

NEW RODENT MATERIAL FROM THE JOHN DAY FORMATION (ARIKAREEAN, MIDDLE OLIGOCENE TO EARLY MIOCENE) OF OREGON

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ABSTRACT

The John Day Formation of Oregon is one of the richest and best studied assemblages in North America. Including seven members and spanning about 20 million years, there are over 150 vertebrate species known from the John Day Formation. The rodent faunas of John Day have not been as well studied as larger mammals, with many families having received little attention in the last hundred years. Here, twenty one species of rodents are described, based on new discoveries and previously unpublished specimens from the John Day Formation. The new material includes four **new genera and species**; the eutypomyid *Allotypomys pictus*, the anchitheriomysine castorid *Microtheriomys brevirohinus*, the eomyid *Proapeomys condoni*, the heteromyid *Bursagnathus aterosseus*; and six **new species**: the sciurine sciurid *Miosciurus covensis*, the eomyids *Apeomys whistleri* and *Neoadjidaumo arctozophus*, the heteromyids *Proheteromys latidens* and *Trogomys oregonensis*, and the sicistine dipodid *Plesiosminthus fremdi*. The problematical eomyid species, “*Florentiamys*” *lulli* Wood, 1936a, is referred questionably as a **new combination**, *?Proapeomys lulli* (Wood, 1936a). Emended diagnoses of *Miosciurus ballovis* (Cope, 1881) and *Proheteromys thorpei* Wood, 1935b, are offered based upon substantially more complete material than was previously known for either. Biostratigraphic ranges of the newly described rodents allow more direct comparison with other contemporaneous faunas from North America. These new rodents also allow better reconstruction of past ecosystems and are vital for understanding how faunas have changed through time in the region.

KEY WORDS: crown height, dental morphology, Dipodidae, Eomyidae, Eutypomyidae, Heteromyidae, John Day Formation, Sciuridae

INTRODUCTION

The fossil record of the John Day Basin of Oregon has been studied for nearly 150 years. An amazingly rich sequence of beds preserved in this region record nearly 40 million years of time, from the middle Eocene through late Miocene. These fossil beds have yielded hundreds of plant and animal species to date, with more discovered regularly. The record of Cenozoic change preserved in the John Day Basin is unique, with well dated volcanic rocks allowing detailed examination of environmental and evolutionary changes through time. Climate and habitats in the region changed dramatically over this interval, as the global and regional climate became cooler and more arid, habitats became more open (Retallack et al. 2000, 2007; Zachos et al. 2001, 2008; Retallack et al. 2004). Both floras and faunas also changed substantially, with some lineages evolving to exploit changing habitats and others vanishing entirely.

The John Day Formation in particular has been studied and published on extensively; the well-known “Cope’s Bible” (1884) was an early summary of the John Day mammals. Recent revisions of the John Day Formation now include seven members, ranging in age from about 39 to 18 Ma (Hunt and Stepleton 2004; Albright et al. 2008). Diversity of fossil plant and animal species from the John Day Formation is incredibly high. The well known Bridge Creek Flora, from the Eocene – Oligocene boundary, currently includes over 100 plant species (Meyer and Manchester 1997). The Oligocene aged Turtle Cove Fauna, the

most well known from the John Day Formation, includes nearly 100 recognized mammal species (Fremd 2010).

While knowledge of the John Day Formation is extensive, there are certainly gaps. Early collections, including the only known specimens for some rodent taxa, have little associated locality or stratigraphic data. Additionally, the abundance of small mammals in these units varies considerably, from predominant to almost unknown in some strata.

To date, over 40 species of rodents have been described from the John Day Formation; most of these were first recognized and described by Cope (1878, 1879, 1881). John Day Formation rodents have received little attention over the last hundred years, with the notable exception of Rensberger’s work on geomyids and aplodontids (1971, 1973, 1983). Many rodent taxa, and in some cases families, are only known from scattered fragmentary remains. This may be attributable to collecting biases, along with the fact that most of the fossils are derived from volcanoclastic paleosol deposits, with some strata strongly biased towards preservation of larger taxa.

Recent focus on collecting small mammals and careful examination of existing collections at John Day Fossil Beds National Monument (JODA) have revealed many new species and occurrences, as well as more complete material of poorly known taxa. The well-defined stratigraphy of the John Day Formation and numerous dated marker

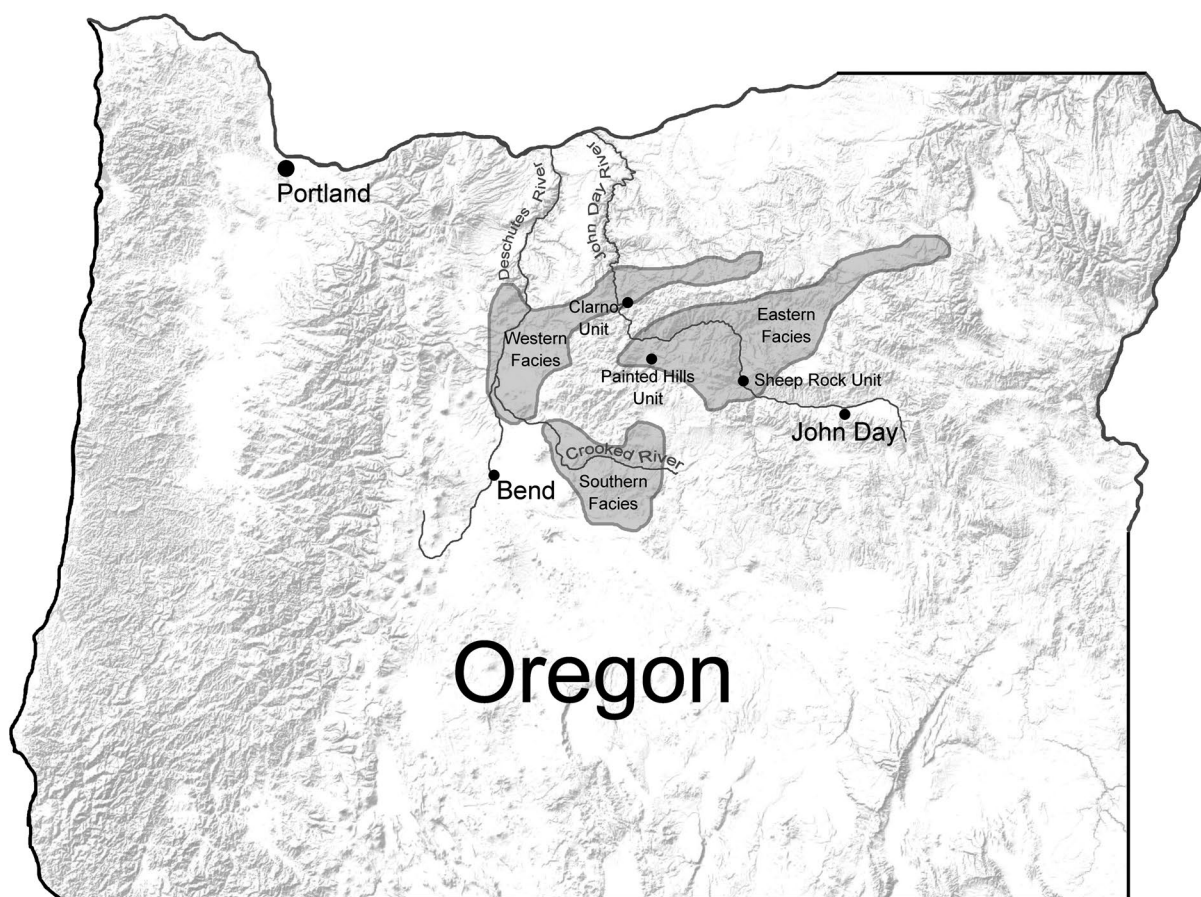


Fig. 1.—Map showing the generalized distribution of the eastern, western, and southern facies of the John Day Formation and the three units of John Day Fossil Beds National Monument. Modified from Robinson et al. (1984) and Albright et al. (2008).

beds (Albright et al. 2008) allow us to place these taxa in a detailed chronological and biostratigraphic context. Study of these new rodents will allow better reconstruction of Oregon's past ecosystems and greater understanding of how faunas in the John Day region have evolved through time.

MATERIALS AND METHODS

Hundreds of localities from the John Day Formation are scattered across central and eastern Oregon, with many protected within John Day Fossil Beds National Monument (JODA) and neighboring Bureau of Land Management lands (Fig. 1). The JODA collection acts as the repository for fossils from public and private lands across the region, including specimens from all three 'facies' of the John Day Formation (Robinson et al. 1984). The specimens described here were found over many years of collecting, mainly done through the efforts of former JODA paleontologist Ted Fremd.

Dental nomenclature used in comparative descriptions follows that of Wood and Wilson (1936) with modifications for heteromyids as in Korth (1997: fig. 1), for castorids

as in Stirton (1935), Huguency (1999), and Wu et al. (2004), and dipodids as in Kimura (2013). Upper teeth are designated by capital letters and lower teeth by lower-case letters (e.g., M1 and m1). The measurements were done using a Wolfe optical micrometer or Mitutoyo Absolute digital calipers to the nearest 0.01 mm. Dimensions of brachydont teeth were taken at the occlusal surface; those species with mesodont or higher-crowned teeth were taken at the base of the crown (maximum dimensions). Measurement of crown height is based only on lower molars and differs for different rodents. The index of crown height for eutypomyids is based on the height of the entoconid divided by the maximum width of the molars taken on unworn or little-worn specimens (Storer 1988). The crown-height index for heteromyids is based on the height of the crown from the base of the enamel to the base of the central valley measured buccally, divided by the maximum width (Korth 1997: fig. 1; Lindsay and Reynolds 2008: 231).

Abbreviations for institutions: **AMNH**, American Museum of Natural History; **CM**, Carnegie Museum of Natural History; **FAM**, Frick Collections, AMNH; **FMNH**, Field Museum of Natural History; **JDNM**, John Day National Monument; **JODA**, John Day Fossil Beds

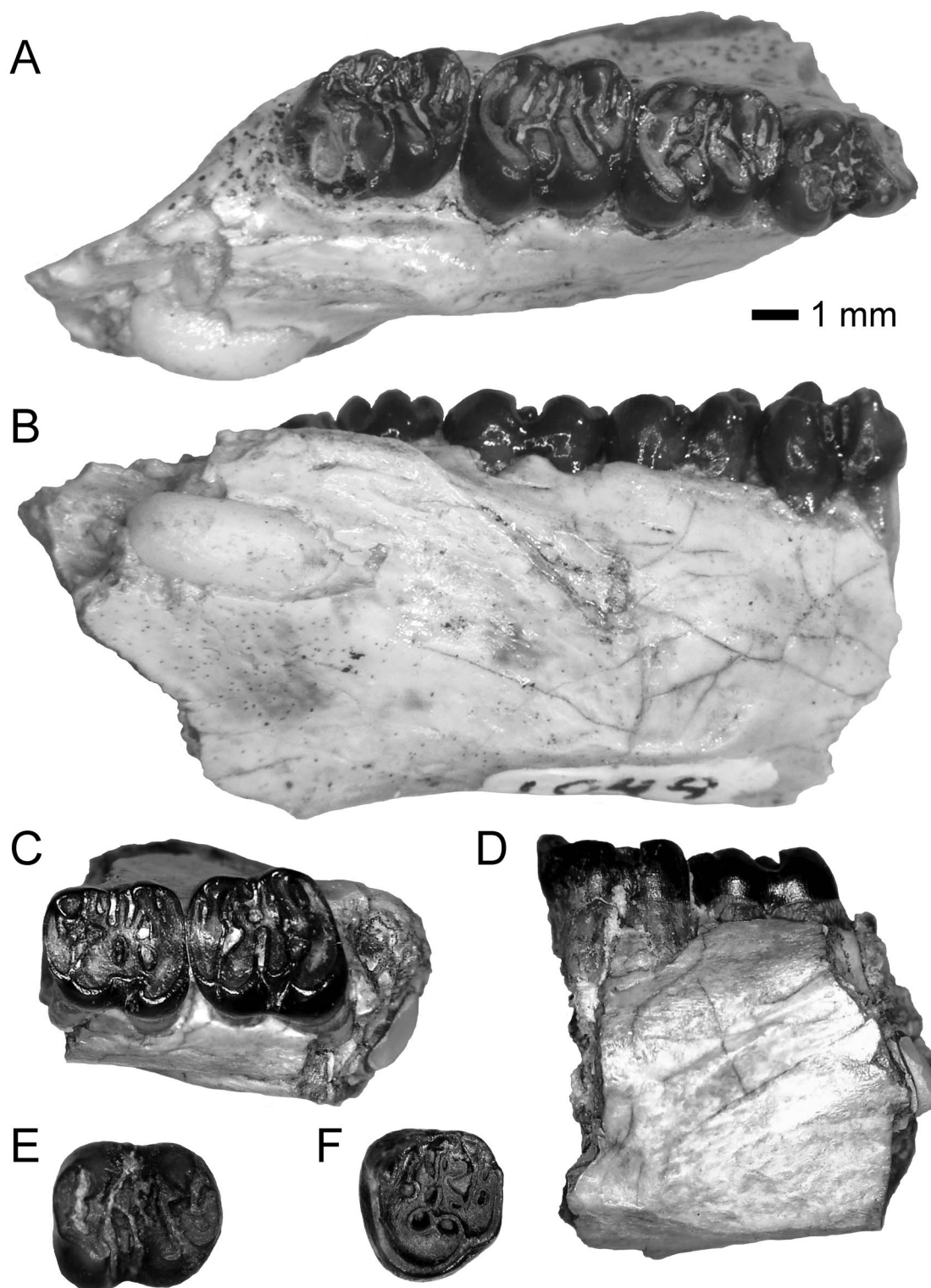


Fig. 2.—Specimens of *Allotypomys pictus*, new genus and species, from the John Day Formation, Oregon. Holotype, JODA 1049, right dentary with p4 to m3. **A**, occlusal and **B**, lateral views JODA 16004, left dentary with p4 and m1; **C**, occlusal and **D**, lateral views, JODA 4972, right m1; **E**, occlusal view; JODA 6420, right M3; **F**, occlusal view. Scale bar equals 1 mm.

TABLE 1. Dental measurements (in mm) of <i>Allotypomys pictus</i> from the John Day Formation. Abbreviations: L , anteroposterior length; W , transverse width; ht/W , crown-height index (= height of entoconid/ transverse width of tooth).														
	i1L	i1W	p4L	p4W	m1L	m1W	ht/W	m2L	m2W	ht/W	m3L	m3W	ht/W	p4–m3
JODA 1049	3.05	1.65	3.09	2.68	3.27	3.28	0.51	3.5	3.61	0.43	3.72	3.13	0.43	13.92
JODA 4972					3.35	2.89	0.60							
JODA 16004					2.85	2.76	0.51	3.12	3.14	0.45				
											M3L	M3W		
JODA 6420											2.74	2.97		

National Monument; **LACM(CIT)**, Natural History Museum of Los Angeles County, California Institute of Technology Collections; **SDSM**, South Dakota School of Mines and Technology, Museum of Geology; **UC**, University of California (Berkeley); **UCMP**, University of California Museum of Paleontology; **UF**, University of Florida Museum; **UWA**, University of Washington; **UWBM**, University of Washington-Burke Museum; **YPM**, Yale-Peabody Museum.

GEOLOGY

The John Day Formation represents an incredibly complex series of strata distributed broadly throughout central and eastern Oregon. These deposits consist primarily of volcanoclastic sedimentary rocks and airfall tuffs, and are approximately 1000 m thick in total (Fisher and Rensberger 1972; Robinson et al. 1984; Bestland and Retallack 1994; Retallack et al. 2000; Albright et al. 2008; McClaughry et al. 2009). Layers throughout the sequence have distinctive lithologies and a series of conspicuous marker units have allowed discontinuous exposures to be correlated at great distances throughout central and eastern Oregon (Albright et al. 2008).

The stratigraphy of the John Day Formation has been extensively examined, starting with Merriam, who divided it into three divisions (lower, middle, and upper) primarily based on color (Merriam 1901). Hay (1963) also defined lower, middle, and upper members based on the widespread Picture Gorge Ignimbrite, his middle member. These units were further refined and subdivided through the work of Fisher and Rensberger (1972), Fremd et al. (1994), Hunt and Stepleton (2004), and most recently Albright et al. (2008). This most recent work has yielded a detailed litho- and chronostratigraphy with radioisotopic and paleomagnetic calibration (Albright et al. 2008: figs. 9–10). As currently recognized, the John Day Formation includes seven members from the middle Eocene to early Miocene, about 39 to 18 Ma (Fig. 1; Hunt and Stepleton 2004; Albright et al. 2008).

Many tuffs have been radioisotopically dated from the John Day Formation, using ⁴⁰Ar/³⁹Ar single-crystal laser-fusion dating of sanidine (Albright et al. 2008). Among

these, the most relevant to this study are the following: A-B Tuff (sanidine tuff of Member G of Robinson) dated 29.75 ± 0.02 Ma, Blue Basin Tuff dated 28.8 Ma, Picture Gorge Ignimbrite (Member H of Robinson) dated 28.7 ± 0.07 Ma, Deep Creek Tuff dated 27.89 ± 0.57 Ma, Biotite Tuff dated 27.14 ± 0.13 Ma, Tin Roof Tuff dated 25.9 ± 0.3 Ma, JD-BC-3 tuff dated 23.79 ± 0.18 Ma, and Across the River Tuff dated 22.6 ± 0.13 Ma (Hunt and Stepleton 2004; Albright et al. 2008). These dates allow us to infer the age of the specimens described here, often to within less than a one million year time span.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821

Family Eutypomyidae Miller and Gidley, 1918

Allotypomys, new genus

Type and Only Species.—*Allotypomys pictus*, new species

Diagnosis.—Smaller than Chadronian, Orellan, and later species of *Eutypomys* Matthew, 1905; larger than Duchesnean species; lophs on cheek teeth broad, not delicate and numerous as in *Eutypomys*; mesoconid on lower molars isolated in early stages of wear, uniting with the mesolophid in late stages of wear; buccal end of mesolophid attached to hypolophid in early wear, center of completed mesolophid attached to hypolophid in late stages of wear; crown height near that of *E. thompsoni* Matthew, 1905, lower-crowned than *E. hibernodus* Korth, 2000, and *E. wilsoni* Korth, 2007a.

Range.—Early Arikareean (early Oligocene) of Oregon.

Etymology.—Greek, *allos*, other; *typos*, shape; *mys*, mouse.

Allotypomys pictus, new species
(Fig. 2; Table 1)

Type Specimen.—JODA 1049, right dentary with p4–m3.

Referred Specimens.—JODA 4972, right m1; JODA 6420, left M3; JODA 16004, left dentary with m1–m2.

Horizon and Locality.—JODA 1049, 6420, 16004 – JDNM 23 (Green Cove), Painted Hills, Wheeler County, OR, lower Turtle Cove Member, John Day Formation; JODA 4972 – JDNM 161, Grant County, OR, upper Turtle Cove Member or Kimberly Member, John Day Formation.

Age.—Early early Arikareean (early Oligocene, Ar1), between A-B Tuff dated 29.75 ± 0.02 Ma and Blue Basin Tuff dated 28.8 Ma (Albright et al. 2008). Note: JODA 4972 comes from an uncertain stratigraphic level, though the outcrop from which it was collected has the Deep Creek Tuff exposed at its base. The overlying exposures include both upper Turtle Cove and Kimberly members strata, indicating occurrence of this taxon either in Ar2 or Ar3.

Diagnosis.—Same as for genus.

Etymology.—Latin, *pictus*, painted: in reference to the Painted Hills from which the type specimen was collected.

Description.—In size (Table 1), the holotype of *A. pictus* is greater than that of *Microeutypomys* Walton, 1993 (Walton 1993: table 1) and Duchesnean species of *Eutypomys* (Storer 1988: tables 7–9), and smaller than Chadronian and later species of *Eutypomys* (Wood 1937:232; Wood 1974: tables 17–19; Wood and Konizeski 1965: table 2; Korth 2007a:32). Storer (1988) measured the crown height of *Eutypomys* species by dividing the height of the entoconid by the maximum width of the molars (ht/W). Based on this index, *A. pictus* is similar in crown height to that of the Chadronian and Orellan species *E. inexpectatus* Wood, 1974, and *E. thompsoni*, lower-crowned than the Orellan *E. hibernodus* and Whitneyan *E. wilsoni* (see Korth 2000: table 2; Korth 2007a), and higher crowned than the Duchesnean species (Storer 1988: tables 7–9).

The p4 is the smallest of the lower cheek teeth, and only known from the holotype (Fig. 2A). It is longer than wide and narrower anteriorly than posteriorly. The anterolingual corner of the tooth is broken away, so the metaconid is missing. The tooth is in the early stage of wear, so there are some small irregularities that outline the major cusps and lophs. These are entirely lacking on the molars, suggesting that they will disappear after only a little more wear. The protoconid is obliquely compressed and the posterior arm of the protoconid does not extend into the center of the tooth. The mesoconid is not continuous with either the protoconid or hypoconid. There is an irregularly sided mesolophid that extends from the lingual margin of the tooth into the center, and is continuous with the mesoconid and hypolophid via very delicate lophules extending from it. The hypolophid extends buccally from the entoconid, connecting with the anterior arm of the hypoconid and center of the posterior cingulid, again, via thin, weak lophules. The posterior cingulid extends from the hypoconid buccally to the lingual edge of the tooth, posterior to the entoconid.

The m1 is approximately equal in length and width. The tooth on the holotype is moderately worn, so unlike p4, there is no indication of enamel irregularities or lophules

anywhere on the occlusal surface of the tooth. However, on the referred specimen, JODA 4972, which is unworn, these minute irregularities are present (Fig. 2E). The anterior width is only slightly less than the posterior width. The metaconid, protolophid, and anterior cingulid form an oval-shaped loop that encloses a small basin. No parts of this loop are connected to the protoconid. The protoconid is obliquely compressed and has a continuous posterior arm that extends to the lingual edge of the tooth, fusing with the metaconid lingually, and leaving an oblique valley between it and the protolophid for the entire width of the tooth. Posterior to the protoconid on the buccal side of the tooth is a large, isolated mesoconid that is roughly oval in shape, parallel to the protoconid. On the lingual half of the tooth is a thin mesolophid that extends from the lingual margin of the tooth buccally, but turns directly posteriorly near the center of the tooth, fusing with the center of the hypolophid. On m1 of JODA 16004, the specimen with the greatest amount of wear, the mesoconid is fused with the buccal end of the mesolophid (Fig. 2C). The hypolophid is continuous from the entoconid to the hypoconid. The entoconid is anteroposteriorly compressed, and the hypoconid is obliquely compressed, parallel to the protoconid and mesoconid. A spur from the entoconid extends posteriorly, joining the posterior cingulid, and isolating a small enamel lake near the center of the posterior cingulid. On the most worn specimen, this enamel lake has been obliterated.

The m2 differs little from m1 in occlusal morphology, but is wider than long, and the anterior width is equal to the posterior width. The m2 on the holotype is slightly less worn than m1, so that there is a distinct valley between the hypolophid and the posterior cingulid for the lingual half of the width of the tooth (Fig. 2A). On the more worn specimen, JODA 16004, this valley has been partially eliminated, and three smaller enamel lakes have formed (Fig. 2C). Also, as in m1, on the more worn specimen, the mesoconid is continuous with the mesolophid, forming a transverse loph that crosses the entire tooth. All other morphologies are the same as in m1.

The m3 is longer than m2, but is narrower. The postero-labial corner of the tooth is broken away, so the hypoconid is not preserved (Fig. 2A). The anterior loop (anterior cingulid, protolophid, metaconid configuration) is the same as in m1 and m2. The protoconid is similar to that of m1 and m2, but does not reach the lingual side of the tooth and fuses with the metaconid. Instead it extends more postero-lingually, ending just short of the entoconid. Between the metaconid and entoconid is a V-shaped loph that runs buccally from the edge of the tooth, then turns back toward the lingual side of the tooth, ending posterior to its point of origin. This loph does not connect directly to the posterior arm of the protoconid or entoconid. The mesoconid is smaller than on m1 and m2 and is continuous with the hypolophid, joining the hypolophid at about its center. The hypolophid extends buccally from the entoconid and appears to fuse with the anterior arm of the hypoconid as well as the loph from the mesoconid. There is also a short posteriorly

directed loph running from the hypolophid, just lingual to the junction of the hypolophid and mesoconid. This short loph isolates two narrow, oblique valleys along the posterior edge of the tooth between it and the entoconid and between it and the lingual end of the posterior cingulid.

The dentary is similar to that of Oligocene species of *Eutypomys*. It is heavy (transversely thick) and slightly concave on the medial side (Fig. 2B). The ascending ramus originates at a point even with the anterior margin of m3. The masseteric scar is a low ridge that extends from the anterior margin of the ascending ramus anteroventrally, ending at mid-depth of the dentary, ventral to the anterior margin of m2. There is a wide, shallow groove that separates the ascending ramus from the tooth row. The pulp cavity for the incisor is an anteroposteriorly elongated oval that originates posterior and lateral to the m3 on the ascending ramus. All other portions of the dentary are missing.

The lower incisor is much narrower transversely than deep. The enamel surface is round and smooth, extending from the medioventral margin to more than half the depth of the tooth on the lateral side. In cross-section, the medial side is slightly concave and the lateral side is strongly convex.

The referred M3, JODA 6420, is heavily worn (Fig. 2F). The tooth is slightly wider than long. The buccal cusps (paracone, metacone) are small and anteroposteriorly compressed into the protoloph and metaloph, respectively. The protocone is large and crescentic, extending for nearly the entire lingual margin of the tooth. The hypocone is circular, smaller than the protocone, and positioned posterior and buccal to the protocone. The remainder of the occlusal morphology is a combination of enamel fossettes and irregular lophs. The anterior cingulum is very short, anterior to the paracone in the anterobuccal corner of the tooth. The protoloph connects the paracone to the protocone, but is irregularly shaped, isolating a small circular enamel lake on its anterior side, and three separate lakes on its posterior side between the protoloph and the mesoloph. The mesoloph is similarly irregular in shape, isolating two enamel lakes on the buccal half of the tooth between it and the metaloph. The metacone is directly connected to the hypocone, which is not continuous with the protocone, forming another circular enamel lake between the hypocone and protocone. The posterior cingulum runs from the hypocone to the metacone along the posterior edge of the tooth. The posterior cingulum is not continuous with the metacone, being divided from it by a minute valley. A very small enamel lake near the center of the posterior cingulum separates it from the center of the metaloph.

Discussion.—*Allotypomys pictus* is one of the latest occurring eutypomyids. The only other species from the Arikareean are *Eutypomys montanensis* Wood and Konizski, 1965, from Montana, and *Eutypomys* sp. from South Dakota (Macdonald 1970). The occurrences of *Allotypomys* from the early Arikareean of Oregon (Ar1) indicate eutypomyids had a broader distribution into the Oligocene than was previously known.

The trends within eutypomyids from the early Eocene (Wasatchian *Mattimys* Korth, 1984) through the late Oligocene (Arikareean *Eutypomys*) are increases in: 1) size; 2) complexity of the occlusal pattern of the cheek teeth; and 3) crown height. In contrast, *A. pictus* is smaller than any of the Chadronian or later eutypomyids, but similar in crown height. The complex pattern of lopholes in later *Eutypomys* is that of very thin lopholes with a pattern that becomes so complex that the major lophs of the molars are no longer recognizable (Korth 2000). In *A. pictus*, the minute lopholes that characterize *Eutypomys* are lacking; the lophs are broadened rather than thinned, making the occlusal pattern simpler.

Allotypomys pictus clearly belongs to a side-branch of the Eutypomyidae that simplifies the occlusal pattern of the molars rather than making them more complicated. The presence of minute irregularities on the lophs of the little-worn p4 of the holotype (JODA 1049) and the referred isolated molar of *A. pictus* (JODA 4972) suggests that it was derived from an ancestor that had irregularities of the enamel, typical of other eutypomyids.

Family Castoridae Hemprich, 1820
Subfamily Anchitheriomyinae Korth, 2001a

Microtheriomys, new genus

Type and Only Species.—*Microtheriomys brevirohinus*, new species.

Diagnosis.—Small beaver; upper and lower cheek teeth unilaterally hypsodont; occlusal surface of cheek teeth with complex pattern of fossettes; P3 lacking; upper tooth rows parallel (not diverging posteriorly); P4 slightly larger than M1; molars longer than wide; rostrum short; posterior palatine foramen entirely within palatine bone.

Range.—Early Arikareean (early and late Oligocene) of Oregon.

Etymology.—Greek, *micro*, small; *therios*, animal; *mys*, mouse.

Discussion.—*Microtheriomys* is referable to the Anchitheriomyinae based on the complexity of the occlusal pattern of the cheek teeth, unilateral hypsodonty of the upper and lower cheek teeth, and position of the posterior palatine foramen. It differs from the other North American anchitheriomyines *Anchitheriomys* Roger, 1898 (including *Amblycastor* Stirton, 1935), *Oligotheriomys* Korth, 1998, and *Miotheriomys* Korth, 2004, in: 1) being markedly smaller; 2) having a shorter rostrum; 3) having P4 nearly equal in size to M1 (P4 much larger in other genera); 4) having upper tooth rows parallel to one another (posteriorly diverging in other genera); 5) having upper and lower molars longer than wide (wider than long in other genera); and 6) having irregular, minute striations on the incisors. *Microtheriomys* lacks the deeply ridged incisors of *Amblycastor*.

and differs from *Oligotheriomys* in the loss of P3 and possessing higher crowned cheek teeth. *Microtheriomys* has ornamented incisors like *Propalaeocastor* Borisoglebskaya, 1967, from Asia, but it differs from that taxon in that: 1) the P4 is not as enlarged; 2) the tooth rows do not diverge; and 3) there is no groove running anteriorly from the posterior palatine foramen.

***Microtheriomys brevihinus*, new species**
(Figs. 3–4; Table 2)

Type Specimen.—JODA 16037, partial skull with base of rostrum and palate, both incisors and right P4–M2, and left P4–M1.

Referred Specimens.—JODA 16477, left M1; JODA 15263, left M1; JODA 7726, right p4; UCMP 76515, right dentary with i1, dp4–m2.

Horizon and Locality.—JODA 16037, 16477 – JDNM 8, Sheep Rock, Grant County, OR, Unit H, Turtle Cove Member, John Day Formation; JODA 15263 – JDNM 9, Blue Basin, Grant County, OR, Unit E, Turtle Cove Member, John Day Formation; JODA 7726 – JDNM 9, Blue Basin, Grant County, OR, Unit G, Turtle Cove Member, John Day Formation. UCMP 76515 – V6685, Picture Gorge 12, Grant Count OR, upper Turtle Cove Member, John Day Formation

Age.—Early early Arikareean (early and late Oligocene, Ar1), between A-B Tuff dated 29.75 ± 0.02 Ma and Deep Creek Tuff dated 27.89 ± 0.57 Ma (Albright et al. 2008).

Diagnosis.—Same as for genus.

Etymology.—Latin, *brevi*, short; Greek, *rhin*, nose: in reference to the short snout of this beaver.

Description.—The partial skull (JODA 16037) is less than half the size of any previously described North American anchitheriomyine (Figs. 3A–D, Table 3; Korth and Emry 1997; Korth and Martin 2007). Although the anterior portion of the rostrum is broken away, it is evident that it was not elongated as in *Amblycastor*. In the latter, the incisive foramina are well anterior to the level of the anterior margin of the zygomatic arch and situated at, or posterior to, the halfway point of the upper diastema. In the skull of *Microtheriomys*, the incisive foramina originate posterior to the anterior margin of the zygomatic arch. In addition, the curvature of the upper incisors also suggests that they will pass the palatal surface at a point not far anterior to the point of breakage of the rostrum. The maxillary-premaxillary suture crosses the midline of the palate near the center of the incisive foramina. The palate is flat between the tooth rows. The maxillary-palatine suture crosses the palate at the level of the anterior portion of the M1. The posterior palatine foramen is large and oval in shape, and lies within the maxillary-palatine suture, even with the middle of the M1.

The base of the zygomatic arch is preserved on the left side of the skull and is sciuromorphic. The infraorbital foramen is ventral to it and laterally compressed with a small crista facialis ventrolateral to it. Much of the anterior part of the orbital wall is preserved on the right side; however, only the sphenopalatine foramen is recognizable dorsal to M1.

The upper incisors are nearly as wide transversely as they are deep and roughly triangular in cross-section. The anterior surface of the incisors is nearly flat, only slightly convex. On the enamel surface of the incisors are minute striations; these are oriented anteroposteriorly but irregular in occurrence (Fig. 3E). The ornamentation seen on the incisors of *Microtheriomys* is not like the distinct ridges present on specimens of *Anchitheriomys*.

The upper cheek teeth of JODA 16037 (Figs. 3F–G) are nearly square in occlusal outline, being slightly longer anteroposteriorly than they are wide (transversely). There is no alveolus for P3 on either side of the skull. The cheek teeth are strongly unilaterally hypsodont, being nearly twice as tall lingually as buccally. The cheek teeth decrease in size from P4 to M2, but only slightly. The occlusal pattern is complex, but similar on all of the cheek teeth.

In each tooth, the four major cusps are recognizable; the paracone and metacone are strongly compressed anteroposteriorly and the protocone and metacone are obliquely compressed (anterolingual to posterobuccal). The mesoflexus is deep, extending lingually and curving posteriorly to form a J-shape, ending at the posterior margin of the tooth (posteroloph). The hypoflexus is short and directed anterobuccally along the posterolateral surface of the protocone. In the P4, the protoloph runs lingually from the paracone, curves anteriorly through the protolophule I to join the anterior edge of the tooth (anteroloph), which isolates the parafofsette. The protolophule II separates a pair of fofofsettes, the premesofossette and the lingual premesofossette. In the molars, protolophule II is absent and the premesofossette is a single buccolingually elongate fofofsette. The posterobuccal quarter of each upper cheek tooth is isolated by the mesoflexus. A loph originates at the buccal edge of the tooth (mesoloph) posterior to the paracone, follows the buccal boundary of the mesoflexus to merge with the endoloph, curves posteriorly, and then fuses with the hypocone at the posterior edge of the tooth. A short metaloph extends lingually from the metacone. The metaloph fuses with the metastyle crest and posteroloph via small lophules (metalophule II), creating a postmesofossette anterior to the metaloph and metafofsette posterior to it.

In each of the teeth there are some slight variations in the form of irregularly sided or accessory lophules. These variations are particularly evident in the right dentition, which shows less wear than the left. On the right P4 of JODA 16037, there is a short transverse metalophule I that connects the metaloph to the hypocone and separates the last portion of the mesoflexus. Also in that right P4, the metastyle crest is only connected to the metacone, with

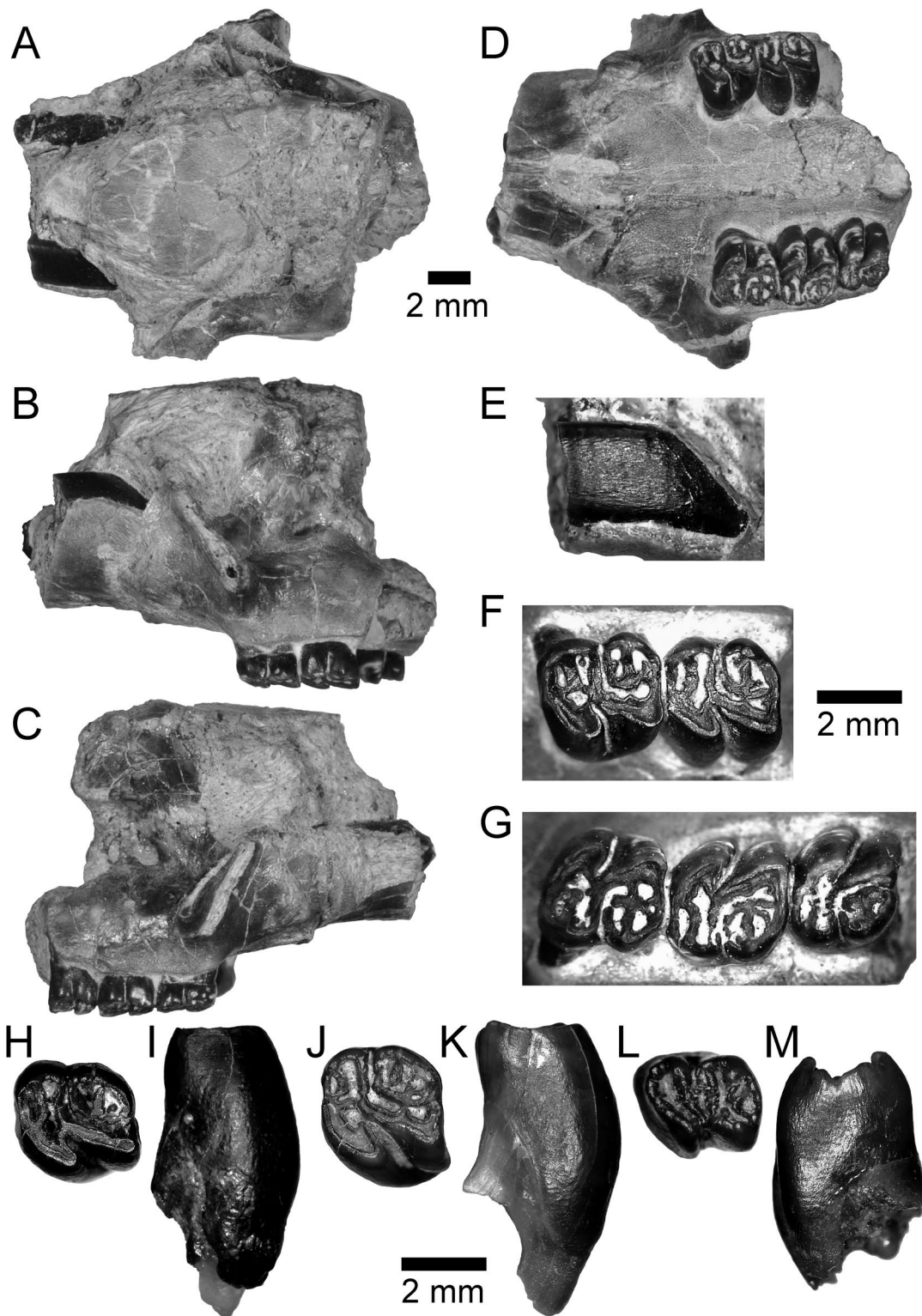


Fig. 3.—Specimens of *Microtheriomys brevirohinus*, new genus and species, from the John Day Formation, Oregon. A–G, Holotype, JODA 16037, partial skull with incisors, right P4 to M2, left P4 to M1; A, dorsal view; B, left lateral view; C, right lateral view; and D, ventral view; E, enlarged dorsal view of left incisor; F, enlarged occlusal view of left P4 to M1; G, enlarged occlusal view of right P4 to M2; H–I, JODA 16477, left M1 or M2; H, occlusal view; I, anterior view; J–K, JODA 15263, left M1 or M2; J, occlusal view; K, anterior view; L–M, JODA 7726, right P4; L, occlusal view; M, anterior view. Scale bars equal 2 mm.

the postmesoflexus open and connected anteriorly to the mesoflexus. In the right M1, the paraflexus is open and the anteroloph is not connected to the paracone.

A juvenile dentary referred to *Microtheriomys* (UCMP 76515) includes i1 and dp4–m2 (Fig. 4). All teeth show little wear. The occlusal pattern of the cheek teeth is complex but the four major cusps are evident as in the uppers. The dp4 has a crescentic anteroconid with the anterolophid, anterior to and between the metaconid and protoconid. The hypoconid and entoconid are anteroposteriorly compressed. The elongated hypoconid fuses to the posterolophid and extends to the posterior edge of the entocoid. Posterior to the anteroconid is a broad parafoesettid. It runs from the protoconid along the posterior edge of the metalophid, but is interrupted centrally by a small lophid. The mesoflexid runs approximately halfway across the tooth ending buccally at a small lopulid. Anterior to the mesoflexid is a small foesettid; posterior to it is a broader foesettid. The hypoflexid is very shallow and directed posterolingually. The metafoesettid is broad, running from the hypoconid to the entoconid, nearly interrupted by a small lophid just buccal to the midline of the tooth.

In the m1, the protoconid and metaconid are worn to a crescent shape and the hypoconid and entoconid are anteroposteriorly compressed. The hypoconid is elongated and fuses with the posterolophid and entoconid as in dp4. Posterior to the anterolophid and anterobuccal to the metaconid is a pair of small foesettids. A broad parafoesettid runs transversely from the lingual edge of the protoconid to the posterior surface of the metaconid. The mesoflexid runs less than half the width of the tooth before fusing to the broad mesofoesettid. As in dp4, the hypoflexid is short and the metafoesettid is broad, though it runs uninterrupted across the entire width of the tooth.

The m2 is almost completely unworn. The occlusal morphology is similar to that of m1. One noticeable difference is that the mesoflexid is much deeper and only a minute foesettid is present anterior to it.

A number of isolated teeth are also referred to *Microtheriomys*, including a pair of upper molars (JODA 15263, 16477) and a lower p4 (JODA 7726). Both upper molars have a pair of small buccal roots and a large lingual root, and clearly show strong unilateral hypsodonty (Figs. 3I, K). JODA 15263 displays less wear than the holotype, showing several additional variations. As in the right P4 of JODA 16037, the metalophule I connects the metaloph to the hypocone, interrupting the mesoflexus. As protolophule II is present but the protocone is not directly connected to the endoloph, the hypoflexus of JODA 15263 is elongate and open on the buccal side of the protocone (in the P4 of JODA 16037 this area is the lingual premesofoesette). The metaloph is not connected to the metacone, with a single large foesette lingual to the metacone (where the postmesofoesette and metafoesette are separated in JODA 16037). The wear of JODA 16477 is slightly less than that of the holotype, but the occlusal pattern is similar.

The referred lower p4, JODA 7726, has almost no wear,

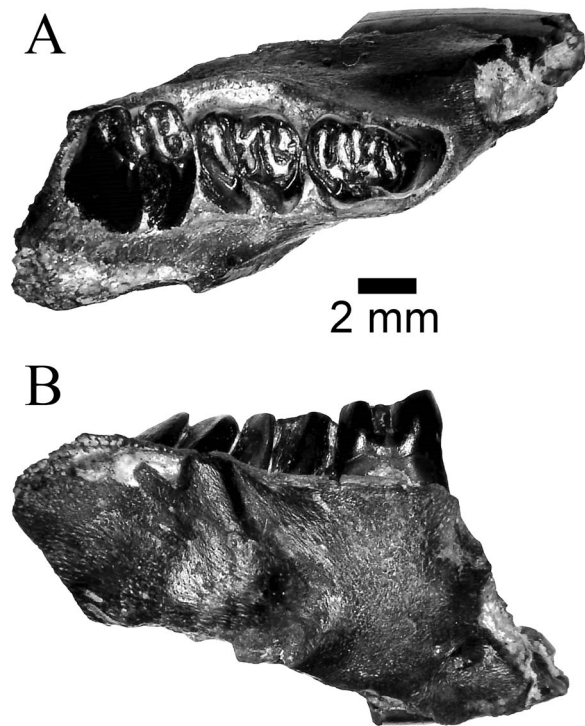


Fig. 4.—Dentary and dp4–m2 of *Microtheriomys brevirohinus*, UCMP 76515, from the John Day Formation, Oregon. A, occlusal view. B, lateral view.

similar to the molars of UCMP 76515, and shows a highly complex occlusal pattern with irregularly folded enamel (Fig. 3L). The tooth is unilaterally hypsodont (Fig. 3M), though not as strongly as the upper molars. All four major cusps are clearly evident, with the protoconid and metaconid substantially higher than the entoconid and hypoconid. The protoconid and metaconid are round, while the entoconid and hypoconid are anteroposteriorly compressed. The hypoconid is particularly elongate, fusing with the posterolophid and connecting to the posterior surface of the entoconid. The protoconid is connected to the entocoid by a narrow loph running posterolingually. The mesoflexid is interrupted by a lophulid in the middle of the tooth, and with wear would run less than halfway across the tooth transversely. A premesofoesettid lies anterior to the buccal edge of the mesoflexid. The hypoflexid is short and directed posterolingually. Two parafoesettids sit anterobuccal to the metaconid and a large parafoesettid runs from the lingual surface of the protoconid to the posterior surface of the metaconid. There is no postmesofoesettid, but a broad metafoesettid runs from the hypoconid to entoconid.

The referred dentary (UCMP 76515) displays morphology similar to that of *Steneofiber* Geoffroy Saint-Hilaire, 1833, with the diastema dropping sharply anterior to the premolar. There is a pair of mental foramina located directly

TABLE 2. Cranial and dental measurements (mm) of *Microtheriomys brevirohinus* specimens from the John Day Formation. Abbreviations: **BCH**, buccal crown-height; **L**, anteroposterior length; **LCH**, lingual crown-height; **W**, transverse width; **ht/W**, crown-height index (= height of entoconid/ transverse width of tooth).

JODA 16037	Rostrum W		12.16						
	Palate W at P4		5.68						
	Palate W at M2		5.68						
	Skull height at M1		13.29						
	Incisive Foramen L		3.61						
		I1L	I1W	P4L	P4W	M1L	M1W	M2L	M2W
	left			2.93	2.67	2.7	2.63		
	right	2.37	2.24	3.03	2.8	2.75	2.69	2.5	2.6
		M1L	M1W	BCH	LCH				
JODA 15263		2.84	2.66	1.83	5.77				
JODA 16477		2.82	2.69	1.97	4.76				
		p4L	p4W	BCH	LCH				
JODA 7726		2.94	2.84	3.79	2.24				
		i1L	i1W	dp4L	dp4W	m1L	m1W	m2L	m2W
UCMP 76515		3.02	2.35	3.22	2.67	3.60	2.93	3.26	2.89

below the anterior root of dp4, in the center of the ramus. The masseteric scar extends anteriorly to below the anterior end of m1. The ascending ramus originates near the middle of m1. The lower incisor has a semi-flattened anterior surface with ornamentation similar to that of I1.

Discussion.—*Microtheriomys* is the smallest and the most primitive anchitheriomyine in some features (parallel tooth rows, P4 not enlarged). These features are also found in Orellan and Whitneyan species of *Agnotocastor* (Stirton, 1935). *Agnotocastor* is similarly characterized by complex patterns on the cheek teeth (Galbreath 1953; Emry 1972; Korth 1996, 2001b). *Microtheriomys* and other anchitheriomyines differ from *Agnotocastor* in having unilateral hypsodonty on the upper and lower cheek teeth. The pattern of the upper cheek teeth in *Agnotocastor* differs in having deeper hypoflexi, shallower mesoflexi, and more numerous small enamel lakes. The rostrum of *Agnotocastor* is also more elongated than in *Microtheriomys* (Stirton 1935: fig. 1; Korth 2001b: figs. 1, 3). *Microtheriomys* is advanced over both *Oligotheriomys* and *Agnotocastor* in the loss of P3 and displaying higher crowned cheek teeth. Unlike *Agnotocastor* and *Anchitheriomys*, *Microtheriomys* has semi-flattened incisors.

Microtheriomys may provide a link between North American beavers and early castorids of Eurasia. In many

features, *Microtheriomys* is most similar to a number of Oligocene and early Miocene beavers from Asia and Europe referred to the genus *Propalaeocastor* (Kretzoi 1974; Wu et al. 2004; Bendukidze et al. 2009). Both *Microtheriomys* and *Propalaeocastor* display the following characters: 1) unilateral hypsodonty, with the lingual side of the upper cheek teeth substantially higher crowned than the labial (Wu et al. 2004); 2) the absence of the P3; 3) P4 being the largest cheek tooth; 4) relatively complex dental pattern; and 5) posterior palatine foramen lies in the maxillary-palatine suture (Wu et al. 2004). However, *Microtheriomys* lacks the groove running anteriorly from the foramen seen in *Propalaeocastor*. Also like *Propalaeocastor*, the incisors of *Microtheriomys* display longitudinal ornamentation (Korth 2004), though not to the extent seen in later anchitheriomyines, *Anchitheriomys* and *Amblycastor*.

Propalaeocastor butselensis (Misonne, 1957) (sometimes referred to as *Asteneofiber* Kretzoi, 1974) from the earliest Oligocene (MP 21) of Belgium is thought to be the likely ancestor of *Steneofiber*, and later castorines, including *Castor* Linnaeus, 1758 (Hugueney 1999; Wu et al. 2004; Stefan 2011). Kretzoi (1974) distinguished *Propalaeocastor butselensis* (= *Asteneofiber butselensis*) from *Steneofiber* based on its smaller size, lower crown height, and more complex cheek-tooth pattern. Hugueney (1999) interpreted *P. butselensis* to be the likely ancestor of *Steneofiber*

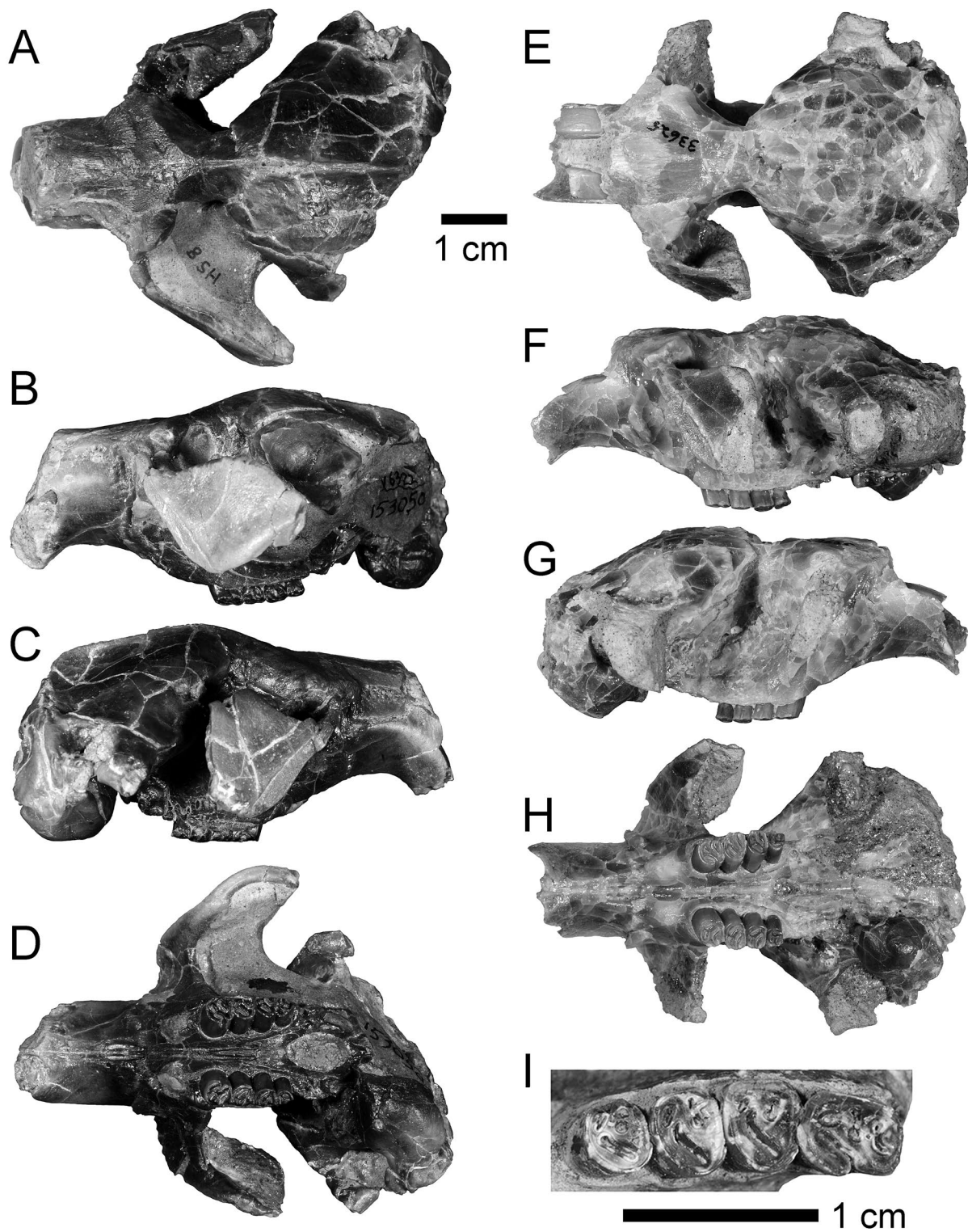


Fig. 5.—Specimens of *Palaeocaster fossor* from the John Day Formation, Oregon. A–D, UCMP 153050, nearly complete skull; A, dorsal view; B, left lateral view; C, right lateral view; D, ventral view; E–H, UWBM 33625, nearly complete skull; E, dorsal view; F, left lateral view; G, right lateral view; H, ventral view; I, UCMP 216045, right partial dentary with p4 to m3; enlarged occlusal view. Scale bars equal 1 cm.

TABLE 3. Cranial, mandibular, and dental measurements (in mm) of *Palaeocastor fossor* from the John Day Formation, with comparative measurements of material from the Harrison Formation of Nebraska. Abbreviations: **L**, anteroposterior length; **W**, transverse width. * indicates estimated measurement due to breakage; the actual measurement should be greater.

	Harrison Fm., Nebraska		John Day Fm., Oregon						Mean
	CM 1217	FMNH 12217	JODA 1653	UCMP 153030	UCMP 76770	UCMP 216045	UWBM 31642	UWBM 33625	
Skull L	72.00	66.28		66.38*				65.73*	67.59
Rostrum W	18.60	17.62		17.27				15.16	17.16
Rostrum Depth	17.50	17.04		18.55				17.12	17.56
Postorb. cons. W	11.16	14.53		9.72				9.43	11.21
Zygomatic W	61.20	55.86		53.40*					56.82
Jugal Depth	13.95	13.47		15.11				15.23	14.44
Max. cran. W	37.02	34.26		35.66*				32.85	34.95
Nuchal W	41.31	37.21		43.74*				35.46*	39.43
Auditory bulla L	13.46	13.84		14.05				13.43	13.70
I1 L	4.77	4.90		5.22				4.99	4.97
I1 W	4.62	4.52		4.55				4.28	4.49
P4-M3 L	14.28	14.22		13.08				12.71	13.57
i1 L	5.46		5.78		5.67	5.42	5.65		5.60
i1 W	5.04		6.39		5.91	5.27	5.34		5.59
p4-m3 L	15.89		15.78			16.62	16.87		16.29
Jaw depth at m1	15.09		16.79			15.78	16.99		16.16

and later castorines, including *Castor*. Based on the morphology of *P. irtyschensis* Wu et al., 2004, from the early Oligocene of China, *Propalaeocastor* was assigned to the Castorinae (Wu et al. 2004). *Microtheriomys* is referred here to the Anchitheriomyinae based on shared features with that subfamily, but further analysis may suggest placement of this taxon within the Castorinae, as it bears a definite similarity to early members of that group.

The presence of *Microtheriomys* in the lower and upper Turtle Cove Member of the John Day Formation reveals greater diversity of beavers in the early Arikareean (Ar1) of Oregon than was previously known. Like *Microtheriomys*, both *Capacikala gradatus* (Cope, 1879) and *Palaeocastor peninsulatus* (Cope, 1881) occur in the Turtle Cove fauna, though both of these genera survive later into the Arikareean, through Ar3.

Subfamily Palaeocastorinae Martin, 1987
Palaeocastor Leidy, 1869

Palaeocastor fossor (Peterson, 1905)
(Fig. 5; Table 3)

Steneofiber fossor Peterson, 1905

Palaeocastor major Romer and McCormack, 1928

Palaeocastor fossor [sic] Stirton, 1935

Fossorcastor fossor (Peterson) Martin, 1987

Referred Specimens.—UWBM 33625, nearly complete skull lacking zygomatic arches, nasals and premaxillaries; UWBM 31642, articulated mandible with incisors, left p4–m3, and right p4–m2; UCMP 153050, nearly complete skull with all teeth, lacking posterior part of zygomatic arches and left side of basicranium and occipital; UCMP 216045, right partial dentary with i1, p4–m3; UCMP 76770, left i1 fragment; JODA 1653, articulated mandible with incisors, right m1–m2.

Horizon and Locality.—JODA 1653 – JDNM-39, Welton's Rhino, Grant County, OR, Kimberly Member, John Day Formation; UCMP 76770 – V6681, Picture Gorge 7, Level 6, Grant County, OR, Kimberly Member; UWBM 33625 – UWA 5929 (UC V6600), Rudio Creek 4, Grant County, OR, Kimberly Member, John Day Formation; UWBM 31642 – UWA 5853, Sutton Main, Wheeler County, OR, Kimberly Member or Johnson Canyon Member, John Day Formation; UCMP 153050 – V6322, Gray Face Bluff (Haystack 8 of Rensberger 1973), Wheeler County, OR, Haystack Valley Member, John Day Formation; UCMP 216045 – V6504, Haystack West, Wheeler County,

TABLE 4. Cranial, mandibular, and dental measurements (in mm) of *Palaeocastor peninsulatus* from the John Day Formation. Abbreviations: **L**, anteroposterior length; **W**, transverse width. * indicates estimated measurement due to breakage; the actual measurement should be greater.

	John Day Fm., OR										Mean
	AMNH 6998	LACM(CIT) 890	JODA 6527	JODA 13207	JODA 15820	JODA 15821	UCMP 56203	UCMP 174834	UCMP 216044	UWBM 51976	
Skull L	64.51	72.78	59.78		70.16	68.86*					66.81
Rostrum W	15.83	14.25	13.72		14.96	15.85		14.41	15.85	13.37	14.78
Rostrum Depth	16.25	18.04	15.43		17.73			16.85	17.21	17.29	16.97
Postorb. cons. W	6.77	8.30	9.96		9.23	9.59		8.90	10.44		9.03
Zygomatic W	47.91*	44.41*	32.12*		49.70	50.62*			47.26*		49.70
Jugal Depth	11.4	8.12	10.88		7.05	8.73		6.55	11.67	6.68	8.89
Max. cran. W	29.84	30.34	26.75		29.70	28.86		28.77	29.5*		29.04
Nuchal W	32.42	29.831	33.66		34.59	31.36		33.63			32.58
Auditory bulla L	14.94	15.89	13.08			15.89		14.70			14.90
I1 L	3.94		4.14		4.18	4.39		4.26		3.94	4.14
I1 W	3.76		3.9		4.08	4.08		4.06		3.72	3.93
P4-M3 L	14.33	14.77	13.2	13.23		13.3		13.49	13.18	13.59	13.64
i1 L					4.49		4.67	4.37		4.08	4.40
i1 W					4.01		4.15	4.15		3.51	3.96
p4-m3 L							16.38	15.02		14.47	15.29
Jaw depth at m1					13.02		14.43*	12.83		12.92	12.92

OR, Haystack Valley Member, John Day Formation.

Age.—Early late Arikareean (late Oligocene, Ar3), between Tin Roof Tuff dated 25.9 ± 0.3 Ma (Albright et al. 2008) and JD-BC-3 tuff dated 23.79 ± 0.18 Ma (Hunt and Stepleton 2004).

Discussion.—The John Day specimens referred here to *P. fossor* do not differ significantly in size or morphology from topotypic specimens from Nebraska (Peterson 1905). The skulls have the massive zygomatic arches, broad cranium and rostrum, and anteriorly flattened incisors characteristic of *Palaeocastor* (Fig. 5). In comparison to other species of the genus, the John Day *P. fossor* material includes skulls and dentitions that are larger than *P. simplicidens* (Matthew, 1907), and *P. nebraskensis* (Leidy, 1856), but smaller than *P. magnus* Romer and McCormack, 1928 (Table 3; also see Peterson 1905; Stirton 1935; Martin 1987, for comparative tables and figures).

Palaeocastor peninsulatus has also been reported from the John Day Formation (Stirton 1935; Flynn and Jacobs 2008). Both *P. peninsulatus* and *P. fossor* have similar occlusal morphology of the cheek teeth and possess flattened incisors (Rybczynski 2007). The skull and cheek-tooth row lengths of the *P. fossor* specimens described here overlap

with those of *P. peninsulatus* specimens known from John Day (Tables 3–4). It is important to note that recent work by Stefen (2010) and Caledo (2014) found neither skull size nor dental morphology may be useful in differentiating palaeocastorine beavers. Both size and crown morphology change dramatically as the teeth wear (Stefen 2010; Caledo 2014), meaning the identification of fossil beavers by dental material alone is difficult. Similarly, the cranial morphology and overall dimensions of *Palaeocastor* change substantially through ontogeny (Caledo 2014).

Though some measures of size overlap, likely as a consequence of young adult and older individuals in the samples, the John Day *P. fossor* specimens can be readily distinguished from *P. peninsulatus*. The *P. fossor* specimens have relatively larger incisors, a more massive jugal on the zygomatic arch, more robust rostrum, broader neurocranium and occipital, and deeper mandible (Tables 3–4; Caledo 2014). The robust cranium and broad, flat incisors of the John Day specimens are consistent with specialization for chisel-tooth digging behavior (Samuels and Van Valkenburgh 2009), which is supported for *P. fossor* by artifactual evidence within burrows (Martin and Bennett 1977). *Palaeocastor peninsulatus* has been inferred to be a primarily scratch digging species (Samuels and Van Valkenburgh 2009; Caledo 2014).

Flynn and Jacobs (2008) indicated the occurrence of *P. fossor* from the lower Turtle Cove Member of the John Day Formation, but from an uncertain locality. However, no specimens of *P. fossor* have been previously described or figured from Oregon (though a cast of UCMP 153050, referred to *P. fossor*, was used for comparison with *P. peninsulatus* material from Montana, Caledo 2014). Given the poor or incomplete locality data associated with many early collections from the John Day Basin, it is likely that this early early Arikareean occurrence reported by Flynn and Jacobs (2008) was erroneous.

In the cladistic analyses of Rybczynski (2007) and Caledo (2014), *P. peninsulatus* was found to be the sister group to the highly fossorial clade of palaeocastorines that includes *P. fossor* and the likely subterranean *Euhapsis* Martin, 1987, and *Fossorcastor*. While *P. peninsulatus* is known and relatively abundant in the lower and upper Turtle Cove Member strata (Ar1 – Ar2), all of the *P. fossor* specimens described here come from above the Tin Roof Tuff, higher in the John Day Formation section (Ar3). The less specialized, scratch-digging *P. peninsulatus* seems to be replaced by the more specialized *P. fossor* through time. This transition corresponds with environmental changes in the region, with habitats opening up as the climate became cooler and drier (Retallack 2004, 2007). The early late Arikareean (Ar3) occurrences of *P. fossor* in Oregon are as early as the earliest records from Montana, Wyoming, and Nebraska, possibly indicating that this specialized fossorial species originated in the Pacific Northwest and then dispersed east.

Family Sciuridae Fischer de Waldheim, 1817
Subfamily Sciurinae Baird, 1857
Tribe Sciurini Burmeister, 1854

Miosciurus Black, 1963

Emended Diagnosis.—Small size; skull narrow, skull roof flat; cranium deeper than in *Protosciurus* Black, 1963; zygomatic plate triangular, facing anterolaterally, bounded by distinct anterior and dorsal ridges; infraorbital foramen ovate and laterally compressed; diastema short; mental foramen high on side of jaw; masseteric fossa ending below m1; teeth low-crowned; conules typically lacking on upper molars; two pairs of roots present on lower cheek teeth, anterior and posterior root pairs partially fused and buccolingually elongated; posterolingual corner of m1–m2 angular; entoconid, mesoconid, and mesostylid distinct on lower molars.

Miosciurus ballovianus (Cope, 1881)
(Fig. 6; Table 5)

Sciurus ballovianus Cope, 1881
Miosciurus ballovianus (Cope) Black, 1963

Type Specimen.—AMNH 6961, crushed skull with mandible with left M1, right M2, left m1–m3, and right m1.

Referred Specimens.—JODA 15369, right maxilla with P3–M2; JODA 15370 (a, b), left dentary with m1–m2, right M2; JODA 12631, right dentary fragment with m1–m2; JODA 12639, right dentary fragment with p4; UCMP 77169, left dentary fragment with partial m1 and m3; UCMP 216053, left dentary fragment with partial m2; JODA 12635, 12642, 14695, p4; JODA 12624, 12626, 12628, 12629, 12630, 12640, 12641, 12644, 12645, m1; JODA 12614, 12616, 12617, 12620, 12622, 12625, 12627, 12633, 12634, 12637, 12638, 12643, m2; JODA 12615, 12618, 12621, 12623, 12632, 12636, m3; JODA 12607, 12609, 12619, P4; JODA 12604, 12605, 12606, 12608, 12610, 12612, 12613, 12646, M1 or M2.

Horizon and Locality.—JODA 15369 and 15370 – JDNM 8, Sheep Rock, Grant County, OR, Unit K1, Turtle Cove Member, John Day Formation; UCMP 216053 – V6429, Reed's Ranch, Haystack 1, Wheeler County, OR, upper Turtle Cove Member or Kimberly Member, John Day Formation; UCMP 77169 – V6322, Gray Face Bluff (Haystack 8 of Rensberger 1973), Wheeler County, OR, Haystack Valley Member, John Day Formation; all other referred JODA specimens – JDNM 140, Campbell Ranch, Gilliam County, OR, Kimberly Member, John Day Formation.

Age.—Late early Arikareean (late Oligocene, Ar2) and early late Arikareean (Ar3), between Deep Creek Tuff dated 27.89 ± 0.57 Ma (Albright et al. 2008) and JD-BC-3 tuff dated 23.79 ± 0.18 Ma (Hunt and Stepleton 2004).

Diagnosis.—Smaller than *M. covensis*, new species (described below); prominent anterostylid present on m1; minute conules present on protoloph and metaloph of P4; dorsal surface of the diastema maintains level of the alveolar margin.

Description.—The p4 is the smallest of the cheek teeth, and wider posteriorly than anteriorly (Figs. 6D–H). The metaconid is the largest cusp and positioned at the anterolingual corner of the tooth, more anterior than the protoconid. A minute anterostylid is present on the anterior edge of the tooth between the major cusps, either central or slightly buccal to center. The ectolophid is complete from the protoconid to the hypoconid, and obliquely oriented, with a small but distinct mesoconid at its center. Along the lingual border of the tooth, a large mesostylid is situated just posterior to the metaconid. The posterior cingulid forms a low ridge that runs the entire width of the tooth, originating at the hypoconid and ending just short of the entoconid. The valley separating the entoconid from the posterior cingulum is minute. It has single, buccolingually elongate anterior and posterior roots.

The lower molars are typically rhomboidal in occlusal outline, not compressed anteroposteriorly, and have an angular posterolingual corner (Figs. 6A–C). The m1 can be distinguished from m2 in being slightly smaller and the shape of the trigonid basin. On m1, the anterior cingulid ends short of the protoconid in a small, but prominent

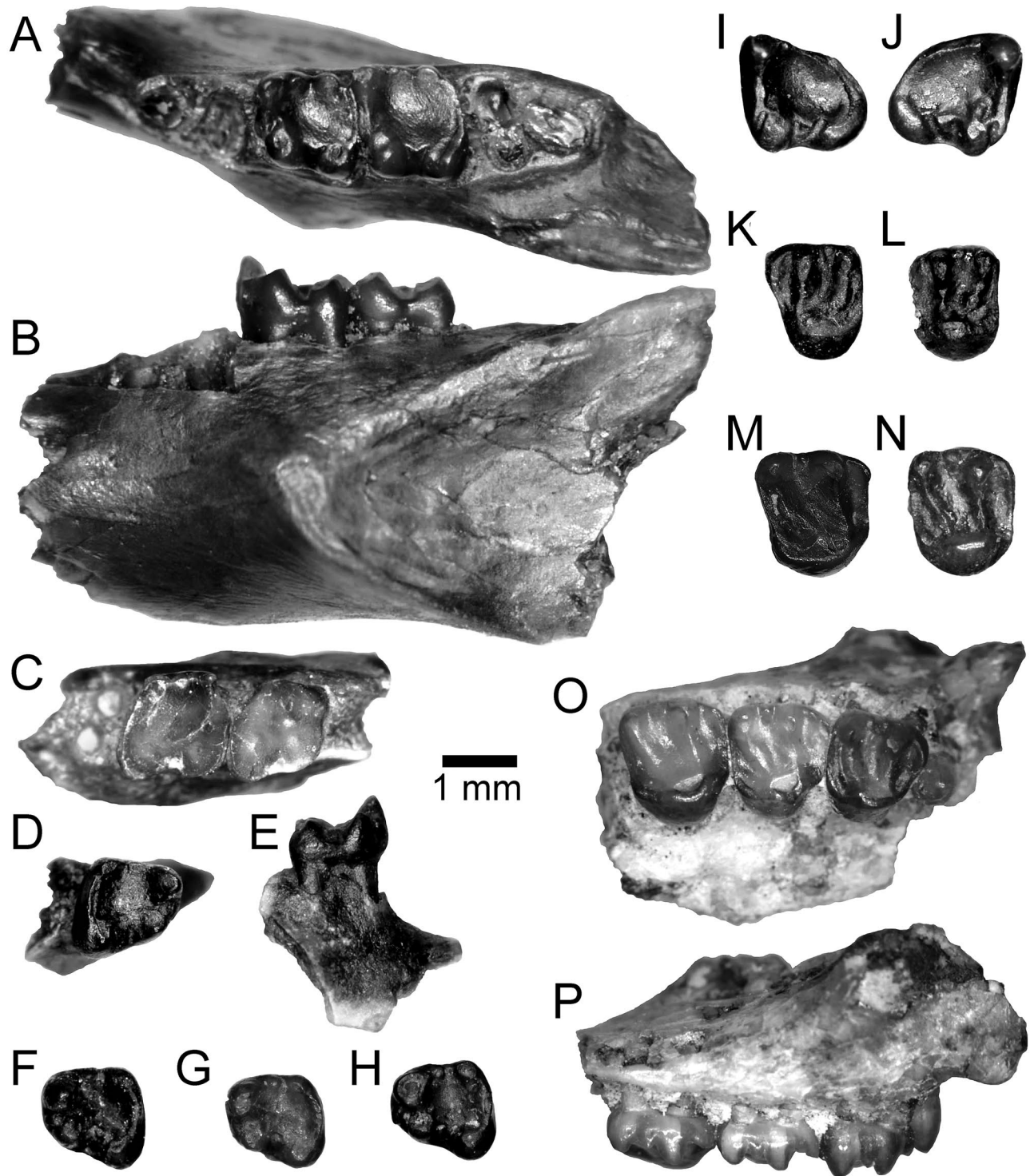


Fig. 6.—Specimens of *Miosciurus ballovianus* from the John Day Formation, Oregon. **A–B**, JODA 15370a, left dentary with m1 and m2; **A**, occlusal view; **B**, lateral view; **C**, JODA 12631, right dentary fragment with m1 and m2; **D–E**, JODA 12639, right dentary fragment with p4; **D**, occlusal view; **E**, lateral view; **F**, JODA 12635, left p4; **G**, JODA 12642, left p4; **H**, JODA 14695, left p4; **I**, JODA 12615, left m3; **J**, JODA 12621, right m3; **K**, JODA 12619, left P4; **L**, JODA 12612, left M1; **M**, JODA 15370b, right M2; **N**, JODA 12610, right M2; **O–P**, JODA 15369, right maxilla with P3 to M2; **O** occlusal view; **P**, lateral view. Scale bar equals 1 mm.

TABLE 5. Dental measurements (in mm) of *Miosciurus ballovis* from the John Day Formation. Abbreviations: **L**, anteroposterior length; **W**, transverse width. Statistical abbreviations: **N**, number of specimens; **M**, mean; **OR**, range of size; **SD**, standard deviation; **CV**, coefficient of variation. Measurements of holotype taken from Black (1963). *, all isolated molars listed as M1.

			P3L	P3W	P4L	P4W	M1L*	M1W*	M2L	M2W
N			1	1	4	4	9	9	2	2
M			0.59	0.69	1.28	1.49	1.36	1.70	1.45	1.74
OR					1.24-1.34	1.38-1.58	1.25-1.47	1.61-1.81	1.44-1.45	1.73-1.75
SD					0.05	0.08	0.08	0.08		
type						1.5	1.7			

	i1L	i1W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W
N	2	2	4	4	10	10	14	13	6	6
M	1.91	1.02	1.39	1.35	1.37	1.42	1.50	1.56	1.64	1.58
	1.82-	1.01-	1.35-	1.33-	1.26-	1.33-	1.33-	1.46-	1.57-	1.55-
OR	1.99	1.03	1.46	1.37	1.47	1.50	1.63	1.70	1.73	1.67
SD			0.05	0.02	0.07	0.05	0.08	0.08	0.05	0.04
CV			3.44	1.27	5.02	3.79	5.18	4.94	3.32	2.81
type					1.5	1.5	1.6	1.6	1.8	1.7

anterostylid. The metalophulid II is complete, forming a roughly circular trigonid basin. On m2, the anterior cingulid extends more buccally, ending either anterior to, or fusing with the protoconid, forming a transversely narrow basin for the trigonid. The anterior width of m1 is slightly less than the posterior width, but in m2 these are nearly equal. Lower molars have distinct entoconids that are continuous with the posterior cingulid on some specimens and separated by a minute valley on others. The mesoconids and mesostylids are generally large, whereas the entocoids are more reduced on some specimens. The anterior roots of m1 and m2 are fused to the alveolar level.

The m3 is the largest of the lower cheek teeth (Figs. 6I–J). Anteriorly, it is similar to m2, but the anterior cingulid is more closely appressed to the protoconid and the metalophulid II is incomplete. The trigonid basin is transverse and narrow, being completely eliminated after moderate wear. A minute anterostylid is present, often represented as a small notch on the anterior side of the protoconid. The tooth is greatly expanded posteriorly. The hypoconid, ectolophid, and mesoconid are as in the anterior molars. Posterior to the hypoconid, the posterior cingulid wraps around the posterior edge of the tooth and is continuous along the lingual side until it joins the metaconid on its posterior side. The entoconid is entirely lacking, and the mesostylid is greatly reduced or absent.

The diastemal portion of the dentary anterior to the p4 drops only slightly below the level of the cheek teeth alveoli in JODA 15370a (Fig. 6B). The masseteric fossa extends anteriorly to the middle of m1, and has prominent boundaries with anterior edges coming to a point. The mental foramen is small, lies anterior to the anterior root

of p4, and is relatively dorsally positioned. The lower incisor is preserved in a pair of specimens (JODA 15370a, JODA 1263) and is relatively anteroposteriorly deep and transversely compressed. The incisor is gently convex on the anterior and lateral sides, and bears no ornamentation on the enamel surface.

The P3 is peg-like, with a single prominent cusp with a minute ridge running posteriorly from the apex (Figs. 6 O–P). P4 is molariform and subquadrate. The anterocone is variable in size in the anterobuccal corner of the tooth. The anterior cingulum runs lingually from the anterocone along the anterior edge of the tooth, ending at the protocone. The protocone is broad and crescentic. The buccal cusps (paracone, metacone) are slightly anteroposteriorly compressed. There is always a distinct mesostyle along the buccal edge of the tooth between the major cusps. The protoloph and metaloph are parallel and continuous to the protocone from the paracone and metacone, respectively. There are minute conules variably present on these lophs. The hypocone is a distinct crescentic cusp at the postero-lingual corner of the tooth, continuous with the protocone anteriorly and the posterior cingulum posteriorly.

M1 and M2 are nearly identical (Figs. 6K–P). The anterior cingulum is larger and extends farther from the protocone in the M1 than M2. In both teeth, the cingulum is widely separated from the protoloph and fuses lingually with the protocone. There is no enlarged anterocone as in P4. The remainder of the occlusal morphology of M1 and M2 is very similar to that of P4. Like the P4, they show variably present minute conules on the protoloph and metaloph. M3 is not represented in the collections.

Some features of the skull can be seen in the preserved

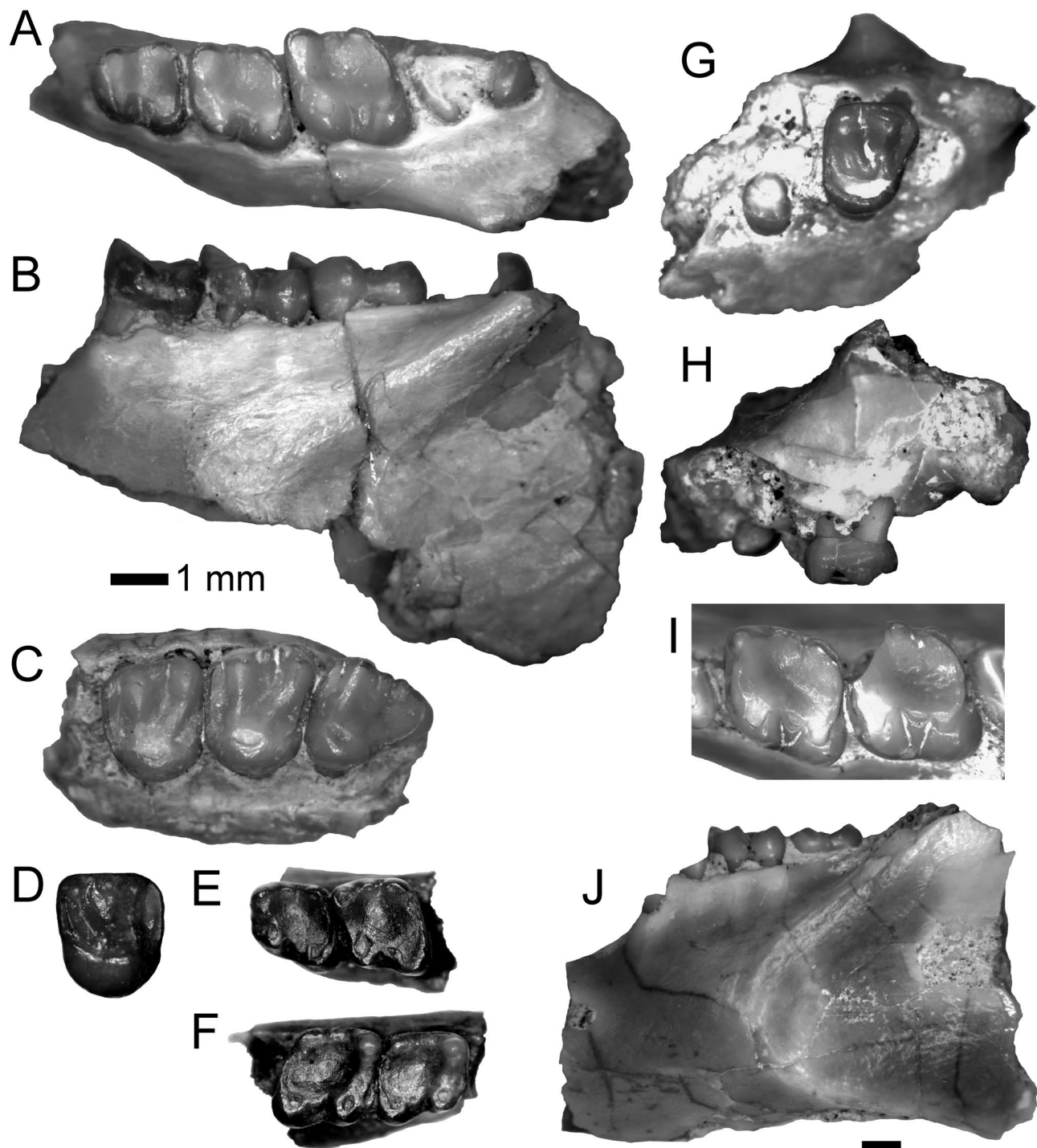


Fig. 7.—Specimens of *Miosciurus covensis*, new species, and *Miosciurus* sp. from the John Day Formation, Oregon. **A–H**, *Miosciurus covensis*; **A–C**, Holotype, JODA 10093; **A**, occlusal view left dentary with p4 to m2; **B**, same as A, lateral view; **C**, right maxilla with M1 to M3; **D**, JODA 3625, right M1; **E**, JODA 15372, left dentary fragment with p4 to m1; **F**, JODA 15373, right dentary fragment with m1 to m2; **G–H**, JODA 3738, right maxilla fragment with P4; **G**, occlusal view; **H**, lateral view. **I–J**, *Miosciurus* sp. JODA 4447, left dentary with m1 to m2; **I**, occlusal view; **J**, lateral view (reduced 2/3). Right scale for A–I, lower left for J. Scale bars equal 1 mm.

TABLE 6. Dental measurements (in mm) of *Miosciurus covensis*. Abbreviations: **L**, anteroposterior length; **W**, transverse width. Measurements of holotype taken from Black (1963).

	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	
JODA 10093			1.73	2.03	1.86	2.21	2.13	1.94	
JODA 3738	1.49	1.70							
JODA 3625					1.83	2.23			
JODA 10289					1.83	2.19			
mean					1.84	2.21			
	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4–m3
JODA 10093	1.61	1.56	1.68	1.78	1.91	1.95			7.65
JODA 7251			1.68	1.70					
JODA 6355			1.65	1.68					
JODA 15372			1.6	1.56	1.66	1.81			
JODA 15373			1.63	1.62	1.79	1.80			
mean			1.65	1.67	1.79	1.85			

portion of the maxilla of JODA 15369. The infraorbital foramen opens anterior to and above P3. While not complete, the preserved portion of the infraorbital foramen in JODA 15369 is clearly ovate in shape and compressed laterally, as it is in the holotype (Black 1963). The posterior border of the anterior root of the zygomatic arch is level with the middle of P4.

Discussion.—Previously, *M. ballovianus* was only known from the holotype, a badly crushed skull with associated cheek teeth (Black 1963). The new sample can be referred to this species by its similar size (Table 5) and morphology of the cheek teeth. These specimens provide a much more complete understanding of this species' morphology, with each cheek tooth represented, other than the M3. The morphology of JODA 15369 agrees with the type, with the laterally compressed infraorbital foramen suggesting that *Miosciurus* was sciuromorphic (Black 1963; Goodwin 2008). The new material of *M. ballovianus* also allows the placement of this species in a biostratigraphic context, with a range spanning the late early Arikareean (Ar2) and early late Arikareean (Ar3).

Miosciurus ballovianus co-occurs with two larger tree squirrels in John Day Formation deposits, with the larger *Protosciurus mengi* Black, 1963, and *P. rachelae* Black, 1963, in the upper Turtle Cove and Kimberly members (Fremd and Whistler 2009). *Miosciurus ballovianus* represents the smallest early tree squirrel in North America, about 50% smaller than *P. condoni* Black, 1963, and 40% smaller than extant *Sciurus* Linnaeus, 1758. The size of *M. ballovianus* suggests a trend towards dwarfism in this lineage through the late Oligocene, as this species is substantially smaller than any earlier squirrel; a hypothesis which

is discussed in greater detail below. The next small tree squirrel known from the fossil record of North America is the Clarendonian *Sciurus olsoni* Emry et al., 2005, which is similar in size to *M. ballovianus* and was likely derived from *Miosciurus* or *Protosciurus*.

Several characters of *M. ballovianus*, like the shape of the diastema of the dentary and partially fused roots on lower cheek teeth, also are similar to the contemporaneous *Nototamias* Pratt and Morgan, 1989. Black (1963) considered *Miosciurus* close to the divergence of arboreal and terrestrial squirrels; these similarities potentially represent features present in the ancestor of the chipmunk and ground squirrel clade (Goodwin 2008). A second species of *Miosciurus* (described below) may help reveal how these species evolved from earlier, larger squirrels.

Miosciurus covensis, new species (Figs. 7A–H; Table 6)

Type Specimen.—JODA 10093, associated left dentary and partial maxilla with p4–m2 and M1–M3, respectively.

Referred Specimens.—JODA 15372 left dentary fragment with m1–m2; JODA 15373, right dentary fragment with m1–m2; JODA 6355, JODA 7251, m1; JODA 3738, maxilla fragment with right P4; JODA 3625, 10289, right M1, 12923, left M2.

Horizon and Locality.—JODA 10093, 12923, 15372, 15373 – JDNM 52, Logan Butte, Crook County, OR, lower Turtle Cove Member, John Day Formation; JODA 7251 – JDNM 171, Grant County, OR, Unit C, Turtle Cove Member, John Day Formation; John Day Formation;

JODA 3738, 6355 – JDNM 9, Blue Basin, Grant County, OR, Units C through D, Turtle Cove Member, John Day Formation; JODA 3625 – JDNM 7, Foree, Grant County, OR, Unit E1, Turtle Cove Member, John Day Formation.

Age.—Early early Arikareean (early Oligocene, Ar1), between A-B Tuff dated 29.75 ± 0.02 Ma and Blue Basin Tuff dated 28.8 Ma (Albright et al. 2008).

Diagnosis.—Larger than *M. ballovianus*; mesoconids and trigonid basins on the lower molars relatively smaller than in *M. ballovianus*; anterostylid of m1 not pronounced as in *M. ballovianus*; dorsal surface of the diastema dips below the alveolar margin; conules lacking on P4; greater mesiodistal expansion of the protocone of M1 and M2 than in *M. ballovianus*.

Etymology.—Latin suffix, *-ensis*, locality; referring to Turtle Cove.

Description.—The cheek teeth are slightly larger than those of *M. ballovianus* (Tables 5–6), but the occlusal morphology is very similar. Only the differences between these species will be described here. The p4 of the holotype is heavily worn (Fig. 7A), so little of the occlusal morphology is recognizable but is generally similar to that of *M. ballovianus*. On m1 and m2, the mesoconid is slightly reduced and the trigonid basins are smaller and not as well defined as in *M. ballovianus* (Figs. 7A, E–F). A small anterostylid is present on the lower molars representing a notch at the anterior edge of the protoconid, but the m1 lacks the prominent anterostylid of *M. ballovianus*.

On the dentary, the preserved posterior part of the diastema surface shows that it dips slightly ventrally rather than maintaining the level of the alveolar margin, as in *M. ballovianus* (Fig. 7B). The structure of the masseteric fossa is similar to that of *M. ballovianus*, extending anteriorly to the level of the m1 and displaying prominent boundaries.

P4 differs only from that of *M. ballovianus* in lacking any evidence of conules on the protocone and metaloph (Fig. 7G). M1 and M2 are as in the type species, except there is a greater mesiodistal expansion of the protocone, as in *Protosciurus*. M3 is not known for *M. ballovianus* but is present on the maxilla of the holotype of *M. covensis* (Fig. 7C). The anterior half of M3 is identical to that of the anterior molars. On the posterior half of the tooth, the hypocone is lacking and the tooth is greatly reduced at its posterolingual corner. The posterobuccal half of the tooth is greatly expanded posteriorly. The mesostyle is doubled. The metacone is not recognizable as a distinct cusp, but is incorporated into a posterior cingulum that wraps around the posterobuccal corner of the tooth.

Similar to the maxillary features of *M. ballovianus* (JODA 15369), in JODA 3738 the infraorbital foramen opens anterior to and above P3 (Fig. 7H). The infraorbital foramen of JODA 3738 is ovate ventrally and compressed dorsally, rather than laterally compressed to the degree seen in *M. ballovianus*. As in *M. ballovianus*, the posterior

border of the anterior root of the zygomatic arch is level with the middle of P4.

Discussion.—*Miosciurus covensis* is larger than the type species, *M. ballovianus*, and varies subtly from it in the morphology of the cheek teeth and dentary (lack of conules on P4, greater mesiodistal expansion of protocone on M1 and M2, smaller trigonid and mesoconid on lower molars, less prominent anterostylid on m1, shape of mandibular diastema). The infraorbital foramen of *M. covensis* is not laterally compressed to the degree seen in *M. ballovianus*; the shape of the infraorbital foramen in *M. covensis* is actually quite similar to that of *P. condoni*, suggesting incipiently sciuriformous jaw musculature.

Miosciurus covensis is the only sciurid documented in strata below the Turtle Cove Unit E, representing the earliest sciurid known from the Pacific Northwest. The presence of this new species indicates a greater diversity of tree squirrels (Sciurini) in the region than previously known. The occurrence of at least five tree squirrel species (*M. ballovianus*, *M. covensis*, *Protosciurus condoni*, *P. mengi*, and *P. rachelae*) in the Arikareean of the John Day Formation is in stark contrast to the fossil record of the later Cenozoic, where tree squirrels are virtually absent across North America (Emry et al. 2005; Goodwin 2008).

Both the size and morphology of *M. covensis* fall somewhat intermediate between the characteristics of *Protosciurus* and the later *M. ballovianus*. *Miosciurus covensis* is smaller than any earlier tree squirrel known, suggesting a trend toward dwarfism in this lineage. This would represent the earliest dwarfing event in the fossil record of the Sciuridae; the extant members of this family include seven independently derived dwarf lineages (Thorington and Hoffmann 2005; Hautier et al. 2009). If *M. covensis* is ancestral to *M. ballovianus*, which is approximately 15 – 20% smaller (Tables 5–6), it would suggest this dwarfing trend continued through the end of the Oligocene.

Based on molecular data, Mercer and Roth (2003) estimated the divergence of the major squirrel clades took place in the late Eocene and early Oligocene. They estimated the early divergence within the Xerinae, the terrestrial squirrels, to be around 28 million years ago (Mercer and Roth 2003). This late Oligocene divergence estimate matches the first appearance of chipmunk-like squirrels and ground squirrels (Black 1972; Steppan et al. 2004; Goodwin 2008). As *Miosciurus* has morphological similarities to both the arboreal and terrestrial squirrel clades, this early Oligocene (Ar1) species may be similar to the ancestor of the earliest terrestrial squirrels.

Miosciurus sp.
(Figs. 7I–J)

Referred Specimens.—JODA 4447, right partial dentary with m1–m2 and associated postcranial fragments.

Horizon and Locality.—JDNM 8B, Hayes Haven, Grant

County, OR, Unit K2, Turtle Cove Member, John Day Formation.

Age.—Late early Arikareean (late Oligocene, Ar2), between Biotite Tuff dated 27.14 ± 0.13 Ma and Tin Roof Tuff dated 25.9 ± 0.3 Ma (Albright et al. 2008).

Measurements.—JODA 4447: m1, length = 1.97 mm, width = 2.26 mm; m2, length = 2.08 mm, width = 2.35 mm; i1, length = 3.27 mm, width = 1.74 mm.

Description.—The dentary is relatively deep for the size of the teeth, and as in *M. covensis*, the diastemal depression is deeper than in *M. ballovianus* (Fig. 7J). The masseteric fossa is shallow and extends anteriorly to below the anterior margin of m1, forming a broad U-shape. The mental foramen is small, located anterior to the anterior root of the p4, and is relatively dorsally positioned. The lower incisor is relatively anteroposteriorly deep and transversely compressed, with gently convex anterior and lateral sides. The incisor bears no ornamentation on the enamel surface.

The m1 is slightly wider than long, and wider posteriorly than anteriorly (Fig. 7I). It is typically rhomboidal in shape with the metaconid more anterior than the protoconid. The metalophulid I extends buccally from the metaconid, ending in an anterostylid anterior and slightly lingual to the protoconid. A minute trigonid basin is formed between it and the metalophulid II that runs lingually from the protoconid. Lingually, there is a doubled mesostylid posterior to the metaconid that is separated from both the metaconid and entoconid by prominent valleys. The mesoconid is large, only slightly smaller than the hypoconid. The posterior cingulid extends from the posterior side of the hypoconid along the posterior edge of the tooth, joining the entoconid at the lingual end. The entoconid is distinct and obliquely compressed, and is only slightly smaller than the hypoconid.

The m2 is similar to m1 in most aspects of morphology, though the metaconid is broken away. It differs from m1 in having some slight irregularities of the enamel in the talonid basin of the tooth, lacking the minute trigonid basin, and having a relatively smaller entoconid. There is one large mesostylid present, but due to breakage it cannot be determined whether it was doubled as in m1.

Discussion.—*Miosciurus* sp. is morphologically very similar to the other species of *Miosciurus* in the John Day fauna in features such as the size of the entoconid on the lower molars and position of the mental foramen. However, it differs from these other species in its larger size, irregularities of the enamel in the basins of the lower teeth, and having multiple mesostylids. The specimen referred to *Miosciurus* sp. is distinguished from the other sciurine in the fauna, *Protosciurus*, in being much smaller and having multiple mesostylids on the lower molars.

Black (1963) described a dentary with p4–m3 from the John Day Formation, YPM 13602, that he called “Genus and Species Indeterminate” (Black 1963:149). This

specimen is similar in size to *Miosciurus* sp., JODA 4447, and may represent the same species. As in JODA 4447, YPM 13602 has a prominent notch between the entoconid and mesostylid of the lower molars. Similar to the other *Miosciurus* specimens described here, YPM 13602 has a shallow diastemal depression. However, the masseteric scar on YPM 13602 extends farther anteriorly (below p4) than the specimen of *Miosciurus* sp. described here and there is no indication of multiple mesostylids (Black 1963: pl. 7, fig. 1). At this time it is impossible to determine whether YPM 13602 belongs to the same species as the referred *Miosciurus* sp. dentary.

Protosciurus Black, 1963

Protosciurus rachelae Black, 1963 (Fig. 8; Tables 7–8)

Referred Specimens.—UCMP 86367, nearly complete skull (lacking anterior end of rostrum) with incisors and left M3; JODA 7276, left P4; JODA 12603, left M1 or M2; JODA 6280, right M3; JODA 12602, right p4; JODA 12601, right m3.

Horizon and Locality.—JODA 6280 – JDNM 35, Round-up Flat, Grant County, OR, Unit K1, Turtle Cove Member, John Day Formation; JODA 7276 – JDNM 8, Sheep Rock, Grant County, OR, Unit K2, Turtle Cove Member, John Day Formation; JODA 12601, 12602, 12603 – JDNM 140, Campbell Ranch, Gilliam County, OR, Kimberly Member, John Day Formation; UCMP 86367 – V6584, Pelecypod, Wheeler County, OR, upper Turtle Cove or Kimberly members, John Day Formation.

Age.—Late early Arikareean (late Oligocene, Ar2) and early late Arikareean (Ar3), between Deep Creek Tuff dated 27.89 ± 0.57 Ma (Albright et al. 2008) and JD-BC-3 tuff dated 23.79 ± 0.18 Ma (Hunt and Stepleton 2004).

Description.—The skull of *P. rachelae*, UCMP 86367, is referred to this species based on size (Table 7) and the lack of a protoconule on the M3 (all other cheek teeth lacking). The skull lacks the anterior part of the rostrum, but is otherwise complete and three-dimensional (Figs. 8A–D). In overall shape it does not differ from that of modern *Sciurus*. Although not complete, the rostrum appears short and widens posteriorly. Dorsally, the nasals and premaxillaries end at the same level, even with the anterior margin of the orbits. The frontals are flat and there is a distinct flattened shelf that forms along the top of the orbits. Only the base of the postorbital process is preserved on the left side of the skull. The frontals end posteriorly at the postorbital constriction, just behind the postorbital process. The parietals are gently convex, forming the dome of the neurocranium; this is unlike the flattened skull roof that characterizes the type of *P. condoni* (Black 1963). Beginning at the posterior base of the postorbital processes are

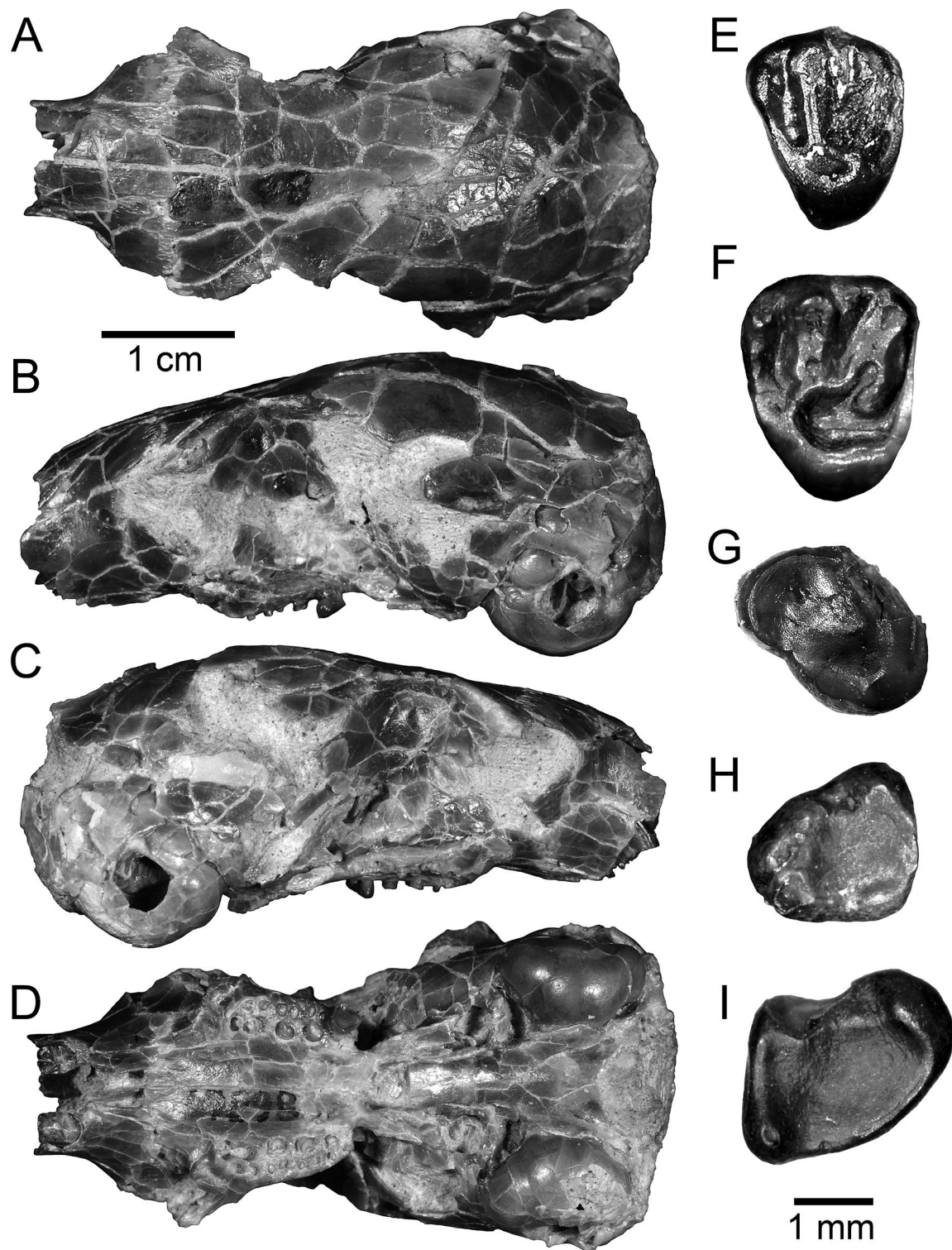


Fig. 8.—Specimens of *Protosciurus rachelae* from the John Day Formation, Oregon. A–D, UCMP 86367, skull with incisors and left M3; A, dorsal view; B, left lateral view; C, right lateral view; D, ventral views; E, JODA 7276, left P4; F, JODA 12603, left M1 or M2; G, JODA 6280, right M3; H, JODA 12602, right p4; I, JODA 12601, right m3. Scale bars equal 1 mm.

TABLE 7. Cranial measurements (in mm) of *Protosciurus* skulls from the John Day Formation. Note that the *P. mengi* specimen, UCMP 86368, is a juvenile.

	<i>P. condoni</i> UO 5171	<i>P. rachelae</i> UCMP 86367	<i>P. mengi</i> UCMP 86368
Length anterior orbit to occiput	50.59	34.83	
Maximum cranial width	29.76	24.16	22.44
Occipital width	28.49	22.67	21.26
Foramen magnum width	8.79	8.02	
Length of bulla	16.22	11.25	10.53
P4-M3 length	17.17	9.61	

low temporal crests that converge at a point approximately two-thirds the length of the parietals. At that point, a single sagittal crest runs posteriorly along the center of the neurocranium, ending at the nuchal crest. The cranium is relatively deeper than in *P. condoni*, more like extant *Sciurus*.

Although the skull is not distorted by crushing, most of the bones are badly cracked. Most of the anterior zygomatic arches are missing on both sides, but there is enough of the base of the arch on the right side to show that it is sciuriform with a slight lateral compression of the infraorbital foramen, similar to the condition in the type specimen (Black 1963: pl. 3, fig. 1). On the right side of the skull, much of the orbital wall is preserved (Fig. 8C). The sphenopalatine foramen, optic foramen, and opening for the sphenoidal fissure are observable and positioned exactly as figured by Wahlert (1974: fig. 1) for Recent *Marmota* Blumenbach, 1779. On the left side, the alisphenoid is preserved and the single opening for the buccinator and masticatory foramina is observable (Fig. 8B). Posterior to the glenoid fossa for the mandible is a large, oval temporal foramen, along the parietal-mastoid suture. The bulla is inflated and circular in outline. The inflation is also evident in the mastoid and the lateral part of the occipital that are above the bulla. The external acoustic meatus is large and circular in outline.

Ventrally, the palate is flat to slightly concave upward (Fig. 8D). The incisive foramina are short, but cannot be measured because they lack their anterior border. The palatine extends anteriorly on the palate to a level even with M2. There is a large, oval posterior palatine foramen in the palatine even with M3. Posterior to the tooth row is the posterior maxillary notch, which is not as deep or anteriorly directed as in *P. condoni*. Posterior to the palate, the structures and foramina are nearly identical to those of *Marmota* (Wahlert 1974: fig. 1). The only observable difference is that the pterygoid flanges on the *P. rachelae* skull are not as large or long as in *Marmota*. In posterior view, the skull only differs from that of *Marmota* in being less wide.

The P4 of *P. rachelae* has not been described previously. An isolated specimen, JODA 7276, is referred to

this species based on size and morphology (Fig. 8E). The specimen is roughly triangular in occlusal outline. There is a distinct, transversely elongated parastyle in the anterobuccal corner of the tooth. A low anterior cingulum runs from it along the anterior edge of the tooth, ending at the protocone. The paracone and metacone are anteroposteriorly compressed. There is a small mesostyle between them along the buccal side of the tooth, and a short loph runs lingually from the mesostyle toward the center of the tooth. The protoloph and metaloph converge on the protocone. There are no conules on these lophs, but there is a slight swelling of the metaloph near its center. The posterior cingulum runs the entire width of the tooth along its posterior edge, extending from the protocone to the metacone.

An M1 or M2 in the collection, JODA 12603, is heavily worn, so fine details of the occlusal morphology cannot be observed (Fig. 8F). The anterior cingulum is only somewhat expanded (Black 1963) and, unlike the upper molars of *P. mengi*, does not extend near the lingual margin of the tooth (Korth 1987a). The protocone is expanded anteroposteriorly, with a swelling at the lingual edge of the posterior cingulum indicating the hypocone. There is a small mesostyle between the paracone and metacone, slightly nearer to the paracone. Circular wear facets on the protoloph and metaloph of JODA 12603 suggest the presence of paired protoconules and metaconules. The upper molars of the holotype (AMNH 7241), as described in Black (1963), show no evidence of conules.

The left M3 of UCMP 86367 is present, and an additional right M3 is in the collection, JODA 6280 (Fig. 8G). The morphology of these teeth is similar to that of the holotype (Black 1963), with a broad protocone, large metacone, and no indication of a protoconule. The M3 of UCMP 86367 is heavily worn, but the parastyle and anterior cingulum are relatively small. The anterobuccal corner of JODA 6280 is broken, but there is a relatively sharp indentation between the protocone and metacone.

The upper incisors of UCMP 86367 are broken, but have a shape consistent with the description of the holotype (Black 1963). The incisors are not strongly transversely compressed, with a flat medial surface and rounded anterior

TABLE 8. Dental measurements (in mm) for *Protosciurus rachelae* from the John Day Formation. Abbreviations: **L**, anteroposterior length; **W**, transverse width.

	I1L	I1W	P4L	P4W	M1 or M2L	M1 or M2W	M3L	M3W	P4–M3L
JODA 7276			1.99	2.58					
JODA 12603					2.24	2.89			
UCMP 86367 L							2.37	2.23	9.44
UCMP 86367 R	3.33	2.42							9.8
JODA 6280							--	2.36	
			p4L	p4W	m3L	m3W			
JODA 12602			2.12	1.92					
JODA 12601					2.68	1.9			

and lateral surfaces. The enamel runs from the anteromedial margin of the tooth and extends approximately one-third of the way down the lateral surface. These features of the incisor are more similar to *Douglassciurus* Emry and Korth, 2001, than extant *Sciurus* (Emry and Thorington 1982).

There is one specimen of p4, JODA 12602, referred to *P. rachelae* (Fig. 8H). The p4 is longer than wide and narrower anteriorly than posteriorly. The metaconid and protoconid are closely spaced, and the protoconid is just slightly more posterior than the metaconid. A very narrow valley separates them anteriorly, but they are connected posteriorly by the metalophulid II. There is a small antero-stylid between the two trigonid cusps along the anterior border of the tooth. There is no indication of a mesoconid, as is characteristic of the species. The hypoconid is large and in the posterobuccal corner of the tooth. The posterior cingulid extends from it along the posterior border of the tooth, ending lingually at the entoconid, which is transversely compressed. The posterolingual corner of the tooth is slightly rounded.

The referred m3, JODA 12601 (Fig. 8I), has morphology similar to that of other material referred to *P. rachelae* (Black 1963; Korth 2009). The trigonid basin is not evident, though a small anterior cingulid is present on the anterior surface of the metaconid and anterolingual portion of the tooth. The tooth is expanded posteriorly, has a large hypoconid, and reduced entoconid, which is continuous with the posterior cingulid.

Discussion.—The skull of *P. rachelae* is remarkably similar to that of Recent tree squirrels. Like *Sciurus*, *P. rachelae* displays a deeper cranium and more domed (convex) skull roof than *P. condoni*. A notable difference from *Sciurus* is the morphology of the temporal crests. As in *P. condoni* (Black 1963: pl. 3, fig. 1a), the temporal crests of *P. rachelae* meet anterior to joining the nuchal crest and form

a short sagittal crest. The infraorbital foramen is laterally compressed and slit-like in *P. rachelae*, but not to the extent seen in extant *Sciurus*. As noted by Black (1963), the structure of the infraorbital foramen in this species suggests that *Protosciurus* only showed the beginnings of sci-uromorphy (Goodwin 2008).

Previously reported material of *P. rachelae* from the John Day Formation lacked detailed locality data (Black 1963); these new specimens allow placement of this species in a stratigraphic context. The presence of *P. rachelae* from the Arikareean John Day Formation is not its earliest occurrence. Several isolated teeth have been referred to this species from the Whitneyan of South Dakota, occurring at a site where specimens of *P. mengi* have also been reported (Korth 2009).

***Protosciurus mengi* Black, 1963**
(Figs. 9–10, 11B; Tables 7, 9)

Referred Specimens.—JODA 4565, left dentary with i1, p4–m3; JODA 5761, partial right dentary with m1–m2; JODA 16035, left dentary with m1–m2; JODA 16036, left dentary with m2–m3; JODA 12696, left p4; JODA 12344, left m1; JODA 3175, left m2; JODA 3176, 4527, left M1 or M2; JODA 12599 left M3; JODA 16483, left maxilla with dP4–M2, unerupted P3–P4; UCMP 86368, partial juvenile skull with incisors and left dP4–M2, partial mandible with incisors, and partial postcranial skeleton (right clavicle, right humerus, left humerus, left radius, left ulna, left metacarpals and some phalanges, left femur, left tibia, right tibia, right metatarsals and proximal phalanges); JODA 16034, fragmentary postcranial bones with complete calcaneum.

Horizon and Locality.—JODA 3175, 3176 – JDNM 8, Sheep Rock, Grant County, OR, Unit E, Turtle Cove Member, John Day Formation; JODA 16034, 16035, 16036 –

JDNM-7, Foree, Grant County, OR, Unit F, Turtle Cove Member, John Day Formation; JODA 5761 – JDNM-22, Lone Pine Beds, Grant County, OR, upper Turtle Cove Member, John Day Formation; JODA 4527, 4565, 12344 – JDNM 8B, Hayes Haven, Grant County, OR, Unit K2, Turtle Cove Member, John Day Formation; JODA 12596, 12599, 12696 – JDNM 140, Campbell Ranch, Gilliam County, OR, Kimberly Member, John Day Formation; JODA 16483 – V6322, Gray Face Bluff (Haystack 8 of Rensberger 1973), Wheeler County, OR, Haystack Valley Member, John Day Formation; UCMP 86368 – V70175, Junction N 2, Wheeler County, OR, unknown horizon, John Day Formation.

Age.—Early early Arikareean (early Oligocene, Ar1) through early late Arikareean (late Oligocene, Ar3), between A-B Tuff dated 29.75 ± 0.02 Ma (Albright et al. 2008) and JD-BC-3 tuff dated 23.79 ± 0.18 Ma (Hunt and Stepleton 2004).

Description.—The fragmentary juvenile skull, UCMP 86368, is in two primary pieces (Figs. 9A–C). The anterior portion of the skull consists of the rostrum, most of the left maxilla, approximately half of the palate, the anterior half of the left zygomatic arch, and skull roof to the anterior border of the parietals. The rostrum is short and strongly tapered anteriorly. The skull roof is flat (in part due to crushing) and there is no indication of any temporal crests. The nasals extend posteriorly to the level of the anterior margin of the orbit, slightly more posterior than the premaxillaries. Due to breakage, there are no postorbital processes preserved, but on both sides of the skull, there is a thin shelf of bone that extends over the top of the orbit. The anterior portion of the preserved zygomatic arch is tilted dorsally, exhibiting the sciuromorphic condition. The infraorbital foramina are not completely preserved in UCMP 86368, but another specimen (JODA 16483) has a laterally compressed, slit-like infraorbital foramen. The palate is gently concave upward and wide. The incisive foramina are small (2.69 mm). The maxillary-premaxillary suture crosses the midline of the palate at the posterior end of the incisive foramina. No other foramina or structures are observable on the anterior fragment.

The posterior fragment is uncrushed and due to the young age of the individual (deciduous teeth present) the sutures are not fused. There is a wide, roughly triangular interparietal at the center of the top of the skull. Only small portions of the posterior edges of the parietals are preserved. There is no evidence of sagittal or temporal crests. The occipital condyles and foramen magnum are obscured by the attachment of vertebral fragments. The auditory bullae are “doughnut” shaped and slightly inflated, and the inflation includes the mastoid bone dorsal to the bulla. The external acoustic meatus is a large circular opening. Ventrally, the basioccipital and posterior edge of the basisphenoid are preserved medial to the bullae, as well as with several foramina along the edges of the bullae. At the pos-

teromedial corner of the bulla is the jugular foramen, coincident with the opening for the carotid canal that pierces the bulla. Posterior and lateral to the jugular foramen on the left side of the skull are two small hypoglossal foramina. At the anteromedial edge of the bulla is the opening for the Eustachian tube. Preserved on the right side of the skull anterior to the Eustachian tube is a large foramen ovale.

The only tooth present in the John Day collection that has not been described is dP4, which is present in both UCMP 86368 (Fig. 9D) and JODA 16483 (Fig. 10H). This tooth is markedly smaller than the upper molars but similar in morphology. The cusps and lophs are bulbous as in all of the cheek teeth. The anterior cingulum is expanded anteriorly at the anterobuccal corner, and the valley separating the anterior cingulum from the protocone is wide. The paracone and metacone are round in outline (not compressed). The protocone and metaloph run from the paracone and metacone, respectively, to the protocone, forming a U-shape that is wider buccally. In both specimens, a small protoconule and metaconule are present in both specimens and the mesostyle is prominent. The protocone is crescentic and wide (anteroposteriorly). The posterior cingulum runs from the protocone to the metacone along the posterior margin of the tooth, forming a wide valley between it and the metaloph. There is no distinct hypocone, but the posterior cingulum is slightly widened at the posterolingual corner of the tooth.

The upper M1 and M2 are characterized by large hypocones and multiple metaconules (Korth 1987a, 2009). The anterior cingulum is large and extends nearly to the lingual margin of the teeth. A parastyle is relatively prominent in the M1 of UCMP 86368 and in JODA 3176, but less so in the M2 of UCMP 86368 and JODA 4527 (Figs. 8D, 9H, N–O). The posterior cingulum runs from the protocone through the hypocone to the metacone along the posterior margin of the tooth, with a narrow, but deep valley between it and the metaloph. The mesostyles of the John Day specimens are variable, being relatively prominent in UCMP 86368, JODA 3176, and 16483, but less distinct in JODA 4527, as in the material described by Korth (1987a). In JODA 16483, fine wrinkles are present in the enamel of the valleys between lophs; this seems to fade with wear (Fig. 10H).

The referred dentaries have morphology typical of *Protosciurus*. In JODA 4565, the diastema is short and the diastemal depression is relatively deep (Fig. 10B). The mental foramen is positioned well below the level of the diastema. The masseteric fossa extends to approximately the middle of the m1 and has prominent boundary ridges.

The lower cheek teeth all display prominent mesoconids and mesostylids, and large entoconids. The metaconids and protoconids are large and separated by a narrow valley. A small anterostylid lies anterior to the protocone, forming a small trigonid basin in all teeth. The p4 is longer than wide and narrower anteriorly than posteriorly (Fig. 10K). In JODA 4565, the metaconid and protoconid are large and separated by a narrow valley. The entoconid is

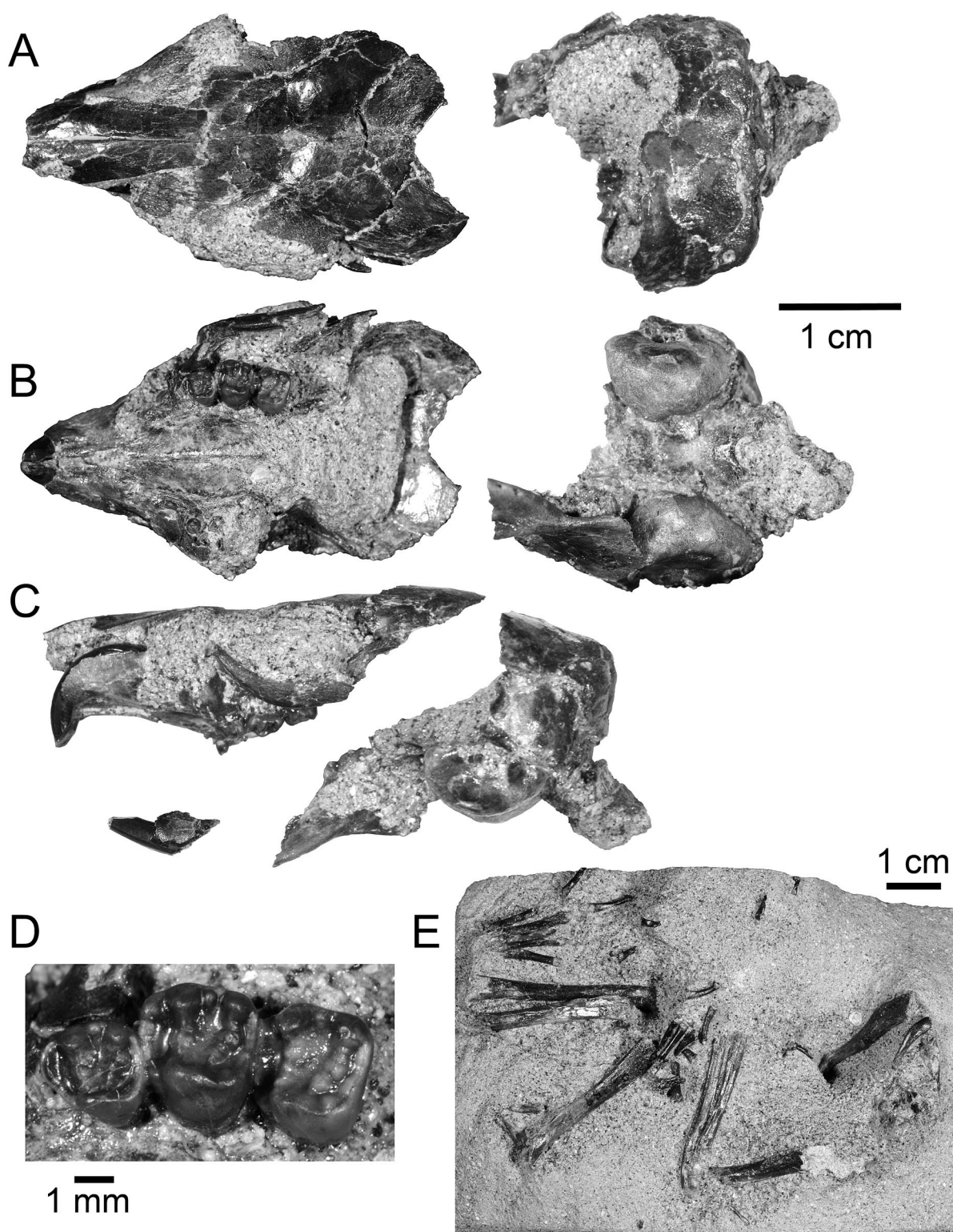


Fig. 9.—Specimens of *Protosciurus mengi* from the John Day Formation, Oregon. UCMP 86368, partial skull (anterior and posterior fragments) with incisors and left dp4 to M2, anterior mandible fragment, and associated postcranial bones; A–C, skull; A, dorsal view; B, ventral view; C left lateral view; D, occlusal view of dp4 to M2; E, partial postcranial skeleton. A–C to same scale (upper right), D to lower left scale, E to lower right scale.

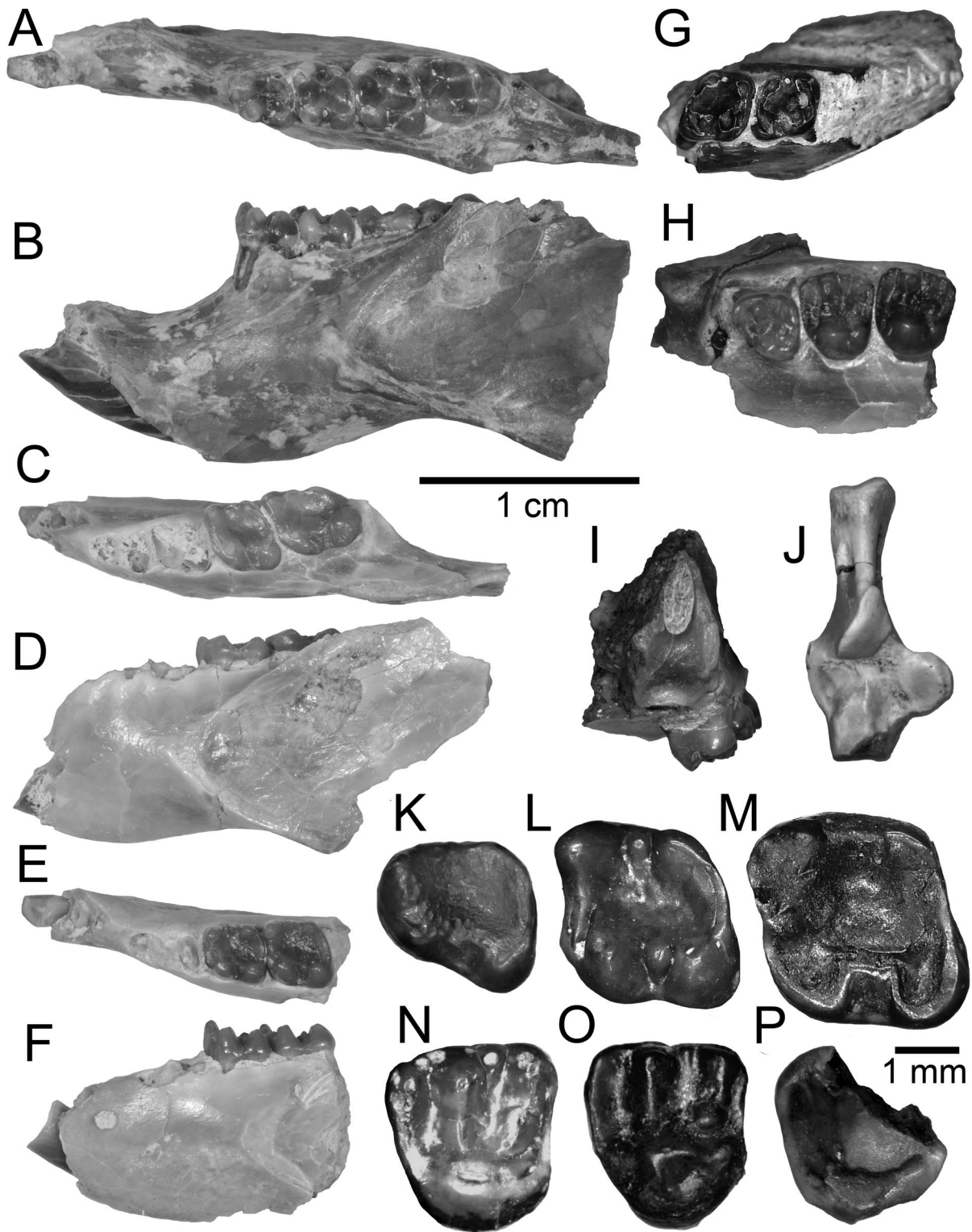


Fig. 10.—Specimens of *Protosciurus mengi* from the John Day Formation, Oregon. A–B, JODA 4565, left dentary with i1, p4 to m3; A, occlusal view; B, lateral views; C–D, JODA 16036, left dentary with m2 and m3; C, occlusal view; D, lateral view; E–F, JODA 16035, left dentary with m1 and m2; E, occlusal view; F, lateral view; G, JODA 5761, partial dentary with m1 and m2; H–I, JODA 16483, left maxilla with dP4 to M2; H, occlusal view; I, anterior view; J, JODA 16034, dorsal view of calcaneum; K, JODA 12696, left p4; L, JODA 12344, left m1; M, JODA 3175, left m2; N, JODA 3176, M1 or M2; O, JODA 4527, M1 or M2; P, JODA 12599, left M3. Scale bars equal 1 cm (A – J) and 1 mm (K–P).

TABLE 9. Dental measurements (in mm) for *Protosciurus mengi* from the John Day Formation.

Abbreviations: **L**, anteroposterior length; **W**, transverse width. Statistical abbreviations: **N**, number of specimens; **M**, mean; **OR**, range of size; **SD**, standard deviation; **CV**, coefficient of variation.

	i1L	i1W	dP4L	dP4W	M1L	M1W	M2L	M2W	M3L	M3W	P4–M3
UCMP 86368	1.98	1.56	2.67	2.71	2.94	3.61	2.79	3.35			
JODA 3176					2.67	3.06					
JODA 4527					2.59	2.98					
JODA 16483			2.74	2.85	3.02	3.49	3.09	3.51			
	i1L	i1W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4–m3
N	4	4	2	2	5	5	6	6	2	2	2
M	2.41	1.54	2.53	2.29	2.50	2.71	2.80	2.95	3.59	2.96	12.11
OR	2.02–2.61	1.28–1.67	2.48–2.58	2.17–2.41	2.30–2.70	2.64–2.77	2.60–2.93	2.77–3.13	3.44–3.73	2.81–3.11	11.49–12.72
SD	0.27	0.17			0.16	0.05	0.11	0.13			
CV	4.65	11.37			7.55	2.00	3.94	4.33			

distinct in all teeth, though it is partially fused with the posterolophid, particularly in the m3. The posterolingual corner of the tooth is slightly rounded. Black (1963) noted that there were fine wrinkles in the enamel of the talonid basin, which is evident in JODA 16035 (Figs. 10E–F). This pitting fades with wear, and is unobservable on the most worn specimens.

The upper and lower incisors of UCMP 86368 have a shape similar to that of other members of the genus. Like *P. rachelae*, the upper incisors are not strongly transversely compressed, and have a flat internal surface and rounded anterior and external surfaces. The enamel of the upper incisor runs from the anterointernal margin of the tooth and extends approximately one-half of the way down the external surface. As in *P. condoni*, the lower incisors are more transversely compressed than the uppers, and the enamel extends slightly more onto the external surface. Like *P. rachelae* described above, features of the incisors of *P. mengi* are more similar to *Douglassciurus* than extant *Sciurus* (Emry and Thorington 1982).

A partial postcranial skeleton is associated with the juvenile skull of *P. mengi*, UCMP 86368. These postcranial elements are articulated and imbedded in a block of matrix (Fig. 9E). Exposed elements include the following: right clavicle, right humerus, left humerus, left radius, left ulna, left metacarpals and some phalanges, left femur, left tibia, right tibia, right metatarsals and proximal phalanges. Epiphyses for all elements are missing, suggesting they were still cartilaginous at this stage of development. In general, the limb bones are relatively gracile, but not as elongate as in *Sciurus* or *Douglassciurus* (Emry and Thorington 1982). However, it is important to note that UCMP 86368 is a juvenile individual and the relative length of these limb elements may be partially due to ontogenetic differences. A mature adult individual of *Protosciurus*

would certainly have had longer limb elements than are seen in this specimen.

An incomplete right clavicle of UCMP 86368 is preserved adjacent to the proximal end of the right humerus. The medial portion of the clavicle and the acromial end are missing, but the morphology of the preserved portion is like that of extant *Sciurus*. The lateral end of the bone is flattened and has a curved anterior surface. Both the left and right humeri are partially preserved, with the medial surface of the right humerus and lateral surface of the left exposed. Relative to their length, the bones appear somewhat stouter than *Sciurus* or *Douglassciurus* (Emry and Thorington 1982), but not nearly as robust as those of *Spermophilus* Cuvier, 1825. The deltopectoral crest appears similar to that of *Sciurus* and *Douglassciurus*, not nearly as prominent as in *Spermophilus*. The medial surface of the right humerus clearly shows the presence of an entepicondylar foramen, as is typical of sciurids.

The left ulna of UCMP 86368 is partially preserved, in apparent articulation with the left humerus and radius. The olecranon process is incompletely preserved, but does appear relatively short compared to the length of the bone, as in *Sciurus*. The ulnar shaft is flattened and appears rather thin at its midshaft, as is the case in *Sciurus* and *Douglassciurus* (Emry and Thorington 1982). A laterally concave interosseus crest is present, beginning near the radial notch and disappearing in the distal third of the ulnar shaft, as in *Sciurus*. In *Douglassciurus* and *Spermophilus*, there is a more distally extended interosseus crest, providing a larger area of attachment for the wrist and digital flexors and extensors (Emry and Thorington 1982). The left radius is partially preserved, but lacks any features that would facilitate comparison to other squirrels. Portions of the left manus are preserved, but these are limited to shafts of several metacarpals and phalanges. While incomplete, these

elements do appear to be elongate and gracile, as in tree squirrels.

The left femur of UCMP 86368 is also partially preserved, in articulation with an exposed portion of the left innominate and the left tibia. Unfortunately, as in the other limb elements, the epiphyses are missing, preventing detailed comparison to other taxa. The third trochanter is broken, but seems to have been relatively prominent, as in *Sciurus* and *Douglassciurus* (Emry and Thorington 1982). The left and right tibiae of UCMP 86368 are partially preserved, with the lateral surface of the left tibia and medial surface of the right exposed. As in *Sciurus*, the tibial crest does not appear to extend much distally onto the shaft. Like the manus, portions of the right pes are preserved, including the shafts of all five metatarsals and several proximal phalanges. These elements are incomplete, but definitely elongate and gracile, as in tree squirrels.

Some additional postcranial material was discovered with several of the *P. mengi* dentaries described here; among these elements was a complete calcaneum (JODA 16034, Fig. 10J). Emry and Thorington (1982) compared the calcaneum of *Douglassciurus jeffersoni* (Douglass, 1901) to those of *Sciurus* and *Spermophilus*. The tuber calcaneus of *Protosciurus* is more elongate and laterally compressed than *Spermophilus* or *Douglassciurus*, but lacks the strong medial curvature seen in *Sciurus*. The lateral ridge of the tuber calcaneus is less prominent than in *Douglassciurus* or *Spermophilus*, providing a relatively small area of attachment for the calcaneo-fibular ligament, but not as small as in *Sciurus*. The sustentacular facet of *Protosciurus* is intermediate in shape and position between the characteristics of *Douglassciurus* and *Sciurus*. Like *Sciurus*, the facet is more medially located and less round than *Douglassciurus*. Unlike *Sciurus*, the sustentacular facet is still well separated from the ectal facet by a prominent groove and is not connected to the distal end of the bone by a broad ridge. The ectal facet has a trapezoidal shape similar to *Douglassciurus*, rather than the roughly triangular shape of *Sciurus*. The peroneal tubercle of *Protosciurus* is long, beginning at a point proximal to the distal edge of the ectal facet and proximal edge of the sustentacular facet and extending to the level of the distal edge of the sustentacular facet. Like *Sciurus*, the peroneal tubercle begins more proximally in *Protosciurus* than in *Spermophilus* or *Douglassciurus*, but the distal extension is also greater than in *Sciurus*. As in *Sciurus*, the peroneal groove of *Protosciurus* is prominent and extends onto the body of the calcaneum.

Discussion.—*Protosciurus mengi* was originally described from the Orellan of Nebraska, based on a single dentary with p4–m3 (Black 1963). Later, Korth (1987a) described the upper dentition and cited two more dentaries from the upper part of the Orellan Member (Orellan C and D), suggesting a later Orellan occurrence of the species. Most recently, specimens referred to this species have been reported from the Whitneyan of South Dakota (Korth 2009).

The occurrence of *P. mengi* from the John Day Formation extends the record of this species into the Arikarean.

There appear to be no changes in morphology or size (Table 8; Black 1963:147; Korth 1987a: tables 1–2) between the oldest and youngest identified specimens of *P. mengi*. The overall cranial morphology of *P. mengi* is similar to that of *P. condoni* and *P. rachelae*, and extant *Sciurus*. The morphology of the zygomatic arch and infra-orbital foramen of *P. mengi* are similar to that of *P. rachelae*, suggesting that *Protosciurus* was not fully sciuromorphic (Black 1963; Goodwin 2008).

Emry and Thorington (1982) demonstrated how similar the Chadronian *Douglassciurus* was to extant *Sciurus*, suggesting there has been little change in tree squirrels since the late Eocene. Based on postcranial similarity to extant tree squirrels, Emry and Korth (1996) referred *D. jeffersoni* to the tribe Sciurini. The postcranial material of *Protosciurus* is very similar to extant *Sciurus* and *Douglassciurus*. While *Douglassciurus* is thought to have retained some primitive characters, intermediate between terrestrial and arboreal squirrels (Emry and Thorington 1982), some aspects of the morphology of *Protosciurus* are more like *Sciurus* than the earlier *Douglassciurus*.

Based on their analysis of *Douglassciurus*, Emry and Thorington (1984) referred to the extant tree squirrel *Sciurus* as a living fossil. The new specimens of *P. rachelae* and *P. mengi*, and their similarity to *Sciurus*, support this suggestion. Both the craniodental and postcranial morphology of *Protosciurus* suggest close relation to extant tree squirrels (Sciurini). The postcranial morphology of *P. mengi*, as in *Douglassciurus*, supports inference of an arboreal lifestyle, like that of extant tree squirrels. This suggests that quite modern tree squirrels were present in the early Oligocene of North America, and have changed little since then. Parsimony and likelihood reconstructions of the most recent common ancestor of squirrels using molecular phylogenetic data (Steppan et al. 2004) are also consistent with inferred arboreality of early squirrels based on their morphology.

Tribe Pteromyini Brandt, 1855
Petauristodon Engesser, 1979

Petauristodon sp.
(Fig. 11A)

Referred Specimen.—JODA 12597, left m3.

Horizon and Locality.—JDNM 140, Campbell Ranch, Gilliam County, OR, Kimberly Member, John Day Formation.

Age.—Early late Arikarean (late Oligocene, Ar3), between Tin Roof Tuff dated 25.9 ± 0.3 Ma (Albright et al. 2008) and JD-BC-3 tuff dated 23.79 ± 0.18 Ma (Hunt and Stepleton 2004).

Measurements.—Length = 2.97 mm; width = 2.64 mm.

Description.—In overall shape, the tooth is similar to the m3 of other sciurids in being expanded posteriorly and narrower posteriorly than anteriorly. The central basin of the tooth is filled with rugose or crenulated enamel. The metaconid is the largest cusp and positioned more anteriorly than the protoconid. The anterior cingulid runs from the metaconid buccally and ends before reaching the protoconid. Rather than being a loph, the cingulid consists of a series of cusps, which are separated from the protoconid by a narrow valley. The metalophulid II (=posterior arm of the protoconid) is short, ending well short of the base of the metaconid. The mesoconid is distinct and isolated from both the protoconid and hypoconid. The posterior cingulid (=posterolophid) is a continuous ridge from the hypoconid to the entoconid that bows strongly posteriorly. The entoconid is small, but distinct, and is continuous with the posterior cingulid. The mesostylid is large and isolated from both the metaconid and entoconid along the lingual edge of the tooth.

Discussion.—The specimen is referable to *Petauristodon* because of its robust cusps, large size, and crenulate enamel in the central basin (Fig. 11A). Due to the limited material available, the species cannot be determined. In size, the JODA specimen most closely approaches that of *P. pattersoni* Pratt and Morgan, 1989, from the Hemingfordian and *P. jamesi* (Lindsay, 1972) from the Clarendonian (Pratt and Morgan 1989: table 1). The degree of enamel crenulation in the JODA specimen is greater than that of *P. pattersoni* from Thomas Farm (Pratt and Morgan 1989).

This is first definite record of *Petauristodon* from the Arikareean, and represents the earliest occurrence of the genus. Elsewhere, Whistler and Lander (2003) listed the genus from the late Arikareean (Ar 3–4) of southern California with question, as did Bailey (1992) from the Arikareean of Nebraska. *Petauristodon* is also known from the Barstovian (Ba1) of Oregon, at Red Basin (Shotwell 1968). This John Day Formation occurrence represents the earliest well-dated record of a ‘flying squirrel’ (Pteromyini of Steppan et al. 2004, Petauristinae of Goodwin 2008) in North America. The age of the John Day occurrence of *Petauristodon* is close to Mercer and Roth’s (2003) estimated divergence of Pteromyini from Sciurini based on molecular data, around 23 million years ago. However, earlier records of ‘flying squirrels’ have been reported; Bell et al. (2003) and Bell (2004) described several species of *Sciurion* Skwara, 1986, from Orellan, Whitneyan, and Arikareean localities within the Cypress Hills Formation of Saskatchewan. Emry and Korth (2007) described several species of *Hesperopetes* Emry and Korth, 2007, from the Chadronian of Wyoming and latest Whitneyan or earliest Arikareean of South Dakota. Though they display crenulated enamel, the relationship of these species to the pteromyines is uncertain (Emry and Korth 2007).

Whether *Petauristodon* was actually a ‘flying squirrel’ (tribe Pteromyini) is uncertain. Emry and Korth (1996)

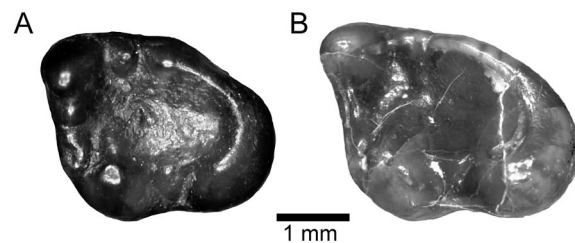


Fig. 11.—Left m3s of specimens of *Petauristodon* sp. and *Protosciurus mengi* from the John Day Formation, Oregon. **A**, *Petauristodon* sp., JODA 12597; **B**, *Protosciurus mengi*, JODA 4565. Scale bar equals 1 mm.

raised doubts about identifying fossil flying squirrels purely from teeth. Pratt and Morgan (1989) and Thorington et al. (2005) questioned the attribution of the genus to the Pteromyini based on characteristics of the dentition and astragalus. It is possible that the dental characters of *Petauristodon* and *Sciurion* may have arisen independently from extant flying squirrels, or may have been retained from some earlier shared ancestor. It is currently unclear whether early ‘flying squirrels’ like *Petauristodon* and *Sciurion* were actually gliding animals, and in the absence of relatively complete postcranial remains this issue will continue to be unresolved (Thorington et al. 2005; Goodwin 2008). The habitat that the John Day *Petauristodon* inhabited seems to be mosaic mixed woodlands, as indicated by the abundance of open habitat-adapted geomyids (*Entoptychus* Cope, 1878), burrowing beavers (*Capacikala* Macdonald, 1963, and *Palaeocastor*), and talpids (*Scalopoides* Wilson, 1960), along with clearly arboreal tree squirrels (*Miosciurus* and *Protosciurus*) (Fremd and Whistler 2009). This type of habitat neither supports nor refutes gliding habits of *Petauristodon*.

Family Eomyidae Winge, 1887
Subfamily Eomyinae Winge, 1887
Tribe Apeomyini Fejfar et al. 1998

Proapeomys, new genus

Type Species.—*Proapeomys condoni*, new species

Referred Species.—?*P. lulli* (Wood, 1936a).

Diagnosis.—Submesodont crown height of cheek teeth; central transverse valley on lower molars persistent and continuous on m1 and m2 for entire width of tooth; lophodont cheek teeth with anterior and posterior transverse loops formed on m1–m2.

Etymology.—Greek, *pro*, before; and referring to the related genus *Apeomys*.

Range.—Arikareean of Oregon.

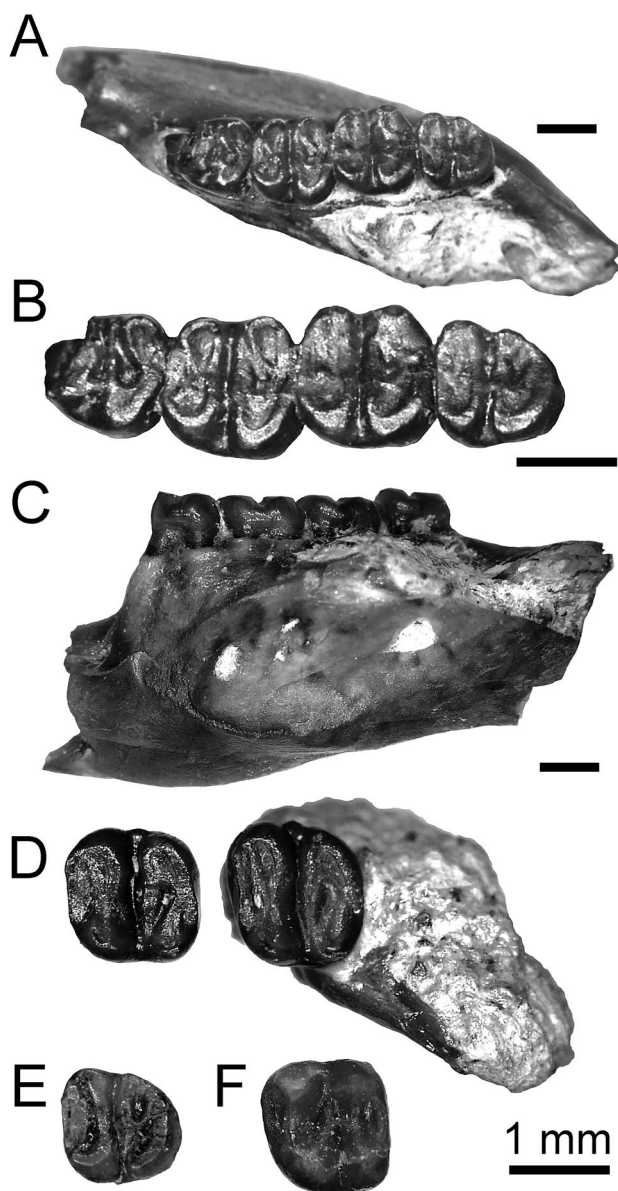


Fig. 12.—Specimens of *Proapeomys condoni*, new genus and species, from the John Day Formation, Oregon. **A–C**, Holotype, JODA 1207, dentary with left p4 (partial) to m3; **A**, occlusal view; **B**, occlusal view (enlarged); and **C**, lateral view; **D**, JODA 16482, right m1 and m2 (note that fragment of dentary adjacent to m2 is not in life position); **E**, JODA 15371, left m3; **F**, JODA 8920, left M1 or M2. Bar scale to the right of each figure. Scale bars equal 1 mm.

***Proapeomys condoni*, new species**
(Fig. 12; Table 10)

Type Specimen.—JODA 1207, dentary with left p4(partial)-m3.

Referred Specimens.—JODA 16482, right m1 and m2;

JODA 15371, isolated left m3; JODA 8920, left M1 or M2.

Horizon and Locality.—JODA 1207, 15371, 16482 – JDNM 9, Blue Basin, Grant County, OR, Unit E, Turtle Cove Member, John Day Formation; JODA 8920 – JDNM 52, Logan Butte, Crook County, OR, lower Turtle Cove Member, John Day Formation.

Age.—Early early Arikareean (early Oligocene, Ar1), between A-B Tuff dated 29.75 ± 0.02 Ma and Blue Basin Tuff dated 28.8 Ma (Albright et al. 2008).

Diagnosis.—Transverse loops of lower molars incomplete; anterior cingulid on lower molars more closely appressed to metalophid (anterior basin smaller) and cheek teeth not as lophate as *?P. lulli*; m3 variably retains anteroposteriorly oriented loph at center, blocking central transverse valley.

Etymology.—Patronym for Thomas Condon.

Description.—The cheek teeth on JODA 1207 are little worn but the anterior part of p4 is broken away (Figs. 12A–B). The cheek teeth are submesodont, but lophate. The p4 is smaller than m1 and m2, but larger than m3. The p4 is approximately equal in width and length, but narrower anteriorly than posteriorly. The metaconid is missing and the protoconid is incomplete on the p4. The entoconid and hypoconid are preserved and are obliquely compressed (entoconid anterolingual-posterobuccally; hypoconid posterolingual-anterobuccally). The hypolophid extends posterobuccally from the entoconid, joining the hypoconid at its posterolingual point. A short posterior cingulid extends lingually from the hypoconid, enclosing a small basin between it and the hypolophid. The ectolophid is complete from the posterior of the protoconid to the hypoconid with a small re-entrant valley along its buccal side. A short mesolophid extends lingually from a small mesoconid at the center of the ectolophid. The mesolophid ends well short of the lingual edge of the tooth within a central transverse valley.

The m1 is slightly larger than p4, wider than long and more rectangular in occlusal outline (anterior width nearly equal to posterior width). The metaconid and protoconid are anteroposteriorly compressed and joined together by a straight metalophid. The anterior cingulid extends lingually from the protoconid along the anterior edge of the tooth, ending short of the metaconid and lingual margin of the tooth, forming an incomplete loop. Posterior to the metalophid is a narrow, deep transverse valley that crosses the entire tooth. The entoconid is obliquely compressed as in the p4 and the hypoconid is crescentic. The entoconid and hypoconid are united posteriorly by the posterior cingulid that extends the entire width of the tooth along its posterior border. The posterior cingulid is convex posteriorly. Arising from the anterobuccal point of the hypoconid is a mesoconid that extends lingually to a point even with the center of the tooth and mesolophid that ends adjacent to the anterobuccal surface of the entoconid. The posterior cin-

TABLE 10. Dental measurements (in mm) of *Proapeomys* from the John Day Formation.
Abbreviations: **L**, anteroposterior length; **W**, transverse width.

TABLE 10. Dental measurements (in mm) of <i>Proapeomys</i> from the John Day Formation. Abbreviations: L , anteroposterior length; W , transverse width.													
<i>P. condoni</i>					M1L	M1W							
JODA 8920					1.24	1.31							
	i1L	i1W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W	p4–m3		
JODA 1207		1.12		1.32	1.30	1.49	1.32	1.49	1.23	1.23	5.45		
JODA 15371									1.12	1.13			
JODA 16482					1.29	1.44	1.33	1.49					
<i>?P. lulli</i>					m1L	m1W	m2L	m2W	m3L	m3W			
YPM 143766					1.22	1.39	1.27	1.49					
JODA 16002								1.42	1.29	1.28			

gulid and mesoconid/mesolophid form a nearly complete loop, with a transversely oriented oval basin.

The m2 is shorter but wider than m1 and nearly identical in occlusal morphology (Figs. 12B, D). The only difference between m2 and m1 is that the anterior cingulid does extend lingually to the edge of the tooth, uniting with the metaconid, isolating a transversely elongated lake between it and the metalophid. In both the m1 and m2 of JODA 16482, there is a minute ?ectostylid at the buccal end of the central transverse valley, between the protoconid and hypoconid (Fig. 12D). Also in JODA 16482, there is a small transversely oriented valley (fourth syncline of Engesser 1999) posterior to the entoconid and anterior to the posterolophid, lingual to the connection of the entoconid and posterolophid. This feature has apparently been lost with wear in the type specimen.

The m3 is the smallest of the cheek teeth and is equal in length and anterior width, but tapers posteriorly. The anterior half of the tooth is similar to that of m1 and m2, but the anterior cingulid and metalophid are of equal height and form a loop. Posterior to the central transverse valley, there is some variation in the two specimens available. In JODA 1207, the entoconid and hypoconid are connected anteriorly by a transverse loph (?mesolophid) and posteriorly by a strongly posteriorly bowed posterior cingulid (Fig. 12B). This isolates a small basin on the posterior half of the tooth. In JODA 15371, the ?mesolophid is interrupted just lingual to the hypoconid by a narrow valley, and there is a short spur that extends posteriorly from the ?mesolophid into the posterior basin. In JODA 15371, there are two distinct loops and no connection between the metalophid and mesolophid (Fig. 12E), but in JODA 1207 there is a small anteroposterior loph (ectolophid) connecting the two and blocking the central transverse valley (Fig. 12B).

The M1 or M2, JODA 8920, is assigned to this species based on its similar size, crown height, and degree of lophodonty (Fig. 12F). It was also collected from the same

horizon (but different locality) as the holotype. The tooth is rectangular in occlusal outline, slightly wider than long. The four major cusps are distinct, at the four corners of the tooth, and equal in size. The protocone is compressed obliquely (anterobuccal to posterolingual) and the hypocone is anteroposteriorly compressed. The anterior cingulum extends lingually from the anterobuccal corner of the tooth to just past its midline, fusing with the anterior arm of the protocone. The protoloph runs directly lingually from the paracone, joining the anterior arm of the protocone at the junction of the anterior cingulum. A mesoloph extends buccally from the protocone, ending well short of the buccal edge of the tooth. Extending posteriorly from the mesoloph, near the center of the tooth, is a short posteriorly directed loph that joins the metaloph at its center. The metaloph runs directly lingual from the metacone to the hypocone and is only slightly bowed anteriorly. The posterior cingulum runs along the posterior border of the tooth connecting with both the hypocone and metacone posteriorly to enclose a small basin. The tooth is slightly higher crowned on its lingual side.

The i1 of JODA 1207 is narrow, but deep; the anterior enamel surface is convex with the enamel extending onto the lateral side. The dentary is slender and is deepest ventral to p4, tapering strongly dorsally posterior to this point. The masseteric scar is marked by dorsal and ventral ridges that meet anteriorly below the p4 in a U-shape. The ascending ramus extends dorsally at the midpoint of m2. The diastemal depression is deep, dropping steeply from in front of p4 to about one-third the depth of the dentary. The mental foramen lies just anterior to the posterior end of the diastema, not far below the diastemal depression, and opens anterodorsally.

Discussion.—The transverse loops on the occlusal surface of the lower cheek teeth of *Proapeomys* are only otherwise known in apeomyines among eomyids. The morphology of

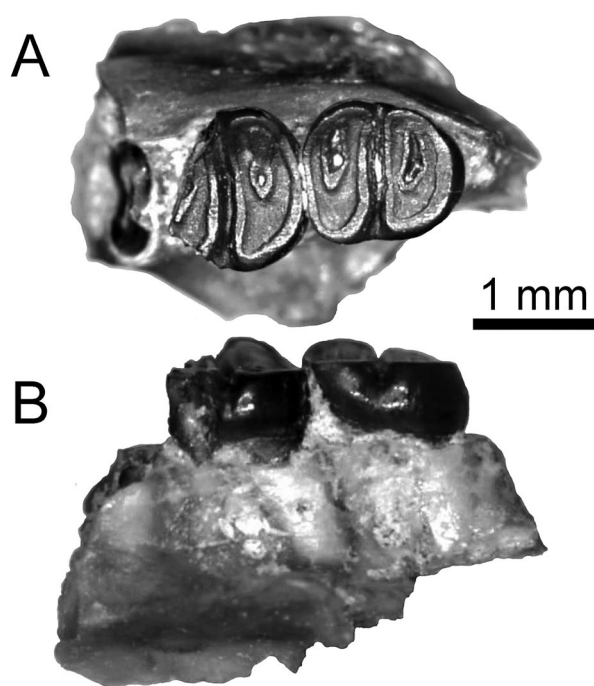


Fig. 13.—Left dentary fragment with m2 (partial) and m3 of *?Proaapeomys lulli* from the John Day Formation, Oregon, JODA 16002. **A**, occlusal view; **B**, lateral view. Scale bar equals 1 mm.

the molars in *P. condoni* differ from those of *Zophoaapeomys* Korth, 2007a, and *Apeomys* Fahlbusch, 1968, in being less lophate with less well-defined loops, and having the cusps more distinct. As in *Proaapeomys*, *Zophoaapeomys* also has incomplete loops, but the cusps of that taxon are less distinct and it is substantially smaller (Korth 2007a, 2008a). Additionally, the central valley in the lower m1 and m2 of *Zophoaapeomys* is blocked lingually by the metaconid and entoconid, while it is continuous in *Proaapeomys*. The loops formed in the molars of *Apeomys* are higher with deeper valleys and the cusps are not recognizable as part of the lophids. The anterior loop in *Apeomys* is oriented obliquely (anterobuccally) and the posterior loop extends for nearly the entire width of the tooth. In *P. condoni*, the anterior loop is narrower anteroposteriorly and transversely, and is not obliquely oriented. Both the posterior and anterior loops are predominantly situated on the lingual side of the tooth due to the presence of distinct, crescentic buccal cusps (protoconid, hypoconid). The p4 and m3 of the type of *P. condoni* retain an anteroposterior loph (ectolophid) that interrupts the central valley, which is not present in *Apeomys*.

The referred upper molar of *P. condoni* is distinct from that of *Zophoaapeomys* and *Apeomys*. The cusps observed in the molars of *P. condoni* and *Zophoaapeomys* are much more distinct than in *Apeomys*. The mesoloph of *P. condoni* runs buccally from the protocone, ends short of the paracone, and has a small posteriorly directed lophule

linking it to the metaloph. In *Zophoaapeomys*, the mesoloph links the hypocone to the paracone, a short “spur” runs posterobuccally from the protocone toward the mesoloph, and the metaloph and mesoloph unite at the hypocone. The mesoloph runs anterobuccally from the hypocone in *Apeomys*, linking the hypocone to the paracone in some specimens. In both *P. condoni* and *Apeomys*, the metaloph and posterior cingulum enclose a small basin.

***?Proaapeomys lulli* (Wood, 1936a), new combination**
(Fig. 13; Table 10)

Florentiamys lulli Wood, 1936a

Jimomys lulli (Wood) Wahlert, 1976

Type Specimen.—YPM 10573, partial dentary with heavily worn left m1–m2.

Referred Specimen.—JODA 16002, dentary fragment with m2(partial)–m3.

Horizon and Locality.—JDNM 8B, Hayes Haven, Grant County, OR, Unit K2, Turtle Cove Member, John Day Formation.

Age.—Late early Arikareean (late Oligocene, Ar2), between Biotite Tuff dated 27.14 ± 0.13 Ma and Tin Roof Tuff dated 25.9 ± 0.3 Ma (Albright et al. 2008).

Diagnosis.—Cheek teeth slightly more lophate and higher crowned than type species, *P. condoni*; central transverse valley continuous on m3.

Description.—The type specimen, YPM 10573, has been described and figured elsewhere (Wood 1936a; Wahlert 1976). Only one additional specimen has been referred to this species, containing m2 and m3 (Fig. 13). The molars in the referred specimen, JODA 16002, are worn, but not to the extent of those of the holotype. The m2 has a broken anterior margin, but it is evident that there are two distinct loops formed by the lophs of the tooth. These loops are larger than those of the holotype due to the earlier stage of wear. Little can be determined about the anterior loop on m2 due to breakage, but the posterior loop is limited to the lingual half of the tooth and tapers to a point at its lingual end. The m3 is slightly smaller than m2. Both loops are complete and limited to the lingual half of the occlusal surface. Both loops are oriented directly transversely and narrow, nearly meeting the edge of the tooth at its anterolingual end.

Discussion.—Wood (1936a) named *Florentiamys lulli* from the John Day beds of Oregon and referred it to a genus of geomyoid known elsewhere from the Arikareean of the northern Great Plains. Even though the holotype of *F. lulli* contained only two molars that were heavily worn, he noted the transverse valley and believed it was similar to the bilophodonty of geomyoids. Later, Wahlert (1976)

named a new genus of geomyoid from the Barstovian of the Great Plains, *Jimomys*, and questionably referred *F. lulli* to his new genus. Wahlert (1976) based his referral on a number of morphologies of the type of “*F.*” *lulli* that were distinct from *Florentiamys*. However, the size, crown height of the cheek teeth, and relative size of the p4 of “*Jimomys*” *lulli* are distinct from the type species of *Jimomys*, *J. labaughi*. The cheek teeth of *Jimomys* are mesodont in crown height (Wahlert 1976: fig. 1) and the molars of “*J.*” *lulli* are brachydont to submesodont. The measurements of *J. labaughi* are approximately 25–30% larger than “*J.*” *lulli* (Wahlert 1976: table 1). Although p4 is lacking in the type of “*J.*” *lulli*, the alveolus is only slightly longer than the molars (Table 9); in *Jimomys* p4 is nearly one and one-half times longer than m1. The occurrence of “*J.*” *lulli* (Arikareean) is also much earlier, approximately 15 million years, than the occurrence of *J. labaughi* (Barstovian). The little-worn specimens referred here to *P. condoni* are believed to belong to the same genus as the holotype of “*Florentiamys*” *lulli* based on similar size, crown height of the cheek teeth, and persistent transverse valley on the molars. The cheek teeth in *P. condoni* have a continuous transverse valley and two-looped morphology of the molars as in ?*P. lulli*, but differ in being lower-crowned with more distinct lingual cusps, displaying incomplete loops, and a complete ectolophid on m3. The differences between *P. condoni* and ?*P. lulli* appear to be due to increased lophodonty and crown height of the latter, which also occurs at a higher stratigraphic level. Due to the incompleteness of the record of ?*P. lulli* it cannot be referred to *Proapeomys* with confidence.

Apeomys Fahlbusch, 1968

Apeomys whistleri, new species
(Fig. 14, Table 11)

Type Specimen.—JODA 12662, right m1 or m2.

Referred Specimens.—JODA 12664, left p4; JODA 12665, left m1 or m2; JODA 12660, maxilla fragment with left P4 and alveolus for M1; JODA 12663, left P4; JODA 12659, left M1 or M2; JODA 12661, right maxilla fragment with M1 or M2.

Horizon and Locality.—JDNM 140, Campbell Ranch, Gilliam County, OR, Kimberly Member, John Day Formation.

Age.—Early late Arikareean (late Oligocene, Ar3), between Tin Roof Tuff dated 25.9 ± 0.3 Ma (Albright et al. 2008) and JD-BC-3 tuff dated 23.79 ± 0.18 Ma (Hunt and Stepleton 2004).

Diagnosis.—Larger than type species, *Apeomys tuerkheimae*, Fahlbusch, 1968; “spur” on metalophid lacking on lower molars (present in European species); central transverse valley on P4 complete, not interrupted by mesostyle.

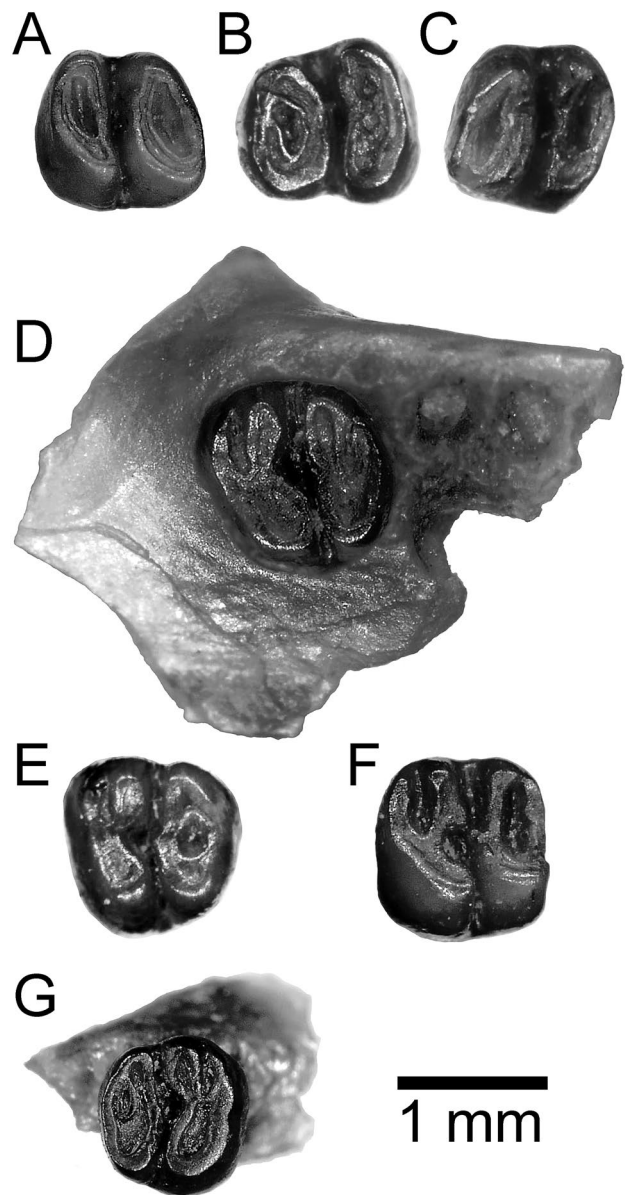


Fig. 14.—Specimens of *Apeomys whistleri*, new species, from the John Day Formation, Oregon. **A**, Holotype, JODA 12662, right m1 or m2; **B**, JODA 12664, left p4; **C**, JODA 12665, left m1 or m2; **D**, JODA 12660, maxilla fragment with left P4 and alveolus for M1; **E**, JODA 12663, left P4; **F**, JODA 12659, left M1 or M2; **G**, JODA 12661, right maxilla fragment with M1 or M2. Scale bar equals 1mm.

Etymology.—Patronym for David Whistler, who has contributed greatly to understanding of North America’s fossil rodents and first recognized the distinctness of this species.

Description.—The p4 and lower molars are mesodont in crown height and have the typical occlusal morphology of *Apeomys*, consisting of two transverse loops with a deep central transverse valley. The anterior loop is not as wide

TABLE 11. Comparative dental measurements (in mm) of *Apeomys whistleri* from the John Day Formation and *A. tuerkheimae* from the Oligocene of Germany (Fahlbusch 1968). Abbreviations: **L**, anteroposterior length; **W**, transverse width. Statistical abbreviations: **M**, mean; **SD**, standard deviation.

<i>Apeomys whistleri</i>		P4L	P4W	M1 or M2 L	M1 or M2W
	JODA 12660	1.21	1.28		
	JODA 12663	1.17	1.20		
	JODA 12659			1.14	1.10
	JODA 12661			1.00	1.24
		p4L	p4W	m1 or m2L	m1 or m2W
	JODA 12664	1.12	1.10		
	JODA 12662 (type)			1.22	1.10
	JODA 12665			1.05	1.10
<i>Apeomys tuerkheimae</i>		P4L	P4W	M1 or M2 L	M1 or M2W
	M			1.01	1.17
	SD			0.04	0.06
		p4L	p4W	m1 or m2L	m1 or m2W
	M	1.13	0.95	1.12	1.09
	SD	0.04	0.05	0.04	0.06

as the posterior, but is complete, outlining a deep oval basin. The posterior loop is complete, but the central basin is anteroposteriorly compressed, leaving only a small linear depression. The worn occlusal surfaces of the lower teeth are concave, as was noted by Fejfar et al. (1998).

The p4 (JODA 12664) displays two complete lophs, with irregularly shaped basins (Fig. 14B). In the anterior loop, the anterolophid and mesolophid are evident, with the anterolophid linking the protoconid to the metaconid, and narrowing near its fusion with the metaconid. The mesolophid runs transversely from the protoconid approximately halfway to the metaconid. Just labial to the entoconid, there is a small anteriorly directed projection from the anterior loph of the posterior loop.

On the lower molars (JODA 12662, 12665), the occlusal surfaces display few details (Figs. 14A, C). The labial cusps (protoconid, hypoconid) and lingual cusps (metaconid, entoconid) are readily apparent on the anterior and posterior loops. The anterior and posterior basins of the lower molars are diagonally inclined, slightly lingually. The small “spur” extending anteriorly from the posterior loph of the anterior loop that is present in European species (Engesser 1999: fig. 30.8) is completely lacking. There are three roots on the lower molars, two anterior and one posterior.

P4 is slightly smaller than the anterior molars (Figs. 14D–E). There is a narrow, deep central transverse valley that separates the protoloph and metaloph, which is continuous across the tooth. The anterior cingulum originates

from the anterior margin of the protoloph and meets with the paracone buccally to partially enclose a small basin, which is variable in size, based on the length of the anterior cingulum. The posterior cingulum runs the entire width of the tooth, meeting the posterior margin of the metacone, enclosing a second basin between it and the metaloph.

M1 or M2 is similar in morphology to P4 but nearly square in occlusal outline (Figs. 14F–G). The lingual cusps are crescentic. The anterior cingulum runs for approximately the buccal half of the tooth, partially enclosing a basin between it and the paracone and protoloph. The protoloph runs anterolingually from the paracone joining the lingual arm of the protocone at the base of the anterior cingulum, giving the protoloph a sharp angle at its center. The metaloph runs directly lingually from the metacone to the hypocone. On one specimen, JODA 12659, there is a short oblique loph that connects the protoloph to the metaloph across the central transverse valley. On the other upper molar (JODA 12661), the central valley is continuous across the tooth. As in P4, the posterior cingulum runs the entire width of the tooth completing a transverse loop from the metacone to the hypocone along with the metaloph.

Discussion.—*Apeomys whistleri* is referable to this otherwise Eurasian genus based on the occlusal morphology of the cheek teeth (consisting of two distinct loops) and the presence of three roots on the lower molars. Korth (2007a) recognized an apeomyine, *Zophoaapeomys*, from the Whitneyan

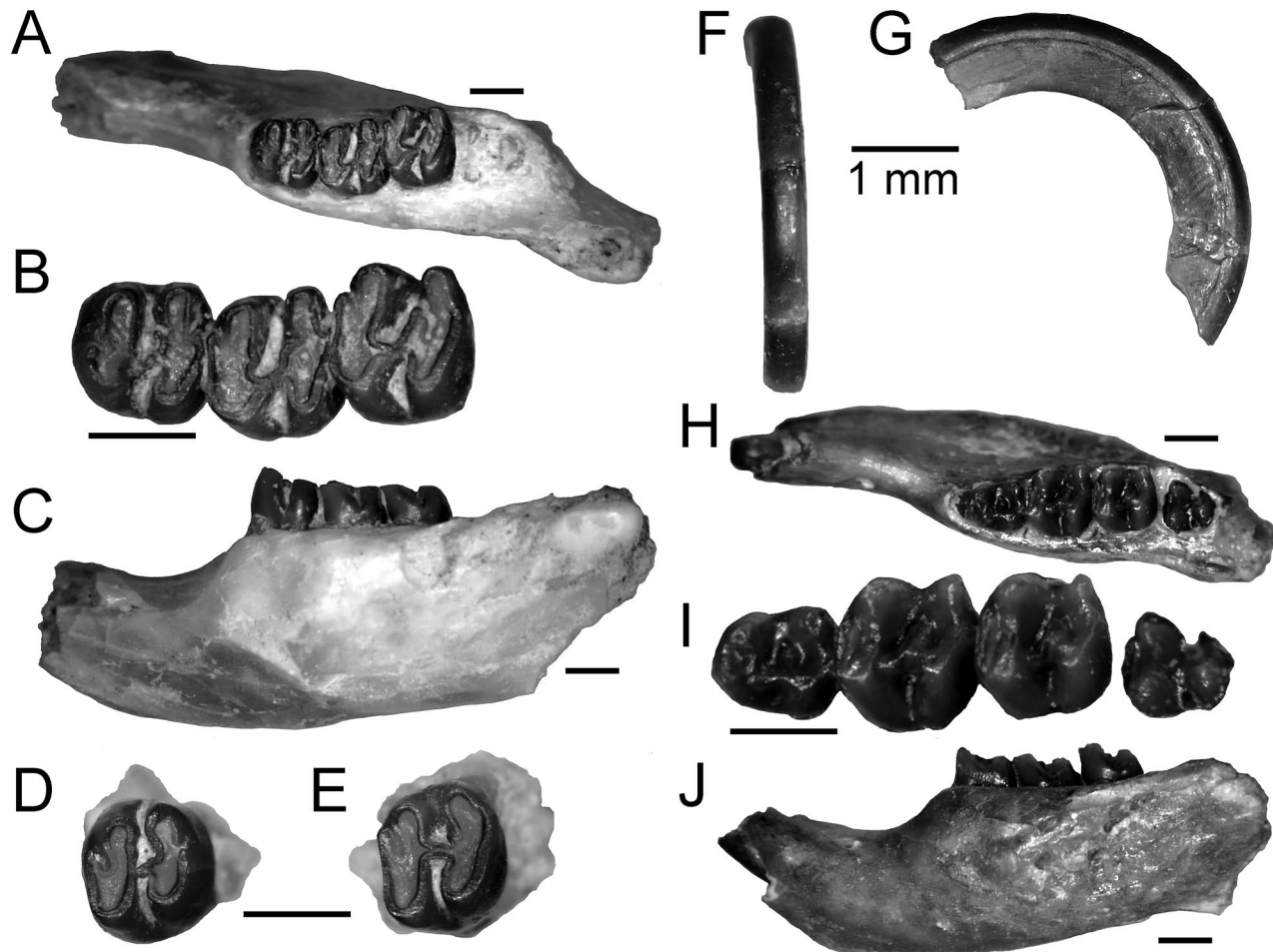


Fig. 15.—Specimens of *Neoadjidaumo arctozophus*, new species, from the John Day Formation, Oregon. A–E, Holotype, JODA 16005; A–C, left dentary with i1, p4 to m2; A, occlusal view; B, occlusal view (enlarged); C, lateral view; D, right P4; E, right M1 or M2; F–G, right I1; F, anterior view; G, lateral view; H–J, JODA 3615, right dentary with i1, dp4 to m2; H, occlusal view of dentary; I, dp4–m2; J, lateral view of dentary. Scale bars equal 1 mm. Scale bars adjacent to appropriate specimen.

and distinguished it from *Apeomys* by the presence of only two roots on the lower molars, more distinct cusps and lower crown-height. *Apeomys whistleri* agrees with the Eurasian species in all these features (see Fahlbusch 1968). However, *A. whistleri* differs from the European *A. tuerkheimae* in its larger size and lack of the “spur” on the metalophid of the lower molars of the latter (Fahlbusch 1968). Like *A. whistleri*, *Proapeomys* and *Zophoapeomys* also lack the “spur” in the lower molars seen in *A. tuerkheimae* (Korth 2007a).

The upper cheek teeth of *A. whistleri* are very similar to *A. tuerkheimae*. In the upper premolars and some lower molars (JODA 12661), the central transverse valley is continuous and separates the protoloph from the metaloph. As in *A. tuerkheimae*, the upper cheek teeth of *A. whistleri* have an enclosed basin between the metaloph and posterior cingulum, and partially enclosed basin between the anterior cingulum, paracone, and protoloph (Fahlbusch 1968).

Several large apeomyines have been described from the Miocene of Nevada, including the Hemingfordian *Megapeomys bobwilsoni* Morea and Korth, 2002, and the early Barstovian *Apeomyoides savagei* Smith et al., 2006. Whereas the occlusal morphology of *Megapeomys* and *Apeomyoides* is similar to *Apeomys*, these taxa are substantially larger (nearly twice as large) and the cheek teeth are higher crowned. Like *Apeomys*, *Apeomyoides* has three roots on the lower molars, while *Megapeomys* has four roots (Smith et al. 2006).

The occurrence of *A. whistleri* is roughly equivalent in age to that of *A. tuerkheimae*, which is known from MP30 and MN1a (Engesser 1999: fig. 30.17), and later than the reported occurrence of the morphologically more primitive *Zophoapeomys* from the Whitneyan and earliest Arikarean of South Dakota and Nebraska (Korth 2007a; Korth and Branciforte 2008) and *Proapeomys* from the early Arikarean of Oregon reported here. Given the presence of two

relatively primitive apeomyines in the early and middle Oligocene of North America, it seems likely that *Apeomys* evolved in North America and dispersed to Europe in the late Oligocene, as suggested by Engesser (1999) and Korth (2007a, 2008a). These records suggest that apeomyines may have originated in North America and later immigrated to Eurasia, possibly including dispersals of: 1) *Apeomys* to Europe in the late Oligocene; and 2) *Megapeomys* either originating in Eurasia and dispersing to North America in the early Miocene, or vice versa.

Tribe Eomyini Winge, 1887
Neoadjidaumo Korth, 2008a

***Neoadjidaumo arctozophus*, new species**
 (Fig. 15; Table 12)

Type Specimen.—JODA 16005, left dentary with p4–m2 with associated I1, right P4 and right M1 or M2.

Referred Specimen.—JODA 3615, right dentary with i1, dp4–m2.

Horizon and Locality.—JODA 16005 – JDNM 52, Logan Butte, Crook County, OR, lower Turtle Cove Member, John Day Formation; JODA 3615 – JDNM 9, Blue Basin, Grant County, OR, Unit D, Turtle Cove Member, John Day Formation.

Age.—Early early Arikareean (early Oligocene, Ar1), type specimen between unnamed tuff dated as 29.07 ± 0.13 Ma and “Upper Tuff” dated 28.86 ± 0.07 Ma (Bestland 1996), referred specimen between A-B Tuff dated 29.75 ± 0.02 Ma and Blue Basin Tuff dated 28.8 Ma (Albright et al. 2008).

Diagnosis.—Larger than the type species; more lophate cheek teeth (deeper valleys); short anterior cingulum on P4 (absent in type species); mesoloph on upper molars almost completely lost; mesostyle present on upper molar.

Etymology.—Greek, *arktos*, north; and *zophos*, west.

Description.—The dentary is slender, typical of eomyids (Figs. 15C, J). The masseteric scar extends anteriorly to below p4 in a U-shape. The ascending ramus originates lateral to m2. The diastema is shallow and nearly as long as the tooth row. The mental foramen is dorsal to the dorso-ventral midline of the dentary, just anterior to the midpoint of the diastema.

The cheek teeth are lophate and mesodont in height. The holotype (JODA 16005) is moderately worn but the molars on the referred specimen are almost entirely unworn. The p4–m2 are wider than long, m2 being the widest. The p4 is narrower anteriorly than posteriorly (Fig. 15B). The metalophid is continuous across the anterior margin of the tooth with the protoconid and metaconid distinguishable only by the presence of a small basin anteriorly. The ectolophid is

short and directed posterolingually across the central valley of the tooth. Both of the hypolophid cusps are anteroposteriorly compressed. The hypolophid is continuous from the entoconid to the hypoconid forming a broad transverse loph. There is a minute “spur” (mesolophid) extending lingually from the center of the hypolophid into the central valley. The posterior cingulid is very short, arising just lingual to the center of the posterior edge of the hypolophid.

The dp4 on the referred specimen (JODA 3615) is smaller and lower-crowned than p4 of the holotype (Figs. 15I–J). It is proportioned as in p4 (narrower anteriorly than posteriorly). A small trigonid is enclosed anteriorly by the anterior cingulid, and posteriorly by metalophid II. The ectolophid is complete for the length of the tooth and a short mesolophid extends into the central basin, ending well short of the lingual margin. The hypolophid is continuous along the posterior margin of the tooth from the hypoconid to the entoconid. There is no distinct posterior cingulid.

The m1 and m2 are similar in occlusal morphology. On the holotype (worn), the anterior cingulid is completely fused with the metalophid and only recognizable at its extreme lingual end (Figs. 15B, I). The anterior cingulid on the referred specimen is attached to the protoconid at its anterobuccal edge and extends lingually for most of the anterior width of the tooth. On the holotype, the ectolophid and hypolophid on m1 are nearly identical to that of p4. The small “spur” (mesolophid) is almost completely fused to the hypolophid, enclosing a small island within the loph. On the m2, the ectolophid is slightly more lingually located and a short mesolophid is recognizable, and closely appressed to the metalophid. It appears likely that after additional wear, the mesolophid will fuse with the hypolophid. On the unworn referred specimen (JODA 3615), a short mesolophid is present and directed posterolingually in both the m1 and m2. In the m1 of the holotype, the hypolophid is a broad loph continuous across the tooth and there is a short posterior cingulid, as in the p4; however, there is no indication of a posterior cingulid on the m2. On the unworn specimen, no posterior cingulid is observable on any of the lower cheek teeth.

P4 is slightly wider than long; the protoloph and metaloph are broad lophs that are oriented transversely, defining a central transverse valley (Fig. 15D). The anterior cingulum is a very short loph that arises from the protoloph just lingual to the paracone and extends buccally for a short distance. The endoloph is very short, near the center of the tooth, and oriented slightly anterobuccally. There is a minute projection from the posterior surface of the protoloph just buccal to its connection with the endoloph, which may be a remnant of the mesoloph. The posterior cingulum arises from the hypocone and extends along the posterior margin of the tooth for a short distance, ending well short of the metacone, isolating a small oval valley between it and the metaloph.

The only upper molar is more worn than the P4 (Fig. 15E). As in the lower molars, the anterior cingulum is

TABLE 12. Dental measurements (in mm) of *Neoadjidaumo arctozophus* from the John Day Formation.
Abbreviations: **L**, anteroposterior length; **W**, transverse width.
*, dp4-m3 length.

	I1L	I1W	P4L	P4W	M1L	M1W					
JODA 16005	1.64	.95	1.24	1.43	1.18	1.47					
	i1L	i1W	dp4L	dp4W	p4L	p4W	m1L	m1W	m2L	m2W	p4-m3
JODA 16005					1.24	1.39	1.14	1.39	1.24	1.38	5.74
JODA 3615	1.20	.64	1.06	0.94			1.11	1.28	1.12	1.18	4.67*

almost completely fused with the protoloph, forming a broad loph. The endoloph is in the center of the tooth, and oriented directly posteriorly, fusing with the center of the broad metaloph. The metaloph is slightly concave posteriorly, but no posterior cingulum is recognizable. A minute “spur” extending from the posterior surface of the protoloph just buccal to its connection with the endoloph may be a remnant of the mesoloph. A distinct mesostyle is present at the buccal end of the central transverse valley. The posterior cingulum extends buccally from the hypocone to along the posterior margin of the tooth and ends just short of the metacone, with a narrow valley between it and the metaloph.

The I1 of the holotype is nearly twice as deep as it is wide (transversely: Figs. 15F–G). It is roughly triangular in cross-section, with flat internal and external surfaces, and a convex anterior surface. The enamel runs from the anterointernal margin of the tooth and extends approximately one-third of the way down the external surface. The lower incisor of the referred specimen has a shape generally similar to the upper incisor of the holotype, though the anterior face is somewhat flattened.

Discussion.—*Neoadjidaumo arctozophus* differs from the type species *N. hemedapus* Korth and Branciforte, 2008, in its substantially larger size (Table 12), and greater crown-height and lophodonty of the cheek teeth. The upper molars of *N. hemedapus* retain a minute mesoloph that is greatly reduced in the upper molar of *N. arctozophus*. Additionally, the P4 of *N. arctozophus* has a short anterior cingulum that is lacking on P4 specimens of the type species.

As noted by Korth (2008a), the cheek teeth of the European *Ritteneria* Schaub, in Stehlin and Schaub, 1951, and derived species of *Rhodanomys* Depéret and Douxami, 1902, are superficially similar to those of *Neoadjidaumo*, but there are some distinct differences. Significantly, the cheek teeth of both European genera are brachydont, not mesodont as in *Neoadjidaumo*. In *Neoadjidaumo*, the mesoloph is reduced and a small mesostyle may be present, the endoloph is complete, and the anterior and posterior cingula are greatly reduced but remain recognizable. The mesoloph on the upper molars of the European genera are

often long, extending obliquely across the tooth, or lost completely but retaining a large mesocone. The endoloph is never complete on the upper cheek teeth of *Ritteneria* and derived species of *Rhodanomys*. The evolutionary sequence from *Eomys* to *Rhodanomys* to *Ritteneria* is well documented in the European record (Engesser 1999). Given these differences, it is very unlikely that *Neoadjidaumo* is part of this lineage.

The occlusal morphology of the unworn molars on the referred specimen, JODA 3615, most closely approach those of the Orellan genus *Metadjidaumo* (Setoguchi 1978; Korth 1981) in crown height, the buccal attachment of the anterior cingulid, and reduction or loss of the posterior cingulid. It is not unlikely that *Neoadjidaumo* was derived from a species of *Metadjidaumo*.

Leptodontomys Shotwell, 1956

Leptodontomys sp. (Fig. 16)

Referred Specimens.—JODA 12699, partial right dentary with m1–m2(partial).

Horizon and Locality.—JDNM 140, Campbell Ranch, Gilliam County, OR, Kimberly Member, John Day Formation.

Age.— Early late Arikareean (late Oligocene, Ar3), between Tin Roof Tuff dated 25.9 ± 0.3 Ma (Albright et al. 2008) and JD-BC-3 tuff dated 23.79 ± 0.18 Ma (Hunt and Stepleton 2004).

Measurements.—JODA 12699: m1, length = 0.79 mm, width = 0.75 mm; m2, width = 0.85 mm.

Discussion.—The morphology of the specimens referred here to *Leptodontomys* differs little from those described elsewhere for *L. (=Adjidaumo) douglassi* (Burke 1934; Korth and Bailey 1992; Korth 2008a [referred to *Pseudoadjidaumo* by Flynn 2008a]). The anterior cingulid extends nearly the full width of the m1 and m2, including both lingual and buccal extensions. The anterior cingulid of the m1

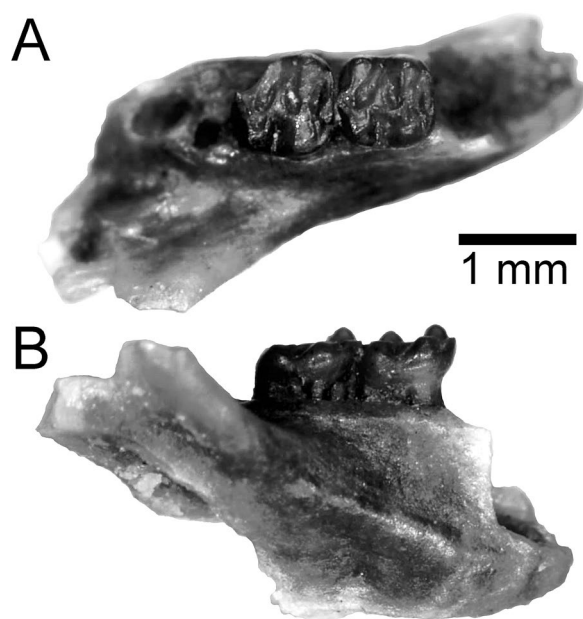


Fig. 16.—*Leptodontomys* sp. from the John Day Formation, Oregon, JODA 12699, right dentary with m1 to m2. **A**, occlusal view; **B**, lateral view. Scale bar equals 1 mm.

of JODA 12699 is not connected to the metalophid, though they would likely be connected at a later stage of wear. In the m2 of JODA 12699 (Fig. 16), the anterior cingulid is weakly joined to the anterior arm of the protoconid and the anterior portion of the metaconid. The posterior cingulid is restricted to the central portion of the tooth, rather than extended lingually adjacent to the entoconid as reported for *L. douglassi* (Korth and Bailey 1992). The lower molars of JODA 12699 are smaller than any recorded for *L. douglassi* (Korth 2008a: table 1; Fremd and Whistler 2009). Because of these differences in morphology and size, the JODA specimen cannot be definitely referred to *L. douglassi*. Korth (2008a) cited a single specimen with upper cheek teeth of *Leptodontomys* sp. from the Arikareean of Nebraska that was similarly smaller than *L. douglassi*. It is possible that *Leptodontomys* sp. from the John Day is the same as the smaller species from Nebraska, but this cannot be verified. The new occurrence of *Leptodontomys* in the late Arikareean indicates a long persistence of the genus in Oregon, as *L. quartzii* Shotwell, 1967, is known from the Barstovian and *L. oregonensis* Shotwell, 1956, is known from the Hemphillian.

Family Heteromyidae Gray, 1868
Subfamily Mioheteromyinae Korth, 1997

Trogomys Reeder, 1960

Type Species.—*Trogomys rupinimenthae* Reeder, 1960.

Referred Species.—*T. ironcloudi* (Macdonald, 1970); and *T. oregonensis*, new species.

Range.—Early Arikareean (late Oligocene) of Oregon and South Dakota; early Hemingfordian of southern California.

Emended Diagnosis.—Small mioheteromyine heteromyid with low-crowned cheek teeth (index for m1 <0.30); trigonid basin of p4 closed anteriorly by converging lophules from metaconid and protostylid; union of metalophid and hypolophid on p4 via centrally sloping posterior sides of protostylid and metaconid, enclosing the trigonid basin posteriorly.

Discussion.—Reeder (1960) named *Trogomys* from the late Arikareean or early Hemingfordian of southern California, and referred it to the Perognathinae based on the lower crown-height of the cheek teeth and central union of the lophs on the lower premolar. *Trogomys* can be distinguished from *Perognathus* Wied-Neuwied, 1839, by the lack of a grooved upper incisor and the morphology of p4. Although *Perognathus* (and the Perognathinae) have been traditionally defined as having a central union of the lophs on p4 (Wood 1935a), this union is not always present in the most primitive members of the Perognathinae (Korth 2007b). The central union of the lophs in *Perognathus* is due to an anteroposteriorly oriented lophule connecting the transverse lophs at their center, a much different morphology than in *Trogomys* where a minute central trigonid basin is formed. Korth (1997) erected the Mioheteromyinae, and included *Trogomys* in this new subfamily based on the morphology of p4 and size of incisive foramina of the skull (Korth 1997: table 5).

The anteriorly and posteriorly closed trigonid basin in the p4 of *Trogomys* is also present in the late Arikareean *Proheteromys ironcloudi* Macdonald, 1970, from South Dakota. The small size and morphology of p4 of the latter make it referable to *Trogomys* rather than *Proheteromys*. A single specimen from the John Day Formation (JODA 4534) is similar in size and crown height of the cheek teeth, and has the enclosed trigonid basin of *Trogomys*, making it referable to the latter genus. Whistler (1983) referred a few specimens from the early Hemingfordian of California to *Trogomys* sp., cf. *T. rupinimenthae*. However, these specimens are much too high-crowned to belong to this genus (Whistler 1984: figs. 13–16).

***Trogomys oregonensis*, new species**
(Fig. 17; Table 13)

Type and Only Specimen.—JODA 4534, left dentary with p4–m3.

Horizon and Locality.—JDNM 8B, Hayes Haven, Grant County, OR, Unit K2, Turtle Cove Member, John Day Formation.

Age.—Late early Arikareean (late Oligocene, Ar2), be-

tween Biotite Tuff dated 27.14 ± 0.13 Ma and Tin Roof Tuff dated 25.9 ± 0.3 Ma (Albright et al. 2008).

Diagnosis.—Similar in size with type species, *T. rupinimenthae*, larger than *T. ironcloudi*; anteroconid on p4 as in *T. ironcloudi* (absent in type species); hypolophid on p4 posteriorly concave and V-shaped (straight in type species); m3 subequal in length and width (shorter than wide in other species).

Etymology.—Latin suffix, *-ensis*, locality; referring to Oregon.

Description.—The cheek teeth of JODA 4534 are in a late stage of wear, so most of the individual cusps cannot be discerned on the molars, but the shape of the lophs and central valley are preserved (Fig. 17). The p4 is the smallest of the cheek teeth, and slightly wider than long. The anterior width is narrower than the posterior width. The protostylid is slightly larger than the metaconid. These cusps are united both posteriorly and anteriorly. Anteriorly, there is a minute central anteroconid that is continuous with both trigonid cusps on an anteriorly bowed anterior cingulid. Posteriorly, both cusps have lophules that slope toward the center of the tooth, uniting with the hypolophid at its center. The outline of the hypoconid and entoconid are recognizable. They are united centrally, forming a posteriorly pointing V-shaped hypolophid. There is no indication of a hypoconulid or hypostylid.

The m1 and m2 are bilophate with a persistent central transverse valley and buccal stylids. Only on m1 is the protostylid identifiable. The metalophid and hypolophid of the m3 are fused centrally, similar to the p4; with additional wear the m2 would have displayed a similar fusion. The molars decrease in size posteriorly. The m1 and m2 are wider than long, and m3 is subequal in length and width. Little else is recognizable on the cheek teeth.

The dentary is slender, with a shallow diastema, and a low ridge marking the masseteric fossa extends anteriorly to below the p4. No other features of the dentary are present due to breakage. The lower incisor is gently curved anteriorly and is relatively narrow (i1 width = 0.86mm).

Discussion.—*Trogomys oregonensis* is referable to this genus based on the lower crown-height of the molars (less than *Proheteromys* Wood, 1932, and *Mookomys* Wood, 1931) and the distinctive morphology of p4 (enclosed trigonid basin). It is distinct from the type species *T. rupinimenthae*, in having a p4 with a distinct anteroconid and having a posteriorly pointing V-shaped hypolophid (straight in *T. rupinimenthae*). It differs from both the type species of *Trogomys* and *T. ironcloudi* in having an m3 equal in width and length. In both the other species, the m3, like the anterior molars, is wider than long.

The occurrence of *T. oregonensis* is from the late early Arikareean (Ar2), while *T. rupinimenthae* does not appear until Ar3 and persists into the Hemingfordian. *Trogomys ironcloudi* is known from Ar1 and Ar2 of Nebraska and Sas-

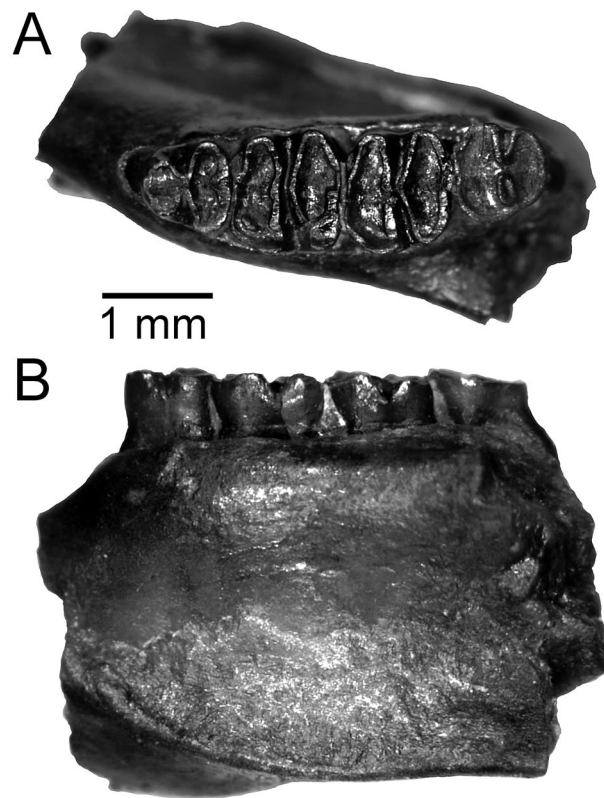


Fig. 17.—Holotype of *Trogomys oregonensis*, new species, from the John Day Formation, Oregon, JODA 4534, left dentary with p4 to m3. A, occlusal view; B, lateral view. Scale bar equals 1 mm.

katchewan (Macdonald 1970; Flynn et al. 2008). Whistler and Lander (2003) also indicated that *Trogomys* occurred in the late Arikareean lower Orange County Sespe and Vaqueros formations of California, which were temporally correlated with the late Arikareean (Ar3) “Kimberly fauna” of Oregon.

Mookomys Wood, 1931

Mookomys sp.
(Fig. 18)

Referred Specimen.—JODA 7900, partial maxilla with right P4 and partial M1, left distal femur.

Horizon and Locality.—JDNM 186, Wheeler County, OR, Haystack Valley Member, John Day Formation

Age.—Early late Arikareean (late Oligocene, Ar3), between JD-BC-3 tuff dated 23.79 ± 0.18 Ma (Hunt and Stepleton 2004) and Across the River Tuff dated 22.6 ± 0.13 Ma (Albright et al. 2008).

TABLE 13. Comparative dental measurements (in mm) of the holotypes of species of *Trogomys*. Abbreviations: **L**, anteroposterior length; **W**, transverse width; **ht/W**, crown-height index = buccal height/transverse width of tooth.

	p4L	p4W	m1L	m1W	ht/W	m2L	m2W	ht/W	m3L	m3W	p4-m3
<i>T. oregonensis</i>											
JODA 4534	0.85	0.92	0.88	1.18	0.29	0.98	1.10	0.35	0.92	0.93	4.06
<i>T. rupinimenthae</i>											
LACM (CIT) 5186	0.82	0.86	0.98	1.15	0.26	0.83	1.15	0.30	0.77	0.88	3.62
<i>T. ironcloudi</i>											
SDSM 634	0.75	0.8	0.85	1.1	0.27	0.85	1.10	—	0.75	0.95	3.20

Measurements.—P4, length = 1.05 mm, width = 1.12 mm; M1, length, = 0.75 mm, width = 1.19 mm.

Description.—The preserved cheek teeth are higher crowned than in specimens of *Trogomys* and *Proheteromys* from John Day (Figs. 18A–B). The P4 is equal in width and length, and slightly narrower than the M1. The protoloph of P4 consists of only a central, slightly medio-laterally broadened conical protocone. The metaloph has the typical three cusps, metacone, hypocone, and hypostyle. The hypocone is the largest and central. Both the other cusps are smaller and slightly more anteriorly placed, making the metaloph slightly convex posteriorly. There is a minute posterior cingulum along the posterior border of the tooth between the hypocone and metacone.

Only the protoloph of M1 is preserved. It consists of three cusps, paracone, protocone, and protostyle, with the protocone being the largest. The protoloph is slightly bowed posteriorly due to the protostyle and paracone being slightly more anterior than the protocone. There is a thin, low anterior cingulum running buccally from the protostyle anterior to the central protocone, uniting buccally with the base of the paracone.

Found associated with the maxilla was the distal end of a left femur (Figs. 18C–E). The diaphysis is straight and round (anteroposterior diameter 1.34 mm, mid-length diameter 1.38 mm). The patellar groove is narrow, elongate, and deep, with high trochlear ridges. The medial and lateral condyles are similar in size, and both condyles are much deeper anteroposteriorly (depth of lateral condyle = 3.54 mm) than they are wide (distal breadth of femur = 2.58 mm).

Discussion.—JODA 7900 is referable to a heteromyid, but differs from the other heteromyids from the John Day in being smaller and having higher-crowned cheek teeth. It most closely resembles *Mookomys* from the Hemingfordian or early Barstovian of Montana (Wood 1931, 1935a; Sutton and Korth 1995) based on crown height. Korth (1997: table 3) demonstrated that *Mookomys* was meso-

dont in crown height rather than brachydont, thus eliminating a number of species referred elsewhere to this genus. Also, the anterior cingulum on M1 is similar to that of *M. thrinax* Sutton and Korth, 1995 (Sutton and Korth 1995: fig. 6A). The John Day specimen differs from the upper cheek teeth of *M. thrinax* in being smaller and having P4 narrower than M1 (P4 equal to M1 width in *M. thrinax*). The cheek teeth of JODA 7900 are similar in size to cheek teeth of *M. altifluminis* Wood, 1931 (Wood 1935a: table II), making it possible that the John Day specimen is referable to this species. Unfortunately, *M. altifluminis* is only known from lower cheek teeth and an upper incisor (Wood 1931; Korth 1997), whereas JODA 7900 consists of a maxilla with upper cheek teeth, making direct comparisons impossible.

The distal femur associated with the maxilla has morphology consistent with that of other heteromyids, and shows features that indicate saltatory locomotion. The high and deep patellar groove with high trochlear ridges indicates movement constrained to a parasagittal plane with little mediolateral motion; this is similar to what is seen in many cursorial and saltatory mammals (Hildebrand 1995; Argot 2002; Fostowicz-Frelik 2007; Salton and Sargis 2009). The high trochlear ridges function to prevent dislocation of the quadriceps tendon from the patellar groove (Anemone 1993). Similarly, the deep medial and lateral condyles indicate saltatory adaptations of this species, as this morphology increases the mechanical advantage of the quadriceps femoris in extension of the knee (Anemone 1993; Anemone and Covert 2000). The medial and lateral condyles are similar in size, suggesting symmetrical loads were applied to the femur during locomotion (Argot 2002), as would be expected from parasagittal limb movement characteristic of saltatory locomotion.

The John Day occurrence of *Mookomys* is from the late Arikareean, just slightly older than the occurrence of the type species, *M. altifluminis* from the Hemingfordian of Montana. A number of other late Arikareean records of *Mookomys* have been reported, though none have been assigned to a species (Lindsay and Tessman 1974; Rasmus-

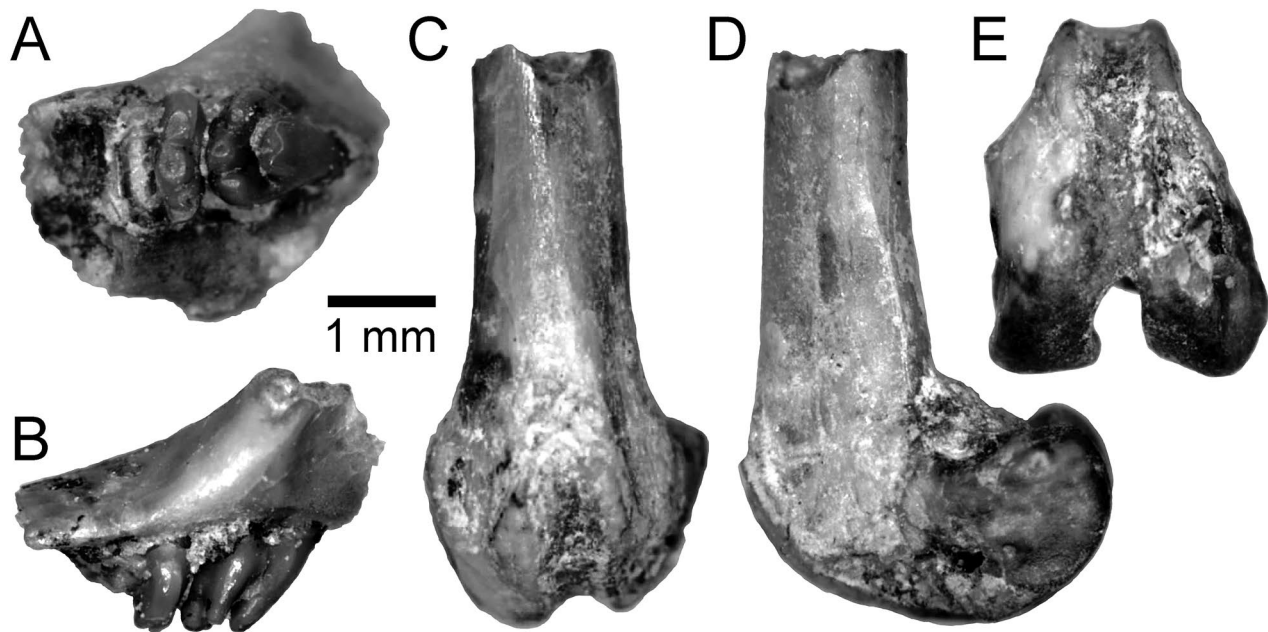


Fig. 18.—Specimens of *Mookomys* sp., JODA 7900, from the John Day Formation, Oregon. **A–B**, right maxilla with P4 and partial M1; **A**, occlusal view; **B**, lateral view; **C–E**, distal femur; **C** anterior view; **D** lateral view; **E**, distal view. Scale bar equals 1 mm.

sen 1989; Bailey 2004; Flynn et al. 2008).

Proheteromys Wood, 1932

Discussion.—*Proheteromys* has long been used as a waste basket genus for early species of heteromyids (Korth 1997). In the most recent review of the geomorph rodents, Flynn et al. (2008) listed 14 different species of *Proheteromys* ranging in age from the Whitneyan to the Barstovian. Of these, four species have been referred to other genera and four of the species previously referred to *Proheteromys* have cheek teeth that are much larger, more brachydont, and more bunodont than the type species of the genus, *P. floridanus* Wood, 1932, and may likely represent a genus of geomyoid or florentiamyid (Table 14). Korth (1997) also suggested that two of the species described from the Arikareean of South Dakota, *P. gremmelsi* (Macdonald, 1963), and *P. bumpi* (Macdonald, 1963), were likely synonyms. Green (2002) suggested that *P. sulculus* Wilson, 1960, was referable to *Mookomys* because of the grooved upper incisor. This allocation was followed by Flynn (2008a). However, the complexity of p4 and distinct morphology of the groove on I1 of *P. sulculus* are distinct from any species of *Mookomys* (Wilson 1960; Korth 1997), so the species should be retained in *Proheteromys*. If all of these referrals are followed, the number of species is limited to seven, known from the Arikareean and Hemingfordian only.

Wood (1932) originally referred *Proheteromys* to the subfamily Heteromyinae. This was followed by most later authors (Simpson 1945; Lindsay 1972; Korth 1994; McKenna and Bell 1997). Wahlert (1993) listed the genus under the heading “Geomyoidea or Heteromyidae, *incertae sedis*.” Korth (1997) suggested that it was questionably referable to the subfamily Mioheteromyinae. Most recently, Flynn et al. (2008) listed the genus under “Basal Heteromyids.” With the description of the skull of *Proheteromys latidens* (below), it is evident that it has the distinctive cranial features of the Mioheteromyinae (Korth 1997) and should be referred to this subfamily.

Proheteromys thorpei Wood, 1935b

(Fig. 19; Tables 15–16)

Type Specimen.—YPM 10571, partial dentary with left incisor and p4–m1.

Referred Specimens.—UWBM 73420, partial dentary with right p4–m3; JODA 1004, partial dentary with right m1–m2; JODA 12657, 16001, right m1.

Horizon and Locality.—UWBM 73420 – Picture Gorge 6 (V6662, Stubblefield 6), Grant County, OR, unknown horizon, John Day Formation; JODA 1004 – JDNM 8, Sheep Rock, Grant County, OR, upper Turtle Cove Member, John Day Formation; JODA 16001 – JDNM 8B, Hayes Haven, Grant County, OR, Unit K2, Turtle Cove Member, John Day Formation; 12657 – JDNM 140, Campbell

TABLE 14. Previously described species referred to *Proheteromys* referred to other genera or suggested as representing a *florentiamyid*.

Species	Generic allocation
<i>P. nebraskensis</i> Wood, 1937	<i>Kirkomys</i> (Korth and Branciforte 2008)
<i>P. fedti</i> Macdonald, 1963	<i>Proharrymys</i> (Korth and Branciforte 2008)
<i>P. parvus</i> (Troxell, 1923)	<i>Kirkomys</i> (Korth 2008c)
<i>P. ironcloudi</i> Macdonald, 1970	<i>Trogomys</i> this paper
<i>P. magnus</i> Wood, 1932	? <i>florentiamyid</i> (Korth 1997)
<i>P. maximus</i> James, 1963	? <i>florentiamyid</i> (Korth 1997)
<i>P. savinensis</i> Albright, 1996	? <i>florentiamyid</i> (Korth 1997)
<i>P. toledoensis</i> Albright, 1996	? <i>florentiamyid</i> (Korth 1997)

Ranch, Gilliam County, OR, Kimberly Member, John Day Formation.

Age.—Late early Arikareean through early late Arikareean (late Oligocene, Ar2 – Ar3), between Biotite Tuff dated 27.14 ± 0.13 Ma and JD-BC-3 tuff dated 23.79 ± 0.18 Ma (Hunt and Stepleton 2004).

Emended Diagnosis.—Intermediate sized, smaller than other Arikareean species and larger than Hemingfordian species; p4 four-cusped; p4 protostylid at anterobuccal corner of the tooth and markedly smaller than metaconid; crown height of lower molars greater than all other species except the Hemingfordian *P. floridanus* and *P. matthewi* Wood, 1935b (mean ht/W index of m1 = 0.39).

Description.—The nearly complete referred dentary, UWBM 73420, is the first specimen allocated to this species that contains all the lower cheek teeth (Figs. 19A–B). The p4 is smaller than the molars and nearly triangular in occlusal outline, narrower anteriorly. The protostylid is minute at the anterobuccal corner of the tooth. The adjacent metaconid is much larger and tapers posteriorly toward the center of the tooth. Anterior and slightly lingual to the metaconid is a minute cuspule. The entoconid and hypoconid are widely separated and oval in outline. Along the posterior edge of the tooth between the hypoconid and entoconid is a small hypoconulid. There are no buccal stylids present.

The m1 and m2 are typical of heteromyids: bilophate with three cusps in each loph, the buccal styler cusps being the smallest. There is an anterior cingulid on the anterobuccal corner of the tooth connecting the protoconid to the protostylid; this anterior cingulid is reduced in m2. The m1 is slightly longer, but narrower than m2. The m3 is the smallest cheek tooth. The m3 protolophid is similar to the anterior molars (but smaller), and the hypolophid has only two cusps, lacking the hypostylid.

The dentary of *P. thorpei* is slender, and in UWBM 73420 there is a deeper diastema than is observed in most other members of the genus (Figs. 19B–C). The masseteric fossa is marked by a low ridge that runs anteriorly from below the m3 and extends anterior to the p4. The ascending

ramus is broken, but slopes posteriorly upward beginning at the m3.

Discussion.—The four specimens referred here to *P. thorpei* are done so based on size, morphology of p4, and crown height of m1 (Table 16). UWBM 73420 contains all of the cheek teeth. Previously only p4 and m1 had been known (Wood 1935b). The p4 of UWBM 73420 differs slightly from that of the holotype. It has the greatly reduced protostylid as in the holotype, but is shorter and has an accessory cuspule on the anterior slope of the metaconid. These differences are viewed here as representing part of an expected amount of variation within a population. The crown height of UWBM 73420 is also very similar to that of the holotype, and higher than most other species of *Proheteromys* (Tables 15–16). The isolated m1s (JODA 12657, 16001) are referred to this species based on their size and morphological similarity to the holotype of the species and UWBM 73420. The second dentary, JODA 1004, can only be referred to the *P. thorpei* based on size, as the p4 is lacking and the m1 and m2 are too worn to measure their crown heights.

The minute protostylid on p4 and the relatively high crowns of the lower molars are the most unique characters of *P. thorpei* and separate it from the other species from the John Day Formation.

***Proheteromys latidens*, new species**
(Figs. 20–21; Tables 15, 17–18)

Holotype.—UCMP 150688, nearly complete skull and associated mandible with complete dentition, partial postcranial skeleton.

Referred Material.—UCMP 82276, partial skull with left P4–M3 and right P4–M1; UCMP 82335, partial dentary with right m1; JODA 12656, 12658, 12697, m1 or m2; JODA 7989, 12651, 12652, P4; JODA 12653, 12654, 12655, M1 or M2.

Horizon and Locality.—UCMP 82276, 82335, 150688

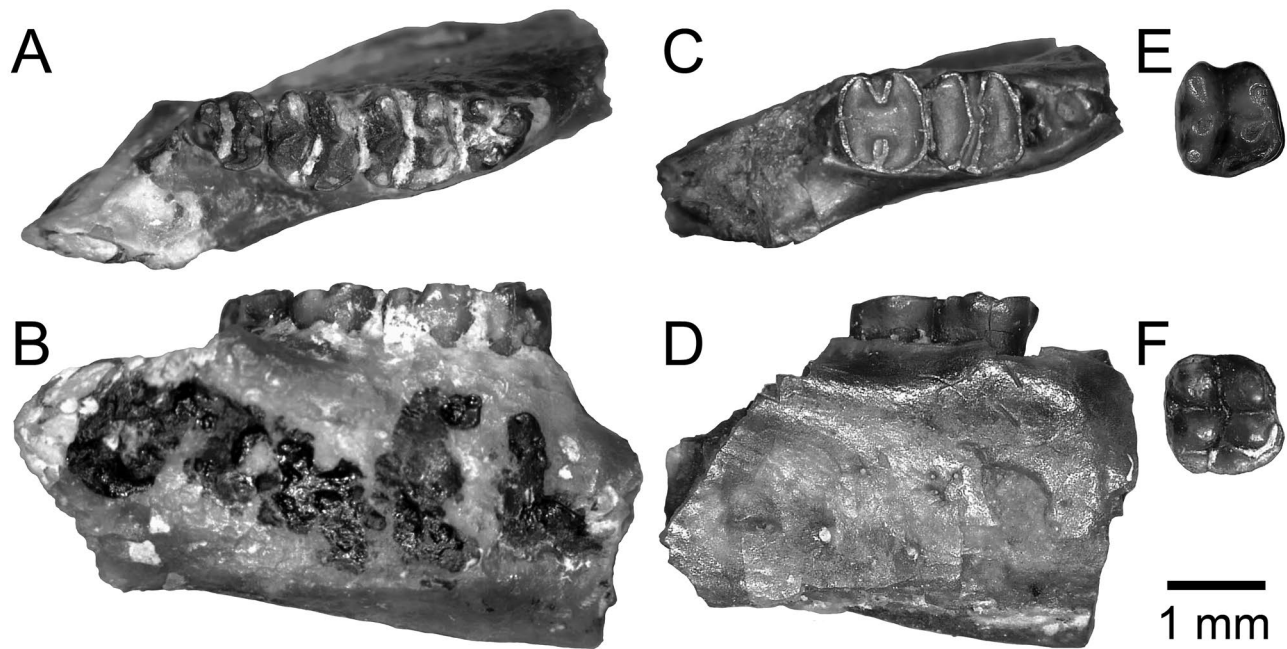


Fig. 19.—Specimens of *Proheteromys thorpei* from the John Day Formation, Oregon. **A–B**, UWBM 73420, right dentary with p4 to m3; **A**, occlusal view; **B**, lateral view; **C–D**, JODA 1004, right dentary with m1 and m2: **C**, occlusal view; **D**, lateral view; **E**, JODA 12657, right m1; **F**, JODA 16001, right m1. Scale bar equals 1 mm.

– V6600, Rudio Creek 4, Kimberly Member, John Day Formation; all JODA specimens – JDNM 140, Campbell Ranch, Gilliam County, OR, Kimberly Member, John Day Formation.

Age.—Early late Arikareean (late Oligocene, Ar3), between Tin Roof Tuff dated 25.9 ± 0.3 Ma (Albright et al. 2008) and JD-BC-3 tuff dated 23.79 ± 0.18 Ma (Hunt and Stepleton 2004).

Diagnosis.—Large size for *Proheteromys*; cheek teeth relatively high-crowned (mean crown-height index = 0.38); molars proportionally wider compared to length than other species (mean L/W = 0.76); metaconid and protostylid of p4 similar in size and fused to one another near their centers, metaconid fuses posteriorly with hypolophid lingual to tooth center producing a small central valley that is open buccally.

Etymology.—Latin, *latus*, wide; and *dens*, tooth.

Description.—The skull of *P. latidens* is larger than that of *Bursagnathus*, new genus (Table 17). In overall morphology, it is similar to other mioheteromyines such as *Mioheteromys* Korth, 1997 (Figs. 20A–E). In overall shape, the skull is low and wide, typical of mioheteromyines. Dorsally, the rostrum is narrow and broadens only slightly posteriorly. The nasals end on the skull roof near the anterior margin of the orbits, and do not extend as far posteriorly as the premaxillaries, as is common in other heteromyids.

The skull roof is flat and low. There is no rim or lip along the dorsal margin of the orbit as in perognathines. Much of the neurocranium is broken away, so little can be determined. However, on the left side, a low ridge is present along the parietal marking the attachment of the temporalis muscle. There is also a small protuberance of the squamosal anterior to the glenoid fossa, as in heteromyines and perognathines.

In lateral view, the surface of the upper diastema slopes gently upward anteriorly (Figs. 20B–C). The large rostral perforation and small bony swelling ventral to it are characteristic of all heteromyids. The anterior root of the zygomatic arch lies well anterior to the P4, with the anteriormost point of the orbit situated approximately halfway between the P4 and rostral perforation. Most of the orbital wall is broken or obscured by matrix. However, the alisphenoid is preserved on the right side of the skull. In this area, there is a large, oval foramen with a small notch along its anterior side. This is interpreted as the accessory foramen ovale, which includes the buccinator and masticatory foramina. The small notch is likely for the latter two foramina. The preserved auditory bulla is rather elongate and somewhat ventrally inflated, but little detail can be determined due to the condition of the specimen.

Ventrally, the incisive foramina are approximately 30% of the total length of the upper diastema, relatively large for a heteromyid (Fig. 20D). The premaxillary-maxillary suture crosses the centerline of the palate just anterior to the posterior border of the incisive foramina. The pal-

TABLE 15. Comparative crown-height indices and length/width proportions (L/W) of m1 for holotypes of *Proheteromys* species. Abbreviations: **L**, anteroposterior length; **W**, transverse width; **ht/W**, crown-height index (ht/W) = buccal height/ transverse width of tooth. * - species possibly synonyms.

	Species	Specimen	ht/W index	L/W m1
ARIKAREEAN	<i>P. gremmelsi</i> *	SDSM 5574	0.31	0.88
	<i>P. bumpi</i> *	SDSM54304	0.34	0.93
	<i>P. latidens</i>	UCMP 150688	0.38	0.79
	<i>P. thorpei</i>	YPM 10571	0.41	0.96
HEMINGFORDIAN	<i>P. cejanus</i>	FAM 25365	0.33	0.96
	<i>P. floridanus</i>	UF 97529	0.39	0.90
	<i>P. matthewi</i>	AMNH 12896a	0.44	0.87
	<i>P. sulculus</i>	KU 10203	0.60	0.96

ate between the tooth rows is better preserved in UCMP 82276 than in the holotype. The palatal surface is flat with two shallow, parallel grooves running anteroposteriorly just lateral to the centerline. The palatine-maxillary suture follows these grooves and crosses the centerline even with the boundary between P4 and M1. There are two oval posterior palatine foramina on either side within the grooves. The most anterior are at the anterior extent of the palatine; the posterior foramina are medial to M2. The preserved portion of the palate suggests the parapterygoid fossa was shallow, as in other mioheteromyines (Korth 1997).

The dentary is slender and elongated (Fig. 20F). The lower diastema dips only slightly below the alveolar surface and is equal in length to the lower tooth row. The mental foramen is high on the dentary, just below the dorsal surface of the diastema near its center and well anterior to the p4. The masseteric fossa is marked by a low ridge that runs along the ventral surface of the ramus from below m3 anteriorly to a point slightly dorsal and posterior to the mental foramen. The angular process is narrow, tapered, and deflected laterally from the horizontal ramus. The ascending ramus slopes gently upward posteriorly beginning at m3. On the lateral side of the ascending ramus is a small, oval knob that marks the posterior end of the incisor. Posterior to it is a shallow broad basin. There is no coronoid process preserved on either side due to breakage. The condyle is preserved on the right dentary (Fig. 20F) and extends posteriorly, with a deep notch at the posterior end of the dentary between the condyle and angular process.

Both the upper and lower incisors are transversely compressed and gently curved on the anterior surface. There are no grooves or ornamentation on the anterior enamel surface. The morphology of the cheek teeth does not vary from the typical heteromyid pattern; both upper and lower molars are composed of two rows of three cusps, and the P4 has an isolated anterior protocone and a three-cusped metaloph. The crown height of the lower molars averages 0.38 (range = 0.31–0.43), which is relatively high (Table

15). The p4 consists of two large metalophid cusps (metaconid, protostylid) that are oval in outline and nearly equal in size, the metaconid being only slightly larger (Fig. 20H). On the holotype, the metaconid has fused posteriorly with the hypolophid and buccally with the protostylid, isolating a small valley at the center of the tooth that is open to the buccal edge. There is no indication of a hypostylid on p4, but this cannot be determined with certainty due to the degree of wear.

The proportions of the molars are wider relative to width than other species of the genus. The ratio of length to width of the lower molars of *P. latidens* averages 0.76, whereas that of other species ranges from 0.87 to 0.96, indicating that the molars are nearly as wide as long (Table 15).

The holotype (UCMP 150688) has some associated postcranial material imbedded in a block of matrix (Fig. 20I), as well as a partially prepared distal femur and tibia (Figs. 20J–K). Exposed elements imbedded in matrix include the right humerus, right astragalus, calcaneum, a partial innominate, a rib, and several vertebrae. The medial surface of the humerus and its proximal end are exposed, allowing the following measurements: total length = 14.71 mm, anteroposterior diameter of the humeral head = 2.46 mm. The humeral head is round and the lesser tubercle sits slightly below it; the shaft is slender and long. The exposed medial epicondyle is small, providing a relatively small site of origin for the wrist and digital flexors. The plantar surface of the astragalus is exposed, allowing the following measurements: total length = 2.97 mm, body length = 1.72 mm, body width = 2.03 mm, navicular facet length 1.30 mm. The astragalar head is large and slightly displaced laterally. The sustentacular and ectal facets are not separated by a sulcus calcaneus. The sustentacular facet extends slightly onto the neck, but is not continuous with the navicular facet, which is highly convex. The lateral surface of the calcaneum is exposed; its tuberosity is relatively slender, while the peroneal tubercle is short and

TABLE 16. Dental measurements (in mm) of *Proheteromys thorpei* from the John Day Formation. Abbreviations: **L**, anteroposterior length; **W**, transverse width; **ht/W**, crown-height index (ht/W) = buccal height/ transverse width of tooth.

	i1L	i1W	p4L	p4W	m1L	m1W	ht/W	m2L	m2W	m3L	m3W	p4–m3
JODA 1004	1.23	0.69			1.00	1.13		1.02	1.16			
JODA 12657					1.07	1.17	0.38					
JODA 16001					1.12	1.17	0.37					
UWBM 73420	1.40	0.64	0.75	0.85	1.02	1.09	0.38	1.02	1.16	0.78	0.85	3.89
YPM 10571 (type)			0.91	0.83	1.14	1.19	0.41					

ends well above the cuboid facet. The femur is only represented by the distal end and the epiphysis is missing. The tibia is elongate and gracile (incomplete length = 22.88 mm, mediolateral diameter = 1.61 mm), with a relatively short but prominent tibial tuberosity (length of tibial spine = 10.26 mm). The proximal medial and lateral condyles are approximately equal in size (anteroposterior length = 3.88 mm, mediolateral breadth = 3.75 mm).

Discussion.—The molars of *P. latidens* differ from those of *P. thorpei* in being larger and relatively wider (Tables 16, 18). The relative width of the molars is unique to *P. latidens* among the species of the genus (Table 15). The p4 is also unique, the metalophid consisting of two large oval cusps that fuse anteriorly before fusing to the hypolophid.

The skull of *P. latidens* is the most complete skull of the genus ever described. It has all of the distinctive features that characterize other mioheteromyines: 1) low, broad skull; 2) slightly inflated bullae; 3) long incisive foramina (greater than 15% diastemal length); and 4) premaxillary-maxillary suture meets the incisive foramina anterior to their posterior end. Most of these features are considered primitive for heteromyids (Korth 1997), and are not unexpected for *Proheteromys*.

However, there is one feature of the skull of *P. latidens* that is clearly more primitive than any previously described heteromyid. The foramina on the ventral alisphenoid differ between subfamilies of heteromyids. In Heteromyinae and previously described Mioheteromyinae, there is a large accessory foramen ovale and a smaller foramen anterior to it, which is a combined foramen for the buccinator and masticatory foramina (Wahlert 1985; Korth 1997: fig. 11). On the skull of *P. latidens*, this anterior foramen is included within the accessory foramen ovale, as evidenced by the small notch along the anterior border. This condition is not known in other heteromyids and is elsewhere only present among geomyoids in eomyids, heliscomyids, and florentiamyids. This is considered the primitive condition for all geomyoids (Korth 1997).

It is also worth noting that in *P. latidens*, the anterior root of the zygomatic arch and anterior wall of the orbit are anterior to the P4, approximately halfway between the P4 and rostral perforation. This is also the condition observed

in the type (UCMP 37134) of *Mioheteromys amplissimus* (Korth 1997), but is not true of extant heteromyids or other previously described fossil heteromyids, where the anterior wall of the orbit lies directly above or just anterior to the P4.

The preserved postcranial material of the holotype (UCMP 150688) allows some inferences to be made on the paleoecology of *Proheteromys*. The humerus length of *P. latidens* (14.71 mm) is greater than the mean length of five individuals of *Perognathus parvus* (Peale, 1848) examined in Samuels and Van Valkenburgh (2008) = 11.80 mm. The relatively small medial epicondyle of the humerus indicates small forelimb muscles, and suggests that *P. latidens* was not specialized for digging like many extant heteromyids (Howell 1932; Hildebrand 1985). The exposed portion of the calcaneum is relatively generalized, unlike the calcaneum of extant highly saltatory heteromyids (Howell 1932). The tibia is gracile and has a relatively elongate tibial tuberosity. The mediolateral diameter of the tibia (1.61 mm) is less than the mean diameter of *P. parvus* (1.78 mm), but the length of the tibial tuberosity (10.26 mm) is greater than the mean in *P. parvus* (6.90 mm). The elongated tibial tuberosity indicates relatively distal insertion of the semimembranosus and semitendinosus muscles, consistent with terrestrial habits (Howell 1932; Samuels and Van Valkenburgh 2008). In total, postcranial morphology suggests that *Proheteromys* was likely terrestrial, rather than saltatory like many heteromyids, and was certainly not specialized for bipedal ricochetal locomotion like dipodomysines (Howell 1932).

Subfamily Perognathinae Coues, 1875

Bursagnathus, new genus

Type and Only Species.—*Bursagnathus aterosseus*, new species.

Diagnosis.—Primitive heteromyid characters: small size; low-crowned cheek teeth (mean molar crown-height index = 0.30); incisors asulcate; temporal foramen retained; incisive foramen length greater than 15% diastema length; stapedial foramen retained in bulla; squamosal not reduced

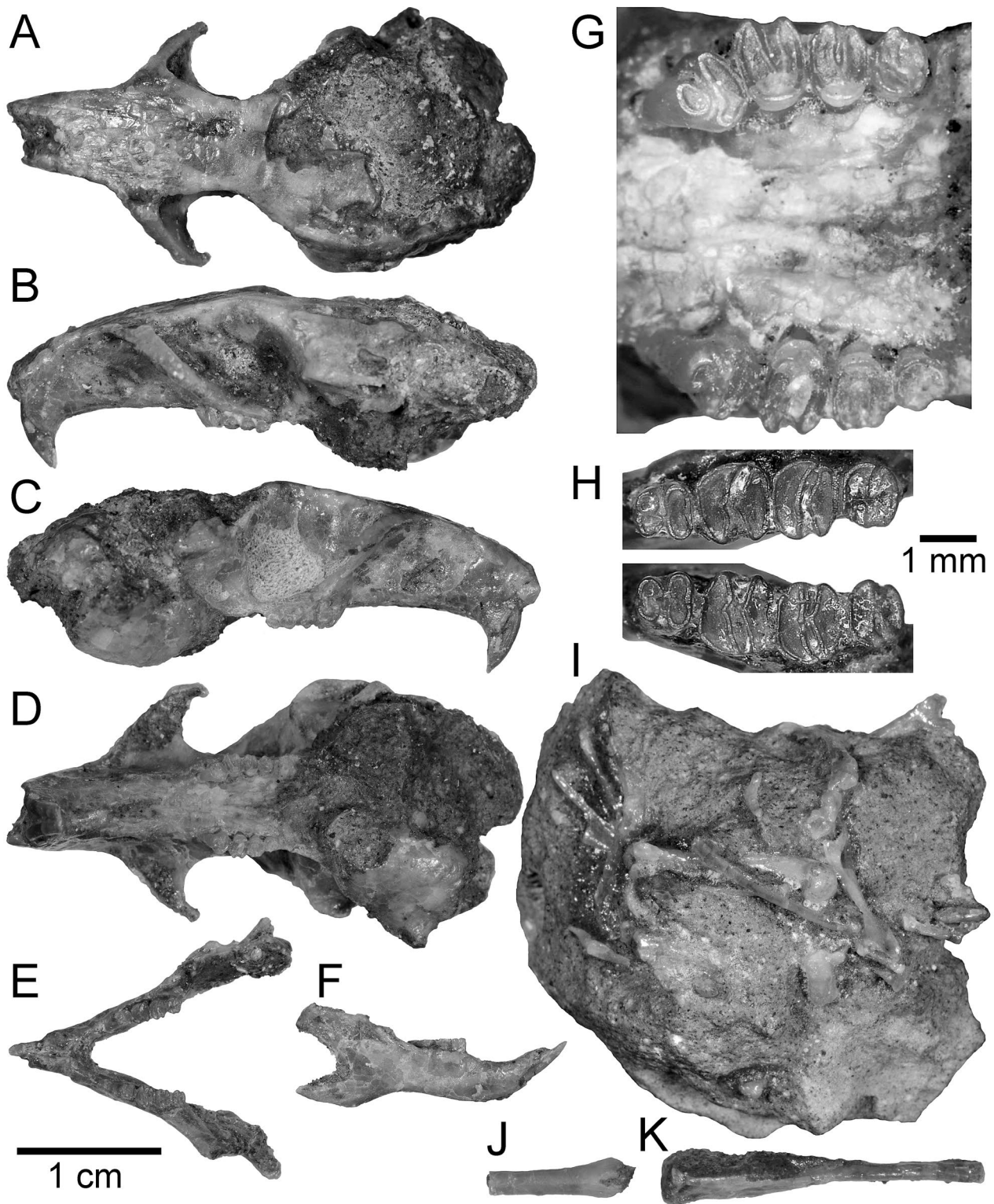


Fig. 20.—Holotype of *Proheteromys latidens*, new species, from the John Day Formation, Oregon, UCMP 150688. **A–D**, cranium; **A**, dorsal view; **B**, left lateral view; **C**, right lateral view; **D**, ventral view; **E–F**, mandible; **E**, occlusal view of mandible, **F**, lateral view of right dentary; **G**, occlusal view of left and right P4–M3; **H**, occlusal view of left and right p4–m3; **I**, partial postcranial skeleton imbedded in matrix; **J**, anterior view of distal end of left femur, **K**, anterior view of incomplete left tibia. Scale bar for **A–F** and **I–K** equals 1 cm (lower left); for **G** and **H** equals 1 mm (center right).

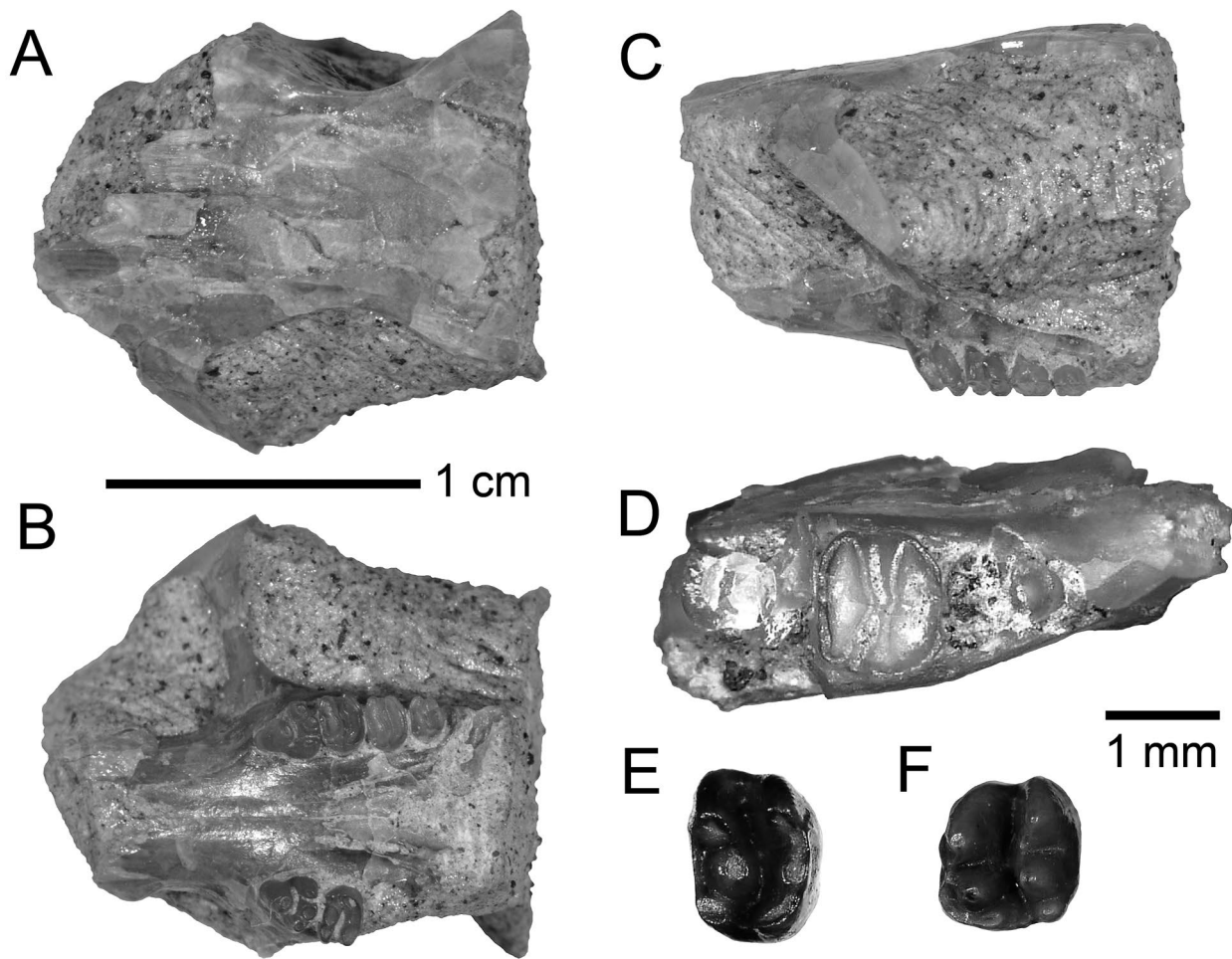


Fig. 21.—Referred specimens of *Proheteromys latidens* from the John Day Formation, Oregon. **A–C**, UCMP 82276, partial skull with left P4 to M3 and right P4 and M1; **A**, dorsal view; **B**, left lateral view; **C**, ventral view; **D**, UCMP 82335, right dentary with m1; **E**, JODA 12653, left M1 or M2; **F**, JODA 12658, left m1 or m2. Scale bar for **A–C** equals 1 cm (left); for **D–F** equals 1 mm (right).

to thin bar dorsal to external acoustic meatus; nasals extend more posteriorly on dorsal side of skull than premaxillaries. Derived perognathine characters: auditory bullae inflated, meeting anteriorly (but no inflation of the mastoid); masticatory and buccinator foramina separate on alisphenoid; accessory foramen ovale lacking; parapterygoid fossa deep; marking for temporalis muscle weakly defined and limited to lateral part of parietals; premaxillary-maxillary suture crosses palate at posterior border of incisive foramen; unossified area present in wall of orbit between alisphenoid and frontal bones; bony flange present along dorsal margin of orbit; p4 with distinct central loph uniting metalophid and hypolophid.

Range.—Late Arikareean (late Oligocene or earliest Miocene) and early Hemingfordian (early Miocene) of Oregon.

Etymology.—Latin, *bursa*, pouch; *gnath*, jaw.

Discussion.—*Bursagnathus* differs from primitive heteromyids (=mioheteromyines) in several features of the skull: 1) inflation of the bulla; 2) deep parapterygoid fossa; 3) separation of the masticatory and buccinator foramina and loss of the accessory foramen ovale on the alisphenoid; 4) presence of an unossified area in the wall of the orbit between the alisphenoid and frontal bones; 5) bony flange along the dorsal margin of the orbit; 6) reduction in the width of the interparietal; and 7) the premaxillary-maxillary suture crosses the midline of the palate at the posterior end of the incisive foramina. All of these features are considered to be derived and shared with perognathines. Dentally, *Bursagnathus* has low-crowned cheek teeth and also has the perognathine central attachment of the metalophid to the hypolophid on p4.

Similarly, *Bursagnathus* differs from heteromyines in the following features: 1) inflation of the auditory bullae;

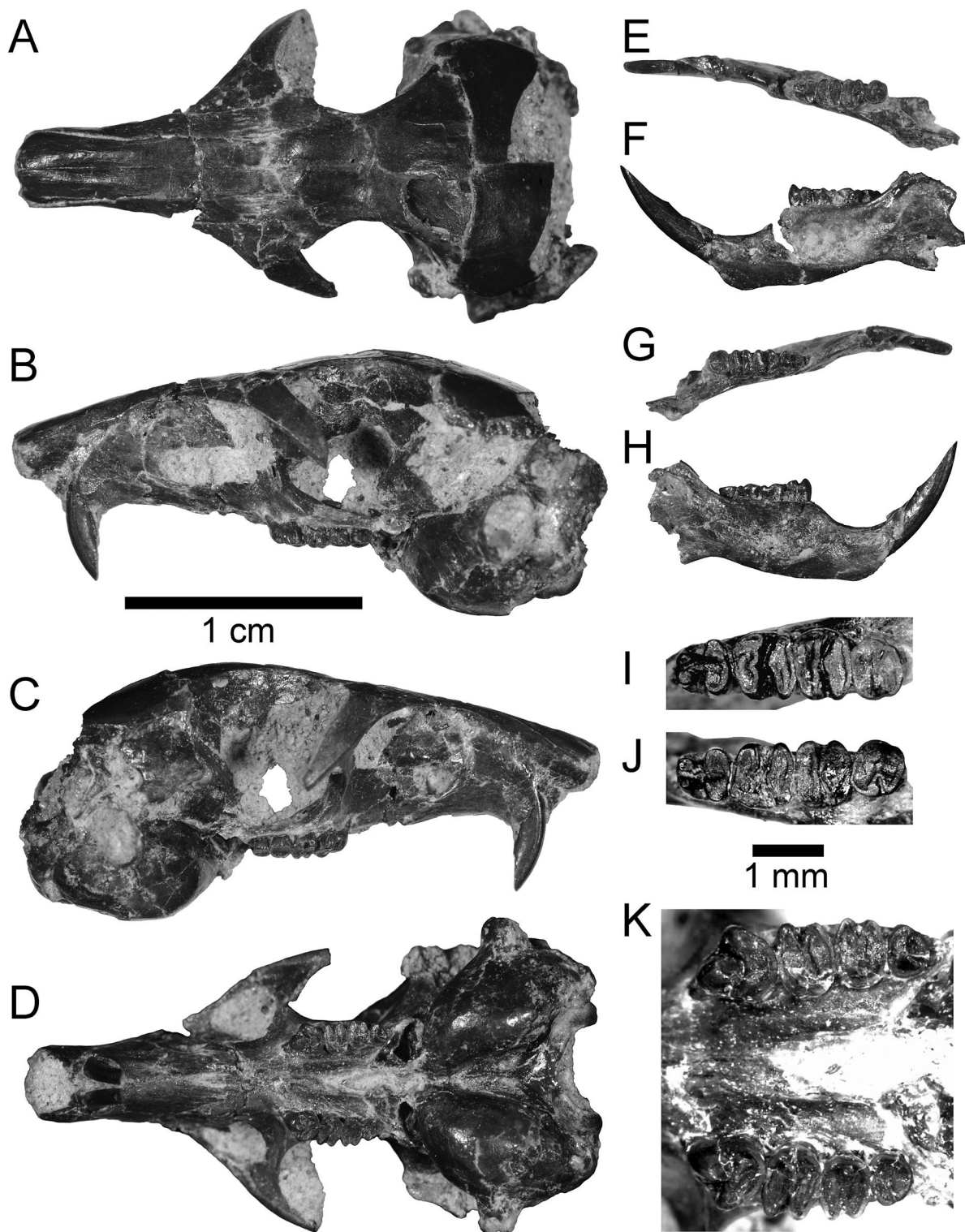


Fig. 22.—Holotype of *Bursagnathus aterosseus*, new genus and species, UCMP 56279, from the John Day Formation, Oregon. **A–D**, cranium; **A**, dorsal view; **B**, left lateral view; **C**, right lateral view; **D**, ventral view; **E–F**, left dentary; **E**, occlusal view; **F**, lateral view; **G–H**, right dentary; **G**, occlusal view; **H**, lateral view; **I**, right p4–m3; **J**, left p4–m3; **K**, ventral view of palate with right and left P4–M3. Scale bar for **A–H** equals 1 cm (left); for **I–K** equals 1 mm (right).

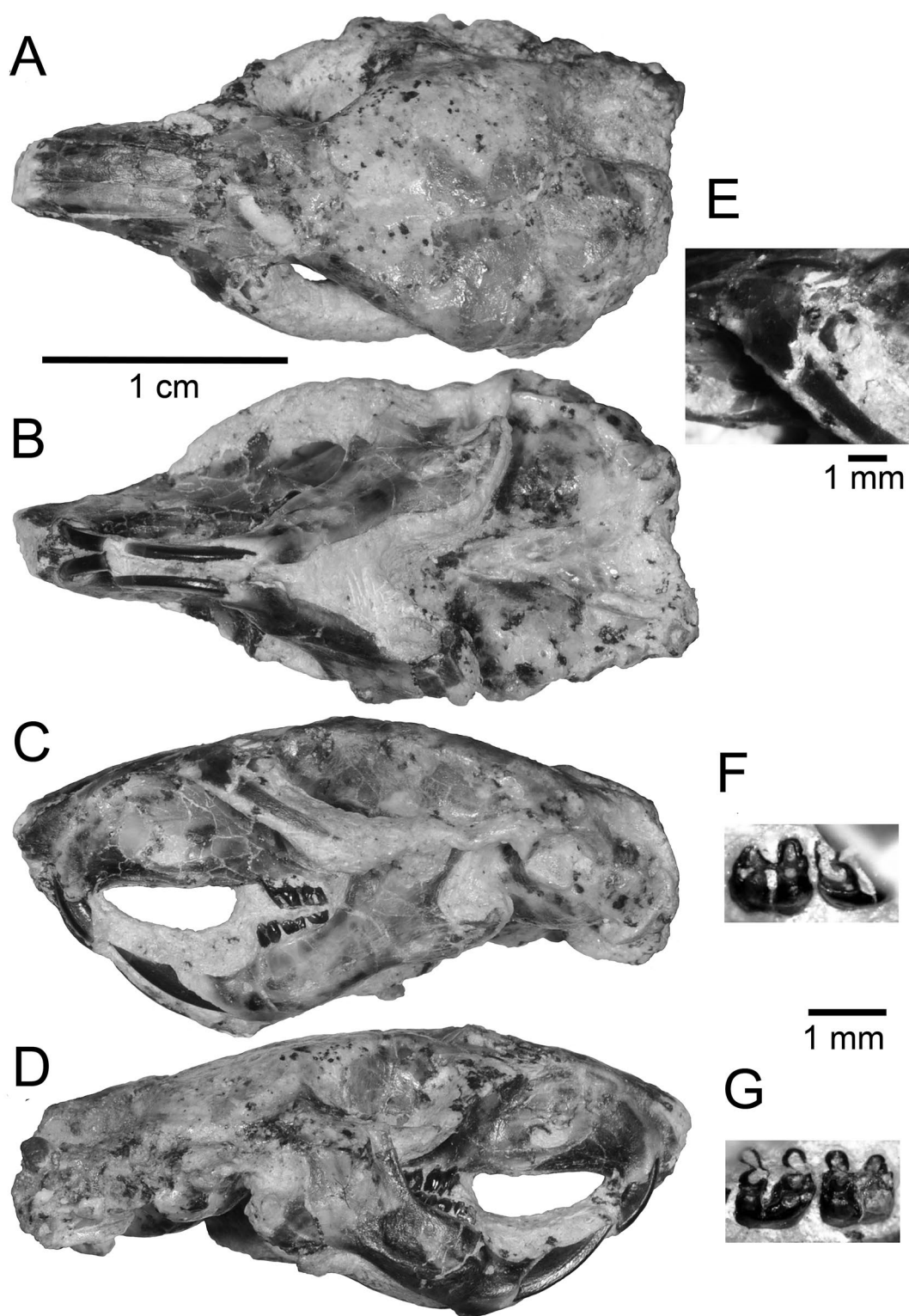


Fig. 23.—Skull and articulated mandible of *Bursagnathus aterosseus*, JODA 7407. **A**, dorsal view; **B**, ventral view; **C**, left lateral view; **D**, right lateral view; **E**, enlarged view of left orbit; **F**, left p4–m1 (anterior to left); **G**, right p4–m1 (anterior to right). Bar scale for **A** – **D** equals 1 cm (left), for **E** equals 1 mm (upper right), and for **F** and **G** equals 1 mm (lower right).

TABLE 17. Cranial measurements (in mm) for *Proheteromys latidens* and *Bursagnathus aterosseus*. * indicates estimated measurement due to breakage, the actual measurement should be greater.

	<i>P. latidens</i>	<i>B. aterosseus</i>	<i>B. aterosseus</i>
	UCMP 150688	JODA 7407	UCMP 56279
Skull length (approximate)	32.47	26.82	24.76
Maximum cranial width	15.42	12.31	11.99
Posterior cranial width (occipitals)	11.88	10.97	9.96
Maximum width at zygomatic arches	--	11.99	--
Nasal length (approximate)	12.19	9.07*	10.91
Maximum rostral width (anterior)	4.38	3.38	3.29
Maximum rostral width (posterior)	5.96	5.11	5.05
Maximum rostral depth (posterior)	6.19	5.61	6.26
Auditory bulla length	10.11	6.48	7.94
Auditory bulla width	7.96	5.12	6.06
Length of incisive foramen	2.65	1.81	1.78
Infraorbital foramen length	2.59	1.41	1.66
Infraorbital foramen depth	2.04	1.27	1.47
Upper diastema length	8.95	6.61	7.25
Dentary length (tip of incisor to condyle)	18.83	15.51	14.33*
Lower diastema length	4.25	2.98	3.49

2) retention of the stapedial foramen in the bulla (lost in heteromyines); 3) narrower interparietal; and 4) the morphology of the lower premolar (non-central union of lophs in heteromyines).

There are a number of derived features of extant perognathines that are not present in *Bursagnathus*. In extant perognathines (*Perognathus* and *Chaetodipus* Merriam, 1889), the incisive foramina are 15% or less of the diastemal length (Wahlert 1985), the upper incisors are sulcate, the squamosal is reduced to a thin bar extending posteriorly above the external acoustic meatus, the inflation of the auditory bulla includes the mastoid, and the temporal foramen is absent. In *Bursagnathus*, we see the following features: 1) length of the incisive foramen ~25% length of upper diastema; 2) upper incisors not sulcate; 3) squamosal not reduced to a thin bar extending posteriorly; 4) bullar inflation not present in adjacent mastoid; and 5) temporal foramen retained.

The most primitive perognathine previously described was *Eochaetodipus* Korth, 2008b, from the late Arikarean of Nebraska. *Bursagnathus* differs from *Eochaetodipus* in having a few more derived characters of the skull. In the alisphenoid of *Eochaetodipus*, the accessory foramen ovale is retained, but this foramen is lost in *Bursagnathus*,

Mioperognathus Korth, 2008b, and extant perognathines. *Eochaetodipus* lacks the bony flange along the dorsal margin of the orbit and the unossified area in the wall of the orbit that are present in *Bursagnathus* and extant perognathines. The auditory bullae of *Bursagnathus* are also more greatly inflated than in *Eochaetodipus*. The marking of the temporalis on the parietals of the skull of *Eochaetodipus* is more pronounced than in *Bursagnathus* and extant perognathines. The lower premolar of *Eochaetodipus* is primitive and lacks the distinctive central loph uniting the two transverse lophs present in *Bursagnathus* that is characteristic of all other perognathines.

Bursagnathus differs from *Mioperognathus* in lacking a number of derived perognathine characters present in the latter: 1) reduction of the squamosal to a thin bar extending posteriorly above external acoustic meatus; 2) sulcate incisors; and 3) bullar inflation extending into adjacent mastoids. Unlike *Mioperognathus*, *Bursagnathus* does seem to display a bony flange along the dorsal margin of the orbit like extant perognathines and dipodomysines. Also, the auditory bullae of *Bursagnathus* are much more ventrally inflated than in *Mioperognathus*, with a ventral extension of the bulla below the level of the upper tooth row, similar to that of *Perognathus*. *Bursagnathus*, like *Chaetodipus* and

TABLE 18. Dental measurements (in mm) of *Proheteromys latidens* from the John Day Formation. **L**, anteroposterior length; **W**, transverse width; **ht/W**, crown-height index (ht/W) = buccal height/ transverse width of tooth. Isolated M1/m1 or M2/m2 listed as M1/m1. Statistical abbreviations: **N**, number of specimens; **M**, mean; **OR**, range of size; **SD**, standard deviation; **CV**, coefficient of variation.

	I1L	I1W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	P4-M3L
N	1	1	6	7	7	7	3	3	3	3	3
M	1.36	0.88	1.32	1.35	0.97	1.39	0.89	1.32	0.77	1.05	4.40
OR			1.21–1.43	1.30–1.41	0.88–1.08	1.22–1.50	0.88–0.90	1.30–1.34	0.74–0.79	0.96–1.10	4.31–4.55
SD			0.10	0.04	0.07	0.10	0.01	0.02	0.03	0.08	0.13
CV			7.94	2.72	6.91	6.98	1.12	1.57	3.44	7.44	2.97
Holotype left			1.42	1.31	1.08	1.45	0.9	1.34	0.78	1.1	4.55
right			1.43	1.37	0.92	1.46	0.88	1.33	0.79	0.96	4.31
	i1L	i1W	p4L	p4W	m1L	m1W	m1 ht/W	m2L	m2L	m3L	m3L
N	1	1	2	2	7	7	6	2	2	2	2
M	1.00	0.95	0.90	0.90	1.05	1.29	0.38	0.96	1.25	0.80	1.03
OR			0.86–0.93	0.87–0.92	0.98–1.19	1.18–1.38	0.31–0.43	0.94–0.98	1.23–1.27	0.77–0.83	1.02–1.03
SD					0.07	0.06	0.05				
CV					6.84	4.90	12.78				
Holotype Left			0.86	0.92	1.04	1.30	0.38	0.98	1.23	0.77	1.02
Right			0.93	0.87	1.08	1.25		0.94	1.27	0.83	1.03

Perognathus, also does not have the marked reduction in the size of the upper molars from M1 to M3 that is characteristic of *Mioperognathus*.

***Bursagnathus aterosseus*, new species**
(Figs. 22–23; Tables 17, 19)

Type Specimen.—UCMP 56279, nearly complete cranium (jugals and occipital missing) with complete dentition and both associated dentaries with complete dentition.

Referred Specimen.—JODA 7407, partially crushed, nearly complete skull (occipital missing) with attached and articulated mandible.

Horizon and Locality.—UCMP 56279 – “Black Bone Hill” = Picture Gorge 1 (UCMP A863, V6666), Grant County, OR, Johnson Canyon Member, John Day Formation; JODA 7407 – JDNM 49A, Picture Gorge 36, Grant County, OR, Rose Creek Member, John Day Formation.

Age.—Late Arikareean (late Oligocene, Ar3? or earliest Miocene, Ar4) to early Hemingfordian (early Miocene, He1). UCMP 56279 was collected from below the Across the River Tuff (22.6 ± 0.13 Ma, Hunt and Stepleton 2004)

at Picture Gorge 1. The Johnson Canyon Member was interpreted by Albright et al. (2008) to span the interval of an unconformity between the Balm Creek and Rose Creek members, and would thus be stratigraphically above the JD-BC-3 tuff dated 23.79 ± 0.18 Ma (Hunt and Stepleton 2004). JODA 7407 was collected from above the basal conglomerate of the Rose Creek Member at Picture Gorge 36. That site has been dated at ~18.8–18.2 Ma biostratigraphically (Hunt and Stepleton 2004) and ~18.7–18.5 Ma or 18.1–17.6 Ma magnetostratigraphically (Albright et al. 2008).

Diagnosis.—Same as for genus.

Etymology.—Latin, *ater*, black; *osse*, bone: in reference to the Black Bone Hill, from which the type specimen was collected.

Description.—The skulls of both specimens are almost entirely complete. The dentaries are nearly complete and separate from the skull in the holotype (UCMP 56279), which retains its three-dimensional shape, but it lacks the zygomatic arches and the occipital and interparietal bones (Fig. 22). In JODA 7407, both dentaries are attached to the skull, obscuring most of the cheek teeth, and there is some dorsoventral crushing of the neurocranium, but both

TABLE 19. Dental measurements (in mm) of *Bursagnathus aterosseus* from the John Day Formation. Abbreviations: **L**, anteroposterior length; **W**, transverse width; **ht/W**, crown-height index (ht/W) = buccal height/ transverse width of tooth.

		i1L	i1W	p4L	p4W	m1L	m1W		m2L	m2W	m3L	m3W	P4–M3L
UCMP 56279	left			1.47	1.29	0.97	1.32		0.86	1.22	0.77	0.89	4.25
	right	1.11	0.75	1.4	1.28	1.02	1.45		0.86	1.18	0.69	0.89	4.07
JODA 7407	left	1.08	0.60	1.34		0.92							
		i1L	i1W	p4L	p4W	m1L	m1W	m1 ht/W	m2L	m2W	m3L	m3W	p4–m3L
UCMP 56279	left			0.93	0.9	0.97	1.13	0.27	0.98	1.20	0.85	1	4.01
	right	1.12	0.63	0.92	0.95	1.03	1.14	0.30	0.97	1.19	0.85	1.05	4.02
JODA 7407	left	1.20	0.53	0.98		1.06							
	right			0.97		1.01							

of the zygomatic arches are mostly intact and only some of the occipitals are lacking (Fig. 23). In general, the skulls are low and wide (see Table 17 for cranial measurements). The dorsal side of the rostrum is tapered anteriorly. The nasals end posteriorly even with the anterior margin of the zygomatic arch. Dorsally, the premaxillae do not extend as far posteriorly as the nasals; this is in contrast to all other perognathines where the premaxillae extend more posteriorly than the nasals. The frontals are flat with no muscle markings, extending posteriorly to a point even with the anterior edge of the posterior attachment of the zygomatic arch. The parietals are also flattened and there is a low ridge marking the limit of the temporalis (less pronounced than in *Eochaetodipus*, more than in *Mioperognathus* and recent perognathines). The neurocranium is widest posterior to the posterior root of the zygomatic arches. Just posterior to this, at the posteroexternal corner of the parietals is an ovate temporal foramen, similar to what is seen in *Eochaetodipus* and *Mioperognathus*. There appears to be a slight ridge on the posterior edge of the parietals representing the nuchal crest, but this area is badly damaged in both specimens so it cannot be determined with certainty. In JODA 7407, an interparietal bone is present and oval in outline (Fig. 23A), similar in shape and size to that of *Eochaetodipus* (Korth 2008b: fig. 1).

In lateral view, the upper diastema is ventrally flattened and slopes slightly dorsally (Figs. 22B–C, 23C–D). The infraorbital foramen and associated rostral perforation are low on the rostrum, even with the center of the upper diastema, and roughly circular in outline. There is a slight swelling of bone at the posteroventral edge of the rostral perforation. The zygomatic arch is sciurormorphous, but the extent of the jugal bone on the zygomatic arch cannot be definitely determined due to distortion and breakage. On the left side of JODA 7407, there is a small bony flange preserved along the dorsal margin of the orbit just posterior to the anterior root of the zygomatic arch (visible in Fig. 20P). This bony flange is very thin and there is some dam-

age to the area, but it is continuous with the anterolateral margin of the frontal bone. Due to breakage, crushing, and matrix on both cranial specimens, not all of the foramina and sutures on the orbital wall can be studied. In JODA 7407, there is an oval-shaped unossified area in the orbital wall at the base of the frontals (Fig. 23C); this seems to be the unossified area between the alisphenoid and frontal bones that includes the ethmoid foramen and characterizes Perognathinae (Wahlert 1995; Korth 2008b). The most visible foramen in the orbital wall is the nasolacrimal, which is at the anterodorsal corner of the orbital wall. On the holotype, the alisphenoid is well preserved and unobscured on both sides. There are two distinct foramina, a dorsal masticatory foramen that opens anterodorsally, and a ventral buccinator foramen that opens anteriorly. Although partially obscured, it appears that that posteroventral edge of the alisphenoid is concave anteriorly and there is no indication of an accessory foramen ovale.

In ventral view, the incisive foramen is near the center of the upper diastema and equal to approximately 25% of the length of the upper diastema (Table 17; Fig. 22D). The maxillary-premaxillary suture on the ventral surface of the diastema crosses the midline of the skull at the posterior end of the incisive foramina. The tooth rows are nearly parallel on the maxilla, diverging only slightly posteriorly. On the holotype, there are two thin, shallow grooves along the palatal surface between the tooth rows. The palatine bone extends anteriorly to a point even with P4, and there is a narrow slit-like posterior palatine foramen within the shallow grooves even with M1. The parapterygoid fossae are deep with a circular venous foramen in the center. The posterior palatine foramen is a slit along the maxillary-palatine suture, posterior to M3, below the lip of the parapterygoid fossa. The pterygoid fossa is deep and contains the opening for the sphenopterygoid canal. The foramen ovale is a narrow opening along the anterolateral side of the auditory bulla. The auditory bullae are strongly ventrally inflated, and extend anteromedially, nearly

touching one another. The ventral inflation of the bullae is so extensive that they protrude below the level of the upper tooth row (Figs. 22C–D). Due to breakage, it is evident that the bullae are made of a single layer of bone. The external acoustic meatus is short and wide with a circular opening, oriented nearly directly laterally. Just posterior to the external acoustic meatus on the ventrolateral surface of the bulla is a small stylomastoid foramen. A stapedial foramen pierces the bulla along its medial side, adjacent to the occipital condyle. Along the medial side of the bulla, at the anteromedial edge is a small fissure between the bulla and basisphenoid. The jugular foramen is along the posteromedial side of the bulla, between the bulla and basioccipital posterior to the stapedial foramen.

The dentary is slender, as is typical of heteromyids (Figs. 22F–H). The lower diastema is a little shorter than the lower tooth row and has a concave dorsal surface. The mental foramen is below the center of the diastema, just dorsal to mid-depth of the dentary. The masseteric scar arises dorsally from the angular process to a point below the center of p4. On the left side of JODA 7407, there is a weak dorsal ridge that originates below m1 and extends anteriorly to below the anterior edge of p4, forming a V-shape with the masseteric scar. The angular process forms a relatively broad shelf that projects ventrolaterally from the ramus and then deflected medially (Figs. 23B–C). There is a weak, laterally flaring superior angular process, as is seen in *Chaetodipus*; this process is not as strongly differentiated from the angular process as in dipodomysines. The coronoid process preserved on the left dentary of JODA 7407 is short and not deflected laterally as in other perognathines. The articular process is distinct and well separated from the smaller coronoid process.

The upper incisors are narrow (transversely) and gently convex on the anterior surface. The enamel is smooth and unornamented, and extends across the anterior face and approximately one-third of the lateral surface of the incisor. The pattern of cusps on the cheek teeth do not vary greatly from the typical bilophate heteromyid pattern (Figs. 22I–K). P4 is the largest of the upper cheek teeth, being longer than any of the molars and subequal in width to M1. It consists of a single-cusped protoloph (protocone) and a three cusped metaloph (metacone, hypocone, and hypostyle). The hypostyle is anteroposteriorly elongated. The molars decrease in size from M1 to M3. The first two molars are wider than long and have two well-defined transverse lophs of three cusps each, with the lingual cusps (=styles) being the smallest. The central transverse valley runs nearly the entire width of the teeth and is persistent even at a very late wear stage. With advanced wear, as in UCMP 56279, the protoloph and metaloph are fused at the lingual edge of the upper molars, blocking the central transverse valley. M3 is nearly circular in occlusal outline, and the cusps cannot be definitely identified due to wear. It appears that the M3 protoloph is three-cusped, and the metaloph two-cusped.

The lower incisor is similar in shape to the upper incisors, but slightly narrower transversely. The lower cheek

teeth, as in other heteromyids, are dominated by two transverse lophs of three cusps each. The p4 is smaller than m1, and the metalophid consists of only two cusps (metaconid, protostylid). On all specimens, the metaconid is slightly larger than the protostylid, but both are circular in shape (Figs. 22I–J). A central loph connects the center of the hypolophid with the posterior sides of the two metalophid cusps. The hypolophid is a broad transverse loph with three cusps. The entoconid and hypoconid are round and similar in size, and on the buccal side of the tooth there is a small hypostylid evident in JODA 7407 (visible in Fig. 23G). In UCMP 56279, the teeth are more worn, and the hypostylid is only evident in that the hypolophid tapers at its buccal end.

The m1 is the largest lower cheek tooth, and the molars decrease in size from m1 to m3. Both lophs of m1 are three-cusped, with the buccal hypostylid and protostylid being the smallest cusps. The anterior cingulid wraps around the anterobuccal corner of the tooth, connecting the protostylid with the anterior side of the protoconid. The transverse valley runs the entire width of the tooth and is persistent even at the advanced wear seen in UCMP 56279. The m2 is similar to m1, but is smaller and does not have the small anterior cingulid. The m3 is the smallest tooth. The metalophid lacks an anterior cingulid and is similar to that of the m2, but the hypolophid is shorter than in the m1 or m2, suggesting that it is two-cusped rather than three-cusped.

Discussion.—*Bursagnathus aterosseus* is a primitive perognathine and approximately contemporaneous with *Eochaetodipus asulcatus* Korth, 2008b, from the late Arikarean of Nebraska. However, it is more derived than *E. asulcatus* in a number of features, and overall it is more morphologically similar to *Mioperognathus willardi* Korth, 2008b, from the late Barstovian of New Mexico and extant perognathines. *Bursagnathus* is smaller than *Eochaetodipus*, both in terms of cranial and dental dimensions, and comparable in cranial size to *Mioperognathus*, though the dentition is consistently larger than in that taxon (Tables 17, 19; Korth 2008b).

The incisive foramina of *Bursagnathus* are proportionate to those of *Mioperognathus*, and relatively longer in than in *Eochaetodipus*, *Chaetodipus*, and *Perognathus*. In both *Bursagnathus* and *Mioperognathus*, the incisive foramina are more than 20% of the length of the upper diastema. This suggests that the shortened incisive foramina of extant perognathines (*Perognathus* and *Chaetodipus*) are a relatively recently derived trait, since the middle Miocene, and were derived independent of the shortened incisive foramina of *Eochaetodipus*. *Bursagnathus* and *Mioperognathus* both lack an accessory foramen ovale on the alisphenoid and have more weakly defined temporal markings on the parietals than *Eochaetodipus*. Like extant perognathines, both taxa also display an unossified area in the wall of the orbit between the frontal and alisphenoid, a derived trait within the subfamily.

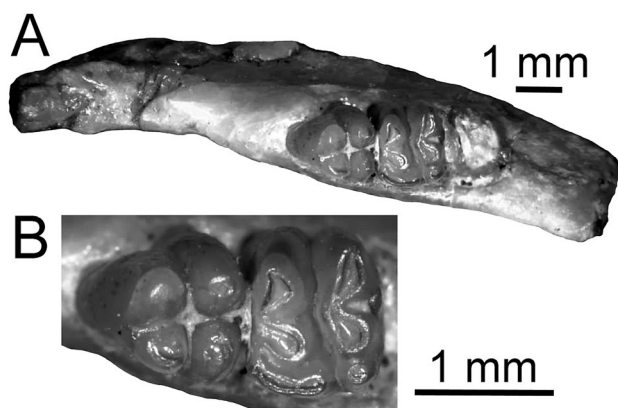


Fig. 24.—Left dentary with i1, p4–m1 of *Tenudomys* sp., JODA 3548, from the John Day Formation, Oregon. **A**, occlusal view of dentary; **B** p4–m1 (enlarged). Scale bars equal 1 mm.

The bullae of *Bursagnathus* are much more inflated than in *Eochaetodipus*, but do not show the inflation of the mastoid seen in *Mioperognathus* and extant perognathines. However, the bulla of *Bursagnathus* is substantially more ventrally inflated than in *Mioperognathus*, more like extant *Perognathus*. Both *Bursagnathus* and *Mioperognathus* display a bulla composed of a single lamina of bone, while *Chaetodipus* and *Perognathus* have trabeculate bone (Korth 2008b).

In at least one specimen of *Bursagnathus* (JODA 7407), a bony flange is present above the orbits. This flange is not present in *Mioperognathus* and is considered a derived trait of Recent perognathines (Korth 2008b). Its presence in *Bursagnathus* indicates this trait was present by at least the early Miocene and was either absent in other fossil perognathine specimens due to its fragility and poor preservation, or it was secondarily lost in *Mioperognathus*. Extant perognathines and *Mioperognathus* display sulcate upper incisors, but *Bursagnathus* does not. This suggests that this trait first appeared in the subfamily in the early or middle Miocene.

Wahlert (1985) suggested that heteromyid subfamilies were not well separated in the Miocene and believed the common ancestor of the subfamilies occurred in the late Oligocene or early Miocene. *Bursagnathus aterosseus* occurs in the latest Oligocene and early Miocene, and bears an array of derived features of perognathines, quite divergent from earlier heteromyids. This suggests that the divergence of perognathines from other heteromyids likely occurred in the late Oligocene. Given the suite of derived characters in *Bursagnathus*, it represents a likely ancestor of more recent perognathines, including *Perognathus* and *Chaetodipus*.

The holotype specimen of *B. aterosseus* (UCMP 56279) was actually included as a calibration point for the perognathine node in a recent molecular phylogeny by Hafner et al. (2007). At that time, the specimen was referred to

as *Perognathus sensu lato*, using a personal communication from Ted Fremd, and assigned an age of 22–20 Ma (Hafner et al. 2007). Using that calibration point and Bayesian methods, the divergence of Perognathinae from Heteromyinae was estimated to be around 21.83 Ma and the divergence of *Perognathus* from *Chaetodipus* around 20.59 Ma (Hafner et al. 2007: fig.3). The more refined age of UCMP 56279, between 23.8 and 22.6 Ma, will allow recalibration of these phylogenies and an overall better understanding of the evolution of heteromyids.

Geomyoidea Family Uncertain
Tenudomys Rensberger, 1973

Tenudomys sp.
(Fig. 24)

Referred Specimen.—JODA 3548, left dentary with i1, p4–m1.

Horizon and Locality.—JODA 3548 – Paratylopus Hill (Haystack Valley), Grant County, OR, Haystack Valley Member, John Day Formation.

Age.—Early late Arikareean (late Oligocene, Ar3), between JD-BC-3 tuff dated 23.79 ± 0.18 Ma and the Across the River Tuff dated 22.6 ± 0.13 Ma (Hunt and Stepleton 2004).

Measurements.—p4: length = 1.44 mm, width = 1.50 mm; m1: length = 1.48 mm, width = 1.83 mm; i1: length = 1.57 mm, width = 1.09 mm.

Description.—The lower incisor is roughly triangular in cross-section, being more narrow transversely than it is anteroposteriorly, and the anterior face is semi-flattened. The cheek teeth are mesodont in height and have bulbous cusps. The p4 has four distinct cusps: two in the metalophid (metaconid, protostylid) and two on the hypolophid (hypoconid, entoconid). All cusps are of nearly equal size and relatively round in occlusal outline. The metalophid cusps are spaced more closely together than the hypolophid cusps, making the tooth wider posteriorly. Deep valleys separate the metalophid and hypolophid, and a shallower anteroposterior valley separates the cusps of each lophid. There is no hypostylid or anterostylid on the tooth, and the hypolophid does not show the anteroposterior compression that is common in some other species of the genus.

The m1 is larger than p4, especially in width (Fig. 24). The metalophid and hypolophid are well defined and separated by a deep transverse valley that runs the entire width of the tooth. The cusps of each lophid join each other at a point between and just anterior to them, forming a shallow V-shape. The anterior cingulid runs posteriorly from the anterobuccal corner of the tooth a short distance, and then ends in a small protostylid that is situated just posterior to the posterior border of the protoconid. The hypostylid is a small, round cuspsule that lies buccal to the hypoconid and

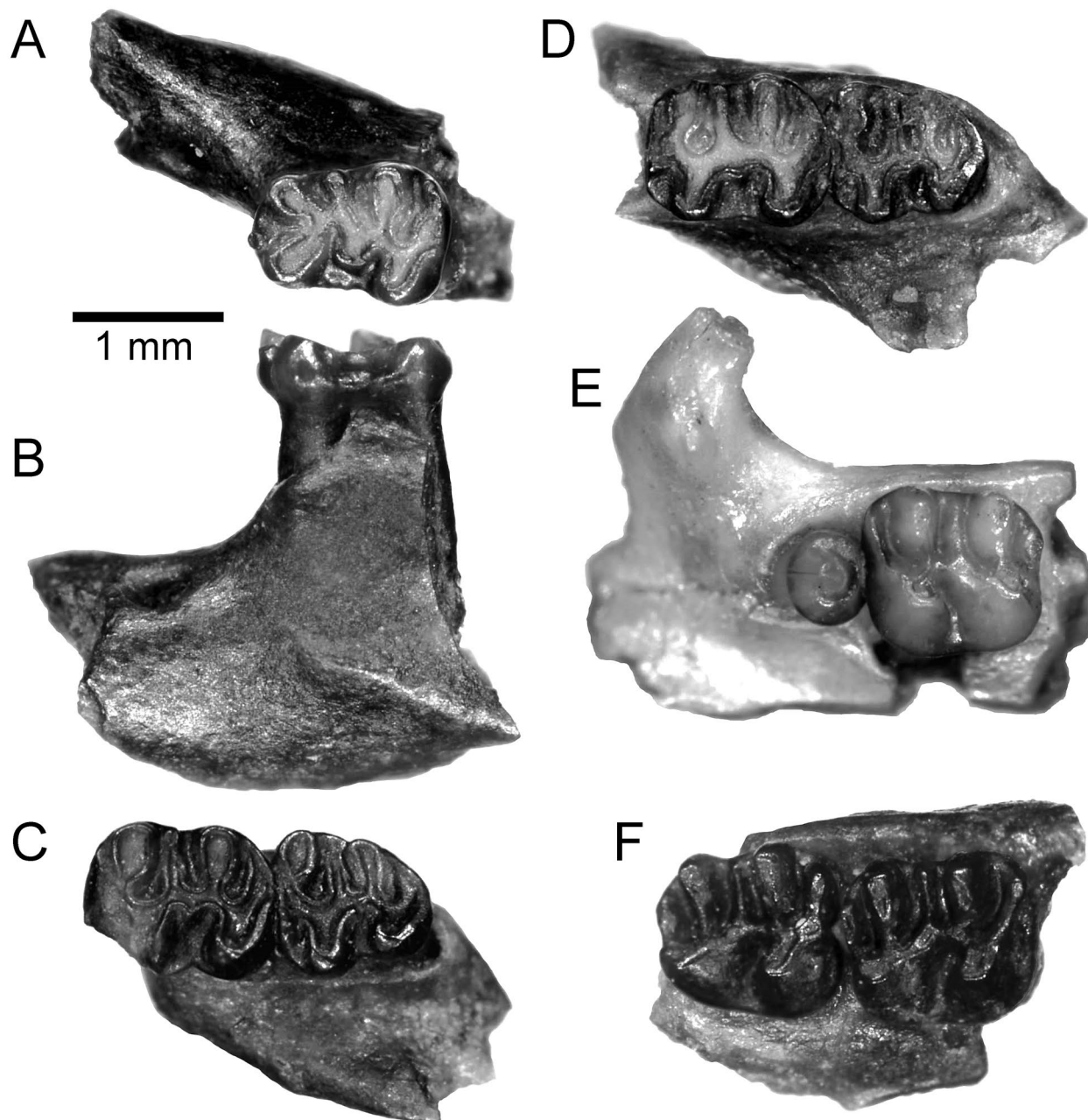


Fig. 25.—Specimens of *Plesiosminthus fremdi*, new species, from the John Day Formation, Oregon. **A–B**, Holotype, JODA 12686, left dentary fragment with m1; **A**, occlusal view; **B**, lateral view; **C**, JODA 12685, left dentary with m2–m3; **D**, JODA 12693, left dentary fragment with m2– m3; **E**, JODA 6951, left maxilla with P4– M1; **F**, JODA 7990, right maxilla with M1–M2: Scale bar equals 1 mm.

aligned with the other two hypolophid cusps. There is a minute hypoconulid at the center of the posterior edge of the tooth, between the major cusps.

Discussion.—JODA 3548 is referable to *Tenudomys* based on Rensberger's (1973) diagnosis of the genus with mesodont cheek teeth and a simple four-cusped occlusal pattern

of p4. It is distinct from other species of the genus by its intermediate size: smaller than *T. macdonaldi* Rensberger, 1973, and *T. dakotensis* (Macdonald, 1963), and larger than *T. bodei* (Wilson, 1949) and *T. basilaris* Korth, 1989. It is most similar to *T. bodei* in the retention of distinctly rounded and separate hypolophid cusps on p4 (Wilson 1949: fig. 5a; Korth 1993: fig. 2B). In *T. macdonaldi*, the

TABLE 20. Dental measurements (in mm) of *Plesiosminthus fremdi* from the John Day Formation. Abbreviations: **L**, anteroposterior length; **W**, transverse width.

	P4L	P4W	M1L	M1W	M2L	M2W
N	6	6	9	9	5	5
M	0.60	0.62	1.27	1.21	1.20	1.14
OR	0.52–0.71	0.58–0.67	1.21–1.34	1.13–1.30	1.15–1.22	1.08–1.20
SD	0.07	0.03	0.04	0.05	0.03	0.06
CV	11.96	5.36	3.47	4.17	2.43	4.85
	m1L	m1W	m2L	m2W	m3L	m3W
N	5	6	8	8	3	3
M	1.32	1.00	1.30	0.99	1.04	0.94
OR	1.24–1.40	0.95–1.03	1.23–1.39	0.93–1.04	1.02–1.07	0.90–1.00
SD	0.06	0.03	0.06	0.04	0.03	0.05
CV	4.50	2.67	4.28	4.16	2.41	5.63
Holotype JODA 12686	1.32	1.03				

hypolophid cusps are broad and transversely compressed (Rensberger 1973: fig. 37a; Korth 1993: fig. 2E).

Although the John Day specimen has a relatively primitive premolar morphology, it occurs in the late Arikarean (Ar3). That means the John Day *Tenudomys* specimen is the youngest reported occurrence of the genus (Flynn et al. 2008). Other reported occurrences include *T. basilaris* from the Orellan of Nebraska, *T. bodei* from the early Arikarean (Ar1) of California, and *T. macdonaldi* and *T. dakotensis* from the early Arikarean of South Dakota (Ar1) (Flynn et al. 2008). Contrary to previous reports (Flynn et al. 2008), there are no known records of *T. macdonaldi* from the John Day Formation and no occurrences in the Kimberly Member.

Family Dipodidae Fischer von Waldheim, 1817
Subfamily Sicistinae Allen, 1901
Plesiosminthus Viret, 1926

Plesiosminthus fremdi, new species
(Fig. 25; Table 20)

Type Specimen.—JODA 12686, left dentary fragment with left m1.

Referred Specimens.—JODA 12685, 12693, partial left dentaries with m2–m3; JODA 12666, 12668, 12671, 12684, 12688, m1s; JODA 6223, 12687, 12689, 12690, 12694, 12695, m2s; JODA 6951, partial left maxilla with P4–M1; JODA 7990, partial right maxilla with M1–M2; JODA 12667, 12669, 12672, 12674, 12683, maxilla fragments with P4; JODA 12675, 12676, 12678, 12680, 12682,

12692, 12700, M1s; JODA 12673, 12679, 12681, 12701, M2s.

Horizon and Locality.—JDNM 140, Campbell Ranch, Gilliam County, OR, Kimberly Member, John Day Formation.

Age.—Early late Arikarean (late Oligocene, Ar3), between Tin Roof Tuff dated 25.9 ± 0.3 Ma (Albright et al. 2008) and JD-BC-3 tuff dated 23.79 ± 0.18 Ma (Hunt and Stepleton 2004).

Diagnosis.—Intermediate sized, similar to *P. sabrae* Black, 1958, larger than *P. clivosus* Galbreath, 1953, smaller than other species; anteroconid on m1 generally minute; connection of ectolophid to metalophid on m1 variable, but when present always lingual to midline of tooth; endoloph on M2 and most M1 joins protoloph at its center (not directly with protocone); length of m3 reduced relative to m2.

Etymology.—Patronym for Theodore Fremd, whose work has redefined the stratigraphy of the John Day Basin and understanding of the region’s fossil record.

Description.—In size, the dentition is relatively small, being smaller than all other North American species except *P. clivosus*, and is roughly equivalent in size to *P. sabrae* (Table 20; Green 1977).

The m1 is narrower anteriorly than posteriorly, with an occlusal pattern of lophs similar to other species referred to *Plesiosminthus* (Fig. 25A). An anteroconid is always present, but minute, in all but one specimen (JODA 12688),

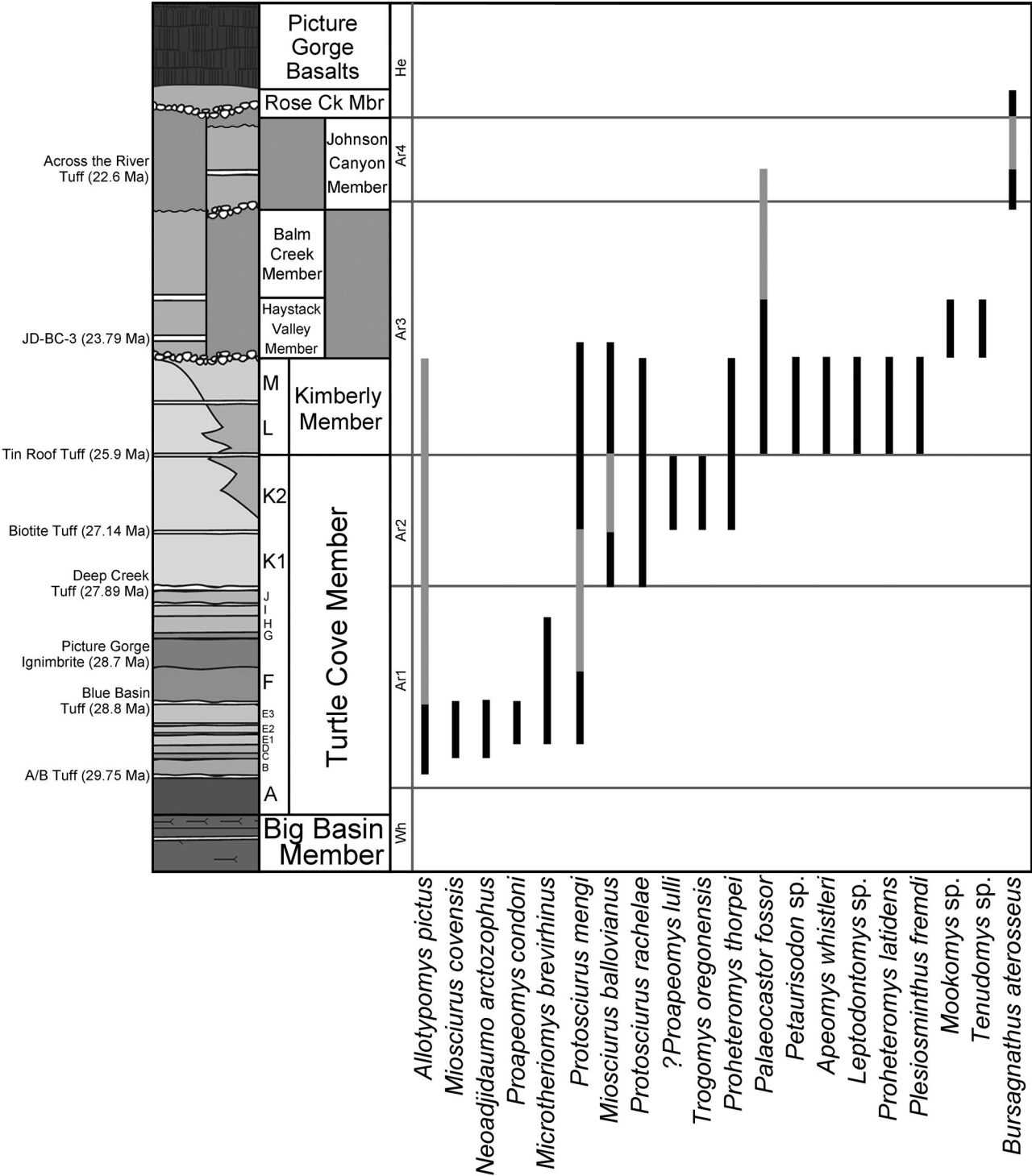


Fig. 26.—Composite stratigraphy of the John Day Formation with stratigraphic ranges for 20 newly described rodents. Stratigraphy and radiometric dates based on Fremd et al. (1994), Hunt and Stepleton (2004), and Albright et al. (2008). Black bars indicate confirmed stratigraphic ranges; grey bars indicate range-throughs or presence at sites with unconfirmed stratigraphic units.

and is positioned at the center or buccal side of the tooth. The protoconid and metaconid are connected by the metalophid, which is bowed posteriorly. The anterior end of the ectolophid is continuous with the metalophid on three of the six specimens of m1. When there is a connection, it is lingual to the midline of the tooth. A mesoconid is always present, but smaller than the major cusps of the tooth. The mesolophid is always long, extending to the lingual edge of the tooth, usually ending in a distinct mesostylid of variable size. The hypolophid runs transversely and is always complete from the entoconid to the anterior arm of the hypoconid. The posterolophid originates on the posterior side of the hypoconid and wraps lingually around the posterior margin of the tooth, ending before reaching the entoconid. A small but distinct hypoconulid is always present and strongly connected to the hypoconid via the posterolophid.

The m2 is the same size as m1, but the anterior and posterior widths are the same, making the tooth rectangular in occlusal outline (Figs. 25C–D). The lingual cusps are placed slightly anterior to the opposing buccal cusp. A low anterolophid extends for the width of the tooth along the anterior margin. A small anterostylid is present at the center or just buccal to the center of the cingulid where the anterior arm of the metaconid joins the anterolophid. Posterior to the junction with the anterolophid, the anterior arm of the protoconid joins the anterior arm of the metaconid. The ectolophid is continuous from the posterior side of the protoconid to the hypoconid. A small but recognizable mesoconid is present at the center of the ectolophid. The mesolophid extends from the mesoconid to the lingual edge of the tooth, posterior to the metaconid. The hypolophid extends buccally from the entoconid, joining the ectolophid and anterior arm of the hypoconid. The hypoconid and posterolophid are similar to that of m1, but the hypoconulid is smaller.

The m3 is only about 80% the length of m2 (range = 78–82%), generally smaller than in other species (Figs. 24C–D). The occlusal pattern of m3 is similar to that of m2, differing only in the narrowing of the tooth posteriorly and the fusion of the lingual end of the posterolophid with the posterior surface of the entoconid.

P4 is a small, circular tooth (Fig. 25E). At the antero-buccal edge is a small conical cusp. The remainder of the tooth is surrounded by a distinct cingulum that isolates a narrow, crescentic valley posterior to the cusp.

M1 is the largest of the upper molars (Figs. 25E–F). It is rectangular in occlusal outline, being slightly longer than wide. The buccal cusps (paracone, metacone) are anteroposteriorly compressed and the lingual cusps (protocone, hypocone) are obliquely compressed. The anteroloph arises from the anterolingual corner of the protocone and extends to the buccal edge of the tooth, anterior to the paracone. A small anterocone is variably present along the anterior cingulum near its center. The protoloph connects the paracone to the posterior arm of the protocone with a slight posterior bend. The endoloph connects to the center of the protoloph on all but two specimens, in which it directly connects to the protocone. The endoloph is continuous from the proto-

loph to the hypocone. A distinct mesocone is present along the endoloph at its center, where the mesoloph arises and runs buccally to the edge of the tooth. The metacone is anteroposteriorly compressed, and the metaloph runs transversely directly from it to the hypocone.

The posteroloph begins at the posterobuccal corner of the hypocone and runs to the buccal edge of the tooth posteriorly to the metacone.

The M2 is similar in morphology to M1, but is slightly smaller (Fig. 25F). The anterocone is variably present. The endoloph never connects directly with the protocone, but joins the protoloph at its center, near its junction with the posterior arm of the protocone. All other features are as in M1. There are no known M3 specimens from the John Day Formation.

Discussion.—*Plesiosminthus* specimens described here had previously been noted from the Campbell Ranch Fauna (Fremd and Whistler 2009), and preliminarily referred to *P. clivosus*. *Plesiosminthus fremdi* is intermediate in size, larger than *P. clivosus*, similar in size to the Hemingfordian *P. sabrae*, and smaller than nearly all other North American species (Table 20; Black 1958:86; Wilson 1960:82; Green 1977: table 3). *Plesiosminthus fremdi* differs from other members of the genus in a number of morphological features, as diagnosed by Black (1958), Green (1977), and Kimura (2013). When coded using the characters listed in Kimura (2013: appendices 1–2), *P. fremdi* shows a unique combination of characters that distinguish it from *P. clivosus*, *P. sabrae*, *P. grangeri* Wood, 1935c, and *P. meridionalis* Comte, 2000, as well as Eurasian taxa. Taxa formerly referred to “*Schaubeumys*” were recently synonymized with *Plesiosminthus* by Kimura (2013).

The anteroconid of the m1 in *P. fremdi* is isolated from the protoconid and metaconid, as is the case for *P. clivosus* and *P. grangeri*, while the anteroconid is absent or lies at the base of the metaconid in *P. sabrae* (Black 1958; Green 1977). The m1 ectolophid of *P. fremdi* is continuous with the metalophid on half of the m1s (three of six specimens). In *P. sabrae* the ectolophid rarely connects with the metalophid (Green 1977), while in *P. clivosus* the ectolophid connects anteriorly to the protoconid and in *P. grangeri* the ectolophid is variable, but usually does not connect to either the metalophid or protoconid. The m1 hypoconulid is absent in *P. clivosus*, and present in *P. fremdi*, *P. sabrae*, and *P. grangeri*. In *P. fremdi* and *P. grangeri*, the m1 hypoconulid is always connected to the hypoconid via a well-developed posterolophid, but in *P. sabrae* the hypoconulid is only weakly connected to the hypoconid (Green 1977). In *P. fremdi* the metaconid of the m2 connects to the anteroconid, as it does in *P. sabrae* and *P. grangeri*; this is unlike *P. clivosus* where it connects to the anterior arm of the protoconid.

The protoloph of the upper molars in *P. fremdi* is complete and attaches to the posterior arm of the protocone in both M1 and M2. In *P. grangeri* the protoloph is variable in M1 and connects to the posterior arm of the protocone

in M2 (Green 1977; Kimura 2013). In *P. clivosus* the protoloph connects to the posterior arm of the protocone in M1 and is incomplete in M2. And in *P. sabrae* the protoloph connects to the mesocone of M1 and is incomplete in M2. Green (1977) also suggested that the endoloph was incomplete on the M2 of *P. sabrae*. In all M2 specimens of *P. fremdi*, the endoloph is complete. In *P. sabrae* and *P. grangeri*, the metacone of the M1 is rounded, while in *P. fremdi* it is strongly anteroposteriorly compressed, as in *P. clivosus*. Kimura (2013) indicated that the metaloph of the M1 is curved and connects to the posterolabial corner of the metacone in *P. sabrae* and *P. grangeri*, but in *P. fremdi* the metaloph is straight and connects to the center of the metacone, as in *P. clivosus*.

The unique features of *P. fremdi* are: 1) the connection of the ectolophid to the metalophid on m1; 2) the relative size of m3 relative to m2 (80% length of m2 versus 86%); and 3) the connection of the endoloph to the protoloph on M1 and M2. On three of the six m1s of *P. fremdi*, the ectolophid is connected to the metalophid. Several other species of the genus have a much higher percentage of incomplete ectolophids on m1, as high as 80% (Black 1958; Green 1977). The anterior connection of the ectolophid is unique in *P. fremdi*, in that it is always lingual to the centerline of the tooth. In all other species, this connection is directly aligned with the center of the metalophid or angled buccally, connecting with the protoconid. The m3 is also relatively smaller in *P. fremdi* than in most other species. Korth (1987b) noted that in North American species of *Plesiosminthus*, the length of m3 averaged between 86 and 88% the length of m2. Only in the Barstovian *P. cartomylos* Korth, 1987b, was it less (76%). The known m3s of *P. fremdi* average only 80% the length of m2. In *P. fremdi*, the endoloph on all the M2s, and all but two specimens of M1, connects anteriorly with the protoloph between the paracone and protocone. Although highly variable (Green 1977), the connection of the endoloph on upper molars of other species is nearly always directly with the protocone.

Plesiosminthus occurs and is common at many localities in the Great Plains from the Arikareean through the Clarendonian, is known from the Hemingfordian of Delaware, and is common from Oligocene and Miocene sites in Europe and Asia (Daxner-Höck 1999; Flynn 2008b). The phylogenetic analysis of Kimura (2013) found *Plesiosminthus* from both Asia and North America to form a clade, sister to a clade that includes *Macrognothomys* Green, 1977, and *Sicista* Gray, 1827, the extant birch mice. That analysis points to at least two dispersal events of *Plesiosminthus* from Asia to North America, with dispersal of the ancestors of *P. clivosus* and *P. grangeri* in the early Arikareean (by 30 Ma) and a later dispersal of *P. meridionalis* (*Plesiosminthus* sp. of Emry and Eschelman, 1998) in the Hemingfordian around 18 Ma (Kimura 2013).

The absence of *Plesiosminthus* through most of the John Day section may be attributable to the ecology of sicistines. Extant birch mice have a semi-prehensile tail and are good climbers, tending to favor forests and relatively

wet habitats (Nowak 2005). Like tree squirrels, the rarity of these rodents may be due to preference for habitats where fossils are less often preserved (Flynn 2008b).

DISCUSSION

Since Cope's (1878, 1879, 1881) initial description of the faunas from the John Day Formation, no complete description of the entire rodent fauna has been published. The only detailed taxonomic studies that have been made are of the allomyine and meniscomyine Aplodontidae (Rensberger 1983) and pleurolicine and entoptychine Geomyidae (Rensberger 1971, 1973). Several reviews of specific families of rodents have also included John Day material: Castoridae (Stirton 1935; Martin 1987); Cricetidae (Wood 1936b; Martin 1980); and Sciuridae (Black 1963). A few species have also been named individually (Sinclair 1905; Miller and Gidley 1918; Wood 1935b, 1936). Most recently, a preliminary description of a microfauna consisting of mainly rodents was reported from the Kimberly Member of the John Day (Fremd and Whistler 2009). In all, over 40 species of rodents had been described from the John Day Formation; the additional material described here substantially improves our understanding of John Day rodents, raising the number to 54 rodent species described to date.

Biostratigraphy

Most early collections from the John Day Formation had poor locality and stratigraphic data, preventing analysis of how faunas changed through the sequence. The work of Fremd et al. (1994) and Albright et al. (2008) allowed the first detailed biostratigraphic assessment of mammals from the John Day Formation. This facilitated modification and recalibration of the Arikareean biozonations, updating the biostratigraphy and biochronology of Tedford et al. (2004). The rodents included in that biostratigraphic framework were some aplodontids, castorids, cricetids, "*Florentiamys*" (referred here to *Proapeomys*), and geomyids, primarily the more well studied John Day rodents (Albright et al. 2008). Here, we add biostratigraphic ranges for a series of species from important, but more poorly known groups, including eomyids, heteromyids, sciurids, a dipodid, and a eutypomyid (Fig. 26). The addition of these taxa allows more direct comparisons of the John Day rodent faunas to those at other sites in North America.

Castorids occur through the entire Arikareean of Oregon, with as many as three taxa co-occurring at one time. *Allotypomys* represents the first eutypomyid to be documented from Oregon, definitely occurring in the early early Arikareean (Ar1) and possibly surviving as late as the early late Arikareean (Ar3). The anchitheriomysine beaver *Microtheriomys* is restricted to the early early Arikareean (Ar1), but occurs through much of that interval. Palaeocastorine beavers are represented by *C. gradatus*, from Ar1 though Ar3, as well as two species of *Palaeocastor*.

Current records of *Palaeocastor* from the John Day Formation suggest the two species do not overlap temporally, with *P. peninsulatus* restricted to units below the Tin Roof Tuff (Ar1 – Ar2) and *P. fossor* above (Ar3 – Ar4?). The appearance of *P. fossor* in the early late Arikareean (Ar3) coincides with its appearance in the Harrison Formation of Wyoming and Nebraska (Flynn and Jacobs 2008).

Squirrel diversity is high through the Arikareean of Oregon, with five putative tree squirrels (Sciurini) and one flying squirrel (Pteromyini). The diversity of Sciurini is in sharp contrast with the Cenozoic record for most of North America, where tree squirrels are relatively rare (Goodwin 2008). The biostratigraphic range of *Miosciurus covensis*, restricted to the early early Arikareean (Ar1), is distinct from *M. ballovianus* (Ar2–Ar3), potentially making these two sciurids characteristic of these late Oligocene intervals in Oregon. Co-occurrence of *M. covensis* with *Protosciurus mengi* in the lower Turtle Cove fauna (Ar1) is followed by co-occurrence of *M. ballovianus* with *P. mengi* and *P. rachelae* in the upper Turtle Cove (Ar2), Kimberly (Ar3), and Haystack Valley faunas (Ar3). The stratigraphic range of *P. condoni* remains uncertain, while the possible gliding squirrel *Petauristodon* is known only from the Kimberly fauna (Ar3). The early late Arikareean (Ar3) occurrence of *Petauristodon* represents the earliest record of the genus in North America, though several earlier records of putative flying squirrels have been reported from the Cypress Hills Formation of Saskatchewan (Bell 2004).

Until now, no eomyids had been described from the John Day Formation, though they had appeared in a number of faunal lists (Fremd and Whistler 2009; Fremd 2010). The eomyids described here display rather restricted stratigraphic ranges, possibly making them useful for characterizing intervals of the Arikareean. *Neoadjidaumo arctozophus* and *Proapeomys condoni* are restricted to the first half of the early early Arikareean (Ar1), *?Proapeomys lulli* is restricted to the late early Arikareean (Ar2), and *Apeomys whistleri* and *Leptodontomys* are known only from the early late Arikareean (Ar3). The *Apeomys* specimens from the late Oligocene of Oregon predate records of the genus in Europe, in the latest Oligocene and early Miocene. However, it is important to note that all of these eomyids are represented by only a few specimens and their distributions may have been wider than is currently known.

Heteromyids, represented by *Trogomys oregonensis* and *Proheteromys thorpei*, first appear in the late Oligocene, late early Arikareean (Ar2), of Oregon. *Proheteromys thorpei* is one of the earliest occurrences of the genus, though *P. bumpi* and *P. gremmelsi* appear earlier, in the early early Arikareean (Ar1) Wounded Knee Fauna of South Dakota (MacDonald 1970). The late Oligocene occurrence of *T. oregonensis* is far older than the early Miocene type species *T. rupinimenthae*. In the early late Arikareean (Ar3), there are three heteromyids, including: *P. thorpei*, *P. latidens*, and *Mookomys* sp. The John Day occurrence of *Mookomys* from the late Arikareean (Ar3) is just slightly older than the occurrence of the type species, *M. altifluminis*, from

the Hemingfordian. The first recognizable perognathine, *B. aterosseus*, appears in the late late Arikareean (Ar4) and survives into the early Hemingfordian (He1). The occurrence of *B. aterosseus*, along with *Eochaetodipus asulcatus* from the late Arikareean of Nebraska, represents the earliest records of the subfamily. Given the similarity of *Bursagnathus* to more recent perognathines, it is possible that the Pacific Northwest represents the region where this important group originated.

The presence of *Plesiosminthus* in the Arikareean of Oregon is significant, as the Arikareean NALMA was defined by the earliest appearance of the genus in Tedford et al. (2004). Though the occurrence of the John Day species in Ar3 is substantially later than the appearance of *Plesiosminthus* in Ar1 of Nebraska, this new record helps facilitate direct faunal comparisons between the two regions.

Paleoecology and Paleoenvironmental Interpretations

The first burrowing rodents known from the fossil record of Oregon appear in the early Arikareean (Ar1). Both *Palaeocastor peninsulatus* and *Capacikala gradatus* are known from the lower and upper Turtle Cove strata. These beavers display cranial morphology consistent with scratch-digging behavior, and the postcranial morphology of *P. peninsulatus* suggests it likely used both its forelimbs and flattened incisors to dig (Samuels and Van Valkenburgh 2009; Caledo 2014). The occurrence of scratch-digging burrowing beavers in the early Arikareean (Ar1) represents the first appearance of burrowing mammals in Oregon, coinciding with cooling and drying of the environment and the expansion of bunch grassland habitats in the Oligocene, between 30 and 27 Ma (Retallack et al. 2000). *Palaeocastor* and *Capacikala* occur prior to the appearance and diversification of geomyids in the late early Arikareean (Ar2), including the well known *Pleurolicus* Cope, 1878, and multiple species of *Entoptychus* (Rensberger 1971, 1973). Morphology of entoptychine geomyids suggests they were also fossorial (Rensberger 1971), and burrows from the Harrison Formation of Nebraska suggest some taxa may have been chisel-tooth digging specialists (Gobetz and Martin 2006). In the early late Arikareean (Ar3), entoptychine gophers diversified and became incredibly abundant (Rensberger 1971).

Corresponding with early late Arikareean diversification of these geomyids, *Palaeocastor fossor* appears. *Palaeocastor fossor* is a specialized tooth-digging beaver species, as evidenced by both craniodental morphology and artifactual evidence (Peterson 1905; Martin and Bennett 1977; Samuels and Van Valkenburgh 2009). From the early Arikareean (Ar1) to early late Arikareean (Ar3), burrowing beavers seem to have transitioned toward a highly fossorial existence (Samuels and Van Valkenburgh 2009), exploiting the expansion of open habitats in the Oligocene (Retallack 2007). The small, abundant entoptychine geomyids and the larger, more specialized *P. fossor* likely partitioned habitats

like extant rodents do, by favoring different soil depths or consistency (Nevo 1999). The presence of highly fossorial burrowing beavers and entomochine gophers in the early late Arikarean clearly indicates the presence of at least partially open habitats at this time. This interpretation is compatible with the paleosol studies of Retallack (2004), who reconstructed these environments as representing grassy woodlands and desert shrublands.

Microtheriomys has craniodental morphology suggesting that it is closely related to *Propalaeocastor* from Eurasia, and thus it may have had very different ecology than other contemporaneous North American castorids. *Propalaeocastor* is thought to be the ancestor of *Steneofiber*, and later castorines (Hugueney 1999; Wu et al. 2004). *Steneofiber eseri* Viret, 1929, displays a specialized grooming claw, which in *Castor* is considered an adaptation for maintaining “non-wettable fur” associated with swimming (Hugueney and Escuillie 1995; Rybczynski 2007). *Propalaeocastor* was not included in the phylogenetic analysis of Rybczynski (2007), but in that analysis, *Steneofiber*, and all other castorines and castoroidines, were inferred to be part of a single semi-aquatic and woodcutting clade that originated in the Oligocene. *Anchitheriomys* was placed as sister to the clade that included Castorinae and Castoroidinae, with uncertain ecology (Rybczynski 2007). However, an anchitheriomyine beaver from the middle Miocene of China, *Anchitheriomys tungurensis* (Stirton, 1934) has postcranial similarities to extant beavers, suggesting it may also have displayed semi-aquatic habits (Stirton 1934). Further analyses, including *Microtheriomys* and *Propalaeocastor*, may indicate that these taxa were similar to the common ancestor of the swimming and woodcutting castorid clade.

The several species of *Protosciurus* known from the Arikarean of Oregon can be interpreted as ecological equivalents to extant tree squirrels. The craniodental structure of these squirrels has long been known to be remarkably similar to *Sciurus* (Black 1963), and we now know that their postcranial morphology was also similar to extant tree squirrels. Extant arboreal rodents display relatively gracile limb elements and elongate digits (Thornington 1972; Samuels and Van Valkenburgh 2008); the morphology of *Protosciurus* is consistent with an arboreal lifestyle. While postcrania of the several small *Miosciurus* species are unknown, their cranial and dental structure suggests a generalized form intermediate between arboreal and terrestrial squirrels (Black 1963). Dwarfing of *Miosciurus* through time, as suggested by the available material, is consistent with this squirrel evolving to avoid competition with the larger *Protosciurus* and potentially exploit a chipmunk-like niche. Persistence of both *Protosciurus* and *Miosciurus* as rare components of burrowing rodent-dominated faunas in the early late Arikarean (Ar3).

Postcranial materials of *Proheteromys latidens* and *Mookomys* sp. reveal locomotor diversity within early heteromyids, with some species already adapted to a saltatory lifestyle in the late Arikarean (Ar3). The John Day occurrence of *Mookomys* represents the earliest occurrence of a saltatory rodent in the Pacific Northwest, likely adapted to take advantage of the expansion of open habitats in the late Oligocene (Retallack et al. 2007). Both *Proheteromys* and *Mookomys* are considered to be relatively primitive among Heteromyidae among recent studies, considered Mioheteromyinae by Korth (1997) and “basal heteromyids” by Flynn et al. (2008), raising the question of whether the common ancestor of extant subfamilies might have been a quadrupedal saltator. This is not an unreasonable assertion given the structure of the recent molecular phylogeny of Heteromyidae by Hafner et al. (2007). That study found the two pocket mouse subfamilies, Perognathinae and Heteromyinae, to be sister groups relative to the Dipodomysinae. Their analysis suggests that these three subfamilies diverged almost simultaneously, near the Oligocene/Miocene boundary (about 22 Ma, Hafner et al. 2007). The occurrence of *Mookomys* from Ar3, combined with the saltatory adaptations characteristic of dipodomysines and perognathines, suggests that the family was likely saltatory prior to divergence of extant subfamilies, and that heteromyines may be secondarily terrestrial/semi-fossorial.

Even though no postcrania are known for *Bursagnathus*, cranial and dental materials are remarkably similar to the extant pocket mice *Perognathus* and *Chaetodipus*. The enlarged auditory bullae of *Bursagnathus* suggest adaptation to open habitats, which were common in Oregon in the late Oligocene and early Miocene. Given the quadrupedal saltatory locomotion of extant pocket mice, similar ecology is likely for earlier perognathines.

The ecology of early sicistines, like *Plesiosminthus*, is unknown. The extant birch mice (*Sicista*) are scansorial and have a semi-prehensile tail. Co-occurrence of *P. fremdi* with several tree squirrel species (*Miosciurus ballovianus*, *Protosciurus mengi*, *Protosciurus rachelae*, and *Petauristodon* sp.) in the Campbell Ranch fauna suggests the presence of relatively wet, forested habitats, as tend to be preferred by extant sicistines (Nowak 2005).

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Conclusions

The additional material described here has added ten new species and four new genera that are exclusive to the John Day fauna, and recognized species of four additional genera that were previously not reported from the fossil record of Oregon. Ongoing work will help place all other rodents from the John Day Formation into a biostratigraphic and evolutionary context. This work will allow comparisons with the more well-known rodent faunas of the Great Plains and greatly improve understanding of the evolution and dispersals of rodents through the Cenozoic of North America.

The rodent faunas of the John Day Formation document ecological and evolutionary response to significant environmental changes in the Oligocene, and facilitate more accurate paleoenvironmental reconstructions. The occur-

rence of open habitat-adapted taxa, like *Palaeocastor* and entoptychine geomyids, along with arboreal taxa, like *Protosciurus* and *Miosciurus*, is consistent with reconstruction of mosaic open woodland environments in the Oligocene of Oregon.

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