# HEMPHILLIAN RODENTS FROM NORTHERN OREGON
# AND THEIR BIOSTRATIGRAPHIC IMPLICATIONS

James E. Martin

Museum of Geology, South Dakota School of Mines and Technology, Rapid City, SD  57701
James.Martin@sdsmt.edu

## ABSTRACT

Hemphillian localities south of the Columbia River in northern Oregon have produced thousands of small mammalian fossils. Castorids, geomyids, cricetids, and a murid described herein were derived from the Arlington, Ordnance, and McKay Reservoir localities.  Large sample sizes allow a greater understanding of the range of variation and ontogenetic changes, as well as paleoecology and biostratigraphic distribution.  Two new taxa are described, *Parapliosaccomys wittei* sp. nov., a geomyine, and *Paronychomys woodburnei*, a hypsodont cricetid.  *Castor*, *Dipoides*, and *Parapliosaccomys* indicate the assemblages are late Hemphillian in age, although certain taxa indicate temporal differences among the localities.  The lower Arlington and Ordnance localities are the oldest, Arlington 15 is medial, and McKay Reservoir is the youngest of the assemblages.  A *Castor-Parapliosaccomys* Concurrent Range Biozone is named for the interval represented by the assemblages from northern Oregon and is correlated to Christmas Valley, OR, possibly Churchhill Butte and Hoye Canyon, NV, as well as with assemblages from the Great Plains at *Pliohippus* Draw, ZX Bar, Mailbox, and Honey Creek, NE.  The appearances of *Prosomys* and *Spermophilus* (*Spermophilus*) at the McKay Reservoir Locality provide another important datum indicating latest Hemphillian time.

## INTRODUCTION

R.W. Wilson's (1937b) review of Hemphillian rodents marked the culmination of investigations begun earlier in that century.  Other than Shotwell's (1956, 1970) works, largely concerned with paleoecology, small mammals from the Hemphillian of the Pacific Northwest have received relatively little attention.  Our collections from northern Oregon (Figure 1) from Arlington, Ordnance, and McKay Reservoir produced very large samples that illustrate intraspecific variation and stratigraphic distribution.

Prior to this research, information of the biostratigraphic distribution of rodents in northern Oregon was limited.  At many of the northern Oregon localities, good exposures, identifiable basalt flows, and the relative absence of channel deposits allowed recognition of vertical distribution of mammalian taxa. The abundant rodents were utilized to determine relative age differences in the Pacific Northwest, and their ranges allowed correlation with other Hemphillian rodent assemblages in North America.

This investigation includes lithostratigraphy, vertebrate paleontology, and correlation in Gilliam, Morrow, and Umatilla counties (Figure 1).  The original Ordnance Locality (=Westend Blowout of University of Oregon) occurred in Morrow County about 16 km south of the Columbia River, formed in a 1.5 square kilometer aeolian blowout.

An assemblage from McKay Reservoir south of Pendleton, Umatilla County, was described (Shotwell, 1956), and we have collected for the past 25 years. These specimens increase morphological knowledge of known species, add new elements, and provide refinement of age and environment of deposition.  The McKay specimens were found along the eastern shoreline from about 150 m of lateral exposure. Vertical distribution is somewhat limited, but fossils were found *in situ* from the upper 15 m of exposure.

The third area, south of Arlington, Gilliam County, consists of 12 localities (including the CIT Krebs Ranch localities).  From 20 square kilometers, localities produced fossils with the greatest vertical distribution, illustrating biostratigraphic and environmental differences.

## METHODS

To organize fossiliferous localities stratigraphically, geological correlations were made among localities.  At Arlington, three distinct lithologies persist through the uppermost exposures where most specimens were found.  Specimens were collected relative to distribution within discrete geological

sections, and lithological reference was made for each taxon. Unfortunately, limited vertical exposure at Ordnance made precise lithostratigraphic integration impossible; correlations were based upon vertebrate similarities.
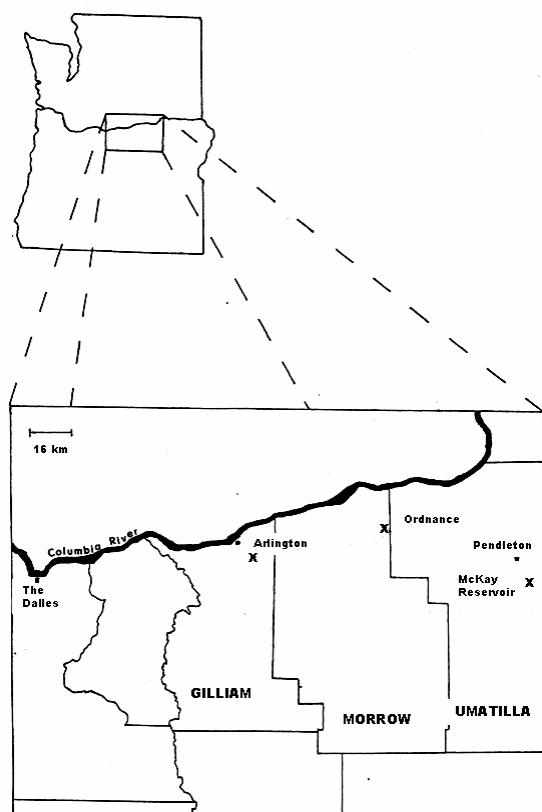


FIGURE 1. Index map of northern Oregon; X=fossil localities.

Close inspection of exposures every three months for five years, with sporadic collecting thereafter, resulted in large collections of rodents. Anthills were collected when available; normally, the stratigraphic source of the anthill debris was easily determined. Although large collections were obtained by surface collection, all fossiliferous sites were washed and screened to insure discovery of rare taxa.

Measurements were obtained under a binocular microscope. Unless otherwise noted, measurements are of maximum dimensions (A-P=anteroposterior; Tr=transverse) expressed in millimeters. Statistical abbreviations include: observed range (OR), mean (X), standard deviation (S), and coefficient of variation (CV). Tooth nomenclature follows Stirton (1936) for castorids, Shotwell (1967a) for cricetids, and Shotwell (1967b) for geomyids. Abbreviations: CIT=California Institute of Technology housed at LACM; LACM=Los Angeles County Museum of Natural History;

SDSM=Museum of Geology, South Dakota School of Mines, Rapid City; UCMP=University of California, Museum of Paleontology, Berkeley; UO=University of Oregon, Eugene; and UWBM=University of Washington, Burke Museum, Seattle. Note that specimens described below without an institutional acronym are from UWBM. Ordnance Locality=UWBM locality A8803; Arlington 3=UWBM B1532; Arlington 4=UWBM B1533; Arlington 5=UWBM B1534; Arlington 7=UWBM C0120; Arlington 8=UWBM C0121; Arlington 9=UWBM C0122; Arlington 11=UWBM C0124; Arlington 13=UWBM C0126; Arlington 14=UWBM C0127; Arlington 15=UWBM C0141; and McKay Reservoir=UWBM C0128.

## HISTORY OF INVESTIGATION

Modern knowledge of the northern Oregon Hemphillian assemblages from the Dalles Group began when Shotwell commenced collecting in the 1950s. He worked at all three areas discussed herein but concentrated primarily on paleoecology (1958). Only the collections from McKay Reservoir were described systematically (Shotwell, 1956). From the Ordnance Locality, a talpid was described (Hutchinson, 1968), and Shotwell (1967b) mentioned the geomyid *Pliosaccomys* from Arlington. Shotwell made an early attempt (1958) at paleoecological evaluation, concluding that Arlington and Ordnance represented a drier environment than at McKay Reservoir, but he did not address whether or not these assemblages were chronologically equivalent.

Newcomb (1971) extended the terminology of the Dalles Formation westward from its type area into the Arlington and McKay Reservoir areas. However, he noted an important consideration: fossils from the type Dalles Fm. were considered Clarendonian, whereas those at Arlington, Ordnance, and McKay Reservoir were Hemphillian.

Fry (1973) discussed northern Oregon assemblages, particularly from the Arlington area. He found fossils from the base of the Arlington section that he believed were Clarendonian or possibly Barstovian (1973:241).

Northern Oregon was intensively investigated when nuclear power plants were proposed near Ordnance and Arlington. As a result, the Dalles Fm. was elevated to group status and subdivided into separate formations (Farooqui et al., 1981). The sedimentary rocks superjacent to the Elephant Mountain Basalt in the Arlington area were termed the Alkali Canyon Formation without reference to the Shutler Fm. that had been utilized since the 1940s. Those rocks overlying the Columbia River Basalt Group south of Pendleton, were named the McKay
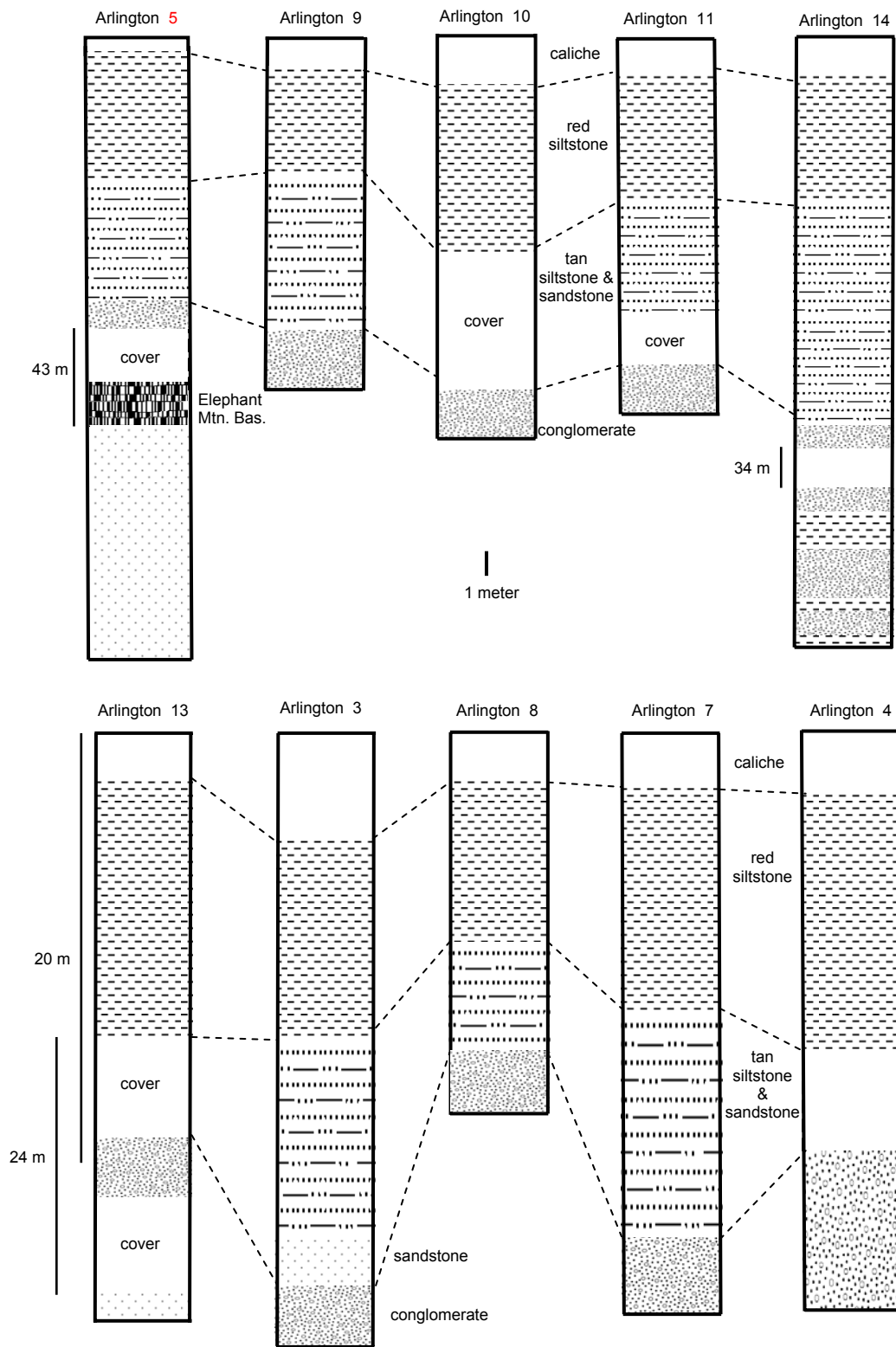
FIGURE 2. Stratigraphic sections of the Alkali Canyon Fm. at the lower Arlington localities.

Formation, based upon the fossiliferous rocks near McKay Reservoir.

Field investigations under my direction began as graduate studies and are continuing. Eight known fossiliferous localities in northern Oregon were re-collected and nine additional sites were found. Collections from these localities have more than doubled the specimen numbers and produced many hitherto unknown taxa. Coprolites from the localities were described, as well (Martin, 1981), and contained taxa that were rare or unknown based upon comparisons with material recovered from screen washing. For example, one coprolite from McKay Reservoir produced the only specimens of *Perognathus* and the rare *Oregonomys sargenti*, taxa adapted for a relatively arid environment (Martin, 1984) in contrast to most others at McKay Reservoir that indicate a riparian environment. Martin (1984) also described the heteromyids, noting that species from Ordnance and Arlington were less derived than those from McKay Reservoir, suggesting a temporal difference. A new chipmunk species and a new genus of large ground squirrel were described by Martin (1998). Larger mammals and insectivores will appear in later contributions.

## LOCAL LITHOSTRATIGRAHPHY

Across northern Oregon, the base of the exposed section is the upper Columbia River Basalt Grp. Schminke (1967) and Newcomb (1971) extended the terminology of the Yakima Basalt and Ellensburg Fm. from central Washington south to the Columbia River. At Arlington, the Pomona Basalt, the oldest unit exposed, forms the bottom of an east-west trending valley. The Rattlesnake Ridge Mbr. of the Ellensburg Fm., the Elephant Mountain Basalt, and the Dalles Grp. (Alkali Canyon Fm.) comprise the valley walls. Of these, the Alkali Canyon Fm. is the most fossiliferous. The Rattlesnake Ridge Mbr. equivalent at Arlington produced specimens that will be described subsequently.

The Alkali Canyon Fm. of the Dalles Grp. at Arlington consists of alternating conglomerates and tuffaceous siltstones and sandstones. A caliche layer caps the ridges that border the east-west valley, except at its western edge where the caliche descends down-section below the Elephant Mountain Basalt and is overlain by Pleistocene aeolian and fluvial deposits. In the lower 30 m of the Alkali Canyon Fm., two conglomeratic layers form prominent benches. A third conglomerate with larger fossils, exposed about 12 m below the caliche layer, persists throughout the region and was utilized as a datum for measured sections (Figure 2). The clasts consist of well-rounded basalt

with minor quartzite, andesite, and metamorphics in a coarse sandy matrix cemented by caliche. At Arlington 3, a coarse, loosely consolidated bluish sandstone and a black basalt sandstone are sporadically distributed above the conglomerate. These sands are overlain by a widespread tan siltstone and sandstone, the primary producer of fossil vertebrates. The caliche was developed in a thick unit of red siltstone, the highest stratigraphic unit of the Alkali Canyon Fm. at most localities. Fewer fossils occurred in the red siltstone than in the underlying tan unit, but yielded associated skeletons. The conglomerate, the tan siltstone and sandstone, and the red siltstone capped by a thick caliche can be traced throughout the area. Only at Arlington 15 were fossils encountered higher in the section. This locality consists of a small, isolated exposure of reddish siltstone about 12 m above the caliche level. At Arlington 13, fossils were reworked from the tan and red units into Pleistocene deposits; therefore, the specimens could not be utilized for biostratigraphic analysis but provided morphological data.

Before cultivation, the Ordnance Locality consisted of a large blowout caused by migrating dunes. Siltstones and coarse sandstones were exposed that overlie the Columbia River Basalt. The detrital units are similar to those exposed at Arlington, but the sands are coarser. Aeolian processes exposed the fossils and basalt clasts, concentrating them in deflation tracts where surface collection produced thousands of specimens.

Shotwell (1956:18) described the deposits at McKay Reservoir as consisting of a 1-1.5 m conglomerate overlying about 60 m of tuffaceous sandstones incised into the northerly dipping Columbia River Basalt. During later investigations, rubble and silt left by the receding water covered the lower half of the section. Only two layers of resistant tan siltstone were exposed about halfway through the section. The upper portion of the section is normally better exposed above a coarse basalt conglomerate containing fragmentary water-worn bones about 12 m below the top of the exposure (Figure 3). Most fossils occur in a white, tuffaceous claystone near the top of the section (Unit 8 of Figure 3), with fewer specimens from a suprajacent red siltstone. A weathered tephra, Unit 10, also contains vertebrates, occurs within the red siltstone, and with another tephra (Unit 4), brackets the principal fossiliferous interval.

## SYSTEMATIC PALEONTOLGY

Of the rodents from northern Oregon, the heteromyids, non-spermophiline sciurids, and rodent specimens from coprolites have been published

Unit 12; basalt cobble conglomerate, 2.5 m: conglomerate with well rounded clasts, ranging up to 20 cm in fine-grained basalt sand matrix, caliche developed at base, unconformable over other units, cutting east-west trending channels to the level of Unit 5, fossils rare

Unit 11; red siltstone/claystone, 1.2-1.4 m: identical to Unit 9, fossils abundant

Unit 10; gray tephra, 0.25-0.55 m: fossiliferous

Unit 9; red siltstone/claystone, 0.5-0.8 m: similar to Unit 7, fossils abundant, normally with black preservation

Unit 8; white claystone, 0.47-0.9 m: blocky weathered surface, fossils abundant, normally with bluish preservation

Unit 7; red claystone, 1.1-1.3 m: tan grading upward to red claystone with small sandy channels, blocky weathered surface, abundant fossils in channels, cut and fill

Unit 6; pinkish white claystone, 1.1 m: resistant clay with cut and fill base,

Unit 5; red claystone, 1.9 m: bright red, fine-grained argillaceous sand and claystone with rootlets, caliche, fossils rare

Unit 4; gray waterlain tephra, 0.4 m

Unit 3; gray claystone, 1.2 m: resistant with manganese-coated root molds, some clay clasts, sand, and scattered 7.5 cm basalt clasts near top, weathered to pocked surface

Unit 2; basalt cobble conglomerate, 1.8 m: conglomerate with well-rounded clasts, ranging from 13-25 cm in fine-grained sand and caliche matrix, cross-bedded, unconformable base, fossils rare

Unit 1; gray claystone, 1.25 m: resistant claystone with minor sandstone channels
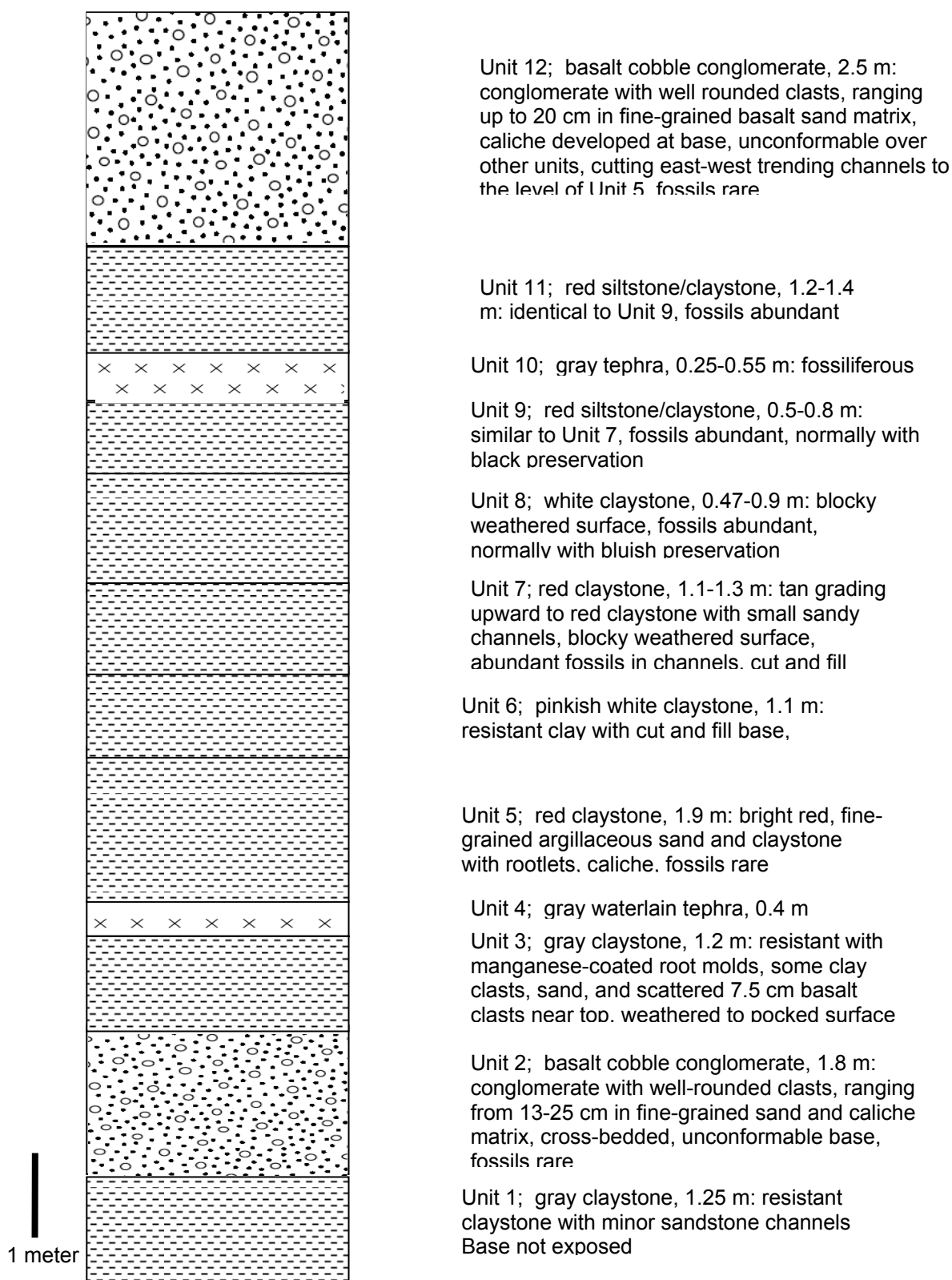Base not exposed

1 meter

FIGURE 3. Stratigraphic section of the McKay Formation at McKay Reservoir.

(Martin, 1984, 1998, 1981, respectively). The castorids, geomyids, cricetids, and murids are described below.

Class MAMMALIA Linnaeus, 1758
Order RODENTIA Bowditch, 1821
Family CASTORIDAE Gray, 1821
Genus *DIPOIDES* Schlosser, 1902
*DIPOIDES* sp. cf. *D. WILSONI*
Figure 4A-B

**Referred Specimens**—SDSM 21075, right dentary fragment with i; UWBM 54459, dentary with p4; 57267, p4; 57897, p4; 57268, m1 or m2 from Ordnance. UWBM 57244, M1 or M2; 57245, M1 or M2; 57246, M3; 57247, m3 from conglomerate at Arlington 4; 57249-57251, M1 or M2 from tan unit at Arlington 7. SDSM 19841, left i; UWBM 57252, M3 from conglomerate and 57253, M1 or M2 from basalt sandstone at Arlington 3. UWBM 57254, dentary with p4-m2 from tan unit at Arlington 11. UWBM 57263, M1 or M2; 57255, M3 from Arlington 13. UWBM 57258, 57890, P4; 57891, P4 (broken); 57259, 57892-57893, M1 or M2; 57260, 57894-57895, M3; 57256, 57261-57262, i; UWBM 57896, m3 from Arlington 15.

**Stratigraphic Source and Age**—Alkali Canyon Fm. of Dalles Grp.; late Hemphillian

**Description**—Although their posterior borders are poorly preserved, the two P4s are strongly curved, high-crowned, rootless, and larger than the molars. A very shallow paraflexus persists to the tooth base and is directly opposite the hypoflexus on 57890, whereas the paraflexus lies posterior to the hypoflexus on 57258. The mesoflexus is crescentic, curves posteriorly on one specimen, but is a transverse flexus on the other. Flexi are inflated and flattened at their terminations, particularly the hypoflexus.

The M1 and M2 at adult wear stages assume a compressed "S" crown pattern with enamel loph borders subparallel and transversely oriented; no specimens possess more than two inflections or fossettes as do those of *D. stirtoni* (Wilson, 1934:22). On upper molars and premolars, enamel thins along the posterior edges and at tooth margins where the lophs meet; enamel is thickest on the leading edges of the anterior and medial lophs.

Because the posterior loph is columnar, the M3 displays a distorted S-pattern (unlike those of *D. tanneri* that never attain an S-pattern) but otherwise is similar to the anterior molars. One M3, 57255 from Arlington 13, is smaller than the other M3 (Table 1) and exhibits a more complex crown pattern, perhaps indicating a different ontogenetic stage. The tooth is rootless, high-crowned, and would assume a modified S-pattern with wear. A small, shallow fossette lies

opposite the narrow termination of the hypoflexus, an inflection that crosses three-fourths of the occlusal surface and slants anteriorly. The mesoflexus curves posteriorly and bifurcates midway across the occlusal surface; one limb typically extends to the lingual margin, but the other is directed posterobuccally. A small fossette lies between the arms of the mesoflexus, and like the anterior fossette, could be easily removed by occlusal wear, but the bifurcating mesoflexus persists to the tooth base. Such a mesoflexus also occurs among the isolated teeth of UMMP 29704 of *D. wilsoni*, whereas UMMP 28158, a palate with third molars also from Saw Rock Canyon, displays the normal mesoflexus. Therefore, *D. wilsoni* possesses the same variations as among the Oregon specimens.
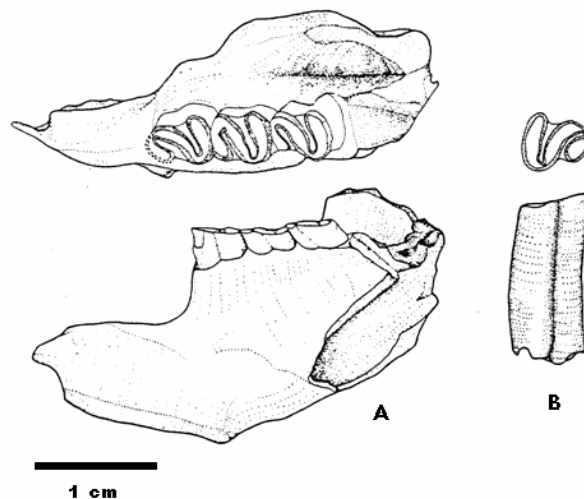


FIGURE 4. *Dipoides* sp. cf. *D. wilsoni*: A) UWBM 57254, right dentary with p4-m2; B) UWBM 57267, left p4.

The dentaries from Arlington and Ordnance resemble a compressed miniature of *D. smithi* from McKay Reservoir. UWBM 57254 from Arlington 11 has the roots of the posterior processes preserved, indicating the ascending ramus was more compact than that of *D. smithi*. Three small mental foramina occur on 57254, one is 3.5 mm anterior to the p4 below the diastema. No specimens of *D. smithi* have a foramen situated this far forward; most foramina occur below the anterior edge of the p4. Moreover, SDSM 21975 possesses only one foramen 1.2 mm anterior to the edge of the premolar. The incisor associated with this dentary fragment has faint crenulations in the enamel, like those of *D. smithi*. However, the incisor is narrower (3.8 mm) than that of *D. smithi*, which is

normally a millimeter larger (e.g. SDSM 27885—4.8 mm, SDSM 27976—5.2, 4.7 mm).

The dentary from Arlington, UWBM 57254 (Figure 4A), contains the only known p4 that has inflated lophid margins, a long middle lophid, and no parastriid. The three premolars from Ordnance (Figure 4B) are similar except that 57897 bears a well-formed parastriid that extends to the tooth base. Inflections of all four premolars have flattened terminations where the enamel thins. Thinning also occurs at the tooth margins where lophids meet; enamel is thick on the posterior edge of each lophid.

The m1 and m2 are composed of the S-shaped occlusal pattern characteristic of *Dipoides* and are similar to the premolar, except that the enamel is thin on the leading edge and no molars in their adult stage exhibit a parastriid. However, 57268 from Ordnance appears to be a broken lower molar that bears a shallow parafossette with thin enamel at its buccal and lingual extremities. Small size and upward taper indicate a young individual.

Except that the transversely compressed posterior lophid forms a convex posterior margin, the m3 resembles the anterior molars. The short posterior lophid of the Arlington specimens contrasts with that of *D. smithi*, on which the posterior lophid is the same width as the medial lophid, and the posterior edge of the tooth is flattened.

**Discussion**—Castorids are rare at Ordnance and Arlington but abundant at McKay Reservoir. Only four specimens of *Dipoides* were obtained at Ordnance. A few more specimens were found in the conglomerate and overlying tan siltstones and sandstones at Arlington. At the highest Arlington locality, Arlington 15, beavers are abundant, reflecting a more aquatic depositional environment (Shotwell, 1958:280).

Shotwell (1955) reviewed the known species of *Dipoides*, using size and the frequency of parastriae(ids) on premolars as diagnostic characters among species. Even with a small sample from Ordnance and Arlington, a size difference can be observed with specimens from McKay Reservoir, especially upper molars (Tables 1-2).

Specimens from Ordnance and Arlington are similar in size to *Dipoides williamsi* Stirton (1936) from Arizona, *D. vallicula* Shotwell (1970) from southeastern Oregon, and *D. wilsoni* Hibbard (1949) from Kansas and smaller than *D. stirtoni* (Wilson, 1934), *D. smithi* (Shotwell, 1955), and *D. tanneri* (Korth, 1998) from Nebraska. Cheek teeth of *D. williamsi* have more elongate medial lophids, a transversely shorter posterior lophid on p4 (3.5 mm compared to 3.75, 4.1, and 4.4), and shorter anterior lophids on molars, resulting in a more delicate, laterally compressed dentition compared to that of northern Oregon species. Although *D. williamsi* is

known by relatively few specimens and some size differences might be the result of intraspecific variation, the poor development of the anterior lophid on the molars appears diagnostic. On available specimens of *D. williamsi*, the anterior reentrant almost isolates the anterior lophid. Anterior lophid thickness from the termination of the anterior reentrant to the anterior edge of the molar has a maximum of 0.29 mm on *D. williamsi*, whereas the minimum thickness is 0.41 mm on Oregon specimens, indicating a very anteroposteriorly narrow and transversely short lophid on *D. williamsi*. The Oregon samples differ in being more robust with a square outline, owing to more complete lophid development.

---

TABLE 1. Dental measurements of *Dipoides* sp. cf. *D. wilsoni*

| | | A-P | Tr |
|---|---|---|---|
| Ordnance: | | | |
| UWBM 54459 | p4 | 4.75 | 3.8 |
| UWBM 57267 | p4 | 5.2 | 4.3 |
| UWBM 57897 | p4 | 5.15 | 3.65 |
| UWBM 57268 | M1 or M2 | | |
| | (broken, juvenile) | 3.75 | 3.4 |
| Arlington: | | | |
| UWBM 57258 | P4 | 5.25 | 4.5 |
| UWBM 57890 | P$^4$ | 4.5 | 4.6 |
| UWBM 57259 | M1 or M2 | 3.9 | 3.45 |
| UWBM 57892 | M1 or M2 | 4.25 | 3.95 |
| UWBM 57893 | M1 or M2 | 3.75 | 3.55 |
| UWBM 57244 | M1 or M2 | 3.85 | 3.95 |
| UWBM 57249 | M1 or M2 | 3.55 | 4.0 |
| UWBM 57253 | M1 or M2 | 3.55 | 3.3 |
| UWBM 57251 | M1 or M2 | 4.4 | 4.1 |
| UWBM 57263 | M1 or M2 | 4.0 | 3.7 |
| UWBM 57246 | M3 | 4.4 | 3.55 |
| UWBM 57255 | M3 | 3.5 | 3.1 |
| UWBM 57260 | M3 | 3.85 | 3.4 |
| UWBM 57894 | M3 | 4.2 | 3.45 |
| UWBM 57254 | p4 | 5.15 | 4.2 |
| UWBM 57254 | m1 | 4.5 | 4.1 |
| UWBM 57254 | m2 | 4.7 | 3.8 |
| UWBM 57247 | m3 | 4.65 | 3.5 |
| UWBM 57896 | m3 | 4.65 | 3.1 |

---

The specimens from Ordnance and Arlington are similar to *D. vallicula*, but are slightly larger. Medially expanded cheek tooth lophs, instead of parallel borders on the lophs; flattened flexi(ids) terminations, rather than broadly expanded terminations; and an anteroposteriorly elongate middle lophid on p4, instead of a compressed lophid distinguish these specimens from those of *D. vallicula*. The latter feature suggests anterior expansion from the parastriid, diagnostic of *D. vallicula* (Shotwell, 1970). Only one p4 from Ordnance possesses a parastriid, and two upper premolars have a shallow paraflexus unlike that of *D. vallicula*, on which a parastriid normally occurs, and the paraflexus crosses at least half of the occlusal surface to abut against the hypoflexus or connects with it to isolate the anterior loph. Therefore, although *D.*

*vallicula* is geographically the closest species within this size range, its morphology differs from that at Ordnance and Arlington.

*Dipoides* from Arlington and Ordnance have size and loph structures similar to those of *D. wilsoni* from Saw Rock Canyon, Kansas. In both groups, lophs are expanded medially rather than exhibiting parallel sides like those of *D. vallicula*. Parastriids are normally absent on the lower premolars of *D. wilsoni*, but three of eleven premolars from Kansas possess the striid. Expanded terminations of the flexi(ids) are often flattened; on those premolars without a parastriid, a tendency exists for bifurcation of the terminations. The paraflexus of *D. wilsoni* is normally absent or short, but on UMMP 28158, the paraflexus joins the hypoflexus to isolate the anterior loph, similar to that of *D. vallicula.*

*D. vallicula*, *D. wilsoni*, and *Dipoides* species from Arlington and Ordnance have variations of the parastriae(ids), but the latter two groups have expanded loph borders and flattened termination of the flexi. Lack of an adequate sample, however, makes positive assignment impractical, so the specimens from northern Oregon are provisionally referred to *D. wilsoni. Dipoides wilsoni* has also been recorded from the upper Snake Creek beds (*Pliohippus* Draw), Nebraska (Skinner et al., 1977), Saw Rock Canyon Local Fauna, Kansas (Hibbard, 1949), and Churchill Butte, Nevada (Kelly and Lugaski, 1999).

_____

TABLE 2. Dental measurements of *Dipoides smithi*

|  |  |  | N | OR | X | S | CV |
|---|---|---|---|---|---|---|---|
| P4 | A-P |  | 10 | 4,25-6.5 | 5.30 | .74 | 13.97 |
|  | Tr |  | 10 | 3,75-5.4 | 4.96 | .27 | 5.42 |
| M1 or M2 | A-P |  | 13 | 3.8-5.3 | 4.62 | .40 | 8.74 |
|  | Tr |  | 13 | 4.0-5.5 | 4.71 | .43 | 9.23 |
| M3 | A-P |  | 6 | 4.3-5.1 | 4.64 | .27 | 5.80 |
|  | Tr |  | 6 | 3.7-4.0 | 3.82 | .11 | 2.95 |
| p4 | A-P |  | 15 | 4.65-7.2 | 5.99 | .73 | 12.25 |
|  | Tr |  | 15 | 4.25-5.7 | 4.83 | .41 | 8.56 |
| m1 | A-P |  | 11 | 4.35-5.75 | 5.25 | .40 | 7.60 |
|  | Tr |  | 11 | 4.3-5.3 | 4.77 | .33 | 6.85 |
| m2 | A-P |  | 11 | 4.55-5.7 | 5.32 | .33 | 6.24 |
|  | Tr |  | 11 | 4.2-5.3 | 4.79 | .38 | 7.82 |
| m3 | A-P |  | 4 | 4.2-5.5 | 4.93 | .59 | 11.99 |
|  | Tr |  | 4 | 3.7-4.6 | 4.25 | .40 | 9.51 |

_____

*DIPOIDES SMITHI* Shotwell 1955

**Referred Specimens**—UWBM 57303-57306, 18 I; 57301, palate with P4-M3; 57302, palate with M1; 57307, 5 maxillae (edentulous); 57308-57317, P4; 57318-57331, M1 or M2; 57332-57336, M3; 57283-57286, 21 i; 57287, dentary with i, p4-m3; 57288, dentary with p4-m3, 57289-57295, dentaries with p4-m2; 57296, dentary with p4; 57297-57298, dentaries with m1; 57300, dentary with m2; 57272, 6 p4; 57273-57276, 14 m1 or m2; 57277, 2 m3 from McKay Reservoir.

**Stratigraphic Source and Age**—McKay Fm. of Dalles Grp.; late Hemphillian

**Description**—These specimens are larger than those from Ordnance and Arlington (Table 2) and add to the sample of *Dipoides smithi* of Shotwell (1955) by including the first known specimens of m3, by providing additional palates and additional dentaries with ascending rami, and by doubling the number of other dental elements.

The incisors of *D. smithi* bear faint crenulations that Shotwell (1970:37) regarded, along with a general size increase, as significant in the evolution toward *Procastoroides*.

On the P4 in the palates, 57301 and 57302, a shallow parastria extends down a fourth of the tooth height, and on all but two premolars, a shallow groove persists down the buccal side. Unlike that of *D. stirtoni*, the paraflexus is poorly formed, appearing only as a notch posterior to the hypoflexus. Therefore, although Shotwell diagnosed *D. smithi* without parastriae on adult premolars, they appear infrequently and are always poorly formed. The hypoflexus termination is normally flattened, and the enamel thins on this anteroposteriorly directed crest. The mesoflexus termination can be flattened or pointed, and the flexus normally curves posteriorly.

The upper molars closely match Shotwell's description (1955:131). A feature not discussed, however, is the enamel thickening on the anterior borders of each loph. The enamel is thinner on the posterior border of the anterior and medial lophs and is thinnest on the posterior border of the posterior loph and where the enamel is oriented anteroposteriorly.

Shotwell (1955:130) noted that the p4 of *D. smithi* infrequently has a parastriid. Of p4, only four possess parastriids that extend to the tooth base. Normally, the premolar and lower molars have expanded loph margins and flattened flexid terminations.

The heretofore unknown m3 assumes the typical "S" pattern and is more anteroposteriorly compressed than that of many *Dipoides* species, particularly on the posterior lophid. Instead of a rounded posterior border like those from Arlington and Ordnance, the tooth is flattened because both sides of the posterior lophid are parallel. In one specimen, 57277, an expanded anterior flexid termination is almost bifurcated.

**Discussion**—Stirton (1935:452) suggested a phylogenetic line leading from *Eucastor* through *Dipoides* to *Castoroides*. After the description of *Procastoroides* (Barbour and Schultz, 1937), Shotwell (1970:39) stated that *Dipoides* gave rise to *Procastoroides*, which evolved into *Castoroides.* Recent investigation suggests that *Dipoides* was

derived from *Prodipoides* (Korth, 2007) and was on a separate clade from *Eucastor* (Korth, 2007). The transition from *Prodipoides* to *Dipoides* involved the extension of the flexi(ids) to the tooth bases instead of being worn to fossettes(ids), loss of metastriae(ids), and increased hypsodonty. From the late Clarendonian of Nebraska, *D. tanneri* (Korth, 1998) is very similar to *D. stirtoni* from the early Hemphillian and appears the least derived species of *Dipoides* with striae(ids) that extend to tooth bases.

When *Dipoides* became established in the Hemphillian, size appears to distinguish two lineages. In the lower Hemphillian deposits at Rome, Oregon, and Thousand Creek, Nevada, a large species, *D. stirtoni*, retains parastriae(ids) on the premolars and fossettes on some molars. Similar structures appear on a smaller species, *D. vallicula* from the lower Hemphillian deposits at Little Valley, Oregon. From the upper Hemphillian, a large species, *D. smithi*, and two small species, *D. wilsoni* and *D. williamsi*, have S-shaped cheek teeth with only infrequent occurrences of the parastriae(ids) on the premolars. Perhaps *D. smithi* evolved from *D. stirtoni* and *D. wilsoni* and *D. williamsi* were derived from *D. vallicula.*

The largest species of *Dipoides*, from the Blancan age, are taxa from which Shotwell (1970) believed *Procastoroides* evolved. These large species must have originated from a plesiomorphic species, such as *D. stirtoni*, because both *D. intermedius* from Hagerman, Idaho, and *D. rexroadensis* from the Rexroad Fm., Kansas (Hibbard, 1941), the Ringold Fm., Washington (Gustafson, 1978) and fluvial deposits in South Dakota (Green, 1977), have a metastria(id) on some teeth (the latter species has a parastriid on p4). The large size of these species and their retention of characters found in early Hemphillian species make a taxon similar to *D. stirtoni* a likely ancestor. However, no such representatives have been found in late Hemphillian assemblages, suggesting that the largest species might be immigrants or their ancestors had a restricted distribution.

Genus *CASTOR* Linnaeus, 1758
*CASTOR* sp. cf. *C. CALIFORNICUS*
Figure 5A-B

**Referred Specimens**—UWBM 57280, 57281, p4; SDSM 27987, m1 or m2 fragment; UWBM 57282, m1 or m2 from McKay Reservoir. SDSM 21074, M3; UWBM 57266, p4; SDSM 21073, m1 or m2; UWBM 46663, m1 or m2 from Ordnance.

**Description**—The M3 is of a young individual based on size (Table 5), strongly curved crown, rootless condition, and crenulated enamel. All flexae exhibit rounded ends. The paraflexus is crenulated, the long mesoflexus curves far posteriorly, and the short

metaflexus is straight. The short hypoflexus has a small fossette adjacent to its rounded end.

Although the lower premolars represent different stages of occlusal wear, all are distinctly curved buccally, similar to the condition of *C. californicus*. One p4 from McKay Reservoir, UWBM 57281 (Figure 5A), is only slightly worn and rootless. UWBM 57280 (Figure 5B) and UWBM 57266 have roots, but the latter specimen from Ordnance is more heavily worn, as can be determined by a metafossettid with a crenulated posterior margin. UWBM 57280 and 57266 have similar crown patterns with a long paraflexid that trends anteriorly so the anterior lophid recurves. The hypoflexid and mesoflexid are opposite, abut one another, and the mesoflexid has a flattened termination. On UWBM 57280, the metaflexid is long, crossing about four-fifths of the occlusal surface, but the metastriid is short, and a metafossettid would soon be formed (e.g. 57266). The paraflexid is of intermediate length, and the mesostriid extends to the tooth base where the enamel pinches in and terminates.
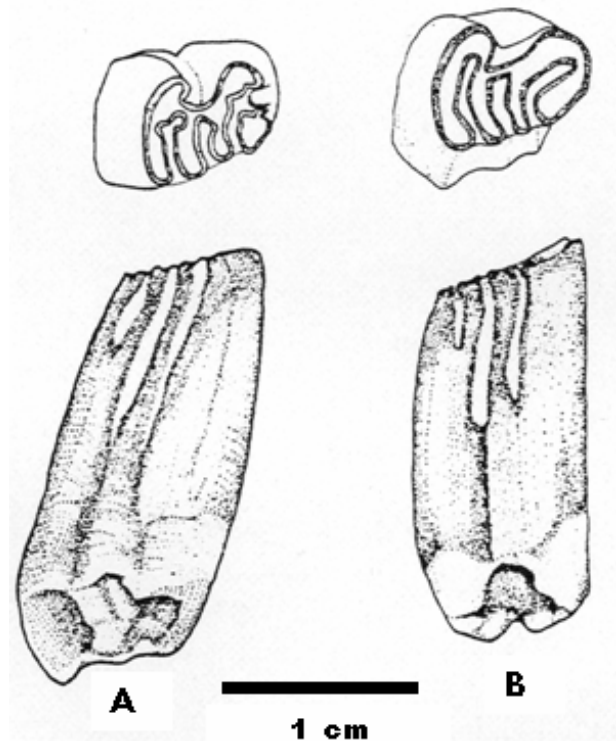


FIGURE 5. *Castor* sp. cf. *C. californicus*: A) UWBM 57281, left p4; B) UWBM 57280, left p4.

The unworn premolar, UWBM 57281, differs in several ways. Crenulations on flexid margins, no root formation, incomplete flexid development, and high crown indicate an early ontogenetic stage of this individual. The parastriid of 57281 is much longer

than those of UWBM 57280 and 57266, extending almost to the tooth base, like the mesostriid. At this wear stage, the cuspate anterior lophid is separated by a shallow fissure from the tooth body.

---

TABLE 3. Comparison of hypostria(ids) lengths of *Castor* from Grandview and Hagerman to *C. californicus*.

| Grandview: | N | OR | X | S | CV |
|---|---|---|---|---|---|
| P4 | 1 | 28.5 | | | |
| M1 or M2 | 5 | 14.1-27.8 | 21.98 | 5.77 | 26.23 |
| p4 | 3 | 19.5-24.8 | 22.7 | 2.82 | 12.41 |
| m1 or m2 | 3 | 10.4-22.5 | 17.63 | 5.77 | 26.23 |
| TOTAL | 12 | 10.4-28.5 | 21.62 | 5.47 | 25.32 |
| | | | | | |
| Hagerman: | | | | | |
| P4 | 5 | 18.5-25.0 | 22.78 | 2.64 | 11.61 |
| M1 or M2 | 16 | 11.25-23.0 | 16.58 | 3.64 | 21.94 |
| M3 | 5 | 10.5-18.0 | 14.8 | 3.05 | 20.63 |
| p4 | 9 | 5.0-23.5 | 13.77 | 5.1 | 37.41 |
| m1 or m2 | 10 | 8.5-21.2 | 13.77 | 4.54 | 32.98 |
| m3 | 2 | 6.5-15.5 | 11.0 | 6.36 | 57.85 |
| TOTAL | 47 | 5.0-25.0 | 15.58 | 4.90 | 31.47 |
| | | | | | |
| *C. californicus* | | | | | |
| P4 | 3 | 9.0-23.5 | 16.17 | 7.25 | 44.85 |
| M1 or M2 | 15 | 10.0-24.1 | 17.7 | 4.13 | 23.34 |
| M3 | 2 | 7.25-16.25 | 11.75 | 6.36 | 54.16 |
| p4 | 5 | 9.8-24.0 | 15.61 | 5.43 | 34.76 |
| m1 or m2 | 10 | 7.3-19.1 | 12.11 | 3.24 | 26.80 |
| m3 | 3 | 4.8-12.3 | 9.43 | 4.05 | 42.93 |
| TOTAL | 40 | 4.8-24.1 | 15.0 | 4.96 | 33.08 |

---

TABLE 4. Comparison of hypostriae(ids) lengths of all teeth of *Castor* from Grandview and Hagerman to those of *C. californicus* from UCMP V3520 and V4855 before and after root formation.

| Before: | N | OR | X | S | CV |
|---|---|---|---|---|---|
| Grandview | 8 | 19.5-28.5 | 24.64 | 2.86 | 11.59 |
| Hagerman | 27 | 10.5-25.0 | 17.99 | 4.31 | 23.97 |
| *C. californicus* | 25 | 11.3-24.1 | 17.74 | 3.71 | 20.94 |
| | | | | | |
| After: | | | | | |
| Grandview | 3 | 10.4-17.8 | 14.1 | 3.7 | 26.24 |
| Hagerman | 17 | 5.0-16.4 | 11.77 | 3.4 | 28.89 |
| *C. californicus* | 12 | 4.8-13.25 | 9.85 | 2.23 | 22.66 |

---

TABLE 5. Dental measurements of *Castor* sp. cf. *C. californicus*

| Ordnance: | | A-P | Tr |
|---|---|---|---|
| SDSM 21074 | M3 | ~7.5 | 6.0 |
| UWBM 57266 | p4 | --- | ~9.0 |
| UWBM 46663 | m1 or m2 | --- | ~9.5 |
| SDSM 21073 | m1 or m2 | 7.9 | 9.1 |
| | | | |
| McKay Reservoir: | | | |
| UWBM 57280 | p4 | 11.7 | 8.5 |
| UWBM 57281 | p4 | 9.0 | 6.7 |
| UWBM 46663 | m1 or m2 | 8.3 | 8.8 |
| SDSM 27987 | m1 or m2 | --- | 13.5 |

---

UWBM 46663 from Ordnance appears to be a lower molar of an old individual as indicated by its lack of curvature, root formation, and crown morphology, but is too poorly preserved for definite assignment. UWBM 21073 is a worn molar whose hypoflexid meets the metafossettid, and the ends of both are squared. The mesofossettid curves anteriorly and has a rounded end. The paraflexid is almost worn to a fossettid with a bifurcated end.

The lower molar from McKay Reservoir, SDSM 27987, has a hypoflexid deflected anteriorly whereas the metaflexid is bent posteriorly. The mesoflexid is straight, whereas the paraflexid has a bifurcated end. Bifurcated ends of paraflexids commonly occur on specimens of extant *Castor canadensis*. (e.g. SDSM R238). UWBM 46663, a lower molar from McKay Reservoir, is water worn and from an old individual as indicated by well formed roots. The paraflexid is crenulated, and the hypoflexid and metaflexid are opposite. With a length of 2.2 mm, the parastriid is the longest lingual inflection. The other two striids are almost obliterated, indicating the posterior flexids would soon be worn to fossettids.

**Discussion**—Only two species of *Castor*, *C. californicus* Kellogg (1911) and *C. accessor* Hay (1927) have been described from the Tertiary of North America. *C. californicus* was described from the Blancan San Joaquin Fm. at Kettleman Hills, California, an assemblage intermediate in age between those of Hagerman and Grand View. The type of *C. accessor* is a p4 from a young individual collected near Froman Ferry, Idaho. Shotwell (1970:39) did not feel that this p4 was an adequate type specimen and designated a dentary with a complete dentition as a plesiotype from nearby Grand View, which Bjork (1970) considered younger than Hagerman. Repenning et al. (1995) indicated that the Froman Ferry assemblage is about a half million years younger than Grand View, which is Blancan V (Repenning, 1987), and that the Hagerman assemblages are as much as 1.3 million years older than Grand View.

Some difficulty has arisen in distinguishing the two species, particularly when evaluating the specimens from Hagerman, which Shotwell (1970) and Gazin (1936) assigned to *C. accessor*, but Zakrzewski (1969) and Stirton (1935) considered as *C. californicus*. Conrad (1980) in an unpublished doctoral dissertation synonymized the two species based on comparisons of a sample from Hagerman with that from Grand View. Repenning et al. (1995) concurred but had only a few teeth from Froman Ferry for comparison. On all observed cheek teeth from the Hagerman assemblages in the Glenn's Ferry Fm., Idaho, from the Kettleman Hills, from Grand View, and from northern Oregon, the hypostriae(ids) extend to the bases of the enamel; however, the hypostriae(ids)

appear longest on those from the Grand View assemblage (Table 3). Comparison of age groups on the basis of root formation (Table 4) reduced the standard deviations, and particularly, the coefficients of variation. Therefore, although not abundant, specimens from McKay Reservoir and Ordnance are not differentiable from *C. californicus* on the basis of available material. The species from Grand View, *C. accessor*, appears more hypsodont, does not have a strongly curved p4, and comes from younger deposits than does *C. californicus*.

These Oregon specimens also appear similar to *C. californicus* from the Ringold Fm. in Washington (Gustafson, 1978). However, too few specimens are known from either the Ringold Fm. or from northern Oregon for precise determination.

## *CASTOR* sp. indet.

**Referred Specimens**—UWBM 57264, cheek tooth fragment from tan unit at Arlington 7. UWBM 57265, cheek tooth fragment from the conglomerate at Arlington 3.

**Description**—These two fragments are the first large castorids from the Arlington localities and are of similar size as those from Ordnance and McKay Reservoir. One specimen consists of a fossette; the other is a fragment with the hypostria and a fossette.

**Discussion**—*Castor* is rare at all northern Oregon localities, particularly at Arlington, where only fragments were found. The paucity of specimens seems to reflect actual abundance. Perhaps the greater abundance of *Dipoides* at McKay Reservoir may indicate that they dominated the riparian habitat in the Hemphillian when *Castor* first appears in North America. At the Ordnance and Arlington localities, inhospitable environment appears to be a factor in the scarcity of *Castor*. *Castor* appears in North America in the late Hemphillian upper Snake Creek Fm. (*Pliohippus* Draw), Mailbox Locality, Santee and Devils Nest Airstrip assemblages, Nebraska (Voorhies, 1990a), and at the northern Oregon localities.

Family GEOMYIDAE Bonaparte, 1845
Subfamily GEOMYINAE Baird, 1857
Genus *PARAPLIOSACCOMYS* Shotwell, 1967b

**Revised Generic Definition**—A geomyine approximately the size of *Phelosaccomys* Korth and Reynolds (1994), *Pliosaccomys dubius* Wilson (1936) and smaller species of *Thomomys*; rostrum arched but not so much as that of *Thomomys*; anterior root of zygomatic arch originating above and opposite P4; mandibular symphysis long, extending back to below p4 resulting in an angular ventral margin of dentary; shallow pit lateral to m3 on dentary; ascending ramus arises lateral to m2; cheek teeth with dentine tracts more than 2 mm extending onto the enamel crown; roots formed on cheek teeth; roots of upper and lower first and second molars fused; cheek teeth higher crowned than those of species of *Pliosaccomys* but lower crowned than those of species of *Thomomys*; P4 protoloph and metaloph unite medially; p4 metalophid composed of three ridges when unworn; bilophate molars anteroposteriorly compressed with shallow medial valleys that do not extend to the tooth base and soon wear away forming a single pillar; unworn lower molars with compressed anterior cingulids, especially on m3.

## *PARAPLIOSACCOMYS WITTEI*, sp. nov.
Figures 6; 7a-e; 8f-h; 9f-h; 10

**Type Specimen**—UWBM 56844, left dentary with p4-m2

**Type Locality**—Arlington 7 (UWBM locality C0120) from the tan unit

**Stratigraphic Source and Age**—Alkali Canyon Fm. of Dalles Grp.; late Hemphillian

**Referred Specimens**—UWBM 56836, 3 I; 56837, 4 I, 6 i; 56838-56839, P4; 56840-56842, M1 or M2; 56843, dentary with i, p4; 56845-56847, dentaries (edentulous); 56855, i; 56848, p4; 56849-56854, m1 or m2 from tan unit at Arlington 7. UWBM 55844-55854, I; 55754, palate (edentulous); 55755-55756, maxillae (edentulous); 55757-55795, P4; 55796-55836, M1 or M2; 55837-55843, M3; 55846, dentary with i, dp4-m1; 55847-55848, dp4; 55668, dentary with i, p4-m2; 55669-55672, dentaries with p4; 55673-55675, dentaries with i; 55676-55677, dentaries (edentulous); 55678-55707, p4; 55708-55745, m1 or m2; 55746-55753, m3 from tan unit at Arlington 14. UWBM 57047, palate (edentulous); 57048-57049, i; 57050, m1 or m2 from tan unit; 57501, I; 57052, M1 or M2; 57053-57054, i; 57055, m3 from base of red siltstone; 57056, 2 I; 57057, i; 57058, dentary with p4-m1 from top of red siltstone from Arlington 5. UWBM 56916, i from tan unit; 56917, P4; 56918, M1 or M2; 56920, dentary with i from base of red siltstone from Arlington 9. UWBM 56883, i; 56884, maxilla (edentulous); 56885, rostrum; 56886-56888, P4; 56889, M1 or M2; 56890-56891, dentaries with p4-m1; 56892, dentary (edentulous); 56893, p4; 56894, m1 or m2; 56895-56896, m3 from tan unit; 56897, i; 56898-56899, palates (edentulous); 56900-56902, M1 or M2; 56907-56909, P4; 56910-56911, m1 or m2 from base of the red siltstone from Arlington 11. UWBM 56803, I from conglomerate; 56804, I; 56805, dentary (edentulous) from basalt sandstone; 56806, i; 56807-56808, P4; 56811-56812, m1 or m2 from top of tan unit; 56813, i; 56814, p4 from base of red siltstone; 56815, m3 from top of red siltstone from Arlington 3. UWBM 56858,
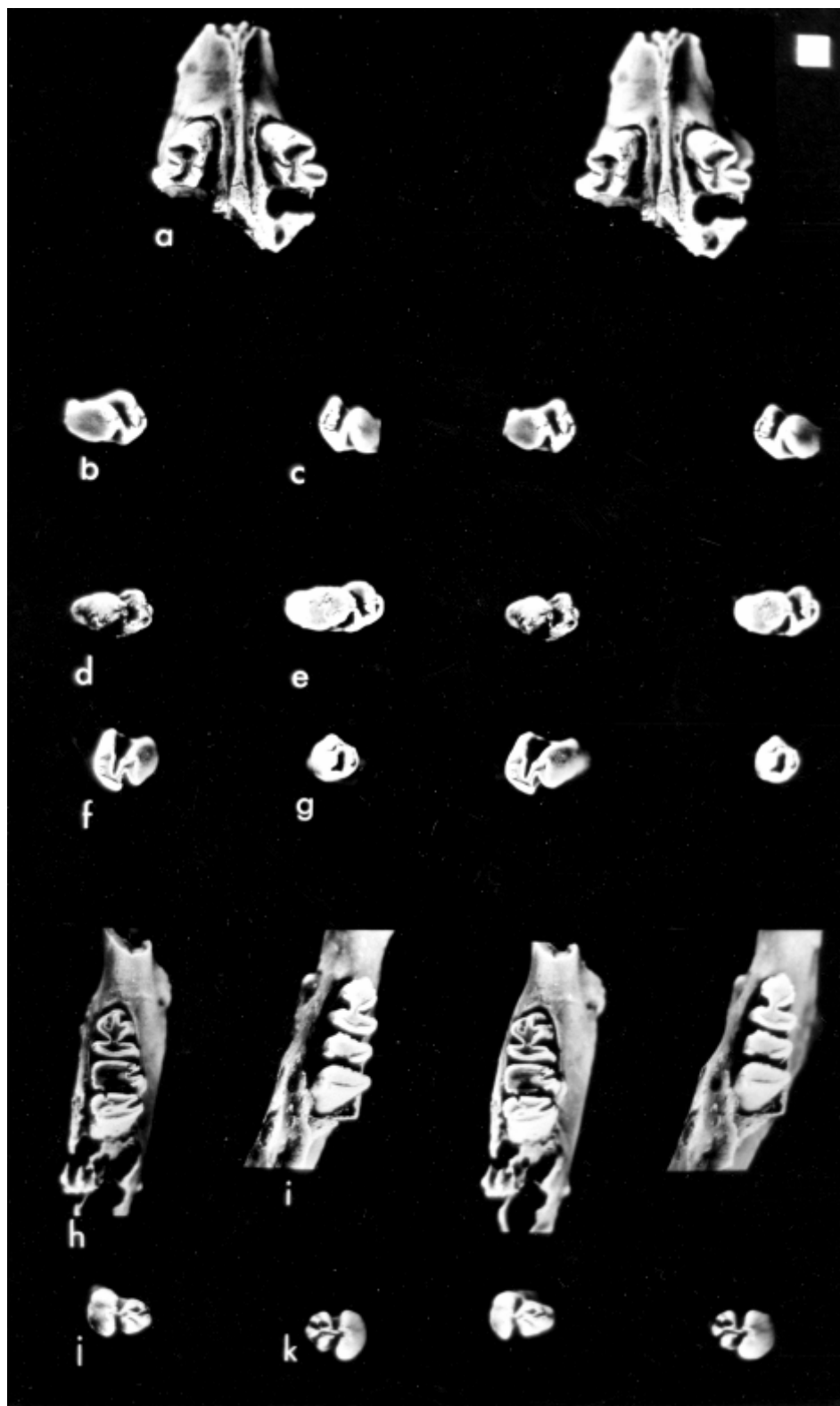
FIGURE 6. *Parapliosaccomys wittei*:  a) UWBM 55483, palate with 2 P4; b) UWBM 55758, left P4; c) UWBM 55757, right P4; d) UWBM 54274, left P4; e) UWBM 54289, left P4; f) UWBM 55793, right P4; g) UWBM 55838, right M3; h) UWBM 56844, left dentary with p4-m2; i) UWBM 55668, left dentary with p4-m2; j) UWBM 55583, left p4; UWBM 55678, right p4.  Buccal is to the top of figures of isolated teeth.  Scale equals one millimeter.

palate (edentulous); 56860, I; 56861-56862, P4; 56859, i from tan unit at Arlington 8. UWBM 56786-56788, P4; 56789-56790, M1 or M2; 56791, 3 i; 56792, i; 56793, dentary (edentulous); 56794-56796, m1 or m2 from conglomerate at Arlington 4. UWBM 56931-56933, 7 I; 56935, maxilla (edentulous); 56936, P4; 56938, i; 56939, dentary with p4; 56940, 57509, dentaries (edentulous); 57060-57601, p4; 57062-57063, m1 or m2, 56937, m3 from Arlington 13. UWBM 55561, I; 55488, rostrum; 55483-55484, palate with 2P4; 54176, palate; 54177, 10 palates (edentulous); 55485-55487, palate (edentulous); 55489-55524, P4; 55525-55553, M1 or M2; 55554-55560, M3; 55572, i; 55562, 55565, 55574-55576, dentaries with p4-m1; 55563-55564, 55566, 55568, 55573, 55577-55581, dentaries with p4; 55557, dentary with m1; 55570-55571, dentary with i; 55569, 55582, dentaries (edentulous); 55583-55613, p4; 55666-55667, dp4; 55614-55654, m1 or m2; 55655-55665, m3 from Ordnance.

**Diagnosis**—shallow rugosities on lateral side of dentary; cheek teeth less hypsodont than those of *Parapliosaccomys oregonensis*; distance from enamel base to base of medial valley on upper and lower first and second molars normally less than 2.0 mm; dentine tracts never over half the tooth length and never exceeding 1.0 mm on p4-m1; medial valleys on molars shallower than on species of *Pliosaccomys* but deeper than on *Parapliosaccomys oregonensis*; metaloph and metalophid on first and second molars Y-shaped with expanded anterior cingulum(id); little expansion of anterior cingulum(id) on third molars; dp4 quadrate and well worn before molars occlude.

**Etymology**—Named for Beverly and Bernhard Witte (pronounced witty) in appreciation for their encouragement and aid in the field and laboratory. Beverly found the type specimen and type locality.

**Description**—UWBM 55754 and 55484 exhibit a slightly arched rostrum, but not so much as that of *Parapliosaccomys oregonensis* from McKay Reservoir or species of *Thomomys*. A medial ridge occurs on all palates of *P. wittei*, and the tooth rows converge anteriorly. The two palates, 55483 (Figure 6a) and 55484, are very old individuals whose premolars had been worn beyond the level of the base of the enamel on the posterior loph. The upper incisors have wide, flat anterior faces with faint grooves close to their medial borders and exhibit the short, chisel-shaped, wear pattern characteristic of *Thomomys*.

Although the cusp disposition on the cheek teeth of *Parapliosaccomys wittei* is very similar to that of *Pliosaccomys dubius* (Wilson, 1936), the teeth of *P. wittei* are higher crowned and exhibit dentinal tracts. The medial valley persists almost to the crown base on

upper and lower first and second molars on species of *Pliosaccomys*, and the distance between the base of the enamel and the base of the valley ranges from 0 to 0.9 mm. This distance varies between 0.9 and 2.1 mm on *P. wittei*, indicating that crown lengthening occurs below the medial valley. Except for slight inflections that never exceed 0.2 mm on some teeth of *P. dubius*, dentine tracts are essentially unknown among species of *Pliosaccomys*. Well formed dentine tracts on *P. wittei* never extend more than 1 mm up the lingual margins of the lower cheek teeth and are not longer than 2 mm on any cheek teeth.

The bilophodont P4 of *P. wittei* normally bears a bicusped protoloph as evinced by the wide protoloph on worn specimens and two small cusps on unworn premolars such as 54274 (Figure 6d), 54289 (Figure 6e), 55757 (Figure 6c), and 55758 (Figure 6b), but some unworn specimens appear to possess only a single cusp. Wilson (1936:22) noted that *P. dubius* might have more than a single cusp on the protoloph of P4, and CIT 1799 supports this contention. A bicusped protoloph also occurs on *Pliosaccomys higginsensis* (Dalquest and Patrick, 1989) from the early Hemphillian Higgins Local Fauna. The lateral profile of the protoloph appears straight as considered diagnostic of *P. higginsensis* (Dalquest and Patrick, 1989), although some variation was noted among specimens of *P. wittei*.

The metaloph of the P4 of *P. wittei* is composed of a metacone, hypocone, hypostyle, and a posterior cingulum that originates at the posterobuccal edge of the hypocone, swings posteriorly around the hypocone, and intersects the hypostyle at the lingual border of the metaloph. The cingulum, which might have functioned to separate lophs of the P4 and M1 for masticatory efficiency, does not extend as far posteriorly as that of *P. dubius* and does not remain as long on the occlusal surface. With occlusal wear a small fossette is formed posterior to the hypocone. On 55793 (Figure 6f), the fossette is divided, but the fossettes do not persist, and the metaloph becomes crescentic. The interior limb of the crescent connects to the protoloph in early wear stages. As wear progresses, the connection shifts medially, resulting in a pattern similar to compressed triangles connected at their apices. This initial loph connection is similar to that of species of *Phelosaccomys* (Korth and Reynolds, 1994; Korth 1998). However, with wear a central basin occurs on upper premolars of the latter species. During late wear, the enamel of *P. wittei* does not persist on the lateral edges of the lophs when the premolar is planed to the level of the dentine tracts. These tracts extend up a third of the metaloph height, but reach only to just above the base of the lateral valley on the protoloph.

The tract heights vary, but the relative difference between lophs remains constant.

The upper molars are all similar except for a size decrease posteriorly (Table 6). All upper molars are bilophodont with a lingual loph connection, but the protoloph is approximately one-fourth longer than the metaloph, whereas on *P. dubius*, the lophs are equal. In *P. wittei*, the protoloph of M1 or M2 consists of a protostyle, protocone, and paracone aligned in a sharp, straight crest. In contrast, the tricusped metaloph is crescentic, curved posteriorly, and resembles the metaloph configuration of the P4 in posterior cingulum development, and for a short time, a fossette. With wear below the external valley, the lophs resemble those of *Thomomys* that narrow externally and form a tear-shaped surface. With wear, the occlusal surface intersects the dentine tracts whose lengths vary more than on the premolars, extending from one-half to two-thirds the height of M1-M2.

The M3 (Figure 6g) is smaller, and more curved than the anterior molars, but cusp morphology is similar. The protoloph is a transverse crest and longer than the metaloph to which it connects both lingually and buccally to form a deep medial fossette. This large fossette persists until the M3 is worn to a pillar and to the level of the dentine tracts, which extend up one-third of the molar height. The unworn metaloph possesses a short cingulum similar to M1-M2, and with wear, a shallow fossette can form.

The deep, robust dentaries of *P. wittei* are not as massive nor have the extremely pointed ventral margin characteristic of *Thomomys* but is more angular than that of *Phelosaccomys* (Korth and Reynolds, 1994). The posterior symphyseal margin of *P. wittei* terminates below the p4, whereas on *P. dubius*, the scar does not extend to the p4, and that of *Thomomys* extends behind the p4. The posteroventral symphysis of *P. dubius* is relatively smooth, whereas that of *P. wittei* is angular and just anteroventral to the anterior termination of the masseteric scar. This scar is bounded by a ridge for insertion of the *M. masseter lateralis* that is usually more distinct than that for the *M. masseter medialis*. The confluence of the ridges lies below the anterior root of p4, and the dorsal ridge for the *M. masseter medialis* extends posterodorsally to the anterior root of the coronoid process, whereas the ventral ridge fades just above the origin of the angular process. Unlike *P. dubius*, the dentary of *P. wittei* has lateral rugosities where bone is molded around the cheek teeth roots, indicating the higher crowned teeth of *P. wittei*.

The posterior dentaries are not as well preserved, except for the ascending ramus of 54187. The coronoid process originates external to m2, and external to m3 is a shallow pit for insertion of the *M.*

TABLE 6. Dental measurements of *Parapliosaccomys wittei*.

| Arlington 7: | | N | OR | X | S | CV |
|---|---|---|---|---|---|---|
| P4 | A-P | 1 | 1.7 | | | |
| | Tr | 1 | 1.75 | | | |
| M1 or M2 | A-P | 3 | 0.8-0.85 | 0.83 | .03 | 3.46 |
| | Tr | 3 | 1.5-1.7 | 1.65 | .13 | 8.02 |
| p4 | A-P | 3 | 1.4-1.85 | 1.68 | .25 | 14.65 |
| | Tr | 3 | 1.3-1.6 | 1.47 | .15 | 10.42 |
| m1 or m2 | A-P | 8 | 0.9-1.05 | .95 | .06 | 6.29 |
| | Tr | 8 | 1.45-1.7 | 1.64 | .09 | 5.59 |
| | | | | | | |
| Arlington 11: | | | | | | |
| P4 | A-P | 3 | 1.25-1.75 | 1.43 | .28 | 19.21 |
| | Tr | 3 | 1.3-1.75 | 1.5 | .23 | 15.28 |
| M1 or M2 | A-P | 4 | 0.7-0.9 | .84 | .10 | 11.30 |
| | Tr | 4 | 1.2-1.7 | 1.5 | .21 | 14.14 |
| p4 | A-P | 6 | 1.6-2.15 | 1.93 | .23 | 11.70 |
| | Tr | 7 | 1.35-1.55 | 1.48 | .06 | 4.30 |
| m1 or m2 | A-P | 6 | 0.9-1.0 | .95 | .06 | 6.66 |
| | Tr | 6 | 1.3-1.65 | 1.52 | .13 | 8.51 |
| m3 | A-P | 2 | 1.0 | | | |
| | Tr | 2 | 1.2-1.3 | 1.25 | .07 | 5.66 |
| | | | | | | |
| Arlington 14: | | | | | | |
| P4 | A-P | 38 | 1.1-2.0 | 1.59 | .23 | 14.18 |
| | Tr | 35 | 1.2-2.0 | 1.62 | .14 | 8.32 |
| M1 or M2 | A-P | 41 | 0.7-1.1 | .94 | .08 | 8.36 |
| | Tr | 40 | 1.05-2.1 | 1.63 | .23 | 14.09 |
| M3 | A-P | 7 | 0.9-1.2 | 1.06 | .11 | 10.73 |
| | Tr | 7 | 1.3-1.5 | 1.41 | .07 | 4.88 |
| p4 | A-P | 29 | 1.1-2.0 | 1.57 | .21 | 13.44 |
| | Tr | 28 | 1.2-1.6 | 1.41 | .16 | 8.21 |
| m1 or m2 | A-P | 39 | 0.8-1.2 | .99 | .08 | 8.26 |
| | Tr | 39 | 1.25-1.85 | 1.48 | .15 | 10.13 |
| m3 | A-P | 8 | 0.8-1.0 | .99 | .06 | 6.46 |
| | Tr | 8 | 1.0-1.4 | 1.21 | .12 | 10.28 |
| | | | | | | |
| Ordnance: | | | | | | |
| P4 | A-P | 40 | 1.1-1.9 | 1.58 | .19 | 11.94 |
| | Tr | 40 | 1.25-1.95 | 1.64 | .18 | 11.06 |
| M1 or M2 | A-P | 29 | 0.75-1.0 | .89 | .06 | 7.06 |
| | Tr | 29 | 1.1-1.85 | 1.58 | .18 | 11.49 |
| M3 | A-P | 7 | 0.8-1.2 | 1.02 | .13 | 13.0 |
| | Tr | 7 | 1.25-1.5 | 1.37 | .10 | 7.25 |
| p4 | A-P | 39 | 1.25-2.05 | 1.65 | .21 | 12.92 |
| | Tr | 39 | 1.1-1.7 | 1.38 | .14 | 10.22 |
| m1 or m2 | A-P | 41 | 0.75-1.1 | .98 | .08 | 8.34 |
| | Tr | 41 | 1.1-1.8 | 1.42 | .17 | 12.52 |
| m3 | A-P | 11 | 0.9-1.1 | 1.01 | .07 | 6.84 |
| | Tr | 11 | 1.1-1.5 | 1.40 | .11 | 8.03 |

| Arlington 3: | A-P | Tr |
|---|---|---|
| UWBM 56807, P4 | 1.60 | 1.50 |
| UWBM 56808, P4 | 1.50 | 1.45 |
| UWBM 56809, p4 | 2.00 | 1.55 |
| UWBM 56818, p4 | 1.85 | 1.65 |
| UWBM 56814, p4 | 1.70 | 1.80 |
| UWBM 56811, m1 or m2 | 1.05 | 1.70 |
| UWBM 56812, m1 or m2 | 0.95 | 1.50 |
| UWBM 56815, m3 | 1.20 | 1.70 |

| Arlington 4: | A-P | Tr |
|---|---|---|
| UWBM 56786, P4 | 1.50 | 1.70 |
| UWBM 56788, P4 | 1.30 | 1.40 |
| UWBM 56789, M1 or M2 | 0.90 | 1.70 |
| UWBM 56790, M1 or M2 | 0.80 | 1.30 |
| UWBM 56795, m1 or m2 | 1.05 | 1.90 |
| UWBM 56796, m1 or m2 | 1.00 | 1.40 |

| Arlington 5: | A-P | Tr |
|---|---|---|
| UWBM 57052, M1 or M2 | 0.85 | 1.25 |
| UWBM 57058, dentary with p4 | 1.30 | 1.10 |
| " " m1 | 0.90 | 1.30 |
| UWBM 57050, m1 or m2 | 0.95 | 1.55 |
| UWBM 57055, m3 | 0.85 | 1.20 |
| | | |
| Arlington 7: | | |
| UWBM 56917, P4 | 1.70 | 1.65 |
| UWBM 56918, M1 or M2 | 0.80 | 1.90 |
| | | |
| Arlington 8: | | |
| UWBM 56861, P4 | 1.40 | 1.25 |
| UWBM 56862, P4 | 1.60 | 1.15 |
| | | |
| Arlington 13: | | |
| UWBM 56936, P4 | 1.40 | 1.55 |
| UWBM 56939, p4 | --- | 1.50 |
| UWBM 57060, p4 | 1.25 | 1.25 |
| UWBM 57061, p4 | 2.05 | 1.40 |
| UWBM 57062, m1 or m2 | 0.90 | 1.75 |
| UWBM 57063, m1 or m2 | 0.80 | 1.40 |
| UWBM 56937, m3 | 1.00 | 1.35 |

_____

*pterygoideus internus*. On 55669 and 54185, the posterior mandibular foramen is above the bone ridge formed by the incisor. The articular process appears similar to that of *Thomomys*, and a distinct incisor capsule is broken from 55668, 54187, and 57059. Above the capsule, a prominent furrow deepens caudally. The dorsal root of the angular process lies below the capsule, whereas the ventral origin is below and behind the m3.

Like those of other geomyines, the lower incisor possesses a euhedral cross section with a wide, flat anterior face. Wear results in a chisel-shaped occlusal pattern.

One dentary, 57058 (Figure 7a), has a newly erupted premolar, and with other isolated specimens, a spectrum of wear stages can be illustrated. When unworn, the p4 is hypsodont, bilophid, and has a medial connection between lophids. Lophids are tricuspid: the hypolophid cusps are arranged in a straight, transverse line, whereas the metalophid resembles a trefoil similar to that of *Thomomys* and *P. dubius*. Normally, as on 55583 (Figure 6j) and the type specimen (Figure 6h), a long, crest-shaped anteroconid is flanked by the metaconid and protoconid. On other p4s, such as 57058, the anteroconid remains conical, and the metaconid and protoconid send short crests anteriorly. Further metalophid complication results from accessory cuspules and ridges in major reentrants. For example, 55678 (Figure 6k) has additional ridges connecting the anteroconid to the metaconid and to the anterior crest of the protoconid. This elaborate metalophid occurs on specimens from Ordnance and Arlington, and is very similar to the unworn p4, CIT 1809, of *P. dubius*, indicating a close phylogenetic relationship. Variation of the unworn p4 metalophid of *P. wittei* might be expected; cusps exist for a short time

before worn away. The geomyines evolved toward the worn occlusal pattern, which is identical among the specimens from Arlington and Ordnance. Moreover, similar variation of the unworn pattern occurs at both sites, indicating conspecificity.

The sharp hypolophid crest is worn into an anteroposteriorly compressed ellipse, but the worn pattern of the p4 of *P. wittei* varies depending on the shape of the unworn metalophid. On specimens with a long anteroconid, wear produces a trefoil on the metalophid with a slight lingual shift of the axis, as exemplified by 55684. The two reentrants between major metalophid cusps persist until late wear stages, and the lingual groove usually extends further down the tooth. Wear on the metalophid with a conical anteroconid results in the shape of a fork with a short middle tine (e.g. 55681). As on 55682, the middle crest fuses with the metaconid, resulting in a single anterobuccal indentation. Further wear causes the lateral crests, which were originally directed toward one another, to fuse, forming a fossettid. In later wear stages, all remnants of the crown pattern are obliterated, and an ovoid shape persists throughout much of the tooth height. The final stage of wear, regardless of original pattern, occurs when the occlusal surface is planed below the upward extent of the dentine tracts, as on 55701. The dentine tracts extend up one-fourth of the length of the hypolophid, measured from the base of the lingual valley, and are never greater than 1 mm. Shotwell (1967b:45) also noted dentine tracts on two p4s from Kreb's Ranch I and II at Arlington.

Two isolated dp4s are known from Ordnance, and another in a dentary with an unerupted m1 (55846, Figure 7b) from Arlington 14. The dp4s are very similar, consisting of four cusps on each side connected by a medial ridge. The only appreciable differences are that 55846 has a cuspule in the middle buccal reentrant and the anterior lingual reentrant is deeper on those from Ordnance. The buccal cuspule is of questionable significance because of limited masticatory utility only in very late wear stages. The slightly deeper reentrant may be of greater utility, but additional specimens are required to determine its intraspecific variation. All three deciduous premolars from northern Oregon are of the same relative hypsodonty and have deeper reentrants than those of *P. dubius*. The molars in the dentaries of CIT 1810, *P. dubius*, and UWBM 55846 are unworn and at about the same eruption stage. The dp4 of CIT 1810, however, is more heavily worn medially, almost to the reentrant valleys, whereas the lophids remain high on 55846. Other differences include the more prominent connection of anterior and posterior lophids with the medial ridge and the long posterior lophid of *P. wittei* compared to the condition of *P. dubius*.
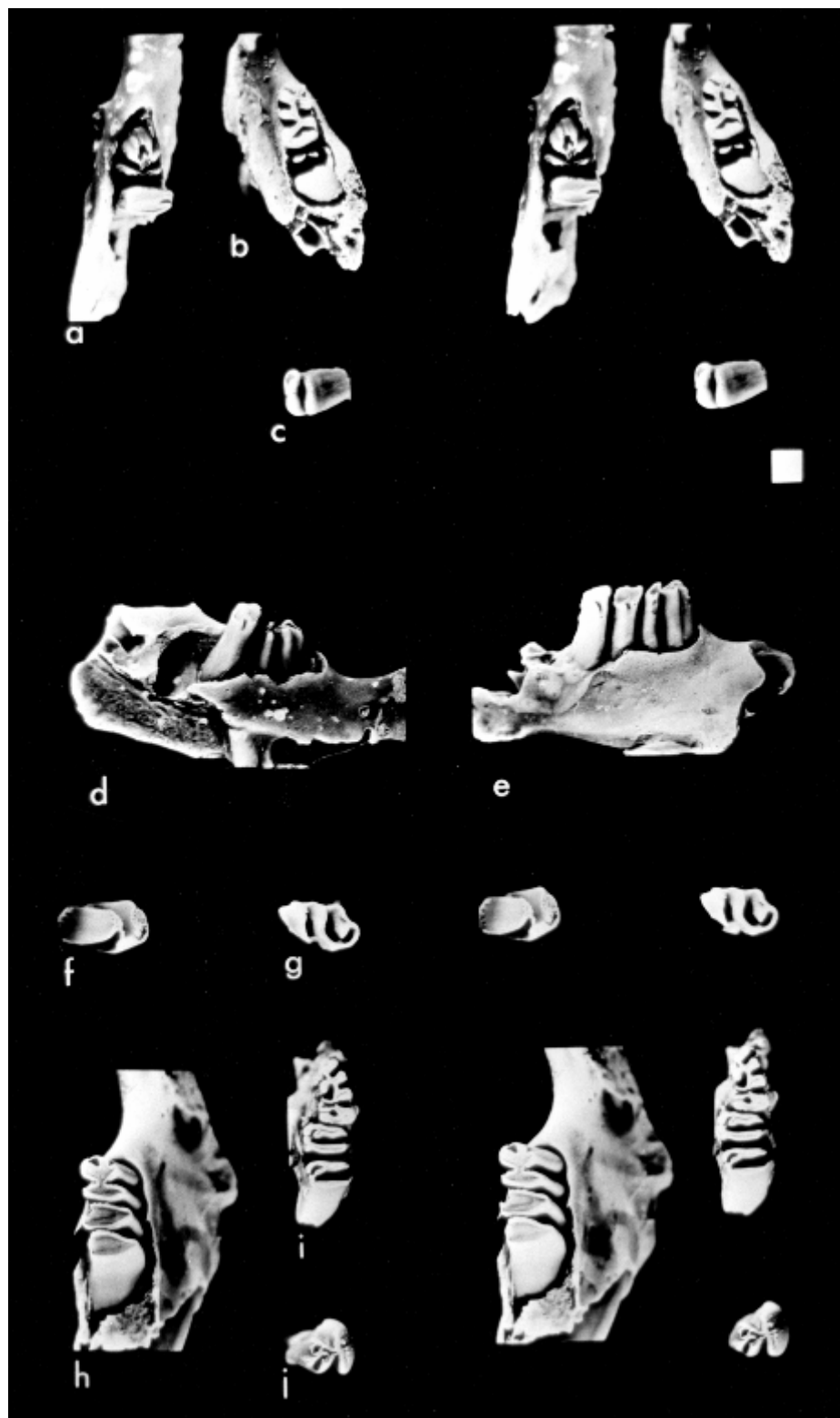
FIGURE 7. *Parapliosaccomys wittei*:  a) UWBM 57058, left dentary with p4-m1; b) UWBM 55846, right dentary with dp4-m1; c) UWBM 55655, right m3; d) UWBM 57058, left dentary with p4-m1, lingual view; e) UWBM 56844, left dentary with p4-m2, type specimen, lingual view. *Parapliosaccomys oregonensis*:  f) UWBM 57642, P4; g) UWBM 57649, left dP4; h) UWBM 57672, left dentary with p4-m2; i) UWBM 57680, right dentary with dp4-m2; j) UWBM 57682, right p4.  Buccal is to the top of figures of isolated teeth.  Scale equals one millimeter.

Many m1 and m2 are known. Unworn molars like 55616 and the unerupted molar in the dentary of 55846 display a long, sharp hypolophid composed of minute cusps that are barely discernible, resulting in a serrated appearance. The metalophid assumes the typical Y-shape of Wood (1935) and is composed of the metaconid, protoconid, and an anterior cingulid that connects to the protostylid. The cingulid is normally continuous around the buccal margin and merges with the hypolophid, or can be separated by a notch on the hypolophid, as is characteristic of *P. dubius*. The notch on the molars of *P. wittei* is seldom as deep as that of *P. dubius* and is almost worn away before the premolar occludes, as on 57058 (Figure 7d). The fissure remains distinct on the molars of *P. dubius*, even after p4 occlusion, such as on the holotype, CIT 1796.

Various wear stages are illustrated by numerous m1 and m2. On 57058, a dentary with a partially erupted p4, the m1 is slightly worn, exhibiting a buccal connection and an incipient medial lophid connection, resulting in a buccal fossettid and a short, shallow lingual valley. The occlusal pattern is almost worn away, and the m1 would have been monolophid when the p4 was completely erupted. Only a lingual indentation would remain to attest to the early bilophid structure. This wear stage is illustrated by the holotype of *P. wittei*: the p4 is slightly worn, the m1 is monolophid with a pointed lingual termination, and the m2 is at the same wear stage as the m1 of 57058. This wear succession differs from that of *P. dubius* and *Pliosaccomys magnus* (Kellogg, 1910) from Thousand Creek, Nevada, on which even after p4 wear, the m1 remains deeply fissured, and the lingual molar ends become pointed only after extreme wear when the crown pattern is removed. Therefore, *P. wittei* is more derived than *P. dubius* or *P. magnus*, more closely approaching the condition of *Thomomys* with monolophid molars with pointed lingual margins.

The m3 of *P. wittei* is bilophid with a medial connection. UWBM 55655 (Figure 7c) is unworn and illustrates a compressed anterior m3 cingulid that does not extend as far anteriorly as that of *P. dubius* or *P. higginsensis*, ending at the buccal metalophid termination, not entering the medial valley. Therefore, the metalophid is narrower than that of *P. dubius*. The m3 lophids of *P. wittei* initially are separate, but through wear, they unite medially and form a monolophid tooth with lingual and buccal indentations.

*PARAPLIOSACCOMYS OREGONENSIS* Shotwell
1967b
Figures 7f-j; 8a-c; 9a-c; 10

**Type Specimen**—UO 3631, dentary with i, p4-m1.

**Type Locality**—McKay Reservoir (UWBM locality C0128).

**Stratigraphic Source and Age**—McKay Fm., Dalles Grp.; late Hemphillian.

**Referred Specimens**—In addition to specimens described by Shotwell (1967b): UWBM 57639, palate (edentulous); 57640, rostrum; 57641, 3 I; 57643-57648, P4; 57649, 2 dP4; 57650-57664, M1 or M2; 57665-57670, M3; 57671, dentary with p4-m3; 57672-57673, dentaries with p4-m2; 57674-57677, dentaries with p4; 57678, dentary with m1-m2; 57679, dentary with i; 57680, dentary with dp4-m2; 57681, 10 i; 57682-57692, p4; 57693-57712, m1 or m2; 57713-57715, m3 from McKay Reservoir.

**Amended Diagnosis**—mandibular symphyseal area larger than that of *Parapliosaccomys wittei*; buccal dentary with prominent rugosities; check teeth as much as 25% higher crowned than those of *P. wittei*; dentine tracts always over half the tooth height, and in adults over 2.0 mm on p4 and m1, ranging from 2.0 to 4.1 mm; distance from enamel base to medial valley base on M1-M2 normally more than 2.0 mm, ranging from 1.3-4.3 mm; molars with very shallow medial valleys that do not persist as long as those of *P. wittei*; dp4 with pointed anterior end; compressed Y-shaped metalophid on lower molars; medial valleys of m1 and usually m2 completely worn away sooner than those of *P. wittei*.

**Description**—The arched rostrum and palate of *P. oregonensis* closely resemble those of *P. wittei* with three subparallel ridges that separate the anteriorly converging tooth rows. The unworn cheek teeth of *P. oregonensis* are more slender (Table 7) and as much as 25% higher crowned than those of *P. wittei*, and the lower molars of *P. oregonensis* are higher crowned than those of *Parapliosaccomys* sp. from Arlington 15 (see description below). The cheek teeth of *P. oregonensis* are also more derived through the evolution of higher dentine tracts. The dentine tract lengths of the lower cheek teeth of *P. oregonensis* and *P. wittei* are mutually exclusive, and only one tract measurement of *Parapliosaccomys* sp. from Arlington 15 falls within the range of *P. oregonensis*. Figures 8 and 9 illustrate a significantly greater dentine tract development on the lower cheek teeth of *P. oregonensis* than those of either *Parapliosaccomys* sp. or *P. wittei*. However, a greater range of overlap occurs on the upper molars. The difference in upper molar tract height of *P. oregonensis* and *P. wittei* is significant, but the measurement of the tract height on the single upper molar of *Parapliosaccomys* sp. falls well within the range of *P. oregonensis*. Perhaps the

development of dentine tracts occurred phylogenetically earlier on the upper molars than on the lower molars, but a greater sample is required for substantiation. An overall increase in dentine tract height can be traced from *P. wittei* to *Parapliosaccomys* sp. to *P. oregonensis*.

Dentine tracts of *P. oregonensis* are not as high as in species of *Thomomys*, whose tracts appear on the occlusal surface before the p4 erupts and so cannot be measured without introducing the factor of differential wear. However, the p4 of *P. oregonensis*, as in 57672, is fully erupted and moderately worn before dentine tracts appear on the occlusal surface of the molars. In addition, the cheek teeth of *P. oregonensis* exhibit root closure in adult forms, whereas the teeth of *Thomomys* remain essentially rootless.

Unlike the P4 of *Thomomys*, that of *P. oregonensis* is curved, lower crowned, and possesses roots. From the unworn premolars, 57642 (Figure 7f) and UO 26096, the protoloph appears composed of a single, transversely elongate cusp, whereas the protoloph of *P. wittei* is normally bicusped. UWBM 57646 of *P. oregonensis* is unusual in the possession of a cuspule on the anterior protoloph face. The P4 metaloph of *P. oregonensis* consists of a small metacone, large hypocone, and distinct posterior cingulum, terminating in a crest-like hypostyle. The cingulum is as large as that of *P. wittei* but slightly more anteroposteriorly compressed than that of *P. dubius*. As noted by Shotwell (1967b:40), numerous cuspules complicate the basic crown pattern. The cuspules vary in position and size and may be a response to selection of a rougher triturating surface on the P4 early ontogenetically after loss of the more complex dP4. The evolutionary advantage of the cuspules is minimal, however, compared to the worn pattern. Except for the earlier occurrence of dentine tracts on the occlusal surface, this worn pattern closely resembles that of *P. wittei* and differs from that of *Thomomys* only in the later occurrence of dentine tracts on the occlusal surface.

TABLE 7. Dental measurements of *Parapliosaccomys oregonensis*.

|          |     | N  | OR        | X    | S   | CV    |
|----------|-----|----|-----------|------|-----|-------|
| P4       | A-P | 7  | 1.25-1.75 | 1.45 | .20 | 13.78 |
|          | Tr  | 7  | 1.25-1.67 | 1.46 | .16 | 10.67 |
| M1 or M2 | A-P | 15 | 0.70-1.0  | 0.84 | .10 | 11.46 |
|          | Tr  | 15 | 1.10-1.71 | 1.55 | .19 | 7.62  |
| M3       | A-P | 5  | 0.90-1.1  | 1.02 | .09 | 8.40  |
|          | Tr  | 6  | 1.20-1.5  | 1.38 | .10 | 7.13  |
| p4       | A-P | 15 | 1.10-2.13 | 1.71 | .28 | 16.27 |
|          | Tr  | 16 | 1.20-1.6  | 1.41 | .14 | 10.00 |
| m1 or m2 | A-P | 20 | 0.80-1.1  | 0.94 | .11 | 11.94 |
|          | Tr  | 19 | 1.0-1.8   | 1.55 | .16 | 10.33 |
| m3       | A-P | 3  | 0.81-1.0  | 0.94 | .11 | 11.71 |
|          | Tr  | 3  | 1.28-1.42 | 1.37 | .08 | 5.54  |

The unworn dP4 (Figure 7g) exhibits more explicitly characters noted by Shotwell (1967b:39). Three transverse lophs unite lingually upon extreme wear; otherwise, the anterior loph that possesses a small buccal cuspule remains separate. The central loph connects via a continuous cingulum that swings around the lingual margin to connect to the rear midpoint of the posterior loph. This cingulum isolates the lingual cusp, forming the Y-shape of Wood (1935), similar to the posterior molar loph.

Upper molar morphology follows closely descriptions by Shotwell (1967b) and is very similar to that of *P. wittei*. Hypsodonty and dentine tract development of *P. oregonensis* are greater than in *P. wittei*, and roots and persistence of the medial valley on M1-M2 after eruption are distinguishing characters from *Thomomys*. The tear-shaped occlusal molar surface of *P. oregonensis* appears earlier than on *P. wittei* but not as early as on *Thomomys*.

Except for height differences of crowns and dentine tracts, the M3 of *P. oregonensis* is very similar to that of *P. wittei*. However, unworn M3s, such as 57666, indicate those of *P. oregonensis* are more anteroposteriorly compressed, resulting in narrower lophs than those of *P. wittei*, which are more cuspate when unworn.

The dentary of *P. oregonensis* resembles that of *Thomomys* and *P. wittei* and represents an intermediate developmental stage. *P. oregonensis* is derived over *P. wittei* in the degree of molding around the cheek teeth roots on the lateral face of the dentary. Although this character is probably ontogenetic, individuals of equivalent dental wear of *P. wittei* do not exhibit the rugosity, even at late wear stages. Masseteric rugosity can be correlated with greater hypsodonty, a feature characteristic of *P. oregonensis* and *Thomomys*, and probably increases surface area for muscle insertion. The mandibular symphysis of *P. oregonensis* ends below the p4 like *P. wittei*, whereas on *Thomomys*, the termination is below the m1. Normally, the pit lateral to m3 for insertion of the *M. pterygoidus internus* is shallow like that of *P. wittei*. On 57679, however, the fossa is deep, but not as deep as that of *Thomomys*. Therefore, the dentary of *P. oregonensis* is similar to that of *P. wittei* but exhibits modifications accentuated in *Thomomys*.

The p4 morphology resembles that of *P. wittei*, although the higher dentine tracts and greater hypsodonty of *P. oregonensis* should be stressed. An unworn p4 of *P. oregonensis*, 57682 (Figure 7j), with root development measures 3.2 mm from the lingual valley base up the crown. At similar developmental stage, 55584-55587 from Ordnance range between 2.6 and 3.0 mm, and 55681 from Arlington 14 measures 2.6 mm, indicating shorter crowns of *P. wittei*. The p4 crown pattern of *P. oregonensis* is very similar to that

of *P. wittei*; however, premolars of *P. oregonensis* have a long, crest-like anteroconid, not the cuspate anteroconid on some p4 of *P. wittei*. Unerupted premolars of *Thomomys* also have an anteroposteriorly elongate anteroconid, suggesting stabilization of the configuration over that of *P. wittei*.
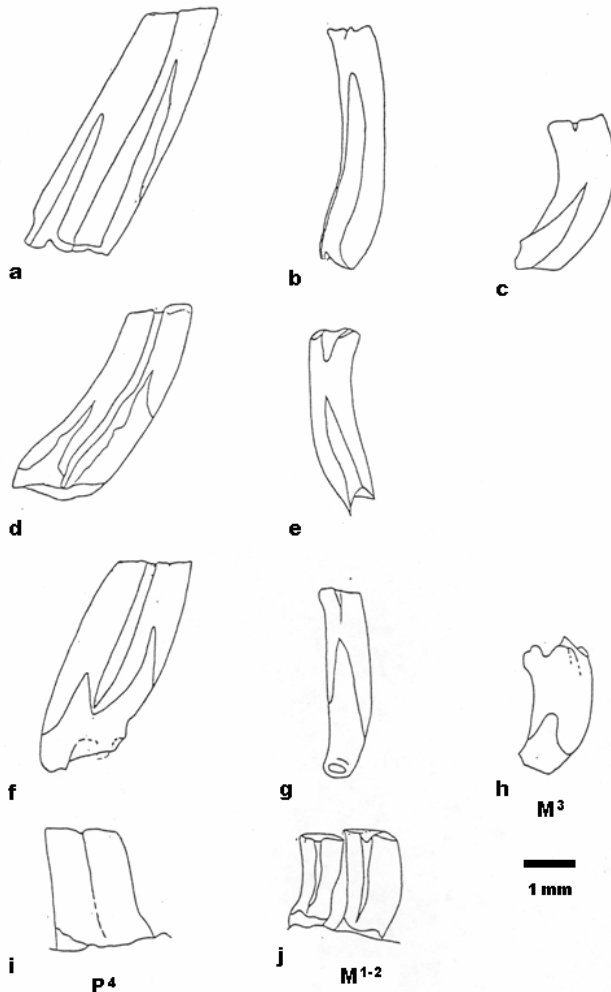
———————————————————————————



FIGURE 8. Dental succession of the upper cheek teeth of *Pliosaccomys* and *Parapliosaccomys*. a) *Parapliosaccomys oregonensis*, UWBM 57648, right P4; b) *P. oregonensis*, UWBM 57653, left M1 or M2; c) *P. oregonensis*, UWBM 57666, left M3; d) *Parapliosaccomys* sp., UWBM 57911, right P4; e) *Parapliosaccomys* sp., UWBM 57914, right M1 or M2; f) *P. wittei*, UWBM 55973, right P4; g) *P. wittei*, UWBM 55815, left M1 or M2; h) *P. wittei*, UWBM 55838, left M3; i) *Pliosaccomys dubius*, CIT 1799, left P4; j) *P. dubius*, CIT 1799, left M1 or M2.

———————————————————————————

The dp4 is like that of *P. wittei*, but the medial ridge connecting the marginal cusps curves buccally, whereas that of *P. wittei* is angular. The anterior dp4 of *P. oregonensis* has a triangular, rather than rectangular outline. The dp4 in the dentaries of 57680

(Figure 7i) of *P. oregonensis* and 55846 of *P. wittei* are worn nearly the same, although the latter may be slightly less worn. The succeeding molars, however, are radically different. The m1 of 55846 is unerupted and reaches only to the base of the dp4, whereas the m1-m2 of 57680 are fully erupted and exhibit occlusal wear. Therefore, eruption and utilization of molars occur earlier in *P. oregonensis* than in *P. wittei*.

The basic morphology of m1-m2 of *P. oregonensis* is similar to that of *P. wittei* with modifications of increased hypsodonty, higher dentine tracts, and more rapid acquisition of the worn pattern. The medial valleys are very shallow, but retention of the anterior cingulid keeps all lophids the same distance apart for masticatory efficiency until the molars are worn to a single pillar. Comparison of 57672 (Figure 7h) to the holotype of *P. wittei* (Figure 7e) demonstrates that the lingual molar valleys are completely worn from *P. oregonensis* sooner than from *P. wittei*, resulting in the tear-shaped occlusal surface of m1-m2 characteristic of *Thomomys*. The m3 of *P. oregonensis* is like that of *P. wittei* except for greater hypsodonty, higher dentine tracts, and a more curved tooth column.

*PARAPLIOSACCOMYS* sp. indet.
Figures 8d-e; 9d-e

**Referred specimens**—UWBM 57908, 4 I; 57909-57913, P4; 57914-57917, M1 or M2; 57918, 7 i; 58335, dentary with p4; 57919-57920, p4; 57921-57925, m1 or m2 from Arlington 15.

**Description**—These specimens are from the highest occurring Arlington locality and represent a more derived species than *P. wittei*. The size (Table 8) and tooth crown patterns are very similar to those of *P. wittei* but are significantly more hypsodont and have higher dentine tracts (Figs. 8-9). However, the relative paucity of specimens and lack of a jaw with more than a single tooth causes me to delay naming this species.

**Discussion**—Another geomyid has been assigned to *Parapliosaccomys* (Lindsay, 1972), but of the eight specimens collected from the Barstow Fm. in California, only three are of taxonomic use. UCMP 78897, an M1 or M2, is larger than any species of *Parapliosaccomys* from Oregon (maximum width=2.15 mm) and possesses a groove down the entire buccal length and has two buccal dentine tracts more similar to those of *Entoptychus* (Rensberger, 1971), rather than *Parapliosaccomys* or *Phelosaccomys*. Furthermore, the cingulum bends symmetrically around the lingual margin instead of angling directly to the protostyle as in *Parapliosaccomys*. On UCMP 78895, m1 or m2, the medial valley extends through to the buccal edge, unlike species of *Parapliosaccomys*, but observed on some specimens of *Pliosaccomys*. The cingulid is

prominent and extends anteriorly in a fashion more similar to that of species of *Pliosaccomys*. Also, the dentine tract extends to the base of the lingual valley, a feature unknown in derived species of *Parapliosaccomys*. The p4, UCMP 78167, if of the same species (no dentine tracts), is similar to worn p4s of *Entoptychus* and *Phelosaccomys* in possession of a medial fossette. These differences, the Barstovian occurrence, and the occurrence of a lineage extending only to the early Hemphillian suggests that the California specimens are an earlier parallel specialization.

A second taxon questionably ascribed to *Parapliosaccomys* was described by Voorhies (1990b), based on specimens from the Barstovian Norden Bridge assemblage from Nebraska. However, Korth and Reynolds (1994) suggested these specimens should be referred to *Phelosaccomys*, a taxon that parallels some features of *Parapliosaccomys*. All other references to *Parapliosaccomys* on the Great Plains (e.g., Korth, 1987; Voorhies, 1990b) likewise have been considered *Phelosaccomys* (e.g., Korth, 1998).

Finally, *Pliosaccomys wilsoni* (James, 1963) from late Clarendonian deposits in the Cuyama Valley, California, has been included within *Mojavemys* (Korth and Chaney, 1999).

*Pliosaccomys dubius* (Wilson, 1936), *P. magnus* (Kellogg, 1910), and *P. higginsensis* (Dalquest and Patrick, 1989) have similar morphologies and come from Hemphillian deposits at Smiths Valley, Thousand Creek, Nevada, and near Higgins, Texas, respectively. These taxa appear to be the base of a lineage whose culmination appears in *Parapliosaccomys oregonensis* and evidently *Thomomys* (Figure 10). *P. dubius*, the genotypic species, has six major cusps on the p4, and the hypolophid on the m1 and m2 is crest-like, rather than cuspate. *P. magnus* was originally described as a species of *Diprionomys* and later regarded as *Cupidinimus* (Wood, 1935). Although the morphological similarities of *P. dubius* and *Cupidinimus magnus* were correctly noted by Wilson (1936:25), the similarities were not taxonomically resolved until Shotwell (1967b) included both species within *Pliosaccomys*. Except that the molars of *P. dubius* eventually wear to a tear shape and a few specimens exhibit incipient dentine tract development, *P. dubius* and *P. magnus* might be considered conspecific. *P. higginsensis* is also similar to *P. dubius* and *P. magnus*, with only relatively slight differences of the upper premolar. *Pliosaccomys* was collected about 45 m below the upper Arlington localities, will be described later, and prove that *Pliosaccomys* is found stratigraphically below occurrences of *Parapliosaccomys*.
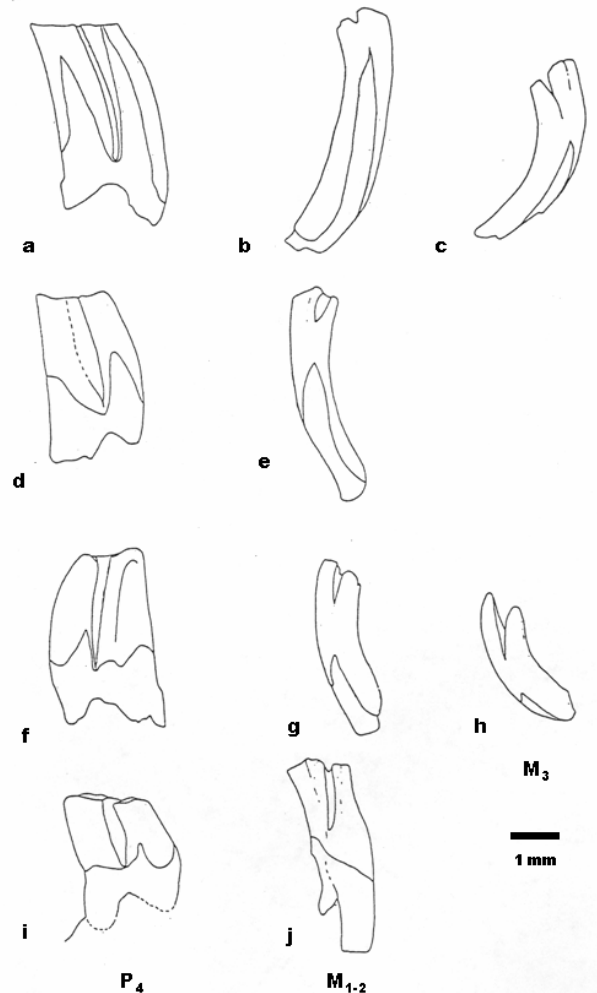


FIGURE 9. Dental succession of the lower cheek teeth of *Pliosaccomys* and *Parapliosaccomys*. a) a) *Parapliosaccomys oregonensis*, UWBM 57683, right p4; b) *P. oregonensis*, UWBM 57705, left m1 or m2; c) *P. oregonensis*, UWBM 57713, left m3; d) *Parapliosaccomys* sp., UWBM 57919, right p4; e) *Parapliosaccomys* sp., UWBM 57922, right m1 or m2; f) *P. wittei*, UWBM 55588, left p4; g) *P. wittei*, UWBM 55627, right m1 or m2; h) *P. wittei*, UWBM 55655, right m3; i) *Pliosaccomys dubius*, CIT 1805, right p4; j) *P. dubius*, LACM 33855, right m1 or m2.

A significant evolutionary step in this geomyine lineage occurs with the appearance of *Parapliosaccomys wittei*. Although size and basic tooth morphology attest to the descent of *P. wittei* from species of *Pliosaccomys*, *P. wittei* possesses much more hypsodont cheek teeth that exhibit well-developed dentine tracts. Many morphological features correlate with increased crown height. An arched rostrum, deep maxilla, rugosity on lateral side of the dentary and deep, pointed dentary are characteristic of *P. wittei* and are accentuated by *Parapliosaccomys oregonensis* and *Thomomys*. The cheek teeth are most diagnostic. The molar roots of *P. wittei* are fused and
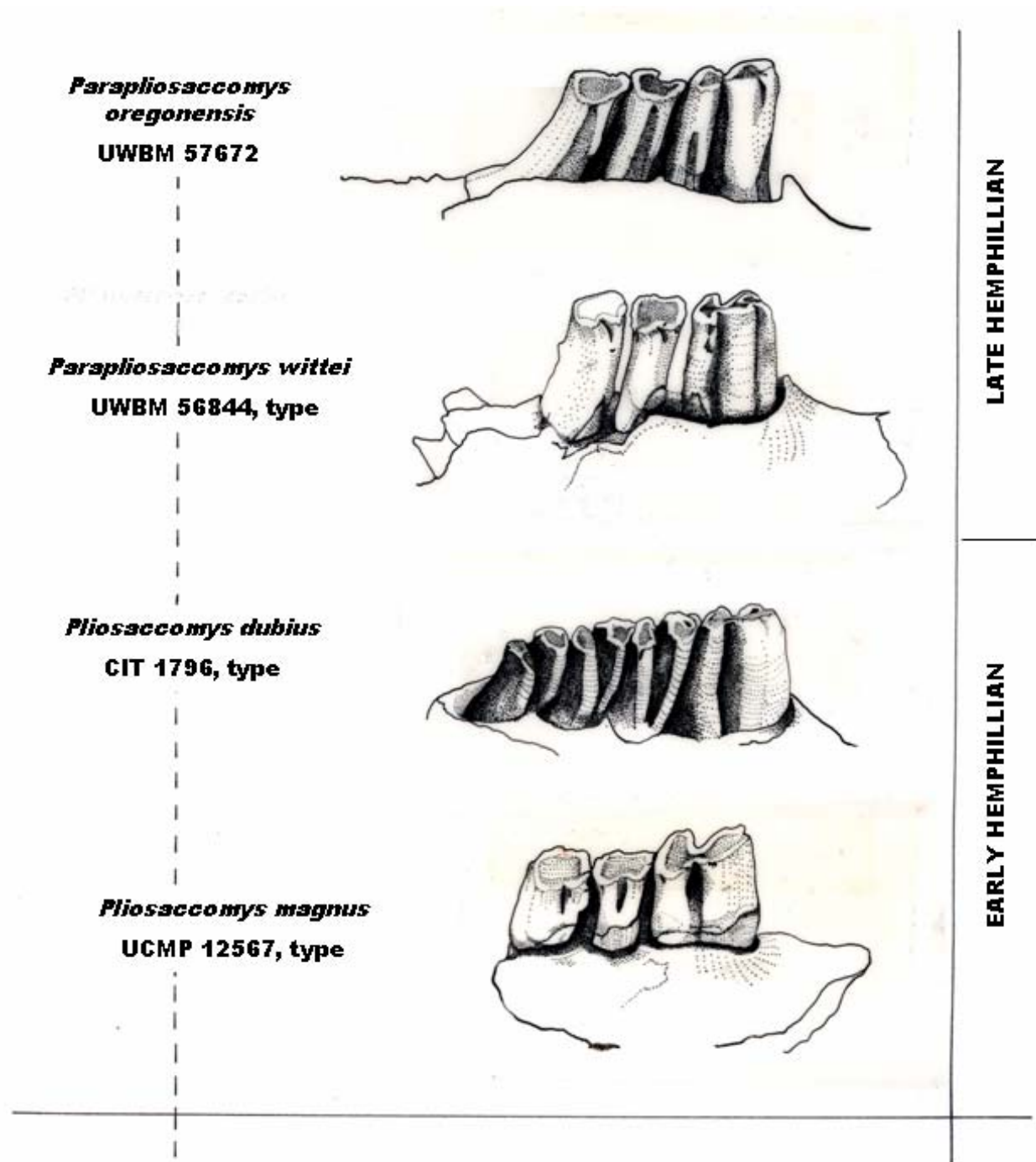
FIGURE 10. Succession of geomyine taxa through the Hemphillian. All are left dentaries, anterior is to right.

the increase in crown height occurs beneath the base of the medial valley that is shallower than that of *Pliosaccomys*. Distinct dentine tracts also occur that never reach to the valley base and are not doubled like those of other geomyines such as *Entoptychus*. The cingula on unworn teeth of *P. wittei* are prominent, although more compressed, especially on the third molars, than those of *Pliosaccomys*. As evolution proceeded, the cingula were functional only early in life and have become reduced; however, even in

*Thomomys* vestiges can be observed on unerupted cheek teeth. The tear-shaped monolophid molars appear to provide occlusal symmetry in *Thomomys*, a configuration on some well worn teeth of *P. dubius* and characteristic of the worn pattern of *P. wittei*.

A more derived stage is represented by *P. oregonensis*. The maxilla and dentary are similar to those of *P. wittei*, although the rostrum is slightly more arched, the lateral side of the dentary has deeper rugosities, and the fossa lateral to m3 is deeper on some specimens of *P. oregonensis*. The teeth of *P. oregonensis* are rooted, but the roots are fused on P4. The teeth have higher crowns and dentine tracts than those of *P. wittei*. However, the dentine tracts do not appear on the occlusal surface as soon as on *Thomomys*, and the medial valleys on the molars of *P. oregonensis* are not as shallow. Many such characters can be observed at different wear stages. When the dp4 is worn, the molars of *P. dubius* and *P. wittei* are unerupted, the molars of *P. oregonensis* have occluded, but deep valleys remain, and the molars of *Thomomys* have almost lost the medial valleys. After occlusion of the p4, the valleys on the molars of *P. wittei* are very shallow, and those of *P. oregonensis* and *Thomomys* have been worn away, resulting in a tear-shaped occlusal outline. Some question concerning ancestry of *Thomomys* is the lack of enamel on the base of the posterior margin of the premolars of *Parapliosaccomys*. However, enamel disappears from the occlusal surface only at extreme wear stages. Therefore, this character would have little impact on the success of the species, and with greater hypsodonty, enamel could occur lower on the premolars. *P. oregonensis* also occurs in late Hemphillian deposits at Churchill Butte, Lyon Co. (Kelly and Lugaski, 1999), and Hoye Canyon, Douglas Co., Nevada (Kelly, 2000).

---

TABLE 8. Dental measurements of *Parapliosaccomys* sp. indet. from Arlington 15.

|  | A-P | Tr |
|---|---|---|
| UWBM 57909, P4 | 1.40 | 1.63 |
| UWBM 57910, P4 | 1.17 | 1.28 |
| UWBM 57911, P4 | 1.25 | 1.32 |
| UWBM 57912, P4 | 1.50 | 1.50 |
| UWBM 57914, M1 or M2 | 0.80 | 1.38 |
| UWBM 57915, M1 or M2 | 0.90 | 1.32 |
| UWBM 57916, M1 or M2 | 0.78 | 1.48 |
| UWBM 58335, dentary with p4 | 1.88 | 1.52 |
| UWBM 57919, p4 | 1.50 | 1.42 |
| UWBM 57920, p4 | 1.80 | 1.28 |
| UWBM 57921, m1 or m2 | 0.90 | 1.50 |
| UWBM 57922, m1 or m2 | 0.90 | 1.50 |
| UWBM 57923, m1 or m2 | 0.90 | 1.56 |
| UWBM 57924, m1 or m2 | 0.91 | 1.40 |

---

The evolutionary modifications in the transition of *Pliosaccomys* species through *Parapliosaccomys*

*wittei* to *P. oregonensis* and thence to *Thomomys* are primarily concerned with changes related to greater hypsodonty. The cranium and dentary have responded to house the hypsodont cheek teeth, and the molars are transformed to a monolophid, tear-shaped pattern. Persistent dentine tracts are developed at points parallel to the occlusal motion. Importantly, most of these changes can be observed stratigraphically superpositioned in the Arlington section. From the lowest localities in the Ellensburg Fm. comes a species of *Pliosaccomys*, from the tan and red siltstones of the Alkali Canyon Fm. comes *Parapliosaccomys wittei*, and from the highest Arlington locality comes an advanced species of *Parapliosaccomys* approaching the condition of *P. oregonensis*.

Family CRICETIDAE Rochebrune, 1883
Subfamily CRICETINAE Murray, 1866
Genus *PARONYCHOMYS* Jacobs, 1977
*PARONYCHOMYS WOODBURNEI*, sp. nov.
Figure 11a-f

**Type Specimen**—UWBM 57789, maxilla with M1-M3.

**Type Locality**—Ordnance Locality (UWBM locality A8803).

**Stratigraphic Source and Age**—Alkali Canyon Fm., Dalles Grp.; late Hemphillian.

**Referred Specimens**—UWBM 57790, maxilla with M1-M3; 57791, maxilla with M1-M2; 57792-57798, maxillae with M1; 57799-57801, M1; 57802-57805, M2; 57806-57807, dentaries with m1-m2; 57808, dentary with m1; 57809-57810, dentaries with m2-m3; 57811-57813, dentaries with m2; 57814-57818, m1; 57819-57827, m2; 57828, m3 from Ordnance. UWBM 57734, maxilla with M1-M2; 57735, maxilla with M2; 57736, dentary with m1-m2; 57737, dentary with i, m1; 57738-57739, dentaries with i; 57740, m1; 57741, m2 from tan unit at Arlington 14. UWBM 57747, dentary with m1; 57748, dentary with i; 57749, dentary (edentulous) from tan unit at Arlington 7. UWBM 57754-57755, dentaries with i from tan unit; 57760, dentary with m1-m2 from the base of the red siltstone from Arlington 11. UWBM 57766, maxilla with M1-M3; 57767, m2 from the base of the red siltstone at Arlington 5.

**Diagnosis**—large cricetid with lophodont cheek teeth inflated at the crown bases; M1 anterocone slanting posteriorly and situated at buccal margin; M2 with flat posterior margin; M3 with large anterior cingulum, metacone, and distinct hypocone; m1 with very closely appressed anteroconid and metaconid; and relatively well developed m3 posteriorly.

**Etymology**—Named for Michael O. Woodburne, who championed the marriage of geology and paleobiology, enhancing both through biostratigraphy.
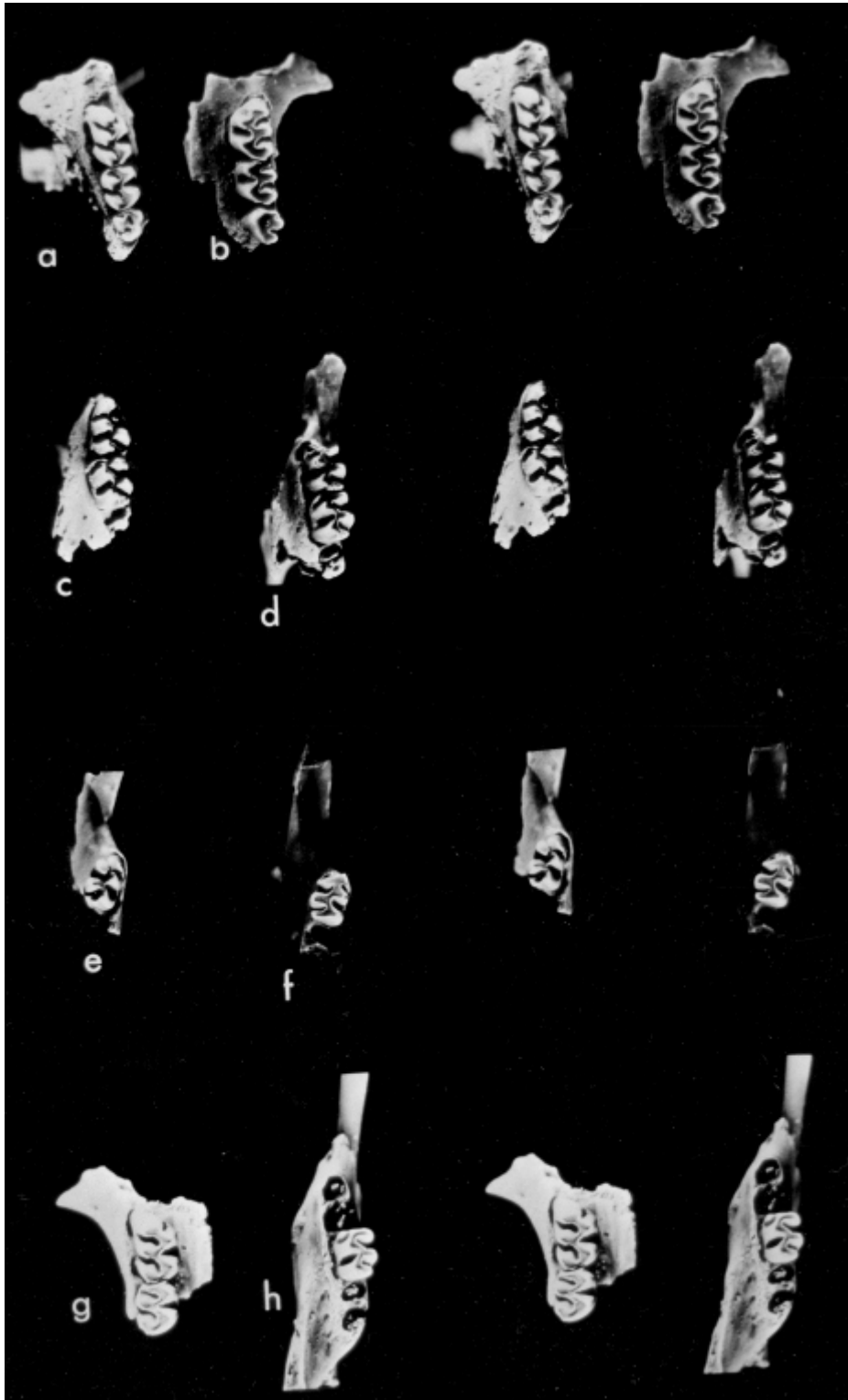
FIGURE 11. *Paronychomys woodburnei*: a) UWBM 57789, right maxilla with M1-M2, type specimen; b) UWBM 57734, left maxilla with M1-M2; c) UWBM 57760, left dentary with m1-m2; d) UWBM 57807, left dentary with m1-m2; e) UWBM 57808, right dentary with m1; f) UWBM 57737, right dentary with m1. *Paronychomys* sp. indet.: g) UWBM 58377, right maxilla with M1-M2; h) UWBM 58376, left dentary with m2. Scale equals one millimeter.

**Description**—Cheek teeth are larger and higher crowned than those of most fossil or extant cricetids. All molars have well defined, symmetrical patterns of alternating cusps with deep reentrants. Molars are normally extremely hypsodont with cusps apparent only when the teeth are unworn, have no mesolophs(ids), and few accessory cuspules that never enter into the occlusal plane. Hypsodonty, simple crown pattern, and large size aligns these teeth with cricetid morphological Group III of Shotwell (1967a).

The teeth of *Paronychomys woodburnei* (Table 9) are very robust (much like its namesake) compared to the delicate, specialized teeth of *P. lemredfieldi* and *P. tuttlei* (Jacobs, 1977) and the even smaller *P. alticuspis* (Baskin, 1979) from Arizona. The cheek tooth row on the three complete maxillae of *P. woodburnei* measures 4.22, 4.26, and 4.30 mm and is longer than that of *P. lemredfieldi* (3.65 and 3.80 mm). The dentition of all Arizona species are more laterally compressed than the brachyodont teeth of *P. woodburnei* that appear slightly less hypsodont. Molar crowns are inflated at their bases, resulting in a bulbous appearance compared to the vertical molar sides of *P. lemredfieldi* and *P. alticuspis*. Of particular importance is the rapid decrease in the tooth row posteriorly on the Arizona species described by Jacobs (1977); *P. woodburnei* has a large M3 with hypocone, whereas those of the Arizona species are reduced with no hypocone.

The M1 (Figure 11a,b) consists of four major cusps arranged in a staggered pattern and a prominent anterocone that slants posteriorly, not rising vertically as in *P. alticuspis*, *P. lemredfieldi*, and *P. tuttlei*. The four cusps are connected by high lophs and this portion of the tooth appears wider transversely than that of the species from Arizona. The posterior cingulum is separate from the metacone in early wear stages (e.g. 57800) but soon fuses, leaving a very angular posterior molar margin. A few variations exist: 57799 has a small fossette in the oblique loph between the paracone and hypocone, 57790 and 57792 have a small cuspule between the anterocone and paracone, and 57795 has a short crest from the anterocone trending posteriorly.

The lophodont M2 also has staggered cusps (Figure 11a,b) and a prominent anterior cingulum. This cingulum keeps the paracone on M2 equidistant from the metacone on M1 as are the paracone and metacone. Separation appears to be the function of cingula, keeping the major cusps the same distance apart, resulting in a symmetrical pattern for masticatory efficiency. Lophs are formed by the posterior margin of M1 and M2 of equivalent width to the major oblique lophs. Another feature functionally related to mastication is the thin enamel on the posterior margin of M1; also, enamel is thickest on the anterior edges of the lophs of the upper molars and on the posterior

margins of the lowers, indicating points of maximum use during mastication. The M2 posterior cingulum is indistinct and the posterior tooth margin is flattened, unlike the pointed terminations of most M2 from Arizona and apparently ?*Paronychomys* sp. from Coffee Ranch (Dalquest, 1983). UWBM 57790 is the only M2 of *P. woodburnei* that exhibits a short, low mesoloph almost fused to the paracone.

The prominent M3 hypocone distinguishes *P. woodburnei* from *P. lemredfieldi* and *P. tuttlei*. The M3 of *P. woodburnei* is quadrate rather than circular like the Arizona species and has a very prominent anterior cingulum that separates the M3 paracone from the M2 metacone. Two large buccal reentrants occur, and a medial fossette is formed between the paracone and protocone. The hypocone is reduced compared to the protocone, perhaps indicating a trend for the condition of the Arizona species.

The dentary of *P. woodburnei* is short, stout (Figure 11,d), has a prominent masseteric scar, and the mental foramen is anterior to the m1 below the diastema.

Normally, the m1 anteroconid and metaconid are very closely appressed (Figure 11c, e-d). On *P. tuttlei*, the anteroconid is well separated from the metaconid in early wear stages, whereas the cusps of *P. lemredfieldi* and *P. alticuspis* are only slightly separated, although perhaps more so than in *P. woodburnei*. Otherwise, the m1 of all species are similar, with a prominent posterior cingulid and high oblique crests connecting major cusps. Two roots occur on all m1 of *P. woodburnei* except 57817 that exhibits a small, short medial root.

Specimens of m2 are very similar among species, consisting of staggered cusps, a short but prominent posterior cingulid, and an anterior cingulid consisting of only a buccal projection. Heavy occlusal wear of the three m3 removed many salient features. Two buccal reentrants occur between the anterior cingulid and the protoconid and between the protoconid and the hypoconid. The posterior half of the tooth is reduced, but perhaps not so much as that of *P. lemredfieldi* or *P. alticuspis*.

**Discussion**—*P. woodburnei* has a relatively unspecialized dentition compared to *P. alticuspis* from the early late Hemphillian White Cone Local Fauna (Baskin, 1979) and *P. lemredfieldi* and *P. tuttlei* from the late Hemphillian Redington Local Fauna (Jacobs, 1977). The teeth of *P. woodburnei* lack vertical walls but are inflated, creating an illusion of lesser hypsodonty. The tooth row is not as reduced as that of the Arizona species described by Jacobs (1977), and the M3 retains a hypocone. The M1 anterocone slants posteriorly unlike the Arizona species and is small and buccally positioned. The M2 lacks a pointed posterior

cingulum, and the anteroconid and metaconid are closely appressed on m1. These features could be considered plesiomorphic, and none would exempt *P. woodburnei* from ancestry of the Arizona species. Therefore, *P. woodburnei* represents a less derived species than those from Arizona and extends the geographic range of the genus into the Pacific Northwest.

*PARONYCHOMYS* sp. indet.
Figure 11g-h

**Referred Specimens**—UWBM 58377, palate with right M1-M2, left M2; SDSM 27897, left M1-M2; UWBM 58376, dentary with m2 from McKay Reservoir.

**Description**—These specimens resemble those of *P. woodburnei* but are larger (Table 10), and therefore, larger than any of the Arizona species. The teeth have crowns inflated just above the roots unlike the Arizona species, a feature particularly evident on M1 (Figure 11g) that has a buccal anterocone, slanting posteriorly like that of *P. woodburnei*. However, the posterior margin of 58377 is very pointed, whereas that of *P. woodburnei* is flattened. The posterior expansion of M1 encroaches on the leading edge of M2, causing compression of the buccal end of the anterior cingulum of the M2. Therefore, enamel on the two margins forms an oblique loph parallel and as long as those connecting the major cusps. A greater enamel loss appears on the posterior edge of the M1, so the anterior enamel border of the M2 assumes a greater role during mastication than did the anterior enamel border of the M2 of *P. woodburnei*. The posterior margin of the M2 of UWBM 58377 and SDSM 27897 are also pointed, unlike the flattened border of *P. woodburnei*.

The dentary and m2 (Figure 11h) are similar to those of *P. woodburnei*, although the lophid between the metaconid and protoconid curves posteriorly, and the posterior cingulid appears slightly enlarged.

TABLE 9. Dental measurements of *Paronychomys woodburnei*.

|  |  | N | OR | X | S | CV |
|---|---|---|---|---|---|---|
| M1 | A-P | 12 | 1.75-2.18 | 2.02 | .12 | 6.00 |
|  | Tr | 12 | 1.25-1.41 | 1.26 | .27 | 21.5 |
| M2 | A-P | 9 | 1.55-1.73 | 1.61 | .08 | 5.10 |
|  | Tr | 9 | 1.17-1.44 | 1.27 | .09 | 6.97 |
| M3 | A-P | 3 | 1.11-1.21 | 1.16 | .05 | 4.35 |
|  | Tr | 3 | 1.06-1.10 | 1.08 | .02 | 1.85 |
| m1 | A-P | 11 | 1.52-1.90 | 1.80 | .11 | 6.30 |
|  | Tr | 11 | 1.13-1.47 | 1.22 | .09 | 7.64 |
| m2 | A-P | 15 | 1.45-1.68 | 1.55 | .07 | 4.36 |
|  | Tr | 15 | 1.05-1.31 | 1.23 | .04 | 3.56 |
| m3 | A-P | 3 | 1.15-1.25 | 1.20 | .05 | 4.18 |
|  | Tr | 3 | 1.00-1.04 | 1.03 | .02 | 2.25 |

**Discussion**—These specimens appear to represent a more derived species than *P. woodburnei*, from which it may have been derived, based upon the bulbous crowns and posteriorly slanting, buccally positioned M1 anterocone. An oblique loph formed by the borders of M1 and M2 indicates modification for increased masticatory efficiency. Also, McKay Reservoir molars appear more hypsodont when comparing specimens with equivalent occlusal wear. From three individuals with worn teeth, hypsodonty cannot be precisely diagnosed, and additional molars should be obtained for species designation. Even so, the McKay Reservoir specimens appear to represent derivation over those of *P. woodburnei* and are at about the same evolutionary stage as *P. tuttlei*.

TABLE 10. Dental measurements of *Paronychomys* sp. indet.

|  | A-P | Tr |
|---|---|---|
| UWBM 58377, maxilla with M1 | 2.50 | 1.49 |
| "      "      M2 | 1.81 | 1.51 |
| "      "      M2 | 1.80 | 1.41 |
| SDSM 27897, maxilla with M1 | 1.8 | 1.40 |
| "      "      M2 | 1.45 | 1.35 |
| UWBM 58376, dentary with m2 | 1.50 | 1.30 |

Genus *COPEMYS* Wood, 1936
*COPEMYS* sp. indet.
Figure 12a-f

**Referred Specimens**—UWBM 57784, I; 57785, maxilla with M1-M2; 57788, M1; 57786-57787, dentaries with m1-m3 from Ordnance. UWBM 57732, dentary with m1-m2; 57733, dentary with m2 from tan unit at Arlington 14. UWBM 57744-57745, maxillae with M1; 57746, dentary with m1-m2 from tan unit at Arlington 7. UWBM 57753, maxilla with M1-M3 from tan unit; 57758, dentary with i, m1-m3; 57759, dentary with m2 from the base of the red siltstone from Arlington 11. UWBM 57763, dentary with m2 from tan unit at Arlington 5. UWBM 57773, dentary with m1-m3 from Arlington 13.

**Description**—The striking staggered cusp arrangement (Figure 12a,d,e) on the small molars (Table 11) and the symmetrical reentrants, including those posterior to the m1 anteroconid, align the taxon with cricetid Group I of Shotwell (1967a). The teeth do not possess the characteristic oblique alignment of protolophule I-anterior hypocone arm and entolophulid-posterior protoconid arm of *Peromyscus* (Lindsay, 1972:75). A persistent mesoloph(id) bisects the interval between the paracone and metacone on the upper molars and the metaconid and entoconid on the lower molars. The prominence of this crest on specimens from Oregon contrasts with that of

*Antecalomys vasquezi* (Jacobs, 1977; Korth, 1998) from the Hemphillian Redington Local Fauna in Arizona but is similar to the condition of *Copemys mariae* from the Clarendonian of Oklahoma and Nebraska (Korth, 1998:330).

The M1 (Figure 12a-c) has a very large bicusped anterocone, which is expanded transversely almost as much as the main tooth body and connected to the protocone slightly lingual of the midline. The anterocone has internal and external crests flaring posteriorly. The external anterocone cusp is higher, paralleling the paracone and metacone, whereas the internal cusp reflects the configuration of the protocone and hypocone. Another similarity to the main body is a buccal crest extending to the paracone, resembling the mesoloph. This structure apparently provides another crest for mastication. The protoloph and metaloph join the posterior edges of the protocone and hypocone, respectively, with a prominent intervening mesoloph (only 57788 has a poorly formed mesoloph). A minute posterior cingulum is almost incorporated into the M1 metaloph, reaching to the metacone base.

Except for a slightly rounded posterior margin, the M2 is square with very symmetrically staggered cusps. A prominent anterior cingulum originates from the protocone, extends anteriorly to the midline, turns buccally, and extends to the molar margin. On 57753 (Figure 12a), the anterior cingulum has a short buccal spur, unlike that of 57785 (Figure 12c). Both specimens exhibit a fossette on the protoloph, a prominent mesoloph that is partially fused to the paracone on 57785, and a short posterior cingulum.

The only known M3, 57753, is anteroposteriorly compressed and half the length of the M1. Anteriorly, the M3 is similar to the M2, but the posterior portion is greatly reduced. The mesoloph and metaloph are fused, the posterior cingulum is lost, and the hypocone is greatly reduced to a lingual spur.

Like the upper molars, the major cusps on the lower molars are symmetrically arranged, but no oblique lophid formation occurs because of a distinct mure from where the mesolophid originates. The m1 is long, rectangular, and has an expanded anteroconid. Although normally single cusped, the anteroconid is expanded laterally to form a lophid and is asymmetrical with a high lingual end that slopes and narrows buccally to terminate in a crest that trends posteriorly. The anteroconid of UWBM 57732 appears doubled, perhaps representing a variation within this taxon, although additional specimens might indicate a separate cricetid. Deep reentrants separate the medially connected anteroconid from the tooth body. The mesolophid and posterior cingulid are slender, normally reach the lingual margin, and exhibit wear, but the internal cusps receive the most wear. The metaconid and entoconid receive slightly less wear and

remain high with anterior oblique wear facets until planed at extreme wear. A faint tubercule lies on the valley floor between the protoconid and hypoconid on 57786 (Figure 12c). All m1s have a wide, long posterior cingulid effectively separating the entoconid from the m2 metaconid.

The m2 is similarly constructed, but the anterior cingulid is anteroposteriorly short with no lingual projection, but the buccal limb is long and wide. The cingulid appears to function similar to that of the posterior cingulid of the m1. The m3 of *Copemys* sp. has no mesoloph, the entoconid and posterior cingulid are reduced, and the internal reentrants would become fossettids with wear.

**Discussion**—The specimens represent a less derived taxon than *Peromyscus*, a cricetine that attained oblique alignment of protolophule I-anterior hypocone arm and entolophulid-posterior protoconid arm. *Peromyscus* was never collected from the same localities as *Copemys* sp. but was found higher in the section at Arlington 15.

Genus *PEROMYSCUS* Gloger, 1841
*PEROMYSCUS* sp. indet.
Figure 12g

**Referred Specimens**—UWBM 57774, 8 I; 57775, maxilla with M1; UO F-8739, dentary with m1-m3; UWBM 57776, dentary with m1-m2; UO F-8740, dentary with m1-m2; UO F-8402, dentary with m1 from Arlington 15. UWBM 58378, palate with left M1-M2, right M1, dentary with m1-m3; 58379, dentary with m2-m3 from McKay Reservoir.

**Description**—The cheek teeth are brachyodont and have the oblique orientation of lophs characteristic of *Peromyscus* (Lindsay, 1972). The molars are very small (Table 12), and the crown patterns are variable as is typical of small, brachyodont cricetids. The only M1 from Arlington 15 exhibits a parastyle, mesoloph, and a medially situated, bicusped anterocone that is very wide, with a crest trending to the parastyle. The major cusps are opposite and oblique loph formation is via the mesoloph whose anteromedial edge is fused to the paracone, encircling a small fossette posterior to the paracone. Therefore, although the cusps lack a staggered arrangement, a pattern of oblique lophs is formed by the mesoloph between the paracone and hypocone.

The M1-M2 from McKay Reservoir have the diagnostic oblique arrangement of lophs. The anterocone of M1 is poorly divided with no crests to the paracone or mesoloph. A short spur appears in the position of the mesoloph. The posterior cingulum is absent on both molars, but the anterior cingulum of the M2 is well formed.
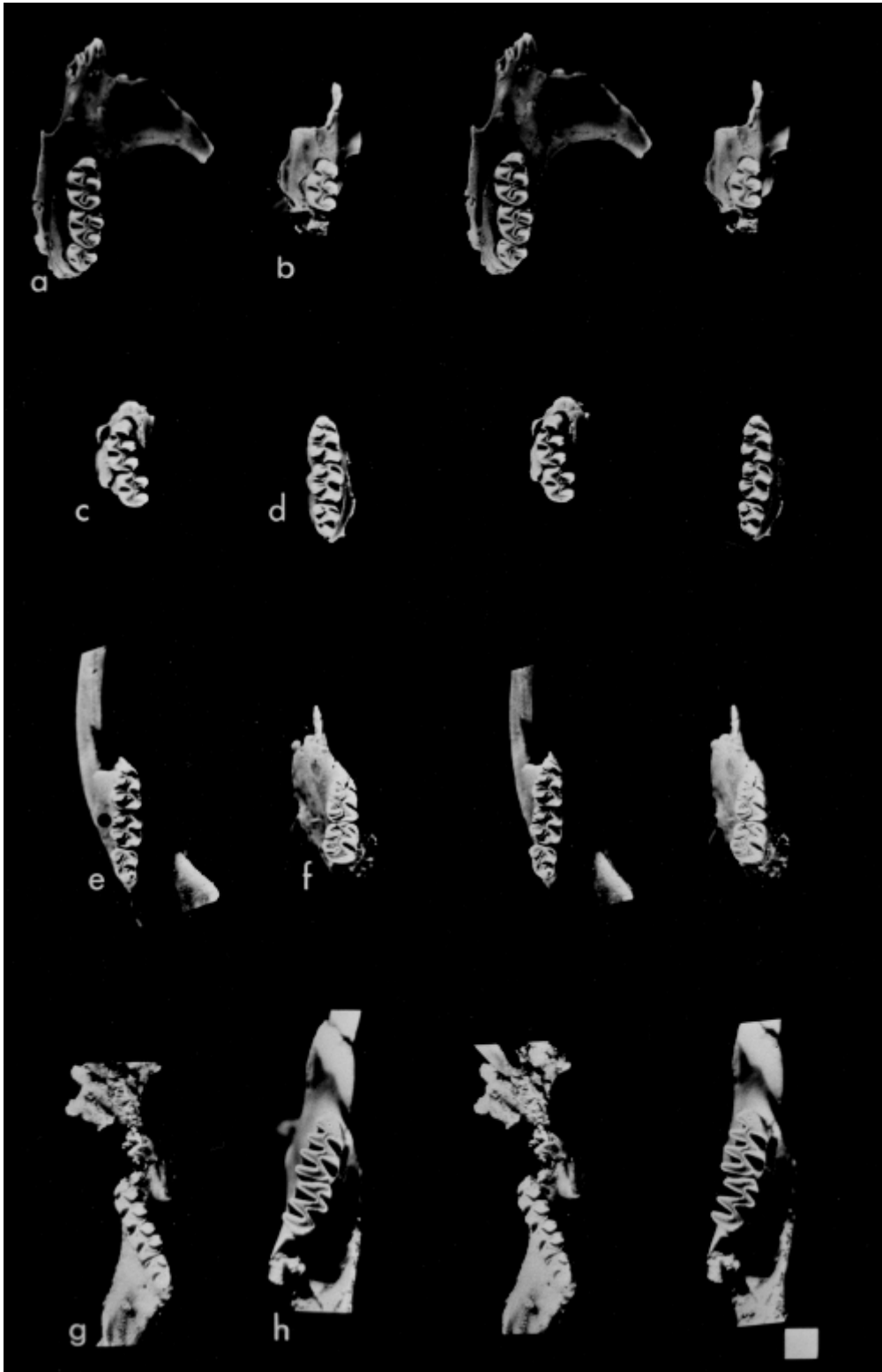
FIGURE 12. *Copemys* sp. indet.: a) UWBM 57753, left maxilla with M1-M3; b) UWBM 57745, left maxilla with M1; c) UWBM 57785, right maxilla with M1-M2; d) UWBM 57786, right dentary with m1-m3; e) UWBM 57758, right dentary with m1-m3; f) UWBM 57732, right dentary with m1-m2. *Peromyscus* sp. indet.: g) UWBM 58378, left dentary with m1-m3. *Prosomys mimus*: h) UWBM 58418, right dentary with m1-m2. Scale equals one millimeter.

More than a single species may be represented by the lower molars from Arlington 15. The molars of UO F-8739 and F-8740 are small with a bicuspid m1 anteroconid. UO F-8402 and UWBM 57776 are slightly larger (Table 12), and the anteroconid is a single cusp. Therefore, additional specimens are required for precise taxonomic determinations.

The m1 of UO F-8739 and F-8740 has a bicuspid anteroconid well divided anteriorly with posterior crests along the buccal and lingual margins. The molar body is composed of staggered cusps connected by oblique lophids and a prominent posterior cingulid. On UO F-8402 and UWBM 57776, the monocuspid anteroconid has a distinct posterior crest extending buccally like *Copemys* sp. The metaconid is isolated on UWBM 57776, but on UO F-8402, is connected to the confluence of the protoconid and anteroconid by a very narrow crest. The lophids of 57776 are obliquely oriented owing to a low mesolophid, unlike UO F-8402. The lower molars from McKay Reservoir are large, especially 58379 (Table 12), but otherwise identical to the m1 of 58378 (Figure 12g) with a single anteroconid, poorly divided from the metaconid.

**Discussion**—As is typical of *Peromyscus*, a wide range of variation occurs. Whether all specimens represent a single species cannot be ascertained on the basis of available material. The crown patterns resemble those of the five specimens of *P. nosher* (Gustafson, 1978) from the Blancan Ringold Fm. in Washington, but that species does not have the well defined, obliquely oriented lophs like those from Arlington 15 and McKay Reservoir.

*Peromyscus* sp. does not occur at Ordnance or the lower Arlington localities. This absence appears to be a function of paleoecology. With the possible exception of 58379, *Copemys* sp. has not been collected from Arlington 15 or McKay Reservoir. The occurrences are not temporally controlled, because *Peromyscus* is known from older Hemphillian deposits (e.g. Rattlesnake Fm., Martin, 1983).

Family MURIDAE Illiger, 1811
Subfamily MICROTINAE Miller, 1896
*PROSOMYS MIMUS* Shotwell 1956
Figure 12h

**Referred Specimens**—UWBM 58418, dentary with m1-m2; SDSM 51295, m1 from McKay Reservoir.

**Description**—SDSM 51295 and UWBM 58418 (Figure 12h) resemble closely the descriptions of Shotwell (1956) with the exception that the m1 of UWBM 58418 has a small fossettid on the anterior loop.

TABLE 11. Dental measurements of *Copemys* sp. indet.

| | A-P | Tr |
|---|---|---|
| Ordnance: | | |
| UWBM 57785, maxilla with M1 | 1.23 | 0.80 |
| " " M2 | 0.89 | 0.78 |
| UWBM 57788, M1 | 1.28 | 0.80 |
| UWBM 57786, dentary with m1 | 1.11 | 0.72 |
| " " m2 | 0.99 | 0.74 |
| " " m3 | 0.80 | 0.68 |
| UWBM 57787, dentary with m2 | 1.07 | 0.90 |
| " " m3 | 0.90 | 0.77 |
| | | |
| Arlington 14: | | |
| UWBM 57732, dentary with m1 | 1.53 | 1.02 |
| " " m2 | 1.32 | 1.11 |
| UWBM 57733, dentary with m2 | 1.18 | 0.96 |
| | | |
| Arlington 5: | | |
| UWBM 57763, dentary with m2 | 1.18 | 0.96 |
| | | |
| Arlington 7: | | |
| UWBM 57744, maxilla with M1 | 1.55 | 0.95 |
| UWBM 57745, maxilla with M1 | 1.60 | 0.98 |
| UWBM 57746, dentary with m1 | 1.39 | 0.95 |
| " " m2 | 1.14 | 1.03 |
| | | |
| Arlington 11: | | |
| UWBM 57753, maxilla with M1 | 1.66 | 1.02 |
| " " M2 | 1.29 | 1.08 |
| " " M3 | 0.87 | 0.96 |
| UWBM 57758, dentary with m1 | 1.89 | 0.97 |
| " " m2 | 1.20 | 0.99 |
| " " m3 | 1.02 | 0.90 |
| UWBM 57759, dentary with m2 | 1.14 | 0.91 |
| | | |
| Arlington 13: | | |
| UWBM 57773, dentary with m1 | 1.46 | 0.97 |
| " " m2 | 1.17 | 1.01 |
| " " m3 | 1.04 | 0.82 |

**Discussion**—This species represents the earliest occurrence of a genus in North America that migrated from Eurasia (Repenning, 1980). Shotwell (1956) named the taxon from McKay Reservoir *Prosomys mimus*. Later, Repenning (1968) assigned the species to *Promimomys* (Kretzoi, 1955), a European genus, but Voorhies (1990a) resurrected *Prosomys*. The fossettid on the m1 of 56418 supports assignment to this microtine; even *Mimomys* from Blancan deposits possesses a reentrant that wears to a fossettid.

No murids were collected at Arlington or Ordnance from thousands of specimens, and particular attention was focused on this rare rodent. Therefore, environmental partitioning seems unlikely; the occurrence at McKay Reservoir indicates later deposition than at Arlington or Ordnance. The species also occurs at the Christmas Valley Locality in south-central Oregon (Repenning, 1968), the Honey Creek and Mailbox assemblages, Nebraska (Voorhies, 1990a), and Wyman Creek Local Fauna, Nebraska

(Tucker, 2003), indicating correlation with McKay Reservoir.

---

TABLE 12.  Dental measurements of *Peromyscus* sp. indet.

|  | A-P | Tr |
| --- | --- | --- |
| Arlington 15: | | |
| UWBM 57775, maxilla with M1 | 1.73 | 1.07 |
| UO F08739, dentary with m1 | 1.38 | 0.85 |
| "        "      m2 | 1.04 | 0.84 |
| "        "      m3 | 0.87 | 0.68 |
| UO F08740, dentary with m1 | 1.30 | 0.83 |
| "        "      m2 | 1.01 | 0.94 |
| UWBM 57776, dentary with m1 | 1.50 | 0.98 |
| "        "      m2 | 1.26 | 0.96 |
| UO F08402, dentary with m1 | 1.56 | 1.04 |
| | | |
| McKay Reservoir: | | |
| UWBM 58378, maxilla with M1 | 1.66 | 1.18 |
| maxilla with M1 | 1.70 | 1.15 |
| "        "      M2 | 1.30 | 1.25 |
| dentary with m1 | 1.55 | 1.05 |
| "        "      m2 | 1.30 | 1.15 |
| "        "      m3 | 1.12 | 0.89 |
| dentary with m2 | 1.37 | 1.15 |
| "        "      m3 | 1.24 | 0.95 |

---

## BIOSTRATIGRAPHY IN NORTHERN OREGON

Rodent distribution from deposits in northern Oregon is illustrated on Figure 13.  With the exception of *Spermophilus wilsoni*, *Spermophilus shotwelli*, and the species of *Castor*, no species overlap occurs between McKay Reservoir and either Ordnance or the lower localities at Arlington.  The highest locality, Arlington 15, appears intermediate between McKay Reservoir and the other localities in northern Oregon.  Moreover, the species at McKay Reservoir and Arlington 15 are normally more derived than their counterparts from lower in the section at Arlington and Ordnance.  Some clades undergo changes reflecting temporal differences.

Some disparity in the rodents at McKay Reservoir may be a function of environment, but a temporal difference exists.  *Parapaenemarmota oregonensis* (Martin, 1998), *Spermophilus mckayensis* (Black, 1963), and *Prosomys mimus* (Shotwell, 1956) are restricted to McKay Reservoir.  The absence of *Parapaenemarmota* from Ordnance and Arlington, a large taxon not easily overlooked, could be interpreted as environmental exclusion.  *Spermophilus mckayensis* is a ground squirrel with an incipiently hypsodont dentition.  Living species commonly occur in relatively arid environments and would be expected at Arlington and Ordnance where the habitat was suitable.  Therefore, the first appearance of this species at McKay Reservoir represents a temporal advance.  *Prosomys mimus* is one of the earliest microtines in

North America and does not occur at older North American localities, even those of similar environment.  Therefore, of the three species restricted to McKay Reservoir, at least two indicate temporal difference.

The brachyodont cricetids change at a generic level within the Arlington localities.  *Copemys* sp., which had not attained an oblique loph arrangement, is replaced at Arlington 15 and McKay Reservoir by *Peromyscus*, a living taxon with oblique loph construction.  These occurrences may be controlled environmentally as *Peromyscus* occurs in older Hemphillian deposits, but *Copemys* does not range higher.

Of genera with different species at McKay Reservoir and the Ordnance and Arlington localities, the more derived species are at McKay Reservoir.  The most convincing taxa to substantiate later deposition at McKay Reservoir are species of *Parapliosaccomys*.  By tracing hypsodonty, dentine tract development, and transition from a bilophodont to monolophodont molar, a successive change occurs.  *P. wittei* from Ordnance and the lower Arlington localities is derived compared to *Pliosaccomys*.  These features are accentuated by *Parapliosaccomys* sp. from Arlington 15 and *P. oregonensis* from McKay Reservoir.

Arlington 15 represents a transition from the assemblages occurring at the lower Arlington localities and Ordnance to that at McKay Reservoir.  *Peromyscus* sp. and *Parapliosaccomys* sp. from Arlington 15 appear morphologically more similar to species at McKay Reservoir than to those occurring geographically closer.  Arlington 15 lies about 15 m above a widespread caliche that caps most of the lower Arlington localities, indicating later deposition.  Superpositional relationships and rodent morphologies indicate the Ordnance Locality and those from below the caliche at Arlington are almost contemporaneous, and Arlington 15 and McKay Reservoir were deposited subsequently.

Biostratigraphic distribution of rodent taxa indicates a zonation for northern Oregon.  Operative ranges may be delineated for *Castor* and *Parapliosaccomys.*  The lowest stratigraphic data for *Castor* sp. cf. *C. californicus* and *Parapliosaccomys wittei* occur at the base of the Arlington section (conglomerate) and at Ordnance.  The datum of *Castor* can also be considered the lowest occurrence of the genus in North America unless a specimen from the Rome assemblage with questionable locality data can be substantiated (Wilson, 1937a); the datum of *Parapliosaccomys* is also a lowest occurrence and with current knowledge also represents the first appearance datum within this geomyine lineage.  The *Parapliosaccomys* occurrence at McKay Reservoir represents its highest stratigraphic datum and at current knowledge the highest occurrence.  Therefore, the

FIGURE 13. Local range biozones of Hemphillian rodents that are included within the *Castor-Parapliosaccomys* Concurrent Range Biozone in northern Oregon.



FIGURE 14. Occurrences within selected late Hemphillian rodent assemblages in western North America.

defining stratotype reference sections extend from the upper conglomerate in Arlington through the red siltstone at Arlington 15 of the Alkali Canyon Fm. and the upper levels from Unit 2 to 12 of the McKay Formation. *C. californicus* extends into the Blancan; therefore, the *Castor-Parapliosaccomys* Concurrent Range Biozone is proposed for the interval in northern Oregon, Christmas Valley, Oregon, and possibly south into western Nevada from the lowest occurrence of *Castor* and *Parapliosaccomys* to the highest occurrence of *Parapliosaccomys*, and may be equated to late Hemphillian time. Also, the first occurrences of *Neotamias malloryi* and *Perognathus stevei* are at the base of the biozone, *Dipoides smithi* is restricted to the interval, and lowest occurrences of *Spermophilus* (*Spermophilus*), *Parapaenemarmota*, and *Cosomys* are higher in the biozone and may define a subzone in the future.

## AGE AND CORRELATION

The localities in northern Oregon correlate with Hemphillian deposits elsewhere (Figure 14) as indicated by the common occurrences of *Plesiogulo*, *Pliotaxidea*, *Paronychomys, Teleoceras*, and smaller species of *Dipoides* (Tedford et al., 2004:218). Hemphillian localities in northern Oregon are slightly younger than others in the Pacific Northwest, with the exception of the Christmas Valley Locality where *Prosomys mimus* is known (Repenning, 1968) and we recently collected *Castor* and *Dipoides*, indicating correlation with McKay Reservoir. The first appearance of *Prosomys* is an important biostratigraphic datum. Late Hemphillian assemblages have also been described from Churchill Butte, Lyon Co. (Kelly and Lugaski, 1999), and Hoye Canyon, Douglas Co., Nevada (Kelly, 2000) where *Parapliosaccomys* occurs. Therefore, these two assemblages are assigned to the *Castor-Parapliosaccomys* Concurrent Range Biozone.

Other Northwest Hemphillian assemblages are older and include those from Rome and Drewsey, southeastern Oregon, and those from Smiths Valley and Thousand Creek, Nevada, based on the occurrence of *Dipoides stirtoni*, *Peromyscus antiquus, Diprionomys parvus*, and species of *Pliosaccomys*. The Rattlesnake assemblage of central Oregon also correlates with these older assemblages, based on the occurrences of *Dipoides stirtoni*, *Peromyscus* (Martin, 1983), and other taxa collected by the author. Based on more derived rodent species from Ordnance, Arlington, and McKay Reservoir, the localities in northern Oregon are younger than those in central and southeastern Oregon, except Christmas Valley.

On the Great Plains, numerous assemblages are similar to those in northern Oregon, such as the Hemphill (Coffee Ranch) assemblage, Texas; the upper Snake Creek (*Pliohippus* Draw), Santee, Mailbox, Devils Nest Airstrip assemblages, Nebraska, and the Edson and Saw Rock Canyon Local Faunas, Kansas. Saw Rock Canyon (Hibbard, 1949, 1953) resembles those in northern Oregon through the occurrence of *Paenemarmota sawrockensis*, *Perognathus mclaughlini*, *Dipoides wilsoni*, and *Peromyscus sawrockensis* and is late Hemphillian or early Blancan (Hibbard, 1964; Bell et al., 2004). *Paenemarmota sawrockensis* resembles *Parapaenemarmota oregonensis* except for smaller size and incomplete p4 trigonid of the latter (Martin, 1998). *Perognathus mclaughlini*, *Dipoides wilsoni*, and *Peromyscus sawrockensis* represent evolutionary stages similar to their counterparts at McKay Reservoir and possibly Arlington 15, but the occurrence of *Ogmodontomys* at Saw Rock suggests a younger age.

Skinner et al. (1977) reviewed the Hemphillian upper Snake Creek assemblages: *Pliohippus* Draw yielded *Castor* sp. cf. *C. californicus* and *Dipoides* sp. cf. *D. wilsoni*, similar to Ordnance and the lower Arlington localities, and the ZX Bar Local Fauna includes *Pliotaxidea* and *Gaillardia thomsoni*, an aquatic mole whose only other known North American occurrence is at McKay Reservoir (Hutchinson, 1968). The Santee assemblage, Nebraska, shares *Dipoides*, *Castor* cf. sp. *C. californicus*, *Paronychomys*, and rhinocerotids (Voorhies, 1990a) with the northern Oregon localities and is slightly younger than McKay Reservoir, where *Protopliophenacomys* is unknown. A fission-track date of 5.0±0.2 Ma was obtained from an ash overlying the Santee assemblage (Voorhies, 1977). The Devils Nest Airstrip assemblage, Nebraska, is similar to Santee (Voorhies, 1990a) but does not contain *Paronychomys*. The Mailbox Locality, Nebraska, contains both castorids, as well as *Ochotona* sp. cf. *O. spanglei, Prosomys mimus*, and *Pliozapus* sp. cf. *P. solus* (Voorhies, 1990a), species that also occur at McKay Reservoir. The Honey Creek Locality, Nebraska (Voorhies, 1990a), is similar, sharing *Ochotona*, *Dipoides*, ?*Prosomys*, and *Pliozapus*; the Wyman Creek Local Fauna, Nebraska (Tucker, 2003), shares *Prosomys*. Therefore, of the late Hemphillian rodent assemblages known from Nebraska, *Pliohippus* Draw, ZX Bar, Honey, Wyman Creek, Mailbox, Santee, and Devils Nest Airstrip correlate with those from northern Oregon, although the latter two appear slightly younger.

Schultz (2002) recognized early, late, and latest Hemphillian assemblages in the Texas panhandle and Oklahoma. From the late Hemphillian, *Dipoides*

occurs at the Optima Local Fauna, and *Spermophilus* (*Otospermophilus*), *Perognathus*, *Paronychomys*?, and *Peromyscus* are recorded from the Coffee Ranch Local Fauna (Dalquest, 1983), which also occur in northern Oregon. The Coffee Ranch Local Fauna has been dated using the fission-track on zircons at 6.6 Ma (Schultz, 2002) and hydrated glass fission-track dates of 4.7 Ma (Izett, 1975:202) and 5.3 Ma (Boellstorff, 1976:65).

In California, the upper Dove Spring Fm. is considered early Hemphillian (Whistler and Burbank, 1992). This portion of the formation includes their *Paronychomys/Osteoborus diabloensis* Assemblage Zone, indicating that *Paronychomys* occurs low in the Hemphillian. All other known occurrences are late or latest Hemphillian.

Several local faunas in the southwestern United States and in Mexico contain taxa similar to those in Oregon. The Yepomera/Matachic assemblage of Chihuahua, Mexico, has been considered late Hemphillian (5.0 to 5.25 Ma) based upon paleomagnetic correlation (Lindsay et al., 2006). *Parapaenemarmota pattersoni* (Wilson, 1949) from Matachic, is slightly more derived than *Parapaenemarmota oregonensis* (Martin, 1998) from McKay Reservoir. From the Redington Local Fauna, Arizona, dated from 5.21 to 6.25 Ma (in Jacobs, 1977), two species of *Paronychomys* and one from the White Cone Local Fauna, Arizona, dated at 6.69 Ma (in Baskin, 1979), appear more hypsodont than those from Ordnance and Arlington, perhaps resembling the species from McKay Reservoir.

Therefore, the northern Oregon assemblages appear to have accumulated during the Hemphillian Age, greater than 5 million years ago, during the late Hemphillian (Hh3) of Tedford et al. (2004) and below the 5.6 Ma *Plesiogulo* extinction datum (Lindsay et al., 1984). The northern Oregon assemblages are younger than most others from the Pacific Northwest, except the Christmas Valley Locality in south-central Oregon, and more closely resemble certain assemblages from the Great Plains and Southwest.

CONCLUSIONS

1. The Hemphillian localities at Ordnance, Arlington, and McKay Reservoir produced thousands of rodent specimens. Of the taxa recovered from McKay Reservoir and Arlington 15, all but *Spermophilus shotwelli*, *Spermophilus wilsoni*, and *Castor* sp. cf. *C. californicus* are more derived and occurred later than those occurring at the Ordnance Locality and the lower localities at Arlington.

2. Taxa from the lower localities at Arlington and Ordnance appear synchronous. The deposits at Ordnance may be slightly older but not significantly.

3. The high proportion of taxa adapted for a riparian environment at McKay Reservoir and Arlington 15 in contrast to the high percentage of taxa specialized for a drier habitat at Ordnance and the lower Arlington localities supports the paleoecological conclusions of Shotwell (1958, 1964), even considering their temporal differences.

4. Taxa first appearing at McKay Reservoir with no generic (or subgeneric) counterparts at the other localities in northern Oregon include: *Spermophilus* (*Spermophilus*) *mckayensis*, the first ground squirrel with incipient hypsodonty; *Prosomys mimus*, the earliest known North American murid that gave rise to later genera (Repenning, 1980); and *Parapaenemarmota oregonensis*.

5. Arlington 15, the stratigraphically highest site at Arlington, appears to represent a temporally intermediate interval between McKay Reservoir and the other lower localities in northern Oregon. The transitional age is based on the appearance of *Peromyscus*, a genus not found at the lower localities at Arlington or Ordnance, and a species of *Parapliosaccomys* more derived than *P. wittei*, but perhaps not so derived as *P. oregonensis* from McKay Reservoir. In contrast, the castorids appear more similar to those from the lower Arlington localities than to *Dipoides smithi* from McKay Reservoir. Therefore, taxa from Arlington 15 resemble those from the lower localities at Arlington and Ordnance, but have greater affinities with those from McKay Reservoir.

6. Different species of the same genus from McKay Reservoir and the other northern Oregon localities indicate a later age for McKay Reservoir. *Oregonomys sargenti* from McKay Reservoir is more derived than *O. pebblespringsensis* based on acquisition of a molariform p4 (Martin, 1984); *Parapliosaccomys oregonensis* possesses more hypsodont teeth with higher dentine tracts than *P. wittei*; and *Paronychomys* sp. from McKay Reservoir may be slightly more hypsodont with a more derived cingular structure of M2 than in *P. woodburnei*.

7. One of the best documented phylogenies of rodents is the *Pliosaccomys-Parapliosaccomys* lineage. *Pliosaccomys dubius, P. magnus*, and *P. higginsensis* appear in the early Hemphillian. *Parapliosaccomys wittei* evolved from species of *Pliosaccomys* by gaining greater hypsodonty, fusing molar roots, and developing dentine tracts on the cheek teeth. These features are accentuated in *Parapliosaccomys oregonensis* from McKay Reservoir. Only root loss and the slightly higher crowned teeth and dentine tracts differentiate the latter species from *Thomomys*.

8. Correlation of the northern Oregon assemblages with those of other Hemphillian sites in the Pacific Northwest indicates that only the Christmas

Valley assemblage is as young, and the interval represented by these assemblages is characterized by the *Castor-Parapliosaccomys* Concurrent Range Zone.

9. The northern Oregon assemblages occurred during the late Hemphillian (Hh3) Land Mammal Age (Tedford et al., 2004) and below the 5.6 Ma *Plesiogulo* extinction datum of Lindsay et al. (1984). Correlatives of the lower Arlington and Ordnance localities include Churchill Butte and perhaps Hoye Canyon, NV, and *Pliohippus* Draw, NE; the late Hemphillian Coffee Ranch Local Fauna appears to be slightly older. Correlatives of the McKay Reservoir and Arlington 15 include Christmas Valley, OR, ZX Bar, Mailbox, and Honey Creek, NE; these localities are slightly older than Santee and Devils Nest Airstrip, NE, and Yepomera/Matachic, Mexico.

## ACKNOWLEDGMENTS

## LITERATURE CITED

Barbour, E.H., and C.B. Schultz. 1937. An early Pleistocene fauna from Nebraska. American Museum Novitiates 942:1-100.

Baskin, J.A. 1979. Small mammals of the Hemphillian age White Cone local fauna, northeastern Arizona. Journal of Paleontology 53(3):695-708.

Bell, C.J., E.L. Lundelius, Jr., R.W. Graham, E.H. Lindsay, D.R. Rues, Jr., H.A. Semen, Jr., S.D. Webb, and R.J. Zakrewski. 2004. The Blancan, Irvingtonian, and Rancholabrean Mammal Ages; pp. 232-314 in Woodburne, M.O. (ed.), Late Cretaceous and Cenozoic Mammals of North America—Biostratigraphy and Geochronology. Columbia University Press.

Bjork, P.R. 1970. The Carnivora of the Hagerman Local Fauna (Late Pliocene) of southwestern Idaho. American Philosophical Society, Transactions 60(7):1-54.

Black, C.C. 1963. A review of the North American Tertiary Sciuridae. Harvard University, Museum of Comparative Zoology, Bulletin 130(3):109-248.

Boellstorff, J.D. 1976. The succession of Late Cenozoic volcanic ashes in the Great Plains: A progress report; in Stratigraphy and Faunal Sequence—Meade County, Kansas. Midwestern Friends of the Pleistocene, 24th Annual Meeting, Kansas Geological Survey, Guidebook, Series 1:1-85.

Conrad, G.S. 1980. The biostratigraphy and mammalian paleontology of the Glenns Ferry Formation from Hammett to Oreana, Idaho. Unpublished Ph.D. dissertation, Idaho State University, Pocatello 334p.

Dalquest, W.W. 1983. Mammals of the Coffee Ranch Local Fauna, Hemphillian of Texas. University of Texas, Texas Memorial Museum, Pearce-Sellards Series 38:1-41.

Dalquest, W.W., and D.B. Patrick. 1989. Small mammals from the early and medial Hemphillian of Texas, with descriptions of a new bat and gopher. Journal of Vertebrate Paleontology 9(1):78-88.

Farooqui, S.M., J.D. Beaulieu, R.C. Bunker, D.E. Stensland, and R.E. Thoms. 1981. Dalles Group: Neogene formations overlying the Columbia River Basalt Group in north-central Oregon. Oregon Geologist 43(10):131-140.

Fry, W.E. 1973. Fossil giant tortoise of the genus *Geochelone* from the late Miocene-early Pliocene of north-central Oregon. Northwest Science 47(4):239-249.

Gazin, C.L. 1936. A study of the fossil horse remains from the Upper Pliocene of Idaho. U.S. National Museum, Proceedings 83(2985):281-320.

Green, M. 1977. *Dipoides* (Rodentia, Castoridae) from Yankton County, South Dakota. Journal of Paleontology 51(1):136-138.

Gustafson, E.P. 1978. The vertebrate faunas of the Pliocene Ringold Formation, south-central Washington. University of Oregon, Museum of Natural History, Bulletin 23:1-62.

Hay, O.P. 1927. The Pleistocene of the western region of North America and its vertebrated animals. Carnegie Institution of Washington, Publication 322B:1-346.

Hibbard, C.W. 1941. New mammals from the Rexroad fauna upper Pliocene of Kansas. American Midland Naturalist 26(2):337-368.

Hibbard, C.W. 1949, Pliocene Saw Rock Canyon fauna in Kansas. University of Michigan, Museum of Paleontology, Contributions 7(5):91-105.

Hibbard, C.W. 1953, The Saw Rock Canyon fauna and its stratigraphic significance. Papers Michigan Academy of Science, Arts, Letters 28:387-411.

Hibbard, C.W. 1964. A contribution to the Saw Rock Canyon local fauna of Kansas. Papers Michigan Academy of Science, Arts, Letters 49:115-127.

Hutchinson, J. H. 1968. Fossil Talpidae (Insectivora, Mammalia) from the later Tertiary of Oregon. University of Oregon, Museum of Natural History, Bulletin 11:1-117.

Izett, G.A. 1975. Late Cenozoic sedimentation and deformation in northern Colorado and adjoining areas; pp. 179-209 in Curtis, B.M. (ed.). Cenozoic History of the Southern Rocky Mountains. Geological Society of America, Memoir 174.

Jacobs, L.L. 1977. Rodents of the Hemphillian age Redington local fauna, San Pedro Valley, Arizona. Journal of Paleontology 51(3):505-519.

James, G.T. 1963. Paleontology and nonmarine stratigraphy of the Cuyama Valley badlands, California. Part I. Geology, faunal interpretations, and systematic descriptions of Chiroptera, Insectivora, and Rodentia. University of California Publications, Geological Sciences 45:1-171.

Kellogg, L. 1910. Rodent fauna of the late Tertiary beds at Virgin Valley and Thousand Creek, Nevada. University of California Publications, Geological Sciences 5(29):421-437.

Kellogg, L. 1911. A fossil beaver from the Kettleman Hills, California. University of California Publications, Geological Sciences 6(17):401-402.

Kelly, T.S. 2000. A new late Hemphillian (Late Miocene) mammalian fauna from Hoye Canyon, west central Nevada. Natural History Museum of Los Angeles County, Contributions to Science 481:1-21.

Kelly, T.S., and T.P. Lugaski. 1999. A Hemphillian (Late Miocene) mammalian fauna from the Desert Mountains, west central Nevada. Southern California Academy of Sciences, Bulletin 98(1):1-14.

Kretzoi, M. 1955. *Promimomys* cor N. G. N. Sp., ein altertumlicher arvicolide aus dem ungarischen Unterpleistozan. Acta geol., Budapest 3:89-94.

Korth, W.W. 1987. New rodents (Mammalia) from the late Barstovian (Miocene) Valentine Formation, Nebraska. Journal of Palentology 61:1058-1064.

Korth, W.W. 1998. Rodents and lagomorphs (Mammalia) from the late Clarendonian (Miocene) Ash Hollow Formation, Brown County, Nebraska. Annals of Carnegie Museum 67(4):299-348.

Korth, W.W. 2007. A new genus of beaver (Rodentia, Castoridae) from the Miocene (Clarendonian) of North America and systematics of the Castoroidinae based on comparative cranial anatomy. Annals of Carnegie Museum 76(2):117-134.

Korth, W.W., and D.S. Chaney. 1999. A new subfamily of geomyoid rodents (Mammalia) and a possible origin of Geomyidae. Journal of Paleontology 73(6):1191-1200.

Korth, W.W., and R.E. Reynolds. 1994. A hypsodont gopher (Rodentia, Geomyidae) from the Clarendonian (Miocene) of California. San Bernardino County Museum Association, Special Publication 94-1:91-95.

Lindsay, E.H. 1972. Small mammal fossils from the Barstow Formation, California. University of California Publications, Geological Sciences 93:1-104.

Lindsay, E.H., N.D. Opdyke, and N.M. Johnson. 1984. Blancan-Hemphillian Land Mammal Ages and Late Cenozoic mammal dispersal events. Annual Review of Earth and Planetary Sciences 12:445-488.

Lindsay, E.H., L.L. Jacobs, and N.D. Tessman. 2006. Vertebrate fossils from Yepomera. Chihuahua, Mexico—the University of Arizona connection; pp. 19-32 in Carranza-Castaneda, O. and Lindsay, E.H. (eds.), Advances in Late Tertiary Vertebrate Paleontology in Mexico and the Great American Biotic Interchange. Universidad Nacional Autonoma de Mexico, Instituto de Geologia, Publication Especial 4.

Martin, J.E. 1981. Contents of coprolites from the Hemphillian of northern Oregon and their significance in paleoecological interpretations. S.D. Academy of Science, Proceedings 60:105-115.

Martin, J.E. 1983. Additions to the early Hemphillian Rattlesnake Fauna from central Oregon. S.D. Academy of Science, Proceedings 62:23-33.

Martin, J.E. 1984. A survey of Tertiary species of *Perognathus*, and a description of a new genus of Heteromyinae; pp. 90-121 in Papers in Vertebrate Paleontology Honoring Robert Warren Wilson. Carnegie Museum of Natural History, Special Publication 9.

Martin, J.E. 1998. A new species of chipmunk, *Eutamias malloryi*, and a new genus (*Parapaenemarmota*) of ground squirrel from Hemphillian deposits in northern Oregon; pp. 31-42 in Martin, J.E. (ed.). Stratigraphy and Paleontology of the West Coast—In Honor of V. Standish Mallory. University of Washington, Thomas Burke Washington State Museum, Research Report 6.

Newcomb, R.C. 1971. Relation of the Ellensburg Formation to extensions of the Dalles Formation in

the area of Arlington and Shutler Flat, north central Oregon. OreBin 33(7):133-142.

Repenning, C.A. 1968. Mandibular musculature and origin of the subfamily Arvicolinae (Rodentia). Acta Zool. Cracov., Krakow 13:29-72.

Repenning, C.A. 1980. Faunal exchange between Siberia and North America. Canadian Journal of Anthropology 1:37-44.

Repenning, C.A. 1987. Biochronology of the microtine rodents of the United States; pp. 236-268 in Woodburne, M.O. (ed.), Cenozoic Mammals of North America-Geochronology and Biostratigraphy. University of California Press.

Repenning, C.A., T.R. Weasma, and G.R. Scott. 1995, The early Pleistocene (latest Blancan-earliest Irvingtonian) Froman Ferry Fauna and history of the Glenns Ferry Formation, southwestern Idaho. U.S. Geological Survey, Bulletin 2105:1-79.

Rensberger, J.M. 1971. Entoptychine pocket gophers (Mammalia, Geomyoidea) of the early Miocene John Day Formation, Oregon. University of California Publications, Geological Sciences 90:1-209.

Schminke, H.U. 1967. Stratigraphy and petrology of four upper Yakima Basalt flows in south-central Washington. Geological Society of America, Bulletin 78:1385-1422.

Schultz, G.E. 2002. Clarendonian and Hemphillian vertebrate faunas from the Ogallala Formation (Late Miocene-Early Pliocene) of the Texas Panhandle and adjacent Oklahoma. Oklahoma Geological Survey, Open-File Report 10-2002:35-71.

Shotwell, J.A. 1955. Review of the Pliocene beaver *Dipoides.* Journal of Paleontology 29:129-144.

Shotwell, J.A. 1956. Hemphillian mammalian assemblage from northeastern Oregon. Geological Society of America, Bulletin 67:717-738.

Shotwell, J.A. 1958. Inter-community relationships in Hemphillian (mid-Pliocene) Mammals. Ecology 39:271-282.

Shotwell, J.A. 1964. Community succession in mammals of the late Tertiary; pp. 135-150 in Imbrie, J. and Newell, N. (eds.), Approaches to Paleoecology. John Wiley and Sons Publishers.

Shotwell, J.A. 1967a. *Peromyscus* of the late Tertiary in Oregon. University of Oregon, Museum of Natural History, Bulletin 5:1-35.

Shotwell, J.A. 1967b. Later Tertiary geomyoid rodents of Oregon. University of Oregon, Museum of Natural History, Bulletin 9:1-51.

Shotwell, J.A. 1970. Pliocene mammals of southeastern Oregon and adjacent Idaho. University of Oregon, Museum of Natural History, Bulletin 17:1-103.

Skinner, M.F., S.M. Skinner, and R.J. Gooris. 1977. Stratigraphy and biostratigraphy of late Cenozoic deposits in central Sioux County, western Nebraska. American Museum of Natural History, Bulletin 158(5):263-370.

Stirton, R.A. 1935. A review of the Tertiary beavers. University of California Publications, Geological Sciences 23(13):391-458.

Stirton, R.A. 1936. A new beaver from the Pliocene of Arizona with notes on the species of *Dipoides.* Journal of Mammalogy 17:279-281.

Tedford, R.H., L.B. Albright, III, A.D. Barnosky, I. Ferrusquia-Villafranca, R.M. Hunt, Jr., J.E. Storer, C.C. Swisher, III, M.R. Voorhies, S.D. Webb, and D.P. Whistler. 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs); pp. 167-231 in Woodburne, M.O. (ed.), Late Cretaceous and Cenozoic Mammals of North America—Biostratigraphy and Geochronology. Columbia University Press.

Tucker, S. 2003, Carnivores and microtine-like rodents from a new late Miocene (Hemphillian) locality in north-central Nebraska. Journal of Vertebrate Paleontology 23(3):105A.

Voorhies, M.R. 1977. Fossil moles of late Hemphillian age from northeastern Nebraska. Nebraska Academy of Sciences, Transactions 4:129-138.

Voorhies, M.R. 1990a, Vertebrate biostratigraphy of the Ogallala Group in Nebraska; pp. 115-151 in Gustavson, T.C. (ed.), Geologic Framework and Regional Hydrology: Upper Cenozoic Blackwater Draw and Ogallala Formations, Great Plains. University of Texas, Bureau of Economic Geology.

Voorhies, M.R. 1990b. Vertebrate paleontology of the proposed Norden Reservoir area, Brown, Cherry, and Keya Paha counties, Nebraska. University of Nebraska, Division of Archaeological Research, Technical Report 82-09:1-173.

Whistler, D.P., and D.W. Burbank. 1992. Miocene biostratigraphy and biochronology of the Dove Spring Formation, Mojave Desert, California, and characterization of the Clarendonian mammal age (late Miocene) in California. Geological Society of America, Bulletin 104:644-658.

Wilson, R.W. 1934. A new species of *Dipoides* from the Pliocene of eastern Oregon. Carnegie Institution Washington, Publication 453:21-28.

Wilson, R.W. 1936. A Pliocene Rodent fauna from Smiths Valley, Nevada. Carnegie Institution Washington, Publication 473:15-34.

Wilson, R.W. 1937a. New middle Pliocene rodent and lagomorph faunas from Oregon and California. Carnegie Institution Washington, Publication 487:1-19.

Wilson, R.W. 1937b. Pliocene rodents of western North America. Carnegie Institution Washington, Publication 487:21-73.

Wood, A.E. 1935. Evolution and relationships of the heteromyid rodents with new forms from the Tertiary of western North America. Carnegie Museum, Annals 24:73-262.

Zakrzewski, R.J. 1969. The rodents from the Hagerman Local Fauna, upper Pliocene of Idaho. University of Michigan, Museum of Paleontology, Contributions 23(1):1-36.