reported. Previously, its latest reported occurrence was from the Chadronian of Texas (Wood, 1974; Anderson, 2008).



**FAMILY APLODONTIIDAE BRANDT, 1855****SUBFAMILY PROSCIURINAE WILSON, 1949A****Genus *Prosciurus* Matthew, 1903*****Prosciurus hogansoni*, new species**

FIGURE 3B–E; TABLE A2

**TYPE SPECIMEN.** NDGS 2720, right partial maxilla with P4–M2 (Figure 3B).

**REFERRED SPECIMENS.** NDGS 2308, right P4; NDGS 2087, partial left M1; NDGS 2233, 2653, M3; FAM 145531, NDGS 1855, dentaries with p4–m3; USNM PAL 642808, dentary with p4–m2; NDGS 2556, dentary with m1–m3; NDGS 2527, dentary with m1–m2; NDGS 2519, 2647, partial dentaries with m2–m3; FAM 14552, dentary with m2; NDGS 2324, left p4; NDGS 2323, right m3.

**OCCURRENCE.** Sampling intervals 2, 5, and 6.

**DIAGNOSIS.** Almost the size of *P. vetustus* Matthew, 1903, smaller than *P. magnus* Korth, 2007, larger than all other species; hypolophid on m2–m3 parallels posterior cingulid, never complete to ectolophid; trigonid basin on m1 closed posteriorly by posterior arm of protoconid, open on m2–m3.

**ETYMOLOGY.** Patronym for John Hoganson, emeritus paleontologist of the North Dakota Geological Survey, who helped establish the North Dakota State Fossil Collection and the Paleontological Resource Management Program at the North Dakota Geological Survey.

**DESCRIPTION.** The P4 is typical of prosciurines in that it has an anteriorly expanded anterocone. The paracone is slightly larger than the metacone. There is a small but distinct parastyle along the buccal margin of P4 on the holotype between the anterocone and the paracone (Figure 3B), but it is lacking on NDGS 2308. The anterior cingulum extends from the lingual end of the anterocone along the anterior margin of the tooth, joining the protocone at its anterobuccal corner. There is a minute cusp and slight flexure in the anterior arm of the protocone between it and the lingual end of the anterior cingulum, indicating a minute protocone crest. The paracone is anteroposteriorly compressed, and the protoloph is continuous to the center of the buccal edge of the protocone. The protoloph bends anteriorly near its center to accommodate a protoconule that is not in alignment with the paracone and protocone. There is a minute mesostyle along the buccal margin of the tooth between the paracone and metacone with a low, short lingual mesoloph extending just slightly into the central basin. The metacone is also anteroposteriorly compressed but not as greatly as the paracone. The metaloph extends anterolingually from the metacone, weakly joining the protoloph just buccal to the protocone. The metaconule is circular in occlusal outline and slightly larger than the protoconule. The posterior cingulum runs along the posterior edge of the tooth, extending from the center of the posterior margin of

the metacone to the posterobuccal corner of the protocone. Just posterior to the apex of the protocone is a slight flexure in the cingulum with a minute hypocone.

M1 is approximately equal in size to P4 (Figure 3B, Table A2). The anterior cingulum extends from the anterobuccal corner of the tooth to a point anterior to the apex of the protocone, where it turns posteriorly to join the protocone. In the anterobuccal corner of the cingulum is an anteroposteriorly compressed parastyle. The valley between the anterior cingulum and the protoloph is wide. A distinct protocone crest extends anterobuccally into the valley from the buccal side of the protocone. The metacone and protoloph are similar to those of P4, but the protoconule is much smaller. The mesostyle is more anteroposteriorly elongated than in P4 and does not have the mesoloph attached lingually. The metacone, metaloph, and metaconule are similar to those of P4, but there is a minute second metaconule between the larger (more lingual) one and the metacone. The metaloph is continuous with the center of the buccal side of the protocone, rather than joining the protoloph as in P4. The hypocone is larger and slightly more lingually situated than in P4.

M2 is generally similar to M1. However, the protoconule is smaller, being barely recognizable within the protoloph. The mesostyle has a low loph extending lingually from it that bends posteriorly and joins the metaloph at a minute second metaconule along the buccal edge of the larger metaconule.

M3 is nearly circular in occlusal outline and smaller than M1 and M2 (Figure 3C, Table A2). The anterior cingulum is as in the anterior molars, but there is no indication of a parastyle. The protocone is transversely compressed. The protoloph is as in the anterior molars, but there is no recognizable protoconule, just a sharp anterior flexure along its center. On NDGS 2653 is a minute lophule that extends anteriorly from the flexure. A distinct protocone crest is present. The posterior half of the tooth is greatly reduced relative to M1 and M2. A minute mesostyle is present but much smaller than the other molars. There is no metacone. The metaloph starts as a narrow, transversely oriented ridge from near the buccal edge of the tooth (just posterior to the mesostyle), then bends posteriorly near the center of the tooth to join a small, triangular metaconule. Two ridges extend from the metaconule; anteriorly, a ridge extends lingually to join the buccal side of the protocone near its center, and posteriorly, a ridge extends posteriorly and slightly buccally to join the posterior cingulum. The posterior cingulum originates at the posterobuccal corner of the protocone and wraps around the posterobuccal side of the tooth, ending along the buccal margin, just posterior to the mesostyle. The hypocone is only a minute cusplike posterior to the protocone at the lingual end of the posterior cingulum. There is a minute lophule in the posterobuccal corner of the tooth between the metaloph and the loph extending posteriorly from the metaconule.

The lower dentitions from Fitterer Ranch were assigned to this species on the basis of size and morphology similar to that of other species of the genus. The dentary does not differ markedly

from other prosciurines (Figure 3E). The masseteric scar ends anteriorly in a narrow U shape below the boundary between m1 and m2. The posterior edge of the diastema dips downward sharply at the anterior root of p4 but curves gently upward to the posterior alveolus of the lower incisor. The mental foramen is approximately at mid-depth of the dentary, just anterior to the posterior margin of the diastema.

The p4 is the smallest of the lower cheek teeth with a trigonid much narrower than the talonid (Figure 3D, Table A2). The trigonid is dominated by the two major cusps (metaconid, protoconid) that are of approximately equal size. The metaconid extends slightly more anteriorly than the protoconid; both are round to ovate in occlusal outline. The trigonid basin is a narrow valley separating these cusps. A minute anterostylid is always present near the center of the anterior opening of the trigonid basin and is attached to a low lophid that attaches to the antero-buccal side of the protoconid. Posteriorly, the trigonid is always closed by the metalophid II, which is complete from the protoconid to the metaconid. The ectolophid is complete from the protoconid to the hypoconid with a large mesoconid at its center but is not straight. The posterior arm of the protoconid and anterior arm of the hypoconid both extend lingually and join the anterior and posterior edges of the mesoconid, respectively. A small lophid extends buccally from the mesoconid that varies in size. The hypoconid is the largest of the cusps and is slightly obliquely compressed (anterolingual-posterobuccal). The entoconid is anteroposteriorly compressed. A distinct mesoconid is always present midway between the metaconid and entoconid. The hypolophid runs buccally from the entoconid, always fusing with the posterolophid near its center. The posterior cingulid originates at the hypoconid and wraps around the posterior margin of the tooth to the entoconid.

The m1 is more nearly rectangular in occlusal outline than p4, but the anterior width (trigonid) is slightly narrower than the posterior width (Figure 3D). The metaconid and protoconid are spaced farther apart than in p4, and the metalophid I is complete along the anterior edge of the tooth. The metaconid is slightly anteroposteriorly compressed, but the protoconid is not. The posterior arm of the protoconid (metalophid II) extends lingually to the base of the metaconid, enclosing the trigonid basin posteriorly. The trigonid basin is small and anteroposteriorly compressed. The remainder of the tooth is similar to that of p4 except that the posterolophid is separated at its lingual end from the entoconid by a narrow valley. The hypolophid bends posteriorly but is variable in that it can end as in p4 near the center of the posterolophid or can extend more buccally, paralleling the posterolophid and ending short of the ectolophid.

The m2 is slightly larger than m1 but is nearly identical in occlusal morphology. The trigonid basin on m2 is always open posteriorly, unlike m1, because the posterior arm of the protoconid never extends far enough lingually to meet the base of the metaconid.

The m3 is the longest of the molars (Figure 3D). The anterior part of the tooth is similar to those of m1 and m2, but the

metaconid is slightly more anteroposteriorly compressed. The trigonid basin is open posteriorly as in m2. The ectolophid is also similar to that of the anterior molars, but the hypoconid is relatively smaller and does not extend buccally as far as in m1 and m2. There is an accessory, minute metastylid anterior to the larger, central mesostylid that is attached to the posterior arm of the metaconid. The hypolophid is similar to that of m2. The posterolophid bows posteriorly much more than in the anterior molars, elongating the tooth.

**DISCUSSION.** This species is clearly referable to *Prosciurus* on the basis of the diagnosis of Vianey-Liaude et al. (2013): P4 subequal to M1 in size, protoconule reduced, metaconule doubled, and metaloph continuous with protocone on upper molars; hypolophid curves posteriorly, variably fusing with the posterolophid, never complete to the ectolophid on the lower molars.

*Prosciurus hogansoni* differs from other species of the genus in being larger than *P. parvus* (Korth, 1989a: table 2) and smaller than *P. magnus* (Korth, 1989a:404, 2009:91). *Prosciurus magnus* lacks the protocone crest present on the upper molars of both *P. vetustus* and *P. hogansoni*. In addition, *P. hogansoni* differs from *P. vetustus* in being slightly larger (Table A2; Wood, 1937:67; Black, 1965:6), having a parastyle on P4, and having a posteriorly closed trigonid basin on m1.

## Genus *Altasciurus* Korth and Tabrum, 2017

### *Altasciurus leonardi*, new species

FIGURE 4; TABLE A3

**TYPE SPECIMEN.** NDGS 2715, left dentary with i1, p4–m3 (Figure 4E).

**REFERRED SPECIMENS.** FAM 96867, 145533, dentaries with p4–m3; FAM 94178, NDGS 1856, dentaries with p4–m2; USNM PAL 642809, FAM 96868, dentaries with m1–m3; FAM 145534, dentary with m1–m2; FAM 96866, dentary with m3; USNM PAL 642814, p4; USNM PAL 642810–642813, NDGS 2656, isolated m2s; FAM 145535, palate with left and right P4–M3; NDGS 2234, maxillary fragment with P4–M1; USNM PAL 642817, NDGS 2299, 2639, isolated P4; USNM PAL 642815, 642816, 642819, NDGS 2294, 2327, isolated M1 or M2; USNM PAL 642818, isolated M3.

**OCCURRENCE.** Sampling intervals 2, 5, and 6.

**DIAGNOSIS.** Close in size to *Prosciurus parvus* Korth, 1989a, smaller than *A. relictus* (Cope, 1873b) and *A. albiclivus* (Korth, 1994a), larger than *A. clausulus* (Korth, 2009). Generic characters: protoconules nearly equal in size to metaconules on upper cheek teeth and metaconules single; hypolophid complete to ectolophid on m2–m3, joins center of posterior cingulid on p4, variable on m1; trigonid basin open posteriorly on lower molars. Specific characters: P4 subequal in size to M1 (P4 larger in *A. albiclivus*); protocone crest lacking on upper molars (present on *A. relictus*); multiple metastylids on lower molars.

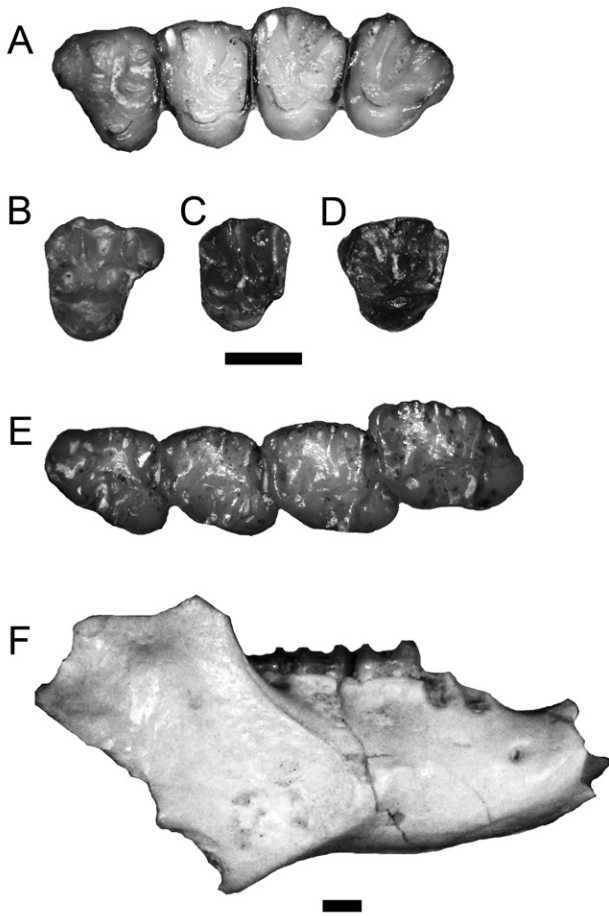


FIGURE 4. Dentition and dentary of *Altasciurus leonardi* from Fitterer Ranch: (A) FAM 145535, left P4–M3; (B) NDGS 2639, right P4; (C) USNM PAL 642815, right M1 or M2; (D) USNM PAL 642818, right M3; (E) NDGS 2715 (holotype), left p4–m3; and (F) USNM PAL 642809, lateral view of dentary. Bar scales = 1 mm; note different bar length in F.

**ETYMOLOGY.** Patronym for Arthur Gray Leonard, the state geologist of North Dakota from 1903 to 1932, who collected some of the first fossils on behalf of the North Dakota Geological Survey.

**DESCRIPTION.** There are no specimens that can be referred to P3 with confidence. The alveolus for P3 is preserved on a few specimens. It is round in outline and positioned lingual to the anterocone of P4.

P4 does not differ greatly from that of other species of the genus (Figure 4A,B). The anterocone is large, D shaped, and limited to the anterobuccal corner of the tooth. A minute parastyle is present on some of the specimens at the posterobuccal corner of the anterocone. The protoloph is continuous from the paracone to the protocone. It runs from the posterolingual edge of the paracone along the posterior side of the protoconule and

joins the center of the buccal side of the protocone via a short loph. There is no indication of a protocone crest, but there is a slight flexure in the anterior cingulum anterior and buccal to the protocone. The protoconule is transversely compressed and only slightly smaller than the metaconule. There is a minute mesostyle at the center of the buccal margin of the tooth, blocking the central transverse valley. On one specimen, FAM 145535, it is attached on its posterior side to the metacone. The metaloph runs from the anterolingual corner of the metacone to the anterobuccal corner of the metaconule. On none of the specimens, including the most heavily worn, NDGS 2234, does the metaloph continue lingually from the metaconule to connect with the protocone or protoloph. The metaconule is slightly larger than the protoconule and slightly transversely compressed but not as much as the protoconule. There is no indication of a hypocone on any specimen. The posterior cingulum runs from the posterior arm of the protocone along the posterior edge of the tooth, ultimately joining the posterior side of the metacone.

M1 is approximately the same width as P4 but is not as long because of the lack of the anterocone (Figure 4A,C). In its place is a small, anteroposteriorly compressed parastyle at the buccal end of the anterior cingulum. The remainder of the occlusal morphology of M1 is similar to that of P4. However, the protoconule is slightly smaller than the metaconule and is less transversely compressed. There is a distinct, but small, hypocone present posterior and slightly buccal to the protocone. A protocone crest is not present on any of the specimens. Only on the most heavily worn specimen, NDGS 2234, does the metaconule connect anteriorly with the protoloph. On this specimen, the anterolingual corner of the metaconule merges with the protoloph and hypocone at the same point. On a few of the specimens, a short spur extends from the metaconule posteriorly or posterolingually, but it never reaches either the metaloph or protocone.

M2 is definitely known from only a single specimen, FAM 145535; all but one of the other specimens are isolated and identified as M1 or M2. The known M2 is slightly larger than the M1, but the occlusal morphology does not differ from M1.

M3 is known from only two specimens, FAM 145535 and USNM PAL 642818 (Figure 4A,D). The anterior half of the tooth is the same as in M1 and M2. The posterior half is greatly reduced and modified. The metacone is reduced to a thin, transverse loph that extends lingually from the buccal edge of the tooth, ending before reaching the lingual side. At its lingual end it joins a loph that runs slightly obliquely, extending anteriorly from the posterior margin of the tooth. There is no hypocone, but there is a bend in the posterior cingulum along the posterior margin of the tooth in its place.

The most complete dentary is USNM PAL 642809, which retains most of the bone, including much of the ascending ramus (Figure 4F). The masseteric scar is similar to that of other species, ending anteriorly below the boundary between m1 and m2 in a U or V shape. However, particularly on USNM PAL 642809, the two margins of the scar fuse below mid-depth of the jaw, lower than in other species. In a few of the specimens, a short

ridge extends slightly more anteriorly from the junction of the dorsal and ventral ridges. The ascending ramus blocks m3 from lateral view and is separated from the body of the ramus by a wide valley. The base of the incisor is marked by a slight swelling on the ascending ramus approximately level with the tooth row on the lateral side of the jaw.

The lower incisor is longer than wide in cross section and nearly flat anteriorly, similar to that of *A. relictus* (Korth, 1989a:402). On the enamel surface are minute irregularities that run nearly parallel to the length of the incisor. These irregularities appear more pronounced than on incisors of other species.

The p4 is the smallest of the lower cheek teeth and narrower anteriorly than posteriorly (Figure 4E). A minute anteroconid is variably present and can be either isolated from the main cusps or connected by a low loph to the protoconid. One specimen, FAM 94178, lacks an anteroconid but has a distinct ridge running anterolingually from the protoconid in its place. The trigonid is blocked posteriorly by the metalophulid II. The ectolophid is complete from the posterior arm of the protoconid to the anterior arm of the hypoconid. The mesoconid is relatively large but smaller than the main cusps. The buccal slope of the mesoconid extends buccally, sometimes forming a distinct buccal mesolophid. The hypoconid is the largest of the cusps and obliquely compressed. It is continuous with the posterior cingulid that wraps around the posterior margin of the tooth, ending just posterior to the posterolingual side of the entoconid. The hypolophid extends buccally from the entoconid and curves slightly posteriorly, joining the center of the posterior cingulid. There is a distinct anteroposteriorly compressed hypoconulid at the center of the posterior cingulid. Along the lingual side of the tooth is a distinct metastylid attached to the lophid extending posteriorly along the lingual edge of the tooth from the metaconid. Anterior to the metastylid is a minute accessory metastylid.

The m1 and m2 are nearly identical and cannot be separated in isolated specimens. In dentaries that contain both, m2 is slightly larger, and the anterior width is nearly equal to the posterior width, wider than in m1. The metaconid is anteroposteriorly compressed and is continuous with the anterior cingulid that runs buccally, attaching to the anterobuccal corner of the protoconid. The posterior arm of the protoconid extends lingually but never reaches the base of the metaconid, leaving the anteroposteriorly compressed trigonid basin open at its posterolingual end. The ectolophid, mesoconid, and posterior cingulid are as in p4. The entoconid is anteroposteriorly compressed, and the hypolophid extends buccally, sometimes curving posteriorly and fusing with the posterior cingulid or curving slightly anteriorly and fusing with the ectolophid, just posterior to the mesoconid. The metastylids are as in p4, a larger one separated from the entoconid by a deep notch and a smaller one anterior to it along the lophid extending posteriorly from the metaconid along the lingual side of the tooth. In some specimens, a short lophulid extends buccally from the larger metastylid (=mesolophid?).

The m2 is nearly identical to m1, but the trigonid is slightly wider and less compressed than in m1 (Figure 4E).

The hypolophid is always continuous with the ectolophid. The doubled metastylids are as in m1. In more worn specimens, the anterior, smaller metastylid is eliminated.

The m3 is the largest of the lower molars, being elongated posteriorly. The anterior part of the tooth is similar to that of m1 and m2, but the metaconid is more anteroposteriorly compressed, and the trigonid basin is more open posteriorly. The mesoconid and ectolophid also echo the morphology of m1 and m2, but the ectolophid is longer. The hypoconid extends much farther posteriorly than in the anterior molars and is positioned more lingually. The entoconid and hypolophid are as in m2. There are always three metastylids on the lingual side of the tooth, continuous with the metaconid. The most posterior one is the largest and is separated from the entoconid as in m1 and m2.

**DISCUSSION.** Although similar in size to those of *Prosciurus parvus*, the cheek teeth of *A. leonardi* differ from those of the former by the morphologies separating these two genera presented by Vianey-Liaude et al. (2013) and Korth and Tabrum (2017). The only morphology that is not consistent with the diagnoses of these two genera is the single metaconule on the upper molars of *P. parvus* (Korth, 1989a: fig. 1B), a character otherwise limited to *Altasciurus*.

The multiple mesostylids on the lower cheek teeth are similar to those of *Campestrallomys annectens* Korth (1989a: fig. 4A,B) from the Orellan of Nebraska. However, m1 and m2 of *C. annectens* are wider than long (Korth, 1989a: table 3), and those of *A. leonardi* are longer than wide or of equal dimensions (Table A3). The upper molars of *C. annectens* have a partial ectoloph connecting the paracone to the mesostyle that is not present in *A. leonardi*.

Other than size (smaller than *A. relictus* and *A. albiclivus*, larger than *A. clausulus*; Korth, 1989a: table 1, 1994a: table 1, 2009: table 1), *A. leonardi* differs from all other species of the genus in the presence of multiple metastylids on the lower molars. It also lacks the protocone crest usually present on upper molars of *A. relictus* (Wood, 1937; Rensberger, 1975; Korth, 1989a).

## FAMILY SCIURIDAE FISCHER DE WALDHEIM, 1817

### SUBFAMILY SCIURINAE FISCHER DE WALDHEIM, 1817

#### Genus *Hesperopetes* Emry and Korth, 2007

#### *Hesperopetes* cf. *H. blacki* Emry and Korth, 2007

FIGURE 5

**REFERRED SPECIMENS.** NDGS 2721, P4; USNM PAL 642821, NDGS 2303, M1 or M2; USNM PAL 642983, p4; USNM PAL 642820, m3.

**OCCURRENCE.** Sampling intervals 2 and 6.

**DESCRIPTION.** NDGS 2721 is a little-worn P4 (Figure 5A; L = 1.18 mm; W = 1.23 mm). The central basin of the

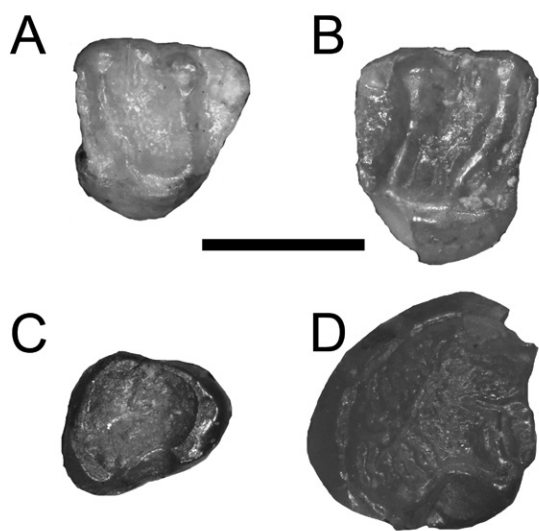


FIGURE 5. Cheek teeth of *Hesperopetes* cf. *H. blacki*: (A) NGS 2721, right P4; (B) NDGS 2303, left M1 or M2; (C) USNM PAL 642983, right p4; and (D) USNM PAL 642820, right m3. Bar scale = 1 mm.

tooth has minute crenulations of the enamel. The anterior cingulum extends nearly the entire width of the tooth, ending lingually even with the center of the protocone. Although the tooth has some breakage at the anterobuccal corner, the parastyle extends anteriorly, making the valley between the anterior cingulum and the protoloph very wide at its buccal end. The buccal cusps (paracone, metacone) are anteroposteriorly compressed. A distinct mesostyle is present along the center of the buccal margin of the tooth, separated from the buccal cusps by narrow valleys and slightly closer to the paracone than the metacone. The protocone is transversely compressed and anteroposteriorly elongated. The protoloph and metaloph are continuous from the buccal cusps to either end of the protocone, making a broad U shape. There is no indication of any conules on either loph. The hypocone is a slight swelling along the posterior side of the tooth, just posterobuccal to the protocone, and is continuous with the posterior cingulum that extends to the buccal edge of the tooth.

NDGS 2303 is a little-worn M1 or M2 (Figure 5B; L = 1.22 mm; W = 1.45 mm). Its overall morphology is similar to that of P4, but the valley between the protoloph and anterior cingulum is not as wide or expanded anteriorly at the anterobuccal corner. A partial ectoloph connects the paracone to the mesostyle. The only other upper molar referable to this species is a heavily worn M1 or M2, USNM PAL 642821 (L = 1.13 mm; W = 1.22 mm). Although none of the crenulations on the enamel surface are retained, the overall morphology is the same as in NDGS 2303.

The p4, USNM PAL 642983, is much smaller than the m3 (Figure 5C; L = 0.97 mm; W = 0.82 mm) but has faint crenulations in the central basin. All of the cusps are weakly developed. The anterior width is less than the posterior width. The

cusps of the trigonid are observable only as small, circular wear facets. The metaconid is smaller and slightly more anterior than the protoconid. Both cusps are fused together anteriorly. A ridge extends posteriorly from the metaconid along the lingual side of the tooth for half its length. A very thin ectolophid extends posterobuccally from the protoconid, joining the hypoconid posteriorly. The hypoconid and entoconid are similarly poorly developed and connected by the posterior cingulid that wraps around the posterior end of the tooth as a low ridge. A narrow valley separates the entoconid anteriorly from the lophid extending from the metaconid.

The m3, USNM PAL 642820, is nearly equal in length and width (Figure 5D; L = 1.54 mm; W = 1.49 mm). The tooth is slightly damaged, but the damage does not seem to have altered the measurements very much. The enamel surface of the central basin of the tooth has minute crenulations. The metaconid is partially broken away but appears to be the tallest of the cusps in the anterolingual corner of the tooth. The anterior cingulid extends buccally from its base along the anterior edge of the tooth, ending in a minute cusplule anterior to the center of the protoconid. The protoconid is relatively small and anteroposteriorly compressed. A short but distinct posterior arm (metalophulid II) extends directly lingually, ending at the base of the metaconid. The ectolophid is complete from the protoconid to the hypoconid with a flexure in the center but no indication of a mesoconid. The hypoconid is mostly broken away but clearly fills the posterobuccal corner of the tooth, extending slightly more buccally than the protoconid. The entoconid is greatly reduced and partially broken. The posterior cingulid curves around the posterior border of the tooth and is continuous along the lingual side (=entolophid), where it ultimately fuses with the posterior side of the metaconid.

**DISCUSSION.** These specimens are clearly referable to *Hesperopetes* on the basis of the crenulated enamel and reduction of the cusps diagnostic of the genus (Emry and Korth, 2007). In size, the specimens are most similar to *H. blacki* (the smallest species of the genus; Emry and Korth, 2007: table 1). However, no p4s, m3s, or M1s or M2s of *H. blacki* have been described previously (the majority of the specimens from Fitterer Ranch). USNM PAL 642820 differs from m3s of other species of the genus in being nearly as wide as it is long. In other species, m3 is much longer than wide (Emry and Korth, 2007: table 1; Korth, 2014: table 7). The P4 from Fitterer Ranch is slightly smaller than the originally referred specimen of *H. blacki* (Emry and Korth, 2007: fig. 2F) but more molariform with a better-developed hypocone and more widely expanded anterior cingulum. Both the topotypic sample of *H. blacki* and the referred material from Fitterer Ranch are too poorly known to make a definite specific identification on the latter material. The m3 from Fitterer Ranch, USNM PAL 642820, is larger than the other specimens referred here to *H. cf. blacki*. It is possible that it represents an additional, larger species of *Hesperopetes*, but because of the limited number of specimens from this locality and the rarity of the species in general, this possibility cannot be verified.

## SUBFAMILY CEDROMURINAE KORTH AND EMRY, 1991

Genus *Cedromus* Wilson, 1949b*Cedromus wardi* Wilson, 1949b

FIGURE 6

REFERRED SPECIMENS. NDGS 2508, partial right maxilla with M2 (partial) to M3; FAM 65762, left maxilla with P3–M2.

OCCURRENCE. Sampling interval 5 only.

MEASUREMENTS. NDGS 2508: M2, W = 2.41 mm; M3, L = 2.44 mm, W = 2.56 mm. FAM 65762: P3, L = 1.09 mm, W = 1.13 mm; P4, L = 2.73 mm, W = 2.91 mm; M1, L = 2.54 mm, W = 2.91 mm; M2, L = 2.36 mm, W = 3.27 mm.

DESCRIPTION. The P3 is nearly circular in occlusal outline and conical in shape. A low ridge runs from the apex of the cusp posterobuccally to the posterior margin of the tooth. Along the lingual side of the tooth is a minute cingulum (Figure 6A).

P4 through M2 are nearly equal in size. The buccal margin of P4 is lengthened by the anterior extension of the anterior cingulum along the buccal side. There is no evidence of a parastyle, but the anterior cingulum bows anteriorly at the anterobuccal corner, forming a large basin between it and the paracone. The anterior cingulum continues lingually from the anterobuccal corner of the tooth and joins the base of the protocone at its lingual end. The paracone is ovate (transversely elongated) and continuous with the protoloph that runs lingually to join the protocone. There is no indication of a protoconule. The metacone is slightly transversely compressed. It is connected anteriorly by an ectoloph that runs directly anterior to join the center of the paracone. At the center of the ectoloph, a short loph extends buccally to the edge of the tooth, where it joins a small mesostyle. The metaloph extends from the anterolingual corner of the metacone and joins the metaconule along its anterior side. The metaconule is also ovate and nearly as large as the metacone. The metaloph continues from the metaconule as a low loph that joins the posterobuccal corner of the protocone. The protocone is the largest of the cusps and is crescentic in occlusal outline. The posterior cingulum extends posteriorly from the apex of the protocone, curves buccally at the posterolingual corner of the tooth, and continues buccally along the posterior margin of the tooth to the metacone.

The only M1 in the Fitterer Ranch sample is on FAM 65762, and it is partially broken along the buccal edge. In overall morphology it is similar to P4 but lacks the expanded anterior cingulum at the anterobuccal corner of the tooth. The ectoloph is preserved on only the posterior half of the tooth. It originates at the posterior edge of the tooth, even with the apex of the metacone, runs directly anteriorly across the metacone, and then curves buccally at the center of the tooth. As in P4, there is no indication of a protoconule in the protoloph. The metaconule is as large as the metacone and circular in occlusal outline. The metaloph ends at the metaconule, isolating the metaconule from the protocone.

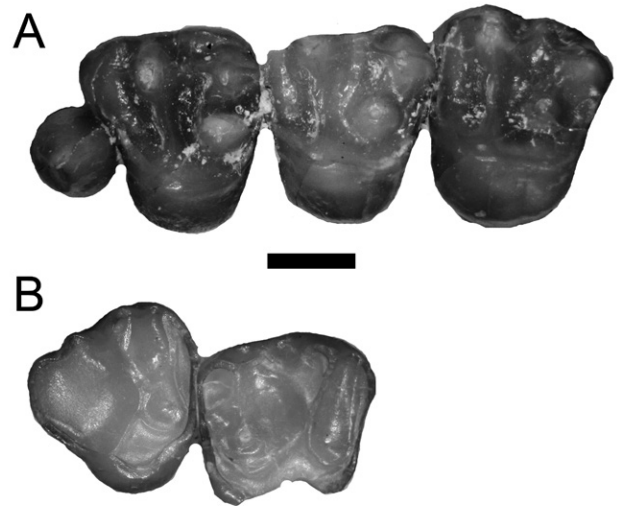


FIGURE 6. Upper cheek teeth of *Cedromus wardi* from Fitterer Ranch: (A) FAM 65762, left maxilla with P3–M2, and (B) NDGS 2508, partial right maxilla with M2 (partial) to M3. Bar scale = 1 mm.

All other features are as in P4. There is no distinct hypocone, but there is a slight swelling on the posterior cingulum at the posterolingual corner of the tooth, posterior to the protocone.

M2 is similar in size and morphology to M1. The ectoloph is complete on both known specimens, and the mesostyle is central along the buccal edge of the tooth, joined by curving ridges from both the paracone and metacone. As in M1, the metaconule is separated from the protocone even on the heavily worn specimen, NDGS 2508 (Figure 6B).

M3 is smaller than the anterior molars and nearly triangular in occlusal outline (Figure 6B). The anterior cingulum and protoloph are as in M1 and M2, but there is a slight flexure in the protoloph near its center with a slight swelling (=protoconule). The paracone is smaller than in M1 and M2 and more anteroposteriorly compressed. The mesostyle is a minute cusp at the center of the buccal edge of the tooth. There appears to be a minute curving ectoloph connecting the paracone to the mesostyle, but it is obscured by wear. The posterior half of the tooth is a simple, broad basin. There is no indication of a hypocone, and the metacone is a minute cusp at the posterobuccal corner of the tooth.

DISCUSSION. The Fitterer Ranch specimens do not differ in size or morphology from previously described upper cheek teeth of *Cedromus wardi* (Wood, 1937: fig. 19 [=Prosciurus sp.]; Galbreath, 1953: pl. 2, fig. C; Korth and Emry, 1991: fig. 5.1). Although Galbreath (1953) originally referred a partial skull with cheek teeth only questionably to this species, the occurrence of associated upper and lower dentitions of *C. wilsoni* from Wyoming has verified his allocation (Korth and Emry, 1991). The Fitterer Ranch specimens are similar to *C. wardi* and differ from *C. wilsoni* by their slightly larger size and complete

ectoloph on the upper molars. The Whitneyan species *C. woodi* Korth, 2015 is larger than *C. wardi* (Wilson, 1949b:32; Korth, 2015: table 1). *Cedromus wardi* is elsewhere known from the Orellan of South Dakota, Colorado, and Nebraska (Goodwin, 2008; Korth, 2015).

## FAMILY CASTORIDAE HEMPRICH, 1820

### Genus *Agnotocastor* Stirton, 1935

**DISCUSSION.** Recently, Li et al. (2017) included most of the North American species previously referred to *Agnotocastor* in the Asian genus *Propalaeocastor* Borisoglebskaya, 1967, retaining only the type species of *Agnotocastor*, *A. praetereadens* Stirton, 1935, in the latter genus. They included only the Eurasian *A. devius* Lytschev and Shevyreva, 1994 in the genus along with the type species. Li et al.'s (2017:8) diagnosis of *Propalaeocastor* included mainly primitive characters but also the unilateral mesodonty of the upper cheek teeth and complex occlusal pattern of all the cheek teeth. Li et al. (2017) separated *Agnotocastor* from *Propalaeocastor* by the simpler occlusal pattern of the cheek teeth of the former. However, *Agnotocastor* was separated from *Propalaeocastor* on the basis of a comparison with only the holotype of *A. praetereadens*, a partial cranium that has heavily worn cheek teeth (Stirton, 1935: fig. 13). Li et al. (2017) apparently did not include the large sample of *A. coloradensis* reported by Galbreath (1953) and possibly topotypic specimens of *A. praetereadens* described from the Whitneyan of South Dakota (Korth, 2014). In these larger samples of *Agnotocastor* (including specimens described herein) it is evident that the cheek teeth contain the more complex occlusal morphology and are not simplified. None of the North American species previously referred to *Agnotocastor* have the unilateral mesodonty (=unilateral hypsodonty) that is present in the upper cheek teeth of *Propalaeocastor* (Li et al., 2017: fig. 4). The buccal height of the upper cheek teeth is typically less than the lingual height on all castorids, but the disparity is much less in *Agnotocastor* than in *Propalaeocastor* or other castorids such as anchitheriomysines. All of the other North American species previously referred to *Agnotocastor* (*A. coloradensis* Galbreath, 1953; *A. galushai* Emry, 1972; *A. readingi* Korth, 1988) should be retained in this genus along with the type species.

No specimens of the Eurasian species cited by Li et al. (2017) have been directly examined as part of this study. However, on the basis of the available figures, *A. devius* appears to have a much simpler occlusal morphology than any other species of either *Agnotocastor* or *Propalaeocastor* (Li et al., 2017: fig. 9) and is not likely referable to either genus.

### *Agnotocastor praetereadens* Stirton, 1935

FIGURE 7; TABLE A4

**REFERRED SPECIMENS.** USNM PAL 648205, right maxilla with P4–M1 and left dentary with m1–m2; USNM PAL 642974, maxilla with P3–M1; FAM 94998, maxilla with P3–P4;

NDGS 2512, maxilla with P4–M2; FAM 96418, maxilla with P4–M3; FAM 96419, NDGS 2513, 2623, P4; NDGS 2531, maxilla with M1–M3; FAM 64079, NDGS 2514, partial maxillae with M2–M3; NDGS 2521, 2522, 2524, 2551, 2671, 2686, M1 or M2; NDGS 2526, M3; NDGS 2511, right dentary with p4–m3, left dentary with p4–m1 and associated upper and lower incisors; FAM 64076–64078, NDGS 2515, dentaries with p4–m3; FAM 95000, dentary with p4–m2; FAM 94991, NDGS 2718, partial dentaries with p4–m1; USNM PAL 642975, right dentary with dp4–m1; NDGS 2667, dp4; FAM 94999, 64081, NDGS 2614, partial dentaries with p4; FAM 94903, isolated left p4; USNM PAL 642806, FAM 64075, dentaries with m1–m3; FAM 64080, right dentary fragment with m1; USNM PAL 642807, NDGS 2523, 2657, m1 or m2.

**OCCURRENCE.** Single specimen from sampling interval 6; all others from sampling interval 5.

**DESCRIPTION.** P3 is preserved only in USNM PAL 642974 (Figure 7B). It is circular in occlusal outline and basically conical in shape. However, the apex of the crown is along the anterobuccal side of the tooth and is obliquely compressed (anterobuccal-posterolingual). Posterior to this cusp are small, low ridges that define a minute hypoflexus that is directed posterobuccally and a metaflexus that is completely enclosed and extends for most of the width of the tooth.

P4 is the largest of the upper cheek teeth. It is roughly rectangular in occlusal outline and slightly wider than long. In the least worn specimens, USNM PAL 642974 and NDGS 2512 (Figure 7A,B), the major lophs (protoloph, metaloph, mesoloph) and cingula are recognizable, but the valleys that separate them are divided by numerous smaller lophules. The anterior cingulum extends from near the center of the anterior border to the buccal edge of the tooth. The buccal cusps (paracone, metacone) are anteroposteriorly compressed, and the lingual cusps (protocone, hypocone) are crescentic. The mesoloph is a thin ridge that runs buccally from the posterobuccal corner of the protocone to the buccal edge of the tooth, fusing anteriorly with the posterior edge of the paracone. The mesoflexus extends for over half the width of the tooth and is slightly curved posteriorly at its lingual end. The posterior cingulum is continuous from the posterobuccal side of the hypocone to the posterolingual side of the metacone. On the specimen with the heaviest degree of wear, FAM 96418 (Figure 7C), all of the fossettes and flexi are still recognizable. The lingual height of the crown is slightly greater than the buccal in unworn specimens, but it is not a marked difference. This difference in crown-height is true for all of the upper cheek teeth.

M1 and M2 are nearly identical to one another and slightly smaller than P4 in the little- to moderately worn specimens. The teeth are markedly shorter than wide even in the little-worn specimens. In overall occlusal morphology they are similar to P4, but the lingual cusps are more obliquely compressed (anterolingual-posterobuccal) than in P4. The number of accessory lophules that cross the valleys is smaller, making the fossettes less complex than in P4. On the heavily worn specimen, only three fossettes remain, the hypofossette, mesofossette, and parafofsette. The former two are elongated; the latter is roughly circular in outline.

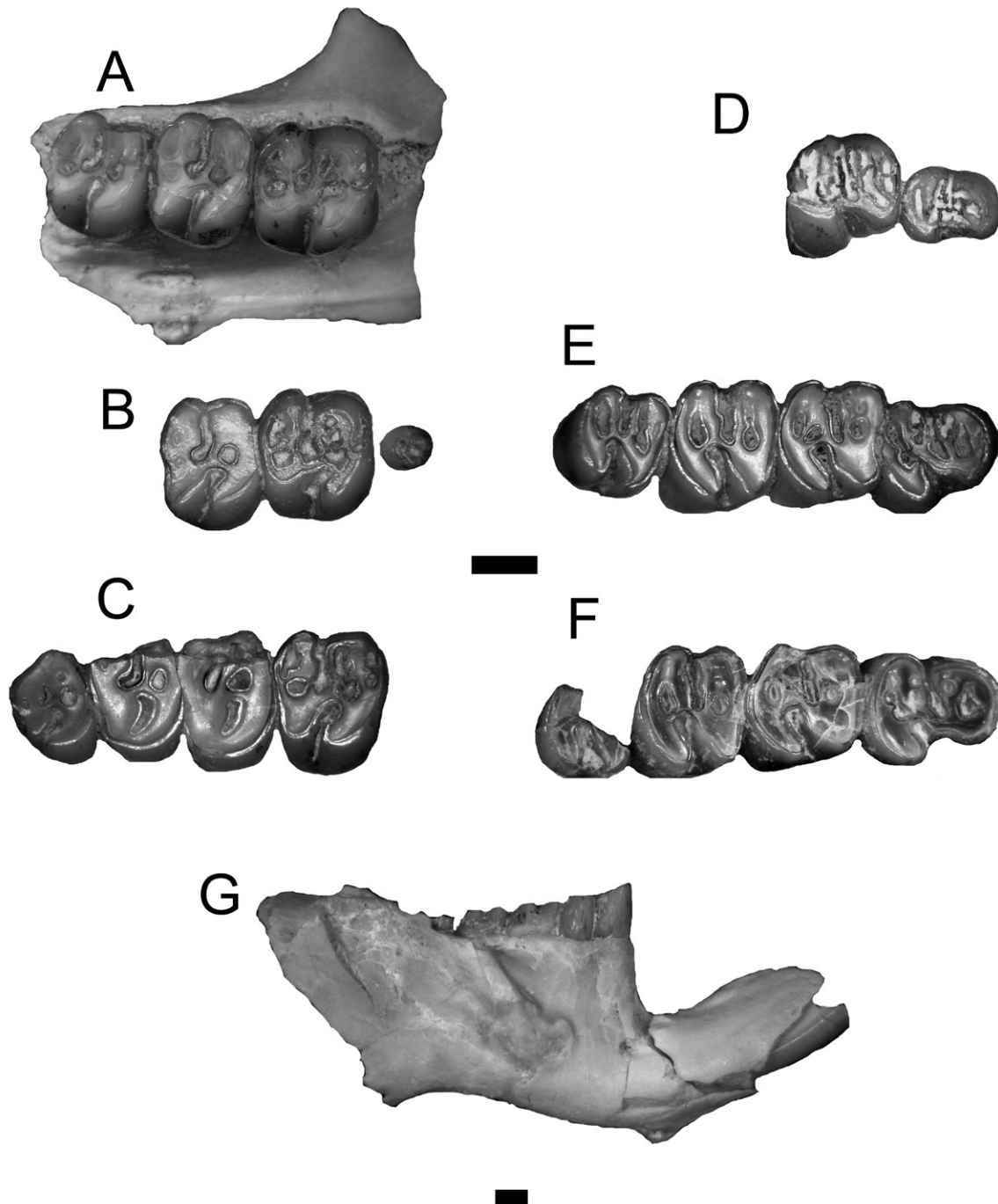


FIGURE 7. Dentitions of *Agnotocastor praetereadens* from Fitterer Ranch: (A) NDGS 2512, left maxilla with P4–M2 (reversed); (B) USNM PAL 642974, right P3–M1; (C) FAM 96418, right P4–M3; (D) USNM PAL 642975, right dp4–m1; (E) FAM 64077, left p4–m3 (reversed); (F) NDGS 2511, right p4–m3 (partial); and (G) NDGS 2511, right lateral view of dentary. Bar scales = 2 mm; note different bar length in G.

M3 is the smallest of the upper cheek teeth and approximately oval in occlusal outline, wider anteriorly than posteriorly. In the least worn specimen, NDGS 2514, the only flexi present are a deep mesoflexus that extends lingually for more than half the width of the tooth, curving posteriorly at its lingual end, and a

shallow hypoflexus oriented roughly anterobuccally. There are six enamel fossettes, two on the posterior half of the tooth between the hypocone and metacone and four on the anterior half. All of the major cusps are greatly reduced in size, with the protocone being the largest. On the most worn specimen, FAM 96418, the



hypoflexus extends deeper into the center of the tooth, and the number of fossettes is reduced to four: two on the anterior half that are circular in outline, a central crescentic one, and a minute one near the posterobuccal corner of the tooth (Figure 7C).

The dentary is similar to that of other species in being deep with a pronounced digastric process and a deep diastema (Figure 7G). The masseteric fossa ends anteriorly below the posterior root of p4 with a strong dorsal ridge extending posteriorly to the anterior edge of the ascending ramus. In lateral view, the ascending ramus blocks m2 and m3. The mental foramen is low on the dentary, below the anterior root of p4, slightly below the level of the most depressed point of the diastema.

One specimen retains a little-worn dp4, USNM PAL 642975 (Figure 7D). The tooth is smaller than specimens of p4 and smaller than the associated m1. It is lower crowned than m1 and oval in outline, narrower anteriorly than posteriorly. The hypolophid is recognizable as a thin, transverse lophid connecting the entoconid and hypoconid. The ectolophid is a thin lophid along the buccal edge of the tooth connecting the protoconid and hypoconid. Two lophids extend posteriorly from the anterior margin of the tooth, converging posteriorly in a V shape, outlining the trigonid basin. No other distinct lophids are recognizable, merely a complex of thin lophulids. The hypoflexid is extremely shallow.

In size, p4 is longer but narrower than m1 (Table A4). The talonid is wider than the trigonid. The anterior cingulid bows anteriorly across the anterior margin of the tooth, connecting the metaconid and protoconid. Both trigonid cusps are small in size and incorporated into the associated lophids. The protoconid is crescentic in occlusal outline. On unworn or little-worn specimens, the protoconid is continuous with the ectolophid, which extends posterolingually to the entoconid at the posterolingual corner of the tooth (Figure 7E). The hypoflexid extends nearly the entire width of the tooth, ending posterobuccal to the entoconid. The mesoflexid extends from the center of the lingual edge of the tooth to the ectolophid. There are two large enamel fossettids anterior to the mesoflexid and two posterior to it. In worn specimens the hypoflexid is interrupted by a minute lophid extending anteriorly from the hypoconid, but the remainder of the flexid continues as in the unworn specimens (Figure 7F). The accessory fossettids are reduced in size in the more worn specimens, but the mesoflexus remains open and deep until extreme wear.

The m1 and m2 are nearly identical in morphology. Both have crowns that narrow anteroposteriorly ventrally, making the occlusal shape change from being approximately equal in length and width on unworn specimens to being much wider than long in late states of wear. A distinct hypoflexid extends posterolingually from the center of the buccal edge of the tooth for nearly half its width, and a mesoflexid extends buccally from the center of the lingual side of the tooth directly transversely to approximately the center of the tooth. Anterior to the mesoflexid are several small enamel fossettids (as many as four), and posterior to the mesoflexid are generally two small enamel fossettids. As the teeth wear, the number of fossettids decreases, ultimately resulting in a single fossettid anterior to the mesoflexus that is circular in outline and a single posterior fossettid that is slightly

transversely elongated. In very late stages of wear, the mesoflexid becomes a fossettid by the closure of its lingual end.

The m3 is the smallest of the lower molars but is generally similar in morphology to m1 and m2 (Figure 7E). However, the length of the tooth does not decrease with wear as in the anterior molars. The occlusal pattern in unworn specimens is slightly simpler than in unworn specimens with fewer accessory fossettids in the former, but worn specimens ultimately attain the same morphology seen in m1 and m2.

**DISCUSSION.** The specimens of *A. praetereadens* from Fitterer Ranch do not differ in morphology or size from those of the large sample previously described from the Whitneyan of South Dakota (Table A4; Korth, 2014: table 8). The Fitterer Ranch specimens differ from Orellan *A. coloradensis* Wilson, 1949b in being smaller (Galbreath, 1953: table 13). Although the molars are similar in size to those of Chadronian *A. galushai* Emry, 1972 and Orellan *A. readingi* Korth, 1988, *A. praetereadens* differs from both in having p4 larger relative to m1 (Emry, 1972: table 1; Korth, 1988: table 1, 2001: table 1). The upper cheek teeth also have a less complex pattern of fossettids than in *A. readingi* and *A. coloradensis* (Galbreath, 1953: fig. 20; Korth, 2001: fig. 2). *Agnotocastor praetereadens* also differs from *A. readingi* in having a deeper diastema on the dentary and a mesoflexus that curves posteriorly on the upper molars (straight in *A. readingi*).

Murphy et al. (1993) listed *Palaeocastor complexus* (= *Neotocastor hesperus*; Flynn and Jacobs, 2008) as occurring in the Fitterer Ranch fauna. However, that report was based on a misidentification, and all specimens previously referred to *P. complexus* from Fitterer Ranch are here referred to *A. praetereadens*. Previously, *A. praetereadens* has been reported only from the Whitneyan (Stirton, 1935; Korth, 1994b; Flynn and Jacobs, 2008). No specimen referable to this species was found in any of the units below sampling interval 5 at Fitterer Ranch (Figure 1).

## Genus *Oligotheriomys* Korth, 1998

### *Oligotheriomys magnus* (Wood, 1937), new combination

FIGURE 8

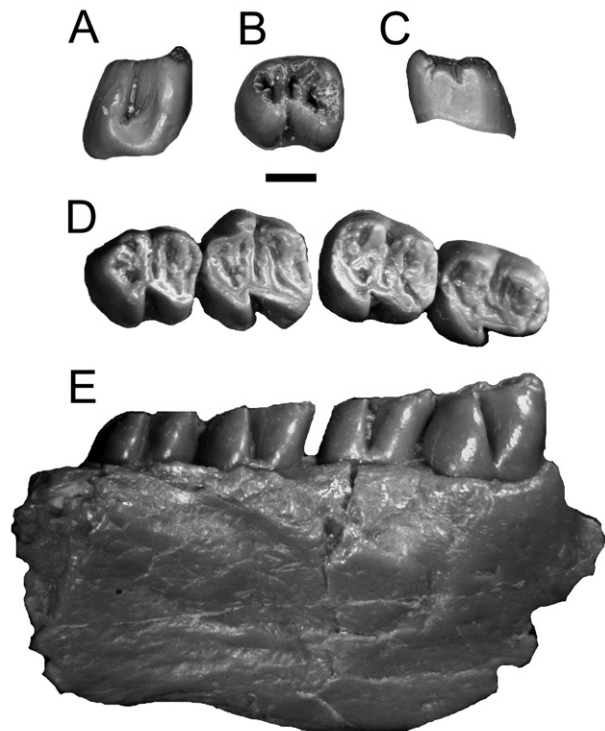
*Eutypomys magnus* Wood, 1937  
 ?*Anchitheriomys magnus* (Wood) Korth, 1994b  
*Oligotheriomys primus* Korth, 1998  
 ?*Oligotheriomys magnus* (Wood) Korth, 2000  
*Propalaeocastor primus* (Korth) Li et al., 2017

**TYPE SPECIMEN.** YPM-PU 13779, right dentary with p4–m3 (Figure 8D,E).

**REFERRED SPECIMENS.** NDGS 2660, right m3; FAM 64016, right maxilla with M1–M2.

**MEASUREMENTS.** NDGS 2660: L = 4.05 mm; W = 3.58 mm; height of the entoconid = 3.03 mm; crown-height index = 0.84.

**OCCURRENCE.** Sampling interval 5 only.



**FIGURE 8.** Holotype and referred specimen of *Oligotheriomys magnus*. (A)–(C) NDGS 2660, right m3: (A) buccal view, (B) occlusal view, and (C) lingual view. (D)–(E) YPM-PU 13779 (holotype, cast): (D) p4–m3, occlusal view, and (E) lateral view of dentary. Bar scale = 2 mm.

**DESCRIPTION.** The occlusal outline of the referred m3, NDGS 2660 (Figure 8B), is nearly rectangular (longer than wide) and convex posteriorly. The occlusal pattern of the tooth consists of recognizable lophids that have multiple wrinkles in the enamel that extend into the basins of the teeth. The metaconid and entoconid are anteroposteriorly compressed, and the buccal cusps (protoconid, hypoconid) are obliquely compressed (posterobuccal-antero-lingual). There are crenulations of the enamel between the metaconid and protoconid, forming a triangular area along the anterior edge of the tooth between these cusps. A complete lophid bows posteriorly and runs from the protoconid to the metaconid, enclosing a crescentic trigonid basin. The hypolophid extends buccally from the entoconid to the ectolophid just anterior to the hypoconid. The ectolophid is highly crenulated, but there is no indication of a mesoconid. There is a triangular mesostylid at the center of the lingual side of the tooth that blocks the central valley (=mesoflexid). The hypoflexid extends for about one-third of the width of the tooth, forming a sharp bend in the ectolophid just anterior to the hypoconid. The posterior cingulid wraps around the posterior edge of the tooth, connecting the hypoconid and entoconid along their posterior sides. Just posterior to the entoconid is a second anteroposteriorly compressed cusp that extends only slightly into the posterior basin between the posterior cingulid and the hypolophid. Korth (2000:

table 2) calculated a crown-height index of *Eutypomys* lower molars by dividing the height of the entoconid by the maximum width of the tooth (Figure 8A,C). This index for NDGS 2660 is 0.84, markedly higher than that for the m3 of species of *Eutypomys* (0.36–0.52). The crown-height index of the type specimen of “*E.*” *magnus* was given as 0.63; however, the specimen is slightly worn (Figure 8D,E). The M1–M2 of this species (= *O. primus*) has been illustrated and described elsewhere (Korth, 1998).

**DISCUSSION.** The isolated lower molar NDGS 2660 is referred to *O. magnus* on the basis of its size and the complexity of its occlusal surface. In overall morphology it most closely approaches that of the m3 of “*Eutypomys*” *magnus* Wood, 1937 but is slightly larger and higher crowned (Figure 8). Korth (2000) suggested that “*E.*” *magnus* might have been included in *Oligotheriomys* but did so questionably because it was known from only lower dentition and the type species of *Oligotheriomys*, *O. primus*, was known from only an upper dentition. The Fitterer Ranch specimen of m3 is markedly similar to that of the holotype (and only known specimen) of “*E.*” *magnus*. The Fitterer Ranch specimen verifies the allocation of “*E.*” *magnus* to *Oligotheriomys*. The holotype of *O. primus* is also from Fitterer Ranch (Korth, 1998), making the assignment of the m3 to this species more likely. The similarity of NDGS 2660 to the m3 of the holotype of “*E.*” *magnus* suggests that the upper dentition originally referred to *O. primus* is also referable to “*E.*” *magnus*, making the former a junior synonym of the latter but maintaining the generic identification as *Oligotheriomys*.

Li et al. (2017) included “*O. primus*” in Eurasian *Propalaeocastor*. *Oligotheriomys* does possess the unilateral mesodonty of the upper molars and complex occlusal pattern observed in *Propalaeocastor* but lacks the diagnostic character of “metaflexus buccally open” of the latter (Li et al., 2017:8) and has an overall greater complexity. In addition, the hypoflexus of the holotype of “*O. primus*” is much shallower than in any illustrated specimen of *Propalaeocastor* (Korth, 1998: fig. 1; Wu et al., 2004; Li et al., 2017: fig. 4). Similarly, the lower molars of *O. magnus* have a more complex occlusal pattern than *Propalaeocastor*, and the diastema of the dentary is not as deep in *O. magnus* (Figure 8E; Li et al., 2017: fig. 6). The lower incisor of *O. magnus* is much narrower (transversely) and is not nearly as flattened anteriorly as in *Propalaeocastor* (Li et al., 2017: fig. 7C). Because of these differences, *O. magnus* (= *O. primus*) should be retained in its own genus.

#### **FAMILY EOMYIDAE WINGE, 1887**

#### **Genus *Adjidaumo* Hay, 1899**

#### ***Adjidaumo minimus* (Matthew, 1903)**

FIGURES 9A–D, 10; TABLE A5

**REFERRED SPECIMENS.** FAM 145539, 94926, NDGS 1858, 2202, 2310, 2693, USNM PAL 643370, 643393, 643415, dentary with p4–m3; NDGS 2643, USNM PAL 643408, 643410, 643418, 643436, dentary with p4–m2; NDGS 2022,

USNM PAL 643339, 643394, 643396, 643422, dentary with p4–m1; USNM PAL 643392, dentary with dp4–m1; NDGS 2568, FAM 94927, dentary with p4; NDGS 2050, 2218, 2583, USNM PAL 643412, dentary with m1–m3; USNM PAL 643383, 643388, 643390, 643405, 643409, 643413, 643421, 643425, NDGS 2025, 2208, 2651, dentary with m1–m2; USNM PAL 643378, 643398, 643403, 643414, 643417, 643420, 643428, dentary with m2–m3; USNM PAL 643215, 643245, 643253, 643292, dp4; NDGS 2001, 2002, 2010, 2011, 2019, 2043, 2066, 2221, 2287, 2329, USNM PAL 643199, 643206, 643222, 643227, 643229, 643237, 643264, 643272, 643285, 643293, 643294, 643296, 643311, 643322, 643349, 643357, 643369, 643371, 643384, 643385, 643399, 643400, 643407, 643426, 643434, p4; NDGS 1999, 2006, 2008, 2021, 2023, 2028, 2031, 2034, 2039, 2044, 2045, 2049, 2051, 2056, 2060, 2062, 2067, 2080, 2213, 2217, 2219, 2230, 2240, 2289, 2293, 2306, 2330, USNM PAL 643087, 643184, 643187–643191, 643193–643196, 643201–643205, 643207–643214, 643216–643218, 643220, 643224, 643226, 643228, 643230–643233, 643236, 643238–643240, 643242–643244, 643247, 643254–643258, 643260–643262, 643266–643271, 643273–643283, 643286–643291, 643295, 643297, 643299, 643301–643309, 643312, 643313, 643315, 643316, 643318–643321, 643344, 643346, 643348, 643353–643356, 643359, 643361, 643363, 643367, 643368, 643372, 643376, 643381, 643386, 643397, 643401, 643404, 643419, 643424, m1 or m2; NDGS 1995, 1998, 2206, 2214, USNM PAL 643185, 643186, 643192, 643197, 643198, 643200, 643219, 643221, 643223, 643225, 643234, 643235, 643241, 643246, 643248–643252, 643259, 643263, 643265, 643284, 643298, 643310, 643314, 643317, 643402, m3; NDGS 2302, 2650, maxilla with P4–M3; NDGS 2642, USNM PAL 643365, 643379, 643423, maxilla with P4–M2; NDGS 2300, 2648, USNM PAL 643352, 643358, 643411, maxilla with P4–M1; USNM PAL 643380, maxilla with P4, M2; USNM PAL 643430, maxilla with M1–M3; USNM PAL 643416, maxilla with M1–M2; USNM PAL 643343, 643427, maxilla with M2–M3; USNM PAL 643435, maxilla with M2–M3 and isolated dP4, P4, three M1s or M2s; USNM PAL 642989, 642998, 643005, 643027, 643054, 643063, 643064, 643076, 643111, 643118, 643132, dP4; NDGS 2004, 2009, 2014, 2041, 2042, USNM PAL 642988, 642994, 643011, 643012, 643024, 643039, 643044, 643049, 643057, 643067, 643082, 643083, 643086, 643102, 643103, 643108, 643109, 643130, 643146, 643147, 643153, 643345, 643347, 643373–643375, 643382, 643406, 643432, 643433, P4; NDGS 2052, 2053, 2057, 2061, 2068, 2069, 2209, 2216, 2288, 2295, 2297, USNM PAL 642990–642993, 642995–642997, 642999, 643000, 643002–643004, 643006, 643008–643010, 643013, 643021, 643023, 643025, 643026, 643028, 643035–643038, 643040–643043, 643045–643048, 643050–643053, 643055, 643056, 643058–643062, 643065, 643066, 643074, 643077–643081, 643084, 643085, 643091, 643094–643101, 643104–643107, 643110, 643112–643117, 643119–643129, 643131, 643133–643145, 643148, 643150–643152, 643154–643160, 643350, 643351, 643360, 643362, 643364,

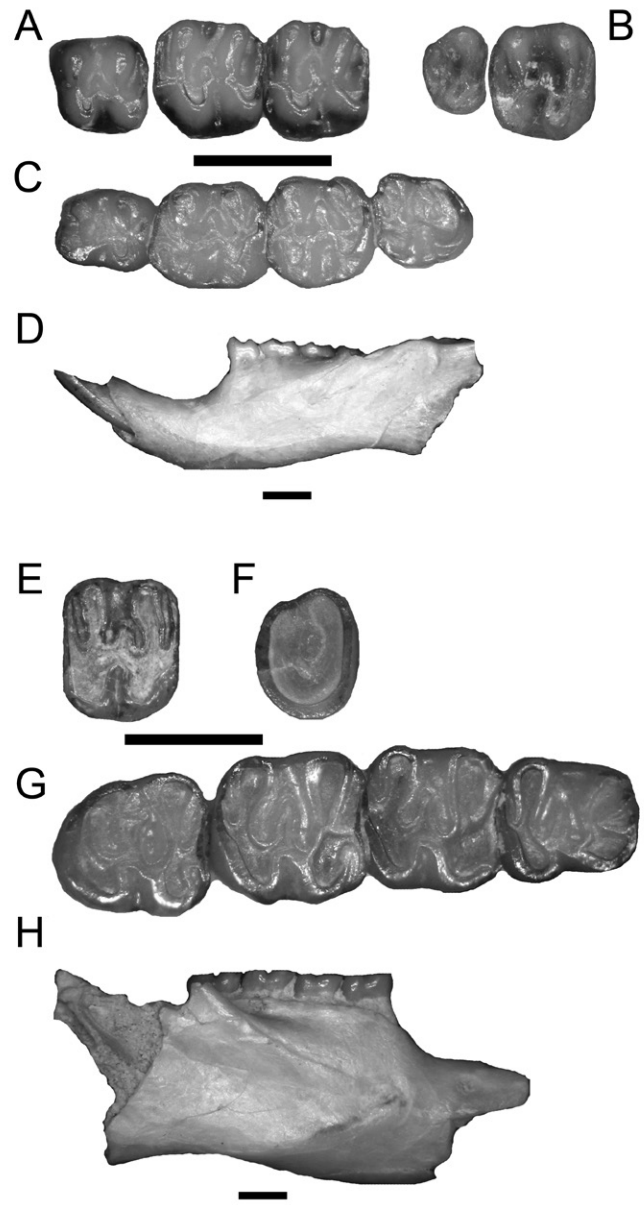


FIGURE 9. Dentition and dentary of *Adjidaumo* from Fitterer Ranch. (A)–(D) *Adjidaumo minimus*: (A) NDGS 2642, left P4–M2; (B) USNM PAL 643435, right M2–M3; (C) NDGS 2693, occlusal view of left p4–m3; and (D) NDGS 2693, lateral view of dentary. (E)–(H) *Adjidaumo minimus*: (E) USNM PAL 643391, right M1 or M2; (F) USNM 643391, right M3; (G) USNM PAL 643437, right p4–m3; and (H) USNM PAL 643437, lateral view of dentary. Bar scales = 1 mm; note different bar lengths in D and H compared with A–C and E–G.

643377, 643389, 643431, M1 or M2; NDGS 2286, USNM PAL 642987, 643001, 643007, 643022, 643075, 643149, M3.

**OCCURRENCE.** Sampling intervals 2 to 6.

**DISCUSSION.** The skull and dentition of *A. minimus* have been described elsewhere in detail (Matthew, 1903; Wood,

1937; Black, 1965; Korth et al., 2015). The specimens from Fitterer Ranch do not differ in morphology from these previous descriptions. In size, the average dimensions of the cheek teeth of the Fitterer Ranch material match those of the topotypic sample from Chadronian Pipestone Springs, Montana (Table A6), but are slightly smaller than those from Flagstaff Rim, Wyoming (Korth et al., 2015: table 2). However, the dimensions of the individual teeth from Fitterer Ranch (Table A5) show a nearly complete overlap in size with the Flagstaff Rim samples (Korth et al., 2015: table 2) and cannot be shown statistically to be significantly different.

The specimens of *A. minimus* are similar in size to those of *Leptodontomys douglassi* reported from the Whitneyan and Arikarean (Burke, 1934:396; Korth and Bailey, 1992: table 1; Korth, 2008a: table 1). However, the Fitterer Ranch specimens differ from the type and referred specimens of *L. douglassi* in having less elongated lower molars (length shorter relative to width). The anterior cingulid is also less well developed in *L. douglassi* and more closely appressed to the metalophid, and the cusps are more marginal in *A. minimus*, not sloped toward the center of the tooth as in *L. douglassi* (Burke, 1934).

*Adjidaumo minimus* was originally known only from the Chadronian (Wood, 1980; Korth, 1994b) but has been previously listed as occurring in the Orellan of Montana (Tabrum et al., 1996; Flynn, 2008). However, that Orellan occurrence was based on an unverified faunal list (Tabrum et al., 1996: table 10). The occurrence of *A. minimus* at Fitterer Ranch clearly extends the range of the species at least into the Orellan.

### ***Adjidaumo minutus* (Cope, 1873a)**

FIGURES 9E–H, 10; TABLE A7

**REFERRED SPECIMENS.** FAM 96879, USNM PAL 643387, dentary with p4–m3; FAM 96874, NDGS 2313, 2589, dentary with p4–m2; FAM 145540, dentary with m1–m3; USNM PAL 643336, NDGS 2517, 2549, dentary with m1–m2; NDGS 2569, dentary with m1; USNM PAL 643300, dp4; NDGS 2290, 2311, USNM PAL 643161, p4; NDGS 2226, 2238, 2291, 2331, m1 or m2; NDGS 2244, 2292, m3; NDGS 2046, left dp4; USNM PAL 643437, right maxilla fragment with M2–M3; USNM PAL 643391, NDGS 2296, 2321, M1 or M2.

**OCCURRENCE.** Sampling intervals 2, 5, and 6.

**DISCUSSION.** The lower dentition of *A. minutus* has been described previously (Wood, 1937). Two maxillary specimens with P4–M2 and P4–M1 have been previously illustrated by Wahlert (1978: fig. 7A) and Korth (1989b: fig. 3D), respectively. The Fitterer Ranch sample of upper dentitions is limited to only three specimens, but one of these, USNM PAL 643437, contains an M3 that has not been previously described. Unfortunately, it is heavily worn, and little of the occlusal pattern is observable. All that remains is a central, transversely elongated enamel ring. In outline, the tooth is much smaller than M2, with the metaloph not as wide as the protoloph. The morphology of the dentary

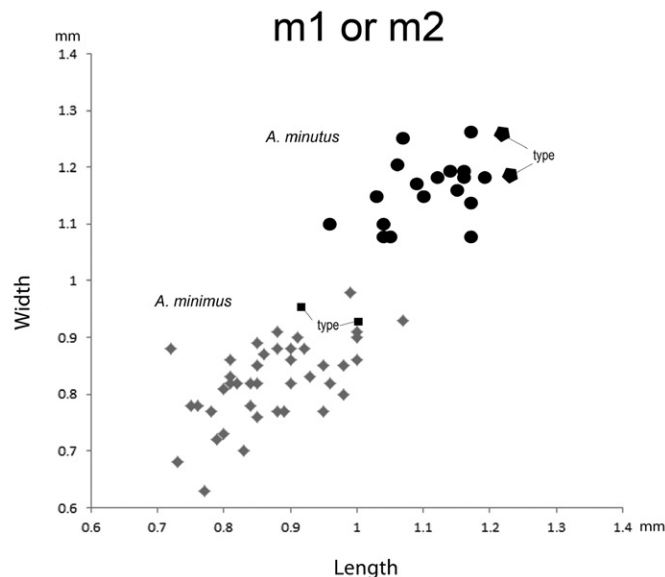


FIGURE 10. Scatter diagram of length versus width of m1 or m2 of *Adjidaumo minimus* (diamonds) and *A. minutus* (circles) from Fitterer Ranch. Measurements for types of *A. minimus* (squares) and *A. minutus* (pentagons) from Wood (1937:240).

and lower cheek teeth (Figure 9G,H) does not differ from that of previously described material (Wood, 1937; Korth, 1989b).

In dental dimensions, the Fitterer Ranch sample of *A. minutus* does not differ from those of the largest previously reported sample from the Orellan of Nebraska (Korth, 1989b: table 2) and can be separated from the specimens of *A. minimus* from Fitterer Ranch graphically (Figure 10) as well as statistically. *Adjidaumo minutus* has been reported elsewhere only from the Orellan (Wood, 1980; Korth, 1994b; Flynn, 2008).

### **Genus *Paradjidaumo* Burke, 1934**

#### ***Paradjidaumo trilophus* (Cope, 1873b)**

FIGURE 11; TABLES A8, A9

**REFERRED SPECIMENS.** NDGS 2307, USNM PAL 643327, partial maxilla with P4–M2; USNM PAL 643016, 643018, 643019, 643029, 643033, 643070, 643071, 643073, 643090, isolated dp4s; USNM PAL 643015, 643034, 643088, isolated P4s; NDGS 2304, 2305, USNM PAL 643014, 643020, 643030–643032, 643068, 643069, 643072, 643089, 643091–643093, isolated M1s or M2s; USNM 643017, M3; NDGS 1859, dentary with right dp4–m3; NDGS 2684, FAM 96896, right dentary with dp4–m2; NDGS 2506, partial dentary with dp4–m1; NDGS 2552, 2564, 2567, FAM 94935, 94967, 94968, 96871, 96880, 145541, 145542, dentaries with p4–m3; NDGS 2309, 2532, 2562, 2586, 2644, 2675, 2685, 2703, dentaries

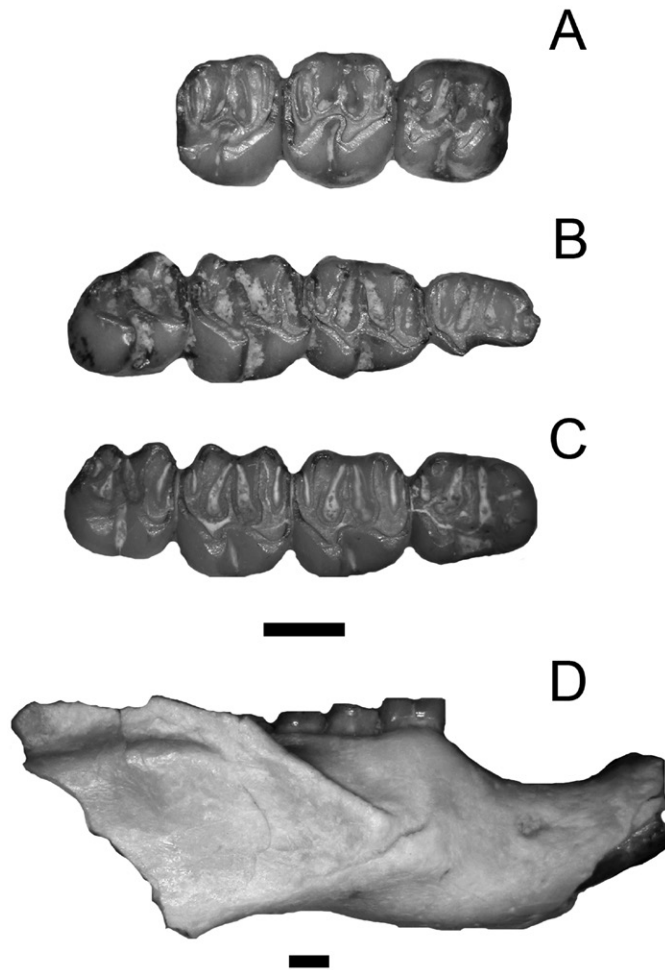


FIGURE 11. Dentition and dentary of *Paradjidaumo trilophus* from Fitterer Ranch: (A) USNM PAL 643327, right P4-M2; (B) NDGS 1859, left dp4-m3 (reversed); (C) NDGS 2567, right p4-m3; and (D) NDGS 2564, lateral view of dentary. Bar scales = 1 mm; note different bar length in D.

with p4-m2; NDGS 698, 2533, 2668, 2694, dentaries with p4-m1; FAM 96878, left dentary with m1-m3; NDGS 2705, FAM 145543, right dentary with m1-m2; FAM 145544, left dentary fragment with m1; USNM PAL 643163, 643169, 643171, 643174, 643180, isolated dp4s; USNM PAL 643166, 643176, 643177, 643179, isolated p4s; NDGS 2659, 2679, FAM 643162, 643164, 643165, 643167, 643170, 643172, 643173, 643175, 643181-643183, isolated m1s or m2s; USNM PAL 643168, 643178, isolated m3s.

**OCCURRENCE.** Sampling intervals 2 through 6.

**DISCUSSION.** This species has been well described elsewhere (Burke, 1934; Wood, 1937; Black, 1965; Korth, 1980, 2013). Korth (1980:933) provided a detailed list of synonymies. The mean dental measurements of specimens in the Fitterer Ranch sample are slightly smaller than in other fossil

assemblages (Tables A8, A9). However, none of these groups can be shown to be statistically different from one another. The crown-height index for the lower molars of the Fitterer Ranch sample of *Paradjidaumo* averages 0.35 (range = 0.21-0.47), identical to that of other samples of *P. trilophus* (Korth, 2013: tables 1, 3). This species is elsewhere known from the late Chardonian to the late Whitneyan (Ch3-Wh2 of Janis et al., 2008; see also Korth, 2007a, 2013, 2014).

**FAMILY HELISCOMYIDAE KORTH, WAHLERT,  
AND EMRY, 1991**

**Genus *Heliscomys* Cope, 1873b**

***Heliscomys senex* Wood, 1935**

FIGURE 12A-G; TABLES A10, A11

**TYPE SPECIMEN.** SDSM 25409, left dentary with p4, m2-m3 (Wood, 1935: fig. 6a).

**REFERRED SPECIMENS.** USNM PAL 642913, left p4; NDGS 2326, USNM PAL 642882-642912, 642957, 642984, m1 or m2; USNM PAL 642914-642920, m3; USNM PAL 642921, left dP4; USNM PAL 642922, 642923, 642940, P4; USNM PAL 642936, 642941, 642942, 642943, M1 or M2; USNM PAL 642924-642927, 642970, M3.

**OCCURRENCE.** Sampling intervals 5 and 6.

**EMENDED DIAGNOSIS.** Premolars large relative to first molars (width of P4 90% that of M1; length of p4 78% that of m1); styler cusps well developed on upper and lower molars; styler cusps on upper molars separated by distinct valley; dental measurements smaller than those of *H. hatcheri* Wood, 1939 and *H. gregoryi* Wood, 1933.

**DESCRIPTION.** The entire sample of *H. senex* consists of isolated teeth. The P4 is typically four cusped, with a central anterior cusp (protocone) and three cusps of the metaloph (metacone, hypocone, hypostyle), with the central hypocone being the largest (Figure 12B). The entostyle is anteroposteriorly elongated.

There is one specimen of a dP4, USNM PAL 642921 (Figure 12A), which is smaller than the P4s. The general pattern of the cusps is similar to that of P4. The hypocone is the largest and much higher than any of the other cusps. The protocone and paracone are of equal size, and the protostyle and entostyle are reduced to low, crescentic ridges at the anterolingual and posterolingual corners of the tooth, respectively.

M1 cannot be separated from M2 by size or morphology. The four main cusps (paracone, protocone, metacone, hypocone) are approximately equal in size and arranged in parallel, transverse rows (Figure 12C). The anterior cingulum extends along the entire anterior edge of the tooth, wrapping around the anterolingual corner. The protostyle and entostyle are smaller than the main cusps but are aligned with the protoloph and metaloph. A distinct valley separates the styler cusps. The posterior

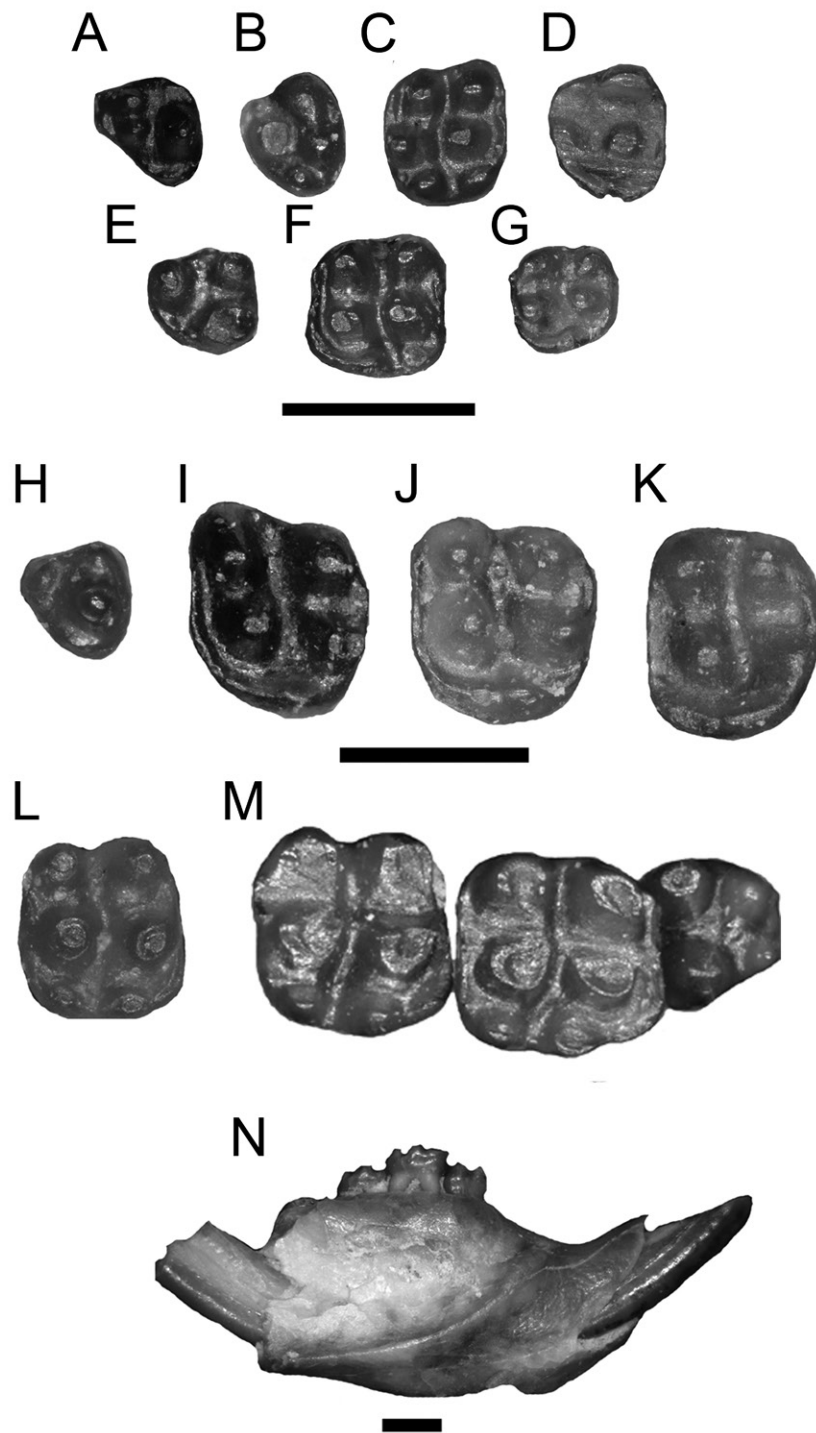


FIGURE 12. Dentitions of *Heliscomys* from Fitterer Ranch. (A)–(G) *Heliscomys senex*: (A) USNM PAL 642921, left dp4; (B) USNM PAL 642940, left P4; (C) USNM PAL 642941, right M1 or M2; (D) USNM PAL 642926, right M3; (E) USNM PAL 642913, left p4; (F) USNM PAL 642895, left m1 or m2; and (G) USNM PAL 642914, left m3. (H)–(N) *Heliscomys borealis*: (H) USNM PAL 642959, left P4; (I) USNM PAL 642928, left M1; (J) USNM PAL 642964, right M2 (reversed); (K) USNM PAL 642939, left M3; (L) USNM PAL 642958, right m3; (M) NDGS 2645, right p4–m3; and (N) NDGS 2645, lateral view of dentary. Bar scales = 1 mm; note different bar length in N.

cingulum is limited to the buccal half of the tooth, posterior to the metacone.

M3 is the smallest molar and ranges from nearly circular to slightly oval in outline (Figure 12D). The protocone is the largest cusp, is situated near the center of the tooth on its anterior half, and is isolated from all the other cusps. The paracone and metacone are reduced to crescentic swellings along the buccal edge of the tooth. The hypocone is variable in size, from small to completely absent. If present, it is along the posterior margin of the tooth near its center. The anterior cingulum is continuous with the lingual cingulum and posterior cingulum, encircling the entire tooth in most cases. A minute protostyle is always present at the anterolingual corner of the tooth. In USNM PAL 642926, the lingual cingulum has a minor break, separating a very small hypostyle from the protostyle.

The p4 is represented by a single specimen, USNM PAL 642913 (Figure 12E). It is narrower anteriorly than posteriorly. The metalophid consists of a large metaconid in the anterolingual corner of the tooth and a protostylid that is a low ridge running along the anterobuccal side of the tooth. The protostylid is separated from the other cusps by a small but deep pit. The cusps of the hypolophid (entoconid, hypoconid) are nearly equal in size, the hypoconid being only slightly larger. They are divided from one another, as well as the cusps of the protolophid, by a deep valley, isolating each of the cusps.

All specimens of m1 and m2 (Figure 12F) are isolated and cannot be separated on the basis of morphology or size. The teeth are typical of those of *Heliscomys*, consisting of two transverse rows, each with two main cusps (metalophid = metaconid, protoconid; hypolophid = entoconid, hypoconid). In a few specimens, the anterior slope of the metalophid cusps converges anteriorly with the anterior cingulid. There are always two stylar cusps (protostylid, hypostylid) along the buccal side of the tooth, smaller than the major cusps. The anterior cingulid extends for nearly the entire width of the tooth and wraps around the anterobuccal corner, then extends posteriorly, ending in the protostylid. On most specimens, there is a minute cuspule at the anterobuccal corner of the tooth within the cingulid. On approximately one-fourth of the specimens, there is a narrow break in the anterior cingulid, separating this anterior cuspule from the protostylid. The posterior cingulid is variable in size along the posterior margin of the tooth. It extends from posterior to the apex of the hypoconid to posterior to the apex of the entoconid.

The m3 is the smallest of the molars (Figure 12G) and narrower posteriorly than anteriorly. The four major cusps are always recognizable, but the hypoconid and entoconid are much more closely spaced, making the talonid narrower. The anterior cingulid is similar to that of the anterior molars and wraps around the anterobuccal corner of the tooth but does not extend as far posteriorly, ending buccal to the protoconid. There are generally no stylar cusps. If there are, only a minute protostylid is present.

**DISCUSSION.** Korth (1995) divided the known species of *Heliscomys* into subgenera, mainly on the basis of the

relative size of P4 to M1 and the greater development of the stylar cusps on the upper molars. The subgenus *Heliscomys* had a relatively narrower P4, less well developed (or absent) stylar cusps, and a continuous lingual cingulum on the upper molars (*H. vetus* Cope, 1873b; *H. senex* Wood, 1935; *H. woodi* McGrew, 1941; *H. mcgreui* Korth, 1989b; and later *H. medius* Korth, 2007a), whereas the subgenus *Syphyriomys* had a P4 nearly as wide as M1. M1 and M2 each have two stylar cusps separated from each other by a distinct valley (*H. hatcheri* Wood, 1933; *H. gregoryi* Wood, 1935; *H. ostranderi* Korth et al., 1991). It was also suggested (Korth, 1995) that the p4 of *H. (Heliscomys)* was more simplified with a central anterior cusp (metaconid), whereas *H. (Syphyriomys)* had a noncentral anterior cusp often accompanied by an additional cusp (protostylid). This latter feature appears quite variable (Galbreath, 1953; Korth et al., 1991), and specimens referred to species of both of these subgenera have both three- and four-cusped p4s. However, it appears that the subgenera can be distinguished by the relative length of p4 to m1. In species with the reduced P4, the p4 length is 60% of the length of m1 or less, and in the species with the relatively larger P4, the p4 length is 70% of the length of m1 or greater (Tables A10, A11), regardless of the number and position of the cusps on p4.

On the basis of the relative length of p4 to m1, the holotype of *H. senex* should belong to the subgenus *Syphyriomys* rather than *Heliscomys*. The specimen referred to *H. senex* by Korth (1995: fig. 1, table 1) from South Dakota, SDSM 25409, consisting of a partial cranium and associated dentaries, cannot be allocated to this species because the holotype of *H. senex* has a p4 that is 75% of the length of m1 even though it is only three cusped. SDSM 25409 is more likely referable to *H. vetus*. In morphology, the Fitterer Ranch p4 is similar to that of the holotype of *H. senex*, consisting of three major cusps and a minute protostylid (Figure 12E; Wood, 1935: fig. 6a).

The holotype of *H. senex*, YPM-PU 13459, is the only previously reported specimen of the species, and the Fitterer Ranch material is the first record of upper dentition of this species, which is compatible in morphology to the species referred to the subgenus *Syphyriomys*. In size, the Fitterer Ranch material is smaller than *H. (S.) hatcheri* and *H. (S.) gregoryi* and has better-developed stylar cusps on the molars than in *H. (S.) ostranderi*. Flynn et al. (2008) considered *H. senex*, *H. gregoryi*, and *H. hatcheri* to be synonyms of the type species *H. vetus*. However, all of the three former species are distinct from *H. vetus* in having the dental morphologies of *Syphyriomys*, unlike *H. vetus*.

### ***Heliscomys borealis*, new species**

FIGURE 12H–N; TABLES A11, A12

**HOLOTYPE.** USNM PAL 642928, left M1 (Figure 12I).

**REFERRED SPECIMENS.** USNM PAL 642959, left P4; USNM PAL 642929–642933, 642935, M1; NDGS 2281, USNM PAL 642962–642967, M2; NDGS 2328, USNM PAL 642934, 642937–642939, M3; NDGS 2645, right dentary with

p4–m2 (m3 fragment); USNM PAL 642944, 642946, 642951–642954, 642956, m1; USNM PAL 642945, 642947, 642948, 642950, 642955, m2; USNM PAL 642958, m3.

**OCCURRENCE.** Sampling intervals 2 and 4 to 6.

**DIAGNOSIS.** Larger than *H. vetus*, smaller than *H. medius* Korth, 2007a and *Megaheliscomys* Korth, 2007b; premolars reduced in size (P4 width 50%–64% that of M1, p4 length 60% that of m1); lingual cingulum continuous on upper molars; entostyle present on M1, but lingual cingulum not interrupted by valley; M2 with transversely compressed entostyle of variable size and no protostyle; lower molars with well-developed styler cusps.

**ETYMOLOGY.** Latin *borealis*, meaning “northern.”

**DESCRIPTION.** P4 is markedly smaller than the molars and smaller than P4s referred to *Heliscomys senex* (see above description). The tooth is roughly triangular in occlusal outline (Figure 12H). The main central cusp is the hypocone at the center of the posterior half of the tooth. The three remaining cusps are markedly smaller: the protocone (anteriorly), the metacone (buccally), and the hypostyle (lingually). The protocone and metacone are circular in outline; the hypostyle is slightly transversely compressed.

The M1s are larger than the upper molars of *H. hatcheri* (Table A12). They consist of two rows of two cusps each, which is typical for heliscomyids, but the paracone is larger than the other cusps, which causes the tooth to be expanded buccally at the anterobuccal corner (Figure 12I). A small mesostyle is just posterior to the paracone. The anterior cingulum originates along the anterior margin of the tooth, even with the apex of the paracone, and continues lingually and is continuous with the lingual cingulum, wrapping around the lingual side of the tooth and ending along the posterior edge of the tooth when it fuses with the hypocone. Along the lingual cingulum, just anterior and lingual to the hypocone, is a distinct, round entostyle. A short posterior cingulum is isolated and extends along the posterior margin of the tooth from the buccal slope of the hypocone to the lingual slope of the metacone.

The M2 is similar in size to the M1 (Figure 12J). The paracone of M2 is not as buccally expanded as in M1, making it more square in occlusal outline. M2 lacks the mesostyle on most specimens. The entostyle is a transversely compressed swelling on the lingual cingulum, lingual to the hypocone.

M3 is the smallest of the upper molars. The four major cusps are arranged as in M1 and M2 (Figure 12K) but are slightly more anteroposteriorly compressed, and the hypocone is more reduced in size (smaller than the other cusps). There is no buccal expansion of the paracone. The cingulum is continuous along the anterior margin of the tooth and continues along the lingual margin to the center of the posterior margin of the hypocone. There are no distinct styler cusps on the lingual cingulum, but a slight swelling lingual to the hypocone is commonly present.

The single dentary, NDGS 2645 (Figure 12N), does not differ from that described elsewhere for *Heliscomys* (Korth et al., 1991). The masseteric scar is a ridge that originates posteriorly

near the ventral margin of the dentary and rises anteriorly to a small shelf, nearly reaching the alveolar margin of the diastema, just posterior to the center of the diastema, which is part of the symphysis. There is a distinct digastric process extending ventrally below the center of the diastema. The mental foramen is dorsal to the anterior end of the masseteric scar. The diastema is nearly as long as the tooth row (3.04 mm) and shallow. The lower incisor is narrower than wide, nearly flattened anteriorly, and the enamel extends approximately one-third the anteroposterior length of the cross section of the tooth on the lateral side.

The only p4 is contained in the only dentary of the sample, NDGS 2645 (Figure 12M). It is smaller than the molars, being only 60% the length and 80% the width of m1. There are four recognizable cusps: metaconid and protostylid (anteriorly) and entoconid and hypoconid (posteriorly). The metalophid cusps are equal in size and slightly smaller than the hypolophid cusps. The anterior cusps are also more closely spaced to one another than the posterior cusps, making the tooth narrower anteriorly. There is a minute cuspule on the anterior slope of the metaconid (=anterostylid). All of the cusps are isolated from one another, with a deep valley separating the metalophid from the hypolophid and an equally deep valley running along the center of the tooth separating the lingual cusps from the buccal cusps.

The m1 and m2 are similar in morphology but distinct enough that the isolated teeth can be separated from one another (Figure 12M). The occlusal surface consists of the four major cusps, which are equally sized, arranged into the two transverse rows. The styler cusps are distinct but always smaller and aligned with the major cusps. The anterior cingulum on m1 extends for nearly the entire width of the tooth anteriorly, then curves posteriorly at the anterobuccal corner of the tooth. The cingulum can be continuous with the protostylid but is usually separated from it by a narrow, shallow valley. The hypostylid is always present and separated from the protostylid by a valley. The posterior cingulum is continuous for nearly the entire width of the tooth but never extends lingually to the edge of the tooth and is not continuous with the hypostylid buccally.

The m2 is similar to m1 in morphology but is slightly wider relative to length than m1. Morphologically, it differs in the development of the anterior and posterior cingulids. The anterior cingulum is limited to the buccal half of the tooth, and the posterior cingulum is limited to the posterior margin of the tooth, even with the apex of the hypoconid to even with the apex of the entoconid.

The m3 is smaller than m1 and m2 but similar in morphology (Figure 12L). It differs from the anterior molars in having the posterior cusps smaller relative to the anterior cusps. The styler cusps are always present but again are relatively smaller than in the other molars. The anterior cingulum is as in m2, but there is no posterior cingulum.

**DISCUSSION.** The size of the cheek teeth of *H. borealis* from Fitterer Ranch is intermediate between those of *H. vetus* and *H. medius* (Table A12; Wood, 1935: table II; Galbreath, 1953: table 11; Korth, 2007a: table 2) but is clearly referable to



the subgenus *Heliscomys* on the basis of the proportions of the premolars and development of the styler cusps on the upper molars (Korth, 1995). *Heliscomys borealis* can also be distinguished from the other species of *Heliscomys* from Fitterer Ranch by its intermediate size. *Heliscomys borealis* is the most widely distributed species of *Heliscomys* stratigraphically from Fitterer Ranch, being known from sampling intervals 2 through 6.

### *Heliscomys* cf. *H. medius* Korth, 2007a

FIGURE 13A,B

REFERRED SPECIMENS. USNM PAL 642960, 642961, M1s.

OCCURRENCE. Sampling interval 6 only.

MEASUREMENTS. USNM PAL 642960: L = 1.01 mm, W = 1.20 mm. USNM PAL 642961: L = 0.99 mm.

DISCUSSION. The two upper molars referred here are larger than any of the other specimens from Fitterer Ranch referred to *Heliscomys*. They do not differ markedly in size or morphology from those of *H. medius* (Korth, 2007a). The species was originally diagnosed as having a distinct protostyle on M1 along with a larger entostyle. Only one of the two M1s from Fitterer Ranch has a protostyle, USNM PAL 642961 (Figure 13B), suggesting that this is a variable character.



FIGURE 13. Cheek teeth of *Heliscomys* cf. *H. medius* and *Kirkomys* sp. from Fitterer Ranch. (A)–(B) *Heliscomys* cf. *H. medius*: (A) USNM PAL 642960, right M1 (reversed), and (B) USNM PAL 642961, right M1 (partially broken). (C)–(E) *Kirkomys* sp.: (C) USNM PAL 642968, left P4; (D) USNM PAL 642969, right M1; and (E) USNM PAL 642949, right m3. Bar scale = 1 mm.

## FAMILY FLORENTIAMYIDAE Wood, 1936

### Genus *Kirkomys* Wahlert, 1984

#### *Kirkomys* sp.

FIGURE 13C–E

REFERRED SPECIMENS. USNM PAL 642949, right m3; USNM PAL 642968, left P4; USNM PAL 642969, left right M1.

OCCURRENCE. Sampling interval 5 only.

MEASUREMENTS. USNM PAL 642968: L = 0.97 mm, W = 1.09 mm. USNM PAL 642969: L = 1.02 mm, W = 1.17 mm. USNM PAL 642949: L = 0.94 mm, W = 0.95 mm.

DESCRIPTION. The P4, USNM PAL 642968, is slightly wider than long (Figure 13C; L = 0.97 mm, W = 1.09 mm) and has the typical geomyoid occlusal pattern of a central protocone in the protoloph and three cusps in the metaloph: metacone, hypocone, and entostyle. The hypocone is central and the largest of all of the cusps. There is a minute cuspule (=paracone) on the buccal slope of the protocone. The protocone is separated from the metaloph by a narrow, transverse valley. The cusps of the metaloph are oval in shape, only slightly anteroposteriorly compressed. There is a short posterior cingulum along the posterior edge of the tooth, from even with the apex of the hypocone to even with the apex of the metacone.

The M1, USNM PAL 642969 (Figure 13D), is slightly larger than P4 (L = 1.02 mm, W = 1.17 mm). The major cusps are arranged in two parallel transverse rows (paracone and protocone in the protoloph and metacone and hypocone in the metaloph) separated by a deep transverse valley. The hypocone and protocone are of equal size and larger than the other cusps. The anterior cingulum originates buccally even with the center of the paracone and extends the entire width of the tooth, curves posteriorly, and is continuous with the lingual cingulum, which wraps around the posterolingual corner of the tooth, then fuses with the posterolingual corner of the hypocone. Along the lingual cingulum are two recognizable cusps. The protostyle is a slight, obliquely compressed swelling at the anterobuccal corner of the cingulum. The entostyle is larger than the protostyle, oval in shape, and directly lingual to the hypocone. The posterior cingulum is a minute spur that extends buccally from the posterobuccal corner of the hypocone and does not reach the buccal edge of the tooth or the posterior side of the metacone.

The m3 referred here, USNM PAL 642949 (Figure 13E), is larger than any of the other m3s from Fitterer Ranch referred to the other species (L = 0.94 mm, W = 0.95 mm) but otherwise typical of geomyoids. The anterior cingulid extends for the entire width of the tooth along its anterior margin, then wraps around the anterobuccal corner of the tooth, extending posteriorly along the buccal side of the tooth as a buccal cingulum for about half its length. The metalophid consists of the two main cusps, the metaconid and protoconid, which are of equal size. Both cusps

are connected to the center of the anterior cingulid by lophids that are angled to meet one another, forming a V shape. There is no indication of a protostylid buccal to the protoconid. The central valley is deep and extends for the entire width of the tooth. The hypolophid is slightly narrower than the metalophid. The cusps of the hypolophid are anteroposteriorly compressed, with the hypoconid being slightly larger than the entoconid. There is a minute hypostylid aligned with the other hypolophid cusps buccal to the hypoconid. There is a minute posterior cingulid along the posterior edge of the tooth posterior to the valley between the entoconid and hypoconid.

**DISCUSSION.** The specimens referred to *Kirkomys* sp. are separable from *Heliscomys* from Fitterer Ranch by their larger size. The P4 referred here is also much larger than that of *H. medius*. Morphologically, they are referable to *Kirkomys* because of their low crown-height index and relatively simple occlusal pattern. The well-developed styler cusps on the upper molar also distinguish it from specimens of *H. medius*.

These specimens are smaller than reported for any other species of *Kirkomys*: *K. nebraskensis* (Wahlert, 1984: table 1 [= *K. milleri*]; Korth and Branciforte, 2007: table 5), *K. parvus* (Korth, 2008b: table 2), and *K. martintau* (Korth, 2008b: table 3, 2014: table 11). The crown-height index of m1 and m2 has been used previously to distinguish between species of *Kirkomys* (Korth and Branciforte, 2007; Korth, 2008b). However, since the only lower molar of *Kirkomys* in the Fitterer Ranch collection is an m3, it cannot be determined. All of the previously referred species of *Kirkomys* are from the Whitneyan.

#### FAMILY CRICETIDAE FISCHER DE WALDHEIM, 1817

#### Genus *Eumys* Leidy, 1856

#### *Eumys brachyodus* Wood, 1937

FIGURES 14, 15; TABLES A13, A14

**REFERRED SPECIMENS.** USNM PAL 642823–642825, 642828–642830, 642832–642843, 642836, 642846, FAM 94173, 94179–94181, 94183, 94879, 94880, 94883–94885, 94915, 94916, 94924, 94942, 94945, 94949–94951, 94956, 94961, 94964, 95005, 95006, 96417, 96863, 96873, 96876, 96886, 96888, 96889, 96891, 96892, 96939, NDGS 729, 1861–1866, 2312, 2528, 2530, 2553, 2557, 2559–2563, 2566, 2571, 2573, 2576, 2584, 2592, 2596, 2598–2600, 2602, 2605–2607, 2609, 2612, 2620, 2624, 2625, 2629, 2632, 2662, 2668, 2672, 2683, 2689, 2692, 2708, 2709, dentaries with m1–m3; USNM PAL 642826, FAM 94171, 94919, 96865, 96882, 96890, 96893, 96897, NDGS 2678, 2695, 2701, 2713 (both left and right sides), dentaries with m1–m2; USNM PAL 642831, 642844, FAM 94174, 94182, 94887, 94889, 94941, 94943, 94947, 96864, 96872, 96884, 96898, NDGS 727, 792, 2283, 2509, 2510, 2548, 2581, 2595, 2613, 2619, 2630, 2635, 2674, 2681, 2702, dentaries with m2–m3; FAM 94886, 94890, 95007,

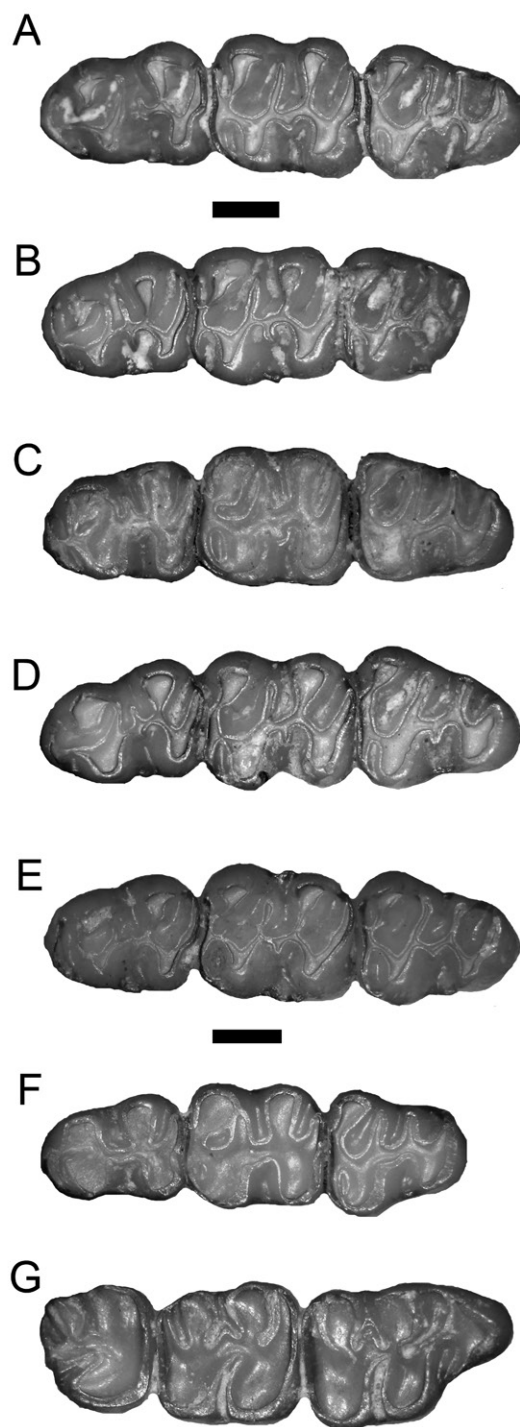


FIGURE 14. Dentitions of *Eumys brachyodus* from Fitterer Ranch: (A) USNM PAL 642823, right m1–m3 (reversed); (B) USNM PAL 642841, left m1–m3; (C) USNM PAL 642830, left m1–m3; (D) USNM PAL 642839, left m1–m3; (E) USNM PAL 642829, left m1–m3; (F) USNM PAL 642837, left m1–m3; and (G) USNM PAL 642847, right M1–M3. Bar scale = 1 mm.

NDGS 2505, 2538, 2541, 2676, 2682, partial dentaries with m1; USNM PAL 642827, FAM 95008, 96881, 96894, NDGS 694, 726, 2516, 2546, 2574, dentary fragment with m2; USNM PAL 642822, NDGS 2542, 2284, dentaries with m3; USNM PAL 642860–642871, NDGS 2322, m1; 62 unnumbered dentaries with cheek teeth in the AMNH collections; USNM PAL 642845, 642872–642878, m2; USNM PAL 642879, 642880, m3; NDGS 2707, partial skull with incisors and right M1–M3 and left M2; FAM 94920, 94962, NDGS 2578, palates with left and right M1–M3; NDGS 2580, palate with right M1–M3 and left M1–M2; USNM PAL 642847, NDGS 2540, palate with right M1–M3 and left M2–M3; NDGS 2771, palate with left and right M1–M2; NDGS 2697, partial palate with left and right M1; NDGS 2617, palate with right M1 and left M1–M2; NDGS 2719, partial palate with left and right M2; FAM 95004, NDGS 2536, 2636, maxillae with M1–M3; NDGS 2670, maxilla with M1–M2; FAM 96877, 96883, NDGS 2590, 2611, 2640, maxillae with M2–M3; USNM PAL 642849–642853, FAM 94960, NDGS 697, 2537, 2544, 2587, 2610, 2637, 2663, M1; USNM PAL 642854, 642855, NDGS 2285, 2543, M2; USNM PAL 642856–642859, M3; seven unnumbered specimens of upper dentitions in the AMNH collections (four palates, two maxillae, and a partial skull).

**OCCURRENCE.** Sampling intervals 1 to 7.

**DISCUSSION.** The most common rodent from Fitterer Ranch is *Eumys*, which is represented by over 300 specimens. All but one of the specimens are referable to *E. brachyodus* because the cheek teeth are equivalent in size and proportionately wider relative to length compared with those of other species of *Eumys* (Tables A12, A13; also see Wahlert, 2004: table 1; Korth, 2010: table 5, 2011: table 3 and appendix).

There is little difference in the mean values of the dimensions of the cheek teeth of *E. brachyodus* from Fitterer Ranch from the different sampling intervals (Tables A13, A14). There is some variation in the size of the specimens from the highest sampling interval, but the sample is extremely small, and all measurements are within the range of those from other sampling intervals, so the mean values are clearly anomalous.

Wood (1937) originally diagnosed *E. brachyodus* as having lophulids from both the metaconid and protoconid directly connected to the anteroconid on m1. Later, it was demonstrated that this morphology, although not always present, was common in m1s of the species and was diagnostic for the species because this type of variation was not found on any other species (Korth, 2010, 2011). This morphology of the doubled lophids occurs on 20% of the Fitterer Ranch sample specimens (Figure 15), a similar percentage to that of Whitneyan samples of *E. brachyodus* from South Dakota (Korth, 2010: table 2, 2011: table 4). Although there is some variation in the proportions of this morphology on m1s from different sampling intervals (Tables A13, A14), the double attachment is present in all sampling intervals except sampling intervals 1 and 7 (Figure 15), which are represented by only 10 and two specimens, respectively.

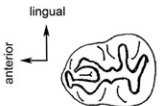



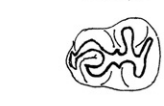
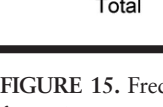
	SAMPLING INTERVALS					Total #	%
	1-2	3	4-5	6	7		
	0	2	28	6	0	36	25
	6	1	21	2	0	30	21
	1	1	25	0	2	29	20
	0	1	24	4	0	29	20
	3	3	9	4	0	19	13
	0	1	1	1	0	3	2
<b>Total</b>	<b>10</b>	<b>9</b>	<b>108</b>	<b>17</b>	<b>2</b>	<b>146</b>	

FIGURE 15. Frequency of morphologies of m1 of *Eumys brachyodus* from Fitterer Ranch separated by sampling intervals.

### *Eumys lammersi*, new species

FIGURE 16

**TYPE AND ONLY SPECIMEN.** USNM PAL 642848, right dentary with m1–m3.

**MEASUREMENTS.** m1: L = 3.01 mm, W = 2.18 mm; m2: L = 2.68 mm, W = 2.53 mm; m3: L = 2.71 mm, W = 2.17 mm; m1–m3: L = 8.51 mm.

**OCCURRENCE.** Sampling interval 5.

**DIAGNOSIS.** Largest species of the genus; molars proportioned as in *E. elegans* (not relatively wider as in *E. brachyodus*); anteroconid on m1 minute, transversely elongated, and connected to metaconid and protoconid by separate lophulids; distinct branch of the posterior cingulid on m1 posterior to hypoconid; m1 longest of the lower molars, m2 and m3 approximately equal in length.

**ETYMOLOGY.** Patronym for George Eber Lammers, formerly of the Manitoba Museum of Man and Nature, who helped get the NDGS paleontology program working at Fitterer Ranch in the 1980s and worked with John Hoganson (NDGS emeritus) on some of the early reports on the fauna from that locality.

**DESCRIPTION.** The proportions of the lower molars (length versus width) of the holotype are similar to those of *E. elegans* and most other species of *Eumys*, distinctly narrower than in *E. brachyodus*. The m1 is the longest of the lower molars, and the m2 and m3 are of nearly equal size, again similar to those

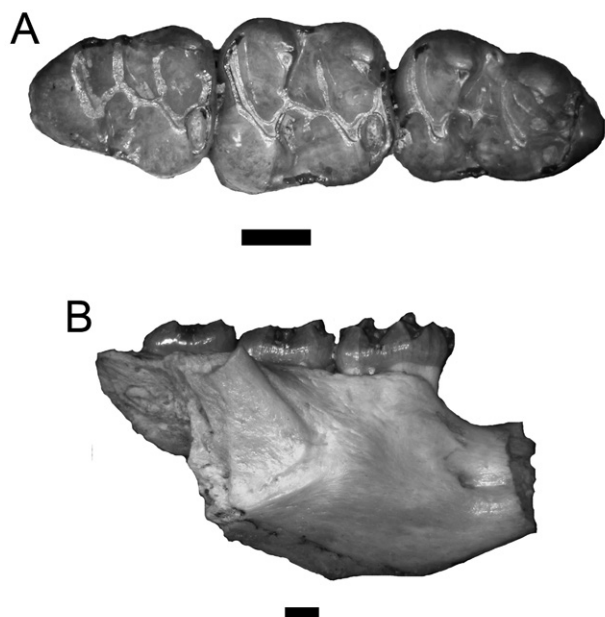


FIGURE 16. Holotype of *Eumys lammersi*, USNM PAL 642848, right dentary with m1–m3: (A) Occlusal view of m1–m3, and (B) Lateral view of dentary. Bar scales = 1 mm; note different bar lengths.

of *E. elegans*. The height of the lophs of the lower molars is the same as that of other species of the genus and not as high as in *Wilsonneumys* Martin, 1980.

The m1 is narrower anteriorly than posteriorly, typical of species of *Eumys* (Figure 16A). The anteroconid is minute and located just buccal to the center line of the tooth along the anterior border. The anteroconid is anteroposteriorly compressed, and the anterior cingulid extends both buccally and lingually from it as a high lophid. Lingually, the cingulid ends even with the apex of the metaconid; buccally, it wraps around the anterobuccal corner of the tooth, ending just before reaching the protoconid. Anteroposterior lophids extend anteriorly from both the metaconid and protoconid, joining the anterior cingulid just lingual and buccal to the anteroconid, respectively, leaving three small basins just posterior to the anterior cingulid. Both the metaconid and protoconid are obliquely compressed (anterolingual-posterobuccal). The trigonid basin is narrow and runs anterobuccally between the metaconid and protoconid, ending in the center of the three basins posterior to the anterior cingulid. The posterior arm of the protoconid extends across the tooth, joining the lophid extending posteriorly from the metaconid along the lingual margin of the tooth. A short ectolophid runs posteriorly from the center of the posterior arm of the protoconid to the center of the hypolophid. At its center, there is a small mesoconid that has two short lophids running perpendicular to it, one extending buccally (buccal mesolophid) and one lingually (mesolophid). Both the buccal and lingual valleys on either side of the ectolophid

are blocked along their lingual and buccal borders by small anteroposteriorly elongated cusps (mesostylid, ectostylid). The entoconid is roughly triangular in occlusal outline. The hypolophid extends buccally from it, joining the posterior end of the ectolophid. The anterior arm of the hypoconid extends lingually, also joining the ectolophid, forming a complete hypolophid. A minute ridge runs down the posterobuccal side of the entoconid from its apex. Because of the small size of this lophid, it will likely disappear after moderate wear. The posterolophid extends from the posterolingual corner of the hypoconid to the posterolingual corner of the tooth in a broad arc. A narrow valley separates the lingual end of the posterolophid from the entoconid. There is no recognizable hypoconulid on m1, but in its place (just lingual to the hypoconid) is a short, posterobuccally oriented cingulid.

The m2 is rectangular in occlusal outline, nearly equal in width anteriorly and posteriorly. The anterior cingulid extends from the anterobuccal corner of the tooth to a point just anterior to the apex of the metaconid. The metaconid and protoconid are similar to those of m1 but more widely separated. As in m1, the anterior arms of the metaconid and protoconid connect anteriorly with the anterior cingulum separately. The metaconid is obliquely compressed, and the protoconid has a V shape. As in m1, the posterior arm of the protoconid extends lingually, ending short of the lingual margin of the tooth, posterior to the metaconid. There is a small oval basin anterior to the protoconid formed by the buccal end of the anterior cingulid, the anterior arm of the protoconid, and the lingual extent of the protoconid. The trigonid basin extends from the anterior cingulid to the point where the posterior arm of the protoconid ends. The ectolophid is as in m1 but lacks the minute (lingual) mesolophid. The buccal and lingual valleys between the metalophid and hypolophid are blocked along the edges of the tooth as in m1. The hypolophid and posterolophid are as in m1, but no accessory posterior cingulid or small loph extends posteriorly from the entoconid as in m1.

The m3 narrows posteriorly, typical of *Eumys*. The anterior half of the tooth is the same as in m2, but the posterior arm of the protoconid does fuse with a posterior arm of the metaconid as in m1, enclosing the trigonid lingually. As in m2, there is only a minute buccal mesolophid on the ectolophid. The posterior half of the tooth is reduced in width. The entoconid is reduced to the lingual end of the hypolophid, the hypoconid is markedly reduced in size relative to m1 and m2, and the basin between the hypolophid and posterolophid is widely open lingually.

Other than its larger size, the dentary of *E. lammersi* does not differ from that of other species of the genus (Figure 16B).

**DISCUSSION.** The molars of the holotype of *E. lammersi* are greater in length than those of any Orellan or Whitneyan species of *Eumys*, including the previously described largest species, *E. cricetodontoides* White, 1954 (see Korth, 2010: table 3). There is no overlap in length of the molars of the type of *E. lammersi* and *E. cricetodontoides* or the large sample of *E. brachyodus* from Fitterer Ranch (Table A13). The lower molars are not as wide relative to length as in *E. brachyodus*

from Fitterer Ranch but are within the range of the other species of *Eumys* (Korth, 2010: table 5). The double connection of the metaconid and protoconid to the anterior cingulid on m1 of *E. lammersi* is similar to that of *E. brachyodus*, but the small posterior cingulid on m1 is not known in any other species of the genus.

The size of m2 of *E. lammersi* is similar to that of the Arikareean *E. eliensis* Black, 1961 and Whitneyan *E. euryodus* Korth, 2010 (Korth, 2010: table 4). However, *E. lammersi* differs from *E. eliensis* in having m1 longer than the posterior molars, whereas the m1 is the shortest of the molars in the latter. *Eumys lammersi* differs from *E. euryodus* in having an m3 subequal in size to m2; in the latter the m3 is distinctly smaller than m2. The m1 of *E. lammersi* is also more elongated than in *E. euryodus* and *E. eliensis*, which have proportions of m1 similar to those of *E. brachyodus* (Korth, 2010: table 5). The double connection of the metalophid to the anteroconid and posterior cingulid on m1 of *E. lammersi* is not present in *E. eliensis* (m1 not known for *E. euryodus*). In the large sample of *Eumys* from Fitterer Ranch, no upper molars are large enough to represent *E. lammersi*.

## Genus *Willeumys* Wahlert, 2009

### *Willeumys viduus* (Korth, 1981)

FIGURE 17

*Scottimus viduus* Korth, 1981

*Willeumys viduus* (Korth) Korth and Tabrum, 2017

**REFERRED SPECIMENS.** NDGS 2301, maxilla with left M1–M2; NDGS 2298, left m1; USNM PAL 642881, right m2; NDGS 730, partial dentary with right m2–m3; NDGS 2547, dentary fragment with right m2.

**OCCURRENCE.** Sampling intervals 2, 5, and 6.

**MEASUREMENTS.** NDGS 2301: M1, L = 2.24 mm, W = 1.33 mm; M2, L = 1.56 mm, W = 1.38 mm. NDGS 2298: m1, W = 1.34 mm. USNM PAL 642881: m2, L = 1.65 mm, W = 1.35 mm. NDGS 730: m2, L = 1.71 mm, W = 1.49 mm; m3, L = 1.62 mm, W = 1.31 mm. NDGS 2547: m2, L = 1.78 mm, W = 1.35 mm.

**DESCRIPTION.** The most complete dentary is NDGS 730, which lacks any bone anterior to the posterior root of m1 and posterior to the posterior end of m3 (Figure 17D). The masseteric scar ends anteriorly in a V shape ventral to the center of the alveolus for m1, at mid-depth of the dentary. The ascending ramus arises lateral to m2 and blocks the majority of m3 from lateral view. Only a fragment of i1 is present, but it is longer than wide in cross section, widest at about one-fourth the anteroposterior length of the cross section of the tooth with a rounded anterior enamel surface that extends approximately one-third the length of the cross section of the tooth. A fragment of the anterior enamel surface is exposed, and the minute ridges typical of the genus are present.

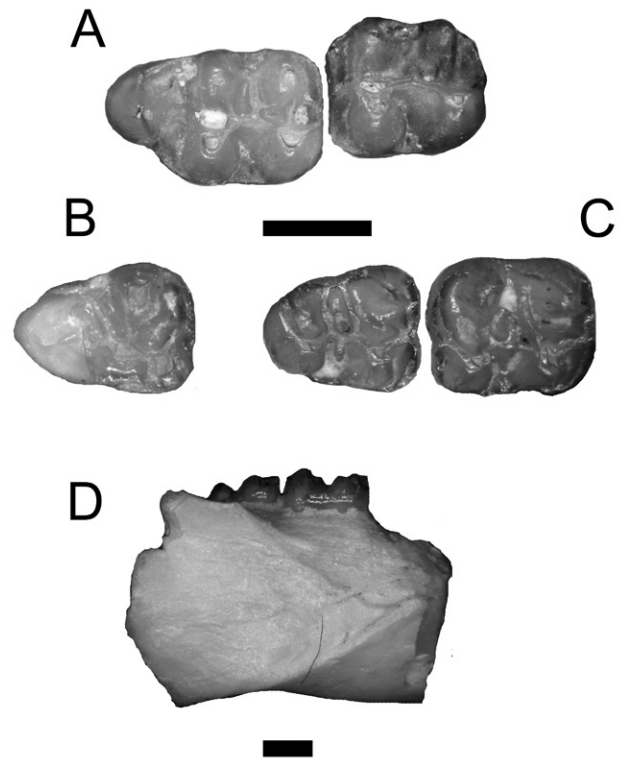


FIGURE 17. Dentition and dentary of *Willeumys viduus* from Fitterer Ranch: (A) NDGS 2301, left M1–M2; (B) NDGS 2298, left m1; (C) NDGS 730, right m2–m3; and (D) NDGS 730, lateral view of dentary. Bar scales = 1 mm; note different bar length in D.

The only m1 in the Fitterer Ranch sample, NDGS 2298, is partially broken on the anterior end, so little of the morphology of the metalophid is preserved (Figure 17B). However, the outline of the tooth is typical of that of cricetids in being narrower anteriorly. The ectolophid is complete, directed posterobuccally from the posterior side of the trigonid to the hypoconid. A long mesolophid extends anterolingually nearly to the lingual edge of the tooth. There is a distinct mesoconid at the center of the ectolophid. The entoconid is slightly anterior to the hypoconid and anteroposteriorly compressed. The posterolophid is continuous from the posterolingual corner of the hypoconid to the posterolingual corner of the entoconid. Just lingual to the hypoconid is a minute lophid extending buccally from the posterolophid.

The m2 is rectangular in occlusal outline (Figure 17C). The anterior cingulid extends for nearly the entire width of the tooth along the anterior border, curving around the anterobuccal corner of the tooth. The metaconid is obliquely compressed (anterolingual-posterobuccal). The anterior arm of the metaconid extends anterobuccally to meet the anterior cingulid near its center. The protoconid is crescentic in outline, and its anterior arm also extends anterolingually to the anterior cingulid. The anterior extensions of both the protoconid and metaconid

either meet at the center of the anterior cingulid, forming a V shape, or are slightly separated from one another, leaving a narrow anteroposterior valley between them. The posterior arm of the protoconid extends posterolingually, ending posterior to the metaconid. It is variable in length, sometimes reaching the posterobuccal edge of the metaconid. The ectolophid is a short, anteroposteriorly directed lophid running from the posterolingual corner of the protoconid to the center of the hypolophid. There is always a minute mesoconid at its center. A short mesolophid and buccal mesolophid are present but vary in height. The entoconid is anteroposteriorly compressed. The hypolophid extends buccally from it, curving slightly anteriorly until it fuses with the posterior end of the ectolophid, where the hypolophid is directed posterobuccally to join the anterior arm of the hypoconid. The hypoconid is also crescentic in occlusal outline. The posterolophid originates at the posterolingual corner of the hypoconid and arcs around the posterior edge of the tooth, fusing lingually with the posterior side of the entoconid. Posterior and slightly lingual to the hypoconid, along the posterolophid, is a short posterior cingulid that extends buccally for a short distance, never reaching the buccal edge of the tooth.

The m3 is known on only NDGS 730. It is wider anteriorly and tapers posteriorly. The anterior portion of the tooth is similar to that of m2, but the anterior arms of the two trigonid cusps are more widely spaced. The posterior arm of the protoconid extends across the entire tooth to the lingual border, just posterior to the metaconid. There is no mesolophid. The entoconid is reduced to a transverse loph (lingual extension of the hypolophid). There is no observable mesoconid, but a short buccal mesolophid is present. The hypoconid is similar in shape to that of m2 but smaller and more anteroposteriorly elongated. The posterolophid forms a broad arc around the posterior end of the tooth, ending on the buccal side of the tooth, just short of the lingual end of the hypolophid.

M1 has a large, wide anterocone that extends from the buccal side of the tooth for more than half its width. The anterocone is rounded anteriorly and flat posteriorly (Figure 17A). It is connected to the protoloph along the buccal edge of the tooth. The valley between the anterocone and protoloph is interrupted by two short lophs, one running posteriorly from the center of anterocone and ending just anterior to the paracone and the second from the lingual corner of the anterocone, connecting with the anterobuccal corner of the protocone. The paracone and metacone are oval in occlusal outline, being slightly wider (transversely) than long. Both the protocone and hypocone are crescentic in outline. The protocone connects to the paracone both anteriorly and posteriorly, forming a small fossette between the two cusps. The entoloph runs from the posterobuccal corner of the protocone to the anterobuccal corner of the hypocone. The mesoloph extends lingually from the center of the entoloph, ending short of the buccal edge of the tooth and fusing with a short, posteriorly directed loph from the apex of the paracone. A short spur also extends posteriorly from the mesoloph, just lingual to the lingual edge of the metacone. The metaloph runs

buccally from the hypocone to the posterolingual corner of the metacone, forming a fossette between the cusps similar to that of the protoloph. The posterior cingulum extends buccally from the posterobuccal corner of the hypocone to the posterobuccal corner of the tooth but is not continuous with the metacone. Near the center of the posterior cingulum is a short anteroposterior loph connecting to the posterolingual corner of the metacone.

M2 is rectangular in occlusal outline. There is no anterocone, but the anterior cingulum extends across the anterior edge of the tooth for nearly its entire width. The cingulum is connected to the protoloph by a short anteroposterior loph that is centered at the anterobuccal corner of the protocone. The major cusps are as in M1. The double connection of the protocone to the paracone is also as in M1, isolating a small enamel fossette between the two cusps. The mesoloph is much shorter than in M1. A small loph runs posteriorly from the paracone, but it ends in the valley between the paracone and metacone and does not connect with the mesoloph. The metaloph extends anterolingually from the metacone, joining the entoloph anterior to the hypocone. There is no accessory anteroposteriorly oriented loph on the mesoloph or the posterior cingulum as in M1.

**DISCUSSION.** The morphology and size of the lower molars referred here to *Willeumys* do not differ from those of *W. viduus* (= *Scottimus viduus*, Korth, 1981: table 2, figs. 6, 7). The accessory lophs on the molars are variably present in the originally referred material of the species.

*Willeumys korthi* was named by Wahlert (2009) on the basis of a single specimen. The distinction between *W. korthi* and *W. viduus* is based on the morphologies of M1/m1 (Korth and Tabrum, 2017). Because there are only minor morphological differences between the first molars of these two species, it is possible they may be synonymous. However, until better samples of *W. korthi* are discovered (known only from the holotype) the actual range of variation for these morphologies cannot be determined. Both *W. korthi* and *W. viduus* are limited to the Orellan (Korth, 1981; Wahlert, 2009; Korth and Tabrum, 2017).

## CONCLUSIONS

Several of the taxa with limited observed stratigraphic ranges at Fitterer Ranch (i.e., *Cedromus*, *Kirkomys*, *Eumys lammeri*, *Heliscomys* cf. *medius*, cf. *Microparamys* sp., and *Oligotheriomys*) are rare (consisting of five or fewer specimens), so their range in the stratigraphic sequence cannot be verified with any confidence at this time. The majority of the remaining species (10 out of 12) are known throughout the section, at least from sampling intervals 2 to 6, with some gaps. The only species that appear to be well enough represented in terms of numbers of specimens but are lacking in the lower sampling intervals (sampling intervals 1 to 3) are *Agnotocaster praetereadens* and *Heliscomys senex*. Those species are known from only sampling intervals 5 and 6, whereas the other well-represented species are found throughout the section. It is possible that the distribution

of species within this sequence might be ecologically related. Sampling intervals 5 and 6 are composed of rocks deposited within a broad paleovalley and a smaller paleochannel, respectively. The fauna preserved in those rocks includes relatively abundant fish, anuran amphibians, and pond snails, which are rarely present in the underlying rocks that form the base of the Brule Formation at Fitterer Ranch. It is possible that the presence of some rodent species only in those sampling intervals may be related to the environmental shift represented by those rocks rather than representative of a broader faunal turnover or a real local first appearance.

The age of the fauna at Fitterer Ranch has been considered both Orellan and Whitneyan (=early to late early Oligocene; Janis et al., 2008: ppendix I). This detailed study of the rodent portion of the fauna has underscored that ambiguity. Of the rodent species recognized, the four newly described species and the indeterminate species of *Kirkomys* Wahlert, 1984 are unique to the fauna; five species are otherwise limited to the Orellan (Table A15), four are elsewhere limited to the Whitneyan, one is known from the Orellan and Whitneyan (*Ischyromys typus*), one ranges from the Chadronian to the Whitneyan (*Paradjidaumo trilophus*), and one is definitely known previously from the Chadronian (*Adjidaumo minimus*, latest Eocene) but also has been reported from the Orellan (Tabrum et al., 1996). The genus *Kirkomys* is elsewhere limited to the Whitneyan (Wahlert, 1984; Korth and Branciforte, 2007; Korth, 2014); however, the Fitterer Ranch material, although not complete enough to recognize a new species, clearly differs from all known species of the genus in its smaller size. Of those species definitely identified from Fitterer Ranch, *E. brachyodus* and *A. praetereadens* are previously reported from only Whitneyan faunas (Prothero and Emry, 2004). Given that evidence, this fauna seems to be transitional between the latest Orellan (Or4: 32.6 to 32.0 Ma) and the early Whitneyan (Wh1: 32.0 to 31.4 Ma), with relict species from the former age mixed with early appearances of typically Whitneyan species. It is possible then that the early Whitneyan (Wh1) may begin at sampling interval 5 with the first occurrence of *A. praetereadens*, although as mentioned above, the restriction of that species to sampling intervals 5 and 6 may be linked to the change in depositional facies.

A review of the nonrodent mammalian fauna at Fitterer Ranch is still underway, but the current results of that work agree with the biostratigraphic information provided by the rodent fauna. Although oreodonts are not as common at Fitterer Ranch as they are in the rocks of the White River Group in southern South Dakota and Nebraska, several well-preserved specimens are known, including one collected a few meters above the base of the Brule Formation (NDGS 2734 from locality NDGS L231). The only oreodont taxa currently identified from sampling intervals 1 through 6 at Fitterer Ranch by these authors are *Miniochoerus starkensis* and *Merycoiodon bullatus* (contra Murphy et al., 1993), both of which are elsewhere restricted to the latest Orellan (Or4) and early Whitneyan (Wh1) North American Land Mammal Ages (NALMAs; Prothero and Emry,

2004). Fitterer Ranch is the type locality for the canid *Osbornodon renjieii*, and the other occurrences of that species within the Great Plains region are from the latest Orellan (Or4) of southern South Dakota and the Whitneyan of southern South Dakota and northwest Nebraska (Welsh, 2014). Thus, a latest Orellan (Or4), early Whitneyan (Wh1), or transitional Orellan-Whitneyan age for the Fitterer Ranch fauna is supported by multiple portions of the mammalian fauna.

Kihm (1990) previously reported on the abundance of specimens of *Eumys brachyodus* and the complete absence of *Eumys elegans* from a locality within the lower third of the Brule Formation in the Little Badlands area of North Dakota. As a result, it was suggested that much of the fauna from the Brule Formation of North Dakota may actually be Whitneyan, contrary to prior reports of an Orellan fauna at the base of the Brule Formation (e.g., Stone, 1972; Hoganson and Lammers, 1985; Kihm and Lammers, 1986). However, studies of cricetids from Brule Formation rocks in the Chalky Buttes area of Slope County, North Dakota, to the southwest of the Little Badlands area reported a predominance of specimens of *Eumys elegans* and none referred to *Eumys brachyodus* (Kihm, 1990; Wahlert, 2004). The presence of *Eumys elegans* is more typical of Orellan faunas than Whitneyan faunas, although a thorough review of that fauna would be needed before a biostratigraphic age could be assigned to the Brule Formation in the Chalky Buttes. Thus, it is possible that deposits of the Brule Formation in different geographic areas of North Dakota may preserve faunas of different biostratigraphic ages, and the age of the fauna at Fitterer Ranch should not be used to infer the age of the basal beds of the Brule Formation throughout the state.

The main nonpaleontological evidence for the age of the Brule Formation rocks at Fitterer Ranch comes from magnetostratigraphy (Prothero, 1996). Those data were also reported in reference to the units defined by Skinner (1951), facilitating easy comparison between that study and the current work. Prothero (1996) collected samples along two sections at Fitterer Ranch, the first spanning from subunits 4A to 6A and the second spanning from subunits 5D to 6F. The lowest sample from subunit 4A showed normal polarity. All subsequent samples up through the bottom portion of subunit 6A showed reverse polarity. Within subunit 6A there was a transition to normal polarity that persisted up through subunit 6E. The five samples from within subunit 6F varied from normal to reverse polarity, with no clear pattern (Prothero, 1996: fig. 5). Those results were interpreted as indicating that the lowest portion of subunit 4A was deposited during Chron C13n (33.2 to 33.7 Ma; Ogg, 2012). That would be a slightly older age than is indicated at this time by the rodent fauna for the basal beds of the Brule Formation at Fitterer Ranch (Or1 or Or2 versus Or4 or Wh1). However, that data point is reported as a Class III site (sensu Opdyke et al., 1977), meaning two samples showed a clear polarity preference but the third sample showed a contradictory polarity preference (Prothero, 1996). It is then possible that the report of normal polarity at the base of subunit 4A is inaccurate; however, samples taken from

elsewhere in the Little Badlands region in that same study also recorded normal polarity from the base of subunit 4A (Prothero, 1996). Alternatively, it is possible that those basal beds were not sampled densely enough in this study to facilitate recognition of an earliest Orellan (Or1) or late early Orellan (Or2) fauna, especially given that very few sites from the basal Brule Formation were available for study. The upper portion of subunit 4A through the lower portion of 6A was deposited during Chron C12r (31.0 to 33.2 Ma; Ogg, 2012), which spanned from the upper portion of the late early Orellan (Or2) through the lower portion of late Whitneyan (Wh2), consistent with the paleontological evidence for those rocks that suggests a latest Orellan (Or4) to early Whitneyan (Wh1) “age” for those rocks. The reverse polarity interval recorded in the upper part of subunit 6A through 6E corresponds to Chron C12n (30.0 to 30.6 Ma; Ogg, 2012) in the middle portion of the late Whitneyan (Wh2) NALMA (Prothero and Emry, 2004). Clear faunal evidence is not available at this time to test that interpretation given the scarcity of paleontological localities within the upper portion of the Brule Formation at Fitterer Ranch, but work continues to address this issue. Overall, the magnetostratigraphic and faunal evidence from Fitterer Ranch is in close agreement (Figure 1).

A recently published review of the Chadron Formation within North Dakota (Boyd and Webster, 2018) noted that the

contact between the Chalky Buttes and South Heart Members of that formation is unconformable, contrary to prior reports (e.g., Stone, 1973; Murphy et al., 1993; Hoganson et al., 1998). The contact between the Chadron and Brule Formations in North Dakota was also previously reported as conformable (e.g., Stone, 1973; Murphy et al., 1993; Hoganson et al., 1998). This study reveals that the basal beds of the Brule Formation at Fitterer Ranch contain either a late Orellan or transitional Orellan-Whitneyan fauna. The underlying rocks of the South Heart Member of the Chadron Formation contain brontotheriid fossils, indicating the preservation of a Chadronian (latest Eocene) fauna in those rocks (Murphy et al., 1993; Boyd and Webster, 2018). Given that paleontological evidence, the contact between the Chadron and Brule Formations at Fitterer Ranch is a disconformity that at a minimum spans from the end of the Chadronian NALMA (33.7 Ma; Janis et al., 2008) to the beginning of the latest Orellan NALMA (32.6 Ma; Janis et al., 2008). As noted previously, the age of the fauna at Fitterer Ranch should not be unilaterally applied to the basal beds of the Brule Formation throughout North Dakota without further study of faunas from different geographic locations. However, given the scale of time represented by the disconformity at Fitterer Ranch, it seems likely that a disconformity is present at that contact throughout North Dakota, although the scale of missing time may vary at different locations.





# Appendix: Tables of Measurements

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TABLE A1. Dental measurements (in mm) for *Ischyromys typus* from Fitterer Ranch. Abbreviations: dP, deciduous upper premolar; p, lower premolar; P, upper premolar; m, lower molar; M, upper molar; L, anteroposterior length; W, maximum width; Min, minimum measurement; Max, maximum measurement; SD, standard deviation; CV, coefficient of variation. A dash (—) indicates data are not available.

Measurement or statistic	Lower Teeth								
	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4–m3
Number of specimens	9	9	18	18	20	20	13	13	8
Mean	3.99	3.37	3.89	3.60	3.87	3.86	3.96	3.57	16.38
Min	3.51	2.88	3.44	3.09	3.43	3.48	3.62	3.25	14.61
Max	4.28	3.60	4.32	4.16	4.38	4.20	4.36	3.81	18.03
SD	0.26	0.21	0.31	0.29	0.28	0.20	0.21	0.18	1.05
CV	6.53	6.10	7.90	8.12	7.13	5.18	5.35	5.05	6.39

Measurement or statistic	Upper Teeth											
	DP4L	DP4W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
Number of specimens	2	2	1	1	2	2	4	4	3	3	2	2
Mean	4.22	3.39	2.15	2.79	3.94	4.19	3.96	3.82	3.80	3.70	3.52	3.12
Min	4.09	3.35	—	—	3.88	4.13	3.73	3.73	3.51	3.53	3.49	3.04
Max	4.34	3.43	—	—	3.99	4.24	4.16	3.91	3.96	3.79	3.54	3.19
SD	—	—	—	—	—	—	0.20	0.07	0.25	0.15	—	—
CV	—	—	—	—	—	—	5.00	1.93	6.62	3.98	—	—

TABLE A2. Dental measurements (mm) for *Prosciurus hogansoni* from Fitterer Ranch. Abbreviations: p, lower premolar; P, upper premolar; m, lower molar; M, upper molar; L, anteroposterior length; W, transverse width; Min, minimum measurement; Max, maximum measurement; SD, standard deviation; CV, coefficient of variation; NDGS, North Dakota Geological Survey. A dash (—) indicates data are not available.

Measurement or statistic	Lower Teeth								
	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4–m3
Number of specimens	4	4	5	5	8	8	6	5	6
Mean	1.81	1.88	1.88	2.01	2.04	2.04	2.42	1.99	8.55
Min	1.64	1.71	1.83	1.79	1.76	1.88	2.20	1.93	8.20
Max	1.89	2.02	1.94	2.28	2.14	2.20	2.73	2.04	9.04
SD	0.12	0.13	0.05	0.19	0.12	0.12	0.17	0.05	0.28
CV	6.41	7.12	2.45	9.58	5.88	6.05	7.08	2.27	3.30

NDGS Specimen No.	Upper Teeth							
	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
2087	—	—	1.85	—	—	—	—	—
2233	—	—	—	—	—	—	2.03	2.15
2308	2.00	2.29	—	—	—	—	—	—
2653	—	—	—	—	—	—	2.13	2.3
2720	2.03	2.32	1.82	2.35	1.84	2.37	—	—

TABLE A3. Dental measurements (mm) for *Altasciurus leonardi* from Fitterer Ranch. Abbreviations: L, anteroposterior length; W, transverse width; N, number of specimens; M, mean; Min, minimum measurement; Max, maximum measurement; SD, standard deviation; CV, coefficient of variation.

Measurement or statistic	Lower Teeth								
	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4-m3
N	6	6	11	11	12	12	6	5	6
M	1.72	1.58	1.59	1.56	1.68	1.68	1.99	1.64	7.37
Min	1.52	1.46	1.37	1.26	1.51	1.53	1.80	1.50	6.60
Max	1.85	1.72	1.82	1.72	1.85	1.90	2.21	1.76	8.00
SD	0.11	0.10	0.16	0.13	0.12	0.11	0.16	0.11	0.53
CV	6.28	6.20	10.01	8.55	7.00	6.60	8.23	6.40	7.19

Measurement or statistic	Upper Teeth									
	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P4-M3	P3-M3
N	6	5	8	8	2	2	3	3	2	2
M	1.75	1.98	1.43	1.85	1.41	2.04	1.63	1.85	6.04	6.59
Min	1.66	1.82	1.24	1.65	1.35	1.94	1.53	1.83	5.88	6.39
Max	1.96	2.13	1.62	2.20	1.46	2.13	1.75	1.88	6.20	6.79
SD	0.12	0.14	0.13	0.19	0.08	0.13	0.11	0.03	0.23	0.28
CV	6.72	7.00	8.76	10.20	5.54	6.60	6.91	1.36	3.75	4.29

TABLE A4. Dental measurements (mm) for *Agnotocastor praetereadens* from Fitterer Ranch. Abbreviations: L, anteroposterior length; W, transverse width; N, number of specimens; M, mean; Min, minimum measurement; Max, maximum measurement; SD, standard deviation; CV, coefficient of variation. A dash (—) indicates data are not available.

Measurement or statistic	Lower Teeth										
	dp4L	dp4W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4-m3
N	2	2	13	13	18	18	9	9	7	6	6
M	3.05	2.31	4.10	3.48	3.24	3.52	3.20	3.65	3.05	3.08	13.37
Min	2.85	2.31	3.58	3.03	3.00	3.15	2.93	3.34	2.66	2.75	12.96
Max	3.25	—	4.74	3.85	4.00	4.16	3.50	3.93	3.32	3.20	14.09
SD	0.28	—	0.36	0.24	0.25	0.21	0.19	0.15	0.23	0.17	0.46
CV	9.27	—	8.89	6.90	7.84	5.90	6.07	4.16	7.49	5.41	3.41

Measurement or statistic	Upper Teeth											
	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P4-M3	P3-M3
N	1	1	8	8	11	11	6	5	7	6	1	1
M	1.42	1.39	3.60	4.12	2.95	3.77	2.95	3.74	2.53	3.09	11.46	12.79
Min	—	—	3.39	3.85	2.84	3.25	2.71	3.44	2.30	2.72	—	—
Max	—	—	3.72	4.50	3.12	4.04	3.15	3.93	2.95	3.36	—	—
SD	—	—	0.11	0.21	0.09	0.26	0.14	0.19	0.21	0.23	—	—
CV	—	—	2.94	5.19	3.20	6.93	4.82	4.97	8.29	7.59	—	—

TABLE A5. Dental measurements (mm) of *Adjidaumo minimus* from Fitterer Ranch. Abbreviations: dp, deciduous lower premolar; dP, deciduous upper premolar; p, lower premolar; P, upper premolar; m, lower molar; M, upper molar; L, anteroposterior length; W, transverse width; Min, minimum measurement; Max, maximum measurement; SD, standard deviation; CV, coefficient of variation. A dash (—) indicates data are not available.

Measurement or statistic	Lower Teeth										
	dp4L	dp4W	p4L	p4W	m1L <sup>a</sup>	m1W <sup>a</sup>	m2L	m2W	m3L	m3W	p4–m3
Number of specimens	5	5	54	55	167	167	37	37	52	51	14
Mean	0.69	0.51	0.72	0.66	0.87	0.83	0.83	0.85	0.77	0.75	3.33
Min	0.63	0.48	0.57	0.53	0.72	0.63	0.65	0.74	0.54	0.62	3.04
Max	0.76	0.53	0.87	0.87	1.07	1.02	0.95	0.97	0.92	1.04	3.64
SD	0.06	0.03	0.07	0.06	0.07	0.07	0.07	0.06	0.07	0.07	0.18
CV	8.01	5.37	9.13	8.54	7.81	8.33	8.21	7.06	9.35	9.45	5.27

Measurement or statistic	Upper Teeth										
	dP4L	dP4W	P4L	P4W	M1L <sup>a</sup>	M1W <sup>a</sup>	M2L	M2W	M3L	M3W	P4–M3
Number of specimens	13	13	52	50	163	152	13	13	14	15	2
Mean	0.74	0.72	0.74	0.81	0.83	0.89	0.82	0.95	0.60	0.67	3.23
Min	0.64	0.58	0.60	0.62	0.65	0.72	0.75	0.83	0.50	0.52	3.22
Max	0.92	0.81	0.88	0.96	1.01	1.07	0.95	1.08	0.82	0.86	3.23
SD	0.08	0.07	0.06	0.07	0.06	0.07	0.07	0.08	0.09	0.09	—
CV	10.59	9.54	8.45	8.80	7.72	7.94	8.15	8.07	14.98	13.13	—

<sup>a</sup>Including isolated teeth of either M1/m1 or M2/m2.

TABLE A6. Dental measurements (mm) of *Adjidaumo minimus* from Pipestone Springs, Montana (topotypic sample including those previously cited by Black, 1965). Abbreviations: p, lower premolar; P, upper premolar; m, lower molar; M, upper molar; L, anteroposterior length; W, transverse width; Min, minimum measurement; Max, maximum measurement; SD, standard deviation; CV, coefficient of variation. A dash (—) indicates data are not available.

Measurement or statistic	Lower Teeth									
	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4–m3	
Number of specimens	9	9	11	11	8	8	4	4	3	
Mean	0.69	0.65	0.88	0.82	0.84	0.86	0.79	0.74	3.38	
Min	0.64	0.56	0.81	0.75	0.75	0.81	0.67	0.70	3.20	
Max	0.74	0.72	0.95	0.90	0.91	0.90	0.90	0.78	3.49	
SD	0.04	0.05	0.05	0.05	0.06	0.03	0.09	0.03	0.16	
CV	5.05	7.76	5.39	5.69	7.42	3.40	11.92	4.45	4.65	

Measurement or statistic	Upper Teeth			
	P4L	P4W	M1L	M1W
Number of specimens	1	1	5	5
Mean	0.73	0.77	0.83	0.93
Min	—	—	0.82	0.89
Max	—	—	0.86	0.98
SD	—	—	0.02	0.04

**TABLE A7.** Dental measurements (mm) of *Adjidaumo minutus* from Fitterer Ranch. Abbreviations: dp, deciduous lower premolar; dP, deciduous upper premolar; p, lower premolar; P, upper premolar; m, lower molar; M, upper molar; L, anteroposterior length; W, transverse width; Min, minimum measurement; Max, maximum measurement; SD, standard deviation; CV, coefficient of variation. A dash (—) indicates data are not available.

Lower Teeth											
Measurement or statistic	dp4L	dp4W	p4L	p4W	m1L <sup>a</sup>	m1W <sup>a</sup>	m2L	m2W	m3L	m3W	p4–m3
Number of specimens	1	1	8	8	14	14	9	9	5	5	7
Mean	0.85	0.50	1.05	0.99	1.09	1.13	1.11	1.18	1.15	1.05	4.78
Min	—	—	0.94	0.94	1.00	1.05	0.96	1.10	1.02	0.97	4.30
Max	—	—	1.18	1.02	1.17	1.21	1.19	1.26	1.25	1.15	5.20
SD	—	—	0.08	0.03	0.06	0.05	0.07	0.05	0.11	0.07	0.28
CV	—	—	7.51	2.64	5.41	4.64	6.48	4.48	9.16	6.83	5.96

Upper Teeth										
Specimen No. and mean	dP4L	dP4W	P4L	P4W	M1L <sup>a</sup>	M1W <sup>a</sup>	M2L	M2W	M3L	M3W
USNM PAL 643437	—	—	—	—	—	—	1.03	1.36	0.81	1.08
USNM PAL 643391	—	—	—	—	0.94	1.16	—	—	—	—
NDGS 2296	—	—	—	—	0.98	1.23	—	—	—	—
NDGS 2321	—	—	—	—	1.13	1.25	—	—	—	—
NDGS 2046	0.92	0.81	—	—	—	—	—	—	—	—
Mean	—	—	—	—	1.02	1.21	—	—	—	—

<sup>a</sup>Including isolated teeth of either M1/m1 or M2/m2.

**TABLE A8.** Dental measurements (mm) for *Paradjidaumo trilophus* from Fitterer Ranch. Abbreviations: dp, deciduous lower premolar; dP, deciduous upper premolar; p, lower premolar; P, upper premolar; m, lower molar; M, upper molar; L, anteroposterior length; W, transverse width; Min, minimum measurement; Max, maximum measurement; SD, standard deviation; CV, coefficient of variation. A dash (—) indicates data are not available.

Lower Teeth											
Measurement or statistic	dp4L	dp4W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4–m3
Number of specimens	9	9	32	31	62	62	34	33	21	19	24
Mean	1.30	0.97	1.36	1.25	1.27	1.32	1.29	1.40	1.27	1.18	5.49
Min	1.13	0.86	1.18	1.12	1.01	1.11	1.14	1.22	1.14	1.03	5.00
Max	1.41	1.02	1.49	1.50	1.54	1.56	1.57	1.72	1.45	1.34	6.29
SD	0.09	0.05	0.07	0.09	0.09	0.10	0.09	0.10	0.08	0.07	0.29
CV	6.62	5.06	5.00	7.06	7.24	7.51	7.22	7.20	6.60	6.01	5.33

Upper Teeth										
Measurement or statistic	dP4L	dP4W	P4L	P4W	M1L	M1W	M2 L	M2W	M3L	M3W
Number of specimens	9	10	10	9	29	28	3	3	3	3
Mean	1.10	1.13	1.24	1.33	1.21	1.38	1.18	1.37	0.91	1.15
Min	0.98	1.01	1.06	1.26	1.02	1.17	1.10	1.29	0.82	1.14
Max	1.29	1.26	1.37	1.43	1.38	1.59	1.23	1.45	0.96	1.15
SD	0.09	0.08	0.10	0.05	0.09	0.11	—	—	—	—
CV	7.85	6.73	7.92	3.79	7.46	7.87	—	—	—	—

TABLE A9. Comparison of mean dental measurements (mm) of *Paradjidaumo trilophus* from different localities. Abbreviations and references for localities: PS, Pipestone Springs, Montana (Black, 1965:29–30); Neb, Sioux County, Nebraska (Korth, 1980: table 2); various, Canyon Ferry, Montana, and Slim Buttes and Blue Ash, South Dakota (Korth, 2013: table 2); FR, Fitterer Ranch (this volume, Table A8). Other abbreviations: NALMA, North American Land Mammal Age; p, lower premolar; P, upper premolar; m, lower molar; M, upper molar; L, anteroposterior length; W, transverse width. A dash (—) indicates data are not available.

		Lower Teeth								
Locality	NALMA	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4–m3
PS	Chadronian	1.41	1.36	1.44	1.51	1.38	1.54	1.29	1.34	5.70
Neb	Orellan	1.49	1.37	1.43	1.47	1.40	1.49	1.38	1.30	5.73
Various	Chadronian-Whitneyan	1.37	1.28	1.36	1.43	1.31	1.42	1.36	1.26	5.60
FR		1.36	1.25	1.27	1.32	1.29	1.40	1.27	1.18	5.49

		Upper Teeth								
Locality	NALMA	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P4–M3
PS	Chadronian	1.30	1.40	1.40	1.60	1.30	1.60	0.90	1.30	5.20
Neb	Orellan	1.51	1.52	1.39	1.60	1.24	1.60	0.97	1.36	5.33
Various	Chadronian-Whitneyan	1.30	1.42	1.30	1.42	1.24	1.48	—	—	—
FR		1.24	1.33	1.21	1.38	1.17	1.37	0.91	1.15	—

TABLE A10. Dental measurements (mm) for *Heliscomys senex* from Fitterer Ranch. Abbreviations: L, anteroposterior length; W, transverse width; m, lower molar; M, upper molar; p, lower premolar; P, upper premolar; Min, minimum measurement; Max, maximum measurement; SD, standard deviation; CV, coefficient of variation. A dash (—) indicates data are not available.

		Lower Teeth					
Measurement or statistic	p4L	p4W	m1 or m2L	m1 or m2W	m3L	m3W	
Number of specimens	1	1	30	32	6	7	
Mean	0.63	0.49	0.81	0.80	0.62	0.62	
Min	—	—	0.72	0.68	0.58	0.57	
Max	—	—	0.92	0.88	0.67	0.71	
SD	—	—	0.06	0.06	0.03	0.05	
CV	—	—	6.83	7.08	5.49	8.56	

		Upper Teeth						
Measurement or statistic	dP4L	dP4W	P4L	P4W	M1 or M2L	M1 or M2W	M3L	M3W
Number of specimens	1	1	3	3	4	3	1	1
Mean	0.62	0.65	0.63	0.74	0.71	0.83	0.58	0.70
Min	—	—	0.57	0.70	0.69	0.76	0.59	0.62
Max	—	—	0.71	0.78	0.75	0.89	0.66	0.75
SD	—	—	0.07	0.04	0.03	0.07	0.03	0.06
CV	—	—	11.76	5.41	3.81	7.87	5.45	8.16

TABLE A11. Mean measurements (mm) of lower cheek teeth of species of *Heliscomys* and relative lengths of p4 and m1. Measurements are from Wood (1935: table II) for holotype of *H. senex*, Wood (1939: table 1) for *H. hatcheri*, Korth et al. (1991: table 1) for *H. ostranderi*, and Wood (1935: table I) and Galbreath (1953: table 11) for *H. vetus*. Abbreviations: p, lower premolar; m, lower molar; L, anteroposterior length; W, transverse width; FR, Fitterer Ranch sample.

Taxon	p4L	p4W	m1-2L	m1-2W	m3L	m3W	p4L/m1L
<i>H. senex</i> (FR)	0.63	0.49	0.81	0.80	0.62	0.62	0.78
<i>H. senex</i> (holotype)	0.62	0.56	0.83	0.86	0.72	0.69	0.75
<i>H. hatcheri</i>	0.63	0.61	0.91	0.90	0.77	0.76	0.69
<i>H. ostranderi</i>	0.49	0.52	0.81	0.79	0.62	0.64	0.63
<i>H. borealis</i> (FR)	0.53	0.72	0.98	0.95	0.76	0.77	0.63
<i>H. vetus</i>	0.51	0.57	0.85	0.84	0.67	0.66	0.60

TABLE A12. Dental measurements (mm) for *Heliscomys borealis* from Fitterer Ranch. Abbreviations: m, lower molar; M, upper molar; p, lower premolar; P, upper premolar; L, anteroposterior length; W, transverse width; Min, minimum measurement; Max, maximum measurement; SD, standard deviation; CV, coefficient of variation. A dash (—) indicates data are not available.

Measurement or statistic	Lower Teeth							
	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W
Number of specimens	1	1	7	8	6	6	2	2
Mean	0.53	0.72	0.98	0.95	0.93	0.99	0.76	0.77
Min	—	—	0.89	0.90	0.88	0.95	0.75	0.73
Max	—	—	1.06	0.99	1.00	1.06	0.76	0.81
SD	—	—	0.06	0.04	0.06	0.04	—	—
CV	—	—	6.02	3.71	6.34	4.41	—	—
Measurement or statistic	Upper Teeth							
	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W
Number of specimens	1	1	8	8	7	7	4	4
Mean	0.49	0.60	0.81	0.94	0.85	0.96	0.75	0.84
Min	—	—	0.72	0.77	0.83	0.93	0.73	0.80
Max	—	—	0.89	1.03	0.87	1.00	0.78	0.87
SD	—	—	0.06	0.08	0.01	0.03	0.02	0.03
CV	—	—	7.08	8.66	1.58	2.79	2.95	3.57



TABLE A13. Dental measurements (mm) and proportions for lower molars of *Eumys brachyodus* from Fitterer Ranch. Abbreviations: m, lower molar, L, anteroposterior length; W, transverse width; Min, minimum measurement; Max, maximum measurement; SD, standard deviation; CV, coefficient of variation. A dash (—) indicates data are not available.

Measurement or statistic	m1L	m1W	m2L	m2W	m3L	m3W	m1-m3	m1L/W	m2L/W	m3L/W
<b>All Sampling Intervals</b>										
Number of specimens	167	179	215	216	175	171	159	165	211	170
Mean	2.39	1.85	2.25	2.07	2.35	2.02	7.08	1.29	1.09	1.17
Min	2.00	1.57	1.84	1.70	1.98	1.64	6.33	1.04	0.90	1.00
Max	2.77	2.24	2.75	2.51	2.71	2.52	8.06	1.57	1.29	1.44
SD	0.16	0.13	0.16	0.14	0.16	0.14	0.34	0.07	0.07	0.08
CV	6.59	7.05	7.20	6.67	6.83	7.11	4.82	5.79	6.32	6.64
<b>Sampling Intervals 1–2</b>										
Number of specimens	14	16	27	27	23	23	18	14	26	23
Mean	2.47	1.91	2.36	2.12	2.36	2.02	7.05	1.30	1.12	1.17
SD	0.16	1.68	2.01	1.81	2.01	1.78	6.44	0.12	0.96	1.00
CV	6.41	2.24	2.75	2.46	2.60	2.29	7.68	9.41	1.29	1.35
<b>Sampling Intervals 3</b>										
Number of specimens	7	7	7	7	7	7	7	7	7	7
Mean	2.30	1.82	2.28	2.08	2.38	2.09	7.00	1.27	1.10	1.14
SD	0.12	0.11	0.16	0.11	0.13	0.14	0.35	0.06	0.05	0.06
CV	5.08	5.98	6.90	5.31	5.33	6.92	5.01	5.11	4.67	5.37
<b>Sampling Intervals 4–5</b>										
Number of specimens	126	133	164	162	131	127	129	125	159	126
Mean	2.39	1.86	2.22	2.06	2.35	2.02	7.08	1.29	1.08	1.16
SD	0.16	0.13	2.04	0.00	2.21	1.84	6.81	0.07	0.00	1.20
CV	6.70	7.01	2.69	2.47	2.71	2.36	8.06	5.35	1.26	1.35
<b>Sampling Intervals 6</b>										
Number of specimens	17	20	12	15	9	9	4	17	12	9
Mean	2.38	1.82	2.32	2.12	2.35	2.00	7.19	1.31	1.11	1.18
SD	0.13	0.12	0.14	0.15	0.21	0.18	0.22	0.06	0.10	0.13
CV	5.47	6.41	5.92	7.11	8.73	9.16	3.08	4.64	9.18	10.67
<b>Sampling Intervals 7</b>										
Number of specimens	2	2	3	3	3	3	3	2	3	3
Mean	2.53	2.19	2.46	2.16	2.51	2.17	7.07	1.16	1.14	1.17
SD	—	—	0.14	0.17	0.11	0.32	0.75	—	0.10	0.13
CV	—	—	5.76	8.03	4.22	14.72	10.56	—	8.67	10.95

**TABLE A14.** Dental measurements (mm) and proportions for upper molars of *Eumys brachyodus* from Fitterer Ranch. Abbreviations: M, upper molar; L, anteroposterior length; W, transverse width; Min, minimum measurement; Max, maximum measurement; SD, standard deviation; CV, coefficient of variation. A dash (—) indicates data are not available.

Measurement or statistic	M1L	M1W	M2L	M2W	M3L	M3W	M1-M3	M1L/W
<b>All Sampling Intervals</b>								
Number of specimens	42	47	43	43	37	37	22	39
Mean	3.10	2.12	2.13	2.09	1.70	1.88	7.05	1.47
Min	2.66	1.67	1.81	1.66	1.30	1.58	6.33	1.22
Max	3.57	2.53	2.51	2.42	2.07	2.21	7.70	1.64
SD	0.26	0.19	0.17	0.18	0.15	0.17	0.42	0.10
CV	8.29	9.18	7.95	8.71	8.72	8.86	5.89	6.99
<b>Sampling Intervals 1–2</b>								
Number of specimens	6	6	5	5	2	2	1	6
Mean	3.25	2.22	2.17	2.22	1.71	1.99	7.04	1.47
SD	0.24	0.11	0.14	0.09	0.18	0.08	—	0.13
CV	7.36	4.95	6.65	4.26	10.75	4.26	—	8.62
<b>Sampling Intervals 3</b>								
Number of specimens	1	1	1	1	2	2	1	1
Mean	2.81	2.07	2.04	2.01	1.71	1.93	6.56	1.36
<b>Sampling Intervals 4–5</b>								
Number of specimens	27	29	32	31	25	25	18	27
Mean	3.07	2.08	2.10	2.05	1.71	1.88	7.05	1.48
SD	0.26	0.22	0.17	0.19	0.16	0.17	0.42	0.10
CV	8.48	10.33	8.01	9.14	9.36	9.12	5.98	6.54
<b>Sampling Intervals 6</b>								
Number of specimens	8	11	5	6	8	8	2	6
Mean	3.11	2.17	2.29	2.15	1.67	1.84	7.31	1.41
SD	0.25	0.16	0.14	0.17	0.12	0.19	0.47	0.10
CV	7.87	7.38	6.11	7.92	7.47	10.13	6.49	6.94

TABLE A15. Occurrence of rodent species at Fitterer Ranch. Abbreviations for ages: C, Clarkforkian; Ch, Chadronian; Or, Orellan; Wh, Whitneyan. An X indicates a species occurs in a particular interval; a dash (—) indicates that it does not.

Species	Sampling intervals				Known range
	1–2	3	4–5	6	
<i>Ischyromys typus</i>	X	X	X	X	Or-Wh
<i>Paradjidaumo trilophus</i>	X	X	X	X	Ch-Wh
<i>Eumys brachyodus</i>	X	X	X	X	Wh
<i>Adjidaumo minimus</i>	X	X	X	X	Ch-?Or
<i>Willeumys viduus</i>	X	—	X	X	Or
<i>Hesperopetes cf. blacki</i>	X	—	—	X	Wh
<i>Prosciurus hogansoni</i> , new species	X	—	X	X	Fitterer Ranch
<i>Altasciurus leonardi</i> , new species	X	—	X	X	Fitterer Ranch
<i>Heliscomys borealis</i> , new species	X	—	X	X	Fitterer Ranch
<i>Adjidaumo minutus</i>	X	—	X	X	Or
cf. <i>Microparamys</i> sp.	X	—	—	—	C-Ch
<i>Oligotheriomys magnus</i>	—	—	X	—	Or
<i>Cedromus wardi</i>	—	—	X	—	Or
<i>Kirkomys</i> sp.	—	—	X	—	Fitterer Ranch
<i>Eumys lammersi</i> , new species	—	—	X	—	Fitterer Ranch
<i>Agnotocastor praetereadens</i>	—	—	X	X	Wh
<i>Heliscomys senex</i>	—	—	X	X	Or
<i>Heliscomys cf. medius</i>	—	—	—	X	Wh

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