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New material of fossil rodents (Mammalia) from the Eocene (Bridgerian-Uintan) Washakie Formation, southcentral Wyoming

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Abstract.—Eight species of rodents are described based on previously unreported fossil material from the early Eocene Adobe Town Member of the Washakie Formation of Wyoming. Among these are two new species: the sciuravid *Pauromys turnbulli* and the cylindrodont *Pareumys flynni*. The overall rodent fauna consists of twelve species. The greatest change in the rodent fauna is between the lower and middle units of the Adobe Town Member; six species having their last occurrence in the lower unit and three species having their first occurrence in the middle unit. This coincides with the boundary of the Bridgerian and Uintan North American Land Mammal Ages.

Keywords: Eocene, Bridgerian, Uintan, Rodentia, dental morphology, Adobe Town Member, Washakie Formation

The Washakie Formation is in the southcentral part of Wyoming and part of the Greater Green River Basin (McCarroll et al. 1996: fig. 1). The stratigraphy and history of investigation of the formation has been presented by Turnbull (1978). The formation has been divided into two members, the subjacent Kinney Rim Member (Twkk), and the overlying Adobe Town Member (Twka). The age of the formation ranges from the early Eocene (Bridgerian North American Land Mammal Age [NALMA]) to the early middle Eocene (Uintan NALMA; Turnbull 1978; McCarroll et al. 1996; Robinson et al. 2004). The material described here is limited to the Adobe Town Member, which has been divided into Lower, Middle, and Upper units. The age of these units has been determined as late Bridgerian NALMA for the lower unit Twka1 (Br3: see Janis et al. 2008, table 0.1 for abbreviations), the early Uintan NALMA for middle unit Twka2 (Ui1), middle Uintan NALMA for the upper unit Twka3 (Ui2).

Fossil mammals from the Washakie Formation have been described as early as the late nineteenth century (Cope, 1884). McCarroll et al. (1996) reviewed the history of investigation of the Washakie Formation and presented a faunal list of the fossil mammals, which included ten species (McCarroll et al. 1996: table 1). Stucky et al. (1996: table 1) similarly reviewed the Sand Wash subbasin of the Washakie Formation and recognized seven species (Stucky et al. 1996) of rodents (Table 1). The fossils described herein do not include material from the subbasin.

Some rodents from the Washakie have been cited in previous systematic studies (e.g., Wood 1962; Turnbull 1991), but

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Table 1.—PREVIOUSLY recognized species of rodents from the Washakie Formation.

McCarroll et al. (1996: table 1)	Stucky et al (1996: table 1)
Upper Adobe Town Member (Twka3 = Ui2)	Sand Wash Sub-basin (Ui1–2)
Paramys compressidens	*Leptotomus bridgerensis*
Pareumys grangeri	*Leptotomus* sp.
Middle Adobe Town Member (Twka2 = Ui1)	*Thisbemys* sp.
Leptotomus leptodus	Ischyromyidae sp.
Leptotomus (?bridgerensis)	*Sciuravus* sp.
Protoptychus hatcheri	*Tillomys* sp. cf. *T. senex*
Lower Adobe Town Member (Twka1 = Br3)	*Namatomys* sp.
Paramys sp.	
Leptotomus bridgerensis	
Thisbemys sp.	
Mysops parvus	
Sciuravus nitidus	
Sciuravus sp.	

there has been no detailed description of the entire rodent fauna. Twelve species are recognized here, six ischyromids, three sciuravids, two cylindrodontids, and a protoptychid. Turnbull (1991) has fully described the protoptychid, *Protoptychus hatcheri* Scott, 1895, so no additional description or discussion of this species is presented here. The species that are represented by the most specimens, two species of the paramyine ischyromyid *Thisbemys* and a previously undescribed sciuravid, are being described elsewhere, so are also not included in this study.

Materials and Methods

All of the material described here is from the collections of the Field Museum of Natural History (FMNH), and was collected for the most part, by W.D. Turnbull or J.J. Flynn and field parties from that institution from the 1940s into the 1990s. Dental terminology for rodents follows that of Wood and Wilson (1936). Lower teeth are designated by lower-case letters, uppers by capital letters (e.g., m1 or M1). All measurements were taken with an optical micrometer to the nearest 0.01 mm. Abbreviations for measurements: L, anteroposterior length; W, transverse width (maximum measurements); for land mammal ages: Wa, Wasatchian; Br, Bridgerian; Ui, Uintan; divisions of each of these ages (Br3, Ui1, Ui2) are as defined by Janis et al. (2008: table 0.1).

This work has been registered in ZooBank with the registration number [LSID].

Systematics

Order Rodentia Bowdich, 1821

Family Ischyromyidae Alston, 1876

Metaparamys Korth and Emry, 2007

Metaparamys compressidens (Peterson, 1919)

Fig. 1A, B; Table 2

Paramys compressidens Peterson, 1919:63
Ischyrodomus compressidens (Peterson), Gidley, 1919:63
Metaparamys compressidents (Peterson), Korth & Emry, 2007

Referred specimens.—FMNH PM 3871, skull fragment with left I1, P3, M1–M3; FMNH PM 169, left dentary with i1, p4–m3; FMNH PM 55361, partial dentary with p4–m2.

Occurrence.—FMNH PM 3871 from early Uintan (Ui1) Middle Adobe Member (Twka2); and FMNH PM 169 and 55361 from middle Uintan (Ui2), Upper Adobe Member (Twka3), Washakie Formation, Sweetwater County, Wyoming.

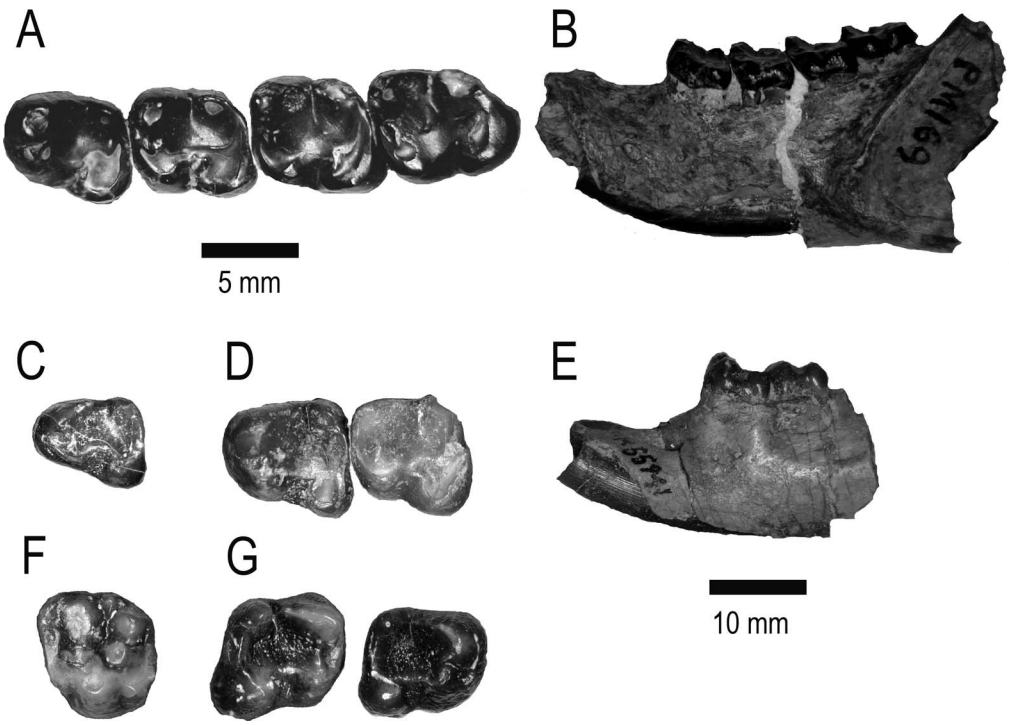

Fig. 1. Dentition and dentaries of paramyine ischyromyid rodents from the Washakie Basin. A, B, *Metaparamys compressidens*, FMNH PM 169. A, left p4–m3, occlusal view. B, lateral view of dentary. C–E, *Uintaparamys bridgerensis*. C, FMNH PM 1504, left dp3. D, E, FMNH PM 55941. D,left p4–m1, occlusal view. E, lateral view of dentary. F–G, *Quadratomus grandis*. F, FMNH PM 55166, left M1, G, FMNH PM 55348, right p4–m1. Occlusal views to same scale (above left), dentaries to different scale (below right).

Discussion.—The material from the Washakie Basin does not differ markedly in size or morphology from previous descriptions of this species (Peterson 1919; Wood 1962; Korth 1988; Korth & Emry 2007). Wood (1962) followed Gidley (1919) in referring this species to the genus *Ischyrotomus* Matthew, 1910, but noted that the cheek teeth were more crenulated than in other species of this genus (a feature more typical of *Paramys*). Later, Korth (1988) returned this species to *Paramys*, its original allocation (Peterson 1919), noting that a number of the specimens referred earlier to this species by Wood (1962) were incorrectly done so. Most recently, Korth & Emry (2007) erected a new genus *Metaparamys* and included "*P.*" *compressidens* as a referred species. The only previously cited specimen of *M. compressidens* from the Washakie Formation was FMNH PM 169 (Wood 1962: 215).

Uintaparamys Kretzoi, 1968

Discussion.—Kretzoi (1968) noted that the genus *Letotomus* was preoccupied, and proposed *Uintaparamys* to replace it. This synonymy was not noted by authors until considerably later. Black (1971) continued the use of *Leptotomus,* and also listed *Tapomys* Wood 1962, as a synonym. In a review of the Tertiary rodents of North America, Korth (1994) listed *Leptotomus* as a valid genus separate from *Tapomys* and made no reference to *Uintaparamys*. McKenna & Bell (1998), in their classification of all mammals, listed both *Leptotomus* and *Uintaparamys* as synonyms of

Table 2.—DENTAL measurements of lower cheek teeth of ischyromyid rodents from the Washakie Formation, Wyoming. Abbreviations: L, anteroposterior length; W, transverse width. All measurements in mm. —, indicates measurement could not be made due to breakage.

FMNH PM #	dp4L	dp4W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4–m3L	i1L	i1W
Metaparamys compressidens													
57082									4.89	3.72			
1504 (left)	4.37	3.58										3.24	2.40
1504 (right)	—	3.57					4.57	4.62				3.55	2.55
61620					4.65	4.19							
55941			4.68	4.51	4.63	4.67						3.35	2.57
Uintaparamys bridgerensis													
55361			4.3	4.1	4.08	3.84	4.02	4.07					
169			4.67	3.97	4.51	4.14	4.61	4.23	5.42	4.16	19.68	3.55	3.37
Quadratomus grandis													
55348			5.02	4.52	5.35	5.02							
Mattimys sp.													
51050					1.35	1.32							

Tapomys. Most recently, Anderson (2008: 316) noted that "...there are generic-level distinctions that warrant a separate genus for *Uintaparamys*." Anderson (2008) listed *Leptotomus* as a junior synonym of *Uintaparamys* and retained *Tapomys* as a distinct genus. This latter allocation is followed here.

Uintaparamys bridgerensis (Wood 1962)
Fig. 1C–E, Table 2

Leptotomus bridgerensis Wood, 1962:88
Uintaparamys bridgerensis (Wood) Anderson, 2008:316

Referred specimens.—FMNH PM 55941, left partial dentary with i1, p4–m1; FMNH PM 1504, left dentary with i1, dp4; FMNH PM 57082, right dentary fragment with m3; FMNH PM 61620 right dentary with i1, partial p4–m1, complete m2 and left m1 or m2.

Occurrence.—FMNH PM 1504 and 57082 from early Uintan (Ui1), Middle Adobe Member (Twka2); FMNH PM 55941 and FMNH 61620 from late Bridgerian (Br3), Lower Adobe Town Member (Twka1), Washakie Formation, Sweetwater County, Wyoming.

Discussion.—The specimens referred here to *Uintaparamys bridgerensis* do not differ in size or morphologically from the material described by Wood (1962) as "*Leptotomus*" *bridgerensis* (Fig. 1C–E, Table 2). Wood (1962: 88) originally limited the occurrence of this species in the Washakie basin to the Bridgerian "lower Washakie of the Washakie basin, Wyoming" (=Br3) and cited the type specimen of the larger "*L*." *leptodus* from the "upper Washakie" (Wood 1962: 73; =Ui1 or 2). All of the specimens cited herein are smaller than "*L*." *leptodus*, and fall within the range of size of the smaller "*L*." *bridgerensis* (Table 2; Wood 1962: tables 25, 30). However, two specimens from the Washakie Basin referred here are from Middle Adobe Member (Ui1), likely the same horizon as the holotype of "*L*." *leptodus*.

Quadratomus Korth, 1984
Quadratomus grandis (Wood, 1962)
Fig. 1F–G, Table 2

Leptotomus grandis Wood, 1962:80
Quadratomus grandis (Wood) Korth, 1984:23

Referred specimens.—FMNH PM 55166, left M1 or M2; FMNH PM 55348, associated right p4 and m1.

Occurrence.—Both specimens from late Bridgerian (Br3), Lower Adobe Town

Member (Twka1), Washakie Formation, Sweetwater County, Wyoming.

Description.—The two lower cheek teeth (FMNH PM 55348) are little-worn and the talonid basins are full of minute crenulations (Fig. 1G); p4 longer than wide, and wider posteriorly than anteriorly; anterior width only slightly less than the posterior width, making the tooth look rectangular in occlusal outline; metaconid in anterolingual corner of tooth, and markedly larger than the protoconid, is crescentic in occlusal outline with lophids extending posteriorly from along lingual side and buccally along anterior margin of tooth. Protoconid markedly smaller than metaconid and posterior to it along buccal margin of tooth. Small, low anterior cingulid extends from anterobuccal corner of protoconid, curves around the anterobuccal corner of tooth, and ends along the anterior margin of tooth before reaching base of metaconid, forming small trigonid basin with narrow opening along both anterior and posterior ends; metaconid cristid descends posterior side of metaconid along lingual side of tooth, but ends before joining entoconid; ectolophid runs posteriorly from the posterolabial corner of the protoconid to the anterolingual corner of the hypoconid; mesoconid not likely present but its presence is obscured by crenulate nature of ectolophid; hypoconid large and round in occlusal outline at posterobuccal corner of tooth; posterolophid runs lingually from posterolingual edge along posterior margin of tooth, ultimately fusing with posterobuccal corner of entoconid; entoconid round in occlusal outline.

The m1 similar in morphology to p4, but protoconid larger and more buccally positioned, giving tooth a more rectangular occlusal outline (Fig. 1G); trigonid basin anteroposteriorly compressed; posterior arm of protoconid extends directly lingually, reaching base of metaconid, enclosing basin posteriorly; anterior cingulid as in p4, ending at anterobuccal base of the metaconid; posterior half of tooth nearly identical to that of p4 except for a distinguishable mesoconid at center of ectolophid.

Referred M1 or M2, FMNH PM 55166, similar in size to lower cheek teeth (L = 4.65 mm, W = 5.16 mm); tooth shows more wear than referred lower teeth, so crenulations are minimal, but still discernable; anterior cingulid runs along anterior margin of tooth from parastyle in anterobuccal corner of tooth to a point anterior to apex of protocone, where it bends posteriorly to join protocone; protoloph consists of large paracone and protocone, and much smaller, centrally placed protoconule; each cusp separated from adjacent cusp by shallow transverse valley; protocone large and central along lingual edge of tooth with short loph running buccally from its center; metaloph consists of large metacone and slightly smaller metaconule (larger than protoconule) that angles slightly anterolingually and converges with protocone just posterior to its center on buccal side; hypocone markedly smaller than protocone and positioned posterior and slightly lingual to apex of the protocone; posterior cingulum extends buccally from hypocone along posterior margin of tooth, ending before reaching posterobuccal corner; distinct mesostyle at the center of buccal side of tooth, midway between major buccal cusps; minor lophule extends only slightly into central valley of tooth.

Discussion.—The dental measurements of the Washakie specimens are only slightly larger than those of the holotype of *Q. grandis* (Table 1; Wood 1962: tables 27, 28), and smaller than the next smallest species of the genus, *Q. grossus* Korth 1985. The p4 is more molariform than that of *Q. grossus* (Korth 1985: fig. 5B) and nearly identical to that of the holotype of *Q. grandis* (Wood 1962: fig. 28J; Korth 1984: fig. 9B, C).

The holotype and previously referred specimens of *Q. grandis* are limited to the

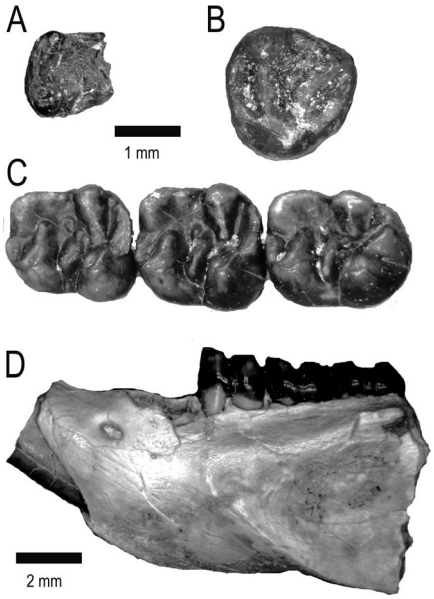

Fig. 2. Dentition and dentary of *Mattimys* and *Tillomys* from the Washakie Basin. A, *Mattmys* sp., FMNH PM 56559, right m1 (partial). B, ?*T. senex*, FMNH PM 1505, left M3. C–D, *T. senex,* FMNH PM 55908. C, left m1–m3, occlusal view. D, lateral view of dentary. A–C to same scale (above), D to different scale (below).

uppermost Huerfano Formation of southern Colorado (early Bridgerian; Br1), slightly older than the Washakie specimens (Robinson 1966; Wood 1962; Korth 1984, 1985).

Mattimys Korth, 1984
Mattimys sp.
Fig. 2A

Referred specimen.—FMNH PM 56559, right dentary fragment with m1.

Occurrence.—Late Bridgerian (Br3), Lower Adobe Town Member, Washakie Formation (Twka1), Sweetwater County, Wyoming.

Description.—Although lacking ventral border, dentary very deep relative to size of preserved molar (approximately = 4 mm); masseteric fossa marked by low ridge that extends anteriorly to below anterior margin of m2.

Enamel surface of m1 finely crenulated (Fig. 2A); anterior border of tooth broken away, so total length of tooth cannot be measured precisely; width can be =1.32 mm; protoconid and metaconid missing, but it appears that posterior arm of protoconid extends across entire tooth, ending at metaconid, enclosing trigonid basin posteriorly; low, but distinct ridge runs posteriorly along lingual edge of tooth from metaconid, ending just anterior to entoconid; ectolophid incomplete; mesoconid small but recognizable; hypoconid larger than the entoconid, and has distinct crenulations on its posterior side; posterior cingulid runs from posterolingual corner of hypoconid along posterior edge of tooth, ending well short of lingual margin; entoconid round in occlusal outline and distinct but short hypolophid extends buccally and slightly posteriorly from it, ending before reaching center of posterior cingulid.

Discussion.—The small size, presence of crenulations on the enamel, complete metalphulid II, and presence of a partial hypolophid on this specimen are nearly identical to that of the earlier Washatchian *Mattimys kalicola* (Matthew 1918: fig. 38; Korth 1984: fig. 32). It differs from the lower molars of known species of the paramyine *Lophiparamys* (also with crenulated enamel) in its slightly smaller size, less-well developed enamel crenulations, and presence of a hypolophid and complete metalophulid II, both lacking in species of *Lophiparamys* (Wood 1962: fig. 56A–E).

The Washakie specimen cannot be definitely referred to the type and only species of the genus *M. kalicola* because of its slightly smaller size (Korth 1984: table 15), and the incompleteness of the specimen. The *Mattimys* specimen from the Washakie is late Bridgerian in age (Br3); the latest occurrence of *M. kalicola* elsewhere is from the late Washatchian (Wa6: Flynn & Jacobs 2008). However, a specimen of similar size to that of the Washakie

Table 3.—DENTAL measurements of lower cheek teeth of sciuravid rodents from the Washakie Formation, Wyoming. Abbreviations: L, anteroposterior length; W, transverse width. All measurements in mm. *, m1 or m2.

FMNH PM#	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4–m3L	i1L	i1W
Tillomys senex											
55908			2.84	1.62	2.90	1.75	3.03	1.67		2.01	1.03
51688*			1.94	1.75							
Pareumys turnbulli											
44685							1.20	1.11			
8026			0.98	0.92	1.23	1.06	1.22	0.95	4.73	1.16	0.52
44683									4.71		
63076	0.61		1.04							1.27	0.63
8027	0.56	0.50	1.20	1.00			1.15		4.36	1.21	0.60
63077	0.55	0.58	1.17	0.94	1.23	1.02			4.65	1.03	0.55
Mean	0.57	0.54	1.10	0.95	1.23	1.04	1.19	1.03	4.61	1.17	0.58

specimen was identified as *Mattimys* sp. from the early Bridgerian (Br2) of Nevada (Emry & Korth 1989).

Family Sciuravidae Miller and Gidley, 1918
Tillomys Marsh, 1872
Tillomys senex Marsh, 1872
Fig. 2B–D, Table 3

Referred specimens.—FMNH PM 55908, left dentary with i1, m1–m3; FMNH PM 51688 left m1 or m2; questionably referred specimen, FMNH PM 1505, right M3.

Occurrence.—FMNH PM 55908 and FMNH PM 51688 from late Bridgerian (Br3), Lower Adobe Town Member (Twka1); FMNH PM 1505 from Middle Adobe Town Member (Ui1); Washakie Formation (Twka2), Sweetwater County, Wyoming.

Description.—Dentary is deep (4.9 mm below m1); length of the diastema short (approximately 2.5 mm) and has sharp dorsal ridge (Fig. 2D); mental foramen high on the dentary, just below dorsal margin of diastema and just anterior to anterior root of p4; masseteric scar U-shaped and ends anteriorly in small, circular depression ventral to anterior margin of m1 at mid-depth of dentary.

Incisor is twice as long as wide in cross-section (Table 3); anterior enamel surface slightly rounded, but nearly flattened; enamel only barely extends onto lateral surface of incisor, and not onto the medial surface.

The p4 not preserved, but from alveolus it was approximately same length as m1, and narrower than wide; m1 and m2 nearly identical and rectangular in outline (longer than wide), m1 slightly narrower anteriorly than posteriorly (Fig. 2C); metaconid slightly obliquely compressed at anterolingual corner of the tooth; protoconid J-shaped with long metalophulid II, nearly reaching base of metaconid; anterior cingulid a short, low loph extending across anterior margin of tooth from anterobuccal part of the metaconid to anterolingual point of protoconid; mesoconid isolated at center of buccal side of tooth and obliquely oriented, slightly nearer hypoconid than protoconid, suggesting that it will fuse with hypoconid first as it wears. On both m1 and m2 of FMNH PM 55908 there is small accessory cuspule in central basin of tooth, just lingual and slightly anterior to lingual end of the mesoconid, cusp is lacking on isolated molar (FMNH PM 51688); entoconid obliquely compressed, low ridge extends buccally and slightly posteriorly from it into central basin, and ends well short of hypoconid; hypoconid obliquely compressed (anterobuccal to posterolingual), and continuous with pos-

terior cingulid that wraps around posterior side of tooth, ending short of the entoconid; small hypoconulid present at buccal end of posterior cingulid, adjacent to apex of hypoconid.

The m3 is longer than m1 and m2 but similar in occlusal morphology (Fig. 2C); only major difference is that in m3, posterior cingulid bows more posteriorly.

M3, FMNH PM 1505, is referred here tentatively to *Tillomys* based on similar size, crown-height, and lophodonty with the lower molars of *Tillomys* from Washakie (Fig. 2B). It is circular in occlusal outline, only slightly wider than long (L = 1.89 mm; W = 2.01 mm); paracone circular in occlusal outline at anterobuccal corner of tooth, and protocone is at center of lingual side of tooth, and slightly elongated (anteroposteriorly); anterior cingulum low, runs from anterolingual corner of paracone along anterior margin of tooth, ending in a small cuspule lingually, just before joining anterobuccal side of protocone; protoloph is broad loph that is complete from paracone to metacone, isolating small valley between it and anterior cingulum (parafossette); central transverse valley (mesoflexus) continuous across entire tooth, and bows anteriorly at its center, is shallowest between protocone and hypocone; small transversely flattened mesostylid at buccal end of central valley; metaloph much shorter than protoloph and bows anteriorly; metacone a small, obliquely compressed cusp at posterobuccal edge of and is joined anteroligually by metaloph, and posterolingually by posterior cingulum; metaloph slightly swelled at is center, indicating a metaconule; hypocone is markedly smaller than protocone, circular in outline, and posterior and buccal to protocone; posterior cingulum runs along posterior border of tooth from hypocone to posterior side of metacone, enclosing small basin (posterofossette).

Discussion.—The two sciuravid genera, *Tillomys* and *Taxymys*, are rare in the fossil record, known from only a few specimens each. The former is only known from lower dentitions, the latter only from upper dentitions. The synonymy of these genera has been discussed over several decades (see Walton & Porter 2008, for historical review). Unfortunately, the synonymy of *Tillomys* and *Taxymys* cannot be resolved at this time. It will be necessary to find associated upper and lower dentitions in order to determine the viability of each of these genera (and species).

The type and referred specimens of both *Tillomys senex* and *Taxymys lucaris* are from Upper Bridger (Br3), Twin Buttes Member, Tabernacle Butte, Wyoming. The dentary and referred lower molar from Washakie are from the Lower Adobe Town Member (Br3) and the questionably referred upper molar (Fig. 2B) is from the Middle Adobe Town Member (Ui1). The occurrence of latter is younger than the previously known occurrence of either *Tillomys* or *Taxymys* (Walton & Porter 2008), although *Taxymys* has been cited as occurring in the Uintan in an unpublished dissertation (Murphey 2001).

Pauromys Troxell, 1923
Pauromys turnbulli n. sp.
Fig. 3A–C, Table 3

Type Specimen.—FMNH PM 8027, right dentary with i1, p4–m1, m3(partial).

Referred Specimens.—FMNH PM 63077, left dentary with i1, p4–m2; FMNH PM 44683, left dentary with i1, m1–m2; FMNH PM 63076, right dentary with i1, p4–m3; FMNH PM 8026, right dentary with i1, m1–m3; FMNH PM 44685, left dentary fragment with m3.

Occurrence.—Early Uintan (Ui1); Middle Adobe Town Member, Washakie Formation (Twka2), Sweetwater County, Wyoming.

Diagnosis.—Slightly larger than *P. perditus* Troxell, 1923; p4 more greatly reduced in size relative to m1 than other species (length p4/length m1 = 0.47); p4 two-rooted with one or two distinct

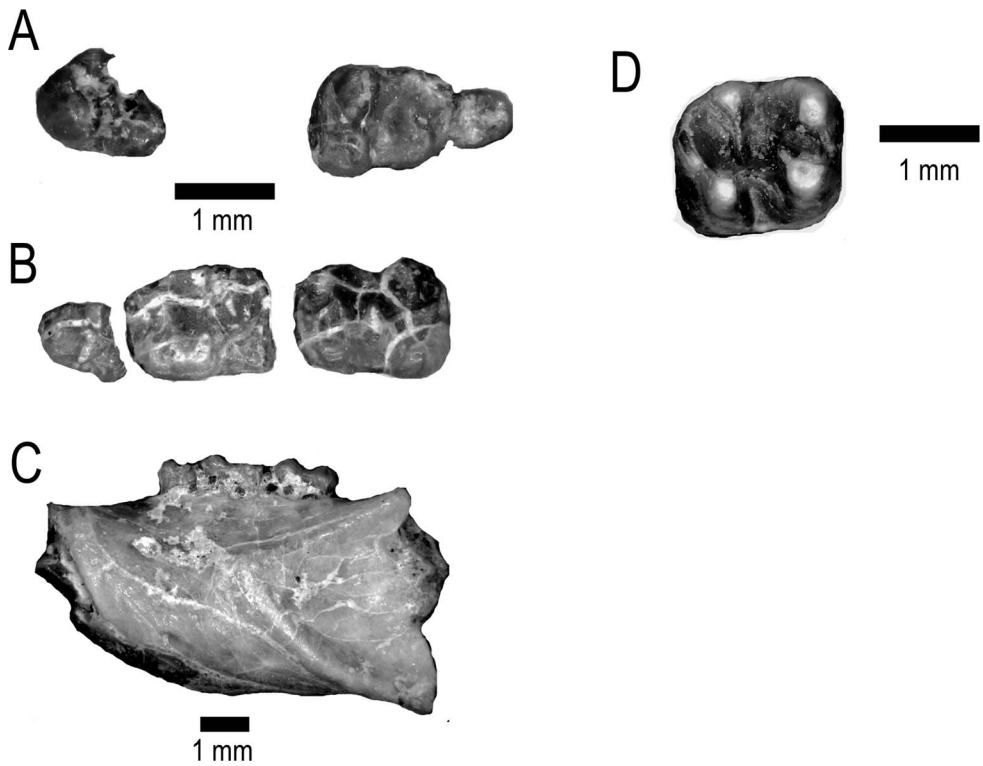

Fig. 3. Lower cheek teeth of *Pauromys* and *Mysops* from the Washakie Basin. A–C, *Pauromys turnbulli*. A, FMNH PM 8027 (holotype), right p4–m1, m3 (partial). B–C, FMNH PM 6377. B, p4–m2, occlusal view. C, lateral view of dentary. D, *Mysops* sp., FMNH PM 55377, right m1 or m2. Occlusal views of cheek teeth to same scale (top and bottom), dentary to different scale (below C).

trigonid cusps; anterior arm of the hypoconid continuous with the mesoconid on lower molars (=partial ectolophid); m3 approximately equal in length to m2.

Etymology.—Patronym for W. D. Turnbull of the FMNH, collector of the bulk of the specimens described herein.

Description.—Dentary is deep relative to size of the dentition, averaging a depth of between 70 to 80 percent length of cheek tooth row (average = 3.4 mm; Fig. 3C); diastema shallow and approximately half length of tooth row (average = 2.2 mm); dorsal surface of diastema dips only slightly below alveolar margin of cheek teeth and has sharp dorsal ridge; mental foramen relatively large for size of dentary, and is approximately one-third the depth of dentary below anterior root of p4; masseteric ridges form a V-shape, ending anteriorly at mid-depth of dentary, ventral to boundary between m1 and m2; anterior margin of ascending ramus even with posterior margin of m3.

The p4 markedly smaller than molars; in the two specimens that contain both p4 and m1, length of p4 is only 47% length of m1. Trigonid cusps (metaconid, protoconid) vary in size in different specimens; on FMNH PM 63077, protoconid is larger than metaconid (Fig. 3B), on FMNH PM 8027, there appears to be only single, large, central cusp (Fig. 3A), and on FMNH PM 63076, cusps approximately the same size; if separate cusps present, metaconid is always more anterior than protoconid; tooth wider posteriorly than anteriorly; entoconid and hypoconid approximately equal in size; no distinct ectolophid or mesoconid on any specimens, but proto-

conid and hypoconid abut one another buccally; minute metastylid on posterolingual slope of metaconid on holotype only.

On the specimens that retain both m1 and m2 (FMNH PM 8026, 63077), m1 is slightly smaller in both length and width (Fig. 3B); both m1 and m2 longer than wide and rectangular in occlusal outline; m1 best preserved on FMNH PM 8027 (Fig. 3A), on all other specimens is heavily worn or broken; m1 narrower anteriorly than posteriorly; metaconid and protoconid approximately equal in size, metaconid being slightly more anterior; trigonid basin open anteriorly, bounded by low anterior cingulid that does not appear to be continuous with either of trigonid cusps, but extends buccally to a point anterior to protoconid; posterior arm of protoconid extends lingually to base of metaconid, closing trigonid basin posteriorly; a minute metastylid on posterior slope of metaconid along lingual side of tooth; mesoconid transversely elongated, but does not connect anteriorly to protoconid, but does connect posteriorly with hypoconid; hypoconid and entoconid larger than cusps of trigonid; short hypolophid extends buccally from entoconid, but ends before reaching hypoconid; hypoconid oval in occlusal outline, and continuous with posterior cingulid, which extends along posterior margin of tooth, but ends well short of entoconid or lingual edge of tooth.

The m2 nearly identical to m1, but wider anteriorly, and anterior cingulid appears to extend slightly more buccally anterior to protoconid (Fig. 3B); FMNH PM 44685 contains m3 that is completely unworn; tooth approximately equal in size to m2; only difference between m3 and m2 is that posterior cingulid bows more posteriorly on m3; connection of mesoconid with hypoconid a lower loph than in m1 or m2, but still present.

Discussion.—*Pauromys turnbulli* is referable to this genus based on its small size, greatly reduced p4, and basic sciuravid occlusal pattern of the molars. *P. trunbulli* differs from *P. lillegraveni* Walsh, 1997, from California in having m2 and m3 of similar length (m3 smaller than m2 in *P. lillegraveni*; Walsh 1997: table 5) and having a two-rooted p4 (one-rooted in *P. lillegraveni*). It differs from *Pauromys* sp. from Utah (Dawson 1968) in having a partial ectolophid on the lower molars and a smaller p4 relative to m1. *P. turnbulli* differs from the type species *P. perditus* from Wyoming in being slightly larger and having the length of m3 nearly equal to that of m2 (m3 longer than m2 in *P. perditus*; Dawson 1968: table 6).

The early Uintan occurrence of *P. trunbulli* (Ui1) is later than that of the Bridgerian *P. perditus* (Br2) and *Pauromys* sp. (Br1), and slightly earlier than the later Uintan *P. lillegraveni* (Ui2: see Janis et al. 2008: appendix 1).

Family Cylindrodontidae Miller & Gidley, 1918

Mysops Leidy, 1871

Mysops sp.

Fig. 3D

Referred Specimen.—FMNH PM 55377, right m1 or m2.

Occurrence.—Late Bridgerian (Br3), Adobe Town Member (Twka1), Washakie Formation, Sweetwater County, Wyoming.

Description.—In size, FMNH PM 55377 significantly smaller than other cylindrodon from fauna (L = 1.65 mm; W = 1.48 mm), described below. Tooth very low-crowned, roughly rectangular in occlusal outline, but slightly wider posteriorly than anteriorly (Fig. 3D); small trigonid basin blocked anteriorly but open posteriorly; metaconid and protoconid equal in size; metaconid slightly anteroposteriorly compressed, protoconid crescentic; posterior arm of protoconid very short; ectolophid much lower than cusps in height, but continuous from posterior side of protoconid to the anterolingual corner of hypoconid; low, but complete hypolophid runs from entoconid to ectolophid, joining

Table 4.—DENTAL measurements of lower cheek teeth *Pareumys flynni* from the Washakie Formation, Wyoming. Abbreviations: L, anteroposterior length; W, transverse width. All measurements in mm. *, m1 or m2.

FMNH PM#	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4–m3L	i1L	i1W
55121			2.06	1.7	1.98	1.99	2.41	1.96		1.71	0.63
55136							2.30	1.94			
55130*			2.08	1.65							
57094*			1.88	1.65							
55060	1.40	1.37	1.82	1.80	1.84	1.93	2.28	1.82	7.58	2.13	1.52
55060	1.36	1.41	1.82	1.60	1.83	1.80	2.20	1.83	7.43	1.96	1.50
Mean	1.38	1.39	1.93	1.68	1.88	1.91	2.30	1.89	7.51	1.93	1.22

it just anterior to its junction with hypoconid. Neither hypoconid nor entoconid show any compression, both nearly circular in occlusal outline; posterior cingulid runs from posterolingual corner of hypoconid along posterior margin of tooth, ending at posterolingual corner but never reaching entoconid, leaving a deep valley between posterior cingulid and entoconid.

Discussion.—The single molar from the Washakie is clearly separable from the other cylindrodontid from the fauna (described below) in its smaller size, lower crown-height, and lower ectolophid and hypolophid.

The three recognized species of *Mysops*, *M. minimus*, Leidy 1871, *M. parvus* (Marsh 1872: =*M. plicatus* Troxell 1923), and *M. fraternus* Leidy 1873, are all known from the Bridger Formation of Wyoming (Walsh & Storer 2008). In addition, all are represented by only a few specimens, which has led to uncertainty as to whether all the species are truly distinct from one another (Wilson 1938; Walsh & Storer 2008). Because only a single tooth is available from the Washakie Formation, no specific identification can be made, nor can any conclusions about the synonymy of the currently recognized species.

Pareumys Peterson, 1919
Pareumys flynni n. sp.
Fig. 4, Table 4

Type specimen.—FMNH PM 55060, left and right dentaries with i1, p4–m3.

Referred specimens.—FMNH PM 55121, right dentary with i1, m1–m3; FMNH PM 55130, 57094 m1 or m2; FMNH PM 55136, left m3; FMNH PM 42080, right M3.

Occurrence.—FMNH PM 55121, 42080, 55130, 55136, from late Bridgerian (Br3), Lower Adobe Town Member (Twka1); FMNH 57094 from early Uintan (Ui1) Middle Adobe Town Member (Twka2); FMNH PM 55060 from later Uintan (Ui2) Upper Adobe Town Member (Twka3), Washakie Formation, Sweetwater County, Wyoming.

Diagnosis.—Similar in size to *P. grangeri* Burke, 1935; p4 equal in length and width (longer than wide in all other species) and smaller relative to the molars than any other species; mesoconid present on m1 of little-worn specimens (absent in all other species).

Etymology.—Patronym for J. J. Flynn of the American Museum of Natural History (formerly of FMNH), the collector of much of the fossil material described here.

Description.—Dentary deep for the size of dentition but transversely narrow (Fig. 4D); depth at m1 of FMNH PM 55060 = 6.83 mm (approximately 90% length of tooth row); deepest ventral to p4 at posterior margin of symphysis; dorsal surface of diastema short but not completely preserved on any specimen, so cannot be measured; dorsal margin of diastema a sharp ridge level with alveolar margin; mental foramen high on side of

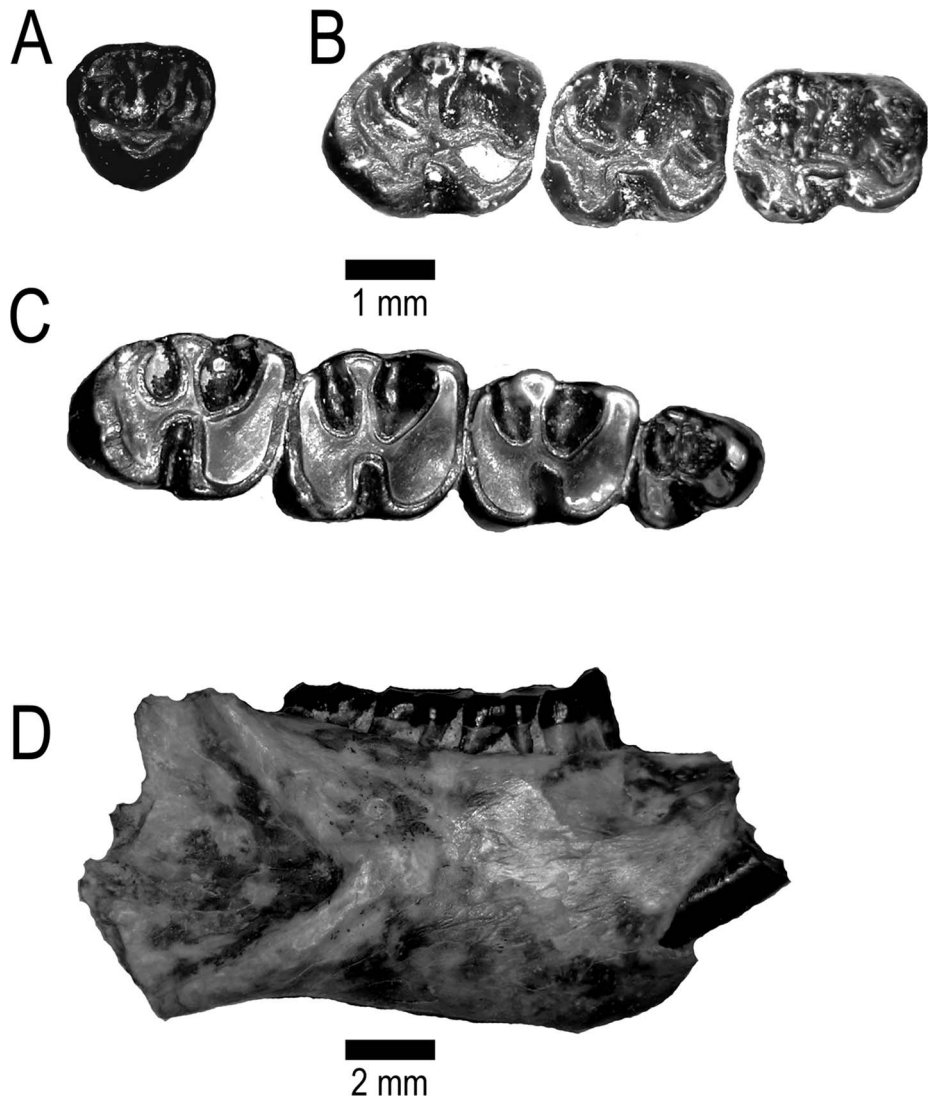

Fig. 4. Cheek teeth of *Pareumys flynni* from the Washakie Basin. A, FMNH PM 42080, right M3. B, FMNH PM 55121, right m1–m3. C–D, FMNH PM 55060 (holotype). C, right p4–m3, occlusal view. D, lateral view of dentary. Occlusal views all teeth to same scale (above), dentary to different scale (below).

dentary, just anterior to p4, at posterior boundary of diastema; ridges marking masseteric fossa high and form V-shape, ending anteriorly below center of m2; anterior margin of ascending ramus arises posterior to tooth row.

The i1 much longer than wide in cross-section; medial surface flattened, anterior enamel surface nearly flattened for most of its width, then curves posteriorly, wrapping around lateral side of tooth, extending posteriorly to more than half cross-sectional length; no grooves or ornamentation on enamel of incisor.

The p4 markedly smaller than any of the molars (Fig. 4C); widest posteriorly, and narrow anteriorly and approximately equal in length and width; trigonid consists of two closely appressed cusps, a smaller and more anterior metaconid and a larger

and slightly more posterior protoconid; a narrow, short valley (anterofossettid) separates these two cusps, but is blocked posteriorly; short loph (metalophid crest) extends posteriorly along lingual side of tooth from anterolingual corner of metaconid, but ends before reaching entoconid; ecotolophid short, connecting posterolingual corner of protoconid with anterolingual corner of hypoconid; hypoconid anteroposteriorly compressed and transversely elongated; buccal valley (hypoflexid) between protoconid and hypoconid relatively short and extends posterolingually; entoconid anteropotseriorly compressed and at posterolingual corner of tooth; low hypolophid extends buccally from it, then meets posterior end of ectolophid where it joins anterolingual corner of hypolophid; posterior cingulid a narrow lophid extending lingually from posterolinigual corner of hypoconid to posterolingual side of entoconid. The two major basins between hypolophid and trigonid (mesoflexid), and between hypolophid and posterior cingulid (metaflexid) deep; enamel within basins is smooth.

Two isolated lower molars cannot be identified as either m1 or m2 with certainty, but in specimens that contain both, m1 slightly smaller than m2 with narrower anterior width. Trigonid of m1 consists of anteroposteriorly compressed metaconid and crescentic protoconid united anteriorly by anterior cingulid and is slightly narrower than talonid (Fig. 4B, C); protoconid extends slightly more posteriorly than metaconid, and posterior arm of protoconid crosses most of tooth, ending before reaching metaconid on moderately-worn specimens; on heavily worn specimens, entire trigonid becomes a wear facet; ectolophid runs posteriorly from protoconid to hypoconid as in p4; on least-worn specimens, FMNH PM 55121 (Fig. 4B) and FMNH PM 55130, there is a slight swelling near its center (mesoconid); hypoconid crescentic in outline, but transversely elongated; buccal valley between buccal cusps short and does not extend very far into basin; posterior half of tooth an in p4, but posterior basin between hypolophid and posterior cingulid (metaflexid) deeper and wider, and posterior cingulid ends lingually before reaching posterior edge of entoconid; a distinct hypoconulid at center of posterior margin of tooth; on completely unworn specimen, FMNH PM 55130, hypoconulid appears as large, distinct cusp.

The m2 nearly identical to m1, but slightly wider anteriorly and posterior arm of protoconid shorter (Fig. 4B, C); m3 longer than m2 but narrower posteriorly; posterior arm of protoconid shorter, leaving trigonid basin more widely open posteriorly; on holotype, there is distinct metastylid that is lacking on m3 of referred specimen, FMNH PM 55121; buccal reentrant valley between protoconid and hypoconid (hypoflexid) is deeper on m3, placing ectolophid nearly at center of the tooth.

The only upper tooth assigned to this species is an M3, FMNH PM 42080 (Fig. 4A). It is assigned to this species due to its compatible size with the lower dentitions and similarity to other cylindrodonts. The tooth is nearly circular in occlusal outline; anterior cingulum extends for entire anterior width of tooth from anterolingual corner of paracone to anterior arm of protocone; at lingual end, abutting protocone is small swelling (protostyle); protoconid anterioposteriorly elongated and transversely compressed; protoloph runs from paracone to center of buccal side of protocone; distinct, circular protoconule present, but connection to the protocone is a very thin loph; distinct hyocone present posterior and slightly buccal to protocone, approximately equal in size to protostyle and is continuous with posterolingual arm of protocone and wraps around posterior margin of tooth, ending at posterobuccal corner of tooth; metaloph not complete, both metaconid and metaconule isolated, metaconule slightly larger.

Table 5.—DENTAL measurements of topotypic sample of *P. grangeri* from Utah. Abbreviations: L, anteroposterior length; W, transverse width. Statistics: mean, ± one standard deviation, observed range, and sample size in parentheses.

Sample	Mean ± Standard Deviation	Range (Sample Size)
p4L	1.70 ± 0.09	1.60–1.80 (4)
p4W	1.66 ± 0.14	1.50–1.80 (4)
m1L	1.76 ± 0.11	1.55–1.90 (10)
m1W	1.66 ± 0.14	1.40–1.85 (9)
m2L	2.06 ± 0.09	2.00–2.20 (5)
m2W	1.84 ± 0.10	1.70–1.95 (5)
m3L	2.13 ± 0.08	2.10 –2.30 (7)
m3W	1.84 ± 0.11	1.70–2.00 (7)
p4–m3L	8.15	(1)
i1L	1.98 ± 0.11	1.90–2.05 (2)
i1W	1.33 ± 0.11	1.25–1.40 (2)

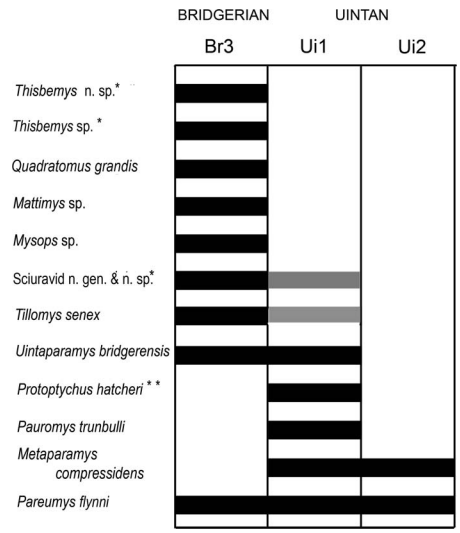

Fig. 5. Occurrence of rodent species throughout the Adobe Town Member of the Washakie Formation. Twk1: Lower (late Bridgerian, Br3); Twk2: Middle (early Uintan, Ui1); Twk3: Upper (middle Uintan, Ui2). Black bars = occurrence; gray bar = possible occurrence. *, species not yet described, **, species described by Turnbull (1991).

Discussion.—Pareumys flynni differs from all other species of the genus in the proportionally smaller p4 that is equal in length and width. In all other species, the p4 is equal or nearly equal in size to m1, and distinctively longer than wide. The molars of *Pareumys flynni* are of a similar size to those of *P. grangeri* (Burke 1935: 8) and *P. boskeyi* (Wood 1973: table 5), larger than those of *P. milleri* (Peterson 1919: 66) and *P.* near *grangeri* (Lillegraven 1977: table 9), and smaller than in *P. guersbergi* (Black 1970: 456). In a large sample of topotypic specimens of *P. grangeri* from the Uinta Basin, Utah in the collections of the Carnegie Museum, the size and proportions of p4 are distinctively different than for *P. flynni* (longer than wide), whereas the dimensions of the molars are very similar (Tables 4, 5).

The presence of a mesoconid on little-worn m1s of *P. flynni* is unusual for cylindrontids. Elsewhere, this feature occurs only in the most primitive genus, *Tuscahomys* Dawson & Beard, 2007, from the earliest Wasatchian.

Although of similar size to the Washakie species, the problematical ?*P. troxelli* Burke 1935, has a distinctive hypolophid morphology of m1 and m2 (continuous with protoconid) that is not present in *P. flynni* but has been reported in some specimens of *P. boskeyi* from Texas (Wood 1973). Because of the variable nature of this morphology, Walsh & Storer (2008) suggested that ?*P. troxelli* might be synonymous with *P. grangeri* pending the description of additional material.

Pareumys flynni is the only rodent species occurs at all three horizons in the Adobe Town Member of the Washakie Formation (Fig. 5).

Conclusions

The greatest change in the rodent fauna in the Washakie Formation is between the late Bridgerian NALMA (Br3) Lower Adobe Town Member and the early Uintan NALMA (Ui1) Middle Adobe Town Member (Fig. 5; Table 6). Five species are limited to the Lower member (two species of *Thisbemys*, *Quadradomus grandis*, *Mattimys* sp., and *Mysops* sp.) with two additional species from the

Table 6.—RODENT species from the Waskakie Formation recognized in this paper. Brackets indicate possible occurrence.

Upper Adobe Town Member (Twka3 = Ui2)
Metaparamys compressidens
Pareumys flynni n. sp.
Middle Adobe Town Member (Twka2 = Ui1)
Metaparamys compressidens
Uintaparamys bridgerensis
Pauromys turnbulli n. sp.
Protoptychus hatcheri
[Sciuravid n. gen. & n. sp.]
[*Tillomys senex*]
Lower Adobe Town Member (Twka1 = Br3)
Uintaparamys bridgerensis
Quadratomus grandis
Thisbemys sp.
Thisbemys n. sp.
Mysops sp.
Mattimys sp.
Sciuravid n. gen. & n. sp.
Tillomys senex

Lower member that are only questionably identified from the Middle member (the undescribed sciuravid and *Tillomys senex*). Only *Uintaparamys bridgerensis* is definitely known, but limited to, both the Lower and Middle members (Br3–Ui1). Two species, *Protoptychus hatcheri* and *Pauromys turnbulli*, are limited to the Middle member (Ui1), and *Metaparamys compressidens* is known from the Middle and Upper members (Ui1–2). Only one species, *Pareumys flynni*, is present at all three horizons in the Adobe Town Member (Br3–Ui2). The occurrence of *Mattimys* from the Lower member (Br3) is the latest occurrence of this genus (Flynn et al. 2008: fig. 23.3).

The two new species, *Pauromys turnbulli* and *Pareumys flynni*, are unique to the Washakie Formation. The occurrence of *Par. flynni* represents the earliest appearance of the genus *Pareumys* (late Bridgerian; Br3) that elsewhere first occurs in the Uintan (Korth 1994; Walsh & Storer 2008). The two new species from the Washakie (*Thisbemys* n. sp. and sciuravid n. gen. & sp.) are also unique to this fauna (Fig. 5).

In the original definitions of the North American Land Mammal Ages (NALMA), Wood et al. (1941) noted that the Washakie Formation straddled the boundary between the Bridgerian and Uintan. Unfortunately, very few rodents were used to define these ages; the only rodent listed as an index fossil for the Uintan was *Protoptychus* and none were listed for the Bridgerian. *Ischyrotomus* (here referred to a species of *Metaparamys*) was listed as first occurring in the Uintan. In the most recent review of the definitions of these ages, Robinson et al. (2004) also cited *Protoptychus* as an index fossil for the Uintan, but also listed *Pareumys* as a first occurrence in the Uintan. In the rodent fauna described here, *Metaparamys* does first appear in the Uintan (Ui1), however the new species of *Pareumys* occurs in the late Bridgerian (Br3) predating the previously known first occurrence of the genus.

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