

# *PaleoBios*

---

OFFICIAL PUBLICATION OF THE UNIVERSITY OF CALIFORNIA MUSEUM OF PALEONTOLOGY



Suzanne G. Strait, Patricia A. Holroyd, Carrie A. Denvir and Brian D. Rankin (2016). Early Eocene (Wasatchian) rodent assemblages from the Washakie Basin, Wyoming.

**Cover photo:** Howard Hutchison excavating at V71237 (Lower Meniscotherium) during July 1971. Polaroid image from field notes of Barbara T. Waters, on file at UCMP.

**Citation:** Strait, S. G., Holroyd, P. A., Denvir, C. A. & Rankin, B. D. 2016. Early Eocene (Wasatchian) rodent assemblages from the Washakie Basin, Wyoming. *PaleoBios*, 33(1). [ucmp\\_paleobios\\_29986](#).

## Early Eocene (Wasatchian) rodent assemblages from the Washakie Basin, Wyoming

SUZANNE G. STRAIT<sup>1</sup>, PATRICIA A. HOLROYD<sup>2\*</sup>, CARRIE A. DENVIR<sup>1</sup> and BRIAN D. RANKIN<sup>2</sup>

<sup>1</sup>Department of Biological Sciences, Marshall University, Huntington, West Virginia 25755 U.S.A.

<sup>2</sup>University of California Museum of Paleontology, Berkeley, California 94720 U.S.A.

Rodent assemblages are described from two early Eocene (Wasatchian North American Land Mammal Age; Graybullian subage) localities from the Main Body of the Wasatch Formation in the Washakie Basin, Wyoming. One locality (UCMP V71237) represents a catastrophic death assemblage and the other (UCMP V71238) is a channel lag which immediately overlies it. Quarrying and screen-washing at these localities has resulted in the recovery of 81 specimens from V71237 and 224 specimens from V71238 and comprising a uniquely rich, stratigraphically controlled sample. The rodent fauna from these localities include *Paramys copei*, *P. taurus*, *Lophiparamys murinus*, *Microparamys hunterae*, *Tuscahomys ctenodactylops*, and *Knightomys* cf. *K. minor*. These specimens provide substantial new morphological data for the previously poorly-known *M. hunterae*, *T. ctenodactylops*, and *L. murinus*. Comparison of relative abundances demonstrates that *T. ctenodactylops* is the most common in both localities, but that the smaller bodied species *M. hunterae* and *Knightomys* cf. *K. minor* are much rarer in the lag deposit.

**Keywords:** Wasatch Formation, Mammalia, Rodentia, diversity, abundance

### INTRODUCTION

Rodents are still relatively poorly known from North American early Eocene assemblages, and localities that produce abundant, relatively complete specimens are rare. Here we describe two rodent assemblages that have produced both. These assemblages derive from two localities, UCMP V71237 (Lower *Meniscotherium*) and UCMP V71238 (Upper *Meniscotherium*) that occur approximately 40 meters above the base of the Wasatch Formation in the Washakie Basin (Fig. 1), an area that in the Eocene had low topographic relief with permanently saturated soils, localized ponds, and large channels (Roehler 1993). UCMP V71237 is an approximately one meter thick muddy siltstone unit that contains a catastrophic assemblage that appears to have formed within days after the death of the animals (Williamson 2001). This locality is dominated by remains of the eponymous condylarth *Meniscotherium tapiacitum* Cope, 1882b. Fossils were hand-quarried, and the remaining matrix was screen-washed to recover additional specimens (J.H. Hutchison, pers. comm. and field notes on file at UCMP). Some of the rodent specimens described here were found during the initial quarrying operation, but the majority were recovered by subsequent screen-washing.

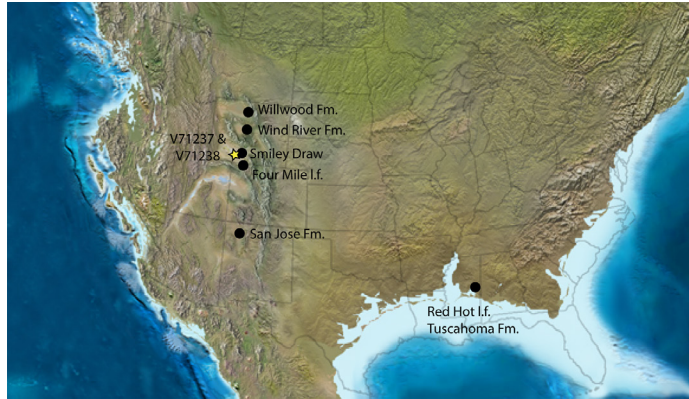
\*author for correspondence

UCMP V71238 is a massive, moderately-indurated sandstone unit that immediately overlies the mudstone of V71237 (Fig. 2). In V71238 fossils are found as lag in approximately 10 cm at the base of this sandstone unit and appear to represent a direct reworking of the underlying mudstone unit. Fossils are recovered from this unit primarily as eroded float, and weathered parts of this unit were screen-washed to recover small specimens.

Williamson and Lucas (1992) and Williamson (2001) presented brief faunal lists for UCMP V71237; Table 1 provides an updated faunal list and Table 2 a comparison between localities V71237 and V71238 based on data generated by more recent work with the UCMP collection. These new data have greater biostratigraphic utility. Rankin and Holroyd (2014) inferred both UCMP V71237 and V71238 to be early Wasatchian (Wa3 of Gingerich 1983; Graybullian subage) based on the co-occurrence of *Homogalax protapirinus* (Wortman, 1896), *Cardiolphus semihians* (Cope, 1882a), *Tetonius matthewi* Bown and Rose, 1987, *Cantius mckennai* Gingerich and Simons, 1977, and *Haplomyilus speirianus* (Cope, 1880b) (see biostratigraphic ranges for these taxa in Gingerich 1983, 1991, Bown and Rose 1987, Clyde 1997, Chew 2005). Based on the range of this biozone in the Bighorn Basin, the age of V71237 and V71238 can be estimated to be approximately 54 Ma (Wing et al. 2000).

**Citation:** Strait, S. G., Holroyd, P. A., Denvir, C. A. & Rankin, B. D. 2016. Early Eocene (Wasatchian) rodent assemblages from the Washakie Basin, Wyoming. *PaleoBios*, 33(1). ucmp\_paleobios\_29986. **Permalink:** <http://escholarship.org/uc/item/6946n7r3>

**Copyright:** Items in eScholarship are protected by copyright, with all rights reserved, unless otherwise indicated.



**Figure 1.** Map showing locations of the Lower (UCMP V71237) and Upper (UCMP V71238) *Meniscotherium* localities and the other rodent faunas discussed in the text.



**Figure 2.** Outcrop of V71237 and V71238, taken in July 2015. Second author (approximately 160 cm for scale).

Together, the fauna from these two localities can serve as a window into the composition of an early Eocene rodent fauna from a floodplain environment. Many previously-described Wasatchian rodents are from surface collections that may have accumulated over considerable spans of time and also tend to be size biased. Additionally, few single localities have sample sizes that approach UCMP V71237 and V71238. Comparison of the two localities provides insights into how differences in depositional environment can produce significantly different perceptions of dominance and relative abundances of small mammals.

## SYSTEMATIC PALEONTOLOGY

### Abbreviations and nomenclature

**FMNH** – Field Museum of Natural History, Chicago, Illinois, USA; **UCMP** – University of California Museum of Paleontology, Berkeley, California, USA; **UM** – University of Michigan, Ann Arbor, Michigan, USA; **UW** – University of Wyoming, Laramie, Wyoming, USA. Upper teeth are designated by upper case letters; teeth of the lower dentition by lower case letters. Specimens bearing more than one tooth are indicated by dashed tooth positions (e.g., M1-2); specimens whose position is indeterminate are indicated by slashed tooth positions (e.g., M1/2). All measurements are in mm and were taken on a Nikon SMZ800 or Leica M125 with ocular micrometers. All measurements were repeated for precision by different researchers. Length = L; width = W; trigonid width = TrW; talonid width = TaW; observed range = OR; standard deviation = SD. Dental nomenclature is as shown in Figure 3 and follows Wood (1962) and Korth (1994).

RODENTIA **BOWDICH, 1821**  
 SCIUROMORPHA **BRANDT, 1855**  
 ISCHYROMYIDAE **ALSTON, 1876**  
 PARAMYINAE (**HAECKEL, 1895**)

*Paramys* **LEIDY, 1871**

*Paramys copei* **LOOMIS, 1907**

Fig. 4

**Referred specimen—UCMP V71238:** UCMP 148758, LM1/2.

**Description and Discussion—UCMP 148758** is a relatively large (L= 3.1, W=3.4) isolated M1/2 that conforms morphologically to those described for *Paramys copei* by Wood (1962), Korth (1984), and Ivy (1990), and is referred here to that taxon.

*Paramys taurus* **WOOD, 1962**

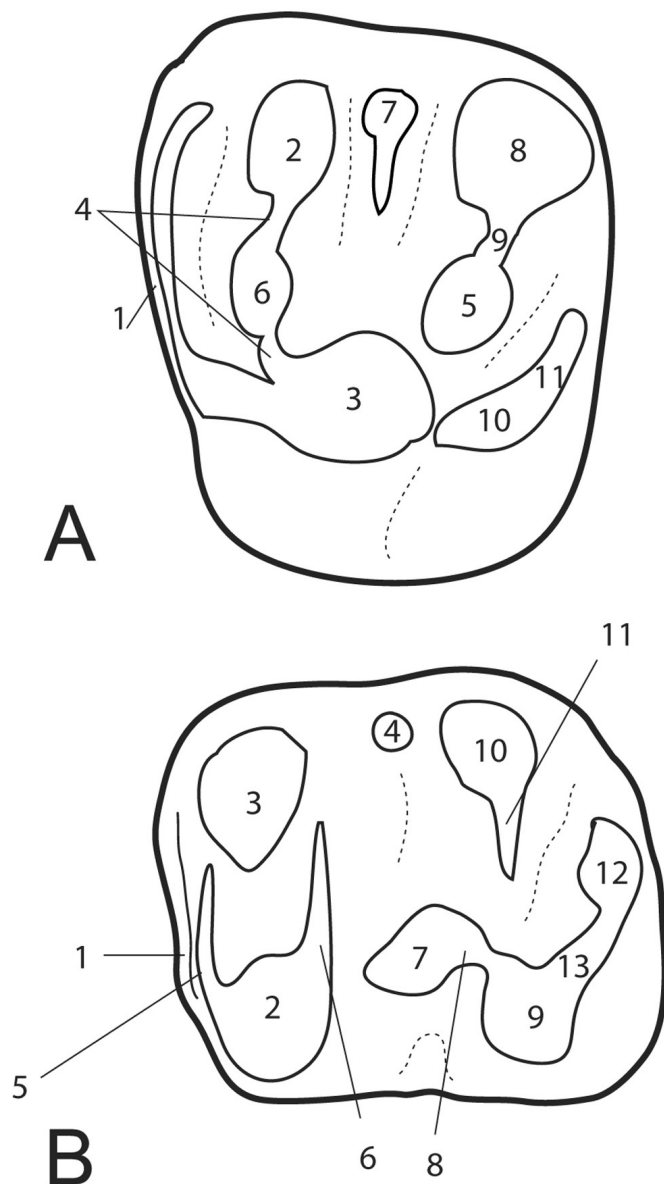
Figs. 4, 5; Tables 3, 4

**Referred specimens—UCMP V71237:** UCMP 148614, 148629, Rp4; UCMP 148630, Lp4; UCMP 148672, Rm1/2; UCMP 148631, Rm3; UCMP 149222, Right dentary with m3; UCMP 148634, LM3.

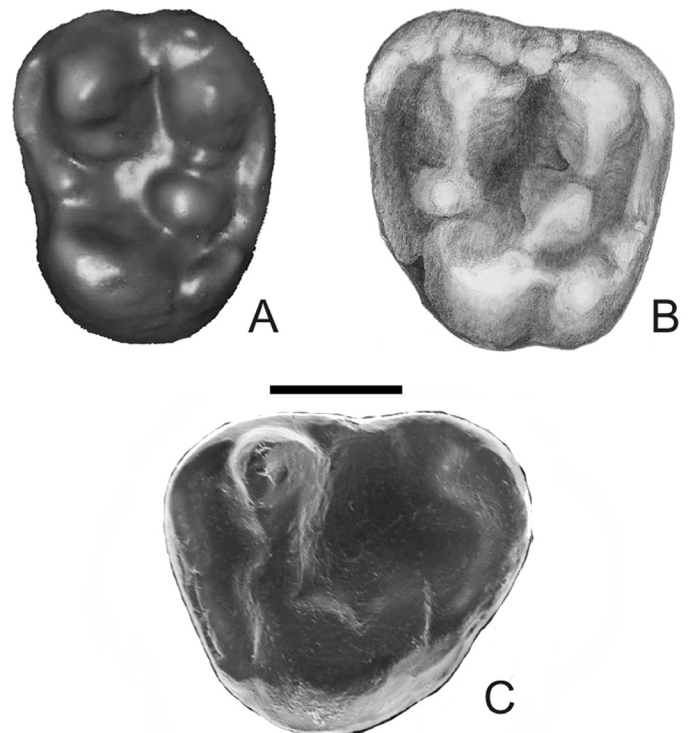
**UCMP V71238:** UCMP 148748, Lp4; UCMP 148749, 151272, Rm1/2; UCMP 148747, Lm1/2; UCMP 148755, 189311, Rm3; UCMP 148751, 148752, 148756, 151273, 151274, Lm3; UCMP 148757, LP4; UCMP 148731, 189305, RM1/2; UCMP 148720, 148759, 151357, LM1/2; UCMP 148784, 189301, LM3.

Table 1. Taxonomic listing of vertebrates from UCMP V71237 and V71238, Wasatch Formation, Wyoming.

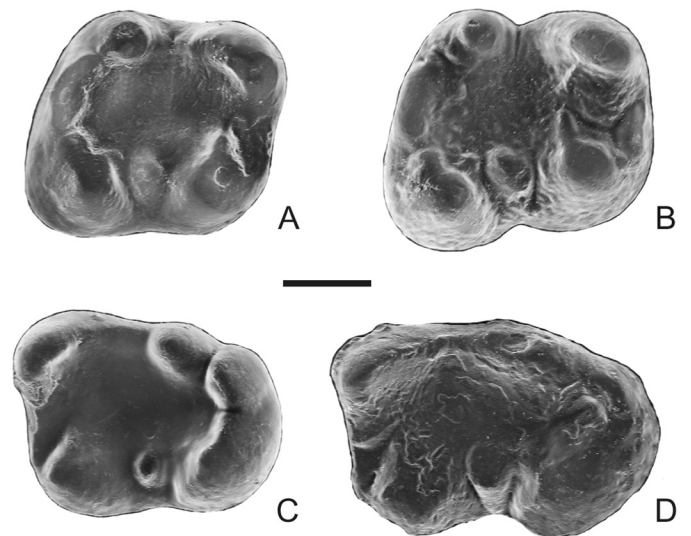
<b>Osteichthyes</b> Huxley, 1880	<i>Peradectes protinnominatus</i> McKenna, 1960	Genus and species indeterminate
Amiiformes Hay, 1929	<i>Miniperadectes</i> sp. Bown and Rose, 1979	Primates Linnaeus, 1758
Amiidae Bonaparte, 1838	Erinacemorpha Gregory, 1910	Microsypidae Osborn and Wortman, 1892
Genus and species indeterminate	Adapisoricidae Schlosser, 1887	<i>Microsyps</i> sp. Leidy, 1872
Lepisosteiformes Hay, 1929	Genus and species indeterminate	cf. <i>Choctawius</i> sp. Beard and Dawson, 2009
Lepisosteidae Cuvier, 1825	Soricomorpha Gregory, 1910	Paromomyidae Simpson, 1940
cf. <i>Lepisosteus</i> sp. Lacépède, 1803	Nyctitheriidae Simpson, 1928	<i>Phenacolemur</i> sp. Matthew, 1915
<b>Reptilia</b> Linnaeus, 1758	<i>Leptacodon</i> sp. Matthew and Granger, 1921	Omomyidae Trouessart, 1879
Crocodylia Gmelin, 1789 sensu Benton and Clark, 1988	<i>Wyonycteris</i> sp. Gingerich, 1987	<i>Tetoniurus matthewi</i> Bown and Rose, 1987
Alligatoridae Cuvier, 1807 sensu Norell et al., 1994	Leptictida McKenna, 1975	<i>Tetonoidea pearcei</i> Gazin, 1962
cf. <i>Allognathosuchus</i> sp. Mook, 1921	Leptictidae Gill, 1872	Adapidae Trouessart, 1879
Squamata Opper, 1811	<i>Palaeictops</i> sp. Matthew, 1899	<i>Cantius mckennai</i> Gingerich and Simons, 1977
Anguimorpha Fürbringer, 1900 sensu Estes et al., 1988	<i>Prodiacodon</i> sp. Matthew, 1929	<i>Copelernus</i> sp. Gingerich and Simons, 1977
Genus and species indeterminate	Order Uncertain	Condylarthra Cope, 1881
Iguania Cuvier, 1817	Aptenodontidae Matthew, 1910	Hypodontidae Trouessart, 1879
Genus and species indeterminate	Genus and species indeterminate	<i>Hyposodus paulus</i> Leidy, 1870
Testudines Batsch, 1788	Cimolestia McKenna, 1975	Apheliscidae Matthew, 1918
Baenidae Cope, 1882a	Didelphodonta McKenna, 1975	<i>Apheliscus</i> sp. Cope, 1875b
<i>Palatobaena gaffneyi</i> Archibald and Hutchison, 1979	Palaeoryctidae Winge, 1917	<i>Haplomylus speiramus</i> (Cope, 1880b)
Kinosternidae Hay, 1892	<i>Aceroryctes dulcis</i> Rankin and Holroyd, 2014	Menisotheriidae Cope, 1874
Genus and species indeterminate	Apatotheria Scott and Jepsen, 1936	<i>Menisotherium tapiacitum</i> Cope, 1882b
Planetochelyidae Hutchison, 2013	Apatemyidae Matthew, 1909	Phenacodontidae Cope, 1881
<i>Planetochelys dithyros</i> Hutchison, 2013	<i>Apatemyx</i> sp. Marsh, 1872	<i>Ectocion osbornianus</i> Cope, 1882a
Family indeterminate	Pantodonta Cope, 1873	Perissodactyla Owen, 1848
<i>Echmatemys testudinea</i> (Cope, 1872)	Coryphodontidae Marsh, 1876a	Equidae Gray, 1821
<b>Aves</b> Linnaeus, 1758	<i>Coryphodon</i> sp. Owen, 1845	<i>Arenalippus</i> (= <i>Hyracotherium</i> ) <i>pernix</i> Marsh, 1876b
Anseriformes Wagler, 1831	Pantolestia McKenna, 1975	Isectolophidae Peterson, 1919
Family indeterminate	Pantolestidae Cope, 1884b	<i>Cardiophus semihians</i> (Cope, 1882a)
Genus and species indeterminate	<i>Amaranthis gregoryi</i> Gazin, 1962	<i>Homogalax protapirinus</i> (Wortman, 1896)
<b>Mammalia</b> Linnaeus, 1758	<i>Palaeosinopa</i> sp. Matthew, 1901	Artiodactyla Owen, 1848
Multituberculata Cope, 1884a	?Pholidota Weber, 1904	Dichobunidae Turner, 1879
Neoplagiulacidae Ameghino, 1890	Palaeanodonta Matthew, 1918	Homacodontinae Marsh, 1894
<i>Ectypodus</i> sp. Matthew and Granger, 1921	Metacheiromyidae Wortman, 1903	<i>Bunophorus robustus</i> Sinclair, 1914
<i>Parectypodus</i> sp. Jepsen, 1930	Genus and species indeterminate	Rodentia Bowdich, 1821
Didelimoiphia Gill, 1872	Tillodonta Marsh, 1875	Ischyromyidae Alston, 1876
Peradectidae Crochet, 1979	Esthonychiidae Cope, 1883	<i>Lophioparamys murinus</i> (Matthew, 1918)
	<i>Esthonyx</i> sp. Cope, 1874	<i>Microparamys hunterae</i> Ivy, 1990
	Carnivora Bowdich, 1821	<i>Paramys taurus</i> Wood, 1962
	Miacidae Cope, 1880a	<i>Paramys copei</i> Loomis, 1907
	Genus and species indeterminate	Cylindrodontidae Miller and Gidley, 1918
	Creodonta Cope, 1875a	<i>Tuscalomys ctenodactylops</i> (Korth, 1984)
	Hyaenodontidae Leidy, 1869	Sciuravidae
	Limnocyoninae Wortman, 1902	<i>Knighthomys</i> cf. <i>K. minor</i> Ivy, 1990



**Figure 3.** Schematic upper (A) and lower molar (B) showing dental nomenclature, modified after Wood (1962) and Korth (1994). Upper molar: 1. anteroloph, 2. paracone, 3. protocone, 4. protoloph, 5. metaconule, 6. protoconule (paraconule of standardized tribosphenic dental nomenclature), 7. mesostyle, 8. metacone, 9. metaloph, 10. hypocone, 11. posteroloph. Lower molar: 1. anterior cingulid, 2. protoconid, 3. metaconid, 4. mesostylid, 5. anterolophid, 6. metalophulid II (metalophid of Wood 1962), 7. mesoconid, 8. ectolophid, 9. hypoconid, 10. entoconid, 11. hypolophid, 12. hypoconulid, 13. posterolophid.



**Figure 4.** *Paramys* spp. upper dentition. A. *Paramys taurus*, UCMP V71238/148757, left P4, B. *Paramys copei*, UCMP V71238/148758, left M1/2, C. *Paramys taurus*, V71237/148634, left M3. Scale bar = 1 mm.



**Figure 5.** Examples of the lower dentition of *Paramys taurus*. A. UCMP V71237/148672, right m1/2, B. UCMP V71238/151272, right m1/2. C. UCMP V71238/151273, left m3, D. UCMP V71238/151274, left m3. Scale bar = 1 mm.

Table 2. Taxonomic comparisons of vertebrates from UCMP V71237 and V71238, Wasatch Formation, Wyoming.

	V71237	V71238	V71237	V71238
Amiidae genus and species indeterminate		X		
cf. <i>Lepisosteus</i> sp.	X	X		
cf. <i>Allognathosuchus</i> sp.		X		
Anguimorpha genus and species indeterminate	X	X		
Iguania genus and species indeterminate		X		
<i>Palatobaena gaffneyi</i>		X		
Kinosternidae genus and species indeterminate		X		
<i>Planetochelys</i> sp.		X		
<i>Echmatemys testudinea</i>	X	X		
Anseriformes genus and species indeterminate		X		
<i>Ectypodus</i> sp.	X	X		
<i>Parectypodus</i> sp.	X	X		
<i>Peradectes protinnominatus</i>	X	X		
<i>Mimoperadectes</i> sp.		X		
Adapisoricidae genus and species indeterminate	X	X		
<i>Leptacodon</i> sp.	X	X		
<i>Wyonycteris</i> sp.	X	X		
<i>Palaeictops</i> sp.	X	X		
<i>Prodiacodon</i> sp.	X	X		
Aptemodontidae genus and species indeterminate	X			
<i>Aceroryctes dulcis</i>	X			
<i>Apatemys</i> sp.	X	X		
<i>Coryphodon</i> sp.	X	X		
<i>Amarammis gregoryi</i>	X	X		
<i>Palaeosinopa</i> sp.	X	X		
Metacheiromyidae genus and species indeterminate			X	
<i>Esthonyx</i> sp.			X	X
Miacidae genus and species indeterminate			X	X
Limnocyoninae genus and species indeterminate			X	X
<i>Microsyoops</i> sp.			X	
cf. <i>Choctawius</i> sp.			X	
<i>Phenacolemur</i> sp.			X	
<i>Tetonius matthewi</i>			X	
<i>Tetonioides pearcei</i>			X	X
<i>Cantius mckennai</i>			X	X
<i>Copelemur</i> sp.				X
<i>Hyopsodus paulus</i>			X	X
<i>Apheliscus</i> sp.				X
<i>Haplomylus speirianus</i>			X	X
<i>Meniscotherium tapiacitum</i>			X	X
<i>Ectocion osbornianus</i>			X	
<i>Arenahippus</i> (= <i>Hyracotherium</i> ) <i>pernix</i>			X	X
<i>Cardiophus semihians</i>			X	X
<i>Homogalax protapirinus</i>			X	X
<i>Bunophorus robustus</i>				X
<i>Lophioperamys murinus</i>			X	X
<i>Microparamys hunterae</i>			X	X
<i>Paramys taurus</i>			X	X
<i>Paramys copei</i>				X
<i>Tuscahomys ctenodactylopus</i>			X	X
<i>Knighthomys</i> cf. <i>K. minor</i>			X	X

**Table 3.** Measurements and descriptive statistics of the upper dentition of *Paramys taurus* from UCMP V71237 and V71238, Wasatch Formation, Wyoming.

	<i>M1/M2</i>		<i>M3</i>	
	L	W	L	W
148720	2.2	2.6		
148731	2.2	2.5		
148759	2.3	2.6		
151357	2.6	3.3		
189305	2.2	2.6		
148634			2.4	2.7
148784			2.4	2.4
189301			2.4	2.7
OR	2.2-2.6	2.5-3.3	2.4	2.4-2.7
Mean	2.3	2.72	2.40	2.60
SD	0.17	0.33	0	0.17

**Table 4.** Measurements and descriptive statistics of the lower dentition of *Paramys taurus* from UCMP V71237 and V71238, Wasatch Formation, Wyoming.

	<i>p4</i>			<i>m1/m2</i>			<i>m3</i>		
	L	TrW	TaW	L	TrW	TaW	L	TrW	TaW
148614	2.3	1.6	1.8						
148629	2.3	1.6	1.9						
148630	2.3	1.5	1.8						
148748	2.2	1.5	1.9						
148672				2.7	2.3	2.5			
148747				-	1.9	2.4			
148749				2.7	2.2	2.2			
151272				2.8	2.2	2.5			
148631							3.2	2.2	2.1
148751							3.3	2.2	2.2
148752							3.3	2.3	2.1
148755							3.1	2.0	2.0
148756							3.1	2.0	2.0
151273							2.8	2.1	1.9
151274							3.3	2.1	2.0
OR	2.2-2.3	1.5-1.6	1.8-1.9	2.7-2.8	1.9-2.3	2.2-2.5	2.8-3.3	2.0-2.3	1.9-2.2
Mean	2.28	1.55	1.85	2.73	2.15	2.40	3.16	2.13	2.04
SD	0.05	0.06	0.06	0.06	0.17	0.14	0.18	0.11	0.10

**Description and Discussion**—These specimens are referred to *Paramys taurus* based on lower teeth with a dominant, obliquely oriented metaconid, trigonid basin restricted to a narrow fissure, strong posterolophids with lophate hypoconulids, talonid cusps marginally placed, and prominent mesoconids. Teeth are variable with wear. In unworn specimens enamel pitting is evident, as are mesostylids. Worn specimens show ectolophid development and posterolophid continuity with the entoconid. The trigonid basin size varies with wear, from a more open condition in unworn specimens but a narrow fissure develops with greater wear. A small accessory cuspule is present on one specimen (UCMP 148752) anterior to the posterolophid. The single P4 (UCMP 148757) from these localities is completely unworn and has equally small hypocone and protoconule. Due to the lack of wear there is no metaloph or protoloph development. There is a small accessory cuspule buccal to the metacone. A small, salient mesostyle is present anterobuccal of the metacone.

MICROPARAMYINAE [WOOD, 1962](#)

*Lophiparamys* [WOOD, 1962](#)

*Lophiparamys murinus* ([MATTHEW, 1918](#))

Fig. 6; Tables 5, 6

**Referred specimens**—UCMP V71237: UCMP 148785, Rp4; UCMP 148786, RP4; UCMP 149221, LP4; UCMP 148674, LM1/2.

**UCMP V71238:** UCMP 148688, 148690, 148691, Lm3; UCMP 151276, LP4; UCMP 235522, LM1/2; UCMP 151277, RM3.

**Emended Diagnosis**—*Lophiparamys murinus* differs from *L. debequensis* [Wood, 1962](#) in its larger size, enamel

**Table 5.** Measurements and descriptive statistics of the lower dentition of *Lophiparamys murinus* from UCMP V71237 and V71238, Wasatch Formation, Wyoming.

	P4		M1/M2		M3	
	L	W	L	W	L	W
148786	1.6	2.2				
149221	1.6	2.2				
151276	1.5	2.0				
148674			1.8	2.2		
235522			2.0	2.3		
151277					2.0	1.8
OR	1.5-1.6	2.0-2.2	1.8-2.0	2.2-2.3	-	-
Mean	1.57	2.13	1.90	2.25	-	-
SD	0.06	0.12	0.14	0.07	-	-

crenulate but less columnar and topographically lower, distinct hypoconulid present on lower molars, anteroposteriorly more transverse upper dentition with shorter protocone arm (*sensu* [Flanagan 1986](#)), P4 metacone is only slightly smaller than the paracone, and P4 lacks a paracone arm (*sensu* [Flanagan 1986](#)). Wood (1962) included as diagnostic characters of *L. murinus* a “strong metalophulid on molars” and accessory cuspules on m3. This character should be emended to a strong metalophulid II on m1-2 and variable development of accessory cuspules of m3. Smaller than *L. woodi* [Guthrie, 1971](#) with coarser crenulations.

**Description**—The following descriptions of lower dentition morphology are additions to those of Matthew (1918), Wood (1962), and Ivy (1990).

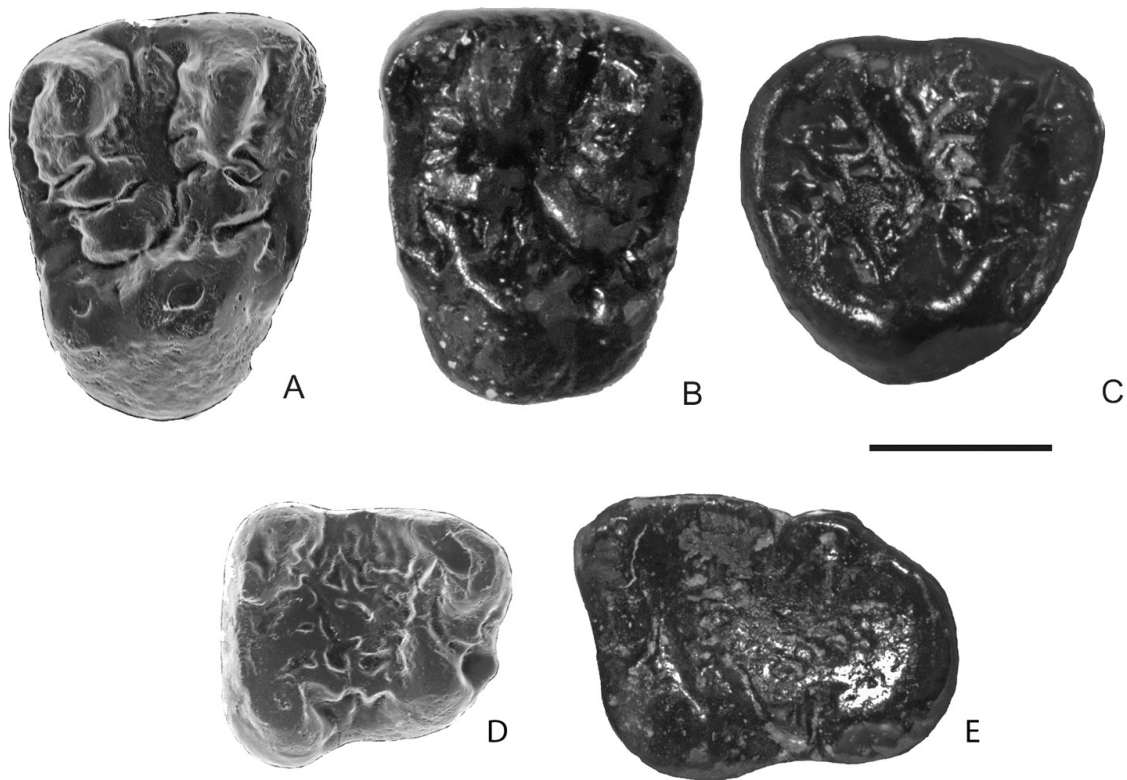
*p4*—The metalophulid II is continuous transversely from the protoconid and ascends up the center of the posterior wall of the metaconid. There is a short, curved anterolophid that arises from the midpoint of the protoconid and terminates at the labial base of the metaconid. A mesoconid is evident, although it is incorporated into the talonid crenulations. A mesostylid is present. The entoconid and hypoconid are distinct. A posterolophid connects the hypoconid to a cuspule just labial of the entoconid, which may represent a hypoconulid.

*m3*—The trigonid crests and basin of the m3 are reduced. The anterolophid is discontinuous with the protoconid, and the metalophulid II is only visible in worn teeth. A distinct mesostylid is present and is similar in size to the mesoconid, however, with wear the mesostylid become less distinctive. In describing the type, Wood (1962) noted the presence of four cuspules between the hypoconid and mesostylid. In the sample at hand, both the hypoconulid and entoconid are present but no additional cuspules are developed, demonstrating the

**Table 6.** Measurements and descriptive statistics of the lower dentition of *Lophiparamys murinus* from UCMP V71237 and V71238, Wasatch Formation, Wyoming.

	<i>p4</i>			<i>m3</i>		
	L	TrW	TaW	L	TrW	TaW
148785	1.6	1.2	1.4			
148688				2.1	1.6	1.5
148690				2.6	1.8	1.7
148691				2.2	1.6	1.5
OR	-	-	-	2.1-2.6	1.6-1.8	1.5-1.7
Mean	-	-	-	2.30	1.67	1.57
SD	-	-	-	0.26	0.12	0.12





**Figure 6.** *Lophiparamys murinus*. **A.** UCMP V71237/148786, right P4, **B.** UCMP V71237/148674, left M1/M2, **C.** UCMP V71238/151277, left M3, **D.** V71237/148785, right p4, **E.** UCMP V71238/148688, right m3. Scale bar = 1 mm.

variability in the crenulate occlusal morphology.

The upper dentition has not been previously described for *Lophiparamys murinus*. Six upper teeth are attributed to *L. murinus* based on size and distinctive crenulate enamel.

**P4**—Unlike the reduced metacone on the P4 of *L. debequensis*, the P4 of *L. murinus* displays a metacone that is only slightly smaller than the paracone. The hypocone is distinct, but smaller than the protocone. A posteroloph extends from the hypocone to the posterolabial corner of the metacone. There is a small, anteroposteriorly compressed mesostyle. The metaconule is doubled, whereas the protoconule is only a single cusp. Due to the crenulated nature of these teeth, both the posteroloph and metaloph are discontinuous. With wear, the lophs become more prominent and converge on the protocone. The anteroloph originates at the midpoint of the protocone. A short protocone crest (sensu Korth 1994) extends between the anteroloph and the protoconule. The paracone arm, observed within the P4 of *L. debequensis* (see Flanagan 1986), is not developed.

**M1/2**—UCMP 148674 and 235522 represent either the

M1 or M2 of *L. murinus*. Both teeth are similar in general morphology to P4 except that the anteroloph on these molars is better developed and more anteriorly projecting.

**M3**—The crown of UCMP 151277 is dominated by a large, rounded protocone and slightly smaller paracone; these cusps are joined by a distinct protoloph. The metacone is indistinct and the area it would normally occupy is merely a flattened, crenulated area confluent with the crenulated trigon basin. No hypocone is present. A small protoconule is developed, however, the presence or absence of a metaconule cannot be determined due to the extent of crenulation. A short, weak metaloph originates from the protocone but only extends approximately to the midpoint of the tooth. The anteroloph arises from near the base of the protocone and extends to the labial edge of the tooth; the enamel of the anteroposteriorly short shelf formed by this loph is crenulate. In comparison to *Lophiparamys debequensis*, the shape of the tooth in *L. murinus* is less triangular and more subrectangular in occlusal outline.

**Discussion**—Specimens of *Lophiparamys* are

comparatively rare in Eocene fossil assemblages. *Lophiparamys murinus* was first described by Matthew (1918) based on an upper and lower dentition. Subsequently, the upper dentition was lost and had never been figured. Ivy (1990) included two additional dentaries with a single molar each. Our sample includes the first occurrence of *L. murinus* from outside the Bighorn Basin and allows us to provide the first detailed description of upper teeth, thereby permitting more diagnostic characters to be identified. The upper teeth described here are relatively primitive among microparamyines due to their subrectangular shape with greater width relative to length when compared to the squarer outline seen in most microparamyines. In its molar proportions, retention of a distinct hypoconulid on the lower molars, distinct conules on upper molars, and less extreme crenulation, *L. murinus* appears to be the least derived species of the genus.

*Lophiparamys woodi* is the most poorly known species of *Lophiparamys*, with only six isolated teeth reported (Guthrie 1971). The original diagnosis for this species is problematic. Guthrie (1971, p. 73) noted as a diagnostic character “lower molars with ... protoconid not connected to anterior cingulum,” even though the only lower tooth position known for *L. woodi* is m3. A distinctive valley, especially evident in unworn specimens, separating the protoconid and anteroloph is primitive for Microparamyini and is most distinctive in posterior molars (Wood 1962, Korth 1984, Ivy 1990). The second diagnostic character of *L. woodi* Guthrie noted was lower molars with the entoconid isolated from posterior cingulum. Entoconid isolation in unworn specimens is diagnostic of Microparamyini as well (Wood 1962). Based on Guthrie’s available sample of *L. woodi*, there are few tooth positions that can be compared across taxa; therefore the distinctiveness between *L. murinus* and *L. woodi* is limited to size and degree of crenulation.

*Microparamys* WOOD, 1959  
*Microparamys hunterae* IVY, 1990  
 (Fig. 7; Tables 7-10)

**Referred specimens**—UCMP V71237: UCMP 148610, right dentary with p4, m1-3; UCMP 148648, 148656, Lp4; UCMP 148671, Lm1; UCMP 148654, 148658, 148659, 149219, 149224, Rm1/2; UCMP 148643, 148660, 148663, Lm1/2; UCMP 148655, Rm3; UCMP 148675, LDP4; UCMP 148650, LP4, UCMP 148638, 152488, RM1-2; UCMP 148611, LM1-2; UCMP 148647, 148651-148653, 148665, 148667, 148670, RM1/2; UCMP 148640, 148641, 148645, 148666, 148669, LM1/2; UCMP 148639, left maxilla with M2+alveolus of M3; UCMP 148642, 148668, RM3; UCMP 148761, 148766, LM3.

**UCMP V71238:** UCMP 148772, 148774, 148782, Rm1/2;

UCMP 148770, 148775, 148776, 148778-148780, Lm1/2; UCMP 148777, Rm3; UCMP 148771, Lm3; UCMP 148762, 148763, 148766, 148768, RM1/2; UCMP 148769, LM1/2.

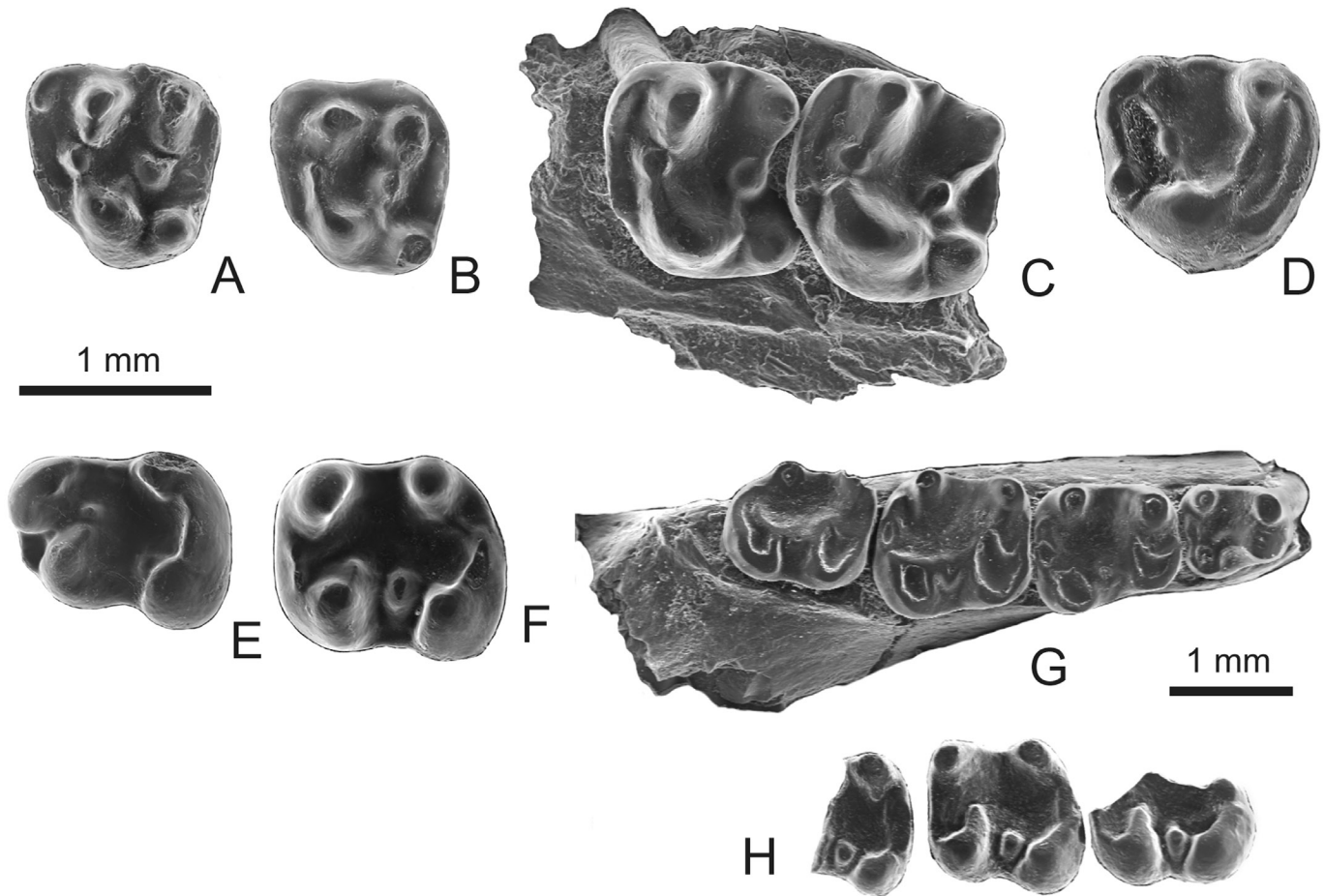
**Emended diagnosis**—Ivy’s (1990) original diagnosis of *Microparamys hunterae* included: same size as *Knightomys* (formerly *Microparamys*) *reginensis* (Korth, 1984) but with only one mental foramen; smaller with a less elongated mesoconid than *M. scopaiodon* Korth, 1984, smaller than *M. minutus* (Wilson, 1937) and *M. cheradius* Ivy, 1990; further differs from *M. cheradius* with a less complete, more oblique metalophulid II, and less well separated anterolophid. With the reallocation of “*M.*” *reginensis* to *Knightomys* (Flanagan 1986), *M. hunterae* is now the smallest known species of *Microparamys*.

Upper dentition and p4 diagnostic characters can now be added to Ivy’s original description including: differs from *M. cheradius* in lacking a P4 mesostyle and having better developed cingula and relatively larger hypocone, giving the tooth a much squarer outline; M1/2 paracone larger and higher than metacone; M1/2 mesostyle present; M1/2 protoloph and metaloph typically discontinuous. Differs from *M. scopaiodon* in that the p4 is double rooted, relatively larger (p4s are approximately the same absolute size in both taxa, but the molars in *M. scopaiodon* much larger), and hypoconid slightly larger.

**Description**—*Microparamys hunterae* was previously only known from the moderately worn type specimen (Fig. 7H) from the early Wasatchian (Wa-2) of the Clarks Fork Basin. This new sample includes the first evidence of the upper dentition, p4, and deciduous teeth, and also permits the examination of variation in the lower dentition.

*p4*—The metaconid is the largest and highest cusp and is located anterior and lingual to the shorter protoconid. These two cusps are separated by a deep fissure in the unworn specimen. A short metalophulid II arises from the protoconid, running lingually and ending at the base of the metaconid. A tiny anteroconid, present immediately anterior to the protoconid, disappears with wear. The trigonid basin is open labially, and no ectolophid is present. In unworn specimens a small, rounded mesoconid is evident. Posteriorly, the talonid basin is closed by a low crest joining hypoconid and entoconid. No distinct hypoconulid is discernable.

*m1/2*—Anteroposteriorly compressed trigonid with metaconid that is higher and more obliquely oriented than the protoconid. Anterolophid well developed enclosing the trigonid anteriorly, but it is not continuous with the protoconid until later wear stages. Metalophulid II does not ascend the metaconid, instead ending near the posteromedial edge of that cusp. Mesoconids are round, isolated, and do not elongate into the talonid basin. Metastylids lacking. The



**Figure 7.** *Microparamys hunterae* from UCMP V71237. **A.** UCMP 148675, left DP4, **B.** UCMP 148650, left P4, **C.** UCMP 148611, left maxillary fragment with M1-M2, **D.** UCMP 148668, right M3, **E.** UCMP 148648, left p4, **F.** UCMP 148660, left m1/2, **G.** UCMP 148610, right dentary with p4-m3, **H.** UM 66968, holotype, right dentary with partial m1, m2, partial m3. Scale bar for A-G = 1 mm and is located between A and F. Scale bar for G-H = 1 mm.

posterolophid is continuous with an anterior-posteriorly compressed, centrally-positioned, small hypoconulid. The entoconid is isolated.

*m3*—*m3* differs from *m1/2* in that the hypoconid is more compressed and continuous with the more lingually positioned hypoconulid.

*Dentary*—Part of the dentary is preserved in UCMP 148610. The full depth of the dentary is not preserved, so we cannot assess whether it is as deep as the specimen described by Ivy (1990). Also, although the bone immediately beneath p4 is present, no mental foramen is visible. Additionally, this specimen clearly lacks the small, second mental foramen beneath the posterior root of p4 seen in some other Wasatchian rodents.

*DP4*—UCMP 148675 is identified as a DP4 based on the expanded anteroloph and narrower lingual portion. Compared to the molars, the cusp tips are more acute, and the lophs are not developed. The paracone is higher than

the metacone, and the mesostyle is very small. There is a small hypocone, and the hypocone and protocone are closer together than in the molars.

*P4*—The upper premolar is relatively shorter than the molars, but still basically square in shape. The paracone and metacone are not marginal; there is a discontinuous cingulum that extends across the buccal margin of the tooth. An anteroloph begins low at the base of the protocone and extends around to the labial margin of the tooth where it widens at the paracone base. The paracone is both slightly higher and larger than the metacone, and there is no distinct mesostyle. The metaconule is larger than the protoconule. The metaloph and protoloph are continuous towards the protocone. The hypocone is a large cusp well separated from both the protocone and metaconule. The posteroloph extends around the metacone to the labial margin of the tooth.

*M1/2*—Upper first and second molars are square in

**Table 7.** Measurements and descriptive statistics of the dentition preserved in maxillae of *Microparamys hunterae* from UCMP V71237 and V71238, Wasatch Formation, Wyoming.

	<i>M1</i>		<i>M2</i>	
	L	W	L	W
148611	1.0	1.1	1.1	1.2
148638	1.1	1.1	1.2	1.1
148639			1.2	1.2
OR	1.0-1.1	1.1	1.1-1.2	1.1-1.2
Mean	1.05	1.10	1.17	1.17
SD	0.07	0	0.06	0.06

occlusal outline with the width typically being equal to, or only slightly larger than, the length. The protocone has a wider base and is more bulbous than the other cusps. The hypocone is large, equal in height to the metacone, but shorter than the protocone. The hypocone is not connected to the metaconule. The paracone is consistently wider and more robust than the metacone. The paracone is also higher, but this height difference becomes substantially reduced with wear. Both conules are present, and the metaconule is typically slightly larger. The protoconule is slightly anterior to the paracone. Both the protoloph and metaloph are typically discontinuous especially in unworn specimens. The metaloph is best developed where it extends from metacone to metaconule. The anteroloph extends only along the buccal two-thirds of the tooth. Most specimens have a diminutive mesostyle, which is typically closer to the paracone than metacone.

*M3*—*M3* are triangular in occlusal outline and reduced posteriorly with a small, marginally-placed metacone, and hypocone absent. There is a small metaconule which with wear forms a partial metaloph. Anteriorly, the protoconule is reduced and incorporated into the protoloph. The mesostyle is weakly to moderately developed. The anteroloph is similar in design to that of the other molars.

**Discussion**—*Microparamys hunterae* was previously only known from UMMP 66968, a fragmentary dentary with moderately worn m1-3 (Fig. 7H). This specimen was allocated to *Microparamys* by Ivy (1990, p. 59) on the basis of “the lack of sciuravid lophate characteristics and the presence of the diagnostic separation of the anterior cingulum.” Wood (1962, p. 158) noted that separation of the anterolophid from the protoconid is a “progressive character, being poorly developed in the Wasatchian forms”, while younger species have a deep valley. Although *M. hunterae* does not have the distinctive valley seen in later-occurring *Microparamys*, the

**Table 8.** Measurements and descriptive statistics of the upper dentition of *Microparamys hunterae* from UCMP V71237 and V71238, Wasatch Formation, Wyoming.

	<i>P4</i>		<i>M1/M2</i>		<i>M3</i>	
	L	W	L	W	L	W
148650	0.9	0.9				
148640			1.1	1.2		
148641			1.2	1.2		
148645			1.2	1.2		
148665			1.0	1.1		
148666			1.1	1.1		
148667			1.1	1.2		
148668			1.2	1.2		
148669			-	1.2		
148670			1.1	1.1		
148676			1.1	1.0		
148761			1.0	1.0		
148762			1.2	1.2		
148763			1.1	1.1		
148766			1.3	1.5		
148768			1.1	1.1		
148769			1.0	1.1		
148647			1.1	1.4		
148651			1.1	1.2		
148652			1.3	1.3		
148653			1.0	1.0		
148642					0.9	0.8
OR	-	-	1.0-1.3	1.0-1.5	-	-
Mean	-	-	1.12	1.17	-	-
SD	-	-	0.09	0.13	-	-

anterolophid is well developed and is not continuous with the protoconid prior to wear; we concur with Ivy’s placement of this taxon.

*Microparamys hunterae* occupies the same size range as *Knightomys reginensis*; however, the Washakie Basin specimens are morphologically distinct from the *K. reginensis* described by Korth (1984) and Flanagan (1986). These specimens differ from *K. reginensis* in the following characteristics of the lower molars: complete lack of metastylids; entoconid is high and columnar and lacks a hypolophid; mesoconid less elongated and does not extend into the talonid basin; and a

**Table 9.** Measurements and descriptive statistics of the dentition preserved in dentaries of *Microparamys hunterae* from UCMP V71237 and V71238, Wasatch Formation, Wyoming.

	<i>p4</i>			<i>m1</i>			<i>m2</i>			<i>m3</i>		
	L	TrW	TaW	L	TrW	TaW	L	TrW	TaW	L	TrW	TaW
148610	0.8	0.6	0.7	1.2	0.9	1.0	1.2	1.0	1.2	1.1	1.0	1.0

**Table 10.** Measurements and descriptive statistics of the lower dentition of *Microparamys hunterae* from UCMP V71237 and V71238, Wasatch Formation, Wyoming.

	<i>p4</i>			<i>m1/m2</i>			<i>m3</i>		
	L	TrW	TaW	L	TrW	TaW	L	TrW	TaW
148648	1.2	0.8	0.9						
148656	1.0	0.7	0.8						
148654				1.2	0.9	1.0			
148663				1.1	0.7	0.8			
148671				1.1	0.9	0.8			
148770				1.4	1.0	1.2			
148772				1.2	1.0	1.2			
148774				1.3	1.2	1.3			
148775				1.2	1.0	1.1			
148776				1.3	1.0	1.1			
148778				1.2	0.8	1.1			
148779				1.2	0.8	0.9			
148780				1.3	1.1	1.0			
148782				1.4	1.2	1.4			
149219				1.2	0.9	1.0			
149224				1.2	1.0	1.1			
148643				1.2	1.0	1.0			
148644				1.3	1.1	1.2			
148658				1.3	1.2	1.3			
148659				1.3	1.0	1.1			
148660				1.2	0.9	1.0			
151278				1.4	1.2	1.3			
148655							1.1	-	0.8
148771							1.1	0.9	0.8
148777							1.2	1.0	1.0
OR	1.0-1.2	0.7-0.8	0.8-0.9	1.1-1.4	0.7-1.2	0.8-1.4	1.1-1.2	0.9-1.0	0.8-1.0
Mean	1.10	0.75	0.85	1.25	1.00	1.10	1.13	0.95	0.87
SD	0.14	0.07	0.07	0.09	0.14	0.16	0.06	0.07	0.12

complete lack of accessory cuspsules in talonid basin. In the upper dentition *K. reginensis* has a distinctive connection between the hypocone and metaconule (hypoloph), which *M. hunterae* lacks.

CYLINDRODONTIDAE MILLER AND GIDLEY, 1821

*Tuscahomys* DAWSON AND BEARD, 2007

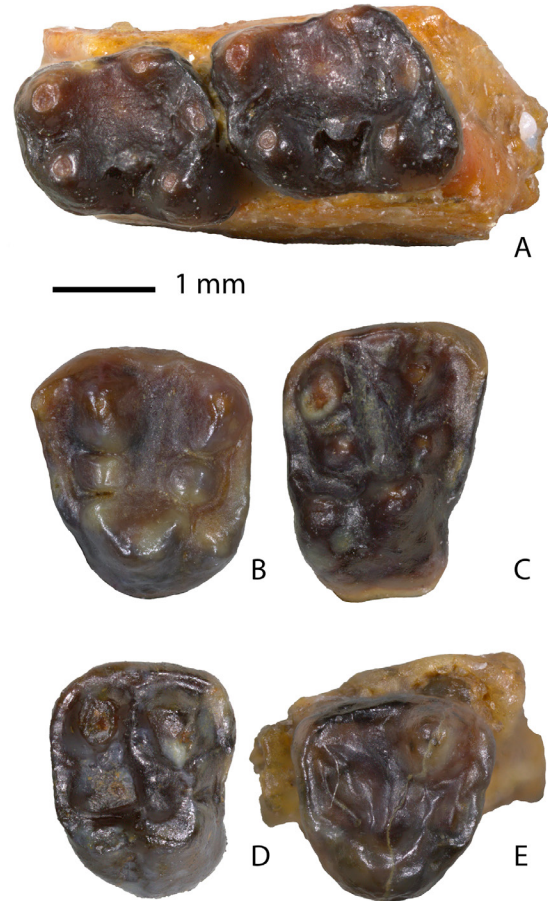
*Tuscahomys ctenodactylops* (KORTH, 1984)

Figs. 8-10, Tables 11-18

**Referred specimens**—UCMP V71237: UCMP 175197, right dentary with p4, m1-2; UCMP 148615, Rdp4; UCMP 148613, right dentary with p4, m1-3; UCMP 148628, left dentary with m1-3; UCMP 148632, 149223, Rm1/2; UCMP 148662, Lm1/2; UCMP 148646, RP3; UCMP 148612, 148624, 148661, right maxillae with P3, M1-3; UCMP 148664, LP3; UCMP 148625, left maxilla with P3, M1-2; UCMP 148616, RP4; UCMP 148673, LP4; UCMP 148626, right maxilla with P4, M1-3; UCMP 148627, left maxilla with M1-2; UCMP 148617-148619, 148636, RM1/2; UCMP 148621, 148622, LM1/2; UCMP 175196, right maxilla with M2-3; UCMP 148633, 148637, RM3; UCMP 148620, 148623, 148635, LM3.

**UCMP V71238:** UCMP 169140, left dentary with p4, m1-3; UCMP 148678, 151320, 152487, Rp4; UCMP 148706, 151321-151324, 151355, Lp4; UCMP 148705, left dentary with m1; UCMP 148746, 171521, right dentaries with m1-2; UCMP 148677, 148683-148686, 148700, 148707, 148750, 151344-151354, 151365, 151366, Rm1/2; UCMP 148679-148682, 148697, 148708, 148710, 151334-151343, 151368, 189308, 189310, 235519, 235521, Lm1/2; UCMP 156869, left dentary with m1-3; UCMP 151369, left dentary with m2-3; UCMP 148687, 148693, 148695, 148696, 148699, 148709, 148711, 151329-151332, 189307, 235520, Rm3; UCMP 148689, 148692, 148694, 148698, 148701-148703, 148753, 148754, 151325-151328, 151333, 189309, Lm3; UCMP 151318, 189313, DP4; UCMP 152485, left maxilla with P3-4; UCMP 189314, RP3; UCMP 152484, LP3; UCMP 148715, 151315, 151316, 151356, 189312, RP4; UCMP 148722, 148723, 148727, 148729, 151311-151314, 189315, LP4; UCMP 148712-148714, 148721, 148728, 148730, 148734, 148736, 148737, 148739, 148742, 148745, 151301-151310, 189302 RM1/2; UCMP 148716-148718, 148724-148726, 148732, 148733, 148735, 148740, 148744, 151293-151300, 151317, 151367, 152486, 189306, LM1/2; UCMP 148738, 148764, 148767, 151279-151284, 189303, RM3; UCMP 148719, 148741, 148743, 151285-151292, 189300, LM3.

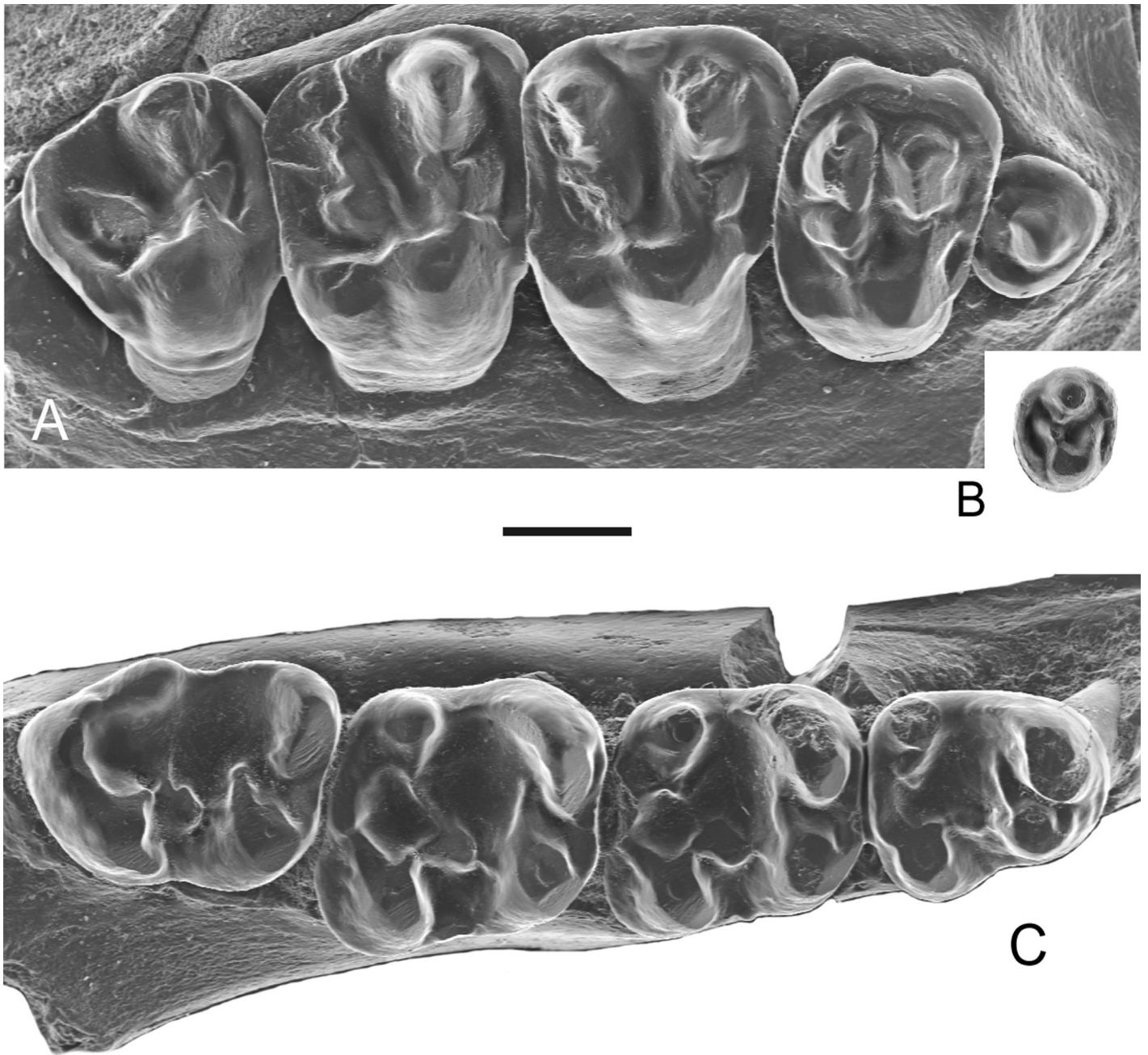
**Emended Diagnosis**—Differs from *T. minor* Dawson and Beard, 2007 and *T. medius* Dawson and Beard, 2007 in larger size, is comparable in size to *T. major*, and is smaller



**Figure 8.** *Tuscahomys ctenodactylops* holotype and paratypes from UW locality V60008. **A.** UW 15008, holotype left dentary with m1-m2, **B.** UW 15009, left M1 or M2, **C.** UW 15263, right M1 or M2, **D.** UW 15262, right P4, **E.** UW 15010, right maxillary fragment with M3.

on average than *T. walshi* Anemone, Dawson, and Beard, 2012 and *T. worlandensis* Rose, Chew, Dunn, Kraus, Fricke, and Zack, 2012. Differs from *T. medius* in having a slightly higher crowned cheek teeth. Differs from *T. medius* and *T. minor* in having a larger M3 metaconule. Differs from *T. walshi* in having relatively narrower posterior molars and a smaller M3.

**Description**—Korth (1984) described *Tuscahomys* (formerly *Reithroparamys*) *ctenodactylops* from a left dentary with m1-m2, an isolated P4, and 3 upper molars from a University of Wyoming locality from near the base of the Wasatch Formation in the Washakie Basin and at approximately the same stratigraphic level as and quite near Roehler's *Coryphodon* Catastrophe Quarry (McGee 2001). Based on the geographic position of the type locality, it lies near the base of Roehler's (1993) master section for the Main Body

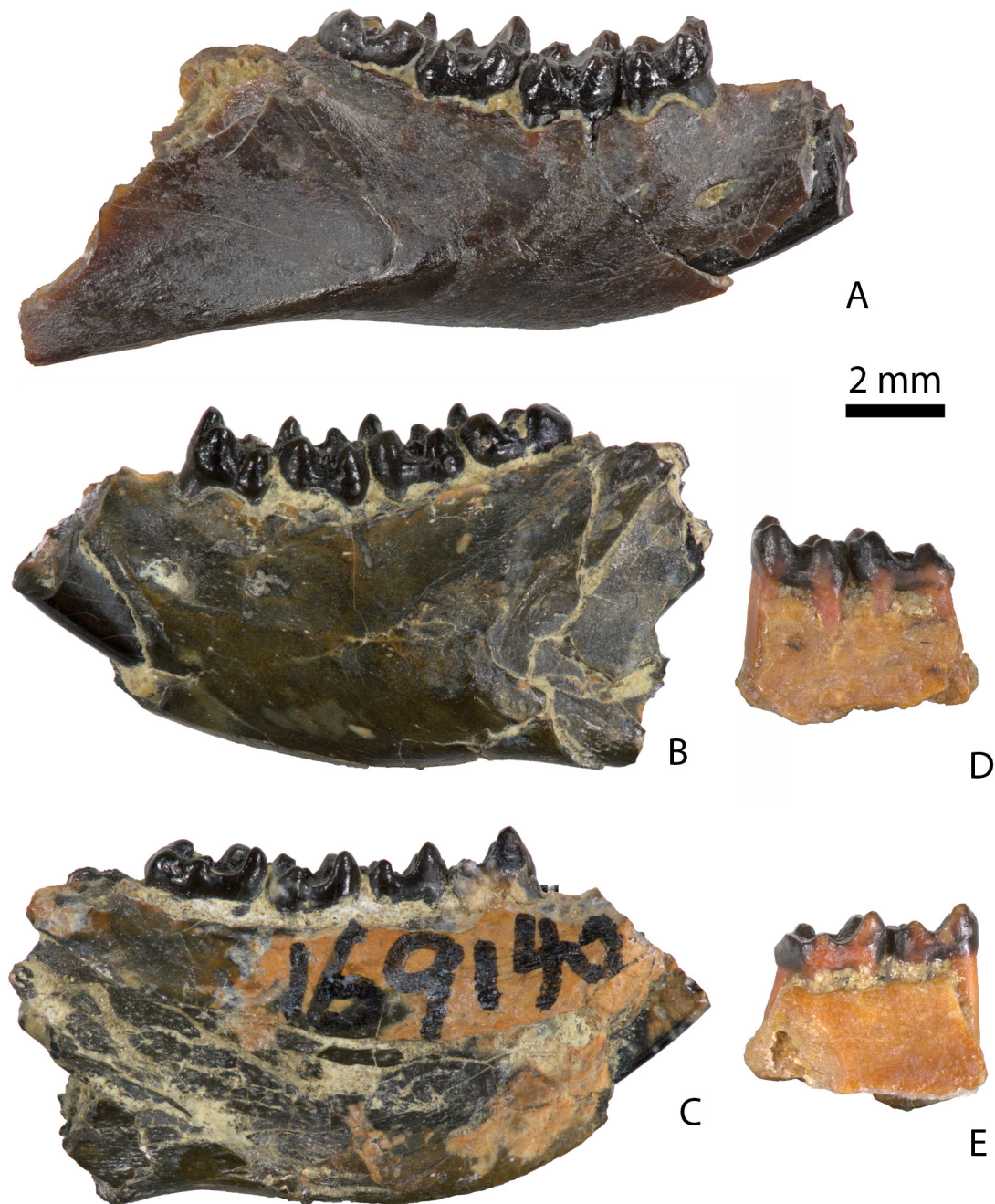


**Figure 9.** *Tuscahomys ctenodactylops* from UCMP loc. V71237. **A.** UCMP 148612, right maxilla with P3-M3, **B.** UCMP 148664, right P3, **C.** UCMP 148613, right dentary with p4-m3. Scale bar = 1 mm.

of the Wasatch Formation and is at approximately the same stratigraphic level as V71237 and V71238 with respect to the base of the formation. This large collection of specimens from V71237 and V71238 provides us with the opportunity to describe all cheek tooth positions, examine individual variation, and expand its diagnosis. We have also included measurements of the holotype (UW 15008) and paratypes, as measurements were not explicitly provided in Korth (1984), and our measurements indicate that the scale bar associated

with the original illustrations was inaccurate. We also include illustrations of the original sample (Fig. 8) as well as exemplars from the collections described here (Figs. 9-10).

*dp4*—These deciduous teeth are heart-shaped, with a narrower lingual portion. Compared to the permanent teeth, the cusp and conule tips are more acute, and lophs are not developed. The cingulum is discontinuous buccally due to wear. A minute mesostyle is variably present. There is a small hypocone, and the hypocone and protocone are more closely appressed than in the molars.



**Figure 10.** *Tuscahomys ctenodactylops*. **A.** UCMP 148613, right dentary in lateral view, **B, C.** UCMP 169140, left dentary in lateral and medial views, **D, E.** UW 15008, holotypes left dentary in lateral and medial view.

*P3*—*P3* is known from four maxillary specimens and two isolated teeth. This tooth position shows extreme variability. Root number varies from one to two and the unworn crowns vary and can include one primary cusp, one primary cusp with a smaller accessory cusp, or two relatively equally size cusps. With wear *P3* looks simple and peg-like.

*P4*—The paracone and metacone are subequal and slightly anteroposteriorly compressed. Korth (1984) stated that the metacone is slightly more buccal than the paracone, but we find that this orientation is variable. The metaconule is much larger than the protoconule. Two of the 10 specimens (UCMP 148673, 148723) have a mesostyle. All cusps are bulbous and



**Table 11.** Measurements and descriptive statistics of the dentition preserved in maxillae of *Tuscahomys ctenodactylops* from UCMP V71237 and V71238, Wasatch Formation, Wyoming.

	<i>P3</i>		<i>P4</i>		<i>M1</i>		<i>M2</i>		<i>M3</i>	
	L	W	L	W	L	W	L	W	L	W
152485	0.7	0.8	1.1	1.2	1.7	1.7				
148625	0.9	1.0	1.7	2.3	2.0	2.6	2.0	2.3		
148612	0.9	1.0	1.6	2.0	2.0	2.3	2.1	2.4	1.9	1.9
148624	1.0	1.4	1.8	2.2	2.0	2.3	2.0	2.3	2.2	2.1
148661	0.8	1.0	1.8	2.4	2.0	2.6	2.0	2.6	2.1	2.1
148626			1.6	1.8	1.8	2.2	1.8	2.0		
148627					1.9	2.3	2.0	2.3		
175196							2.0	2.5	2.1	2.2
OR	0.7-1.0	0.8-1.4	1.1-1.8	1.2-2.4	1.7-2.0	1.7-2.6	1.8-2.1	2.0-2.6	1.9-2.2	1.9-2.2
Mean	0.86	1.04	1.60	1.98	1.91	2.29	1.99	2.34	2.08	2.08
SD	0.11	0.22	0.26	0.44	0.12	0.30	0.09	0.19	0.13	0.13

protoloph and metaloph develop with wear. In most cases the slight buccal cingulum is restricted to the area between the paracone and metacone. However, in a few specimens (e.g., UCMP 148612, 148625, 148722, and 148729) this cingulum is continuous with both the anteroloph and posteroloph. The hypocone is very small (even smaller than the metaconule), and is only separated from the protocone by a slight groove.

*M1/2 and M3*—Molars are as described by Korth (1984), with the following additional observations. *M1/2* are narrow teeth, with the width being greater than the length. In *M3* the length and width measurements are essentially equal. In *M1/2* mesostyles are variable in their development, even within the same tooth row (e.g., UCMP 148626). The conules are relatively large, but the metaconule is wider than the more anteroposteriorly compressed protoconule. The hypocone and protocone are relatively internal, resulting in a sloped appearance to the crown lingual to these cusps. On maxillae having both *M1* and *M2*, there is little difference in morphology. The only consistent difference is that the lingual slope is steeper and the tooth is absolutely wider in *M1* than *M2*. Korth (1984) reported the metacone of *M3* to be absent, but some specimens in our sample (e.g., UCMP 148637) retain very small metacones. Additionally, on *M3* the presence of a minute hypocone is variable and they lack a distinctive mesostyle.

*dp4*—UCMP 148615 is the sole deciduous premolar of this taxon and is slightly smaller than the permanent premolars. It is a molariform teeth with a very narrow trigonid

relative to the talonid. The metaconid is much larger than the protoconid, but does not show the anteroposterior compression or obliquity characteristic of the permanent cheek teeth. An anteroconid and metalophulid II are present. An ectolophid and hypolophid are both present. In permanent teeth, the hypoconid and entoconid are comparable in size; however, in the *dp4* the hypoconid is high and columnar; the entoconid and hypoconulid are smaller and confluent with the posterolophid.

*p4*—These are the first known *p4*s of this species. The trigonid is dominated by an enlarged metaconid which is equal in size to the *m1* metaconid. The shorter and narrower protoconid is labial to the mid-line and closely appressed to the metaconid, but separated from it by a v-shaped valley. With slight-medium wear the metalophulid II descends from the posterolingual corner of the protoconid and terminates posterior to the metaconid at the midline of the cusp. The mesoconid is small and round, located immediately posterior to the protoconid. Ectolophids only develop with wear. The bulbous hypoconid is wider, but not higher, than the entoconid. The entoconid is isolated from the posterolophid, which with wear connects the hypoconulid to the hypoconid. The hypoconulid is centrally positioned, anteroposteriorly compressed, and is more lophate than cuspidate. A short crest arises from the base of the entoconid and is directed toward the hypoconulid but does not meet it. This crest is not apparent in worn specimens.

*m1/2*—The trigonid is moderately higher than the talonid. In unworn specimens the metaconid is markedly higher and

**Table 12.** Measurements and descriptive statistics of the upper premolars of *Tuscahomys ctenodactylops* from UCMP localities V71237 and V71238, Wasatch Formation, Wyoming, and from UW locality V6008, Wasatch Formation, Wyoming. Note that the observed range, mean, and standard deviation exclude UW 15262.

	<i>P3</i>		<i>P4</i>	
	L	W	L	W
148646	0.7	0.9		
148664	1.0	0.7		
152484	1.1	1.4		
148616			1.8	2.5
148673			2.0	2.5
148715			1.6	2.3
148722			1.6	2.4
148723			1.9	2.6
148727			1.7	2.4
148729			1.5	2.0
151311			1.7	2.1
151312			1.6	2.2
151313			1.6	2.3
151315			1.8	2.3
151316			1.6	2.1
151317			2.0	2.4
151356			1.6	2.6
189312			2.0	2.6
189313			2.0	3.0
189315			1.6	2.4
UW 15262			1.8	2.7
OR	0.7-1.1	0.7-1.4	1.5-2.0	2.0-3.0
Mean	0.93	1.00	1.74	2.39
SD	0.21	0.36	0.18	0.24

its base is slightly wider than the protoconid. The metaconid is positioned marginally and slightly obliquely oriented, but the protoconid is angled more lingually. Both anterolophid and metalophid II are present, but their expression varies. The mesoconids are large, filling the space between the protoconid and hypoconid. In some unworn teeth (e.g., UCMP 148700) a very slight ectolophid is visible. However, early in wear the ectolophid disappears, and the mesoconid eventually becomes confluent with the anterolingual edge

of the hypoconid. The rounded mesoconid is positioned just labial of the midline and posterior to the protoconid, leaving a shelf-like area immediately labial to it. In some specimens this shelf is enclosed by a buccal cingulid. A hypolophid is consistently present and is typically directed from the entoconid toward the mesoconid. In some cases, this crest connects with the mesoconid. Hypoconulids are elongated and lophate, connected to the larger hypoconid by a continuous protolophid and separate from the entoconid. Although Korth (1984) stated that m1 is smaller than m2, it is not possible to distinguish isolated teeth due to the amount of variability present in the sample.

*m3*—The third molar has not previously been reported. The third molar is similar to m1-m2 in form, except the talonid is subequal to or narrower than the trigonid. The hypoconulid is more posteriorly positioned, higher, and connected to both entoconid and hypoconid. The hypolophid is obliquely oriented and with wear this crest joins the mesoconid.

*Dentary*—All three specimens that preserve this area (UCMP 148613, 148628, and 148705) bear two mental foramina: one larger foramen beneath the anterior root of p4 and a second smaller foramen beneath the posterior root of p4. The dentary is best preserved in UCMP 148613 and 169140 (Fig. 10). The dentary is deep relative to the height of the teeth. The diastema between the p4 and incisor is short and has a sharply defined ridge. Two mental foramina are present. The anterior foramen is larger, more oval and located beneath the anterior root of p4, approximately at half the height of the dentary. The smaller mental foramen is circular and slightly ventral and posterior to the former, occurring under the posterior root of p4. The masseteric fossa is deeply excavated and delineated by rounded ridges coming down from the coronoid process of ascending ramus and forward from the angular process. A small protuberance is present at the anteriormost point where the ridges meet, beneath m2. The angular process of the dentary is broken, but the base of it shows that it would have extended ventrally as well as posteriorly. The ventral border of the angular process shows striations for muscle attachments. On the lingual side the pterygoid fossa is posteroventral to the m3. The labial side is convex, whereas the lingual side is too damaged to determine if it was concave or flattened. The symphyseal surface is lightly rugose and extends posteriorly only to a spot slightly anterior to p4.

**Discussion**—Originally described by Korth (1984) as a species of *Reithroparamys*, Dawson and Beard (2007) reasigned this species to the genus *Tuscahomys*. Based on our expanded sample of this species, we have included an emended diagnosis of *T. ctenodactylops* above. This diagnosis does not include many of the characters that have previously appeared

**Table 13.** Measurements and descriptive statistics of the upper M1 or M2 of *Tuscahomys ctenodactylops* from UCMP localities V71237 and V71238, Wasatch Formation, Wyoming and from UW locality V6008, Wasatch Formation, Wyoming. Note that the observed range, mean, and standard deviation exclude UW 15009 and 15263.

	MI/M2			MI/M2	
	L	W		L	W
148617	2.0	2.3	151295	2.1	2.1
148618	2.1	2.3	151296	2.0	2.2
148619	2.0	2.5	151297	2.1	2.1
148621	2.0	2.2	151298	1.9	2.2
148636	2.0	2.6	151299	2.0	2.1
148714	2.0	2.6	151300	2.0	2.1
148716	2.0	2.5	151301	1.9	2.2
148717	1.9	2.0	151302	2.0	2.3
148718	-	1.9	151303	2.0	2.4
148721	2.0	2.5	151304	2.0	2.2
148724	2.1	2.2	151305	2.0	2.1
148725	2.0	2.4	115306	2.0	2.3
148726	1.8	2.6	115307	2.0	2.3
148728	1.9	2.1	115308	2.0	2.3
148730	2.0	2.0	151309	2.2	2.4
148732	2.1	2.7	151310	1.9	2.1
148733	2.1	2.1	151367	2.0	2.3
148734	2.1	2.7	189302	2.2	2.5
148735	2.0	2.2	189306	1.8	2.9
148736	2.2	2.4	235522	2.0	2.3
148739	1.9	2.4	UW 15009	2.1	2.6
148740	1.9	-	UW 15263	2.1	2.8
148742	2.0	2.0			
148744	2.0	2.0	OR	1.8-2.2	1.9-2.9
151293	2.0	2.3	Mean	2.00	2.29
151294	1.9	2.3	SD	0.09	0.22

in diagnoses for other species of *Tuscahomys*, including P4 protocone position, upper cheek tooth anterior cingulum development, and relative protoconule size (see Dawson and Beard 2007), talonid width, entoconid height, and cusp isolation (see Anemone et al. 2012), and P4 hypocone size/presence (see Rose et al. 2012). These characters are too variable and/or too difficult to reliably quantify within our sample and easily erased with wear.

Comparisons of our samples to the holotype and the four specimens of the hypodigm (Fig. 8) reveal several differences.

The lower molars of the holotype and the upper molars included in the type series fall within the range of metric and morphological variation seen in the V71237 and V71238 samples. However, the P4 described by Korth (1984) (UW 15262) is larger than any of the specimens from V71237 and V71238 and falls within the size range of *Tuscahomys walshi*. The crown is more rectangular rather than squarish, and the ectocingula is not continuous across the labial side of the tooth, but is discontinuous labial to the metacone. The central trough is deeper and separates the paracone and

**Table 14.** Measurements and descriptive statistics of the upper M3 of *Tuscahomys ctenodactylops* from UCMP V71237 and V71238, Wasatch Formation, Wyoming, and from UW V6008, Wasatch Formation, Wyoming. Note that the observed range, mean, and standard deviation exclude UW 15010.

	M3	
	L	W
148620	2.0	2.0
148622	1.8	2.3
148623	2.0	2.0
148633	2.2	2.2
148635	2.0	2.0
148637	1.9	1.8
148719	2.1	2.2
148738	2.0	2.1
148741	2.1	-
148743	2.0	2.1
148764	2.0	2.0
148767	2.0	1.9
151279	2.2	2.1
151280	2.0	2.0
151281	2.0	2.1
151282	2.1	2.0
151283	2.1	2.1
151284	2.1	2.1
151285	2.0	2.0
151286	2.0	2.0
151287	2.2	2.1
151288	2.1	2.1
151289	2.2	2.2
151290	2.1	2.1
151291	2.1	2.0
151292	2.1	2.0
189300	1.8	1.9
189303	2.2	2.1
UW 15010	2.0	2.0
OR	1.8-2.2	1.8-2.3
Mean	2.05	2.06
SD	0.11	0.11

metacone, and both conules and the hypocone are better developed and more inflated at their bases. In all these features, the P4 ascribed to the type series of *T. ctenodactylops* resembles *T. walshi*.

While *Tuscahomys minor*, *T. medius*, and *T. worlandensis* can be readily differentiated from *T. ctenodactylops* based on size, separating *T. major* and *T. walshi* from *T. ctenodactylops* is more difficult, as these overlap in size. *Tuscahomys major* is currently known from 10 specimens that document the following tooth positions: DP4, P4, M1 or M2, and m2 (Dawson and Beard 2007, Beard and Dawson 2009). Comparing *T. major* with our measurements of the enlarged sample of *T. ctenodactylops*, *T. major* teeth fall within the range of *T. ctenodactylops* for m2, P4, and the type sample of M1 or M2. They differ by less than a tenth of a millimeter for DP4, and the only notably different tooth is the very wide M1 or M2 referred to *T. major* after its initial description (CM 81754; Beard and Dawson 2009). Dawson and Beard's (2007) only morphological character differentiating *T. major* and *T. ctenodactylops* is P4 metaconule size. The P4 of *T. major* are worn and variation for this character is not known. The only other possible morphological difference between these similarly-sized species may be more consistent presence of mesostyles in *T. major*. This variation in mesostyle size and the limited size differences may not be sufficient to distinguish *T. major* from the expanded sample of *T. ctenodactylops*.

By contrast, *Tuscahomys walshi* can be more readily differentiated from *T. ctenodactylops* based on selected dental characters (see diagnosis), but there is overlap in the size ranges for these two species. Although it is easy to look at these assemblages from limited stratigraphic and geographic ranges and detect the differences between *T. ctenodactylops* and *T. walshi*, identifying specimens from other areas and/or which are only represented by selected isolated teeth is likely to be challenging. Additionally, the existence of both species in the same geographic basin and at different times also suggests the possibility that these represent lineage-segments (*sensu de* Queiroz 1998, 1999) and future work may find them to be taxonomically indistinct.

#### SCIURAVIDAE (MILLER AND GIDLEY, 1918)

*Knightomys* GAZIN, 1962

*Knightomys* cf. *K. minor* IVY, 1990

Fig. 11; Table 19

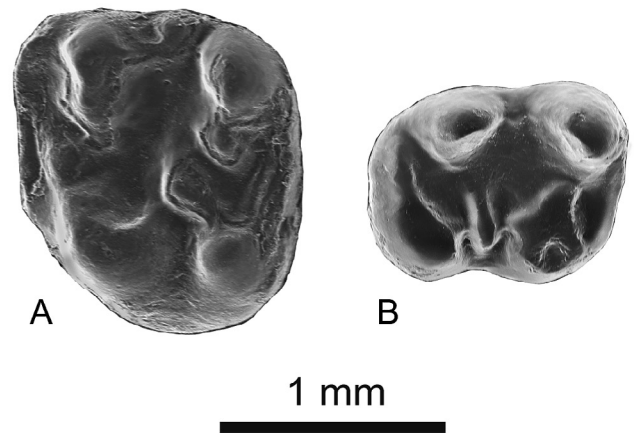
**Referred specimens**—UCMP V71237: UCMP 148657, Rm3; UCMP 148649, LM1/2.

**Table 15.** Measurements and descriptive statistics of the dentition preserved in dentaries of *Tuscahomys ctenodactylops* from UCMP localities V71237 and V71238, Wasatch Formation, Wyoming, and the holotype from UW locality V6008, Wasatch Formation, Wyoming. Note that the observed range, mean, and standard deviation exclude UW 15008.

	<i>p4</i>			<i>m1</i>			<i>m2</i>			<i>m3</i>		
	L	TrW	TaW	L	TrW	TaW	L	TrW	TaW	L	TrW	TaW
175197	1.9	1.3	1.4	2.2	1.7	1.9	2.2	1.9	2.1			
148613	1.9	1.2	1.5	1.9	1.4	1.7	2.0	1.7	1.9	2.4	1.6	1.6
169140	1.8	1.3	1.5	1.9	1.4	1.7	2.0	1.7	1.9	2.5	1.7	1.7
148705				2.0	1.7	1.9						
148746				2.3	1.6	1.9	2.4	1.8	2.0			
171521				2.0	1.6	1.8	2.1	1.8	2.0			
148628				1.8	1.5	1.7	2.0	1.8	1.9	2.4	1.8	1.6
156869				2.1	1.6	1.9	2.3	2.0	2.1			
151369							2.2	1.8	1.9	-	1.8	-
UW 15008				2.1	1.5	1.8	2.3	1.8	2.0			
OR	1.8-1.9	1.2-1.3	1.4-1.5	1.8-2.3	1.4-1.7	1.7-1.9	2.0-2.4	1.7-2.0	1.9-2.1	2.4-2.5	1.6-1.8	1.6-1.7
Mean	1.87	1.27	1.47	2.03	1.56	1.81	2.15	1.81	1.96	2.43	1.73	1.63
SD	0.06	0.06	0.06	0.17	0.12	0.10	0.15	0.10	0.09	0.06	0.10	0.06

**Table 16.** Measurements and descriptive statistics of the lower premolars of *Tuscahomys ctenodactylops* from UCMP V71237 and V71238, Wasatch Formation, Wyoming.

	<i>p4</i>		
	L	TrW	TaW
148678	1.4	1.6	-
148706	2.0	1.5	1.6
151320	2.0	1.4	1.7
151321	2.0	1.4	1.7
151322	1.9	1.4	1.7
151323	1.9	1.4	1.6
151324	2.0	1.3	1.6
151355	1.9	1.4	2.1
151487	1.9	1.3	1.5
OR	1.4-2.0	1.3-1.6	1.5-2.1
Mean	1.89	1.41	1.69
SD	0.19	0.09	0.18



**Figure 11.** *Knightomys* cf. *K. minor*. A. V71237/148649, left M1/2, B. V71237/148657, right m3.

**UCMP V71238:** UCMP 148781, Rdp4; UCMP 148765, LP4.

**Description—*P4***—The *P4* is an anteroposteriorly short tooth dominated by lophs. The protocone is rounded and the protoloph and metaloph are continuous towards this cusp. The anteroloph is relatively small, whereas the posteroloph is shelf-like and the hypocone is incorporated as a small bulge at its lingual end. The paracone and metacone, although

**Table 17.** Measurements and descriptive statistics of the lower m1 or m2 of *Tuscahomys ctenodactylops* from UCMP V71237 and V71238, Wasatch Formation, Wyoming.

<i>m1/m2</i>				<i>m1/m2</i>			
	L	TrW	TaW		L	TrW	TaW
148632	2.3	1.9	2.0	151341	2.1	1.8	1.9
148662	2.2	1.9	2.0	151342	1.8	1.4	2.0
148677	2.2	1.5	1.8	151343	2.0	1.6	1.7
148679	2.0	1.6	1.8	151344	2.2	1.8	1.9
148680	2.2	1.9	2.0	151345	2.1	1.6	2.1
148681	2.1	1.9	2.2	151346	2.0	1.8	2.0
148682	2.2	1.7	2.0	151347	2.0	1.6	2.0
148683	2.2	1.8	1.7	151348	2.1	1.6	1.9
148684	2.1	1.6	1.8	151349	2.3	1.9	1.9
148685	2.3	2.1	-	151350	2.3	1.9	2.0
148697	2.2	1.9	2.1	151351	2.0	1.6	2.1
148700	2.2	2.0	2.2	151352	2.2	1.9	1.9
148707	2.2	1.9	1.9	151353	2.1	-	2.0
148708	2.3	1.9	1.9	151354	2.3	2.0	-
148710	2.1	1.5	1.8	151365	2.1	1.7	-
148750	2.3	2.1	2.2	151366	2.0	1.8	2.0
149223	2.1	2.2	2.2	151368	2.1	1.6	1.8
151334	2.0	1.5	1.7	189310	2.2	1.9	2.0
151335	2.1	1.5	1.7	235519	-	1.6	-
151336	2.2	1.6	1.7	235521	2.4	1.8	-
151337	2.0	1.6	1.9				
151338	2.3	1.6	1.8	OR	1.8-2.4	1.4-2.2	1.7-2.2
151339	2.3	1.9	1.7	Mean	2.16	1.76	1.93
151340	2.3	1.6	2.0	SD	0.12	0.19	0.15

broken, are closely appressed and there is no evidence of a buccal cingulum.

*M1/2*—Although the upper molar is in the same size range as the specimens of *Microparamys* from these localities, it differs significantly from them in that there is a distinct connect from the hypocone to the metaconule, typical of *Knightomys*. This specimen also has a double metaconule, protoconule anteriorly displaced, and a mesostyle connected to paracone by faint crest. The metacone is higher than the paracone.

*dp4*—Based on size and morphology UCMP 148781 is tentatively identified as *Knightomys*. This tooth has typical deciduous characteristics including thinner enamel, splayed roots, and trigonid composed of a small, isolated

centrally-positioned anteroconid and labio-lingually aligned protoconid and metaconid. The trigonid is narrower than the open, wide talonid basin. The metaconid is higher and slightly larger than the protoconid. No metalophulids are present, and the protoconid and metaconid are separated by a distinct valley. A slight but distinct ectolophid is present, but a mesoconid is absent. The talonid is longer than the trigonid with labio-lingually aligned entoconid and hypoconid. No hypolophid is present, but the entoconid, hypoconid, and small centrally-positioned hypoconulid are joined by a low posterolophid.

*m3*—The m3 is moderately worn. The trigonid is only slightly higher than the talonid. There is a small trigonid

**Table 18.** Measurements and descriptive statistics of the lower m3 of *Tuscahomys ctenodactylops* from UCMP V71237 and V71238, Wasatch Formation, Wyoming.

	<i>m3</i>		
	L	TrW	TaW
148687	-	-	2.0
148689	2.6	1.8	1.7
148692	2.3	1.7	1.6
148693	2.8	1.9	1.9
148694	2.5	1.9	1.8
148695	2.6	1.9	1.8
148696	2.8	1.8	1.9
148698	2.7	1.9	1.8
148699	2.5	1.8	1.7
148701	2.8	1.8	1.7
148702	2.5	1.8	1.7
148703	2.6	1.8	1.7
148709	2.5	1.5	1.5
148711	-	-	1.6
148753	2.6	1.8	1.7
148754	2.5	1.8	1.8
151325	2.5	1.7	1.7
151326	2.4	1.7	1.5
151327	2.7	1.8	1.6
151328	2.4	1.7	1.6
151329	2.7	2.0	1.7
151330	2.6	1.7	1.9
151331	2.7	1.9	1.5
151332	-	-	1.8
151333	2.5	1.9	1.6
189309	2.6	1.9	1.8
OR	2.3-2.8	1.5-2.0	1.5-2.0
M	2.58	1.80	1.72
SD	0.13	0.11	0.13

basin delimited by both metalophulids I and II. There is a very small mesostylid in the valley between the metaconid and entoconid. The mesoconid is slightly lingual to the midline of the protoconid and hypoconid and extends as a low loph into the talonid basin. The entoconid is separated from the

**Table 19.** Measurements and descriptive statistics of the dentition of *Knighthomys* cf. *K. minor* from UCMP V71237 and V71238, Wasatch Formation, Wyoming.

	<i>m3</i>			<i>P4</i>		<i>M2</i>	
	L	TrW	TaW	L	W	L	W
148657	1.4	1.2	1.1				
148765				1.0	1.2		
148649						1.2	1.3

posterolophid by a shallow valley and the basin is lingually open. The hypoconid is bulbous and continuous with the posterolophid. No distinct hypoconulid is present.

**Discussion**—These teeth are in the size range for both *K. minor* and *K. cremneus* Ivy, 1990. They are assigned to *K. cf. K. minor* based on lower molar distinctions from *K. cremneus* including: a much smaller posteroloph and less bunodont cusps, metalophulid II comprising only the protoconid arm, and open talonid basin.

#### DISCUSSION

The presence of massive sandstone units within this portion of the Wasatch Formation suggests an active floodplain environment in which catastrophic flooding may have had an impact on the terrestrial communities. This inference is supported by the presence of two catastrophic assemblages within the lowermost 40 meters of the formation, including UCMP V71237 (Lower *Meniscotherium*) as well as UCMP V72193 (Roehler's *Coryphodon* Catastrophe Quarry) (Roehler 1993, McGee 2001). Based on the limited degree of disarticulation, Williamson (2001) inferred that the remains of *Meniscotherium tapiacetum* in UCMP V71237 were buried very shortly after death, likely within a matter of weeks, during a single fluvial event. Williamson (2001) further noted that the absence of smaller skeletal elements of *Meniscotherium* in the assemblage suggested that it was a winnowed assemblage that had undergone limited transport. UCMP V71238 is a channel lag assemblage, typical of many vertebrate accumulations that occur in the fossil record. Given the unique depositional history of UCMP V71237, we can hypothesize that it may more accurately reflect the composition of the local early Eocene mammalian community than assemblages that accumulated as the result of more active fluvial processes.

To assess rodent assemblage composition and the extent to which the rodents from these two sites may reflect the composition of the original mammalian community, we calculated total number of specimens (TNS) and minimum number of individuals (MNI) for each of the rodent taxa based on counts of the cheek teeth (Table 20). Additionally,

**Table 20.** Summary of total number of specimens (TNS) and minimum number of individuals (MNI) from each locality.

Species	UCMP V71237		UCMP V71238	
	TNS	MNI	TNS	MNI
<i>Paramys copei</i>	0	0	1	1
<i>P. taurus</i>	7	2	19	5
<i>Lophiparamys murinus</i>	4	1	6	3
<i>Microparamys hunterae</i>	34	2	20	2
<i>Tuscahomys ctenodactylops</i>	33	5	171	18
<i>Knightomys</i> cf. <i>K. minor</i>	2	1	1	1

we calculated the TNS of all mammalian taxa from each quarry, using only the last two premolars and molars to generate values comparable to those of rodents. The TNS of mammals from UCMP V71237 is 397, with 78 of these representing rodents (i.e., 19.6% of the total fauna). Within UCMP V71238, the TNS of mammals is 1101, with rodents (n=196) representing 17.8%. These relative percentages for rodents based on TNS are comparable to values reported for Wasatchian quarries in the Bighorn Basin (Silcox and Rose 2001, Strait 2001) and Four Mile fauna of northwestern Colorado (Bown 1979) and are significantly higher than those from Bighorn Basin surface collections, where rodents generally represent less than 10% of fossils recovered (Bown 1979, Clyde 1997, Silcox and Rose 2001). Although UCMP V71237 is unusual in having a relatively high proportion of the rare condylarthran *Meniscotherium*, representing 27.7% of TNS, it appears that the relative abundance of rodents within the fauna as a whole is comparable to that known from other quarried or screen-washed Wasatchian sites. That the relative abundances of rodents in quarried or screen-washed Wasatchian localities falls generally between 13–20% of TNS strongly suggests that these values accurately reflect the abundances of these animals on the Eocene landscape and highlights their importance in these ecosystems.

Examination of the TNS and MNI data (Fig. 12) for individual rodent taxa reveals that the dominant taxa at UCMP V71237 and V71238 are *Tuscahomys ctenodactylops* and *Microparamys hunterae*, although at a gross level their abundances differ significantly between the two levels, and whether TNS or MNI is employed. *Paramys taurus* and *Lophiparamys murinus* are the next most abundant, and *Knightomys* cf. *K. minor* and *P. copei* make up a minor part of the fauna, with *P. copei* absent from UCMP V71237.

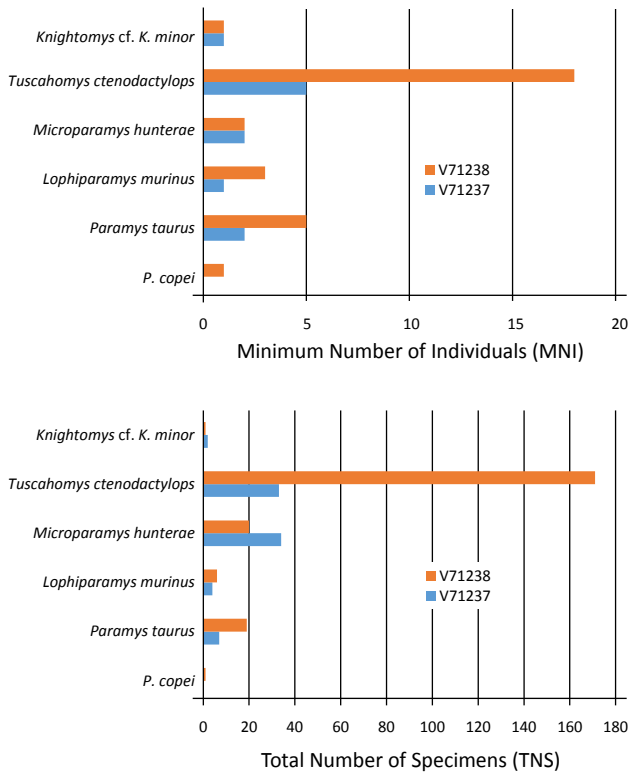
#### Comparison with other early Wasatchian rodent assemblages

Although rodents are fairly common at many early Eocene sites, few rodent assemblages have been systematically

described. The only rodent assemblages of comparable age to the UCMP V71237 and V71238 are those from early Wasatchian (Wa3, early Graybullian) localities from the Clarks Fork Basin described by Ivy (1990). The Clarks Fork Basin assemblages are dominated by *Acritoparamys atwateri* (Loomis, 1907) and *Paramys taurus*, with rarer appearances of *P. copei*, *P. pycnus* Ivy, 1990, *Microparamys cheradius*, *Lophiparamys murinus*, *Knightomys cremneus*, and *Reithroparamys* cf. *R. debequensis* Wood, 1962. As noted by Ivy (1990), the rarity of smaller rodents (e.g., *P. pycnus*, *M. cheradius*, and *L. murinus*) is likely the result of the assemblages being almost entirely comprised of surface collections, a collecting technique that is known to undersample smaller specimens.

In a slightly older, earliest Wasatchian (Wa0) screen-washed site from the southeastern Bighorn Basin, Strait (2001) reported *Acritoparamys atwateri* as the dominant taxon, with rarer occurrences of *Paramys taurus* and *P. copei*. Expanded samples have revealed that many of the specimens previously identified as *A. atwateri* represent a new species near *Tuscahomys* and that this taxon is the dominant rodent (Strait 2006) within this assemblage; this taxon is also now known to be the dominant rodent in other earliest Wasatchian sites (Gingerich and Smith 2006, Rose et al. 2012). In the central Bighorn Basin where somewhat younger, middle Wasatchian (Wa4 and Wa5) quarries have produced abundant rodents (see Silcox and Rose 2001), *Paramys* cf. *P. taurus* is frequently the most common taxon, with the single exception being within the rodent fauna from the McNeil Quarry, where *Knightomys* sp. dominates. In these faunas, *Knightomys* is otherwise a less common element, as are cf. *Acritoparamys atwateri* and cf. *P. copei*. A number of other rodent taxa have been reported from the mid-Wasatchian (Wa3–5; Graybullian) of the Bighorn Basin (see Wood 1962, Korth 1984), but all of these are based on only a single fossil or just a handful of specimens from unknown stratigraphic horizons. Within the Greater Green River Basin, *Tuscahomys* is extremely abundant at the slightly younger (Wa4) Smiley Draw locality where it co-occurs with two additional, unspecified rodent taxa (Anemone et al. 2012).





**Figure 12.** Relative abundance of rodents from UCMP V71237 and V71238 based on total number of specimens (TNS) and minimum number of individuals (MNI).

Despite the differences in collecting methodologies between these assemblages and the limited number of reported rodent occurrences, there are nonetheless notable and measurable differences in the composition of the Wasatchian faunas from Wyoming. In particular, *Acritoparamys* is absent in the Washakie Basin localities, and *Tuscahomys* and *Microparamys* are the dominant taxa in UCMP V71237 and V71238 but rare in the Clarks Fork and central Bighorn Basin samples younger than Wa0. *Knightomys* also appears to be somewhat more common in the stratigraphically younger Bighorn Basin quarries than in the Washakie Basin sample presented here.

More geographically distant areas show greater dissimilarity to the Washakie Basin rodents. Whereas the Wa0 fauna from the Tusahoma Formation in Mississippi is dominated by *Tuscahomys*, with the genus represented by three species, the remainder of the rodent fauna is comprised of five members of the Paramyidae, including one species of *Paramys*, a species questionably referable to *Franimys* Wood, 1962, a species otherwise only known from Europe (*Corbarimys* Marnat, 1989), and another two undetermined species (Dawson and Beard 2007, Beard and Dawson 2009). Other families of rodents are not yet known from there. Comparing the UCMP V71237 and V71238 assemblages with Flanagan's (1986) late

Graybullian to Lysitean screen-washed assemblages from the San Jose Formation in New Mexico, *Apatosciuravus*, *Mattimys* Korth, 1984, and *Pauromys* spp. are present in the southern fauna, but are absent in the Washakie and Bighorn Basin samples, although Korth (1984) has reported the occurrence of *Apatosciuravus* from unspecified localities in the Bighorn Basin and from the Four Mile fauna. *Paramys copei* is shared among all three of these basins, and slightly younger species of *Paramys*, *Knightomys*, and *Lophiparamys* are all present.

This brief summary of rodent distributions highlights several aspects of early Eocene biogeography. The rodent faunas of the Western Interior (where reported to date) all share the common taxa *Paramys copei* and *P. taurus* and species of *Microparamys*. Even rare taxa, i.e., *Lophiparamys murinus* and the genus *Knightomys*, appear to be geographically widespread in the western United States. Not surprisingly, the greatest similarity of the V71237 and V71238 assemblages is with the nearby Smiley Draw local fauna (Anemone et al., 2012). What is less expected is the similarity of V71237 and V71238 to Wa0 assemblages in both the Bighorn Basin and Mississippi, specifically in the presence and dominance of *Tuscahomys* species. Anemone et al. (2012) suggested that *Tuscahomys* was part of a suite of commonly co-occurring taxa that include *Meniscotherium* that may characterize a distinct ecotype. We concur that this is one possible explanation for these distributions; however, we are more cautious in our interpretations. *Meniscotherium* occurs in many localities and has a broad geographic range (Williamson and Lucas, 1992), and we have very incomplete knowledge of what taxa consistently co-occur with it throughout its range. The hypothesis that *Meniscotherium* and *Tuscahomys* co-occurrences can be used as ecological indicators is certainly suggested by current data, but we feel this hypothesis needs additional faunal data to be rigorously tested.

#### SUMMARY

Here, we comprehensively described the rodent fauna from UCMP V71237 and V71238 (Lower and Upper *Meniscotherium*), two stratigraphically closely spaced but sedimentologically and taphonomically distinct localities in the Main Body of the Wasatch Formation of early Wasatchian (Wa3) age from the Washakie Basin of Wyoming. Notable occurrences include representatives of *Lophiparamys*, *Knightomys*, *Paramys taurus* and *P. copei*. Additionally, these assemblages include some of the best preserved, most complete specimens of *Tuscahomys ctenodactylops* and *Microparamys hunterae* described to date and which add

considerable new morphologic information. Counts of specimens reveal that *Tuscahomys* is the most abundant taxon in both localities and that *Microparamys* is notably under-represented in UCMP V71238 relative to the occurrence of this taxon within UCMP V71237, a likely taphonomic size bias resulting from depositional differences.

Comparison with other Wasatchian assemblages demonstrates that these two Washakie Basin assemblages differ considerably from those recovered from contemporaneous and slightly younger assemblages within the more northerly Willwood Formation. The rodent fauna from UCMP V71237 and V71238 is also notably different from the stratigraphically younger faunas of the Wind River and San Jose formations. Somewhat surprisingly, however, the fauna from these two localities shares some elements not only with the geographically close but slightly younger, middle Wasatchian (Wa4) Smiley Draw local fauna but also those from the earliest Wasatchian (Wa0) of the Tuscahoma Formation in Mississippi and Willwood Formation of the Bighorn Basin, Wyoming.

#### ACKNOWLEDGMENTS

The recovery of specimens from UCMP V71237 and V71238 was accomplished with support from the National Science Foundation to the late D.E. Savage and from the Annie M. Alexander Endowment of the UCMP. We thank J.H. Hutchison for his assistance in the field and his insights into the collecting history of these sites. M. Dawson, A. Tabrum, P. D. Gingerich and G. F. Gunnell, K. D. Rose, and L. Vietti are thanked for access to comparative material. Figure 4a laser scan was made by N. Smith, Figure 4b was prepared by M. Spears, and D. Neff is thanked for SEM imaging. S.G S. was supported by NSF DEB 020881; C.A.D. received a Marshall University undergraduate tuition waiver and NASA undergraduate research grant; and B.D.R. was supported by the Doris O. and Samuel P. Welles Research Fund to the UCMP. R.L. Anemone and two anonymous reviewers are thanked for their constructive comments.

#### LITERATURE CITED

- Alston, E.R. 1876. On the classification of the order Glires. *Proceedings of the Zoological Society of London* 44:61-98.
- Ameghino, F. 1890. Los plagiulacideos argentines y sus relaciones zoológicas, geológicas, y geográficas. *Boletín des Instituto geográfico argentino* 11:143-201.
- Anemone, R.L., M.R. Dawson, and K.C. Beard. 2012. The early Eocene rodent *Tuscahomys* (Cylindrodontidae) from the Great Divide Basin, Wyoming: phylogeny, biogeography, and paleoecology. *Annals of Carnegie Museum* 80: 187-205.
- Archibald, J. D. and J. H. Hutchison. 1979. Revision of the genus *Palatobaena* (Testudines, Baeniedae), with description of a new species. *Postilla* 177:1-19.
- Batsch, A. J. G. C. 1788. Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien. Akademische Buchhandlung, Jena. 528 pp.
- Beard, K. C. and M. R. Dawson. 2009. Early Wasatchian mammals of the Red Hot local fauna, uppermost Tuscahoma Formation, Lauderdale County, Mississippi. *Annals of Carnegie Museum* 78:193-243.
- Benton, M. J. and J. M. Clark. 1988. Archosaur phylogeny and the relationships of the Crocodylia. Pp. 295-338 in M. J. Benton (ed.). *The Phylogeny and Classification of the Tetrapods. Volume 1: Amphibians, Reptiles, Birds*. Clarendon Press, Oxford.
- Bonaparte, C. L. 1838. *Selachorum tabula analytica. Nouvelles Annales des Sciences Naturelle* 2.
- Bowdich, T. E. 1821. An analysis of the natural classifications of Mammalia for the use of students and travellers. J. Smith, Paris. 115 pp.
- Bown, T.M. 1979. Geology and mammalian paleontology of the Sand Creek facies, lower Willwood Formation (lower Eocene), Washakie County, Wyoming. *Geological Survey of Wyoming, Memoir* 2:1-151.
- Bown, T. M. and K. D. Rose. 1979. *Mimoperadectes*, a new marsupial, and *Worlandia*, a new dermopteran, from the lower part of the Willwood Formation (early Eocene), Bighorn Basin, Wyoming. *Contributions from the Museum of Paleontology, The University of Michigan* 25:89-104.
- Bown, T. M. and K. D. Rose. 1987. Patterns of dental evolution in early Eocene anatomorphine primates (Omomyidae) from the Bighorn Basin, Wyoming. *Journal of Paleontology* 61 (Supplement to no. 5):1-162. (The Paleontological Society Memoir 23).
- Brandt, J.F. 1855. Beiträge zur nahern Kenntniss der Säugethiere Russlands. *Mémoires de l'Académie Impériale des Sciences de Saint-Petersbourg* 69:1-375.
- Chew, A. 2005. Biostratigraphy, paleoecology and synchronized evolution in the early Eocene mammalian fauna of the central Bighorn Basin, Wyoming. Ph.D. dissertation, The Johns Hopkins University, Baltimore, Maryland. 661 pp.
- Clyde, W.C. 1997. Stratigraphy and mammalian paleontology of the McCullough Peaks, Northern Bighorn Basin, Wyoming: Implications for Biochronology, Basin Development, and Community Reorganization across the Paleocene-Eocene boundary. Ph.D. dissertation, Dept. of Geology, University of Michigan, Ann Arbor, Michigan. 271 pp.
- Cope, E. D. 1872. On a genus of Pleurodira from the Eocene of Wyoming. *Proceedings of the American Philosophical Society* 12:472-477.
- Cope, E. D. 1873. Fourth notice of extinct Vertebrata from the Bridger and the Green River Tertiaries. *Paleontological Bulletin* 17:1-4.
- Cope, E. D. 1874. Report upon the vertebrate fossils discovered in New Mexico with descriptions of new species. Pp. 589-606 in Annual Report of the Chief of Engineers, U. S. Army, Appendix FF. Washington, D. C.
- Cope, E. D. 1875a. On the supposed Carnivora of the Eocene of the Rocky Mountains. *Paleontological Bulletin* 20:1-4.
- Cope, E. D. 1875b. Systematic catalogue of Vertebrata of the Eocene of New Mexico, collected in 1874. *Geographic Explorations and Surveys west of the 100<sup>th</sup> Meridian*, G. M. Wheeler, Corps of

- Engineers, U. S. Army, Washington, D. C.* 4:37-282.
- Cope, E. D. 1880a. On the genera of the Creodonts. *Proceedings of the American Philosophical Society* 19:76-82.
- Cope, E. D. 1880b. The northern Wasatch fauna. *American Naturalist* 14: 908-909.
- Cope, E. D. 1881. On some Mammalia of the lowest Eocene beds of New Mexico. *Proceedings of the American Philosophical Society* 19:484-495.
- Cope, E. D. 1882a. Contributions to the history of Vertebrata of the lower Eocene of Wyoming and New Mexico, made during 1881. *Proceedings of the American Philosophical Society* 34: 139-191
- Cope, E. D. 1882b. Synopsis of the Vertebrata of the Puerco epoch. Supplement on a new *Meniscotherium* from the Wasatch Epoch. *Proceedings of the American Philosophical Society* 20: 461-471.
- Cope, E. D. 1883. On the mutual relations of the bunotherian Mammalia. *Journal of the Academy of Natural Sciences of Philadelphia* 33: 77-83.
- Cope, E. D. 1884a. The Tertiary Marsupialia. *American Naturalist* 18: 686-697.
- Cope, E. D. 1884b. Second addition to the knowledge of the fauna of the Puerco Epoch. *Proceedings of the American Philosophical Society* 21: 309-324.
- Crochet, J.-Y. 1979. Diversité systématique des Didelphidae (Marsupialia) Européens Tertiaires. *Géobios* 12:365-378.
- Cuvier, G. 1807. Sur les différentes espèces de crocodiles vivants et sur leur caractère distinctifs. *Annales du Muséum National d'Histoire Naturelle* 10: 8-66.
- Cuvier, G. 1817. Le Règne Animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des Animaux et d'introduction à l'anatomie comparée. Volume 4. Chez Déterville, Paris. 255 pp.
- Cuvier, G. 1825. Recherches sur les ossements fossiles, où l'on rétablit les caractères de plusieurs animaux dont les révolutions des globe ont détruit les espèces, third edition. Volume 3. G. Dufour et E. d'Ocagne, Paris, France. 412 pp.
- Dawson, M.R., and K.C. Beard. 2007. Rodents of the family Cylindrodontidae (Mammalia) from the earliest Eocene of the Tuscaloosa Formation, Mississippi. *Annals of Carnegie Museum* 76: 135-144.
- de Queiroz, K. 1998. The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. Pp. 57-75 in D.J. Howard and S. H. Berlocher (eds.). *Endless Forms: Species and Speciation*. Oxford: Oxford University Press.
- de Queiroz, K. 1999. The general lineage concept of species and the defining properties of the species category. Pp. 49-80 in R.A. Wilson, (ed.). *Species: new interdisciplinary essays*. Massachusetts Institute of Technology Press, Cambridge, Massachusetts, p49-89.
- Flanagan, K.M. 1986. Early Eocene rodents from the San Jose Formation, San Juan Basin, New Mexico. *Contributions to Geology, University of Wyoming, Special Paper* 3:197-220.
- Fürbringer, M. 1900. Zur vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln. *Jenaische Zeitschrift für Naturwissenschaft* 34:215-718.
- Gazin, C. L. 1962. A further study of the lower Eocene mammalian faunas of southwestern Wyoming. *Smithsonian Miscellaneous Collection* 144: 1-98.
- Gill, T. 1872. Arrangement of the families of mammals with analytical tables. *Smithsonian Miscellaneous Collections* 11:1-98.
- Gingerich, P.D. 1983. Paleocene-Eocene faunal zones and a preliminary analysis of Laramide structural deformation in the Clark's Fork Basin, Wyoming. *Wyoming Geological Association Annual Field Conference Guidebook* 34:185-195.
- Gingerich, P. D. 1987. Early Eocene bats (Mammalia, Chiroptera) and other vertebrates in freshwater limestones of the Willwood Formation, Clark's Fork Basin, Wyoming. *Contributions from the Museum of Paleontology, The University of Michigan* 27:275-320.
- Gingerich, P.D. 1991. Systematics and evolution of early Eocene Perissodactyla (Mammalia) in the Clarks Fork Basin, Wyoming. *Contributions from the Museum of Paleontology, University of Michigan* 28:181-213.
- Gingerich, P. D. and E. L. Simons. 1977. Systematics, phylogeny, and evolution of early Eocene Adapidae (Mammalia, Primates) in North America. *Contributions from the Museum of Paleontology, The University of Michigan* 24:245-279.
- Gingerich, P.D., and T. Smith. 2006. Paleocene-Eocene land mammals from three new latest Clarkforkian and earliest Wasatchian wash sites at Polecat Bench in the northern Bighorn Basin, Wyoming. *Contributions from the Museum of Paleontology, University of Michigan* 31: 245-303.
- Gmelin, J. F. 1789. *Linnei Systema Naturae*. G. E. Beer, Leipzig. 1057 pp.
- Gray, J. E. 1821. On the natural arrangement of vertebrate animals. *The London Medical Repository Monthly Journal and Review* 15: 296-310.
- Gregory, W. K. 1910. The orders of mammals. *Bulletin of the American Museum of Natural History* 27:1-254.
- Guthrie, D.A. 1967. The mammalian fauna of the Lysite Member, Wind River Formation, (early Eocene) of Wyoming. *Memoirs of the Southern California Academy of Sciences* 5:1-53.
- Guthrie, D. A. 1971. The mammalian fauna of the Lost Cabin Member, Wind River Formation (lower Eocene) of Wyoming. *Annals of Carnegie Museum* 43:47-113.
- Hay, O. P. 1892. The batrachians and reptiles of the State of Indiana. *Annual Report of the Indiana Department of Geology and Natural Resources* 17: 409-602.
- Hay, O. P. 1929. Second bibliography and catalogue of the fossil Vertebrata of North America. *Publications of the Carnegie Institute of Washington* 390:1-2003.
- Haeckel, E. 1895. *Systematische Phylogenie der Wirbeltiere (Vertebrata)*. Dritter Theil des Entwurfs einer systematischen Stammesgeschichte. Berlin, Verlag von Georg Reimer. 660 pp.
- Hutchison, J. H. 2013. New turtles from the Paleogene of North America. Pp. 477-497 in D. B. Brinkman, P. A. Holroyd, and J. D. Gardner (eds.). *Morphology and Evolution of Turtles*. Springer, New York.
- Huxley, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. *Proceedings of the Zoological Society of London*

- 43: 649-662.
- Ivy, L.D. 1990. Systematics of late Paleocene and early Eocene Rodentia (Mammalia) from the Clarks Fork Basin, Wyoming. *Contributions from the Museum of Paleontology, University of Michigan* 28: 21-70.
- Jepsen, G. L. 1930. New vertebrate fossils from the lower Eocene of the Bighorn Basin, Wyoming. *Proceedings of the American Philosophical Society* 69:117-131.
- Korth, W. 1984. Earliest Tertiary evolution and radiation of rodents in North America. *Bulletin of Carnegie Museum of Natural History* 24:1-71.
- Korth, W. 1994. The Tertiary record of rodents in North America. New York: Plenum Press. 310 pp.
- Lacépède, B. G. E. 1803. *Histoire Naturelle des Poissons: V. Plassan*, Paris, France. 803 pp.
- Leidy, J. 1869. The extinct mammalian fauna of Dakota and Nebraska including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. *Journal of the Academy of Natural Sciences of Philadelphia* 7: 8-472.
- Leidy, J. 1870. Remarks on a collection of fossils from the western Territories. *Journal of the Academy of Natural Sciences of Philadelphia* 22:109-110.
- Leidy, J. 1871. Notice of some extinct rodents. *Proceedings of the Academy of Natural Sciences of Philadelphia* 22:230-232.
- Leidy, J. 1872. On fossil vertebrates in the Early Tertiary Formation of Wyoming. *Fifth Annual Report of the United States Geological and Geographical Survey of the Territories by F. V. Hayden*: 353-372.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tomus I: Regnum animale. Editio decimal, reformata. Laurenti Salvii, Stockholm.*
- Loomis, F.B. 1907. Wasatch and Wind River rodents. *American Journal of Science* 4:123-130.
- Marandat, B. 1989. Mammifères nouveaux de l'Ilerdien des Corbières et du Minervois (Bas-Languedoc, France). *Palaeovertebrata* 19:161-167.
- Marsh, O. C. 1872. Preliminary description of new Tertiary Mammals. Parts I-IV. *American Journal of Science* 4:122-128, 202-224.
- Marsh, O. C. 1875. New order of Eocene mammals. *American Journal of Science* 9:239-250
- Marsh, O. C. 1876a. On some characters of the genus *Coryphodon*. *American Journal of Science*, 3:425-428.
- Marsh, O. C. 1876b. Notice of new Tertiary mammals. *American Journal of Science* 12: 401-404.
- Marsh, O. C. 1894. Description of Tertiary artiodactyles. *American Journal of Science* 48: 259-274.
- Matthew, W. D. 1899. A provisional classification of the freshwater Tertiary of the West. *Bulletin of the American Museum of Natural History*, 12:19-75.
- Matthew, W. D. 1901. Additional observations on the Creodonta. *Bulletin of the American Museum of Natural History* 14: 1-38
- Matthew, W. D. 1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. *Memoirs of the American Museum of Natural History* 9:291-567.
- Matthew, W. D. 1910. On the skull of *Apternodus* and the skeleton of a new artiodactyl. *Bulletin of the American Museum of Natural History* 28: 33-42.
- Matthew, W. D. 1915. Part IV: Entelonychia, Primates, Insectivora (part). In W. D. Matthew and W. Granger (auths.), A revision of the lower Eocene Wasatch and Wind River faunas. *Bulletin of the American Museum of Natural History* 34:429-434.
- Matthew, W. D. 1918. A revision of the lower Eocene Wasatch and Wind River faunas. Part IV. Insectivora (continued), Glires, Edentata. *Bulletin of the American Museum of Natural History* 38: 565-657.
- Matthew, W. D. 1929. Preoccupied names. *Journal of Mammalogy* 10:171.
- Matthew, W. D. and W. Granger. 1921. New genera of Paleocene mammals. *American Museum Novitates* 13:1-7.
- McGee, E. 2001. A mass death accumulation of *Coryphodon anthracoides* (Mammalia: Pantodonta) at Roehler's *Coryphodon* Catastrophe Quarry (lower Eocene, Wasatch Formation), Washakie Basin, Wyoming. Pp. 317-333 in G.F. Gunnell (ed.). *Eocene Biodiversity: Unusual Occurrences and Rarely Sampled Habitats*. Kluwer Academic/Plenum Publishers, New York.
- McKenna, M. C. 1975. Towards a phylogenetic classification of the Mammalia. Pp. 21-46 in W. P. Luckett and F. S. Szalay (eds.). *Phylogeny of the Primates: A Multidisciplinary Approach*. Plenum Press, New York.
- Miller, G. S., Jr. and J. W. Gidley. 1918. Synopsis of the supergeneric groups of rodents. *Journal of the Washington Academy of Sciences* 8: 431-448.
- Mook, C. C. 1921. *Allognathosuchus*, a new genus of Eocene crocodylians. *Bulletin of the American Museum of Natural History* 44: 105-110.
- Norell, M.A., J. M. Clark, and J. H. Hutchison. 1994. The Late Cretaceous alligatoroid *Brachychampsia montana* (Crocodylia): new material and putative relationships. *American Museum Novitates* 3116: 1-26.
- Oppel, M. 1811. *Die Ordnungen, Familien und Gattungen der Reptilien, als Prodrum einer Naturgeschichte derselben*, J. Lindauer, München. 87 pp.
- Osborn, H. F. and J. L. Wortman. 1892. Fossil mammals of the Wasatch and Wind River beds. Collection of 1891. *Bulletin of the American Museum of Natural History* 4: 81-147.
- Owen, R. 1845. *Odontography; a treatise on the comparative anatomy of the teeth*. Hippolyte Bailliere, London. 655 pp.
- Owen, R. 1848. Description of teeth and portions of jaws of two extinct Anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by Marchioness of Hastings in the Eocene deposits on the Wight: with an attempt to develop Cuvier's idea of the Classification of Pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London* 4:103-141.
- Peterson, O. A. 1919. Report upon the material discovered in the upper Eocene of the Uinta basin by Earl Douglass in the years 1908-1909, and by O. A. Peterson in 1912. *Annals of Carnegie Museum* 12: 40-168.

- Rankin, B. D. and P. A. Holroyd. 2014. *Aceroryctes dulcis*, a new palaeoryctid (Mammalia, Eutheria) from the early Eocene of the Wasatch Formation of southwestern Wyoming. *Canadian Journal of Earth Sciences* 51: 919-926.
- Roehler, H.W. 1993. Eocene climates, depositional environments, and geography, Greater Green River Basin, Wyoming, Utah, and Colorado. U.S. Geological Survey Professional Paper 1506F. U.S. Government Printing Office, Washington. 74 pp.
- Rose, K. D., A. E. Chew, R. H. Dunn, M. J. Kraus, H. C. Fricke, and S. P. Zack. 2012. Earliest Eocene mammalian fauna from the Paleocene-Eocene Thermal Maximum at Sand Creek Divide, southern Bighorn Basin, Wyoming. *University of Michigan Papers on Paleontology* 36:1-122.
- Schlosser, M. 1887. Die Affen, Lemuren, Chiropteren, Insektivoren, Marsupialier, Creodontier und Carnivoren des Europäischen Tertiärs und deren Beziehungen zu ihren lebenden und fossilen außereuropäischen Verwandten: Part 1. *Beiträge zur Palaontologie und Geologie, Osterreich-Ungarns und des Orients* 6: 1-224.
- Scott, W. B. and G. L. Jepsen. 1936. The mammalian fauna of the White River Oligocene. Part I, Insectivora and Carnivora. *Transactions of the American Philosophical Society* 28:1-153.
- Silcox, M.T., and K.D. Rose. 2001. Unusual vertebrate microfaunas from the Willwood Formation, early Eocene of the Bighorn Basin, Wyoming. Pp. 131-164 in G.F. Gunnell (ed.), *Eocene Biodiversity: Unusual Occurrences and Rarely Sampled Habitats*. Plenum Press.
- Simpson, G. G. 1928. A new mammalian fauna from the Fort Union of southern Montana. *American Museum Novitates* 297: 1-15.
- Simpson, G. G. 1940. Studies on the earliest primates. *Bulletin of the American Museum of Natural History* 77: 185-212.
- Sinclair, W. J. 1914. A revision of the bunodont Artiodactyla of the middle and lower Eocene of North America. *Bulletin of the American Museum of Natural History* 33: 267-295.
- Strait, S.G. 2001. New Wa-0 mammalian fauna from Castle Gardens in the southeastern Bighorn Basin. *University of Michigan Papers on Paleontology* 33:127-143.
- Strait, S.G. 2006. Rodents from the dawn of the Eocene. Abstracts, Climate and Biota of the Early Paleogene, Bilbao, Spain:134.
- Trouessart, E. L. 1879. Catalogue des Mammifères vivants et fossiles. *Revue et Magazine de Zoologie pure et appliqué* 7:219-285.
- Turner, H. N., Jr. 1849. On the evidence of affinities afforded by the skull in the ungulate Mammalia. *Proceedings of the Zoological Society of London* 17: 147-158.
- Wagler, J. G. 1831. Einige Mittheilungen über Thiere Mexicos. *Isis v. Oken*, 5: 510-535.
- Weber, M. 1904. Die Säugetiere. Einführung in die Anatomie und Systematik der recenten und fossilen Mammalia, Verlag Von Gustav Fischer, Jena, Germany. 866 pp.
- Williamson, T.E. 2001. *Meniscotherium* mass-death assemblages. Pp. 335-360 in G.F. Gunnell (ed.), *Eocene Biodiversity: Unusual Occurrences and Rarely Sampled Habitats*. Kluwer Academic/Plenum Publishers, New York.
- Williamson, T.E., and S.G. Lucas. 1992. *Meniscotherium* (Mammalia: "Condylarthra") from the Paleocene-Eocene of western North America. *New Mexico Museum of Natural History Bulletin* 1:1-75.
- Wilson, R. W. 1937. Two new Eocene rodents from the Green River Basin, Wyoming. *American Journal of Science* 34:447-456.
- Wing, S.L., H. Bao, and P.L. Koch. 2000. An early Eocene cool period? Evidence for continental cooling during the warmest part of the Cenozoic. Pp. 137-238 in B. T. Huber, K. G. MacLeod and S. L. Wing (eds.), *Warm Climates in Earth History*. Cambridge University Press, Cambridge.
- Winge, H. 1917. Udsigt over Insectaedernes Indbyrdes Slaegtskab, Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening, *Copenhagen* 68: 83-203.
- Wood, A.E. 1959. Rodentia. In McGrew, P.O. (ed.), *The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming*. *Bulletin of the American Museum of Natural History* 117:157-169.
- Wood, A. E. 1962. The Early Tertiary Rodents of the Family Paramyidae. *Transactions of the American Philosophical Society* 52:1-261.
- Wood, A.E. 1965. Small rodents from the early Eocene Lysite Member, Wind River Formation of Wyoming. *Journal of Paleontology* 39:124-134.
- Wortman, J. L. 1896. Species of *Hyracotherium* and allied perisodactyls from the Wasatch and Wind River beds of North America. *Bulletin of the American Museum of Natural History* 8: 81-110.
- Wortman, J. L. 1902. Studies of Eocene Mammalia in the Marsh collection, Peabody Museum. Part I. Carnivora. Paper 7. *American Journal of Science* 13: 197-206.
- Wortman, J. L. 1903. Studies of Eocene Mammalia in the Marsh collection, Peabody Museum. Part II. Primates. Suborder Cheiromyoidea. *American Journal of Science* 16: 345-368.
- Wortman, J. L. and W. D. Matthew. 1899. The ancestry of certain members of the Canidae, the Viverridae, and Procyonidae. *Bulletin of the American Museum of Natural History* 12:109-139.